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High value of ecological information for river connectivity restoration

Suresh Andrew Sethi • Jesse R. O’Hanley • Jonathon Gerken • Joshua Ashline • Catherine Bradley

Suresh Andrew Sethi (Corresponding author)
US Geological Survey, New York Cooperative Fish and Wildlife Research Unit, Cornell University, 211 Fernow Hall, Cornell University, Ithaca NY 14853
e. suresh.sethi@cornell.edu
p. +1 607.255.7273
f. +1 607.255.1895

Jesse R. O’Hanley
Kent Business School, University of Kent, Canterbury CT2 7PE UK

Jonathon Gerken • Joshua Ashline • Catherine Bradley
US Fish and Wildlife Service, Fisheries and Ecological Services, Anchorage AK 99503 USA

Abstract

Context Efficient restoration of longitudinal river connectivity relies on barrier mitigation prioritization tools that incorporate stream network spatial structure to maximize ecological benefits given limited resources. Typically, ecological benefits of barrier mitigation are measured using proxies such as the amount of accessible riverine habitat.

Objectives We developed an optimization approach for barrier mitigation planning which directly incorporates the ecology of managed taxa, and applied it to an urbanizing salmon-bearing watershed in Alaska.

Methods A novel river connectivity metric that exploits information on the distribution and movement of managed taxon was embedded into a barrier prioritization framework to identify optimal mitigation actions given limited restoration budgets. The value of ecological information on managed taxa was estimated by comparing costs to achieve restoration targets across alternative barrier prioritization approaches.

Results   Barrier mitigation solutions informed by life history information outperformed those using only river connectivity proxies, demonstrating high value of ecological information for watershed restoration. In our study area, information on salmon ecology was typically valued at 0.8-1.2M USD in costs savings to achieve a given benefit level relative to solutions derived only from stream network information, equating to 16-28% of the restoration budget.

Conclusions   Investing in ecological studies may achieve win-win outcomes of improved understanding of aquatic ecology and greater watershed restoration efficiency.

Keywords: anadromous, conservation planning, fish passage, Life Cycle Connectivity Index, optimization, Pacific salmon, spatial network

1. Introduction

Landscape scale impacts of artificial stream barriers (e.g., dams and road crossings) include both physical and ecological changes. Stream barriers alter flow regimes (Costigan and Daniels 2012), change sediment accumulation dynamics (Renwick et al. 2005), and can increase flood damage from poorly maintained or undersized water conveyance structures (Gillespie et al. 2014). Stream barriers also drive significant ecological change within watersheds by restricting fish (Nislow et al. 2011) and macroinvertebrate (Sethi et al. 2004) movements, and potentially reduce habitat quality for aquatic organisms (Lessard et al. 2003, Aust et al. 2011). Effective river connectivity restoration is logistically challenging and costly. In urban areas, one often faces technical difficulties and high costs working in congested areas. In rural areas, sites may be remote or require private landowner permission to gain access. Costs to repair, replace, or remove barriers to restore natural flow regimes can range from the tens of thousands to millions of US dollars (USD; Text S1), particularly when bridges need to be constructed. Thus, efficient stream barrier mitigation planning has become a top watershed management priority (e.g., Fullerton et al. 2010, Beechie et al. 2013).

Recently proposed methods for river connectivity restoration planning explicitly take into account the spatial structure of river barrier networks and employ sophisticated optimization techniques to maximize restoration benefits given available resources (Kemp and O’Hanley 2010, King and O’Hanley 2016). Owing to limited knowledge and understanding of species distributions, dispersal patterns, and habitat use in most watersheds, the ecological benefits of stream barrier restoration efforts are typically measured using proxies in the form of habitat connectivity indices (e.g., O’Hanley et al. 2013a). Although useful for describing high-level habitat connectivity patterns (e.g., connectivity between upstream areas and the sea), reliance on physical connectivity metrics may mask the importance of fine-scale dispersal and habitat use dynamics of focal management taxa. Aquatic plants and animals are patchily distributed within riverine ecosystems, and mobile taxa often make regular seasonal movements within catchments, including anadromous Pacific salmon which must migrate from oceans to freshwater habitats to complete their life cycle (Groot and Margolis 1991). Field-based studies have a long tradition of successfully informing the instream ecology of aquatic plants and animals; however, these efforts are costly and time consuming. Thus, it may appear impractical to expect detailed ecological information to be included in barrier prioritization efforts alongside information relating to spatial stream networks, barrier locations, and mitigation costs.

