



Human Influence on the Spatial Structure of Threatened Pacific Salmon Metapopulations

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Abstract: *To remain viable, populations must be resilient to both natural and human-caused environmental changes. We evaluated anthropogenic effects on spatial connections among populations of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) (designated as threatened under the U.S. Endangered Species Act) in the lower Columbia and Willamette rivers. For several anthropogenic-effects scenarios, we used graph theory to characterize the spatial relation among populations. We plotted variance in population size against connectivity among populations. In our scenarios, reduced habitat quality decreased the size of populations and hydropower dams on rivers led to the extirpation of several populations, both of which decreased connectivity. Operation of fish hatcheries increased connectivity among populations and led to patchy or panmictic populations. On the basis of our results, we believe recolonization of the upper Cowlitz River by fall and spring Chinook and winter steelhead would best restore metapopulation structure to near-historical conditions. Extant populations that would best conserve connectivity would be those inhabiting the Molalla (spring Chinook), lower Cowlitz, or Clackamas (fall Chinook) rivers and the south Santiam (winter steelhead) and north fork Lewis rivers (summer steelhead). Populations in these rivers were putative sources; however, they were not always the most abundant or centrally located populations. This result would not have been obvious if we had not considered relations among populations in a metapopulation context. Our results suggest that dispersal rate strongly controls interactions among the populations that comprise salmon metapopulations. Thus, monitoring efforts could lead to understanding of the true rates at which wild and hatchery fish disperse. Our application of graph theory allowed us to visualize how metapopulation structure might respond to human activity. The method could be easily extended to evaluations of anthropogenic effects on other stream-dwelling populations and communities and could help prioritize among competing conservation measures.*

Keywords: anthropogenic, connectivity, network, spatial analysis, viability

Influencia Humana sobre la Estructura Espacial de Metapoblaciones de Salmón del Pacífico Amenazadas

Resumen: *Para permanecer viables, las poblaciones deben ser resilientes a cambios ambientales tanto naturales como causados por humanos. Evaluamos los efectos antropogénicos sobre las conexiones espaciales entre poblaciones de salmón Chinook (*Oncorhynchus tshawytscha*) y arco iris (*O. mykiss*) (designadas como amenazadas por el Acta de Especies en Peligro de E. U. A.) en la cuenca baja de los ríos Columbia y Willamette. Para varios escenarios de efectos antropogénicos, utilizamos teoría de grafos para caracterizar la relación espacial entre poblaciones. Graficamos la varianza en el tamaño poblacional contra la conectividad entre poblaciones. En nuestros escenarios, la reducción en la calidad del hábitat disminuyó el tamaño de las poblaciones y las presas hidroeléctricas en los ríos provocaron la extirpación de varias poblaciones, lo cual redujo la conectividad. La operación de criaderos de peces incrementó la conectividad entre poblaciones y condujo a*

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poblaciones heterogéneas o panmícticas. Con base en nuestros resultados, consideramos que la recolonización de la cuenca alta del Río Cowlitz en otoño y primavera, se podría restablecer la estructura metapoblacional de esas especies a condiciones cercanas a las históricas. Las poblaciones que podrían conservar la mejor conectividad serían las que habitan los ríos Molalla (Chinook en primavera), bajo Cowlitz o Clackamas (Chinook en otoño) y el Santiam (arco iris en invierno) y Lewis (arco iris en verano). Sin embargo, las poblaciones en estos ríos fueron fuentes putativas, ya que no siempre fueron las más abundantes o localizadas en el centro. Este resultado no habría sido obvio si no hubiéramos considerado las relaciones entre las poblaciones en un contexto metapoblacional. Nuestros resultados sugieren que la tasa de dispersión controla las interacciones entre las poblaciones que componen las metapoblaciones de salmón. Por lo tanto, los esfuerzos de monitoreo podrían llevar al entendimiento de las tasas reales de dispersión de peces silvestres y criados. Nuestra aplicación de la teoría de grafos nos permitió visualizar como puede responder la estructura metapoblacional a la actividad humana. El método podría ser extendido fácilmente a evaluaciones de efectos antropogénicos sobre otras poblaciones y comunidades que habitan en ríos y podría ayudar a priorizar entre medidas de conservación en competencia.

Palabras Clave: análisis espacial, antropogénico, conectividad, red, viabilidad

Introduction

Human activities can change landscapes over greater spatial and temporal extents than natural disturbances to which organisms have adapted (Vitousek et al. 1997). Long-lasting and widespread changes may alter spatial relations among populations and thereby reduce resilience of a metapopulation to further changes. Here we use *metapopulation* to mean a suite of interacting, spatially distributed populations that persist despite locally dynamic demographic and environmental conditions (Hanski 1998). A population within a metapopulation is characterized by distinct genetic, ecological, or life-history attributes. Spatial structure among populations lends stability to a metapopulation by buffering against localized catastrophic events; extirpated populations can be recolonized by neighboring populations (Kallimanis et al. 2005). Spatial structure may also maintain or increase genetic diversity, which can increase resilience to spatially extensive disturbances (Fox 2005).

Human activity that reduces habitat amount or quality decreases the number of individuals that can be supported in a metapopulation (Moilanen & Hanski 1998), and actions that fragment habitats can reduce the ability of organisms to disperse among populations (With et al. 2006). Removal of dispersal barriers, translocation of wild individuals, or release of animals reared in captivity can increase exchange of individuals among populations (henceforth, connectivity). However, high levels of connectivity (Rahel 2007) may increase synchrony among populations, making a metapopulation less resilient to change.

Comparison of presumed historical with observed current-day metapopulation structures can inform choices among alternative conservation approaches (Crooks & Sanjayan 2006). Harrison and Taylor (1997) propose a conceptual framework to describe metapopulation forms (Fig. 1a). In this framework, metapopulation structure ranges from well-mixed populations (effectively

one panmictic or patchy population) to largely isolated remnant populations, in which dispersal among populations is low and persistence of individual populations is unlikely, especially when each population has few individuals (nonequilibrium metapopulation). Variance in the size of individual populations ranges from low (classic metapopulation) to high (mainland-island metapopulation, in which the metapopulation is sustained by one or more large source populations). Harrison and Taylor's (1997) concept can be used as a basis for assessing potential conservation measures. For example, if a classic metapopulation were separated into smaller, more isolated populations by human activities, increasing connectivity might increase probability of metapopulation persistence. For mainland-island metapopulations, conserving or reconstructing habitat for large source populations would be necessary for the metapopulation to persist. To maintain metapopulations transformed into patchy or panmictic populations, it might be necessary to increase or reintroduce spatial structure.

