[mortality]

THESIS

ECOLOGICAL EVALUATION OF TWO SYMPATRIC STRAINS OF CUTTHROAT TROUT

Submitted by

John R. Trojnar

In partial fulfillment of the requirements

for the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

June, 1972

ABSTRACT

ECOLOGICAL EVALUATION OF TWO SYMPATRIC STRAINS OF CUTTHROAT TROUT

A study was conducted on North Michigan Lake, Colorado, during the summer of 1971 to learn more about the role intraspecific variability can play in fishery management programs. Ecological differences between the Pikes Peak and Snake River cutthroat were investigated through food and habitat preference and angling vulnerability.

The Snake River cutthroat was more vulnerable to angling than the Pikes Peak cutthroat. This vulnerability was a result of ecological divergence through differences in feeding habits. The Snake River cutthroat fed mainly on surface organisms, thus making them more susceptible to the anglers who fished primarily with flies on the surface. The Pikes Peak cutthroat was highly selective for zooplankton.

It is believed that the Pikes Peak cutthroat had a higher rate of mortality prior to and during the study period.

The North Michigan Lake study illustrates only one example of the many ways intraspecific variability in fish can be utilized. Ecological, behavioral, and physiological differences can have a great influence on growth, survival, and angling vulnerability. The greatest challenge and potential of genetic variability is the establishment of two or more interacting populations in a single environment to more efficiently utilize the resources of the lake, thus maximizing fish production.

John R. Trojnar
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, Colorado 80521
June, 1972

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Fishery scientists have long been aware of genetic variability present in fish populations. Since the advent of fish culture the genotypes of various species of trout have been rigorously selected and altered to produce domesticated strains for efficient hatchery production. These include early spawning and maturity, increased growth rate and fecundity, tolerance to warm water and crowding, and resistance to disease (Donaldson and Olson, 1956). The process of selection for useful hatchery traits has diverted the gene pools from genetic homeostasis accumulated by natural selection in the parental stocks. The problem of artificial versus natural selection and its implications to fishery management has been largely ignored.

Almost totally overlooked in management programs is the genetic variability present in natural populations as a result of natural selection. Mayr (1963) has described various ways in which speciation and intraspecific differentiation develops. Ricker (1959) discussed the influence of environment and genetics on many intraspecific differences that distinguish various stocks of Pacific salmon and steelhead trout, *Salmo gairdneri*. Definite heritable differences exist between summer and winter stocks of steelhead (Smith, 1960, 1969). Genetic integrity is maintained in these anadromous species by reproductive isolation as a result of the homing instinct to natal streams. The cutthroat trout, *Salmo clarki*, is a good example of a polytypic species. A long evolutionary history of diverse stocks in different geographical regions under various environmental conditions has created a wide range of genetic variability within this species.

There are numerous examples in which intraspecific variability is even maintained in sympatric populations. Behnke (In press) reviewed the tremendous variability exhibited by the arctic char, Salvelinus alpinus. Fenderson (1964) found sympatric populations of dwarf and normal forms of lake whitefish, Coregonus clupeaformis, in five Maine lakes. Kokanee salmon, Oncorhynchus nerka, demonstrate great variability. Averett and Espinosa (1968) found differences in site selection and time of spawning between two groups of kokanee introduced in Odell Lake, Oregon. Vernon (1957) studied three races of kokanee in Kootenay Lake, British Columbia. Also in Kootenay Lake, Cartwright (1961) investigated two races of rainbow trout which differed in growth rate and age at maturity. The spawning habits of one of the races, the large Gerrard rainbow, were observed by Hartman (1969). In New York, Zilliox and Youngs (1958) studied the large and small races of smelt, Osmerus eperlanus mordax, in Lake Champlain. Khan and Qadri (1970) presented data on four different races of lake trout, Salvelinus namaycush, in Lake Superior. Discrete populations of Atlantic herring, Clupea harengus harengus, in the Gulf of St. Lawrence were described by Messieh and Tibbo (1971).

The evolutionary process works to diverge populations to partition the environment through specialization where the environment has been continuous for a long period. A good example is the species flocks in the great lakes of Africa (Greenwood, 1959). North America has a rather depauperate fauna because of recent glaciation. The establishment of two or more sympatric populations to more effectively utilize the total environment is a promising area. My study at North Michigan Lake is a start in the investigation of such a management practice.

During the past 20 years, concern that inbreeding and domestication have put the hatchery trout at a competitive disadvantage when stocked in natural waters has resulted in many studies comparing hatchery and wild trout. Some have ended with ambiguous results (Adelman and Bingham, 1955; Mason, Brynildson, and Degurse, 1967; and Smith, et al., 1969). Others demonstrated the superiority of wild strains of trout. Miller (1953) found poor winter survival of hatchery-reared cutthroat trout. When wild and hatchery rainbow trout were stocked as fingerlings in Lake De Smet, Wyoming, the wild trout were 11 times more abundant when they returned to the inlet of the lake to spawn (Muellar and Rockett, 1962). Cordone and Nicola's (1970) study of Beardsley Reservoir, California, showed poor returns of the Whitney and Virginia strains of rainbow trout which have a long history of domestication in comparison to the recently domesticated Shasta strain and the wild Kamloops rainbow. In experiments conducted in the Adirondack Mountains of New York, wild strains of brook trout, *Salvelinus fontinalis*, were superior to domestic strains in growth and survival (Webster, 1954; Flick and Webster, 1964; and Flick, 1971).

Miller (1957) states that although traits selected for in the hatchery are not deleterious *per se*, they may have genetic linkages which are at a selective disadvantage in nature while being unimportant in the artificial hatchery environment. Vincent (1960) and Moyle (1969) showed some behavioral differences between wild and hatchery strains of brook trout which may account for lower survival of hatchery trout in the wild. Miller (1958) suggests that the inability of the hatchery trout to compete with the wild resident population, not only for food but for space and cover as well, results in higher mortality of these fish.

A good example of differences in performance of a strain in a hatchery environment and in the wild is the University of Washington strain of rainbow trout, popularly known as the Donaldson rainbow. No one can dispute the superiority of this strain in Dr. Donaldson's hatchery. However, Soldwedel and Pyle (1968, 1969) found very little difference between it and a domestic New Jersey strain of rainbow trout when placed in the wild. When Menasveta (1961) compared the Donaldson strain with the domesticated Lake Chelan strain, he found the Donaldson strain had poorer survival, a slower growth rate, and a poorer return to the creel. Despite such results, Minnesota is proclaiming the Donaldson rainbow as its "dream trout" (Woods, 1971).

The genetic background of a fish is very important to its survival after being placed in a natural environment. Fry or fingerlings, particularly, must be subjected to the rigors of the wild for one or more years before they enter the fishery. The only consideration given to genetic background in the past has been between wild and domestic strains of trout. Practically no attention has been given to the differences between wild strains of trout despite the ecological, behavioral, and physiological differences that might be exploited by the fishery scientist.

Present Study

My study was conducted during the summer of 1971. It was designed to learn more about intraspecific differences in cutthroat trout which could serve as a basis for more sophisticated, scientifically based fishery management programs. North Michigan Lake was chosen for the study because it had received stockings of three strains of cutthroat trout during the past few years. Rainbow trout, rainbow x cutthroat hybrids, brook trout, longnose suckers (*Catostomus catostomus*), and a few brown trout (*Salmo trutta*) are also present in the lake. In 1968 grayling, *Thymallus arcticus*, were stocked in the lake. However, none were observed in either angler or gill net catches from the lake, and only one was seen caught below the dam.

My study evaluated differences in the ecology of the different strains of cutthroat coexisting in a single environment as reflected in food habits, habitat preference, and vulnerability to angling.

Cutthroat Strains

The three strains of cutthroat trout stocked in the lake were: Pikes Peak, Snake River, and Lahontan.

The Pikes Peak cutthroat, most likely a hybrid between the greenback cutthroat, *S. clarki stomias*, and the Yellowstone cutthroat, *S. clarki lewisi*, is one of the four strains commonly used by Colorado. The brood stock is maintained in a lake controlled by the City of Colorado Springs located in the mountains near Pikes Peak.

The Snake River cutthroat is an unnamed subspecies found in the Snake River between Jackson Lake, Wyoming, and Palisades Reservoir on the Idaho-Wyoming border. This strain is atypical of other interior cutthroat because of its fine, peppery spotting and silver-like appearance. Unlike other cutthroat it has held its own in the face of introductions of other trout and still remains the dominant fish in its native range (Beal, 1959). A hatchery brood stock has been maintained since 1949 and is being selected for earlier spawning. The Snake River cutthroat used in this study came from this source. Eggs are also taken from a brood stock in the Lake of the Woods near Jackson, Wyoming, which is stocked with cutthroat taken from the Snake River. Wyoming is currently making extensive use of the Snake River cutthroat.

The Lahontan cutthroat, S. clarki henshawi, is native to the Lahontan basin of Nevada and eastern California. The decline of the large Lahontan cutthroat of Pyramid Lake has been documented by Sumner (1940). The population now used as a source of eggs is located in Heenan Lake, California. The fish now in Heenan Lake were originally taken from the Carson River and have hybridized to a limited extent with rainbow trout. Calhoun (1944) extensively studied the food habits of this strain in Heenan Lake. Unlike the Snake River cutthroat, this strain is very difficult to raise in the hatchery. Evidently because of an evolutionary history of being predaceous on native chubs, it has been found necessary to add a protein supplement to the normal hatchery diet. Unlike other cutthroat which are spotted more posteriorly, the Lahontan is evenly spotted with spots extending onto the head and stomach region.

DESCRIPTION OF STUDY AREA

North Michigan Lake is located in north-central Colorado at the headwaters of the North Platte River system. Although situated in the montane zone, as defined by Shelford (1963), it is at a relatively low elevation of 8920 ft (2719 m). The lake has a drainage area of 25 sq miles (65 sq kilometers), a surface area of 66 acres (27 hectares), and an approximate maximum depth of 43 ft (13 m). The ice-free period is approximately from June 1 to the first or middle part of October. Ice thickness reached depths of approximately 3 ft during the winter.

Grass Creek and North Fork Michigan Creek, the two main tributaries of North Michigan Lake, have concrete fish traps located several hundred feet above the lake.

The bottom is extremely variable. Organic muck, silt and clay, gravel and rubble, and stick and leaf litter are present.

Unlike many montane lakes, North Michigan Lake is mesotrophic in nature. Heavy algal blooms occur during August and September, and dense growths of rooted macrophytes occur to depths of 10 ft. Extensive cattle grazing, a lumber camp approximately 1 mile upstream from the lake, and campers may all make a significant contribution to the nutrients entering the lake.

The lake was formed when a dam was constructed in 1962 and has been stocked annually since 1964 (Table 1).

TABLE 1. Numbers of fish stocked in North Michigan Lake.

Size of fish stocked	Year of Stocking 1964	1965	1966	1967	1968	1969	1970
					100,000*		
2"				48,000	24,000**	6,600	7,130
			10,000*	15,800	26,600	33,000***	33,500
2-4"			15,000				
4-6"	2,700	2,020	1,000	1,023			3,150

* Grayling

** Snake River cutthroat

*** Lahontan cutthroat

All others are Pikes Peak cutthroat

METHODS AND MATERIALS

Biological Parameters

Fish distribution and abundance

Vertical and horizontal gill nets were set twice monthly from June through September.

One sample with a horizontal net was taken through the ice in March. During the month of June, horizontal nets were set at four locations at each sampling period. Due to the excessive catch of longnose suckers, it was decided to set only one horizontal net at each sampling period. The "experimental" net was 150 ft long and 4 ft high and had mesh sizes ranging from 3/4 inch to 1-3/4 inch. The gill net was set perpendicular to the shore with the smallest mesh nearest shore. The location of the sets of the last three months of the study is given in Figure 1.

The vertical gill nets consisted of three 12 x 40 ft panels. Each panel consisted of two 6 x 40 ft panels of different mesh sizes sewn together and was attached to a 10 ft aluminum roller. The pairing of the mesh sizes of the panels were as follows: 1/2" with 5/8", 3/4" with 1", and 1-1/4" with 1-1/2". The rollers were attached in tandem, and the nets were set at Station 4 (Figure 1). Each panel was marked at 10-foot intervals so that the depth of each individual fish could be recorded. A spreader bar was placed at a depth of 20 ft, and a metal conduit pipe served as a weight across the bottom of the net. Window sash weights of 24 lbs each served as anchors at each end of the roller tandem.

