REPRINT FROM
Calif. Fish and Game 76(3): 161–173 1990

GROWTH AND LONGEVITY OF GOLDEN TROUT, *ONCORHYNCHUS AGUABONITA,* IN THEIR NATIVE STREAMS [1]

ROLAND A. KNAPP
AND
TOM L. DUDLEY
Department of Biological Sciences and
Marine Science Institute
University of California
Santa Barbara, California, U.S.A. 93106

Golden trout, *Oncorhynchus aguabonita,* from 17 streams in the Kern Plateau region of the Sierra Nevada, California, were aged using otoliths, and growth rates were determined using length-age and weight-age relationships. Growth rates, condition factors, and densities of trout were correlated with site-specific biological and physical factors using stepwise multiple regression techniques. These stream populations were highly stunted, and individuals attained quite old ages (9 years). Densities were usually low and high density had a significant negative effect on growth ($P < 0.001$). In addition, growth was positively affected by amount of aquatic vegetation, amount of bank vegetation, stream channel stability, and elevation. While site-specific factors such as trout density may influence trout growth, the low growth rates throughout the study area were probably due to the low productivity of these unstable montane streams and the short growing period at high elevations.

INTRODUCTION

Golden trout, *Oncorhynchus aguabonita,* formerly *Salmo aguabonita,* have been widely introduced throughout the United States of America and other parts of the world, but are endemic to only two watersheds, both in the southern Sierra Nevada mountains of California (Fisk 1983). There are two subspecies of the golden trout; *O. a. aguabonita* is native to the headwaters of the South Fork Kern River and Golden Trout Creek and *O. a. whitei* is native to the Little Kern River, Tulare County. Golden trout were initially thought to be most closely related to cutthroat trout (Jordan 1892), but are now understood to belong to the rainbow trout series (Berg 1987).

Although the golden trout is the official California state fish, its natural history in native habitats is poorly understood. What is known of golden trout natural history is primarily based on introduced populations of lake-dwelling fish (Fisk 1983). In these populations, spawning is typically initiated in June and continues through July. Eggs hatch in 29 to 50 days, and after 2–3 weeks in the gravel the fry emerge and grow rapidly during the first summer. They reach approximately 4.5 cm by age one year, 12 cm at two, and 19 cm at three years of age (Needham and Vestal 1938, Fisk 1983). Lake fish reach reproductive maturity at three years of age and may survive to spawn as many as three times. The maximum recorded age is six years. Golden trout from streams rarely achieve lengths greater than 18 cm and ages of such populations are unknown (Fisk 1983). Factors which influence growth rates of stream populations are also unknown.

---

[1] Accepted for publication April 1990.

Growth rates of trout can vary markedly in relation to temperature, food ration, and density (Elliott 1982). In many cases, the differences within a species may be greater than those between species. Under good conditions, non-anadromous trout in streams may achieve a length greater than 40 cm after only three years (Carlander 1969). Growth is often retarded at higher elevations, due to lower temperatures and a shorter growing season. Purkett (1951) reported that three-year old rainbow trout, *Oncorhynchus mykiss,* formerly *Salmo gairdneri,* averaged 29 cm at 1,600 m and 24 cm at 1,850 m, and a 24-year old brook trout, *Salvelinus fontinalis,* reached only 24 cm at 3,322 m in a low productivity Sierra Nevada lake (Reimers 1979). If higher elevation habitats have lower fish densities than lower sites, however, reduced competition at higher sites may result in faster growth rates (McAfee 1966).

In this paper, we report on ages, growth, and population densities of golden trout, *O. a. aguabonita,* from 12 of its native streams in the Golden Trout Wilderness, Inyo National Forest. Five additional study streams contained populations introduced from nearby native populations around the turn of the century. These included three sites on the eastern edge of the Golden Trout Wilderness and two sites in Kings Canyon. Several populations in the Golden Trout Wilderness have been the subject of an intensive management project to preserve the native habitat and gene pool of the golden trout (Fisk 1983). Brown trout, *Salmo trutta,* had been introduced to the South Fork Kern River drainage, and these predators and competitors were removed by California Department of Fish and Game biologists from 1976 to 1982. Golden trout were transplanted extensively during this operation, though trout were not transplanted into any of our study streams. Our objective was to provide information on golden trout ages and growth rates from stream populations and to determine what biological and physical factors affected trout growth rate, condition, and density.

STUDY SITES

The 17 study streams all originate on or near the Kern Plateau of the southern Sierra Nevada (Inyo and Tulare counties, California; Figure 1). Most are tributaries of the South Fork Kern River or Golden Trout Creek, both within the Golden Trout Wilderness. Three streams flow eastward into the Owens Valley and two are tributaries of the Kings River in the southern portion of Kings Canyon National Park and drain into the Central Valley.

