RELATIVE CONTRIBUTIONS OF CLIMATE VARIATION,

LAKE TROUT PREDATION, AND OTHER FACTORS

TO THE DECLINE OF YELLOWSTONE LAKE CUTTHROAT TROUT

DURING THE THREE RECENT DECADES

by

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STATEMENT OF PERMISSION TO USE

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ABSTRACT

The relative contributions of climate variation, lake trout *Salvelinus namaycush* predation, and other factors to the recent, three-decade decline of the lacustrine-adfluvial (i.e., a life-history form consisting of fish that mostly live in a lake but spawn in an inflowing tributary) Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (YCT) population of Clear Creek, a Yellowstone Lake tributary, were evaluated. Strong growth of that population's storied spawning run between the early 1960s and 1978, when the run peaked at about 70,000 fish, had been considered key evidence of recovery of the lake's YCT population from formerly excessive angler harvest and other adverse factors. Thus the run's subsequent, almost continuous decline to about 500 fish in 2007 was perplexing. Gillnet catches of YCT at established lake locations likewise indicated a concurrent decline in the lake-wide YCT population. Prominent among the factors that may have importantly affected the YCT population during the recent decades was predation by the illegally introduced, reproducing, nonnative lake trout discovered in Yellowstone Lake in 1994. Data mainly taken from YCT in the spawning run (n = 29 years) and gillnet catch (n = 30 years) were examined for information useful to specifying the Leslie matrix of a dynamic, age-structured model that had climate as a covariate. The model, fitted to spawning run size and mean total length (TL) of YCT in the run during 1977–2007 (n = 29 data years), explained 87% of variation in observed run size, 86% of variation in observed mean TL, and strongly suggested that climate (as indexed by total-annual air degree-days > 0°C measured on the lake's north shore) had an important effect on recruitment of age-0 YCT to subsequent spawning runs. Results also suggested that an effect of lake trout predation on survival of age-1 to age-5 YCT became apparent only during the recent decade. The important test of ongoing efforts to control lake trout in Yellowstone Lake and thereby limit their predation on YCT – on the basis of data for YCT – will occur when climatic conditions improve for YCT recruitment to the Clear Creek and other YCT spawning stocks of the lake.

CHAPTER ONE

PROLOGUE TO THE STUDY

Introduction

When the first scientific survey of the fishes of Yellowstone National Park (YNP) was conducted, in 1889, Yellowstone Lake and its tributaries reportedly abounded with "red-throated" trout (Jordan 1891), known today as Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri*. By mid-twentieth century, however, a marked decline in that Yellowstone cutthroat trout (YCT) population was evident, and was mainly attributed to excessive angler harvest (Benson and Bulkley 1963) and, more recently, to reduced natural reproduction that accompanied hatchery-driven, spawn-taking operations (Gresswell and Varley 1988). During subsequent decades, the YCT recovery that accompanied increasingly restrictive angling regulations and elimination of spawn-taking seemingly substantiated the assumed adverse effects of those former factors (Gresswell and Varley 1988; Gresswell et al. 1994).

Obligate stream spawners, adult YCT from Yellowstone Lake have been observed during the spawning season in 68 of the lake's approximately 124 possible (i.e., dependent upon annual water availability) inflowing tributaries (Gresswell and Varley 1988). The fish also spawn in the lake's outlet stream, the Yellowstone River (Kaeding and Boltz 2001). Total spawner number and several other attributes of the annual YCT spawning run in one tributary, Clear Creek, have been periodically estimated for several decades. The resulting data time series is the longest (but not the only) for YCT in

Yellowstone Lake, and some of its indices have been used to depict trends in the lake's YCT population. For example, strong growth of the spawning run between the early 1960s and 1978, when it peaked at about 70,000 fish (Figure 1.1), was considered key evidence of recovery of the lake's YCT population from the formerly excessive harvests and other adverse factors (Gresswell and Varley 1988; Gresswell et al. 1994). Consequently, the run's subsequent, almost continuous decline to about 6,000 fish in 1994 – despite greatly restrictive angling regulations and a concurrent downward trend in estimated total-annual YCT harvest – was perplexing, particularly to YNP managers. Although several subsequent annual YCT spawning runs were somewhat larger than 6,000 fish, Clear Creek run size showed another downward trend between 1998 and 2007 (Figure 1.1). Catches of YCT in gill nets routinely set during fall at established Yellowstone Lake locations likewise indicated a concurrent, marked decline in the YCT population (Koel et al. 2005).

Three factors were prominent among those that may have importantly affected, either individually or collectively, the dynamics of the YCT population of Yellowstone Lake during the three recent decades. First, a reproducing population of lake trout *Salvelinus namaycush*, a highly piscivorous species not indigenous to YNP, was discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996). Because introduced lake trout elsewhere had adversely affected native cutthroat trout, the National Park Service (NPS) soon began what became an intensive capture-and-removal program aimed at controlling the lake trout population (Ruzycki et al. 2003; Koel et al. 2005).

Second, *Myxobolus cerebralis*, a nonnative myxozoan parasite and causative agent of "whirling" disease in several salmonid fishes, including YCT (Hedrick et al.

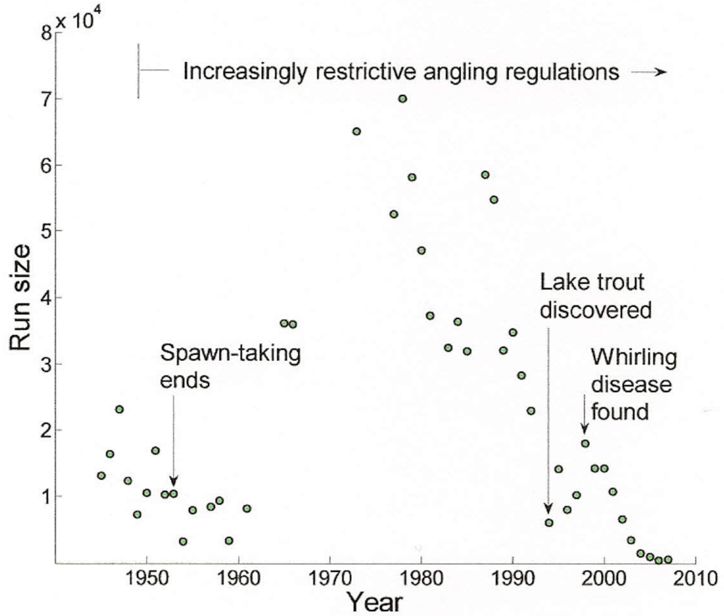

Figure 1.1. Number of Yellowstone cutthroat trout counted in the annual spawning run in Clear Creek, Yellowstone National Park, during 46 years between 1945 and 2007. Also indicated are key events that may have affected that spawning population.

1999), was found in Yellowstone Lake's YCT in 1998 (Koel et al. 2005). Initially detected in the YNP region in Montana's Madison River in 1994, whirling disease was believed to have caused a substantial decline in that river's rainbow trout *O. mykiss* population during the early 1990s (Vincent 1996). In YNP, Koel et al. (2005, 2006) suggested the evident near elimination of the YCT spawning run in Pelican Creek, which enters Yellowstone Lake about 2 km southeast of the lake outlet, was due to whirling disease. That conclusion was based on the observation that 75–100% of hatchery-produced YCT fry held in cages in Pelican Creek in 2000 or 2001 subsequently tested positive for the whirling disease parasite (Koel et al. 2006). The creek's spawning run had totaled nearly 30,000 YCT in 1981. Ways of eliminating or controlling *M. cerebralis* in the Yellowstone Lake drainage are not yet apparent (Koel et al. 2006).

Third, years with below-average stream discharges, often the result of severe drought, were especially frequent in the Yellowstone Lake region during the past three decades. Elsewhere, low stream discharges have been shown to negatively affect the reproduction of stream-spawning fishes, including oncorhynchids (e.g., Brett 1951; Selifonov 1987; Lawson et al. 2004). In YNP, Koel et al. (2005) reported that reduced Yellowstone Lake surface elevations during dry years exposed natural alluvial deposits of sand and gravel near the mouths of inflowing tributaries, and late-summer tributary flow was often entirely subsurface when passing through the deposits. Those authors speculated that the deposits prevented migration to the lake of YCT fry produced in the tributary that year. Also, in a preliminary investigation that led to the present study, Kaeding (1996) presented a simple regression model for a spawning run that consisted of age-4 to age-6 fish whose relative abundances were proportional to total-annual Yellowstone Lake discharge (an assumed index of annual water availability in the lake's spawning tributaries) 4–6 years earlier, respectively. The regression explained 63% of the variation in size of the Clear Creek spawning run between 1969 and 1994, and suggested annual water availability had an important effect on recruitment of YCT to the Clear Creek spawning run.

The goal of this study was to evaluate the relative contributions of climate variation, lake trout predation, and other factors to the decline of the lacustrine-adfluvial (i.e., a life-history form consisting of fish that mostly live in a lake but spawn in an inflowing tributary; Varley and Gresswell 1988) YCT population of Clear Creek. Before that goal could be achieved, however, it was necessary to accomplish several initial objectives, presented herein in separate chapters. Those objectives culminated with development of a dynamic, age-structured model of the population. The model was "dynamic" in that it accounted for the potential effects of several population characteristics and time-varying environmental factors on the population; and "age-structured" because it embodied the age structure (and its associated demographic characteristics) of the YCT population.

Objectives by Chapter

In brief, the first objective of Chapter Two was to identify a robust predictor of Clear Creek's discharge and temperature during the annual YCT spawning period from among several local climate variables (e.g., air temperature, precipitation) and total-annual Yellowstone Lake discharge. If certain of the variables (whose data time series were long and effectively complete) showed statistical associations with the creek's discharge and temperature (whose data time series were sporadic), it would be useful as a predictor variable in the YCT population model for years when discharge and creek temperature were not measured. The second objective was to determine the degree of statistical association among the local climate variables across the Yellowstone Lake drainage. If those associations were extensive, certain of the variables may be useful as broad predictors of seasonal discharge or temperature of the lake's tributaries as a whole and thus would be important to investigations of the lake's collective YCT population.

For Chapter Three, objectives were to (1) document the procedures for operation of the Clear Creek trap and gillnet sampling and (2) examine the data for captured YCT to identify demographic characteristics useful to specifying a Leslie (1945, 1948) matrix. That matrix will be a key part of the model of the lacustrine-adfluvial YCT population of

Clear Creek (Chapter Five). Because knowledge of the accuracy of extant age estimates for YCT was important to interpreting the somatic growth of YCT, reliability of those estimates also was assessed.

Objectives of Chapter Four were to examine the time-series data for YCT caught in the Clear Creek trap or gill nets and identify (1) associations between population metrics within and between capture methods, as well as temporal trends in metrics, and (2) evidence of temporal shifts in the mean total length (TL) of three distinct YCT size-classes and the factors that may have caused the shifts. Attaining the first objective will reveal the extent to which the YCT in the Clear Creek spawning run are like those of YCT in any particular area of the lake or the lake as a whole, whereas attaining the second objective will reveal factors that should be included in the model (Chapter Five).

For Chapter Five, objectives were to (1) develop a dynamic, age-structured model of the lacustrine-adfluvial YCT population of Clear Creek; (2) separately estimate the parameters for the full model, as well as for each of its two main components (i.e., climate and predation), and compare the various observed and predicted trajectories for run size and mean TL of YCT in the run; and (3) draw conclusions about the factors that may have importantly affected the dynamics of that YCT population during the three recent decades. Improved understanding of the historic dynamics of this key lacustrine-adfluvial YCT population will be important to the management of YCT in Yellowstone Lake, as well as to assessment of the efficacy of the ongoing lake trout control program.

Finally, Chapter Six's objectives were to summarize the major conclusions of the study and make recommendations for management and research.

CHAPTER TWO

EFFECTS OF LOCAL CLIMATE VARIABLES ON SEASONAL DISCHARGE AND TEMPERATURE OF CLEAR CREEK AND THEIR APPLICABILITY TO OTHER STREAMS IN THE YELLOWSTONE LAKE DRAINAGE

Introduction

Reproductive success of *Oncorhynchus* fishes (i.e., Pacific salmon, cutthroat trout, rainbow trout, and their allies) is often positively associated with the magnitude of seasonal stream discharge, perhaps owing to mobilization and removal of fine (potentially smothering) sediments from stream gravels where fertilized eggs were subsequently deposited and incubated, the provision of additional spawning substrate, or other factors (e.g., Brett 1951; Selifonov 1987; Lawson et al. 2004). Likewise, stream temperature, itself a covariate of stream discharge, can affect spawning time, reproductive success, and early-life survival (Kocik and Taylor 1987). For example, when available food is not limiting, elevated temperature results in more rapid body growth, and larger, more energy-rich age-0 coho salmon *O. kisutch* that are more likely to survive the winter (e.g., Holtby 1988; for a comprehensive review involving numerous fishes, see Hurst 2007). Thus predominance in the population of a year-class of oncorhynchids may be greatly affected by the biomass of its parent stock (which is positively associated with total egg output) and interactions of water quantity and temperature during the early life of age-0 fish in their natal stream or downstream rearing area (Kocik and Taylor 1987; Selifonov 1987; Lawson et al. 2004). However, collection of the data for the physical environment needed to estimate such relations may be prohibitively costly, particularly for stream discharges and when relevant streams are numerous and in remote areas.

Obligate stream spawners, adult YCT from Yellowstone Lake have been observed during the spawning season (~June) in 68 of the lake's approximately 126 inflowing tributaries (Gresswell et al. 1997). The YCT also spawn in the lake's outlet stream, the Yellowstone River (Kaeding and Boltz 2001). Soon after emerging from stream gravels in July or August, most age-0 YCT emigrate to the lake (Ball and Cope 1961; Gresswell and Varley 1988). Thus the period during which these young fish are influenced by the environmental conditions of their natal stream is short.

Attributes of YCT in the annual spawning run and concurrent creek discharge and temperature of one tributary, Clear Creek, have been periodically sampled for several decades. The resulting data time series is the longest for the YCT of Yellowstone Lake, and some of its indices have been used to depict trends in the lake-wide YCT population (e.g., Gresswell et al. 1994), including a marked downward trend evident during the past decade and hypothesized to be due to predation by nonnative lake trout (Koel et al. 2005). The illegally introduced lake trout had been discovered in the lake in 1994 (Kaeding et al. 1996).

The investigation described here was a key, initial component in the development of a dynamic, age-structured model of the lacustrine-adfluvial YCT population of Clear Creek. Because data for Clear Creek's discharge and temperature were sporadic within and among years, the first objective of the chapter was to identify a robust predictor of the creek's discharge and temperature from among several local climate variables and

Yellowstone Lake discharge (all of which had long, mainly complete data time series; described below).

In mountainous regions of the western United States, seasonal stream discharge is largely controlled by winter snow accumulation and subsequent snowmelt (Redmond and Koch 1991; Barnett et al. 2005). Also, seasonal stream temperatures have been shown to have a positive, linear association with seasonally “moderate” air temperatures (i.e., 0–20 °C) like those of the study area (e.g., Mohseni and Stefan 1999). If those or other variables examined in the present chapter were statistically associated with Clear Creek’s discharge or temperature, they may be useful as predictor variables in the developing model.

The chapter’s second objective was to determine the degree of statistical association among the local climate variables across the Yellowstone Lake drainage. If those associations were extensive, certain of the variables may be useful as broad predictors of seasonal discharge or temperature of the lake’s tributaries as a whole and thus would be important to investigations of the lake’s collective YCT population.

Study Area

Yellowstone Lake, in YNP, lies approximately 2,357 m above mean sea level, has a surface area of 34,100 ha, shoreline length of 277 km, mean depth of 43 m, and maximum depth of 131 m (Kaplinski 1991; Morgan 2007). Often considered the largest high-elevation (i.e., > 2,000 m) lake in North America, Yellowstone Lake mainly lies within an ancient volcanic caldera (Morgan et al. 2007) and has a surrounding, essentially undeveloped drainage of 2,230 km^2 (Koel et al. 2006). The drainage lies entirely within (and constitutes most of) the Yellowstone climate division of the U.S. National Climate Data Center (Redmond and Koch 1991).

Clear Creek begins nearly 2,762 m above mean sea level and flows west though coniferous forest for about 19 km before reaching the east shore of Yellowstone Lake (Figure 2.1). As a tributary of the lake, Clear Creek is of moderate size. Its watershed encompasses 2.6% of the drainage that surrounds the lake (Koel et al. 2006). Clear Creek discharge can exceed 10 m^3/s during spring runoff but usually drops below 1 m^3/s by August.

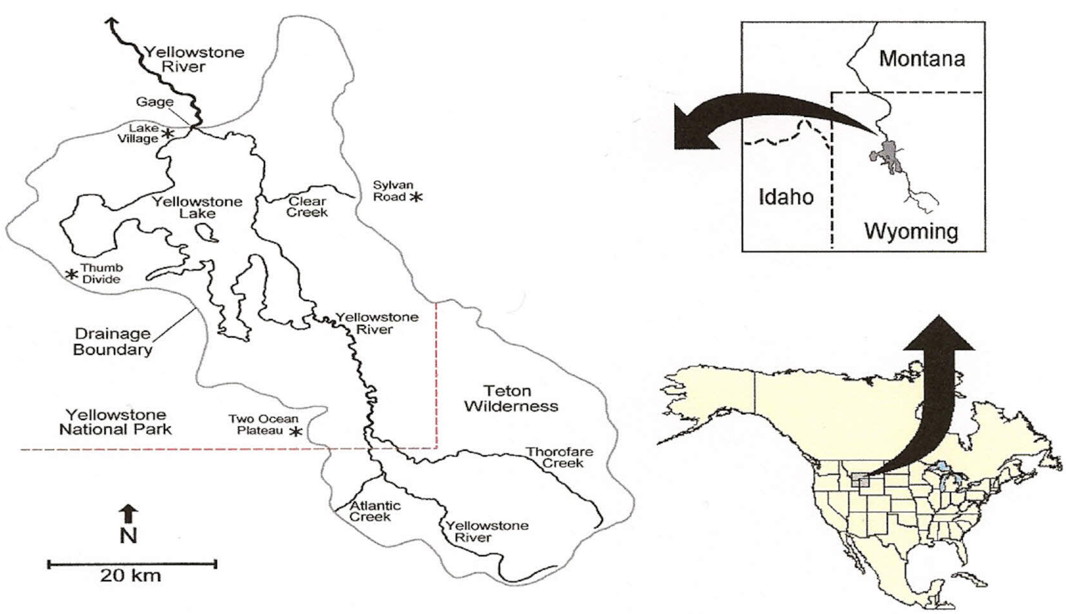

Figure 2.1. Map of the Yellowstone Lake drainage, Yellowstone National Park and Teton Wilderness Area, Wyoming. Among the numerous tributaries of the lake, only the Yellowstone River and Clear Creek are indicated, as are two additional headwater streams, the locations of snow-water measurement (✱), and the river gage at the lake outlet.

Methods

Data Sources

Clear Creek discharge and temperature data (described below) were obtained as electronic databases or taken directly from field data sheets stored in the files of either the former U.S. Fish and Wildlife Service (USFWS) Yellowstone Fisheries Assistance Office (data collected between 1977 and 1995) or present NPS Fisheries and Aquatic Sciences Program in YNP (1996–2004 data). Before the data were otherwise examined, their time series were plotted within years to identify abrupt shifts in values that may have indicated recording or other errors. Ostensibly erroneous data were either compared against original data sheets and corrected when necessary or excluded from further analyses when an otherwise uncorrectable error in the original data was apparent.

Stream Discharges

Standard measurement techniques (employing either mechanical or electronic flow meters) were used to periodically estimate Clear Creek discharge during most annual fish-trap operations (mid-May through July). Discharge was estimated daily or less frequently (e.g., high creek discharge often precluded estimates because personnel could not safely wade the creek) near a staff gage mounted on a steel fence post driven into the creek bottom about 100 m upstream from the trap, which was built near the creek's mouth. Stage-discharge relations for Clear Creek were available for 19 years. For each annual relation, discharge was measured on an average of 29.4 days (range, 6–57 days). Creek stage (i.e., height; measured using the gage) was recorded during discharge estimation as well as periodically throughout the work day (approximately 0700–2400 hour, although more limited in recent years). Routine measurements of creek stage during trap operations were available for 23 years. Creek stage was measured on an average of 358.2 occasions (range, 59–553 occasions) each year and 5.7 occasions each measurement day.

For the Yellowstone River, estimated mean-daily discharges at the Yellowstone Lake outlet (gage site 06186500; Figure 2.1) were obtained from a U.S. Geological Survey Internet web site (http://waterdata.usgs.gov/mt/). Discharge estimates were available for 1927–2007, except data were not collected during October 1982–September 1983 or October 1986–September 1988 (i.e., water years [1 October–30 September] 1983, 1987, and 1988).

Snow-water Measurements

Measurements of the water content of accumulated snow (i.e., snow-water equivalent [SWE]) on about April 1 (the approximate time of maximum-annual SWE at high elevations in YNP) were obtained from either a Natural Resources Conservation Service (NRCS) web site (http://www.wcc.nrcs.usda.gov/cgibin/state-site.pl?state=WY&report=snowcourse) or Phillip E. Farnes (Research Scientist, Snowcap Hydrology, and retired NRCS Hydrologist, Bozeman, Montana). The four locations of SWE measurement (Figure 2.1) were in disparate areas in or near the Yellowstone Lake drainage: (1) the area north of the lake (Lake Village location; site code 10E04, but named "Lake Camp"; 2,371 m elevation); (2) the Clear Creek area east of the lake (Sylvan Road; 10E05; 2,191 m); (3) the upper Yellowstone River drainage south of the lake (Two Ocean Plateau; 10E17S; 2,816 m); and (4) the area west of the lake (Thumb Divide; 10E07; 2,432 m). Although in the adjacent Middle Creek drainage, the Sylvan Road location was 8 km from the drainage divide with the headwaters of Clear Creek. Two Ocean Plateau was on the drainage divide with the Snake River. Measurements of SWE were available for each of the four locations from the 1930s through 2004, except measurements at Sylvan Road were not collected in 1992 or 1993 and ended in 1995.