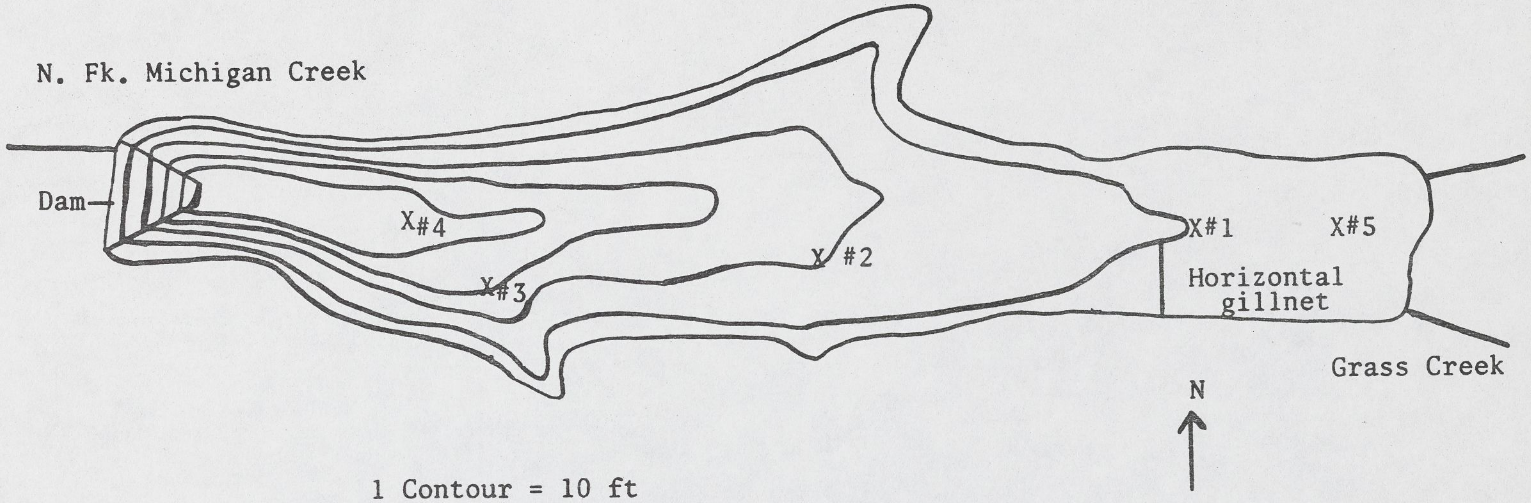

FIGURE 1. Map of North Michigan Lake and location of sampling stations.

Age and growth of fish

Lengths and weights were recorded for all fish in the sample. Stomach samples were taken from all cutthroat, rainbow, and rainbow x cutthroat hybrids, five longnose suckers, and approximately 10 brook trout on each sampling date. Numbers, frequency of occurrence, and reconstructed volumes were used in the analysis of the food items.

Otoliths were stored in water, then examined under a dissecting microscope using reflected light. Brook trout otoliths were submerged in glycerin before being read. Because cutthroats, rainbows, and their hybrids have otoliths which are large and thick, they were baked as described by Lawler and McRae (1961) for 30 minutes at 175-180° C before being submerged in glycerin and read.

Creel census

No attempt was made to estimate the total catch or angler use of the reservoir. The creel census was designed merely to find out what forms were entering the catch and in what percentage throughout the fishing season. Angler interviews were made late in the morning and just before dark.

Plankton

Plankton samples were taken twice a month at Station 4 (Figure 1) on the day the gill nets were set. Three 30 ft vertical hauls with a #20 mesh plankton net 30 cm in diameter served as a pooled sample which was preserved in 10% formalin. Zooplankton was enumerated using a Palmer counting cell. Phytoplankton was evaluated qualitatively.

Bottom fauna

Bottom samples were taken twice monthly at depths of 5, 10, 20, 30 and 40 ft (Figure 1). Each sample (four grabs with àn Ekman dredge, 1 sq ft) was sieved through a wash bucket 30 cm in diameter with a #30 mesh wire cloth bottom. Samples were preserved with rose bengal dye and formalin and examined using a sugar flotation method as described by Lackey and May (1971).

Physical Parameters

Oxygen and temperature measurements were taken twice a month at noon at Station 4 (Figure 1) on the day the gill nets were set. A temperature profile was taken using a thermistor. Depth and temperature were recorded only when there was a temperature change. Oxygen determinations were made to the nearest mg/l using a Hach oxygen kit. Four samples were taken at depths of 5, 15, 25, and 35 ft, corresponding to the mid-depths of the four 10-foot sections of the vertical gill net.

RESULTS AND DISCUSSION

Temperature and Oxygen

Temperature remained fairly cool throughout the summer, with 63° F (17.3° C) being the maximum surface temperature recorded (Figure 2). The lake became thermally stratified in August, at which time anaerobic conditions developed at depths greater than approximately 20 ft (Figure 3). Data from the late September sampling seems to indicate that the lake was in the process of "turning-over." The temperature was fairly uniform; however, anaerobic conditions still persisted at a depth of 35 ft. At no time were fish stressed as a result of a combination of low oxygen and high temperatures.

Benthic Fauna

Bottom samples revealed a lack of variety in the organisms present. Chironomid larvae, snails, and oligochaetes made up the major portion of the organisms (Table 2). Chironomid pupae, damselfly and mayfly naiads, and larval *Chaobrus* occurred in very reduced numbers. Samples at 5 and 10 ft contained many more organisms than those at 20, 30 and 40 ft. Any other generalizations, especially quantitative, would be unwise because the bottom was extremely difficult to sample due to a steep bottom gradient, rocks, and tree branches. Although the amphipod *Hyalella azteca* and water mites were present in stomach samples, none were found in the bottom samples.

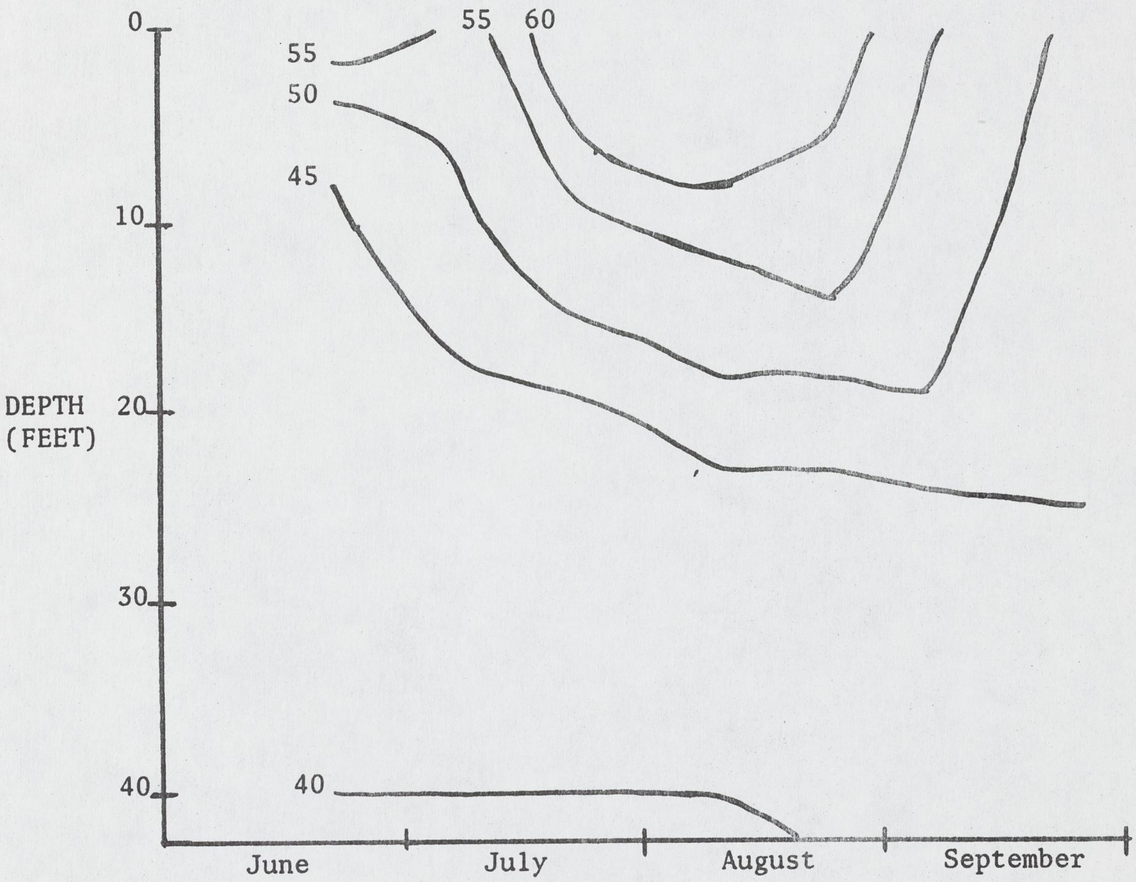

FIGURE 2. Temperature (°F) profile in North Michigan Lake throughout the study period.

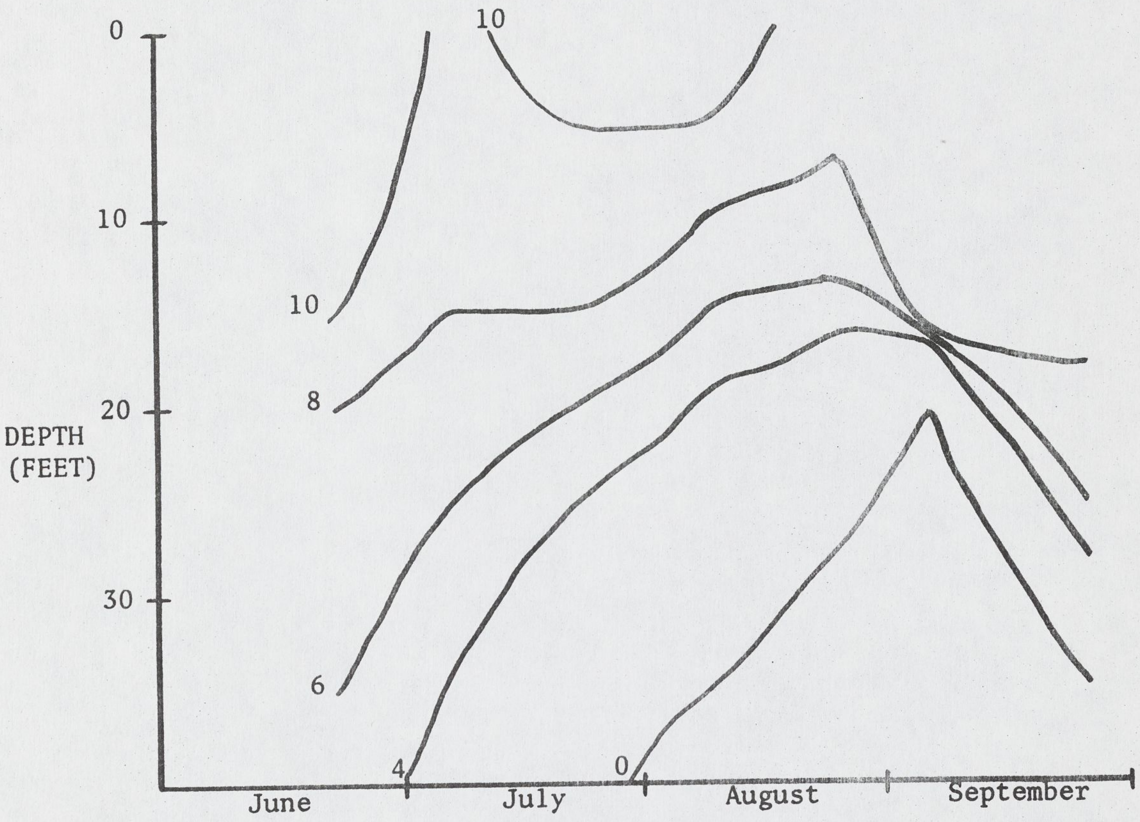

FIGURE 3. Oxygen (mg/l) profile in North Michigan Lake throughout the study period.

TABLE 2. Numbers and volumes (ml) of major organisms found in bottom samples of North Michigan Lake. (One sample composed of organisms sorted from 1 sq. ft of bottom.)

