ABUNDANCE AND POPULATION DYNAMICS OF INVASIVE NORTHERN PIKE *ESOX LUCIUS*, YAMPA RIVER, COLORADO, 2004–2010

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Executive Summary

Northern pike *Esox lucius* was introduced into the Yampa River basin in the 1970's and is now considered one of the basin's most problematic invasive aquatic species. Its high abundance, habitat use that overlaps with most native fishes, and ability to consume a wide variety of life stages of native fishes, including large adults, are impediments to the recovery of endangered fishes in the upper Colorado River basin. In response, mechanical removal of the species was implemented from 2004-2010 by the Upper Colorado River Endangered Fish Recovery Program. The goals of this study were to assess effectiveness of northern pike removal efforts to date and predict the ability of those efforts to achieve removal targets. Objectives to achieve those goals included development of comprehensive age- or size-structured abundance estimates and estimation of immigration rates.

We analyzed mark-recapture records of 8,929 individual northern pike from three reaches of the Yampa River (Hayden to Craig, HC [designated as a "buffer zone" between upstream pike populations and downstream native fish critical habitat]: river mile [RM] 171.0–134.2; South Beach-Little Yampa Canyon-Juniper, SLJ: RM 134.2–91.0; Maybell-Sunbeam, MS: RM 88.7–58.5) from 2004–2010. Overall, capture probability estimates per sampling occasion (pass) were low: averaging 0.17 for an average-length northern pike (465 mm total length). Survival rate estimates for average-length northern pike were highest in downstream reach MS, averaging 0.54 (range: 0.36–0.71) across annual time intervals, followed by middle reach SLJ (average: 0.32, range: 0.18–0.48), and then upstream reach HC (average: 0.25, range: 0.12–0.38). Annual abundance estimates followed the opposite pattern: highest each year in HC (range: 1192–3951), followed by SLJ (659–2446), and lowest in MS (range: 233–645). Years with highest abundance included 2004 and 2009 for all reaches.

In reach HC, an average of 32% of the estimated northern pike population was removed each year (range: 11–40%). Changes in abundance due to combined effects of recruitment and immigration averaged 496% (range: 40–2038%). Results were similar in reach SLJ: mean annual removal rate of northern pike was 35% (range: 14–52%) and annual population changes averaged 491% (range: -28–2075%). In reach MS, average removal rate was 32% despite lower densities, and annual population increases between sampling intervals were 144% (range: -52–459), again due to combined effects of recruitment and immigration. Recruitment and immigration effects could not be estimated separately due to sparseness of the data. Population changes between sampling intervals averaged 144% (range: -52–459).

Too few young northern pike were captured to produce age-structured abundance estimates and recruitment rates. Therefore, we utilized growth rate information to accomplish a similar objective in reaches HC and SLJ. Most young northern pike captured in reach HC were produced in 2004, followed by 2006, 2008, and 2009, in descending order. In reach SLJ, most northern pike were produced in 2009, 2004, 2006, and 2008, in descending order. High reproductive success may have been expected in the high-discharge years 2008 and 2009 because of increased spawning habitat availability, but peak flows in 2004 were the lowest of the 2004-2010 study period. Thus, the relationship between Yampa River flow patterns and northern pike spawning success and annual recruitment is uncertain.

Immigration rate estimation in our tag-recapture analysis was precluded by too few movements among study reaches, so we used all captures within a broader dataset to describe northern pike movement in the Yampa River basin. Yampa River reaches included: Lake Catamount (CAT, upstream of RM 205.0), Above Hayden (AH, RM 205.0–171.0), HC, SLJ, MS, Lily Park (LP, RM 55.5–44.8), and Yampa Canyon (YC, RM 44.8–0.0). Green River reaches included: Lodore Canyon (GRc, RM 360.0–345.1), Echo to Split (GRb, RM 345.1–321.0), and middle Green River (GRa, RM 321.0–247.0). Of 1,911 individual northern pike with multiple captures, 21% of these fish (*n* = 394) changed reaches. Of those 394 northern pike, 90% of movements were to a downstream reach, either within the Yampa River or to the Green River. The reach with the largest proportion of northern pike movement out of the reach was AH at 34%, and reach HC just downstream had the next highest rate of movement at 19%. We detected 18 northern pike originally tagged in CAT and later recaptured from 2004–2011in Yampa or Green River reaches. Northern pike also moved from the Yampa River basin downstream into the Green River: nine into upstream GRc, five into middle GRb (all at or near the Green-Yampa River confluence), and 10 into downstream GRa. We detected 121 northern pike that moved from off-channel ponds in the Yampa River basin (where they had been stocked after removal from the river) to Yampa River or Green River study reaches.

In addition to our movement description from tagged fish recaptures, analysis of length–frequency histograms of young northern pike from our recruitment investigations provided additional information on pike movement. Specifically, we noted the appearance of older cohorts of fish in reaches where they were absent in previous years, which suggested immigration. For example, in 2008, no age-0 and few age-1 fish were captured in reach HC in sampling that extended through early July when both age classes could have been detected. In 2009, both 2007 and 2008 cohorts were well-represented there. Hence, those young northern pike may have moved in from another reach or off-channel source. It is possible they moved upstream from downstream reach SLJ, but a similar scenario was observed in SLJ: few 2007 or 2008 northern pike were captured in those years (despite sampling into July), but the 2007 cohort was more abundant than expected as age-2 fish in 2009. Thus, young northern pike found in those reaches were most likely the result of immigration from upstream reaches.

Targeted sampling of young northern pike through space and time is necessary to better understand recruitment and immigration patterns in the Yampa River. However, even without specific estimates of those processes, we demonstrated through northern pike movement, survival rate, and abundance estimate data that current removal efforts are inadequate to permanently reduce pike abundance in the Yampa River. This is mainly because combined recruitment and immigration rates exceed removal rates. In lower-density reaches such as downstream reach MS, which is further downstream from known spawning areas and reservoirs, increased removal combined with lowered recruitment and immigration may reduce northern pike densities down to target levels. However, in higher-density reaches upstream, other control efforts, such as northern pike source management and spawning disruption, in addition to increased removal would be required to overcome annual population increases from recruitment and immigration. This information should allow managers to better evaluate the role of removal in the "buffer zone" on populations in downstream critical habitat and explore more effective means to reduce northern pike abundance, which should assist with recovery of native fishes.

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KEY WORDS

northern pike, upper Colorado River, endangered fishes, non-native predator, invasive species, population dynamics, demographic parameters, movement, management

INTRODUCTION

Introduction and establishment of non-native fish in western rivers of the USA are major threats to conservation of native fish assemblages (Minckley and Deacon 1968; Moyle et al. 1986; Stanford and Ward 1986; Carlson and Muth 1989; Minckley and Deacon 1991; Olden et al. 2006). In the upper Colorado River basin (UCRB), non-native fish invasions began over 100 years ago, with introduction of channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, and salmonids. In the 1970's, small-bodied species such as red shiner *Cyprinella lutrensis* were expanding rapidly (Vanicek et al. 1970; Holden and Stalnaker 1975b; Holden and Stalnaker 1975a), and potential negative effects of that species and other small-bodied fishes have been documented (Haines and Tyus 1990; Dunsmoor 1993; Ruppert et al. 1993; Muth and Snyder 1995; Bestgen et al. 2006a). More recently, piscivores such as smallmouth bass *Micropterus dolomieu* and northern pike *Esox lucius* have established and are now common in the Yampa River and other locations in the UCRB (Wick et al. 1985; Anderson 2002; Anderson 2005; Bestgen et al. 2006b; Burdick 2008; Johnson et al. 2008; Martin et al. 2010; Battige 2013; Francis and Ryden 2013; Skorupski et al. 2013; Webber and Jones 2013; Martinez et al. 2014).

The predatory threat of large-bodied, piscivorous taxa such as northern pike and smallmouth bass is substantial. For example, based on results of a bioenergetics model, Johnson et al. (2008) ranked smallmouth bass and northern pike as the first- and second-most problematic invasive species because of their high abundance, habitat use that overlaps with most native fishes, and ability to consume a wide variety of life stages of native fishes in the Colorado River basin. Expanded populations of piscivores such as northern pike impede conservation actions aimed at recovery of four endangered fishes in the UCRB: Colorado pikeminnow *Ptychocheilus* *lucius*, razorback sucker *Xyrauchen texanus*, humpback chub *Gila cypha*, and bonytail *Gila elegans* (U.S. Fish and Wildlife Service 2002a; U.S. Fish and Wildlife Service 2002b; U.S. Fish and Wildlife Service 2002c; U.S. Fish and Wildlife Service 2002d). Northern pike are especially problematic because they are capable of consuming nearly all life stages of native fishes, including adult Colorado pikeminnow (J. Hawkins, pers. obs.), which is the native apex predator of the UCRB. Evidence that northern pike may be a potent predatory problem in the Yampa River includes the declining abundance of Colorado pikeminnow from 2000-2003 to a relatively low level in 2006-2008, in spite of abundance increases in the four other major population areas in the Green River basin during the same time period (Bestgen et al. 2010a).

In response to the predatory threat posed by non-native northern pike, the Upper Colorado River Endangered Fish Recovery Program initiated efforts to control such species via mechanical removal beginning in 1999 (Hawkins et al. 2005; Martinez et al. 2014). Interim goals for removal actions have been established for the Yampa River and include reducing density of northern pike and increasing composition of the small-bodied fish community to 10-30% native fishes. Average density calculated from Petersen mark-recapture abundance estimates for northern pike ≥ 300 mm total length (TL) from 2004–2010 was 30.8 pike/mile in the Yampa River from Hayden, Colorado, downstream to Craig, Colorado, which was considered a "buffer zone" between upstream pike populations and downstream endangered fish critical habitat (Finney and Haines 2008; Webber 2008; Webber 2009; Webber 2010; Martinez et al. 2014). Average density for the same time period in critical habitat of the middle Yampa River, where endangered fish reside, was 10.2 pike/mile (Martin et al. 2010; Wright 2010; Martinez et al. 2014). The interim target for critical habitat is 3 pike/mile (Valdez et al. 2008) or the equivalent of current Colorado pikeminnow density (1.9 pikeminnow/mile in 2008; (Bestgen et al. 2010a)), whichever is lower. Colorado pikeminnow captures in 2012 and 2013 were $n = 6$ and $n = 8$, respectively, resulting in even lower abundance and density estimates (K. Bestgen, pers. comm.). To date, substantial information has been collected on distribution, population abundance, size structure, and movements of northern pike concurrent with removal actions throughout the UCRB. Removal efforts vary in intensity and effectiveness across stream reaches where northern pike exist, but only in a few areas are those efforts thought to approach levels of removal needed to enhance survival prospects for native fishes (Badame et al. 2008; Burdick 2008; Hawkins et al. 2009). Further, limited understanding of population level effects of removal actions inhibits the ability of managers to understand effectiveness of removal programs and formulate a comprehensive control strategy that will effectively reduce populations of northern pike and enhance prospects for recovery of native fish populations.

Goal and objectives

Goals for this study were to assess effectiveness of northern pike removal efforts to date and predict the ability of those efforts to achieve removal targets. Objectives to achieve those goals included development of comprehensive age- or size-structured abundance estimates and estimation of immigration rates (Bestgen et al. 2010a).

Comprehensive abundance estimates conducted at appropriate temporal and spatial scales coupled with immigration information should result in a better understanding of abundance dynamics of northern pike populations in the Yampa River. This understanding will allow managers to evaluate effectiveness of removal in all reaches, including the “buffer zone”, on northern pike populations in downstream critical habitat, assess immigration from sources upstream of critical habitat, and explore more effective means to reduce pike abundance and subsequently, assist with recovery of native fishes.

STUDY AREA

The upper Colorado River basin covers portions of Wyoming, Utah, Colorado, New Mexico, and Arizona (Figure 1). The basin is bordered by the Rocky Mountains on the east and various ranges to the west. Main drainages include the Green River, upper Colorado River, and San Juan River subbasins and the downstream boundary is defined by Lee Ferry below Glen Canyon Dam, Arizona. The scope of this study is restricted primarily to the Yampa River basin in northwest Colorado (Figure 2). The basin experiences a relatively natural hydrograph driven by snowmelt runoff (Figure 3), although a few relatively small upstream reservoirs exist: Stagecoach Reservoir and Lake Catamount upstream on the Yampa River, and Elkhead Reservoir on Elkhead Creek (Figure 2). Additional sampling and tag recapture data from middle and upper Green River was used in some analyses.

METHODS

Data

northern pike captures resulted from targeted non-native species removal efforts and from other UCRB studies where fishes were captured, such as Colorado pikeminnow abundance estimate sampling (Bestgen et al. 2010a; Osmundson and White 2014) and fish community monitoring downstream of Flaming Gorge Dam on the Green River (Bestgen et al. 2010b).

northern pike were captured by boat, raft, and backpack electrofishing; “block-and-shock” sampling (closing off large backwater mouths with trammel nets while electrofishing); seining; electric seining; gill, fyke, and trammel netting; and angling. We obtained most northern pike data for this study from the non-native species database created in Microsoft Access by Andre Breton (Larval Fish Laboratory/Colorado Cooperative Fish and Wildlife Unit, Colorado State University, Fort Collins, Colorado). The database was constructed to model population dynamics of Smallmouth Bass in the UCRB (Breton et al. 2013a; Breton et al. 2014) and many of those records originated from a dataset maintained by U. S. Fish and Wildlife Service (USFWS), Grand Junction, Colorado. Additional northern pike data were obtained directly from Colorado Parks and Wildlife (CPW) biologists who have performed work in the study area. Those records were added to Breton’s database, but not to the USFWS dataset.

We conducted thorough error-checking and standardization of database records prior to inclusion in a final data set for analyses. A series of queries was used to detect errors within and among records including missing or erroneous Floy® tags, multiple tag deployments, duplicate records, incorrect recapture designations, and incomplete location data. Acquisition of records and compilation of the final data set for analysis consumed about 11 months of time by the senior author, and nearly 50% of the project budget.

Groups

In order to detect differences in northern pike population parameters and estimate movement/immigration throughout the Yampa River, encounter histories were grouped by initial capture reach. From upstream to downstream, reaches were defined as: Lake Catamount (CAT, upstream of river mile [RM] 205.0), Above Hayden (AH, just upstream of Steamboat Springs downstream to Hayden, RM 205.0–171.0), Hayden to Craig (HC, RM171.0–134.2) South Beach-Little Yampa Canyon-Juniper (SLJ, RM 134.2–91.0), Maybell-Sunbeam (MS, RM 88.7–58.5), Lily Park (LP, RM 55.5–44.8), and Yampa Canyon (YC, RM 44.8–0.0; Figure 4). Recaptures from the following Green River reaches were included: Lodore Canyon (GRc, upstream of Yampa River confluence, RM 360.0–345.1), Echo to Split (GRb, Echo Park, Colorado, at Yampa River confluence downstream to Split Mountain boat ramp near Jensen, Utah, RM 345.1–321.0), and middle Green River (GRa, Split Mountain boat ramp downstream to the Duchesne River confluence, RM 321.0–247.0; Figure 4). Reach delineations and groupings were based on recent sampling history and differences in stream geomorphology present in some reaches. Our initial intention was to produce age-structured or size-structured abundance estimates and to group the data accordingly; however, insufficient data in many reaches precluded such estimation.

Time

All annual sampling events were organized into four passes each year: one marking pass and three recapture/removal passes. Effort among reaches and investigators was not synchronized and sampling occurred in some reaches and years more frequently than in others; regardless, all sampling events were allocated to four passes each year to best achieve a balanced study dataset for analysis purposes. Multiple encounters of an individual within a pass were considered one encounter.

Statistical modeling

Data were analyzed in Program MARK (White and Burnham 1999) using the robust design (Cormack 1964; Jolly 1965; Seber 1965; Kendall and Pollock 1992; Kendall et al. 1995), which allows estimation of multiple population parameters through the use of relatively longer (e.g., annual) primary sampling sessions and more closely-spaced secondary sampling occasions (passes). Data was insufficient to incorporate a multi-state component to the robust design analysis (Brownie et al. 1993), which would estimate transition rates (movement) among reaches between the primary sampling sessions. Huggins closed-capture abundance estimation models (Huggins 1989; Huggins 1991) were used for analysis of secondary sampling data, because they permit inclusion of individual covariates, such as fish length (Bestgen et al. 2010a). The effect of length on capture probability (and other parameters) is generally an important feature of capture-recapture studies of fishes (Peterson et al. 2004; Dauwalter and Fisher 2007; Korman et al. 2009). For records lacking length information (approximately 0.3%), we substituted mean length of northern pike from the same sample.

Parameters of interest in the primary ("open population") sampling sessions include: *S*, the probability of survival from the start of one sampling session (year) to the start of the next (therefore, 1 – *S* = mortality, which in this study includes removal and other mortality causes); γ'' ("gamma-double-prime"), the probability of being absent from the study area and unavailable for capture given that the animal <u>was</u> present during the previous sampling session; and γ' ("gamma-prime"), the probability of being absent from the study area and unavailable for capture given that the animal <u>was not</u> present on the study area during the previous sampling session. For secondary ("closed population") sampling occasions (passes), *p* is the probability of initial capture and *c* is the probability of recapture. In order to include individual covariates, population abundance estimates in the study area (*N*) are conditioned out of the likelihood in Huggins closed capture models and, instead, are derived parameters.

Assumptions under the closed robust design include: there are no additions or deletions of animals across secondary sampling occasions; survival probability is the same for all individuals in the population, regardless of availability for capture; and temporary emigration is either completely random, Markovian, or based on a temporary response to first capture.

A priori model set

After preparing the final dataset for analysis, we used the previously identified reaches and covariates to build an a priori model set. Additional effects were modeled directly within MARK. Survival rate, *S*, model structures included the following effects:

constant – one survival rate estimate for all individuals and intervals across the study period;

reach – survival rate estimates vary by initial capture reach;

interval – each (annual) interval has a unique survival rate estimate; interval is defined as the start of one primary sampling session to the start of the next;

length – survival rates are (linearly on logit scale) related to total length (mm) of fish at first capture; a squared term ($length^2$ on logit scale) was added to model the more plausible quadratic relationship of survival changing with increasing length; we used length at first capture, rather than estimating fish length through time (e.g., Breton et al. 2013b), because most fish were relatively large and slower growing and recapture intervals were usually short. Mean initial capture length of any northern pike subsequently recaptured was 529 mm TL. From

2004–2009, 81% of first recaptures occurred within the same year as initial captures. Within-year growth of those fish with length information for both captures was 4 mm, on average. Temporary emigration probabilities, γ'' and γ', model structures included the following effects:

Constant Markovian – one γ'' estimate and one γ' estimate for all individuals and intervals across the entire study period;

random – $\gamma'' = \gamma'$;

no movement – $\gamma'' = \gamma' = 0$.

Initial capture and recapture probabilities, *p* and *c*, model structures included the following effects:

constant – one capture or recapture probability estimate for all individuals and occasions across the study period;

reach – capture or recapture probability estimates vary by initial capture reach;

pass – capture or recapture probability estimates vary by sampling occasion;

year – capture or recapture probabilities for each set of annual sampling passes differ from those for sets of passes in other years;

length, length^2 – capture or recapture probabilities are related to fish total length (mm) at first capture;

threshold – length above which capture or recapture probabilities plateau;

discharge (*Q*) – capture or recapture probabilities are related to mean May discharge of the Yampa River (USGS gauge 09251000); we investigated if *Q* could be used as a surrogate for the more complex time-varying model structures.

$c = p$ – recapture probability is equal to initial capture probability.

$c \neq p$ – recapture probability is not equal to initial capture probability.

Run procedure and model selection

For each parameter, effects were modeled individually, additively, and as interactions. We ran all models using the logit link to maintain a monotonic relationship with the continuous individual covariate, length. Model selection was conducted with Akaike's information criterion (AIC, Akaike 1973). Models with lower AIC values are considered more parsimonious and closer to the unknown "truth" that produced the data (Burnham and Anderson 2002). The AIC values reported by Program MARK are based on a modified version of the criterion, denoted AIC_c, which adjusts for small sample size bias (Sugiura 1978; Hurvich and Tsai 1989; Burnham and Anderson 2002) and converges to AIC when sample size is large.

