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EFFECTS OF BEAVER ON TROUT IN SAGEHEN CREEK, CALIFORNIA

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During the past several decades there has been a tremendous increase in the number of beavers (*Castor canadensis* Kuhl) in the United States as a result of protection from trapping, and transplantation of breeding stocks. This increase has been accompanied by a growth of interest in the effect that beavers have on other animals, particularly trout. No evaluation of beaver-trout relationships has heretofore been attempted in California and this fact provided the stimulus for the present study.

Sagehen Creek was deemed an appropriate situation for this investigation for several reasons. Since beaver were first introduced into this stream in 1945 (Hensley, 1946) and have been largely undisturbed by man, the effects upon trout of a relatively new and still-expanding beaver population could be determined. Also, since three species of trout, rainbow trout (*Salmo gairdnerii* Richardson), brown trout (*Salmo trutta* L.), and brook trout (*Salvelinus fontinalis* (Mitchill)), are present in Sagehen Creek, any differential effect of beaver on the individual species could be assessed. Finally, this creek is typical of many small streams on the eastern slope of the northern Sierra Nevada.

Arising from two permanent cold (37 to 38°F.) springs at an elevation of 7,400 ft., Sagehen Creek meanders through about 13 mi. of meadow, forest, and sagebrush before emptying into the Little Truckee River at an altitude of 5,800 ft. Melting snows contribute heavily to the stream flow during spring and summer. Minimum fall flows between 1.3 and 2.6 cu. ft. per sec. and maximum spring flows between 38 and 149 cu. ft. per sec. occurred during the years 1954–59 at the Sagehen Creek Project (Fig. 1). Water temperatures over 70°F. in the main stream channel are rare and of short duration. Winter conditions are severe, since the extreme minimum temperatures for the 1954–60 period ranged from –12 to –30°F. and the maximum snow packs ranged from 48 to 131 in. in depth.

When the study began, there were four separate beaver colonies in Sagehen Creek. Since it was not feasible to study all of them in detail, it was decided to study one colony intensively and the others extensively. The so-called "Rockslide Colony" (Figs. 1 and 2) was selected for intensive study because it occupied an area believed to be most representative of average ecological conditions in the stream. Field work was begun in the winter of 1954 and was completed by the summer of 1957.

The beavers of the Rockslide Colony maintained a complex system of 14 dams, and the resulting ponds, together with the dams, could affect trout in a number of ways. In an attempt to determine the effects of beavers and their workings upon trout, a program was set up to study: 1) the physical characteristics of beaver pond and stream areas; 2) the bottom faunas present in pond and stream and the utilization of these organisms by trout; 3) the trout populations present in pond and stream habitats; and 4) the effect beaver dams have on trout spawning migrations.

This study was undertaken while the writer was employed by the University of

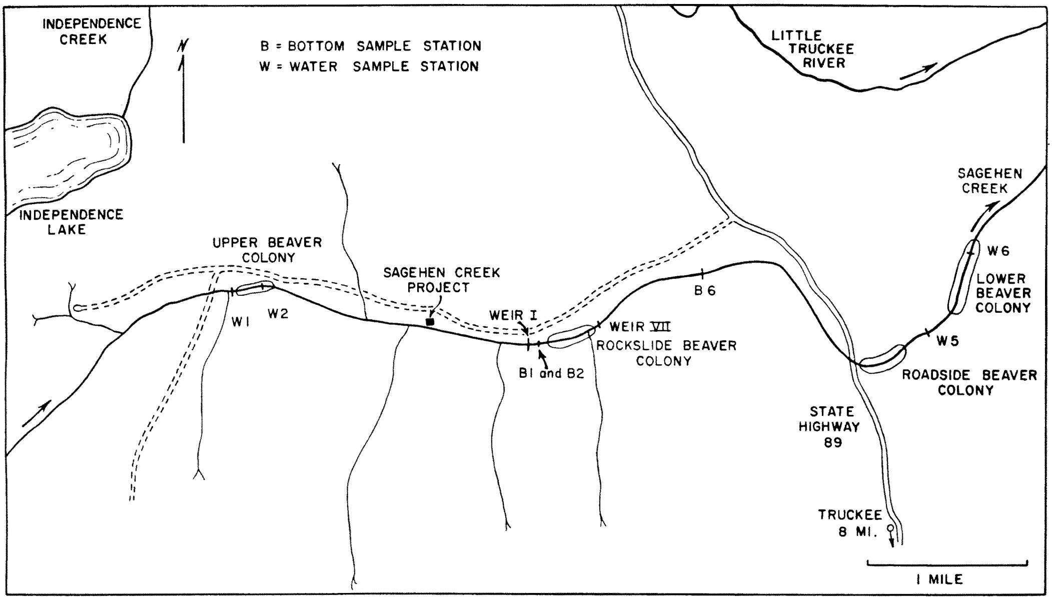

FIG. 1. Reference map of Sagehen Creek and surrounding area.

California, Department of Zoology, at the Sagehen Creek Project. Many of the facilities at the Project were provided by the Max C. Fleischmann Foundation. A. Starker Leopold, Paul R. Needham, and Robert L. Usinger provided valuable guidance and encouragement throughout the study. Aid with various phases of the field work was given by Gerardus C. deRoth, Joseph G. Hall, Robert S. Hoffmann, and by many students who were employed at the Project during the summers. Mrs. Emily Reid prepared the figures. The author is indebted to all these people and grateful for their help.

PHYSICAL CHARACTERISTICS OF BEAVER POND AND STREAM AREAS

General Physical Characteristics

Water velocity was greater in stream than in pond situations. In August the average water velocity at stream stations B1, B2, and B5 was 1.03 ft. per sec. while no measurable velocity occurred in the beaver ponds at B3 and B4 (Figs. 1 and 2). The lack of current in the ponds permitted the deposition of silt on the pond bottoms, where it accumulated to the extent of 1 or 2 ft. in old ponds. Typical stream bottom consisted of rubble, gravel, sand, and occasionally hard-pan, rock, and silt. Differences in water velocities and bottom types were found to influence kinds and standing crops of bottom organisms.

There were some important differences between the vegetations associated with beaver pond and stream areas. Following impoundment of water by beavers, some riparian trees were killed, particularly lodgepole pine (*Pinus contorta* Dougl.). Aspen (*Populus tremuloides* Michx.) occasionally was flooded and killed, but this species in or near a beaver pond was usually cut by beavers for food and for building dams or lodges. Downed aspens formed an interlacing tangle over some ponds and provided ideal trout cover. Bushy willows (*Salix* sp.) grew along parts of the stream and seemed to thrive around the edges of many beaver ponds (Hall, 1960). The aquatic water buttercup (*Ranunculus aquatilis* L.) was more prevalent in ponds than in running waters.

