

Competitive release modifies the impacts of hydrologic alteration for a partially migratory stream predator

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Abstract – Understanding ecological effects of altered stream flows is an essential objective. In a comparative field study of juvenile steelhead trout (*Oncorhynchus mykiss*) that compared natural- and reduced-flow sites, we used mark–recapture modelling and information theory to quantify spatially and temporally explicit patterns of density, specific growth rate, survival and outmigration; and test predictions for biotic and abiotic drivers. Densities were lower in water withdrawal treatments, resulting in lower intraspecific competition and, higher specific growth rate and survival. We observed yearly differences in density and intraspecific competition, with a negative relationship between density and specific growth rate over a wide range of densities, but reductions in survival only at the highest densities. Moreover, individual variability within sites was important. At high density (sites and years), survival related negatively to body size. In contrast, when overall density was lower, specific growth rate was negatively related to body size. Lastly, individuals were more likely to outmigrate when they had larger body size, lower survival or reared in habitats with reduced flows, and these patterns appeared mediated by the intensity of intraspecific competition. Our results underscore the harsh bioenergetic conditions induced by higher temperatures and densities during summer baseflow (relative to other seasons), particularly for larger fish demanding more resources, and suggest a density-dependent mechanism for why this period is important for regulating salmonid populations. We found that a complex combination of natural (e.g., density) and anthropogenic (e.g., withdrawal) factors affected juvenile salmon populations and life history expression in the face of altered flows.

Key words: density dependence; Pollock's robust design; partial migration; AlC_C ; anadromous; self-thinning

Introduction

Natural variation in hydrologic regimes has been shown to have significant effects on river food webs (Power et al. 2008; McHugh et al. 2010; Stanley et al. 2010). As demands on water resources continue to increase, anthropogenic impacts on instream flows are increasingly common, resulting in growing concern over their impact on stream ecosystems (Grantham et al. 2010). Potential impacts may be complex and include a suite of integrated effects to the abiotic and biotic conditions in streams and adjacent habitats. Abiotic impacts of lower instream flows are not limited to an altered hydrograph, but include changes to temperatures, stream velocities, habitat connectivity,

habitat heterogeneity, energy transport and substrate characteristics (Ligon et al. 1995; Elliott & Parker 1997; Poole & Berman 2001; Poff et al. 2006). Such physical changes influence the biotic interactions of stream organisms through impacts on productivity, relative abundance and diversity patterns, and the susceptibility to invasive species (Power et al. 1995; Poff et al. 1997; Hart & Finelli 1999; Bunn & Arthington 2002).

As both an upper trophic-level predator in freshwater systems and a valuable commercial, recreational and cultural resource, salmonids are a vital component of food webs in temperate to arctic ecosystems. Salmonid populations are likely to be particularly vulnerable to flow alterations as each specific life cycle

stage of a migratory existence can be independently and differentially impacted by physical changes to in-stream habitat. Additionally, trophic interactions that propagate to upper trophic levels have been shown to be mediated by annual and subannual variations in flow (Power et al. 2008; Kurlle & Cardinale 2011). As such, these populations can provide an informative model organism for studying the effect of environmental change and the complex impacts to upper trophic levels when community structure and function is anthropogenically altered (Arthaud et al. 2010). Impacts on juveniles during their freshwater existence are often experienced directly through a change in food supply or an increase in temperatures (Connor & Pflug 2004; Richter & Kolmes 2005) or more subtly as a change in trophic structure (Power et al. 1995). For adults returning to freshwater to spawn, changes in the timing, duration and magnitude of high and low flow periods have the potential to limit the area of or accessibility to spawning habitats (Hatten et al. 2009). At each stage of the life cycle, indirect or compensatory mechanisms mediated through food web dynamics or competition may complicate our interpretation of hydrologic effects (Johnson et al. 2009).

For migratory populations, altered flow conditions in freshwater can have direct impacts on the demographics of rearing life history stages, ultimately impacting viability of the returning adult population (Arthaud et al. 2010). For instance, increased temperatures and other impacts to energetic costs (e.g., active metabolism, prey availability) can impact growth rate and survival of juvenile salmonids (Jager et al. 1997; Nislow et al. 2004; Piccolo et al. 2008). Additionally, reduced recruitment or increased crowding alters density and intraspecific interactions (Keeley 2001; McKinney et al. 2001; Alonso-Gonzalez et al. 2008; Kennedy et al. 2008). These effects bear unique consequences for migratory species when they impact the timing or condition of outmigrating individuals (Satterthwaite et al. 2010). A number of factors in rearing habitats influence the likelihood of migration initiation or the probability to survive that migration including growth rates, growth efficiencies and survival probabilities (Nicieza & Metcalfe 1997; Forseth et al. 1999; Zabel & Williams 2002; Horton et al. 2009). Furthermore, for partially migratory species, conditions in freshwater habitats impact the decision of if and when to migrate (Morinville & Rasmussen 2003; Olsson et al. 2006). As returning migrant salmonids have considerably larger body size and higher fecundity than resident individuals, the number of migrant individuals and the successful return of those individuals has the potential to impact population viability (Jonsson & Jonsson 1993; Achord et al. 2003).

The overarching objectives of this study were to quantify the demographic impacts of reduced stream

flow to a population of juvenile steelhead trout (*Oncorhynchus mykiss*) and to contrast the relative strengths of abiotic and biotic effects resulting from altered flows on juvenile salmonid growth rate, survival and outmigration. Over a 2-year period in a 4th-order watershed, we marked and recaptured individuals and compared populations that were impacted by water withdrawal to those experiencing a natural hydrograph. Specifically, we were interested in the patterns of growth rate and survival from summer to fall when both growth opportunity and water withdrawal were high, as well as the subsequent impacts to outmigration in the winter and spring. We predicted that hydrologic alterations would negatively impact abiotic conditions (e.g., increase temperature, reduce stream flow and habitat area) that would, in turn, have negative impacts on juvenile steelhead growth rate and survival. Further, we were interested in whether the effects of density through intraspecific competition would offset or enhance the effects of altered abiotic conditions for juvenile growth rate and survival. We predicted that biotic factors would have the strongest effects in unaltered sites, as expressed in reductions in density over time as resource-limited individuals grow and require more resources per individual (i.e., self-thinning slopes suggesting if populations are at carrying capacity), whereas density-independent abiotic factors would drive growth rate and survival in impacted sites. Lastly, as outmigration tendencies are driven by growth rate and survival in freshwater habitats, we expected both local density and reduced instream flow to impact the proportions of residents versus migrants as well as the size of outmigrating fish in this partially migratory population. To determine the strength of habitat and intraspecific competitive effects in explaining survival and outmigration patterns, we defined mark-recapture models *a priori* and assessed the support for each of these models/hypotheses using an information-theoretic approach.

Methods

Study area

Lapwai Creek Watershed (LCW), which drains an area of 70,700 hectares, flows as a fourth-order stream into the Clearwater River in northern Idaho, USA (Fig. 1). LCW ranges in elevation from 239 to 1463 m and includes the main stem of Lapwai Creek and its tributaries, Mission, Sweetwater and Webb Creek. The watershed supports a federally threatened, naturally reproducing population of headwater spawning A-run steelhead (one year of ocean residency leading to a smaller adult body size compared to B-run steelhead, which typically spend two years

in the ocean and spawn in larger streams), which are listed as part of the Snake River Distinct Population Segment (NMFS 2006a,b). Diversion dams have significant impacts on instream flows from April to October in Sweetwater and Webb Creek, whereas Mission Creek and the upper portions of Lapwai Creek have unaltered hydrologic regimes. The water storage and diversion system is complex, but simply put, water diversions can equal the rate of summer flows in Webb and Sweetwater Creeks, potentially drying streambeds below the dams (NMFS 2006a). We conducted the study during the base flow period of 2008 and 2009. We identified base flow period on the hydrograph as a relatively constant flow rate that is at/near the lowest level of the year. Flows over the diversion dams during the irrigation season, but particularly in July and August, were higher in 2009 than 2008 (U.S. Geological Service, <http://waterdata.usgs.gov/id/nwis>). Of the stream habitat accessible to anadromous fishes, the upper half cuts deeply through basalt rock creating relatively steep canyons and confined channels, whereas at lower elevations, stream gradients decrease and valleys and stream channels widen. Anthropogenic impacts exist throughout the watershed and include dryland cropland, cattle grazing, silviculture, removal of riparian cover and channel geomorphic modification (Richardson & Rasmussen 2007).