Here, we provide empirical evidence that the cost savings obtained by including life-history information into river connectivity restoration planning may be substantial. Using Coho salmon (Oncorhynchus kisutch) from the Big Lake watershed in Alaska, U.S.A. as a test case, we develop a novel river connectivity metric termed the Life Cycle Connectivity Index (LCCI) which exploits ecological information on the focal managed taxon. Subsequently, the LCCI is embedded into a barrier optimization framework that identifies optimal portfolios of stream barrier mitigation actions given a limited budget. Unlike existing connectivity metrics, LCCI takes into account the spatial relationship of distinct habitats required throughout the freshwater component of a focal taxon life cycle together with life stage-specific information on dispersal behavior and barrier passability. Another key feature of the LCCI metric is the ability to identify habitat bottlenecks across life stage transitions attributable to impaired watershed connectivity. The index can be adapted to model the life cycles of freshwater migratory species of conservation concern other than Pacific salmon.

A suite of observational fields studies on Coho salmon in the Big Lake watershed were used to inform the LCCI barrier optimization model in the test case, including adult spawning salmon surveys, analysis of juvenile summer rearing and overwinter habitat use, and assessment of outward migration dynamics of smolts. Restoration benefits were compared to a suite of common alternative barrier prioritization approaches, including random project selection, project scoring and ranking based upon habitat area, and an optimization model that maximizes a generic index for longitudinal river connectivity. Finally, we estimated the value of information for Coho salmon ecology in the Big Lake watershed by comparing restoration budgets needed to achieve a given level of LCCI for the different barrier prioritization approaches.

2. Methods

Case study area

The ≈300 km^2 Big Lake watershed is located in the rapidly urbanizing Matanuska-Susitna valley near Anchorage, Alaska, U.S.A (Figure 1). This subarctic system, which terminates at saltwater in upper Cook Inlet, is low-gradient with off-channel habitat dominated by lakes and wetlands (Curran and Rice 2009). Coho salmon are a numerically and socioculturally dominant salmon species in the Big Lake watershed, supporting commercial fisheries in Cook Inlet, and sport and subsistence fisheries within the drainage. Coho salmon in this system are hypothesized to utilize most of the watershed across freshwater life stages, exhibiting ontogenetic and seasonal migrations within drainages (e.g., Ashline 2017). As such, this species is the focal management taxon for fish passage restoration, serving as an umbrella species nesting the stream connectivity needs of other fish taxa. Human population in the valley has grown 50% per decade since 1990 (U.S. Census Bureau 2017), resulting in increased road and housing infrastructure with associated stream crossing works. Currently, 42 of the 60 extant stream crossing projects (culverts) in the Big Lake watershed partially or fully impede fish passage (Table S1.3). A combination of federal, state, borough, and non-governmental groups are coordinating fish passage restoration in the Big Lake watershed, resulting in a need to prioritize stream barrier mitigation efforts given limited restoration budgets.

Figure 1 approximately here

Life Cycle Connectivity Index

The Life Cycle Connectivity Index incorporates the spatial distribution of freshwater life stage-specific habitats and interlinks them via intermediary dispersal through the stream network. Stream barriers, such as culverts, inhibit dispersal from one habitat type to another, thus reducing fish passage connectivity and potentially limiting habitat availability for specific life stages. In the present application, we parameterized the LCCI to represent the predominate Coho salmon life cycle pattern in the Big Lake watershed, utilizing information from a suite of field studies implemented from 2011 to 2015 (see below; additional detail provided in Text S1).

A semelparous species, adult Coho salmon in the study area typically migrate from the ocean to discrete freshwater spawning beds from July to October (Figure S1.1). Spawning bed locations were identified using radio tag telemetry and stream surveys by U.S. Fish and Wildlife Service (Foley et al. forthcoming). Eggs incubate overwinter, and young of year fish emerge in late Spring and distribute to preferred summer rearing grounds made up of wider and shallower mainstem reaches in the Big Lake watershed (Bradley et al. 2017, Sethi et al. 2017). In Autumn, juvenile fish redistribute to preferred lake habitats to overwinter, generally the nearest suitable lake (Sethi et al. 2013, Ashline 2017). In the following Spring, age 1 juvenile fish then return to summer rearing mainstem habitats and ultimately back to their respective overwinter lake habitat locations. While age 1 fish do not necessarily seek out the same summer rearing reaches they utilized as age 0 fish, we modeled the age 0 overwinter-to-age 1 summer rearing-to-age 1 overwinter dispersal phase as a cyclic out-and-back route based upon movements of Passive Integrated Transponder (PIT) tagged fish (Ashline 2017). After two winters in freshwater, fish out-migrate from overwinter lake habitats as smolts to rear to adulthood in the ocean. Survival estimates of individually PIT-tagged Coho salmon smolts in the study watershed indicated high cumulative mortality along the outward migration (Text S1). Subsequently, we represented the relative values of the origination habitats for outward smolt migration by including a habitat discount factor equal to migration related mortality. While Coho salmon exhibit plasticity in rearing habitat use and smolt timing, the life history strategy described above is believed to reflect the predominant Coho salmon life history in the Big Lake watershed using information generated from primary studies in the system.

