

Prepared in cooperation with the Bureau of Reclamation

**Theoretical Life History Responses of Juvenile
Oncorhynchus mykiss to Changes in Food Availability
Using a Dynamic State-Dependent Approach**

Open-File Report 2013–1154

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By Jason G. Romine, Joseph R. Benjamin, Russell W. Perry, Lynne Casal, Patrick J. Connolly, and
Sally S. Sauter

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**U.S. Department of the Interior
U.S. Geological Survey**

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Conversion Factors and Datums

Conversion Factors

SI to Inch/Pound

Multiply	By	To obtain
Length		
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
Flow rate		
millimeter per day (mm/d)	0.03937	inch per day (in/d)
cubic meter per second (m ³ /s)	70.07	acre-foot per day (acre-ft/d)
Heat Capacity		
joules per gram (j/g)	0.239	calories per gram (c/g)

Datums

Horizontal coordinate information is referenced to North American Datum of 1983 (NAD 83).

Altitude, as used in this report, refers to distance above the vertical datum.

Theoretical Life History Responses of Juvenile *Oncorhynchus mykiss* to Changes in Food Availability Using a Dynamic State Dependent Approach

By Jason G. Romine, Joseph R. Benjamin, Russell W. Perry, Lynne Casal, Patrick J. Connolly, and Sally S. Sauter

Abstract

Marine subsidies can play an important role in the growth, survival, and migratory behavior of rearing juvenile salmonids. Availability of high-energy, marine-derived food sources during critical decision windows may influence the timing of emigration or the decision to forego emigration completely and remain in the freshwater environment. Increasing growth and growth rate during these decision windows may result in an altered juvenile population structure, which will ultimately affect the adult population age-structure. We used a state dependent model to understand how the juvenile *Oncorhynchus mykiss* population structure may respond to increased availability of salmon eggs in their diet during critical decision windows. Our models predicted an increase in smolt production until coho salmon eggs comprised more than 50 percent of juvenile *O. mykiss* diet at the peak of the spawning run. At higher-than-intermediate levels of egg consumption, smolt production decreased owing to increasing numbers of fish adopting a resident life-history strategy. Additionally, greater growth rates decreased the number of age-3 smolts and increased the number of age-2 smolts. Increased growth rates with higher egg consumption also decreased the age at which fish adopted the resident pathway. Our models suggest that the introduction of a high-energy food source during critical periods of the year could be sufficient to increase smolt production.

Introduction

Oncorhynchus mykiss (*O. mykiss*) shows a wide range of life histories (Thorpe, 2007). This species adopts both anadromous (steelhead) and non-migratory (rainbow trout) life histories with many variants in between. The many life-history trajectories used by *O. mykiss* represent a remarkably complex fitness-based cost benefit analysis. This has allowed *O. mykiss* to persist in the Pacific Northwest of the United States despite overfishing, loss of habitat, complete blockages to migratory pathways, and increased mortality during seaward migration (*sensu* Hilborn and others, 2003). Typically, the cost of seaward emigration is higher mortality; however, the rewards are larger size and associated greater fecundity, a worthwhile gambit for some of these fish (steelhead). In contrast, fish that remain in small freshwater systems have lower mortality rates, but also have slower growth and an order of magnitude lower fecundity (rainbow trout) than their anadromous counterparts. The tradeoffs between survival probability and the genetic contribution to the next generation are driving forces behind the relative contribution of these pathways to the population.

Life-history pathways of *O. mykiss* are influenced by genetics and environmental conditions, which in turn affect the physiology of the fish (Thorpe and others, 1998; Zimmerman and Reeves, 2000; Christie and others, 2011). Thorpe and others (1998) suggested that the diversity of life-history patterns of salmonids could be explained by growth patterns at critical periods or decision windows during the year relative to genotype. For example, if resources were adequate during a critical decision window and a fish was growing faster than its genetic predisposition, then the fish might continue the maturation process and remain resident rather than emigrate to the ocean. The basis for this hypothesis is that excess growth is converted to lipid stores, which in turn allow the fish to continue the maturation process by diverting excess growth to gonad development. Although growth rate can be a predictor of life-history trajectories, genetic variability also is involved, thereby diluting the absolutism of growth rate or lipid availability as predictive variables (Thorpe and others, 1998).

Satterthwaite and others (2009) presented a model based on growth, fecundity, freshwater survival, and smolt-to-adult survival rate (SAR) to predict the life-history trajectories of juvenile *O. mykiss* in coastal California streams. This model provides a unique approach to predicting life-history pathways of juvenile *O. mykiss* under a given set of growth and survival rates. Although it was developed for California systems, it may be parameterized for other regions such as the Methow River (Benjamin and others, 2013). The model provides a platform to evaluate how changes in growth as a result of habitat change, food availability, and fish density may affect the age-structure of the juvenile population.

Reintroduction of extirpated species can reinstate key ecological processes that were previously absent. For instance, the reintroduction of wolves (*Canis lupis*) into Yellowstone National Park in the Western United States has resulted in altered herbivore feeding patterns and thereby changed patterns of woody plant regeneration over large areas (Ripple and Beschta, 2004). Species introductions or reintroductions likely will affect the associated ecosystem. The reintroduction of coho salmon (*Oncorhynchus kisutch*) into the Methow River system inevitably will alter ecological relationships within this system. However, the manner in which those relationships will be altered remains unclear because of the complex ecological effects that anadromous salmonids have on aquatic biota (Gresh and others, 2000; Naiman and others, 2002; Schoonmaker and others, 2003).

Adult anadromous salmonids are an energy-rich, marine-derived subsidy to freshwater systems and can transfer significant quantities of nutrients such as carbon, nitrogen, and phosphorus from the ocean to freshwater environments where they can be diffused across trophic levels. However, there is little consensus regarding the effect of marine derived nutrients on the growth and survival of fishes within the freshwater environment (Bilby and others, 1998; Lang and others, 2006; Harvey and Wilzbach, 2010). This discrepancy may be linked partially to studies in which salmon carcasses have been added to streams as opposed to studies where natural salmon runs occur. For carcass-addition studies, nutrients may be transmitted to fish either directly through consumption of carcass material or indirectly through increased primary and secondary production (Merz and Moyle, 2006). In the studies of indirect nutrient transmission through increased production, direct consumption of eggs can also provide an important energy source that affects fish growth and life-history expression (Moore and others, 2008; Armstrong and others, 2010). Therefore, reintroduction of extirpated salmon species may have positive effects on other target species. Coho salmon spawn in the fall throughout the Pacific Northwest. In the Methow River system, spawning coho salmon could provide a critical pre-winter food source in the form of eggs that would contribute to increased growth of juvenile

O. mykiss and other resident fishes. Late-fall spawning also coincides with the hypothesized smolt decision window (Satterthwaite and others, 2009). Changes in growth during this period could influence whether juveniles adopt a resident or anadromous life-history pathway and the age at which a given pathway is followed.

