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Fluctuations in Trout Populations and Their Implications for Land-Use Evaluation

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Abstract.—We describe the magnitude of fluctuations in trout populations in several widely separated streams in the intermountain region of the western United States, and consider the potential effect of such fluctuations on land-management planning. Trout populations included native and exotic species, self-reproducing and hatchery-maintained populations, and assemblages that ranged from monospecific to diverse. Annual fluctuations in population statistics were generally large, and some fluctuations were related to geographic setting and trout species. For individual species, fluctuations in all statistics were typically less in the Rocky Mountain study areas than in the Great Basin, but, for the total salmonid community, the situation was reversed. Numerical population fluctuations frequently did not parallel fluctuations in biomass. Except in cases of irregular occurrence, populations of brook trout *Salvelinus fontinalis*, particularly those in Rocky Mountain study areas, were numerically the most stable; those of allopatric cutthroat trout *Salmo clarki* in the Great Basin were the least stable numerically. However, biomass of allopatric cutthroat trout was one of the most stable population statistics, and biomass fluctuations were greater for Rocky Mountain brook trout than for most other species. Allopatry and sympatry were not obviously related to species-specific fluctuations, though there was some tendency for total salmonid fluctuations in number to be lower, and changes in biomass to be higher, in diverse assemblages. In all cases where a species occurred sporadically or regularly but as a minor member of the local assemblage, fluctuations were typically large. The total salmonid community tended to fluctuate less than individual populations, except when fry of anadromous chinook salmon *Oncorhynchus tshawytscha* were present. It is apparent that inherent trout population fluctuations must be considered within the framework of land-use planning if fishery goals are also going to be achieved. Habitat-based models to evaluate the effects of land uses and habitat enhancement efforts frequently fail to incorporate these fluctuations. For this reason, we concluded that such models often have little utility in predicting sizes or biomass of salmonid populations in the intermountain west.

Common land uses such as logging, livestock grazing, mining, and stream channelization can cause reductions in game-fish populations. Conversely, increases in game-fish populations have commonly been associated with stream enhancement projects, nongame-fish control efforts, and forest and range rehabilitation efforts. Such practices may cause fish population changes, but it is often difficult to prove their influence. Fish populations are dynamic and may fluctuate considerably, even over relatively short periods of time, regardless of human influence. Consequently, managers seeking to assess the effects of land-use practices on fish populations must understand the nature and causes of such fluctuations as fully as possible.

Population fluctuations have received considerable attention in classical ecology, but seem to be less well acknowledged in fisheries research. Some researchers (e.g., Crisp et al. 1974; Hunt 1974; O'Connor and Power 1976; Martin 1980; Moyle and Vondracek 1985) have reported high annual variations in biomass of stream-fish populations, but others (e.g., Burns 1971; Gard and Flittner 1974; Hunt 1976; Eggleshaw and Shackley 1977) have reported relatively low annual biomass fluctuations for some fish populations. This contrast demonstrates the need to evaluate each situation individually to determine local population characteristics over time before conclusions are drawn about the effects of land use practices. Point estimates of population statistics made before and after treatment without regard to whether or not the population normally fluctuates, or when during a population cycle the samples may have been taken, reduce the strength of conclusions that may be drawn.

Currently, many models are being developed to allow prediction of trout biomass from habitat conditions (Bovee 1978; Binns and Eiserman 1979; USFWS 1980). These are appealing as management aids because any land-use or fisheries-management project that produces quantifiable changes in habitat conditions can be evaluated for anticipated effects on trout populations. Although development of these models is a worthy effort, they seem to be based on the implicit assumption that trout populations should be naturally stable, and that instability is due to overt changes in habitat conditions. If model parameters (e.g., habitat conditions) remain relatively stable from year to year, the model should predict stability[1] in associated trout populations. If the populations actually are not stable, correction factors that incorporate density-related interactions need to be incorporated into the model.

To assess the ubiquitousness, frequency, and magnitude of fluctuations in wild trout populations, we selected four streams in the northern Rocky Mountains in Idaho and five streams draining into the Great Basin in Utah and Nevada. We evaluated fluctuations in several populations of (predominantly) wild trout in both allopatric and sympatric situations over time periods of up to 11 years. During this study, wide and unusual fluctuations in climatic conditions occurred, which caused some of the highest and lowest streamflows on record. Such conditions may be expected to exacerbate normal fluctuations and possibly bias studies that ignore the likelihood of population fluctuations. We have endeavored to present this information in a fashion that underscores the manager's need to understand the characteristics of the fish population under consideration, and we propose methods for applying this knowledge to management-oriented decision making. Consequently, we present data on hatchery-maintained populations, on small but stable natural populations, and on populations for which we have as few as 3 years of data to provide managers with as broad a data base as possible with which to assess the potential inherent fluctuation in trout population statistics.

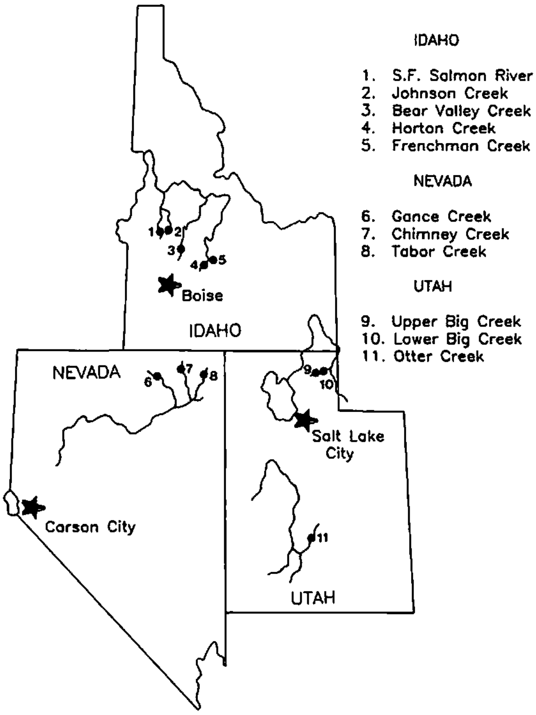

FIGURE 1.—Sites (numbered) where fish population fluctuations were studied in the intermountain region of the western USA.