We selected six study reaches (Fig. 1) in a stratified random procedure that included two reference sites (Upper Mission and Upper Lapwai) representing natural hydrologic regimes and four hydrologically impacted sites (Lower Webb, Middle Sweetwater, Lower Sweetwater and Lower Lapwai). All sites were relatively close in stream network space (e.g., no two sites were separated by more than 15 km) and were comparable in size and flow rate. Lower Sweetwater and Lower Lapwai were located at approximately 300–400 m in elevation, while the other sites were located between 500–600 m. Year-round resident fish included dace (*Rhinichthys*; mix of longnose and speckled species), sculpin (*Cottidae*), bridgelip sucker (*Catostomus columbianus*), northern pikeminnow (*Ptychocheilus oregonensis*), reddsideshiner (*Richardsonius balteatus*) and chiselmouth (*Acrocheilus alutaceus*). Summer and fall biomasses were dominated by steelhead, dace and sculpin.

Sampling of steelhead populations

We sampled steelhead populations at each site with multiple pass depletion techniques (three pass) using a Smith-Root LR-24 electrofisher (Smith-Root, Inc., Vancouver, WA, USA) in 100 m reaches, each of which was long enough to encompass several repeating stream habitat types (streams typically averaged

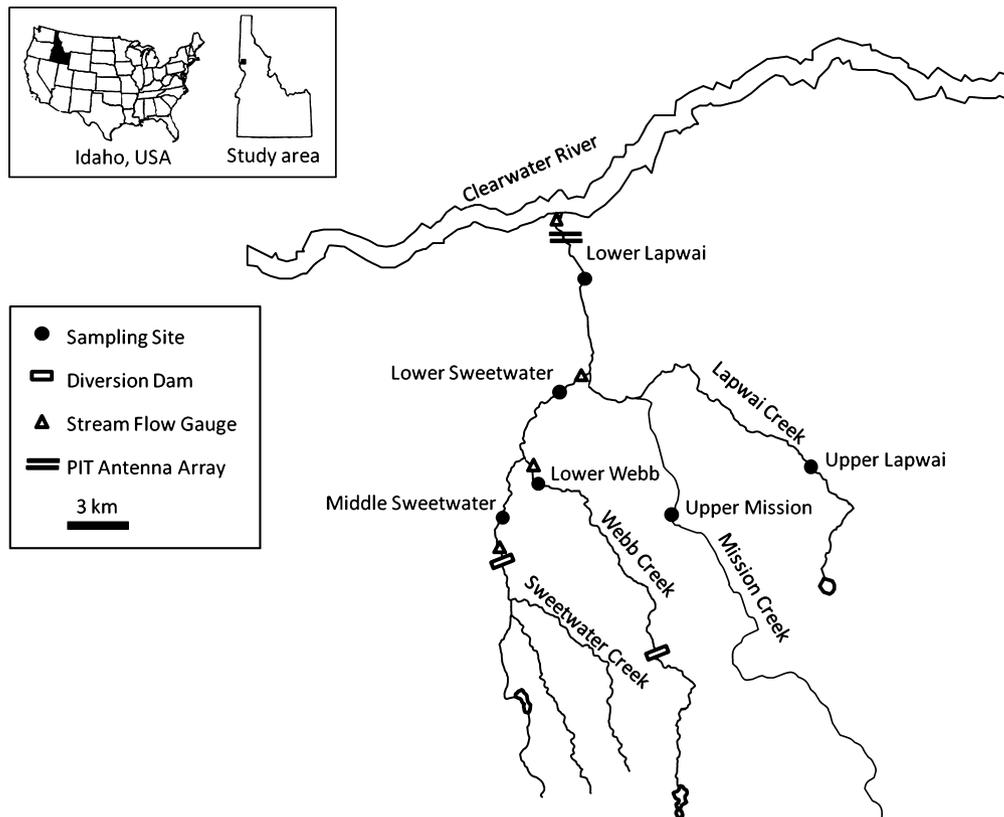


Fig. 1. Map of Lapwai Creek watershed, located in northern Idaho, USA.

between 3 and 5 m in width). We set block nets to ensure a closed population for the three passes. In 2008, we sampled steelhead at each site three (Lower Webb and Lower Lapwai) or four times from late June to early October (4 weeks between visits). In 2009, we sampled each site five times from early June to late September (3 weeks between visits). To minimise stress of capture and handling on fish, we conducted our electrofishing efforts when water temperatures were <17 °C.

We held captured fish in buckets filled with aerated stream water at ambient stream temperatures and minimised the time that fish were handled out of the water. We anaesthetised steelhead with tricaine methanesulfonate (MS-222), then measured fork length (FL) [to 1 mm] and mass [to 0.1 g], and inserted 12.50×2.07 mm, 134.2 kHz ISO passive integrated transponder (PIT) tags (Biomark, Inc., Boise, ID, USA) into the ventral body cavity of individuals over 65 mm FL. We estimated tag retention and survival ($>99\%$) from both off-site training sessions and field trials, wherein we assessed fish post-tagging. To record PIT tag codes, we used a FS-2001F-ISO reader (Biomark, Inc.). PIT tags assign a unique code to each fish so that we could track the fate of individuals.

Reductions in instream flow

Stream flow gauges operated by United States Geological Survey (USGS) and Bureau of Reclamation (BOR) were in close proximity to four of our sampling sites (Lower Webb, Middle Sweetwater, Lower Sweetwater and Lower Lapwai), with no surface water inputs or losses occurring between each site and stream gauge. To estimate the proportion of water removed by the diversion dams, we used continuous measures from these stream gauges coupled with a previous model developed for the watershed that estimates average instream flow under scenarios where diversions were not present (Day 2009). We assumed the two reference sites to be operating at 0% reduction due to the lack of water diversions in this part of the watershed. In Lower Lapwai, a site that combines both impacted and nonimpacted hydrographs, we estimated the per cent reduction using the estimated natural flow (i.e., without diversions) from Sweetwater Creek (Day 2009) combined with the actual inputs from Lapwai and Mission Creek. The results from this analysis include the period from January 1, 2008 to September 30, 2008, but are representative for the withdrawal effects across years.

Steelhead density and specific growth rate

We determined age distributions of juvenile steelhead using body size histograms, where bimodal distribu-

tions separated subyearling and yearling fish. We calculated densities (individuals m^{-2}) of both subyearling and yearling fish based upon population estimates from depletion efforts (Zippin 1956, 1958; Carle & Strub 1978). We then measured specific growth rate (SGR) of recaptured fish, which closely approximates (geometric) mean daily change in mass, as:

$$SGR = 100 \times [(\ln(m_{t+1}) - \ln(m_t))/t] \quad (1)$$

where m_t = mass in grams at capture, m_{t+1} = mass in grams at recapture and t = time, or the number of days between date of capture and recapture (i.e., growth period) (Wootton 1990; Elliot & Hurley 1995). We calculated multiple SGR estimates for those individuals that were captured more than two times in a sampling season. Not all time periods between capture and recapture were equal, so we expressed SGR as a function of time (day^{-1}). Further, to eliminate small decimals, we use the convention of expressing SGR as $\% day^{-1}$. Due to small numbers of recaptures and consistently high SGR among individuals at the impacted sites, we pooled SGR estimates from these sites.

