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Contemporary controls and future predictions of non-native
smallmouth bass range expansion into salmon-rearing habitat

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Abstract

Contemporary controls and future predictions of non-native smallmouth bass range expansion into salmon-rearing habitat

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Non-native fishes have been stocked in freshwater ecosystems throughout the world to support recreational fishing opportunities. Since their initial introduction and establishment many of these species have spread, and future range expansions of non-native fishes in response to climate change are imminent. Although only a subset of non-native species have been shown to cause ecological harm, in some cases their impacts to recipient ecosystems are dramatic and span multiple levels of biological organization ranging from the genome to the ecosystem.

Smallmouth bass (*Micropterus dolomieu*; hereafter referred to as bass), a cool-water fish native to central and parts of eastern North America, provide a compelling example of the potential ecosystem consequences of introducing a novel predator. Their introduction has resulted in reduced growth of other native predators and induced changes in the behaviour, distribution and at times caused the local extirpation of prey fish species. In the Pacific Northwest region of the United States, bass have been purposely stocked over the past century to promote recreational fisheries in rivers, lakes and reservoirs, where their potential to overlap with salmonids residing in headwater habitats was considered to be minimal. Many bass

populations have greatly expanded from their initial introduction sites and there is increasing concern that they may now seasonally occupy upstream areas where endangered salmonids rear. Climate-induced stream temperature warming and land-use management practices are likely to enable range expansions of predatory bass farther into salmon rearing grounds, potentially adding more stress on an already highly threatened group of cold-water fishes.

I combined a field observation dataset with correlative and mechanistic models to determine the contemporary controls on bass distribution, and predict the future range expansion of bass into salmon-bearing streams of the Pacific Northwest. In my study system, the John Day River (a tributary of Columbia River), I found the upstream expansion of bass into salmon rearing areas is largely controlled by water temperature. My distributional surveys revealed that bass overlap with juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in a considerable amount of their early summer rearing habitat. Using a series of linked models, I predicted how the thermal regime of the John Day River is likely to change as a result of anticipated climate change, and in turn, how bass and juvenile Chinook salmon distributions are likely to respond to climate-induced stream warming. The results of this work suggest that bass will occupy an increasingly large portion of juvenile Chinook salmon rearing habitat in the future, and this pattern is likely to be repeated in many stream systems where these species co-exist. This is of broad conservation concern given that salmon have to deal with both the direct stress of warming streams, as well as increasing spatial and temporal overlap with piscivorous bass.

I also investigated the potential for riparian vegetation restoration to ameliorate some of the water temperature increases predicted due to climate warming, to provide a tool to maintain salmon rearing habitat and keep bass from expanding their range upstream. I found that restoration could provide this dual benefit and that spatially prioritized restoration will result in a

greater return-on-investment in terms of reducing bass abundance while increasing thermally suitable habitat for rearing Chinook salmon in the face of climate change.

In my third chapter I used physiology to examine the strong correlative relationship I observed between bass upstream extent and water temperature in Pacific Northwest streams. In this work I employed bioenergetic models, calibrated with input data from the study system, to show that bass upstream extent is determined by temperature-constrained growth of their earliest life history stage (i.e., young-of-year bass). I found that upstream, the scope for growth collapses in young-of-year bass because their ability to consume food declines rapidly as temperatures cool. Reduced growth of young bass, in turn, would lead to recruitment failure of bass populations if they spawned their young too far upstream due the size-selective overwinter mortality on age 0 bass. Adult bass exert a large degree of parental care for their young, so the distribution of the population as a whole is determined by conditions that are suitable for the growth of their progeny. By knowing which life-history stage determines bass distribution in temperate streams, managers can target strategies to diminish the growth performance of that stage to reduce the range expansion of bass into salmon habitat.

Overall, this work (1) provides insight into contemporary controls on the distributions of a non-native fish in mid- to high-latitude river systems, (2) demonstrates that bass are moving into salmon habitat presently (a pattern that is likely repeated in many river systems in the Pacific Northwest where bass are broadly distributed), and (3) provides management relevant tools to anticipate and prevent the future range expansion of bass farther into salmon-bearing streams.

In my final chapter I broaden my focus of freshwater conservation and assess the national scale potential of National Parks to serve as protected areas for native U.S. fish. I found that

although most parks were not designed with freshwater conservation in mind, nearly two-thirds (62%) of native US fishes reside in national parks. Using a conservation planning approach that integrated fish diversity representation provided by parks and their current and future ecological threats and management challenges, I identified 50 parks that could serve as a foundation for a nationally comprehensive freshwater protected area system. While the NPS has limitations as the potential basis for an aquatic protected area network, I argue it provides considerable representation of freshwater fish diversity that should be taken into account during systematic conservation planning for freshwaters.

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DEDICATION

To my daughter, Mayla Marine Lawrence. May you pursue your passions, whatever those may be.

CHAPTER 1

SPATIOTEMPORAL PATTERNS AND HABITAT ASSOCIATIONS OF SMALLMOUTH BASS (*MICROPTERUS DOLOMIEU*) INVADING SALMON REARING HABITAT

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Abstract

1. Smallmouth bass (*Micropterus dolomieu*) have been widely introduced to fresh waters throughout the world to promote recreational fishing opportunities. In the Pacific Northwest (U.S.A.) upstream range expansions of predatory bass, especially into subyearling salmon rearing grounds, is of increasing conservation concern, yet has received little scientific inquiry. Understanding the limitations to bass upstream colonization, the habitat characteristics that influence bass distribution and the timing and extent of bass and salmon overlap is needed to develop management strategies that mitigate potential ecological impacts of bass.
2. We employed a spatially continuous sampling design to determine the extent of bass and subyearling Chinook salmon (*Oncorhynchus tshawytscha*) sympatry in the North Fork John Day River (NFJDR), a free-flowing river system in the Columbia River Basin that contains an upstream expanding population of non-native bass. Extensive (i.e. 53 km) surveys were conducted over two years and during an early and late summer period of each year, because these seasons provide a strong contrast in the river's water temperature and flow condition. Classification and regression trees were applied to determine the primary habitat correlates of bass abundance at reach and channel unit scales.
3. Our study revealed that bass seasonally occupy up to 22% of the length of the mainstem NFJDR where subyearling Chinook salmon occur, and the primary period of sympatry between these species was in the early summer and not during peak water temperatures in late summer. Where these species co-occurred, bass occupied 60-76% of channel units used by subyearling Chinook salmon in the early summer and 28-46% of the channel

units they occupied in the late summer. Because these rearing salmon were well below the gape limitation of bass, this overlap could result in either direct predation or sublethal effects of bass on subyearling Chinook salmon. The upstream extent of bass increased 10 to 23 km (2009 and 2010, respectively) as stream temperatures seasonally warmed, but subyearling Chinook salmon were also found farther upstream during this time.

4. Our multi-scale analysis suggests that bass were selecting habitat based on antecedent thermal history at a broad scale, and if satisfactory temperature conditions were met, mesoscale habitat features (i.e. channel unit type and depth) played an additional role in determining bass abundance. The upstream extent of bass in the late summer corresponded to a high-gradient geomorphic discontinuity in the NFJDR, which likely hindered further upstream movements of bass. The habitat determinants and upstream extent of bass were largely consistent across years, despite marked differences in the magnitude and timing of spring peak flows prior to bass spawning.
5. The overriding influence of water temperature on smallmouth bass distribution suggests that managers may be able limit future upstream range expansions of bass into salmon rearing habitat by concentrating on restoration activities that mitigate climate or land-use related stream warming. These management activities could be prioritized to capitalize on survival bottlenecks in the life-history of bass and spatially focused on landscape knick points such as high-gradient discontinuities to discourage further upstream movements of bass.

Introduction

Non-native piscivorous fishes have been stocked in freshwater ecosystems throughout the world to support recreational fishing opportunities (Eby *et al.*, 2006). Since their initial introduction and establishment many of these species have spread, with and without additional human assistance (Johnson, Arlinghaus & Martinez, 2009), and future range expansions of non-native fishes in response to climate change are imminent (Rahel & Olden, 2008). Although only a subset of non-native species have been shown to cause ecological harm, in some cases their impacts to recipient ecosystems are dramatic and span multiple levels of biological organization ranging from the genome to the ecosystem (Cucherousset & Olden, 2011).

Smallmouth bass (*Micropterus dolomieu* Lacepède; hereafter referred to as bass), a cool-water fish native to central and eastern North America, provide a compelling example of the potential ecosystem consequences of introducing a novel predator. Smallmouth bass have been widely stocked in freshwater ecosystems in Africa, England, Europe, Japan and Russia (Quinn & Paukert, 2009), as well as many regions in North America (Schade & Bonar, 2005; Carey *et al.*, 2011). Their introduction has resulted in reduced growth of other native predators (Vander Zanden, Casselman & Rasmussen, 1999) and induced changes in the behaviour, distribution and at times caused the local extirpation of prey fish species (MacRae & Jackson, 2001; Jackson & Mandrak, 2002; Hughes & Herlihy, 2012). The impact of smallmouth bass introductions outside of the U.S. has gone largely unstudied, although recent work in Japan and South Africa suggest bass are having similar effects there (Iguchi *et al.*, 2004; Woodford *et al.*, 2005).

In the Pacific Northwest region of the United States, bass have been purposely stocked over the past century to promote recreational fisheries in rivers, lakes and reservoirs, where their potential to overlap with salmonids residing in headwater habitats was considered to be minimal

(Lampman, 1946). Many bass populations have greatly expanded from their initial introduction sites (e.g. LaVigne *et al.*, 2008) and there is increasing concern that they may now seasonally occupy upstream areas where some salmonids rear. As a result, smallmouth bass has been identified as a factor contributing to the decline of wild populations of Pacific salmon (*Oncorhynchus* spp.) now listed under the U.S. Endangered Species Act (Sanderson, Barnas & Wargo Rub, 2009; Carey *et al.*, 2011). Climate-induced stream temperature warming (Isaak *et al.*, 2011) and land-use management practices (e.g. removal of riparian vegetation) are likely to enable range expansions of predatory bass further into salmon rearing grounds, potentially adding more stress on an already highly threatened group of cold-water fishes (Ruckelshaus *et al.*, 2002).

Prior studies examining the impact of smallmouth bass on salmonids in the Pacific Northwest have focused largely on predation of salmon smolts as they move through the hydropower corridor of the Columbia River. Bass predation on outmigrating salmon smolts is highly variable, ranging from 0-35% of the total wild salmon run (Sanderson *et al.*, 2009). This variability is primarily associated with the abiotic conditions (e.g. temperature, water clarity, flow) that occur when these species overlap (Carey *et al.*, 2011) and the size and origin of the salmon smolts available for bass consumption (Fritts & Pearsons, 2006). The largest predatory impacts of bass on salmon to date have been documented where small subyearling ocean-type Chinook salmon (*Oncorhynchus tshawytscha* Walbaum) emigrate from their natal sites when temperatures are warm enough to allow for bass activity ($>10^{\circ}$ C, Poe *et al.*, 1991; Fritts & Pearsons, 2004). Bass predation is much lower or non-existent on larger yearling salmon smolts that outmigrate earlier in the year when river temperatures are cooler (Poe, Shively & Tabor, 1994). Little is known about the potential sympatry between bass and salmon that spend

extensive periods rearing in river systems. For example, stream-type Chinook salmon spend their first year in rivers before outmigrating the following spring as yearlings. Salmonids with this type of life history are more likely to encounter bass during their first summer rearing period. Although potential impacts are unknown to date, river conditions during this period favour bass activity and subyearling salmon are within the size range that is vulnerable to bass predation.

Upstream range expansions of bass in Pacific Northwest rivers are likely limited by temperature, but no studies have (1) documented the seasonal use of upstream areas by bass or (2) attempted to identify limiting factors that may prevent their further upstream expansion. High-gradient reaches characteristic of mountainous river systems may also play a role in limiting the upstream extent of bass by serving as barriers to movement, especially during high flows. Understanding the limitations to bass upstream colonization, the habitat characteristics that determine bass distribution and the timing and extent of bass and salmon overlap is needed to develop management strategies that mitigate potential impacts of bass in salmon rearing habitats.

Recent studies of smallmouth bass in their native range suggest that the primary habitat variables that influence their distribution depend on the scale of study, corresponding to an increasingly prominent hierarchical view of fish-habitat relationships (Brewer *et al.*, 2007; Dauwalter *et al.*, 2007). However, no prior studies have used a spatially continuous sampling methodology (i.e. sampling all channel units over a survey extent) to characterize multi-scale bass-habitat relationships across a river valley segment. Spatially continuous data provide the unique opportunity to understand how discontinuities in reach-scale physical habitats (e.g. geomorphic constrictions; Poole, 2002) affect fish distribution and upstream extent, and

simultaneously allow an assessment of catchment-scale environmental drivers on distributional patterns (Fausch *et al.*, 2002). Continuous surveys also allow the researcher to change the spatial scale of analysis (i.e. sample grain) to assess across-scale fish-habitat relationships.

We employed a spatially continuous sampling design to determine the extent of smallmouth bass and subyearling Chinook salmon sympatry in the North Fork John Day River (NFJDR hereafter), a river system that supports both a recreational fishery for non-native bass and contains one of the healthiest remaining stream-type Chinook salmon stocks in the Pacific Northwest (McClure *et al.*, 2003). Using these data, we determined the primary habitat variables that influence the distribution of bass in the NFJDR, and by changing the grain of our analysis, we tested if these variables depend on the scale of study. We conducted our study over two years to determine if there was year-to-year consistency in the primary habitat variables that explained bass distribution. Extensive surveys were conducted in early and late summer to determine seasonal variation in bass and Chinook salmon distribution in the NFJDR. Finally, we investigated potential factors that limit the upstream extent of bass in the NFJDR, including the influence of geomorphically defined discontinuities that disrupt more continuous longitudinal gradients in habitat. These data are essential to manage bass populations and to prevent further range expansion of non-native bass in river systems by providing information at spatial scales (e.g. 10-100 km) of management relevance.

Methods

Study area description

The free-flowing NFJDR originates in the Blue Mountains of Northeastern Oregon and is a major tributary of the John Day River, which drains into the Columbia River (Fig. 1.1). Chinook salmon migrate upstream to their spawning areas in the NFJDR primarily from May to June and hold in the stream until spawning occurs in September (Lindsay *et al.*, 1985). The majority of Chinook salmon fry emerge from spawning redds from March to April. These fry grow and develop in the NFJDR and its tributaries until the following February-May, when they outmigrate as yearlings. Thermally suitable habitat for Chinook salmon holding and rearing (considered <24° C; McCullough, 2001) is compromised in the NFJDR from a legacy of mining, livestock overgrazing and water withdrawals for irrigation.

According to Shrader & Gray (1999), smallmouth bass have been present in the Columbia River since at least the 1930s, but they were not found in the John Day River mainstem above river kilometre (RKM) 16, due to the impassable Tumwater Falls. In the 1960s Oregon Game Commission biologists began to consider stocking bass above Tumwater Falls, but the decision took several years because of concerns that bass may prey on migrating salmon smolts. The risk to yearling salmon smolts from predatory bass was ultimately deemed to be low given that smolts outmigrate when water temperatures are cold (2-7° C) and the river is high and turbid, factors that are likely to reduce the risk of bass predation. Although they were not noted in Shrader & Gray's (1999) report, the risks to subyearling Chinook salmon that rear instream during their first summer were probably considered negligible given that bass were to be introduced far downstream of subyearling Chinook salmon rearing grounds. Ultimately, smallmouth bass were introduced to the lower mainstem of the John Day River in 1971 (Shrader

& Gray, 1999). Bass were released 42 km below the confluence of the mainstem with the NFJDR, and where the NFJDR drains into the mainstem. Since that time bass have moved progressively upstream, and recent surveys conducted by the authors reveal that bass are now seasonally sympatric with subyearling Chinook salmon in the NFJDR, 80-142 km upstream of their original release site (depending on which initial introduction site is considered their source), as well as in the upper reaches of the Middle Fork and mainstem John Day River. Although only 80 adult bass were released in the initial stocking effort (and no subsequent releases were required), the John Day River and its tributaries now host a prized recreational bass fishery, and bass are protected within the John Day River by a take limit of 5 individuals per day, per angler.

Other fishes observed in the NFJDR study extent included resident and anadromous rainbow trout (*Oncorhynchus mykiss* Walbaum), mountain whitefish (*Prosopium williamsoni* Girard), northern pikeminnow (*Ptychocheilus oregonensis* Richardson), largescale (*Catostomus macrocheilus* Girard) and bridgelip (*Catostomus columbianus* Eigenmann) suckers, longnose (*Rhinichthys cataractae* Valenciennes) and speckled (*Rhinichthys osculus* Girard) dace, reddsider shiner (*Richardsonius balteatus* Richardson), and multiple species of sculpin (*Cottus* spp).

Temperature and discharge monitoring

Pendent temperature loggers (Onset Electronics, Onset, Massachusetts, U.S.A.) were deployed in the NFJDR to record annual water temperatures over the longitudinal extent of the survey area (RKM 52-105), with loggers positioned at RKM 52, 58, 66, 73, 86 and 105.

Temperature was recorded hourly over the summer (i.e. June to August) and every other hour in the winter (September to May) in 2009 and 2010. Additional loggers ($n = 13$ in 2009, $n = 16$ in 2010) were deployed every 1-2 kilometres immediately prior to the early summer survey and

were recollected at the end of the late summer survey each year. These loggers recorded temperature at a 1-hour interval.

We used degree days $>10^{\circ}\text{C}$ (hereafter called degree days) rather than instantaneous temperatures during the survey to describe the thermal history of the fish prior to and during the survey period, and to better capture the differences in temperature dynamics between the 2009 and 2010 survey years. A 10°C degree day threshold was chosen because bass are generally inactive and growth does not occur below this temperature (Shuter & Post, 1990). Degree days were calculated over the survey extent by summing the average daily temperature minus the 10°C threshold from May 1 of each survey year through the last day of the survey. Because we did not install loggers until June in 2009, we used data from the U. S. Forest Service (measured hourly at RKM 99 from May 1, 2009) to determine degree days until our temperature sampling began. Temperature loggers were not deployed every river kilometre, so degree days were extrapolated across the survey extent based on a linear relationship between degree days and RKM in the study area (June 2009 model $R^2 = 0.98$; August 2009 model $R^2 = 0.97$; July 2010 model $R^2 = 0.97$; August 2010 model $R^2 = 0.99$).

Discharge during the survey period was determined based on a U. S. Geological Survey (USGS) long-term flow gage (station 14046000) stationed on the NFJDR at RKM 24. This station provided daily discharge data ($\text{m}^3\text{ s}^{-1}$) from 1929 until present, allowing us to compare discharge conditions in 2009 and 2010 immediately prior to and during our surveys, as well as place our surveys in a historical context of long-term flow conditions.

Fish distribution and habitat surveys

We conducted spatially continuous fish distribution surveys of the NFJDR in the early summer (June 21-26, 2009; June 29-July 5, 2010) and late summer (August 6-11, 2009; August 18-23, 2010), for a total of four surveys over two years. Stream surveys were conducted from the NFJDR confluence with the Middle Fork John Day River (RKM 52) to Trough Creek (RKM 105), for a survey extent of 53 km. With the exception of the August 2009 survey, a one-kilometre reach (RKM 100-101) was not surveyed because this canyon reach contained rapids that were dangerous to snorkel. Preliminary surveys in 2008 revealed the RKM 52-105 survey extent represented the transition zone where bass seasonally utilized habitat in near proximity to, or overlapping with, rearing Chinook salmon. Chinook salmon spawning distribution in the NFJDR varies from year to year, with a downstream extent of redds at RKM 85 and an upstream extent at RKM 177 (Jeff Neal, personal communication).

The timing of the distributional surveys was chosen to correspond to seasonally disparate flow and temperature conditions in the John Day River and to allow a comparison of bass and subyearling Chinook salmon sympatry during the early summer high flow, cooler temperature, period and the low-flow, high temperature, late summer condition. The timing of the early summer survey was also chosen to observe bass spawning in the NFJDR.

Fish distributional surveys were conducted utilizing a modified version of a method developed by Torgersen *et al.* (1999; 2006), a spatially continuous survey technique of fish populations and their associated habitats where all channel units (i.e. riffles, glide-like riffles, glide-like pools, pools) were sampled over the study extent. Fishes were counted in each channel unit using two-person teams. Channel units were differentiated by changes in surface velocity and depth profile. Snorkelers surveyed each channel unit from downstream to upstream,

first moving up one side of the stream, floating down the thalweg and then moving up the opposite bank. If the opposite bank was too shallow to snorkel, then only one bank and the thalweg were snorkeled. Snorkelers noted the species and number of each of the fishes observed. The abundance of bass adults (age 1 and older, >10 cm) and subyearling Chinook salmon are reported here. Water visibility was measured using a modified Secchi disk, a 25 cm length of 2.5 cm diameter PVC pipe, coloured alternately black and white. With the tube immersed in the water, the snorkeler moved slowly away from the tube until it was no longer visible, and then the distance between the snorkeler and the tube was measured. Average visibility was 6 m (standard deviation = 2 m), and visibility was lower during the high flow early summer survey compared to the late summer period; decreases in visibility may have resulted in underestimation of counts in the early summer.

A shore-based surveyor used a global positioning unit (GPS) to georeference and delineate the channel unit. The surveyor also recorded habitat variables including the dominant and sub-dominant substratum (%), mean and maximum depth (m), unit length (m), average wet width (m), riparian cover along the stream bank (%), and large boulder coverage in the channel unit (%). Substrata, riparian cover, and boulder cover were visually estimated; wet width and unit length were determined using a laser range finder; depth was determined by the snorkeler. Stream gradient was measured over the survey extent in a geographical information system (GIS) using 1:24,000 USGS digital raster graphics by marking points where topographic contours crossed the stream, and then calculating the elevation change over the distance separating each point.

Long channel units (>100 m) were subsampled using the following rule: If the channel unit was ≤ 300 m, the snorkeler surveyed 100 m of habitat, skipped 100 m, and then snorkelled

the remaining habitat. If the channel unit was >300 m, the snorkeler surveyed 100 m and then skipped 200 m; this subsampling procedure was repeated until the unit ended. Because riffle habitat was difficult to snorkel due to high water velocities in the early summer and shallow conditions in the late summer, riffles were snorkelled in areas with depths typically >0.25 m: all other habitat within riffles (<0.25 m) was considered too shallow for adult bass (Orth & Newcomb, 2002; Dauwalter *et al.*, 2007). This may have resulted in some underestimation of subyearling Chinook salmon numbers if they reside in very shallow sections of riffles, but previous surveys within the NFJDR (Torgersen *et al.*, 2006), and other studies suggest that subyearling Chinook salmon typically occur in slower, deeper habitats (Everest & Chapman, 1972; Hillman, Griffith & Platts, 1987; Roper, Scarnecchia & La Marr, 1994).

Bass and subyearling Chinook salmon distribution was assessed across the longitudinal continuum of the NFJDR at two scales: the channel unit scale and at a 1-km scale. The 1-km scale was chosen to describe reach-level fish-habitat relationships. Counts of each species per RKM (where RKM 0 represents the NFJDR confluence with the John Day River main stem) were determined using a custom binning script in R (version 2.13.0; R Development Core Team). Because some long channel units were subsampled, we extrapolated counts to estimate total fish per channel unit based on a fish per unit length metric. Pools were snorkelled completely so no extrapolation was required. Riffles were treated differently because (1) we snorkelled ‘useable’ habitat, and (2) applying fish count estimates from ‘useable’ habitat to extrapolate counts to large sections of riffles that were unusable (i.e. extremely shallow) would have resulted in overestimates of fish numbers. In extremely shallow sections of riffles, we assumed that adult bass and subyearling Chinook salmon abundance was zero.

To define the upstream extent of bass reproductive activities, any bass nest encountered during the early summer surveys (i.e. late June and early July) was noted and its position was recorded using a GPS. Nest counts presented in the results represent conservative estimates because counts from sampled areas were not extrapolated to unsampled portions of channel units.

Statistical analysis

Bass-habitat relationships were analysed using a recursive partitioning algorithm widely known as classification and regression trees (CART). CART is a useful technique to model ecological data because it can handle a combination of continuous and discrete explanatory variables, it is relatively insensitive to outliers and it can accommodate both non-linear and interactive relationships between the explanatory variables and the response variable (Olden, Lawler & Poff, 2008). The goals of the statistical analysis were to explore the primary habitat correlates of bass distribution, and to determine if the relative importance of these variables changed seasonally and at different spatial scales. Thus, the analysis was completed at two scales (i.e. channel unit and 1-km binned reach scale data), and each of the four surveys was assessed separately (i.e. 2009 and 2010 early summer models, and 2009 and 2010 late summer models), for a total of eight models.

Reach-scale regression trees were built with bass count per kilometre as the response variable. The explanatory variables included degree days, gradient ($\text{m}\cdot\text{km}^{-1}$), length-weighted average maximum depth (m), channel wet width (m), percent riparian cover (%), percent large boulder cover (%) and a velocity and substratum score. The velocity metric employed in the model was semi-quantitative and was calculated by (1) determining the percent of each RKM

composed of riffle, glide-like riffle, glide-like pools and pool habitat; (2) multiplying the contribution of each of these unit types by 4,3,2,1, respectively (to represent fast to slow velocity units) and (3) summing the result. Therefore, velocity scores for each RKM range between 1 and 4 depending on the overall occurrence of each unit type within that kilometre. Substratum score represents a composite score determined by multiplying the field-measured substrata data (i.e. percent dominant and subdominant substratum) by a score (5 = bedrock, 4 = boulder, 3 = cobble, 2 = gravel, 1 = sand), adding up that total and then applying a logarithmic transformation. This method resulted in an increasing score as substratum size increased. Trees were built using 10-fold cross-validation and were pruned based on the 1-standard-error rule (De'ath & Fabricius, 2000) with the *rpart* library in R.

At the channel unit scale, the response variable for the regression trees was bass adults per km², measured as the channel unit wet width multiplied by the unit length. The response variable at this scale was highly heteroscedatic, so it was log (x+1) transformed prior to analysis (Moisen, 2008). The continuous explanatory variables included in the channel unit scale models were degree days, channel gradient (m·km⁻¹), mean unit depth (m), max unit depth (m), channel wet width (m), percent riparian cover (%), percent large boulder cover (%) and substratum score (as calculated previously). Unit type (i.e. riffle, glide-like riffle, glide-like pool and pool), a non-continuous explanatory variable representing a channel unit's velocity and depth profile, was included as a factor-type variable in models at this scale. Trees were built using 10-fold cross-validation. Because we were interested in describing rather than predicting bass-habitat relationships at the channel unit scale, the tree was allowed to grow one additional branch beyond the 1-standard-error-rule commonly used for pruning the tree (i.e. model simplification) during regression tree building.

Results

Stream physical characteristics during the surveys

The seasonal stream temperature profile and hydrograph of the NFJDR is typical of a snow-melt driven Pacific Northwest river system, with peak discharge in the late spring/early summer period and maximum temperatures during the summer low flow period (typically in early August). Average daily water temperatures during the early summer surveys were similar over the study extent between 2009 and 2010 (Table 1.1). Stream temperatures observed during both late summer surveys were also similar (Table 1.1), but they were depressed compared to temperatures recorded prior to and after each survey. For example, in late summer 2009 the peak summer temperature recorded at RKM 52 (27.6° C) was observed four days prior to the survey initiation. A heavy rainstorm occurred during this survey, causing the average daily temperature recorded at RKM 52 to drop 10° C. Degree days accumulated at both the downstream (i.e. RKM 52) and upstream areas of the survey extent (i.e. RKM 105) were higher in 2009 compared to 2010 during early and late summer, reflecting the earlier warming that year (Fig. 1.2a).

Discharge was also similar between early summer surveys in 2009 and 2010 (Table 1.1), although the timing and magnitude of peak discharge was different between years (Fig. 1.2b). Peak monthly-mean flow in 2009 occurred in May and although it was high relative to the 80-year historical average (152 vs. 102 m³ s⁻¹, Fig. 1.2b), the timing of the peak matched the long-term record. A large snow pack and a relatively cold spring delayed the peak monthly-mean discharge in 2010, which occurred in June. The magnitude of the 2010 June mean monthly discharge was also high, reaching 123 m³ s⁻¹. A heavy rain storm increased the range of

discharge observed during the late summer 2009 survey and tripled the maximum discharge observed at that time compared to 2010 (Table 1.1).

Fish distribution and bass-Chinook salmon sympatry

Bass occurred in the lower region of our survey extent during the early summer in 2009 and 2010, with an upstream extent of RKM 77 and 79, respectively (Fig. 1.3). Peaks in bass counts differed spatially between years during these surveys, as revealed by the kilometre-scale distributional data. Bass were nesting during the early summer survey in both years, and the majority of nests were found in the lower survey region. The numbers of nests observed (i.e. 37 in 2009, 40 in 2010), and the position of the most upstream nest were comparable between years (i.e. RKM 74 in 2009, RKM 75 in 2010). At the beginning of the survey, seven-day average daily (7DAD) minimum, mean and maximum temperatures at the upstream-most nest were 12.7° C, 15.0° C, and 17.6° C, in 2009 and 15.1° C, 17.3° C, and 19.6° C in 2010, respectively. The upstream extent of adult bass largely coincided with the upstream extent of bass nests in 2009 and 2010, where few adult bass were upstream of the most upstream nest.

The upstream extent and the numbers of bass observed greatly increased in the late summer survey, suggesting bass were moving up from below the lower survey extent (Fig. 1.3). Bass distribution was patchy during the late summer in both years, and similar to the early summer surveys, the spatial position of peak counts varied between years. The late summer upstream extent of bass was similar between years, but some bass penetrated further upstream in 2009 (i.e. up to RKM 100) compared to 2010 (i.e. up to RKM 89). Bass had completed nesting before the late summer survey, as no nests were observed. 7DAD minimum, mean and

maximum temperatures where the most upstream bass were observed in late summer were 16.1° C, 18.8° C, and 22.1° C, in 2009 and 16.1° C, 19.9° C, and 24.8° C in 2010, respectively.

Subyearling Chinook salmon co-occurred with bass at both the channel unit (e.g. the same pool) and reach scale (i.e. within the same RKM), but the extent of overlap was higher in the early summer compared to the late summer (Fig. 1.3). The downstream extent of subyearling Chinook salmon in the early summer was consistent across years, with Chinook salmon found downstream to RKM 52 in 2009 and RKM 53 in 2010, although small numbers of Chinook salmon may have occurred downstream of our survey extent. In early summer, subyearling Chinook salmon numbers increased from downstream to upstream, but the pattern was more pronounced in 2010 compared to 2009. The spatially continuous nature of the survey revealed that, similar to bass, subyearling Chinook salmon distribution was patchy over the survey extent, and the (reach scale) peaks in subyearling Chinook salmon distribution were not spatially similar between survey years. 7DAD minimum, mean and maximum temperatures where the downstream-most subyearling Chinook salmon were observed in early summer were 14.3° C, 16.7° C, and 19.2° C, in 2009 and 15.9° C, 18.2° C, and 20.5° C in 2010, respectively.

Bass and Chinook salmon co-occurred from RKM 52-77 in early summer 2009 (25 km total), and RKM 53-79 in 2010 (26 km total). Within this area of overlap, bass occurred in 60% (2009) to 76% (2010) of the channel units occupied by subyearling Chinook salmon. Given that rearing Chinook salmon persist until RKM 165 (*Torgersen et al., 2006*), and thus occur over 113 km of the NFJDR, bass occurred in 22% of the length of the mainstem NFJDR where subyearling Chinook salmon are typically present.

The overall extent of sympatry between bass and subyearling Chinook salmon declined in the late summer period in 2009 (14 km) and 2010 (21 km) (Fig. 1.3). Bass occupied 28% (2009)

to 46% (2010) of the channel units where subyearling Chinook salmon occurred within this area of overlap. The late summer downstream extent of subyearling Chinook salmon in 2009 was RKM 87 and RKM 69 in 2010, although very few Chinook salmon were observed this far downstream during this period. 7DAD minimum, mean, and maximum temperatures at the most downstream site occupied by subyearling Chinook salmon at this time were 16.5° C, 19.5° C, and 23.1° C in 2009, and 18.2° C, 21.6° C, and 24.9° C in 2010. The majority of the subyearling Chinook salmon were observed above RKM 100 in August of both years.

Bass-habitat relationships

Water temperature, quantified here as degree days, was the strongest predictor of bass distribution at the reach (i.e. kilometre) scale in both seasons and both years (Fig. 1.4). No other habitat variable was selected through the CART analysis at this scale. Pruned regression trees built to predict bass km^{-1} had an R^2 of 0.74 (RSME = 5.4, $P < 0.0001$) and 0.59 (RSME = 18.0, $P < 0.0001$) for early and late summer in 2009, respectively, and 0.77 (RSME=5.9, $P < 0.0001$) and 0.70 (RSME = 13.0, $P < 0.0001$) for early and late summer in 2010, respectively. Early summer kilometre scale trees split on 137 degree days (and subsequently on 111 degree days) in 2009 and 141 degree days (and subsequently on 113 degree days) in 2010. Late summer kilometre-scale trees split based on 628 degree days in 2009 and 675 degree days in 2010. Both late summer regression trees had only one split and two terminal nodes.

At the channel unit scale, degree days and other habitat features, including mean and max depth, channel unit type (e.g. riffle, pool) and wetted channel width were the primary correlates of bass density (Fig. 1.5). For all seasons and years, temperature and habitat variables operated in a hierarchical manner to predict the density of bass, and degree days consistently represented

the first regression tree split. In the early summer 2009, slower velocity channel units (i.e. glide-like riffles, glide-like pools and pools) where accumulative degree days exceeded 107, and particularly channel units with 122 or more degree days, supported the highest bass densities (model performance: $R^2 = 0.68$, RMSE = 5.77, $P < 0.0001$, Fig. 1.5a). Similarly for early summer 2010, channel units with > 113 degree days had the highest bass densities, particularly in glide-like riffle, glide-like pool and pool units with greater than 140 degree days accumulated ($R^2 = 0.66$, RMSE = 3.85, $P < 0.0001$, Fig. 1.5b). Deeper channel units also supported higher densities of bass compared to shallow units; for example, units with 113-140 degree days with mean depths exceeding 0.55 m had 9 times higher bass densities than thermally comparable, but shallower units. In late summer 2009, bass were typically present in warmer channel units with degree days exceeding 611, whereas bass were absent or rare in cooler units (Fig. 1.5c). In warmer channel units, bass density on average was lower in riffle habitats compared to glide-like riffles, glide-like pools and pools, and within these channel unit types, densities were highest in units with greater maximum depth. Habitat correlates of bass density in late summer 2010 were similar to 2009. Cooler channel units (degree days < 666) typically supported lower bass densities, with the exception of glide-like pool and pools units where degree days exceeded 602 (Fig. 1.5d). In the warmer regions of the river (degree days > 666), channel unit type was the second most important variable; riffle units had a lower density of bass compared to all other unit types. In both riffle and non-riffle habitats, units with greater maximum depth had higher bass densities. The 2009 and 2010 late summer models explained similar proportions of the overall variability in bass density at the channel unit scale, with an R^2 of 0.71 in 2009 (RMSE=6.52, $P < 0.0001$) and 0.68 (RMSE=5.77, $P < 0.0001$) in 2010.

Limits to upstream movement

Continuous sampling revealed that the upstream extent of bass corresponded with a discontinuity in channel geomorphology (Fig. 1.6). In August 2009, bass were found just below a high-gradient river segment (8 m km^{-1}), where the NFJDR becomes highly constrained in a canyon at RKM 100. The upstream extent of bass in 2010 was RKM 89, right downstream of a segment where three tributaries (i.e. Camas, Meadowbrook and Desolation Creek) enter the NFJDR, greatly increasing its contributing basin area. This segment is also immediately downstream from a series of reaches with increasing gradient, decreasing channel width and a depression in maximum river temperatures, as measured by forward looking infrared remote sensing (*FLIR*; *ORDEQ, 2010*). Subyearling Chinook salmon distribution increased greatly upstream of the high-gradient discontinuity at RKM 100 (Fig. 1.3b, 1.3d), suggesting it might be a barrier to bass and Chinook salmon sympatry during the late summer.

Discussion

This study demonstrates that smallmouth bass have greatly expanded their upstream range from their initial introduction site, such that they now inhabit Chinook salmon rearing habitat in the NFJDR. At the maximum extent of overlap, smallmouth bass occupied nearly a quarter of the length of the mainstem NFJDR where subyearling Chinook salmon occurred. This area represents the interface between the upstream extent of ‘coolwater’ bass and the downstream extent of ‘coldwater’ Chinook salmon. Upstream invasions by bass, although largely undocumented, are believed to be common in river systems throughout the Pacific Northwest (Carey *et al.*, 2011) and other regions (e.g. Ellender, Weyl & Swartz, 2011). Despite the ubiquity of smallmouth bass in river systems, the majority of previous studies have focused

on their invasions in temperate lakes (e.g. Vander Zanden *et al.*, 2004; Sharma, Herborg & Therriault, 2009). The piscivorous nature of bass and their documented impacts on native fish communities (Jackson, 2002) make their invasions in rivers a cause for conservation concern.

Our seasonal surveys revealed that the primary period of bass and Chinook salmon sympatry in the NFJDR occurred in the early summer prior to the stream reaching peak water temperatures. Bass were nesting throughout this zone of sympatry during the early summer period. Because male bass generally do not feed while nesting (Hanson & Cooke, 2009), spawning may reduce the potential predation of bass on subyearling Chinook salmon at this time. However, not all bass engage in spawning activities each year (Raffetto, Baylis & Serns, 1990), and females may not greatly reduce their feeding during spawning. If smallmouth bass feed prior to spawning (Tabor, Shively & Poe, 1993; Fritts & Pearsons, 2004), or if only a small fraction of the overall bass population reduces feeding activities to spawn in the NFJDR, subyearling Chinook salmon could be highly vulnerable to smallmouth bass during this period of peak overlap.

Late summer surveys revealed a decreased extent of overall sympatry between bass and subyearling Chinook salmon, although bass and Chinook salmon overlapped at the upper extent of bass distribution within the NFJDR at this time. By comparing the early and late summer surveys, it is clear that bass moved upstream and the overall numbers of bass increased in the survey extent. Upstream migrations of smallmouth bass have been observed in other river systems, and these movements may be motivated by bass seeking river segments suitable for spawning (Lyons & Kanehl, 2002) or may be the result of density dependent processes (DeAngelis, Godbout & Shuter, 1991).

In both survey years, subyearling Chinook salmon were no longer observed in the lower NFJDR survey extent in late summer. Although the fate of these salmon is unknown, several mechanisms could account for this pattern. First, subyearling Chinook salmon could move upstream in response to downstream warming. Water temperatures in our lower survey extent regularly approach, and at times exceed, 24° C (Fig. 1.2), the upper thermal tolerance of juvenile Chinook salmon (McCullough, 2001). Subyearling Chinook salmon may also move from downstream areas into adjacent cooler tributaries as stream temperatures warm. Surveys of tributaries in the John Day River system provide evidence that subyearling Chinook salmon utilize tributaries far downstream of known spawning habitat (Lindsay *et al.*, 1985); this has been documented in other river systems as well (Murray & Rosenau, 1989; Scrivener, Brown & Andersen, 1994). Predation may also account for the observed loss of subyearling Chinook salmon from the lower survey extent. Although we did not collect direct evidence of smallmouth bass predation on subyearling Chinook (i.e. diet samples), prior studies have shown that smallmouth bass can have high predation rates on small subyearling Chinook salmon when water temperatures are high (Tabor *et al.*, 1993; Fritts & Pearsons, 2004; Tabor *et al.*, 2007). Stream-type subyearling Chinook salmon that overlapped with bass in the NFJDR during early summer were similar in size (i.e. mean 50 mm fork length; Lawrence, unpublished data) to the ocean-type subyearling Chinook salmon that bass preyed heavily upon in other studies (i.e. mean 57 mm fork length; Fritts & Pearsons, 2004). Northern pikeminnow, a native predator present in our survey extent, may also prey on subyearling Chinook salmon in the NFJDR, but they were far less abundant than smallmouth bass in the study area (Lawrence, unpublished data). Finally, temperature-mediated competition with other species, such as redbreasted sunfish, who feed on drift with subyearling Chinook salmon, but prefer warmer temperatures may also reduce the growth

or exclude subyearling Chinook salmon from the lower survey extent as water temperatures seasonally warm (Reeves, Everest & Hall, 1987). Further study is needed to weigh the relative influence of these mechanisms on subyearling Chinook salmon seasonal distribution and to more fully understand the implications of bass and Chinook salmon sympatry. Degree days $> 10^{\circ}\text{C}$, an ecologically-relevant temperature threshold above which bass are generally active and growth occurs (Shuter & Post, 1990), was the primary determinant of bass abundance at both reach and channel unit scales. Our results revealed strong year-to-year consistency in the influence of water temperature in the distribution of bass in the NFJDR in both early and late summer. This consistency, and previous research (summarized by Armour, 1993), suggests that water temperature determines bass distribution in cold water rivers. Given this mechanistic underpinning, it is likely that these results could be applied to many other river systems experiencing upstream range expansions of smallmouth bass.

Our multi-scale analysis suggests that bass selected habitat based on antecedent thermal history at a broad scale, and if satisfactory temperature conditions were met, mesoscale habitat features (i.e. channel unit type and depth) played an additional role in determining bass abundance. In the lower, warmer section of the NFJDR, bass were more abundant in deeper channel units, and typically those with slow (i.e. pools and glide-like pools) and intermediate (i.e. glide-like riffles) water velocity. Depth was also a significant predictor of adult bass density in spatially extensive (Dauwalter *et al.*, 2007) and temporally intensive (Dauwalter & Fisher, 2008) studies of smallmouth bass in their native range. Water depth is important in the early summer period because bass must avoid constructing nests in channel reaches that are susceptible to dewatering (leaving eggs and fry stranded) as stream discharge declines into the summer. In the late summer, when the NFJDR was at base flow and riffle habitat was extremely

shallow, longitudinal patterns in bass abundance were influenced by channel unit type (i.e. riffles vs. non-riffle units) and channel depth. Riffles at this discharge would impede adult bass movement and occupancy, whereas in non-riffle habitat, water depth is important to provide cover for bass and to allow for their movement within the channel unit. Prior studies demonstrate that adult bass typically do not occupy riffle habitat (Schlosser, 1987; Ebert & Filipek, 1991).

Water temperature may operate through several mechanisms to limit bass upstream extent in coldwater river systems such as the NFJDR. In the early summer, bass spawn and therefore must select temperatures that are not only suitable for their own physiology, but they also must establish their nests in areas with temperatures that are appropriate for the development of their young. Temperature directly effects the development of bass eggs and the growth of young-of-the-year bass (Shuter *et al.*, 1980). Temperature-growth relationships differ for adult and young-of-the-year bass; young-of-the-year bass grow optimally at temperatures significantly greater (29° C; Shuter & Post, 1990) than those that provide optimal growth for adult bass (22° C; Whitley, Hayward & Rabeni, 2002). This difference is likely to influence how far bass move upstream prior to spawning. Young-of-the-year growth is particularly important in north temperate river systems, where bass must obtain a minimal size to survive a winter starvation period (Shuter *et al.*, 1980). Bass nesting in areas with temperature regimes that are not sufficient to achieve this growth minimum would be selected against because their offspring would not survive to spawn. In a central Appalachian river, Martin & Petty (2009) found bass in cold streams in relatively close proximity to warm streams, but not in cold streams separated by significant distances from warm segments. They attributed this pattern to a similar mechanism,

i.e. the need for adult bass to spawn in water with temperatures suitable for the development of their young.

In the late summer, adult temperature-growth relationships are likely to govern the upstream extent of bass. After spawning, a portion of the bass population continued to move upstream of their nesting grounds, as evidenced by the difference between their early versus late summer upstream extent. The water temperature observed at the uppermost occurrence of bass during this time was similar in 2009 and 2010 (i.e. 7DAD mean 18 and 19° C, respectively). This consistency suggests that these temperatures may be the coolest water that bass can occupy and still maintain positive growth given the availability of food in the NFJDR. As upstream temperatures become increasingly cold, bass would have reduced, zero, or negative growth regardless of food availability (Whitledge, Hayward & Zweifel, 2003).

