Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bears visiting streams from DNA

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Abstract: Spawning Yellowstone cutthroat trout (*Oncorhynchus clarki*) provide a source of highly digestible energy for grizzly bears (*Ursus arctos*) that visit tributary streams to Yellowstone Lake during the spring and early summer. During 1985–87, research documented grizzly bears fishing on 61% of the 124 tributary streams to the lake. Using track measurements, it was estimated that a minimum of 44 grizzly bears fished those streams annually. During 1994, non-native lake trout (*Salvelinus namaycush*) were discovered in Yellowstone Lake. Lake trout are efficient predators and have the potential to reduce the native cutthroat population and negatively impact terrestrial predators that use cutthroat trout as a food resource. In 1997, we began sampling a subset of streams ($n = 25$) from areas of Yellowstone Lake surveyed during the previous study to determine if changes in spawner numbers or bear use had occurred. Comparisons of peak numbers and duration suggested a considerable decline between study periods in streams in the West Thumb area of the lake. The apparent decline may be due to predation by lake trout. Indices of bear use also declined on West Thumb area streams. We used DNA from hair collected near spawning streams to estimate the minimum number of bears visiting the vicinity of spawning streams. Seventy-four individual bears were identified from 429 hair samples. The annual number of individuals detected ranged from 15 in 1997 to 33 in 2000. Seventy percent of genotypes identified were represented by more than 1 sample, but only 31% of bears were documented more than 1 year of the study. Sixty-two (84%) bears were only documented in 1 segment of the lake, whereas 12 (16%) were found in 2–3 lake segments. Twenty-seven bears were identified from hair collected at multiple streams. One bear was identified on 6 streams in 2 segments of the lake and during 3 years of the study. We used encounter histories derived from DNA and the Jolly-Seber procedure in Program MARK to produce annual estimates of grizzly bears visiting streams. Approximately 68 grizzly bears visited the vicinity of cutthroat trout spawning streams annually. Thus, approximately 14–21% of grizzly bears in the Greater Yellowstone Ecosystem (GYE) may have used this threatened food resource annually. Yellowstone National Park (YNP) is attempting to control the lake trout population in Yellowstone Lake; our results underscore the importance of that effort to grizzly bears.

Key words: cutthroat trout, DNA, grizzly bear, lake trout, *Oncorhynchus clarki*, *Salvelinus namaycush*, spawning, *Ursus arctos*, Yellowstone

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Yellowstone Lake is one of the last remaining undisturbed natural habitats for native Yellowstone cutthroat trout (*Oncorhynchus clarki*, Varley and Gresswell 1988). This population is in jeopardy because of the presence of non-native lake trout (*Salvelinus namaycush*), which were discovered in the lake in 1994. Research suggests that lake trout have been in Yellowstone Lake for >25 years, and that illegal introductions occurred through the mid 1990s (Munro et al. 2001). Declines in native populations of cutthroat trout have occurred in other lakes where lake trout have been introduced (Kaeding et al. 1996). Without control of lake trout in Yellowstone Lake, McIntyre (1996) estimated the cutthroat trout population would decline as much as 90%. A decline of this magnitude could dramatically decrease food availability for an estimated 42 wildlife species, including grizzly bears (*Ursus arctos*, Schullery and Varley 1996).

Each spring and early summer, cutthroat trout enter tributary streams of Yellowstone Lake to spawn. Grizzly bear feeding on spawning cutthroat trout has been documented since the mid 1970s (Mealey 1980, Reinhart 1990, Mattson and Reinhart 1995; W.P. Hoskins, 1975, Yellowstone Lake tributary study, Interagency Grizzly Bear Study Team, Bozeman, Montana, USA). Cutthroat trout provide a food resource that is high in protein and lipid content (Pritchard and Robbins 1990) during a time when bears recoup nutritional losses incurred during hibernation (Mattson et al. 1991*a*). In comparison, lake trout spawn in deep lake waters and are mostly unavailable to terrestrial predators.

Peak numbers of spawning cutthroat trout and indices of bear use declined on streams near the developments of Grant Village and Lake (front-country streams) during 1990–95 (Reinhart et al. 1995). It is unknown whether declines of cutthroat trout and subsequent bear use are directly related to lake trout or other factors, such as changes in streams due to the fires of 1988 or effects of other recently discovered exotics (such as whirling disease [*Myxobolus cerebralis*]). It is also unknown whether similar declines in spawner numbers have occurred in tributary streams remote from human developments and roads (back-country streams).

During 1997–2000, we conducted stream surveys of spawning cutthroat trout and grizzly bear use on a sample of tributary streams to Yellowstone Lake. Our primary objective was to determine if changes in spawner numbers and grizzly bear use had occurred since the previous surveys (1985–87) and the discovery of lake trout. Our secondary objective was to estimate the number of grizzly bear visiting streams using DNA amplification and genotyping techniques (Mowat and Strobeck 2000). This information would establish a benchmark of bear numbers for future comparison and allow us to assess the impact of potential loss of this food resource to the grizzly bear population in the GYE.

Study area

We investigated spawning cutthroat trout and associated grizzly bear activity on tributary streams to Yellowstone Lake, YNP. Yellowstone Lake (centered at 44.47°N, 110.37°W) is in the southeastern portion of YNP (Fig. 1) and the approximate center of the current distribution of grizzly bears in the GYE (Schwartz et al. 2002). Outflow from Yellowstone Lake is part of the Yellowstone–Missouri–Mississippi River systems (Marston and Anderson 1991). The lake is oligotrophic, occurs at an elevation of 2,358 m, has a mean depth of 42 m, and a maximum depth of 98 m. Yellowstone Lake has approximately 176 km of shoreline and a surface area of 354 km^2.

Mean maximum and minimum temperatures at Lake Ranger Station, YNP, were –5.3°C and –16.6°C, respectively, during January and 21.7° and 3.5° C, respectively, during July (Temperature and Precipitation Station, Yellowstone Lake, Wyoming, USA, 1948–99). Precipitation averaged 51 cm annually, with 420 cm falling as snow, mostly between October and April. The lake is typically frozen from December until late May or early June.

Forest cover surrounding Yellowstone Lake is predominately lodgepole pine (*Pinus contorta*) in the western and northern portions of the drainage basin. Mixed stands of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine occur on the eastern and southern portions of the drainage basin. Mixed grass–sedge (*Carex* spp.) or grass–forb meadows are common along stream corridors west and north of the lake.

The only fish native to Yellowstone Lake, other than cutthroat trout, is the longnose dace (*Rhinichthys cataractae*; Simon 1962). In addition to lake trout, other introduced fish in the lake are redside shiners (*Richardsonius balteatus*), longnose suckers (*Catostomus catostomus*), and lake chub (*Couesius plumbeus*; Gresswell and Varley 1988).

