Steelhead Life History on California's Central Coast: Insights from a State-Dependent Model

WILLIAM H. SATTERTHWAITE*

Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California Santa Cruz, Santa Cruz, California 95064, USA

MICHAEL P. BEAKES

Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California Santa Cruz, Santa Cruz, California 95064, USA; and National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, California 95060, USA

ERIN M. COLLINS

California Department of Fish and Game, 8175 Alpine Avenue, Suite F, Sacramento, California 95826, USA

DAVID R. SWANK

Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California Santa Cruz, Santa Cruz, California 95064, USA; and National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, California 95060, USA

JOSEPH E. MERZ

Cramer Fish Sciences, 126 East Street, Auburn, California 95603, USA; and Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, California 95064, USA

ROBERT G. TITUS

California Department of Fish and Game, 8175 Alpine Avenue, Suite F, Sacramento, California 95826, USA

SUSAN M. SOGARD

National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, California 95060, USA

MARC MANGEL

Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California Santa Cruz, Santa Cruz, California 95064, USA

Abstract.—Steelhead *Oncorhynchus mykiss* display a dizzying array of life history variation (including the purely resident form, rainbow trout). We developed a model for female steelhead in coastal California (close to the southern boundary of their range) in small coastal streams. We combined proximate (physiological) and ultimate (expected reproductive success) considerations to generalize the notion of a threshold size for emigration or maturity through the development of a state-dependent life history theory. The model involves strategies that depend on age, size or condition, and recent rates of change in size or condition during specific periods (decision windows) in advance of the actual smolting or spawning event. This is the first study in which such a model is fully parameterized based on data collected entirely from California steelhead populations, the majority of data coming from two watersheds the mouths of whose rivers are separated by less than 8 km along the coast of Santa Cruz County. We predicted the occurrence of resident life histories and the distribution of sizes and ages at smolting for steelhead rearing in the upstream habitats of these streams. We compared these predictions with empirical results and show that the theory can explain the observed pattern and variation.

Rainbow trout *Oncorhynchus mykiss* display highly variable life histories. They are facultatively anadromous and iteroparous, as both resident and anadromous forms potentially spawn repeatedly. Among anadromous fish (steelhead), there is great variability in age at emigration and age at return, along with the probability of repeat spawning. Thorpe (2007) identified 32 possible life history trajectories for steelhead, and this

large diversity of life histories presents a great challenge for managing the species. Changes in freshwater conditions (e.g., due to water management or climate change) may alter demographic rates along the fish's current life history trajectories and send fish on alternative life history pathways with radically different demographic results. Understanding when this will happen is a key challenge. Here we illustrate how state-dependent life history theory can help meet this challenge by predicting life history responses to the unique environmental conditions faced by steelhead on California's central coast.

Although there is clearly evidence for some degree of genetic control over the life histories exhibited by individual steelhead (Tipping 1991; Martyniuk et al. 2003), there is also substantial evidence for plasticity in life history in response to the environment (Zimmerman and Reeves 2000). For instance, anadromous steelhead may spawn resident offspring (rainbow trout), and the offspring of rainbow trout may emigrate to the ocean (Pascual et al. 2001; Thrower et al. 2004; Olsen et al. 2006; Ciancio et al. 2008). Thus, a model used to predict life histories in steelhead should allow for a combination of genetic and environmental effects, tailored to the local environments experienced by the specific populations of interest.

Steelhead are widely distributed in streams draining into the northern Pacific Ocean. Across this geographic range, life histories often vary in predictable ways (though with considerable variation both across and within regions). For example, steelhead from more northerly streams (where productivity and growth rates are lower) often smolt at older ages than do steelhead from southerly streams (Busby et al. 1996; Savvaitova et al. 2001), and resident populations are often found above barriers to anadromy.

The steelhead in central California are of particular interest for several reasons. These fish are near the southern limit of the species range, facing environmental conditions quite distinct from more northerly steelhead populations. In the Mediterranean climate, temperatures are typically high relative to northern populations; mild winters and productive, high-flow springs support the highest growth rates (Hayes et al. 2008). By contrast, rainfall is low and streamflow can become very low during the summer and fall, when growth is most strongly limited. Furthermore, small, flashy coastal streams frequently feature sandbar-closed estuaries during low-flow periods that may provide ideal growing habitat (Thorpe 1994; Bond et al. 2008; Hayes et al. 2008) but also constrain potential emigration and return dates to periods when streamflow is high enough to breach the sandbar.

In developing predictive models, the alternative life history pathways available to steelhead can be viewed in the context of demographic and life history tradeoffs (Mangel 1994; Thorpe et al. 1998; Mangel and Satterthwaite 2008). Larger females are more fecund (Allen and Sanger 1960; DuBois et al. 1989) and, while the effect of size on male reproductive success is often difficult to quantify and is usually frequency dependent (Jones and Hutchings 2001), large males are at a competitive advantage in acquiring mates. The quantitative analysis here applies to female fish, whose strongly size-dependent fecundity would tend to favor the anadromous life history owing to enhanced growth opportunities in the ocean. At the same time, survival in the ocean can be low and size dependent (Ward and Slaney 1988; Ward et al. 1989; Bond et al. 2008), tending to favor delayed smolting at larger sizes. Since the process of emigration itself or long delays before emigration can both carry substantial mortality risk, maturity as a freshwater resident might offer a sufficient survival advantage to be favored under some conditions, or we might expect a mixture of anadromous and resident fish. One goal of our work is to identify these conditions.

Since at least as early as 1957, we have had conceptual models of smolting based on a threshold size for emigration (Elson 1957; as applied to Atlantic salmon *Salmo salar*, which has a facultatively anadromous, iteroparous life history similar to that of steelhead). More recent work used the growth rate during a specific period as a cue for migration, assuming that a high growth rate will take fish to a critical size for ocean survival before ocean entry (e.g., "smolting size"; Peven et al. 1994; see Hayes et al. 2008 for a comparison of growth trajectories against a 150-mm minimal ocean entry size). While useful for predicting large-scale behavior patterns, this approach cannot account for the wide variation observed in individual smolt sizes (e.g., Shapovalov and Taft 1954), nor can it explain the apparent importance of growth rate as well as size in determining saltwater readiness (Mangel 1994; Metcalfe 1998; Thorpe et al. 1998).

Mangel (1994) and Thorpe et al. (1998) describe a life history modeling framework that more comprehensively compares the different life history options available to Atlantic salmon (and potentially to steelhead–rainbow trout) and allows for individual variability in both their physiological responses to the environment and their resulting life history pathways. These models involve strategies that depend on age, size or condition, and the recent rate of change in size or condition during specific periods (decision windows) in advance of the actual smolting or spawning event. The idea of decision windows in Atlantic salmon
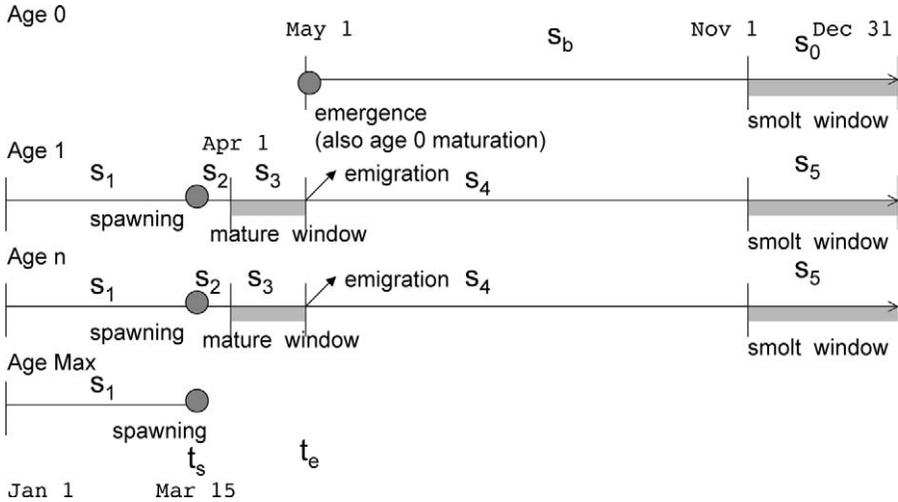
FIGURE 1.—Timeline of the model of steelhead life history. The intervals are designated according to their corresponding survival rates (s_p), as described in the appendix.

has received empirical support (summarized in Thorpe et al. 1998) as has the idea of genetically determined physiological thresholds that vary among populations (Piche et al. 2008).