Depth	Date	Chironomid larvae		Gastropoda		Oligochaete	
		Number	Volume	Number	Volume	Number	Volume
5 feet	6/21	---	---	---	---	---	---
	7/6	207	.40	50	.40	63	.10
	7/23	46	.05	22	.15	23	.04
	8/9	13	.026	1	.008	10	.02
	8/26	34	.05	11	.05	16	.032
	9/7	17	.10	12	.05	6	.012
	9/24	52	.20	39	.20	112	.10
10 feet	6/21	126	.70	20	.05	0	---
	7/6	107	.30	12	.10	47	.15
	7/23	59	.10	29	.05	44	.05
	8/9	35	.10	6	.05	9	.018
	8/26	93	.30	0	--	24	.05
	9/7	90	.30	6	.05	12	.024
	9/24	22	.05	44	.20	17	.02
20 feet	6/21	4	.008	0	--	5	.01
	7/6	8	.016	0	--	2	.004
	7/23	21	.05	0	--	10	.02
	8/9	36	.15	0	--	69	.10
	8/26	8	.016	0	--	16	.032
	9/7	9	.018	0	--	0	--
	9/24	13	.10	0	--	11	.05
30 feet	6/21	17	.10	0	--	0	--
	7/6	13	.05	0	--	0	--
	7/23	34	.15	0	--	0	--
	8/9	49	.20	0	--	0	--
	8/26	14	.028	0	--	0	--
	9/7	3	.006	0	--	0	--
	9/24	17	.10	0	--	0	--
40 feet	6/21	3	.006	0	--	0	--
	7/6	4	.008	0	--	0	--
	7/23	1	.002	0	--	0	--
	8/9	0	--	0	--	0	--
	8/26	0	--	0	--	0	--
	9/7	0	--	0	--	0	--
	9/24	1	.002	0	--	0	--

Phytoplankton and Aquatic Plants

During the months of June and July various species of green algae (Chlorophyta) were predominant, although in very low numbers. During the latter part of July the blue-greens (Cyanophyta) *Anabaena* and *Aphanizomenon* increased in abundance and became a "bloom" by early August. From the end of August through September, there was a bloom of *Ceratium* (Pyrrhophyta) with varying amounts of *Anabaena*, *Aphanizomenon*, and *Volvox* (Chlorophyta). Parvin Lake is most suitable for making comparisons because of its similar productivity and elevation. Lackey (1971) found that *Ceratium* reached its peak of abundance earlier in Parvin Lake and never became dominant as it did in North Michigan Lake. The bloom of *Anabaena* and *Aphanizomenon* started at the same time of the year in both lakes but lasted for a longer duration in Parvin Lake.

The development of thick beds of the rooted macrophytes *Elodea* and *Potomageton* coincided with the algal blooms of August and September.

Zooplankton

Rotifers, copepods, and the cladocerans, *Daphnia* and *Bosmina*, were the dominant zooplankters. The cladocerans, *Ceriodaphnia*, *Diaphanosoma*, and *Chydorus*, occurred infrequently. *Polyarthra*, *Felinia*, and *Keratella* made up most of the rotifers, as they did in Parvin Lake. In contrast, Lackey (1971) found that they were most abundant during the winter and early spring and very scarce during the summer.

The relative abundance of zooplankton throughout the summer months is given in Figure 4. Rotifers were the dominant zooplankters except in late July-early August when copepods were the most abundant. The

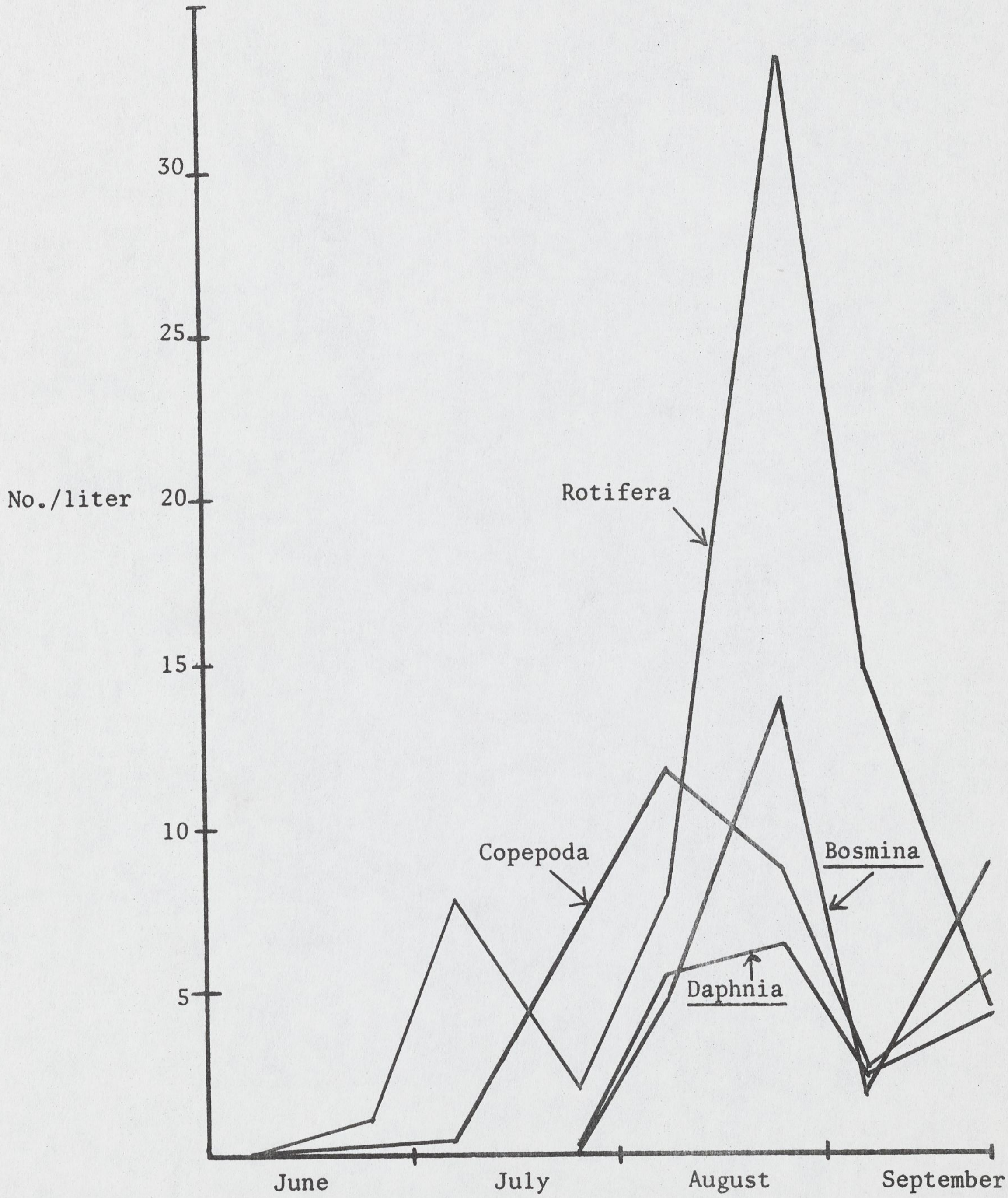

FIGURE 4. Relative abundance of zooplankton in North Michigan Lake during the study period.

highest abundance of rotifers was reached in late August. Peaks of *Daphnia* and *Bosmina* also occurred in late August. It appears that copepods, *Daphnia*, and *Bosmina* were again increasing in late September.

Fish

Vertical distribution

Fish moved into deeper waters as the season progressed. In general fish were concentrated in the upper 10 ft of water during June and July. They went down to 20 ft in August and to 30 ft in September (Figure 5). Although there are no striking relationships between oxygen and temperature and fish distribution, in general fish avoided areas with less than 5 mg/l oxygen and preferred mid 50° F water temperatures.

Vertical distribution of zooplankton, particularly *Daphnia*, was not determined. Areas of high abundance of zooplankton may have had a significant effect on fish distribution, particularly during the months of August and September.

Differences in vertical distribution between species and between the two strains of cutthroat were not apparent. Rainbow trout were caught only in the upper 10 ft, but the small sample size precludes a definitive statement.

There was a sudden increase in the vertical gill net catch of suckers in late July, continuing through early September. Such a pelagic existence is reflected in the occurrence of zooplankton in their stomachs at this time.

Depth (ft)	June 4 Temp. and O_2	June 4 Type	June 22 Temp. and O_2	June 22 Type	July 6 Temp. and O_2	July 6 Type	July 23 Temp. and O_2	July 23 Type	August 10 Temp. and O_2	August 10 Type	August 27 Temp. and O_2	August 27 Type	September 6 Temp. and O_2	September 6 Type	September 25 Temp. and O_2	September 25 Type
	48°F		57°F		54°F		63°F		62°F		61°F		57°F		48°F	
5		3 PP 3 BT 4 RT 3 S	10 mg/l	4 SR 4 PP 8 BT 2 RT 3 S	9 mg/l	4 SR 3 PP 1 S	10 mg/l	6 SR 3 PP 1 RT 13 S	10 mg/l	2 SR 1 PP 4 BT 26 S	9 mg/l	1 SR 9 BT 5 RT	9 mg/l	1 PP 6 BT	9 mg/l	4 BT 2 RT
10	43°F		44°F		47°F		54°F		57°F		59°F		54°F		47°F	
15			10 mg/l	1 SR 1 PP	8 mg/l	1 BT	8 mg/l	1 BT 1 S	6 mg/l	1 SR 3 BT 10 S	5 mg/l	2 SR 3 PP 10 BT 8 S	9 mg/l	1 SR 2 PP 5 BT 9 S	9 mg/l	3 PP 1 S
20	41°F		42°F		44°F		44°F		48°F		47°F		49°F		46°F	
25			9 mg/l	1 PP	6 mg/l		4 mg/l		1 mg/l		1 mg/l		0 mg/l	8 S	6 mg/l	1 SR 3 PP 2 S
30	40°F		41°F		42°F		41°F		42°F		42°F		43°F		45°F	
35			6 mg/l		5 mg/l		3 mg/l		0 mg/l		0 mg/l		0 mg/l	1 PP	0 mg/l	

BT = Brook trout; PP = Pikes Peak; RT = Rainbow trout; SR = Snake River; S = Suckers

FIGURE 5. Vertical distribution of fish at 10 foot intervals in North Michigan Lake.

Differences in gill net catch

Vertical and horizontal gill net catches reveal differences among species in their susceptibility to these two methods of capture (Table 3). Horizontal gill nets accounted for 76% of the brook trout and 79% of the suckers netted, but only 42% of the Pikes Peak cutthroat, 45% of the Snake River cutthroat, and 36% of the rainbows. Rainbow and cutthroat trout appear more evenly distributed, while brook trout and suckers were more bottom oriented.

There is no differential susceptibility to either type of gill net by the two strains of cutthroat. Consequently, a combined set of a horizontal and vertical gill net can be considered one unit of effort, and the combined gill net catch serves as a reliable indicator of the relative abundance of Pikes Peak and Snake River cutthroat in the lake.

Relative abundance and biomass

It is impossible to estimate the actual percentage of each species present in the lake because different species had different vulnerability to the two forms of nets used. However, a look at the relative numbers and their weights in relation to the total gill net catch would be useful in getting some idea of how the lake's energy is being channeled (Table 4). It is interesting to note that only about 12% of the numbers and 10% of the weight of the total gill net catch represented introduced cutthroat trout. Approximately 50% of the numbers and 27% of the weight could be considered as potentially contributing to the sport fishery. A large portion of the lake's productivity is being channeled into an unused resource - the longnose sucker population.

TABLE 3. Percentage of each species or strain caught by the two methods of gillnetting in North Michigan Lake. Numbers are in parenthesis.

Gillnet	Pikes Peak	Snake River	Rainbow	Brook	Sucker
Horizontal	42% (22)	45% (19)	36% (8)	76% (195)	79% (324)
Vertical	58% (30)	55% (23)	64% (14)	24% (60)	21% (88)

TABLE 4. Percentage of total numbers and weight each species or strain contributed to the gillnet catch in North Michigan Lake. Actual numbers or weight (Kg) are given in parenthesis.

	Pikes Peak	Snake River	Rainbow	Brook	Sucker
Numbers	6.6% (52)	5.4% (42)	2.8% (22)	32.6% (255)	52.6% (412)
Weight	4.2% (5.2)	5.3% (6.5)	2.0% (2.5)	16% (19.8)	72.5% (89.7)

Growth

Growth curves for brook trout and cutthroat trout, using simple linear regression are shown in Figure 6. There is no difference between the two strains of cutthroat. The growth of the age II brook trout and Pikes Peak cutthroat is interesting. By the end of their third summer, the brook trout were larger than the Pikes Peak cutthroat. However, as three-year-olds the cutthroats are always larger. This could mean that either the cutthroat normally undergoes considerable growth during the winter, or for some reason the 1969 year class of Pikes Peak cutthroat has a reduced growth rate.

Maturity

A striking phenomenon not readily explained is the high incidence of immaturity among both brook and cutthroat trout (Table 5). Twelve of 14 age II brook trout examined in August-September samples were immature, as well as 15 of 24 of age III. Both age IV females were mature. Previous studies in the Rocky Mountain area show that almost all brook trout are mature at age II and all are mature by age III (Holton, 1953; Allen, 1956; and Rabe, 1957).

