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Use of naturally occurring mercury to determine the importance of cutthroat trout to Yellowstone grizzly bears

Laura A. Felicetti, Charles C. Schwartz, Robert O. Rye, Kerry A. Gunther, James G. Crock, Mark A. Haroldson, Lisette Waits, and Charles T. Robbins

Abstract: Spawning cutthroat trout (*Oncorhynchus clarki* (Richardson, 1836)) are a potentially important food resource for grizzly bears (*Ursus arctos horribilis* Ord, 1815) in the Greater Yellowstone Ecosystem. We developed a method to estimate the amount of cutthroat trout ingested by grizzly bears living in the Yellowstone Lake area. The method utilized (*i*) the relatively high, naturally occurring concentration of mercury in Yellowstone Lake cutthroat trout (508 ± 93 ppb) and its virtual absence in all other bear foods (≤6 ppb), (*ii*) hair snares to remotely collect hair from bears visiting spawning cutthroat trout streams between 1997 and 2000, (*iii*) DNA analyses to identify the individual and sex of grizzly bears leaving a hair sample, (*iv*) feeding trials with captive bears to develop relationships between fish and mercury intake and hair mercury concentrations, and (*v*) mercury analyses of hair collected from wild bears to estimate the amount of trout consumed by each bear. Male grizzly bears consumed an average of 5 times more trout/kg bear than did female grizzly bears. Estimated cutthroat trout intake per year by the grizzly bear population was only a small fraction of that estimated by previous investigators, and males consumed 92% of all trout ingested by grizzly bears.

Résumé : Les truites fardées (*Oncorhynchus clarki* (Richardson, 1836)) en fraye constituent une ressource alimentaire potentiellement importante pour les grizzlis (*Ursus arctos horribilis* Ord, 1815) dans l'écosystème du Grand Yellowstone. Nous avons mis au point une méthode pour estimer la quantité de truites fardées ingérées par les grizzlis vivant dans la région du lac Yellowstone. La méthode utilise (*i*) la concentration naturelle et relativement élevée de mercure chez les truites fardées du lac Yellowstone (508 ± 93 ppb) et son absence virtuelle (≤6 ppb) dans les autres aliments des ours, (*ii*) des dispositifs pour récolter à distance des touffes de poils des ours qui visitent les cours d'eau de fraye de la truite fardée (utilisés de 1997 à 2000), (*iii*) des analyses d'ADN pour déterminer l'identité et le sexe des grizzlis qui ont laissé ces touffes de poils, (*iv*) des essais alimentaires chez des ours en captivité afin d'établir la relation qui existe entre l'ingestion de poissons et de mercure, d'une part, et la concentration de mercure dans le poil, d'autre part, et (*v*) le dosage du mercure dans le poil d'ours sauvages afin d'estimer la quantité de chair de truite consommée par chaque ours. Les grizzlis mâles consomment en moyenne 5 fois plus de chair de truite par kg d'ours que les femelles. L'ingestion annuelle estimée de chair de truite par la population d'ours n'est qu'une petite fraction de celle obtenue par des chercheurs antérieurs; de plus, les mâles consomment 92 % de toute la chair de truite ingérée par les grizzlis.

[Traduit par la Rédaction]

Introduction

Spawning cutthroat trout (*Oncorhynchus clarki* (Richardson, 1836)) are a highly digestible, energy- and protein-rich food resource that is readily accessible to grizzly bears (*Ursus arctos horribilis* Ord, 1815) in the Greater Yellowstone Ecosystem (GYE) (Pritchard and Robbins 1990; Mattson and Reinhart 1995). Until recently, Yellowstone Lake was the last pristine habitat for native Yellowstone cutthroat trout (Kaeding et al. 1996). However, non-native lake trout (*Salvelinus namaycush* (Walbaum in Artedi, 1792)) were discovered in 1994 and found in substantial numbers in the lake in 1995. Because lake trout are efficient predators of cutthroat trout, lake trout have the potential to reduce the

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cutthroat trout population by 80%–90% (McIntyre 1995). A decline of this magnitude may negatively impact 28 wildlife species that feed on cutthroat trout, including the threatened grizzly bear. 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 the deeper water of the lake (Schullery and Varley 1996).

Previous studies of grizzly bear use of spawning cutthroat trout in the tributaries of Yellowstone Lake found or suggested that (*i*) 59 of the 124 tributaries to the Lake contained spawning cutthroat trout and 36 of those streams showed evidence of fishing by bears, (*ii*) a minimum of 44 individual bears fished those streams in 1987, (*iii*) female grizzly bears used the vicinity of streams more consistently and made greater use of the spawning cutthroat trout than did males, and (*iv*) 90% of the bears' diet during the spawning season was cutthroat trout (Reinhart and Mattson 1990; Mattson and Reinhart 1995). A more recent study conducted from 1997 to 2000 that used hair snares and DNA analyses identified 74 individual grizzly bears (64% male : 36% female) and estimated that 60 bears per year (12%–18% 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). Because of the large number of grizzly bears using the Yellowstone Lake area, determining the nutritional importance of cutthroat trout to both individual grizzly bears and the population is critical for evaluating the ecological impact of the loss of this food resource.

