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Abstract:

Freshwater ecosystems are declining in quality globally, but a lack of data inhibits the identification of areas valuable for conservation across national borders. We developed a biological measure of conservation value for 6 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, though 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 that 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.

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). However, 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). However, 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 in salmon persistence (Zabel et al. 2006), and freshwater habitat drives the life-history diversity that is critical for resilience (Mantua & Francis 2004). However, 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 answerthe 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 6 anadromous Pacific salmon species: coho (*Oncorhynchus kisutch*), chum (*O. keta*), chinook (*O. tshawytscha*), 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 km^2, but remaining catchments ranged from 92 to 44,600 km^2. 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, agency reports, other information, and expert judgment from 1950-2005 to estimate life-history richness and average annual wild salmon abundance. We focused on 1998-2005because 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 and 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

$$\mathrm{CV}_i = \frac{1}{2}\sum_{j=1}^{s}\frac{A_{ij}}{\sum_{i=1}^{t} A_{ij}} + \frac{1}{2}\sum_{j=1}^{s}\frac{R_{ij}}{\sum_{i=1}^{t} R_{ij}}, \quad (1)$$

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 of 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

$$A = W_c C + W_e E \quad (2),$$

$$A = W_c C / H \quad (3), \text{ or}$$

$$A = W_e E / (1 - H) \quad (4),$$

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 3 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:

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

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

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

(6)

where A_j is abundance of a species in catchment j, $A_{\text{predicted},i}$ is the abundance predicted by our multivariate regression models for catchment i, and $A_{known,i \rightarrow c}$ 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 0-4, depending on whether fall, winter, spring, and/or summer migration timings were present. Richness for pink salmon ranged from 0-2, 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 consideredpartially 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 2-tailed binomial test. Ideally, HCV catchments would have a higher proportion protected.

Human influence

Conversion of land to agricultural, urban, or timber 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 1.0. 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% to 92% of variability (Table 2). Occupied stream length was a significant, positive term in all models, whereas occupied lake area was 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.

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 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 were 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 inHigh-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). 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 ρ= -0.72, $p = 4\text{x}10^{-166}$; UR ρ = -

0.45, p = 2x10^{-54}; DM ρ = -0.57, p = 1x10^{-90}; HCH ρ = -0.42, p = 3x10^{-36}). Percentage of each catchment within conservation areas showed a weaker, negative correlation to latitude (ρ= -0.14, p = 8x10^{-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 ($r^2 < 0.1$, Fig. 4), although agriculture (p = 3x10^{-25}) and dams (p = 2x10^{-12}) were negatively correlated to CV. Urbanization was negatively but insignificantly correlated to CV. Variance in CV decreased with 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 = 3x10^{-10} and p = 3x10^{-22}, respectively). For comparison, catchment area was positively correlated to CV (p = 8x10^{-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: **Error! Reference source not found.**:

$$CV = 0.0061 - 0.0077\text{AG} + 0.0053\text{UR} - 0.0031\text{DM} + 0.0020\text{PRT} + 0.0044\text{HCH}$$

(7).

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

$$CV = 0.0060 - 0.0023\text{DM} + 0.00056\text{PRT} + 0.0014\text{HCH} \qquad (8),$$

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 nonconservation 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 nearshore 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. However, these patterns are not apparent in our data. We believe 2 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. However, 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). However, 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 fine scale of our analysis. At a wider scale, regions that are highly transformed – such as Puget Sound and California – 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. However, 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 proactive 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

Abell, R. 2002. Conservation biology for the biodiversity crisis: a freshwater follow-up. Conservation Biology 16:1435-1437.

Abell, R., J. D. Allan, and B. Lehner. 2007. Unlocking the potential of protected areas for freshwaters. Biological Conservation 134:48-63.

Allendorf, F. W., D. Bayles, D. L. Bottom, K. P. Currens, C. A. Frissell, D. Hankin, J. A. Lichatowich, W. Nehlsen, P. C. Trotter, and T. H. Williams. 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology 11:140-152.