Width and surface area of the stream were increased by ponding. The average width in July at 1,340 randomly chosen stream stations in the upper half of the creek was 11.3 ft.; the average width at 208 stations in the Rockslide and Upper Colonies was 16.6 ft. Beaver Ponds 1 through 13 in the Rockslide Colony (Fig. 2) were found to have a total surface area of 1.273 a. in summer. Following a nearly complete removal of dams by a flood in December 1955, the surface area diminished to 0.873 a., a decrease of 32 percent.

The character of winter ice cover was found to be considerably different in the beaver ponds from that in the faster running waters. During most of the winter, the ponds were continuously capped with several inches of shelf ice overlaid with varying amounts of snow. Anchor ice did not form on

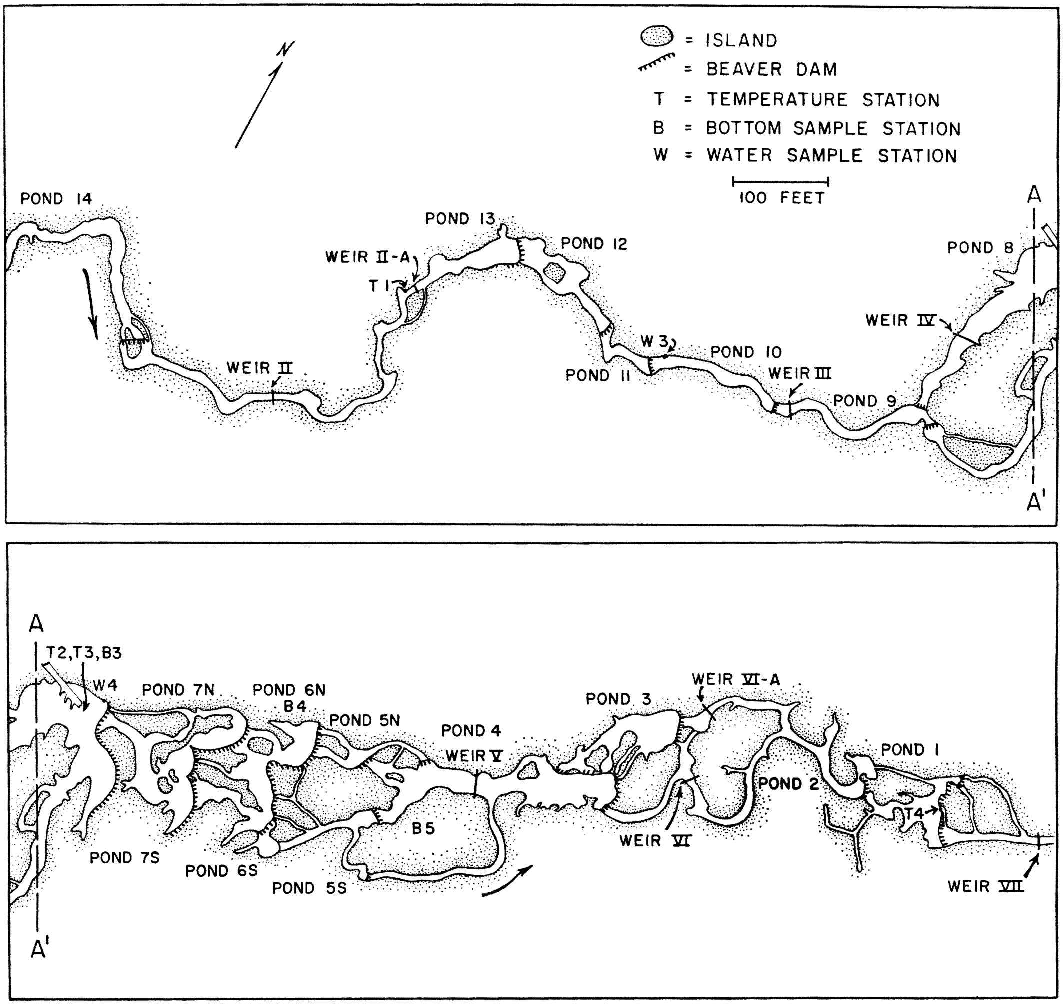

FIG. 2. Map of the Rockslide Beaver Colony on Sagehen Creek.

the pond bottoms. This may have been prevented by the entrance of relatively warm ground water. On the other hand, on cold nights the stream froze almost solid in many riffles where anchor ice built up from the bottom to form dams, and melting and breakup of anchor ice greatly disturbed the stream substrate.

Water Temperatures Above and Below a Pond Series

Monthly averages of late afternoon temperatures of water entering and leaving contiguous ponds in the Rockslide Colony (Stations T1 and T4 in Fig. 2) are shown graphically in Fig. 3. It is evident that water leaving the ponds was colder than that entering at all times of the year except during the spring months, when high flows obliterated any local influences. A small spring with a July temperature of 43°F. entered the Rockslide ponds and doubtless helped cool the water in summer when the flow was low. In midwestern and eastern United States, warming of beaver ponds on summer afternoons has often been reported (Patterson, 1950; Adams, 1953; Reid, 1952). High temperatures may kill trout directly or provide a habitat more suitable for other fish, thus exposing trout to competition with these forms.

In addition to the afternoon temperature series, temperatures of water entering and leaving Rockslide ponds were recorded every 4 hr. for a 24-hr. period once each season. Water leaving the beaver ponds between midnight and noon in summer and fall averaged 3.7°F. warmer than entering water. At other seasons and times, water leaving the ponds was cooled an average of 1.4°F. The ponds

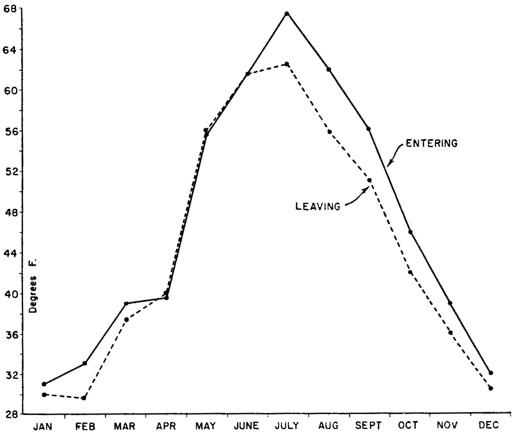

FIG. 3. Monthly averages of afternoon temperatures of water entering and leaving the Rockslide Beaver Colony on Sagehen Creek.

appeared to stabilize water temperatures because pond waters were not influenced as greatly as were stream waters by changes in air temperature.

