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Influence of Basin-Scale Physical Variables on Life History Characteristics of Cutthroat Trout in Yellowstone Lake

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Abstract.—Individual spawning populations of Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* differ in life history characteristics associated with broad spatial and temporal environmental patterns, but relationships between specific life history characteristics of Yellowstone cutthroat trout and physical aspects of the environment are poorly understood. We examined basin-scale physical characteristics of tributary drainages and subbasins of Yellowstone Lake in relation to timing (peak and duration) of lacustrine–adfluvial Yellowstone cutthroat trout spawning migrations and mean length of cutthroat trout spawners in 27 tributaries to the lake. Stream drainages varied along gradients that can be described by mean aspect, mean elevation, and drainage and stream size. Approximately two-thirds of the variation in the timing of the peak of the annual cutthroat trout spawning migrations and average length of spawners was explained by third-order polynomial regressions with mean aspect and basin area as predictor variables. Because most cutthroat trout ascend tributaries soon after peak runoff, it appears that the influence of basin-scale physical variables on the date of the migration peak is manifested by the pattern of stream discharge. Spawner length does not seem to be a direct function of stream size in the Yellowstone Lake watershed, and aspect of the tributary basin seems to have a greater influence on the body length of cutthroat trout spawners than does stream size. Mechanisms that explain how the interaction of basin-scale physical variables influence spawner length were not investigated directly; however, we found evidence of distinct aggregations of cutthroat trout that are related to physical and limnological characteristics of the lake subbasins, and there is some indication that lake residence may be related to tributary location.

Fishes exhibit more intraspecific phenotypic variability than most other taxa (Allendorf et al. 1987). Intraspecific variation of life history characteristics (e.g., food habits, age composition, timing of spawning migration, and meristic and morphometric characters) has been documented for anadromous and potamodromous fishes across extensive geographic scales (e.g., Leggett and Carscadden 1978; Sinclair 1988; Jonsson and L'Abée-Lund 1993) and even within individual drainage basins (e.g., Riget et al. 1986; Larson and McIntire 1993; Gresswell et al. 1994). However, high phenotypic variation in fishes does not seem to be associated with increased genotypic variability, suggesting a strong linkage to environmental factors (Allendorf 1988; Healey and Prince 1995).

There is some evidence of a direct relationship between life history and habitat diversity. For example, Schaffer and Elson (1975) concluded that mean age of first spawning for anadromous Atlantic salmon *Salmo salar* was a heritable life history trait influenced by river size and that commercial fishing disrupted the natural age composition of spawning runs by removing older age-classes. Beacham (1984) found that chum salmon *Oncorhynchus keta* are morphometrically related to water availability and flow in natal streams. Jonsson and Sandlund (1979) identified environmental factors that influenced the existence of small and large mature males in fluvial stocks of

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brown trout *Salmo trutta* in Norway. Riget et al. (1986) reported that three distinctive ecological forms of Arctic char *Salvelinus alpinus* within a single large lake in west Greenland exhibited distinctive habitat, feeding, and reproductive characteristics.

Such spatial and temporal variability among fish stocks has been recognized for decades in commercial fisheries (Sinclair 1988). Pioneering work on Pacific salmon *Oncorhynchus* spp. led to a growing appreciation of the importance of intraspecific variability in species persistence and evolution (Ricker 1972; Taylor 1991; Healey and Prince 1995), and the stock concept has been applied to commercial fisheries management (Larkin 1981; Sinclair 1988). Despite this information base, demographic principles such as the stock concept have been applied only rarely to management of potamodromous salmonids in the United States, except in the Great Lakes (Loftus 1981; Spangler et al. 1981). Instead, potamodromous salmonid management has been dominated by put-and-take stocking of hatchery fish (Evans and Willox 1991; Krueger and May 1991), and in most cases stocked fish have been nonnative species, subspecies, or strains (Behnke 1992). In recent decades, however, managers and researchers have become increasingly interested in life history variation within and among populations of native potamodromous salmonids (Jonsson and Sandlund 1979; Elliot 1994), and in the importance of identifying and protecting this diversity (Allendorf and Leary 1988; Dizon et al. 1992; Gresswell et al. 1994). Concern about the role of land-use practices in the extirpation of indigenous fishes has renewed interest in the interaction of habitat and salmonid life history (Healey and Prince 1995; Reeves et al. 1995).

Recent efforts to document the status and management of potamodromous forms of cutthroat trout *Oncorhynchus clarki* (Gresswell 1988; Young 1995) provide one example. Cutthroat trout are broadly distributed from coastal rivers in the Pacific Northwest to interior streams and lakes of the Great Basin and Rocky Mountains (Behnke 1992). Earliest fossil records of the species date to the Miocene (Stearley and Smith 1993). Since then, cutthroat trout have diverged into 14 subspecies (Behnke 1988). Differences in life history strategies across the range of Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri*, perhaps the most abundant potamodromous cutthroat trout subspecies, represent a complex array of responses to environmental variation (Varley and Gresswell 1988; Gresswell 1995).

At the ecosystem scale, individual spawning populations of Yellowstone cutthroat trout differ in life history characteristics associated with spatial and temporal environmental patterns. Gresswell et al. (1994) summarized some of the life history variables (e.g., abundance and mean length of spawning adults and temporal pattern of spawning migrations) that can be used to differentiate individual spawning populations of Yellowstone cutthroat trout in the Yellowstone Lake drainage. The relationship between life history organization of Yellowstone cutthroat trout and physical environment is not adequately understood, however, because the information necessary to examine these relationships is scarce and environmental degradation is widespread. The fishery database of the U.S. Fish and Wildlife Service and U.S. National Park Service for Yellowstone Lake is a notable exception. Although these data were not collected specifically to address population–environment interactions, they represent one of the most extensive sources of information on cutthroat trout in the world.

The purpose of this paper is to examine specific life history traits of adfluvial cutthroat trout spawning populations in Yellowstone Lake relative to physical characteristics of tributary drainages and subbasins in the lake. Using fishery data collected during the mid-1980s, we sought to answer the following questions: What basin-scale physical variables differentiate tributary drainages in the Yellowstone Lake watershed? What are the relationships between physical characteristics of tributary drainages and time of the peak in the cutthroat trout spawning migration, duration of spawning migration, and mean length of cutthroat trout spawners from individual tributaries? Is variation in length and growth of mature cutthroat trout detectable among subbasins of the lake? Finally, what are some of the ecological and management implications of the observed life history variation of cutthroat trout in the Yellowstone Lake watershed?

Background

Yellowstone Lake supports at least 68 lacustrine–adfluvial populations of cutthroat trout that return to natal streams to spawn (Gresswell et al. 1994). Homing of spawning cutthroat trout to natal streams, return of spawning cutthroat trout to the same stream in successive years, and return of experimentally displaced spawners in the same year

all have been documented, and straying appears to be 3% or less (Ball 1955; Cope 1957; McCleave 1967). Furthermore, Benson and Bulkley (1963) suggested that mature cutthroat trout may exhibit fidelity to specific regions of the lake throughout the summer.

Yellowstone cutthroat trout spawn between April and August in tributaries to Yellowstone Lake (Ball 1955; Cope 1956, 1957; Jones et al. 1986), and timing (peak and duration) of annual spawning migrations varies among streams (Gresswell et al. 1994). Yellowstone cutthroat trout spawners remain in tributaries from 1 to 3 weeks (Ball and Cope 1961). Although estimates of instream spawning mortality approach 50% in some cases (13–48%; Gresswell 1995), iteroparity is common (Gresswell and Varley 1988).

Several weeks after emergence, most larval Yellowstone cutthroat trout emigrate to the lake, but some may overwinter in their natal streams (Welsh 1952; Benson 1960). Evidence of extended residence has been observed in some streams (Gresswell et al. 1994). Immature cutthroat trout occupy pelagic areas of Yellowstone Lake where zooplankton are abundant and predator density is low (Gresswell and Varley 1988). Mature cutthroat trout generally reside in the littoral zone. Macroinvertebrates, such as *Gammarus lacustris, Hyallela azteca,* and a variety of aquatic insects dominate the diet of larger cutthroat trout in the lake (Benson 1961; Jones et al. 1990).

Yellowstone Lake and its watershed have not been subjected to large-scale environmental degradation because they are in a national park. Hatchery supplementation and high levels of angler harvest during the first half of the Twentieth Century led to alterations of Yellowstone cutthroat trout population structure and changes in species composition in the lake. Hatchery operations were suspended in the mid-1950s, and harvest has been restricted since the early 1970s. A shift in population structure toward a greater proportion of older and larger fish has been documented since the implementation of more restrictive angling regulations (Gresswell and Varley 1988; Gresswell et al. 1994). The relatively low level of anthropogenic environmental disturbance in the Yellowstone Lake ecosystem, coupled with a fishery database that extends back to the late 1940s, provides a unique opportunity to study the interactions among basin-scale physical characteristics of tributary drainages and life history attributes (i.e., spawning migration timing and spawner length) of Yellowstone cutthroat trout.

