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Setting spatial conservation priorities despite incomplete data for characterizing metapopulations

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## Abstract

Management of spatially structured species poses unique challenges. Despite a strong theoretical foundation, practitioners rarely have sufficient empirical data to evaluate how populations interact. Rather, assumptions about connectivity and source-sink dynamics are often

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30 based on incomplete, extrapolated or modeled data, if such interactions are even considered at  
all. Therefore, it has been difficult to evaluate whether spatially structured species are meeting  
conservation goals. We evaluated how estimated metapopulation structure responded to  
estimates of population sizes and dispersal probabilities, and to the set of populations included.  
We then compared outcomes of alternative management strategies that target conservation of  
35 metapopulation processes. We illustrated these concepts for Chinook salmon (*Oncorhynchus*  
*tshawytscha*) in the Snake River, USA. Our description of spatial structure for this  
metapopulation was consistent with previous characterizations. We found substantial differences  
in estimated metapopulation structure when we had incomplete information about all populations  
and when we used different sources of data (3 empirical, 2 modeled) to estimate dispersal,  
40 whereas responses to population size estimates were more consistent. Together, these findings  
suggest that monitoring efforts should target all populations occasionally and populations that  
play key roles frequently, and that multiple types of data should be collected when feasible.  
When empirical data are incomplete or of uneven quality, analyses using estimates produced  
from an ensemble of available datasets can help conservation planners and managers weigh near-  
45 term options. Doing so, we found tradeoffs in connectivity and source dominance in  
metapopulation-level responses to alternative management strategies that suggest which types of  
approaches may be inherently less risky.

**Keywords:** uncertainty, spatial structure, dispersal, source-sink, conservation

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## **Introduction**

Management of metapopulations (Hanski 1998) poses particular challenges, and setting  
conservation goals can be difficult if movements among populations are not understood (e.g.,  
Ying et al. 2011). There is a rich literature on the theory of population structure and its emergent  
55 properties (Holt 1996, Keeling 2002, Clobert et al. 2012). For example, metapopulations can  
exhibit source-sink dynamics, wherein populations with net demographic surpluses support those  
with net deficits (Pulliam 1988, Heinrichs et al. 2016). Spatial distribution of populations across  
a landscape can promote resilience by reducing the likelihood that all populations will  
experience the same disturbances (Kallimanis et al. 2005, Good et al. 2008). Spatial structure

60 also increases genetic diversity through local adaptation and reduced genetic exchange, which in turn can increase the long-term resilience of the species (Fox 2005).

Despite the strong theoretical understanding of metapopulation processes, practitioners rarely have sufficient empirical data to evaluate how populations interact (Harrison and Taylor 1997, Lowe and McPeck 2014). Rather, assumptions about dispersal and source-sink dynamics  
65 are often based on incomplete, extrapolated or modeled data. Therefore, it has been difficult to evaluate whether spatially structured species are meeting conservation benchmarks. This is especially true for metapopulations in freshwater lotic systems, which do not meet assumptions of classic metapopulation models due to the dendritic nature of stream networks (Fagan 2002, Moilanen et al. 2008, Seymour and Altermatt 2014). Estimates of dispersal among such  
70 populations are crucial for understanding how they interact and for predicting how they will respond to disturbance. Technological advances in mark-recapture, genetic, and modeling methods have led to expansive and growing datasets suited to estimating dispersal. Yet in many cases, limitations specific to each of these methods have prevented a comprehensive analysis (Erős and Campbell Grant 2015, Heino et al. 2015).

75 For species both spatially structured and for which conservation concern is high, a diverse portfolio of populations may be key to long-term persistence through natural and anthropogenic stressors (Anderson et al. 2013, Griffiths et al. 2014). Therefore, consideration of metapopulation processes should inform conservation priorities. For example, an understanding of source-sink relationships can help identify appropriate strategies for reintroduction or  
80 recolonization of animals into habitats from which they have been extirpated (Holland and Bennett 2011, Anderson et al. 2014). Comparing levels of synchrony in demographic trends among populations relative to past levels may suggest whether changes in artificial propagation or sportfish stocking programs are appropriate (Moore et al. 2010, Fox et al. 2013). Understanding spatial relationships among populations may help to prioritize habitat restoration  
85 activities. For instance, improvements in rearing or breeding areas may increase the size of a population, but it may be more beneficial to improve connectivity by restoring habitat in migratory corridors (Cooper and Mangel 1999, Sawyer et al. 2013). These considerations are becoming increasingly challenging as climate change alters habitat conditions and phenology of biological processes (Schiffers et al. 2013, Gienapp et al. 2014, Schuetz et al. 2015).

90 In this paper, our objectives were to: (1) evaluate how estimates of metapopulation  
structure were influenced by population size, methods and data used to estimate dispersal, and by  
the set of populations for which data were available; and (2) evaluate alternative management  
strategies despite uncertainty. We illustrated these concepts for Chinook salmon (*Oncorhynchus*  
*tshawytscha*) in the Snake River, USA. For the first objective, we evaluated how estimated  
95 metapopulation structure differed across a range of abundance estimates using dispersal data  
from three empirical and two modeled sources with different population sets. We asked: how  
sensitive are estimates of metapopulation structure to data gaps or to inaccurate information?  
Answers can help identify management decisions that could be misguided by mis-specified  
metapopulation structure and can highlight locations where additional data can most improve  
100 understanding. For the second objective, we used all available information to compare a suite of  
management scenarios to evaluate how metapopulation structure may respond to strategic  
aspects of recovery efforts, such as increasing the size of certain populations or decreasing  
dispersal by individuals reared in captivity. We asked: What can be learned about tradeoffs  
between alternative management strategies using the information we have? Answers can guide  
105 evaluation of whether current management practices are meeting conservation goals for spatially  
structured populations and what can be done to improve metapopulation function.

## Methods

### *Study area*

110 Our analyses encompassed streams used for spawning and rearing by spring/summer  
Chinook salmon in the Snake River below Hells Canyon Dam and its major tributaries in Idaho,  
Oregon and Washington states, USA (**Figure 1**). The landscape in the surrounding drainages  
ranges from arid grassland to mountainous forest. Many streams are within federally protected  
wilderness areas and are relatively pristine. Others have been influenced by human activities  
115 such as livestock grazing, water diversions, timber harvest, and ore mining. Juveniles generally  
spend one year in freshwater rearing habitats before beginning migration to the Pacific Ocean.  
After 1–4 years in the ocean, adults travel up to 1,500 km to return to their natal streams and  
reproduce. During both migrations, fish navigate 8 hydropower facilities.

The Snake River spring/summer Chinook salmon evolutionarily significant unit (ESU),  
120 one of several along the Pacific Rim, is listed as threatened under the U.S. Endangered Species

Act (ESA; NMFS 2005). Populations within the ESU are considered to be at high risk of extinction within the next 100 years (NMFS 2013). Within this ESU, 32 populations were previously identified by a group of experts and assigned to five “major population groups” (MPGs) within which populations are thought to be more closely related based on a combination of geography, life history patterns, demographic trends, genetic attributes, and environmental information (ICTRT 2003, 2005). Population boundaries are relatively stable through time, although the extent of spawning reaches can vary annually. Populations in the Clearwater River basin are not formally part of the listed ESU, but artificial propagation programs have led to significant natural production in recent years.

At present, abundance and production of natural-origin fish in this ESU are substantially lower than historical estimates. Wild Chinook salmon were functionally extirpated from several tributaries due to mining practices that degraded habitat or to construction of impassable dams (Table 1). Fish hatcheries are operated in all MPGs except the Middle Fork Salmon River. Hatcheries operate to support numbers of wild fish spawning (i.e., conservation programs), provide fish for harvest (i.e., fishery enhancement programs), or both (Naish et al. 2008). Conservation programs primarily use local brood stock in order to maintain genetic diversity, whereas fishery enhancement programs may have used nonlocal broodstock. We did not distinguish between hatchery-origin spawners from each type of program in our analyses.

#### *Estimating ESU structure*

We used constructs from graph theory to describe spatial relationships among populations within the ESU (Schick and Lindley 2007, Erős et al. 2011, Fullerton et al. 2011). Populations were depicted as nodes (circles in figures), with geographic location given by position and population size represented by diameter. Dispersal among populations was represented by edges (arrows in figures), with line thickness representing magnitude and arrows denoting direction. Graph theoretical techniques have been successfully applied to evaluate human impacts to metapopulation structure in a wide variety of aquatic ecosystems (Saunders et al. 2015). To construct graphs, we created a matrix of potential transitions among populations, calculated as the product of population size and the probability of dispersal (data described below). Diagonals in the transition matrix represent the number of fish homing and recruiting to their natal population; off-diagonal elements are emigration (columns) or immigration (rows) between each pair of populations. Edge weights ( $w$ ), the number of individuals emigrating minus

those immigrating divided by donor population size, represented realized net dispersal. In graphs, we constructed edges between populations  $i$  and  $j$  if the donor population contributed more than  $z = 1\%$  of net recruitment to the recipient (Schick and Lindley 2007).

155 We calculated a suite of patch-level metrics (**Figure 2**) to characterize properties of each population pertaining to its role in the metapopulation. These metrics helped identify populations that were isolated (not connected to any others), the degree of independence (where recruitment in a population is more strongly driven by reproduction than by immigration) and which populations functioned as sources or pseudo-sinks (the latter are populations with abundances  
160 that are supplemented by immigration from other populations but which may be self-sustaining in the absence of immigrants). The metrics are complementary, yet there was some conceptual overlap. Therefore, we computed a principal components analysis (PCA) to reduce dimensionality of population metrics and to help visualize how populations differed in their roles as metapopulation components. The PCA enabled us to compare two populations with respect to  
165 multiple metrics simultaneously. For instance, both populations may be well connected, but one may be a source and the other a pseudo-sink.

We also computed a suite of graph-level metrics (**Figure 2**) that allowed us to compare how metapopulation structure differed among various scenarios (described below). Graph-level metrics characterized properties of the entire metapopulation such as the fraction of isolated  
170 populations, the fraction of potential connections realized, the fraction of fish migrating, and whether the graph was dominated by sources or by pseudo-sinks. For graph-level metrics, we used boxplots to inspect differences among results.

