The Shiraz model: a tool for incorporating anthropogenic effects and fish–habitat relationships in conservation planning

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Abstract: Current efforts to conserve Pacific salmon (*Oncorhynchus* spp.) rely on a variety of information sources, including empirical observations, expert opinion, and models. Here we outline a framework for incorporating detailed information on density-dependent population growth, habitat attributes, hatchery operations, and harvest management into conservation planning in a time-varying, spatially explicit manner. We rely on a multistage Beverton–Holt model to describe the production of salmon from one life stage to the next. We use information from the literature to construct relationships between the physical environment and the necessary productivity and capacity parameters for the model. As an example of how policy makers can use the model in recovery planning, we applied the model to a threatened population of Chinook salmon (*Oncorhynchus tshawytscha*) in the Snohomish River basin in Puget Sound, Washington, USA. By incorporating additional data on hatchery operations and harvest management for Snohomish River basin stocks, we show how proposed actions to improve physical habitat throughout the basin translate into projected improvements in four important population attributes: abundance, productivity, spatial structure, and life-history diversity. We also describe how to adapt the model to a variety of other management applications.

Résumé : Les efforts actuels pour la conservation des saumons du Pacifique (*Oncorhynchus* spp.) se basent sur une variété de sources d'information, dont les observations empiriques, les opinions d'experts et les modèles. Nous élaborons ici un cadre pour incorporer dans la planification de la conservation, de façon variable dans le temps et explicite dans l'espace, des données détaillées sur la croissance de population dépendante de la densité, sur les caractéristiques de l'habitat, sur les opérations de pisciculture et sur la gestion de la récolte. Nous utilisons un modèle de Beverton–Holt à plusieurs niveaux pour décrire la production de saumons d'un stade à l'autre de leur cycle. Des renseignements tirés de la littérature nous servent à établir les relations entre l'environnement physique et les paramètres de productivité et de capacité requis par le modèle. Comme exemple de l'utilisation possible du modèle pour la planification de la récupération par des responsables des politiques de gestion, nous appliquons notre modèle à une population menacée de saumons chinook (*Oncorhynchus tshawytscha*) du bassin de la Snohomish dans le Puget Sound, Washington, É.-U. En incorporant des données additionnelles sur les opérations de pisciculture et sur la gestion de la récolte pour les stocks du bassin de la Snohomish, nous montrons comment les actions prévues pour améliorer l'habitat physique dans l'ensemble du bassin résultent en des améliorations anticipées de quatre caractéristiques démographiques importantes, soit l'abondance, la productivité, la structure spatiale et la diversité des cycles biologiques. Nous décrivons aussi comment adapter le modèle à une gamme d'autres usages de gestion.

[Traduit par la Rédaction]

Introduction

Salmon populations throughout the Pacific Northwest have declined dramatically over the past century owing to a variety of anthropogenic impacts and changes in climate (National Research Council 1996; Ruckelshaus et al. 2002). A necessary step in developing salmon recovery plans involves estimating the relative effects of habitat degradation, hatchery operations, harvest management, and hydropower dams (i.e., "the four Hs"), as well as interactions with other species and other environmental factors on salmon population status (Ruckelshaus et al. 2002). This task is often difficult when

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dealing with salmon, however, because of the variety of freshwater, estuarine, and marine habitats that they occupy during their diverse life history (Mobrand et al. 1997; Greene and Beechie 2004; Sharma et al. 2005). Population models offer a useful way of integrating the effects of the four Hs on salmon populations, particularly models that incorporate these effects on life-stage-specific survival or capacity. Nonetheless, most models provide population viability analyses to estimate population growth rates and threat of extinction (e.g., Kareiva et al. 2000; Ellner and Fieberg 2003; Wilson 2003) without any specific allowances for density-dependent dynamics caused by the direct interaction between habitat conditions and fish population performance (Greene and Beechie 2004; Zabel et al. 2006).

Modeling fish–habitat relationships is not a new endeavor. For salmon in particular, a rich literature exists describing how changes in the quantity and quality of habitat affect the survival of various life stages (e.g., Tappel and Bjorn 1983; Chapman 1988; Kondolf 2000). Although some studies have modeled the influence of in-stream habitat attributes on the survival of salmon at specific life stages (e.g., Lisle and Lewis 1992; McHugh et al. 2004), only recently have researchers done so across the entire life cycle, demonstrating the importance of various habitat changes on the overall population dynamics of salmon (see Nickelson and Lawson 1998; Greene and Beechie 2004; Sharma et al. 2005). Additionally, changes in land use by humans will continue to affect salmon populations through their indirect effects on habitat-forming processes (Beechie and Bolton 1999; Regetz 2003). Predicting the impacts of current and future alterations to salmon habitat requires a holistic modeling perspective that captures not only the expected future population size, but also detailed information on stock productivity, spatial structure, and the diversity of life-history types (Lichatowich et al. 1995; Mobrand et al. 1997; McElhany et al. 2000).

Here we outline a framework for incorporating the effects of habitat change, hatchery operations, and harvest management actions on salmon population status for use in recovery planning. The Shiraz model utilizes a set of user-defined relationships among habitat attributes, fish survival, and carrying capacity to evaluate population performance across space and time. The model allows us to translate the effects of changes in habitat conditions resulting from land-use restoration and protection actions into consequences for salmon population status and likelihood of recovery. Furthermore, the Shiraz model provides estimates of the four important criteria for describing viable salmon populations (VSP): abundance, productivity, spatial structure, and diversity (McElhany et al. 2000). We illustrate our model framework using available data from the Snohomish River basin, which contains two of the 22 remaining populations of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound listed as threatened under the Endangered Species Act (National Marine Fisheries Service 1999). A multi-stakeholder recovery planning group in the Snohomish River basin has adopted population-specific salmon recovery targets to describe salmon population attributes necessary for viability. In collaboration with them, we evaluated the potential consequences of habitat conservation alternatives (Bartz et al. 2006) for salmon population status using the Shiraz model. Our analyses subsequently helped the policy group refine their conservation

alternatives and select a preferred recovery plan based on the predicted outcomes for the two Chinook salmon populations in their basin.

Materials and methods

Study area and species

The Snohomish River basin is located north and east of Seattle, Washington, USA (Fig. 1), and the river's estuary runs adjacent to Everett, Washington. Agricultural, urban, and suburban land use dominate the lower (western) region of the watershed, whereas forests largely cover the upper (eastern) region that extends to the crest of the Cascade Mountains. The two Chinook populations in the basin generally return to the river in the summer and spawn in the fall (Ruckelshaus et al. 2006). Most juveniles migrate as sub-yearlings, spending some time rearing in the Snohomish River estuary before continuing into the Pacific Ocean, but a small fraction of juveniles rear for a year in the stream and migrate as yearlings. Two hatchery facilities in the basin rear three distinct stocks of Chinook salmon (see Hatchery operations below). Other salmonid species in the basin include coho (*O. kisutch*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon and bull trout (*Salmo confluentus*).

### Fish stocks and life history within the modeling framework

The Shiraz model framework (Fig. 2) begins by assigning fish to various "stocks" that might represent (*i*) different life-history types (e.g., ocean-type vs. stream-type Chinook), (*ii*) different origin (e.g., wild or hatchery fish), or (*iii*) different species. Coincident with assigning fish to their respective stocks, one must specify each life-history trajectory, a description of the habitat types that an individual traverses throughout its life cycle and the time spent in each. This could take the simple case of only considering spawners and their subsequent offspring that recruit back to freshwater, or it could assume a much more detailed form. In the Snohomish case study, we used the following life-history stages: mature adults returning from the ocean to rivers, spawning adults that survived harvest, eggs, fry, smolts, and ocean ages 1–5. We considered only ocean-type Chinook salmon that go to sea after only a few months of rearing in freshwater habitat (Healey 1991).

