Contributed Paper

Range-Wide Selection of Catchments for Pacific Salmon Conservation

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Abstract: Freshwater ecosystems are declining in quality globally, but a lack of data inhibits identification of areas valuable for conservation across national borders. We developed a biological measure of conservation value for six species of Pacific salmon (Oncorhynchus spp.) in catchments of the northern Pacific across Canada, China, Japan, Russia, and the United States. We based the measure on abundance and life-history richness and a model-based method that filled data gaps. Catchments with high conservation value ranged from California to northern Russia and included catchments in regions that are strongly affected by human development (e.g., Puget Sound). Catchments with high conservation value were less affected by agriculture and dams than other catchments, although only 1% were within biodiversity reserves. Our set of high-value areas was largely insensitive to simulated error, although classification remained uncertain for 3% of catchments. Although salmon face many threats, we propose they will be most likely to exhibit resilience into the future if a complementary mosaic of conservation strategies can be proactively adopted in catchments with healthy salmon populations. Our analysis provides an initial map of where these catchments are likely to be located.

Keywords: conservation planning, freshwater protected areas, landscape variables, northern Pacific, Oncorhynchus, salmon

Selección de Siti os de Captación en Toda el Área de Distribución para la Conservación de Salmón del Pacífico

Resumen: Los ecosistemas dulceacuícolas están declinando globalmente en cantidad, pero la falta de datos inhibe la identificación de áreas valiosas para la conservación afuera de fronteras nacionales. Desarrollamos una medida biológica del valor de conservación para seis especies de salmón del Pacífico (Oncorhynchus spp.) en áreas de captación en el Pacífico del norte en Canadá, China, Japón, Rusia y Estados Unidos. Basamos la medida en la abundancia y riqueza de la historia de vida y en un método basado en modelos que llenó vacíos de datos. Las áreas de captación con alto valor de conservación se extendieron desde California hasta Rusia e incluyeron áreas de captación en regiones que están fuertemente afectadas por el desarrollo humano (e.g., Puget Sound). Las áreas de captación con alto valor de conservación fueron menos afectadas por agricultura y presas que las demás áreas, aunque solo 1% estuvo dentro de reservas de biodiversidad. Nuestro conjunto de áreas de alto valor fue insensible al error simulado, aunque la clasificación permaneció incierta para 3% de las áreas de captación. Aunque los salmones enfrentan muchas amenazas, proponemos que es muy probable que exhiban resiliencia en el futuro si se puede adoptar un mosaico complementario de estrategias de conservación proactivamente en áreas de captación con poblaciones sanas de salmón. Nuestro análisis aporta un mapa inicial de la ubicación potencial de estas áreas.

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Palabras Clave: áreas dulceacuícolas protegidas, *Oncorhynchus*, Pacífico del norte, planificación de la conservación, salmón, variables de paisaje

Introduction

A major advance for conservation in recent decades has been the ability to target conservation efforts globally to areas where the impact will be greatest (Brooks et al. 2006). Nevertheless, aquatic ecosystems have lagged behind in this regard, because data are rarely available for international planning (Abell 2002; Brooks et al. 2006). Large-scale aquatic planning is particularly needed for Pacific salmon (*Oncorhynchus* spp.). More than 278 populations are extinct globally (Augerot 2005), and deteriorating aquatic habitat is a major driver of declines (National Research Council 1996).

To date, regional policies in reaction to declines—primarily catch restrictions and habitat restoration—have dominated salmon conservation (Rahr & Augerot 2006). Nevertheless, conservation is most successful when proactive interventions target viable populations before declines require socially divisive and expensive recovery (Jennings 2000). Proactive catchment conservation can include conservation areas, habitat-protection legislation, best-practices land management, maintenance of natural hydrology, and exclusion of non-native or hatchery species (Saunders et al. 2002). Proactively protecting a range-wide portfolio of catchments would be a long-term strategy for ensuring freshwater salmon production in the face of uncertain future climate and human activities (Mantua & Francis 2004; Rahr & Augerot 2006). Although salmon use many marine habitats, population viability models highlight freshwater conditions as more important to salmon persistence (Zabel et al. 2006), and freshwater habitat drives the life-history diversity that is critical for resilience (Mantua & Francis 2004). Nevertheless, freshwater conservation planning for salmon across their range has not yet been possible.