In this study, our goal was to simulate the potential shifts in life-history decisions by juvenile *O. mykiss* in response to the addition of coho salmon eggs, a seasonally available, high-energy food source. We used linked life history (Satterthwaite and others, 2009) and bioenergetics models (Hanson and others, 1997) to examine how contribution of coho salmon eggs to the diet of *O. mykiss* influenced their life-history trajectory. We parameterized our model to emulate conditions in Beaver Creek, a small tributary of the Methow River where *O. mykiss* are likely to interact with spawning coho salmon in the future. Our goal was not to predict outcomes for Beaver Creek, but, rather, to understand the potential effect of egg subsidies on *O. mykiss* in small streams similar to Beaver Creek where such interactions will play out. Additionally, predicting the relative contribution of eggs to the diet of *O. mykiss* is difficult owing to spatial (e.g., spawning versus non-spawning habitat) and temporal (e.g., seasonal and inter-annual) variation in abundance of both *O. mykiss* and coho salmon. We circumvented this complexity by simulating a wide range of relative contributions of eggs to the diet of *O. mykiss*. Although spatial and temporal variation in egg subsidies to *O. mykiss* will ultimately control the observed distribution of life-history trajectories, our approach allowed us to gain insights about the magnitude of egg subsidies required to alter life-history trajectories.

Description of Study Area

Historically, the Methow River in north-central Washington, USA, supported a large population of coho salmon with an estimated 20,000–30,000 adults returning to the river annually (Mullan, 1984; Mullan and others, 1992). This coho salmon run was blocked by dam construction at the mouth of the Methow River in 1915 (Wahle and Pearson, 1984). At the time of this study, coho salmon are being reintroduced to the Methow River Basin. Annual smolt releases have ranged from 250,000 to 1 million since inception of the program in 1997. The program has resulted in adult returns increasing from less than 1,000 to more than 20,000.

We used a population of *O. mykiss* in Beaver Creek to parameterize our models. Beaver Creek is a tributary to the Methow River and is at a mean altitude of 505 m (fig. 1). Beaver Creek is a third-order stream with a mean base flow of 0.05 m³/s (Martens and Connolly, 2010). Ichthyofauna in Beaver Creek is dominated by *O. mykiss*, but other native and non-native fishes are present, including Chinook salmon (*O. tshawytscha*), brook trout (*Salvelinus fontinalis*), and shorthead sculpin (*Cottus confusus*; Martens and Connolly, 2010).

Within Beaver Creek, *O. mykiss* smolt at age 2 to age 4. Most juvenile steelhead (66 percent) smolt at age 2, while approximately 30 and 4 percent smolt at age 3 and age 4, respectively (P.J. Connolly, U.S. Geological Survey, unpub. data, 2010). Along with the migratory population, resident *O. mykiss* compose approximately 20 percent of the population in Beaver Creek. These fish mature at age 1 to age 4.

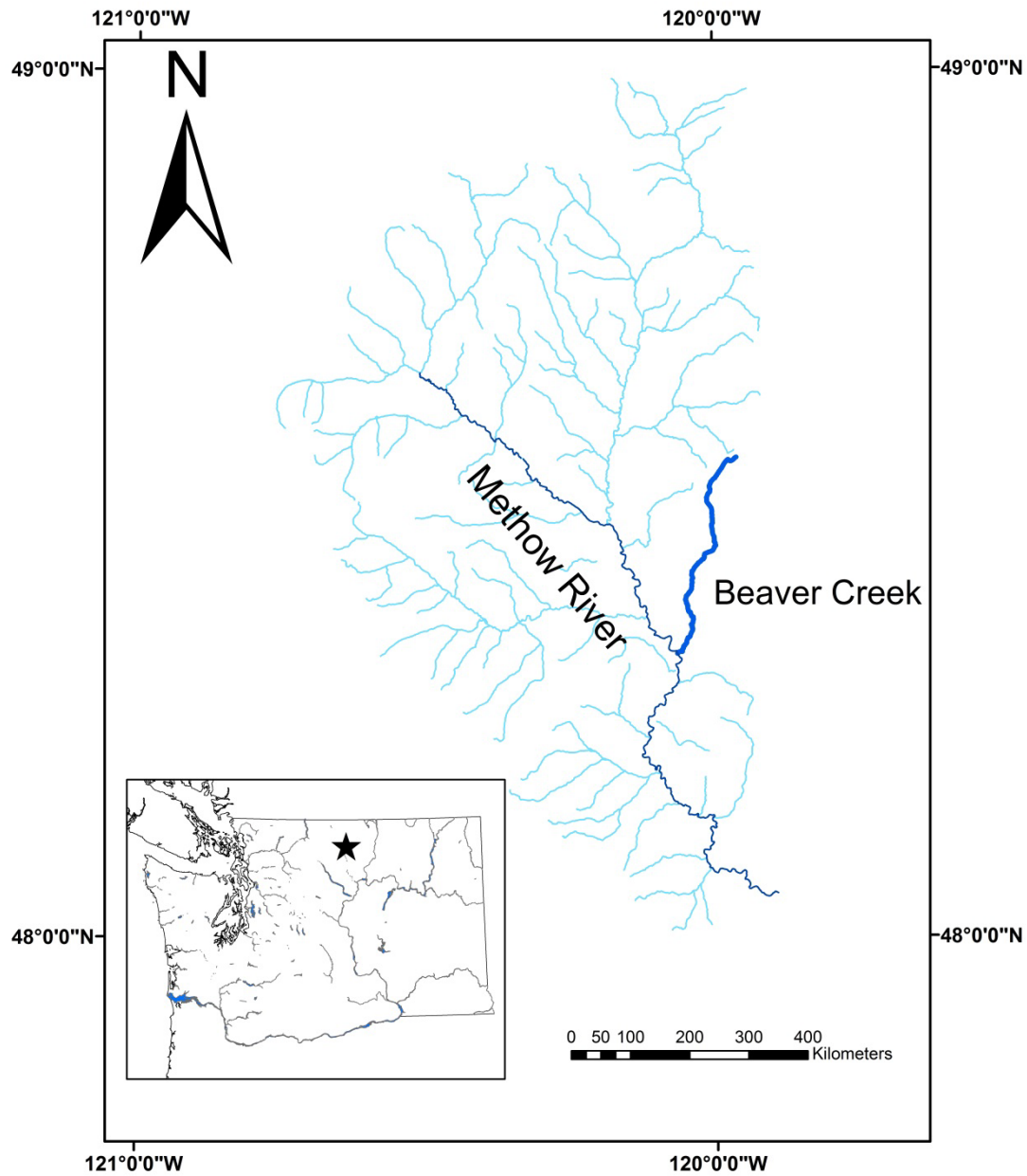


Figure 1. Map of Methow River Basin showing location of study area in Beaver Creek, a tributary of the Methow River in north-central Washington. Darker water bodies represent Beaver Creek and Methow River. Base map created from the National Hydrography Dataset (NHD). NHD provided by U.S. Geological Survey in cooperation with U.S. Environmental Protection Agency, USDA Forest Service, and other Federal, State and local partners.