Study Areas

The geographic diversity of our study areas (Figure 1) provided a wide range of environmental conditions and species assemblages for analysis and comparison (Table 1). The Idaho study streams were largely sinuous and flowed through wet meadows. They contained wild resident populations of bull trout *Salvelinus confluentus* and brook trout *S. fontinalis,* anadromous and resident populations of steelhead and rainbow trout *Salmo gairdneri,* and anadromous populations of chinook salmon *Oncorhynchus tshawytscha* in various proportions; principal among the other species were mountain whitefish *Prosopium williamsoni* and sculpin *Cottus* spp. The Utah and Nevada study areas were less sinuous, flowed through relatively dry meadow areas, and contained wild populations of cutthroat trout *Salmo clarki* or wild and hatchery-reared populations of brown trout *Salmo trutta,* rainbow trout, and brook trout; nongame species included sculpins, daces *Rhinichthys* spp., and suckers *Catostomus* spp.

Methods

We randomly selected a 549-m section on each stream, except on Horton Creek, where a 488-m section was used, and Upper Big Creek, where we expanded the effort to include 732 m of stream. We used either Smith-Root (models V or VII) or Coffelt model VVP-2C electrofishers[2] (Platts et al. 1983) to sample fish populations.

[1] The term "stability" is frequently used but often poorly understood and inadequately measured. We are using the term qualitatively such that stable populations are those that show little variability about a long-term average size over time.

[2] The use of trade, firm, or corporate names in this paper is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

TABLE 1.—Characteristics and fish species assemblages of study streams in the northern Rocky Mountains and Great Basin.

Stream	Hydrographic basin[a]	Riparian vegetation	Recreational fishing	Fish species[b]	Streambank condition
South Fork Salmon River	Salmon River (UC)	Sedge (sod)	None	DV	Stable
Johnson Creek	Salmon River (UC)	Willow-sedge	Slight	B, D[c]	Stable
Bear Valley Creek	Salmon River (UC)	Willow-sedge	Light	CS, RT, B, DV, W, Sc	Moderately stable
Horton Creek	Salmon River (UC)	Sedge (sod)	None	B	Stable[d]
Frenchman Creek	Salmon River (UC)	Willow-sedge	Moderate	CS, RT[c], B, DV[c], W, Sc	Stable
Gance Creek	Humboldt River (EL)	Sagebrush-grass	Moderate	CT, Sc	Unstable
Chimney Creek	Mary's River (EL)	Sagebrush-grass	None	CT	Very unstable
Tabor Creek	Humboldt River (EL)	Sagebrush-grass	Heavy	RT, B, Sc, D	Unstable
Big Creek	Bear River (B)	Sagebrush-grass	Heavy	RT, CT, BT, S, Sc	Very unstable
Otter Creek	Sevier River (B)	Sagebrush-grass	Heavy	RT, BT, B[c]	Moderately stable

[a] Basin abbreviations: UC = upper Columbia; EL = eastern Lahontan; B = Bonneville.
[b] Species abbreviations: CS = chinook salmon; RT = rainbow trout; CT = cutthroat trout; B = brook trout; DV = bull trout; BT = brown trout; W = mountain whitefish; Sc = sculpin; D = dace; S = sucker.
[c] Uncommon.
[d] Horton Creek banks were stable within the section containing fish, unstable elsewhere.

Study areas were usually sampled on or near August 1 of each year (unless weather conditions or the demands of a full sampling schedule required some deviation in sampling times). We chose the early August date on the assumptions that streamflows would be low enough for effective sampling, that young of the year would be large enough to collect easily, that competitive interactions would be maximal, and that fish would be relatively stationary because of territorial behavior. Many of the species considered here maintain home areas during the summer months, including rainbow trout (Edmunson et al. 1968), brook trout (Shetter 1968), and brown trout (Eggleshaw and Shackley 1977). Schlosser (1982) has also shown that competition for local resources is most important during the summer.

Population estimates were based on a removal–depletion sampling strategy coupled with a maximum likelihood computer algorithm that determined the most likely true population size from the removal pattern (Platts et al. 1983; Van Deventer and Platts 1983, 1985). Downstream movements of fish were prevented by block nets placed across the lower ends of the study areas. In 1975 and 1976, two removal passes of equal effort were used, but high variance in the population estimates led us to implement a four-pass removal strategy in 1977. All trout were counted and weighed to the nearest 0.1 g; total lengths were measured to the nearest millimeter. Population statistics for individual species were summed to provide values for all salmonids collected; for streams with anadromous salmon, values for total salmonids were considered with and without the contribution of the salmon fry.

To assess population fluctuations, we used two measures of stability. The maximum relative fluctuation (M_s) was defined as the percentage difference between the highest and lowest value of each population statistic relative to the lowest value:

$$M_s = \frac{X_{max} - X_{min}}{X_{min}} \times 100;$$

X_{max} = largest annual value and X_{min} = smallest annual value. This statistic relates the largest observed change to the smallest observed value during the study period, and gives an indication of the magnitude of potential volatility for each population statistic evaluated.

Average relative fluctuation (A_s) was used to describe the magnitude of changes in each population statistic with respect to the mean value of that statistic over the course of the study:

$$A_s = \frac{X_{max} - X_{min}}{X_{avg}} \times 100;$$

X_{max} and X_{min} are as above and X_{avg} = average value over the entire study period.