Next, we used Statistical Analysis Software© (http://www.sas.com/en_us/home.html) to conduct multiple regression bootstrapping and determine whether the strength of abiotic and biotic drivers on SGR differed between years. As residuals were non-normal, we used a nonparametric approach. With SGR as the response variable, we tested for the importance of the following predictor variables: temperature, reach-scale total biomass (gm^{-2}) and FL (mm). We did not conduct a model selection approach; rather we analysed a single model containing all three predictor variables. We excluded the first growth period from 2009 because that year we began sampling several weeks earlier when temperature and flow conditions were not comparable to the rest of the sampling periods. Also, a portion of the subyearling population was too small to PIT tag, so we restricted the analysis to yearling steelhead. We quantified the average temperature experienced by steelhead within each growth period using HOBO® TidbiT v2 instream temperature loggers (Onset Computer Corporation, Bourne, MA, USA) at each site (measurements every 15 min). Next, we used total biomass, calculated using depletion estimates of abundance. We included subyearling fish in biomass estimates as they have the potential to affect yearling fish through exploitative competition (Harvey & Nakamoto 1997). Finally, because the average FL of yearling fish varied among sites and over time, we considered each fish's time-specific relative size at each site by dividing each individual's FL over the

average FL of all yearlings captured during the site visit (called relative length score). A length score of 1 indicates a yearling fish of average size compared to other fish at the site on that visit, a score above 1 a fish larger than average and a score below 1 a fish smaller than average. We used biomass and FL measures from the beginning of each growth period.

Steelhead intraspecific competition

To assess density-dependent effects, we established relationships between changes in individual size and density. As fish increase in size, they require more resources to survive, and if individuals in a local population are faced with limiting resources through crowding, any additional increases in the size of individuals must be balanced by losses through either emigration or mortality (*sensu* Elliott 1993). The resulting negative relationship between average body size of a cohort and the density of fish in that cohort (i.e., self-thinning) provides evidence for density-dependent mortality (Armstrong 1997; Dunham & Vinyard 1997; Grant et al. 1998; Rincon & Lobon-Cervia 2002; Keeley 2003). Furthermore, the slope of the self-thinning line may suggest the mechanism by which density-dependent changes are occurring (e.g., metabolic demand, minimum territory size or food consumption) (Dunham & Vinyard 1997; Grant et al. 1998). To calculate the slope of the self-thinning line at each site, we determined the least squares best fit line between the natural log of the average mass (g) and the natural log of the density (individuals m^{-2}) of steelhead in the 2008 subyearling cohort over the 2-year study.

Steelhead survival

We estimated apparent survival (Φ) using Pollock's robust design (Pollock 1982; Kendall & Nichols 1995; Kendall et al. 1995, 1997). The robust design, like the more commonly used Cormack-Jolly-Seber (CJS), estimates apparent survival between capture sessions. In our case, each site visit was a capture session and we estimated survival between each visit. Thus, we had four capture sessions in 2008 (three survival intervals) and five capture sessions in 2009 (four survival intervals). The robust design differs from the CJS model in that it estimates capture rate within each single capture session (i.e., site visit), as opposed to between two successive capture sessions. It does so by utilising *secondary* capture sessions, which in our case were the three electrofishing passes we made during each site visit. Moreover, by estimating capture rate within each capture session/site visit, the robust design allows estimation of an additional parameter, which occurs between capture sessions.

This additional parameter provides an estimate of dispersal from the study reach. We modelled temporary dispersal from the study reach (e.g., a fish is caught on visit 1, absent from the site on visit 2 and returns to the site on visit 3). By including temporary dispersal terms, the robust design improves estimates of capture rate and by extension apparent survival. Adapting the methods of Horton et al. (2009), we selected the two top models for each of capture rate and temporary dispersal rate, creating four pair-wise combinations. Then, we analysed each survival model structure four times, once with each of the four pair-wise combinations.

In 2008, we could not include two sites in the survival analysis, Lower Lapwai and Lower Webb, because decreased sampling visits, low densities and minimal recaptures resulted in a reduced data set that did not conform to the model structure. Thus, we modelled apparent survival at four sites in 2008. In 2009, densities and recapture rates at the impacted sites were low and we combined all fish from these sites into one group, which we refer to as the impacted sites group, resulting in three sites/groups for which we estimated apparent survival. A more thorough description of the survival model construction and justification is available for this article online (see Supporting Information 'Data S1').

We defined candidate model sets using Program MARK (White & Burnham 1999; White 2010) and assessed the fit of each model using Akaike's Information Criterion adjusted for small sample sizes (AIC_C) (Burnham & Anderson 2002). The parameter of interest to us was apparent survival, which we modelled with ecologically based hypotheses in mind to understand patterns and potential drivers. We developed candidate models for the remaining parameters using a variety of covariates/structures (e.g., variability across site, time, local density and individual body length); however, the goal was to find a well-supported model that would improve survival estimates, as opposed to quantifying patterns and drivers. Our survival model structures/hypotheses considered both spatial variation (water withdrawal effects, density effects and site effects) and temporal variation (full time-dependence and linear trend over the summer), as well as combinations of both spatial and temporal variation within single models (additive variation across space and full space- and time-dependence). Additionally, we included models with individual covariates of relative length score (defined above) using the logit link function provided in Program MARK (Table 1). A description of our model selection approach as well as the full set and structure of all models tested for each parameter is available for this article online (see Supporting Information 'Data S1' and Tables S1 and S2).

Table 1. Candidate set of Pollock’s robust design models (Pollock 1982; Kendall & Nichols 1995; Kendall et al. 1995, 1997) for predicting apparent survival of yearling juvenile steelhead from Lapwai Creek watershed, Idaho, USA.

Model Description	Hypothesis
Constant	No pattern
Site	Unknown spatial variation
Time	Unknown temporal variation
Site and time (full model)	Unknown spatial and temporal variation
Site and linear trend over time	Unknown spatial variation and temporally varying density dependence
Site and time (additive model)	Unknown spatial variation and basin-wide temporal pattern
Water withdrawal	Altered habitat
Water withdrawal and time (full model)	Altered habitat and unknown temporal variation
Water withdrawal and linear trend over time	Altered habitat and temporally varying density dependence
Water withdrawal and time (additive model)	Altered habitat and basin-wide temporal pattern
Density	Spatially varying density dependence
Density and time (full model)	Spatially varying density dependence and unknown temporal variation
Density and linear trend over time	Spatially and temporally varying density dependence
Density and time (additive)	Spatially varying density dependence and basin-wide temporal pattern

Each of the above 14 models was also constructed with inclusion of relative length score individual covariate to test for effects of body size on survival, for a total of 28 different survival model structures. Density was estimated from depletion estimates at the beginning of each survival interval. For a more detailed explanation of the specific covariates included in each model and the number of parameters in each model (which differs between the analyses for 2008 and 2009 due to different numbers of sites and capture occasions in each year), see Supporting Information ‘Data S1’ and Table S1, which is available online.

We considered all models within two AIC_C points of the top model as having support from the data and compared the Akaike weights (w_i) of supported models, where higher Akaike weights indicate better support for models. We present model-averaged estimates of monthly apparent survival. For individual covariates, for which we had no method of model averaging, we present those included in strongly supported models (Burnham & Anderson 2002).

Steelhead outmigration

We predicted outmigration patterns of yearling steelhead following the 2008 sampling season. Damage to detection equipment prevented analysis following the 2009 season. While fish may have eventually outmigrated in 2009, the decision to delay migration for a year is also of interest, as this will be affected by conditions experienced in the freshwater-rearing habitat. Lower Webb dried during the summer and Lower Lapwai acted as a migration corridor (as evidenced by relatively low recapture rates during the summer and high outmigration rates); thus, we did not include these sites.

Because steelhead are partially migratory (i.e., both resident and migratory individuals within a single population) (Jonsson & Jonsson 1993), it is necessary to differentiate between one of three fates: mortality in headwater streams, residency (or delayed outmigration) in headwater streams or outmigration. First, to account for mortality in headwater streams, we estimated the number of yearling steelhead that survived to the start of the migratory season (we first detected outmigration in October, several weeks after we stopped estimating summer survival, and outmigration continued until April). This population consisted of fish that we captured/recaptured in the electrofishing reaches on the final visit, *plus* individuals that we estimated as alive but not recaptured – either missed or dispersed. To populate this latter group of fish, we applied the top survival model from the 2008 sampling season (for specific model structure, see Supporting Information ‘Table S1’, ‘model 2 + length’), which included site effects and body size individual covariate (we did not use model-averaged parameter estimates because we wanted to include individual covariate estimates). Thus, the probability of surviving to the start of the migratory season depended upon the number of survival intervals as an individual’s last capture/recapture and the body size of the individual relative to its conspecifics at the site. For this analysis, we assumed that our survival estimates, which we developed for fish residing in our study reaches, applied to habitats adjacent to our study reaches. Additionally, because we detected outmigration shortly after we stopped measuring survival, we assumed that fish were free to leave the watershed starting in October, thus limiting our bias in assuming high and equal survival across sites between October and the actual date of an individual fish’s outmigration.