The data requirements of these models are formidable, requiring a description of freshwater growth; survival rates in freshwater, during emigration, and in the ocean; expected adult return size; and size-specific fecundity. Ideally, all of these data would be watershed specific. To date, we know of no study that has attempted to fully parameterize such a model (but see Mangel 1996; Mangel and Satterthwaite 2008), let alone with data from a single geographic location. In this paper, we present a state-dependent life history model (Mangel and Clark 1988; Clark and Mangel 2000) for steelhead (specifically tailored to the seasonal patterns on California's central coast) based on data collected entirely from California steelhead populations, the majority of the data coming from two watersheds (Scott and Waddell creeks) the mouths of whose rivers are separated by less than 8 km along the coast of Santa Cruz County, California (37°N, 122°W). We compare these predictions with smolt age data reported by Shapovalov and Taft (1954) and unpublished observations of patterns in residency.

Methods

Conceptual framework.—We assume that smolt transformation and sexual maturation are processes that must be initiated in advance of the actual acts of emigration or spawning. We further assume that there are specific decision windows in advance of these events during which a fish commits itself to one

developmental pathway or another based on its current size and recent growth rate. We assume that the way in which a fish responds to its size and growth rate during these windows is under genetic control and thus that natural selection will tend to favor response strategies that maximize fitness (see Hazel et al. 1990).

For simplicity, we assume that the major events in a steelhead's life (emergence from the gravel, the smolting decision window, the maturation decision window, spawning, and emigration to the ocean) occur at fixed times each year. The timing of these events may vary from year to year based on environmental conditions, but we seek only to find general rules of thumb that steelhead development are predicted to follow based on the consistent general timing of these events and the environmental conditions driving them (Høgåsen 1998). Further, photoperiod as a cue probably constrains large changes in timing from year to year (Clarke 1989; Duston and Saunders 1992).

Specifically, we assume the timing of events described in Figure 1, which is inferred from previous studies of these systems (Shapovalov and Taft 1954; Hayes et al. 2008) and our own field observations. Fish spawn in early spring (nominally March 15), and fry emerge from the gravel in late spring (May 1). Smolts emigrate in midspring (May 1) at age 1 or older. Hayes et al. (2008) describe fish that may begin migration at various times only to spend long periods rearing in freshwater lagoons formed by sandbars at the river mouth prior to ocean entry. We do not explicitly model this life history pathway in this paper but instead focus on direct emigration to the ocean. We infer the existence of a 2-month decision window (Metcalfe et

al. 1988; Mangel 1994; Thorpe et al. 1998) preceding smolting, nominally running from November 1 to December 31. We assume a 1-month maturity decision window nominally running from April 1 to April 30, 10.5 months in advance of spawning. We postulate that the maturity decision window should in general come earlier in the year than the smolting decision window because spawning occurs earlier in the year than does emigration, and (especially for females) sexual maturity probably involves more substantial physiological investment and more time for complete development.

In year 0, the maturity decision window could precede emergence, and the next maturity window would not come until after potential spawning at age 1. To provide the option of spawning at age 1, for age-0 fish we determined the optimal maturity decision for fish based on their size on November 1 and then identified combinations of emergence date and growth rate that yield fish of those sizes, identifying conditions immediately after emergence that are predicted to lead to maturity.

We do not expect that fish follow these exact decision rules or that fish project expected fitness according to the equations presented below. Rather, we expect that natural selection should favor fish that respond to the cues available to them about their environment and growth and developmental status in ways that lead to realized life history trajectories similar to those predicted to yield the highest fitness. We use the word "decision" in the same sense as Gotthard (2008), not implying a cognitive process but instead a series of developmental switches along alternate physiological pathways.

State variables.—We use stochastic dynamic programming (SDP; Mangel and Clark 1988; Clark and Mangel 2000) to identify the optimal developmental pathways for a female steelhead, given its current size, age, and growth. Table 1 presents a full list of variable names, values used, and data sources for the model. As a measure of fitness, we use expected total lifetime reproduction. We do not account for generation time effects owing to uncertainty as to the appropriate baseline population growth rate. The costs of delayed reproduction are highly sensitive to population growth rate (large costs occurring if populations are growing rapidly, but if populations are stable over the long run, changes in generation time do not affect fitness. If populations are declining, as may be the case for steelhead recently, increased generation time actually increases fitness (Gardner and Mangel 1997).

Working backward through time from the possible endpoints of a fish's life, we describe its expected fitness as a function of three state variables: (1) its fork length l (mm), (2) an indicator g of whether it has initiated sexual maturation ($g = 0$ representing immature fish, $g = 1$ representing maturing fish), and (3) an indicator e of whether it is preparing to smolt ($e = 1$) or not ($e = 0$). We use fork length as opposed to other length measures to facilitate comparison with field data; for brevity, we will refer to this quantity as simply length for the remainder of the paper. At the end of decision windows, a fish is described by an additional state variable, b (its length at the beginning of that window) that allows calculation of its growth rate over the course of the decision window as described below. Thus, at any time (t, measured in days since January 1 of the year the fish emerged) we seek to specify the expected lifetime fitness $F(l, b, g, e, t)$ of a fish on the basis of its state variables, the state variable b being dropped except at the end of a decision window.

Dynamic programming equations.—We calculate terminal reward separately for resident rainbow trout and emigrating steelhead. Resident rainbow trout receive a terminal reward at the latest possible spawning event but can also accrue fitness during earlier spawning events. We assign expected lifetime fitness to steelhead at the time of emigration, implicitly accounting for potential repeat spawning at the time of first emigration.

The fitness of a resident rainbow trout at the time of final spawning, T_{sf}, is

$$F(l, g, e, T_{sf}) = \begin{cases} \phi(l) & \text{if } g = 1, \\ 0 & \text{otherwise.} \end{cases} \quad (1)$$

That is, a sexually mature fish receives a fitness benefit based on its size-dependent egg production $\phi(l)$, which is described below. A sexually immature fish receives no fitness at the time of spawning and has no potential for future fitness since this is the last possible spawning event for that fish.

Fish spawning at earlier times (generically denoted by t_s) receive a similar fitness increment if sexually mature, along with their expected lifetime fitness at the next time step if they survive. When assigning future fitness, fish are assumed to select the optimal developmental pathway available to them at any point in the future, given their state at that time. This depends upon time-dependent survival $s(t)$ and size, developmental pathway, and time-dependent growth to new size $l'(l, g, e, t)$ so that

$$F(l, g, e, t_s) = \begin{cases} \phi(l) + s(t) \cdot F[l'(l, g, e, t_s), g, e, t_s + 1] \\ \quad \text{if } g = 1, \\ s(t) \cdot F[l'(l, g, e, t_s), g, e, t_s + 1] \\ \quad \text{otherwise.} \end{cases} \quad (2)$$

In equation (2), we assume that there is no survival cost of spawning per se, and the baseline simulations

TABLE 1.—Variable baseline and alternative values used, and citations for parameters in the state-dependent model of steelhead life history. See Methods for further details.

Symbol	Definition[a]	Baseline value	Variants	Source[b]
t	Time			
	Date of emergence	121		
t_s	Date of resident spawning	74		
t_e	Date of emigration	121		
	Date of start of smolting window	305		
	Date of end of smolting window	365		
	Date of start of maturity window	91		
	Date of end of maturity window	121		
F	Expected lifetime egg output, given current state and time			
l	Fork length (mm)			
b	Fork length (mm) at the start of the decision window			
g	Maturity switch: 1 = maturing, 0 = immature			
e	Smolting switch: 1 = smolting, 0 = freshwater physiology			
$\phi(l)$	Length-specific egg production of resident female spawners	$0.0974(l/10)^{2.1169}$		Shapovalov and Taft (1954)
	Resident survival through spawning event per se	1	0.417	Shapovalov and Taft (1954), Ward et al. (1989)
Φ	Expected lifetime egg production of an anadromous female	7,100		Shapovalov and Taft (1954)
$\sigma(l)$	Size-specific marine survival from smolting to first spawning	$0.84 \exp(-8.657 + 0.0369l)/[1 + \exp(-8.657 + 0.0369l)]$	capped at 0.433 or halved across the board	Bond (2008), Shapovalov (1967), Shapovalov and Taft (1954)
l	Time- and state-dependent expected future size, calculated as follows: growth (mm/d) through Dec 31 of first year of fish's life	0.119 mm/d	up to 150% of baseline	Hayes et al. (2008)
	Specific growth rate in length during winter (Nov–Jan) for age-1+ fish	0.0093633	up to 150% of baseline	Hayes et al. (2008)
	Specific growth rate in length during spring (Feb–Apr) for age-1+ fish	0.00210447	up to 150% of baseline	Hayes et al. (2008)
	Specific growth rate in length during summer (May–Jun) for age-1+ fish	0.00049033	up to 150% of baseline	Hayes et al. (2008)
	Specific growth rate in length during fall (Aug–Oct) for age-1+ fish	0.00023787	up to 150% of baseline	Hayes et al. (2008)
	Asymptotic size achievable in freshwater	250 mm	500 mm	
	Fraction of baseline growth (in length) achieved by maturing fish	0.83	1	
s_p	Freshwater survival over the following periods:			
s_b	Deposition of egg to start of age-0 smolting decision window	0.0087	(Shared by all trajectories, so never varied)	Tuned to yield $R_0 = 1$ for optimal strategy in baseline scenario
s_0	Smolting decision window, age-0 fish	0.519	(Shared by all trajectories, so never varied)	Burns (1971)
s_1	End of smolt window to spawning, age-1+ fish	0.701	Raised to 0.50 or 0.25	Allen (1986)
s_2	Spawning to start of maturity window, age-1+ fish	0.931	Raised to 0.50 or 0.25	Allen (1986)
s_3	Maturity window, age-1+ fish	0.702	Raised to 0.50 or 0.25	Allen (1986)
s_4	End of maturity window to start of smolting window, age-1+ fish	0.393	Raised to 0.50 or 0.25	Burns (1971), Allen (1986)
s_5	Smolting decision window, age-1+ fish	0.753	Raised to 0.50 or 0.25	Allen (1986)

