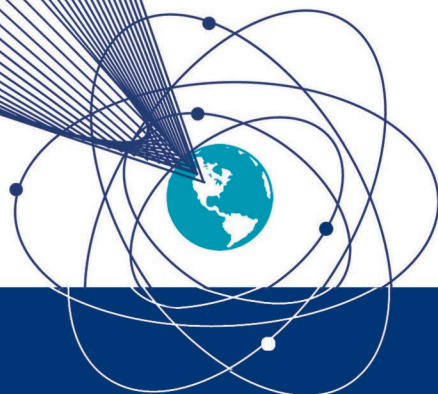


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IJS



INTERMOUNTAIN JOURNAL OF SCIENCES

The Intermountain Journal of Sciences (IJS) is a regional peer-reviewed journal that encourages scientists, educators and students to submit their research, management applications, or viewpoints concerning the sciences applicable to the intermountain region. Original manuscripts dealing with biological, environmental, health and human development, mathematics, molecular-cellular, pharmaceutical, physical and social sciences are welcome.

Co-sponsors/publishers include the Montana Academy of Sciences, the Montana Chapters of The Wildlife Society and The American Fisheries Society. It is the intent of the governing bodies of the co-sponsoring organizations that this journal replace and standardize printed proceedings from the respective annual meetings. Format and style should follow the *Guidelines for Meeting Abstracts Submitted to the Intermountain Journal of Sciences, 1st revision 2016*.^{*} It is the policy of the editorial board that abstracts from presentations at annual meetings be published in the last issue of *IJS* for that year of the annual meeting. Submission of manuscripts for review and publication without regard to membership is encouraged.

Baseline funding is provided by the co-sponsoring organizations. Long-term funding will be derived from page charges assessed manuscript authors at \$60/page, sponsoring organizations at \$40/page for annual meeting abstracts and annual subscriptions: student - \$6, regular member - \$15, patron member - \$25, international member - \$25 and library - \$25. One time subscriptions are: life member - \$150 and sustaining subscriber - \$2,500.

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The *Intermountain Journal of Sciences* (IJS) is a fully refereed journal.

Manuscripts are submitted to the Editor-in-Chief (EIC) for initial consideration for publication in the IJS. This review shall include, but not be limited to, appropriateness for publication in IJS, correct formatting and inclusion of a letter of submittal by the author with information about the manuscript as stated in the "Guidelines for manuscripts submitted to the *Intermountain Journal of Sciences*" (Dusek 1995, 2007) available on the IJS website, www.intermountainjournal.org under the Publish tab. This cover letter must also include a statement by the author that this paper has not been submitted for publication or published elsewhere. The EIC notes the date of receipt of the manuscript and assigns it a reference number, IJS-xxxx. The EIC forwards a letter of manuscript receipt and the reference number to the corresponding author. The corresponding author is the author who signed the submittal letter.

Three hard or digital copies of the submitted manuscript, with copies of the "Guidelines and checklist for IJS referees" attached are forwarded to the appropriate Associate Editor. The Associate Editor retains one copy of the manuscript and guidelines for his/her review, and submits a similar package to each of two other reviewers. A minimum of two reviewers, including the Associate Editor, is recommended for each manuscript. The two reviewers are instructed to return the manuscript and their comments to the Associate Editor. The Associate Editor then returns all manuscript copies and reviewer comments plus a recommendation for publication, with or without revisions, or rejection of the manuscript to the EIC. This initial review process is limited to 30 days.

The EIC then reviews the recommendations and all comments and notifies the corresponding author of the results of the review and the publication decision.

ACCEPTANCE

For accepted manuscripts, each copy of the manuscript containing comments thereon and other comments are returned to the corresponding author. Revised manuscripts are to be returned to the EIC in hard copy and four copies if further review is required. These copies can be submitted in digital form by email. The revised manuscript shall be returned to the EIC within 14 days of notification. Review of the revised manuscript by the Associate Editor and reviewers shall be completed and returned to the EIC within 14 days. An accepted manuscript will then be forwarded to the Managing Editor (ME) for final processing.

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Each manuscript that is rejected for publication is returned by the EIC to the corresponding author along with the reasons for rejection. The author is also advised that the manuscript may be resubmitted, provided all major criticisms and comments have been addressed in the resubmitted manuscript. The resubmitted manuscript may be returned to the initial review process if deemed appropriate by the EIC. If the manuscript is rejected a second time by either the EIC or the Associate Editor and reviewers, no further consideration will be given for publication of the manuscript in IJS. The corresponding author will be notified of this decision.

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Each manuscript submitted by an Associate Editor shall be reviewed by the EIC and a minimum of two other reviewers with expertise in the subject being addressed. Each manuscript submitted by the EIC shall be forwarded with the necessary review materials to the ME or chairman of the editorial board, who will serve as the EIC for that manuscript.

ABSTRACTS

Only abstracts submitted from the annual meetings of the sponsoring organizations will be published in IJS. Other submissions of abstracts shall be considered on a case-by-case basis by the Editorial Board. Sponsoring organizations shall collect abstracts, review them for subject accuracy, format them in Microsoft Word and email them to Rick Douglass, the EIC (RDouglass@mtech.edu), on or before November 1. Each abstract shall be reviewed by the EIC to assure proper grammar, compliance with IJS Guidelines and for publication in the December issue of IJS. The Guidelines for Submitting Meeting Abstracts (Presentation or Poster) are available as a pdf on the IJS website under the Publish tab.

COMMENTARY

Submissions concerning management applications or viewpoints concerning current scientific or social issues of interest to the Intermountain region will be considered for publication in the "Commentary" Section. This section will feature concise, well-written manuscripts limited to 1,500 words. Commentaries will be limited to one per issue.

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LITERATURE CITED

Dusek, Gary L. 1995, revised 2007.

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Revised guidelines are available on the Intermountain Journal of Sciences web site: (www.intermountainjournal.org)

DIET OF BURBOT AND IMPLICATIONS FOR SAMPLING

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ABSTRACT

Burbot (*Lota lota*) are an apex piscivore that were illegally introduced to the Green River drainage, Wyoming, raising concerns for the conservation and management of fishes throughout the basin. However, relatively little is known about the diet of non-native burbot. The objectives of this research were to characterize diet composition of burbot and identify differences in diet composition as a function of sampling gear. Diet composition was characterized using frequency of occurrence, percent by number, and percent by weight to identify the importance of each prey type to burbot. Diet composition was compared across gears to identify the relationship between gear and diet. Fishes were present in the stomach contents of nearly all burbot sampled and composed 62–100 percent of the stomach contents of burbot greater than 300 mm. Prey diversity was greatest in diets of burbot sampled with small-mesh hoop nets. Results from the current study provide important information on the diet of non-native burbot and highlight the potential influence of gear on diet studies.

Key Words: Burbot, Gear bias, Diet, Green River, Wyoming

INTRODUCTION

Burbot (*Lota lota*) are the only freshwater species of the family Gadidae and have a circumpolar distribution throughout Europe, Asia, and North America (Stapanian et al. 2010). Burbot have been categorized as opportunistic piscivores (Rudstam et al. 1995, Amundsen et al. 2003) with fish typically dominating the diet of burbot greater than 400 mm (Rudstam et al. 1995, Schram et al. 2006). Fratt (1997) evaluated prey consumption of burbot in Green Bay, Lake Michigan, Wisconsin, and reported that 55 percent of stomach contents (by volume) of burbot less than 400 mm were fishes. Bailey (1972) reported greater than 90 percent occurrence of fishes in the diet of 119–742 mm burbot in Lake Superior, Wisconsin and Michigan. The author suggested that burbot were important competitors with other large piscivores in the system due to their non-selective diet and high consumption rates. Although burbot are apex piscivores throughout their native distribution (Cott et al. 2011),

relatively little is known about how burbot function in food webs in systems where they are non-native.

In Wyoming, burbot represent native and non-native populations and are a primary management concern for state, federal, and tribal natural resource agencies. Burbot are native to the Tongue and Wind-Bighorn river drainages, but are considered either rare (Wind-Bighorn River drainage) or extirpated (Tongue River, Krueger and Hubert 1997). In the Green River drainage, burbot were illegally introduced into Big Sandy Reservoir in the 1990s (Gardunio et al. 2011). Since their initial introduction, burbot have been found from Flaming Gorge Reservoir (FGR) to the confluence of the New Fork and Green rivers. The rapid expansion of burbot in the Green River has increased concern for the management of sport fishes and conservation of native fishes in the system. The Green River supports economically, socially, and ecologically important fishes including brown trout

(*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), Colorado River cutthroat trout (*O. clarkii pleuriticus*), roundtail chub (*Gila robusta*), bluehead sucker (*Catostomus discobolus*), and flannelmouth sucker (*C. latipinnis*). Managers have hypothesized that burbot compete with and (or) directly consume native fishes and economically important trout species. However, relatively little is known about how non-native burbot may affect the trophic dynamics of recipient systems.

Negative effects of introduced species are often not exclusive to a single mechanism. For example, both predation and resource competition may occur between native and non-native species. Mills et al. (2004) evaluated interactions between non-native western mosquitofish (*Gambusia affinis*) and native least chub (*Notichthys phlegenthontis*) in Walter Spring, California and found that adult mosquitofish greater than 30 mm fed extensively on 9–13 mm least chub. Once least chub were too large to be consumed by western mosquitofish, they were negatively influenced by resource competition. Similarly, non-native burbot likely influence native fishes through multiple mechanisms. Cott et al. (2011) investigated the trophic ecology of burbot relative to lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*), and lake whitefish (*Coregonus clupeiformis*) in four boreal Canadian lakes using stable isotope analysis. Burbot and lake trout were both described as top-level piscivores in the lakes, and burbot were thought to play a particularly important role in structuring fish assemblages via predation and competition. In the Green River drainage, burbot have been hypothesized to alter the system through resource competition (i.e., habitat, food) and predation (Gardunio et al. 2011). For instance, Gardunio et al. (2011) suggested that burbot outcompete smallmouth bass (*Micropterus dolomieu*) for available prey in FGR as evidenced by declining catch rates of smallmouth bass following establishment of burbot. Despite concerns regarding the influence of burbot on the trophic dynamics

of the Green River fish assemblage, little empirical data on diet are available for non-native burbot.

Information on diet is fundamental for understanding how a given species may influence the food web of a system (Garvey and Chipps 2012). Although a number of analytical techniques are available to quantify dietary information (e.g., bioenergetics modeling, stable isotope analysis), identification of gut contents is a commonly used technique. Gut contents are ideally quantified over extensive spatial and temporal scales to capture seasonal and temporal variation in diet (Hyslop 1980, Garvey and Chipps 2012). However, short-term diet studies can provide valuable data that answer narrow questions (e.g., fish- versus invertebrate-dominated diet, consumption of native fishes) and can be used to guide future management decisions and research foci.

Sampling techniques are an important consideration when describing the diet of fishes (Bowen 1996). Active gears, such as electrofishing often select for sedentary individuals (Reynolds and Kolz 2012). Sedentary individuals are not actively foraging, and studies using information predominantly from sedentary individuals may underestimate the amount or inaccurately describe the types of food consumed by fish in the population. Alternatively, fish captured with passive gears often contain greater amounts of food than those caught by active gears. For instance, Hayward et al. (1989) reported that the amount of food in yellow perch (*Perca flavescens*) stomachs was greater in fish caught with gill nets than those caught by trawling in Lake Erie, Ohio. Furthermore, passive entrapment gears can sample non-target prey species increasing the potential for post-capture consumption by piscivorous species. Breen and Ruetz (2006) examined the diets of two bowfin (*Amia calva*) and eight yellow bullhead (*Ameiurus natalis*) captured in fyke nets stocked with round goby (*Neogobius melanostomus*), banded killifish (*Fundulus diaphanous*), and bluntnose minnow (*Pimephales notatus*).

The authors reported that a single bowfin consumed 35 percent of the fish stocked in a fyke net, suggesting that piscivory is likely high in entrapment gears. Therefore, the choice of sampling technique has the potential to influence diet composition by either sampling active or sedentary fish or by confounding diet composition by post-capture piscivory.

Although the influence of sampling gear on diet analysis has been recognized for decades (Hayward et al. 1989), certain instances (e.g., target species, habitat) dictate when a particular sampling gear is used. For instance, burbot are cold-water stenotherms that prefer deep habitats (Klein et al. 2015a) and are most often sampled using passive gears such as hoop nets, cod traps, and gill nets (Bernard et al. 1991, Spence 2000). Considering the need to accurately describe the diet of non-native

burbot, we sought to evaluate the influence of passive-entrapment (hoop nets) and active (electrofishing) gears on diet composition of burbot in the Green River. In addition, we provide a short-term description of non-native burbot diet. Although we understand that short-term diet studies do not capture the spatio-temporal variability in diet, we argue that any description of diet of non-native burbot will be useful for directing management actions and future research. For instance, information on diet of non-native burbot is invaluable for understanding if targeted suppression of the species is needed in the Green River.

METHODS

The Green River originates in the Wind River Range of western Wyoming and is a primary tributary of the Colorado River (Fig. 1). The Green River basin covers

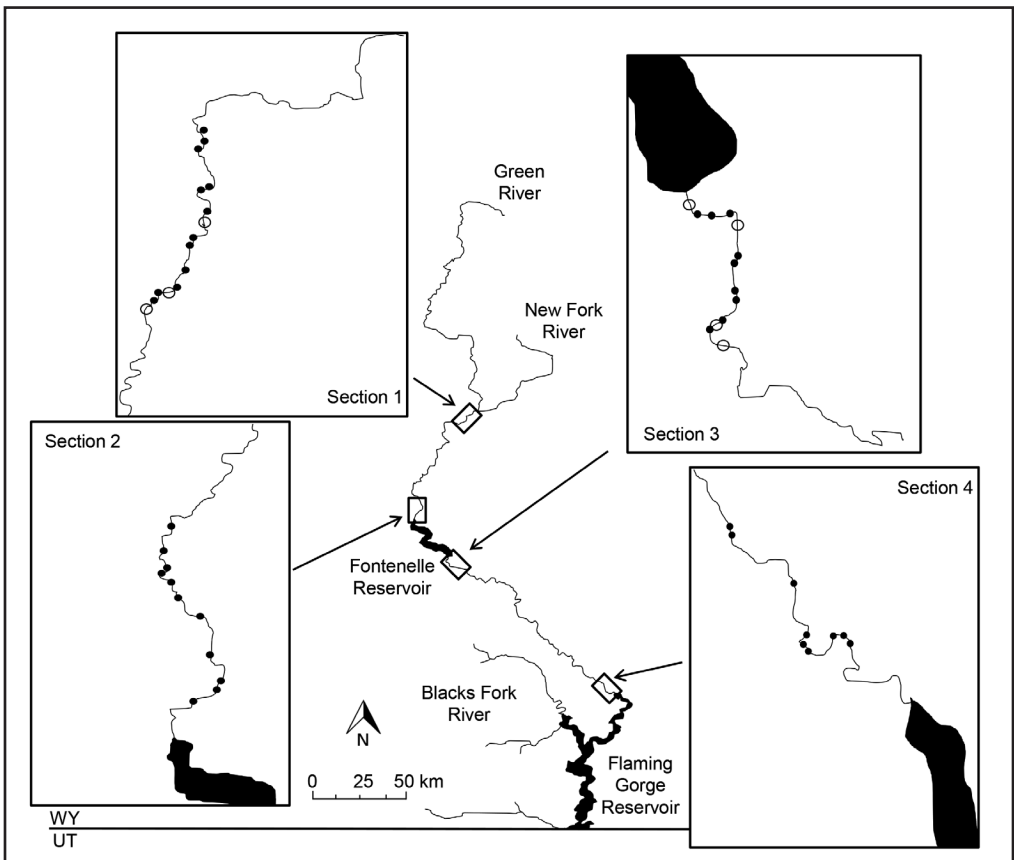


Figure 1. River sections used for Burbot sampling in the Green River, Wyoming during the summer and autumn (2013). Boxes depict each section in detail, with sites sampled in the summer (solid black circles) and autumn (open black circles).

parts of Wyoming, Colorado, and Utah. The headwaters are characterized by high-gradient runs interspersed with pool-riffle habitat (Kurtz 1980). From its headwaters, the Green River flows for approximately 235 km before entering Fontenelle Reservoir. From Fontenelle Reservoir downstream to the confluence of the Big Sandy River, the Green River is characterized by long runs averaging 450 m (Wiley 1974). From the Big Sandy River confluence to Flaming Gorge Reservoir, the Green River is relatively low gradient (Wiley 1974). Sampling was conducted in the Green River, Wyoming, from August through November 2013. The river was divided into four sections to allocate sampling effort (Klein et al. 2015b). Each river section was then divided into 150-m long reaches. Reaches were sampled using night electrofishing, small-mesh hoop nets (6.4-mm bar mesh), and large-mesh hoop nets (19-mm bar mesh). A total of 28 reaches was sampled over a 9-day period such that each reach was sampled three times with each gear. An additional 12 reaches were opportunistically sampled with either night electrofishing, small-mesh hoop nets, or large-mesh hoop nets to obtain additional diet samples.

Small-mesh hoop nets were 3.0 m long, had seven 0.6-m diameter hoops, and constructed of 6.4-mm bar mesh. Large-mesh hoop nets had an overall length of 2.9 m with four 0.91-m diameter hoops and were constructed of 19-mm bar mesh. Cod ends were anchored upstream and nets were positioned parallel to the current. A single net was baited with dead white sucker (*Catostomus commersonii*) (a non-native species common in the system) and fished for approximately 24 hours in a given reach. Bait was placed in a perforated plastic container attached in the cod end of each net. Equal effort was used at each reach and catch was recorded as the number of fish per sampling event.

A float boat equipped with a Smith-Root VVP-15B electrofisher (Smith-Root, Vancouver, Washington) powered by a 5,000 W generator was used for night electrofishing. Power output was

standardized with a frequency of 45Hz and duty cycle of 45 percent at 2,750–3,250 W (Miranda 2009). A 2.4-m long dip net with 6-mm bar knotless mesh was used by a single netter positioned on the bow of the boat. Electrofishing was initiated at the uppermost point of each 150-m reach and preceded downstream until the entire reach had been sampled.

All captured burbot were weighed (nearest 1.0 g) and measured for total length (nearest 1.0 mm). On the final sampling event for each reach, all captured burbot were euthanized with an overdose of MS-222 (tricaine methanesulfonate, Western Chemical, Inc., Ferndale, Washington). The anterior portion of burbot stomachs were removed, preserved in 10 percent formalin, and returned to the University of Idaho for diet analysis.

Stomachs were opened and rinsed to ensure the removal of all contents. Seventy-five stomachs were empty and removed from further diet analysis. Prey items were enumerated and weighed to the nearest 0.01 g by taxonomic category. Non-fish categories included Insecta, (*Orconectes* spp.), Gastropoda, Amphipoda, rocks, and unknown material. Fish categories consisted of longnose dace (*Rhinichthys cataractae*), speckled dace (*R. osculus*), redbside shiner (*Richardsonius balteatus*), utah chub (*Gila atraria*), white sucker × flannelmouth sucker hybrid, mountain whitefish (*Prosopium williamsoni*), rainbow trout, burbot, mottled sculpin (*Cottus bairdii*), unknown catostomid, and unknown salmonid. Prey items identified as fish, but not assigned to taxonomic group were categorized as unidentified fish. Diagnostic structures were used when whole items were unavailable. For example, *Orconectes* spp. prey items were counted using the number of identifiable heads.

Burbot were grouped into 50-mm length bins. Proportions of diet categories by number and weight were calculated for individual burbot and averaged for each 50-mm length group. Diet composition was also categorized as frequency of occurrence, percent by number, and percent by weight

for each gear type (night electrofishing, small-mesh hoop net, and large-mesh hoop net). Frequency of occurrence was calculated as the number of individuals with prey items of a particular category divided by the total number of individuals with stomach contents. Percent by number was calculated as the number of items of each prey type divided by the total number of food items enumerated for each fish and then averaged across individuals with stomach contents. Similarly, percentage by weight was calculated as the average proportional weight of each prey category across individuals with stomach contents. Standard error was calculated for both percent by number and percent by weight for each category.

A multivariate analysis of variance (MANOVA) was used to identify differences in diet composition by gear type (Johnson 1998, Chipps and Garvey 2007). Analysis of variance (ANOVA) was then used to test for differences between gear types for a given diet category (Ott and Longnecker 2010). If differences in count data were observed between gears for a given diet category, a Tukey-pairwise comparison was used to detect differences between gears. All tests were considered significant at $\alpha = 0.05$.

RESULTS

In total, 231 burbot were sampled for diet analysis (Table 1). Night electrofishing sampled 156 burbot, small-mesh hoop nets sampled 68 burbot, and seven burbot were sampled using large-mesh hoop nets. Burbot sampled using night electrofishing

averaged 418 mm (\pm SE; \pm 11 mm) in length; whereas, burbot sampled with hoop nets had a mean length of 334 mm (\pm 12 mm). Burbot sampled using large-mesh hoop nets averaged 340 mm (\pm 40 mm) in total length.

Fish were observed in nearly all burbot stomachs ($n = 211$) and varied from 25–100 percent by number across lengths (Fig. 2). Unidentified fish accounted for the greatest proportion of stomach contents among length bins, except for 200–249 mm. Non-fish contents were observed in all length bins, except for 700–749 mm ($n = 1$). Diversity of prey items was greatest for 300–349 mm and 450–499 mm burbot. Proportions of prey items varied little between percent by number and weight for all burbot length categories. Fish made up 62–100 percent of the diet by number for burbot greater than 300 mm. Fish in the diet of burbot 150–300 mm represented 25–86 percent by number. Of the identified fishes, salmonids were 2–25 percent by weight of the contents for 250–699 mm burbot. Burbot less than 350 mm consumed a higher proportion of non-fish prey items relative to burbot greater than 350 mm. Of these non-fish prey items, insects were 14–67 percent by number for burbot 150–349 mm (Fig. 2). *Orconectes* spp. were observed in stomach contents of 250–699 mm burbot, but did not account for more than 15 percent by number or 11 percent by weight.

Overall diet composition varied by gear. Diversity of ingested prey items was greatest for burbot captured in small-mesh hoop nets (Table 2). White sucker \times flannelmouth

Table 1. Summary statistics for burbot (*Lota lota*) sampled from the Green River, Wyoming in August–November 2013. Burbot were sampled using night electrofishing, small-mesh hoop nets, and large-mesh hoop nets.

Sampling gear	<i>n</i>	Total length (mm)			
		\bar{x}	SE	Minimum	Maximum
Night electrofishing	156	418	11	31	719
Small-mesh hoop net	68	334	12	125	606
Large-mesh hoop net	7	340	40	178	497
All gears	231	391	9	31	719

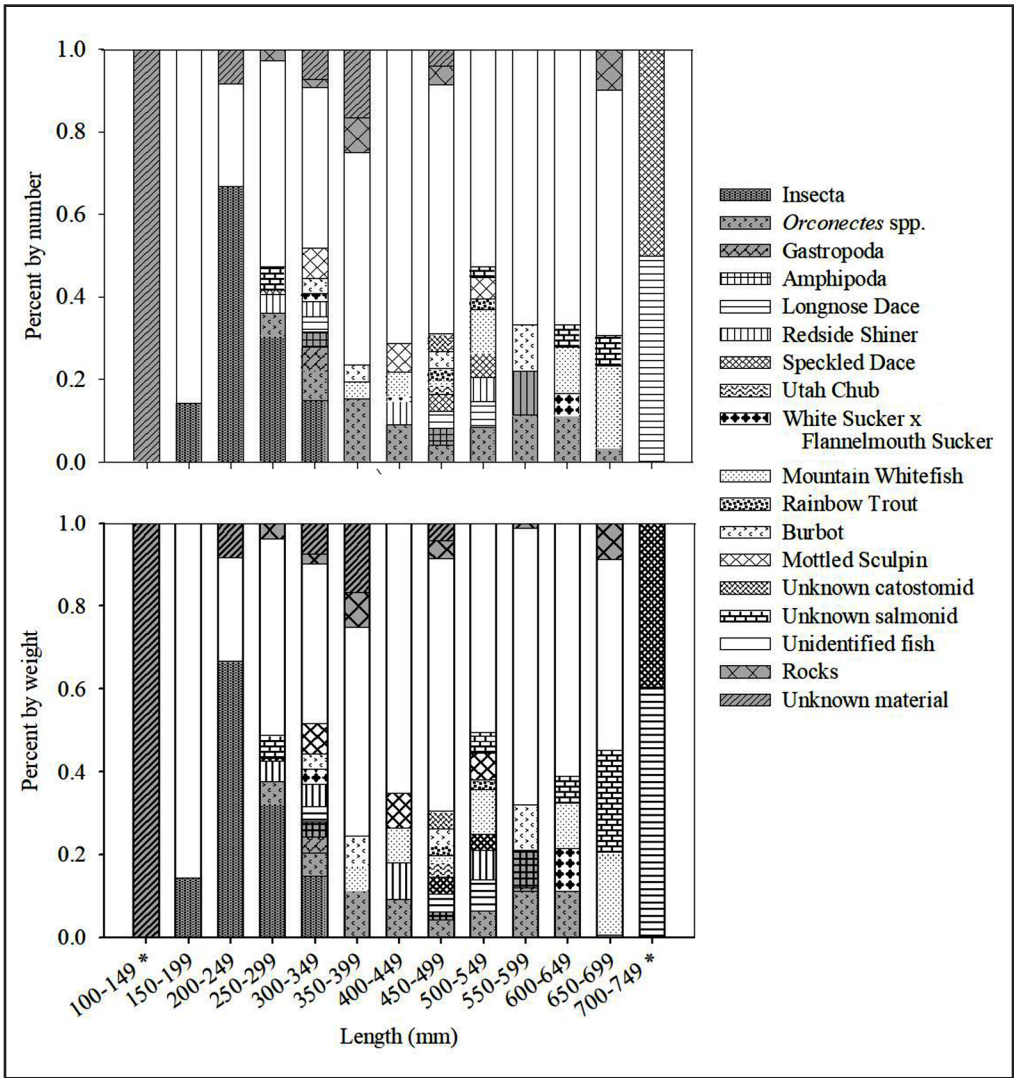


Figure 2. Diet composition of Burbot sampled from the Green River, Wyoming in August–November 2013. Diet composition presented as average percent by number (upper panel) and average percent by weight (lower panel) for Burbot by 50-mm length bin. Asterisks indicate diet samples obtained from a single fish.

sucker, unknown catostomid, burbot, and mottled sculpin were only observed in the diet of burbot captured in small-mesh hoop nets. Utah chub was only observed in stomachs from night electrofishing. Cyprinids represented nearly 10 percent of the diet of burbot caught in small-mesh hoop nets. Invertebrates composed 27 percent by number of stomach content in burbot caught by night electrofishing. The percent by weight of fish in the diet of burbot was similar among gears: 67 percent

for night electrofishing, 84 percent for small-mesh hoop nets, and 87 percent for large-mesh hoop nets (Table 2). Results of the MANOVA revealed a significant difference in diet composition among gear types ($F_{2,153} = 1.72$; $P < 0.02$). The ANOVA identified four diet taxa that were different among gears. The diet of burbot captured with small-mesh hoop nets contained significantly higher numbers of reidside shiner ($F_{2,153} = 3.83$; $P < 0.03$), white sucker × flannelmouth sucker hybrid ($F_{2,153} = 3.53$;

Table 2. Diet composition of burbot (*Lota lota*) sampled from the Green River, Wyoming in August–November 2013. Diet composition is presented as frequency of occurrence (FO), mean percent by number (%N), and mean percent by weight (%W) for night electrofishing, small-mesh hoop net, large-mesh hoop net, and all gears combined. Numbers in parentheses represent one standard error.

