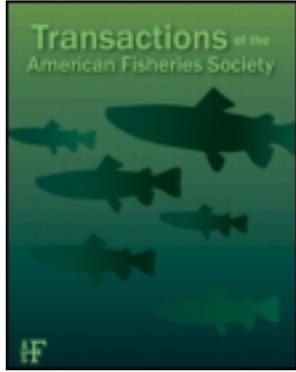


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State-Dependent Migration Timing and Use of Multiple Habitat Types in Anadromous Salmonids

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ARTICLE

State-Dependent Migration Timing and Use of Multiple Habitat Types in Anadromous Salmonids

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Abstract

Anadromous salmonids vary considerably in their age at ocean entry, their timing of ocean entry within a year, and the extent to which they use multiple habitat types within freshwater. To better understand habitat use and movement timing, we developed a broadly applicable model of state-dependent movements among multiple habitats, which was parameterized based on a case study of steelhead *Oncorhynchus mykiss* in a California coastal watershed with a seasonally closed lagoonal estuary. The model correctly predicted population-level patterns, including predominance of anadromy and a dominant smolt age of 2 years. In addition, the new model predicted the occurrence of small, lagoon-rearing fish (displaying smoltlike migratory behavior) that returned upstream and did not enter the ocean until the next year, whereas large fish emigrated from the lagoon into the ocean. The new model predicted all-or-nothing habitat use for fish of a given size, but we observed a mix of strategies for fish of the same size. Our modeling suggests that a mortality–growth rate tradeoff can explain much of the life history variation, but this tradeoff alone cannot drive a mixture of habitat use strategies by fish of a similar state (i.e., length). We predicted that a mixed strategy may develop as a consequence of density-dependent reduction in growth rates, arising as more individuals recruit to the originally preferable habitat. Higher risk in the higher-growth habitat may halt recruitment to the high-growth habitat even before growth rates are equalized. Uncertainty in rewards associated with the higher-growth habitat may also favor a mixed strategy in which only some fish accept the higher risk associated with increased growth

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opportunity. This model framework can be used to predict movement timing and use of multiple habitats for other salmonids and in other systems.

A relatively well-developed conceptual and computational theory describes variation in age-specific movements by salmonids between freshwater and ocean environments. First developed for Atlantic salmon *Salmo salar* (Mangel 1994; Thorpe et al. 1998) and then extended to Arctic char *Salvelinus alpinus* (Rikardsen et al. 2004) and steelhead *Oncorhynchus mykiss* (anadromous rainbow trout; Mangel and Satterthwaite 2008; Satterthwaite et al. 2009, 2010), these models allow predictions of life history patterns on the basis of tradeoffs between opportunities for growth and survival. These state-dependent life history models typically operate at the level of two habitats (i.e., freshwater versus ocean) and predict life history timing at the level of years (e.g., smolt at age 1 or smolt at age 2). Thus, they do not account for fine-scale variation important in some salmonid life histories. For example, many salmonids use estuarine habitats for varying time periods, and this phase of their life cycle is distinct from their use of either upstream or ocean habitats (Thorpe 1994; Miller and Sadro 2003; Koski 2009). In addition to variation in age at emigration, there can be considerable individual variability in the within-year timing of ocean entry (Fisher 1994; Bottom et al. 2005).

In population-level tests, state-dependent models developed by Satterthwaite et al. (2009, 2010) successfully predicted the frequency of resident and anadromous steelhead in two California Central Valley populations and correctly predicted the predominance of anadromy and the most frequent age of smoltification on the central California coast (Sogard et al. 2012). These models predicted life histories of individuals on the basis of their current state (size) and expected survival probabilities and state dynamics (growth) associated with different habitats, with resultant effects on expected lifetime fitness. However, to date there are no published tests of state-dependent life history predictions from these models at the individual fish level. Such tests will increase the usefulness of models as management tools; by learning where current models fail, we can identify and then incorporate important mechanisms that have been omitted and we can identify life stages for which more data are needed.

We revisited a state-dependent steelhead life history model that was developed by Satterthwaite et al. (2009), and we applied it to growth rates documented in the upper Scott Creek (central California coast) watershed by Hayes et al. (2008). Although it correctly predicted the approximate age structure of smolts, the model missed some details of life history in Scott Creek and nearby Waddell Creek (Shapovalov and Taft 1954; Hayes et al. 2011), namely the presence of small (<100 mm fork length [FL]) fish among the downstream migrants and some fish that rear in a downstream lagoon but then return upstream rather than entering the ocean. The model predicted a minimum size of

100–110 mm in December for fish to initiate the smoltification process, but smaller fish have been observed migrating downstream with elevated levels of gill Na^+ , K^+ ATPase (Hayes et al. 2011), an enzyme that provides an index of saltwater readiness (Zaugg and McLain 1972). In addition, some fish have been observed to migrate to and overwinter in the lagoon, migrate back upstream in fall, and overwinter upstream before smolting and emigrating in the following spring (Shapovalov and Taft 1954; Hanson 2008; Hayes et al. 2011). These discrepancies between model predictions and empirical observations may have arisen because Satterthwaite et al. (2009) neglected the potential for the high-risk–high-reward lagoon habitat to influence steelhead life history trajectories. Here, we apply a newly developed model to this lagoonal system as a case study for the treatment of state-dependent use of multiple habitat types by salmonids, but our methods can be generalized in a straightforward manner.

METHODS

Our study consisted of a combination of model development and empirical work carried out in the Scott Creek watershed. First, to test the predictions of the new model and the Satterthwaite et al. (2009) model at the individual level, we reconstructed the life histories of individually marked fish with known sizes and growth rates. Second, we estimated survival rates in upstream and lagoon habitats. Third, we developed a broadly applicable state-dependent model of anadromous salmonid movement among multiple habitat types (upstream, lagoon, and ocean), allowing for weekly movement decisions. As a case study, we parameterized the model for female steelhead in the Scott Creek system. The model used growth and survival data as inputs, but observed life histories were not model inputs. Finally, we assessed the parameterized model's ability to reproduce observed life history patterns in Scott Creek, and we performed algebraic analyses of the model to draw general conclusions that need not be tied to any specific system.

Study site.—Scott Creek (Figure 1) is a small, 70-km² coastal watershed located 100 km south of San Francisco in central California (37°02'28"N and 122°13'50"W). Anadromous fish can access approximately 23 km of stream between the estuary and natural upstream barriers of the main stem and the three main tributaries (Hayes et al. 2008). Flow is highly variable, with winter peak flows reaching 28 m³/s (Hayes et al. 2008). Summer and autumn flows may be reduced to 0.08 m³/s during an average year, and during extreme droughts the stream may run dry in the lower reaches. A sandbar typically forms in the summer or fall, closing off the estuary to form a freshwater lagoon with occasional saltwater input from storm surges.