There are 124 tributaries to the lake (System of Numbering Yellowstone Waters SONYEW; Varley et al. 1976, Jones et al. 1986), and spawning trout have been documented in 48% ($n = 59$) of them. Streams without spawning trout exhibit insufficient flows, steep gradients, incompatible substrates, natural or artificial blocks, or are thermally influenced with incompatible chemical composition. Spawning of cutthroat trout occurs from ice-off through late July or early August (Reinhart 1990, Reinhart et al. 1995). Grizzly bears feed on these trout primarily from mid May through July (Reinhart and Mattson 1990). Bear activity, concurrent with spawning, has been documented on 93% ($n = 55$) of streams and

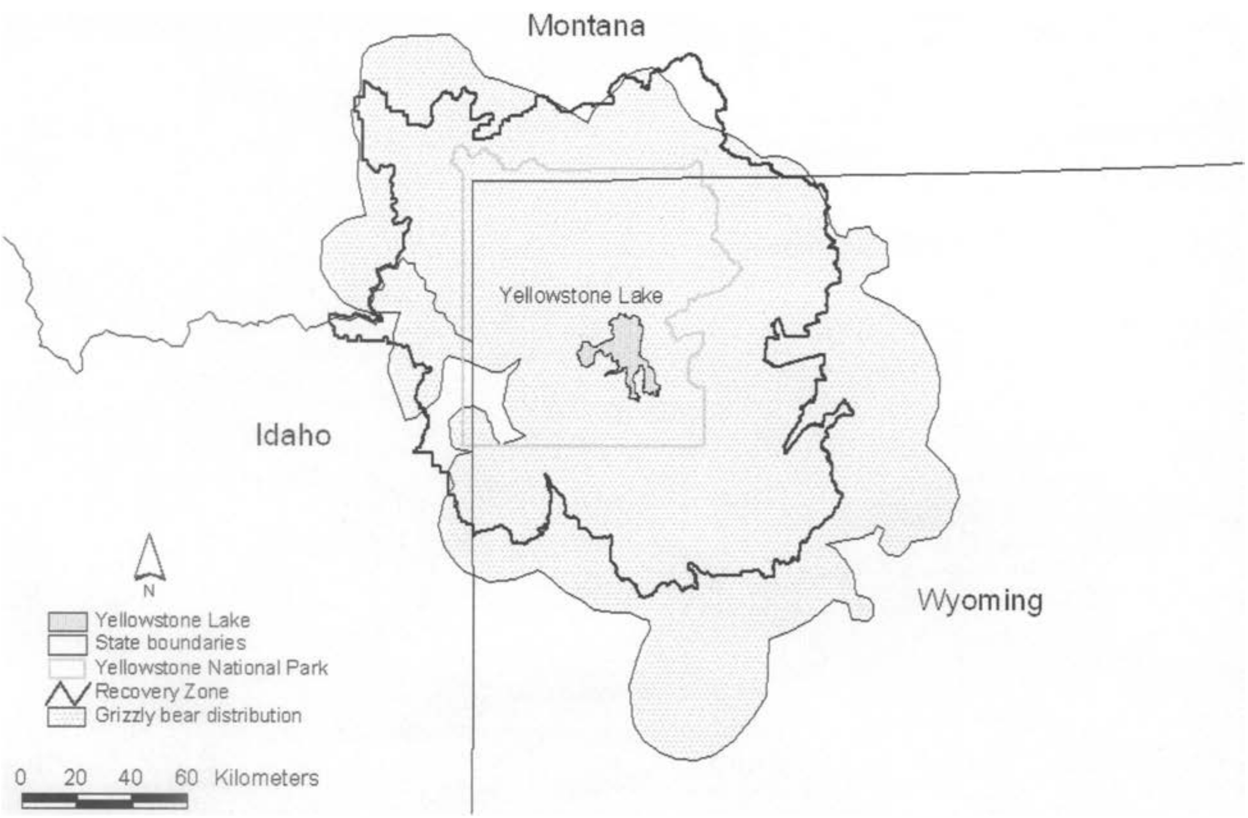

Fig. 1. Greater Yellowstone Ecosystem, including Yellowstone Lake, the boundaries of Yellowstone National Park, and an estimate of the current distribution of grizzly bears in the Greater Yellowstone Ecosystem from Schwartz et al. (2002).

evidence of bears fishing has been found on 61% ($n = 36$) of streams (Reinhart and Mattson 1990).

Other important foods used by grizzly bears in the GYE include ungulates, primarily elk (*Cervus elaphus*) and bison (*Bison bison*), which are consumed as carrion (Green et al. 1997, Mattson 1997) and as prey (Gunther and Renkin 1990, Mattson 1997). Summer aggregations of army cutworm moths (*Euxoa auxiliaris*) occur on high-elevation talus slopes in the southeastern portion of the GYE and are consumed by grizzly bears during late July through September (Mattson et al. 1991*b*). Seeds from whitebark pine (*Pinus albicaulis*) probably are the most important late summer and fall food (Kendall 1983, Mattson et al. 1991*a*). Mattson et al. (1991*a*) described other vegetal foods used by grizzly bears in the GYE.

Methods

Spawner numbers and duration

During 1997–2000, we surveyed spawning fish in 25 streams, including 12 front-country and 13 back-country streams (Fig. 2). This sample represented 46% of streams exhibiting spawning runs and 75% of streams with prior evidence of grizzly bear fishing (Reinhart 1990). Front-country streams included 6 Lake Area and 6 West Thumb streams. Back-country streams included 8 West Shore and 5 East Shore streams. Streams were surveyed weekly from ice-off through the end of cutthroat trout spawning activity, which usually occurred during mid-August. Data collection followed procedures described by Reinhart (1990) and Reinhart et al. (1995) and included a visual count of spawning trout through the upstream extent of the run. Stream courses were surveyed to the same extent during both study periods, and streams were considered the sampling unit for most comparisons.

To assess whether declines in numbers of spawning trout were evident between our surveys and those of Reinhart (1990) for 1985–87, we computed the difference in median peak counts ($\text{median}_{1997\text{–}2000} - \text{median}_{1985\text{–}87}$) and the difference in median duration of spawning activity for each stream. Differences were