Conservation planning typically involves identification of areas of high conservation value, assessment of existing conservation areas, and identification of priorities (Groves et al. 2002). Conservation value in this context is based on the number and viability of species or ecosystems (Groves et al. 2002). The data for these analyses, however, contain uncertainty from measurement error, temporal variation, systematic bias, and other sources (Elith et al. 2002). Viability in particular has been difficult to assess, and proxies of uncertain accuracy, such as habitat integrity, are often used (Groves et al. 2002). Conservation-value uncertainty can increase the risk of misdirected conservation efforts but is rarely evaluated (Elith et al. 2002).

After identifying areas of high conservation value, planners often use gap analyses to assess existing conservation areas and to identify areas that are poorly protected (Jennings 2000; Scott et al. 2001). Gap analyses define conservation areas as those that do not allow extractive uses (Jennings 2000; Groves et al. 2002). The identification of high-conservation-value areas and gaps then guides the setting of conservation priorities when considered alongside economics, future threats, and feasibility (Groves et al. 2002).

Previous conservation planning for salmon evaluated extinction risk in limited regions, but was not intended to aid proactive conservation or to evaluate conservation areas (e.g., Nehlsen et al. 1991; COSEWIC 2004; Gustafson et al. 2007). Spurred by range-wide conservation efforts of the Wild Salmon Center, we designed our research to identify catchments with high conservation value for salmon and to answer the questions: (1) Do existing conservation areas of the North Pacific include catchments of high conservation value? (2) Is the degree of human influence a valid proxy for salmon conservation value? and (3) Is the set of high-conservation-value catchments sensitive to errors in the data? We did not identify conservation priorities or consider economics and nonbiological factors.

Methods

Study Area

The study area (Fig. 1) covered 74% of the range of six anadromous Pacific salmon species: coho (*Oncorhynchus kisutch*), chum (*O. keta*), chinook (*O. tschawytscha*), pink (*O. gorbuscha*), sockeye (*O. nerka*), and steelhead (*O. mykiss*) (Augerot 2005). We excluded catchments where occupied stream length data were not readily available, including Honshu (Japan), Korea, Mexico, Yukon Territory (Canada), and the Arctic.

To standardize river comparisons, we used Hydro1K catchments, which is the only available global data set (USGS 2003a). In our study area 80% of catchments were 1,000 to 10,000 km², but remaining catchments ranged from 92 to 44,600 km². We therefore tested for a catchment area effect in our results.

Conservation Value

We defined conservation value so as to estimate the number and viability of our 6 target species in each of 1046 catchments. We compiled published literature,
Figure 1. Quality of salmon abundance data used to calculate conservation value (CV), displayed as the percentage of species in each catchment for which data of a certain spatial scale were available: (a) data available at the scale of individual catchments or smaller and (b) data available that spanned multiple adjacent catchments (data records were allocated to individual catchments).

agency reports, other information, and expert judgment from 1950–2005 to estimate life-history richness and average annual wild salmon abundance. We focused on 1998–2005 because this period had the most consistent data. A list of sources is available from http://www.stanford.edu/~mpinsky/salmon/.

We ranked highest catchments that contained large populations and high life-history richness for our target species. We also weighted rare species more heavily (inverse to overall abundance and to the number of catchments occupied). Rarity-weighted indices ensure that areas with uncommon species are prioritized (Winston & Angermeier 1995). We used abundance and life-history richness as indicators of population viability within species with the assumption that larger and more diverse populations have a lower extinction risk (Winston & Angermeier 1995; Hilborn et al. 2003).

Therefore, our measure of conservation value (CV$_i$) was

$$ CV_i = \frac{1}{2} \sum_{j=1}^{s} \frac{A_{ij}}{\sum_{i=1}^{t} A_{ij}} + \frac{1}{2} \sum_{j=1}^{s} \frac{R_{ij}}{\sum_{i=1}^{t} R_{ij}}, $$

where $A_{ij}$ is the log abundance of species $j$ in catchment $i$, $R_{ij}$ is the life-history richness of species $j$ in catchment $i$, $s$ is total number of species, and $t$ is total number of catchments. We log-transformed abundance to homogenize variance. Indices similar to ours include the index of centers of density, a rarity-weighted metric of fish density (Winston & Angermeier 1995).

To delineate a set of catchments most likely to be of interest to conservation planners, we classified the highest scoring 20% as of high conservation value (HCV). This cutoff was arbitrary but informative for exploring patterns.

The input data contained uncertainty related to measurement error, temporal variation, and different abundance-estimation methods. We evaluated the effect of uncertainty on CV by producing 1000 replicate data sets after adding a random error term to each $A_{ij}$ and $R_{ij}$ value. With 10% probability, one life history was added or subtracted from $R_{ij}$. A normally distributed error term was added to $A_{ij}$ with an expectation of zero and a standard deviation equal to 50% of $A_{ij}$. Errors of 25–75% are common in salmon counts (Ruckelshaus et al. 2002).

