FOOD HABITS OF THE WESTERN WHITE SUCKER

IN

LONETREE RESERVOIR-SUMMER OF 1952

By

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WM 192b

Problem in Fish Management

May 28, 1953

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INTRODUCTION

In 1950, members of the Colorado Cooperative Fisheries Research Unit began an ecological survey of Lonetree Reservoir, Larimer County, Colorado. The survey is part of a long range program aimed at improving the warm water fishing in Lonetree and other similar irrigation reservoirs.

This report is based on a laboratory examination of intestinal contents of the western white sucker (Catostomus commersoni suckleyi Girard) taken from Lonetree Reservoir.

COLLECTION OF SPECIMENS

All of the fish used in this study were collected with gill nets, in Lonetree Reservoir, during the months of June, July and August, 1952. The nets were set daily and the fish were removed the following morning. The weight, length and sex of each fish was determined and recorded and a scale sample was placed in a coin envelope. When the fish was cut open for sex determination, the intestine was also examined. If the intestine was in good condition and contained sufficient material to warrant examination, it was cut free at the pharynx and anus and was carefully removed. All of the digestive organs were left intact, given a code number, wrapped in cheesecloth and preserved in a 10 percent formalin solution.

It should be pointed out that taking suckers by gill net has some disadvantages. Since the fish are often entrapped in the nets for several hours before they are removed, many of them die and start to decompose.

LABORATORY PROCEDURE

A 1 c.c. sample was removed from the most anterior part of the intestine. This sample was placed in a 10 c.c. graduated centrifuge tube and diluted with water to the 5 c.c. level. The tube was agitated until the contents were thoroughly mixed, then the mixture was poured into a watch glass. The material was stirred with a probe until a homogeneous suspension was obtained. A 1 c.c. sample was drawn off with a widemouth pipette and placed in a container for microscopic inspection.

At the beginning of the study, a Sedgwick-Rafter cell was tried for counting the organisms under the microscope. Since the cell has a capacity of 1 c.c., the sample filled it to the point that the organisms were bunched together so closely that an accurate count could not be made.

Counting and identifying the organisms was simplified by marking off a Petri plate into 40 divisions and substituting it in place of the Sedgwick-Rafter cell. The area of the Petri plate permitted a wider and thinner distribution of the material, thereby, easing the task of separating the organisms and debris.

A dissecting microscope was used for counting the organisms, however, a compound microscope was used to identify many of the smaller individuals. The identifiable invertebrate organisms were tallied by actual count then multiplied by 5 which was the dilution of the sample. All plant material and debris was considered separately and was recorded as an estimated percentage of the total sample volume. The data was recorded on standard fish stomach analysis sheets.

An attempt was made to classify all organisms as to their genus, but in some representatives this was impossible because they were partially digested. Some of the scientific names have been changed to conform with those used by Pennak (1953).

In the tabular presentation of the data (Tables 1 and 2), the volume and frequency of occurrence of the debris is not shown because it may create an erroneous interpretation of the results. An analysis of the debris is given elsewhere in the report.

The writer is indebted to Dr. O. W. Olsen, Dr. J. R. Olive and Dr. T. O. Thatcher of Colorado A&M College for assistance in identifying many of the organisms.

DISCUSSION OF FOOD HABITS

The suckers examined, in the study, were between 8.1 and 16.5 inches in length with an average of 11.8 inches. Although some of them may not have been sexually mature, they were all of sufficient size to be considered as adults. The findings of Stewart (1927) indicate that suckers acquire adult feeding habits by the time they reach a length of 3 inches.

The data from this study shows that Diptera larvae represented more than half of the animal diet of suckers in Lonetree Reservoir. Of this group, midge larvae (Tendipes) were, by far, the most abundant. Although Tendipes pupae appeared in 40 percent of the intestines examined, they were never present in very great numbers.

Kutkuhn (1953) found that phantom midge larvae (Chaoborus) represented 34 percent of the bottom fauna in Lonetree Reservoir. However, these organisms constituted a very small part of the sucker diet. Their low frequency of occurrence may be due to the fact that the larvae are inhabitants of deep water, where the absence of oxygen prohibited the fish from feeding.

The only other genus of Diptera which was utilized was the larvae of the biting midge (Bezzia).

Two forms of caddis fly larvae were fed upon infrequently by the suckers. Limnephilidae larvae were taken most often during the month of June, and Oecetis larvae were taken only during the late summer. Neither of these insects could be considered an important food item.

Fragments of two small ants were found in the intestines of two suckers, that were collected in the month of August. Their appearance was thought to be incidental.

Entomostracans were found to be second in numbers and occurrence in the food of suckers in Lonetree Reservoir. Studies made by Nurnberger (1930) show that these organisms are a major food of the common white sucker in a Minnesota lake. Although both copepods and cladocerans are quite small, their great numbers increase their importance as a food item.

The extremely high numbers of free-living nematodes (Dorylaimus), which were found during the study, indicate that they are a very important food of the sucker in Lonetree Reservoir. Surveys, in other localities, by Stewart (1927), Nurnberger (1930), Thorpe (1942) and Harrison (1950) fail to show an occurrence of nematodes in the food of suckers. However, Moore (1952) found Dorylaimus to be present in 54 percent of 82 carp specimens taken from Lonetree. This leads to the assumption that nematodes may be very abundant in the reservoir. It is probable that the fish ingested them accidentally, along with the green plant fragments. Since the nematodes are vegetable feeders, which live in and around plants of the littoral zone, this may account for their failure to show up in dredging samples that have been taken in the deeper portions of the reservoir.

The constant and frequent occurrence of Hydracarina in the sucker intestine samples may indicate that these individuals are a preferred sucker food. Although their numerical count was low, the specimens found were large enough to provide an appreciable amount of nutrition.

One sucker contained two vertebrae of a small unidentified fish, but this information is not shown in the tables.

Green plant fragments were utilized, by the suckers, throughout the summer. Tender shoots and rootlets were the most common forms ingested. Plant fragments usually are one of the staple foods of suckers, but in Lonetree Reservoir rooted plants are not available to fish except during times of high water. The suckers used in this study were taken after the water in the reservoir had started to recede, thus much of the shoreline had no form of vegetation. This scarcity of vegetation is reflected in the low volume of plant fragments which occurred in the samples.

Filamentous algae was present in 50 percent of the intestines examined, but it represented a minor part of the total diet. *Spirogyra* and *Mougeotia* were the only two genera that could be

Table 1. The Summer Foods of 40 Western White Suckers in Lonetree Reservoir, Colorado, 1952, Expressed as the Percentage of Each Food Item and the Percentage of Occurrence.

Class	No. of Items	% of Each Food Item	% of Freqency Occurrrence
Entomostraca	6,073	28.0	80.0
Copepoda			
Cyclops	3,440	19.0	55.0
Cladocera	1,598	9.0	57.5
Chydorus	425	2.4	30.0
Alona	395	2.2	5.0
Ilyocryptus	375	2.2	12.5
Bosmina	203	1.1	17.5
Daphnia	200	1.1	7.5
Ostracoda	35	Trace	5.0
Hydracarina	238	1.0	50.0
Nematoda			
Dorylaimus	2,455	14.0	77.5
Insecta			
Diptera	10,172	56.0	87.5
Tendipes L.	8,202	53.8	85.0
Tendipes P.	200	1.0	40.0
Bezzia L.	125	0.6	15.0
Chaoborus L.	115	0.6	17.5
Tricoptera	155	1.0	22.5
Limnephilidae L.	105	0.7	10.0
Oecetis L.	50	0.3	12.5
Total	17,544	100.0	
Green Plant Fragments *		5.2	87.5
Seeds*		0.3	22.5
Filamentous Algae*		2.8	50.0
Diatoms*		1.0	17.5
Desmids*		0.7	2.5

L-Larvae *-Estimated Percentage
P-Pupae

Table 2. The Summer Foods of 40 Western White Suckers in Lonetree Reservoir, Colorado, 1952-Showing the Average Number of Items Per 1 c.c. of and Percentage of Frequency Occurrence.
BY MONTHS

Class	June (9) Ave. No.	June (9) % of Occ.	July (6) Ave. No.	July (6) % of Occ.	August (25) Ave. No.	August (25) % of Occ.
Copepoda						
Cyclops	0.5	11	251.6	16	77.0	75
Cladocera						
Chydorus	19.7	77	25.0	83	50.6	52
Alona	0.0	0	0.0	0	15.8	8
Ilyocryptus	0.5	11	1.6	15	14.4	12
Bosmina	1.4	22	1.6	15	7.2	16
Daphnia	0.0	0	0.8	15	7.8	8
Ostracoda	0.0	0	0.0	0	1.4	8
Hydracarina	4.7	55	6.6	50	6.2	48
Nematoda						
Dorylaimus	123.8	77	25.7	83	47.4	56
Diptera						
Tendipes L.	275.5	100	239.1	83	226.4	80
Tendipes P.	6.6	66	0.8	15	5.8-	40
Bezzia L.	13.3	55	0.0	0	0.2	4
Chaoborus L.	0.0	0	6.6	33	3.0	20
Tricoptera						
Limnephilidae	2.7	22	4.0	50	0.0	0
Oecetis L.	0.0	0	0.0	0	2.0	16
Plant Fragments		100		83		84
Seeds		22		0		28
Filamentous Algae		88		83		28
Diatoms		22		0		0
Desmids		11		,0		0

Number in parenthesis indicates number of fish examined .
L.- Larvae
B.- Pupae

identified. Suckers are considered to be heavy algal feeders in waters where the clinging types of algae are found. In Lonetree Reservoir, free-floating algae is the type most commonly observed and is not easily taken by bottom feeding fish.

Diatoms of three genera, namely, Cymatopleura, Fragilaria and Navicula appeared only in the suckers that were netted during the month of June. Although they were usually found in trace amounts, one intestine was half filled with them.

Closterium was the only desmid found in the samples. Several of these minute plants were present in the same fish that was gorged with diatoms.

Inorganic, plant and animal debris represented an estimated 58 percent of the total volume of the samples examined. Of this material, 23.5 percent was sand, mud and silt; 18 percent was plant debris and 16.5 percent was animal remains. This is a rather high figure, but Leonard (1940) discovered that organisms present in the debris appeared to be in direct proportion to those occurring in the recognizable materials. It is this writer's opinion that a similar condition existed in the specimens examined in this study.

COMPETITION

An overpopulation of suckers is quite common in many Colorado reservoirs. In the Lake States, the larger predatory species, such as the northern pike (Esox lucius) and Great Lakes muskellunge (Esox masquinongy masquinongy), tend to control the sucker population. Since no large predatory fish inhabit Lonetree

Reservoir, suckers have become quite numerous. The results of gill netting during 1950, 1951 and 1952 show that suckers rank second in the numbers of fish collected (Fisk 1952).

Although this study is limited to data covering a three-month period, it does indicate that suckers consume an appreciable quantity of organisms that are utilized by game fishes of Lonetree Reservoir (Fisk 1953, Kutkuhn 1953). Half of the diet of young largemouth black bass (*Micropterus salmoides salmoides*) and young yellow perch (*Perca flavescens*) was made up of dipterous larvae and entomostracans. Both of these forms were found to be a major food of suckers.

Suckers have been known to eat large numbers of fish eggs, but not one egg was found in the 40 intestines examined. In the author's opinion, the destruction of aquatic vegetation is the primary evil of suckers in Lonetree Reservoir. Because plant life is so scarce, any curtailment of its growth will have an injurious effect upon the food chain.

SUMMARY

The intestines of 40 adult western white suckers taken from Lonetree Reservoir, Colorado, during the summer of 1952 were examined to determine the food habits of the fish.

The main food of the suckers was midge larva (Tendipes). Second in importance was entomostracans, of which, approximately one-third were copepods and two-thirds were cladocerans. The nematode *Dorylaimus* was an important food item and appeared in great numbers. Plant foods were taken regularly but not in as great a volume as other surveys have shown.

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COLORADO A & M COLLEGE

FORT COLLINS

DEPARTMENT OF W. M. - 190

Experiment No. .... **Course No. or Division** ......

Name of Student Roger Barnhart

Names of Associates ....

Title of Experiment Humpback Brown Trout of S. Platte

Date Performed ....

Date Presented ....

Returned for Correction ....

Date of Final Presentation ....

Grade ....

File No. ....

Group No. . . .

x80-

Report on Fish Problem Concerning

The Humpbacked Brown Trout

Submitted to:

Dr. H. A. Tanner

Leader Colo. Cooperative

Fishery Research Unit

Forestry Department

By:

Roger A. Barnhart
Colorado A.& M. College
December 17, 1954

Report on Fish Problem - Fall Quarter 1954

Introduction:

While working for the Game and Fish Department of Colorado and the Colorado A.& M. Cooperative Research Unit on the south fork of the S. Platte River near Deckers, Colorado this summer (1954), it was noted that this section of stream contained substantial numbers of a "humpbacked" brown trout (Salmo trutta). Our work consisted largely of a creel census where we contacted the fisherman personally and collected data on his catches. This "humpback" trout was quite commonly found in the catch.

This trout has a large "hump" of flesh on its dorsal side, usually directely in front of the dorsal fin. It was found that the humpbacked fish did not attain the lengths of the normal brown. Due to this fleshy hump the fish had surprising weight in relation to its length. In all other appearances, the fish seemed quite healthy. The trout does not appear to be hindered physically by this hump. It was able to put up a very strong battle when hooked, even jumping at times.

Later on a fresh fish was dissected and there appeared to be a skeletal difference. The humpbacked trout seemed to have a compaction of vertebrae in the region of the hump. This aroused an interest in this fish. There were many local theorys for this type fish, none of which seemed feasible. After this a number of the humpbacked trout were collected and preserved in formalin. They were brought back to the Colorado A.& M. campus this summer to Dr. Tanner. A problem was assigned to me concerning this fish.

Problem:

To determine the true cause of the humpbacked trout by:

1. Finding any structural differences in the humpbacked brown trout compared with the normal trout.
2. Discovering the influence of heredity on the humpback brown.
3. Collecting information of age-growth studies of "humpback" brown and normal trout.

Accomplishments to Date:

The first attempt on the problem was made in trying to remove the flesh from the preserved "humpback" trout. Boiling was tried and served only to garden the tissues of the fish more. After this, little was done for a time. Then a trip was made back to the area where we had worked this summer. Fresh humpbacked trout were collected by means of an electrical shocking unit.

While there , eggs were stripped from the late spawning trout and crosses were made between male and female humpbacks, normal males and females, a normal male and humpback female, and a humpback male and a normal female. These eggs were brought back to Fort Collins and placed at the Belleview hatchery to be hatched and reared.

A number of the fresh humpback fish were returned to Fort

Collins and frozen. Since then the flesh has been removed from half of them by cooking. It was found that the meat came off rather well if cooked long enough. Oh the other hand, the skeleton of a fish cooked too long will fall apart.

The skeletons of the fresh fish were examined closelh. There is a definite compaction of vertebrae on the humpbacked trout. On some of the more humped fish the vertebrae are almost impossible to ascertain because of the compaction and often a fusion of two vertebrae. The compaction does not accur throughout the entire skeletal length but primarily in the anterior regions. It is not always the same vertebrae however. There is no reduction in the number of vertebrae in the humpbacked trout. Both the normal and the humpbacked fish have fifty-six true vertebrae. It is easy to see how the compaction can be a cause of the shorter humpbacked trout. The length of the individual vertebrae of two of the trout were measured but nothing could be determined by these measurements.

Scale samples were collected this summer as part of the creel census. A number of the scales have been read and the age of the fish determined. There seems to be no dradtic differences in the age-growth relationships betwiin the humpback and normal trout although inough of the scales have not been read as yet to make any definite conclusions.

Pictures were taken of the skeletons of the fish but have not been developed yet.

Things to be Accomplished:

Of course, the main thing desired is to get a final answer on the humpback trout. It is hoped that this can be done during winter quarter, 1954-5. Briefly it will be accomplished by:

1. Having the pictures developed and taking some additional shots.
2. Finishing reading the scales and establishing some conclusions on age-growth relationships.
3. Removing the meat from some fish;especially the preserved specimens.
4. Gathering all posseble data on the skeletons and coming to some conclusions on physiological differences.
5. Determining the results of the fish crosses from the hatched fish and concluding the significance of heredity in respect to the problem.