[a] All dates are days of the year from January 1.
[b] May have required intervening calculations and analyses (see text).

were carried out given this assumption. Alternatively, we might calculate the survival cost of spawning per se as follows. Ward et al. (1989) suggest that large emigrating fish have an ocean survival rate of about 43.3%. However, Shapovalov and Taft (1954) report a ratio of 15 second-time spawners to 83 first-time

spawners, suggesting that in a population which has reached a stable age distribution, survival to second spawning is 15/83, or 18.1%. Assuming that the extra mortality must come from the costs of spawning, this would suggest a spawning survival rate of 18.1/43.3, or 41.7%. This probably overestimates the true cost of

spawning in resident rainbows as their smaller size and lower metabolic demands might make recovery easier in the food-poor river environment, and an average spawning survival rate of 56% has been reported for mature Atlantic salmon parr in Newfoundland (Myers 1984; Berglund 1992; summarized in Fleming 1996). Nevertheless, we use the probably pessimistic estimate of 41.7% spawning survival.

For emigrating steelhead, we assign all fitness at the time of emigration, implicitly accounting for multiple spawnings. Emigrating smolts receive fitness based on their expected size-dependent survival when they leave the river system $\sigma(l)$ and the expected lifetime fecundity of a steelhead Φ, including its size-dependent fecundity at first return and additional fitness from repeat spawnings, discounted by the probability of kelt survival as described below. We assume that the size of a returning steelhead is independent of its size at emigration (Sutherland 1973; Pearson 1993; Snover et al. 2005), which may also be justifiable in light of data suggesting that size only accounts for a small amount of the variation in fitness within the class of large anadromous females (Seamons et al. 2004). Fish following other developmental pathways at this time (t_e) receive their expected fitness in the next time period, if they survive. Thus,

$$F(l, g, e, t_e)$$
$$= \begin{cases} \sigma(l)\Phi & \text{if } e = 1, \\ s(t) \cdot F[l'(l, g, e, t_e), g, e, t_e + 1] & \text{otherwise.} \end{cases}$$
$$(3)$$

At the end of the maturation decision window (t_{dg}), fish currently uncommitted to either developmental pathway are assumed to select the maturation pathway that maximizes their expected fitness, while fish committed to a pathway continue along that pathway. Mathematically,

$$F(l, b, 0, 0, t_{dg}) = s(t) \cdot \max_g \{F[l''(l, b, g, 0, t_{dg}), g, e, t_{dg} + 1]\},$$
$$F(l, g, e, t_{dg}) = s(t) \cdot F[l''(l, b, g, e, t_{dg}), g, e, t_{dg} + 1]$$
$$\text{if already committed,} \quad (4)$$

where $l''(l, b, g, e, t)$ is the expected size resulting from growth between time t and time $t + 1$, updated on the basis of how quickly the fish grew over the decision window as determined by comparing l to $l'(b, g, e, t - 1)$, as described below.

The top equation indicates that a previously uncommitted fish will smolt if the product of ocean survival at its expected size at emigration and lifetime reproductive output of a returning steelhead is greater than the expected lifetime fitness of a fish that remains a parr and grows to a larger size before making an

optimal decision in the future, each option being discounted by the expected mortality between the decision window and reproduction. The bottom equation indicates that if a fish has already committed to a life history pathway, it cannot change its trajectory.

Similarly, uncommitted fish are assumed to select the optimal smolting pathway at the end of the smolt decision window (t_{de}), while other fish continue along their previous path, that is,

$$F(l, b, 0, 0, t_{de}) = s(t) \cdot \max_e \{F[l''(l, b, 0, e, t_{de}), g, e, t_{de} + 1]\},$$
$$F(l, g, e, t_{de}) = s(t) \cdot F[l''(l, b, g, e, t_{de}), g, e, t_{de} + 1]$$
$$\text{if already committed.} \quad (5)$$

For any other time period, fish continue along their designated developmental pathway, that is,

$$F(l, g, e, t) = s(t) \cdot F[l'(l, g, e, t), g, e, t + 1]. \quad (6)$$

We assume that once a developmental pathway has been initiated, it cannot be abandoned; thus, sexually mature fish cannot later smolt and smolting fish cannot mature in freshwater. This may not be appropriate for males (Shapovalov and Taft 1954) but appears appropriate for females.

Parameterization and data sources.—To characterize the size-dependent production of eggs of fish maturing in freshwater, we used the equation

$$\phi(l) = 0.974 \cdot (l/10)^{2.1169}, \quad (7)$$

where l is measured in millimeters (Shapovalov and Taft 1954:148). This same equation provides a good fit to the egg production of smaller rainbow trout as measured by Allen and Sanger (1960), estimating the average rainbow's fecundity within 5% of the reported value.

We determined the size-dependent expected marine survival of emigrating smolts,

$$\sigma(l) = 0.84 \frac{e^{-8.657 + 0.0369l}}{1 + e^{-8.657 + 0.0369l}}, \quad (8)$$

as follows: First, we estimated size dependence in the relative survival of hatchery smolts by fitting a logistic model to data from Scott Creek (Bond et al. 2008). Second, we rescaled so that the predicted survival for the modal length of wild age-2 Waddell Creek smolts moving downstream (165 mm; Shapovalov and Taft 1954) would match their reported average survival (6%; Shapovalov 1967). This rescaled smolt survival function also corresponded within 1% of survivals reported by Shapovalov (1967) for age-1 and age-3 smolts, length at age inferred from Shapovalov and Taft (1954).

This two-step process was made necessary by the

nature of our respective data sources on smolt survival for central California creeks. In Bond et al. (2008), a large number of hatchery fish were released, all marked as hatchery fish but not uniquely identifiable. A subsample of 542 of these fish were measured before release. Fifty-two of these fish were recaptured heading upstream to spawn, their length at ocean entry estimated by scale reading (see Bond et al. 2008 for details). To estimate size dependence in relative survival, we grouped the lengths of released and surviving fish into 10-mm bins and used maximum likelihood techniques to fit a logistic function modeling survival as a function of length, calculating survival within each bin based on its midpoint length and assuming binomial error in the data. This assumed that the measured subset of released fish was the entire starting population, and since this is not true, the final survival estimate would need to be adjusted down accordingly. However, it would also need to be adjusted up to account for the (unpublished) trapping efficiency of returning spawners and to account for the higher survival of wild versus hatchery smolts (Ward and Slaney 1990). Further, historic (and evolutionarily relevant) smolt survivals in these watersheds may be better represented by the data of Shapovalov (1967) since ocean survival of steelhead seems to have declined since 1990 (Ward 2000), but the data of Shapovalov (1967) alone do not allow estimating size effects with high resolution.

Since very few large (>220-mm) smolts were released, the estimated survival rates for large smolts implied by the model may be unreasonably high. Alternatively, for some of the sensitivity analyses discussed below we set a maximum survival probability of 43.3% based on the data of Ward et al. (1989).

The expected lifetime fecundity of a returning steelhead (Φ) was calculated on the basis of data presented in Shapovalov and Taft (1954). We derived a value of 7,100 for this variable by calculating the average across years of the expected fecundity of the average-sized steelhead at its first spawning (Table 32 in Shapovalov and Taft 1954), plus the expected fecundity of the average second- and third-time spawners discounted for survival based on the relative numbers of new and repeat spawners. This corresponds to the fecundity of a 668-mm fish in a single spawning event according to equation (7), within the size range of returning steelhead but larger than any resident rainbow trout in these streams (maximum of ~300 mm, with very few fish >250 mm).