To formulate LCCI , let N^{SP}, N^{SR0}, N^{WR}, N^{SR1} be the sets of spawning (SP), age 0 summer rearing (SR0), winter rearing (WR), and age 1 summer rearing (SR1) habitat areas of a river network indexed by i, j, k, and ℓ, respectively. Index o denotes the ocean. Index $w \in \{\mathrm{SP}, \mathrm{SR0}, \mathrm{WR}, \mathrm{SR1}, \mathrm{SM}\}$, meanwhile, is used to indicate a dispersal step with w equal to SP for ocean-to-spawning ground dispersal (immigrating adults), SR0 for spawning-to-summer rearing dispersal (age 0 juveniles), WR for age 0 juvenile summer rearing-to-overwinter dispersal, SR1 for age 1 juvenile overwinter-to-summer rearing out and back dispersal, and SM for overwinter-to-ocean smolt out-migration at the end of Coho salmon juvenile freshwater life cycle.

Let F be the set of "feasible" dispersal paths starting from and terminating at the ocean, where a path is feasible if the distance d_{st} between habitat areas s and t for any given dispersal step w does not exceed some maximum dispersal distance, r^{w}:

$$F = \{(o, i, j, k, \ell, o) | i \in N^{\mathrm{SP}}, j \in N^{\mathrm{SR0}}, k \in N^{\mathrm{WR}}, \ell \in N^{\mathrm{SR1}}, d_{oi} \le r^{\mathrm{SP}}, d_{ij} \le r^{\mathrm{SR0}}, \\ d_{jk} \le r^{\mathrm{WR}}, d_{k\ell} \le r^{\mathrm{SR1}}, d_{ko} \le r^{\mathrm{SM}}\} \qquad \text{Eq. 1}$$

The amount of stream network habitat (including lakes) of life stage specific type $m \in \{\mathrm{SP}, \mathrm{SR0}, \mathrm{WR}, \mathrm{SR1}\}$ in area s is denoted by h_s^w. The total amount of habitat of type m that can be reached from area s assuming no barriers are present is denoted by H_s^m. The term H_s^m, which serves a normalization factor in the LCCI (see below), is calculated by summing over all destination areas t that are reachable from s through a feasible dispersal path (i.e., $H_s^m = \sum_{t \in D_s} h_t^m$, where D_s is the set of destination habitat areas reachable from s such that subpath (s,t) is contained in F).

The passability $p_b(d,a)$ of an individual barrier b is assumed to be directional (d) and age (a) specific, with $d \in \{\mathrm{up}, \mathrm{dwn}\}$ for upstream (up) and downstream (dwn) travel, respectively, and $a \in \{\mathrm{ad}, \mathrm{juv0}, \mathrm{juv1}, \mathrm{sm}\}$ for adults (ad), age 0 juveniles (juv0), age 1 juveniles (juv1), and smolts (sm), respectively. Passability, as defined in Kemp and O'Hanley (2010), represents the proportion of fish (in the range 0-1) that are able to successfully navigate a barrier. Cumulative passability P_{st} between two habitat areas s and t denotes the proportion of fish that are able to pass all intervening barriers lying between s and t and is calculated by multiplying individual barrier passability values along the path from s to t taking into account the age of the fish and direction of travel. Hence, $P_{st} = \prod_{b \in B_{st}} p_b\left(\mathrm{dir}_{st}^b, a\right)$, where B_{st} is the set of intervening barriers between s and t and dir_{st}^b defines the direction of travel past barrier b when going from source area s to destination area t. The overall passability $P_{oijk\ell o}$ of any feasible path $(o,i,j,k,\ell,o) \in F$ is evaluated by taking the product of each dispersal step: $P_{oijk\ell o} = P_{oi} \times P_{ij} \times P_{jk} \times P_{k\ell} \times P_{ko}$.