Arnold, C. L., Jr., and C. J. Gibbons. 1996. Impervious surface coverage: the emergence of a key environmental indicator. Journal of the American Planning Association 62:243-258.

Augerot, X. 2005. Atlas of Pacific Salmon: the first map-based status assessment of salmon in the north Pacific. University of California Press, Berkeley.

Bartz, K. K., K. M. Lagueux, M. D. Scheuerell, T. Beechie, A. D. Haas, and M. H. Ruckelshaus. 2006. Translating restoration scenarios into habitat conditions: an initial step in evaluating recovery strategies for Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 63:1578-1595.

Beach, D. 2002. Coastal sprawl: the effects of urban design on aquatic ecosystems in the United States. Pew Oceans Commission, Arlington, Virginia.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, and A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. Science 313:58-61.

Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. da Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. Science 291:125-128.

Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecological Applications 17:66-80.

Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 60:1057-1067.

COSEWIC. 2004. Canadian species at risk, November 2004. Committee on the status of endangered wildlife in Canada.

Dormann, C. F., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609-628.

Elith, J., M. A. Burgman, and H. M. Regan. 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distributions. Ecological Modeling 157:313-329.

European Commission Joint Research Centre (ECJRC). 2004. Global Land Cover 2000 database: Global Product v1.1. ECJRC, Ispra, Italy. Available from http://www-tem.jrc.it/glc2000 (accessed September 2005).

Good, T. P., R. Waples, and P. Adams. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Tech. Memo., NMFS-NWFSC-66, 598 p. U.S. Department of Commerce, Seattle, Washington.

Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V.

Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: putting conservation science into practice. BioScience 52:499-512.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009-1020.

Harper, D. J., and J. T. Quigley. 2005. A comparison of the areal extent of fish habitat gains and losses associated with selected compensation projects in Canada. Fisheries 30:18-23.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the United States of America 100:6564-6568.

Jennings, M. D. 2000. Gap analysis: concepts, methods, and recent results. Landscape Ecology 15:5-20.

Jones, E. L., III, T. J. Quinn II, and B. W. Van Alen. 1998. Observer accuracy and precision in aerial and foot survey counts of pink salmon in a southeast Alaska stream. North American Journal of Fisheries Management 18:832-846.

Kalashnikov, V. D. 1997. Electric power industry of the Russian Far East: status and prerequisites for cooperation in north-east Asia. Workshop on the Future of Regional Electric Power Grids in Northeast Asia. Khabarovsk Economic Research Institute, Far Eastern Branch of Russian Academy of Sciences, Honolulu, Hawaii.Levin, P. S., and J. G. Williams. 2002. Interspecific effects of artificially propagated fish: an additional conservation risk for salmon.

Conservation Biology 16:1581-1587.

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 with threatened salmon. Proceedings of the Royal Society of London Series B-Biological Sciences 268:1153-1158.

Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554-568.

Mantua, N. J., and R. C. Francis. 2004. Natural climate insurance for Pacific Northwest salmon and salmon fisheries: finding our way through the entangled bank. Pages 127-140 in E. E. Knudsen and D. MacDonald, editors. Fish in our future? Perspectives on fisheries sustainability. American Fisheries Society, Bethesda, Maryland.

McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. E. Jordan. 2003. A large-scale, multispecies status, assessment: anadromous salmonids in the Columbia River Basin. Ecological Applications 13:964-989.

Mohseni, O., H. G. Stefan, and J. G. Eaton. 2003. Global warming and potential changes in fish habitat in U.S. streams. Climatic Change 59:389-409.

Montgomery, D. R. 2000. Coevolution of the Pacific salmon and Pacific rim topography. Geology 28:1107-1110.

National Research Council 1996. Upstream: salmon and society in the Pacific Northwest.

National Academy Press, Washington, District of Columbia.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific Salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16:4-21.

Newell, J. 2004. The Russian Far East: a reference guide for conservation and development. Daniel and Daniel Publishers, McKinleyville, California.

