# A quantitative framework for the analysis of habitat and hatchery practices on Pacific salmon 

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Received 26 June 2003; received in revised form 8 July 2004; accepted 28 July 2004


#### Abstract

We developed a model to capture the interaction of two factors (habitat and hatchery indicators) on salmon abundance, and provide a framework for evaluating alternative restoration actions for salmon in the northwestern United States, assuming specific ocean conditions and harvest rates. We modeled different hypothetical coho salmon population trajectories in Issaquah creek (King County, western Washington, USA) as a function of land-use change and hatchery supplementation. The model can be tailored to address individual problems, areas and questions.


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Keywords: Modeling; Habitat; Hatchery-interactions; Land use; Salmon

## 1. Introduction

With numerous stocks of Pacific salmon already extirpated and with dozens of additional stocks being considered for listing under the Canadian Species at Risk

[^0]Act (SARA), there is a growing concern about how to design the appropriate management actions to conserve and restore these stocks (Murray and Wood, 2002). Pacific salmon are impacted by a wide range of human activities such as modifications to freshwater and estuarine habitats, harvests, and hatchery practices, and any plan to conserve and rebuild salmon should consider the interaction of all of these factors (Kareiva et al., 2000). In addition to these anthropogenic impacts, much of the recent change in salmon abundance can be ascribed to changes in ocean conditions (Coronado and Hilborn, 1998; Francis and Hare, 1994). This pa-
per intends to integrate these separate components and provide a model to evaluate different management alternatives in a watershed geared to salmon conservation and restoration.

### 1.1. Habitat

In the Pacific Northwest, the quality and quantity of freshwater salmon habitat for spawning and rearing has declined due to stream blockage, forestry, agriculture and urbanization (NRC, 1996; Bisson et al., 1997). We focus on coho salmon (Oncorhynchus kisutch) as they are dependent upon freshwater conditions. Efforts to relate coho abundance to habitat quality and quantity have been attempted in recent years. Bradford et al. (1997) examined data from 106 coho streams from California to Alaska that reported counts of smolts at weirs and found stream length and latitude (spatial location) to be the only variables related to smolt production. Sharma and Hilborn (2001) used a subset of Bradford's data (1997) from the Puget Sound region and found that greater pool and pond densities were associated with greater smolt densities, while greater road density and steeper stream gradient were associated with lower smolt densities. In addition, habitat enhancement measures often have been based on perceptions of what is good habitat quality for a particular species and have entailed short-term treatments to meet these perceptions, such as woody debris placement and spawning channel construction (Beechie et al., 1994, 1996). Roper et al. (1997) suggested that restoration measures can be successful in maintaining fish populations in the future if there is a shift from restoration of instream habitat features to restoration of watershed processes.

Models either individual-based (Wildhaber and Lamberson, 2004; Van Winkle et al., 1998) or based on external forcing variables such as flow (Lopes et al., 2004) show how habitat characteristics affect fish abundance and distributions in a stream. As such, availability of different types of habitat could affect overall abundance as shown by Nickelson et al. (1992a). Nickelson et al. (1992b) showed that after construction of in-stream and side channel habitat, the rearing density of juvenile coho in the restored streams was similar to that of juveniles in natural areas. Our model uses survival from one life-stage to the next, measurable habitat
characteristics, and land coverage data for the watershed of concern to simulate population trajectories for coho salmon.

### 1.2. Hatcheries

A great deal of debate has centered on the beneficial and detrimental aspects of hatchery programs (ISAB, 2003). The artificial rearing conditions, use of limited number of broodstock, and the selection of specific traits by hatchery managers has lead to both phenotypic and genotypic divergence of hatchery fish from their indigenous sources as seen in on a single stock of steelhead (Chilcote et al., 1986). Even though evidence for this in coho is limited there is abundant literature on similar species like Atlantic salmon, rainbow trout and brown trout to hypothesize that this could possibly be the case for Pacific salmon (and in our case coho). A divergence from hatchery and wild fish may manifest itself behaviorally (Vincent, 1960; Fenderson et al., 1968; Jenkins, 1971; Dickson and MacCrimmon, 1982), physiologically (Woodward and Strange, 1987), morphologically (Taylor, 1986; Flemming and Gross, 1993), and genetically (Allendorf and Phelps, 1980; Ryman and Stahl, 1980; Cross and King, 1983; Vuorinen, 1984; Verspoor, 1988). These changes can occur within only a few generations of domestic rearing (Mason et al., 1967; Reisenbichler and McIntyre, 1977; Chandler and Bjornn, 1988; Reisenbichler and Rubin, 1999). In addition, Emlen (1991) modeled a hypothetical scenario showing that with a $5 \%$ interbreeding of individuals, a non-trivial reduction in fitness was possible. Such reductions may take many generations to recover even if caused by a single hybridizing event (Emlen, 1991).

As more and more salmon stocks in the Pacific Northwest were depleted, high harvest levels were sustained in some fisheries by salmon produced in hatchery programs. However, due to poor broodstock protocols and hatchery practices, straying of hatchery fish has occurred in many streams in the Pacific Northwest (Lutch et al., 2003; Evans et al., 1997; Nickelson et al., 1986). We model hypothetical survival schedules by life-stage on hatchery-wild composite fish in this paper, and use the model to show how different artificial propagation programs could hypothetically affect natural spawners, using total spawners as our measure of performance.

### 1.3. Harvest and ocean conditions

The effect of harvest on the productivity of salmon populations has been recognized for over a century (Taylor, 1996; Smith and Tim, 1994). Biologists understanding of where salmon migrate, particularly where Chinook and coho migrate, and are harvest is based primarily on the analysis of coded-wire-tag (CWT) data on hatchery indicator stocks and a few natural stocks (CTC, 2001; Cormack and Skalski, 1992). Harvest has easily been identified as affecting salmon simply because it is obvious that those salmon caught do not survive to spawn, as a result harvest reductions generally have been the first management action taken to sustain salmon populations (Taylor, 1996). In addition, the importance of ocean conditions in salmon productivity has only recently become widely accepted. While the problem has been discussed for many decades, the work of Pearcy (1992) and Francis and Hare (1994) showed that many of the major changes in salmonid abundance could be related to changes in ocean conditions.

For our purposes, we kept the ocean and harvest regimes constant in the model, but this could easily be modified to be stochastic and each parameter could be increased or decreased depending on predictions (ocean) and policy decisions (harvest rates).