Depending on the data available for a catchment, our abundance estimates came either directly from other researchers’ estimates of abundance or indirectly from estimates of spawning adults, catch, harvest rates, or multiple-regression equations we developed to predict abundance. This database, with citations, is available from http://www.stanford.edu/~mpinsky/salmon/.
To convert catch and escapement to abundance, we used one of the following equations

\[ A = W_c C + W_e E \]  
(2)

\[ A = W_c C / H, \]  
(3)

or

\[ A = W_e E / (1 - H) \]  
(4)

where \( A \) is abundance, \( W_c \) is percent wild fish in the catch, \( C \) is fisheries catch, \( W_e \) is percent wild salmon among spawning adults, \( E \) is spawning adults (escapement), and \( H \) is harvest rate. We assumed harvest rates were similar for the same species in nearby catchments. In rivers with salmon hatcheries, we counted only fish spawned in the wild. Available data dictated our selection of Eqs. 2, 3, or 4. When we had a choice, we chose the equation that used data with the finest spatial resolution.

We included catch and escapement in our abundance estimate because we focused on freshwater habitat, and abundance is the most complete measure of freshwater productivity. In addition, abundance does not vary directly with fishing effort, as opposed to either catch or escapement. Finally, data gaps precluded use of either catch or escapement exclusively across the study area.

Estimates of abundance were not available for all catchments and, where available, an estimate’s spatial extent did not always match our catchments. These possibilities presented three challenges: data spanned a portion of the area occupied by a species within a catchment; data were unavailable; and data had an area of inference that spanned multiple catchments.

Where data spanned part of a catchment, we expanded abundance across the entire catchment proportional to occupied stream length:

\[ A = \frac{L_{\text{unknown}}}{L_{\text{known}}} A_{\text{known}} + A_{\text{known}}, \]  
(5)

where \( A \) is abundance of a species, \( L_{\text{unknown}} \) is occupied stream length of that species in the section of catchment with unknown abundance, \( L_{\text{known}} \) is occupied stream length in the section with known abundance, and \( A_{\text{known}} \) is known abundance.

For catchments with no data, we created multivariate regression models to extrapolate abundance from landscape variables. Variables included occupied stream length, elevation, relief, distance from coast, and catchment area (Table 1). Perimeter and area of occupied lakes were also included for sockeye. Because these models relied on occupied stream length, we could not extrapolate outside our study area.

For cases where a record spanned multiple catchments (e.g., many ocean catch records), we allocated abundance to individual catchments. The allocation was
proportional to predicted abundance from the extrapolation models, but was scaled so the sum across catchments was equal to the overall abundance record:

$$A_j = \frac{\sum_{i=1}^{c} A_{\text{predicted}, i} A_{\text{known}, 1 \rightarrow c}}{A_{\text{predicted}, j}}$$

where $A_j$ is abundance of a species in catchment $j$, $A_{\text{predicted}, i}$ is abundance predicted by our multivariate regression models for catchment $i$, and $A_{\text{known}, 1 \rightarrow c}$ is overall abundance recorded for the set of catchments $1$ through $c$ (of which catchment $j$ is a member). In the Klamath and Sacramento rivers, we allocated abundance evenly across catchments because occupied stream length was not available from which to predict abundance.

We caution that our abundance estimates come from many different sources in which a wide variety of methods were used, so they are rough approximations rather than precise estimates. This is the nature of data available for wide-scale conservation planning for salmon. We use simulated errors (see above) to evaluate the effects of this uncertainty on our comparisons among catchments.

Migration timing is a key life-history trait because it facilitates temporal isolation between populations and allows divergence at other traits (Quinn et al. 2000). We defined life-history richness per catchment per species so that it ranged from 0 to 4, depending on whether fall, winter, spring, and/or summer migration timings were present. Richness for pink salmon ranged from 0 to 2, depending on whether odd- or even-year runs were present.

Conservation Areas

For our gap analysis, we assumed conservation areas protected a catchment if they covered over 90% by area. We defined conservation areas as International Union for Conservation of Nature (IUCN) category I or II biodiversity reserves (WDPA Consortium 2006). Conservation may occur in other categories, but categories I and II are solely for conservation and research. We chose this narrow definition because aquatic ecosystems are often the first affected when management becomes less strict (Saunders et al. 2002). Our 90% threshold was motivated by research indicating that aquatic ecosystems degrade when 10% or more of a catchment has been altered dramatically (e.g., into impervious surfaces) (Arnold & Gibbons 1996; Beach 2002). We also considered partially protected basins (50–90% coverage).