NIMA (National Imagery and Mapping Agency). 2000. Vector map level 0 (VMAP0), edition 003. NIMA, Washington, District ofColumbia. Available from http://geoengine.nga.mil (accessed 1 July2004).

Pess, G. R., D. R. Montgomery, E. A. Steel, R. E. Bilby, B. E. Feist, and H. M. Greenberg. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 59:613-623.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2005. nlme: linear and nonlinear mixed effects models. R package version 3.1-66. R Foundation for Statistical Computing, Vienna.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104:5732-5737.

Pressey, R. L. 1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems? Conservation Biology 8:662-668.

Quigley, J. T., and D. J. Harper. 2006. Compliance with Canada's Fisheries Act: a field audit of habitat compensation projects. Environmental Management 37:336-350.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. Evolution 54:1372-1385.

Rahr, G., and X. Augerot. 2006. A proactive sanctuary strategy to anchor and restore high-priority wild salmon ecosystems. Pages 465-489 in R. T. Lackey, D. H. Lach and S. L. Duncan, editors. Salmon 2100: the future of wild Pacific salmon. American Fisheries Society, Bethesda, Maryland.

Ratner, S., R. Lande, and B. B. Roper. 1997. Population viability analysis of spring chinook salmon in the South Umpqua River, Oregon. Conservation Biology 11:879-889.

Rodrigues, A. S. L., et al. 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428:640-643.

Ruckelshaus, M. H., P. S. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific Salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33:665-706.

Saunders, D. L., J. J. Meeuwig, and A. C. J. Vincent. 2002. Freshwater protected areas: strategies for conservation. Conservation Biology 16:30-41.

Scott, J. M., R. J. F. Abbitt, and C. R. Groves. 2001. What are we protecting? The United States conservation portfolio. Conservation Biology in Practice 2:18-19.

USACE (U.S. Army Corps of Engineers). 2006. National inventory of dams. USACE, Alexandria, Virginia. Available from http://crunch.tec.army.mil/nidpublic/webpages/nid.cfm (accessed March 2006).

USGS (U.S. Geological Survey). 2003a. Hydro1k documentation. USGS, Sioux Falls, South Dakota. Available from http://lpdaac.usgs.gov/gtopo30/hydro/readme.asp (accessed April 2006).

USGS (U.S. Geological Survey). 2003b. SRTM30 V1 Documentation. USGS, Sioux Falls, South Dakota. Available from ftp://e0srp01u.ecs.nasa.gov/srtm/version1/SRTM30 (accessed September 2005).

WDPA Consortium (World Database on Protected Areas). 2006. World database on protected areas 2006. International Union for Conservation of Nature and UN Environment Programme World Conservation Monitoring Centre, Cambridge. .

Winston, M. R., and P. L. Angermeier. 1995. Assessing conservation value using centers of population density. Conservation Biology 9:1518-1527.

Zabel, R. W., M. D. Scheuerell, M. M. McClure, and J. G. Williams. 2006. The interplay between climate variability and density dependence in the population viability of chinook salmon. Conservation Biology 20:190-200.

Table 1. Variables used to calculate conservation value of salmon within catchments (biological), to extrapolate abundance of salmon within catchments (environmental), and for correlation against conservation value (human influence).

Variable	Description	Transformation	Sources[a]
Biological			
A	wild adult abundance, by species	log(x+1)	3,4
R	Life-history richness (number of run timings), by species	none	3,4
Environmental			
STR:region[b]	occupied stream length, by species (m)[b]	log(x+1)	3, 4
AR	catchment area (km^2)	log(x+1)	1
DST	distance to coast from catchment centroid (m)	log(x+1)	1
ELEV	mean elevation (m)	none	5
REL	relief (standard deviation of elevation) (m)	none	5
LKAR[c]	area of occupied lakes (m^2)	log(x+1)	2, 3, 4
LKPM[c]	perimeter of occupied lakes (m)	log(x+1)	2
Human Influence			
AG	percent of catchment in agriculture (%)	arcsin(sqrt[x])	6
UR	percent of catchment urbanized (%)	arcsin(sqrt[x])	6
DM	index of river fragmentation by large dams (0-1) [d]	arcsin(sqrt[x])	2, 3, 8
HCH	percent of Pacific salmon species with hatcheries located in the catchment (%)	arcsin(sqrt[x])	3, 4
PRT	percent of catchment area within nationally designated protected areas (%)	arcsin(sqrt[x])	7