Study Area

Physical setting.—At an elevation of 2,357 m, Yellowstone Lake is the largest high-altitude lake (elevation > 2,000 m) in North America. Surface area is about 34,000 ha, and the shoreline length is 239 km (Kaplinski 1991). Vegetation in the drainage basin (261,590 ha, Benson 1961) is predominately lodgepole pine *Pinus contorta* forest and subalpine meadows. Tertiary andesite and Quaternary rhyolite underlie much of the drainage, but Tertiary sedimentary deposits are present in several tributary drainages in the southern portion of the basin (USGS 1972). Postglacial lacustrine, fluvial, and deltaic deposits are common at lower elevations within the basin, recording periods when lake level was more than 24 m above the present surface (Richmond 1976).

A total of 124 tributaries to Yellowstone Lake have been identified (Hoskins 1974, 1975; Jones et al. 1986, 1987), but several are ephemeral. With a drainage area of almost 110,000 ha, the Yellowstone River upstream from Yellowstone Lake is the largest tributary, draining about 42% of the watershed. Because this tributary to the lake's Southeast Arm is remote (Figure 1), it has been sampled irregularly, and we have omitted it from our analysis. Pelican Creek, which enters the lake's north end, has the second largest drainage area (17,656 ha). Pelican, Chipmunk, Beaverdam, Clear, Columbine, Sedge, Arnica, Solution, Grouse, and Cub creeks (Figure 1) account for 31% of the total lake drainage area. Eighty-one tributaries have drainage areas less than 100 ha; some cover only 5 ha, and they collectively represent 1% of the study area.

Of the 11 streams with the largest drainages, 9 empty into the South Arm, Southeast Arm, and along the east shore of the lake (Figure 1). Arnica Creek and Solution Creek flow into West Thumb. None of the tributary drainages larger than 2,000 ha enter along the west shore of Yellowstone Lake. Spawning has been observed in 68 tributaries (Figure 2), but 16 of these are used only in years of high stream discharge (Jones et al. 1987).

Yellowstone Lake comprises a north–south-oriented main basin and six subbasins (Kaplinski 1991). The main basin, defined by the 80-m depth contour, extends northwest from the Southeast Arm (Figure 3). West Thumb is the largest of the second-order subbasins. Strong prevailing winds from the southwest generate surface currents toward the northeastern shore, bottom currents back to the southwest, and upwelling in West Thumb

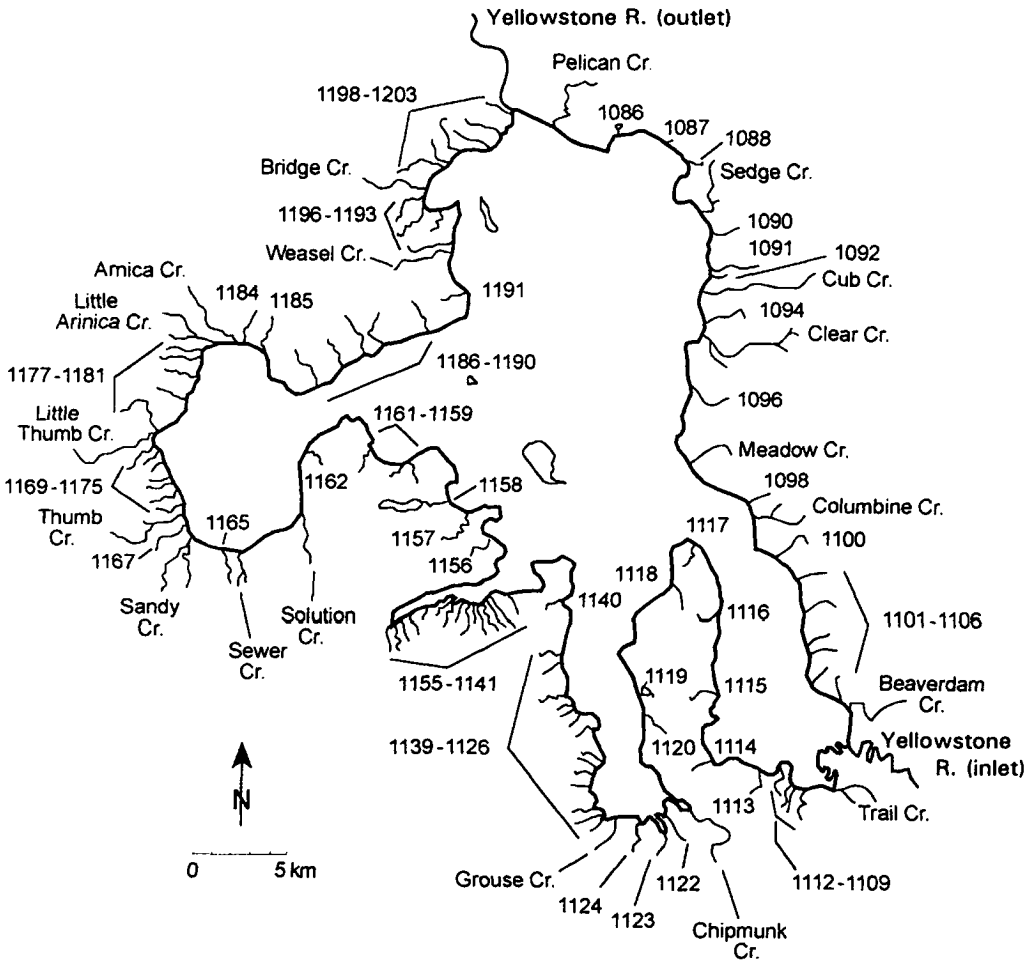

FIGURE 1.—Yellowstone Lake and tributaries. Streams are identified by the first four digits of the 15-digit number designated by the system for numbering streams and lakes in Yellowstone National Park (Mahony and Lentsch 1986). See Figure 3 for lake basins and other features.

(Benson 1961). The northern portion of the lake has two subbasins, one south of the Yellowstone River outlet, and a second in Mary Bay, a hydrothermal explosion crater (Wold et al. 1977). Three other subbasins, South Arm, Flat Mountain Arm, and the channel connecting West Thumb to the main lake basin, occupy areas carved by Late Pleistocene fluvial and glacial activity (Kaplinski 1991). South Arm is relatively protected from prevailing winds and has two large tributaries, Chipmunk and Grouse creeks.

Fishes.—Yellowstone cutthroat trout and longnose dace *Rhinichthys cataractae* are native to Yellowstone Lake (Simon 1962). Redside shiner *Richardsonius balteatus*, lake chub *Couesius plumbeus*, and longnose sucker *Catostomus catostomus*, were introduced and have become established during this century (Gresswell and Varley 1988). Yellowstone cutthroat trout and longnose suckers are distributed throughout the lake basin. Redside shiners, lake chub, and longnose dace are limited to shallow areas around the shoreline, exclusive of islands.

In 1994, lake trout *Salvelinus namaycush* were collected for the first time from Yellowstone Lake (Kaeding et al. 1996). In addition to potential competitive interactions (e.g., Marrin and Erman 1982; Griffith 1988) between the two salmonid species, Yellowstone cutthroat trout likely will be the major prey of the piscivorous lake trout (Marnell 1986, 1988; McIntyre 1995). Although the presence of this aggressive predator may substantially alter the abundance and demography of Yellowstone cut-