Recruitment

Lack of balanced fish size-structure across reaches and time precluded age-specific northern pike abundance estimation and, thus, estimation of recruitment rates. Few age-0 fish, in particular, were captured due to sampling techniques better-suited to capture adult sizes (e.g., boat or raft electrofishing). Therefore, we used growth rate information to understand northern pike recruitment. For each study year, we calculated weekly length frequencies (in 10-mm-length increments) for northern pike from two study reaches with the most recapture data: HC and SLJ. Those fine-scale length frequencies generated through time allowed us to distinguish possible age-1 pike (the smallest fish captured in the first few weeks of sampling, typically in early spring) from likely age-0 pike (small individuals captured in the last few weeks of sampling, typically in late spring or early summer). We "grew" individuals from that first, approximate age-classification to the end of their current growing season using two methods. First, we calculated growth rates based on changes in length between recapture intervals for northern pike ≤ 300 mm TL in this dataset. Second, we used growth rates from a more complex equation including Growing Degree Day units (GDD) and latitude (Rypel 2012):

$$(1)\ \log(\text{growth rate} + 1,\ \text{mm}\cdot\text{GDD}^{-1}) = (\text{slope} * \text{latitude}) + \text{intercept}$$

where average latitude for the study area was 40.5° and average monthly GDD were obtained for Maybell, Colorado, 1958–2006, from the Western Regional Climate Center website (http://www.wrcc.dri.edu/). The study which generated the above relationship found no significant difference (ANCOVA, $p = 0.32$) between growth rates of northern pike from lentic and lotic environments in North America.

After computationally growing the individuals, we had more accurate minimum and maximum lengths for the two age groups. Finally, we could assign age-1 northern pike back to the year they were produced in order to characterize recruitment. This process also allowed us to detect absence of young northern pike from a reach in one year and later presence of those cohorts in order to identify possible immigration.

Movement, escapement, translocation

In addition to including temporary emigration parameters in our MARK analysis, we further described northern pike movement among study reaches. Capture events were not grouped by passes, as in the mark-recapture analysis. Instead, all encounters of each northern pike were included, regardless of time elapsed between captures. Distance traveled (river miles), direction traveled, time elapsed in days (d), reach changes, reservoir escapement, and recaptures after translocation were calculated for each recapture event. For entire northern pike capture histories, net distance traveled (difference between first and last capture locations, in river miles) and total distance traveled (sum of distances on all legs of capture history, in river miles) were calculated.

RESULTS

Parameter estimation data summary

We limited the dataset for parameter estimation to three reaches (upstream Hayden to Craig, middle South Beach-Little Yampa Canyon-Juniper, and downstream Maybell-Sunbeam, Figure 4) and seven years (2004–2010) that had comparable mark-recapture efforts, in order to achieve a balanced study design for analysis in Program MARK. The dataset contained 8,929 individual northern pike ranging in size from 59–1120 mm TL (mean: 465 mm TL). The smallest fish tagged and released was 137 mm, while the smallest fish tagged, released, and recaptured was 152 mm. Mean length was largest for northern pike from reach MS (519 mm TL), followed by reach HC (484 mm TL) and reach SLJ (411 mm TL). There was a downward trend in mean northern pike length through time for each reach (Figures 5, 6, and 7), but an increase in 2008 in all reaches. Proportions of larger northern pike (> 450 mm TL and > 600 mm TL) generally declined throughout the study period in all reaches (Figure 8). Northern pike in both size categories in SLJ and those > 600 mm TL in MS declined to less than half of 2004 levels by 2010. Northern pike were most abundant in capture samples in reach HC and in 2004 and 2005, in particular (Table 1). Number of northern pike captured declined in a downstream direction such that only 9.8% of all pike were from reach MS. Number of northern pike captured varied across years in reaches SLJ and MS, but was highest in 2004, the first year of relatively widespread removal sampling.

Boat, raft, and "block-and-shock" electrofishing accounted for 69% of sampling hours but contributed 98% of initial captures of individual northern pike in the parameter estimation dataset. Fyke netting made up 31% of sampling hours and contributed 2% of initial captures of individual northern pike in the dataset. Northern pike were captured from one to three times (maximum of two recaptures), for a total of 10,018 capture events of 8,929 individuals (Table 2). Only 1,052 northern pike were ever recaptured after initial tagging and release, and 81% of first recaptures of those fish occurred within the same year as initial captures. Of the 7,877 northern pike encountered only once, 13% were released alive on marking passes but never seen again; the remainder were translocated (78%), sacrificed for further study (3%), or died from other causes (6%).

Of the 8,929 individual northern pike included in the parameter estimation dataset, 7,098 were translocated (Table 2) to three sites within the Yampa River basin (Yampa State Park Headquarters pond, Yampa River State Wildlife Area ponds, and Loudy-Simpson ponds) and one site in the White River basin (Rio Blanco Lake). Of 6,147 northern pike translocated upon initial capture, 274 fish (4.5%) had incomplete or no tagging information.

Model selection

We included 43 models in the final analysis (Table 3), with the number of parameters ranging from 3 to 108. The model with the lowest AIC_c value carried 72% of AIC_c weight; the next two closest models were within 5 AIC_c points of the top-ranked model and together constituted another 25% of AIC_c weight (total AIC_c weight = 97%). The only difference between the top three models was the threshold value of fish length assigned to the capture probability structure. Therefore, the top-ranked model will be used for all further inference.

Capture probability

The top-ranked model produced 108 estimable parameters. Initial capture probability of northern pike was modeled with 98 parameters (Table 4). Structure for each of seven years contained an intercept, two reach parameters (HC and SLJ), three passes, reach and pass interactions, plus linear and quadratic effects of length with a threshold of 600 mm TL, which constrained p to remain constant for northern pike larger than that size. The intercept for each year represented initial capture probability for northern pike from the third reach (MS) during the fourth pass. Models where $c \neq p$ were inestimable, due to high levels of removal and low recaptures in some reaches and years. Since the top-ranked model defined $c = p$ (recapture probability = initial capture probability), estimates were identical and the two parameters will collectively be referred to as "capture probability" or "p" hereafter.

The model ultimately produced 84 northern pike capture probability estimates back-transformed from logit values: one length-dependent estimate for fish captured in every reach (n = 3) X year (n = 7) X pass (n = 4) combination. Of the 84 capture probabilities estimated for an average-length (465 mm TL) northern pike, 70% were less than 0.20. Average $\hat{p}$ across all reaches, passes, and years for that size fish was 0.17 (range: 0.03–0.51). Annual capture probability was highest in 2008 (0.22) and lowest in 2009 (0.13), averaging across reaches and passes (Table 5). Reach SLJ produced the highest average $\hat{p}$ (0.24), which was likely due to longer and more intensive sampling seasons there, which included late-season efforts that began in 2010 aimed at disruption of smallmouth bass spawning (Hawkins et al. 2010; Breton et al.

2014). Reaches HC and MS produced lower estimates (0.15 and 0.13, respectively), but there was considerable variation through time in all reaches (Table 6). When averaging across reaches and years, pass 2 produced the highest capture probability (0.23); however, the highest $\hat{p}$ was 0.51, obtained during pass 4 in 2010 from reach SLJ. Since actual sampling passes were combined to achieve a balanced dataset over all years and reaches, the $\hat{p}$'s through time represent only generalizations of temporal patterns.

The positive logit value for length combined with a negative value for length^2 resulted in capture probability rates that increased (and sometimes peaked, then decreased) to 600 mm TL (the threshold defined by the top-ranked model), then plateaued for larger northern pike. Curve shapes and northern pike lengths with maximum capture probabilities varied by reach, year, and pass (84 possible curves; see Figure 9 for examples).

Temporary emigration

In the 108-parameter top-ranked model, temporary emigration was modeled with the 2-parameter "no movement" structure ($\gamma'' = \gamma' = 0$), precluding estimation. In short, this means that observable northern pike remained observable, while the unobservable fish remained unobservable (no movement into or out of the study area as a whole). Gamma values were fixed to 0 and not included in total parameter count. See DISCUSSION for reasons this structure was included in the top-ranked model.

Survival and abundance

In the 108-parameter top-ranked model, survival of northern pike was modeled with 10 parameters in additive structure: an intercept, two reach parameters (HC and SLJ), five intervals (time period from the start of one annual sampling session to start of the next), and both linear and quadratic effects of length (Table 7). The intercept represented survival for northern pike in the third reach (MS) in the last time interval. Survival estimate calculations for the other reaches included addition of the negative logit value of the intercept to the negative logit value of each reach. Thus, the larger logit value for northern pike initially captured in downstream reach MS (intercept, −2.03) suggested higher survival than those from upstream reaches SLJ (−2.03 + −0.98 = -3.01) or HC (−2.03 + −1.38 = -3.41). The larger positive logit value for 2004–2005 suggested highest northern pike survival in that interval, while survival in the 2008–2009 interval was lowest.

The model ultimately produced 18 northern pike survival rate estimates back-transformed from logit values: six time-varying, length-dependent $\hat{S}$'s for fish captured in each of three reaches. Survival rate estimates for average-length northern pike (465 mm TL) initially captured in downstream reach MS averaged 0.54 (range: 0.36–0.71) across all intervals and were the highest in the study area (Figure 10). The survival rates in upstream HC averaged 0.25 (range: 0.12–0.38) and middle SLJ averaged 0.32 (range: 0.18–0.48). Survival rates were lowest in intervals 2005-2006 and 2008-2009, but higher in other years, in all reaches. The patterns of survival rates over years largely parallel each other in trend direction because the estimating model was additive, but vary in magnitude because of reach differences.

The positive logit value for length combined with a negative value for length^2 resulted in bell-shaped, length-dependent survival estimate curves for each reach (Figure 11). Survival rates increased up to 625 mm TL then decreased for larger northern pike. Due to the additive structure of the survival portion of the model, length at maximum survival was identical; however, curve magnitude varied by reach and interval.

Northern pike population abundance estimates, $\hat{N}$, were highest in the upstream reach HC (range: 1192–3951) and lowest in downstream reach MS (range: 233–645) and varied by year (Table 8, Figure 12). Years of highest abundance were 2004, 2005, and 2009 in reach HC; 2004 and 2009 in SLJ; and 2004, 2007, and 2009 in MS; abundance was relatively low in all reaches from 2006-2008. Confidence intervals were wide in 2004 for the SLJ estimate and in 2009 for both the HC and SLJ estimates.

Removal efforts

In order to more accurately describe the interaction of northern pike survival rates, abundance estimates, and removal effects within each reach, we calculated mean survival rates for the average-length pike captured each year for each reach. That resulted in mean survival rates of 0.25 (range: 0.13–0.41) for northern pike captured in HC, 0.30 (0.18–0.48) in SLJ, and 0.57 (0.40–0.75) in downstream MS (Table 9). Estimates differed slightly from those presented above, which were all calculated with the average-length northern pike for the entire dataset (465 mm TL) for comparison. Furthermore, we added to abundance estimates any northern pike captured and removed in sampling (for pike or other species) that occurred prior to annual marking passes (when multiple agencies tried to synchronize and maximize marking effort).

For each reach, we summarized abundance estimates, survival rate estimates, and numbers of northern pike removed through time, then calculated removal rates, mortality rates, and population increases (Tables 10, 11, and 12). For example, in reach HC (Table 10), the population abundance estimate for 2004 was 3,465 and 1,139 northern pike were removed from the reach that year, resulting in a removal rate of 33%. Average-size northern pike in that reach were estimated by our analysis to survive the 2004–2005 interval (start of sampling in 2004 to start of sampling in 2005) at a rate of 0.41 and, therefore, not survive (due to mortality and removal combined, 1 – *S*) at a rate of 0.59 (column "Mortality: total"). We were then able to separate mortality rates from removal rates: 59% of the population estimate died or was removed and we calculated that 33% had been removed, so 26% of the population estimate was subject to mortality (59% - 33%, column "Mortality: other"). Number of northern pike predicted by the 2004–2005 survival rate estimate to remain in the reach at the end of interval and to be sampled in 2005 was 1,421 (3,465 * 0.41). The difference between that value and the abundance estimate for 2005 was 2,551 (3,972 – 1,421, column "Recruitment & Immigration"), which was 180% of the predicted value (2,551/1,421, column "R & I/predicted"). Similar tables were constructed for each reach and results, converted to densities, are graphically displayed in Figures 13, 14, and 15.

The relative effects of northern pike removal compared to other mortality factors varied among reaches, with other factors being strongest/highest upstream and declining downstream. In most years, other mortality rates exceeded removal rates in reaches HC and SLJ (Tables 10 and 11); however, removal always exceeded other mortality in reach MS, a function of higher survival rates there (Table 12). Removal may be the only mechanism to reduce northern pike in reach MS, as other mortality factors only accounted for 12% of population reductions, on average. While removal rates varied widely in reaches HC and SLJ (11–49% and 14–52%, respectively; Tables 10 and 11), years with the smallest proportions of northern pike removed sometimes had largest estimates of pike predicted to remain at the end of the intervals, which demonstrated the need for continued removal in those reaches as well.

Abundance estimates in reaches HC and SLJ were higher than abundances predicted to remain at the end of the previous intervals for all years, except 2005 in reach SLJ (Tables 10 and

11). The increases were due to combined recruitment and immigration and were, on average, nearly 500% (range: -28–2075%) higher than predicted abundances in those reaches. In reach MS, where survival was highest, population increases due to combined recruitment and immigration were approximately 144% of predicted abundance, on average (range: -52–459%; Table 12).

The pattern of higher abundance than was predicted to remain by the previous interval's survival rate estimate was apparent in every year in HC (Figure 13), every interval except 2004-2005 in SLJ (Figure 14), but only in 3 of 6 intervals in MS (Figure 15). In reaches HC and SLJ, abundance declined after 2005 and 2004, respectively, and remained low until the 2008-2009 interval, when it increased substantially. Abundance estimates for 2009 were imprecise for both reaches, but even densities computed using the lowest estimates of the 2009 95% confidence intervals were seven to nine times higher than what was predicted to remain at the end of 2008–2009 intervals in each reach. In the lower density, downstream reach MS, predicted densities were closer to and sometimes even higher than subsequent abundance estimate densities (Figure 15).

Recruitment

Combined recruitment and immigration rates exceeded combined removal and mortality rates most years, but separate estimates of recruitment and immigration could not be obtained by our mark-recapture analysis due to sparseness of the data. To further investigate northern pike recruitment, we assigned young pike captured in reaches HC and SLJ to age classes and production years. Hydrologic conditions of those years were then used to characterize recruitment. Too few young northern pike were captured in reach MS to include it in these recruitment analyses.

For 37 pairs of northern pike within-year captures from our parameter estimation dataset (n = 8,929 individuals) where initial capture length was < 301 mm TL, average growth rate between captures was 0.56 mm/d. Average monthly Growing Degree Day units from May to September at Maybell, Colorado (1958–2006), ranged from 117 to 527 (Table 13). The resulting average growth rate between May and September calculated from Equation 1 (in METHODS) was 0.54 mm/d (range: 0.20–0.88 mm/d). Estimated age-1 northern pike lengths at the end of September each year calculated using both methods were within 1–3% of each other, with the exception of one 4% difference. We estimated age-0 northern pike in reach HC to range in length from 107–176 mm TL at the end of September for any given study year (2004–2010). September length estimates of age-1 northern pike in HC ranged from 193–340 mm TL. In reach SLJ, age-0 northern pike ranged from 95–253 mm TL and age-1 fish from 176–346 mm TL at the end of September. Age-1 northern pike were then assigned back to the years in which they were produced.

In reach HC, only seven age-0 northern pike were captured throughout the study period and captures of age-1 fish exceeded that of age-0 fish every year (Table 14). Thus, estimated age-0 northern pike captured in that reach were almost entirely made up of age-1 fish captured in subsequent years and assigned back to production years. In contrast, numbers of age-0 northern pike actually captured in reach SLJ exceeded numbers of subsequently captured age-1 pike for every pair of study years except 2007–2008, when only 5 young pike were captured.

Many young northern pike captured in reach HC were apparently produced in the relatively dry year 2004, followed by 2006, 2008, and 2009, in descending order, with the latter two years being relatively wet and with high peak flows (Table 14, Figure 16). Few northern pike were apparently produced in 2005 and 2007. It should be noted that very few age-0 northern pike were captured in reach HC in any year they were produced (7 total from 2004-2010). Of young northern pike captured in reach SLJ, most were produced in 2009 and 2004, with fewer produced in other years, particularly 2005 and 2007 (Table 14).

Movement, escapement, translocation

We employed a wider range of records than was used in the parameter estimation dataset to describe northern pike movement: 10 reaches were included in the Yampa and Green rivers (Figure 4), in the period 2000–2012. We included recapture events outside the scope of this study when available; however, data compilation from those years was not complete and our use was opportunistic.

The resulting dataset consisted of 1,911 individual northern pike captured from two (n = 1,538) to ten (n = 1) times. Time elapsed between first and last captures ranged from 1 d to over 8 years. Total distance traveled ranged from 0 to 241.4 river miles (mean: 12.0). Of the 1,911 individuals with multiple captures, the movements of 394 (21%) resulted in a reach change, while those of 1,396 (73%) resulted in no reach change. The remaining 121 individuals (6%) were translocated, escaped, and then were recaptured. We describe those fish separately, below.

Of the 1,911 individual northern pike with multiple captures, > 70% originated in reaches HC and SLJ. This was expected, given that sampling was more frequent there than in upstream reaches and abundances were higher than in downstream reaches. Of the 394 northern pike making reach changes during their capture histories, most (36%) originated in HC. However, the reach with the largest portion of its northern pike leaving was AH (34%), followed by HC (19%; Table 15).

Northern pike reach changes were predominantly in a downstream direction: 90% moved to a downstream reach, either within the Yampa River or to the Green River. Approximately 9% made upstream reach changes, while the remaining 1% moved upstream, then back to their original reaches. Downstream movements covered from one (83%) to eight reaches. Upstream and "up, then back" movements only ever covered one or two reaches (Table 16). Proportions of movements in a downstream direction were highest for northern pike originating in upstream reaches CAT and AH (100% each; downstream was the only available direction from these reaches), followed by HC (94%), MS (93%), LP (83%), and SLJ (74%).

Of northern pike making reach changes in any direction, those initially captured in downstream reach LP made the largest total movements (all legs of movement history combined): 52.1 river miles, on average (Table 17). Although there were only six fish originating from reach LP that made reach changes, they traveled long distances both upstream and downstream. Maximum distance traveled by northern pike from LP was 70.9 river miles upstream to reach SLJ, the longest upstream distance traveled by any fish making a reach change. Northern pike that were initially captured in CAT and then changed reaches (n = 18) traveled the next longest distances: 49.4 river miles on average (maximum: 241.4 river miles downstream to the middle Green River, GRa). Northern pike initially captured in MS traveled an average of 47.9 river miles (maximum: 120.4 river miles downstream to GRa). Northern pike originating in AH, HC, and SLJ traveled similar distances (28.0, 26.8, and 33.8 river miles on average, respectively). Maximum distances traveled were 229.4, 174.1, and 150.3 river miles, respectively, all downstream to reach GRa.

For the 1,396 northern pike remaining in initial study reaches throughout their capture histories, net movements of 57% were in a downstream direction, 23% resulted in no change, and 19% were in an upstream direction. Net distance traveled (difference between river miles of first and last captures) was low, on average: 2.7 river miles downstream (range: 29.3 river miles upstream to 35.8 river miles downstream, both by pike within reach SLJ; Table 18). Maximum total distance traveled within a reach, regardless of direction, was 50.9 river miles, by a northern pike captured three times in reach SLJ in less than one year.

Of the 394 northern pike making reach changes, 18 originated in Lake Catamount. Of those 18, nine were last captured in reach AH, five in HC, and one each in SLJ, MS, YC, and GRa. Nearly all (n = 17) were initially tagged in CAT on 18 April 2003, then subsequently captured in the Yampa River or Green River from 2004 to 2011 (Table 19). The remaining northern pike was initially tagged in CAT in 2006 and recaptured in the Yampa River in 2007. Notably, none of the 864 northern pike tagged in Stagecoach Reservoir in 2003 (Orabutt 2006) was ever recaptured, except one fish whose provenance was doubtful given its growth rate between captures (K. Rogers, CDPW, pers. comm. *in* Fitzpatrick 2008). Approximately 2,200 northern pike had been tagged in Lake Catamount from 2003 to 2007. Northern pike had not been tagged in Elkhead Reservoir prior to this study, so escapement could not be described.

We detected 24 northern pike that moved downstream from the Yampa River basin into the Green River: nine into upstream Lodore Canyon (GRc), five into Echo-Split reach (GRb), and ten into middle Green (GRa). Initial capture reaches ranged from CAT down to LP (Table 20).

In the dataset used for movement description, we counted 10,276 northern pike translocated out of Yampa River reaches to one site in the White River basin (Rio Blanco Lake) and to three sites within the Yampa River basin and adjacent to reach HC, in particular (Yampa State Park Headquarters pond, near Yampa River RM 158.0; Yampa River State Wildlife Area ponds, near Yampa River RM 154.0; and Loudy-Simpson ponds, near Craig, Colorado, and Yampa River RM 139.0). Approximately 5% (n = 465) of translocated northern pike were not tagged. Of fish translocated to any of the three Yampa River basin sites, 121 were subsequently captured in one of the Yampa River or Green River study reaches (Table 21). Translocation sites were adjacent to reach HC and a large portion of recaptures of translocated northern pike occurred in that reach (80%). Only 3% of recaptures were from the next upstream reach AH and 11% came from the next downstream reach SLJ.