In addition to water temperature, channel morphology may also play an important role in determining the upstream extent of bass in mountainous regions. Our spatially continuous sampling technique revealed that a geomorphic discontinuity may restrict the upstream movement of bass in the NFJDR during late summer. In both survey years, bass were not found above a highly confined, high-gradient canyon segment at RKM 100. In 2009, bass were present in a pool immediately downstream of this feature. We conducted an extensive survey of the peer-reviewed literature to determine the highest stream gradient that bass could overcome; however, given that most studies of bass are in relatively low gradient river systems in their native range, this gradient threshold is unknown. Brewer *et al.* (2007) surveyed almost 2000 reaches in Missouri and found that smallmouth bass rarely occupied areas with gradients exceeding 10 m km⁻¹ (i.e. 8 out of 1994 reaches) and were not found in reaches with channel gradients >25 m km⁻¹. Dauwalter *et al.* (2007) measured smallmouth bass abundance in 1800

channel units of streams in Oklahoma and found that bass were absent from any units exceeding 10 m km^{-1} gradient. Although bass may not reside in relatively high-gradient stream segments, they could potentially pass through them. Burton & Odum (1945) found that bass did not occur in reaches with gradients ranging from 8 to 10 m km^{-1} , but they were present upstream of them. The authors reported occurrence, not abundance, so it is unknown how many bass were able to overcome these high-gradient segments. The high-gradient segment in the NFJDR was 8 m km^{-1} , which may deter bass from moving farther upstream, especially because this feature coincided with cold water temperatures. However, based on the limited literature available, it is unlikely to completely prevent their movement. Year-to-year variation in upstream water temperature will likely determine if bass move far enough upstream to encounter this high-gradient feature, and thus, will alter its influence on bass upstream movement – i.e. in some years cold water temperatures downstream of this feature will prevent bass upstream movement before bass encounter this high-gradient segment. This appeared to happen in 2010, when a late snow melt delayed the warming of water temperatures in the upper NFJDR, and so bass upstream extent was 11 km below this high-gradient feature. However, climate-related warming is projected to increase stream temperatures in the John Day River (Ruesch *et al.*, in press) and many other rivers in the Pacific Northwest (Isaak *et al.*, 2011), and therefore high-gradient features that become more common upstream are likely to play an increasingly prominent role in determining bass upstream range expansions.

Managers may be able prevent or at least limit upstream range expansions of bass in salmon-bearing rivers by (1) capitalizing on aspects of the life history of bass (i.e. the need for sufficient age-0 growth to overcome winter starvation), and (2) use natural landscape knickpoints such as high-gradient discontinuities to deter the upstream movement of bass. Managers could

establish target temperature criteria to prevent over-winter survival of young-of-the-year bass in salmon rearing areas (e.g. the United States Environmental Protection Agency has water temperatures standards above which salmonids are physiologically and competitively disadvantaged; EPA, 2003). Chu *et al.* (2006) found that young-of-the-year survival had the greatest influence on population dynamics of bass; thus, by reducing recruitment, managers may be able to slow the invasion by non-native bass populations in rivers. Also, with relatively limited geographic information (e.g. gradient derived from a topographic map) managers could identify moderate- to high-gradient knickpoints on the landscape that naturally deter upstream movements of bass. These locations could function as a ‘first front’ to prevent range expansions by bass. For example, this information could be used to spatially prioritize protection (e.g. conservation of intact riparian vegetation) or restoration activities (e.g. re-vegetation of riverbanks) to maintain cold water temperatures above these geomorphic features. This could provide multiple disincentives to bass to further penetrate salmon rearing grounds. Similar strategies could be applied to limit the upstream range expansion of bass in other river systems, and these approaches may constrain upstream movements of other non-native cool and warm-water predatory species.

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References

- Armour, C.L. (1993) Evaluating temperature regimes for protection of smallmouth bass. p. 27. United States Department of the Interior, Fish and Wildlife Service, Resource Publication 191, Washington, D.C.
- Brewer, S.K., Rabeni, C.F., Sowa, S.P. & Annis, G. (2007) Natural landscape and stream segment attributes influencing the distribution and relative abundance of riverine smallmouth bass in Missouri. *North American Journal of Fisheries Management*, **27**, 326-341.
- Burton, G.W. & Odum, E.P. (1945) The distribution of stream fish in the vicinity of Mountain Lake, Virginia. *Ecology*, **26**, 182-194.
- Carey, M.P., Sanderson, B.L., Friesen, T.A., Barnas, K.A. & Olden, J.D. (2011) Smallmouth bass in the Pacific Northwest: a threat to native species; a benefit for anglers? *Reviews in Fisheries Science*, **19**, 305-315.
- Chu, C., Collins, N.C., Lester, N.P. & Shuter, B.J. (2006) Population dynamics of smallmouth bass in response to habitat supply. *Ecological Modelling*, **195**, 349-362.
- Cucherousset, J. & Olden, J.D. (2011) Ecological impacts of nonnative freshwater fishes. *Fisheries*, **36**, 215-230.
- Dauwalter, D.C. & Fisher, W.L. (2008) Spatial and temporal patterns in stream habitat and smallmouth bass populations in eastern Oklahoma. *Transactions of the American Fisheries Society*, **137**, 1072-1088.
- Dauwalter, D.C., Splinter, D.K., Fisher, W.L. & Marston, R.A. (2007) Geomorphology and stream habitat relationships with smallmouth bass (*Micropterus dolomieu*) abundance at

- multiple spatial scales in eastern Oklahoma. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 1116-1129.
- De'ath, G. & Fabricius, K.E. (2000) Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, **81**, 3178-3192.
- DeAngelis, D.L., Godbout, L. & Shuter, B.J. (1991) An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. *Ecological Modelling*, **57**, 91-115.
- Ebert, D.J. & Filipek, S.P. (1991) Evaluation of feeding and habitat competition between native smallmouth bass (*Micropterus dolomieu*) and rainbow trout (*Oncorhynchus mykiss*) in a coolwater stream. In: *The First International Smallmouth Bass Symposium*. (Eds D.C. Jackson), pp. 49-54. American Fisheries Society, Nashville, Tennessee.
- Eby, L.A., Roach, W.J., Crowder, L.B. & Stanford, J.A. (2006) Effects of stocking-up freshwater food webs. *Trends in Ecology & Evolution*, **21**, 576-584.
- Ellender, B.R., Weyl, O.L.F. & Swartz, E.R. (2011) Invasion of a headwater stream by non-native fishes in the Swartkops River system, South Africa. *African Zoology*, **46**, 39-46.
- EPA (2003) EPA Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards. EPA 910-B-03-002. Region 10 Office of Water, Seattle, WA.
- Everest, F.H. & Chapman, D.W. (1972) Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. *Journal of the Fisheries Research Board of Canada*, **29**, 91-100.
- Fausch, K.D., Torgersen, C.E., Baxter, C.V. & Li, H.W. (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience*, **52**, 483-498.
- Fritts, A.L. & Pearsons, T.N. (2004) Smallmouth bass predation on hatchery and wild salmonids in the Yakima River, Washington. *Transactions of the American Fisheries Society*, **133**, 880-895.
- Fritts, A.L. & Pearsons, T.N. (2006) Effects of predation by nonnative smallmouth bass on native salmonid prey: the role of predator and prey size. *Transactions of the American Fisheries Society*, **135**, 853-860.
- Hanson, K.C. & Cooke, S.J. (2009) Nutritional condition and physiology of paternal care in two congeneric species of black bass (*Micropterus* spp.) relative to stage of offspring development. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, **179**, 253-266.
- Hillman, T.W., Griffith, J.S. & Platts, W.S. (1987) Summer and winter habitat selection by juvenile Chinook salmon in a highly sedimented Idaho stream. *Transactions of the American Fisheries Society*, **116**, 185-195.

- Hughes, R.M. & Herlihy, A.T. (2012) Patterns in catch per unit effort of native prey fish and alien piscivorous fish in 7 Pacific Northwest USA rivers. *Fisheries*, **37**, 201-211.
- Iguchi, K., Matsuura, K., McNyset, K.M., Peterson, A.T., Scachetti-Pereira, R., Powers, K.A., Vieglais, D.A., Wiley, E.O. & Yodo, T. (2004) Predicting invasions of north American basses in Japan using native range data and a genetic algorithm. *Transactions of the American Fisheries Society*, **133**, 845-854.
- Isaak, D.J., Wollrab, S., Horan, D. & Chandler, G. (2011) Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. *Climatic Change*, DOI 10.1007/s10584-10011-10326-z.
- Jackson, D.A. (2002) Ecological effects of *Micropterus* introductions: the dark side of black bass. In: *Black Bass: Ecology, Conservation, and Management*. (Eds D.P. Philipp & M.S. Ridgway), pp. 251-264. American Fisheries Society, Bethesda, Maryland.
- Jackson, D.A. & Mandrak, N.E. (2002) Changing fish biodiversity: predicting the loss of cyprinid biodiversity due to global climate change. In: *American Fisheries Society Symposium*. (Eds N.A. McGinn), pp. 89-98, Bethesda, Maryland.
- Johnson, B.M., Arlinghaus, R. & Martinez, P.J. (2009) Are we doing all we can to stem the tide of illegal fish stocking? *Fisheries*, **34**, 389-394.
- Lampman, B.H. (1946) *The Coming of the Pond Fishes*, Metropolitan Press, Portland, Oregon.
- LaVigne, H.R., Hughes, R.M., Wildman, R.C., Gregory, S.V. & Herlihy, A.T. (2008) Summer Distribution and Species Richness of Non-native Fishes in the Mainstem Willamette River, Oregon, 1944-2006. *Northwest Science*, **82**, 83-93.
- Lindsay, R.B., Knox, W.J., Flesher, M.W., Smith, B.J., Olsen, E.A. & Lutz, L.S. (1985) Study of wild spring Chinook salmon in the John Day River system. Vol. DE-A179-83BP39796. Oregon Department of Fish and Wildlife, Portland, Oregon.
- Lyons, J. & Kanehl, P. (2002) Seasonal movements of smallmouth bass in streams. In: *Black bass: Ecology, Conservation, and Management*. (Eds D.P. Philipp & M.S. Ridgway), pp. 149-160. American Fisheries Society, Bethesda, Maryland.
- MacRae, P.S.D. & Jackson, D.A. (2001) The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 342-351.
- Martin, R.W. & Petty, J.T. (2009) Local stream temperature and drainage network topology interact to influence the distribution of smallmouth bass and brook trout in a Central Appalachian Watershed. *Journal of Freshwater Ecology*, **24**, 497-508.
- McClure, M.M., Holmes, E.E., Sanderson, B.L. & Jordan, C.E. (2003) A large-scale, multispecies status, assessment: anadromous salmonids in the Columbia River Basin. *Ecological Applications*, **13**, 964-989.

- McCullough, D.A., S. Spalding, D. Sturdevant, and M. Hicks. (2001) Summary of technical literature examining the physiological effects of temperature on salmonids. U.S. Environmental Protection Agency, Issue Paper 5, EPA-910-D-01-005, Seattle.
- Moisen, G.G. (2008) Classification and regression trees. In: *Ecological Informatics*. (Eds S.E. Jorgensen & B.D. Fath), pp. 582-588, Vol. 1.
- Murray, C.B. & Rosenau, M.L. (1989) Rearing of juvenile chinook salmon in nonnatal tributaries of the lower Fraser River, British Columbia. *Transactions of the American Fisheries Society*, **118**, 284-289.
- Olden, J.D., Lawler, J.J. & Poff, N.L. (2008) Machine learning methods without tears: a primer for ecologists. *Quarterly Review of Biology*, **83**, 171-193.
- ORDEQ (2010) John Day River Basin total maximum daily load (TMDL) and water quality management plan (WQMP). p. 167, Portland, Oregon.
- Orth, D.J. & Newcomb, T.J. (2002) Certainties and uncertainties in defining essential habitats for riverine smallmouth bass. In: *Black bass: ecology, conservation, and management*. (Eds D.P. Philipp & M.S. Ridgway), pp. 251-264. American Fisheries Society, Bethesda, Maryland.
- Poe, T.P., Hansel, H.C., Vigg, S., Palmer, D.E. & Prendergast, L.A. (1991) Feeding of predaceous fishes on outmigrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society*, **120**, 405-420.
- Poe, T.P., Shively, R.S. & Tabor, R.A. (1994) Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake Rivers. In: *Theory and application in fish feeding ecology*. (Eds D.J. Stouder & K.L. Fresh & R.J. Feller), pp. 347-359. University of South Carolina, Columbia, South Carolina.
- Poole, G.C. (2002) Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology*, **47**, 641-660.
- Quinn, S. & Paukert, C. (2009) Centrarchid fisheries. In: *Centrarchid Fishes: Diversity, Biology, and Conservation* (Eds S.J. Cooke & D.P. Philipp), pp. 312-339. Wiley-Blackwell Chichester, United Kingdom.
- Raffetto, N.S., Baylis, J.R. & Serns, S.L. (1990) Complete estimates of reproductive success in a closed population of smallmouth bass (*Micropterus dolomieu*). *Ecology*, **71**, 1523-1535.
- Rahel, F.J. & Olden, J.D. (2008) Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, **22**, 521-533.
- Reeves, G.H., Everest, F.H. & Hall, J.D. (1987) Interactions between the redbreast shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon - the influence of water temperature. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 1603-1613.

- Roper, B.B., Scarnecchia, D.L. & La Marr, T.J. (1994) Summer Distribution of and Habitat Use by Chinook Salmon and Steelhead within a Major Basin of the South Umpqua River, Oregon. *Transactions of the American Fisheries Society*, **123**, 298-308.
- Ruckelshaus, M.H., Levin, P., Johnson, J.B. & Kareiva, P.M. (2002) The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics*, **33**, 665-706.
- Ruesch, A., Torgersen, C.E., Lawler, J.J., Olden, J.D., Peterson, E.E., Volk, C. & Lawrence, D.J. (in press) Projected climate-induced habitat loss for salmonids based on a network model of stream temperature. *Conservation Biology*.
- Sanderson, B.L., Barnas, K.A. & Wargo Rub, A.M. (2009) Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? *Bioscience*, **59**, 245-256.
- Schade, C.B. & Bonar, S.A. (2005) Distribution and abundance of nonnative fishes in streams of the Western United States. *North American Journal of Fisheries Management*, **25**, 1386-1394.
- Schlosser, I.J. (1987) The role of predation in age-related and size-related habitat use by stream fishes. *Ecology*, **68**, 651-659.
- Scrivener, J.C., Brown, T.G. & Andersen, B.C. (1994) Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) utilization of Hawks Creek, a small and nonnatal tributary of the upper Fraser River. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1139-1146.
- Sharma, S., Herborg, L. & Therriault, T.W. (2009) Predicting introduction, establishment and potential impact of smallmouth bass. *Diversity and Distributions*, **15**, 831-840.
- Shrader, T. & Gray, M.E. (1999) Biology and management of John Day River smallmouth bass. Oregon Department of Fish and Wildlife. Portland, Oregon.
- Shuter, B.J., Maclean, J.A., Fry, F.E.J. & Regier, H.A. (1980) Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Transactions of the American Fisheries Society*, **109**, 1-34.
- Shuter, B.J. & Post, J.R. (1990) Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society*, **119**, 314-336.
- Tabor, R.A., Footen, B.A., Fresh, K.L., Celedonia, M.T., Mejia, F., Low, D.L. & Park, L. (2007) Smallmouth bass and largemouth bass predation on juvenile Chinook salmon and other salmonids in the Lake Washington basin. *North American Journal of Fisheries Management*, **27**, 1174-1188.
- Tabor, R.A., Shively, R.S. & Poe, T.P. (1993) Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. *North American Journal of Fisheries Management*, **13**, 831-838.

- Torgersen, C.E., Baxter, C.V., Li, H.W. & McIntosh, B.A. (2006) Landscape influences on longitudinal patterns of river fishes: spatially continuous analysis of fish-habitat relationships. *American Fisheries Society Symposium*, **48**, 473-492.
- Torgersen, C.E., Price, D.M., Li, H.W. & McIntosh, B.A. (1999) Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications*, **9**, 301-319.
- Vander Zanden, M.J., Casselman, J.M. & Rasmussen, J.B. (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, **401**, 464-467.
- Vander Zanden, M.J., Olden, J.D., Thorne, J.H. & Mandrak, N.E. (2004) Predicting occurrences and impacts of smallmouth bass introductions in north temperate lakes. *Ecological Applications*, **14**, 132-148.
- Whitledge, G.W., Hayward, R.S. & Rabeni, C.F. (2002) Effects of temperature on specific daily metabolic demand and growth scope of sub-adult and adult smallmouth bass. *Journal of Freshwater Ecology*, **17**, 353-361.
- Whitledge, G.W., Hayward, R.S. & Zweifel, R.D. (2003) Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. *Transactions of the American Fisheries Society*, **132**, 316-325.
- Woodford, D.J., Impson, N.D., Day, J.A. & Bills, I.R. (2005) The predatory impact of invasive alien smallmouth bass, *Micropterus dolomieu* (Teleostei: Centrarchidae), on indigenous fishes in a Cape Floristic Region mountain stream. *African Journal of Aquatic Science*, **30**, 167-173.

Table 1.1 Thermal and discharge characteristics of the North Fork John Day River during the early and late summer surveys in 2009 and 2010.

Season	Year	Survey dates	Average daily temp (°C)		Discharge (m ⁻³ s ⁻¹)
			RKM 52	RKM 105	RKM 24
<i>Early</i>	2009	21-26 June	13.7-20.2	10.0-16.2	21.6-30.0
<i>summer</i>	2010	29 June-5 July	16.0-19.9	13.2-17.0	24.1-34.6
<i>Late</i>	2009	6-11 August	17.4-23.9	15.1-19.3	3.5-11.9
<i>summer</i>	2010	18-23 August	18.5-24.1	15.4-20.8	3.1-3.7

Average daily water temperatures (°C) represent the range in mean temperatures during the survey period at river kilometre (RKM) 52 and 105, corresponding to the downstream and upstream survey extent. Stream discharge (m⁻³ s⁻¹) represents the range in discharge during the survey period. Stream discharge was measured at RKM 24, the site of a USGS long-term flow gauge.

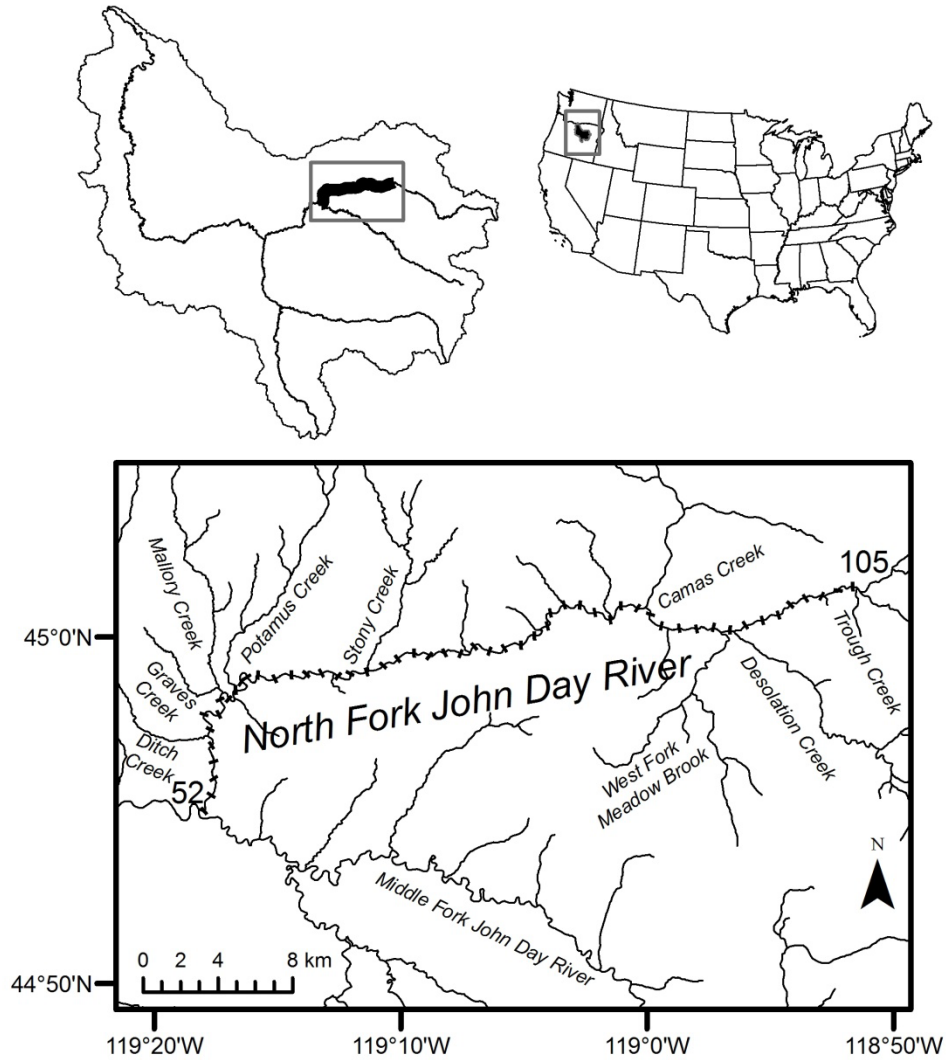


Fig. 1.1

Site map showing the survey extent of the North Fork John Day River (NFJDR) in northeastern Oregon, USA. Surveys were conducted from RKM 52, at the confluence with the Middle Fork John Day River, to Trough Creek at RKM 105. Hatching along the survey extent demarcates 1-km bins used in the reach scale analysis.

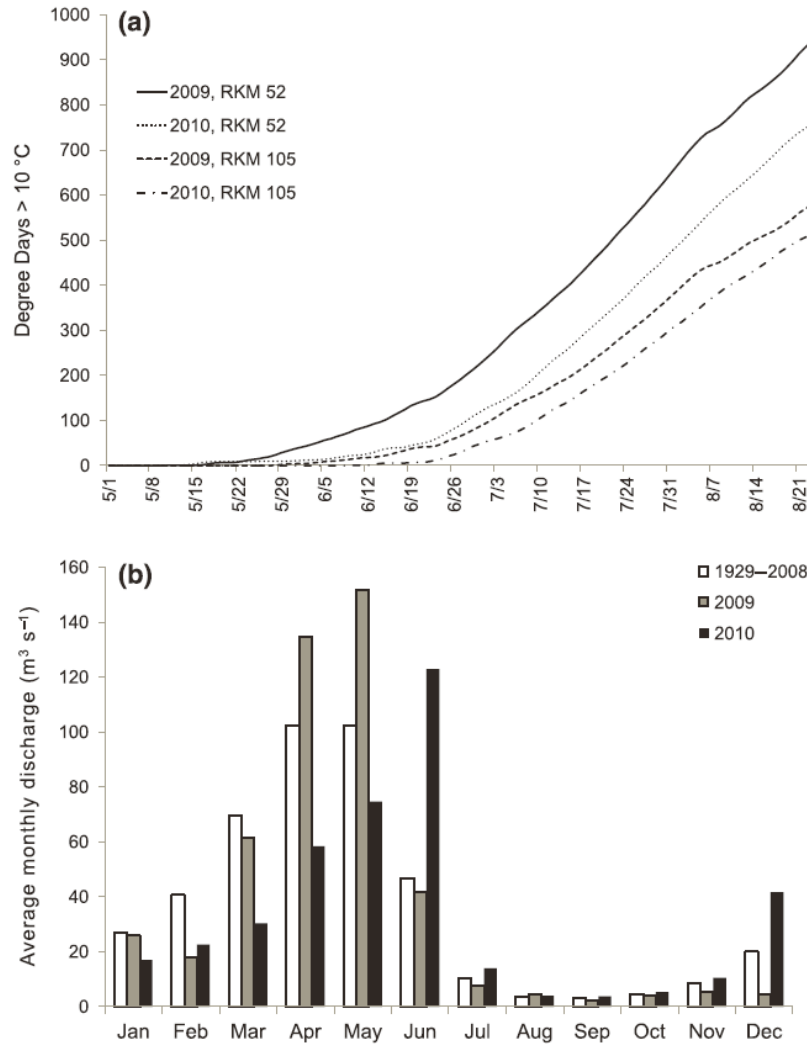


Fig. 1.2

Temperature and discharge conditions of the NFJDR during the survey period. (a) Degree days (DD) > 10° C accumulated from 1 May until 23 August for each survey year at the downstream (RKM 52) and upstream extent of the survey area (RKM 105); (b) Average monthly discharge in 2009 and 2010 compared to the 59-year (1929-2008) monthly mean discharge, measured at a USGS gauge station at RKM 24.

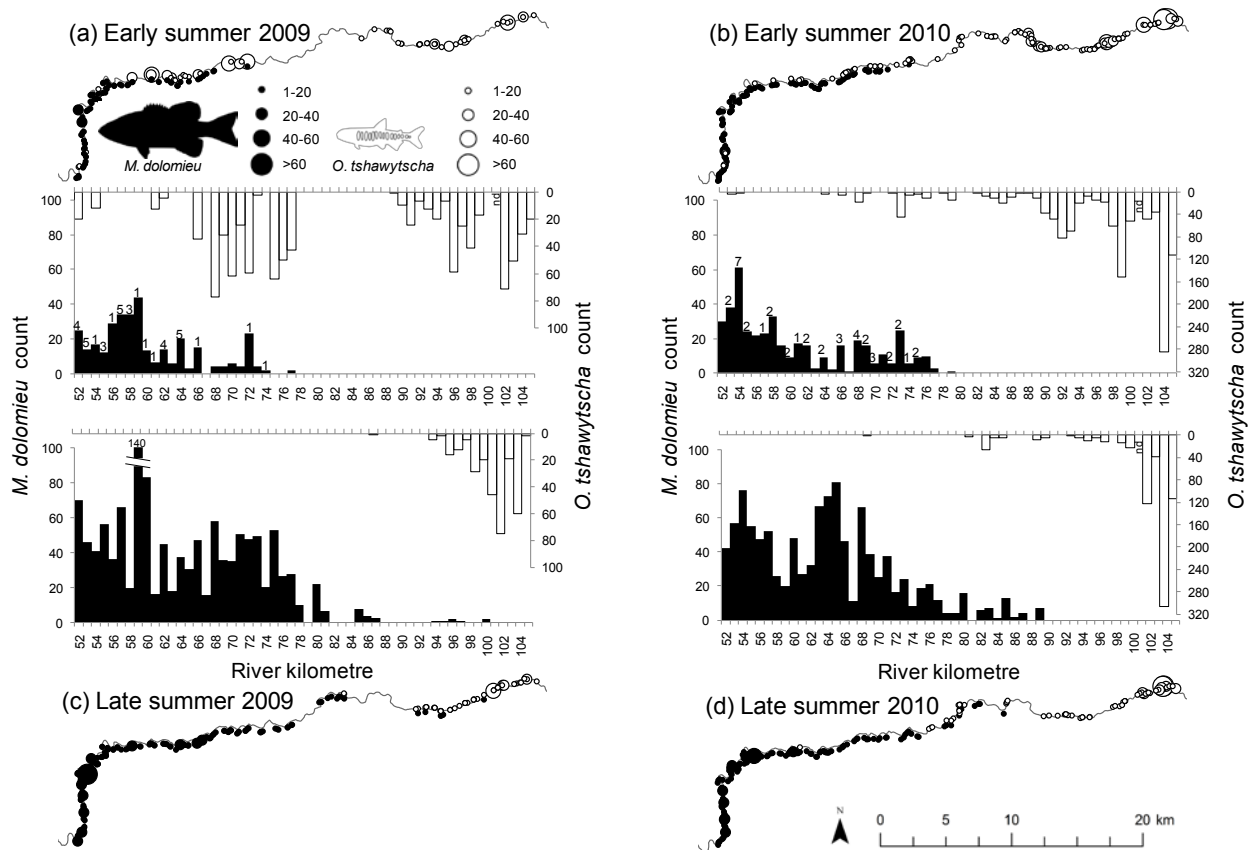


Fig. 1.3

Early and late summer distribution of bass and subyearling Chinook salmon in the NFJDR over the survey extent at channel unit and reach (i.e. 1-km) scales. Circles displayed on the stream hydrography symbolize channel unit counts of bass (filled symbols) and Chinook salmon (open symbols). The symbols are offset from the hydrography to allow for better visualization of channel units in which bass and subyearling Chinook salmon co-occur. Bars represent counts of bass (filled) and subyearling Chinook salmon (open) km⁻¹ at the reach scale. RKM 100 was not surveyed (nd = no data) in June 2009, July 2010 and August 2010. Note that bass were found below the survey extent and subyearling Chinook salmon were found above it. (a) Early summer 2009 bass and Chinook salmon distribution at channel unit and reach scales. Numbers above bass km⁻¹ counts represent the number of bass nests observed km⁻¹. Nest counts were not extrapolated to unsampled areas (see methods); (b) Early summer 2010 bass and Chinook salmon distribution at channel unit and reach scales. Numbers above bass km⁻¹ counts represent the (unextrapolated) number of bass nests observed km⁻¹; (c) Late summer 2009 bass and Chinook salmon distribution at channel unit and reach scales. The axis break at RKM 59 at the reach scale denotes a count of 140 bass km⁻¹; (d) Late summer 2010 bass and Chinook salmon distribution at channel unit and reach scales.

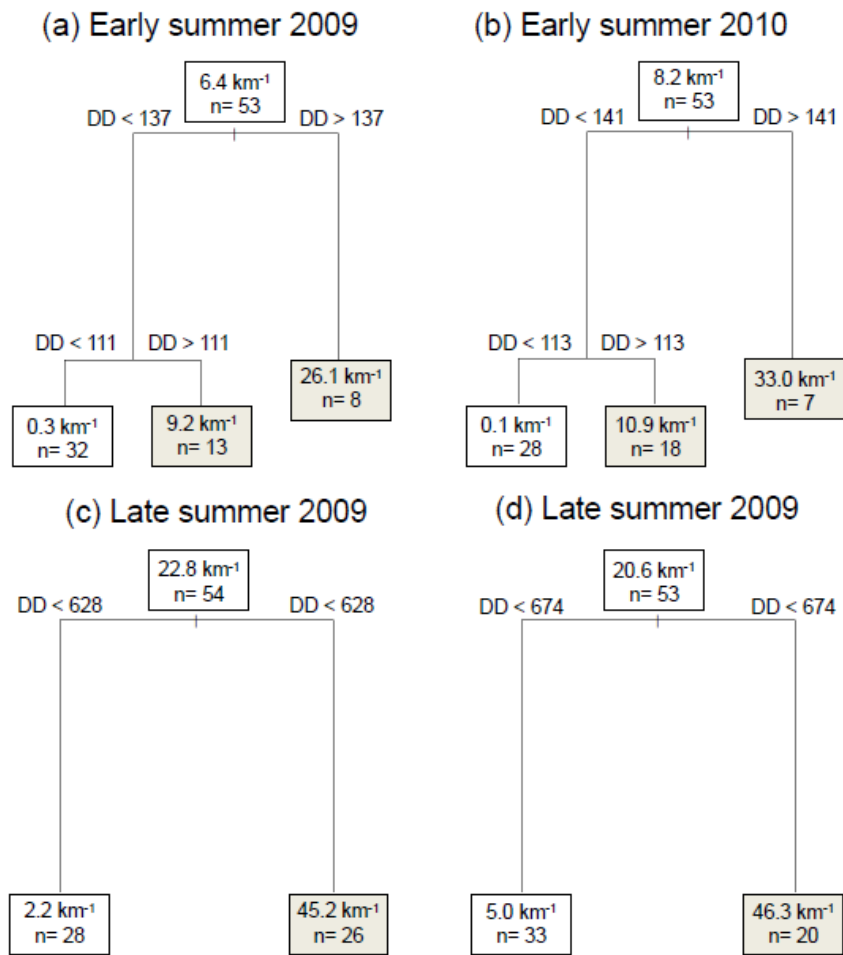


Fig. 1.4

Regression tree analysis of reach (i.e. kilometre) scale bass abundance as a function of the explanatory variables for (a) early summer 2009, (b) early summer 2010, (c) late summer 2009 and (d) late summer 2010 surveys. Parent and terminal (i.e. child) nodes of each tree are represented by a square. The number within each node denotes the mean bass count km⁻¹ and the number (n) of river kilometres (i.e. sample size) in that node. DD = degree days > 10° C. Terminal nodes with grey-fill had greater bass abundance than the global average (i.e. the root node).

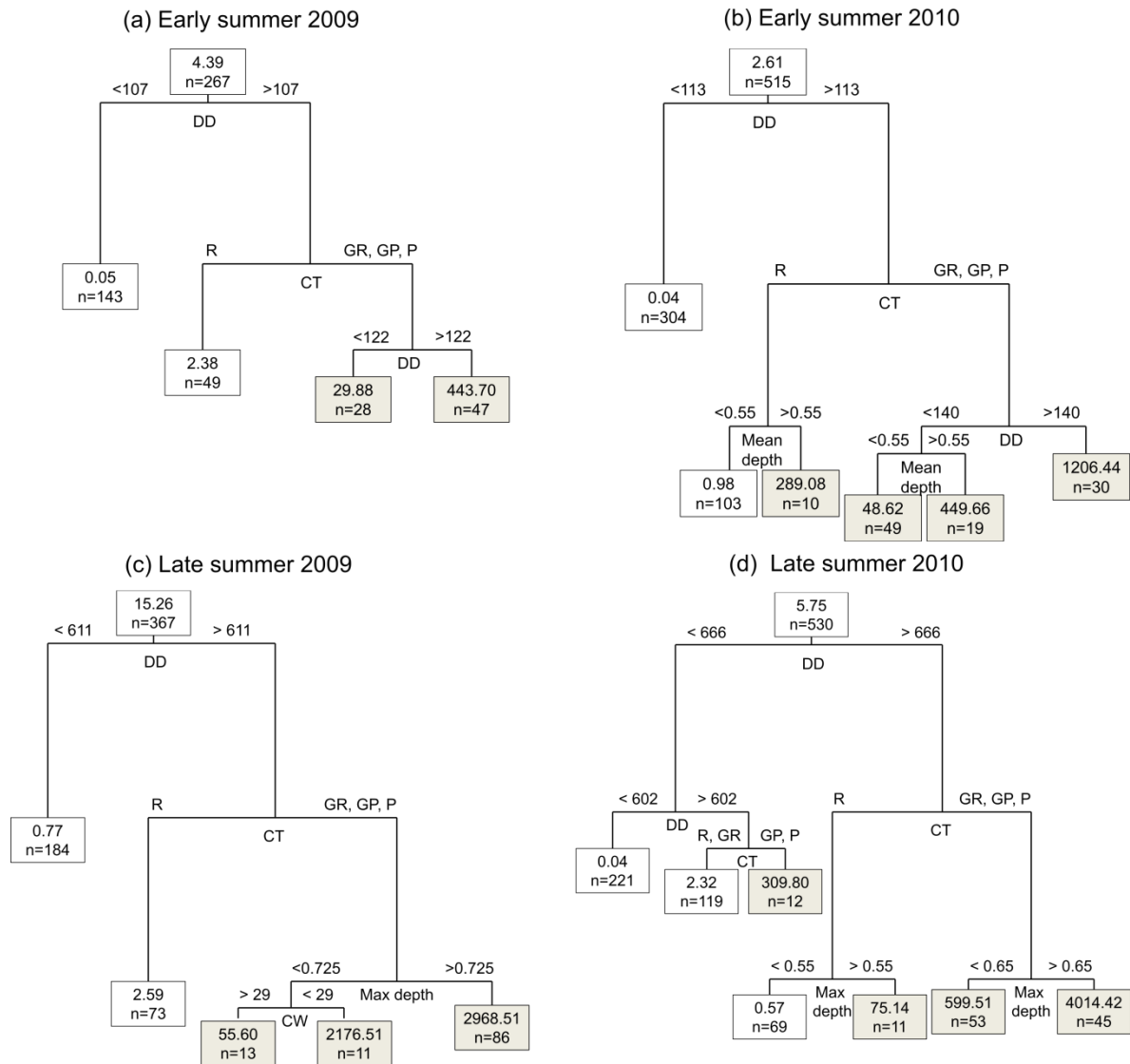


Fig. 1.5

Regression tree analysis of channel unit scale bass density (km^{-2}) as a function of the explanatory variables for (a) early summer 2009, (b) early summer 2010, (c) late summer 2009 and (d) late summer 2010 surveys. Parent and terminal (i.e. child) nodes of each tree are represented by a square. The number within each node denotes the mean bass density (km^{-2}) and the number (n) of channel units (i.e. sample size) in that node. DD = degree days $> 10^\circ \text{C}$; CT = channel unit type, where R = riffle, GR = glide-like riffle, GP = glide-like pool, P = pool; CW = channel width (m); mean and max depth (m). Terminal nodes with grey-fill had greater bass density than the global average (i.e. the root node).

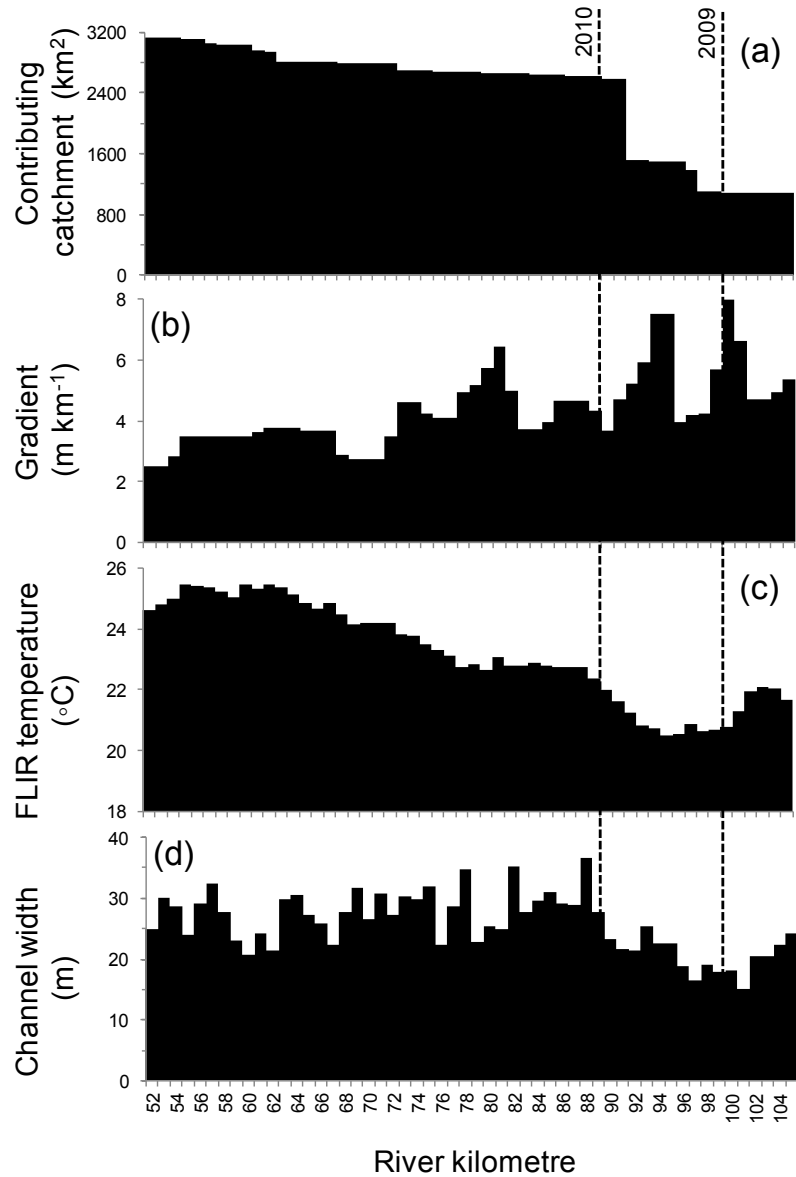


Fig. 1.6

Reach-scale habitat characteristics showing variability over the survey extent of the NFJDR. (a) contributing catchment area of the NFJDR, where large changes in area indicate tributary confluences; (b) gradient over the survey extent; (c) stream temperatures measured using airborne thermal remote sensing conducted at peak temperatures (i.e. early August). This stream temperature profile was formed from a composite of two helicopter flights of the NFJDR with FLIR cameras (ORDEQ, 2010); (d) channel wet widths measured during August 2010 survey. Dashed vertical lines denote the spatial position of the upstream most bass in late summer 2009 and 2010, which corresponded with a relatively large change in contributing area, gradient, remote sensing-based stream temperature and channel width.

CHAPTER 2

THE INTERACTIVE EFFECTS OF CLIMATE CHANGE, RIPARIAN MANAGEMENT, AND A NON-NATIVE PREDATOR ON STREAM-REARING SALMON

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Abstract

Predicting how climate change is likely to interact with myriad other stressors that threaten species of conservation concern is an essential challenge in aquatic ecosystems. This study provides a framework to accomplish this task in salmon-bearing streams of the northwestern United States, where land-use related reductions in riparian shading have caused changes in stream thermal regimes, and additional warming from projected climate change may result in significant losses of coldwater fish habitat over the next century. Predatory non-native smallmouth bass have also been introduced into many northwestern streams and their range is likely to expand as streams warm, presenting an additional challenge to the persistence of threatened Pacific salmon. The goal of this work was to forecast the interactive effects of climate change, riparian management, and non-native species on stream-rearing salmon, and to evaluate the capacity of restoration to mitigate these effects. We intersected downscaled global climate forecasts with a local-scale water temperature model to predict mid- and end-of-century temperatures in streams in the Columbia River basin; we compared one stream that is thermally impaired due to the loss of riparian vegetation and another that is cooler and has a largely intact riparian corridor. Using the forecasted stream temperatures in conjunction with fish-habitat models, we predicted how stream-rearing Chinook salmon and bass distributions would change as each stream warmed. In the highly modified stream, end-of-century warming may cause near total loss of Chinook salmon rearing habitat and a complete invasion of the upper watershed by bass. In the less modified stream, bass were thermally restricted from the upstream-most areas. In both systems, temperature increases resulted in higher predicted spatial overlap between stream-rearing Chinook salmon and potentially predatory bass in the early summer (2-4-fold increase) and greater abundance of bass. We found that riparian restoration could prevent the

extirpation of Chinook salmon from the more altered stream, and could also restrict bass from occupying the upper 31 km of salmon rearing habitat. The proposed methodology and model predictions are critical for prioritizing climate-change adaptation strategies before salmonids are exposed to both warmer water and greater predation risk by non-native species.

Introduction

Global climate change and a complex amalgam of other environmental stressors threaten to undermine the structure and function of freshwater ecosystems (Woodward et al. 2010). In stream systems, climate-related increases in water temperatures have already been widely observed (Kaushal et al. 2010, Isaak et al. 2012) and both the rate and magnitude of warming is predicted to increase as air temperatures rise over the next century (Mote and Salathé 2010). Many streams are already highly altered by land-use related removal of riparian vegetation that reduces stream shade and water use for irrigation that lowers flow, both of which make streams more susceptible to warming. As a result, elevated water temperature is one of the foremost water quality problems for rivers in the United States, and there are mounting concerns that climate-related warming will further intensify this problem (USEPA 2002).

Climate-related stream warming will have direct, and in some cases, dramatic effects on populations of coldwater organisms such as salmon, many of which are already considered threatened or endangered as a result of a variety of human-related stressors (Ruckelshaus et al. 2002). Many salmonid species are expected to lose significant portions of their current distributions as thermally suitable habitat declines (Ruesch et al. 2012). For example, climate change-induced stream warming is projected to result in the loss of almost half (47%) of thermally suitable habitat for all trout in the interior western United States (Wenger et al. 2011).

Salmon populations in increasingly warmer streams exist in fragmented systems that limit movement to thermally favorable environments. Habitat fragmentation may also prevent ‘rescue’ effects from other, more stable, populations if parts of stream networks become unsuitable for migration (Rieman et al. 2007). The ultimate consequences of stream warming for salmon populations will vary by species and region, but the most dramatic effects are likely to be observed in areas that form the southern periphery of their range where even small amounts of climate warming may push temperatures above the thermal tolerances of these species (Mantua et al. 2010, Beer and Anderson 2011).

Beyond the direct effect of thermally stressful temperatures, salmon must also cope with non-native species including warm-water predators that will expand into salmon rearing areas as streams warm. However, with the exception of Wenger et al. (2011), most investigations of climate change impacts on salmon have not considered fish community interactions, or the potential interactive effects of invasive species and stream warming on salmon populations (Rahel and Olden 2008). Smallmouth bass (*Micropterus dolomieu*; bass hereafter), a predatory non-native fish species that has been introduced throughout the range of salmon in the Pacific Northwest (Carey et al. 2011), may be particularly problematic for salmon populations faced with climate-warmed streams. Bass can consume large proportions of salmon runs (up to 35%) under certain conditions, such as when small subyearling Chinook salmon (*Oncorhynchus tshawytscha*) co-occur with bass when water temperatures are warm enough to make bass metabolically active (Fritts and Pearsons 2004, Sanderson et al. 2009). Projections of bass range expansion under scenarios of climate change have only been completed for lake-dwelling bass (Sharma et al. 2009), and although bass occupy many salmon-bearing rivers, no previous study has forecast the upstream range expansion of stream-dwelling bass as streams warm. Although

bass are generally considered a warm-water fish compared to salmon, our previous research has documented that bass and subyearling Chinook salmon co-occur where upstream migrant bass overlap with the downstream range of stream-rearing Chinook salmon (Lawrence et al. 2012). In situations where these species overlap, bass may prey on stream-rearing salmon directly, or cause sublethal effects such as reductions in the growth of subyearling salmon resulting from stress and the use of sub-optimal habitats when bass are present (Kuehne et al. 2012).

In a changing climate, watershed managers are faced with the challenge of translating broad-scale climate projections into anticipated local changes to determine where restoration actions could be undertaken to reduce potential impacts on salmon populations (Naiman et al. 2012). Translating regional climate forecasts to local scale predictions is a re-occurring need, and the gap between these scales leaves many managers with little guidance on how to adapt their present-day management efforts to climate change. Low-risk actions can be undertaken in the face of such uncertainty that would benefit a given system even if climate change forecasts are not ultimately realized (Lawler et al. 2010, Rieman and Isaak 2010). Ultimately, managers need (1) a way to quantify how climate change may affect watersheds at multiple scales, and (2) decision tools to evaluate management actions that can offset the effects of future stream warming.

