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Is Metapopulation Theory the Best Guide for Recovering Snake River Fall Chinook Salmon in the 21st Century?

--Manuscript Draft--

Manuscript Number:	
Article Type:	Research Article
Full Title:	Is Metapopulation Theory the Best Guide for Recovering Snake River Fall Chinook Salmon in the 21st Century?
Short Title:	Metapopulation theory guides salmon recovery
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Keywords:	metapopulation spatially-structured population dams population fragmentation translocation life history diversity hatchery supplementation population recovery conservation reliance
Abstract:	US policy towards recovering Evolutionarily Significant Units (ESU) protected by the Endangered Species Act has been guided ecological theory applied in a one-size-fits-all manner. Theory suggests that recovery can be achieved by enhancing population abundance, productivity, spatial structure, and diversity. In this study, we assessed the future risk of extirpation for the Snake River fall Chinook salmon (Oncorhynchus tshawytscha). Following a recent upsurge in abundance, recovery goals seek to improve spatial structure by adding a new upstream spawning area and increase diversity by decreasing reliance on hatchery production. We evaluated recovery options targeting spatial structure and diversity by using mechanistic and statistical models to assess population viability (PVA). Both PVA models suggest that the ESU is currently viable, and both indicate that hatchery inputs could be reduced by an order of magnitude without elevating risk to the ESU. To evaluate goals related to spatial structure, i) we evaluated covariation between existing spawning areas and ii) we simulated operation of a trap-and-transport system to provide access to historical spawning habitat above a complex of dams and return juveniles downstream. Spawner abundances among current spawning areas below the dams were highly synchronized, suggesting increased ESU risk. Counter to our expectations based on theory, conditions under which adding the upstream spawning area reduced ESU risk were narrow. Success required a significant amount of new spawning habitat, continued access to current spawning habitat, and high round-trip survival for salmon using the new habitat. This leads us to caution that recovery options based on theory should not be applied wholesale without regard to the human interventions needed to implement them and the assumptions on which the theories are based.
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Opposed Reviewers:	
Additional Information:	
Question	**Response**
Financial Disclosure	This research was funded by Idaho Power Company through a contract with Oak Ridge National Laboratory (ORNL), which is managed by UT-Battelle, LLC, for the

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April 25, 2015

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Dear PLOS One Editors:

Please consider this manuscript entitled ""Is Metapopulation Theory the Best Guide for Recovering Snake River Fall Chinook Salmon in the 21st Century?" for publication in PLOS One. Recovery goals for all at-risk salmon populations are derived from metapopulation theory, which seeks to enhance spatial diversity by establishing multiple populations. US policy toward species conservation relies in part on the concept of the 'rescue effect' as having broad applicability across species and habitats. Our study quantified the future viability of the Snake River fall Chinook salmon population that has special protection under US law. We evaluated recovery options including hatchery support and establishment a new upstream population by implementing trap and transport programs in both directions (up and downstream) using two population viability models. Our results suggested that minimal hatchery support is required to ensure viability over a 100-y time horizon with access to spawning areas below Hells Canyon Dam. Model projections also suggested that adding a conservation-reliant population above the dams would improve viability only for a narrow range of parameters. This outcome suggests to us that, in general, spatial diversity created through artificial management of a second main-stem population may not necessarily increase viability of the conjoined populations. This result leads us to question the wholesale application of metapopulation theory in setting recovery goals. We review other theoretical studies that have previously suggested that the 'rescue effect' has a much smaller role than is generally assumed to be the case. This leads us to recommend that more-pragmatic and realistic models of management-dependent species are required to guide recovery efforts.

We would like to request Dr. Brian McKenzie as our editor.

Best regards,

Henriette I. Jager
Senior Research Scientist
Oak Ridge National Laboratory

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April 25, 2015

Is Metapopulation Theory the Best Guide for Recovering Snake River Fall Chinook Salmon in the 21st Century?

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Abstract

US policy towards recovering Evolutionarily Significant Units (ESU) protected by the Endangered Species Act has been guided ecological theory applied in a one-size-fits-all manner. Theory suggests that recovery can be achieved by enhancing population abundance, productivity, spatial structure, and diversity. In this study, we assessed the future risk of extirpation for the Snake River fall Chinook salmon (*Oncorhynchus tshawytscha*). Following a recent upsurge in abundance, recovery goals seek to improve spatial structure by adding a new upstream spawning area and increase diversity by decreasing reliance on hatchery production. We evaluated recovery options targeting spatial structure and diversity by using mechanistic and statistical models to assess population viability (PVA). Both PVA models suggest that the ESU is currently viable, and both indicate that hatchery inputs could be reduced by an order of magnitude without elevating risk to the ESU. To evaluate goals related to spatial structure, i) we evaluated covariation between existing spawning areas and ii) we simulated operation of a trap-and-transport system to provide access to historical spawning habitat above a complex of dams and return juveniles downstream. Spawner abundances among current spawning areas below the dams were highly synchronized, suggesting increased ESU risk. Counter to our expectations based on theory, conditions under which adding the upstream spawning area reduced ESU risk were narrow. Success required a significant amount of new spawning habitat, continued access to current spawning habitat, and high round-trip survival for salmon using the new habitat. This leads us to caution that recovery options based on theory should not be applied wholesale without regard to the human interventions needed to implement them and the assumptions on

which the theories are based.

Keywords: metapopulation, spatially-structured population, dam, translocation, life history diversity, hatchery, population viability, risk, conservation reliance

Introduction

Species conservation has been guided by ecological theories that relate risk of extirpation to each of four properties: abundance, productivity, spatial structure, and diversity [1]. Decisions to list species under the US Endangered Species Act (ESA) has often been based, in part, by analyses of their extinction and re-colonization dynamics of collections of populations, or metapopulations [2]. Three well-known examples of this are the Florida panther (*Felis concolor coryii*), marbled murrelet (*Brachyramphus marmoratus*), and red-cockaded woodpecker (*Strix occidentalis caurina*) [3]. Policies seeking to recover threatened and endangered species have also been strongly influenced by principles from metapopulation theory [1, 4, 5]. This paper focuses on an ESA-listed salmon ESU (Evolutionarily Significant Unit) that has specific recovery goals: i) to avoid destroying habitat patches (spawning areas) faster than they are naturally created, ii) to protect habitat that is suitable but currently unoccupied, iii) to maintain historical distances among spawning areas to maintain natural straying rates, and iv) to expand spawning areas to span their historical range [5].

The prevailing paradigm in conservation biology is that connectivity is a necessary feature of healthy and resilient Pacific salmon populations [4, 6, 7]. Metapopulations occupy discrete spawning areas separated by unsuitable habitat and connected by low rates of dispersal

through straying [2]. For salmon ESUs that function as metapopulations, infrequent straying provides a hedge against spatially heterogeneous risks. Spawning areas that are not used in one year may be recolonized by straying salmon that originated in neighboring spawning areas via the "rescue effect" [8].

Recovery goals for ESA-listed salmon ESUs favor dendritic over linear spatial arrangements of spawning areas in river networks [9]. The theory is that tributary spawning areas can protect against catastrophes concentrated in one sub-basin [5, 10, 11] and increase the opportunity for spawners originating from neighboring sub-basins to recolonize empty habitat following local extirpation [5, 12]. When numbers spawning in different spawning areas fluctuate independently, areas with few spawners in one year are more likely to be recolonized by strays from more-productive spawning areas nearby, thereby increasing the viability of the metapopulation as a whole [13]. Therefore, the degree of synchrony exhibited by sub-populations can be important [13, 14].

Our study focuses on the Snake River fall Chinook salmon ESU. The Snake River ESU's spawning run declined to very low levels for many years prior to its listing as federally threatened in 1992 [15]. Recently, the number of spawners returning to Lower Granite Dam has increased to pre-dam levels, and these high abundances have persisted for longer than one generation (i.e., from parental breeding to return of offspring to breed) (Figure 1).

Historically, the Middle Snake River provided the core spawning area for Snake River fall Chinook salmon. The quality of this habitat was high in part because groundwater inputs moderated temperatures, resulting in fast incubation and early emergence by juveniles. A large fraction of the historical spawning habitat was blocked by construction of Swan Falls Dam, the

first dam constructed on the Snake River in 1901. Following construction of Swan Falls Dam, spawning was limited to the Marsing Reach of the Snake River, which still had some diminished benefit from the groundwater inputs upstream (Groves and Chandler 2005). Construction of Brownlee Reservoir (the first of a three reservoir Complex) blocked access to the Marsing Reach in 1958. Passage was attempted at Brownlee Dam, but those efforts ceased in 1964, when it was evident that downstream passage of juveniles was not successful. The majority of spawning now occurs below the Hells Canyon Complex of dams (Brownlee, Oxbow, and Hells Canyon, "the Complex"), three dams in the mainstem Snake River between the head of Lower Granite Reservoir and Hells Canyon Dam (Figure 2).