The viability of species living in stream networks is likely to decrease in response to habitat fragmentation (Fagan 2002; Wiens 2002). Dunham and Rieman (1999) evaluated influences of habitat amount and fragmentation by roads on the spatial distribution of populations of bull trout (*Salvelinus confluentus*) that were assumed to function as a metapopulation. Populations of anadromous Pacific salmon (*Oncorhynchus* spp.) are also useful in the investigation of the effects of humans on spatial dynamics of metapopulations of riverine fish (Schtickzelle & Quinn 2007). Salmon populations have asynchronous dynamics. Reproduction is spatially segregated, and although most salmon return to natal streams to spawn, a small proportion disperse to neighboring streams (Quinn 2005). Because salmon are diadromous, their abundance is influenced by ocean conditions that affect growth. Yet population sizes in any given year are expected to respond similarly to ocean conditions because individuals from multiple populations co-occur while at sea (Quinn

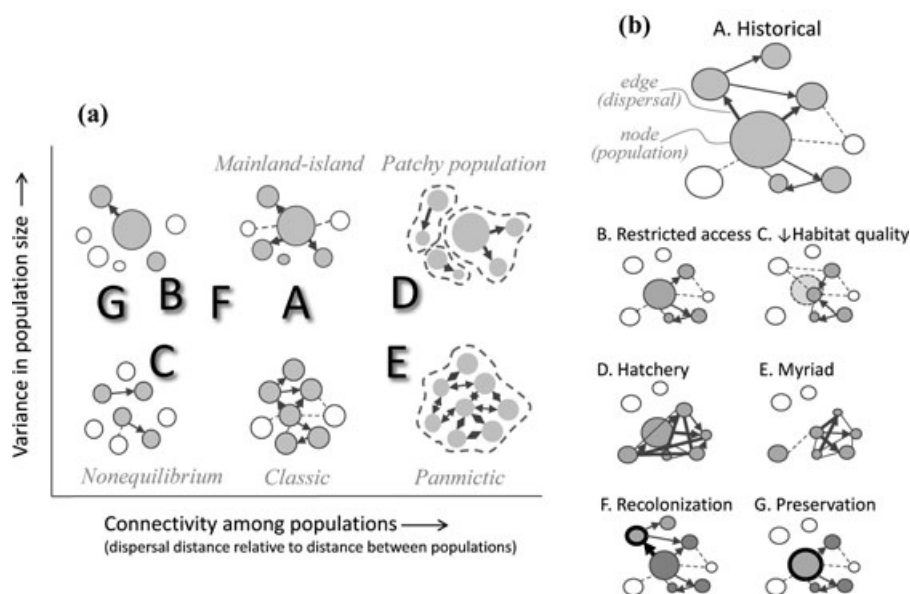


Figure 1. Theoretical framework for describing the spatial structure of metapopulations, adapted from figures in Harrison and Taylor (1997): (a) possible metapopulation spatial structures, given information about population sizes, dispersal capability, and distance among populations and (b) graph representations of a hypothetical Pacific salmon metapopulation for the human-influence scenarios (described in Table 1) (filled circles, extant populations; open circles, extirpated populations; solid lines, existing connections; dashed lines, past connections; circle size reflects population size; arrows, dominant direction of dispersal; circles with heavy outline, populations to be reestablished or preserved; letters on [a], hypothesized spatial position of the scenarios identified in [b]). Position of scenario G (preservation) in (a) illustrates the condition of the metapopulation if the population identified for preservation were lost.

2005). Asynchronous population dynamics and the high fidelity of most salmon to natal streams are likely due to adaptations by fish to the local conditions they experience during reproduction in freshwater.

It is difficult to quantify spatial structure of salmon metapopulations because the distances over which salmon travel are vast (up to thousands of kilometers). Genetic analyses help clarify levels of connectivity (Neville et al. 2006); however, genetic data often cannot distinguish between historical and present-day population structures because genetic change lags behind habitat alteration (Poissant et al. 2005). Use of isotopic markers with distinct signatures in different locations can help one discern the origin of salmon (Barnett-Johnson et al. 2010). Isaak et al. (2007) extended incidence function model measures originally applied in terrestrial landscapes to explore the relations among habitat size, quality, and connectivity for salmon within a watershed. Graph or network theory can help identify spatial relations between animal populations across extensive areas (Urban et al. 2009). In graph or network theory, nodes represent the size and spatial position of elements (e.g., populations, habitat patches) and edges represent permeability or the relative strength of connections among elements (Fig. 1b). Quantitative estimates can be calculated that describe the cohesion and con-

nectivity among elements and how overall metapopulation structure might change if any of these elements were altered in position or size. Despite its widespread application in terrestrial systems (Urban & Keitt 2001; Brooks 2006) and in some marine environments (Trembl et al. 2008), graph theory has not often been applied to freshwater ecosystems. Schick and Lindley (2007) used graph theory to evaluate how the sequential addition of hydropower dams altered the spatial structure of spring-run Chinook salmon (*O. tshawytscha*) in the Sacramento and San Joaquin basins (central California, U.S.A.).

We used graph theory to evaluate whether human actions have influenced the spatial structure of Chinook salmon and steelhead (*O. mykiss*) in the lower Columbia and Willamette rivers (western Oregon and Washington, U.S.A.). We compared the presumed historical spatial structure among populations with structure under present-day conditions: anthropogenic barriers to movement, reduced habitat quality, and fisheries management. We considered these conditions within the conceptual framework of Harrison and Taylor (1997) so we could prioritize conservation of populations or connections that would alter metapopulation structure to most resemble historical populations, which presumably were viable.