[a] Key: 1, Hydro1k catchments (USGS 2003a); 2, VMAP level 0 (NIMA 2000); 3, interviews with fisheries biologists (see online materials at www.stanford.edu/~mpinsky/salmon/); 4, State and

provincial data sets (see online material); 5, SRTM30 (USGS 2003b); 6, Global land cover (European Commission Joint Research Centre 2004); 7, World Database on Protected Areas (WDPA Consortium 2006); 8, U.S. National Inventory of Dams (USACE 2006), Canadian provincial ministry data, and published sources (Kalashnikov 1997; NIMA 2000; Newell 2004).

[b] Hydrographic scale and methods for measuring salmon distribution vary across region (Asia [AS], Alaska [AK], British Columbia [BC], and Washington/Oregon/Idaho [WOI]). Abundance models were fit against the interaction between occupied stream length and region.

[c] Lake area and lake perimeter were only included in models for sockeye.

[d] See Methods for description of the index of river fragmentation

Table 2. Models of salmon abundance calculated by ordinary least squares or by generalized least squares.*

	Ordinary least squares			*Generalized least squares*		
Species (r^2, p)	variable	coefficient	p	variable	coefficient	p
Chinook	intercept	-0.00264	0.997	intercept	0.44	0.598
(0.812,	STR:AK	0.683	2.66E-82	STR:AK	0.681	1.11E-72
<0.00001)	STR:BC	0.653	2.00E-122	STR:BC	0.562	4.84E-78
	STR:AS	0.453	5.56E-23	STR:AS	0.454	1.49E-16
	STR:WOI	0.546	1.56E-70	STR:WOI	0.537	3.70E-52
	AR	0.155	0.0132	AR	0.21	0.000678
	REL	0.00106	0.0349	ELEV	0.000601	0.00756
	DST	-0.113	0.00839	DST	-0.194	0.00234
Chum	intercept	0.484	0.584	intercept	1.75	0.12
(0.916,	STR:AK	0.929	1.44E-100	STR:AK	0.934	1.44E-97
<0.00001)	STR:BC	0.982	3.86E-118	STR:BC	0.902	2.29E-72
	STR:AS	0.63	1.80E-86	STR:AS	0.664	2.25E-68
	STR:WOI	0.526	2.85E-21	STR:WOI	0.558	8.46E-25
	AR	0.125	0.123	REL	0.00263	7.62E-05
	REL	0.00125	0.00973	DST	-0.188	0.0411
	DST	-0.142	0.0343			
Coho	intercept	1.09	0.129	intercept	1.98	0.0553
(0.83,	STR:AK	0.874	6.09E-111	STR:AK	0.843	3.62E-79
<0.00001)	STR:BC	0.86	2.52E-129	STR:BC	0.783	1.10E-78
	STR:AS	0.434	1.89E-35	STR:AS	0.38	7.89E-20
	STR:WOI	0.333	1.95E-32	STR:WOI	0.375	5.31E-23
	REL	0.000902	0.0852	REL	0.00202	0.00493