The length–frequency histograms we constructed for investigations into northern pike recruitment, where computationally "grown" young pike were assigned back to the years they were produced, proved useful in identifying immigration into reaches. Specifically, they revealed appearance of older cohorts of fish in reaches where younger age-classes were not captured in previous years. For example, in reach HC for year 2006, very few age-0 (produced in 2006) and low numbers of age-1 (produced in 2005) northern pike were captured in sampling that continued through late June (Figure 17). In 2007, those 2006 and 2005 cohorts were well-represented in the sample. No age-0 (2007) fish were captured that year, as sampling ceased in late May during that low flow year. In higher flow year 2008, sampling extended through early July, so we would expect to see age-0 fish, if present, and certainly the 2007 cohort as age-1 fish. Few, if any, were captured, but both cohorts were captured in 2009. Hence, the young northern pike captured in 2009 in reach HC may not have been produced there in 2007 and 2008. It is possible they immigrated from downstream reach SLJ, but we found a similar scenario there to that described for HC: few 2007 or 2008 northern pike were captured in those years (despite sampling into July), but the 2007 cohort was well-represented as age-2 fish in 2009 (Figure 18).

DISCUSSION

Our analysis of northern pike mark-recapture records from the Yampa River, 2004–2010, showed highest pike abundance upstream and highest survival downstream. Population increases due to combined recruitment and immigration outweighed population reductions through combined removal and mortality for most years in upstream reaches. Mortality rates exceeded removal rates in upstream reaches for most years; however, years with lowest rates of removal often corresponded to highest predicted abundance at the end of those intervals. Downstream, removal was the primary mechanism of northern pike population reductions.

Based on our analysis of growth rates and length–frequency histograms, reproductive success by northern pike was not necessarily linked to a particular flow pattern or magnitude. Most young northern pike captured in upstream reaches were produced in 2004, the year with lowest peak discharge of the study period, and 2009, a year with high peak flows and protracted runoff. That analysis also revealed that young northern pike may not have been produced in the study reaches in which they were captured. Age-0 and age-1 cohorts were missing from 2007 and 2008 samples in two reaches, but both cohorts were more abundant in 2009, suggesting immigration.

Northern pike movements were primarily downstream within and among Yampa River study reaches. Recaptures were also detected in the Green River, both upstream and downstream of the Yampa River confluence. We documented northern pike escapement from Lake Catamount and from three translocation sites.

Tag loss

Tag loss in mark-recapture studies can lead to biased estimates of survival and abundance (Seber and Felton 1981). It causes survival rate to be estimated too low, because a tagged fish that loses its tag but is still alive is an apparent mortality in the analysis. Tag loss also causes abundance to be estimated too high, because fewer tags are available for recapture even though the tagged fish is still in the population which reduces the estimated probability of capture. We investigated tag loss among all northern pike records obtained for this study. We found 232 records of northern pike containing multiple tags recorded upon a single capture event. The multiple tags included either two Floy® tags or a Passive Integrated Transponder plus a Floy® tag. Loss (or no subsequent recording) of one Floy® tag was found in the histories of 32 individuals (12.2%). Total time at large before detection of tag loss ranged from 1d to 4 years (average: 408 d). Average time elapsed from last capture with both tags to next capture with tag loss was 396 d.

Very little information on Floy® tag loss from riverine esocids was available in the literature for comparison. Annual Floy® tag loss for northern pike from Minnesota lakes was estimated to be < 2% (Pierce and Tomcko 1993), resulting in a 4% adjustment to abundance estimates. That same study noted 7.7% short-tem (March to April) Floy® tag loss from dorsally-tagged northern pike in the Mississippi River (Pierce and Tomcko 1993).

While the tag loss rate calculated for Yampa River northern pike was higher than in the Mississippi River, it may be an overestimate. There were few within-sampling-season captures of northern pike with multiple tags ($n = 9$), so comparable, finer-scale calculations of tag retention were not possible. Also, as many as five different groups of biologists have conducted work in the same Yampa River reaches through time. While that work contributed to the double-tagged fish we used in this estimate, it also resulted in confused protocols in early years; older, worn tags may have been pulled out, not reported, and replaced with new tags, or one of two tags may have simply not been reported. Most importantly, we suspect that variation in tags and/or techniques among years may be largely responsible for the loss rate we estimated. For example, northern pike initially double-tagged in 2003 comprised 56% of fish analyzed for tag loss, but none actually lost their tags upon recapture. Northern pike initially double-tagged in 2004, however, made up only 34% of the multiple-tag data but 88% of individuals with lost tags. For those reasons and in the absence of a controlled study, we deem 12.2% tag loss to be an overestimate and did not adjust survival or abundance estimates accordingly.

Abundance estimates

Northern pike population abundance in all reaches was relatively low from 2006-2008, then increased in 2009. Abundance estimates for 2009 were imprecise for reaches HC and SLJ, but densities computed using the lower limits of the confidence intervals were still seven to nine times higher than what was predicted to remain at the end of 2008–2009 intervals in each reach. We investigated explanations for the high 2009 abundance estimates, including the possibility of an influx of young fish after the high discharge year of 2008. However, we were unable to demonstrate that high discharge years were correlated with increased northern pike reproductive success, and while numbers of small fish captured in reach SLJ increased in 2009 (Figure 6), similar increases were not observed in other reaches (Figures 5 and 7). High discharge may contribute to northern pike population increases in other ways, such as redistribution of fish throughout the river or escapement of multiple age-classes through reservoir spills.

For the most part, northern pike abundance estimates in this study followed a similar pattern to those estimated for reach HC in Recovery Program Project 98b and for reaches SLJ, MS, and LP in Project 98a, 2004–2010, but estimates of abundance by year tended to be greater in the present study (Figure 19, http://www.coloradoriverrecovery.org/documents-publications/work-plan-documents/project-annual-reports.html#III.). Our estimates were up to four times higher in 2009 and two to three times higher in some other years, despite the fact that Project 98a sampling included reach LP and this study did not. A factor contributing to consistently higher abundance estimates in this study was incorporation of fish lengths and individual capture probabilities. Projects 98a and 98b generated mark-recapture abundance estimates only for northern pike > 300 mm TL using the Petersen estimator, which employs a single capture probability for all individuals. In this study, fish < 300 mm TL made up 17% of the dataset and the top-ranked model structure allowed capture probability to vary by fish length. Because capture probabilities were lowest for smaller northern pike in this study (see Figure 9 for examples), actual captures of those sizes represented more fish in the population than captures of larger fish. Thus, inclusion of all northern pike lengths and length-dependent capture probabilities both contributed to higher abundance estimates than in previous analyses that did not incorporate those factors.

Lengths of individual northern pike notwithstanding, capture probabilities among years in Project 98a (reaches SLJ, MS, and LP) were similar from 2004 through 2007 at 0.22–0.23, highest in 2008 at 0.28, and lowest in 2009 at 0.15; capture probability estimates were not available for Project 98b, reach HC. In this study, annual capture probability was also highest in

2008 (0.22) and lowest in 2009 (0.13), averaging across reaches, passes, and northern pike lengths (Table 5).

Removal efforts

Removal levels varied widely across years, particularly in reaches HC and SLJ and were highest in 2010 for both reaches. Accordingly, “other” mortality (death and emigration) varied widely but accounted for more than half of northern pike population reductions there in most years. Our movement description revealed that nearly 20% of northern pike with multiple captures emigrated out of reaches HC and SLJ (Table 15); thus, the remainder of “other” mortality was actual death of pike. While the benefit of removal may be questioned in light of those results, removal of northern pike early in the year reduces predation on and competition with native species throughout the summer, before mortality occurs. Furthermore, years with lowest rates of removal (e.g., 2009 in HC, 2004 and 2009 in SLJ) often corresponded to highest predicted abundance at the end of those intervals (Tables 10 and 11), so removal remains an important population control tool in those reaches.

Rates of northern pike mortality in the Yampa River basin were comparable with those observed for harvested northern pike populations elsewhere. For example, in seven Minnesota lakes (Pierce and Tomcko 2003), annual mortality rates of pike ranged from 36–63% and were not related to density or production. Those rates were similar to total (removal + death + emigration) mortality rates of 43-75% for northern pike in the three reaches of the Yampa River. The seven Minnesota populations exhibited wide ranges in productivity and other variables, but were all were considered sustainable recreational fisheries at those exploitation rates. Pierce and Tomcko (2003) concluded that northern pike production and populations were resilient when recruitment was not limited by availability of habitat for reproduction. Although total mortality (removal plus other) rates in the Yampa River basin were often higher than in those Minnesota lakes, escapement of adult fish from reservoirs and abundant reproductive habitat within- and off-channel provide virtually unlimited sources of annual pike production to sustain the population. Thus, even higher mortality rates from removal and other causes, in combination with reduced recruitment and immigration, may be needed to reduce Yampa River northern pike populations from sustainable to a less viable state.

In lower-density reaches with less recruitment and immigration pressure, such as downstream MS, increased removal efforts could push northern pike densities down to target levels of 3 pike/mile (Valdez et al. 2008) or current Colorado pikeminnow density, whichever is lower. However, in higher-density reaches upstream, the level of removal required to surpass population increases is unlikely to be achieved without additional control measures. Furthermore, the UCRB Nonnative and Invasive Aquatic Species Prevention and Control Strategy (Martinez et al. 2014) posits that current density targets are likely too high in the face of residual, main channel propagules and propagule pressure outside critical habitat (i.e., in upstream reaches and off-channel sources).

Contributing to those propagules are northern pike that escape from reservoirs and former translocation sites. Some of the escapement we summarized had been previously documented for discrete river reaches by Finney and Haines (2008), by Martin et al. (2010), and in numerous annual project reports to the UCRB Recovery Program since then. This synthesis added several records to that documentation. Translocation of northern pike to some sites (Loudy Simpson ponds and Yampa River SWA ponds) ceased in 2011 and pike removal efforts in Lake Catamount began in 2007. However, continued presence of northern pike in and escapement from reservoirs and other sources remain threats to native fish recovery (Johnson et al. 2014; Martinez et al. 2014).

Recruitment

Based on our analysis of growth rates and length–frequency histograms, reproductive success by northern pike was not necessarily linked to a particular flow pattern or magnitude. Successful northern pike spawning and rearing require rising water temperatures; inundated vegetation associated with pools, gradually sloping banks, flooded meadows, marshy areas connected to rivers, and backwaters; and stable water levels (Carbine 1941; Franklin and Smith 1963; Bry 1996; Hill 2004). In the Yampa River, availability of inundated vegetation in lentic habitats is limited in some reaches and controlled by spring discharge levels (i.e., higher spring snowmelt runoff results in more inundated vegetation along shorelines, in backwaters, and in connected off-channel ponds; Nesler 1995). Given the proclivity for northern pike to spawn in flooded vegetation and floodplain habitat, greater reproductive success may have been expected in 2008 and 2009 due to the higher-than-average peak flows and protracted high flows, respectively (Figure 16). However, many young northern pike captured in reach HC were apparently produced in the relatively dry year 2004, followed by 2006, 2008, and 2009, in descending order (Table 14). Few northern pike were apparently produced in 2005 and 2007. Of young northern pike captured in reach SLJ, most were produced in 2009 and 2004, with fewer produced in other years, particularly 2005 and 2007 (Table 14). The hydrograph of 2004 (a year in which many of the young northern pike captured in 2004 and 2005 were produced) did not resemble that of 2008 or 2009. Peak flows were the lowest of the study period in 2004: < 6000 cfs. Runoff did begin slightly earlier than in some other years, providing the necessary spawning habitat sooner. However, that early inundation also occurred in 2007 – the year in which the lowest number of young northern pike subsequently captured was produced. Conversely, in 2005, runoff began similarly to other years and peak streamflow was higher than that of 2009; but that year resulted in the second lowest number of young northern pike subsequently captured. Such variation in discharge and northern pike production among years conflicts with the conventional wisdom that higher flows result in higher pike productivity in the Yampa River. Nesler (1995) also found no relationship between northern pike abundance and discharge magnitude from 1987–1991, a period of mostly low flows.

One possible explanation for the numbers of northern pike apparently produced in the low-peak-flow year 2004 and subsequently captured as age-0 or age-1 fish in reaches HC and SLJ is successful reproduction and escapement from upstream reservoirs, such as Lake Catamount. The dam at that reservoir spilled every year from 1999 to 2010, with mean spill duration of 196 d (Johnson et al. 2014). Spills in 2004 and 2005 each totaled approximately 200 d and certainly could have contributed to the numbers of age-0 and age-1 fish (as well as other age-classes) captured in those years. However, spill duration in 2007 was one of the longest in the dataset: approximately 220 d (Johnson et al. 2014), but sampling that year and in 2008 resulted in the lowest numbers of young northern pike captured in reaches HC and SLJ. Thus, no relationship between reservoir spill duration and young northern pike captures could be established.

Ultimately, capture of young northern pike during this study was incidental, given that timing of sampling varied annually and boat electrofishing suited to capture of large-bodied fish was the dominant sampling technique. Indeed, in reach HC only 7 age-0 northern pike were captured throughout the study period. Well-timed, targeted sampling of age-0 and age-1 northern pike under a variety of environmental conditions would be necessary to identify sources, estimate recruitment rates, and better understand the factors that advantage (and disadvantage) pike reproduction in this system. Resulting data may reveal relationships among spawning, discharge, and temperature, similar to those generated for smallmouth bass in the Yampa River basin and northern pike in Browns Park of the Green River (Appendix A), that could be used to disadvantage northern pike reproduction and recruitment and aid endangered species recovery (Bestgen et al. 2007; Hill and Bestgen 2014; Bestgen and Hill *draft report*).

Movement and immigration

Directly estimating northern pike immigration rates within our MARK analysis was not possible with available data. Only 394 of more than 10,000 northern pike from all 10 Yampa River reaches made reach changes throughout their capture histories. That already low number dropped considerably when reaches were limited to three, captures were allocated to passes, and multiple within-pass contacts were considered one capture for parameter estimation. Furthermore, “within-year” reach changes do not contribute to transition rates, which are calculated between primary (annual) sampling sessions only. Therefore, too few reach-to-reach movements among years remained to adequately estimate transition rates. Still, we proceeded with the robust design for our analysis, which included temporary emigration parameters to estimate movement rates of northern pike to/from the three central study reaches, collectively. However, models with any structure other than $\gamma'' = \gamma' = 0$ (no movement) produced inestimable parameters or implausible estimates with exceptionally wide confidence intervals. There were simply too few northern pike emigrations off of and onto the study area to estimate γ'' and γ'. While information from those parameters would have been useful, it would not have revealed origins or destinations of those fish. Thus, our recruitment investigation and movement description provided accounts of northern pike dispersal throughout the basin.

Most northern pike movements were downstream, whether by changing reaches or moving within the same reach, and some were long distances. For example, northern pike escaped Lake Catamount and traveled downstream 241.1 river miles (maximum distance in this study) to the middle Green River before capture and removal. Similarly, northern pike from the Yampa River moved downstream into the Green River and then upstream, and were the likely source for a reproducing population upstream of Lodore Canyon in Browns Park National Wildlife Refuge (Bestgen et al. 2006b). Little information on northern pike movements within lotic systems is available in the literature. In a Belgian river, six northern pike radio-tagged for just over a year made some degree of upstream spawning movement followed by a downstream movement, but only three proceeded further downstream than their initial winter tagging locations (Ovidio and Philippart 2005). However, those northern pike only occupied up to 25 km (15.5 miles) of river, including spawning migrations. Northern pike changing reaches in this study traveled twice that far, on average, throughout their capture histories (Table 17), and those movement rates may be conservative due to effects of removal. That is, 10,276 northern pike from the movement analysis dataset were translocated out of the Yampa River, which interrupted capture histories and reduced movement rates within and among reaches. Regardless of movement distances and rates, propensity for downstream movement increased the risk of northern pike establishment in other portions of the UCRB.

Movement among Yampa River reaches may not be restricted to adult northern pike. Our recruitment investigations revealed that young northern pike captured in reaches HC and SLJ likely were not produced there. Very few age-0 northern pike were captured in reach HC in any year, but age-1 fish were more abundant in all subsequent years. It is possible that young northern pike in reach HC immigrated upstream from reach SLJ, given that many more age-0 northern pike were captured there each year. In Yampa River surveys from 1987–1991, Nesler (1995) found no young-of-year or juvenile northern pike in reaches downstream of Craig, Colorado, and found little difference between upstream and downstream movement rates. Our movement description, however, found that 90% of northern pike reach changes were in a downstream direction, making colonization of HC by age-0 pike from SLJ less likely.

Young northern pike could feasibly have immigrated into HC and SLJ from upstream reach AH, a stretch with known pike spawning habitat, as well as from off-channel ponds and reservoirs (Hill 2004; Fitzpatrick and Winkelman 2009; Martinez et al. 2014). Unfortunately, little sampling was conducted in AH during the time frame of this study following the main stem surveys in 2004 and 2005. Sampling ceased in late April and early May of those years, so young northern pike were not detected and no inferences can be made. We did investigate data collected in 2009 from the confluence of the Yampa River with Walton Creek, an area known to produce many northern pike (B. Atkinson, CPW, pers. comm.). In one day of October sampling, a preponderance of age-0 northern pike was captured – many times the numbers captured over weeks of sampling downstream (Figure 20). We note that gear targeting smaller fish was used (electric seine) and 2009 numbers do not explain the appearance of 2007 and 2008 fish downstream. However, the limited sampling in Walton Creek illustrates the level of productivity present upstream of the buffer zone. Mark-recapture sampling was conducted in upper AH after this study. During 2012, 36% of northern pike captured were age-0 or age-1 (H. Crockett, CPW, pers. comm.), further demonstrating that upstream reaches of the Yampa River are relatively important sources of pike production.

We evaluated above the possibility that reservoir spills and escapement of young northern pike from Lake Catamount may have obscured any relationship between discharge and pike reproduction, but did not find consistent support for it. Similarly, escapement of young age-classes from reservoirs may explain the appearance of cohorts previously absent in sampling of reaches HC and SLJ. Spill durations in 2009 were > 200 d at Lake Catamount and approximately 40 d at Elkhead Reservoir (Johnson et al. 2014), and could have resulted in escapement of 2007 and 2008 northern pike cohorts, which were not captured in river samples those years. In the absence of similarly-timed sampling from year to year, however, it is unknown when and where the "missing" cohorts first appeared in the river.

Targeted sampling of young northern pike through space and time is necessary to better understand the species' recruitment and immigration patterns in the Yampa River. Even without specific estimates of those processes, however, we demonstrated through movement, survival rate, and abundance estimate data that current removal efforts in the buffer zone and critical habitat are by themselves inadequate to reduce northern pike abundance; future control efforts also need to reduce recruitment and immigration. In addition to increased removal efforts, other northern pike control actions may include: identification of spawning locations; prevention of access to spawning locations; spawning disruption; and control of off-channel sources. Continued widespread distribution and abundance of northern pike in the Yampa River and elsewhere will limit efforts to restore or enhance populations of native and endangered fishes.

CONCLUSIONS

- Northern pike abundance was highest in upstream reach Hayden-to-Craig (HC), followed by middle reach South Beach-Little Yampa Canyon-Juniper (SLJ), then downstream reach Maybell-Sunbeam (MS).
- Northern pike survival was highest in downstream reach MS, followed by middle reach SLJ, then upstream reach HC.
- In upstream, higher-density reaches HC and SLJ, northern pike abundance estimates in spring were nearly always higher than abundances predicted by survival rate estimates to remain after the previous period; the differences were attributed to combined effects of recruitment and immigration.
- In downstream, lower-density reach MS, combined recruitment and immigration of northern pike was lower than in upstream reaches, likely a result of upstream removal efforts; those efforts also reduce immigration into reaches further downstream.
- Northern pike removal rates varied widely among years for all reaches and likely are not sufficient to reach removal targets with continued immigration and recruitment from resident and upstream propagules.
- Northern pike recruitment and immigration rates could not be directly estimated with available data.
- There was no clear relationship between discharge and northern pike recruitment: 2004, 2006, 2008, and 2009 had variable flow peaks and durations, but most young pike later captured were produced in those low and high flow years.

- Young northern pike may immigrate into endangered fish critical habitat, likely from upstream.
- Most northern pike movement among reaches was in a downstream direction.
- Northern pike escaped from Lake Catamount and three translocation sites.

RECOMMENDATIONS

- Conduct targeted sampling for young-of-year northern pike through space and time to identify primary sources of pike production and understand factors that affect it; such information can then be used to disadvantage future pike spawning and recruitment.
- Prevent or disrupt northern pike spawning and/or recruitment.
- Continue or increase northern pike removal in critical habitat and upstream to reduce downstream movement in the Yampa and Green rivers.
- Prevent or reduce escapement of (or eliminate) northern pike from off-channel sources and reservoirs.
- Tag northern pike, including upstream of critical habitat, if evaluation of control efforts is warranted.
- Construct sampling design for any future northern pike mark-recapture study.