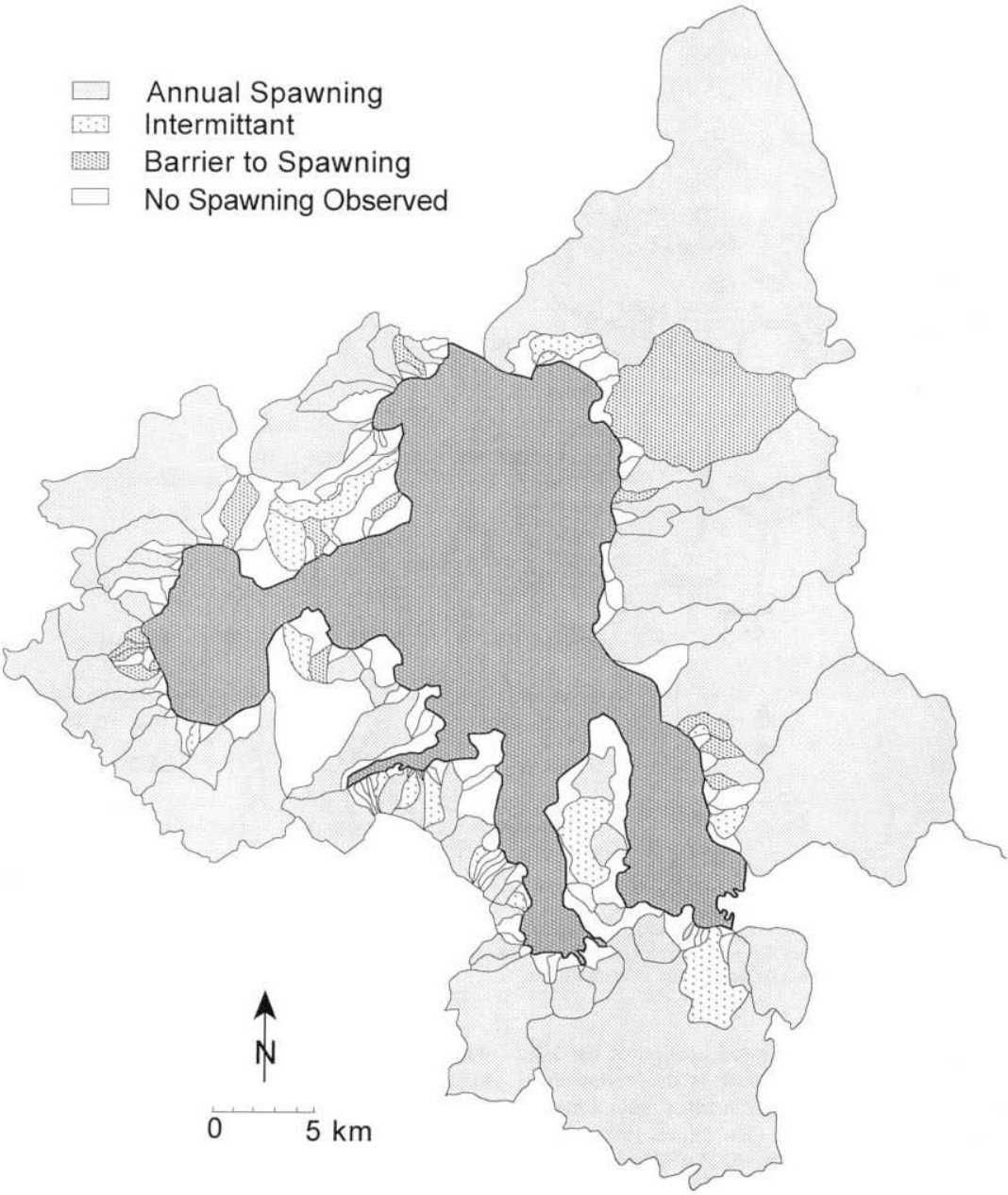

FIGURE 2.—Drainage areas above Yellowstone Lake (darkest shading) used by adfluvial Yellowstone cutthroat trout for spawning.

throat trout in the lake (McIntyre 1995), data used in our analysis (1979–1992) were collected before lake trout numbers had increased to a point of detection. Therefore, we have assumed that the influence of lake trout on the results and interpretation of this study have been small.

Methods

Physical characteristics.—Basin-scale physical variables were compiled for 115 tributaries (Table 1). These data were obtained from a geographical information system (GIS) maintained in Yellowstone National Park. Several additional physical

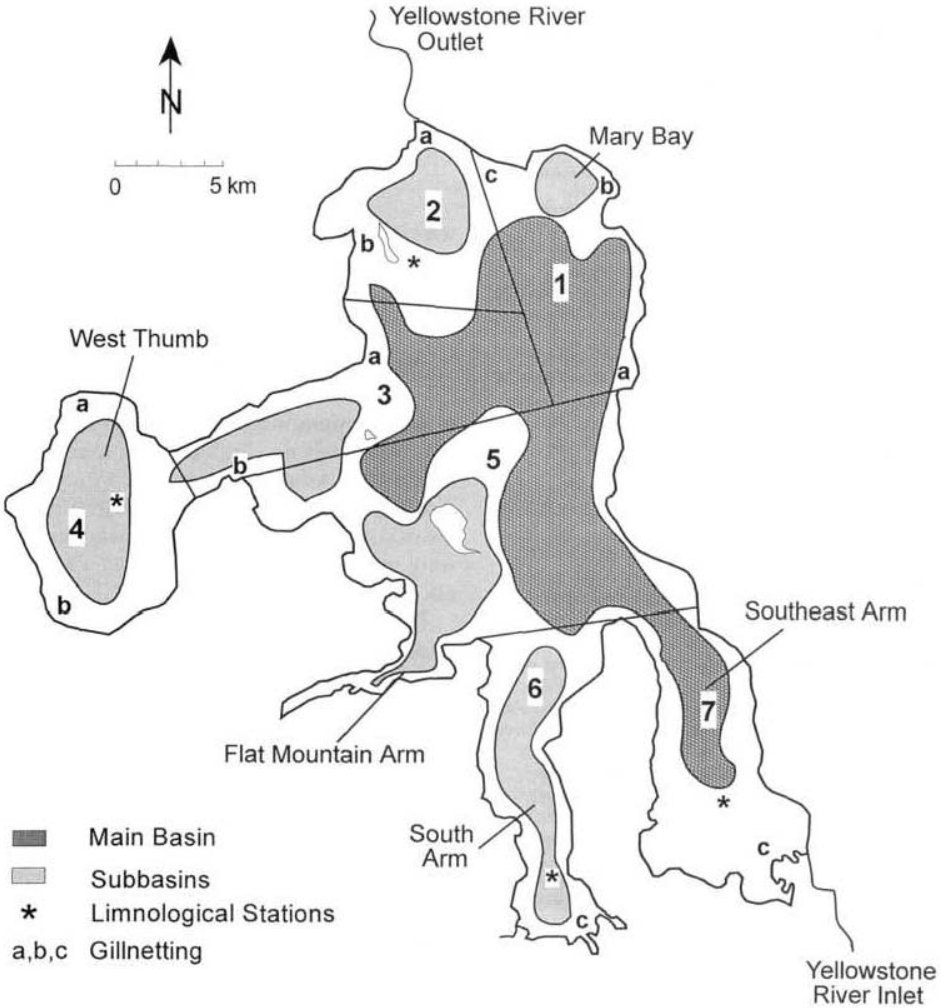

FIGURE 3.—Creel survey, gill-net, and limnological sampling stations, Yellowstone Lake. Lake subbasins correspond to bathymetric mapping by Kaplinski (1991). For management purposes, the lake has been partitioned (straight lines) into seven areas: (1) Mary Bay, (2) Yellowstone River outlet and Bridge Bay, (3) channel connecting West Thumb to the main lake basin, (4) West Thumb, (5) Flat Mountain Arm and Frank Island, (6) South Arm, and (7) Southeast Arm.

variables were obtained from U.S. Geological Survey 7.5-minute topographic maps (Table 1): location of tributary stream mouth; longitudinal tributary profile (slope and intercept; Hack 1957); stream order and link number (Leopold et al. 1964); main-stem length, slope, and maximum elevation; and lengths of stream (km) and percentages of total stream length below the 2,440-m and 2,395-m elevational contours.

Life history characteristics.—Between 1985 and 1987, 27 spawning streams were visited once every 2 weeks from late May through July to assess the progress of the cutthroat trout spawning migration; each stream was monitored in at least two of the three study years. Fish were counted in a 100-m reference section by observers walking along the shoreline (Jones et al. 1986, 1987; Reinhart 1990). An estimate of mean total length of spawners was obtained from samples of cutthroat trout collected from each stream by electrofishing in the reference section during the peak migration (Jones et al. 1986, 1987; Table 2). More detailed data on migration pattern and spawner length were obtained at Clear Creek, where a weir was used

TABLE 1.—Physical variables for 115 tributaries of Yellowstone Lake obtained from the Yellowstone National Park geographical information system (GIS, U.S. National Park Service, Yellowstone National Park) and from topographic maps (7.5-minutes series, U.S. Geological Survey, Reston, Virginia).

Variable (source)	Method of estimation
Drainage basin size (GIS)	Estimated by summing area (ha) of each geological bedrock type within the individual stream drainages
Geological bedrock type (GIS)	Recorded as percentage of total drainage area (ha); the 26 geological types were grouped into four major categories: Tertiary andesite, Quaternary rhyolite, Quaternary surficial deposits (detritus, hot-spring deposits, and hydrothermal explosion deposits), and sandstone (including sandstone, limestone, siltstone, and shales)
Link number (map)	Number of first-order tributaries within each stream drainage (Leopold et al. 1964)
Location of tributary stream mouth (map)	Coordinates of the mouth of each tributary to Yellowstone Lake designated by the universal transverse mercator (UTM) grid system (Grubb and Eakle 1988)
Longitudinal profile (map)	Described by slope and intercept of the linear regression of linear distance from the main-stem source and elevation (Hack 1957). Main stem was defined as the longest continuous channel in each individual stream basin. Distance from the source and elevation were recorded in meters at each elevational contour along the main stem. The natural logarithm of distance was the predictor variable in the regression, and elevation was the response variable
Maximum elevation (map)	Elevation (m) at the main stem source
Mean aspect (GIS)	Weighted mean estimated by multiplying the midpoint of each 15-degree aspect class (ranging from 1 to 360 degrees) by the area estimated for that class and summing for all classes; the sum was divided by the total area of the drainage
Mean elevation (GIS)	Weighted mean estimated by multiplying the midpoint of each 10-m elevation class by the area estimated for that class and summing for all classes; the sum was divided by the total area of the drainage
Mean slope (GIS)	Weighted mean estimated by multiplying the midpoint of each 10-degree slope class by the area estimated for that class and summing for all classes; the sum was divided by the total area of the drainage
Proportion of stream in low-elevation reaches (map)	Length of stream (km) and percentage of total stream length below the 2,440-m and 2,395-m elevational contours (lake level ≈ 2,360 m)
Stream order (map)	Designation according to Leopold et al. (1964)
Weighted main-stem slope (map)	Weighted mean slope of the main stem for each tributary estimated by multiplying the midpoint between elevational contours (m) and summing for all intervals; the sum was divided by the total length of the main stem
Water yield (GIS)	Total precipitation for each stream drainage basin calculated by multiplying the midpoint of each 40-cm precipitation class (based on a 30-year mean, 1960–1990) by the area in the class and summing

to collect migrating fish in 1987 (Jones et al. 1988). All individuals moving upstream were tallied, and the lengths (total length, nearest 5 mm) of 75 cutthroat trout spawners were measured daily. Once a week an additional 100 cutthroat trout spawners were measured (nearest 1 mm) and weighed (nearest 2 g) at Clear Creek.