Methods

Dynamic State-Dependent Model

We followed the methods of Satterthwaite and others (2009) to simulate life-history patterns of juvenile *O. mykiss* in Beaver Creek under different scenarios of coho salmon egg availability. Satterthwaite and others (2009) developed a dynamic state-dependent model (DSDM) that incorporated both proximal and ultimate approaches to predict age at smolting and becoming resident. We parameterized the model to emulate demographics of *O. mykiss* in north-central Washington (growth, survival, and fecundity). The DSDM relies on growth information during critical “decision windows” throughout the year (fig. 2). At the end of the critical decision windows, the optimal life-history strategy is selected based on the size and growth of the fish. At each decision window, three choices are assessed by the model—wait until the next window, begin to mature, or begin the smoltification process. We based the timing of the windows on field observations and previously published literature for the area. Decision windows were assumed to be fixed periods in time when physiological, morphological, and behavioral changes may begin, depending on the size of the fish (Thorpe and others, 1998; Satterthwaite and others, 2009). These windows included an average spawning date of May 1, an average date of fry emergence from the gravel of June 15, an average date of smolt emigration of June 1 (Peven and others, 1994; Snow and others, 2008), and discrete periods of time when smoltification or maturation are initiated. In the life-history model, the optimal fitness pathway for a fish is selected based on growth during the window and length at the end of each decision window. We estimated that the smolting decision window for juvenile *O. mykiss* in Beaver Creek was between October 1 and December 31, about 6 months prior to emigration as was suggested by Thorpe and others (1998) and Satterthwaite and others (2009). The decision window for maturing fish at age 1 and older was set between May 1 and June 1. This decision was assumed to occur about 1 year before spawning, owing to the metabolic cost of the maturation process. The maturation decision window for young-of-the-year fish was based on growth from emergence to October 1.

Fitness estimation was based on survival in freshwater, SAR, and size-dependent fecundity (Satterthwaite and others, 2009). Data were unavailable for the egg-to-emergence survival rate within the Methow River Basin; therefore, we estimated that rate at 6.5 percent based on a coastal steelhead population in southwest British Columbia (Ward and Slaney, 1993). The remaining freshwater survival rates were estimated at 50 percent annually, which is within the range of survival rates of other *Oncorhynchus* species throughout the Columbia River Basin (Bradford, 1995).

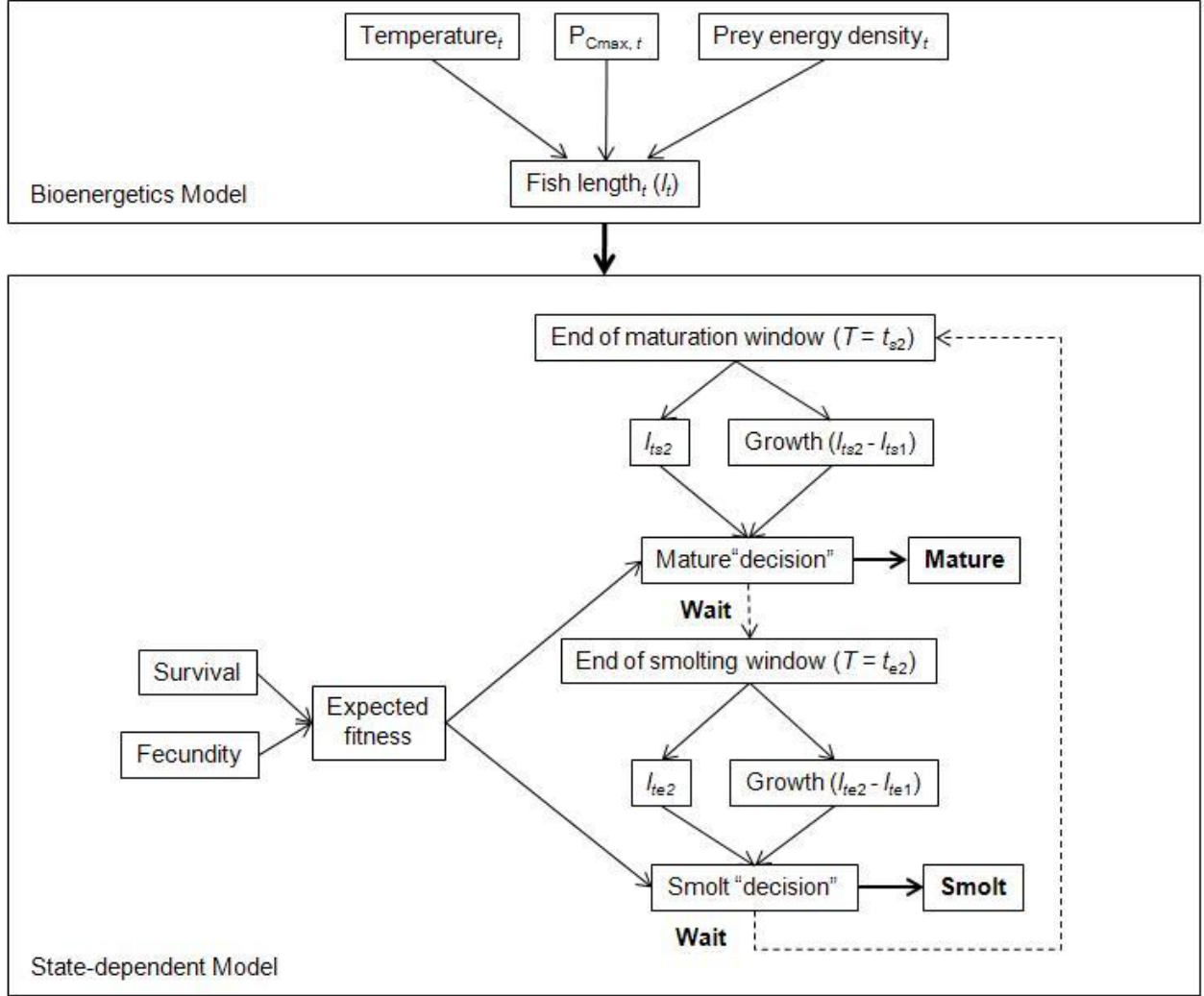


Figure 2. Conceptual diagram of linkages between the bioenergetics model and the state-dependent life history model. The bioenergetics model simulates the length of each fish (l) at time (t). The state-dependent model then predicts life-history trajectories either to mature and spawn as a rainbow trout (s) or to emigrate as a steelhead smolt (e) as a function of expected fitness, growth over discrete time windows (t_{s1} to t_{s2} or t_{e1} to t_{e2}), and length at the start of the window. The dashed line indicates no trajectory has been selected and individual fish loop through the model until a trajectory is chosen.

Length dependent, SAR ($\sigma(l)$) was estimated from the release of 50,000 *O. mykiss* in the Methow River using a Cormack-Jolly Seber mark-recapture model:

$$\sigma(l) = 0.36 \frac{e^{-6.171+0.03843l}}{1+e^{-6.171+0.03843l}}. \quad (1)$$

Length-specific fecundity of resident female rainbow trout ($\phi(l)$) was estimated from Hodge (2010) for *O. mykiss* in the Klamath River Basin,

$$\phi(l) = 0.2128 * l^{2.4301}. \quad (2)$$

This model provided a good fit to fecundity data from Wells Dam (Snow and others, 2008) which is located near the mouth of the Methow River. Average lifetime fecundity of anadromous females was estimated at 5,545 based on returns of wild steelhead to Wells Dam from 2000 to 2006 (Snow and others, 2008). Although a small percentage of steelhead spawn in multiple years, we considered the contribution of repeat spawning events to be negligible and, therefore, only one spawning event was considered in the fitness estimation.