Roger Barnhart

note:

Dr. Tanner,

I feel that I have done very poor work on this problem to date and I sense that you feel the same way on the subject. I have not spent nearly enough time on it. I am really very interested in this fish problem and hope that this next quarter I will be able to show some satisfactory results. I am sure that I will have a good deal more time to spend on it during winter quarter. I am upset personally that I have showed so poorly on a subject concerned directly with my major. It seems as though I have been required to spend time on subjects which were not so closely allied to my field of study but were nevertheless to go down on my grade record. I do not intend to do this in the future because such a study as this fish problem will be of far more value in future years to me, I am sure.

Sincerely,

Roger Barnhart

A STUDY OF FOOD COMPETITION BETWEEN THE TROUT SALMO AND THE NEWLY INTRODUCED MOUNTAIN WHITEFISH PROSOPIUM WILLIAMSONI (GIRARD) IN THE CACHE LA POUDRE RIVER

Submitted to

Dr. Harold K. Hagen

Professor of Fish Management

Colorado A. and M. College

By

David J. Jones

Fish Management Student

Fort Collins, Colorado

February 26, 1957

627½ South Loomis
Fort Collins, Colorado

February 26, 1957

Doctor Harold K. Hagen
Professor of Fish Management
Colorado Agricultural and Mechanical College
Fort Collins, Colorado

Dear Doctor Hagen:

In compliance with your request of January 7, 1957, I am submitting the following report concerning the food competition between the Mountain Whitefish and the trout in the Cache la Poudre River.

The report covers the food organisms found in the Cache la Poudre River, also the food habits of the whitefish, rainbow, and brown trout, and the populations of these three species in the river. This study was seriously limited because I was not able to take samples from this river.

I conclude that the whitefish and the trout do compete for food and that this may become a serious problem if the whitefish population increases.

Sincerely,

David J. Jones

DJJ:ng

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A STUDY OF

FOOD COMPETITION BETWEEN THE TROUT SALMO

AND THE

NEW MOUNTAIN WHITEFISH PROSOPIUM WILLIAMSONI (GIRARD)

IN THE

CACHE LA POUDRE RIVER

INTRODUCTION

OBJECT OF THE REPORT

The object of this study is to determine whether there is a probability of active food competition between the newly introduced whitefish and the trout in the Cache la Poudre River in Colorado. The trout population includes annually stocked Rainbow and naturally reproducing German Brown Trout. This problem was assigned by Dr. Harold K. Hagen, Professor of Fish Management. The study was made, and this report is submitted to fulfill the requirements of the course, Problems in Fisheries Studies.

ABSTRACT

The most common organisms found in many mountain streams of the United States are aquatic earthworms, beetles, true flies, mayflies, stoneflies, and caddis flies. Mayflies are the most abundant of these in the Cache la Poudre River. Rainbow and brown trout feed mostly on true flies, mayflies, caddis flies, leafhoppers, beetles, scuds, snails, clams, and fresh water shrimp. True flies, caddis flies and mayflies were the favorite food organisms of the whitefish. The rainbows are stocked annually at the rate of one hundred fish per every one-fifth mile during the spring and summer. There are approximately thirty-three brown trout per two hundred feet of the river. There has been a total of 1225 whitefish planted at four locations on the river.

METHODS AND SCOPE

The quantity and quality of the food organisms as well as the population of fish in the Cache la Poudre River were determined. Also, an investigation of the food habits of the Mountain Whitefish, Rainbow Trout, and German Brown Trout was made.

Some data on the food organisms in the river was obtained from a sample, but most of this information was taken from the literature. The fish population of the river was determined from the information supplied by the Colorado Game and Fish Department and the Fish Management Classes of Colorado A. and M. College. The food habits of the fish were determined only from the available literature, and no stomach samples were taken because of limited time and funds.

CONCLUSIONS

The conclusions of the report are:

(1) The Cache la Poudre River contains nearly the same types and numbers of trout food organisms as other trout streams.

(2) The Mountain Whitefish, Rainbow Trout, and the German Brown Trout eat generally the same organisms.

(3) With the present population of whitefish, there is probably no serious competition; however, as the whitefish population increases, this competition may become serious.

The study of this problem should be pursued more fully in the future by taking stomach samples and watching the population trends of these fish in the Cache la Poudre River.

NATURE OF THE PROBLEM

The Colorado Game and Fish Department has undertaken the project of establishing the Mountain Whitefish in the Cache la Poudre River. The following report and study were made to determine if there is food competition between these whitefish and the trout presently found in the river. This problem was my assignment for the Problems in Fisheries Studies course taught by Dr. Harold K. Hagen. The information on the fish food in the river and the food habits of the fish was taken from the literature. The population of the fish in the river was considered in determining the degree of food competition as well as the effects of the competition between the trout and whitefish.

FOOD ORGANISMS

Quality

The search of the literature revealed that aquatic earthworms (Oligochaeta), beetles (Coleoptera), true flies (Diptera), mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddis flies (Trichoptera), were the most commonly found organisms in the many mountain streams of the United States. (Appendix A.) The 1950 study made on Convict Creek in California showed that all six of the above named orders of organisms were present in the stream during the winter. The insects, as well as the worms, were all found dwelling on the bottom of the stream, which is their natural habitat, (Maciolek and Needham, 1951). Waddell Creek in California also has similar bottom life during the winter. The study on this stream during the summer found plant lice (Hemiptera) floating in the water, although they are terrestrial insects, (Needham, 1940). Scuds (Amphipoda), flatworms (Platyhelamenthes), and crayfish (Decapoda) live along with the aquatic insects in a trout stream in West Virginia, (Surber, 1936). (Appendix A.)

Two separate studies on the Cache la Poudre River are being considered in this report. One is an extensive study made in 1950 at an area just below the Fort Collins' water works, which includes samples from all bottom types. The most important bottom types in the Cache la Poudre are silt that is found in pools and rubble, and rocks and gravel, in the riffle, fast running areas. Midges (Tendipedidae), black flies (Simulidae), net-winged midges (Blepharaceridae), and snipe flies (Rhagionidae), are the families of the true flies that were found. The caddis flies of the Cache la Poudre River belong to two families: Brachycentridae and Hydropsychidae. Only one family, Pteronarcidae, of the stoneflies was found in this study. Baetidae and Heptageniidae were the two families that represented the mayflies in the study area, (Gruchy, 1951).

In the spring and fall of 1956 the Fish Management Classes of Colorado A. and M. College made population studies of the Cache la Poudre, at which time they also took bottom samples of the study areas. All of the samples except one, however, have been lost. This one sample was taken in an area with a silt bottom by the means of a Peterson dredge in April, 1956. The sample contained aquatic earthworms, Tendipedidae, Brachycentridae, and Hydropsychidae, (Hagen, 1956).

The Cache la Poudre River, as determined by this limited study, has nearly the same types of organisms as other trout streams in the United States.

<u>Quantity</u>

The oranisms in Convict Creek were classified in two groups, (Maciolek and Needham, 1951). These are the organisms that were taken in bottom samples and the organisms that were caught in nets as they drifted down stream. Caddis flies were the most numerous organisms found in the bottom sample.

Beetles and mayflies were also numerous in the bottom samples. (Table 1.) Of the drifting organisms the caddis flies were again the most numerous, with mayflies and beetles also present in important numbers.

Table 1. The Percentages by Numbers of the Organisms Taken in the Bottom Samples and Drift Net Samples in Convict Creek, California, (Maciolek and Needham, 1951).

Organism	Percent of total numbers in all of the tow types of samples	
	Bottom Samples	Drift Samples
Caddis flies (Trichoptera).	28.3%	28.5%
Mayflies (Ephemeroptera).	19.4%	23.8%
True flies (Diptera).	14.0%	2.3%
Stoneflies (Plecoptera)	3.0%	2.3%
Aquatic earthworms (Oligochaeta)	10.7%	10.7%
Beetles (Coleoptera).	22.0%	27.0%
Miscellaneous	2.6%	3.1%

In the Waddell Creek study, silt was found to be the most productive bottom type in the stream. The silt bottom areas produced 3.47 grams of organisms per square foot. Rubble and course gravel produced 1.84 grams and 1.27 grams of food organisms respectively. Fine gravel, muck, and sand produced considerably less organisms. Samples were taken from riffles, fast running sections, during the four seasons, and the spring samples were found to be the most productive. During the spring there were 4.92 grams of food organisms per square foot of bottom area. The weight of the food present dropped to 1.94 grams per square foot in the summer and 2.14 grams per square foot in the fall. Only .73 grams of organisms were found per square foot in the winter samples.

Comparison of the relative abundance of the organisms showed mayfly nymphs, immature mayflies, to be the most abundant in the riffle areas and the true fly larvae most abundant in the pools, (Needham, 1940). (Table 2.)

Table 2. The Percentages of the Total Organisms in the Riffle and Pool Areas in Waddell Creek, California, (Needham, 1940).

Organism	Riffle	Pools
Mayfly numphs	39.6%	41.2%
Caddis fly larvae & pupae	21.3%	1.2%
Stonefly nymphs	14.7%	4.1%
True fly larvae & pupae	13.8%	46.7%
Beetle larvae & pupae	7.6%	2.6%
Crayfish and Scuds	3.7%	.2%

This study shows there is considerably less available food in the winter than in the other seasons. This condition may be partially caused by the action of anchor ice. Anchor ice is slushy ice that forms on the bottom of rivers when the water is super cooled. This anchor ice washes downstream as the water warms and knocks some organisms free from the bottom. The organisms are then temporarily available, but the supply soon becomes depleted. Also, ice damming causes severe fluctuations in water flow which frequently leaves the organisms exposed to the air where they are killed by extreme temperatures. This hypothesis was demonstrated by taking bottom samples from Convict Creek before ice formed and again after the ice left in the spring. The first sample contained 107 organisms per square foot while the sample taken after the ice had left the stream contained only thirty-six organisms, (Reimers, 1957).

In the West Virginia stream considered in this report, scuds (Gammarus) were by far the most numerous organisms. The scuds numbered fifteen hundred per square foot in June. Caddis flies were the second most numerous organisms in the stream. October and November were the months during which they averaged 129 individuals per square foot, which was their greatest abundance, (Surber, 1936). (Table 3.)

Table 3. The Average Populations per Month of the Important Organisms in a stream in West Virginia, (Surber, 1936).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Scuds	260	310	310	500	800	1500	900	1000	750	200	400	300
Mayflies	87	82	14	35	32	42	70	86	57	78	85	30
Caddis Flies	70	60	69	87	96	85	30	33	44	129	129	61
Beetles	35	38	39	29	43	61	69	62	103	90	93	37
True flies	23	37	35	26	50	17	16	34	16	13	41	13
Total insects	215	217	157	177	221	205	185	215	220	310	348	141

The highest number of insects was 348 per square foot in November and the lowest was 141 per square foot in December.

The one sample from the Fish Management Classes' studies taken in a silt bottom area in April 1956 contained 1.35 grams, wet weight, of organisms per square foot. Aquatic earthworms were predominant in the sample, with 135 worms per square foot. There were 129 midge larvae and pupae; also, there were twenty-one caddis fly larvae in the sample.

July and April were the low and high months respectively in organism production in the 1950 study on the Cache la Poudre River. Mayflies made up 37.75 per cent of the total population over the year. (Table 4.) The true flies and caddis flies were 31.47 per cent and 20.71 per cent of the total population respectively, (Gruchy, 1951).

Table 4. The Monthly Average Populations of Bottom Organisms per Square Foot of Substrate in the Cache la Poudre River, (Gruchy, 1951).

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Aver-age	% of pop.
Mayflies	2.8	2.6	2.1	10.4	21.0	19.1	31.7	18.1	40.6	54.1	20.3	37.75%
True flies	.3	2.9	7.1	24.6	34.3	15.2	11.7	30.6	34.1	9.4	17.0	31.71%
Stoneflies	.1	7.7	10.2	9.2	6.3	7.4	2.3	3.1	3.7	2.8	5.3	9.83
Caddis flies	.9	1.9	13.4	19.6	14.8	24.0	11.3	8.2	10.6	6.3	11.11	20.71%
Total	4.2	15.0	32.3	63.8	76.5	65.7	57.0	60.0	88.9	72.7	53.7	100%

The largest monthly average in this study was 88.9 organisms per square foot, thus indicating that the Cache la Poudre is less productive than Convict Creek, which had a high of 107 organisms per square foot. However, the other sample of the Cache la Poudre River contained 285 organisms. The stream in West Virginia had the highest production, with 348 per square foot.

FOOD AND FEEDING HABITS

Trout

The Rainbow Trout, Salmo gairdnerii, feed nearly exclusively on insects. These insects are generally in the larval "worm" stage, but insect adults are readily eaten when available.

In a study made in the winter at Convict Creek in California, it was found from a sample of fifty-three rainbows that true flies were the most frequently eaten insects. Caddis flies were second, and mayflies were the third most numerous insects found in this sample. (Table 5.) Aquatic earthworms, beetles, and stone flies were also found in the trout stomachs, (Maciolek and Needham, 1951).

Table 5. The Organisms Found in the Stomachs of 53 Rainbows Taken from Convict Creek, California, from December 29 to March 22, (Maciolek and Needham, 1951).

Food Organism	Percentage of Total Number
True flies (Diptera)	54.9%
Caddis flies (Trichoptera)	21.5%
Mayflies (Ephemeroptera)	14.1%
Beetles (Coleoptera)	3.9%
Aquatic earthworms (Oligochaeta)	3.4%
Stoneflies (Plecoptera)	.8%
Miscellaneous	1.4%

The trout in Convict Creek were noted to be active during the entire winter, and there was no apparent reduction of their feeding activity, (Maciolek and Needham, 1951).

A study made in the winter of 1956 on the same stream showed that sixty percent of all of the items found in the stomachs were indigestible debris. There was an average of eleven food items per fish, of which mayflies were the most abundant. The mayflies made up 42.8% of the total diet while the true flies and caddis flies constituted 33.5% and 16.8% respectively. The trout showed no lack of desire to feed in the cold weather but, rather, there was a lack of food for them to eat, (Reimers, 1957).

The rainbows sampled in the summer in Waddell Creek also ate more mayflies than any of the other insects. (Table 6.) Others eaten in order of their importance were true flies, caddis flies, beetles, and stoneflies, (Needham, 1940).

Table 6. The Foods Consumed by 80 Rainbow Trout Caught during May, June, and July in Waddell Creek, California, (Needham, 1940).

Food Organisms	Percent of Total Number
Mayflies	37.1%
True flies	17.8%
Caddis flies	18.7%
Beetles	7.9%
Ants, bees, and wasps	6.6%
Stoneflies	3.3%
All others	8.6%

Ten rainbows were taken from the Merced River (in the Yosemite Valley of California), in which leafhoppers were the most important food item. This sample was taken in October when the leafhoppers were abundant on the trees near the river. Beetles, both adults and larvae, were the next most abundant insects found in the ten stomachs, (Needham, 1935). (Table 7.)

Table 7. The Food Organisms Found in 10 Rainbow Trout Taken from the Merced River, Yosemite Valley, California in October, (Needham, 1935).

Food Organisms	Percent of Total Number
Leafhoppers	35.5%
Aquatic beetles (Coleoptera)	35.3%
True flies (Diptera)	13. %
Caddis flies (Trichoptera)	7.3%
Mayflies (Ephemeroptera)	2.7%
Stoneflies (Plecoptera)	2.5%
Miscellaneous	3.7%

Scuds (Gammarus) were the favorite food of the rainbow in a stream in West Virginia. Mayfly nymphs were also found in many stomachs of the sampled rainbow, (Surber, 1936). (Table 8.)

Table 8. The Foods of 131 Rainbows Taken in August from a West Virginia Stream, (Surber, 1936).

Organisms	Number of fish in which these were found
Scuds (Gammarus)	98
Mayfly nymphs (Baetis)	59
June beetles (Scarabidae)	56
Midge fly larva (Tendipedidae)	48
Caddis fly pupae (Glossosoma)	46
Ants (Formicidae)	46
Midge fly pupae (Tendipedidae)	41
Crayfish (Cambarus)	35
Grasshoppers (Acrididae)	31
Wasps (Hymenoptera)	30
Algae	28
Ground beetles (Carabidae)	25
Water boatmen (Corixidae)	24
Snails (Mullusca)	23
Caddis fly larva (Glossosoma)	19

Three orders of insects seem to be the staple food items for the rainbows during the winter, spring, and early summer. These are mayflies, true flies, and caddis flies, all of which have aquatic swelling immature stages. They are eaten while on the stream bottom or while drifting, if they have been dislodged and carried down stream. In the summer and fall the numbers of terrestrial insects increased in the diets of the rainbow. Leafhoppers, June beetles, ants, grasshoppers, and wasps are the most important terrestrial insects that the rainbows ate as the insects fell into the water. Aquatic beetles and scuds, and other fresh water crustaceans were also important in the diet of the rainbows during summer. Rainbows' diet generally is determined by the number and kind of food organisms present in the streams.

