The Use of Vertebral Number in Systematic Studies of Western North American Trouts of the Genus *Salmo*

Submitted

by

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Abstract

This study, by a Fisheries Science major at Colorado State University, evaluates the use of the number of vertebrae in distinguishing species and subspecies in the western North American trouts in the genus Salmo. Dr. Robert Behnke, Assistant Leader of the Cooperative Fishery Unit, supervised the project. The species of Salmo included the rainbow trout, Salmo gairdneri, cutthroat trout, Salmo Clarki, and golden trout, a group of forms belonging to the golden trout complex--currently recognized as three species. Speci~~es~~mens were categorized according to the basin from which they were collected. Vertebral counts taken in this and previous studies indicate that this character is effective for species diagnosis. ~~Other~~ Experimental ~~results~~ studies have shown that environmental factors may cause different vertebral numbers within the same genotype. Contradicting studies indicate that fish which develop rapidly have fewer vertebrae. Other studies indicate a small variation within a species from north~~ern~~ to south~~ern location~~. Findings indicate that differences in latitude and environment do not significantly alter the genotypically determined vertebral number. Hybrids between species have a number of vertebrae intermediate to that of the parent species. Vertebral number is an effective character to differentiate species and subspecies.

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Introduction

This study evaluated the use of the number of vertebrae in distinguishing species and subspecies in the western North American trouts of the genus Salmo. Dr. Robert Behnke, Assistant Leader of the Cooperative Fishery Unit supervised the project.

Just how many species and subspecies should be recognized in the genus Salmo is not known. Almost 50 species and subspecies have been named. Opinions vary to the other extreme that all named species belong to a single variable species. There is some disagreement on the definition of species and subspecies, but the main problem is that the genus Salmo is widely distributed in western North America and is highly variable and reproductive isolation is weak between species. Another complicating factor is that all of the trouts are fully capable of hybridizing. Comprehensive data is not available to denote how many phylogenetic lines are represented and because of this there is a need for a character of the species which would allow comparison of hundred and thousands of specimens. This character should be an accurate reflection of the genotype. The observed differences should truly indicate divergence and therefore, suggest the origins and affinities of the fish.

Methods

Under the supervision of Dr. Robert Behnke, Salmo were collected from throughout western North America. The fish were grouped according to the basin and region from which they were collected. Dr. Behnke provided supplementary counts from some of the basins. (A basin is a drainage system or geographical area whose waters are interconnected in a single river system or a segment of such a system.) The basins which fish were taken from were: Columbia River, Sacramento, Lahontan, Bonneville, Kern River, California, Rio Grande, Alvord, Colorado River, Snake River, Yellowstone Lake, South Platte, and the Pacific Coast including California, Oregan Washington, Canada, Alaska, and Mexico. (See map).

The fish were grouped according to the species and subspecies. The rainbow trout, Salmo gairdneri, collected were native to Pacific Coast waters but they have since been widely introduced throughout the West. Cutthroat trout, Salmo clarki, were collected including many subspecies from various basins. The golden trout complex is probably a separate major evolutionary line of western Salmo and it comprises four distinct groups: California golden trout, Salmo aguabonita, Mexican golden trout, Salmo chrysogaster, Gila trout, Salmo gilae, and the Apache trout which as not yet been named. Also included in the collection are other undescribed forms. These include what will probably become a new subspecies of cutthroat trout and a species from isolated basins which appears to be intermediate between rainbow and cutthroat in many characters. The parent species of this intermediate group reflect characteristics of the rainbow and cutthroat species. Some of the museum specimens were collected as long ago as the 1870's and 1880's, but the vertebral counts were only recently made.

The vertebral counts were made by X-raying the specimens and taking the counts from the negative. Every centrum in the vertebral column was counted including the last few centra in the caudal region of the fish. With the use of X-rays one hundred or more specimens could easily be counted in a day by one person.

Data

The coastal subspecies of cutthroat, Salmo clarki clarki, and the rainbow, Salmo gairdneri, provide a good basis for comparison of vertebral numbers of two species. Mottley (1937) found the mean for the cutthroat trout to be 61.7 and a mean of 63.5 for the rainbow species. Our study, based on many more specimens from more diverse localities found a mean in the coastal cutthroat subspecies to be 61.5 for 304 fish from Alaska, Washington, Oregon, and California. A total of 466 rainbow trout have a mean of 62.7. These trout were collected from Alaska to California. A comparison of the two species shows a mean difference of 1.2 more vertebrae in the rainbow species. Most of the cutthroat species vertebral number were in the range of 60 to 63. The majority of the rainbow specimens ranged from 61 to 64. This indicates that most rainbow specimens had at least one more vertebrae than the cutthroat species and that the vertebral number would be a good character for differientiation of the two species. (See Tables I and II).

There have been varied opinions on the vertebral numbers in trouts. Jordan (1894) thought the rainbow trout had only 60 vertebrae. He believed the species named <u>Salmo gairdneri</u> by Richardson in 1836, which had sixty-four vertebrae, was a salmon. Kendall (1921) thought two different species of rainbows, a freshwater, landlocked species and an anadromous steelhead species could be differentiated by vertebral number. Later his findings were found to be in error because he had made his conclusions from only a few specimens. Mottley (1936) concluded that all the British Columbian rainbows were of a single species. But, until now, there have been no published comparisons between species and subspecies using so many specimens from such a large geographical area to evaluate the efficacy of vertebral number, as a taxonomic character. The number of vertebrae in the golden trout complex has never been published.

Jordan (1894) pointed out the fact that there is a slight change in vertebral number from North to South. The mean values of vertebral number of the rainbow and cutthroat species indicate a slight but not consistant trend from North to South, of decreasing vertebral number. Alaska showed a 63.0 mean from 161 fish, while 271 California rainbows have a mean of 62.4. However, one contradicting fact was that the highest vertebral numbers occurred in rainbow trout taken from Rio Hondo and Las Adjuntas in Mexico. They did not show a lower number of vertebrae than the fish which were collected from Alaska, even though they lie much farther south than the Alaskan fish. The 50 specimens showed a vertebral mean of 64.4. (See Table IIa). Dr. Behnke believes that this group may be a relict population. The amount of environmental influence on vertebral numbers of these populations is not known, but considering other populations from the geographical area, the influence must be small. In the cutthroat trout there is a difference of 1.1 vertebrae from Alaska to Oregon and California. (See table 1). Alaska's numbers are based on 181 fish and California's and Oregon's mean values came from 100 fish. Hubbs (1922, 1925) found the number of vertebrae in herring to decrease with an increase in temperature. Hubbs concluded that the vertebral number in fish was within genetically determined limits and that it was "a function of the rate of development rather than the result of environmental controlled selections of certain genotypes which have specific numbers." Mottley (1937) in his study of rainbow trout described the increased temperature decreases the number of vertebrae under laboratory conditions. Gabriel (1944) correlated vertebral number with a measure of the time of development. He revealed that there was a gradual increase in vertebral number with increased time of development caused by lower temperatures. Many authors have experienced the same results. Garside (1966) summarizes the findings of many results of the effect of temperature on vertebral number. But it must be remembered that fish grown in laboratory conditions (constant temperature, constant oxygen level, etc.) are different that fish grown in the wild; trout reproduce only in a narrow temperature range in nature. Our study pointed out that hatchery grown trout in Verdi Fish Hatchery and a hatchery near Hot Creek, California of the same genotype may vary in vertebral number. The eggs were all taken from Heenan Lake and hatched in these two hatcheries. Fish hatched at Hot Creek, California showed a mean of 60.8. This difference of .5 vertebrae per fish can be best explained by the indication that the Verdi Fish Hatchery probably raised their fish at a lower temperature than the Hot Creek Hatchery and that these fish developed slower. The above data shows that fish grown in constant environmental conditions (with higher temperatures) in a hatchery may develop at a faster rate and usually have less vertebrae. (See table Ia).

The use of vertebral number in systematic studies appears to be highly useful in the golden trout complex. These species all have lower vertebral numbers than those of the rainbow and cutthroat. (See table 111). The mean values of the golden complex indicate a value of 59.9 for Apache trout, 60.5 for the Gila trout, 59.5 for the golden trout and down to 57.8 for the Mexican Golden trout. The golden trout was thought first described as cutthroat to be a subspecies of the Kern River rainbow by Jordan (1894). Ferguson (1916) believed that the golden trout was not derived from the Kern rainbow and entered the Kern drainage long before the rainbow. The low vertebrae count mean (59.5) for the golden trout indicates that the golden trout is not derived from the rainbow. Needham and Gard (19~~59~~64) believe that Salmo aguabonita may have close affinities with two other species of golden-like trouts, the Mexican golden trout, Salmo chrysogaster and the Gila trout, Salmo gilae. An undescribed form of golden-like trout, called the Apache trout found in only a few streams in the White Mountains in Arizona strongly suggests a close relationship to Salmo aguabonita. Our vertebra~~e~~l counts of the Mexican golden (57.8), Gila trout (60.5) and the Apache trout (59.9) point out this relationship. (See table III).

The use of vertebral number in determining subspecies may be useful in some instances. A subspecies of the cutthroat trout found in the South Platte and Arkansas basins exhibits a lower number of vertebrae than any other subspecies. The greenback trout, Salmo clarki stomias, typically has about one less vertebrae than other cutthroat trout. The only pure strain of this subspecies occurs in the South Platte basin.

The Big Thompson, Rock Creek Lake, Bear Lake and Albion Creek and a headwater tributary of the Little Poudre have vertebral counts less than 60.7 indicating that this subspecies does have a mean less than the average cutthroat. This information was based on seventy-eight counts. (See table Ib). The Piute trout, Salmo clarki seleniris, is another unique subspecies. Vertebral counts support the zoogeographical evidence that seleniris is derived from an isolated population of Salmo clarki henshawi. The mean of the vertebral number of the henshawi subspecies was found to be 61.5 from 129 fish collected in an isolated part of the Lahontan Basin. We found a mean of 61.8 for the Piute trout which is close to the mean found for the henshawi subspecies. Another subspecies, Salmo clarki humboldtensis, is also believed to be derived from the henshawi subspecies. The vertebral number which we found for this subspecies is 61.7. This number is again very close to the mean value of the henshawi subspecies which indicated that the humboldtensis subspecies may be a derivative of the henshawi subspecies.

The Piute trout revealed another interesting fact about vertebral numbers. Specimens collected in 1933 (table Ic) showed a mean vertebral count of 61.8. Fish collected in 1956 also had a mean of 61.8. These figures indicate that the vertebral numbers have remained consistent over a period of 23 years. This points out that environmental and other conditions for the Piute have probably remained consistant also.

The vertebral number may be useful for naming and distinguishing unknown species found in southern Oregon and in the Upper Sacramento Basin. The group in the Upper Sacramento have a mean of 62.1.~~vertebral per fish~~. This value was calculated from 91 fish taken from 12 creeks and rivers in the area. (See table Vb). It is thought that this group of fish may be a rainbow and cutthroat intermediate, since the vertebral counts taken from fish in this area range from 60 to 65. The group of fish from southern Oregon were taken from many desiccating basins in this region. The 37 specimens showed a mean of 63.5 vertebrae. These may also be a rainbow-cutthroat intergrade or it is also believed they may be a primitive intermediate evolutionary line.

Since the species of Salmo have been introduced into many waters, it has been found that rainbow, cutthroat, and the golden trouts are fully capable of hybridization. (Hybridization is a fertile mating of two species, but it may result from the crossing of subspecies of the same species or a result of both.) This has created a problem in recognizing a species by its vertebral number. Out data indicated that hybridizing has occurred in many area. Apache trout in Oak and Becker Creeks, (See table IIIa), have hybridized with the rainbow trout. The vertebral numbers show a wide variation (59-63) and indicate that the hybrids (mean=61.0) between the species (rainbows- approximately 63 and Apache trout- approximately 59) are intermediate of these parents species. A golden, rainbow, cutthroat hybrid occurs in the North Platte River. The range is from 59 to 62 with a mean of 60.4. This population indicates a greater golden trout influence with a mean value very close to the vertebral count of the golden trout, which is 59.~~9~~5. (See table IV).

Conclusions

Our study indicated that the the number of vertebrae is useful as a character for species diagnosis. Particularly it is important in recognizing the three main lines of *Salmo* species: cutthroat, rainbows and goldens. This character may be useful in distinguishing some subspecies of the cutthroat group. Vertebral number may be useful in determining some now unknown species. Changes in latitude showed no clear cut trend of different vertebral number from North to South within a species. Evidence shows hybrids between species have an intermediate number of vertebrae of the parent species. Since it is possible to differentiate a large number of specimens in a short time by the use of this character, demonstrating the practical use of vertebral numbers, ~~is thereby~~ proven.

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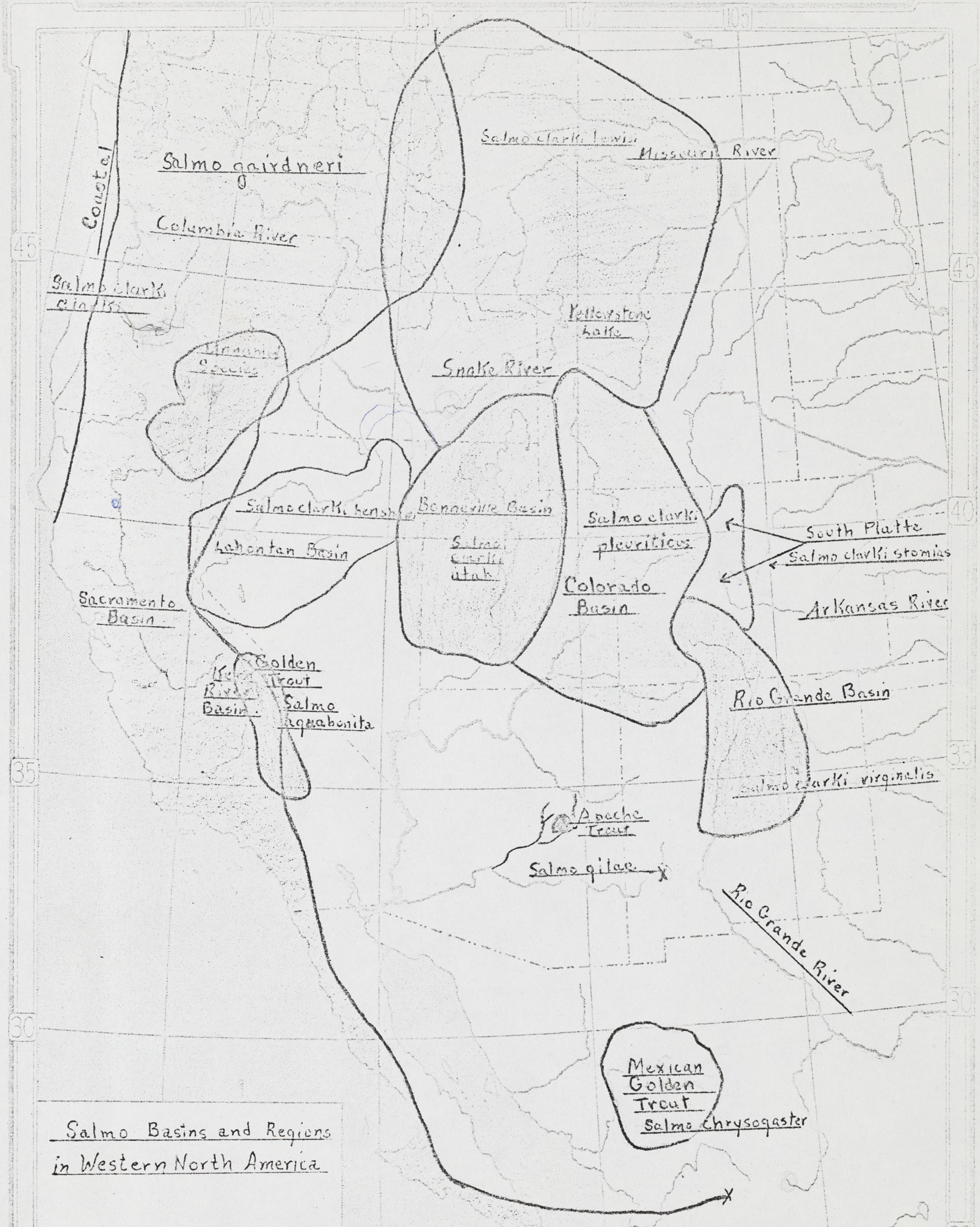
APPENDIX

Cartocraft Desk Outline Map. Western United States. No. 7177



Salmo Basins and Regions in Western North America

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Table I

BASIN: Cutthroat Regions (Salmo clarki)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Coastal													
Alaska	181					6	57	70	42	6			61.9
Washington	23					2	3	7	9	1	1		62.5
California and Oregon	100				5	28	31	26	7	2	1		61.0
Total Coastal	304				5	36	91	103	58	9	2		61.7
lewisi													
Canada	102				2	33	36	25	5	1			61.0
Yellowstone	72					8	25	32	7				61.5
Total lewisi	174				2	41	61	57	12	1			61.3
henshawi													
Lahontan Hatchery fish	55				3	10	26	16					61.2
Lahontan Basin fish	74				1	3	20	36	12	2			61.9
Total henshawi	129				4	13	46	52	12	2			61.5
stomias													
East slope, Arkansas River	52				2	5	24	18	3				61.3
Total stomias	52				2	5	24	18	3				61.3
macdonaldi total	6					4	2						60.3
Other subspecies													
Western Slope Col. R.	39					5	16	13	4	1			61.5
Colorado River	68					5	19	31	12				61.9
Alvord Basin	45					3	19	19	4				61.5
Lahontan (Piute trout)	49						12	36	1				61.8
Bonneville	65					1	5	26	29	2	2		62.5
Humboldt	125					3	44	69	9				61.7
East Slope, South Platte	312			1	18	96	117	68	12				60.8
Snake River	57						12	23	19	1			62.2
Rio Grande	112					8	43	46	15				61.6
Total Salmo clarki	1537			1	31	220	516	561	188	16	4		61.5

Table Ia

BASIN: Lahontan (Salmo clarki henshawi)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Hatchery fish													
Heenan Lake California-1948 hatched at Hot Creek California	9				1	2	4	2					60.8
Lily Pad Lake California hatched in hatchery	21					1	11	9					61.4
Verdi Fish Hatchery-1952	25				2	7	11	5					61.3
Total	55				3	10	26	16					61.2
Lahontan Basin	6						1	4	1				62.5
Lake Tahoe- 1872,1876	2							2					62.0
Lake Tahoe	2						1			1			62.5
Winnemuccal	2								2				63.0
Truckee River	26						7	12	6	1			62.0
Summit Lake	28				1	2	8	15	2				61.7
Carson River Murray Canyon	6					1	3	2					61.1
Walker River	2							1	1				62.5
Total	74				1	3	20	36	12	2			61.9

Table Ib

BASIN: East Slope-South Platte
(*Salmo clarki stomias* and hybrids)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
* Big Thompson- 1967	31					15	15	1					60.6
* Rock Creek Lake	3				1	1		1					60.2
Morraine Park- 1889	4							2	2				62.5
* Bear Creek- 1889	1				1								59.0
* Albion Creek- 1957, 1963, 1964	39			1	6	22	9	1					60.1
Black Hollow- 1963, 1964, 1967	42				1	14	16	10	1				61.9
* South Fork Little Poudre above Pingree	4					2	1	1					60.6
Roaring Creek- 1963, 1964	48					12	29	7					60.9
* North Boulder Creek- 1963, 1964	56				6	25	22	3					60.4
Hague Creek (Poudre tributary)	7						2	4	1				61.9
Corral Creek- 1966, 1967	22						6	14	2				61.8
Trap Creek- 1966, 1967	29				3	5	9	11	1				61.1
Neota Creek- 1966, 1967	17						6	9	2				61.8
Bennett Creek- 1967	7							4	3				62.4
Cache la Poudre Headwaters- 1967	2						2						61.0
Total	312			1	18	96	117	68	12				60.8
* *Salmo clarki stomias*													
Total	78			1	8	40	25	2					60.2

Table Ic

BASIN: Lahontan Basin (Salmo clarki seleniris) Piute trout

Some hybrids between rainbow and cutthroat trout

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Piute trout													
Silver King Creek- 1939	13						4	8	1				61.8
Silver King Creek- 1933	26						6	20					61.8
Silver King Creek (above falls)-1956	10						2	8					61.8
Total	49						12	36	1				61.8
Hybrids													
Silver King Creek (below falls)- 1956	19				1		3	7	6	2			62.2
Total	19				1		3	7	6	2			62.2

Table Id

BASIN: East Slope-Arkansas River
Salmo clarki stomias and Salmo clarki macdonaldi

COLLECTION SITE	N	VERTEBRAL NUMBERS											MEAN
		56	57	58	59	60	61	62	63	64	65	66	
Salmo clarki stomias													
Twin Lakes- 1889	23				1	1	11	10					61.3
Arkansas River- 1889	12					1	7	3	1				61.3
South Huerfano Creek -1963	17				1	3	6	5	2				61.2
Total	52				2	5	24	18	3				61.3
Salmo clarki macdonaldi													
Twin Lakes- 1889	6					4	2						60.3
Total	6					4	2						60.3