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Table 1. Initial captures of northern pike by reach and year from the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

Reach	Year							
	2004	2005	2006	2007	2008	2009	2010	total
HC	1221	1282	489	630	449	427	768	5266
SLJ	517	355	335	619	291	291	375	2783
MS	164	85	127	202	122	101	79	880
total	1902	1722	951	1451	862	819	1222	8929

Table 2. Capture frequency and final disposition of northern pike captured in three reaches of the Yampa River, Colorado (Hayden to Craig, river mile [RM] 171.0–134.2; South Beach-Little Yampa Canyon-Juniper, RM 134.2–91.0; Maybell-Sunbeam, RM 88.7–58.5), 2004–2010.

Disposition	Capture frequency			
	1	2	3	total
Released alive	998	25	1	1024
Translocated	6147	917	34	7098
Dead	518	72	2	592
Preserved	214	1		215
total	7877	1015	37	8929

Table 3. Closed robust design models and model selection criteria to estimate survival ($\hat{S}$), temporary emigration (ɣ'' and ɣ') and capture probability ($\hat{p}$, $\hat{c}$) for northern pike from three reaches of the Yampa River, Colorado (Hayden to Craig, river mile [RM] 171.0–134.2; South Beach-Little Yampa Canyon-Juniper, RM 134.2–91.0; Maybell-Sunbeam, RM 88.7–58.5), 2004–2010. AIC_c = Akaike's Information Criterion, adjusted for small sample size bias; Delta AIC_c = AIC_c – minimum AIC_c; AIC_c Weight = ratio of delta AIC_c relative to entire set of candidate models; Model Likelihood = ratio of AIC_c weight relative to AIC_c weight of best model; K = number of parameters; Deviance = log-likelihood of the model – log-likelihood of the saturated model. Effects included: no variation (.); initial capture reach (reach); interval, year, or pass (time); Q (discharge); and fish total length at capture (length and length^2).

Model	Delta AIC_c	AIC_c Weights	Model Likelihood	K	Deviance
{S(reach+time+length2) γ'',γ'(no mvmnt) p(reach*yr*pass+length2)threshold600 c(=p)}	0	0.716	1.00	108	26182.12
{S(reach+time+length2) γ'',γ'(no mvmnt) p(reach*yr*pass+length2)threshold700 c(=p)}	2.93	0.165	0.23	108	26185.05
{S(reach+time+length2) γ'',γ'(no mvmnt) p(reach*yr*pass+length2)threshold800 c(=p)}	4.42	0.078	0.11	108	26186.54
{S(reach+time+length2) γ'',γ'(no mvmnt) p(reach*yr*pass+length2) c(=p)}	6.91	0.023	0.03	108	26189.03
{S(reach+time+length) γ'',γ'(no mvmnt) p(reach*yr*pass+length2) c(=p)}	8.48	0.010	0.01	107	26192.82
{S(reach+time) γ'',γ'(no mvmnt) p(reach*yr*pass+length2) c(=p)}	9.25	0.007	0.01	106	26195.81
{S(reach+time+length2) γ'',γ'(no mvmnt) p(reach*yr*pass+length2)threshold500 c(=p)}	22.04	0.000	0	108	26204.16
{S(reach+time+length2) γ'',γ'(no mvmnt) p(reach*yr*pass+length) c(=p)}	78.25	0	0	101	26275.87
{S(reach+time+length) γ'',γ'(no mvmnt) p(reach*yr*pass+length) c(=p)}	89.02	0	0	100	26288.84
{S(reach+time) γ'',γ'(no mvmnt) p(reach*yr*pass+length) c(=p)}	89.22	0	0	99	26291.25
{S(reach*time) γ'',γ'(no mvmnt) p(reach*yr*pass+length) c(=p)}	97.87	0	0	109	26277.77
{S(reach+time) γ''(0) γ'(1)no mvmnt p(reach*time) c(=p)}	364.646	0	0	92	26582.04
{S(reach*time) γ''(reach) γ'(reach) p(reach*time) c(=p)}	372.155	0	0	101	26569.775
{S(reach*time) γ''='(rndm,reach*time) c(=p)}	372.156	0	0	101	26569.776
{S(reach*time) γ''='(rndm,reach*time,no constr) p(reach*time) c(=p)}	374.363	0	0	102	26569.775
{S(reach*time) γ''(0) γ'(1)no mvmnt p(reach*time) c(=p)}	374.363	0	0	102	26569.775
{S(reach*time) γ''(reach*time, no constr) γ'(reach*time) p(reach*time) c(=p)}	377.126	0	0	104	26568.115
{S(time) γ''(0) γ'(1)no mvmnt p(reach*time) c(=p)}	390.531	0	0	90	26612.296
{S(reach+time) γ''(0) γ'(1)no mvmnt p(reach+time) c(=p)}	1754.719	0	0	50	28062.111
{S(reach*time) γ''(reach) γ'(reach) p(yr*pass) c(=p)}	1902.957	0	0	46	28218.730
{S(reach*time) γ''(reach*time, no constr) γ'(reach*time) p(yr*pass) c(=p)}	1919.750	0	0	54	28218.729
{S(reach*time) γ''(reach*time, no constr) γ'(reach*time) p(reach*pass) c(=p)}	2046.095	0	0	32	28390.945

Continued.

Table 3. Continued.

Model	Delta AIC_c	AIC_c Weights	Model Likelihood	*K*	Deviance
{S(reach+time) γ''(0) γ'(1)no movmnt p(pass*Q+length) c(=p)}	2358.824	0	0	17	28734.397
{S(reach+time) γ''(0) γ'(1)no movmnt p(reach+pass+Q+length) c(=p)}	2401.574	0	0	16	28779.180
{S(reach+time) γ''(0) γ'(1)no movmnt p(pass+Q+length) c(=p)}	2416.816	0	0	14	28798.481
{S(reach+time) γ''(0) γ'(1)no movmnt p(pass*Q) c(=p)}	2581.260	0	0	16	28958.866
{S(reach+time) γ''(0) γ'(1)no mvmnt p(yr*length) c(yr*length)}	3670.207	0	0	36	30006.789
{S(reach+time+length,length^2) γ''(0) γ'(1)no mvmnt p(reach*yr) c(=p)}	3806.576	0	0	31	30153.488
{S(reach+time) γ''(0) γ'(1)no mvmnt p(yr*reach) c(=p)}	3832.002	0	0	29	30183.032
{S(reach+time) γ''(0) γ'(1)no movmnt p(Q+length,length^2) c(=p)}	3845.184	0	0	12	30230.901
{S(reach*t) γ''(reach*t, no constr) γ'(reach*t) p(yr*reach) c(=p)}	3848.731	0	0	44	30168.682
{S(reach+time) γ''(0) γ'(1)no movmnt p(reach+Q+length) c(=p)}	3882.668	0	0	13	30266.360
{S(reach+time) γ''(0) γ'(1)no movmnt p(reach+Q*length) c(=p)}	3884.557	0	0	14	30266.222
{S(reach+time) γ''(0) γ'(1)no movmnt p(Q*length) c(=p)}	3901.923	0	0	12	30287.640
{S(reach+time+length,length^2) γ''(0) γ'(1)no movmnt p(year-int) c(=p)}	4002.721	0	0	17	30378.294
{S(reach+time+length,length^2) γ''(0) γ'(1)no movmnt p(year-ident) c(=p)}	4002.721	0	0	17	30378.294
{S(reach+time+length,length^2) γ''(0) γ'(1)no mvmnt p(reach*Q) c(=p)}	4057.807	0	0	16	30435.413
{S(reach+time+length,length^2) γ''(0) γ'(1)no mvmnt p(reach) c(=p)}	4088.877	0	0	13	30472.569
{S(reach+time+length,length^2) γ''(0) γ'(1)no movmnt p(Q) c(=p)}	4107.305	0	0	12	30493.022
{S(reach+time+length,length^2) γ''(0) γ'(1)no movmnt p(.) c(=p)}	4115.097	0	0	11	30502.837
{S(reach+time+length,length^2) γ''(0) γ'(1)no movmnt p(.) c(.)}	4117.048	0	0	12	30502.765
{S(reach+time+length,length^2) γ''(0) γ'(1)no movmnt p(Q) c(.)}	4118.454	0	0	13	30502.146
{S(.) γ''(.) γ'(.) p(.) c(.) PIM}	4202.549	0	0	3	30606.403

Table 4. Parameter estimates, standard errors (SE), and upper and lower 95% confidence limits (CL) for the function of logit *p*, capture probability, of northern pike in three reaches of the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2); SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0); 2004–2010 = sampling years; length and length^2 = individual covariates. Each year's intercept represents capture probability for pike from reach MS (Maybell-Sunbeam, RM 88.7–58.5) during pass 4.

Parameter	Estimate	SE	95% CL	
2004 intercept	-9.10	1.713	-12.463	-5.746
2004 HC	-0.44	0.408	-1.237	0.361
2004 SLJ	2.54	0.425	1.707	3.373
2004 pass1	-0.09	0.273	-0.621	0.448
2004 pass2	0.91	0.234	0.453	1.369
2004 pass3	-0.57	0.308	-1.178	0.029
2004 HC*pass1	0.57	0.310	-0.042	1.173
2004 HC*pass2	0.80	0.268	0.279	1.330
2004 HC*pass3	2.25	0.334	1.593	2.904
2004 SLJ*pass1	-1.61	0.330	-2.256	-0.963
2004 SLJ*pass2	-1.65	0.282	-2.199	-1.095
2004 SLJ*pass3	-1.24	0.360	-1.947	-0.535
04length	0.02	0.007	0.006	0.034
04length^2	-0.000013	0.000007	-0.000028	0.000001
2005 intercept	-4.02	1.105	-6.184	-1.854
2005 HC	-14.56	84.774	-180.720	151.594
2005 SLJ	-0.70	0.401	-1.485	0.084
2005 pass1	-0.44	0.280	-0.990	0.108
2005 pass2	-2.07	0.439	-2.928	-1.207
2005 pass3	-0.39	0.278	-0.939	0.152
2005 HC*pass1	14.41	84.774	-151.751	180.561
2005 HC*pass2	17.57	84.774	-148.590	183.725
2005 HC*pass3	13.80	84.774	-152.352	179.961
2005 SLJ*pass1	1.34	0.344	0.666	2.016
2005 SLJ*pass2	3.06	0.482	2.112	4.001
2005 SLJ*pass3	1.28	0.344	0.601	1.951
05length	0.01	0.005	-0.004	0.016
05length^2	-0.000001	0.000006	-0.000012	0.000009
2006 intercept	-6.46	1.499	-9.400	-3.523
2006 HC	-0.01	0.374	-0.744	0.721
2006 SLJ	0.45	0.370	-0.277	1.172
2006 pass1	0.94	0.280	0.394	1.490
2006 pass2	0.32	0.298	-0.267	0.901
2006 pass3	0.31	0.305	-0.286	0.911
2006 HC*pass1	-1.40	0.320	-2.028	-0.773
2006 HC*pass2	0.28	0.325	-0.358	0.915
2006 HC*pass3	-0.98	0.347	-1.662	-0.302
2006 SLJ*pass1	-0.56	0.323	-1.197	0.068
2006 SLJ*pass2	-0.19	0.342	-0.863	0.476
2006 SLJ*pass3	-0.87	0.362	-1.584	-0.166
06 length	0.02	0.007	0.004	0.030
06length^2	-0.000015	0.000007	-0.000029	-0.000001

Continued.

Table 4. Continued.

Parameter	Estimate	SE	95% CL	
2007 intercept	-3.31	1.248	-5.755	-0.863
2007 HC	-0.29	0.410	-1.091	0.516
2007 SLJ	0.92	0.403	0.135	1.713
2007 pass1	-1.13	0.283	-1.690	-0.579
2007 pass2	0.17	0.211	-0.239	0.588
2007 pass3	0.31	0.201	-0.088	0.701
2007 HC*pass1	1.21	0.315	0.596	1.832
2007 HC*pass2	0.75	0.244	0.274	1.229
2007 HC*pass3	-0.25	0.245	-0.726	0.236
2007 SLJ*pass1	0.75	0.317	0.129	1.370
2007 SLJ*pass2	0.22	0.246	-0.264	0.700
2007 SLJ*pass3	-0.71	0.247	-1.194	-0.226
07length	0.00	0.006	-0.007	0.015
07length^2	-0.000003	0.000007	-0.000016	0.000010
2008 intercept	-8.71	1.844	-12.327	-5.098
2008 HC	0.84	0.433	-0.014	1.685
2008 SLJ	1.35	0.453	0.456	2.234
2008 pass1	0.93	0.342	0.259	1.600
2008 pass2	1.46	0.329	0.814	2.103
2008 pass3	0.39	0.375	-0.348	1.121
2008 HC*pass1	-1.98	0.379	-2.726	-1.241
2008 HC*pass2	-2.02	0.360	-2.728	-1.318
2008 HC*pass3	-0.66	0.398	-1.436	0.126
2008 SLJ*pass1	-1.30	0.408	-2.099	-0.500
2008 SLJ*pass2	-0.94	0.384	-1.696	-0.190
2008 SLJ*pass3	-0.84	0.437	-1.700	0.014
08length	0.03	0.008	0.010	0.041
08length^2	-0.000025	0.000008	-0.000042	-0.000009
2009 intercept	-9.12	2.032	-13.102	-5.136
2009 HC	0.05	0.508	-0.949	1.044
2009 SLJ	2.54	0.518	1.523	3.555
2009 pass1	0.31	0.324	-0.327	0.944
2009 pass2	0.79	0.302	0.194	1.377
2009 pass3	0.28	0.329	-0.369	0.921
2009 HC*pass1	-0.28	0.373	-1.008	0.453
2009 HC*pass2	0.51	0.339	-0.150	1.177
2009 HC*pass3	-0.15	0.376	-0.889	0.585
2009 SLJ*pass1	-1.75	0.372	-2.482	-1.025
2009 SLJ*pass2	-3.14	0.385	-3.891	-2.381
2009 SLJ*pass3	-1.64	0.373	-2.372	-0.908
09length	0.02	0.009	0.004	0.040
09length^2	-0.000018	0.000010	-0.000037	0.000002
2010 intercept	-5.31	0.951	-7.175	-3.446
2010 HC	-0.56	0.497	-1.529	0.418
2010 SLJ	2.29	0.526	1.263	3.326
2010 pass1	-0.17	0.344	-0.842	0.506
2010 pass2	0.34	0.314	-0.274	0.956
2010 pass3	-0.16	0.347	-0.840	0.522
2010 HC*pass1	1.29	0.403	0.498	2.078
2010 HC*pass2	2.43	0.369	1.702	3.149
2010 HC*pass3	1.07	0.411	0.265	1.876
2010 SLJ*pass1	-1.84	0.414	-2.648	-1.023
2010 SLJ*pass2	-0.96	0.360	-1.661	-0.251
2010 SLJ*pass3	-2.13	0.424	-2.957	-1.296
10length	0.01	0.004	0.002	0.018
10length^2	-0.000006	0.000005	-0.000016	0.000003

Table 5. Mean, minimum, and maximum capture probability estimates, $\hat{p}$, for average-length (465 mm total length) northern pike in the Yampa River, Colorado, 2004–2010. Estimates were averaged across all study reaches (Hayden to Craig, river mile [RM] 171.0–134.2; South Beach-Little Yampa Canyon-Juniper, RM 134.2–91.0; Maybell-Sunbeam, RM 88.7–58.5) and passes.

	all reaches, passes		
year	mean $\hat{p}$	min $\hat{p}$	max $\hat{p}$
2004	0.16	0.04	0.48
2005	0.15	0.03	0.35
2006	0.19	0.08	0.32
2007	0.15	0.04	0.32
2008	0.22	0.09	0.43
2009	0.13	0.06	0.45
2010	0.19	0.06	0.51
mean	0.17	0.03	0.51

Table 6. Capture probability estimates by reach, year, and pass for average-length (465 mm total length) northern pike from the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

Year	Pass				average
	1	2	3	4	
		HC			
2004	0.07	0.21	0.20	0.04	0.13
2005	0.10	0.35	0.06	*	0.17
2006	0.10	0.24	0.08	0.15	0.14
2007	0.09	0.20	0.09	0.09	0.12
2008	0.09	0.13	0.17	0.21	0.15
2009	0.07	0.20	0.07	0.06	0.10
2010	0.16	0.49	0.13	0.06	0.21
average	0.10	0.26	0.12	0.10	0.15
		SLJ			
2004	0.14	0.31	0.13	0.48	0.26
2005	0.20	0.22	0.20	0.09	0.18
2006	0.29	0.24	0.14	0.22	0.22
2007	0.18	0.32	0.18	0.24	0.23
2008	0.24	0.43	0.22	0.31	0.30
2009	0.16	0.07	0.17	0.45	0.22
2010	0.12	0.36	0.10	0.51	0.27
average	0.19	0.28	0.16	0.33	0.24
		MS			
2004	0.06	0.15	0.04	0.07	0.08
2005	0.12	0.03	0.12	0.17	0.11
2006	0.32	0.20	0.20	0.15	0.22
2007	0.04	0.13	0.15	0.11	0.11
2008	0.23	0.33	0.15	0.10	0.20
2009	0.08	0.12	0.08	0.06	0.09
2010	0.08	0.13	0.08	0.10	0.10
average	0.13	0.16	0.12	0.11	0.13

* There was no pass 4 in reach HC in 2005.

Table 7. Parameter estimates, standard errors (SE) and upper and lower 95% confidence limits (CL) for the function of logit *S*, survival rate, of northern pike captured in three reaches of the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2); SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0); 2004–2005, 2005–2006, and 2006–2007, 2007–2008, 2008–2009 = survival intervals; length and length^2 = individual covariates. The intercept represents survival of pike from reach MS (Maybell-Sunbeam, RM 88.7–58.5) through interval 2009–2010.

Parameter	Estimate	SE	95% CL	
intercept	-2.03	1.127	-4.241	0.175
HC	-1.38	0.274	-1.919	-0.845
SLJ	-0.98	0.273	-1.510	-0.441
2004–2005	0.42	0.375	-0.313	1.158
2005–2006	-1.02	0.370	-1.748	-0.299
2006–2007	-0.35	0.372	-1.078	0.381
2007–2008	0.23	0.392	-0.541	0.995
2008–2009	-1.05	0.464	-1.956	-0.137
length	0.01	0.004	0.001	0.016
length^2	-0.000007	0.000004	-0.000014	0.0000002

Table 8. Population abundance estimates ($\hat{N}$), standard errors (SE) and 95% confidence intervals (CI) for northern pike in three reaches of the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

	HC			SLJ			MS		
Year	$\hat{N}$	SE	95% CI	$\hat{N}$	SE	95% CI	$\hat{N}$	SE	95% CI
2004	3439	519	2632 – 4708	2444	1003	1255 – 5547	645	224	365 – 1312
2005	3951	523	3108 – 5187	843	107	675 – 1103	233	50	164 – 369
2006	1410	223	1066 – 1962	849	150	630 – 1237	257	37	204 – 353
2007	1825	229	1454 – 2364	1071	74	948 – 1243	594	136	406 – 962
2008	1192	176	920 – 1626	659	157	461 – 1121	235	32	189 – 319
2009	3568	1514	1711 – 8124	2446	1459	938 – 7476	500	171	280 – 995
2010	1445	132	1232 – 1759	792	149	587 – 1202	296	91	179 – 559

Table 9. Mean total lengths (TL) and associated survival rate estimates ($\hat{S}$) for northern pike captured annually in three reaches of the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

	HC		SLJ		MS	
interval	mean TL (mm)	$\hat{S}$	mean TL (mm)	$\hat{S}$	mean TL (mm)	$\hat{S}$
2004-2005	539	0.41	457	0.48	604	0.75
2005-2006	470	0.13	477	0.18	556	0.40
2006-2007	490	0.23	418	0.28	501	0.55
2007-2008	420	0.31	377	0.38	439	0.66
2008-2009	519	0.14	467	0.18	558	0.40
2009-2010	453	0.29	340	0.30	500	0.64
mean	484	0.25	411	0.30	519	0.57

Table 10. Annual abundance ($\hat{N}$), removal rate, and survival rate ($\hat{S}$) estimates, plus associated mortality, recruitment, and immigration (R & I) rates, for northern pike from the Hayden to Craig reach (river mile 171.0–134.2) of the Yampa River, Colorado, 2004–2010. Mortality = death, emigration, and removal.

Year	Interval	N_t	removed (n)	removed (%)	$\hat{S}$ (%)	Mortality: total (100-$\hat{S}$, %)	Mortality: other (total - removed, %)	predicted to remain (N_t *$\hat{S}$)	Recruitment & Immigration (N_{t+1} - predicted)	R & I/predicted (%)
2004		3465	1139	33						
	04-05				41	59	26	1421	2551	180
2005		3972	1143	29						
	05-06				13	87	58	516	1055	204
2006		1571	591	38						
	06-07				23	77	39	361	1463	405
2007		1825	534	29						
	07-08				31	69	40	566	626	111
2008		1192	411	34						
	08-09				14	86	52	167	3401	2038
2009		3568	375	11						
	09-10				29	71	60	1035	410	40
2010		1445	705	49						
average				32	25	75	46			496

Table 11. Annual abundance ($\hat{N}$), removal rate, and survival rate ($\hat{S}$) estimates, plus associated mortality, recruitment, and immigration (R & I) rates, for northern pike from the South Beach-Little Yampa Canyon-Juniper reach (river mile 134.2–91.0) of the Yampa River, Colorado, 2004–2010. Mortality = death, emigration, and removal.