To bridge the science-management gap and gain knowledge of the interactive effects of multiple stressors in freshwater ecosystems, we studied how non-native smallmouth bass, riparian land-use, and climate change will act together to affect an evolutionary significant Chinook salmon population in the John Day River (JDR) Basin, a tributary of the Columbia River. To accomplish this task we combined downscaled regional climate change forecasts of air temperature and streamflow with a fine-scale stream temperature model to determine future

thermal regimes of streams in the JDR for mid- and end-of-century time periods. The stream temperature forecasts in turn were input to statistical fish-habitat models, developed from data within the study area, to forecast how habitat will change for stream-rearing salmon and to predict the upstream spread of non-native bass into salmon habitat. We also explored the ability of riparian vegetation restoration to reduce climate-related warming in the JDR basin, and, in turn provide the dual conservation benefit of (1) maintaining rearing-habitat for salmon in the face of stream warming, and (2) limiting the upstream invasion of predatory bass into salmon rearing areas.

Methods

Study area

This study was conducted in the North Fork (NFJDR) and Middle Fork (MFJDR) tributaries of the JDR (21,000 km² basin area), which collectively drain 6,800 km² and originate in the Blue Mountains of north-eastern Oregon (Fig. 2.1). The JDR is of high conservation importance because it is one of the largest free-flowing rivers in the interior Columbia River Basin. Both tributaries receive precipitation predominantly in the form of snow and rain in November through May. Snow melt in late spring, typically peaking in April and May, causes high flows in the JDR basin that decline over June and July until the low flow summer period that occurs from August through September. Air temperatures within the study area range from winter lows of -18° C to summer highs exceeding 30° C.

The NFJDR and MFJDR provide contrasting thermal conditions that allow for an assessment of the responses of subyearling Chinook salmon and bass to climate and land-use induced changes in stream temperatures. The NFJDR is a relatively cool system that flows

through colluvial and alluvial canyons to alluvial valleys with gradients up to 30 m km^{-1} (3.00%) in the upper basin to 2.4 m km^{-1} (0.24%) in the lower section of the study area at elevations from 662 m (at the confluence of the MFJDR) to 1691 m. The MFJDR is a tributary of the NFJDR and is warmer and less steep; it flows through alluvial canyons and valleys with a maximum gradient of 15 m km^{-1} (1.50%) in the upper river to 0.6 m km^{-1} (0.06%). Elevations within the MFJDR study region are 662-1245 m. Summer baseflow in both systems is provided by snowmelt fed springs, which persist longer into the summer in the NFJDR. Although both tributaries have been altered due to land use and resource extraction, the riparian corridor of the NFJDR is largely intact because the North Fork John Day Wilderness Area and the Umatilla National Forest protect the upper NFJDR. Land adjacent to the lower NFJDR has experienced some removal of riparian vegetation due to livestock grazing. By contrast, land adjoining the MFJDR is mostly privately owned and has experienced significant riparian vegetation removal by grazing cattle; many parts of the river are wide and shallow as a result of bank erosion. Private landowners, the Nature Conservancy, the Confederated Tribes of the Warm Springs Nations, the Malheur National Forest, and the Oregon Department of Parks and Recreation are currently engaged in restoration projects to re-vegetate and re-meander parts of the upper MFJDR.

Fish populations in the NFJDR and MFJDR

The JDR supports the largest entirely wild run of Chinook salmon in the Columbia River basin, and may serve as a source to Chinook populations in the lower main stem Columbia River that are listed as threatened under the U.S. Endangered Species Act. Spring Chinook salmon spawn in the upper NFJDR and MFJDR and their offspring rear in these streams during their first year of life as subyearlings. The rearing and spawning habitat of Chinook salmon has been

increasingly constrained to the upper basins of both rivers due to thermal alterations related to land use (e.g., riparian vegetation removal) and water withdrawals for irrigation. Water temperatures throughout the NFJDR and MFJDR are often at or near the thermal tolerances for Chinook salmon (Torgersen et al. 1999). Particularly warm years, such as 2007 and 2013, have caused mass-mortality of adult Chinook salmon that hold in pools of the MFJDR when maximum water temperatures exceed 28°C (e.g., 2007) or water temperature increases rapidly (e.g., 2013).

At the downstream end of their distribution in the NFJDR and MFJDR, subyearling Chinook salmon seasonally overlap with non-native bass (Lawrence et al. 2012). Bass were introduced to the lower NFJDR in 1971 (Shrader and Gray 1999), but have subsequently moved upstream in both the NFJDR and the MFJDR. Bass move upstream and enter the lower (i.e., downstream) rearing areas of subyearling Chinook salmon when water temperatures warm from June to August.

Modeling framework

We linked a series of models to predict the distribution of bass and subyearling Chinook salmon in response to stream warming caused by global climate change. First, we used global climate change forecasts of air temperature and stream flow, downscaled to our study region as inputs into a local-scale water temperature model. This water temperature model was used to generate future forecasts of stream temperatures that were then input to bass and subyearling Chinook salmon distribution models, which were based on observed fish-temperature relationships in the JDR basin. Our forecasts of future fish distributions were based on these relationships because water temperature determines the seasonal distribution of bass and

Chinook salmon in the JDR basin (Lawrence et al. 2012). Details on each of the individual models that compose this framework are provided below.

Stream temperature modeling

We used the mechanistic stream temperature model Heat Source (Version 8.0.8, Boyd and Kasper 2003) to forecast stream temperatures resulting from climate change and various riparian vegetation restoration scenarios. This model uses high-resolution spatially continuous landscape data, coupled with deterministic mass and heat transfer processes to simulate water temperatures and flow dynamics. The Oregon Department of Environmental Quality (ORDEQ) produced a calibrated Heat Source temperature model of the NFJDR and MFJDR as part of a total maximum daily load (TMDL) assessment (ORDEQ 2010a). We employed the ORDEQ model but changed the air temperature inputs and boundary conditions (i.e., headwaters and tributary stream temperature and flow) to reflect downscaled climate change predictions for these variables. Details on generating future air temperature and boundary condition forecasts in a form suitable for input to the Heat Source model are provided in Appendix A. All other variables were unchanged from the calibrated model (e.g., we assumed no change in riparian condition in response to changing flow). We chose to use Heat Source to model stream temperatures because it accounts for the spatially explicit role of vegetative shading in the determination of stream temperature, as well as the conditions upstream of each temperature prediction point. This allowed us to apply spatially explicit vegetation restoration scenarios to determine the capacity for management activities to offset stream warming caused by climate change.

Climate data

Climate forecasts were derived from the Parallel Climate Model, Version 1 (PCM1) general circulation model (GCM), which was used because it exhibited low bias for simulating observed climate for the region (Littell et al. 2011). We modeled a mid-range forecast from 2030-2059 (hereafter referred to as the ‘2040’ period), and an end-of-century period ranging from 2070-2099 (i.e., the ‘2080’ period). For each period, the PCM1 GCM was run with a middle-of-the-road A1B greenhouse gas emission scenario (IPCC 2007). GCM projections were downscaled to a $1/16^\circ$ resolution (~ 6 km) and a daily forecast using the spatially explicit delta method (Littell et al. 2011). This method extracts the historical variability in air temperature and precipitation and applies that variability to the future climate prediction. Downscaled PCM1 flow forecasts for NFJDR and MFJDR tributaries and the upstream boundary conditions were produced with a Variable Infiltration Capacity model provided by Wenger et al. (2011) and Hamlet et al. (2010; details in Appendix A). Forecasts of daily boundary condition water temperatures were produced by parameterizing an independent non-linear regression model relating forecasted air temperature to stream temperature at each model boundary (Appendix A). To compare future projections of warming to the present period, we calculated daily air temperatures and boundary conditions (i.e., water temperature and flow) over the 30-year period from 1977-2006. This period was chosen because it constrained the description of climate to the most current Pacific Decadal Oscillation shift that occurred in 1977 (Hamlet et al. 2007). Future climate predictions were calculated as daily means with the same variability that was observed in the present condition (i.e., 1977-2006).

Model domains in space and time

For the NFJDR, the model domain encompassed 120 river kilometers (RKMs), starting just above the confluence of the MFJDR with the NFJDR (RKM 53) to Baldy Creek (RKM 172) (Fig. 2.1). The model domain of the MFJDR contained 102 RKM, starting at RKM 12 and extending to RKM 113. These areas were chosen because they include the upstream extent of bass within each basin (Lawrence et al. 2012) and extend upstream where bass do not currently reside but may move as a result of climate-induced stream warming. Stream temperature was modeled from June 15 to August 31 in the NFJDR and May 1 to October 31 in the MFJDR. The calibrated NFJDR model period was shorter due to ORDEQ time constraints when they originally developed the models (ORDEQ 2010a).

Stream temperature model output

We used a custom R script (version 2.13.0, R Development Core Team) to convert the Heat Source water temperature output (generated at an hourly time step every 200 m along the stream) to mid- and end-of-century 7-day-average-daily (7DAD) mean water temperatures at a reach (1 km) scale in early and late summer. We modeled early and late summer distributions of bass and subyearling Chinook salmon because these periods captured both the period of high-potential overlap (i.e., early summer) and high-potential for bass upstream movement (i.e., late summer; Lawrence et al. 2012). These periods also provided a contrast in temperature and flow conditions; during the early summer period (i.e., late June), the tributaries were on the declining limb of the snowmelt hydrograph, and thus discharge was high and water temperature was cool. In the late summer (i.e., early August), the streams were at base flow and usually at or near their peak water temperatures.

Watershed restoration scenarios

We investigated a range of restoration scenarios to determine the potential to mitigate climate-induced stream warming, limit the range expansion of bass, and minimize habitat loss for rearing Chinook salmon within the JDR basin. The restoration approaches currently pursued in the basin (and in many river systems throughout the Pacific Northwest) include active or passive riparian restoration. Active restoration involves the re-planting of overgrazed vegetation, whereas passive restoration is conducted by fencing off the riparian corridor to prevent livestock from grazing there and to allow the natural recruitment and re-growth of vegetation. The Heat Source model accounts for the spatially explicit role of vegetative shading in the heat balance equation of the stream, and therefore, allowed us to simulate vegetation re-growth on the landscape and then determine its potential to cool the stream. Current vegetation was mapped every 50 m along the riparian corridor of the NFJDR and MFJDR from remote sensing imagery by ORDEQ as part of the Heat Source modeling process. The resulting GIS layer described the height of vegetation and its density, as well as its spatial position within 100 m of the river channel. An automated spatial analysis program sampled the vegetation layer to extract input for the Heat Source model including vegetation height, basal elevation, density and proximity to the stream (ORDEQ 2010a). Heat Source uses this information to determine the amount of shade that riparian vegetation provided every hour at each model distance step over the model temporal domain, accounting for the sun's position and shading provided by topography (e.g., canyons), termed 'effective shade'. ORDEQ (2010a) also estimated the 'potential' vegetation along the riparian corridor of the NFJDR and MFJDR, i.e., the vegetation that would be present without human and livestock impacts. The process of estimating potential vegetation is summarized in

Appendix C and full details of the restored vegetation characteristics are described in ORDEQ (2010b).

Because complete restoration of the riparian corridor is unlikely, we tested restoration of riparian habitat across a range of management scenarios. To prioritize those areas of the river that should be restored first, we ran the Heat Source model using the current vegetation configuration and in the fully restored condition, and then calculated the difference (i.e., the ‘potential effective shade’) between shade provided under the current condition of the riparian corridor and the shade provided under a fully restored vegetation scenario. Potential effective shade was determined on July 15, the warmest day of the model calibration year (2002). In an effort to compare realistic restoration segment sizes, we aggregated the 50-m reaches into 600-m segments, which are typical of fencing projects in the basin based on 91 projects from 1984-2008 (Powell et al. 2008). These restoration segments were compared by averaging the potential effective shade across the twelve finer scale (50 m) reaches that composed the broader segment, and then segments were arranged from high to low in terms of their potential to increase the shade of the stream. The area encompassing the North Fork John Day Wilderness area (RKM 120.3-164.1) has relatively un-impacted vegetation, and therefore was not considered for potential restoration within this study. This aggregation scheme resulted in a total of 129 segments in the NFJDR and 169 segments in the MFJDR. We ran scenarios where we restored the top 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100% of restoration segments, and we compared the thermal profile of the river under these different scenarios in the 2080s. Additionally, we compared the potential to reduce warming as a result of climate change given a more ‘opportunistic’ restoration scenario by randomly choosing the same percentages of segments without regard for their potential effective shade. This method simulated restoration that is

conducted where it is feasible due to land availability or other social constraints. Although it would have been desirable to prioritize restoration by running all potential combinations of restoration segments and determining those combinations that would most effectively lower the stream temperature, the run time of the model (3-5 hours) and number of potential simulations (the factorial of 129+169 segments) were not feasible with our computing resources.

Fish distribution models

Bass and subyearling Chinook salmon distribution models were built based on fish and habitat surveys conducted in late June and early August of 2009 (MFJDR and NFJDR) and 2010 (NFJDR only; Lawrence et al. 2012). Lawrence et al. (2012) revealed that bass abundance in the study area had a positive non-linear relationship to water temperature at a broad scale, and if satisfactory temperatures were available, greater water depths were (linearly) associated with greater bass abundance. For this study, we built a Bayesian hierarchical model to quantify this hierarchical habitat selection at two spatial scales. At a broad “segment” scale, we used temperature as a predictor of bass abundance, and within segments, we used depth as a predictor at a finer 1 km “reach” scale.

We delineated the two spatial scales using constrained hierarchical clustering, which is similar to ordinary hierarchical clustering with the additional constraint that objects can only be agglomerated if they are contiguous (Gordon and Birks 1972). The goal was to define segments (3 km in length or greater) that contained reaches (defined here as 1 km) with similar geomorphic and thermal characteristics. Clustering of individual (1 km) reaches into segments was based on contributing watershed area (m^2), average channel width (m), and average stream temperature, as measured from airborne thermal infrared (TIR) remote sensing (Torgersen et al.

2001). The TIR dataset was provided by ORDEQ (2010a), and represents approximate maximum summer temperature. The TIR dataset was employed because it captured small scale spatial variation in surface water temperature (e.g., thermal anomalies associated with springs, groundwater input, and hyporheic exchange). Watershed area was determined from Netmap (www.netmaptools.org). Channel width was measured in August 2010 during the fish distribution survey (Lawrence et al. 2012). Clustering was carried out based on a column-standardized Euclidean distance matrix calculated with the CONISS agglomerative clustering method (Grimm 1987) in R with the *rioja* package (Juggins 2012). Segments in the NFJDR ($n = 10$) and MFJD ($n = 9$) ranged in length from 3 to 10 km and were defined according to spatial patterns in channel geomorphology (e.g., channel width and major tributary confluences) and stream temperature.

The hierarchical model for bass abundance had a non-linear model to quantify the segment-scale relationship with temperature and a linear model to quantify the reach-scale relationship with depth. At the reach-scale, estimated abundance was assumed to follow a Poisson distribution, and the rate parameter was a linear function of mean abundance in the segment and the average maximum depth:

$$y_{ij} \sim \text{Poisson}(\lambda_{ij})$$

$$\lambda_{ij} = \bar{y}_j + \beta \times \text{depth}_{ij}$$

where y_{ij} is the observed bass abundance in the i th reach of the j th segment, λ_{ij} is the rate parameter of the Poisson distribution, \bar{y}_j is the mean abundance at the j th segment, and β quantifies the relationship between reach-scale (average maximum) water depth and deviations from the segment mean abundance. Reach-scale depth, depth_{ij} , was mean centered within each

segment. At the segment scale, mean bass abundance was assumed to be normally distributed, dependent on segment-scale water temperature. The relationship between bass abundance and temperature at the segment-scale was estimated using a logistic equation:

$$\bar{y}_j \sim N(\mu_j, \tau_y)$$

$$\mu_j = \frac{K}{1 + n_0 \times e^{-r \times temp_j}}$$

where \bar{y}_j is the mean abundance at segment j ; μ_j and τ_y are the mean and precision of the normal distribution, respectively; K , n_0 , and r are the parameters of the logistic equation; and $temp_j$ is the average 7DAD mean temperature of all reaches within segment j . Temperature data were derived from water temperature loggers deployed during the fish surveys over the model longitudinal extent (Lawrence et al. 2012) and were centered based on the mean and scaled by the standard deviation across the study region. We choose to model the 7DAD mean because it represents the central tendency of temperature and is biologically relevant to bass and subyearling Chinook (see model below). Based on data from temperature loggers, we found that 7DAD maximum and minimum were highly correlated with the 7DAD mean at the 1 km scale. The following ‘uninformative’ prior distributions were used to specify the likelihood structure (Gelman et al. 2004):

$$\begin{array}{ll} \beta \sim N(0, \tau_\beta) & \tau_y \sim \Gamma(1, 0.1) \\ \tau_\beta \sim \Gamma(1, 0.1) & K \sim \Gamma(2, 0.5) \\ n_0 \sim \Gamma(2, 0.5) & r \sim \Gamma(2, 0.5) \end{array}$$

The model was fit in WinBUGS Version 1.4.3 (Lunn et al. 2000) called from R with the R2WinBUGS package (Sturtz et al. 2005). Separate early summer and late summer models were developed to describe the relationship between bass and temperature. Each model had the same

structure (as described above) but was fit with data collected from early and late summer bass distribution surveys (Lawrence et al. 2012). Model performance was measured using pseudo- R^2 values, which were 0.73 for the early summer model, and 0.71 for the late summer model. No spatial autocorrelation was detected in the model residuals. To predict the future spatial distribution of bass, we used the 7DAD mean water temperatures forecasted for early and late summer of the 2040s and 2080s in the fitted Bayesian hierarchical model, and then obtained the median of the posterior predictive distribution of bass abundances per reach (e.g., Boone et al. 2012).

To forecast how the availability of salmon rearing habitat in the NFJDR and MFJDR may change by the 2040s and 2080s, we fitted a model to relate subyearling Chinook salmon distribution to stream temperature. The subyearling Chinook salmon model was based solely on temperature. Therefore, we used logistic regression (Hosmer and Lemeshow 2000) with 7DAD mean water temperature to develop a species distribution model at the reach scale (1 km) that used observations of subyearling Chinook salmon in the JDR basin from Lawrence et al. (2012). The model fit in R had an area-under-the-curve (of the receiver operator characteristic curve) of 0.89. Unlike the bass model, where we fit separate early and late summer models, we fit only one subyearling Chinook salmon model with data from late summer. In this case, we were primarily interested in defining thermally suitable habitat for subyearling Chinook salmon, but water temperatures in the early summer surveys (i.e., in 2009 and 2010) were not warm enough to observe thermal restrictions in their distribution. However, we postulated that early summer temperatures in 2040 and 2080 may be warm enough to restrict subyearling Chinook salmon from occupying parts of the NFJDR and MFJDR. To predict the future spatial distribution of subyearling Chinook salmon in early and late summer, we applied stream temperature forecasts

to the fitted regression model and reported the probability of salmon presence over the longitudinal extent of the models.

Results

Water temperatures in both of the studied tributaries are forecast to increase as air temperatures rise and discharge changes over the next century. The 7DAD mean water temperature of the NFJDR in the early summer is forecasted to increase 1.2° C by 2040 and 2.3° C by 2080 (averaged over the longitudinal profile of the river, relative to the 30-year norm of temperatures in the current condition; Appendix B). In the late summer, 7DAD means in the NFJDR are projected to increase 1.5° C by 2040 and 2.0° C by 2080. Forecasted 7DAD mean water temperatures of the MFJDR exceed estimates for the NFJDR. An average increase of 1.6° C by 2040 and 3.2° C by 2080 is predicted for the MFJDR in the early summer, and increases of 1.1° C by 2040 and 1.7° C by 2080 are predicted in the late summer.

Bass abundance and upstream extent

As stream temperatures warm, bass are predicted to move upstream in both the NFJDR and MFJDR relative to their distribution in 2009 (Figs. 2.2 and 2.3). For example, the upstream extent of bass in the NFJDR in early summer was RKM 76.7 (modeled = 75, Fig. 2.2A) but is forecast to increase to RKM 91 by 2040 (Fig. 2.2B) and RKM 114 by 2080 (Fig. 2.2D). Bass upstream extent increased between early and late summer in 2009 (from RKM 76.7 to 99.7; modeled = 96; Fig. 2.2A, F), and similarly, bass are forecasted to move farther upstream in the late summer period as the stream warms. By 2040, bass are forecasted to move an additional 29 km upstream (to RKM 125 compared to RKM 96; Fig. 2.2G) in the late summer; by 2080, bass are predicted to move up to RKM 132 (a total of 36 km compared to the 2009 modeled upstream

extent; Fig. 2.2I). Larger increases in upstream distribution are forecasted for the MFJDR where the entire upstream extent of the river is forecasted to be thermally suitable for bass by 2040 in both early and late summer (Fig. 2.3B, G). This represents an overall increase in upstream extent of 67 km in the early summer and 48 km in the late summer by 2040.

In both systems, bass abundance is predicted to increase in 2040-2080 (Figs. 2.2 and 2.3). In the NFJDR, 2080 forecasts of early summer abundance of bass are at or near carrying capacity (K in the model) in 38 km (RKM 53-90; Fig. 2.2D), and late summer bass abundance is variable but near carrying capacity in 62 km (RKM 53-114; Fig. 2.2I). The early summer forecast of bass abundance for 2080 in the MFJDR shows a similar trend; however, bass reach the carrying capacity over a longer stretch of river (97 km; RKM 12-108; Fig. 2.3D) due to higher forecasted water temperatures. In late summer, bass abundance is near carrying capacity in 69 km in 2080 (RKM 12-80; Fig. 2.3I).

Probability of subyearling Chinook salmon presence

The probability of subyearling Chinook salmon presence is negatively related to water temperatures. Therefore, as water temperatures increase, the availability of Chinook salmon rearing space decreases. In both seasons and both tributaries, subyearling Chinook salmon are forecasted to have a lower probability of presence by the 2040s and 2080s (Figs. 2.2 and 2.3). In the NFJDR, the probability of presence in the early summer remains high ($p > 0.8$) by the 2040s (Fig. 2.2B), and this is sustained by the 2080s, although their probability of presence is somewhat reduced below RKM 90 (Fig. 2.2D). In the contemporary climate (i.e., 2009), the rearing space available to subyearling Chinook salmon decreased between early and late summer as a result of seasonal warming (Fig. 2.2A, F), but this seasonal reduction is greater in 2040 and

2080 (Fig. 2.2B vs. G; 2.2D vs. I). If we define thermally suitable habitat for subyearling Chinook salmon as areas where their probability of presence is ≥ 0.5 (which corresponds to 19.5°C in our model), then thermally suitable habitat in the NFJDR during late summer occurs upstream of RKM 98 in 2009 (Fig. 2.2F), RKM 126 in 2040 (Fig. 2.2G), and RKM 132 in 2080 (Fig. 2.2I).

The MFJDR is warmer than the NFJDR (Appendix B) and currently has a lower probability of subyearling Chinook salmon presence. However, the additional warming forecasted for 2040 and 2080 may result in an even greater loss in rearing habitat in the MFJDR (Fig. 2.3). In the early summer, thermally suitable habitat for subyearling Chinook salmon is found throughout the MFJDR in 2009 (RKM 12-112; Fig. 2.3A) but only occurs upstream of RKM 26 in 2040 (Fig. 2.3B) and RKM 73 in 2080 (Fig. 2.3D). In late summer, thermally suitable Chinook salmon habitat occurs upstream from RKM 57 in 2009 (Fig. 2.3F) but only occurs in 4 km by the 2040s (RKM 96-99; Fig. 2.3G) and in 0 km by the 2080s (Fig. 2.3I). In 2009, the probability of occurrence for subyearling Chinook salmon in late summer was greater than 0 throughout the MFJDR (Fig. 2.3F), whereas by 2080, probability of presence exceeded 0 only in the upper 33 km of the MFJDR in the late summer, with a maximum probability of 0.38 (Fig. 2.3I).

Bass and subyearling Chinook salmon overlap

As water temperatures warm by 2040 and 2080, the overlap between bass and subyearling Chinook salmon may increase substantially in the early summer (Figs. 2.2B, D and 2.3B, D), but may show only limited change in the late summer (Figs. 2.2G, I and 2.3G, I). If overlap is defined as 1-km reaches where bass abundance ≥ 1 and the probability of subyearling

Chinook salmon presence is ≥ 0.5 , then the total early summer overlap between bass and Chinook salmon in the NFJDR may nearly double from 23 km in 2009 to 39 km by 2040, and nearly triple to 62 km by 2080. In the MFJDR, early summer overlap between bass and subyearling Chinook salmon may nearly quadruple from 23 km in 2009 to 86 km by 2040, but then may decrease to 40 km by 2080, as the distribution of subyearling Chinook salmon becomes constrained to the upper river.

As was observed in 2009 (Figs. 2.2F and 2.3F), late summer overlap between bass and subyearling Chinook salmon by 2040 and 2080 is minimal in the NFJDR (Fig. 2.2G, I) and the MFJDR (Fig. 2.3G, I). As bass move upstream by 2040 and even farther upstream by 2080, so do subyearling Chinook salmon, and therefore their overall overlap may not change. In the MFJDR, there is some potential for co-occurrence between bass and subyearling Chinook salmon in the upper river ($RKM \geq 77$), but in all reaches where bass are predicted to be present, the probability of Chinook salmon presence is <0.5 .

Restoration of riparian vegetation to reduce stream temperatures

The restoration of stream-side vegetation had a relatively small capacity to lower early summer 7DAD mean temperatures of the NFJDR in 2080 (Fig. 2.4A). Riparian restoration in the NFJDR resulted in a relatively greater reduction in 7DAD mean temperatures in late summer (Fig. 2.4B), with a maximum reduction of 1.6° C (average reduction = 0.8° C) given 100% restoration. Complete restoration of the NFJDR riparian corridor in 2080 in either season was not capable of achieving the 7DAD mean temperatures modeled for 1977-2006 (Fig. 2.4A, B).

Restoration had a more pronounced effect on stream temperature in the MFJDR (Fig. 2.4C, D). Similar to the NFJDR, riparian restoration resulted in greater reductions in 7DAD

mean temperatures in the late summer compared to the early summer. The maximum reductions in early summer 7DAD mean temperatures achievable by complete restoration of the MFJDR riparian zone was 1.8° C (mean = 1.0° C), where the greatest effect of restoration on temperature was observable in the downstream reaches of the river (Fig. 2.4C). In the late summer, restoration was effective at reducing temperatures in both the lower and upper MFJDR, with a maximum capacity to reduce 7DAD mean temperatures by 2.5°C (mean = 1.6° C) under complete riparian vegetation restoration (Fig. 2.4D). No amount of riparian restoration was capable of achieving the 7DAD mean temperatures modeled during the early summer current condition (Fig. 2.4C). However, restoring 50% of the MFJDR by 2080 is forecasted to decrease water temperatures to what they were in 1977-2006 in the lower river during late summer (Fig. 2.4D). Riparian restoration along the entire MFJDR by 2080 lowered the 7DAD mean water temperature below the 1977-2006 average in downstream areas in late summer (<RKM 50), but this was not the case in the upper river (Fig. 2.4D). This is likely due to the greater scope for increasing effective shade in downstream portions of the MFDJR relative to some upstream areas in that basin (Appendix C, Fig. C-1).

The influence of riparian restoration on fish distributions

The restoration of riparian areas indirectly influenced bass and Chinook salmon distributions through modification of stream temperatures. The capacity of restoration to reduce the abundance and upstream extent of bass by 2080 was lower in the NFJDR (Figs. 2.2 and 2.5A, B) compared to the MFJDR (Figs. 2.3 and 2.5C, D). This illustrates the limited capacity of riparian restoration to reduce 7DAD mean water temperatures within the NFJDR relative to the MFJDR. In the NFJDR, 50% restoration of riparian vegetation by 2080 slightly reduced the early summer upstream expansion of bass, thereby lowering their upstream-most occurrence to

RKM 109 (Fig. 2.2E), compared to RKM 114 in the un-restored condition (Fig. 2.2D). Restoration did not reduce the upstream extent of bass in the late summer in the NFJDR (Fig. 2.2I vs. 2.2J). The overall abundance of bass in the NFJDR decreased with increasing restoration (Fig. 2.5A, B). Complete restoration of the riparian corridor by 2080 was capable of reducing the overall abundance of bass in the NFJDR by up to 13% in the early summer (Fig. 2.5A), and 11% in the late summer (Fig. 2.5B). In the MFJDR, restoration of 50% of the landscape is not likely to reduce the upstream extent of bass in the early summer of the 2080s (Fig. 2.3E), but it is likely to prevent large numbers of bass from moving into the upper river in the late summer. Bass are forecasted to occupy the entire MFJDR in late summer by 2080 (Fig. 2.3I), but simulations of 50% restoration restricted bass from most of the upper 31 km of river (> RKM 81; Fig. 2.3J). Restoration reduced the overall abundance of bass in the MFJDR in the 2080s by up to 5% in the early summer (i.e., 100% vs. 0% restoration of the MFJDR in 2080; Fig. 2.5C), and resulted in up to a 43% reduction in overall bass abundance in the late summer of the 2080s (Fig. 2.5D). In both the NFJDR and MFJDR, restoration in specific ‘priority’ areas outperformed random restoration in reducing the overall abundance of bass for a given level of restoration investment (Fig. 2.5).

The effect of restoration on subyearling Chinook salmon occurrence was most apparent in the MFJDR where the potential for increasing stream-side shade was greater. In the NFJDR, thermally suitable habitat for subyearling Chinook salmon occurred throughout the river in the early summer of the 2080s, with or without restoration (Fig. 2.2D, E). Increasing amounts of restoration increased the overall probability of Chinook salmon occurrence in the NFJDR by up to 3% during early summer (Fig. 2.6A) and up to a 10% in late summer (Fig. 2.6B). In the MFJDR, 50% restoration increased the amount of thermally suitable habitat for subyearling

Chinook salmon by 36 km in the early summer of the 2080s ($RKM \geq 37$ compared to $RKM \geq 73$ in the un-restored condition; Fig. 2.3D,E). During this period, the overall probability of subyearling Chinook salmon occurrence increased by up to 85% through restoration (Fig. 2.6C). In the late summer of the 2080s, thermally suitable rearing habitat in the MFJDR is totally unavailable to subyearling Chinook salmon without restoration (Fig. 2.3I); however, restoration of 50% of the riparian corridor may provide 19 km of the MFJDR (upstream of RKM 90) that is available for rearing (Fig. 2.3J). Restoration of the MFJDR resulted in a 506% increase in the probability of subyearling Chinook salmon occurrence in the late summer of the 2080s compared to no restoration (Fig. 2.6D). In both tributaries, prioritized restoration had a greater effect on the probability of subyearling Chinook salmon presence than random restoration (Fig. 2.6), but this effect was most apparent in the MFJDR (Fig. 2.6C,D).

The effect of restoration on the overlap between bass and subyearling Chinook salmon was variable for NFJDR and MFJDR. In the NFJDR, restoration decreased the extent of overlap between bass and subyearling Chinook salmon by 5 km in the early summer of the 2080s, and increased the probability of Chinook salmon where they co-occurred (Fig. 2.2D, E). In the MFJDR, the spatial extent of early summer overlap of bass and Chinook salmon increased with restoration by 2080, but this mainly reflected an overall increase in the probability of subyearling Chinook salmon presence rather than a shift in bass upstream extent (Fig. 2.3D, E). Late summer co-occurrence of bass and subyearling Chinook salmon by 2080 was minimal with no restoration in the NFJDR and MFJDR; however, restoration may prevent bass from occupying the upper MFJDR and increase the capacity of these areas to support subyearling Chinook salmon (Fig. 2.3I, J).

Discussion

The forecasts of climate change presented in our study suggest that extensive stream warming by the middle and end of this century will allow non-native bass to occupy an increasingly large portion of tributaries within the John Day River basin, and subyearling Chinook salmon rearing habitat will be reduced. This pattern is likely to be repeated in streams throughout the Pacific Northwest where temperatures are forecasted to increase (Isaak et al. 2012), and where bass are widely introduced (Carey et al. 2011). The forecasts are particularly severe for the MFJDR where rearing habitat for subyearling Chinook salmon (without riparian restoration) will nearly disappear if the 2080 projections of climate change occur. The losses in salmonid habitat projected for the John Day River basin and the broader interior Columbia River basin represent some of the highest potential declines in the range of Chinook salmon. This region is part of the southern extent of Chinook salmon distribution where the contemporary climate regularly approaches (and sometimes exceeds) the thermal tolerances of the species (Mantua et al. 2010).

Our study is one of the first attempts to forecast interactions between bass and Chinook salmon distribution based on seasonal water temperature patterns and climate change. Based on our 2009 surveys, we observed that the early and late summer period correspond to different degrees of sympatry between these fishes. The early summer is a time of high overlap between bass and subyearling Chinook salmon. This overlap most likely occurs because subyearling Chinook salmon disperse downstream after emergence in March to June due to displacement from high spring flows, displacement for upstream feeding sites resulting from intraspecific competition, or due to purposeful downstream movement (Murray and Rosenau 1989, Bradford and Taylor 1997). In the NFJDR and MFJDR, subyearling Chinook salmon are commonly

observed downstream of their downstream-most redd sites (Lindsay et al. 1985). In these downstream non-natal areas, bass emerge from winter torpor as temperatures rise from 10 to 15° C and begin building nests in anticipation of spawning (Armour 1993). At this time, water temperatures are still cool enough to allow for occupancy by Chinook salmon, but not so cold that they prevent bass from occupying the area and nesting. As summer temperatures increase, subyearling Chinook salmon vacate warm areas, moving upstream or into cooler tributaries, or are lost to predation. Some bass also move upstream (as documented by Lawrence et al. 2012) but not far enough to maintain the relatively high degree of overlap observed between bass and subyearling Chinook salmon in the early summer. It is likely that the much warmer stream temperatures observed during the late summer isolate bass and subyearling Chinook salmon due to physiological differences in thermally-mediated growth and consumption. Thus, the relative extent of overlap between bass and Chinook salmon is much lower in late summer compared to early summer.

We forecast that sympatry between bass and subyearling Chinook salmon will increase dramatically in the early summer as streams warm through the 2040s and 2080s. In the NFJDR, increases in water temperature in the early summer were enough for bass to significantly expand in upstream distribution, but not great enough to restrict subyearling Chinook salmon from occupying the lower extents of the modeled domain. Thus, overlap in this system increased in the early summer period by the 2040s and 2080s. In the MFJDR, forecasted warming in the early summer enabled bass to occupy the entire modeled extent of the river. The warming achieved by 2040, however, does not exclude subyearling Chinook salmon from occupying much of the lower MFJDR. Therefore, overlap between bass and rearing Chinook salmon is likely to be high during the early summer in the 2040s. However, as early summer warming

progresses into the 2080s, the degree of warming is such that a large fraction of the habitat will become thermally unsuitable for subyearling Chinook salmon. Thus, the spatial overlap between bass and Chinook salmon will decrease. This difference leads to the counter-intuitive result that as the riparian zone of the MFJDR is restored by the 2080s (and water temperatures are lowered) the expected overlap between bass and Chinook salmon in the early summer increases. In this situation, the degree of cooling achieved through the restoration in the MFJDR is enough to enhance the probability of subyearling Chinook salmon presence, but may not be enough to prevent bass from occupying the upper river. In the late summer, bass are forecasted to advance farther into previously suitable Chinook salmon rearing habitat in both river systems. In the late summer, however, warm water temperatures maintain spatial separation between bass and Chinook salmon, i.e., the relatively minimal amount of overlap observed between these fishes in 2009 is maintained by the 2040s and 2080s because both species move upstream as temperatures warm in the late summer. In the case of subyearling Chinook salmon, they have a limited distance to move upstream before reaching ephemeral headwater areas. Thus, even though the sympatry between bass and subyearling Chinook salmon did not increase as bass moved farther upstream by 2080, the total thermally suitable habitat available to subyearling Chinook salmon decreased significantly (i.e., 34 km in the NFJDR [a 55% reduction]; and 56 km in the MFJDR [a 100% reduction]).

In addition to the large increases in bass upstream extent forecasted over the next century, the overall abundance of bass is also forecasted to increase within the NFJDR and MFJDR. A broader degree of early season overlap combined with larger numbers of bass in Chinook salmon rearing areas may enhance predation of bass on subyearling Chinook salmon. The extent to which bass consume subyearling Chinook salmon in the upper JDR basin is not known, but bass

have been shown to feed heavily on small subyearling Chinook salmon when they co-occur in the Yakima River system (Fritts and Pearsons 2004). Fritts and Pearsons (2004) attributed this degree of predation to both the small size of rearing Chinook salmon when they overlap with bass and the relatively warm stream temperatures during their co-occurrence that stimulate bass metabolism and, thus, consumption. Similarly, in the NFJDR and MFJDR, bass overlap with subyearling Chinook salmon that are comparable in size to those observed in the Yakima River, and this overlap occurs when water temperatures are warm enough to enable bass feeding. Subyearling Chinook salmon may be particularly vulnerable because they do not initially recognize bass as predators, an oversight resulting from a lack of shared evolutionary history between predator and prey (Kuehne and Olden 2012). Bass may also have sub-lethal effects on subyearling Chinook salmon by causing stress and inhibiting feeding and growth (Kuehne et al. 2012).

The carrying capacity of streams to support bass may also change in the future, although we did not address this change in our model structure. The total number of bass forecasted to occupy the study system is determined partly by the observed carrying capacity of bass, as parameterized in the bass model with 2009 and 2010 data. However, the carrying capacity could increase as temperatures warm by enhancing the overwinter survival of bass, or through demographic processes such as increased reproduction. If the carrying capacity of bass increases as the NFJDR and MFJDR warm, then it is possible that our future estimates of bass abundances are conservative, especially in the lower river where bass are forecasted to reach the model carrying capacity over large spatial extents. One important caveat is that food availability may limit increases in bass carrying capacity, but the extent to which stream productivity will increase as temperatures increase is still unclear. Ultimately, accounting for these potential

changes in carrying capacity would require a deterministic demographic model (e.g., Peterson and Kwak 1999). Such models represent an avenue for future research when forecasting bass populations that occupy salmon-bearing streams, but they require more data than statistical models.

Other stream variables may also determine how bass and subyearling Chinook salmon populations respond to climate change, depending on the context of the river system. For example, we accounted for alterations in stream flow associated with climate change in terms of its influence on stream temperature, but we did not model the direct effects of changing stream discharge on bass and subyearling Chinook salmon. In the Pacific Northwest, many snow-melt systems (such as the tributaries presented in this study) are predicted to become rain-dominated systems over the next century (Elsner et al. 2010, Reidy Liermann et al. 2012). This change from relatively predictable and gradual declines in flow to more rapid stream discharge changes could have direct effects on bass spawning nests and fry, which are susceptible to scour and may be displaced under high flows (Smith et al. 2005). The transition from snow to rain-dominated systems can also have direct negative consequences on salmon recruitment if the winter discharge is large enough to mobilize the stream bed and scour salmon eggs residing in the substrate (Goode et al. 2013). Additionally, geomorphic features may limit the upstream intrusion of bass in mountainous river systems, even if these areas are thermally suitable. For example, high-gradient segments of rivers are common in upstream reaches, and these areas may not be accessible by bass. The extent to which bass can move through high-gradient segments, especially at high flow, is unknown at this time (Lawrence et al. 2012). Also, stream substrates change longitudinally, and therefore, as bass move upstream, they may have difficulty finding appropriately sized spawning gravels (Lukas and Orth 1995, Dauwalter and Fisher 2007).

Differences in basin productivity, due to geology and land-use could also lead to different responses to climatic trends by bass and Chinook salmon, given their thermal tolerances are also contingent on food supply (Beauchamp 2009). Together, these factors could be incorporated into future efforts to predict the response of bass and Chinook salmon to climate change.

Restoring riparian vegetation may offset climate-induced losses in thermally suitable Chinook salmon rearing habitat and may reduce the expansion of bass into upstream stream habitats. Riparian restoration may be particularly useful in small to mid-sized streams ($\leq 5^{\text{th}}$ order) if shade provided by riparian vegetation is the primary determinant of stream temperature (Johnson 2004, Cristea and Burges 2010). Our results showed that the capacity of restoration to offset some of the warming forecasted by the 2080s varied by both season (i.e., early vs. late summer) and by stream (i.e., NFJDR vs. MFJDR). In both streams, restoration had a greater capacity to reduce late summer temperatures compared to early summer temperatures. This is likely because stream flow declines seasonally, and by late summer these streams are shallower and more prone to warming, a time when riparian shading has the greatest potential to provide a cooling benefit.

Riparian restoration had a greater potential to reduce stream temperatures forecast for the 2080s in the MFJDR than the NFJDR, and given its potential cost, restoration may have a greater return-on-investment if employed there. The upper NFJDR has a largely intact riparian corridor and therefore has a smaller capacity to increase effective shade than the MFJDR (i.e., there is a relatively small difference between current and potential effective shade in the NFJDR; Appendix C). Additionally, the lower NFJDR has a smaller total magnitude of restored effective shade compared to the lower MFJDR (Appendix C, Fig. C1). This is likely the result of (1) smaller channel widths in the MFJDR, which allow for more effective shading of the stream if

restored, and (2) differences in the Ecoregion-Physiographic regions between these stream systems, which in turn, influence the tree heights in the riparian canopy and the foliage density predicted after restoration (see Appendix C for details). Cristea and Burges (2010) found a similar pattern when they investigated the potential for riparian vegetation restoration to offset climate-induced temperature increases in the Wenatchee River system in Washington; narrower streams could achieve greater effective shade after restoration and thus resulted in greater shade-related temperature decreases compared to larger streams. In the MFJDR there are many opportunities to increase stream shade because most riparian areas have been heavily grazed by either current or past ranching activities (Beschta and Ripple 2005) and disturbed by historical dredge mining. Parts of the upper MFJDR are currently undergoing riparian restoration, as well as other forms of restoration including stream channel re-meandering. Hydrology also plays an important role in determining thermal regimes (Caissie 2006). For example, reducing irrigation-related water removals has the capacity to reduce stream temperature, especially during summer baseflow conditions. The relative magnitude of benefits from streamflow and riparian vegetation restoration are likely to be system specific. In the MFJDR, ORDEQ (2010a) estimated that vegetation restoration had a greater capacity to reduce stream temperature compared to flow restoration. Despite this, instream flow restoration will certainly be a valuable stream temperature restoration tool in many systems in the Pacific Northwest (Beechie et al. 2013).

In our study, prioritized restoration outperformed opportunistic restoration in providing the dual benefit of reducing bass abundance and increasing the probability of subyearling Chinook salmon occurrence. The priority restoration segments we identified (Appendix C, Figs. C2 and C3) could be used to allocate limited restoration funds to the segments where restoration would have the biggest ecological benefit for salmon. If our forecasts of stream warming by the

2080s occur, restoration will likely be the only way to prevent extirpation of spring Chinook salmon from the MFJDR. Another important consideration in evaluating the effectiveness of restoration in mitigating climate change is that the magnitude of stream temperature reduction achievable through restoration depends partly on the metric used to define temperature. We used 7DAD mean but if we used 7DAD maximum, greater reductions in stream temperature may have been observed. This pattern has been shown experimentally by shading streams (Johnson 2004). Although reductions in the 7DAD mean temperature may be relatively small for the NFJDR, a greater reduction in the 7DAD maximum may be achievable through restoration.

There are uncertainties associated with forecasts of global warming, and these uncertainties have to be considered when prioritizing adaptation strategies. For example, Arismendi et al. (2012) showed that some streams become cooler even when the regional climate trends reflect overall warming. Additionally, the GCM that we downscaled is one of many projections of climate change available for the region. Lawler et al. (2010) suggest that it is important to use low-risk adaptation strategies that are robust to this uncertainty—that is, they benefit the ecosystem even if the exact magnitude of warming is unknown. In stream systems, riparian restoration provides one such low-risk adaptation strategy because riparian vegetation also provides coarse-woody habitat and terrestrial food subsidies to streams (Wipfli and Baxter 2010). Restored riparian vegetation also retains sediment, stabilizes banks, and reduces erosion (Beechie et al. 2013). These changes may have an additional cooling effect not currently considered in our modeling approach.

Climate-induced stream warming is likely to occur throughout the interior Western United States, and other regions in the United States and the world (Poff et al. 2002, Wenger et al. 2011). In our study, we provide a mechanism to translate regional-scale climate forecasts into

local-scale changes in fish distribution. The stream temperature model we employed was mechanistic and spatially explicit and therefore provided a means to evaluate the extent to which riparian restoration can ameliorate warming. We believe this approach could be applied in many other streams where the data inputs are already available (i.e., downscaled climate forecasts, stream temperature models, fish-temperature relationships).

Climate change affects species directly and indirectly through myriad stressors that are already present in the ecosystem (Nelson et al. 2009). For example, additional warming in the MFJDR (a river system that is currently considered thermally impaired due to riparian vegetation removal) may result in the extirpation of the Chinook salmon unless riparian restoration is undertaken to increase shade and offset the impacts of climate change. This outcome is starkly different from that projected for the NFJDR where a relatively intact riparian corridor supports cool water habitat, even in the face of climate-induced stream warming. Climate change will also affect stream rearing salmon by enabling the range expansion of predatory non-native species such as bass. The interactive effects of climate-change, riparian land-use, and introduced species will determine the future of rearing salmon populations. This work highlights the potential for restoration to mitigate some of the effects of climate change, especially in systems with a high degree of current riparian vegetation alteration and spreading non-native species.