To test whether HCV catchments had a different proportion in conservation areas than did non-HCV catchments, we used a two-tailed binomial test. Ideally, HCV catchments would have a higher proportion protected.

Human Influence

Conversion of land to agricultural, urban, or timber uses degrades salmon habitat (Pess et al. 2002); dams impede migration (McClure et al. 2003); and hatchery salmon compete with wild salmon (Levin & Williams 2002). Conservation areas can prevent some of these impacts. Therefore, we used linear regression to investigate the relationship between CV and agriculture, urbanization, dams, hatcheries, and conservation areas (Table 1). A timber data set for our study area is not yet available. We also tested whether human influence declined with latitude because this would be the simplest proxy if successful.

To estimate dam impacts, we calculated the percentage of stream kilometers within each catchment located above dams, weighted by cumulative impedance to fish passage. Impedance values were 0.1 (partially passable dams) or 1 (impassable dams), and impedance values were accumulated with each additional dam encountered up to a maximum of 1. We included dams >10 m and so excluded small impediments, which were numerous in some catchments.

Statistical and GIS Methods

To create abundance models, we used 2 multiple regression approaches: ordinary least squares (OLS) and generalized least squares (GLS) with exponential, spatially autocorrelated errors (Dormann et al. 2007). Latitude and longitude were used as spatial covariates in GLS errors. Ignoring spatial autocorrelation in regression can cause excessive type I errors, lead to erroneous inclusion of terms, and cause estimation errors for model coefficients. We simplified models with Akaike’s information criterion (AIC) and step-wise removal of terms from a full model that included all independent variables. To explore relationships between CV and human influence, we used multiple regression methods (OLS and GLS) and single regressions between CV and human influence variables.

We used R 1.14 (R Foundation for Statistical Computing, Vienna) with the nlme package (Pinheiro et al. 2005) for statistical analysis. Geographic calculations were executed in ArcGIS 9.2 (ESRI, Redlands, California) with a Lambert equal area projection.

Results

Models of Salmon Abundance

Salmon abundance data were available in many regions, although data were sparser in Russia and spatial resolution varied between regions (Fig. 1). For example, many records in Alaska, Russia, and Japan spanned multiple catchments (Fig. 1b).

Models for species abundance were highly significant, and the OLS models explained 78–92% of variability
Table 2. Models of salmon abundance calculated by ordinary least squares or by generalized least squares.*