## *Data*

### 175 **Population size**

We estimated the size of populations as the geometric mean of spawners presumed wild (i.e., unmarked) for brood years 1999-2008 (i.e., fish that returned to spawn between 2000 and 2012; **Table 1, Table S1**). Spawner abundance estimates were derived from a combination of redd counts, carcass surveys, and adults observed annually at weirs or in index spawning  
180 reaches. These data were collected by multiple agencies and compiled by NMFS (2010). For populations lacking the full time series, we relied on agency reports to estimate spawner abundances.

## Dispersal

185 We define *dispersal* probability as the probability of emigration by an individual from its natal population into a non-natal population to reproduce. For salmon, this is termed donor-based *straying* (Keefer and Caudill 2013); in this paper we use the two terms interchangeably. We considered dispersal estimated from five sources: (1) coded wire tag (CWT) data; (2) passive integrated transponder (PIT) tag data; (3) genetic estimates of migration rates; (4) a hydrologic distance model; and (5) a habitat attraction model. Each approach to estimating dispersal  
190 probabilities had a distinct suite of strengths and assumptions (**Table 2**). For instance, tagging approaches did not confirm whether animals had successfully contributed offspring to the population. Past events may have influenced current patterns of genetic variation. Models assumed that movement was driven by a simple mechanism (distance or habitat quality). Due to data limitations, we were unable to incorporate relationships between dispersal probability and  
195 sex, age, size, life history stage, demographic characteristics, and environmental conditions (Keefer and Caudill 2013, Westley et al. 2013, Westley et al. 2015).

### Coded wire tag data

200 We queried observations of hatchery fish implanted with coded wire tags (CWT) (PSMFC 2014). The database contains records contributed by various organizations; there is no systematic recovery program. We used recoveries of spring/summer Chinook salmon brood years 2000–2009 in the Snake River basin and retained only records that were presumed final destinations (where tags were collected from carcasses on spawning grounds or from adults returning to hatcheries) and omitted recoveries from locations that may have been “en route” to  
205 intended spawning locations (e.g., the mainstem Columbia, Snake and Salmon rivers). We calculated dispersal probabilities as the proportion of fish released as juveniles from a population that were recovered as adults in a non-natal population. We aggregated data within population boundaries and averaged dispersal probabilities across years. To be conservative, we treated missing values (i.e., no data available for a population pair) as zeroes when averaging straying  
210 rates but omitted missing values when averaging homing rates. There was an annual average of 323 returning fish (range: 4 to 48 fish per population).

### Passive integrated transponder tag data

215 We queried observations of wild fish implanted with passive integrated responder (PIT)  
tags (CBR 2014). We used final detections of spring/summer Chinook salmon brood years 2002-  
2008 in the Snake River basin; we omitted detections of returning adults for locations that may  
have been “en route” to intended spawning locations such as in lower mainstems and at dams, as  
well as records for tags that were likely not attached to a live fish. We recognize that records  
may not represent the final destination (i.e., fish may have continued to move but not been  
220 detected again) or the *intended* final destination (i.e., fish died after the last detection but before  
making it to the spawning grounds). We calculated dispersal probabilities as the proportion of  
fish tagged as juveniles from a population whose final detection as adults occurred in a non-natal  
population. We aggregated data within populations and across years as described for CWT data.  
There were data for an annual average of 112 returning fish (range: 1 to 20 fish per population).

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### Genetic data

We evaluated genetic connectivity by estimating pairwise migration rates among a subset  
of populations for which we had microsatellite genotypic data (Van Doornik et al. 2011, Van  
Doornik et al. 2013). We computed estimated effective population sizes and genetic distances,  
230 and then used these to estimate pairwise migration rates (Wright 1931).

We estimated the effective number of breeders ( $N_b$ ) for each collection site, in each year,  
with genetic linkage disequilibrium (Hill 1981) using the computer program LDNE with bias  
correction for finite population and sample sizes (Waples 2006, Waples and Do 2010). We then  
calculated the harmonic mean  $N_b$  across years and multiplied by population-specific generation  
235 time (Myers et al. 1998, McPherson et al. 2006, Waples et al. 2010) to obtain an estimated  
evolutionarily effective size ( $N_e$ ) for each population.

To estimate pairwise genetic distances among all populations, we combined genetic data  
across collection years within populations and calculated pairwise  $G''_{ST}$ , a multilocus equivalent  
of the  $F_{ST}$  fixation index standardized for heterozygosity and for a limited number of populations  
240 (Meirmans and Hedrick 2011). When populations are small, genetic distance estimates are  
upwardly biased (Waples 1998) so we subtracted  $1/2N_b$  from the pairwise genetic distance  
estimates (where  $N_b$  is the harmonic mean for the pair of populations in question). Finally, we  
estimated pairwise migration  $m$  from the relationship



$$G_{ST}'' = \frac{1}{\left(4N_e \frac{d^2}{(d-1)^2}\right) m + 1} \quad [\text{Eq. 1}]$$

where  $N_e$  is the harmonic mean of the  $N_e$  estimates for the pair of populations in question and  $d$  is the finite number of subpopulations (Wright 1943, Slatkin and Voelm 1991).

We recognize a variety of simplifying assumptions that go into this estimate (**Table 2**), and we also recognize different perspectives and conclusions based on effective gene flow and movement of individuals among locations and breeding aggregates. Unsourced populations could be responsible for significant indirect gene flow among our study populations. Therefore, our genetic estimate should be viewed as an “effective” migration rate, including both direct migration of successfully spawning individuals moving from one population to another, as well as indirect gene flow mitigated through a stepping stone effect via “ghost” populations (Beerli 2004, Slatkin 2005). In our study system, the size of such a mitigating effect is unknown and may vary across river basins and through time.

#### Missing data

Coverage across populations differed depending on the data source (**Table S7**). Missing data can influence the interpretation of metapopulation structure (Moilanen and Nieminen 2002, Slatkin 2005). Therefore, we filled missing cells in dispersal matrices (i.e., unsourced dispersal between population pairs) using a hybrid bootstrap-simulation approach. We consider the potential impact on estimated metapopulation structure of omitting populations in the *Sensitivity analysis* and *Information scenarios* sections.

Plots of empirical estimates of dispersal versus hydrological distance, or distance along the river network between each pair of populations (**Figure S1; Table S8**), suggest a relationship whereby dispersal probabilities decline exponentially with distance between populations (**Figure 3**). Similar relationships with distance have been found for steelhead (Pearse et al. 2007) and are common for other species (Lowe and McPeck 2014).

Yet there is substantial complexity in the shape of this relationship. To capture uncertainty in estimating dispersal for missing cells and to propagate its effect through estimation of metapopulation structure, we used the following approach.

(1) For each type of empirical data (CWT, PIT and genetic), we used generalized nonlinear least squares (nlme package for R; Pinheiro et al. 2014) to fit an exponential decay dispersal kernel (Clark et al. 1998):

$$p_{ij} = \exp\left(-\left|\frac{d_{ij}}{\alpha}\right|^c\right) \quad [\text{Eq. 2}]$$

where  $\alpha$  (in km) is a dispersion parameter (the rate of decay from the source),  $c$  is a dimensionless shape parameter controlling the degree of kurtosis, and  $d_{ij}$  is hydrologic distance between populations  $i$  and  $j$ . The  $\alpha$  parameter is related to the dispersal ability of the species, and  $c$  controls the shape of the kernel's tail ( $c < 1$  gives a fat tail;  $c = 1$  is exponential). For each dataset, there was a strong homing tendency and a fat tail suggesting occasional long distance dispersal by a few individuals (**Figure 3**).

(2) Next, we filled missing cells in the dispersal matrix. The value  $s$  representing estimated dispersal from population  $i$  to population  $j$  was obtained by randomly drawing a sample from a lognormal distribution of possible dispersal probabilities at that distance:

$$s_{ij} = p_{ij} \times \ln N(\mu, \sigma^2) \quad [\text{Eq. 3}]$$

where  $\mu = 0$ ,  $\sigma^2 = 0.5$ , and  $p_{ij}$  is the predicted value from the fitted dispersal curve from Equation 2. We chose a lognormal distribution to ensure that sampled values were usually  $\leq p_{ij}$  but occasionally were very large. We stress that this sampling was only used to fill cells with missing data; empirical data were preserved when available. This gave one instance of a complete matrix of estimated dispersal probabilities for a given type of data.

(3) To ensure that columns summed to 1 (i.e. homing and straying summed to 100%), we column-standardized the matrix, preserving homing probabilities and adjusting straying probabilities proportionally.

(4) We used the filled dispersal matrix from step 3 and spawner abundances to estimate metapopulation structure as described above. We constructed graphs, computed summary metrics and stored results.

(5) We repeated the first 4 steps 1,000 times and interpreted the median result.

#### Hydrologic distance model

We pooled all 3 sources of empirical data (CWT, PIT, and genetic) to fit a curve using Equation 2. Fitted parameters were  $\alpha = 2.0$  and  $c = 0.32$ . Instead of deterministically using the

300 predicted values, however, we introduced stochasticity by following steps 2-5 above. In step 2, we did not preserve any empirical estimates. Instead, each cell in the matrix was filled with a random sample using Equation 3.

#### Habitat attraction model

305 Conceivably, fish may be attracted to stray into a population due to social stimuli during migration or if they are able to detect (e.g., via olfaction of water chemistry or conspecifics) that the quality of spawning habitat is more attractive than what they are likely to find in their natal stream. We began with the first two steps of computing dispersal probabilities using the hydrologic distance model. Dispersal probabilities resulting from step 2 were then multiplied by the ratio of habitat quality in a given population to habitat quality in the natal population (this  
310 ratio ranged from 0 to 1). Habitat quality was represented by an index of intrinsic potential spawning habitat based on stream width, gradient, valley width, and sediment characteristics described in Cooney and Holzer (2006) (**Table 1**). We continued with steps 3-5.

#### Ensemble dispersal estimate

315 We also computed a dispersal matrix using all available information weighted equally so that we could evaluate the influence of missing data, and to have a common source of dispersal data for characterizing existing conditions and for evaluating management scenarios. The combined (hereafter, 'ensemble') dispersal matrix was calculated by first producing four instances of complete dispersal matrices estimated from CWT data, PIT tag data, genetic data,  
320 and the habitat attraction model. We then took the median of the four matrices (i.e., element by element), and column-standardized the result (**Table S9**). As before, we incorporated uncertainty by using the median result of 1,000 estimates of metapopulation structure. The ensemble dispersal probabilities differed from those estimated using the hydrologic distance model in two ways: (1) empirical stray rates were preserved (only cells with no data were estimated); and (2)  
325 empirical values were combined with estimates from the habitat attraction model.