Cutthroat trout were examined in the March, June, and early July samples. Nineteen of 21 age III Pikes Peak and 18 of 19 Snake River cutthroat of that same age were immature. In the late fall sample in which gonadal development should have progressed to a considerable extent only a single Snake River cutthroat, a male, out of five examined exhibited developing testes. Hayden (1967) found that more

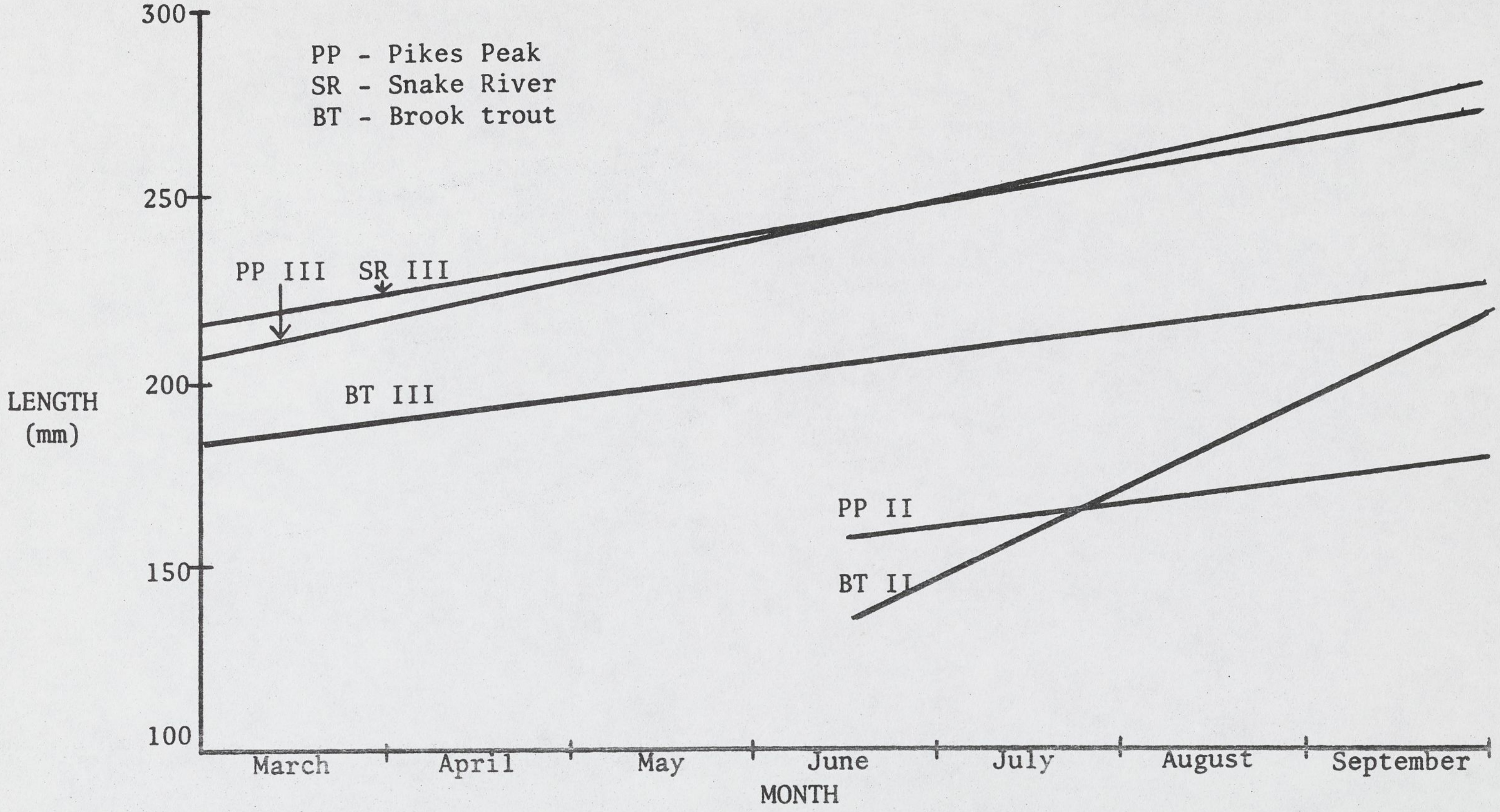

FIGURE 6. Growth curves (linear regression) of two and three-year-old cutthroat and brook trout in North Michigan Lake.

TABLE 5. Incidence of maturity of brook trout and cutthroat trouts in North Michigan Lake.

Species and degree of maturation	Age II		Age III		Age IV		Age V	
	Male	Female	Male	Female	Male	Female	Male	Female
Brook trout								
Immature	6	6	7	8	0	0	0	0
Mature	2	0	3	6	0	2	0	0
Pikes Peak								
Immature	0	0	6	13	0	1	0	0
Mature	0	0	2	0	0	1	1	0
Snake River								
Immature	0	0	10	8	0	0	0	0
Mature	0	0	1	0	0	0	0	0

than 80% of the Snake River cutthroat mature at ages III and IV, with more males maturing at an earlier age than females. Similar results on different strains of cutthroat have also been found by Irving (1955) and Drummond (1965).

A search of the literature revealed no satisfactory explanation as to the cause of this observed late maturation. Parasites and inadequate diet, suggested as a possible cause by Vladykov (1956), do not apply to North Michigan Lake. Grachev (1971) reports that egg development of chum salmon, *Oncorhynchus keta*, can proceed from stage to stage only after certain levels of fat content are achieved. Fish in the March sample appeared to have adequate deposits of fat. Certain unknown environmental conditions are probably present which account for this late maturity, since both brook and cutthroat trout are similarly affected.

Survival

No Lahontan cutthroat occurred in the gill net catch indicating very poor survival of this strain.

Based on the 1968 stocking records, the Snake River cutthroat comprised 48% and the Pikes Peak 52% of the cutthroat stocked. If survival of the two strains were the same, a similar ratio would appear in the gill net catch of three-year-old cutthroat. The Snake River cutthroat made up 58% of the gill net catch. Using a Chi-square statistical analysis with Yate's correction factor, there is a suggestion that the gill net catch is different from the expected catch ($P < .08$). Such a probability may not warrant a definitive statistical pronouncement because of the small sample size. However, there is circumstantial evidence which suggests that the Snake River cutthroat probably had better survival from the time of stocking to the start of the study. Trends in gill net and angler catches suggest that the Pikes Peak suffered higher mortality than the Snake River cutthroat during the summer.

An unknown but substantial number of Snake River cutthroat probably left the lake after being stocked in 1968. In the spring of 1970, one year before the study began, Dr. Stephen Flickinger (Personal communication) caught numerous Snake River cutthroats in the creek below the dam. In addition, angler catches in the inlet and outlet close to the lake during the study period revealed a 2 to 1 ratio of Snake River to Pikes Peak cutthroat.

It is consistent with their life history in the Snake River that they would exhibit downstream migratory behavior when young. Hayden (1967) found that spawning occurs in tributary streams of the Snake River. Resulting young migrate down to the Snake River as young-of-the-year and as yearlings. Such a situation could conceivably have been duplicated in North Fork Michigan Creek. It has been the experience of Wyoming biologists that the Snake River cutthroat will leave a lake if an outlet exists.

One factor that may artificially inflate the number of Pikes Peak cutthroat attributed to the 1968 stocking is recruitment from natural reproduction in the inlets. Any three-year-old cutthroat naturally reproduced in the inlet, and which subsequently migrated to the lake, would be classified as a Pikes Peak since this was the only cutthroat stocked prior to 1968.

Individual gill net catches of cutthroat trout throughout the year suggests some interesting trends (Figure 7). Although the sample sizes are small there seems to be a decrease in the catch of age III Pikes Peak cutthroat as the season progresses, indicating possible mortality. In spite of the greater rate of removal of the Snake River cutthroat by anglers, the gill net catch of this strain remained remarkably constant. A Chi-square analysis comparing the one sample in March and the June and July samples to the expected ratios of the two strains when stocked revealed no statistical difference. However, the ratio of the two strains of cutthroat of age III in the August and September samples was statistically different ($P < .025$) than expected if survival was equal between the two lots of fish. This drop in the number of Pikes Peak cutthroat is supported by the fact that this strain composed 26% of the anglers' cutthroat catch in June and July, as opposed to only 14% in August and September.

It will be interesting to observe if substantial numbers of Snake River or Pikes Peak cutthroat are present in the lake in the spring of 1972, for only four Pikes Peak cutthroat of age IV or older were caught in the gill nets the entire year. This would indicate poor survival between the ages III and IV. This cannot be due to spawning mortality because few cutthroat in the lake are mature at age III.

Food habits

To make the discussion of food habits less cumbersome, and at the same time ecologically more meaningful, food organisms were classified into one of three categories: benthic, pelagic, or surface (Figure 8).

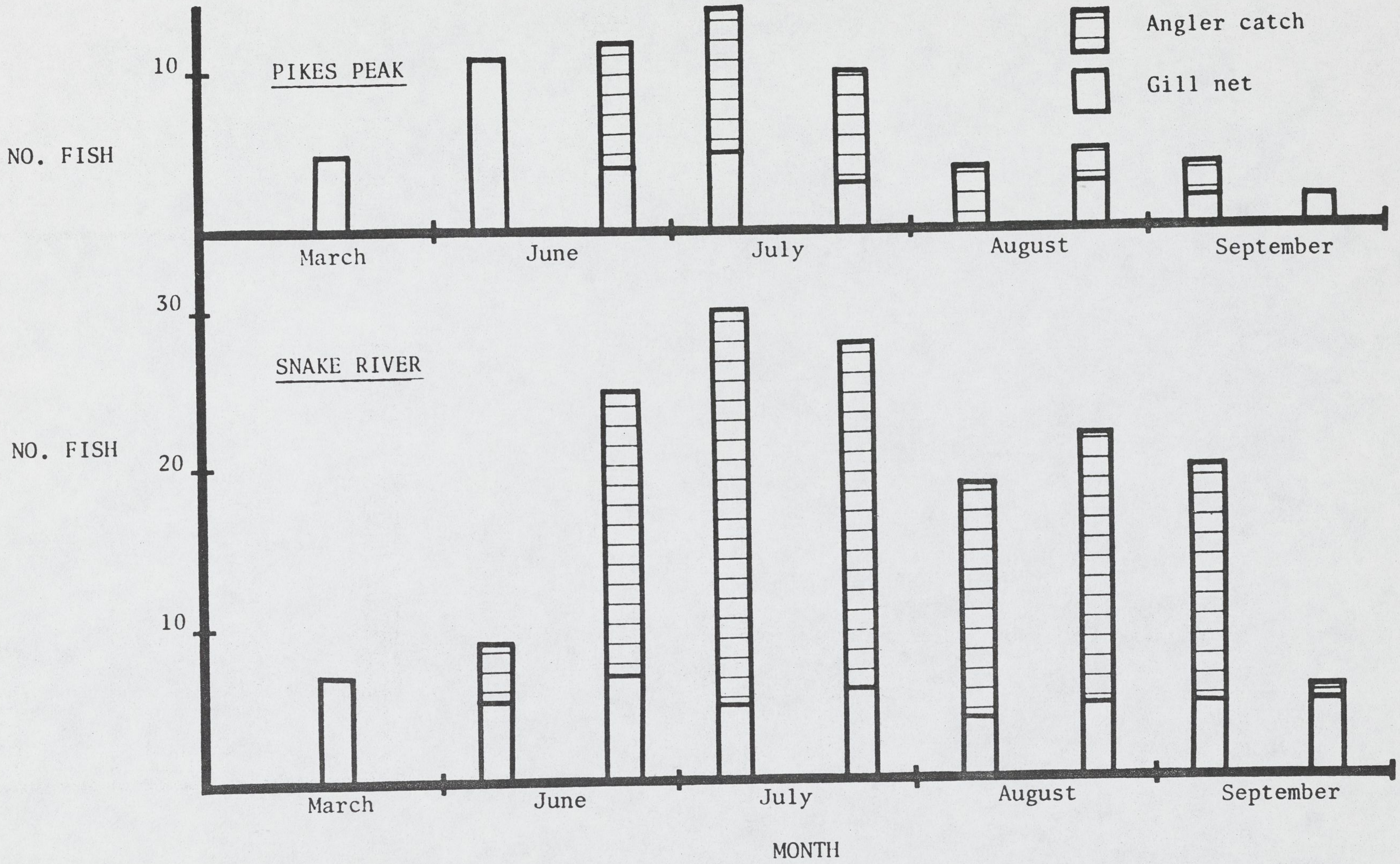

FIGURE 7. Gill net catch and anglers catch of three-year-old cutthroat in North Michigan Lake. (No angling sample was taken in March).