Methods

Study Area

Our study area encompassed the Columbia River and tributary watersheds from the mouth to The Dalles Dam (308 river km), including the Willamette River. Collectively, these watersheds drain 47,046 km² from the Cascade Mountains in western Oregon and Washington (U.S.A.). Natural phenomena that affect the landscape have included large fires, landslides, and volcanic eruptions in the uplands and floods in the lowlands. Dominant upland human activities include hydropower dams and forestry. Lowland land uses include agriculture and urban and rural residential development, which are concentrated in the Willamette Valley and near the city of Portland. Four anadromous salmonids occur in the study area: Chinook, coho (*O. kisutch*), chum (*O. keta*), and steelhead.

We focused on Chinook salmon and steelhead because these species exhibit complex and diverse life histories (Waples et al. 2009), are widely distributed in the region, and are the species for which the most credible data are available. The study area encompassed 2 evolutionarily significant units (ESUs) (i.e., groups of populations that are geographically, ecologically, and evolutionarily unique [Waples 1991]) of Chinook and 2 steelhead ESUs, each of which is designated as threatened under the U.S. Endangered Species Act. We modeled spring Chinook, fall Chinook, winter steelhead, and summer steelhead as separate metapopulations because temporal separation of spawning is likely sufficient to isolate populations occurring sympatrically and the boundary delineating the upper Willamette and lower Columbia ESUs may not be a dispersal barrier. The same could be true for the eastern border of our study area, where fish may stray above The Dalles Dam into the upper Columbia River, but we believe the dam is a deterrent to such movement. We did not consider the small probability that fish might stray outside the Columbia River basin (Hendry et al. 2004).

Scenarios

We developed 7 scenarios through which to evaluate the effects of anthropogenic changes to the spatial structure of salmon metapopulations and to identify possible actions to conserve viable metapopulations (Table 1). The historical scenario depicted hypothetical conditions before European settlement. In this scenario, we assumed only natural barriers limited fish access to streams; fish were of wild origin; and habitat quality and fish abundance were minimally affected by native peoples.

Four scenarios accounted for anthropogenic change: restricted access (access to streams limited to areas below impassable hydropower dams, but other conditions remained as in the historical scenario); reduced habitat quality (fish restricted to areas below dams and

instream habitat quality decreased relative to historical conditions); presence of hatchery fish (fish restricted to areas below dams and an increased probability of dispersal by hatchery fish relative to dispersal rates of wild fish); and myriad (multiple factors, including restricted stream access due to dams, reduced habitat quality, presence of hatchery fish, fish harvest, unfavorable oceanic conditions, and other unknown environmental factors). The myriad scenario best represents presumed present-day conditions.

We devised 2 conservation scenarios (baseline of each was the restricted-access scenario): recolonization (identification of the one extirpated population [i.e., disconnected by a migration barrier] that would most increase connectivity if reestablished) and preservation (identification of the one extant population that would most decrease connectivity if extirpated).

Analyses

Populations

We defined populations as in Myers et al. (2006), the boundaries of which were synonymous with watersheds (Supporting Information). There were 16 and 22 populations of spring and fall Chinook, respectively, 22 of winter steelhead, and 6 of summer steelhead.

We represented the geographical location of each population as a single point in space (Supporting Information). This location was the midpoint of documented fish occurrences within the primary mainstem river for which the watershed was named (ODFW 2004; WDFW 2007). For steelhead and fall Chinook, the lower extent we considered was the confluence of a river with the Columbia River. Because spring Chinook generally spawn at higher elevations than fall Chinook (Quinn 2005; Myers et al. 2006), the lower extent coincided with the intersection of each river with the 100-m elevation contour. In areas below this contour, fish were largely designated as present (rather than as spawning or rearing) in fish-distribution data maintained by the Oregon and Washington departments of fish and wildlife. For the historical scenario and the reestablished population in the recolonization scenario, we also included streams above hydropower dams where fish were documented historically. For scenarios including hatchery fish (hatchery and myriad scenarios), we used midpoints of present-day fish distributions for 2 spring Chinook hatcheries, middle fork Willamette, and McKenzie because releases occur nearer to these areas than to the hatchery facilities. We positioned other populations at hatchery facilities because exact release locations were unknown.

We used an index to represent the potential sizes of populations (n_i) because we lacked sufficient empirical data on sizes for all populations. This index (IPkm) measured the intrinsic physical potential of a stream system to

Table 1. Scenarios of human influence and parameters used to model salmon metapopulations in each scenario.

Parameter	Scenario						
	historical (pre-European settlement conditions)	restricted access (presence of impassable barriers)	reduced habitat quality (some reduction in habitat quality)	hatchery (fish hatcheries in some populations)	myriad (multiple an- thropogenic and natural stressors)	recolonization (identify key populations to reestablish)	preservation (identify key populations to preserve)
Population size ^b	IPkm, assuming only natural barriers	IPkm below dams	IPkm below dams × habitat quality index	IPkm below dams	IPkm below dams × popu- lation performance index	IPkm below dams	IPkm below dams
Population location	midpoint of historical distribution	midpoint of current distribution	midpoint of current distribution	hatchery locations	hatchery locations	midpoint of current distribution	midpoint of current distribution
Dispersal per generation (m) (%) (Chinook, steelhead)	2, 5	2, 5	2, 5	5, 8	5, 8	2, 5	2, 5
Dispersal distance (α) (km)	100	100	100	125	125	100	100
Population connection	0.01	0.01	0.01	0.01	0.01	0.01	0.01
threshold (z)	no change	loss of some populations	some pop- ulations become smaller	more con- nections among populations	unknown	increased con- nectivity if population reestablished	decreased con- nectivity if population extirpated
Predicted result							change in population size, range in population sizes
							change in distances among populations 0.5–15
							25–300
							0.0025–0.2

^aDescription of how parameters were adjusted in sensitivity analyses.^bIPkm, intrinsic habitat potential index multiplied by accessible stream length in kilometers (see Supporting Information for a description of IPkm and its variants).

support salmon and was based on species-specific associations with channel gradient, discharge, and channel-to-valley width ratio (Burnett et al. 2007). A full explanation of this index is in Supporting Information. Briefly, we derived geospatial data from a 10-m digital elevation model, and for each stream reach (1:100,000) we calculated the value of the index as the geometric mean of channel gradient, discharge, and channel-to-valley width ratio, multiplied by reach length. For each population, we summed values for all reaches in documented fish distributions, which essentially weighted accessible stream length to indicate how many kilometers might support fish.