Taxon	Night electrofishing			Small mesh hoop net			Large mesh hoop net			All gears		
	FO	% N	% W	FO	% N	% W	FO	% N	% W	FO	% N	% W
Insecta	0.17	17.48 (3.76)	17.48 (3.76)	0.02	1.04 (1.04)	1.64 (1.64)	0.00	0.00	0.00	0.12	11.86 (2.58)	12.04 (2.60)
Orconectes spp.	0.09	6.89 (2.39)	6.30 (2.33)	0.10	7.29 (3.33)	5.60 (3.00)	0.00	0.00	0.00	0.09	6.79 (1.88)	5.88 (1.79)
Gastropoda	0.01	0.03 (0.03)	0.07 (0.07)	0.04	3.13 (2.31)	2.10 (2.08)	0.00	0.00	0.00	0.02	0.98 (0.71)	0.69 (0.64)
Amphipoda	0.03	2.82 (1.61)	2.25 (1.33)	0.00	0.00	0.00	0.00	0.00	0.00	0.02	1.86 (1.07)	1.49 (0.88)
Longnose Dace	0.04	2.62 (1.45)	3.00 (1.55)	0.02	2.08 (2.08)	2.08 (2.08)	0.00	0.00	0.00	0.03	2.37 (1.15)	2.62 (1.20)
Speckled Dace	0.01	2.30 (1.26)	1.99 (1.14)	0.13	0.94 (0.66)	0.45 (0.32)	0.00	0.00	0.00	0.04	1.81 (0.86)	1.45 (0.76)
Redside Shiner	0.04	0.32 (0.32)	0.53 (0.53)	0.04	6.59 (2.79)	8.78 (3.78)	0.00	0.00	0.00	0.04	2.24 (0.91)	3.05 (1.24)
Utah Chub	0.01	0.49 (0.49)	0.79 (0.79)	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.32 (0.32)	0.52 (0.52)
White Sucker x Flannelmouth Sucker	0.00	0.00	0.00	0.06	2.31 (1.47)	4.03 (2.80)	0.00	0.00	0.00	0.02	0.71 (0.46)	1.24 (0.87)
Mountain Whitefish	0.05	3.72 (1.75)	3.93 (1.80)	0.04	2.43 (1.72)	3.05 (2.20)	0.20	10.0 (10.00)	14.93 (14.93)	0.05	3.53 (1.30)	4.01 (1.44)
Rainbow Trout	0.01	0.65 (0.65)	0.57 (0.57)	0.02	1.04 (1.04)	0.93 (0.93)	0.00	0.00	0.00	0.01	0.75 (0.53)	0.66 (0.47)
Burbot	0.00	0.00	0.00	0.08	7.29 (3.64)	7.98 (3.87)	0.00	0.00	0.00	0.03	2.24 (1.15)	2.46 (1.22)
Mottled Sculpin	0.00	0.00	0.00	0.10	7.87 (3.74)	8.20 (3.91)	0.00	0.00	0.00	0.03	2.42 (1.18)	2.52 (1.23)
Unknown salmonid	0.04	1.33 (0.72)	2.50 (1.24)	0.04	3.13 (2.31)	3.23 (2.36)	0.00	0.00	0.00	0.04	1.84 (0.85)	2.64 (1.09)
Unknown catostomid	0.00	0.00	0.00	0.02	2.08 (2.08)	2.08 (2.08)	0.00	0.00	0.00	0.01	0.64 (0.64)	0.64 (0.64)
Unidentified fish	0.60	54.51 (4.67)	53.62 (4.68)	0.56	46.53 (6.56)	43.60 (6.94)	1.00	80.00 (12.25)	71.88 (17.27)	0.60	52.87 (3.73)	51.12 (3.81)
Rocks	0.06	2.97 (1.52)	3.10 (1.54)	0.00	0.00	0.00	0.20	10.00 (10.00)	13.19 (13.19)	0.04	2.28 (1.05)	2.47 (1.10)
Unknown material	0.04	3.88 (1.91)	3.88 (1.91)	0.06	6.25 (3.53)	6.25 (3.53)	0.00	0.00	0.00	0.04	4.49 (1.66)	4.49 (1.66)

$P < 0.04$), burbot ($F_{2,153} = 4.82$; $P < 0.01$), and mottled sculpin ($F_{2,153} = 5.48$; $P < 0.006$) in their stomachs than other gears.

DISCUSSION

Our results suggest non-native burbot from the Green River have similar diets to burbot found in their native distribution. In the current study, 25-100 percent of the stomach content (by weight) for non-native burbot contained fish. Schram et al. (2006) reported that fishes constituted greater than 90 percent by weight of the diet of burbot greater than 400 mm in the Apostle Islands of Lake Superior, Wisconsin. Similarly, Fratt et al. (1997) described the diet of burbot in Green Bay and western Lake Michigan and reported that 94 percent by volume was fishes. Additionally, the consumption of fish by burbot is often reported as being positively related to fish length. Amundsen et al. (2003) observed that percent by number of fish prey items increased from 30 percent in 100–200 mm burbot to nearly 100 percent for burbot greater than 400 mm in the subarctic Pasvik watercourse of northern Norway and Russia. Similarly, Tolonen et al. (1999) concluded that the probability of burbot consuming fish was positively correlated with length in Kilipisjärvi, a lake in northern Finland. In the current study, an average of 56 percent (by weight) of the diets of burbot less than 300 mm contained fish; whereas, diets of fish greater than 300 mm contained an average of 82 percent fish. The observed differences between the diets of small and large non-native burbot is likely related to ontogenetic diet shifts associated with behavior and gape limitation. Small burbot (<300 mm) are likely gape limited as evidenced by Damsgard's (1995) commonly used (Stockwell et al. 2010, Harrison et al. 2013) prey vulnerability model (maximum prey length (cm) = $[0.535 \times \text{predator length (cm)}] - 0.487$). Based on Damsgard's model, a 300 mm burbot could only ingest a 155 mm prey item. Although small burbot could theoretically consume fish roughly half their body size, prey items may not be available for some burbot due to a lack of

spatial overlap between predator and prey. Burbot occupy deep habitats with rocky substrate (Dixon and Vokoun 2009, Klein et al. 2015a); whereas, many juvenile stream-dwelling fishes occupy shallow habitats to avoid predation (Schlosser 1987, Delbert-Lobb and Orth 1990). Harrison et al. (2013) suggested that burbot move into the littoral zone during the crepuscular period to forage. However, the authors noted a size-structured pattern in depth distribution; whereby, small burbot did not exhibit pronounced diel movements compared to large burbot. The authors suggested that small burbot avoid foraging in littoral zones to reduce interspecific and intraspecific predation. As such, small burbot in the Green River may be constrained to a diet composed primarily of invertebrates until they are no longer gape limited or the threat of size-dependent predation is negligible. Regardless of the exact mechanism resulting in the diet of non-native burbot, our results suggest burbot may negatively influence the trophic dynamics of the Green River.

Non-native species can negatively influence recipient ecosystems through various mechanisms including predation, competition, and hybridization (Vitule et al. 2009). For example, Ruzycski et al. (2003) suggested non-native lake trout negatively influenced the persistence of Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) in Yellowstone Lake, Wyoming, by consuming approximately 14 percent of the vulnerable cutthroat trout population in a single year. Similarly, Saunders et al. (2014) described the diet of burbot in FGR and concluded that *Orconectes* spp. occurred in 78-85 percent of the stomachs. The authors suggested non-native burbot could negatively influence smallmouth bass populations in FGR through competition for *Orconectes* spp. Although our results indicate that non-native burbot do not consume high proportions of *Orconectes* spp., the abundance of fish in burbot diet suggest the species could alter the trophic dynamics of the Green River through direct predation and competition. Klobucar et al. (2016) concluded that burbot in FGR

consume an estimated 45,400 kg of fish annually assuming a population size of 80,000 burbot. Although a population estimate of burbot is not available for the Green River, the results of Klobucar et al. (2016) suggest burbot in the Green River could negatively influence fish populations through direct predation. Furthermore, Klobucar et al. (2016) estimated that burbot diets in FGR contained an average of 32 percent (by weight) fish; whereas, our results indicate that fish constituted an average of 75 percent (by weight) of burbot diet in the Green River. As such, burbot may have a higher per capita rate of predation in the Green River compared to predation rates in FGR. In addition to direct predation, non-native burbot may negatively influence fish populations and species assemblages through indirect effects. Knudsen et al. (2010) reported that burbot negatively influenced Arctic charr (*Salvelinus alpinus*) populations through direct predation and predation-induced shifts in resource use (i.e., habitat, diet). Although additional research is likely needed to understand the influence of non-native burbot on the food web of the Green River, the presence of an apex piscivore in the system is a concern for the conservation and management of native and sport fishes.

Although we describe diet composition of non-native burbot, inferences should be made with caution. Burbot were sampled from August to November and the diet data presented here likely do not reflect seasonal variations in diet. Rudstam et al. (1995) concluded that the diet of burbot in Green Bay, Lake Michigan, was dominated by alewives (*Alosa pseudoharengus*) in winter and spring, and shifted to rainbow smelt (*Osmerus mordax*) in summer and autumn. Similarly, Chisholm et al. (1989) reported that largescale sucker (*Catostomus macrocheilus*) were most important to burbot in Libby Reservoir, Montana, in autumn and winter; whereas, yellow perch dominated burbot diets in spring. Burbot in FGR primarily consumed northern crayfish in the autumn and increase piscivory in the winter (Klobucar et al. 2016). The authors

suggested that reduced activity due to colder water temperatures in the winter subjected resident fishes to increased levels of predation by burbot. If burbot in the Green River exhibit similar seasonal diet shifts, piscivory may increase in the winter further threatening native and sport fish species.

Our results suggest diet composition is likely influenced by gear type. Specifically, selectivity for small-bodied fishes in entrapment gears could bias diet analysis due to post-capture piscivory by target species. Merriner (1975) used multiple sampling techniques (i.e., gill nets, haul seines, trawls, and pound nets) to characterize the diet of weakfish (*Cynoscion regalis*) in Pamlico Sound and waters near Morehead City, North Carolina. The author reported contrasting occurrences of diet items in relation to gear type and only observed thread herring (*Opisthonema oglinum*) in stomachs of weakfish captured with pound nets. Interestingly, diet of burbot captured by small-mesh hoop nets in the current study contained a majority of small-bodied fishes such as redbreasted shiners and mottled sculpin. Alternatively, larger-bodied fish such as mountain whitefish were observed in the diet of burbot captured by large-mesh hoop nets. The fact that burbot consumed higher proportions of small-bodied fishes in small-mesh hoop nets may be the result of the size selectivity of small- and large-mesh hoop nets. For example, 1,258 redbreasted shiners were captured in small-mesh hoop nets over the course of the study; whereas, no redbreasted shiners were caught in large-mesh hoop nets. Bowen (1996) cautioned that large fish captured in entrapment gears may feed on prey types disproportional to natural occurrences or consume prey not normally in the diet. Duffy et al. (2011) quantified the number of juvenile salmonids (*Oncorhynchus* spp.) that had been consumed by piscivores in downstream migrant traps in Prairie Creek, California. Adult Coastal cutthroat trout (*O. clarkii clarkii*) captured in live boxes consumed five to six times as many juvenile salmonids as those sampled using other techniques. Thus, greater occurrence of

redside shiner, white sucker × flannelmouth sucker, burbot, and mottled sculpin in diets of burbot captured in small-mesh hoop nets may have been an artifact of opportunistic feeding behavior associated with sampling gear. Based on our data, a single sampling technique would have yielded a different diet composition for burbot in the Green River. White sucker × flannelmouth sucker, unknown catostomid, burbot, and mottled sculpin were only observed in the diet of burbot captured in small-mesh hoop nets, and utah chub was only observed in stomach contents of burbot captured by night electrofishing. Burbot are often sampled using passive entrapment gears (e.g., hoop nets, cod traps) due to the habitat use (e.g., deep water) of the species. As such, diet collected from burbot sampled using entrapment gears may not adequately reflect what burbot would consume under normal conditions.

Our results suggest the diet of non-native burbot was similar to the diet of burbot within their native distribution. Non-native burbot are a functional apex piscivore and have the potential to influence trophic dynamics in the Green River. As such, managers of the Green River may want to focus efforts on understanding how an apex piscivore may influence species interactions in the system. As additional research will likely require further diet analysis, managers should be cognizant of the potential biases associated with using entrapment gears. Although entrapment gears are commonly used to sample burbot, alternative sampling techniques should be used for diet studies focused on the species. Gill nets or similar passive sampling techniques (e.g., trammel nets) are effective for sampling benthic species (e.g., burbot) in lentic systems (Beauchamp et al. 2009). However, gill nets are not effective in high-current velocities typical of many small, non-wadeable rivers; therefore, active techniques such as electrofishing may be the best alternative (Klein et al. 2015a). Collectively, our results highlight the importance of gear selection for diet studies while providing

baseline data on diet of non-native burbot in the Green River.

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SEASONAL MOVEMENTS AND ANGLER EXPLOITATION OF AN ADFLUVIAL WALLEYE POPULATION IN THE MISSOURI RIVER, MONTANA

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ABSTRACT

An unauthorized introduction of walleye in Canyon Ferry Reservoir (CFR) challenges fisheries managers as the population pioneers new habitat upstream in the Missouri River. Montana Fish, Wildlife & Parks (MFWP) confirmed walleye in the river upstream of CFR in 2007. Angler tag returns suggested walleye were abundant in the river. It was unknown if these were adfluvial walleye originating in CFR, or a discrete fluvial population. Understanding seasonal movements and ecology of walleye in the river will allow managers to effectively monitor and manage these fish. The objectives of this study were to monitor radio and anchor-tagged walleye movements to quantify movements and determine if two distinct populations exist, establish spatial and temporal densities within the river, and calculate exploitation rates of walleye by anglers in the river. Overall, most radio-tagged walleye relocated in the river, 88 percent river and 100 percent CFR implanted fish, exhibited seasonal adfluvial movements suggesting, similar to other studies, that two distinct walleye populations are not present. Adfluvial walleye were concentrated in the lower 6.4 km of the river during the annual ascending hydrograph, maintained maximum upstream extent throughout the summer, and out-migrated into CFR by late fall. Radio-tagged walleye only used the river between 17 March and 27 November. We estimated walleye exploitation rates were 21 percent for CFR-tagged walleye and 13 percent for river-tagged walleye. Exploitation rates for anchor-tagged walleye in this study reflect CFR exploitation rates (18% from 2010-2014) just prior to this study. These results suggest that adfluvial Missouri River walleye are seasonally abundant and exploited at similar rates as lacustrine CFR walleye, but no changes to current river walleye management strategies are recommended. In addition, routine walleye population monitoring surveys and a creel survey are warranted as the adfluvial CFR walleye population continues to adapt, expand, and establish.

Key Words: walleye, adfluvial, Missouri River, exploitation, radio telemetry, radio tag, anchor tag, reservoir fisheries Montana

INTRODUCTION

In 1989, a novel population of walleye (*Sander vitreus*) was discovered in Canyon Ferry Reservoir (CFR) in central Montana (MFWP 1991). Based on back-calculated length at age, walleye were likely introduced into CFR in the early 1980's (Yerk 2000). Given abundant spawning habitat (McMahon 1992), this population was expected to prosper. Concern over this new population, and its effects on one of the most popular recreational fisheries in Montana (Colby and Hunter 1989) prompted

an investigation of the basic biology of the species in the upper Missouri River system to understand the potential trophic level and community changes that could occur as the fish community approached an equilibrium. In addition, an upstream range extension into the Missouri River was possible since reservoir walleye populations routinely migrate to tributary river spawning locations, typically in early spring (Forney 1963, Scott and Crossman 1973, Olsen et. al 1978), and a sizeable proportion may persist in deep pools throughout the river during

the summer and out-migrate to the reservoir each fall (McMillan 1984).

Indeed, in 2003, Montana Fish, Wildlife & Parks (MFWP) confirmed the use of the Missouri River by walleye, when an angler harvested a 381 mm walleye in the river 3.9 km upstream from CFR. In 2007 MFWP captured a walleye in the lower 3.9 river km (rkm) during a semi-annual spring survey. Anglers reported catching 32 additional walleye, anchor-tagged in CFR, from 2004 through 2015 within the river, but no additional walleye were sampled in the river by MFWP biologists during that period (MFWP, unpublished data).

Canyon Ferry Reservoir is one of the most popular recreational fisheries in Montana. Historically nearly 100,000 anglers annually targeted yellow perch (*Perca flavescens*) and rainbow trout (*Oncorhynchus mykiss*). However, with the introduction of walleye, the management goal shifted in 2000 to include walleye as part of quality multi-species fishery (MFWP 2010). The management goals for the river section between Toston and CFR have been to manage the walleye population to minimize predation impacts on existing rainbow trout, brown trout (*Salmo trutta*), and forage species and to provide a low-level sport fishery (MFWP 2010). Angler caught Walleye tag returns steadily increased from the river section from 2007-2015 and raised questions about whether walleye density was increasing in the river or if greater catch was a function of more anglers using the river. Furthermore, increasing walleye use of the river has implications for the management and monitoring of CFR.

The objectives of this study were to: 1) describe walleye movements between CFR and Missouri River, 2) determine if two distinct walleye populations existed in the area (i.e., fluvial or adfluvial river walleye), 3) determine the seasonal density of walleye in the Missouri River, and 4) determine angler exploitation rates of walleye in the Missouri River. Results from this study could be used to evaluate management strategies for the Missouri River to achieve management goals for CFR (MFWP 2010).

STUDY AREA

Canyon Ferry is a 35,000-surface acre reservoir on the mainstem Missouri River, in central Montana. Canyon Ferry Dam construction was completed in 1954 and the reservoir is operated by the US Bureau of Reclamation (BOR) as a flood storage facility (Pick-Sloan Flood Control Act 1944). In order of intended purpose, CFR is managed by the BOR for flood control, hydroelectric power generation, irrigation, and recreation. Reservoir elevations are typically held stable through 1 March where the target elevation is 1154.3 (m) to ensure there is storage space suitable to buffer spring runoff. The recreation pool elevation is 1157.3 (m) and the target date is 1 July. The average annual reservoir elevation fluctuation from 2000-2015 was 4.6 m (range 3.4-6.4 m).

Yellow perch abundance in CFR is primarily limited by walleye predation in conjunction with limited spawning habitat (i.e., aquatic vegetation) due to seasonal fluctuations in reservoir elevation from reservoir operations (MFWP 2010). Yellow perch in CFR are currently protected by the most conservative species specific harvest regulation in Montana (10 daily and in possession) (MFWP 2010). Rainbow trout are managed by stocking hatchery raised fish, and size at stocking has increased (i.e., CFR was historically planted with fingerlings) to catchable sized fish (greater than 203 mm) over the years to maximize survival from walleye predation. Canyon Ferry Reservoir is one of the top three most fished waters in Montana and creel surveys found that anglers increasingly preferred pursuing walleye (Table 1).

The Missouri River section of the study area was 37.3 rkm from the inlet of CFR upstream to Toston Dam (Fig. 1). Water flow in the upper Missouri River basin are controlled primarily by Hebgen Dam on the Madison River and two minor storage reservoirs on the Jefferson (Clark Canyon Reservoir) and Ruby (Ruby Reservoir) rivers. Mean annual discharge at the U.S. Geological Survey (USGS) Toston gage,

Table 1. Biennial statewide pressure survey rankings (Rank) by study area section and percentages of CFR creel surveyed anglers targeting Walleye (%), 1991-2015.

Year	Study Area Section	1991		1993		1995		1997		1999		2001		2003	
		Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%
	Canyon Ferry Res.	6	--	1	--	1	--	2	3.6	1	16.8	3	33	3	41.1
	Missouri River	61	n/a	105	n/a	102	n/a	147	n/a	133	n/a	81	n/a	79	n/a

Year	2005		2007		2009		2011		2013		2015		Mean		
	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	Rank	%	
	Canyon Ferry Res.	3	(68)	3	(49)	1	(34)	3	24	5	59.8	5	32	3	40
	Missouri River	158	n/a	96	n/a	92	n/a	106	n/a	119	n/a	69	n/a	104	n/a

just downstream from Toston Dam, from 1989-2015 was 127 m³/s and the mean annual water temp was 9°C. The river has been managed by MFWP exclusively as a wild trout fishery (i.e., reproduction is natural except periodic brown trout plants through 1998). Walleye were included as a management priority in the river in 2010 and identified as a “low-level” angling opportunity (MFWP 2010). This section of the Missouri River historically has 10 times less annual angling pressure as CFR and ranks, on average, as the 104th fishery in the Montana since 1991 (Table 1).

METHODS AND MATERIALS

To evaluate fish behavior, location, and movement from the reservoir and river we used both active and passive methods. We used radio telemetry to track movements of fish year-round, but sample size was limited by funding. To increase the sample size, and to be able to compare angler return rates for exploitation, we tagged additional walleye to confirm radio telemetry results during this study. We adjusted for tag loss by utilizing tag loss rates established during a 2007-08 CFR walleye tagging evaluation (MFWP, unpublished data). We compared tag reporting rates established during anchor tagging efforts on CFR from 2010-2015 (MFWP 2016).

In the reservoir, we captured fish at the same locations in April and May in 2015 and April in 2016 using non-baited “Merwin” floating traps with shore leads similar to those described by Hamilton et. al (1970). Each trap net measured 2.5 m tall, 2.5 m wide, and 2.5 m long “spiller” and “pot” capture chambers with 3 m tall leads varying in length from 14 m to 38 m (adjusted throughout annual surveys for reservoir elevation changes) and all netting panels were 25 mm mesh

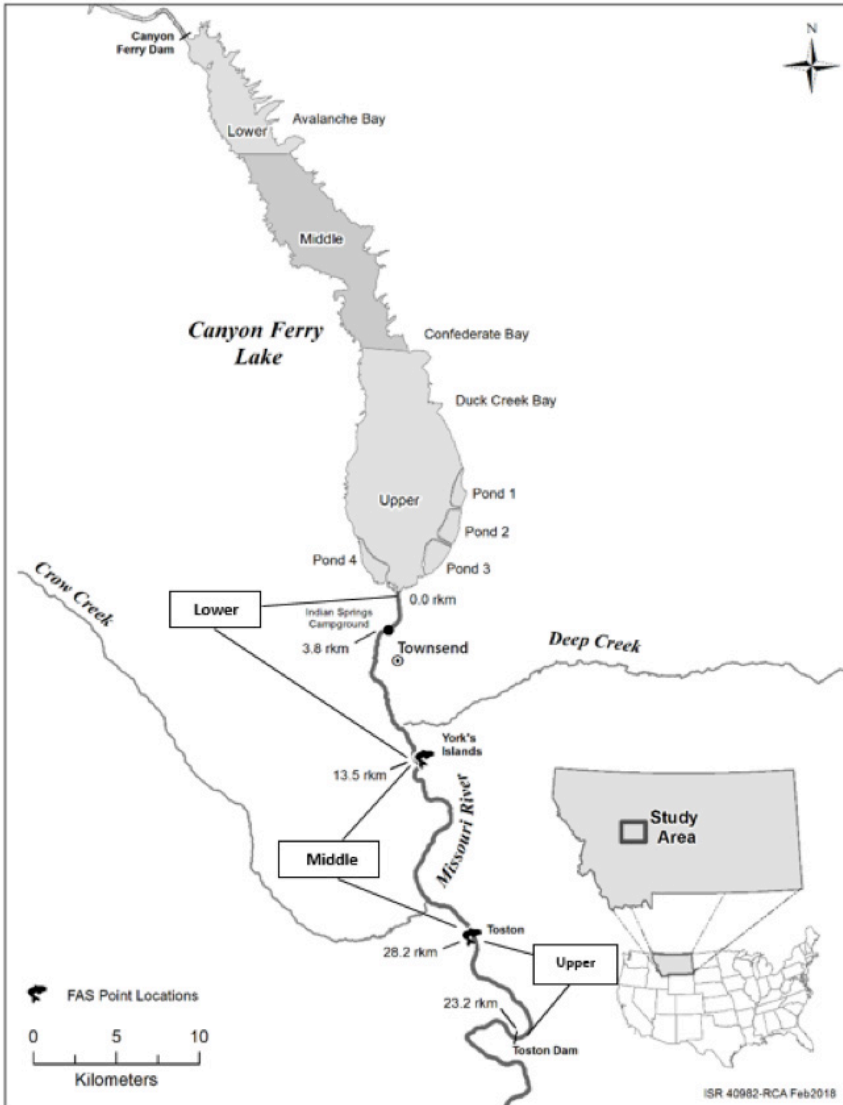


Figure 1. Study area map of the Upper Missouri River from Canyon Ferry Reservoir to Toston Dam.

(bar measure). We set traps on the south end of CFR near the Silos recreation area (west) and the Dust Abatement Pond #1 (east; Fig. 1). We fished Merwin traps 24 hrs/day, for 116 days at both trapping locations during both years. Trapping effort between the two CFR sites was 41 percent on the east and 58 percent on the west, with differential sampling between the two caused by high wind fouling trap sets on the east shore, a common occurrence during spring sampling.

Walleye were captured in the Missouri

river upstream of CFR from late March to early June in 2015, 2016 and 2017 (Table 2) by electrofishing the river margins using a 6 m aluminum jet boat mounted electrofishing system with two boom mounted anodes. AC power from a 5,000-watt generator was routed through a *Coffelt VVP-15* rectifying unit to produce approximately 200 V and 7.25 Amps of smooth DC.

Once captured, all Fish were weighed to the nearest gram (g), measured for total length (mm), and inspected for sex using

Table 2. Shocking effort (minutes shocked (min)) and total number of captured walleye, rainbow trout, brown trout, mountain whitefish (*Prosopium williamsoni*), common carp (*Cyprinus carpio*), and burbot (*Lota lota*) in the Missouri River, by river reach (rkm), during spring-time surveys.

Date	Shocking Time (min)	River Reach (rkm)	Walleye ¹	Rainbow Trout	Brown Trout	No. of Fish Captured			
						Suckers ²	Mountain Whitefish	Common Carp	Burbot
3/20/15	136	13.5-0.08	--	99	31	215	55	--	--
3/27/15	121	37.0-17.9	--	99	28	295	135	--	--
4/6/15	21	4.0-0.8	--	12	6	25	5	--	--
4/14/15	97	35.4-24.8	--	35	15	50	75	9	--
4/20/15	109	24.1-16.3	--	60	16	35	49	35	--
4/27/15	66	4.0-0.8	11	46	7	46	5	43	2
4/30/15	153	13.5-0.8	11	44	21	213	42	183	--
5/1/15	101	17.7-13.2	5	81	16	165	98	28	--
5/4/15	58	37.0-28.2	5	31	25	115	32	23	--
5/7/15	114	6.4-1.5	31	30	26	222	10	99	--
5/20/15	69	13.5-6.4	10	21	22	150	40	59	--
5/29/15	29	13.8-10.5	5	8	8	100	25	50	--
4/6/16	46	3.9-0.8	10	29	3	28	5	30	--
4/19/16	42	3.9-0.8	26	10	2	40	--	50	--
4/26/16	136	13.5-0.8	27	42	8	147	18	92	--
5/3/16	60	3.9-0.8	20	52	7	115	8	150	3
5/17/16	47	3.9-0.8	18	29	3	62	--	53	3
5/25/16	114	13.5-0.8	16	18	34	190	25	105	--
6/2/16	81	6.4-0.8	90	13	10	124	5	171	4
4/11/17	61	4.2-0.8	39	39	3	60	6	32	--
4/20/17	68	13.5-6.4	7	35	5	83	25	38	--
4/24/17	64	6.4-0.8	67	16	13	50	1	69	--
4/25/17	32	37.0-34.4	--	19	1	133	8	--	--
5/1/17	73	6.4-0.8	40	11	1	100	2	64	--
5/8/17	74	6.4-0.8	42	31	5	184	1	147	1
5/15/17	35	3.9-1.5	7	10	7	50	1	22	--
6/5/17	51	3.4-1.8	10	2	14	65	--	82	--
Total	2058		497	922	337	3062	676	1634	13

¹Includes recaptured Walleye

²Combined count for White Suckers and Longnose suckers

methods described by Beard et. al (1997). We tagged all walleye with Floy brand FD-94 T-bar anchor tags on the left front spinous dorsal fin (Grisak et. al 2012). A subset of walleye greater than 406 mm were surgically implanted with Lotek model SR-11-25 and MCFT-3FM transmitters (in 2015) or MCFT-3FM transmitters (in 2016) using the external antennae method (Bunt and Cooke 2001). These transmitters had 876 and 584-day life expectancies respectively.