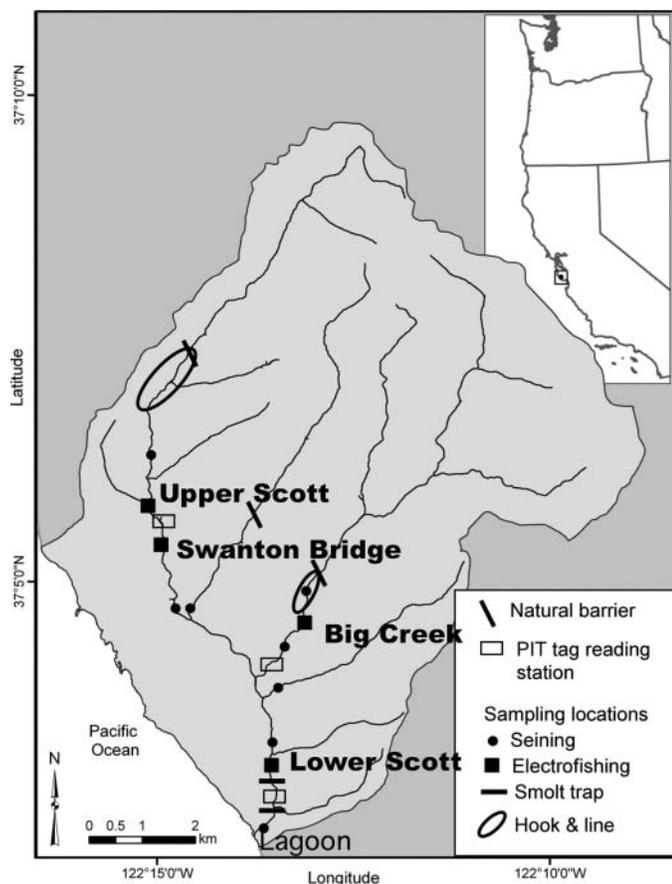


FIGURE 1. The Scott Creek watershed study system in central California, with sampling sites indicated (PIT = passive integrated transponder).

Conditions in the lagoon provide for accelerated growth rates (Hayes et al. 2008). This enhanced growth may come at the cost of reduced survival, as at least some coastal lagoons carry elevated mortality risk (Smith 1990) and there is seasonal variation in the suitability of lagoon habitat for fish rearing (Hayes et al. 2011). Saltwater intrusion can result in stratified conditions and a hypoxic bottom layer. High lagoon temperatures can facilitate increased growth but can also increase metabolic costs. Predation risk may also be particularly high in the lagoon (Hayes et al. 2011). Growth in the lagoon is density dependent (Hayes et al. 2008). The estuary typically reopens after winter storms in November through January.

Field observations.—We followed the life histories of marked individual fish that were first sampled using three-pass-depletion electrofishing at four sites on Scott Creek (Figure 1). We sampled in June, October, and December (June 2006–June 2008 and June 2009–December 2010; U.S. Endangered Species Act restrictions prevented electrofishing in spring). We measured weight (g) and FL (mm) and marked all 65-mm and larger fish with passive integrated transponder (PIT) tags, following the methodology described by Sogard et al. (2009). To test model predictions of movement and life histories based on fish size, we

reconstructed life histories of individual fish using recaptures of PIT-tagged fish from continued electrofishing, downstream migrant traps, lagoon seining, and resightings made by instream PIT tag readers (Figure 1; details in Hayes et al. 2011). We then classified fish into one of the following five categories based on subsequent recaptures or resightings, given that we knew their size and location in December: (1) lost fish, which had no further record for greater than 1 year after capture in December; there was no information on movement or life history trajectories for these fish; (2) stationary fish, which were recaptured or resighted within 1 km of their original location in March–October of the following year; earlier or later resightings were treated as lost unless further resightings were made; (3) instream relocators, which moved over 1 km either upstream or downstream but remained above the migrant trap; (4) downstream migrants, which were observed passing through the downstream trap or were caught by lagoon seining the following year but were not subsequently resighted upstream; and (5) lagoon visitors, which were seen passing through the downstream trap or were captured in the lagoon and then were resighted upstream less than a full year later.

Satterthwaite et al. (2009) predicted a 100–110-mm size threshold for downstream movement. Thus, all fish smaller than this size were predicted to fall into category 2 or 3; larger fish were predicted to fall into category 4; and no fish were predicted to belong to category 5. To test these predictions, we used a χ^2 test to compare the frequency of migratory fish (downstream migrants or lagoon visitors; i.e., categories 4 and 5) and non-migratory fish (stationary fish or instream relocators; i.e., categories 2 and 3) that were larger or smaller than 105 mm FL in December.

Results of the new model (described later) predicted that some small fish would move downstream but would rear in the lagoon temporarily before returning upstream (i.e., category 5). Some fish rearing in the lagoon may die or escape detection upstream even if they return, resulting in the classification of actual lagoon visitors as a mixture of categories 4 and 5. We therefore compared the overall shape of the size distributions of migratory (categories 4 and 5) versus nonmigratory (categories 2 and 3) fish by using a Kolmogorov–Smirnov (K–S) test to determine whether downstream migrants were larger than fish remaining upstream. Since the new model predicted ocean entry by large fish and upstream return by small fish, we used a second K–S test to compare the size frequency distribution of visitors with that of downstream migrants. We performed these tests in R software (R Development Core Team 2011).

Survival estimates.—We estimated upstream survival rates for age-0 fish from quantitative depletion electrofishing in Scott Creek (Pollock and Otto 1983, their equation 17). We generated seasonal abundance estimates at the start and end of summer (June to October), fall (October to December), and winter–spring (December to June). We calculated daily survival rates at the three upstream-most sites during June 2006 through June 2008 (data from 2009 were excluded due to a major fire in the

upper watershed during August 2009). For age-1 and older (age-1 +) fish (identified based on site-dependent size distribution breaks averaging 83 mm FL in June, 87 mm FL in October, and 92 mm FL in December), we used PIT tags to track individual capture histories over time and we used Program MARK (White and Burnham 1999) to estimate survival and recapture probabilities within each of the sites and seasons. The best-supported model contained seasonal variation in apparent survival but a constant capture probability.

We estimated lagoon survival based on changes in density inferred from multiple estimates using mark–recapture techniques between late July and early October 2007–2009. We conducted monthly lagoon sampling during lagoon closure (July–November) with a 30- × 2-m nylon beach seine following the methods described by Bond et al. (2008). During 2007 and 2008, we seined once per month and used recaptures of PIT-tagged fish to calculate monthly lagoon population estimates. In 2009, we estimated the monthly lagoon population using a 2-d mark–recapture sampling design. On the first day, fish were captured, tagged, and released into the lagoon. We seined again 1–7 d later and estimated population size based on the proportion of recaptured fish in the second sample (see Appendix for details). We generated maximum likelihood estimates of monthly lagoon population size using the Ricker elaboration of the Petersen method (Ricker 1975) implemented via *mrClosed* in the *FSA* package (Ogle 2011) for R. We assumed a closed population during this period so that density changes reflected

survival. The lagoon was closed during this time, so no fish could emigrate to the ocean. Immigration to the lagoon during this period is low but is not zero (Hayes et al. 2011, their Figure S1). We assumed that lagoon survival was constant year-round based on limited data, and we considered October to be our final density estimate because substantial migration out of the lagoon and back upstream occurs in November (Hayes et al. 2011).