Temperatures Within One Beaver Pond

The surface and bottom water temperatures at the deepest point in Pond 8 (T2 and T3 in Fig. 2) were recorded periodically on late afternoons for 1 year. Surface temperatures were higher than bottom temperatures during all seasons except winter, when the temperatures at these two stations were about the same (Fig. 4). Afternoon warming of surface waters would have been caused by exposure to warm air and radiant energy. The generally homothermous condition of the pond in winter was maintained by the permanent cover of ice and snow which prevented rapid heat exchange between pond and atmosphere.

In order to check the possibility that temperature stratification was present in Pond 8 in summer, a vertical series of temperatures was taken on a July afternoon. Homothermous water (excluding the very surface) of 67.5°F. extended down to the 24-in. level. Below this upper layer of water, there was a sharp drop in temperature of 4°F. to the 32-in. level followed by a somewhat lesser drop of 2°F. between this level and the bottom at 44 in. Temperatures in the pond were stratified; this may be of importance to trout since the cool lower layer could be used as a retreat during hot days.

Temperature Extremes

The highest water temperature measured, 72.5°F. on August 4, 1955, was at the surface of Pond 8. The lowest temperature, 29°F. on January 25 and 26, 1955, occurred in water flowing out of the Rockslide ponds. This low water temperature may have been the result of supercooling or, more likely, of encasement of the thermometer bulb by ice. Embody (1921) stated that good yields of brook, brown, and rainbow trout occur in New York streams with summer temperatures of 79, 83, and 85°F., respectively. Fry, *et al.* (1946) found the ultimate upper and lower lethal temperatures for brook trout to be 78°F. and below 32°F., respectively. Adams (1953) reported that wild brook trout endured temperatures higher than 80°F. (maximum 83°F.) for a period of 5.5 hr. The highest water temperature (and probably also the lowest) recorded during the present study were within the tolerance ranges of the three trout species.

Water Chemistry

A diurnal series of water samples was taken each season from Pond 8 (W4) and from the stream above (W3) at 4-hr. intervals. Single samples were collected at stream and pond stations in the Upper (W1 and W2) and Lower (W5 and W6) Colonies each season. Dissolved oxygen and methyl orange and phenolphthalein alkalinities in the samples were determined by use of methods outlined in Welch (1948). A *p*H meter was used to assess the degree of acidity.

Water samples from Pond 8 exhibited a yearly range in dissolved oxygen of 7.7 to 11.9 p.p.m., in *p*H of 6.9 to 7.9 units, and in methyl orange alkalinity of 26 to 70 p.p.m. (Table 1). No phenolphthalein alkalinity was found. Almost identical data were obtained from the samples collected at the stream station (W3) above Pond 8. Unlike the condition in the Rockslide Colony, slight decreases in dissolved oxygen (maximum of 1.8 p.p.m.) and *p*H (maximum of 0.6 unit) occurred as the water passed through the Upper and Lower Colonies. Many workers have reported lower dissolved oxygen and *p*H levels in beaver ponds than in the running waters above them (Salyer, 1935; Wilde, *et al.*, 1950; Adams, 1953; Rupp, 1955). The abundant growth of vegetation in the Rockslide ponds may have maintained oxygen and *p*H levels equal to those in the stream above.

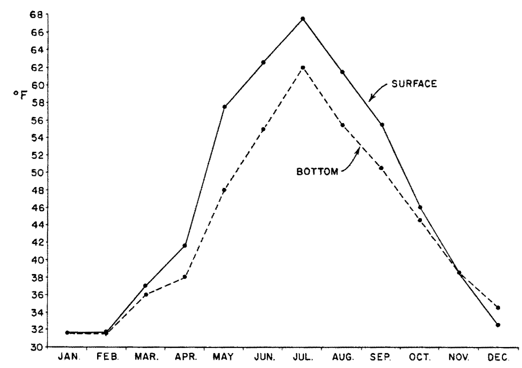

FIG. 4. Monthly averages of afternoon temperatures of water at the surface and bottom of Beaver Pond 8 on Sagehen Creek.

TABLE 1.—WATER ANALYSIS OF ROCKSLIDE BEAVER POND 8 IN SAGEHEN CREEK
(Ranges of values over 24-hr. periods)

Date	Water Temperature Degrees F.	Dissolved Oxygen (p.p.m.)	*p*H	Methyl Orange Alkalinity (p.p.m.)	Oxygen Percentage Saturation
April 28, 1954	36.0–49.0	9.1–10.4	6.9–7.4	26–29	96–101
July 30, 1954	51.0–66.0	7.7– 9.8	7.4–7.9	62–67	102–113
Nov. 3, 1954	35.0–42.5	9.8–11.0	7.4–7.8	68–70	98–102
Jan. 25, 1955	32.5–33.5	11.1–11.9	7.5–7.8	63–65	98–104

Though little change in the chemistry of the water occurred as it passed through beaver ponds, elevational and seasonal changes did occur. The water gained an average of 19 p.p.m. in methyl orange alkalinity as it traveled from the Upper to the Lower Colonies. Evidently the longer period of contact of the water with the limestone substrate accounts for this increased alkalinity. The fact that dissolved oxygen was highest in winter and lowest in summer was apparently related to the oxygen-holding capacity of water at different temperatures. Alkalinity was much lower in spring than at any other season and was accompanied by a relatively low *p*H. These changes probably resulted from increased dilution of dissolved bicarbonates by high spring runoff from melting snows.

Trout have long been considered to have high oxygen requirements. Needham (1938) stated that the oxygen content of trout waters should be at least 4 p.p.m. However, trout have been known to live for a limited time under some amazingly low oxygen tensions where temperatures were not excessive. Gutsell (1929) found that some brook trout accustomed to low oxygen tensions survived for a day in water with as low as 1.2 p.p.m. of dissolved oxygen at 59.9°F.; some rainbow trout survived dissolved oxygen tensions as low as 1.6 p.p.m. (66.2 to 68°F.) for a few days. Brook trout in the Bean River, New Hampshire, survived in water temporarily containing only 1.1 p.p.m. of oxygen at 52°F. (Jahoda, 1947).

In the present study, the lowest amount of dissolved oxygen (7.3 p.p.m. at 66°F.) was in a Lower Colony pond in July; the highest (11.9 p.p.m. at 32.5°F.) was in Pond 8 in January. Sagehen waters were always nearly saturated or supersaturated with oxygen.