We actively relocated fish by using truck, boat, and airplane and maintained a stationary data logging receiver located near the mouth of the river (reservoir/river interface) to determine movement to and from CFR (Fig. 1). A Lotek model SRX_800 BCV4.1 receiver was used for mobile tracking. We actively searched for radio-tagged walleye, throughout the entire river section and CFR, primarily focused on the shallow (depths < 10 m) upper sub-section and shallow shoreline habitat throughout the middle and lower reservoir sub-sections, approximately weekly from Spring to Fall (truck or boat) and monthly (truck or airplane) during the winter. A Lotek model SRX_400 W32CT receiver was used as the stationary data logging receiver annually from Spring to early Winter. We removed the stationary receiver in the winter to avoid significant annual river ice jams.

We divided the reservoir into three historically standardized fisheries survey sections (lower, middle, and upper) (MFWP 2016) and locations of radio-tagged and angler reported or MFWP surveyed anchor-tagged fish were recorded according to these sections (Fig.1).

We classified the river in three sub-sections (lower, middle and upper), based on boat launch access, that measured 13.5 km, 14.6 km, and 9.2 km, respectively (Fig. 1) and a total of 2,015 minutes of shock time was expended. Sample time by section was 72 percent lower, 16 percent middle, 10 percent upper. Differential sampling by section was caused by fish density as we determined that walleye densities were concentrated downstream of rkm 6.4 during annual sampling timeframes (Table 2). We

recorded locations of telemetered fish to the nearest 0.2 rkm and angler reported or MFWP captured anchor-tagged fish were recorded to the nearest 0.2 rkm, landmark or river sub-section (Fig. 1). We monitored mean daily river discharge using the USGS gaging station on the Missouri River at Toston, MT (USGS gage 06054500) during this study.

We hypothesized that fish in the reservoir and river would be discrete localized populations. Radio-tagged fish movement data was analyzed using Chi square goodness of fit tests. We used two sample ANOVA to determine if walleye movements into the river were significantly different between tag type, section implanted, and sex. We used anchor-tagged walleye to verify seasonal radio telemetry movements and evaluate whether exploitation rates from angler captured anchor-tagged fish were similar to rates established in CFR just prior to this study. We related tagged walleye river movements and river discharge, using a correlation coefficient, to determine how annual discharge influenced walleye movement. The significance level for all tests was $\alpha=0.05$.

RESULTS

Fish Movement

Reservoir tagged walleye – In CFR we implanted radio transmitters in six male and three female walleye. Lengths averaged 466 mm (range 409-533 mm) and weights averaged 945 g (range 544-1588 g). We anchor-tagged 175 walleye. Walleye lengths averaged 356 mm (range 254-818 mm) and weights averaged 457 g (range 95-5987 g) and included 95 males, 16 females and 64 unidentified.

All reservoir implanted walleye were relocated in 2015 and 2016, 30 percent were relocated in 2017, and each fish was relocated an average of six times (range 2-11). Relocations in the river occurred in 2015 from April 16 to November 19, in 2016 from March 17 to November 27, and in 2017 from May 22 to July 11. Overall, 39 percent

($n=20$) of reservoir radio-tagged walleye observations were made in the river section, exclusively within the lower river section (range 1.1-12.6 km), and 61 percent ($n=31$) were within the reservoir. One female was relocated at rkm 12.6 and one male was relocated at rkm 3.9, which represented the upstream extent of CFR tagged walleye by sex. Ninety percent of walleye relocation were in the upper reservoir ($n=28$), with 10% of relocations within the middle reservoir ($n=3$), and no relocations in the lower reservoir.

Anchor-tagged walleye in 2015 were reported by anglers within the river between 28 April and 14 September and the reservoir between July 10 and 15. In 2016, anchor-tagged walleye were only reported by anglers within the reservoir from 9 April to 26 September. Anchor-tagged walleye in 2017 were reported by anglers within the river on 24 April and in the reservoir between 29 March and 17 June.

River tagged walleye – In the Missouri river upstream from CFR, we implanted radio transmitters in 8 male and 10 female walleye with an average length of 513 mm (range 419-724 mm) and an average weight of 1389 g (range 526-3856 g). We anchor-tagged 457 walleye including 266 males, 46 females and 109 unidentified sex. Missouri River anchor-tagged walleye lengths averaged 399 mm (range 178-724 mm) and weights averaged 629 g (range 45-3856 g).

Ninety-two percent of fish radio-tagged in the river were relocated in 2015, 88 percent in 2016, and 42 percent in 2017. Mean relocations per fish was 12 (range 3-37). Radio-tagged walleye were relocated in the river in 2015 from 27 April to 24 October, in 2016 from 6 April to 5 October, and in 2017 from 11 April to 13 August. We relocated walleye throughout the entire river (range 0.0-37.3 rkm). Distribution in the reservoir was likely under represented due to deep water detection limitations throughout middle and lower reservoir sub-sections. We located a single female radio-tagged walleye approximately 24.1 linear km from the river inlet (within the lower reservoir section),

and a male was located approximately 16.1 linear km from the inlet (within the middle reservoir section).

In 2015 anglers caught river anchor-tagged fish within the river between 15 July and 12 October and within the reservoir on 24 August in 2015. Walleye anchor-tagged in the river in 2016 were caught by anglers within the river from 3 May to 1 October in 2016 and on 12 July in 2017. In 2016, river anchor-tagged walleye were caught by anglers in the river from 15 May to 19 September in 2016 and 10 May to 20 August in 2017. River anchor-tagged walleye from 2017 were caught by anglers within the river between 1 May and 7 September and the reservoir between 5 May and 25 July.

Population Definition

Radio-tagged walleye movement was not localized to CFR or the river ($\chi^2=0.62$, $df=3$, $P=0.43$) as 88 percent of river and 57 percent of CFR implanted fish moved into an adjacent study section and 96% of walleye relocated in the river exhibited seasonal adfluvial movements. Angler caught anchor-tagged walleye were localized to their section ($\chi^2=30.11$, $df=3$, $P<0.01$), and relocation sites were similar to the seasonal locations displayed by radio-tagged walleye in the river.

Average upstream movement in the river was significantly different between reservoir and river radio-tagged fish ($F=1.68$; $df=48$; $P<0.01$). Both sexes from each section migrated into the river similarly. No significant difference in upstream river movement was observed between males and females implanted within the same section from either the reservoir ($F=1.77$; $df=13$; $P=0.14$) or river ($F=1.69$; $df=32$; $P=0.18$).

Mean upstream migrations of radio-tagged walleye from each section into the river were significantly different ($F=1.68$; $df=37$; $P<0.01$). Overall, radio-tagged river walleye moved further upstream (mean 17.1 rkm, SE: 2.1) than radio-tagged reservoir tagged walleye (2.4 rkm, SE: 0.9) within the river. Mean upstream capture locations for anchor-tagged walleye from each section

into the river were not significantly different ($F=1.70$; $df=27$; $P=0.13$). Overall, walleye anchor-tagged in the reservoir were captured further upstream (mean 15.4 rkm, SE: 11.0) than walleye anchor-tagged in the river (8.9 rkm, SE: 1.6).

Radio-tagged male walleye were significantly longer than anchor-tagged male walleye and lengths in the reservoir ($F=1.66$; $df=95$; $P<0.01$) and river ($F=1.65$; $df=287$; $P=0.01$). However, radio-tagged male walleye lengths were not significantly different between the river and reservoir ($F=1.81$; $df=10$; $P=0.17$), but anchor-tagged male walleye lengths were significantly different between the river and reservoir ($F=1.65$; $df=372$; $P<0.01$) as larger fish were sampled and tagged in the river (average 405 mm, SE: 4.5) than in the reservoir (average 358 mm, SE: 4.5).

Female walleye lengths were not significantly different between tag types in the reservoir ($F=1.73$; $df=17$; $P=0.09$) or river ($F=1.68$; $df=44$; $P=0.28$). Radio-tagged female walleye lengths were not significantly different between sections ($F=1.79$; $df=11$; $P=0.65$) but walleye anchor-tagged in the river were significantly longer (average 556 mm, SE: 13.4) than those tagged in CFR (average 469 mm, SE: 46.8).

Seasonal use by tagged fish

Overall, 96 percent of river walleye captured for this study were found in the lower river sub-section, specifically from rkm 1.1 to 6.4. Despite an overall decrease in sampling effort in the river section between 2015 and 2017 (1,074, 526, and 458 minutes shocked), the number of walleye captured and tagged each year (75, 195, and 197 fish tagged) increased.

For radio-tagged river walleye, 63 percent of relocations came from the lower river sub-section, 15 percent in the middle, 15 percent in the upper and 7 percent in CFR. Overall, 66 percent of river telemetered walleye migrated into the river multiple years, 22 percent one year, and 12 percent were never relocated in the river. Six multi-year migrants returned to within

a mean of 0.4 rkm (range 0-1.6 rkm) from their maximum upstream relocation the previous year.

Walleye radio-tagged in CFR were only located in the lower river sub-section. Overall, 29 percent of CFR telemetered walleye migrated into the river multiple years, 29 percent only one year, and 42 percent were never observed in the river. Two multi-year migrants returned to within a mean of 7.5 rkm (range 0-11.5 rkm) maximum upstream location the previous year.

Increasing springtime river discharge and movement into the river were related for river ($R^2=0.15$) and reservoir ($R^2=0.07$) telemetered walleye. River migrants, especially those located within the upper river sub-section, did not reach maximum upstream extent in the river until after peak river discharge occurred in early summer each year. These movements were confirmed by anchor-tagged walleye as none were reported by anglers earlier than 15 July from the upper sub-section despite anecdotal evidence of walleye angling effort throughout the entire river from spring to fall.

Exploitation

Thirty-One walleye anchor-tagged in CFR were caught by anglers or MFWP personnel for an overall reporting rate of 18 percent. Of those, 90 percent were caught or captured in CFR and 10 percent were in the river. Fifty-Three walleye anchor-tagged in the river were caught and reported by anglers or MFWP personnel for an overall reporting rate of 12 percent. Of those, 28 percent were caught or captured in CFR and 72 percent in the river. Estimated exploitation, corrected for tag loss, was 21 percent (range 19.9-21.5%) for CFR and 13 percent (range 7-20%) for river anchor-tagged Walleye.

DISCUSSION

Walleye tagged and relocated in the Missouri River upstream from CFR were observed throughout all sub-sections in the river, and all relocated telemetered fish

out-migrated to CFR. Walleye found in the river that were initially radio-tagged in CFR migrated only into the lower sub-section of the river and then out-migrated. No radio-tagged fish (regardless of capture location) overwintered in the river. No anchor-tagged fish were caught or captured in the river outside the timeframe observed by radio-tagged fish. Thus, this study suggests that two distinct resident populations are not present, but that a proportion of CFR walleye exhibit adfluvial movement.

We strived to capture and tag fish uniformly across all sections, however, this does not reflect seasonal walleye distribution throughout the river. Our results suggest that walleye, during the spring (April to early June), were primarily in the lower sub-section of the river, reach maximum upstream extent throughout the summer, and out-migrate to CFR in the fall. Also, multi-year radio-tagged river migrants showed signs of site fidelity. These movements could be related to deep pool riverine (McMillian 1984, Hanson 2006) habitat availability throughout the summer, although this remains mostly unknown.

Although walleye with radio tags were slightly longer than anchor-tagged fish, there was no difference in how far they moved upstream, and seasonal adfluvial behavior was observed by fish from both tag types. Size differences, albeit slight, between lacustrine and adfluvial sampled CFR walleye suggest that seasonal river inhabitants may grow larger than lacustrine CFR walleye. This could be explained by sampling selectivity or capture method, but we hypothesize that adfluvial walleye may be slightly larger in the river compared to CFR due, potentially, to differences seasonal thermal conditions (i.e., max water temperature near 26°C in 2015; USGS gage 06054500), forage availability (i.e., relatively large quantities of yellow perch, white suckers (*Catostomus commersonii*), and longnose dace (*Rhinichthys cataractae*) may be available in the river compared to reservoir; Traxler 2017) or other unknown variables.

Average estimated CFR anchor tag exploitation reported by other studies in this area was 18 percent (range 17-20 percent; MFWP *unpublished data*). The overall anchor tag reporting rate from this study (13 percent) was similar to the average reporting rate of 11.8 percent (range 8-14; MFWP 2016) percent during CFR anchor tag studies from 2011-2016. One major study, which compared nearly 50 walleye populations across North America (Baccante and Colby 1996) found that most exploitation rates varied from 3-30 percent. Data from this study suggest that exploitation is currently similar between reservoir and river caught walleye. Overall, anchor tagged fish exploitation in this study was likely underrepresented as only fish tagged in 2015 were at-large for 3 years. Moreover, river tagged fish exploitation was 38 percent less than reservoir tagged fish and could be explained by river walleye migration timing with a combination of lower reservoir angling effort in early spring/late fall, specifically for walleye, and overall angling pressure differences (approximately 10-times more reservoir pressure on average) between sections over time.

Anchor tag returns may have been biased by angler timing. Based on MFWP creel data from 2015-2017 (MFWP 2016, MFWP 2017, MFWP *unpublished data*), few anglers sought walleye in April (averaged 24 per year or 1.4% of annual anglers surveyed) and October (averaged 18 anglers or 1.2% of annual anglers surveyed). Even fewer anglers historically sought walleye during the winter fishing months (MFWP 2010). Therefore, it is not surprising that no anchor-tagged fish, especially river captured walleye, were reported by anglers within the reservoir from late fall to early spring each year.

Though not the intent of this study, we found that electrofishing was more efficient than Merwin traps for capturing walleye in this study. Walleye CPUE for electrofishing the river section averaged 0.23 fish per minute (SE 0.18) and trap nets in the reservoir averaged <0.01 fish per minute (SE 0.0). An active capture method,

like electrofishing, may be a more efficient survey tool for future walleye surveys in the reservoir.

Lastly, though not the intent of this study, female walleye were observed in the river during electrofishing and one appeared reproductively ready and was expressing eggs. Other studies in Montana have shown walleye, or sauger (*Sander canadensis*), from the same genus, spawn in rivers (Jaeger et al. 2005, Bellgraph 2006, Grisak et al. 2012) and the timing of movements of walleye from CFR into the Missouri River are similar to other studies (Paragamian 1989, DePhilip et al. 2005, Hanson 2006). In a separate 2017 survey we confirmed young-of-the-year walleye in the river during beach seine surveys, indicating that natural reproduction may be occurring. Downstream early life history drift of age-0 walleye has been documented for river spawning walleye populations (Corbett and Powles 1986, Mitro and Parrish 1997) and could explain our survey results. Results from this study, in conjunction with results from other walleye surveys in the study area, have helped develop a better understanding of walleye life history in the upper Missouri River drainage from Canyon Ferry Dam to Toston Dam.

CONCLUSION AND MANAGEMENT IMPLICATIONS

The timing and movements of walleye into the Missouri River upstream of Canyon Ferry Reservoir were poorly understood prior to this study. Future walleye management strategy assessments within the study area should consider seasonal adfluvial walleye movement throughout the study area and we recommend that walleye be designated as seasonally abundant and well-distributed throughout the river. Based on tag returns and radio telemetry relocations, walleye in this study were observed throughout all river sub-sections from spring to fall. Size differences between CFR and river tagged walleye were observed and necessitate a better understanding of basic walleye biology differences such as growth, diet, spawning success between the river

and reservoir. In order to fully monitor and manage the CFR walleye population, we recommend a standardized walleye electrofishing survey within the river section.

Angling pressure estimates in the river indicate a steady increase in angling pressure over time since 1991 with a high of 10,635 angler days in 2015 (MFWP 2017). Anecdotal evidence indicates that river section anglers, specifically boat anglers, are pursuing walleye at an increasing rate in recent years. Angling pressure estimates in the reservoir also indicate a steady increase in angling pressure over the same period and a record high of over 133,220 angler days in 2009. Anglers pursuing walleye in the reservoir, based on summer creel evaluations from 1996-2016, increased from zero percent in 1996 to 33 percent by 2001 and the mean thereafter observed was 45 percent (range 24-77%). Thus, we assume that more anglers are pursuing walleye in the river as the population expands into the river. Angling dynamics in this unique sport fishery have likely changed, since walleye expansion into the river in the mid-2000's, and we recommend a creel survey be considered to better understand angler trends in the river upstream of CFR.

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TRENDS IN YELLOWSTONE RIVER BASIN WATER SUPPLY AS INTERPRETED THROUGH HYDROLOGIC ANALYSIS, 1898-2007

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ABSTRACT

The Yellowstone River and its tributaries provide an important case study in the changes in magnitude and timing of discharge. As part of a review of water demands on the river and potential effects on fish and other aquatic biota, we assessed long term trends (1898-2007) and more recent changes (1970-2007) in the hydrographs of the Yellowstone River and its tributaries using data from 18 USGS Hydro-Climatic Data Network Stations. We evaluated seven variables used to characterize the discharge: 1) annual discharge, 2) magnitude of discharge, 3) absolute annual minimum discharge, 4) monthly discharge, 5) date when half of annual volume passed station, 6) date when maximum daily mean occurred, and 7) date when discharge returned to baseflow. Declines in volume and magnitude of annual and seasonal discharges are present in the basin, more so in areas where there are no water storage facilities. Timing of flow events are occurring earlier in the year throughout the basin, leaving less water in the summer and fall when water demands are the greatest. The appearances of significant trends have increased over the period 1970-2007, and it is expected that they will continue without serious changes in the basin. Lessened flows and altered timing stands to greatly affect all users of water in the basin, as is occurring in the rest of western North America. Effects on the native biota inhabiting the river can also be expected.

Keywords: Montana, streamflow, discharge, instreamflows, fishes

INTRODUCTION

In the past century, substantial declines in annual discharges have been documented throughout many of the rivers and streams of the western United States. Changes observed in magnitude and timing of runoff (Cayan et al. 2001; Stewart et al. 2004, 2005; Gibson et al. 2005), and the magnitude of peak discharge have been attributed to a wide range of human activities on the landscape (Zelt et al. 1999; Gibson et al. 2005). Observed changes in the timing of discharge have been most commonly characterized as an earlier peak and an earlier runoff pattern

(Cayan et al. 2001; Regonda et al. 2004; Stewart et al. 2004, 2005; Gibson et al. 2005). In interior river basins with temperate climates, most annual discharge (often 50 to 80 percent of the total; Stewart et al. 2004) originates from snowmelt in spring and early summer. Despite high spring flows, discharge by late summer can be low, water withdrawals for human uses high as a percentage of total daily discharge, and instream water shortages severe. Earlier runoff and declining annual discharge can result in less water available for late summer demands for all competing uses (fish and wildlife, municipal, industrial, irrigation, etc.). Earlier runoff can also result in a protracted period of baseflow conditions and in severe cases can result in decreases

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in average baseflow because of diminished groundwater recharge (Arnell 1999).

Such changes in runoff can have substantial implication for ecological processes and aquatic communities in rivers. The quantity and timing of discharge is of critical importance in a free-flowing river for fish and fish habitat. Ecological processes can be regulated by the timing of peak discharge (Poff et al. 1997) and by the timing and magnitude of baseflow. Decreased volume, earlier discharge, and lower and longer periods of base flow can have negative impacts on the local fauna and a river's ecological functioning during the dry season. Many fish species in different areas have evolved specialized adaptations effective under the historic timing of runoff. They subsequently can develop a dependence on these cues (Cayan et al. 2001; Stewart et al. 2004, 2005; Gibson et al. 2005). Low water conditions reduce a river's ability to buffer against high temperatures and pollution, and can potentially disconnect riverine habitats causing isolation and mortality of native

fauna (Gido et. al 2010). Late summer is a time when habitat for native fish and aquatic life can be minimal and potentially limiting due to decreased discharge and warmer water temperatures (Arismendi et al. 2012).

The Yellowstone River and its tributaries provide an important case study of the changes in magnitude and timing of discharge (Fig. 1). The Yellowstone River mainstem, which is unregulated, and its tributaries experience a dominant bi-modal natural hydrograph because of snow melt dominated flows. The first rise is a response to early melting of snow in lower elevation areas in the basin, usually occurring in the early spring (March or April). A second, more significant rise happens later in the summer when most of the snowpack in the higher elevations is being depleted (late May or June; Vorosmarty et al. 2000).

Irrigation withdrawals are the largest of all water withdrawals in the Yellowstone River Basin (YRB; approximately 96.5 percent; Miller and Quinn 1997). Irrigation withdrawals persist through late summer into the fall with many water

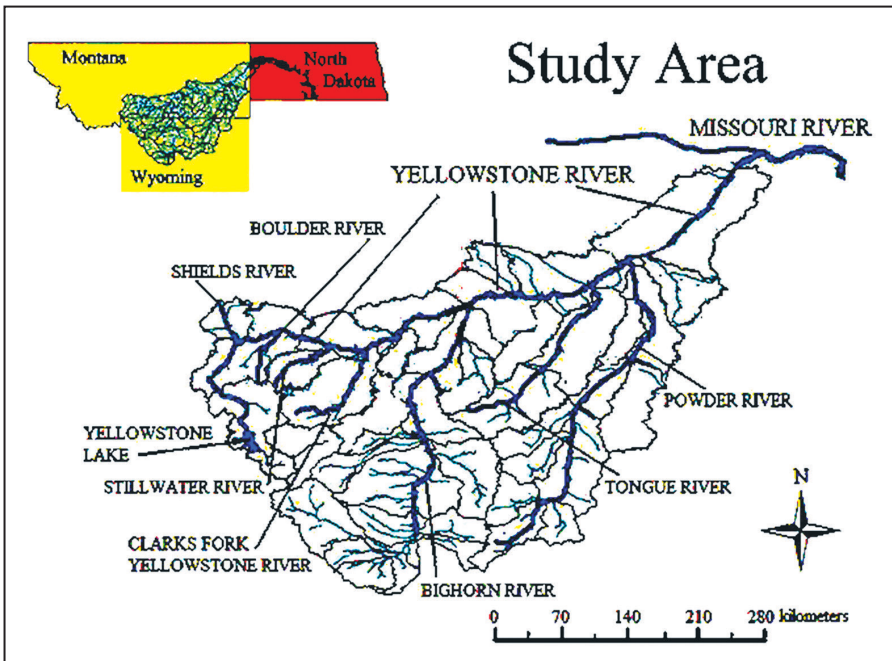


Figure 1. United State Geological Survey (USGS) Hydro-Climatic Data Network sites on the Yellowstone River and its seven major tributaries: Shields River, Boulder River, Stillwater River, Clarks Fork of the Yellowstone River, Bighorn River, Tongue River, and Powder River.

permits expiring as late as October 31 (MTDNRC 2008). Determining the effects of this dominant water use on the natural hydrograph in the basin is crucial to understanding potential effects on fish and other aquatic life.

The magnitude of absolute minimum flows for rivers varies widely throughout the basin. Some of the rivers frequently or periodically experience near zero flow conditions (e.g., the Powder River; Hubert 1993), whereas others continue to flow at levels that may or may not provide sustainable conditions for the aquatic life dependent upon it. Absolute minimum flow is a direct reflection of the ground water table along a river, and can be used to determine the amount of use or overuse throughout time (Smakhtin et al. 2001). The gradual reduction in surface water supply from groundwater development can lead to ecological effects that may not be fully realized for years. It also greatly complicates the administration of water rights.

As a first step in understanding water supply, use, and demands in the YRB, we conducted an analysis of the trends in monthly flows at its gauging stations over the period 1898-2007. The objective of this study was to assess long term trends and recent changes in the hydrographs of the Yellowstone River and its tributaries based on timing and magnitude of peak flows, seasonal flows, and base flows. Detailed time series analyses were used to test statistical validity of any apparent trends (Parrett 2006).

METHODS

To evaluate the hydrographs within the YRB, we downloaded data available online from 18 United States Geological Survey (USGS) Hydro-Climatic Data Network stations on the Yellowstone River and its seven major tributaries: Shields River, Boulder River, Stillwater River, Clarks Fork of the Yellowstone, Bighorn River, Tongue River, and Powder River (Table 1; Fig. 2). We chose sites that were near the origin, the confluence, and state borders of the rivers to better detect any changes. On all but three of the tributaries (Shields, Boulder, and

Stillwater), at least two sites were chosen for analysis. The following USGS stations were used: The Yellowstone River near Livingston, MT (USGS 06192500), at Billings, MT (USGS 06214500), at Miles City, MT (USGS 06309000), and near Sidney, MT (USGS 06329500); Shields River near Livingston, MT (USGS 06195600); the Boulder River at Big Timber, MT (USGS 06200000); the Stillwater River near Absarokee, MT (USGS 06205000); the Clarks Fork Yellowstone River near Belfry, MT (USGS 06207500), and near Edgar, MT (USGS 06208500); the Bighorn River at Kane, WY (USGS 06279500), near St. Xavier, MT (USGS 06287000), and Bighorn River at Tullock Creek near Bighorn, MT (USGS 06294500); the Tongue River near Dayton, WY (USGS 06298000), at the State Line near Decker, MT (USGS 06306300), and at Miles City, MT (USGS 06308500); and the Powder River at Sussex, WY (USGS 06313500), at Moorhead, MT (USGS 06324500), and near Locate, MT (USGS 06326500). The Sidney station (USGS 06329500) was used to represent the basin output and overall trend because the station was established in 1910, and the flow at this site represents nearly all of the total annual discharge leaving the basin as runoff. All calculations were made using the data available during the chosen periods. In general, data were complete for these stations over the period of 1898 to 2007 (Table 1).

Seven variables used to characterize the discharge, four for aspects of volume and three for aspects of timing, were obtained or computed from the USGS records (Stewart et al. 2004; Smakhtin et al. 2001). The four variables chosen to depict discharge volume were: 1) annual discharge, i.e., the total volume of discharge past a station during an individual water year (October 1 to September 30), 2) magnitude of peak discharge, i.e., the largest magnitude of daily averaged discharge past a station within an individual water year, 3) absolute annual minimum discharge, i.e., smallest annual magnitude of daily averaged water flowing past a station within an individual water year, and 4) monthly discharge –

Table 1. USGS Hydro-Climatic Data Network sites.

Code	Site Number	River	Location	Period of Data
1	06192500	Yellowstone	Livingston, MT	1898 - 1905, 1929 – 2007
2	06195600	Shields	Livingston, MT	1979 – 2007
3	06200000	Boulder	Big Timber, MT	1948 - 1953, 1956 – 2007
4	06205000	Stillwater	Absarokee, MT	1911 - 1914, 1936 – 2007
		Clarks Fork		
5	06207500	Yellowstone	Belfry, MT	1922 – 2007
		Clarks Fork		
6	06208500	Yellowstone	Edgar, MT	1922 - 1969, 1987 – 2007
7	06214500	Yellowstone	Billings, MT	1905, 1928 – 2007
8	06279500	Bighorn	Kane, WY	1929 – 2007
9	06287000	Bighorn	St. Xavier, MT	1935 – 2007
10	06294500	Bighorn	Bighorn, MT	1946 – 2007
11	06298000	Tongue	Dayton, WY	1919 – 2007
12	06306300	Tongue	Decker, MT	1961 – 2007
13	06308500	Tongue	Miles City, MT	1939 - 1941, 1946 – 2007
14	06309000	Yellowstone	Miles City, MT	1923, 1929 – 2007 1939, 1940, 1950 - 1957,
15	062313500	Powder	Sussex, WY	1979 – 2007
16	06324500	Powder	Moorhead, MT	1930 – 2007
17	06326500	Powder	Locate, MT	1939 – 2007
18	06329500	Yellowstone	Sidney, MT	1911 – 2007

i.e., average discharge during each month at a station. Three of the four variables had one value per year per station and the fourth variable (mean monthly discharge) had 12 values per year per station. The three variables chosen to depict timing of discharge were: 5) date during the water year when half of the annual volume of flow has passed a station, 6) date during the water year when the maximum daily mean was achieved, 7) date of return to baseflow (discharges below the 50th percentile flows) after spring rise.