We estimated freshwater survival based on values reported for coastal streams in northern California (Burns 1971; Allen 1986; Bley and Moring 1988), adjusted for model time intervals as described in the appendix. Taken together, these estimates yield an annual survival of 14% for age-1 and older (hereafter, age-1+) fish.

Freshwater growth rates.—We modeled growth rates as described for upstream fish in Hayes et al. (2008). Age-0 fish grew at 0.119 mm/d until October 31 of their first year of life, regardless of size. Older fish grew in length at season-dependent specific growth rates (in length) of 0.0938%/d during winter (November–January), 0.211%/d during spring (February–April), 0.0496%/d during summer (May–July), and 0.0237%/d during fall (August–October).

This model allows growth to unlimited sizes; however, bioenergetic models suggest limits on the sizes that fish can achieve in a given environment (West et al. 2001). For the majority of computations here, we cap the length achievable in freshwater at 250 mm (although growing to this length at the rates reported by Hayes et al. [2008] would take over 5 years, far longer than most fish would be expected to live), allowing for longer lengths when performing sensitivity analyses, as specified.

Although we lack detailed data on the energetic costs of smolting and maturing, maturity in particular is likely to carry a significant energetic cost, ovaries making up a substantial fraction of body weight in adult females. Based on the calculation that 19% of an adult rainbow trout's body weight might be ovaries (Allen and Sanger 1960), we reason that approximately 19% of mass growth in a maturing rainbow goes into gonadal development rather than somatic growth. The exact effect of this reduction in growth in mass on growth in length depends on the size of the fish; however, for fish 35–250 mm long, growth in length is always 82–84% of baseline, so we reduce growth in maturing fish to 83% of baseline. In Results, we report the impact of eliminating this reduction in growth rate for maturing fish.

At the end of decision windows (see equation 5), we updated expected growth based on recent growth by comparing length at the end of the window with that which would be predicted based on length on the start of the window, that is,

$$\nu = [l/l'(b, g, e, t-1)]^{\rho}, \qquad (9)$$

$$l''(l, b, g, e, t) = \nu \cdot l'(l, g, e, t), \qquad (10)$$

where l is the length of the fish at the end of the decision window and b is the length of the fish at the start of the decision window (thus, $l'[b, g, e, t-1]$ is the expected size of the fish at the end of the decision window). Values of ρ near 0 imply that fish ignore recent growth rates; values near 1 imply that recent
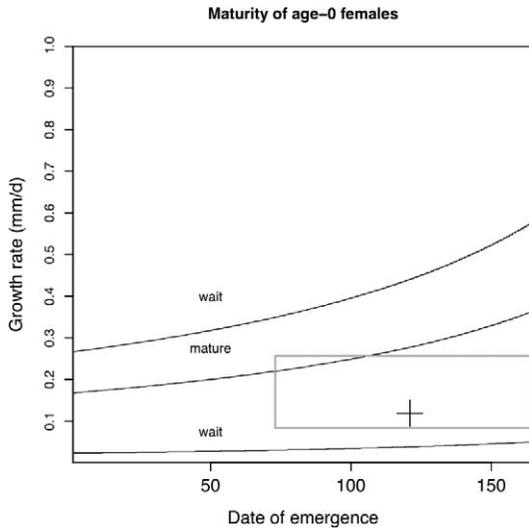
FIGURE 2.—Combinations of emergence date (days since January 1) and growth rate for which age-0 females are predicted to mature as parr. The cross indicates the model predictions of size and growth rate during the decision window, the gray box the estimated range of emergence dates and growth rates from Hayes et al. (2008 [raw data and inferred maximal and minimal growth rates; see Methods]). The dark lines represent the boundaries between the combinations for which we predict that fish will mature and those for which we predict that fish will remain immature.

growth factors heavily into expected size in the future. For the computations presented here, we use $\rho = 0.3$.

Model outputs.—For any combination of sizes at the start and end of each decision window, the model generates a prediction as to whether an optimally behaving fish will smolt or mature under those conditions. This allows us to generate phase-space plots of optimal decisions as a function of size at the end of the decision window and growth over the course of the window. This allows the identification of size thresholds for smolting, although the size threshold may change depending on growth rate, illustrated by nonvertical lines separating regions of size–growth phase space with different predicted behaviors.

By comparing the optimal state-dependent decisions with the expected growth trajectories of individual fish, we can also predict the ages at which fish first smolt or mature. We make predictions for the most common life history trajectory given average growth or predict distributions of life histories for fish growing faster or slower than average. Since age advances over the winter, a prediction that fish will initiate smolting at age a implies they will actually emigrate at age $a + 1$, and fish starting to mature at age a will first spawn at age $a + 1$.

To compare our predictions of emergence date and growth rate-dependent age-0 maturity against the expected range of emergence dates and growth rates in the field, we estimated the bounds on emergence dates as those sample dates on which Hayes et al. (2008; raw data for their Figure 3) captured fish smaller than 27 mm FL. We set the lower bound for age-0 growth rate as 2 SE below the lowest estimated mean from Hayes et al. (2008; their Table 3) and estimated the upper bound on growth rates based on the apparent fastest-growing individual in the raw data for their Figure 3, with one individual 72 mm longer than typical emergence length 280 d after the inferred earliest emergence date. We compare size- and growth-rate-specific smolting predictions for age-0 fish against the range of sizes for age-0 fish at the end of the year reported in the raw data for Figure 3 of Hayes et al. (2008), the upper and lower bounds on potential age-0 growth taken as the lowest and highest estimates from their Table 3 (± 2 SEs). For older fish, we compare state-dependent predictions against the size ranges predicted for those intervals by Hayes et al. (2008; their Figure 7), growth rates based on mean specific growth rate applied to the sizes fish would be at the start of the decision window. However, Hayes et al. present 90% confidence intervals on the size achieved by a fish growing at the mean time-dependent growth rate rather than a 90% confidence interval on lengths reached by individually variable fish. With a large sample size, fish may spread over a much wider range of sizes than the 90% confidence interval on the mean; thus, fish may cover an even wider range of size at age than the figures in Hayes et al. (2008) suggest.

We programmed the model in R (R Development Core Team 2007); the code is available upon request from the corresponding author.

Results

Baseline

Along a typical growth trajectory, female fish are predicted to neither initiate maturation nor begin smolting at age 0 (Figures 2, 3a). Compared with the emergence dates and growth rates seen in the field, only the very largest–earliest emerging and fastest-growing age-0 fish are predicted to initiate maturity (Figure 2). Even larger age-0 fish are predicted to smolt (Figure 3a), but it seems unlikely that age-0 fish can grow this large in upstream habitats. The model also predicts that age-0 fish with growth rates very near zero would mature since they will take a very long time to reach a size at which they can smolt with an appreciable chance of marine survival, and the model allows some egg production even at arbitrarily small size.
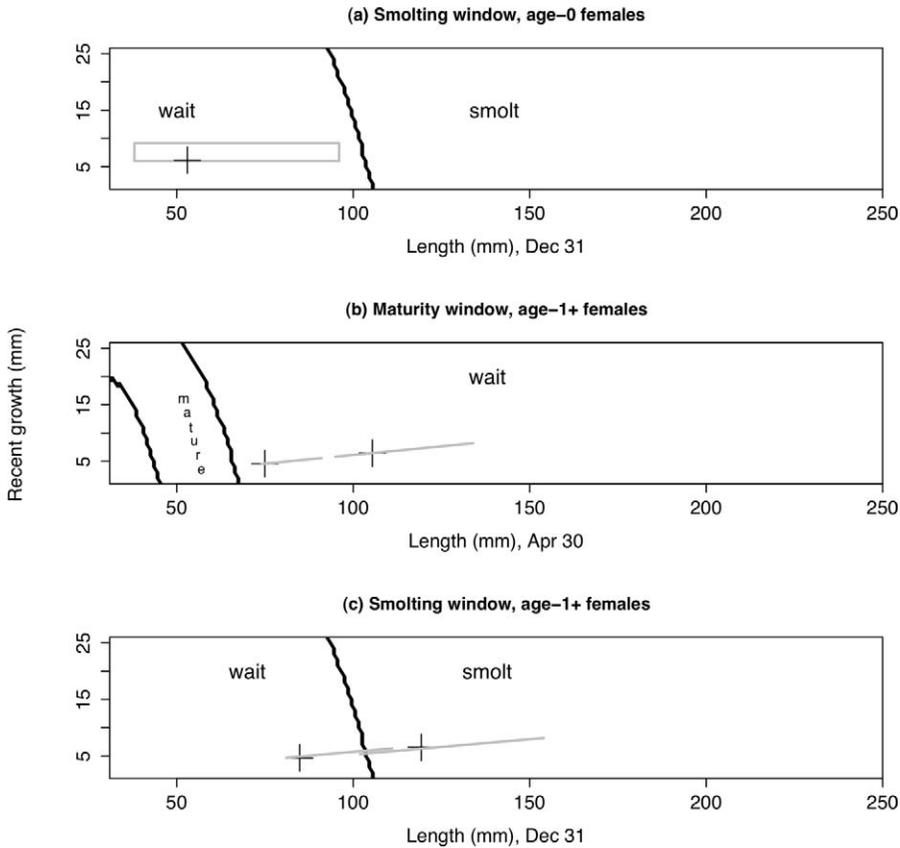
FIGURE 3.—Phase-space graphs for predictions of **(a)** the age-0 smolting decision, **(b)** the age-1+ maturity decision, and **(c)** the age-1+ smolting decision for female fish. In (a), the cross indicates the model predictions of size and growth rate during the decision window, the gray box the estimated range of sizes and growth rates from Hayes et al. (2008 [raw data and inferred maximal and minimal growth rates; see Methods]). In (b) and (c), the crosses indicate the model predictions of size and growth rate during the decision window for age-1 (left) and age-2 (right) fish, the gray lines the range of sizes predicted for these intervals by Hayes et al. (2008; their Figure 7). Recent growth is defined as growth over the course of the decision window.