To differentiate between resident and migratory population segments, we used an array of two pass-through PIT antennas set up in parallel (4 m apart) at the mouth of Lapwai Creek (Fig. 1) to detect outmigration of PIT-tagged steelhead (note that we may be misclassifying some migrants as residents if individuals decide to migrate in subsequent years). This array spanned the width of the stream, and the detection fields were large enough to reach the surface of the water in all but the highest flow conditions. We assumed the two antennas operated independently of one another and calculated detection efficiency, E_{array} , as:

$$E_{array} = 1 - [1 - (d_{1+2} \times (d_2 + d_{1+2})^{-1})] \times [1 - (d_{1+2} \times (d_1 + d_{1+2})^{-1})] \quad (2)$$

where d_{1+2} is the number of tag detections at both antennas, d_1 is the number of tag detections at the

upstream antenna and d_2 is the number of tag detections at the downstream antenna (Zydlewski et al. 2006). Tag detection efficiencies at the Lapwai array were 0.96. This is likely an overestimation of detection efficiency, as we were unable to test the independence of the two parallel PIT antennas and 4 m apart may not have been enough to ensure independence; however, as the detection field included the entire water column under most conditions, we expect the arrays were operating near independence and that detection efficiencies were indeed high. In early April, high flows damaged the antenna array and compromised tag reading efficiencies; however, juvenile salmonid PIT detection systems at the hydropower dams along the Snake and Columbia Rivers, which began operation in late March, allowed us to quantify outmigration [arrays are operated by the Columbia PIT Tag Information System (PTAGIS), managed by the Pacific States Marine Fisheries Commission, available at <http://www.ptagis.org>]. While yearling steelhead would be expected to have high survival travelling between Lapwai Creek and the PTAGIS arrays, detection efficiency at any one dam would have varied rather highly (e.g., between 0.104 and 0.689) as flow volume, spill volume and the degree of smoltification changed over time (Faulkner et al. 2010). This makes it difficult to estimate detection efficiency, especially considering that each fish has multiple chances of detection as it migrates through the hydropower system. Unfortunately, there was no period of overlap when both our antennas at Lapwai Creek and the antennas along the hydropower system were both operating, which would have allowed some useful comparisons. As we were unable to confidently estimate detection efficiency, we ran our outmigration models under two different scenarios: 0.9 approximates the value we estimated at the Lapwai array, whereas 0.6 offers a comparison in the case that we overestimated detection probability.

We used Program MARK (White & Burnham 1999; White 2010) to develop multistrata live recaptures models that predicted probability of outmigration (Hestbeck et al. 1991; Brownie et al. 1993). In addition to survival and capture rate, these models can estimate the probability of transitioning between different strata (ψ). We have two strata: the headwaters area, where resident fish remain, and outmigration as measured by PIT tag detection arrays at the watershed mouth or the hydropower dams (see above). We defined a model with two capture occasions, the first representing all PIT-tagged yearling steelhead estimated to be alive at the end of the summer sampling season (see above) and the second representing the detection of outmigrating steelhead. Between the two capture occasions, we fixed survival in both strata to one and recapture probability in the

headwater stratum to zero because we did not repeatedly sample throughout the outmigration season, rather we assumed high and similar survival across sites. Secondly, we fixed the transition rate between the migration stratum to the headwaters stratum to 0 (this assumes that once a fish outmigrates, it does not return to the watershed). Lastly, we conducted two model runs by fixing probability of capture (= detection efficiency) in the migration stratum (i.e., at the PIT antennas) to 0.9 and 0.6 (see above).

We structured models to consider outmigration patterns at different spatial scales (i.e., watershed, subbasin, site and individual) and then used AIC_C to compare the strength of these models to suggest drivers of outmigration. We modelled various combinations of the following outmigration predictors/scenarios: site-specific (site level), the average of individual SGR estimates for each site (site level – we did not have large enough sample size to include SGR at the individual level), survival according to the top survival model in the 2008 analysis (both site and individual level), the highest recorded density at a site over the summer sampling (site level), the density recorded on the last site visit (site level) and whether water withdrawal occurred at the site (subbasin level). We also included the following body size measures: relative length score (individual-across-site level), average FL at each site on the last sampling visit (site level) and a watershed-wide relative length score, which we calculated the same as the site metric except we pooled individuals from all sites (individual-across-watershed level) (Table 2).

We considered all models within two AIC_C points of the top model as having support from the data (Burnham & Anderson 2002). Due to the small number of sites and lack of multiple years of data, we did not consider the specific relationship suggested by the parameter estimates, but if the 95% confidence interval did not cross zero, we considered the direction of the relationship (i.e., positive or negative). Also, we tested the sensitivity to covariates by plugging the greatest and least observed covariate value into the top model containing the covariate of interest.

Results

Instream flow

The removal of water from Webb and Sweetwater Creeks resulted in quantifiable reductions in instream flow. Early in the calendar year, a snowmelt-driven hydrograph maintained high flows and the canal system removed only a small proportion of total available water. However, as discharges decreased, larger proportions of available water were removed. At the

Table 2. Candidate set of multistrata live recaptures models (Hestbeck et al. 1991; Brownie et al. 1993) for predicting outmigration of yearling juvenile steelhead from Lapwai Creek watershed, Idaho, USA.

Model Parameters	Spatial Resolution	No. of Parameters
Survival	Site	7
Specific growth rate	Site	7
Average body length	Site	7
Survival, specific growth rate	Site	8
Survival, average body length	Site	8
Specific growth rate, average body length	Site	8
Survival, specific growth rate, average body length	Site	9
Survival	Individual	7
Site-specific relative body length	Individual	7
Watershed-wide relative body length	Individual	7
Survival, site-specific relative body length	Individual	8
Survival, watershed-wide relative body length	Individual	8
Water withdrawal	Subbasin	7
Highest density	Site	7
Last density	Site	7
Withdrawal, highest density	Site	8
Withdrawal, last density	Site	8
Withdrawal, site-specific relative body length	Individual	8
Withdrawal, watershed-wide relative body length	Individual	8
Highest density, site-specific relative body length	Individual	8
Highest density, watershed-wide relative body length	Individual	8
Last density, site-specific relative body length	Individual	8
Last density, watershed-wide relative body length	Individual	8
Withdrawal, highest density, site-specific relative body length	Individual	9
Withdrawal, highest density, watershed-wide relative body length	Individual	9
Withdrawal, last density, site-specific relative body length	Individual	9
Withdrawal, last density, watershed-wide relative body length	Individual	9
Site	Site	9
Site, site-specific relative body length	Site	10
Site, watershed-wide relative body length	Site	10
Null	Watershed	6

The 'Model Parameters' column lists all the covariates included in each model. For 'Spatial Resolution' we describe the finest spatial scale of the model. When counting the number of parameters in a model, we included parameters which we set to a fixed value.

Lower Webb, Middle Sweetwater and Lower Sweetwater sites, instream flows were reduced by as much as 80–90% relative to the expected natural flow. The greatest reductions occurred in June and early July. The reduction in instream flow at Lower Lapwai was not as pronounced when compared to natural flows at the Upper Mission and Upper Lapwai sites (Fig. 2). By late July, smaller proportions of water were removed and flows reflected more natural levels, but remained below predicted natural levels. Periodic precipitation events resulted in increased spill over the

diversion dams and brief periods of less % reduction (Fig. 2).