With this in place, LCCI is given by:

$$\mathrm{LCCI} = 100 \times \sum_{(o,i,j,k,\ell,o) \in F} E_{oi}^{\mathrm{SP}} \times E_{ij}^{\mathrm{SR0}} \times E_{jk}^{\mathrm{WR}} \times E_{k\ell}^{\mathrm{SR1}} \times P_{ko}$$

$$= 100 \times \sum_{(o,i,j,k,\ell,o)\in F} \left(\frac{P_{oi} h_i^{\mathrm{SP}}}{H_o^{\mathrm{SP}}}\right) \times \left(\frac{P_{ij} h_j^{\mathrm{SR0}}}{H_i^{\mathrm{SR0}}}\right) \times \left(\frac{P_{jk} h_k^{\mathrm{WR}}}{H_j^{\mathrm{WR}}}\right) \times \left(\frac{P_{k\ell} h_\ell^{\mathrm{SR1}}}{H_k^{\mathrm{SR1}}}\right) \times P_{ko}$$

$$= 100 \times \sum_{(o,i,j,k,\ell,o)\in F} \frac{\left(h_i^{\mathrm{SP}} h_j^{\mathrm{SR0}} h_k^{\mathrm{WR}} h_\ell^{\mathrm{SR1}}\right)}{\left(H_o^{\mathrm{SP}} H_i^{\mathrm{SR0}} H_j^{\mathrm{WR}} H_k^{\mathrm{SR1}}\right)} P_{oijk\ell o} \qquad \text{Eq. 2}$$

where the terms E_{oi}^{SP}, E_{ij}^{SR0}, E_{jk}^{WR}, and $E_{k\ell}^{\mathrm{SR1}}$ represent, respectively, the effective amount of spawning habitat in area i reachable from the ocean o, the effective amount of age 0 summer rearing habitat in area j reachable from area i, the effective amount of winter rearing habitat in area k reachable from area j, and the effective amount of age 1 summer rearing habitat in area ℓ reachable from area k. LCCI is formed by taking the product of E_{oi}^{SP}, E_{ij}^{SR0}, E_{jk}^{WR}, and $E_{k\ell}^{\mathrm{SR1}}$ times the cumulative passability of winter-to-ocean dispersal P_{ko} and then summing over all feasible dispersal paths in F. The last equality in equation 2 demonstrates how LCCI is defined in terms of habitat amounts (parameters h_s^m and H_s^m) and cumulative passabilities (variables $P_{oijk\ell o}$). The index is normalized onto a 0 to 100 scale, with 0 indicating one or more life stage specific habitat types is completely inaccessible and 100 indicating that all life stage specific habitats are fully accessible. By assumption, proportionate reductions in the accessibility of each life-stage specific habitat type contribute equally to LCCI reductions. The LCCI index could be expanded to include weights expressing the relative importance of different habitat types, however, we took the approach that significant restrictions in accessibility of any habitat type would lead to survival bottlenecks and thus chose to weight accessibility reductions equally across all habitat types.

Barrier mitigation prioritization

To cost-effectively target culvert mitigation actions in the Big Lake watershed, we developed an optimization model to maximize LCCI subject to a budget constraint. The LCCI metric is used by the optimization model to simultaneously determine i) which habitat type exhibits the greatest reduction in accessibility given stream barriers~~is in least supply~~ and ii) which portfolio of barriers if mitigated would increase the~~ supply~~ accessibility of the most limiting habitat via changes in the cumulative passabilities $P_{oijk\ell o}$ of feasible paths. Mitigation of a barrier (i.e., culvert replacement or removal) was assumed to restore full passability for all Coho salmon life stages.

As formulated above, the cumulative passability terms $P_{oijk\ell o}$, in equation 2 are nonlinear. To avoid solving a nonlinear optimization model, a mixed integer linear programming reformulation of the model was devised by applying the "probability chain" concept developed by O'Hanley et al. (2013b). Full details of the optimization model and input information are provided in Supplemental Text S1.