Most age-0 fish are predicted to wait until age 1 or older before committing to a life history trajectory. Only very small age-1+ fish, smaller than any age-1+ fish that have been sampled, are predicted to mature at age 1 (Figure 3b) since such fish would take a very long time to reach smolting size and would very likely die first. Among age-1 fish, those growing at the expected rate would be predicted to forego smolting as well, but the larger and faster-growing age-1 fish (those 104 mm or longer on December 31 if growing as expected) are predicted to initiate smolting and thus emigrate at age 2 (Figure 3c). Almost all remaining fish are predicted to be large enough to initiate smolting at age 2 and therefore emigrate at age 3.

Thus, among fish with varying emergence times and growth rates, we predict that the very fastest- and earliest-emerging fish will mature as parr, none will emigrate at age 1, some of the faster-growing fish will

emigrate at age 2, most of the remainder will emigrate at age 3, and a few fish will emigrate at age 4. However, it must be realized that each year of delay carries a substantial risk of mortality. Thus, among fish that actually live long enough to commit to a life history trajectory, we predict relatively few mature parr, a substantial number of age-2 and age-3 emigrants, and very few age-4 emigrants.

These predictions are largely consistent with the emigrant ages inferred from scale readings of spawners in Waddell Creek by Shapovalov and Taft (1954), as summarized in Figure 4. However, they report age-1 emigrants as well. Although some of these presumed age-1 emigrants may actually be older fish incorrectly aged because of a lack of annulus formation in the estuarine habitats (Hayes et al. 2008), fish as small as 60–70 mm have been observed migrating down lower Scott Creek (Hayes et al. 2008), and these fish may be
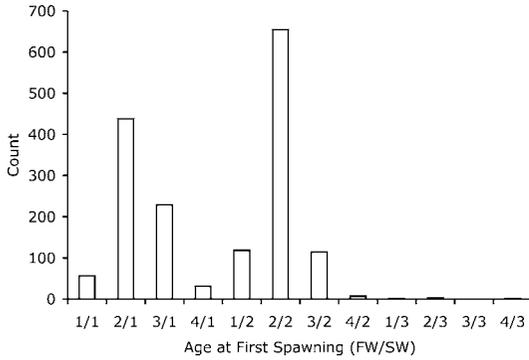
FIGURE 4.—Inferred age (freshwater [FW]/saltwater [SW]) at first spawning for Waddell Creek females in 1933–1942 (adapted from Table 28 in Shapovalov and Taft 1954).
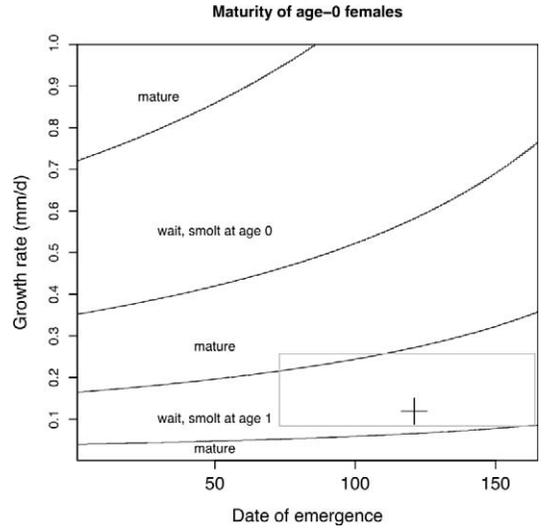

FIGURE 5.—Combinations of emergence date (days since January 1) and growth rate for which age-0 females are predicted to mature as parr, given high stream survival, no limit on the long-term sizes achievable in freshwater, and a low limit on the survival of large smolts. See Figure 2 for additional details.

on course to emigrate at age 1. In addition, Figure 4 may underrepresent the proportion of age-1 emigrants if they have lower ocean survival than the older smolts.

Our model predicts that fish need to be at least 104 mm in December to initiate smolting (and thus approaching 129 mm by May). However, Hayes et al. (2008; their Figure 6) report some fish considerably smaller than this moving downstream and possibly smolting, with the majority of smaller fish moving down earlier in the year. Such fish may be taking advantage of superior growth opportunities in the estuary before entering the ocean (Thorpe 1994; Bond et al. 2008), such that they enter the ocean at sizes near what would be predicted for larger fish emigrating directly from the upstream habitats. A further compli-cation interpreting these data are that not all fish migrating downstream are smolting; some may simply be competitive subordinates displaced from upstream habitats (Leider et al. 1986; Keeley 2001).

The prediction that very few females will mature in freshwater is harder to test against published results. Resident populations are found above multiple water-falls in the Scott Creek watershed, but these waterfalls act as barriers to anadromy so resident life histories would be expected. Some mature resident rainbow trout have been observed spawning below the falls; however, it is unclear how many of these fish were originally spawned below the falls rather than migrat-ing downstream from resident populations above the falls.

Sensitivity Analyses

We reran our model after changing key assumptions or parameter estimates to assess the sensitivity of model predictions. These sensitivity analyses serve two purposes. First, there is uncertainty associated with all of the parameter estimates entering into the model, so it

is important to assess how robust the predictions of the model are to changes in each parameter, to quantify the uncertainty, and to prioritize future data acquisition. In addition, these sensitivity analyses may predict the response of steelhead to alterations in the environment, such as changes in temperature, food supply, and survival.

Evolved behavioral thresholds would probably take many generations to change in response to a new environment. Over the short term we expect fish to still select developmental pathways based on their old size thresholds. Thus, changes in growth might lead to different ages at smolting (for example), but over the short term these changes would be made based on old decision rules. By contrast, changes in survival (river or ocean) would not lead to different sizes during the decision windows and thus would not lead to different life history pathways over the short term. However, following the old decision rules in new conditions may lead to reduced fitness. Over the long term, new decision rules might be expected to evolve, possibly leading to the loss of some life history pathways.

Effects of Growth Rates: Short Term

Over the short term, we predict that changes in growth rates will mainly affect age at smolting. If age-1+ fish grow faster, even more would be expected to initiate smolting at age 1 and emigrate at age 2. Overall, this would shorten generation time and lessen
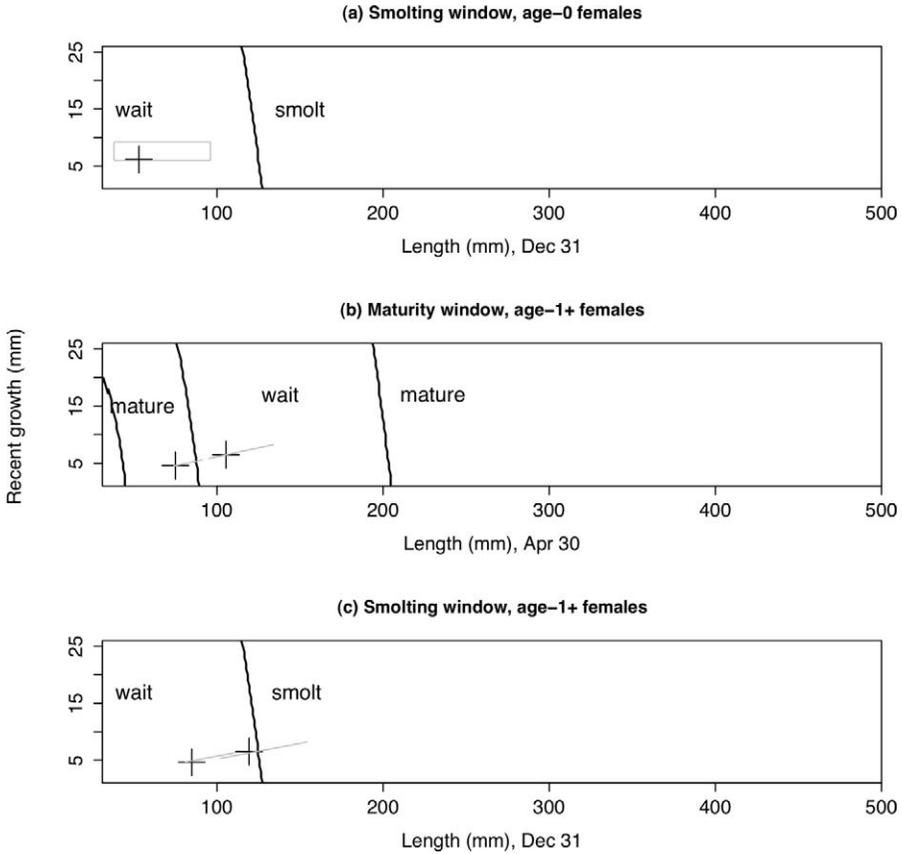
FIGURE 6.—Phase-space graphs for predictions of **(a)** the age-0 smolting decision, **(b)** the age-1+ maturity decision, and **(c)** the age-1+ smolting decision for female fish, given high stream survival, no limit on the long-term sizes achievable in freshwater, and a low limit on the survival of large smolts. See Figure 3 for additional details.