Year	Interval	N_t	removed (n)	removed (%)	$\hat{S}$ (%)	Mortality: total (100-$\hat{S}$, %)	Mortality: other (total - removed, %)	predicted to remain (N_t *$\hat{S}$)	Recruitment & Immigration (N_{t+1} - predicted)	R & I/predicted (%)
2004		2444	467	19						
	04-05				48	52	33	1175	-333	-28
2005		843	288	34						
	05-06				18	82	48	151	698	462
2006		849	254	30						
	06-07				28	72	42	236	835	353
2007		1071	558	52						
	07-08				38	62	10	402	257	64
2008		659	269	41						
	08-09				18	82	41	117	2432	2075
2009		2550	357	14						
	09-10				30	70	56	756	132	17
2010		889	459	52						
average				35	30	70	39			491

Table 12. Annual abundance ($\hat{N}$), removal rate, and survival rate ($\hat{S}$) estimates, plus associated mortality, recruitment, and immigration (R & I) rates, for northern pike from the Maybell-Sunbeam reach (river mile 88.7–58.5) of the Yampa River, Colorado, 2004–2010. Mortality = death, emigration, and removal.

Year	Interval	$\hat{N}_t$	removed (n)	removed (%)	$\hat{S}$ (%)	Mortality: total ($100-\hat{S}$, %)	Mortality: other (total - removed, %)	predicted to remain ($\hat{N}_t * \hat{S}$)	Recruitment & Immigration ($\hat{N}_{t+1}$ - predicted)	R & I/predicted (%)
2004		645	139	21						
	04-05				75	25	4	482	-249	-52
2005		233	74	32						
	05-06				40	60	28	94	163	174
2006		257	100	39						
	06-07				55	45	6	142	452	318
2007		594	193	32						
	07-08				66	34	2	391	-155	-40
2008		235	105	45						
	08-09				40	60	15	94	430	459
2009		524	107	20						
	09-10				64	36	16	334	21	6
2010		355	129	36						
average				32	57	43	12			144

Table 13. Average monthly Growing Degree Day units (GDD), Maybell, Colorado, 1958–2006 (Western Regional Climate Center website: http://www.wrcc.dri.edu/), and resulting northern pike growth rates (Rypel 2012). Growing Degree Day units are computed as the difference between the daily average temperature and the base temperature (50°) and are summed for the entire month.

	Month					
	May	June	July	August	September	average
GDD (base 50)	117	308	527	468	197	323
growth rate (mm/d)	0.20	0.51	0.88	0.78	0.33	0.54

Table 14. Captures of age-0 and age-1 northern pike from two reaches of the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (RM 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0).

Year	# age-0 captured	# age-1 captured in following year	total captures produced in year
		reach HC	
2004	1	270	271
2005	0	34	34
2006	3	104	107
2007	0	11	11
2008	0	90	90
2009	1	85	86
2010	2		
		reach SLJ	
2004	101	12	113
2005	15	12	27
2006	36	15	51
2007	2	3	5
2008	27	15	42
2009	91	54	145
2010	55		

Table 15. Number of northern pike (NP) that were captured multiple times and changed reaches, Yampa and Green rivers, 2001–2012. CAT = Lake Catamount (upstream of river mile [RM] 205.0), AH = Above Hayden (RM 205.0–171.0), HC = Hayden to Craig (RM 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5), LP = Lily Park (RM 55.5–44.8).

initial reach	# of NP with multiple captures	% of all multiple captures	# of NP making reach changes	% of NP leaving reach	% of all reach changes
CAT	18	1	18	*	5
AH	279	15	95	34	24
HC	746	39	142	19	36
SLJ	617	32	104	17	26
MS	204	11	29	14	7
LP	47	2	6	13	2
total	1911		394		**

* NP captured multiple times within CAT were not included in the movement analysis; therefore 100% of pike in this table would have left CAT.

** Column does not sum to 100% due to rounding.

Table 16. Direction of reach changes and number of reaches covered by northern pike movements in the Yampa and Green rivers, 2001–2012.

Direction	# of reaches moved								total
	1	2	3	4	5	6	7	8	
downstream	297	32	9	7	6	3	1	1	356
upstream	33	2							35
up, then back	3								3
total	333	34	9	7	6	3	1	1	394

Table 17. Net and total distances traveled by northern pike that left initial capture reaches in the Yampa River, Colorado, 2001–2012. Net distance is the sum of upstream (negative value) and downstream (positive value) distances traveled throughout the capture history of a fish. Total distance is the sum of absolute values of distances traveled throughout the capture history of a fish. CAT = Lake Catamount (upstream of river mile [RM] 205.0), AH = Above Hayden (RM 205.0–171.0), HC = Hayden to Craig (RM 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5), LP = Lily Park (RM 55.5–44.8), RM = river miles.

initial reach	reach length (RM)	*n*	mean net distance (RM)	maximum upstream net distance (RM)	maximum downstream net distance (RM)	mean total distance (RM)	maximum total distance (RM)
CAT		18	49.4	*	241.4	49.4	241.4
AH	34.0	95	27.4	*	229.4	28.0	229.4
HC	36.7	142	26.5	-5.7	174.1	26.8	174.1
SLJ	43.2	104	22.3	-43.5	150.3	33.8	150.3
MS	30.2	29	41.0	-56.4	120.5	47.9	120.5
LP	10.7	6	28.5	-70.9	54.9	52.1	70.9
total/mean		394	27.7			31.9	

* No upstream movements

Table 18. Net and total distances traveled by northern pike that did not leave initial capture reaches throughout their capture histories in the Yampa River, Colorado, 2001–2012. Net distance is the sum of upstream (negative value) and downstream (positive value) distances traveled throughout the capture history of a fish. Total distance is the sum of absolute values of distances traveled throughout the capture history of a fish. AH = Above Hayden (RM 205.0–171.0), HC = Hayden to Craig (RM 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5), LP = Lily Park (RM 55.5–44.8), RM = river miles.

reach	reach length (RM)	*n*	mean net distance (RM)	maximum upstream net distance (RM)	maximum downstream net distance (RM)	mean total distance (RM)	maximum total distance (RM)
AH	34.0	181	0.7	-19.5	14.6	2.7	28.4
HC	36.7	511	2.2	-22.1	33.5	2.9	33.5
SLJ	43.2	500	4.2	-29.3	35.8	8.0	50.9
MS	30.2	168	2.5	-21.9	29.7	5.2	29.7
LP	10.7	36	-0.1	-5.7	3.5	2.1	11.9
total/mean		1396	2.7			5.1	

Table 19. Initial captures of northern pike from Lake Catamount, Colorado, and recaptures in reaches of the Yampa and Green rivers, Colorado. CAT = Lake Catamount (upstream of river mile [RM] 205.0), AH = Above Hayden (RM 205.0–171.0), HC = Hayden to Craig (RM 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5), LP = Lily Park (RM 55.5–44.8), YC = Yampa Canyon (RM 44.8–0.0), GRa = middle Green (RM 321.0–247.0).

Initial CAT capture date	recapture date	reach	recapture date	reach	recapture date	reach	*n*
18-Apr-03	14-Apr-04	AH	20-Apr-04	AH			1
	20-Apr-04	AH	5-May-06	SLJ			1
	26-Apr-04	AH					1
	28-Apr-04	AH					7
	29-Apr-04	AH					1
	4-May-05	AH	25-Apr-06	HC	9-May-06	HC	1
	10-May-06	HC					1
	15-Jun-06	HC					1
	22-Apr-08	LP	12-Jun-09	YC			1
	1-May-08	GRa					1
	6-Jul-11	HC					1
18-Apr-06	18-May-07	MS					1

Table 20. Initial capture and recapture reaches of northern pike that moved from the Yampa River basin, Colorado, to the Green River, Colorado and Utah, 2001–2012. CAT = Lake Catamount (upstream of river mile [RM] 205.0), AH = Above Hayden (RM 205.0–171.0), HC = Hayden to Craig (RM 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5), LP = Lily Park (RM 55.5–44.8), GRc = Lodore Canyon (RM 360.0–345.1), GRb = Echo to Split (RM 345.1–321.0), GRa = middle Green (RM 321.0–247.0).

Initial reach	Recapture reach		
	middle Green (GRa)	Echo-Split (GRb)	Lodore (GRc)
CAT	1		
AH	1		1
HC	1		2
SLJ	4	2	
MS	3	2	3
LP		1	3
total	10	5	9

Table 21. Translocation sites and numbers of northern pike stocked (*n*) after removal from the Yampa River, Colorado, 2000–2012.

Translocation site	adjacent Yampa RM	*n*	untagged	Recapture reach							Recapture	% of
				AH	HC	SLJ	MS	LP	GRc	GRa	total	escapes
Yampa State Park Headquarters pond	158.0	2676	301		1	1		1			3	2.5
Yampa River State Wildlife Area ponds	154.0	3299	23	4	79	4	4				91	75.2
Loudy-Simpson ponds	139.0	2758	32		17	8			1	1	27	22.3
Rio Blanco Reservoir	White River basin	1234	13									
Not recorded*		309	96									
total		10276	465	4	97	13	4	1	1	1	121	100

* All from 2004; either Loudy-Simpson ponds or Rio Blanco Lake.

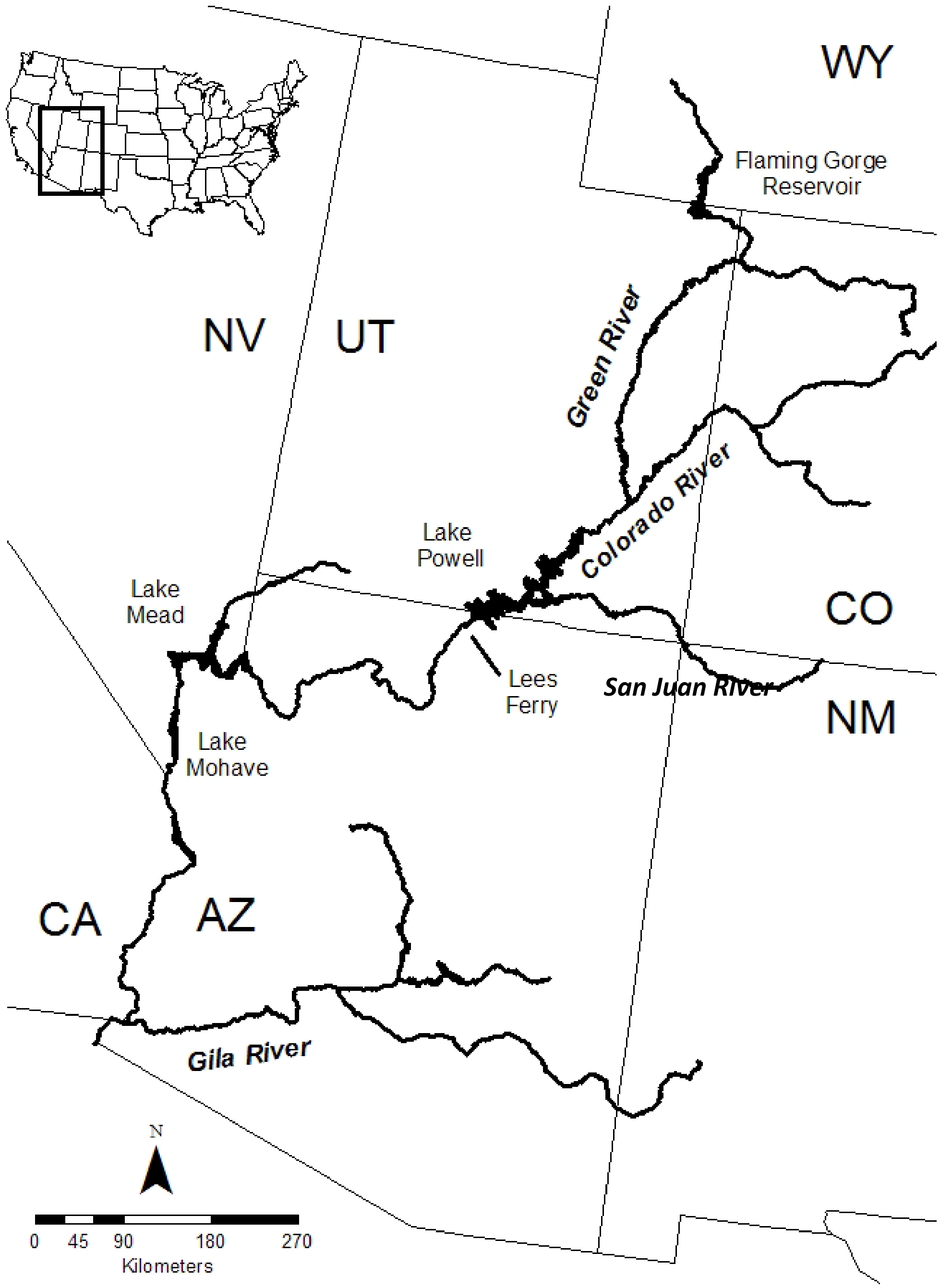


Figure 1. Map of the Colorado River basin. Lee Ferry divides the Upper and Lower Colorado River basins.

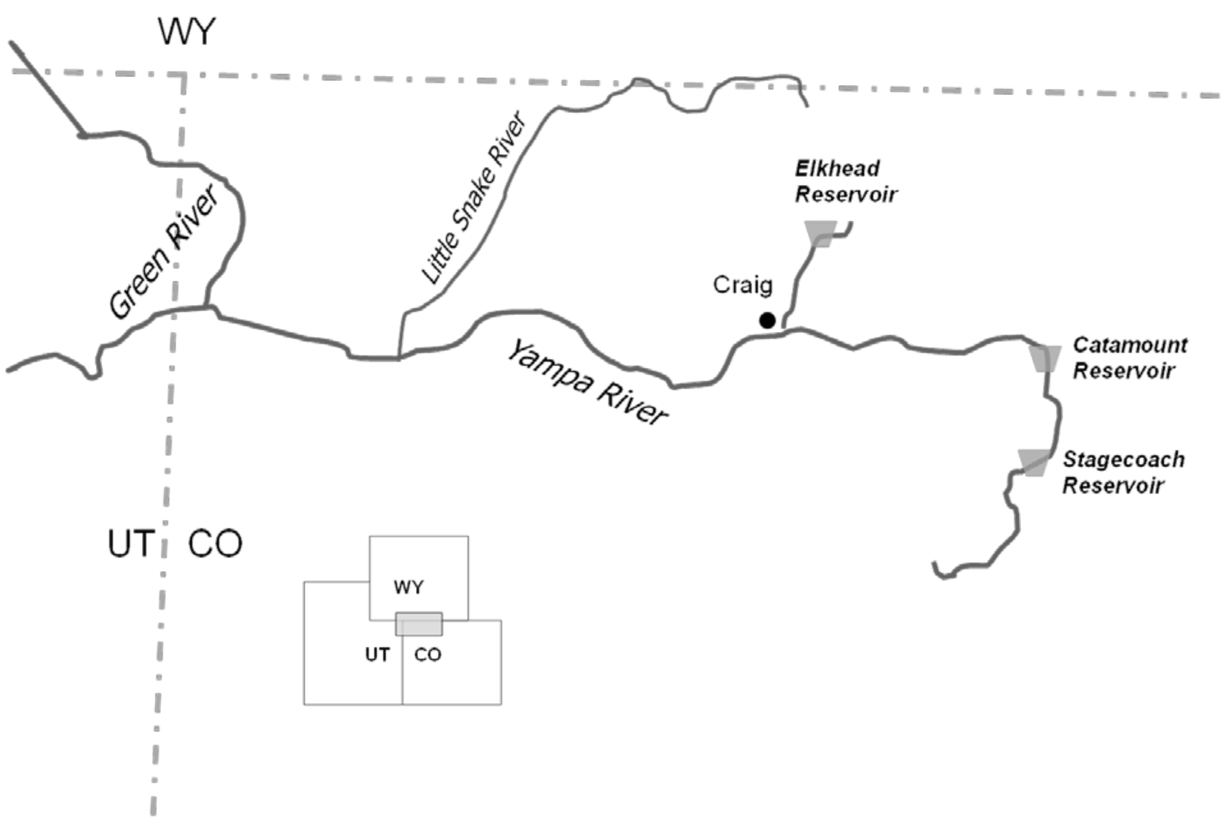


Figure 2. Map of Yampa River basin, Colorado.

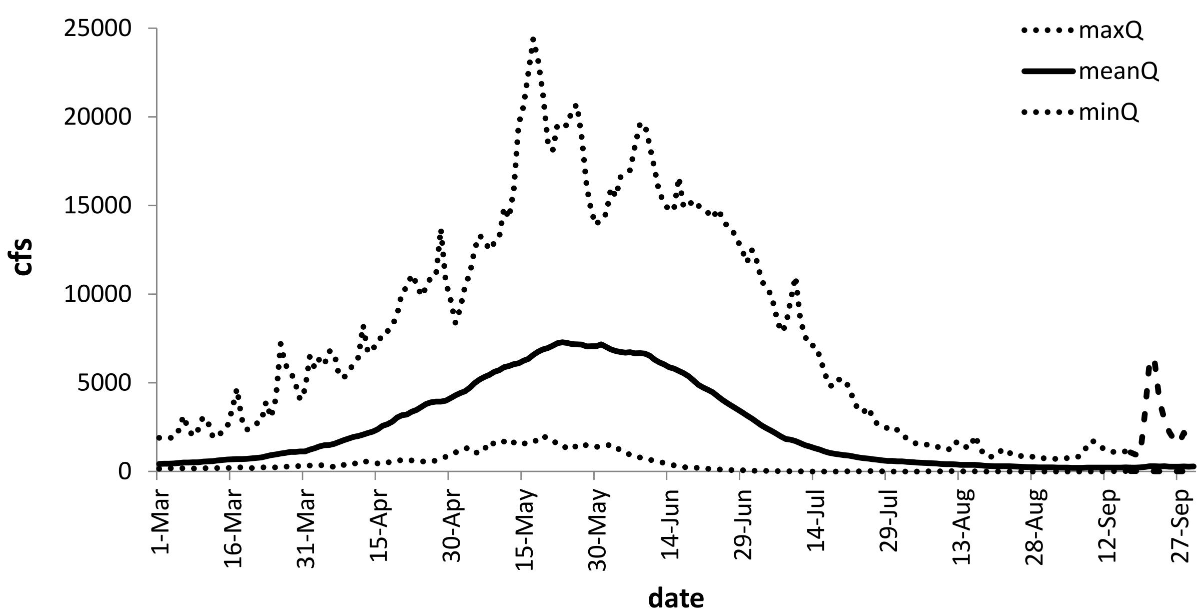


Figure 3. Mean daily discharge (cubic feet per second, cfs) of the Yampa River near Maybell, Colorado (U.S. Geological Survey gage 09251000), for years 1917–2013.