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Literature Cited

- Arismendi, I., S. L. Johnson, J. B. Dunham, R. Haggerty, and D. Hockman-Wert. 2012. The paradox of cooling streams in a warming world: regional climate trends do not parallel variable local trends in stream temperature in the Pacific continental United States. *Geophysical Research Letters* 39:L10401.
- Armour, C. L. 1993. Evaluating temperature regimes for protection of smallmouth bass. United States Department of the Interior, Fish and Wildlife Service, Resource Publication 191, Washington, D.C., USA.
- Beauchamp, D. A. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *American Fisheries Society Symposium* 70:1-19.
- Beechie, T., H. Imaki, J. Greene, A. Wade, H. Wu, G. Pess, P. Roni, J. Kimball, J. Stanford, P. Kiffney, and N. Mantua. 2013. Restoring salmon habitat for a changing climate. *River Research and Applications*. doi: 10.1002/rra.2590.
- Beer, W. N., and J. J. Anderson. 2011. Sensitivity of juvenile salmonid growth to future climate trends. *River Research and Applications* 27:663-669.
- Beschta, R. L., and W. J. Ripple. 2005. Rapid assessment of riparian cottonwood recruitment: Middle Fork John Day River, Northeastern Oregon. *Ecological Restoration* 23:150-156.
- Boone, E. L., B. Stewart-Koster, and M. J. Kennard. 2012. A hierarchical zero-inflated Poisson regression model for stream fish distribution and abundance. *Environmetrics* 23:207-218.
- Boyd, M., and B. Kasper. 2003. Analytical methods for dynamic open channel heat and mass transfer: Methodology for heat source model Version 7.0. Page 204. Oregon Department

of Environmental Quality, Portland, Oregon, USA,
<http://www.deq.state.or.us/wq/tmdls/docs/tools/heatsourcemanual.pdf>.

Bradford, M. J., and G. C. Taylor. 1997. Individual variation in dispersal behaviour of newly emerged Chinook salmon (*Oncorhynchus tshawytscha*) from the upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1585-1592.

Caissie, D. 2006. The thermal regime of rivers: a review. *Freshwater Biology* 51:1389-1406.

Carey, M. P., B. L. Sanderson, T. A. Friesen, K. A. Barnas, and J. D. Olden. 2011. Smallmouth bass in the Pacific Northwest: a threat to native species; a benefit for anglers? *Reviews in Fisheries Science* 19:305-315.

Cristea, N. C., and S. J. Burges. 2010. An assessment of the current and future thermal regimes of three streams located in the Wenatchee River basin, Washington State: some implications for regional river basin systems. *Climatic Change* 102:493-520.

Dauwalter, D. C., and W. L. Fisher. 2007. Spawning chronology, nest site selection and nest success of smallmouth bass during benign streamflow conditions. *American Midland Naturalist* 158:60-78.

Elsner, M., L. Cuo, N. Voisin, J. Deems, A. Hamlet, J. Vano, K. Mickelson, S.-Y. Lee, and D. Lettenmaier. 2010. Implications of 21st century climate change for the hydrology of Washington State. *Climatic Change* 102:225-260.

Fritts, A. L., and T. N. Pearsons. 2004. Smallmouth bass predation on hatchery and wild salmonids in the Yakima River, Washington. *Transactions of the American Fisheries Society* 133:880-895.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. *Bayesian data analysis*, second edition. Chapman and Hall, Boca Raton, Florida, USA.

Goode, J. R., J. M. Buffington, D. Tonina, D. J. Isaak, R. F. Thurow, S. Wenger, D. Nagel, C. Luce, D. Tetzlaff, and C. Soulsby. 2013. Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins. *Hydrological Processes* 27:750-765.

Gordon, A. D., and H. T. B. Birks. 1972. Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. *New Phytologist* 71:961-979.

- Grimm, E. C. 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* 13:13-35.
- Hamlet, A. F., P. Carrasco, J. Deems, M. M. Elsner, T. Kamstra, C. Lee, S.-Y. Lee, G. Mauger, E. P. Salathe, I. Tohver, and L. Whitely Binder. 2010. Final Project Report for the Columbia Basin Climate Change Scenarios Project. Climate Impacts Group, University of Washington, Seattle, Washington, USA.
<http://www.hydro.washington.edu/2860/report/>.
- Hamlet, A. F., P. W. Mote, M. P. Clark, and D. P. Lettenmaier. 2007. Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. *Journal of Climate* 20:1468-1486.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied Logistic Regression*. Wiley, New York, New York, USA.
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. *Climatic Change* 113:499-524.
- Johnson, S. L. 2004. Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 61:913-923.
- Juggins, S. 2012. Analysis of quaternary science data. R package 'rioja' version 0.7-3. Newcastle University, Newcastle, UK. <http://cran.r-project.org/>.
- Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment* 8:461-466.
- Kuehne, L., and J. D. Olden. 2012. Prey naivety in the behavioural responses of juvenile Chinook (*Oncorhynchus tshawytscha*) salmon to an invasive predator. *Freshwater Biology* 57:1126-1137.

- Kuehne, L. M., J. D. Olden, and J. J. Duda. 2012. Costs of living for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in an increasingly warming and invaded world. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1621-1630.
- Lawler, J. J., T. H. Tear, C. Pyke, M. R. Shaw, P. Gonzalez, P. Kareiva, L. Hansen, L. Hannah, K. Klausmeyer, A. Aldous, C. Bienz, and S. Pearsall. 2010. Resource management in a changing and uncertain climate. *Frontiers in Ecology and the Environment* 8:35-43.
- Lawrence, D. J., J. D. Olden, and C. E. Torgersen. 2012. Spatiotemporal patterns and habitat associations of smallmouth bass (*Micropterus dolomieu*) invading salmon-rearing habitat. *Freshwater Biology* 57:1929-1946.
- Lindsay, R. B., W. J. Knox, M. W. Flesher, B. J. Smith, E. A. Olsen, and L. S. Lutz. 1985. Study of wild spring Chinook salmon in the John Day River system. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.
- Littell, J. S., M. M. Elsner, G. S. Mauger, E. Lutz, A. F. Hamlet, and E. Salathe. 2011. Regional climate and hydrologic change in the Northern U.S. Rockies and Pacific Northwest: internally consistent projections of future climate for resource management. Preliminary project report, USFS JVA 09-JV-11015600-039. Prepared by the Climate Impacts Group, University of Washington, Seattle, Washington, USA.
http://ceses.washington.edu/picea/USFS/pub/Littell_etal_2010/.
- Lukas, J. A., and D. J. Orth. 1995. Factors affecting nesting success of smallmouth bass in a regulated Virginia stream. *Transactions of the American Fisheries Society* 124:726-735.
- Lunn, D., A. Thomas, N. Best, and D. J. Spiegelhalter. 2000. WinBUGS - a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* 10:325-337.
- Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change* 102:187-223.
- Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. *Climatic Change* 102:29-50.
- Murray, C. B., and M. L. Rosenau. 1989. Rearing of juvenile chinook salmon in nonnatal tributaries of the lower Fraser River, British Columbia. *Transactions of the American Fisheries Society* 118:284-289.

- Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences*. doi: 10.1073/pnas.1213408109
- Nelson, K. C., M. A. Palmer, J. E. Pizzuto, G. E. Moglen, P. L. Angermeier, R. H. Hilderbrand, M. Dettinger, and K. Hayhoe. 2009. Forecasting the combined effects of urbanization and climate change on stream ecosystems: from impacts to management options. *Journal of Applied Ecology* 46:154-163.
- ORDEQ. 2010a. John Day River Basin total maximum daily load (TMDL) and water quality management plan (WQMP). State of Oregon, Department of Environmental Quality, Portland, Oregon, USA.
- ORDEQ. 2010b. John Day River Basin total maximum daily load (TMDL) Appendix C: Estimate of natural potential vegetation in the John Day Basin. State of Oregon, Department of Environmental Quality, Portland, Oregon, USA.
- Peterson, J. T., and T. J. Kwak. 1999. Modeling the effects of land use and climate change on riverine smallmouth bass. *Ecological Applications* 9:1391-1404.
- Poff, N. L., M. M. Brinson, and J. W. J. Day. 2002. Aquatic ecosystems and global climate change. Pew Center on Global Climate Change.
- Powell, R. M., P. D. Alley, L. Goin, and J. Kehrberg. 2008. John Day River Sub-basin Fish Habitat Enhancement Project. Annual Report. Oregon Department of Fish and Wildlife, John Day, Oregon, USA.
- Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22:521-533.
- Reidy Liermann, C. A., J. D. Olden, T. J. Beechie, M. J. Kennard, P. B. Skidmore, C. P. Konrad, and H. Imaki. 2012. Hydrogeomorphic classification of Washington state rivers to support emerging environmental flow management strategies. *River Research and Applications* 28:1340-1358.
- Rieman, B. E., D. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce, and D. Myers. 2007. Anticipated climate warming effects on bull trout habitats and populations across the

- interior Columbia River basin. *Transactions of the American Fisheries Society* 136:1552-1565.
- Rieman, B. E., and D. J. Isaak. 2010. Climate change, aquatic ecosystems, and fishes in the Rocky Mountain West: implications and alternatives for management. General Technical Report RMRS-GTR-250. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, Colorado, USA.
- Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33:665-706.
- Ruesch, A., C. E. Torgersen, J. J. Lawler, J. D. Olden, E. E. Peterson, C. Volk, and D. J. Lawrence. 2012. Projected climate-induced habitat loss for salmonids in the John Day river network, Oregon, U.S.A. *Conservation Biology* 26:873-882.
- Sanderson, B. L., K. A. Barnas, and A. M. Wargo Rub. 2009. Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? *BioScience* 59:245-256.
- Sharma, S., L. Herborg, and T. W. Therriault. 2009. Predicting introduction, establishment and potential impact of smallmouth bass. *Diversity and Distributions* 15:831-840.
- Shrader, T., and M. E. Gray. 1999. Biology and management of John Day River smallmouth bass. Oregon Department of Fish and Wildlife. Portland, Oregon, USA.
- Smith, S. M., J. S. Odenkirk, and S. J. Reeser. 2005. Smallmouth bass recruitment variability and its relation to stream discharge in three Virginia rivers. *North American Journal of Fisheries Management* 25:1112-1121.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* 12:1-16.
- Torgersen, C. E., R. N. Faux, B. A. McIntosh, N. J. Poage, and D. J. Norton. 2001. Airborne thermal remote sensing for water temperature assessment in rivers and streams. *Remote Sensing of Environment* 76:386-398.
- Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications* 9:301-319.

USEPA (U.S. Environmental Protection Agency). 2002. National water quality inventory: report to congress, 2002 reporting cycle. Page 39, Washington, D.C., USA.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America* 108:14175-14180.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries* 35:373-387.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B-Biological Sciences* 365:2093-2106.

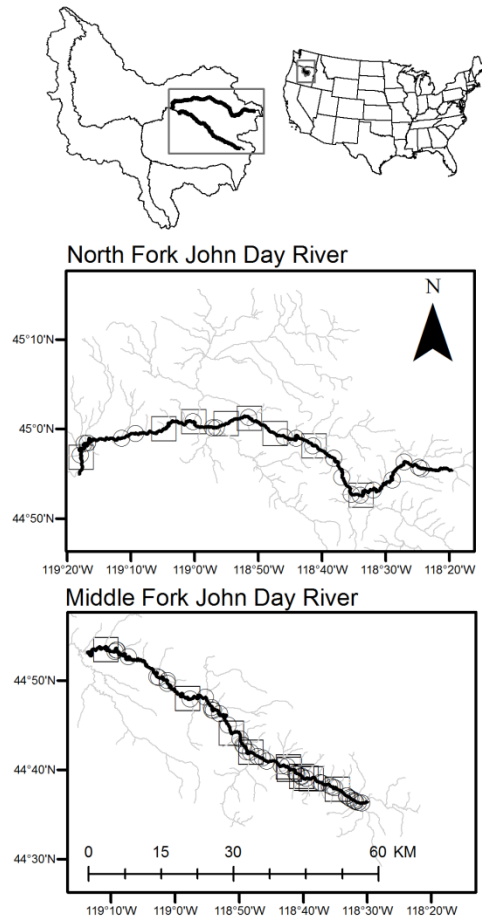


Fig. 2.1

Map of the NFJDR and MFJDR showing the extent of the model domain for each river (black line), the spatial position of modeled tributaries (i.e., the boundary conditions) where they intersect with the mainstem NFJDR and MFJFR (○), and the spatial location of the meteorological nodes where air temperatures were input (□).

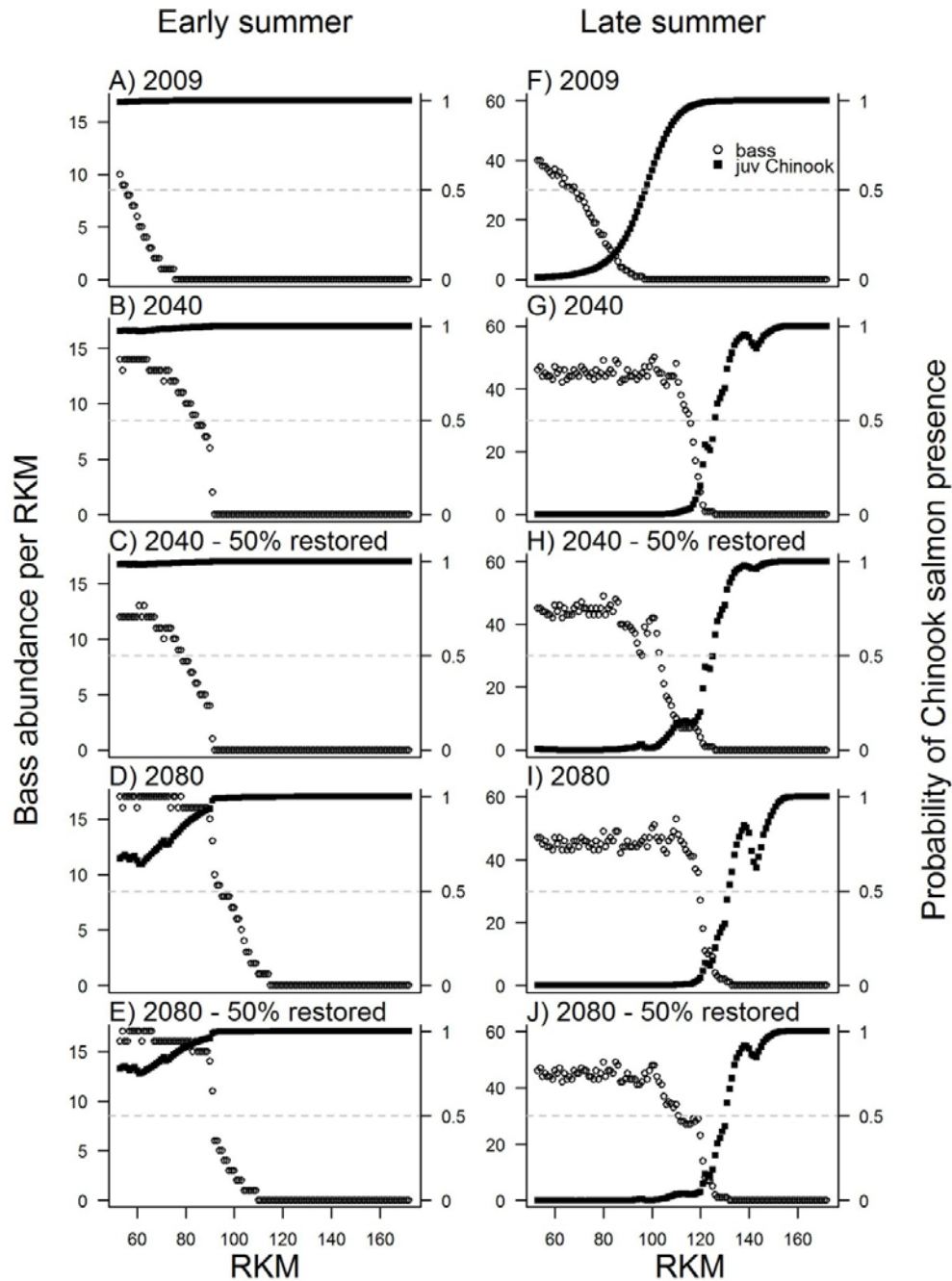


Fig. 2.2

Modeled bass and subyearling Chinook salmon distribution over the longitudinal profile of the NFJDR in early summer (A) 2009, (B) 2040, (C) 2040 with the top 50% of segments restored, (D) 2080, (E) 2080 with the top 50% of segments restored, and late summer forecasts in (F) 2009, (G) 2040, (H) 2040 with the top 50% of restoration segments restored, (I) 2080, (J) 2080 with the top 50% of restoration segments restored. The 2009 bass distributions, rather than a 1977-2006 average, are shown because bass have expanded in the study area over that period, and 2009 represents the most up-to-date known spatial distribution of bass. RKM – river kilometer. The dotted gray line in each panel indicates the probability of subyearling Chinook salmon presence equals 0.5.

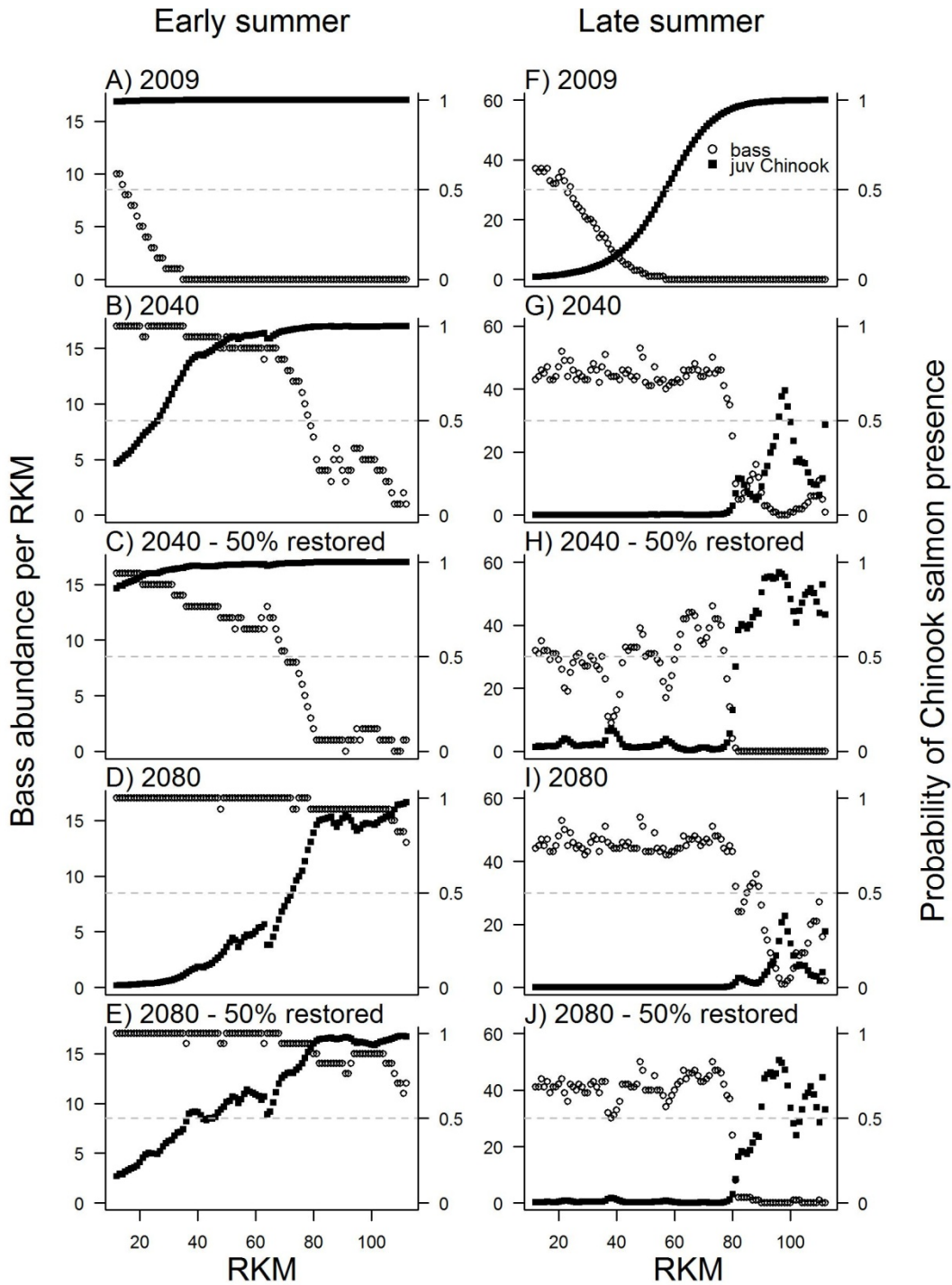


Fig. 2.3

Modeled bass and subyearling Chinook salmon distribution over the longitudinal profile of the MFJDR in early summer (A) 2009, (B) 2040, (C) 2040 with the top 50% of segments restored, (D) 2080, (E) 2080 with the top 50% of segments restored, and late summer forecasts in (F) 2009, (G) 2040, (H) 2040 with the top 50% of restoration segments restored, (I) 2080, (J) 2080 with the top 50% of restoration segments restored. RKM – river kilometer. The dotted gray line in each panel indicates the probability of subyearling Chinook salmon presence equals 0.5.

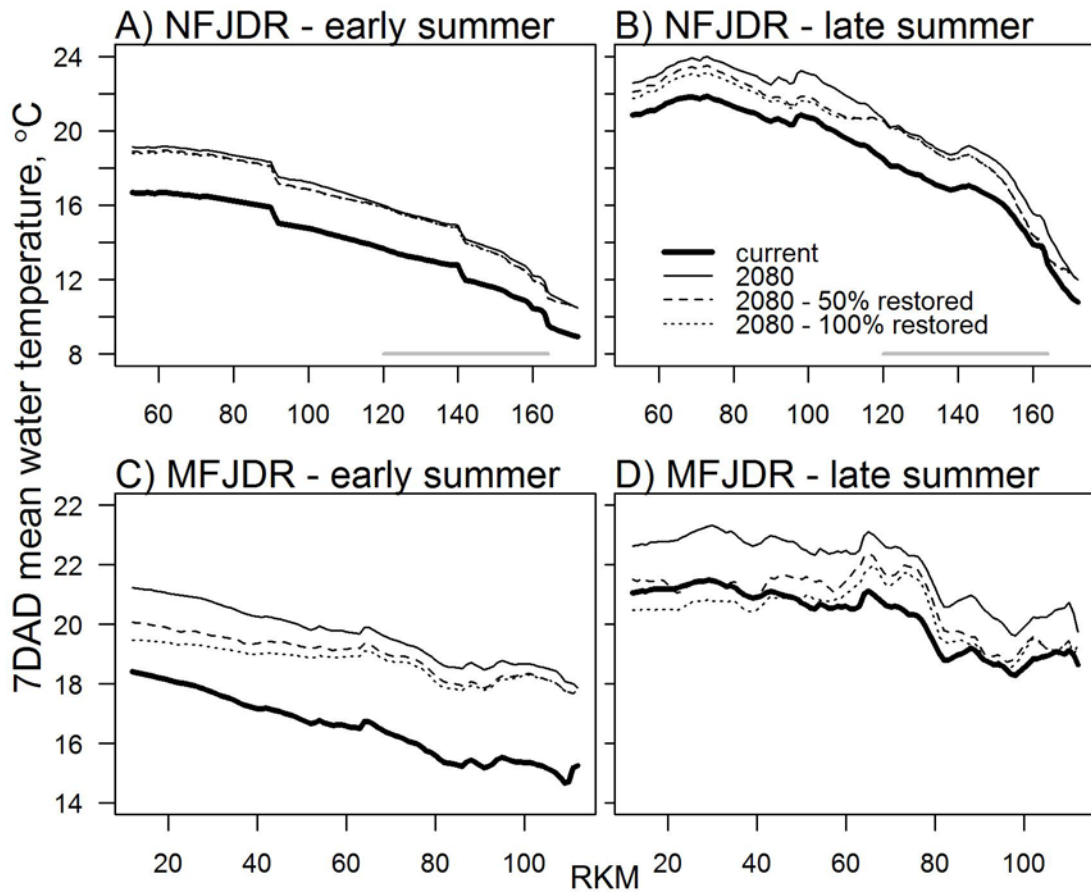


Fig. 2.4

7DAD mean water temperature along the longitudinal continuum (RKM – river kilometer) for the current condition, 2080, and 2080 with 50 and 100% restoration for the NFJDR in (A) early summer, and (B) late summer, and the MFJDR in (C) early summer, and (D) late summer. The grey horizontal line in (A) and (B) from RKM 120 to 164 represents an existing conservation area where vegetation is already considered to be at maximum height and density; therefore restoration was not considered there.

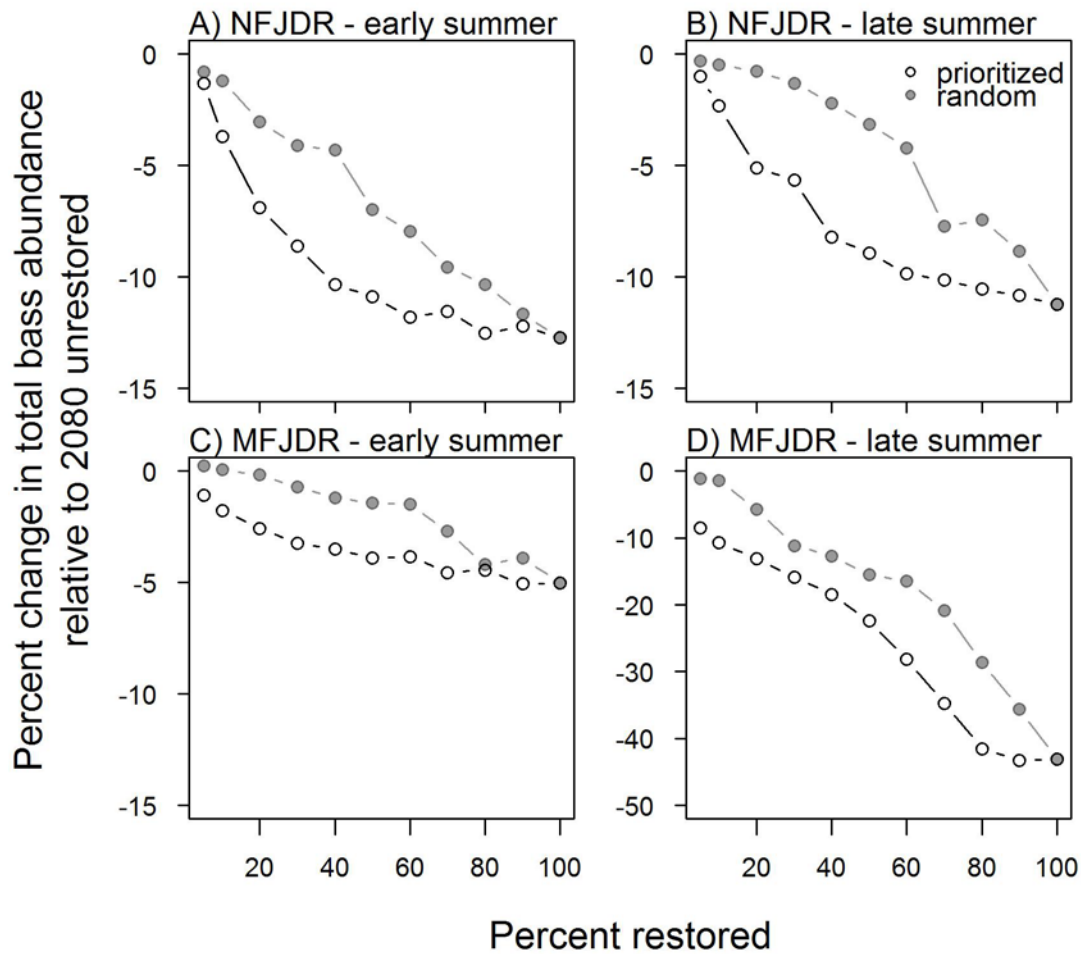


Fig. 2.5

Percent change in the total bass abundance (i.e., over the entire model domain) in 2080 with increasing levels of riparian restoration for the NFJDR in (A) early summer, and (B) late summer, and the MFJDR in (C) early summer, and (D) late summer. Open circles (\circ) indicate prioritized restoration for a given level of restoration (from 5-100%) where segments that resulted in the greatest enhancement of effective shade were restored first. Filled circles (\bullet) indicate restored segments were chosen randomly.

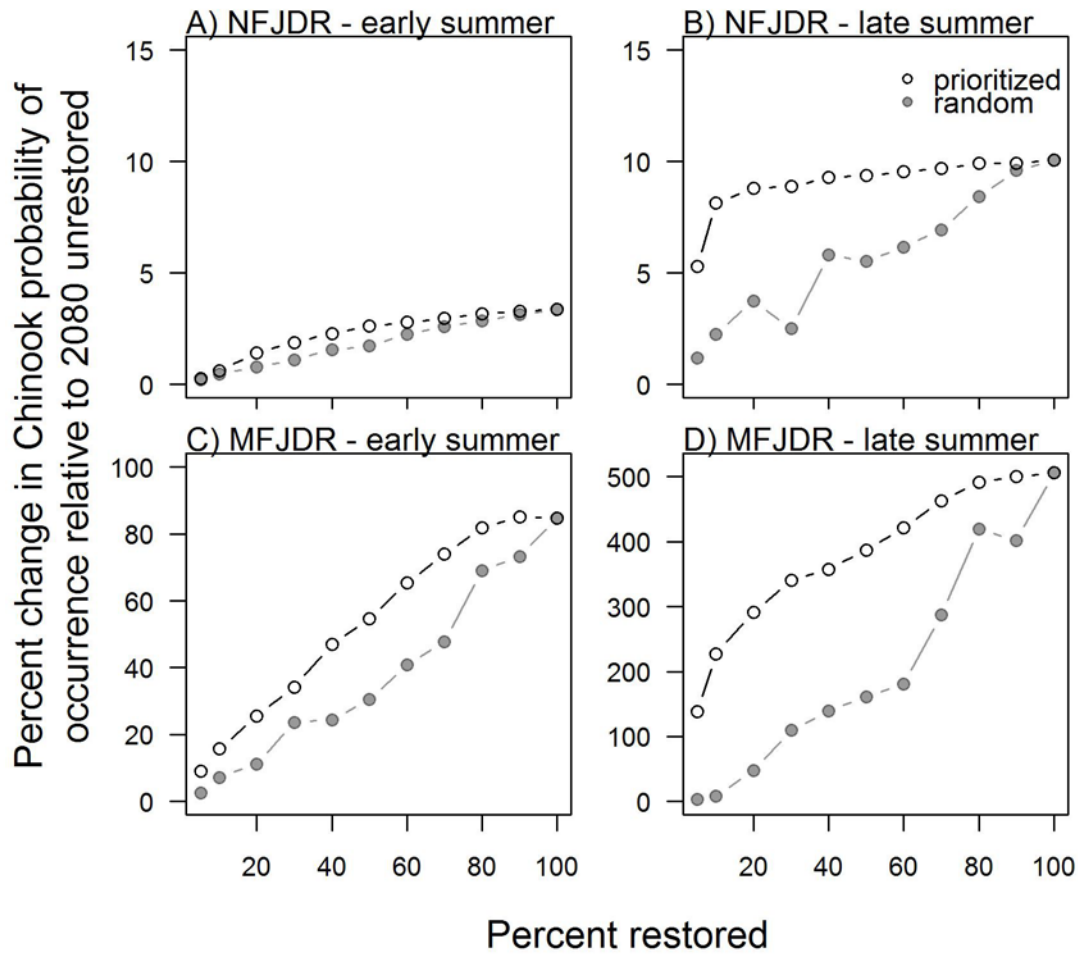


Fig. 2.6

Percent change in the subyearling Chinook salmon probability of occurrence (summed over the entire model extent) in 2080 with increasing levels of riparian restoration for the NFJDR in (A) early summer, and (B) late summer, and the MFJDR in (C) early summer, and (D) late summer. Open circles (○) indicate prioritized restoration for a given level of restoration (from 5-100%) where segments that resulted in the greatest enhancement of effective shade were restored first. Filled circles (●) indicate restored segments were chosen randomly.

Chapter 2 Appendix A

Air temperature forecasts along the stream corridor

Forecasts of air temperature, one of the primary physical drivers of stream temperature, were input to Heat Source at meteorological nodes along the mainstem of each river ($n = 8$ nodes for the NFJDR, $n = 10$ nodes MFJDR; Fig. 2.1). To assign downscaled air temperature forecasts to the meteorological nodes of the NFJDR and MFJDR, we used a geographic information system (GIS) to identify the GCM grid-cell that contained each node. To account for elevation differences between the grid-cell forecasts of air temperature and air temperature that would occur at each meteorological node, we first determined the mean elevation of the GCM cell and then adjusted the air temperatures to the elevation of the corresponding node, based on an lapse rate of 6° C per km (Hamlet and Lettenmaier 2005).

To provide input to the Heat Source model, we had to generate hourly temperature estimates from the downscaled daily averages. To simulate diurnal variation in air temperature, we calculated the hourly deviation (i.e. difference) from the daily mean temperature for every day of the model run in the calibrated model (year 2002). We then applied these deviations to the present (1977-2006) and future climate scenarios, so that while the daily means were the same as that produced at the daily time step in the downscaled GCMs, the hourly temperatures exhibited the seasonal diurnal variation as observed in 2002.

Water temperature forecasts at upstream model boundary and tributaries

Heat Source required stream temperature data at both the upstream model boundary and for the tributaries that flow into the stream within the model domain (collectively referred to here

as ‘boundary conditions’). Forecasted stream temperatures at each boundary were determined in a two step process.

First, we parameterized an independent non-linear regression model relating daily air temperature to daily stream temperature for each model boundary. In the NFJDR a Michaelis-Menten regression was used. We chose an asymptotic air-to-water temperature relationship because as air temperatures rise, so does evaporative cooling, and hence stream temperatures rise at a slower rate at elevated air temperatures (Mohseni and Stefan 1999). For the MFJDR, we used a 4-parameter logistic curve to generate the air-water temperature relationship because the model period began earlier and extended later than the NFJDR model (Mohseni et al. 1998). Air-water temperature relationships were parameterized using data from the original ORDEQ model calibration year (2002), when water temperature loggers were placed instream at each boundary and air temperature was monitored from the closest real-time meteorological station (NFJDR: ~ 40 km from upstream boundary; MFJDR: ~ 20 km from the upstream boundary). Mohseni et al. (1998) showed that when using non-linear regression to model stream temperatures, there is no significant effect of distance on goodness of fit when weather stations were within 244 km of the modeling site.

Second, we input (lapse adjusted) forecasts of air temperature from the downscaled GCM into each regression to determine the future predicted stream temperature at that boundary. Air temperatures were derived from the GCM cell that contained the meteorological station used to originally develop the air-water temperature relationship. Stream temperature forecasts produced from the regression models occur at a daily time step, but the Heat Source model required hourly stream temperatures at the boundary conditions to run the model. We followed

the same approach described above for the mainstem meteorological nodes to simulate diurnal variation in stream temperature for the boundary conditions.

Flow forecasts at upstream model boundary and tributaries

To determine water flow at the upstream boundary condition of the NFJDR during the future periods, we followed the method ORDEQ used in their initial calibration. Their boundary flow was input by multiplying the daily average flow at a downstream United States Geological Survey (USGS) gage station (RKM 24.6, station 14046000) by a modifier that was determined based on the ratio of flow measured at the boundary and that recorded at the gage station during the model calibration summer (ORDEQ 2010). We determined the future upstream boundary flow by multiplying forecasted flow at the gage station by the established ratio of gage-to-boundary flow (Hamlet et al. 2010).

We compared modeled flow forecasts at the USGS gage site for the current period relative to the measured gage flow during the same period, and detected large discontinuities in predicted flows from the end of the month to the beginning of the next (6/30 to 7/1, 7/31 to 8/1; Hamlet et al. 2010). To alleviate this problem, we created a calibration factor for every day in the model period (1977 -2006) that represented the ratio between modeled flow versus measured flow at the gage station. We then applied those daily calibrations to the future modeled flow predictions for the 2040s and 2080s. Daily flows in the Heat Source model at the boundary represented the log normal average of flow at the USGS gage site over the 30-year period (given that flows were not normally distributed over this period) multiplied by the gage site-to-boundary flow ratio as described above.

The future upper boundary condition flows for the MFJDR were determined differently, because Hamlet et al (2010) did not produce corresponding flow forecasts for the USGS gage station ORDEQ used to establish boundary flow (RKM 24.0, gage 14044000). Instead, we employed daily flow forecasts from Wenger et al. (2011), who used a Variable Infiltration Capacity (VIC) model to route downscaled CIG forecasts of precipitation to individual National Hydrography Layer (NHD) stream segments in streams throughout the western United States, including our study area. We used the Wenger et al. (2011) forecasts based on the same periods, GCM, emission scenario (A1B), and delta downscaled products that were used to forecast air temperatures. The Wenger et al. (2011) flow forecasts generally overestimated flow forecasts during summer low flow (Wenger et al. 2010), which was observable when we compared their predictions to measured flow for a segment of the MFJDR that was gauged. To account for this overestimate, we created a daily calibration factor for every day in the model simulation period over the 1977-2006 period by calculating the ratio of flow from the Wenger et al. (2011) modeled forecast at the USGS gauging station to measured flow at that site. Those calibration factors were then applied to the NHD segment containing the MFJDR upstream boundary to generate daily flow forecasts (over 30 years; 1977-2006) for the current period, and the 2040s and 2080s. We used a log-normal average of daily flow rather than the arithmetic average because of a non-normal distribution of flows over the 30 year period.

The Wenger et al. (2011) projections were also used to produce flow forecasts for the tributaries that input water into the NFJDR (n = 22) and MFJDR (n= 44) along the model domain. A GIS was used to identify and pair the boundary river segments within the Heat Source model to the NHD flow forecasts described above. These flow forecasts were calibrated using the same calibration factors generated for the MFJDR boundary, and represent a log

normal average (n=30 years) of daily flow for each of the periods of interest in this study (current, 2040, 2080).

Chapter 2 Appendix B

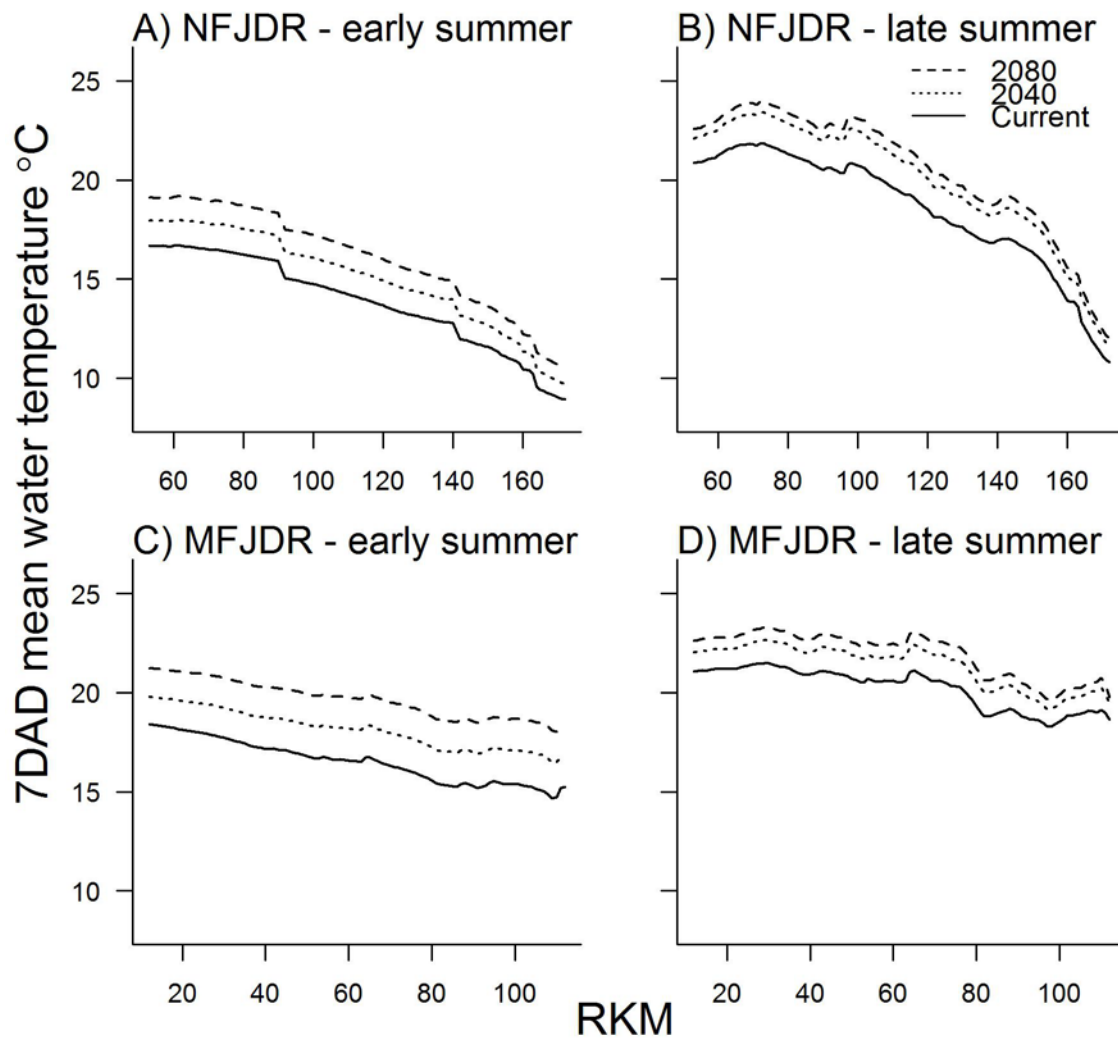


Fig. B-1

Forecasts of the longitudinal profile of stream temperature (7DAD mean) in the NFJDR (A) during early summer, (B) during late summer, and in the MFJDR (C) during early summer, (D) during late summer. Current (1977-2006), 2040, and 2080 represent the 30 year average 7DAD mean temperatures. RKM – river kilometer.

Chapter 2 Appendix C

Restoration potential: NFJDR versus MFJDR

The potential for riparian restoration to ameliorate climate-induced stream warming varied in our study streams. In the NFJDR restoration had relatively little potential to offset warming, while in the MFJDR restoration resulted in a noticeable reduction in stream temperature. The lower capacity of restoration to reduce temperatures in the NFDJR is related to two factors. First, the upper NFJDR is a protected area (from RKM 120 to 164), and throughout that area, the effective shade provided by the riparian corridor is already high (Fig. C-1). ORDEQ considered this area to already contain the maximum potential riparian vegetation (in terms of tree height and foliage density). Second, the lower NFJDR has both a smaller scope to increase effective shade (i.e., the difference between effective shade provided by current vegetation and restored vegetation is small relative to the MFJDR) and the magnitude of effective shade achievable in the lower NFJDR is smaller than that the potential effective shade in the lower MFJDR (Fig. C-1). This is likely a function of (1) smaller channel widths in the MFJDR, which allow for more effective shading of the stream if restored, and (2) differences in the Ecoregion-Physiographic (EP) regions between these stream systems, which in turn, influence both the tree heights in the riparian canopy and the foliage density predicted after restoration. The method of defining these EP regions and their associated potential vegetation relies on basin-specific historic assessments, plant association studies, observations during by ORDEQ during the Total Maximum Daily Load monitoring, and the literature (ORDEQ 2010). Ultimately, every reach within the landscape is assigned an explicit EP region with associated vegetation characteristics after identifying the valley form and ecoregion of that reach.