We converted daily survival into weekly survival for use in the life history model. For model parameterization, we used the seasonal arithmetic means of annual estimates upstream and we assumed that lagoon survival was constant at the July–October value. For lagoon survival, we averaged 2007 and 2009 estimates, excluding the highly uncertain 2008 estimate (Appendix Table A.1). We also assumed that upstream survival of age-1 + fish from December to June was the same as their October–December value, since estimates from December to June would be biased low by substantial emigration during that period.

Formulating a state-dependent movement model with multiple habitats.—We modeled weekly movement between upstream, lagoon, and ocean habitats for presumed anadromous fish (Figure 2), based on assumed trade-offs between growth rate and mortality risk in different habitats and the concomitant costs and benefits in terms of expected lifetime reproductive success. We assumed that individual behavior depends on state (in this case, length) and identified optimal state-dependent behaviors that maximized expected lifetime fitness (Mangel and Clark 1988; Clark and Mangel 2000). We assumed that survival of

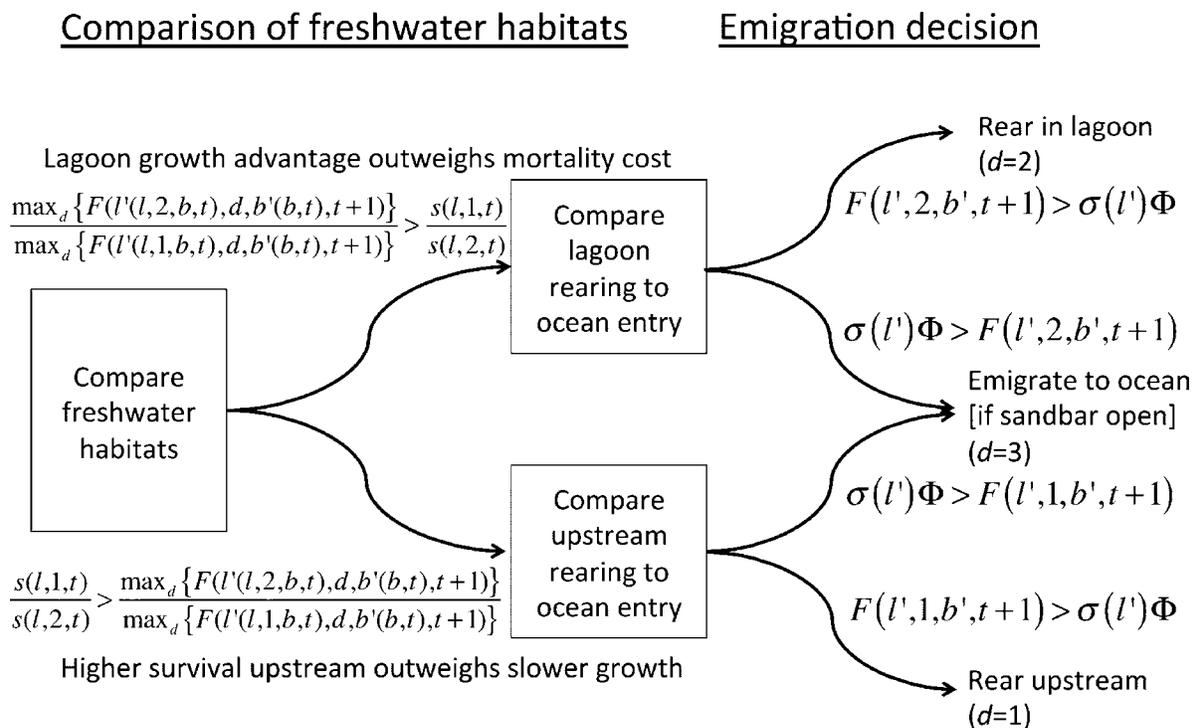


FIGURE 2. Flow chart of a conceptual model of steelhead life history and movement decisions in the Scott Creek system. See Table 1 for definitions of parameters, and see Methods for a description of equations. Note that emigration to the ocean is only possible when the lagoon is not closed by the sandbar.

TABLE 1. Model parameters used to predict steelhead movement and habitat selection in the Scott Creek system, California.

Symbol	Parameter description
l	Fork length (mm)
t	Time (weeks since January 1 of birth year)
x	Location (1 = upstream, 2 = lagoon)
d	Movement decision (1 = upstream, 2 = lagoon, 3 = ocean)
b	Ratio of expected current lagoon growth to long-term average
l'	Expected value of l after growth one time step in the future
s	Weekly survival probability
T	Terminal time (maximum freshwater residency)
o	Status of lagoon (1 = open, 0 = closed, intermediate = probability of being open)
σ	Emigrant survival
Φ	Lifetime fecundity of returning steelhead

emigrating smolts is size dependent, so rapid freshwater growth has the potential to increase marine survival but may decrease freshwater survival. Costs and benefits of changes in growth rates are predicted to vary through time depending on fish size and time of year. Time of year is important because time-varying growth opportunities and survival rates change the relative risks and rewards of upstream versus lagoon habitats and because emigration to the ocean is only possible when the lagoon is open.

We restricted the model to anadromous fish because there is evidence for a degree of genetic predisposition to anadromy in Scott Creek *O. mykiss* below barriers to anadromy (Pearse et al. 2009). We did not explicitly model initiation of the parr-smolt transformation because there is evidence for seasonal gill Na^+ , K^+ ATPase upregulation even in upstream fish (Hayes et al. 2004, 2011; Hanson 2008). Combined with overall high saltwater tolerance of Scott Creek yearlings (Beakes et al. 2010), this suggests an ability to quickly adopt a saltwater-tolerant physiology.

Expected lifetime fitness (F) of a fish is a function of state variables consisting of length l , position x (1 = upstream, 2 = lagoon), and time t (in weeks since January 1 of the birth year; Table 1). We let b denote an expected rescaling of lagoon growth rates (relative to the long-term mean), accounting for density dependence (Hayes et al. 2008); b decreases as the number of fish in the lagoon increases.

Following the work of Hayes et al. (2008), we assumed that age-0 fish upstream grew at a rate of 0.119 mm/d, whereas older fish and fish in the lagoon grew at location- and season-dependent specific growth rates r_{xt} (Table 2; Hayes et al. 2008), with a maximum (asymptotic) freshwater length of 250 mm (Satterthwaite et al. 2009). Thus, if $l(t)$ is the size (FL, mm) at the start of week t , the expected size at the start of the next

TABLE 2. Seasonal weekly specific growth rates (SGR; relative change in fork length [mm] per week, see Methods) for upstream-rearing and lagoon-rearing steelhead.

Season	Upstream SGR	Lagoon SGR
Winter (weeks 44–4) ^a	0.0066	0.0150
Spring (weeks 5–17)	0.0148	0.0258
Summer (weeks 18–30)	0.0017	0.0295
Fall (weeks 31–43)	0.0035	0.0231

^aWeeks 44–4 for winter indicates week 44 in the first year to week 4 in the subsequent year.

week depends on the current size, location, rescaled lagoon growth rate (if the fish is currently in the lagoon), and seasonal (dependence on t) effects:

$$l(t+1) = l'(l, x, b, t) = \begin{cases} l(t)(1 + r_{1t}) & \text{if } x = 1 \text{ (upstream)} \\ l(t)(1 + br_{2t}) & \text{if } x = 2 \text{ (lagoon)} \end{cases} \quad (1)$$

We let $s(l, x, t)$ denote freshwater survival from one week to the next.