Trout can live successfully in waters displaying wide ranges in hydrogen-ion concentration. Greene, *et al.* (1933) found brook trout ponds in the upper Hudson River area with *p*H's ranging from 5.4 to 7.1, while Creaser (1930) concluded that the range of voluntary toleration of brook trout to *p*H extended from 4.1 to 9.5. The highest *p*H recorded in Sagehen Creek (7.9) was in the stream above the Lower Colony in July and the lowest (6.9) was in Pond 8 in April.

Since all water quality data determined were well within the lethal limits for trout (where these are known), it is concluded that the slight changes in water chemistry in some of the ponds had no appreciable effect upon trout.

The changes imposed on a stream by damming are those associated with the transposition from a typical lotic to a lentic environment. The physical attributes of ponds appear to offer trout habitat superior to that in streams except for the obvious deficiency of spawning gravels. Greater living space, better cover, slower water velocity, less severe ice conditions, and more stable water temperatures occur in the ponds.

FOODS AND FEEDING OF TROUT IN BEAVER POND AND STREAM AREAS

Samples of the bottom faunas were obtained each season from four stream stations and two Rockslide beaver ponds. Stream-bottom types sampled were gravel (B1), rubble (B2), silt (B6), and rubble between two beaver ponds (B5). Two samples were obtained with a square-foot Surber sampler at each rubble or gravel stream station. At the silt-bottomed stream station, two ¼-sq.-ft. Ekman dredge hauls were taken in summer and spring, one in fall, and none in winter. Pond station B3 was in a comparatively old pond built before 1951, but B4 was in a newer pond built in 1952 or 1953. Four Ekman dredge hauls were obtained from each pond (except in summer when eight were taken), two from shallow areas and two from the deepest points in the ponds.

Surber and Ekman samplers were selected for use since they were the most practical ones available for sampling riffles and ponds, but both fail to catch the entire bottom faunas within their borders. The Surber sampler misses organisms not dislodged from the stream bottom or not washed into the net. Many organisms escape the Ekman since its jaws invariably close on some object that keeps them slightly apart.

A sieve with openings of 0.59 mm. was used to separate the bottom fauna from fine debris. Sieves with openings this large (the one used by most workers in the past) fail to catch many young midges (Jonasson, 1955). Undoubtedly many small organisms were not recovered in the present study. But since these minute organisms weigh so little, it is doubtful that their omission resulted in significantly lower sample weights, although numbers of organisms would be conservatively counted.

The sorted bottom samples were weighed to the nearest 0.01 g. after being pressed against blotting paper for 1 min. Most of the organisms were identified to genus by the use of two references, Usinger (1956) and Pennak (1953); a list of organisms appears in Table 2. Statistical comparisons of averages in this and subsequent sections of this paper were made using the *t* test (Dixon and Massey, 1957, p. 121).

Kinds of Bottom Organisms

The combined stream stations (B1, B2, B5) yielded 81 categories of organisms whereas the combined pond stations (B3, B4) had only 42 for all seasons. That the stream displayed a more diverse assemblage of life than the ponds was to be expected since it presents a relatively heterogeneous environment. A beaver pond, on the other hand, is quite homogeneous and a broad assortment of animal types would not be anticipated there.

Some of the important kinds of organisms found in the ponds were *Sialis* larvae, several genera of chironomid larvae, *Palpomyia* and *Chrysops* larvae, and *Pisidium* and oligochaete adults. Dominant organisms in the stream were *Alloperla, Cinygmula,* and *Ephemerella* nymphs, as well as *Glossosoma* and *Cricotopus* larvae.

Numbers and Weights of Bottom Organisms

Average total numbers and weights of organisms at the beaver pond stations were much greater than those at the stream sta-

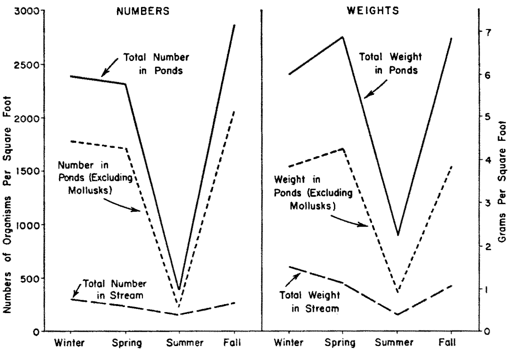

FIG. 5. Average seasonal numbers and weights of bottom organisms in beaver pond and stream areas of Sagehen Creek. Data from pond stations B3 and B4 and stream stations B1, B2, and B5 are combined.

tions during each season (Fig. 5). When all seasons were averaged together, the ponds contained 1,992 organisms (5.50 g.) and the stream contained 239 organisms (1.03 g.)/sq. ft. (differences significant at the 1 percent level). In New Mexico, Huey and Wolfrum (1956) also found beaver ponds to be much richer in bottom organisms than were stream areas. Contradictory data were obtained in Maine, where beaver pond bottoms contained fewer organisms per unit area than did various stream types (Rupp, 1955).

In accounting for the greater standing crop of organisms in the Sagehen ponds than in the stream, we might first consider temperature differences. The bottom temperature of Pond 8 varied less than did that of the entering stream. Temperature stability in the ponds might have provided more satisfactory conditions for the organisms. Since water chemistry was so similar in pond and stream, it is unlikely that this affected bottom faunas. Perhaps the two most pertinent differences lie in the substrate and current. The basic nutrients contained in the silt of the ponds would be more readily available to plant life because of the much greater surface area of silt particles. Current is slower in the ponds and would not carry away bottom fauna as readily as it would in the stream. Neill (1938), Sprules (1941), and Abell (1956) consider current the most important factor affecting bottom faunas.

The summer standing crop of bottom organisms in the ponds was significantly lower (1 percent level) than the crops at other seasons (Fig. 5). In the stream, weights were significantly lower (5 percent level) in summer, but numbers were not lower. That fewer organisms were sampled in the ponds in summer was anticipated, since the emergence of adult insects reached its peak then and incoming generations of larvae were too small to be taken by samplers. These data indicate that season must be taken into account when a stream is to be assessed as to its productivity.

Many mollusks lived in the pond bottom, but few of these forms were present in the stream (Table 2). These mollusks were mostly clams (*Pisidium*), but included a few snails (*Physa* and *Gyraulus*). Since much of the weight of these forms is composed of shell and because clams are virtually uneaten by trout in Sagehen Creek, a comparison of pond and stream life was made with mollusks excluded (Fig. 5). Though faunal differences between pond and stream were not as pronounced, the average numbers and weights of organisms in pond samples were still significantly higher (1 percent level) than were those in stream samples.