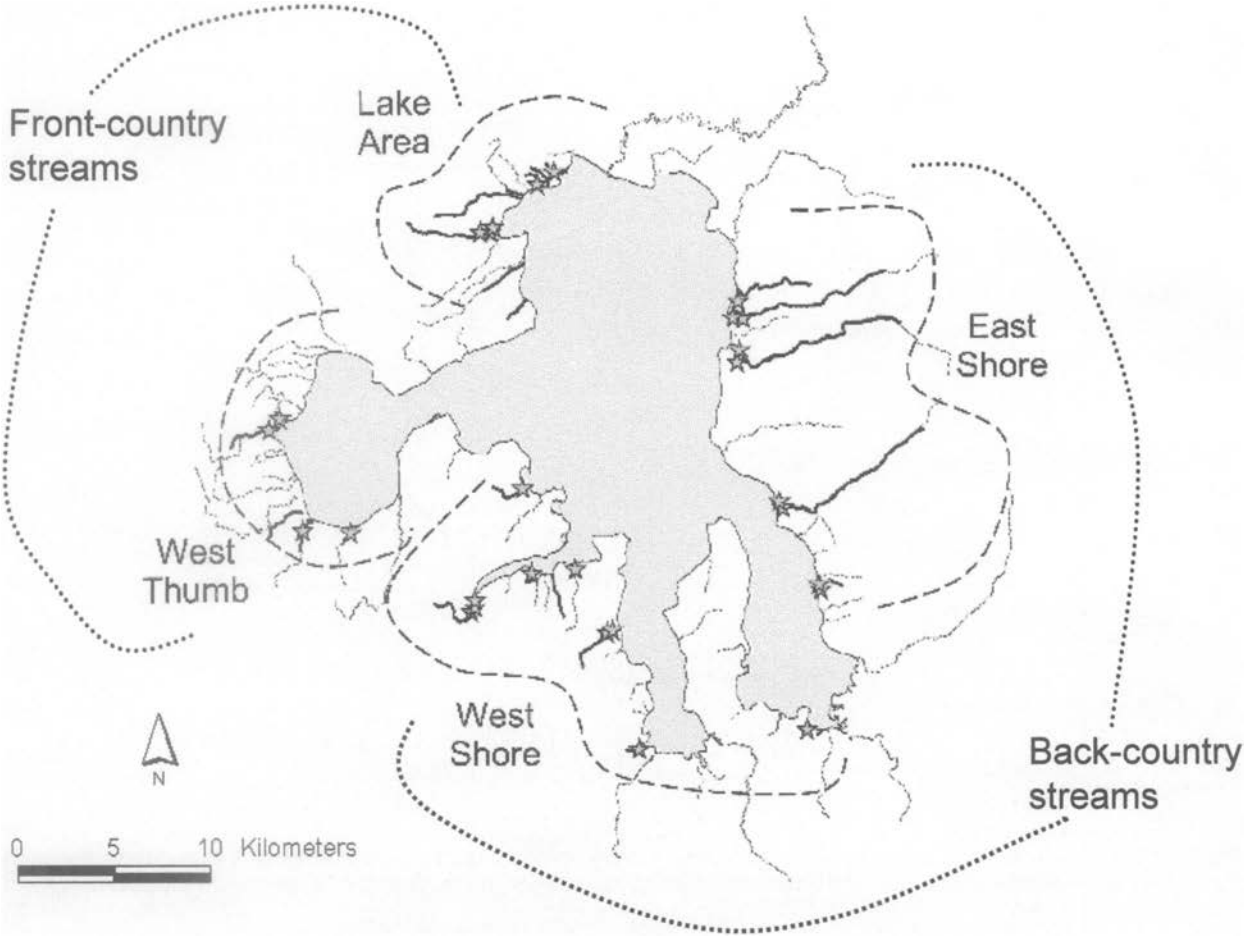

Fig. 2. Cutthroat trout spawning streams surveyed and location of grizzly bear hair-snagging sites (stars) on tributary streams in 4 areas surrounding Yellowstone Lake, Yellowstone National Park, 1997–2000.

summarized by computing the median difference by lake portion. For peak counts, we only used observations from streams where spawning trout were observed during ≥ 2 annual surveys during each study. For duration, if spawning trout were present in streams during the initial survey, the week previous to the initial survey was assumed to be the earliest week of spawning. Although surveyed during 1997–2000, Arnica Creek was excluded from West Thumb comparisons because it was poisoned during 1985–87 to eliminate brook trout (*Salvelinus fontinalis*).

Indices of bear activity

Bear activity associated with streams was determined by documenting fish remains left by feeding bears, scats, and bear tracks along stream courses (Reinhart 1990) and was done in conjunction with weekly fish surveys. All observed bear sign were removed from stream courses during weekly surveys. Track measurements were used to estimate the minimum number of grizzly and black bears (*Ursus americanus*) that visited spawning streams prior to each survey. Tracks that varied by more than 1.5 cm in pad width (of either the front or rear foot), by species or by association (e.g., adult with young), were considered to be from different bears. The total number of visits by bears based on track surveys did not necessarily reflect the number of different bears that fished spawning streams because some bears traveled among streams. However, the average numbers of bear visits/stream/week provided an index to use of the cutthroat trout resource and a method to compare species-specific activity between studies. To assess whether changes in bear use of spawning streams were evident between our surveys and results reported by

Reinhart (1990) for 1985–87, we computed the median difference in scats, fish remains, and grizzly bear visits/stream/week using the same procedure described previously for assessing changes in spawner numbers.

Estimates of bear numbers on streams

Hair-snagging techniques (Haroldson and Anderson 1997) were used to obtain hair from bears visiting the vicinity of streams for use in DNA genotyping. During 1997 and 1998, 14 and 15 snagging sites were deployed on 10 and 11 streams, respectively. Baited hair-snagging sites were placed on only 1 stream in the Lake area and 1 in West Thumb during 1997–98 due to concern for public safety in these front-country areas. The remaining sites were distributed among back-country East Shore ($n=3$) and West Shore ($n=6$) streams. During 1999 and 2000, we deployed 26 and 28 hair snags, respectively, on 19 streams. This increased effort was primarily due to use of unbaited hair snags of barbed wire stretched diagonally across bear trails or fishing spots. Each stream had 1–3 hair-snagging sites >1.5 km apart, depending on the length of the spawning run and streamside topography. All snagging sites were established prior to onset of spawning runs. Cattle blood was used as an attractant (Haroldson and Anderson 1997) at all baited sites. All hairs caught on a single barb of the perimeter wire were treated as a single sample for DNA analysis and collected using sterile techniques. Samples with ≥10 hairs were shipped to the University of Idaho, Moscow, Idaho, for DNA analysis.

Laboratory procedures. All DNA extraction and polymerase chain reaction (PCR) was performed in a low-quantity DNA room dedicated to processing bone, scat, and hair samples to avoid contamination errors. We attempted to extract DNA from all samples with ≥5 visible roots. This minimum was intended to provide enough DNA to avoid genotyping errors in microsatellite analysis of samples with low quantities of DNA (Taberlet et al. 1997, 1999; Goossens et al. 1998). In 1997–99, DNA was extracted using 200 μl of 5% Chelex solution (Walsh et al. 1991) and purified with a Geneclean II Kit (Bio101MP Biomedical, Irvine, California, USA). In 2000, DNA was extracted using a Qiagen tissue kit (Qiagen Inc., Valencia, California, USA) using standard protocols. Species identification was performed by amplifying a 145–165 base pair section of the mitochondrial DNA (mtDNA) control region that has a 13–20 base pair deletion in grizzly bears relative to black bears (Shields and Kocher 1991, Waits 1996) using primers described in Murphy et al. (2000). Products from the PCR were separated and analyzed using an Applied Biosystems (ABI; Foster City, California, USA) 377 DNA Sequencer.