We assigned wild and hatchery fish to different stocks, which allowed us to track separate changes in their survival due to varying environmental effects or harvest policies. It also enabled us to investigate the impact of various hatchery operations on overall stock performance. Another important concept in the Shiraz model is stock transformation, such that at the time of spawning, individuals from one stock can change their stock identity. For example, the progeny of hatchery fish that stray and naturally spawn are considered wild fish in the next model generation. Another possible application might include a life-history type that depends on estuarine rearing whereby a small fraction (maybe 5%) of nonestuarine-rearing fish transform into estuarine-rearing fish.

Spatial resolution

As the model is spatially explicit, the user must decide what level of spatial resolution to consider. Explicitly modeled spatial units could be as broad as an entire watershed or

1598

Can. J. Fish Aquat. Sci. Vol. 63, 2006

Fig. 1. Map of the Snohomish River basin (Washington, USA) showing the primary reaches of the Snoqualmie, Skykomish, and Snohomish rivers (thick black lines) and the 62 subbasins (thin black lines). Also shown are the locations of the tribal (H_T) and state (H_S) salmon hatcheries (stars) and Sunset Falls (SF), a natural barrier to anadromous fish.
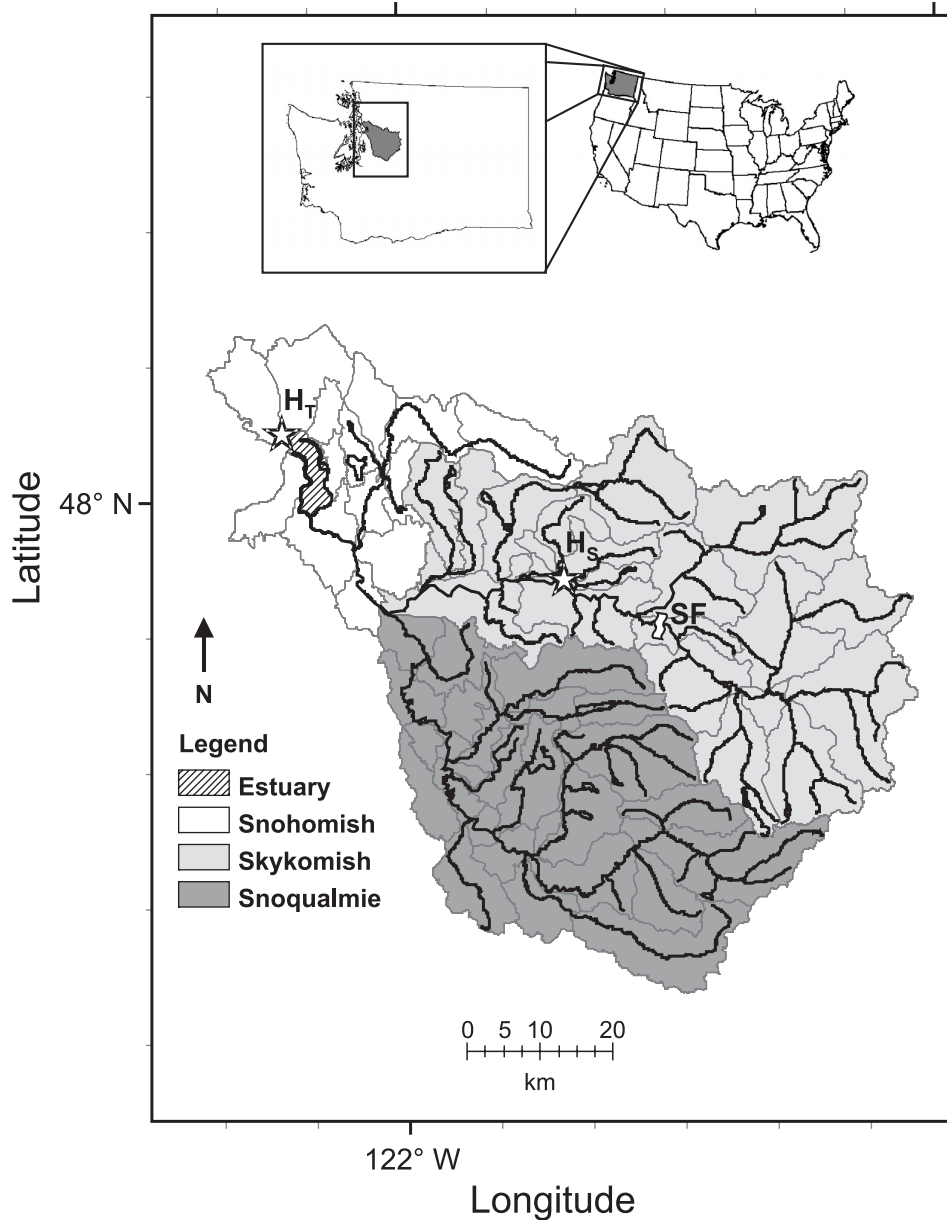
as fine as individual stream reaches, but once defined, the model assumes that all spatial units are identical in size with respect to fish movement (see below). The Shiraz model tracks fish during their freshwater residency and seaward migration within each unit, and subsequent spawners return to their natal locations to spawn unless they stray. For this case study, we used the 62 subbasins within the Snohomish River watershed (including the estuary) as our level of spatial resolution (Fig. 2). These subbasins ranged in size from 12.2 to 246 km², and the total length of stream within each subbasin ranged from 0.34 to 98 km. We treated the estuary and ocean as one "subbasin" each because of the relatively large spatial scales over which fish use them and the limited survival data with which to parameterize the model. The model is structured such that another application could split freshwater, estuarine, and marine habitats into a variety of

spatial units, depending on available data and user preferences.

Temporal resolution

The model generally operates on an annual time scale but considers that several life-stage transitions might occur within a given year (e.g., spawning of eggs and the emergence of the fry from the gravel). This allows fish of different species, stocks, or life-history stages to interact with one another in the various spatial units. By defining a beginning and an end year, the model allows for forward projections of population size by stock, life stage, and location.

Habitat indicators

We use the underlying physical environment as the primary driver of fish population dynamics. Therefore, the user must

Fig. 2. Conceptual diagram of the Shiraz model framework indicating how various anthropogenic impacts (four Hs) can be used to drive biological responses of fish through a life-cycle model. The influence of human land use and natural landscape processes on habitat attributes is treated in Bartz et al. (2006).
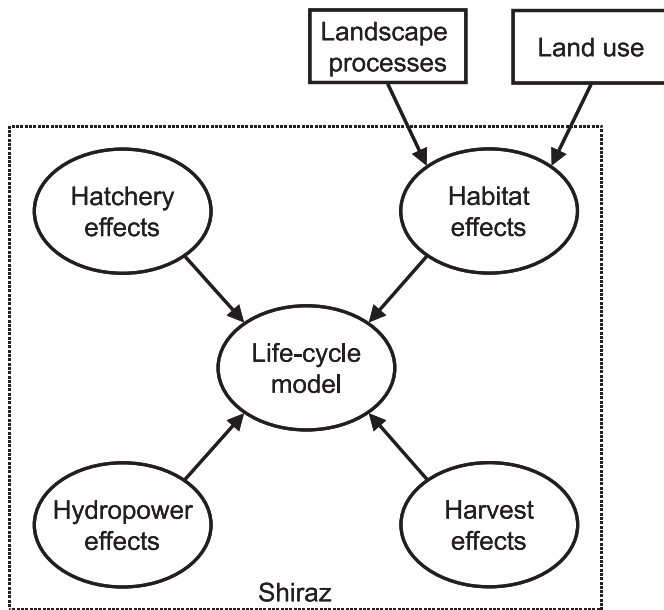
specify a set of habitat indicators that potentially affect fish population status for each area of interest. These can be detailed physical factors such as stream gradient or width, percentage of pools, riparian vegetation cover, or habitat quantities such as juvenile rearing area, spawning area, etc. Habitat indicators can change over time gradually by exponential or logistic growth (or decay) but do not change from year to year in a stochastic way in this model. For those kinds of inputs (e.g., stream flow or temperature), the user must define stochastic variables as described below. For our case study, we relied on physical habitat indicators for estimating the capacity of juvenile and adult salmon and for predicting prespawning mortality and the survival of eggs to fry because of availability of data and functional relationships (see Bartz et al. 2006).