The following life history information was obtained from each tributary: (1) spawning migration peak, measured as mean day of year (counted from January 1) when the greatest number of cutthroat trout spawners were observed in each tributary; (2) duration of spawning migration, expressed as mean number of days that cutthroat trout spawners were observed in individual spawning streams; and (3) mean total length (mm) of cutthroat trout spawners sampled in the spawning streams.

Daily counts of cutthroat trout spawners and stream gauge height information collected at Clear Creek during a 10-year period between 1979 and 1991 (1979–1981, 1983–1984, 1987–1991) were used to investigate the relationship between migration timing and peak stream discharge. Spawner counts were tabulated relative to the date of peak discharge, and fish moving on each day (relative to the peak discharge) were summed for the entire sample. Finally, the proportion of the fish migrating daily was plotted relative to the day of peak discharge.

Analysis.—Statistical analyses were accomplished by using Number Cruncher Statistical Systems (Hintze 1992). Among-stream distributions of physical and life history variables were tested for normality (Kolmogorov–Smirnov normality test), and variables that were not normally distributed were transformed to a logarithmic scale ($\log_{10}$). Principal components analysis (PCA) was used to identify basin-scale physical characteristics that were most useful in discriminating among 115 tributary drainages in the Yellowstone Lake

TABLE 2.—Date (day of year counted from January 1) of peak abundance and duration of the annual cutthroat trout spawning migration and mean length of cutthroat trout spawners in 27 tributaries to Yellowstone Lake, 1985–1987. Streams are numbered as in Figure 1.

Stream	Peak of spawning migration (day of year)			Duration of spawning migration (d)			Mean length (mm) of spawners (sample size)
	Mean	Maximum	Minimum	Mean	Maximum	Minimum	
1091	165	168	159	33	42	23	386 (8)
1095	172	182	163	65	78	52	382 (4,412)
1103	184	185	182	28	28	27	376 (28)
1111	164	170	158	40	40	39	305 (31)
1113	161	163	159	42	42	41	342 (27)
1123	160	165	154	35	42	27	363 (33)
1126	157	157	156	38	42	33	374 (58)
1127	157	157	156	44	55	33	368 (11)
1138	165	171	155	43	49	35	331 (23)
1146	167	178	155	23	29	13	316 (18)
1155	179	198	158	67	74	56	359 (122)
1164	155	165	149	37	63	22	354 (125)
1166	158	170	145	71	74	68	349 (87)
1167	147	155	138	72	74	70	357 (69)
1168	158	170	145	26	26	26	349 (104)
1169	166	170	161	92	169	40	342 (100)
1176	169	177	161	46	53	38	346 (351)
1177	166	170	161	52	64	40	351 (167)
1179	158	171	145	41	63	18	365 (45)
1180	158	171	145	23	28	18	346 (14)
1182	158	171	145	55	74	45	369 (51)
1192	162	171	153	22	25	19	337 (28)
1197	149	171	127	45	61	33	358 (54)
1198	157	167	147	31	35	26	357 (93)
1199	150	154	146	44	47	41	333 (13)
1201	147	154	140	58	75	41	358 (86)
1203	143	154	131	96	176	40	344 (60)

watershed. Using data from all tributaries for which information was available increased the likelihood that results would be representative of tributaries in the Yellowstone Lake watershed as a whole. Correlation matrices of physical variables were used in the analysis to reduce the effects of scaling and unequal variances among variables. After initial analysis, variables with low component loadings (<0.40) were eliminated, and the remaining variables were reanalyzed via varimax rotation (Tabachnick and Fidell 1989).

Relationships among physical variables and life history characteristics for the 27 streams were subjected to ecological response surface analysis (Bartlein et al. 1986). First-, second-, and third-order polynomial regressions with one and two predictor variables were analyzed in an attempt to find the model that explained the most variation in the response variable. Predictor variables were selected from the set of physical variables that displayed the highest component loadings (correlation between variables and an individual component) for each of the first three components of the PCA. Specific predictor variables were chosen on the basis of relative component loading, ease of measurement, and accuracy and precision of variable measurement. Separate relationships were developed for each of the three response variables (mean date of spawning migration peak, mean duration of spawning migration, and mean length of cutthroat trout spawners).

Yellowstone Lake.—For management purposes, Yellowstone Lake has been divided into seven zones (Figure 3) that approximate the subbasins described above (Jones et al. 1982; Kaplinski 1991). Digitized depth profiles for these zones were entered into a GIS database at the Pacific Northwest Experimental Station (U.S. Forest Service, Corvallis, Oregon). Mean depth and littoral area (percent of lake surface area represented by water < 10 m deep) were estimated for each zone (Table 3). From 1977 to 1982 limnological data, including water transparency (Secchi disc), surface water temperature, and pH at 2 m depth, were collected at stations in the South Arm, Southeast Arm, West Thumb, and Stevenson Island (Figure 3); these data were obtained in July during thermal stratification.

Creel surveys reflected effects of angling regulations through time and variations in angling in-

TABLE 3.—Mean length and growth index (P) of cutthroat trout captured in gill nets from six of seven management zones in Yellowstone Lake, 1978–1992; mean depth and percent of total area shallower than 10 m, estimated from digitized depths provided by Kaplinski (1991); mean pH and mean surface water temperature obtained from four sample stations in Yellowstone Lake, 1978–1984; and mean number of cutthroat trout harvested annually from the Yellowstone Lake fishery 1978–1992.

Variable	Lake management zone					
	1	2	3	4	6	7
Mean length of prespawners	389	385	386	373	414	408
Growth index (P)	2.62	2.66	2.57	2.48	2.75	2.71
Percent of area < 10 m deep	18.8	17.9	9.8	14.5	23.4	22.5
Mean depth (m)	66.5	45.5	66.9	59.7	45.0	55.9
pH	7.39	7.39	7.39	7.33	7.54	7.38
Temperature (°C)	11.1	11.1	11.1	9.9	11.3	11.2
Mean annual harvest	2,451	17,882	2,999	7,101	913	731

tensity among zones. The number of cutthroat trout harvested in each of the seven management zones was estimated annually by a volunteer postal survey, the Volunteer Angler Report (VAR; Varley et al. 1976). Adjustments for card return bias were applied to all estimates, and procedures for data collection and estimation were unchanged from 1978 through 1992.

Indices of population length structure and relative abundance were determined from fish collected by experimental gill nets in six of the seven management zones. Gill nets were set in Yellowstone Lake annually from 1978 through 1992 during the third week of September. Eleven sites (Figure 3) were sampled each year during a 5-d sample period, and five nets were set overnight at a site once during the sample period. Monofilament nets were 38 m long, 1.5 m deep, and comprised 7.6-m-long panels of 19-, 25-, 32-, 38-, and 51-mm (bar measure) mesh netting. Nets were set perpendicular to shore in water 1.5–5-m deep and spaced approximately 100 m apart.

Cutthroat trout from each net were arranged from longest to shortest, measured to the nearest 1 mm (total length), and weighed to the nearest 2 g. Sex and stage of maturity were determined from the gonads; individuals judged to have sufficient gonadal development to spawn in the subsequent spring were designated as prespawners. Scales were collected from the longest fish and from every third fish in the length-ordered cline. Age was back calculated from scales; sample sizes ranged from 169 to 347 fish annually. Criteria developed by Laakso and Cope (1956) were used to detect lack of first year annuli, and age was adjusted upward if necessary. Mean length was calculated for all fish in an age-group at each sample site.

Growth parameters were obtained by the Brody–von Bertalanffy procedure (Ricker 1975). The Brody growth coefficient (K) and the theoretical asymptotic length (L_∞) were estimated by fitting mean length for each age-group to a specialized form of the von Bertalanffy growth formula (surface factor D = 1; Pauly 1984). For among-site comparisons, L_∞ was converted to asymptotic weight (W_∞) via a length–weight functional relationship (Ricker 1975) that was determined annually from all fish captured at the respective site, and the resulting value was combined with K to estimate the index of growth performance (P; Pauly 1979) for that site and year.

Analysis of gillnetting data focused on among-zone differences in length and growth of cutthroat trout. To compensate for interannual variation in the proportion of immature cutthroat trout captured in gill nets, among-zone comparisons of length and growth were limited to prespawners (individuals with sufficient gonadal development to spawn the following spring). Repeated-measures analysis of variance (ANOVA; Maceina et al. 1994) was used for comparisons of mean length and growth performance index (P). Lake zone was the primary factor of interest. Sample year was added to the model as a fixed factor, and netting sites were nested within zones. Multiple mean comparisons were obtained using Newman–Keuls procedures. Relationships among fish length and growth, zone environment, and angler harvest were investigated by calculating Pearson correlation coefficients for mean length of prespawners, growth index (P), limnological parameters, and mean number of cutthroat trout harvested annually.