A suite of 6 microsatellite loci (G1A, G10B, G10C, G10L, G10M, G10P) was used for individual identification (Paetkau et al. 1995). Woods et al. (1999) described methods used for PCR conditions and ABI gel separation. Genotypes for each sample were determined using the Genescan 3.0 and Genotyper 3.5 software packages (Applied Biosystems, Foster City, California, USA). After genetic analyses were completed, the database was searched for matches to identify unique genotypes. Two approaches were used to filter the data and remove genotyping errors. First, single capture individuals (genotypes seen only once) were genotyped again at all loci. Second, the dataset was screened for samples that differed at only 1 locus or at 2 loci in a pattern that could be explained by allelic dropout. Then, the locus or loci were reamplified for both samples. There was not enough DNA to regenotype single capture individuals from the 1997 dataset. Any samples that were observed only once and not reliably regenotyped were removed from the dataset to prevent retention of genotyping artifacts.

Excluding errors in genetic analysis, a difference in genotypes between samples is proof that they originate from different animals. However, samples with identical genotypes could match for the surveyed loci but actually represent 2 individuals that would display different genotypes if more loci were examined. Thus, a statistical basis for match declarations must be used. We calculated the probability of identity for siblings ($P[ID]_{sibs}$; Woods et al. 1999, Waits et al. 2001) and used a threshold value of <0.05 for accepting genotypes (Woods et al. 1999). We also calculated the average $P(ID)_{sibs}$ for recaptures in the dataset.

All samples that met the statistical criterion for unique individuals were analyzed to determine sex by amplifying the Amelogenin locus using primers SE47 and SE48 as described in Ennis and Gallagher (1994). Products from the PCR were separated by size on an ABI 377 and scored using Genescan 3.0 and Genotyper 3.5. To ensure accuracy, all samples were genotyped a minimum of 2 times.

Statistical procedures. We tallied unique individuals identified annually from all sampled streams to estimate the minimum number of bears visiting streams. We also used the open-population Jolly-Seber (J-S) routine in Program MARK (White and Burnham 1999) to estimate number of grizzly bears visiting streams. To maintain a constant sampling area and intensity, we restricted the J-S analysis to the 10 streams sampled all 4 years and generated an annual encounter history for

Table 1. Median and range of earliest week, latest week, and duration of spawning activity from 4 areas of Yellowstone Lake, Yellowstone National Park, 1997–2000.

Lake portion	Earliest[a] week median (range)	Latest week median (range)	Median duration, weeks (range)	*n*
Lake Area	4th week May (4th week Apr–2nd week Jun)	2nd week Jun (4th week May–1st week Jul)	3 (1–6)	23
West Thumb	4th week May (2nd week May–2nd week Jun)	2nd week Jun (3rd week May–2nd week Jul)	3 (1–7)	20
West Shore	3rd week May (2nd week May–1st week Jul)	1st week Jul (1st week Jun–2nd week Aug)	6 (2–7)	26
East Shore	4th week Jun (4th week May–1st week Jul)	4th week Jul (2nd week Jun–2nd week Aug)	6 (2–9)	16

[a]If spawning trout were present in streams during initial survey, earliest week was estimated as the previous week.

each individual encountered on those streams. We used Akaike Information Criterion adjusted for small samples (AIC_c) to assess an *a priori* suite of models (Burnham and Anderson 2002) and model averaging (White et al. 2001) to estimate annual number of grizzly bears visiting spawning streams.

Selection of our *a priori* models was based on a variety of factors. We expected that survivorship for independent bears ($\geq$2 years old and the bears most likely to be captured) would be high (Eberhardt et al. 1994, Eberhardt 1995) and constant; hence, we considered alternative models with constant and time dependent apparent survival. We assumed the number of bears visiting streams would be relatively constant in the short term (4-year duration of study); thus, we considered alternative models containing a fixed lambda (1.0), an estimated constant lambda, and a time varying lambda. Finally, it seemed likely that capture probability would vary among years, given the vagaries of natural food abundance and its effect on the number of bears visiting streams, thus we modeled capture probability as year-dependent.

Results

Spawner numbers and duration

Breakup of ice on Yellowstone Lake during 1997–2000 averaged 15 May (range 8–20 May). Spawning trout were typically observed in West Thumb, West Shore, and Lake Area streams shortly after breakup of ice (Table 1). Earliest spawning activity observed in East Shore streams generally lagged other lake portions by 3–4 weeks, usually starting during the fourth week in June. Duration of spawning activity was longest on West and East Shore streams, probably because these areas contained more and larger streams which provided for larger cohorts of fish. Peak counts of spawning trout also varied considerably (Table 2) and likely were influenced by factors including flows, extent of stream course, drainage basin, and abundance of cohort classes available for spawning.

We observed no decline in peak numbers of fish between 1985–87 and 1997–2000 surveys on front country Lake Area streams or the back-country East Shore streams (Fig. 3a). Peak numbers of spawning trout increased on back-country West Shore streams, but declined on the front-country West Thumb streams (Fig. 3a).

Duration of spawning activity was shorter during 1997–2000 than 1985–87 on all lake portions except West Shore streams (Fig. 3b). Although the earliest week of spawning was similar between study periods among all areas of the lake, latest week of spawning tended to be earlier during 1997–2000, accounting for observed differences.

Indices of bear activity

Back-country West Shore and East Shore streams had greater numbers of grizzly bear visits per week than front-country Lake Area and West Thumb streams (Table 2). We observed a maximum of 5 bear visits/stream/week during the study period. Generally, streams with more spawning trout had more bear visits. Flat Mountain Creek (West Shore) had more use than any other stream, averaging 1.8 bear visits/week. Delusion Creek had the fewest bear visits of all back-country streams, with an average of 0.1 visits/week. We observed a maximum of 2 bear visits/week on Lake Area and West Thumb streams. Bridge and Lodge creeks were the most frequently used streams in the Lake Area, each averaging 0.2 grizzly bear visits/week. Little Thumb Creek, the most frequently used stream in West Thumb, averaged 0.4 visits/week. No grizzly bears visited Stream 1167 in West Thumb during the study period.

Median differences in frequency of grizzly bear visits per week between the study periods indicate a decline in grizzly bear use of streams around most of Yellowstone

Table 2. Peak counts of spawning cutthroat trout, grizzly visits/week, number of scats, and number of fish remains documented annually on tributary streams from 4 portions of Yellowstone Lake, Yellowstone National Park, 1997–2000. Track width differences of >1.5 cm were used to differentiate individual bears.