The comparisons mentioned above are on a unit-area basis. If the standing crop of organisms in the entire Rockslide Colony were compared to that which the same area would support as a stream, an even greater difference would be evident because a ponded stream covers much more area than one without ponds.

No consideration has been given in the foregoing comparisons to relative turnover rates. Allen (1951) estimates that in the Horokiwi Stream the total annual production of the whole bottom fauna must be well over 17 times that of the average standing crop on a numerical basis, or 100 times on a weight basis. These data indicate a very high turnover rate in the bottom fauna. While a thorough treatment of this question is impossible with the data available here, it is known that many genera of midges (the dominant pond organisms) have several generations per year and that most genera of mayflies, stoneflies, and caddisflies (the dominant stream organisms) have only one generation per year. On this basis, the turnover rate of dominant organisms in the ponds would be higher than that for dominant organisms in the stream. The greater richness shown for ponds might therefore be enhanced if turnover rates of bottom faunas were considered.

Comparison of Sampling Stations

Reports have been made that although new ponds are good trout producers for a few years, their yields then gradually decrease (Salyer, 1935; Adams, 1953). Presumably this trend would also be followed by trout foods. At the Rockslide Colony, the new pond possessed somewhat larger numbers and weights of bottom organisms than did the old pond, but the differences were not significant at the 5 percent level.

It has long been known that the character of stream substrate exerts a tremendous influence on numbers and kinds of organisms living there. Stream bottom types are usually listed in the following order of decreasing productivity: rubble, gravel, sand, and bedrock. There are conflicting data in regard to the importance of silt. Needham (1929) and Pate (1932) found silt to be the most productive substrate type while later Pate (1933) found that small rubble actually exceeded silt in productivity.

In Sagehen Creek, silt was clearly the most productive stream bottom type studied in terms of numbers and weights of organisms, and gravel was the least productive. Average standing crops of bottom organisms from stream and pond habitats indicate the following sequence in decreasing productivity: beaver pond, stream silt, rubble between beaver ponds, rubble in stream, and gravel in stream.

Utilization of Food by Trout

It has been shown that the beaver ponds contained greater numbers and weights of bottom organisms than did the stream.

TABLE 2.—NUMBERS OF BOTTOM ORGANISMS PER SQUARE FOOT COLLECTED AT BEAVER POND AND STREAM SAMPLE STATIONS IN SAGEHEN CREEK (Annual averages listed)

Organisms[1]	STREAM STATIONS				POND STATIONS	
	B1	B2	B5	B6[2]	B3	B4
Nematoda a.					0.3	0.5
Oligochaeta a.	1.3	2.3	0.6	35.3	37.4	55.9
Hydracarina a.	0.9	1.4	0.8	1.3	0.8	1.5
Pteronarcella n.	0.1					
Pteronarcys n.			0.1			
Peltoperla n.	0.5		0.1			
Nemoura n.	3.6	1.3	21.6		1.0	0.3
Capnia n.			0.5			
Eucapnosis n.	0.1					
Acroneuria n.	0.1	0.9	0.8			
Isoperla n.	0.4	0.1				
Arcynopteryx n.	1.0	3.6	1.4			0.3
Isogenus n.	0.1	0.8	0.8			
Alloperla n.	28.5	10.0	4.0	0.7	0.5	0.8
Paraperla n.			0.4			
Rhithrogena n.	11.1	3.6	2.4			
Cinygmula n.	38.3	21.9	7.9			
Iron n.	0.5	1.4	1.4			
Ironodes n.			0.1			
Siphlonurus n.		3.3				
Paraleptophlebia n.	1.3	2.5	4.6			
Ephemerella levis n.	5.9	8.1	3.5			1.8
E. tibialis n.	0.3	0.1	0.8			
E. doddsi n.	1.1	2.5	0.3			
E. flavilinea n.	0.6	1.8	1.0			0.5
E. coloradensis n.	0.8	1.1	0.3			
E. micheneri n.			0.1			0.3
E. delantala n.	2.5	0.9				
E. cognata n.	2.4	1.4	0.4			0.8
E. soquele n.	0.9		0.5			
E. hecuba n.		0.3				
Baetis n.	1.5	2.9	4.1			
Sialis l.	0.1		3.3	30.0	64.1	28.9
Rhyacophila l.	2.9	5.1	0.4		0.5	0.3
Glossosoma l.	9.0	34.9	6.5		0.3	
Glossosoma p.	0.1	0.6			0.3	
Agapetus l.	4.6	8.5	0.6			
Chimarra l.		0.1				
Wormaldia l.	0.1	1.0	0.1			
Psychomyiidae l.		0.3				
Hydropsyche l.	0.4	4.1	6.0			0.3
Hyropsychidae p.	0.1					
Hydroptila l.			0.6		5.0	12.0
Neophylax l.	3.0	3.0	3.3			
Limnephilidae A l.				0.7	0.3	
Limnephilidae B l.	4.0	3.3	1.3			
Limnephilidae C l.			0.1	4.7		0.3
Limnephilidae D l.	0.3					
Limnephilidae E l.	0.3	0.3	0.3			
Limnephilidae F l.	0.3	0.3				
Limnephilidae p.	0.5	0.8	0.9			
Heteroplectron l.	0.1	1.1	0.9	2.0	8.5	1.5
Micrasema l.	1.4	2.5	0.3			
Agabinus l.		0.1				0.3
Helophorus a.		0.1				
Paracymus a.			0.1			
Zaitzevia a.	4.0	1.3	0.3	0.7		
Zaitzevia l.	4.5	3.6	0.9		0.3	0.3
Narpus a.	6.8	2.4	0.8			
Narpus l.	0.3	0.3	0.4	0.7		
Lara a.					0.3	
Tipula l.						0.8
Antocha l.	0.8	11.3	5.9			