Mattson and Reinhart (1995), in the most extensive study of grizzly bear use of spawning cutthroat trout, made several critical assumptions that, if incorrect, could lead to an overestimate of the nutritional importance of cutthroat trout. Those assumptions included the following: (*i*) bears that had one or more radiotelemetry relocations within 500 m of a known spawning stream during the spawning season ate cutthroat trout and (*ii*) food habits estimated from feces collected adjacent to spawning streams represented the diet of all bears that had one or more relocations within 500 m of a spawning stream.

To avoid making these assumptions while determining the nutritional importance of cutthroat trout, we sought a predictor of trout consumption that could be measured in grizzly bear hair. Mercury, a biological contaminant that accumulates in many aquatic ecosystems, is readily absorbed and deposited in hair in proportion to its intake (Huckabee et al. 1973; Ben-David et al. 2001; Fournier et al. 2002). Recently, Yellowstone Lake cutthroat trout were found to contain relatively high levels of naturally occurring mercury (W.C. Shanks, letter to Yellowstone National Park Superintendent Finley dated 9 September 1999). Thus, we hypothesized that the mercury content of the hair of Yellowstone grizzly bears could be a direct measure of cutthroat trout intake if cutthroat trout were the only significant dietary source of that element.

Methods

Study area

The Greater Yellowstone Ecosystem (GYE) includes Yellowstone National Park (YNP) and Grand Teton National Park and adjacent federal, state, and private lands in portions of Montana, Wyoming, and Idaho. The GYE contains the headwaters of three major continental-scale river systems: the Missouri and Mississippi, Snake and Columbia, and Green and Colorado rivers. Long, cold winters and short summers characterize the climate of the GYE (Marston and Anderson 1991). Grizzly bears use habitats that range from 1500 to 3600 m (Schwartz et al. 2003). At low elevations, foothill grasslands or shrub steppes occur. With increasing moisture, open stands of Rocky Mountain juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), and Douglas-fir (*Pseudotsuga menziesii*) occur. Lodgepole pine (*Pinus contorta*) dominates at mid-elevations where poor soils formed from rhyolite predominate. With increasing elevation, spruce–fir or subalpine forests dominate. Engelmann spruce (*Picea engelmannii*) and whitebark pine (*Pinus albicaulis*) form the upper treeline. Alpine tundra occurs at the highest reaches of all major mountain ranges (Patten 1963; Waddington and Wright 1974; Despain 1990).

Yellowstone Lake is a high-elevation (2358 m), oligotrophic lake that covers 35 391 ha, has a mean depth of 42 m, and has a basin capacity of 14×10^9 m^3 (Benson 1961). The lake is usually frozen from December until May or June (Reinhart and Mattson 1990). The Yellowstone Lake watershed area is estimated to be 261 590 ha. The west and north drainages of the Yellowstone Lake basin contain small streams draining from low-relief plateaus with lodgepole pine forests and alluvial meadows, whereas the east and southeast drainages are characterized by higher relief mountain topography, closed-canopy mixed forests, and subalpine slopes (Reinhart and Mattson 1990).

Field collection of bear foods

Major plant and animal foods consumed by grizzly bears (Mattson et al. 1991) were collected throughout the GYE to determine their mercury content and thereby determine whether cutthroat trout had a unique mercury signature relative to all other foods. Plant samples included whitebark pine nuts; the foliage of clover (*Trifolium* spp.), fireweed (*Epilobium angustifolium* subsp. *angustifolium*), sticky geranium (*Geranium viscosissimum*), horsetails (*Equisetum arvense*), meadow thistle (*Cirsium scariosum*), strawberry (*Fragaria* spp.), cow parsnip (*Heracleum maximum*), dandelion (*Taraxacum* spp.), lanceleaf springbeauty (*Claytonia lanceolata*), bluebells (*Mertensia ciliata*), sedges (*Carex raynoldsii* and *C. praticola*), and grasses (*Bromus anomalous*, *Phleum alpinum*, *Agropyron caninum*, *Poa* spp., *Danthonia* spp., and *Festuca idahoensis*); the bulbs or roots of oniongrass (*Melica spectabilis*), biscuitroot (*Lomatium triternatum*), false truffles (*Rhizopogon* spp.), and yampa (*Perideridia gairdneri*); and fleshy fruits or berries from huckleberry (*Vaccinium globulare*), currant (*Ribes* spp.), strawberry (*Fragaria* spp.), serviceberry (*Amelanchier alnifolia*), roses (*Rosa woodsii*), and russet buffaloberry (*Shepherdia canadensis*) (Mealey 1975; Kendall 1983; Mattson et al. 1991). Collected animal matter included cutthroat trout from 11 spawning tributaries of Yellowstone Lake and one tributary of Trout Lake in the northeast corner of YNP, lake trout, bison (*Bison bison bison* (Linnaeus,

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1758)), elk (*Cervus elaphus* Linnaeus, 1758), moose (*Alces alces* (Linnaeus, 1758)), and mule deer (*Odocoileus hemionus* (Rafinesque, 1817)). All foods were stored frozen at −20 °C.