Lake portion	Stream	SONYEW[a]	Years surveyed	Years with spawners	Median (range) of peak spawners	Median (range) grizzly visits/week	Median (range) total annual scats	Median (range) total annual fish remains
Lake Area	Weasel	1192	4	1	3 (3–3)	0.1 (0–2)	0.0 (0)	0.0 (0)
	Bridge	1196	4	4	476 (149–657)	0.2 (0–2)	0.0 (0)	2.5 (2–5)
	Wells	1198	4	4	15 (4–49)	0.1 (0–2)	0.0 (0)	0.0 (0)
	Incinerator	1199	4	3	47 (4–59)	0.1 (0–1)	0.0 (0)	0.0 (0–1)
	Hatchery	1201	4	4	68 (36–94)	0.1 (0–1)	0.0 (0–4)	2.0 (0–3)
	Lodge	1203	4	4	60 (29–115)	0.2 (0–1)	1.0 (0–2)	1.0 (0–4)
West Thumb	Sewer	1164	4	4	21 (15–54)	0.2 (0–2)	0.0 (0)	0.0 (0)
	Sandy	1166	4	4	88 (33–107)	0.2 (0–2)	0.0 (0–1)	0.0 (0–1)
	1167	1167	4	3	22 (3–57)	0.0 (0)	0.0 (0)	0.0 (0)
	Little Thumb	1176	4	4	142 (74–155)	0.4 (0–1)	0.5 (0–2)	0.0 (0–4)
	1177	1177	2	1	59 (59–59)	0.1 (0–1)	1.5 (1–2)	0.5 (0–1)
	Arnica	1183	2	2	88 (15–161)	0.3 (0–1)	0.0 (0)	0.0 (0)
West Shore	1113	1113	4	3	137 (111–201)	1.3 (0–4)	2.5 (1–10)	8.5 (3–17)
	East Eagle	1126	3	3	88 (79–138)	1.0 (0–3)	10.0 (2–20)	1.0 (1–13)
	West Eagle	1127	3	3	27 (27–40)	0.8 (0–2)	0.0 (0–4)	1.0 (1–2)
	1138	1138	4	4	816 (409–1153)	1.4 (0–5)	9.0 (1–31)	17.5 (7–49)
	1141	1141	2	2	202 (116–288)	0.6 (0–3)	6.5 (5–8)	3.0 (1–5)
	Grizzly Bay	1150	4	4	58 (23–40)	0.6 (0–4)	2.5 (1–7)	3.5 (0–17)
	Flat Mountain	1155	4	4	1505 (456–1711)	1.8 (0–5)	10.0 (1–25)	11.0 (7–20)
	Delusion	1158	4	1	28 (28–28)	0.1 (0–1)	0.0 (0)	0.0 (0–2)
East Shore	Little	1091	2	2	46 (36–56)	0.8 (0–4)	9.5 (1–18)	1.0 (1)
	Cub	1093	4	4	822 (754–2986)	1.6 (0–4)	3.0 (1–18)	6.0 (1–9)
	Clear	1095	4	4	2349 (261–4429)	1.1 (0–4)	5.0 (0–14)	6.0 (2–8)
	Columbine	1099	4	4	1081 (461–1249)	1.0 (0–3)	0.0 (0–1)	0.5 (0–2)
	Foam	1107	3	2	73 (47–99)	0.5 (0–2)	4.0 (3–7)	0.0 (0–5)

[a]System of numbering Yellowstone waters.

Lake (Fig. 4a), particularly Lake Area and East Shore streams. However, grizzly bear visits did not differ between study periods on West Shore streams (Fig. 4a).

Although we were unable to associate scats and fish remains found along streams to grizzly or black bear, they do indicate bear activity along streams. Comparisons of annual totals of scats (Fig. 4b) and fish remains (Fig. 4c) detected along streams suggest a general decline in use between studies. This trend was most evident from scats left by bears along West Thumb and West Shore streams and from fish remains left along West Thumb streams (Fig. 4c).

Estimates of bear numbers on streams

We collected 981 hair samples of which 650 were determined to be from grizzly bears. Among grizzly bear samples, success rate for replication and amplification of DNA was 71% (annual range = 61–76%), resulting in 461 genotyped samples (Table 3). We excluded 32 samples that were genotyped because they did not meet the $P(ID)_{sibs}$ threshold. Average $P(ID)_{sibs}$ for the data set was 0.018, meaning 1 of 55 sibling pairs (or pairs of individuals that share half their genes) were expected to match at the genotyped loci.

Minimum number of bears identified annually from all streams sampled ranged from 15 during 1997, to 33 during 2000 (Table 3). Cumulatively, 74 unique genotypes were identified from 429 hair samples that met the $P(ID)_{sibs}$ threshold (Table 3). Tests for sex determination failed for 24 (32.4%) grizzly bears. Of the 50 genotypes for which sex was determined, 18 (36%) were female and 32 (64%) were male.

Twenty-two (29.7%) bears were identified from only 1 sample. Fifty-one (68.9%) bears were detected during only 1 year. Among individuals detected multiple years, 14 (18.9%) were observed 2 years, 8 (10.8%) 3 years, and 1 (1.4%) individual was detected all 4 years. Most genotyped bears were detected in only 1 portion of the lake ($n = 62$, 84%), whereas 11 bears were detected in 2 lake portions (15%), and 1 bear in 3 (1%). The majority of the 74 unique individuals were detected on back-country (West and East Shore) streams. Only 18% of unique individuals were known to visit front-country streams of West Thumb ($n = 9$) and Lake area ($n = 4$).

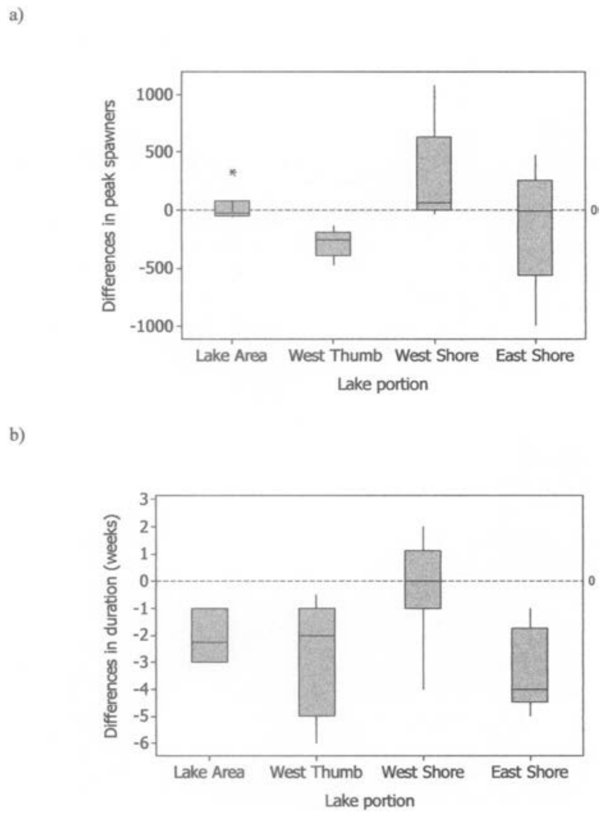

Fig. 3. Box plots of (a) difference in median peak counts for each stream between study periods (median $_{1997–2000}$ – median $_{1985–87}$) and (b) difference in median duration of spawning activity between study periods for tributary streams from 4 areas of Yellowstone Lake, Yellowstone National Park. Top and bottom box edges represent the 25th and 75th percentiles. The horizontal line inside the box is the median, and the whiskers extend to the largest and smallest difference within 1.5 times the box length. Extreme values appear as symbols above or below whiskers.