We used dynamic state variable modeling (Mangel and Clark 1988; Clark and Mangel 2000) to determine the weekly state-dependent movement decision d (1 = remain or move upstream; 2 = remain or move downstream; 3 = emigrate to the ocean [only possible when the estuary is open]) that maximized the expected lifetime fitness. We calculated movement decisions for a range of b to explore the effects of different lagoon densities on predicted movement.

Dynamic state variable models involve assigning expected lifetime fitness to all states at the latest possible time T and then working backwards. Optimal decisions at each previous time step are then identified using expected state dynamics, conditioned on the (already determined) fitness values associated with future states expected for each possible decision. Since the oldest smolts in this region emigrate at age 4 (Shapovalov and Taft 1954), we chose a terminal time T corresponding to 5 years (260 weeks). Thus, any fish remaining in freshwater through the end of its fifth year had zero fitness, so that

$$F(l, x, b, T) = 0. \quad (2)$$

Expected lifetime fitness of fish emigrating to the ocean was determined by their size-dependent expected survival to first spawning $\sigma(l)$ and lifetime reproductive output Φ (conditioned on making their first return, but including repeat spawnings):

$$F_{\text{ocean entry}} = \sigma(l)\Phi. \quad (3)$$

Based on the reported size-dependent relative survival of hatchery smolts from Scott Creek (Bond et al. 2008) and the age-dependent marine survival of wild fish from nearby Waddell

Creek (Shapovalov and Taft 1954), we estimated:

$$\sigma(l) = 0.84 \frac{e^{-8.657+0.0369l}}{1 + e^{-8.657+0.0369l}}, \quad (4)$$

where l is FL in millimeters (Satterthwaite et al. 2009), and survival is 0 for fish smaller than 125 mm (c.f., Bond et al. 2008). Satterthwaite et al. (2009) estimated that Φ is 7,100 eggs. We assumed that fecundity of returning fish was independent of their size at emigration, in part because (1) size at emigration is generally a poor predictor of size at return (Sutherland 1973; Pearson 1993; Snover et al. 2005) and (2) size only explained a small amount of variation in fitness among anadromous female steelhead (Seamons et al. 2004).

Ocean entry is only possible if the lagoon is open, with probability $o(t)$. If $o(t)$ was less than 1, movement decision 3 ($d = 3$) resulted in fish emigrating if the sandbar was open upon arrival in the lagoon or rearing in the lagoon for at least one time step if the sandbar was closed. In forward iterations, $o(t)$ was known for fish in the lagoon, and depending on model implementation $o(t)$ could be known (taking the form of an indicator function) or unknown (a time-dependent probabilistic function) for fish upstream. To generate the results presented here, we used a constant $o(t)$ that took only values of 0 or 1. We assumed a lagoon opening date of January 16 and a closing date of August 5, the means of 1989–2003 data on sandbar closure for Scott Creek.

We assumed that movement occurred at the end of the week, so fish grew and survived according to their current location. For t less than T , a fish emigrating to the ocean received expected fitness governed by equation (4), conditioned on survival and growth during the intervening week. However, a fish moving to upstream habitat ($d = 1$) or to the lagoon or downstream ($d = 2$; also the result of movement decision 3 if the lagoon is closed) had an expected survival $s(l, x, t)$; if it survived, the fish was expected to grow to size $l'(l, x, b, t)$ based on its current location. This set the fish's starting conditions for the next week in the newly selected habitat, so future fitness was conditioned on d rather than x . Thus,

$$F(l, x, b, t) = \max_d \left\{ \begin{array}{l} s(l, x, t)F[l'(l, x, b, t), d, b'(b, t), t+1] \text{ if } d < 3, \\ s(l, x, t)\sigma[l'(l, x, b, t)]\Phi \text{ if } d = 3 \text{ and } o(t) = 1, \\ \text{or otherwise if } d = 3 \text{ and } o(t) < 1 \\ s(l, x, t)\{o(t)\sigma[l'(l, x, b, t)]\Phi + [1 - o(t)] \\ \times F[l'(l, x, b, t), 2, b'(b, t), t+1] \} \end{array} \right\}, \quad (5)$$

where $b'(b, t)$ describes dynamics in expected lagoon growth from one week to the next. In the backward iteration (Clark and Mangel 2000), we determined optimal decisions for all combinations of state variables (l, x , and b) and weeks (t). Thus,

we assumed that knowledge about lagoon state b was easy to acquire, either through direct sampling or information gained from flow rates upstream, local density of conspecifics, or an evolutionary expectation of seasonal dynamics.

Generating life history predictions.—We solved the dynamic programming equation (5) for our site-specific parameterization to generate predictions of state-dependent behavior for Scott Creek fish, and we compared those predictions with the observed movements of individuals of different sizes. We performed forward simulations where individual fish made decisions based on the known state of the lagoon, including its suitability for growth as affected by the locations of other fish (i.e., in forward simulations, $b[t]$ varied among fish based on a dominance or priority hierarchy and how many fish were already in the lagoon).

The model can also generate general predictions that are not tied to the particular system through analytical or graphical solutions of the dynamic programming equation. For example, based on equation (5), the decision (made at time $t - 1$) to use the lagoon at time t depends on a comparison of the expected fitness of being in the lagoon at time t ,

$$s(l, 2, t)\max_d F[l'(l, 2, b, t), d, b'(b, t), t+1], \quad (6)$$

and the expected fitness of returning to or remaining upstream at time t ,

$$s(l, 1, t)\max_d F[l'(l, 1, b, t), d, b'(b, t), t+1]. \quad (7)$$

Assuming that $\sigma(l)$ is monotonically increasing (equation 4; also see Ward et al. 1989; McGurk 1996), that $s(l, x, t)$ never decreases with increasing l (Sogard 1997; Carlson et al. 2008), and that fish never shrink (i.e., for $l_1 > l_2$, $l'[l_1, x, b, t] > l'[l_2, x, b, t]$), it follows that $F(l_1, x, b, t)$ will be greater than $F(l_2, x, b, t)$ for all x, b , and t if l_1 is greater than l_2 . In other words, given that a fish is currently alive and free to relocate, it is always advantageous to be larger (the costs of achieving that larger size have already occurred, thus the conditioning on being alive). Therefore, $\max_d \{F[l'(l, 2, b, t), d, b'(b, t), t+1]\}$ exceeds $\max_d \{F[l'(l, 1, b, t), d, b'(b, t), t+1]\}$, so a fish is only predicted to remain or return upstream if the survival advantage upstream outweighs the expected lifetime benefits associated with faster growth:

$$\frac{s(l, 1, t)}{s(l, 2, t)} > \frac{\max_d \{F[l'(l, 2, b, t), d, b'(b, t), t+1]\}}{\max_d \{F[l'(l, 1, b, t), d, b'(b, t), t+1]\}}. \quad (8)$$

That is, although it is always better for a fish to be larger rather than smaller, the risk of growing large may outweigh the associated advantage that larger size confers upon expected lifetime reproductive success.