Steelhead density

Densities of yearling juvenile steelhead were consistently greater in the reference sites than in the impacted sites during both 2008 and 2009, often by up to an order of magnitude (Fig. 3a,b). At the reference sites, densities declined as the summer progressed, whereas those at the impacted sites remained relatively constant over the summer. In one exception, Middle Sweetwater in 2008, the density of yearling fish at the end of the season was comparable to that at the reference sites, but densities started lower at Middle Sweetwater relative to the reference sites and did not decline over the summer (Fig. 3a,b). We found no subyearling steelhead at Middle Sweetwater during either year, and we observed little to no subyearling recruitment at Lower Sweetwater and Lower Lapwai. Subyearling recruitment was greater in Lower Webb, particularly in 2008, but was typically several times less than at the reference sites. Excluding Middle Sweetwater in 2008, at impacted sites, we rarely caught more than five yearling individuals on a given visit at each 100-m electrofishing reach. At impacted sites, densities were greater in 2008 than 2009 for both yearling and subyearling age classes.

Densities at the two reference sites varied between 2008 and 2009. During both years, Upper Lapwai had greater yearling densities than Upper Mission. Moreover, densities at both sites were greater in 2008 than 2009, and the difference in density between the sites was greater in 2008. Subsequently, the decline in density over the sampling season was greater in 2008, specifically at Upper Lapwai, the site-year combination with the greatest yearling densities (Fig. 3a,b). Subyearling densities were consistently greater in Upper Lapwai than Upper Mission in both years.

Steelhead specific growth rate and intraspecific competition

Individual SGR of yearling fish was greater in the impacted sites (all four sites pooled) than in both Upper Mission and Upper Lapwai for both years. In 2008, yearling SGR at the impacted sites was slightly negative during July, but was positive during the remainder of the summer. In contrast, yearling SGR at Upper Mission and Upper Lapwai was negative or near zero throughout the entire sampling period and became less negative over time. In 2009, our June sampling revealed that SGR of yearling fish during this period was the greatest of the study. SGR from July to September 2009, the period comparable to the

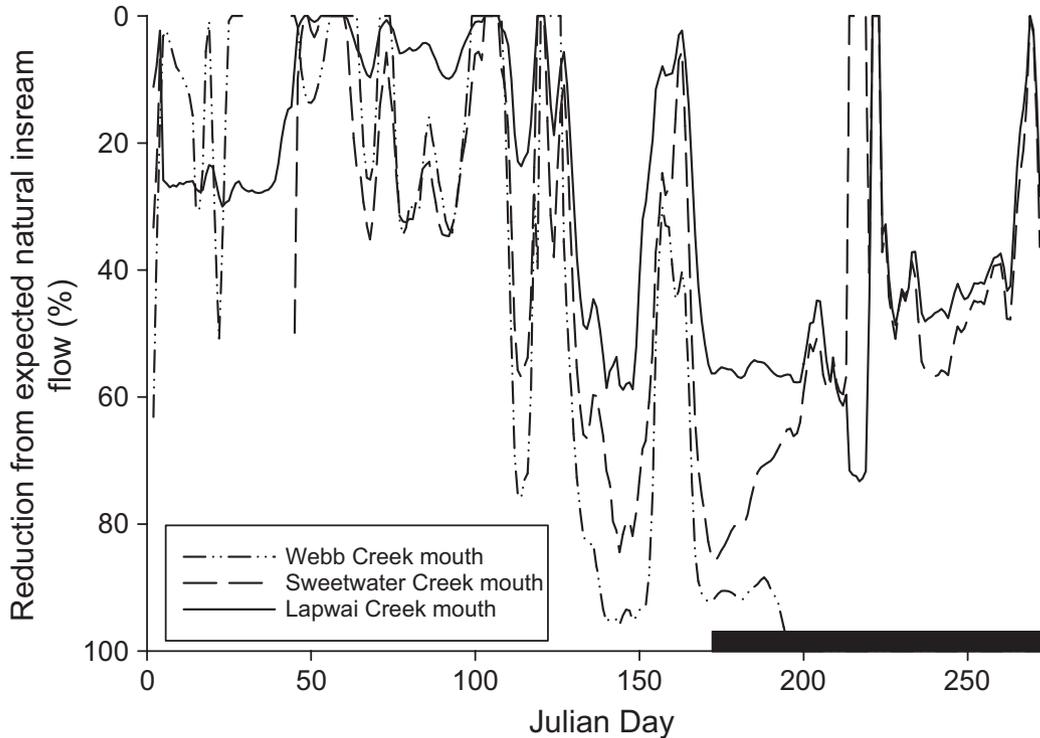


Fig. 2. Per cent reduction from natural in-stream flow due to water diversions at the mouths of three creeks in Lapwai Creek watershed, Idaho, USA. Data include the period from January 1 to September 30, 2008 and are based off a model by Day (2009). The black bar indicates sampling period.

timing of sampling in 2008, was greater than in 2008 and positive for most of the summer. In general, 2009 SGR at each site decreased over time. By the end of the summer, Upper Mission and Upper Lapwai had SGR values near zero, whereas SGR at the impacted sites was 0.55% per day (Fig. 4a,b).

The bootstrap multiple regression analysis indicated variable effects of biomass and individual length on SGR between years. Both the 2008 $\{F_{3,180} = 6.12; P = 0.0002\}$ and 2009 $\{F_{3,157} = 5.98; P = 0.0008\}$ models were significant. In 2008, there was a negative relationship with biomass {standardised coefficient = -0.0450 ; $P < 0.0001$; 95% confidence interval = $(-0.0672, -0.0231)$ }, while the effects of temperature $\{P = 0.3928\}$ and individual length $\{P = 0.1976\}$ were not significant. Biomass was also a significant predictor of SGR in 2009, but this time, the relationship was positive {standardised coefficient = 0.1559 ; $P = 0.0076$; 95% confidence interval = $(0.0437, 0.2691)$ }. Furthermore, in 2009, there was a significant relationship with individual length, where larger fish grew slower {standardised coefficient = -0.5859 ; $P = 0.0198$; 95% confidence interval = $(-1.0789, -0.1022)$ }. As in 2008, the effect of temperature was insignificant $\{P = 0.5984\}$.

Both Upper Lapwai and Upper Mission exhibited evidence of self-thinning, indicative of intraspecific competition, although the effect was considerably

stronger and statistically significant at Upper Lapwai. The self-thinning relationships were single phase (i.e., linear) with R^2 values of 0.29 and 0.78 for Upper Mission and Upper Lapwai, respectively. Slopes of the self-thinning lines were -0.29 ($P = 0.2142$) and -0.69 ($P = 0.0084$) for Upper Mission and Upper Lapwai, respectively. We were unable to calculate self-thinning relationships in the impacted sites due to low densities.

Steelhead survival

The effective sample size for apparent survival models in 2008 was $N = 567$ (176 recapture events) and in 2009 was $N = 502$ (257 recapture events). In 2008, survival (Φ) models with site effects and individual (i.e., relative length score) covariates had support from the AIC_C model selection analysis. The sum of the w_i 's for these models was 0.6592, suggesting strong support for this model structure (Table 3). The model-averaged parameter estimates reflected the strong site effects. Survival was nearly constant over time and similar among Middle Sweetwater, Lower Sweetwater and Upper Mission, though slightly lower at Lower Sweetwater. Meanwhile, survival at Upper Lapwai was nearly constant over time, but was considerably lower compared to the other three sites (Fig. 5a). All top models that included