Among 23 bears observed during multiple years, 16 were detected only within the same lake portion and 6 were detected within the same and different lake portions. One individual was detected on streams from 2 lake portions during 2 years.

The number of individual bears identified per stream varied from 0 to 17 (Fig. 5). No individual bears were detected on 3 streams. On 2 of these streams, Sandy Creek in West Thumb and Hatchery Creek in the Lake Area, grizzly bear hair was obtained but not amplified and replicated to an individual genotype. No hair samples were obtained from Lodge Creek in the Lake Area. The number of streams at which individual bears were

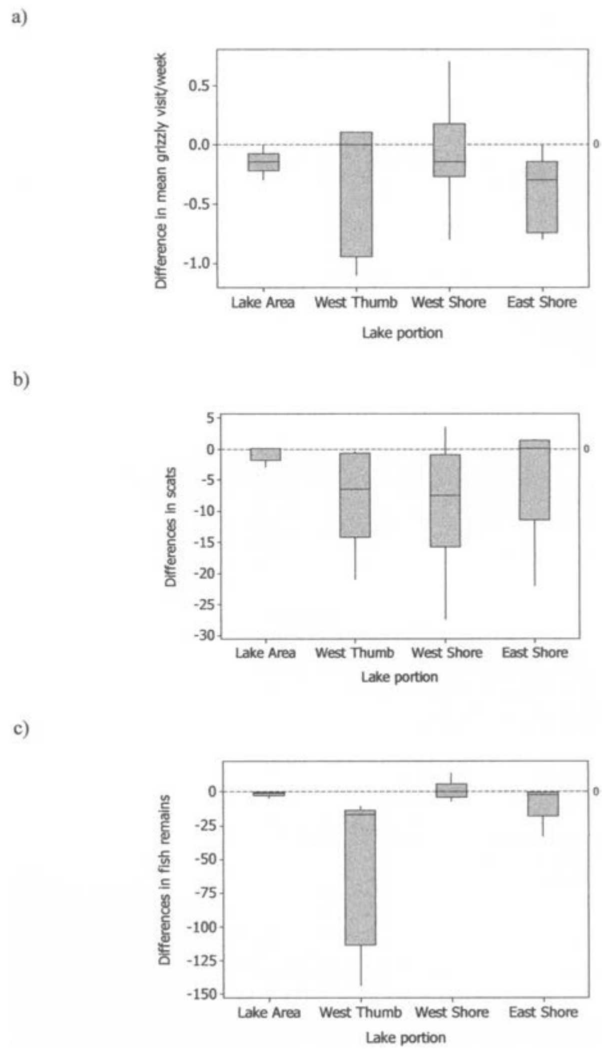

Fig. 4. Box plots of (a) difference in mean grizzly bear visits/week for each stream between study periods ($median_{1997–2000}$ – $median_{1985–87}$), (b) difference in median total scats counted annually, and (c) difference in median total fish remains counted annually for tributary streams from 4 areas of Yellowstone Lake, Yellowstone National Park. Top and bottom edges of the box represent the 25th and 75th percentiles. The horizontal line inside the box is the median, and the whiskers extend to the largest and smallest difference within 1.5 times the box length. Extreme values appear as symbols above or below whiskers.

detected ranged from 1 to 6; most bears ($n = 47$, 64%) were known from only 1 stream. For bears found during multiple years, 5 were seen on the same streams only, 4 were observed from different streams among years, and 14 were detected from the same and different streams.

Table 3. Summary of bear hair samples collected at cutthroat trout spawning streams on Yellowstone Lake, Yellowstone National Park, and analyzed for individual identification using $P(ID)^{a}_{sibs} < 0.05$, 1997–2000.

Year	Streams sampled	Hair snares	Hair samples collected	Samples with >10 hairs	Samples DNA extracted	Species identification: Grizzly bear	Species identification: Black bear	Grizzly bear samples genotyped (%)	Samples identified (%) to individual grizzly using $P(ID)_{sibs} <$ 0.05	Individual grizzly bears	Cumulative frequency of unique grizzly bears
1997	10	14	360	193	143	101	42	62 (61)	57 (56)	15	15
1998	11	15	332	173	158	113	45	84 (74)	83 (73)	28	40
1999	19	26	529	318	301	238	63	165 (69)	154 (65)	31	57
2000	19	28	472	297	273	198	75	150 (76)	135 (68)	33	74

[a]$P(ID)_{sibs}$ = probability of identity for siblings.

Sixty-one individual bears were encountered on the 10 streams that were sampled all 4 years during 1997–2000. Three of the 8 *a priori* models had $\Delta AIC_c \leq 2$ and thus had strong support (Burnham and Anderson 2002). The model containing constant apparent survival, time-dependent capture probability, and lambda fixed at 1 provided the best fit to the data; second best was a model where all parameters were constant and lambda was fixed at 1 (Table 4). The top 2 models produced estimates of 62 and 76 grizzly bears visiting the vicinity of spawning streams, respectively, but the confidence intervals of these estimates were wide (Table 5). Model averaging over all 8 models produced an estimate of 68 grizzly bears (95% CI = 30–106; Table 5) visiting the vicinity of the 10 sample streams annually.

Discussion

Reinhart and Mattson (1990) reported an increase in the number of streams fished by bears from 1974–75 to 1985–87 and attributed the increase primarily to changes in fishing regulations that resulted in more large fish in Yellowstone Lake. The period 1974–75 also was a time of transition from bears making substantial use of human foods to relying more on native foods following the closure of garbage dumps in the GYE (Reinhart and Mattson 1990). Our results, along with those of Reinhart et al. (1995), indicate the number of cutthroat trout spawning in Yellowstone Lake tributaries declined during 1989–2000 compared with 1985–87. This trend was most pronounced on the tributaries of West Thumb where both peak counts and duration declined. Indices of grizzly bear activity on West Thumb streams also declined. Only in West Shore streams were peak counts and durations greater or similar to those reported by Reinhart and Mattson (1990), as were indices of bear use. A notable decline in spawning trout was also observed at the Clear Creek fish trap, on the East Shore, where just under 60,000 spawners were counted in 1987, but only 12,000 were counted in 2000 (Yellowstone Center for Resources 2002).