TABLE 2.—Continued

Organisms[1]	Stream Stations				Pond Stations	
	B1	B2	B5	B6[2]	B3	B4
Dicranota l.			0.3			
Erioptera l.					0.3	0.3
Hexatoma A l.		0.1	0.1	3.3	0.8	1.5
Hexatoma B l.	0.1		0.1	0.7		
Limnophila l.	0.1					
Tipulidae l.	0.3	0.4				
Liriope l.			1.1	108.0	1.6	4.8
Pericoma l.	12.0	5.1		4.0		
Simuliidae l.	0.8	0.3				
Simuliidae p.	0.1	0.1	0.1			
Chironomidae A l.				160.7	697.5	1,258.9
Chironomidae B l.				442.0	262.3	209.0
Chironomidae C l.				32.7	167.3	6.3
Chironomidae D l.	8.6	24.6	94.9	4.7		2.5
Chironomidae E l.				10.0	2.3	4.5
Chironomidae l.	8.9	23.3	123.6		0.3	0.3
Paratendipes p.					0.6	0.5
Prodiamesa p.					0.4	
Tanytarsus p.					1.0	0.3
Hydrobaenus A p.	0.3		5.3			
Hydrobaenus B p.		0.3	2.6			
Diamesa p.			0.3			
Cricotopus p.			2.0			
Pelopia p.			0.8			
Chironomidae p.	0.1		0.1		0.3	
Palpomyia l.	0.3	0.4	0.4	38.0	9.3	17.5
Chrysops l.		0.1		0.7	6.5	11.5
Tabanus l.				0.7		
Empididae l.						0.3
Unident. l. and p.		1.0				1.3
Pisidium a.	1.3	0.9	2.6	276.7	466.6	617.8
Physa a.			0.1			1.8
Gyraulus a.	0.1			0.7	0.3	2.1
Totals	180.4	213.8	325.9	1,159.0	1,737.0	2,248.6
Numbers of samples	8	8	8	6	20	20

[1] a, adult; n, nymph; l, larva; p, pupa.
[2] No sample was taken at B6 in winter.

Here, an attempt will be made to determine whether or not trout were actually utilizing the more abundant foods present in the ponds, and the relative roles of bottom fauna and drift food in the diet of the trout.

Stomachs from 142 brook, brown, and rainbow trout were obtained from stream and pond sites during the year. Angling and electric shocking were used to collect the trout. Organisms in stomachs were identified to the same taxonomic level as in bottom samples and are listed in Table 3. Adult insects not present in bottom samples were grouped as "drift."

Kinds of bottom organisms eaten by trout.—Trout from the ponds contained 72 kinds of organisms whereas stream trout contained 61. Since there was a greater variety of organisms in the stream habitat, the reverse of the above would have been expected. However, many stream forms were eaten by pond trout and a few pond forms were eaten by stream trout. Some stream organisms found in abundance in pond trout were *Cinygmula*, *Paraleptophlebia*, and *Baetis* nymphs, *Neophylax*, *Micrasema*, and simuliid larvae. Pond organisms found in stream trout were Limnephilidae A larvae and Nematoda.

Clearly there is some mechanism of food exchange between ponds and stream. One possibility is that organisms are dislodged from their homes and float from one habitat to the other. Also, the trout themselves may move between habitats. Short riffles often occur between ponds and it is likely that trout from the downstream ponds enter these areas to feed.

In July of 1955, a two-way fish trap was placed at the head of Pond 13 (Weir II-A in Fig. 2) to determine the extent of trout movement at that time. During a 3-week period, only two trout were caught by the traps. It is concluded that very little movement occurred into or out of the ponds in summer. There are of course seasonal movements associated with spawning activities in spring and autumn.

Numbers of bottom organisms eaten by trout.—In the 142 stomachs analyzed, 7,897 bottom organisms were classified for an average of 56 per stomach. More organisms were present, but were too disintegrated for identification.

Stomachs taken during the summer months contained an average of only 15 bottom organisms. This apparent low food intake in summer correlated with the low numbers in the bottom samples at that season. However, a trout's metabolism is highest in summer and a high intake of food at this season would seem to be essential. It is known that the digestive rate in trout increases with an increase in water temperature (Hess and Rainwater, 1939; Reimers, 1957). Therefore, a higher intake of food in summer by the Sagehen trout may have occurred, even though the number of organisms recognizable at any one time was low.

On the assumption of equal availability of pond- and stream-bottom organisms, an interesting comparison may be made. Brown and brook trout from the ponds contained an average of over two and four times as many bottom organisms, respectively, as did their counterparts from the stream. The reverse is evident with rainbow trout, since they contained over twice as many bottom organisms in the stream as they did in the ponds. Perhaps this species difference in feeding accounts for the observation that brook and brown trout often do well in ponds whereas rainbow trout usually do better in stream situations.

Selection or availability of bottom organisms to trout.—To this point no consideration has been given to the numbers of different kinds of organisms eaten by trout in relation to their abundance in the bottom fauna. In an attempt to relate these two phenomena, the "forage ratio" of Hess and Swartz (1941) is employed. This ratio is determined by the following formula:

$$\text{Forage ratio} = \frac{\frac{n}{N}}{\frac{n^1}{N^1}}$$

where n = the number of any given organism in the stomachs, N = the total number of organisms in the stomachs, n^1 = the number of the same organism in the bottom samples, and N^1 = the total number of food organisms in the bottom samples. A forage ratio of 1 indicates that a particular organism occurs in the stomachs in the same frequency as it occurs in the bottom samples, and that the trout are eating it at random. A ratio of more than 1 indicates that the organism is either being selected by the trout or is readily available; a ratio of less than 1 indicates that the trout are not selecting the organism or that it is not readily available.

In using the forage ratio, it is assumed that organisms are equally available to the sampling device and the fish, and that bottom foods and stomachs are adequately sampled. These assumptions may not be entirely justified, but the use of this ratio is still the best method available for relating foods present in a habitat to foods eaten by fish. Forage ratios for the more important organisms will be considered here.

1. Important pond organisms: The most numerous organisms in the pond bottom and in the stomachs of pond trout were immature midges (Chironomidae, Diptera). If all seasons, trout species, and genera of chironomids are grouped, a forage ratio of 0.8 is derived. In reality, trout ate more midges than were recorded since these are

small, rapidly disintegrating forms which are often difficult to recognize. Midge larvae live buried in the silt, and in order for a forage ratio as high as 0.8 to exist, trout must be seeking these forms for food. Pate (1932) reported that trout were observed rooting in the bottom silt and eating midge larvae as they floated away.

The clam *Pisidium* was second in abundance in the pond bottom fauna but only three individuals appeared in all the stomachs.

Although numerous in the pond, oligochaetes were found in only two pond trout. It may be that more were eaten, but that they were too soft-bodied to remain recognizable for long in the stomachs. They, like clams, were largely unavailable and unselected.

Sialis larvae were eaten mainly by brown trout in winter and spring, the forage ratios being 1.3 and 3.5, respectively. These hellgrammites crawl around and are more available to trout than are quiescent forms living in the substrate. Their value as food is probably high since individual larvae are large.

All trout from ponds except winter rainbows ate *Palpomyia* larvae at all seasons in fair numbers. The forage ratio for summer brook trout was a high 10.1. These delicate dipterans are even smaller than midges and undoubtedly more were eaten than were recorded. Because of their small size, they are of only moderate food value to trout.