<table>
<thead>
<tr>
<th>Species (r², p)</th>
<th>Ordinary least squares</th>
<th>Generalized least squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>variable</td>
<td>coefficient</td>
</tr>
<tr>
<td>Chinook</td>
<td>intercept</td>
<td>-0.00264</td>
</tr>
<tr>
<td>(0.812, &lt;0.00001)</td>
<td>STR:AK 0.683</td>
<td>2.66E-82</td>
</tr>
<tr>
<td></td>
<td>STR:BC 0.653</td>
<td>2.00E-122</td>
</tr>
<tr>
<td></td>
<td>STR:AS 0.453</td>
<td>5.56E-25</td>
</tr>
<tr>
<td></td>
<td>STR:WOI 0.546</td>
<td>1.56E-70</td>
</tr>
<tr>
<td></td>
<td>AR 0.155</td>
<td>0.0132</td>
</tr>
<tr>
<td></td>
<td>REL 0.00106</td>
<td>0.0349</td>
</tr>
<tr>
<td></td>
<td>DST -0.113</td>
<td>0.00839</td>
</tr>
<tr>
<td>Chum</td>
<td>intercept</td>
<td>0.484</td>
</tr>
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<td>(0.916, &lt;0.00001)</td>
<td>STR:AK 0.929</td>
<td>1.44E-100</td>
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<td></td>
<td>STR:BC 0.982</td>
<td>3.86E-118</td>
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<td></td>
<td>STR:AS 0.63</td>
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</tr>
<tr>
<td></td>
<td>STR:WOI 0.526</td>
<td>2.85E-21</td>
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<td></td>
<td>AR 0.125</td>
<td>0.125</td>
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<tr>
<td></td>
<td>REL 0.00092</td>
<td>0.0852</td>
</tr>
<tr>
<td></td>
<td>DST -0.0992</td>
<td>0.079</td>
</tr>
<tr>
<td>Coho</td>
<td>intercept</td>
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<td>(0.83, &lt;0.00001)</td>
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<td></td>
<td>STR:BC 0.86</td>
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<td></td>
<td>STR:AS 0.434</td>
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</tr>
<tr>
<td></td>
<td>STR:WOI 0.335</td>
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<tr>
<td></td>
<td>REL 0.000902</td>
<td>0.0852</td>
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<tr>
<td></td>
<td>DST -0.0992</td>
<td>0.079</td>
</tr>
<tr>
<td>Pink</td>
<td>intercept</td>
<td>1.97</td>
</tr>
<tr>
<td>(0.853, &lt;0.00001)</td>
<td>STR:AK 0.916</td>
<td>4.41E-81</td>
</tr>
<tr>
<td></td>
<td>STR:BC 0.933</td>
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<td></td>
<td>STR:AS 0.853</td>
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<td></td>
<td>STR:WOI 1</td>
<td>1.66E-41</td>
</tr>
<tr>
<td></td>
<td>AR 0.152</td>
<td>0.0675</td>
</tr>
<tr>
<td></td>
<td>REL 0.00121</td>
<td>0.0351</td>
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<tr>
<td></td>
<td>DST -0.272</td>
<td>0.000102</td>
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<td>Sockeye</td>
<td>intercept</td>
<td>1.32</td>
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<td>4.63E-38</td>
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<td></td>
<td>STR:BC 0.71</td>
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<tr>
<td></td>
<td>STR:AS 0.634</td>
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</tr>
<tr>
<td></td>
<td>STR:WOI 0.28</td>
<td>1.41E-05</td>
</tr>
<tr>
<td></td>
<td>LKAR 0.204</td>
<td>7.69E-16</td>
</tr>
<tr>
<td>Steelhead</td>
<td>intercept -1.37</td>
<td>9.08E-05</td>
</tr>
<tr>
<td>(0.778, &lt;0.00001)</td>
<td>STR:BC 0.462</td>
<td>8.41E-162</td>
</tr>
<tr>
<td></td>
<td>STR:AS 0.616</td>
<td>1.87E-20</td>
</tr>
<tr>
<td></td>
<td>STR:WOI 0.439</td>
<td>2.35E-102</td>
</tr>
<tr>
<td></td>
<td>AR 0.187</td>
<td>2.17E-05</td>
</tr>
<tr>
<td></td>
<td>ELEV 0.000227</td>
<td>0.0717</td>
</tr>
<tr>
<td></td>
<td>REL -0.00135</td>
<td>0.00129</td>
</tr>
</tbody>
</table>

*The r² and p values refer to ordinary least-squares models. See Table 1 for variable codes.

(Tables 2). Occupied stream length was a significant, positive term in all models, while occupied lake area was also significant and positive for sockeye. Each model retained at least one landscape variable, but the variables differed between models. When included, catchment area, elevation, and relief were positive terms, whereas distance from coast was negative. We lacked sufficient data to fit a term for steelhead-occupied stream length in Alaska (STR:AK) and therefore did not extrapolate steelhead abundance in Alaska.

The OLS and the GLS models estimated similar magnitudes and signs of coefficients (Table 2). For all species the abundances predicted by OLS and GLS models were significantly correlated (Pearson r > 0.88, p < 10⁻¹²). Because GLS accounts for spatial autocorrelation, we used the GLS models to extrapolate and allocate abundance.

Location of Catchments of High Conservation Value

Catchments had CVs ranging from 0 to 0.021 (median 0.0046). The HCV catchments clustered at mid-latitudes, with a majority falling between 50°N and 60°N (Fig. 2). Some HCV catchments were located as far south as 5°N.
as northern California (40°N), whereas others were in highly developed areas such as Puget Sound and the Columbia River. Japan and China had no HCV catchments, whereas Russia had 55, Canada had 52, Alaska had 72, and the contiguous United States had 29 (14%, 33%, 32%, and 14% of the latter 4 regions’ catchments, respectively). Most HCV catchments were near the coast. Kamchatka, coastal British Columbia, and Bristol Bay stood out as dense HCV aggregations.

The set of HCV catchments was not highly sensitive to simulated error (Fig. 2). Of the 208 catchments originally classified as HCV, 17 (8%) were incorrectly reclassified as non-HCV in >25% of simulations. In addition, 14 non-HCV catchments (1.7%) were incorrectly reclassified in >25% of simulations. We considered these 31 catchments (3%) borderline between HCV and non-HCV.

To remove area effects, we ranked catchments by their residuals after regressing CV against catchment area. This new HCV set was 93.4% identical to our original set.