Table Ie

BASIN: Coastal Region (Salmo clarki clarki)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Alaska													
Lake Barnhof and mouth of Parloff Creek- 1959	5						1	4					61.8
Makaka Point Stream Alaska- 1957	30					1	9	11	9				62.0
Lake #1 Hawkins Island Alaska- 1957	19							3	12	4			63.1
Hasselberg Lake Alaska 1957	27						7	13	6	1			62.0
Bell Creek Alaska (salt water)- 1954	1							1					62.0
Reflection Lake Alaska 1954	2						2						61.0
Herman Creek Alaska- 1954	3					1	1		1				61.3
Long Lake Alaska- 1954	8						5	3					61.4
Ketchikan, Luck Lake- 1959	17					1	3	10	3				61.9
Herman Creek- 1954	8					1	5	2					61.1
Lake near Stakini River mouth- 1958	5					1	4						60.8
Taku River at Flannigan Slough- 1958	3						3						61.0
Quinsara Lake (tributary Cambell River)- 1958	23						9	12	2				61.7
Middle Quinson Lake- 1958	30					1	8	11	9	1			62.0
Total	181					6	57	70	42	6			61.9
Washington													
Tanner Creek Washington 1909	6								4	1	1		63.5
Crescent Lake Washington- 1896	4							2	2				62.5
Lake Southerland Washington- 1898	9					1	2	5	1				61.7
Clearwater Creek Washington- 1957	4					1	1		2				61.8
Total	23					2	3	7	9	1	1		62.5

Table Ie continued

BASIN: Coastal Region (Salmo clarki clarki)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
California and Oregon													
Grassy Lake Oregon- 1957	30				3	15	9	3					60.4
Bible Creek Oregon- 1957	15				1	3	5	5	1				61.1
Little North Fork Kitches River- 1953	8						4	3	1				61.6
Fall Creek Oregon- 1959	2						2						61.0
Whiskey Creek- 1959	9						3	6					61.7
Gate Creek Oregon- 1953	23					5	5	6	4	2	1		61.8
Penn Creek California- 1957	12				1	4	3	3	1				60.9
Klamath River California- 1924	1					1							60.0
Total	100				5	28	31	26	3	2	1		61.0

Table If

BASIN: Rio Grande (Salmo clarki virginalis)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Rio Chiquito- 1966	18					5	10	3					60.9
Rio Grande, New Mexico Sandoval County	6						5		1				61.33
Indian Creek Tularosa Basin- 1966	11						1	7	3				62.2
Indian Creek-1967	2						1	1					61.5
Indian Creek and Rio Seco- 1960	30						9	16	5				61.8
Rio Grande del Norte -1889	6						1	4	1				62.0
South Fork Trinchera Creek- 1967	10					2	2	3	3				61.6
Main Fork Trinchera Creek- 1967	6					1	2	3					61.5
Trinchera Creek- 1967	15						7	6	2				61.5
Bear Creek- 1967	6						3	3					61.5
Rio Puerco- 1874	2						2						61.0
Total	112					8	43	46	15				61.6

Table Ig

BASIN: Snake River (Salmo clarki lewisi)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Hatchery fish													
Hatchery- 1967	2						1	1					61.5
Total	2						1	1					61.5
Afton- 1967	2							2					62.0
Snake River- 1967	6						2	2	2				62.0
Game Creek- 1955	25						5	14	4	2			62.1
Game Creek- 1955	10						4	4	2				61.8
Fish Creek- 1957	4						1		3				62.5
West Fork Irving Creek- 1934	10							1	8	1			63.0
Total	57						12	23	19	1			62.2

Table Ih

BASIN: Yellowstone (Salmo clarki lewisi)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Atlantic Creek- 1967	42					4	15	19	4				61.5
Yellowstone Lake and tributary- 1954	30					4	10	13	3				61.5
Total	72					8	25	32	7				61.5

Table Ii

BASIN: Canada (Salmo clarki lewisi)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Pickle Jar Lakes Alberta- 1959	35				2	24	9						60.2
George Creek Alberta- 1957	28					7	14	7					61.0
Ware Creek Alberta- 1957	35					2	11	16	5	1			61.8
Issac Creek - 1929 British Columbia	3						1	2					61.8
Issac Creek- 1929	1						1						61.0
<u>Total</u>	112				2	33	36	25	5	1			61.0

Table Ij

BASIN: Humboldt Basin (_Salmo clarki humboldtensis_)

Humboldt trout

VERTEBRATE NUMBERS

COLLECTION SITE	N	58	59	60	61	62	63	64	MEAN
Humboldt drainage	12				2	10			61.9
Humboldt River	4					4			62.0
Humboldt River	2				1		1		62.0
Marys River	5			1	1	3			61.4
Pablo Creek	2				1	1			61.5
Star Creek	1					1			62.0
Round Mountain	1					1			62.0
Beaver Creek	27				7	19	1		61.8
South Fork Little Humboldt	13			2	7	4			61.2
Nelson Creek	7				4	3			61.4
Rock Creek	4				2	2			61.5
South Fork Rock Creek	16				8	5	3		61.6
Humboldt River and Marys' River	11				2	8	1		61.9
Toe Jam Creek	16				8	5	3		61.69
Lewis Creek	2					2			62.0
Rock Creek	2				1	1			61.5
Total	125			3	44	69	9		61.7

Table Ik

BASIN: Bonneville (Salmo clarki utah)

VERTEBRAL NUMBERS

COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Logan River- 1894	2							2					62.0
Wilson Spring Provo Basin- 1915	1								1				63.0
Utah Lake- 1889	6						1	1	2	1	1		63.0
City Creek	1								1				63.0
Provo Utah	9							1	6	1	1		63.1
Pine Creek Nevada- 1958	28					1	3	12	12				62.3
Lehman Creek- 1938	2							2					62.0
Beaver Creek Utah	8						1	4	3				62.3
Weber River Utah	4							1	3				62.8
Utah, former tributary to Little Cottonwood creek- 1967	4							3	1				62.3
Total	65					1	5	26	29	2	2		62.5

Table II

BASIN: Alvord Basin, *(Salmo clarki)*

COLLECTION SITE	N	VERTEBRAL NUMBERS 56	57	58	59	60	61	62	63	64	65	66	MEAN
Alvord Basin: Willow Creek- 1952	7						1	4	2				62.1
Willow Creek- 1934	9					1	1	5	2				61.9
Alvord Basin: Virgin Creek- 1934	29					2	17	10					61.3
Total	45					3	19	19	4				61.5

Table Im

BASIN: Colorado River (Salmo clarki pleuriticus)

		VERTEBRATE NUMBERS							
COLLECTION SITE	N	58	59	60	61	62	63	64	MEAN
Stillwater Creek (Colorado tributary)	14				3	3	8		62.4
Pole Creek (Green River tributary)	10			1	2	7			61.6
Wheatfield Creek, New Mexico (San Juan Basin)	10			2	4	3	1		61.3
North Fork Escalante Creek-1950	12				3	6	3		62.0
Current Creek Utah	3					3			62.0
West Fork Dry Creek Colorado	3				1	2			61.7
East Fork Dry Creek Colorado	4				2	2			61.5
Payne Creek (tributary Little Delores River)	4			1		3			61.2
Roubideau Creek Colorado	1				1				61.0
Washington Gulch Colorado	2					1	1		62.5
Busk Creek Colorado	3			1	2				60.7
Hill Creek Colorado (White River tributary)	2				1	1			61.5
Total	68			5	19	31	12		61.9

Table In

BASIN: Western Slope - Upper Columbia River

Salmo clarki VERTEBRATE NUMBERS

COLLECTION SITE	N	58	59	60	61	62	63	64	MEAN
Creston, Montana	39			5	16	13	4	1	61.5
Total	39			5	16	13	4	1	61.5

Table II

BASIN: Rainbow Regions (*Salmo gairdneri*)

COLLECTION SITE	N	VERTEBRAL NUMBERS											MEAN
		56	57	58	59	60	61	62	63	64	65	66	
Coastal													
Alaska	167					1	7	40	78	39	2		63.0
Washington and Oregon	28							6	12	10			63.2
California	271					9	57	87	78	32	8		62.4
Total coastal	466					10	64	133	168	81	10		62.7
Canada	176					1	1	28	77	58	10	1	63.2
Mexican Rainbow	67			1		4	6	7	7	22	17	3	63.8
Total Salmo gairdneri	709			1		15	71	168	252	161	37	4	62.9

Table IIa

BASIN: Coastal Region (Salmo gairdneri) (page 1)
with Canada and Mexico

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Alaska													
Brooks River	7								6	1			63.1
Outlet Whiskey Lake	21							4	13	3	1		63.0
Inlet Whiskey Lake	3								3				63.0
Wood River System	30						1	11	14	4			62.7
Bedlam Lake	20					1	5	13	1				61.7
Brooks Lake	16							1	9	6			63.3
Big Kitoi Lake	5								1	4			63.8
Big Kitoi Creek	5								4	1			63.2
Tebay Lake	22							5	9	7	1		63.2
Tikchik River	11							3	7	1			62.8
Alagnak River	27						1	3	11	12			63.3
Total	167					1	7	40	78	39	2		63.0
Washington and Oregon													
North Fork Salmonberry River	26							4	12	10			63.2
Spencer Creek	2							2					62.0
Total	28							6	12	10			63.2
California													
Waddell Creek	5					2	1	2					61.0
San Lorenzo River	9						2	4	3				62.1
Russian River	8						2	4	2				62.0
McCloud River- 1893	5						1	1	2	1			62.8
McCloud River and Clairborne Creek	10						1	1	5	2	1		63.1
*Klamath River	175					7	42	57	50	15	4		62.4
Pine Creek	8							1	1	4	2		63.9

Table IIa

BASIN: Coastal Region (Salmo gairdneri) (page 2)
with Canada and Mexico

VERTEBRAL NUMBERS

COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
California (continued)													
San Pablo Creek	26						1	4	10	10	1		63.2
Santo Domingo River	25						7	13	5				61.9
Total	271					9	57	87	78	32	8		62.4
Canada													
Moberly Creek, Alberta	32								9	16	6	1	64.0
Riske Creek, B.C.	25						1	8	9	6	1		62.9
Fish Lake, B. C.	33							3	26	4			63.0
Loon Lake, B. C.	24					1		7	8	8			62.9
Trout Lake, B. C.	25							8	11	5	1		63.0
Bear Lake, B. C.	7								1	5	1		64.0
Coquinaila River, B. C.	30							2	13	14	1		63.5
Total	176					1	1	28	77	58	10	1	63.2
Mexico													
San Ignacio Creek	17			1		4	5	6	1				61.1
Las Adjuntas	23								2	10	10	1	64.4
Rio Hondo	27						1	1	4	12	7	2	64.3
Total	67			1		4	6	7	7	22	17	3	63.8

* Snyder, J. O. 1940 California Fish and Game, Volume 26:2, pp. 96-138.

Table III

BASIN: Apache trout, Golden trout, Gila trout and hybrids of the above with hybrids of rainbows and cutthroats

COLLECTION SITE	N	VERTEBRAL NUMBERS											MEAN
		56	57	58	59	60	61	62	63	64	65	66	
Hybrids													
North Platte cutthroat x golden x rainbow	19				1	13	2	3					60.4
Apache trout x rainbow	12				1	4	4	1	1	1			61.0
Kern River Golden x rainbow	104			1	4	16	33	30	16	4			61.5
Lahontan Basin Rainbow x cutthroat	19				1	3	7	6	2				62.2
Apache trout	170			5	35	79	38	7	4	2			60.1
Gila trout and hybrids	79				4	20	24	16	12	3			61.1
Mexican Golden trout with hybrids	147	15	32	42	25	26	7						58.3
Pure Apache trout	117			5	29	63	20						59.9
Total													
Pure Golden trout													
Total	180			21	84	61	14						59.4
Pure Gila trout													
Total	42				4	16	17	4	1				60.5
Pure Mexican golden trout Total	103	15	32	41	11	1	3						57.8

Table IIIa

BASIN: Apache Indian Reservation
Apache trout and hybrids

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
* Ord Creek	27			1	7	13	6						59.9
* Bonita Creek	16			2	3	8	3						59.8
* Big Bonita Creek	5					5							60.0
* Reservation Creek	21			2	8	10	1						59.5
Sand Creek	10				2	4	3		1				60.4
* Squaw Creek	6				1	4	1						60.0
* Flash Creek	6				2	2	2						60.0
* Crooked Creek	5				1	3	1						60.0
Moon Creek	4					2	2						60.5
* Hughey Creek	3				1	1	1						60.0
Big Diamond Creek	11				2	2	6	1					60.5
Diamond Creek	12				1	4	3	4					60.8
* Deep Creek	23				4	14	5						60.0
* Firebox Creek	5				2	3							59.6
Becker Creek	4							1	2	1			63.0
Oak Creek, tributary to Verde River hybrids, collected -1915	12				1	4	4	1	1	1			61.0
White R. -	20												59.5
Total	170			5	35	79	38	7	4	2			60.1
* Apache trout **Total**	117			5	29	63	20						59.9

Table IIIb

BASIN: Mexico Region (*Salmo chrysogaster*)

(Mexican Golden Trout)

		VERTEBRAL NUMBERS												
COLLECTION SITE	N	55	56	57	58	59	60	61	62	63	64	65	66	MEAN
Rio Verde- Rio Fuerte	50	1	7	19	19	3		1						57.4
Km 24- Rio Fuerte	3		1	2										56.7
Rio Sinaloa	23		6	10	7									57.0
Rio Culiacan	27			1	15	8	1	2						58.4
Total	103	1	14	32	41	11	1	3						57.8

Table IIIc

BASIN: Southwestern New Mexico (*Salmo gilae*)
and Hybrids

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
* Diamond Creek	25				2	10	8	4	1				60.5
* Main Diamond Creek	17				2	6	9						60.6
South Diamond Creek	6					2	3		1				61.0
Gila River	9						1	4	3	1			62.4
Langstrough Creek	22					2	3	8	7	2			62.2
Total	79				4	20	24	16	12	3			61.1
* *Salmo gilae*													
Total	42				4	16	17	4	1				60.5

Table IIId

BASIN: Kern River Basin (Salmo aquabonita)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Rock Creek	5			2	1	2							59.0
Whitney Creek	12			1	2	8	1						59.7
Cottonwood Lakes	8			1	3	2	2						59.7
Volcano Creek	23			2	15	4	2						59.3
Golden Trout Creek	33			3	23	5	2						59.3
Cottonwood Creek	33			1	11	18	3						59.7
South Fork of Kern	34			6	14	11	3						59.4
Mulkey Creek	32			5	15	11	1						59.4
Total	180			21	84	61	14						59.4

Table IVa

BASIN: East Slope-North Platte (Hybrids)

					VERTEBRAL NUMBERS								
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Roxy Ann Outlet (Red Canyon)- 1966 cutthroat cross golden cross rainbow	19				1	13	2	3					60.4
Total	19				1	13	2	3					60.4

Table IVb

BASIN: Kern River (*Salmo aquabonita*, *Salmo gairdneri gilberti* and *Salmo whitei* hybrids)

		VERTEBRAL NUMBERS										
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Coyote Creek Below falls	7				1	1	1	2	1	1			59.9
Whitney Creek	3					2	1						60.3
Rock Creek	6						4	1	1				61.4
Little Kern Creek	1						1						61.0
Kern River	3					1	1	1					61.0
Wallace Creek	3						1	2					61.7
Wallace Creek	1					1							60.0
Shotgun-Pistol Creek	5						3	2					61.4
Little Kern River	4					1	2	1					61.0
Rifle Creek	4					2	1	1					60.9
Culver Lake	4					1	2	1					61.0
Upper Fustan Meadow	7					2		3	1	1			61.4
Chagoopa Creek	9							3	5	1			62.8
Salmon Creek	15			1	2	2	5	2	3				60.9
Kern River	19					2	9	5	2	1			61.5
King's River	3							2	1				62.3
Kern River	3				1			1	1				61.3
Upper Siberia Creek	7					1	2	3	1				61.7
Total	104			1	4	16	33	30	16	4			61.5

Table V

BASIN: Regions of Unknown Species

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Southern Oregon	37						2	5	12	9	7	2	63.5
Upper Sacramento	91					4	24	27	26	7	3		62.1
Total	128					4	26	32	38	16	10	2	62.6

Table Va

BASIN: Southern Oregon (Unknown species)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Malhver Basin, Silvies River	10									3	5	2	64.9
Chewavcan Basin	6								4	2			63.3
Goose Lake, Cottonwood Creek	6						1	1	2	2			62.8
Fort Rock Basin, Buck Creek	6								3	2	1		63.7
Warner Basin, Honey Creek	8						1	4	3				62.3
Klamath Lake	1										1		65.0
Total	37						2	5	12	9	7	2	63.5

Table Vb

BASIN: Upper Sacramento (unknown rainbow cutthroat intermediate)

		VERTEBRAL NUMBERS											
COLLECTION SITE	N	56	57	58	59	60	61	62	63	64	65	66	MEAN
Sheephaven Meadows	21					2	15	4					61.1
Moosehead Creek	9						1	5	3				62.2
Lost River	7						1	4	1	1			62.3
Trout Creek	3								3				63.0
Star City Creek	3							1	2				62.7
Racoon Creek	1								1				63.0
Snowslide Creek- 1967	3							2		1			62.7
Koske Creek- 1967	3							2	1				62,0
Hawkins Creek- 1967	10					2	6	2					61.0
Edson Creek	5						1	4					61.8
North Fork Pit River	6							3	3				62.5
Clairborne Creek	20								12	5	3		63.6
Total	91					4	24	27	26	7	3		62.1

TYPES OF FOOD CONSUMED BY RAINBOW TROUT(*Salmo gairdnerii*) ON THE ISLAND OF KAUAI, HAWAII.

Prepared for FW300

28 FEBRUARY 1973

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Fishery Report on Types of Foods Consumed by Rainbow Trout (Salmo gairdnerii) on the Island of Kauai, Hawaii.

This report is basically on the types of food consumed by Kokee rainbow trout. Most of the information was obtained from ~~a wide~~ a wide variety of sources ranging from Geology to Crustaceans. The rest of the report came from the author's true life experience of fishing and living on Kauai. It starts out with a brief description of the island of Kauai and how its trout streams were formed. Then there is a report on the fishing areas at Kokee and methods of sampling food organisms. The majority of the report is concentrated on a survey of foods eaten by Kokee trout and a brief description of each type of food. I hope you can see from the data in my report that there are excellent amounts of food sources available at Kokee and absolutely no need for any more or newer types of food sources.

Contents

Introduction

What's that!? Did I read the title right "trout fishing" in Hawaii?? Impossible you say, well on the island of Kauai there is even a trout fishing season. The island of Kauai is the oldest and northern most isle in the chain of five main islands. It is situated approximately 160° longitude and 22° latitude. It has an area of 555 square miles and its highest point is Mt. Kahili rising 5,170 feet high. The trout fishing area is located on a high plateau called Kokee. (altitude app. 5,000 ft) The Kokee trout streams were originally formed centuries ago by eroding of a central volcanic crater into an elevated, vast swamp. This swamp is called the Alakai swamp and it covers nearly one-fourth the surface area of Kauai. Since the rainfall in some years is more than 600 inches; you can see water is no problem. Most of the river valleys of Kauai were formed by cool, clear, filtered, swamp water (average temp. of water between 50-60°F) seeping over the eroded crater's edge. The area which we are concerned with is where this seepage of water begins. This area is the location of Kokee's surprising trout streams.

History of Trout on Kauai

Of all the trout and salmon introduced into Kauai's streams only the rainbow trout (Salmo gairdnerii) seem to survive. Even at that survival is marginal because of the lack of colder water temperatures necessary for successful natural spawning. Although some fortunate fish do spawn successfully it is not adequate enough for a reasonable trout season. Thus, even as early as 1920 annual shipments of fry and eggs were planted in the streams at Kokee.

Fishing Area at Kokee

In order to better understand what types of foods are consumed by the island trout we should take a brief look at the fishing area at Kokee. Fishing is permitted in the Kokee Ditch System, the Puu Lua Reservoir, the Kauaikinana Stream, the Kauaikoi Stream, the Waiakoali Stream, the Mohihi Stream, the Koaie Stream, the Waialae Stream, and parts of the Kokee Stream. Except for the Koaie and Waialae Streams each of the other four streams are diverted into an extensive ditch system. The Kokee Ditch System was formed by way of diversion dams, tunnels, and flumes. The main system joins together in an area called the Black Pipe or Hale Manu junction and from then on the ditch flows into the Puu Lua Reservoir.

Methods of Sampling Food Organisms

(this section is taken directly out of a pamphlet, thus one footnote will be used)

Standard methods developed by fishery biologists for the examination of streams were used. Water, air temperatures, and pH values were taken in pratically all the waters examined. The pH values were determined by using a Hellige Pocket Comparator, Model 605, with four permanent, glass, color standards. These gave a range from 2.0 to 9,5. The quantitative Surber stream bottom foods net was used where feasible for taking stream foods samples, but the extremeeruggedness and irregularity of the bottom areas in most cases, prevented the collection of quantitative fish food samples. In lieu of this, qualitative samples were obtained by hand picking and by sieving and washing the foods out of gravel, algae, mosses, and from stones using a 30-mesh soil sieve and 14-mesh handscreen. Fish specimens and stomachs were preserved in formaldehyde and food organisms in 70 per cent alcohol. Fish were collected by angling and netting.[1]

[1] P. R., Needham, A Fisheries Survey of the Streams of Kauai and Maui with Special Reference to Rainbow Trout (Salmo gairdnerii), (Honolulu, Hawaii, Division of Fish and Game Board of Commissioners of Agriculture and Forestry, January 1950), pp. a to c.

Survey of Food Eaten by Kokee Rainbow Trout

(again this section is taken directly out of a pamphlet, thus one footnote will be used)

In tables A and B will be found the breakdown of the foods found in the stomachs of rainbow trout caught in the Kokee area. Since the foods eaten in the ditch below Puu Ka Pele Lookout vary considerably from those eaten by trout in the ditch below Hale Manu and upper Kokee, tables A and B lists the foods eaten from these three separate areas.