Field collection and analysis of bear tissues

Grizzly bear hair samples were collected from May to mid-August of 1997 through 2000 using hair snares set 51 cm above the ground along cutthroat trout spawning streams surrounding Yellowstone Lake (Haroldson et al. 2005). The number of streams sampled per year ranged from 10 to 19 and included both front country (West Thumb and Lake) and backcountry (East and West Shore) streams. Amplification of mtDNA was used to identify hair samples to species (Murphy et al. 2000), microsatellite loci were used for individual identification (Woods et al. 1999), and polymerase chain reaction (PCR) co-amplification of X and Y chromosomes was used for sex determination (Ennis and Gallagher 1994). Female bears were identified by the presence of the X chromosome PCR product and the absence of the Y chromosome PCR product. Male bears were identified by the presence of both X and Y chromosome PCR products. To minimize the possibility of an error in sex identification, all samples were genotyped a minimum of two times. If results were faint or ambiguous, a third PCR was attempted. In over 200 analyses of samples of known sex, no errors in sex identification have occurred using this protocol. Field and laboratory methods are described in more detail in Haroldson et al. (2005).

All plant and animal tissue samples were freeze-dried and ground prior to mercury analysis. Hair samples collected from the same bear in the same year were pooled and analyzed as a single sample. Hair samples collected from the same bear in different years were analyzed separately to determine interannual variation in mercury content. Samples were analyzed at the US Geological Survey laboratories in Denver, Colorado. Samples were digested in a nitric acid – sodium dichromate solution, diluted with 12 mL of water, preserved with a 1% nitric acid – sodium dichromate solution, and analyzed for total mercury using continuous-flow cold-vapor atomic absorption spectrometry using a PerkinElmer 3030B spectrophotometer (Kennedy and Crock 1987).

Feeding trials using captive grizzly bears

Six 3-year-old captive grizzly bears (three male and three female siblings) were used in a year-long feeding trial to determine the relationship between consumption rates of mercury-contaminated trout and bioaccumulation of mercury in hair, plasma, and whole blood. Bears were housed at the Washington State University Bear Research, Education, and Conservation Facility in Pullman, Washington. Two bears were born in captivity, two were wild-caught from the GYE, and two were wild-caught from the Northern Continental Divide Ecosystem. Bear mass ranged from 69 kg in the spring to 136 kg in the fall.

In the summer of 2001, 2800 kg of lake trout and 360 kg of cutthroat trout were collected from Yellowstone Lake. These fish were gillnetted as part of the park's annual effort to control the lake trout population. Freshly netted fish were stored frozen in waxed cardboard boxes and shipped to Washington State University, where they were stored (−20 °C) until fed to grizzly bears. In the feeding trials, we wanted to simulate the normal time course of cutthroat trout consumption by GYE grizzly bears. Although spawning trout are available from as early as 4 May to as late as 17 August, the average duration of trout availability in 22 streams is 33 ± 14 days, with peak spawning numbers occurring from 4 June to 21 June (Haroldson et al. 1999, 2000, 2001).

Thus, we began the feeding trials on 30 May 2002 and fed fish to bears for 33 days. One male and one female bear were not fed fish and served as controls. The remaining bears were fed either ad libitum (one male and one female) or 50% ad libitum (one male and one female). The two ad libitum bears were housed in concrete-floored pens and fed only trout during the 33-day experimental period. The two bears receiving 50% ad libitum fish began eating 1 day later than the ad libitum bears, as their daily fish allotment was determined from the preceding day's ad libitum intake. Bears receiving fish were fed 89% lake trout and 11% cutthroat trout, as not enough cutthroat trout were available for the entire trial. Prior to and after the 33 days of fish-feeding (ad libitum bears) or throughout the study (for the two control bears and the 50% ad libitum bears), all bears were fed limited amounts of low-mercury commercial bear chow (21% crude protein, Command Chunk, Land O' Lakes Feeds, Seattle, Washington), apples, and grazed low-mercury white clover (*Trifolium repens*) 12 h/day (Table 1).

Blood and hair samples were collected at the start of the feeding trial, at the end of the 33 days of fish-feeding, and once a month thereafter until the bears hibernated in early November. All hair measurements were taken and samples collected from captive bears along the middle of the back where hair would be most likely sampled when wild bears

Table 1. Mercury concentration in parts per billion (mean ± SD, 100% dry matter basis) of foods fed to captive grizzly bears (*Ursus arctos horribilis*) and consumed by grizzly bears in the Greater Yellowstone Ecosystem.