The German Brown Trout, Salmo trutta, eat generally the same organisms as the rainbows, although in different proportions.

The 1951 study on Convict Creek showed caddis fly larvae are the favorite food of the browns. The true flies were the second most important food item, with aquatic earthworms, beetles, mayflies, and stoneflies also important food items, (Maciolek and Needham, 1951). (Table 9.)

Table 9. The Organisms Found in the Stomach of 40 Brown Trout Taken from Convict Creek during the Winter of 1951, (Maciolek and Needham, 1951).

Food	Percent of Total Number
Caddis flies	37.2%
True flies	31.6%
Mayflies	11.6%
Beetles	7.4%
Aquatic earthworms	4.7%
Stoneflies	2.8%
Miscellaneous	4.7%

Mayflies were by far the most important brown trout food in Waddell Creek. The Mayflies were 79.3 percent of the total food of the browns taken during that study. Caddis flies, true flies, and aquatic earthworms made up 9.5 percent, 2.5 percent, and 2.1 percent respectively, (Needham, 1940).

Snails and small clams (Mollusca) were the most important food items of the browns in Hot Creek, Mono County, California. The other items of importance were fresh water shrimp (Decapoda), caddis flies and damsel flies (Odonata), (Needham, 1935). (Table 10.)

Table 10. The Foods Consumed by Eight German Brown Trout from Hot Creek, Mono County, California, (Needham, 1935).

Food	Percent of Total Foods
Snails and small clams (Mollusca)	55.6%
Fresh water shrimp (Decapoda)	33.3%
Caddis flies (Trichoptera)	7.9%
Damsel flies (Odonata)	2.5%
Miscellaneous	.7%

<u>Mountain White Fish</u>

The Mountain White Fish is a gamefish native to the intermountain area of several western states, including western Colorado. The whitefish is not closely related to trout, but is has similar food and habitat requirements. A thorough study of the food habits of the whitefish were made on samples taken from the Yellowstone and Gallatin Rivers in Montana. Both adults and young fish were collected and their stomach contents analyzed. Midge larvae were found to be most important food items of the young whitefish, (Laakso, 1950). (Table 11.)

Table 11. Table of Stomach Contents of 35 Fingerling Whitefish Taken from the Yellowstone River in June and July, (Laakso, 1950).

Food organism	Average number of items per fish June 22	July 21
True flies (Diptera)		
Black fly larvae (Simuliidae)	0	1.0
Midges (Tendipedidae)		
Larvae	32.2	25.8
Pupae	3.0	8.3
Adults	2.7	1.0
Caddis flies (Trichoptera)		
Psychomyiidae larvae	1.5	.0
Hydropsychidae larvae	1.0	1.0
Mayfly nymphs & adults (Ephemeroptera)	2.0	1.0
Stonefly nymphs (Plecoptera)	0	1.0

The food of the adult whitefish, although composed almost entirely of immature insects, was quite different from that consumed by fingerlings. Also the average volume of food per stomach was more than twice as great in the fish over sixteen inches long than in the group less than fourteen inches long. May flies, stoneflies, caddis flies, and true flies were the most important food items of the whitefish in the Yellowstone River. Fish eggs, snails, water mites, and ants were found only as traces in the samples. The family Rhyacophilidae of the caddis flies was the most important food found in the samples taken in the spring. (Table 12) The most important food in the summer was the Baetidae family of the mayflies, while the Lepidostomatidae family of the caddis flies and the Tendipedidae family of the true flies were the most important families of food items in the fall and winter respectively, (Laakso, 1950).

Table 12.

The Important Food Organisms Found in the Stomachs of Adult Whitefish During the Year Taken from the Yellowstone River, Montana, (Laakso, 1950).

	Average number of organisms per fish			
Food	Spring	Summer	Fall	Winter
Mayflies				
Heptageniidae		13.2	3.5	3.6
Baetidae	4.0	52.8	5.7	7.3
Caddis flies				
Lepidostomatidae		trace	154.8	24.1
Hydropsychidae	1.0		6.6	6.1
Leptoceridae	1.0	trace	trace	
Bachycentridae	1.0	8.3	11.4	trace
Rhyacophilidae	81.5	trace	trace	29.4
True flies				
Simuliidae		5.3	17.2	67.0
Tendipedidae	3.0	13.9	36.5	195.0
Stoneflies				
Pteronarcidae	5.0	trace	3.0	trace
Perlodidae	4.0	trace	14.6	13.4
Water mites (Hydracarina)		10.9		
Fish Eggs			13.3	trace

The whitefish of the Gallatin River ate nearly the same insects as those in the Yellowstone River. The most important food item in both summer and fall was the Tendipedidae family, instead of being the most important food in the winter as it was in the Yellowstone River, (Table 13.) The Hydroptilidae family were the insects most often eaten during the spring in the Gallatin River, and the Hydropsychilidae family was the preferred food item in the winter, (Laakso, 1950).

This difference in food habits can probably be attributed to the availability of the organisms, rather than different tastes of the fish.

Table 13. The Important Food Organisms Found in the Stomachs of Adult Whitefish During the Year Taken from the Gallatin River, Montana, (Laakso, 1950).

	Average number of organisms per fish			
Food	Spring	Summer	Fall	Winter
Mayflies				
Heptangeniidae . . .	trace	trace	trace	trace
Baetidae	11.6	3.5	trace	trace
Caddis flies				
Lepidostomatidae . .	46.1	trace	40.5	27.3
Hydropsychidae . . .	717	4.3	8.9	57.0
Hydroptilidae . . .	64.1	trace	4.6	trace
Brachycentridae . .	12.9	trace	9.4	27.5
Rhyacophilidae . . .	trace	trace	8.1	trace
True flies				
Tendipedidae	53.2	16.8	53.1	50.1
Stone flies				
Pteronarcidae. . . .	6.0	2.0	trace	13.7
Perlodidae	5.7	trace	21.0	9.9

Evaluation

It is noted that rainbows prefered true flies, caddis flies, mayflies, beetles, and scuds. Brown trout prefered caddis flies, true flies, snails and clams, and shrimp. The whitefish ate more mayflies, true flies, and caddis flies than any other organisms in the stream. Competition is therefore very likely between these three species.

The Whitefish and the brown trout tend to feed on the bottom more than the rainbow. However, as pointed out earlier, when food is scarce trout will eat anything they can get.

The proportions of caddis fly larvae, stonefly nymphs, and whitefish eggs were approximately the same for the browns and whitefish in the Gallatin River. A comparison of stomach contents taken from December to February showed that the whitefish contained five times as much food per stomach as the trout. This would indicate that whitefish have more foraging ability than trout. Both species eat surface organisms as a supplement to aquatic organisms during the summer, (Laakso, 1950)

POPULATION

Trout

The rainbow trout do not naturally reproduce in the Cache la Poudre River and are stocked annually by the Colorado Game and Fish Department.

The Game and Fish Department starts their stocking program near the first of April. They plant a five-gallon bucket of legal sixed rainbow every one-tenth mile of the river that is in the national forest lands. They do no stocking in areas privately owned that are not open to public fishing. The legal-sized rainbow average eight to eleven inches long and there are approximately one hundred trout per five gallon can. The trout were planted approximately every two weeks, (Till, 1957). At this rate of stocking it can be assumed that there would be 300 rainbows every 520 feet by the start of fishing season, which is near the end of May.

The Game and Fish Department continue this general stocking program throughout the summer until Labor Day, after which there is no stocking. There is no information on the rainbow population during the fishing season, but it is assumed to gradually decrease from opening day of the fishing season to the end of the fishing season, October 31. It is believed that very few rainbows survive the fishing season and live through the winter. The data from the population studies of the Fish Management Classes revealed that only eleven rainbows remained in a two hundred foot section of the Cache la Poudre River on October 6, 1956, (Hagen, 1956).

A direct-current shocker was used to capture the fish for this study. The estimated efficiency of this operation was that seventy-five percent of the existing fish were caught. Therefore, the population of rainbows in the two hundred feet in October was about fifteen, as contrasted to approximately 115 rainbows at the start of the season and the additional fish added during the season.

The same section of river when studies in April of 1956 produced five rainbows or about half the number found in the fall, (Hagen, 1956). If similar results are found this spring, it would indicate that, in this particular situation, the fisherman are the greatest enemy of the rainbow and not the severe winter conditions or food competition.

The brown trout do reproduce in the Cache la Poudre River and are not stocked by the Game and Fish Department. The Fish Management Classes' studies last spring found that there were an average of thirty-three browns per two hundred feet of the river. The one section with records available on this fall's study yielded fifty-seven brown trout last spring, and it yielded ninety legal sized brown trout this fall, (Hagen, 1956). One of these things may have caused this apparent increase. One is that the trout may have moved into that area in the fall. Another is a greater efficiency in the crew collecting them in the fall; while the third possibility is that the very small brown trout were not recorded in the spring, and they grew enough during the summer to be counted in the fall study.

Combining the two calculated populations gives a total population of approximately 148 trout per two hundred feet of river during the summer and about 40 trout in the same length section in the winter.

The trout that were caught in the spring study were all tagged with metal jaw tags. These tags have numbers on them which were recorded along with the length and weight of the fish before it was released back into the stream. During the season eight of these tags were returned by the fisherman that caught the fish, and five of the tagged fish were recaptured in the shocking operation this fall.

The thirteen brown trout were all measured, and the growth was calculated. The average growth per fish during the summer was .89 inches per one hundred days with the range in growth from zero to 4.07 inches per one hundred day, (Hagen, 1956). This rate of growth can be considered fairly good.

Mountain Whitefish

The Mountain Whitefish were introduced into the Cache la Poudre River in the spring of 1956. The original plant of 475 adult white fish was made just downstream from the Poudre Ponds Rearing Station. (Appendix B)

A total of 750 whitefish were planted in three placed this fall. These places were upstream from the rearing station, at the junction of Roaring Creek and the Cache la Poudre River, and near the Big South Fork Camp Grounds. Presently the total number of adult whitefish that have been stocked in the Cache la Poudre River is 1225. The Game and Fish Department plan to stock approximately this same number in 1957 and 1958, which, if they all lived, would give a total population of 3675 white fish in the river, (Till, 1957).

The whitefish are adapted to spawning and reproducing in the Cache la Poudre River. They spawn in the fall when the river is clear and the water level is not fluctuating; also, they naturally spwn in gravel and rubble riffle areas which are numerous in the river. Female whitefish from ten to seventeen inches long will produce 1420 to 7270 eggs respectively, (Brown, 1952). Thus the whitefish should reproduce and increase its numbers until there is a large established population. This will mean that if the river can support only a given number of fish, some of these fish will now be whitefish instead of trout. This is particularly true in the winter, when both the whitefish and brown trout will inhabit the area. The number of rainbows, however, will still be determined by the state's stocking program, but the rainbows may experience increased food competition in the summer.

CONCLUSIONS

The Chahe la Poudre River contains nearly the same types and numbers of food organisms as most other trout streams. These organisms are the types that whitefish and trout readily eat, and the Cache la Poudre is suitable to maintain a population of whitefish. The Rainbow Trout, German Brown Trout, and the Mountain Whitefish all prefer the same three orders of insects as food. Thus there is food competition between these fish when they live in the same area.

At the present time there are comparatively few whitefish in the Cache la Poudre River, therefore there is probably no serious food competition. However, if the whitefish population increases, they will compete seriously for food with the trout. Another possibility is that the whitefish will not be able to increase its numbers because of the competition from the trout. This condition would result in failure of establishing whitefish in the Cache la Poudre River by the Game and Fish Department.

I recommend that the problem be studied more thoroughly in the next year or two by taking samples of the fish from the river. Their stomach contents should be examined as well as the population trends of the fish.

APPENDIX

APPENDIX A

Figure 1. Illustrations of Typical Representatives of the following: (
(Pennak, 1953).

A. Aquatic Earthworms, adult, (Dorsal view)

B. Beetles, adult, (Dorsal view)

C. True Flies, larva, (Lateral view)

D. Mayflies, nymph, (Dorsal view)

E. Stoneflies, nymph, (Dorsal view)

F. Caddis Flies, larva, (Dorsal view)

APPENDIX B

Map of the upper portion of the Cache la Poudre River

Supplimentary Legend

A. Location of the population study sections:

Section 11, Township 8 North, Range 75 West.

Section 32, Township 9 North, Range 74 West.

B. Location of bottom sample:

Section 35, Township 9 North, Range 75 West.

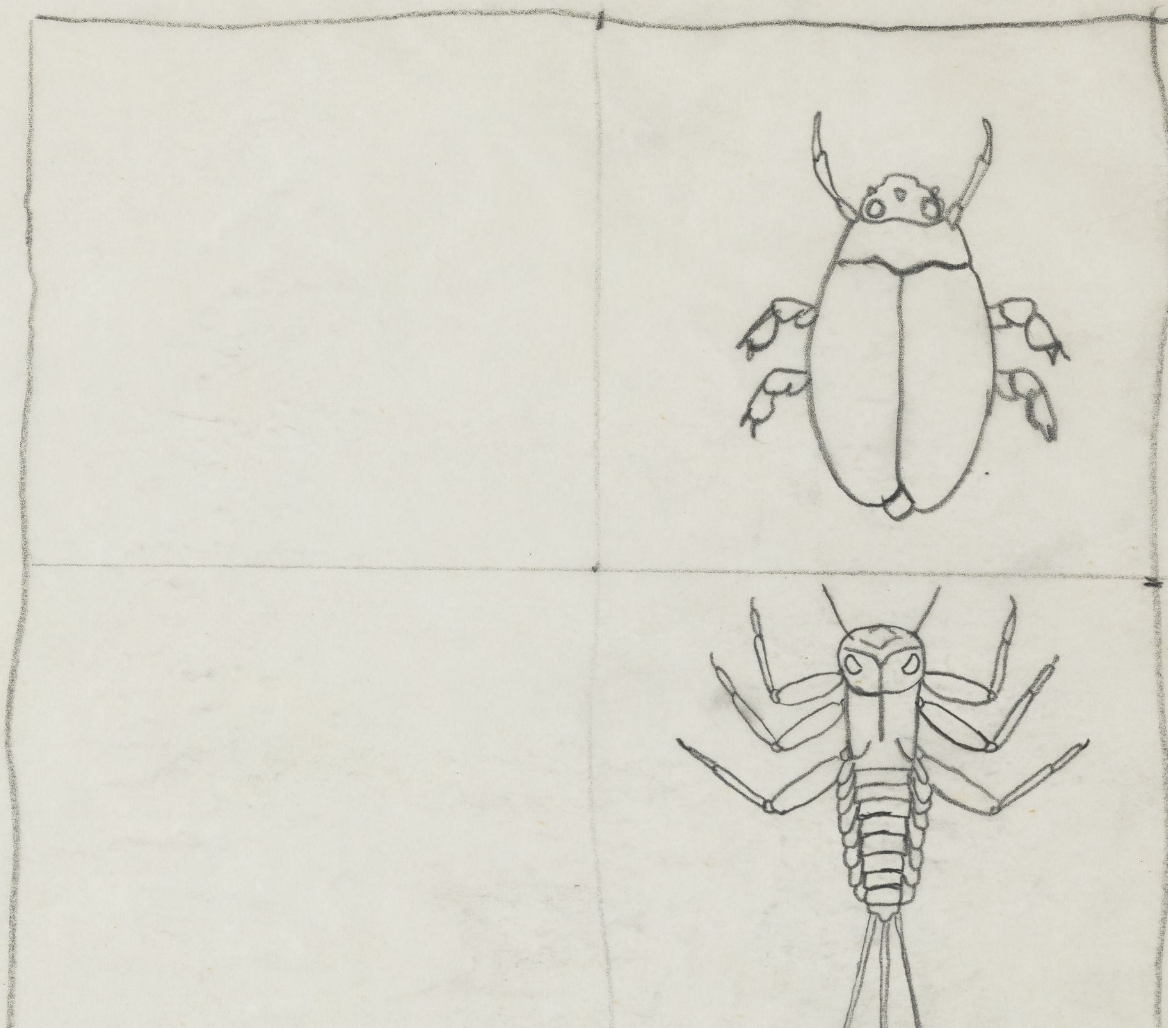
C. Location of the whitefish plantings:

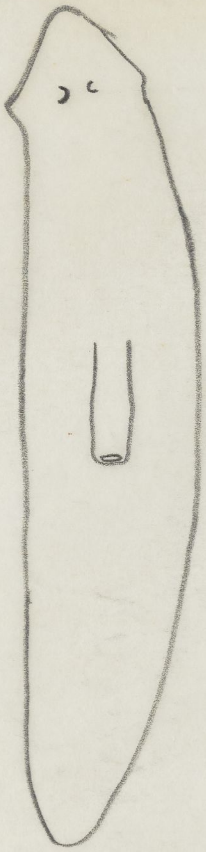
Section 32, Township 9 North, Range 75 West.