### 1.4. Integrated modeling approach using all factors

Numerous models exist in the ecological literature such as Leslie Matrix models (Caswell, 2000), density dependent models (Schafer, 1954; Beverton and Holt, 1957; Ricker, 1975) and stochastic simulation models to project population trajectories (Kareiva et al., 2000; Dennis et al., 1991). In recent years, due to the impacts of human development on our resources, numerous species have decreased in abundance in relation to historic levels (Dennis et al., 1991). At the same time, the ecological literature has captured innovative modeling approaches tying land use to population viability. For example, Alexander and Sheilds (2003) model the relationship between land use and a species (penguins) health and persistence, Ji and Jeske (2000) model the use of different habitat types by birds (Pintails) by different life-history stages, and Ahearn (1998) model the affect of human interactions in en-
vironments which have multiple users. Others such as Radeloff et al. (1999), have used Geographic Information Systems (GIS) to model species forest interactions and simulate population trajectories. For some marine organisms, Valavanis et al. (in press) modeled the relationship between essential fish habitat, GIS, and population persistence.

However, for salmon populations, these approaches have been limited in scope. Jessop (1998) modeled the effect of land use on habitat quality and the consequential population dynamics of brown trout, and Bartholow (1994) modeled the affect of flow fluctuations on Chinook salmon survival and distribution from spawning till they leave the river. In our model, we took into account interactions between sub-populations (e.g., hatchery and wild populations) that result in competition for resources, and therefore bring into play density dependence limitations of the population. Beverton-Holt equations such as those in Moussali and Hilborn (1986) can be applied to combined wild and hatchery stocks, or to wild stocks alone (Beverton and Holt, 1957; Ricker, 1975) to model density dependence. We used an approach similar to the population viability analysis for Oregon coastal coho stocks of Nickelson and Lawson (1998). Our modeling approach is unique as it is mechanistic in nature, and captures land management actions and their effects on the population dynamics.

Adkison (1994) explored the genetics of hatchery supplementation programs with a very detailed model and found it difficult to detect a strong impact of domestication. In addition, genetic affects of hatchery fish on the overall stock dynamics has been hypothesized using complicated genetic models calculating effective population size (Ford, 2002). We simplify these effects with an exponential decay parameter that affects survival of fish as a function of a hatchery effect. The consequences of genetic interaction between wild and hatchery fish have received little attention by population dynamics modelers, and this is the first approach that takes into account the effect of fitness on the population dynamics of Pacific salmon.

Mathematical modeling can be used as a tool to understand implications of different management actions (Hilborn and Mangel, 1997; Hilborn and Walters, 1992; Starfield and Bleloch, 1991; Walters and Holling, 1990; Clark, 1985). In this paper, we present a model for Pacific Salmon that weighs all the factors that affect the
stock recruit dynamics. Based on a desired minimum population level, and the opportunity for different user groups (e.g., fishing constituencies, habitat protection advocates or genetic fitness advocates) we can use this model to weigh different options much in the same way that Starfield and Bleloch (1991) weigh different alternatives for wildlife management. This paper hypothesizes how direct measures of habitat can be integrated into a model similar to that of Moussali and Hilborn (1986). The sensitivity of the population size or trajectory to changes in any specific habitat can easily be calculated through this model and the potential for genetic impacts of hatchery/supplemented fish on wild spawning fish can be considered simultaneously. The model provides a framework for complete analysis of the life history of salmon, synthesizing the interaction between habitat, hatchery production, harvest rates and ocean survival. This framework has great potential not only for analysis of habitat changes, but also as an approach by which to evaluate "essential fish habitat" (Valavanis et al., in press; DOC, 1997).

## 2. Materials and methods

### 2.1. General model framework

The basic model of salmon population dynamics is the spawner recruit model (Hilborn and Walters, 1992) and one commonly used for coho and Chinook salmon is the Beverton-Holt model (1957):
$R_{t+1}=\frac{a S_{t}}{b+S_{t}}$
where $R_{t+1}$ is the recruits in time $t+1, S_{t}$ is the spawners in time $t$, and $a$ and $b$ are parameters of the model. This model can be applied to stage-based populations and allow for a harvest rate $\left(u_{t}\right)$ as follows:
$N_{i+1, t+1}=\frac{a N_{i, t}}{b+N_{i, t}}\left(1-u_{t+1}\right)$
where $N_{i, t}$ is the number of individuals in stage $i$ at time $t$. In this case, the subscript $t$ refers to the generation of salmon, ignoring the fact that many salmon return to spawn at different ages.

Moussali and Hilborn (1986) used a sequence of Beverton-Holt models to represent the different lifehistory stages of salmon and further modified the above
models to directly relate the model parameters to habitat quality and quantity.
$N_{i+1, t+1}=\frac{N_{i, t}}{\left(1 / p_{i, t}\right)+\left(1 / c_{i, t}\right) N_{i, t}}$
where $N_{i, t}$ is the number of individuals alive at the beginning of life-history stage $i$ at time $t, p_{i}$ is the "productivity" at stage $i$ (the maximum survival rate from stage $i$ to $i+1$ ) and $c_{i}$ is the "capacity" (the maximum number of individuals that will survive from stage $i$ at time $t$ to stage $i+1$ at time $t+1$ ).

This model can be used to represent a six-stage lifehistory model, tracking spawners $\left(N_{1, t}\right)$, eggs $\left(N_{2, t}\right)$, emergent fry $\left(N_{3, t+1}\right)$, summer parr $\left(N_{4, t+1}\right)$, smolts $\left(N_{5, t+2}\right)$ and adults $\left(N_{6, t+2}\right)$, allowing for both ocean survival rate $\left(o_{t+2}\right)$, and harvesting $\left(u_{t+3}\right)$, to change over time (note, the time subscript is calendar year for the coho life-cycle starting with spawners $N_{1}$, at a particlaur year $t$. The juvenile life cycle occurs in $t+1$, in $t+2$ smolts emigrate, the adult's life-cycle stage occurs in $t+2$, and the adults mature in year $t+3$ during which they are either harvested or return to their natal streams to spawn. For modelling, we ignore the small proportion of the population maturing in year $t+2$ ).

For the above notation and for the coho life-cycle, $p_{1}$ is fecundity per spawner, $c_{1}$ is the carrying capacity for eggs, $p_{2}$ is the survival from egg to fry at low densities, $c_{2}$ is the maximum fry production as determined by the total amount of rearing area available, $p_{3}$ is the maximum fry to summer parr survival, $c_{3}$ is the maximum production of summer parr dependent on summer rearing area, $p_{4}$ is the maximum summer parr to smolt survival, $c_{4}$ is the maximum production of smolts dependent on over-wintering rearing area. For the ocean cohort and harvest rate the following equations are used:
$N_{6, t+2}=\frac{N_{5, t+2}}{\left(1 / o_{t+2}\right)+\left(1 / c_{5, t+2}\right) N_{5, t+2}}$
$N_{1, t+3}=N_{6, t+2}\left(1-u_{t+3}\right)$
where $o_{t+1}$ is the maximum smolt to adult survival (under average ocean conditions), $c_{5}$ is the maximum ocean capacity (we keep the ocean carrying capacity at a very high value to minimize effects of density dependence, as this is unlikely), and $u_{t+3}$ is the harvest rate for adults returning to spawn.