Sample	Mercury content
Yellowstone animal matter	
Cutthroat trout (*Oncorhynchus clarki*)	
Gillnetted in Yellowstone Lake	530±90 (6)
Caught in Yellowstone Lake spawning streams	508±93 (16)
Caught in Trout Lake spawning stream	485 (2)
Lake trout (*Salvelinus namaycush*)	
Gillnetted in Yellowstone Lake	430±60 (6)
Ungulates (bison, elk, moose, and mule deer)	all ≤6 (10)
Yellowstone plant matter	
Foliage, roots and bulbs, fruits and berries in GYE	all ≤6 (47)
Washington State University bear foods	
White clover (*Trifolium repens*)	6 (1)
Apples (*Malus* spp.)	≤6 (2)
Commercial bear chow	≤6 (2)

Note: Numbers in parentheses are sample sizes.

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moved under hair snares. Prior to the start of the feeding trial, two 10 cm × 10 cm patches along the back of each bear were shaved to simplify measurements and sampling of newly growing hair. The length of newly growing hair was measured during each sampling. The study complied with the principles and guidelines of the Canadian Council on Animal Care and was approved by the Washington State University Institutional Animal Care and Use Committee (protocol ASAF 3181).

Statistical analyses

Linear least squares regression (PROC REG; SAS Institute Inc. 1998) was used to model the mercury relationships. We used an ANOVA and least squares means to test for differences between the mercury content of foods consumed by Yellowstone grizzly bears and between the mercury content of male and female grizzly bears (PROC GLM and LS Means, SAS Institute Inc. 1998).

Results

Mercury in Yellowstone grizzly bear foods

The only significant source of mercury in foods consumed by grizzly bears in the GYE was cutthroat trout (Table 1), which contained a minimum of 88 times more mercury than either plants or ungulates (F = 118.55, P < 0.0001). Gillnetted cutthroat trout had slightly higher mercury concentrations (530 ± 90 ppb) than did cutthroat trout caught in spawning streams (508 ± 93 ppb) and gillnetted lake trout (430 ± 60 ppb), although these differences were not significantly different (F = 1.45, P = 0.2972). Dry matter content of spawning cutthroat trout was 27.8% ± 2.0%. Spawning cutthroat trout caught in the single spawning stream for Trout Lake also had elevated mercury levels (Table 1).

Mercury content of Yellowstone grizzly bear hair

Of the 74 bears identified from hair snares set on cutthroat trout spawning streams flowing into Yellowstone Lake (Haroldson et al. 2005), 42 (19 males, 14 females, and 9 unknowns) left enough hair for mercury analyses (Fig. 1). Most of the bears sampled (17 of 19 males, 11 of 14 females, and 8 of 9 unknowns) used backcountry streams exclusively. The hair mercury content ranged from 17 to 2600 ppb. Males had higher mean mercury concentrations in their hair (526 ± 639 ppb) than did females (134 ± 282 ppb) (F = 4.93, P = 0.0336). Five bears (three males, one female, and one unknown) were sampled in two successive years. All five maintained qualitatively similar hair mercury concentrations between years. Of the bears of known sex with ≥200 ppb mercury in their hair, 92% were males. Of bears of known sex with <100 ppb mercury in their hair, 75% were female.

Captive bear feeding trials

Blood mercury levels peaked at the end of trout-feeding before declining toward background levels prior to hibernation (Fig. 2). Bear hair began growing in early May and continued growing into October at a rate of approximately 1.5 cm/month. The mercury content of the hair grown by each bear during a particular month tracked that bear's average monthly plasma mercury content, with a considerable enrichment in hair (Fig. 3). Mercury content of the fully grown hair collected in October increased curvilinearly with increasing fish and mercury intake (Fig. 4). However, the curvilinearity was minimal and there was virtually no variation due to sex or any other variable except total fish and mercury intake.

Estimates of cutthroat trout intake by Yellowstone grizzly bears

We estimated intake of cutthroat trout for each wild grizzly bear by solving the equation in Figure 4B for the observed hair mercury concentrations (Fig. 1). Annual intake ranged from 2.4 to 1090 g cutthroat trout/kg bear. Mean annual fish intake by male grizzly bears was over 5 times greater (135 g/kg bear) than the mean annual fish intake by females (26 g/kg bear).

Discussion

All grizzly bears identified by hair samples as having been at spawning cutthroat trout streams consumed trout, as indicated by elevated mercury signatures. However, our data indicated that male grizzly bears were the primary consumers of cutthroat trout, in contrast to the conclusion of Reinhart and Mattson (1990) and Mattson and Reinhart (1995) that females fed more heavily on trout. While there may be many potential explanations for the contradictory findings, the most likely ones include (*i*) the differing methods and assumptions in the two types of studies and (*ii*) a significant decline in cutthroat trout between 1975–1989 (Reinhart and Mattson 1990; Mattson and Reinhart 1995) and 1997–2000 (current study), with a resultant change in bear behavior. As for the differing methods and assumptions, Reinhart and Mattson (1990) estimated sex and age composition of bears near streams based on track analyses, and Mattson and Reinhart (1995) used telemetry locations to determine proximity of collared bears to trout streams. Both authors inferred equality between time spent by bears in proximity to spawning streams and trout ingestion, although they lacked any support for that claim. Our results indicate that proximity as determined by their 500 m threshold is not proportional to level of consumption.