Section 31, Township 9 North, Range 75 West.

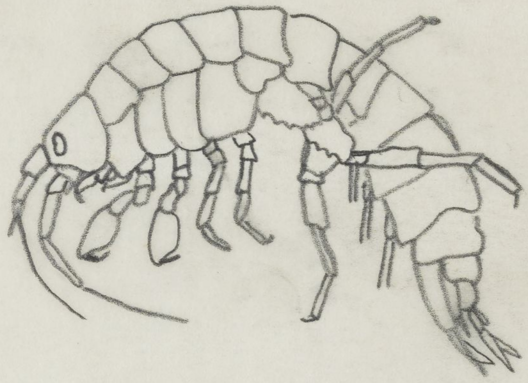
Section 30, Township 9 North, Range 74 West.

Section 3, Township 8 North, Range 72 West. (Not Shown)

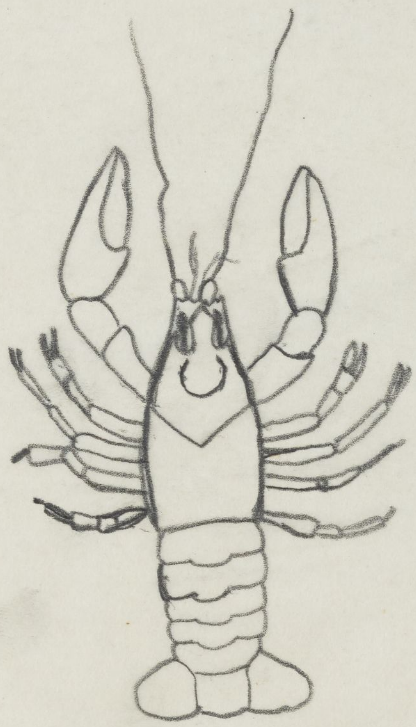




Euplanaria X 15.



Gammarus fasciatus X 5



Procambarus X 0.7

APPENDIX A

Figure 2. Illustrations of Typical Representative of the following: (Pennak, 1953).

A. Flatworms, adult, (Ventral view)

B. Scuds, adult, (Lateral view)

C. Crayfish, adult, (Dorsal view)

SPECIATION OF SEVERAL

SALMONIDAE

by

W. H. Dieffenbach

In partial fulfillment of requirements of Z - 180

EVOLUTION

March 2, 1964

SPECIATION OF SEVERAL

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INTRODUCTION

The problem of multiplication of species lies in explaining how a natural population is divided into several reproductively isolated populations. Mayr (1963), lists nine modes of multiplication of species (Table 1). Geographic isolation, resulting in speciation is the most important and frequent mode by which incipient species are formed. Although few incipient species move up to the rank of full species, due to extinction, we still recieve an adequate number of new species to fill the available niches.

The most important isolating mechanism achieved during speciation are the ethological barriers. They may vary from obvious behavorial patterns, such as fall spawning vs. spring spawning to very complex and subtle actions each requiring a correct reaction before mating can take place.

The speciation of the Family Salmonidae has progressed most rapidly since the Pleistocene. In Europe, Asia, and North America glaciation lead to isolation of various parental Salmonidae forms and differentiation followed. Incomplete speciation of the members of the Salmonidae is exhibited by the frequency of successful hybridization

INTRODUCTION

The p

within the genera *Coregonus*, *Salvelinus*, and *Salmo.*

Table 1. Potential modes of Multiplication of Species

Multiplication of species

- A. Instantaneous speciation
  - 1. Genetical
    - a. Single mutation in asexual species
    - b. Macrogenesis
  - 2. Cytological, partially or wholly sexual species
    - a. Chromosomal mutation
    - b. Autopolyploidy
    - c. Amphiploidy
- B. Gradual speciation
  - 1. Sympatric speciation
  - 2. Semigeographic speciation
  - 3. Geographic speciation
    - a. Isolation of a colony
    - b. Extinction of intermediate links in a chain of populations which the terminal ones had already acquired reproductive isolation

SPECIATION OF THE GENUS COREGONUS

The genus Coregonus is a group of many plastic species which evolved in the recent geological periods of the Pleistocene. The whitefishes evolved allopatrically and now live as sympatric species without sterility barriers.

The genus originated in Asia, during the early Pleistocene. The whitefishes spread across the Bering Sea via the Beringian Land Bridge (Map 1) into North America and westward into Scandinavia. Speciation into the existing Coregonid species occurred in the late Pleistocene. In eastern Siberia and Arctic Alaska (plus the Yukon Valley), the ice sheets were insiginificant and the whitefishes of these areas have resided side by side for a long period of time Walters (1955). Thus the whitefishes of this area have had a long period of time to become stabilized while the whitefishes of Canada and Scandinavia were moved about, isolated as allopatric species, and once again tossed together after the last glaciation into what is now a large group of incompletely evolved sympatric species.

As expressed by Wynne-Edwards (1952), Walters (1955), Vladykov (1954), and Svardson (1957), the best and possibly only reliable characteristic for separating the species of the genus Coregonus is the number of gill rakers. This

INTRODUCTION

characteristic was tested by Svardson (1957) when he transplanted species of Coregonus into different habitats in attempts to induce a change in the gill raker number. In 12 cases of transplantation the mean gill raker count remained unchanged or diverged from that of the parental stock on an average of less than two.

In North America there are 14 species of Coregonus Bailey (1960). For this paper two of the best known whitefishes, the world-wide distributed broad whitefish, Coregonus nasus (Pallas), and the North American humpback whitefish, C. clupeaformis (Mitchell) will be discussed. Synonyms for the humpback whitefish, C. clupeaformis, include C. kennicotti (Gilbert), C. richardsoni (Gunther), and C. nelsoni (Bean).

The broad whitefish is distributed across the Arctic and subarctic from the Mackenzie River system in northwest Canada, across Alaska, into Siberia and westward to Scandinavia.

There is disagreement amoung the various authors about the spawning period of the broad whitefish. Berg (1948), and Svardson (1957) state that the broad whitefish spawns in the fall in Siberia and Europe, while Walters (1955) says the spawning season is in the early summer. It is possible that all reports are accurate inthe description of spawning time. Under varying evolutionary stress on different continents the species could develop different spawning periods. The question then is, are these populations of the same species if they have different spawning times? Using the rainbow trout, Salmo gairdneri (Richardson), as an example, it is evident morphologically that the rainbow trout is a definite species but it has populations that spawn in spring, summer and fall. Spawning time is not as significant as many other taxonomical characters in the determining of valid speciation.

The taxonomic variation between the broad whitefish and humpback whitefish is summerized by Lindsey (1962), in a study of the whitefishes of the Yukon and Mackenzie River drainages. The species occupy the same waters without apparent interbreeding and can be distinguished consistantly by the use of two taxonomical characters (gill raker length and interorbital width). If these characters are genetical then it can be accepted that the two species are not interbreeding and hence are distinct species. Although these characters varied within the species at different geographic areas, the variation between species was consistant. The humpback whitefish consistantly maintained a higher orbital width and gill raker length (at all stages of life) than did the broad whitefish. Admittedly the area chosen by Lindsey is one of the few places in the world where the whitefish populations are stable. The

...ering Strait land bridge. Continental outlines reflect sea level 120 feet lower than at the pres-... ...ased on soundings in United States Navy Hydrographic Office Map 2560 (June, 1948, ed.). ...and rivers not shown. Present-day land features are solid black; land now submerged is white; ...shaded. 1. Siberia. 2. Alaska. 3. Land bridge. 4. Chukchi Embayment. 5. Arctic Ocean. 6. Ber-... sea. 7. St. Matthew Island. 8. St. Lawrence Island.

stability of these populations is due to the lack of glacial interference and meddling during the late Pleistocene, also mentioned earlier.

Svardson (1957), discusses the plasticity of the genus *Coregonus* in Scandinavia. He states that spontaneous hybrid...

are found in nature. These hybrids can be mistaken for a third species of whitefish in lakes and streams which are known to have two species. No major morphological differences exist but the species may be separated by their minor differences including gill raker counts and ecological habitat.

The breakdown of species in the whitefish group through hybridization, plus the lack of taxonomical differences in those areas of recent glaciation demonstrates the incompleteness of the speciation of thegenus Coregonus. The incomplete speciation of the whitefish has caused man, with his desire to make everything fit neatly into a scheme, much confusion and resulted in a great number of conflicting versions of the story of speciation of the Coregonus.

SPECIATION OF THE GENUS SALMO
IN NORTH AMERICA

The parental members of the genus Salmo made their way across from Siberia to North America via the Beringian Land Bridge (Map 1), during the period the Laurentian Ice Sheet covered much of the northeastern part of the continent. The land bridge theory is strongly supported by the presence of saltwater intolerant species common to Asia and North America on St. Lawrence Island in the Bering Sea. Lanham (1962), points out the existance of a trout similar to the North American cutthroat trouts on Kanchatka, a Siberian peninsula, as evidence that the genus Salmo originated in Asia as a cutthroat-like trout.

The parent type Salmo moved southward down the Pacific coast and spread inland through the major river systems, including the Columbia and Colorado Rivers. Migration up either the Columbia or Colorado River would give the parent Salmo access to the pluvial lakes of the Great Basin more than 50,000 years ago. It is during the pluvial lake period that speciation of the members of the genus Salmo is believed to have began.

In the pluvial lakes fluctuating water levels, daming and flooding, headwater capture and other factors were constantly at work. Any of these factors could have isolated a part of the parent Salmo in an area where isolated from the main population, an incipient species could attempt to evolve into a full species.

The rainbow trout, Salmo gairdneri (Richardson), Gila trout, S. gilae (Miller), and possibly the recently noted Arizona cutthroat trout (no scientific name), all began to diverge during the period of pluviation.

The rainbow trout followed the receeding ice up the west coast and is now found as far north as Prince William Sound, Alaska. The Gila trout and the Arizona cutthroat trout have remained within a few hundred miles of their suspected place of origin. The Gila trout in the Gila River system of New Mexico and the Arizona cutthroat trout in the White River of Arizona, both rivers are part of the Colorado River system.

Cytological studies by Simon and Dollar (1963), indicate the cutthroat trout to be a valid species since it is distinct with respect to chromosome number and morphology. The diploid number of the rainbow trout is 60, consisting of 16 acrocentric and 44 metacentric chromosomes. Twenty-two acrocentric and 42 metacentric chromosomes make up the diploid compliment of 64 in the cutthroat trout. Arm numbers are 104 and 106 respectively. (Fig. 1 & 2).

The following scheme (Fig. 3) is presented by Simon and Dollar to explain the change in the chromosomal makeup

Fig 1

Fig 2

Fig 3

of the cuttroat and rainbow trouts:

> The transition is presumed to have taken place by two alterations of the haploid chromosome set; the first a reduction of chromosome number by centric fusion of two acrocentric chromosomes, and the second a reduction in arm number by one centromere shift. The loss of one arm from a metacentric chromosome in the haploid set could also account for the observed differences in arm number, but this seems less likely, as large deficiencies are usually lethal. Support for the choice of a centromere shift is also suggested by chromosome measurements which show a "new" and larger acrocentric pair in the rainbow complex.

In considering the possibility that the rainbow trout is more primitive we must find a means for a increase in chromosome number from 60 to 64. Chromosome number could be increased by misdivision, but then we must have an increase of 4 chromosomes in the diploid number, either an increase of 4 or 8 ~~chromo~~depending upon the morphology of the chromosomes duplicated, an increase of from zero to 4 metacentric chromosomes, or an increase of from 0 to 4 acrocentric chromosomes. None of these conditions are met.

Chromosome number comparison of the different species in the genus *Salmo*, show the rainbow trout, and the Atlantic salmon, *S. salar* (Linnaeus), with 60 diploid chromosomes, the cutthroat trout, *S. clarki* (Richardson), with 64, and the brown trout, *S. trutta* (Linnaeus), with 80 diploid chromosomes.

Although chromosome number of the brown trout does not seem to fit in with the rest of the genus *Salmo*, it must be taken into consideration that the Atlantic salmon, rainbow trout and cutthroat trout are all natives to the North American continent while the brown trout is only native to Europe. The brown trout is the only member of the freshwater Salmos which spawns in the fall. The difference in chromosome number, native range and spawning time strongly sugguest that the brown trout of Europe was subjected to very different evolutionary stress, including lack of competition from other members of the genus *Salmo*.

To extend the idea that like chromosome number alone means necessity of close relationship, Wright (1955), leads to the classification of the brown trout in the genus *Salvelinus*. The commonly known and well studied members of the genus Salvelinus, brook trout, *Salvelinus fontinalis* (Mitchill), lake trout, *Salvelinus namaycush* (Walbaum), and the Arctic char, *Salvelinus alpinus* (Linneaus), have 84, 84, and 80 diploid chromosomes respectively. The brown trout with 80 chromosomes fits very well into the group until taxonomically we study the expression of the chromosomes. The brown trout has a toothless flat vomer, exhibits dark spots on a light background, and has fewer than 200 scales in its lateral line, all characters of the genus *Salmo* and opposite of the genus *Salvelinus*.

Mayr (1963) states that well defined and reproductively isolated species may completely agree structurally in their chromosomes and differ only in their gene contents. The old theory of instantaneous speciation through chromosomal mutation can not be substantiated.

Speciation by means of genic or chromosomal alteration is not possible without the species or population passing through a stage of heterozygosity. It would be during this period of heterozygosity that selection against the new genic makeup would occur. In large interbreeding species such as the fishes, heterozygosity would be selected against unless a small portion of the entire population was isolated. The period of time required for speciation will vary with the species and combination of processes of speciation involved. Many of the species of the family Salmonidae are sibling species which ecological isolation is responsible for the present evolutionary situation, Svardson (1961).

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A MORPHOLOGICALLY BASED STUDY OF THE <u>GILA</u> COMPLEX OF THE UPPER COLORADO RIVER DRAINAGE

FOR

Dr. Robert Behnke
FW 130
Systematic Ichthyology

by

Paul Holden

INTRODUCTION:

The cyprinid genus Gila is presently divided into four subgenera; Gila, Siphateles, Snyderichthyes and Richardsonius which includes the former genus Clinostomus (Uyeno, 1961). This study is concerned with the systematics of the subgenus Gila of the Colorado River basin with emphasis on the upper basin forms presently recognized as Gila r. robusta, G. robusta elegans and G. cypha.

Baird and Girard (1853), working on fish collected by the Pacific Railroad Surveys, described the genus Gila and several species from the Colorado River basin, included were G. robusta and G. elegans. Cope and Yarrow (1875) named several Gila based on collections of the Wheeler Survey in southwestern United States, included was G. seminuda from the Virgin River, Utah.

By 1896, 14 species and 5 genera had been used for the Colorado River basin Gila. The revision of Jordan and Evermann (1896) reduced these to 2 genera (Gila and Leuciscus) and 5 species. Listed in Gila were 3 species, robusta, elegans and seminuda, with 6 synonyms. Leuciscus contained 2 species, intermedius and niger, with 3 synonyms.

Ellis (1914), with little critical examination, suggested that robusta and elegans might be considered one polymorphic species with a subspecies seminuda. Jordan, Evermann and Clark (1930) retained robusta, elegans and seminuda as full species, and the two species of Leuciscus listed by Jordan and Evermann (1896) were both included under Tigoma gibbosa (Baird and Girard).

Miller (1946) described a new species, G. cypha, from the Grand Canyon of Arizona and suggested that robusta and elegans were only subspecies. Tanner (1950) named a new species, G. jordani from the

White River of Nevada, it is presently considered a subspecies of *G. robusta*.