Results

Tributary Drainages

Stream drainages in the Yellowstone Lake basin varied along multivariate gradients of basin-scale

TABLE 4.—Component loadings (correlation between variables and an individual component) for principal components analysis (PCA) of cutthroat life history in 115 Yellowstone Lake tributaries. The percent of variation explained by individual components after varimax rotation of physical variables is shown in parentheses under the component number.

Variable	PCA component 1 (33%)	2 (24%)	3 (14%)	4 (7%)
Drainage basin area	−0.90			
Andsesite (% of basin)			0.74	
Rhyololyte (% of basin)				
Mean aspect (basin)			0.87	
Mean slope class (basin)				
Average elevation (basin)		−0.81		
UTM[a]-east			0.80	
UTM[a]-north				0.93
Stream order	−0.80			
Maximum elevation (basin)		0.90		
Total length of tributary	−0.84			
Slope of profile regression		−0.85		
Intercept of profile regression		−0.85		
Weighted mean slope (basin)	0.78			
Water yield (mean for basin)	−0.89			
Link number	−0.79			
Length of stream below 2,440-m elevation	−0.91			

[a] Universal transverse mercator (coordinates of the stream mouth).

physical variables (Table 1). Approximately 71% of the variation among 115 tributaries was expressed in the first three components of the rotated PCA. The first component was dominated by variables associated with stream length and drainage basin size (Table 4). Basin elevation and stream profile variables characterized the second component, and mean aspect and location (UTM–east) were the primary variables in the third component. The fourth component was represented by the location variable (UTM–north), and it accounted for an additional 7% of the variation among streams.

Life history variables measured for fish in the subset of 27 spawning streams varied extensively (Table 2). Mean length of cutthroat trout spawners ranged from 305 to 386 mm. Date of peak spawning ranged from day 143 (late May) to day 184 (early July) during the study period. Duration of spawning migrations averaged about 47 d but varied in individual streams from 22 to 96 d. Among-year variation in migration duration was greatest in populations with the longest periods of spawning.

Drainage area, mean elevation, and mean aspect were chosen to represent the first, second, and third components as predictor variables for polynomial regression analysis (Table 5). Mean elevation and aspect of the tributary drainage were directly related to the date of the spawning migration peak, but none of the predictor variables produced statistically significant relationships with duration of spawning migration (Table 5). In linear regressions with single predictor variables, about 50% of the variation in date of peak migration was attributable to either mean aspect ($P \leq 0.01$, $r^2 = 0.51$) or mean elevation ($P \leq 0.01$, $r^2 = 0.48$) alone (Table 5). The best predictor of the date of the spawning migration peak was a third-order polynomial regression of drainage area and mean aspect ($P \leq 0.01$, $R^2 = 0.64$).

The resulting response curve provided a reasonable representation of the complex relationship between the basin-scale physical variables (drainage area and mean aspect) and the peak of the

TABLE 5.—Coefficients of determination (R^2) for first- (linear), second- (quadratic), and third-order (cubic) polynomials describing relationships among physical (predictor) variables that characterize the drainage basin and life history (response) variables that describe attributes of annual Yellowstone cutthroat trout spawning migrations in 27 tributaries to Yellowstone Lake. Asterisks denote $P \leq 0.05$* or $P \leq 0.01$**.

Basin-scale variables	Date of peak migration			Mean length of spawners			Mean duration of migration		
	Linear	Quadratic	Cubic	Linear	Quadratic	Cubic	Linear	Quadratic	Cubic
Log_{10}ha (hec)	0.06	0.06	0.07	0.12	0.13	0.33	0.00	0.02	[a]
Mean elevation (melv)	0.48**	0.48**	[a]	0.02	0.11	[a]	0.09	0.19	0.22
Mean aspect (masp)	0.51**	0.52**	[a]	0.07	0.33**	0.36**	0.06	0.13	[a]
Hec, melv	0.48**	0.53**	[a]	0.12	0.39	[a]	0.11	0.28	[a]
Hec, masp	0.51**	0.54**	0.64**	0.15	0.53**	0.63*	0.08	0.30	0.49
Melv, masp	0.57**	0.61**	[a]	0.08	0.34	[a]	0.09	0.21	[a]
Hec, melv, masp	0.57	[b]	[b]	0.16	[b]	[b]	0.12	[b]	[b]

[a] Correlation matrix becomes singular.
[b] Insufficient sample size.

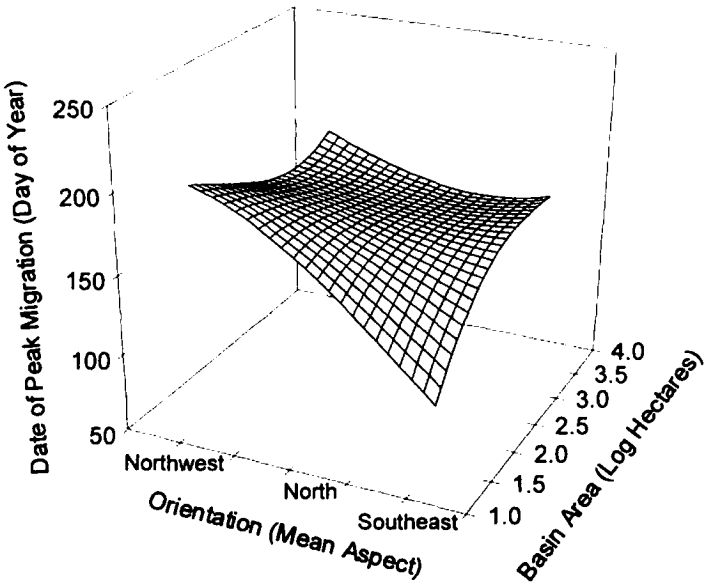

FIGURE 4.—Ecological response surface predicted by a third-order polynomial regression with drainage basin area ($\log_{10}$ ha) and mean aspect as predictor variables and date of peak cutthroat trout spawning migration in 27 tributaries to Yellowstone Lake as the response variable.

spawning migration (Figure 4). The response surface suggests that in smaller drainages, spawning migration peaks earlier in tributaries with a predominately southern aspect than in tributaries with a northern orientation. The importance of aspect diminishes in larger drainages, however. A trend toward later migration peaks accompanies increasing drainage size, but the rate of change appears to be affected by basin orientation. Thus, peak migrations are predicted to occur earliest in small basins with a predominantly southeastern aspect; large drainages with a predominantly northwestern aspect support the latest migration peaks.

The cutthroat trout spawning migration in Clear Creek was directly related to the pattern of stream discharge during the spring runoff. When the numbers of cutthroat trout spawners entering Clear Creek daily were summed over time (10 sample years between 1979 and 1991) in relation to the relative date of peak stream discharge, the majority of cutthroat trout spawners migrated upstream after peak stream discharge (Figure 5). During individual years, 87% (1981) to 98% (1987) of the cutthroat trout spawners migrated upstream after the peak stream discharge (mean, 92%).

Mean aspect was the only individual predictor variable that yielded a statistically significant relationship with mean length of cutthroat trout spawners (Table 5). Variation in mean length of cutthroat trout spawners was best explained by a third-order polynomial regression, with drainage size and mean aspect as predictor variables (Table 5; $P \leq 0.05$, $R^2 = 0.63$). Mean length of spawners appeared to be relatively constant in drainages with a southeastern orientation, regardless of drainage size, but in north-oriented tributaries mean length of spawners was related to drainage size (Figure 6). Spawners with the longest total length occurred in large drainages with a northwest orientation, and spawners with the shortest total length were found in small drainages with a similar orientation. Mean length of spawners in smaller drainages declined as basin orientation shifted from southeast to northwest; in large basins, spawner length generally increased from the southeast to the northwest.

Yellowstone Lake

Among-zone, among-site, and among-year differences in mean length of cutthroat trout prespawners were significant (ANOVA; $P < 0.05$), but interactions of zone and year were not ($P > 0.05$). The shortest prespawners were in zone 4 (West Thumb), the longest were collected in zones 6 (South Arm) and 7 (Southeast Arm) (Table 6). Mean length of cutthroat trout from zone 4 was significantly different from that in zones 6 and 7 (Newman–Keuls multiple comparison; $P \leq 0.05$).