cumulative exposure to freshwater mortality risk, boosting fitness. If age-1+ fish grew more slowly, more of them would be expected to delay smolting, at the cost of extra instream mortality risk and longer generation times. However, changes in growth rate are never predicted to promote age-1+ fish maturing in freshwater over the short term. Among age-0 fish, more rapid growth might lead to more of the fastest-growing fish maturing, and some might even reach sizes sufficient for smolting without using the estuarine habitat.

It seems that faster growth favors initiating maturation as an age-0 fish but not as an older fish for two reasons. First, for age-0 fish there is a shorter period of time between the maturity decision window and the next spawning opportunity than there is for older fish, so in general it is easier to select for maturation in age-0 fish. In addition, even fast-growing age-0 fish are generally too small to have a high probability of marine survival as smolts, so moderate increases in growth rate tend to favor maturity in age-0 fish. By contrast, fast-growing older fish are usually large enough to have a good chance of marine survival, and further boosts in their growth rate increase marine survival even more and further reward smolting.

Hayes et al. (2008) report that fish in the estuary can reach large sizes, for which the model would predict smolting or maturing in year 0. Age-0 fish using the estuarine habitat often grow large enough that smolting is predicted, but some of the slowest-growing estuarine fish could end up at sizes where maturation is predicted rather than smolting. However, achieving this rapid growth as an age-0 fish requires movement down into the estuary, which may effectively commit a fish to ocean entry if the large flows that historically breached the sandbar also forced many fish into the ocean. A detailed analysis of the effects of estuarine growth on life history predictions awaits the collection of estuary-specific mortality rates and possibly a consideration of frequency-dependent strategies, as the growth advan-
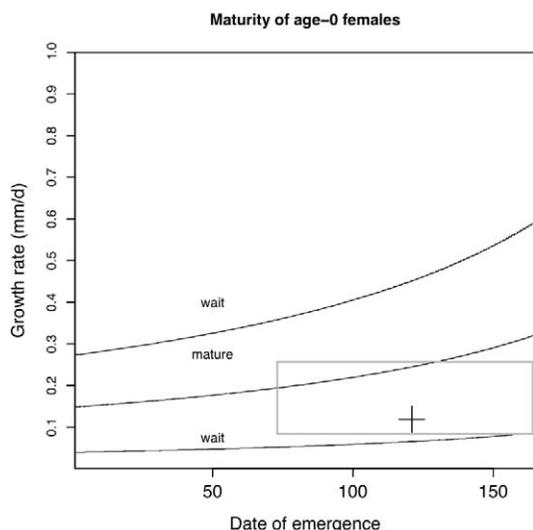
FIGURE 7.—Combinations of emergence date (days since January 1) and growth rate for which age-0 females are predicted to mature as parr if the growth in length is 17% slower in maturing fish. See Figure 2 for additional details.

tage of the estuarine habitat may disappear if too many fish utilize it given negative density dependence in estuarine growth (Hayes et al. 2008).

Effects of Growth Rates: Long Term

Increases in growth rate while maintaining a 250-mm maximum size achievable in freshwater increases the likelihood that some fish mature as parr, but fish emerging later or growing more slowly are still predicted to smolt rather than mature, often smolting at younger ages. Larger maximum size leads to delayed smolting at large sizes if very high marine survival of large smolts is allowed, but fish are predicted to mature instream if maximal freshwater size is unlimited and marine survival is capped at 43.3%, as suggested by the data of Ward et al. (1989).

Effects of Freshwater Survival

With a maximum size of 250 mm and allowing very high marine survival of large smolts, small increases in freshwater survival (to an annual survival of 36%, allowing 1% of fish to live past 4 years) favor delayed smolting rather than maturing in freshwater, even eliminating the prediction that the very fastest-growing parr would mature. Capping smolt marine survival at 43%, as suggested by the data of Ward et al. (1989), does not change this nor does increasing the maximal freshwater size to 500 mm, which only leads to an expectation of further delayed smolting. If the asymptotic size limit is raised and the marine survival

of large smolts is capped, a mixture of mature parr and smolting fish is predicted, residency being predicted for the fastest-growing age-0 fish (Figure 5) and the slowest-growing older fish (Figure 6b). Large older fish are also predicted to mature (Figure 6b); however, it is unlikely any fish could reach sizes approaching 200-mm FL at age 1 or even age 2, and fish growing well enough to reach these sizes at older ages are typically predicted to smolt at age 1 or 2 instead (Figure 6c).

If freshwater survival is boosted even further to 61% annually (allowing 1% of fish to live past 8 years), fish are predicted to always smolt at older ages and larger sizes if there is a 250-mm size limit in freshwater and high survival of large smolts. If one keeps a 250-mm size limit but limits the survival of large smolts, no fish would be predicted to smolt or mature as age-0 fish along typical growth trajectories, but older fish are predicted to show a mix of smolting and maturing as residents. Given a 500-mm size limit in freshwater, with extremely high freshwater survival fish are always predicted to adopt the resident strategy regardless of large smolt marine survival.

Effects of Marine Survival

As the marine survival of smolts decreases, fish are increasingly predicted to follow a resident life history pattern. When ocean survival is halved from its baseline value, fish are predicted to mature as parr along any expected growth trajectory. Obviously, if ocean survival is reduced to zero, smolting is never predicted and the resident strategy becomes favored exclusively. This may explain the occurrence of resident populations above waterfalls in the Scott Creek watershed since any emigrant would leave no descendants in the above-falls population.

Effects of Spawning Survival

Any reduction in the survival of spawning residents is predicted to further favor smolting over maturing in freshwater, and indeed, if the spawning event itself carries a 59% mortality risk maturity in freshwater is never predicted. The actual cost of spawning in residents is probably lower, but this suggests that it may be harder to evolve a resident strategy than the baseline model predicts.

Effects of Costs of Maturing

If the energetic costs of maturing do not reduce growth in length, the size threshold for maturity in age-0 fish moves down to increasingly overlap with the earliest-emerging, fastest-growing parr (Figure 7). In addition, the raw data from Hayes et al. (2008; their Figure 3) suggest that some fish are growing as fast as

0.4 mm/d up until June, and fish growing at this rate are predicted to mature as parr. However, we still predict very few mature parr, since it appears that such growth cannot be maintained for the rest of the year (or the fast-growing fish are moving down to the estuary).

Discussion

A condition-dependent life history model, as implemented by stochastic dynamic programming, can successfully predict most of the observed life history patterns displayed by central coast steelhead females in the field. The model predicts few, if any, resident females, and it is unclear how many resident females spawn in these streams absent input from above-waterfall populations, although field observations suggest there are very few. The model is largely successful predicting the age of smolts as well, matching Shapovalov and Taft's (1954) observation that most returning steelhead in Waddell Creek emigrated after 2 or 3 years in freshwater.

The observations of small fish moving downstream in Scott Creek (Hayes et al. 2008) and the inferred occurrence of age-1 smolts in Waddell Creek (Shapovalov and Taft 1954) might seem surprising in light of model predictions based on upstream growth rates. However, it is well established that juvenile fish utilizing the estuarine habitat can grow much more rapidly than fish remaining upstream (Hayes et al. 2008), and such rapidly growing fish would be expected to smolt at young ages. The model described above can be readily modified to incorporate the possibility of rapid growth in the estuary. Making quantitative predictions about estuarine use, however, requires parameterization with respect to predation risk in the estuary, costs of movement into the estuary (and back out for fish that do not smolt), and possibly a consideration of density-dependent effects since the estuary may not remain a superior growth environment if too many fish move downstream to use it. Further, modeling the use of the estuary may require considering bet-hedging strategies (Slatkin 1974) since the physical quality and temporal duration of the estuary is variable from year to year (Hayes et al. 2008). For example, if the lagoon is inundated with seawater, stratification and anoxic conditions can develop, reducing prey abundance and thus growth rates.