Stochastic variables

The Shiraz model uses two methods for addressing uncertainty in model inputs. The first approach requires the user to specify parameters for any of three statistical distributions (uniform, normal, lognormal) from which the model will draw random variates at each time step. Variates then replace the otherwise constant parameter values in the functional relationships or the static estimates of habitat condition used in the functional relationships (Appendix A). Because variability tends to be highly correlated across space, the normal method is to draw one random variate for each major section of a watershed per time step and tie survival rates to this variate over most, if not all, areas. Second, one can estimate the overall effect of stochastic variables by using a Monte Carlo approach whereby the model is run a specified number of times while drawing random variates. Model output (e.g., the number of spawners by area) is evaluated at some time point during each Monte Carlo simulation, typically at the

end of a prespecified number of years. At the end of all simulations, summary statistics such as the mean and variance are computed for the output variables of interest. This approach is useful for evaluating the effects of various harvest management strategies, hatchery operations, or changes in ocean conditions.

Initial conditions

In addition to habitat values, functional relationships, and movement criteria specified below, the Shiraz model requires the user to set other initial conditions for a model run. This includes specifying how many individuals of each life stage and stock are alive and the proportion of each life stage occupying each geographical area. At a minimum, one must designate the initial number and spatial distribution of spawners so that the model can track subsequent life stages through space and time. However, one could also specify an entire age distribution across all life stages.

The model scenarios

We modeled three different scenarios to reflect our best estimates of the differences in physical habitat under pre-European settlement conditions (historical), present land use and management and policies (current path), and proposed future policies (test case). The Snohomish Basin Salmonid Recovery Technical Committee developed a set of management actions that consisted of restoring riparian habitat, removing dikes and revetments, decommissioning roads, etc. We transformed their set of potential actions under the test case into changes in physical habitat (see Bartz et al. 2006) and used them as inputs into the Shiraz model to evaluate the potential population response of Chinook salmon within the basin. We also assumed that hatchery operations and harvest rates would continue as implemented under the current path and therefore did not make any adjustments under the test case.

Model formulation

The model development begins with a multistage Beverton–Holt model (Moussalli and Hilborn 1986):

$$(1) \qquad N_{s+1} = \frac{N_s}{\dfrac{1}{p_{s \to s+1}} + \dfrac{1}{c_{s+1}} N_s}$$

where the number of fish surviving to their next life-history stage (N_{s+1}) is a function of the number alive at the current life stage (N_s), their survival or productivity to the next stage ($p_{s \to s+1}$), and the capacity of the environment to support them (c_{s+1}). The parameters p and c can assume fixed values or be functions of the environment (see below). Furthermore, at each life stage, p and c can be a single-point estimate or the product of several estimates, such that

$$(2) \qquad p_{s \to s+1} = \prod_r p_{s \to s+1, r}$$

$$(3) \qquad c_{s \to s+1} = \prod_r c_{s \to s+1, r}$$

where r represents the number of functional relationships for a given life stage. The basic habitat model consists of specifying how habitat indicators and stochastic variables relate to productivity and survival. A range of functional forms is avail-

1600

Can. J. Fish Aquat. Sci. Vol. 63, 2006

Table 1. The parameter values and functional relationships affecting the productivity (survival) and capacity of each life stage for the Shiraz application to the Snohomish River basin.

Life-stage transition	Productivity (p)	Life stage	Capacity (c)
Spawners[a] to eggs	f_1(temperature)[b]	Eggs	$2500 \cdot c_1$(habitat)[c]
Eggs to fry	f_2(temperature, flow, sediment)[d]	Fry	c_2(habitat)[e]
Fry to smolt	0.332	Smolts	c_3(habitat)[f]
Smolts to 1-ocean	0.033	1-ocean	∞
1-ocean to 2-ocean	0.6	2-ocean	∞
2-ocean to 3-ocean	0.7	3-ocean	∞
3-ocean to 4-ocean	0.8	4-ocean	∞

Note: Unless otherwise noted, parameter values come from Greene and Beechie (2004). See Materials and methods section for details regarding the forms of the functional relationships.

[a]Spawners are first converted to potential eggs (eq. 18) before applying eq. 1.

[b]Prespawning mortality is a nonlinear function of temperature (Cramer 2001).

[c]The egg capacity equals an index of spawner fecundity (5000 eggs per female), divided by 2 to account for females only, times the estimated spawner capacity from B. Sanderson (Northwest Fisheries Science Center, 2725 Montlake Boulevard E., Seattle, WA 98112, USA, unpublished data). See Bartz et al. (2006) for details.

[d]Egg-to-fry survival is a nonlinear function of temperature (Velsen 1987; Beacham and Murray 1989), river flows (Seiler et al. 2003), and fine sediment (Tappel and Bjorn 1983).

[e]Fry capacity is derived from the detailed habitat analyses described in Bartz et al. (2006).

[f]Smolt capacity is derived from the detailed habitat analyses described in Bartz et al. (2006).

able to develop these relationships, including simple linear, exponential, and line segments (Appendix A).

Functional relationships

For our case study, we used habitat-based functions to relate various attributes of the physical environment to the productivity (survival) and capacity of several life stages. For survival, these included the transitions from spawners to eggs and from eggs to fry. For capacity, these included eggs, fry, and smolts. These functional relationships vary across space but we omit the area subscripts below for simplicity. First, we modeled the prespawning survival of adults in the river (p_1) as a nonlinear function of water temperature (T_{pre}, in °C) during a portion of the spawning period (15 July through 15 August), based on the analyses of Cramer (2001), such that

$$(4) \quad p_1 = \begin{cases} 1 & \text{if } T_{pre} < 16 \\ 1 - 0.15(T_{pre} - 16) & \text{if } 16 \leq T_{pre} < 22.6 \\ 0.01 & \text{if } T_{pre} \geq 22.6 \end{cases}$$

We used three separate relationships for estimating the effects of the physical environment on egg-to-fry survival. The first, a nonlinear function ($p_{2,1}$) of water temperature (T_{inc}) during the incubation period (15 September through 15 February), is a series of line segments fit from data in Velsen (1987) and Beacham and Murray (1989), where

$$(5) \quad p_{2,1} = \begin{cases} 0.273 T_{inc} - 0.342 & \text{if } 1.3 \leq T_{inc} < 4.7 \\ 0.94 & \text{if } 4.7 \leq T_{inc} < 14.3 \\ -0.245 T_{inc} + 4.44 & \text{if } 14.3 \leq T_{inc} < 18.1 \\ 0.01 & \text{if } T_{inc} \geq 18.1 \end{cases}$$

Second, we modeled egg-to-fry survival as a linear function ($p_{2,2}$) of the normalized mean flow during the incubation period (Q^*). To do so, we mapped the maximum daily mean flow during the incubation period (Q) onto the interval [0,1] by dividing it by the maximum flow (Q_{max}) for a 100-year period as predicted by Sumioka et al. (1998). Seiler et al.

(2003) presented a flow–survival relationship across the egg-to-smolt stages, but we wanted it for the egg-to-fry stage only. Therefore, we assumed that the entire flow effect manifested itself during the egg-to-fry transition and divided all of Seiler and colleagues' survival estimates by the fry-to-smolt survival ($p_{fs} = 0.332$) reported by Greene and Beechie (2004). We then fit the following relationship between our newly estimated egg-to-fry survival and normalized flow (Q^*):

$$(6) \quad p_{2,2} = \begin{cases} 0.58 - 0.844 Q^* & \text{if } Q^* < 0.675 \\ 0.01 & \text{if } Q^* \geq 0.675 \end{cases}$$

Lastly, egg-to-fry survival was also modeled as a nonlinear function of the percent fine sediment (<6.3 mm) in the spawning gravel ($p_{2,3}$). Based on data from Tappel and Bjornn (1983), we developed the following relationship between egg-to-fry survival and the proportion of fine sediment (f)

$$(7) \quad p_{2,3} = \begin{cases} 0.95 & \text{if } f < 0.268 \\ -3.32f + 1.81 & \text{if } 0.268 \leq f < 0.544 \\ 0.06 & \text{if } f \geq 0.544 \end{cases}$$

We then combined the three terms for egg-to-fry survival according to eq. 2. For the remaining productivity and capacity parameters necessary for describing the complete life cycle, we used either point estimates from the literature or model-driven values (Table 1).