#### *Sensitivity analysis*

To explore how missing data or inaccurate estimates of population size or dispersal could affect results, we conducted a sensitivity analysis. We used observed spawner abundance for

330 wild fish during 1999-2008, the ensemble dispersal dataset, and included all 32 ESA-listed  
populations to estimate baseline metapopulation structure; we considered this to be the ‘truth’.  
We then evaluated how the metapopulation responded when we altered a random set of 5, 10, or  
20 populations in one of three ways: (1) the size of selected populations was increased or  
335 decreased by 50%, (2) dispersal from selected populations was increased or decreased by 50%,  
or (3) selected populations were omitted (i.e., assumed not to be part of the metapopulation). We  
ran 1000 simulations for each situation. To evaluate how changes to a single population could  
influence the metapopulation, we repeated this analysis but modified only one population at a  
time.

#### 340 *Information scenarios*

We explored how estimated metapopulation structure could be influenced by the  
completeness and accuracy of available data. By placing results from these scenarios in the  
context of results from the sensitivity analysis, we aimed to learn how robust ESU structure was  
to inaccuracies in available information.

345 To evaluate how *population size* influenced metapopulation structure, we varied  
population size estimates while holding constant the dispersal probabilities (ensemble) and the  
set of populations (all 32 ESA-listed populations). We considered four population sizes (**Table  
S1**): (1) estimated spawner abundance during the late 1800s, computed by multiplying an  
estimate of potential spawners in the Snake River (400,000 fish; Chapman 1986) by a  
350 population-specific index of spawning habitat potential (Cooney and Holzer 2006) (*hist*); (2)  
observed spawner abundance during 1962-1971, a period when fish were moderately abundant  
coincident with favorable ocean conditions, fewer hydropower dams, and prior to the  
construction of fish hatcheries in the Snake River (*mod*); (3) observed spawner abundance for  
wild fish during the recent decade, 1999-2008 (*wild*); and (4) observed abundance of both wild  
355 and hatchery fish observed on the spawning grounds, 1999-2008 (*w+h*). Comparisons across  
these representations gave insight to how metapopulation structure might have changed over  
time. Both the moderate and historical scenarios included estimates of abundance in the four  
populations believed to be functionally extirpated presently. Comparisons between *w+h* and *wild*  
360 scenarios enabled us to evaluate the potential contribution of the number of hatchery-origin  
spawners.

To evaluate how the *type of data used to estimate dispersal* influenced metapopulation structure, we varied dispersal estimates while holding constant population size (recent wild spawner abundance) and the set of populations (all 32 ESA-listed populations). We compared metapopulation structure estimated using dispersal probabilities computed from CWT data, PIT tag data, genetic data, the hydrologic distance model, and the habitat attraction model.

Finally, we evaluated how estimated metapopulation structure reflected the specific *set of populations* included. We used recent wild spawner abundance and the ensemble dispersal probabilities, but varied the set of populations, considering only sets of populations for which single-source dispersal information was available (10, 13, and 16 of the 32 populations for CWT, PIT, and genetics, respectively). We also evaluated how inclusion of populations in the Clearwater River would alter estimated metapopulation structure. We were interested to see whether potential straying by hatchery-origin fish from the Clearwater could have any influence on listed populations in other MPGs.

### 375 **Management scenarios**

We used scenarios to investigate how alternative management strategies or environmental stressors might alter interactions among salmon populations. These scenarios were intended to address strategic aspects of ESU recovery (i.e., increasing size of certain populations via habitat restoration or decreasing dispersal by hatchery-origin fish), rather than specific tactics used in each population. Management scenarios compared a representation of existing conditions from the recent decade (*R*) to a variety of alternative scenarios (**Table 3**). For all scenarios, we used ensemble dispersal probabilities and included all 32 ESA-listed populations. Wild spawner abundances were used for all scenarios except those for which we were explicitly interested in the influence of hatchery fish. For hatchery influence scenarios, we increased (*H+*) or decreased (*H-*) the number of hatchery spawners in populations with hatcheries and also increased dispersal probabilities, as some evidence suggests hatchery fish may stray at higher rates (Keefer and Caudill 2013, Ford et al. 2015). For habitat alteration scenarios, we increased or decreased the number of spawners by 50% in all populations (*A+* or *A-*), populations designated by the HSRG (2009) as primary (*P+* or *P-*), and populations designated as stabilizing (*S+* or *S-*). We also examined a scenario that increased abundance in the four functionally extirpated populations (**Table 1**) to 10% of the historical estimate (*F*).

We visualized how salmon metapopulations in each scenario differed from baseline conditions with a PCA. The biplot showed metapopulations (each scenario represented by one point) in relation to graph-level metrics. By plotting the first two principal components, we reduced six different but related metrics to two essential elements: the degree to which the metapopulation is dominated by a few large source populations (y-axis) and connectivity among populations (x-axis) (Harrison and Taylor 1997, Fullerton et al. 2011). This plot allowed us to evaluate how different scenarios influenced the relative position of a metapopulation along each of these axes, regardless of absolute magnitudes.

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## Results

### *Estimated ESU structure*

In the estimated present-day metapopulation, populations within an MPG shared more connections than those between MPGs (**Figure 4**). Interactions were often strongest between populations near the mouths of adjacent rivers. This result was supported by the relationship between genetic distance  $F_{ST}/(1-F_{ST})$  and hydrologic distance for Salmon River populations (**Figure S2**).

Populations that were most independent, or sustained primarily by individuals that accurately homed rather than by immigrants, included the Imnaha, Lostine, Tucannon, Pahsimeroi, and Catherine (**Table S10; Figure 4**). Dispersal from these populations was generally lowest, suggesting that they were also the most isolated populations. Conversely, well-connected populations included Yankee Fork Salmon, EF Salmon, Bear Valley, Salmon River below Redfish Lake, and Camas. Populations acting as the strongest sources included upper Middle Fork Salmon, Chamberlain, Secesh, Bear Valley, and Minam, whereas those acting as the strongest pseudo-sinks included upper Grande Ronde, Sulphur, Yankee Fork Salmon, Loon, and Camas.

### *Sensitivity analysis*

Compared to the unmodified baseline metapopulation structure, effects on metapopulation structure were generally smallest when we altered the size of a random subset of constituent populations and largest when we used a reduced set of populations; altered dispersal had intermediate but considerable effects (**Figure 5**). In most cases, the medians and variance in

metrics were comparable to baseline structure. Variability in responses arose because the metapopulation responded differently to the particular set of populations that had been altered in a given simulation, as well as to our stochastic sampling of dispersal curves. Effect size increased with the number of populations altered. The most notable effects were when 20 populations were omitted and when we altered dispersal from 20 or 10 populations. Removing populations caused the fraction of migrants and the fraction of edges to decrease whereas the fraction of sources and fraction isolated increased. Increasing dispersal for a random subset of populations caused an increased fraction of migrants and fraction of edges. Decreasing dispersal caused a decreased fraction of migrants and edges and an increased fraction isolated. The fraction of sources relative to sinks was highly sensitive to the specific set of populations altered; this metric was more responsive to altered population size and inclusion than to dispersal.

Changes to certain individual populations had more influence on the ESU than others. The fraction of edges was unduly influenced by changes to the upper Middle Fork Salmon, South Fork Salmon mainstem, Panther Creek, and Big Sheep Creek, among others (**Figure 6**). A reduction in the fraction of edges was notable when the upper Middle Fork population was omitted, when this population decreased in size, and when dispersal from this population decreased but was relatively unchanged when either population size or dispersal increased.

### *Information scenarios*

Estimated metapopulation structure was idiosyncratic and depended on the particular combinations of empirical data used to estimate size and dispersal, and which populations were included. As spawner abundance decreased from the late 1800s (*hist*) through a period when spawners were moderately abundant (*mod*) to conditions in the recent decade (*wild*), we estimated that both the number and fraction of fish migrating decreased and source dominance increased slightly (**Figure 7; Table S11**). The fraction of isolated populations was lowest in the estimated historical metapopulation and highest for the metapopulation with moderate spawner abundance. The fraction of edges was lowest with moderate spawner abundance and highest with recent estimates of spawner abundance. When we included both hatchery and wild spawners ( $w+h$ ), we found a slightly larger number but smaller fraction of fish migrating and a higher fraction of sources than when we considered wild fish only (**Figure 7**). This resulted in slightly fewer isolated and more connected populations but similar inter-MPG interactions.

455 Dispersal probabilities and the corresponding fraction of migrants were highest when  
estimated using models (*hab*, *hyd*), lowest when estimated from genetic data (*gen*), and  
intermediate for the tag-recapture methods (**Figure 7; Table S11**). For both tag methods (*cwt*,  
*pit*), fish exhibited a strong homing tendency; when straying occurred, it tended to be into nearby  
populations (**Table S2, Table S3**) but PIT tag data revealed several rare instances of long-  
distance straying into the Upper Columbia River ESU. Use of genetic data yielded a  
460 metapopulation dominated by more sources and fewer sinks than metapopulations estimated  
using other data sources. Despite having the lowest dispersal probabilities, the metapopulation  
estimated using genetic data had more edges and fewer isolated populations than we saw with  
tag-based estimates (**Figure 7**). Because the relationship between genetic dispersal and distance  
had a fat tail, long-distance dispersal by a few individuals was more frequent, i.e., many  
465 populations exchanged a small number of fish. The ensemble dispersal estimate mediated values  
that were especially high in one dataset and low in another (i.e., the net effect was reduced or  
cancelled).

When we included only a subset of populations, we found a reduced fraction of migrants  
and edges and an increased fraction of sources and isolated populations (**Figure 7; Table S11**).  
470 Inclusion of populations in the Clearwater River caused a higher fraction of migrants and  
reduced fraction of sources and isolated populations.

Metapopulation structure as characterized using any single dispersal dataset sometimes  
produced responses outside of what we might have expected based on the sensitivity analyses.  
For instance, using a modeled dispersal estimate produced a much larger fraction of migrants  
475 than the sensitivity analysis scenario that had the strongest likelihood of altering this metric (the  
scenario in which we increased dispersal from 20 random populations by 50%). However, the  
fraction of edges increased only about as much as the sensitivity analysis scenario where we  
increased dispersal in five random populations (compare **Figures 7 and 5**).