The southern portion of the Sierra Nevada was largely unaffected by the Pleistocene glaciation which shaped the valleys north of the Kern Plateau (Jahns 1954). Consequently, most of the stream valleys in this region consist of broad alluvial flats separated by low granitic ridges sparsely vegetated with lodgepole, *Pinus contorta,* and foxtail, *P. balfouriana,* pines. The meadows range in elevation from 2,300 to 3,200 m, and are composed of relatively unconsolidated granitic sands and fine sediments. They are more subject to erosion and degradation than meadows in the glaciated Sierra Nevada (Albert 1982).

Characteristics of the individual streams are provided in Table 1. The streams of this region are typically of low gradient and stream bottoms consist of unstable sand and occasional gravels and cobble. Meanders are common in the unconfined meadow flats, and most streams are relatively wide and shallow.

Discrete riffle-pool sequences are largely absent. The banks are generally steep-sided, rarely densely vegetated, and active erosion sites are common. True riparian vegetation is absent, except for mesic herbs and occasional willow shrubs, *Salix* spp. In-stream cover which can be used by trout is rare. As a consequence of stream openness, summer stream temperatures fluctuate greatly, ranging daily from 3° to 22°C. Golden trout are the only fish species inhabiting the study streams.

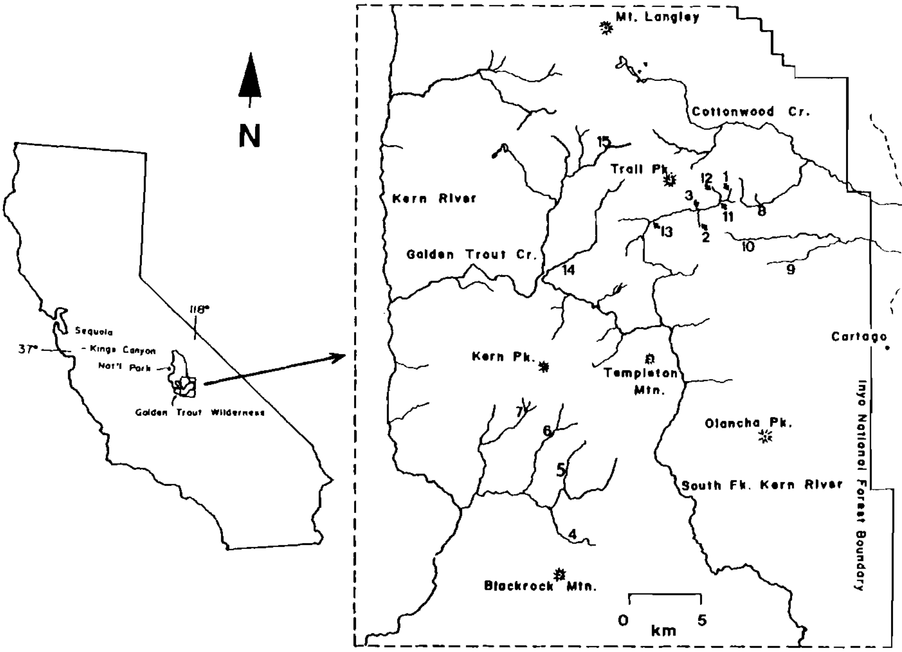

FIGURE 1. Map of California showing study sites on the Kern Plateau. Study sites are numbered and correspond to numbers in Table 1. The two study sites in Kings Canyon National Park (16, 17) are not shown.

MATERIALS AND METHODS

Sampling occurred during the summers of 1983 and 1984. At each site, a 100 m linear transect was established along a representative stream section, and all samples were taken from this section. The section was mapped three-dimensionally to assess geomorphological characteristics such as meander patterns, width/depth relationships, and pool/riffle ratios. Two bottom substrate cores (15 cm deep x 8 cm diam) were taken and partitioned into five sediment size classes with sieves (mesh sizes = 2.0, 1.0, 0.5, and 0.1 mm—particles larger than 2 cm were hand separated from the 2 mm sieve). The three largest size classes were weighed in the field and the two smallest size classes were returned to the laboratory for more accurate weighing.

Invertebrates were collected with a 30 cm x 30 cm modified Hess sampler. The sampler was pushed approximately 10 cm into the substrate and the substrate within the sampler was vigorously stirred by hand. Any suspended

TABLE 1. Stream Characteristics for Study Sites shown in Figure 1. The Sample Sizes Used to Calculate Condition (K) and Density (#/m²) are Given as #/100 m.