Total biomass (B_t), the estimated total trout weight, and areal biomass (B_a), the estimated trout weight per unit surface area, were computed as

$$B_t = NW \text{ and } B_a = \frac{B_t}{lw};$$

N = estimated trout population size, W = mean trout weight, l = length of the stream section, and w = mean width of the study section. Stream width and depth were determined by the transect method described in Platts et al. (1983).

Results

Bull Trout

Bull trout were the only fish inhabiting the South Fork Salmon River (SFSR) study area, and their numbers fluctuated considerably over the 11-year period (Appendix). Although their maximum numerical fluctuation (M_s = 486%) was lower than the combined average for all species in all areas (M_s = 643%), their average fluctuation (A_s = 234%) was higher than the overall average (A_s = 148%) (Table 2). In contrast, bull trout in the Bear Valley Creek study area, where they are part of a rather diverse assemblage of species, exhibited wide maximum fluctuation in numbers (M_s = 1,017%) but smaller average fluctuation (A_s = 198%) than in the SFSR study area. The largest population sizes for both study areas occurred during years of unusually low streamflow (1977 for both, 1979 also for SFSR); during the rather wet years of 1983–1985, bull trout populations in the SFSR study area were depressed.

Fluctuations in bull trout biomass were slightly higher in SFSR than in Bear Valley Creek. (Data and comparisons, here and subsequently, refer only to the respective study areas.) Fluctuations in average length, however, were higher in Bear Valley Creek, and length fluctuations in both Bear Valley Creek and SFSR were lower than fluctuations in any of the other population statistics. In both study areas, the lowest population sizes (1978) corresponded to low biomass levels and very high mean lengths, suggesting poor recruitment of young-of-the-year fish that year. Conversely, the largest populations, which occurred during different years for the two study areas, were related to low mean fish size and nearly maximal biomass, indicating good recruitment.

Rainbow Trout

Population statistics for rainbow trout, particularly numbers of fish, generally fluctuated a great deal (Appendix; Table 2). Maximum numerical fluctuation was greatest in Bear Valley Creek (M_s = 2,040%), where the rainbow trout population was composed of unknown proportions of resident and anadromous fish. Average numerical fluctuation of the Bear Valley Creek population (A_s = 188%), however, was within the range for other populations (A_s = 125–279%). In Johnson Creek, rainbow trout occurred irregularly in the samples and were seldom very abundant. In Otter and Tabor creeks, they were the dominant fish species, and most of them were hatchery-reared fish. Numerical fluctuation of rainbow trout in Upper Big Creek was the lowest among the study areas, but still high (M_s = 660%, A_s = 125%); these fish were also predominantly hatchery individuals.

Except in Johnson and Upper Big creeks, observed fluctuations of rainbow trout biomass were much less than numerical fluctuations. Maximum and average fluctuations in total and areal biomass were quite low in Otter Creek, and even the Bear Valley Creek population exhibited lower-amplitude fluctuations in biomass than in numbers.

Mean lengths fluctuated much less than mean weights; the Tabor Creek population exhibited the largest fluctuations in both attributes. In Bear Valley and Johnson creeks, where the populations consisted of only wild fish, fluctuations were typically higher than for the hatchery-reared populations in Utah. Rainbow trout in Tabor Creek, Nevada, did have rather large fluctuations in these statistics, because fingerlings were stocked in 1981 instead of the usual catchable-size fish (see Appendix for mean fish sizes).

Brook Trout

Maximum and average fluctuations in brook trout population sizes were among the lowest observed for any species (Appendix; Table 2), lower than the overall average for all species in all areas. The Horton Creek population, which coexisted with only a small population of sculpin, exhibited the highest fluctuations in population size (M_s = 368%, A_s = 119%), and the Bear Valley Creek population, which coexisted with several salmonid species, mountain whitefish, and sculpin, exhibited the lowest fluctuations in population size (M_s = 63%, A_s = 45%). In Otter Creek, numbers of brook trout fluctuated considerably, but, as in the case of Bear Valley Creek bull trout and Johnson Creek rainbow trout, the species occurs somewhat irregularly there.

In all study areas, fluctuations in brook trout biomass were greater than numerical fluctuations. Overall, Frenchman Creek, where a healthy population of brook trout interacted chiefly with variable numbers of anadromous salmon and sculpin, contained a brook trout population with the most stable characteristics, though the Johnson Creek population typically exhibited the smallest average relative fluctuations in brook trout biomass. The large maximum population fluctuation in Ot-

TABLE 2.—Observed maximum (Max) and relative fluctuations in estimated trout population sizes, total and area biomasses, and mean fish weights and lengths by species and study area for the period 1975–1985. Fluctuations are expressed as percentages of the minimum or average yearly values (maximum or mean fluctuations, respectively).