Hatchery operations

The model simulates hatchery operations from two perspectives: the number of eggs taken from returning spawners and the number of juveniles released back into the river. The user specifies the number of eggs to take each year and the stock from which they are to be taken. After accounting for hatchery mortality as a result of egg takes, any remaining fish may be allowed to spawn in the wild. For hatchery releases, the user must specify the life stage(s) of fish (e.g., subyearlings, yearlings), the number of fish of each stage to release, and the location within the watershed where the fish should be released. After release, hatchery fish follow survival

and capacity rules, whether similar to or different from, those applied to the wild fish. Any returning adults are also subject to harvest as described below.

The Snohomish River basin has two operating hatcheries with Chinook salmon programs: the Tulalip Tribe's Bernie Kai-Kai Gobin Hatchery directly north of the estuary on Tulalip Bay and the Washington Department of Fish and Wildlife's (WDFW) Wallace River Hatchery much farther upstream (Fig. 2). We modeled hatchery releases according to the current schedules used by both hatchery management programs (Table 2). The Bernie Kai-Kai Gobin Hatchery releases juveniles from two different fish stocks at the sub-yearling stage immediately upstream of Tulalip Bay in Puget Sound. These fish interact with wild fish and other hatchery stocks in the estuary and nearshore areas. The Wallace River Hatchery releases fish from one stock at two different ages, subyearling and yearling; both size classes migrate to the estuary shortly after their release from the hatchery and interact with any wild fish along the way.

Fish movement

Within the model, fish can move between areas, and once movement takes place, Shiraz tracks the number of fish by life stage, stock, year, area of birth, and current area of residence. The model directs adult fish (with specified stray rates) to return to their natal areas when spawning takes place while allowing for movement at any number of life-history stages. This movement can be specified either by a fixed preference (i.e., the proportion of fish moving from area i to area j) or by letting the fish migrate to an area based on their expected survival in that area according to an ideal free distribution (IFD; sensu Fretwell 1972). For each freshwater life stage s and stock k where movement occurs, the user must specify a matrix of constant movement probabilities ($\mathbf{M}_{s,k}$), which should represent the physical structure of the watershed and realistic downstream migration patterns. In our case, the probability of moving from one area to another is independent of the actual size of the area. For IFD movement, the expected "fitness" (ϕ) for a stage s of stock k in an area i is

$$(8) \qquad \phi_{s,k,i} = \frac{1}{\left(\dfrac{1}{p_{s,k,i}} + \dfrac{N_{s,i}}{c_{s,k,i}} \right)}$$

where N is the total number of fish and p and c are the productivity (survival) and capacity, respectively. The idea is that fish "sample" the environment during their early life stages and then move to maximize fitness for all fish. Furthermore, we provide a parameter μ for a "mixed" solution, so that the spatial allocation can be weighted by the intrinsic movement probability and by trying to maximize survival, where

$$(9) \qquad \pi_{s,k,i \to j} = \left(M_{s,k,i \to j} \right)^{\mu} \cdot \left(\frac{\phi_{s,k,i}}{\phi_{s,k,\max}} \right)^{(1-\mu)}$$

and $\phi_{s,k,\max}$ is the maximum fitness across all areas for a given life stage and stock. The number of fish after movement (N) in an area j is then

Table 2. The name, stocks, release life stage (age), and targeted release numbers for the two hatcheries operating within the Snohomish River basin.

Hatchery name	Fish stock	Life stage	Annual releases
Bernie Kai-Kai Gobin	Summer	Fingerling	1 500 000
	Fall	Fingerling	200 000
Wallace River	Summer	Fingerling	1 000 000
	Summer	Yearling	250 000

$$(10) \qquad N_{s,k,j} = \pi_{s,k,i \to j} \, N_{s,k,j}$$

In our example, we chose to let fry move downstream according to a specified movement matrix without any specific knowledge of the quality of the habitat (i.e., $\mu = 1$). In this case, juveniles fill up their natal habitat first and then migrate downstream to the next available subbasin without moving upstream again (i.e., no rheotaxis). This is analogous to an ideal free distribution for a territorial organism, usually referred to as an "ideal despotic distribution" (Fretwell 1972; Tregenza and Thompson 1998). We adopted this latter approach because we are unaware of any evidence of salmon following IFD movement rules.

When returning to freshwater habitat to spawn, anadromous salmonids generally exhibit strong homing tendencies for their natal sites, but we know that some level of straying exists (Groot and Margolis 1991). Therefore, the model allows the user to input straying rates from one area to another by stock. When combined with stock transformations, this useful construct can mimic the observed contribution of hatchery-origin fish to the natural spawning population. We applied the observed straying rates of hatchery fish to natural spawning grounds estimated from recoveries of otoliths on the spawning grounds that were thermally marked in the hatchery, thereby distinguishing the fish as hatchery origin (Rawson et al. 2001). Based on otolith recovery data, we assumed that only 3% and 1% of Tulalip hatchery fish strayed into the Snoqualmie and Skykomish rivers, respectively, and became part of the wild population. For fish from the Wallace Hatchery, however, we assumed that 1% and 28% of adults strayed into the Snoqualmie and Skykomish rivers, respectively (Kit Rawson, Tulalip Tribes, and Curt Kraemer, Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, WA 98012, USA, unpublished data).

Harvest policies

Fish in the ocean mature at age-specific rates. If the model application is to include fishery catch, those fish maturing in the ocean and returning to freshwater are then subject to harvest. We allowed for two possible harvest management policies: a constant escapement goal or a constant harvest rate. When managing for constant escapement, the model allows a set number of adult fish to "escape" the fishery and return to freshwater before harvesting the remaining spawners. Under a constant harvest rate policy, the model treats harvest as another source of mortality by taking a set proportion of the returning adult fish (z_c). Therefore, the harvest rate for a given year (z_t) becomes

1602

Can. J. Fish Aquat. Sci. Vol. 63, 2006

$$(11) \quad z_t = \begin{cases} 1 - \dfrac{\text{escapement}}{\sum \text{adults}} & \text{if constant escapement policy} \\ z_c & \text{if constant harvest policy} \end{cases}$$

The harvest rate on wild and hatchery fish is potentially stochastic, and if so, the realized harvest rate ($z*$) becomes

$$(12) \quad z_t^* = z_t \varepsilon_t$$

where ε_t is a random variate drawn from a uniform, normal, or lognormal distribution. For our purposes, we only adopted a constant harvest rate policy with $z_t = 0.22$ with $\varepsilon_t \sim N(1.0, 0.02)$ based on data from 1999–2003 provided by the co-managers (Kit Rawson, Tulalip Tribes, and Curt Kraemer, Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, WA 98012, USA, unpublished data). Some fish from the Snohomish are caught at sea in troll fisheries, but the majority are harvested within Puget Sound in gillnet and purse-seine fisheries. We made no distinction between the two nor did we consider size-selective harvest. We also assumed no change in harvest rate when moving from the current path scenario to the test policy case.