	DST	-0.0992	0.079	DST	-0.181	0.0354

Pink	intercept	1.97	0.0444	intercept	3.02	0.0155
(0.853,	STR:AK	0.916	4.41E-81	STR:AK	0.907	8.49E-78
<0.00001)	STR:BC	0.933	1.65E-118	STR:BC	0.824	2.04E-76
	STR:AS	0.853	1.10E-88	STR:AS	0.845	1.58E-76
	STR:WOI	1	1.66E-41	STR:WOI	0.96	5.25E-38
	AR	0.152	0.0675	REL	0.00272	0.000377
	REL	0.00121	0.0331	DST	-0.272	0.00653
	DST	-0.272	0.000102			
Sockeye	intercept	1.32	0.0506	intercept	1.25	0.0759
(0.836,	STR:AK	0.695	4.63E-38	STR:AK	0.699	3.38E-38
<0.00001)	STR:BC	0.71	3.72E-43	STR:BC	0.717	7.14E-44
	STR:AS	0.634	6.26E-47	STR:AS	0.634	1.28E-46
	STR:WOI	0.28	1.41E-05	STR:WOI	0.292	6.61E-06
	DST	-0.102	0.0728	DST	-0.0967	0.104
	LKAR	0.204	7.69E-16	LKAR	0.201	2.29E-15
Steelhead	intercept	-1.37	9.08E-05	intercept	-1.27	0.000122
(0.778,	STR:BC	0.462	8.41E-162	STR:BC	0.467	1.48E-117
<0.00001)	STR:AS	0.616	1.87E-20	STR:AS	0.601	3.72E-20
	STR:WOI	0.439	2.35E-102	STR:WOI	0.517	2.99E-103
	AR	0.187	2.17E-05	AR	0.151	0.000113
	ELEV	0.000227	0.0717			
	REL	-0.00135	0.00129			

* The r^2 and p values refer to ordinary least squares models. See Table 1 for variable codes.

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).*

		Protected area coverage (% of catchment)		
		Protected (>90)	Partially protected (50-90)	Unprotected (<50)
All catchments		2.5	2.9	95
HCV catchments		1.4	6.3	92
Chinook	presence	2.5	4.8	93
	abundance	1.6	6.9	92
Chum	presence	1.7	3.3	95
	abundance	1.4	4.5	94
Coho	presence	4.0	4.8	91
	abundance	2.9	18	79
Pink	presence	1.7	3.8	95
	abundance	3.1	10	87
Sockeye	presence	5.0	5.6	89
	abundance	4.5	17	78
Steelhead	presence	2.0	3.6	94

	abundance	0.05	2.1	98

* Catchments are classified according to whether protected areas cover >90%, 50-90%, or <50% of a catchment's area. Species are summarized by presence/absence and by total abundance.