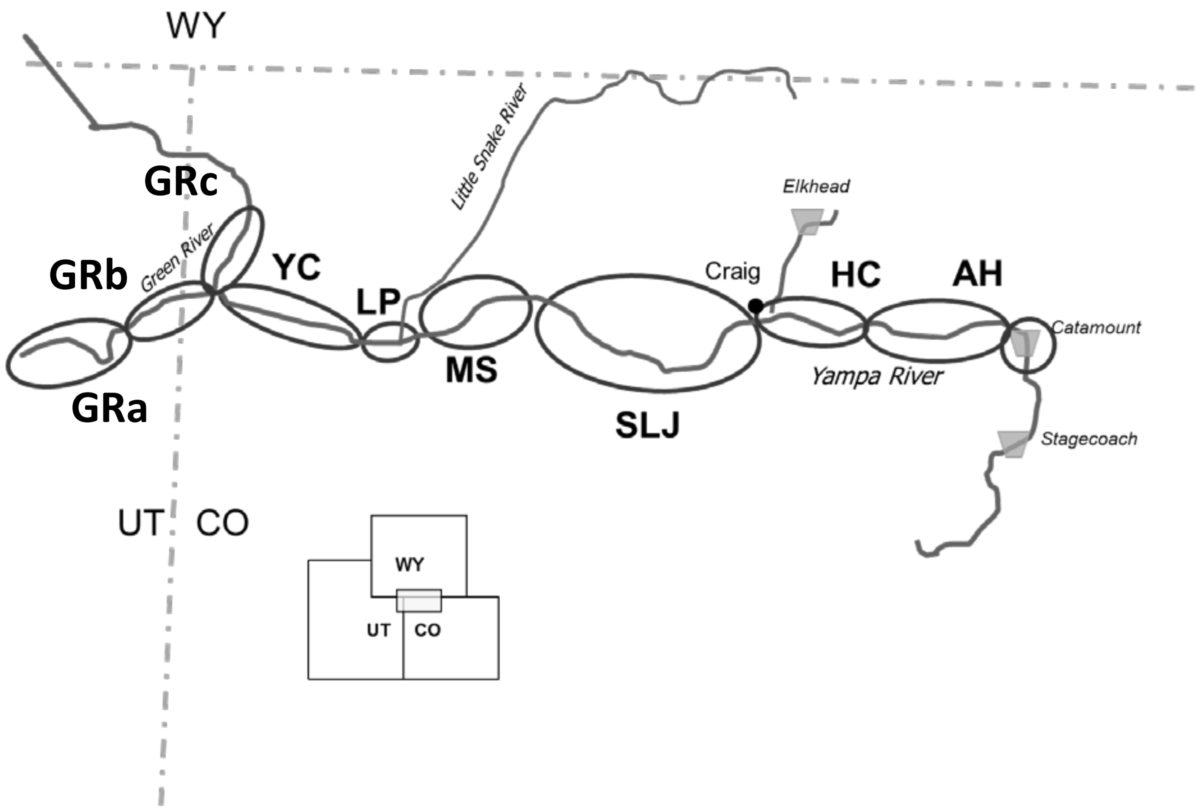


Figure 4. Study reaches within the Yampa River and portions of the Green River. Lake Catamount (upstream of river mile [RM] 205.0), AH = Above Hayden (205.0–171.0), HC = Hayden to Craig (RM 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5), LP = Lily Park (RM 55.5–44.8), YC = Yampa Canyon (RM 44.8–0.0), GRc = Lodore Canyon (RM 360.0–345.1), GRb = Echo to Split (RM 345.1–321.0), GRa = middle Green (RM 321.0–247.0).

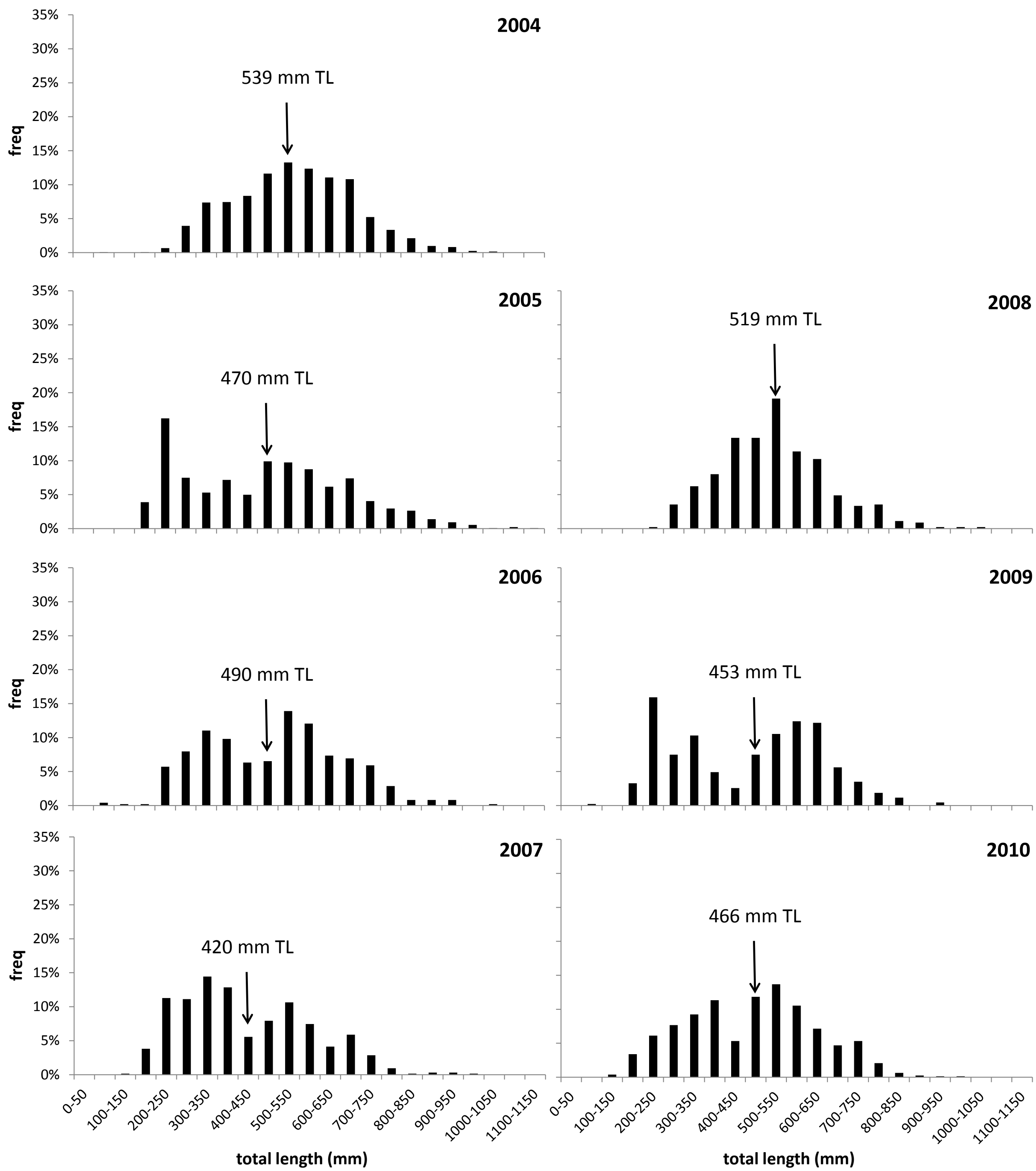


Figure 5. Length–frequency histograms of northern pike captured in reach HC (Hayden to Craig, river mile 171.0–134.2) of the Yampa River, Colorado, 2004–2010. Arrows and corresponding values represent mean northern pike length for each year. TL = total length.

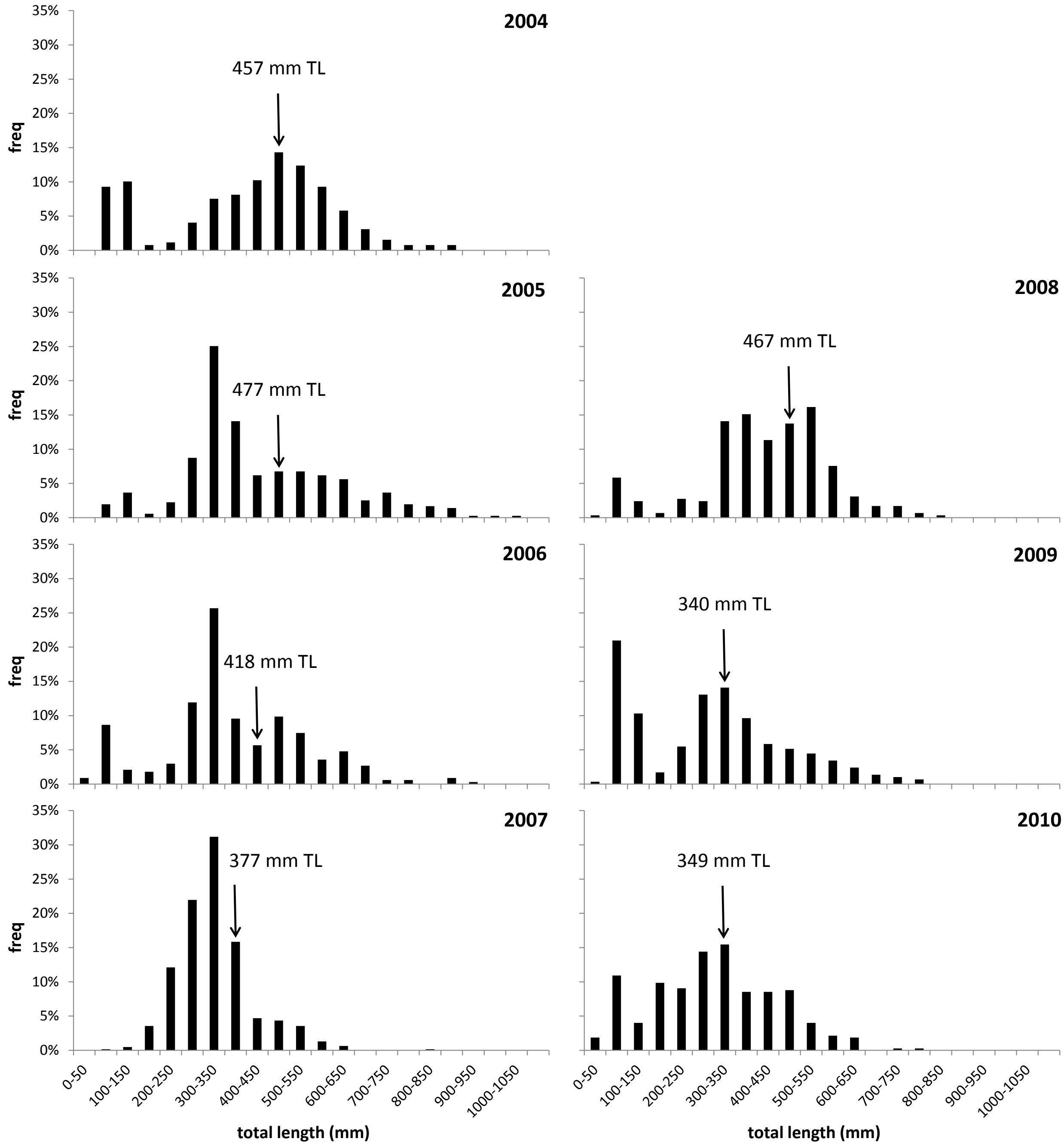


Figure 6. Length–frequency histograms of northern pike captured in reach SLJ (South Beach-Little Yampa Canyon-Juniper, river mile 134.2–91.0) of the Yampa River, Colorado, 2004–2010. Arrows and corresponding values represent mean northern pike length for each year. TL = total length.

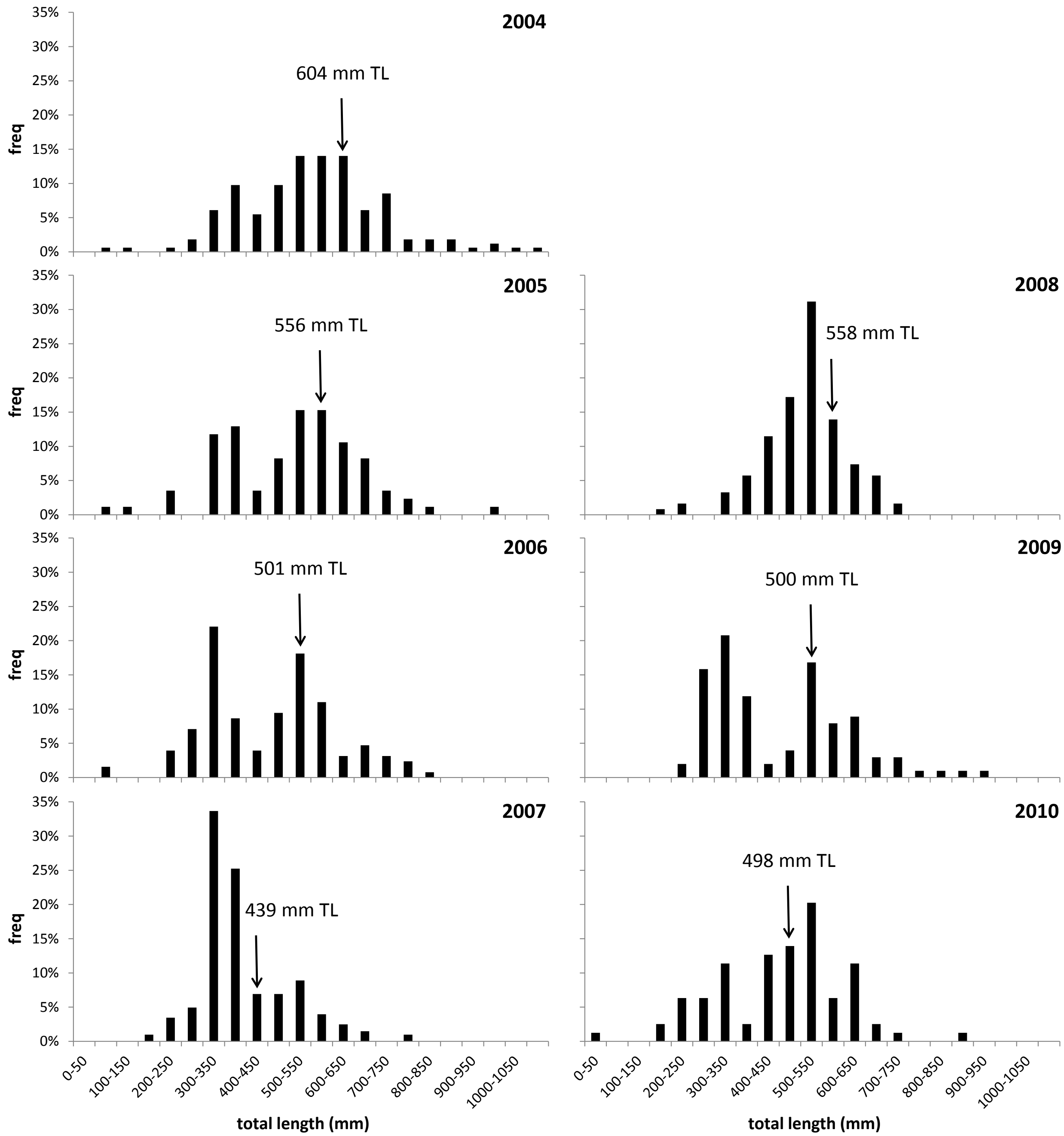


Figure 7. Length–frequency histograms of northern pike captured in reach MS (Maybell-Sunbeam, river mile 88.7–58.5) of the Yampa River, Colorado, 2004–2010. Arrows and corresponding values represent mean northern pike length for each year. TL = total length.

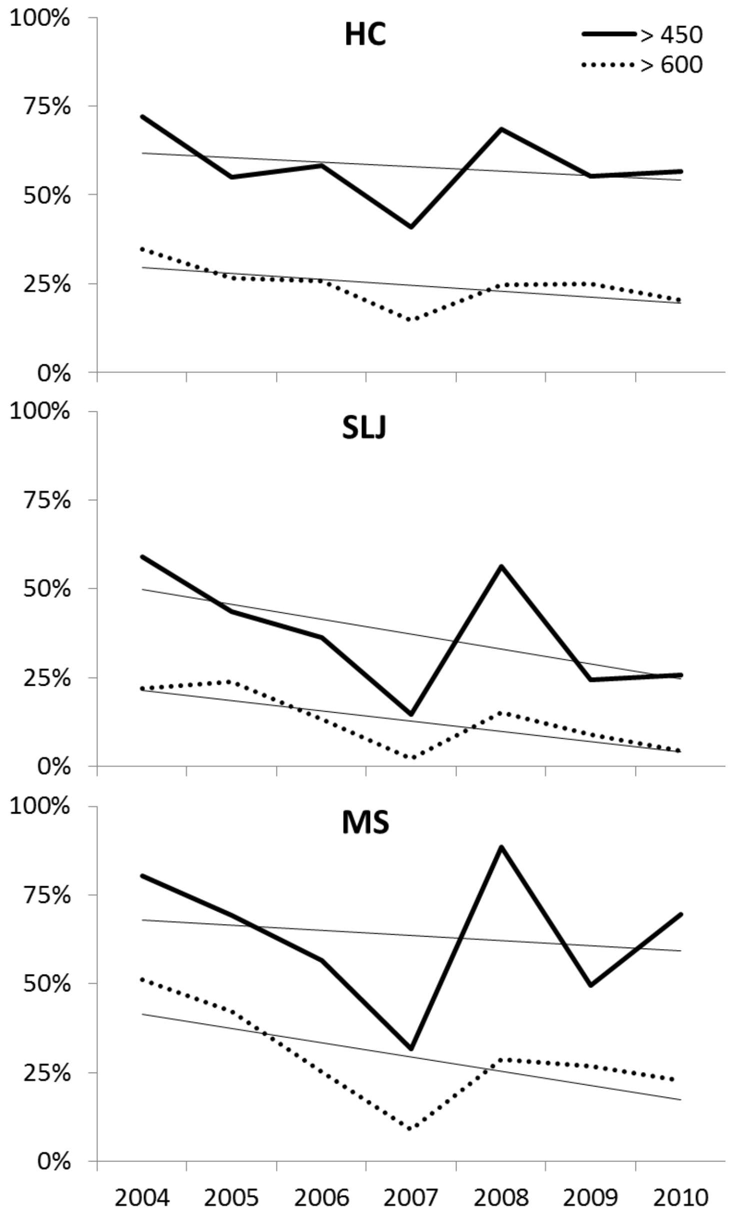


Figure 8. Percent frequency of northern pike > 450 mm TL (solid line) and > 600 mm TL (dotted line) captured in three reaches of the Yampa River, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

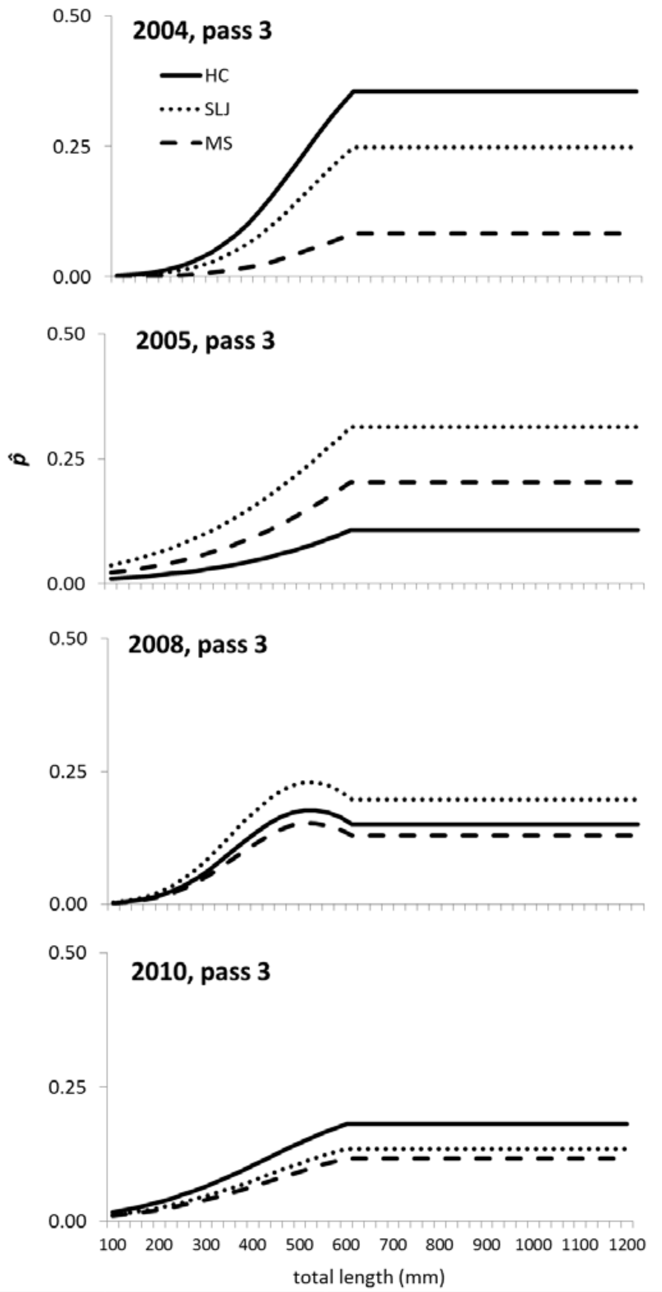


Figure 9. Examples of length-dependent capture probability estimate ($\hat{p}$) curves by year, pass, and reach. The top-ranked model contained a threshold length (600 mm total length), above which probabilities plateaued. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

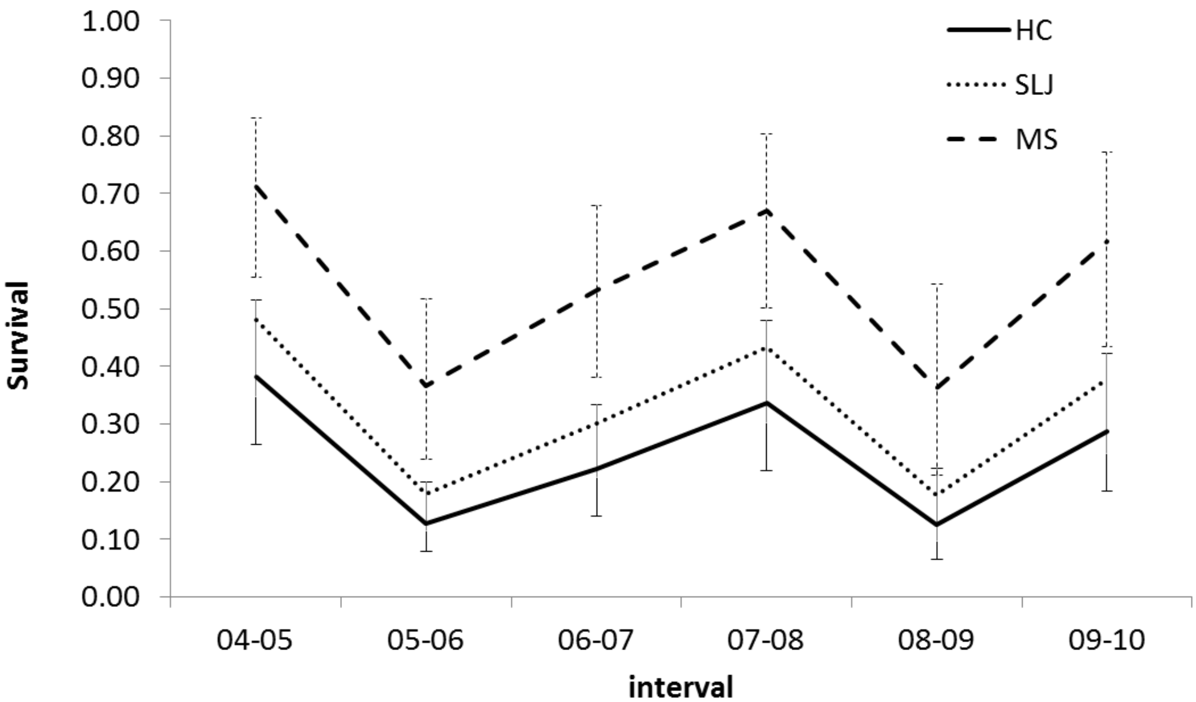


Figure 10. Survival rate estimates and 95% confidence intervals for average-length (465 mm total length) northern pike captured in three reaches of the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5). Confidence intervals for SLJ estimates overlapped those of HC and MS in all years and are not displayed to aid clarity.