Maturation and spawning

Each year, a proportion of adults from each stock k mature based on their stage s ($m_{s,k}$; Table 3). The number of fish returning to the river and subject to harvest is thus

$$(13) \quad N_{s,k,\text{return},t} = m_{s,k} N_{s,k,\text{ocean},t}$$

Those remaining in the ocean then follow eq. 1 and parameter values in Table 1 for transition to the next stage. The subsequent number surviving harvest and returning to the river is

$$(14) \quad N_{s,k,\text{river},t} = (1 - z_t) N_{s,k,\text{return},t}$$

Although all fish in the ocean are treated as one large pool, the model actually tracks them by their natal location. Some fish surviving harvest stray from their natal locations upon return based on a straying matrix ($\mathbf{Y}$) that identifies the proportion of fish straying from a particular natal location i to a spawning area j. The number of fish spawning (S) in a location j is then

$$(15) \quad S_{s,k,j,t} = \sum_i Y_{i,j} N_{s,k,i,t}$$

For the hatchery fish returning to a reach, some (or all) are removed for hatchery egg take (E) to meet the hatchery's minimum egg quota (E_{quota}), so that

$$(16) \quad E_{s,k,i,t} = \min(S_{s,k,i,t}, E_{\text{quota}})$$

Any remaining fish are allowed to spawn in the natural environment and become part of the wild stock:

$$(17) \quad S_{s,\text{wild},i,t} = S_{s,\text{hatchery},i,t} - E_{s,k,i,t}$$

In our case study, all of the adults returning to the Tulalip hatchery are harvested and their broodstock is taken from the Wallace hatchery, but some of the Wallace fish are allowed to spawn in the wild (Kit Rawson, Tulalip Tribes, and Curt Kraemer, Washington Department of Fish and Wildlife, 16018 Mill Creek Boulevard, Mill Creek, WA 98012, USA, unpublished data).

Table 3. The proportion of adult salmon in the ocean that mature and return to the river to spawn, by age and stock (Pam Goodman, Northwest Indian Fisheries Commission, 6730 Martin Way East, Olympia, WA 98516, USA, unpublished data) and the age-specific fecundity (eggs per female) (Greene and Beechie 2004).

Stage (s)	Age	Stock-specific maturation rates (m)			Fecundity (f)
		Wild	Tulalip	Wallace	
5	2	0.02	0.03	0.02	2500
6	3	0.13	0.18	0.14	4848
7	4	0.60	0.90	0.82	5710
8	5	1.0	1.0	1.0	6664

Spawners from all stocks (k) and areas (i) in a given year t are then transformed into total potential eggs ($N_{1,k,i,t}$) according to

$$(18) \quad N_{1,k,i,t} = \sum_s P_s S_{s,k,i,t} f_s$$

where P_s is the proportion of females of stage s (= 0.5 for all stages), $S_{s,k,i,t}$ is the number of spawners of a given stage s, and f_s is the stage-specific fecundity (Table 3).
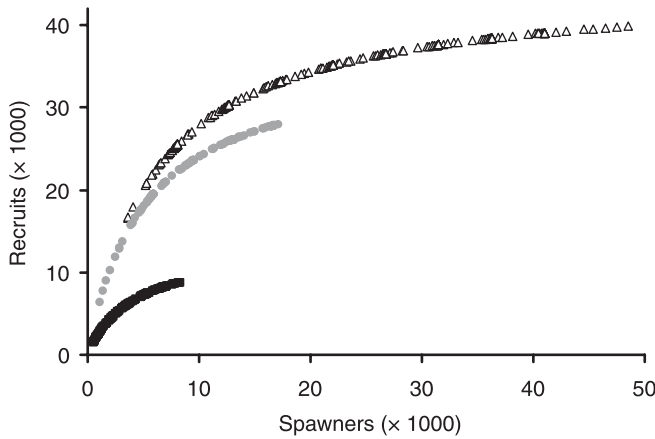
Sensitivity analyses

As a first step toward identifying the type and location of potential restoration actions in the Snohomish River basin, we conducted a sensitivity analysis of the model following the basic parameterization for the "current path" described above. By systematically increasing the productivity or capacity estimates for various life stages while holding all other values constant, we estimated the change in the number of spawners throughout the entire basin. We did so for the following model parameters: adult capacity, juvenile (fry and smolt) capacity, egg-to-fry survival, and fry-to-smolt survival. For the capacity estimates, we replaced the estimates under the current path with those estimated under historical conditions. For the survival estimates, we simply increased those under the current path by 10% of their estimated value (e.g., an egg-to-fry survival of 5% became 5.5%). In addition to changing the parameter values across the entire basin at once, we also changed the parameter values in one of four select geographical regions (the estuary, mainstem reaches, lowland streams, and headwater streams) while keeping all others constant.

Results

The first metric for classifying viable salmon populations (VSP) is abundance. Under the current path parameterization, the model produced smolt and spawner abundances similar to those observed in the Snohomish River basin. Our mean egg-to-fry survival rate was 7.7% compared with the average 7.1% for stream-type Chinook based on data reviewed by Bradford (1995). Shiraz tended to overestimate the number of wild spawners (8383) compared with the average 3700 (95% confidence interval (CI): 3249–4146) estimated by the Puget Sound Technical Recovery Team from 1965 to 2002. Nevertheless, they have also witnessed an increase in wild spawners in recent years, with 10 600 wild fish returning in 2004. The number of modeled smolts (611 400) was close to that estimated from screw traps on the river (800 200) from 2001 to 2003 (Brian Kelder, Tulalip Tribes, 7515 Totem

Fig. 3. Modeled spawner–recruit relationships for the wild stocks only under the historical (open triangles), test case (shaded circles), and current path (solid squares) scenarios. Recruits are simply the number of adults returning to spawn.


Fig. 4. Maps of the spatial distribution of the predicted number of spawners under (*a*) historical, (*b*) test case, and (*c*) current path scenarios. The estimate of the equilibrium spawner abundance is listed under each name.

Beach Road, Tulalip, WA 98271, USA, unpublished data). On average, hatchery fish constituted a majority of the returning spawners in our modeled populations, with 46% and 17% coming from the Wallace and Tulalip hatcheries, respectively. The remaining 37% of those surviving the fishery came from wild spawners or from hatchery fish that strayed and spawned in the wild. These model predictions varied somewhat from the observed stock composition where an average of 53% of spawning fish from 1971 to 2002 originated from hatcheries. From 1993 to 2002, however, hatchery fish represented 68% of the returning spawners observed in the basin, which is closer to our model result of 63%.

In addition to population abundance, stock productivity represents the second of the important VSP criteria for viable salmon populations. The estimates of productivities and carrying capacities from the stock–recruit relationship of wild fish varied under the three different scenarios (Fig. 3). For the historical case, the estimated intrinsic productivity was 7.34 recruits per spawner with a capacity of 44 881 recruits. Under current conditions, however, the estimated productivity was much lower at 3.15 recruits per spawner with a capacity of 13 203 recruits. We estimated an improvement in the test case with an estimated productivity of 7.05 recruits per spawner and a capacity of 36 359 recruits.