BENTHIC

CHIRONOMIDAE LARVAE
AMPHIPODA
HYDRACARINA
GASTROPODA
ODONATA
EPHEMEROPTERA
COLEOPTERA (AQ.)
TRICOPTERA LARVAE

SURFACE

COLEOPTERA (TERR.)
HYMENOPTERA
DIPTERA
HEMIPTERA
ORTHOPTERA
CHIRONOMIDAE ADULT

PELAGIC

ZOOPLANKTON
CHIRONOMIDAE PUPAE

FIGURE 8. Classification of food items in North Michigan Lake.

Distinct differences occurred in the food habits. Figure 9 shows the percentage by volume each food category was consumed by the trout for the four months. The Pikes Peak cutthroat's diet was predominantly zooplankton (68.5%). Surface insects, mostly terrestrial insects, composed the major portion of the diet of the Snake River cutthroat (67.7%). The brook trout fed more on benthic organisms than the cutthroat. Although 56% of the food eaten by brook trout was from the pelagic zone, in contrast to the Pikes Peak cutthroat which fed mostly on zooplankton, half of the pelagic organisms consumed by brook trout were chironomid pupae. More than half (54.2%) of the food consumed by rainbow trout consisted of benthic organisms, but a small sample size and a few fish having many snails in their stomachs probably biased the results. However, stomach samples from large rainbow trout indicate that at least this portion of the population fed almost exclusively on snails.

Figure 10 gives the percentage each food category contributed to the diet throughout the summer months. Although the two strains of cutthroat and the brook trout fed on the same organisms, they differed in the degree each food category was exploited. Benthos made up a major portion of the food in early June. Surface insects, mostly terrestrial hymenopterans, were eaten in late June. In early July chironomid pupae became abundant and made up the major portion of the brook trout's diet. In late July brook trout continued to feed on chironomid pupae, while the Snake River cutthroat ate chironomid adults and terrestrial insects. The Pikes Peak cutthroat fed on terrestrial insects and benthos. Starting in August, the Pikes Peak cutthroat fed almost totally on zooplankton. Brook trout fed on zooplankton, but

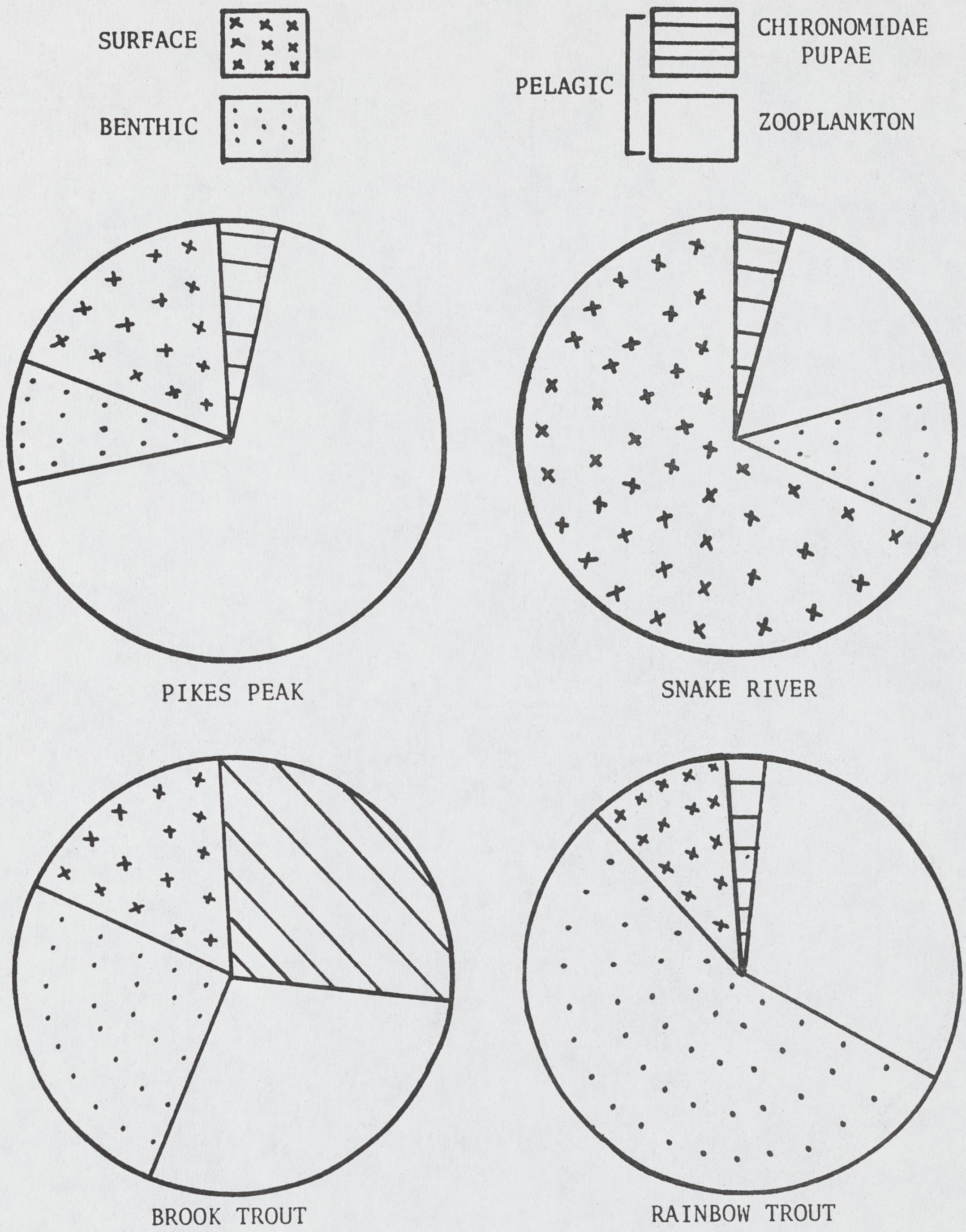

FIGURE 9. Percentage (by volume) consumption of each food category by trout in North Michigan Lake.

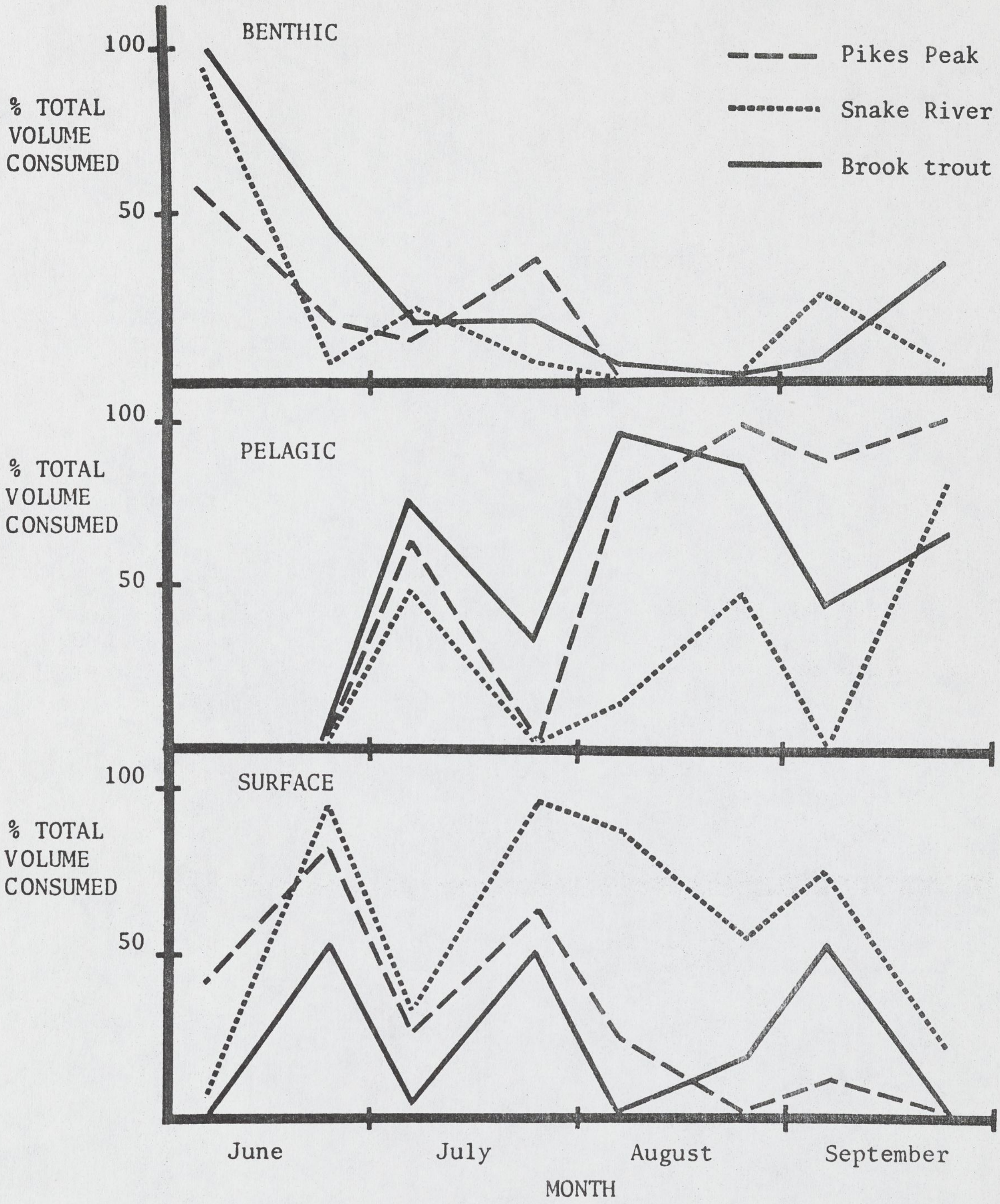

FIGURE 10. Percentage (by volume) contribution of each food category to the diet of trout throughout the summer months in North Michigan Lake.

still continued to feed on chironomid pupae to an extent. Terrestrial insects continued to make up the main portion of the diet of the Snake River cutthroat. It was not until late September, when all other food organisms were scarce, that zooplankton became the dominant food of the Snake River cutthroat.

Figure 11 shows the relative abundance of *Daphnia* and on the same time scale the portion of *Daphnia* in the diets of the trouts. The amount of *Daphnia* in the stomachs of brook trout and Snake River cutthroats seem to reflect the relative abundance of that organism in the environment. Particularly striking are the coincidental peaks in late August and the low points in early September. There is virtually no coincidental drop in *Daphnia* consumption by the Pikes Peak cutthroat, indicating a high degree of selectivity on the part of this strain for this organism.

Table 6 gives the frequency of occurrence of each food category. It is noteworthy that almost four out of five Snake River cutthroats had eaten at least one surface organism. The degree of overlap into other food categories is indicated by the sum of the frequencies for a particular strain or species. It seems that the Snake River cutthroat, in addition to feeding on the surface, is also more opportunistic than the others. This would be expected of a fish with an evolutionary history in a large river environment.