#### 480 ***Management scenarios***

Compared to the present-day scenario (*R*), connectivity among populations was higher  
and the metapopulation was more dominated by a few large sources when hatchery influence  
increased (*H+*) (**Figure 8; Table S12**). Conversely, when the influence of hatchery fish  
decreased (*H-*), connectivity was reduced and source dominance slightly increased.



485 In all other scenarios, we used only wild fish and did not modify dispersal, so differences  
in connectivity among scenarios were emergent properties resulting from altered source/sink  
relationships when population size differentials changed. We found reduced connectivity and  
source dominance when habitat quality was decreased in all populations (*A-*) or in populations  
designated as ‘primary’ (*P-*) (**Figure 8**). Habitat improvements in all populations (*A+*) or in  
490 populations designated as ‘stabilizing’ (*S+* and *S-*) had little effect but habitat improvements in  
primary populations (*P+*) increased both connectivity and source dominance marginally. All  
habitat improvement scenarios had less effect on connectivity and a comparable effect on source  
dominance as hatchery scenarios.

Estimated metapopulation structure changed dramatically when we re-established the  
495 four extirpated populations (*F*). This scenario had the lowest source dominance but higher  
connectivity than all scenarios except the increased hatchery influence scenario (*H+*).  
Lookingglass drew immigrants from nearby populations, whereas Panther interacted in complex  
ways with its neighbors, sending fish to the North Fork Salmon but receiving many more fish  
from populations in the lower Middle Fork Salmon. Asotin and Big Sheep remained isolated.

500 Individual populations responded differently to management scenarios. For example, in  
Chamberlain Creek, neither independence nor flow direction responded appreciably to any  
scenario, whereas both metrics were strongly influenced by many scenarios in the upper Grande  
Ronde population (**Figure S15**).

## 505 **Discussion**

Our study illustrated that missing or inaccurate data can have substantial influence on  
estimated metapopulation structure. We found that in general, omission of populations had the  
greatest potential to misrepresent metapopulation structure. Metrics of metapopulation structure  
were also influenced considerably by dispersal estimates, and to a lesser degree by estimated  
510 population size. The common practice of managing individual populations independently may be  
overlooking the influence of and reliance on neighboring populations. Our results suggest that  
monitoring efforts should target all populations occasionally and populations that play key roles  
frequently, and that multiple types of data should be collected when feasible.

When empirical data are incomplete or of uneven quality, analyses using estimates  
515 produced from an ensemble of available datasets can help conservation planners and managers

weigh near-term options. Our estimate of metapopulation structure for the Snake River spring/summer Chinook salmon evolutionarily significant unit (ESU), based on all available information, was congruent with previous findings (ICTRT 2003, 2005, Thorson et al. 2014, Jorgensen et al. 2015). Interestingly, we found more interactions among populations within the Middle Fork Salmon River than expected, given that no fish hatcheries are operated there. The mouths of rivers used by these populations are closely spaced, which may promote straying opportunities. We had few empirical data for estimating dispersal rates among these populations, so we remain unsure whether this finding represents a real example of the influence of dendritic stream network structure on dispersal processes. Some studies suggest that dendritic network structure can influence metapopulation structure (Mari et al. 2014, Yeakel et al. 2014) whereas others found no effect (Webb and Padgham 2013).

Below, we use our findings for this salmon metapopulation and the questions posed in the introduction as guides to consider (1) how information level can influence management options for spatially structured populations and how monitoring can be targeted to reduce uncertainty, and (2) what can be learned about tradeoffs of alternative management decisions despite uncertainty.

### ***Impact of information level on metapopulation characterization***

At least four pieces of information are paramount to accurately describing spatially-structured populations: the number of component populations, inter-population dispersal, the size of individual populations, and their spatial arrangement (Lande 1988, Moilanen and Nieminen 2002, Sutherland et al. 2014). We evaluated how sensitive our characterization of the Snake River salmon metapopulation was to the first three of these and indirectly to the fourth (populations retained their locations throughout our analyses, but spatial configurations of subsets differed).

### **Set of populations**

We found that failure to account for all populations had a larger effect than did potential inaccuracies in the size of populations or dispersal rates. Unknowingly (or intentionally) ignoring “ghost” populations may cause managers to think that populations are more isolated than they really are. Such a belief may result in prescriptions to enhance connectivity among populations,

which may unintentionally decrease local adaptation and increase synchrony among populations (Paradis et al. 1999, Fox et al. 2013), rendering them less resilient to widespread stressors. If one of the missing populations is a large or centrally located source, a nearby sink population could  
550 artificially appear to be highly productive and function independently (Cooper and Mangel 1999). Managers may choose to protect the sink population without knowing that its status relies heavily on an unknown neighbor. To avoid these pitfalls, we recommend that monitoring be as spatially inclusive as possible. This may mean collecting basic information for all populations occasionally instead of, or in addition to, the common practice of more intensely monitoring only  
555 a few index populations. Basic information will be sufficient for populations having low potential to interact with other populations (e.g., those located far from others or with demonstrated independence). However, for populations suspected of having significant interactions (e.g., centrally located or large populations or those with the potential to be influenced by artificial propagation), more accurate empirical estimates could substantially  
560 improve understanding about metapopulation structure and how it changes through time. If information of consistent quality is not available for all populations, using modeled data or ensembles created using a variety of data may be preferable to permitting data gaps. Only by considering the metapopulation as a whole can managers envision how changes in one population might cascade to other populations.

565 The specific set of populations omitted sometimes caused responses in opposite directions and with vastly different magnitudes, suggesting that certain populations have stronger roles in the metapopulation than others or, alternatively, that spatial juxtaposition of populations is important. Hand et al. (2016) found that relationships between climatic variation and metapopulation processes were not consistent across steelhead metapopulations in the Columbia  
570 River basin, and suggested that practitioners should be wary in extrapolating conclusions from one metapopulation to another. Heinrichs et al. (2016) found that strong source-sink dynamics emerged in theoretical metapopulations under a diverse combination of potential controlling factors, suggesting that emergent properties are not easily predictable based on patterns in underlying data.

575

## Dispersal

Dispersal estimates also influenced our characterization of metapopulation structure considerably. Our sensitivity analysis revealed that over- or under-estimating dispersal for a random subset of 5, 10, or 20 populations affected estimates of connectivity and isolation but did not influence trends in the proportion identified as sources. Had we used only modeled estimates of dispersal, we may have concluded that the metapopulation was too-well connected and suggested taking measures to decrease connectivity (Jackson and Pringle 2010, Rahel 2013) when in reality there may be multiple isolated populations in need of intervention to avoid extinction. Conversely, had we used a single type of empirical estimate of dispersal, we may have falsely assumed interactions among populations to be too low and suggested steps to enhance connectivity.

Using genetics dispersal estimates painted a very different picture of metapopulation structure than when we used other approaches. It only took a few successful long distance dispersal events to maintain genetic connections among populations (i.e., the dispersal curve had a fat tail) whereas tag-recapture data and distance-based dispersal models were less likely to detect rare events. A genetics approach conveys the movement of genes among populations whereas a demographic approach conveys movement and productivity of individuals (Lande 1988, Kanno et al. 2014). The two may be complementary ways of characterizing metapopulations, each providing a valuable perspective for managers. Using genetic data is more relevant for measuring and maintaining genetic diversity over generations, whereas using demographic information may highlight more immediate conservation concerns such as identifying a population at imminent risk of extinction.

Monitoring dispersal remains a key challenge (Lowe and McPeck 2014). Most ecologists would agree that empirical estimates are favorable compared to modeled estimates because they are more likely to represent real processes. Yet empirical estimates are expensive to collect and are constrained by the unique suite of assumptions specific to each data type. Until a more complete mechanistic understanding of dispersal is available, it seems prudent to monitor dispersal using multiple techniques when possible. Monitoring a common subset of populations would enable comparison across methods and years. Ultimately, we felt that using an approach that included empirical estimates for dispersal where available (i.e. our ensemble dataset) was best because this dataset muted some of the extreme values seen in individual datasets. If biases

associated with each empirical dataset were known, a better approach would be to weight estimates before combining them.

610 Monitoring dispersal from the natal population to the population in which animals reproduce may not completely represent dispersal processes for species with complex life history strategies such as salmon. For instance, Copeland et al. (2014) found that a substantial proportion of juvenile spring/summer Chinook salmon in the Snake River rear downstream from their natal streams. Given that imprinting is believed to occur throughout their stream occupancy, this behavior could influence homing accuracy (Westley et al. 2013). Other approaches for 615 estimating dispersal might prove to be great resources for filling gaps and expanding our understanding about dispersal. For instance, recent studies have identified rearing habitats by analyzing chemical signatures in fish otoliths (ear bones) and water from different streams (Kennedy et al. 2002, Hamann and Kennedy 2012). Radiotelemetry data are accumulating for this ESU as well (Keefer and Caudill 2013) that could provide important information about 620 populations for which we currently know little. For other species, information reported by citizen scientists (e.g., the Christmas bird count or trends in social media discussions) could be useful sources of information (Donnelly et al. 2013, Kirilenko and Stepchenkova 2014).

### **Population size**

625 Our characterization of metapopulation structure was least influenced by estimates of population size. In the sensitivity analysis, the proportion of sources was more responsive than connectivity measures to perturbations in size for a random subset of populations. Estimates of metapopulation structure in earlier times (moderate and historical abundance scenarios) had higher numbers of fish migrating but fewer sources and connections. In addition to abundance 630 declines across the whole ESU, changes in metapopulation structure from historical to recent scenarios also reflect the loss of the four populations now considered to be functionally extirpated (we have already demonstrated the influence of missing populations). Estimated metapopulation structure may be robust to estimates of population size as long as relative sizes (i.e., compared to one another) are reasonably realistic. However, source-sink dynamics may be 635 misunderstood if size is inaccurately estimated for populations that are near in space and very different in size. Therefore, increasing abundance for a subset of populations by improving habitat or bolstering hatchery fish production may be safest when managers are reasonably

confident that any resulting change in source-sink dynamics will have a neutral or positive effect on conservation goals.

640 For the well-studied Snake River spring/summer Chinook salmon ESU, we had high confidence in spawner abundance estimates for most populations (i.e., those that have been monitored consistently for decades). Those for which we had lower confidence were unlikely to play key roles, based on our assessment. Continued tracking of population sizes will be necessary to explore how population interactions may be changing. Population productivity – the  
645 proportion of fish from each population that return to reproduce – may better reflect population size than spawner abundance. However, productivity estimates are often difficult to obtain and monitoring abundance as a proxy has a long history in species management.