### 2.2. Habitat data

To directly relate stream productivity to freshwater quality and capacity ( $p_{i}, c_{i}$ ) we assumed that freshwater quality is directly related to land use in the basin. While there are many ways this could be done within the general model framework proposed here, for the purpose of this analysis we used land cover information for a watershed (Lunetta et al., 1997). This data set was created to assist in watershed prioritization and analysis of salmonid habitat. It categorized the Lake Washington/Cedar River drainage in eight sub-units called Washington area units (WAU). We use data from the Tiger and Lake Sammamish WAUs (Table 1), and stream segments in which the gradient of the stream was between 0 and $4 \%$ because coho do not generally use habitat with steeper gradients (Lunetta et al., 1997) as reaches greater than $4 \%$ gradient have a high stream velocity. Stream velocity is difficult to obtain due to year to year variability in flow, and as gradient is highly correlated to stream velocity, we used it as the basis for stream areas in our model.

A habitat matrix (Table 2) derived from expert opinion (Gino Lucchetti, King County Department of Natural Resources, Seattle, WA) was used to transform stream areas in the land-use classes to estimate different types of available habitat (in $\mathrm{m}^{2}$ ) for the respective WAU's.

The stream habitat categories were based on the Fisheries Habitat Relationships (FHR, Bisson et al., 1981). The seven categories were pools, cascades, glides, riffles, runs, spawning gravel, and other (Table 2). We did not distinguish between pools and ponds which would have required estimates of pond area, a stream-specific attribute not obtainable from land-use characteristics. The pools category encompasses all pool and pond habitats available (i.e., trench pools, plunge pools, lateral scour pools, mid-channel scour pools, dammed pools, alcoves, beaver ponds and backwater pools).

To estimate the amount of a habitat type $j$ in watershed $k$ at time $t\left(H_{k, j}\right)_{t}$, we begin with the area $\left(\mathrm{m}^{2}\right)$ of stream in watershed $k$ with the $0-4 \%$ gradient $\left(A_{k}\right)$ and the percent of area in watershed $k$ in land-use class $q$ at time $t\left(L_{q k}\right)_{t}$ : old growth, second growth, etc. from Table 1. The percent of stream habitat types $j$ (pools, cascades, glides, riffles, rapids/runs and other) found in land-use class $q\left(M_{j, q}\right)$ is taken from Table 2 and
is assumed to be constant over time. We estimate the amount of habitat type $j$ in watershed $k$ at time $t\left(H_{k, j}\right)_{t}$ via the equation:

$$
\begin{equation*}
\left[H_{k, j}\right]_{t}=A_{k} \times \sum_{q=1}^{n}\left[\left[M_{j, q}\right] \times\left[L_{q, k}\right]_{t}\right] \tag{6}
\end{equation*}
$$

### 2.3. Habitat incorporated into the Beverton-Holt model

Capacity estimates were calculated for the different watersheds dependent on the different types of land use and available stream habitat. Nickelson et al. (1992a) estimated how many individuals in each life-history stage, $i$ (eggs, fry, parr and pre-smolts) could be maintained per square meter of each habitat type $j\left(D_{j, i}\right)$. We used these estimates (Table 3) to calculate stagespecific capacities for watershed $k$ in life-history type $i$ at time $t\left(c_{k, i}\right)_{t}$. Incidentally, the $\left(c_{k, i}\right)_{t}$ corresponds to the $c_{i}$ in Eq. (3) for a particular life-stage, for a particular watershed $k$, and thus have a time dynamic. Since the data resolution for carrying capacity (Table 3) gives us only five life-stages, spawners to egg, egg to fry, fry to winter pre-smolt, pre-smolt to smolt and smolt to adult, we had to assume there was no density dependence from fry to summer parr and incorporated only the productivity parameter from this life-cycle stage:
$\left[c_{k, i}\right]_{t}=\sum_{j=1}^{n}\left[H_{k, j}\right]_{t} \times\left[D_{j, i}\right]$
The productivities for each stage $\left(p_{i}\right)$ are assumed to be related to the land use in each watershed-implicitly incorporating the impact of land use on the hydrologic regime, so that a watershed with a high percentage of old growth forest would have higher productivity (survival) than an urbanized area because stream flows would be more stable, sediments loads would be less, summer temperatures would be lower, etc. For a given watershed $k$, we used an average of the percent area in each land-use class $\left(L_{q, k}\right)_{t}$ weighted by its relative productivity ( $E_{i, q}$ in Table 1 ) and the overall survival from one stage to the next $\left(\mathrm{Sr}_{i}\right)$ obtained from Nickelson's research (Table 4, Tom Nickelson, Oregon Department of Fish and Wildlife, Corvallis, OR, USA, personal communication). For purposes of our modeling, we have made $E_{i, q}$ a constant that does not change by life-stage (we could change this dependent

Table 1
Washington area units and the respective land-use area in square meters for stream reaches having slopes between 0 and $4 \%$ (EPA western Washington Watershed Screening data, Lunetta et al., 1997)

| Land-use category | Tiger | Lake Sammamish | Total watershed area | Productivity scalar $(E)^{\text {a }}$ |
| :--- | :--- | :--- | :--- | :--- |
| WAU units |  |  |  | 1.00 |
| Old growth | - | - | - | 0.95 |
| Second growth | 621,016 | 417,970 | 222,484 | $0,003,904$ |
| Shrubs | $1,824,359$ | 389,593 | $2,213,952$ | 0.80 |
| Other forest | 7,884 | 46,492 | 54,375 | 0.50 |
| Ponds, lakes and water | $2,976,399$ | 954,064 | $3,930,463$ | 0.40 |
| Agriculture, rural and urban | 86.92 | 23.97 | 110.88 |  |
| Stream kms $(0-4 \%)$ | 173,834 | 47,933 | 221,766 |  |
| Stream area $\left(\mathrm{m}^{2}\right)$ |  |  |  |  |

Note: For modelling purposes we used the stream area for both WAU's as Issaquah creek passes through both (this is probably a high estimate).
${ }^{\text {a }}$ Productivity scalar (E) used in Eq. (8) for basing stage-based survival estimates.