It will be noted that the red shrimp, (Gammarus), formed over

TABLE A

SUMMARY OF FOODS EATEN BY KAUAI RAINBOW TROUT*

FOOD GROUP	NUMBER EATEN PER FISH			PER CENT OF TOTAL NUMBER OF FOOD ANIMALS		
	Hale Manu	Kokee Stream	Lower Ditch	Hale Manu	Kokee Stream	Lower Ditch
Red Shrimp	2.0	0.0	55.8	9.6	0.0	64.7
Aquatic Sowbugs	0.0	0.0	12.7	0.0	0.0	14.7
Angle Worms	0.6	1.9	1.2	3.1	12.4	1.3
Midge Larvae	0.1	0.0	1.8	0.6	0.0	2.1
True Flies	0.1	1.0	2.1	0.6	6.6	2.4
Beetle Larvae	0.5	0.1	1.4	2.4	0.8	1.6
Damselfly Nymphs	1.0	5.2	0.0	4.9	33.8	0.0
True Bugs	0.5	0.1	0.9	2.4	0.8	1.1
Moth Larvae	0.3	1.3	2.0	1.2	8.3	2.4
Millipedes	15.4	5.3	5.1	74.1	34.7	5.9
Centipedes	0.0	0.0	0.5	0.0	0.0	0.6
Ants, Bees, Wasps	0.0	0.0	1.2	0.0	0.0	1.5
Snails	0.1	0.1	0.3	0.6	0.8	0.3
Algae	--	--	----	+	+	+
Miscellaneous**	0.1	0.2	1.2	0.6	1.8	1.4
TOTALS	--	--	--	--	--	--

*Based on Stomachs from 29 Rainbow Trout Ranging in Size from 3-7/8" - 16-1/2" overall Length.

**Misc. includes: 1) Parts of Termites, 2) Earwig, 3) Unidentified

TABLE B

SUMMARY OF FOODS EATEN BY KAUAI RAINBOW TROUT*

FOOD GROUP	ESTIMATED AVERAGE PER CENT BY VOLUME PER FISH			TOTAL NO. FOOD ANIMALS Number of stomachs		
				8	8	13
	Hale Manu	Kokee Stream	Lower Ditch	H. Manu	Kokee	L. Ditch
Red Shrimp	2.1	0.0	43.5	16	0	725
Aquatic Sowbugs	0.0	0.0	3.5	0	0	165
Angle Worms	1.9	36.4	8.2	5	15	15
Midge Larvae	0.1	0.0	0.5	1	0	23
True Flies	0.2	0.5	1.9	2	8	27
Beetle Larvae	0.4	0.1	1.6	4	1	18
Damselfly Nymphs	4.0	18.1	0.0	8	41	0
True Bugs	0.5	0.3	0.4	4	1	12
Moth Larvae	1.9	6.8	3.5	2	10	26
Millipedes	84.5	17.4	12.2	124	42	66
Centipedes	0.0	0.0	0.3	0	0	7
Ants, Bees, Wasps	0.0	0.0	3.3	0	0	16
Snails	0.4	0.3	3.9	1	1	4
Algae	3.4	11.5	10.5	+	+	+
Miscellaneous**	0.1	0.2	4.1	1	2	16
TOTALs	--	--	--	168	121	1120

**Misc. (continue) 3) Large invertebrate animal, 4) Spiders, 5) Seeds, vegetative matter other than Algae.

64 per cent of the total number of food items taken by fish in the ditch below Puu Ka Pele Lookout. Over 55 were found per stomach. No shrimp were found in the stomachs of fish from upper Kokee Streams. Isopods were likewise very important in the lower ditches forming almost 15 per cent of the total number of items eaten by fish from that area. No isopods were found in the stomachs of fish taken below Hale Manu or in the upper Kokee waters.

Angle worms and millipedes were likewise very important items in the diet of the fish examined. While comparatively few angle worms were found per stomach, they average 36.4 per cent by volume of the food of fish taken from the upper Kokee waters. Likewise, they formed 12.4 per cent of the total number of food items found in the stomachs of fish from this region. Millipedes were important both in numbers and volume for they formed 74 per cent, 34 per cent, and 5.9 per cent, respectively of the numbers of items eatenbby fish taken below Hale Manu, upper Kokee, and the Puu Ka Pele ditch. By volume, they bulk larger than any other single item forming over 84 per cent in the case of Hale Manu fish, 17 per cent of upper Kokee fish, and 12.2 per cent of the foods from fish in the lower ditch.

In summary, the dominant fish foods of the ditch below Puu Ka Pele Lookout were of red shrimp, isopods, angle worms, and millipedes. Fish from the ditch below Hale Manu subsisted largely on millipedes and red shrimp. Miscellaneous items made up the bulk of the remainder. Upper Kokee fish, on the other hand, were depending principally on angle worms, damselfly nymphs, and millipedes. The principal difference between the upper and lower areas was that streams above Kokee lacked red shrimp and isopods.

Practically all the stomachs opened contained some green algae. This is commonly found in rainbow trout and they are the only trout known to consistently eat it. Most of the stomachs contained small amounts, but occasionally large masses as big as the ends of one's thumb would be found in stomachs of Kokee fish.

Miscellaneous items such as midge larvae, adult flies, true bugs, moth larvae, snails, and other miscellaneous items showed that a surprising amount of food was falling into the water from the land. Moth larvae were particularly abundant though occuring in lesser amounts than foods such as shrimp, angle worms, and millipedes. Rainbows from upper Kokee where food conditions are much poorer had doubtless eaten algae as a direct source of food. In some cases it is eaten merely to secure the organisms living in it.[2]

Description of Food Organisms

(listed in three categories and in alphabetical order)

<u>Dominant Aquatic Foods:</u>

Aquatic Angleworms- The probable order is Plesiopora, but no information on genus or species. Species measuring approximately 5 to 8 cm. were observed in pools of all streams. Trout seem to like these worms because none were observed in certain pools where fish were present.

Damselfly Nymphs- The order is Odonata and the suborder Zygoptera. This suborder contains one of the most interesting and remarkable of all the endemic groups of Hawaiian insects, <u>Megalagrion</u>, and it is the only aquatic group that is developed to any extent.[1]

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[2] Ibid., pp. 16-18.

[1] E.C., Zimmerman, Insects of Hawaii, Vol. 2, 1st ed., (Honolulu, University of Hawaii Press: 1948) p. 341.

The nymphs of this species, unlike any other known form, have adapted themselves to a life on land.[2] The naiads crawl about in search of their prey in the ground littler beneath dense clumps of fern.[3]

[2] Ibid., p. 343.

[3] Ibid., p. 343.

Dragonfly Nymphs- The order is Odonata and the suborder is Anisoptera. Anax strenuus is the genus species on Kauai. The voracious larvae are known to eat a variety of organisms among which are earthworms, damselfly and dragonfly naiads (even their own relatives), fly larvae (Chironomidae), Hydrobius beetle larvae (Hydrophilidae), crustaceans such as shrimps, sowbugs, and amphipods, molluscs such as Physa, Lymnaea, and Melania, tadpoles, smallfish, and almost any available insect that happens to fall into the water.[4]

[4] Ibid., p. 334.

Isopods- This is Class Crustacea and Subclass Malacostraca. The order here is Isopoda and the species we are interested in is Asellus communis. This is a fresh-water species about 15mm. long and more commonly called sow bugs or pill bugs.

Midge Larvae- There are many kinds of midge larvae such as beetle larva (Hydrophilidae) and mosquito larva (Family Culicidae), but probably the most prominent type is the large torrent midge larvae Telmatogeton torrenticola. It is commonly found on the rocks in the streams flowing out of the mountains.[1] It is dis-

[1] D. E., Hardy, Insects of Hawaii, Vol. 10, 1st ed., (Honolulu, University of Hawaii Press: 1960) p. 162.

tinguished from other Hawaiian species by the large size, the large simple claws of the male, and by the reduced hairy vestitule of the body.[2] It is called large torrent midge larvae because it thrives in swift water and measures a huge 6.0mm. in lenght. Although abundant in the past this species is becoming exceedingly rare to find today.

Red Shrimp- The genus is Gammarus, but species is unknown. The local name for this species is called "opae". It is a transparent crustacean with tiny red spots on its back. Like the torrent midge larvae, the red shrimp too has decreased through time. Once ab abundant in many of Kauai's cold clear streams this species has decreased to only a minute number.

Dominant Land Foods:

Ants- The order is Hymenoptera and the family is Formicidae. Formicidae is the only family of ants in the Hawaiian Islands. This family includes harvester ants, carpenter ants, mound-building ants, field ants, and others.[1] There are seven sub-families from this one family and numerous more genuses. Thus, classifly down to genus species is just about impossible. Anyway these ants literally fall into the food chain of trout and are readily eaten as a delicacy.

Beetles- The order is Coleoptera. This is the largest order of insects with species numbering approximately 300,000.[2] Since

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[2] Ibid., p. 162.

[1] D. J., Borror and R. E., White, A Field Guide to the Insects, 1st ed., (Boston, Houghton Mifflin Company: 1970) pp. 344-346.

[2] Ibid., pp. 146-147.

the number of species is so numerous describing each species found on Kauai is virtually impossible. These beetles are almost everywhere and feed on all sorts of plant and animal materials.[3] They are abundant on vegtation ; they occur under bark, stones, and other objects; many are found on or in the ground, in fungi, rotting vegetation, dung, and carrion.[4] The beetles enter the food chain of trout by way of natural falling into the streams or floods.

Damselflies- Again the order is Odanta and the suborder is Zygoptera. The genus *Megalagrion* are among the largest and most striking in the fauna. Rivers and ponds have their representative species, as do wet banks and waterfalls.[1] The nine species found on Kauai are as follows; *adytum*, *endytum*, *heterogamias*, *kauaiense*, *orobates*, *oresitrophum*, *vagabundum*, *williamsoni*, and *pacificum*.[2] Damselflies like dragonflies are eaten by larger trout while darting along the surface of the water.

Dragonflies- Again the order is Odonata and the suborder is Anisoptera. The species *Anax strenuus* is not only the largest Hawaiian dragonfly, but it is also the largest Hawaiian insect.[3] *Anax strenuus* is mostly a mountain species and is only occasionally seen in the lowlands, and the only in certain places.[4] It seems

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[3] *Ibid*., p. 147.

[4] *Ibid*., p. 147.

[1] E. C., Zimmerman, *Insects of Hawaii*, Vol. 2, 1st ed., (Honolulu, University of Hawaii Press: 1948) p. 343.

[2] *Ibid*., pp.350-357.

[3] *Ibid*., p. 332.

[4] *Ibid*., p. 334.

to prefer the deep canyons and cool stream pools of the mountains and breeds up to 6,000 feet or more.[5] In the highlands of Kauai, the adults fly close to the ground over a grassy, semi-swamp, expertly flushing small moths.[6] They eat a great variety of flying insects, including large native damselflies.[7] The dragonflies are attacked by larger trout while cooling themselves in the streams.

Earthworms or Angleworms- The order is Opisthopora and the genus is Lumbricus, but species is unknown. This earthworm is very similar to the huge North American worm Lumbricus terrestris or more commonly called "night crawlers". These worms usually enter the food chain by way of floods where earth in which they are embedded is eroded into the streams.

Millipedes- The class is Diplopoda and the order Colobognatha, but the genus species is unknown. These diplopods lie by the thousands on the surface of stones in shallow and swift water. They range in size approximately from 2 to 3 centimeters. The millipeds enter the water by natural falling or by floods.

True Bugs- The order is Hemiptera with suborders Gymnocerta and Cryptocerata. Again, this order has too many species to write detailed descriptions even of each family. Important families are as follows: Cydnidae (burrower, ground, and negro bugs), Pentatomidae (shield bugs and stink bugs), Coreidae (squash bugs), Lygaeidae (chinch bugs), Tingidae (lace bugs and tingids),

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[5] Ibid., p. 334.

[6] Ibid., p. 334.

[7] Ibid., p. 334.

Enicocephalidae (gnat and unique heahed bugs), Reduviidae (reduviids, assassin, and kissing bugs), Nabidae (nabids and damsel bugs), Anthocoridae (flower bugs), Cryptoostemmatidae (jumping ground bugs), Miridae (leaf bugs), Saldidae (shore bugs), Hebridae (velvet water bugs), Mesoveliidae (water treaders), Veliidae (smaller water striders), Notonectidae (back-swimmers), and Corixidae (water boatman).[1] The majority of families eaten by Kokee trout come from the last six families listed.

(1) In the family Saldidae or shore bugs is the genus Saldula which is commonly found along the edges of streams or oozing banks in the mountains.[2]

(2) In the family Hebridae or velvet water bugs is the genus Merragata which is a predaceous little bug that walks about on the surface of ponds, streams, and puddles, and readily submerges to explore submerged vegetation.[3]

(3) In the family Mesoveliidae or water treaders is the genus Mesovelia mulsanti which is a long-faced bug located in lowland reservoirs, ponds, and taro patches, but it also ventures into the mountains in some areas.[4]

(4) In the family Veliidae or smaller water striders is the genus Microvelia vagus which is a common predaceous water bug from sea level to about 7,000 feet.[5] It is found among such

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[1] E. C., Zimmerman, Insects of Hawaii, Vol. 3, 1st ed., (Honolulu, University of Hawaii Press: 1948), p. 220.

[2] Ibid., p. 221.

[3] Ibid., p. 225.

[4] Ibid., p. 227.

water plants as duckweed and inhabits ponds, puddles and running water.[6]

(5) In the family Notonectidae or back-swimmers is the genus *Buenoa pallipes* which obtain their common names from the fact that they actually swim on their backs.[7] This species is abundant in the lowlands, although it does extend its range to a few thousand feet elevation, and it flies actively.[8] It is a voracious feeder on almost all kinds of insects, including mosquito wrigglers, which it can capture and hold with its stout fore legs.[9]

(6) In the family Corixidae or water boatmen is the genus *Trichocorixa reticulata* which looks more like some kind of a leafhopper than a bug.[10] It is common in brachish pools in the lowlands, but sometimes ventures up into the mountains.[11]

True Flies- Like most of Class Insecta the flies or Order Diptera number too numerous to be described in detail. Order Diptera is divided into two suborders Nematocera and Brachycera. From these suborders families Tipulidae (crane flies), Psychodidae (moth flies), Stratiomyidae (soldier flies), Bombyliidae (beeflies), Scenopinidae (window flies), and Empididae (dance

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[5] *Ibid.*, p. 228.

[6] *Ibid.*, p. 228.

[7] *Ibid.*, p. 232.

[8] *Ibid.*, p. 232.

[9] *Ibid.*, pp. 232-233.

[10] *Ibid.*, p. 234.

[11] *Ibid.*, p. 234.

flies and empid flies) are the only ones established in the islands. The flies enter the food chain by probably flying right into the water's reflection.

Miscellaneous Foods:

Algae and various plant seeds- Rainbow trout are the only trout that seems to consume green algae (species unknown). If animal foods are scarce it seems that more algae is eaten. Also, various wild seeds are eaten when available to trout.

Bees and Wasps- These insects are from the Order Hymenoptera. Because of the lush flora, wasps and especially bees are abundant in the Kokee region. They get themselves trapped because of the water's reflection.

Centipedes- Centipedes are from the Class Chilopoda. They are common animals found in soil and debris, under bark, in rotting wood, and in similar protected places.[1]

Crayfish- The class is Crustacea and Order Decapoda. These animals were brought in from the continental United States as a possible food source. Even though this idea did not work out as planned the genus *Cambarus* served as a excellent food source for fresh-water bass and trout. They are now thriving in most of Kauai's reservoirs. In Puu Lua Reservoir at Kokee these creatures are the major diet for trout. They have not established themselves in the streams, possibly because of an unstable environment for reproduction.

Earwig- The order is Dermaptera. The genus *Anisolabis* is the

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[1] D. J., Borror and R. E., White, *A Field Guild to the Insects*, 1st ed., (Boston, Houghton Mifflin Company: 1970) pp. 50-51.

probable genus at Kokee. This genus is found in rotten logs, under bark and stones, and in the soil of the mountain areas.

Frogs and Toads- These two cousins from the Class Amphibia are also abundant along the swampy banks of each stream. As you walk along the banks you can hear them splashing into the water and maybe into the hungry mouths of some trout.

Grasshoppers, Cockroaches, Locusts, Mantids, Katydids, Leaf Insects, Stick Insects, and Crickets- For these insects the order is Orthoptera. Because of the lush vegetation these insects are profusely abundant. Like most hopping or flying insects they enter the water because of its reflection.

Minnow~~e~~s- The only minnows at Kokee are located in Puu Lua Reservoir. I do not know what kind of minnows they are, but the locals call them "mosquito fish" (genus. Gambusia). There are no minnows of any kind in the streams and even now I have no idea why none were introduced.

Mammals- Probably the only mammals to be consumed by Kauai's rainbow trout are mice. There are four main types of rats or mice in the islands all from the genus <u>Rattus</u>. These are the black rat, brown rat, Hawaiian rat, and the house rat.

Moths and Butterflies- These insects are from the Order Lepidoptera. Like the bees and wasps these insects thrive in the cool rain forest of Kokee. Also like bees and wasps they get caught by the reflection of the water.

Snails- I have no idea what types of snails are eaten by rainbow trout. Still, in the nineteen 40's or 50's a small univalve mollusc called "vi" could be found in most of Kauai's streams. Today, this species has all but become extinct.

Spiders- The class is Arachnida and the Order Arancida. They usually fall prey to trout as they walk along the water's surface.

Termites- The order is Isoptera. The species of termite that we are concern with comes from the genus Neotermes. Neotermes connexus is the largest termite in Hawaii and its length may reach nearly 20mm.[1] It is typically a forest insect which may range from 500 feet up to about 5,000-foot level.[2] It is common in dead stumps, logs, limbs, and dead parts of living trees.[3]

Trout eggs- Even though the water temperature is often too warm for reproduction the adult trout continues the natural process of spawning. Many times these eggs are uncovered by flash floods and then become a tasty treat for nearby fish.

Trout (fingerlings)- Most trout become carnivorous after they become two to three years-old. Thus, during the annual spring plantings most of the young trout are consumed by the larger hold-over trout.

Conclusion

Fron this report it is obvious that there is no food problem affecting the trout at Kokee. As you have seen there was a multitude of aquatic and land foods to satisfy each and every fishes taste. Thus, any recommendations to introduce a new or exotic food source should be ignored by this author's opinion. Such a

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[1] E. C., Zimmerman, Insects of Hawaii, Vol. 2, 1st ed., (Honolulu, University of Hawaii Press: 1948) pp. 170-171.

[2] Ibid., p. 171.

[3] Ibid., p. 171.

species could cause problems beyond the scope of the ordinary fishery biologist. An exotic species could cause breaks in the already stable food web of the Kokee rainbow trout.

special note: Mayflies, caddisflies, & stoneflies were introduced as a potential source of food for the trout, but it seems that the environmental conditions in the islands were not suited for them.

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HOOKING MORTALITY OF CUTTHROAT TROUT

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3-7-73

Fulfilling the requirements for JT330 and FW300

ABSTRACT

Factors affecting survival of adult cutthroat trout released by anglers were studied at Yellowstone Lake in 1967 and 1968. Twelve hundred a nd ssventy five trout were caught with single hooke and worms, and by casting with treble hook lures. Fish were held in liveboxes from 10 to 99 days.

Trout caught in prespawnig condition with lures did not incur higher mortality than fish not in reproductive condition. Hooking mortality was high in trout caught by the troll and worm method. high water temperatures increased the frequency of deep hookings and the rate of immediate mortality in troll caught trout. Temperatures between 37 and 62° F did not influence any growth of fungus on any of the fish.

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INTRODUCTION

One of the main problems in fisheries management is that there is a great death toll in fish due to hooking mortality. Many fish are returned to the water by fisherman because they are not legal size or right species, and beacause some anglers only fish for sport. If this type of management proves to be harmful then a new policy must be enforced in order to protect fish.

The area that was studied was at Yellowstone Lake, which is situated on the Continental Divide in the south- central part of Yellowstone National Park, Wyoming. It is located at an elevation of 7,731 feet and encompasses anarea of 1,396 square miles. The lake is maintained by snow runoff and springs having a maximum depth of 320 feet. Field work was conducted from June 1 through mid September in 1967 and 1968.

In 1961 at Yellowstone Lake the National Park Service adopted a fishing for fun program involving the release of uninjured fish. Questions were being raised by biologists about the effectiveness of fishing for fun program. Biologists believed that fish were dying after release due to hooking mortality. The program was discontinued by the National Park Service and U.S. Fish and Wildlife Service so that a more thorough investigation of hooking mortality could be studied.

Research was done in 1967 and 1968 to study certain aspects of catch and return fishing at Yellowstone Lake. The influence of water temperature, angling techniques on survival of released fish, and response of trout to certain physiological stresses associated with hooking and handling were examined.

There were several objectives in this study which would prove vital to further ~~to~~ future fishery management. They are as follows: 1) hooking mortality of cutthroat trout caught in prespawning condition 2) whether deep hooked trout have a better chance for survival when the hook is not removed 3) relationships between water temperature and immediate mortality in trout caught by the troll and worm method 4) corrosion rate of hooks left in trout and 5) whether external fungal infection was evident from catch and return fishing.

The fish being studied, the cutthroat trout, is recognized easily from the crimson slash marks on each side of the throat beneath the lower jaws and is now restricted to the high mountain regions.

The cutthroat trout spawns in the spring from April to June depending on the water temperature. Spawning takes place in gravel areas in running water. The female constructs a nest by scooping out a depression in the gravel with her body and fins and then the fertilized eggs are buried in the gravel by the female. The fry emerge late in the summer.

The particular species of cutthroat trout being studied was Salmo clarki lewisi which is indigenous to the Yellowstone Lake area.