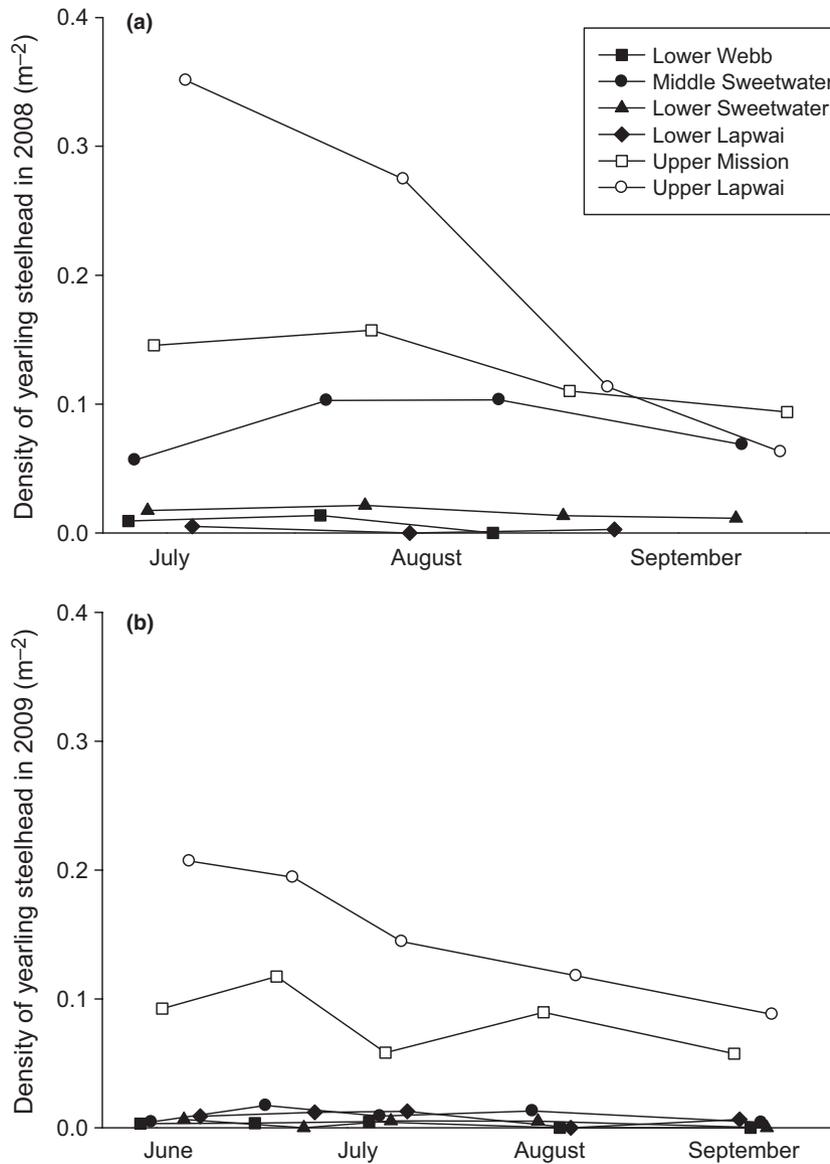


Fig. 3. Densities of yearling steelhead (individuals m^{-2}) from six study sites in Lapwai Creek watershed, Idaho, USA. Data were collected between July and September, 2008 (a) or between June and September, 2009 (b). Closed symbols indicate sites impacted by a water diversion project, and open symbols represent sites with a relatively unaltered hydrologic regime.

length individual covariates indicated that survival was lesser for larger fish (Fig. 5b).

In contrast to 2008, survival in 2009 was described by temporal variation, but not spatial variation. Three of the supported models had time effects only and a cumulative w_i of 0.2966. The other supported model had time effects plus an additive term for density (Table 3). Also in contrast to 2008, there was little support for models that included the relative length score individual covariate. The best supported model that included individual length covariate had a w_i of only 0.0446, and the parameter estimates typically had slopes near zero and 95% confidence intervals that included zero. According to model-averaged parameter estimates, survival was lowest early in the sampling season, highest in late July/early August and then decreased slightly, by the end of September (Fig. 5c).

Steelhead outmigration

We estimated that 28, 11, 72 and 48 tagged yearling steelhead survived to the start of the migratory season for Middle Sweetwater, Lower Sweetwater, Upper Mission and Upper Lapwai, respectively. We detected 45 steelhead at the PIT detection arrays (29 of these at the PTAGIS arrays on or after March 25, 2009). The number of detected migrants by site (proportion outmigrating) was 10 (0.36), 3 (0.27), 13 (0.18) and 19 (0.40) for Middle Sweetwater, Lower Sweetwater, Upper Mission and Upper Lapwai, respectively. The average fork lengths (standard error) of yearling steelhead at the end of the sampling season for Middle Sweetwater, Lower Sweetwater, Upper Mission and Upper Lapwai were 147.0 (1.59), 148.7 (1.48), 121.7 (0.73), and 129.5 (0.82), respectively.

When detection efficiency was set at 0.9, we found support for three outmigration models (Table 4). The top model included water withdrawal and highest density covariates, where outmigration probability was greater at higher densities and was greater from water withdrawal sites compared to reference sites, at a given density (Fig. 6a). This model also included site-specific relative body length, where larger individuals were more likely to outmigrate (Fig. 6b). The other two models used survival alone and survival coupled with site-specific relative body length. Individual covariates were important, as site-specific relative body length was included in two of the supported models and the survival estimates used in the third supported model relied upon measures of site-specific relative body length. With detection efficiency fixed at 0.6, there was one supported model, which was the same as the top model when detection efficiency was 0.9. For this top model, compared to when detection efficiency was fixed at 0.9, both estimated outmigration rates (0.736, 0.551, 0.282 and 0.733 for Middle Sweetwater, Lower Sweetwater, Upper Mission and Upper Lapwai, respectively) and standard errors (0.146, 0.175, 0.094 and 0.130 for Middle Sweetwater, Lower Sweetwater, Upper Mission and Upper Lapwai, respectively) were larger. Site averaged estimated outmigration rates from the top model when recapture rate was fixed at 0.9 agreed closely with actual proportions of outmigrants (the latter is reported in the previous paragraph). When detection efficiency was fixed at 0.6, the models estimated higher site-averaged outmigration rates than those actually observed.

Considering the strength of support and direction of the relationships for individual variables with detection efficiency set at 0.9, survival was negatively related to outmigration rate, whereas site-specific relative body length was positively related, and both variables had strong support because their 95%

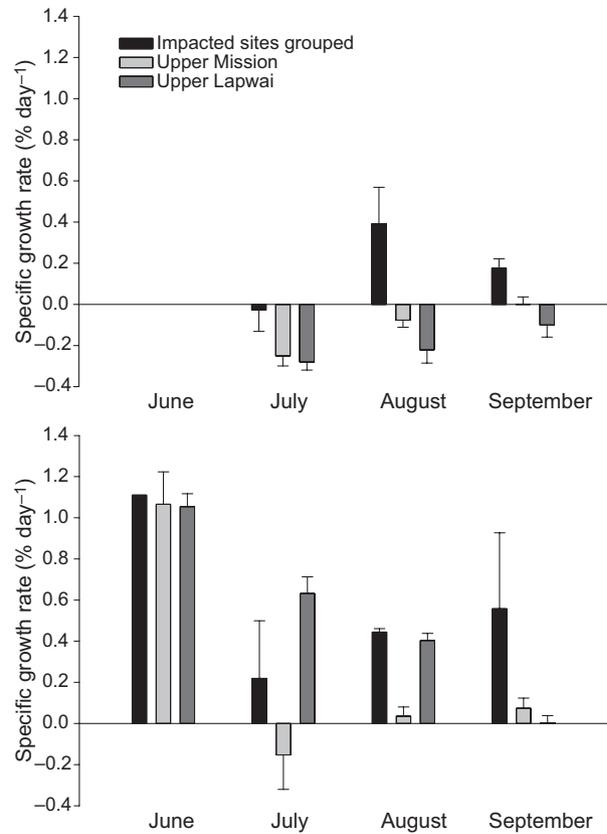


Fig. 4. Specific growth rate (% day⁻¹) of yearling steelhead from Lapwai Creek watershed, Idaho, USA. The impacted sites group includes data from four sites impacted by a water diversion project, and the other two sites have a relatively unaltered hydrologic regime. Data were collected between July and September, 2008 (a) or between June and September, 2009 (b). Error bars indicate ± 1 standard error.

confidence intervals did not include zero in any of our models. For watershed-wide relative body size, the 95% confidence interval always crossed zero. In one case each for withdrawal and highest density, confidence intervals did not include zero, and the

Table 3. AIC_c results for Pollock's robust design mark-recapture models of yearling steelhead apparent survival for both the 2008 and 2009 sampling seasons in Lapwai Creek watershed, Idaho, USA.