Table 2
Conversion matrix transforming stream area (\%) to specific stream habitat characteristics as estimated by a local expert Gino Lucchetti, King County Department of Natural resources, Seattle, Washington

| Land type/stream habitat type | Pools (\%) | Cascades (\%) | Glides (\%) | Riffles (\%) | Rapids/runs (\%) | Other (\%) |
| :--- | :--- | :--- | :--- | :--- | :---: | :---: |
| Old growth | 60 | 0 | 5 | 30 | 5 | 0 |
| Second growth | 50 | 0 | 10 | 30 | 10 | 0 |
| Shrubs | 40 | 0 | 10 | 40 | 10 | 0 |
| Other forest | 20 | 0 | 20 | 40 | 0 | 0 |
| Ponds, lakes and water | 0 | 0 | 0 | 50 | 100 | 0 |
| Agriculture, rural and urban | 10 | 0 | 20 | 0 | 0 |  |

Table 3
Capacity estimates of juvenile coho per square meter of habitat dependent upon season (based on Nickelson et al., 1992a,b)

| Life-cycle stage <br> (habitat type) | Egg-fry <br> (spring) | Spring fry-winter pre-smolt <br> (summer) | Winter pre-smolt-smolt <br> (winter) |
| :--- | :--- | :--- | :--- |
| Pools | 2.275 | 1.55 | 0.7625 |
| Cascades | 0 | 0.2 | 0 |
| Glides | 1.8 | 0.08 | 0.1 |
| Riffles | 1.2 | 0.01 | 0.01 |
| Rapids | 0.6 | 0.01 | 0.01 |
| Other | 1.8 | 1.05 | 0.5 |
| Spawning gravel | 0 | 0 | 0 |

Table 4
Density independent survival rates for coho salmon

| Survivals from life-cycle stages | Nickelson's study | Life-cycle stage-based survivals | Estimated survivals |
| :--- | :---: | :--- | :---: |
| Egg to smolt | 0.2 | Egg to spring fry | 0.67 |
| Spring fry to smolt | 0.3 | Spring fry to summer parr | 0.6 |
| Summer par to smolt | 0.5 | Summer parr to winter | 0.56 |
| Winter pre-smolt to smolt | 0.9 | Winter pre-smolt to smolt | 0.9 |
| Spawn to egg | 1250 | Spawner to egg | 1250 |

on different life-history-based productivities which are a function of habitat conditions in the watershed).
$p_{i, t}=\operatorname{Sr}_{i} \times \frac{\sum_{q=1}^{n}\left[E_{i, q}\right] \times\left[L_{q, k}\right]_{t}}{\sum_{q=1}^{n}\left[L_{q, k}\right]_{t}}$
where $p_{i}$ is the density independent productivity for stage $i$ dependent on the relative importance/relationship between productivity and land use in that stream; $E_{i, q}$, scalar showing the importance of land-use type ( $q$ ) for overall productivity (in Table 1); $\mathrm{Sr}_{i}$, average maximum survival rate from one stage to the next in the freshwater life history of coho given average conditions (Table 4) under a baseline in the best possible habitat suited for their survival. Please note, that the life cycle-based productivities $\left(p_{i}\right)$ is equivalent to the productivities in Eq. (3), and have a time dimension to them.

We rewrite Eq. (3) in terms of the land use-based productivity and capacity estimates, by freshwater lifehistory stage for coho in watershed $k$ as:

$$
\begin{align*}
& N_{k, i+1_{t}} \\
& =\frac{N_{k, i_{t}}}{1 /\left(\operatorname{Sr}_{i} \times\left(\sum_{q=1}^{n}\left[E_{i, q}\right] \times\left[L_{q, k}\right]_{t} / \sum_{q=1}^{n}\right.\right.} \\
& \left.\quad \times\left[L_{q, k}\right]_{t}\right)+1 /\left(A_{k} \times \sum_{j=1}^{n}\left[\left[\sum_{q=1}^{n}\left[M_{j, q}\right]\right.\right.\right. \\
&  \tag{9}\\
& \\
& \left.\left.\left.\left.\quad \times\left[L_{q, k}\right]_{t}\right] \times\left[D_{j, i}\right]\right)\right]\right)\left[N_{k, i_{t}}\right]
\end{align*}
$$

All these stages occur at the different seasonal or monthly time-steps, but in the same calendar year timestep shown in Eq. (3), other than the smolt life-cycle stage, which occurs in the next year.

### 2.4. Hatchery domestication incorporated into the Beverton-Holt model

The number of coho eggs produced in the wild in a given year is a function of the number of spawners returning, the number of eggs per spawner, and the carrying capacity of the stream. We assume a 50:50 sex ratio in the spawners and the maximum number of eggs that are successfully deposited and fertilized to be 2500 per female. This leads to a maximum of 1250 eggs deposited per spawner $\left(p_{1}\right)$. The carrying capacity for eggs $\left(c_{1}\right)$ in the stream is calculated and defined as in the previous section. Thus the number of eggs suc-
cessfully deposited and fertilized in a given year, takes the form of Eq. (4) as in the previous section.

At the egg stage, a domestication index is calculated for the cohort. This index is the average number of generations a certain gene spends in the hatchery stock, labeled as AHG, with higher average hatchery generations (AHG) symbolizing decreased genetic "wildness". This could be referred to as the average breeding value of fitness in nature. As more and more hatchery fish interact with natural fish, this averagebreeding values decline in the natural population. If no natural fish enter the hatchery stock, then the hatchery population increases its average hatchery generations by one with each returning cohort. If natural coho breed in the hatchery, then the hatchery population's average hatchery generations increases by less than one because natural coho will inherently have a lower number of hatchery generations than the hatchery stock, and a higher average breeding value than exclusively hatchery fish. If zero hatchery fish spawn in the stream, then the wild stock's average hatchery generations will remain at zero over time. As the number of hatchery fish that spawn in the stream increases, the natural stock's average number of hatchery generations will increase. The following equation can be used to calculate the average number of hatchery generations for the eggs of both populations:

$$
\begin{equation*}
\mathrm{AHG}_{\mathrm{W}, t+1}=\frac{\left(\left(N_{1, t}^{\mathrm{W}} \times \mathrm{AHG}_{\mathrm{W}, t}\right)+\left(N_{1, t}^{\mathrm{H}} \times \mathrm{AHG}_{\mathrm{H}, t}\right)\right)}{N_{1, t}^{\mathrm{W}}+N_{1, t}^{\mathrm{H}}} \tag{10}
\end{equation*}
$$

where $\mathrm{AHG}_{\mathrm{W}, t+1}$ is the average hatchery generation of the wild stock's next cohort (e.g., the eggs) based on the number of hatchery strays $\left(N_{1, t}^{\mathrm{H}}\right)$ spawning in the wild and natural or wild $\left(N_{l, t}^{\mathrm{W}}\right)$ fish spawning in the wild, weighted by the domestication factor of each stock's cohort. Similarly, we can calculate a $\mathrm{AHG}_{\mathrm{H}}$ for the hatchery stock intermingling with some wild fish. This domestication index will be the same for all the life-stages of the subsequent cohort, and will not change until the progeny come back to spawn in calendar time, $t+3$.

The number of individuals that survive from one life-cycle stage to the next is predicted by a Beverton-Holt model where maximum stage-based survival $\left(p_{i, t}\right)$ and carrying capacity $\left(c_{i, t}\right)$ are calculated according to Eqs. (8) and (7), respectively. The stage-
based survival is then adjusted for the effect of domestication according to the equation:
$p_{i, t}^{\prime}=p_{i, t} \mathrm{e}^{-\theta_{i} \times\left(\mathrm{AHG}_{s}\right)}$
where $\theta$ represents the rate at which survival decreases with respect to increasing generations of domestication at a particular life-cycle stage ( $i$ ) and $s$ indicates whether we are modeling hatchery or wild populations as the productivity function will be dependent on the number of hatchery fish spawning with natural fish in the natural or hatchery environment. Data from Reisenbichler and Rubin (1999) suggests that $\theta$ could be between 0.1 (egg/fry to yearling survival) to 0.25 (egg/fry to adult survival) depending on the cumulative life-stages affected. In our simulations we used values of theta of 0.05 (Table 5) that might effect survival from one life-stage to the next (in scenario 3d, Table 5 we model an overall impact from egg/fry to adult as that modeled by Reisenbichler and Rubin, 1999).