For the historical scenario and the reestablished population in the recolonization scenario, we represented potential population size with IPkm for all streams historically accessible to fish. In present-day scenarios, we limited fish distributions to areas below impassable barriers. For the reduced habitat quality and myriad scenarios, we multiplied IPkm by an estimate (0 to 1) of habitat quality or population performance, respectively (Table 1). Habitat quality represented current instream habitat conditions and risk of continued deterioration of habitat conditions due to anthropogenic stressors. Population performance comprised empirical data on trends in salmon abundance and productivity, estimated proportion of hatchery fish, harvest rates, habitat quality, and other environmental conditions. Estimates were derived by the Willamette-Lower Columbia Technical Recovery Team, a body of experts convened by NOAA (National Oceanic and Atmospheric Administration) Fisheries (as required by the Endangered Species Act) to assess population status, risk of extinction, and recovery goals (see Supporting Information for details).

Dispersal

We modeled probability of dispersal among populations as the product of m , the proportion of fish that attempt to disperse (stray) from their natal population, and $\mathbf{P}$, a matrix describing the probability of successful dispersal between each pair of populations. The probability that individuals dispersing from population i would successfully recruit into population j was represented by p_{ij} . We used a dispersal kernel that causes the probability of successful dispersal to decrease exponentially as distance between populations increases (Schick & Lindley 2007):

$$p_{ij} = \frac{1}{2\alpha} \exp \left[- \left| \frac{d_{ij}}{\alpha} \right| \right], \quad (1)$$

where α is the maximum distance a fish will disperse and d_{ij} is distance along the midline of the stream network between node coordinates (distance matrices in Supporting Information). We standardized movements to account for differences in population sizes (off diagonals in $\mathbf{P}$ divided by column sums).

Salmon likely do not swim to their natal spawning ground and then stray into another watershed. Rather, as they migrate from the sea to their spawning location, they choose which stream to ascend at each tributary junction they encounter. Thus, the probability of straying may depend more on which decisions the fish make than on distances among populations. To test this possibility, Schick and Lindley (2007) devised a wrong-turn model and found the resulting graph and its ecological interpretation to be very similar to that from the more parsimonious model of distance among populations that incorporated fewer untestable assumptions. Moreover, results of previous studies show that genetic diversity increases as the watercourse distance separating Pacific salmon populations increases (Hendry et al. 2004; Myers et al. 2006). Given their strong homing ability (Quinn 2005), we reasoned that salmon would be more likely to stray to populations that are close to their natal population.

We used stray rates of 2% for Chinook salmon and 5% for steelhead to globally parameterize m for all population pairs (Hendry et al. 2004; Keefer et al. 2005) (Supporting Information). Stray rates likely differ among populations, and values may be influenced by factors we did not consider in our models, but we lacked precise data for these populations. There are also few data on which to base α . Wild and hatchery Chinook and hatchery steelhead in the upper Columbia River are unlikely to travel beyond 100 km on average from their natal population (ICBTRT 2003). Therefore, we parameterized α as 100 km for both species. Some evidence suggests hatchery fish may stray at higher rates (Keefer et al. 2005; Quinn 2005) and over greater distances (ICBTRT 2003; Myers et al. 2006) than wild fish. Therefore, in the hatchery and myriad scenarios, where hatchery fish were present, we set m to 5% for Chinook and 8% for steelhead and α to 125 km for both species. We later evaluated the sensitivity of results to these parameter values.

Spatial Structure

We described the spatial structure ($\mathbf{S}$) of each metapopulation in each scenario as the product of population size ($\mathbf{n}$), stray rate (m), and the probability of successful dispersal ($\mathbf{P}$) (Supporting Information). Diagonals in $\mathbf{S}$ represent recruitment within a population; off-diagonal elements represent emigration (lower triangle) or immigration (upper triangle) between each pair of populations. We calculated the weight of interaction between populations ($\mathbf{W}$) as the number of individuals immigrating or emigrating divided by the number of individuals that recruited into their natal population. We used this information to construct graphs to evaluate differences in spatial structure among scenarios. Nodes in these graphs represent populations, and the position of a node is the geographical location of a population. The node

Table 2. Population connectivity metrics used to evaluate the spatial structure of salmon metapopulations.

Metric	Level of metric	Description	Equation*	Value range
Node strength	patch	relative contribution of a population; represents how pivotal a population is to overall graph structure; does not indicate whether individuals primarily emigrate from or immigrate to the population	$=s_{i \rightarrow j} + s_{j \rightarrow i}$	>0
Independence	patch	measure of population isolation (Schick & Lindley 2007); higher values indicate greater reliance on recruitment than on immigration	$\frac{s_{ii}}{s_{ii} + s_{j \rightarrow i}}$	0–1
Relative strength	patch	number of fish emigrating from (positive values) or immigrating into (negative values) a population relative to recruitment within the population	$= \frac{s_{i \rightarrow j} - s_{j \rightarrow i}}{s_{ii}} * 100$	any
Total edge weight	graph	cumulative magnitude of all edge weights (connections among populations)	$\sum w_{i \rightarrow j} + \sum w_{j \rightarrow i}$	>0
Graph connectance	graph	ratio of connections (edges) to the maximum possible connections among all populations	$\frac{\sum e_{i \rightarrow j} + \sum e_{j \rightarrow i}}{n_{\text{tot}}^2 - 1}$	0–1
Unconnected nodes	graph	the fraction of isolated populations with no connections	$\frac{\sum n_{e=0}}{n_{\text{tot}}}$	0–1

*Key: $s_{i \rightarrow j}$, emigration from population i to population j ; $s_{j \rightarrow i}$, immigration to population i from population j ; s_{ii} , recruitment within the population; w , weight (magnitude) of dispersal among populations; e , edge or population connectivity (i.e., edge having $w > 0.01$); $n_{e=0}$, a population that has no edges; n_{tot} , total number of populations.

diameter corresponds to population size. Weighted arrows, or edges, connect the populations and represent the direction and magnitude of dispersal among populations. Populations i and j were connected (i.e., had an edge) if w_{ij} or $w_{ji} > a$ threshold z , which we set initially to 0.01, as in Schick and Lindley (2007). For population connections included in the final graph, direction of the connection and magnitude equaled $|w_{ij} - w_{ji}|$.