		Fluctuation (%)									
				Biomass							
		Number		Total (g/reach)		Areal (g/m²)		Mean weight (g)		Mean length (mm)	
Stream[a]	Years of data	Max	Mean	Max	Mean	Max	Mean	Max	Mean	Max	Mean
Bull trout											
S. Fork Salmon R.	11	486	234	204	112	245	125	190	95	59	44
Bear Valley Cr.	5	1,017	198	99	64	207	114	462	156	135	87
Rainbow trout											
Bear Valley Cr.	5	2,040	188	273	102	453	134	580	175	130	83
Johnson Cr.	9	1,300	272	1,164	206	1,010	191	568	177	83	57
Upper Big Cr.	3	660	125	575	126	766	142	22	20	18	16
Otter Cr.	5	1,000	190	192	125	215	132	396	188	68	56
Tabor Cr.	6	1,073	279	274	135	240	133	1,042	145	165	82
Brook trout											
Bear Valley Cr.	5	63	45	263	115	451	164	247	108	57	42
Johnson Cr.	9	163	95	248	105	281	120	129	87	51	40
Horton Cr.	7	368	119	454	171	570	183	225	111	55	43
Frenchman Cr.	8	93	61	217	127	231	141	251	127	73	54
Otter Cr.	3	240	103	933	220	985	222	470	164	67	51
Cutthroat trout											
Upper Big Cr.	3	288	126	62	51	45	37	140	90	48	40
Gance Cr.	8	448	133	255	137	193	124	186	108	89	68
Chimney Cr.	4	772	135	193	94	150	87	502	161	113	84
Brown trout											
Otter Cr.	5	754	183	287	117	297	122	219	128	76	59
Average, per trout population											
	6	673	155	356	125	396	136	352	128	80	57
All trout, by stream											
S. Fork Salmon R.	11	486	234	204	112	245	125	190	95	59	44
Bear Valley Cr.[b]	5	124	71	220	98	388	143	119	75	47	40
Bear Valley Cr.[c]	5	664	171	317	107	410	128	114	69	43	35
Johnson Cr.	9	162	94	247	105	279	119	210	117	49	40
Horton Cr.	7	368	119	454	171	570	183	225	111	55	43
Frenchman Cr.[b]	8	93	61	217	127	231	141	251	127	73	54
Frenchman Cr.[c]	8	525	201	258	114	274	126	524	185	212	109
Upper Big Cr.	3	113	73	37	31	76	55	16	15	28	25
Otter Cr.	5	564	176	176	104	183	109	233	120	80	57
Tabor Cr.	6	1,073	279	274	135	240	133	1,042	145	165	82
Gance Cr.	8	448	133	255	137	193	124	186	108	89	68
Chimney Cr.	4	772	135	193	94	150	87	502	161	113	84
Average, all trout, per stream											
All[b]	7	420	138	228	111	256	122	297	107	76	54
All[c]	7	518	162	242	111	262	119	324	113	89	59

[a] S. = south; R. = river; Cr. = creek.
[b] Does not include anadromous chinook salmon.
[c] Includes anadromous chinook salmon.

ter Creek (M_s = 240%) was associated with apparently random variations in the rather small population.

Mean lengths of brook trout fluctuated little in any of the study areas; mean weights fluctuated considerably more. Frenchman Creek, despite its relatively stable population, revealed the largest fluctuations in brook trout length (M_s = 73%, A_s = 54%) and weight (M_s = 93%, A_s = 61%) among the Idaho study areas; the next largest changes were in Bear Valley Creek, the only other Idaho stream we studied that contained anadromous fish. Among all streams, Otter Creek had the highest fluctuations in brook trout length (M_s = 67%, A_s

= 51%) and weight (M_s = 240%, A_s = 103%), due to the irregular nature of that population.

Cutthroat Trout

Cutthroat trout populations were entirely self-sustaining in all study streams. Although most of the populations were resident and coexisted with nongame species, Chimney Creek had only a small resident population, a typically large population of fry produced by migratory adults from the nearby Mary's River, and no nongame species. Physical conditions are also quite variable in Chimney Creek (Platts et al. 1985; Nelson et al. 1987), so it is not surprising that maximum (M_s = 772%) and average (A_s = 135%) numerical fluctuations were greatest there (exclusive of Lower Big Creek, for which there are only 2 years' data). Gance Creek, which contains resident fish of the same (presumably) Humboldt race of Lahontan cutthroat trout *S. c. henshawi* as Chimney Creek, also exhibited large fluctuations in cutthroat trout population sizes. Gance Creek also has highly variable physical conditions (Platts et al. 1985; Platts and Nelson, unpublished) and a cutthroat trout population that is known to be quite unstable (Platts and Nelson 1983). In Upper Big Creek, the small population of Yellowstone cutthroat trout *S. c. bouvieri* was numerically more stable, though additional years of data collection might change our assessment of this population.

Biomasses of cutthroat trout populations were more stable than those of most other trout populations studied. In Chimney and Gance creeks, this stability was no doubt due to the overwhelming preponderance of young of the year in most samples (up to 97% in the Chimney Creek samples: Nelson et al. 1987). Cutthroat trout length fluctuations were generally low, being greatest in Chimney Creek (M_s = 113%, A_s = 84%).

Brown Trout

Brown trout in Otter Creek were chiefly mature individuals, and their numbers fluctuated considerably. Both maximum (M_s = 754%) and average relative (A_s = 183%) fluctuations were above the combined average for all species (Appendix; Table 2).

Otter Creek is a regulated stream without large fluctuations in flow. This physical stability and the preponderance of adult fish may be responsible for the relatively low fluctuations in the stream's brown trout biomass. All biomass estimates for this population fluctuated less than the corresponding overall averages; the lowest fluctuations were observed in total biomass (M_s = 287%, A_s = 117%).

Even though most brown trout in Otter Creek were adults, fluctuations in fish length and weight were close to overall study averages. Mean lengths were more stable than mean weights.

Total Salmonids

In general, fluctuations in population statistics for all species as a group (exclusive of anadromous salmon) were less than for individual species in sympatric situations. The principal exception to this generality occurred in Bear Valley Creek, where fluctuations in brook trout statistics were less than the corresponding fluctuations in statistics for total salmonids; for other species in Bear Valley Creek fluctuations exceeded the corresponding fluctuations for total salmonids.

Inclusion of anadromous salmon in the total salmonids category increased the numerical fluctuations of total salmonids considerably. In the Bear Valley Creek study area, maximum and average numerical fluctuations increased by 435 and 141%, respectively, when salmon were considered (M_s = 664%, A_s = 171%). Similarly, in the Frenchman Creek study area, maximum and average numerical fluctuations with salmon included (M_s = 525%, A_s = 201%) increased by 465 and 230%, respectively.