The trichopteran larva *Heteroplectron* was present in fair numbers in the pond bottom and was eaten by all pond trout. Brook trout in summer made the most use of this large, available caddis worm (forage ratio, 10.1). Housed in a hollow stick, it crawls about on the pond floor.

Brown trout ate many *Liriope* larvae (Diptera) in winter and spring and forage ratios were high, 19.1 and 22.8, respectively. These rather large, fleshy larvae should be of considerable food value to brown trout.

The two snails, *Gyraulus* and *Physa*, were not numerous in the bottom fauna, but were certainly selected by brown and brook trout. In spring, forage ratios for *Physa* eaten by brook and brown trout were 91.8 and 81.8, respectively. Summer forage ratios for *Gyraulus* consumed by brook and brown trout were 10.2 and 721. These two mollusks, especially the large *Physa*, appear to be very important trout foods.

2. Important stream organisms: In the stream as in the ponds, immature chironomids were the most important bottom organisms. The forage ratio for stream midges eaten by all trout at all seasons was 1.1.

The ephemeropteran *Cinygmula*, most important in the bottom fauna, was taken by trout in winter and spring in moderate numbers (forage ratio for spring rainbows, 0.4). These nymphs should be readily available to trout, but apparently were not selected.

Glossosoma trichopteran larvae were eaten by rainbows at all seasons, but principally in spring (forage ratio, 0.7). Spring and summer brook trout also ate this form, the forage ratio being a high 5.7 in summer. *Glossosoma* larvae live in sand cases attached to rocks and are moderately available to trout.

Although present in good numbers in the bottom fauna and quite available, *Alloperla* nymphs (Plecoptera) were almost untouched by the trout. A few nymphs turned up in brown and rainbow stomachs, but forage ratios were very low.

The abundant *Ephemerella* nymphs (Ephemeroptera) were eaten by all trout, especially rainbows in spring (forage ratio, 1.2).

The plecopteran *Nemoura* was eaten by all trout in winter and spring. Particular attention was paid the nymphs by winter rainbows (forage ratio, 1.2). This form should be available, since it crawls about on rocks.

Neophylax trichopteran larvae were eaten by all trout, particularly brown trout (winter forage ratio, 40.0). These larvae, living in gravel cases, are moderately available and certainly selected. Because they are large and fleshy, their food value would be high.

In summary, brook and brown trout living in ponds were making good use of the

TABLE 3.—NUMBERS OF ORGANISMS IN 142 TROUT STOMACHS COLLECTED FROM POND AND STREAM AREAS OF SAGEHEN CREEK

Organisms[1]	Stream Rainbows				Pond Rainbows			Stream Browns			Pond Browns			Stream Brooks			Pond Brooks		
	W[2]	Sp	Su	F	W	Sp	Su	W	Su	F	W	Sp	Su	W	Sp	Su	W	Sp	Su
Nematoda a.	1		2	2									1						
Gordioidea a.			1																
Oligochaeta a.							1	1								2		1	
Hydracarina a.			4	1			1				1			2	1	38		4	13
Pteronarcella n.						1					1	2							
Pteronarcys n.											1							1	
Peltoperla n.	1																1		
Nemoura n.	20	45		2	103	9		3			20	1		5	3		10	57	
Capnia n.		1																	
Filipalpia n.		3			1														
Acroneuria n.		1																	
Isoperla n.	1				3	1								1			2		
Arcynopteryx n.	2							2											
Isogenus n.				1	2														
Alloperla n.	2	1	1	1	10			1			5	1					14		
Rhithrogena n.		5			9						2	1		1	2		3	2	
Cinygmula n.	12	51			28	5		6			11			2	8		12	6	
Iron n.		5			1	1		1			1	2							
Ironodes n.		5			2						1			1	1				
Ameletus n.	5										5	2		3					
Paraleptophlebia n.	16	9	2	1	40			6		1	28	2		3		1	5	7	1
Ephemerella levis n.	6	7			9			2			10	1					11	2	1
E. tibialis n.		7			1	1		1							1				
E. doddsi n.	3	10	1									1							
E. flavilinea n.	2	4		7							1	5							
E. coloradensis n.	1	5		1								2						1	
E. delantala n.						3													
E. cognata n.							1												
Ephemerella n.		3	1	2			1			1		3					1		1
Baetis n.	8	27	2	2	16	1					2	1	1		1		2	7	1
Baetidae n.						1													
Sialis l.	4	3			1		1	3			39	63	2				1	4	1
Rhyacophila l.	1	21	3	2	2	1	1				4	4						6	2
Glossosoma l.	8	46	1	10	1	2									3	6	1		
Glossosoma p.						4													2
Agapetus l.			3																
Hydropsyche l.	2	4	1	1								2					1	1	
Neophylax l.	7	3	5	27	1	2	1	12	2	15	46	5			1	2		12	3

TABLE 3.—Continued

Organisms[1]	Stream Rainbows				Pond Rainbows			Stream Browns			Pond Browns			Stream Brooks			Pond Brooks		
	W[2]	Sp	Su	F	W	Sp	Su	W	Su	F	W	Sp	Su	W	Sp	Su	W	Sp	Su
Limnephilidae A l.									7										6
Limnephilidae B l.		1	61	13						7						85			
Limnephilidae C l.		2	1					3		2	6	2			2		4	1	
Limnephilidae E l.	1	10		1										1					
Limnephilidae F l.	1	226													106				
Limnephilidae G l.	6		12					2	1			3	2		5	4		8	3
Limnephilidae H l.												3							
Limnephilidae l.							6									1			
Limnephilidae p.		26				23	2					34							
Heteroplectron l.			7	4			1	3	2		6	2				3	4		2
Lepidostoma l.			1										2					1	3
Micrasema l.	14	35	15	11	4	3	14			1	1	6		3	33	16	2	15	1
Trichoptera p.		316	71	8		1						4				6			53
Agabinus l.				1								2							
Helophorus a.			1	1	1								1					2	
Paracymus a.		3	1			1													1
Zaitzevia a.							6												
Narpus a.							5												
Lara l.																	1		
Tipula l.					1						1	1							
Prionocera l.					1						2								
Antocha l.	2				1														
Hexatoma B l.		2																	
Tipulidae A l.		4	1					1				1			1				
Tipulidae p.												3							1
Liriope l.	1	1									54	9							
Pericoma l.												1							
Simuliidae l.	1	216	6		70	9					29	7			5		3	78	
Simuliidae p.	2	1										1			8			11	
Chironomidae A l.					71	25	42				884	317	4				142	229	44
Chironomidae B l.					18	2					49	7					14	8	10
Chironomidae C l.											7							2	
Chironomidae D l.	159	20	2	1	2						2	3		16	1	1	764	14	1
Chironomidae l.	496	65	37	4				95						69	2	7			
Paratendipes p.			1										2						
Tanytarsus p.						9						15							
Hydrobaenus p.						45		1											
Diamesa p.	6							4											