Conservation Areas in High-Conservation-Value Catchments

Only 2.5% of catchments were protected by conservation areas (>90% coverage), whereas an additional 2.9% were partially protected (50–90% coverage). Most protected catchments were in the United States (73%), with 15% in Russia and 12% in Canada. Of HCV catchments, 1.4% were protected and 6.3% were partially protected. We could not reject the null hypothesis that HCV and non-HCV catchments had an equal proportion protected ($p = 0.39$).

Steelhead and chum were the least protected by conservation areas, with only 0.05–1.5% of total abundance included within protected catchments (Table 3). Sockeye were the most protected, with 5% of sockeye catchments and 4% of abundance located in protected catchments.

Correlation of Conservation Value to Human Influence

Across our study area, human impacts were consistently lowest at latitudes above 55°N (Fig. 3, Spearman correlation with latitude: AG $\rho = -0.72$, $p = 4 \times 10^{-166}$, UR $\rho = -0.45$, $p = 2 \times 10^{-54}$, DM $\rho = -0.57$, $p = 1 \times 10^{-90}$, HCH $\rho = -0.42$, $p = 3 \times 10^{-36}$). Percentage of each catchment within conservation areas showed

Table 3. Protected-area gap analysis for catchments of the northern Pacific expressed as percentage of all catchments, of high-conservation-value (HCV) catchments, or of salmon contained within national protected areas (IUCN categories I and II).*

<table>
<thead>
<tr>
<th>Species</th>
<th>Protected area coverage (% of catchment)</th>
<th>protected (&gt;90)</th>
<th>partially protected (50–90)</th>
<th>unprotected (&lt;50)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All catchments</td>
<td></td>
<td>2.5</td>
<td>2.9</td>
<td>95</td>
</tr>
<tr>
<td>HCV catchments</td>
<td></td>
<td>1.4</td>
<td>6.5</td>
<td>92</td>
</tr>
<tr>
<td>Chinook presence</td>
<td></td>
<td>2.5</td>
<td>4.8</td>
<td>93</td>
</tr>
<tr>
<td>abundance</td>
<td></td>
<td>1.6</td>
<td>6.9</td>
<td>92</td>
</tr>
<tr>
<td>Chum presence</td>
<td></td>
<td>1.7</td>
<td>3.3</td>
<td>95</td>
</tr>
<tr>
<td>abundance</td>
<td></td>
<td>1.4</td>
<td>4.5</td>
<td>94</td>
</tr>
<tr>
<td>Coho presence</td>
<td></td>
<td>4.0</td>
<td>4.8</td>
<td>91</td>
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<tr>
<td>abundance</td>
<td></td>
<td>2.9</td>
<td>18</td>
<td>79</td>
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<tr>
<td>Pink presence</td>
<td></td>
<td>1.7</td>
<td>3.8</td>
<td>95</td>
</tr>
<tr>
<td>abundance</td>
<td></td>
<td>3.1</td>
<td>10</td>
<td>87</td>
</tr>
<tr>
<td>Sockeye presence</td>
<td></td>
<td>5.0</td>
<td>5.6</td>
<td>89</td>
</tr>
<tr>
<td>abundance</td>
<td></td>
<td>4.5</td>
<td>17</td>
<td>78</td>
</tr>
<tr>
<td>Steelhead presence</td>
<td></td>
<td>2.0</td>
<td>3.6</td>
<td>94</td>
</tr>
<tr>
<td>abundance</td>
<td></td>
<td>0.05</td>
<td>2.1</td>
<td>98</td>
</tr>
</tbody>
</table>

*Catchments are classified according to whether protected areas cover >90%, 50–90%, or <50% of a catchment’s area. Species are summarized by presence or absence and by total abundance.
a weaker, negative correlation to latitude \((p = -0.14, \ p = 8 \times 10^{-6})\), even though catchments with the largest percent protected were at higher latitudes (Fig. 3).

Regressions between CV and single human influence variables had low explanatory power \((r^2 < 0.1, \ \text{Fig. 4})\), although agriculture \((p = 3 \times 10^{-25})\) and dams \((p = 2 \times 10^{-12})\) were negatively correlated to CV. Urbanization was negatively but insignificantly correlated to CV. Variance in CV decreased with greater influence from agriculture and dams; thus, highly transformed catchments were almost uniformly of low CV, whereas lightly influenced catchments had variable CV. Percentage of catchment protected and hatcheries were positively correlated to CV \((p = 3 \times 10^{-10} \ \text{and} \ p = 3 \times 10^{-22}, \ \text{respectively})\). For comparison, catchment area was positively correlated to CV \((p = 8 \times 10^{-7})\), but had lower explanatory power \((r^2 = 0.023)\) than all human influence variables except urbanization.