Our model directly considers only female steelhead. Optimal strategies are much harder to identify for male steelhead, where the connection between size and fecundity is less clear (Jones and Hutchings 2001) and the mating success of small males is probably frequency dependent (Gross 1991; Hutchings and Myers 1994). Quantitative predictions of male behavior would require fully parameterized functions describing male fitness as influenced by individual size as well as the frequency of individuals adapting all possible strategies, and we know of no data sets suitable for this purpose. However, all else being equal, small resident males are at a disadvantage because of female mating preferences and male–male conflict, but this disadvantage is reduced as smolt survival decreases. Since our model predicts that changes in anadromy versus residency are driven by trading off the fecundity advantage of large size against the risk of mortality in emigrating smolts, a reduced reward for large size would tend to favor residency. Thus, we expect qualitatively similar patterns in conditions that favor anadromy versus residency, the expectation being that smaller changes are needed to favor residency in males (Hendry et al. 2004; Snover et al. 2006). Among anadromous males, we would expect similar patterns in smolt ages as displayed by females since males and females should face a similar tradeoff in terms of ocean survival at small size versus greater risk of freshwater mortality if delaying smolting until a larger size is achieved. However, the threshold sizes for smolting at each age would probably increase as smolt survival would need to be higher to compensate for a smaller fecundity advantage of anadromous fish. Depending on how these increased threshold sizes compared with size at age for various growth trajectories, some change in smolt ages might be expected, male smolts probably being older and larger.

Given the broad success of the model in describing current life histories, it is instructive to use the model to ask about the likely effects of changes in growth rate and survival due to changes in the riparian environment or climate. Over the short term, only changes in growth rate would be predicted to immediately change life histories. Faster growth easily skews smolt ages toward younger fish, the concurrent result being that more fish would survive until smolting (assuming the larger fish did not suffer increased density-dependent mortality). Conversely, reduced growth rates (upstream or as the result of estuary degradation) would probably lead to older smolts, as fewer fish would survive long enough to emigrate. These predictions are largely consistent with observed geographic gradients in productivity and smolt ages (streams with slower growth having older smolts; Savvaitova et al. 2001), and with observed responses to improved growth environments for juveniles (Ward et al. 2008).

Faster growth might also lead to more fish adapting a resident life history. However, much larger changes in growth rate would be required to change the balance between anadromy and residency than would be required to change the balance of smolt ages, and if freshwater growth rate increases too much, we would

instead predict that age-0 fish would smolt rather than mature. The very fastest growth rates only favor maturity as a resident if the fast growth is accompanied by a very large maximum size achievable in freshwater. Thus, compared with the predictions of Thorpe et al. (1998), our model focusing on ultimate fitness criteria is more restrictive in its predictions as to when good growing conditions would favor the evolution of resident strategies. While it is difficult to propose a proximate mechanism by which fish might assess their likely asymptotic size, it does seem plausible that natural selection will not favor fish that respond to rapid growth (during only part of the year) by maturing as parr if environmental conditions significantly limit maximum sizes supportable in freshwater during other seasons. For example, if poor food availability and high temperatures during the summer and fall limit maximum sizes, rapid growth during the spring alone is not a reliable indicator of potential for large size in the future, and fish maturing in response to rapid growth during the spring would have poor fitness and be unlikely to pass on this strategy.

Over evolutionary time, if marine survival remains unchanged, the replacement of anadromy with resident life histories would seem to require increases in the maximal sizes achievable in freshwater and not just increases in the maximal growth rate for small fish. For streams with strong seasonal variation in growth rate and a "lean period" supporting little to no growth, such an increase in asymptotic size may be difficult to realize.

Although increased stream survival might seem to improve the conditions for residents and favor resident strategies, our models suggest that it will simply favor older, larger smolts (at least for females) unless accompanied by large increases in the asymptotic size achievable in freshwater. This is because of the large size and fecundity advantage of anadromous females, an advantage so large that residents would need to survive for many repeat spawnings to match it. To the extent that stream survival is density dependent (Ward and Slaney 1993), we might expect low densities to correspond to higher survival and thus delayed smolting, although this effect might be obscured if low densities also led to more rapid growth.

A much bigger concern with respect to the loss of anadromy would be decreased ocean survival. While it is not clear how ocean survival would be readily affected by most river conditions, loss or degradations of estuaries could be a major contributor if fish are smaller at ocean entry as a result (Thorpe 1994; Bond et al. 2008). Alterations to stream temperatures might also have a deleterious effect if they cue smolts to begin migrating at inappropriate times, and flow alterations that affect the timing of sandbar formation and breaching could interfere with emigration and return as well. In addition, ocean survival of steelhead may have declined since 1990 (Ward 2000), and if this represents a permanent decline it may pose a threat to the anadromous life history over the long term.

Although changes in stream temperature would need to have very large effects on growth rates before they would be predicted to significantly alter the balance between anadromy and residency, other physiological effects of temperature bear consideration as well. Increased mortality due to higher temperatures could favor smolting at younger ages, having as a possible consequence the production of smaller smolts with poorer marine survival. In addition, high temperatures at crucial periods might interfere with the smolting process per se (Adams et al. 1975; Hoar 1988; McCullough 1999).

In conclusion, our approach to modeling steelhead life histories shows considerable promise in explaining the existing patterns of life history variation and may be useful in predicting responses to environmental changes. Over the short term, we predict altered growth rates will most likely change life history trajectories, particularly age at smolting. Over the long term, it appears that survival probabilities, particularly in the marine environment, are most important in selecting for residency versus anadromy. This modeling approach holds promise for explaining existing life history patterns and evolutionary responses to environmental changes in other steelhead populations as well as other facultatively anadromous species such as Atlantic salmon (Thorpe et al. 1998), brown trout *Salmo trutta*, brook trout *Salvelinus fontinalis*, Arctic char *S. alpinus* (Rikardsen et al. 2004), masu salmon *O. masou*, Dolly Varden *S. malma*, and cutthroat trout *O. clarkii*, especially if coupled to environmentally driven models of growth and survival.

References

Adams, B. L., W. S. Zaugg, and L. R. McLain. 1975. Inhibition of saltwater survival and Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Transactions of the American Fisheries Society 104:766–769.

Allen, G. H., and G. A. Sanger. 1960. Fecundity of rainbow trout from actual count of eggs. Copeia 1960:260–261.

Allen, M. A. 1986. Population dynamics of juvenile steelhead trout in relation to density and habitat characteristics. Master's thesis. Humboldt State University, Arcata, California.

Berglund, I. 1992. Growth and early maturation in Baltic salmon (*Salmo salar*) parr. Canadian Journal of Zoology 70:205–211.

Bley, P., and J. R. Moring. 1988. Freshwater and ocean survival of Atlantic salmon and steelhead: a synopsis. U.S. Fish and Wildlife Service Biological Report 88(9).

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242–2252.

Burns, J. W. 1971. The carrying capacity for juvenile salmonids in some northern California streams. California Fish and Game 57:44–57.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.

Ciancio, J. E., M. Pascual, M. Botto, M. Amaya, S. O'Neal, C. Riva Rossi, and O. Iribarne. 2008. Stable isotope profiles of partially migratory salmonid populations in Atlantic rivers of Patagonia. Journal of Fish Biology 72:1708–1719.

Clarke, W. C. 1989. Photoperiod control of smolting: a review. Physiology and Ecology Japan 1:497–502.

Clark, C. W., and M. Mangel. 2000. Dynamic state variable models in ecology: methods and applications. Oxford University Press, New York.

DuBois, R. B., S. D. Plaster, and P. W. Rasmussen. 1989. Fecundity of spring- and fall-run steelhead from two western Lake Superior tributaries. Transactions of the American Fisheries Society 118:311–316.

Duston, J., and R. L. Saunders. 1992. Effect of 6-, 12-, and 18-month photoperiod cycles on smolting and sexual maturation in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 49:2273–2280.

Elson, P. F. 1957. The importance of size in the change from parr to smolt in Atlantic salmon. Canadian Journal of Fish Culture 21:1–6.

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379–416.

Gardner, S. N., and M. Mangel. 1997. When can a clonal organism escape senescence? American Naturalist 150:462–490.