The two methods used in this research were: 1) mark and recapture and 2) confinement. Fish were marked according to different methods of capture and released. Certain tags were used in each experiment in order to separate the losses attributed to different treatments. The disadvantages to this method is that large numbers of fish must be tagged for sufficient return. Tags ~~also~~ should not cause an increase in the vulnerability to predators and cause any injury to the fish. Mortality due to tagging may cause an error in data.

The confinement method is used because(of the advantage it has in that) the total sample is used in analysis and also mortality is observed directly. There are three assumptions to this method and they are: 1) mortality is not caused by abrasion damage to fish 2) stress of confinement does not cause mortality 3) temperature and dissolved oxygen does not contribute to mortality.

MATERIALS and METHODS

MATERIALS

Vessels

The U.S. Fish and Wildlife Service and the Yellowstone Park Company donated a 19 foot cabin boat and a small utility craft. A 16 foot aluminum electrofishing boat, which contained a built in 150 gallon livewell aerated by a venturi- ram intake system, was used to collect control fish.

Rods and Reels

Zebco rods and reels were used and they are as follows:

model 330 level-wind casting reels and matching 3366 rods
model 4490 open-face spinning reels and rods
model 101 closed face spin casting rod and feel combinations

Lures and Hooks

Hooks were No. 4 carbon steel bait hooks coated with an epoxy enamel compound. Trolling lures consisted of brass, copper, and nickel 1.05 inches long and 0.65 inches across.

Confinement Facilities

A portable livesled was suspended on the port side of 19 foot boat for contemporary confinement of fish. Fish were shaded by means of plywood panels. Four inch and eight inch fish were held in liveboxes.

Electrofishing Equipment

A single phase, 60 cycle, 115 volt, alternating current generator with an input capacity of 1200 watts was used. A multitop transformer permitted selection of 50 to 700 volts in 50 volt increments.

METHODS and RESULTS

EXPERIMENT I- Hooking mortality of prespawning trout

For this experiment, treble hooks were used to catch trout in prespawning and nonspawning conditions. These fish were then confined in livebox for 10 days. Control groups were used for both conditions.

As the prespawning trout entered Clear Creek to spawn in late June of 1967 and 1968, the fish were caught with lures and then placed in a 5- gallon pail of stream water. Within 15 seconds they were transferred to liveboxes. Control fish were transferred in the same manner after being in Clear Creek.

Nonspawning trout were caught offshore from French Island by lure casting. The nonspawning control group were elctrofished by night.

Observations were made daily during the first 5 days and on alternate days thereafter.

Out of 357 trout, 201 were caught by hook and line. The results showed by the Chi-square analysis that there was no significant difference in mortality of spawning and nonspawning trout. See Table 1.

$X^2=.o2$ d.f.=1 P>1

EXPERIMENT II- Survival of trout with hooks not removed

Trout were caught in the South Arm with trolled hooks and worms. Fish were caught between 3 feet and 10 feet.of water and were then placed immediately into a livesled. Fish were considered deeply hooked if the hook was not visible when the mouth was closed; otherwise they were considered superficial (lip hooked). The lip hooked trout were released and the deep hooked trout were separated from the lure by breaking the 2-lb. test leader leaving the hook and tag with the fish.

Table 1-- Hooking mortality of spawning and nonspawning cutthroat trout caught with treble hook lures

	Nonspawning trout		Spawning trout	
	Control	Hook/ line	Control	Hook/ line
No. in sample	63	102	93	99
No. mortalities	0	3	4	1
Per cent mortality	0	2.94	4.30	1.01

Observations of fish in the livebox were made every three hours on the first day, at 12 hour intervals the next 2 days, and on alternate days thereafter. Mortalities were studied by autopsy, X-ray, and stomach analysis.

In this experiment 253 trout out of 422 or 59% were deeply hooked. The water temperature ranged from 37°-64° F and the results showed that deeply hooked trout died as the water temperature rose. Table 2 Chi-square test showed that a) frequency of deep hookings X^2=28, d.f.=3, b) rate of immeeiate mortality X^2=16, d.f.+3and c) losses at the first 24 hours X=10, d.f.=3.

Mortality during the first 30 days is described in Fig. 1 showing a decrease from 253 to 71 fish. Between the 60 and 93 day, 13 out of 23 remaining trout died and survival of trout with hooks left in was slightly over 50 % of original group at the end of 30 days.

EXPERIMENT III- <u>Hook corrosion</u>

The deep hooked trout in the preceding experiment had hooks of known weight left in them and later recovered and reweighed on the same balance used for initial weighing. Corrosion was determined by weight change. Hooks were recovered from live trout at 10, 20, 30, and 90 daysand from dead fish as mortalities occurred.

Tags and leaders were removed from recovered hooks in the field. The hooks were dipped in 95 % ethyl alcohol, rinsed in water, air dried, sealed in envelopes, and then stored in air tight container.

Before rewighing the hooks, they were immersed in boiling water for two minutes, then given two 15 second dips in 10 % glacial acetic acid. After a final rinse in distilled water, hooks were dried in an oven for 3 minutes at 104°F.

Table 2 - Effect of water temperature on frequency of deep hooking and 24 hour mortality of cutthroat trout caught by trolled single hooks and worms

	*****				
Water Temperatures F	37-45	51- 52	57 - 60	Above 60	
No. trout caught	n_1=132	n_2= 113	n_3= 109	n_4=68	T=422
No. deep hooked	n_1'= 56	n_2'= 79	n_3'=67	n_4'=51	T=253
Per cent deep hooked	42.4	69.9	61.5	75	$\bar{X}$=59.9
Mortality when hooks not removed from fish					
No. immediate	n_1 = 0	n_2=13	n_3=8	n_4=13	T=34
Per cent immediate	0	16.5	11.9	25.5	$\bar{X}$=13.42
No. after 24 hours	n_1' = 1	n_2'=16	n_2'=16	n_4'=17	T=50
Per cent after 24 hours	3.33	20.2	23.9	33.3	$\bar{X}$=20.47

T = the sum of the observations within the group = Σn_i

$\bar{X}$ = the overall mean or the average

Hook corrosion was determined from 149 hooks taken from the esophogeal and stomach areas of live and dead trout. The estimated rate of corrosion for 129 hooks in the esophagus of trout was 0.139 mg per day ± 0.0239 mg. True mean corrosion rate was between 0.114 and 0.162mg per day with 95 % confidence Fig. 2. Mean weight loss of hooks in the esophagus for 90 days was 12.47 which is 5.65 % of the mean original weight of the hooks.

EXPERIMENT IV- Water temperature and mortality of lure caught trout

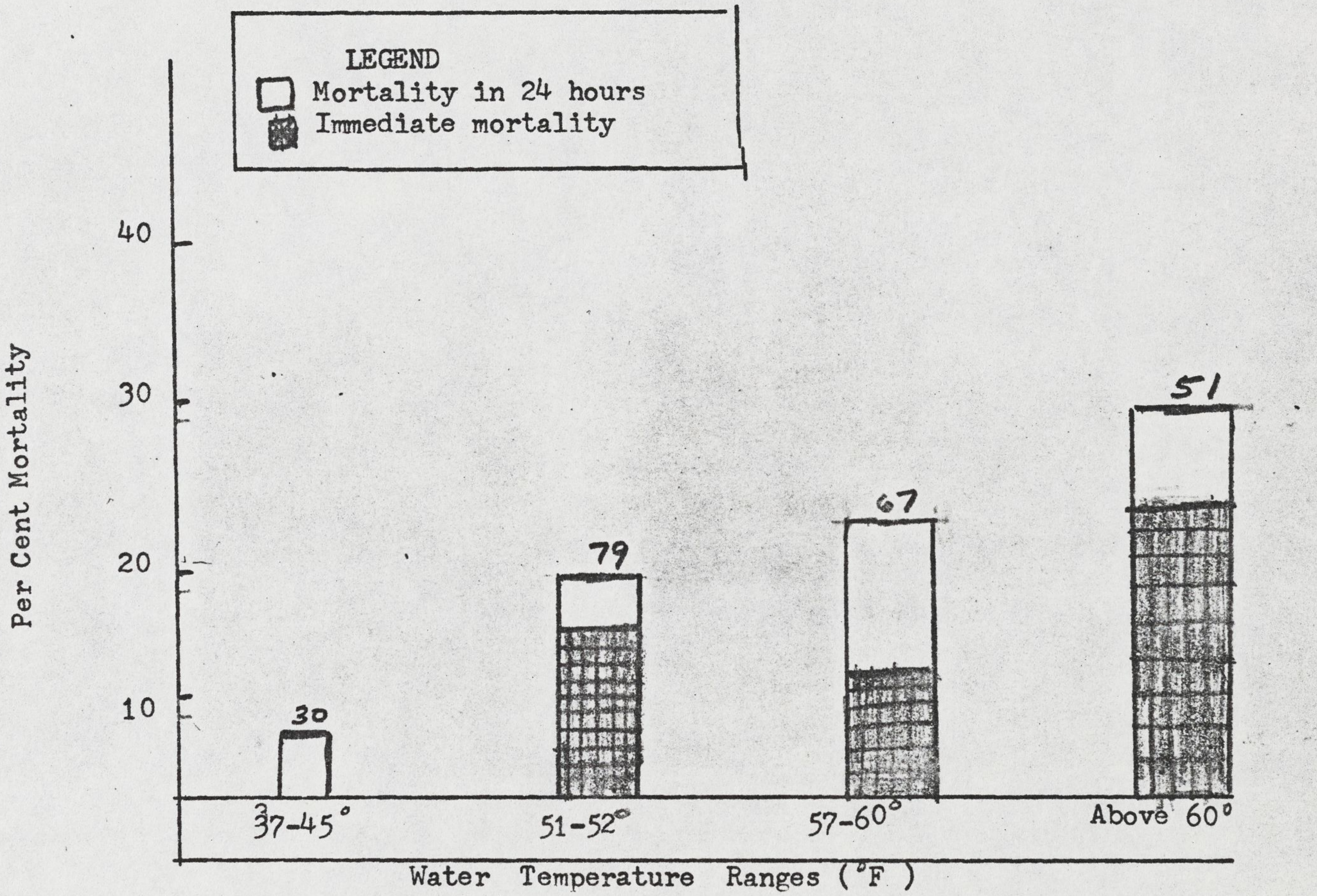
Treble - hook lures were used to catch trout and these fish were held for 30 days. Losses were observed over the full range of water temperatures at Yellowstone Lake. Observations were made daily during the f first four days and on alternate days thereafter. Trout caught by hooks and lines were adipose fin clipped prior to release for identification if recaptured.

Treble hook lures were used to catch 352 trout and 126 control fish were caught by electroshocking. The water temperature ranged from 37°- 62°F and the results showed that there was no significant difference in the loss of trout due to temperature change.(X^2=2, d.f.=2 P>.05) . Table 3. No control fish were lost.There were only 18 mortalities in this experiment.

EXPERIMENT V- Disease

Trout were examined for external infection in preceding experiment.Of the 334 trout that survived the preceding experiment non were infected with fungal growth.

Figure 1 - Relationship between water temperature and mortality of deep hooked cutthroat trout when hooks not removed.



(Numbers Above Bars Indicate Sample Sizes)

Table 3 - Mortality of cutthroat trout caught with treble hook lures at different water temperatures

Temperature Range °F	37 - 49°	46 - 55°	58 - 62°
No. trout caught	102	200	50
No. mortalities	3	13	2
Per cent mortality	2.94	6.50	4.0

CATCH RETURN of PRESPAWNING TROUT

Hooking Mortality of Prespawning Trout

The experiments in the Clear Creek area showed that cutthroat trout in spawning or nonspawning condition may be expected to survive if lure caught.

Whether post-spawning survival is impaired by hooking and handling of trout in prespawning condition is not important at Yellowstone Lake because a) natural spawning mortality is high b) Contributions of post-spawners to the fishery is negligible and c) less than 2 % of the trout reproduce a second time.

TROLLING with the SINGLE HOOK and WORM

Frequency of Deep Hooking

Trout that were deeply hooked by single hooks and bait showed poor survival.

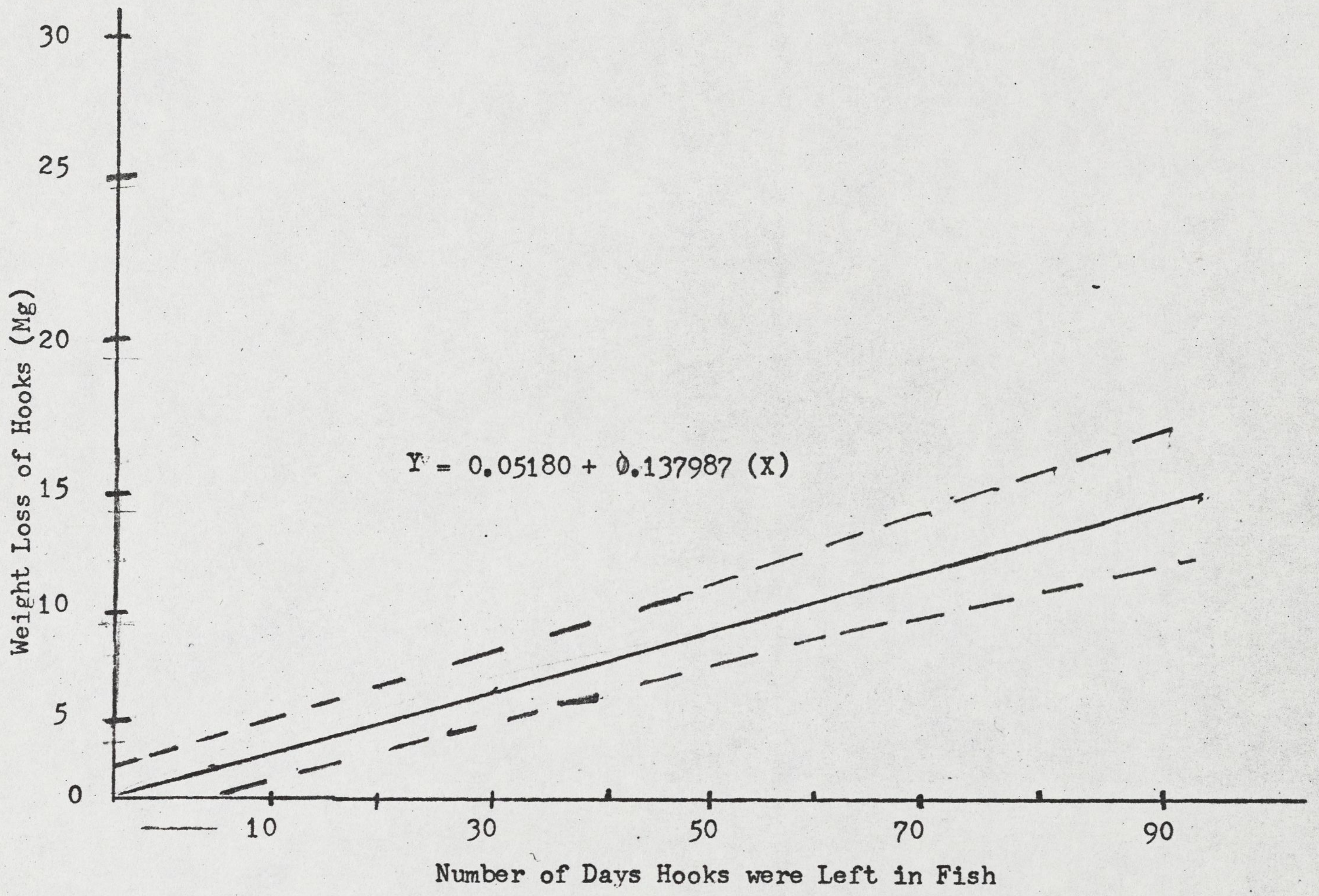
Deep Hooking and Water Temperature

High water temperatures were correlated with deep hooking in troll caught cutthroat trout (FIG.2). Frequency of deep hooking increased from 42.4 % to 75 % as temperatures rose. At elevated temperatures it is believed that cutthroat trout manifest a higher energy potential by altering their manner of attacking the lure resulting in deep hooking.

Hook Removal Versus Hook Left In

This test showed that mortality increased when the hook was taken out. Death toll 88.5 %;whereas, when the hook was left in mortality averaged 34.5 %.

Figure 2 - Corrosion of 12° hooks in the esophogeal region of cutthroat trout with 95 % confidence bands



Hook Corrosion

The results of hook corrosion of cutthroat trout are:1) probability that a No. 4 single hook will dislodge from the esophagus is low 2)hooks in the esophagus corrode slowly; should any vital function be impaired, death would probably occur before the hook would deteriorate sufficiently to be eliminated 3) hooks in the stomach may be eliminated within 120 days in trout that consume and digest food 4) cutthroat trout with a No. 4 hook in the esophagus or stomach are physically able to feed on plankton, but feeding may be abnormal.

SUMMARY

The establishment of catch and return fishing in different areas may prove to be destructive or it could possibly be a useful management technique. The goal of the experiment was to predict fish losses under given conditions.

The techniques used in this research was used to determine the survival rate of cutthroat trout by evaluating the influence of water temperature and angling techniques at Yellowstone Lake. A total of 1,275 trout were caught by hook and line in the summers of 1967 and 1968. Two hundred and nineteen trout were caught for control methods. Fish were taken by trolling with single hook and worm and treble hook lures. The trout we re kept in liveboxes from 10 to 93 days for observations.

There was no significant difference in the mortality of prespawning and nonspawning trout. The possiblity of using spawning stocks for seasonal fishing is questionable.

By use of the troll and worm method, mortality was considerably high. Deep hooked trout survived better when the hooks were not removed. The increase of water temperature increased the mortality rate.

No signs of external fungal infection appeared on any of the trout.

Fishing for Fun

Although a policy of catch and return of prespawning trout in tributaries to Yellowstone Lake may be adopted, several factors must be considered.Such factors are that fisherman may harm fish when they are returned to the water or that fish may br taken illegally from the lake. This policy may pr prove to be beneficial by reducing the fishing pressure on spawning trout. The contradiction to this is that spawning trout must not be interrupted by anglers.This program should not enforced until more is known about the effects of hooking and handling on post- spawning survival.

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THE RIO GRANDE CUTTHROAT TROUT

by
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for
FW300
ICHTHOLOGY

THE RIO GRANDE CUTTHROAT TROUT

The cutthroat trout, Salmo clarki, is an example of a polytypic species. Throughout its geographical range, from Alaska to California and inland throughout the Great Basin and the Rocky Mountain region, the species has numerous subspecies. One of these subspecies is the Rio Grande cutthroat Salmo clarki virginalis.

Coronado's expedition to the New world in 1539 made reference to the Rio Grande cutthroat trout. The expedition found that: "There were very good trout in the upper Pecos River" Rostlund (1952:25). Since that time little new information on the native trout of the Rio Grande basin has emerged. The type locality of the Rio Grande cutthroat trout S. c. virginalis is Ute Creek, Colorado.

HISTORICAL REVIEW

The U.S. Army established Fort Massachusetts on Utah Creek (now Ute Creek) in Costilla County, Colorado in 1852. Ute Creek eventually flows into the Rio Grande in the San Luis Valley. The first collection of Rio Grande trout was made by a Pacific Railroad Survey expedition in 1853. Girard (1856) examined these specimens and described a new species, "Salar virginalis". Fort Massachusetts was abandoned in 1858 and Fort Garland was established six miles to the south. Rio Grande trout were collected later from near Fort Garland and were examined by Cope who described a new species "Salmo spirulus" (Cope, 1872). Sangre de Cristo Pass, probably Sangre de Cristo Creek, was the type locality. Cope had known of Girard's description of virginalis from Ute Creek, but at that time the typological concept for species was prevalent in taxonomy and Cope thought that Spilurus was a valid species because it was: "Not so slender as virginalis."

Confusion of the type locality of virginalis caused later authors to consider "Utah Creek" a tributary to Utah Lake, and the name spilurus was used for the Rio Grande cutthroat, while virginalis was applied to the Bonneville basin trout. The name virginalis given by Girard in 1856 is the first scientific name used for the Rio Grande trout.

DISTRIBUTION

The original range of the Rio Grande trout is unknown. Cope (1886) mentioned two "black-spotted" trout with "teeth on the basihyal bone", from southern Chihuahua, Mexico. Because of this report, most published distributions list the range extending south to Chihuahua. Unfortunately, the fate of Cope's specimens and their exact location is unknown. Cope listed the locality as: "Streams of the Sierra Madre, at an elevation of 7,000 and 8,000 feet, in the southern part of the State of Chihuahua near the boundaries of Durango and Sinaloa." His site could be in the Rio Conchos drainage, tributary to the Rio Grande in Chihuahua, or possibly streams flowing west into the Gulf of California. Trout collections from around the Gulf of California have been discussed by Needham and Gard (1959) from various Pacific Coast streams, but no trout have been reported from the Rio Conchos. The probability remains that during the colder periods of the pleistocene, cutthroat trout did range throughout the Rio Grande system into Mexico and may still persist in isolated populations in Rio Conchos, Behnke (1967).

The presence of native trout in Texas has never been authenticated, Hubbs (1957). McKittrick Creek in the Guadalupe Mountains contains the only population of self-reproducing trout in Texas today, and they are introduced rainbow trout.

Danial (1878) related his fishing experience in a letter to Forest and Stream. While working as assistant surgeon in the Second Texas Rifles during the Civil War, Danial thought he remembered fishing for trout at San Felipe Spring, a tributary to the Rio Grande near Del Rio on the Mexican border. While stationed at Fort Davis, Danial recalled catching many trout from the Limpia River (tributary of the Pecos River).