Figures

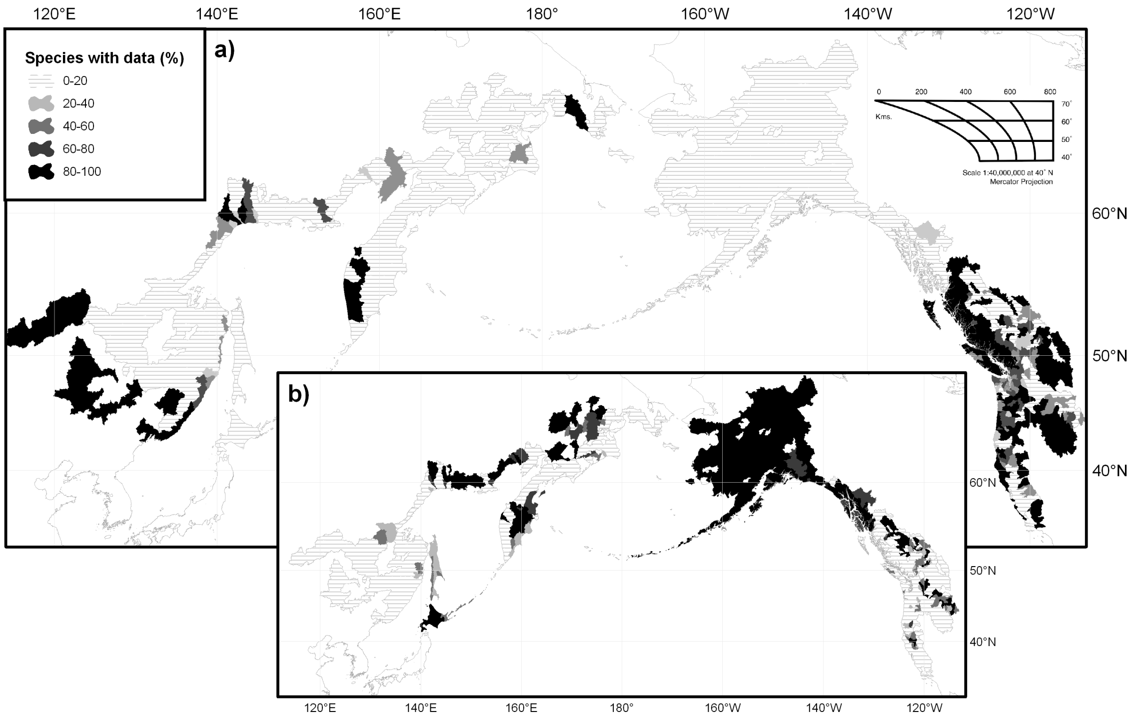

Fig. 1. Quality of salmon abundance data used to calculate conservation value (CV), displayed as the percentage of species in each catchment for which data of a certain spatial scale were available: a) data available at the scale of individual catchments or smaller and b) data available that spanned multiple adjacent catchments (data records allocated to individual catchments).

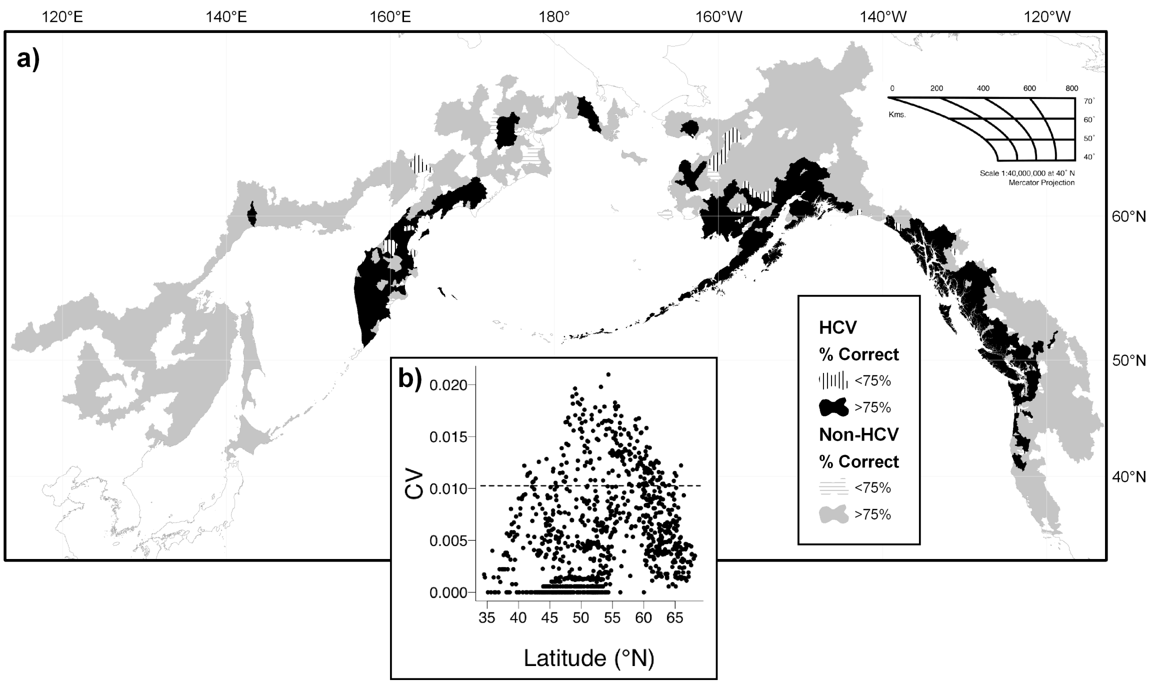

Fig. 2. a) High conservation value (HCV, black) and non-HCV catchments (grey) of the northern Pacific. Lined catchments were correctly reclassified in <75% of trials when error was simulated. b) Conservation value (CV) plotted against latitude. Catchments above the dotted line were classified as HCV.

