



Contrasting Past and Current Numbers of Bears Visiting Yellowstone Cutthroat Trout Streams

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ABSTRACT Spawning cutthroat trout (*Oncorhynchus clarkii bouvieri*) were historically abundant within tributary streams of Yellowstone Lake within Yellowstone National Park and were a highly digestible source of energy and protein for Yellowstone's grizzly bears (*Ursus arctos*) and black bears (*U. americanus*). The cutthroat trout population has subsequently declined since the introduction of non-native lake trout (*Salvelinus namaycush*), and in response to effects of drought and whirling disease (*Myxobolus cerebralis*). The trout population, duration of spawning runs, and indices of bear use of spawning streams had declined in some regions of the lake by 1997–2000. We initiated a 3-year study in 2007 to assess whether numbers of spawning fish, black bears, and grizzly bears within and alongside stream corridors had changed since 1997–2000. We estimated numbers of grizzly bears and black bears by first compiling encounter histories of individual bears visiting 48 hair-snag sites along 35 historically fished streams. We analyzed DNA encounter histories with Pradel-recruitment and Jolly-Seber (POPAN) capture-mark-recapture models. When compared to 1997–2000, the current number of spawning cutthroat trout per stream and the number of streams with cutthroat trout has decreased. We estimated that 48 (95% CI = 42–56) male and 23 (95% CI = 21–27) female grizzly bears visited the historically fished tributary streams during our study. In any 1-year, 46 to 59 independent grizzly bears (8–10% of estimated Greater Yellowstone Ecosystem population) visited these streams. When compared with estimates from the 1997 to 2000 study and adjusted for equal effort, the number of grizzly bears using the stream corridors decreased by 63%. Additionally, the number of black bears decreased between 64% and 84%. We also document an increased proportion of bears of both species visiting front-country (i.e., near human development) streams. With the recovery of cutthroat trout, we suggest bears that still reside within the Lake basin will readily use this high-quality food resource. © 2014 The Wildlife Society.

KEY WORDS black bear, capture-mark-recapture, cutthroat trout, grizzly bear, Jolly-Seber, Pradel-recruitment, robust design.

The availability of high-quality foods has a significant influence on grizzly bear (*Ursus arctos*) survival and reproduction (Schwartz et al. 2006). Spawning cutthroat trout (*Oncorhynchus clarkii bouvieri*) were once a locally important food available to grizzly bears within the Yellowstone Lake basin of Yellowstone National Park (YNP; Mealey 1975, Pritchard and Robbins 1990, Mattson

and Reinhart 1995). Grizzly bears fished for cutthroat trout in at least 36 (61%) of the 59 known trout spawning tributaries to Yellowstone Lake (Hoskins 1975, Reinhart and Mattson 1990). As recently as the late 1990s, an estimated 14–21% of the grizzly bear population in the Greater Yellowstone Ecosystem (GYE) had access to cutthroat trout in tributaries of Yellowstone Lake (Haroldson et al. 2005).

Since the introduction of non-native lake trout (*Salvelinus namaycush*) and whirling disease (*Myxobolus cerebralis*) and the occurrence of a persistent drought, the cutthroat trout population of Yellowstone Lake has declined by 90% (Koel et al. 2005, 2006). Lake trout were discovered in Yellowstone Lake in 1994 (Keading et al. 1996, Koel et al. 2003). Young

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lake trout compete with cutthroat trout for macroinvertebrates, and each adult lake trout has the potential to consume 50 to 90 cutthroat trout annually (Gerstung 1988, Elrod and O'Gorman 1991, Donald and Alger 1993, Stapp and Hayward 2002). Lake trout, unlike cutthroat trout that spawn in small streams in late spring and summer, are not accessible to bears and other wildlife because they spawn in deeper areas of the lake (Schullery and Varley 1996). Whirling disease was discovered in Yellowstone Lake in 1998 (Koel et al. 2006). The disease destroys head cartilage of young trout, resulting in loss of equilibrium, skeletal deformities, and inability to feed normally or avoid predators (Yellowstone Center for Resources 2002). Finally, a drought with less snowfall and warmer summers has reduced stream flows and the number of streams available for cutthroat trout spawning (Haroldson et al. 2005; Rood et al. 2005, 2008). Without spring floods, gravel bars formed by wave and ice action at the mouths of smaller streams block spawning cutthroat trout in spring and prevent fry from entering the Lake in the fall.

Grizzly bears and black bears (*U. americanus*) cohabit the GYE. Numerous studies have shown that sympatric black bears and grizzly bears segregate resource use, with grizzly bears often excluding black bears from high-quality, concentrated foods (Welch et al. 1997, Jacoby et al. 1999, Rode et al. 2001, Robbins et al. 2004, Mattson et al. 2005). Within YNP, black bears often avoid grizzly bear feeding sites, such as cutthroat trout spawning streams (Barnes and Bray 1967, Reinhart and Mattson 1990, French et al. 1994, Green et al. 1997). However, changes in the numbers of available cutthroat trout could change this dynamic along trout streams. Total numbers of cutthroat trout consumed by grizzly bears has declined since the 1980s: 20,910/year in the late 1980s, 2,266/year in the late 1990s, to 302/year during the period of this study (Stapp and Hayward 2002, Felicetti et al. 2004, Fortin et al. 2013). Fortin et al. (2013) recently documented significant decreases, on a per bear basis, in annual consumption of cutthroat trout by grizzly bears (72% decline for consumption by males, no decrease by females) and black bears (69%; equal decline by males and females) between the late 1990s and the late 2000s. Recent consumption levels have been estimated to be very low, with male and female grizzly bears and black bears consuming on average 7, 3, and 6 trout/year/bear, respectively. Grasses, sedges, and forbs are now likely the primary bear foods found along stream corridors.