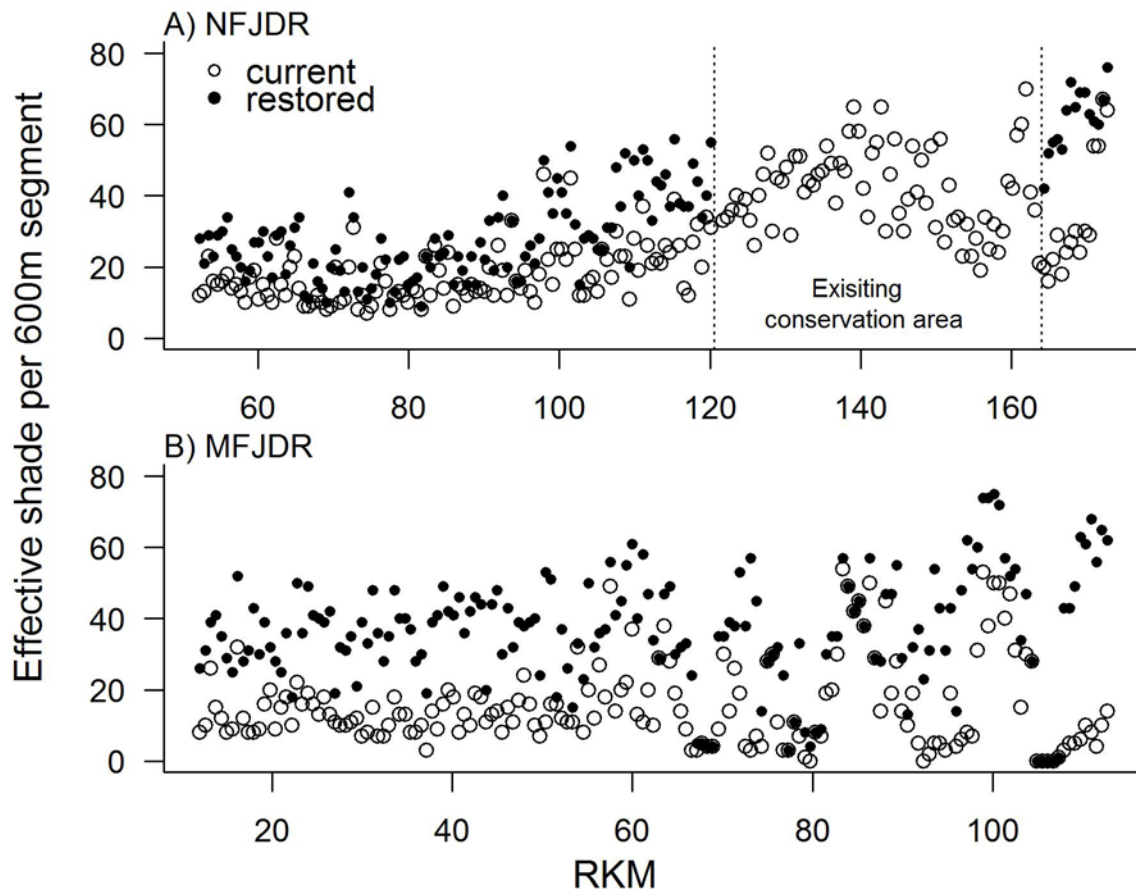


Fig. C-1

The average effective shade for each restoration segment for the current riparian vegetation on the NFJDR and the MFJDR, and the effective shade if the riparian corridor were restored to the system potential vegetation. A conservation area already exists in the NFJDR, and there the vegetation is assumed to be at the system potential (i.e., the maximum height and density of riparian vegetation). Effective shade was calculated for July 15, the warmest day during the calibration year (2002).

Spatial allocation of restoration effort

We prioritized riparian restoration efforts based on the capability of a given restoration segment (600 m in length) to create effective shade. Those segments where restoration created the largest increase in effective shade (compared to the current effective shade; termed ‘effective shade enhancement’) were restored first. We compared 129 potential restoration segments in the NFJDR, and 169 in the MFJDR. For each stream we restored the top 5, 10, 20, 30, 40, 50, 60,

70, 80, and 90% of segments, prioritized by their capacity to enhance shade. This prioritization method resulted in a non-random spatial positioning of restoration across the longitudinal profile of the NFJDR (Fig. C-2) and MFJDR (Fig. C-3). In both river systems, the greatest enhancements in effective shade resulted from restoration in the upper (i.e., upstream) stream sections, while a relatively small number of lower river segments were prioritized for restoration based on this criteria. As the percent of the landscape restored increased the spatial prioritization along the river corridor became more heterogeneous, but still occurred largely in a downstream order. We compared prioritized to opportunistic restoration, where opportunistic restoration was represented by randomly choosing restoration segments according to the same percentage of restoration investment, but without regard for their capability to enhance effective shade. The spatial positioning of this opportunistic restoration is shown in Fig. C-2 and C-3, to provide contrast to the prioritized restoration efforts.

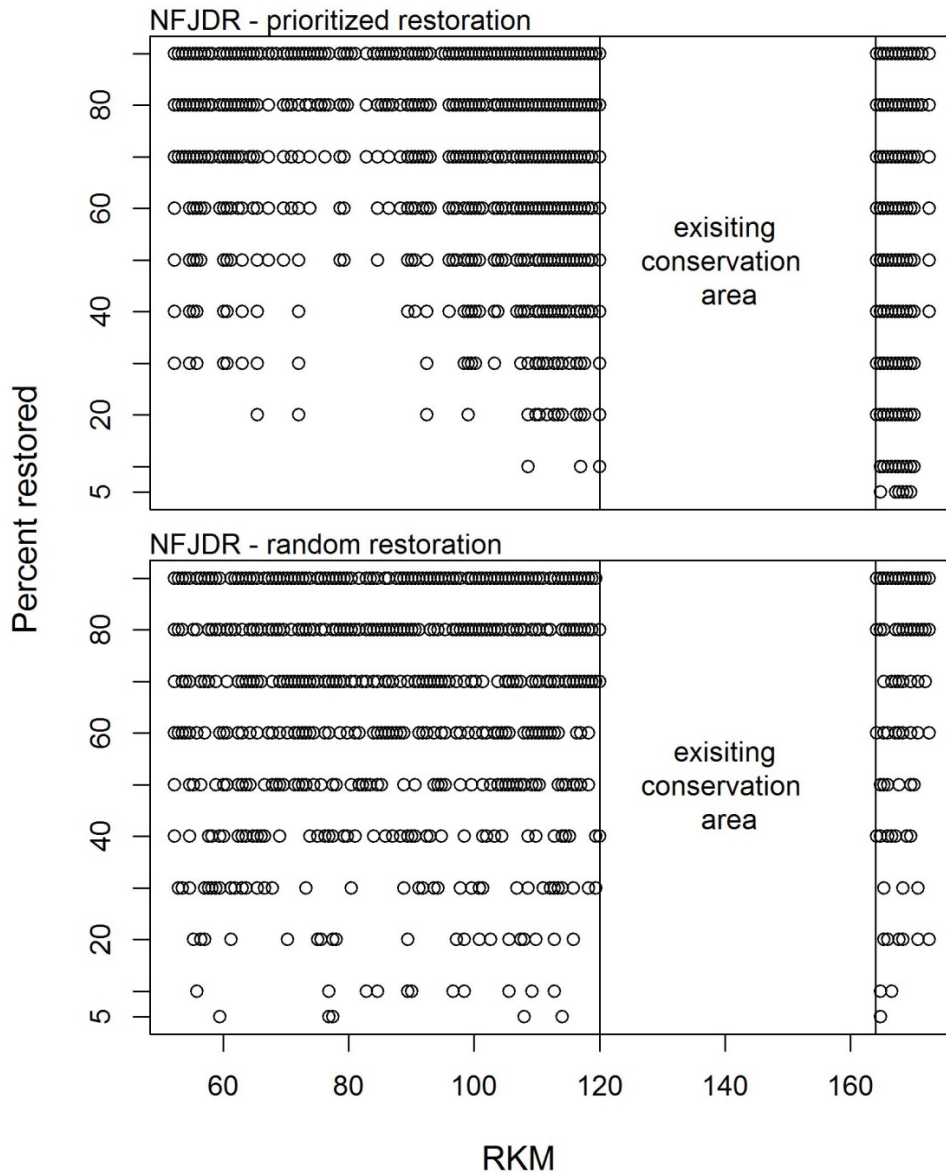


Fig. C-2

Spatial arrangement of prioritized and random restoration allocation from downstream (RKM52) to upstream (RKM 172) in the NFJDR. Each point represents a 600 m restoration segment. Restoration effort ranged from 5% of potential segments (6 of 129 segments) to 90% (116 of 129 segments), prioritized based on each segments potential to enhance of effective shade within that segment relative to other segments. Random restoration represents the random selection of segments at the same level of effort (i.e., 5 to 90%), without regard to their potential to enhance effective shade.

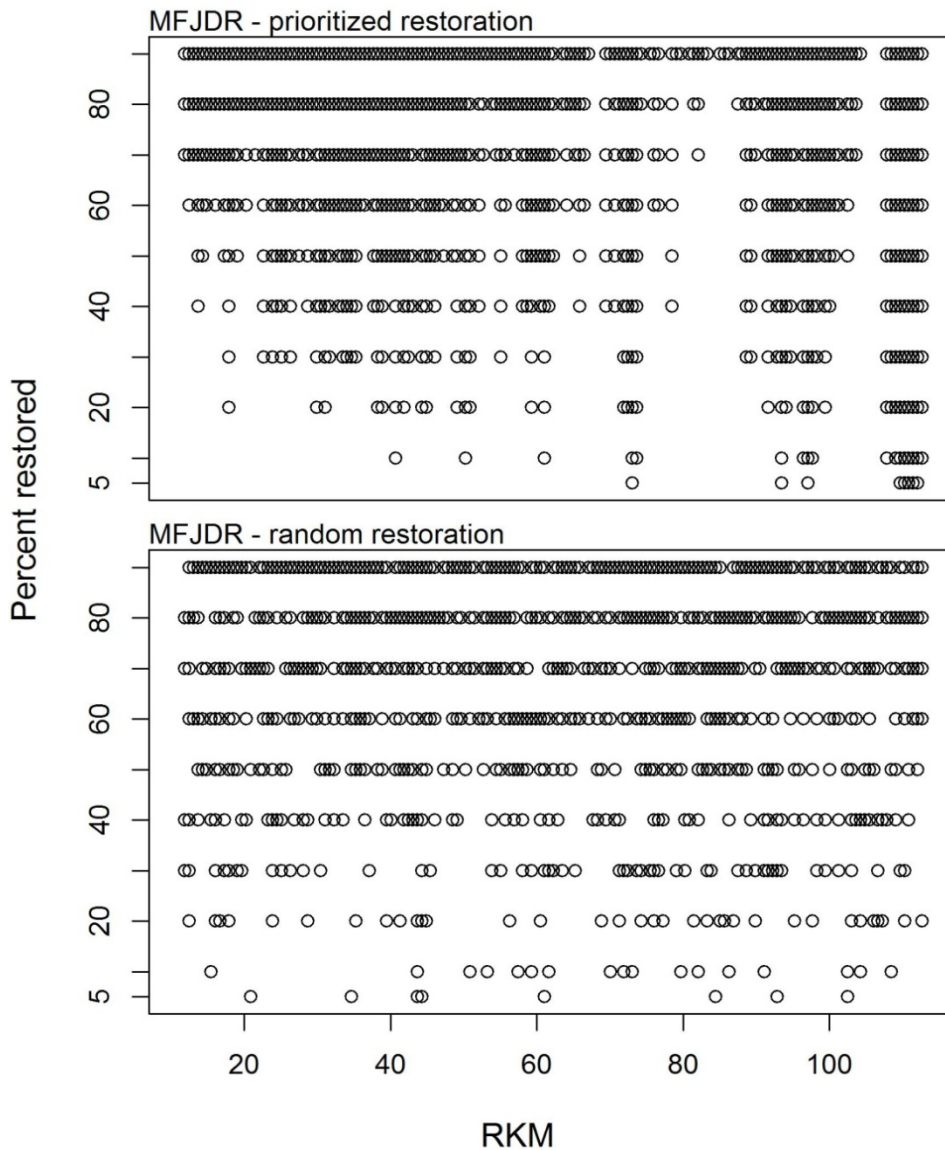


Fig. C-3

Spatial arrangement of prioritized and random restoration allocation from downstream (RKM12) to upstream (RKM 112) in the MFJDR. Each point represents a 600 m restoration segment. Restoration effort ranged from 5% of potential segments (8 of 169 segments) to 90% (152 of 169 segments), prioritized based on each segments potential to enhance of effective shade within that segment relative to other segments. Random restoration represents the random selection of segments at the same level of effort (i.e., 5 to 90%), without regard to their potential to enhance effective shade.

Chapter 2 Appendix Literature Cited

- Hamlet, A. F., P. Carrasco, J. Deems, M. M. Elsner, T. Kamstra, C. Lee, S.-Y. Lee, G. Mauger, E. P. Salathe, I. Tohver, and L. Whitely Binder. 2010. Final Project Report for the Columbia Basin Climate Change Scenarios Project, <http://www.hydro.washington.edu/2860/report/>.
- Hamlet, A. F., and D. P. Lettenmaier. 2005. Production of temporally consistent gridded precipitation and temperature fields for the continental United States. *Journal of Hydrometeorology* 6:330-336.
- Mohseni, O., and H. G. Stefan. 1999. Stream temperature air temperature relationship: a physical interpretation. *Journal of Hydrology* 218:128-141.
- Mohseni, O., H. G. Stefan, and T. R. Erickson. 1998. A nonlinear regression model for weekly stream temperatures. *Water Resources Research* 34:2685-2692.
- ORDEQ. 2010. John Day River Basin total maximum daily load (TMDL) and water quality management plan (WQMP). Page 167, Portland, Oregon.
- Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America* 108:14175-14180.
- Wenger, S. J., C. H. Luce, A. F. Hamlet, D. J. Isaak, and H. M. Neville. 2010. Macroscale hydrologic modeling of ecologically relevant flow metrics. *Water Resources Research* 46.

CHAPTER 3

PHYSIOLOGY DEFINES INVASION EXTENT OF A RIVERINE FISH

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Reference: to be submitted

Abstract

Few studies have used physiology to identify key mechanisms that underlie a species' distributional extent. Given the magnitude of environmental changes anticipated in the coming decades, there is an immediate need to produce robust, mechanistic-based, predictions of how species are likely to respond. To address this challenge, we combined landscape observations of the distribution of an aquatic invasive ectotherm (smallmouth bass; *Micropterus dolomieu*) in two Pacific Northwestern streams with mechanistic models to illustrate how physiology determines their distributional range. We hypothesized that the range limits of this species resulted from temperature-dependent constraints on growth. To test this hypothesis we leveraged the strong upstream-downstream thermal gradient present in our study system and used bioenergetic models to determine the effect of temperature on growth across all life-history stages of bass at increasingly upstream (i.e., colder) sites. In doing so we identified that growth in the earliest life-history stage of bass (age 0) was the most temperature-sensitive. Upstream, scope for growth collapses in young-of-year bass because their ability to consume food declines rapidly as temperatures cool. Our field data on the upstream extent of bass reproduction revealed that the majority of adult bass position their upstream-most spawning nests to maintain temperature-dependent consumptive capacity, and therefore, sufficient growth scope for age-0 progeny. This pattern was repeated in both of our study streams, and explained why bass positioned their nests twice as far upstream in the warm stream we studied compared to the cold one. The placement of spawning nests by adult bass is subject to strong evolutionary selection in temperate systems: if young-of-year bass do not achieve sufficient growth in their first summer they are unlikely to survive an overwinter starvation period. Consumptive capacity and growth in older bass (age 3-4) was far less sensitive to temperature compared to young bass. Our field

surveys revealed that some larger bass moved upstream as the study stream warmed into late summer, and these movements were most likely undertaken to alleviate the metabolic and waste costs associated with increasing seasonal temperatures. However, given that adult bass return to their spawning grounds every spring, the more temperature-sensitive young-of-year bass set the upstream range limit of this species in temperate streams. By knowing which life-history stage determines a species' distribution, managers can target strategies to either enhance or diminish the growth performance of that stage, depending on their objectives.

Introduction

In recent years, many ecologists have called for mechanistic-based investigations to understand the underlying controls on species distributions. Kearney and Porter (2009) argue that species' physiology provides the optimal template to build mechanistic models that address many of the uncertainties inherent in correlative approaches. For example, mechanistic models do not rely on the assumption that species distributions are at equilibrium with their environment. Therefore, they can be especially useful when predicting how a species range may change in response to climate change (Deutsch et al. 2008, Huey et al. 2009, Kearney et al. 2010) or the extent to which a non-native species may spread in a novel environment (Tucker et al. 2010, Ibáñez et al. *in press*).

Ectothermic organisms provide an excellent model to test physiological hypotheses that underlie species persistence, given (1) the well developed physiological theory of these organisms, and (2) their internal temperature matches the external environment, and therefore key physiological rates, such as metabolism, growth, and consumption directly respond to alterations in environmental conditions (Huey et al. 2012). Energy balance equations have been

developed for ectotherms that allow one to determine the climatic cost an animal endures to live at a particular location (Kearney and Porter 2009). Animals will not persist in an area if they run a negative energy budget, because even maintenance metabolism has an energetic cost, not accounting for the fact that animals need to grow to reproduce. Thus, there have been several examples that show the promise of using physiology to explain distributional patterns in terrestrial (Kearney and Porter 2004, Monasterio et al. 2011) and aquatic vertebrate ectotherms (Coleman and Fausch 2007, Pörtner and Peck 2010, Gifford and Kozak 2012), as well as in invertebrates (Hoogenboom and Connolly 2009, Leroux et al. 2013), and bacteria (Lennon et al. 2012).

The limits of species' ranges are often constrained by environmental tolerance, and in many ectotherms that tolerance differs between life history stages (Pörtner and Farrell 2008, Beauchamp 2009). As a consequence, the most sensitive life-history stage may set the distributional limits of all other life stages. For example, adult stream-type Chinook salmon stage in rivers months before spawning, and are more sensitive to warm water temperatures than their fry or juveniles due to temperature-dependent constraints on their aerobic scope (Pörtner and Farrell 2008). Thus, adequate staging conditions for adult salmon are likely to limit where stream-type Chinook populations as a whole can persist. Identifying the most sensitive physiological stage of a given species life history is essential for the conservation of native species, and for invasive species, it provides insight into vulnerabilities that could be harnessed to control their spread. Both of these applications are essential to deal with contemporary ecological issues and for future planning to develop the most effective adaptation strategies to climate change.

Here we use a landscape-scale observation dataset, paired with mechanistic models to examine if physiology can explain our observations of the range limits of non-native smallmouth bass (*Micropterus dolomieu*) in river systems in the Pacific Northwest. We hypothesized that the upstream distribution of this species resulted from temperature-dependent constraints on growth. To test this hypothesis, we leveraged the strong upstream-downstream thermal gradient present in our study system and used bioenergetic models to determine the effect of temperature on bass growth at increasingly upstream (i.e., colder) sites. We carried out our analysis across all life history stages of bass (from young-of-year to adult) to determine if temperature-sensitivity of bass growth changed as they matured, and to identify stage-specific bottlenecks that may set the range limits for other ages. In this work, we draw on observations of bass distributions in two river systems with contrasting thermal regimes to test the repeatability in our understanding of physiology-based range limits of smallmouth bass.

Methods

Study organism

Smallmouth bass (bass hereafter) are native to the central and parts the eastern United States, but have been introduced globally (Quinn and Paukert 2009). In many freshwater ecosystems, their introduction is associated with the loss of native prey assemblages, the displacement of prey fishes from their optimal habitat for growth, and the reduction in the growth of competing predators because bass are omnivorous, opportunistic predators with high food demand (Vander Zanden et al. 1999, Zweifel et al. 1999, Jackson 2002). In the Pacific Northwestern United States, the upstream invasion by non-native bass has caused wide-spread

conservation concern (Carey et al. 2011) given their demonstrated impacts on endangered Pacific salmon (Sanderson et al. 2009, Kuehne et al. 2012).

At a broad scale, climate is hypothesized to control the upper latitudinal distribution of bass due increasing overwinter mortality of young bass as growing seasons decline and winters become more severe (Shuter and Post 1990). Young-of-year bass (YOY hereafter) must have a summer growing season of sufficient duration to reach a critical minimum size, otherwise they are likely to die of starvation due to the depletion of their energy reserves during minimal feeding winter months. Smaller fish have a smaller capacity to store energy relative to larger individuals. The critical size required for overwinter survival varies with winter duration (Shuter et al. 1980). With increasing latitude, longer more severe winters require YOY bass to achieve greater growth in a shorter summer period; ultimately a latitude is reached where the combination of winter duration and too short a growing season prevents the overwinter survival of YOY bass, and therefore their recruitment to the second year of life. Size dependent overwinter survival in bass has been demonstrated in both field and laboratory studies (Oliver et al. 1979, Curry et al. 2005). Other researchers have suggested that attaining a critical size is more important for reducing risk of predation than overwinter starvation (Lyons 1997, Garvey et al. 1998), especially at lower latitudes (Suski and Ridgway 2009). Taken together, a rich body of literature supports the premise that first summer growth is a critical component of successful recruitment and determinant of year class strength in young bass.

Mid- to high-latitude river systems bear some of the same characteristics of thermal gradient that are thought to control the broad scale northern range limits of bass—i.e., they transition from wide and warm systems downstream to narrow and cold systems upstream. However, in rivers the thermal gradient occurs over a much finer spatial domain than the

latitudinal pattern in temperature because downstream-to-upstream changes in elevation, snow-melt driven flows, and canopy shading shift rapidly in river systems. We hypothesized this strong gradient in thermal regime was likely to control the upstream extent of bass in high elevation river systems where YOY bass have reduced opportunity for first-summer growth and have to withstand an increasingly severe winter as they move upstream. This dual challenge to YOY survival is a critical determinant of year class strength and is likely to serve as a strong selective mechanism for where adult bass reproduce on the landscape. If bass spawn too high in the watershed, their young will be unlikely to achieve the size threshold required (and hence the needed accumulation of energy reserves) to survive winter.

Adult male bass provide extensive care for their young (first description, Beeman 1924). Each spring they construct spawning nests, and if they successfully reproduce they guard their nest until their have young transitioned through a series of developmental stages, starting as eggs, metamorphosing into non-swimming fry, and ultimately fry swim out of their nests and begin exogenous feeding (Cooke et al. 2002). This pattern of parental care is important to consider when investigating distributional patterns of adult bass because reproducing bass are strongly tied to their nesting grounds, for up to 6 weeks, during the early summer (Armour 1993). Lawrence et al. (2012) documented that all adult bass (i.e. males and females) reside within the nesting areas, and do not move upstream of the reproductive zone until later in the summer. In prior work we used correlative techniques to illustrate the upstream extent of bass is likely to be temperature driven (Lawrence et al. in press). Here we use bass physiology to provide a mechanism to explain that correlation.

Study system

We measured bass distribution in the John Day River (JDR) basin, a snow-melt fed tributary of the Columbia River, supporting one of the last remaining (entirely) wild populations of Chinook salmon. Smallmouth bass were first introduced to the lower North Fork John Day River in 1971 to support recreational fishing opportunities. Since that time bass have expanded upstream from their introduction site and now reside throughout the basin, although their abundance declines in the headwaters of the JDR (Lawrence et al. 2012). In 2009 we conducted a seasonally repeated, spatially continuous snorkel survey of the North Fork John Day River (NFJDR hereafter) and the Middle Fork John Day River (MFJDR) to describe the (size-specific) distribution of bass and their upstream extent (Fig. 3.1). The survey covered 53 km in the NFJDR and 54 km in the MFJDR. The bass survey extent in the NFJDR extended from river kilometer 0 (RKM hereafter; defined as the confluence of the NFJDR and the MFJDR) to RKM 53.9, where RKM increases in an upstream direction. In the MFJDR we surveyed bass distribution from RKM 11.7 (measured from the NFJDR/MFJDR confluence) to RKM 65.7 (Fig. 3.1). These surveys had both a small sampling grain (i.e. almost every channel unit was sampled) and a large extent (Schneider 2001). Surveys were conducted during June 16-24, and repeated August 1-11, 2009. Bass were spawning during the June survey, so we also documented the spatial distribution of bass nests. A detailed description of the survey methods can be found in Lawrence et al. (2012).

Modeling framework

We used the Wisconsin bioenergetic model (Hanson et al. 1997), with input data from our study site, to determine growth and consumption patterns of bass at increasingly upstream

sites in the NFJDR and MFJDR. We modeled age 0 (YOY), 1, 2, 3, and 4 year old bass to identify age-specific constraints on growth over the longitudinal continuum of the river. This framework allowed us to test our hypothesis that the nesting distribution and upstream extent of bass reproduction in temperate river systems is determined by reductions in growth opportunities, which ultimately have fatal consequences if YOY bass do not achieve a minimum size required to overwinter. We used bioenergetic parameters sets from Shuter & Post (1990) for bass whose starting weight was <50 g (i.e. age 0-2 year olds) and Whitley et al. (2003) for age 3-4 bass, as recommended by Whitley et al. (2003, see Appendix A). The Whitley et al. (2003) bioenergetics model also provided us a mechanistic approach to investigate if our observations of the size distribution of adult bass from downstream to upstream could be explained based on size-dependent physiology.

Bioenergetics is an energy-balance approach that uses fish physiology and first principals to solve the energy equation: $Growth = Consumption - (Waste\ losses + Metabolism)$. Typically, growth is measured and consumption is solved for in this equation. We estimated growth using scales collected from adult bass in the NFJDR, just upstream of the confluence with the MFJDR (0.2 km upstream, n=29). For reference we call this the ‘calibration’ site. At the calibration site we solved the bioenergetics equation to estimate the daily amount of food (units: g/d) required to achieve the observed growth. Most inputs required for bioenergetic modeling were field-derived from the NFJDR (see below). We carried out this process for age 0, 1, 2, 3, and 4 year old bass, where age 0 represented YOY bass spawned in June.

Once we had established the food consumption required to achieve the observed growth for each age class of bass, we then modeled the growth achieved by those age classes at increasingly upstream sites (including and beyond where bass currently reside) if they ate the

same biomass of food as bass at the downstream (calibration) site. This allowed us to investigate the role of temperature in determining bass growth, given a fixed amount of daily consumption (i.e., food availability). One important note is that the capacity for bass to process food decreases as temperatures become colder (i.e., their maximal consumption, C_{\max} , goes down). Therefore, if the consumption rate of bass at a given site, on a given day, exceeded their temperature and size dependent C_{\max} , we set consumption to their maximal level on that day (i.e., the proportion of their $C_{\max} = 1$, or $p = 1$ in the bioenergetics literature). This prevented us from modeling physiologically unrealistic scenarios of consumption and growth. This approach also allowed us to evaluate temperature-regulated controls on consumptive capacity under fixed food availability.

Bioenergetic inputs

Solving the bioenergetic equation to determine seasonal consumption requires data on (1) bass growth (i.e. bass weight at the beginning and end of the growing season), (2) bass energy density, (3) bass diet, (4) the energy density of bass prey, (5) for reproductive bass (i.e., age 3 and older in the NFJDR), the loss of mass associated with spawning, and (6) the thermal experience of the bass over the growth season. The derivation of these inputs is given below.

Growth for age 0-4 bass was determined from adult bass pectoral scales collected by hook and line sampling primarily at the calibration site in subsequent years ($n = 51$ fish). For each bass we measured length-at-age from scale annuli and age back-calculation was calculated using the Fraser-Lee method (Devries and Frie 1996). Bass length-at-age was converted to weight-at-age (as required for bioenergetic modeling) using the length-weight equation $W = 0.0000116 * TL^{3.02}$ ($R^2 = 0.99$; $n = 109$; $p < 0.00001$, min TL = 22, max TL = 298). We assumed all

annual growth occurred over our modeling window (fry = time from emergence to October 31; adult = May 1 to October 31).

We also determined spawning losses and age-at-spawning from the bass that were collected for growth estimation. Spawning losses and age-at-spawning were determined by weighing bass gonadal tissue relative to whole body weight, and age as determined from scales. For age 2-4 bass, diets were determined by a combination of gastric lavage in the field, or by freezing bass and dissecting their stomach contents in the lab. Prey items in bass stomachs were identified to the lowest possible taxonomic unit, wet weighed, and then these units were pooled into 8 overall prey groups, based on similarity of prey energy density in each group. This allowed us to calculate the percent of wet weight that each group contributed to the overall bass diets. Diets were collected seasonally and represent May 1- July 1 (n=20 diets), July 1- August 1 (n=13), and August 1-October 31 (n=15). Diet results and energy densities are shown in Appendix A (Table A-1). Other required bioenergetic inputs (i.e., YOY and adult bass energy density, prey energy density, and age 0-1 diet) were derived from published estimates. All inputs and their sources are detailed in Appendix A (Table A-2).

The water temperatures bass experienced over the 2009 growing season were derived from data loggers deployed in the study streams. Data collection details are below.

Temperature monitoring

Water temperature is a key input in bioenergetic modeling, given physiological rates are determined by temperature in ectotherms. To characterize the thermal experience of bass at increasingly upstream sites in 2009 we deployed continuously recording temperature loggers (HOBO pendant, Onset Electronics, Onset, MA, U.S.A.) across 90 km of stream habitat in each

of our study systems (Fig.3.1). In the NFJDR, we logged temperatures from the calibration site (RKM 0.2) to RKM 89.5 (n=22 loggers). In the MFJDR, we monitored temperature from just above the NFJDR/MFJDR confluence (RKM 0.07) to RKM 89.3 (n=18 loggers). Temperature was recorded hourly over the summer (i.e. May–August) . We extracted the 7 day average daily mean (7DAD mean) from each logger and used it as input into the bioenergetic models described below. Not all loggers were deployed by May, so linear relationships between loggers deployed later (i.e. at the end of June) were developed during a time when both loggers were instream. Those linear relationships were then used to back-calculate May to late June temperature at a given site ($R^2=0.97-0.99$).

We logged winter temperatures (every 2 hours from September to June) at a subset of our spring-summer logging sites to characterize winter duration at increasingly upstream sites in the NFJDR and MFJDR, where winter duration was defined as the number of days that elapse when water temperatures drop below 10° C in the fall to when they rise above 10° C in the spring (Fig. 3.2; Shuter et al. 1980). The 10° C metric was chosen because bass cease feeding when water temperature drop below this threshold (Munther 1970, Oliver et al. 1979). We used the Shuter et al. (1980) index of winter duration to determine the size YOY bass need to attain at increasingly upstream sites in the NFJDR and MFJDR to survive their first winter. The equations for this index are:

$$L_0 = 0.0188d + 1.48$$

$$L_{100} = 0.0328d + 3.39$$

Where L_0 represents any length of YOY bass (cm) below which survival is 0% and L_{100} is the minimum length of YOY bass required for 100% overwinter survival; d is the duration of winter; i.e. the number of days when the water temperature was less than 10° C.

Modeling YOY growth from downstream to upstream

We modeled YOY growth using 4-stage models (Fig. 3.2). These models were run at each RKM where we had temperature data for the NFJDR and the MFJDR (Fig. 3.1, n=40 sites total). The following rule set for each stage was employed:

- 1) YOY were spawned when water temperature reached 15° C, a well documented thermal threshold that signals the onset of spawning in a wide range of bass populations (Armour 1993). Bass in the NFJDR were observed spawning at this temperature in 2009 (Lawrence unpublished data).
- 2) Bass incubate as eggs, and the duration of incubation (D_{inc} in days) prior to hatching is defined according to the equation: $D_{inc} = 83.2e^{-0.1606T}$, where T is the average post-spawning temperature (°C) for the incubation period (Shuter et al. 1980). Here we calculated T as the average 7DAD mean temperature for 7 days after reaching the 15° C threshold that initiates spawning.
- 3) Once bass eggs hatch they undergo further development in the nest before swimming up and beginning to feed exogenously. The duration of this developmental period (D_{dev} in days) was determined with the equation: $D_{dev} = 134e^{-0.1606T}$, where T is the average post-hatching temperature (°C; Shuter et al. 1980). We calculated T as the average 7DAD mean temperature for 7 days after the eggs hatched. Development from egg deposition (Stage 1) to fry swim up (Stage 3) took 10 to 18 days over the spatial domain of the

model (90 km), averaging 14 days in the area where bass nests were observed in 2009.

This corresponds to the range found in previous studies (Tester 1930, Ridgway and Friesen 1992, Warren 2009).

- 4) Once YOY bass were free-swimming fry, we initiated the bioenergetics model, with the physiological parameter set developed by Shuter and Post (1990). The initial weight of YOY bass was set to 0.01 g. At each site, the daily food consumption (g/d) derived from the calibration site (described below) was input into a custom R-based implementation of the bioenergetics model (version 2.13.0, R Development Core Team). We tracked growth until the model ended on October 31, 2009. If the assigned amount of food exceeded the YOY bass C_{max} on a given day, then they were fed C_{max} ($p=1$) that day. Because temperature limited consumption in cold upstream areas, the total modeled consumption varied across sites. October 31st was chosen as the model end date to ensure we captured the whole growing season available to YOY bass. The 7DAD mean temperature was 8.26° C at the NFJDR calibration site on this date, having dropped below 10° C on October 24, 2009.

The daily food amount (i.e., food availability in g/d) input into the bioenergetics model at all upstream sites was determined at the calibration site by (1) running the first 3 stages of the model with the temperature data from the calibration site and (2) once bass emerged from the nest, we solved the bioenergetics equation for daily consumption (g), given the observed growth of YOY bass in 2009. The average growth of YOY bass at this site was 67 mm (SD = 9, length range = 55-96 mm, weight range = 2.1-11.2 g, n = 51). Scale-estimated growth matched the size of the same cohort of bass collected the following spring using a seine (mean TL = 66 mm, SD = 5, length range = 57-75 mm, weight range = 2.3-5.3 g, n = 22). The calibration model was run

from fry emergence until October 31, 2009. All other bioenergetic inputs used to solve the bioenergetic equation at the calibration site (e.g., YOY energy density, diet, prey energy density) were kept constant when running bioenergetics models at increasingly upstream sites. When modeling growth at increasingly upstream sites, YOY bass were assumed to complete their growing season at that site (and not move downstream). We assumed YOY bass did not make long-range downstream movement, given we observed the same (2009) cohort in 2010 (now Age 1 bass) at the upstream-most nesting position (Lawrence et al. 2012). Other studies have found that YOY and Age 1 bass do not migrate (Lyons and Kanehl 2002).

Modeling age 1-4 bass growth from downstream to upstream

The growth of juvenile and adult bass (age 1-4) were modeled on a daily time step from May 1, 2009 to October 31, 2009 because these age classes were assumed to start feeding once water temperatures exceeded 10° C (Fig. 3.2, Step 5). For each age class of bass (1, 2, 3, 4) we determined the daily food consumption (g/d) required to attain the growth observed at the calibration site (NFJDR RKM 0.2) by solving the bioenergetics equation based on scale-derived growth information for each age-class. We then input the daily food consumption observed at the calibration site (used as a proxy for food availability) into bioenergetics model runs at each upstream site and recalculated the growth of that age class using a custom R version of the Wisconsin bioenergetics model. Like the YOY model, if the g/d of food input into the model exceeded the physiological capacity of bass to process it (i.e., $p > 1$), we fed them at C_{\max} ($p=1$). For age 3 and 4 fish, we applied spawning losses equal to 6% of their mass on June 4, 2009. This weight loss was determined from field collected bass (see above) and June 4 was the date water temperatures reached 15° C at the calibration site. All other bioenergetic inputs used to solve the bioenergetic equation at the calibration site (e.g., adult bass energy density, diet, prey

energy density) were kept constant when running bioenergetics models at increasingly upstream sites.

Results

Controls on bass nest distribution

The majority of bass nests observed in the NFJDR (i.e., 90%) occurred in the lower survey extent, below RKM 12.8 (Fig. 3.1). A few satellite nests occurred upstream of the downstream cluster, with the most upstream nest observed at RKM 22.4. Nests in the MFJDR occurred over a broader spatial extent, where 90% of nests were observed below RKM 27.7. The most upstream nest in the MFJDR was twice as far upstream (i.e., at RKM 44.7) as compared to the NFJDR. The growing degree days exceeding 10° C (GDD>10° C hereafter) available to YOY bass at the position where 90% of nests were observed was very similar between systems (971 in the NFJDR, 976 in the MFJDR; Fig. 3.3A, B). GDD>10° C at the most upstream nest in the NFJDR was 914 and 880 in the MFJDR. The spatial pattern of GDD>10° C shows that the MFJDR (Fig. 3.3B) was considerably warmer than the NFJDR (Fig. 3.3A).

The modeled growth of YOY bass, as reflected by weight at the end of the growing season, declined from downstream to upstream in the NFJDR and MFJDR (Fig. 3.3C, D), although the decline was more rapid in the colder NFJDR. We translated end weight (g) to end length (mm) using a NFJDR-derived weight-to-length regression (see methods) to evaluate overwinter survival of the observed nests in 2009. Fig. 3.3E and 3.3F shows the majority of bass place their nests within the zone where the total length attained by their YOY is sufficient to allow some probability of winter survival. If overwinter survival drops linearly (as suggested by Shuter et al.1980) between 100% and 0% at a given RKM, then survival for YOY bass in the

NFJDR would range from 9-19% for the majority of the observed nests (i.e. 90%), and 10-27% in the MFJDR. YOY bass collected from the NFJDR RKM 0.2 site had an end-of-winter size range from 55-96 mm (mean = 67mm; back-calculated from scales), which translates to a 0-75% range in overwinter survival (mean = 19%, Fig. 3.3E). YOY produced at the most upstream sites in the NFJDR and MFJDR (i.e. the relatively rare satellite nests) would not be expected to survive winter.

The reduction in modeled growth can be mechanistically explained by examining YOY bass consumption from downstream to upstream. Similar to growth, total modeled consumption declined across this continuum, with more rapid reductions in the NFJDR compared to the MFJDR (Fig. 3.3G,H). At the most downstream sites in the NFJDR and MFJDR, YOY bass were feeding below C_{\max} ($p=0.91$). However, at upstream sites, YOY bass consumption became increasingly temperature limited—that is, although food was available to YOY bass at these sites, temperatures were too cold for them to physiologically process it. In this situation we modeled YOY bass as feeding at their C_{\max} (i.e., $p=1$; details in methods), but their C_{\max} also declined as temperature declined (Fig. 3.3G, H). Overall, the temperature-dependent decline in consumptive capacity resulted in declining growth, as observed in Fig. 3.3C and 3.3D. Most bass nests occurred at, or downstream of the position in the stream, where YOY bass consumption became temperature constrained (Fig. 3.3G, H). Water temperature was cooler across the NFJDR relative to the MFJDR, and therefore consumption limitation was more severe with increasing upstream position in the NFJDR, relative to the MFJDR. This most likely explains why bass nest farther upstream in the MFJDR. In both systems, bass nests became more scarce as consumptive capacity declined to the point where YOY growth was insufficient for overwinter survival (Fig. 3.3E, F).

Consumption and Growth patterns of Age 1 to Age 4 bass

Similar to Age 0 bass (YOY), Age 1 and 2 bass experienced reduced consumption with increasing upstream extent, especially upstream of RKM 22, the site of the most upstream observed nest in the NFJDR (Fig. 3.4A). This reduction in Age 1 and 2 consumption was also driven by temperature-dependent limitations on consumptive capacity (Appendix B), although their consumption was less sensitive to declining temperature compared to YOY bass (Fig. 3.4A). Reduced consumption, in turn, led to reduced growth of Age 1 and 2 bass with increasing distance upstream (Fig. 3.4B). Overall, the reductions in growth relative to growth observed at RKM 0.2 (the calibration site) was greatest for Age 0 (up to 93% reduction), less for Age 1 (up to 58%), and even less for Age 2 (up to 43%) bass. At RKM 22, growth of Age 1-2 bass did not differ greatly from the downstream calibration site (Fig. 3.4B).

For Age 3 and 4 bass, consumption was far less temperature-constrained compared to Age 0-2 bass (Fig. 3.4A). At RKM 22, Age 3-4 bass consumption was equal to their consumption at RKM 0.2. In Age 3 bass, consumption declined somewhat with increasing upstream extent (i.e., a 14% reduction at RKM 48, a 35% reduction at RKM 89). Temperature effects on Age 4 bass consumption were even less (i.e., a 2% reduction at RKM 48, a 8% at RKM 89). Temperature-constraints on consumption only limited growth in Age 3 bass at the most upstream site (RKM 89; Fig. 3.4B), where their end weight was reduced by 26% relative to the growth observed downstream at RKM 0.2. Age 4 bass grew more with increasing upstream extent, even though their total consumption declined slightly (Fig. 3.4A,B).

The growth of young bass (Age 0-2) was more sensitive to temperature than older bass (Age 3-4) because of allometric differences in how their consumption capacity changed with temperature relative to metabolic and waste costs. As temperatures cooled progressively

upstream, the total energy consumption declined in Age 3 fish, but energy losses due to metabolism and waste did as well (Fig. 3.5A). Because the energy consumed by Age 3 bass exceeded their energy losses, they maintained scope for growth up until the most upstream site (RKM 89; Fig. 3.5A). By contrast, energy consumption in Age 0 bass dropped quickly upstream of RKM 8 (Fig. 3.5B), because maximum feeding was progressively more limited as temperatures declined upstream. In the case of Age 0 bass, the energy they consumed dropped faster than the alleviation in metabolic and waste costs (Fig. 3.5B), and so Age 0 fish had an increasingly limited scope for growth beyond RKM 22 (where the most upstream nest occurs). This Age 0 pattern was repeated in Age 1 and 2 fish, although their energy consumption did not decline as quickly as with Age 0 bass (Appendix B). The balance between energy consumed and energy lost due to waste and metabolism also explains how Age 4 bass could consume slightly less food upstream, but grow larger than at downstream sites (Fig. 3.4A,B). In this case, the metabolic and waste costs of Age 4 bass declined faster than their consumptive capacity decreased upstream, and relieved from those costs, they had a greater scope for growth. Energy losses due to waste and metabolism accounted for an increasing amount of the total energy budget in larger (older) bass. For example, at RKM 0.2 metabolic plus waste costs comprised 63, 71, 73, 78, and 84% of the energy budget in age 0 to age 4 fish, respectively. For Age 4 bass, energy losses due to waste and metabolism declined upstream (79% at RKM 22, 74% at RKM 48, 72% at RKM 89). Thus, as long as sufficient food is available, Age 4 fish will grow larger at cooler upstream temperatures.

The differences in age-specific constraints on scope for growth also provides a mechanism to explain seasonal movement patterns of different age classes of bass. In the NFJDR some larger (i.e. older) bass moved upstream in late summer, while smaller (younger)

bass did not (Fig. 3.6). During the early summer, the upstream extent of all age classes of bass occurred near the upstream-most nest (Fig. 3.6A). In late summer, a small portion of the age 2-4 bass population had moved upstream (as far as RKM 48, 23 km beyond the early summer bass extent). Bass <100 mm (age 1) stayed at, or downstream of, RKM 22 in late summer. The proportion of total bass >200 mm (age 3-4 fish) observed from downstream to upstream increased slower than the proportion of total >100 mm fish counted, providing additional evidence that some large bass may utilize upstream areas to reduce their metabolic demands. Nonetheless, the total number of >200 mm bass (n=360) was small compared to >100 mm bass (n=867), so smaller bass still outnumbered larger bass in upstream areas (data not shown).

Discussion

By combining field observations with bioenergetic modeling, this study provides a physiological basis to understand distributional constraints in the aquatic ectotherm, smallmouth bass. We demonstrated the scope for growth of YOY bass is more temperature sensitive than all other life history stages, and this sensitivity is driven by temperature-dependent constraints on consumptive capacity in YOY fish. Our field observations of bass upstream spawning extent, when assessed using this physiological framework, revealed that the majority of adult bass place their nests at a position in the stream where their young still have scope for consumption, and therefore, growth. This is essential because young bass must achieve a critical size to survive an overwinter period of starvation (Shuter et al. 1980). In both study streams, bass did not nest upstream of a position on the landscape where overwinter survival was unlikely. Winter duration also increases upstream, which provides additional disincentives for bass to place nests too far upstream given the energy required to survive a longer winter increases (while scope for growth and growing season simultaneously decline). Therefore, bass nest positioning is likely

under strong evolutionary selective pressure in mid- to high-latitude rivers that have long winters and relatively short growing seasons. Additionally, although some adult bass undergo post-spawning dispersal upstream, all adult bass return to their spawning grounds every spring (Lawrence et al. 2012). Thus, the most temperature-sensitive YOY life stage determines the upstream extent of all life stages of bass in this study system. Stage-specific temperature-limited scope for growth is likely to underlie range limits in many ectothermic species, given they are subject to same laws of allometry and their physiology is temperature-dependent (Shuter et al. 2012).

Our study also demonstrated that the relationship between temperature and scope for growth changes with life stage, and allometric changes are likely to explain why some adult bass moved upstream of their spawning grounds, while young bass did not. In this case, consumption capacity, and therefore scope for growth, declined rapidly with temperature in small bass (age 0-2), while for large bass (age 3 and age 4) consumptive capacity declined slowly. Metabolic and waste costs also decline with temperature, and so as long as food and consumptive capacity is available, reducing these costs benefit larger fish. Our results also demonstrated that metabolic costs become an increasing portion of the energy budget as bass grow larger, an allometric relationship well-established in metabolic theory (Gillooly et al. 2001). Therefore larger animals are more likely to benefit from reducing these costs, relative to smaller/younger fish. The relief from increasing metabolic costs associated with increased size also explains the apparent paradox of large bass growing more at cooler upstream temperatures while their total consumption declines. In this case, their consumptive capacity declined more slowly than metabolic and waste costs, and therefore their growth scope increased. However, if food becomes limiting upstream, then the energetic relief provided by cooler temperatures will be

outweighed by a lack of energy to support growth. While a reduction in primary and secondary productivity is anticipated in upstream sites (as temperatures cool and the riparian canopy closes the stream to direct sun), the shape of the productivity versus distance upstream curve has not been documented in Pacific Northwest streams. Therefore, we did not incorporate declining production (i.e., food availability) in our analysis. For small bass, the large reduction in consumptive capacity we observed with declining temperatures, strongly suggests temperature is more likely to set their upstream extent than food availability. In this case, no matter how much food is available upstream, small bass will not be able to process it, given the cooler temperatures found there.