SITE NO	*SITE*	*ELEVATION m*	*WIDTH, DEPTH*	*POOL RIFFLE*	*STABILITY RATING*	*% BANK VEGETATED*	*% STREAM VEGETATED*	*# FISH 100 M*	*# FISH M*	*CONDITION (K)*
1	NE MULKEY	2950	10.8	0.76	50	61	64	31	0.09	1.40
2	BEAR	2930	20.8	0.06	102	90	92	13	0.14	1.16
3	MULKEY/BEAR	2880	11.7	0.30	135	85	[illegible]	58	0.11	1.32
4	CASA VIEJA	2560	4.2	0.21	59	100	56	[illegible]	0.11	1.45
5	LONG	2850	6.9	0.40	72	76	41	27	0.05	1.17
6	RED ROCK	2650	5.3	0.26	81	—	22	8	0.04	1.1[illegible]
7	COLD	2780	3.3	1.65	94	90	44	41	0.07	1.44
8	ROUND	3000	10.6	0.26	126	71	53	32	0.08	1.29
9	DIAZ	3030	12.8	0.07	147	9	7	29	0.06	1.4[illegible]
10	ASH	3050	9.0	0.53	78	90	81	16	0.03	1.32
11	UPPER MULKEY	2930	3.4	0.39	84	89	48	18	0.17	1.16
12	MULKEY CS	2950	7.5	0.37	83	90	28	16	0.06	1.25
13	LOWER MULKEY	2850	28.6	0.12	132	55	52			1.10
14	TUNNEL	2730	12.9	0.25	123	80	63	11	0.02	1.14
15	STOKES	2970	10.1	0.42	92	82	15	40	0.06	1.40
16	WF FERGUSON	2730	6.5	0.61	69	73	11	21	0.07	1.30
17	PARADISE	2780	6.0	0.19	57	89	42	12	0.02	1.12

organisms and other organic material was washed into a 330 µm mesh net attached to the downstream end of the sampler. Samples were preserved in 70% ethanol for size partitioning and species identification in the laboratory. Four samples were collected from riffles at each site.

Bank condition was characterized every meter along one randomly chosen 100 m section of stream bank within the study site. At each point, we noted the type of vegetation, whether or not the stream edge was bare, the presence or absence of aquatic vegetation (macrophytes and algae), and whether or not the bank was undercut. If the bank was undercut, the extent of undercutting was measured.

The Pfankuch stream stability rating was calculated for each site (Pfankuch 1975). This index is based on a visual assessment of subjective measures related to stream channel stability, including bank condition, substrate type, vegetative cover, width-depth ratio, and pool-riffle ratio. Stream channel stability is negatively correlated with the index value. For example, narrow, deep streams with overhanging banks and substrates composed mostly of cobble and gravel receive a lower score than wide, shallow streams with highly eroded banks and substrates composed mostly of sand and silt.

Fish were collected by electroshocking (Smith-Root Model 11 Electrofisher). Three passes were conducted at each site in order to obtain a regression estimate for population size (Seber and LeCren 1967). However, this method was not appropriate for the study streams, since the first pass often produced fewer fish than the second and third passes. Because of the limitations of population estimates based on the regressions, the data were used to estimate minimum densities within the stream sections. Fish were retained in buckets until all passes were completed and then measured.

The standard lengths (SL) of all captured fish were measured to the nearest mm on a measuring board. We estimated weights by immersing the fish in a graduated cylinder containing a known volume of water and recording the volume of water displaced. We assumed, and verified in the laboratory, that the specific density of fish tissue was similar to that of water (1.0 g/ml). Therefore, a fish that displaced 50 ml of water was recorded as weighing 50 g. Ten fish from each site, representing a range of sizes, were sacrificed and preserved in 95% ethanol and returned to the laboratory for age determinations. Smaller samples were preserved from three streams which contained few fish. In addition, 10 juveniles (< 1 year of age) were collected from each site where they were present. Since electroshocking did not effectively capture juveniles, they were instead collected using handnets.

Both scales and otoliths (sagittae) were used for age determination; annuli and presumed daily growth increments of otoliths were examined at 100–400X in oil immersion under a light microscope (Campana and Neilson 1985). Otoliths from fish > 3 years old were first ground with carborundum 600 grit to enhance transparency, while otoliths from younger fish were viewed directly.

We investigated the importance of 24 biological and physical site characteristics in determining golden trout growth, condition (K), and density. Site characteristics included riparian stream cover, substrate size composition, bank condition, gradient, elevation, suspended particulates, stream surface area, stream width/depth ratios, pool/riffle ratios, watershed area, abundance of bank and instream vegetation, fish density, stream channel stability, and aquatic insect abundance. Data were analyzed using stepwise multiple regression procedures. The effects of stream channel stability on trout growth, condition, and density were analyzed separately since the stability index incorporated many of the other independent variables.

In stepwise multiple regression procedures in which fish growth (SL/age, weight/age) or condition were included as dependent variables, each fish was a separate observation. When fish density was entered as the dependent variable, each stream was a separate observation. Proportional data were arc-sine square root transformed. The required significance level for inclusion in the regression model was $p < 0.15$. Only those fish more than one year old were used in the analyses since young of the year were present in only five of the study streams when collections were made in 1983.