A major assumption of our mercury accumulation method was that the mercury concentration in hair collected from wild bears from May to mid-August had the same relationship to cutthroat trout intake as that generated using hair collected from captive bears in October (i.e., Fig. 4). Grizzly bear hair collected adjacent to spawning streams in May through July was very likely fully grown hair from the preceding year, i.e., October hair. Bears have one molt/year in which new hair starts growing in late spring and summer as abundant, high-protein foods are consumed, and old hair is not lost until new hair is well along in its growth cycle. Thus, it is unlikely that the hair caught in the Yellowstone hair snares grew prior to the bears' feeding on spawning cutthroat trout and therefore carried an unrepresentative or abnormally low mercury signature. Because newly growing hair takes up the trout mercury signature very quickly (Figs. 2 and 3), any new hair snagged late in the spawning season (i.e., August) after the old hair had been shed would carry a mercury signature slightly higher than that of fully

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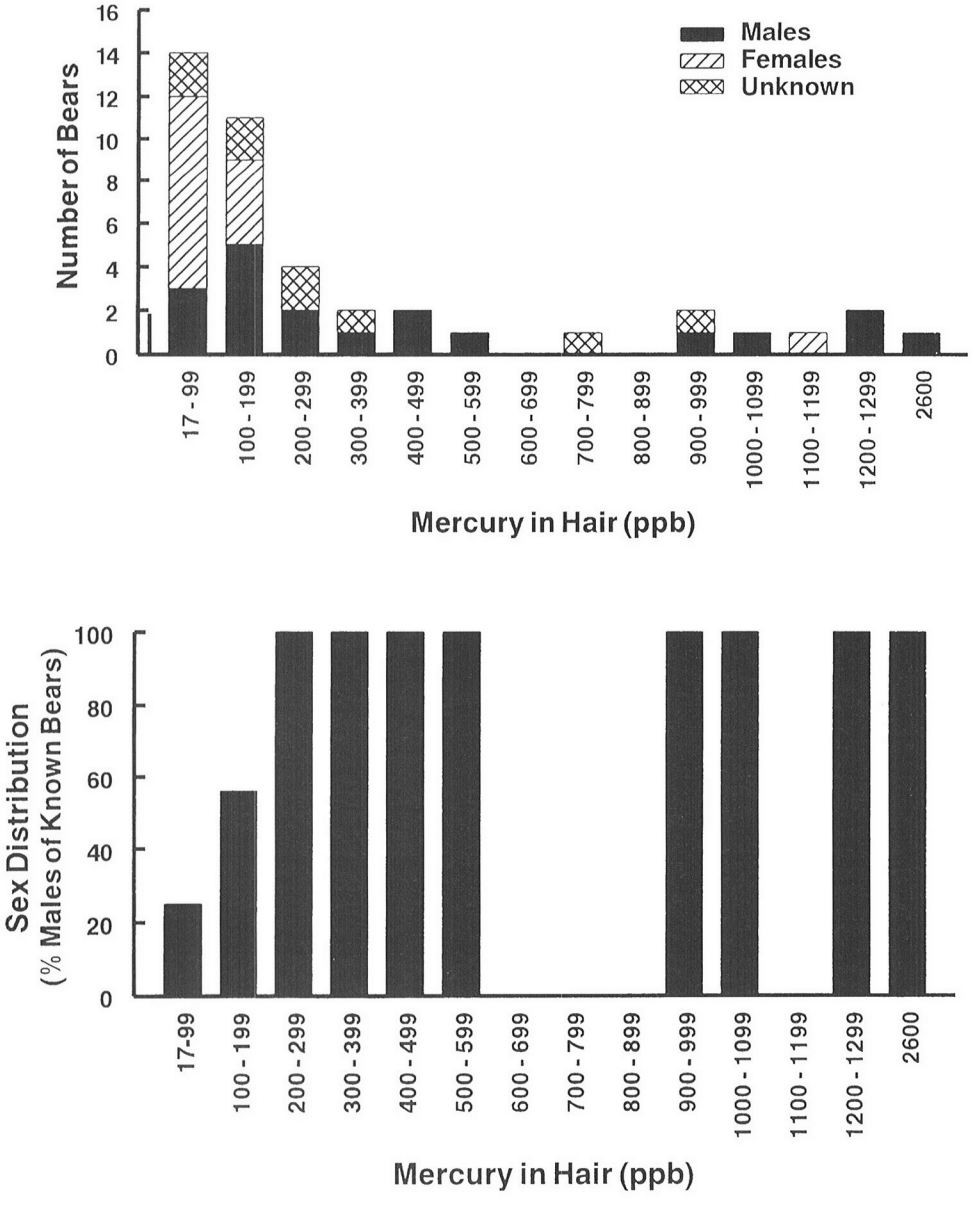
Fig. 1. The amount of mercury (100% dry matter basis) in hair collected from 42 grizzly bears (*Ursus arctos horribilis*) that encountered hair snares adjacent to cutthroat trout (*Oncorhynchus clarki*) spawning streams flowing into Yellowstone Lake between 1997 and 2000. The dark bar at the far left of the top graph is the background level of 6 ppb.



grown October hair. This occurs because the hair produced after trout-feeding has a decreasing mercury content that ultimately dilutes the higher hair mercury levels produced during trout-feeding. However, this error is relatively small (~8% for the captive bears when comparing hair collected in early August and early October) and should not differ between males and females.