Physiology based approaches that decipher the mechanisms that set range limits of invasive ectotherms could be leveraged by managers to reduce the probability of their establishment, control their spread, or reduce their impacts in areas where they are already established. For example, in the study region bass are expanding into critical areas used by juvenile salmon to rear (Lawrence et al. 2012). This is cause for widespread conservation concern, given the endangerment of many salmon populations with the Pacific Northwest (Ruckelshaus et al. 2002) and the documented negative effects of bass on juvenile salmon (Sanderson et al. 2009, Carey et al. 2011, Kuehne et al. 2012). Additionally, bass are predicted to persist farther upstream into salmon rearing areas as streams warm due to climate change (Lawrence et al. *in press*). In this situation, restoration measures aimed at cooling water temperatures (such as include enhancing riparian shade and reducing irrigation-related water withdrawals) could reduce the growth of YOY bass, and thus, decrease their overwinter survival. This will ultimately have demographic consequences for bass populations by diminishing overall recruitment, and in turn, may reduce their impact on rearing salmon.

Developing mechanistic approaches to understand the contemporary distributions of ectotherms is also essential to produce reliable predictions of how a given species is likely to respond to environmental change (Kearney and Porter 2009). For example, this approach allowed us to examine how key variables such as temperature mechanistically determine the distributional extent of bass in stream systems. In the case of conservation efforts, these approaches will provide us far more certainty we are targeting the right variable that either limits (in the case of invasive species) or enhances the distribution of our target species (in the case of native species recovery efforts). Additionally, using a mechanistic approach may also allow researchers to identify an environmental correlate (such as $GDD > 10^{\circ} C$ demonstrated here) that could be reliably applied to predict ectotherm distributions in other systems where data deficiencies preclude a physiological assessment.

Finally, many investigations that aim to predict how species distributions are likely to respond to climate change focus on a single life history stage of an organism. For example, many studies use adult thermal tolerance to anticipate climate-induced distributional changes in species of conservation concern (Eaton and Scheller 1996). This approach has merit if we know *a priori* which stage determines a species distribution, and then develop predictions based on that stage (e.g., Beer and Anderson 2011). However, often the most climate-sensitive stage is unknown. In this study we investigated how physiology changed through the life history of a species, and in doing so, we identified a climate-sensitive life history stage that sets the distributional limits of all other life history stages. We anticipate the framework developed here could be employed to identify similar stage-specific environmental sensitivity in many other species. This information, in turn, could be leveraged for a variety of applied ecological purposes.

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Literature Cited

- Armour, C. L. 1993. Evaluating temperature regimes for protection of smallmouth bass. United States Department of the Interior, Fish and Wildlife Service, Resource Publication 191, Washington, D.C.
- Beauchamp, D. A. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *American Fisheries Society Symposium* 70:1-19.
- Beeman, H. W. 1924. Habits and propagation of the small-mouthed black bass. *Transactions of the American Fisheries Society* 54:92-107.

- Beer, W. N., and J. J. Anderson. 2011. Sensitivity of juvenile salmonid growth to future climate trends. *River Research and Applications* 27:663-669.
- Buckley, L. B., M. C. Urban, M. J. Angilletta, L. G. Crozier, L. J. Rissler, and M. W. Sears. 2010. Can mechanism inform species' distribution models? *Ecology Letters* 13:1041-1054.
- Carey, M. P., B. L. Sanderson, T. A. Friesen, K. A. Barnas, and J. D. Olden. 2011. Smallmouth bass in the Pacific Northwest: a threat to native species; a benefit for anglers? *Reviews in Fisheries Science* 19:305-315.
- Coleman, M. A., and K. D. Fausch. 2007. Cold summer temperature limits recruitment of age-0 cutthroat trout in high-elevation Colorado streams. *Transactions of the American Fisheries Society* 136:1231-1244.
- Cooke, S. J., D. P. Philipp, and P. J. Weatherhead. 2002. Parental care patterns and energetics of smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*) monitored with activity transmitters. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80:756-770.
- Curry, R. A., S. L. Currie, S. K. Arndt, and A. T. Bielak. 2005. Winter survival of age-0 smallmouth bass, *Micropterus dolomieu*, in north eastern lakes. *Environmental Biology of Fishes* 72:111-122.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105:6668-6672.
- Devries, D. R., and R. V. Frie. 1996. Chapter 16: Determination of age and growth. Pages 483-512 in B. R. Murphy and D. W. Willis, editors. *Fisheries Techniques*, Second Edition. American Fisheries Society, Bethesda, Maryland.
- Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41:1109-1115.
- Garvey, J. E., R. A. Wright, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2414-2424.

- Gifford, M. E., and K. H. Kozak. 2012. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography* 35:193-203.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248-2251.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0 for Windows. Center for Limnology, University of Wisconsin-Madison and the University of Wisconsin Sea Grant Institute.
- Hoogenboom, M. O., and S. R. Connolly. 2009. Defining fundamental niche dimensions of corals: synergistic effects of colony size, light, and flow. *Ecology* 90:767-780.
- Huey, R. B., C. A. Deutsch, J. J. Tewksbury, L. J. Vitt, P. E. Hertz, H. J. A. Perez, and T. Garland. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B-Biological Sciences* 276:1939-1948.
- Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367:1665-1679.
- Ibáñez, I., J. Diez, L. P. Miller, J. D. Olden, C. J. B. Sorte, D. M. Blumenthal, B. A. Bradley, C. D'Antonio, J. S. Dukes, R. Early, E. D. Grosholz, and J. J. Lawler. *in press*. Integrated Assessment of Biological Invasions. *Ecological Applications*.
- Jackson, D. A. 2002. Ecological effects of *Micropterus* introductions: the dark side of black bass. Pages 251-264 *in* D. P. Philipp and M. S. Ridgway, editors. *Black Bass: Ecology, Conservation, and Management*. American Fisheries Society, Bethesda, Maryland.
- Jiménez-Valverde, A., A. T. Peterson, J. Soberon, J. M. Overton, P. Aragon, and J. M. Lobo. 2011. Use of niche models in invasive species risk assessments. *Biological Invasions* 13:2785-2797.
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334-350.
- Kearney, M., and W. P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119-3131.

- Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* 3:203-213.
- Kuehne, L. M., J. D. Olden, and J. J. Duda. 2012. Costs of living for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in an increasingly warming and invaded world. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1621-1630.
- Lawler, J. J., and J. D. Olden. 2011. Reframing the debate over assisted colonization. *Frontiers in Ecology and the Environment* 9:569-574.
- Lawrence, D. J., J. D. Olden, and C. E. Torgersen. 2012. Spatiotemporal patterns and habitat associations of smallmouth bass (*Micropterus dolomieu*) invading salmon-rearing habitat. *Freshwater Biology* 57:1929-1946.
- Lawrence, D. J., B. Stewart-Koster, J. D. Olden, A. S. Ruesch, C. E. Torgersen, J. J. Lawler, D. P. Butcher, and J. K. Crown. *in press*. The interactive effects of climate change, riparian management, and a non-native predator on stream-rearing salmon. *Ecological Applications*.
- Lennon, J. T., Z. T. Aanderud, B. K. Lehmkuhl, and D. R. Schoolmaster. 2012. Mapping the niche space of soil microorganisms using taxonomy and traits. *Ecology* 93:1867-1879.
- Leroux, S. J., M. Larrivee, V. Boucher-Lalonde, A. Hurford, J. Zuloaga, J. T. Kerr, and F. Lutscher. 2013. Mechanistic models for the spatial spread of species under climate change. *Ecological Applications* 23:815-828.
- Lyons, J. 1997. Influence of winter starvation on the distribution of smallmouth bass among Wisconsin streams: A bioenergetics modeling assessment. *Transactions of the American Fisheries Society* 126:157-162.
- Lyons, J., and P. Kanehl. 2002. Seasonal movements of smallmouth bass in streams. Pages 149-160 *in* D. P. Philipp and M. S. Ridgway, editors. *Black bass: Ecology, Conservation, and Management*. American Fisheries Society, Bethesda, Maryland.
- Monasterio, C., L. P. Shoo, A. Salvador, I. Siliceo, and J. A. Diaz. 2011. Thermal constraints on embryonic development as a proximate cause for elevational range limits in two Mediterranean lacertid lizards. *Ecography* 34:1030-1039.

- Munther, G. L. 1970. Movement and distribution of smallmouth bass in middle Snake River. *Transactions of the American Fisheries Society* 99:44-53.
- Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Transactions of the American Fisheries Society* 108:130-136.
- Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. Niche dynamics in space and time. *Trends in Ecology & Evolution* 23:149-158.
- Porter, W. P., and M. Kearney. 2009. Size, shape, and the thermal niche of endotherms. *Proceedings of the National Academy of Sciences of the United States of America* 106:19666-19672.
- Pörtner, H. O., and A. P. Farrell. 2008. Physiology and Climate Change. *Science* 322:690-692.
- Pörtner, H. O., and M. A. Peck. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* 77:1745-1779.
- Quinn, S., and C. Paukert. 2009. Centrarchid fisheries. Pages 312-339 in S. J. Cooke and D. P. Philipp, editors. *Centrarchid Fishes: Diversity, Biology, and Conservation* Wiley-Blackwell Chichester, U.K.
- Ridgway, M. S., and T. G. Friesen. 1992. Annual variation in parental care in smallmouth bass, *Micropterus dolomieu*. *Environmental Biology of Fishes* 35:243-255.
- Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33:665-706.
- Sanderson, B. L., K. A. Barnas, and A. M. Wargo Rub. 2009. Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? *Bioscience* 59:245-256.
- Schneider, D. C. 2001. The rise of the concept of scale in ecology. *Bioscience* 51:545-553.
- Seebacher, F., and C. E. Franklin. 2011. Physiology of invasion: cane toads are constrained by thermal effects on physiological mechanisms that support locomotor performance. *Journal of Experimental Biology* 214:1437-1444.

- Shuter, B. J., A. G. Finstad, I. P. Helland, I. Zweimuller, and F. Holker. 2012. The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences* 74:637-657.
- Shuter, B. J., J. A. Maclean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Transactions of the American Fisheries Society* 109:1-34.
- Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:314-336.
- Simmons, A. D., and C. D. Thomas. 2004. Changes in dispersal during species' range expansions. *American Naturalist* 164:378-395.
- Suski, C. D., and M. S. Ridgway. 2009. Winter biology of centrarchid fishes. Pages 264-292 *in* S. J. Cooke and D. P. Philipp, editors. *Centrarchid Fishes: Diversity, Biology, and Conservation*. Wiley-Blackwell, West Sussex, United Kingdom.
- Tester, A. L. 1930. Spawning Habits of the Small-Mouthed Black Bass in Ontario Waters. *Transactions of the American Fisheries Society* 60:53-61.
- Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conratt. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577-581.
- Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11:2234-2250.
- Tucker, A. J., C. E. Williamson, K. C. Rose, J. T. Oris, S. J. Connelly, M. H. Olson, and D. L. Mitchell. 2010. Ultraviolet radiation affects invasibility of lake ecosystems by warm-water fish. *Ecology* 91:882-890.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464-467.
- Warren, M. L., Jr. 2009. Centrarchid identification and natural history. Pages 375-533 *in* S. J. Cooke and D. P. Philipp, editors. *Centrarchid Fishes: Diversity, Biology, and Conservation*. Wiley-Blackwell, West Sussex, U.K.

- Whitledge, G. W., R. S. Hayward, and R. D. Zweifel. 2003. Development and laboratory evaluation of a bioenergetics model for subadult and adult smallmouth bass. *Transactions of the American Fisheries Society* 132:316-325.
- Woodward, F. I. 1990. The impact of low-temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 326:585-593.
- Zweifel, R. D., R. S. Hayward, and C. F. Rabeni. 1999. Bioenergetics Insight into Black Bass Distribution Shifts in Ozark Border Region Streams. *North American Journal of Fisheries Management* 19:192-197.

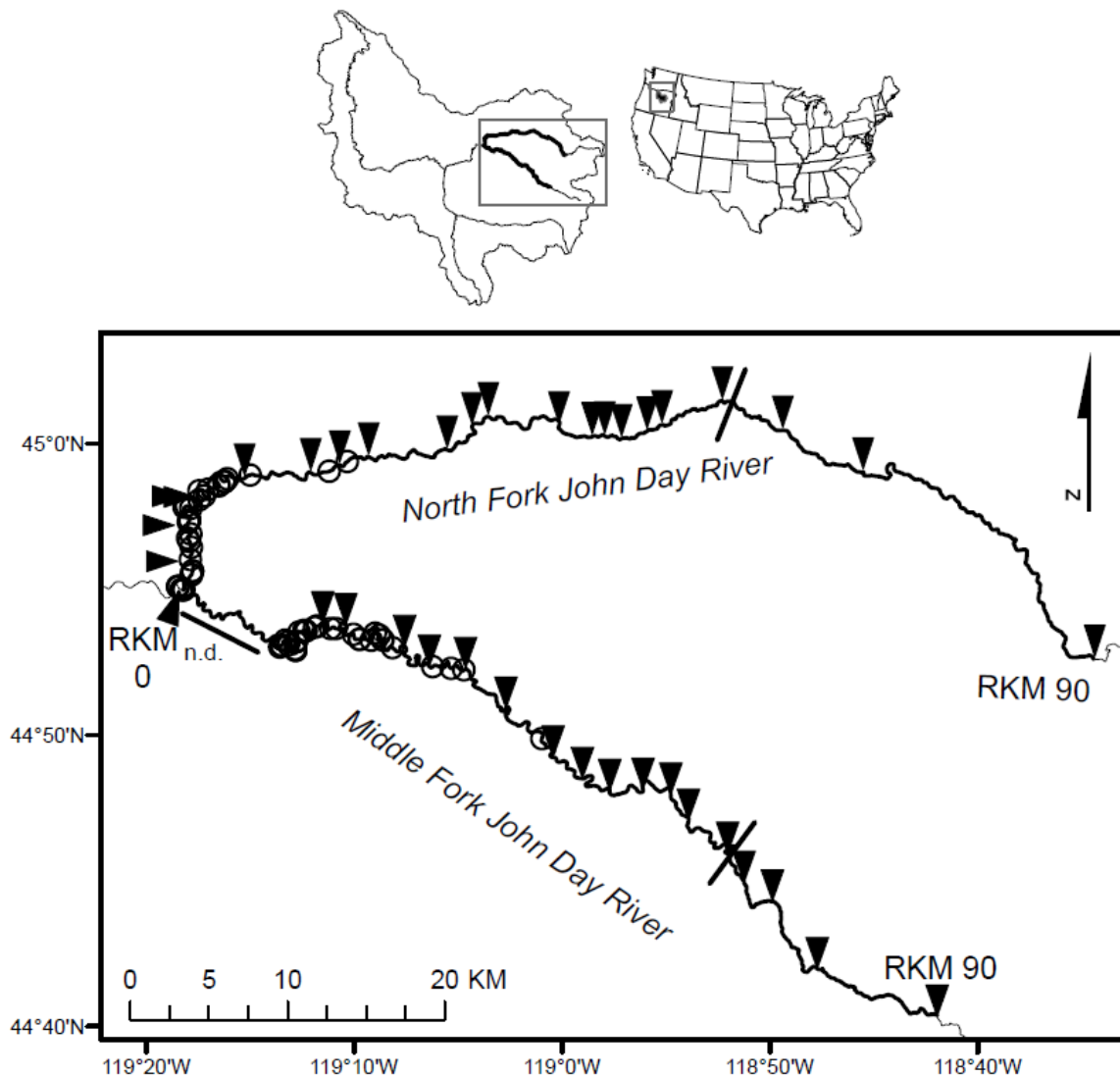


Fig. 3.1

Map of the NFJDR and MFJDR showing the extent of the study domain. RKM 0 represents the confluence of the NFJDR and MFJDR. Temperature logger positions (▼) and bass nests (○) are shown. Bass distribution surveys were conducted from RKM 0 (downstream) to RKM 53.9 (upstream) in the NFJDR and RKM 11.7 to RKM 65.7 in the MFJDR; the upstream extent of field surveys of bass are indicated with a solid line. n.d. – no data.

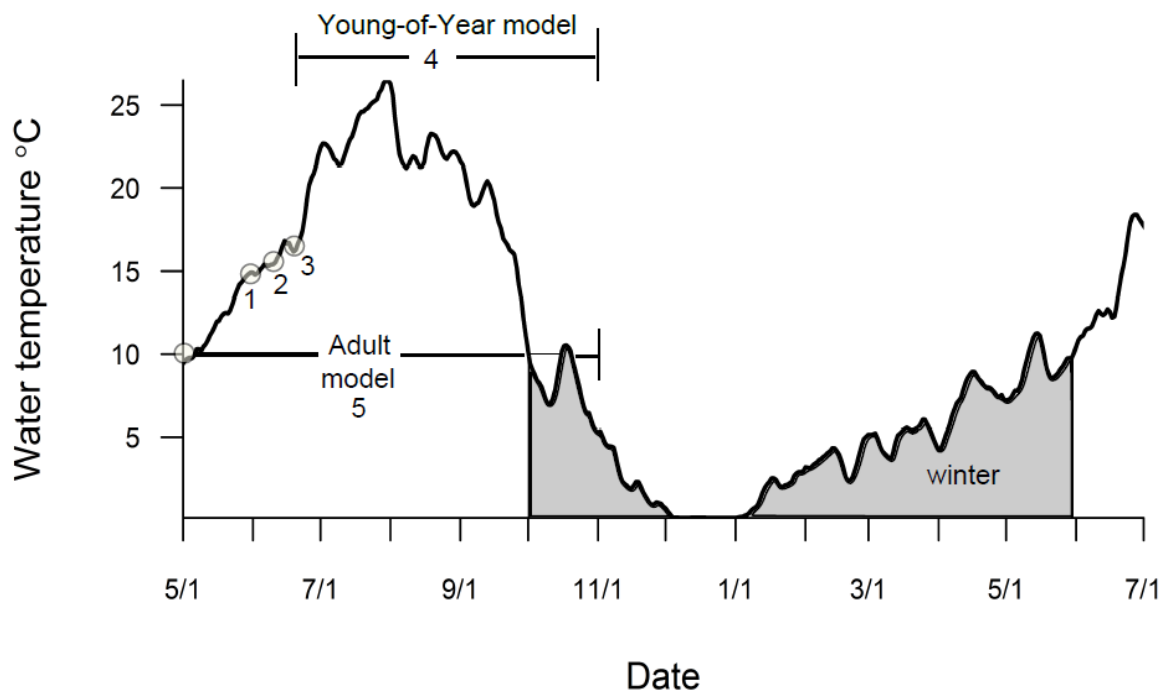


Fig. 3.2

7DAD mean water temperature at the NFJDR model calibration site (RKM 0.2) from May 1, 2009 to July 1, 2010. The young-of-year bass model consisted of 4 stages: 1) bass spawn when water temperatures reach 15° C, 2) bass eggs hatch into fry, 3) bass fry rise from the nest, and 4) bass fry begin to feed exogenously and the bioenergetics model starts. The model stopped on October 31, 2009. The time elapsed between stages 1→2 and 2→3 was determined by temperature-dependent equations (see methods). The age 1 to 4 bass bioenergetics models (5) ran from 5/1/2009 to 10/31/2009. The winter period, used to calculate winter duration, represents the days when temperatures were < 10° C, a threshold when bass stop feeding.

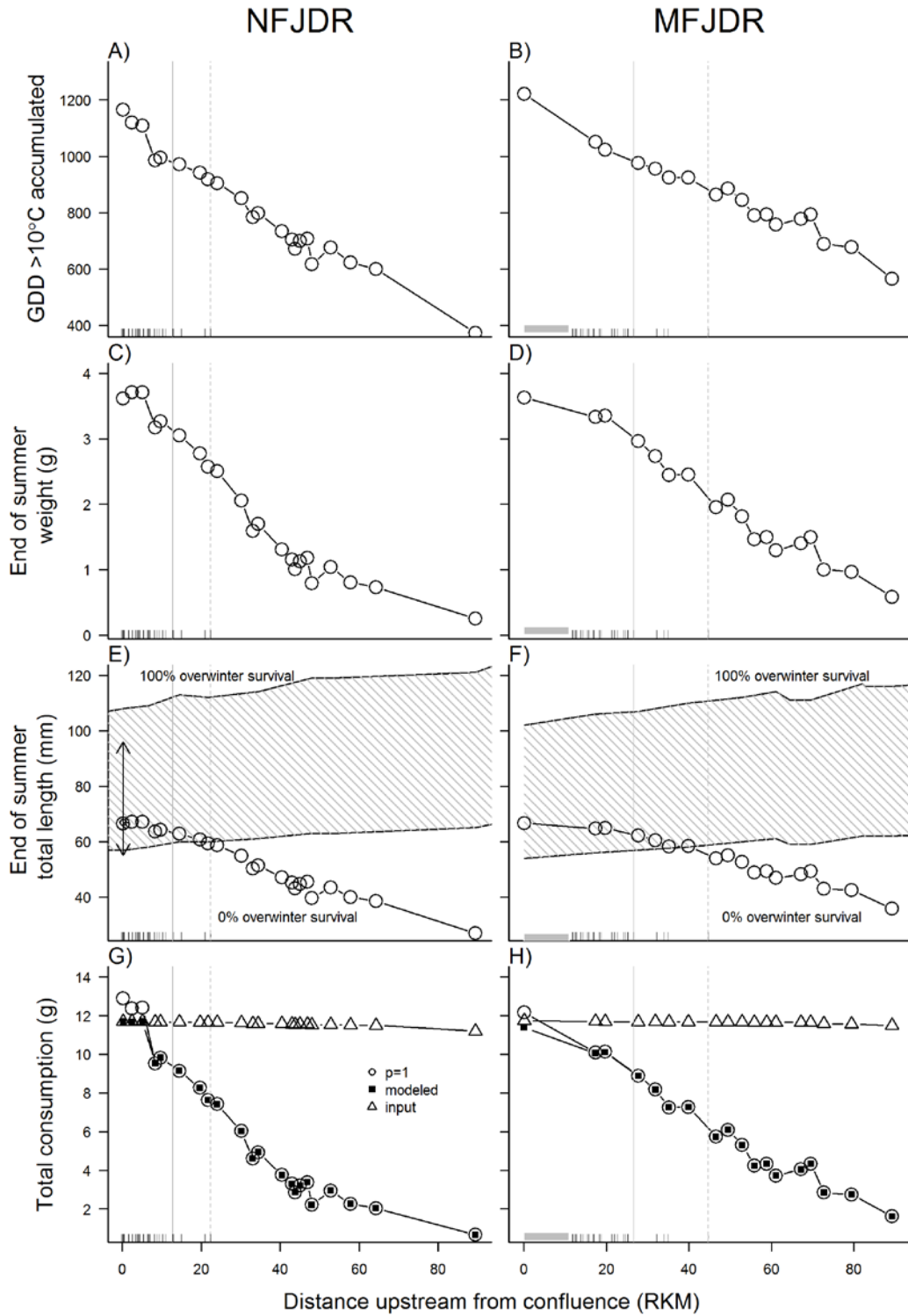


Fig. 3.3

The rug that runs along the x-axis on all panels indicates the spatial position of bass nests observed during the June 2009 survey. In the MFJDR we did not conduct nest surveys below RKM 11.7, but we anticipate nests were present from RKM 0 to RKM 11.7 (indicated by a solid gray bar adjacent to the rug). The vertical lines in all plots indicate the spatial position where

90% of nests were observed (counting from downstream; solid lines) and where the most upstream nest was found (dashed line). Growing degree days $> 10^{\circ}\text{C}$ accumulated by bass fry from the day of nest emergence until October 31, 2009 is shown across RKM in the NFJDR (A) and the MFJDR (B). The end weights of young-of-year bass on the last day of the growing season (October 31, 2009) are shown in the NFJDR (C) and the MFJDR (D). The total length of young-of-year bass at the end of the growing season is shown in the NFJDR (E) and MFJDR (F). The arrow in (E) indicates the range in young-of-year bass lengths observed from bass scales collected from the NFJDR. The hashed area in (E) and (F) indicates how the size of young-of-year bass required to survive winter varied across RKM in 2009. Within the hashed zone overwinter survival varies linearly from 100% to 0% (at a given RKM). If bass fall in the 0% zone they are not anticipated to survive winter. Total consumption (summed across the whole model simulation) of young-of-year bass by RKM is shown in the NFJDR (G) and MFJDR (H). $p = 1$ (open circles) indicates the maximum total consumption of bass at a given RKM (p is the proportion of C_{max} , where 1 = 100%). The triangles represent the total amount of food available for consumption across RKM, as determined from the total consumption observed at the NFJDR calibration site. If food available for consumption was greater than consumption capacity ($p = 1$) at a given RKM, then YOY bass were modeled as feeding at $p = 1$. Filled squares indicate the actual modeled consumption across RKM for young-of-year bass.

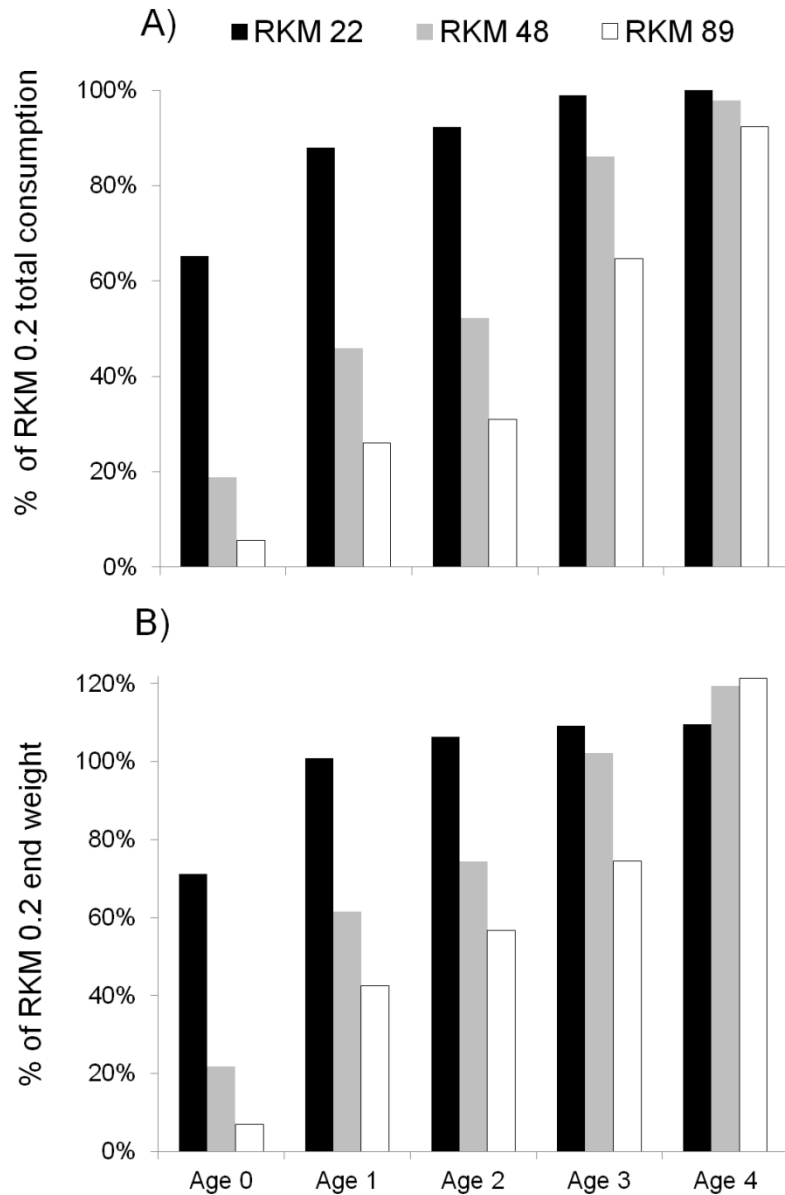


Fig. 3.4

(A) The percent of total consumption (summed over the model period) at NFJDR RKM 22, 48, and 89 relative to the downstream calibration site (RKM 0.2) for age 0-4 bass. (B) The percent of modeled end weight of bass at NFJDR RKM 22, 48, 89 relative to the downstream calibration site for age 0-4 bass. RKM 22 was the site of the most upstream bass nest in the NFJDR in early summer, and RKM 48 was the upstream-most site where adult bass were observed in late summer 2009.

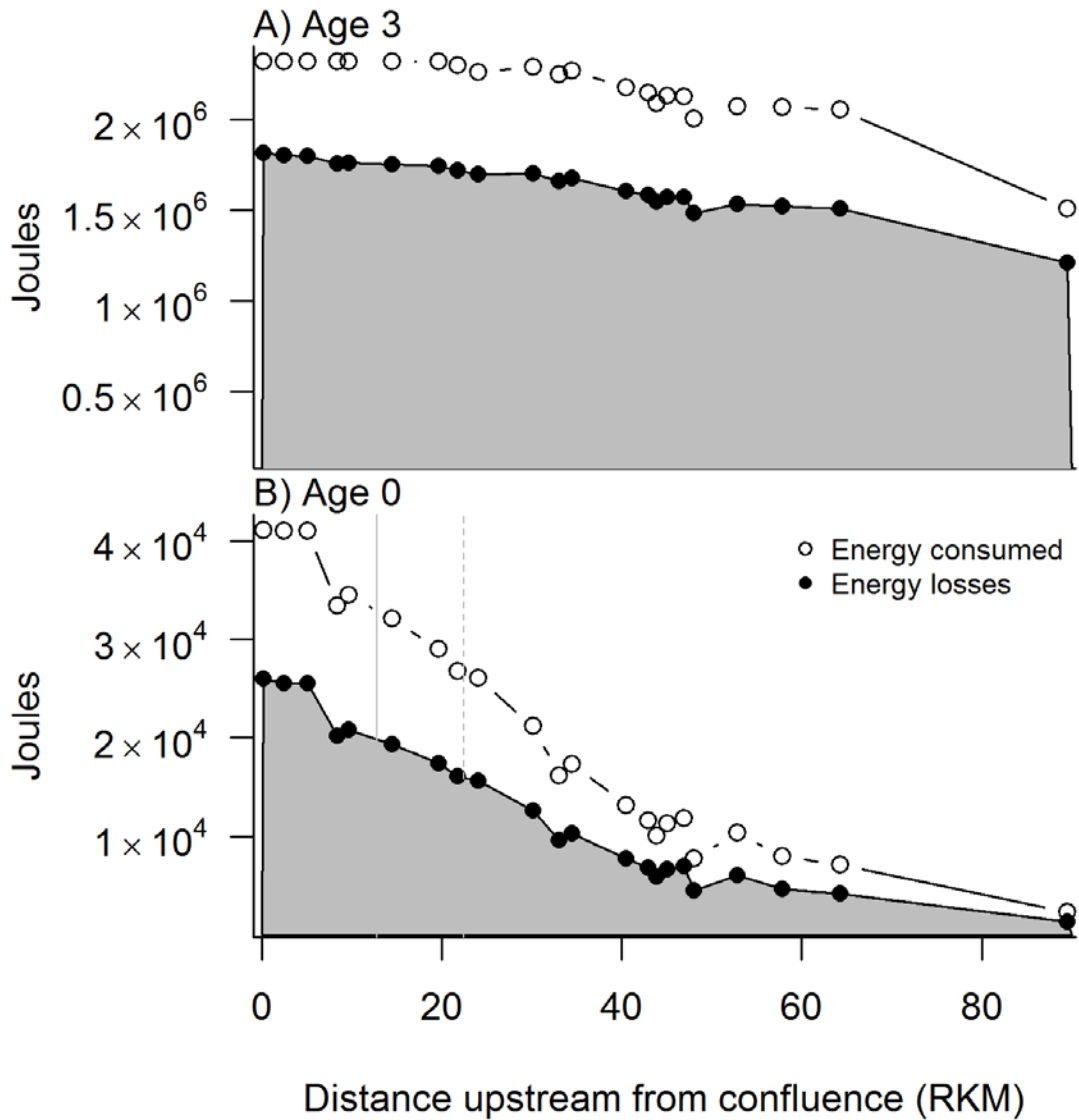


Fig. 3.5

The total energy consumed and energy lost (summed over all days of the model) for Age 3 bass (A) and Age 0 bass (B) across RKM in the NFJDR. If energy consumed exceeds energy losses, this indicates scope for bass growth. The vertical lines in (B) indicate the spatial position where 90% of nests were observed (counting from downstream; solid lines) and where the most upstream nest was found (dashed line).

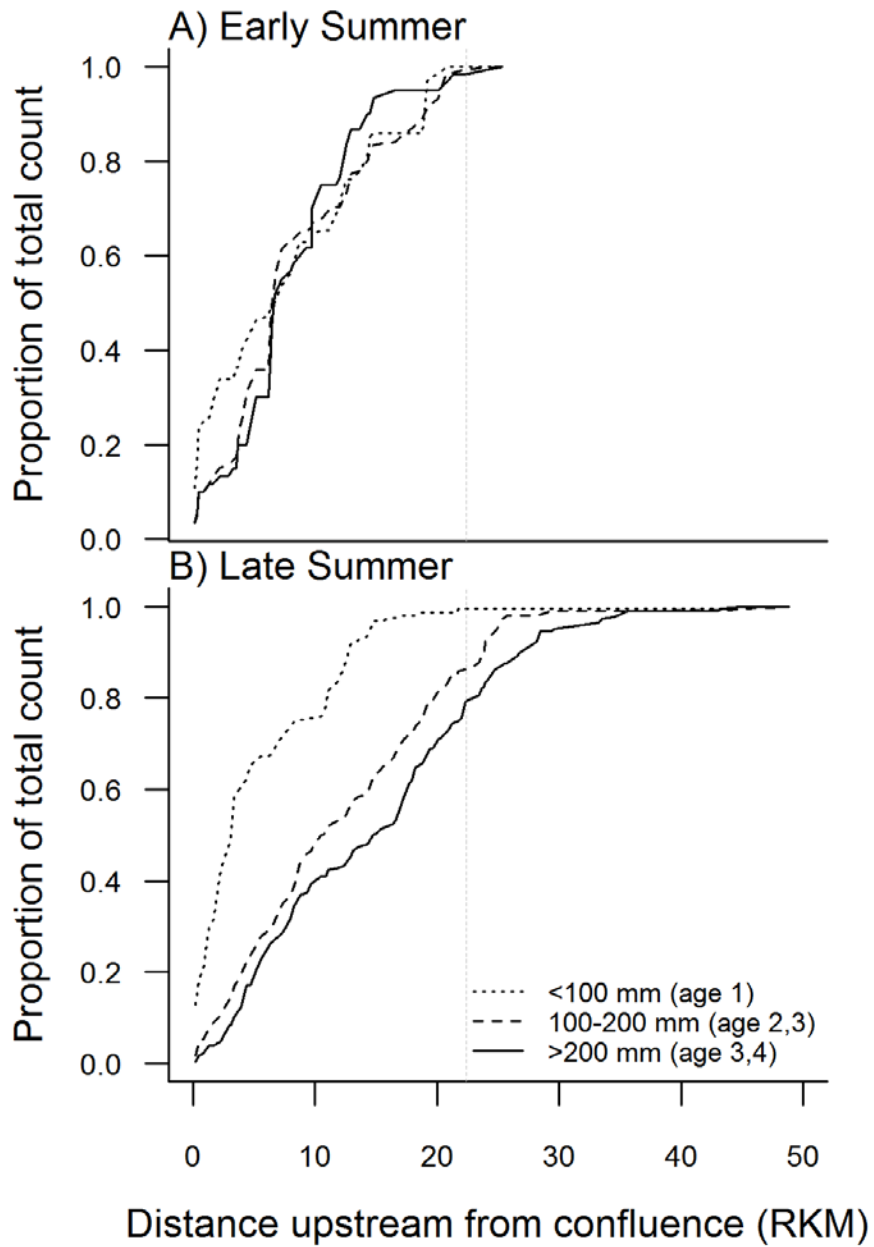


Fig. 3.6

The cumulative proportion of the total count of 3 size classes of bass observed across RKM in the NFJDR in (A) early and (B) late summer 2009. Approximate ages for each size class of bass are given in the legend.

Chapter 3 Appendix A

Table A-1. Seasonal diets determined from bass 168-300 mm TL (avg = 242 mm). Bass were collected from the NFJDR/MFJDR confluence (RKM 0) to NFJDR RKM 25.45.

Prey groups	Prey	Average wet weight contribution to diet per season			Energy density (Joules/g)	Source
		5/1-7/1 (n=20)	7/1-8/1 (n=13)	8/1-10/31 (n=15)		
Aquatic invertebrate larvae, rigid body	Coleoptera, Trichoptera	2.2%	1.1%	0.1%	4272	McCarthy et al. (2009)
Aquatic invertebrate larvae, soft body	Diptera	0.0%	0.0%	0.0%	2746	McCarthy et al. (2009)
Aquatic nymph	Diptera, Ephemeroptera, Insecta, Odonata, Plecoptera	28.8%	14.2%	36.9%	3076	McCarthy et al. (2009)
Aquatic other	Annelida, Arthropoda, Gastropoda, Insecta, Nematoda	21.4%	9.9%	7.9%	2789	McCarthy et al. (2009)
Crayfish	<i>Pacifastacus leniusculus</i>	0.0%	2.5%	11.3%	3318	McIntyre (2004)
Fish	Possible species indicted below ¹	46.3%	40.2%	26.7%	4696	Parrish et al. (2006)
Terrestrial invertebrate adults	Coleoptera, Collembola, Hemiptera, Hymenoptera, Orthoptera, Thysanoptera	0.0%	6.8%	11.2%	5250	McCarthy et al. (2009)
Winged insect	Diptera, Ephemeroptera, Lepidoptera, Odonata, Plecoptera, Trichoptera	1.2%	25.3%	5.8%	4225	McCarthy et al. (2009)

¹ Juveniles of rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*Oncorhynchus tshawytscha*), northern pikeminnow (*Ptychocheilus oregonensis*), largescale sucker (*Catostomus macrocheilus*), bridgelip sucker (*Catostomus columbianus*). Juvenile and adult forms of longnose dace (*Rhinichthys cataractae*), speckled dace (*Rhinichthys osculus*), redbelt shiner (*Richardsonius balteatus*), multiple species of sculpin (*Cottus* spp).

Table A-2. Bioenergetics model parameter set and model inputs for Age 0-4 bass.

Age	Bioenergetic model parameters ¹	Start weight (g)	End weight (g)	Start total length (mm)	End total length (mm)	Calibration site p-value ²	Total consumption at calibration site (g)	Predator energy density (Joules/g) ³	Prey energy density (Joules/g) per season ⁴			Spawning losses ⁵	Scale sample size ⁶
									5/1-7/1	7/1-8/1	8/1-10/31		
0	Shuter & Post 1990	0.01	3.62	10	67	0.907	11.70	4186	3509	3509	3509	na	51
1	Shuter & Post 1990	3.62	18.50	67	116	0.874	61.50	4186	3509	3509	3509	na	46
2	Shuter & Post 1990	18.50	57.86	116	171	0.860	149.77	4186	3804	4173	3853	na	31
3	Whitledge et al. 2003	57.86	152.71	171	227	0.696	593.91	5175	3804	4173	3853	6%	21
4	Whitledge et al. 2003	152.71	221.06	227	257	0.453	632.46	5175	3804	4173	3853	6%	4

¹ Per Whitledge et al. (2003) suggestion, we used the Shuter & Post (1990) smallmouth bass parameter set for bass < 50 g. When bass start weight exceeded 50 g we used the Whitledge et al. (2007) model.

² The p-value was determined by running the bioenergetics model with known growth at the NFJDR RKM 0.2 calibration site and solving the mass-balance equation to determine bass consumption required to achieve the observed growth

³ Hanson et al. (1997) predator energy density was used for Age 0-2 bass. Gravel et al. (2010) adult bass energy density was used for Age 3-4.

⁴ Bass aged 0-1 were assumed to eat primarily immature aquatic invertebrates (Dauwalter and Fisher 2008). We used McCarthy et al. (2009) to estimate their energy density. Age 2-4 bass diets were seasonally determined from fish collected in the NFJDR (n=48). The prey energy density was determined by averaging the energy density of their prey, given their % wet weight contribution to the total diet. The details of these diets can be found in Table A-2.

⁵ Spawning losses for Age 3 and 4 fish were determined from fish collected in the NFJDR by weighing gonad mass relative to total body mass (n=18).

⁶ Scales were collected from adult bass and used to back-calculate length-at-age for Age 0-4 bass

Chapter 3 Appendix B

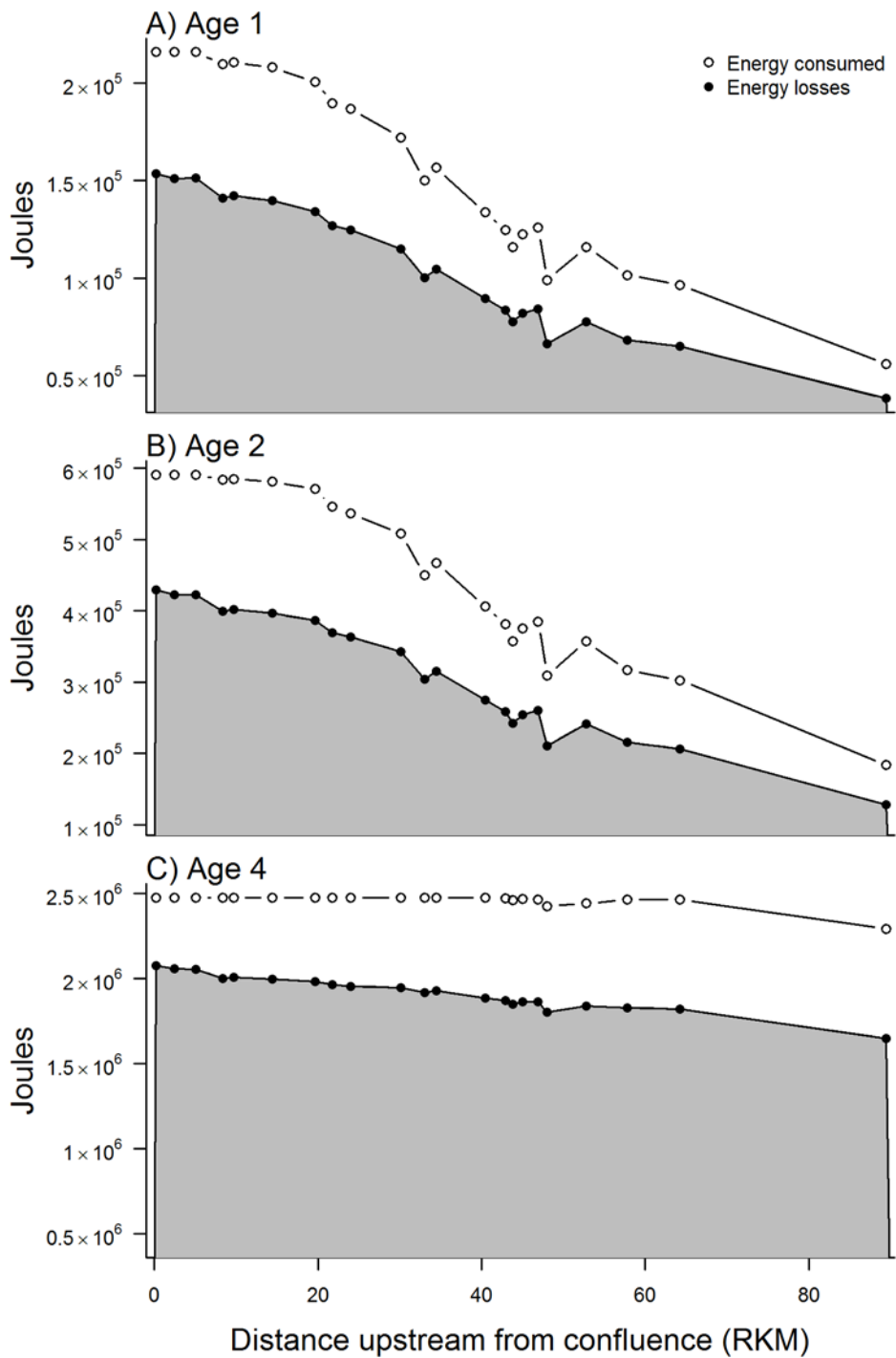


Fig. B-1

The total energy consumed and energy lost (summed over all days of the model) for Age 1 bass (A), Age 2 (B), and Age 4 bass (C) across RKM in the NFJDR. If energy consumed exceeds energy losses this indicates scope for bass growth.

Chapter 3 Appendix Literature Cited

- Dauwalter, D. C., and W. L. Fisher. 2008. Spatial and temporal patterns in stream habitat and smallmouth bass populations in eastern Oklahoma. *Transactions of the American Fisheries Society* 137:1072-1088.
- Gravel, M. A., P. Couture, and S. J. Cooke. 2010. Comparative energetics and physiology of parental care in smallmouth bass *Micropterus dolomieu* across a latitudinal gradient. *Journal of Fish Biology* 76:280-300.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0 for Windows. Center for Limnology, University of Wisconsin-Madison and the University of Wisconsin Sea Grant Institute.
- McCarthy, S. G., J. J. Duda, J. M. Emlen, G. R. Hodgson, and D. A. Beauchamp. 2009. Linking Habitat Quality with Trophic Performance of Steelhead along Forest Gradients in the South Fork Trinity River Watershed, California. *Transactions of the American Fisheries Society* 138:506-521.
- McIntyre, J. K. 2004. Bioaccumulation of mercury and organochlorines in the food web of Lake Washington. Master of Science thesis. University of Washington, Seattle, Washington, USA.
- Parrish, J. K., K. Haapa-aho, W. Walker, M. Stratton, J. Walsh, and H. Ziel. 2006. Small-bodied and juvenile fishes of the mid-Columbia region including keys to diagnostic otoliths and cranial bones. Draft Version, March 2006. University of Washington, Seattle, WA. 137p.
- Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:314-336.