For each metapopulation-scenario combination, we calculated 3 population-level (patch) and 3 metapopulation-level (graph) metrics that measured different aspects of connectivity (Table 2). To explain as much of the variability among connectivity metrics as possible with a single metric, we used principal components analysis to merge the 6 metrics into 1 score: the first principal component. We then plotted this score (x-axis) against the standard deviation of population size (y-axis) to assess metapopulation structures in terms of Fig. 1a.

Sensitivity Analyses

We assessed the effects of several assumptions on connectivity metrics by conducting a sensitivity analysis for each of the parameters (Table 1). To investigate how population size influenced graph structure, we evaluated symmetric changes in population size by either doubling or halving the size of all populations simultaneously; changes in population-size differential, where the variance among individual population sizes was increased or decreased by 50%; effects of tripling the size of only the largest population; and randomly assigning the size of each population from the distribution of original popu-

lation sizes ($n = 50$ resamples). We evaluated sensitivity to distance among populations by simultaneously relocating all populations either downstream or upstream by halving or doubling their original distance from the river mouth. We then simultaneously evaluated sensitivity of results to the remaining 3 parameters: dispersion, percentage of fish straying, and the population-connection threshold (see Table 1 for ranges tested). Varying the threshold value affected only graph-level metrics and visualization on maps. By definition, it could not affect patch-level metrics.

Results

Compared with Chinook salmon, populations of steelhead had higher connectivity despite similar stream distances among populations (Table 3; Fig. 2). This pattern was consistent across scenarios and was driven by both the larger populations and higher assumed stray rate of steelhead (Table 1).

The first principal component explained 90%, 77%, 56%, and 64% of variation among the 6 graph metrics of connectivity for fall Chinook, spring Chinook, winter steelhead, and summer steelhead, respectively. Only the first principal component was significant in a randomization test, with $p < 0.001$, <0.01 , 0.014, and 0.014, respectively; therefore, we used this as our metric of connectivity in subsequent analyses.

Our results suggested that in the absence of presumed human influence (historical scenario), spring Chinook and winter steelhead were structured as mainland-island metapopulations. The structure of fall Chinook

Table 3. Summary of estimated salmon population sizes (IPkm or variant) and connectivity among populations (6 graph metrics) for all species-scenario combinations.

Population and metric ^b	Scenario ^a					
	Historical	Restricted Access	Reduced habitat quality	hatchery	Myriad	Recolonization ^c Preservation ^c
Spring Chinook						
IPkm or variant	307 (92, 470)	166 (0, 410)	100 (0, 286)	166 (0, 410)	48 (0, 241)	upper Cowlitz 210 (1, 410) Molalla 125 (0, 337)
node strength	12.7 (8.1, 19.1)	8.7 (0.0, 12.6)	6.3 (0.0, 9.4)	22.3 (0.0, 33.0)	10.3 (0.0, 19.2)	9.5 (0.0, 12.7) 7.5 (0.0, 11.0)
independence	0.98 (0.93, 0.99)	0.98 (0.94, 1.0)	0.98 (0.95, 1.0)	0.96 (0.87, 1.0)	0.97 (0.82, 1.0)	0.98 (0.94, 1.0) 0.99 (0.95, 1.0)
relative strength	-0.2 (-5.1, 0.7)	0.0 (-3.8, 1.0)	0.0 (-3.5, 0.9)	-0.1 (-9.2, 2.6)	0.0 (-16.5, 2.2)	-0.1 (-4.0, 1.1) 0.0 (-3.2, 1.0)
total edge weight	1.51	1.32	1.30	1.82	1.91	1.35 1.28
graph	0.038	0.021	0.017	0.092	0.092	0.021 0.017
connectance						
unconnected	7/16	8/16	10/16	4/16	5/16	8/16 9/16
nodes						
Fall Chinook						
IPkm or variant	146 (34, 404)	112 (15, 257)	77 (12, 212)	112 (15, 257)	60 (7, 184)	upper Cowlitz 116 (25, 316) lower Cowlitz 108 (6, 244)
node strength	6.5 (3.1, 9.8)	5.3 (2.0, 8.3)	3.6 (1.3, 5.5)	13.6 (5.8, 20.5)	7.2 (3.0, 11.0)	5.9 (2.4, 8.6) 4.7 (0.2, 6.8)
independence	0.97 (0.91, 0.99)	0.98 (0.93, 1.0)	0.98 (0.93, 0.99)	0.94 (0.83, 0.99)	0.94 (0.79, 0.99)	0.98 (0.92, 0.99) 0.98 (0.93, 1.0)
relative strength	-0.4 (-6.7, 1.3)	-0.1 (-5.6, 1.0)	-0.1 (-4.6, 1.1)	-0.5 (-12.8, 2.4)	-0.9 (-21.3, 2.9)	-0.3 (-6.0, 1.2) 0.0 (-5.0, 1.0)
total edge weight	1.87	1.70	1.65	2.78	2.67	1.77 1.63
graph	0.019	0.015	0.015	0.065	0.065	0.019 0.017
connectance						
unconnected	11/22	14/22	12/22	2/22	2/22	13/22 12/22
nodes						
Winter steelhead						
IPkm or variant	357 (59, 911)	160 (2, 738)	98 (1, 479)	160 (2, 738)	118 (1, 509)	upper Cowlitz 174 (17, 738) south Santiam 156 (0, 735)
node strength	41.1 (22.2, 67.2)	27.2 (1.5, 52.7)	15.1 (1.0, 34.8)	39.8 (0.0, 90.5)	27.4 (0.0, 63.6)	28.2 (16.0, 53.1) 25.5 (0.0, 52.1)
independence	0.94 (0.73, 0.97)	0.94 (0.77, 1.0)	0.94 (0.78, 1.0)	0.92 (0.55, 1.0)	0.93 (0.48, 1.0)	0.94 (0.77, 0.99) 0.95 (0.77, 1.0)
relative strength	-1.4 (-31.4, 2.5)	-1.3 (-24.6, 3.0)	-1.2 (-23.2, 3.1)	-0.4 (-74.9, 5.1)	-0.1 (-100, 5.0)	-1.3 (-25.2, 3.2) 0.00 (-24.2, 2.7)
total edge weight	3.88	3.64	3.35	5.42	5.15	3.82 3.49
graph	0.119	0.080	0.084	0.145	0.136	0.091 0.074
connectance						
unconnected	0/22	4/22	4/22	4/22	4/22	3/22 5/22
nodes						
Summer steelhead						
IPkm or variant	236 (187, 532)	176 (147, 243)	144 (71, 166)	176 (147, 243)	149 (84, 187)	north fork Lewis 176 (72, 243)
node strength	30.2 (22.5, 42.7)	18.5 (16.8, 21.3)	13.0 (11.6, 13.5)	31.0 (25.9, 33.5)	22.2 (20.4, 24.6)	18.5 (9.2, 21.3)
independence	0.93 (0.91, 0.97)	0.95 (0.92, 0.97)	0.96 (0.86, 0.97)	0.91 (0.88, 0.95)	0.93 (0.82, 0.95)	0.96 (0.92, 0.98)
relative strength	-2.0 (-4.4, 1.8)	-0.3 (-3.2, 2.1)	1.4 (-11.6, 2.1)	-1.2 (-5.0, 3.9)	1.6 (-14.9, 3.3)	0.3 (-3.4, 1.8)
total edge weight	1.34	1.28	1.32	1.46	1.51	1.23 1.23
graph	0.500	0.367	0.400	0.733	0.700	0.300 0.300
connectance						
unconnected	0/6	0/6	0/6	0/6	0/6	1/6
nodes						