Year	Model No.	Model Description	ΔAIC_c	w_i	No. of Parameters
2008	2 + length	Site	0.0000	0.23049	25
2008	2 + length	Site	0.2536	0.20304	28
2008	2 + length	Site	1.3028	0.12016	26
2008	2 + length	Site	1.5630	0.10550	29
2009	3	Time	0.0000	0.13406	26
2009	3	Time	0.4094	0.10924	29
2009	3	Time	1.8440	0.05332	25
2009	14	Density + time	1.9996	0.04933	27

Table includes all survival (Φ) models within two AIC_c points of the top survival model. The same model number and description can appear multiple times for survival models because each survival model was paired with one of four combinations of the top two temporary dispersal models and the top two probability of capture models. A model number with '+ length' in the 'Model No.' column indicates that relative length score individual covariate was included in the model. The 'Model No.' column refers to descriptions in the Supporting Information, which is available for this article online (see Supporting Information 'Data S1', and 'Tables S1 and S2').

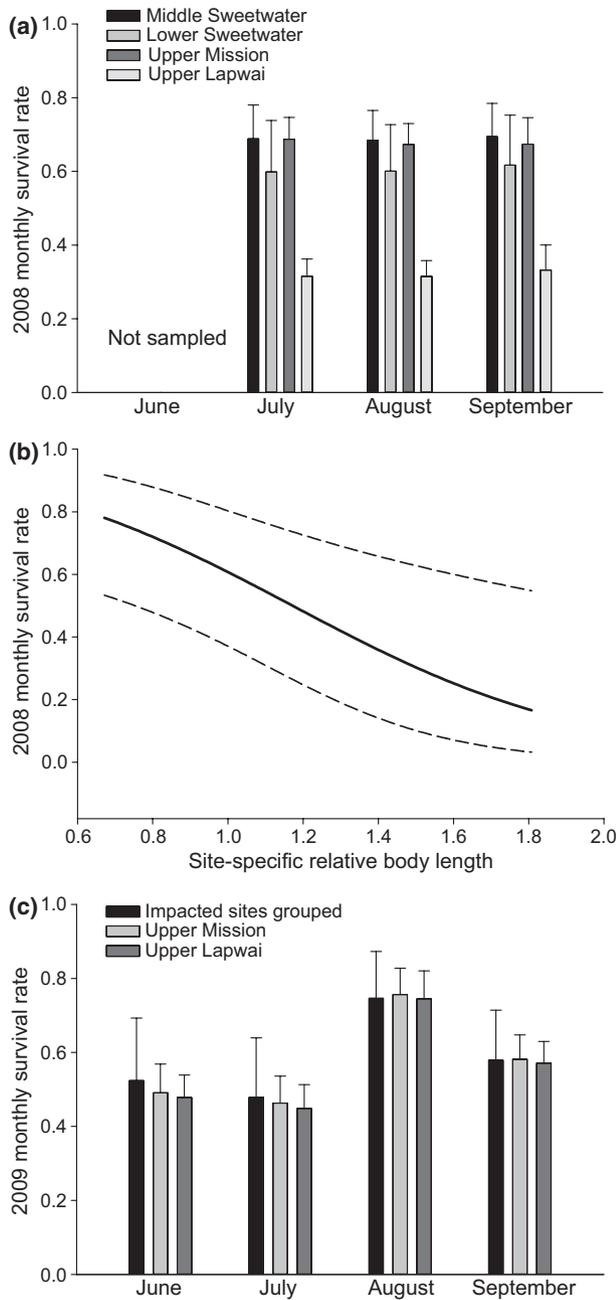


Fig. 5. Monthly apparent survival for yearling steelhead from Lapwai Creek watershed, Idaho, USA according to a mark–recapture analysis. Data indicate model-averaged estimates of site-specific survival in 2008 (a), a representative relationship of relative body-length-specific survival, taken from the top model (model 2 + length) in 2008 for the Upper Lapwai site in August (b), and model-averaged estimates of site-specific survival in 2009 (c). Error bars indicate ± 1 standard error (a, c), and dashed lines indicate the 95% confidence interval (b).

relationships were both positive. For highest density, this occurred for the best-supported model of the model set. The 95% confidence intervals for last density always included zero. The above relationships for individual parameters held mostly consistent when detection efficiency was changed to 0.6, particularly

Table 4. Supported multistrata live recaptures models (i.e., within 2 AIC_C points of the top model) and the null model to predict outmigration of yearling steelhead from Lapwai Creek watershed, Idaho, USA following the 2008 summer sampling season. Detection efficiency fixed at 0.9.

Model Description	Model Set	ΔAIC_C	w_i	No. of Parameters
Water withdrawal, highest density, site-specific relative body length	Water withdrawal and density	0	0.2286	9
Survival, site-specific relative body length	Individual covariates	0.9509	0.1421	8
Survival	Individual covariates	1.6321	0.1011	7
Null model	No variation	9.1165	0.0023	6

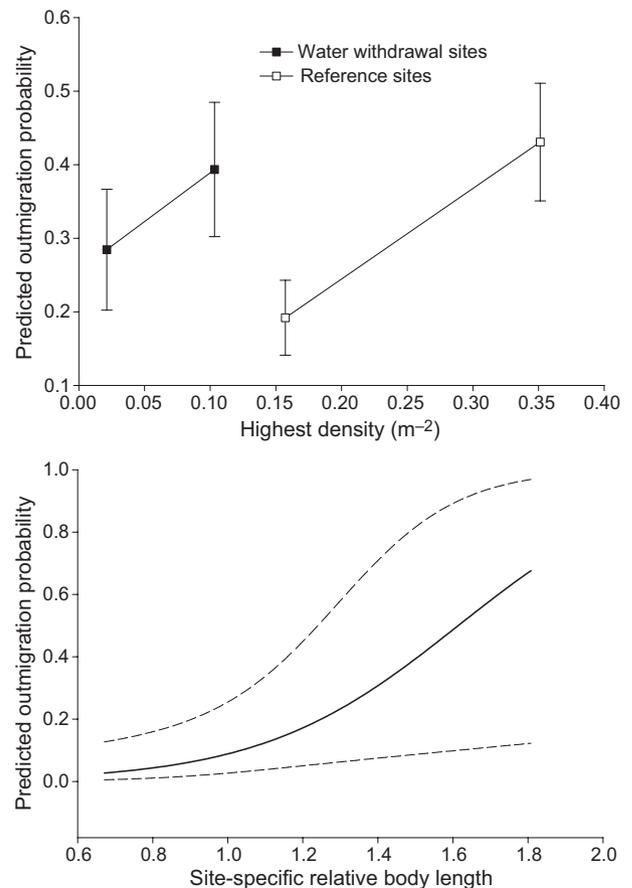


Fig. 6. Outmigration probabilities for yearling steelhead from four study sites in Lapwai watershed, Idaho, USA, during winter 2008/spring 2009. Estimates are from the top model (i.e., lowest AIC_C score) from a multistrata mark–recapture analysis, where detection efficiency was fixed at 0.9. We used density and the presence of water diversion activities to predict outmigration (a), as well as site-specific relative body length (b). Error bars indicate ± 1 standard error (a), and dashed lines indicate the 95% confidence interval (b).

for parameters in supported models. Site-specific relative body length was the most sensitive covariate (Fig. 6b). Highest density, survival and watershed-wide relative body length were moderately sensitive, and last density was the least sensitive.

Discussion

We observed marked differences in steelhead demographics (density, SGR, survival and outmigration) between flow-impacted streams and naturally flowing reference streams. Densities in impacted streams were considerably lower and this appeared to result in higher SGR and survival in impacted streams. High SGR and survival rates indicate that rearing conditions were good and did not limit population size or density. Rather, water withdrawal may have placed limits on the population size of spawning adults (e.g., through periodic drying of the streambed and high mortality of eggs or fry), thus limiting recruitment and density in impacted streams (Jager et al. 1997; Hatten et al. 2009). Large reductions from natural flow levels in the spring months, of which we found evidence, may prevent adults from reaching prime spawning locations. Additionally, habitat changes associated with reduced instream flow (e.g., hyporheic exchange, sediment transport, temperature) may have reduced the success of incubating eggs, which require cool, well-oxygenated water for proper development (Geist et al. 2006; Heywood & Walling 2007).