The presence of lake trout is a likely reason for the decline in spawning cutthroat trout in West Thumb streams and a primary factor in the general population decline of the Yellowstone Lake cutthroat trout. Lake trout are highly predatory on cutthroat trout; older age classes of lake trout may eat 50–90 cutthroat trout/year (Yellowstone Center for Resources 2002). Lake trout have significantly reduced native trout populations in other lakes where they have been introduced (Gerstung 1988, Donald and Alger 1993). Younger age classes of lake trout also compete with cutthroat trout for macroinvertebrates (Elrod and O'Gorman 1991). Without

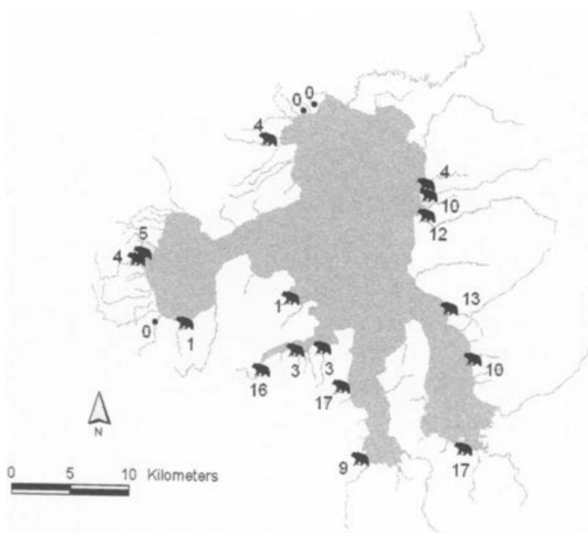

Fig. 5. Number of individual grizzly bears identified on cutthroat trout spawning streams surrounding Yellowstone Lake, Yellowstone National Park, 1997–2000.

Table 4. Jolly-Seber model results from Program MARK from encounter histories derived from streams sampled all 4 years during 1997–2000. Estimated parameters are apparent survival (*phi*), capture probability (*p*), lambda, and population size (*N*). Time dependent parameters in models are represented by (*t*), while (.) indicates that the model uses a single estimate for the parameter.

Model	AIC_c[a]	Delta AIC_c	AIC_c weights	Model likelihood	Parameters	Deviance
Phi(.)*p*(*t*)lambda(1.0)[b]	153.7204	0.0000	0.3282	1.0000	6	28.9170
Phi(.)*p*(.)lambda(1.0)	154.0261	0.3057	0.2817	0.8583	3	35.9469
Phi(.)*p*(.)lambda(.)	155.6017	1.8813	0.1281	0.3904	4	35.3332
Phi(.)*p*(*t*)lambda(.)	155.8098	2.0894	0.1155	0.3518	7	28.6570
Phi(*t*)*p*(*t*)lambda(1.0)	156.4827	2.7623	0.0825	0.2513	8	26.9232
Phi(*t*)*p*(.)lambda(.)	158.1465	4.4261	0.0359	0.1094	6	33.3431
Phi(*t*)*p*(*t*)lambda(.)	158.8086	5.0882	0.0258	0.0785	9	26.7830
Phi(.)*p*(*t*)lambda(*t*)	163.5879	9.8675	0.0024	0.0072	9	31.5623

[a]Akaike Information Criteria adjusted for small sample size.
[b]Initial population size (*N*) is estimated, but notation of the models without (*N*) is most appropriate.

control, lake trout may reduce the cutthroat trout population in Yellowstone Lake by as much as 90% (McIntyre 1996). During 1994–2000, over 43,500 lake trout were removed from Yellowstone Lake in gillnetting operations intended to lessen their impact on cutthroat trout, and 85% of all lake trout removed were caught in the West Thumb area (P. Bigelow, YNP, personal communication). Catch per unit effort also was much higher (3.00) in the West Thumb area than the main basin (0.82), suggesting the greatest density of lake

Table 5. Real parameter estimates for grizzly bear encounter histories derived from DNA analysis of hair samples obtained on cutthroat trout spawning streams all 4 years during 1997–2000. Results are from models with AIC_c[a] ≤ 2 and model averaging. Estimated parameters are apparent survival (*phi*), capture probability (*p*), lambda, and population size (*N*). Time dependent parameters in models are represented by (*t*), while (.) indicates that the model uses a single estimate for the parameter.

				95% confidence interval	
Model	Parameter	Estimate	Standard error	Lower	Upper
Phi(.)*p*(*t*) lambda(1.0)[b]	*Phi*	0.833	0.112	0.507	0.897
	p_1	0.241	0.071	0.129	0.488
	p_2	0.429	0.117	0.227	0.720
	p_3	0.439	0.120	0.232	0.708
	p_4	0.371	0.104	0.197	0.792
	Lambda	1.000	0.000	1.000	1.000
	N	61.939	14.607	40.866	129.732
Phi(.)*p*(.)lambda(1.0)	*Phi*	0.930	0.120	0.260	0.998
	p	0.300	0.074	0.177	0.461
	Lambda	1.000	0.000	1.000	1.000
	N	76.018	17.608	50.052	121.217
Phi(.)*p*(.)lambda(*t*)	*Phi*	0.965	0.122	0.024	1.000
	p	0.300	0.075	0.176	0.463
	Lambda	1.055	0.070	0.927	1.202
	N	70.168	17.136	45.434	115.005
Model averages	Phi_1	0.843	0.159	0.337	0.983
	Phi_2	0.897	0.141	0.303	0.994
	Phi_3	0.885	0.135	0.365	0.990
	p_1	0.265	0.084	0.133	0.457
	p_2	0.366	0.117	0.177	0.608
	p_3	0.376	0.120	0.181	0.621
	p_4	0.342	0.102	0.175	0.559
	$Lambda_1$	1.006	0.047	0.913	1.098
	$Lambda_2$	1.005	0.047	0.913	1.098
	$Lambda_3$	1.006	0.048	0.913	1.099
	N	68.016	19.179	30.426	105.606

[a]Akaike Information Criteria adjusted for small size.
[b]Initial population size (*N*) is estimated, but notation of the models without (*N*) is most appropriate.

trout is there (Yellowstone Center for Resources 2002). Although not proof of cause and effect, this evidence implicates lake trout as a factor in the decline of spawning cutthroat trout in West Thumb streams.

Wildfire and whirling disease are other potential factors contributing to cutthroat trout decline; however, evidence suggests their impacts are secondary to the presence of lake trout. During extensive wildfires in YNP in 1988, a large portion of the watersheds on the west side of Yellowstone Lake burned, whereas watersheds on the east side of the lake did not. Approximately 21% of the forest canopy on the West Shore watershed burned, but no decline in abundance of spawning trout was evident. In fact, peak numbers increased on West Shore streams after the fires of 1988. In contrast, West Thumb streams, where we observed a decline in spawning fish, lost only 3% of their forest canopy to fires. Evidence also indicates abundance of spawning fish may be declining due to shorter duration of runs in the East Shore watershed, where no fires occurred. The lack of correlation between the amount of canopy burned and spawner numbers suggests fire probably was not the primary cause of the decline in spawner numbers at West Thumb streams, but may have been a factor in the increase in numbers of spawning trout on West Shore streams (Gresswell 1999).