Other information of earlier trout collections in texas was supplied by Taylor (1878) in a note to Forest and Stream. Taylor wrote that Dr. D. I. Hunter, a Confederate Army Surgeon, stationed at Fort Davis on the Limpia River, thought eastern brook trout (Salvelinus fontimalis) inhabited the Limpia River. Taylor also told of a buffalo hunter who recalled catching "wagon loads" of "speckled trout" in the Texas Panhandle from streams of the Canadian and Red Rivers. Taylor confirmed the storywith a D. S. Hinkle who worked with Emory's Boundry Survey in the Panhandle area. The Texas Panhandle extended into part of the present day New Mexico at that time. Johnson (1880) noted in Forest and Stream that he didn't believe that trout existed in texas. He stated: "There may be genuine trout in Texas, but if so they are very far from the limits of civilization for I have fished Texas waters since 1848 and never saw a speckled trout other than what is called in the South 'salt water trout' and in the North 'weak fish'". The existance of native trout in the Canadian River system has not been clearly shown. An article in Forest and Stream by an anonymous author (1877) signing himself as "Apache" mentioned that Rio Grande cutthroat trout were abundant...."at the headwaters of the Vermejo."

Colorado Division of Wildlife records do not list any stream named Vermejo in the Rio Grande basin. The reference likely refers to the Vermejo River in the Canadian River Basin of New Mexico. A fish survey by the New Mexico Department of Fish and Game in the Canadian River basin from 1953 to 1956 listed many excellent trout streams in the headwater tributaries of the Canadian River in the Sangre de Cristo Mountains. Fishes found in the streams included brown, brook and rainbow trout. But the report stated:"native cutthroat still dominate most of the upper-most headwaters." The term "native trout" is used to denote cutthroat trout in general, without reference to indigenous or introduced species or subspecies. Extensive introductions of cutthroat trout (mostly Yellowstone lake stock) have been made in the Canadian River basin since 1907. It is not known if cutthroat trout were present before man's activities. The evidence that trout naturally ocurred in the Canadian River basin is inconclusive. There are no known documented records or preserved specimens collected before introductions occurred.

The most southern population found to date is in Indian Creek on the Mescalero Apache Indian Reservation in southern New Mexico. Indian Creek is a tributary to Three Rivers whose waters disappear in the desert of the Tularosa Valley, north of the White Sands National Monument. In the late Pleistocene the Tularosa valley contained a large lake and was probably a tributary to the Rio Grande (Hubbs and Miller 1948).

Due to the topography and steep gradient it is doubtful that the present population is a natural occurrence from the Tularosa basin, but more likely carried over from the Pecos basin by man. The large, sparse spots resemble museum specimens of Pecos cutthroat more than they do the _S. c. virginalis_ of the Rio Grande. The Indian Creek population may be the only known pure stock of Pecos cutthroat. The native trout of the Rio Grande most likely originated from the Colorado River and/or the Arkansas River Drainages. The sharp escarpment of the Sangre de Cristo Range in Colorado, seperating the Arkansas and the Rio Grande drainages would suggest that headwater transfer more likely occurred from the Colorado drainage into the Rio Grande.

SYSTEMATICS

Published accounts of the Rio Grande trout are of little value for the recognition of Rio Grande trout from other cutthroat trout. Most of the early reports consisted of general comments of morphology and spotting patterns, which are essentially worthless for distinguishing the Rio Grande populations from other geographical group of the variable cutthroat trout species. The description of specimens collected by Jordan (1891) from the Rio Grande at Del Norte, Colorado, provided the basis for most later taxonomic descriptions of the Rio Grande subspecies. Jordon stated that the Del Norte specimens had rather large spots..."more or less confined to the dorsal and caudal fins and region between them, though often in the young ,extending on the head." He added: "this form is apparently wholly identical with var. _pleuriticus_, except that in the specimens examined the scales are less crowded forward, so that the number in a lengthwise series is less. I count 155 to 160 in Rio Grande specimens; 185 to 190 in those from Colorado." The amount of information that can be abstracted from the available literature on Rio Grande cutthroat trout provides no real basis

The amount of information that can be found in the available literature on the Rio Grande cutthroat trout provides no real basis for seperating this group from the cutthroat trout of the Colorado River, the Bonneville basin or of Yellowstone Lake.

The most obvious character which tneds to distinguish the Rio Grande trout from the other cutthroat is an adipose fin rimmed with a black border."The Basibranchial teeth are exceedingly minute; not visible above the mucous membrane covering the basibranchial plate, and observable only under magnification and much eye sraining probing with a needle" (Behnke 1967). The interpretation of the presence of basibranchial teeth must be made with caution in this case.

The speicmens from the upper Rio Grande basin have medium spots, mostly concentrated in the posterior region. Anterior to the dorsal fin the spots are less numerous, smaller, and mainly located above the lateralline. Posteriorly from the dorsal fin the spots are larger and more evenly distributed above and below the lateral line.(Behnke 1967).

Characteristics of the Rio Grande cutthroat trout show: Vertebrae-(61-62), gillrakers-(18-20), pyloric caeca-(36-42), scales above lateral line and in lateral line series-(38-42 and 158-172), basibranchial teeth-(present but typically few and poorly developed 3-6), pelvic fin rays-(9), and spotting pattern(moderate size spots arranged symetrically on body, concentrated on region posterior to dorsal fin, spots tupically absent from top of head) from wallace and Behnke (1974).

SUMMARY

More information is needed on the life history and distribution of the Rio Grande cutthroat trout to determine if and where pure populations exist. when found, these populations should be protected to maintain the gene pool for future study and use.

Rm. 316

EVOLUTION
IN THE
SPRING FAUNA

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EVOLUTION IN THE SPRING FAUNA

INTRODUCTION

As a group, aquatic animals exhibit diverse survival abilities. They have adapted to a range of habitat stabilities from intermittent streams and temporary ponds to the extreme constancy of great ocean depths. Aquatic metazoans live in water temperatures from 0° C to 50° C (Mitchell 1974) and in salinities from zero to 280 grams per liter (Hutchinson 1957, Frey 1963). They exist as isolated populations or within extremely diverse communities and have been able to adapt to almost all aquatic habitats on Earth (Table 1).

When compared to other habitats, water has several properties which make it unique for life. The high specific heat (1 cal/gm-C°), high heat of fusion (80 cal/gm), and high heat of vaporization (539 cal/gm) add to the thermal stability, and properties such as density, viscosity, surface tension, and solvency are of paramount importance to aquatic animals.

Springs represent a special aquatic habitat tending toward constancy in physical and chemical properties, and often posses a characteristic fauna (Table 2). Structurally they are part of the surface waters lying at the interface between the ground water and stream habitats. Quantitatively springs are an unimportant part of the total aquatic habitat on Earth (Table 1), but biologically they are very important.

It is the purpose of this term paper to show that spring habitats are important in the evolution of many aquatic animals and as a genetic refuge during times of environmental stress.

Table 1. Distribution of water on Earth.

Source	Volume (miles^3)	Percent of Total
Atmosphere	3,100	0.001
Surface Waters		
Freshwater lakes	30,000	0.009
Saline lakes	25,000	0.008
Streams	300	0.0001
Subsurface Waters		
Soil moisture	16,000	0.005
Ground water		
Less than 0.5 mi deep . . .	1,000,000	0.31
Greater than 0.5 mi deep . .	1,000,000	0.31
Ice Caps and Glaciers	7,000,000	2.15
Oceans	317,000,000	97.2
TOTAL	326,000,000	100

(United States Department of the Interior 1968)

SPRINGS AS HABITATS

Before entering directly into the discussion of the biology and evolution in springs, a general overview of springs as habitats is instructive. The distribution, classification, origin, physical and chemical factors, and general biology of springs will be discussed.

Distribution

Meinzer (1927) examined the largest springs in the United States and found 65 with a flow in excess of 100 cubic feet per second (2840 liters per second). He found that most of these large springs originated in limestone or volcanic lithology. Large springs (24) issuing from limestone occur in central Texas, northern Florida, and southern Missouri. Large springs (38) issuing from volcanic rocks, but not geothermally heated, occur in northern California, central Oregon, and southern Idaho. He also identified three other large springs in Montana issuing from sandstone.

Meinzer (1927) estimated that there were hundreds of springs in the United States with flows in excess of 10 cfs (284 l/sec) and thousands in excess of 1 cfs (28.4 l/ sec). Beckman and Hinchey (1944) estimated there were 10,000 springs in the Missouri Ozarks. Other studies of springs from Tennessee (Sun, et al. 1963), Iowa (Tilly 1968), Kansas (Swineford and Frye 1955), and California (Waring 1915) indicate their widespread distribution across the United States. Peale (1886) lists many mineral springs, and White (1968), Waring (1965), and Pearl (1972) provide data on thermal springs of the world. The thermal springs of the United States are associated with volcanic areas, and include all western states plus Arkansas, Georgia, Virginia, and West Virginia (Waring 1965). Springs in the Fort Collins, Colorado, area tend to be small and are concentrated along the eastern edge of the Rocky Mountains where disrupted metamorphic and sedimentary rocks provide conditions favorable for springs. Therefore, springs are widely distributed across the United States and other countries, with concentrations of large springs in especially favorable climate and geology. Many springs are continuously connected to the streams and lakes in the drainage basin while others are disconnected or isolated by varying distances.

As an indication of the widespread distribution of springs throughout the world, the following references are to a small fraction of spring biological studies: Australia (Bayly and Williams 1973);

Austria (Findenegg 1959, Thurner 1965); Azores (Brock and Brock 1967); Bulgaria (Apostolov 1971, Kownacki and Kownacka 1974); Canada (Van Everdingen 1969, Marsh 1974); Corsica (Reid 1968,1969a,b); Denmark (Nielsen 1950a,b,1951, Berg 1951, Thorup 1963,1966,1970a,b,1974a,b, Bengtsson 1967, Iversen 1973b); England (Carpenter 1927,1928, Elton 1956,1966, Round 1960,1964,1965, Elbourn 1965); Germany (Thienemann 1912, 1949, Brehm 1930, Schwoerbel 1959, Wichard 1970, and many others); Iceland (Tuxen 1944, Brock and Brock 1966, Starmuehlner 1969); India (Jana 1973); Israel (Por 1963,1968, Kahan 1961, 1963,1972, Chervinski 1968, Mazor and Molcho 1972, Dor 1974); Italy (Zanandrea 1955, Toffoletto 1960); Japan (Komatsu 1964); Lapland (Engelhardt 1957); Mexico (Milstead 1960, Minckley 1962,1969, Miller and Minckley 1963, Miller 1964,1968, Hubbs and Miller 1965, Cole and Minckley 1966, Taylor 1966, Minckley and Cole 1968a,b); Netherlands (Maas 1959); New Zealand (Stoner 1923, Winterbourn 1968,1969,1973, Wells and Taylor 1970, Marshall 1973); Nigeria (Lincoln 1972); Poland (Kubik 1970, Skalna 1973); Romania (Robert and Munteanu 1966); Sardinia (Masala 1969); Spain (Alvarez 1964); Turkey (Schutt 1964, Schuett and Bilgin 1970); USSR (Belyshev 1957, Egorova, Pozmogova, and Loginova 1973); and Yugoslavia (Petrovski 1966).

Classification

Classification schemes for springs have been devised by discharge (Meinzer 1927), thermal properties (Tuxen 1944), degree of constancy (Tuxen 1944), source morphology (Bornhauser 1913), stream longitudinal succession (Illies and Botosaneanu 1963), and chemical properties (hard, soft, mineralized, de-oxygenated). Quite often springs constitute the headwaters of a stream so that springs fit into the longitudinal zonation scheme. Illies and Botosaneanu (1963) proposed the crenon (spring region), rhithron, and potamon regions from the headwaters to lower reaches, respectively. The crenon is divided into the eucrenon, the spring source, and the hypocrenon, the spring brook. The point where spring waters lose their characteristics derived underground and become the rhithron is not exactly defined. The terms rheocrene, limnocrene, and helocrene also have been adopted (Hynes 1970). The rheocrene is a spring that flows directly from its source into the spring brook, while a limnocrene first forms a headpool at the source. A helocrene defines a marshy spring source.

Origin

Springs are a natural part of the Hydrologic Cycle (Figure 1). Water evaporates from the oceans, moves inland as atmospheric moisture, falls to the land as precipitation, and flows back to the oceans while acting as a major geologic force in determining land morphology. A percentage of the total precipitation is concentrated into brooks and streams and forms the surface runoff which is obvious to everyone. Much less obvious is the percentage of total precipitation which infiltrates into the soil and then percolates through the various, and often devious, small pore spaces of the soil and underlying rock. The percentage of total precipitation entering the soil can vary widely (0-100%) depending on the land surface and climatic factors; however, most often more than half of the total precipitation will enter the soil to become part of the subsurface water. Table 1 gives an indication that this may be true since far more water is present in subsurface than surface systems. The percolating water continues down through more and more compacted soil until it reaches the water table. The water table is that depth at which all the pore spaces are filled with water and which there is a gradient flow like an underground stream. The water table is usually formed by an underlying strata of rock which is impervious to the passage of water and forces it to flow

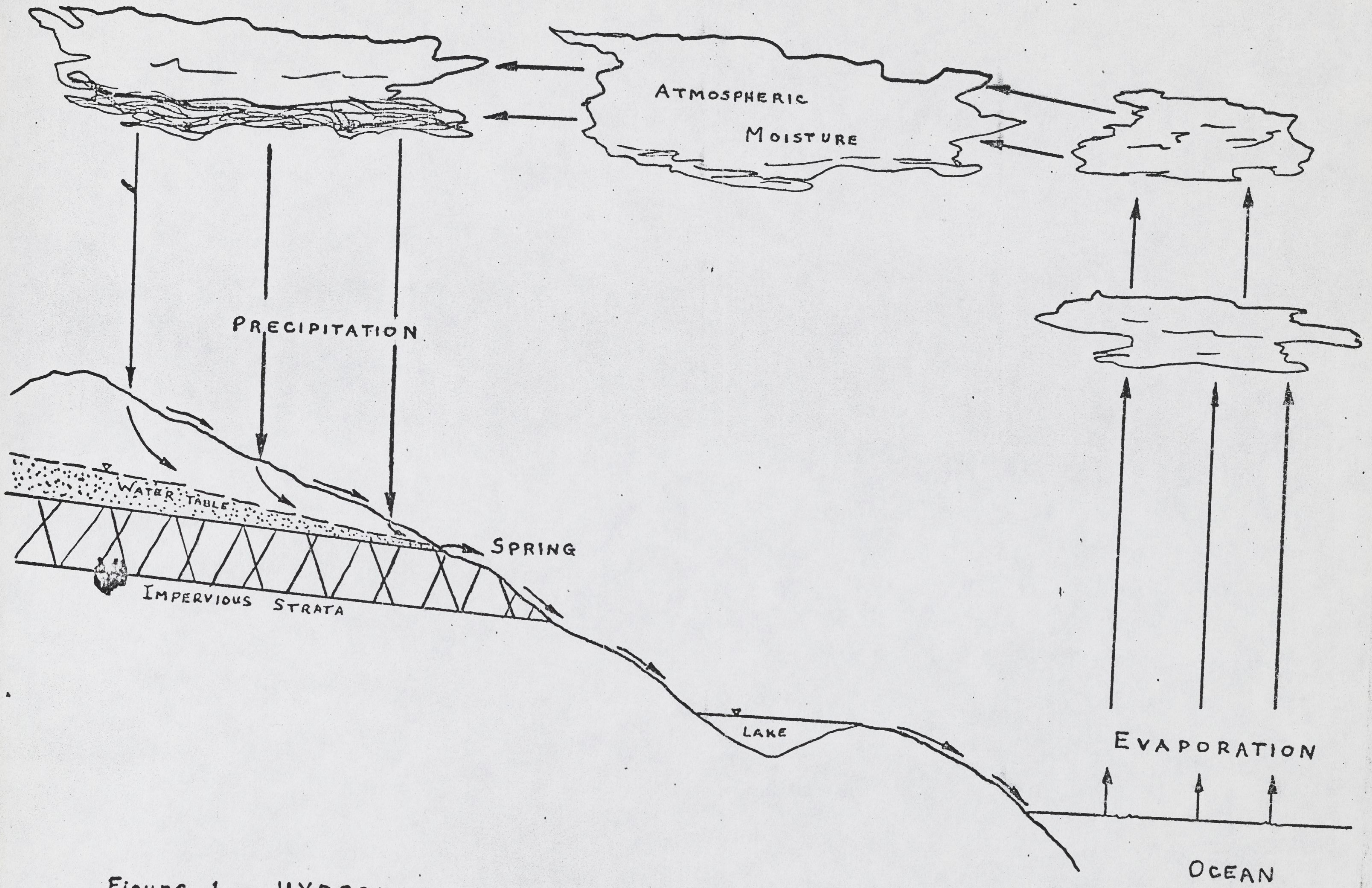

Figure 1. HYDROLOGIC CYCLE

in a lateral direction. The velocity of flow is quite likely very slow since the small interstices create friction. If the impervious strata extends to the ground surface, the underground flow is forced to issue as a spring, that can then continue as part of the surface water or depending on the channel substrate downstream may sink back into the ground. If the underground strata does not force the flow to issue as springs, the water may continue along its underground gradient to possibly enter a stream or lake or an underground storage basin.

There are many alternates to the above described "typical" water movement and origin of springs. Often a geologic fault will act as a barrier to flow, forming a spring at the ground surface. The velocity of underground flow will vary considerably depending on the pore size and in very porous volcanic rock the flow can be quite fast.

Underground streams can form in limestone strata. Percolating water contacts the limestone and dissolves small portions. Over a long geologic time, this gradual dissolving of the limestone can form large caverns and underground channels through which the water can flow freely. This water then issues as spring where the limestone intersects the ground surface. It is also possible for these underground channels to be completely filled with water when the entire region has subsided (Meinzer 1927).

Physical and Chemical Factors

The physical and chemical factors of springs are intimately associated with the particular soil and underlying strata through which the water has moved. Several of these factors are discussed below.

Many investigators of springs have noted their constancy in flow, temperature, and chemical properties (Meinzer 1927, Berg 1951, Noel 1954, Odum 1957a, Teal 1957, Abbott and Hoese 1960, Minshall 1968, Tilly 1968, Stern and Stern 1969, Wilhm 1970). After understanding the origin of springs, it is not difficult to imagine the reasons for constancy in these factors. Passage of the prcipitation slowly through the soil and underlying strata gives it time to adjust its temperature, even out its flow, and accumulate typical minerals. A thunderstorm will cause surface streams to change rapidly, but the necessary slow flow through the soil dampens the flow and delays its peak. If there is a large underground basin feeding water toward the spring, the effect of the thunderstorm will not even be noticed in the spring flow, temperature, or chemical properties. It is only when the percolating waters flow swiftly through coarse material and when the underground basin is small that the spring is not constant. This is especially true when examining a spring for seasonal changes. A spring will only maintain its constancy through the year and periods of drought if it has some underground storage to draw on and if the water movement through the soil is impeded.

Normally, the temperature of springs is close to the mean annual air temperature for the region (Hynes 1970). As the water flows away from the spring source, it becomes more and more affected by heating and cooling from the air and the temperature fluctuations become wider. The distance downstream of the spring source where the temperature fluctuations become that of a normal stream vary with the size of springbrook, amount of shading, and the climate. For example, in a small Kentucky springbrook, the temperature was relatively constant at the source, 25 meters downstream there was a slightly noticeable annual fluctuation, and at 350 meters a definite seasonal cycle from summer highs to winter lows existed (Minshall 1968).

In contrast the exceptionally large Silver Springs in Florida did not change its temperature at all in over 8000 meters (Odum 1957a). In certain localities, the spring temperature can be much higher than the mean air temperature due to geothermal heating from volcanic activity (Waring 1965).

The chemical conditions of spring waters are also constant and are derived from their underground contact with the soil and rocks. Springs vary in their dissolved oxygen content from near zero to 100% saturation. Those near zero will rapidly take in oxygen downstream by diffusion. Such anoxic springs will lack visible life except for bacteria and blue-green algae (Hynes 1970). The spring may issue with high concentrations of carbon dioxide accumulated from the high content in the soil from decomposing organic matter (Gilluly, Waters, and Woodford 1968). These high concentrations will also rapidly diffuse out. In areas where the spring water has passed through limestone strata, there will be high concentrations of calcium and bicarbonate ions due to the solution of limestone ($CaCO_3$) by water and carbon dioxide. Various other ions such as Na^+, Mg^{++}, Cl^-, and $SO_4^=$ can ocassionally be common in mineral springs. Often these mineral springs are associated with thermal springs because of the greater solubility.

The major diurnal and seasonal variable in springs is the amount of light. The seasonal cycle can be greatly modified by spring side shading from vegetation.

Biological Factors

From a biological viewpoint, springs do not necessarily have to be large to be inhabited by life. The only requirement for life is that they allow the aquatic organism to complete their life cycle.

Because of variations in geologic history, evolution, species interactions, and spring habitat, a variety of aquatic organism will be found in springs throughout the world. Table 2 represents generalizations that have been made about the typical biota of cold and hot springs.

Table 2. Characteristic aquatic biota in cold and hot springs.

COLD SPRING	HOT SPRING (>40° C)
Bacillariophyta (diatoms)	Cyanophyta (blue-green algae)
Turbellaria (planaria)	Nematoda (nematodes)
Amphipoda (sideswimmers)	Ostracoda (ostracods)
Isopoda (aquatic sow bugs)	Hydracarina (water mites)
Plecoptera (stoneflies)	Odonata (dragonflies/damselflies)
Trichoptera (caddisflies)	Hydrophilidae (scavenger beetles)
Dytiscidae (diving beetles)	Dytiscidae (diving beetles)
Tendipedidae (midges)	Tendipedidae (midges)
Simuliidae (black flies)	Stratiomyiidae (soldier flies)
Sphaeriidae (fingernail clams)	Ephydridae (shore flies)
Gastropoda (snails)	Gastropoda (snails)
Oligochaeta (aquatic earthworms)	Oligochaeta (aquatic earthworms)

(Brues 1927, Pennak 1953, Tuxen 1944, Teal 1957, Minckley 1963, Minshall 1968, Tilly 1968, Winterbourn 1968, Hynes 1970)

Because of the constant temperature of springs, certain species have become stenothermal and are restricted to springs (Pennak 1953, Hynes 1970). Other organisms may be in limestone springs because of high hardness. The spring fauna is often considered to have low diversity, but may have large numbers of individuals (Pennak 1953, Teal 1957, Minshall 1968). Often the amphipods, isopods, or midges dominate the numbers in cold springs(Minckley 1963, Minshall 1968). The low diversity in springs suggests that many aquatic organisms need a fluctuating environment to complete their life cycle. Hynes (1970) found that part of the low diversity in springs may be due to recent glaciation.