The two primary concerns for this ESU are lack of spatial structure and diversity [9, 16]. A recent review of the Snake River fall Chinook salmon ESU determined that it still faces a moderate risk, mainly because hatchery-reared fish comprise a large (>70%) fraction of the population [17]. Such high levels of hatchery support can mask other problems, creating the illusion that habitat conditions and risks are fine, when they are not [18]. Hatchery support may also compromise the ability of the ESU to adapt to future conditions by artificially mixing genotypes and hindering local adaptation [19, 20].

Artificial mixing is a particular concern in this ESU because plasticity in juvenile life history has emerged, and this aspect of phenotypic diversity is likely to play a meaningful role in how fall Chinook salmon adapt to local conditions during freshwater residence. A new yearling life history has emerged primarily from juveniles produced in one of the major spawning aggregates in the Clearwater River [21]. Because adult returns from juveniles outmigrating as yearlings are higher on average, this new life history may be reducing ESU risk. However, the

current practice of collecting broodstock to support the ESU through hatchery supplementation programs likely results in interbreeding among returning adults that exhibited different juvenile life histories. Thus, hatchery operation will likely reduce homing to natal spawning areas and impede the ability of this ESU to develop life history strategies tailored to spawning and rearing in specific environments, e.g., below dams where temperatures are moderated vs. in unregulated tributaries.

Protecting the Snake River major spawning area below Hells Canyon Dam has been identified as a priority [9, 22]. The majority of redds are built in the mainstem of the Snake River, but spawning also occurs in the lower reaches of major tributaries to the Snake River, including the Clearwater, Imnaha, Grande Ronde, Salmon, and Tucannon Rivers. Among these, the Clearwater River is the most significant tributary spawning area, supporting upwards of 50 percent of natural spawning in the ESU in some years. Because there are high rates of straying among spawning areas [23], these tributaries, along with the upper and lower Snake River mainstem, are considered one population. However, lack of spatial structure continues to be raised as a concern. Because there is presently only one population in this ESU, the ESU is considered vulnerable to catastrophes and to artificially elevated levels of immigration from downstream populations caused by hatchery operations outside the Snake River basin [24, 25]. The strategy identified as having the greatest long-term potential to reduce ESU-level risks associated with spatial structure and diversity is to re-establish fall Chinook Salmon in the Snake River upstream of the Complex [22]. However, the degree to which different spawning areas buffer this ESU against risks [26] has not been evaluated. Snake River spring Chinook Salmon

were recently identified as having the highest ‘portfolio’ risk among salmon stocks in western North America because of the synchrony among spawning areas [27].

In this paper, we use Population Viability Analysis (PVA) to address questions that might help guide restoration efforts related to increasing spatial and phenotypic diversity. In addition, we assessed historical trends and correlations among salmon returning to different spawning areas in the Snake River to assess whether they play an important role in buffering the ESU through recolonization following local extirpation. We address three questions: i) *Is the Snake River ESU downstream of the Complex viable?* ii) *How does the spatial structure and diversity influence the viability of the current ESU downstream of the Complex*? and iii) *Under what conditions would adding a new spawning area upstream of the Complex increase viability*?

Methods

To address these questions, we considered results from two types of models: i) a *statistical* PVA assumes that historical trends will continue into the future, and ii) a *mechanistic* PVA to simulate viability under future management.

Statistical PVA model (S-PVA)

The idea of an S-PVA is that a model is fitted to a historical time series of censused abundances [28] and then projected forward in time. Including density dependence in the model generally improves the predictions of statistical PVA models [29, 30]. We obtained 33 y of historical data for female spawners returning to Lyons Ferry or LG Dam in year t, S_t, for the post-dam building period, t = 1975 to 2013. A stochastic generalization of the Ricker model (Equation 1) was fitted using generalized least squares, with an exponential model for covariance

to describe residual autocorrelation. From the parameters estimated, we obtained equilibrium abundance a / b and intrinsic productivity, e^{a}. Parameter r (the 'range') estimates the time (y) over which spawner returns are autocorrelated.

$$
\begin{aligned}
S_t &= S_{(t-X)}\, e^{a - b\, S_{(t-X)} + \varepsilon}, \\
S_{(t-X)} &= \sum_{x=3,4,5\ years} p_x\, S_{(t-x)}\,, \\
Cov(\varepsilon(x_i), \varepsilon(x_j)) &= r\, e^{-\left(\frac{|x_i - x_j|}{r}\right)} \\
S_t &= \text{spawners year t};\ p_x = \text{proportion returning at age } x
\end{aligned}
\tag{0}
$$

For only unmarked (i.e., presumed wild) adult females, parameter estimates were a = 0.289, b = -0.00031, r = 5.6 y (residual SE = 0.742; total df = 33; residual df = 31). For both marked and unmarked adult females at LGR, parameter estimates for the Ricker model above were a = -0.4446, b = -0.00028, r = 6.1 y, (residual SE = 1.20; total df = 33; residual df = 31). Parameter b is a measure of density dependence, where parameter $b \neq 0$ (p = 0.002) indicates that density dependence is present. Using the fitted models, we evaluated viability by simulating 1,000 projections for 100 y into the future as described in Appendix A.

Mechanistic PVA model (M-PVA)

Our M-PVA model is described in detail in [31]. The model tracks groups of females sharing values of each of four attributes: 1) original spawning population of origin, 2) age in years, 3) juvenile life history [32], and 4) marking status (to indicate trapping or relocation). We projected 100 y into the future to assess future risk of extirpation.

The M-PVA includes both simulation control parameters that are varied in a systematic way (set P_{NEW}; Table S1) and fixed parameters fixed (Table S1). Many parameters enter into key model processes through stochastic formulations (Table S2).

We adopted a multi-modeling approach that combined M-PVA results from a sample from the joint posterior distribution of parameters in set P_{MYS} of poorly known parameters (Table S3). This distribution was defined by using the Bayesian multi-parameter modeling procedure of Piou, Berger (33), as described by [31]. We evaluated 47 parameter combinations for egg-smolt survival below HCD, S_{EGG}, minimum number of adults migrating upstream captured during the historical period, K_{trap_min}, ocean survival upon entry as age-0 juveniles, S_{OC_min}, and the ratio of yearling reservoir survival to sub-yearling survival for age-0 juveniles, S_{RES_OC}.

For each combination of values from P_{MYS}, we simulated 250 replicate populations using distinct random-number streams. In addition to i) the likelihood of persistence for 100 y into the future, we report the following values for each replicate: ii) population trend, λ, where $\lambda = 1$ separates populations that are growing from those that are declining, iii) time to extinction, iv) average and final female spawners, v) smolt-to-adult return ratio to LGR by juvenile life history, vi) estimated carrying capacity, vii) total juveniles stocked by destination and age, and viii) total translocated individuals. In reporting these results, we excluded the first five years to reduce dependence on initial conditions.

Simulation Experiments

Is the Snake River ESU downstream of the Complex viable?

We compared risk of extinction to 100 y produced by each of our PVA models with those previously developed by others for this ESU by using statistical models [17, 34]. The Interior Columbia Basin Technical Recovery Team (TRT) used statistical PVA models to develop 'TRT' risk isoclines based on salmon abundance and productivity [35].

How is viability downstream of the Complex influenced by hatchery support?

To address the policy goal of protecting phenotypic diversity by reducing hatchery influence [19], we simulated the S-PVA and M-PVA with and without hatchery operations supported by brood-stock collection below Lower Granite Dam. For the S-PVA, we compared future viability estimates based on the model fitted only to unmarked returning females with that including both marked and unmarked females. For the M-PVA, we compared projections with different quotas, *Up1_Quota*, controlling the numbers of broodstock removed at Lower Granite Dam and used to supplement (add hatchery-reared juveniles to) the population downstream of the Complex.

How is viability downstream of the Complex influenced by spatial structure?

We quantified the potential role played by spatial structure in reducing risk for the current population downstream of the Complex. To evaluate the benefits of current spatial structure conferred by lack of synchrony, we quantified year-to-year correlations between historical redd (nest) counts for the primary spawning areas.

Under what conditions would reestablishing an upstream spawning area improve viability?

To determine whether naturally produced juveniles in the new population would enhance viability of the ESU, we compared ESU viability under the *status quo* to future translocation scenarios involving trap and transport of adults to a new spawning area upstream of the Complex, reproduction in the new spawning habitat, and migration back downstream. We used the M-PVA because statistical PVAs cannot be used to project viability under different future conditions: S-PVAs assume the future will be the same as the past. Translocation simulations were performed for all combinations of parameters that control both the numbers of spawners transported upstream of the Complex and their success in producing offspring that survive to return to the habitat downstream of the Complex (set P_{NEW}, Table S4).