The parameter ρ , which is a measure of how much recent growth experience influences the decision process, was set at 0. A value of 0 indicates that recent growth during a decision window does not influence the decision; whereas, a value of 1 indicates recent growth has a very high influence on the decision process (Satterthwaite and others, 2009). We set the value to 0 to accommodate the weight loss experienced by juveniles as they enter the early winter months. Satterthwaite and others (2009) set $\rho=0.3$ for their simulation based on an *O. mykiss* population in central California, USA. Additionally, model simulations were run for values of ρ from 0 to 0.6 to show the sensitivity of the model to changes in this parameter. To further explore sensitivity to parameter values, we also varied the SAR cap from 0.33 to 0.39 and freshwater survival from 0.47 to 0.53.

Bio-Energetics Model

We used the Wisconsin bioenergetics model (Hanson and others, 1997) to simulate fish growth based on diet and temperature. Baseline growth was established by fitting the model to growth data from passive integrated transponder (PIT)-tagged juvenile *O. mykiss* that were at liberty in Beaver Creek for more than 100 days. Parameters for the bioenergetics model were those developed by Railsback and Rose (1999). Diet was constructed from available data (Bellmore, 2011). From November 1 (day 305) to March 31 (day 90), aquatic insects constituted 95 percent of the diet and terrestrial insects constituted 5 percent of the diet. From April 1 (day 91) to October 31 (day 304), aquatic insects constituted 65 percent of the diet and terrestrial insects constituted 35 percent of the diet (fig. 3). Water temperature used in the model was developed following the methods of Mohseni and others (1998). This model assumes that the relationship between air temperature and water temperature incorporates factors that influence water temperature such as shading, hydrology, and atmospheric conditions. Water temperature was sampled daily in Beaver Creek 1–2 times per hour from (1) October 25, 2005, to April 23, 2007; (2) March 27, 2009, to March 17, 2010; and (3) July 13 to December 31, 2010. Continuous average daily air temperature was recorded at a weather station near the mouth of the Methow River by the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (2013). Water temperature then was predicted using a 7-d moving average of air temperature. We used daily water temperature averaged across 5 years in the bioenergetics model. Based on this diet regime and water temperature profile, we estimated the proportion of maximum consumption (P_{Cmax}) for each fish. Mean proportion of maximum consumption was estimated at 0.34 (standard deviation of 0.14). This value was used to simulate baseline growth.

The bioenergetics model then was used to simulate growth based on different levels of coho salmon egg availability. Coho salmon eggs were introduced into the diet by assuming a normal distribution of egg availability centered about a peak spawning date of October 15. The maximum proportion of coho salmon eggs in the diet was varied from 0 (baseline scenario) to 1 in each simulation. For example, under the 0.50 coho salmon egg scenario, the proportion of coho salmon eggs in the diet was 0.50 at the peak of spawning. Diet prior to and after peak

spawning in this scenario always consisted of less than 50 percent coho salmon eggs and was determined by the aforementioned normal distribution. The range scenarios evaluated could be equated to 0 spawners (0 scenario) to maximum number of spawners in the system (1 scenario) where superimposition is occurring at a greater frequency and eggs are readily available in high densities. Aquatic and terrestrial insects in the diet were discounted proportionally when coho salmon eggs became available (fig. 3). Gape limitation also was imposed to mimic realistic feeding opportunity. Only fish larger than 72 mm were able to exploit eggs as a food resource (Armstrong and others, 2010). Other than changes in coho salmon egg availability in the diet, we assumed diet composition was constant on an annual basis, with only daily ration varying randomly for each fish on each day of the simulation. Initial lengths for the model were taken from available data for Beaver Creek. Average length of young-of-the-year *O. mykiss* in Beaver Creek on August 1 was 55 mm (standard deviation of 0.14). To generate an initial distribution of lengths, we randomly sampled, with replacement, from a dataset of lengths for Beaver Creek. For each simulation, 2,000 random start lengths were drawn with replacement. This random draw simulated fish hatching at different times to mimic realistic spawn variability and subsequent emergence within the population. Asymptotic length was set at 400 mm based on empirical data from north-central Washington.

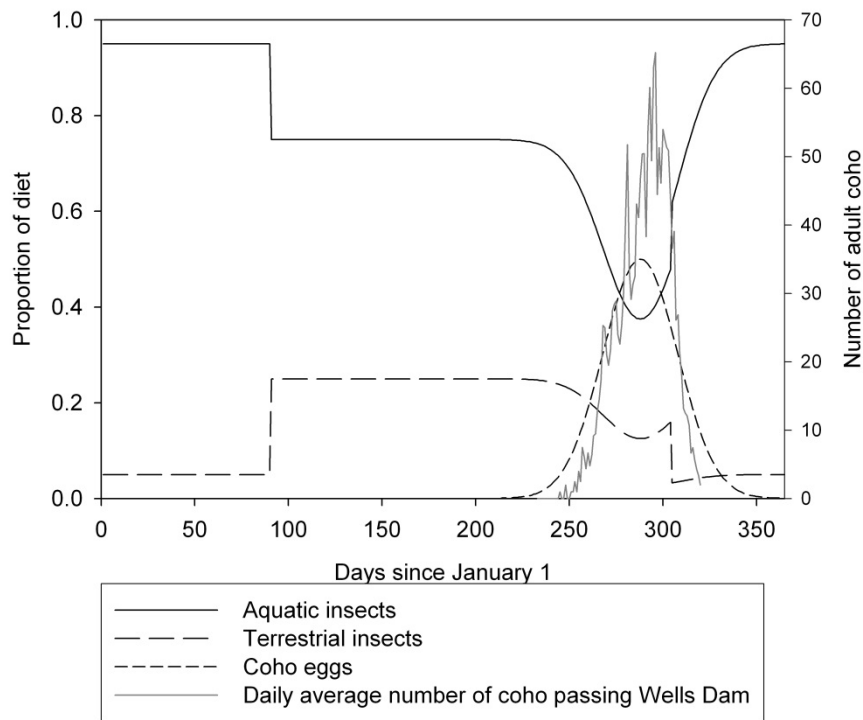


Figure 3. Graph showing diet composition throughout the year for a single coho salmon egg abundance scenario, Beaver Creek, a tributary of the Methow River in north-central Washington. Gray line represents daily average number of adult coho salmon passing Wells Dam from 2002 to 2012.