### ***Managing metapopulations despite uncertainty***

650 The recovery plan for the Snake River spring/summer Chinook salmon ESU identifies targets for abundance, productivity, diversity, and spatial structure that will need to be met for the ESU to be considered viable, i.e. at low risk of extinction in 100 years (NMFS 2013). We did not measure productivity over time and therefore cannot directly evaluate progress toward recovery plan targets, which are defined in terms of long-term viability. Moreover, identifying  
655 specific recovery actions necessary for each population was beyond the scope of this analysis. However, our analysis comparing alternative management strategies can provide a baseline for conservation planning that can be updated adaptively as new information becomes available and can guide near-term solutions. Comparisons of scenarios highlight suites of actions that are most or least likely to influence long-term risk.

660 Our results suggest that safe bets are strategies that increase habitat quality, especially in populations identified as having primary roles (i.e., large or central sources). Although we saw no benefit to the metapopulation of habitat improvements in supplementary populations (those likely to be pseudo-sinks), managers will need to also consider the ecological and cultural value of such populations. Comparison of management strategies can also suggest how actions will  
665 affect a specific population. For example, Chamberlain Creek maintained its independence despite increased interaction with neighboring populations in habitat improvement scenarios. Riskier strategies include those that have the potential to alter source-sink dynamics by inadvertently failing to protect key populations (i.e., unknown sources or stepping stone

populations), opening new areas or drastically improving habitat quality in previously extirpated  
670 areas, and supplementing with artificially reared individuals. The effect on the metapopulation of  
“stepping stone” populations could be positive by providing a source of immigrants, but could  
also distract individuals away from more suitable breeding locations (Kramer-Schadt et al.  
2011). Recovery activities that involve active movement of live animals such as managed  
relocation or assisted migration should consider the potential to impact resident animals (Lawler  
675 and Olden 2011, Olden et al. 2011).

In our analysis, we assumed equal reproductive success of wild and hatchery fish. In  
scenarios in which we included effects of hatchery fish, populations having hatcheries exported  
more fish to neighboring populations. Wild populations are not completely isolated from  
hatchery programs, so if real, such interactions could influence viability. Previous analyses have  
680 suggested that hatchery fish have had minimal influence on genetic diversity in this ESU despite  
high numbers of hatchery strays on spawning grounds (Van Doornik et al. 2011, Matala et al.  
2012, Van Doornik et al. 2013). Others found reduced fitness of offspring from hatchery parents  
(Christie et al. 2014). Hatchery fish may impact the fitness of wild fish through demographic or  
ecological interactions such as competition for mates by spawners or competition for resources  
685 by juveniles (Naish et al. 2008, Buhle et al. 2009). Including hatchery fish in our spawner  
estimates did not alter interactions between MPGs. These results seem consistent with recent  
hatchery practices in this ESU in which broodstock are primarily selected from sources within  
the same MPG (HSRG 2009). Naturally spawning fish in the Clearwater are presumably derived  
from hatchery stocks, and therefore might be expected to stray into other populations. When we  
690 included Clearwater populations in the metapopulation, we saw the potential for increased  
interaction with populations in the lower Snake River. However, the habitat occupied at present  
(upper reaches of the South Fork Clearwater, Lochsa and Selway rivers) is sufficiently distant  
from the other populations that straying would have to be high to generate a detectable effect.

## 695 *Conclusions*

We have shown how data limitations can influence perceptions about metapopulation  
structure for a species for which we have a relatively large amount of information. Data gaps and  
dispersal estimates had the greatest potential to influence results. Many species have fewer data  
available upon which to base conservation and management decisions (Heide-Jørgensen et al.

700 2012). In data-poor situations, simple characterizations of metapopulation structure should be used cautiously. However, managers cannot always wait until better data or better models are available. In these cases, even basic analyses can highlight opportunities in the near term. The approach for evaluating metapopulation structure that we employed here is straightforward and transparent. When data are sparse, this will be a safer approach than using a more detailed model  
705 that makes untestable assumptions. Results could be used to explore potential starting points for more comprehensive modeling efforts (e.g., Harrison et al. 2011, Heard et al. 2013, Piana et al. 2014, Sutherland et al. 2014). In our opinion, the best use of results from analyses such as those we presented will be in guiding future monitoring efforts. As new empirical information is collected, analyses can be updated to more accurately describe metapopulation structure and how  
710 it is changing over time (Thorson et al. 2014, Westley et al. 2015).

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**Table 1.** Characteristics of Snake River spring/summer Chinook salmon populations.

Code	Population	Status of wild fish <sup>a</sup>	Conservation		Spawner abundance <sup>d</sup>	Estimated donor-based dispersal rate <sup>e</sup>					
			status <sup>b</sup>	Hatchery <sup>c</sup>		hyd	hab	cwt	pit	gen	ens
<i>Lower Snake River</i>											
nTu	Tucannon River	Extant	Primary	Integrated	127	0.151	0.150	0.000	0.010	NA	0.052
nAs	Asotin Creek	Extirpated	Stabilizing	None	1	0.157	0.137	NA	NA	NA	0.105
<i>Grande Ronde/Imnaha</i>											
gWe	Wenaha River	Extant	Primary	None	393	0.153	0.156	NA	NA	0.032	0.112
gLo	LookingGlass Creek	Extirpated	Stabilizing	Integrated	1	0.151	0.151	0.041	0.041	0.054	0.079
gLs	Lostine River	Extant	Primary	Integrated	312	0.150	0.157	0.029	0.020	0.017	0.045
gMi	Minam River	Extant	Primary	None	410	0.154	0.154	NA	NA	0.024	0.118
gCa	Catherine Creek	Extant	Primary	Integrated	84	0.152	0.154	0.114	0.000	0.032	0.063
gUm	Upper Grande Ronde	Extant	Stabilizing	Integrated	29	0.146	0.153	NA	0.500	0.056	0.194
iMa	Imnaha River	Extant	Primary	Integrated	480	0.139	0.147	0.004	0.016	0.020	0.031
IBs	Imnaha Sheep Creek	Extirpated	Stabilizing	None	4	0.148	0.141	NA	NA	NA	0.109
<i>South Fork Salmon River</i>											
lSa	Little Salmon River	Extant	Stabilizing	Segregated	174	0.150	0.148	0.001	NA	0.019	0.063
sMa	S Fork Salmon River	Extant	Primary	Segregated	891	0.159	0.163	0.129	NA	0.029	0.085
sSe	Secesh River	Extant	Primary	None	517	0.144	0.148	NA	NA	0.020	0.114
sEf	E Fork S Fork Salmon R	Extant	Primary	Integrated	183	0.146	0.141	NA	NA	0.031	0.113
<i>Middle Fork Salmon River</i>											
mCh	Chamberlain Creek	Extant	Primary	None	633	0.145	0.154	NA	NA	NA	0.108
mLm	Mid Fork Salmon lower	Extant	Contributing	None	38	0.143	0.141	NA	NA	NA	0.110
mBi	Big Creek	Extant	Primary	None	155	0.151	0.163	NA	0.000	0.023	0.079

mCa	Camas Creek	Extant	Primary	None	70	0.152	0.152	NA	NA	NA	0.107
mLo	Loon Creek	Extant	Primary	None	72	0.140	0.147	NA	NA	NA	0.112
mUm	Mid Fork Salmon upper	Extant	Primary	None	220	0.145	0.154	NA	NA	NA	0.104
mSu	Sulphur Creek	Extant	Primary	None	38	0.152	0.159	NA	0.000	NA	0.062
mBe	Bear Creek	Extant	Primary	None	381	0.152	0.143	NA	NA	NA	0.108
mMa	Marsh Creek	Extant	Primary	None	113	0.142	0.149	NA	0.000	0.024	0.090
<b><i>Upper Salmon River</i></b>											
uPn	Panther Creek	Extirpated	Stabilizing	None	1	0.159	0.163	NA	NA	NA	0.116
uNf	N Fork Salmon River	Extant	Contributing	None	70	0.148	0.161	NA	NA	NA	0.116
uLe	Lemhi River	Extant	Primary	None	97	0.150	0.158	NA	0.000	NA	0.061
uLm	Salmon River (lower)	Extant	Contributing	None	143	0.153	0.153	NA	NA	NA	0.112
uPa	Pahsimeroi River	Extant	Primary	Segregated	148	0.155	0.150	0.007	0.016	0.019	0.038
uEf	E Fork Upper Salmon R	Extant	Contributing	None	256	0.139	0.153	NA	NA	NA	0.111
uYf	Yankee Fork Salmon	Extant	Stabilizing	Integrated	30	0.145	0.147	0.098	NA	NA	0.213
uVa	Valley Creek	Extant	Contributing	None	82	0.139	0.152	NA	0.000	0.043	0.066
uUm	Upper Salmon River	Extant	Primary	Segregated	324	0.143	0.143	0.003	0.057	0.034	0.063

<sup>a</sup> Status of populations assigned by ICTRT (2003, 2005). Geographic boundaries of populations were also defined by the Interior Columbia Technical Recovery Team.

<sup>b</sup> Status of populations assigned by HSRG (2009) based on recovery criteria (NMFS 2013) representing the contribution of the population to a viable 'major population group'

<sup>c</sup> Indicates type of hatchery program, if any. Segregated programs are operated to produce fish for harvest and may use nonlocal broodstock whereas integrated programs are aimed at conservation (i.e., bolstering numbers of wild fish using local broodstock)

<sup>d</sup> Abundance of natural-origin spawners over a recent 10-year period (see **Table S1** for estimates including hatchery fish and for past time periods)

<sup>e</sup> Estimate of dispersal from the population to all other populations by data type, where hyd=hydrologic distance model; hab=habitat attraction model; cwt=coded wire tags; pit=passive integrated transponder tags; gen=genetic data; ens = ensemble dataset; NA = no data available

**Table 2.** Basis of dispersal estimates used to assess structure of the Snake River spring/summer Chinook salmon metapopulation.