Water and Air Temperatures and Precipitation

Hand-held thermometers were used to periodically measure Clear Creek temperature throughout the work day, usually concurrent with measurements of creek stage. Recording thermometers (mechanical in one or two early years and electronic in 2001 and parts of 2000 and 2002) and minimum-maximum thermometers were infrequently used. Measurements of creek temperature during fish-trap operations were available for 26 years. During annual operations, creek temperature was measured on an average of 59.2 days (range, 18–77 days), although measurements were less frequent after 2001.

Daily minimum and maximum air temperatures at Lake Village (NRCS site code WY5345, but named “Lake Yellowstone”) were obtained from Phillip E. Farnes. Because air temperatures were manually logged daily at about 0800 hour, the lowest temperature mechanically recorded during the preceding 24-hour period probably occurred during early morning of the logging day, whereas the highest temperature occurred sometime during the preceding calendar day (Phillip E. Farnes, personal communication). Accordingly, maximum-daily air temperatures were moved back one calendar day in the data time series for use in the present study. Measurements of daily precipitation at Lake Village also were obtained from Phillip E. Farnes. At Lake Village, year-round measurements of precipitation were available for water years 1949–2004 and of air temperature for water years 1928–2007, although temperature measurements were not complete for 5 years prior to 1949 and temperature data for those years are not examined herein.

Statistical Analyses

Correlation analysis (Pearson-type) was used to examine associations among Yellowstone Lake discharge, local climate variables (described below), and Clear Creek discharge and temperature, whereas multiple linear regression was used to identify which of those variables best explained variation in creek discharge or temperature (Neter et al. 1996). When multiple predictor variables were examined (interactions were not considered) using multiple regression, an all-possible-linear-regressions procedure (Hintze 2001) was used to identify quantitative predictors that best explained variation in creek discharge or temperature. The procedure ranked candidate models according to their number of predictors, coefficient of determination (r^2) or multiple determination (R^2), and Mallow's C_p criterion but did not allow categorical predictors. When categorical predictors also were considered, a hierarchical-forward-with-switching search algorithm (which treated categorical predictors as "dummy" variables) in multiple-regression procedure was used to identify candidate models. Only regression models that had a significant ($P < 0.01$) F statistic for the analysis of variance (ANOVA) and significant

($P < 0.01$) t statistic for each predictor coefficient were considered informative and are reported herein.

Preparatory Data Analyses

Estimation of Missing Lake Discharges: Estimated mean-daily Yellowstone River discharges at the Yellowstone Lake outlet were averaged within water years (i.e, as mean-annual discharge) for use in analyses. Because discharge data were not available for three water years that encompassed a period when data were available for the YCT spawning run, the missing mean-annual discharges needed to be estimated. Regression of mean-annual lake discharge for the 78 years for which data were available on concurrent mean-annual Yellowstone River discharge at Corwin Springs (gage site 06191500; http://waterdata.usgs.gov/mt/), 108 km downstream from Yellowstone Lake, revealed a significant relation ($r^2 = 0.96$; $F_{1, 76} = 1{,}767$; $P < 0.001$). That relation (Appendix A) was used to estimate mean-annual Yellowstone Lake discharge (hereafter, Lake Q) for the three water years for which data were not available.

Creek Discharge: Regression of $\log_e$ measured Clear Creek discharge on two predictor variables (i.e., $\log_e$ concurrent creek stage and measurement year [a categorical predictor]) revealed a significant relation (Appendix A; $R^2 = 0.94$; $F_{19, 537} = 474$; $P < 0.001$) with significant effects of both predictors. Pair-wise comparisons of stage-discharge relations between consecutive years (similarly performed using regression) revealed significant ($P < 0.01$) differences between relations in 9 of 13 possible instances. Thus creek stage was an important predictor of discharge but the stage-discharge relations were mainly year-specific, probably owing to movement of the steel post and its attached gage during winter.

Consequently, only routine stage measurements for the 19 years that had stage-discharge relations were further examined. Although temporal trends in creek stage differed somewhat among years, consistent similarities also were apparent: (1) seasonal variation in stage was larger than diel variation within years; (2) diel variation was larger on the ascending limb of the seasonal hydrograph (i.e., during spring runoff, which is forced largely by snow melt in YNP [Graumlich et al. 2003; Barnett et al. 2005]) than on the descending limb; and (3) during spring runoff, highest creek stage occurred near midnight and lowest near mid-day. Because routine measurement of Clear Creek stage most consistently occurred between 0900 and 1500 hour, only minimum-daily Clear Creek discharge (hereafter, Creek Q) was estimated, by applying the lowest creek stage recorded that day in the stage-discharge relation for that year.

Creek Temperature: Clear Creek temperatures measured by either electronic-recording or hand-held thermometers revealed a diel trend that had lowest temperature near dawn and highest temperature in early evening. To ensure consistency in measurements examined among years, lowest temperature recorded between 0300 and 0900 hour and highest temperature recorded between 1400 and 2000 hour were considered the daily minimum and maximum temperatures. Mean-daily temperature (hereafter, Creek T) was calculated as the average of the daily minimum and maximum temperatures.

Data Reduction

Variation among daily measurements for each variable was reduced by data summation within one of two temporal scales. On the broad scale, Lake Village air temperature (as degree-days > 0°C, calculated on the basis of mean-daily air temperature; hereafter, Lake Village DDs) and Lake Village precipitation were each summarized on a water-year basis, as Lake Q had been summarized. Along with measures of SWE, the aforementioned variables (except Lake Q) were collectively termed the "local climate variables." On the narrow temporal scale, variation in Creek Q and Creek T was reduced by summation of data for each variable within years and semi-month periods (hereafter, semi-months) during late May–late July; the first semi-month consisted of the first 15 days of the month and the second semi-month consisted of the remaining days. Unlike shorter (e.g., daily) time scales, use of semi-months eliminated the need to consider time lags in data analyses (Mohseni and Stefan 1999).

For Creek Q, data were available for all days in 44 semi-months between 1979 and 2004. For an additional 30 semi-months among those years, Creek Q was available for an average of 11 days (range, 5–15 days) across periods that averaged 13.3 days (range, 10–15 days). The area-under-the-curve method (Hintze 2001), which employed the trapezoidal rule (thus interpolating intervening, missing data), was used to calculate total Creek Q across the measurement period within each of the 30 partially represented semi-months. If the measurement period was less than the entire semi-month, total Creek Q during the period was proportionally increased to represent the semi-month. Creek T, available for all days in 56 semi-months between 1977 and 2001, was summed as total semi-month degree-day (> 0 °C; hereafter, Creek DDs) values within years.

Results

Trends in Lake Discharge and Lake Village Degree-days

Although considerable inter-annual variation occurred within both variables, the broad trend in Lake Q between 1927 and 2007 was concave downward, whereas that for Lake Village DDs between 1928 and 2007 was concave upward (Figure 2.2). A quadratic fit of these data suggested Lake Q broadly peaked during the 1960s and early 1970s, when the concurrent trend in Lake Village DDs was near its lowest point.

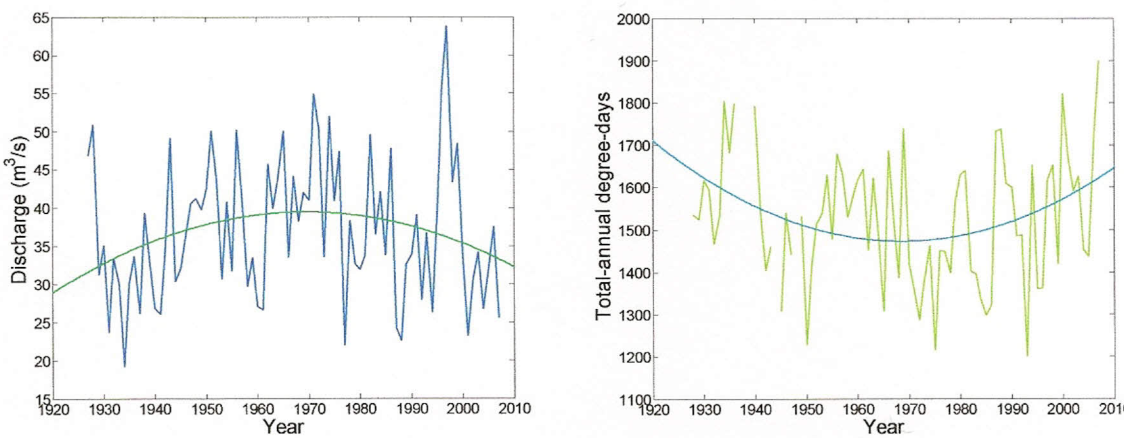

Figure 2.2. Mean-annual discharge (m^3/s) of the Yellowstone River at the Yellowstone Lake outlet (left; water years 1927–2007), and total-annual Lake Village degree-days (right; water years 1928–2007). Broad trends are suggested by the smooth curves, which are fits of a quadratic model to the data.

Associations Among Lake Discharge and Local Climate Variables

Significant ($P < 0.05$) associations occurred between 19 of the 21 possible paired combinations of Lake Q and the local climate variables (Table 2.1). Associations were

Table 2.1. Correlation coefficients (*P*-value in parentheses) for the paired combinations of Yellowstone Lake discharge and the local climate variables, Yellowstone Lake area, Yellowstone National Park. DDs = Lake Village DDs; Ppt = precipitation; SWE = snow-water equivalent; Q = discharge; ns = not significant ($P \geq 0.05$). Number of data pairs (years) for each correlation is given in brackets.

	Local climate variable					
Variable	Total-annual Lake Village DDs	Total-annual Lake Village Ppt	Lake Village SWE	Sylvan Road SWE	Thumb Divide SWE	Two Ocean SWE
Mean-annual Lake Q	-0.427 (<0.001)[75]	0.609 (< 0.001)[55]	0.803 (< 0.001)[68]	0.751 (< 0.001)[56]	0.774 (< 0.001)[67]	0.803 (< 0.001)[75]
Total-annual Lake Village DDs		-0.325 (0.016)[55]	ns	ns	-0.261 (0.039)[63]	-0.292 (0.014)[70]
Total-annual Lake Village Ppt			0.665 (< 0.001)[55]	0.438 (0.003)[44]	0.513 (< 0.001)[55]	0.574 (< 0.001)[55]
Lake Village SWE				0.811 (< 0.001)[55]	0.836 (< 0.001)[66]	0.842 (< 0.001)[68]
Sylvan Road SWE					0.829 (< 0.001)[56]	0.769 (< 0.001)[56]
Thumb Divide SWE						0.700 (< 0.001)[67]

considered strong (i.e., absolute value of correlation coefficient [*r*] > 0.60) among most combinations of Lake Q, Lake Village precipitation, and SWE at each of the four locations. Negative associations always involved Lake Village DDs, as did the two associations that were not significant.

<u>Seasonal Trends in Creek Discharge and Temperature</u>

Semi-month Creek Q had already increased from its seasonal low when measurements began in late May, most often reached its seasonal high in early June, then steadily declined (Figure 2.3). Semi-month Creek DDs was lowest during the two semi-months of increasing and highest Creek Q and steadily increased thereafter (Figure 2.3).

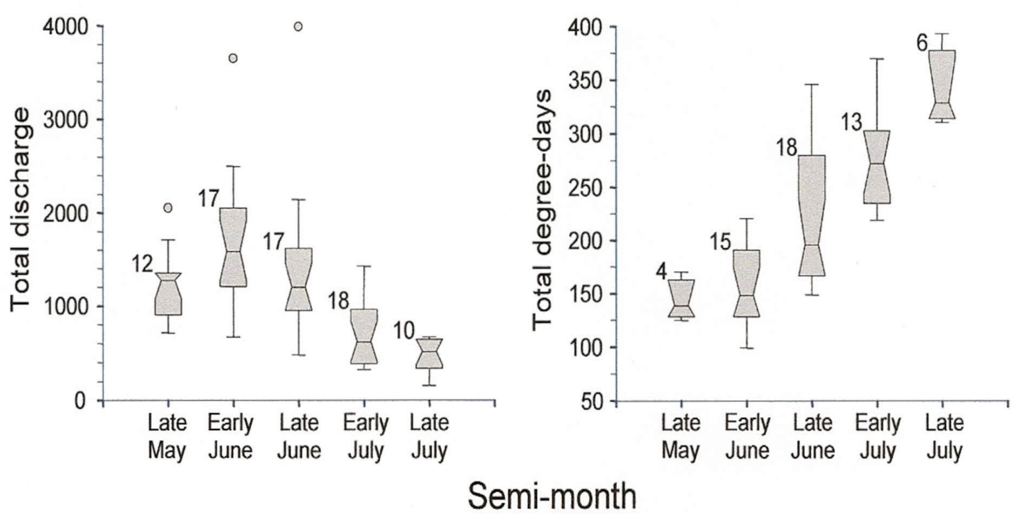

Figure 2.3. Box plots of total semi-month discharge (i.e., sum of daily creek Qs; left) and total semi-month Lake Village DDs (right) for Clear Creek, Yellowstone National Park. Plots indicate the median value at the box notch, the interquartile range (IQR) by the box itself, and the range of values by horizontal lines at the ends of the vertical lines; outliers (i.e., data values > 1.5 IQR from the box) are indicated by circles. Numbers indicate number of measurements (years).

Associations Between Lake Discharge, Local Climate
Variables, and Creek Discharge and Temperature

Significant ($P < 0.05$) associations between Lake Q or local climate variables and semi-month Creek Q were few (4 of 35 instances) and involved either Lake Q or Lake Village DDs (Table 2.2). In these four instances, Creek Q was positively associated with Lake Q or negatively associated with Lake Village DDs, except the association with Lake Village DDs was positive in late May. In contrast, significant associations between Lake Q or local climate variables and semi-month Creek DDs occurred in 13 of 35 instances, none of which were in late May, however. Among these 13 instances, associations of Creek DDs with the various measures of water availability were consistently negative, whereas those with Lake Village DDs were positive.

Regression of Creek Discharge and Temperature
on Lake Discharge and Local Climate Variables

Regression of semi-month Creek Q on two predictor variables, semi-month sequence number within years (a discrete, quantitative predictor) and Lake Village DDs revealed a significant relation (Appendix A; $R^2 = 0.35$; $F_{2,\,71} = 19.4$; $P < 0.001$) with significant effects of both predictors. (As a variable in this context, semi-month sequence number defined the temporal relation among semi-months.) Similarly, a significant relation (Appendix A; $R^2 = 0.31$; $F_{2,\,71} = 16.0$; $P < 0.001$) was evident when Lake Q was substituted for Lake Village DDs. The search algorithm also indicated that distinguishing between semi-months for which the area-under-the-curve method was used and those for which Creek Q data were complete (i.e., method treated as a categorical predictor) had no effect on model selection.

Table 2.2. Correlation coefficients (*P*-value in parentheses) for associations between Yellowstone Lake discharge and the local climate variables and total semi-month discharge and Lake Village DDs of Clear Creek, Yellowstone Lake area, Yellowstone National Park. DDs = Lake Village DDs; Ppt = precipitation; SWE = snow-water equivalent; Q = discharge; ns = not significant ($P \geq 0.05$). Number of data pairs (years) for each correlation is given in brackets.

		Local climate variable					
Semi-month	Mean-annual Lake Q	Total-annual Lake Village DDs	Total-annual Lake Village Ppt	Lake Village SWE	Sylvan Road SWE	Thumb Divide SWE	Two Ocean SWE
				Creek discharge			
Late May	ns	0.730 (0.007)[12]	ns	ns	ns	ns	ns
Early June	ns	ns	ns	ns	ns	ns	ns
Late June	0.619 (0.008)[17]	-0.720 (0.001)[17]	ns	ns	ns	ns	ns
Early July	ns	-0.719 (<0.001)[18]	ns	ns	ns	ns	ns
Late July	ns	ns	ns	ns	ns	ns	ns
				Creek degree-days			
Late May	ns	ns	ns	ns	ns	ns	ns
Early June	-0.660 (0.007)[15]	0.668 (0.007)[15]	ns	ns	ns	ns	ns
Late June	-0.707 (0.001)[18]	0.650 (0.004)[18]	-0.655 (0.003)[18]	-0.490 (0.039)[18]	ns	-0.594 (0.009)[18]	-0.561 (0.015)[18]
Early July	-0.682 (0.010)[13]	0.632 (0.020)[13]	-0.570 (0.042)[13]	ns	ns	-0.625 (0.022)[13]	ns
Late July	ns	0.821 (0.045)[6]	ns	ns	ns	ns	ns

Regression of semi-month Creek DDs on three predictor variables, semi-month sequence number, Lake Q, and Lake Village DDs, revealed a significant relation (Appendix A; $R^2 = 0.84$; $F_{3, 52} = 92.9$; $P < 0.001$) with significant effects of all predictors. Together, semi-month sequence number and Lake Q explained 79% of the variation in semi-month Creek DDs (Appendix A; $R^2 = 0.79$; $F_{2, 53} = 97.1$; $P < 0.001$), whereas semi-month sequence number and Lake Village DDs explained 78% of that variation (Appendix A; $R^2 = 0.78$; $F_{2, 53} = 95.9$; $P < 0.001$).

Discussion

Important statistical associations were found among Lake Q and the local climate variables, as well as between those variables and semi-month Creek Q and Creek DDs. In particular, there were strong associations among Lake Q and SWE at the four, geographically disparate locations in or near the Yellowstone Lake drainage. Redmond and Koch (1991) showed that seasonal stream discharge was largely controlled by winter snow accumulation and subsequent snowmelt in the YNP region and other mountainous areas of the western United States. Thus the statistical associations found in the present study indicated Lake Q is a useful, composite predictor of the magnitude of seasonal stream discharge (specifically, during the YCT spawning and embryo-incubation seasons) throughout the Yellowstone Lake drainage.

Strong associations also were found among Lake Village DDs and semi-month Creek Q and Creek DDs. Likewise, Mohseni and Stefan (1999) showed that stream temperature had a positive, linear association with “moderate” air temperatures like those examined in the present study (i.e., 0–20°C), although stream discharge (particularly discharge resulting from nearby snowmelt) importantly affected the relation. In the present study, such an effect of snowmelt on Creek T was evident in late May. In addition, Lake Village DDs and semi-month sequence number explained 35% of variation in semi-month Creek Q, and Lake Q and semi-month sequence number or Lake Village DDs and semi-month sequence number explained 79% and 78% of variation in semi-month Creek DDs, respectively. Thus Lake Q and, especially, Lake Village DDs are useful covariates of semi-month Creek Q and Creek DDs. Moreover, because Redmond and Koch (1991) showed that Lake Village DDs were strongly associated with similar temperature measures within the Yellowstone climate division – of which the Yellowstone Lake drainage is the major part – it is reasonable to assume that Lake Village DDs is a predictor of stream temperatures during the YCT spawning season throughout the Yellowstone Lake drainage.

A surprising result of this work may have been that Creek Q and Lake Q were almost entirely unassociated among semi-months. Those associations may be weak. Alternatively, the annual stage-discharge relations for Clear Creek may have been importantly biased because high creek discharges could not be measured and used in estimating relations and – that point notwithstanding – measurements of creek stage were few when at their diel high, i.e., near midnight. These data limitations may have affected the correlations with Lake Q, the measurement of which was not similarly inhibited. This problem with measurement of creek discharge also may explain why associations between Creek DDs and Lake Q or the local climate variables were more often significant than those involving Creek Q, namely, available data allowed estimation of mean-daily creek temperatures but not mean-daily creek discharges, and the mean-daily data were more representative of the creek.

The only negative associations between variables involved measures of precipitation (or Lake Q) and air temperature. Redmond and Koch (1991) reported precipitation and air temperature during March–October were negatively associated in the Yellowstone climate division. Those authors also showed that the climate variables were strongly associated with a Pacific North America index (a measure of the dominant mode of winter circulation over the eastern Pacific Ocean and North America) and, to a lesser extent, with the Southern Oscillation Index (a measure of atmospheric conditions in the equatorial Pacific Ocean).

The local climate variables examined in the present study were useful predictors of semi-month Creek Q and Creek DDs, and even more precise predictive models of Clear Creek Q and DDs based on these data may be attainable. Although such detailed models may be important to studies of the creek's lacustrine-adfluvial YCT spawning stock, Clear Creek is but one of many Yellowstone Lake tributaries used by spawning YCT and detailed predictive models for the creek would have unknown precision in their application to other streams in the drainage. Importantly, this study also revealed associations among local climate variables and the creek's discharge and temperature that were also plausibly associated with discharges and temperatures of the lake's tributaries in general.

Statistical associations among local climate variables across the Yellowstone Lake drainage, and strong associations between those variables and semi-month Creek Q and Creek DDs, indicated Lake Q and, in particular, Lake Village DDs are useful as broad indices of seasonal discharge and temperature of the lake's tributaries as a whole. Temperature of Yellowstone Lake's surface, near which age-0 YCT (as well as older fish) rear after they emigrate from their natal tributaries (Benson 1961), also are strongly associated with ambient air temperature (Hostetler and Giorgi 1995). Thus Lake Village DDs will be used as an environmental variable and index of climate in subsequent analyses.

CHAPTER THREE

AGE, GROWTH, MATURITY, AND FERTILITY OF YELLOWSTONE LAKE CUTTHROAT TROUT

Introduction

When the first scientific survey of the fishes of YNP was conducted, in 1889, Yellowstone Lake and its tributaries reportedly abounded with "red-throated" trout (Jordan 1891), known today as Yellowstone cutthroat trout. Subsequent sampling of YCT from the lake has been routinely performed for several decades (e.g., Gresswell and Varley 1988; Gresswell et al. 1994). In particular, on Clear Creek, one of 68 of Yellowstone Lake's inflowing tributaries known to be used by spawning YCT, a trap has been used to capture YCT in the annual spawning run (Gresswell and Varley 1988). Likewise, in the lake itself, gill nets set at established locations have routinely caught YCT (Koel et al. 2005). Nevertheless, demographic data – in particular those necessary for estimating parameters for matrix population models (e.g., Caswell 2001) – are meager for YCT, from Yellowstone Lake or elsewhere (Meyer et al. 2003).

Matrix population models "provide a link between the individual and the population, built around a simple description of the life cycle" and have become widely used in studies of population dynamics (Caswell 2001). The basic matrix population model of the Leslie (1945, 1948) form (Equation 3.1; Caswell 2001),

$$\mathbf{n}(t+1) = \mathbf{A}(t) \times \mathbf{n}(t) , \qquad (3.1)$$

consists of the rate matrix **A**(t) and state column vector **n**(t). (For matrices and vectors in matrix applications, time [i.e., t] is indicated parenthetically to distinguish it from matrix or vector elements, which are designated by subscripts.)