The four volume variables used were annual discharge, peak discharge, annual minimum discharge, and average monthly discharge (in m³/s). They were calculated based on daily statistics from the USGS gauging records for the entire period of record at all 18 stations (Table 1).

The first of the three timing variables (the date of the water year when half of the

flow has passed the gauging station) was calculated using historic daily averages from the USGS gauging records for the entire period of record at 9 of the 18 stations (1-5, 8, 11, 15, and 18) to detect for trends in timing of center mass of discharges in the basin. For this variable, the temporal centroid of streamflow (CT) measurement, a measurement of runoff timing (Stewart et al. 2004), was used to determine whether the snowmelt runoff in the basin is trending earlier or later in the water year. The CT used was the flow-weighted timing, or 'center of mass' of streamflow calculated as

$$CT = \Sigma(t_i q_i) / \Sigma q_i,$$

where t_i is the time in days from the beginning of the water year and q_i is the corresponding streamflow for water year day i (Stewart et al. 2004). The CT measurement was chosen because it is easily and reliably determined, insensitive

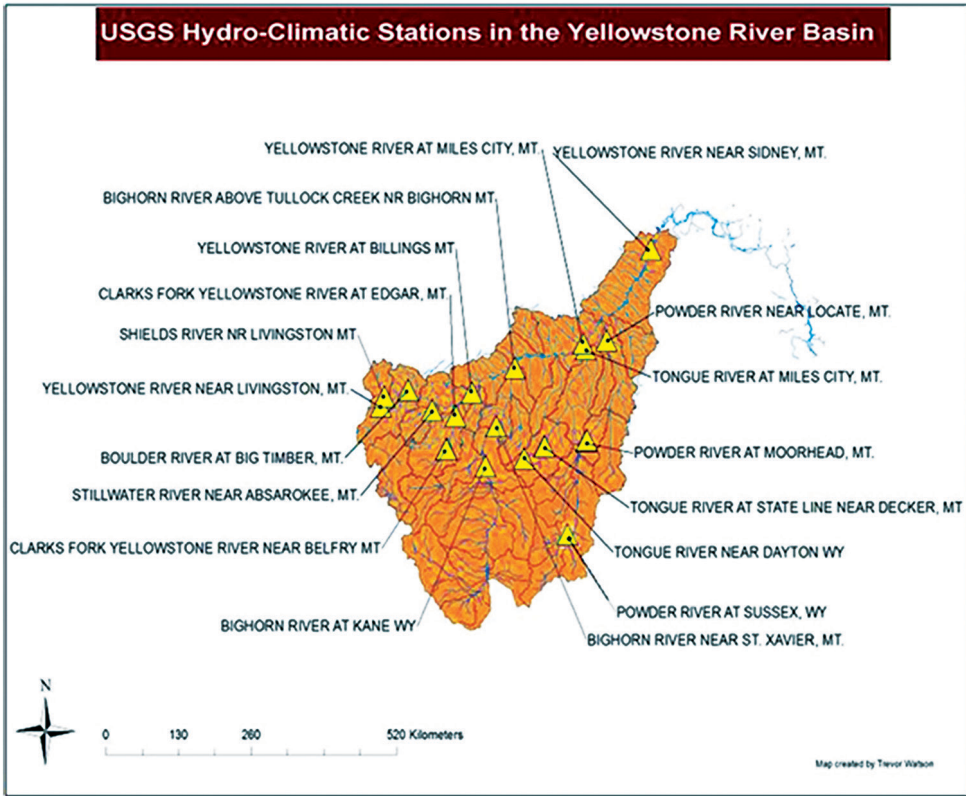


Figure 2. United State Geological Survey (USGS) Hydro-Climatic Data Network sites on the Yellowstone River and its seven major tributaries: Shields River, Boulder River, Stillwater River, Clarks Fork of the Yellowstone River, Bighorn River, Tongue River, and Powder River.

to spurious variations in flow, and it can be used to compare basins in different climatic regimes (Stewart et al. 2004). It has also been used effectively to detect a shift in timing of snowmelt runoff in many rivers in the Northwest (Roos 1987, 1991; Wahl 1992; Dettinger and Cayan 1995; Cayan et al. 2001; Stewart et al. 2004, 2005). The average CT was calculated from daily flow volumes for each of the eight snowmelt-dominated tributaries in the basin. The CT measurement was used only for the stations near the headwaters of the rivers, except on the Shields, Boulder, and Stillwater where there was only one station available, and the Yellowstone River where CT was also calculated at Sidney, site of the lowermost gauging station on the mainstem.

For the second timing variable, annual peak discharge, we obtained peak discharge values and dates of occurrence for each

water year from the USGS gauging records for the entire period of record at all 18 stations. We then fit the Julian date with the water year calendar and found the water year day that the peak discharges occurred.

For the third timing variable, baseflow, daily mean discharges were used for 17 of the 18 stations and the date of return to baseflow was calculated. Baseflow was identified as when the discharge equaled or exceeded 50 percent of the time, also known as Q50, as outlined by Smakhtin et al. (2001). We determined the water day when discharge, after the ‘spring rise’ fell below the Q50 designation. In years when the base flow was not met before the end of the water year, the last day of the water year (365; September 30) was used as its measurement. One of the 18 gauging stations, the site near St. Xavier on the Bighorn (site 9), was excluded because of its unnatural flows

owing to its location directly downstream of Yellowtail Dam on the Bighorn River.

Prior to trend analyses, for each variable, Loess (local polynomial regression fitting) smoothing was used to serve as a visualization tool to better evaluate the data. The Loess smoothing approach to linear and non-linear regression (NIST/SEMATECH 2006) is best described as fixing a low-degree polynomial to small subsets of the data surrounding each point in the data set. Using weighted least squares, the polynomial fit was given more weight to data points near the response data being estimated and less to the ones further away (Appendix 1 in Watson 2014).

Seven null hypotheses were evaluated in the YRB: There were no changes or trends in 1) annual discharges, 2) magnitude of peak discharges, 3) magnitude of absolute annual minimum discharge, 4) average monthly discharges, 5) date of the CT measurements, 6) date of maximum daily means, and 7) date when flows return to baseflow conditions.

A non-parametric approach was used to test for trends for all seven variables. The four volume variables were tested for association between time and discharge; the three timing variables were tested for association between time and day, based on counts of concordant and discordant pairs. Tests were made using the Mann-Kendall Trend Analysis (Kendall Tau (KT)) test (Higgins 2004). Two analyses were run for each site, one using the entire time series of data present and the other from 1970 to 2007 based on observations of the Loess plots (Watson 2014). We separated the results (slopes) as positive or negative and assessed their significance at $P = 0.1$. Anything with a $P > 0.10$ was determined to have no statistical trend, $0.05 < P < 0.10$ to have a trend detected but not significant, $P < 0.05$ to be significant, and $P < 0.01$ to be highly significant (Higgins 2004). Pearson's correlation coefficient (parametric), and the Spearman's rank correlation coefficient test (non-parametric) were used to measure the correlation between the two variables time and discharge for the four volume measurements and time and water day for the three timing

measurements. The correlation coefficients ranged from -1 to 1 (Watson 2014).

RESULTS

Overall, annual discharges, magnitudes of peak discharge, and baseflow tended to decline on the tributaries free of upstream reservoirs. Runoff also tended to occur earlier in more recent years.

Magnitude of Discharge

Annual Average Discharge

Although we observed variability in the average annual discharge for all rivers when considering the entire period of record, there was far less variability at individual sites over the more recent period (1970-2007). There were highly significant declining trends at sites 3, 11, 12, and 18 ($P < 0.01$), significant declining trends at sites 2, 8, 9, 10, and 17 ($P < 0.05$), and no sites with negative but insignificant trends ($0.05 \leq P \leq 0.10$) when evaluated over the entire periods of record (Fig. 3). All sites but 7 and 15 had negative slopes (Kendall Tau; KT) over their entire periods of record.

There was more consistent evidence of declines in the average annual discharge for all rivers over the period 1970-2007 with highly significant declining trends at sites 3, 4, 7-14, and 18 ($P < 0.01$), significantly declining trends at sites 1, 2, 5, 16, and 17 ($P < 0.05$), and no sites with negative but insignificant trends ($0.05 \leq P \leq 0.10$). All sites had negative slopes (KT) over the period 1970-2007 (Fig. 3).

Magnitude of Annual Peak Discharge

Similar variability in the magnitude of annual peak discharge was observed for all rivers and their individual sites studied when considering their entire periods of record and over the more recent period 1970-2007. There were highly significant declining trends at sites 3, 8, 9, 14, 16, 17 and 18 ($P < 0.01$), significant declining trends at sites 12 and 13 ($P < 0.05$), and one site (2) with a negative but insignificant trend ($0.05 \leq P \leq 0.10$) when evaluating the entire period of record (Fig. 4). All sites but 1, 5, and 7 had negative slopes (KT) for the entire period of record.

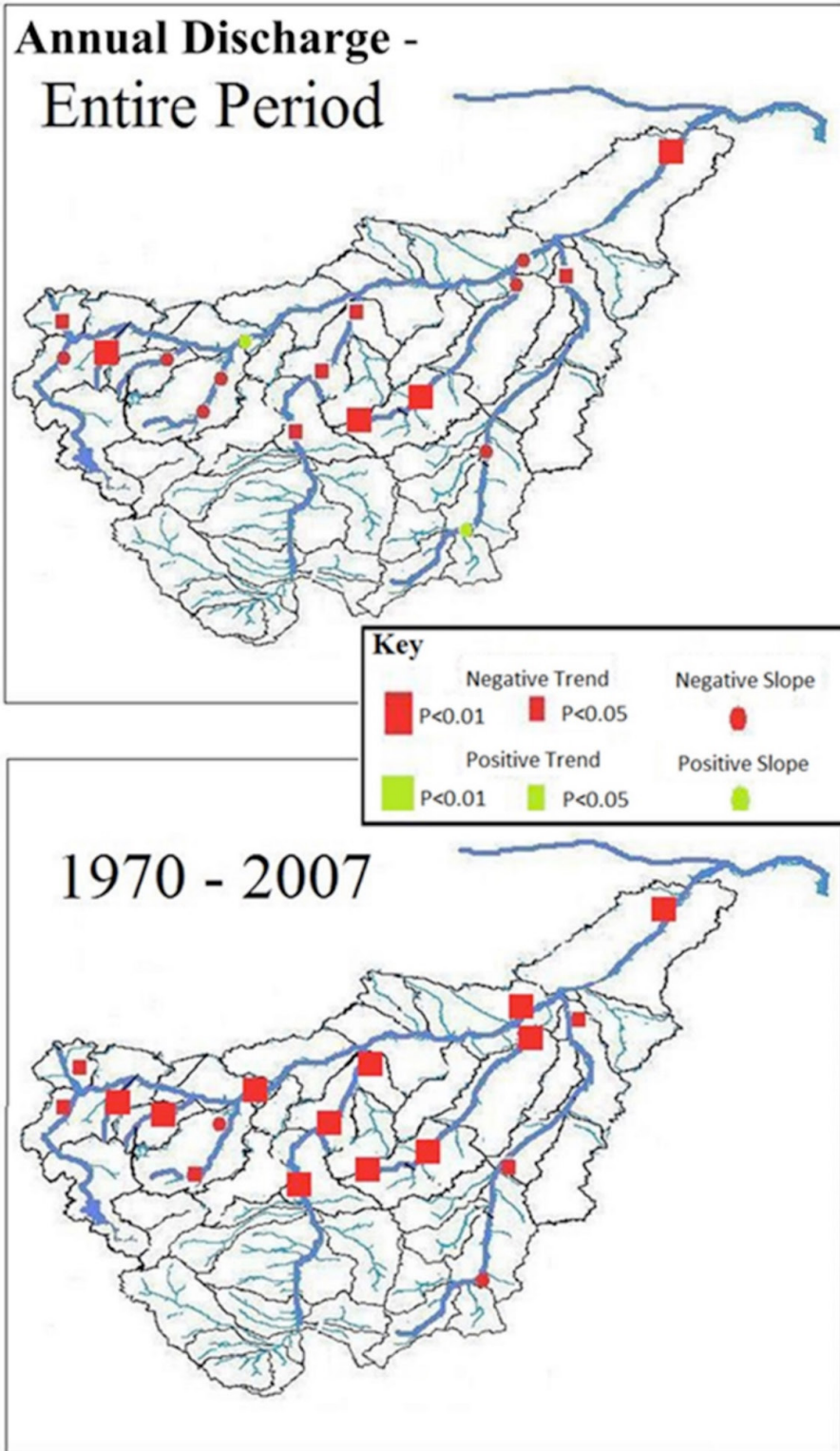


Figure 3. Trend analyses for annual discharge in the YRB a) for entire data periods, and b) from 1970 to 2007.

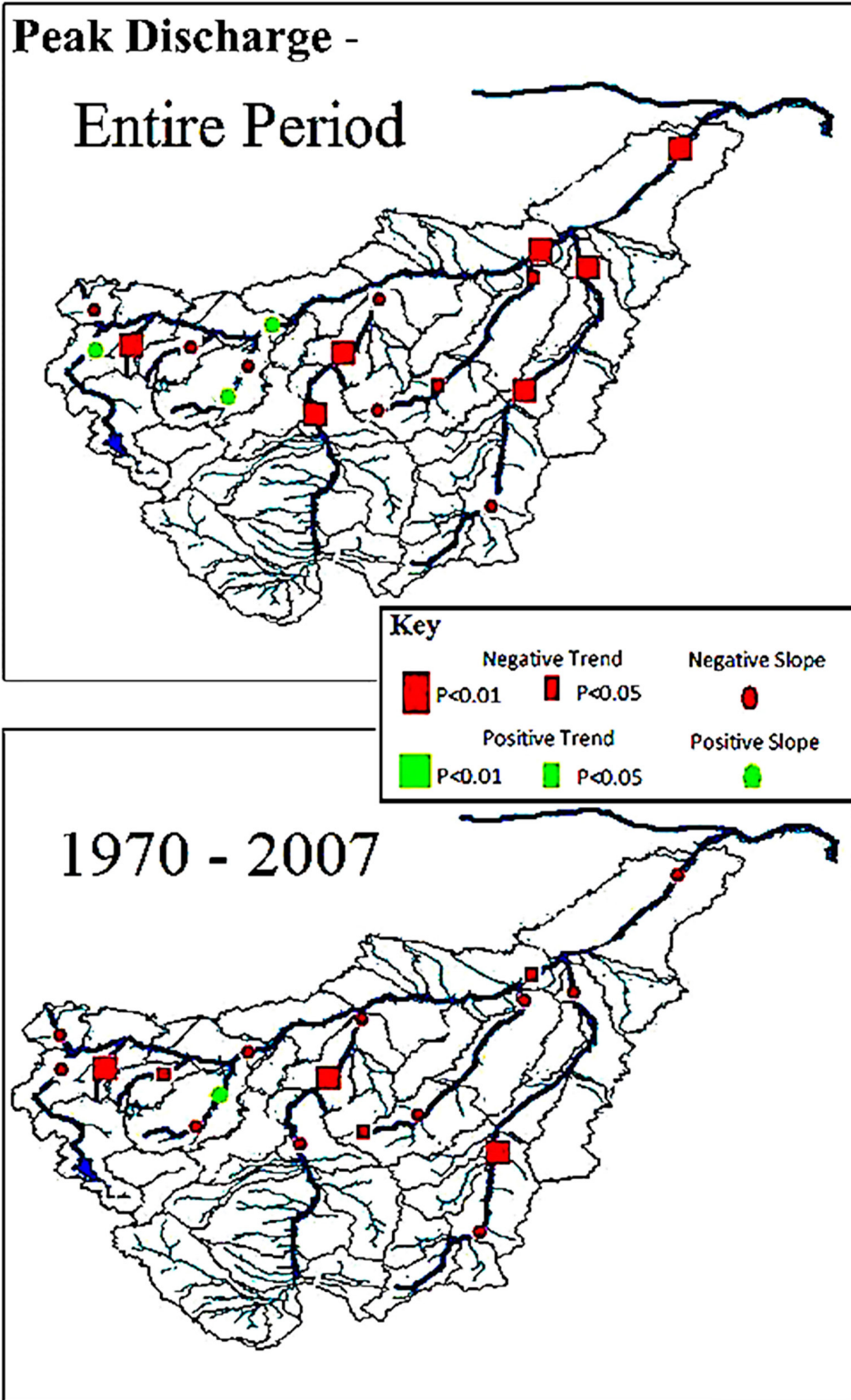


Figure 4. Trend analyses for magnitude of peak discharge in the YRB a) for the entire period and b) from 1970 to 2007.

For annual peak discharge over the period 1970-2007, we found highly significant declining trends at sites 3, 9, and 16 ($P < 0.01$), significantly declining trends at three sites ($P < 0.05$), and negative but insignificant trends at 3 sites ($0.05 \leq P \leq 0.10$). All sites but site 3 had negative slopes (KT) for the period 1970-2007 (Fig. 4).

Absolute Annual Minimum Discharge

Absolute annual minimum discharge showed highly significant ($P < 0.01$) declining trends at sites 2, 5, and 6, highly significant ($P < 0.01$) increasing trends at sites 8, 9, 10, and 14, significantly declining trends at sites 3, 11, and 12 ($P < 0.05$), and significantly increasing trends at site 16 ($P < 0.05$). (Fig. 5).

Over the period 1970-2007 sites 2, 3, 5, 8, 11, 12, 13, 15, and 18 exhibited highly significant declining trends ($P < 0.01$), and significantly declining trends at site 17 ($P < 0.05$). No significant positive trends ($P < 0.05$) were found in the basin for the period 1970-2007. (Fig. 5)

Average Monthly Discharges

Monthly discharges changed similarly throughout the basin by season regardless of river, with only a few deviations. A majority of the 18 sites on the eight rivers experienced declines late spring, summer, and early fall months (May-October), while showing increases in monthly discharges during the other months. The lowest station in the basin, Site 18 Yellowstone River near Sidney, Montana was a clear depiction of this pattern, showing the most summer and fall months with significant declines, while the other months experienced increasing flows. Overall there was little difference in decreasing versus increasing trends, but there were more sites with significantly and very significant decreasing trends than there were with increasing trends (Table 2).

Timing of Discharge

Overall, both the date of the CT measurement and the return date of baseflow measurements tended to occur days earlier during the more recent period evaluated within the YRB.

Centroid of Discharge

The center-time discharge results showed highly significant trends toward earlier runoff events at sites 8 and 18 ($P < 0.01$), no sites with significant trends towards earlier runoff ($P < 0.05$), and two sites (5 and 11) with insignificant trends but trending towards earlier runoff ($0.05 \leq P \leq 0.10$). All nine sites showed negative slopes however when evaluating the entire period of record for each site (Table 3).

Over the period 1970-2007, there were no sites with highly significant trends towards earlier runoff ($P < 0.01$), significant trends towards earlier runoff at sites 4, 5, and 7 ($P < 0.05$), and zero insignificant trends ($0.05 \leq P \leq 0.10$). All but site 8 exhibited negative slopes indicating earlier runoff events for the period 1970 to 2007 (Table 3).

Annual Peak Discharge

Annual peak discharge showed the least significance in changes or trends of all variables evaluated. No sites showed highly significant trends ($P < 0.01$). We found a significant trend ($P < 0.05$) toward earlier annual peak discharge at site 1, and found three sites (5, 7 and 8) with insignificant but negative trends ($0.05 \leq P \leq 0.10$) in the basin for their entire periods of record (Fig. 6; Table 4).

Similar results were found when evaluating the date of annual peak discharge for the more recent period 1970-2007. Sites 1 and 5 had highly significant trends ($P < 0.01$) towards earlier in the year, no sites showed significant trends ($P < 0.05$), and 1 site showed insignificant but negative trends ($0.05 \leq P \leq 0.10$) toward earlier in the year in the basin for the period 1970-2007 (Fig. 6; Table 4).

Annual Baseflow Conditions

Baseflow conditions showed highly significant ($P < 0.01$) trends towards earlier in the year at sites 5, 10 and 18, significant trends ($P < 0.05$) toward earlier in the year at sites 3 and 4, and site 8 had insignificant but negative trends ($0.05 \leq P \leq 0.10$) toward earlier in the year over their entire periods of record (Table 5; Fig. 7).

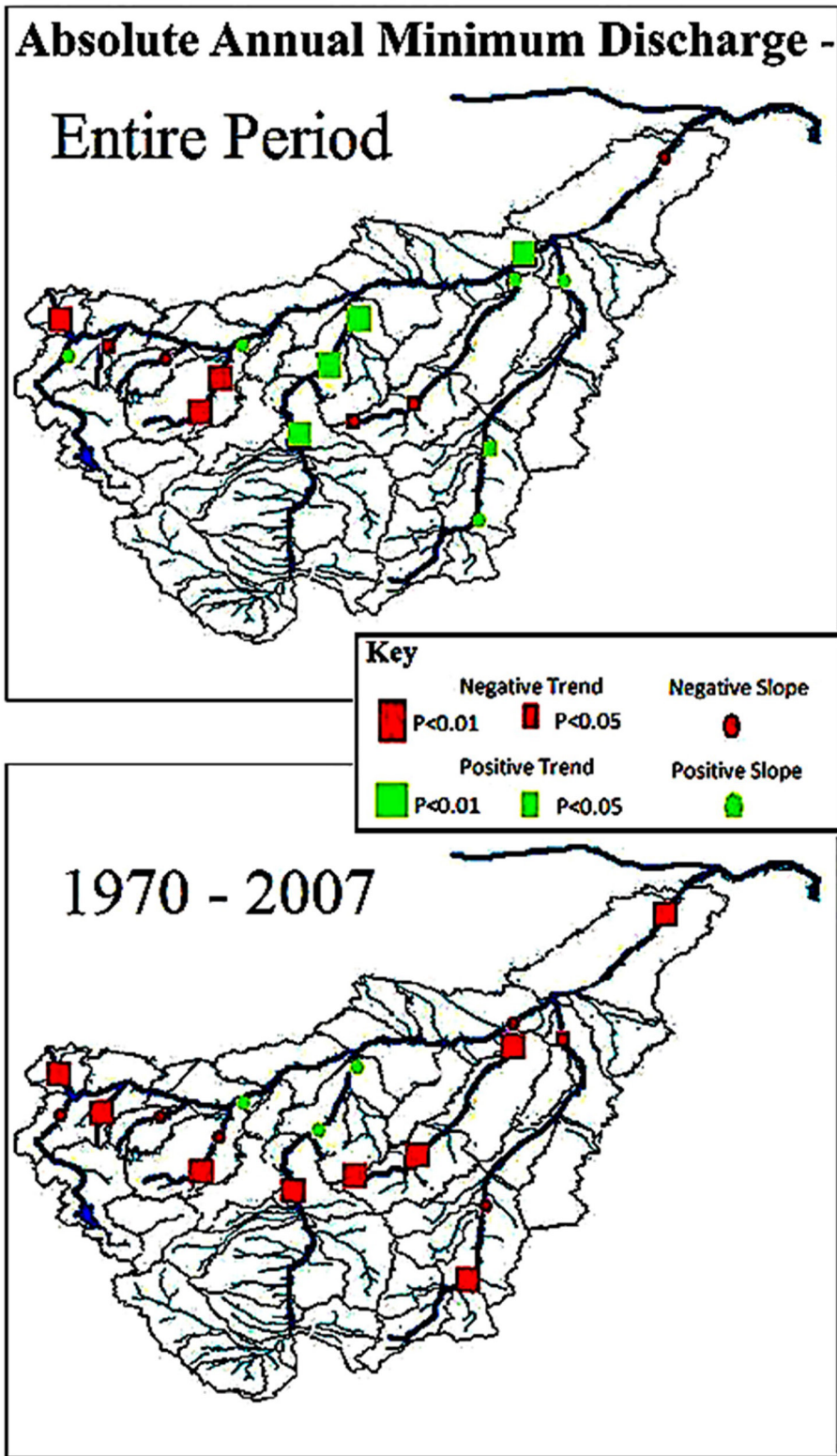


Figure 5. Trend analyses for absolute minimum annual discharge in the YRB a) for the entire period and b) from 1970 to 2007.

Table 2 Significant trend results for Annual Monthly discharges.

Months	Decrease			Increase		
	P<0.01	0.01≤P≤0.05	Trending Down*	P<0.01	0.01≤P≤0.05	Trending Up*
January	2	1	3	3	5	4
February	3	1	3	3	2	6
March	1	3	8	1	0	5
April	0	2	9	1	0	6
May	2	2	8	0	2	4
June	6	2	10	0	0	0
July	1	5	11	0	0	1
August	3	1	8	0	0	6
September	4	1	7	0	0	6
October	1	2	5	0	0	10
November	1	4	3	0	1	9
December	3	2	2	2	1	8
Totals	27	26	77	10	11	65

*Trending down or up but not statistically significant 0.05≤P≤0.10.

Over the period 1970-2007, sites 1, 4, 7, and 13 exhibited highly significant trends (P<0.01) towards an earlier onset of baseflow conditions, significant trends (P<0.05) towards an earlier onset of baseflow conditions at sites 3, 5, 8, 10, and 18, and sites 7 and 14 changed to negative trends. (Fig. 7; Table 5).

Overall, for the seven variables, we rejected all seven of the null hypotheses evaluated. There were many significant (P<0.05) and highly significant (P<0.01) trends identified for the variables throughout the basin. The significant results were scattered throughout and are summarized in detail in Watson (2014).

DISCUSSION

Hydrographic trends from the tributaries and the mainstem provide consistent indications that the historic magnitude and volume of discharge is declining in the YRB. Similar results have been documented in similar snow melt dominated systems along the Rocky Mountains in North America and the Pacific Northwest (Rood et al. 2005; Schindler and Donahue 2006; Luce and Holden 2009). For example, Rood et al. (2005) found that there were

significant declines in total annual flow for many Rocky Mountain watersheds near the hydrographic apex of North America, and Luce and Holden (2009) found that the Pacific Northwest was experiencing the same declines.

Although several studies of various river systems in the West show that there are quantified changes occurring in the observable hydrograph (Lapp et al 2005; Rood et al. 2005; Mote et al. 2005; Barnett et al 2005; Cayan et al 2001), most focus on how it affects the timing of water and less so on the amount of water (Luce and Holden 2009). Part of this bias is due to the science of climate modeling, where there is greater confidence in temperature increases regionally (and thus changes in timing of runoff) than what will occur with magnitude of discharge resulting from precipitation at smaller scales in the Western region (Lapp et al. 2005; Rood et al. 2005; Mote et al. 2005).

The analyses also indicate that the declines in the YRB are prevalent basin-wide from headwaters to mouth (Watson 2014; Figs. 3-7). In contrast, some other studies (e.g., Rood et al. 2005) that identified declines in discharge, saw within-basin differences, e.g., greater changes in higher

Table 3. Trend analysis results for CT measurements in the Yellowstone River Basin.