The OLS model explained 28% of the variation in CV, and AIC retained all terms, leaving the reduced model as

\[
CV = 0.0061 - 0.0077AG + 0.0053UR - 0.0031DM + 0.0020PRT + 0.0044HCH. \quad (7)
\]

All terms were significant at \(p < 10^{-5}\), except for urbanization \((p = 0.059)\). The reduced GLS model was

\[
CV = 0.0060 - 0.0023DM + 0.00056PRT + 0.0014HCH \quad (8)
\]

because AIC removed the urbanization and agriculture terms. This removal suggests the OLS urbanization and agriculture terms were artifacts of spatially autocorrelated errors. The remaining terms in the GLS model (dams, hatcheries, and percent protected) had the same signs as in the OLS model. All terms in the GLS model were significant at \(p < 10^{-8}\), except percent protected \((p = 0.15)\).

For comparison we also fitted models after removing catchment-area effects (models were fit to residuals after a linear regression of CV against area). The OLS and GLS coefficients were of the same sign and similar magnitude to the models fit without removing area effects.

**Discussion**

Using a data set of abundance and life-history diversity coupled with abundance models and a metric of...
population viability, we identified catchments across the North Pacific that are likely to contain highly viable populations of salmon. This set of catchments can provide the biological information needed to choose conservation priorities for proactive salmon conservation. Existing conservation areas contained few high-value catchments. As expected, higher conservation value was associated with conservation areas and low habitat transformation, but was unexpectedly associated with greater hatchery influence. Latitude was a poor proxy for conservation value, although measures of human influence were somewhat better.

Existing Conservation Areas

Existing conservation areas have been criticized for inadequately capturing biodiversity, but have rarely been analyzed across multiple countries. In an analysis of terrestrial vertebrates, Rodrigues et al. (2004) found that global conservation areas capture more species than a randomly distributed network. Factors driving this pattern could include designation of conservation areas in sites with higher species richness and a higher loss of biodiversity outside conservation areas (Bruner et al. 2001; Rodrigues et al. 2004). Countering this pattern are tendencies to designate conservation areas for nonbiodiversity reasons (e.g., recreation or scenery) and away from economically valuable locations (Pressey 1994).

Why are conservation areas less effectively sited for salmon? In part, the conflict between human development and habitat is particularly acute for salmon, potentially forcing conservation areas into less ideal locations. For coho, Burnett et al. (2007) found the least protective land management and the highest threats in the most productive habitat (low-elevation floodplains), whereas conservation areas are more common in less productive headwaters.

At the same time, few conservation areas are created explicitly for aquatic ecosystems or salmon (Saunders et al. 2002; Abell et al. 2007). Without formal consideration of salmon in conservation-area designation, few conservation areas will be located on valuable habitat, particularly where it conflicts with human development.

Existing conservation areas may not effectively mitigate threats and prevent salmon declines. Salmon require a connected network of habitats that exceeds the extent of most conservation areas. In some tributaries of the Columbia River, wilderness designation (IUCN category I) prevents threats from urbanization and agriculture, but cannot mitigate the extensive system of dams below these catchments (McClure et al. 2003). Threats to salmon also propagate downstream as hydrologic alterations (Poff et al. 2007) as well as laterally from hill slopes via overland flow. For example, roads are commonly allowed in multiple-use conservation areas, but roads increase sedimentation and can degrade freshwater habitats (Saunders et al. 2002). In addition, conservation areas do not prevent effects from climate change in marine or freshwater habitats, including delayed near-shore upwelling and warmer stream temperatures (Logerwell et al. 2003; Mohseni et al. 2003). Salmon, however, are...
most likely to show resilience to climate change and poor ocean conditions in areas where other stresses are minimal, such as within full-catchment conservation areas (Mantua & Francis 2004).

Our results suggest that existing conservation areas do not protect catchments important to Pacific salmon. Increased attention to salmon during conservation-area creation and management would begin to reverse this trend. In addition, efforts outside formal conservation areas will likely be important to salmon, including best-practices land management, maintenance of natural hydrology, and exclusion of hatcheries.

**Human Influence as Proxy for Conservation Value**

Because the northern half of our study area contained the catchments least affected by humans, a focus only on these northern latitudes (e.g., northern Russia and Alaska) may appear to be a reasonable strategy to target the most viable salmon populations. Our results caution against this simplistic approach. We found HCV catchments distributed in both the northern and southern latitudes of the North Pacific, including in regions heavily affected by human activities (e.g., the Columbia River and Puget Sound). Regions such as mainland Russian Far East that are less affected by humans did not rank as highly because species richness among our focal species was lower. Inclusion of masu salmon (O. masou), present only in Asia, would likely move some HCV catchments to Russia or Japan.