CHAPTER 4

NATIONAL PARKS AS PROTECTED AREAS FOR U.S. FRESHWATER FISH DIVERSITY

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Reference: Lawrence, D. J., E. R. Larson, C. A. R. Liermann, M. C. Mims, T. K. Pool, and J. D. Olden. 2011. National parks as protected areas for U.S. freshwater fish diversity. *Conservation Letters* 4:364-371.

Abstract

We assessed the representation of freshwater fish diversity provided by the National Park Service (NPS) and the potential for parks to serve as freshwater protected areas (FPA) in the United States. Although most parks were not designed with freshwater conservation in mind, nearly two-thirds (62%) of native US fishes reside in national parks. However, only 18% of the nation's highly imperiled fish species are represented within the NPS. The ability for parks to serve as protected areas depends on activities upstream from their boundaries and we found that a substantial part of these watersheds have some form of conservation status. Using a conservation planning approach that integrated fish diversity representation provided by parks and their current and future ecological threats (i.e., climate change, dams, watershed impervious surface, invasive species) and management challenges (i.e., land stewardship beyond park boundaries), we identified 50 parks that could serve as a foundation for a nationally comprehensive freshwater protected area system. While the NPS has limitations as the potential basis for an FPA network, it provides considerable representation of freshwater fish diversity that should be taken into account during systematic conservation planning for freshwaters.

Introduction

Globally, freshwater ecosystems are under severe anthropogenic pressure and as a result their rich biological resources are rapidly diminishing (Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010). Humans now appropriate >50% of available freshwater run-off (Jackson *et al.* 2001; Sabo *et al.* 2010), over one million dams fragment river systems (Nilsson *et al.* 2005; Poff *et al.* 2007), species invasions are globally widespread (Leprieur *et al.* 2008), and projected climate change will introduce both new challenges and interact with the many other stressors to which fresh

waters are exposed (Rahel & Olden 2008; Woodward *et al.* 2010). The end result is that freshwater faunas are among the most imperiled worldwide (Vié *et al.* 2009; Olden *et al.* 2010), where extinction rates far exceed their marine and terrestrial counterparts (Ricciardi & Rasmussen 1999; MEA 2005).

Scientists have recently begun to explore the potential of establishing freshwater protected areas (FPAs) as one approach to curtail biodiversity loss in freshwater ecosystems. Originally developed for terrestrial areas, and applied over the past two decades to marine systems, protected areas have emerged as a leading tool for conservation. The challenges of planning protected areas for freshwater ecosystems are great due to their hydrologic requirements of longitudinal, lateral, and groundwater connectivity (Barmuta *et al.* 2010). Thus, many contemporary design ideas for terrestrial and marine protected areas are not transferable to FPAs (Abell *et al.* 2007; Nel *et al.* 2009a). Additionally, FPAs must be implemented at the appropriate spatial scale, as many threats originate outside of protected area boundaries.

One of the first steps in designing a representative network of FPAs is taking stock of what is contained within current protected area systems, given that many existing terrestrial reserves house freshwater habitats. Reserves that combine protection for terrestrial and freshwater resources could be prioritized to promote efficient spending of limited conservation dollars (Abell *et al.* 2010). While some regional US assessments of aquatic resources have been completed (e.g., USGS Aquatic GAP program), national scale empirical information on freshwater resources within terrestrial protected areas is lacking. Of the few national studies that have inventoried freshwater species contained within existing protected areas (Lyle & Maitland 1992 - UK; Keith 2000 - France; Tognelli *et al.* 2008 - Chile), none have considered the current

and future anthropogenic threats or the management challenges that may jeopardize the long-term conservation of biodiversity within those protected areas.

In this study we provide the first national assessment of representation for native freshwater fishes provided by the National Park Service (NPS), America's longest standing conservation system. Although many NPS units were established for the conservation of terrestrial features, parks are found across a majority of North American ecoregions and thus have potential to provide national-scale representation for freshwater fish diversity. The persistence of freshwater ecosystems is strongly tied to the health of their contributing watersheds so we quantified the ecological threats to park watersheds including percent impervious land surface, hydrologic alteration and fragmentation by dams, invasive species and projected climate change. We also assessed the management challenges to utilizing NPS units as FPAs based on the amount of park watersheds in some form of conservation status. We used a conservation planning approach to integrate these results (i.e., fish diversity representation, ecological threats, and management challenge) to identify priority parks that could serve as the core members of a FPA network to protect freshwater fish diversity across the US. Prioritization is key since funding is limited and the actions required to protect freshwater ecosystems contained in NPS units have high potential costs, including protracted legal action to secure water rights to parks, and the need to develop cooperative management agreements across multifarious stakeholders to protect the upstream watersheds of a park outside of park boundaries. Finally, we identify watersheds in the US that should be prioritized for future conservation action to provide representation for native fish species that are not currently in the NPS.

Methods

To assess national fish faunal representation provided by the NPS, we collated records for all freshwater species that presently occur within 147 park service units using the NPSpecies database (native occurrences only) and compared them to fish occurrence across all major watersheds of the United States (6 digit Hydrologic Unit Code, HUC). A detailed description of all fish distribution datasets used in this study is provided in the online supplementary material. The 147 parks considered in this analysis were chosen from the broader set of parks evaluated by the NPS Inventory and Monitoring program (n=283 parks), because these parks are managed first and foremost for conservation of their natural resources and thus have the greatest potential to serve as FPAs (see online supplementary material for more details on park selection). Although fish occurrence within the NPSpecies database is internally validated we undertook a secondary validation of each park species list. This validation consisted of a timed (30 minute) review where we compared park species lists from the NPSpecies database to scientific literature, NPS and USGS reports, and gray literature related to the park and, if necessary, contacted park managers for additional information. In 74 hours of effort we added 226 occurrence records to the total 3,084 records of interest. We also evaluated ecoregion-scale (Abell *et al.* 2008) representation provided by parks by comparing the suite of species contained within the network of NPS units in a given ecoregion to the species that reside within all watersheds of that ecoregion (NatureServe 2004).

The ability of NPS units to serve as FPAs depends on both threats to their contributing watersheds and the capacity to manage activities in these watersheds. To address these issues we first delineated the watersheds of all parks considered here in a GIS (see online supplementary materials for details). We intersected each park's watershed layer with a series of threat metrics

to develop a cumulative current and projected future ecological threat index for all parks. Threats computation was standardized, allowing for comparison of threats across parks (see below). Current threat was comprised of four metrics describing major sources of anthropogenic disturbance in each park's contributing watershed, including 1) percent impervious land cover, 2) habitat fragmentation (number of upstream dams/watershed area), 3) flow alteration (total upstream reservoir storage capacity/long-term mean annual discharge), and 4) degree of species invasiveness within parks (non-native : native fish species richness). Future ecological threat was assessed as 1) projected percent impervious surface for 2100 (EPA Spatially Explicit Regional Growth Model; A2 greenhouse gas scenario), 2) projected climate changes in annual mean temperature and percent departure in annual mean precipitation (2100 A2 scenario), and 3) invasion potential, determined by adding all non-native fish species in watersheds adjacent to or within a park's watershed but not yet in park boundaries to the current non-native richness, and then recalculating the ratio of non-native : native richness. Current habitat fragmentation and hydrologic alteration were also included in the future ecological threat index calculation since there are no available forecasts of how these threats will change.

We calculated a 'management challenge' index for each park based on the total area of a park's watershed within its boundary, as well as the percent of a park's watershed in some form of conservation holding (i.e., federal, state, tribal and local governments, and conservation easements). Ecological threat and management challenge metrics were rescaled using a cumulative distribution frequency (CDF) to develop a relative index of threat ranging from 0 to 1 and then treated additively to calculate each of the major threat indices (following Vörösmarty *et al.* 2010). Data sources used to generate each threat index are described in the online supplementary material.

Park threat indices and data on faunal representation were used in the conservation planning software Marxan to identify a minimum set of priority parks that could provide representation for all native freshwater fishes contained in the NPS. Marxan prioritizes sites based on the conservation features they contain, relative to the costs of utilizing a site within the reserve system, and solves the minimum set problem, i.e., finding the smallest number of sites that provide adequate representation with the lowest costs (Possingham *et al.* 2000). In separate analyses, we determined the prioritization of parks based on the occurrence of species in each park and their 1) current ecological threats, 2) future ecological threats, and 3) management challenges, where threats were calculated as costs in Marxan (see online supplementary material for more details). We conducted a sensitivity analysis of park selection by Marxan to 1) determine the influence of the different threat layers on park prioritization, and 2) determine how rare species affected park choice (see online supplementary material). Finally, we conducted another conservation planning analysis to identify watersheds that contain the native fish species not currently within the NPS. To accomplish this, we ran Marxan using our national fish occurrence by watershed database with a goal of prioritizing watersheds that could capture the species not in the NPS (see online supplementary material for detailed methods). We report highly ‘irreplaceable’ watersheds, that is, those watersheds that were selected frequently by our Marxan analysis.

Results

National parks provide representation for 61.7% of the native freshwater fishes that occur in the United States (478 out of 775 total species), and cover a broad range of fish families (Table S1). NPS units afford variable faunal coverage for their associated ecoregions, with an average representation of 49.5% of species (SD = 21.9%, Fig. 4.1). Representativeness is not a function of species richness of the surrounding ecoregion; ecoregions with high native richness are not more or less represented by their network of national parks than ecoregions with low richness ($R^2 = 0.01$, $p=0.47$). Seven ecoregions lacked NPS units that meet our criterion for analysis, three of which occur completely within the US (Apalachicola, Lahontan, Oregon Lakes) and four of which only marginally occur within the US ($\leq 17\%$ of total ecoregion area in the US, Guzman – Samlayuca, Sonora, St. Lawrence, Upper Saskatchewan). Parks provide relatively poor representation for species of conservation concern, currently supporting populations of 27 of the nation's 153 highly imperiled fish species (17.6%). Highly irreplaceable watersheds that contain the fish species not currently represented by parks are broadly distributed across 29 different US ecoregions, but are located primarily in the speciose southeastern US, and species-poor but highly endemic faunas of the southwest and western ecoregions (Fig. 4.2).

Using Marxan we identified 50 priority parks that could provide representation for all native species within the NPS (Fig. 4.1, Table S2). With a goal of capturing at least one occurrence of all 478 species currently in the park network, each Marxan analysis (current and future ecological threat and management challenge as costs) selected parks similarly. The average Pearson's correlation coefficient among analyses was 0.93, with a range of 0.89-0.95 (see sensitivity analysis in online supplementary material, Table S3). Overall, the 50 parks prioritized were comprised of a minimum set of 46, 47, and 46 parks chosen based on current,

future threats, and management challenge cost layers respectively, with a high degree of overlap in their solutions (i.e., only four parks were chosen by a single threat index). Approximately one-third (29.7%) of all native fish species contained in the NPS occur in only one park across all parks considered in this study (n=147 parks, Fig. 4.3A), and 42.7% of the species had only a single representation within the network of 50 parks prioritized in the Marxan analysis (Fig. 4.3B).

The optimal solution derived from the prioritization analysis was driven by the large number of species that are rare within the NPS, defined as species occurring in ≤ 2 parks, which account for 212 of the 478 native US fishes. Parks containing these species (66 parks of the 147 total) have significantly higher current and future ecological threats and lower management potential than parks not containing rare species (Table 1). Together, the large number of rare species distributed across disparate parks (45% of the parks assessed) constrained the Marxan solution to include parks with high threats in the conservation portfolio (Table S2). Parks were chosen differently based on whether rare species were required in the Marxan solution (Table S2, Table S3).

In terms of watershed management challenges, 61 (41%) of the NPS units we assessed have $\geq 90\%$ of their upstream watersheds outside of park boundaries while only 24 parks (16%) contain their own headwaters ($<1\%$ of park watershed outside of the park boundary, Fig. 4.4A). However, 58 parks (39%) have $\geq 90\%$ of upstream watersheds in some form of conservation status (i.e., federal, state, local government land, private land with conservation easements, and tribal land, Fig. 4.4B). We also assessed the congruence of ecological threats and management challenges across the park network to identify potential conservation opportunities. Sixteen of the 50 parks (32%) prioritized by Marxan have below average current ecological threats and

management challenge, representing parks with high FPA potential (relative threat indices <0.5 for both; Fig. 4.5, lower left quadrant). Over one-third (36%) of the parks chosen by Marxan have both above average current ecological threat and management challenge (Fig. 4.5, upper right quadrant). These units were selected largely because they contain rare species, whereas their ecological threats and management challenges make their conservation potential relatively low.

Discussion

Overall, NPS units contain almost two-thirds of the freshwater fish species within the US, providing the first evidence that the NPS could serve as a foundation for a nationally comprehensive FPA system. By applying a systematic planning approach that considers the distribution of fish species across the park network, as well as an assessment of the current and future ecological threats to parks, we identified 50 national parks that provide representation for all freshwater fish in the NPS. The conservation planning approach employed here was constrained by the fact that many fishes are rare within the park system, and these rare species are present in disparate parks (i.e., not all rare species are present within a few parks of the NPS). Thus, many high risk parks had to be included in the conservation portfolio. We recognize there are other means to employ conservation planning software to prioritize parks. For example, high threat parks could be excluded, or ‘locked out’, from potential conservation planning solutions. In an exploratory analysis, we found that if all parks with ≥ 0.75 threats (for any of the three threat indices, range 0 - 1, $n = 60$ parks) were excluded from the prioritization process, 83.7% of native US fish species (400/478 species) in the NPS could be still be represented in as few as 35 national parks.

The representation provided by the NPS is encouraging given that most parks were not established for the conservation of freshwater features. Of the 38% of native fish species unrepresented by parks (n=297 species), more than half (n=171) are highly endemic (i.e., nationwide they are present in ≤ 2 HUC6 watersheds), so it is not surprising that parks designed mainly for terrestrial conservation did not include these species. Further, nearly half (n=126) of the 297 fish species not currently represented within the NPS are considered nationally imperiled and 80% (n=101) of these imperiled species are highly endemic. The relatively low representation of imperiled species within national parks highlights one limitation of using the NPS as a foundation for a national FPA network. Conservation efforts often prioritize the most threatened fauna, so unless parks are established that contain these species, conservation investment for imperiled freshwater fishes will have to be directed outside of the NPS. Our study also identified watersheds that could be prioritized for future conservation action to provide representation for the remaining fish species not presently represented in the NPS (Fig. 4.2). These watersheds may contain non-NPS protected areas, that, if managed in conjunction with the priority parks we identified, could provide representation for all US native freshwater fishes. The highly irreplaceable watersheds we identified also informs the NPS or other conservation organizations where new protected areas could be placed to establish a fully comprehensive system of freshwater fish representation.

A major constraint to utilizing NPS units as FPAs is that their ecological integrity is subject to anthropogenic disturbances that occur outside of park boundaries. This is one of the main criticisms of applying the terrestrial protected area approach to freshwater ecosystems (Dudgeon *et al.* 2006; Abell *et al.* 2007; Nel *et al.* 2009b). Our findings illustrate that while

most parks have the vast majority of their watersheds outside of park boundaries, the contributing watersheds of many NPS units is held in some form of conservation status. Although public ownership of land does not guarantee protection of its waters (Pringle 2000), it increases the feasibility of establishing an integrated watershed protection program. Forming partnerships with surrounding land owners (both public and private) will be essential to maintaining the aquatic resources currently contained within parks. Establishing these sorts of partnerships is easier said than done, but there is precedent for such cooperation within the NPS (Hamin 2001) and the recently introduced National Fish Habitat Conservation Act (S. 1214, H.R. 2565) aims to further enhance cooperation across government entities to provide regional and national scale conservation planning for freshwater resources.

One of the strengths of this study is that it allows park managers to understand the role each park plays in supporting freshwater fish diversity at the national scale. Prior to the NPS Inventory and Monitoring program (NPS I&M, first phase completed in 2008) the NPS did not have biotic inventories to catalogue species contained within most parks (Stohlgren *et al.* 1995), let alone biodiversity data at broader scales. By combining NPS I&M data with our national fish database, this work will assist the NPS to understand each parks' contribution to the broader national fish diversity puzzle, and could assist the development of new policy that supports a comprehensive, network-based conservation strategy. This approach is currently used in the National Wildlife Refuge System, whose policies explicitly put each refuge in the landscape context of all others (USFWS 2001). Additionally, by systematically assessing threats to park watersheds, we provide the NPS a means to compare and prioritize parks based not only on the diversity of freshwater fishes within park borders, but also based on the landscape potential to protect these fishes (Table S2). Prioritizing units within the NPS will be essential because the

action required to protect the hydrologic regime of park watersheds will likely be time consuming and costly. For example, Pringle (2000) found that the NPS was engaged in legal adjudications to secure water rights for over 50 different parks.

Given data limitations, we could not address all possible watershed threats to NPS units. Additional research describing nutrient, heat, or chemical pollution to park watersheds and threats from non-fish invaders within parks is also needed to further characterize parks' FPA potential. Migratory species that occur within parks will also be faced with downstream impediments to their movement into and out of a potential reserve, and non-migratory species may still require other sites outside of park boundaries for spawning, rearing, or overwintering. Another limitation of our analysis is that the NPSpecies dataset only contains presence/absence data. The relatively high representation of fish species found in the NPS likely overestimates the ability for parks to serve as FPAs because some fish populations in NPS units may be in decline or represent only sink or migratory populations. Assessing the population status of fishes contained in the NPS, and particularly rare species contained in high threat parks, will be essential to determine if parks are the best strongholds for US fishes or if other sites with higher conservation potential would be better suited to their protection. Monitoring of some of these fish populations is planned or ongoing as part of the NPS Vital Signs Monitoring Program (Fancy *et al.* 2009). Information on population viability for fish species within the park system does not currently exist at a national scale, and should represent an area of active research if the idea of implementing protection of freshwater resources within parks is carried forward. Also, many (29.7%) native fish species that occur within the NPS are found in only one park unit (Fig. 4.3). A single representation of each species is unlikely to provide adequate buffer against many of the threats that may impinge on fishes within the NPS. Thus, while the NPS may serve as the

foundation for a FPA system for freshwater fishes in the US, redundant representation of these species will be required to provide the much needed assurance that these species will not be lost in the future.

Finally, freshwater fish may not be good surrogates for other freshwater biodiversity such as amphibians, crayfish, or mussels (Lawler *et al.* 2003), and a more taxonomically comprehensive analysis would be valuable in identifying the utility of NPS units as potential FPAs more broadly. Such analyses may become possible as more national park inventories are completed, and our prioritization framework and delineation of park watersheds, threats, and management potential should be useful for this purpose.

Overall, this study contributes to the developing debate on the utility of protected areas for freshwater conservation by examining the role that existing terrestrial reserves may play in representing freshwater species. While the NPS has limitations as the potential basis for an FPA network, it provides considerable representation of freshwater fish diversity that should be taken into account during systematic conservation planning for freshwaters. We also hope that this nationwide analysis of freshwater fish representation in a terrestrial reserve network, combined with a simultaneous assessment of ecological threats and management challenges to these reserves, provides an evaluation framework transferable to other countries and regions.

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ERL, CRL, MCM, TKP, and JDO conceived the idea of the study and developed the datasets.

DJL conducted the data analysis. DJL and JDO wrote the manuscript.

References

- Abell R., Allan J.D., Lehner B. (2007) Unlocking the potential of protected areas for freshwaters. *Biol Conserv* **134**, 48-63.
- Abell R., Thieme M., Ricketts T.H., Olwero N., Ng R., Petry P., Dinerstein E., Revenga C., Hoekstra J. (2010) Concordance of freshwater and terrestrial biodiversity. *Conser Lett*. doi: 10.1111/j.1755-263X.2010.00153.x
- Abell R., Thieme M.L., Revenga C., Bryer M., Kottelat M., Bogutskaya N., Coad B., Mandrak N., Balderas S.C., Bussing W., Stiassny M.L.J., Skelton P., Allen G.R., Unmack P., Naseka A., Ng R., Sindorf N., Robertson J., Armijo E., Higgins J.V., Heibel T.J., Wikramanayake E., Olson D., Lopez H.L., Reis R.E., Lundberg J.G., Perez M.H.S., Petry P. (2008) Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. *Bioscience* **58**, 403-414.
- Barmuta L.A., Linke S., Turak E. (2010) Bridging the gap between ‘planning’ and ‘doing’ for biodiversity conservation in freshwaters. *Freshwat Biol* **56**, 180-195.
- Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.I., Knowler D.J., Lévêque C., Naiman R.J., Prieur-Richard A.H., Soto D., Stiassny M.L.J., Sullivan C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol Rev* **81**, 163-182.
- Fancy S.G., Gross J.E., Carter S.L. (2009) Monitoring the condition of natural resources in US national parks. *Environ Monit Assess* **151**, 161-174.
- Hamin E.M. (2001) The US National Park Service's partnership parks: collaborative responses to middle landscapes. *Land Use Policy* **18**, 123-135.
- Jackson R.B., Carpenter S.R., Dahm C.N., McKnight D.M., Naiman R.J., Postel S.L., Running S.W. (2001) Water in a changing world. *Ecol Appl* **11**, 1027-1045.
- Keith P. (2000) The part played by protected areas in the conservation of threatened French freshwater fish. *Biol Conserv* **92**, 265-273.

- Lawler J.J., White D., Sifneos J.C., Master L.L. (2003) Rare species and the use of indicator groups for conservation planning. *Conserv Biol* **17**, 875-882.
- Leprieur F., Beauchard O., Blanchet S., Oberdorff T., Brosse S. (2008) Fish invasions in the world's river systems: When natural processes are blurred by human activities. *PLoS Biol* **6**, 404-410.
- Lyle A.A., Maitland P.S. (1992) Conservation of freshwater fish in the British Isles: the status of fish in National Nature Reserves. *Aquat Conserv: Mar Freshwat Ecosyst* **2**, 19-34.
- MEA. (2005) *Millennium Ecosystem Assessment: Ecosystems and human well-being: wetlands and water synthesis*. World Resources Institute, Washington DC, USA.
- NatureServe. (2004) Downloadable animal datasets. NatureServe Central Databases. Available from: www.natureserve.org/getData/dataSets/watershedHucs/index.jsp. Accessed 24 January 2009.
- Nel J.L., Roux D.J., Abell R., Ashton P.J., Cowling R.M., Higgins J.V., Thieme M., Viers J.H. (2009a) Progress and challenges in freshwater conservation planning. *Aquat Conserv: Mar Freshwat Ecosyst* **19**, 474-485.
- Nel J.L., Reyers B., Roux D.J., Cowling R.M. (2009b) Expanding protected areas beyond their terrestrial comfort zone: Identifying spatial options for river conservation. *Biol Conserv* **142**, 1605-1616.
- Nilsson C., Reidy C.A., Dynesius M., Revenga C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science* **308**, 405-408.
- Olden J.D., Kennard M.J., Leprieur F., Tedesco P.A., Winemiller K.O., García-Berthou E. (2010) Conservation biogeography of freshwater fishes: recent progress and future challenges. *Divers Distrib* **16**, 496-513.
- Poff N.L., Olden J.D., Merritt D.M., Pepin D.M. (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proc Natl Acad Sci USA* **104**, 5732-5737.
- Possingham H.P., Ball I., Andelman S. (2000) Mathematical methods for identifying representation reserve networks. pp. 291-305 in S. Ferson, M. Burgman editors. *Quantitative methods for conservation biology*. Springer-Verlag, New York, NY.

- Pringle C.M. (2000) Threats to US public lands from cumulative hydrologic alterations outside of their boundaries. *Ecol Appl* **10**, 971-989.
- Rahel F.J., Olden J.D. (2008) Assessing the effects of climate change on aquatic invasive species. *Conserv Biol* **22**, 521-533.
- Ricciardi A., Rasmussen J.B. (1999) Extinction rates of North American freshwater fauna. *Conserv Biol* **13**, 1220-1222.
- Sabo J.L., Sinha T., Bowling L.C., Schoups G.H.W., Wallender W.W., Campana M.E., Cherkauer K.A., Fuller P.L., Graf W.L., Hopmans J.W., Kominoski J.S., Taylor C., Trimble S.W., Webb R.H., Wohl E.E. (2010) Reclaiming freshwater sustainability in the Cadillac Desert. *Proc Natl Acad Sci USA* **107**, 21263-21270.
- Stohlgren T.J., Quinn J.F., Ruggiero M., Waggoner G.S. (1995) Status of biotic inventories in US National Parks. *Biol Conserv* **71**, 97-106.
- Tognelli M.F., De Arellano P.I.R., Marquet P.A. (2008) How well do the existing and proposed reserve networks represent vertebrate species in Chile? *Divers Distrib* **14**, 148-158.
- USFWS. (2001) 601 FW 3.7(C). National Wildlife Refuge System biological integrity, diversity, and environmental health. Available from: www.fws.gov/policy/601fw3.pdf. Accessed 22 December 2010.
- Vié J.C., Hilton-Taylor C., Stuart S.N., editors. (2009) *Wildlife in a Changing World - An Analysis of the 2008 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.
- Vörösmarty C.J., McIntyre P.B., Gessner M.O., Dudgeon D., Prusevich A., Green P., Glidden S., Bunn S.E., Sullivan C.A., Liermann C.R., Davies P.M. (2010) Global threats to human water security and river biodiversity. *Nature* **467**, 555-561.
- Woodward G., Perkins D.M., Brown L.E. (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philos Trans R Soc Lond, Ser B: Biol Sci* **365**, 2093-2106.

Table 4.1. Median (M) current and future ecological threat and management challenge for parks with and without rare species. Differences in median threats between these sets of parks were tested using the Mann-Whitney Rank Sum test. All were statistically significant ($p < 0.05$).

	Parks that contain rare species (n=66)			Parks that do not contain rare species (n=81)			P
	M	25% PCT	75% PCT	M	25% PCT	75% PCT	
Current ecological threat	0.59	0.36	0.79	0.41	0.15	0.68	0.003
Future ecological threat	0.59	0.35	0.77	0.44	0.19	0.73	0.04
Management challenge	0.64	0.37	0.80	0.41	0.14	0.66	<0.001

Fish Diversity Representation

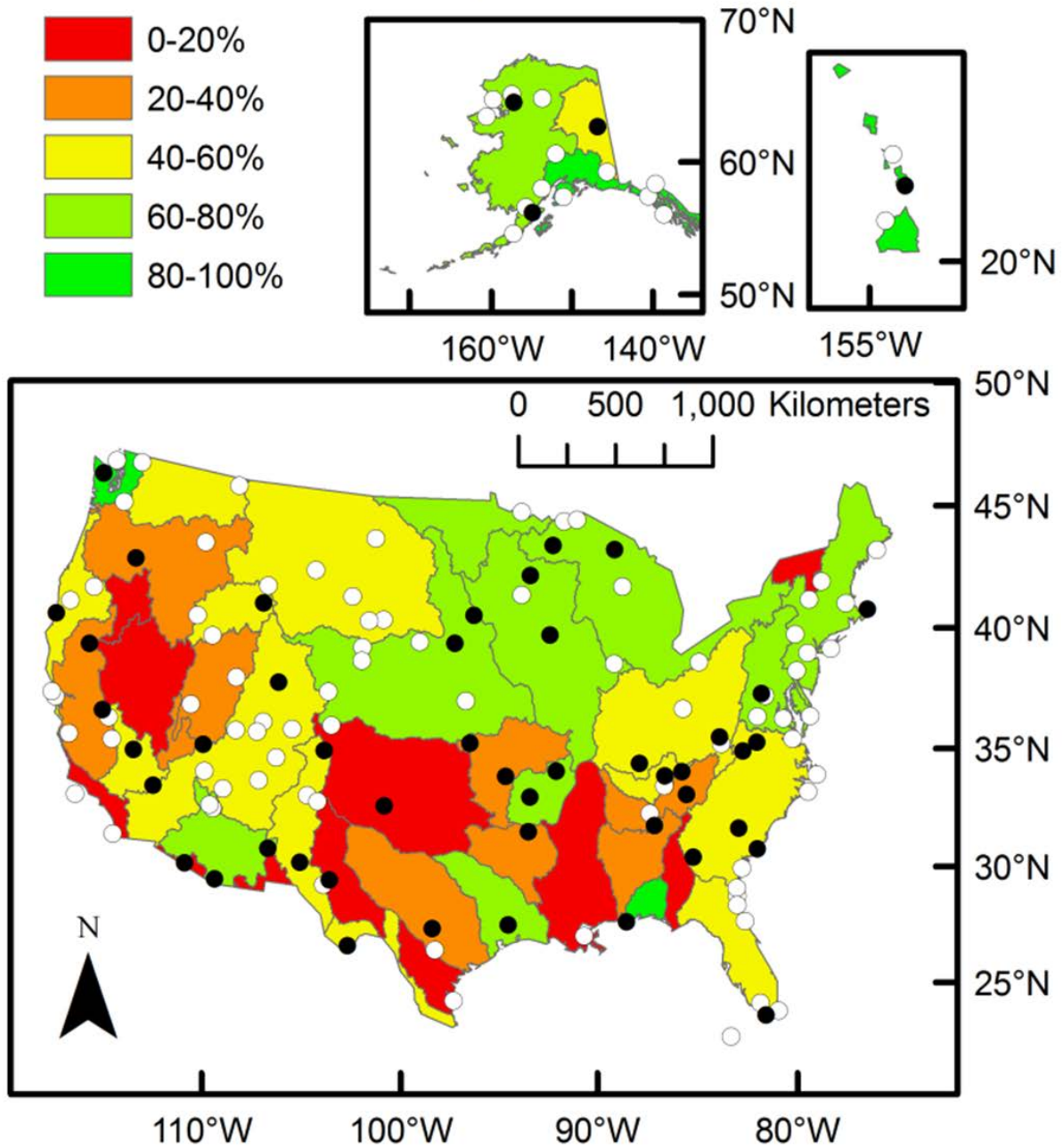


Fig. 4.1

Percent of native fish species represented by parks for each ecoregion, with NPS units selected (filled circles) and not selected (open circles) in our systematic planning analysis. Park symbols represent their geographic centroid, but are not drawn to scale. Ecoregion and park identification can be found in the online supplementary materials (Fig. S1, Table S1).

Irreplaceability

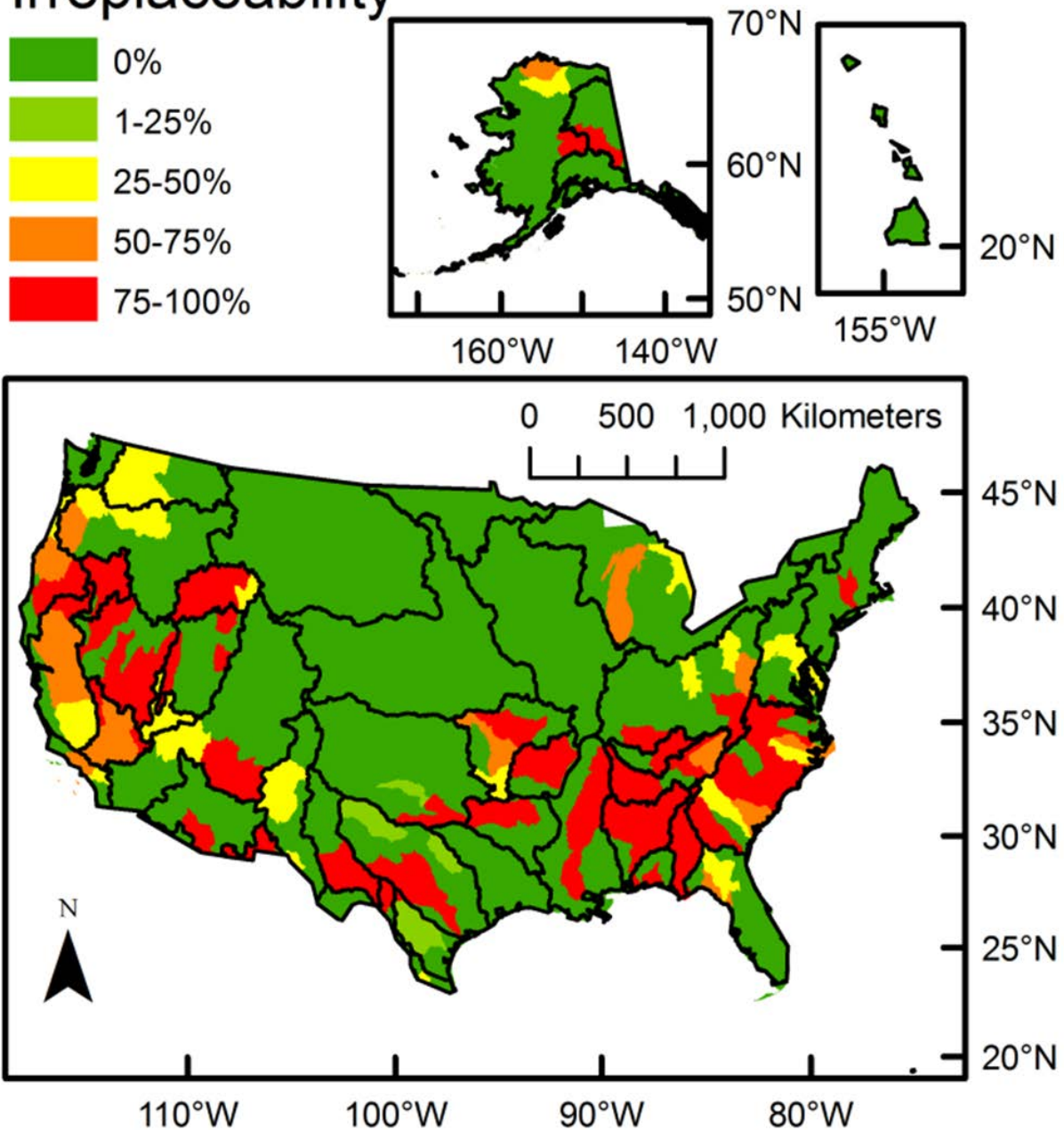


Fig. 4.2

Irreplaceability (i.e., selection frequency by the Marxan conservation planning software) of watersheds in the US that contain the remaining 297 freshwater fish species that do not occur in any NPS unit.

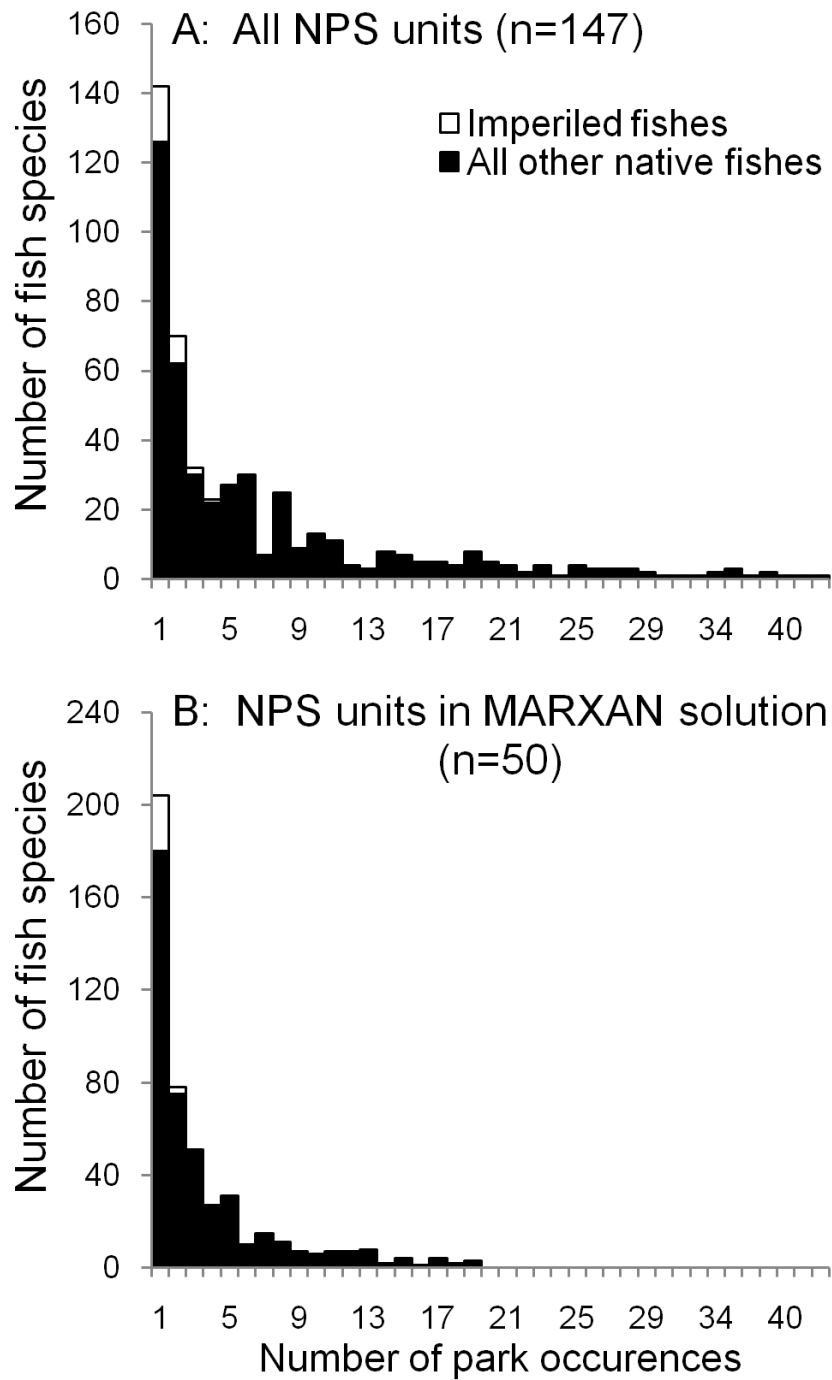


Fig. 4.3

Number of park occurrences for native US species (n=478) within the NPS. (A) Frequency of species occurrence in all NPS units considered in this study and (B) within NPS units prioritized by the Marxan conservation planning analysis.

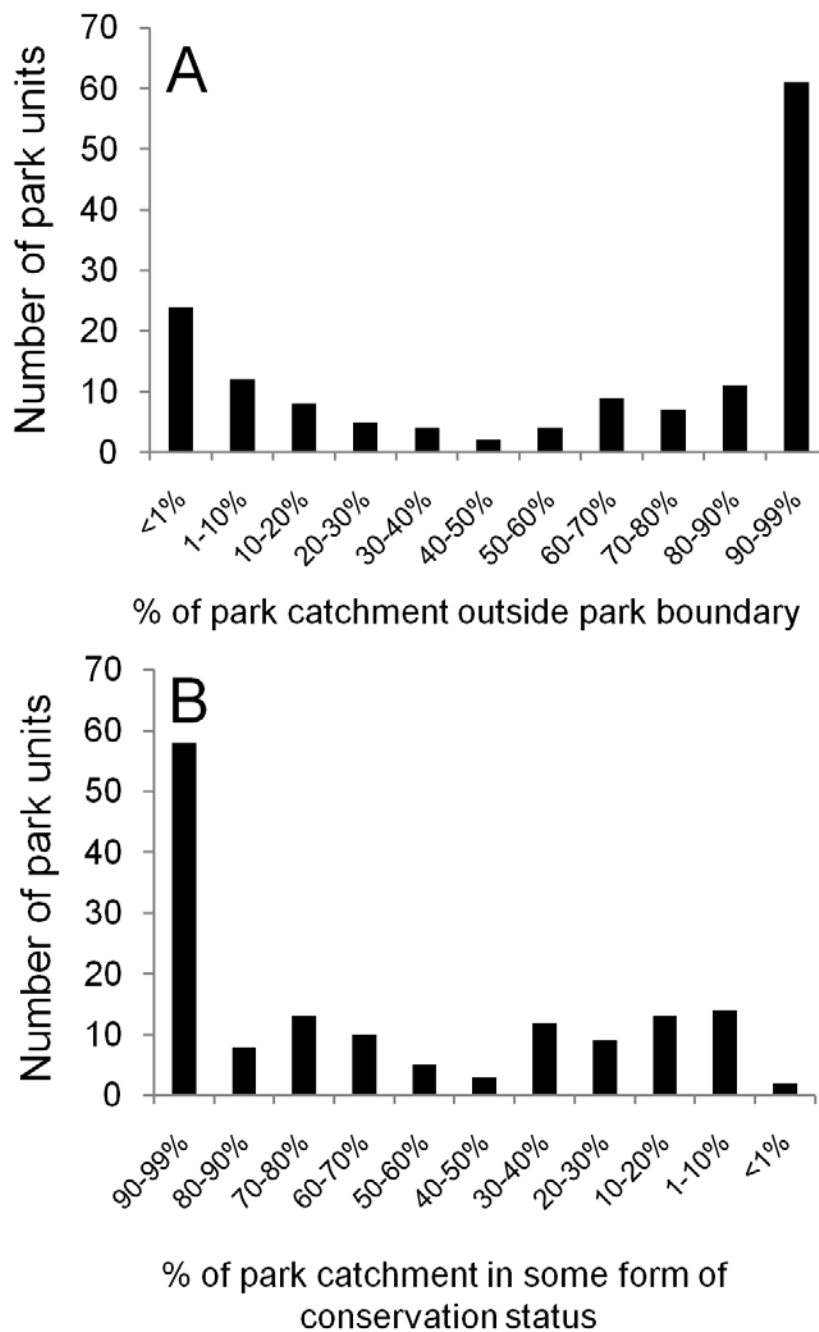


Fig. 4.4

Frequency distribution of NPS units based on (A) the percent of each park's watershed outside of that park's boundary and (B) the percent of a given park's watershed in some form of conservation status (i.e., federal, state, local government land, private land with conservation easements, and tribal land).

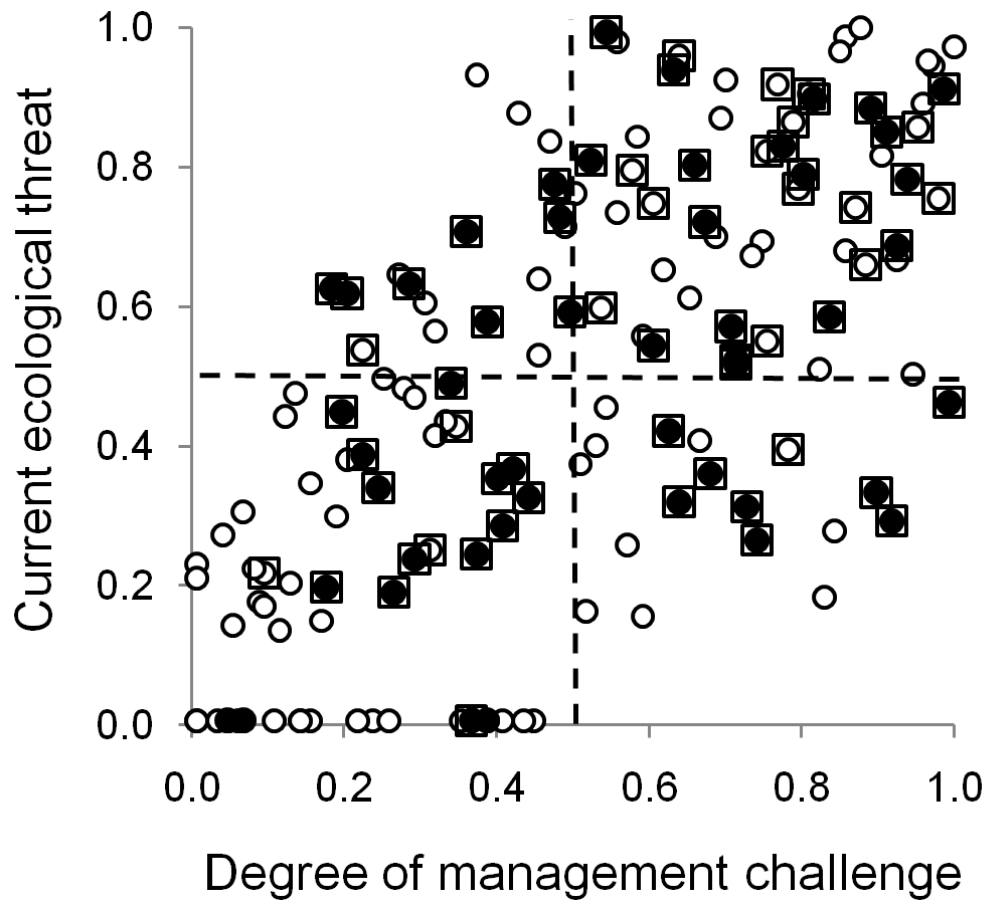


Fig. 4.5

Park current ecological threat as a function of management challenge (based on the percent of a park's watershed in some form of conservation status), with NPS units selected (filled circles) and not selected (open circles) in our systematic planning analysis. Parks with a square outline contain at least one rare species.