USGS Sites	Kendall Tau			Pearson's Correlation			Spearman's Correlation		
	KT Statistic	P-value	Pearson	Pearson	P-Value	Spearman	Spearman	P-Value	
Yellowstone River at Livingston	All Data 1970	-0.094 0.21	-0.142	-0.152	0.2044	-0.152	-0.152	0.1731	
Shields River	All Data	-0.175	-0.232	-0.266	0.1614	-0.266	-0.266	0.1068	
Boulder River	All Data 1970	-0.132 -0.080	0.3199 0.3758	-0.179 -0.150	0.3531 0.2596	-0.198 -0.120	-0.198 -0.120	0.3036 0.3682	
Stillwater River	All Data 1970	-0.177 -0.053	0.119 0.5155	-0.256 +0.427	0.1212 0.0002***	-0.271 -0.069	-0.271 -0.069	0.0993* 0.5695	
Clarks Fork River at Belfry	All Data 1970	-0.302 -0.122	0.0137** 0.0962*	-0.435 -0.181	0.0113** 0.0959*	-0.425 -0.182	-0.425 -0.182	0.0136** 0.0928*	
Bighorn River at Kane, WY	All Data 1970	-0.254 -0.220	0.0252** 0.0044***	-0.319 -0.297	0.0509* 0.0082***	-0.351 -0.315	-0.351 -0.315	0.0308*** 0.05**	
Tongue River near Dayton, WY	All Data 1970	+0.007 -0.145	0.9499 0.0646*	-0.002 -0.229	0.9882 0.0465**	+0.018 -0.212	+0.018 -0.212	0.9154 0.0658*	
Powder River at Sussex, WY	All Data 1970	-0.241 -0.082	0.0346** 0.5183	-0.381 -0.045	0.0184** 0.8112	-0.346 -0.121	-0.346 -0.121	0.0332** 0.5175	
Yellowstone River at Sidney	All Data 1970	-0.149 -0.298	0.309 < 0.0001***	-0.289 -0.382	0.1712 0.0001***	-0.220 -0.421	-0.220 -0.421	0.3005 < 0.0001***	
		-0.098	0.3856	-0.137	0.4111	-0.15	-0.15	0.3626	

* Insignificant trend; P < 0.10
 ** Significant; P < 0.05
 *** Highly Significant; P < 0.01

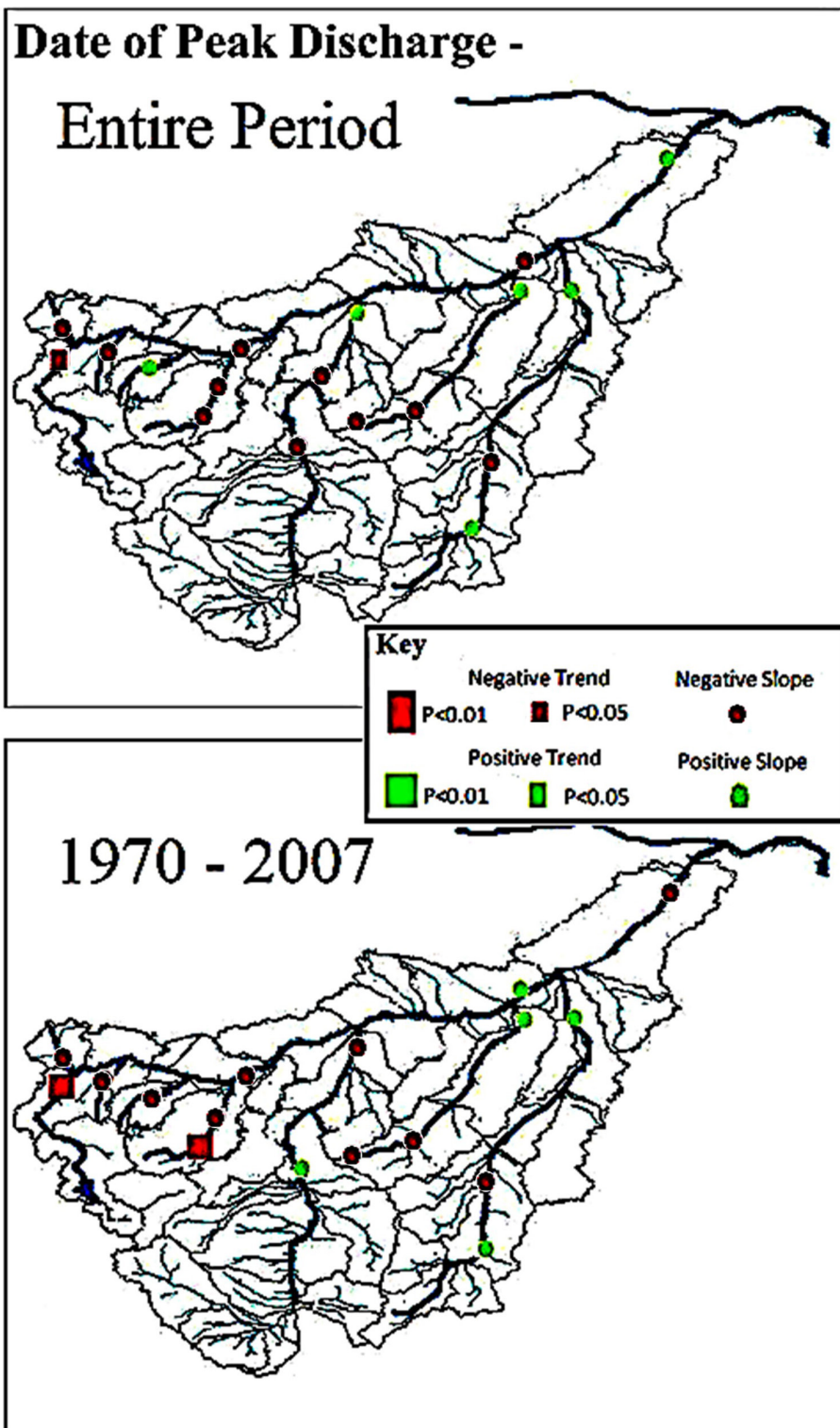


Figure 6. Trend analyses for peak discharge date in the YRB a) for the entire period and b) from 1970 to 2007.

Table 4. Trend analysis results for timing of annual peak discharge dates in the Yellowstone River Basin.

USGS Sites	Kendall Tau			Spearman's Correlation		
	KT Statistic	P-value	Pearson Correlation	Spearman Correlation	P-Value	P-Value
Yellowstone River at Livingston	All Data 1970	-0.197 0.0103**	-0.266 0.003***	-0.275 -0.481	0.0153** 0.0023***	0.0119** 0.0023***
Shields River	All Data	-0.020	0.8806	-0.045	0.8149	0.9656
Boulder River	All Data 1970	-0.052 -0.180	0.5699 0.1213	-0.055 -0.245	0.6768 0.1382	0.5945 0.1065
Stillwater River	All Data 1970	+0.059 -0.048	0.4621 0.6776	+0.106 -0.079	0.3609 0.6356	0.4259 0.6949
Clarks Fork River at Belfry	All Data 1970	-0.133 -0.298	0.0725* 0.0097***	-0.183 -0.386	0.0916* 0.0166**	0.0639* 0.007***
Clarks Fork River at Edgar	All Data 1970	-0.087 -0.067	0.3063 0.6722	-0.203 +0.004	0.0965* 0.9865	0.2523 0.8012
Yellowstone River at Billings	All Data 1970	-0.137 -0.150	0.0737* 0.1900	-0.153 -0.216	0.1732 0.1931	0.0711* 0.1656
Bighorn River at Kane, WY	All Data 1970	-0.137 +0.001	0.0781* 0.99	-0.150 +0.191	0.1906 0.2496	0.0803* 0.8545
Bighorn River at St. Xavier	All Data 1970	-0.036 -0.034	0.6542 0.7627	-0.293 -0.188	0.0119** 0.2599	0.6288 0.7328
Bighorn River near Bighorn	All Data	+0.111	0.4405	+0.158	0.452	0.4603
Tongue River near Dayton, WY	All Data 1970	-0.101 -0.207	0.1952 0.0682*	-0.141 -0.309	0.2192 0.0592*	0.1780 0.0527*
Tongue River at Stateline	All Data 1970	-0.080 -0.019	0.4353 0.8701	-0.053 -0.046	0.7233 0.7851	0.5251 0.9750

Table 4. Continued

USGS Sites	Kendall Tau		Pearson's Correlation		Spearman's Correlation	
	KT Statistic	P-value	Pearson	P-Value	Spearman	P-Value
Yellowstone River at Livingston	All Data	-0.197	0.0103**	-0.266	0.0153**	0.0119**
Tongue River at Miles City	All Data	+0.04.5	0.599	+0.077	0.5391	0.601
	1970	+0.063	0.58	+0.082	0.6239	0.6386
Yellowstone River at Miles City	All Data	-0.047	0.5463	-0.093	0.4136	0.4871
	1970	-0.121	0.2958	-0.057	0.7347	0.3131
Powder River at Sussex, WY	All Data	+0.048	0.6828	-0.053	0.7599	0.6701
	1970	+0.153	0.2827	+0.159	0.449	0.321
Powder River at Moorhead	All Data	-0.097	0.2147	-0.135	0.2403	0.1976
	1970	-0.089	0.4454	-0.103	0.5501	0.3419
Powder River at Locate	All Data	+0.024	0.7686	+0.054	0.6563	0.844
	1970	+0.126	0.2683	+0.154	0.3566	0.3933
Yellowstone River at Sidney	All Data	+0.041	0.569	+0.059	0.567	0.5526
	1970	-0.077	0.5047	-0.021	0.8987	0.5560

* Insignificant trend; $P < 0.10$

** Significant; $P < 0.05$

*** Highly Significant; $P < 0.01$

Table 5. Trend analysis results for return date of baseflow conditions after spring pulse in the Yellowstone River Basin.

USGS Sites	Kendall Tau			Pearson's Correlation			Spearman's Correlation		
	KT Statistic	P-value	Pearson Correlation	Pearson Correlation	P-Value	Spearman	Spearman's Correlation	P-Value	
Yellowstone River at Livingston	All Data 1970	-0.123 0.1072	0.0031***	-0.199 -0.462	0.0732* 0.0035***	-0.194 -0.472	0.0807* 0.00274**		
Shields River	All Data	-0.193	0.1481	-0.125	0.5189	-0.268	0.1606		
Boulder River	All Data 1970	-0.198 -0.292	0.0311** 0.0114**	-0.272 -0.364	0.0388** 0.0247**	-0.309 -0.415	0.0184** 0.0095***		
Stillwater River	All Data 1970	-0.168 -0.344	0.0339** 0.003***	-0.223 -0.440	0.0516* 0.0057***	-0.232 -0.482	0.0422** 0.0022***		
Clarks Fork River at Belfry	All Data 1970	-0.26D -0.232	0.0005*** 0.0435**	-0.362 -0.440	0.0006*** 0.0057***	-0.375 -0.471	0.0004*** 0.0029***		
Clarks Fork River at Edgar	All Data 1970	-0.118 -0.044	0.1599 0.7853	-0.196 +0.004	0.1064 0.9871	-0.173 -0.058	0.1561 0.8031		
Yellowstone River at Billings	All Data 1970	+0.031 -0.316	0.6868 0.0057***	+0.038 -0.444	0.7355 0.0053***	+0.039 -0.464	0.7338 0.0033***		
Bighorn River at Kane, WY	All Data 1970	-0.142 -0.232	0.0664* 0.0435**	-0.146 -0.296	0.1988 0.0715*	-0.199 -0.343	0.0792* 0.0349**		
Bighorn River near Bighorn	All Data 1970	-0.080 -0.186	0.3856 0.1288	-0.263 -0.335	0.0485** 0.0568*	-0.131 -0.283	0.3308 0.1101		
Tongue River near Dayton, WY	All Data 1970	-0.239 -0.294	0.0037*** 0.013**	-0.312 -0.409	0.0058*** 0.0108**	-0.316 -0.389	0.0051*** 0.0156**		
Tongue River at Stataline	All Data 1970	-0.162 -0.154	0.1221 0.1889	-0.190 -0.253	0.2058 0.1306	-0.241 -0.245	0.1072 0.1435		

Table 5. Continued

USGS Sites	Kendall Tau			Pearson's Correlation			Spearman's Correlation		
		KT Statistic	P-value	Pearson	P-value	Spearman	P-value	Spearman	P-Value
Tongue River at Miles City	All Data	-0.029	0.7461	+0.033	0.7993	-0.035	0.7915	-0.035	0.7915
	1970	-0.058	0.6235	-0.109	0.5267	-0.090	0.6025	-0.090	0.6025
Yellowstone River at Miles City	All Data	-0.033	0.6686	-0.048	0.6996	-0.057	0.6180	-0.057	0.6180
	1970	-0.360	0.0017***	-0.535	0.0005***	-0.512	0.0010***	-0.512	0.0010***
Powder River at Sussex, WY	All Data	+0.130	0.2917	+0.125	0.489	+0.169	0.348	+0.169	0.348
	1970	-0.077	0.6021	-0.256	0.2280	-0.112	0.6015	-0.112	0.6015
Powder River at Moorhead	All Data	-0.074	0.3461	-0.105	0.3644	-0.103	0.3738	-0.103	0.3738
	1970	-0.126	0.2816	-0.184	0.2832	-0.197	0.2485	-0.197	0.2485
Powder River at Locate	All Data	-0.032	0.7013	-0.189	0.1194	-0.037	0.7615	-0.037	0.7615
	1970	-0.079	0.4891	-0.226	0.1723	-0.100	0.5488	-0.100	0.5488
Yellowstone River at Sidney	All Data	-0.213	0.0026***	-0.262	0.0103**	-0.307	0.0025***	-0.307	0.0025***
	1970	-0.254	0.0268**	-0.362	0.0257**	-0.385	0.0169**	-0.385	0.0169**

* Insignificant trend; P < 0.10

** Significant; P < 0.05

*** Highly Significant; P < 0.01

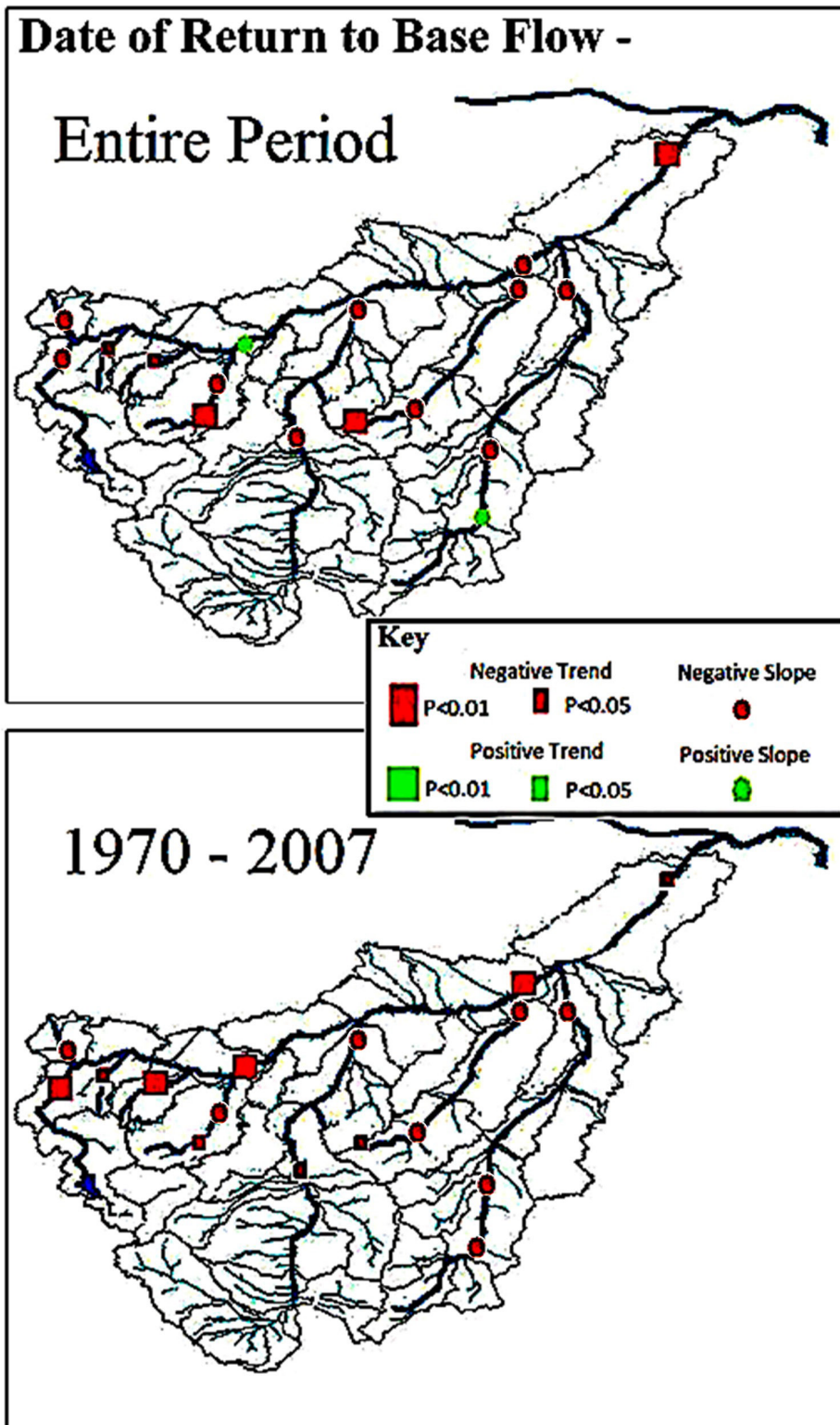


Figure 7. Trend analyses for date of return to baseflow in the YRB a) over the entire period, and b) from 1970 to 2007.

elevation areas than in areas lower in the basin. Much of this difference may be the result of the Yellowstone River mainstem and its tributaries having few large storage reservoirs that can unnaturally alter runoff patterns differentially between the tributaries and mainstem.

However, results of the regulated portions of the YRB (e.g., Bighorn and Tongue Rivers) must be interpreted more cautiously because of potential effects of reservoirs and dam releases. For evaluating the date of return to baseflow, the exclusion of the St. Xavier on the Bighorn River (site 9) from analysis was implemented because of unnatural flows owing to its location directly downstream of Yellowtail Dam (completed 1967) on the Bighorn River. This variable would be likely to be especially affected by dam operations. Other Bighorn River Basin tributary impoundments potentially influencing time series analyses results include Buffalo Bill Reservoir (completed 1910) on the Shoshone River and Boysen Reservoir (completed 1952) on the Wind River. The effects of the completion of Yellowtail Dam in 1967 can be considered, at least indirectly, by comparing results from the entire time series for three Bighorn River stations (Kane, WY: 1929-2007; St. Xavier, MT, 1937-2007; Bighorn, MT, 1946-2007) with those of the post Yellowtail Dam period 1970-2007. Although trends for these stations were similar between the two periods for most variables (e.g., annual discharge (Fig. 3), peak discharge (Fig. 4), date of peak discharge (Fig. 6), and date of return to base flow (Fig. 7), a notable difference occurred in the absolute minimum discharge (Fig. 5). Less positive trends in the more recent period (1970-2007) may reflect the effects of retaining water in the spring for later release, leading to higher minimum discharge in many years. Absolute minimum discharge trends also differ markedly in the Tongue River between the entire time series and the more recent period (1970-2007; Fig. 5). How impoundments affect the hydrograph in these systems will vary depending on reservoir operations in response to annual

water conditions and demands in each basin.

In addition to magnitude of discharge, the significantly altered timing of runoff found in this study in the YRB is consistent with that reported in numerous studies in the West (Cayan et al. 2001; Baron et al. 2002; Regonda et al. 2004; Stewart et al. 2004, 2005; Gibson et al. 2005; Mote et al. 2005; Rood et al. 2008). For example, Cayan et al. (2001) found that not just hydrological fluctuations in spring snowmelt, but also phenological fluctuations as well with earlier onset of bloom timing dates for lilacs (*Syringa vulgaris*) and honeysuckles (*Lonicera tatarica* and *Lonicera korolkowii* stopf), both strongly related to the springtime temperature variations observed mainly since the 1970's. Mote et al. (2005) also found that the rising temperatures in the west, no matter the cause, were resulting in declines in snow water equivalent (SWE) for snow packs in the west, primarily in the Cascades of Oregon. It has been argued that the most important changes occurring in the hydrological cycle in the West is the declining snowpack accumulation and earlier runoff timing caused by temperature changes (Barnett et al. 2008).

Although occasional significance in trends was found when looking at the three timing variables basin-wide, the most prevalent statistically significant trends were those indicating an earlier return of baseflow conditions (Fig. 7; Table 5). Other studies have reported similar results for return to baseflow (Baron et al. 2002; Regonda et al. 2004; Stewart et al. 2004, 2005; Gibson et al. 2005; Rood et al. 2008). For example, Rood (2008) found the greatest changes in late summer flows, when demands are the greatest, were observed in the rivers draining the east slope of the Rocky Mountains, some at a rate of 0.2 percent per year. The substantial onset of earlier runoff and earlier return to baseflows in the basin reported here suggest that the free-flowing Yellowstone River and most of its tributaries are going to be measurably affected by these changes if observed trends remain the same.

The scope of our study was limited largely to an analysis of discharges along

with an investigation of water withdrawals in the basin. (Watson 2014; Watson et al., In Press). We were unable, with existing constraints, to specifically investigate broader climatic indices such as precipitation and air temperature, nor to evaluate the issue of climate change. Although the contributing causes of observed changes in this study may be many, hydrograph changes such as we observed have been attributed in various studies to increasing consumptive water use within river basins (Baron et al. 2002; Mote et al. 2005; Rood et al. 2005, 2008) and to climate change (Vorosmarty et al. 2000; Schindler and Donahue 2006; Hall et al. 2015; Dettinger et al. 2015). For example, the magnitude of peak discharge can be affected by anthropogenic activities such as irrigation withdrawals, land use practices increasing runoff, damming of rivers, as well as changes in climate (Zelt et al. 1999; Gibson et al. 2005). Changes in the timing of peak discharge in relation to climatic factors can also differ depending on the subsurface geology as it affects how shallow and deep pathways for water contribute to the streamflow (Safeeq et al. 2013). The observed changes in stream flow magnitude and volume are thus generally consistent with current perspectives on declining snowpack, climate change, and anthropogenic forcing (e.g., water withdrawals; Vorosmarty et al., 2000; Meehl et al., 2004; Barnett et al., 2005; Mote et al., 2005; Lapp et al., 2005; Leppi 2010). The cause of the more recent changes (i.e., the 1970-2007 analysis) in magnitude and timing appears to coincide well with estimates of warming and prolonged droughts studied during the same period (Vorosmarty et al., 2000; Schindler and Donahue 2006; IPCC 2007).

There are major potential implications for competing water uses and agricultural development with declining discharges and earlier returns to baseflow. With lower discharges, especially during low flow periods, future water allocation decisions can be expected to become increasingly difficult, especially in over allocated systems, such as the Powder River. With

earlier base flow, and demand for water in the basin persisting into the fall with irrigation water users withdrawing water until they harvest crops, an earlier return to baseflow will result in more users being affected on a more frequent basis. This change toward earlier baseflows may impact water allocation decisions (Dettinger 2015), and require modified water allocation strategies, such as establishing a water use hierarchy based on beneficial use or policy changes on salvage water allocations.

Of major concern is how hydrograph changes will affect each region specifically, and if the prolonged droughts and warming are going to become the norm (IPCC 2007; Luce and Holden, 2009). Lower discharge values and earlier return to baseflow have major implications for the YRB's rivers (Schindler 2001; Schindler and Donahue 2006; Arismendi et al. 2012). As the flows decline, the ability of rivers to dilute pollutant loads and avoid thermal thresholds is reduced (Schindler 2001). As the rivers are affected by an earlier onset of snowmelt and decreased discharges due to climatic and anthropogenic factors such as withdrawals (Poff et al. 1997), there will be fewer cold days and nights (IPCC 2007), warmer and more frequent hot days (IPCC 2007), and duration and frequency of droughts will increase in most land areas (Gibson et al. 2005). The natural flow reductions and reductions from withdrawals will provide little protection against rising stream temperatures (Schindler 2001; IPCC 2007). Also, it is predicted that the trend of lessening snow packs and more rising temperatures will continue (IPCC 2007). Declining trends in the magnitude and earlier return to baseflow in the highly turbid, low gradient lower mainstem will result in the water temperature increasing substantially (Arismendi et al. 2012). Site 18, representing the mouth of the YRB watershed, near Sidney, Montana, had very noticeable declines in all variables, especially since 1970. For the distinctive native fish community and important fisheries of the lower Yellowstone River (White and Bramblett 1993), the result from

the Sidney Site (18), the most downriver, most cumulative site is of major concern because it provides the most accurate indication of how much water can be expected in that portion of the river.

Alterations in the magnitude and timing of flows identified in this study can be expected to affect the ecology of the river in many ways (Schindler 2001). Lower magnitude peak discharges and earlier timing of peak discharge could pose potential threats to fish and other aquatic or riparian species keying into them as cues for reproduction. Quantity and quality of in-river habitat for aquatic fauna will also be affected by the amount and timing of discharge and resulting temperature changes (Schindler 2001; Sabo and Post 2008). Declines in magnitude of discharge and earlier timing of runoff can thus be expected to have cascading effects through the ecosystem for fishes, aquatic organisms, riparian habitat and various ecological processes. Efforts to stabilize hydrographs in the face of anthropogenic factors such as irrigation withdrawals, the adjudication process, and human-induced climate change will be necessary to if the historical habitat and fauna of the Yellowstone River is to be maintained. To monitor the situation, analyses such as this study should be updated regularly to assess trends. Although the long period of analysis used in this study leads to confidence in the conclusions, continual updating of the study will provide insight into the potential influence of extreme drought or flood years on such analyses and to the conclusions reached.

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MODEL FOR CLASSIFYING AND MONITORING SERAL STAGES WITHIN AN IDAHO FESCUE TYPE: BIGHORN NATIONAL FOREST, WY

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ABSTRACT

An ecological vegetation model was developed in sedimentary soils on the Bighorn National Forest, Wyoming to classify seral stages within an Idaho Fescue (*Festuca idahoensis*) type. Two key plant species based on canopy cover (%), Idaho fescue and rosy pussytoes (*Antennaria rosea*), provide the required information for the model to classify seral stages and monitor vegetation trends. Three seral stages were quantitatively identified by multivariate statistical analyses for classification and had an overall accuracy of 98 percent. All three seral stages were significantly different from each other ($P < 0.05$). These seral stages provide managers three quantitative options to evaluate alternatives and meet management objectives. Application of this model within the Idaho Fescue ecological type is simple to apply, repeatable, accurate, and cost effective for field applications and management.

Key words: plant succession, diversity, canopy cover, management, grazing, wildlife

INTRODUCTION

Grasslands are a very important resource for livestock, wildlife, fisheries, watersheds, and recreation on the Big Horn Mountains in Wyoming. Management agencies periodically assesses plant community composition based on successional status or trend as part of its management program, but how are these data to be interpreted? Plant succession concepts have been used and applied for many years on rangelands for management and monitoring (Sampson 1919). Still major impacts have frequently occurred before being detected (Kershaw 1973, Block et al. 1987). This study presents a validated ecological model with key variables derived from field data to evaluate vegetation resources and monitor trends based on patterns of seral stage succession.

Grassland vegetation for the Big Horn Mountains has been evaluated for various years and includes the effects of livestock grazing on the vegetation (Beetle 1956,

Hurd and Pond 1958, Beetle et al. 1961, Hurd 1961). Monitoring changes of plant species diversity within and among the ecological seral stages from early to late succession provides a framework to assess influences associated with natural events and resource management. Quantitative ecological models with minimal input from field data can accurately measure changes in vegetation from natural and induced stresses that will provide resource managers information to achieve desired conditions or goals (Uresk 1990, Benkobi et al. 2007, Uresk and Mergen 2014).

The successional status of the Idaho Fescue (*Festuca idahoensis*) type in sedimentary soils on the Bighorn National Forest, Wyoming was based on site data collected by Beetle (1956). The objectives of this current study were: 1) to develop an ecological classification model with seral stages for the Tongue Ranger District, 2) provide field sampling and monitoring protocols.

STUDY AREA

This study was conducted on the Bighorn National Forest within north central Big Horn Mountains, Wyoming. The Idaho Fescue type for the grasslands are found in extensive open areas (Beetle 1956). Soils are sedimentary. Annual precipitation averages 53 cm at Burgess Junction, Bighorn National Forest (2463 m elevation) and ranges from 30 to 54 cm based on years from 1989 to 2017. Average monthly temperature ranges from 7.7 to 16.7^oC with a yearly average of 1.7^oC (HPRCC 2018). Growing season at Burgess Junction is 66 days.