Only frequency of occurrence of the food items of the longnose sucker was recorded (Table 7). Because the sucker does not have a definite stomach region, it would be very difficult to have the same

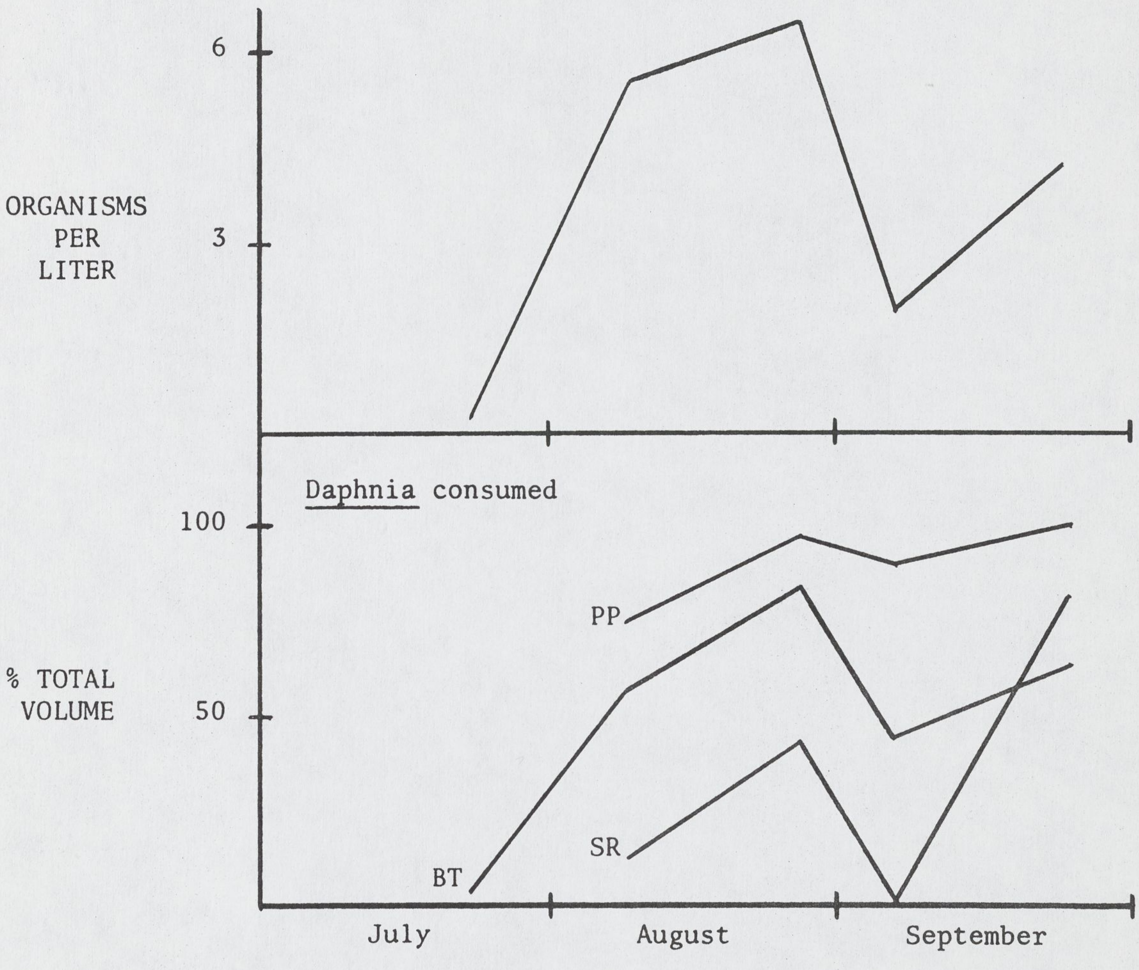

FIGURE 11. Relative abundance of *Daphnia* and its contribution to the diets of the cutthroat and brook trout in North Michigan Lake.

TABLE 6. Frequency of occurrence of each food category in the species or strains of trout in North Michigan Lake.

Category	Pikes Peak	Snake River	Brook trout	Rainbow trout
Benthic	32	43	50	50
Pelagic	52	27	36	25
Surface	36	78	25	35
	120	148	111	110

TABLE 7. Frequency of occurrence of food items in the stomachs of longnose suckers in North Michigan Lake.

Food items	June-July (n=15)	August-September (n=20)
Zooplankton	13	75
Chironomidae larvae	33	25
Gastropoda	7	5
Algae	7	55
Detritus	40	5
Mud	40	10

proportionate sample of intestine for each individual. The sucker also indiscriminantly takes in detritus and food organisms which it mascerates thus rendering it difficult to separate different food items.

In June and July the suckers fed mainly on the bottom. However, in August and September they were more pelagic, and 75% of those sampled had zooplankton in their stomachs. Unlike the trout which fed totally on Daphnia, the suckers also ate Bosmina to a limited extent. Similar exploitation of zooplankton by the longnose sucker has already been documented by Hayes (1956) in Shadow Mountain Reservoir, Colorado. If suckers are serious competitors with the trout in the lake it would be during August and September, and they would have the most effect on the Pikes Peak cutthroat. A casual relationship with the apparent mortality of the Pikes Peak cutthroat during this period cannot be proven; however, such a possibility cannot be ruled out.

Creel census

The lake was divided into three general fishing areas (Figure 12). Section I, the shallow end of the lake, received the heaviest fishing pressure and produced the best fishing in June and July. Fishing in sections II and III improved as the summer progressed when the fish moved into deeper water. These areas provided the best fishing in August and September.

The stocking record of 1968, the relative abundance of three-year-old cutthroat as indicated by the gill net catch, and the relative angler catch of the two strains of cutthroat are given in Table 8. A Chi-square statistical analysis comparing the difference between

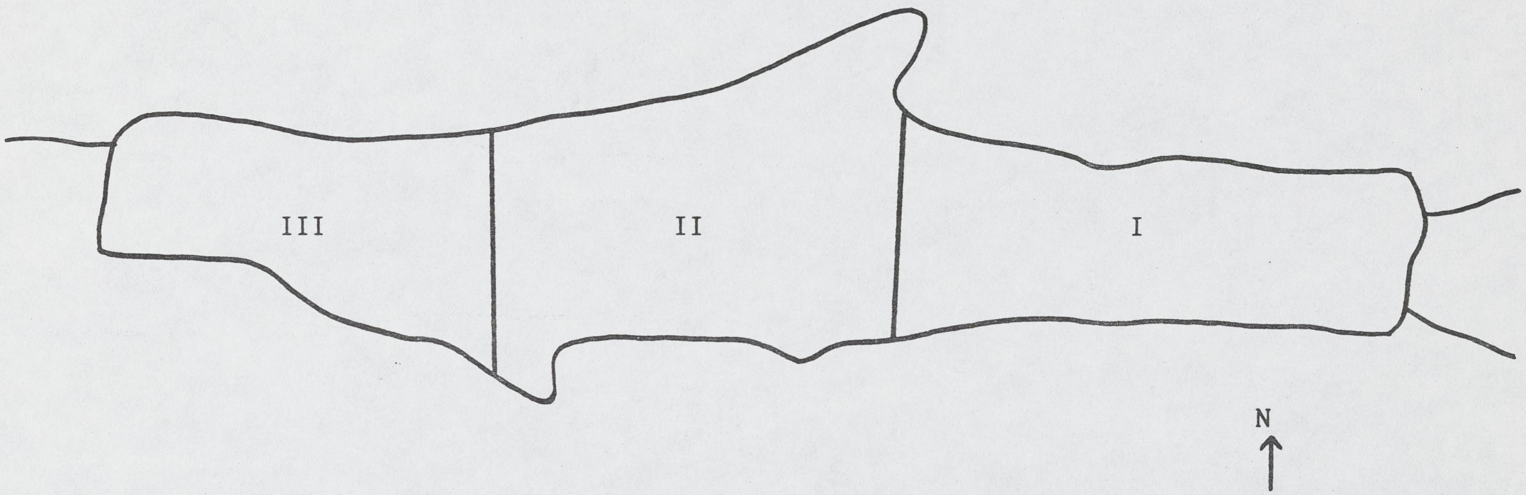

FIGURE 12. General fishing areas on North Michigan Lake.

the expected angler catch and the actual angler catch was highly significant ($P < .005$). Clearly the Snake River cutthroat is more susceptible to angling. This may be due to a combination of two factors. A large portion of the diet of the Snake River cutthroat came from the surface, and most of the fishermen fished on the surface. The Snake River cutthroat also appears to be more opportunistic in its feeding behavior.

GENERAL APPLICATION

Genetic variability in fish populations offers a myriad of possibilities in fishery management programs.

Two basic approaches might be considered to evaluate different strains. The first is the predictive approach. A strain (or strains) is selected to fit a certain set of biological and environmental conditions of a particular body of water under consideration. The selection of strains would be based on the known life histories of several strains being considered.

There are numerous examples of this approach. Two lakes in Wyoming known as Seven and Eight Mile Reservoirs have high concentrations of dissolved solids. After brook trout failed to survive in these waters the Lahontan cutthroat was stocked. This subspecies of cutthroat has been subjected to an ever-increasing saline environment during the past several thousand years, since desiccation of pluvial Lake Lahontan. The introduction proved successful (LaRivers, 1962). Van Velson (1969) studied the life history of the large migratory rainbow of Lake McConaughy, Nebraska, which uses tributaries of the North Platte River 100 miles above the lake to spawn. Wyoming has a series of reservoirs on the North Platte. Wishing to establish a self-sustaining rainbow population, but with inadequate spawning areas in the vicinity of the reservoirs themselves, the McConaughy rainbow will be tried. Eggs will be planted in tributaries above the reservoirs in hope that they will migrate down to the reservoirs to grow and return to the tributaries to spawn. King (1963) described the life history of the large predaceous rainbow of Eagle Lake, California. It relies very heavily on the tui chub, *Gila bicolor*, for food. With an ever-growing problem of the related Utah chub, *G. atraria*, in Flaming Gorge Reservoir, a fish is needed to utilize and perhaps control this rough fish and at the same time be more vulnerable to angling than the brown trout. Knowing that the Utah chub is similar to the tui chub, Wyoming is now considering stocking the Eagle Lake rainbow in Flaming Gorge Reservoir.

The life history of the Henry's Lake cutthroat and the conditions of the lake itself, as described by Irving (1955), suggests that this particular strain of cutthroat might provide an alternative in some lakes in which the rainbow is currently stocked. Henry's Lake, Idaho, is a very atypical cutthroat lake, being shallow and eutrophic. This cutthroat is a hybrid of several subspecies of cutthroat and the rainbow trout, making it very heterogeneous. Cowdrey Lake in the North Park area of Colorado was stocked with this strain in December, 1971, in an attempt to learn more about its potential in fishery management programs. Raleigh and Chapman (1971) stated that the Henry's Lake strain does not do well in a stream environment.

The other basic approach one can take in evaluating different strains is the stocking of two or more strains under a wide variety of biological and physical conditions and observing how they perform. Such was the case in North Michigan Lake. Genetically distinct strains were used but no prior work was done with the Pikes Peak cutthroat, and no one could predict how the Snake River cutthroat, which had an evolutionary history in a large river environment, would behave in a lake environment. Because of this, further studies should concentrate on these two strains in other waters in order that we may select the best strain for a particular set of biological and physical parameters. Colorado currently uses four different strains of cutthroat trout, and such an evaluative approach should be taken with these strains. This would be similar to the work done by Flick and Webster (1969, 1970, 1971) on various strains of wild and domestic brook trout.

Briefly, the most common goals of fishery management programs would be desirable growth of fish and good survival resulting in an ultimate high return to the angler. Such goals can be greatly influenced by the strain or combination of strains used.

Growth rate can be affected in any number of ways. A strain that grows to a large size probably has a strong evolutionary selection as a predator, such as the Lahontan cutthroat and the Eagle Lake rainbow. The food habits of the large Gerrard rainbow of Kootenay Lake have not been documented, but it probably forages on kokanee salmon while the "normal" rainbow of the lake probably feeds on invertebrates. The way a strain interacts with other species can also affect its growth rate. Nilsson and Filipsson (1972) described a sympatric population of dwarf and normal char. Ordinarily, one would expect the plankton feeder to be the dwarf form, but this is not the case. The dwarf form is the benthic feeder because it must compete with the brown trout which is also present. It is possible that the dwarf races of whitefish (Fenderson, 1964) and smelt (Zilliox and Young, 1958) result from such an interaction. Distinct genetic differences between these races result in different behavioral patterns when they are sympatric.

Dwarfism is not genetically controlled but is the outcome of the ecological interaction between distinct genotypes. When a dwarf population of whitefish was placed in a lake without other whitefish, growth rate was normal (Roderick, 1965).

In other instances of growth differential there appears to be no ecological differences which may have affected the rate of growth. In some instances one strain may be able to assimilate food more efficiently. Mohler (1966) found that the Green Lake (Minn.) strain of smallmouth bass, Micropterus dolomieui, had a greater efficiency of food (minnows) utilization than the Elk River (Mo.) strain. Growth differences of wild and domestic strains of brook trout and their hybrids (Flick and Webster, 1969, 1970, 1971) are a result of genetic differences. Because of the lack of data the cause of such growth differences can only be speculated. Both behavioral and physiological differences may be at work.

The genetic background of a strain has a great influence on survival as well as growth. The ability of the Lahontan cutthroat to withstand high concentrations of dissolved solids has already been mentioned. Genetic control of migratory behavior of young fish can have a great influence on the success of introductions into new waters. Such genetic control has been established for sockeye salmon, Oncorhynchus nerka, by Raleigh (1967) and Brannon (1967) and for cutthroat trout by Raleigh and Chapman (1971) in which entirely different migratory patterns are necessary for fry in the inlets and outlet to return to the lake. Northcote (1962) showed that environmental stimuli were responsible for such migratory behavior in the rainbow trout of Loon Lake, British Columbia. This probably is not true for all populations of this species. Raleigh (1967) reported an attempt in New Zealand to establish a stream resident population of rainbow trout with ova from a lake inlet population. The resultant fry and fingerlings moved downstream past a fish trap, and the population failed to establish itself. A second attempt with ova from a stream resident population succeeded.