The number of individuals that survive from one life-cycle phase to the next can be estimated as:
$N_{i+1, t+1}=\frac{N_{i, t}}{\left(1 / p_{i, t}^{\prime}\right)+\left(1 / c_{i, t}\right) N_{i, t}}$
The numbers of individual in any stage is calculated using Eqs. (11) and (12), with each stage having its own $\theta$ to determine the effect of domestication on survival. The number of smolt released by the hatchery is a linear function of the number of spawners returning to the hatchery times a spawner-smolt conversion factor, set equal to 2000 per female or 1000 per spawner (Bill Tweit, Washington Department of Fish and Wildlife (WDFW), Olympia, WA, USA, personal communication). The number of hatchery and wild smolts which survive to adults is based on density independent survival adjusted for each stock's level of domestication (e.g., setting $c_{5, t+1}$ in Eq. (8) to an extremely large number representing infinity).

### 2.5. Ocean conditions and harvest

Ocean survival and harvest are assumed constant in the runs we show in this analysis but any pattern could be used in the model. The equations used were similar to Eqs. (4) and (5) shown previously in the existing models section.

### 2.6. Simulating population trajectories with Issaquah creek watershed

We illustrated the model with data from Issaquah creek (includes the WAU of Lake Sammamish and Tiger, Table 1). All scenarios modeled begin with 336 natural spawners, the average number of spawners observed between 1995 and 1999 (Bill Tweit, WDFW, Olympia, WA, USA, personal communication). Based on our model assumptions (by using the productivity scalars in Table 1), the freshwater rearing capacity is approximately 380 spawners. We started our simulations at 336 spawners, based on average spawners observed on the Issaquah. Hence, without habitat change, harvest or a hatchery, the present natural population will approach equilibrium at 380 spawners.

We simulated four possible scenarios (Table 5):

## 1. Habitat effects

For this scenario, the available land area is converted from seral stage to urban areas at a specified rate per year. We have partitioned this simulation into three different scenarios to illustrate the effect of converting land use from the older seral stages to urban and agricultural areas at a slow rate ( $1 \%$ annually, scenario 1 a ), a rapid rate ( $5 \%$ annually, scenario 1 b ), and finally habitat renewal from urban/agricultural areas to early seral stages ( $1 \%$ annually, scenario 1c).
2. No domestication effect

We partitioned this simulation into two scenarios: one with static habitat conditions (scenario 2a), and one with changing habitat conditions similar to scenario 1a (scenario 2b). A hatchery is introduced on the fourth generation with 100 hatchery fish. The hatchery capacity is 400 fish. The number of smolts produced per hatchery female is 2000 (or 1000 per spawner). The initial average hatchery generations is 5 for the hatchery population and 0 for the wild population. The natural spawners include hatchery spawners that stray at a rate of $10 \%$. All other parameters for the scenario are obtainable from Table 5.
3. Domestication effects

Everything is the same as scenario 2 above, except that there is an average hatchery generation effect and this effect is exacerbated over life-stages. We model marginal to pronounced effects on survival over life-stages, and in the final trajectory model

Table 5
Starting values used in each simulation, with respect to the baseline optimum conditions possible

| Parameters | Baseline | Scenario 1: <br> habitat effects ${ }^{\text {a }}$ | Scenario 2: no domestication effect ${ }^{\text {b }}$ | Scenario 3: <br> domestication effects ${ }^{\text {c }}$ | Scenario 4: <br> domestication <br> effect with <br> hatchery <br> shutdown ${ }^{\text {d }}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Initial wild (W) | 336 | 336 | 336 | 336 | 336 |
| Initial hatchery (H) | 0 | 0 | 100 | 100 | 100 |
| $p_{1}$ (fecundity in eggs/female) | 2,500 | 1,585 | 1,585 | 1,585 | 1,585 |
| $c_{1}$ | 37,892,675 | 37,892,675 | 37,892,675 | 37,892,675 | 37,892,675 |
| $p_{2}$ (egg to fry survival) | 0.67 | 0.42 | 0.42 | 0.42 | 0.42 |
| $c_{2}$ | 319,231 | 316,665 | 316,665 | 316,665 | 316,665 |
| $p_{3}$ (fry to summer parr to winter pre-smolt) | 0.33 | 0.13 | 0.13 | 0.13 | 0.13 |
| $c_{3}$ | 58,570 | 49,019 | 49,019 | 49,019 | 49,019 |
| $p_{4}$ (winter pre-smolt to smolt) | 0.9 | 0.57 | 0.57 | 0.57 | 0.57 |
| $c_{4}$ | 24,549 | 17,387 | 17,387 | 17,387 | 17,387 |
| Theta | 0 | 0 | 0 | 0.05 | 0.05 |
| Initial $\mathrm{AHG}_{\mathrm{H}}$ | na | na | 5 | 5 | 5 |
| Initial $\mathrm{AHG}_{\mathrm{W}}$ | 0 | 0 | 0 | 0 | 0 |
| Wild smolt to adult survival | 0.11 | 0.11 | 0.11 | 0.11 | 0.11 |
| Hatchery female spawner to smolt fecundity | 2000 | na | 2,000 | 2,000 | 2,000 |
| Hatchery smolt to adult survival | 0.035 | na | 0.035 | 0.035 | 0.035 |
| $U_{\text {w }}$ | 0 | 0 | 0.05 | 0.05 | 0.05 |
| $U_{\text {h }}$ | 0 | 0 | 0.9 | 0.9 | 0.9 |
| Hatchery stray rate | 0 | 0 | 0.1 | 0.1 | 0.1 |
| Wild stray rate | 0 | 0 | 0.02 | 0.02 | 0.02 |
| Change in land use from one category to the other | 0 | 0.01 | 0 | 0 | 0.01 |
| Hatchery capacity | na | na | 400 | 400 | 400 |
| Hatchery shutdown in generation | na | na | na | na | 7 |
| Dilution of hatchery effect ( $\mathrm{AHG}_{\mathrm{w}}$ ) from one generation to the next | na | na | na | na | 0.9 |