Another major assumption in the current study was that bears visiting hair snares and leaving samples adequate for mercury analyses were representative of all bears that were fishing. The possibility exists that bears proficient at fishing avoided hair snares and, therefore, did not leave enough hair for mercury analyses. Although we recognize the possibility of this error, the chances of a significant error seem small, as barbed wire hair snares were stretched diagonally across bear trails or known fishing spots to purposefully sample as many bears as possible (Haroldson et al. 2005).

As for the possibility that a potential decline in numbers of cutthroat trout could explain the contradictory results, the peak numbers and duration of spawning declined significantly between 1985–1987 and 1997–2000 in the streams of the West Thumb area (Haroldson et al. 2005). This was likely due to the high concentration of lake trout in that area. However, peak numbers and duration of spawning in East and West Shore backcountry streams remained constant or even increased during the same time frame (Haroldson et al. 2005). Because peak numbers and duration of spawning of cutthroat trout in a particular stream are indices only, we cannot exclude the possibility of a lake-wide decline in cutthroat trout numbers affecting bear behavior. For example,

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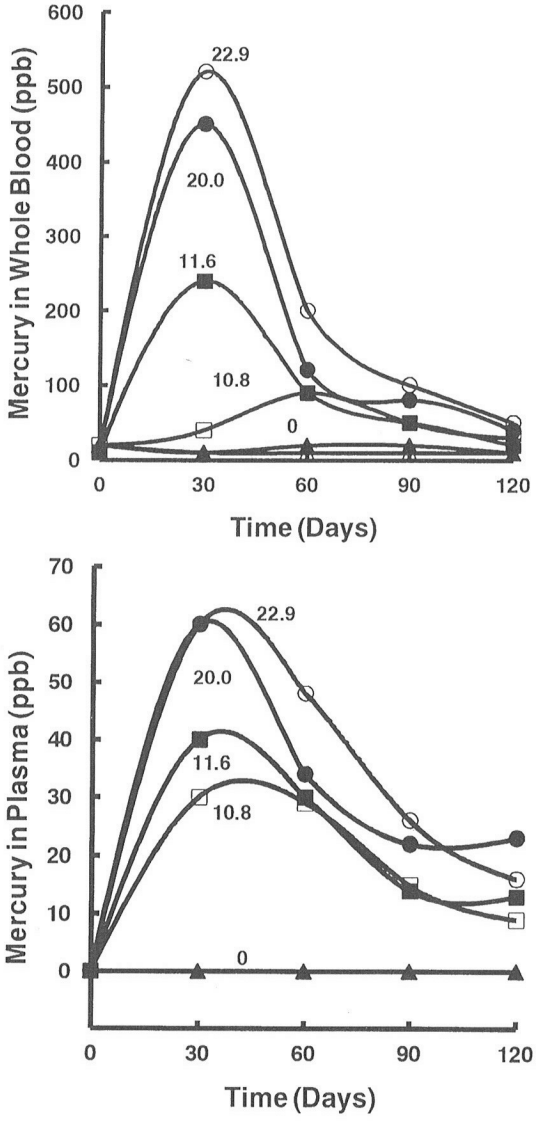
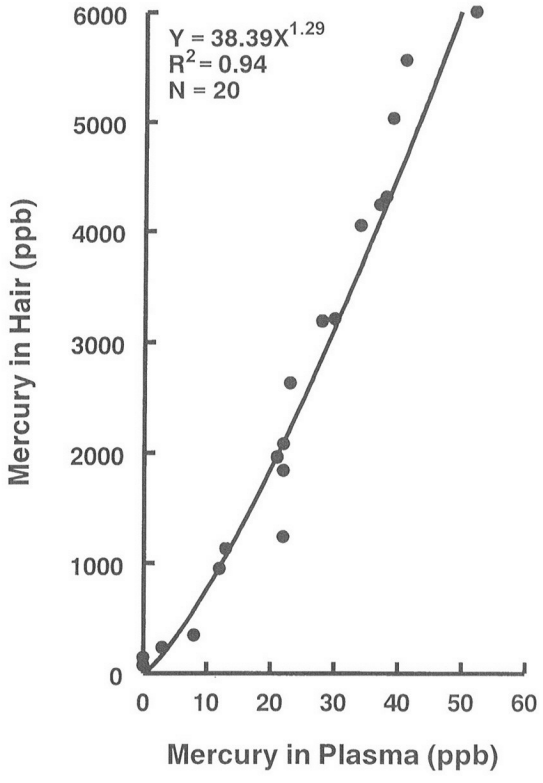
Fig. 2. The relationships between Yellowstone Lake trout consumption and captive grizzly bear plasma and whole blood mercury concentrations. Trout were fed in the ratio of 89% lake trout (*Salvelinus namaycush*) and 11% cutthroat trout and had a dietary mercury concentration of 441 ppb. Trout were fed at ad libitum (two bears) and 50% ad libitum (two bears) levels. Trout-feeding occurred between 30 May and 1 July 2002, before and after which low-mercury foods were fed. Two bears (controls) received no trout and were fed low-mercury foods throughout the study. The numbers accompanying each line are the amounts of mercury (mg) in trout consumed per bear during the entire 33-day feeding trial.