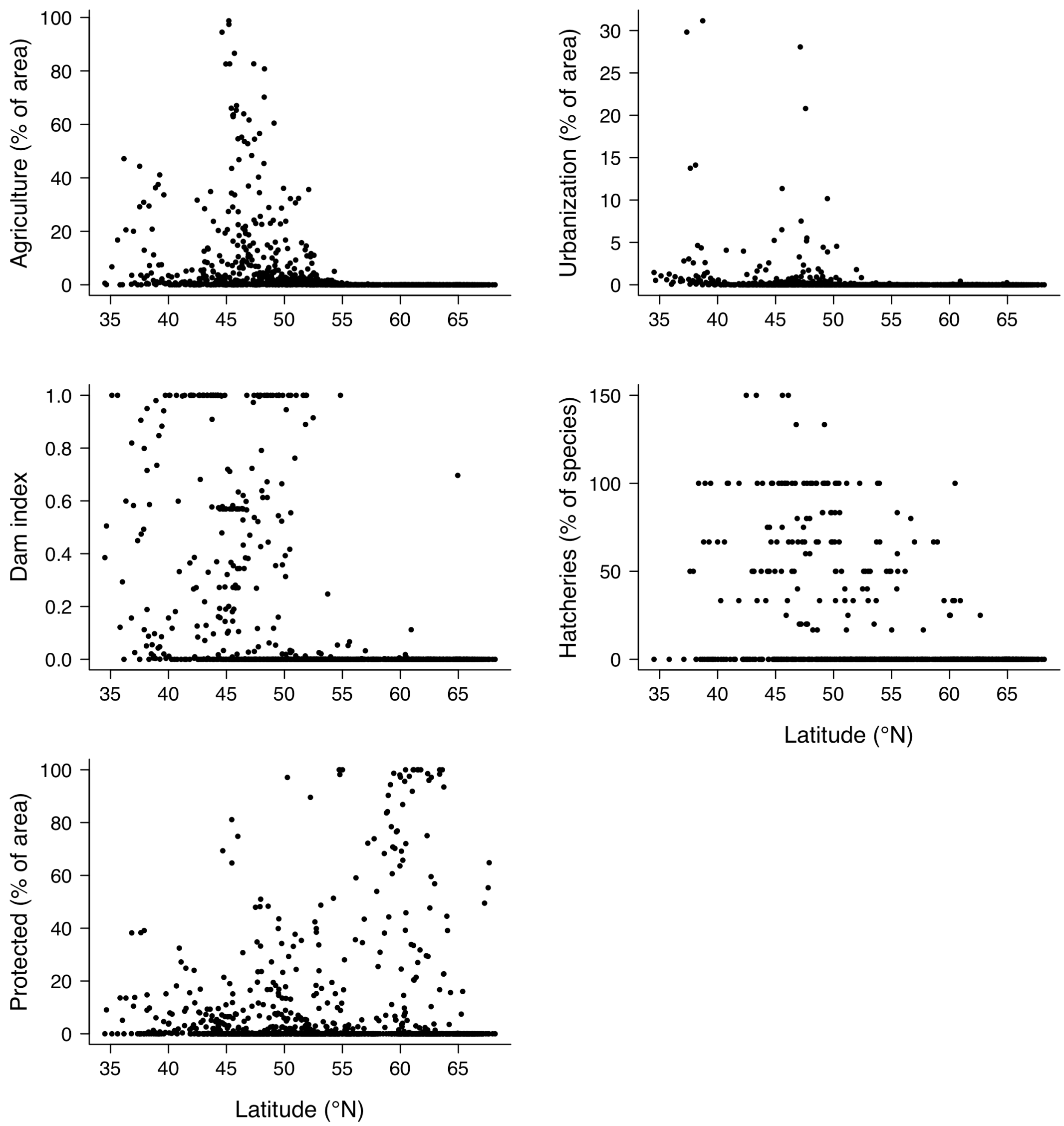

Fig. 3. Variation with latitude of human influence and percentage of catchment contained within nationally designated conservation areas.