Under current hatchery practices below Lower Granite Dam (LG) [36], 20% of adults migrating upstream to spawn are captured (Figure 3). We assumed that a second trap was operated below Hells Canyon Dam (HC) to capture 80% of those female spawners passing above LG between years 2020 and 2080 (i.e., this excludes those removed as hatchery broodstock below LG). The simulated trap-and-transport system collects females at a trap below Hells Canyon Dam (Figure 3) and transports them to a new spawning area upstream of the Complex (*Trap2_up* in Tables S1, S4). During the first 10 y of simulated trapping, females trapped at LG were translocated upstream of the Complex, but thereafter only adult females with marks indicating that they were previously juveniles produced from the upstream spawning areas were transported. Female adults returning to the HC trap marked as being of hatchery origin were not translocated to above the Complex. Simulated production of juveniles in the new spawning area

depends on habitat capacity upstream of the Complex (ratio *Kfact* in Table S4), which is controlled by density dependence in the spawner-recruitment relationship.

After spawning in the new habitat, we assumed that proportion, *Trap_rate_down*, of juveniles were captured in a trap upstream of Brownlee Reservoir, and trucked downstream. These survived at an average rate, *Struck* = 0.8. The remainder migrated through the Hells Canyon Complex with survival *Sriver* = 0.3. Because summer water temperatures in the Snake River above and within Brownlee Reservoir are relatively warm and would not allow over summer rearing, we assumed that all juveniles reared in the new upstream population migrated as sub-yearlings as they did before construction of the Complex [32].

We analyzed results from the translocation simulation experiments for three hatchery scenarios, broodstock quotas (levels 0, 25, 100, and 1,600) applied to females trapped below Lower Granite Dam (LG trap in Figure 3). The scenario with a quota of zero implies no hatchery operation. We constructed a composite index of relative survival from Brownlee to Lower Granite Dam, *Stot* = *New_Sfact* x (*Struck_LGR* x *Trap_rate_down* + *Sriver_LGR* x (1−*Trap_rate_down*) to aid in interpreting results.

Results and Discussion

Is the Snake River fall Chinook salmon ESU downstream of the Complex viable?

Risk assessments for the Snake River ESU using statistical PVA models have become more optimistic as the historical time series used to fit them has included recent, higher abundances. Prior to the post-2006 resurgence, a random-walk model (e.g., no density dependence) for the period 1980-2000 found that population trends were below replacement

[34]. Estimated population trend was higher when hatchery returns were assumed not to spawn (λ = 0.96, with a range of 0.76 to 1.18; triangle in Figure 4A) than when hatchery and wild fish were assumed to reproduce equally (λ = 0.88) [34]. By 2012, the prognosis had improved [17] and projected risk based on abundance and productivity was low (Figure 4A). Our results emphasize one limitation of S-PVAs: projected risk can be sensitive to the length of the historical record. As suggested for this ESU, results from short time series have later turned out to be in error [37, 38]. Reasons for the broad up-surge in Columbia and Snake River salmon returns (not just this ESU) are debated, but a cooling phase in the ocean is almost certainly a factor, as are hatchery inputs.

We superimposed abundance and productivity estimated by this study and previous studies on 'TRT' risk isoclines for the Snake River ESU [39] (Figure 4). Risk estimated by projecting our S-PVA based on 1980-2013 data matched TRT risk categories; both suggest very low risk (open and filled circles in Figure 4). According to our S-PVA, fewer than 2% of 10,000 replicate simulations reached extinction (i.e., zero females) within 100 y, regardless of initial abundance. Our S-PVA estimated an equilibrium abundance of 932 unmarked female adults (1,588 for both) and a productivity of 1.335 for unmarked females (1.56 for both).

Risk levels projected by the M-PVA differed from those of the TRT (Figure 4). M-PVA-simulated extinction risk was high without production from hatchery-origin females, but very low with minimal hatchery inputs (i.e., *Quota* = 25 returning females used as broodstock with equal fitness to wild-origin adults) (Figure 5B). One difference between the models that is most likely to account for the higher risk without supplementation is that the M-PVA assumes a higher survival of offspring produced in the hatchery, whereas the S-PVA assumes equal fitness for

hatchery and wild females. Both models were constrained to match the historical record, which included an increase in hatchery supplementation over time.

How is viability downstream of the Complex influenced by hatchery support?

Both PVA models support the idea that lowering current inputs by an order of magnitude would meet diversity goals without adverse effects on abundance or productivity. For the S-PVA, the risk was very low with or without hatchery returns (circles in Figure 4). For the M-PVA, projected risk of extirpation was minimal over a 100-y time horizon with hatchery support. However, the average abundance of female spawners was higher in simulations with higher broodstock quotas (Figure 5, top). The projected population growth rate, λ, was slightly below one for the quota of 25 females (taken from the adults trapped 20% of the time) and slightly above one for a quota exceeding 100 females (Table 1; Figure 5, bottom). Simulated risk of extirpation before 100 years was zero, even with very low levels of hatchery supplementation, but increased to 0.68 without any supplementation (Table 1). Without the hatchery, no simulations reached extirpation before 16 y (average = 56 y). The distribution of trends in M-PVA simulations with no hatchery (LG trap quota = 0) produced an average population trend less than one, $\lambda = 0.915$, with a range from 0.52 to 1.08 (Figure 5). Hatchery supplementation decreased M-PVA-simulated risk from high (>25% chance in 100 y) for simulations with no hatchery to very low (<1% chance in 100 y) [17] (Figure 5B).

Our analysis suggests that hatchery inputs could be scaled back considerably without increasing other elements of risk, such as productivity (population trend) or abundance. Approximately 1,600 females removed below Lower Granite Dam are used as broodstock at

Lyons Ferry Hatchery [40], yet according to our projections, only 25 females were required to manage risk and above 100 female broodstock, the ESU showed an increasing population trend.

Our PVA simulations did not quantify the genetic risks associated with homogenization by hatchery-reared salmon. Genetic studies have not uncovered evidence of genetic bottlenecks in this ESU [41, 42] and genetic diversity remains high [43]. This is not surprising because the demographic support provided by supplementation protects genetic diversity [44]. Nevertheless, homogenization by mixing in hatchery breeding has reduced genetic structure and has likely prevented adaptation to local conditions in different spawning areas [43].

How is viability influenced by spatial structure?

Levels of straying among spawning areas in the Snake River ESU have been high [23]. The highest pairwise correlations were among spawning areas in the upper and lower mainstem Snake River, and a tributary, the Clearwater River (Figure 6), all belonging to the Snake River ESU. Pairwise correlations between redd counts in the lower Snake River and in two Columbia River spawning areas were still significant, but lower than those in the Snake River (0.34 in the Hanford reach; 0.45 in the Deschutes River). With such high correlations, it is likely that fluctuations leading to low numbers of spawners in one area will coincide with low abundances of returning adults hatched in neighboring spawning grounds [26]. Thus, the spatial structure downstream of the Complex has limited recolonization value because abundances in different spawning areas fluctuate in synchrony.

Under what conditions would reestablishing an upstream spawning area improve viability?

Two main arguments in favor of adding an upstream population are: i) to gain additional spawning habitat and ii) to protect against catastrophic loss of the current population downstream of the Complex. In our simulation experiments, the relative benefit provided by adding a new population upstream of the Complex differed depending on the level of hatchery support from broodstock removed below LGD (progeny released downstream of the Complex.).

No hatchery.— For the case with no supplementation to the extant population below the Complex, none of the translocation scenarios out-performed the scenario with no translocation (*Trap_rate_up* = 0). Productivity downstream of the Complex was too weak to support a second population. Linear regression analysis showed that measures of viability decreased with upstream trapping rate, and were not affected by the three other translocation parameters in Table 2. The model for average female spawners, $S = 112.7 - 125.8$ *Trap_rate_up*, explained 65% of variation without regard to the conditions upstream of the Complex. A similar model for time to extirpation, $T = 38.1 - 32$ *Trap_rate_up*, explained 86% of variation in T, with nearly identical relationships for different levels of relative survival around the Complex (*Stot*).