Results

The baseline simulation (no egg contribution to the diet) predicted 80 percent of juveniles would smolt at age 2 and age 3, with the remaining juveniles becoming resident at age 1 and age 2 (fig. 4). The base model simulation also predicted that there would be more age-3 smolts than age-2 smolts (a contradiction of the empirical data that has been collected for Beaver Creek), and approximately 20 percent of the juveniles would mature at age 2. As coho salmon eggs were increased from 0 to 60 percent in the diet, the proportion of age-2 smolts increased to a maximum of 84 percent, and then decreased. Age-3 smolts decreased to 0 as the contribution of coho salmon eggs increased in the diet. Juveniles were not predicted to undergo smoltification at ages greater than age 3.

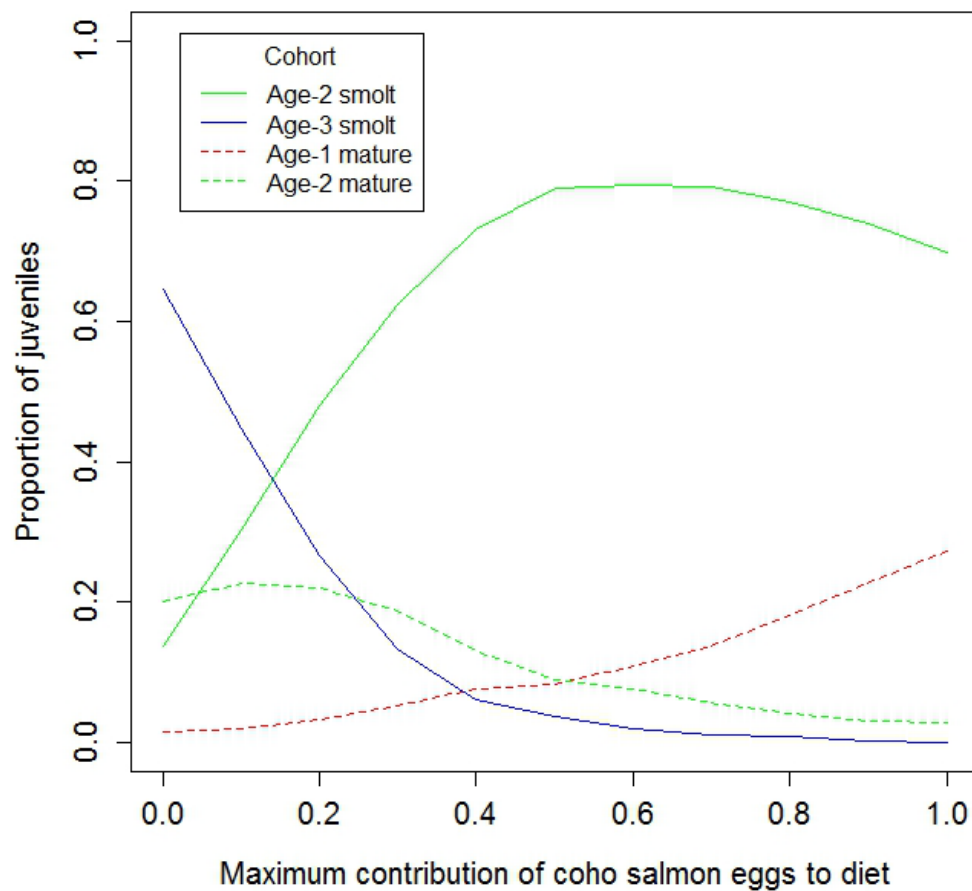


Figure 4. Graphs showing simulated proportions of each life-history pathway as a function of maximum egg contribution to the diet at the peak of the spawning run. (Freshwater survival=0.51, SAR cap=0.36, $\rho=0$).

Maturing fish primarily were age 1 and age 2. As coho salmon eggs increased in the diet, age-2 maturing fish increased slightly to 23 percent and then decreased to 3 percent (fig. 4). As age-2 maturing fish decreased, age-1 maturing fish increased from 1 percent at baseline to 28 percent for the maximum coho salmon egg scenario. Juveniles were not predicted to undergo the maturation process at ages greater than age 2. As coho salmon eggs increased in the diet, mean growth rate increased for all categories. On average, fish that grew an order of magnitude faster than other fish (0.015 mm/d, fig. 5) matured at age 1. Fish that grew 0.006 mm/d began smoltification at age 2 in the optimal scenario for age-2 smolt production.

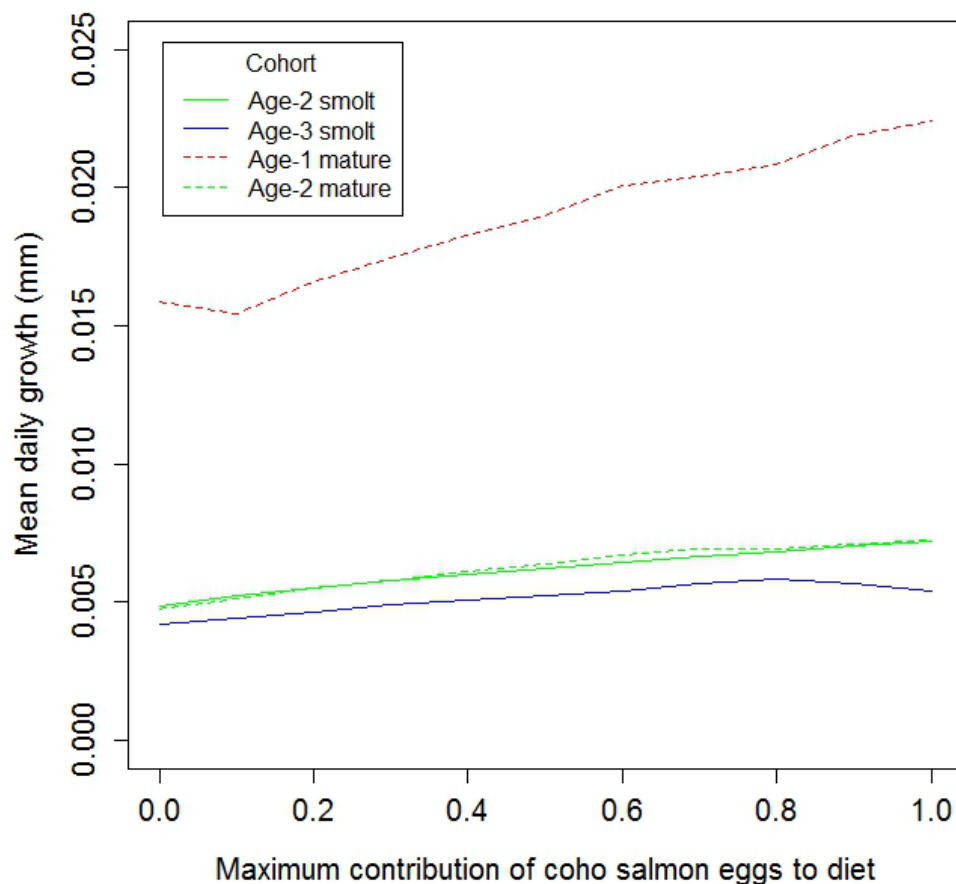


Figure 5. Graph showing mean daily growth by juveniles by life history pathway. Only age-2 and age-3 smolts were predicted. Maturing resident fish only were predicted to occur at age 1 and age 2.