There are two outstanding instances of almost complete failure to establish a population despite repeated massive stockings. Although the exact reasons for such failures were not mentioned, the inability of these fish to compete with other species already present is very likely the reason. Heimer (1970) mentions annual stockings of hundreds of thousands of eyed eggs and cutthroat fingerlings in Priest Lake, Idaho, which resulted in practically no return. Although the strain used was not specified, it was probably from Henry's Lake. Lea (1968) reports a similar situation in Independence Lake, California. This lake received repeated stockings of rainbow trout and the Lahontan cutthroat from Heenan Lake. Although the Lahontan cutthroat native to Independence Lake maintains itself only through natural reproduction, it still is the dominant fish in the lake. The same Heenan Lake strain of Lahontan cutthroat apparently did not do well in North Michigan Lake.

The ultimate goal of a reasonably high return to the angler is naturally affected by the survival of the fish. However, differential angling vulnerability is something that has not been critically studied but merits consideration. Flick and Webster (1971) found that the wild Canadian Assinica strain of brook trout was easier to catch than the domestic strains, but the wild Horn Lake strain was more difficult to catch. The Green Lake strain of smallmouth bass was found by Divine (1968) to be more susceptible to angling than the strain from Jacks Fork of the Current River, Missouri.

It is clearly ecological differences between the Snake River and Pikes Peak cutthroat which made the Snake River cutthroat the more valuable fish for the angler in North Michigan Lake. The North Michigan Lake study is perhaps the first study to attempt to definitely link ecological differentiation at an intraspecific level to angling vulnerability.

Such ecological differences and related catchability raises serious questions concerning the use of gear restrictions. By limiting the use of certain types of gear we may be selecting for one particular strain and underharvesting another. By limiting fishing to flies and lures on North Michigan Lake, one immediately selects for the surface feeding Snake River cutthroat because the vast majority of the people fished with a fly and bubble on the surface. It would be interesting to see if more Pikes Peak cutthroat would enter the catch if bait fishing was permitted. Wales and Borgeson (1961) cite an unpublished report by H.D. Boles in which the wild Kamloops rainbow was found to be more vulnerable to fly fishing than a domestic rainbow strain. Flick and Webster (1971) report that the Assinica strain of brook trout was more vulnerable under fly fishing only regulations but that this was not the case when most of the fishing was done with worms. The presence or absence of forage or competitor species may also be important. Bennett and Childers (1957) found that smallmouth bass alone in ponds were more easily caught on artificial flies and other artificial surface lures than in ponds where they co-existed with red-ear and green sunfish.

In the latter case the smallmouth bass were seldom observed feeding at the surface, and most were caught by fishermen using underwater plugs or live minnows.

Differential growth rate between strains can also affect angler success, particularly if size limits are in effect. In two studies, one involving cutthroat trout (Donaldson, Hansler, and Buckridge, 1957) and the other with brook trout (Greene, 1952), there was a disproportionately low return of the wild trout strain the first year but a very high return the following year because they were slower growing. It would seem advantageous to use two strains with different growth rates in situations where stocking can only be done every two or three years. This would provide a more constant recruitment of fish of catchable size into the fishery.

Before we can make full use of the potential of intraspecific genetic variability to fishery management, we need an awareness and a greater understanding of ecological interactions between fish populations. This largely takes the form of competition for food and space and strategies to avoid competition. Studies between two sympatric species of dace (Gee and Northcote, 1963), sympatric populations of brook trout and arctic char (Everhart and Waters, 1956; Saunders and Power, 1969), cutthroat trout and yellow perch (Echo, 1954), and between brook trout, rainbow trout and kokanee (Chapman, Campbell, and Fortune, 1967) are good examples of food and habitat segregation.

Perhaps the greatest contributor to our knowledge of species interaction has been Nils-Arvid Nilsson of Sweden with his work with brown trout and arctic char (1955, 1960, 1963, 1965; and Nilsson and Anderson, 1967) and several species of whitefish (1958, 1960; and Lindstrom and

Nilsson, 1962). Char were found to be more pelagic and fed on plankton while the brown trout occupied the littoral areas and fed on bottom organisms and terrestrials. Similar differences were found between different species of whitefish. He explains such differences as a result of interactive segregation. This is a process in which minute differences in food preference could be magnified during periods of short supply through a combined effect of innate preference and conditioning. Food that is slightly preferred by one species in relation to the other is "scrambled" away before the other species has learned to use it. It does not appear that interactive segregation is solely responsible for the ecological differentiation present in North Michigan Lake. Nilsson observed the strongest selectivity in times of food scarcity, particularly in the fall. Such was not the case in my study where it seems that innate behavioral patterns played an important role, because selectivity was also observed in times of food abundance. It is consistent with the theory of interactive segregation that suckers and the Pikes Peak cutthroat would both feed on the abundant zooplankton in August and early September. But why didn't the Snake River cutthroat feed on zooplankton to a similar extent?

Genetic differences within a species can often times result in ecological and behavioral differentiation, which is normally thought to exist only between species. There are numerous examples of sympatric populations of a species, which according to Mayr's (1963) criteria of reproductive isolation and ecological differentiation, could be considered biological species. Savvaitova (1970) described two sympatric populations of Dolly Varden char, *Salvelinus malma*. She refers to them as arctic char, but Behnke (In press) gives reasons why they are not this species. No real morphological differences existed. The only significant difference between them was manifested in their food habits: one a "mollusk-eater" and the other a "predator." Four races of the Sevan trout, Salmo ischchan, exist in Lake Sevan, U.S.S.R. Ecological divergence is reflected in such morphological differences as gillrakers, mouth position and body shape (Dadikyan, 1971). The sympatric population of a dwarf and normal arctic char studied by Nilsson and Filipsson (1972) has already been discussed.

It is clear to the student of ecology that the goal of the evolutionary process is to increase stability in the ecosystem. This has been brought about through diversity and ecological divergence. Similar situations of ecological divergence could easily be established by stocking different strains into the same lake as has already been done in North Michigan Lake. This suggests a great, virtually untried potential in the use of intraspecific variability for fishery management. Although it has not received major consideration in fishery management in the past, maximizing fish production in a body of water will take on increasing importance in the years to come. This can only come about through more imaginative and innovative thinking and consequently greater utilization of the available food organisms. Fish culturists have long recognized this fact, and they call it mixed or polyculture (Yashouv, 1963, 1966; Tang, 1970). Investigations conducted at Castle Lake, California illustrate this point. Early studies suggested greater utilization of ecological niches because yield was increased when rainbow trout were stocked on top of an already existing population of brook trout (Wales and German, 1956; Wales and Borgeson, 1961). A subsequent study by Swift (1970) revealed why this happened. When brook trout were alone in Castle Lake 45% of their food by volume consisted of terrestrial insects. When brook trout and rainbow trout were present, benthic organisms made up 75.9% for the brook trout but only 18.5% for the rainbow in terms of energy intake. In contrast, 55.9% of the energy intake of the rainbow trout was terrestrial insects, as opposed to only 14.1% for the brook trout. It appears that as a result of interactive segregation with the rainbow, the brook trout switched from terrestrials to benthic organisms, principally dragonfly naiads. The brook and rainbow trout together made a greater utilization of the food resources than either species would by itself. However, there is still an available food item because chironomid larvae, which make up 83.8% of the benthic energy, was little exploited.

Perhaps the most desirable strain to have in combination with other strains is one that would feed on the surface, typical of the Snake River cutthroat in North Michigan Lake. The Lahontan cutthroat of Independence Lake also fed on the surface to a large extent (Lea, 1968). Efficient utilization of allochthanous food would enable the fish production of the lake to exceed the limits placed on the lake by its own total net primary production.

The fact that the phenotypic expression of a strain is a product of its genotype and the environment should always be kept in mind whenever strains are being evaluated. Schofield (1965) demonstrated the importance of environmental conditioning in the survival of different lots of fish stocked in Honnedaga Lake, New York, which is acidic and has a high concentration of zinc. Wohlfarth and Moav (1970), using three strains of carp, contrasted the effects of genetic variation as influenced by the time of hatching on growth rate and viability. Both parameters had considerable influence. Maturity can also be environmentally as well as genetically controlled. The Assinica strain of brook trout matured at the age of III+ in Black Pond and II+ in Follensby Jr. Pond; these waters are only separated by a few miles (Flick and Webster, 1969). There is also the apparent late maturity of the fish in North Michigan Lake which is environmentally induced (phenotypic expression) and not innate (genotypic control). Food habits are greatly influenced by food availability. The Pikes Peak cutthroat showed a high selectivity for zooplankton. However, what type of food segregation between the two strains of cutthroat would exist if *Daphnia* was not abundant? What would be the diet of the Pikes Peak cutthroat if the Snake River cutthroat was not in North Michigan Lake? Only future studies can determine the role the biological and physical environment played in the ecological differences observed in North Michigan Lake. But one fact is clear. When populations representing two distinct genotypes of a single species were present in North Michigan Lake, they ecologically segregated and exhibited selective feeding habits. This situation almost certainly made more efficient use of the total food supply and increased cutthroat biomass above what would have been if only one population existed.

CONCLUSIONS

The North Michigan Lake study revealed the great potential intraspecific variability of fish can play in fishery management. Besides greater survival of the Snake River cutthroat, ecological differences between the Pikes Peak and Snake River cutthroat played a significant role in angling vulnerability. The poor survival of the Lahontan cutthroat indicated that more research is required to determine the conditions necessary to effectively use this strain.

Although the Snake River cutthroat appears to be a better strain to use in North Michigan Lake, it is not likely to be the panacea for all cutthroat trout management problems. Similar evaluative programs under a variety of conditions are needed in order to clarify the potential role of the Snake River cutthroat in management programs.

My study was only a beginning in the investigation of the potential role that genetic diversity, as a result of natural selection, can play in management programs. Initiated with the full realization that the study would create more questions than it would answer, there is hope that these questions will serve as a stimulus for future investigations.

LITERATURE CITED

Adelman, H.M., and J.L. Bingham. 1955. Winter survival of hatchery-reared and native brook trout. Prog. Fish-Cult. 17(4):177-180.

Allen, G.H. 1956. Age and growth of the brook trout in a Wyoming beaver pond. Copeia 1956(1):1-9.

Averett, R.C., and F.A. Espinosa, Jr. 1968. Site selection and time of spawning by two groups of kokanee in Odell Lake, Oregon. Jour. Wildl. Mgmt. 32(1):76-81.

Beal, F.R. 1959. For the cutthroat, a brighter outlook. Wyoming Wildlife. 23(8):7-9.

Behnke, R.J. 1972. The Salmonid fishes of recently glaciated lakes. Part I: Subfamily Salmoninae, Part II: Subfamily Coregoninae. In: Salmonid Communities of Oligotrophic Lakes Symposium. J. Fish. Res. Bd. Canada. 29(6):In press.

Bennett, G.W., and W.F. Childers. 1957. The smallmouth bass, Micropterus dolomieui, in warm-water ponds. Jour. Wildl. Mgmt. 21(4):414-424.

Brannon, E.L. 1967. Genetic control of migration behavior of newly emerged sockeye salmon fry. International Pacific Salmon Fisheries Commission. Progress Report No. 16. 31 p.

Calhoun, A.J. 1944. The food of the black-spotted trout, Salmo clarki henshawi, in two Sierra Nevada Lakes. Calif. Fish Game. 30(2):80-85.

Cartwright, J.C. 1961. Investigation of the rainbow trout of Kootenay Lake, British Columbia. Management Publication No. 7 of the B.C. Fish and Game Branch. 46 p.

Chapman, D.W., H.J. Campbell, and J.D. Fortune, Jr. 1967. Summer distribution and food of Kokanee and trout in Elk Lake, Oregon. Trans. Amer. Fish. Soc. 96(3):308-312.

Cordone, A.J., and S.J. Nicola. 1970. Harvest of four strains of rainbow trout, Salmo gairdneri, from Beardsley Reservoir, California. Calif. Fish Game. 56(4):271-287.

Dadikyan, M.G. 1971. The causes of divergence of the Sevan trout, (Salmo ischchan (Kessler)). Voprosy Ikhtiologii. 11(4):555-564. (In Russian).

Divine, G. 1968. A study of smallmouth bass in ponds with special consideration of minnows and decapods as forage. Master of Arts Thesis, University of Missouri. 115 p.

Donaldson, L.R., D.D. Hansler, and T.N. Buckridge. 1957. Inter-racial hybridization of cutthroat trout, Salmo clarkii, and its use in fisheries management. Trans. Amer. Fish. Soc. 86:350-360.

Donaldson, L.R., and Paul R. Olson. 1956. Development of rainbow trout brood stock by selective breeding. Trans. Amer. Fish. Soc. 85:93-101.

Drummond, R.A. 1965. Reproduction and harvest of cutthroat trout at Trappers Lake, Colorado. Master of Science Thesis, Colorado State University. 68 p.