Elements in the first row of the $m \times m$ rate matrix **A**(t) (where m is maximum age, in years in the present study) are age-specific fertilities (F_x; i.e., the per-capita, age-x contribution of young to age 1), whereas elements in the immediate sub-diagonal are age-specific survival probabilities (s_x; the proportion of age x individuals that survive to age x + 1). Remaining matrix **A**(t) elements are zero. Thus matrix **A**(t) for an organism whose maximum age is 4 and maturity onset occurs at age 3 is:

$$\begin{bmatrix} 0 & 0 & F_{1,3}(t) & F_{1,4}(t) \\ s_{2,1}(t) & 0 & 0 & 0 \\ 0 & s_{3,2}(t) & 0 & 0 \\ 0 & 0 & s_{4,3}(t) & 0 \end{bmatrix}$$

The state column vector **n**(t) is the age-frequency distribution for the population at time t. Matrix multiplication of **A**(t) and **n**(t) (i.e., Equation 3.1) projects **n**(t) forward one time step, yielding the state vector (i.e., **n**(t + 1)) at time t + 1.

Objectives of the present chapter were to (1) document the procedures for operation of the Clear Creek trap and gillnet sampling and (2) examine the data for captured YCT to identify demographic characteristics useful to specifying a Leslie (1945, 1948) rate matrix. That matrix will be part of a model of the lacustrine-adfluvial YCT population of Clear Creek (Chapter Five). Because knowledge of the accuracy of extant age estimates for YCT was important to interpreting the somatic growth of YCT and assigning fecundities to age-classes, reliability of those estimates also was assessed.

Methods

Study Area

Yellowstone Lake has been classified as mesotrophic to moderately eutrophic on the basis of phosphorus concentration, transparency, and primary productivity (Kilham et al. 1996; Theriot et al. 1997). For a large (surface area, 34,100 ha), high-elevation (2,357 m above mean sea level) lake, appreciable nutrient enrichment from geothermal springs (Morgan 2007) may be unique in Yellowstone Lake.

Native fishes of Yellowstone Lake are YCT and longnose dace *Rhinichthys cataractae*, whereas longnose sucker *Catostomus catostomus*, redside shiner *Richardsonius balteatus*, lake chub *Couesius plumbeus*, and lake trout *Salvelinus namaycush* are established, nonnative species (Benson 1961; Kaeding et al. 1996). The minnow species inhabit only vegetated bays and other littoral areas; YCT, longnose sucker, and lake trout are found throughout the lake. Longnose sucker may have been introduced to Yellowstone Lake as a bait fish in the early 1920s, whereas the nonnative minnows (likewise probably introduced as bait fishes) were not found there until about mid-century (Benson and Bulkley 1963). The illegally introduced, reproducing population of lake trout was discovered in the lake in 1994 (Kaeding et al. 1996).

Field Procedures

Trap Operation: Clear Creek was one of 14 Yellowstone Lake tributaries (including the lake outlet) on which traps, periodically operated near the tributaries' mouths, caught YCT in annual spawning runs during the first half of the twentieth century (Arnold 1967; Gresswell and Varley 1988). Captured ripe fish were artificially spawned and released upstream from the trap, along with captured and released unripe fish. Resulting young YCT, reared in a hatchery on the lake's north shore, were stocked back into the lake or elsewhere, primarily as fry. When such spawn-taking activities ended, in 1953, periodic trap operation continued for purposes of research sampling of YCT (Ball and Cope 1961; Gresswell and Varley 1988). Among the tributaries that had traps, the data time series was longest and most comprehensive for Clear Creek.

Procedures for Clear Creek trap operations did not substantively change during the past four decades, although the trap was not operated in all years and data collection was most comprehensive after 1976. The YCT in annual spawning runs were usually counted between about mid-May and late July. Before 1989, upstream migrants were counted as they were removed from the trap, processed (described below), and released upstream. (The trap's weir spanned the entire width of the creek.) In addition, during daylight when fish were especially abundant, workers counted YCT seen moving upstream through a narrow weir opening. Beginning in 1989, an electronic fish counter was employed in the opening and only YCT that were processed for additional data were trapped and manually counted.

Each week beginning in 1977 up to 100 trapped YCT were measured to TL (mm) and for mass (g); sex was determined from external characteristics and the occurrence of expressible gametes; and scales were taken from 20 fish for use in age estimation. When scales had been taken from 10–15 YCT within one of the consecutive 10-mm intervals that constituted the range in TL measurements that year, scales were no longer taken from YCT in that interval. Each day as many as 75 additional trapped YCT were similarly measured to TL, classified to sex, and tabulated within consecutive 5-mm intervals of fish length. Measurement of Clear Creek discharge and temperature, also performed during trap operations, was described in Chapter Two.

For the present study, data for trapped YCT (or caught in gill nets; described below) were obtained as electronic data bases or taken directly from field data sheets stored in files of either the former USFWS Yellowstone Fisheries Assistance Office (data through 1995) or present NPS Fisheries and Aquatic Sciences Program in YNP (1996–2007 data). Data for trapped YCT were those collected during the 29 years of trap operation between 1977 and 2007 (trap not operated in 1986 or 1993). During that time, run size peaked at about 70,000 fish in 1978 and showed an almost continuous decline to about 6,000 fish in 1994. Although several subsequent annual YCT spawning runs were somewhat larger than 6,000 fish, Clear Creek run size showed another downward trend between 1998 and 2005 (Koel et al. 2005) and consisted of about 500 YCT in both 2006 and 2007 (Figure 1.1). (In spring 2008, high creek discharge destroyed the trap and weir.) Altogether between 1977 and 2007, 73,568 trapped YCT had been measured to TL, 20,775 had been measured for mass (mass data not taken in 1985), 70,034 had their sex determined, and 3,168 fish had been estimated for age (age data not available for 1996 or 2004–2007).

Gillnetting: In 1969, the USFWS (then fisheries technical advisor to the NPS in YNP) began to also use gill nets to annually sample the YCT of Yellowstone Lake. Initially, one net was set in mid-September at each of 21 sites around the lake. In 1977, four nets were set at each site. Finally, beginning in 1978, five nets were set at each of 11 of the original 21 sites (Figure 3.1). Those 11 sites were chosen on the basis of among-site similarity in YCT catch and, collectively, a preponderance of the longnose sucker catch (Jones et al. 1977). Set in the afternoon and retrieved the next morning, gill nets were 38 m long; 1.5 m deep; and consisted of five ordered, 7.6-m panels of 19-mm, 25-mm, 32-mm, 38-mm, or 51-mm (bar measure) monofilament netting. Beginning with the smallest mesh in water about 1.5 m deep, nets at each site were set perpendicular to the shoreline and about 100 m apart.

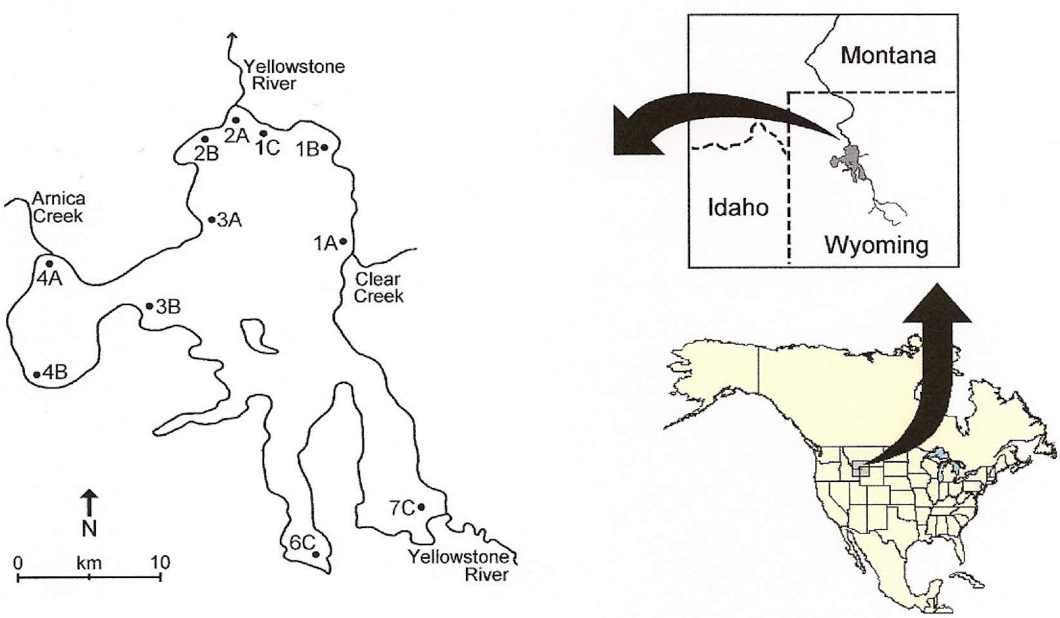

Figure 3.1. Map of Yellowstone Lake, Yellowstone National Park, showing the Yellowstone River inlet (lower right) and outlet (top), the lower part of Clear Creek, Arnica Creek, and the 11 gillnet sampling sites (●) and their codes.

Fish (longnose sucker and lake trout were similarly examined) captured in each net were arranged from longest to shortest and measured to TL and for mass; stage of maturity (i.e., immature or mature) and sex (when possible) were determined by gross examination of excised gonads. Mature fish whose developing gonads indicated the fish would have spawned the next year were further assigned to the "prespawner" (Ball and Cope 1961) maturity stage. Scales used in subsequent age estimation were removed from every third YCT in the length-ordered array, beginning with the longest fish.

Gillnetting occurred in 36 years between 1969 and 2007. Gillnetting did not occur in 1973, 1975, or 1993, at sites 3A and 3B (Figure 3.1) in 1969, sites 3A through 7C in 1971, or at sites 3A and 6C in 2006. Mean number of YCT caught per gill net peaked at about 19 fish in the mid-1980s and subsequently showed an almost continuous decline to about 8 fish in 2005 (Koel et al. 2005), a catch rate similar to that in 2006 and 2007. Among the 21,138 YCT gillnetted between 1969 and 2007, each had been measured to TL, 20,890 had been measured for mass, 19,759 had both determinable sex and stage of maturity (sex and maturity stage inadequately determined in 2006), and 6,599 fish had been estimated for age (age data not available for 1996 or 2004–2007).

Fecundity of Yellowstone Cutthroat Trout

The effect of YCT TL on fecundity was examined for 68 YCT collected from the Clear Creek spawning run in 1984 (Jones et al. 1985) and 40 YCT collected from Arnica Creek runs in 1950 or 1951 (Welsh 1952). (The effect of mass on fecundity was not examined because mass data were not provided by Welsh [1952].) Arnica Creek enters Yellowstone Lake on the north shore of West Thumb (Figure 3.1).

Scale-based Yellowstone Cutthroat Trout Ages

In Yellowstone Lake, whether or not age-1 YCT form a detectable, initial annulus mainly depends upon fish size in spring, when seasonal somatic growth begins and resulting scale annuli are formed. In spring, large age-1 YCT have scales sufficiently large to record a new annulus but small age-1 fish do not (Laakso and Cope 1956). Consequently, small YCT form their initial annulus the next year, as age-2 fish whose scales may have especially numerous circuli through the annulus. Laakso and Cope (1956) examined YCT scales from Yellowstone Lake and concluded that, when more than seven circuli were evident through the first annulus, the fish had been "small" when age 1. Accordingly, its annulus-based age should be increased by one year. That criterion had been consistently applied by the nine known, successive scale analysts (i.e., analysts 1 to 9) who determined the extant YCT ages. The general reliability of those age estimates was assessed by comparing TL at gillnet capture of scale-based age-2 and age-3 YCT to TL of age-2 or age-3 YCT indicated by length frequency (i.e., the Petersen method; e.g., Hilborn and Walters 1992) across years (and, consequently, scale analysts) and in more detail for analyst 8, whose age estimates were most consistent with the length-frequency data.

Statistical Analyses

Correlation analysis (Pearson-type; Neter et al. 1996) was used to examine linear temporal trends in female proportions in annual spawning runs and among prespawner YCT in annual gillnet catches across years. For calculations of proportions of mature and prespawner female and male YCT in gillnet catches, data frequencies were binned within years and consecutive, 20-mm intervals of YCT TL. To reduce variation, minimum sample size for each bin was set at 5 fish. Confidence intervals (CI, 95% in all instances) for proportions (p) were calculated as $\hat{p} \pm 1.96SE$, where $SE = \sqrt{\hat{p}(1-\hat{p})/n}$ (Neter et al. 1996). MATLAB (MathWorks 2005; curve-fitting toolbox) was used to a fit 3-parameter logistic model (Equation 3.2),

$$\hat{p} = a/(1 + b \cdot (\exp(-c \cdot TL))) \ , \quad (3.2)$$

to maturity proportion-TL and prespawner proportion-TL relations. Linear regression (Neter et al. 1996) was used to estimate the slope coefficient for linear relations between proportions for sexes and their maturity stages. Multiple linear regression (Neter et al. 1996) was used to estimate the effect of YCT TL and capture stream (a categorical predictor) on fecundity.

Growth of YCT was examined by fitting (MathWorks 2005; curve-fitting toolbox) TL at capture to scale-based age for individual YCT using Equation 3.3,

$$L_t = L_\infty \cdot [1 - \exp(-(\omega / L_\infty) \cdot t)] \ , \quad (3.3)$$

which is a modification (proposed by Gallucci and Quinn 1979) of the original von Bertalanffy growth model (von Bertalanffy 1938) that has L_t as TL at time (age) t and ω and L_∞ as parameters to be estimated. Unlike the original model, Equation 3.3 has interpretable units (i.e., TL/yr [specifically, annual growth rate near t_0] and asymptotic TL, respectively). Because informative differences in age estimates were evident among the various analysts of YCT scales and the estimates of analyst 8 were most consistent with the length-frequency data, data used in analyses of YCT growth were grouped within three periods: pre-analyst 8, analyst 8, and post-analyst 8.

Results

Length-frequency Distributions

Most measured YCT in spawning runs were 360–419 mm TL (72.6% of YCT; overall TL range, 240–633 mm) and estimated to be 4–6 years old (range, 3–10 yr) on the basis of scale annuli. Gillnetted YCT were 100–565 mm TL and had mean estimated scale-based age of 3.5 years (range, 1–10 years). The combined length-frequency distribution for YCT in spawning runs was unimodal and nearly normal in shape, whereas that for gillnetted YCT was tri-modal (Figure 3.2). The conspicuous size-classes centered around 180 mm TL and 250 mm TL in the distribution for gillnetted YCT predominantly consisted of age-2 and age-3 fish, respectively. (During gillnetting, age-0 YCT had only recently emigrated from their natal streams and were about 35 mm TL, whereas age-1 YCT were 100–120 mm TL. No age-0 YCT and only a few age-1 YCT were gillnetted [Appendix C].) The third size-class of gillnetted YCT consisted of fish > 299 mm TL, i.e., predominantly age 4 and older. The histogram for that size-class was concordant with that for YCT in the spawning run (Figure 3.2).

Female Proportions

Estimated female proportion in spawning runs averaged 0.61 (CI, 0.59, 0.64) and had no linear temporal trend, but showed marked oscillation during the recent decade (Figure 3.3). Annual sample size averaged 2,415 YCT (range, 397–5,575 fish). Estimated

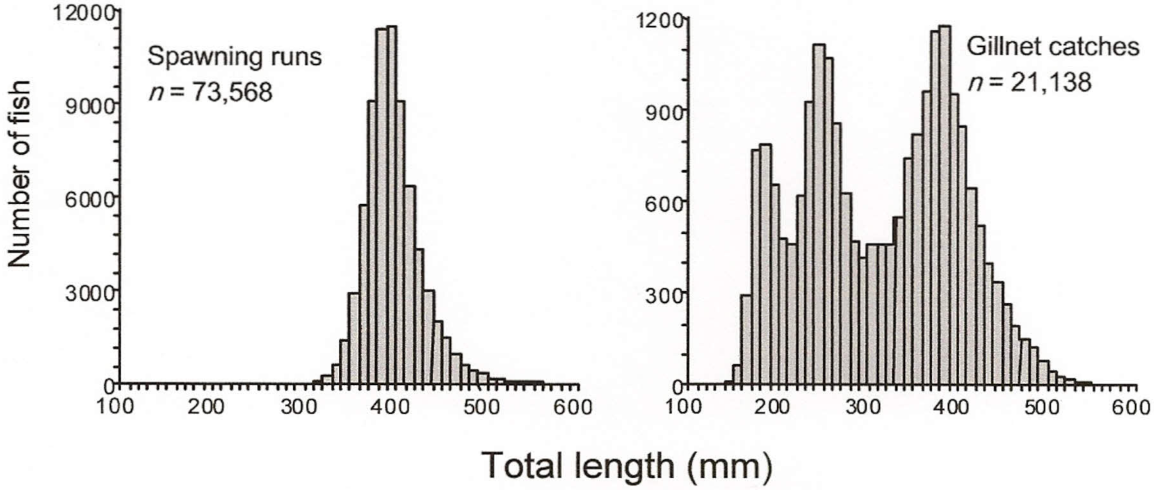

Figure 3.2. Combined length frequency of Yellowstone cutthroat trout in 29 annual spawning runs of Clear Creek, 1977–2007 (nine fish > 599 mm TL [all males] caught during 2005–2007 are not shown), and of Yellowstone cutthroat trout in 36 annual gillnet catches, Yellowstone Lake, 1969–2007.

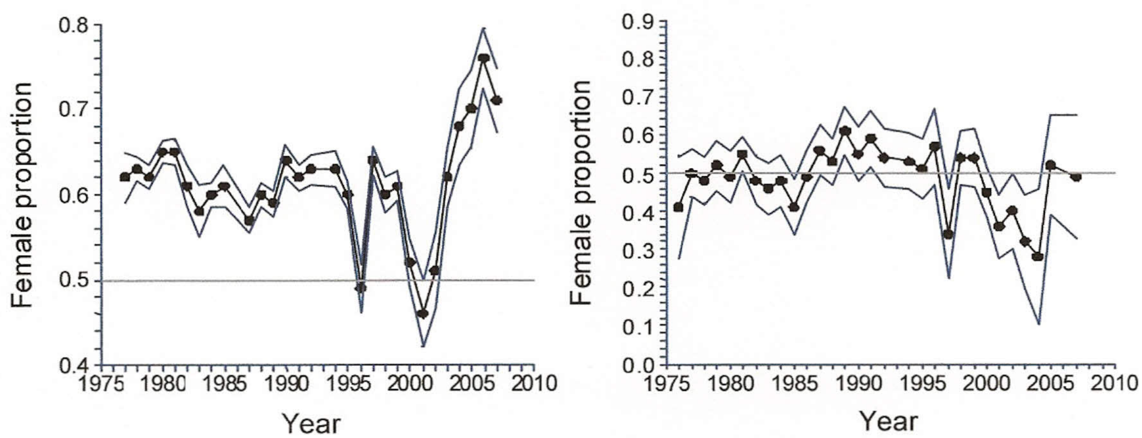

Figure 3.3. Estimated proportion of female Yellowstone cutthroat trout in 29 annual spawning runs of Clear Creek, 1977–2007 (left), and among prespawner Yellowstone cutthroat trout in 35 annual gillnet catches (maturity stage was inadequately determined in 2006), Yellowstone Lake, 1969–2007 (right). Lines above and below data points connect upper or lower 95% confidence intervals for estimates; the horizontal line indicates equal proportions between sexes.

female proportion among prespawner YCT in annual gillnet catches averaged 0.48 (CI, 0.45, 0.51; Figure 3.3). Average sample size was 35 YCT (range, 25–442 fish). There was no linear temporal trend in female proportion among gillnetted prespawner YCT.

Maturity-Total Length and Prespawner-Total Length Relations

Maturity proportion-TL relations for gillnetted female and male YCT were similar and logistic (Figure 3.4; Table 3.1). The onset of maturity occurred when fish reached 200–250 mm TL; about half the fish of both sexes were mature when 330 mm TL; and 90% or more YCT $\geq$ 400 mm TL were mature. Prespawner proportion-TL relations for gillnetted female and male YCT also were similar and logistic (Figure 3.4; Table 3.1); about 70% of YCT $\geq$ 400 mm TL were prespawners.

Linear regression of female maturity proportion on male maturity proportion (i.e., data in Figure 3.4) revealed a strong, positive association (Appendix A; $r^2 = 0.942$; $F_{1, 367} = 5{,}921$; $P < 0.001$); the proportion of mature females was on average larger than that of mature males across TL bins (female slope, 1.043; CI, 1.017, 1.070 [male slope, 1.000]). Similar regression of female prespawner proportion on female maturity proportion indicated a positive association (Appendix A; $r^2 = 0.823$; $F_{1, 399} = 1{,}853$; $P < 0.001$); about 66% of mature females were also prespawners (slope, 0.658; CI, 0.628, 0.688). For male YCT, results of the regression analysis were similar (Appendix A; $r^2 = 0.793$; $F_{1, 434} = 1{,}663$; $P < 0.001$; slope, 0.617 [CI, 0.587, 0.646]).