^a Described in Table 1.^b Defined in Table 2. Patch-level metrics (first 4 under each species) are median values (10th percentile, 90th percentile); graph-level metrics (last 3) are calculated on the entire graph and therefore have no variance.^c Recolonization scenario (not available for summer steelhead) results show reconnection to the extirpated population (named above values) that would most improve connectivity among populations; preservation scenario results show removal of the extant population (named above values) or connection to that population that would most decrease connectivity among populations (see Supporting Information for population locations).

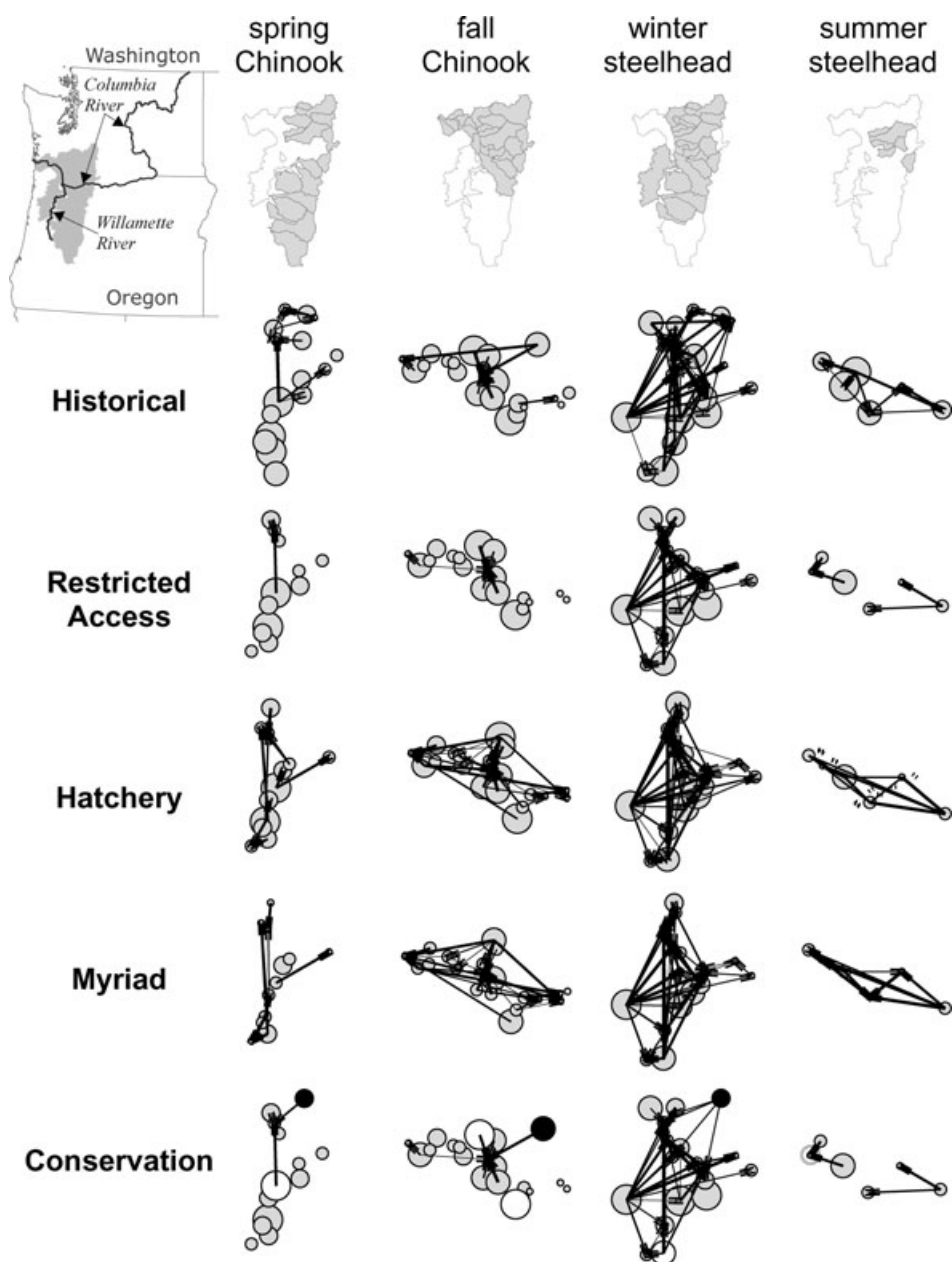


Figure 2. Graphs illustrating spatial structure of salmon metapopulations resulting from human-influence scenarios (historical, restricted access, hatchery, myriad; defined in Table 1) for each salmon species (columns) and resulting from both conservation scenarios (reestablishment of the one extirpated population that would most increase connectivity and preservation of the one extant population that would most decrease connectivity if extirpated) (black circles, populations that, if recolonized, would yield the largest increases in connectivity among populations; open circles, existing populations that would most disconnect the graphs if not preserved). For clarity, the scenario of reduced habitat quality is not shown because it is similar to the restricted-access scenario. The spatial extent of populations included in each salmon metapopulation is shown in the top row (see Supporting Information for names of populations).

metapopulations fell between classic and mainland-island. Summer steelhead populations were structured as a classic metapopulation (Fig. 3). These classifications are intended only to illustrate potential historical conditions and form the basis for relative comparisons among other scenarios.