Data type	Source	Strengths	Simplifying Assumptions	References
Coded wire tag mark recapture (cwt)	Regional Mark Information System (RMIS) database ( <a href="http://www.rmipc.org/">http://www.rmipc.org/</a> ); downloaded in September 2012; data in <b>Table S2</b>	<ol style="list-style-type: none"> <li>1. empirical measurements of observed straying (tags were collected from carcasses so the final location is the presumed intended spawning location)</li> <li>2. many years of data</li> </ol>	<ol style="list-style-type: none"> <li>1. all populations are monitored equally</li> <li>2. fish collected on the spawning grounds produce viable offspring that will contribute to the gene pool</li> <li>3. recovery efficiency is high and consistent across populations, and tag effects are negligible</li> <li>4. dispersal probabilities are representative of wild fish</li> <li>5. dispersal probabilities are independent of broodstock origin and hatchery practices</li> </ol>	Westley et al. (2013, 2015)
Passive integrated transponder tag mark recapture (pit)	PIT Tag Information System ( <a href="http://www.ptagis.org">www.ptagis.org</a> ), accessed via Columbia River Data Access in Real Time (DART) ( <a href="http://www.cbr.washington.edu/dart/query/pit_basin">www.cbr.washington.edu/dart/query/pit_basin</a> ); downloaded in July 2013; data in <b>Table S3</b>	<ol style="list-style-type: none"> <li>1. empirical information about movement of <i>wild</i> fish</li> <li>2. growing database</li> </ol>	<ol style="list-style-type: none"> <li>1. all populations are monitored equally</li> <li>2. juveniles are tagged within their natal population</li> <li>3. fish detected on the spawning grounds produce viable offspring that will contribute to the gene pool</li> <li>4. detection efficiency is high and consistent across populations, and tag effects are negligible</li> <li>5. last recorded detection represents final spawning location</li> </ol>	Keefer et al. (2008)
Genetic migration rates (gen)	DNA microsatellite dataset collected and analyzed by D. Van Doornik and P. Moran, NOAA Fisheries; data in <b>Table S4</b>	<ol style="list-style-type: none"> <li>1. movement of genes (rather than adults) is measured (samples are from juvenile salmon)</li> </ol>	<ol style="list-style-type: none"> <li>1. samples reflect allele frequencies in discrete breeding aggregates</li> <li>2. microsatellite markers are selectively neutral</li> <li>3. populations are at migration/drift equilibrium</li> <li>4. migration is symmetrical between members of a given population pair</li> <li>5. pairwise analysis violates the island model implicit in our</li> </ol>	Van Doornik et al. (2011, 2013)

			estimation of migration	
			6. generations are non-overlapping	
Hydrologic distance model (hyd)	Modeled; data in <b>Table S5</b>	<ol style="list-style-type: none"> <li>1. ease of application and can be calculated for all populations (no data gaps)</li> <li>2. flexible; parameters can be adjusted for different species</li> </ol>	<ol style="list-style-type: none"> <li>1. inter-population distance is a surrogate for rigor and difficulty of movement as fish navigate upstream</li> <li>2. exponential decay is an appropriate model form to represent dispersal</li> <li>3. probability of dispersal between population pairs is equally likely in both directions</li> </ol>	Schick and Lindley (2007); Clark et al. (1998)
Habitat attraction model (hab)	Dispersal probabilities from distance model (above), modified by relative habitat quality; data in <b>Table S6</b>	1-2. same as above	<ol style="list-style-type: none"> <li>1-3. same as above</li> <li>4. fish react to potential habitat quality</li> <li>5. our index of habitat quality is appropriate</li> </ol>	Murphy et al. (2010)

**Table 3.** Scenarios for evaluating potential effects of conservation and management actions on the spatial structure of Snake River spring/summer Chinook salmon.

Code	Scenario name	Spawner abundance <sup>a</sup>	Populations included <sup>b</sup>	Populations altered	Abundance multiplier	Dispersal multiplier <sup>f</sup>
R	Recent.wild	Wild	Extant	None		
H+	Hatchery.inc	All	Extant	Having hatcheries <sup>c</sup>	1.5	1.5
H-	Hatchery.dec	All	Extant	Having hatcheries <sup>c</sup>	0.5	0.5
A+	Habitat.inc	Wild	Extant	Extant	1.5	
A-	Habitat.dec	Wild	Extant	Extant	0.5	
P+	Primary.inc	Wild	Extant	Primary <sup>d</sup>	1.5	
P-	Primary.dec	Wild	Extant	Primary <sup>d</sup>	0.5	
S+	Stabilizing.inc	Wild	Extant	Stabilizing <sup>e</sup>	1.5	
S-	Stabilizing.dec	Wild	Extant	Stabilizing <sup>e</sup>	0.5	
F	Fix.extirpated	Wild	Extant & Extirpated	Extirpated	0.1 * historical	not suppressed

<sup>a</sup> Calculated for brood years 1999-2008; wild = wild spawners; all = both wild and hatchery-origin spawners

<sup>b</sup> excluding Clearwater River populations; extant = support wild fish populations; extirpated = no longer support sustainable wild fish populations (Asotin, Lookingglass, Big Sheep and Panther Creeks)

<sup>c</sup> populations that have hatcheries within their boundaries

<sup>d</sup> populations reported by the HSRG (2009) as necessary to achieve viability

<sup>e</sup> populations reported by the HSRG (2009) to be of lowest conservation concern

<sup>f</sup> we used ensemble dispersal probabilities (combined across 4 sources) for all scenarios

## List of Figures

**Figure 1.** Major population groups (MPG) and individual populations of Snake River spring/summer Chinook salmon. Hatched lines indicate functionally extirpated populations. See **Figure S1** for tag-recapture and genetics sampling locations.

**Figure 2.** Analytical metrics. Patch-level metrics describe individual population attributes; graph-level metrics summarize all populations in the evolutionarily significant unit (ESU). Key:  $s_i$  = spawner abundance for population  $i$ ,  $s_{i \rightarrow j}$ , number of fish emigrating from population  $i$  to population  $j$ ;  $s_{ij}$ , recruitment to the natal population;  $w$ , weight of dispersal between populations;  $e$ , edge (i.e., inter-population connection having  $w > z$ );  $n$ , total number of populations;  $n_{e=0}$ , a population that has no edges;  $n_i$ , population  $i$ . Metrics denoted with an asterisk (\*) are influenced by  $z$  (set to 0.01 in analyses).

**Figure 3.** Dispersal probability estimated from coded wire tag (CWT) data, passive integrated transponder (PIT) tag data and genetic data, plotted against hydrologic distance between population pairs. Top left: all empirical data together; other panels depict fitted curves and 95% confidence intervals for each type of empirical data.

**Figure 4.** Top: Graph depicting source-sink dynamics for populations of Snake River spring/summer Chinook based on ensemble dispersal estimates and recent abundance of wild spawners. Bottom: biplot of patch metrics of metapopulation structure with symbols denoting contribution of populations to MPG-level viability (HSRG 2009; NOAA Fisheries 2013).

**Figure 5.** Sensitivity analysis results, showing resulting metapopulation structure metrics (y-axes; defined in **Figure 2**) when population size (left column), dispersal estimate (middle column), or population set (right column) was altered in a subset of populations. Integers in the x-axis are the number of random populations that were altered in each of 1000 simulations; white = value increased; dark gray = value decreased; gray = populations omitted. For each boxplot, thick lines are medians, boxes are 1st and 3rd quartiles, and whiskers are 5th and 95th percentiles. For comparison, 'true' values computed using the ensemble dispersal dataset and

wild spawners in the recent decade for all populations except those in the Clearwater (n=32) are depicted behind boxes as a gray rectangle (1st and 3rd quartiles) and horizontal lines (dashed=median; dotted=5th and 95th). These and the y-axes are comparable within a row and with the same row in **Figure 7**.

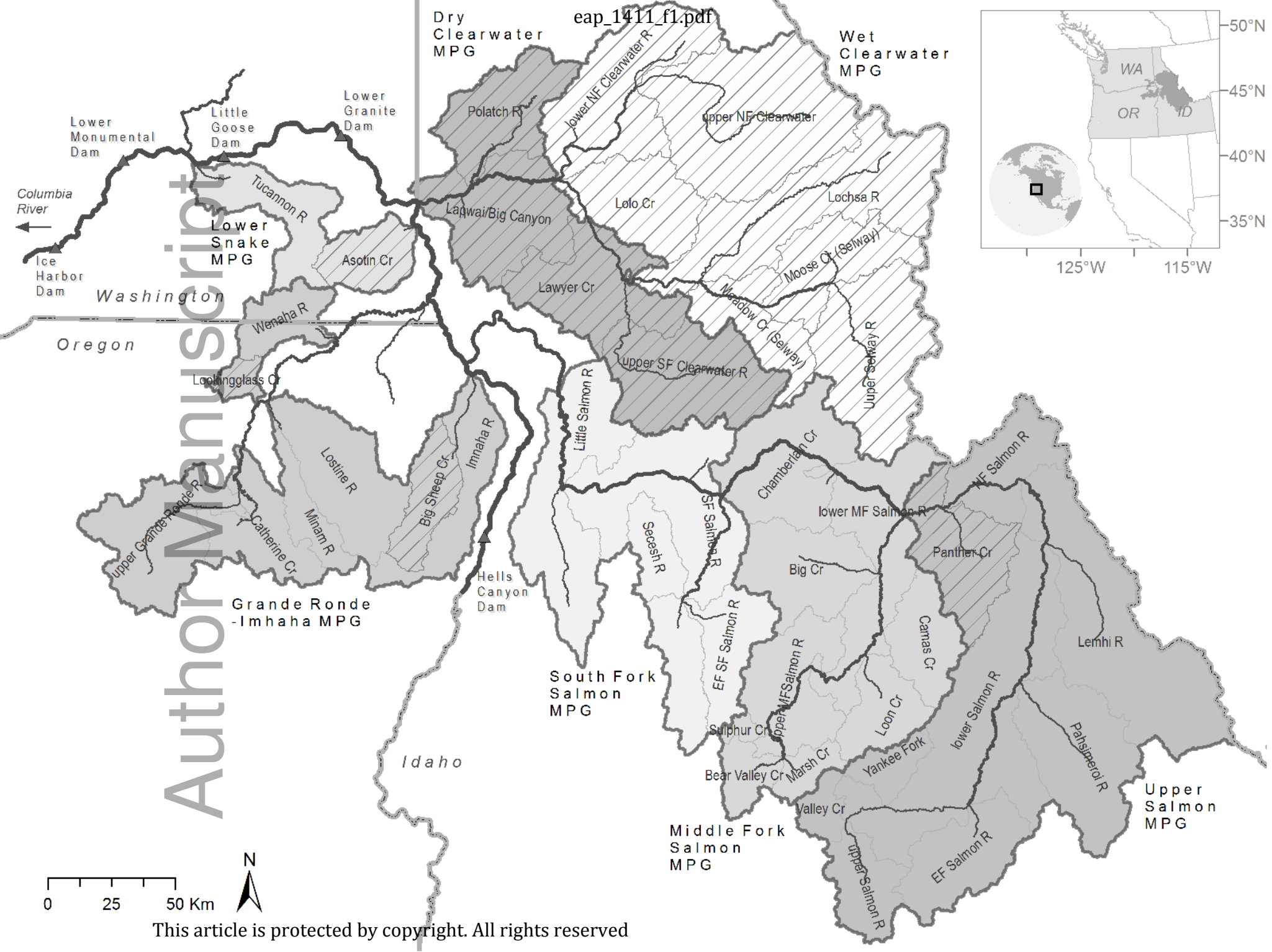
**Figure 6.** Sensitivity analysis results, showing the percent change in the fraction of edges in the metapopulation (see **Figure S3** for other metrics) resulting from changes to a single population (x-axis; names in **Table 1**). Horizontal dashed lines represent ‘true’ values’ using the combined dispersal dataset and all populations except those in the Clearwater (n=32). Gray boxes are major population groups: LoSn=lower Snake; GrIm=Grande Ronde/Imnaha; SfSa=SF Salmon; MfSa=MF Salmon; UpSa=Upper Salmon.