RESULTS

A total of 376 fish from 17 streams were weighed and measured during 1983. Of these, 176 fish from 15 streams were preserved for age determinations. In 1984, an additional 20 fish were preserved from two streams from which no samples had been collected in 1983.

Scales were unsuitable for age determination since annuli were non-existent. In contrast, annuli were easily counted on nearly all otoliths, possibly due to the large and discrete differences in seasonal temperature cycles (Campana and Neilson 1985). Based on annuli counts, golden trout frequently lived more than five years; the oldest was nine years old. We did not validate annulus formation, but are confident that our age estimates are accurate, since otoliths accurately reflected ages of fish up to 23 years old in an extremely stunted brook trout population (Reimers 1979).

Inter-annular increments were present on all otoliths and were assumed to be produced daily. Daily increment production has been verified in several fish species closely related to golden trout including steelhead trout (Campana 1983), chinook salmon (Neilson and Geen 1982), and sockeye salmon (Marshall and Parker 1982). The number of increments between successive annuli ranged from 90–120. Although it is not known for golden trout whether growth ceases when increment formation stops, the increment counts suggest a period of rapid growth of between three and four months per year (June–September). Growth at other times of the year is probably very slow.

Otoliths from young-of-year trout always showed a distinct discontinuity, after which increments were clearly reduced in width (Figure 2). We believe this represents the date at which alevins emerged from the gravel after depletion of the yolk sac. Similar discontinuities were reported from otoliths of sockeye salmon (Marshall and Parker 1982) and correspond to the date of first feeding.

Lengths of golden trout for all age classes are shown in Figure 3. First year growth was rapid, after which fish grew at a slower rate, especially after the fifth year. The length of golden trout for ages 1–9 was fitted to an equation of the form $y_{sl} = 7.30 + 4.02 \ln x_{age}$ ($R^2 = 0.51$, $p < 0.0001$, $n = 138$; Table 2). Weight followed a pattern similar to length, but was more variable (Figure 4). The weight of trout of ages 1–9 was fitted to an equation of the form $y_{wt} = 2.85 + 19.90 \ln x_{age}$ ($R^2 = 0.30$, $p < 0.0001$, $n = 138$; Table 2). When fit to a logarithmic equation, the length-weight relationship for all trout was [$\ln w = -3.59 + 2.70 \ln l$] ($R^2 = 0.90$, $p < 0.0001$, $n = 343$).

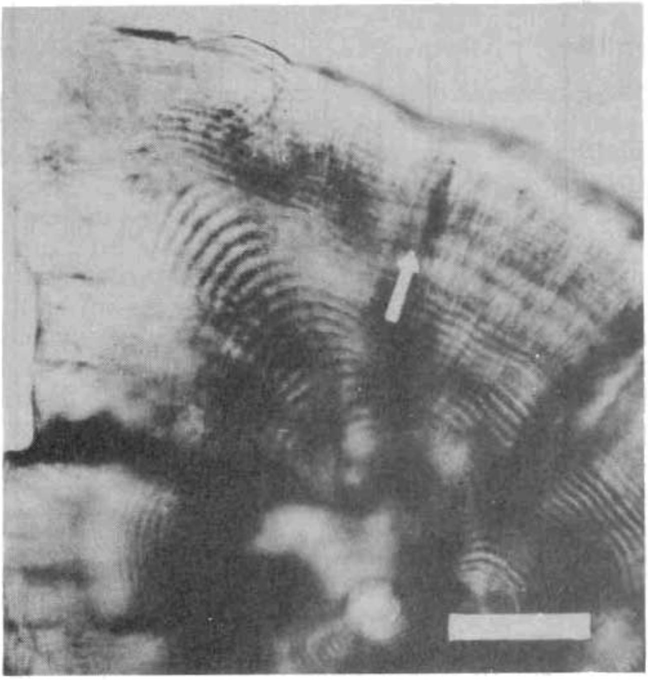

FIGURE 2. Otolith from a 2.5 cm golden trout. Arrow points to suggested emergence mark. Scale bar = 100 μm.

Age-length data was also fitted to a Von Bertalanffy growth function (FISHPARM computer software—Prager et. al. 1987). The Von Bertalanffy equation for all collected fish was $l_t = 15.5(1 - \exp(-0.42[t + 0.54]))$. The asymptotic length for this sample of golden trout was 15.5 cm.

The effects of site characteristics on trout growth (measured as SL/age) were evaluated for 95 fish from 12 streams using stepwise multiple regression. The remaining 43 fish were eliminated because their associated stream variables contained missing values. Fish age accounted for most (62%) of the variation in trout growth explained by the model (Table 3). The percent of stream length covered with aquatic vegetation also added significantly to the model and explained 2% of the variation in trout growth. Fish density (number of fish/m^2) did not vary much between sites (Table 1) and did not explain a significant amount of the variation in trout growth.