Hatchery supplementation.—In scenarios with hatchery supplementation downstream of the Complex, those translocation scenarios with the highest levels of carrying capacity in the upstream population (*New_Kfact)* and the highest trapping rates for downstream juvenile migrants upstream of Brownlee Reservoir (*Trap_rate_down*) produced average spawner numbers exceeding those in the no-translocation scenario (*Trap_rate_up* < 0.125, far right in Figure 7A). This is illustrated for the case of quota = 100 females trapped and transported at the HC trap by showing a grid of box-whisker plots for MPVA-simulated average female spawners

(Figure 7A) and population trends (Figure 7B). Note that the majority of simulations in scenarios with high carrying capacities, *KF* and scenarios with high relative survival from above Brownlee to Lower Granite Dam, *Stot* surpassed the average spawner abundance without translocation (i.e., *status quo*, quota = 0, horizontal line in Figure 7A and B). Translocation scenarios with lower *Stot* and carrying capacity did not produce higher spawner abundances (Figure 7A), on average, than those with no translocation. Population trends show a marked decrease for the case when all spawners are relocated above the Complex (Figure 7B), thereby losing access to downstream spawning habitat

The results reported above are intuitively reasonable. Simulating the addition of a new population upstream of the Complex was beneficial when habitat capacity exceeded that below HC and when survival from the new, upstream habitat to LG Dam exceeded 0.515 x egg-to-smolt survival. This survival threshold is close to that of sub-yearling salmon produced downstream of the Complex to the time they pass LG Dam ($S_{LG,0}$ = 0.63). Some differences might be expected as all juveniles reared upstream of the Complex would likely migrate at age-0, whereas a portion of juveniles from the Clearwater tributary in the population downstream of the Complex exit as yearlings.

How likely is it that habitat capacity and survival would be this high? Following the construction of Brownlee Dam, efforts were made to trap and transport adult salmon above the dam and to collect and pass downstream migrants around Brownlee Dam. Adult salmon passed around the dam continued to migrate to the Marsing reach (Figure 2) [45]. For the return trip, a large barrier net with traps was constructed in the reservoir a few km above Brownlee Dam to collect juvenile salmon for downstream transport. However, passage efforts were discontinued

by 1964 because migrating age-0 juvenile fall Chinook salmon experienced poor survival traveling through the reservoir prior to reaching the barrier net. Juveniles remaining in the stratified reservoir over summer would have faced temperatures exceeding 26.7°C and dissolved oxygen concentrations below 3 ppm [46], conditions considered at the time to be as poor as any found within the species' range [45]. Survival at these temperatures would be unlikely [47].

Summer water quality in Brownlee Reservoir has deteriorated since then [48]. Historic spawning and incubation habitat have been degraded by heavy sedimentation and nutrient loading from agriculture. Consequently, the survival of incubating eggs in the Marsing Reach is low [49-51]. In terms of metapopulation structure, the Marsing Reach appears to be a demographic 'sink', and effort spent on connecting habitat below and above a dam would likely be harmful [52]. Considerable improvement in survival over historical values would be needed to meet the thresholds identified by the M-PVA as beneficial to the ESU. There is hope, however, that a basin-wide process to improve water quality by implementing riparian restoration efforts and reducing nutrient inputs from agricultural lands will restore the Marsing reach to the pre-dam 'source' habitat that it once was.

Establishing a spawning area upstream of the Complex could contribute to future viability in three ways: 1) by providing additional spawning habitat and increasing carrying capacity for the ESU, 2) by recolonizing spawning areas downstream of the Complex following a catastrophe, and 3) by reducing reliance on homogenizing management practices (e.g., hatcheries), leading to the development of distinct phenotypes. Beyond issues with habitat quality, restored access to spawning habitat upstream of the Complex might not provide the expected benefits associated with either spatial or phenotypic diversity. If catastrophic loss of

habitat downstream of the Complex occurred, recolonization of spawners destined for areas upstream of the Complex would require safe transit through the reach to the trap below Hells Canyon Dam. This might or might not be possible depending on the nature of the catastrophe. With regard to developing a genetically distinct upstream population, it may not be possible for a second population to be artificially managed such that there is no genetic mixing, and attempts to do so would increase reliance on hatcheries. Origin-specific tagging of juveniles, with no tag loss or error in recognition, would be required so that adults of BR origin could be selectively trapped-and-transported above Brownlee Dam. BR-origin adults not captured at Hells Canyon Dam would continue to inter-breed with the extant population downstream of the Complex.

Broader implications

We believe that basing recovery planning on simple rules derived from theory can be misguided. These theories make assumptions that are too simple to apply wholesale in setting policies to guide management of riverine species at risk. However, classic metapopulations are rare in natural systems (Cooper and Mangel 1999)[52], and even rarer in human-modified systems that support conservation-reliant species [53]. In particular, the classic metapopulation paradigm has limited relevance for either the pre-dam or post-dam Snake River ESU. Fall Chinook salmon are an “ocean-type” race. They tend to spawn in main channels of large rivers and exit quickly, in contrast to “stream-type” spring Chinook salmon, which spawn in smaller tributaries and remain longer in freshwater. The potential to diversify spatial structure is more limited for mainstem fishes that normally occupy a more-linear (less-dendritic) arrangement of habitat. For metapopulations with a core-satellite structure, conservation of the core population is a priority [22, 52]. The Snake River fall Chinook salmon ESU now consists of a single population with one

large, core spawning area below Hells Canyon Dam and a few satellite spawning areas in two tributaries, the Clearwater and Grande Ronde Rivers.

Two hallmarks of the metapopulation paradigm in conservation biology are the ideas that connected populations are less likely to go extinct [54] and that dendritic stream populations are better protected than those in a non-dendritic arrangement [4, 55]. Yet, theoretical studies have demonstrated that "rescue" by neighboring populations requires levels of migration (i.e., straying) to be low to prevent synchronization [52, 56] and that dendritic arrangements are not always best [57]. Straying rates among spawning areas used by the Snake River ESU are very high, and, as we showed, redd counts in these spawning areas tend to rise and fall together. Constructive measures to increase spatial structure might seek to reduce levels of straying and increase genetic isolation among spawning areas downstream of the Complex. For the highly managed Snake River ESU, two policy changes that could help to reduce straying are 1) to reduce hatchery inputs and 2) to enforce 100% marking policies to permit sorting at traps. In their assessment of incorporating spatial structure and diversity into recovery planning, Fresh, Graeber (1) also highlighted the need to understand the role played by hatcheries, which can cause 'sink' habitats to look like 'source' habitats [18]. Our M-PVA results suggest that this is the case for the Snake River Chinook salmon ESU.

To preserve life-history diversity, "human caused factors such as habitat changes, harvest pressures, artificial propagation and exotic species introduction should not substantially alter variation in traits such as run timing, age structure, size, fecundity, morphology, behavior, and molecular genetic characteristics" [9]. The potential for life history diversification produced by differences in thermal regimes (e.g., below tributary dams or where groundwater influx is

high) is intriguing. Future research to explore resilience to catastrophes may show that thermal diversity, which may or may not correspond spatially to nested basins in developed rivers, could help to enhance population viability.

Beyond this particular ESU, we see important questions that should be addressed in the recovery of salmonids. How can the theoretical framework for managing spatially structured populations be used to represent real rivers and the positive and negative influences of human alterations, such as hatcheries, dams, and nearby land use? Clearly salmon will be entering a new realm, as a result of human activities and climate change [58]. Research efforts should focus on the design of more realistic and pragmatic recovery plans for salmonids in developed rivers, particularly for many ESUs that are conservation reliant.

Acknowledgements

Dell Simmons and Tom Cooney (NOAA Fisheries) provided ocean exploitation data for this analysis. Stuart Rosenberg (IPC) and Deborah Milks (Lyons Ferry Hatchery) contributed back-calculated spawner return counts used in the diffusion modeling.Collegial reviews were provided by Nathan Sutton and Dr. Brenda Pracheil (ORNL).

Figure legends

Figure 1. Historical hatchery and wild adults returning to spawn above Lower Granite Dam on the Snake River, Idaho, USA.

Figure 2. Major rivers and dams of the Lower and Middle Snake River basin. Fall Chinook salmon currently spawn in the mainstem and several tributaries below Hells Canyon Dam. The proposed new spawning area in the Marsing reach above Brownlee Dam was used by many spawners before the dam was built.

Figure 3. Schematic of simulated trap-and-transport program showing two spawner traps, one below Lower Granite Dam and one below Hells Canyon Dam. A juvenile trap above Brownlee Dam would be used to collect juvenile Chinook salmon and transport them to Lower Granite Dam.

Figure 4. We illustrate projected Snake River fall Chinook salmon ESU risk of extirpation within 100 y. A vertical line (productivity, $\lambda = 1$) separates growing and declining ESUs. Estimates are superimposed on TRT isoclines describe risk in terms of productivity and abundance, very low risk: <1%, low risk: 1 to 5%, moderate risk: 5 to 25%, high risk: >25% [Source: Interior Columbia Basin Technical Recovery Team (39)]. S-PVA results are shown for unmarked ('wild', solid circle) and total adult females (open circle). M-PVA results are shown as square symbols with shading indicating the simulated hatchery broodstock quota: open=0, light grey=25 y^{-1}, grey=100 y^{-1}, and filled=1600 y^{-1}. In addition, we present risk estimates from an earlier [up triangle, McClure, Holmes (34)] and a recent study [down triangle, Cooney (17)] of this ESU.