Productivity and capacity, at each life-stage is estimated using Eqs. (10)-(12). Time dynamics are not captured in this Table as the productivity and capacity change with changes in land use and hatchery strays.
${ }^{\text {a }}$ This is for scenario 1a, for pronounced degradation this is 0.05 scenario 1 b , and for regeneration (scenario 1 c ) it is 0.01 from urban areas to third growth (shrubs).
${ }^{\mathrm{b}}$ The second trajectory (scenario 2 b uses the rapid declining habitat conditions of scenario 1 b .
${ }^{c}$ The theta variable is the exponential loss in baseline survival in a specific life-stage. Each trajectory shows theta effecting survival across life-stages (second one till fry, third till parr fourth till adult (Fig. 3) and fifth till adult and loss in habitat from the baseline conditions of scenario 1a).
${ }^{d}$ The third scenario is used for the hatchery decline. After shutdown the scenario modeled uses the same improvement in habitat as shown in scenario 1c or static conditions after the seventh generation.
domestication effects with declining habitat conditions (scenario 1a). $\theta$ (Eq. (11)) has the value of 0.05 , with the hatchery effect maximizing at $25 \%$ of the base period survivals in each life-stage, i.e. with one hatchery generation we will have $96 \%$ of the base period survival (weighted by land use-based pro-
ductivity, Eq. (8)) for each life-stage. For the first scenario (scenario 3a), we have no domestication effect shown. The marginal effect modeled occurs till the egg-fry life-cycle stage (scenario 3b), the third scenario models a egg to summer parr effect (scenario 3c), the fourth scenario modeled an egg
to adult effect (scenario 3d) and the final scenario assumes an egg to adult effect with the hatchery shutdown (scenario 3e).
4. Domestication effect with hatchery shutdown The starting parameters and the AHG effect are the same as scenarios 2 and 3, except that the hatchery shuts down after 21 years (seven generations). All the fish returning then spawn in the wild. All three scenarios here have the hatchery effect from the egg to summer parr life-cycle stage (scenario 3c above), with declining habitat conditions of scenario 1a. We illustrate what happens after the hatchery shutsdown. The scenarios illustrate a slow decline in habitat conditions (same as scenario 1a), and we name this scenario 4 a . We separate this scenario from two other scenarios to illustrate population trajectories resulting from static habitat (scenario 4b), and improving habitat (scenario 4 c , similar parameters as scenario 1c). The domestication effect dilutes over time by $10 \%$ per generation in the natural progeny.

### 2.7. Sensitivity analysis on parameter choice

We perform a sensitivity analysis on the key parameters in the model that generate the habitat-based productivity and capacity, particularly the productivity scalars (scenario 5) and the habitat matrix (scenario 6, Table 2). Additional sensitivity on the magnitude of the effect (estimate of $\theta$ ) is also illustrated (scenario 7).

## 3. Results

### 3.1. Simulation of population trajectories

### 3.1.1. Scenario 1: habitat effects

We observe (Fig. 1) through the simulation how productivity declines over time at different rates (scenarios 1 a and 1 b ). In addition, in 60 years ( 20 generations of the same brood) we observe changes in the carrying capacity in the stream. In the first case, with a slow rate of change, this decline is gradual. This is a result of the change in pool and pond areas for rearing juvenile coho in the stream, as well as the productivity of coho from previous life-stages.


Fig. 1. Changes in capacity and productivity with change in land use in Lake Sammamish, WA. Inset: (a) changes in freshwater productivity with generations; (b) changes in freshwater capacity with generations; and (c) natural spawning trajectories due to changes in productivity and capacity. The three scenarios $1 \mathrm{a}, 1 \mathrm{~b}$ and 1 c correspond to declining habitat, rapid decline in habitat and improving habitat, respectively.

In scenario 1 b , a rapid annual habitat decline of 5\% from seral to urban areas results in both productivity and capacity declines that are steeper in slope, causing extinction (defined as 0 spawners) in 45 years (15 generations).

In scenario 1c, we illustrate what would happen if stream quality could improve by land buy-back mechanisms and converted to the early seral stage classes from urban and agricultural areas at the rate of $1 \%$ per year. Over time, conditions improve and over 60 years ( 20 generations) the populations begin to increase.

### 3.1.2. Scenario 2: no domestication effect

For no domestication effect to take place, a hatchery supplementation program would help recover and boost the natural run (Fig. 2), and provide additional harvest opportunity from the supplemental fish. We have different harvest rates on hatchery stocks with minimal impacts on natural stocks to model hypothetical contrasts, and to have minimal impacts from a hatchery (supplemental) program that dwarfs the natural run in magnitude. We separated this scenario into two cases. Scenario 2a models a population trajectory with static habitat conditions. The population gets a boost and stays there as there is no difference in survival of the progeny of the hatchery and wild fish.


Fig. 2. No domestication effect on the natural populations due to hatchery fish spawning in the wild: (a) changes in productivity due to changes in freshwater conditions; (b) changes in freshwater capacity; and (c) natural spawning trajectories (a combination of natural and hatchery fish). The two trajectories shown are with static and declining habitat conditions.

In scenario $2 b$, rapidly declining habitat conditions (scenario 1 b ) nullify the effect of the hatchery supplementation program. We observe that the natural run seems to be rebuiliding under a short time frame (Fig. 2), but due to loss in habitat productivity and capacity, the natural run declines. This decline is gradual over time, and depends on the rate of habitat loss, and the magnitude of the artificial propagation program.

### 3.1.3. Scenario 3: domestication effect

As the natural stock gets domesticated due to the strays from the hatchery program, we investigate different hypotheses on spawner to adult survivals. Each trajectory simulated amplifies the effect by affecting survival at different life-stages (Fig. 3). We model a marginal effect that occurs only in the egg to fry lifestage (scenario 3b), a mid effect that occurs till the pre-smolt life-stage (scenario 3c), and an extreme effect that occurs in all life-stages till adult (scenario 3d). The final trajectory modeled declining habitat with extreme effects (scenario 3e).

We observe that initially the hatchery adds to the natural production with the strays, but over time the domestication of the stock causes the natural run to dwindle in numbers (Fig. 4). In a short time scale, observers think the stock is rebuilding but this recovery is soon dwarfed by a decline in the following years. As the genetic component effects survival (fitness) from one life-stage to the next (shown through different trajectories effecting survival in single or multiple life-stages of coho, Fig. 4), the productivity decline gets steeper and the overall spawner trajectory has a steeper nega-


Fig. 3. Effect of domestication on overall survival used in the modeling exercise for scenario 3 .


Fig. 4. Effect of domestication due to adverse genetic effects reducing survival of the natural populations. Each of the spawning trajectories show declining survivals due to compounding of the average hatchery generations effect over multiple life cycles of the natural populations (which has the AHG component). Scenario 3 b is an effect from egg-fry, scenario 3 c is an effect from egg-summer parr, scenario 3d is an effect from egg-adult, and scenario 3 e is the effect from egg to adult with declining habitat conditions.
tive slope. Since the overall capacity in freshwater is intertwined with productivity (Moussali and Hilborn, 1986), the freshwater rearing capacity also declines, even if the habitat characteristics don't decline (scenarios $3 \mathrm{~b}-3 \mathrm{~d}$ ). This effect is more pronounced if we have declining habitat conditions in addition to a loss in genetic fitness being passed on to the natural stock (scenario 3e).