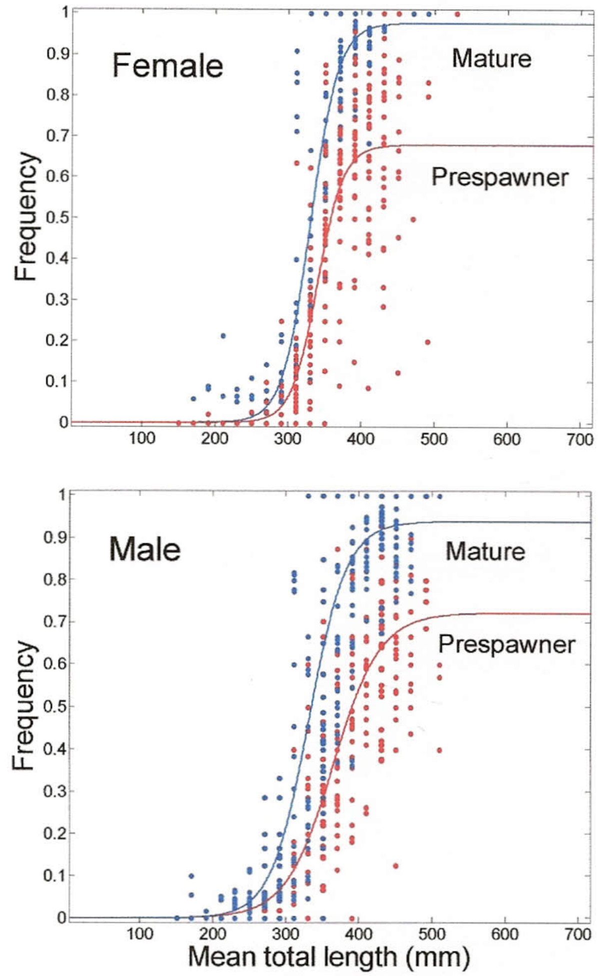

Figure 3.4. Estimated proportions of mature and prespawner female and male Yellowstone cutthroat trout in annual gillnet catches, Yellowstone Lake, 1969–2007, within 20-mm intervals of fish length. Lines represent fits of Equation 3.2 to the data.

Fecundity of Yellowstone Cutthroat Trout

Capture location (i.e., Clear Creek or Arnica Creek) had no significant effect on the otherwise significant relations between YCT fecundity and TL. Nevertheless, for the pooled relation, TL explained only 27% of the variation in fecundity (Table 3.2; Figure 3.5).

Table 3.1. Estimated parameters (and their 95% confidence bounds, in parentheses) for fits of a 3-parameter logistic model (Equation 3.2) to the maturity proportion-TL relations and prespawner proportion-TL relations for gillnetted female (F) and male (M) Yellowstone cutthroat trout. Mean total length (TL) and the standard deviation (SD) of TL were the used normalizing constants.

Sex	Mean TL	SD TL	r^2	Parameter		
				a	***b***	***c***
				Maturity		
F	307.5	86	0.91	0.976 (0.945, 1.006)	3.313 (2.666, 3.959)	4.583 (3.972, 5.195)
M	321.9	94	0.84	0.938 (0.901, 0.976)	1.437 (1.179, 1.696)	3.645 (3.071, 4.22)
				Prespawner		
F	307.5	86	0.83	0.680 (0.648, 0.711)	6.26 (3.881, 8.638)	4.878 (3.913, 5.843)
M	321.9	94	0.81	0.723 (0.676, 0.770)	3.76 (2.991, 4.53)	2.923 (2.429, 3.416)

Scale-based Yellowstone Cutthroat Trout Ages

Three observations suggested that, apart from analyst 8, analysts frequently missed an annulus on scales taken from age-2 and age-3 YCT: (1) mean TL at capture of YCT estimated to be age 2 or age 3 on the basis of scale annuli showed low among-year variation and frequent low values during the period when analyst 8 interpreted scales (i.e., 1986–1995, 2003a; Figure 3.6); (2) when the scales taken from YCT in 2003 were interpreted by analyst 8, his length-at-age results markedly differed from those of analyst 9 for that year and were similar to the 1986–1995 period (Figure 3.6); and (3) approximate ranges in TL of age-2 and age-3 YCT revealed by length frequency (Figure 3.2) were most concordant with the respective ranges in YCT length-at-age determined by analyst 8 (Figure 3.6).

Table 3.2. Estimated parameters (and their 95% confidence bounds, in parentheses) for fits of fecundity to total length for individual Yellowstone cutthroat trout from Clear and Arnica creeks, using the linear model *Fecundity* = ($b \cdot$ TL) + c.

				Parameter	
Location	N	r^2	P	b	c
Clear Creek	68	0.32	< 0.001	4.92 (3.16, 6.68)	-626.4 (-1,282, 29.46)
Arnica Creek	40	0.22	0.002	2.087 (0.8068, 3.368)	344 (-121.5, 809.4)
Both	108	0.27	< 0.001	3.599 (2.4609, 4.7371)	-160.3 (-580.6, 259.9)

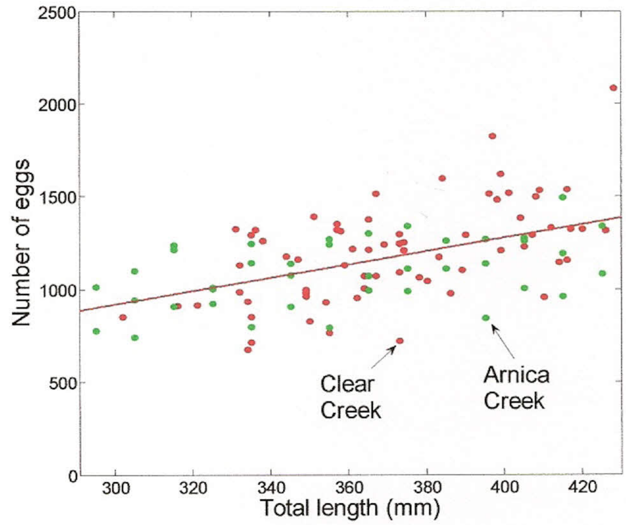

Figure 3.5. Relation between fecundity and total length of 68 Yellowstone cutthroat trout collected from Clear Creek in 1984 and 40 Yellowstone cutthroat trout collected from Arnica Creek in 1950 or 1951, Yellowstone Lake. The line is the best linear fit to the data.

Nevertheless, an additional pattern evident in the age estimates of analyst 8 indicated the criterion of Laakso and Cope (1956) did not provide a definitive means of distinguishing YCT that formed an annulus when age 1 from those that did not. The YCT examined by analyst 8 and whose scales had only two annuli and 4–7 circuli through the first annulus, thus making the fish age 2 according to Laakso and Cope's (1956) criterion,

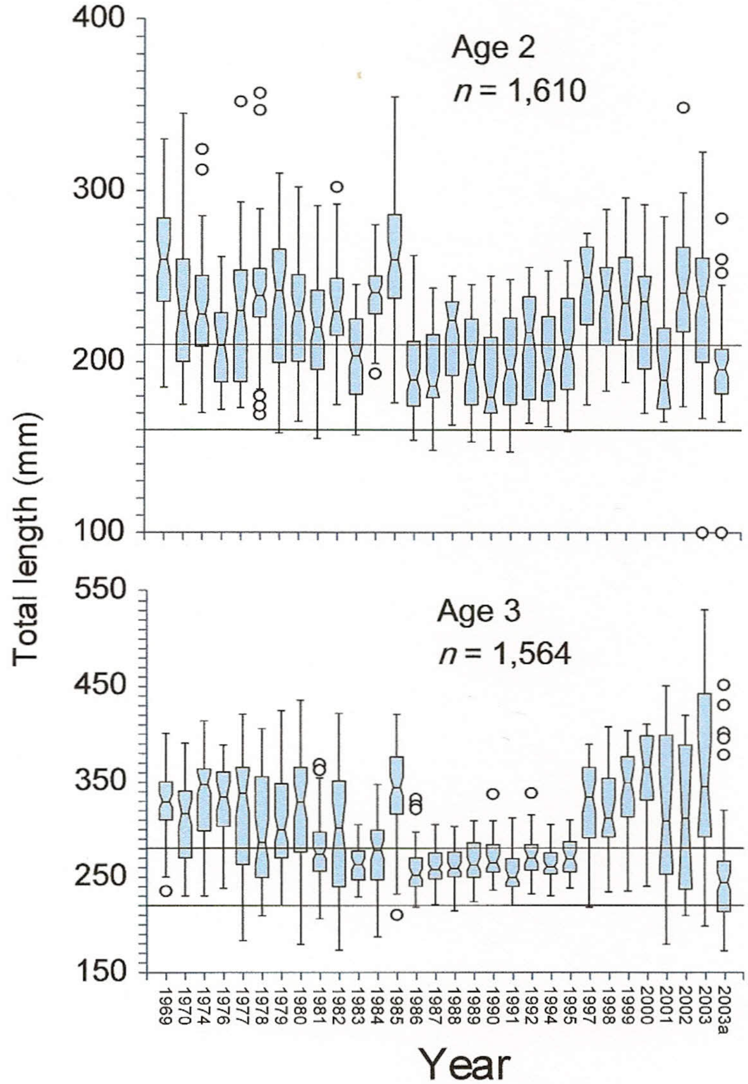

Figure 3.6. Box plots of the TLs of scale-based age-2 and age-3 Yellowstone cutthroat trout in 29 annual gillnet catches from Yellowstone Lake, 1969–2003. Plots indicate the median value (box notch), interquartile range (entire box), and the full range of values (whiskers). Outliers (i.e., values > 1.5 interquartile range from the median) appear as open circles. Paired horizontal lines delimit the approximate range in TL of age-2 or age-3 Yellowstone cutthroat trout indicated by length frequency (Figure 3.2). Data for 2003 are separated into those based on scale interpretations by analyst 9 (2003) and analyst 8 (2003a).

had strongly bimodal length-frequency distributions that straddled those of age-classes 2 and 3 (Figure 3.7). Such bimodal distributions were also evident when annual data were examined.

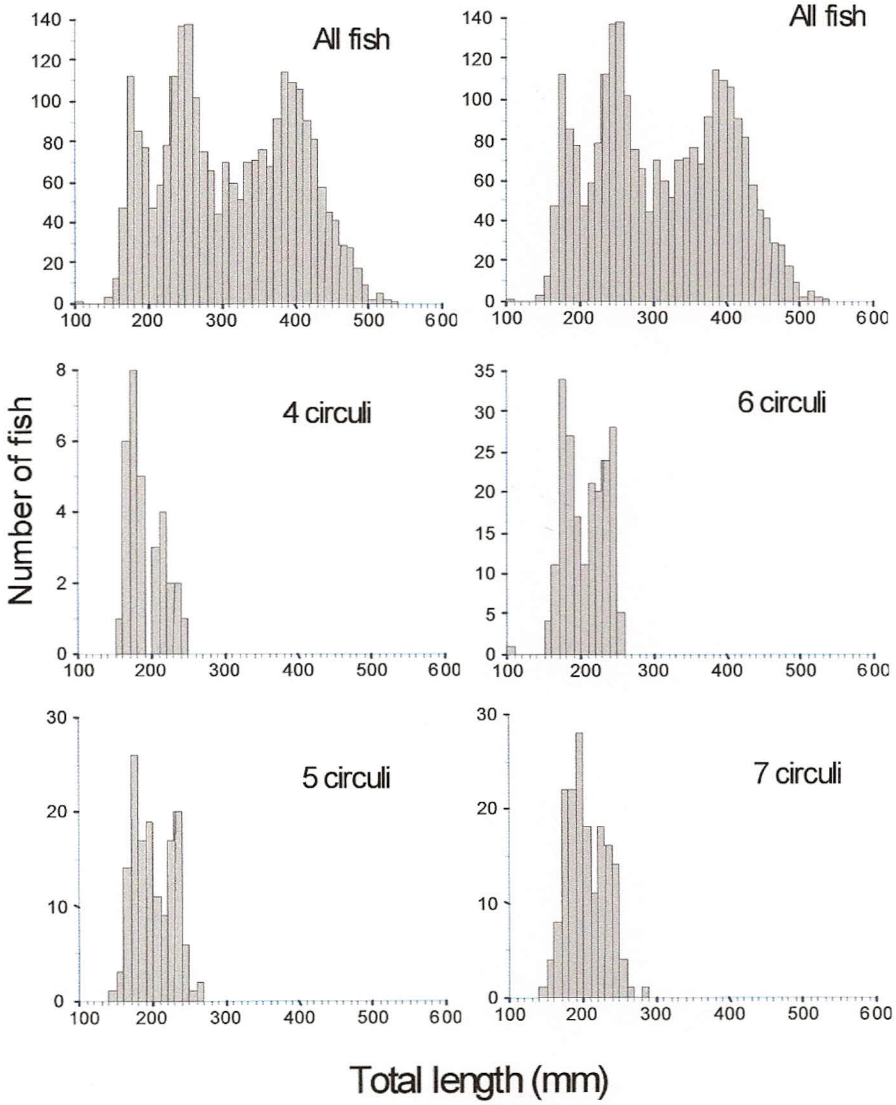

Figure 3.7. Length frequency of all gillnet-caught Yellowstone cutthroat trout whose scales were examined by analyst 8 (duplicate upper figures) and, among those fish, of Yellowstone cutthroat trout whose scales had only two annuli and 4–7 circuli through the first annulus.

Growth of Yellowstone Cutthroat Trout

The fits of YCT TL to age using Equation 3.3 were significant for each of the three periods and differed among periods (Table 3.3; Figure 3.8). Compared to the other periods, the parameter L_∞ was significantly higher and the parameter ω significantly lower for the period when analyst 8 examined scales.

Table 3.3. Estimated parameters (and their 95% confidence bounds, in parentheses) for fits of TL at capture to scales-based age using Equation 3.3. Data used in analyses were grouped within three periods: pre-analyst 8, analyst 8, and post-analyst 8.

Period	N	r^2	Parameter	
			L_∞	ω
Pre-analyst 8	3,264	0.73	466.5 (458.4, 474.6)	168.7 (165.6, 171.9)
Analyst 8	2,487	0.90	600.9 (589.2, 612.6)	120 (118.5, 121.6)
Post analyst 8	1,081	0.81	526.1 (512.4, 539.8)	174.8 (169.6, 179.9)

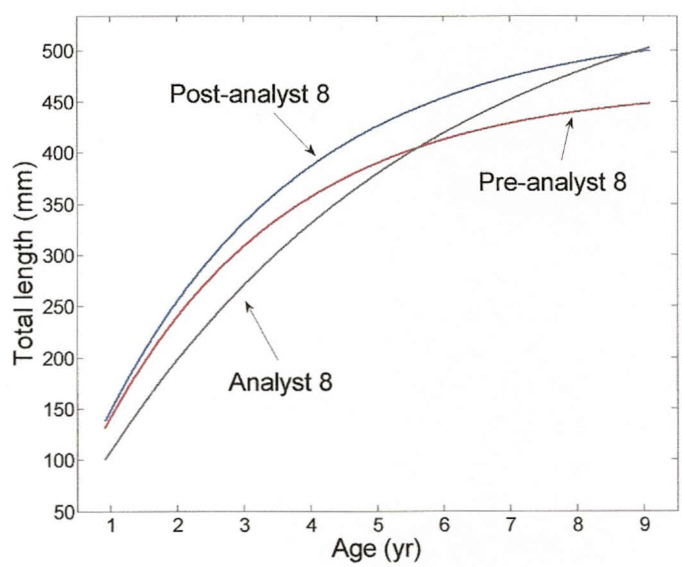

Figure 3.8. Best-fit curves for the relation between total length at capture and scale-based age, using Equation 3.3, for Yellowstone cutthroat trout collected from Yellowstone Lake during three periods relative to the work of analyst 8.

Discussion

Accuracy of the scale-based YCT ages was affected by two evident sources of error, a frequently overlooked scale annulus and an inability to unequivocally identify fish within a single cohort on the basis of scale characteristics. As one would expect, the "knife-edge" nature of Laakso and Cope's (1956) criterion rendered its validity for every YCT improbable. Lentsch and Griffith (1987) reported that missing first-year annuli on scales was common among inland salmonids in the western U.S. and the occurrence of first-year annuli was positively associated with the number of degree-days experienced by the fish during its first year of life. Nevertheless, when the age estimates of analyst 8 were used in analyses, the estimated growth parameters L_∞ and ω were most concordant with empirical observations of age-1 TL and maximum TL of YCT in Yellowstone Lake. Although errors also were evident in analyst 8's age estimates, the data suggested his estimates were most representative of YCT age (and, thus, growth). Temporal differences in fits of YCT TL at capture to scale-based age using the modified von Bertalanffy growth model (Equation 3.3) probably resulted from varying ageing error among scale analysts, rather than differences in YCT growth rate. Had temporal differences in growth occurred among YCT and a population-density effect been important to somatic growth rate, asymptotic TL (i.e., L_∞) should have been largest when population density was lowest, i.e., during the most-recent period. Such differences were not apparent in the scale-based data, however.

Those points notwithstanding, definitive knowledge of maximum YCT age is not essential to delimit the Leslie matrix (whose square dimensions are maximum age in years, in this case) for the planned population model. Maximum YCT longevity of about 10 years, suggested by the extant scale-based estimates, was equal to that similarly estimated for YCT in Idaho streams (Meyer et al. 2003). Thus 10 years is a plausible approximation of maximum YCT age in Yellowstone Lake.

Elements in the first row of the Leslie matrix are age-specific fertilities, i.e., the per-capita, age-specific contribution of young to age 1. Thus fertilities are the products of first-year survival probability, age-specific female proportion, age-specific maturity proportion, and age-specific fecundity. The present study provided important insights into the last three of these demographic characteristics, each of which is discussed below. Furthermore, because Equation 3.3 defined a relation between YCT length and age, it provided an objective link between the Leslie matrix and YCT maturity proportion and fecundity, both of which were conditioned on YCT TL rather than age.

Female proportion showed no linear temporal trend in either the spawning run or among prespawner YCT in the gillnet catch. Predominance of female YCT in the spawning run but not the gillnet catch suggested some male prespawners do not participate in spawning in Clear Creek. Moreover, the female proportion of Clear Creek runs (mean, 0.61) may be historically stable. Ball and Cope (1961) reported average female proportion in annual Clear Creek spawning runs between 1945 and 1953 was 0.58. During that period, average female proportion in annual spawning runs in five additional Yellowstone Lake tributaries ranged from 0.56 to 0.61 (Gresswell et al. 1994). In any case, the results indicated female proportion in the spawning run may be treated as a random variable (with its estimated mean and associated measure of uncertainty) in the product series that constitutes the fertilities in the planned Leslie matrix.

The maturity proportion-TL relation and prespawner proportion-TL relation for gillnetted YCT were logistic. However, only about 70% of YCT $\geq$ 400 mm TL were prespawners (i.e., would have spawned the next spring). Used in conjunction with the somatic-growth model (Equation 3.3), the prespawner-TL relation (and its associated measures of uncertainty) for female YCT could be used to assign a prespawner proportion to each age-class in the fertility product series.

The statistically weak fecundity-TL relation for YCT was not unexpected. Fecundity – like its covariate, somatic weight – is highly variable among individual adult fish of any particular TL, even within a single cohort. For YCT, the amount of variation in fecundity explained by TL (27%) was similar to that reported by Rounsefell (1957) for sockeye *O. nerka* (31–32%) and pink salmon *O. gorbuscha* (12–16%). Thus the third component of the fertility product series is the YCT fecundity-TL relation and its associated measures of uncertainty, similarly used in conjunction with the somatic-growth model. In sum, the results of this study have provided important insights into the fertilities and dimensions of the planned Leslie matrix.

CHAPTER FOUR

TEMPORAL ASSOCIATIONS IN TOTAL LENGTH AND OTHER METRICS BETWEEN CUTTHROAT TROUT IN THE SPAWNING RUN AND GILLNET CATCH, AND EVIDENCE OF A LAKE-WIDE POPULATION SHIFT

Introduction

The extent to which the characteristics of YCT in the Clear Creek spawning run were like those of YCT in any particular area of the lake or the lake as a whole was unknown. Such associations needed to be better understood because the nonnative lake trout appeared especially numerous in the west-central lake area, where actions to remove lake trout have been almost entirely targeted (Koel et al. 2005). If the Clear Creek population primarily inhabited that lake area, the population may have been especially affected by lake trout predation. Alternatively, if the population primarily inhabited a lake area where lake trout ostensibly were few, such predation may have had little effect on the dynamics of the YCT population.

Objectives of the present chapter were to examine the time-series data for YCT caught in the Clear Creek trap or gill nets between 1977 and 2007 (when data collection was most comprehensive; Chapter Three) and identify (1) associations between population metrics within and between capture methods, as well as temporal trends in metrics, and (2) evidence of informative, temporal shifts in the mean TL of three distinct YCT size-classes and the factors that may have caused the shifts. An effect of lake trout predation on YCT TL was anticipated, on the basis of preliminary evidence described below. Attaining the first objective will reveal the extent to which the YCT in the Clear Creek spawning run were like those of YCT in any particular area of the lake or the lake as a whole, whereas attaining the second objective will reveal the factors that should be included in the model (Chapter Five).

Methods

Associations Between Metrics of Cutthroat Trout in the Spawning Run and Gillnet Catch

Statistical associations between $\log_e$ run size, female proportion, mean TL, and standard deviation (SD) in TL of YCT in the annual Clear Creek spawning run, as well as between $\log_e$ mean catch per gill net and similar metrics for prespawner YCT (i.e., YCT whose developing gonads indicated the fish would have spawned the next year) in annual gillnet catches, were examined using correlation analysis (Pearson-type; Neter et al. 1996). Associations between metrics of YCT in the run and those of prespawner YCT gillnetted the preceding fall were similarly examined.

For analyses within capture methods, gillnet data were examined on a lake-wide basis. For analyses between methods, data for the 11 gillnet sampling sites were partitioned among 3 lake areas (Figure 4.1): Area 1 consisted of sampling sites in the north-northeast lake area and at which only one lake trout had been caught (at site 2A) during the routine fall gillnetting of the present study; Area 2 consisted of sites in the west-central lake area where, since 1997, lake trout were often caught in those gill nets (among the 100 lake trout caught in the nets between 1997 and 2007, all but one were caught at sites 3A–4B) and the ongoing capture-and-removal program mainly targets lake

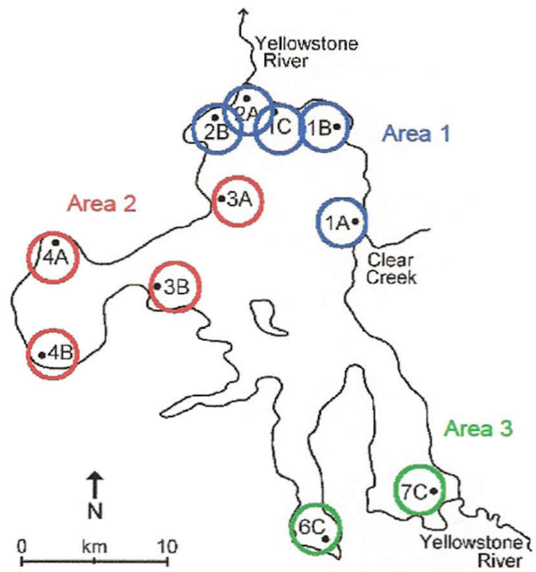

Figure 4.1. Map of Yellowstone Lake, Yellowstone National Park, showing Clear Creek, the 11 gillnet sampling sites (●), their codes, and the three lake areas among which the sites were partitioned for data analyses.

trout (Koel et al. 2005); and, Area 3 consisted of the two, southern sampling sites, which were greatly removed from the other sites. Results of these and the preceding analyses revealed the extent to which the metrics of YCT in the Clear Creek spawning run were like those of YCT in any particular area of the lake or the lake as a whole.