Echo, J.B. 1954. Some ecological relationships between yellow perch and cutthroat trout in Thompson Lakes, Montana. Trans. Amer. Fish. Soc. 84:239-248.

Everhart, W.H., and C.A. Waters. 1965. Life history of the Blueback trout (Arctic char, Salvelinus alpinus (Linnaeus)), in Maine. Trans. Amer. Fish. Soc. 94(4):393-397.

Fenderson, O.C. 1964. Evidence of subpopulations of Lake Whitefish, Coregonus clupeaformis, involving a dwarfed form. Trans. Amer. Fish. Soc. 93(1):77-94.

Flick, W.A. 1971. New trout for old waters. The Conservationist, June-July 1971:18-21.

Flick, W.A., and D.A. Webster. 1964. Comparative first year survival and production in wild and domestic strains of brook trout, Salvelinus fontinalis. Trans. Amer. Fish. Soc. 93(1):58-69.

__________. 1969, 1970, and 1971. Brandon Park fish management reports for 1968, 1969, and 1970. Dept. of Conservation, Cornell University.

Gee, J.H., and T.G. Northcote. 1963. Comparative ecology of two sympatric species of dace (Rhinichthys) in Fraser River System, British Columbia. J. Fish. Res. Bd. Canada. 20(1):105-118.

Grachev, L.Y. 1971. Variation in the number of oocytes in chum salmon (Oncorhynchus keta (Walb.)) during the marine period. Voprosy Ikhtiologii. 11(4):686-696. (In Russian).

Greene, C.W. 1952. Results from stocking brook trout of wild and hatchery strains at Stillwater Pond. Trans. Amer. Fish. Soc. 81:43-52.

Greenwood, P.H. 1959. Evolution and speciation in the Haplochronis (Pisces, Cichlidae) of Lake Victoria. XVth International Congress of Zoology (1958). Sect. II, Paper 2.

Hartman, G.F. 1969. Reproductive biology of the Gerrard stock rainbow trout. In: Symposium on Salmon and Trout in Streams. H.R. MacMillan Lectures in Fisheries. Inst. Fish., Univ. British Columbia: 53-67.

Hayden, P.S. 1967. The reproductive behavior of the Snake River cutthroat in three tributary streams in Wyoming. Snake River Cutthroat Trout Study. Part I. Cooperative Research Project 4. Wyoming Game and Fish Commission. August, 1967. 105 p.

Hayes, M.L. 1956. Life history studies of two species of suckers in Shadow Mountain Reservoir, Grand County, Colorado. Master of Science Thesis, Colorado State University. 126 p.

Heimer, J.T. 1970. Survival and growth of resident and stocked cutthroat trout in Priest and Upper Priest Lakes. Idaho Fish and Game Department Project No. F-53-R-5. August, 1970. 1-23 p.

Holton, G.D. 1953. A trout population study on a small creek in Gallatin County, Montana. Jour. Wildl. Mgmt. 17(1):62-82.

Irving, R.B. 1955. Ecology of the cutthroat trout of Henry's Lake, Idaho. Trans. Amer. Fish. Soc. 84:275-296.

Khan, N.Y., and S.U. Qadri. 1970. Morphological differences in Lake Superior lake char. J. Fish. Res. Bd. Canada. 27:161-167.

King, V.L. 1963. First progress report of the Eagle Lake Rainbow trout fishery. Inland Fisheries Administrative Report No. 63-9. The Resources Agency of California, Dept. of Fish and Game. 18 p.

Lackey, R.T. 1971. Effects of artificial destratification on a lake ecosystem. Ph.D. Thesis. Colorado State University. 71 p.

Lackey, R.T., and B.E. May. 1971. Use of sugar flotation and dye to sort benthic samples. Trans. Amer. Fish. Soc. 100(4):794-797.

LaRivers, Ira. 1962. Fishes and fisheries of Nevada. Nevada State Fish and Game Commission. 782 p.

Lawler, G.H., and G.P. McRae. 1961. A method for preparing glycerin-stored otoliths for age determination. J. Fish. Res. Bd. Canada. 18(1):47-50.

Lea, R.N. 1968. Ecology of the Lahontan cutthroat trout, Salmo clarkii henshawi, in Independence Lake, California. Master of Arts Thesis, University of California, Berkeley. 95 p.

Lindstrom, T., and Nils-Arvid Nilsson. 1962. On the competition between whitefish species. In: The exploitation of natural animal populations. (E.D. LaCren and M.W. Holdgate - Eds.). Oxford University Press: 326-340.

Mason, J.W., O.M. Brynildson, and P.E. Degurse. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Trans. Amer. Fish. Soc. 96(3):313-319.

Mayr, Ernst. 1963. Animal Species and Evolution. Belnap Press of Harvard University Press, Cambridge, Mass. 797 p.

Menasveta, Deb. 1961. Effects of interracial hybridization on growth, mortality, and yield of rainbow trout (Salmo gairdneri, Richardson). Ph.D. Thesis, University of Washington. 154 p.

Messieh, S.N., and S.N. Tibbo. 1971. Discreteness of Atlantic Herring (Clupea harengus harengus) populations in spring and autumn fisheries in the southern gulf of St. Lawrence. J. Fish. Res. Bd. Canada. 28:1009-1014.

Miller, R.B. 1953. Comparative survival of wild and hatchery-reared cutthroat in a stream. Trans. Amer. Fish. Soc. 83:120-130.

__________. 1957. Have the genetic patterns of fishes been altered by introductions or by selective fishing? J. Fish. Res. Bd. Canada. 14(6):797-806.

__________. 1958. The role of competition in the mortality of hatchery trout. J. Fish. Res. Bd. Canada. 15(1):27-45.

Mohler, H.S. 1966. Comparative seasonal growth of the largemouth, spotted, and smallmouth bass. Master of Arts Thesis, University of Missouri. 99 p.

Moyle, P.B. 1969. Comparative behavior of young brook trout of domestic and wild origin. Prog. Fish-Cult. 31(1):51-56.

Muellar, J.W., and Louis C. Rockett. 1962. Effect of harvest, migration, and stocking on rainbow trout spawning potential in a Wyoming lake. Trans. Amer. Fish. Soc. 91(1):63-68.

Nilsson, Nils-Arvid. 1955. Studies on the feeding habits of trout and char in North Swedish lakes. Inst. Fresh. Res. Drottningholm. 36: 163-225.

__________. 1958. On the food competition between two species of Coregonus in a North Swedish lake. Inst. Fresh. Res. Drottningholm. 39: 146-161.

__________. 1960. Seasonal fluctuation in the food segregation of trout, char, and whitefish in 14 North Swedish lakes. Inst. Fresh. Res. Drottningholm. 41: 185-205.

__________. 1963. Interaction between trout and char in Scandinavia. Trans. Amer. Fish. Soc. 92(3):276-285.

Nilsson, Nils-Arvid. 1965. Food segregation between salmonid species in North Sweden. Inst. Fresh. Res. Drottningholm. 46: 58-71.

Nilsson, Nils-Arvid and Göte Andersson. 1967. Food and growth of an allopatric brown trout in northern Sweden. Inst. Fresh. Res. Drottningholm. 47: 118-127.

Nilsson, Nils-Arvid and Olof Filipsson. 1972. Characteristics of two discrete populations of arctic char (Salvelinus alpinus L.) in a North-Swedish lake. Inst. Fresh. Res. Drottningholm. 51: 90-108.

Northcote, T.G. 1962. Migratory behavior of juvenile rainbow trout, Salmo gairdneri, in outlet and inlet streams of Loon Lake, British Columbia. J. Fish. Res. Bd. Canada. 19(2):201-270.

Rabe, F.W. 1957. Brook trout populations in Colorado beaver ponds. Master of Science Thesis, Colorado State University. 104 p.

Raleigh, R.F. 1967. Genetic control in the lakeward migrations of sockeye salmon (Oncorhynchus nerka) fry. J. Fish. Res. Bd. Canada. 24(12):2613-2622.

Raleigh, R.F., and D.W. Chapman. 1971. Genetic control in lakeward migrations of cutthroat trout fry. Trans. Amer. Fish. Soc. 100(1):33-40.

Ricker, W.E. 1959. Evidence for environmental and genetic influence on certain characters which distinguished stocks of the Pacific salmons and steelhead trout. Unpublished manuscript. 103 p.

Roderick, T.H. 1965. Inbreeding - is it important in natural populations? Maine Fish and Game, Fall (1965).

Saunders, L.H., and G. Power. 1969. The arctic char, Salvelinus alpinus (Linnaeus), of Matamek Lake, Quebec. Canadian Naturalist. 96: 919-934.

Savvaitova, K.A. 1970. Morphological features and variability of the Lake-River form of the arctic char (Salvelinus alpinus (L.)) from the Kamchatka River basin. Voprosy Ikhtiologii. 10(2):203-217. (In Russian).

Schofield, C.L. 1965. Water quality in relation to survival of brook trout, Salvelinus fontinalis (Mitchill). Trans. Amer. Fish. Soc. 94(3):227-235.

Shelford, V.E. 1963. The Ecology of North America. University of Illinois Press, Urbana. 609 p.

Soldwedel, R., and A.B. Pyle. 1968. The survival and growth of three strains of rainbow trout (Salmo gairdneri) under conditions of high natural temperatures with and without other fishes. New Jersey Dept. of Conservation and Economic Development Miscellaneous Rept. No. 29. 10 p.

__________. 1969. The Donaldson strain of rainbow trout in New Jersey - comparisons with the New Jersey hatchery strain are made with regard to several characteristics. New Jersey Dept. of Conservation and Economic Development, Div. of Fish and Game, Bureau of Fisheries, Freshwater Fisheries Lab., Miscellaneous Rept. No. 31. 25 p.

Smith, S.B. 1960. A note on two stocks of steelhead trout (Salmo gairdneri) in Capilano River, British Columbia. J. Fish. Res. Bd. Canada. 17(5):739-742.

__________. 1969. Reproductive isolation in summer and winter races of steelhead trout. In: Symposium on Salmon and Trout in Streams. H.R. MacMillan Lectures in Fisheries. Inst. Fish., Univ. British Columbia: 21-51.

Smith, S.B., T.G. Halsey, R.A.H. Sparrow, and G.E. Stringer. 1969. The comparative survival of wild and domestic juvenile rainbow trout planted in British Columbia Lakes. British Columbia Fish and Wildlife Branch, Fish Mgmt. Rept. 61. 9 p.

Sumner, F.H. 1940. The decline of the Pyramid Lake fishery. Trans. Amer. Fish. Soc. 69: 216-224.

Swift, M.C. 1970. A qualitative and quantitative study of trout food in Castle Lake, California. Calif. Fish Game, 56(2):109-120.

Tang, Y.A. 1970. Evaluation of balance between fishes and available fish food in multispecies fish culture ponds in Taiwan. Trans. Amer. Fish. Soc. 99(4):708-718.

Van Velson, R.C. 1969. Migration dynamics in rainbow trout. Master of Science Thesis, Colorado State University. 97 p.

Vernon, E.H. 1957. Morphometric comparison of three races of kokanee (Oncorhynchus nerka) within a large British Columbia lake. J. Fish. Res. Bd. Canada. 14(4):573-598.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (Salvelinus fontinalis Mitchill). Trans. Amer. Fish. Soc. 89(1):35-52.

Vladykov, V.D. 1956. Fecundity of wild speckled trout (Salvelinus fontinalis) in Quebec lakes. J. Fish. Res. Bd. Canada. 13(6):799-841.

Wales, J.H., and D.P. Borgeson. 1961. Castle Lake investigation - third phase: rainbow trout. Calif. Fish Game. 47(4):399-414.

Wales, J.H., and E.R. German. 1956. Castle Lake investigation - second phase: eastern brook trout. Calif. Fish Game. 42(2):93-108.

Webster, D.A. 1954. A survival experiment and an example of selective sampling of brook trout (Salvelinus fontinalis) by angling and rotenone in an Adirondack pond. N.Y. Fish and Game J. 1(2):214-219.

Wohlfarth, G., and Rom Moav. 1970. The effects of variation in spawning time on subsequent relative growth rate and viability in carp. Bamidgeh. 22(2):42-47.

Woods, Don. 1971. The Donaldson ... our dream trout. The Minnesota Volunteer, May-June, 1971: 42-46.

Yashouv, A. 1963. Increasing fish production in ponds. Trans. Amer. Fish. Soc. 92(3):292-297.

__________. 1966. Mixed fish culture - an ecological approach to increase pond productivity. FAO Fisheries Report. No. 44, Vol. 4. Proceedings of the World Symposium on warm water pond fish culture: 258-273.

Zilliox, R.G., and W.D. Youngs. 1958. Further studies of smelt in Lake Champlain. N.Y. Fish and Game J. 5(2):164-174.