The barrier optimization model was parameterized as follows. Barrier culvert locations were snapped to a spatial stream network using the Barrier Analysis Tool add-in for ArcGIS (Hornby 2013). Culvert mitigation cost estimates were generated by U.S. Fish and Wildlife Service engineers (Dekker and Rice 2016). Culvert passabilities were based upon a categorical green-grey-red fish passage ratings system implemented by the Alaska Department of Fish and Game (O'Doherty 2010), and subsequently translated to upstream/downstream and life stage specific passability values using expert judgement of U.S. Fish and Wildlife Service biologists (J. Gerken and J. Ashline; Text S1). Life stage specific dispersal distances were informed by a combination of recorded movements of PIT tagged fish from the Big Lake system (Gerken and Sethi 2013, Ashline 2017) and expert opinion of U.S. Fish and Wildlife fisheries biologists (J. Gerken and J. Ashline). Locations of spawning, age 0 summer rearing, age 1 summer rearing, and overwinter habitats were assigned by U.S. Fish and Wildlife fisheries biologists using primary information on Coho salmon habitat use and movement behavior from in situ ecological studies described previously. Finally, a smolt origination habitat (age 1 overwinter locations) discount factor was specified as the estimated survival of individually PIT-tagged Coho salmon smolts migrating out from different Big Lake sub-basins (Text S1).

The barrier mitigation optimization approach outlined above benefits from information on the stream network configuration as well as detailed fish ecology information when deciding which barriers are selected for mitigation. For comparison, three other barrier prioritization methods were implemented (Table S1.1-S1.2): i) a more conventional optimization approach that maximizes a generic index of stream connectivity (dendritic connectivity index, DCI; Cote et al. 2009), ii) a scoring and ranking based approach, and iii) random selection of mitigation projects. The DCI-informed barrier optimization model maximizes accessible upstream length given a budget (King and O'Hanley 2016). The scoring and ranking approach sorts barriers according to their upstream habitat gain divided by cost (i.e., net increase in passability times net upstream length divided by mitigation cost) and selects projects in rank order as outlined in O'Hanley and Tomberlin (2005). Random project selections represents an uninformed approach to river connectivity restoration planning. Ironically, this approach may characterize many real world situations where ~~ad hoc decisions are driven by~~ budget sideboards, jurisdictional issues, and project access dominate restoration decisions. Twenty iterations of random project selection were carried out at each budget level.

Value of ecological information

To gain understanding about the value of ecological information in river connectivity restoration, we compared the management budget required to achieve a given connectivity benefit outcome from the LCCI maximizing model versus that from the DCI maximizing model. The DCI maximization model only considers physical connectivity within the ~~spatial~~ stream network, while the LCCI model is further informed by fish ecology information (Text S1). The difference in cost between these two models to achieve a specified level of LCCI, therefore, provides a partial estimate of the (marginal) value of focal taxon ecological information. We refer to this as a "partial" value of information estimate owing to other benefits that may arise with investments in stream network or ecological information such as spillover benefits of information for other habitat or population management applications. For comparison, the costs to obtain the Coho salmon ecology information from studies referenced in the Big Lake drainage were estimated at ≈ 0.5M (2015 USD).

Habitat accessibility ratios

Following the specification of the distribution of life stage specific habitats, dispersal paths, and barrier passabilities used to construct the LCCI metric, we investigated the impact of fish passage restrictions on Coho salmon life cycle habitat needs by calculating the proportion of habitat associated with a life stage transition that is accessible for a proposed set of barrier mitigation actions. A habitat accessibility ratio of 1.0 indicates that 100% of the potentially available habitat at the next life stage is accessible; values <1.0 indicate habitat accessibility is restricted by the presence of fish passage barriers.

3. Results

Under the existing set of stream barriers, less than half (LCCI = 49.2) of river habitat in the Big Lake watershed ~~is currently~~ available to meet the life cycle needs of Coho salmon is currently accessible (i.e., for 0 restoration budget). Stream barrier impacts on life stage specific habitat accessibility were most pronounced for the age 0 summer rearing-to-winter rearing dispersal phase, followed by the out-and-back age 1 winter rearing-to-summer rearing transition (Figure 2). Other life stage transition habitat needs were largely unrestricted by stream barriers.

Figure 2 approximately here

As a group, optimization-based approaches (LCCI and DCI maximization) strongly outperformed both scoring and ranking and random project selection. Among the various barrier prioritization schemes, the LCCI maximization approach was most cost-efficient (Figure 3a), outperforming all other approaches across all budget levels. Under this approach, full connectivity (LCCI = 100) for Coho salmon can be restored with a budget of 6.8M USD, requiring mitigation of 29 out of 60 barriers. In contrast, the DCI maximization, scoring and ranking, and random project selection approaches required 7.6M (36 barriers mitigated), 8.4M (44 barriers), and 12.0M USD (mean budget value across 20 iterations; range in number of barriers mitigated = 53 to 60) to restore full connectivity, respectively.