Evidence of Temporal Shifts in Cutthroat Trout Total Length

Near the end of the last century, YCT > 500 mm TL began to appear in the Clear Creek spawning run and annual gillnet catch; such large YCT had not been previously captured by these methods (Appendix B and C). Consequently, statistical change points in the data times series for YCT TL were hypothesized. To examine that possibility, piecewise-polynomial (linear herein) regression models (Seber and Wild 1989) were fitted to temporal-trend data for YCT mean TL to identify change points, which may have appeared as corners in the data trend. The algorithm (Hintze 2001) estimated starting parameter values from the data, used an optimization routine to refine parameter estimates, and estimated change points (and their 95% confidence intervals) in the trend. For these analyses, gillnetted YCT (both sexes combined) were separated into the three size-classes that were prominent in the length-frequency distributions (Figure 3.2), i.e., 100–199 mm TL, 200–299 mm TL, and > 299 mm TL, and primarily consisted of age-2, age-3, and > age-3 YCT, respectively (Chapter Three).

Results

Associations Between Metrics of Cutthroat Trout in the Spawning Run and Gillnet Catch

Within capture methods, mean TL of YCT in spawning runs showed a significant ($P < 0.01$) negative association with run size, which showed a decreasing temporal trend (Table 4.1). Standard deviation in TL of run YCT was positively associated with mean TL. Similarly, mean TL of gillnetted prespawner YCT was negatively associated with mean number of prespawner YCT caught per gill, which also showed a decreasing temporal trend. Female proportion was negatively associated with mean TL; associations involving SD TL were not significant.

Between capture methods, lake-wide, $\log_e$ mean number of prespawner YCT caught per gill net was positively associated with $\log_e$ run size the following year ($r = 0.866$; $P < 0.001$; $n = 25$). On the basis of lake area, significant ($P < 0.01$) associations occurred between 7 of the 9 possible paired combinations of data for YCT in the spawning run and gillnet catch from Area 2 (Table 4.2), whereas 4 of 9 possible

Table 4.1. Correlation coefficients, *P*-values, and samples sizes (number of years) for associations between metrics of Yellowstone cutthroat trout in annual spawning runs in Clear Creek or between the metrics of prespawner Yellowstone cutthroat trout in annual gillnet catches, 1977–2007. CPUE = mean catch per gillnet night. Significant ($P < 0.01$) associations appear in boldface.

Clear Creek spawning run					Prespawner gillnet catch				
Variable	$\log_e$ run size	Female proportion	Mean TL	SD TL	**Variable**	$\log_e$ CPUE	Female proportion	Mean TL	SD TL
Calendar year	**-0.867**	0.088	**0.758**	**0.570**	Calendar year	**-0.792**	-0.352	**0.827**	0.165
	<0.001	0.651	**<0.001**	**0.001**		**<0.001**	0.061	**<0.001**	0.394
	28	29	**29**	**29**		**29**	29	**29**	29
$\log_e$ run size		-0.423	**-0.943**	**-0.729**	$\log_e$ CPUE		**0.586**	**-0.859**	-0.194
		0.025	**<0.001**	**<0.001**			**<0.001**	**<0.001**	0.313
		28	**28**	**28**			**29**	**29**	29
Female proportion			0.430	0.429	Female proportion			**-0.516**	0.285
			0.020	0.020				**0.004**	0.134
			29	29				**29**	29
Mean TL				**0.714**	Mean TL				0.177
				<0.001					0.358
				29					29

Table 4.2. Correlation coefficients, *P*-values, and samples sizes (number of years) for associations among metrics of Yellowstone cutthroat trout in annual spawning runs in Clear Creek, 1977–2007, and prespawner YCT caught in gill nets set in three Yellowstone Lake areas the preceding September. CPUE = mean catch per gillnet night. Significant ($P < 0.01$) associations appear in boldface.

		Lake area, prespawner variable								
		1			**2**			**3**		
Location	**Variable**	$\log_e$ CPUE	Mean TL	SD TL	$\log_e$ CPUE	Mean TL	SD TL	$\log_e$ CPUE	Mean TL	SD TL
Clear Creek run	$\log_e$ run size	**0.703** **< 0.001** **26**	**-0.924** **< 0.001** **26**	-0.251 0.216 26	**0.895** **< 0.001** **26**	**-0.953** **< 0.001** **26**	**0.521** **0.006** **26**	**0.779** **< 0.001** **25**	**-0.877** **< 0.001** **25**	-0.157 0.454 25
	Mean TL	**-0.581** **0.001** **27**	**0.929** **< 0.001** **27**	0.241 0.226 27	**-0.836** **< 0.001** **27**	**0.946** **< 0.001** **27**	**-0.538** **0.004** **27**	**-0.734** **< 0.001** **26**	**0.862** **< 0.001** **26**	0.129 0.529 26
	SD TL	-0.307 0.119 27	0.490 0.010 27	0.407 0.035 27	-0.489 0.010 27	**0.528** **0.005** **27**	-0.086 0.671 27	-0.415 0.035 26	0.480 0.013 26	0.383 0.054 26
Lake Area 1	$\log_e$ CPUE		**-0.631** **< 0.001** **29**	0.027 0.890 29	**0.778** **< 0.001** **29**	**-0.720** **< 0.001** **29**	0.210 0.274 29	**0.791** **< 0.001** **28**	**-0.588** **0.001** **28**	-0.075 0.704 28
	Mean TL			0.106 0.583 29	**-0.872** **< 0.001** **29**	**0.965** **< 0.001** **29**	**-0.501** **0.006** **29**	**-0.788** **< 0.001** **28**	**0.963** **< 0.001** **28**	-0.021 0.914 28
	SD TL				-0.045 0.819 29	0.095 0.622 29	0.067 0.730 29	0.141 0.474 28	0.159 0.419 28	0.185 0.345 28
Lake Area 2	$\log_e$ CPUE					**-0.92** **< 0.001** **29**	0.468 0.010 29	**0.762** **< 0.001** **28**	**-0.830** **< 0.001** **28**	-0.153 0.438 28
	Mean TL						**-0.551** **0.002** **29**	**-0.838** **< 0.001** **28**	**0.906** **< 0.001** **28**	0.056 0.776 28
	SD TL							0.384 0.044 28	-0.417 0.027 28	0.199 0.31 28
Lake Area 3	$\log_e$ CPUE								**-0.751** **< 0.001** **28**	-0.005 0.978 28
	Mean TL									-0.025 0.898 28

paired combinations were significant for both Areas 1 and 3. Absolute values of the significant correlation coefficients (r) were consistently greater in Area 2 than were those values for corresponding variables in the other areas. The statistical associations did not suggest greatest similarity between YCT in any two lake areas.

Evidence of Temporal Shifts in Cutthroat Trout Total Length

Temporal trends in mean TL of YCT in the spawning run and three size-classes of gillnetted YCT each showed a change point in their respective data time series, although confidence intervals for change points were broad and the fit was statistically weakest for gillnetted YCT 200–299 mm TL (Figure 4.2). Estimated changes points occurred in the 1990s, except that for gillnetted YCT 200–299 mm TL was near 1985. Shape of fitted curves was upward concave, except that for gillnetted YCT 200–299 mm TL was downward concave. Equations for the fitted piecewise-polynomial regression models appear in Appendix A.

Discussion

Temporal increases in mean TL of YCT in the spawning run and of prespawners in the gillnet catch and concurrent declines in run size and prespawner catch were suggestive of an effect of YCT population density on the somatic growth of the fish. Similarly, a concurrent increase in mean TL of YCT 100–199 mm long was indicated by the piecewise-polynomial regression results, which also suggested statistical change points in the temporal trends for each of those variables. However, importantly contrasting those similar trends was that for mean TL of gillnetted YCT 200–299 mm

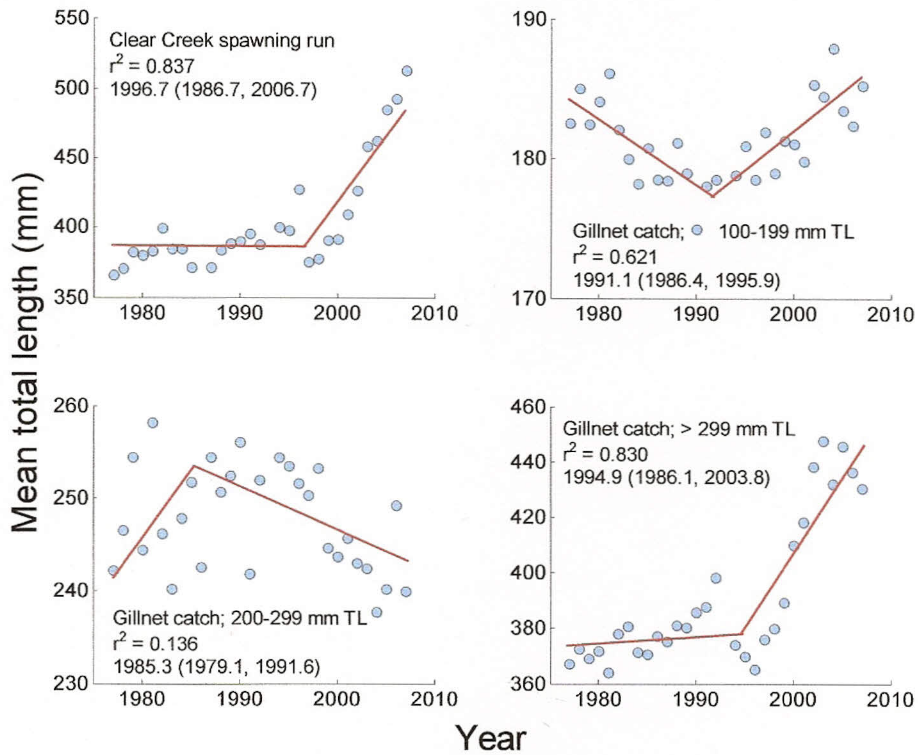

Figure 4.2. Temporal trends in mean TL of Yellowstone cutthroat trout in 29 annual spawning runs of Clear Creek, and in Yellowstone cutthroat trout 100–199 mm TL, 200–299 mm TL, and > 299 mm TL in 30 annual gillnet catches from Yellowstone Lake, 1977–2007. Lines indicate the best fit of a linear-linear piecewise-polynomial regression model to the data. Change points (year) in trends and their 95% confidence intervals are indicated.

long, which generally declined during the past two decades.

Collectively, these concurrent trends in mean YCT TL suggested that lake trout predation had reduced YCT population density which, in turn, resulted in increased somatic growth of YCT. Among the 158,302 lake trout measured and removed (total removed, 268,479 lake trout) from Yellowstone Lake between 1994 (when the fish were discovered) and 2007 as part of the ongoing control program, the longest was 962 mm TL (Patricia Bigelow, NPS, unpublished data). The inter-quartile range for measured lake trout was 288–416 mm TL. Ruzycki et al. (2003) found that 90% of YCT eaten by lake trout in Yellowstone Lake had TL that was 20–45% that of their predator; smallest piscivorous lake trout were 320 mm TL; the smallest YCT found in a lake trout stomach was 65 mm TL. Thus age-0 YCT, which were about 35 mm TL when they emigrated from Clear Creek in July and August, were not important prey for lake trout in Yellowstone Lake. Instead, most YCT susceptible to lake trout predation were age-1 and older, except YCT > 500 mm TL were effectively invulnerable to predation. Therefore, YCT 200–299 mm TL were particularly susceptible to the size-selective predation of lake trout in an ostensibly growing population, which reduced mean TL of the YCT size-class. Collectively, these trends provided evidence of a YCT population shift that resulted from lake trout predation. Whether that population shift was indicative of a broader “regime” shift, i.e., a reorganization of the Yellowstone Lake ecosystem from one relatively stable state to another (e.g., Steele 1996; Folke et al. 2004), is unknown.

Comparisons of YCT metrics between capture methods indicated YCT in the Clear Creek spawning run could not be unequivocally assigned to any of the three lake areas. Moreover, although YCT in Area 3 were ostensibly removed from most lake trout predation, the trends in metrics of these YCT were like those of YCT in Areas 1 and 2. This suggested either the effects of lake trout predation on YCT were more widespread across Yellowstone Lake than otherwise suspected or lake-wide factors apart from lake trout predation were acting on YCT populations across the three lake areas. The possibility that factors apart from lake trout affected the dynamics of the lacustrine-adfluvial YCT population of Clear Creek during the three recent decades will be further examined in Chapter Five.

CHAPTER FIVE

A DYNAMIC, AGE-STRUCTURED MODEL OF THE LACUSTRINE-ADFLUVIAL YELLOWSTONE CUTTHROAT TROUT POPULATION OF CLEAR CREEK

Introduction

Size and other attributes of the annual YCT spawning run of Clear Creek have been periodically estimated for several decades. Descriptions of routine operation of the Clear Creek fish trap, data taken from captured YCT, and demographic characteristics of these fish (as well as of YCT caught in gill nets routinely set in the lake itself) were detailed in Chapter Three. In Chapter Two, total-annual Lake Village DDs was found to be statistically associated with Clear Creek discharge and temperature during the YCT spawning season. In Chapter Four, trends in mean TL of YCT in three size-classes suggested lake trout predation has reduced YCT population density and, in turn, YCT somatic growth has increased. Also, comparisons of YCT characteristics between capture methods (i.e., fish trap or gill nets) suggested that either the effects of lake trout predation on YCT were more widespread across Yellowstone Lake than otherwise suspected or lake-wide factors apart from lake trout predation were acting on YCT populations across lake areas.

Objectives of the present chapter were to (1) develop a dynamic, age-structured model of the lacustrine-adfluvial YCT population of Clear Creek; (2) separately estimate the parameters for the full model, as well as for each of its two main components (described below), and compare the various observed and predicted trajectories for run size and mean TL of YCT in the run between 1977 and 2007; and (3) draw conclusions about the factors that may have importantly affected the dynamics of that YCT population during that period. Improved understanding of the historic dynamics of this key lacustrine-adfluvial YCT population will be important to the management of YCT in Yellowstone Lake, as well as to assessment of the efficacy of the ongoing lake trout control program.

Three potential factors were examined (below) and dismissed from further consideration in model development because the evidence indicated they did not importantly affect the dynamics of the lacustrine-adfluvial YCT population of Clear Creek during the study period.

Angler Harvest

Excessive angler harvest – the principal concern of former managers of YCT in Yellowstone Lake – was deemed responsible for the decline in the lake's YCT population evident near mid-twentieth century (Benson and Bulkley 1963). Subsequent, greatly restrictive angling regulations – particularly those implemented in the 1960s – led to the population recovery evident in Clear Creek run size through the 1970s (Gresswell and Varley 1988; Figure 1.1). Through 1953, however, the run also was subjected to routine, intensive, hatchery-based spawn-taking (Chapter Three). Consequently, recovery of the Clear Creek spawning run to its measured high in the late 1970s also may have been attributed, to an unknown degree, to the cessation of spawn-taking.

That point notwithstanding, whether angler harvest or hatchery-based spawn-taking (or both) had major effects on the lacustrine-adfluvial YCT population of Clear

Creek was immaterial to model development because both factors were no longer operating considerably before the data examined in the present study were collected. Spawn-taking activities had ceased in 1953. In addition, estimates of total-annual angler harvest of YCT from Yellowstone Lake – taken from creel surveys (data for 1950–1976) or the Volunteer Angler Report system (1977–2007) – showed increasing YCT harvests during the 1950s, a sharp decline in harvests beginning with increasingly restrictive angling regulations in the mid-1960s, and no reported YCT harvests in 2006 or 2007 (Figure 5.1). Because the decline in the Clear Creek run during the past three decades occurred when the lake-wide angler harvest of YCT had already been reduced by more than 70% from its highest levels and was further declining, angler harvest was dismissed as a factor that importantly affected the Clear Creek population during 1977–2007.

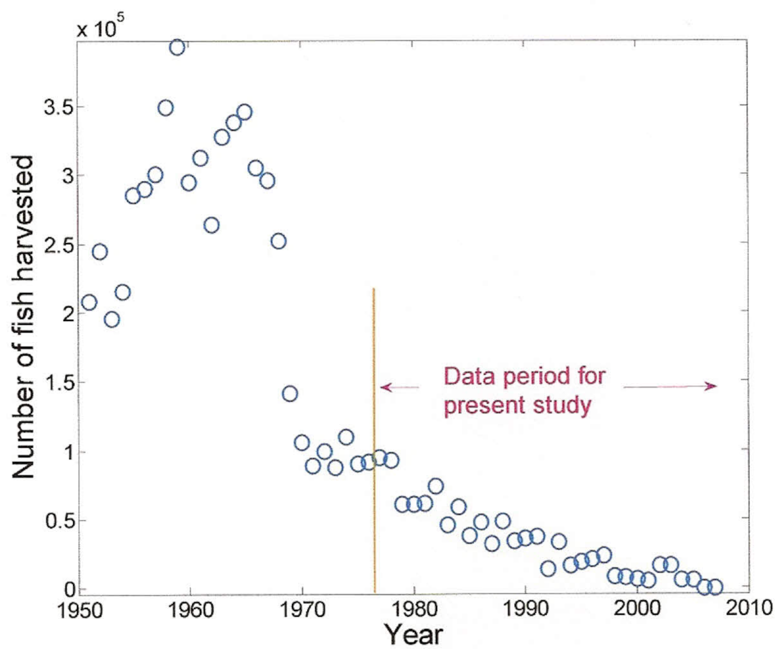

Figure 5.1. Estimated total-annual harvest of Yellowstone cutthroat trout by anglers, Yellowstone Lake, for the 58 years between 1950 and 2007. Also delimited is the period during which data used in the present chapter were collected.

Population Density

Density-dependent effects on survival rates of fishes (and other higher organisms) have been difficult to plainly establish (e.g., Shepherd and Cushing 1990; Murdoch 1994; Turchin 1999; White 2008). The Clear Creek spawning run began its mainly declining trend in the late 1970s, more than a decade before lake trout were discovered in the lake and two decades before whirling disease was found there (Figure 1.1; Chapter Three). Had density-dependent factors led to increased YCT survival during the 1980s, those effects were not evident in these data because run size continued to decline. Thus possible density-dependent effects on the survival of YCT were dismissed as factors important to model development.

Whirling Disease

Whirling disease was found in Yellowstone Lake in 1998 (Koel et al. 2006). Murcia (2007) recently used data for environmental characteristics, intermediate-host occurrence, and fish-host infection from Clear Creek and two other tributaries of Yellowstone Lake to develop a qualitative, risk-ranking system for parasite establishment and whirling disease in YCT. She tested more than 100 wild YCT fry collected from various Clear Creek locations during summer 2002 and 2003; none tested positive for the whirling disease parasite. In a preceding study of hatchery-produced YCT fry held in cages in Clear Creek in 2000, only one fry tested positive for the parasite (Koel et al. 2006). Murcia (2007) concluded that Clear Creek was characterized by water temperatures, velocities, conductivity, and nutrient concentrations that were each low, as well as having little to no organic content in the sediment, characteristics which collectively made YCT in Clear Creek at low risk of whirling disease infection. Thus whirling disease was dismissed as a factor that importantly affected the dynamics of the lacustrine-adfluvial YCT population of Clear Creek and from further consideration in model development.

Methods

Empirical Data

Principal empirical data were those taken from YCT caught in the trap during spawning runs between 1977 and 2007. This period was chosen because, as described in chapters Three and Four, the encompassed data were the most definitive for YCT and they provided insights (supported by data taken from YCT routinely caught in gill nets during the period) important to structuring the model (described below).

Model Structure

The model had two components: a model of somatic growth of individual fish and a population model. Somatic growth of fish was according to Equation 5.1,

$$L_t = L_\infty \cdot [1 - \exp(-(\omega / L_\infty) \cdot t)] \ , \qquad (5.1)$$

a modification (proposed by Gallucci and Quinn 1979) of the original von Bertalanffy growth model (von Bertalanffy 1938), described in Chapter Three.

The population model (Equation 5.2),

$$\mathbf{n}(t+1) = \mathbf{A}_n(t) \times \mathbf{n}(t) \ , \qquad (5.2)$$

was of the time-variant, nonlinear, Leslie form (Caswell 2001) and consisted of the rate matrix $\mathbf{A}_n(t)$ and state column vector $\mathbf{n}(t)$. For time-variant, nonlinear models, one or more elements in matrix $\mathbf{A}_n(t)$ are functions either of environmental variation, the population-state vector $\mathbf{n}$ (thus the n subscript of $\mathbf{A}$), or both. The model was "dynamic" in that it accounted for potential effects of population characteristics or environmental factors on $\mathbf{A}$ and "age-structured" because it embodied the age structure (and its associated demographic characteristics) of the YCT population. The lacustrine-adfluvial YCT population of Clear Creek represented an "ideal" birth-pulse population (Caswell 2001) for simulation using Leslie matrices because spawning (and subsequent embryo incubation) was limited to a short time period and, therefore, the fish effectively reproduced on their birthday.

Matrix multiplication of $\mathbf{A}_n(t)$ and $\mathbf{n}(t)$ (i.e., Equation 5.2) projected $\mathbf{n}(t)$ forward one time step, yielding the state vector (i.e., $\mathbf{n}(t + 1)$) at time $t + 1$. All population projections and accompanying analyses (described below) were carried out with programs written in MATLAB (MathWorks 2005) by the author, unless otherwise indicated.