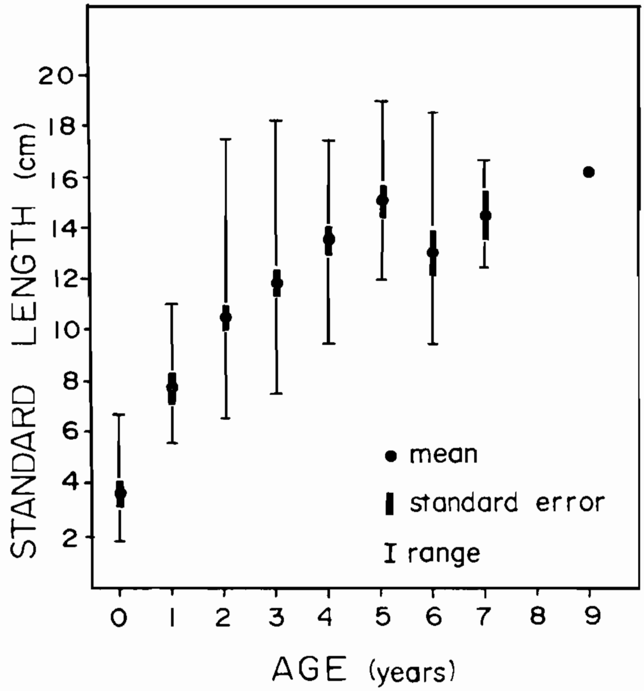

FIGURE 3. Golden trout lengths by age class. Sample sizes for age classes 1–9 are given in Table 2. N = 58 for age 0.

TABLE 2. Actual and Predicted Standard Lengths and Weights of Trout of Ages 1–9. See Text for Equations.

	AGE CLASS (YEARS)								
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
n	10	27	47	28	10	10	5	0	1
predicted length (cm)	7.3	10.1	11.7	12.9	13.8	14.5	15.1	15.6	16.1
actual length (cm)	7.1	9.8	11.8	13.2	15.0	13.1	14.2	—	16.1
predicted weight (g)	2.9	16.6	24.7	30.4	34.9	38.5	41.6	44.2	46.6
actual weight (g)	6.4	14.0	23.9	31.7	47.3	33.2	33.2	—	55.0

TABLE 3. Results of Stepwise Multiple Regression Analysis of Trout Growth Measured As SL/age ($n = 95$). Variables Are Listed As They Entered The Model. See Text for Definition of Independent Variables.

Variable	*Slope*	*P*	*R^2*
fish age	−0.76	0.0001	0.62
% stream vegetated	0.95	0.005	0.02
fish density (#/m^2)	−3.53	>0.10	0.01

When growth was measured as weight/age, regression analysis for 87 fish from 11 streams indicated that golden trout density explained the largest amount of the variation in growth (21%; Table 4). Elevation did not vary much between sites (Table 1), but still explained 8% of the variation in trout growth. The percent of the bank covered by vegetation explained an additional 7% of the variation.

TABLE 4. Results of Stepwise Multiple Regression Analysis of Trout Growth Measured as Weight/Age (n = 87). Variables are Listed as they Entered the Model. See Text for Definition of Independent Variables.

Variable	*Slope*	*P*	R^2
fish density (#/100 m)	−0.19	0.0001	0.21
elevation (m)	0.01	0.0001	0.08
% bank vegetated	7.99	0.004	0.07

Condition factors ranged from 1.16 to 1.47, with a mean of 1.34 ± 0.11 S.E. (Table 1). Although 106 fish were used in the model, none of the site-specific stream variables satisfied the minimum significance level for entry into the regression model.

Multiple regression analyses using fish density (measured as the number of fish per 100 m of stream and as the number of fish per m^2) as the dependent variable resulted in none of the site variables satisfying the minimum required significance level for entry into the regression model. Four streams were eliminated from the analysis because of missing values.

The Pfankuch stream stability rating was significantly correlated with fish growth measured as weight/age ($r=-0.35$, $p=0.0001$, $n=138$), but not as SL/age ($r=-0.09$, $p>0.30$, $n=138$). The correlation between the stream stability rating and fish density measured as the number of fish/100 m was marginally significant ($r=0.44$, $p=0.08$, $n=16$), but the stream stability rating and fish density measured as the number of fish/m^2 were not significantly correlated ($r=0.05$, $p>0.50$, $n=16$). Trout condition was also not significantly correlated with the stream stability rating ($r=-0.07$, $p>.15$, $n=343$).