### 3.1.4. Scenario 4: domestication effect with hatchery shutdown

The hatchery is shut down after operating for seven generations (21 years). Consequently, there is a spike in the population immediately after that due to the excess hatchery fish spawning in the wild. As, we no longer have any hatchery effects on the natural stock, and the domestication factor dilutes over time (domestication


Fig. 5. Rebuilding a natural run with a supplementation boost and then shutting down the program. Trajectories model improving habitat (scenario 4c), static habitat (scenario 4b) and declining habitat (scenario 4c) after shutdown.
declines in the natural stock at the rate of $10 \%$ per successive generation), the run rebuilds slowly as a result of improved survival over time (Fig. 5).

After the hatchery shuts down, we illustrate three hypothetical scenarios. In scenario 4 a , the habitat decline continues at the rate as in scenario 1a. Consequently, after the hatchery shuts down, the temporary boost that is observed in the population gets nullified as the productivity and capacity of the natural stock is low. The population continues to decline at a slow rate.

In scenario 4 b , the habitat conditions remain static. However, as the freshwater productivity and capacity are low, the population stabilizes at low levels of abundance. In scenario 4 c , we observe that with improving habitat conditions (same change in land-use parameters as in scenario 1c), the population slowly rebuilds over time. Ideally, the supplementation should take place while habitat improvements are being made. Thus, when a hatchery is shutdown, the natural population is capable of sustaining itself due to the


Fig. 6. Sensitivity to productivity and capacity parameters based on the habitat portion of the formulation of the Beverton-Holt. Inset: (a) changes in productivity based upon watershed land use and its relation to instream productivity described in Eq. (12); (b) changes to capacity estimates due to changes in in-stream and side channel pool habitat available by land-use types (Eqs. (10) and (11)).
improved habitat conditions. A important distinction to note is that stock recovery only occurs if the present habitat quality and quantity improves over time.

### 3.2. Sensitivity analysis of parameters used in the model

### 3.2.1. Habitat and stream interactions effects

The model is sensitive to parameters such as the habitat matrix (Table 2), and the scalar effect on weighting baseline productivity by land use in the watershed modeled (parameter $E$ in Eq. (8)). Productivity estimates are based on survival from one life-stage to the next (scenario 5), weighed in effect by land-use and the productivity scalar $E$ (Eq. (8)). All three scenarios (Fig. 6a) illustrated assume no change in land-use over the time line displayed.

Scenario 5a illustrates initial parameter values used in our model simulations. Scenarios 5 b and 5 c show how sensitive productivity is to these productivity scalar estimates. In scenario 5 b, we model a productivity scalar having equal weighting for the old, second and third (shrub) growth, and $60 \%$ of the baseline for the other three land classes (lakes, other forests, and urban and agriculture). Using these assumptions, productivity estimates would be double those in our initial simulations. The third scenario is essentially maximum baseline productivity from egg to smolt of $20 \%$ (equal weighting for all classes, scenario 5c). This illustrates an extreme hypothesis that productivity is independent of land use and will be the maximum for all watersheds in all areas. In all probability, these productivities would vary by watershed and land use in the watershed.

Depending on the habitat matrix (Table 2 and Fig. 6b) chosen, we illustrate different capacity estimates obtained on the stream. As the figure illustrates, most juvenile rearing capacity is limited by the amount of in-channel and side channel pools, and ponds (Nickelson et al., 1992a,b). Scenario 6a illustrates the Nickelson model (1992a,b). If in reality this distribution changes by land use as shown by the histogram from old growth to second growth, the rearing capacity estimates will be low as in Scenario 6a. However, as the amount of pool area in the other types of habitat is estimated to be equally distributed, or is higher in third growth and urban areas, the overall smolt rearing capacity will increase as illustrated by scenarios 6 b and 6 c .

### 3.2.2. Sensitivity based on the Hatchery Domestication effect

Scenario 3 illustrates the effect of domestication over the separate life-stages (Fig. 3). The magnitude of the effect of theta $(\theta)$ on the overall survival from egg-adult was discussed in scenarios two and three. Here, we illustrate the effect of the magnitude of theta on overall survival (scenario 7). We assumed that this effect $(\theta)$ is occurring over all life-stages (the last case of scenario 3 ). It is evident that the more severe the magnitude of theta, the greater the effect on overall survival (Fig. 7). Scenario 7a shows us a minor effect of theta $(\theta=0.01)$. A more severe effect is shown in scenario 7 b with $\theta=0.025$, and scenario 7 c uses a value of $\theta=0.05$. Scenario 7c is the value we used in scenario 3d previously.


Fig. 7. Sensitivity to the magnitude of the hatchery domestication effect $(\theta)$ over all life-stages. The figure shows the relative difference in survival from no effect.

### 3.2.3. Other parameters that would effect population trajectories simulated

We have modeled the effect that assumptions in the habitat conversion matrix, the productivity scalars and the hatchery effects have on the overall population dynamics. Other parameters that would affect the population trajectories are the ocean survival and the harvest rates. In addition, we have assumed instantaneous effects from a change in the land-use to changes in the instream habitat (that effects productivity and capacity) in a watershed. We have assumed similar instantaneous effects with the hatchery populations spawning in the natural environment affecting the progeny in the subsequent cohort. These effects could have some time delay characteristics, and may not occur until a few generations later.

## 4. Discussion

Most of the scenarios presented above are realistic scenarios that are prevailing in numerous watersheds across western Washington, Oregon, California, parts of British Columbia, Vancouver Island and Alaska. Land management and forest practices have modified the watersheds so drastically from historic base levels that in a decadal time scale, productivities (related to water quality), and capacity (related to water quantity) are in all probability, significantly different (Lestelle et al., 1996; Lichatowich et al., 1995). In addition, hatchery practices, not designed for supplemental purposes, but with one sole purpose; to increase fish production due to an observed decline in natural production caused by habitat modifications and overfishing, have modified the existing natural populations to such levels that original life-history traits of natural salmon populations have changed (Nickelson et al., 1986). A third level of complexity is ocean conditions and how they affect the overall survival of salmon stocks (Francis and Hare, 1994; Coronado and Hilborn, 1998). Besides these, the human interaction as large communities depend on fisheries on salmon for their subsistence and livelihood, makes these problems extremely difficult to address.