The constant conditions in springs allow for a continuous production of aquatic organisms; however, many still synchronize their development with seasonal variations in light (Hynes 1970). The main source of energy for the aquatic fauna can vary between local primary production of algae (aufwuchs) and higher plants in the spring (Odum 1957a, Abbott and Hoese 1960, Brock 1967, Stockner 1968, Doemel and Brock 1971) or detritus imported into the spring from terrestrial vegetation (Teal 1957, Elton-1966, Minshall, G.W. 1967,1968 Tilly 1968, Wilhm 1970).

Water cress (*Rorippa nasturtium-aquaticum*) is the typical higher aquatic plant found in cold springs throughout the world. Other common emergent, floating, and submerged higher plants include *Veronica*, *Juncus* (rush), *Scirpus* (bulrush), *Carex* (sedge), *Lemna* (duckweed), *Ranunculus* (water buttercup), and various mosses. Diatoms dominate the algae of cold springs and blue-green algae, especially *Phormidium*, *Schizothrix*, *Synechococcus*, and *Mastiglocladus*, dominate in hot springs (Ruttner 1963, Brock 1967, Stockner 1968,1971, Brock and Brock 1969).

FACTORS OF EVOLUTION IN SPRINGS

The following discussion concentrates on the factors of evolution in springs and shows how they can function as genetic refuges. Most of the examples are drawn from literature on invertebrates and fishes; however, ocassional references are made to amphibians and reptiles. The greatest amount of research on the North American spring biota has occurred in the Great Basin, southwestern states, southeastern states, and northern Mexico. Several important contributions have also been made in Massachusetts (Teal 1957), Iowa (Tilly 1968), Wyoming (Brues 1924,1927), and Washington (Stockner 1968,1971).

Dispersal and Colonization

It is well known that aquatic organisms have varying abilities to disperse (vagility) and colonize new habitats. These abilities are very important for the spring biota because they affect gene flow and determine the species composition in any habitat. Dispersal of aquatic organisms can occur either along water connections, across the land surface, or through the air. The mechanisms can be active of passive and may vary with the life cycle. Dispersal to small isolated springs, especially those widely separated by deserts, is mainly a matter of chance. These small isolated springs are often compared to islands in the ocean where the chance of dispersal is related to the size of the island (spring), the distance from the mainland population, and the vagility of the organism.

Dispersal of the aquatic biota along water connections seems the most obvious because it does not require the organism to exist in the hostile, desiccating, land environment. Many springs form the headwaters of streams or flow into lakes, and a direct route of invasion is available, especially for aquatic organisms that can maneuver against the current. Fish are a good example of aquatic organisms that can actively disperse along water connections; they are only stopped by steep waterfalls or other environmental barriers such as low dissolved oxygen, high temperature, and salinity. Passive dispersal occurs along water connections by drift of organisms with lake or stream currents, especially during periods of flood flow.

Once the aquatic organism leaves the water for dispersal overland or through the air, it must be somehow protected from desiccation. Certain life stages of aquatic organisms are adapted for terrestrial life or are resistant to desiccation. Others may be protected by enclosure in mud, leaves, or within the alimentary tract of the transporting organism.

Many adult forms of aquatic insects actively disperse overland by their powers of flight (Fernando 1958,1959, Macan 1961, Maguire 1963, Stewart and Murphy 1968). Because of their chitinous exoskeleton they are protected from desiccation and can freely fly across land or past water barriers to colonize new springs. Because many aquatic insects are rather weak fliers (mayflies, caddisflies, stoneflies, and some true flies), winds may aid or frustrate their movement, and dispersal to isolated springs may only occur ocassionally and in a random manner.

Except for adult aquatic insects and a few fish (catfish), dispersal overland or through the air is passive. Transport is by birds, insects, or other animals, or by physical forces such as the wind (Gislen 1948, Maguire 1963, Stewart and Schlichting 1966, Revill, Stewart, and Schlichting 1967, Stewart, Milliger, and Solon 1970, Milliger, Stewart, and Silvey 1971, Solon and Stewart 1972, Sides 1973). The transported organism is usually prevented from desiccation by being in a resistant or resting life stage, such as a cyst, spore, resting egg, anabiosis, cocoon, winter egg, gemmule, epsiblastic egg, or statoblast, or by being enclosed in mud, leaves, or alimentary tract. Aquatic species within the taxonomic groups Protozoa, Rotatoria, Tardigrada, Bryozoa, Oligochaeta, Cladocera, and possibly Nematoda and Gastrotricha have a cosmopolitan distribution (Pennak 1953) because they have resistant stages or are easily protected from desiccation during transport. Since these organisms can cross most barriers with relative ease, endemic species do not get a chance to form with the constant interchange of genetic information. Aquatic organisms within the Ostracoda, Amphipoda, Isopoda, Decapoda, Hydrcarina, Gastropoda, and Pelecypoda (Pennak 1953,1959) and the fishes (Hubbs and Miller 1948b, Minckley 1969, Armstrong and Williams 1971, Hubbs, Miller, and Hubbs 1974) are more often endemic in springs because they do not form resistant life stages and are only rarely passively dipersed overland.

The environments of most areas of the world have changed greatly through geologic history. Organisms once perfectly adapted to a particular environment during one geologic period often become extinct or quite rare during a later geologic period and new environment. Scattered within the new environment may be found small pieces of the old environment. The organisms restricted to this old environment are called relict species. Relict species are often found in springs and represent a special case of dispersal and colonization. Their existence in the present habitat can be explained by dispersal and colonization during an earlier and more favorable geologic period. As the environment changed, they became restricted to the only remaining fragments of the old envirenment.

Both cold and hot springs are known to contain relict species. Examples include Apatidea muliebris (caddisfly), Asellus bivittatus (isopod), Capnia bifrons (stonefly), Crenichthys nevadae (spring fish), Crenobia alpina (planaria), Empetrichthys latos (poolfish), Feltria romijni (water mite), Gammarus bousfieldi (amphipod), Melanopsis spp. (snails), Monodella relicta (crustacean), Relictus solitarius (dace), and Terrapene coahuila (turtle). Relict species in cold springs are adapted to lower water temperatures as were once common during the last Ice Age. With the present warmer environmental conditions, cold springs provide the necessary habitat for these glacial relicts. Likewise, relict species adapted to high temperatures are found in thermal springs of presently cold climates. Therefore, springs function as true genetic refuges for relict species by providing them with a similar environment to the past. It is also possible that with future environmental changes, that springs could provide preadapted aquatic organisms for invasion of the new habitat. Springs are able to act as genetic refuges mainly because of their constancy.

Isolation

Genetic isolation and subsequent adaptation to specific environments causes divergence in species populations so that with sufficient time new species are formed. Springs with direct connections to streams and lakes generally do not provide strict enough genetic isolation so that an endemic spring biota can evolve. Even in physically isolated springs, the cosmopolitan fauna described above have no problems of adequate dispersal so that genetic interchange occurs freely and the various populations do not diverge.

Relatively complete isolation exists for certain aquatic organisms with low vagility in the springs lying above the fall line of the Appalachian Mountains. Migration can occur downstream quite readily; however, upstream movement is restricted for many organisms by steep waterfalls. Within these springs are found many endemic forms, especially among the amphipods (Gammarus spp.), isopods (Asellus spp.), and darters (Etheostoma spp.)(Howell and Caldwell 1965; Cole and Minckley 1961, Walker 1961, Ramsey and Suttkus 1965, Bowman 1967, Armstrong and Williams 1971).

Extreme isolation exists for aquatic organisms with low vagility at springs located within dry areas. The springs have no direct connection with other water bodies and thus active dispersal along water routes do not presently exist. Dispersal can only occur actively in adult insects or passively in others. For fishes these springs represent complete isolation. Three areas in North America have numerous springs located within a desert and a highly endemic fauna exists: Great Basin; southwestern United States; and Coahuila, Mexico.

The Great Basin of the United States comprises the deserts of Nevada and parts of Utah, Oregon, and California. Water is not an apparent feature of the present landscape, but evidence shows that during various pluvial periods of the Pleistocene epoch the climate of the Great Basin was much wetter and systems of lakes and streams were prevalent (Hubbs, Miller, and Hubbs 1974). During this wetter time it was possible for the aquatic fauna to actively disperse throughout the interconnected drainage systems. The last pluvial period is believed to have ended from 10,000 to 30,000 years ago and since then there has been extensive drying in the area. Once interconnected drainage systems became disconnected and lakes and streams dried up, extinguishing their aquatic biota. In certain locations, small springs were the only permanent aquatic habitats which continued until present. It is within these small springs that remnants and descendants of the pluvial fauna have persisted until present. The springs acted as a genetic refuge and as a new environment to which subsequent adaptation occured.

The fish fauna of the Great Basin has been studied in much greater detail and correlated with the geologic history more than the invertebrate fauna(Hubbs 1940b; Miller 1946,1948,1950, Hubbs and Miller 1948b; Hubbs, Miller, and Hubbs 1974). Fish genera such as *Crenichthys*, *Cyprinodon*, *Empetrichthys*, *Eremichthys*, *Gila*, *Moapa*, *Relitus*, and *Rhinichthys* have unique species, subspecies, and races within the various isolated springs. For example, there are five species of pupfish within the Death Valley system (*Cyprinodon diabolis*, *C. milleri*, *C. nevadensis*, *C. radiosus*, and *C. salinus*). Their habitats are dependent upon closely associated but physically isolated small springs. Speciation between *C. milleri* and *C. salinus* is estimated to have occurred in 2000 years (LaBounty and Deacon 1972). Rapid divergence has also occurred in *C. nevadensis* since six subspecies and many races have been described (Miller 1948). Turner (1974) studied the biochemistry of these five pupfish species and found that they were very similar, indicating little genetic divergence for these traits. However, the morphological distinctness of the species led him to suggest that different parts of the genome evolve at different rates; morphological traits evolve faster than biochemical traits.

The few studies of aquatic fauna other than fish also indicate a high degree of endemism in the Great Basin. The black toad, <u>Bufo exsul</u>, exists around springs in the California desert (Myers 1942). The snail fauna has several endemic forms restricted to springs. <u>Stagnicola pilsbryii</u> has been found only from a spring in western Utah (Russell 1971, Taylor, Walter, and Burch 1963) and unique species of the Hydrobiidae, <u>Fontelicella</u>, have been found in springs of southern Nevada (Gregg and Taylor 1965). There are certainly many evolutionary studies possible for the invertebrates and vertebrates of the Great Basin springs.

The southwestern states of Texas, New Mexico, and Arizona have numerous springs isolated by intervening dry areas. Many of these are mineral springs and some have large flows from limestone strata (Noel 1954, Stevenson and Peden 1973, Stevenson and Buchanan 1973). The fish fauna of the Southwest is better known than the invertebrate fauna. The pupfishes <u>Cyprinodon bovinus</u>, <u>C</u>. <u>elegans</u>, <u>C. macularius</u>, <u>C. tularosa</u>, and several undescribed species are common or endemic in springs (Minckley 1973, Stevenson and Buchanan 1973, Echelle and Miller 1974, Miller and Echelle 1975). Likewise, there is a high degree of endemism in the livebearing fish, <u>Gambusia</u> spp. (Hubbs 1971, Peden 1973). Several endemic spring amphipods have been reported (Cole and Bousfield 1970, Stevenson and Peden 1973).

Cuatro Cienegas, Coahuila, Mexico, is another area that contains a highly endemic aquatic fauna dependent upon spring flow (Minckley 1969).

The present aquatic habitats consist of springs or channels and marshes dependent upon spring flow. The whole area has been isolated from surrounding areas for a considerable geologic time and individual springs and their outflows are separated from others. These springs also occur in a desert area. The investigation of the biota of Cuatro Cienegas has been much broader than for other areas and is continuing at present. Reptiles, amphibians, fishes, and invertebrates have received some study (Minckley 1969). One of the most interesting endemic species is an aquatic boxturtle, Terrapene coahuila (Webb, Minckley, and Craddock 1963, Brown 1971). Members of this genus in other areas are all terrestrial. Several new isopods have been described from the aquatic habitat (Minckley and Cole 1968b, Cole and Minckley 1970). The mollusc fauna is considered to be one of the most endemic in the Western Hemisphere (Taylor 1966). Many new genera within the Hydrobiidae have been described from this area. The fish fauna is also highly endemic with new species described in Cyprinodon (Miller 1964,1968), Gambusia (Minckley 1962), Lucania (Hubbs and Miller 1965), and Xiphophorus (Miller and Minckley 1963). Milstead (1960) lists 14 relict reptiles and amphibians.

Human activity can also have an effect on the isolation and preservation of the aquatic fauna. Dr. Robert J, Behnke of Colorado State University recently travelled to Iran to study the fish fauna. In the dry central basin, he found no permanent water for fish life except where quanats had been dug. A quanat is an underground tunnel which extends into a ground water aquifer, tapping and transporting the water toward a city. The quanat has a certain slope so that it eventually brings the water to the ground surface, just like a spring. Fish would hide in the quanat during the day, but come out at night to feed. This is a special case where a "spring" acted as a genetic refuge.

Characteristics of Spring Fishes

Although there is considerable variation, spring fishes tend to exhibit certain common morphological characteristics. Extreme isolation in small springs with low current and little or no competition or predation appears to have caused a convergence on several similar characteristics (Hubbs 1940b, Hubbs and Miller 1948b, Howell and Caldwell 1965, Hubbs, Miller, and Hubbs 1974).

The desert spring fishes are generally small and sluggish, dull colored, and with a chubby body form. They are adapted for a mid-level depth in quiet water, having a deep caudal peduncle and an enlarged, terminal, and oblique mouth. Their fins are small, short, rounded, and supported by fewer and weaker rays. The anterior body parts are enlarged and the dorsal and anal fins are positioned more to the posterior. The scales are loosely arranged and the sensory canals, barbels, and other dermal senses are reduced. It is interesting that many of these characteristic have been noted for the darters in the isolated Alabama springs (Howell and Caldwell 1965).

Various investigators have attempted to correlate certain morphological characters to temperature and salinity. Miller (1948, 1950) found that fish in warm springs tend to have fewer meristic segments, posteriorally placed dorsal fin, enlarged head and eyes, reduced size, and reduced pelvic fins. Fish at high salinities tend to have increased meristic segments. Bisson and Bond (1971) found an isolated population of Rhinichthys osculus in an Oregon warm spring (24°-27°C) differing from adjacent populations by lacking maxillary barbels. Chervinski (1968) noted the effect of high temperature and salinity on spring populations of cichlids. Hubbs (1959) found an high incidence of vertebral deformities in Gambusia populations from warm springs. Hubbs (1940b) and Miller (1950) speculated that speciation was faster in warm spring fish. A constant, warm temperature provides conditions for year around breeding and rapid growth to maturity so that the number of generations per year is larger. Increased temperature and salinity will increase the mutation rate, which along with genetic drift will cause some variation in characters.

Genetic Drift

Genetic drift is that phenomenon whereby certain alleles are fixed or lost randomly in a small population. Alleles are fixed or lost in the population by a random process rather than by selection, and the genotype trends toward a homozygous condition and loss of hybrid vigor. Populations of 10,000 are not affected by genetic drift, but populations less than 100 are highly susceptible to random fluctuations (Dobzhansky 1970). Genetic drift can be important in changing gene frequencies for small populations especially when the selective advantage of different alleles for a trait is about the same. It requires a high selective advantage to overcome drift in small populations.

Small isolated springs often have small species populations. The numbers often fluctuate seasonally with the quantity of incident radiation and food availability. The Devil's Hole pupfish, Cyprinodon diabolis, is an example of a small, fluctuating population. Its total habitat amounts to 45 m^2 and population size varies from 50-100 to 700-800 as algal density changes with the season (Minckley and Deacon 1973). Population sizes small enough for genetic drift to be an important evolutionary factor undoubtably occurs in many other fishes and invertebrates of springs.

Associated with the idea of genetic drift is the genetic consequence of founding a spring population from a small sample of the total species population. The small founding population will have less genetic variation than the species population and there is less for evolution to work with. The chance for extinction is much higher for the founding group than for the total species population. Close inbreeding and loss of vigor occurs in the small group (Dobzhansky 1970). Many spring populations have undoubtably been founded by long distance, rare dispersal of a few individuals. Likewise, during the shrinkage of aquatic habitats since the last pluvial period in the Great Basin, populations founded in the small springs each represented a small portion of the total genetic variation. Therefore, the evolution of a spring fauna might be expected to show some aberrant forms.

While it is difficult to separate the effects of genetic drift from selection and other evolutionary factors, there exist in the spring fauna literature many references to dwarfism, melanism, and loss of pelvic fins. Small body size probably is selected for because of the small habitat, but it may also be the result of a homozygous condition determined by genetic drift. The Devil's Hole pupfish is very small (15-20 mm), dark, and lacks pelvic fins (Wales 1930, Minckley and Deacon 1973). Dwarfism has been noted for the darter _Etheostoma ditrema_ from Alabama and Georgia springs (Ramsey and Suttkus 1965); the spring darter _E. nuchale_ in Alabama (Howell and Caldwell 1965); various spring subspecies of the dace _Rhinichthys osculus_ in Oregon, Nevada, and Wyoming (Bisson and Bond 1971, Hubbs, Miller, and Hubbs 1974, Hubbs and Kuhne 1937); the spring cyprinodont _Lucania interioris_ from Mexico (Hubbs and Miller 1965); the dragonfly _Lestes uncatus_ from a USSR spring (Belyshev 1957); and the hydrobiid snails from springs of the western United States and Turkey (Gregg and Taylor 1965, Schuett and Bilgin 1970).

Species Interactions in Springs

Isolation of fauna in springs alters normal biotic interactions. Since springs tend to have lower species diversity, the interactions become simpler. Food webs have decreasing complexity and may approximate food chains. Dependence on single food items increase.. The predominant food of the desert spring cyprinodont fishes is algae, indicating a shortening of the food chain so that more energy is available. The desert spring fishes have also been isolated without competition or predation pressures and show a degeneration in sensory structures. When these fish are exposed to game fish or other exotics introduced into their habitat by human action, they show an inability to compete or to protect themselves (Miller 1961, Minckley and Deacon 1968, Pister 1974). Desert spring fishes of the Great Basin have sometimes been forced into unusual interactions. The dessication of their pluvial habitats caused fishes adapted for stream life and those adapted for lake life to be brought together in small springs. Normally the two types would not be associated, but they both occur in springs and may hybridize very extensively (Hubbs 1940b).

Competitive exclusion would seem to be a possible interaction within springs, but it is difficult to demonstrate. If a species becomes isolated in a spring and evolves so that it is superbly adapted to its environment, it is likely to exclude a closely related form from colonizing in the same spring. Since the trophic relations are simplified, the highly adapted form is likely to be exploiting most of the resources, leaving little for an invading species.

The simple trophic relations and dependence on few food items in springs creates the possibility for two species at different trophic levels to coevolve. While coevolution is also difficult to prove, it has been suggested as occurring within at least one spring. Clear Spring, Texas, has an endemic predator species, _Gambusia_ _heterochir_, which preys on an endemic amphipod, _Hyalella_ _texana_. Recent introduction of _Gambusia_ _affinis_ as a competitor did not alter the predator-prey relationship. _G.heterochir_ continued to feed on Hyalella texana while Gambusia affinis fed on insects (Hubbs 1971, Stevenson and Peden 1973).

In closing, it should be noted that the spring fauna may be related to the interstitial fauna and the cave (troglobitic) fauna. Both of these special faunas need oxygenated ground water and other special requirements to exist. They have become specially adapted in body form and behavior to live in these unusual conditions. Since they may be located physically adjacent to springs, members of these faunas may be found in springs. However, not all springs are closely associated with these faunas (Hynes 1970).

SUMMARY

Springs are widely distributed and are small, unique aquatic habitats having constant environmental conditions controlled by regional geology and climate. The characteristic stenothermal spring biota has low diversity, but high individual numbers. Dispersal and gene flow occurs freely for organisms with resistant life stages, giving a cosmopolitan fauna. Other organisms can be strictly isolated to springs because of low vagility and lack of aquatic interconnections. Desert springs represent extreme isolation, especially for fishes, and act as genetic refuges. Adaptation to small springs creates similar characters in fishes. Genetic drift, while difficult to clearly prove, seems likely to operate in many small isolated spring populations. Dwarfism occurs in many spring species. Species interactions are altered in springs due to the low diversity and simpler trophic relations. Competitive exclusion and coevolution may occur in springs.

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"There is little water in the Ceriso at the best of times, and that little brackish and smelling vildy, but by a lone juniper where the rim of the Ceriso breaks away to the lower country, there is a perpetual rill of fresh sweet drink in the midst of lush grass and watercress."

Mary Austin, 1903

<u>The land of little rain</u>.