The relative abundance of cutthroat trout may influence bear mortality rates. For other major food items (e.g., whitebark pine [*Pinus albicaulis*] nuts, ungulates, and army cutworm moths [*Euxoa auxiliaris*]), conflicts between grizzly bears and humans increase in the GYE during years of low availability but decrease when these preferred foods are abundant. During years of poor food availability, bears often seek alternative foods at lower elevation, in more densely human-populated front-country areas of the ecosystem (Gunther et al. 2007). Given a decreased number of trout, we were interested in whether a shift to greater use of the front-country by grizzly bears and black bears has occurred.

Studies in 1987 that used track counts and radio-telemetry locations from instrumented bears estimated that a minimum of 44 grizzly bears fished for cutthroat trout in Yellowstone Lake streams (Reinhart and Mattson 1990, Mattson and Reinhart 1995). More recently (1997–2000), researchers used DNA analyses of bear hair samples, identified 74 grizzly bears (64% male and 36% female), and estimated that 68 bears/year (14–21% of the GYE grizzly bear population) visited the spawning streams and immediate area around Yellowstone Lake during the cutthroat trout spawning season (Haroldson et al. 2005). However, this research only sampled 22 of the 36 streams that historically were used by grizzly bears. Hair samples from black bears were also collected, but individual encounter histories were not modeled to estimate abundance.

We initiated a 3-year study in the spring of 2007 to assess whether numbers of cutthroat trout and numbers and distribution of both bear species had changed since earlier studies. Given the large reduction in the cutthroat trout population, we hypothesized that 1) fewer grizzly bears would now be visiting cutthroat trout streams, 2) current spatial distribution of grizzly bears and black bears would differ from previous years, as bears range more widely during the cutthroat trout spawning season, seeking other foods to replace trout, 3) grizzly and black bear use of front-country areas near human developments would now be higher, and 4) given a lesser number of grizzly bears using cutthroat trout along streams, an equal or greater number of subordinate, more herbivorous black bears would visit streams, exploiting remaining trout and succulent, relatively nutritious forbs and grasses growing in streamside habitats.

STUDY AREA

We conducted our investigation on tributary streams that empty into Yellowstone Lake, YNP (44.47°N, 110.37°W), a high-elevation (2,358 m), oligotrophic lake located in the southeastern portion of YNP and in the approximate center of the GYE. The Yellowstone Lake watershed, estimated at 261,590 ha, comprises the headwaters of the Yellowstone–Missouri–Mississippi Rivers (Marston and Anderson 1991).

The drainage basin was predominately forested, with lodgepole pine (*Pinus contorta*) dominating the western and northern portion and mixed stands of spruce (*Picea engelmannii*), fir (*Abies lasiocarpa*), and pine found more abundantly in eastern and southern portions of the basin. The west and north drainages of the Yellowstone Lake basin contained small streams draining from low relief plateaus through lodgepole pine forests and alluvial meadows. The east and southeast drainages come from higher relief topography, closed canopy mixed forests, and subalpine slopes (Reinhart and Mattson 1990). In total, 124 streams flow into Yellowstone Lake, 48% ($n = 59$) of which contain spawning cutthroat trout (Reinhart and Mattson 1990). Historically, spawning took place from early to late May until late July to early August, with grizzly bears feeding on trout from mid-May through July (Reinhart 1990, Reinhart and Mattson 1990).

METHODS

We estimated the number of bears visiting stream corridors with capture-mark-recapture (CMR) methods. We coupled hair-snagging sessions over multiple years with microsatellite genotyping to determine species, sex, and individual identity. We used scent-lured, barbed wire stations with ≥ 3 trees streamside throughout the study area (Haroldson and Anderson 1997), and all streams we sampled ($n = 35$) historically contained spawning fish and bear fishing activity (Reinhart and Mattson 1990). Each stream had 1–2 hair-snag sites at least 0.5 km apart, depending on length of the spawning habitat and streamside topography. We established all snagging sites before onset of spawning runs. We used fresh cattle blood as the attractant (Haroldson and Anderson 1997). We treated all hairs caught on a single barb of the site perimeter as a single sample for DNA analysis, and we collected samples using sterile techniques. However, when we found multiple samples along a continuous string of barbs, we selected only 1 sample for DNA analysis. Although Tredick et al. (2007) found that this method of sub-sampling may underestimate abundance within high-density populations, the paucity of samples at snag sites during any single survey in our study suggested such error was small. Additionally, we never witnessed observable differences in composition (underfur vs. guard hair) or color of hair samples adjacent to one another. We selected samples with ≥ 10 hairs for DNA analysis (Haroldson et al. 2005). We checked hair-snag sites bi-weekly, weather permitting, from ice-off on Yellowstone Lake until 15 August.

Using our stream-specific genetic results from hair samples, we tabulated the numbers of grizzly and black bears visiting front-country (i.e., within 1 mile of a roadway or other human development) and backcountry streams. We used proportions, bounded by binomial confidence intervals ($n = \text{total number of streams}$), to assess differences in front-country and backcountry visitation between species and study periods.

We deployed 3 remote cameras at randomly selected hair-snag locations in each of the 6 zones around Yellowstone Lake: East Shore, Southeast Arm, South Arm, West Shore, West Thumb, and Lake Village. We used visual references to judge height and relative size (adult males vs. subadult males and adult females) of bears. We then attempted to match collected samples with those bears captured in photos by establishing entry or exit points along the barbed wire perimeter. We numbered barbs in a manner allowing identification of location of collection on the camera image. This camera effort, supplemented with ages known for bears that had been tagged during a previous capture, allowed for an estimate of the age structure of bears that visited the tributary streams.