For Chinook (fall and spring runs) and winter steelhead, there were fewer populations in present-day scenarios than in the historical scenario because several populations were extirpated by large hydropower dams (e.g., in the Cowlitz and Lewis rivers). Both connectivity and variance in size of populations decreased in the restricted-access scenario and decreased even further in the scenario with reduced habitat quality (Table 3 & Fig. 3). Although variance in population size also decreased in the

hatchery and myriad scenarios, connectivity increased, especially for the hatchery scenario (Table 3 & Fig. 2). Hatcheries typically moved spring Chinook populations a short distance downstream but moved fall Chinook and steelhead upstream, so the majority of increases in connectivity were due to higher stray rates rather than to distances among populations. Population structure in the hatchery scenario was primarily patchy for spring Chinook and winter steelhead and panmictic for fall Chinook, whereas the myriad scenario showed a panmictic population structure for all 3 metapopulations (Fig. 3).

The shifts in population structure for summer steelhead from historical to present-day scenarios differed from the patterns for other species, but generally

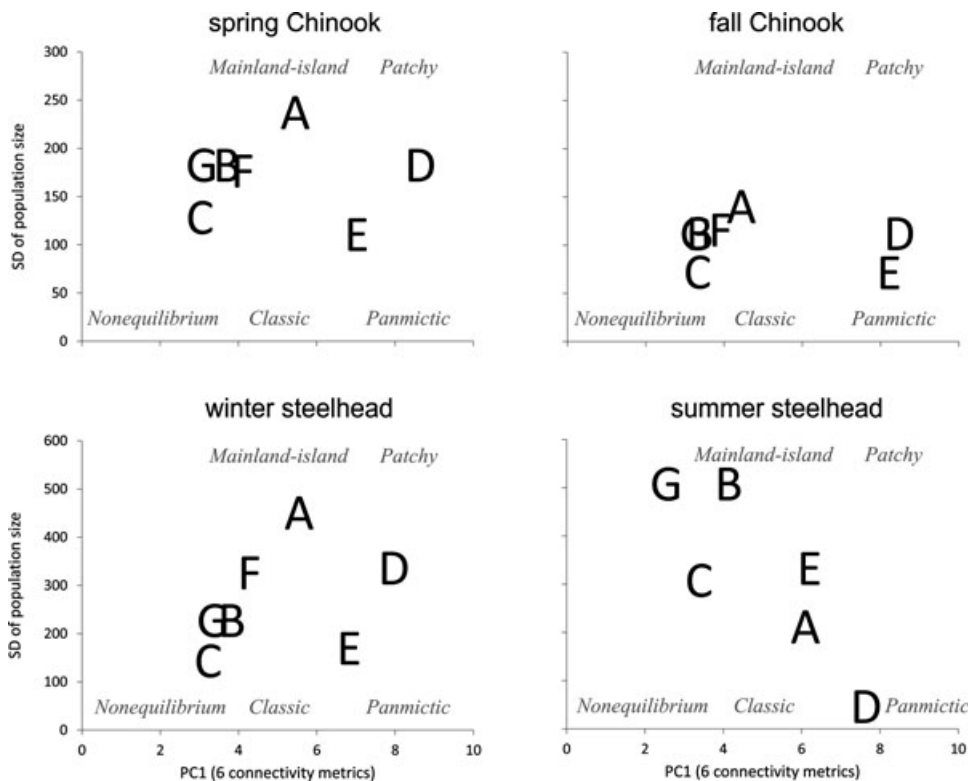


Figure 3. Placement of salmon metapopulations predicted under scenarios of human influence (A, historical; B, restricted access; C, reduced habitat quality; D, hatchery; E, myriad; F, recolonization; and G, preservation; the descriptions of which are in Table 1) within the theoretical framework illustrated in Fig. 1 (y-axis, SD in population size, as estimated with the habitat index IPkm or a scenario-specific variant [see Table 1]; x-axis, first principal component (PC1) merging 6 metrics of connectivity [Table 2]; scores are centered and scaled to facilitate comparison).

followed similar trends along the connectivity axis (Fig. 3). There were 6 populations of summer steelhead, and none were extirpated, but accessible stream length was reduced by dams for some populations.

In the recolonization scenario, the largest increase in connectivity for all 3 metapopulations resulted from reestablishment of the upper Cowlitz population (no populations of summer steelhead were extirpated). Node strength was strongest for these populations historically. In the preservation scenario, the populations that contributed the most to maintaining existing connectivity levels differed by species: Molalla population for spring Chinook, Lower Cowlitz or Clackamas for fall Chinook, south Santiam for winter steelhead, and north fork Lewis for summer steelhead. The recolonization scenario, in which we added a population, had a metapopulation structure more similar to historical conditions than did the preservation scenario, in which we removed a population (Fig. 3).

Most connectivity metrics were sensitive to increased variance in sizes of different populations, but not to identical changes in all populations (which preserved link strengths) (Supporting Information). Larger-size differentials yielded higher connectivity because more individuals emigrated from larger to smaller populations. Conversely, node strength responded to fixed changes in population size but not to changes in variance. Increasing the size of only the largest population substantially increased connectivity. Permutation of original population sizes yielded similar median connectivity levels,

but with considerable variance. Sensitivity to distances among populations differed among metrics. Population independence increased a small amount when populations were farther apart, but there were fewer unconnected populations. This finding suggests that the juxtaposition of all populations relative to one another may be more important than distance among population pairs. We found connectivity metrics to be relatively insensitive to changes in the dispersion parameter α at distances <60 km. However, connectivity metrics were sensitive when proportion of fish straying was large and when the threshold for connection between populations was small, both situations that enhance connectivity.