Vegetation in the open meadows on the Tongue Ranger District is dominated by Idaho Fescue type in which Idaho Fescue is the dominant grass (Beetle 1956). Other grasses and grasslikes are mountain brome (*Bromus marginatus*), Sandberg bluegrass (*Poa secunda*) and sedges (*Carex* spp). Common forbs are lupine (*Lupinus*), rosy pussytoes (*Antennaria rosea*), oldman'whiskers (*Geum triflorum*), Hookers sandwort (*Arenaria hookeri*) and Rocky mountain phlox (*Phlox multiflora*). Additional information and overview on species richness, vegetation characteristics, topography, soils, and climate are presented by Beetle (1956), Beetle et al. (1961) and Hurd (1961). Plant nomenclature follows USDA-NRCS (2018).

METHODS

Data used for this study are from Beetle (1956). Beetle collected data on eighty six transects (sites) that consisted of 10 units per transect. Each unit consisted of four square foot nested frames (0.372 m²/unit or 3.72 m²/transect). Within each square foot frame, visual estimates of cover for each plant species were collected and averaged by unit and transect. The method was defined as the square-foot cover estimate and sampling was conducted over a three year period; 1953, 1954, and 1955.

Preliminarily, data of minor plant species were removed from analyses with mean values of ≤ 1 percent (Uresk and Mergen 2014). The remaining 16 plant

species were used as variables for analyses following procedures by Uresk (1990).

Principal component analyses reduced 16 plant species to 6. Data for the six plant species were subjected to a nonhierarchical cluster analyses (ISODATA) to group the sites (Ball and Hall 1967, del Morel 1975). Stepwise discriminant analysis further reduced 6 species to Idaho fescue and rosy pussytoes. Data for these two species were analyzed with ISODATA for final groupings (seral stages) and provided Fisher classification coefficients to assign groupings defined as seral stages (SPSS 2003, Uresk 1990). Misclassification error rates were estimated with cross validation using a jackknife or "leave one site out" procedure (SPSS 2003). With the cross validation procedure, each site was classified by the discriminant functions derived from all the other sites other than the one left out. Once classified it becomes one of the other sites. The developed model was tested and validated on random sites located in the field on the USDA-Forest Service, Tongue Ranger District for two years, 2005 and 2006.

RESULTS

A total of 16 major plant species and total canopy cover (two dimensional cover) on 86 sites are presented in Table 1. Additional plant species for grasses-sedges forbs are presented by Beetle (1956), and Hurd (1961). After initial data reduction, six species: Idaho Fescue; rosy pussytoes, old man's whiskers, sedges, timber oat grass (*Danthonia intermedia*), and Rocky Mountain phlox remained for further analyses. Additional data reduction with discriminant analyses resulted in two plant species, Idaho Fescue and rosy pussytoes. Cluster analyses of these two species grouped the data into three seral stages; early, intermediate, and late based on plant succession.

The distributions of Idaho Fescue and rosy pussytoes within the three seral stages show the ecological dynamics of these species throughout the system from early to late plant succession (Fig. 1, Table 2). These

Table 1. Average canopy cover (%) and standard errors (in parentheses) for common plant species and other variables by seral stages in sedimentary soils on the Bighorn National Forest, WY (Beetle 1956). Seral stages are significantly different from each other ($P < 0.05$)

Species or variable	Late ¹ n = 35 ²	Intermediate n = 12	Early n = 39
common yarrow <i>Achillea millefolium</i>	2.3(0.3)	2.6(0.7)	4.3(0.5)
pale agoseris <i>Agoseris glauca</i>	1.9(0.4)	0.3(0.1)	2.7(0.5)
slender wheatgrass <i>Elymus trachycaulus</i>	1.3(0.2)	0.3(0.2)	3.3(0.7)
sosy pussytoes <i>Antennaria rosea</i>	5.5(3.9)	21.5(1.4)	2.4(0.4)
Hooker's sandwort <i>Arenaria hookeri</i>	5.3(0.7)	8.4(2.3)	2.8(0.3)
sedge <i>Carex spp</i>	9.9(1.1)	19.1(1.7)	8.6(1.4)
field chickweed <i>Cerastium arvense</i>	3.3(0.5)	0.5(0.3)	4.0(0.6)
timber oatgrass <i>Danthonia intermedia</i>	3.7(0.7)	1.1(1.1)	3.3(0.6)
Idaho fescue <i>Festuca idahoensis</i>	24.9(1.0)	17.4(2.0)	9.5(0.6)
old man's whiskers <i>Geum triflorum</i>	04.6(0.8)	5.5(1.7)	4.5(0.9)
silky lupine <i>Lupinus sericeus</i>	2.6(0.6)	1.5(1.4)	3.1(1.0)
Rocky Mountain phlox <i>Phlox multiflora</i>	4.0(0.6)	3.0(1.2)	4.0(0.8)
Sandberg bluegrass <i>Poa secunda</i>	3.3(0.3)	3.1(0.5)	4.1(0.5)
Potentilla <i>Dasiphora spp</i>	2.4(0.4)	0.6(0.2)	3.6(0.6)
Rocky Mountain spikemoss <i>Selaginella densa</i>	2.4(0.8)	3.0(1.4)	1.1(0.4)
common dandelion <i>Taraxacum officinale</i>	1.3(0.3)	0.6(0.5)	3.6(0.7)
Total cover ¹	97.3(2.8)	86.7(2.8)	66.8(2.0)

¹ Two dimension cover of individual plant species

² Number of sites.

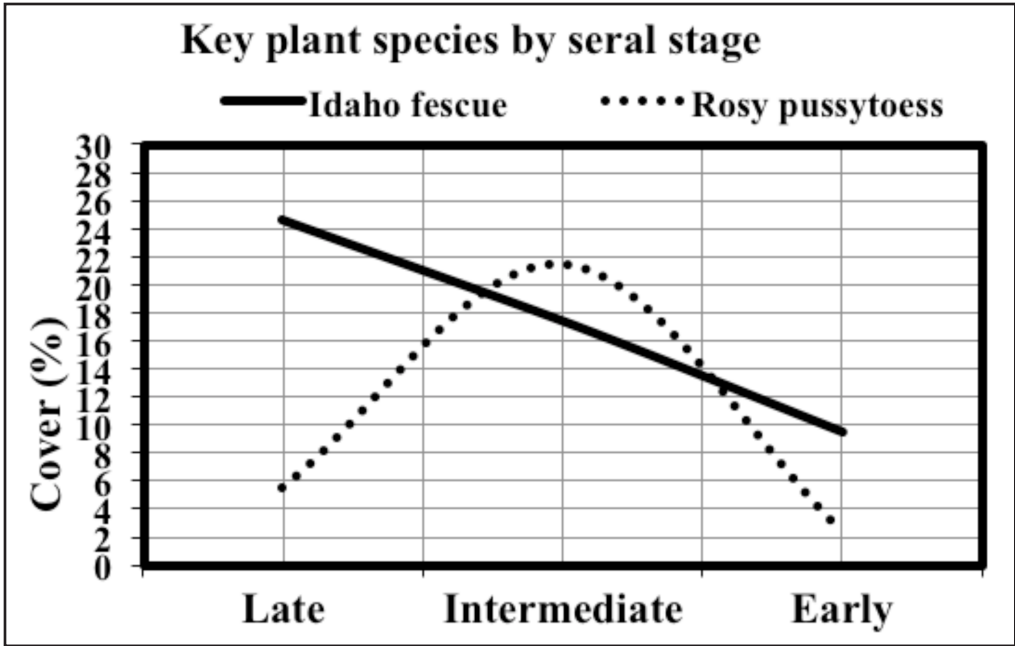


Figure 1. Canopy cover of key variables, Idaho fescue and rosy pussytoes displayed throughout three seral stages in the Idaho fescue association in sedimentary soils on the Bighorn National Forest, WY (Beetle 1956).

Table 2. Mean canopy cover (%) of key plant species for three seral stages within an Idaho Fescue association in sedimentary soils on the Bighorn National Forest, WY (Beetle 1956).

Seral	n	MEAN CANOPY COVER	
		Idaho fescue	Rosy pussytoes
Late	35	24.5	5.5
Intermediate	12	17.4	21.5
Early	39	9.5	2.4

n = number of sites

three seral stages were significantly different from each other ($P < 0.05$). Idaho fescue dominated the late seral stage (25% cover) followed by rosy pussytoes (6% cover). The intermediate seral stage was greatest for rosy pussytoes (22% cover) followed by Idaho fescue (17% cover). Both plant species in the early seral stage had low canopy cover with 10 percent and 2 percent for Idaho fescue and rosy pussytoes, respectively.

Fisher's classification discriminant

function coefficients present the biotic potential and significance of each plant species for predicting and classifying seral stages (Table 3). The species with the greatest coefficient by seral stage expresses the biological indicator value of these two plants within this ecological type. An example of applying the discriminant function coefficients for new field data collected on a site to calculate seral stage assignment and monitoring is presented in Table 4. A seral stage assignment is determined by multiplying Idaho fescue and rosy pussytoes canopy cover for each seral stage (row) and the products are summed

Table 3. Fisher's discriminant function coefficients for classification of seral stages of key species within an Idaho fescue association in sedimentary soils on the Bighorn National Forest, WY (Beetle 1956).

Species	Late	Intermediate	Early
Idaho fescue	0.868	0.558	0.331
Rosy pussytoes	0.376	1.689	0.169
Constant	-12.935	-24.112	-2.89

(+ and -) including the constants for the score in each row. The greatest positive or the least negative score assigns the seral stage for this site. For this example, the site is assigned to early seral stage of plant succession with a value of **3.43** (Table 4). Developed coefficients may be programed into a personal digital assistant (PDA) for assignments of seral stages in the field for classification and monitoring at 98 percent accuracy.

Late seral stage

Idaho fescue dominated the late seral stage with 25 percent canopy cover for 35 sites (Table 1). Sedges provided 10 percent, followed by rosy pussytoes, Hooker’s sandwort, old man’s whiskers, and Rocky Mountain phlox with 6 percent, 5 percent and 5 percent, respectively. Eleven other plant species displayed less canopy cover. Total canopy cover was 97 percent.

Intermediate seral stage

Rosy pussytoes contributed the greatest cover with 22 percent (Table 1). Sedges exhibited 19 percent cover, Idaho fescue 17 percent, Hooker’s sandwort 8 percent, and old man’s whiskers 6 percent. The other 11 plant species displayed lower cover. Total canopy cover was 87 percent. Twelve sites were in the intermediate seral stage.

Early seral stage

All canopy cover values for plant species in the early seral stage were low ranging from 1 percent to 10 percent for 39 sites (Table 1). Idaho fescue provided the greatest cover at 10 percent followed by

sedges, old man’s whiskers with 9 percent and 5 percent correspondingly. Total canopy cover was 67 percent.

DISCUSSION

The ecological model we present for Idaho fescue type on sedimentary soils is based on plant community succession and classification by seral stage. Plant dynamics and species changes between and among seral stages are quantitative estimates and they may be applied to meet resource management objectives. Disturbances such as livestock and wildlife grazing, fire, and climatic factors will move plant species associations within and between seral stages for the ecological type (Beetle 1956, Beetle et al. 1961, Hurd 1961).

The quantitative model developed was based on canopy cover (Beetle 1956) and defined three seral stages which may serve as resource management objectives. These seral stages represent a continuum over the landscape but are discrete categories for purposes of management. The model can be applied to allotments and/or pastures. Seral classification and monitoring between and among the stages is based on two key species, Idaho fescue and rosy pussytoes, with a 98 percent accuracy. Livestock grazing intensity and length of time may be adjusted to modify present seral stages to meet planned resource management objectives (Beetle 1956, Beetle et al. 1961, Hurd 1961, Severson and Urness 1994). A particularly useful feature is that of monitoring intra-seral stage changes to estimate movement toward or away from a

Table 4. An example of assigning seral stages by using Fisher’s discriminant coefficients with site data collected by Beetle (1956) in the Idaho fescue association in sedimentary soils on the Bighorn National Forest, WY.

Seral Stage	Idaho fescue (Coeff ¹ * Cover	+	Rosy pussytoes (Coeff * Cover)	Constant	=	Score
Late	(0.868 * 16	+	0.376 * 6)	-12.935	=	3.209
Intermediate	(0.558 * 16	+	1.689 * 6)	-24.112	=	-5.050
Early	(0.331 * 16	+	0.169 * 6)	-2.89	=	3.43²

¹ Coeff = coefficient

² Assigned serial stage

management objective. Periodic collections of plant community data for evaluation with application of the model are an important asset in evaluating the resources. The model is quantitative, accurate, repeatable, and cost effective.

Managing for all three seral stages is a preferred alternative and provides for plant and animal diversity within the Idaho fescue type. The recommendation is to have 10-15 percent of the landscape in early and late seral stages with approximately 70 percent in the intermediate stage (Kershaw 1973, Mueller-Dombois and Ellenberg 1974). A mosaic of seral stages across the landscape will provide optimum plant and animal diversity (Rumble and Gobeille 1998; Fritcher et al. 2004; Uresk and Mergen 2014). Management for a single seral stages is not adequate or practical for multiple use management based on abundance and species diversity. The intermediate seral stage that approximates 70 percent of the recommended landscape and is approximately equal to moderate grazing (Beetle et al. 1961). This equates to band 5 on the modified Robel pole for the Tongue Ranger District on the Bighorn National Forest, Wyoming (Uresk and Juntti 2008).

Collection of new field data for a relative small site to determine seral stage classification and monitoring canopy cover only requires data collection of two key plants, Idaho fescue and rosy pussytoes. Two transects, 20 m in length with 20 Daubenmire frames (20 cm x 50 cm) per transect that equates to 4 m² per site (Daubenmire 1959). Beetle (1959) reported 3.7m² per site. Transects are widely spaced ≥ 20 m at a minimum for a total of 40 quadrats each spaced 1m apart per transect. Two sites per section (640 acres) are recommended (Benkobi et al. 2007). Species should be at or near full expression for growth. Collection of data may be yearly or 3 to 5 year intervals. For further information see USDA-Forest Service website (Uresk et al. 2010).

The model we present is restricted to the Idaho fescue type, however the protocol used to develop the ecological model

has been applied and used by managers on montane to prairie grasslands (Uresk 1990, Uresk et al. 2012, Uresk and Mergen 2014). Additional 15 vegetation types for developed ecological models with publications that have been applied and used by managers are presented by Uresk et al. (2010). In many cases, the development of these models would be useful in interpreting voluminous plant community data for other geographical areas and community composition of plant species.

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THE GENETIC STRUCTURE OF AMERICAN BLACK BEAR POPULATIONS IN THE SOUTHERN ROCKY MOUNTAINS

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ABSTRACT:

Large and wide-ranging carnivores typically display genetic connectivity across their distributional range. American black bears (*Ursus americanus*) are vagile carnivores and habitat generalists. However, they are strongly associated with forested habitats; consequently, habitat patchiness and fragmentation have the potential to drive connectivity and the resultant structure between black bear subpopulations. Our analysis of genetic structure of black bears in the southern Rocky Mountains of Wyoming and Colorado ($n = 296$) revealed two discrete populations: bears in northern Wyoming were distinct ($F_{ST} = 0.217$) from bears in southern Wyoming and Colorado, despite higher densities of anthropogenic development within Colorado. The differentiation we observed indicates that bears in Wyoming originated from two different clades with structure driven by the pattern of contiguous forest, rather than the simple distance between populations. We posit that forested habitat and competitive interactions with brown bears reinforced patterns of genetic structure resulting from historic colonization. Our work suggests that forested habitat is an important force structuring populations in the southern Rocky Mountains, even for populations of highly vagile carnivores.

Key words: competition, connectivity, landscape, microsatellite, Ursidae

INTRODUCTION

Highly mobile mammals, especially those that display plasticity in their resource use, are often well-connected by dispersal and exhibit little genetic structure (i.e., genetic variation between subpopulations; Evanno et al. 2005) across their range (Wayne and Koepfli 1996). Such connectivity is especially evident among carnivores, which generally possess strong dispersal power (Lee and Vaughan 2003). For example, forest carnivores such as lynx (*Lynx canadensis*) and martens (*Martes americana*) exhibit little genetic structure across much of their distributional range

in North America (Schwartz et al. 2002; Kyle and Strobeck 2003), and puma (*Puma concolor*) populations are panmictic across the central Rocky Mountains (Anderson et al. 2004). Even populations of carnivores inhabiting systems featuring strong barriers to dispersal, such as island archipelagos, can exhibit much connectivity and gene flow between populations (Paetkau et al. 1998). There are, however, notable exceptions with wolverines (*Gulo gulo*) in Scandinavia (Walker et al. 2001) and wolves (*Canis lupus*) in northeastern Europe displaying significant genetic structure (Hindrickson et al. 2013).

American black bears (*Ursus americanus*) are habitat generalists with strong dispersal power (Lee and Vaughn 2003); nevertheless, genetic differentiation has been documented during the assessment of cross-continental translocation efforts (Triant et al. 2004) and along the southern periphery of black bear range in Florida and Arizona (Dixon et al. 2006; Atwood et al. 2011). Previous studies examining the drivers of genetic diversity among black bear populations have attributed structure to isolation by distance (Triant et al. 2004; Pelletier et al. 2012), or barriers from topography (Cushman et al. 2006; Bull et al. 2011) and habitat loss (Csiki et al. 2003; Triant et al. 2004; Dixon et al. 2006; Onorato et al. 2007; Atwood et al. 2011). The amount of forest cover, in particular, can structure bear populations by limiting gene flow when forest cover is naturally patchy or fragmented due to anthropogenic change (Bull et al. 2011).

Forest cover not only provides suitable habitat for black bears but it also buffers interspecific interactions with brown bears (*Ursus arctos*; Aune et al. 1994; Apps et al. 2006). Competition between black and brown bears in western North America can influence the spatial distribution of these species (Apps et al. 2006) with coexistence facilitated by niche partitioning (Herrero 1972; Aune et al. 1994). When brown bears are present, black bears possess smaller territories and are displaced from open habitats into forested areas (Holm et al. 1999). Among carnivores, such competition and niche partitioning can also be an important barrier to gene flow and even lead to genetic structuring, especially for the subordinate competitor (e.g., Ruiz-Gonzalez et al. 2015).

While much attention has focused on how habitat loss and fragmentation and anthropogenic barriers reduce genetic connectivity (Sawaya et al. 2014) and increase genetic structure (Coster and Kovach 2012), anthropogenic development is not a uniform dispersal barrier (Bull et al. 2011). In particular, bears in urbanized landscapes demonstrate flexibility in

behavior and resource use (Kirby et al. 2016) and in some cases, even benefit from human development (Beckmann and Berger 2003).

To date, little is known about the subpopulation structure of black bears in the southern Rocky Mountains. Previous work on black bear phylogeography revealed three haplotypes structured into nine regional groups across North America, with bears in Colorado and the southern Rocky Mountains belonging to a group separate from those in Montana and the northern Rocky Mountains (Puckett et al. 2015). Since bear populations throughout Wyoming were not sampled, the origin of these populations and finer-scale population structure in this region are unknown. Herein, we analyzed the genetic population structure of black bears across the southern Rocky Mountains to identify the clade to which this previously unsampled region belongs and assessed the potential importance of landscape features in determining population structure. We hypothesized that black bears in northern and central Wyoming would belong to different clades when compared to southern Wyoming and Colorado and that this southern clade would display less genetic structure and more connectivity compared to the northern clade, due to the greater amount of contiguous forest.

STUDY AREA

We collected hair from hunter-harvested black bears ($n = 150$) during the fall 2011 hunting season throughout their range in Colorado, which encompasses the western two-thirds of the state, including the Front Range in the northeast and San Juan Mountains in the southwest. We sampled bears in Wyoming ($n = 146$) from baited hair traps and from hunter-harvested bears from 1994 through 1997 at three study sites: the Tetons in the Black Rock area outside the Moran Junction entrance to Grand Teton National Park, the Bighorn Mountains, and the Medicine Bow Mountains (Fig. 1). The Tetons are a continuation of the central Rocky Mountains of Montana and Idaho with vegetation communities transitioning

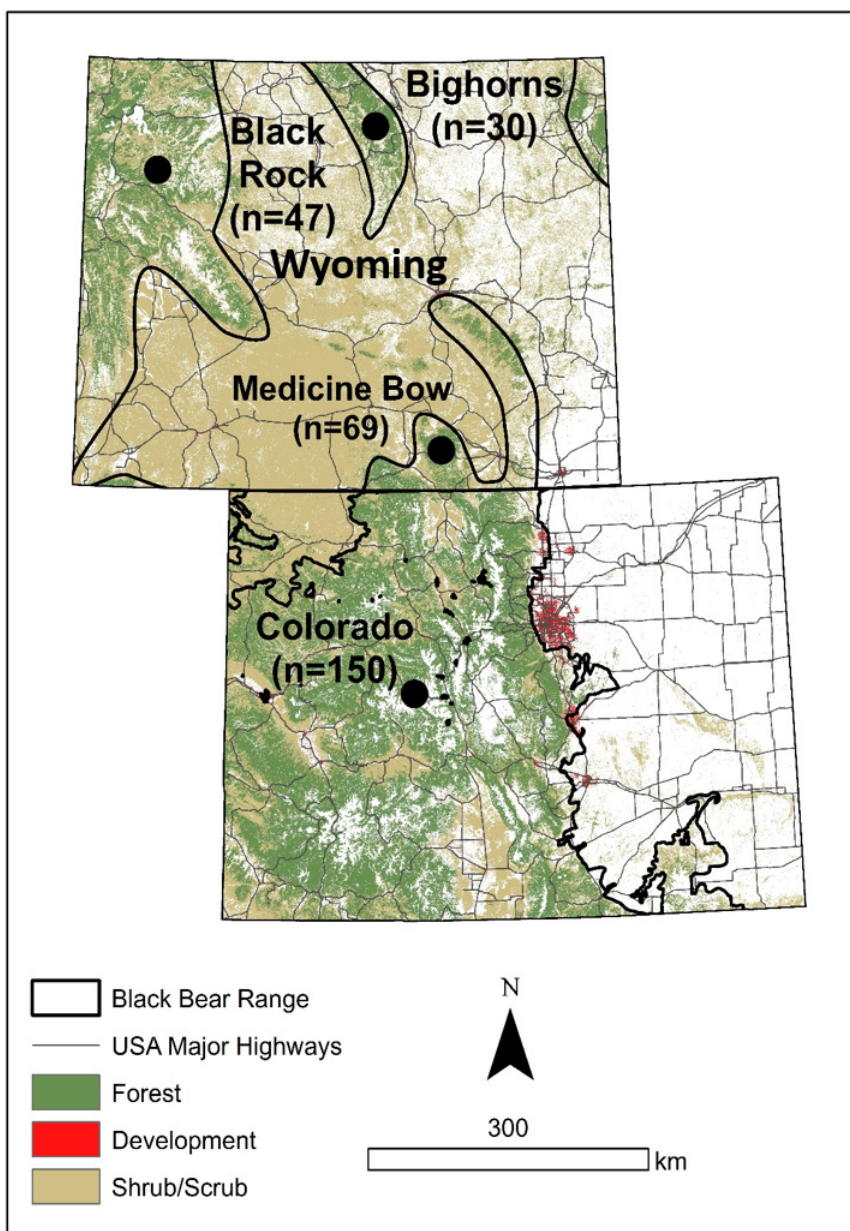


Figure 1 The geographic range of black bears across Wyoming (Buskirk 2016) and Colorado (Colorado Parks and Wildlife) with forest, shrub, and development land cover (Homer et al. 2015) and the major roadways (U.S. Interstates, State Highways, U.S. Routes; ESRI). Black bear range is delineated by the black line and sample locations are defined by the center point of each sample area in the Black Rock Mountains, Bighorn Mountains, Medicine Bow Mountains, and in Colorado. The area of shrub/scrub in central Wyoming represents the Wyoming Basin.

from aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*) to ponderosa pine (*Pinus ponderosa*) and subalpine tundra at higher elevations. The

Bighorn Mountains are an isolated range in north-central Wyoming separated from the Tetons by sagebrush (*Artemisia* spp.) shrubland. In southeastern Wyoming, the

Medicine Bow Mountains are an extension of the Front Range of the Colorado Rocky Mountains, consisting of subalpine tundra, coniferous forests mixed with aspen, ponderosa pine, and pinyon-juniper (*Juniperus* spp.) at lower elevations (Knight et al. 2015). The Wyoming Basin, which stretches from northeastern to southwestern Wyoming, is comprised of shrub-steppe habitat which is dominated by sagebrush, grassland, and intermixed with short-grass prairie. The basin limits the dispersal of forest-obligate bird and mammal species (Findley and Anderson 1956) and similarly may limit dispersal between black bears in northern and southern Wyoming, leading to genetic differentiation between subpopulations (McDonald et al. unpubl. data).

MATERIALS AND METHODS

We extracted deoxyribonucleic acid (DNA) from intact follicles from the Colorado and Wyoming bears following standard procedures using a QIAGEN DNeasy Blood and Tissue Extraction Kit (QIAGEN, Valencia, CA). We genotyped bears using four microsatellite loci: G1A, G10C, G1D, and G10L (Paetkau and Strobeck 1994). Microsatellites were amplified under the following conditions: initial denaturing at 94°C for 2 min; 33 cycles of amplification at 94°C for 30 s, 56°C for 30 s, 72°C for 1 min; final elongation of 72°C for 5 min; incubation at 4°C. The total reaction volume was 12 µl and contained 7.5 µl of dH₂O, 1.25x PCR buffer, 0.25 mM of deoxynucleoside triphosphate, 0 to 1.56 mM of MgCl₂, 0.33 µg/µl of Bovine Serum Albumen, 1 U of Taq DNA polymerase, 0.33 µM of fluorescently labeled forward primer and reverse primer, and 1.5 to 2.0 ng/µl of DNA. Fragment sizes for the Colorado bears were determined using an ABI 3730 DNA Analyzer (Applied Biosystems) and scored in GeneMapper (Applied Biosystems). The alleles from the Wyoming bears were initially scored using electrophoresis on a 25-cm, 7% polyacrylamide gel. We used a 350-bp genetic ladder on a Li-Cor 4200-S

automated DNA sequencer to assess allele sizes and genotyped individuals using GeneImagIR™, version 3.0 software. To test whether allelic scoring of the Colorado bears and of the Wyoming bears was consistent, we randomly selected 20 DNA samples of the genotyped bears from Wyoming, amplified, and scored these samples following the conditions described above for the Colorado bears. We adjusted the alleles from the Wyoming bears based on observed allele frequency distributions per locus as described in a previous study of black bears (Paetkau 1997; Csiki et al. 2003). Alleles at locus G1A and at locus G10C aligned with the published base pair sizes and were not adjusted; we decreased alleles at G1D by one base pair, and increased alleles at G10L by one base pair if they were 171 base pairs or less, or by two base pairs if they were greater than 171 base pairs.

We calculated allele frequencies, observed (H_o) and expected heterozygosity (H_e ; GENEPOP v. 4.2), and the polymorphism information content (CERVUS v. 3.0.7; Kalinowski et al. 2007) and tested for departures from Hardy-Weinberg equilibrium and genotypic linkage equilibrium (GENEPOP v. 4.2) for the Colorado and Wyoming populations separately (Raymond and Rousset 1995), applying a Bonferroni correction (Rice 1989). We tested for genetic differentiation between populations using pairwise F_{ST} (Weir and Cockerham 1984) values for each locus separately and for all loci combined. To further assess the genetic structure of bears in Colorado and Wyoming, we tested for isolation by distance with a Mantel test (Rousset 2008) with genetic distance expressed as $F_{ST}/(1 - F_{ST})$ and geographic distance expressed as the natural logarithm of the distance in kilometers between populations. We defined the geographic location of the three populations in Wyoming using the center point of each of the three sample areas. Due to the broad distribution of black bears in Colorado, we represented the Colorado sample area with the bear capture site that was geographically closest to Wyoming. We

calculated the straight-line distance between each population (ArcGIS version 10.4.1, Environmental Systems Research Institute). We then evaluated the influence of habitat type, defined broadly as forest and shrub/scrub habitat, which is dominated by shrubs and trees less than five meters tall (Homer et al. 2015; Jonkel and Miller 1970), on black bear population structure. We calculated the proportion of forest and shrub land cover along the straight-line distance between sites using 2011 National Landcover Data and weighted the simple distances between sites by the estimated proportions (Geospatial Modeling Environment version 0.7.2, Spatial Ecology). We then estimated isolation by distance through forest and shrubland habitat types.