total cutthroat trout numbers counted at a weir on Clear Creek, a backcountry East Shore stream, were over 58 000 in 1987 but had declined to a maximum of 14 000 per year between 1997 and 2000 (Yellowstone Center for Resources 2002). Thus, we cannot dismiss the possibility that the differences between the conclusions of the current study and those of Reinhart and Mattson (1990) and Mattson and Reinhart (1995) are real and can be attributed to a declining cutthroat trout population.

Fig. 3. The average monthly mercury content of grizzly bear plasma and the mercury content of the hair grown during that month in six captive grizzly bears fed varying levels of lake and cutthroat trout.



While others have compared the cutthroat trout spawning streams of Yellowstone Lake with the salmon spawning streams of Alaska (Craighead et al. 1995; Mattson and Reinhart 1995), the two can be quite different both temporally and spatially. Cutthroat trout spawning occurs primarily in spring and early summer, whereas salmon spawning occurs primarily in summer and fall. Bears have very different food drives during those seasons (Hilderbrand et al. 1999*a*). Also, cutthroat trout spawning streams are typically smaller than salmon spawning streams and thus contain a potentially valuable food resource that is spatially defendable. Adult male grizzly bears would be expected to dominate such a food resource (Stonorov and Stokes 1972; Jacoby et al. 1999), especially if availability is less than male requirements.

Our results may help clarify anomalies in Mattson and Reinhart's (1995) observations that females living in the vicinity of cutthroat trout spawning streams first reproduced at a later age and had smaller litters than females elsewhere in the Greater Yellowstone Ecosystem. They had difficulty rationalizing these observations relative to their conclusion that female grizzly bears consuming trout should have been in better condition and, therefore, more productive than those not eating fish. Our data suggest that trout are not consumed in large quantities by most female grizzly bears and, thus, females living in the Yellowstone Lake area have a poorer quality diet than suggested by Mattson and Reinhart (1995).

Using data from Reinhart and Mattson (1990), Mattson and Reinhart (1995), and Mattson (1997), Stapp and

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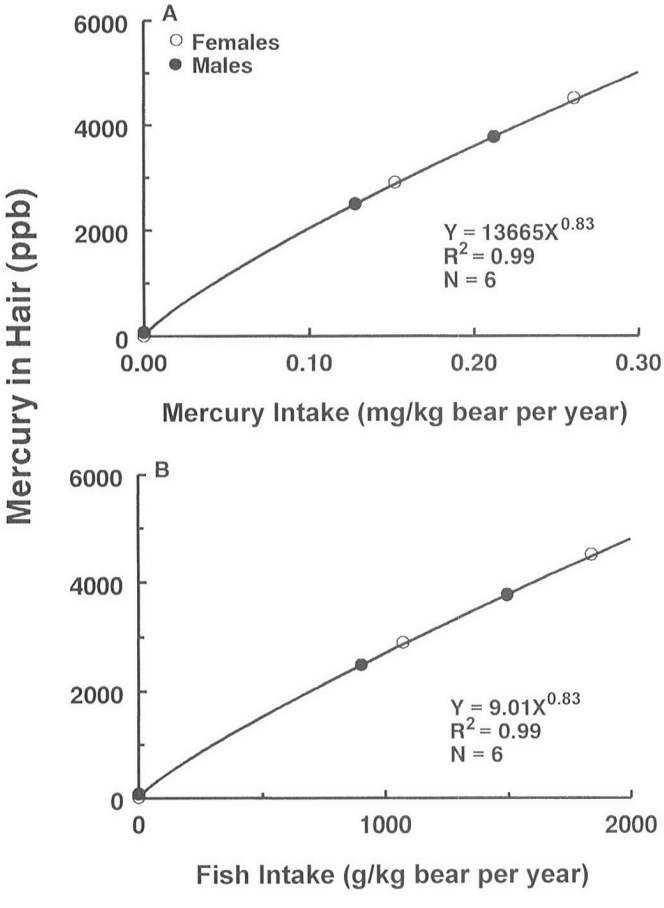
Fig. 4. The relationships between mercury consumption, hair mercury concentration, and Yellowstone Lake cutthroat trout intake by six captive grizzly bears. The hair was collected in early October and, therefore, is fully grown hair. Trout were fed in the ratio of 89% lake trout and 11% cutthroat trout and had a dietary mercury concentration of 441 ppb. Trout were fed at ad libitum (two bears) and 50% ad libitum (two bears) levels. Trout-feeding occurred between 30 May and 1 July 2002, before and after which low-mercury foods were fed. Two bears (controls) received no trout and were fed low-mercury foods throughout the study. The cutthroat trout intake values associated with a given hair mercury concentration are adjusted for the difference in the mercury concentration between the mixed lake trout – cutthroat trout diet fed during the study (441 ppb) and that of spawning Yellowstone Lake cutthroat trout (508 ppb dry mass or 141 ppb fresh mass) (Table 1). All other foods consumed by both wild and captive bears contained ≤6 ppb mercury. Fish and mercury intakes are based on the mean body masses of the captive bears during the 33 days of trout feeding.