Genetic Analysis

We submitted hair samples to Wildlife Genetics International (Nelson, BC, Canada) for genetic analyses. To avoid contamination errors, all amplified DNA was kept and analyzed in an isolated facility separate from all genomic DNA. We attempted DNA extraction from all samples with

4 or more visible roots (20 or more shafts for underfur-dominated samples). This minimum number was chosen as a conservative check on data quality, ensuring that extracts contained enough DNA to avoid genotyping errors in samples with low quantities of DNA (Goossens et al. 1998; D. Paetkau, Wildlife Genetics International, personal communication). DNA was extracted using a Qiagen (Valencia, CA) tissue kit under standard protocols.

We used 2 methods for species identification. Yellowstone grizzly bears have even-numbered allele lengths at microsatellite marker G10J, whereas black bears have exclusively odd-numbered alleles (Kendall et al. 2009; D. Paetkau, unpublished data). We observed no individuals with both an even and an odd-numbered allele at this marker; we subsequently based initial species identifications on this pattern. Once genotypes were finalized for all microsatellite markers, we used multilocus clustering (program Genetix; Belkhir et al. 2004) to confirm species, limiting the analysis to 8 markers other than G10J to ensure independence. The species implied by the 2 methods were always the same.

Correct assignment of genotypes to individual bears relies upon the selection of a proper set of markers (high variability) and a rigorous protocol of sample culling and error checking, without the need to employ probability of identity statistics (Paetkau 2003). Using genetic data from other contemporary GYE samples, we used a highly variable suite of 9 microsatellite markers (G1D, G10B, G10H, G10J, G10L, G10P, MU23, MU51, and MU59) to identify individual grizzly and black bears (Haroldson et al. 2010). Polymerase chain reaction conditions and primer sets were as described in Paetkau et al. (1998).

We culled samples that failed to yield at least 5 markers with high scoring confidence or that showed signs of origination from 2 or more individuals (i.e., had > 2 alleles at multiple markers) from the dataset. We reamplified and reanalyzed those exceeding this cutoff, but not yielding a full 9-locus genotype, after which we used another cull to remove any sample that did not have high-confidence scores for all markers. Finally, we scrutinized 1-mismatch (1-MM) pairs (pairs of genotypes matching at all but 1 marker) and 2-MM pairs. If not reduced to a 0-MM pair by visual scrutiny, we reamplified and reanalyzed the markers causing mismatch, as described by Paetkau (2003). We determined sex of each individual grizzly and black bear using the amelogenin system (Ennis and Gallagher 1994).

Relative Availability of Spawning Fish

We systematically observed all streams that we sampled with hair-snag sites for cutthroat trout to determine median peak numbers of fish and median duration of spawning activity (as in Haroldson et al. 2005). Bi-weekly, 2–3 people counted numbers of spawning individuals as they walked alongside the stream. We conducted the surveys along the span of the stream that the hair-snag sites encompassed, from the mouth to the uppermost hair snag. These sections represented the historical length of spawning activity on most streams.

We understand that these methods have limitations in our ability to document each cutthroat trout within the stream.

However, these methods were necessary because 1) more accurate alternatives were financially and logistically infeasible, and 2) they were used in previous studies, to which we compare our results (e.g., Haroldson et al. 2005). We compared median values and used a χ^2 test for equality of proportions to assess differences between studies using the R programming environment (R Development Core Team 2010, version 2.15.1, www.r-project.org, accessed 10 Oct 2011).

Abundance and Trend

We constructed individual encounter histories for each grizzly bear and black bear identified at hair-snap sites. We assessed annual grizzly bear superpopulation (i.e., total number of bears visiting the vicinity of tributary streams) and growth rate (λ) estimates during the current study (2007–2009) with a robust Pradel-recruitment model (Pollock and Otto 1983, Pradel 1996). These modeling techniques allowed for annual estimates of the numbers of bears visiting these streams, as well as rate of entry into or exit from the study area (i.e., linear stream reaches). We assumed demographic closure of grizzly bears within the study area during each summer sampling period, given high annual survival rates of grizzly bears in the GYE and the absence of births during this time of the year (Eberhardt et al. 1994; Schwartz et al. 2006, 2010). We performed robust modeling on an a priori set of models (Table 1). Our sample sizes allowed us to separately estimate male and female parameters.

Because we were interested in directly comparing estimates from our work with those from the previously published 1997–2000 dataset, we used an open-population POPAN model to estimate abundance on tributary streams with the 2007–2009 encounter data (Schwarz and Arnason 1996, Haroldson et al. 2005). For comparisons between studies, we trimmed encounter histories to match capture effort in Haroldson et al. (2005). To achieve comparable spatial and temporal scale in capture effort between datasets, we used

Table 1. Model variables, Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c from top model (ΔAIC_c), model weights (w_i), number of parameters (K), and model deviance for the robust Pradel-recruitment analysis of encounter data from grizzly bears visiting tributary streams of Yellowstone Lake, Yellowstone National Park, Wyoming, 2007–2009.

| Model | AIC_c | ΔAIC_c | w_i | K | Deviance |
|--|---------|----------------|-------|-----|----------|
| $\Phi(\cdot) f(\cdot) p(t)^{a,b}$ | 456.584 | 0.000 | 0.392 | 23 | 402.970 |
| $\Phi(s) f(s) p(t)^b$ | 457.296 | 0.713 | 0.274 | 25 | 398.205 |
| $\Phi(\cdot) f(\cdot) p(\cdot)$ | 457.948 | 1.365 | 0.198 | 11 | 434.267 |
| $\Phi(s) f(s) p(s)$ | 461.322 | 4.739 | 0.037 | 15 | 428.185 |
| $\Phi(t) f(t) p(t)$ | 461.783 | 5.200 | 0.029 | 25 | 402.692 |
| $\Phi(s) f(s) p(s+t)^c$ | 461.816 | 5.232 | 0.029 | 27 | 397.092 |
| $\Phi(\cdot) f(\cdot) p(s)$ | 462.269 | 5.685 | 0.023 | 14 | 431.541 |
| $\Phi(s+t) f(t) p(t)$ | 463.294 | 6.711 | 0.014 | 27 | 398.571 |
| $\Phi(t) f(s+t) p(t)$ | 466.432 | 9.849 | 0.003 | 27 | 401.709 |
| $\Phi(s+t) f(s+t) p(t)$ | 467.496 | 10.912 | 0.002 | 29 | 396.978 |
| $\Phi(\cdot) f(\cdot) p(t) d(t)^a$ | 470.600 | 14.016 | 0.000 | 35 | 381.653 |
| $\Phi(s \times t) f(s \times t) p(s \times t)^c$ | 505.107 | 48.524 | 0.000 | 44 | 385.172 |

^a Φ , apparent survival; f , recruitment rate; p , capture probability; c , recapture probability.