Various Methods for Controlling the Spawning Times of Fishes

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Various Methods for Controlling the Spawning Times of Fishes

Roger Rouch

Introduction

Control of the spawning times of fishes can be an important tool for the fish culturist. The fish farmer wants to be able to supply the correct number and size of fish at the time his consumer is in need of them. However, the natural spawning time of the fish may not coincide with the demands or quantity and quality of the fry. For example, if rainbow trout which normally spawn in the spring were to spawn in November, the fall progeny would have a 4 month longer growing period than spring progeny, making it possible to stock a much larger fish for a summer stocking program. Bait minnow orders may peak at a time when the bait farmer's supply is low. If he could control the spawning time of his minnows, supply and demand might coincide more closely. Other conditions, such as the availability of labor, weather conditions, and hatchery carrying capacity might be improved by advancing or delaying the natural spawning time of the fish.

Investigations show that spawning action is controlled by a releasing mechanism in the central nervous system. This mechanism starts the spawning action when the fish receives certain stimuli through vision, scent, sound, or physical contact (Fabricius, 1950). A certain series of stimuli is required by each variety of fish to release the action. Should this series of stimuli be delayed, the thresholds of the stimuli required may be lowered by hormones being secreted by the sexual organs as an internal stimulus, or spawning may occur with no observable stimulus if the action is delayed long enough. The external and internal requirements for spawning suggest that there are two routes of action which may change the spawning time. The external stimuli may be artificially altered to induce spawning at an earlier date, or the fish may be deprived of the required series of stimuli until a more desirable spawning time. Another method of changing the spawning time would be to introduce chemicals causing the sexual organs to secrete hormones, thus lowering the threshold of external stimuli required.

Methods for Altering Spawning Times

In some fishes certain components of the activating series of stimuli are sufficiently dominant to change spawning times by advancing or delaying only one or two of them. Experiments with brook trout (Corson, 1955; Allison, 1951), blueback salmon, and other fish species indicate that the dominant stimulus among salmoniods is exposure to light. Studies conducted by B. W. Corson on controlling the spawning time of the fall-spawning brook trout show that by assimilating the lengthening summer days and then the shortening fall days earlier than they occur, November-spawning brook trout can be induced to spawn as early as August. And by maintaining the length of the summer day artificially when the shorter days of fall begin, spawning can be delayed by about six weeks. By delaying the spawning season, the fighting and injury caused by the spawning urge is prevented. Generally, salmoniod fishes constantly exposed to 8 hours of daylight spawn 1 or 1½ months early, fish with 0 hours of daylight spawn 2 weeks to 1 month early, and fish with 16 to 24 hours of light spawn up to 3 months later than normal. Using a brood stock which had advanced or delayed spawning due to the use of artificial light conditions the previous year will result in high losses due to egg deformities if used again the following year with a similar spawn controlling technique. When working with largemouth bass it is necessary to combine abnormal light conditions with a depressed water temperature until spawning is desired, and then gradually increase the water temperature to a normal spawning temperature of 20°C (Carlson, 1973). Using this method, largemouth bass have been induced to spawn during the months of December, January, February, May, June, and July. Artificial lights can be added to raceways at a small cost by using 200 watt lights suspended about 2 meters above the raceway. However, reducing normal daylight can be expensive if the raceways are not already in an enclosed facility.

One of the dominant stimuli to the release mechanism for many warmwater fishes is the temperature of the water. Many warmwater fishes have a certain minimum temperature which must exist for a period of time before they will spawn. By adding cold water to the water supply, spawning can be delayed for a short period of time. By keeping the water temperature between 16° and 18°C, the spawning of catfish can be delayed 20 to 30 days (Meyer, et al., 1973). At the desired time of spawning, the water temperature is allowed to rise above the threshold spawning temperature, and the spawning action ensues. The minimum spawning temperatures of certain fishes are shown in Table 1. The water can be warmed above this minimum before it would normally rise above that temperature by taking advantage of the warmer water of small shallow brood ponds, a practice common among catfish farmers.

By altering other water conditions, spawning time of some warmwater species can be changed (Meyer, 1973). The spawning of golden shiners can be delayed by heavily crowding brood fish in a clean pond. Spawning begins soon after the fish are stocked in a freshly filled pond at a reduced density. Goldfish can be induced to spawn by lowering the water level and quickly restoring it by adding fresh water.

The temperature shock of a low water level being rapidly raised by adding fresh cold water may be necessary to induce goldfish to spawn. Some methods of catfish culture allow the sexes to be separated to delay spawning.

Sexual maturation may also be advanced by injecting fish with pituitary material (Ball, 1954), providing an internal stimulus for the release mechanism. Pituitaries of dead fish are removed and injected into the body cavity of the fish. Spawning usually occurs within a couple days after the last injection. Pituitaries from different species have varied potentcies and effects upon other species (Table 2). There are several chemical treatments used to prepare the pituitary glands for injection, but fresh or frozen glands can be used where precisely measured injections can be sacrificed for cost and time advantages. As little as ¼ of a carp pituitary can stimulate spawning in minnows. Generally, 4 to 8 milligrams of carp pituitary per kilogram of fish is used. Only the female needs be injected, and injections are made at 3 to 48 hour intervals. A series of 3 injections is common, with spawning beginning shortly after the last injection. Methods and results are well enough established to warrant the injection of carp pituitary in catfish, minnows, carp, buffalofish, and others in commercial operations. Research on trout (Hassler, et al., 1939) and salmon (Burrows, 1952) has been less productive. While some positive results have been obtained with these species, further experimenting will be necessary before this method of advancing spawning times can benefit the producer of commercial fish. Obtaining and injecting the pituitary can be an expensive operation, but it may eliminate or aid hand stripping of some pond cultured species. Similar results can be obtained by using human chronic gonadotropin (Sneed and Clements, 1957) which can be easily obtained from drug companies. Injected channel catfish have spawned in aqaria as small as 24 liter capacity (Riggs and Sneed, 1959).

Selective breeding is another tool which the fish culturist may use to alter the normal spawning time. Fish are selected on the basis of size, disease resistance, and other advantageous qualities. The high quality fish are spawned. After reaching sexual maturity, the offspring of these fish will spawn within an interval of around 3 months, with some spawning earlier, and some spawning later than normal. By selectively breeding early or late spawners, whichever is desired, a new spawning time can be established after several generations (Leitritz, 1959). Selective breeding of rainbow trout has developed strains spawning in nearly all months of the year.

Discussion

It is logical to suppose that the use of controlled photoperiods, controlled water conditions, hormone injections, genetic selection, or combinations of these can bring about year-around production of any species. Hatchery and rearing functions might be further segregated due to the potential year-around use of each. Productivity of hatchery assets could be greatly increased. As more knowledge is gained about varying spawning times, hatcheries may wish to propagate one species during one season and a different species during the alternate season, or they may wish to specialize in the year-around production of a single species. The possibilities of altering spawning times hold a great potential for the fish culturist and offer a challenge to the research scientist.

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Table 1.--Mimimum spawning temperatures of certain fish

Species	Temperature (°C)
Black Bass	18
White Bass	13
Catfish	21
Goldfish	16
Golden Shiner	21
Fathead Minnow	18

Table 2.--Effectiveness of injections of fish pituitary into several species of fish

Test Species	Source of Pituitary	Test Results
Common sucker	Carp	Positive
Common sucker	Sucker	Negative
Black bass	Carp	Negative
Black bass	Black bass	Slightly positive
Chub sucker	Carp	Slightly positive
Chub sucker	Chub sucker	Negative
Chub sucker	Common sucker	Negative
Bluegill	Bluegill	Positive
Bluegill	Carp	Negative
Bluegill	Redear sunfish	Negative
Grey mullet	Salmon	Positive
Blueback salmon	Salmon	Negative
Buffalofish	Carp	Positive

Behnke

COMPREHENSIVE EXAM

for

Dr. Gary White

By
Charles Gowan
April 2, 1993

Question 1. Significant Digits.

Introduction

My answer is divided into three sections. In the first, I present a summary of the "classical" view of significant digits, how they are interpreted, and the accepted rules for reporting them. Included is an evaluation of how the rules would be applied to the situation presented in the question. In the second section, I outline an analytical approach to the question. Finally, the last section discusses a simple simulation model I developed to explore the question empirically.

The Classical View

When considering discrete variables, such as the number of offspring produced by an individual, significant digits are of little concern. A bird fledges some whole number of young, and reporting that result as 4 is no less accurate than a report of 4.0000000. In fact, the latter result would seem absurd. If the average number of young fledged is calculated from a census, the number of significant digits reported is dependent upon the judgment of the investigator. Some may feel that the average rounded to the nearest whole number is most appropriate, but others would include one or more significant digits to the right of the decimal place. Neither is an error because, even thought the average is a continuous number, the fact that it was calculated from two discrete integer values makes it an exact number (give or take some rounding). Therefore, one answer to the question posed in the exam is that many significant digits could be reported if, for some reason, the distance measurements were being made on items which came only in very distinct length categories.

Continuous variables are more troublesome. Significant digits for reporting numerical results from measurements on continuous variables are used to convey an implied limit to precision, that limit being defined by the accuracy with which the original measurements were made. For example, if the weight of a fledgling bird was measured with a digital scale reading to 0.1 g, a report of 8.3 g would imply that the true weight was somewhere between 8.25 and 8.35 g. Thus, the implied limits always carry one more figure beyond the last significant one measured (Sokol and Rohlf, *Biometry, 2nd Edition*). This may be the basis for the editorial rule that the mean of a set of data can be reported to one significant digit over the original data. However, as will be discussed in a moment, this rule does not match the accepted standards for such disciplines as chemistry.

It is clear that precision is a relative term. One reason is that no measurement of a continuous variable can be exactly precise, and so precision is based on the resolution of the measuring device, not any absolute criterion. A second reason is that not all authors agree on what the implied limits are when a given number of significant digits is reported. The "rule" presented in the previous paragraph that the implied limit is +/- 5 units in the digit to the right of the last significant digit comes from Sokol and Rohlf, and Zar

(*Biostatistical Analysis, 2nd Edition*). However, Masterton and Slowinski (*Chemical Principles, 4th Edition*) state that the implied precision is +/- 1 unit in the last significant digit. For the bird-weight example, this would mean the report of 8.3 g implies a limit of 8.2 to 8.4. Much to my dismay, I have not been able to locate any text which provides a mathematically rigorous analysis of significant digits. It appears that the limits of precision implied by a given number of significant digits does not have a clearcut definition across all disciplines.

Although the interpretation of significant digits varies, there is better agreement on how the number of significant digits is determined in the mathematical manipulation of measured values. For addition and subtraction involving measured values with different numbers of significant digits, the rule is that the result is rounded such that it contains the same absolute uncertainty as the least precise measurement. For example, 273 + 0.62 = 273.62, rounded to 274 as a final answer (the rules for rounding will not be discussed here). For multiplication and division, the number of significant digits in the least precise estimate is retained in the answer. For example, 23.3 x .1257 = 2.91624 rounded to 2.92 (three significant digits in 23.3 and in 2.92). As with the limits of precision, I could not find any rigorous mathematical treatment of these rules. They appear to be based on the "weakest link" concept. Moreover, these rules also do not match the "journal editors'" rule that averages can be reported to 1 significant digit beyond the precision of the measurements. Thus, all rules appear to be *ad hoc,* but intuitively satisfactory.

With regard to the example given in the exam question, we must first address how many significant digits are implied when measurements are taken to the nearest 10 meters (10, 20, 30 etc.). I believe the correct answer is one. Although a measurement of 20 m implies two significant digits, the fact the measurement could only be made to the nearest 10 m indicates the true limits of precision are 15 to 25 m. According to Sokol and Rohlf's interpretation (discussed above), this level of precision equates to 1 significant digit. Another way to see this is to write the value in scientific notation (i.e. 20 = 2 x 10^1). The exponential portion of the notation is simply a decimal place-holder; all the information from the measurement is contained in the "2".

Using the strict rules provided two paragraphs ago, the average of measurements made to the nearest 10 m should properly contain only 1 significant digit. For example, if the sample was 10, 10, 20, 30, 40, the sum would be 9 x 10^1 (one significant digit) and the mean would be 2.25 x 10^1 rounded to 2 x 10^1 or 20. If the "journal" rules were applied, two significant digits could be reported and the answer would be 2.3 x 10^1 or 23. Under no rules that I have found, would an answer of 22.5 (or 22.50, etc.) be considered appropriate.

A Mathematical Analysis

I mentioned earlier that I could find not a mathematical treatment of the issue of significant digits. This was disturbing to me because I am not a theoretical mathematician.

Therefore, to try to get somewhere with this question, I went back to first-principles. To evaluate the "correctness" of reporting apparently precise mean estimates based on imprecise field measurements, I decided to examine the magnitude of the bias in the mean estimate compared to the true parameter value. I reason that if the expected bias of an estimator using imprecise field data is negligible, it may be appropriate to report the estimate to a higher number of significant digits than is contained in the field data. I also examined the variance of the mean estimate from imprecise data compared to the variance of the mean based on exact measurements.

To complete the analysis, I assume each measurement (x) is an independent random sample from a continuous probability density function. I will refer to x as a measured length for convenience. When samples are collected within k discrete length classes, the effect is to reduce the continuous density function to a k-celled multinomial with parameters n (sample size) and p_i (each p_i is equal to the continuous density function integrated over the range between the lower and upper bounds of a each length category). However, depending on the shape of underlying distribution, the mean of the discretized measurements could be biased. If so, the magnitude of the bias will depend on the size of the length interval (the bin size) relative to the total range of the x variable. It is intuitively obvious that as the number of categories approaches infinity, the difference between measuring lengths exactly and measuring them within categories vanishes. In discussing these topics, I will assume the bin sizes are equal for each of the k length classes.

Assume that the value assigned to each measurement is the middle of each length category (i.e. a measurement of 10 indicates the true measurement is between 5 and 15 units). Assume also that there is no measurement error such that each measurement is accurately recorded in the correct length category. I will discuss three probability density functions to evaluate the effect the shape of the continuous function, and the bin size selected, has on the expected mean value of the categorical observations.

The uniform distribution is the easiest to deal with. If exact measurements were taken of n independent random samples from a uniform distribution, the expected value of the sum would equal the sum of the individual expected values:

$$E[x1+x2+...xn] = E[x1]+E[x2]+...E[xn] \qquad \text{eq. 1}$$

If that same set of samples was measured using categorical methods, each recorded length measurement would have some error associated with it (the difference between the center-point of the bin and the actual length of the sample). Once each random sample is collected, the error is a constant, c. Therefore,

$$E[x1+c1+x2+c2......xn+cn] = (c1+c2+...cn)+E[x1]+E[x2]+....E[xn]. \qquad \text{eq. 2}$$

However, in a uniform distribution, sum of the c_i terms within each bin should equal zero since, if n is large, it is just as likely for the true length of a random sample to be larger than the mid-point of the bin as it is to be smaller. Thus, the c_i terms cancel out for large sample sizes. Therefore Eq. 2 reduces to Eq. 1. The consequence is that the sample mean of the two sampling procedures (continuous and categorical) have the same expected value. This result holds for any bin-size.

The sampling variance of the sum of the exactly-measured values equals the sum of the individual variances:

$$Var(x1+x2+x3....xn) = Var(x1) + Var(x2)+Var(x3)+......Var(xn). \qquad \text{eq. 3}$$

The standard error of the exactly-measured sample mean equals Var(xi)/n^.5

The categorically-measured variables would have a constant included, but this does not influence the variance of the sum:

$$Var[x1+c1+x2+c2......xn+cn] = Var[x1]+Var[x2]+....Var[xn]. \qquad \text{eq. 4}$$

Therefore, The standard error of the categorically-measured sample mean also equals Var(xi)/n^.5.

Thus, for the uniform distribution with equal bin-sizes (and the categorical measurements taken at the center of each bin), the sample mean and its standard error have the same expected values whether the data are collected with exact measurements or categorical ones. If the sample size is large, it may be proper to report more significant digits in the mean than were found in the sample data.

To consider the normal distribution, eqs. 1 and 2 can again be invoked. However, within each bin, it is no longer correct that a the true length of a random sample is as likely to be larger than the mid-point of the bin as smaller. If the mid-point of a particular bin is less than the mean of the normal distribution, the number of samples that are larger than the midpoint will tend to be greater than the number of samples that are smaller (Figure 1). There will be a systematic bias in the measurement errors within each bin. However, given that the distribution is symmetrical, the positive bias for bins less than the distribution's mean will be canceled by the negative bias for bins greater than the mean. Therefore, the expected mean of the categorical sample should again equal the mean of the exact measurements. The variance terms remain equal because the constant terms do not influence the variance. Similarly to the uniform, it may be appropriate to report more significant digits in the mean of the discretized samples than were in the samples themselves.

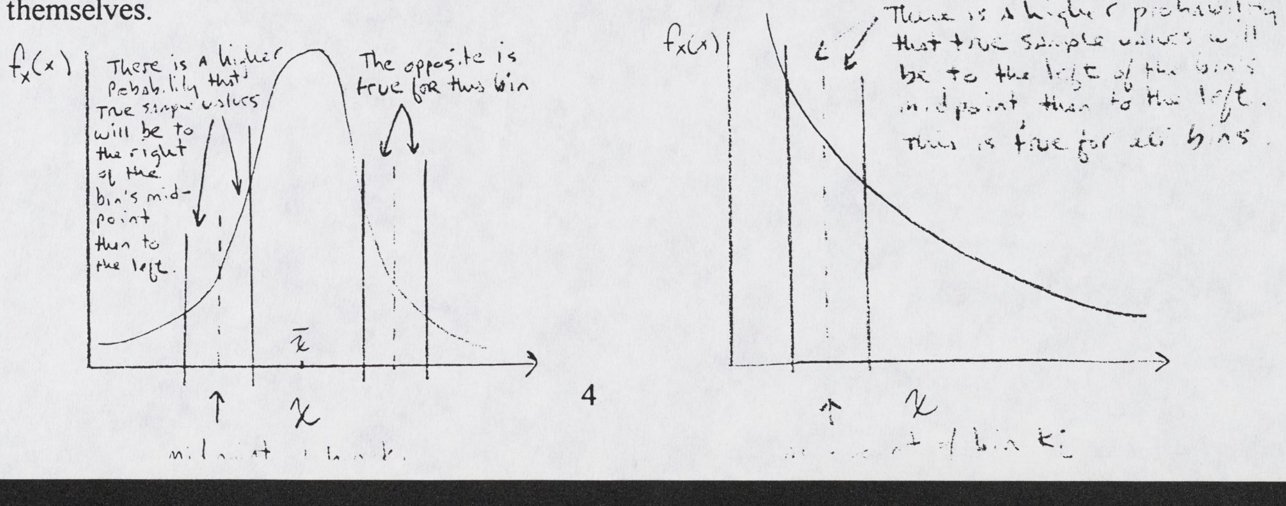

Figure 1

Lastly, I will consider a non-symmetrical distribution, the exponential. Again, eqs. 1 and 2 are correct. As with the normal, the errors within each bin will not tend to cancel one another out. There will tend to be more samples with true lengths which are less than the bin's midpoint, than there are samples which are larger (Figure 1). Unlike the normal, this will be true for all bins and so the bias will be systematic. The average value of c for each bin will be positive and the sum of the categorical samples will tend to overestimate the true sum of the exact samples. Therefore, the mean of the distribution will be over-estimated using the categorical data. Again, the variance will not be effected. Under these circumstances, including more significant digits in the mean than there were in the samples would be fully misleading because the sample mean is known to be biased. Highly precise, biased data are the worst of all worlds.

A Simulation Approach

To confirm the general conclusions just presented, I programmed a simple BASIC model which produces random variables from the uniform distribution (to 8 significant digits). For the simulation results presented here I selected the interval [0, 100] (with mean 50). A given number of random numbers was generated and the true mean and standard error of the mean were calculated. From this, 95% confidence limits were constructed (using z values) and a test made for coverage of the true parameter value (50). Similarly, each random number was assigned to a bin (i.e. the continuous uniform distribution was discretized). The number of bins (and thus bin size) could be specified by the user. In addition, the user could specify whether the categorical measurement for each random sample would be "recorded" as the center-point or the upper or lower bound of the bin. I used this convention to evaluate the effect on coverage of systematic within-bin bias in the error terms. It was faster to use this method to simulate the effect of the error-term bias than to write separate code for the exponential distribution. Controlling how the categorical measurements were recorded was analogous to having measurements correspond to the center-point of each bin in an asymmetrical density function. As with the exact random numbers, the categorical data were averaged, a standard error and 95% confidence interval calculated, and a test for coverage made.

To evaluate the effect of sample size, the above calculations were performed for sample sizes of 10, 100, and 1,000 random numbers. For all sample sizes, coverage was estimated using 1,000 iterations. A different random number seed was used for each iteration. I will report the results of only one run for each sample size (with 1,000 iterations), but I did run several sample sizes more than once to confirm that the results I report are representative. There was not time for additional analysis.

Coverage calculated using the actual (8-bit) values of the random numbers was approximately the anticipated 95% for sample sizes of 100 and 1,000 (Table 1).

However, coverage dropped below 95% when sample sizes were reduced to 10. Coverage calculated using the discretized sampling method with the center of the bin as the discretized value was very similar to the undiscretized results for all sample sizes. The average width of the 95% confidence intervals was also very similar for the two methods. Both results agree with the analytical predictions. Also as expected, coverage was significantly reduced if either the high or low boundary of the bin was used as the discretized value. The magnitude of the error increased as the number of bins decreased. This indicates that systematic bias introduced by discretizing a non-symmetrical density function will reduce coverage. However, the width of the 95% confidence intervals remain approximately equal to the undiscretized results. When applied to a non-symmetrical density function, the discretization approach is likely to introduce significant bias in the estimate of the mean, although this will not be detectable in the form of increased variance. I did one additional run using 100 bins (1% of the range of the distribution), a sample size of 100 and with the discretized value set equal to the lower bound of the bin. The resulting coverage (93.5%) was very similar to that obtained from undiscretized data (93.7%), indicating that if the bin size is small enough (about 1%), the discretization method is essentially as accurate as the undiscretized method.