Gotthard, K. 2008. Adaptive growth decisions in butterflies. Bioscience 58:222–230.

Gross, M. R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology 72:1180–1186.

Hazel, W. N., R. Smock, and M. D. Johnson. 1990. A polygenic model for the evolution of and maintenance of conditional strategies. Proceedings of the Royal Society of London B 242:181–187.

Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J.

Smith, E. C. Anderson, A. J. Ammann, and R. B. MacFarlane. 2008. Steelhead growth in a small central California watershed: upstream and estuarine rearing patterns. Transactions of the American Fisheries Society 137:114–128.

Hendry, A. P., T. Bohlin, B. Jonsson, and O. K. Berg. 2004. To sea or not to sea? Anadromy versus nonanadromy in salmonids. Pages 92–125 *in* A. P. Hendry and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, London.

Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 275–345 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume XIB. Academic Press, New York.

Høgåsen, H. R. 1998. Physiological changes associated with the diadromous migration of salmonids. Canadian Special Publication of Fisheries and Aquatic Sciences 127.

Hutchings, J. A., and R. A. Myers. 1994. The evolution of alternative mating strategies in variable environments. Evolutionary Ecology 8:256–268.

Jones, M. W., and J. A. Hutchings. 2001. The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. Heredity 86:675–684.

Keeley, E. R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82:1247–1259.

Leider, S. A., M. W. Chilcote, and J. J. Loch. 1986. Comparative life history characteristics of hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 43:1398–1409.

Mangel, M. 1994. Climate change and salmonid life history variation. Deep Sea Research, II (Topical Studies in Oceanography) 41:75–106.

Mangel, M. 1996. Computing expected reproductive success of female Atlantic salmon as a function of smolt size. Journal of Fish Biology 49:877–882.

Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey.

Mangel, M., and W. H. Satterthwaite. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. Bulletin of Marine Science 83:107–130.

Martyniuk, C. J., G. M. L. Perry, H. K. Mogahadam, M. M. Ferguson, and R. G. Danzmann. 2003. The genetic architecture of correlations among growth-related traits and male age at maturation in rainbow trout. Journal of Fish Biology 63:746–764.

McCullough, D. A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. Prepared for the U.S. Environmental Protection Agency, Region 10, Seattle.

Metcalfe, N. B. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):93–103.

Metcalfe, N. B., F. A. Huntingford, and J. E. Thorpe. 1988.

Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. Journal of Animal Ecology 57:463–474.

Myers, R. A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 89:53–61.

Olsen, J. B., K. Wuttig, D. Fleming, E. J. Kretschmer, and J. K. Wenburg. 2006. Evidence of partial anadromy and resident-form dispersal bias on a fine scale in populations of *Oncorhynchus mykiss*. Conservation Genetics 7:613–619.

Pascual, M. A., P. Bentzen, C. Riva Rossi, G. Mackey, M. Kinnison, and R. Walker. 2001. First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. Transactions of the American Fisheries Society 130:53–67.

Pearson, G. A. 1993. An analysis of the growth of returning North Esk Atlantic salmon (*Salmo salar*) over the period 1963–1993. Master's thesis. University of Wales, Bangor.

Peven, C. M., R. R. Whitney, and K. R. Williams. 1994. Age and length of steelhead smolts from the mid-Columbia River basin, Washington. North American Journal of Fisheries Management 14:77–86.

Piche, J., J. A. Hutchings, and W. Blanchard. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. Proceedings of the Royal Society of London B 275:1571–1575.

R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org. (April 2007).

Rikardsen, A. H., J. E. Thorpe, and J. B. Dempson. 2004. Modeling the life history variation of Arctic charr. Ecology of Freshwater Fish 13:305–311.

Savvaitova, K. A., K. V. Kuzischin, and D. S. Pavlov. 2001. Population structure of mikizha in the rivers of Kamchatka and North America. Pages 138–155 *in* D. S. Pavlov and K. A. Savvaitova, editors. The Pacific noble salmons and trouts of Asia. Scientific World, Moscow.

Seamons, T. R., P. Bentzen, and T. P. Quinn. 2004. The effects of adult length and arrival date on individual reproductive success in wild steelhead trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 61:193–204.

Shapovalov, L. 1967. Biology and management of steelhead trout in California. California Department of Fish and Game, Inland Fisheries Administrative Report 67-7, Sacramento.

Shapovalov, L., and A. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*), with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game, Fish Bulletin 98:1–373.

Slatkin, M. 1974. Hedging one's evolutionary bets. Nature (London) 250:704–705.

Snover, M. L., G. M. Watters, and M. Mangel. 2005. Interacting effects of behavior and oceanography on growth in salmonids with examples for coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 62:1219–1230.

Snover, M. L., G. M. Watters, and M. Mangel. 2006. Top-down and bottom-up control of life history strategies in coho salmon (*Oncorhynchus kisutch*). American Naturalist 167:E140–E157.

Sutherland, D. F. 1973. Distribution, seasonal abundance, and some biological features of steelhead trout, *Salmo gairdneri*, in the North Pacific Ocean. U.S. National Marine Fisheries Service Fishery Bulletin 71:787–826.

Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17:76–93.

Thorpe, J. E. 2007. Maturation responses of salmonids to changing developmental opportunities. Marine Ecology Progress Series 335:285–288.

Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12:581–599.

Thrower, F. P., J. J. Hard, and J. E. Joyce. 2004. Genetic architecture of growth and early life history transitions in anadromous and derived freshwater populations of steelhead. Journal of Fish Biology 65(Supplement A):286–310.

Tipping, J. M. 1991. Heritability of age at maturity in steelhead. North American Journal of Fisheries Management 11:105–108.

Ward, B. R. 2000. Declivity in steelhead trout recruitment at the Keogh River over the past decade. Canadian Journal of Fisheries and Aquatic Sciences 57:298–306.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 44:1110–1122.

Ward, B. R., and P. A. Slaney. 1990. Returns of pen-reared steelhead trout from riverine, estuarine, and marine releases. Transactions of the American Fisheries Society 119:492–499.

Ward, B. R., and P. A. Slaney. 1993. Egg-to-smolt survival and fry-to-smolt density dependence of Keogh River steelhead. Canadian Special Publication of Fisheries and Aquatic Sciences 118:209–217.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853–1858.

Ward, B. R., P. A. Slaney, and D. J. F. McCubbing. 2008. Watershed restoration to reconcile fisheries and habitat impacts at the Keogh River in coastal British Columbia. Pages 587–602 *in* J. Nielsen, J. J. Dodson, K. Friedland, T. R. Hamon, J. Musick, and E. Verspoor, editors. Proceedings of the Fourth World Fisheries Congress. American Fisheries Society, Symposium 49, Bethesda, Maryland.

West, G. B., J. H. Brown, and B. J. Enquist. 2001. A general model for ontogenetic growth. Nature 413:628–631.

Zimmerman, C. E., and G. H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57:2152–2162.

Appendix: Survival Estimates

We estimated freshwater survival from reports by Burns (1971) for North Fork Caspar Creek and Allen (1986, as reported in Bley and Moring 1988) for the Mad River in coastal northern California; s_b includes survival from the egg stage until early October. Because it includes an unobservable egg-to-alevin-to-fry transition, we simply tuned s_b retrospectively so that the model generated average lifetime reproductive output $R_0 = 1$ for an egg forming a newly emerged fish that follows the optimal strategy. We estimated s_0 (the survival of age-0 fish from November 1 to December 31) as 0.519, the square root of the 4-month June–October survival for age-0 fish reported by Burns (1971), preferring the estimate from Caspar Creek over that from Mad River because its geographic setting is more similar to that of Scott Creek.

Allen (1986, as reported in Bley and Moring 1988) reported first-winter survivals of 26–70% for Mad River steelhead. To generate a point estimate for monthly survival, we took the sixth root of the geometric mean of these values, yielding a monthly survival estimate of 0.868 for the winter. For summer survival, we performed similar calculations on the 6–24% first-summer survival estimates (we did not use the second-summer estimates since they were probably confounded low by emigration), yielding an estimated monthly summer survival of 0.702. We treated October–March as winter and April–September as summer, although we used a separate estimate for the ambiguous June–October period.

We then estimated s_1 (survival from January 1 to March 15) as $0.868^{2.5}$, or 0.701. We estimated s_2 (survival from March 16 to March 31) as $0.868^{0.5}$, or 0.931. We estimated s_3 (survival from April 1 to May 1) as 0.702. We estimated s_4 (survival from May 1 to November 1) as 0.702×0.56 for age-1+ fish, the survival from June to October reported by Burns (1971), for a final estimate of 0.393. We estimated s_5 (survival from November 1 to December 31) as 0.868^2, or 0.753. Taken together, these estimates yield an annual survival of 14% for age-1+ fish.