Bailey, et. al. (1960) mentioned only *G. robusta* and *G. cypha* as full species, this was probably based on Miller's opinion. Uyeno (1961) established some of the relationships between fishes allied to the genus *Gila* in an osteological study. His classification is the one presently recognized.

The present classification of *G. r. robusta* and *G. robusta elegans* does not fit the idea of subspecies being geographical units of species, for these two forms are sympatric. It suggests rather that these forms are ecosubspecies which show rapid parallel evolution in disjunct yet similar habitats, and therefore precludes the idea of a single evolutionary line for each form.

ANNOTATED SYNONYMY OF THE SUBGENUS GILA OF THE COLORADO RIVER BASIN:

Gila robusta robusta - Widely distributed in the Colorado River basin.

Gila robusta Baird and Girard, Proc. Acad. Nat. Sci. Phil., VI 1853, 368, Zuni River.

Gila gracilis Baird and Girard, Proc. Acad. Nat. Sci. Phil., VI 1853, 369, Zuni River. Synonymized by Jordan and Evermann (1896). Gunther, Catalog Fishes, VII, 1868, 241; placed Gila in genus Leuciscus and substituted L. zunnensis for G. gracilis because gracilus was occupied in Leuciscus.

Gila grahami Baird and Girard, Proc. Acad. Nat. Sci. Phil., VI 1853, 389, Rio San Pedro, tributary to Rio Gila, Arizona. Syn. by Jor. & Ever. (1896).

Ptychocheilus vorax Girard, Proc. Acad. Nat. Sci. Phil., VIII, 1856, 209, Locality unknown. Syn. by Jordan and Gilbert (1883).

Gila affinis Abbot, Proc. Acad. Nat. Sci. Phil., X, 1860. 474, type erroneously ascribed to Kansas River. Syn. Jor. & Ever. (1896).

Gila nacrea Cope, Hayden's Geol. Surv., Wyoming for 1870, 1872, 441, tributary of Green River, Fort Bridger, Wyoming. Syn. Jor. & Gil. (1883).

Gila robusta seminuda - Virgin River of Utah, Nevada and Arizona.

Gila seminuda Cope and Yarrow, Zool. Wheeler's Expl. W. 100th Mer., V, 1875, 666, Rio Virgin, Utah. Tentatively retained here as a distinct subspecies pending further study.

Gila robusta jordani Remnant White River of Nevada.

Gila jordani Tanner, Great Basin Nat., X, 1950, 31-36, White River, Lincoln Co., Nevada. Tentatively retained here as in La Rivers (1963) as a subspecies. It is probably closely related to G. r. robusta but may be closer to G. r. intermedia of the Gila River basin of Arizona. No work has been done on this form since it was described by Tanner.

Gila robusta intermedia - Restricted to the Gila River division of basin in Arizona and New Mexico.

Gila gibbosa Baird and Girard. Proc. Acad. Nat. Sci. Phil., IX, 1856, 206, Rio San Pedro, Arizona. Listed as Squalius intermedius by Jor. and Gil., 1883; listed as Leuciscus

Jor. & Ever. (1896). Put in Tigoma gibbosa by Jordan, Evermann and Clark (1930).

Tigoma intermedia Girard, Proc. Acad. Nat. Sci. Phil., XIII, 1856, 206, Rio San Pedro, Arizona. Listed as Squalius intermedius by Jor. & Gil. (1883). Listed as Leuciscus intermedius by Jor. & Ever. (1896). Synonymized under Tigoma gibbosa by Jor. Ever. & Clark (1930).

- didn't name new sp. - only placed Gila gibbosa B.&G. in this genus.

Tigoma gibbosa Girard, Proc. Acad. Nat. Sci. Phil., XIII, 1856, 207, Gila River, Arizona. Synonymized under Squalius niger by Jor. & Gil. (1883). Placed under Leuciscus niger by Jor. & Ever. (1896). Used as Tigoma gibbosa by Jor.,Ever. & Clark (1930).

Gila nigra Cope, Wheeler Surv., Zool. V, 1875, 663, Ash and San Carlos creeks, Arizona. Listed as Squalius niger by Jor. & Gil. (1883). Listed as Leuciscus niger by Jor. & Ever. (1896). Synonymized under Tigoma gibbosa by Jor., Ever. & Clark (1930).

Squalius lemmoni Rosa Smith, Proc. Calif. Acad. Sci., 1884, 3, Rillito Creek, Arizona. Syn. under Leuciscus intermedius by Jor. & Ever. (1896).

An explanation of the synonymy of intermedia is in order. This form was described twice in each of the genera Gila and Tigoma before 1880. Jordan and Gilbert (1883) placed them in the genus Squalius and revised the 4 species to 2, S. niger and S. intermedius. Synonymized under niger was Gila gibbosa, Tigoma gibbosa and Gila nigra; gibbosa was preoccupied in Squalius so niger was used. Tigoma intermedia became S. intermedius.

Jordan and Evermann (1896) kept the 2 species recognized by Jordan and Gilbert (1883) but changed the genus from Squalius to Leuciscus, and synonymized under intermedius, S. lemmoni.

Jordan, Evermann and Clark (1930) combined the two Leuciscus species of Jordan and Evermann (1896) to Tigoma gibbosa. Since this time the form has been placed as a subspecies of Gila robusta under the name intermedia. Examination of the literature shows the species

Gila gibbosa Baird and Girard, Proc. Acad. Nat. Sci. Phil., VII, 1854, 28, Rio Santa Cruz, Arizona. Synonymized in Squalius niger by Jor. & Gil. (1883). Placed in Leuciscus niger by name _gibbosa_ has priority for this form in the genus _Gila_, and that the present use of _intermedia_ is in error.

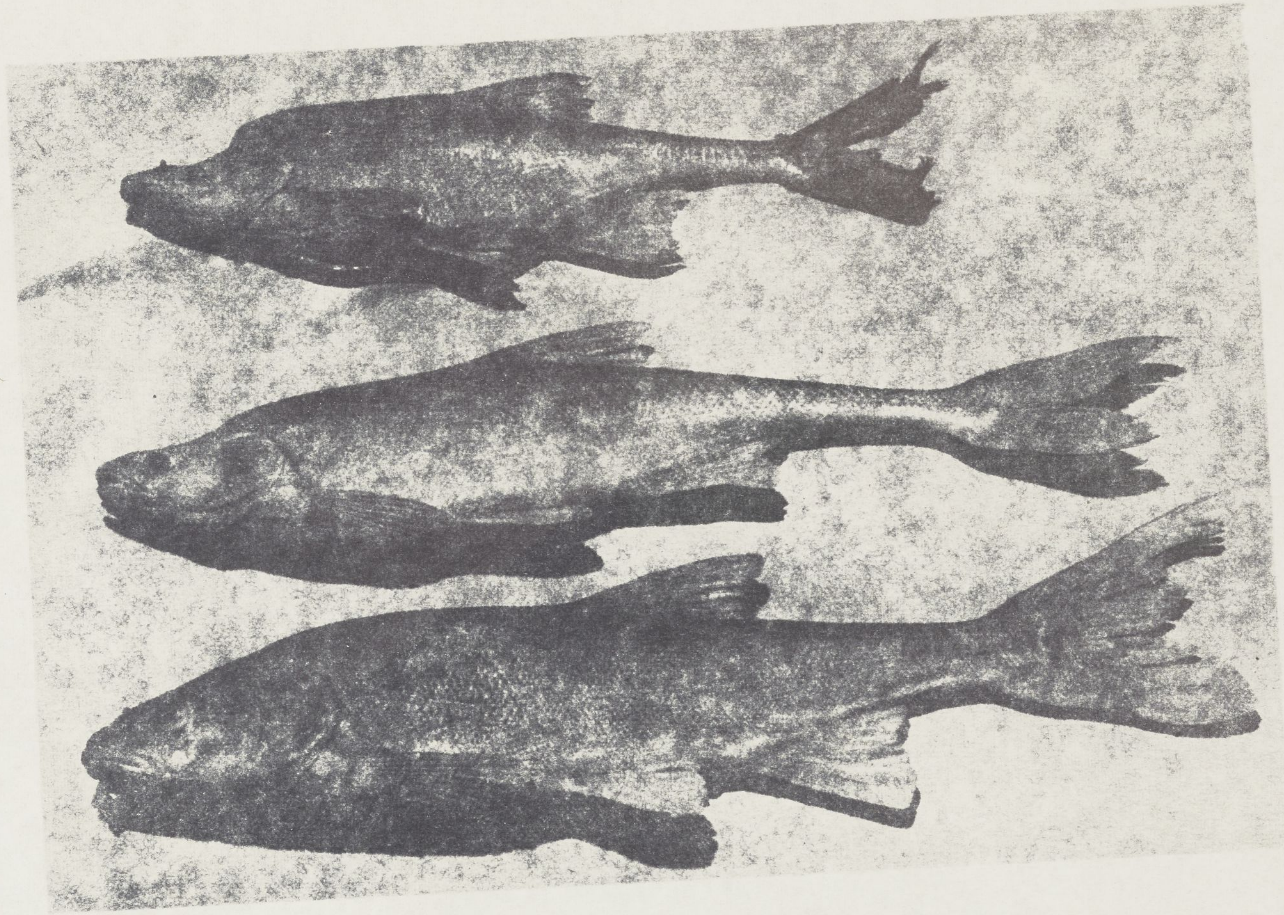
DESCRIPTION AND DISTRIBUTION OF THE FORMS:

The large amount of taxonomic confusion in these forms can be attributed to: instability of a few morphologic characters, notably squamation; and an apparent cline in morphology adapted for varying current conditions. The present ecosubspecies concept is primarily based on this adaptive morphology. The most generalized form, _robusta_, is hypothesized to be a slow to moderately swift current form; _elegans_ is the intermediate form with characters adapted for life in large swift rivers; _cypha_ shows morphology highly adapted for life at or near the bottom of torrential, turbid channels.

As the most generalized, _robusta_ is usually fully scaled, more robust than the other two, and a nuchal hump is absent or greatly reduced. The very streamlined _elegans_ has a pencil-like caudal peduncle, has reduced squamation on dorsal, ventral and peduncle regions and a well developed nuchal hump. The extreme form, _cypha_, is characterized by a long, fleshy snout, a very abrupt nuchal hump, thin caudal peduncle and few scales. (Refer to Figure 1)

All three are endemic to the Colorado River basin; _robusta_ and _elegans_ were once common throughout the basin, but now are scarce in the Gila River division and the large, lower basin reservoirs. Distribution and abundance of _cypha_ has not been investigated in great depth. The type speciman of _cypha_ was collected in the Grand Canyon of Arizona. It has been reported from the Dinosaur National Monument area of the Green River in eastern Utah, and I have several specimens from the Lake Powell area of northern Arizona which morphologically fit the description of _cypha_.

FIGURE 1

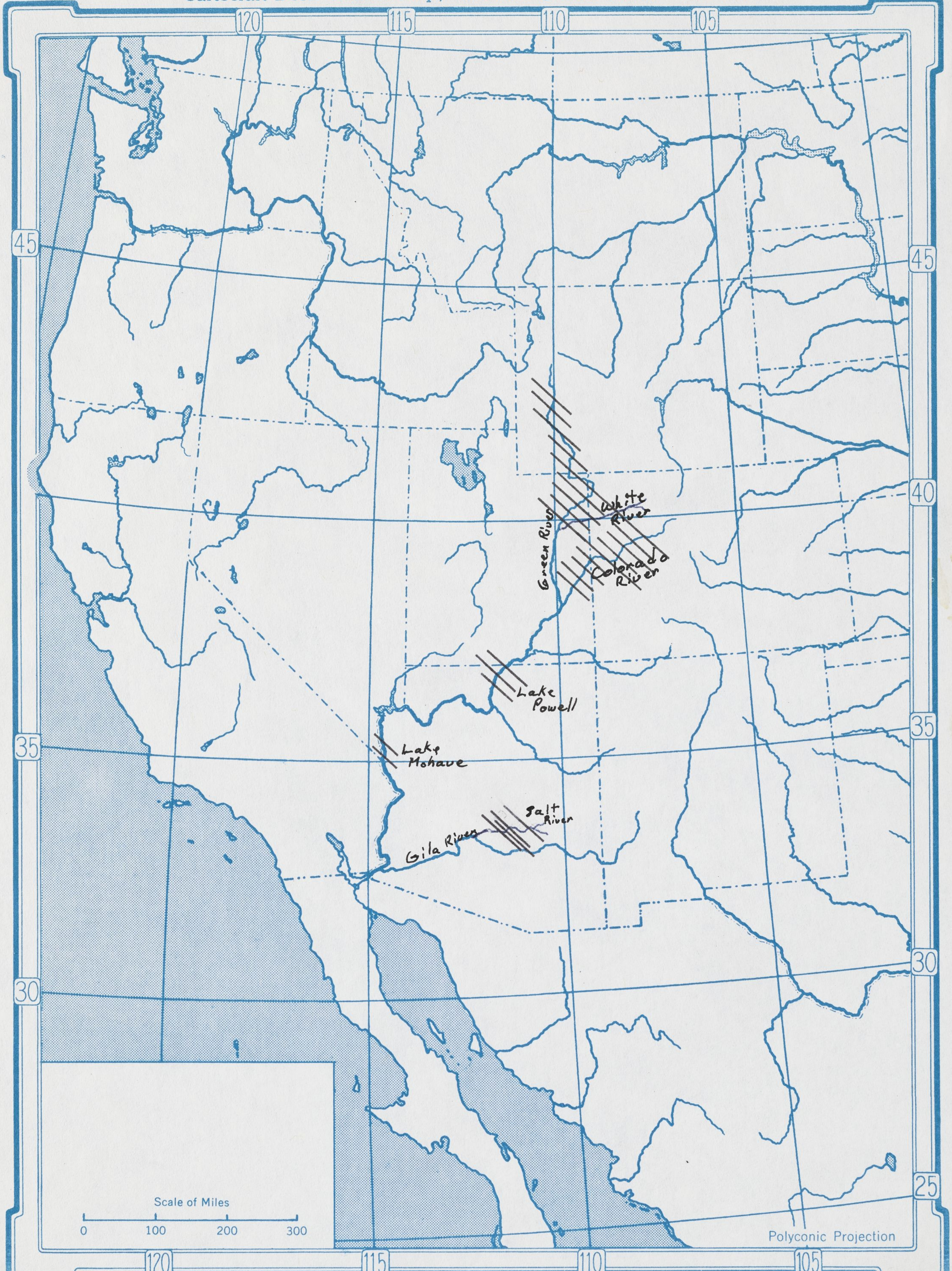


Gila cypha

Gila robusta elegans

Gila robusta robusta

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



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PROCEDURES:

To date, 212 specimens have been partially or wholly examined. They represent collections from the upper Green River, White River (Colorado), parts of the Colorado River and the Salt River of the Gila River basin of Arizona. (Refer to Map 1)

A total of 35 morphometric characters will be recorded for each fish according to Hubbs and Lagler (1958). X-rays have been taken of 103 of the specimens for vertebral and fin ray counts, the remaining 109 will be x-rayed in the near future. The vertebral count includes the urostyle and the 4 Weberian ossicles.

The taximetrics program for computers outlined by Rogers and Estabrook (1966) will be used to help in classifying the fish. Preliminary work with this program demonstrated efficacy in grouping the forms. At present only 17 specimens have been tested with this program.

PRELIMINARY FINDINGS:

The data collected to date indicates that robusta and elegans are probably two species. Table 1 is a comparison of the forms for 4 meristic characters. This data shows robusta and elegans to be very distinct throughout their range, indicating they are species rather than ecosubspecies as previously hypothesized.

Eighteen characters were used in the taximetrics program which showed strong seperation between the two forms. Several characters that have been tested for only a few (approx. 30) specimens, but seem useful for seperating robusta and elegans, are: head length/standard length, peduncle depth/ standard length, head depth/standard length, distance from caudal base to anal fin origin/ standard length.