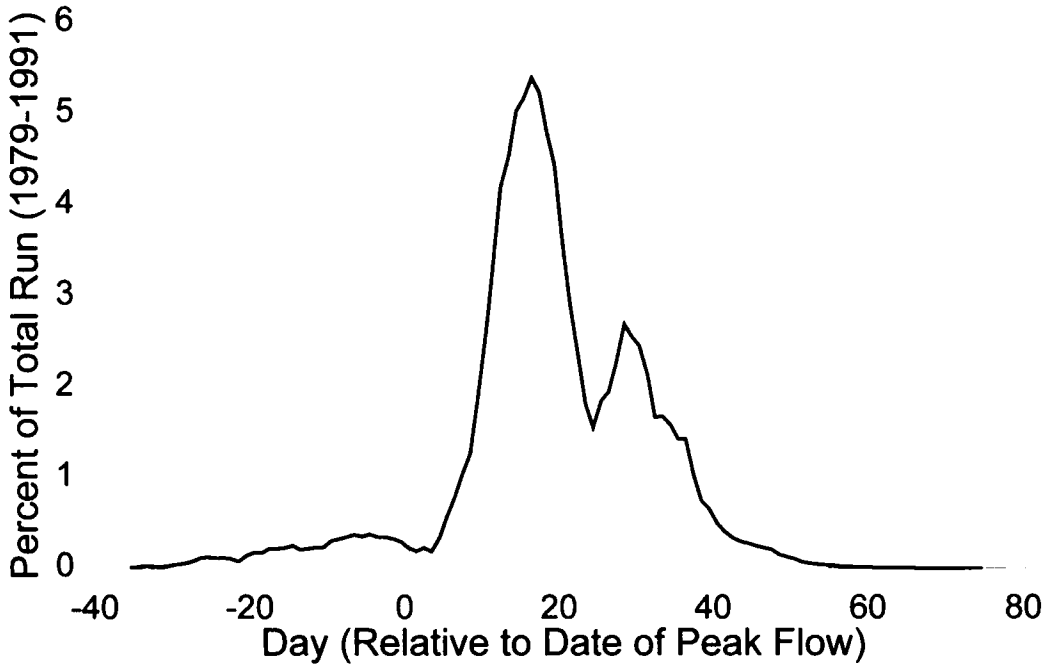

FIGURE 5.—Generalized pattern of Yellowstone cutthroat trout spawning migration into the Clear Creek tributary to Yellowstone Lake. Spawner counts from 1979–1981, 1983–1984, and 1987–1991 were arranged relative to the peak discharge date (0) in each year of sampling. Fish moving a given number of days before or after the peak discharge date were summed for the entire period (e.g., all fish moving 3 d before or 12 d after a discharge peak were summed across years), and daily sums were converted to percentages of all migrants counted in the 10 sampling years.

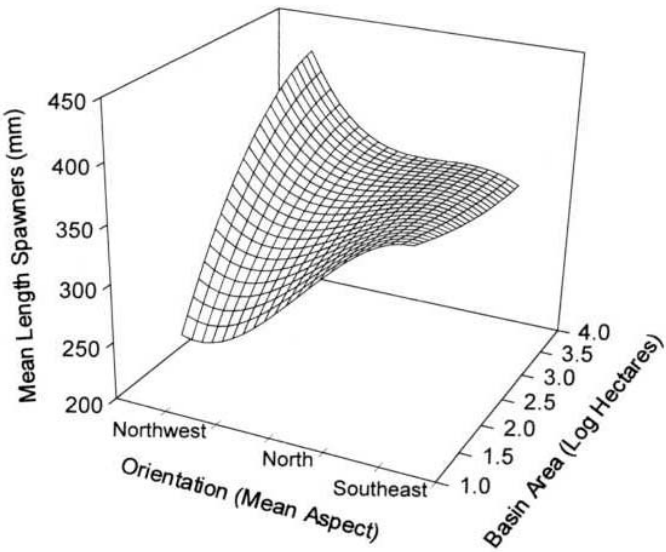

FIGURE 6.—Ecological response surface predicted by a third-order polynomial regression with drainage basin area ($\log_{10}$ ha) and mean aspect as predictor variables and mean length of cutthroat trout spawners in 27 tributaries to Yellowstone Lake as the response variable.

TABLE 6.—Comparison (repeated-measures ANOVA) of mean length of prespawners and growth index (P) of cutthroat trout caught in six of seven management zones in Yellowstone Lake, 1978–1992.

Lake zone	Sample size	Mean length of prespawners (mm)	Significantly different zones[a]	Mean growth index (P)[b]
4	28	373	7, 6	2.48
2	42	385	6	2.66
3	28	386	6	2.57
1	28	389		2.62
7	14	408	4	2.72
6	14	414	4, 2, 3	2.75

[a] Newman–Keuls multiple means comparisons: $P \leq 0.05$.
[b] Growth indexes did not vary significantly among lake zones (Newman–Keuls $P > 0.05$).

Differences in the growth index among the zones of Yellowstone Lake were not significant (ANOVA: $P > 0.05$; Table 6). Differences attributable to effects of netting site and sample year were significant ($P \leq 0.05$), but the interaction effect of the zone and year was not ($P > 0.05$).

Cutthroat trout length and growth in disparate areas of Yellowstone Lake were related to physical and limnological characteristics of individual subbasins (Table 7). The relationships between mean length of prespawners and littoral area (proportion of lake surface area represented by water < 10 m deep; $r = 0.78$; $P = 0.07$), pH ($r = 0.77$; $P = 0.07$), and water temperature ($r = 0.73$; $P = 0.10$) were all positive. Growth index exhibited positive relationships with mean surface temperature ($r = 0.84$; $P = 0.04$), proportion of littoral area ($r = 0.81$; $P = 0.05$), and pH ($r = 0.75$; $P = 0.09$). Coefficients of correlation suggested weak (negative) linear associations between mean angler harvest of cutthroat trout and both mean length of prespawners and the growth index from six management zones (Table 7).

Discussion

Our data suggest that physical characteristics of spawning tributaries in the Yellowstone Lake basin influence life history traits of adfluvial cutthroat trout spawners in complex ways. Basin area, mean aspect, and elevation of tributary drainages appear to affect timing of cutthroat trout spawning migration. The strongest relationship was described by a third-order polynomial regression with drainage basin area and mean aspect as predictor variables. The shape of the resulting response surface implies that the hydrological factors determined by basin area and aspect favor spawning in mid-June (approximate day of year, 165) in most drainages (Figure 4). Optimal spawning conditions apparently occur earlier in small drainages with southeasterly aspect than in northwest-oriented drainages with a large drainage area. The predicted pattern follows the general progression of snowmelt in the Yellowstone Lake basin, which occurs earliest at lower elevations along the western and northern portions of the basin (i.e., drainages with southeastern and southern aspects). Warmer air temperatures at low elevations and direct radiation on south-facing slopes influence this temporal and spatial progression. For example, peak discharge in Pelican Creek, which drains much of the northern portion of the Yellowstone Lake basin (southern aspect), often occurs 2 weeks before it does in Clear Creek, a tributary draining the higher elevation of the Absaroka Mountains in the eastern basin (northwest aspect). Arnica Creek flows into West Thumb from the west (southeast aspect), and discharge usually peaks by mid-May.

Because drainage area, elevation, and aspect

TABLE 7.—Pearson correlation coefficients (P in parentheses) between mean length and growth index of cutthroat trout prespawners captured in gill nets in six management zones in Yellowstone Lake and limnological variables characterizing the zones and the mean number of cutthroat trout harvested annually from each zone, 1978–1992.

Variable	Variable 1	2	3	4	5	6
1 Mean length of prespawners						
2 Growth index (P)	0.92 (0.01)					
3 Mean depth (m)	0.45 (0.37)	−0.62 (0.19)				
4 Proportion of area < 10 m deep	0.78 (0.07)	0.81 (0.05)	−0.61 (0.19)			
5 Mean pH	0.77 (0.07)	0.75 (0.09)	0.56 (0.25)	0.55 (0.26)		
6 Mean surface water temperature (°C)	0.73 (0.10)	0.84 (0.04)	0.24 (0.64)	0.42 (0.41)	0.61 (0.20)	
7 Mean annual harvest	−0.53 (0.27)	−0.19 (0.71)	0.41 (0.41)	−0.21 (0.69)	−0.31 (0.55)	−0.20 (0.70)

strongly affect the annual hydrograph in fluvial systems (Morisawa 1968), the influence of physical drainage basin characteristics on migration timing is not surprising. Water flow is related to the timing of upstream migration for many fish species (Jonsson 1991). In Clear Creek, the peak of the Yellowstone cutthroat trout spawning migration generally occurs following peak runoff as discharge decreases and water temperature increases (Jones et al. 1990); during 10 sample years between 1979 and 1991, 87–98% (mean, 92%) of the cutthroat trout spawners moved upstream after the date of the annual peak discharge (Figure 5). This pattern appears to be typical of Yellowstone cutthroat trout throughout their range (Ball and Cope 1961; Thurow and King 1994; Gresswell 1995). Among-year variation in the timing of annual spawning migrations is directly related to annual weather patterns that determine the amount of annual precipitation and the timing of snowmelt and runoff; however, the pattern of discharge among tributaries is constrained by the physical configuration of the tributary drainages.

A direct relationship between length of migrating salmonid spawners and stream size (stream length and discharge) has been noted in some fluvial systems (Schaeffer and Elson 1975; Beacham and Murray 1987; Jonsson et al. 1991). It has been argued that large rivers require higher energy expenditures for fish to reach spawning areas (Schaeffer and Elson 1975) and that larger females may be better able to dig and cover redds in larger rivers (Beacham and Murray 1987). The relationship between spawner length and tributary size does not appear to be universal, however, and L'Abée-Lund et al. (1989) did not find significant relationships between mean adult length of anadromous brown trout and river size. In the Yellowstone Lake watershed as well, there does not appear to be a simple relationship between spawner length and tributary drainage size. None of the polynomial regressions with spawner length as the response variable and basin size as the only predictor variable were statistically significant (Table 5). When basin size and mean aspect were combined as predictor variables, however, the resulting third-degree polynomial explained substantial variation in spawner length.