The abundance and spatial distribution (the third VSP criterion) of wild spawners across the landscape in the current path differed considerably from our best approximation of that under historical conditions (Fig. 4). Overall, we estimated that the Snohomish River basin currently produces only 17% of the historical number of spawners (26% if we include hatchery fish). Although only 34 of 62 subbasins currently support spawners, we estimated that 37 of them did historically. The six additional South Fork Skykomish subbasins that support spawners currently, but not historically, result from an active management decision by WDFW to truck spawners above Sunset Falls, a naturally occurring anadromous barrier. The abundance and spatial structure of spawners increased considerably under the test case (Fig. 4). We projected a 137% increase in abundance of wild fish, resulting in spawner levels that would be 41% of our historical estimate (53% of historical if we also include hatchery fish).
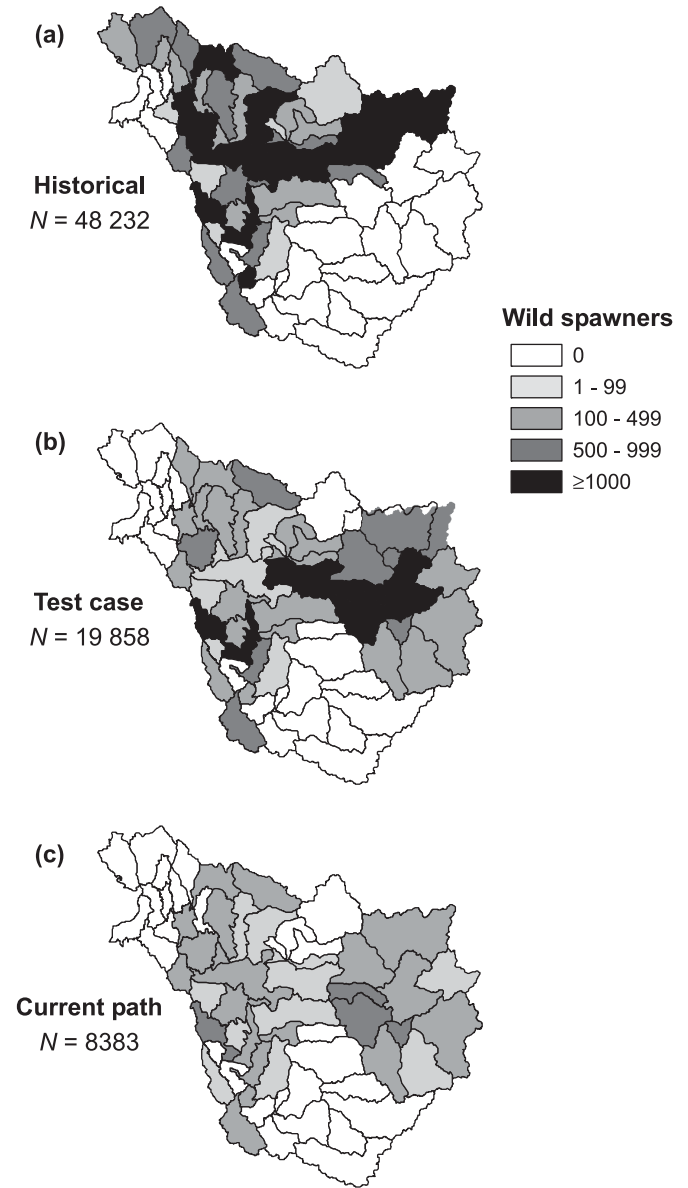
Additionally, we found spawners expanding their range into a total of 36 subbasins, including those above Sunset Falls as we assumed that the active management would continue as currently implemented. Furthermore, the Skykomish and Snoqualmie rivers responded differently to the proposed test case such that they showed increases from the current path of 149% and 123%, respectively.

The fourth VSP attribute used to guide salmon recovery efforts throughout the Pacific Northwest is diversity, which includes genetically based variation and environmentally induced phenotypic variation in life-history traits. Although we did not model differences in genetic composition of the populations, we calculated the proportion of spawners from model runs that breed in various habitat types. We used this as an index for inferring the potential expression of varying life-history traits under different habitat, hatchery, and harvest conditions that we

1604

Can. J. Fish Aquat. Sci. Vol. 63, 2006

Fig. 5. The proportion of spawners under historical (open bars), test case (shaded bars), and current (black bars) scenarios across a diversity of spawning habitats represented by EPA level-IV ecoregions (Omernik 1995).
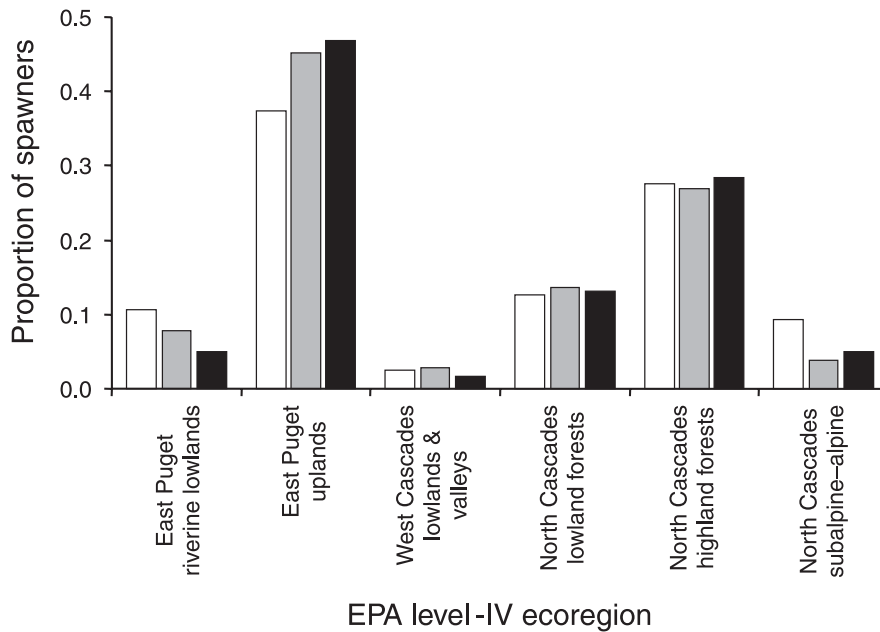
Fig. 6. Results of the initial model sensitivity analyses of the "current path" parameterization to identify appropriate restoration actions. In each case, the value of interest was increased while all other model parameters were held constant.
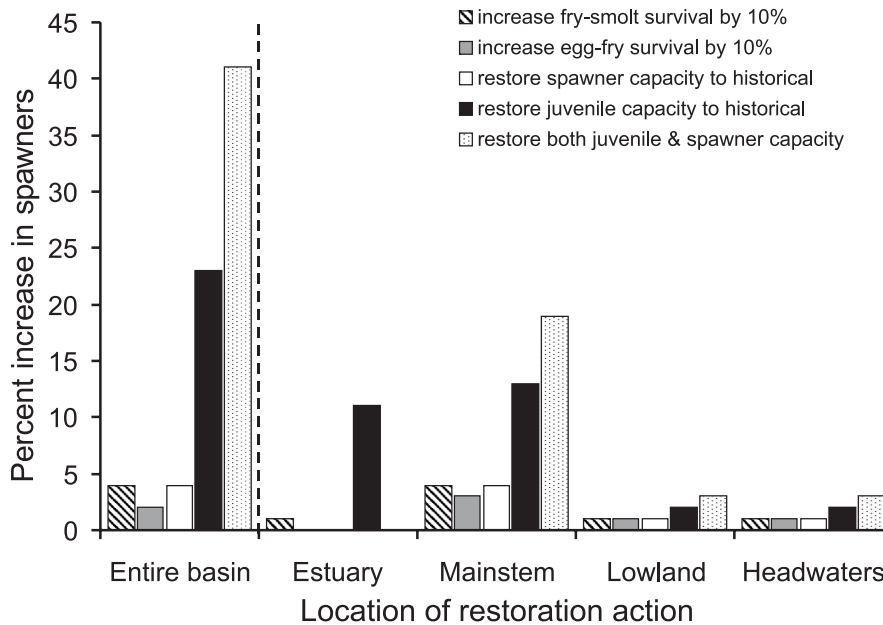
modeled (e.g., potential differences in spawning migration timing). By far, the majority of fish spawned in the East Puget uplands under all three scenarios, followed by North Cascades highland forests (Fig. 5). Although we found no significant differences in the percentage of fish spawning in each of the ecoregions among the three scenarios, the difference between the policy test case and historical conditions ($\chi^2 = 5.8$, df = 5, $P = 33$) was much less than that between the current path and historical condition ($\chi^2 = 7.8$, df = 5, $P = 17$).

Our sensitivity analysis revealed that increasing adult capacity had very little effect on the predicted number of spawners by itself (Fig. 6). When we increased juvenile capacity to

our historical estimate, however, the predicted number of spawners increased substantially, but the effect was most prominent in the estuary and mainstem reaches, with very little impact in the peripheral lowland and headwater reaches (Fig. 6). Interestingly, we observed a synergistic effect of increasing both adult and juvenile capacity such that those improvements resulted in percentage increases in spawner abundance that were greater than the sum of the individual actions. Overall, increasing egg-to-fry or fry-to-smolt survival had less of an impact than improving capacity, but it did have a greater impact in the estuary and mainstem reaches than in the lowland and headwater reaches (Fig. 6).