^b (t) , time-dependent effects; (s) , sex-dependent effects; (\cdot) , null effects.

^c + indicates additivity between variables; \times indicates an interactive effect between variables.

1998–2000 capture data from the Haroldson et al. (2005) dataset and from only 10 streams sampled during each study (i.e., equal sampling effort). We similarly analyzed unpublished CMR data on black bears identified from the same dataset for 1997–2000. All POPAN modeling efforts included identical a priori sets of models that included all possible models with either time varying (t) or constant (\cdot) values of apparent survival (ϕ), capture probability (p), and probability of entry (p_{ent}). We pooled males and females for each POPAN analysis because data from the 10 common streams were too sparse to model sexes separately.

We implemented both modeling procedures using Program MARK (White and Burnham 1999). To compare models within our candidate model sets, we used Akaike's Information Criterion adjusted for small sample size (AIC_c); we considered the model with the lowest AIC_c value as most supported by the data. In cases where pairs of models had $\Delta AIC_c \leq 2$, we considered the simpler model to be the most parsimonious (Arnold 2010). We model-averaged parameter estimates across all candidate models to incorporate model uncertainty (White et al. 2001). We assessed goodness of fit of our most generalized model (i.e., global model) within Program RELEASE (Burnham et al. 1987). We estimated the overdispersion parameter, \hat{c} , in all cases with median \hat{c} and bootstrapping. In cases in which we detected overdispersion, we corrected AIC_c values accordingly, producing quasi- AIC_c ($QAIC_c$) values to assess model parsimony.

RESULTS

Numbers of Spawning Cutthroat Trout

During 2007–2009, spawning activity occurred in an average of 15 of the 35 streams we surveyed each year ($SE = 4.546$; Table 2). The peak number of fish observed per successful run increased each year, as did the proportion of streams with successful runs (Fig. 1b). Only 2 streams supported spawning activity during every year of the study. The highest peak number of fish observed among all streams during an individual survey was 25, and the median peak number of spawners on all streams was 2.5 fish. We observed no spawning activity on 7 streams (20%). Median duration of spawning activity ranged from 1 week (Lake Village area streams) to 3 weeks (West Shore streams), although some streams had runs lasting 7 weeks (Table 3). Of those streams sampled both during our study and by Haroldson et al. (2005), we found spawning activity in 16 of 22 surveyed streams, as compared to 22 of 22 streams from 1997–2000 ($\chi^2_1 = 4.825$, $P = 0.028$; Fig. 1a). During the same time interval between studies, the median peak count on streams decreased by a median of 98.4%, or 71 fish ($n = 22$ streams, range = 3–2,348 fish; Table 2). Since 1997–2000, median duration of spawning runs decreased in all portions of the Lake, with the most drastic decline seen within East Shore streams (6-week to 2-week median duration of spawning activity; Table 3).

Genetic Analysis of Hair

We collected 1,535 hair samples from 48 streamside hair-snap sites during 2007–2009. We genetically analyzed 877

Table 2. Spawning activity indices for cutthroat trout on streams surveyed within each portion of Yellowstone Lake, Yellowstone National Park, Wyoming, 1997–2000 and 2007–2009. Median number of peak spawners includes those years with documented spawning activity, as in Haroldson et al. (2005).

| Lake portion | 1997–2000 study | | | 2007–2009 study | | | % decrease (range) in median peak counts |
|--------------|------------------|-----------------------|--|------------------|-----------------------|--|--|
| | Streams surveyed | Streams with spawners | Median (range) peak annual no. spawners ^a | Streams surveyed | Streams with spawners | Median (range) peak annual no. spawners ^a | |
| East shore | 5 | 5 | 822 (36–4,429) | 8 | 6 | 2 (0–8) | 99.8 (95.7–100) |
| West shore | 7 | 7 | 88 (23–1,711) | 12 | 10 | 3 (0–25) | 98.5 (97.7–100) |
| West thumb | 6 | 6 | 74 (3–161) | 11 | 11 | 3 (1–17) | 87.2 (68.2–96.6) |
| Lake village | 4 | 4 | 31 (3–94) | 4 | 1 | 0 (0–1) | 100.0 (93.3–100) |

^a Of all stream-years.

(57%) samples that met our pre-determined criteria. Of these, 746 (85%) samples were assigned a 9-locus genotype, and average heterozygosity of this 9-locus suite allowed for reliable identification of individuals. We estimated the per-locus error rate in our analysis at 0.002 (Kendall et al. 2009). From these samples, we identified 63 unique grizzly bears (42M:21F) and 27 black bears (17M:10F).

Temporal and Spatial Distribution of Identified Bears

Fourteen black bears (8M:6F) visited streams during only 1-year of the study, 10 (8M:2F) visited during 2 years, and 3 visited all 3 years (1M:2F). Twelve black bears visited only 1 sampled stream (6M:6F), 8 bears visited 2 streams (5M:3F),

and 7 visited 3 or more streams (6M:1F). In contrast, 11 grizzly bears visited hair-snag sites all 3 years (7M:4F), 23 in only 2 years (11M:12F), and 29 in only 1 year (24M:5F). Twenty-five grizzly bears visited only 1 stream (20M:5F), 16 visited only 2 streams (8M:8F), 11 visited 3 streams (5M:6F), and 11 bears visited 4 or more streams (9M:2F).