The relationship between mean aspect of a tributary drainage and the length of cutthroat trout spawners may not appear to be straightforward, but in the Yellowstone Lake watershed, mean aspect of a tributary drainage reflects stream location as well as orientation and exposure to the sun. The apparent influence of geographic location of streams on the length of spawners is consistent with observed differences in mean length of cutthroat trout prespawners from different areas of the lake. Although the length of prespawning cutthroat trout may be affected by angler harvest in the lake, systematic observed differences in fish length among subbasins cannot be explained by angler harvest alone (Table 7). Furthermore, correlations with water temperature, pH, and littoral area (proportion of area < 10 m deep) among lake zones suggest that growth and length of mature cutthroat trout are related to variables within the lacustrine environment. Benthic production is generally highest in littoral portions of lakes (Wetzel 1983), and increased water temperatures encountered in shallow littoral areas can influence fish growth through effects on food quality and quantity, and by changes in consumption rate and growth efficiency (Wootton 1990). In Yellowstone Lake, crustaceans and aquatic insect larvae dominate the diet of mature cutthroat trout; Benson (1961) reported that food abundance and reproduction were related to depth distribution, feeding, and movements of these fish.

Analysis of tagging studies from Yellowstone Lake suggests that cutthroat trout spawners remain together after returning to the lake following spawning. Ball and Cope (1961) summarized angler returns of cutthroat trout that had been tagged in spawning streams but angled in various parts of the lake. When adjusted for variation in angler effort among zones (Benson and Bulkley 1963), the results suggest that about 75% of the fish tagged in streams tributary to the South Arm and West Thumb were later recaptured in the subbasins fed by these streams. In our study, mean length of prespawning cutthroat trout from West Thumb and the South Arm differed significantly (Table 6). Almost two-thirds of the fish tagged in Pelican Creek, a tributary to the north shore, were recaptured in the northern part of the lake. Distribution of fish from Clear Creek (a northeastern tributary) is more complicated. The largest single accumulation of tagged fish from Clear Creek, almost 50% of the fish tagged there, were later caught in the South Arm, and they apparently remained together throughout the summer. In our study, cutthroat trout prespawners from the South Arm were the largest fish sampled in Yellowstone Lake, and these observations may partially explain why cutthroat trout spawners in Clear Creek typically exhibit a longer average length than spawners from other major tributaries in the northern portion of

the lake (Pelican Creek and Cub Creek; Jones et al. 1980, 1982).

The level of straying among cutthroat trout spawning populations in Yellowstone Lake is low (< 3% annually); however, genetic differences among populations (as measured by protein electrophoresis and mitochondrial DNA) have not been observed (D. K. Shiozawa, Brigham Young University, and R. N. Williams, Clear Creek Genetics, unpublished data). Apparently, straying and a lack of strong environmental selective pressures during the relatively short time since Yellowstone cutthroat trout reinvaded the Yellowstone River drainage after the last glaciation (approximately 12,000 years ago; Gresswell et al. 1994) have not allowed detectable genetic differentiation among the cutthroat trout spawning populations. Although there is no evidence of genetic differentiation among spawning populations in the Yellowstone Lake watershed, these populations can be separated by such phenotypic characteristics as mean length, mean age of spawners, and fecundity (Gresswell et al. 1994). Because phenotype reflects the interaction of genotype and environment, phenotypic diversity among populations of cutthroat trout in the Yellowstone Lake basin may be linked to environmental diversity among tributary drainages and within Yellowstone Lake (Healey and Prince 1995; Frissell et al. 1997). Tributaries to Yellowstone Lake vary in stream length, drainage basin area, elevation, stream profile, mean aspect, and location within the Yellowstone basin. These basin-scale factors can influence hydrological pattern, temperature regime, sediment loading, woody debris distribution, instream habitat features, bank stability, and other characteristics of streams (Frissell et al. 1986; Allan 1995; Imhof et al. 1996). Moreover, lake subbasins vary in water depth, proportion of littoral area, water temperature, and pH (Table 3), and these characteristics can directly influence food quality and quantity and thereby fish growth (Wetzel 1983; Wootton 1990).

We have presented evidence that timing of the annual Yellowstone cutthroat trout spawning migration and length of cutthroat trout spawners in tributaries to Yellowstone Lake are related to physical characteristics of the tributary watersheds, specifically to drainage aspect and tributary size. Furthermore, in Clear Creek, migration timing is associated with seasonal pattern of stream discharge. Average length of cutthroat trout spawners appears to be related to a complex interaction of drainage basin size and location of individual tributary streams in the Yellowstone Lake watershed. Statistically significant differences in length of mature cutthroat trout from different portions of the lake suggest that distribution of individuals within the lake is not random, and this distribution may influence the length of spawners in tributary streams. Although average length and growth of cutthroat trout appear to be related to their distribution in the lake, we cannot infer a direct genetic relationship between these life history characteristics and subbasin residence. The observed differences are probably phenotypic responses to variation in food quality and quantity related to dissimilarities in subbasin littoral area, surface water temperature, and other limnological characteristics.

This study has three important implications for fisheries management in freshwater lacustrine systems. First, our results underscore the organizational and developmental complexity of organisms in aquatic systems. There were no simple linear relationships among physical properties of tributaries or lake subbasins and life history characteristics of cutthroat trout in Yellowstone Lake. On the contrary, it is apparent that life history organization is influenced by a suite of physical variables. Some of these controls (e.g., climate and topography) function over broad temporal and spatial scales, and others (e.g., weather patterns and substrate composition) are focused at the local scale for short periods of time. Conditions within the natal stream are highly variable when compared to those encountered in the disparate areas of the lake. Within populations, cutthroat trout must adapt locally to the interactions of physical, chemical, and biological factors in both habitats.

Another important implication of this study is related to the character of habitat in lacustrine systems at a basin scale. The relatively pristine condition of the Yellowstone Lake drainage has contributed to the maintenance of habitat diversity that has enabled concomitant expression of variation in cutthroat trout life history traits. Habitat diversity and associated population diversity probably have contributed to the persistence of cutthroat trout in the Yellowstone Lake basin and supported recovery of the fishery from the effects of angler harvest and hatchery fish stocking that diminished in the 1970s (Gresswell and Varley 1988; Gresswell et al. 1994). Our results underscore the importance of maintaining habitat and population diversity for the persistence of potamodromous salmonids. Those management activities that lead to environmental simplification and homogeneity ultimately may have substantial negative effects

on biological organization at the levels of local populations and metapopulations (den Boer 1968; Harrison and Quinn 1989; Hanski 1991).

Finally, it is important to acknowledge that the influence of management activities will not be uniform across a watershed. For instance, fishing regulations that govern the number and size of fish that can be harvested may affect some areas of a lake more than others. This disparity implies that decisions probably should be based on more vulnerable subpopulations of fish rather than on most abundant groups or even on basin-wide averages. Similarly, the effects of nonnative species introductions may not be distributed equally within a lake basin. In Yellowstone Lake for example, recent evidence suggests that the highest densities of lake trout are found in the portion of the lake where length of adult cutthroat trout is the smallest (J. D. McIntyre, Yellowstone National Park, personal communication). Such information can be used to better predict the consequences of a particular event or activity and provide insight into possible counter measures to reduce negative repercussions.

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References

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London.

Allendorf, F. W. 1988. Conservation biology of fishes. Conservation Biology 2:145–148.

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology 2:170–184.

Allendorf, F. W., N. Ryman, and F. M. Utter. 1987. Genetics and fishery management: past, present, and future. Pages 1–20 *in* N. Ryman, and F. M. Utter, editors. Population genetics and fishery management. University of Washington Press, Seattle.

Ball, O. P. 1955. Some aspects of homing in cutthroat trout. Proceedings of the Utah Academy of Sciences, Arts, and Letters 32:75–80.

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.

Bartlein, P. J., I. C. Prentice, and T. Webb III. 1986. Climatic response surfaces from pollen data for some eastern North American taxa. Journal of Biogeography 13:35–57.

Beacham, T. D. 1984. Age and morphology of chum salmon in southern British Columbia. Transactions of the American Fisheries Society 113:727–736.

Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44:244–261.

Behnke, R. J. 1988. Phylogeny and classification of cutthroat trout. Pages 1–7 *in* Gresswell (1988).

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph 6, Bethesda, Maryland.

Benson, N. G. 1960. Factors influencing production of immature cutthroat in Arnica Creek, Yellowstone Park. Transactions of the American Fisheries Society 89:168–175.

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

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

Cope, O. B. 1956. Some migration patterns in cutthroat trout. Proceedings of the Utah Academy of Sciences, Arts, and Letters 33:113–118.

Cope, O. B. 1957. Races of cutthroat trout in Yellowstone Lake. Pages 74–84 *in* Contributions to the study of subpopulations of fishes. U.S. Fish and Wildlife Service Special Scientific Report—Fisheries 208.

den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18:165–194.

Dizon, A. E., C. Lockyer, W. F. Perrin, D. P. Demaster, and J. Sisson. 1992. Rethinking the stock concept: a phylogeographic approach. Conservation Biology 6:24–36.

Elliot, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, UK.