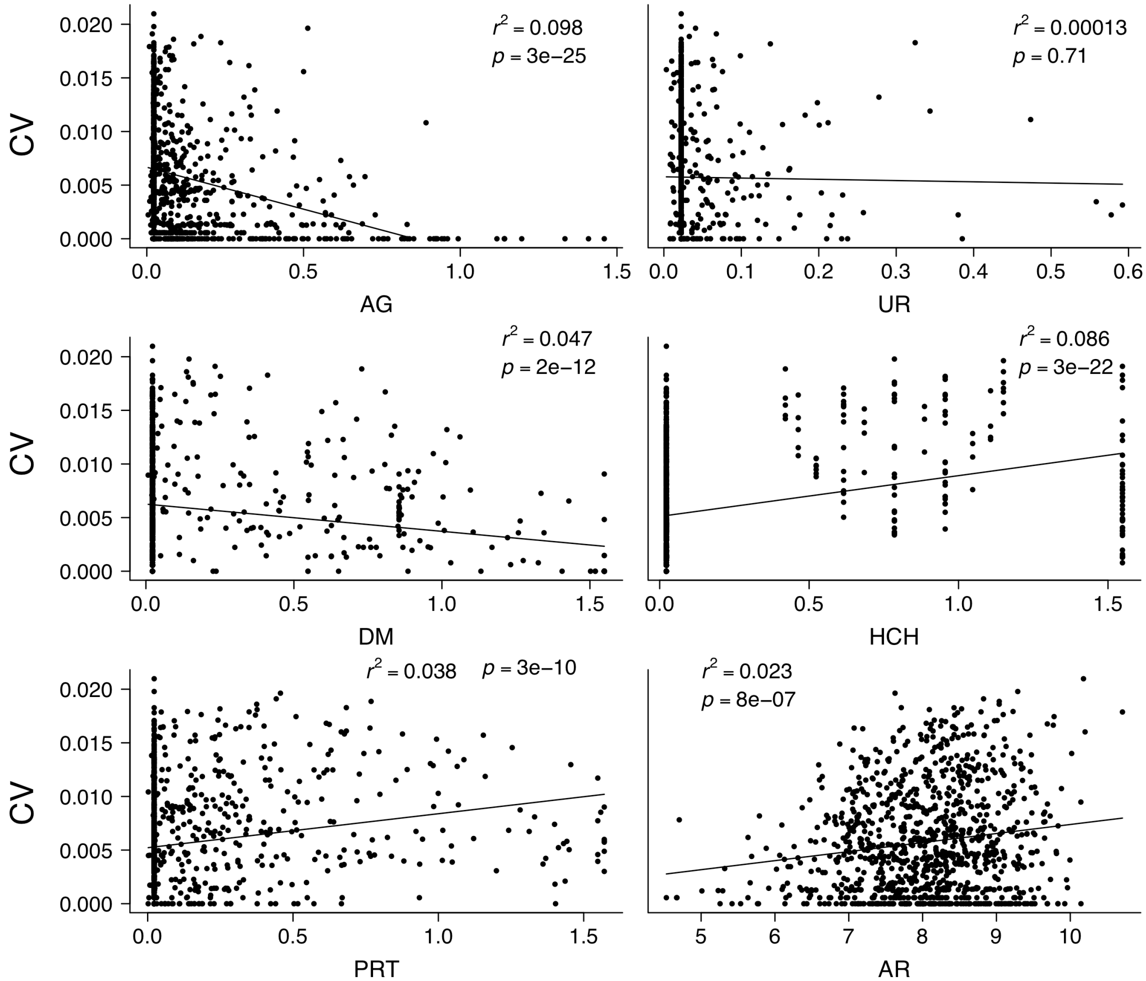

Fig. 4. Conservation value (CV) plotted against (transformed) human influence, percent of catchment protected, and catchment area. The line is the best-fit. See Table 1 for descriptions of variables and transformations.