DISCUSSION

Scales proved unsatisfactory for aging golden trout in this study. Reimers (1958) experienced similar difficulties with scales taken from brook trout from an alpine Sierra Nevada lake. Otoliths, however, proved highly suitable for age determinations. The oldest fish sampled was 16.1 cm SL and was in its tenth year of growth, making it the oldest golden trout on record. Six and seven year old fish were common. Other species of trout occasionally attain similar ages in streams (*O. mykiss*—7 years, Greeley 1933; *O. clarkii*—10 years, Oregon State Game Comm. 1950; *S. trutta*—8 years, Sigler 1952). Most other records of salmonids near 10 years of age or greater are from lake populations (Fenderson 1954, Sumner 1948) or are sea-run individuals (Sumner 1962).

The exceptionally low productivity of streams occupied by golden trout may be a factor in their longevity as well as their retarded growth. In one remarkable case, Reimers (1979) found that introduced brook trout, *Salvelinus fontinalis,* survived for up to 24 years of age in a high altitude, low productivity Sierra Nevada lake. Reimers accounted for their exceptional age by their minimal energetic costs. Activity was reduced by low temperatures in conjunction with extreme food depletion. These fish became highly stunted and did not reproduce until age 16, when population densities declined and allowed food levels to increase and make reproduction possible. Considerable evidence correlates stunting due to reduced food ration and low temperature with enhanced longevity (McCay et al. 1956, Comfort 1963). Golden trout were clearly stunted, suggesting that their increased longevity may be the result of an analogous situation.

In streams, golden trout growth rates are much lower than the rates reported from lake populations (Needham and Vestal 1938, Curtis 1934, McAfee 1966). This agrees with considerable information regarding other species of trout (Carlander 1969), and may be due to several factors. In lakes, fish have access to zooplankton and large prey items not available in streams. This is particularly true following introduction of new populations (including *O. aguabonita*) to fishless lakes, before the prey community composition has been altered (Needham and Vestal 1938). Fish feeding behavior is different in lakes and streams; in streams, fish must expend energy maintaining position and feeding in fast currents (Jenkins 1969, Smith and Li 1983), reducing energy available for growth.

Regression analyses suggested that several factors may influence the growth of golden trout in our study streams. When growth rate was measured as standard length/age, most of the variation was explained by age (Table 3); younger age classes grew more rapidly than older age classes. The amount of the stream covered with aquatic vegetation was positively correlated with trout growth. Aquatic vegetation often provides important habitat for invertebrates and may promote higher invertebrate abundance and diversity (Dudley et al. 1986). Thus, aquatic vegetation may increase the amount of food available to golden trout.

Weight at each age class showed much more variation than size at each age class (Figures 3 and 4). Since weight can be modified over a shorter time period than length, growth rates based on weight may have been more sensitive to the effects of the site variables used in the analyses than growth rates based on length. Growth rates measured as weight/age were affected by numerous site variables (Table 4). Sites with higher fish density (number of fish/m^2) contained fish with significantly slower growth rates. Increased fish density may result in decreased growth rates by decreasing per capita food availability or by increasing competition for foraging sites or cover (Chapman 1966, Chapman and Bjornn 1969, Elliot 1984). Such competition could force fish to expend energy on agonistic interactions instead of on growth.

Density measured as the number of fish/100 m may be a better predictor of growth rates than density measured as the number of fish/m^2 if these trout populations are limited more by the availability of cover than by foraging sites. Nearly all cover in the study streams occurred along the banks and was heavily utilized by fish. Foraging sites were generally in mid-stream and may not have been in short supply in the study streams, since individuals often changed sites without interactions from conspecifics.

Fish from higher elevation streams had higher growth rates than those from lower elevations. McAfee (1966) suggested that if higher elevation habitats have lower fish densities than lower sites, reduced competition at higher sites may result in faster growth. However, our analyses should have removed any density effect and we are thus unable to provide a satisfactory explanation for this relationship.

There was a positive relationship between the amount of streambank vegetation and trout growth. Overhanging vegetation provides cover for fish and may increase the number of terrestrial insects available to trout.