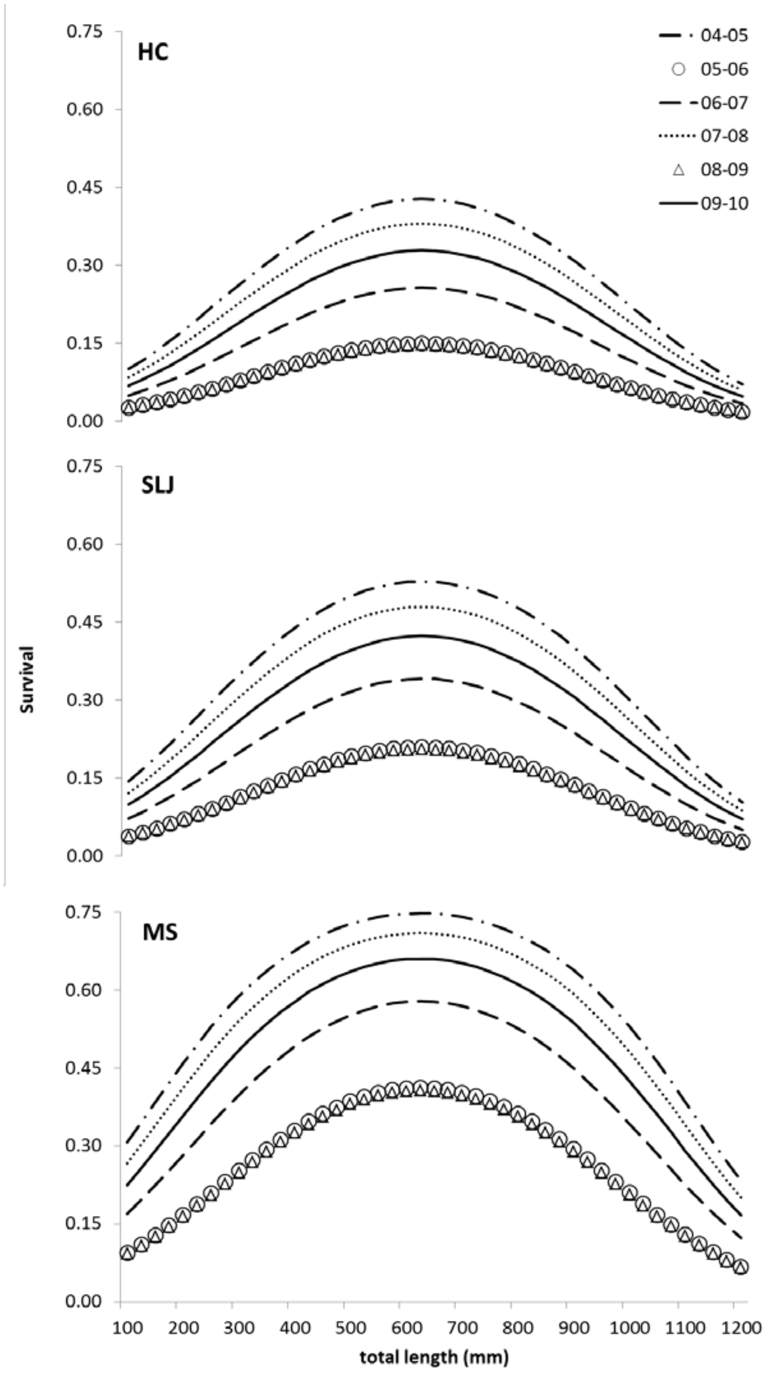


Figure 11. Length-dependent survival rate estimates for northern pike captured in three reaches of the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

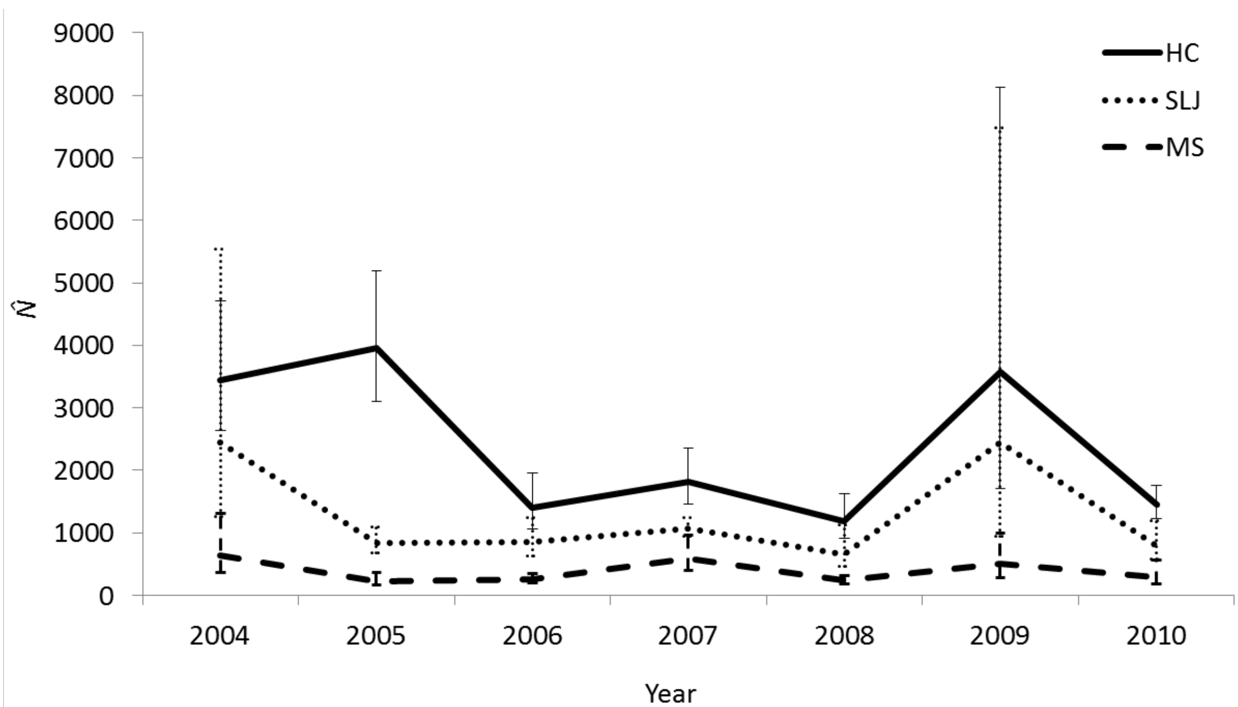


Figure 12. Abundance estimates ($\hat{N}$) and 95% confidence intervals for northern pike in the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5).

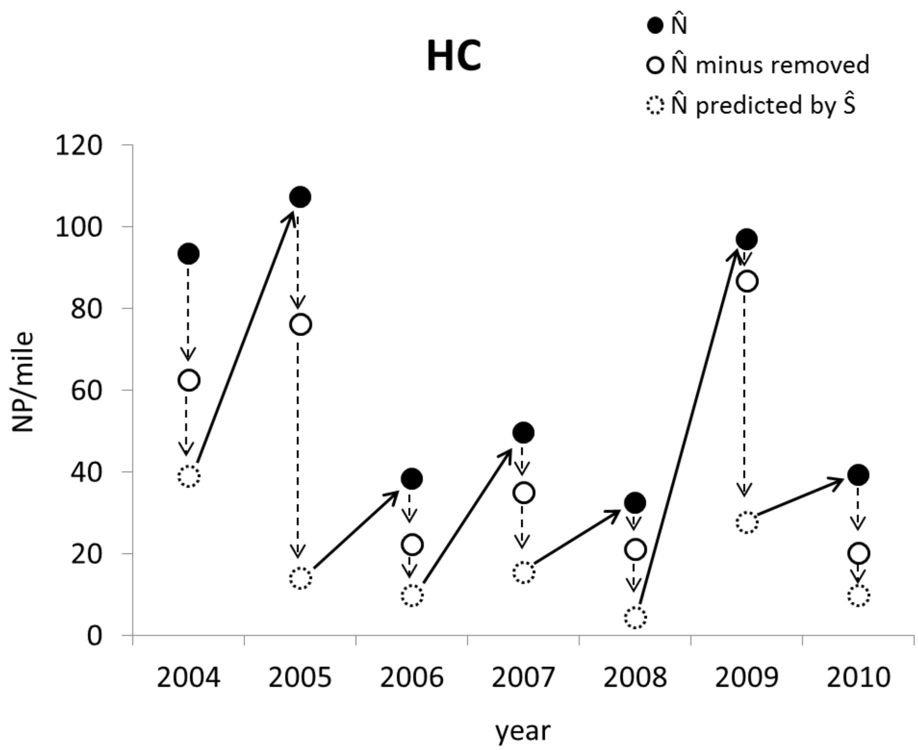


Figure 13. Annual abundance estimates ($\hat{N}$, filled circles), abundance estimates minus numbers removed each year ($\hat{N}$ minus removed, open circles), and predicted abundance remaining after annual survival rate estimate was applied ($\hat{N}$ predicted by $\hat{S}$, dashed circles) expressed as densities for northern pike (NP) in reach Hayden to Craig (HC, river mile 171.0–134.2) of the Yampa River, Colorado, 2004–2010. Dashed arrows indicate reductions in densities due do removal and other mortality factors, solid arrows indicate increases in density due to recruitment and immigration.

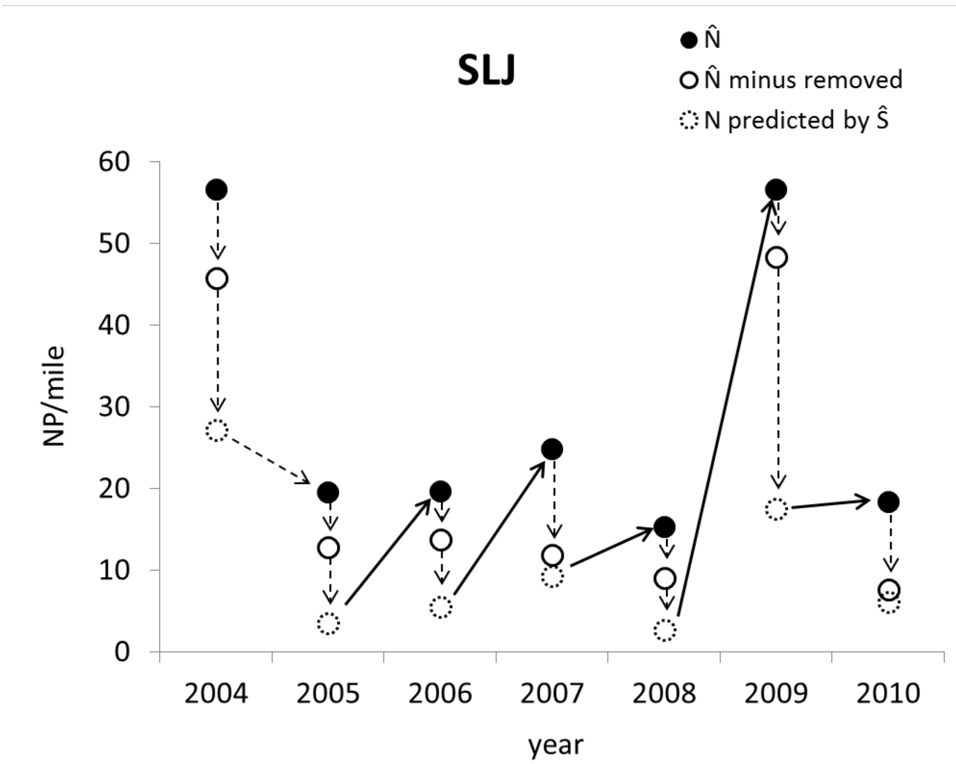


Figure 14. Annual abundance estimates ($\hat{N}$, filled circles), abundance estimates minus numbers removed each year ($\hat{N}$ minus removed, open circles), and predicted abundance remaining after annual survival rate estimate was applied ($\hat{N}$ predicted by $\hat{S}$, dashed circles) expressed as densities for northern pike (NP) in reach South Beach-Little Yampa Canyon-Juniper (SLJ, river mile 134.2–91.0) of the Yampa River, Colorado, 2004–2010. Dashed arrows indicate reductions in densities due do removal and other mortality factors, solid arrows indicate increases in density due to recruitment and immigration.

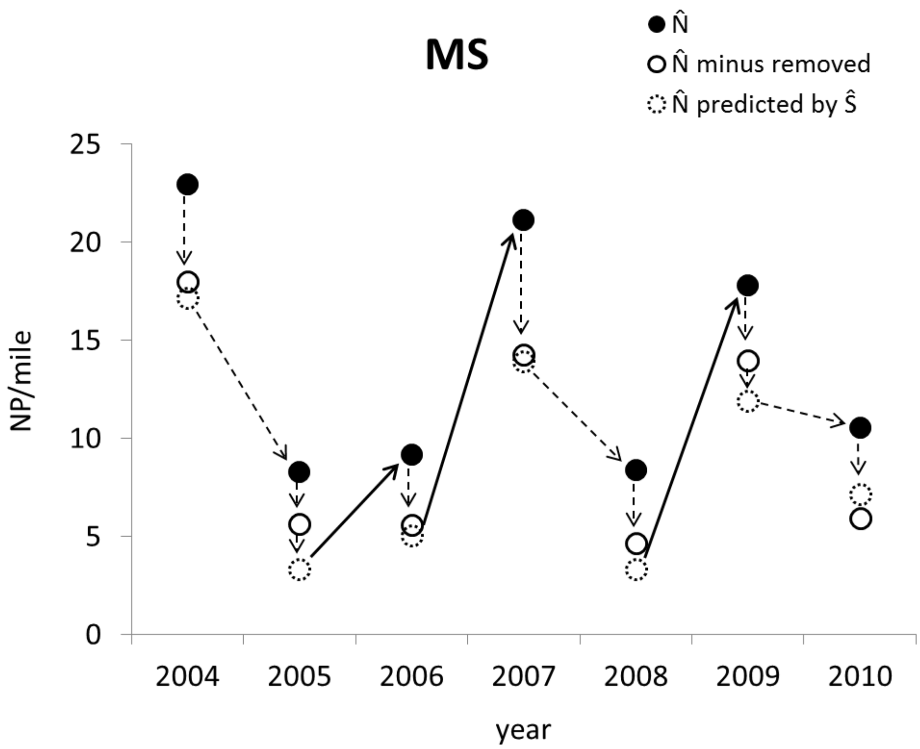


Figure 15. Annual abundance estimates ($\hat{N}$, filled circles), abundance estimates minus numbers removed each year ($\hat{N}$ minus removed, open circles), and predicted abundance remaining after annual survival rate estimate was applied ($\hat{N}$ predicted by $\hat{S}$, dashed circles) expressed as densities for northern pike (NP) in reach Maybell-Sunbeam (MS, RM 88.7–58.5) of the Yampa River, Colorado, 2004–2010. Dashed arrows indicate reductions in densities due do removal and other mortality factors, solid arrows indicate increases in density due to recruitment and immigration.

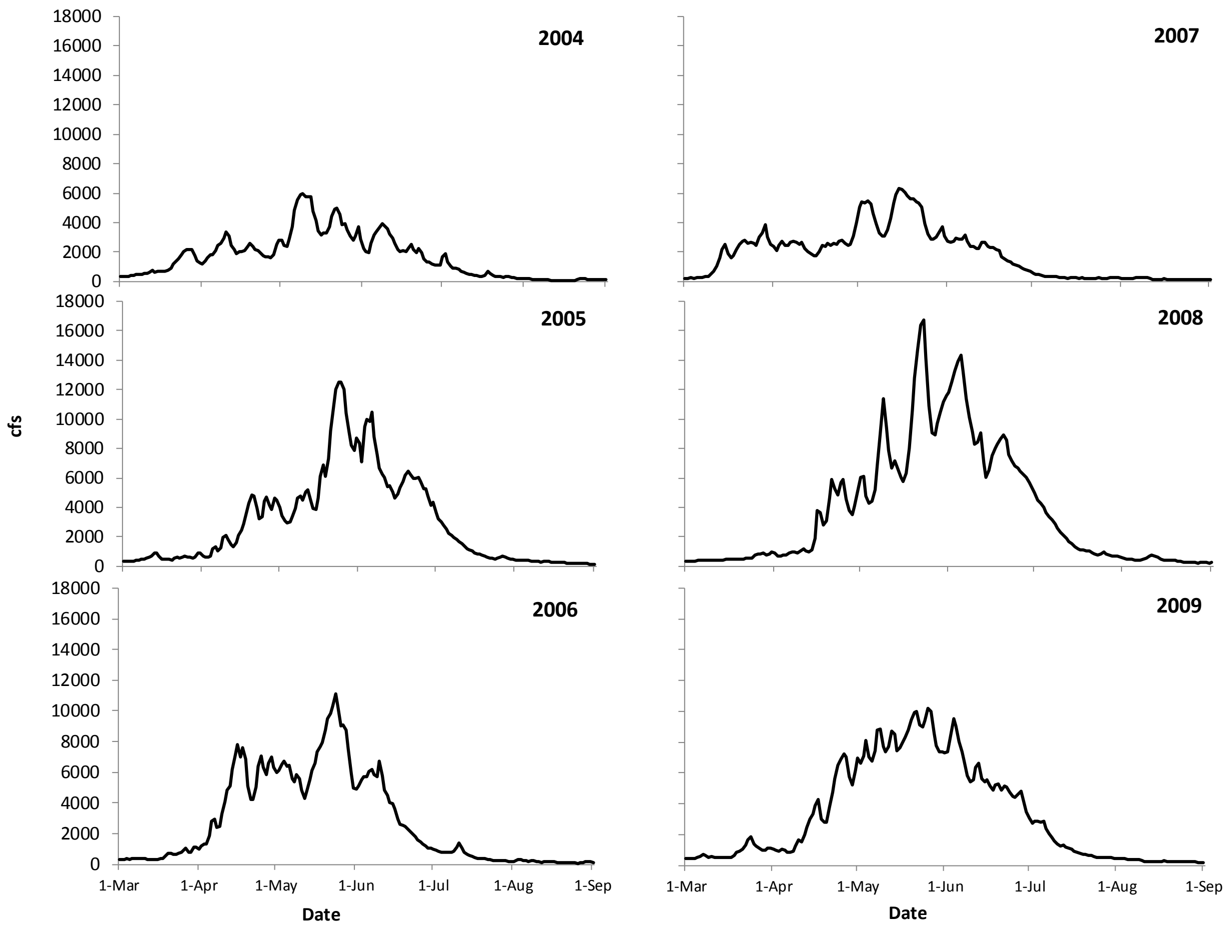


Figure 16. Mean daily discharge of the Yampa River near Maybell, Colorado (U.S. Geological Survey gage 09251000), 2004–2009. cfs = cubic feet per second.