Maximum relative fluctuations in biomass increased somewhat when anadromous salmon were included in the total salmonids, but average fluctuations often decreased. The highly heterogeneous salmonid community in Bear Valley Creek was less affected by the inclusion of anadromous salmon than the brook trout-dominated community in the Frenchman Creek study area. Except for the total biomass estimates, which showed an increase in maximum fluctuation from 220 to 317% (a 44% change) and an increase in average relative fluctuation from 98 to 107% (an 8% change), maximum biomass fluctuations increased no more than 6% and average fluctuations declined no more than 11% in the Bear Valley Creek study area. In contrast, increases in maximum biomass fluctuations with inclusion of anadromous salmon in the Frenchman Creek study area were all greater than 17% and decreases in average relative fluctuations uniformly exceeded 10%.

Bear Valley Creek normally contains large numbers of small fish and relatively few larger fish, which is not true of Frenchman Creek. Consequently, fluctuations in fish-size statistics were little changed with inclusion of salmon fry in Bear

Valley Creek, but increased considerably in Frenchman Creek. In the former area, for example, maximum mean weight and length fluctuations actually decreased by 4 and 9%, respectively, but increased by 464 and 190%, respectively, in Frenchman Creek.

Discussion

Natural Variability

The combined 93 sample years of time-trend information collected during our 11-year study period demonstrate clearly that trout populations normally exhibit large annual fluctuations, in contrast to some other studies that have demonstrated lower levels of variability. Eggleshaw and Shackley (1977), for example, reported rather similar brown trout biomasses from year to year in a Scottish stream, whereas we observed considerable (M_s = 297%, A_s = 122%) fluctuation in brown trout biomass (areal) in our Otter Creek study area. Similarly, Hunt (1976) reported that brook trout numbers in a Wisconsin spring-fed stream varied only 15% over time. Our data from Horton (also a spring-fed stream), Johnson, and Frenchman creeks indicate that, in some western streams at least, naturalized brook trout populations may be much less stable, with maximum and relative fluctuations in areal biomass as high as 570 and 183%, respectively. Martin's (1980) study on the Nawash experimental watershed in Canada suggests that brook trout population density also may vary considerably in eastern North America, where the species is native.

The cutthroat trout we studied were of two subspecies, Yellowstone in Utah and (presumably) Humboldt (or Lahontan) in Nevada. The latter exists under highly variable habitat conditions, and exhibits extreme fluctuations in population statistics. The population variability may be a means to cope with environmental variability (Platts and Nelson 1983; Nelson and Platts 1987), because Humboldt cutthroat trout persist and flourish under conditions often considered inimical to trout, and have withstood introductions of exotic species. Moyle and Vondracek (1985) reported that Lahontan cutthroat trout, which are generally considered the same subspecies as Humboldt cutthroat trout, were driven to extinction in Martis Creek by the introduction of other trouts. This is a typical occurrence in the eastern Sierra Nevada portion of the Lahontan Basin (P. Moyle, University of California, personal communication). Nevertheless, in Gance Creek, on the opposite side of the Lahontan Basin where rainbow trout have been repeatedly introduced, cutthroat trout remain as the only resident trout, presumably because of their adaptation to local conditions (Behnke and Zarn 1976; Behnke 1979).

Regier and Henderson (1973) have suggested that large population fluctuations in allopatric species may indicate an impending change in the local aquatic system. We have shown, however, that large-scale fluctuations in the population characteristics of trout in western streams are common, apparently normal occurrences, and that fluctuations for allopatric populations may exceed those of species in diverse assemblages. Consequently, mere observation of large-scale fluctuations does not necessarily imply an impending change. Divergence from average population level or sudden change in a fluctuation pattern may be more indicative of population changes.

Trout Habitat Models

Our data on trout fluctuations were collected during companion studies of fish habitat conditions (e.g., extent of undercuts, pool–riffle relationships, riparian vegetal cover conditions, etc.) that are not reported here. These analyses of habitat conditions revealed, except for Gance and Chimney creeks, only small annual variations in apparent suitability for trout. There were, however, some rather violent variations in streamwide environmental factors among the study areas, including floods, low flows, and winter icing (Platts et al. 1985). The association of small annual changes in habitat suitability with high levels of population variability leads us to question conclusions drawn from studies that are not designed to account for population fluctuations, and it highlights the pitfalls of reliance on habitat-based models that have been insufficiently tested. Underlying assumptions of habitat-based models such as the habitat evaluation procedures (HEP) and habitat suitability indexes (HSI: USFWS 1980), the instream flow incremental methodology (IFIM: Bovee 1978), and the habitat quality indexes (HQI: Binns and Eiserman 1979) are that fish biomass is largely habitat-limited and that fish populations are always at carrying capacity. Neither of these assumptions is necessarily appropriate in every circumstance (see Mathur et al. 1985 for a discussion of these weaknesses in IFIM).

Had any of these commonly used habitat-oriented models been employed to predict fish biomass in our study areas, they probably would have predicted nearly the same values from year to year because the critical habitat variables for the models changed little during the study period or fluctuated in a manner unrelated to local fish populations. The habitat-based models currently available simply would not have accounted for the fluctuations that occur normally in trout populations, and therefore cannot be expected to produce reliable predictions. Persons and Bulkley (1984) attempted to predict cutthroat trout biomass in our Gance Creek study area using the riverine cutthroat trout HSI model (Hickman and Raleigh 1982), and found poor correspondence between predicted and observed biomasses; the latter sometimes was higher than the former. Although this disparity may be due in part to racial differences between the (presumably) Humboldt strain of cutthroat trout in Gance Creek and the cutthroat trout subspecies used to develop the individual suitability indexes for habitat components, Persons and Bulkley (1984) also found that the model (which they considered sufficiently similar to the rainbow trout HSI model) provided poor predictions of rainbow trout biomass in our Big, Otter, and Tabor creek study areas.