Figure 3 approximately here

Whereas the DCI maximization approach utilizes only spatial stream network information, the LCCI maximization method also incorporates Coho salmon ecology information garnered from the Big Lake watershed when selecting stream barrier mitigation projects. The performance differences between the two approaches, therefore, can be attributed to the inclusion of Coho salmon ecology information. For restoration budgets less than 1.0M USD, the LCCI- and DCI-based optimization approaches produced comparable restoration benefits (Figure 3a). At larger budgets, substantially greater restoration benefits could be achieved by the LCCI maximization approach. Put another way, the LCCI maximization approach achieves any desired level of connectivity at lesser cost than any other prioritization approach tested. Cost-savings attributable to including salmon ecology information for the LCCI-based optimization approach ranged as high as 1.6M USD (at a target of LCCI = 95; Figure 3b). Above restoration targets of LCCI = 55, the value of salmon ecology information averaged 1.0M USD in cost savings (inner quartile range = 0.8M to 1.2M USD), which equates to an average of 25% of the restoration budget (inner quartile range = 17 to 27%) relative to the next best barrier mitigation prioritization scheme.

4. Discussion

River ecosystems have complex spatial structures driven by geology, flow regimes, and climate (Naiman and Bilby 1998). Riverine organisms have evolved to take advantage of these conditions (e.g. Schlosser 1991). For example, a wide range of fish species migrate between freshwater and saltwater ecosystems as part of their reproductive strategy (Gross et al. 1988), and many resident lotic species have distinct habitat needs across spawning, juvenile, and adult life stages (e.g., fish: Aadland 1993, insects: Mérigoux and Dolédec 2004; mussels: McRae et al. 2004). As a result, the impact of stream barriers on riverine populations will depend on both the physical structure of the stream network as well as the distribution of habitat types throughout watersheds. Except in rare cases where habitats are uniformly distributed throughout a drainage, stream barrier mitigation approaches based purely on the physical configuration of stream networks may produce outcomes which are suboptimal with regard to species’ habitat needs.

The Big Lake watershed example demonstrates several benefits which arise when stream barrier mitigation planning directly incorporates life history information on the distribution and movement of the focal management taxon. Perhaps of greatest interest is that the value of information regarding fish habitat and passage needs can be substantial in terms of connectivity restoration cost savings—funding that could be used to mitigate additional stream barriers or be put to other watershed restoration uses. The Coho salmon case study demonstrated typical savings of 25% of the total restoration budget (for restoration budgets > 1.0M USD; Figure 3b). Furthermore, whereas longitudinal connectivity (DCI) always improved with increasing restoration budgets for the barrier mitigation optimization approach which utilized information only on the river network structure, this strategy occasionally produced lower LCCI restoration benefit outcomes with budget increases (e.g., at 3.2M or 4.5M USD in Figure 3a). This indicates that gains in restoration benefit from additional barrier mitigation funding may not always be positive when ignoring the life history of managed taxa. ~~Furthermore, the barrier mitigation optimization approach which utilized information only on the stream network without taking into consideration Coho salmon life history (DCI maximization) occasionally produced lower LCCI restoration benefit outcomes with increases in the restoration budget (e.g., at 3.2M or 4.5M USD in Figure 3a), indicating that the gains in restoration benefit from additional barrier mitigation funding may not always be positive when ignoring the life history of managed taxa.~~ While our results here focus on Coho salmon, many freshwater ~~fish~~ taxa exhibit life stage specific habitat preferences and migration patterns (e.g., Schlosser 1991). We expect barrier mitigation cost savings associated with life history informed prioritization efforts may arise in a wide range of management contexts.