Discussion

From our simulations, we found that human activities altered the spatial structure among populations of anadromous Pacific salmonids. Although we cannot be certain about the exact structure of historical metapopulations, resilience was likely high. In modern cases in which salmon have naturally colonized new habitat, stray rates are temporarily elevated and colonization occurs rapidly (Pess 2009). There is also abundant evidence that spatial structure and diversity lend stability and resilience to populations of Pacific salmon (Good et al. 2008; Schindler et al. 2010). Consideration of the relations between population size (Bulman et al. 2007) and connectivity

(Harveson et al. 2006) on spatial structure could inform conservation decisions that would maximize metapopulation persistence.

Potential Effects of Managing Spatial Structure

If population size is indeed tied to the amount and quality of freshwater habitat, then we think protecting or restoring areas that can support large source populations will increase metapopulation stability by increasing the number of individuals available to increase the size of or recolonize nearby populations. For Chinook salmon, we found that existing populations with the highest potential to function as sources were the Molalla (spring Chinook), lower Cowlitz, and Clackamas (fall Chinook) populations. These populations were all centrally located and were the largest in each metapopulation. Less clear to interpret was the influence of source population location on metapopulation structure. For instance, we found that the south Santiam and north fork Lewis populations were source populations for winter and summer steelhead, respectively. The south Santiam population is the fourth-largest population and is peripherally located, yet it had the most potential to decrease connectivity if extirpated. Similarly, the north fork Lewis population was the second-smallest population of summer steelhead, yet its position relative to other populations made it important for conserving connectivity, even though its current size is a small fraction of its historical size (inferences about summer steelhead spatial structure should be drawn with caution because there were only 6 populations). The largest populations may not function as sources (Cooper & Mangel 1999). The common practice of protecting the largest population ignores the function of that population within the metapopulation.

A next step in prioritizing populations for conservation may be to evaluate existing habitat quality and the potential for increasing habitat quality. Doing so may help prioritize among populations that would otherwise be rated similarly. For example, we identified 2 fall Chinook populations that would most increase connectivity. The Clackamas currently has higher habitat quality than the lower Cowlitz (Supporting Information). Given limited funding, one might choose to either preserve the Clackamas or to improve habitat quality for the lower Cowlitz, depending on costs, feasibility, and other conservation objectives.

Prioritizing populations for reintroduction depends on the potential for that population to increase connectivity within the metapopulation. Reestablishing populations that were historically sources would probably increase metapopulation persistence the most. Our results suggest that for spring and fall Chinook and winter steelhead, providing access to the upper Cowlitz River would increase metapopulation persistence to a greater extent than would reintroductions above dams in the Cispus,

Tilton, Big White Salmon, Lewis, or other watersheds. A greater number of historically suitable stream kilometers might be regained in the upper Cowlitz than in other watersheds. For anadromous species in stream networks, barriers located nearer to the river mouth block proportionally more of a population's habitat (and may even block habitat for multiple populations) (Fagan 2002). Decisions about restoring connections to extirpated populations also require consideration of potential trade-offs. For instance, barrier removal may increase pathways for invasion by nonnative species (Fausch et al. 2009).

We suggest that synchrony be guarded against. Our results suggest that dispersal rate strongly controls connectivity within salmon metapopulations. Thus, to understand how hatchery fish influence metapopulation structure, it will be necessary to better quantify stray rates and whether they differ between wild and hatchery fish. Straying is a natural process that can enable metapopulations of wild salmon to persist despite localized catastrophes (Quinn 2005; Pess 2009). However, sustained high stray rates by small numbers of fish or even relatively low stray rates by large numbers of fish can increase connectivity and move a metapopulation toward a patchy or panmictic structure. If hatchery-reared fish do stray at higher rates than wild fish (as we assumed in our hatchery and myriad scenarios), then continual elevated straying by hatchery fish could mask declines in wild fish populations. A short-term increase in population size could be offset by increased gene flow and lead to a loss of local adaptations. Over time, increased straying could increase synchrony among populations, as has been observed for some Chinook populations in the Snake River (Moore et al. 2010). Increases in synchrony and related decreases in genetic diversity may limit the ability of salmon to withstand widespread environmental changes (Greene et al. 2010).

Lessons from Graph Theory

Graph theory is relatively simple to implement and allows characterization of spatial structure of populations at fine spatial extents (e.g., Erös et al. 2010) and at coarser spatial extents, as we have done here. Its utility depends on how nodes and connections are characterized, which can be challenging in stream networks (Grant et al. 2007). Nonetheless, our results helped us identify trade-offs among freshwater conservation options that would not have been immediately obvious without consideration of the metapopulation dynamics in the area. As the climate changes, shifts in ocean currents and distributions of at-sea resources and fishes are expected. With improved understanding of these potential changes, graph theory could be used to explore how anthropogenic changes to ocean environments also affect the spatial structure of salmon populations.

Graph theory could easily be extended to evaluate connectivity among populations of other anadromous

species, nonmigratory species, and communities in stream networks with internal structure. Such an approach could further illuminate source-sink dynamics for small stream-dwelling fishes (Waits et al. 2008) and population vulnerability to stressors (Woodford & McIntosh 2010) or community diversity (Brown & Swan 2010) with respect to spatial position within a stream network. Additionally, graph theory might be particularly useful for evaluating trade-offs in the removal of dispersal barriers (Spens et al. 2007; Fausch et al. 2009). Evaluating trade-offs can be difficult. By constructing scenarios of how populations and communities respond to human stressors, as we have done, it is possible to prioritize conservation actions.

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Supporting Information

A map of named populations (Appendix S1), an explanation of our calculation of indices of population size (Appendix S2), watercourse distances and estimates of stray rates (Appendix S3), graphing methods used to assess metapopulation spatial structure (Appendix S4), and sensitivity analysis results (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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