Summary and Recommendations

Sokol and Rohlf recommend that when discretizing a continuous function for sampling, the level of measurement resolution should permit the construction of between 30 and 300 bins. Based on the simulation results, this seems a reasonable rule, although a smaller number of bins could be adequate if the underlying distribution is nearly uniform.

The analysis presented above indicates that, with large sample sizes, discretization of a continuous function can provide a reasonable approximation for estimating means. However, I believe it would be still be misleading to report a mean value having three digits to the right of the decimal when the sample was only accurate to the nearest 10 whole units. The intuitive rules established for reporting results in journals appear reasonable to me, and I have no recommendations for a simpler or more accurate rule.

Table 1. Simulation results based on 1,000 iterations per sample size.

		Sample Size					
		10	10	100	100	1000	1000
Number of Bins and Location of Discretized Value		Continuous Data	Discretized Data	Continuous Data	Discretized Data	Continuous Data	Discretized Data
10 Midpoint	Coverage	.922	.924	.951	.949	.949	.962
	Mean Interval Width	35.28	35.09	11.30	11.24	3.58	3.56
5 Midpoint	Coverage	.927	.940	.950	.951	.937	.938
	Mean Interval Width	35.16	34.47	11.33	11.10	3.57	3.50
10, Lower Boundary *	Coverage	.915	.887	.941	.587	.947	.001
	Mean Interval Width	35.45	35.26	11.30	11.25	3.58	3.59
5, Lower Boundary *	Coverage	.924	.776	.956	.041	.949	.000
	Mean Interval Width	35.20	34.52	11.29	11.05	3.58	3.51
100, Lower Boundary *	Coverage			.937	.935		
	Mean Interval Width			11.31	11.31		

* Similar results are obtained using the upper boundary.

Question 2. The population rate of increase.

Introduction

Before addressing the three parts of the question directly, I would like to provide an explicit definition of λ. The definitions pertain not to the basic equation, N_{t+1}/N_t, but to the conditions under which the calculations are made. The definitions follow the recommendations by Graeme Caughley in several of his publications (ex: JWM 35(4):658-663. 1971). The most basic form of λ is provided when the values of N are calculated without regard to the total population density or age-structure. Thus, any time estimates of N at two or more different periods are available, this most basic form of λ is the result. Some caution is warranted in that, for birth-pulse populations such as most game animals, the estimates should be made at approximately the same time each year. The most direct calculation method of an average rate over several years is obtained by regressing ln(N) versus time. The slope is the value r and λ equals e^r.

The second form of λ is similar to the first, but is corrected to reflect the theoretical rate under a stable age distribution. As such, age-specific rates of survival (l_x) and fecundity (m_x) must be available (this will be discussed later in this answer). A life table is constructed, the l_x and m_x schedules are assumed to be fixed, and r (and thus λ) is calculated by iteratively solving the equation:

$$\Sigma l_x e^{-r} m_x = 1 \qquad \text{eq. 1}$$

The final form of λ is similar to the second, but the l_x and m_x schedules must be developed under conditions of very low density. The r value calculated from these data is the "intrinsic" rate of increase for the population in the given environment under conditions of no resource limitation. The λ calculated from r has the same implications.

For much of my response to this question, I will be concerned with the most basic form of λ, that calculated directly from N_{t+1}/N_t (or by regressing ln(N) on time to determine r). The symbols λ_s and λ_i will denote the stable age distribution and intrinsic values, respectively.

Question 2a: Estimating λ when actual N is unknown.

It would be an unusual situation if the sizes of wild populations were known precisely. Therefore, λ is generally always based on estimated population sizes, rather than census information. The major criterion for obtaining accurate estimates of λ would be that reliable estimates of N_{t+1} and N_t are available. However, because λ is the ratio of the two population estimates, systematic bias in the estimates would not produce bias in λ. This is similar to the rational of using the Jolly-Seber model to calculate survival rate even though population size estimates may be biased. This criterion should not be too difficult to achieve if mark-recapture estimates are made each year using the same techniques, marking methods, etc. Poor estimates of λ could result if population estimation methods were changed from year-to-year such that undetected bias was present in all estimates and this bias was in opposite directions. This effect could be particularly acute if *ad hoc* methods were used to generate population estimates. Although it would be tempting to base λ estimates on some type of population index, such methods are usually unreliable and do not include variance estimators.

Including a measure of precision on λ would obviously be of importance. Thus, the quantity $\mathrm{Var}(N_{t+1}/N_t)$ must be calculated. Assuming the two population estimates are independent, and that there is no process covariance between the two years, I believe the correct formula (from the delta method) would be:

$$\mathrm{Var}(N_{t+1}/N_t) = (1/N_t)^2 * \mathrm{Var}(N_t) + (-N_{t+1}/N_t^2)^2 * \mathrm{Var}(N_{t+1}). \qquad \text{eq. 2}$$

Caughley (JWM 35(4):658-663) warns that some investigators have mistakenly calculated the stable-age λ_s using Eq. 2.1 based on either age at death data or a single age distribution estimate based on a one-time sample. He points out that such calculations are tautological because such data already assume that $r_s = 0$.

Question 2.b: Misleading λ values

By the wording in the question, I will assume that the actual value of λ is known (i.e. Type I or Type II errors have not been made when it is stated that λ is $<$ or $>$ 1). Under the circumstance that λ is known to be > 1, the population could still be "in trouble" if the number of individuals were so low that stochastic birth or death processes could lead to extinction. Because λ is simply a ratio, the absolute size of the population is not represented. For example, although a population increase from 5 animals to 10 animals in a year results in $\lambda = 2$, any number of natural stochastic events could result in the loss of the entire population. Another situation where λ could be misleading would be if the calculations were based on an overall increase in a metapopulation in which many of the subpopulations were actually declining. For example, one subpopulation may increase from 100 to 200 animals in a year, but three other subpopulations decrease from 50 to 25 animals. The overall λ value is 1.1, but 3/4 of the subpopulations are heading for collapse. The problems given in these two examples could be compounded if the small populations resulted in significant losses of genetic diversity such that the species was much less capable of surviving future environmental variation.

Another way an $\lambda > 1$ could be misleading would be if the increase in numbers between years was a result of an unstable age structure. When a population does not have a stable age structure, even deterministic life-table models show fairly wide swings in total abundance from time step to time step. If very accurate estimates of λ were made, by chance, between time steps in which the fluctuation was upward, a long-term average decline in the population may be masked. Given that stochastic changes in habitat quality and quantity change l_x and m_x schedules through time, a stable-age structure may be difficult to establish in most natural populations. This could lead to the relatively wide population fluctuations just described. A particularly serious example would be a case where a certain environmental perturbation leads to increased juvenile survival for one or more years, but the long-term effects are a decrease in overall habitat suitability. For example, clearcuts in an area may temporarily make raptor prey very available during the fledgling period, but could ultimately make the area unsuitable for sustaining populations. Thus, several strong recruitment years may give the impression that the population was healthy, when in fact the trend would be downward over the long term.

In similar ways, $\lambda < 1$ may not indicate that the population is in trouble. A very large population of thousands of individuals may experience several years or more of decline due to stochastic environmental effects (drought, for example), but be in no real danger of extinction. This would be especially true for long-lived species adapted to "weather" relatively harsh, but temporary, conditions. Another example would be any cyclic species such as voles in the northern latitudes in which the populations periodically undergo drastic declines in abundance, but persist over the long-term. An unstable age structure may cause a large decrease in abundance between years, but not indicate any long-term threat to the species. Finally, if all measurements are taken within one sub-population which, due to stochastic events, is declining, one may get the mistaken impression that the metapopulation as a whole is on the decline. An interesting example of this type of effect was found by Robert Hunt in his studies of fish-population responses to habitat improvement in Lawrence Creek, Wisconsin. The populations in unimproved downstream sections of the stream declined by nearly 30 percent over the three years following improvement to upstream reaches. However, these declines were accompanied by a 30 to 60 percent increase in fish abundance in much longer stream sections within and adjacent to the improved reaches. Hunt comments that the stream appeared to react as a unit to the habitat improvement, but that if only sub-reaches were analyzed, one could draw exactly the wrong conclusion regarding population changes.

2c. Other problems with estimates of λ

As for any statistical estimate with an associated variance, hypothesis testing regarding the true value of that estimate is subject to Type I and Type II errors. If the null hypothesis is that $\lambda >= 1$, conservation biologists would be most concerned with Type II errors (loggers with Type I). Naturally, there are ways to control these error rates, but if a species is already rare, sample sizes and other determining factors may be beyond the investigator's control. The last resort would be to increase the α-level.

Another consideration is the biology and life history of the species. A very long-lived species with a low reproductive rate (one offspring every other year, for example) may have an λ rate always very close to 1 even under the best of circumstances. Very small changes in the environment which influence birth and death rates may cause λ to fall just below 1. While the difference may be all but impossible to detect statistically, such a species would eventually go extinct.

In summary, λ is probably one of the easiest to calculate and most meaningful population parameters. There is no more fundamental aspect of a population than if it is increasing, decreasing, or remaining constant.

Question 3. Paradigms

Kuhn (1970, *The Structure of Scientific Revolutions*) defines paradigms as "universally recognized scientific achievements that for a time provide model problems and solutions to a community of practitioners" The most universally held paradigm in the natural sciences is the theory of evolution through natural selection. "Survival of the fittest" is a closely-related paradigm. "Predators mostly take the weak and sick" is a specific application of the survival of the fittest paradigm. The relationship between these widely-held beliefs points out something fundamental about biological paradigms: they are almost all rooted, somehow, in the natural selection paradigm. At times the connection is direct (survival of the fittest), but at others the connection is less tangible. For example, the natural selection paradigm is often an implicit assumption within a second paradigm (predators mostly take the weak and sick).

Another paradigm is that biological populations are in equilibrium with their biotic and abiotic environment. Mathematical and empirical studies of interspecific competition, predator/prey cycles, habitat availability versus use, and many others are based on this paradigm. However, within the last 10 to 15 years this paradigm is coming under increasing attack. An influential paper in this regard was May's (1974) on the chaotic behavior of the logistic equation (Science 186:645-647). When r-values exceed 2 in the logistic, stable cycles result in which the population overshoots and then undershoots K. Even higher r-values produce completely chaotic effects. This result was surprising because May (1974) did not incorporate time-lags, age-structure or other complications to produce the chaotic behavior. This was an indication that even the most "deterministic" system could behave chaotically and may not be well-described by equilibrium theory. There is now a rich body of theory regarding non-equilibrium processes and stochastic events, but time constraints preclude a more detailed discussion (for one good summary see Chesson and Case in *Community Ecology*, Harper and Row, 1986).

Another paradigm in the natural sciences states that more diverse ecosystems are more stable. MacArthur first proposed this based on considerations of Eltonian pyramids and food web complexity. May (1973) used a theoretical mathematical approach to examine the issue and concluded that more complex ecosystems should be less stable (*Stability and Complexity in Model Ecosystems*, Princeton Univ. Press). May's findings aside, conservation biologists strongly adhere to this paradigm as evidenced by the simple phrase "maintain biodiversity".

The paradigm I wish to discuss in detail is the paradigm of restricted movement in adult stream fish (juvenile fish are known to commonly disperse long distances from their parents spawning areas). I am interested in this topic because the paradigm does not appear to hold in the streams I am studying, a situation which has guided much of my research. Further, the paradigm offers an interesting example of how data interpretation, rather than the data themselves, can sometimes shape an entire field of study. In the summary to follow, I concentrate on the types of experiments which were done relative to the restricted movement paradigm (RMP), but go light on the literature citations simply because there are so many. I have a detailed review manuscript available if you would like more information.

The RMP has been in force since the 1959 publication of Shelby Gerking's article *The Restricted Movement of Fish Populations* (Biological Review, 34:221-242). In that paper Gerking summarized the results of studies he and several other investigators completed on both warm- and cold-water stream fish populations. The basic study design was similar in all the studies. Stream fish were collected in different reaches of a river (usually about 50 m in length), given marks unique to each section, and released. After a period of time ranging from several days to years, the sections were resampled and the distances moved by the fish were recorded. Almost invariably, the conclusion of the investigators was that the fish had moved very little. Similar studies have been conducted numerous times since Gerking's 1959 publication, all using very similar techniques and almost all reporting very similar results. Through this repeated "verification", the RMP has become one of the best-accepted generalizations regarding stream-fish behavior.

The only serious deviation from the RMP paradigm is the acknowledgment that a small fraction of most populations is mobile. This is based on the infrequent recapture of fish relatively long distances from the point of release. Some consider these "transients" to be sub-dominant fish which cannot successfully defend a territory (Jenkins 1969, Animal Behavior Monographs 2:56-123), while others have shown that mobile individuals are successful at finding and exploiting under-utilized resources (Naslund 1990, J. Fish. Biol. 36:401:404). A quantitative method to determine if a mobile fraction is present in a population based on the frequency distribution of movement distances has been developed (Stott 1967, J. Animal Ecology 36:407:423). Several authors have applied the method to salmonids and all have found a "small" mobile fraction.

The results of the studies Kurt Fausch, Steve Riley and I have been conducting in six high-elevation trout streams in Colorado could also be interpreted as supporting the RMP. The study reach in each stream is 500 m long, divided into contiguous 250 m treatment (habitat enhancement) and control reaches. Each year, 3-pass removal population estimates are made with total capture efficiencies over 90 percent per stream section per year. All fish Age 1+ and older are given a fin clip unique to the section of capture. The study has been ongoing since 1987, and provides the same type of raw data most investigators use to determine fish movements. For example, of the fish recaptured from a previous year's release, an average of 94 percent remain in their home section. Consistent with how most movement studies have been conducted, this would be interpreted as evidence of very restricted fish movements.

The error in concluding that fish movement is restricted is only apparent when one considers the number of unmarked adult trout captured each year. Because capture rates of the Age I+ fish are very high, and because fin regeneration is extremely rare, we would expect that after one or two years, all the Age II+ and older fish in the population would bear fin clips from previous years. However, an average of 52% of Age II+ and older fish captured each year are not clipped. That is, about 1/2 the population present within a given stream reach in one year consists of individuals which have moved into the section since the previous year. Under these circumstances it is obviously misleading to report that 94% of recaptured fish did not move, when in fact, we recapture far less than 1/2 of the total number released.

Our study provides a realistic picture of movement (about 1/2 the population moves at least 250-500 m per year) because we achieve very high capture efficiencies. As a result, we can tell fish are moving based on the capture of *unmarked* fish. In essentially all the studies reporting restricted movement, the authors base their conclusions solely on the recapture of marked fish.

How many recaptures are these results based on? Similar to our study, typically less than 50% (Table 2). This situation did not alarm early investigators because sampling efficiency was low and so capturing unmarked fish during resampling was not considered unusual. Also, fish mortality rates are high, and recapture rates of less than 50% were attributed to the marked fish simply dying. Regarding this last point, an interesting circularity developed over the years. Investigators estimating fish survival found low "apparent" survival and concluded that true survival was also low because fish movement was known to be restricted. Those studying movement concluded that movement was restricted because unrecaptured fish were assumed to have died. The RMP is largely built upon this circularity.

Table 1. Percentage of all marked fish eventually recaptured at least once in various movement studies. Studies discussed in the text but not included here indicate that percent recapture data were not reported or could not be calculated from information given in the publication. Literature citations available upon request.

Study*	Time Between Samples	Percent Recaptured
Shetter and Hazzard 1938	1 month	3-53
Shuck 1945	1 year	15
Stefanich 1952	3 months	47-52
Funk 1955	Various (angler returns)	1
Miller 1957	1-24 months	59
Smith and Saunders 1958	35 days	13-14
Saunders and Gee 1964	14-123 days	76
Shetter 1968	Various (most w/in 37 days)	9-10
Edmundson et al. 1968	1-14 days	60
Mense 1975	1 year	62
Jackson 1980	1-2 months	0-73 (mean 48)
Harcup et al. 1984	21 / 35 / 42 days	72 / 61 / 56
Bachman 1984	1 year	60-83 (mean 72)
Larson 1988	8 months	14
Heggenes 1988b	1 year	26
Nakano et al. 1990	1 month	45
Heggenes et al. 1991	14 days	60

I should note that I am not saying all fish populations show high movement rates. There have been several reliable studies which do provide non-circular evidence of restricted fish movements. To claim *all* fish move would be as misleading as claiming that none do.

What are the management implications of the RMP? The most important is the view that stream fish populations are composed of fairly isolated sub-populations living within limited stream reaches. The recent emphasis being placed on "watershed management" is based on the idea that perturbations in one part of the watershed eventually influence other parts. I do not argue this point. However, with regards to fish, it seems equally probable that the fish could move to the perturbation. For example, a poorly designed culvert at a road crossing could block the upstream movements of fish. Our studies show that when fish do move, about 75% of them go in the upstream direction. Assuming this is somehow adaptive (the paradigm of natural selection rears its head again), blocking these movements could have serious consequences throughout the watershed. In the hydroelectric projects I worked on as a consultant, fish ladders were not required on streams with only "resident" (as opposed to anadromous) populations. This was based on the knowledge that stream fish do not move much, so why would we need ladders?

A second consequence of managing fish under the RMP is that it seems possible to have hatchery stocks and wild fish coexist within the same stream. Hatchery fish can be planted within one section and not threaten wild fish in other sections. For a stream like the Cache la Poudre in which the hatchery fish are almost immediately removed by intense angling pressure, this is probably true. However, for streams with less angling, there is the potential for genetic dilution or other problems as the two populations become mixed through fish movements.

A basic technique in stream fish management is the use of special regulations. Generally, these regulations take the form of size limits or catch-and-release regulations designed to "recycle" fish within the fishery. The goal is to produce more and/or larger fish. It is not uncommon for certain sections of a stream to be designated as catch-and-release while adjacent sections remain under normal regulations, permitting anglers to keep 8 or more fish per day. The RMP justifies this approach because it is assumed there is little interaction between populations within the different sections. At times these regulations are successful, but often they are not. When they are not, it is usually assumed the reason is related to compensatory mortality or limiting factors other than fishing pressure. These assumptions may lead to other management decisions. However, if there is a significant amount of fish movement, failure of the special regulations could result simply from the fact that the standard regulations are really being applied to the entire population.

The final management implication I will consider has to do with the effects of habitat enhancement. Under the RMP, habitat enhancement is assumed to benefit only the population within the enhanced reach. However, in our study in Colorado, we have found significant fish population increases not only in the treatment sections, but in the controls also. It is interesting to note that other investigators have reported similar findings, but generally ignored the phenomenon because they were operating under the RMP. Instead, population increases in treated reaches have been credited to increased over-winter survival. However, this conclusion is not based on rigorous survival estimates, but on the RMP. Since fish movements are "known" to be rare, the benefit of habitat enhancement must result from *in situ* processes. Given the obviously harsh nature of the winter stream environment, it is natural to implicate increased over-winter survival as the causative mechanism. Thus, adherence to the RMP may be leading to other spurious conclusions. The good news is that habitat enhancement may provide benefits over a length of stream much longer than the improved reach.

In summary, paradigms are a central part of biology. They provide the foundations upon which most of the work we do is based. However, they can be mistaken at times for inviolable natural laws which need not be questioned or tested. This is unfortunate because, when they are tested, exceptions are almost invariably found. For example, much of the work stream fish biologists do, the management recommendations they make, and the research they conduct, is based on the paradigm of restricted fish movement. Our studies in Colorado streams indicate that the RMP may not be applicable to Rocky Mountain trout streams. Understanding the dynamics of stream fish populations is complicated when significant movement must be accounted for, but reliable management may not be possible if we stick to the RMP paradigm.

Department of Fishery and Wildlife Biology
College of Natural Resources

MEMORANDUM

March 26, 1993

To: Kurt Fausch

From: Gary C. White

Re: Comprehensive Exam Questions for Charles Gowan

The following are my questions for the written portion of Mr. Gowan's comprehensive exam. He can have the questions on Monday morning, March 29, and should turn in his responses by Friday afternoon, April 2. He is allowed to use any reference material or computer software, but cannot discuss these questions with any person.

1. A common perception held by researchers is that the precision of a parameter estimate cannot be any greater than the precision of the data used to construct the parameter estimate. This perception is translated into practice in the publication of the parameter estimate in a journal article, where editors often restrict the number of digits in the reported estimate. A commonly invoked rule is that the mean of a set of data can not be reported to >1 significant digit over the original data. Suppose you have collected a sample of distances, measured to the nearest 10 meters, i.e., 10, 20, 30, etc. Can you legitimately report a mean distance estimated to 0.001 meter, e.g. 20.234? Why or why not? What conditions would be necessary for such a precise estimate? Can you formulate a simple rule for the statistically naive, or is any rule misleading? You can apply some of your mathematical and statistical knowledge to provide a rigorous analysis of this problem. Be sure to specify any assumptions you make as part of this analysis.

2. Biologists have examined the population rate of increase, $\lambda = N_{t+1}/N_t$, to decide whether a species is "in trouble" and should be listed as a threatened or endangered species. Consider the following scenarios when interpreting the value of λ and deciding whether a species is in trouble.

a. How can λ be estimated when actual population sizes, i.e. N_t, are unknown?

b. The true value of λ is presumably a function of habitat, both quantity and quality. When might the true value of λ be misleading, i.e., $\lambda > 1$ and the species ~~not~~ be "in trouble", or $\lambda < 1$ and the species is Not "in trouble".

c. What are some additional problems in the use of λ when only an estimate and its associated precision is known, i.e., we cannot observe λ exactly?

3. The fisheries and wildlife professions have a number of paradigms that are held by the average professional, e.g., predators mostly take the weak and sick. What are some additional paradigms? Select one of your examples and examine its validity, and the implications of its application to the quality of management.

Hatchery Plants [illegible]