At finer spatial scales than our analysis, the negative impacts of agriculture and dams on salmon abundance and diversity are well understood (National Research Council 1996). Our data show these effects apply generally throughout the salmon range. In particular, the low variance of CV we found at high levels of land transformation supports this conclusion.

The negative impacts of hatcheries are also well understood at fine scales. For example, research in the Snake River shows a negative association between hatchery releases and wild chinook and steelhead survival (Levin et al. 2001; Levin & Williams 2002). Nevertheless, these patterns are not apparent in our data. We believe two factors may explain this discrepancy. First, the countries with the highest abundance and diversity of salmon (Canada and the United States) also have many hatcheries. Hatchery effects may not have overcome biogeographic factors that also drive salmon abundance and diversity.

Second, we excluded hatchery fish by counting fish born in the wild. Nevertheless, this method does not exclude second-generation hatchery fish born to strays. We may therefore overestimate wild abundance near hatcheries. For 12 Oregon steelhead populations, 0–60% of spawning fish are of hatchery origin (Chilcote 2003). Although wild-spawning hatchery salmon reduce population productivity (Chilcote 2003), overall abundance may still increase if the increase in spawners compensates for decreased productivity. The extent to which hatcheries artificially enhance run sizes through strays has not been examined carefully, but the phenomenon may be widespread.

Although our model for CV left substantial variability unexplained, an $r^2$ of 20–40% is typical of other attempts to explain salmon responses to catchment variables, even across much smaller geographies (Pess et al. 2002). Nevertheless, the relatively low explanatory power of our CV model suggests that human influence is of limited utility as a proxy for salmon conservation value. Instead, we suggest that CV be measured from biological metrics (e.g., abundance and diversity), including when applied to other freshwater species.

An exception may be those catchments highly transformed by agriculture and dams. These are unlikely to be valuable for conservation, as shown by their low CV and low variance of CV. We caution, however, that this conclusion stems in part from the particular scale of our analysis. At a wider scale, regions that are highly transformed—such as Puget Sound and California—still contain catchments that are valuable. Historically, conservation areas have been designated in remote regions both because they are pristine and because it is politically less difficult to do so. Nevertheless, salmon conservation will likely need to take place not only in those regions that are remote, but also those where the conflicting needs of humans and salmon must be negotiated rather than avoided.

**Limitations**

Although we extend existing conservation-value indices by including life-history richness, we excluded many important factors that affect viability. These factors include climate change and interbreeding with hatchery salmon (Levin & Williams 2002). Our approach should also not be confused with data-intensive population viability analyses that attempt to quantitatively predict future extinction risk (Ratner et al. 1997).

At the coarse scale of our analysis, interpretation of our results must be cautious. Our life-history data may suffer from omission errors, particularly in regions with little research. For example, low life-history richness in Russia may result from evolutionary forces related to geomorphology and climate (Montgomery 2000), but additional surveys are required to verify this is not an artifact of sparse sampling.

Our abundance data also contain uncertainty, both from field surveys and from our analysis. Although the locations of HCV catchments appear robust to randomly distributed errors, error may also vary nonrandomly across our study area. For example, error varies between field survey methods (Jones et al. 1998), and survey methods vary between jurisdictions. We expect more error in
remote regions and those without large fishing industries. Error estimation in salmon surveys remains rare, making a detailed error assessment difficult.

Implications

Our range-wide set of high conservation value catchments is the first for salmon, complementing local and regional efforts toward salmon recovery and conservation (Allendorf et al. 1997; COSEWIC 2004; Good et al. 2005; Bartz et al. 2006). Our analysis highlights many of the most diverse and abundant salmon populations across the northern Pacific and so can guide investment in proactive conservation. For example, the Wild Salmon Center will use these results to plan a distributed network of salmon rivers on which to focus conservation efforts.

As salmon conservation becomes international, we recommend increased protection of highly viable and resilient salmon populations before declines begin. A mosaic of strategies on the ground will be needed, including conservation areas, riparian buffer zones, management for natural hydrology and connectivity, risk-averse catch management, and low-impact land uses consistent with ecosystem health. Although salmon face many threats, we propose these species will be most likely to exhibit resilience into the future if this new level of integrated conservation strategies can be adopted in a distributed set of healthy freshwater ecosystems that support abundant and diverse salmon populations.

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Literature Cited


Levin, P. S., R. W. Zabel, and J. G. Williams. 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries...