Mathur et al. (1985) discussed several limitations of IFIM and physical habitat simulation (PHABSIM) models that are relevant to our results. The most important of these is the reliance of these models on weighted useable area (WUA), a composite habitat index variable based on habitat area weighted by its composite suitability (involving depth, velocity, and substrate conditions) for a particular species; WUA is assumed to vary with flow, and is used to predict biomass (Milhaus et al. 1984). Mathur et al. (1985) pointed out that decreasing flows should result in reduced fish populations by such models, a contention they refuted by citing Kraft (1972), who showed that an 80% flow reduction for 90 d in a brook trout stream effected redistribution of the fish but caused no decline in abundance. In addition, Persons and Bulkley (1984) showed significant negative correlations between cutthroat trout biomass and both average stream depth and water velocity in cutthroat trout streams. Our concurrent habitat studies have also shown relatively low trout abundance and biomass levels during periods of high flow, when living space would be abundant, and, conversely, high abundance and biomass during low flows. In Johnson Creek, for example, brook trout were 27% below their 9-year average abundance in 1976 (Appendix), when the creek was 6% above average in width and 9% above average in depth (Platts and McHenry, unpublished). In western streams, increased width, depth, and velocity may be indicative of high spring flows or floods, which have occurred in many of our streams (Platts et al. 1985), and which can reduce fish populations by reducing spawning success (Seegrist and Gard 1972; Nelson 1986) and food availability (Elwood and Waters 1969). Although living space often may be a good indicator of potential trout biomass or abundance, other factors, including inherent and unpredictable fluctuations in fish abundance and biomass, may limit the predictive value of living space or available habitat.

Normal fluctuations in population statistics should be included in any predictive model aimed at prescribing land-management practices, habitat-enhancement projects, or mitigation efforts, or at detecting influences of nearby land uses. The HQI model, for example, was developed from one-time population evaluations on a large number of streams (Binns and Eisermann 1979), which may or may not have been sampled at a time when populations were at an average size or biomass level. In addition, predictive relationships based on biomass estimates from a large number of streams may inadequately account for unique factors that influence local fish populations in a particular stream—especially when, as with PHABSIM, the model relies on physical variables that may not be most important in the situation under consideration (Conder and Annear 1987). With the data in this report, we could have demonstrated that fish populations in our study areas were either beneficially or deleteriously influenced by surrounding land uses merely by selecting one year or another to represent the characteristics of the population. It is unlikely that competent fisheries biologists would knowingly be so biased or haphazard, but use of predictive models that fail to account for natural variability may inadvertently result in similar errors.

Study Designs

Large variations in biomass and abundance of trout populations can easily mask the effects of land uses or enhancement efforts. We have shown that changes in fish populations may be, in the short run, unrelated or only weakly related to the habitat attributes normally considered important. Consequently, single-point evaluations of fish populations to determine management effects may detect population conditions unrelated or only weakly related to the management activity. This produces a quandary: we do not want to fail to recognize a degrading effect if one is present, but we also want to avoid erroneously attributing a significant effect to something that was only coincidentally related to fish population characteristics. The best solution lies in the development of adequate study designs, proper sampling techniques, and competent data analysis.

Hall et al. (1978) stated that the traditional watershed study design, with its long-term, pretreatment calibration, and subsequent posttreatment evaluation, cannot overcome error introduced by fluctuating fish populations. They recommended paired treatments with corresponding controls (that is, areas essentially like the treatment area but lacking the treatment itself) to improve sensitivity of the data for detection of environmental change. In our ongoing studies of livestock–fishery interactions, we have used a replicated treatment–control study design, with either two controls per treatment or two sets of paired treatment and control sites per study area. This approach allows assessment of the normal fluctuations in population statistics or habitat characteristics so that changes large enough to be of concern to managers can be detected (Platts et al. 1985). We continue to have difficulty, however, in isolating smaller environmental changes related to land-use activities from normal variability. The chief benefit of our designs is that normal fluctuation patterns, which are assumed to be similar in adjacent treatment and control sites, can be detected and eliminated from the final analysis; after treatment begins, divergence in the pattern of fluctuations between treatment and control areas indicates treatment-induced effects.

Spatial Variation

Spatial variation in trout numbers may be even greater than temporal variation (Hall and Knight 1981). The potential for spatial variation must be considered in any study design, including paired treatment–control studies. In the 17 study areas used in our livestock–fishery studies, from which the data in this report originated, we selected control sites that were as close to the treatment site as possible; they were most often contiguous. We have seldom observed large variations in population statistics among nearby treatments and controls; populations in adjacent or nearby sites may have different sizes, but their trends generally parallel each other.

As distance increases between sites that are to be compared, however, error induced by spatial variation can be expected to increase. In our study areas, the factors that limit trout populations are seldom point-source influences, and nonpoint-source factors usually express themselves over wide areas. Treatments and controls that are close together and closely comparable allow error due to spatial variations to be identified and reconciled in time-trend analyses, and promote the detection of nonpoint-source influences.

Carrying Capacity

The concept of carrying capacity (K) is somewhat ambiguous in the context of trout populations. Rounsfell and Everhart (1953, drawing on work by Krumholz 1948) defined K as "the upper limit of weight of species or combination of species that can be supported by a body of water over an extended period of time." This is probably applicable to fish populations in lakes or ponds, with which Krumholz was working, but may be inappropriate for application to stream-fish populations because habitat characteristics and resource availability may fluctuate considerably. Burns (1971) defined K for salmonid populations in streams as "the greatest weight of fishes that a stream can naturally support during the period of least available habitat," to which he appended Moyle's (1949) stipulation that K "should be considered a mean value around which a population fluctuates." These considerations introduce the potential for defining average, maximum, minimum, and instantaneous values for carrying capacity that must not be confused. In management applications, the most important of these seems to be long-term or average carrying capacity. Upward changes in this capacity would spell success for an enhancement effort; downward changes would indicate deleterious influences from land-use practices. The length of time over which a population should be studied to determine long-term carrying capacity will vary with the population's fluctuation potential. Highly variable populations may require several years of pre- and posttreatment monitoring before conclusions about the effects of a specific land use can be drawn.