Figure 5. M-PVA simulation results for annual quotas for females removed from the river to use as broodstock in the hatchery below Lower Granite Dam, 0, 25, 100, and 1,600 with no translocation of excess females. The boxes illustrate model responses including the average number of female spawners (top graph) and population trend (bottom graph). The box encloses 25th and 75th percent of results from 47 parameter sets. Horizontal lines show the mean (dashed) and median (solid), whiskers indicate the 10th and 90th percentile, and all outliers are depicted by solid symbols.

Figure 6. Correlations among redd counts indicating the degree of synchrony among spawning areas currently used by the Snake River fall Chinook salmon ESU.

Figure 7. Distribution of M-PVA-simulated (A) average female spawners and (B) population trends. Each plot represents a different level for the ratio of habitat capacity above Brownlee Dam to that below Hells Canyon Dam, *KF* and survival from above Brownlee to Lower Granite Dam, *Stot.* Results for each set of parameters can be compared to the scenario with no translocation (Spawner trapping rate = 0, horizontal dashed lines). Results are illustrated for the scenario with a hatchery broodstock quota of 100 females y^{-1}.

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Table 1. Comparison of LPVA simulation results for multi-parameter simulations without a hatchery below Lower Granite Dam (quota=0), and three hatchery scenarios, with a range of annual broodstock quotas. We report the average ± SD and (minimum–maximum) over 200 replicate populations.

Quota, # females (*Up1_Quota*)	Risk of extirpation	Years to extirpation	Population trend, λ	Female spawners	Smolt-to-adult (sub-yearling)	Smolt-to-adult return (yearling)
0	0.989 (1.0 – 0.84)	39.5 ± 8.73 (26 – 59)	0.827 ± 0.043 (0.737 – 0.998)	118.3 ± 45.1 (54 – 284)	0.0036 ± 0.0008 (0.0025 – 0.0064)	0.0026 ± 0.0005 (0.0019 – 0.0040)
25	0.0 (0.0 – 0.0)	> 100 y	0.992 ± 0.002 (0.987 –	470.4 ± 166.9 (228 – 1072)	0.0042 ± 0.0009 (0.0029 – 0.0073)	0.0136 ± 0.0031 (0.0091 – 0.0200)

			0.998)			
100	0.0 (0.0 – 0.0)	> 100 y	1.005 ± 0.002 (1.002 – 1.009)	1,498 ± 357 (911 – 2,686)	0.0043 ± 0.009 (0.0029 – 0.0073)	0.0163 ± 0.0035 (0.0113 – 0.0237)
1,600	0.0 (0.0 – 0.0)	> 100 y	1.023 ± 0.002 (1.018 – 1.026)	5,832 ± 1,444 (912 – 2,687)	0.0043 ± 0.001 (0.0030 – 0.0075)	0.029 ± 0.005 (0.0202 – 0.0398)

Appendix A. Statistical PVA Simulations

For a range of initial spawner returns between 20 and 200 females, we simulated by brood year, accumulating spawners of ages 3-6 with constant proportions, P_x, from earlier years in the historical record to maintain realistic autocorrelation (Equation 1). For each replicate simulation, a random starting year, *t'*, was used when drawing from *nyrs* = 30 years of historical data with the ability to compare returns in year t and t-5. The historical time series was repeated (wrapped around) as needed to complete the 100-y runs. The algorithm is given below:

$$
\begin{aligned}
&r = 1 : nrep \quad \# \textit{Loop over replicates} \\
&\quad tr = \text{uniform}(1, nyrs) \quad \# \textit{Draw start year at random} \\
&\quad tt = 1 : 100 \quad \# \textit{Loop over future years, tt} \\
&\qquad t = tt + 6 \quad \# \textit{Add number of age classes} \\
&\qquad S_t = \sum\nolimits_{age=1}^{6} \left[P_{age} \cdot N_{t-age}^{r} \right] \quad \# \textit{Spawners broodyear } t \\
&\qquad tr = \begin{cases} tr + 1, \; tr \le nyrs \\ 1, \; otherwise \end{cases} \quad \# \textit{Update historical year used} \\
&\qquad \text{Draw } \hat{Y}_{tr}, \text{a prediction, } \log\left(\frac{R_{tr}}{S_{tr}}\right) \\
&\qquad \text{Draw } \hat{\varepsilon}_{tr}, \text{ a residual, } \log\left(\frac{R_{tr}}{S_{tr}}\right) \\
&\qquad N_t^r = S_{t-k} \, e^{\hat{Y}_{tr} + \hat{\varepsilon}_{tr} + b S_{t-k}} \\
&\quad next \; t \\
&next \; r
\end{aligned}
$$

Figure 1 time series
Click here to download Figure: Fig1-IPC-SnakeESU-HistoricalReturns.JPG