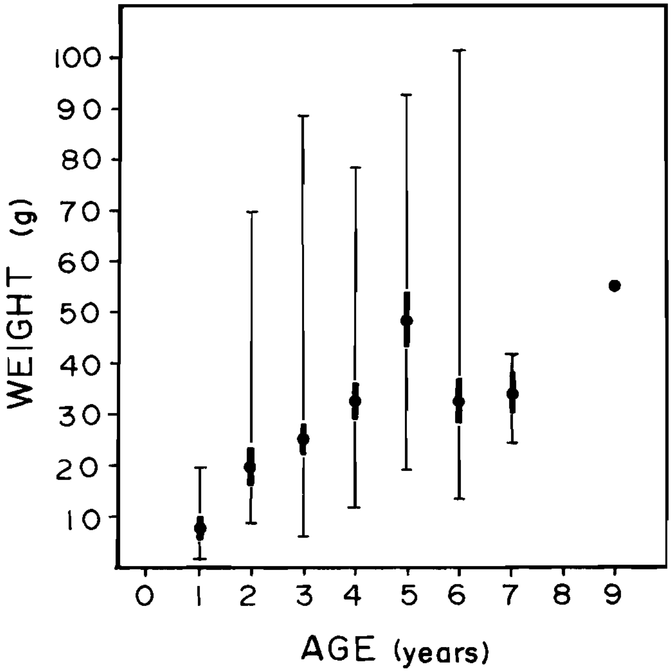

FIGURE 4. Golden trout weights by age class. Samples sizes for each age class are given in Table 2.

The negative correlation between the Pfankuch stream stability rating and trout growth (weight/age) suggests that trout from streams with higher channel stability gained weight faster than those from streams with lower channel stability. Similar effects of channel stability on fish growth have been found for rainbow trout (Van Velson 1979) and brown trout (Dahlem 1979) and were suggested to result from increased food and cover.

Condition factors for 343 trout ranged from 0.90 to 2.16. Despite this variability, our calculated mean K was 1.34, which is similar to K values estimated for lake populations of golden trout (K = 1.315 in Needham and Vestal 1938, 1.34 in Curtis 1934). Apparently, populations of golden trout achieve quite similar condition relationships, even in very different habitats. K values of other trout species vary considerably among habitats, but it appears that trout in montane streams have K values similar to those of golden trout, ranging from 1.15 to 1.63 (Carlander 1969). This uniformity in condition even among different trout species may explain why none of the measured site characteristics affected trout condition in our analysis.

Trout density was not affected by any of the measured site characteristics used in the regression analysis. This analysis should be interpreted with caution, however, as each stream was considered as a separate observation and only 13 streams were used in the analysis. Thus, even if any site characteristics (e.g. amount of suitable spawning gravel or aquatic insect biomass) did affect trout density, the analysis may have lacked the power to detect such effects. The marginally significant correlation between trout density (number of fish/100m) and the Pfankuch stream stability rating suggests that less stable stream channels support higher densities of fish. Although we are unable to provide an explanation for this relationship, it may suggest that fish grew more slowly in streams with lower channel stability because of higher trout densities.

In summary, several site variables affected trout growth. Trout density, trout age, and the Pfankuch stream stability rating were negatively correlated with trout growth while the amount of aquatic vegetation, the amount of bank vegetation, and elevation were positively correlated with trout growth. Differences between sites in stream stability, trout density, bank vegetation, and aquatic vegetation may all influence trout growth by increasing or decreasing the amount of available food or cover. Small increases or decreases in the availability of food or cover may be important in these low productivity streams. However, the low growth rates of golden trout throughout the study area were probably a result of the low productivity of these unstable montane streams and the short period of time available each year for rapid trout growth.

ACKNOWLEDGMENTS

We thank many people for their assistance in organizing and conducting this research, including Scott Cooper, Jon Diehl, Jim Killiam, the other Scott Cooper, and Carla D'Antonio of the University of California, Ralph Giffen and Robin Hamlin of the U.S. Forest Service, and Steve DeBenedetti of the National Park Service. We also thank William Hayden for supplying us with the FISHPARM software and Bill Berg for clarifying the systematics of golden trout. We particularly appreciate the guidance, enthusiasm and philosophical wisdom of Phil Pister of California Fish and Game. The people of Cottonwood Pack Station did an admirable job of figuring out where we were. Research was in part funded by California Water Resources Center Grant No. W628 and National Science Foundation Grant No. BSR83-05837.

LITERATURE CITED

Albert, C. P. 1982. A survey of factors influencing the condition of the stream zone in the Golden Trout Wilderness. M.A. Thesis, Sonoma State University, California. 65 p.

Berg, B. 1987. Evolutionary genetics of rainbow trout, *Parasalmo gairdneri* (Richardson). Unpublished Ph.D. dissertation, U.C. Davis. 184 p.

Campana, S. E. 1983. Feeding periodicity and production of daily growth increments in the otoliths of steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*). Can. J. Zool., 61: 1591–1597.

Campana, S. E. and J. D. Neilson. 1985. Microstructure of fish otoliths. Can J. Fish. Aq. Sci., 42: 1014–1032.

Carlander, K. D. 1969. Handbook of Freshwater Fishery Biology. Iowa State University Press, Ames, Iowa. 752 p.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. Am. Nat., 100: 345–358.

Chapman, D. W. and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153–177 *in* T. G. Northcote, ed. Symposium on salmon and trout in streams. University of British Columbia, Vancouver, B.C.