Estimates of the value of ecological information presented here are specific to the restoration planning aims in the Big Lake watershed; however, this valuation only partially encompasses the benefits associated with investments to improve the understanding about stream taxa ecology. Investments in obtaining ecological information in one watershed provide value to other watersheds by either directly informing focal taxa connectivity and habitat needs, or at a minimum, providing a priori information to guide field design and analyses of ecological studies. For example, the detailed Coho salmon life stage habitat use and migration behavior from the Big Lake watershed is likely applicable to other nearby watersheds for which salmon fish passage restoration efforts are planned. Furthermore, the synthesis of habitat use and migration behavior generated by the LCCI-based barrier prioritization analysis contributed novel ecological insight by identifying which freshwater life stages of Coho salmon are most impacted by stream barriers. In the Big Lake watershed, stream barriers most strongly impacted the redistribution of age 0 juveniles from summer rearing grounds to overwinter habitats (Figure 2, SR0:WR). At this life stage transition, these juvenile fish have relatively weak dispersal capabilities and are sensitive to stream barriers as they migrate upstream to overwinter lake habitats. Interestingly, age 0 fish were found to be largely unaffected by impaired stream connectivity during their emergence and first summer of rearing prior to overwinter redistribution (Figure 2, SP:SR0). This is because few barriers occur along mainstem reaches and because age 0 juveniles typically disperse only short distances from the spawning beds where they hatch to nearby suitable summer rearing reaches. Effectively, nearly all age 0 summer rearing habitat is accessible without mitigating any extant stream barriers.

Results here indicate efficiency gains for watershed-scale connectivity restoration planning when using life history informed barrier mitigation optimization approaches and especially highlight the poor performance of random mitigation project selection. In the present application, restoration planning centered on a single taxon of interest with ecological studies focused on Coho salmon to inform the prioritization of barrier mitigation efforts. River connectivity management in many systems may also center on a single taxon (e.g., Pacific salmon and lamprey; Jackson and Moser 2012); however, at larger spatial scales encompassing multiple watersheds, watershed connectivity restoration may focus on multiple taxa or guilds (Neeson et al. 2015). In such cases, the incorporation of life history information into stream barrier mitigation efforts may require selection of a representative taxon such as a diadromous species with a life history that encompasses both the lower and upper portions of watersheds and thus nests other fish species' connectivity needs. Alternatively, it may be possible to construct barrier mitigation models which incorporate life history for more than one focal species. We suspect this latter case may characterize a growing number of systems where managers must balance promoting the distribution of native species with restricting the expansion of invading aquatic species (Fausch et al. 2009). In this case, a life cycle connectivity index for a focal endemic species could be specified, while imposing a constraint on a separate life cycle connectivity index for the invader.

5. Acknowledgments

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6. Data accessibility

Stream network and culvert information are digitally archived (doi:10.7910/DVN/AFIMSI). Analyses of adult spawning distribution data are available in (Foley et al. forthcoming), summer rearing habitat use in (Bradley et al. 2017), and juvenile migration data in (Gerken and Sethi 2013, Ashline 2017).

7. Figure Captions

Figure 1. Big Lake watershed, Alaska U.S.A. Circles represent the location of fish passage barriers (culverts) throughout the drainage.

Figure 2. Life stage habitat accessibility ratios. Values represent the proportion of accessible habitat associated with a particular life stage transition depending on barrier mitigation actions solutions produced by the Life Cycle Connectivity Index maximization approach. A habitat ratio of 1.0 indicates that 100% of potentially available habitat at the next life stage is accessible; values <1.0 indicate habitat accessibility is restricted by fish passage barriers. Boxplots (whiskers: minimum and maximum; circles: median; boxes: inner quartile range) show habitat ratio value for solutions to the LCCI maximization model across all budgets ranging from 0M to 6.8M (in 1000 USD increments). Abbreviations: O = ocean, SP = spawning grounds, SR0 and SR1 = summer rearing age 0 or 1, WR = winter rearing. Note, because juveniles follow an out-and-back dispersal along the age 0 winter rearing-to-age 1 summer rearing-to-age 1 winter rearing transitions, WR:SR1 and SR1:WR have equivalent habitat ratios (SR1:WR not shown).

Figure 3. Stream barrier prioritization results for the Big Lake watershed, Alaska, U.S.A. (a) Life Cycle Connectivity Index (LCCI) levels for a suite of four barrier prioritization approaches and restoration budget sizes (DCI = Dendritic Connectivity Index; see Materials and Methods for prioritization approach descriptions). Results for the random project selection approach are presented as mean LCCI outcome ± 1.0 standard deviation for 20 iterations at each budget size. The LCCI maximization approach achieves 100% LCCI at a restoration budget of 6.8M (2015 USD). (b) Value of ecological information calculated as the added cost required for the DCI maximization approach to achieve a given level of LCCI in M USD (black line, left axis) and

added cost for the DCI maximization approach as percentage of the restoration budget (gray line, right axis).