Hayward (2002) estimated that Yellowstone grizzly bears annually consume 20 910 spawning cutthroat trout, or approximately 1.6% of the spawning population. The mercury-based estimates of annual trout intake from this study for an average adult male (195 kg) and female (135 kg) in the GYE (Blanchard 1987) are 26 and 4 kg of fish/bear, respectively. Based on an average cutthroat trout mass of 468 g (Stapp and Hayward 2002), adult male and female grizzly bears in our sample consumed an average of 55 and 8 trout/year, respectively. The maximum trout intake for the male with the highest hair mercury level was 180 kg (385 fish) and that for the female with the highest hair mercury level was 44 kg (94 fish). Based on an annual visitation of the streams by approximately 60 grizzly bears, 38 males and 22 females (Haroldson et al. 2005), and the average trout intake by adult male and female grizzly bears, 2266 cutthroat trout would be consumed: 2090 trout by male grizzly bears and 176 trout by female grizzly bears. This level of grizzly bear trout consumption is only 11% of that estimated by Stapp and Hayward (2002) and <2% of the amount of cutthroat trout being consumed by lake trout (Ruzycki et al. 2003).

Potential explanations for the differing estimates of fish intake by grizzly bears between Stapp and Hayward (2002) and the current study include (*i*) the differing methods and assumptions and (*ii*) a significant decline in cutthroat trout between 1975–1989 (Reinhart and Mattson 1990; Mattson and Reinhart 1995) and 1997–2000 (current study) leading to a dramatic decline in grizzly bear consumption. The major assumptions leading to the high fish intake estimates of Stapp and Hayward (2002) were that any bear identified within 500 m of a spawning cutthroat trout stream consumed trout and that cutthroat trout composed 90% of their energy intake. Our results do not support either assumption.

As discussed earlier, a major assumption of this study is that hair collected from wild grizzly bears was either the preceding year's fully grown hair or new hair that was collected after most of the annual trout intake had occurred. Either the old or new hair in these situations would be labeled with a mercury concentration indicative of the actual amount of trout ingested based on the captive bear standards if the hair was growing during trout consumption (i.e., Fig. 4). Although some of the hair samples collected from wild bears in August could have been new hair, trout intake estimates using those samples would overestimate the true cutthroat trout intake by approximately 8% and, therefore, would not contribute to the current low estimates.

In summary, we cannot exclude the possibility of a systematic error in any study (Reinhart and Mattson 1990; Mattson and Reinhart 1995; current study) leading to erroneous conclusions. Similarly, the conclusions of all studies may be correct and indicative of the ongoing effects of a declining cutthroat trout population on Yellowstone grizzly bears. An additional study is needed to test the assumptions of each study and to determine the nutritional and ecological value of spawning cutthroat trout to Yellowstone grizzly bears while significant populations of cutthroat trout remain.

Because bioaccumulation of mercury is relatively high in aquatic food systems, the estimation of fish intake by grizzly bears from mercury concentrations may extend beyond the GYE and Yellowstone Lake (Clarkson 1992; Duffy et al. 1998; Ben-David et al. 2001; Bowles et al. 2001). For example, if spawning salmon (*Oncorhynchus* spp.) are the only significant contributor of mercury to salmon-feeding brown bear populations, hair mercury levels would be useful for quantifying the amount of salmon consumed by bear populations in Alaska and Canada (Ben-David et al. 2001, current study). Previous estimates of salmon intake by bears required multiple captures of the same bear (Hilderbrand et al. 1999*b*). Estimates based on hair mercury levels and appropriately timed captive bear feeding trials would require only one capture or could be done remotely with hair snares.

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Finally, significant mercury consumption and accumulation could have negative health consequences for Yellowstone grizzly bears (Lippmann 2000; Fournier et al. 2002). Because no controlled studies have examined the interaction of mercury intake and reproduction by grizzly bears, we cannot exclude the possibility that the reduced reproductive success reported by Mattson and Reinhart (1995) for adult females living in the Yellowstone Lake area relative to the rest of the ecosystem was due to the negative consequences of mercury ingestion. However, captive adult grizzly bears ($n = 6$) other than those used in this study that were fed large amounts of salmon (240 ppb mercury) over multiple years had hair mercury concentrations of 4778 ± 631 ppb. These bears appear completely healthy, are now 18 years old, and have produced numerous sets of healthy twin cubs (L.A. Felicetti and C.T. Robbins, personal communication). The hair mercury levels of the captive bears were 9–35 times higher than those of male and female grizzly bears in Yellowstone. Thus, we do not expect detrimental health consequences associated with the levels of mercury consumption currently occurring in the grizzly bears of the Greater Yellowstone Ecosystem.

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