Whirling disease was first discovered in Yellowstone Lake in 1998, although it had likely been present in the lake before then (Yellowstone Center for Resources 2002). Whirling disease has been verified at many locations throughout the lake (Yellowstone Center for Resources 2002). The disease primarily affects young cutthroat trout by destroying head cartilage, resulting in loss of equilibrium, skeletal deformities, and inability to avoid predators or to feed normally. Although the current level of infection appears to be low, expansion of this parasite in the Yellowstone Lake basin could seriously affect the cutthroat trout population (Yellowstone Center for Resources 2002). It is unlikely that whirling disease has been present long enough to have been the primary cause for the observed decline in spawning cutthroat trout in West Thumb streams; however, it may have been a contributing factor.

Cutthroat trout rank as one of the highest quality grizzly bear foods in the GYE (Mealey 1980, Pritchard and Robbins 1990) and may influence the distribution of bears over a large area (Mattson and Reinhart 1995). It is important to know how many grizzly bears currently use spawning trout and how important fish are to the bears that feed on them. Using mercury in grizzly bear hair collected during this study, Felicetti et al. (2004) concluded that male bears consumed 5 times more trout than female bears and estimated annual intake per animal was far below the numbers suggested by Mattson and Reinhart (1995). Our findings indicate a decline in use of fish; however, numbers of grizzly bears using the vicinity of spawning streams remains similar to previous levels. Given that availability of spawning trout has declined, use of streams by males versus females may be very different between the study periods. Behaviorally, we expect males to dominate use of a more limited resource, and this prediction is consistent with the sex ratio we observed from hair samples.

From DNA analysis of grizzly bear hair we detected 74 individual grizzly bears that frequented (and likely fished) spawning streams tributary to Yellowstone Lake. A minimum of approximately 30 bears visited spawning streams annually during 1999 and 2000. These years represent our most consistent effort during which just over 70% of streams that bears fished were sampled.

Initially we investigated the robust design (Pollock 1982) for estimating abundance. However, it became apparent from high estimates of emigration (animals unavailable for capture) and low estimates of survival relative to results obtained from telemetry (Eberhardt 1995) and the J-S models, that we were likely violating the assumption of geographic closure during secondary sampling sessions. This seemed likely for a number of reasons, including (1) differences in timing of trout availability among lake portions within secondary sampling periods, and (2) sampling along linear features, which, because of their proximity to the lake, essentially were home-range boundaries. Kendall (1999) indicated that an open-population approach is more appropriate if an animal enters and leaves the study area once during sampling.

The Jolly-Seber estimator is known to produce biased abundance estimates if capture heterogeneity is high, movement into the study area does not correspond to 1 entry and 1 exit, and no temporary movement occurs (Kendall 1999). Boulanger et al. (2002) suggested that permanent movement is more likely with longer-term studies in which yearly sampling is used. Such was the case in our 4-year study. Given potential negative biases, our estimate of 68 bears visiting spawning streams annually seems reasonable. Although our estimate was derived from encounter histories obtained from 10 streams sampled during all 4 years, all portions of the lake were represented in this sample and 82% of the bears genotyped were identified from these streams. In addition, nearly 40% of bears identified were detected on multiple streams, usually within the same portion of the lake. Estimates of apparent survival (Table 5) were consistent with rates obtained from telemetry (Eberhardt 1995), and capture probabilities were within the range estimated for other hair capture–DNA studies (Boulanger et al. 2002). Considered together, these findings support our contention that the estimate of 68 bears visiting spawning streams around Yellowstone Lake is reasonable.

Several other factors likely affected our ability to detect individuals and influenced our estimates. Cubs-of-the-year likely passed under the barbed wire without leaving a sample. In addition, because we used only 6 microsatellite loci in our DNA analysis, we may have influenced capture histories by excluding 32 samples for which $P(ID)_{sibs}$ was not met. These sampling biases likely resulted in under-detection of individual bears, especially cubs-of-the-year and closely-related individuals. Because females are typically more philopatric than males, females may have been particularly under-detected in the sample due to proximity of mother–daughter and female sibling pairs. On the other hand, females may have had higher capture probabilities than males. Adult female grizzly bears have smaller home-ranges and greater home-range fidelity than adult males (Blanchard and Knight 1991) and therefore, fewer alternative areas for foraging. Subadult females establish home ranges near their mother's range (Blanchard and Knight 1991). Thus, adult and subadult females should have a high probability of detection at specific areas within their home ranges that contained high-quality food resources such as cutthroat trout. In contrast, adult male grizzly bears in the GYE have very large home ranges and exhibit less home range fidelity than females (Blanchard and Knight 1991). Adult males may forage in more locations, making detection in a specific area of their home-range less probable. Weaned male offspring generally make substantial movements away from the maternal range (Blanchard and Knight 1991) and would be less likely to be recaptured and detected during multiple years of our study. These sampling biases likely contributed to the lack of precision of our abundance estimates.

Also of interest is an estimate of the portion of grizzly bears in the GYE that seasonally forage on spawning trout. Minimum grizzly bear population estimates averaged 326 bears for the GYE during 1997–2000 (Haroldson and Frey 2001). Keating et al. (2002) estimated the number of female grizzly bears with cubs-of-the-year in the GYE as 41 in 1997, 41 in 1998, 36 in 1999, and 60 in 2000; using the average (45) from that study and the estimated proportion of adult females (0.274) in the populations (Eberhardt and Knight 1996), approximately 500 bears were present in the GYE annually during 1997–2000. Using these estimates, approximately 14–21% of grizzly bears in the GYE visited the vicinity of spawning streams annually. These calculations do not reflect uncertainty which clearly accompanied each estimate.

A gradual change in the availability of a resource, such as cutthroat trout, may allow bears to change and use alternative foods. This accommodation may be occurring with the use of spawning trout; indices of use have decreased and estimates of trout consumption by bears are low (Felicetti et al. 2004). However, other key grizzly bear foods in the GYE also face threats and likely will decline (Reinhart et al. 2001). Probably the most important of these is whitebark pine, which is susceptible to white pine blister rust (*Cronartium ribicola*). Although current infections rates in the GYE are low and have been for some time, the disease may eventually kill much of the whitebark pine in the ecosystem (Koteen 1999, Smith and Hoffman 2000). The cumulative effects of potential reduction or loss of cutthroat trout and whitebark pine seed on the demographics of grizzly bears in the GYE is unknown. Public land managers need to consider the potential reduction of these foods when planning for long-term conservation of grizzly bears in the GYE.

Whether lake trout, whirling disease, or some other factor is the primary cause, cutthroat trout, an important, high-quality food, are declining, as is their use by grizzly bears. We recommend further monitoring of spawning cutthroat trout and associated grizzly bear use to determine the impacts a declining cutthroat trout population will have on grizzly bear population dynamics in the GYE.

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