Equation (8) yields the prediction of all-or-nothing downstream migration if $s(l, x, t)$ is independent of l . In the case of length-dependent survival, it predicts purely length-dependent

TABLE 3. Seasonal weekly survival probabilities for upstream-rearing steelhead. No estimate was made for age-1 and older (age-1 +) fish from December to June (of the next year) since it would be highly confounded with emigration. For comparison, weekly survival in the lagoon from July to October was estimated as 0.913. Estimates and confidence intervals for individual year–site combinations are reported in Table A.1.

Time period	Age-0 weekly survival probability	Age-1 + weekly survival probability
Jun–Oct	0.962	0.958
Oct–Dec	0.958	0.945
Dec–Jun	0.955	

downstream migration (i.e., complete migration at all lengths if the condition in equation 8 is not met, and no migration otherwise). Thus, a mixture of movement strategies among fish of the same size is only consistent with this model formulation if b varies across fish.

RESULTS

Survival Estimates

Estimated weekly survival upstream varied seasonally and was always higher upstream than in the (assumed constant) lagoon (Tables 3, A.1).

Size Dependence and Timing of Movement

In general, we predicted (Figure 3) that the greatest use of the lagoon occurred in spring and summer. The habitat identified as optimal varied with the magnitude of the growth advantage offered by the lagoon relative to upstream (smallest advantage in Figure 3a, largest in Figure 3d). Under the baseline lagoon growth advantage, we predicted that fish as small as 50–60 mm would rear in the lagoon in late spring and early summer (weeks 17–29) and would continue to rear there during summer (weeks 30–42), a time when lagoon growth rates were highest. Fish were largely predicted to either return or remain upstream during fall and early winter (week 43 to week 3 the following year), especially if the growth advantage in the lagoon was reduced (Figure 3a, b). We predicted that fish would avoid the lagoon in winter and early spring if lagoon growth was reduced to 70% of baseline (still 22% higher than upstream, weeks 4–16; Figure 3a). When lagoon use in winter was predicted at all, it was generally not predicted for the smallest fish. Lagoon use at this time was generally only predicted for (1) fish approaching 100 mm that could reach a large smolt size before lagoon closure or (2) fish that could achieve the maximum possible size and then emigrate to the ocean with only brief exposure to elevated risk in the lagoon. The banding in Figure 3 occurs because we allowed fish to move every week; thus, if fish could reach a “target” size by the end of a particular season by spending only part of the season in the lagoon, they were predicted to move back and forth repeatedly.

A larger growth advantage in the lagoon (i.e., growth = 125% of baseline) led to the prediction that even smaller fish rear in the

lagoon during spring (Figure 3d). When the estuary was open to the ocean (weeks 3–31), we generally predicted that only fish near the asymptotic length would emigrate to the ocean, except shortly before the lagoon was expected to close. At this time, fish longer than approximately 150 mm FL were predicted to emigrate to the ocean.

Empirically, the overall size distributions of fish moving downstream versus those remaining upstream were significantly different (K–S test: $D = 0.27$, $P = 0.0063$; Figure 4a). Although downstream movement the following year was more likely for fish longer than 105 mm FL in December (27 of 36 fish, 75%) than for smaller fish (58 of 123 fish, 47%) and although this difference was statistically significant (Yates $\chi^2 = 7.60$, $P = 0.0058$), many fish smaller than 105 mm FL moved downstream and some very large fish remained upstream. Among the 85 fish that moved downstream, only smaller fish ($n = 3$, all ≤ 81 mm) were later resighted upstream, suggesting that small fish may rear in the lagoon but return upstream later, whereas larger fish rear in the lagoon and then emigrate to the ocean. However, sample sizes were limited, and this pattern was not statistically significant (K–S test: $D = 0.59$, $P = 0.27$; Figure 4b).

Mixed Strategies

In our model, movement is entirely predicted by state (of the fish and of the lagoon); for a given lagoon state, all fish of a particular size with the same expectation of lagoon growth make the same movement decision (equation 8). However, field observations demonstrated that fish of the same size were often found in different habitats, reflecting different movement decisions (Figure 4).

To explore the effects of lagoon growth rate variation on migration, we plotted optimal decisions for fish as a function of FL and the ratio between realized and baseline lagoon growth rates for four time periods: week 17 (peak migration; Figure 5a), week 31 (just before lagoon closure; Figure 5b), week 43 (as lagoon growth rate drops to its lowest value in late fall; Figure 5c), and week 3 of the next year (initial reopening of the lagoon; Figure 5d). If lagoon growth rate was at least 70% of baseline, only the largest fish were predicted to emigrate directly to the ocean well before the lagoon closed (Figure 5a, d). When lagoon closure was imminent, the minimum size for ocean entry decreased (since it is the last chance for ocean entry during that year) and fish that were too small to enter the ocean were predicted to return upstream (Figure 5b). Fish (especially small fish) were predicted to avoid the lagoon in fall (Figure 5c) or winter (Figure 5d), particularly if the lagoon growth advantage was reduced.

DISCUSSION

Survival

We consistently estimated survival of steelhead to be higher upstream than in the lagoon. This difference in survival and