In the realm of endangered species management, managers need to make rational decisions on what protective measures to take that would have the most significant long-term benefits on the stock of concern. The tool developed here gives us a framework to evalu-

Table 6
Using the model to obtain different objectives

| Scenario | Policy objective | Option A: option 1 (habitat <br> driven) | Option B: option 2 <br> (hatchery driven) | Option C: option 3 (balance <br> of habitat and hatcheries) |
| :--- | :--- | :--- | :--- | :--- |
| 8 | Double natural spawners in <br> 20 generations with no <br> change in harvest statusqou | Improve habitat at the rate <br> of $0.34 \%$ per year from <br> agricultural and urban areas <br> to third growth | Increase hatchery capacity <br> to 1016 fish and supplement <br> from present generation | Increase hatchery capacity to <br> Assumes no hatchery <br> influence at start time and |
|  |  | no harvest |  |  |

Alternatives between habitat improvement, hatchery supplementation and a combination of the two.
ate alternative strategies (Starfield and Bleloch, 1991; Clark, 1985), such as hatchery supplementation versus habitat restoration versus harvest restrictions, and also provides target reference points for management, given the existing and future conditions. We illustrate the use of this tool with some hypothetical objectives. For example, a possible objective (with the same parameter values as scenario 3 b above) could be to double the natural spawners over the next 20 generations. Possible solutions to this objective are that we either improve habitat by $0.2 \%$ from urban areas to third growth areas (Table 6, scenario 8a) or supplement without any habitat improvements (Table 6 , scenario 8 b) by increasing the hatchery capacity to 1016 adults. We could also obtain this goal by a combination of the two, namely sup-
plement by increasing hatchery capacity to 600 adults with some partial habitat improvements (Table 6, scenario 8c). There are numerous permutations of the last scenario of which only one has been shown on the table. Depending on the economic and social costs associated with an option, the best possible option could be devised using a cost function (Clark, 1985) and minimizing the cost associated with an outcome.

An alternative objective may be to maximize harvest in a certain time frame (we again assume the same parameter values as in scenario 3b). To accomplish this objective, we need a high hatchery output (Table 6 , scenario 9 b ). Habitat alterations cannot make the target fishery catch that high, as the habitat cannot produce beyond a certain number of fish (Table 6 , scenario 9 a).

In a balanced scenario harvest rates could increase on the natural component of the run after the natural run sizes are greater than a 1000 fish (Table 6, scenario 9c). As in the previous case, there are a number of permutations of hatchery supplementation and habitat modifications that could achieve this objective, and only one solution is presented here. However, the adverse impacts of the strays from the surplus hatchery fish may eventually cause genetic swamping of the natural origin populations in the streams. As in the previous case the best option could be estimated using a cost function (Clark, 1985) and minimizing the cost associated with an outcome.

A third possible objective could be to increase the fitness or productivity of the natural population to 50 smolts per spawner (almost double the present value) on average and a minimum spawning population of 1000 fish by the 20th generation. This can only be achieved by changing the habitat (Table 6, scenario 10a) as the final objective is fitness of the natural stock. In this scenario, you could only model a minimal harvest on the natural stock (5\%) and this rate could be increased over time, but the overall catch will always be lesser than that modeled if a hatchery were operating. Depending on a cost associated with harvest loss, this objective may not be feasible to all the user groups involved in the process.

It should be noted that management measures for sustainable harvest are tied to these parameter estimates of productivity and capacity shown in the previous scenarios. Hence as productivity improves on a stock, the harvest rate it can sustain also increases, as does the maximum sustainable yield for the stock (Moussali and Hilborn, 1986). If productivity levels decline however, and harvest pressures do not, populations will be overfished, and reduced to low abundances, as was seen in numerous coho stocks in Oregon and Washington in the late 1990s (Nickelson and Lawson, 1998).

The model presented here is an illustrative tool (as shown in Table 6) to understand the dynamics of all these variables interacting with one another simultaneously. It provides a framework to evaluate different management policies under one common thread (Table 6 above). However, it is sensitive to parameter choice (Figs. 3, 6 and 7), and to provide a more accurate picture, a concrete experimental design to test productivities by land use and stream type should be developed for the watershed and species being mod-
eled. In addition, our modeled assumption, that there is no time delay affect between land-use changes and consequential changes in-stream habitat functionality (related to productivity, and capacity by life-stage for the stock of concern), is probably inaccurate.

In terms of understanding the interactions with hatchery fish, the AHG concept is oversimplified, and issues of competition and fitness as well as loss of genetic integrity would have to be addressed (Reisenbichler and Rubin, 1999; Nickelson et al., 1986; Chilcote et al., 1986). However, with this simple accounting mechanism, all these factors are addressed to some extent by the AHG term. The model trajectories are sensitive to the exponential decline parameter (theta), and further research needs to be conducted to detect if such effects exist on natural populations of concern. There is no uniform solution to all given stocks or watersheds, but all these factors should be taken into account, when designing a model tailored to individual areas and questions. In an approach similar to Nickelson and Lawson (1998), we could introduce stochasticity in the parameters used and model multiple simulations of the previously described scenarios to make this model more probabilistic in nature.

## 5. Conclusion

The model presented here allows for the potential of density dependence in each life-history stage, and as such provides a framework for a complete life-cycle analysis. Most previous models have simply calculated either the carrying capacity at one or two stages as a function of habitat (Nickelson et al., 1992a, b; Nickelson and Lawson, 1998), or ignored density dependence and dealt only with survival through various life-history stages (Kareiva et al., 2000). By relating the carrying capacity and productivity at each life-history stage to specific habitat quality and quantity, the model provides a general approach for relating field data on survival versus measurable habitat characteristics, and carrying capacity. Finally, the model provides a framework for complete analysis of the salmon life history, synthesizing the interaction between habitat, hatchery production, harvest rates and ocean survival. This framework has great potential not only for analysis of habitat changes, but also an approach for evaluation of "essential fish habitat", a term that is fast becoming an
important measure for reproductive success (Valavanis et al., in press; DOC, 1997).

In conclusion, as most models in population dynamics, Pacific salmon life-cycle models are no different, and change with space and time. An adaptive management framework (Lee, 1993) should address management concerns for Pacific salmon, especially for stocks at critical or low abundance levels. The mathematical model presented here can provide policy makers a common thread to evaluate population trajectories across a watershed (watersheds) using a common set of assumptions. This has been the missing step in setting region specific objectives for Endangered Species Act (ESA) stocks of Pacific salmon. Particular attention needs to be made to improvements in habitat along with hatchery practices, as these could possibly compliment one another. A holistic design for Pacific salmon involves developing stock production relationships that incorporate habitat and hatchery-interactions. Target management objectives for endangered species recovery could then be related to estimates of improved productivity, maximum yield or maximum production in a watershed through land-management actions, in-stream habitat modifications, and hatchery reform.

## Acknowledgments

We acknowledge Mark Maunder and Robert Francis for helping in the initial model design. We acknowledge Tom Nickelson, Pete Bisson, Gino Lucchetti, Tim Beechie and George Pess for help in the habitat development; Reg Reisenbichler and Gayle Brown for help with the hatchery-interactions; and Bill Tweit for coho data on Issaquah creek. We also wish to thank the Quantitative Ecology and Resource Management Department at the University of Washington, the Washington Sea Grant Program and National Marine Fisheries Service for supporting this research.

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