Elements in the first row of the $m \times m$ rate matrix $\mathbf{A}_n(t)$ (where m is maximum age, in years) were age-specific fertilities (F_x; the per-capita, age-x contribution of young to age 1), whereas elements in the immediate sub-diagonal were age-specific survival probabilities (s_x; the proportion of age x individuals that survive to age x + 1). Remaining matrix $\mathbf{A}_n(t)$ elements were zero. The matrix' dimensions were 10 × 10, i.e., the approximate maximum age (10 yr) for YCT in Yellowstone Lake (Chapter Three). Thus matrix $\mathbf{A}_n(t)$ for the lacustrine-adfluvial YCT population of Clear Creek, whose maturity onset occurred about age 3 (Chapter Three), was:

$$\begin{bmatrix} 0 & 0 & F_{1,3}(t) & F_{1,4}(t) & F_{1,5}(t) & F_{1,6}(t) & F_{1,7}(t) & F_{1,8}(t) & F_{1,9}(t) & F_{1,10}(t) \\ s_{2,1}(t) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{3,2}(t) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{4,3}(t) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{5,4}(t) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{6,5}(t) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{7,6}(t) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_{8,7}(t) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{9,8}(t) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{10,9}(t) & 0 \end{bmatrix}$$

Because Equation 5.1 defined a relation between YCT TL and age, it provided an objective link between the population model and YCT fecundity (Chapter Three), which was conditioned on YCT TL (rather than age).

The fertilities and survival probabilities of a Leslie matrix cannot all be constants because the population would either grow exponentially without limit or crash to extinction. Instead, the population is regulated by variation in the fertilities and survival probabilities of its member organisms. Such variation results from environmental effects on those variables, and demographic stochasticity. Clearly, the trend in the lacustrine-adfluvial YCT population of Clear Creek (Figure 1.1) indicated population regulation, although the factors effecting that regulation were unknown.

Constant Model Parameters

A simple model (i.e., one with few, ostensibly key parameters to be estimated) was sought because such models afford better understanding of the factors that importantly affect the dynamics of the population. Accordingly, the model utilized as constants several parameters for which the empirical data suggested a plausible parameter value. Those parameters (Table 5.1) included the female proportion of the run and the fecundity-TL relation (i.e., the relation's intercept and slope; Clear Creek and Arnica Creek YCT data combined), both of which were detailed in Chapter Three.

Table 5.1. Parameters treated as constants in the model of the lacustrine-adfluvial YCT population of Clear Creek.

Description	**Value**
Female proportion of run	0.612
Intercept of fecundity-TL relation	-160.33
Slope of fecundity-TL relation	3.6
A in Equation 5.3	510.1
B in Equation 5.3	0.1604
C in Equation 5.3	0.000429
Intercept for linear fit to ascending limb of length-frequency histogram for run	-4.346
Slope for linear fit to ascending limb of length-frequency histogram for run	0.0138
Survival probability, age 6	0.5092
Survival probability, age 7	0.4415
Survival probability, age 8	0.1918
Survival probability, age 9	0.0100

Analyses described in Chapter Three suggested that population density affected YCT somatic growth. To estimate the broad nature of that potential relation, mean TL of YCT in the annual Clear Creek spawning run was plotted against run size the preceding year. (In Chapter Four, run size was shown to be a plausible index of population density.) Results revealed a strongly negative, nonlinear relation (Figure 5.2) that was closely fit ($r^2 = 0.93$; $P < 0.01$) by a ratio of first-order polynomials model (Equation 5.3),

$$\overline{TL} = (A + Bx) / (1 + Cx), \tag{5.3}$$

that had A, B, and C as its parameters (Table 5.1) and x as run size the preceding year. Use of the relation in the model is described below.

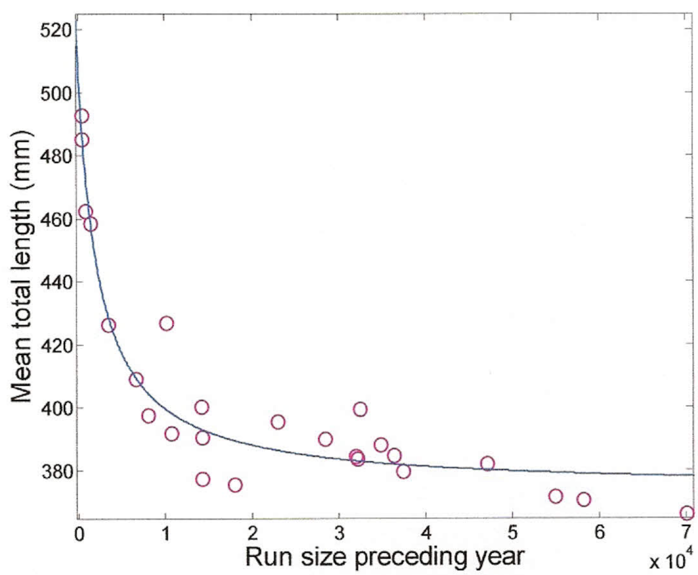

Figure 5.2. Relation between mean total length of Yellowstone cutthroat trout in the annual Clear Creek spawning run and run size the preceding year, 1977–2007. The line is the best fit of Equation 5.3 to the data.

Not all YCT in the lacustrine-adfluvial population of Clear Creek participated in the annual spawning run – immature YCT remained in the lake. A relation was needed to distinguish run fish from the remainder of the simulated population. That relation was based on linear fits to the ascending limb for each annual, scaled (i.e., proportioned to have its maximum at unity) length-frequency distribution for YCT in the run, for data pooled within each of four separate periods arbitrarily based on decades. The fits showed that slope for the relation was similar during the two earliest periods but greatly reduced during the most-recent period (Figure 5.3). Because a possible effect of lake trout predation on mean TL of YCT in the Clear Creek spawning run may have begun in the late 1980s (Chapter Four), the pooled linear relation (Table 5.1) for the ascending limb of

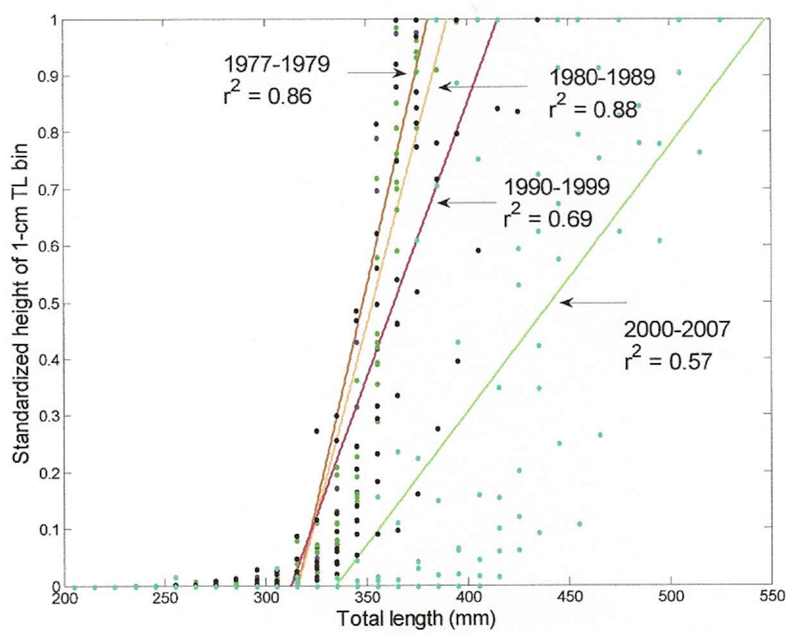

Figure 5.3. Relation between the scaled height of the ascending limb of the length-frequency distributions (1-cm bins) for Yellowstone cutthroat trout caught in the Clear Creek trap and the mean TL of fish in the bin during four separate periods. Years encompassed by periods are indicated. Lines are simple linear regression fits of the data (TL > 300 mm TL) for each period.

the run's length-frequency histograms for 1977–1989 was used to distinguish run fish from the remainder of the population. This was accomplished by multiplying each age-specific TL for the population (i.e., Equation 5.1) at that time step by the TL-specific probability obtained from the linear relation.

Elements in the immediate sub-diagonal of the Leslie matrix are the age-specific survival probabilities. Survival probabilities for age 6–9 YCT were estimated by applying an age-length key (Hilborn and Walters 1992) to the average of the normalized (scaled to sum to unity) length-frequency distributions for YCT in spawning run between 1977 and 1989. That period was chosen because the encompassed annual length-frequency distributions were similar in shape (Appendix B) and, as described above, ostensibly representative of the population before a possible effect of lake trout predation became apparent. Also important and discussed in Chapter Three, the descending limbs of the length-frequency distributions for YCT in spawning runs and concurrent gillnet catches were concordant. Thus the descending limbs of the length-frequency distributions for run fish were indicative of size frequency of the YCT population within the encompassed TL range.

To create the age-length key, a normal (Gaussian) model was fit (MathWorks 2005; curve-fitting toolbox) to the scaled (i.e., scaled such that its maximum was unity) length-frequency distribution for each scale-based age-class in the samples taken from the spawning run (Chapter Three). The age estimates (entirely those of analyst 8) were pooled within age-classes among years because they were too few for annual analyses and showed no important differences among years; also, YCT estimated as age 9 or older were pooled into the 9+ age-class because they totaled only 10 fish (Table 5.2). The probability that YCT within each consecutive, 1-cm bin of the run's length-frequency distribution were of a particular age was estimated by dividing the probability for the age by the sum of all probabilities across all ages for the bin; collectively, these probability proportions constituted the age-length key.

Table 5.2. Parameter estimates (mm) and their 95% confidence intervals for Gaussian fits to the scaled, age-specific length-frequency distributions for age-4–9+ Yellowstone cutthroat trout in the Clear Creek spawning run, Yellowstone Lake, 1987–1994. Age estimates were those of analyst 8.

Age-class	R^2	μ	**95% CI**	σ	**95% CI**
4	0.89	332.9	(331.1, 334.7)	21.53	(19, 24.05)
5	0.99	366	(365.5, 366.6)	19.25	(18.47, 20.04)
6	0.99	400.3	(399.9, 400.8)	22.91	(22.32, 23.49)
7	0.99	432.2	(431.8, 432.6)	16.04	(15.49, 16.59)
8	0.82	453.1	(450.8, 455.4)	20.97	(17.73, 24.21)
9+	0.87	483.3	(482.4, 484.3)	9.731	(8.551, 10.91)

Age structure of the spawning run was estimated by multiplication of the age-length key (a matrix) and the average length-frequency distribution for the spawning run (a column vector) between 1977 and 1989. Stochastic variation was applied by treating the parameters μ and σ for each Gaussian model as normal random variables whose values were based on the outcomes of curve fitting (Table 5.2). Altogether, 250,000 estimates of spawning-run age structure were performed. Age-specific survival probabilities for YCT in the spawning run were estimated by dividing the abundance of each age-class by the abundance of the preceding age-class. Only survival probabilities that fell in the interval 0, 1 were further examined because values > 1 indicated the age-class had not fully recruited into the run. Results suggested YCT fully recruited into the Clear Creek spawning run at age 6 (Figure 5.4); the mean estimated survival probability for each age-class was used as a constant parameter in the model (Table 5.1).

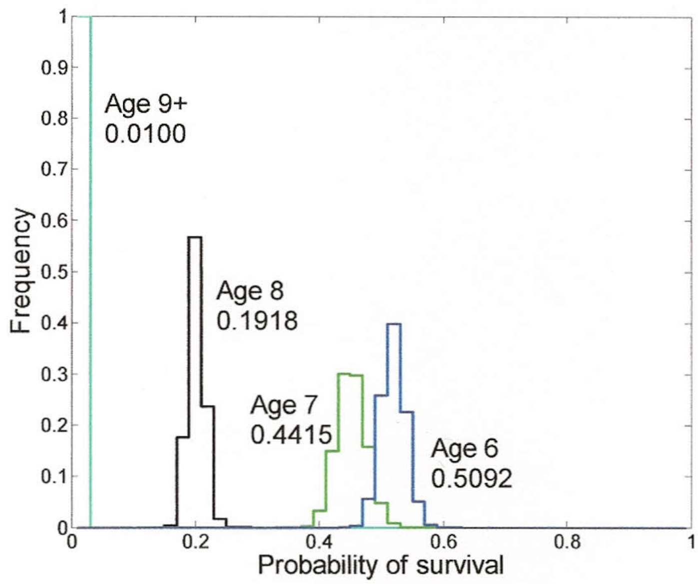

Figure 5.4. Histograms of estimated annual survival probability of age-6–9+ Yellowstone cutthroat trout in the Clear Creek spawning run, 1987–1994. Mean value for each age-class is indicated.

Estimated Model Parameters

Six parameters were estimated as part of the modeling process (Table 5.3). Reproductive success of *Oncorhynchus* fishes elsewhere has been associated with seasonal discharge and temperature of their spawning streams (Chapter Two). In the present study, annual Yellowstone Lake discharge was shown to generally peak in the early 1970s and its overall trend was a few years in advance of that of size of the Clear Creek spawning run (compare Figures 1.1 and 2.2). In Chapter Two, total-annual Lake Village DDs (> 0°C) was shown to be associated with spawning-season discharge and

Table 5.3. Parameters whose statistical characteristics were estimated by modeling the lacustrine-adfluvial Yellowstone cutthroat trout population of Clear Creek. Lower and upper bounds delimit parameter spaces potentially searched during model fitting.

Description	**Lower and upper bounds**
β in Equation 5.4	0.1–12
Maximum first-year survival probability	0.0001–0.0400
ω in Equation 5.1	150–285
L_∞ (in part) in Equation 5.1	20–125
Start year, predation effect on survival probability	1972–2006
Rate survival probability reduced	-2.0–0.0

temperature of Clear Creek. Accordingly, it was hypothesized that recruitment of age-0 YCT to the Clear Creek spawning run was associated with Clear Creek discharge and temperature, as indexed by Lake Village DDs. That association was described by a Gompertz model (Equation 5.4),

$$f(x) = \exp((\alpha / \beta) \cdot (1 - \exp(\beta x))), \qquad (5.4)$$

chosen because it provided a wide variety of intuitively applicable curve shapes (i.e., functional responses to predictor x), including no effect of the predictor, and its application required that only one parameter (i.e., β) be estimated (parameter α was set as a constant, 0.005, because variation in α had little effect on curve shape). Three contrasting curves for the Gompertz model, which included the arbitrarily set lower and upper bounds for searches of the parameter space, are shown in Figure 5.5. Estimates of total-annual Lake Village DDs (Chapter Two) were scaled to the interval 0, 1 for use as the predictor x (Equation 5.4). Because studies of a wide variety of fishes have indicated first-year survival was remarkably low, often on the order of 0.01 or less, lower and upper bounds for the parameter space for maximum first-year survival examined during model fitting (described below, along with the need for such bounding) were arbitrarily set at 0.0001, 0.0400.

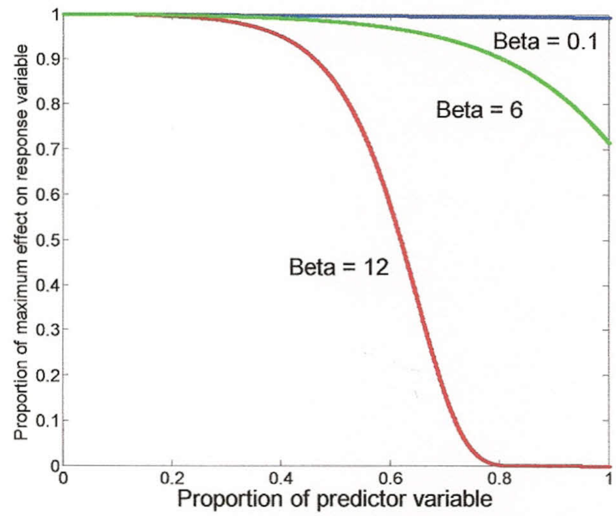

Figure 5.5. Three contrasting example curves for the Gompertz model used in the present study. The curves differ only in the parameter β (Equation 5.4).

Parameter ω in Equation 5.1 was among those estimated and had its upper and lower bounds broadly based on the 95% confidence intervals obtained by fitting Equation 5.1 to data for all scale-aged YCT caught in gill nets (i.e., pooled data for all scale analysts; Chapter Three). Also estimated was parameter L_∞ in Equation 5.1 but as a value added to the deterministic estimate of the mean TL of YCT in the spawning run derived using Equation 5.3. In this way, the effect of YCT population density on YCT somatic growth was included in the model. Specifically, the age-specific fertilities (F_x) of matrix $\mathbf{A}_n(t)$ (Equation 5.2) were estimated as the products of (1) the female proportion of the run, (2) the density-conditioned somatic-growth model, (3) the fecundity-TL relation, and (4) the product of maximum first-year survival and the result of the Gompertz model for that time step (year). Upper and lower bounds for the L_∞ (in part) parameter space were delimited on an initial, trial-and-error basis (Table 5.3).

The final two parameters to be estimated pertained to the effect of lake trout predation on the survival probabilities of age-1 to age-5 YCT. Lake trout had been discovered in Yellowstone Lake in 1994 and data taken from those fish suggested lake trout had reproduced in the lake since at least 1989 (Kaeding et al. 1996). Munro et al. (2005) used natural chemical markers in otoliths to identify the probable source and date of introduction of lake trout into Yellowstone Lake. They concluded that the oldest lake trout in their sample had chemical signatures like those of lake trout from nearby Lewis Lake (where the fish had been introduced by the U.S. Fish Commission in 1890; Evermann 1893) and that lake trout had been illegally introduced into Yellowstone Lake during the late 1980s. Using virtual population analysis, Ruzycki et al. (2003) estimated 8,300 age 3–5 and 3,000 age 6–23 lake trout in Yellowstone Lake in 1996. Although discovered in the lake in 1994, lake trout were not caught in the gill nets used to routinely sample YCT in fall until 1997. Moreover, among the 100 lake trout caught in those nets between 1997 and 2007, all but one (caught at station 2A in 2005) were caught at stations 3A–4B and their catch rates have generally increased across years (Figure 5.6). Collectively, these data suggested an introduced lake trout population whose initial, successful reproduction occurred in the 1980s and whose population mainly inhabited the west-central area of the lake and was rapidly expanding (and finally exceeded its detection threshold) in the 1990s.

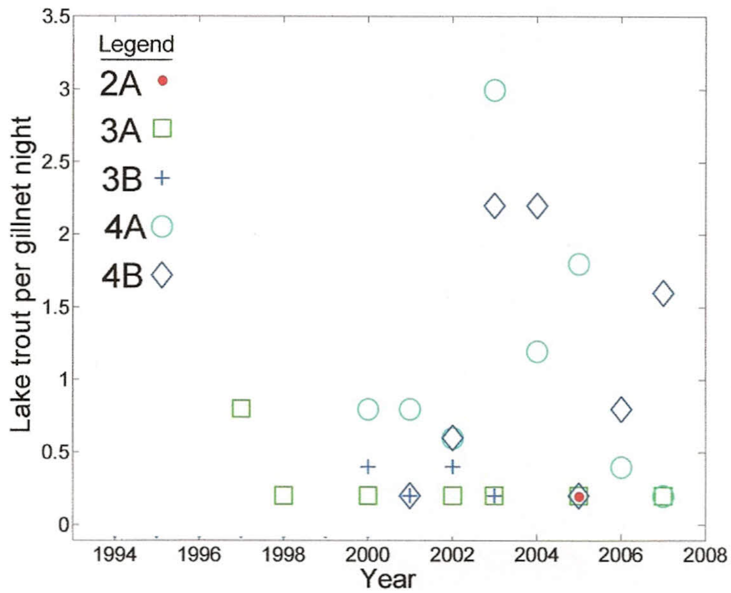

Figure 5.6. Non-zero catch rates for lake trout caught in gill nets at sampling sites 2A, 3A, 3B, 4A and 4B, Yellowstone Lake, 1994–2007 (see Figure 3.1 for locations of sampling sites).

Furthermore, among the 158,302 lake trout measured and removed (total removed, 268,479 lake trout) from Yellowstone Lake between 1994 and 2007 as part of the ongoing control program, the longest was 962 mm TL (Patricia Bigelow, NPS, unpublished data). The inter-quartile range for all measured lake trout was 288–416 mm TL. Ruzycki et al. (2003) found that YCT eaten by lake trout in Yellowstone Lake had TL that was 11–57% that of their predator; the TL of 90% of YCT prey was 20–45% that of their predator; smallest piscivorous lake trout were 320 mm TL; and, the smallest YCT found in a lake trout stomach was 65 mm TL.

These data suggested age-0 YCT, which were about 35 mm TL when they emigrated from Clear Creek in July and 100–120 mm TL more than one year later when caught in gill nets (but as yearling fish; Chapter Three), were not important prey for lake trout in Yellowstone Lake. Instead, most YCT prey of lake trout were age 1 and older, particularly YCT < 300 mm TL (~ age 4; Chapter Three). Moreover, the rate of that predation ostensibly increased with size of the lake trout population. Accordingly, the final two parameters estimated were (1) the year that lake trout predation began to reduce the survival probability of age-1 through age-5 YCT (the base survival probabilily for these fish was arbitrarily set as 0.5092, i.e., that of age 6 fish [Table 5.1]) and (2) the linear rate of that reduction. Year was necessarily treated as an integer value whose lower and upper bounds were arbitrarily set at 1972, 2006, whereas the rate term (represented in computer code as the slope of a linear relation) had arbitrarily bounds of -2.0, 0.0 (Table 5.3).

Model Start Year and Population

In 1965 and 1966, Clear Creek run size was tallied as about 36,000 fish (Figure 1.1). Accordingly, the start year (i.e., $t = 0$) for model simulations was set as 1965 and the 36,000 run fish were equally and arbitrarily divided among age-classes 3–5 and placed in state-vector elements $\boldsymbol{n}_{3,1}(1) - \boldsymbol{n}_{5,1}(1)$. In addition, an arbitrary 72,000 fish (i.e., 2× the starting run size) was placed in each of $\boldsymbol{n}_{1,1}(1)$ and $\boldsymbol{n}_{2,1}(1)$.

Model Assumptions

In addition to the basic assumption that the empirical data were representative of the lacustrine-adfluvial YCT population of Clear Creek, several assumptions were important to implementing the model: (1) Its structure embodied the key factors that effected the dynamics of the YCT population. Of course, this was determined by how well the model fit the data. (2) The dynamics of the lacustrine-adfluvial YCT population of Clear Creek were independent of other YCT spawning stocks in Yellowstone Lake, and there was no appreciable movement of fish among spawning stocks. Indeed, those other populations did not exist in the simulations. (3) The simulated population, whose start year was set at 1965, had reached a stable age distribution by 1977, i.e., the first year of the pre-lake trout period, when model-fitting began.