Discussion

Models offer a quantitative framework for assimilating data, identifying important features of the environment, predicting future outcomes, and evaluating the potential effects of various decisions (Hilborn and Mangel 1997). In particular, life-cycle models provide scientists and policy makers with a tool for studying how changes in vital rates affect the overall population dynamics of species. In a conservation context, these models are often used to estimate population growth rates and the threat of extinction (e.g., Kareiva et al. 2000; Ellner and Fieberg 2003; Wilson 2003). In these instances, the most valuable models incorporate a variety of data related to the all of the external (e.g., habitat, exploitation) and internal (e.g., density-dependent) processes that affect the various life stages, while maintaining the flexibility to include new data or assumptions as to how the system of interest operates (Boyce 1992). The Shiraz model is designed to do just that.

Viable salmon populations (VSP) are defined by four important metrics: abundance, productivity, spatial structure, and diversity (McElhany et al. 2000). Important consideration of all of these performance measures is necessary when setting recovery goals and planning restoration actions (Boyce 1992). The Shiraz model framework allowed us to evaluate changes in these VSP parameters under various scenarios. Just as with any other model, Shiraz should be used in conjunction with empirical data and viewed as merely one of several tools available in the planning process. Scenarios offer an effective way of bringing stakeholders together to confront issues of concern (Bennett et al. 2003), and the Shiraz model framework offers the opportunity for salmon-recovery groups to explore the consequences of those scenarios for fish populations. By including harvest, hatchery, and habitat effects in the scenarios, we can obtain more realistic projections than models that consider only habitat.

By using a combination of empirical data and modeling efforts and exploring the outcomes of very different protection and restoration scenarios, we were able to present the decision makers in the Snohomish Basin Recovery Planning Group with clear choices for possible strategies. Our original sensitivity analyses suggested that restoration actions aimed at improving juvenile rearing habitat in the estuary and lower mainstem reaches would have the best chance of improving overall population performance. This essentially confirmed the independent assessment of regional biologists and planners who classified those areas as degraded (<50% intact) or moderately degraded (50%–80% intact) relative to historical conditions because of urbanization and agricultural activities (Snohomish Basin Salmonid Recovery Technical Committee 2004).

Our results indicated that the test case alternative would result in approximately 41% of the estimated historical spawner abundance. This population level would not reach the recovery goal of 80% of historical abundance adopted by the planning group (Snohomish Basin Salmonid Recovery Technical Committee 2004). Nevertheless, there are several reasons why we expect that we underestimated the potential response of salmon to recovery actions. First, our analyses do not capture the full spectrum of restoration measures proposed by the technical committee because of our inability to ascribe changes to in-stream habitat attributes from the entire suite of actions (Bartz et al. 2006). Second, the projected increases in the quantity of juvenile rearing habitat could also produce subsequent increases in the quality of available habitat and improve survival rates, a possibility that we were unable to account for in the model owing to the lack of a predictive relationship between habitat quantity and quality. Third, we used several fixed parameters from Greene and Beechie (2004) that might also improve with positive changes in habitat. For example, the survival from smolts to age-2 adults was fixed at a particularly low value (0.033), and given improvements in growth during the parr and smolt stages, we would expect concurrent increases in marine survival (Holtby et al. 1990; Koenings et al. 1993; Zabel and Williams 2002). Similar arguments would apply to our underestimates of the parameters for stock–recruit models. Fourth, improvements in spawner escapements should increase the amount of marine-derived nutrients and energy delivered to this ecosystem in the form of carcasses and gametes that are important to the growth and survival of stream-dwelling salmonids (Bilby et al. 1998; Wipfli et al. 2003) and the overall health of the surrounding ecosystem (Cederholm et al. 1999; Naiman et al. 2002; Schindler et al. 2003). Fifth, our test case used the same hatchery and harvest policies as those currently implemented in the Snohomish River basin, but future recovery decisions will almost certainly involve changes in those plans as well. Therefore, our results should be taken as a conservative estimate of the population response to the proposed restoration actions under the test case.

As mentioned above, we chose relatively few functional relationships for implementation in the Shiraz model. We did so for several reasons. First, models are only as good as their input variables, and we were limited by the availability of both habitat-specific data (e.g., temperature, fine sediment) and functional relationships for relating those data to fish productivity and capacity. Therefore, we felt it wiser to rely on literature values when we could not derive our own parameter estimates or functional relationships. Second, simpler models tend to be more generally applicable to other systems and the results are easier to understand (Gunderson and Holling 2001). Third, our goal was to develop a transparent framework for using detailed fish–habitat relationships to assess large-scale responses of fish populations to changes in habitat, hatchery operations, and harvest levels. Using relatively simple models as planning tools with a collection of stakeholders can be an important step toward effective management (Carpenter 2002; Bennett et al. 2003), and Shiraz is designed to be used in such a manner. Finally, although understanding the historical causes of population decline is important, concentrating on the potential response of fish to future remediation activities is more important for recovery efforts (Ruckelshaus et al. 2002), and the Shiraz model framework does this.

Our model structure relied on the underlying stage-specific Beverton–Holt relationship of Moussalli and Hilborn (1986). Other model forms such as the Ricker model (Ricker 1954) or a hockey stick model (Barrowman and Myers 2000) could be potentially employed, but the underlying model assumptions would need to be addressed to avoid potential problems (e.g., a nonunimodal spawner–recruit curve). We are aware of another model that also uses the multistage Beverton–Holt model to

1606

Can. J. Fish Aquat. Sci. Vol. 63, 2006

drive transitions from one life stage to another. The ecosystem diagnosis and treatment (EDT) model has also been applied to salmon restoration problems in the Pacific Northwest, but there is no formal publication describing the methods or functional relationships (see http:// www.mobrand.com/MBI/library.html). Furthermore, it does not allow for stochasticity, nor does it provide outputs of the number of individuals of a given life stage by spatial location across time.

Because the Shiraz model is a flexible framework, it could be adopted for use with other fish species, whether marine or freshwater. For example, the 1996 reauthorization of the Magnuson–Stevens Fishery Conservation and Management Act established that the conservation of essential fish habitat (EFH) is an important component of building and maintaining sustainable fisheries throughout US waters. The Act requires cooperation among the National Marine Fisheries Service, the eight regional fishery management councils, fishing participants, federal and state agencies, and others in achieving EFH protection, conservation, and enhancement. By relating the amount and kind of habitat to fish productivity and capacity, the Shiraz model easily could be used by this collection of stakeholders to establish EFH by determining the relationship of changes in both population parameters to changes to habitat.

Acknowledgments

References

Barrowman, N.J., and Myers, R.A. 2000. Still more spawner–recruitment curves: the hockey stick and its generalizations. Can. J. Fish. Aquat. Sci. **57**: 665–676.

Bartz, K.K., Lagueux, K., Scheuerell, M.D., Beechie, T.J., Haas, A., and Ruckelshaus, M.H. 2006. Translating restoration scenarios into habitat conditions: an initial step in evaluating recovery strategies for Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **63**: 1578–1595.

Beacham, T.D., and Murray, C.B. 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. Can. J. Zool. **67**: 2081–2089.

Beechie, T., and Bolton, S. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. Fisheries, **24**: 6–15.

Bennett, E.M., Carpenter, S.R., Peterson, G.D., Cumming, G.S., Zurek, M., and Pingali, P. 2003. Why global scenarios need ecology. Front. Ecol. Environ. **1**: 322–329.

Bilby, R.E., Fransen, B.R., Bisson, P.A., and Walter, J.K. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Can. J. Fish. Aquat. Sci. **55**: 1909–1918.

Boyce, M.S. 1992. Population viability analysis. Annu. Rev. Ecol. Syst. **23**: 481–506.

Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. Can. J. Fish. Aquat. Sci. **52**: 1327–1338.

Carpenter, S.R. 2002. Ecological futures: building an ecology of the long now. Ecology, **83**: 2069–2083.

Cederholm, C.J., Kunze, M.D., Murota, T., and Sibatani, A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries, **24**: 6–15.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Trans. Am. Fish. Soc. **117**: 1–21.