Summary

Trout populations in western U.S. streams may, under normal circumstances, undergo wide fluctuations in population characteristics. It would be ideal if a manager or researcher could just determine the size, biomass, and structure of a trout population before and after implementation of a land use, stream enhancement project, etc., and simply compare the two results to ascertain the effect of the treatment—but reality demands more sophisticated techniques. Instead, the characteristics, including inherent temporal fluctuation, of the population in question should be well known so that their effects on data interpretations are minimized. Without such knowledge, it would be too easy to collect data before treatment at a high population level and afterward at a coincidentally low level, and vice versa. Similarly, population models based on habitat characteristics may be unsuitable at their present level of development because they do not take into account that populations may fluctuate in a manner somewhat independent of fluctuations in habitat characteristics; further, such models frequently ignore potential density-dependent influences. We believe that fishery specialists need to turn away from a reliance on instantaneous evaluations of trout populations or habitat characteristics, and to develop better management plans and better ways to assess enhancement efforts or land use practices in watersheds. Trout populations are not necessarily stable entities and should not be regarded as such.

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Appendix

Annual fluctuations in estimated trout populations, total and areal biomass, mean weights, mean lengths, and standard errors by species and study area for the period 1975 to 1985. Est. is estimate; NA is not available.

Year	Population estimate		Estimated biomass			Weights (g)		Lengths (mm)	
				Areal (g/m^2)					
	Number	SE	Total (g)	Est.	SE	Mean	SE	Mean	SE
			Bull trout: South Fork Salmon River						
1975	401	29.90	6,240	2.2	0.65	15.6	4.41	88.1	2.69
1976	258	73.97	3,106	1.1	0.36	12.0	1.41	87.5	3.17
1977	811	8.60	9,432	3.6	0.23	11.6	0.51	91.7	1.29
1978	321	3.86	5,601	2.1	0.20	17.5	1.40	100.8	2.34
1979	1,511	17.21	9,081	3.9	0.31	6.0	0.36	63.4	1.01
1980	682	13.66	5,429	2.2	0.19	8.0	0.55	70.8	1.57
1981	386	11.91	5,335	2.1	0.24	13.8	1.40	95.3	2.13
1982	448	7.92	4,977	1.9	0.19	11.1	1.02	79.3	2.30
1983	369	12.17	3,716	1.4	0.14	10.1	0.90	84.9	2.27
1984	349	10.17	5,040	2.2	0.29	14.4	1.72	92.7	2.83
1985	356	9.02	4,343	1.8	NA	12.2	1.07	90.8	2.41
			Bull trout: Bear Valley Creek						
1976	49	82.32	249	0.0	0.08	5.1	1.70	67.3	6.50
1977	67	2.33	328	0.1	0.02	4.9	0.98	60.5	3.05
1978	6	0.00	165	0.0	0.00	27.6	3.56	142.2	1.45
1979	12	1.02	257	0.01	0.00	21.4	5.08	114.1	14.82
1980	20	0.25	278	0.1	0.02	13.9	4.19	84.3	11.54
			Rainbow trout: Bear Valley Creek						
1976	86	6.45	653	0.1	0.02	7.6	1.20	76.7	3.14
1977	15	0.56	428	0.1	0.03	28.6	6.45	125.4	10.91
1978	5	0.06	175	0.0	0.01	35.1	7.79	145.4	9.12
1979	107	2.64	552	0.1	0.02	5.2	0.83	63.2	3.35
1980	58	7.10	537	0.1	0.02	9.3	1.54	85.6	4.26

Appendix

Continued.