As an upper trophic-level predator, intraspecific interactions appeared to strongly influence SGR and survival in the naturally flowing reference habitats. At these sites, the highest initial densities were associated with the steepest decline in density over the summer, suggesting an impact on survival. While the survival analysis did not suggest a strong density relationship, we did observe lower survival at the Upper Lapwai site in 2008, which coincides with the highest densities and steepest decline in density observed throughout the study. There was also a negative relationship between total biomass and SGR in 2008, the highest density year, and average SGR at a site was often negative. Taken together, our results suggest a partitioning of the effects of density dependence between SGR and survival (Keeley 2001; Einum et al. 2006). We found that in a relatively high-density year, SGR was impacted negatively across a wide range of densities, but that survival was reduced only at the highest densities (Imre et al. 2005). Furthermore, survival rates were lower for larger individuals, but body size did not affect individual SGR. In contrast, in a relatively low-density year, there was not a negative relationship between density and either survival or SGR across sites. However, within sites, SGR, but not survival, was impacted and larger fish grew slower. These patterns suggest that under intense intraspecific competition, all individuals grow slowly, and when abiotic conditions are stressful, as they are during warm summer months, larger individuals have the hardest time meeting bioenergetic requirements, and as a result some perish. In contrast, when competition is less

severe and more homogenous across space, the impacts of competition may be limited mostly to SGR (not survival) and there may not be large differences in SGR across sites, rather stronger impacts on the larger individuals within each site.

The body size effects on SGR and survival are interesting because larger body size is often expected to confer a competitive advantage and therefore higher fitness (Post et al. 1999). However, as body size increases, so do the overall consumptive requirements for individuals to maintain minimum metabolic function. Therefore, when temperatures are warm and per capita food resources are scarce, we should expect to see disproportionately large impacts on the bioenergetic requirements of larger individuals (Diana 2004). Interestingly, in cooler spring and fall months, large body size is more likely to become a competitive advantage as individuals increase consumption relative to metabolic expenditures and take full advantage of their ability to displace smaller fish from prime feeding habitats. Nevertheless, the bioenergetically stressful summer months had strong impacts on outmigration patterns in the first year of the study when densities were higher and survival was lower. Recent modelling of the bioenergetics of these populations has supported the likelihood that periodic high thermal maxima impose disproportionately negative effects on the growth of larger-sized *O. mykiss* (Myrvold and Kennedy, 2014). We were unable to measure outmigration in the second year of this study when densities were lower and body size impacted SGR rather than survival. If the reduced densities resulted in less harsh summer-rearing conditions, it is possible that conditions in summer months would play a relatively smaller role compared to those in other seasons.

The results of our self-thinning analysis further support the importance of intraspecific interactions at sites with natural flows and high densities. The slope at Upper Lapwai (-0.69) was most similar to self-thinning models that implicate foraging limitations, which converge on a slope of -0.73 (Grant et al. 1998). However, the food consumption hypothesis (i.e., that competition is driven by foraging limitations) assumes constant availability of food across the entire growing season, and these slopes are difficult to accurately quantify in the field, thus caution must be used in interpreting the results (Steingrímsson & Grant 1999). The slope at Upper Mission was not as steep as at Upper Lapwai, but may be taken to suggest some level of density-dependent interactions, albeit reduced from those of a population at true carrying capacity. Alternatively, different mechanisms (e.g., space vs. food) may operate within these different sites (Keeley 2003). Densities at the flow-altered sites remained constant and comparatively low over time, suggestive of no self-thinning effects in these habitats.

In migratory salmonid populations, when density dependence acts strongly in freshwater habitats, a trade-off exists where an individual must maximise both pre- and postmigratory vital rates (Bohlin et al. 1993; Morinville & Rasmussen 2003). That is, low growth efficiency (i.e., the proportion of energy intake used on growth) and survival of rearing fish will increase the propensity to outmigrate, as individuals balance mortality risks and seek out habitats with greater growth potential (Forseth et al. 1999); however, larger individuals are more likely to survive the migration; thus, low growth rates act to delay or limit outmigration (Horton et al. 2009). These potentially competing demands may create complex patterns in the size of migrant fish and the proportion of fish that outmigrate, particularly when spatial and temporal variations in physical (e.g., temperature and water withdrawal) and biological (e.g., intraspecific competition) conditions impact growth rate and survival (Olsson et al. 2006).

We identified spatial patterns of outmigration and suggested factors that drive an individual to remain as a resident (or delay outmigration) versus outmigrate from the watershed. Our models tended to perform better than the null only when we included individual covariates of body size, suggesting the importance and power of considering variation down to the level of the individual (Zabel et al. 2005). Additionally, we were able to predict outmigration probability by considering the effects of local density, as well as individual-based parameters (e.g., body size and survival) that were associated with density (Olsson et al. 2006; Horton et al. 2009). Further support for the importance of competition comes from our finding that body size compared to other individuals at a site was a more useful predictor than was body size compared to all individuals in the watershed. This suggests a trade-off, where fish wait to outmigrate as long as possible and only the largest individuals leave, but the amount of time they can afford to wait (and the body size they reach) will be less in higher density sites where intraspecific competition is intense (Forseth et al. 1999). Also, interesting was the finding that the highest density observed during the summer was a useful predictor, but the last observed density was not. Had we only measured density at the end of the summer, which seems logical due to its temporal proximity to the outmigration season, we would have seen relatively similar densities across sites; however, by repeatedly sampling over time, we observed that locally high densities earlier in the summer reduced survival and SGR, with apparent lasting effects into other seasons and life history stages. Water withdrawal also appeared to impact outmigration. According to the top model, for a given density, outmigration tendencies were higher

for individuals in flow-impacted habitats relative to reference habitats. Drying of the streambed below the diversion dams has been observed periodically over the last century, and the associated increased risk of mortality may have resulted in selection for rearing individuals to leave. The number of sites provides limited overlap in density between the impacted and reference sites; however, the goal of considering outmigration effects remains important to understand how hydrologic regimes affect life history variability and the long-term persistence of local populations (Beechie et al. 2006).

Summary and Implications

The differences we observed in the SGR, survival and life history decisions for a stream predator have important implications for habitat conservation as well as our understanding of population dynamics in complex systems. Our results across a paired watershed illustrate the complex response of these systems to alterations in hydrologic function coupled with effects of local density and intraspecific competition. While water withdrawal apparently influenced recruitment, the impacts of altered flow to SGR and survival were negligible and were likely mediated through a positive response to low density. Meanwhile, it remains important to understand how the intensity of intraspecific competition interacts with altered instream habitat to determine the conditions experienced by rearing salmonids, as these conditions have both direct (e.g., growth rate and survival) and indirect (e.g., drivers of migration patterns and reproductive capacity) effects on population dynamics. The proportion of migrant individuals can have implications for population-level reproductive capacity, as can survival of individuals during migration, both of which are affected by conditions in freshwater-rearing habitats. We found that site-specific covariates (e.g., local density, demographics, habitat alteration), when combined with individual covariates (e.g., body size), provided good predictions of outmigration patterns. To provide a mechanistic understanding of how habitat alteration influenced life history strategies, our models incorporated both biotic drivers of migratory decisions across spatial scales as well as the direct impacts of water withdrawal. While successful at suggesting drivers, our work underscores the complexities of identifying demographic impacts for an organism with a complex life cycle undergoing the direct and indirect effects of environmental change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Survival model description and selection.

Table S1. Candidate set of models under Pollock’s robust design for estimating survival, temporary movement and capture probability of overyearling juvenile steelhead in Lapwai Creek watershed, Idaho, USA.

Table S2. AIC_C results for Pollock’s robust design mark–recapture models of juvenile steelhead capture probability and temporary movement models for both the 2008 and 2009 sampling seasons in Lapwai Creek watershed, Idaho, USA.