8. Figures

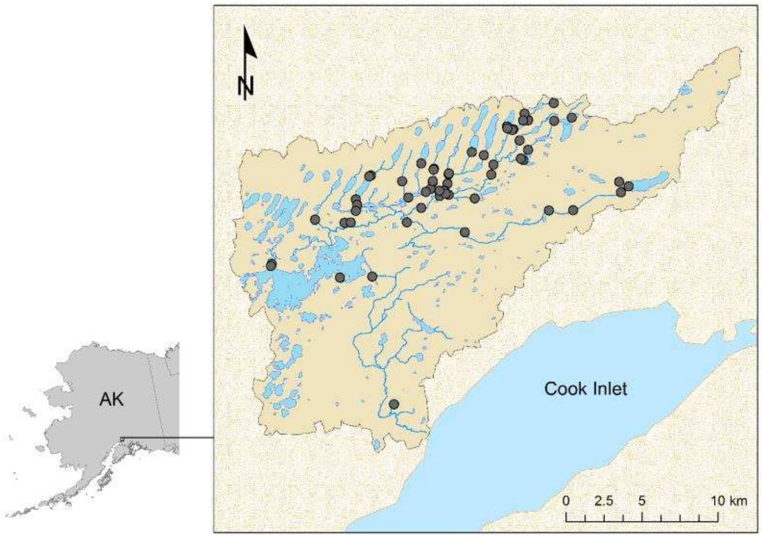

Figure 1.

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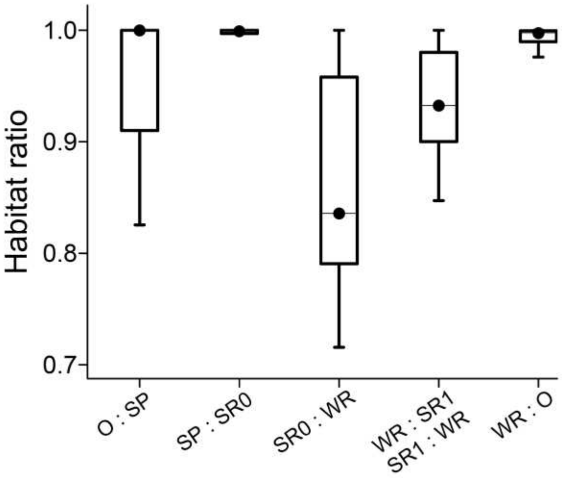

Figure 2.

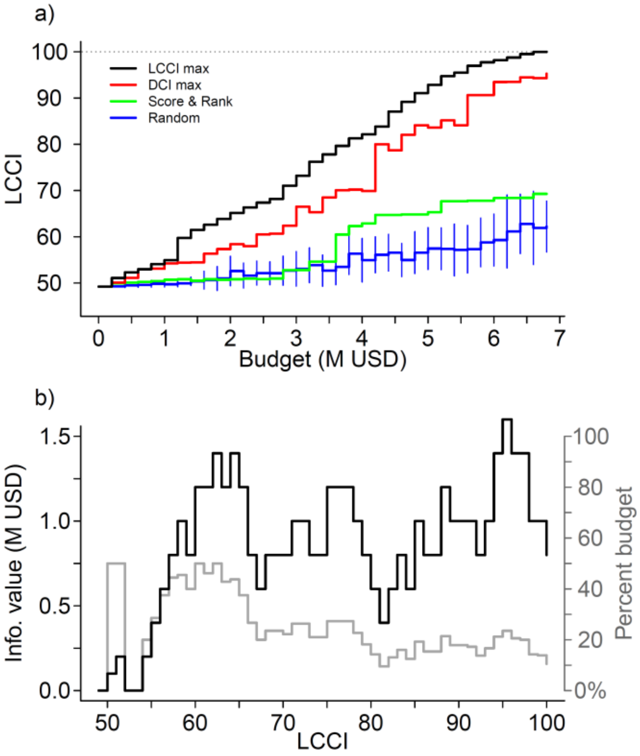
a)
100
90
80
70
60
50
LCCI
LCCI max
DCI max
Score & Rank
Random
0
1
2
3
4
5
6
7
Budget (M USD)
b)
1.5
1.0
0.5
0.0
Info. value (M USD)
100
80
60
40
20
0%
Percent budget
50
60
70
80
90
100
LCCI

Figure 3.

9. References

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10. Supplementary material

Supplemental Text S1: Life Cycle Connectivity Index and barrier mitigation prioritization methods detail.