TABLE 1

	Principle Dorsal Fin Rays					Principle Anal Fin Rays						Vertebrae (including urostyle & 4 Weberian ossicles)							Gill Rakers (combined anterior and posterior counts of first left arch)					
	8	9	10	11	$\bar{X}$	7	8	9	10	11	$\bar{X}$	45	46	47	48	49	50	$\bar{X}$	18-20	21-23	24-26	27-29	30-32	$\bar{X}$
<u>Gila</u> <u>r</u>. <u>robusta</u>																								
Green R.	1	49			9.0	1		36	13		9.2	3	12	2				46.0	2	26	16	2		23.4
Colorado R.		13			9.0			11	2		9.2	3						46.0		3	11	2		24.6
White R.		17			9.0			15	2		9.1	2	13	1	1			46.0		4	12	1		24.6
Salt R.		6			9.0			6			9.0		5	1				46.2		3	3			24.1
<u>Gila</u> <u>r</u>. <u>elegans</u>																								
Green R.		4	77	6	10.0			1	69	16	10.2			1	12	21	6	48.8		1	8	33	44	29.3
Colorado R. - Lake Mohave		1	3		9.8			2	2		9.5											1	3	31.3
<u>Gila</u> <u>cypha</u>																								
Lake Powell area	1	2	3		9.3				4	2	10.3									1	3	2		26.0
Colorado R. (unknown)		1			9.0				1		10.0			1				47.0		1				22.0
<u>elegans</u> x <u>cypha</u> ?																								
Lake Powell area	1	13	7		9.3				19	2	10.1		2	5	6	2		47.5		1	3	15	3	28.1
Green R.		4			9.0			2	2		9.5			1				47.0		1	3			24.5
<u>robusta</u> x <u>elegans</u> ?																								
Green R.		1	2		9.7			1	2		9.7		1	2				46.7		1	2			24.7
White R.		1			9.0			1			9.0		1					46.0				1		28.0

A few characters that are similar in both forms are: pelvic fin rays, usually 9-9; caudal fin rays, invariably 19; pharyngeal teeth, usually 2,5-4,2 but several other combinations have been found; lateral line scale count, 75-96 for *robusta* with a mean of about 82, 75-99 for *elegans* with a mean of about 85.

The status of *G. cypha* is not clear yet. Only a few specimens were available for examination, therefore no decisive statement can be made about this form. Only 2 specimens have been characterized in the literature (Miller, 1946) thus the intraspecific variation of this form is unclear. The main criteria outlined by Miller (1946) and used here for distinguishing *cypha* are: 1) An abrupt nuchal hump (Compare *cypha* and *elegans* in Figure 1). 2) A prominent fleshy snout and subterminal mouth. 3) A small eye in comparison to either *robusta* or *elegans*.

Many of the specimens from the Lake Powell area seem to be intergrades between *elegans* and *cypha*. The data from these fish have not been ~~run through the computer~~ computerized, when this is done their relationship to the other forms may be better understood. Four specimens from the Green River also fall into this questionable category.

One specimen from the White River and 3 from the Green River are possible hybrids of *elegans* and *robusta*. The taximetrics program will be of use in alligning these fish also.

COMPARISON WITH OTHER WORK:

Miller (1946:414) compares *intermedia*, *robusta*, *seminuda*, *elegans* and *cypha* for 6 characters. My data disagrees with his in a few instances. Miller considers *robusta* as fully scaled; my data shows this form to be variable, usually being fully scaled but a few were found with reduced scalation on the dorsal, ventral and peduncle regions. These few approach *elegans* in this character. Miller considers *seminuda* as an intergrade between *robusta* and *elegans*, but he does not give locality information on the 5 fish characterized. I am reserving the name *seminuda* for *Gila* from the Virgin River of Utah, Nevada and Arizona which are reported to be distinct (Personal communication between James Deacon and Robert Behnke).

The *robusta* Miller examined were from the Gila River system of Arizona; they agree in character with the *robusta* I examined from the upper basin. The *elegans* he used were from the middle and lower Colorado river, these also agree in character with the *elegans* of the upper basin. Miller's chart shows a good seperation between *robusta* and *elegans* for 5 of the 6 characters used, pelvic fin rays were the same, 9-9. The comparison of my data to his indicates that all specimens of each form are quite identical to each other throughout the Colorado River basin, and that each form is distinct; suggesting two species rather than subspecies. In other words the intraspecific variability is less than the interspecific, indicating two monophyletic gene pools with perhaps limited hybridization and not polyphyletic ecosubspecies.

Gila *r.* *intermedia* as characterized by Miller (1946), and Barber and Minckley (1966) seems to be a distinct form. It differs from *robusta* in dorsal and anal fin ray counts (8-8 as apposed to 9-9 for *robusta*)and general body morphology, expecially the peduncle depth (deeper in *intermedia*). This form has been reported to live sympatrically with *robusta* and *elegans*, but no reports of hybridization between *intermedia* and either of the other two have appeared in the literature. Specimens of the 3 forms collected together from the Salt River of Arizona by Gilbert and Schofield (1898) were examined by Dr. Minckley (Arizona State Univ.), and he reported them as being distinct from each other. This indicates that intermedia may be a valid species.

G. r. jordani of the White River of Nevada appears very close to robusta in meristic characters but differs in general body morphology, being more robust or chunky (Tanner, 1950).

Miller (letters to Donald Franklin) and Hagen (1962) have reported cypha from the Green River in Dinosaur National Monument. I have seen several of the specimens referred to and found they lacked an abrupt nuchal hump, and the snouts were not well developed. These were some of the questionable fish mentioned earlier as possible intergrades between cypha and elegans. Further study may show these characters to be more variable in cypha than presently thought.

ECOLOGICAL DATA:

Ecological data on the Colorado basin Gila is scarce. Virtually no life history data has been published for any of the forms although some data for robusta and elegans should be forthcoming (Vanicek,1967 Ph.D. thesis, Utah State Univ.).

The distribution pattern of the forms I examined indicates robusta is found in the large, swift, warm rivers (Middle Green) and also in the large, cool tributaries (Upper Green, White R., Upper Colorado R.). It appears that elegans is restricted to the swift, warm rivers (Green below Flaming Gorge and main Colorado). The extreme morphology of cypha suggests it lives in very swift water. The little data we have from collections supports this hypothesis.

EVOLUTION AND PHYLOGENY:

The evolution of the Colorado basin Gila is undoubtedly integrally tied with the geological history of that basin. Unfortunately this history is somewhat obscure at the present time. Several general trends seem to be indicated though (Smith, 1966).

1.) The Colorado Plateau, what is now the upper Colorado basin, uplifted in the late Miocene and probably had parts draining to lower basins to the west, south and southeast.

2.) By early Pliocene a continuous river to the Pacific through southern California probably was established.

3.) The Kaibab Upwarp during the early-mid Pliocene separated the upper and lower basins, and ponded the upper basin waters.

4.) The river became continuous again in the late Pliocene when the water was raised enough to flow over the Kaibab Upwarp.

5.) Connections were severed between the Colorado and White rivers during a period of aridity in the late Pleistocene.

The Colorado basin has over 80% endemism in its primary fish fauna which is the highest of any North American river basin. The approximately 27 endemic species indicate a long history with much geographical isolation.

Gila is considered the most primitive American cyprinid genus (Miller, 1958A). The genus Ptychocheilus was probably derived from a Gila-like ancestor (Uyeno, 1961) as was the tribe Plagopterini, the spinedaces (Miller and Hubbs, 1960). Species of Ptychocheilus probably originating from a Colorado basin form are found presently in the Sacramento and Columbia basins. Miller (1965) suggests these species had evolved by the late Pliocene.

The tribe Plagopterini comprised of 3 genera and 6 species is endemic to the middle and lower Colorado basins. The spinedaces strongly indicate the opportunities for geographic isolation and speciation associated with the early Colorado River basin.

Gila robusta jordani probably represents a population of *robusta* that has recently become isolated in the White River, and subsequent limited habitat has selected towards the present chunky morphology.

The classification of *seminuda* of the Virgin River is tentative until specimens are examined. Therefore I will not speculate on its evolution or phylogeny here.

The Gila river system undoubtedly was the site of origin for *intermedia*. The time period involved and the ancestral form are not so clear. Miller (1958B) says the Gila division probably did not join the Colorado until the Quaternary. Smith (1966) infers that the Gila-Colorado connection is much older, at least mid-Pliocene. The Gila River and the White River-Virgin River area have several fish species in common, and both have several endemics. This suggests both a connection between the two and a long period of isolation. It is possible that both systems were connected by the Colorado until mid Pliocene, at which time the Gila River system became isolated. It then rejoined the Colorado in late Pliocene. This is merely speculation on my part but it is a possibility.

The relationships of *intermedia* to the other members of the subgenus may give us information on the phylogeny of the *Gila*. *G. atraria* of the Bonneville basin is the most primitive living species of the genus according to Uyeno (1961). It is possible that this form and *intermedia* may be closely related. If so this would suggest an early origin for *intermedia*. *G. orcutti* of southern California and *G. purpurea* and *G. ditaenia* of northern Sonora, Mexico seem to be closer to each other than to any other form (Miller, 1945). These forms probably originated from the Colorado basin, and most likely the lower Colorado basin. They show affinities to intermedia in several morphologic characters (fin ray and lateral line scale counts). It is possible therefore that intermedia or the ancestor of intermedia gave rise to these 3 isolated forms, orcutti, ditaenia and purpurea.

The Gila of the Rio Grande basin (pandora and nigrescens) probably came from a Colorado basin ancestor. Their likely mode of introduction to the Rio Grande probably parallels that for Pantosteus plebeius suggested by Smith (1966).

The extreme morphology of cypha suggests evolution in a torrential habitat. Present distribution information indicates the Grand Canyon-middle basin area as the probable center. This area is relatively new, dating from the late Pliocene (Smith, 1966), therefore cypha is probably of more recent origin than either robusta or elegans (see below). Its extremely modified morphology also suggests a rather recent origin, probably coming from an elegans-like incestor.

The origin of robusta and elegans was probably early-mid Pliocene. A mid Pliocene fossil Gila from Arizona had modifications for swift water much like the present forms (Uyeno and Miller, 1965). A low vertebrae count indicates it may be closer to robusta than elegans. It was found in the Bidahochi Formation which is presently part of the Little Colorado River system. This suggests that robusta may have evolved in the upper basin during the time it was ponded by the Kaibab Upwarp. It is possible then that elegans evolved at the same time as robusta in the lower basin. Both possibly came from a common ancestor that was much like the present robusta.

Another theory on the evolution of these two forms is that robusta is the older form; when the river became segmented a population was isolated in a fairly swift current area and subsequent selection produced *elegans.* Again the ponding of the upper basin does not suggest a swift habitat so the lower basin seems the most likely site for the origin of *elegans*.

The only form whose origin is well founded is *jordani*, the evolution of the other forms is pure speculation at this point. A better understanding of the relationships of the forms involved may give us new input and help solve this problem.

It is evident from this discussion that the Colorado basin provided ample opportunity for independant speciation.

FUTURE STUDIES:

To prove the hypothesis that *robusta* and *elegans* are species, reproductive isolation must be established. If this isolation exists, what are the mechanisms causing it? Are they ecological or behavioral? Is there a spatial or temporal difference in spawning between the forms? If the two interbreed, are the hybrids fertile? These questions must be answered before a definite statement can be made about the classification of *robusta* and *elegans*, or for that matter any of the Colorado basin *Gila*.

Future studies should start with filling in the geographical gaps in our collections. More specimens are needed from the Grand Canyon and lower Green River. These areas may contain the answers to many questions concerning the morphologic diversity exhibited by the fish of the Colorado River.

Once the morphologic diversity is known, we will have an idea on how to approach ecological and genetic studies. Investigations to determine the niche of each morphologic form and extent and mechanisms of reproductive isolation between the forms should be undertaken. If known hybrids could be produced, then standard specifications would be available for comparison with suspected natural hybrids.

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A LITERATURE REVIEW OF ENVIRONMENTAL INFLUENCE ON REPRODUCTIVE PHYSIOLOGY AND MIGRATION IN FISHES

by

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ABSTRACT

Schreck, C.B. A literature review of environmental influence on reproductive physiology and migration in fishes. Report for PS 560, Environmental Physiology, Fall Quarter, 1968.

A literature review of environmental physiology in fishes is presented in this paper. The paucity of information on physiological processes and the multiplicity of literature on the migratory aspects of reproduction necessitate the discussion of three pertinent aspects: 1) Environmental, including the influence of light, temperature, water flow, and physical characteristics of the water; 2) physiological, including the affects of the environmental aspects on the organism's reproduction, primarily via the pituitary and/or thyroid; and 3) migratory, including the ability of adults and fry to home, and the directional cues used in this process. It is concluded that thermal regimes and photoperiodicity are the most influential environmental parameters, both initiating gonad development and timing sexual activity. Other extrinsic stressors, however, may also be intricately involved. Reproductive processes in fishes are controlled by pituitary and thyroid hormones; the physiological condition of the organism and extraneous physical features of the environment are also influential. Thus, an environmental-cortex-hypothalamic-hypophysis-gonadal mechanism

is propsed. Both adult and juvenile fishes have the propensity to home. Olfaction, temperature sensitivity, celestial navigation and other cues direct the fish in this process; genetics, however, may also be involved. Essentially, further study is needed in all of the areas mentioned here.

INTRODUCTION

A synthesis of the available literature discussing the environmental influence on piscine reproductive physiology is of great reference value. A broad definition of reproduction is employed so as to include not only the gonadal development and processes but also the more extrinsic factors of the spawning migration because of their integral role in parental success. There is a great paucity of critical and detailed information about the physiology of fishes. Contrarily, the multitudinous literature on homing, migration, and natural history of this group is beyond the scope of this presentation; only selected references are included to provide a broad perspective but not an exhaustive review of these aspects.

Teleosts (higher bony fishes) exhibit most of the sexual reproductive mechanisms found in the Animal Kingdom, and they have developed several specializations unique among the vertebrate animals (Hoar, 1957a). It is almost impossible to draw any generalizations from so varied a group. This can easily be appreciated when one realizes that the phyletic differences between the three major groups, the cyclostomes, elasmobranchs, and boney fishes, are actually much greater than that separating the latter taxon from man. For instance, some species (e.g., the cyprinodont Ozyrias latipes) have no period of sexual inactivity, ovulation being alomost as continuous as spermatogenesis (Amoroso and Marshall, 1960). At the other extreme are the species such as the salmons in which the gonads mature only once and death inevitably follows. The ceratioid angler-fish (Photocorynus spiniceps) is aberrant in that the male or males become parasitic on the female which is many times their size. The males of this species are permanently affixed to the female and dependent on her for their food supply (Norman, 1963). Gymnogenesis is also found among fishes, the entire species consisting solely of females; some members of the genus Xiphophorus reproduce by this means. The great majority of fishes are egg layers; some elasmobranchs and very few bony fishes, however, are viviparous.

Matthews and Marshall (1956) give an excellent presentation of the temporal factors affecting morphological changes in the reproductive systems of various fishes, and Brieder and Rosen (1966) exhaustively list all that is currently known about the "modes of reproduction in fishes." Nowhere, however, can a complete discussion be found on the relationships between the environment and the reproductive processes of fish. To portray the environmental reproductive physiology in its broadest aspects, both natural and experimental conditions are considered in this review.

REVIEW OF THE LITERATURE

The material under discussion is considered from three aspects: 1) the environmental, including cyclic and stressor phenomena; 2) the physiological, including endocrine and sexual features; and 3) the migratory, including homing and orientation of both adult and juvenile fish.

Environmental Aspects:

Breeding activity in fishes is usually characterized by marked seasonal rhythms (Amoroso and Marshall, 1960). The environmental parameters are manifested in various ways, although their net effect on the organism are essentially the same. Some aquatic habitats (e.g., rivers) are subject to cyclic changes or variations not encountered in terrestrial ecosystems. Most phenomena that set biological clocks or induce physiological responses are, however, ubiquitous in nature.

Water flow can trigger reproductive responses in certain fishes. John (1963) found that the reproductive cycle of the speckled dace, *Rhinichthys osculus*, is bimodal, with discrete peaks in early spring and late summer if precipitation is normal. Drought and the consequent overcrowded, undernourished populations may cause a failure in reproduction. John concluded that "rising temperature, increasing daylength, and perhaps flowing water are essential and adequate stimuli for spring reproduction, but decreasing daylength, declining temperature, and flowing water are inadequate stimuli for late-summer reproduction. Reproduction is greatest in the spring with streams swollen from melting snow and in late summer following freshets or flash floods. A single flood in late summer induces spawning; a single flood in early summer does not." Basically, however, the reproductive period of Rhinichthys seems to be regulated by the photoperiod. Pickford and Atz (1957) reported that in addition to photoperiod, certain Brazilian fishes require waterflow, occurrence of rain, a critical temperature range, and possibly a certain lunar cycle to induce spawning. Changes in turbidity and chemical content of the water (e.g., pH, hardness, salinity, and dissolved gases) may also be involved.