Model predictions were very sensitive to changes in ρ (fig. 6). An increase in ρ of 0.1 could shift a population from one almost entirely composed of maturing residents to a population entirely composed of smolts, and vice versa. For the baseline scenario simulation where ρ was varied from 0 to 0.6, predicted proportions of the population smolting varied widely (fig. 6). As ρ increased, the proportion of age-3 smolts generally decreased as the proportion of age-2 smolts increased. Age-2 smolts then decreased and age-1 smolts increased to constitute the entire population at $\rho=0.6$. The percentage of the population predicted to mature followed a different pattern. As ρ increased, age-1 maturing fish increased, and then decreased as age-3 maturing fish increased. Age-3 maturing fish decreased as age-2 maturing fish increased, then subsequently decreased. Maturing fish generally decreased as ρ increased, and smolting fish increased as ρ increased for the conditions set in the simulation.

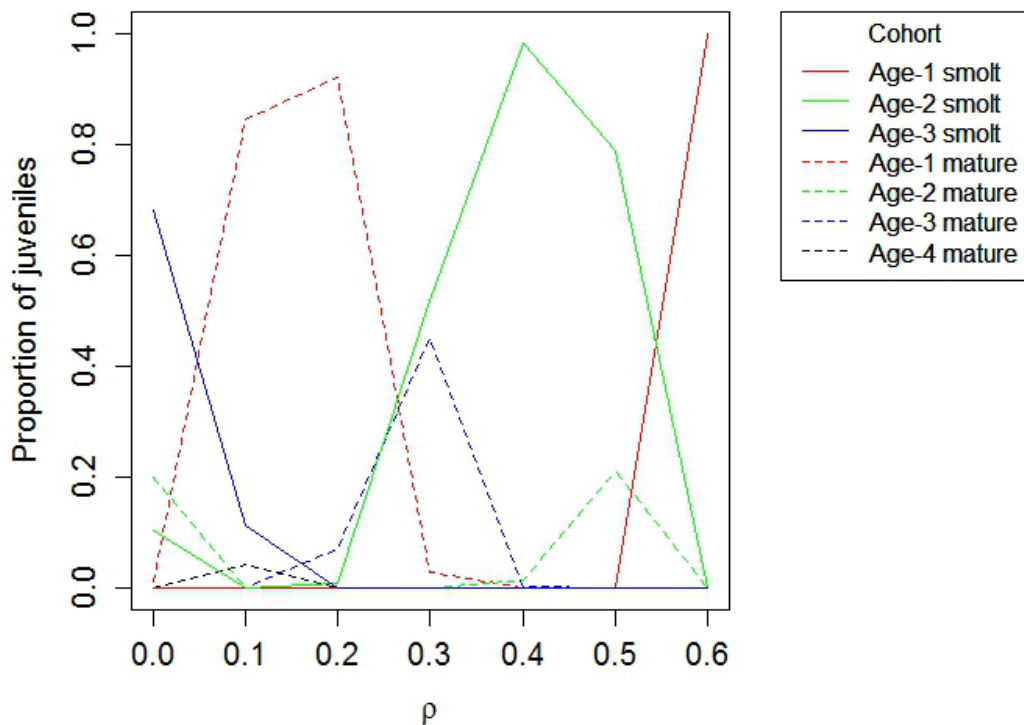


Figure 6. Graph showing results of simulations showing predicted population structure for different values of ρ run under the baseline scenario. Freshwater survival was set at 0.50 and SAR was capped at 0.36.

Simulations of all possible combinations of ρ and the SAR cap showed somewhat similar trends in smolt production in relation to ρ (figs. 7 and 8). Low freshwater survival, high SAR cap values, and high ρ produced the greatest number of smolts. As freshwater survival increased, numbers of juveniles predicted to smolt decreased, but this could be offset by higher values of ρ . When freshwater survival was set at the highest value (0.53), SAR cap and ρ had to be at the highest levels to produce smolts; otherwise, no smolts were predicted to be produced.

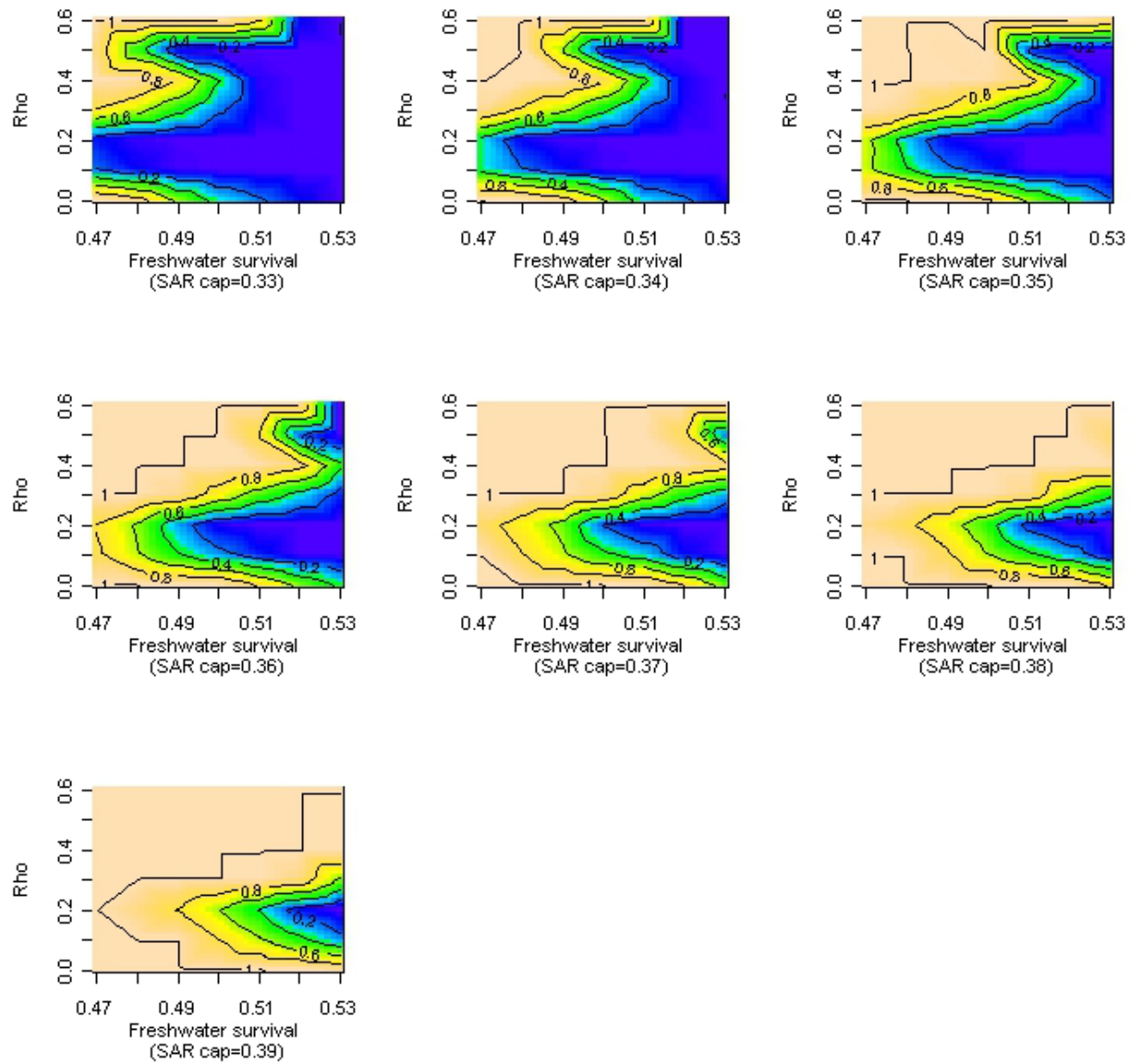


Figure 7. Graphs showing results of simulations showing relationship between freshwater survival, ρ , and smolt production for all values of SAR cap. Contours represent percentage of juvenile population smolting under different scenarios. Scale increases from dark (0=0 percent smolt production) to light (1=100 percent smolt production).