Comfort, A. 1963. Effect of delayed and resumed growth on the longevity of a fish (*Lebistes reticulatus* Peters) in captivity. Gerontologia, 8(2): 150–155.

Curtis, B. 1934. The golden trout of Cottonwood Lakes (*Salmo aguabonita* Jordan). Amer. Fish. Soc., Trans., 64: 259–265

Dahlem, E. A. 1979. The Mahogany Creek Watershed—with and without grazing. Pages 31–34 *in* O.B. Cope, ed. Forum on grazing and riparian/stream ecosystems, Trout Unlimited, Inc.

Dudley, T. L., S. D. Cooper, and N. Hempill. 1986. Effects of macroalgae on a stream invertebrate community. N. Amer. Benthol. Soc., J., 5: 93–106.

Elliott, J. M. 1982. The effects of temperature and ration size on the growth and energetics of salmonids in captivity. Comp. Biochem. Physio., 73(1): 81–91.

Elliot, J. M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–1983. J. Anim. Ecol., 53: 327–350.

Fenderson, C. N. 1954. The brown trout in Maine. Maine Fish Bull., 2: 16 p.

Fisk, L. 1983. Golden trout of the High Sierra. Calif. Fish and Game, 16 p.

Greeley, J. R. 1933. The growth rate of rainbow trout from some Michigan waters. Amer. Fish. Soc., Trans., 63: 361–378.

Jahns, R. H. 1954. Geology of Southern California. California Division of Mines and Geology, Bulletin 170.

Jenkins, T. M. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *S. gairdneri*) resident in a mountain stream. Anim. Behav. Monogr., 2: 57–123

Jordan, D. S. 1892. Description of the golden trout of Kern River. Bien. Rept. St. Bd. Fish. Comm., Calif., 5: 62–65.

Marshall, S. L. and S. S. Parker. 1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. Can. J. Fish. and Aquat. Sci., 39: 542–547.

McAfee, W. R. 1966. Golden trout. Pages 216–221 *in* A. Calhoun, ed. Inland Fisheries Management. Calif. Dept. Fish and Game.

McCay, C. M., F. Pope, and W. Lunsford. 1956. Experimental prolongation of the life span. Pages 29–39 *in* R. L. Craig, ed. Problems of aging, 28th Grad. Sympos. New York Acad. Medicine, 1955. George Eliot Books, New York. 221 p.

Needham, P. R., and E. H. Vestal. 1938. Notes on growth of golden trout (*Salmo agua-bonita*) in two High Sierra lakes. Calif. Fish and Game, 24(3): 273–279.

Neilson, J. D. and G. H. Geen. 1982. Otoliths of chinook salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors influencing their production. Can. J. Fish. Aquat. Sci., 39: 1340–1347.

Oregon State Game Commission. 1950. Annual report, Fishery Division, 1951. 238 p.

Pfankuch, D. 1975. Stream reach inventory and channel stability evaluation. USDA Forest Service, Northern Region. 26 p.

Prager, M. H., S. B. Saila, and C. W. Recksiek. 1987. FISHPARM: A microcomputer program for parameter estimation of nonlinear models in fishery science. Old Dominion University Research Foundation. Technical Report 87-10.

Purkett, C. A., Jr. 1951. Growth rate of trout in relation to elevation and temperature, Amer. Fish. Soc., Trans., 80: 251–259.

Reimers, N. 1958. Conditions of existence, growth, and longevity of brook trout in a small, high altitude lake of the eastern Sierra Nevada. Calif. Fish and Game, 44: 319–333.

Reimers, N. 1979. A history of a stunted brook trout population in an alpine lake: A lifespan of 24 years. Calif. Fish and Game, 65: 196–215.

Seber, G. A. F., and E. D. LeCren. 1967. Estimating population parameters from catches large relative to the population. J. Anim. Ecol., 36: 361–643.

Sigler, W. F. 1952. Age and growth of the brown trout, *Salmo trutta fario* Linnaeus, in Logan River, Utah. Amer. Fish. Soc., Trans., 81: 171–178.

Smith, J. J. and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Pages 173–180 *in* L. G. Noakes et al., eds. Predators and prey in fishes. W. Junk Publ., The Hague, Netherlands.

Sumner, F. H. 1948. Age and growth of steelhead trout, *Salmo gairdnerii* Richardson, caught by sport and commercial fishermen in Tillamook County, Oregon. Amer. Fish. Soc., Trans., 75: 77–83.

Sumner, F. H. 1962. Migration and growth of the coastal cutthroat trout in Tillamook County, Oregon. Amer. Fish. Soc., Trans., 91(1): 77–83.

Van Velson, R. 1979. Effects of livestock grazing upon rainbow trout in Otter Creek. Pages 53–55 *in* O. B. Cope, ed. Forum—Grazing and Riparian/Stream Ecosystems, Trout Unlimited, Inc.