Lewis (1963) propounded that fishes may be crowded to such an extent that reproduction is inhibited. Inhibiting substances, if they exist, have not yet been identified; they may simply constitute a toxic concentration of waste materials. According to Lewis, Swingle claimed that fishes may produce a substance due to crowding that represses reproduction.

Courtship activities may induce intense nervous excitement that is responsible for nuptial coloration (Crew, 1952). This nervous stimulation may control the deposition of pigment and guanin in the skin for breeding "plumage"; a more intense coloration can be associated with a higher metabolism.

The environment helps to determine the age of maturation in fishes; the more eutrophic (to a point) is the habitat, the earlier the maturation. This can directly influence the reproductive period of a species. Brown (1957) stated that the age at which female Atlantic salmon return to spawn for the first time varies; those growing faster and migrating earlier, home to their spawning grounds at a younger age than do those which grew more slowly and migrated later. Also, an increase in population density may induce stunting in certain species (Morris, 1966) and thus possibly influence reproduction.

Dissolved substances in the ambient medium that can penetrate gill membranes and reach the pituitary, thyroid, or gonad can cause a reproductive response. Hoar (1957a) reported an experiment illustrating the effect of dissolved steroids on gonadal development. Jacobi, cited by Marshall (1956), further confirmed this by showing that eels need salt in their surrounding water for genital development. That is, eels cannot reproductively mature unless they are in salt water. Contrarily, the salmons (*Salmo salar* and those of the genus *Oncorhynchus*) can become completely ripe in freshwater although the sea is an integral part of their normal life histories.

Viox (1967) stated that 20 out of 40 male cutthroats (S. clarki) from Newton Lake, Wyoming, had eggs in addition to testes. This condition is clearly the product of dissolved materials; the excesses of magnesium (300 p.p.m. or above) and sulfates (900 p.p.m. or above) in the lake are probably responsible for the hermaphroditism.

Light and temperature, possibly working in concert, are undoubtedly the most influential of the environmental parameters. The latter is generally a direct product of the former; as daylength increases so does water temperature. Consequently, it is almost impossible in field situations to determine which, if not both, of these variables is responsible for reproductive control. The following experiments illustrate how light and temperature initiate or time spawning in fishes.

The cichlid Tilapia when exposed to a greater amount (duration?) of light breeds earlier and at a considerably smaller size than siblings not recipients of this amount (Brown, 1957). Hoar and Robertson (1959) showed under controlled conditions, that goldfish raised with a 16 hour illumination-8 hour dark periodicity had an increase in ovary size (maturation) as opposed to those with an 8 hour light-16 hour dark regime. Hoar (1957a) reported evidence found by Baggermann that further substantiates the reproductive control by a light-temperature mechanism. Sticklebacks transferred from sea in December

(6° C, 8 hour daylight) to the laboratory (20° C, 16 hour daylight) built nests within 4 weeks. " Six-month old fish (hatched in April and May), if brought into the laboratory in October and held at 20° C with 16 hours illumination, will mature in 50 days but fail to mature in 8 months with only 8 hours illumination." The acceleration produced by 16 hours of light was markedly delayed at temperatures below 20° C.

Light without a thermal component can regulate trout reproduction. Different photoperiodic regimes markedly affect gonadal cycles of both male and female brook trout (Salvelinus fontinalis). Henderson (1963) also pointed out that the influence of long or short photoperiods depends upon the respective phase of gametogenesis in progress and on the photoperiod in effect during earlier stages of the gonadal cycle. The maturation of the "gonads may be regulated by the normal seasonal changes of day length.... An accelerated light regime can hasten the time of functional maturity in adult trout, but is without effect when applied to maturing fish in which gametogenesis is taking place for the first time." This stimulative effect of the environment is probably dependent upon the operation of a "hypothalamic-hypophyseal mechanism." The following data supports Henderson's conclusions. "The rate of gonadal development is the same at 16° as it is at 8.5° provided that the fish are exposed to natural day lengths.

If fish are subjected to long or short photoperiods, the gonadal response at 16° is quite different from that at 8.5°." The changes in quantitiy of gonadotropins released from the anterior pituitary probably mediate the environmental stimulation of reproduction; Hoar (1957) stated that constant darkness causes hypertrophy and eventual atrophy of the endocrine system of the characin <u>Astyanox</u>.

Ahsan (1966) preformed experiments demonstrating different photoperiods at various temperatures do not appear to dominate any stage of the spermatogenetic process of the lake chub, <u>Couesius plambeus</u>. He presented evidence showing that an endogenous rhythm was also present that may be partially responsible for the timing of testicular changes. Harrington (1956, 1959) presented other experiments of this nature.

It is interesting to note that trout living in the northern hemisphere are operating under a photoperiodic regime 6 months apart from those in the southern hemisphere. As a consequence, spawning of the two geographic populations are separated by exactly one-half of a year. It would be of great value to study the life history of the trout in Lake Titicaca which lies essentially on the equator. Does the great increase in light extend the period of spawning?

The <u>fate of the gametes</u>, once independent of the gonad, also determines reproductive success. In most fishes the sex products are shed into the water and perish within minutes unless they unite (Hoar, 1957b). Proper nutrition is essential for gamete development (Lewis, 1963).

The eggs of the fishes are either pelagic (buoyant and generally with a thin non-adhesive membrane) or demersal (sink and have a hard, smooth, or adhesive membrane); the former is generally the rule in marine species and the latter in freshwater forms (Boyd and Hamilton, 1952). The pelagic eggs contain an oil glob-ule (s), serving possibly as a food source and/or for buoyancy. Mann (1964) stated that the eggs of the fat minnow (*Sarcocheilichthys variegatus*) produce a substance that activates and attracts spermatozoa, thus causing their aggregation around the micropyle area. Hafez (1968) pointed out, with reference to domestic animals, that there may be a seasonal variation in metabolic activity of sperm. The fertility and hatchability of eggs are affected by the female's ambient conditions during mating and by the environment of the eggs of birds prior to incubation.

Spermatozoa in fishes are commonly stored for prolonged periods; possibly for that reason they contain a high lipid concentration (Mann, 1964). Parkes (1960) cited Yanagimachi who found that herring spermatozoa retain their fertilizing capacity to a small extent for 12 hours in 8 to 10° C sea water. Mature sperm of the kilifish *Fundulus heteroclitus* are capable of maintaining motility following a 150,000 r X-ray exposure. The eggs fertilized by these spermatozoa, however, have high mortality or give rise to abnormal embryos. The X-ray probably changes the state of DNA polymerization of the sperm chromatin (Mann, 1964). Mann (1964) further reported that the sperm of some fish are very sensitive to pH changes. The addition of water or dilute salt solutions to trout semen provokes a short-lived burst of activity followed by a gradual decline in motility. Oxygen has an activity effect on sperm motility and prolongs its duration. A dilutent containing 0.15 % potassium chloride in contrast to sodium chloride has no activating effect; the addition of potassium ions to a suspension of motile sperm in sodium chloride solution can render them motionless. This "reaction" is reversible. Manncites Schlenk's proposed explanation that trout spermatozoa show great activity upon dilution with water or sodium chloride solution but not with trout seminal plasma because of the high potassium content of the plasma (80 mg/100 ml). The rapid increase of motility after dilution with water decreases the potassium concentration in the seminal fluid, thus the potassium ions from the sperm cells can flow into the surrounding medium. Apparently, the potassium both preserves the sperm's energy by inducing quiescence and engenders a state of "preparedness for action" ('Bewegungsbereitschaft').

Physiological Aspects:

Árvay (1967) concluded, with reference to man, that the endocrine processes are a product of the environment and are held in unity by the nervous system. He proposed a "cortex-hypothalamo-hypophysis-gonad system." The endocrine functions are so intimately intertwined with reproduction in fishes that one cannot be mentioned without the other. There are several factors that confound a physiological discussion of fish reproduction.

There is very little known about the physiology of fishes. There are two glandular tissues present in "all" fishes for which there is no known function. These are the corpuscles of Stannius associated with the kidney, and the urophysis or caudal neurosecretory system located in proximity with the spinal cord in the caudal peduncle (Bern, 1967). Honma (1959a, b) indicated that these glands may be involved somehow in migration or reproduction of the ayu (Plecoglossus altivelis); both showed marked histological developments during the spawning migration. Bern (1967) stated that aldosterone and prolactin are apparently lacking in fishes. Tomlinson, McBride, and Geiger (1967), however, cited a report that the former was present in salmon plasma. The only chemically-identified sex hormone to date (1960) found in any cold-blooded vertebrate is 17B-estradiol, discovered by Hisaw and Ringler in the dogfish shark, Squalus suckleyi

(Dodd, 1960).

Another obstacle in the path of a physiological discussion is the ignorance about fish nutrition. As Black (1957) reported, many species fast during spawning and migration periods; consequently, ion balance can become upset. For instance, it is not known whether or not migrating adult salmon have the biochemical ability to digest or assimilate food.

Presently, almost nothing is known about sex determination in fishes. In fact, it is not known whether or not fishes have sex chromosomes; to date, one report shows evidence that these are present in the goldfish. There are three factors that must be considered here: 1) The genetic control, 2) polymorphism of sex, and 3) the environmental influence on sex determination. The synbranchiform fish Monopterus albus starts its reproductive cycle as a functional female; males are produced only by sex reversal. This may be a genetic "switch mechanism [designed] to maintain the full reproductive power of the population immediately after periods of critical conditions, and to prolong the reproductive capacity of many members of the population in fishes with sexual succession" (Liem, 1963). Sex reversal in the poeciliid Xiphophorus is not uncommon (Crew, 1952), and in one form, the entire population is female, reproducing by gymnogenesis. One variety of Poeciliopsis also consists only of females; the sperm of any closely allied species is needed to stimulate development of the triploid ova, but there is no actual penetration (Schultz, 1967). That the environment influences sexual differentiation can be seen from the monoecious cutthroat population previuosly mentioned.

Chemicals may also induce sexual development (Amoroso and Marshall, 1960). Yamamoto and Kasjishima (1968) artificially induced sex reversal in goldfish in both directions; that is, they produced heterogametic females (Carassius auratus males are normally XY) and genetically female males. This was done by administering estrogens or androgens, respectively, during the critical period of gonadal determination; the hormones were ingested in the food.

Aberrant reproductive developments are encountered in the ceratioid angler-fish and in the cyprinidont, subfamily Rivulinae. As mentioned above, female Photocorynus are permanently parasitized by the male of the species, to such a degree, in fact, that the female provides nourishment for the male through her bloodstream. These fish, then, may be considered pseudohermaphrodites. Numerous species of the toothcarps inhabit ephemeral ponds of tropical Africa and South America. During dry periods, the adults perish, but the previously deposited fertilized eggs resist the six month period of desiccation and hatch when the rainy seasons come (Peters, 1963).

Dodd (1960) stated that in teleosts, as in cyclostomes (jawless fish), but unlike all other vertebrates, the embryonic gonad is a single structure probably homologous to the gonadal cortex of other vertebrates. Auxocytes (early oöcytes) are usually the most prominent cells in the teleostian primordial gonad; this may be a possible protogynous condition. D'Anoca, according to Dodd, reported that both gonia are initially present, the spermatogonia being less obvious due to their smaller size. It is believed that a genetically mediated sex determining inductor substance(s) is secreted by certain gonadal stroma cells. "The chemical nature of the inductor substances is unknown, though they are thought by some workers to be identical with the sex steroids.... Exogenous androgens and oestrogens can, under certain experimental conditions, exert an effect on sex differentiation" (Dodd, 1960).

Forbes (1961) presented an excellent review of reproductive endocrinology in fishes, and Honma (1959b, 1961) studied these processes in the ayu. Hormones have recently come into use by the fish-culturist to artificially induce spawning; there is much current literature on this subject (Stevens, 1966).

The hormones of the pituitary (gonadotropins) and gonads (androgens, estrogens, perhaps progesterone) are intimately involved in the regulation and timing of reproduction and the control of its physiology. Seasonal variations of the environment affects the pituitary. Hoar 1957a) reported that the middle glandular area" of this gland has gonadotropin activity and that it fluctuates seasonally. Although temperature might act directly on the gonads and thyroid, or water salinity might modify the ionic and osmotic content of the blood thus stimulating the thyroid, the pituitary is generally the bridge between the receptor organs and the rest of the endocrine system. Hoar concludes that the pituitary produces the tropic hormones in fishes; changes in the thyroid or other glands do not normally occur in the absence of the hypophysis. "It is possible then, that changes in the external environment may also effect the activity of the pituitary. Those materials which can penetrate gill membranes will reach the pituitary readily."

It is not known if the pituitary controls any part of the sexual cycle of cyclostomes; the accessory olfactory organ, however, is glandular and may be associated with gonad development. Dodd (1960) further stated that the source of teleost gonadotrophin is probably the basophil (cyanophil) cells in the middle glandular region of the pituitary. This cell type increases in number and activity during gonad maturation. The hypophysectomy of male Gobius paganellus by Vivien, reported by Dodd, caused the testes to become atrophic, and two glands on the ejaculatory duct of the vas deferens were greatly reduced in size. The females exhibited follicular atresia and ovarian involution.

Degenerative changes occur in the pituitary of Atlantic and Pacific salmon during sexual maturation; at this time, the meso-adenohypophysis undergoes great cell multiplication and hypertrophy (Van Overbeeke, 1967). Lyophilized pituitary extract obtained at seasonal intervals from the perch, _Perca fluviatilis_, has been used to experimentally time its gonadotropin content (Swift and Pickford, 1965). This pituitary extract was administered to hypophysectomized male _Fundulus heteroclitus_ by interperitoneal injection. The "...maximal gonadotrophin content of the hypophysis, reflected in stimulation of regressed testes and onset of nuptial coloration in the assay fish, coincided with the peak of the natural reproductive cycle in April. In August the pituitary was depleted of gonadotrophin." Amoroso and Marshall (1960) reported that photoperiodic control of pituitary function was illustrated by experiments in which precocious sexual maturity was achieved by control of illumination in a variety of fish. There is morphological evidence that suggests direct nervous connections between the different peripheral sense organs and the pituitary.

The _thyroid_, probably controlled by the pituitary, may also be closely involved in the regulation and preparation of the reproductive processes in fishes. Matty (1960) reported that the changes observed in the teleost thyroid was related to reproduction; spawning occurred immediately following the period of greatest histological activity of the gland. Swift (1955) injected labeled iodine (I^{131}) into brown trout, _Salmo trutta_, periodically throughout the year. By measuring the radioactivity of the thyroid with a G-M tube at various times after the administration, he was able to determine the activity of the gland by plotting the decrease in counts over time. The slope of the line thus obtained was, according to Swift, directly related to the thyroid's incorporation of iodine and therefore its activity. He found that the brown trout's peak thyroid activity was in midsummer (long day length, warm water). The maturation of the gonads commenced in females during June and in males during July and was completed during October. Thus the thyroid "prepared" the gonad for spawning, and these cycles were by seasonal rhythms. In 1959, however, Swift (1959) reported that the thyroid activity of S. trutta was inversely related to water temperature except for a short burst of activity in July. The generalization was later made that thyroid activity increases at spawning time because of the increased rate of loss of administered radio-iodine by the brown trout and because of the great increase in production of labelled thyroxine by Fundulus heteroclitus (Swift, 1960). Honma and Tamura (1963) reported on thyroid and pituitary functions in the ayu.

Crew (1952) stated that the physical condition of Oncorhynchus during spawning may actually be pathological. Tomlinson, McBride, and Geiger (1967) found in force-fed or unfed migrating adult sockeye salmon in freshwater that the flesh "water and sodium content increased and the potassium content decreased...." They concluded that starvation "plays no part in bringing about degenerative changes observed in skeletal muscles of migrating, spawning sockeye salmon...;the development of the gonads is in some manner directly concerned in the changes, for the skeletal muscles of sexually developing sockeye has been found to show marked benefit from feeding after the fish were gonadectomized, and a similar effect has been observed in unspawned male sockeye which commenced feeding some 6 months after the time when they would normally have spawned." They also stated that the changes in the flesh may be indirectly induced by hormones, and they cited several reports showing that adrenal corticoids injected into trout influenced the concentrations of sodium and potassium in the blood and the excretion of sodium through the gills. Possibly for osmotic regulation, "the king salmon, when it returns to fresh water to spawn, immediately increases its production of slime, and the skin thickens considerably by the time the fish reaches the spawning ground" (Van Oosten, 1957). It is interesting to note that freshwater trouts, more primitive than the salmon, also develop a thickened epidermis during spawning.