During 2007–2009, 21 of 63 grizzly bears ($33 \pm 5.9\%$ [$\pm 95\%$ CI]) visited the vicinity of streams located near human development, defined as front-country ($n=15$ streams; Fig. 2). This proportion was not significantly different from an expected proportion based upon the relative sampling intensity of front-country streams ($43 \pm 6.2\%$; $P=0.359$). During 1997–2000, a significantly smaller proportion of grizzly bears ($18 \pm 4.2\%$ of identified) visited front-country streams than would be expected ($37 \pm 6.1\%$; $P=0.027$). The proportion of male grizzly bears ($69 \pm 7.1\%$) in the current study visiting the vicinity of back-country streams (Fig. 2) did not differ from 1) the overall proportion of males sampled in this study ($P=0.999$) or 2) expectations from an estimated GYE-wide sex ratio of 50% males ($P=0.071$; Haroldson 2012). The proportion of grizzly bears that visited front-country streams that were female ($43 \pm 10.8\%$) did not differ from our study-wide sex ratio of $33 \pm 5.9\%$ females ($P=0.590$). When compared to grizzly bears, a significantly greater proportion of black bears (8 male and 7 female black bears; $56 \pm 9.5\%$ of total number identified) visited front-country hair snags during 2007–2009 ($P \leq 0.001$). For 1997–2000, the same proportion of grizzly bears and black bears ($27 \pm 6.7\%$) visited front-country streams.

We obtained 178 photographs of bears from snag site cameras. Although we identified the age-class of as many as 7 new grizzly bears and 5 new black bears each year from the images, the majority of age class information came from known-age bears (i.e., previously live-captured). We determined age classes for 37 of the 63 snag-captured grizzly bears. We classified 7 grizzly bears (5M:2F) as subadults at time of sampling. The average age of known-aged grizzly bears that visited snag sites was 11 years old. The youngest known age of sampled bears at snag sites was 4. We never obtained pictures of dependent young at snag sites. Because approximately 41% of sampled bears were unassigned to age or age-class, we cannot rule out the possibility of presence of dependent young along stream corridors. Age classes of 6 of the 27 unique black bears were determined from camera images. All were adults.

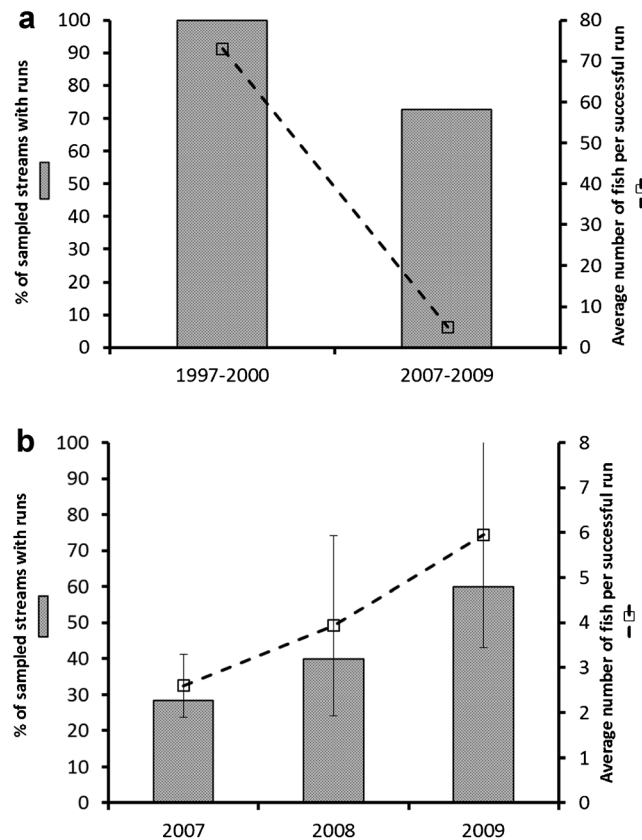


Figure 1. Percentage of sampled streams with runs and average number of cutthroat trout per successful run within 22 common streams between 1997–2000 and 2007–2009 datasets (a) and within the entire 35-stream dataset from 2007–2009 (b), Yellowstone Lake, Yellowstone National Park. Frame b includes 95% confidence intervals. For any given year, a successful run occurred if fish (as few as 1) were present on a stream in that year.

Table 3. Duration of cutthroat trout spawning activity on streams within each portion of Yellowstone Lake, Yellowstone National Park, Wyoming, between the 1997–2000 and 2007–2009 survey efforts.

| Lake portion | 1997–2000 study | | | 2007–2009 study | | |
|-------------------|----------------------------------|---|---|----------------------------------|---|---|
| | Median duration in weeks (range) | Earliest week median (range) | Latest week median (range) | Median duration in weeks (range) | Earliest week median (range) | Latest week median (range) |
| East shore | 6 (2–9) | 4th week Jun (4th week May–1st week Jul) | 4th week Jul (2nd week Jun–2nd week Aug) | 2 (1–5) | 4th week May (3rd week May–2nd week Jul) | 2nd week Jun (4th week of May–2nd week of Jul) |
| West shore | 6 (2–7) | 3rd week May (2nd week May–1st week Jul) | 1st week Jul (1st week Jun–2nd week Aug) | 3 (1–7) | 1st week Jun (4th week May–4th week Jun) | 3rd week Jun (1st week Jun–2nd week Jul) |
| West thumb | 3 (1–7) | 4th week May (2nd week May–2nd week Jun) | 2nd week Jun (3rd week May–2nd week Jul) | 2 (1–7) | 4th week May (1st week May–3rd week Jun) | 2nd week Jun (4th week of May–2nd week of Jul) |
| Lake village area | 3 (1–6) | 4th week May (4th week Apr–2nd week Jun) | 2nd week Jun (4th week May–1st week Jul) | 1 (1–1) | 4th week Jun (none) | 4th week Jun (none) |