Evans, D. O., and C. C. Willox. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycush*, by stocking of non-native stocks. Canadian Journal of Fisheries and Aquatic Sciences 48:134–146.

Frissell, C. A., W. J. Liss, R. E. Gresswell, R. K. Nawa, and J. L. Ebersole. 1997. A resource in crisis: changing the measure of salmon management. Pages 411–444 *in* D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Gresswell, R. E., editor. 1988. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pages 36–54 *in* M. Young, editor. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-GTR-256.

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 and Aquatic Sciences 51(Supplement 1):298–309.

Gresswell, R. E., and J. D. Varley. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. Pages 45–52 *in* Gresswell (1988).

Griffith, J. S., Jr. 1988. Review of competition between cutthroat trout and other salmonids. Pages 134–140 *in* Gresswell (1988).

Grubb, R. G., and W. L. Eakle. 1988. Recording wildlife locations with the universal transverse mercator (UTM) grid system. U.S. Forest Service Research Note RM-483.

Hack, J. T. 1957. Studies of longitudinal stream profiles in Virginia and Maryland. U.S. Geological Survey Professional Paper 294-B.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17–38.

Harrison, S., and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos 56:293–298.

Healey, M. C., and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. Pages 176–184 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Hintze, J. L. 1992. Number cruncher statistical systems, version 5.03. Jerry L. Hintze, Kaysville, Utah.

Hoskins, W. P. 1974. Yellowstone Lake tributary survey project. Interagency Grizzly Bear Study Team, Bozeman, Montana.

Hoskins, W. P. 1975. Yellowstone Lake tributary study. Interagency Grizzly Bear Study Team, Bozeman, Montana.

Imhof, J. G., J. Fitzgibbon, and W. K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):312–326.

Jones, R. D., P. E. Bigelow, R. E. Gresswell, and R. A. Valdez. 1982. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report 1981, Yellowstone National Park, Wyoming.

Jones, R. D., D. G. Carty, R. E. Gresswell, C. J. Hudson, and D. L. Mahony. 1987. Fishery and aquatic management program in Yellowstone National Park. U. S. Fish and Wildlife Service, Technical Report 1986, Yellowstone National Park, Wyoming.

Jones, R. D., D. G. Carty, R. E. Gresswell, and D. L. Mahony. 1988. Fishery and aquatic management program in Yellowstone National Park. U. S. Fish and Wildlife Service, Technical Report 1987, Yellowstone National Park, Wyoming.

Jones, R. D., and five coauthors. 1986. Fishery and aquatic management program in Yellowstone National Park. U. S. Fish and Wildlife Service, Technical Report 1985, Yellowstone National Park, Wyoming.

Jones, R. D., and five coauthors. 1990. Fishery and aquatic management program in Yellowstone National Park. U. S. Fish and Wildlife Service, Technical Report 1989, Yellowstone National Park, Wyoming.

Jones, R. D., J. D. Varley, D. E. Jennings, S. M. Rubrecht, and R. E. Gresswell. 1980. Fishery and aquatic management program in Yellowstone National Park. U. S. Fish and Wildlife Service, Technical Report 1979, Yellowstone National Park, Wyoming.

Jonsson, B., and J. H. L'Abée-Lund. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. Journal of Fish Biology 43(Supplement A):1–16.

Jonsson, B., and O. T. Sandlund. 1979. Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta* m. *fario*) in Søre Osa River system, Norway. Environmental Biology of Fish 4:43–54.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research 66:20–35.

Jonsson, N., L. P. Hansen, and B. Jonsson. 1991. Variation in age, size, and repeat spawning of adult Atlantic salmon in relation to river discharge. Journal of Animal Ecology 60:937–947.

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.

Kaplinski, M. A. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wy-

oming. Master's thesis. Northern Arizona University, Flagstaff.

Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48:66–76.

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

L'Abée-Lund, J. H., and six coauthors. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. Journal of Animal Ecology 58:525–542.

Larkin, P. A. 1981. A perspective on population genetics and salmon management. Canadian Fish Culturist 38:1469–1475.

Larson, G. L., and C. D. McIntire. 1993. Food habits of different phenotypes of threespine stickleback in Paxton Lake, British Columbia. Transactions of the American Fisheries Society 122:543–549.

Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35: 1469–1478.

Leopold, L. B., M. G. Wollman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman, San Francisco.

Loftus, K. H. 1981. Where are we now? Canadian Journal of Fisheries and Aquatic Sciences 38:1464–1465.

Maceina, M. J., P. W. Bettoli, and D. R. DeVries. 1994. Use of a split-plot analysis of variance design for repeated-measures fishery data. Fisheries 19(3):14–20.

Mahony, D. L., and L. D. Lentsch. 1986. SONYEW revised: numbering Yellowstone waters. U.S. Fish and Wildlife Service, Yellowstone National Park, Wyoming.

Marnell, L. F. 1986. Impacts of hatchery stocks on wild fish populations. Pages 339–347 *in* R. H. Stroud, editor. Fish culture in fisheries management. American Fisheries Society, Fish Culture Section and Fisheries Management Section, Bethesda, Maryland.

Marnell, L. F. 1988. Status of the westslope cutthroat trout in Glacier National Park, Montana. Pages 61–70 *in* Gresswell (1988).

Marrin, D. L., and D. C. Erman. 1982. Evidence against competition between trout and nongame fishes in Stampede Reservoir, California. North American Journal of Fisheries Management 2:262–269.

McCleave, J. D. 1967. Homing and orientation of cutthroat trout (*Salmo clarki*) in Yellowstone Lake, with special reference to olfaction and vision. Journal of the Fisheries Research Board of Canada 24: 2011–2044.

McIntyre, J. D. 1995. Review and assessment of possibilities for protecting the cutthroat trout of Yellowstone Lake from introduced lake trout. Pages 28–33 *in* J. D. Varley, and P. Schullery, editors. The Yellowstone Lake crisis: confronting a lake trout invasion. U.S. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

Moreau, J. 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. Pages 81–113 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Morisawa, M. 1968. Streams: their dynamics and morphology. McGraw-Hill, New York.

Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of Von Bertalanffy's Growth Formula. Kiel University, Berichte aus dem Institute für Meereskunde 63, Kiel, Germany. (Not seen; cited *in* Moreau 1987.)

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. International Center for Living Aquatic Resources Management Studies and Reviews 8, Manila.

Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Pages 334–349 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17, Bethesda, Maryland.

Reinhart, D. P. 1990. Grizzly bear habitat use on cutthroat trout spawning streams in tributaries of Yellowstone Lake. Master's thesis. Montana State University, Bozeman.

Richmond, G. M. 1976. Surficial geological history of the Canyon Village quadrangle, Yellowstone National Park, Wyoming, for use with map I-642. U.S. Geological Survey Bulletin 1427.

Ricker, W. E. 1972. Heredity and environmental factors affecting certain salmonid populations. Pages 19–160 *in* R. C. Simon, and P. A. Larkin, editors. The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, Vancouver.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Riget, F. F., K. H. Nygaard, and B. Christensen. 1986. Population structure, ecological segregation, and reproduction in a population of Arctic char (*Salvelinus alpinus*) from Lake Tasersuaq, Greenland. Canadian Journal of Fisheries and Aquatic Sciences 43:985–992.

Schaffer, W. H., and P. F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56:577–590.

Simon, J. R. 1962. Yellowstone fishes. Yellowstone Library and Museum Association, Yellowstone Interpretive Series 3, Yellowstone National Park, Wyoming.

Sinclair, M. 1988. Marine populations. University of Washington Press, Seattle.

Spangler, G. R., A. H. Berst, and J. F. Koonce. 1981. Perspectives and policy recommendations on the relevance of the stock concept to fishery management. Canadian Journal of Fisheries and Aquatic Sciences 38:1915–1921.

Stearley, R. F., and G. R. Smith. 1993. Phylogeny of the Pacific trouts and salmons (*Oncorhynchus*) and genera of the family Salmonidae. Transactions of the American Fisheries Society 122:1–33.

Tabachnick, B. G., and L. S. Fidell. 1989. Using multivariate statistics. HarperCollins, New York.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:195–207.

Thurow, R. F., and J. G. King. 1994. Attributes of Yellowstone cutthroat trout redds in a tributary of the Snake River, Idaho. Transactions of the American Fisheries Society 123:37–50.

USGS (U.S. Geological Survey). 1972. Geologic map of Yellowstone National Park. U.S. Geological Survey, Miscellaneous Geological Investigations I-711, Washington, DC.

Varley, J. D., and R. E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. Pages 13–24 *in* Gresswell (1988).

Varley, J. D., and six coauthors. 1976. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report 1975, Yellowstone National Park, Wyoming.

Welsh, J. P. 1952. A population study of Yellowstone blackspotted trout (*Salmo clarki*). Doctoral dissertation. Stanford University, Stanford, California.

Wetzel, R. G. 1983. Limnology, 2nd edition. Saunders, Philadelphia.

Wold, R. J., M. A. Mayhew, and R. B. Smith. 1977. Bathymetric and geophysical evidence for a hydrothermal explosion crater in Mary Bay, Yellowstone Lake, Wyoming. Journal of Geophysical Research 82:3733–3738.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London.

Young, M. K., editor. 1995. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-GTR-256.