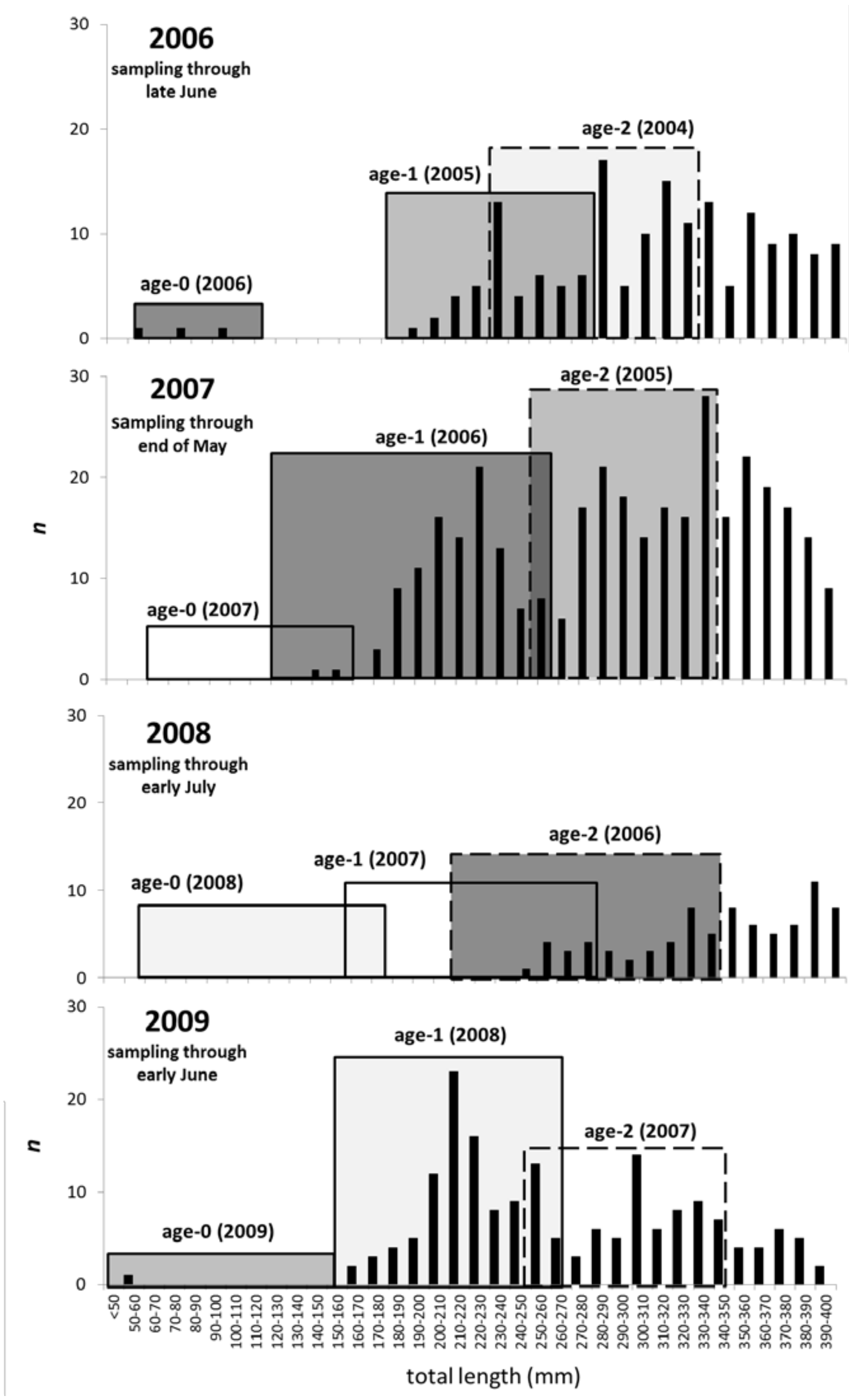


Figure 17. Length–frequency histograms for northern pike captured in reach HC (Hayden to Craig, river mile 171.0–134.2), Yampa River, Colorado, 2006–2009. Boxes encompassing age-groups were based on timing of actual captures and estimates of seasonal growth from this study. Dashed boxes represent age-2 length ranges in April sampling only.

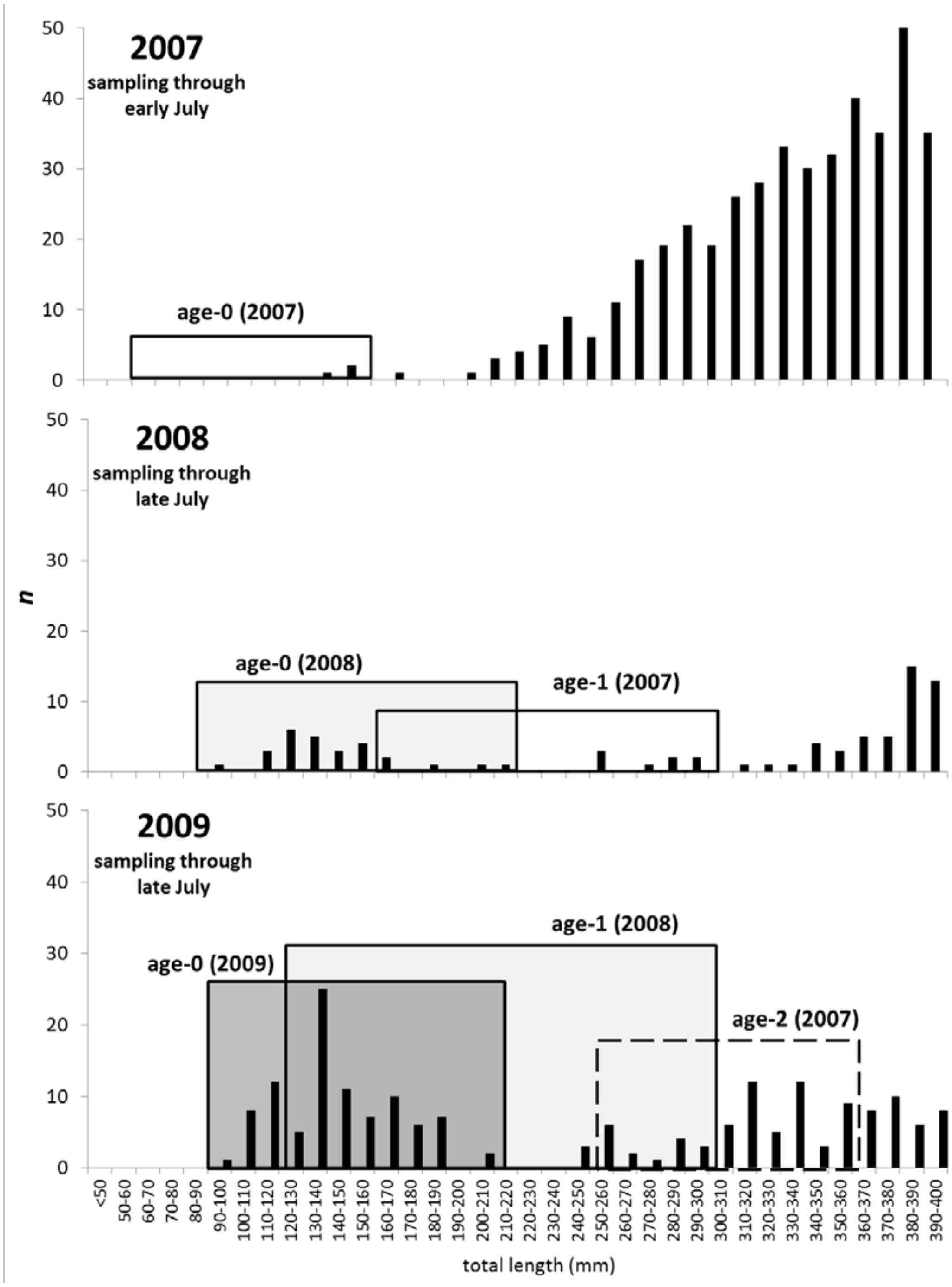


Figure 18. Length–frequency histograms for northern pike captured in reach SLJ (South Beach-Little Yampa Canyon-Juniper, RM 134.2–91.0), Yampa River, Colorado, 2007–2009. Boxes encompassing age-groups were based on timing of actual captures and estimates of seasonal growth from this study. Dashed boxes represent age-2 length ranges in April sampling only.

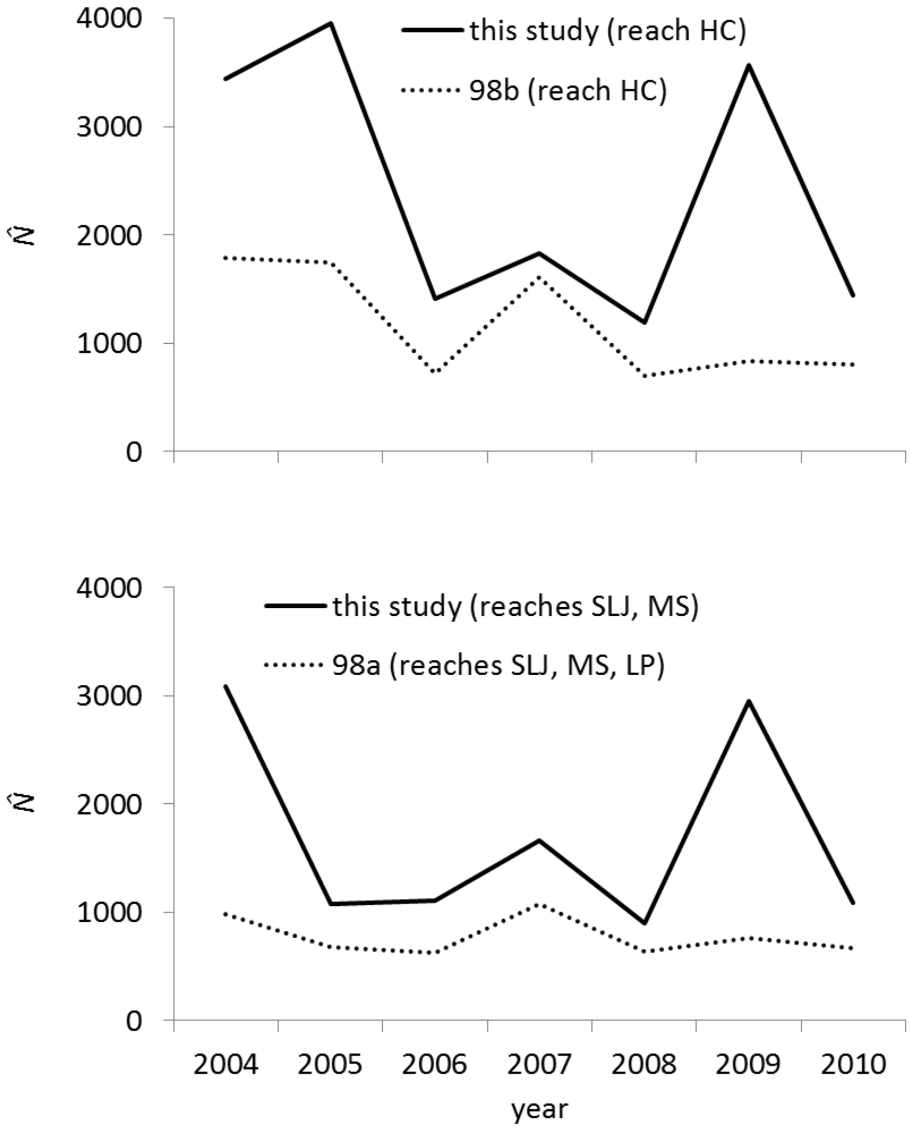


Figure19. Comparison of abundance estimates ($\hat{N}$) generated in this study to those from Recovery Program projects 98b (top) and 98a (bottom) for northern pike from the Yampa River, Colorado, 2004–2010. HC = Hayden to Craig (river mile [RM] 171.0–134.2), SLJ = South Beach-Little Yampa Canyon-Juniper (RM 134.2–91.0), MS = Maybell-Sunbeam (RM 88.7–58.5), LP = Lily Park (RM 55.5–44.8).

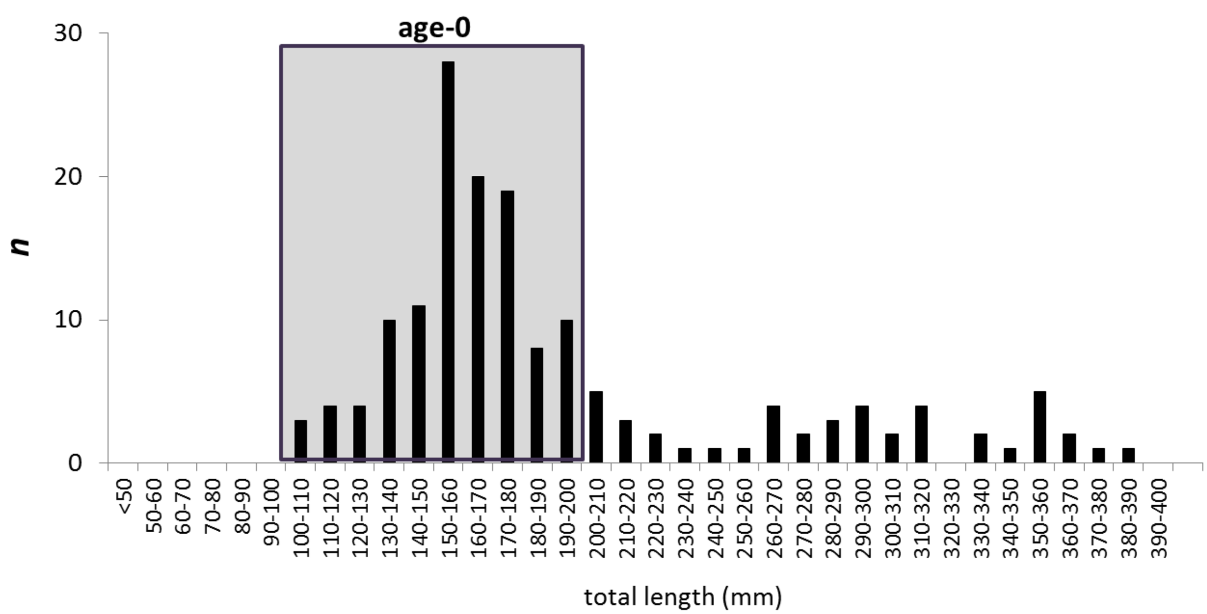
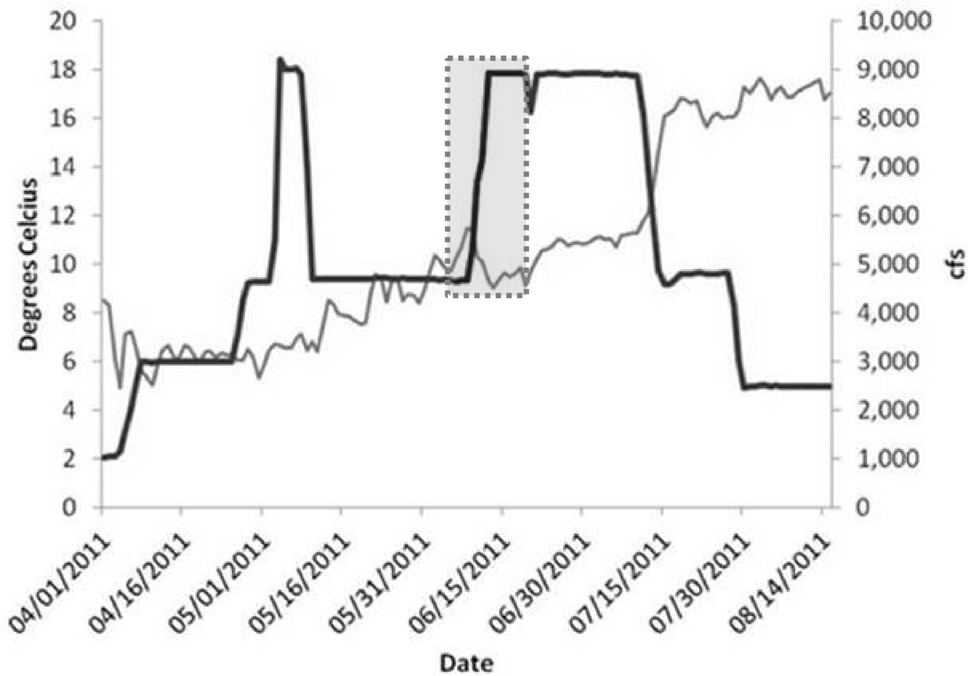


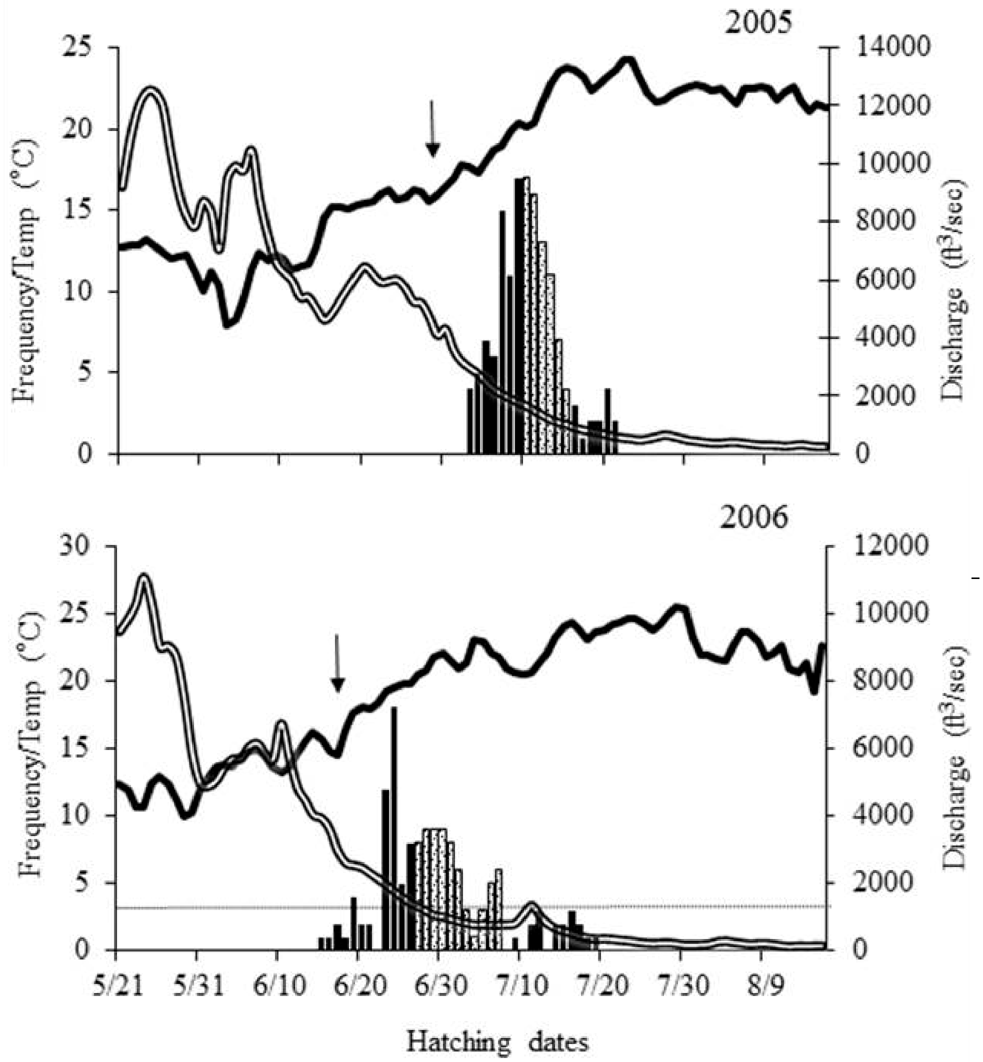
Figure 20. Length–frequency histogram for northern pike captured at the confluence of Walton Creek and the Yampa River, Colorado, 2 October 2009. Age-0 size range estimate based on early season lengths of age-1s and late-season lengths of age-0s calculated from growth rates for pike in other reaches of this study.

APPENDIX A

Examples of spawning, streamflow, and water temperature data relationships that may be used to disadvantage northern pike and smallmouth bass reproduction and recruitment.



A.1. Water temperature (gray line) and streamflow (in cubic feet per second, cfs; black line) at Brown's Park National Wildlife Refuge (USGS gage 09234500), 2011. The shaded gray box indicates northern pike spawning activity based on otolith-aged young-of-year pike collected in seine samples.



A.2. From Figure 2 in Bestgen and Hill (draft report): Frequency distribution of hatching dates for age-0 smallmouth bass captured in Little Yampa Canyon, Yampa River, Colorado, 2005-2011. Water temperature data (solid line) and discharge data (U. S. Geological Survey Gauge 09251000, double line) were collected from a site near Maybell, Colorado. The vertical arrow represents onset of mean daily water temperatures >16°C. The three cohorts of age-0 smallmouth bass in histograms were derived by dividing the distribution into approximately equal thirds through time, and are indicated by filled (cohort 1), open dotted (cohort 2), and filled (cohort 3) bars proceeding from left to right.