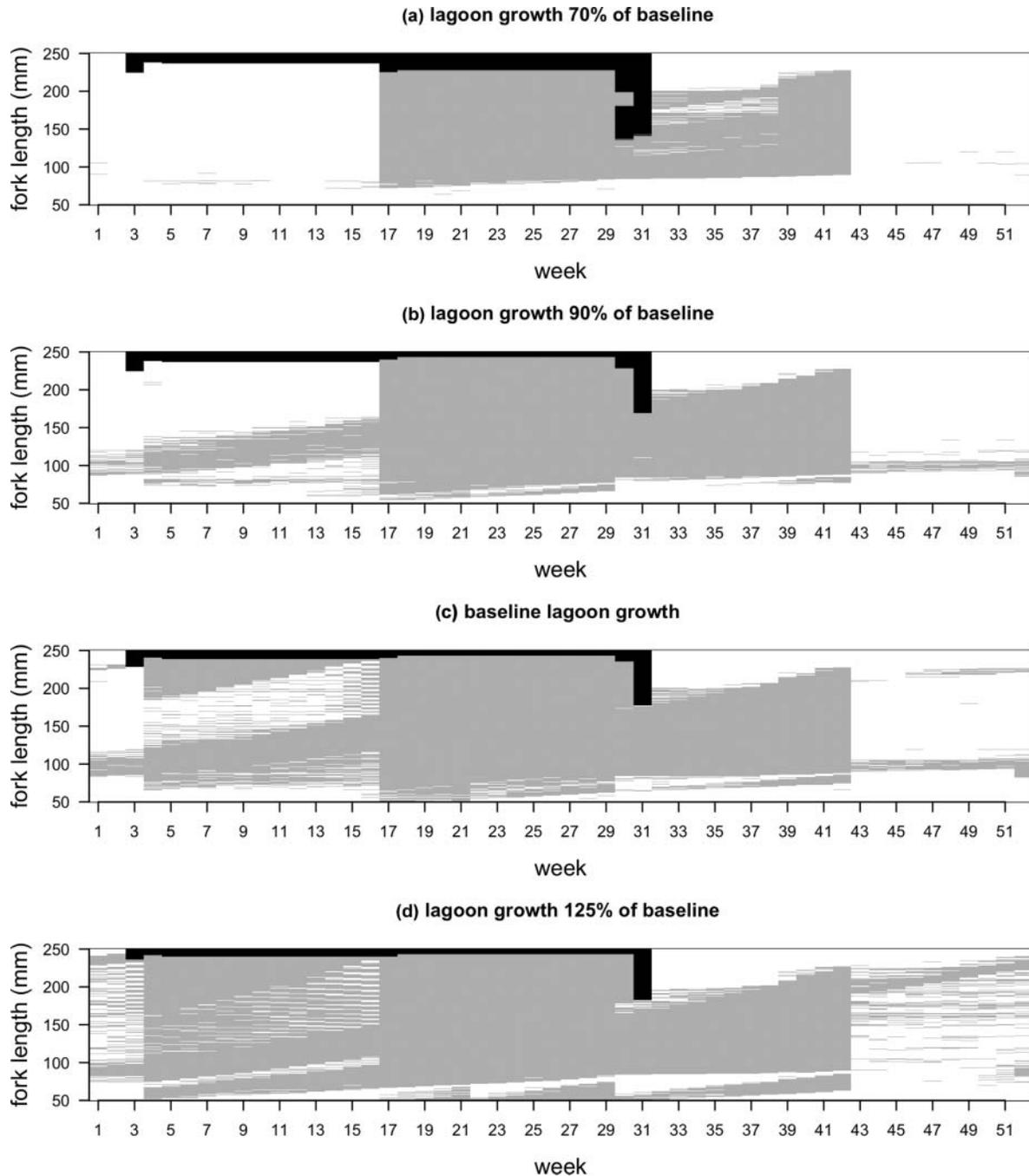


FIGURE 3. Predicted optimal rearing habitat for steelhead of varying sizes (y -axis) at different times of year (x -axis). White indicates that upstream rearing is optimal, gray shading indicates that lagoon rearing is optimal, and black shading indicates that emigration to the ocean is optimal. We explore the effects of varying growth rate in the lagoon by scaling growth rate to (a) 70%, (b) 90%, (c) 100%, or (d) 125% of the baseline (multiyear mean as given in Table 2).

the higher growth rates in the lagoon (Hayes et al. 2008) provide the necessary conditions for a tradeoff between a relatively high-risk, high-reward habitat (the lagoon) and a relatively low-risk, low-reward habitat (upstream). Our results suggest that this tradeoff is a major driver of habitat selection in this system.

Limited data forced us to assume constant survival in the lagoon. However, this assumption is unlikely to have a major effect on our results because our model predicted low use of the lagoon in late fall, when survival may be lower due to low dissolved oxygen levels and increased salinity (Hayes et al. 2011).

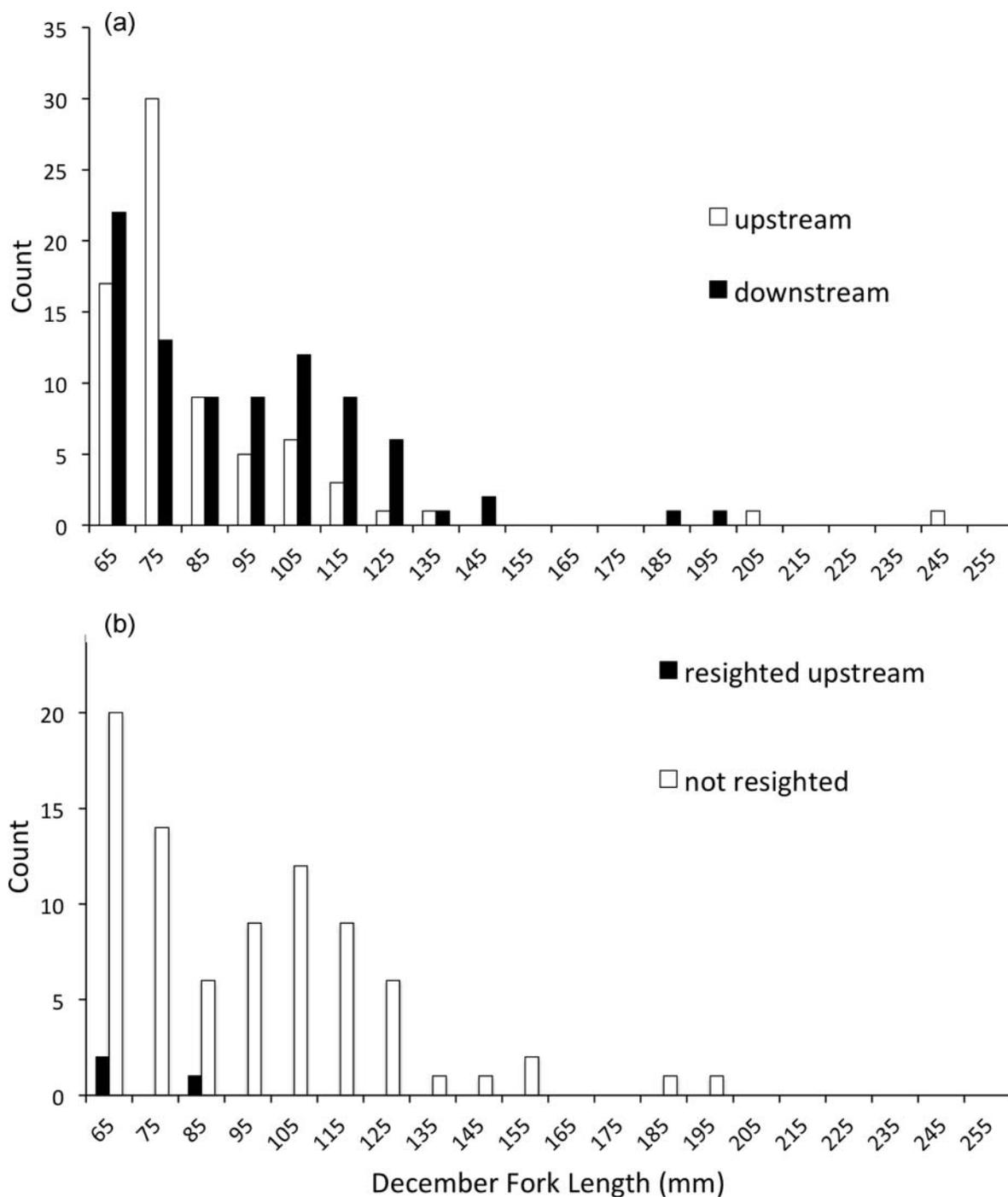


FIGURE 4. Fork length (FL) distributions of steelhead measured upstream in December and classified on the basis of different inferred movement patterns during the subsequent spring: (a) comparison of FL distributions for fish known to have moved downstream later that year (downstream) and fish known to have remained upstream for an extended period (upstream); and (b) comparison of FL distributions for downstream migrants that were resighted upstream and downstream migrants that were never resighted.