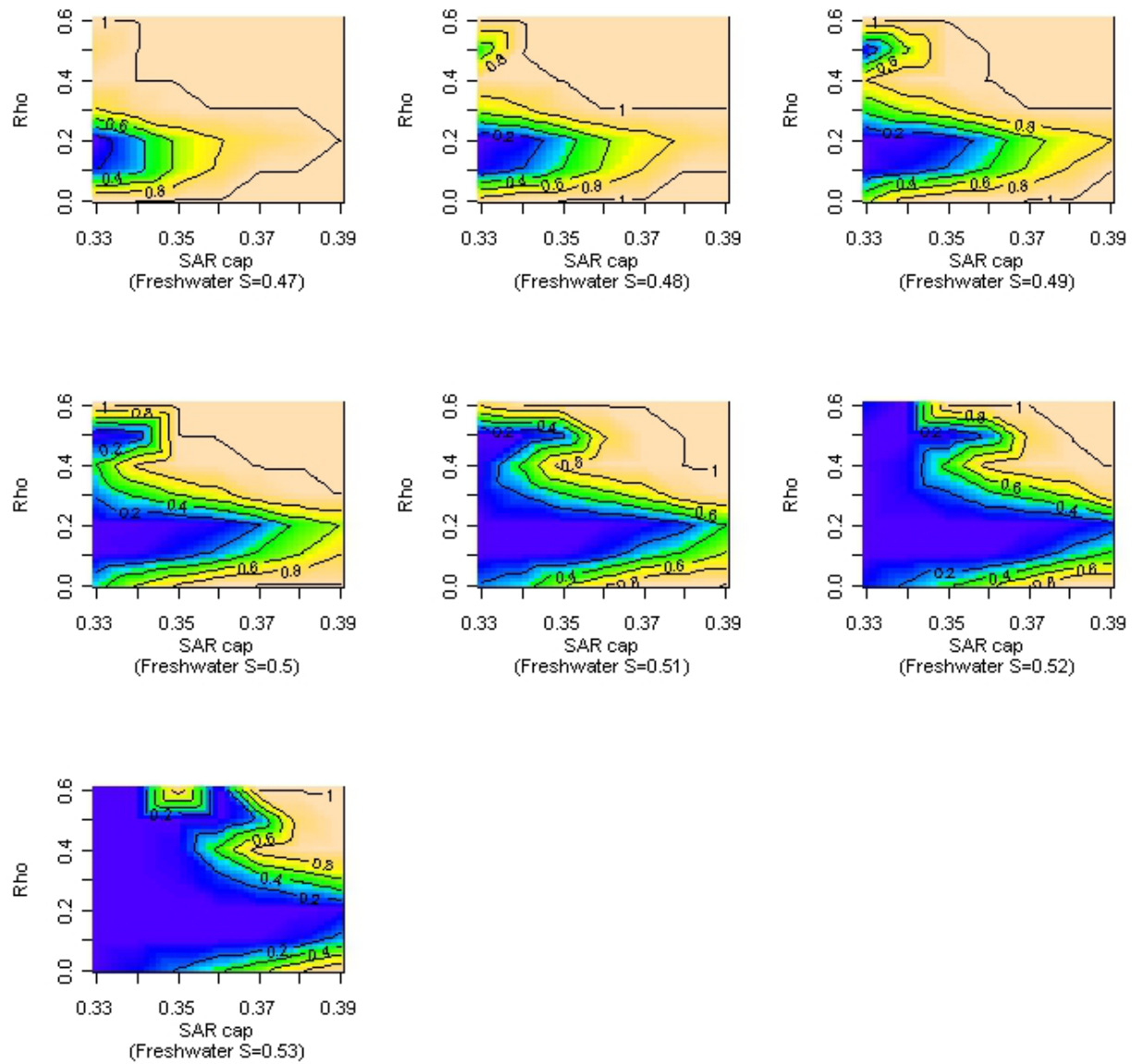


Figure 8. Graphs showing results of simulations showing relationship between SAR cap, ρ , and smolt production for all values of freshwater survival (S). Contours represent percentage of juvenile population smolting under different scenarios. Scale increases from dark (0=0 percent smolt production) to light (1=100 percent smolt production).

Discussion

For this study, we analyzed the extent to which the population structure of *O. mykiss* could be altered by adding a high energy food source (salmon eggs) just prior to the onset of winter. Our model simulations show that increased availability of coho salmon eggs could change the life-history pathways of rearing *O. mykiss*. Both age-2 smolt production and the number of juveniles becoming resident at age 1 were predicted to increase, which suggests the presence of an optimal threshold for producing greater numbers of smolts.

Our model predicted that the greatest percentage of smolts would occur at intermediate levels of coho salmon egg availability. At the highest levels of coho salmon egg availability, most fish began smoltification at age 2, but more than 20 percent of the juveniles were predicted to become mature at age 1. This should be expected given the much higher growth rates. Higher growth rates would mean greater lipid production and allow the maturation process to continue. Thorpe and others (1998) reported similar findings. These findings indicate that high contribution of eggs to the diet could tip the fitness balance towards adoption of a resident life-history strategy.

We did not explicitly model food item encounter rates within our simulations. For example, not all fish within the system would likely be able to take advantage of coho salmon eggs because of spatial mismatch between juvenile *O. mykiss* and spawning coho salmon. However, we randomly selected daily consumption for each fish throughout the simulations in an attempt to mimic encounter rates of food items. Therefore, even in the scenario where coho salmon eggs were available for 100 percent of the diet, a fish that had a very low consumption value would not benefit as much as a fish with a high consumption value. By taking this approach, we have attempted to account for spatial heterogeneity in food items (Moore and others, 2008).

The DSDM was very sensitive to small changes in survival. A 1 percent change in survival yielded large shifts in the predicted life-history pathways for the base scenario. Such a small change in survival is well within the confidence limits of most survival estimates. As such, the model likely is better suited for evaluating relative changes among alternative scenarios than predicting actual changes in populations given the inherent uncertainty in system response to coho salmon reintroduction. It is unlikely that a 1 percent change in survival would result in true population structure shifts as predicted by the model.