Model Variations

Three variations of the model were each separately examined. The first was the "full" model, which included all of the parameters described above. The second, termed the "climate" model, consisted of the full model without the lake-trout predation component. Finally, the "predation" model was the full model without the climate component, i.e., the Gompertz model (Equation 5.4).

Model Fitting

Objective Function: The objective function was that which was minimized in the fitting process for the model. The objective function (Equation 5.5),

$$SST = \sum_{j=1977}^{2007}((N_{pj} - N_{oj})^2 + (\overline{TL}_{pj} - \overline{TL}_{oj})^2) \ , \tag{5.5}$$

was the total sum of squared differences (i.e., "sum of squares"; *SST*) between the observed annual run size (N_o) and run size predicted (N_p) by the model and between the observed mean TL of run fish $(\overline{TL}_o)$ and mean TL predicted by the model $(\overline{TL}_p)$ across years (*j*). (Estimation of the predicted data is described below.) Prior to calculation of objective-function values, the observed and predicted data for each variable were standardized (i.e., calculated as *z*-scores) and thus given equal weight between parameters.

Simulated Annealing: Fitting the model of the lacustrine-adfluvial YCT population of Clear Creek to the data entailed a search for the suite of four, five, or six parameters (Table 5.3) – dependent upon the particular model – that minimized the objective function and was accomplished using simulated annealing (MathWorks 2005; genetic algorithm and direct search toolbox). The simulated annealing algorithm (Kirkpatrick et al. 1983; Cerny 1985) mimics the process of annealing in metallurgy by (1) randomly choosing candidate parameter values from the parameter space according to a “cooling” or “re-annealing” schedule, (2) evaluating the objective function on the basis of the proposed parameter value (i.e., only one parameter was varied at a time), and (3) accepting the proposed parameter value when the value of the objective function decreased (i.e., a better fit of the model to the data was achieved) or the value increased or remained unchanged but other criteria were met. If the proposed parameter value is not accepted, the preceding value is restored and the search is resumed. As annealing “temperature” is reduced and the algorithm converges on a function solution, a smaller portion of the parameter space is searched. The simulated annealing solver more rapidly converges on a solution if the search area for each parameter is objectively bounded in parameter space. Accordingly, the initial upper and lower bounds for each parameter were established (Table 5.3). Parameter seeds (i.e., starting values) for each search were randomly drawn from the uniform distribution defined by the upper and lower bounds for each parameter. The lowest value for the objective function achieved after 100 fits of the model to the data was considered indicative of the global minimum in parameter space.

Predicted Run Size and Mean Total Length of Run Fish, and Comparison of Model Fits

Predicted Clear Creek run size and mean TL of YCT in the run were calculated by placing the parameter estimates at the assumed global minimum in their respective model positions and projecting the model population forward from 1965 through 2007. Start-year spawning run and population were described earlier. Linear regression (Neter et al. 1996) was used to determine how well the models predicted run sizes and mean TLs.

Results

The full, climate, and predation models each explained 87%, 73%, and 47% of variation in observed Clear Creek run size and 86%, 49%, and 72% of the variation in observed mean TL of run fish, respectively, between 1977 and 2007 (Figure 5.7). The climate model closely predicted run size but failed to closely predict mean TL of run fish in 2006 and 2007. In contrast, the predation model closely fit observed mean TL of run fish but portrayed (explained below) only the broad decline in observed run size during 1977–2001. Estimates of the parameters maximum s_0, Gompertz β, ω, L_∞ (in part), start year for lake trout predation effect, and the rate of that effect on survival probability at the assumed global minimum were 0.011, 10.04, 231.3 mm, 62.5 mm, 1998, and -0.120 for the full model; 0.019, 11.02, 264.5 mm, 42.5 mm, (na), and (na) for the climate model; and 0.003, (na), 272.5 mm, 36.0 mm, 2001, and -0.295 for the predation model,

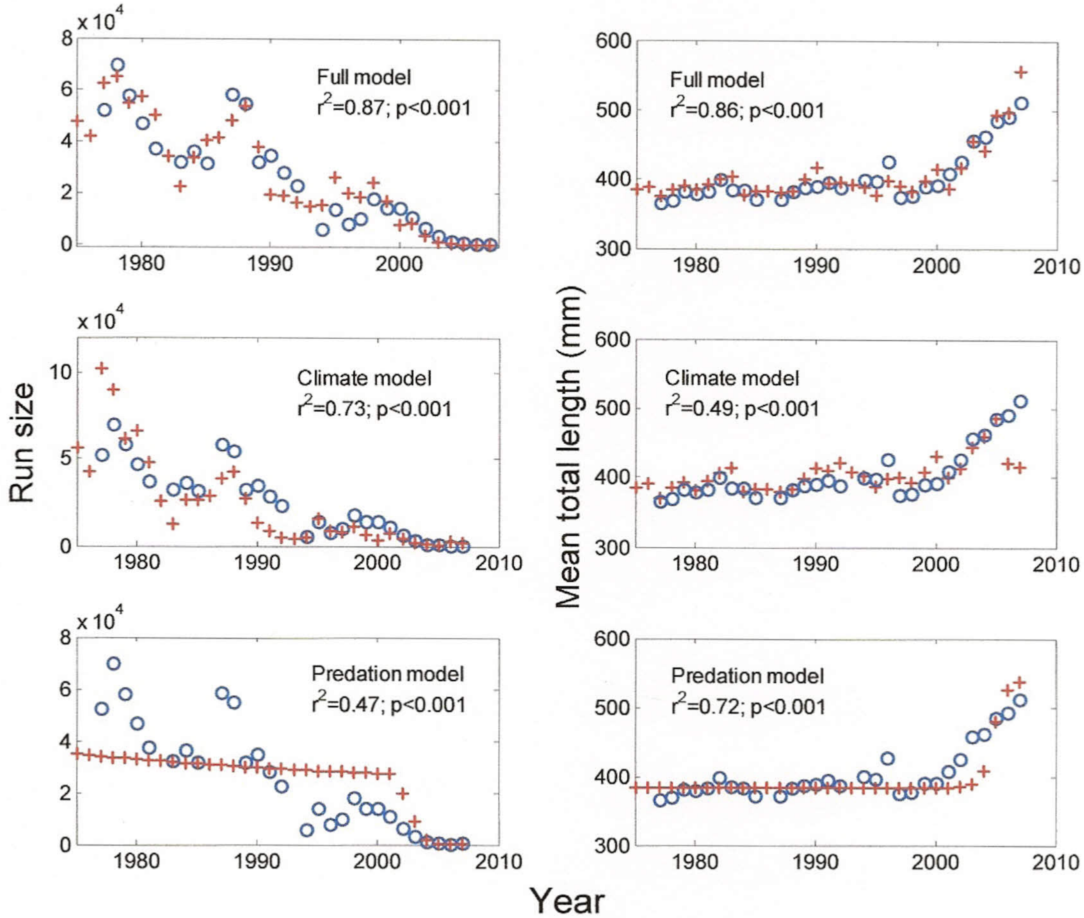

Figure 5.7. Relation between observed size of the annual spawning run of lacustrine-adfluvial Yellowstone cutthroat trout in Clear Creek and run size predicted by each of three models (left), and between the observed and predicted mean total lengths of fish in the run (right), 1977–2007. Observed data appear as open circles; predicted data as plus signs. Number of observed data points differs between variables because mean total length but not run size was estimated in 1982.

respectively. The estimated maximum s_0 of 0.003 for the predation model defined a population in continual numeric decline since the start year (Figure 5.7). Curves for the Gompertz model on the basis of the β parameter estimates for the fitted full model and climate model are shown in Figure 5.8.

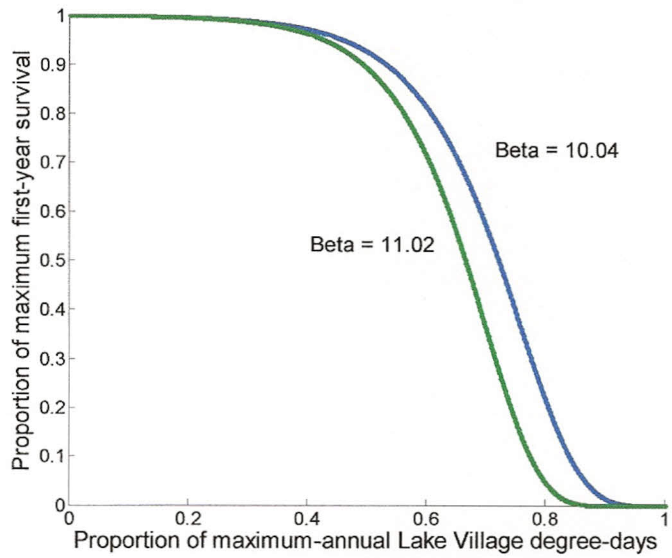

Figure 5.8. Curves for the Gompertz model (Equation 5.3) when $\beta = 10.04$ or 11.02.

Discussion

The fitted models provided insights into the factors that importantly affected the dynamics of the lacustrine-adfluvial YCT population of Clear Creek during the three recent decades. Among those insights was that climate, as indexed by Lake Village DDs, had an important effect on recruitment of age-0 YCT to subsequent spawning runs. Although the characteristics of climate that individually or collectively affected first-year survival of YCT are unknown (see Chapter Two for a discussion of pertinent literature), results of these analyses plainly indicated such recruitment was greatest in years when Lake Village DDs were low and accompanying annual stream discharges were high.

The fitted models also suggested that an effect of lake trout predation on the YCT population had only recently (i.e., during the past decade) become apparent if at all. That latter possibility is based on the observation that the strength of a lake trout effect weighs heavily on the two, most-recent data points for mean TL of YCT in the run, which were not well-fit by the climate model. It may seem enigmatic that, in contrast, lake trout predation may have begun to affect size structure of the YCT population one decade earlier, in the 1990s (Chapter Four). One possible explanation for this divergence is that lake trout predation was mainly directed at immature YCT and sufficient YCT survived to mature and reproduce. Moreover, because those surviving, mature YCT grew well and had greater length-at-age than their pre-lake trout predecessors, they also had greater fecundity. Thus total egg production of the spawning population was not importantly diminished by lake trout predation during the initial years of a lake-trout predation effect on YCT population structure. (Recall that, in the context of the present study, model-fitting in part consisted of finding the values of parameters ω and L_∞ [in part] that best fit the deterministic fecundity-TL relation in the context of the overall model fit.)

Climate variation and, perhaps, lake trout predation appear to have importantly affected the lacustrine-adfluvial YCT population of Clear Creek during the recent three decades. Moreover, these data clearly indicate that assessment of the effects of lake trout predation on YCT – and thereby indirectly assessing the efficacy of the ongoing lake trout control program – will require the use of models that include both climate variation and lake trout predation.

If the important effect of climate on recruitment of age-0 YCT to subsequent spawning runs described in the present study is real, the adult YCT population of Yellowstone Lake would have experienced appreciable recruitment during the 1960s and early 1970s, when the climate was generally cooling and concurrent water availability was increasing (see Figure 2.2 for trends in climate, as indexed by annual water availability and Lake Village DDs). That growing adult population was indicated by strong spawning runs in Clear Creek in 1965 and 1966 (Figure 1.1). Moreover, because greatly restrictive angling regulations began to be implemented in the 1960s, the YCT population would have benefitted from both increased recruitment of adults and reduced angler harvest. The relative importance of these two factors to population growth during the 1970s is unknown and an intriguing question.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

This study undertook a comprehensive examination of the extensive data for the YCT of Yellowstone Lake and had as its goal to evaluate the relative contributions of climate variation, lake trout predation, and other factors to the decline of the lacustrine-adfluvial YCT population of Clear Creek. Strong growth of the YCT spawning run of Clear Creek between the early 1960s and 1978, when it peaked at about 70,000 fish, was considered key evidence of recovery of the lake's YCT population from formerly excessive angler harvest and other adverse factors. Thus the run's subsequent, almost continuous decline to about 500 fish in 2007 was perplexing. Catches of YCT in gill nets routinely set during fall at established Yellowstone Lake locations likewise indicated a concurrent, marked decline in the YCT population. During the past decade, that decline was primarily attributed to predation by the illegally introduced, reproducing, nonnative lake trout discovered in Yellowstone Lake in 1994.

Data mainly taken from YCT in the spawning run and gillnet catch were closely examined for information useful to objectively specifying the model's Leslie matrix. The subsequent full model, as well as its two components, were each fitted to spawning run size and mean TL of YCT in the run during 1977–2007. The full model explained 87% of variation in observed run size and 86% of the variation in observed mean TL during the period and strongly suggested that climate (as indexed by total-annual Lake Village DDs measured on the lake's north shore) had an important effect on recruitment of age-0 YCT to subsequent spawning runs. The results also suggested that the effect of lake trout predation on the spawning population began to be apparent only during the recent decade if at all.

Because an effect of lake trout predation on YCT may have only recently emerged, whether or not ongoing efforts to control lake trout in Yellowstone Lake have importantly limited that predation cannot yet be assessed. An important, future test of efficacy of the lake trout removal program – on the basis of data for the YCT population – will occur when climatic conditions improve for YCT recruitment to the Clear Creek and other YCT spawning stocks of Yellowstone Lake and additional data for these fish are available. Comparison of data taken from YCT in that future period to those predicted by the full model of the present study would provide one important means of assessing control-program efficacy.

Accordingly, future research should include development of models that incorporate uncertainty into parameter estimates – probably employing a Bayesian approach (e.g., Lee 2009) – either based upon the current model or another model. Such models would be especially important to assessments of the lake trout control program based on the above comparisons. In any case, results of the present study provided a firm foundation upon which to conduct additional modeling research. Perhaps most importantly, those results also showed that assessing the effects of lake trout predation on YCT requires use of models that include environmental effects apart from lake trout predation.

Consequently, routine sampling of YCT, updating of data bases (biological and physical), and comprehensive examination of these data are essential. The biological data examined in the present study should continue to be collected. The trap and weir on Clear Creek were destroyed by spring flooding in 2008; those structures should be restored and made operable as soon as possible. Consideration also should be given to recording whether captured YCT were "tangled," "gilled," or "wedged" in gill nets (in the sense of Hamley 1975) and to setting complimentary net gangs in deeper water at each sampling site. Those deeper nets may capture the ostensibly substantial portion of age-2 YCT that does not occupy the littoral areas now targeted by the gillnet sampling program in mid-September. If so, it may become possible to estimate gillnet selectivity, population length frequency, and annual survival probability for age-2 and older YCT. Distinguishing among YCT that were tangled, gilled, or wedged in nets is essential to the estimation of gillnet selectivity and related statistics (e.g., Hamley 1975).

Estimation of population length frequency using gillnet data would be an important step toward development of a dynamic, age-structured model based on gillnetted YCT. Such a model could distinguish among YCT in the three lake areas of the present study, for example, and would also be of considerable importance to assessing the efficacy of the lake trout control program. The control program for lake trout is almost entirely directed at the west-central (West Thumb and Breeze Channel) lake area. Almost certainly the lake trout population is growing in other lake areas.

LITERATURE CITED

Arnold, B.B. 1967. A ninety-seven year history of fishery activities in Yellowstone National Park, Wyoming. Unpublished draft manuscript. U.S. Bureau of Sport Fisheries and Wildlife, Albuquerque, N.M.

Ball, O.P., and O.B. Cope. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service, Research Report 55, Washington, D.C.

Barnett, T.P., J.C. Adam and D.P. Lettenmaier. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303–309.

Benson, N.G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish and Wildlife Service, Research Report 56, Washington, D.C.

Benson, N.G., and R.V. Bulkley. 1963. Equilibrium yield and management of cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service, Research Report 62, Washington, D.C.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181–213.

Brett, J.R. 1951. A study of the Skeena River climatological conditions with particular reference to their significance in sockeye production. Journal of the Fisheries Research Board of Canada 8(3):178–187.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Second edition. Sinauer Associates, Inc. Publishers. Sunderland, MA. 722 pp.

Cerny,V. 1985. A thermodynamical approach to the travelling salesman problem: an efficient simulation algorithm. Journal of Optimization Theory and Applications, 45:41–51.

Evermann, B.W. 1893. A reconnaissance of the streams and lakes of western Montana and northwestern Wyoming. Bulletin of the U.S. Fish Commission 11:3–60.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson and C.S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Reviews in Ecology, Evolution and Systematics 35:557–581.

Gallucci, V.F., and T.J. Quinn, II. 1979. Reparameterizing, fitting, and testing a simple growth model. Transactions of the American Fisheries Society 108: 14–25.

Graumlich, L.J., M.F.J. Pisaric, L.A. Waggoner, J.S. Littell and J.C. King. 2003. Upper Yellowstone River flow and teleconnections with Pacific Basin climate variability during the past three centuries. Climate Change 59:245–262.

Gresswell, R.E., and J.D. Varley. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. American Fisheries Society Symposium 4:45–52.

Gresswell, R.E., W.J. Liss and G.L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries Aquatic Sciences 51(Supplement 1):298–309.

Gresswell, R.E., W.J. Liss, G.L. Larson and P.J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. North American Journal of Fisheries Management 17:1046–1064.

Hamley, J.M. 1975. Review of gillnet selectivity. Journal of the Fisheries Research Board of Canada 32:1943–1969.

Hedrick, R.P., T.S. McDowell, K. Mukkatira, M. Georgiadis and E. MacConnell. 1999. Susceptibility of selected inland salmonids to experimentally induced infections with *Myxobolus cerebralis*, the causative agent of whirling disease. Journal of Aquatic Animal Health 11:330–339.

Hilborn, R., and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York. 570 pp.

Hintze, J. 2001. Number Cruncher Statistical Systems. Kaysville, Utah.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 45:502–515.

Hostetler, S.W., and F. Giorgi. 1995. Effects of a $2 \times CO_2$ climate on two large lake systems: Pyramid Lake, Nevada, and Yellowstone Lake, Wyoming. Global and Planetary Change 10:43–54.

Hurst, T.P. 2007. Review paper: causes and consequences of winter mortality in fishes. Journal of Fish Biology 71:315–345.

Jones, R.D., J.D. Varley, D.E. Jennings, S.M. Rubrecht and R.E. Gresswell 1977. Fishery and aquatic management program in Yellowstone National Park: annual technical report for 1976. U.S. Fish and Wildlife Service, Yellowstone National Park, Wyoming.

Jones, R.D., D. Carty, R.E. Gresswell and L.D. Lentsch. 1985. Fishery and aquatic management program in Yellowstone National Park: technical report for 1984. U.S. Fish and Wildlife Service, Yellowstone National Park, Wyoming.

Jordan, D.S. 1891. A reconnaissance of streams and lakes of Yellowstone National Park, Wyoming, in the interest of the U.S. Fish Commission. Bulletin of the U.S. Fish Commission 9:41–63.

Kaeding, L.R. 1996. Evaluation of the monitoring program for Yellowstone cutthroat trout in Yellowstone Lake. Unpublished report to the National Park Service, Yellowstone National Park. U.S. Fish and Wildlife Service, Bozeman, Montana.

Kaeding, L.R., G.D. Boltz and D.G. Carty. 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. Fisheries 21(3):16–20.

Kaeding, L.R., and G.D. Boltz. 2001. Spatial and temporal relations between fluvial and allacustrine Yellowstone cutthroat trout, *Oncorhynchus clarki bouvieri*, spawning in the Yellowstone River, outlet stream of Yellowstone Lake. Environmental Biology of Fishes 61(4):395–406.

Kaplinski, M.A. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wyoming. M.S. Thesis. Northern Arizona University, Flagstaff. 82 pp.

Kilham, S.S., E.C. Theriot and S.C. Fritz. 1996. Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. Limnology and Oceanography 41(5):1052–1062.

Kirkpatrick, S., C.D. Gelatt and M.P. Vecchi. 1983. Optimization by simulated annealing. Science 220(4598):671–680.

Kocik, J.F., and W.W. Taylor. 1987. Effect of fall and winter instream flow on year-class strength of Pacific salmon evolutionarily adapted to early fry outmigration: a Great Lakes perspective. American Fisheries Society Symposium 1:430–440.

Koel, T.M., P.E. Bigelow, P.D. Doepke, B.D. Ertel and D.L. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout declines and impacts to bears and anglers. Fisheries 30(11):10–19.

Koel, T.M., D.L. Mahony, K.L. Kinnan, C. Rasmussen, C.J. Hudson, S. Murcia and B.L. Kerans. 2006. *Myxobolus cerebralis* in native cutthroat trout of the Yellowstone Lake ecosystem. Journal of Aquatic Animal Health 18:157–175.

Laakso, M., and O.B. Cope. 1956. Age determination in Yellowstone cutthroat trout by the scale method. Journal of Wildlife Management 20:138–153.

Lawson, P.W., E.A. Logerwell, N.J. Mantua, R.C. Francis and V.N. Agostini. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 61:360–373.

Lee, P.M. 2009. Bayesian Statistics: an Introduction, 3rd edition. Wiley, New York. 352 pp.

Lentsch, L.D., and J.S. Griffith. 1987. Lack of first-year annuli on scales: frequency of occurrence and predictability in trout of the western United States. Pages 177–188 *in* R.C. Summerfelt and G. E. Hall (eds.) The Age and Growth of Fish. Iowa State University Press, Ames.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

Leslie, P.H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35:213–245.

MathWorks. 2005. MATLAB: the Language of Technical Computing. Version 7.1.0.124 (R14). The MathWorks, Natick, MA.

Meyer, K.A., D.J. Schill, F.S. Elle and J.A. Lamansky, Jr. 2003. Reproductive demographics and factors that influence length at sexual maturity of Yellowstone cutthroat trout in Idaho. Transactions of the American Fisheries Society 132:183–195.

Mohseni, O., and H.G. Stefan. 1999. Stream temperature/air temperature relationship: a physical interpretation. Journal of Hydrology 218:128–141.

Morgan, L.A. (Ed.). 2007. Integrated geoscience studies in the greater Yellowstone area—volcanic, tectonic, and hydrothermal processes in the Yellowstone geoecosystem. U.S. Geological Survey Professional Paper 1717.

Munro, A.R., T.E. McMahon and J.R. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 62:79–87.