Size Dependence of Movement

Our empirical results for size-dependent individual movement were not fully consistent with the predictions of Satterthwaite et al. (2009). Although larger fish were more likely to

move downstream, our observations were not consistent with a size threshold for downstream migration. Our observations are consistent with the new model's prediction that anadromous steelhead juveniles from a range of sizes would rear in the lagoon

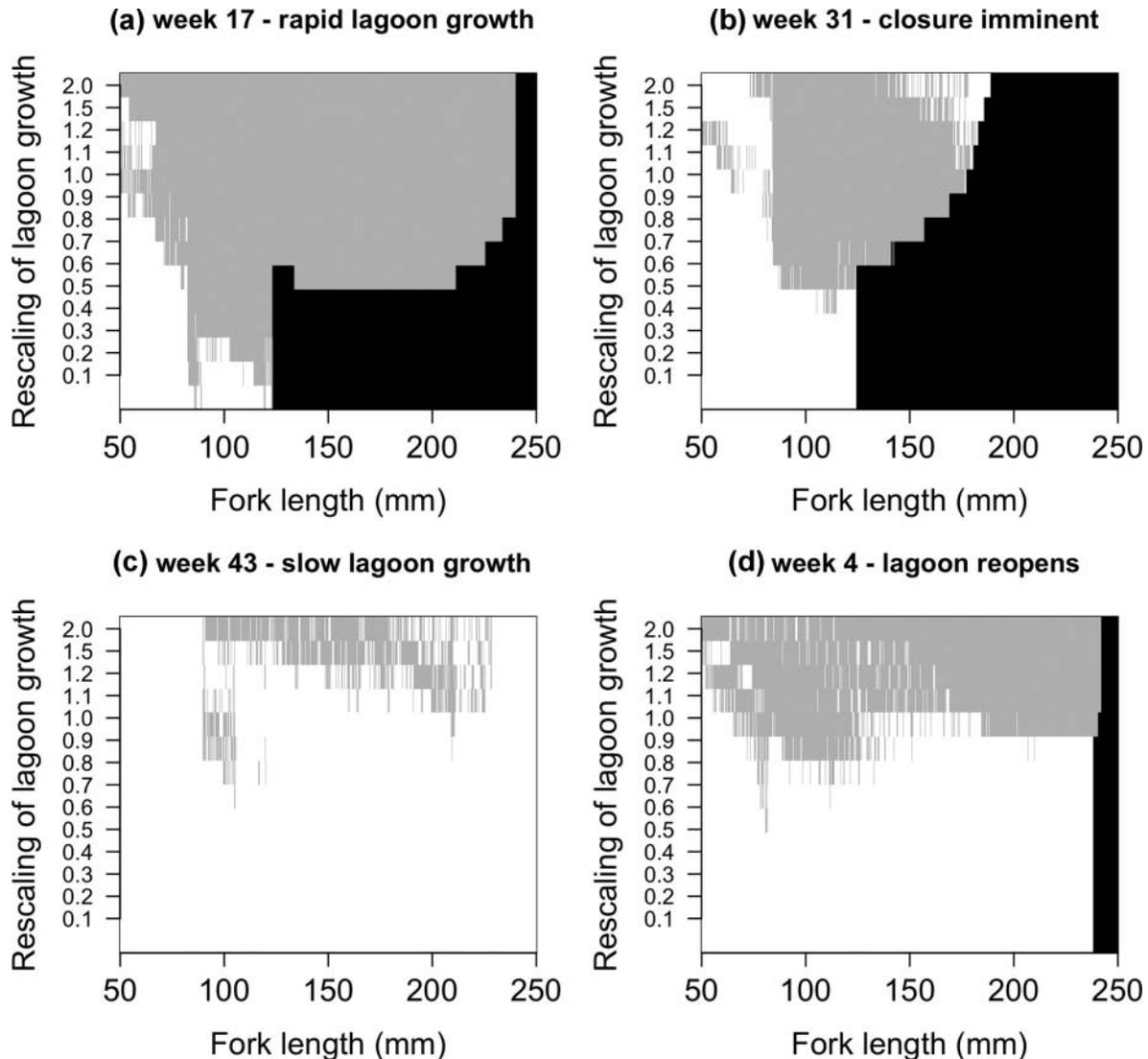


FIGURE 5. Predicted movement decisions of steelhead as a function of fork length (*x*-axis) and the rescaling of lagoon growth rate relative to its baseline given in Table 2 (*y*-axis) for different time periods, including (a) the onset of the period of most rapid growth in the lagoon (week 17), (b) the period immediately before lagoon closure (week 31), (c) the onset of the slowest period of growth in the lagoon (week 43), and (d) the initial reopening of the lagoon (week 4). White denotes fish that are predicted to move or stay upstream, gray shading denotes fish that are predicted to rear in the lagoon, and black shading denotes fish that are predicted to enter the ocean.

during spring. We further predicted that larger fish emigrate to the ocean before lagoon closure, whereas smaller fish delay emigration for at least another year. This result is consistent with the results of Hayes et al. (2011), who found that small fish entering the lagoon were more likely than large fish to be resighted in the lagoon after it closed (when ocean emigration that year was no longer possible).

Timing of Movement

We predicted and field observations demonstrated (Hayes et al. 2011) that movement behavior was time dependent, with the greatest movement to the lagoon occurring in spring, when the lagoon growth advantage was highest. Consistent with this

prediction, Hayes et al. (2011, their Figure 4a) found that the greatest downstream migration occurred in March and April. We also predicted that lagoon use would be low in the fall. Consistent with this prediction, Hayes et al. (2011, their Figure 4b) reported little or no downstream migration during this time as well as an increased upstream detection rate for fish that were previously in the lagoon (Hayes et al. 2011, their Figure 3a).

Mixed Strategies

Conditioned on state, the model predicted all-or-nothing lagoon use by steelhead, but we observed that within a fixed size-class, there was a mix of fish remaining upstream or migrating to the lagoon. This discrepancy could reflect the fact

that our state variable was length rather than lipid level (McMillan 2009), metabolic rate (Morinville and Rasmussen 2003), or other states that are not well reflected by length (Thorpe 2007). The observed mix of strategies for fish with similar sizes could therefore reflect fish responding to different internal states according to consistent “decision rules.” However, the mix of strategies displayed by fish of the same apparent state could also result from density dependence in lagoon growth rates (Hayes et al. 2008) if accompanied by some ordering of movements among fish. Increasing fish density in the lagoon would reduce the growth advantage it offers and would favor upstream rearing.

We assumed that recruitment to the lagoon stops when the marginal increase in growth rate available to the next fish moving downstream is too small to compensate for increased lagoon mortality risk, requiring that the movement decisions of individual fish reflect the tradeoff between the growth rates that are achievable upstream versus downstream. Although the mechanisms for acquiring such information are unknown, the final size at age of lagoon-rearing fish appears to vary little across years (Hayes et al. 2008), suggesting that fish in this system have evolved strategies for adjusting their usage of the lagoon in response to achievable growth.