Abundance and Trend—Grizzly Bears

Estimates from robust modeling.—Goodness-of-fit testing upon the 2007–2009 encounter histories using our most general model resulted in a \hat{c} value of 1.77. Lebreton et al. (1992) suggested that values <3 do not indicate issues with overdispersion of data. Sensitivity simulations indicated that a 77% change in \hat{c} of the best-fitting model resulted in a 2.7% change in model weight, indicating robustness to overdispersion. Capture probabilities from our robust Pradel modeling were near or above rates of 0.20 (mean of all capture sessions of 0.22); capture probabilities <0.20 often result in imprecise abundance estimates (i.e., inflated confidence intervals) when population size is estimated to

be <100 (Boulanger et al. 2002). Our AIC_c values indicated that the most parsimonious model (model 1) using the robust Pradel-recruitment procedure estimated apparent survival (ϕ) and recruitment rate (f) as invariant across sex or time but with a time-dependent capture rate (p ; Table 1). Also, 2 other models had ΔAIC_c values less than 2: one had ϕ and f varying between male and female grizzly bears and p varying with time (model 2), and another in which all 3 parameters were invariant across sex and time (model 3).

From 2007 to 2009, point estimates for abundance of male and female grizzly bears increased each year, ranging from 46 to 59 individuals (Fig. 3a). However, we found no significant change in the number of grizzly bears visiting streams in successive years ($\lambda = 1.140$, $SE = 0.086$, $95\% \text{ CI} = 0.972\text{--}1.308$). Model averaged estimates of abundance from the robust model also supported this trend in years 2007 and 2008. As indicated by the most parsimonious model in earlier analyses, estimates of apparent survival for the 2 intervals between summer sampling sessions did not differ (Tables 1 and 4). Although point estimates for male survival (0.848) and female (0.928) survival did not differ statistically, such estimates would reflect substantial differences in mean life span between sexes (Tables 1 and 4).

POPAN modeling: Within and between study estimates.—POPAN modeling of the current dataset resulted in lower variance in total number of bears visiting the vicinity of tributary streams. During 2007–2009, we estimate 48 (95% $CI = 42\text{--}56$) male and 23 (95% $CI = 21\text{--}27$) female grizzly bears visited historically fished tributary streams. Because of the paucity of animals captured during the earlier study (1997–2000) that were subsequently recaptured in this study, we were unable to merge the 2 datasets and analyze parameters of interest during the interval between studies. Under equal effort, model averaged estimates of grizzly bear abundance on 10 common streams in both studies differed (Fig. 3b), with an estimate of 73 grizzly bears (95% $CI = 59\text{--}88$) in 1998–2000 and 27 grizzly bears (95% $CI = 24\text{--}30$) in 2007–2009.

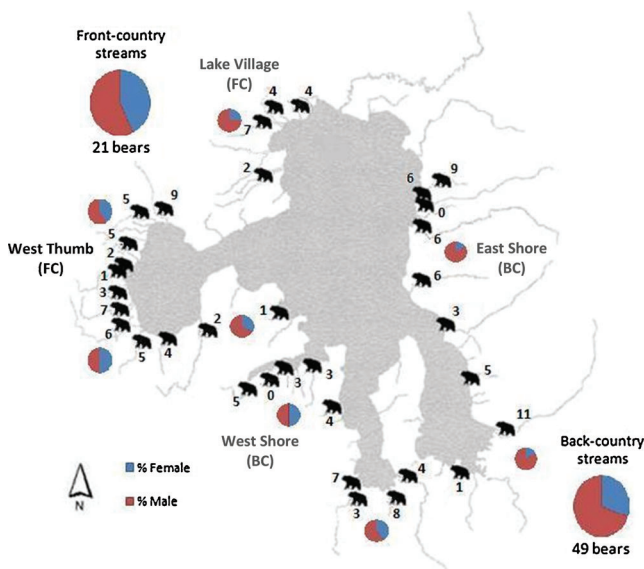


Figure 2. Number of individual grizzly bears identified at hair-snags on each tributary stream sampled ($n = 34$), Yellowstone Lake, Yellowstone National Park, 2007–2009. Streams within lake areas are labeled front-country (FC) or backcountry (BC), depending on proximity to human development. Pie charts indicate sex ratios in representative areas around Yellowstone Lake.

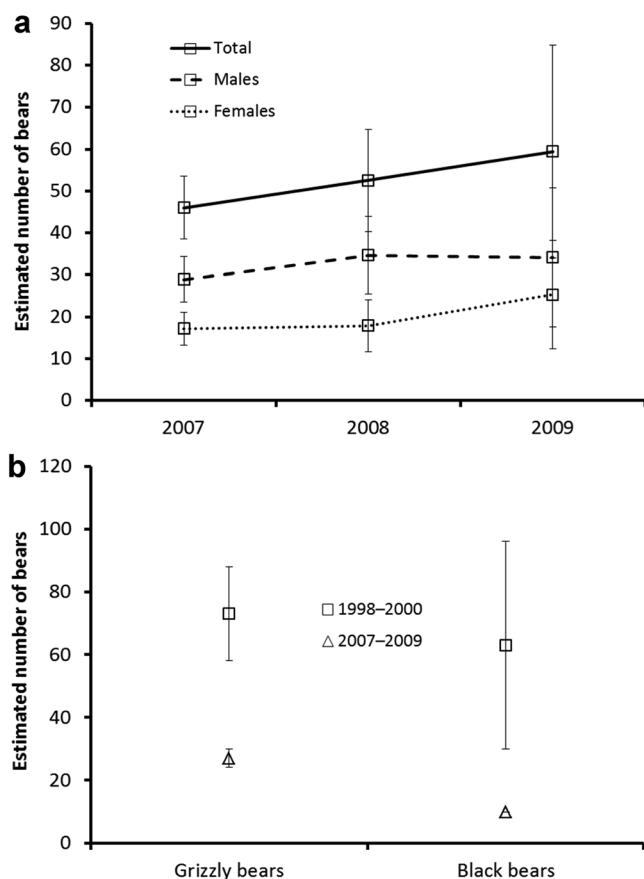


Figure 3. Robust estimates of annual number of male and female grizzly bears visiting 35 streamside hair-snag sites, 2007–2009 (a), and abundance estimates of grizzly bears (derived from a POPAN model) visiting hair-snag sites on the 10 common streams between the 1998–2000 and 2007–2009 studies (b), Yellowstone Lake, Yellowstone National Park. Bars indicate 95% confidence intervals.