Cramer, S.P. 2001. The relationship of stream habitat features to potential for production of four salmonid species. Final Report to the Oregon Building Industry Association. S.P. Cramer and Associates, Gresham, Oreg.

Ellner, S.P., and Fieberg, J. 2003. Using PVA for management despite uncertainty: effects of habitat, hatcheries, and harvest on salmon. Ecology, **84**: 1359–1369.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey.

Greene, C.M., and Beechie, T.J. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **61**: 590–602.

Groot, C., and Margolis, L. 1991. Pacific salmon life histories. UBC Press, Vancouver, B.C.

Gunderson, L.H., and Holling, C.S. 2001. Panarchy: understanding the transformations in human and natural systems. Island Press, Washington, DC.

Healey, M.C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver, B.C. pp. 311–394.

Hilborn, R., and Mangel, M. 1997. The ecological detective — confronting models with data. Princeton University Press, Princeton, New Jersey.

Holtby, L.B., Andersen, B.C., and Kadowaki, R.K. 1990. Importance of smolt size and early ocean growth to interannual variablity in marine survival of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **47**: 2181–2194.

Kareiva, P., Marvier, M., and McClure, M. 2000. Recovery and management options for spring/summer chinook salmon in the Columbia River basin. Science (Washington, D.C.), **290**: 977–979.

Koenings, J.P., Geiger, H.J., and Hasbrouck, J.J. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effect of smolt length and geographic latitude when entering the sea. Can. J. Fish. Aquat. Sci. **50**: 600–611.

Kondolf, G.M. 2000. Assessing salmonid spawning gravel quality. Trans. Am. Fish. Soc. **129**: 262–281.

Lichatowich, J.A., Mobrand, L.E., Lestelle, L.C., and Vogel, T.S. 1995. An approach to the diagnosis and treatment of depleted Pacific salmon populations in Pacific Northwest watersheds. Fisheries, **20**: 10–18.

Lisle, T.E., and Lewis, J. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. Can. J. Fish. Aquat. Sci. **49**: 2337–2344.

McElhany, P., Ruckelshaus, M.H., Ford, M.J., Wainwright, T., and Bjorkstedt, E. 2000. Viable salmonid populations and the recov-

ery of evolutionary significant units. US Department of Commerce, NOAA Tech. Memo. No. NMFS-NWFSC-29.

McHugh, P., Budy, P., and Schaller, H. 2004. A model-based assessment of the potential response of Snake River spring–summer Chinook salmon to habitat improvements. Trans. Am. Fish. Soc. **133**: 622–638.

Mobrand, L.E., Lichatowich, J.A., Lestelle, L.C., and Vogel, T.S. 1997. An approach to describing ecosystem performance "through the eyes of salmon". Can. J. Fish. Aquat. Sci. **54**: 2964–2973.

Moussalli, E., and Hilborn, R. 1986. Optimal stock size and harvest rate in multistage life history models. Can. J. Fish. Aquat. Sci. **43**: 134–141.

Naiman, R.J., Bilby, R.E., Schindler, D.E., and Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems, **5**: 399–417.

National Marine Fisheries Service. 1999. Endangered and threatened species; threatened status for three chinook salmon evolutionarily significant units (ESUs) in Washington and Oregon, and endangered status for one chinook salmon ESU in Washington. Federal Register, **64**: 14308–14328.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, DC.

Nickelson, T.E., and Lawson, P.W. 1998. Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model. Can. J. Fish. Aquat. Sci. **55**: 2383–2392.

Omernik, J.M. 1995. Ecoregions: a spatial framework for environmental management. *In* Biological assessment and criteria: tools for water resource planning and decision making. *Edited by* W. Davis and T.P. Simon. Lewis Publishing, Boca Raton, Fla. pp. 49–62.

Rawson, K., Kraemer, C., and Volk, E. 2001. Estimating the abundance and distribution of locally-produced chinook salmon throughout a large river system using thermal mass-marking of otoliths. North Pac. Anadromous Fish Comm. Tech. Rep. **3**: 31–34.

Regetz, J. 2003. Landscape-level constraints on recruitment of chinook salmon (*Oncorhychus tshawytscha*) in the Columbia River basin, USA. Aquatic Conservation: Marine and Freshwater Ecosystems, **13**: 35–49.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. **11**: 559–623.

Ruckelshaus, M.H., Levin, P.S., Johnson, J.B., and Kareiva, P.M. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annu. Rev. Ecol. Syst. **33**: 665–706.

Ruckelshaus, M.H., Currens, K., Graeber, B., Fuerstenberg, B., Rawson, K., Sands, N.J., and Scott, J. 2006. Independent populations of chinook salmon in Puget Sound. US Department of Commerce, NOAA Technical Memorandum. In press.

Schindler, D.E., Scheuerell, M.D., Moore, J.W., Gende, S.M., Francis, T.B., and Palen, W.J. 2003. Pacific salmon and the ecology of coastal ecosystems. Front. Ecol. Environ. **1**: 31–37.

Seiler, D., Neuhauser, S., and Kishimoto, L. 2003. 2002 Skagit River 0+ chinook production evaluation. Washington Department of Fish and Wildlife, Olympia, Wash.

Sharma, R., Cooper, A.B., and Hilborn, R. 2005. A quantitative framework for the analysis of habitat and hatchery practices on Pacific salmon. Ecol. Model. **181**: 231–250.

Snohomish Basin Salmonid Recovery Technical Committee. 2004. Snohomish River Basin ecological analysis for salmonid conservation. Snohomish County Surface Water Management Division, Everett, Wash.

Sumioka, S.S., Kresch, D.L., and Kasnick, K.D. 1998. Magnitude and frequency of floods in Washington. US Geological Survey Water Resources Investigations Rep. No. 97-4277, Washington, D.C.

Tappel, P.D., and Bjorn, T.C. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. N. Am. J. Fish. Manag. **3**: 123–135.

Tregenza, T., and Thompson, D.J. 1998. Unequal competitor ideal free distribution in fish? Evol. Ecol. **12**: 655–666.

Velsen, F.P.J. 1987. Temperature and incubation in Pacific salmon and rainbow trout: compilation of data on median hatching time, mortality, and embryonic staging. Can. Data Rep. Fish. Aquat. Sci. No. 626.

Wilson, P.H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer chinook. Conserv. Biol. **17**: 782–794.

Wipfli, M.S., Hudson, J.P., Caouette, J.P., and Chaloner, D.T. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Trans. Am. Fish. Soc. **132**: 371–381.

Zabel, R.W., and Williams, J.G. 2002. Selective mortality in chinook salmon: what is the role of human disturbance? Ecol. Appl. **12**: 173–183.

Zabel, R.W., Scheuerell, M.D., McClure, M.M., and Williams, J.G. 2006. The interplay between climate variability and density dependence in the population viability of Chinook salmon. Conserv. Biol. **20**: 190–200.

Appendix A

Table A1. Description of the various functional relationships between an indicator variable (X) and the response variable (Y, either p or c).

Functional relationship	Equation
Constant value	$Y = p_1$
Constant multiplier	$Y = p_1 X$
Exponential	$Y = p_1 \exp(p_2 X))$
First-order impact[a]	$Y = \exp(p_1(X - X_N))$
Second-order impact[a]	$Y = \exp(p_1(X - X_N) + p_2(X - X_N)^2)$
Third-order impact[a]	$Y = \exp(p_1(X - X_N) + p^2(X - X_N)^2 + p_3(X - X_N)^3)$
Line segments[b]	$Y = \begin{cases} f_1(X) & \text{for} \quad X \le x_1 \\ f_2(X) & \text{for} \quad x_1 < X \le x_2 \\ f_3(X) & \text{for} \quad x_2 < X \end{cases}$

[a]For first- through third-order impacts, X_N represents some normal condition against which the observed variable is compared.

[b]For line segments, $f_1(X)$ is a straight line fit between the points x_0, Y_0 and x_1, Y_1; $f_2(X)$ is a straight line fit between the points x_1, Y_1 and x_2, Y_2, etc.