Alternative Explanations

We have laid out in precise mathematical notation the hypothesis that juvenile salmonid life history trajectories result from a tradeoff between survival and growth rates in alternate environments. The tradeoff varies for fish of different sizes and may also vary among individuals of the same size due to density dependence in growth rates combined with priority or dominance effects. Alternately, the mix of habitat use strategies may reflect a balanced polymorphism resulting from coexisting genotypes subjected to fluctuating selection. Another possibility is that habitat use is a probabilistic rather than deterministic function of individual state, reflecting a “bet-hedging” polymorphism. Under this scenario, some fraction of the population settles for the lower-mean but lower-variance strategy (Cohen 1966; Slatkin 1974).

We assumed that size at ocean entry is the dominant driver of emigrant survival. Thus, fish were predicted to wait until just before lagoon closure for ocean entry if lagoon growth was good and the fish had not already reached their maximum possible length. With suitable data, we could modify the emigration survival function ($\sigma[I]$) to be time dependent as well (Scheuerell et al. 2009). We might then predict fish emigrating earlier at smaller sizes to match temporal patterns in favorable ocean conditions.

Management Implications and Extensions to Other Systems

Our results suggest a strong selective advantage to the facultative use of lagoon or estuarine habitats, but the diversity of observed strategies suggests that the advantage offered by high-risk–high-reward habitat is temporally variable and

thus sensitive to environmental changes, both natural and anthropogenic. Our model provides a quantitative framework for predicting short-term (plastic) and long-term (evolutionary) impacts of changes in lagoon–estuarine conditions and lagoon–ocean connectivity on population dynamics and life history diversity (Mangel and Satterthwaite 2008). This model could be readily adapted to address pressing questions in other systems. For example, other salmonids commonly use multiple habitat types, including estuaries (Thorpe 1994), and may exhibit repeat migrations as have been observed for “nomad” coho salmon *O. kisutch* (Miller and Sadro 2003; Koski 2009). Variable migration timing within a year is a distinguishing characteristic of life history diversity both among different runs of Chinook salmon *O. tshawytscha* (Fisher 1994) and within runs (Williams 2006; Miller et al. 2010).

Multiple-habitat, variable-timing systems like these cannot be fully described by simpler models (e.g., Thorpe et al. 1998; Rikardsen et al. 2004; Satterthwaite et al. 2009), and more detailed, individual-based models (e.g., Railsback and Harvey 2002) require substantially more data or assumptions to fully parameterize them. Thus, our approach is an effective compromise between model complexity and fidelity to nature.

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Appendix: Detailed Survival Estimates and their Uncertainty

Confidence Interval Calculation

Upstream survival, age 0.—We estimated weekly survival of age-0 steelhead based on the ratio between the estimated number of age-0 fish at the end of the interval (N_d) and the estimated number of age-0 fish at the start of the interval (N_0), scaled to the length of the interval (d) in days:

$$\left(\frac{N_d}{N_0}\right)^{\frac{1}{d}}$$

We generated binomial confidence intervals on the ratio between initial and final counts (Harte 2002) and scaled them to weekly survival as done previously.

Upstream survival, age 1 and older.—The 95% confidence intervals on apparent survival estimates were calculated automatically by Program MARK by analyzing sites separately and using the best model (chosen based on Akaike's information criterion scores), which incorporated seasonal variation in apparent survival with a constant capture probability.

Lagoon survival.—We estimated weekly survival of steelhead in the lagoon as

$$\left(\frac{N_d}{N_0}\right)^{\frac{1}{d}},$$

where d is the number of days between initial and final density estimates.

Our estimates of N_0 and N_d were based on Ricker's (1975) modification of the Petersen method applied to paired mark-recapture censuses of an assumed closed population. If N is

the (unknown) total number of fish, M is the number of fish marked on the first occasion, n is the total number (marked or not) of fish captured on the second occasion, and m is the number of marked fish that were recaptured on the second occasion, the probability density for N follows a hypergeometric distribution:

$$p(N|M, n, m) = \frac{\binom{M}{m} \binom{N-M}{n-m}}{\binom{N}{n}}.$$

We used Metropolis algorithm Markov-chain Monte Carlo methods (Gelman et al. 2004) implemented in R (R Development Core Team 2011) to draw 200,000 samples for N_0 and N_d with probabilities proportional to the probability density function as applied to the data for each year. This is equivalent to a Bayesian posterior distribution for the probability of N taking on different values given a uniform prior on N .

We used these chains (starting at the maximum likelihood estimate) of estimates for N_0 and N_d to create a chain of estimates for their ratio and thus for apparent survival by using the Geweke (1992) diagnostic to ensure convergence and the Raftery and Lewis (1995) approach to ensure adequate chain length, as implemented by the coda package (Plummer et al. 2010) in R.

In 2008, only one marked fish was recaptured after the initial July sampling event (i.e., $m = 1$). This led to extreme uncertainty in the July estimate of N and Monte Carlo Markov chains that would not converge. We do not present credible intervals for the 2008 estimate, and we do not include it in the long-term mean used to parameterize the life history model.

TABLE A.1. Seasonal weekly apparent survival probabilities (95% confidence [credible] intervals [CIs] in parentheses) for steelhead by age-class, year, and location (see Figure 1) in the Scott Creek system. No estimate was made for age-0 survival at the Swanton Bridge site in 2006 because of problems with the June electrofishing event. The 95% CIs were calculated as described in the Appendix text. For the 2008 lagoon survival, no CIs were estimated and the maximum likelihood estimate should be interpreted with caution because only a single marked fish was recaptured after the first marking event. December–June values are from December of the specified year to June of the subsequent year (NA = not applicable).

Site and year	Time period		
	Jun/Jul–Oct	Oct–Dec	Dec–Jun
Age 0			
Upper Scott, 2006	0.960 (0.955–0.965)	1.007 (NA)	0.938 (0.929–0.947)
Upper Scott, 2007	0.952 (0.947–0.958)	0.965 (0.956–0.972)	0.959 (0.951–0.966)
Swanton, 2006		0.954 (0.947–0.961)	0.944 (0.935–0.951)
Swanton, 2007	0.952 (0.947–0.957)	0.938 (0.927–0.948)	0.944 (0.932–0.954)
Big Creek, 2006	0.983 (0.978–0.987)	0.935 (0.919–0.949)	0.981 (0.974–0.986)
Big Creek, 2007	0.961 (0.955–0.967)	0.948 (0.935–0.959)	0.963 (0.953–0.972)
Age 1 and Older			
Upper Scott, 2006	0.967 (0.913–0.987)	0.979 (0.75–0.999)	
Upper Scott, 2007	0.957 (0.918–0.978)	0.928 (0.855–0.965)	
Swanton, 2006	0.947 (0.902–0.972)	0.953 (0.886–0.981)	
Swanton, 2007	0.956 (0.93–0.973)	0.956 (0.896–0.982)	
Big Creek, 2006	0.965 (0.922–0.985)	0.925 (0.836–0.967)	
Big Creek, 2007	0.955 (0.924–0.974)	0.933 (0.867–0.967)	
All Ages			
Lagoon, 2007	0.917 (0.848–0.972)		
Lagoon, 2008	0.809 (NA)		
Lagoon, 2009	0.908 (0.878–0.94)		