**Figure 7.** Metrics describing metapopulation structure for the Snake River spring/summer Chinook salmon ESU comparing results across different population sizes (left column), different datasets used to estimate dispersal (middle column), and different sets of populations (right column). Metrics (y-axes) are defined in **Figure 2**. Abbreviations in the x-axes are, for the left column: hist = historical abundance in the late 1800s, mod = wild spawner abundance for brood years 1962-1971 when fish were moderately abundant; w+h = wild and hatchery spawner abundance for brood years 1999-2008. Abbreviations for the middle column: hyd = hydrologic distance model; hab = habitat attraction model; cwt = coded wire tag data; pit = passive integrated transponder tag data; gen = genetic data. Abbreviations for the right column: a:43 = all populations in the ESU including Clearwater populations (n=43); c:10 = populations for which coded wire tag data existed (n=10); p:13 = populations for which passive integrated transponder tag data existed (n=13); gen = populations for which genetic data existed (n=16). For comparison, values computed using the ensemble dispersal dataset and wild spawners in the recent decade for all populations except those in the Clearwater (n=32) are depicted behind boxes as a gray rectangle (1st and 3rd quartiles) and horizontal lines (dashed=median; dotted=5th and 95th). These and the y-axes are comparable within a row and with the same row in **Figure 5**. See **Figures S4-S12** for additional exploration of these patterns.

**Figure 8.** Top: theoretical framework for describing the spatial structure of metapopulations, adapted from figures in Harrison and Taylor (1997). Bottom: salmon ESU as predicted by management scenarios placed in this framework. Metric names (vectors) in **Figure 2** and scenario names (points) in **Table 3**. For clarity, scenario S- is not shown because it is nearly identical to S+. See **Figures S13-15** for additional exploration of the effects of management scenarios on the ESU and on individual populations.

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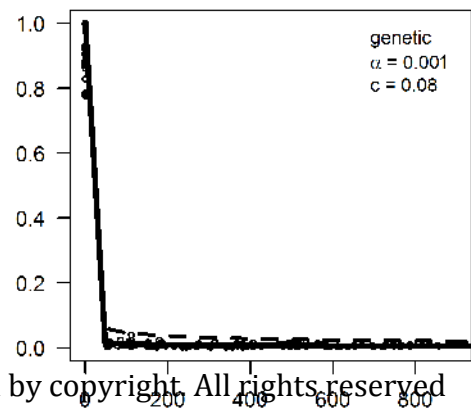
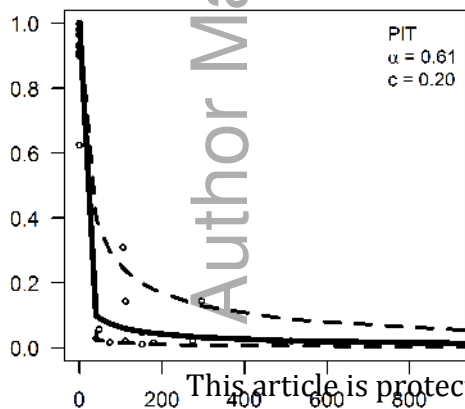
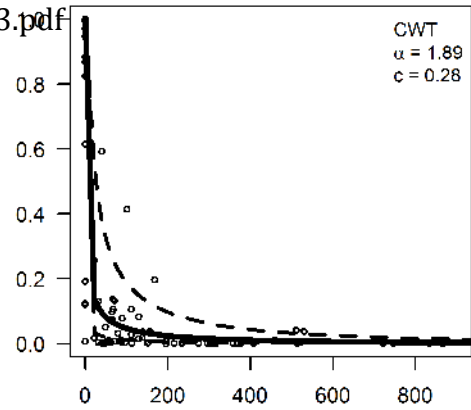
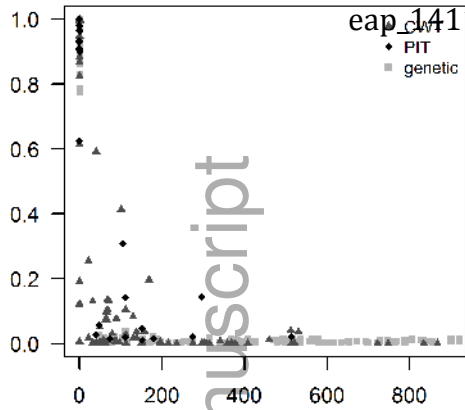


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Metric (value)	Description	eap_1411_f2.pdf	Equation	Illustration
<b>Patch (population)</b>				
NodeStrength (> 0)	represents how pivotal a population is to overall graph structure; does not indicate whether individuals primarily emigrate from or immigrate into the population		$S_{i \rightarrow j} + S_{j \rightarrow i}$	
OutWeights (> 0)	sum of outbound connection weights (InWeights = sum of inbound)		$\sum_i w_{i \rightarrow j}$	
Independence (0 - 1)	measure of population isolation (Schick & Lindley 2007); higher values indicate greater reliance on recruitment than on immigration		$\frac{S_{ii}}{S_{ii} + S_{j \rightarrow i}}$	
FlowDirection (any value)	number of fish emigrating from or immigrating into a population relative to recruitment within the population; negative numbers indicate net emigration and positive indicate net immigration		$\frac{S_{j \rightarrow i} - S_{i \rightarrow j}}{S_{ii}}$	
<b>Graph (ESU)</b>				
fSrcs-fSinks* (-1 - 1)	fraction of sources (populations with more outbound than inbound connections) minus fraction of pseudo-sinks (opposite)		$\frac{\sum n_{e_{i \rightarrow j} > e_{j \rightarrow i}}}{n} - \frac{\sum n_{e_{i \rightarrow j} < e_{j \rightarrow i}}}{n}$	
fIsolated* (0 - 1)	fraction of isolated populations (those with no connections)		$\frac{\sum n_{e=0}}{n}$	
fEdges* (0 - 1)	fraction of all potential inter-population connections (edges)		$\frac{\sum e_{i \rightarrow j} + \sum e_{j \rightarrow i}}{n^2 - 1}$	
rDispersal (0 - 1)	realized donor-based dispersal		$\frac{\sum w_{i \rightarrow j}}{\sum w}$	
fMigrants (0 - 1)	fraction of fish migrating (vs. homing)		$\frac{\sum S_{i \rightarrow j} + \sum S_{j \rightarrow i}}{\sum s}$	
sdPopSize (>0)	standard deviation of spawner abundance		$sd(s)$	

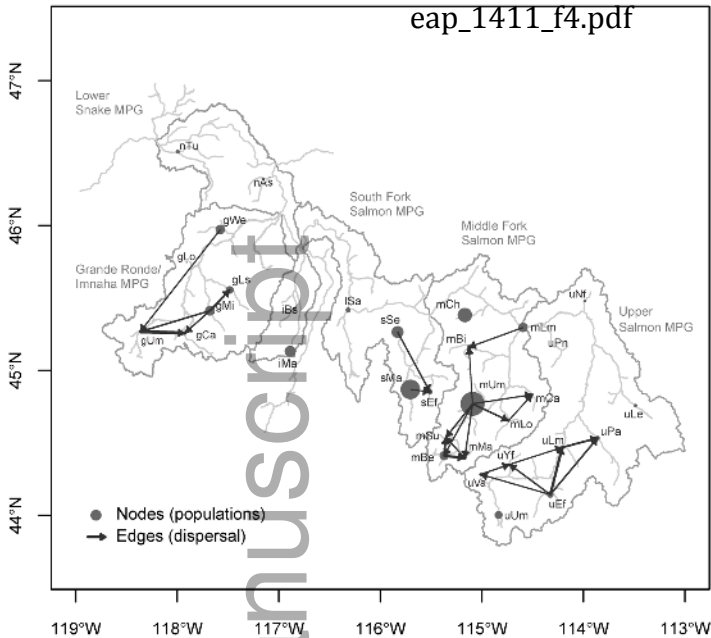
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Dispersal probability



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Hydrologic distance (km)



Populations:

Lower Snake MPG:

nTu: Tucannon  
nAs: Asotin

Grande Ronde/Imnaha MPG:

gWe: Wenaha  
gLo: Lookingglass  
gLS: Lostine  
gMi: Minam  
gCa: Catherine  
gUm: upper Grande Ronde  
iMa: Imnaha  
iBs: Big Sheep

South Fork Salmon MPG:

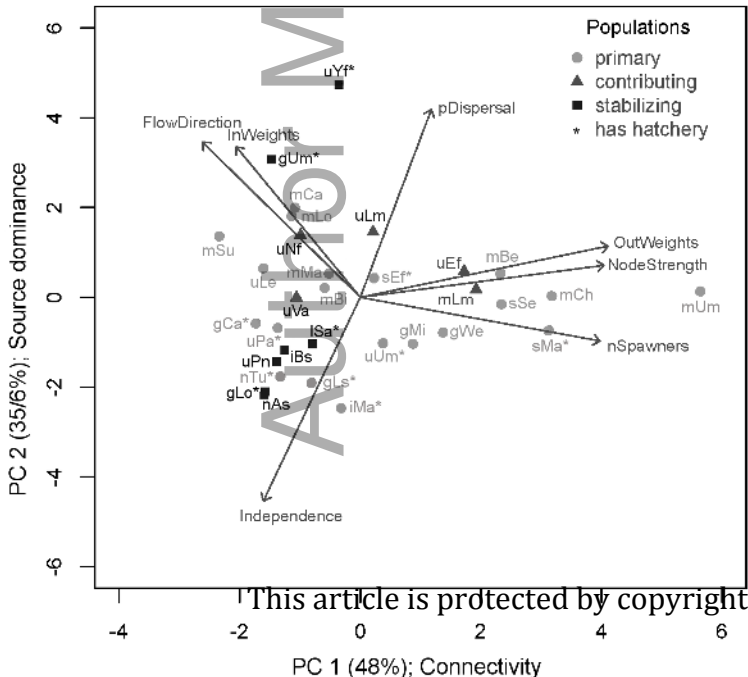
iSa: Little Salmon  
sMa: South Fork Salmon  
sSe: Secesh  
sEf: East Fork SF Salmon

Middle Fork Salmon MPG:

mCh: Chamberlain  
mLm: lower Middle Fork Salmon  
mBi: Big  
mCa: Camas  
mLo: Loon  
mUm: upper Middle Fork Salmon  
mSu: Sulphur  
mBe: Bear Valley  
mMa: Marsh

Upper Salmon MPG:

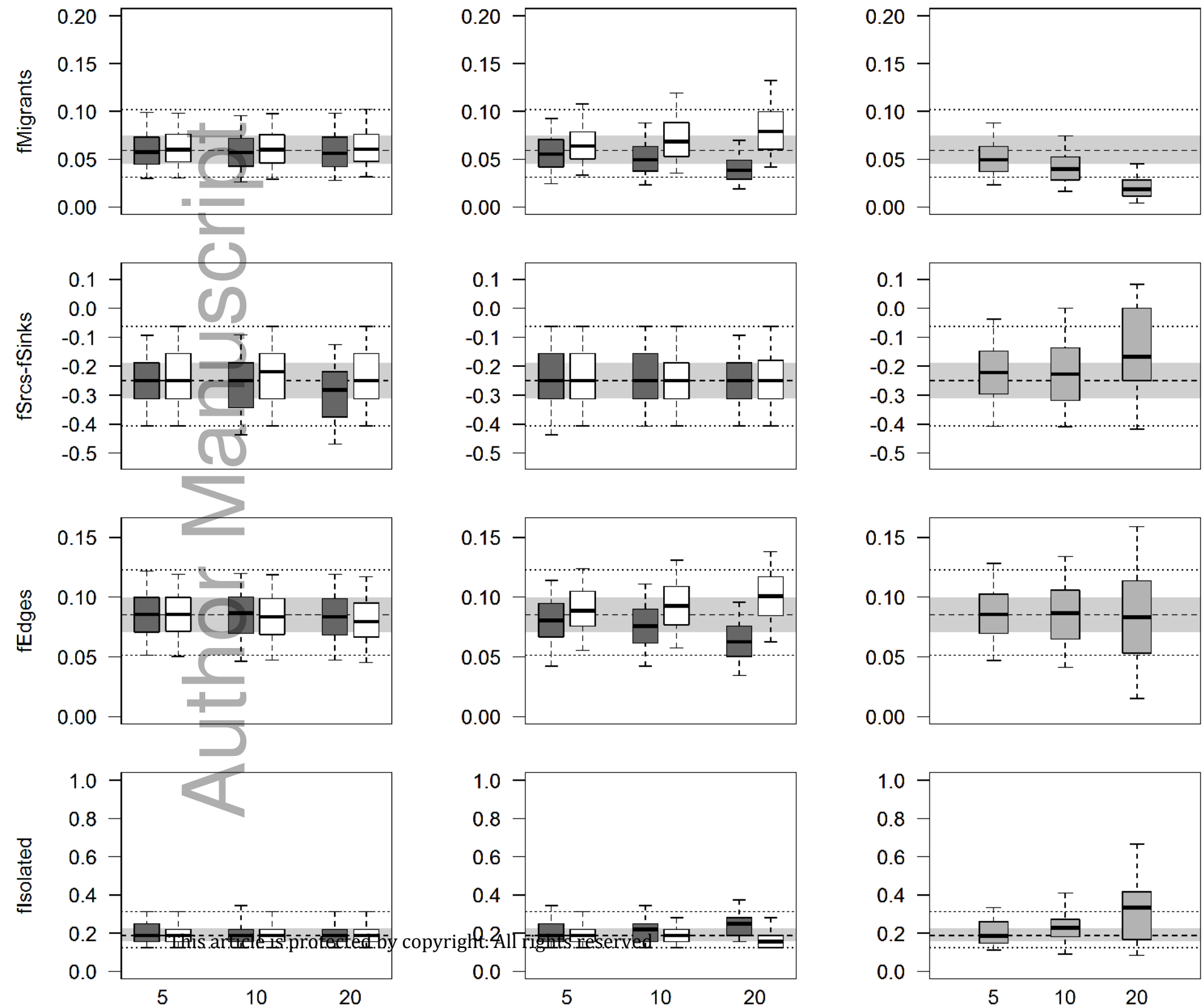
uPn: Panther  
uNf: North Fork Salmon  
uLm: lower Upper Salmon  
uLe: Lemhi  
uUm: upper Upper Salmon  
uEf: East Fork Salmon  
uYf: Yankee Fork Salmon  
uVa: Valley



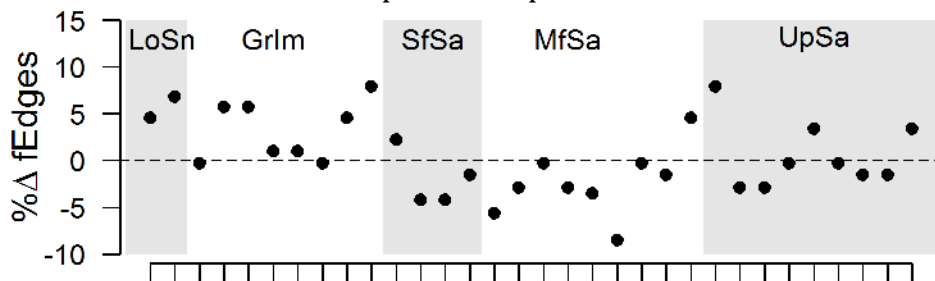
Population size

Dispersal estimate

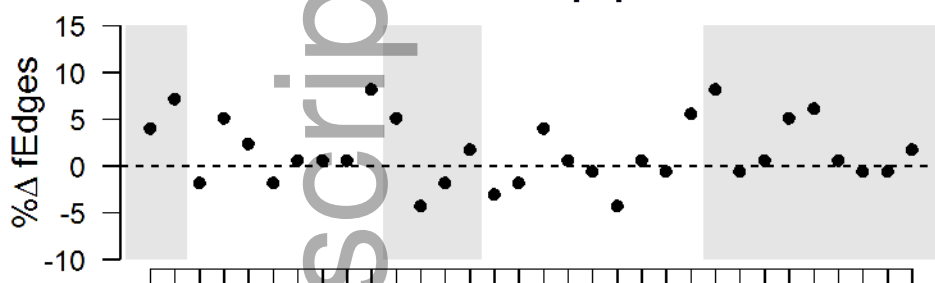
Population set



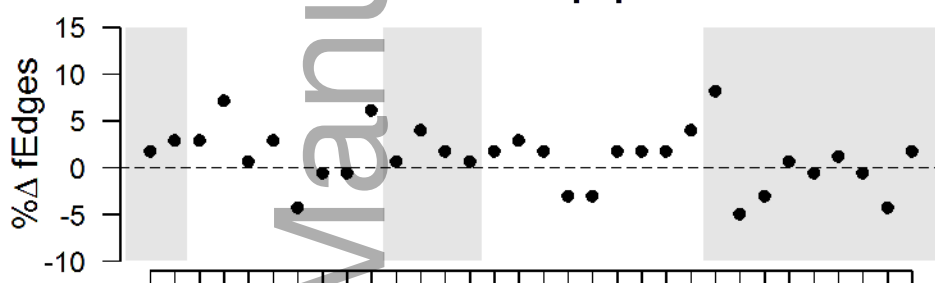
omit the population



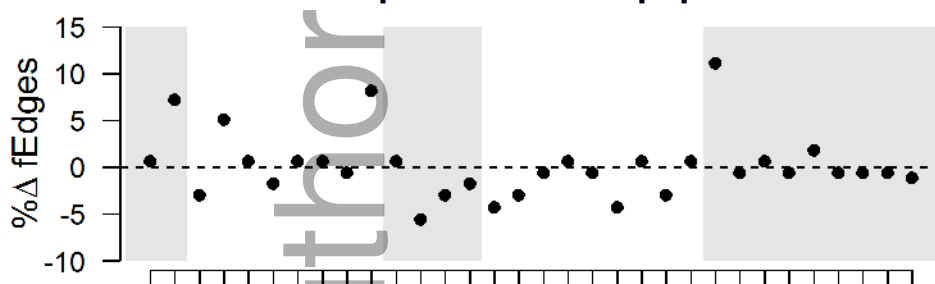
0.5 \* size of the population



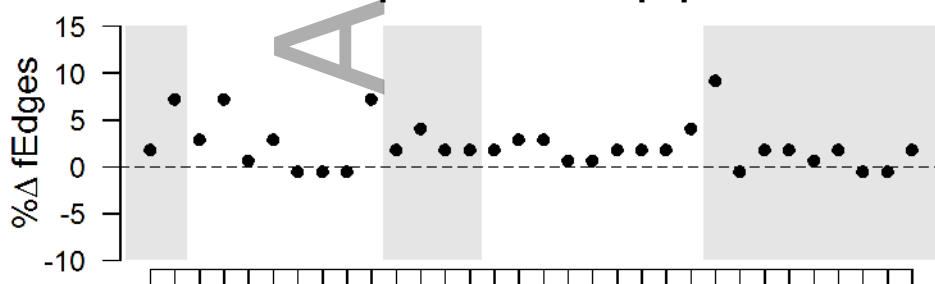
1.5 \* size of the population



0.5 \* dispersal from the population



1.5 \* dispersal from the population



nTu nAs gWe gLO gLS gLi gLa gAm gIva gIas iLa sIva sIse sIef mIn mIn Bi mCa mCo mUm mUe mUe mUa uIn uIn f uIn e uIn a uIn f uYa uIn

Population

Population size

Dispersal estimate

Population set