Chapter 4 Supplementary Materials

Fish distribution data

NPS data from the I&M program consists of presence/absence records of $\geq 90\%$ of the fish species occurring within park borders (NPS 2009). These records are based on voucher specimens, scientific references (reports or datasets), and park observation reports. Once validated by experts, the species list for each park is housed in the National Park Service Biodiversity Database (NPSpecies for short, NPS). We extracted the freshwater fish data (defined as fish requiring freshwater habitat during at least one life history stage) from the NPSpecies database on January 25, 2010. Only species currently residing in the park were used (i.e., historic occurrences were discarded). Sub-species were not included for the analysis because they are not described in equivalent detail across the all datasets used in this study. At the time of our study, most but not all of the park species lists in NPSpecies were validated. Therefore, we undertook a secondary validation for each of the 147 parks of interest. Validation consisting of a timed (30 minute) review during which we compared the species list from the NPSpecies database to scientific literature, NPS and USGS reports, and gray literature related to the park and, if necessary, contacted park managers for additional information. In 74 hours of effort we added 226 occurrence records to the total 3,084 records of interest.

Fish species occurrence at the national and ecoregion scale were derived from two databases; the NatureServe Central Database (NatureServe 2004) and the USGS Nonindigenous Aquatic Species Database (NAS, USGS 2004). Fish occurrences from both databases were used at the 6 digit Hydrologic Unit Code (HUC) level of resolution. The NatureServe database documents native US fish occurrence for the conterminous US (i.e., excludes Alaska and

Hawaii) and is based on location data compiled from a state and natural heritage program and supplemented using scientific literature and expert review. We derived 6 digit HUC native fish species occurrence for Alaska using range maps from Mecklenburg *et al.* (2002). Native fish occurrences for Hawaii were derived from FishBase (Froese and Pauly 2010) and were assigned to the Hawaiian Islands freshwater ecoregion as a whole (not a specific 6 digit HUC in Hawaii). The USGS NAS database documents non-indigenous species occurrence in US, including both translocated and exotic species, and includes the conterminous US, Alaska, and Hawaii. USGS NAS fish occurrence data were obtained from scientific literature, museum records, databases, monitoring programs, state and federal agencies, professional communications, online reporting forms, and Aquatic Nuisance Species (ANS) hotline reports. To avoid any taxonomic issues associated with collating species records from three databases (NPSpecies, NatureServe, USGS NAS) we converted all taxonomy to that used by FishBase.

To develop ecoregion-scale fish occurrence lists we first assigned each 6 digit HUC to an ecoregion using Arc-GIS (Version 9.3). Then fish assemblages for each ecoregion were determined by combining the fish occurrence for all HUCs contained within that ecoregion. Each ecoregion contained at least one 6 digit HUC, but usually had more. In some cases 6 digit HUCs spanned adjacent ecoregions. We assigned these HUCs to ecoregions using their geographic centroid (i.e., the center area of the HUC). NPS units were assigned to ecoregions and their species lists were collated in an analogous fashion. This allowed us to compare the fish species present within an ecoregion to those present within the network of parks within that ecoregion. To ascertain the level of representation for fish species of conservation concern we assigned fishes a conservation rank using the NatureServe ranking system (NatureServe 2010). We used

only G1 and G2 ranked species – those fishes with the highest level of imperilment – to determine NPS representation of imperiled species.

Parks considered in the analysis

In 2008 the NPS completed the first phase of the Inventory and Monitoring (I&M) program, whose primary goal was to catalog the biodiversity (i.e., fishes, amphibians, reptiles, birds, mammals, plants) contained within units of the NPS. Parks included in the I&M program were a subset (n=283) of the total parks in the NPS (n=~390 in the NPS), chosen from the broader set of parks because they contained ‘any’ natural resources (NPS 2009). Parks within the I&M have a broad range of designations, including battlefields, battlefield parks, military parks, historical parks, historic sites, lakeshores, memorials, monuments, parks, parkways, preserves, reserves, recreation areas, rivers, wild and scenic rivers and riverways, scenic trails, seashores, and an ‘other designation’ category. Although all parks must conform to the Organic Act (1916), which mandates the conservation of natural features within parks, the more than 20 different park designations are, in practice, managed according to one of three primary NPS values – the preservation of natural, historic, or recreational values (Dilsaver 1994; Hamlin 2001). We used only those parks from the I&M program established primarily for their natural value, because their central management goal is the conservation of natural features within the site. We did, however, include natural historic parks because many of these parks were large and contained significant natural resources. Although ‘parkways’ and ‘scenic trails’ did fit into to the broader class of parks preserved primarily for their natural value (termed here ‘natural value

parks'), these park types were excluded from our analysis since they generally consist of a trail with a relatively small buffer. Natural value parks in Alaska, Hawaii, and the contiguous United States were considered in the analysis. Parks based in American territories (e.g. National Park of American Samoa, the Virgin Islands) were not included because GIS data was lacking to complete the full threat analysis for these units. Thus, a total of 181 parks were assessed, composed of historical parks (n=25), lakeshores (n=4), monuments (n=63), parks (n=55), preserves (n=9), reserves (n=2), rivers (n=5), seashores (n=10), and wild and scenic rivers and riverways (n=8). Thirty four parks considered for the analysis lacked fish data because there were no fish populations or freshwater features within the park boundaries, leaving a total of 147 parks in our study.

Park watershed delineation

Assessment of the ecological threats and management potential of NPS units required identification of the contributing watershed for each park. Park watersheds were defined by first identifying all stream lines that flow through a given park. We used the NHD-Plus Value Added Attribute (VAA-COM) Object Navigator Tool to navigate all upstream flowlines, including tributaries that contribute flow to a given streamline based on NHD-Plus 1:100K hydrography. Once all of the contributing flowlines were identified we intersected these flowlines with their associated NHD-Plus watershed. All contributing watersheds and the park boundary were combined (using union and dissolve features in Arc-GIS) to develop a 'whole watershed' for each park. Park boundaries were included in the watershed because other non-stream aquatic

features (e.g. lakes, wetlands) may contain fish that the stream-based watershed determination technique alone would not have captured.

Assessment of ecological threats to parks and their management challenges

Park cumulative threat index computation

We developed a relative index to rank each park's current and projected future threat in relation to all other parks. We also computed a relative index of the management challenge to using a park as an FPA. These indices were subsequently used as cost layers in separate analyses in the Marxan conservation planning software. Each major index (current ecological threat, future ecological threat, management challenge) represents a composite of a series of individual threat metrics additively combined. Current ecological threat was comprised of four metrics describing major sources of anthropogenic disturbance in each park's contributing watershed, including 1) percent impervious land cover, 2) habitat fragmentation (number of dams/watershed area), 3) flow alteration (reservoir storage capacity/mean annual discharge), and 4) within parks, we determined the degree of species invasiveness (non-native: native fish species richness). Future ecological integrity was assessed as 1) projected percent impervious land cover for 2100 (according to the EPA Spatially Explicit Regional Growth Model, based on the A2 greenhouse gas scenario), 2) projected climate changes in annual mean temperature and percent departure in annual mean precipitation based on a 2100 A2 scenario, and 3) invasion potential, determined by adding all non-native species in the watersheds adjacent to or within a park's watershed but not

yet in park boundaries to the current non-native richness, and then recalculating the ratio of non-native : native richness. Current habitat fragmentation and hydrologic alteration were included in the future ecological threat index calculation since there currently are no available forecasts of how these threats will change. The management challenge index for each park was calculated based on the total area of a park's watershed within its boundary, as well as the percent of a park's watershed in some form of conservation holding (i.e., federal, state, tribal and local governments, and conservation easements). Details on data sources and processing for each threat metric are provided below.

The relative level of each threat metric considered in our analyses was compared across parks using a cumulative distribution function (CDF, Vörösmarty *et al.* 2010), a rescaling technique that places the park score for each threat on a scale from 0 to 1 based on the frequency distribution of values for that threat across all parks. If the value for a given threat was truly considered 0 for a park, that score was set to 0 and was excluded from the CDF (Vörösmarty *et al.* 2010). A cumulative threat score for each analysis (i.e., current threats, future threats, management challenge) was determined by summing the CDF scores for each threat metric considered in that analysis, and then a CDF was run to determine how parks ranked against each other in terms of cumulative threat. Weighting of threat metrics within a given analysis was not employed when generating cumulative scores because we had no *a priori* reason to rank one threat more serious than another in terms of preserving fish diversity within a park. The results of this analysis are presented in Table S2.

Individual threat metric derivations

Percent impervious surface on contributing watershed

The degree of impervious surface cover on the contributing watershed of each park was determined using National Land Cover Database (NLCD) 2001 land-cover data (30 m resolution, Homer *et al.* 2004), and projected in the future using the EPA Spatially Explicit Regional Growth Model (EPA 2009a). The EPA SERGoM model predicts future impervious surface by predicting changes in human population, allocates that human density to housing density, and then predicts percent impervious surface for 1 km² grid cells based on the predicted housing density. Various growth scenarios are available for use in the SERGoM model. We used the A2 (high growth) scenario to be consistent with the climate change model (see below). While this is the least conservative model of future growth in impervious surface cover, the model does not include impervious surface related to commercial lands so it still likely to be an underestimate of future impervious surface cover. Commercial lands contributed 14% of the total US impervious surface cover in 2001(EPA 2009b). The SERGoM model does not have future projections for Alaska, Hawaii, or watersheds outside the US border that contribute to watersheds of parks within the US (e.g. Glacier National Park). Each of these cases was treated differently. For Alaska parks we assumed no growth in impervious surface, the most conservative situation. Large increases in impervious surface in Alaskan park watersheds are not likely given that for most parks (10 of 16) the contributing watershed of parks was almost contained completely within the park boundaries (i.e., headwater parks with $\leq 5\%$ of their watershed outside of park boundaries). Similarly, for the three Hawaiian parks we assumed no change in impervious surface cover in the future scenario. Hawaiian parks had mostly self-contained headwaters (median = 2.0% of park watershed outside of park border, range = 0.00 to 16.9%), so again major changes in impervious surface cover were considered unlikely. For parks with watersheds

that cross trans-national borders we assumed that changes in impervious surface would be consistent with the projected changes within US boundaries (i.e., the same percentage of contributing watershed was projected to have impervious surface inside and outside the US).

Dam density

We calculated dam density (dams km⁻²) on the contributing watershed of each park as an index of hydrologic fragmentation within and upstream of the park. US dam data was derived from the National Inventory of Dams (NID; n = 79,777). When park watersheds were outside of the US border we used the Global Reservoir and Dam Database (GRAND; n= 6,879).

Percent hydrologic alteration

We assessed the degree of flow alteration within park watersheds by determining the summed reservoir storage capacity (cf yr⁻¹) for all dams occurring within the watershed and then dividing that capacity by the summed mean annual discharge (cf yr⁻¹; following Nilsson *et al.* 2005) for all stream segments that occur within the park. Data were derived from NID and GRAND datasets (see above). Mean annual discharge was determined using the unit-runoff method and was calculated for the most downstream segment of each flowline moving through a given park.

Invasive species established within parks and future invasion potential

We assessed the threat posed by non-native species currently within NPS units and non-native species with a strong potential to invade parks. We used the ratio of non-native to native fish diversity to assess the threat posed by non-native species within parks, rather than the total number of non-native species, to control for differences in productivity across parks that would naturally support more species diversity.

Non-native fish species currently residing in parks were identified based on the ‘nativity’ status assigned to each species within a given park, as provided in the NPSpecies database. For those species where the status was listed as ‘unknown’ in NPSpecies and for species that we amended during the timed literature review, we assigned native/non-native status based on the designation in the adjoining 6-digit HUC watersheds. If the species was considered native to any 6-digit HUC contained within a park’s watershed, then the species was considered native to the park.

Future invasion potential for each park was determined by tallying all non-native species, both translocated (from North America) and exotic (from other continents) that occur within any 6-digit HUC that overlaps a park’s watershed, but are not currently established within the park. These species were added to the current list of non-native species established within the park and then we recalculated the ratio of non-native: native richness.

Climate analysis: Temperature and precipitation

Changes in annual mean temperature and precipitation (percent departure from present) were determined for each NPS unit using Climate Wizard (www.climatewizard.org 2010). We compared the present (1961-1990) mean annual temperature and precipitation to the future (2070-2099) using an ensemble average of 10 General Circulation Models with a high emission scenario (SRES, A2). Annual mean temperature and precipitation departure data within Climate Wizard has a 12K resolution for the lower 48 US states, and 50K resolution for AK and Hawaii. Climate data was downloaded as a raster for the conterminous US, Alaska, and Hawaii, and using Arc-GIS, we determined the departure (change in mean annual temperature in degree C,

and percent change in mean annual precipitation) by averaging the value of all raster cells occurring within a park unit's boundary.

Management Challenge

The degree of management challenge for each park was determined based on two metrics. First, we calculated the percentage of each park's watershed outside of park boundaries. This metric provides a measure of the degree of control a given park has over activities that may influence water supply (via water withdrawals and dam construction), habitat fragmentation (via dam construction), and the land-use on the park's contributing watershed (including clearing of forested land and increases in impervious surface). Second, we used the recently updated Conservation Biology Institute Protected Area Database (PAD, CBI 2010) to quantify the amount of each parks' contributing watershed in some form of conservation status. This included federal, state, and local government lands, tribal land, and private land under conservation easements. This index provides a measure of potential for the NPS to cooperatively manage the contributing watershed of park freshwater ecosystems.

Conservation planning approach to prioritize parks and US watersheds for conservation

Using Marxan to prioritize parks

Park threat indices and data on faunal representation were used in the conservation planning algorithm Marxan to identify those parks most critical for providing comprehensive representation of freshwater fishes in the US. Marxan prioritizes sites based on the conservation

features they contain, relative to the costs of utilizing a site within the reserve system, and solves the minimum set problem, i.e., finding the smallest number of sites that provide adequate representation with the lowest costs (Possingham *et al.* 2000). In separate analyses, we determined the prioritization of parks based on the occurrence of species in each park and 1) current ecological threats, 2) future ecological threats, and 3) management challenges, where threats were calculated as costs in Marxan.

Three input files are used by Marxan to determine the minimum set solution. First the planning unit file contains all of the conservation sites (i.e., parks) to be prioritized and their costs (range 6.8-1000). Second, the species file contains all of the freshwater fishes to be represented, the number of occurrences for each of these species required by the final solution, and the relative weights (termed ‘species penalty factor’) for each species that serves as a penalty if that species is not included in the final solution of parks chosen by Marxan. Initially weights for all species were set to 1. Weights were increased to 2 for those species not included in initial runs of Marxan, a standard calibration procedure used in Marxan (Ardron *et al.* 2008). This insured that all native US species present in the NPS were represented in the Marxan solution (at least one occurrence). We also tested our problem set with all SPFs set to 2, 10, 100, and 1000 but this did not change the parks (number and their identity) in the final Marxan solution. The third input file is a species occurrence by park matrix. One hundred runs of Marxan were completed for each of the three analyses (current ecological threat, future ecological threat, management challenge), with 5000 iterations per run. A sensitivity analysis was run to determine if additional iterations changed the Marxan solution (i.e., the parks chosen). Iterations of 5,000, 10,000, 10^5 , 10^6 , and 10^7 did not change the parks selected. This is because the dataset was fairly small and because of the data structure (i.e., many rare species spread across disparate

parks). Simulated annealing with two-step iterative improvement was used as the prioritization algorithm. Because we were interested in prioritizing previously established parks, rather than creating a clustered set of new protected areas, we did not employ the boundary length modifier option in Marxan.

Marxan generated a best solution for each analysis, that is, a list of parks chosen in the best run from the 100 total runs of Marxan with the same cost layer. The best run is defined as the lowest cost solution that meets all of the conservation goals (i.e., at least one occurrence for each native US fish species here). The best parks chosen by each analysis were compared to determine how the different threat layers influenced park selection.

Sensitivity analysis of Marxan solution of NPS units to prioritize

With a goal of comprehensive representation for all 478 species present within the NPS, we completed a sensitivity analysis to determine how and whether the cost layer influenced park selection. In separate analyses, Marxan was conducted with the following cost layers: 1) equal costs across all parks, 2) current ecological threats, 3) future ecological threats, and 4) management challenge. A description of methods used to calculate ecological threats and management challenge is provided above. To determine the sensitivity of the Marxan solution to these different cost layers we compared the ‘best solution’ from each Marxan analysis using a Pearson’s correlation coefficient (R). The best solution is those parks chosen in the best run from a total of 100 runs of Marxan with the same cost layer. The best run is defined as the lowest cost solution that meets all of the conservation goals. We present correlation coefficients, not statistical significance, since the large number of units (and hence, elevated

degrees of freedom) makes many correlations appear statistically significant despite low values. Instead, we were interested in comparing the degree of overlap (correlation) between the solutions under different cost conditions.

With a goal of complete representation for all fish species within NPS units, parks were chosen similarly, regardless of differences in the cost layers, or whether cost were equal across parks (Table S3). Best solutions for runs with equal threat, current ecological threat, future ecological threat, and management challenge cost layers had correlation coefficients ranging from 0.81 to 0.95 (average 0.89; Table S3).

To determine the influence of rare species on the Marxan solution we performed a complementary analysis with rare species removed from the dataset (i.e., species that occur in ≤ 2 units; 212 species). With rare species excluded the best solution varied based on the cost layer (Table S3). The average correlation coefficient among Marxan solutions with this representation requirement was 0.49 (range 0.38-0.62). The strongest correlation between parks chosen in the best solution were based on current and future ecological threat (Pearson's $R = 0.62$). Correlation for parks chosen in the best solution with and without threats was also much lower when rare species were excluded (Pearson's $R = 0.46$ for equal threats versus current ecological threats, 0.50 for future ecological threats, 0.38 for management potential).

Finally, parks were chosen differently based on whether rare species were required in the Marxan solution (Table S2, Table S3,). This was expected, especially given the representation requirements are much lower if rare species are not required (i.e., the number of species required in the solution). The average correlation coefficient for the best solution between the two scenarios (rare species required versus not required) was 0.21 (range 0.16-0.26; Table S3).

Overall, this analysis highlights that the optimal Marxan solution was driven by the large number of rare species within the NPS (defined as species occurring in ≤ 2 parks), which accounted for 212 of the 478 of native US species. Together, the large number of rare species spread across a disparate set of parks (45% of the parks assessed) constrained the Marxan solution and resulted in some parks being included in the conservation portfolio regardless of their costs.

Using Marxan to prioritize watersheds that contain native fish species not currently represented by the NPS

We conducted an additional Marxan analysis to identify and prioritize watersheds that contain the native fish species not currently within the NPS (n= 297 species). Here HUC 6 watersheds were treated as potential conservation ‘sites’ (i.e., the site input file). The species file required by Marxan included only those 297 species not currently represented in a NPS unit. Finally, our ‘site by species’ file consisted of a matrix of these 297 species by each site (i.e., HUC 6 watershed) where they occur. All watersheds were treated as having equal costs, that is, no threat layer was applied to HUC 6 watersheds that would affect their selection frequency by Marxan. Similar to the prior Marxan analysis, one hundred runs of Marxan were completed with 5000 iterations per run and simulated annealing with two-step iterative improvement was used as the prioritization algorithm. We report here the frequency that each watershed was chosen based on 100 runs of Marxan (defined as their irreplaceability, or ‘summed solution’ in Marxan terminology). This allowed us to identify highly irreplaceable watersheds, that is, those watersheds that were selected most frequently by our Marxan analysis.

References

Ardron J.A., Possingham H.P., Klein C.J., eds. (2008) *Marxan Good Practices Handbook*. Pacific Marine Analysis and Research Association, Vancouver, BC.

CBI. (2010) The Conservation Biology Institute. PAD-US 1.1 (CBI Edition). Corvallis, OR. Available from: databasin.org/protected-center/features/PAD-US-CBI. Accessed 21 June 21 2010.

Climate Wizard (2010) Available from: www.climatewizard.org. Accessed 7 May 2010.

Dilsaver L.M., editor. (1994) *America's national park system: the critical documents*. Rowmand & Littlefield Publishers, Inc., London.

EPA (2009a) ICLUS v1.2 User's Manual: ArcGIS Tools and Datasets for Modeling US Housing Density Growth. U.S. Environmental Protection Agency, Global Change Research Program, National Center for Environmental Assessment, Washington, DC. Available from: oaspub.epa.gov/eims/eimscomm.getfile?p_download_id=494082. Accessed 25 April 2010.

EPA. (2009b) Land-Use Scenarios: National-Scale Housing-Density Scenarios Consistent with Climate Change Storylines. U.S. Environmental Protection Agency, Global Change Research Program, National Center for Environmental Assessment, Washington, DC. Available from: oaspub.epa.gov/eims/eimscomm.getfile?p_download_id=489947. Accessed 25 April 2010.

Froese R., Pauly D. (2010) FishBase. Available from: www.fishbase.us/search.php. Accessed 16 January 2010.

Global Reservoir and Dam Database. (2010). Available from <http://atlas.gwsp.org/>. Accessed 4 May 2010.

Hamin E.M. (2001) The US National Park Service's partnership parks: collaborative responses to middle landscapes. *Land Use Policy* **18**, 123-135.

Homer C., Huang C.Q., Yang L.M., Wylie B., Coan M. (2004) Development of a 2001 National Land-Cover Database for the United States. *Photogramm Eng Remote Sensing* **70**, 829-840.

Mecklenburg C.W., Mecklenburg T.A., Thorsteinson L.K. (2002) *Fishes of Alaska*. American Fisheries Society, Bethesda, Maryland.

National Inventory of Dams. (2010). Available from <https://nid.usace.army.mil>. Accessed 4 May 2010.

NatureServe. (2004) Downloadable animal datasets. NatureServe Central Databases. Available from: www.natureserve.org/getData/dataSets/watershedHuCs/index.jsp. Accessed 24 January 2009.

NatureServe. (2010) NatureServe Conservation Status. Available from: www.natureserve.org/explorer/ranking.htm. Accessed 24 January 2009.

Nilsson C., Reidy C.A., Dynesius M., Revenga C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science* **308**, 405-408.

NPS. (2009) Strategic plan for natural resource inventories: FY 2008 - FY 2012. National Resource Report NPS/NRPC/NRR-2009/094. Available from: science.nature.nps.gov/im/inventory/Inventory_Strategic_Plan.pdf. Accessed 20 December 2008.

NPS. (2010) The National Park Service Biodiversity Database (NPSpecies). Available from: science.nature.nps.gov/im/apps/npspp/index.cfm. Accessed 25 January 2010.

Possingham H.P., Ball I., Andelman S. (2000) Mathematical methods for identifying representation reserve networks. pp. 291-305 in S. Ferson, M. Burgman editors. *Quantitative methods for conservation biology*. Springer-Verlag, New York, NY.

USGS. (2004) Nonindigenous Aquatic Species Database. Available from: nas.er.usgs.gov/. Accessed 20 January 2009.

Vörösmarty C.J., McIntyre P.B., Gessner M.O., Dudgeon D., Prusevich A., Green P., Glidden S., Bunn S.E., Sullivan C.A., Liermann C.R., Davies P.M. (2010) Global threats to human water security and river biodiversity. *Nature* **467**, 555-561.

Table S1. Families of freshwater fishes present in the NPS (n=147 parks) and for the entire US. Sub-species were not included in the analysis.

	Species count in NPS	Species count for US	% of species represented in NPS
Acipenseridae	7	8	88%
Amblyopsidae	4	6	67%
Amiidae	1	1	100%
Anguillidae	1	1	100%
Aphredoderidae	1	1	100%
Atherinopsidae	2	3	67%
Catostomidae	43	62	69%
Centrarchidae	27	31	87%
Characidae	1	1	100%
Cichlidae	0	1	0%
Clupeidae	8	8	100%
Cottidae	15	27	56%
Cyprinidae	151	248	61%
Cyprinodontidae	7	15	47%
Elassomatidae	3	6	50%
Eleotridae	3	3	100%
Embiotocidae	0	1	0%
Esocidae	4	4	100%
Fundulidae	17	24	71%
Gadidae	1	1	100%
Gasterosteidae	3	3	100%
Gobiidae	2	3	67%
Goodeidae	0	4	0%
Hiodontidae	2	2	100%
Ictaluridae	25	39	64%
Lepisosteidae	5	5	100%
Moronidae	3	3	100%
Mugilidae	1	1	100%
Osmeridae	4	5	80%
Percidae	86	179	48%
Percopsidae	1	2	50%
Petromyzontidae	14	19	74%
Poeciliidae	6	14	43%
Polyodontidae	1	1	100%
Salmonidae	23	37	62%
Sciaenidae	1	1	100%
Syngnathidae	1	1	100%
Umbridae	4	4	100%

Table S2. Park threat ranking (0-1) and selection in the best solution by the MARXAN conservation planning software. MARXAN analyses were run with three separate cost layers: 1) current ecological threat, 2) future ecological threat, 3) management potential, with (*) and without (◆) rare species required in the solution. Selection of a park by MARXAN is indicated by the following abbreviations: ALL – parks chosen by all three analyses; C – parks chosen based on current ecological threat layer only; F – parks chosen based on future ecological threat layer only; M – parks chosen based on management challenge layer only; C&F – parks chosen based on current and future ecological threat layers; C&M – parks chosen based on current ecological threat and management challenge layers; F&M – parks chosen based on future ecological threat and management challenge layers. If rare species (i.e., present in ≤ 2 parks) were present in a park the Rare Species column contains a Y.

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN◆ Selection (Rare Species Excluded)	Rare species?
101	Alaskan Coastal	Alagnak	National Wild and Scenic Rivers & Riverway	0.01	0.02	0.35		C	
101	Alaskan Coastal	Aniakchak	National Monument	0.01	0.01	0.01			
101	Alaskan Coastal	Bering Land Bridge	National Preserve	0.01	0.29	0.24			
101	Alaskan Coastal	Cape Krusenstern	National Monument	0.01	0.25	0.01			
101	Alaskan Coastal	Denali	National Park	0.01	0.14	0.14		C	
101	Alaskan Coastal	Gates Of The Arctic	National Park	0.01	0.23	0.11			
101	Alaskan Coastal	Katmai	National Park	0.01	0.04	0.05	F		

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
101	Alaskan Coastal	Kobuk Valley	National Park	0.01	0.22	0.07	C&M	C&M	
101	Alaskan Coastal	Lake Clark	National Park	0.01	0.09	0.16			
101	Alaskan Coastal	Noatak	National Preserve	0.14	0.27	0.12			
102	Upper Yukon	Yukon - Charley Rivers	National Preserve	0.01	0.12	0.39	F		
103	Alaska & Canada Pacific Coastal	Glacier Bay	National Park	0.17	0.03	0.10		M	
103	Alaska & Canada Pacific Coastal	Kenai Fjords	National Park	0.23	0.19	0.01			
103	Alaska & Canada Pacific Coastal	Klondike Gold Rush	National Historical Park	0.01	0.07	0.44		C	
103	Alaska & Canada Pacific Coastal	Mount Rainier	National Park	0.38	0.33	0.20		M	
103	Alaska & Canada Pacific Coastal	North Cascades	National Park	0.20	0.24	0.13		M	
103	Alaska & Canada Pacific Coastal	Olympic	National Park	0.35	0.16	0.40	ALL	C&F	Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
103	Alaska & Canada Pacific Coastal	San Juan Island	National Historical Park	0.61	0.63	0.65			
103	Alaska & Canada Pacific Coastal	Sitka	National Historical Park	0.16	0.01	0.59		F	
103	Alaska & Canada Pacific Coastal	Wrangell - St Elias	National Park	0.01	0.08	0.06			
109	English - Winnipeg Lakes	Voyageurs	National Park	0.46	0.61	0.54			
116	Laurentian Great Lakes	Apostle Islands	National Lakeshore	0.24	0.35	0.37	ALL		Y
116	Laurentian Great Lakes	Cuyahoga Valley	National Park	0.82	0.93	0.76			Y
116	Laurentian Great Lakes	Grand Portage	National Monument	0.41	0.70	0.67			
116	Laurentian Great Lakes	Indiana Dunes	National Lakeshore	0.92	0.95	0.77			Y
116	Laurentian Great Lakes	Isle Royale	National Park	0.22	0.24	0.10		ALL	Y
116	Laurentian Great Lakes	Pictured Rocks	National Lakeshore	0.33	0.33	0.44	ALL		Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
116	Laurentian Great Lakes	Sleeping Bear Dunes	National Lakeshore	0.60	0.59	0.54			Y
118	Northeast US & Southeast Canada Atlantic Drainages	Acadia	National Park	0.93	0.95	0.37			
118	Northeast US & Southeast Canada Atlantic Drainages	Assateague Island	National Seashore	0.48	0.36	0.14			
118	Northeast US & Southeast Canada Atlantic Drainages	Cape Cod	National Seashore	0.62	0.71	0.20	ALL		Y
118	Northeast US & Southeast Canada Atlantic Drainages	Fire Island	National Seashore	0.15	0.44	0.17			
118	Northeast US & Southeast Canada Atlantic Drainages	Marsh-Billings-Rockefeller	National Historical Park	0.97	0.99	0.85			
118	Northeast US & Southeast Canada Atlantic Drainages	Minute Man	National Historical Park	1.00	0.99	0.88			
118	Northeast US & Southeast Canada Atlantic Drainages	Morristown	National Historical Park	0.65	0.97	0.62			

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
118	Northeast US & Southeast Canada Atlantic Drainages	Saratoga	National Historical Park	0.16	0.44	0.52			
118	Northeast US & Southeast Canada Atlantic Drainages	Upper Delaware	National Wild and Scenic Rivers & Riverway	0.90	0.98	0.81			Y
118	Northeast US & Southeast Canada Atlantic Drainages	Valley Forge	National Historical Park	0.95	0.97	0.97			
120	Columbia Glaciated	Glacier	National Park	0.41	0.49	0.32			
121	Columbia Unglaciaded	John Day Fossil Beds	National Monument	0.52	0.21	0.71	ALL		Y
121	Columbia Unglaciaded	Nez Perce	National Historical Park	0.55	0.65	0.76			Y
122	Upper Snake	City Of Rocks	National Reserve	0.01	0.31	0.22			
122	Upper Snake	Grand Teton	National Park	0.71	0.92	0.36	ALL		Y
122	Upper Snake	Hagerman Fossil Beds	National Monument	0.40	0.39	0.53			

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
123	Oregon & Northern California Coastal	Crater Lake	National Park	0.31	0.18	0.07			
123	Oregon & Northern California Coastal	Lewis and Clark	National Historical Park	0.39	0.16	0.78			Y
123	Oregon & Northern California Coastal	Muir Woods	National Monument	0.01	0.39	0.41			
123	Oregon & Northern California Coastal	Oregon Caves	National Monument	0.21	0.07	0.01			
123	Oregon & Northern California Coastal	Point Reyes	National Seashore	0.61	0.48	0.31		F	
123	Oregon & Northern California Coastal	Redwood	National Park	0.72	0.27	0.67	ALL		Y
125	Sacramento - San Joaquin	Devils Postpile	National Monument	0.44	0.26	0.33			
125	Sacramento - San Joaquin	Lassen Volcanic	National Park	0.45	0.50	0.20	M		Y
125	Sacramento - San Joaquin	Pinnacles	National Monument	0.53	0.55	0.46			
125	Sacramento - San Joaquin	Sequoia and Kings Canyon National Parks	National Park	0.50	0.69	0.25		C	

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
125	Sacramento - San Joaquin	Yosemite	National Park	0.63	0.76	0.18	ALL	M	Y
127	Bonneville	Great Basin	National Park	0.27	0.48	0.04			
127	Bonneville	Timpanogos Cave	National Monument	0.73	1.00	0.56			
128	Death Valley	Death Valley	National Park	0.63	0.54	0.29	ALL		Y
128	Death Valley	Mojave	National Preserve	0.24	0.46	0.29	C&F		Y
129	Vegas - Virgin	Zion	National Park	0.59	0.59	0.50	ALL		Y
130	Colorado	Arches	National Park	0.56	0.50	0.32			
130	Colorado	Black Canyon Of The Gunnison	National Park	0.84	0.80	0.59			
130	Colorado	Canyon De Chelly	National Monument	0.48	0.37	0.28			
130	Colorado	Canyonlands	National Park	0.96	0.87	0.64			Y
130	Colorado	Capitol Reef	National Park	0.88	0.75	0.43			

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
130	Colorado	Dinosaur	National Monument	0.94	0.78	0.63	ALL	ALL	Y
130	Colorado	Grand Canyon	National Park	0.98	0.82	0.56			
130	Colorado	Mesa Verde	National Park	0.84	0.88	0.47			
130	Colorado	Wupatki	National Monument	0.87	0.82	0.69			
131	Gila	Gila Cliff Dwellings	National Monument	0.29	0.29	0.41	ALL	ALL	Y
131	Gila	Montezuma Castle	National Monument	0.56	0.51	0.59			
131	Gila	Organ Pipe Cactus	National Monument	0.19	0.20	0.27	ALL		Y
131	Gila	Tumacacori	National Historical Park	0.90	0.93	0.82	ALL		Y
131	Gila	Tuzigoot	National Monument	0.86	0.84	0.79			Y
132	Upper Rio Grande - Bravo	Bandelier	National Monument	0.93	0.96	0.70			
132	Upper Rio Grande -	Great Sand Dunes	National Park	0.39	0.60	0.22	ALL	F&M	Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
	Bravo								
132	Upper Rio Grande - Bravo	Guadalupe Mountains	National Park	0.47	0.44	0.29			
132	Upper Rio Grande - Bravo	White Sands	National Monument	0.37	0.74	0.42	ALL		Y
133	Pecos	Carlsbad Caverns	National Park	0.49	0.41	0.34	ALL		Y
133	Pecos	Pecos	National Historical Park	0.37	0.66	0.51		C	
135	Lower Rio Grande - Bravo	Big Bend	National Park	0.80	0.58	0.66	ALL		Y
139	West Texas Gulf	Padre Island	National Seashore	0.01	0.05	0.14			
140	East Texas Gulf	Lyndon B. Johnson	National Historical Park	0.46	0.46	0.99	ALL		Y
140	East Texas Gulf	San Antonio Missions	National Historical Park	0.86	0.89	0.95			Y
141	Sabine - Galveston	Big Thicket	National Preserve	0.79	0.54	0.80	ALL	C	Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
142	Upper Missouri	Badlands	National Park	0.75	0.73	0.61			Y
142	Upper Missouri	Devils Tower	National Monument	0.95	0.80	0.97			
142	Upper Missouri	Little Bighorn Battlefield	National Monument	0.69	0.76	0.75			
142	Upper Missouri	Theodore Roosevelt	National Park	0.67	0.72	0.73			
142	Upper Missouri	Wind Cave	National Park	0.64	0.52	0.46			
142	Upper Missouri	Yellowstone	National Park	0.54	0.65	0.22			Y
143	Middle Missouri	Agate Fossil Beds	National Monument	0.50	0.43	0.95			
143	Middle Missouri	Florissant Fossil Beds	National Monument	0.71	0.90	0.49			
143	Middle Missouri	Homestead	National Monument	0.97	0.94	1.00			
143	Middle Missouri	Missouri	National Wild and Scenic Rivers & Riverway	0.88	0.86	0.89	ALL	M	Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
143	Middle Missouri	Niobrara	National Wild and Scenic Rivers & Riverway	0.67	0.61	0.93		C&F	
143	Middle Missouri	Pipestone	National Monument	0.33	0.42	0.90	C&F		Y
143	Middle Missouri	Rocky Mountain	National Park	0.65	0.69	0.27			
143	Middle Missouri	Scotts Bluff	National Monument	0.68	0.56	0.86			
144	US Southern Plains	Alibates Flint Quarries	National Monument	0.31	0.38	0.73	ALL	ALL	Y
145	Ouachita Highlands	Hot Springs	National Park	0.99	0.78	0.54	ALL		Y
146	Central Prairie	George Washington Carver	National Monument	0.27	0.35	0.74	ALL		Y
146	Central Prairie	Tallgrass Prairie	National Preserve	0.81	0.67	0.52	M		Y
147	Ozark Highlands	Buffalo	National River	0.32	0.18	0.64	ALL		Y
147	Ozark Highlands	Ozark	National River	0.36	0.28	0.68	ALL	ALL	Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
148	Upper Mississippi	Effigy Mounds	National Monument	0.69	0.91	0.93	ALL		Y
148	Upper Mississippi	Mississippi	National River	0.66	0.88	0.88		ALL	Y
148	Upper Mississippi	Saint Croix	National Wild and Scenic Rivers & Riverway	0.57	0.77	0.71	ALL		Y
149	Lower Mississippi	Jean Lafitte	National Historical Park	0.76	0.47	0.98			Y
150	Teays - Old Ohio	Bluestone	National Wild and Scenic Rivers & Riverway	0.74	0.68	0.87			Y
150	Teays - Old Ohio	Hopewell Culture	National Historical Park	0.70	0.79	0.69			
150	Teays - Old Ohio	Mammoth Cave	National Park	0.59	0.57	0.84	ALL	C&M	Y
150	Teays - Old Ohio	New River Gorge	National River	0.83	0.71	0.78	ALL		Y
151	Cumberland	Big South Fork	National River	0.54	0.40	0.61	ALL		Y
152	Tennessee	Cumberland Gap	National Historical Park	0.58	0.67	0.39	ALL		Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
152	Tennessee	Great Smoky Mountains	National Park	0.73	0.73	0.48	ALL	C&M	Y
152	Tennessee	Obed	National Wild and Scenic Rivers & Riverway	0.77	0.64	0.80		F	Y
152	Tennessee	Russell Cave	National Monument	0.18	0.17	0.83			
153	Mobile Bay	Little River Canyon	National Preserve	0.52	0.41	0.71	ALL		Y
154	West Florida Gulf	Gulf Islands	National Seashore	0.34	0.09	0.24	ALL	ALL	Y
156	Florida Peninsula	Big Cypress	National Preserve	0.76	0.62	0.50			
156	Florida Peninsula	Biscayne	National Park	0.99	0.81	0.86			
156	Florida Peninsula	Canaveral	National Seashore	0.14	0.10	0.05		ALL	
156	Florida Peninsula	Cumberland Island	National Seashore	0.26	0.11	0.57			
156	Florida Peninsula	Dry Tortugas	National Park	0.01	0.14	0.03			

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
156	Florida Peninsula	Everglades	National Park	0.78	0.63	0.48	ALL		Y
156	Florida Peninsula	Fort Frederica	National Monument	0.01	0.12	0.45			
156	Florida Peninsula	Fort Matanzas	National Monument	0.28	0.20	0.84			
156	Florida Peninsula	Timucuan Ecological and Historic Preserve	National Preserve	0.51	0.34	0.82			
157	Appalachian Piedmont	Appomattox Court House	National Historical Park	0.42	0.37	0.63	ALL		Y
157	Appalachian Piedmont	Booker T. Washington	National Monument	0.29	0.29	0.92	ALL	C&F	Y
157	Appalachian Piedmont	Cape Hatteras	National Seashore	0.30	0.22	0.19			
157	Appalachian Piedmont	Cape Lookout	National Seashore	0.01	0.15	0.26			
157	Appalachian Piedmont	Colonial	National Historical Park	0.80	0.83	0.58			Y
157	Appalachian Piedmont	Congaree	National Park	0.91	0.86	0.99	ALL		Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
157	Appalachian Piedmont	Fort Pulaski	National Monument	0.89	0.84	0.96			
157	Appalachian Piedmont	Fort Sumter	National Monument	0.01	0.12	0.37	ALL		Y
157	Appalachian Piedmont	Ocmulgee	National Monument	0.78	0.53	0.94	ALL		Y
158	Chesapeake Bay	Chesapeake and Ohio Canal	National Historical Park	0.85	0.90	0.91	ALL	ALL	Y
158	Chesapeake Bay	George Washington Birthplace	National Monument	0.22	0.31	0.08			
158	Chesapeake Bay	Harpers Ferry	National Historical Park	0.82	0.85	0.90			
158	Chesapeake Bay	Shenandoah	National Park	0.43	0.52	0.35		M	Y
159	Southern California Coastal - Baja California	Cabrillo	National Monument	0.35	0.56	0.16			
159	Southern California Coastal - Baja California	Channel Islands	National Park	0.18	0.32	0.09			
828	Hawaiian Islands	Haleakala	National Park	0.20	0.03	0.18	ALL	C&F	Y

Ecoregion ID	Ecoregion	Park Name	Park Type	Current Ecological Threat	Future Ecological Threat	Management Challenge	MARXAN* Selection (Rare Species Included)	MARXAN [♦] Selection (Rare Species Excluded)	Rare species?
828	Hawaiian Islands	Kalaupapa	National Historical Park	0.25	0.06	0.31			Y
828	Hawaiian Islands	Kaloko-Honokohau	National Historical Park	0.44	0.05	0.12		M	

Table S3. Pearson’s correlation coefficients for the best solution chosen by MARXAN with four different cost layers, with and without rare species included in the analyses.

	Rare species?	Included	Included	Included	Included	Excluded	Excluded	Excluded	Excluded
	Cost layer	Current ecological threat	Future ecological threat	Management challenge	Equal threat	Current ecological threat	Future ecological threat	Management challenge	Equal threat
Cost layer	Rare species?								
Current ecological threat	Included	1							
Future ecological threat	Included	0.95	1						
Management potential	Included	0.94	0.89	1					
Equal threats	Included	0.87	0.86	0.81	1				
Current ecological threat	Excluded	0.26	0.21	0.26	0.18	1			
Future ecological threat	Excluded	0.20	0.20	0.20	0.16	0.62	1		
Management potential	Excluded	0.25	0.20	0.25	0.16	0.56	0.42	1	
Equal threats	Excluded	0.22	0.21	0.22	0.22	0.46	0.50	0.38	1

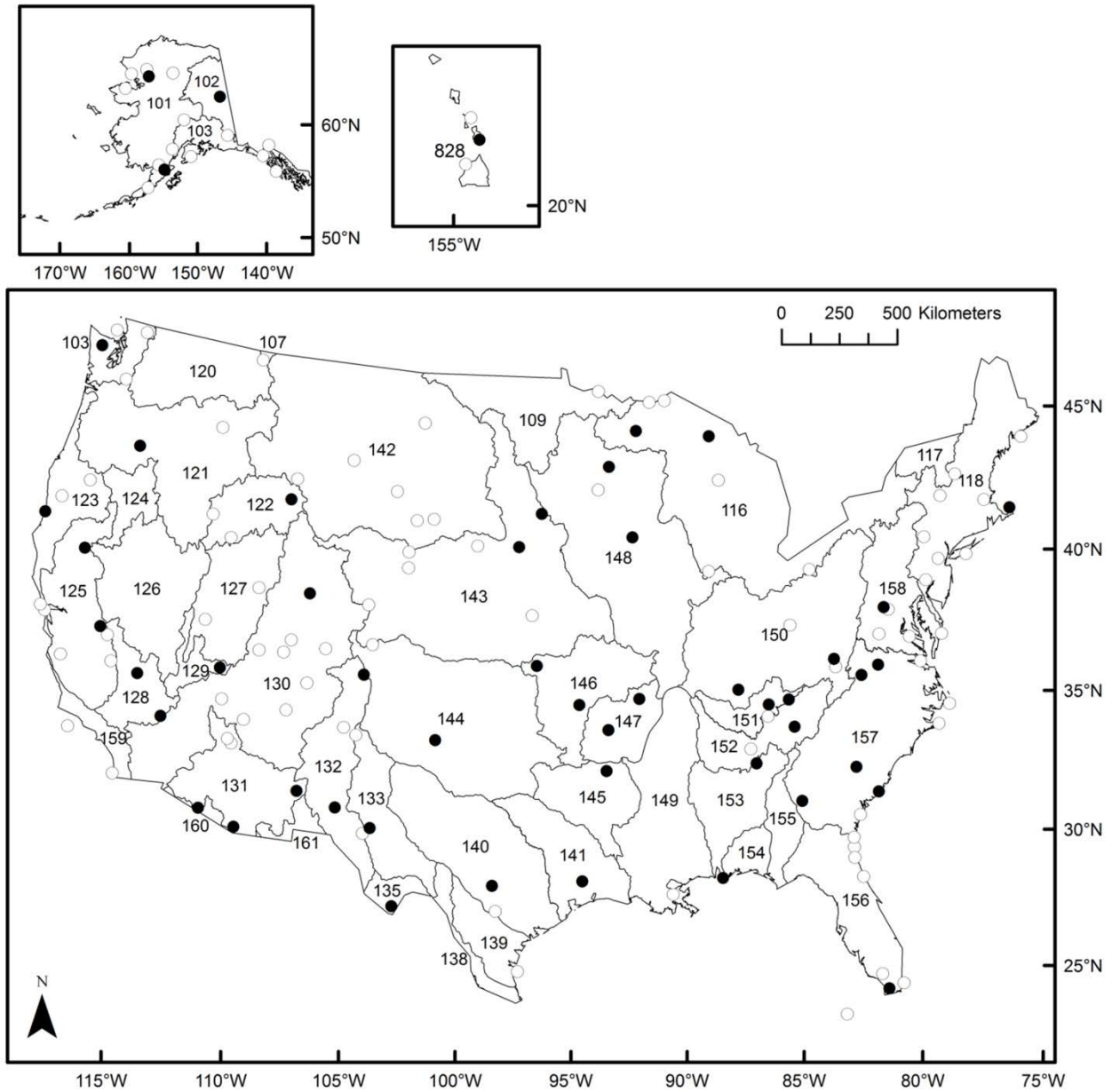


Fig. S1

Freshwater ecoregions of the US and the geographic centroid of NPS units selected (filled circles) and not selected (open circles) in our conservation planning analysis. The number within each ecoregion represents the ecoregion identifying number (i.e., Ecoregion ID, see Table S2 for ecoregion names and the parks contained within each).