To cluster individuals by genotype in the absence of geographic information, we used STRUCTURE version 2.3.4 (Pritchard et al. 2000). We performed ten independent runs of $K = 1 - 10$, where K indicates the number of populations based on genotypic similarity, with and without population gene flow at 50,000 Markov chain Monte Carlo repetitions and a burn-in period of 5,000. We used the admixture model due to expected gene flow among the populations. The final K value was selected by plotting K ($K = 1 - 10$) versus the ΔK ($\Delta K = m([L''K])/s[L(K)]$) where $L(K) = \ln P(D)$ and selecting the best fit (Evanno et al. 2005).

RESULTS

All four loci, G1A, G10C, G1D, and G10L, were polymorphic, with average observed heterozygosity ranging from 0.38 in Wyoming to 0.50 in Colorado (Table 1). The Black Rock population and the Medicine Bow populations departed from Hardy-Weinberg equilibrium and one pair of loci (G1A and G10L) exhibited linkage disequilibrium ($P = 0.002$).

Gene flow was highest between the Bighorn and Black Rock populations ($F_{ST} = 0.023$, weighted distance = 132.73 km) and between the Colorado and Medicine Bow populations ($F_{ST} = 0.029$, weighted distance = 63.21 km) and lowest between the Black Rock and Medicine Bow populations ($F_{ST} = 0.279$, weighted distance = 339.08 km; Table 2). Tests of isolation by distance indicated genetic structure between the bears at the four study sites. Isolation by the straight-line distance between sites showed a positive but non-significant relationship ($r^2 = 0.58$, $P = 0.08$). Isolation by distance of forest and shrub cover between sites were positive and significantly related ($r^2 = 0.72$, $P = 0.03$; Fig. 2).

Population assignment tests revealed two genetically distinct populations because ΔK reached the maximum value ($\Delta K = 12.7$) at $K = 2$. When we used our four sampling locations as predefined populations, STRUCTURE clustered 79% of the bears

Table 1. Allelic richness (A_r), base pair size (BP), observed (H_o) and expected (H_e) heterozygosity, and polymorphism information content (PIC) for Colorado ($n = 150$) and Wyoming ($n = 146$) black bear populations at 4 microsatellite loci (G1A, G10C, G1D, and G10L).

Location	Locus	A_r	BP	H_o	H_e	PIC
Colorado	G1A	6	201-216	0.50	0.50	0.68
	G10C	3	114-120	0.52	0.48	0.30
	G1D	6	186-200	0.49	0.51	0.73
	G10L	11	158-191	0.48	0.52	0.87
Wyoming	G1A	6	197-211	0.27	0.73	0.74
	G10C	6	114-126	0.43	0.57	0.45
	G1D	8	186-198	0.43	0.57	0.77
	G10L	17	154-193	0.39	0.61	0.91

Table 2. Pairwise F_{ST} and distance (both straight-line and weighted) between black bear sampling locations in the Black Rock Mountains in northwestern Wyoming ($n = 47$); Colorado ($n = 150$), the Medicine Bow Mountains in south-central Wyoming ($n = 69$), and the Bighorn Mountains in northern Wyoming ($n = 30$).

	F_{ST}	Straight-line Distance (km)	Distance Weighted by Forest and Shrub (km)
Black Rock/Bighorns	0.023	236.62	132.73
Colorado/Medicine Bow	0.029	77.68	63.21
Colorado/Bighorns	0.158	404.72	253.41
Black Rock/Colorado	0.198	443.95	411.14
Medicine Bow/Bighorns	0.234	344.09	241.56
Black Rock/Medicine Bow	0.279	419.82	339.08

from Colorado and 86% of the bears from the Medicine Bow Mountains into one population and 92% of the bears from the Black Rock Mountains and 94% of the bears from the Bighorn Mountains into another. Without predefined populations, 87% of the bears from Colorado and 91% of the bears from the Medicine Bow Mountains were clustered into one population and 98% of

the bears from the Black Rock Mountains and 100% of the bears from the Bighorn Mountains were clustered into the other (Fig. 3).

DISCUSSION

Although bears possess strong dispersal power, black bears in the southern Rocky Mountains can be separated into two

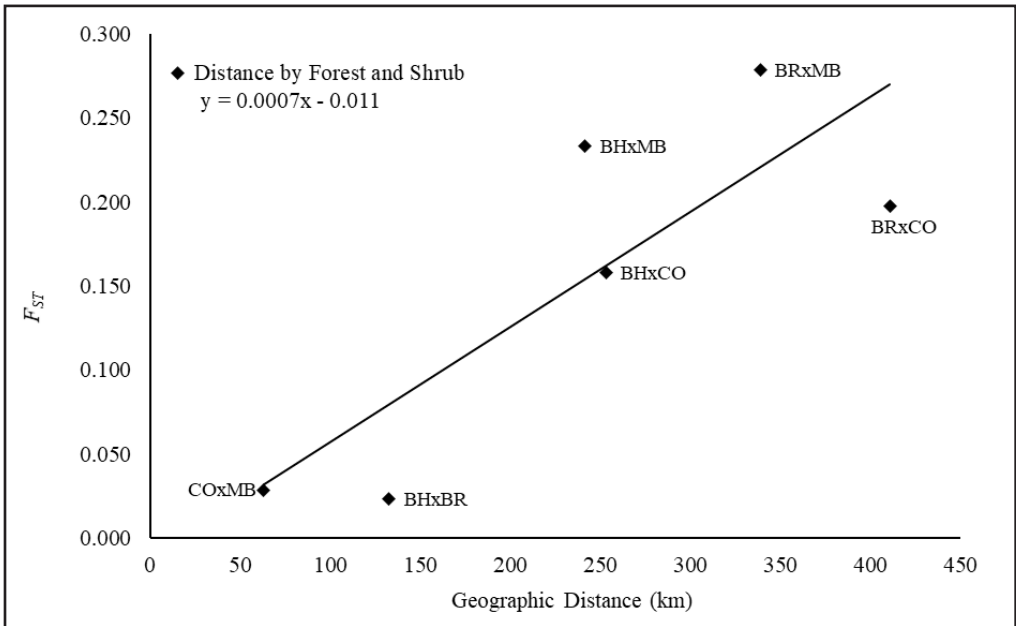


Figure. 2 Results of isolation by distance analysis showing distance weighted by the proportion of forest and shrubland between populations (Medicine Bow Mountains = MB, Black Rock Mountains = BR, Bighorn Mountains = BH, Colorado = CO) compared to the pairwise genetic distance (F_{ST}). The F_{ST} between Medicine Bow and Black Rock Mountains and between Medicine Bow and the Bighorn Mountains each are higher than expected given the distance through bear habitat between populations indicating that the Wyoming Basin may limit dispersal between these populations.

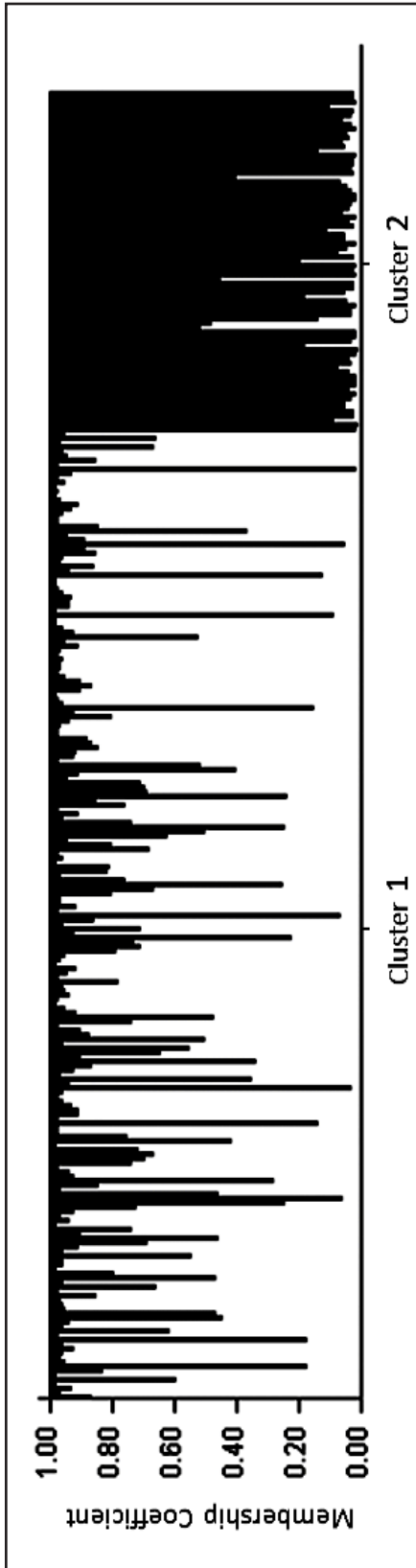


Figure 3. The proportional membership of each individual black bear in the two clusters STRUCTURE identified without predefined populations. The white segment represents Cluster 1 (Colorado and Medicine Bow Mountains) and the black segment represents Cluster 2 (Black Rock Mountains and Bighorn Mountains).

discrete genetic populations. Black bears in northern Wyoming (Black Rock and the Bighorn Mountains) clustered into one distinct population and bears in southern Wyoming and Colorado clustered into another. These results reveal the origin of bears throughout a heretofore unsampled region within their distributional range; in particular, that black bears along the southern part of Wyoming belong to the previously described southern genetic group extending from Colorado south through New Mexico, while black bears in north and central Wyoming belong to the northern clade that ranges from Montana into Canada. The level of divergence we detected between northern Wyoming and the southern Wyoming/Colorado complex was within the range of F_{ST} values reported by other studies on black bear population structure. The divergence we observed was lower compared to black bear populations in Louisiana, where populations were augmented with bears from Minnesota and formed two distinct populations ($F_{ST} = 0.206$; Triant et al. 2004). On the other hand, the level of divergence we observed was much greater than those reported for populations sampled elsewhere in relatively contiguously forested regions and originating from the same phylogenetic cluster (Puckett et al. 2015) in eastern North America. In Ontario, black bears displayed weak structure ($F_{ST} = 0.06$) resulting from isolation by distance across much of their distribution with the exception of a geographically isolated population (Pelletier et al. 2012). Similarly, in New Hampshire black bears exhibited low levels of genetic structure ($F_{ST} = 0.014$) despite increasing anthropogenic pressures (Coster and Kovach 2012) and bears sampled in the forests of South Carolina are considered to be one population ($F_{ST} = 0.023$; Drewry et al. 2012). Our estimated F_{ST} were most similar to those observed in the highly fragmented forests of Florida ($F_{ST} = 0.224$; Dixon et al. 2006) and

southeast Arizona ($F_{ST} = 0.112$; Atwood et al. 2011). Altogether, our findings suggest that the amount of forest cover between populations, which facilitates dispersal in black bear populations elsewhere (Cushman et al. 2006; Bull et al. 2011), is the primary driver of genetic structure when comparing bears in the northern clade (Black Rock and Bighorns) to those in the southern Rocky Mountains (Colorado and Medicine Bow).

Given that Colorado has a higher human population density and greater anthropogenic development (Table 3), our findings that Colorado bears exhibited greater connectivity compared to bears at the three study sites in Wyoming may be unexpected. However, development does not necessarily act as a barrier to bear movement (Coster and Kovach 2012) and can increase foraging availability (Kirby et al. 2016) and enhance survival (Beckmann and Berger 2003). In addition to a higher housing density, Colorado features twice as much forested area compared to Wyoming (United States Forest Service 2016), which may support panmixia of black bears. Our findings support the notion that habitat connectivity via forest cover plays a dominant role, rather than anthropogenic development, in black bear connectivity and regional genetic structure.

We propose that the biological mechanisms behind our finer-scale findings that bear genetic structure is explained by patterns of habitat connectivity, not only simple distance between subpopulations, is a consequence of colonization, habitat associations, and historic competitive interactions. The current distribution of black bears is explained by patterns of dispersal out of glacial refugia (Puckett et al. 2015) and the divergence we observed between bears in northern and southern

Wyoming appears to have resulted from this historic pattern of colonization. We propose that this historic structure has been reinforced by the strong association between black bears and forest cover throughout their distributional range. Forested habitats confer abundant food resources (Jonkel and Cowan 1971), enhanced denning opportunities (Johnson et al. 1978), and increased vegetative cover for movement and dispersal (Herrero 1972). The absence of contiguous forest across large regions of Wyoming may limit bear dispersal between northern and southern Wyoming, strengthening historic patterns of genetic structure in this region. In addition, black bear use of forested habitats is enhanced in areas where they are sympatric with brown bears. Such behavior has been observed near the Black Rock study site, where black bears selected for forest and avoided open habitats in the presence of brown bears (Holm 1998; Schwartz et al. 2002). The presence of brown bears in northwestern Wyoming likely restricts black bears to forested areas and decreases gene flow between populations separated by open habitat, particularly across the Wyoming Basin, resulting in the structure we observed. Since brown bears occur in open habitats more often than forested areas (Herrero 1972; McLellan and Hovey 2001), it is unlikely that brown bears were common in Colorado forests, leading to the sort of panmixia found in black bears in Canada (Pelletier et al. 2012). The extirpation of brown bears elsewhere in North America has altered black bear habitat use and distribution through competitive release: in Labrador, black bears expanded habitat use into the tundra (Veitch and Harrington 1996) and in California, black bears colonized the central coast, creating a population distinct from

Table 3. The population density, housing density, and total road density, including primary, secondary, and rural roads (United States Census Bureau 2012), per square kilometer in Colorado and Wyoming.

Location	Population	Housing Units	Roads
Colorado	18.7	8.21	1.09
Wyoming	2.22	1.03	0.98

other neighboring populations (Brown et al. 2009). While it is difficult to disentangle habitat-mediated competition from the various habitat requirements of black bears across their range, we believe that both are important factors reinforcing the historic population structure of bears in this region. Our study reveals the phylogenetic origin of black bears in the southern Rocky Mountains and the importance of historic colonization events, habitat associations, and competition in shaping the current population genetic structure of bears in this region. Our findings identify that biological mechanisms, not merely distance, can structure populations of a highly vagile carnivore. Understanding the drivers of population structure is important for the long-term conservation and management of large carnivores, particularly in increasingly altered landscapes, where a suite of novel conditions is impacting carnivore population connectivity.

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SYNERGISTIC EFFECTS OF ROAD CLOSURE, CLIMATE AND VEGETATION CHANGE ON ELK COUNTS: IMPLICATIONS FOR MANAGEMENT

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ABSTRACT

Increasing our understanding of the effects motor vehicles have on elk populations is vital to their management and past research has consistently shown that elk avoid roads and traffic. However, the fine-scale impact of traffic volume is rarely quantified and the environmental context experienced by elk at the time of disturbance is systematically ignored in these studies. We use an experimental design where roads are opened or closed to motorized traffic at specific times of year, and where motorized traffic has been quantified. We provide an environmental context to the study of the impacts of road closure on elk counts by accounting for climatic and vegetation changes over the course of the study. We specifically quantify the impact of road access, vegetation green-up, and snow dynamics on Rocky Mountain elk (*Cervus canadensis nelsoni*) counts along the main road in the Gros Ventre River drainage, WY, before and after two gates were sequentially opened to the public during the spring and early summer of 2010–2014. Elk counts increased with snow depth along the main road, and counts decreased as snow receded and vegetation greened over a 5-year period ($p < 0.001$). An increase in vehicle traffic resulted in a significant decline in elk counts ($p < 0.001$), which decreased at a rate of 1.42% for each unit increase in vehicle traffic. Our results indicate that gate closures in the Gros Ventre River Drainage decreased vehicle-related anthropogenic disturbance for elk, and that environmental variables affect elk counts and distribution further. Wildlife managers should consider both motorized vehicle traffic and the environmental context elk experience when managing road access in elk habitat.

Key words: *Cervus canadensis*, Elk, Climate, NDVI, Road, Traffic, Winter Severity Index.

INTRODUCTION

Roads are important for recreational access, commerce, and firefighting activities, but can have negative effects on animal distributions and habitat use. Fahrig et al. (2009) synthesized 79 studies covering 131 species and 30 species groups, concluding that “the negative effects of roads on animal abundance outnumbered the positive effects by a factor of 5”, and that effects on large mammals were predominantly negative. Motorized travel can reduce abundance of some species near travel areas by displacing them towards areas of less motorized

use – a direct impact. This could displace animals to lesser quality habitats, indirectly resulting in poorer fitness, and possibly abundance – an indirect impact. Because of the importance of elk-related recreation in the Western United States, previous studies focused on the impacts of roads and motorized-traffic on elk (Bolon 1994).

Early research assessed the effects of roads on elk distribution and habitat use, focusing on the density of fecal pellet groups and distance from roads as indicators of habitat use. A decrease in the relative density of pellets with increasing proximity to roads indicated an aversion to roads. For

instance, elk (*Cervus canadensis nelsoni*) in the Blue Mountains of Washington reduced habitat use within 0.5 miles from roads that were open to motorized traffic and preferred habitat further from main forest roads. Perry et al. (1977) showed elk reduced habitat use near roads by up to 95% compared to similar habitat away from roads. Lyon (1979) found elk regularly preferred similar habitats further from roads. The effect was most pronounced in areas where road densities were as low as 1 mile of road per sq. mile. Subsequent studies using radiotelemetry data of collared elk supported these results, whereby elk consistently avoided habitat near open roads as opposed to similar habitat away from roads (Marcum 1975, Hershey et al. 1976, Irwin et al. 1983, Edge et al. 1987). Witmer et al. (1985) observed that elk in Oregon used habitat within 500 meters of open roads half as much as predicted for similar habitat farther away from roads. Elk telemetry data further suggested that open road densities negatively correlated with elk telemetry points (Burcham et al. 1998) and that elk avoided human disturbance, and particularly vehicle activity, preventing them from utilizing desirable habitat (Morgantini et al. 1979).

With modern quantitative tools, models became better at predicting the probability of elk using specific areas of a landscape (McCorquodale 2013). Rowland et al. (2000) used elk telemetry data to reconsider the question of how road density models predicted elk habitat effectiveness. Their work also suggests elk avoided open roads, though a distance to road approach predicted elk habitat use better than a road density approach. One of the best variables for predicting elk habitat use in northeastern Oregon was distance from high-use and medium-use roads (Johnson et al. 2000), whereby elk use probability increased as distance from roads increased. Traffic volume also affects elk distribution. For instance, the likelihood of observing western Montana elk decreased as traffic volume increased (Edge and Marcum 1991). An Arizona study of elk wearing Global Positioning System (GPS) collars correlated

with hourly traffic data revealed the probability of elk occurring near highways decreased with increased traffic volume (Gagnon et al. 2007).

Although the scientific literature indicates that motorized use of roads negatively impacts elk, an understanding of how environmental factors known to impact elk movement, habitat use, and fitness, interact with impacts of motorized use of roads is currently lacking. For example, snowpack has been shown to limit the survival and reproduction of elk in many ecosystems (Post and Stenseth 1999, Garrott et al. 2003). Plant green-up is also closely tied to elk ecology such as seasonal migration and habitat use (Hebblewhite and Merrill 2007, Parker et al. 2009, White et al. 2010), and elk populations tend to select habitat patches at peak Normalized Difference Vegetation Index (NDVI) values during spring migration (Merkle et al. 2016).

Such environmental metrics likely mediate the relationships that exist between elk, road closure/openness, and vehicle traffic. Spring distributions of elk is closely associated with greater photosynthetic activity of spring vegetation as determined using NDVI (Hebblewhite and Merrill 2007, Parker et al. 2009, Merkle 2016), and elk migrating through intact wilderness areas to summer ranges inside Yellowstone National Park have been experiencing an increasing rate and shorter duration of green-up, coinciding with warmer spring and summer temperatures, reduced spring precipitation, and an unusually severe regional drought (Middleton et al. 2013). Indeed, while comparing migratory and resident herds of elk in Yellowstone National Park, Middleton et al. found that although habitat quality was still advantageous to elk nutrition on summer range, those conditions had declined over a 21-year period as they observed a reduction in green-up duration of 27 days over that time period (Middleton et al. 2013). They further observed a lack of a similar trend on the range of resident elk, and observed that some residents appeared to gain a nutritional subsidy from agriculture. These findings suggest that elk

should be spending less time on their higher elevation summer ranges, and more time at lower elevations where nutritional subsidies are available and where the durations of green-up may be less impacted by warming; however, this is also where anthropogenic disturbances related to road access and traffic exist.

While much of this research described above supports a negative correlation between elk and roads or traffic, certain factor such as green-up and local weather conditions may complicate this relationship further. To address cause and effect between elk and traffic, we use an experimental design where roads are opened or closed to road traffic at specific times of year, where vehicle traffic has been quantified, and where environmental factors that could potentially affect elk seasonal habitat use and abundance have been accounted for. We have the unique opportunity to study the relative impacts of vehicle traffic and environmental variables (winter severity, snow depth, and green-up) on a large population of elk in the Gros Ventre Drainage, Wyoming, USA. We use climatic and vegetation indices to provide an

environmental context for the impact of road closures on elk counts and use of low elevation habitat shared with recreationists. We specifically test: i) whether elk counts increase when roads were closed to motorized traffic; ii) the relative contribution of spring vegetation quality, winter severity, and snow depth in explaining changes in elk counts, along with road closure; and iii) the relationship between increased traffic volume and elk sightings.

STUDY AREA

The Gros Ventre River Drainage is located on the Bridger-Teton National Forest in Northwestern Wyoming (Fig. 1). Elevation ranges from approximately 2,000 to 3,422 meters. Valley bottoms are dominated by sagebrush grassland (*Artemisia* spp.) and grassland steppe ecotypes. The dominate sagebrush species are the threetip sagebrush (*Artemisia tripartita*) and the big sagebrush (*Artemisia tridentata*). Other common shrub species include Douglas rabbitbrush (*Chrysothamnus viscidiflorus*) and rubber rabbitbrush (*Ericameria nauseosa*). Grass species include Idaho

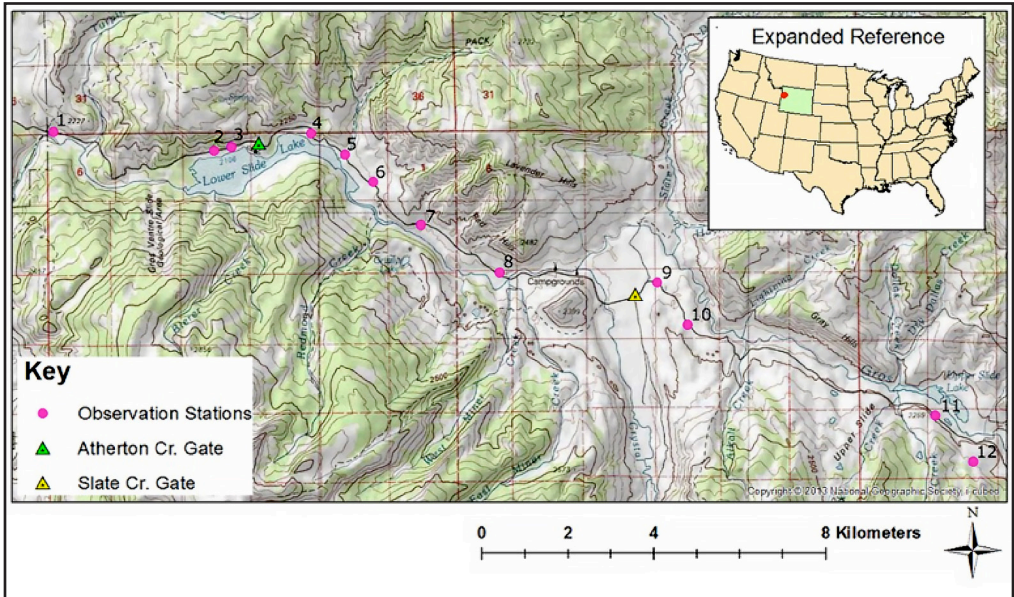


Figure 1. Locations of observation stations and gates along the main Gros Ventre road, Bridger-Teton National Forest, WY, 2010–2014.

fescue (*Festuca idahoensis*), Montana wheatgrass (*Agropyron ulbicans*), thickspike wheatgrass (*Agropyron dasystachyum*), Sandberg bluegrass (*Poa secunda*), western needlegrass (*Stipu occidentalis*), sedge (*Carex sp.*), silvery lupine (*Lupinus sereciuss*), and rose pussytoes (*Antennaria rosea*). Surrounding upland slopes are comprised of a mix of sagebrush grassland, grassland steppe, and forest ecotypes dominated by the quaking aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), limber pine (*Pinus flexilis*), and whitebark pine (*Pinus albicaulis*).

Ungulate species present include mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Large carnivore species present include grey wolves (*Canis lupus*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), pine marten (*Martes Americana*), bobcats (*Lynx rufus*), lynx (*Lynx Canadensis*), cougars (*Puma concolor*), and wolverine (*Gulo gulo*).

Long, cold winters with considerable snowfall and short, cool summers characterize the local climate. In the nearby town of Jackson, Wyoming (elevation 1,901 meters), 22 km from our study area, temperature extremes range from -52°C during the winter to 36°C during the summer (USFWS 2007). Total average annual precipitation is 38.6 cm, with 60% coming in the form of winter snow and the remainder from rainfall. Total annual snowfall averages 228 cm.

The Jackson Elk Herd

The Gros Ventre River Drainage provides year-round habitat for a portion of the Jackson Elk Herd; including summer habitat for about 30% of that herd (Smith 2000). The population management objective, set by the Wyoming Game and Fish Department (WGFD)

for a 15-year period beginning 2007, is approximately 11,000 animals (USFWS 2007). Management of the Jackson Elk Herd includes seasonal hunting (rifle and archery) and supplemental winter feeding on the National Elk Refuge and in the Gros Ventre Drainage. The population numbered as high as 19,657 elk in the mid-1990s, but harvests have brought that number within 2,000 individuals of the 11,000 elk objective (USFWS 2007). Elk utilize lower elevations of the Gros Ventre Drainage as winter range and spring calving grounds and migrate to higher elevation summer ranges within and outside of the drainage including into the Gros Ventre Mountains, Yellowstone National Park, and Grand Teton National Park.

The Gros Ventre River Drainage

As a result of the 2009 Bridger-Teton National Forest decision to designate a new motorized vehicle route system across the Forest's North Zone, many changes in motorized use occurred in the Gros Ventre drainage. This included changes to the main Gros Ventre Corridor Road referred to as the Gros Ventre road, which is a two-lane gravel road that follows the drainage bottom. Prior to the 2009 Bridger-Teton National Forest motorized travel decision, the primary uses of the road include hiking, wildlife viewing, fly-fishing, hunting (elk included), OHV use, snowmobiling, cross country skiing, camping, and horseback riding as primary activities: <https://www.fs.fed.us/visit/destinations>. Beginning in 2010, one of the changes made in the Gros Ventre road was a seasonal closure to cars and trucks that begins on 15 December and extends through 1 June, while snowmobiling was still allowed. This seasonal road closure involved the closure of two gates: Atherton Creek Gate (open 1 May; lower Gros Ventre watershed) and Slate Creek Gate (open 1 June; middle watershed). The Bridger-Teton National Forest wanted a better understanding of wildlife distributions (including elk) and the effectiveness of seasonal travel restrictions in reducing wildlife disturbance in the Gros Ventre

drainage. This study aims to improve understanding of the effectiveness of these travel management efforts by investigating elk distribution in the Gros Ventre drainage before, during, and after road segments are opened to the public.