Murcia, S. 2007. *Myxobolus cerebralis* in native cutthroat trout of three spawning tributaries to Yellowstone Lake: a qualitative ecological risk assessment. Ph.D. dissertation, Montana State University, Bozeman. 154 pp.

Murdoch, W.W. 1994. Population regulation in theory and practice. Ecology 75(2):271-287.

Neter, J., M.H. Kutner, C.J. Nachtsheim and W. Wasserman. 1996. Applied Linear Statistical Models, 4th edition. WCB/McGraw-Hill, New York. 1408 pp.

Redmond, K.T., and R.W. Koch. 1991. Surface climate and streamflow variability in the western United State and their relationship to large-scale circulation indices. Water Resources Research 27(9):2381–2399.

Rounsefell, G.A. 1957. Fecundity of North American Salmonidae. Fishery Bulletin 57: 451–468.

Ruzycki, J.R., D.A. Beauchamp and D.L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13(1):23–37.

Seber, G.A.F., and C.J. Wild. 1989. Nonlinear Regression. John Wiley and Sons, New York. 768 pp.

Selifonov, M.M. 1987. Influence of environment on the abundance of sockeye salmon (*Oncorhynchus nerka*) from the Ozernaya and Kamchatka rivers. Canadian Special Publications in Fisheries and Aquatic Sciences 96:125–128.

Shepherd, J.G and D.H. Cushing. 1990. Regulation in fish populations: myth or mirage? Philosophical Transactions: Biological Sciences 330(1257):151–164.

Steele, J.H. 1996. Regime shifts in fisheries management. Fisheries Research 25:19–23.

Theriot, E.C., S.C. Fritz and R.E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park, Wyoming, U.S.A. Arctic and Alpine Research 29(3):304–314.

Turchin, P. 1999. Population regulation: a synthetic view. Oikos 84(1):153–159.

Varley, J.D., and R.E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. American Fisheries Society Symposium 4:13–24.

Vincent, E.R. 1996. Whirling disease and wild trout: the Montana experience. Fisheries 21(6):32–33.

Welsh, J.P. 1952. A population study of Yellowstone blackspotted trout (*Salmo clarkii lewisi* Girard). Ph.D. dissertation. Stanford University. 183 pp.

White, T.C.R. 2008. The role of food, weather and climate in limiting the abundance of animals. Biological Review 83:227–248.

APPENDICES

APPENDIX A

EQUATIONS FOR FITTED REGRESSION MODELS

NOT OTHERWISE DESCRIBED IN TABLES, BY CHAPTER AND PAGE.

Chapter Two

Page 15

Lake Q = -3.4202 + 0 .4661*Corwin Springs Q* ;

ln Creek Q (m^3/s) = 1.7179 + 2.9079*ln gage height* (m) + 8.3986E-02(*Year 1980*) - 0.1930(*Year 1981*) - 0.5691(*Year 1983*) - 0.2118(*Year 1984*) - 0.5132(*Year 1987*) - 0.4281(*Year 1988*) - 1.7341E-02(*Year 1990*) + 2.0987E-03(*Year 1991*) - 8.1660E-02(*Year 1992*) + 5.2953E-02(*Year 1995*) - 1.0694(*Year 1997*) - 0.8953(*Year 1998*) - 1.2449(*Year 1999*) - 0.1122(*Year 2000*) - 0.2471(*Year 2001*) - 0.2462(*Year 2002*) - 0.2564(*Year 2003*) - 0.2596(*Year 2004*)

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Creek Q = 7833 - 1.809*Lake Village DDs* - 593.1*SemiMonthSeqNo* ;

Creek Q = 4189 + 0.6133*Lake Q* - 588.8*SemiMonthSeqNo* ;

Creek DDs = -765.6 + 0.1622*Lake Village DDs* - 0.0494*Lake Q* + 122.4*SemiMonthSeqNo* ;

Creek DDs = -461.2 - 6.902E-02*Lake Q* + 118.3*SemiMonthSeqNo* ;

Creek DDs = -914.3 + 0.2288*Lake Village DDs* + 119.5*SemiMonthSeqNo*

Chapter Three

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FemaleMaturityProportion = 1.272E-02 + 1.043*MaleMaturityProportion* ;

FemalePrespawnerProportion = -7.330E-03 + 0.6580*FemaleMaturityProportion* ;

MalePrespawnerProportion = -4.335E-03 + 0.6167*MaleMaturityProportion* ;

Chapter Four

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Mean TL YCT Clear Creek spawning run = -9187 + 4.795*Year* + ((*Year* - 1996.7) × 4.738 × SIGN(*Year* - 1996.7)) ;

Mean TL gillnetted YCT 100–199 mm TL = 161 + 8.379E-03*Year* + ((*Year* - 1991.1) × 0.5114 × SIGN(*Year* - 1991.1)) ;

Mean TL gillnetted YCT 100–199 mm TL = -660 + 0.460*Year* + ((*Year* - 1985.3) × -0.9157 × SIGN(*Year* - 1985.3)) ;

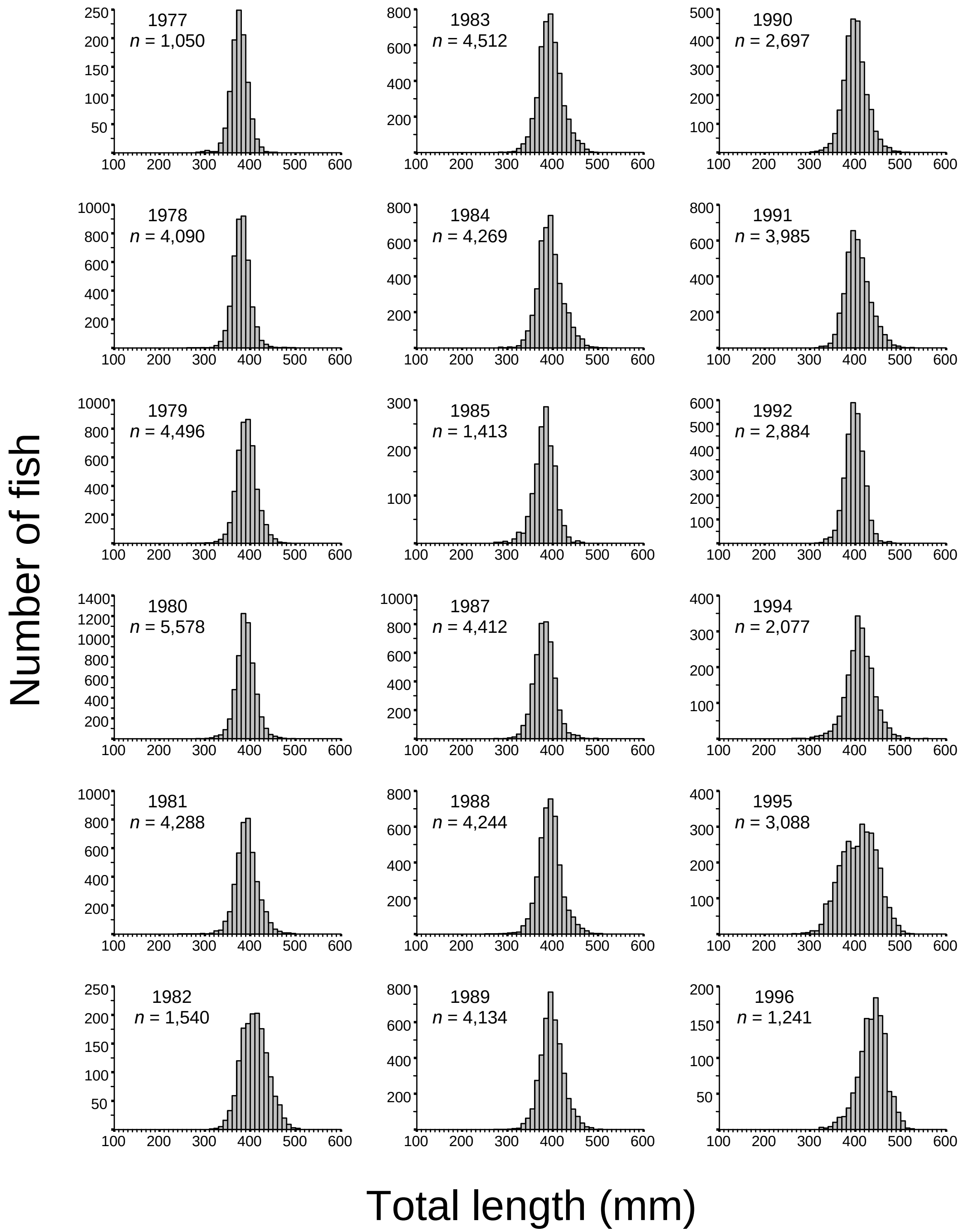
Mean TL gillnetted YCT 100–199 mm TL = -5163 + 2.778*Year* + ((*Year* - 1994.9) × 2.550 × SIGN(*Year* - 1994.9))

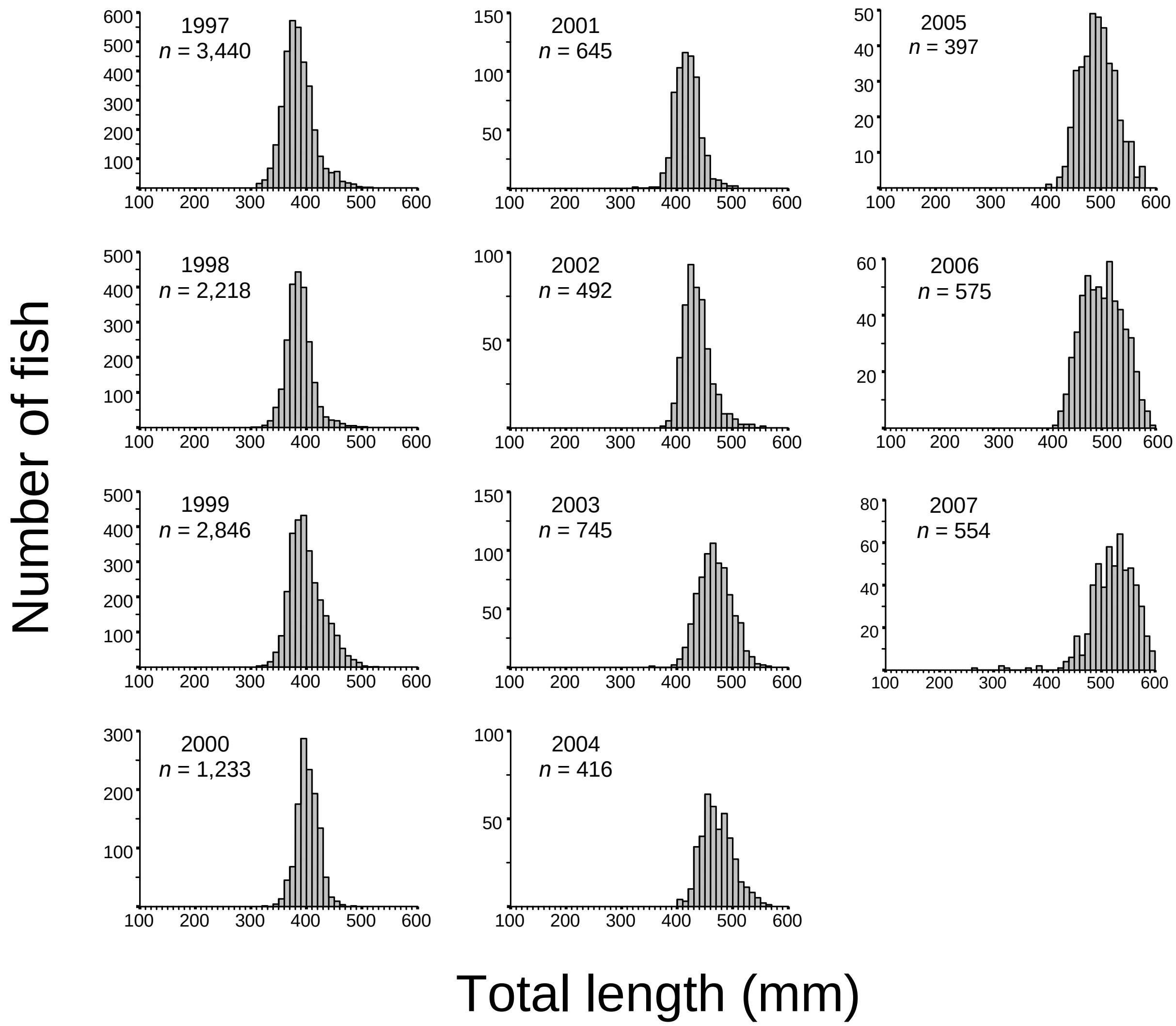
<u>APPENDIX B</u>

LENGTH FREQUENCY OF YELLOWSTONE CUTTHROAT TROUT IN

29 ANNUAL SPAWNING RUNS OF CLEAR CREEK, 1977–2007

(NINE FISH > 599 MM TL CAUGHT DURING 2005–2007 ARE NOT SHOWN).

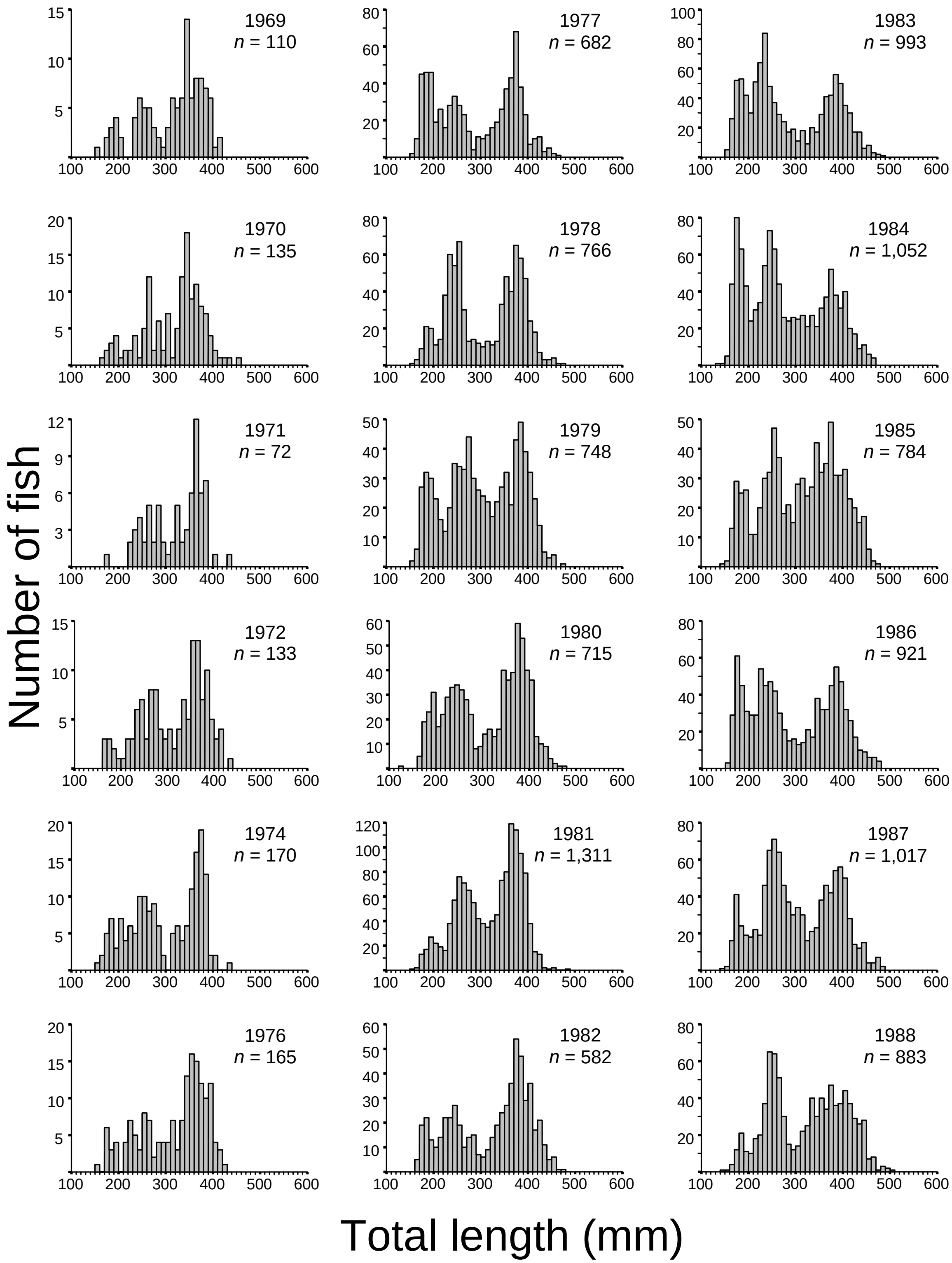

1977
n = 1,050
1983
n = 4,512
1990
n = 2,697
1978
n = 4,090
1984
n = 4,269
1991
n = 3,985
1979
n = 4,496
1985
n = 1,413
1992
n = 2,884
1980
n = 5,578
1987
n = 4,412
1994
n = 2,077
1981
n = 4,288
1988
n = 4,244
1995
n = 3,088
1982
n = 1,540
1989
n = 4,134
1996
n = 1,241
Number of fish
Total length (mm)

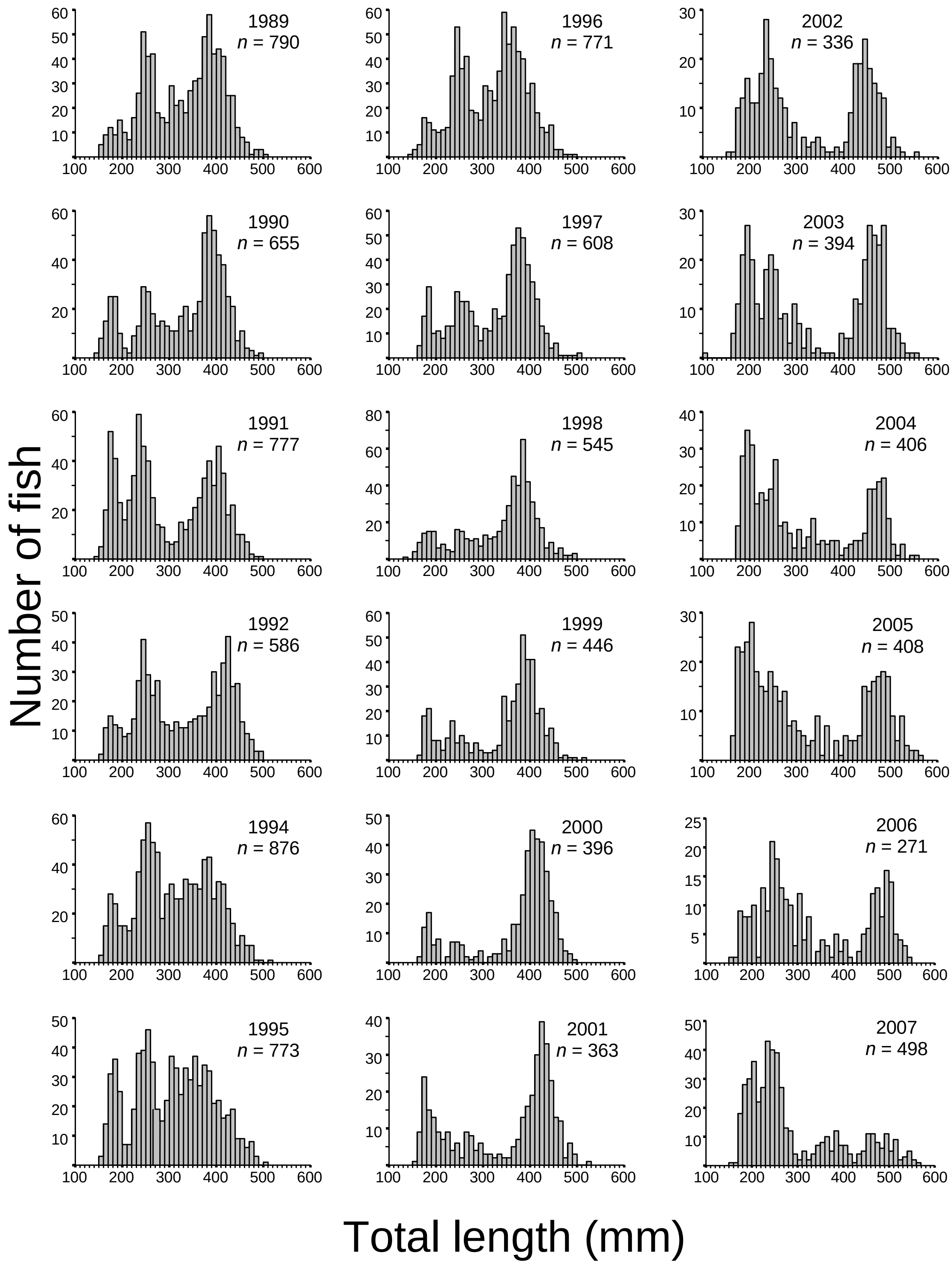

1997
n = 3,440
1998
n = 2,218
1999
n = 2,846
2000
n = 1,233
2001
n = 645
2002
n = 492
2003
n = 745
2004
n = 416
2005
n = 397
2006
n = 575
2007
n = 554
Number of fish
Total length (mm)

APPENDIX C

LENGTH FREQUENCY OF YELLOWSTONE CUTTHROAT TROUT IN

36 ANNUAL GILLNET CATCHES, YELLOWSTONE LAKE, 1969–2007.


1969
n = 110
1977
n = 682
1983
n = 993
1970
n = 135
1978
n = 766
1984
n = 1,052
1971
n = 72
1979
n = 748
1985
n = 784
1972
n = 133
1980
n = 715
1986
n = 921
1974
n = 170
1981
n = 1,311
1987
n = 1,017
1976
n = 165
1982
n = 582
1988
n = 883
Number of fish
Total length (mm)


1989
n = 790
1996
n = 771
2002
n = 336
1990
n = 655
1997
n = 608
2003
n = 394
1991
n = 777
1998
n = 545
2004
n = 406
1992
n = 586
1999
n = 446
2005
n = 408
1994
n = 876
2000
n = 396
2006
n = 271
1995
n = 773
2001
n = 363
2007
n = 498
Number of fish
Total length (mm)