Abundance—Black Bears

Using POPAN modeling of the full 1998–2000 dataset, we estimated that 78 black bears (95% CI = 28–128) visited the 22 streams sampled during that study. With a similar analysis on 2007–2009 black bear CMR data, we estimated an abundance of 28 bears (95% CI = 23–33) visited the vicinity of historically fished tributary streams. After standardizing temporal and spatial effort of both studies, we estimated that 63 (95% CI = 30–96) black bears visited the vicinity of tributary streams in the previous study (Fig. 3b). Attempts to

Table 4. Model-averaged estimates and standard error (SE) of parameters for male and female grizzly bears from robust modeling, Yellowstone Lake tributary streams, Yellowstone National Park, Wyoming, 2007–2009.

| Parameter | Females | Males |
|---------------------------------|---------------|---------------|
| Apparent survival (ϕ) | | |
| 2007–2008 | 0.930 (0.055) | 0.852 (0.093) |
| 2008–2009 | 0.926 (0.059) | 0.843 (0.098) |
| Recruitment (γ) | | |
| 2007–2008 | 0.221 (0.097) | 0.293 (0.103) |
| 2008–2009 | 0.217 (0.096) | 0.289 (0.101) |
| Population change (λ) | | |
| 2007–2008 | 1.151 (0.119) | 1.144 (0.136) |
| 2008–2009 | 1.143 (0.121) | 1.132 (0.139) |

standardize effort left the 2007–2009 data very sparse, with a minimum number of 10 animals visiting snag sites. As a result, we were unable to obtain estimates and confidence intervals of abundance with the POPAN analysis.

DISCUSSION

The number of grizzly bears visiting tributary streams of Yellowstone Lake and the number of spawning cutthroat trout in those streams decreased during the past decade. The decline in cutthroat trout spawning activity was more widespread than previously documented (Reinhart and Mattson 1990, Mattson and Reinhart 1995, Koel et al. 2003, Haroldson et al. 2005, Gunther et al. 2007). The number of bears visiting any single cutthroat trout spawning stream during the 1998–2000 study increased at a decreasing rate with increases in trout numbers along individual streams (Fig. 4a). However, we found no relationship between trout numbers and numbers of bears in the current study (Fig. 4b), presumably because the low

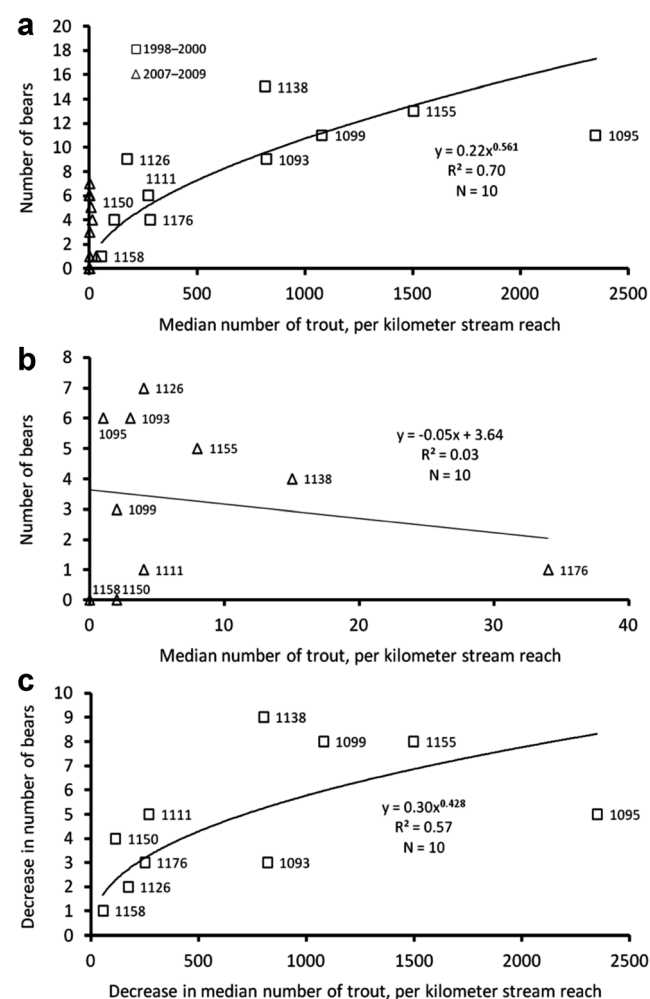


Figure 4. Relationships between the number of bears and median number of cutthroat trout observed for each common tributary stream sampled, 1998–2000 and 2007–2009 (a) and 2007–2009 exclusively (b), Yellowstone Lake, Yellowstone National Park. We also present the relationship between decreases in numbers of fish and bears along streams between study periods (c). Individual streams are labeled (e.g., 1093 and 1176 are numbers assigned by Yellowstone Park personnel).

density of remaining trout ($\leq 1\%$ of historical numbers) can no longer be efficiently exploited by grizzly bears. Grizzly bears are not likely continuing to visit stream corridors in the search for cutthroat trout (Haroldson et al. 2005, Fortin et al. 2013).