Year	Population estimate: Number	Population estimate: SE	Estimated biomass: Total (g)	Areal (g/m²): Est.	Areal (g/m²): SE	Weights (g): Mean	Weights (g): SE	Lengths (mm): Mean	Lengths (mm): SE
Rainbow trout: Johnson Creek									
1975	14	0.96	190	0.1	0.06	13.5	7.62	75.0	15.30
1976	2	1.00	85	0.1	0.04	45.3	31.35	137.0	48.00
1977	4	0.79	90	0.1	0.01	22.6	1.89	129.8	4.75
1978	4	0.00	125	0.1	0.01	31.3	4.97	137.5	10.36
1979	2	0.00	97	0.1	0.07	48.6	47.55	97.0	65.00
1980	1	0.00	15	0.0	NA	15.0	0.00	110.0	0.00
1981	2	0.00	35	0.0	0.01	17.5	8.05	114.5	20.50
1982	11	0.37	98	0.2	0.02	8.9	2.84	91.8	6.35
1983	3	0.68	22	0.0	0.01	7.3	3.37	86.0	18.45
Rainbow trout: Upper Big Creek									
1981	38	0.52	5,740	2.4	0.18	151.1	9.22	242.4	4.64
1982	36	0.04	5,008	1.8	0.11	139.1	6.99	235.9	4.32
1983	5	0.00	850	0.3	0.14	170.0	86.27	206.0	41.91
Rainbow trout: Otter Creek									
1979	21	0.39	2,899	1.3	0.28	138.1	29.36	191.0	24.27
1980	43	0.70	3,059	1.1	0.12	71.1	7.07	171.2	7.65
1981	77	1.61	7,223	3.0	0.34	93.8	9.95	184.0	5.42
1982	36	1.08	3,425	1.4	0.12	95.1	7.33	199.4	4.17
1983	7	0.14	2,471	1.0	0.26	353.0	96.33	287.9	37.76
Rainbow trout: Tabor Creek									
1979	111	2.01	8,277	4.1	0.32	74.6	4.95	178.4	3.84
1980	114	2.13	12,379	5.7	0.46	108.6	7.62	187.4	8.70
1981	1,302	22.98	13,098	6.4	0.47	10.1	0.64	82.5	1.05
1982	654	7.24	30,954	13.8	0.77	47.3	1.97	150.1	1.76
1983	193	2.59	14,869	6.3	0.34	77.0	3.04	185.0	2.44
1984	184	4.15	21,147	7.6	0.52	114.9	4.34	218.9	3.59
Brook trout: Bear Valley Creek									
1976	63	3.70	1,259	0.2	0.04	20.0	3.63	100.4	6.80
1977	92	0.70	2,853	0.7	0.11	31.0	4.46	112.7	5.91
1978	88	0.97	787	0.1	0.03	8.9	1.88	71.8	4.23
1979	103	1.25	2,151	0.4	0.05	20.9	2.65	104.7	4.48
1980	94	3.68	1,969	0.4	0.07	21.0	4.11	93.8	5.83
Brook trout: Johnson Creek									
1975	318	4.06	3,911	2.2	0.19	12.3	0.90	91.8	2.17
1976	266	12.21	6,200	3.6	0.31	23.3	1.29	112.3	2.54
1977	241	1.25	6,056	4.1	0.33	25.1	1.54	117.7	2.79
1978	327	2.78	5,451	3.4	0.28	16.7	1.00	94.3	2.27
1979	533	3.34	8,539	5.9	0.40	16.0	0.61	105.3	1.28
1980	346	8.08	3,796	2.5	0.24	11.0	0.84	78.0	2.79
1981	210	7.52	2,453	1.5	0.20	11.7	1.36	81.4	3.06
1982	553	8.61	7,305	4.5	0.31	13.2	0.64	101.5	1.29
1983	465	5.40	8,272	4.7	0.32	17.8	0.88	104.1	2.07
Brook trout: Horton Creek									
1978	19	0.72	341	0.5	0.21	17.9	6.92	82.8	11.93
1979	72	0.35	1,102	1.8	0.26	15.3	2.01	102.8	3.84
1980	77	0.90	1,887	2.9	0.27	24.5	1.95	112.5	3.87
1981	59	4.88	445	0.7	0.14	7.5	1.29	72.4	4.21
1982	33	0.79	367	0.4	0.11	11.1	2.70	86.5	5.61
1983	89	0.92	928	1.3	0.23	10.4	1.80	84.6	3.85
1984	62	3.35	1,277	1.7	0.33	20.6	3.69	105.6	6.07

Appendix

Continued.

Year	Population estimate		Estimated biomass			Weights (g)		Lengths (mm)	
				Areal (g/m²)					
	Number	SE	Total (g)	Est.	SE	Mean	SE	Mean	SE
				Brook trout: Frenchman Creek					
1976	567	17.22	8,324	4.0	0.30	14.7	1.02	94.1	1.79
1977	617	2.94	12,858	7.0	0.33	20.8	0.95	103.5	1.79
1978	500	4.09	6,665	3.5	0.30	13.3	1.13	76.8	2.23
1979	795	6.64	4,722	2.5	0.22	5.9	0.51	60.0	1.20
1980	716	17.52	5,248	2.7	0.22	7.3	0.57	71.3	1.42
1981	625	13.94	4,056	2.1	0.15	6.5	0.43	70.0	1.21
1982	411	4.39	6,568	2.9	0.22	16.0	1.05	96.0	2.02
1983	778	7.73	7,111	3.1	0.27	9.1	0.72	79.1	1.27
				Brook trout: Otter Creek					
1979	0	NA	0	0	NA	0	NA	0	NA
1980	0	NA	0	0	NA	0	NA	0	NA
1981	13	0.41	169	0.1	0.01	13.0	1.46	104.7	2.62
1982	17	69.55	1,260	0.5	2.09	74.1	26.21	174.6	26.40
1983	5	0.20	122	0.0	0.01	24.4	3.71	128.0	4.75
				Cutthroat trout: Upper Big Creek					
1981	80	2.33	3,954	1.7	0.22	49.4	6.00	157.3	5.10
1982	41	0.81	3,843	1.4	0.13	93.7	8.36	204.5	5.70
1983	159	1.97	6,223	2.0	0.23	39.1	4.36	137.7	3.56
				Cutthroat trout: Gance Creek					
1978	207	1.35	2,900	3.3	0.49	14.0	1.84	79.3	3.78
1979	619	10.96	4,556	5.0	0.74	7.4	1.07	55.4	1.77
1980	1,135	12.57	10,294	9.8	0.88	9.1	0.68	62.3	1.54
1981	1,040	6.49	7,197	7.1	0.57	6.9	0.47	70.5	1.24
1982	518	10.52	3,678	3.7	0.37	7.1	0.61	69.9	1.52
1983	476	5.82	3,679	3.4	0.37	7.7	0.77	73.2	1.55
1984	1,091	4.31	5,346	4.3	0.36	4.9	0.35	64.0	1.03
1985	506	4.07	5,393	1.8	NA	13.2	0.88	97.3	1.84
				Cutthroat trout: Chimney Creek					
1981	53	0.00	1,018	1.3	0.17	19.2	2.29	127.8	4.03
1982	462	1.38	1,474	1.9	0.27	3.2	0.41	59.9	0.83
1983	420	5.19	2,978	3.3	0.42	7.1	0.86	66.1	1.95
1984	280	2.13	2,915	2.5	0.38	10.4	1.47	70.8	2.94
				Brown trout: Otter Creek					
1979	26	0.19	7,187	3.2	0.23	276.4	16.47	283.4	5.38
1980	153	3.13	7,187	5.3	0.49	92.9	7.98	184.7	4.90
1981	222	6.40	19,265	8.0	0.90	86.8	8.79	161.0	5.53
1982	44	0.68	4,975	2.0	0.36	113.1	19.77	187.2	12.40
1983	91	2.61	15,422	5.9	0.64	169.5	16.75	224.6	7.93