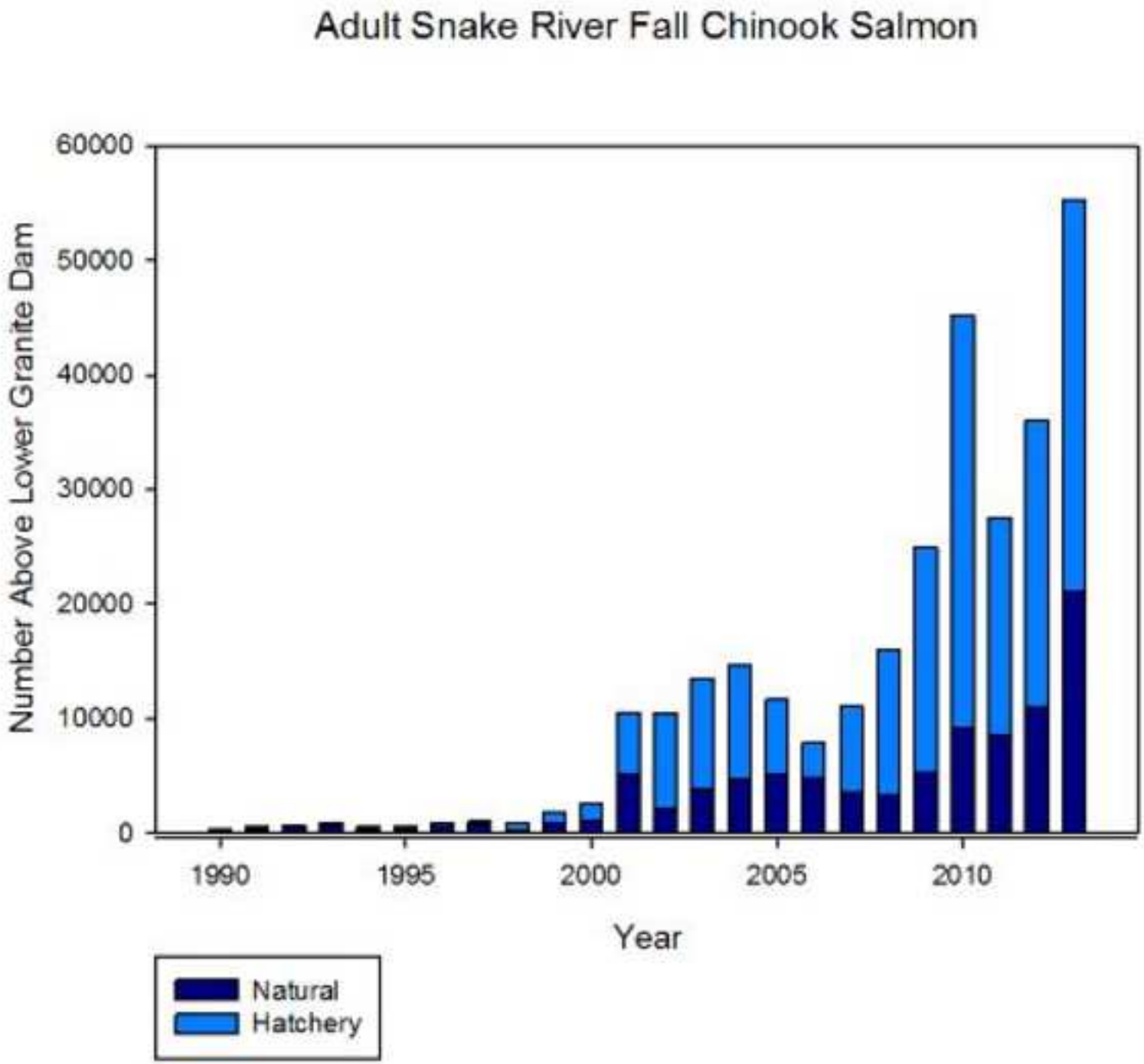

Figure 2 map
Click here to download Figure: Fig2-map-FC_Habitat.jpg

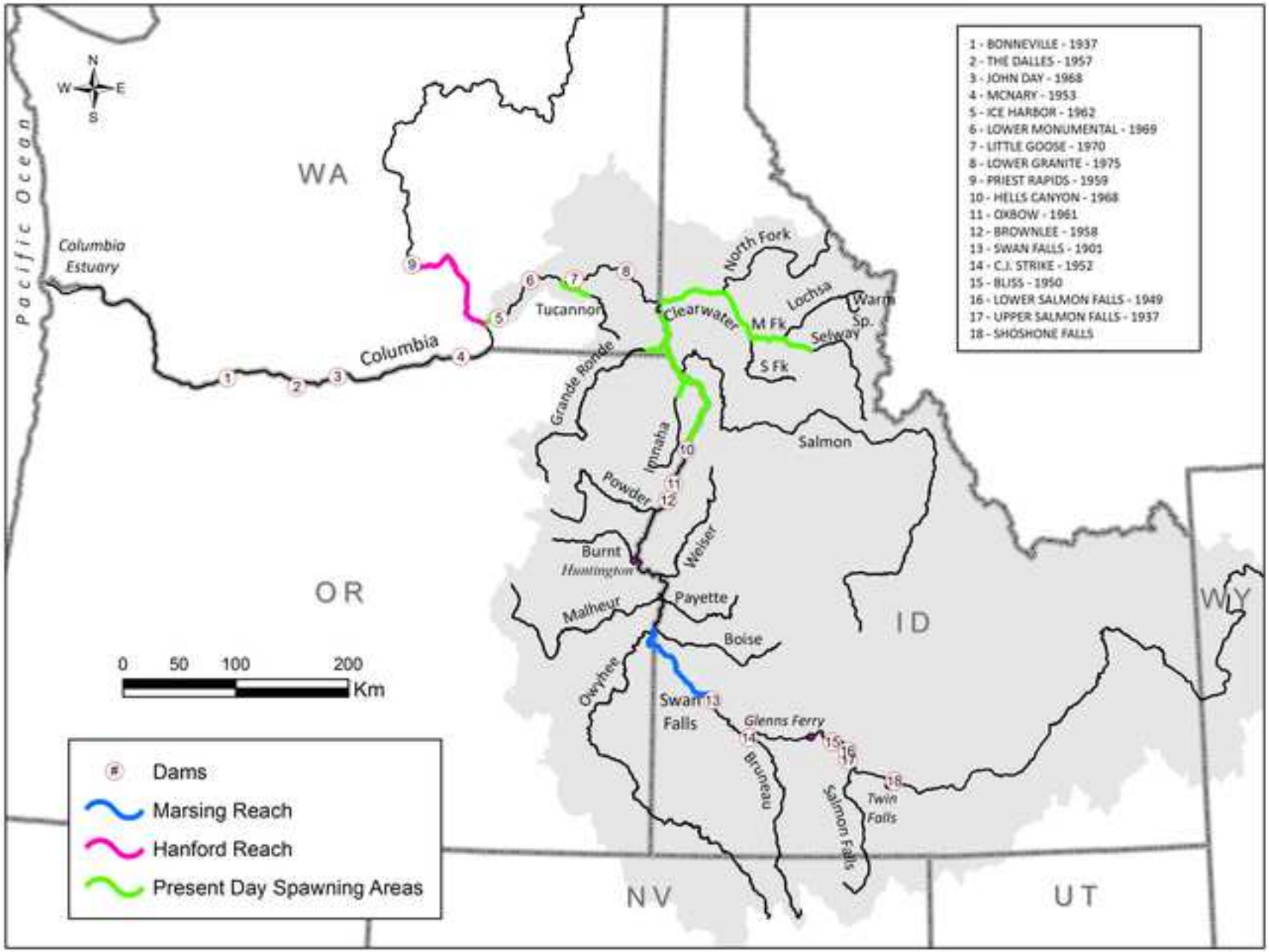

Figure 3 - trap diagram
Click here to download Figure: Fig3. Two-Trap-Diagram.png