We predicted more grizzly bears would frequent front-country streams relative to 1997–2000 given the loss of available cutthroat trout and because other food resources can be found near developed areas around Yellowstone Lake (Gunther et al. 2004). The shift from an absence of grizzly bears in front-country streams (1997–2000) to a more uniform distribution between front-country and backcountry streams recently may indicate that a transition towards greater front-country use by grizzly bears is underway. A more pronounced shift has occurred with black bears. Grizzly bears and black bears equally visited front-country streams from 1997 to 2000, whereas current front-country use by black bears far outpaces grizzly bears. These changes in spatial distribution of both species around the lake may be a direct response to declines in the availability of cutthroat trout. Further, larger body size and caloric demand may have led grizzly bears to seek higher-quality foods (i.e., elk) outside of the Yellowstone Lake basin.

The age and sex distribution of grizzly bears visiting hair-snag sites in this study (19% subadults, 54% adult males, and 27% adult females) does not differ from current estimates for the larger Yellowstone population (22% subadults, 39% adult males, and 39% adult females; $\chi^2_2 = 3.0$, $P = 0.223$; Knight and Eberhardt 1985, Haroldson 2012). However, a slight bias in sex ratio may have been introduced by our study design. Models in which capture probability (P) varied by sex were less supported than those assuming no difference in P between males and females (Table 1). Also, estimates within the Northern Continental Divide Ecosystem using hair-snag techniques similar to our effort observed female-dominated sex ratios (58–69% female; Kendall et al. 2008, 2009). Thus, we conclude that more males than females are continuing to visit cutthroat trout spawning streams, a finding similar to that of Haroldson et al. (2005). This trend may be a behavioral artifact of historically male-dominated consumption of trout along tributary streams of Yellowstone Lake, as several bears may continue to occupy the same home ranges they did a decade earlier (Felicetti et al. 2004). Additionally, male bears may have an increased chance of encountering hair-snag sites because of higher rates of movement and larger home range sizes (2–3 times) than females in Yellowstone (Blanchard and Knight 1991).

Ten-year estimates of trout consumption indicate that it has not been a significant food for female grizzly bears for some time (Felicetti et al. 2004, Fortin et al. 2013). Hence, we considered whether the use of cutthroat trout by future generations may be in jeopardy because of the loss of traditional foraging knowledge, passed from mothers to cubs. However, with a well-documented natural history as an opportunistic omnivore capable of substantial foraging plasticity especially in the GYE (Fortin et al. 2013, Gunther et al. 2014), we are certain that bears, if abundant, will once again return to the use of this high-quality food resource.

Estimates of the number of black bears visiting stream corridors has declined from 1998–2000 to 2007–2009 (Fig. 3b) by as much as 84%. We predicted the opposite, as a lesser grizzly bear presence along streams might allow increased exploitation by black bears of plant foods growing in streamside habitats (e.g., Mattson et al. 2005). However, the reduction in black bear numbers, as with grizzly bears, may be a direct response to the decrease in cutthroat trout. Fortin et al. (2013) observed that trout intake by black bears visiting tributary streams of Yellowstone Lake decreased by 69% during the past decade. Hence, current numbers of cutthroat trout no longer support the effective foraging of this resource by either bear species.

Unlike Haroldson et al. (2005), we used a robust model to produce annual superpopulation estimates of grizzly bears near tributary streams, thereby assuming geographic closure. We found, when modeling apparent survival (ϕ) and recruitment rate (f), a generalized model fit equally as well as the constrained, fixed-value models (likelihood ratio tests; $P = 0.675$, $P = 0.122$, and $P = 0.796$, for summer sessions of 2007, 2008, and 2009, respectively), indicating that the estimated values of ϕ and f during summer sampling sessions did not statistically differ from 1 and 0, respectively. These findings support our conclusion that reasonable geographic closure occurred during summer sessions, which allowed us to proceed with a robust modeling effort.

The slight increases in spawning numbers observed during our study (Fig. 1b) may have occurred because 1) an increase in the amount of spawning habitat for cutthroat trout became available after high stream-flows in 2008 and 2009 removed impeding gravel bars, and 2) an increased effort to remove lake trout from Yellowstone Lake may have increased cutthroat trout survival (Koel et al. 2010). Current trends (through summer of 2012) continue to show increases in the trout population, especially in some West Thumb streams, yet numbers are still $< 5\%$ of historical spawning numbers (Gunther et al. 2011; E. Reinertson, National Park Service, personal communication). Although the 15-year gill-netting effort to control numbers of invasive lake trout within Yellowstone Lake has slowed population growth, a harvest much greater than the current effort is required to induce a population decline (Syslo et al. 2011).

MANAGEMENT IMPLICATIONS

Since the late 1990s, we have documented an increased proportional use of front-country stream corridors by grizzly bears and black bears, which could lead to increases in bear-human conflicts (Gunther et al. 2004). As such, National Park Service priority should be placed on recovering and sustaining a healthy trout population, especially in back-country reaches of tributary streams, to aid in reducing future bear-human conflicts. We found evidence of a very slow recovery of the cutthroat trout spawning population, which has yet to reach levels that could be efficiently exploited by grizzly bears or black bears. For example, although the median number of cutthroat trout per stream during the current study was 2.5 fish, a single male grizzly bear in the earlier study consumed 55 trout annually (Felicetti

et al. 2004). Consequently, we suggest that the number of spawning trout per stream will have to reach approximately 400 fish/km of stream (i.e., the inflection point of the first derivative [slope] of the equation in Fig. 4a) before large numbers of grizzly and black bears once again specialize on this food. If the Yellowstone Lake cutthroat trout population can be recovered to such levels, grizzly and black bears that still reside within the lake basin will readily find and use this high-quality food resource, potentially returning both species to higher use of backcountry habitat. For these reasons, we endorse the ongoing gillnetting efforts to control numbers of lake trout in Yellowstone Lake.

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