METHODS

Data Collection

Elk Statistics and Gate Timing – We counted elk at 12 observer stations along a 23 km stretch of the Gros Ventre road at elevations ranging from 2,073 to 2,378 meters during spring, 2010–2014 (Fig. 1). The road was divided into three sections A, B, and C by gates at Atherton Creek (open 1 May; lower Gros Ventre watershed) and Slate Creek (open 1 June; middle watershed). The sequential opening of the gates by the USFS provided progressively greater levels of public access (all types of access, including motorized) to the middle and upper portion of the watershed during spring (Fig. 2). We tested the effect of gate closure (i.e. both gates closed, Atherton gate open and Slate Cr. Closed, or both gates open) on elk counts using the statistical framework described below. The twelve observation stations were

located in “viewsheds” intentionally spaced along the road to prevent observers from counting the same elk more than once. A project crew consisting of two teams of two trained citizen-science volunteers travelling in a vehicle collected observations for approximately 10 minutes at each station (data collection at stations 9, 11 and 12 was 20 minutes each due to larger viewsheds). Observations began at station 1 at 0600 and ended at station 12. All stations were visited by observers during a survey day, weather and road conditions permitting. The crews completed twelve surveys per year, from 21 April–12 May and 20 May–11 June, between 2010 and 2014.

Winter Severity Index and Snow Depth

We obtained precipitation and temperature (TEMP) data from the Gros Ventre Summit SNOTEL site (43°39 N, 110°13 W; 2,667 m) operated by the U.S. Natural Resources Conservation Service. In addition to using daily snow depth as a variable, we created a winter severity index (WSI) described by Baccante et al. (2010). First, we calculated a monthly WSI (mWSI) for the 6 months beginning 1 November and ending 30 April by combining mean monthly air temperature in degrees Celsius (TEMP) and mean monthly

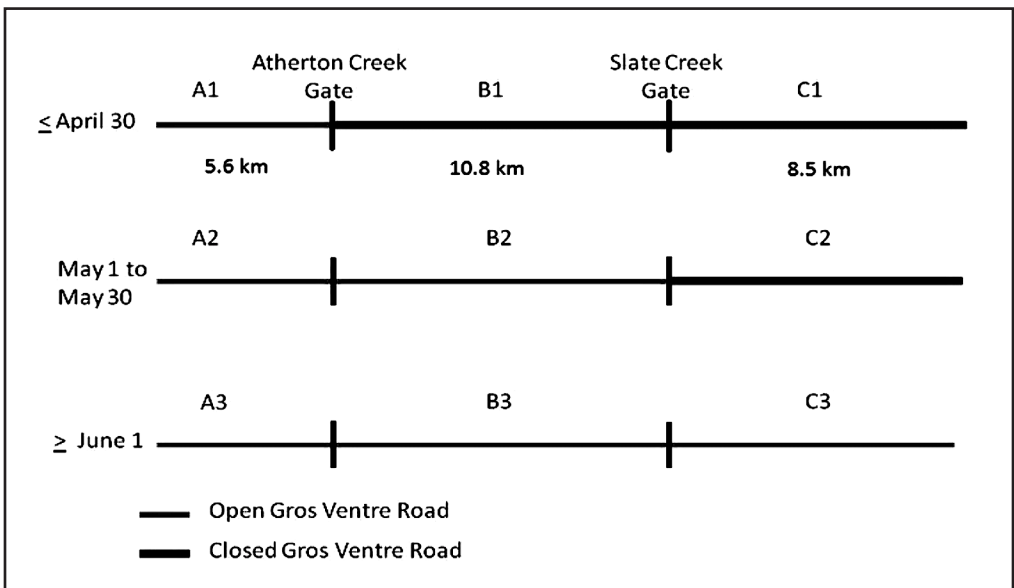


Figure 2. Road sections, travel status, and gates along the Gros Ventre Road, WY, 2010–2014.

snowfall in centimeters (SNOW) as follows: if $TEMP \leq -25^{\circ}C$ then $mWSI = 4 \times SNOW$; if $TEMP > -25^{\circ}C$ and $\leq -15^{\circ}C$ then $mWSI = 3 \times SNOW$; if $TEMP > -15^{\circ}C$ and $\leq -5^{\circ}C$ then $mWSI = 2 \times SNOW$; if $TEMP > -5^{\circ}C$ then $mWSI = 1 \times SNOW$. The total WSI for each year was calculated as the sum total of the six mWSI's for that year. Since the mWSI's began in the November of one calendar year and ended in the following calendar year, the WSI represented the year in which that winter ended. More severe winters with lower temperatures and/or increased snowfall were indicated by higher WSI values.

NDVI – NDVI has become widely used in ecological studies and measures the ratio of near infrared to red light reflected by vegetation (Pettorelli et al. 2005) and plant biomass (Muñoz et al. 2010), and is acknowledged as a good measure of green-up. We acquired Normalized Difference Vegetation Index (NDVI) data from the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD13Q1 Version 6 product provided to the public by the U.S. Geological Survey (USGS) Agency (Didan 2015). This USGS product provided a vegetation index (NDVI) which showed the relative “greenness” of vegetation produced by an algorithm that used the reflectance bands of red, blue, near infrared, and middle infrared light reflected from the Earth. The data were recorded by MODIS placed on two National Aeronautics and Space Administration (NASA) satellites. The resulting data provided pixels representing a $250m^2$ area NDVI value for 16-day time periods. We selected the following sites to measure green-up: stations one, eight, and nine (numbered starting from West to East). Each site represented a $250m^2$ area (one pixel) lying within each of the three sections of the Gros Ventre road. To simplify comparisons, the NDVI value of each $250m^2$ pixel was matched to the elk count for that pixel's road section and 16-day time range.

Vehicle Traffic – Using a traffic counter placed near the Atherton Creek gate by

USFS engineers, we estimated daily numbers of vehicles on the Gros Ventre road during 2010 and 2011, the only years such information was available. These data allowed a separate analysis of the impact of actual traffic on elk counts.

Data Analyses

When investigating elk count differences across gate opening scenarios, the Shapiro-Wilk test for normality of the residuals ($p < 0.001$) and QQ-plot, a statistical and visual way to assess normality of the residuals (Shapiro and Wilk 1965), both indicated that the residuals were not normally distributed. We thus used a non-parametric Kruskal-Wallis test, appropriate when residuals are not normally distributed (Kruskal and Wallis 1952), to determine differences in elk counts across gate opening scenarios.

We used Poisson regression analyses to evaluate changes in elk counts (response variable of interest) with respect to the timing of gate opening, NDVI, snow depth, and WSI separately and in combination. Poisson regression models are log-linear and thus appropriate in modelling positive count data as a function of both categorical and continuous explanatory variables (Kleinbaum et al. 1998). We first ensured that none of the explanatory variables were collinear by calculating variance inflation factors (VIF) using the “vif” function in R (i.e. a $VIF > 10$ is indicative of collinearity; Fox and Weisberg 2011). We defined Poisson regression models that tested for the singular, additive and interactive effects of non-collinear explanatory variables on elk counts (when it made biological sense) and compared these models using Akaike's Information Criterion (‘AIC’, Akaike 1973).

Note that due to smaller sample size and in an effort to conserve degrees of freedom, traffic data were analyzed separately using univariate Poisson regression modeling, as we only had 2 years (2010-11) of traffic data as opposed to 5 years for aforementioned analyses (2010-2015). For this analysis, we considered the impact of vehicle traffic data on elk count to test whether an increase in

traffic related to a decrease in elk counts. Using AICc model selection, we compared it to a model that allowed vehicle traffic to interact with gate timing of opening to test whether the potential negative impact of vehicle traffic on elk counts augmented as gates opened.

Regression beta coefficients, 95% confidence intervals, and p-values were used to indicate the effect and relative influence of each explanatory variable on elk counts. All analyses were performed in RStudio.

RESULTS

Elk Drainage Use

The Kruskal-Wallis test indicated significant differences in elk counts as a function of gate timing ($p < 0.001$). Counts for 705 station visits ranged from 0 to 510 elk, totaling 12,519 elk sightings over the five-year study period. Elk counts were greatest when both Atherton and Slate Cr. Gates were closed and were lowest when both gates were open (Fig. 3).

Environmental Factors and Elk Counts

Variance inflation factors were all < 5 for all predictors tested ($\text{vif}(\text{WSI})=2.61$;

$\text{vif}(\text{Timing})=1.85$; $\text{vif}(\text{NDVI})=2.41$; $\text{vif}(\text{Snow})=4.06$) suggesting a lack of collinearity among all predictors tested. Although we had the possibility to test all explanatory variables of interest as well as interactions between them, considering snow depth and WSI in conjunction within the same Poisson regression model seemed uninformative and redundant. When excluding this possibility, the best performing model retained an effect of snow depth, NDVI, and timing of gate opening on elk count. This model largely outperformed any other model that was part of the model selection process (Table 1: AICc weight = 1) and outranked the next best performing model by 335 AICc points (Table 1). Within the best performing model, additive effects of NDVI, snow depth, and gate timing were retained, along with interactions between NDVI and gate timing, and between snow depth and gate timing. Each predictor had a significant effect ($p < 0.05$) on elk counts (Table 2). On their own, NDVI and snow depth both had a negative impact on elk counts, however, the negative effect of snow depth on elk counts was much subtler than that of NDVI (Table 2, Fig. 4). When considering an interaction between snow

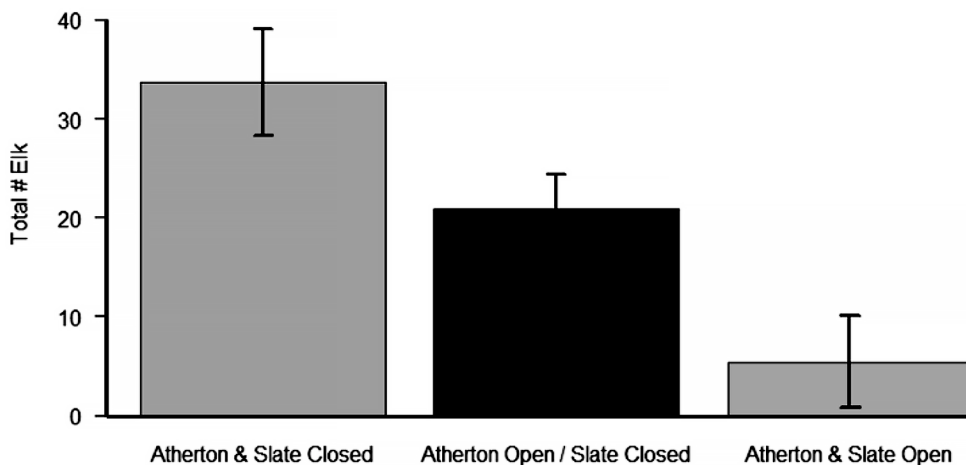


Figure 3. Differences among elk counts in response to the timing of gate opening along the Gros Ventre Road, WY. Data was collected between April 21 and June 11 for 2010-2014.

Table 1. Poisson regression models testing for the effect of Winter Severity Index (WSI), the Normalized Deviance Vegetation Index (NDVI), gate timing (Timing), snow depth (SD) and relevant interactions (‘:’) on elk counts. K represents the number of parameters in the model. Best performing model based on AICc is presented in bold.

Predictors	K	AICc	Delta AICc	AICc weight	LogLikelihood
NDVI:Timing+SD:Timing	7	33087.97	0.00	1	-16536.91
NDVI:Timing+WSI:Timing	7	33422.80	334.83	0	-16704.32
SD:Timing	4	34137.89	1049.92	0	-17064.92
NDVI:Timing	4	36617.82	3529.84	0	-18304.88
WSI:Timing	4	37278.49	4190.52	0	-18635.22
NDVI+SD+Timing	5	34644.48	1556.51	0	-17317.20
NDVI+WSI+Timing	5	34965.26	1877.29	0	-17477.59
NDVI+SD	3	35666.12	2578.15	0	-17830.04
NDVI+WSI	3	36008.60	2920.63	0	-18001.28
SD+Timing	4	35088.20	2000.23	0	-17540.07
NDVI + Timing	4	34972.02	1884.05	0	-17481.98
Timing	3	37074.07	3986.10	0	-18534.02
SD	2	36938.24	3850.27	0	-18467.11
NDVI	2	36085.85	2997.87	0	-18040.91
WSI	2	41379.54	8291.56	0	-20687.76

Table 2. Performance of predictors from the best-fitting Poisson regression model selected in table 1 (in bold). Predictors include: Snow Depth (SD), the Normalized Deviance Vegetation Index (NDVI), gate timing (i.e. Timing1: both gates were closed; Timing2: Atherton creek gate was open; Timing3: both Atherton and Slate creek gates were open; see Fig. 2) and relevant interactions (‘:’) on elk counts.

Predictors	β	95% C.I. -		z-values	P-values
		lower bound	upper bound		
Intercept (Timing1)	3.7125	3.6231	3.8016	81.5180	<0.001
NDVI	-0.4146	-0.6159	-0.2132	-4.0360	<0.001
SD	-0.0010	-0.0017	-0.0003	-2.7870	0.005
NDVI:Timing2	-3.3349	-3.4895	-3.1801	-42.2550	<0.001
NDVI:Timing3	-4.5911	-4.7985	-4.3865	-43.6840	<0.001
SD:Timing2	0.0067	0.0061	0.0072	24.5150	<0.001
SD:Timing3	0.0105	0.0090	0.0121	13.2580	<0.001

depth and gate opening, the relationship between snow depth and elk count became more positive as gates opened (i.e. Timing1: both gates were closed; Timing2: Atherton creek gate was open; Timing3: both Atherton and Slate creek gates were open; see Table 2, Fig. 2), but remained statistically weak. When considering the interaction between NDVI and timing of

gate opening, the impact of NDVI on elk count became more negative as gates opened (Table 2, Fig. 4).

Vehicle Traffic impacts on Elk Counts
 In a separate analysis that involved more limited data (2010-2011) on the impact of actual vehicle traffic on elk counts, we observed a negative relationship between vehicles and elk counts (Fig. 4). The Poisson

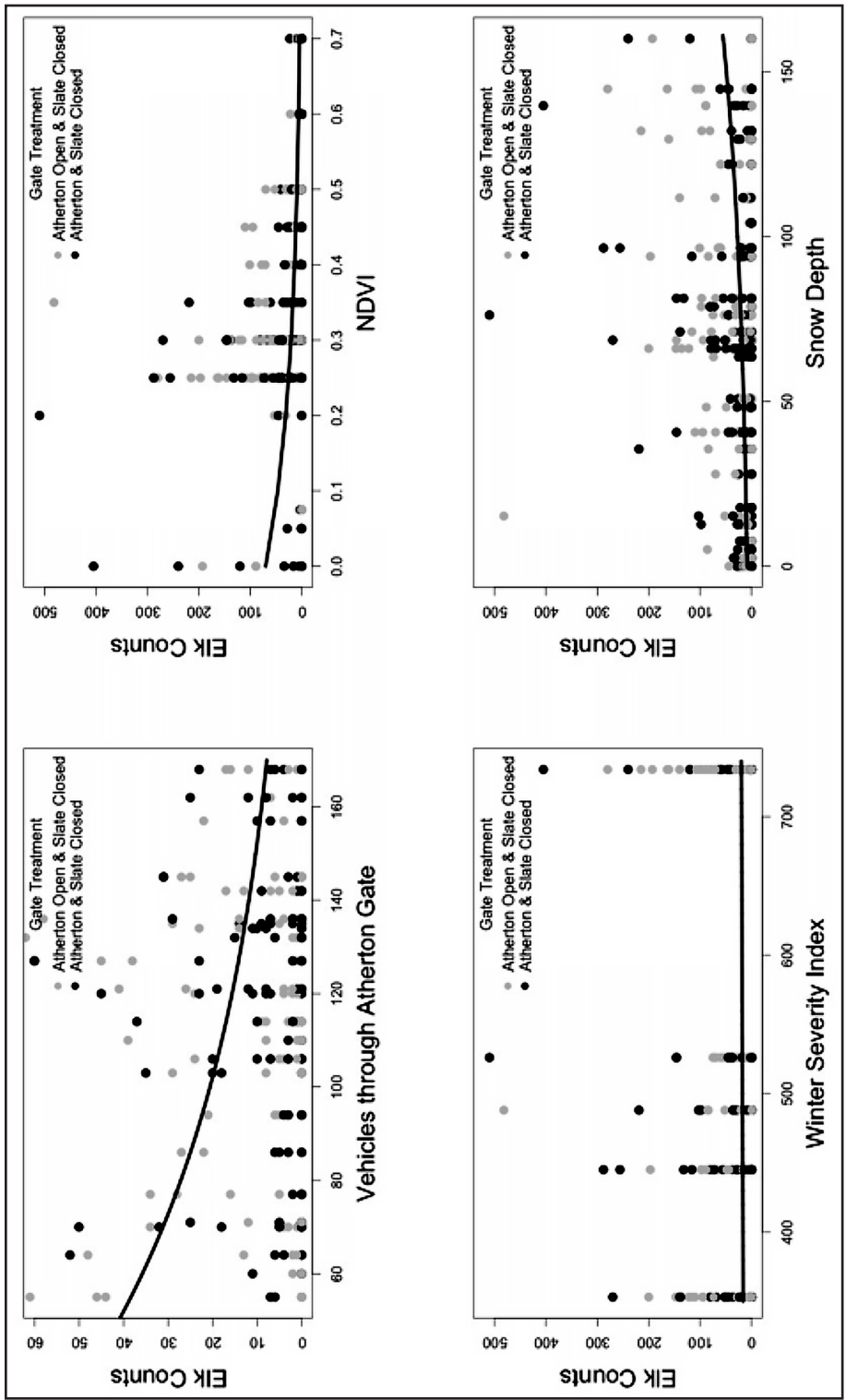


Figure 4. Regression of elk counts against A) snow depth, B) Winter Severity Index (WSI), C) the Normalized Difference Vegetation Index (NDVI), and D) the number of vehicles passing through Atherton Gate, WY. Data was collected between April 21 and June 11 for 2010-2014 for top-right and bottom panels, and between April 21 and June 11 for 2010 & 2011 for top-left panel.

regression model that accounted for an interaction between traffic and timing of gate opening (AICc = 14199) outperformed the model that only accounted for vehicle traffic by 486 AICc points. Estimates from the best performing model are presented in Table 3 and indicate that, as gates opened through the spring, the impact of vehicle traffic on elk counts became increasingly negative.

DISCUSSION

Our analyses support the hypotheses that: i) elk counts increase when roads are closed to motorized travel, as suggested by previous studies; ii) The relative contribution of spring vegetation quality (NDVI) and snow depth were important in explaining changes in elk counts, and interacted with road closure; and iii) the negative impact of traffic was exacerbated when all gates were open to the general public.

Roads and Elk in Context

The novelty of this work lies in the consideration that interactions between the timing of gate opening and environmental covariates can potentially shape elk use of migration corridor, and thus elk counts in the spring and summer within such habitats. Indeed, the best performing model retained an interaction between NDVI and gate timing, and snow depth and gate timing, on elk counts. These interactions indicate that the impact of gate timing on elk counts is mitigated by environmental conditions, whereby an increase in spring green up and a

decrease in snow depth lead to a progressive decline in elk counts as gates progressively open. These synergistic effects suggest that both environmental and anthropogenic factors can influence elk counts.

It is especially important to consider the impact of gate closure and traffic within the environmental context that elk are experiencing year-to-year, since failure to do so could bias management recommendations. In the Western US, an increasing frequency of spring snow storms is predicted in response to climate change (Cayan et al. 2006) and a narrower green-up window has already been observed in response to warmer spring-summer temperatures and reduced spring precipitation (Middleton et al. 2013). The latter could have potential influences on elk seasonal distribution and migration (Middleton et al. 2013). Because herbivores, such as elk, time their migration phenology to that of the forage they depend on for body mass gains and fitness, one would expect elk to remain at lower elevations for a longer period of time in the spring in response to spring snowstorms while “surfing the green-wave” (Bischof et al. 2012, Aikens 2017).

Environmental impacts on elk counts

Our results suggest that elk congregate at lower elevations when snow depth was at its peak and gates were closed, and migrate up in elevation as NDVI increased. Smallidge et al. (2003) and Bischof et al. (2012) similarly observed elk migration from lower to higher elevation in association

Table 3. Estimates from Poisson regression model testing for the effect of vehicle traffic (Traffic) and timing of gate opening (Timing; i.e. Timing1: both gates were closed; Timing2: Atherton creek gate was open; Timing2: both Atherton and Slate creek gates were open; see Fig. 2) on elk counts.

Predictors	β	95% C.I. -		z-values	P-values
		lower bound	upper bound		
Intercept	3.9555	3.8623	4.0484	83.3390	<0.001
Traffic:Timing1	-0.0041	-0.0060	-0.0023	-4.3770	<0.001
Traffic:Timing2	-0.0075	-0.0085	-0.0066	-15.6700	<0.001
Traffic:Timing3	-0.0142	-0.0150	-0.0133	-31.7260	<0.001

with a vegetative “greenwave”. Only recently have ecologists documented the true role migration corridors, such as the Gros Ventre Drainage, play in shaping herbivore phenology and population dynamics. Although their importance in enabling animals to move between winter and summer ranges has long been understood, their actual use as key transitional habitat for herbivores such as mule deer and elk has only recently been better acknowledged. Migratory corridors are economically and ecologically important for animals which closely time their movements to track spring green-up (Aikens 2017). White et al. (2012) also found that elk numbers at lower elevations increased with greater snowpack. Counts were performed in the spring and summer, which might explain the very weak relationship between elk counts and snow depth pre-road access, as one would expect a strong and positive relationship between counts and snow depth, independently of gate closure.

Traffic Impacts on Elk Counts

Traffic volume was negatively correlated with elk counts. For every 1 vehicle increase passing through Atherton gate, there was a corresponding 1.42% decrease in elk counts when all gates were open (Table 3), suggesting that vehicle traffic had a negative impact on elk abundance in the Gros Ventre River drainage. The daily average number of vehicles through Atherton gate steadily increased from approximately 49 in April, 103 in May, 153 for June, and 233 for July during years 2010 and 2011. Our results align with findings from the literature that document the negative effects of vehicle traffic volume on elk abundance (McCorquodale 2013).

Elk counts were significantly less when roads were open, but whether this was primarily due to the negative impact of motorized traffic or natural migration behavior away from lower elevation roads is difficult to discern with the data at hand. A large number of elk were documented in the drainage well into the end of May in

most years (>100 individuals, Appendix A). We were still able to observe a progressive decrease in elk counts over the spring and summer months, after the sequential opening of the gates. The impact of vehicle traffic on elk count was negative by itself (Fig. 4), which supports the hypothesis that elk avoid traffic. This adds to the literature in that past studies mostly focused on highways and their impact on elk habitat use (e.g. Edge and Marcum 1991, Gagnon et al. 2007). Here we show that motorized travel along improved gravel roads has the potential to displace elk.

Limitations, Future Work, and Management Implications

More accurate assessments of elk abundance generally follow the Capture-Mark-Recapture or Resight methods that account for imperfect detection. In this case, a point-count distance sampling approach would have been appropriate (Buckland et al. 1993) and provided a more standardized data collection approach, something to consider for future studies. Another factor that could have biased our study is the timing of survey visits. Elk are crepuscular animals most active in the evening and dawn. Stations visited later in the morning might have had less elk activity and undercounted elk compared to sites visited earlier. Another open question is whether elk would respond to traffic differently if the road was open year around? Anecdotal evidence suggests that elk on feed grounds near Jackson Hole show little response to continued vehicle traffic.

Even provided such limitations, this study establishes a systematic point-count approach to estimating elk abundance in the Gros Ventre drainage, in that we have already identified environmental and anthropogenic factors that are susceptible to affect availability to detection in elk (Williams et al. 2002). Namely, the timing of gate opening, vehicle traffic, winter snow depth and spring vegetation quality have all been found to affect the probability of counting elk and thus their availability for detection. We suggest conducting point

count studies pre-vegetation green-up, when elk are still utilizing the lower elevations of the Drainage, and would encourage point-count surveys before any gate opening to maximize availability to detection.

Our research suggests that both climatic variables and vehicle traffic synergistically affect elk counts and distribution. This is important because a forecasted increase in the frequency of spring snow storms in the Western US, coupled with the general prediction that peak NDVI will intensify, but narrow in the spring (Middleton et al. 2013). This may delay spring migration to higher elevation and force elk to remain in the drainage in the spring while overlapping with recreationists and road use. If forced to migrate upwards in the spring to avoid traffic and anthropogenic disturbance before green-up, this could create a mismatch between elk migration and peak NDVI, which could ultimately affect elk fitness and persistence. If additional resources were to become available to managers, the deployment of GPS collars on elk would help inform fine-scale migration from wintering to summering grounds in response to road closure or openness, traffic volume when gates are open, and year-to-year variability in environmental conditions. Our results collectively outline the importance of considering the environmental context and climatic conditions elk experience when managing for road closures and recreation. We suggest that the positive impact of road closure to elk within the Gros Ventre drainage will continue to become more pronounced in the future given the projected effects of climate change on snow dynamics and green-up in the western United States.

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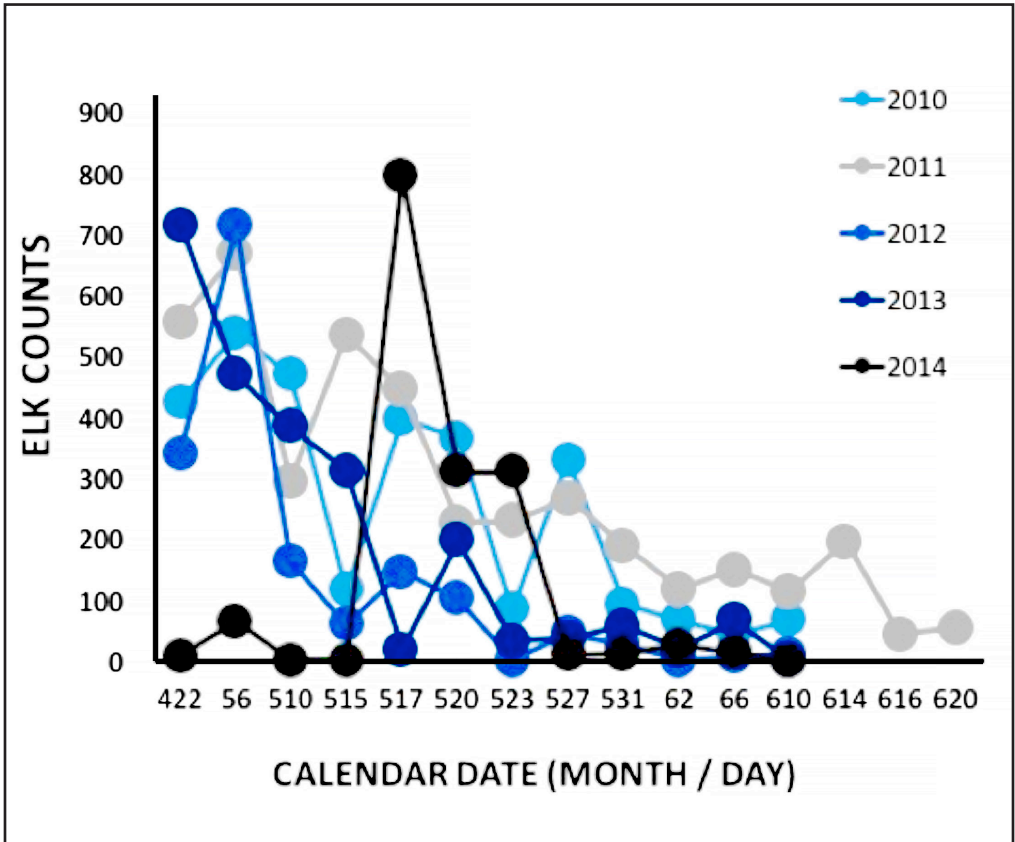
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Appendix A. Elk counts throughout spring, summed over 12 observatory points at each date along the Gros Ventre Road, WY. Data were collected between April 21 and June 11 for 2010-2014.



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