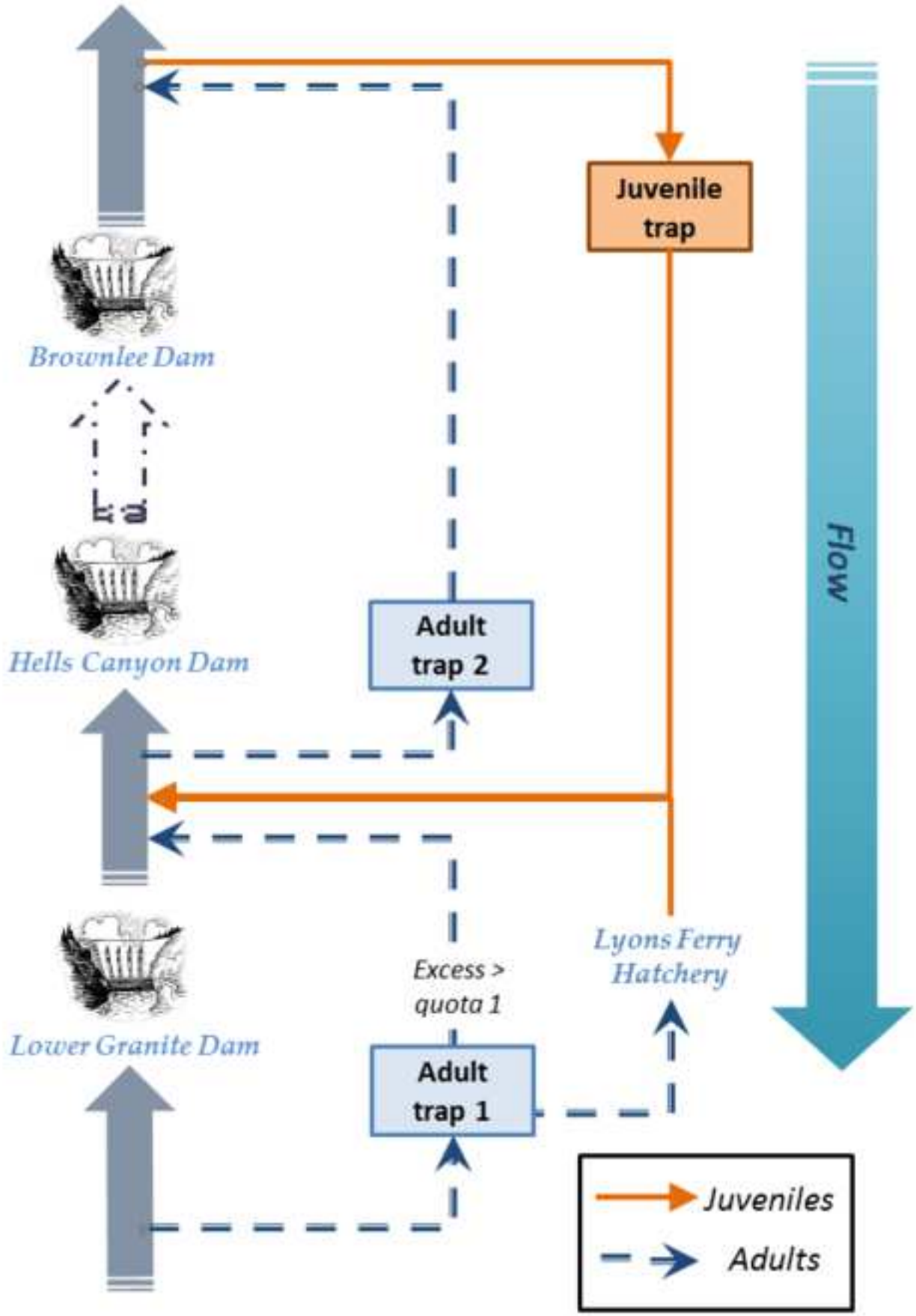

Figure 4 TRT risk
Click here to download Figure: Fig4-TRT-risk4.JPG

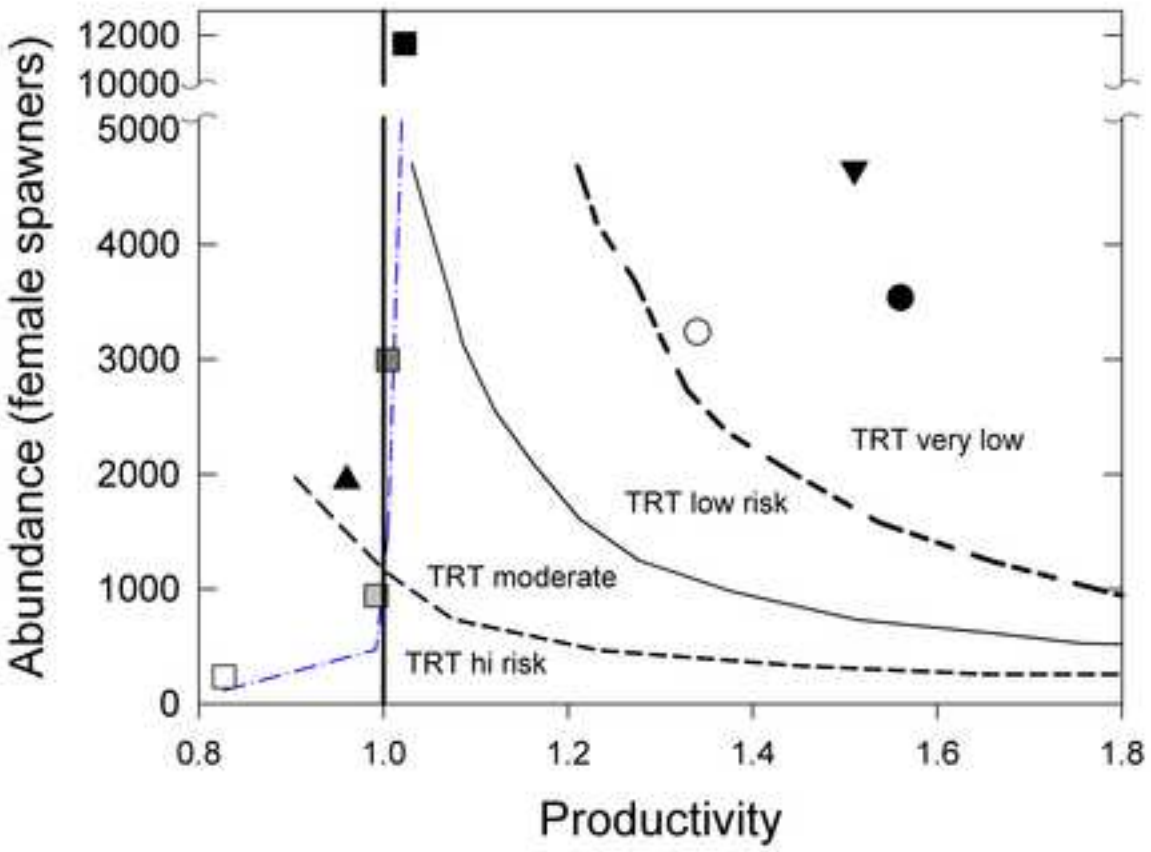

Figure 5 box-whiskers
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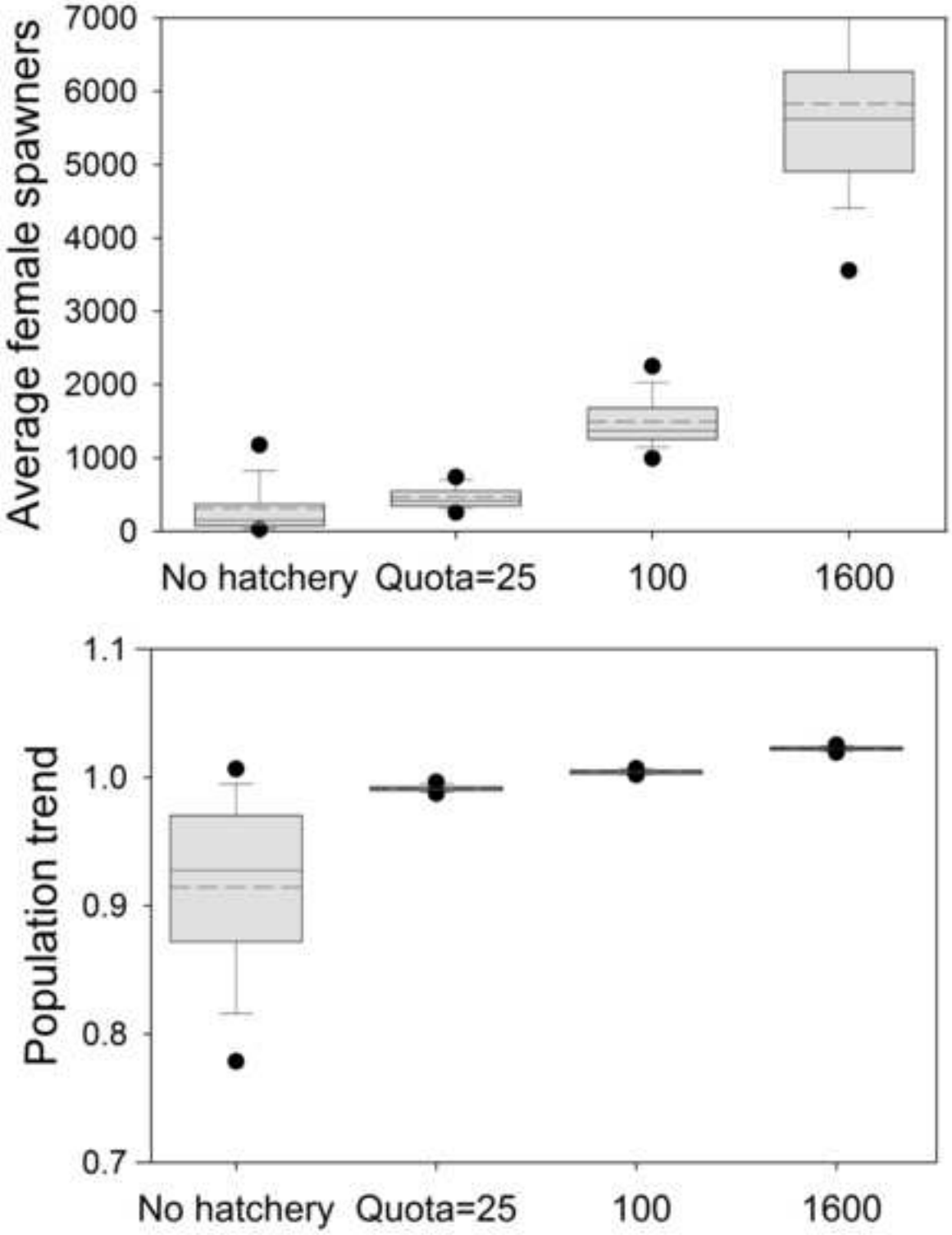

Figure 6 correlations
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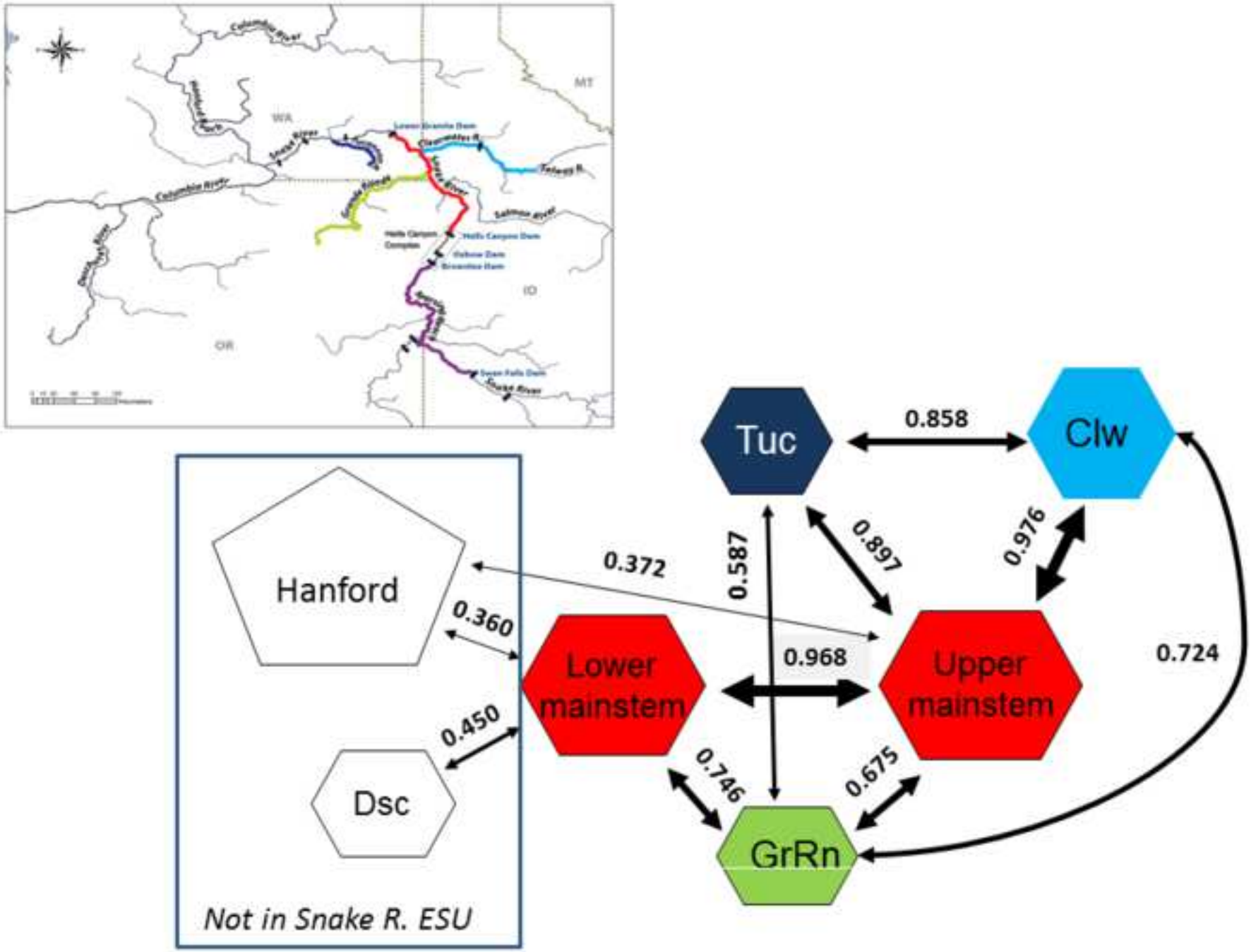