Our simulation results show the sensitivity of this model to the ρ parameter, in that small changes in ρ can lead to complete shifts in the predicted population structure. Moreover, there are little data to support an appropriate value for this parameter. The use of ρ as a parameter in future scenarios should be limited to that of a tuning parameter for model adjustment and agreement. Satterthwaite and others (2009) state that the ρ parameter defines the extent to which recent growth influences the decision process. This is indeed the case because of the structure of the fitness function; however, there are no biological or empirical data to support the estimation of this parameter other than tuning ρ to fit the observed population structure. Future studies should be aimed at improving estimates of this value.

Density-dependent effects were not included in this model. An increase in the residual population could induce a density-dependent response in mortality, growth, or emigration. Given the fitness function in the state-dependent model, decreased freshwater survival owing to competition or lack of resources would result in greater selection for the anadromous life-history

pathway (Satterthwaite and others, 2009). The decision windows or ultimate cues are based on genetically predetermined and relatively rigid thresholds when compared to proximal decisions influenced by environmental cues and population densities. These thresholds allow for a much wider range of variation in life-history pathways that were not modeled in this study.

Likewise, we did not account for the potential competitive effects between juvenile coho salmon and juvenile *O. mykiss*. Competition for resources and piscivory could reduce freshwater survival, thereby pushing more juveniles towards the anadromous pathway. Although some studies have reported slight negative effects on sympatric salmonids resulting from the introduction of hatchery raised coho salmon, predicting the response to such interspecific competition is difficult (Murdoch and others, 2005; Satterthwaite and others, 2009; Pess and others, 2011). However, Pearsons and Temple (2007) and Temple and Pearsons (2012) found little negative effect on *O. mykiss* from supplementation of coho salmon in the Yakima River Basin. The trade-off between an increased high-energy food source and increased competition for that resource owing to the addition of coho salmon is not known and may negate the positive growth attributed to coho salmon egg consumption, resulting in no change in the population structure (Mangel and Satterthwaite, 2008).

Our model did not explicitly include a metric for lipid stores, which has been shown to be positively correlated to the maturation process (for example, Thorpe and others, 1998; Thorpe, 2007). Fat content estimates for fish typically are estimated from a function that includes both length and weight (Bull and others, 1996). As such, weight, which was derived from the bio-energetics model, could be viewed as a proxy for lipids given the linear relationship between weight and fat content as estimated by Bull and others (1996) and used by Thorpe and others (1998). If a term for lipids was included within our model, the outcome would be identical owing to the use of proximal changes in weight to determine life-history pathways. We predicted fish with the fastest growth rates to mature. This is consistent with the correlation of lipid stores and maturing status.

The effect of marine-derived nutrients (MDN) is somewhat difficult to disentangle from other pathways of trophic transfer. Uchiyama and others (2008) reported little-to-no positive effect of increased MDN on sockeye salmon (*O. nerka*) productivity and suggested that environmental conditions played a more important role. Harvey and Wilzbach (2010) reported no increase in growth of juvenile salmonids following carcass addition. This is likely owing to the lower energy density value of fish tissue (1,300 J/g) versus that of salmon eggs (7800 J/g). Lang and others (2006) found slight increases in growth of juvenile coho salmon owing to increased MDN and suggested little long-term benefit from increased MDN in the form of overwinter survival or increased smolt production. These studies did not project the potential long-term consequences or potential changes in life-history patterns that could arise from a more productive ecosystem over larger temporal scales. These studies are in contrast to the findings of Moore and others (2008), which found large changes in *O. mykiss* growth owing to increases in sockeye salmon egg subsidies. Although carcass subsidies are important within the system, they may have a lesser benefit to rearing salmonids than MDN in the form of eggs. Bilby and others (1998) reported increased densities of juvenile coho salmon and steelhead following carcass and egg addition. Furthermore, they reported up to a 39 percent increase in the proportion of marine-derived nitrogen in juvenile muscle tissue following carcass addition. Scheuerell and others (2007) also found increased growth in juvenile *O. mykiss* upon the arrival of spawning salmonids

owing to consumption of eggs rather than carcasses, as their diet was primarily comprised of eggs. Although we did not include fish flesh within the diet of modeled juveniles, our results would not likely change given the lack of immediate contribution of carcasses to fish growth and the relatively low energy density value.

Although our baseline scenario was somewhat indicative of the actual population, age-4 smolts were not predicted in any of the scenarios even though they occur within the study area. Given the resolution and movements of juveniles within the system, age-4 smolts may not be of Beaver Creek origin, but instead may come from the much cooler headwaters of another tributary and may grow much slower than our model predicted. During the fitting of the growth model to the mark recapture data, it was observed that fish in the upper reaches grew much slower than fish in the lower reaches or closer to the mouth of Beaver Creek where it drains into the Methow River. Additionally, our model did not predict any age-1 smolts despite higher growth rates. Satterthwaite and others (2009) predicted that an increased growth rate would lead to younger smolts, whereas our results suggest slightly increased numbers of resident fish. This likely is owing to differences in model parameterization, namely freshwater asymptotic length (250 mm in the American River versus 400 mm in the Methow River) and differential survivorship. These differences stem from the presence of larger, fluvial *O. mykiss* in the Methow River that are absent in California rivers.

Freshwater survival was empirically estimated; however, because of the dynamic nature of the system, resolution of the data only allowed for annual estimates. (An interesting approach for future studies would be to examine model sensitivity to seasonal changes in mortality.) Additionally, freshwater survival did not vary across fish sizes, but may be size-dependent. The study system is somewhat cold-limited compared to the American River (Satterthwaite and others, 2009), owing to heavy winter snows that ice over the entire system. Overwinter mortality likely is the current limiting factor in this fish population; however, given the dynamics of the system, determination of size-based overwinter survival on wild juveniles is not currently feasible. Departures from baseline growth owing to increased growth from feeding on eggs may or may not increase overwinter survival (Connolly and Petersen, 2003).

Our results reflect the importance and variability in growth of juvenile steelhead and the resultant life-history pathways. Our approach has linked fitness with environmental conditions and trophic conditions creating a predictive platform that may be easily altered to test hypotheses regarding changes in bioenergetics, stream temperatures, and flow regimes. When egg availability was high (greater than 70 percent), juveniles grew at a faster rate that resulted in increased numbers of fish maturing in freshwater and fewer numbers of smolts. This conclusion is consistent with hatchery findings that suggest extremely fast- and slow-growing juveniles will become resident, while moderately growing juveniles will tend to smolt at later ages (Berejikian and others, 2011).

The coho salmon reintroduction program offers a unique opportunity to monitor the potential consequences of a renewed ecological interaction between coho and other salmonids within the system. Given the great changes within the ecosystem and the potential changes owing to climate change (Benjamin and others, 2013), it is unlikely that the renewed interaction will be representative of a past condition within the Methow. Coho salmon were once dominant in this system and displacement and competition are likely to occur, resulting in changes to the trophic dynamics of the system. Future monitoring of the system will afford the only means to evaluate the true predictive power of our approach.

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