McBride (1967) used histological examination to show extensive degenerative changes in the thyroid, pancreas, and kidney during gonad development of unfed adult sockeye salmon. There was an increase in the large follicles of the thyroid paralleling gonadal maturation, and when fully matured there was a decrease in cell height and cell number. Regression of the kidney followed gonadal development; there was a sclerosis of the glomerular capillary bed, thickening of Bowman's capsule, decrease in number of lymphoid cells, and a concomittant increase in the pigmentation of kidney parenchyma. During sexual ripening of unfed fish the pancreas exhibited changes in the exocrine portion; there was a shrinkage in the size of the caeca as well as a reduction in the amount of exocrine, zymogenous tissue. Endocrine tissue exhibited hyperplasia. Feeding prevented the deterioration of the thyroid, while it delayed and reduced that of the kidney and pancreas in the adult sexually-ripening sockeye.

Robertson, et. al. (1961) examined the changes occurring in blood constituents of migrating adult king salmon (*O. tshawytscha*). They reported that the glucose content of the blood increased to about twice that found in salmon in the sea, but rarely was glucose present in the urine. The sodium and potassium concentrations decreased. Cholesterol values rose during migration and then decreased during spawning to concentrations lower than those of premigrants. Total proteins exhibited diminution as did the protein-bound iodine. There was a progressive rise in the concentration of 17-hydroxycorticosteroids to very high levels at the time of spawning; consequently, concomittant syndromes of Cushing's disease were observed in both physiological and histological features.

Sexual ripening in the stickleback, *Gasterosteus*, induces hypertrophy of the muscles of the pectoral fins so that the fish can "fan" the water over its nest (Marshall, 1956).

A *delay in fertilization* (spawning) of 4 to 7 days in brown trout caused a slight excess of males; under the same conditions, rainbows produced an excess of females (Huxley, 1923). In the rainbow, this late fertilization lead to: 1) an increase in mortality, especially in the early stages; 2) a decrease in growth rate; 3) an increase in anomolies, mainly a shortening of the operculum; and 4) males were more suseptible to these conditions than were the females. This may possibly indicate chromosomal degeneration or an increase in mutations.

Honma (1961) and Honma and Tamura (1962) studied seasonal gonadal changes in the salmonoid fish *Plecoglossus altivelis*.

Migratory Aspects:

Some species of fish spawn in one type of aquatic environment but grow and mature in another. Breeding migrations are almost universal among fishes (Marshall, 1956). The anadromous species of Salmonidae provide good examples, wandering to the sea as juveniles, developing sexually, and then returning to freshwater to spawn. The eels of the genus *Anguilla*, contrarily, are catadromous (spawn in seawater but mature in freshwater). Considering these migratory species, two pertinent facets of reproductive success must be considered. First, for various adaptive reasons, the adult fish must be able to locate their spawning grounds although often from several thousands of miles away. Secondly, the juveniles must have the propensity for finding the waters where they will mature. The following discussion is limited to broad concepts and physiological aspects of these two phenomena to represent the reproductive processes of fishes in toto.

Fishes have a great ability to home with a great degree of accuracy (Larimore, 1952; Miller, 1954). Various mechanisms have been proposed to explain how fishes attain this end. It is, of course, very difficult to correlate the senses of these aquatic vertebrates with those of terrestrial forms. Nevertheless, the qualities associated with smell, taste, and sight with reference to mammals have their homologues (or analogues) in the poikilotherms.

Olfaction is highly developed in fishes and seems to be of prime importance in the ability to home. Walker and Hasler (1949) found that the bluntnose minnow (Pimephales notatus) could discriminate between varieties of the same species of plants at a dilution of parts per million. Lepomis megalotis (longear sunfish) apparently use nasal cues for homing. Gunning (1959) showed that this species, while blinded, could return to within a very close proximity of where it was first captured when displaced downstream but could not do so when transferred upstream. Sunfish with nasal pits occluded moved randomly when displaced in either direction.

Another sense highly developed in some fishes is taste. Bardach, Todd, and Crickmer (1967) demonstrated that blinded, olfactory impaired catfish of the genus *Ictalurus* could locate distant chemical cues by the means of taste alone, using true gradient searching in the absence of a current. "...unilateral deprivation of taste receptors which are spread over the body and barbels of the animals caused pronounced circling toward the intact side. The relation of swimming paths of the fish to the chemical in the water suggested that comparisons of the concentrations were made in time and space."

Bérziņš (1949) illustrated that temperature indirectly determines the orientation of pelagic fishes. The fish follow the narrow thermal layer to which they are best adapted, eventhough this temperature zone varies in depth due to the wind and other physical factors.

Marshall (1956) stated Paton's conclusion that the "state of nutrition is the main factor determining migration...; when the salmon has accumulated a sufficiently large store of material, it returns to the rivers which were its original habitat." The accumulation of iodine and the subsequent formation of thyroid hormone may be a vital component of the physiology of migrating adult salmon (Hoar, 1957).

Donaldson and Allen (1957) reared silver salmon (*Oncorhynchus kisutch*) in a Washington hatchery. The fingerlings were then marked and divided between two other hatcheries on different streams but within the same system as the first. Following two months of orientation, they were released to migrate to sea. Of the returning adults, none came back to the hatchery of their birth; they returned to the respective river from where they had been released. Adult silver salmon were captured by Wisby and Hasler (1954) in Issaquah Creek and its east fork. The olfactory pits of one-half were occluded; all were then displaced one mile below the junction of the two streams. The control group was able to repeat the same choice at the junction while the experimental group distributed themselves randomly. Hartman (1964) showed that migrating sockeye (O. nerka), when transferred to the mouths of other lake tributaries from the one where they were first captured, returned to the tributary of their original choice.

The thyroid gland may play some role in the migration of juvenile fish. Eales (1963) used histological and radiochemical criteria to show that "fry migrants (pink and chum salmon) have relatively inactive thyroids, while yearling migrants (sockeye and coho) have active thyroids."

Brown trout fry were observed to drift downstream at night with maximum movement occurring in the early hours of the evening and onset being associated with sunset (Elliot, 1966). The downstream drift occurred when the water temperature was below 14°C. This critical temperature possibly initiated the movement, but some other mechanism must have controlled it. Lyon (1904) reported that fish normally face upstream in a river. This orientation is not due to a rheotropic control but is rather dependent on the fact that, if the fish were to drift with the current, the surroundings would appear to be moving past them. Thus rheotaxis is due to a visual cue and not to changes in pressure. To illustrate, Lyon placed a fish in a bottle and pulled it through a trough of water; eventhough there was no current in the bottle, the fish faced in the apparent upstream direction. Fry, then, apparently lose visual contact with their environment during the dark hours and passively drift downstream. Ali and Hoar (1959) explained the physiological mechanism involved in the salmon. Through histophysiological examination of retinas, they found that the eye was incompletely dark-adapted at the time of greatest downstream migration (about 7-9 PM in the salmon). The movement of the rods and cones is in direct proportion to the logarithm of the light intensity, due to redistribution of retinal epithelial pigment. As light intensity falls, rheostatic responses fail, and the fish pass downstream with the current. Hoar (1953) found that schooling species of salmon are active at night and swim near the surface. Consequently, they are displaced downstream shortly after hatching. Elevated temperatures and hyperthyroidism may modify this reaction to currents and hasten downstream movement. Stream dwelling forms are associated with the bottom and display inactivity by night. Eventhough darkness causes loss of visual contact, the fish can use thigmotactic responses to hold their position.

MacInerny (1964) examined the five species of Pacific salmon fry for temporal salinity preferences. He concluded that the sequence began with a preference for freshwater, then gradually changed in the direction of increasing salinity, and ended with a preference for seawater concentration. The timing of this selected preference parallels that of the natural migration from river to ocean. Apparently, "the juvenile Pacific salmon are able to use estuarial salinity gradients as one of the directional cues in their seaward migration." It is interesting to note that *O. kisutch* attains a larger size in Lake Michigan than in the ocean, although it never contacts a saline environment.

Celestial navigation may also be involved in juvenile orientation. Johnson and Groot (1963) studied the seaward migration of sockeye smolts through a lake system by direct observation and tagging. The migration was well oriented and non-random, and all the fish moved at the same time in all of the lake's regions. Movement was near the surface, diurnal, and maximum during the evening crepuscular. There was an increase in rate of swimming as the season progressed due to a greater drive by the fish; this rate of travel was related to the hours of sunshine on previous days.

The rainbows (Salmo gairdneri) of Loon Lake, British Columbia, spawn in the inlet and outlet streams of the lake and in a tributary to the outlet. The progeny of these trout must swim in the correct direction to reach the lake; in fact, those hatched in the tributary must move downstream to the outlet and then upstream to the lake. Northcote (1962) found that the fry in the inlet (13°C or below) moved at night and did not contact the substrate; the onset being in the early evening and the greatest movement in the middle of the night. In the outlet (15°C or above), the fry came in frequent contact with the bottom during the night, thus holding thier position at night and swimming upstream during the day. Laboratory studies confirmed the movement of fry downstream when in water below 13°C and upstream when in water above 15°C. Reciprocal transplants into both the inlet and outlet proved that this condition was not genetic.

There must certainly also be a genetic basis for homing. Both Brannon (1967) and Raleigh (1967) reported that the migratory behavior of newly emerged sockeye salmon was genetically controlled. Adult cutthroat trout in Yellowstone Lake had the ability to home to a certain tributary when while blinded and nasally impaired (McCleave, 1967). This may be due to a genetic involvement, but McCleave did not consider the role of either the pineal or parietal eye or the sense of taste.

RESEARCH PROPOSALS

As previously mentioned, very little is known about the general physiology of fishes; the area of reproduction comprises only a fraction of this knowledge. Essentially, research is needed on all aspects of environmental reproductive-physiology. The life histories of many freshwater species have been determined, but there is a veritable lack of such information about marine or non-commercial forms. The most immediate research needed is the investigation of fish endocrinology. The chemical identification of hormones is totally wanting, and target organs and responses must be identified. Thereafter, intrinsic and extrinsic variations in hormonal balance must be understood before the knowledge of environmental aspects can be appreciated. An investigation of sex determination and a concomittant study of gonad differentiation would add greatly to the total picture of fish reproduction. Many current authors are answering vital questions about fish migrations. Here, also, an endocrineological study must be undertaken to explain many of the phenomena already reported. The morphology, behavior, and physiology (biochemistry) of salmon at sea is in dire need of investigation.

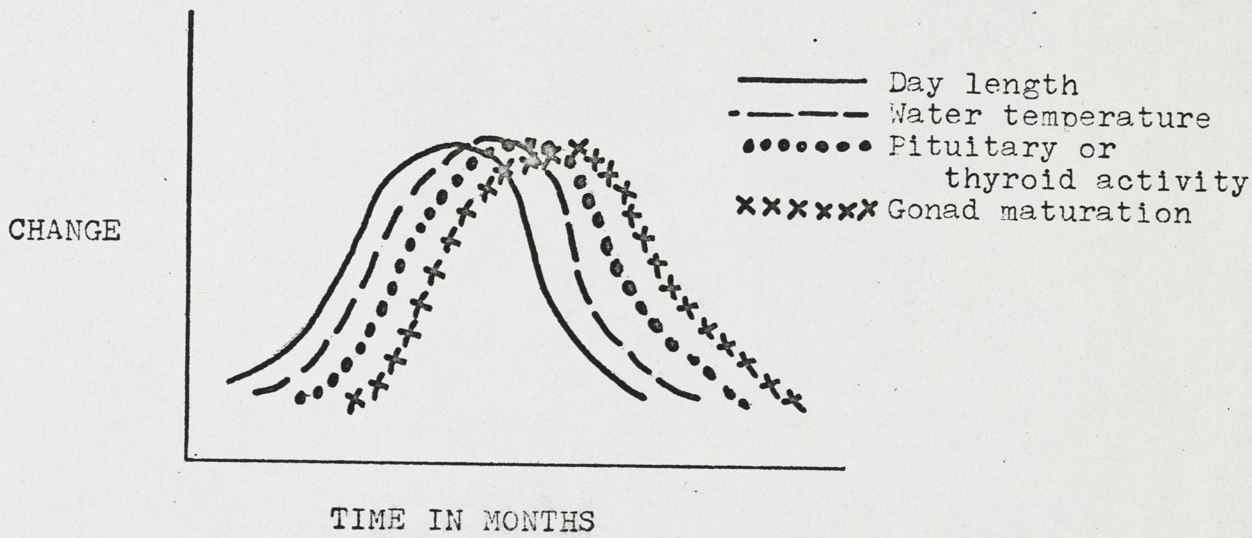
CONCLUSION AND SUMMARY

This paper reviewed the literature discussing reproductive processes and migrations of fishes as influenced by the environment. Several aspects of the reproductive functions were considered: sexual, gonad development, and spawning migration. The following generalization by Hoar (1957a) is an apropos summary of the information presented here. "Recurring cycles of growth, migration, and reproduction are associated with cyclical changes in the activity of endocrine glands. Sometimes these rhythms occur under constant environmental conditions, but in the majority of cases they follow seasonal or diurnal cycles;...endocrine activity of fish is frequently modified by light. In addition, activities of poikilothermous animals are dependent on environmental temperature, and this variable may well affect the endocrine production along with other processes. Osmotic differences, salinity, odors, or tastes may also have an effect."

The environment can exert its influence on piscine reproductive physiology in several ways. Water flow, crowding, courtship activities, age at maturation, materials in the ambient medium (including the physical characteristics of the water) affect reproduction. Some of these parameters, but primarily the first, may serve as a timing signal to induce spawning; all of the above are somehow involved in proper gonad development. Light and temperature are probably the most important controlling factors. These two environmental manifestations generally are found in concert, long day length-warm water, etc.. Photoperiodicity and/or temperature regimes are responsible for setting the biological clocks associated with reproduction. The organism probably meters light through its duration; a certain day length may initiate maturation of the gonads and another may trigger spawning. Temperature can exert its effects either through the stimulus induced by the summation of thermal units or by the monitoring of a certain critical temperature. As in light, one temperature (number of thermal units?) may cause gonadal development and another spawning responses. A recent Sigma Xi Seminar given at Colorado State University by Dr. Brown suggested that geomagnetic phenomena (associated possibly with solar or lunar tides) may also be involved in the timing of cyclic processes.

The sex products of fishes are usually at the mercy of the environment once they become independent of the gonad.

The physiology of fish reproduction is controlled by the environment via the nervous and endocrine systems. Light and temperature regimes influence pituitary activity which inturn acts on the thyroid and gonad, both of which may be directly affected by these conditions. The physical condition of the species as well as the time of of fertilization of the ova influences reproductive capacity. Generally, an environment-cortex-hypothalamus-hypophysis-gonad mechanism is responsible for reproductive control. The following illustration shows how reproductive physiology is timed by variance in cyclic environmental phenomena.



These curves may be shifted with respect to one another; they serve merely to illustrate that an environmental cycle induces an endocrine response which inturn times the gonadal rhythm.

Sex determination in fishes is as yet poorly understood. It is believed that fish go through a bisexual stage prior to gonad differentiation. Sex reversal and monosexual species are natural occurrences.

The migration of adult fish to spawning areas and the movement of the young to the parental habitat are dependent on cues from the environment. Adult fishes can home to a certain tributary of a river system from several thousands of miles away. Olfaction is probably one of the most important senses used in this process; taste, temperature sensitivity and celestial navigation may also be involved. The state of nutrition of the organism is the main factor determining when adult fish will migrate. Young fish have salinity preferences in addition to those directional cues used by their parents. Again, olfaction is of prime importance. Visual contact with the environment in conjunction with a critical water temperature can determine if a juvenile fish will move with or against a river's current. In a large lake network celestial navigation may be heavily relied upon by the migrants. A basic genetic foundation may also be involved.

There is a veritable lack of knowledge in all of the areas presented here. Further study is most importantly needed in the areas of fish endocrinology, sex determination, and gonad differentiation. An understanding is also needed of the developments taking place in the salmon while at sea.

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