Figure 7a

Click here to download Figure: Fig7a-Grid-Boxplot.spawners-Quota100.pdf

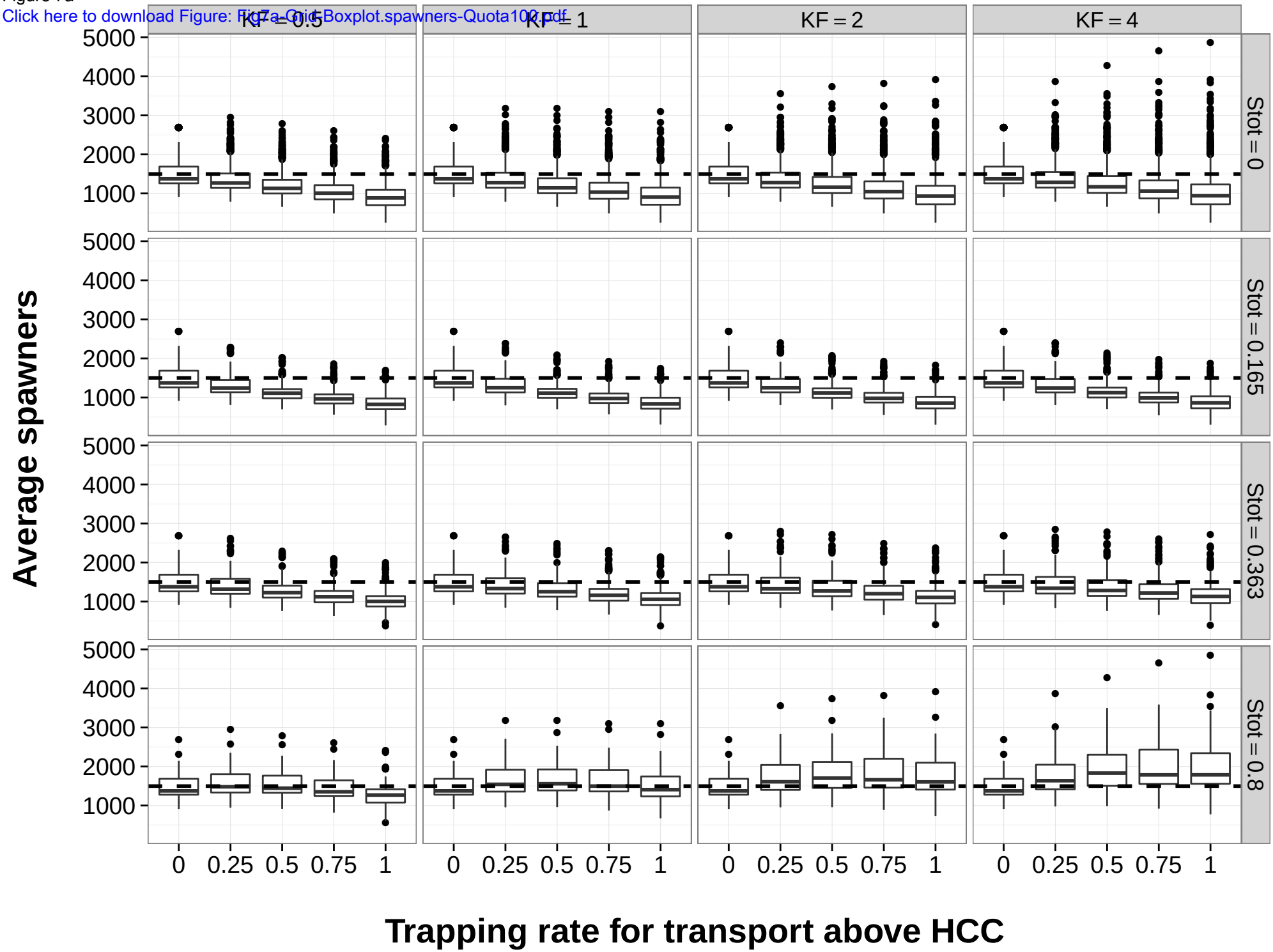

Figure 7b

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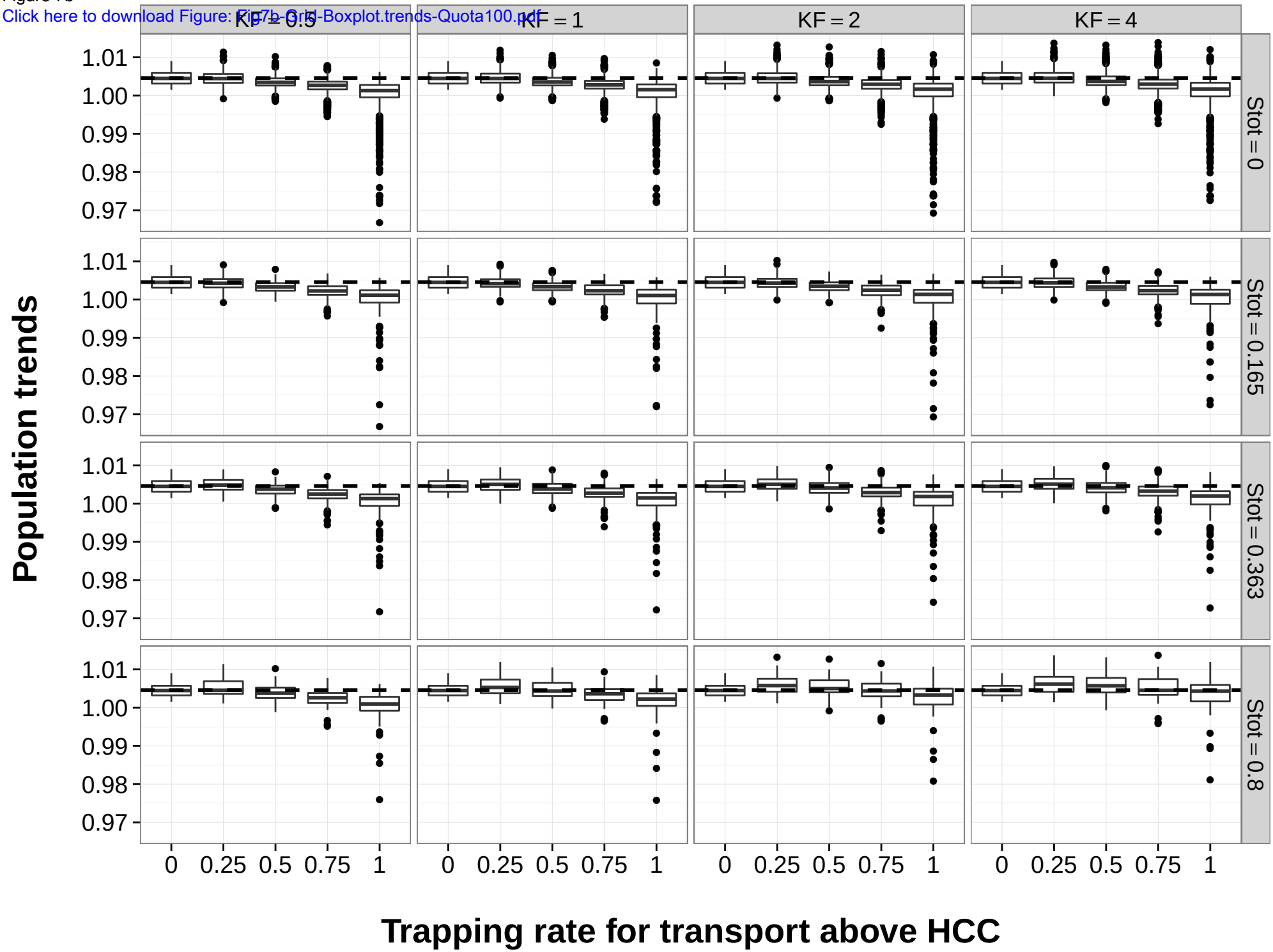

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