TABLE 3.—Continued

Organisms[1]	Stream Rainbows				Pond Rainbows			Stream Browns			Pond Browns			Stream Brooks			Pond Brooks		
	W[2]	Sp	Su	F	W	Sp	Su	W	Su	F	W	Sp	Su	W	Sp	Su	W	Sp	Su
Cricotopus p.	68	1	1	4				126				2		39		1			
Chironomidae p.	132	8	9	3			9				2	72	19	10		17	60	178	4
Palpomyia l.	4	3	4			1	1				5	3	2				3	14	6
Chrysops l.												1	3						
Tabanus l.			4																
Empididae l.							1												
Pisidium a.											1							1	1
Physa a.			2								1	11	3					14	3
Gyraulus a.												2	32					6	1
Salmo a.											1								
Cottus a.															2			1	
Total organisms	995	1,206	264	111	399	151	94	273	12	27	1,229	610	74	156	186	190	1,061	694	165
No. of stomachs	10	10	10	8	10	3	5	4	2	1	8	10	12	4	7	14	4	10	10
No. of bottom organisms per stomach	99	121	26	14	40	50	19	68	6	27	154	61	6	39	27	14	265	69	17
Drift organisms	4	41	327	49	2	20	84		43	5	2	27	168	1	1	120		28	69
Grand total	999	1,247	591	160	401	171	178	273	55	32	1,231	637	242	157	187	310	1,061	722	234
Total no. of organisms per stomach	100	125	59	20	40	57	36	68	28	32	154	64	20	39	27	22	265	72	23
Avg. total length of trout (mm.)	169	173	179	176	177	204	169	180	207	152	210	238	217	148	174	144	160	152	161

[1] a, adult; n, nymph; l, larva; p, pupa.
[2] W, winter; Sp, spring; Su, summer; F, fall.

abundant pond bottom fauna whereas in the stream, rainbow trout were utilizing bottom fauna to the greatest extent.

Neill (1938) states that brown trout feed on the whole range of animals present, taking them in proportion to their accessibility and representation in the environment. This conclusion cannot be supported by this study, since some seemingly unavailable organisms were eaten by trout in large numbers and some common forms were used scarcely at all. Allen and Claussen (1960) also found selective feeding by brook trout in a Wyoming beaver pond. There seems to be a definite element of selection in the foraging habits of trout.

Drift organisms in the diet of trout.—Drift organisms, or those not part of the bottom fauna, represented about half of the summer diet of all trout combined (Table 3). A few drift items were consumed in spring, but almost none were eaten in winter. The over-all average contribution of drift to the diet of Sagehen trout—pond and stream samples combined—was 11 percent.

When the species of trout are considered separately, it appears that brown trout depended more on drift in summer than did the other trouts (Table 3). On a numerical basis, drift accounted for 78 and 69 percent of the brown trout's summer food in stream and pond respectively. Brook trout depended least on drift food since 39 and 29 percent of its food in stream and pond was drift, whereas rainbow trout consumed an intermediate amount of these foods. All trout living in the stream depended more on drift foods than did those inhabiting ponds.

Most of the adult insects grouped as drift lived in the bottoms of stream and pond before they emerged. This further minimizes the contribution of strictly terrestrial insects to the diet of Sagehen trout. The trout of this stream live largely on aquatic insects.

FISH POPULATIONS IN BEAVER POND AND STREAM AREAS

Fish populations in Pond 14 and in stream sections at the Sagehen Creek Project and near B6 (Figs. 1 and 2) were censused each August between 1954 and 1957. The pond measured 221 ft. in length and had a surface area of 0.0555 a. It was atypical in that it was long and narrow, but it was chosen for sampling because the stream could be diverted around it. The stream sections at the Project and near B6 had lengths of 149 and 150 ft. and surface areas of 0.0391 and 0.0429 a., respectively.

Populations were measured by the diversion and draining method described by Needham and Rayner (1939). The stream was diverted, the pools pumped dry, and the fish were removed, measured to total length, weighed, and marked with jaw tags. They were returned to the stream when water was restored in the channel. This method is most accurate for determining fish populations, since nearly all fish over 25 mm. in length are captured.

Trout Populations

Species and numbers.—The total numbers of each trout species sampled during the entire study in the beaver pond and in an equal length of the combined stream sections are given in Table 4. Rainbow trout were dominant in both habitats and accounted for slightly over one-half the population of each. Brook trout were second in abundance and brown trout were least abundant. The unusual paucity of brown trout in the pond may be due to the fact that it lies near the upper altitudinal limit of the range of this species.

Average numbers of trout in the pond

TABLE 4.—TOTAL NUMBERS OF TROUT PRESENT IN BEAVER POND 14 AND IN THE COMBINED STREAM SECTIONS OF SAGEHEN CREEK FROM 1954 TO 1957 (221 ft. of each habitat compared)

Trout Species	Beaver Pond 14		Combined Stream Sections	
	Number	Percentage	Number	Percentage
Brown trout	39	24	21	13
Brook trout	42	25	52	32
Rainbow trout	85	51	88	55
Totals	166	100	161	100

and in an equal length of combined stream sections for the 4-yr. period were similar, being 41 and 40, respectively. On a trout-per-acre basis, averages of 747 and 664 were determined for pond and combined stream sections, respectively (differences not significant at 5 percent level). In contrast, Huey and Wolfrum (1956) found four times as many trout in pond as in comparable stream sections. They used electric shocking for censusing, and since this method misses many small trout so numerous in stream sections, their low figure for stream trout may be exaggerated.

Size of trout.—Whereas there were about as many trout in the stream as in the pond, the pond fish proved to be much larger. Between 1954 and 1957, there were 30 trout over 200 mm. long in the pond, but only 11 trout of this length occurred in an equal length of combined stream sections. (One 628-mm. brown trout from the pond was the largest trout ever recorded in Sagehen Creek.) The average total length of trout in the pond was 147 mm. whereas that in the stream was only 110 mm. (difference significant at 1 percent level). Rutherford (1955) also found longer brook trout in beaver ponds than in stream areas in Colorado. On the other hand, the Sagehen stream sections contained more fry. Forty trout under 75 mm. long were present in the pond; only 58 of these small trout were taken in the combined stream sections.

The average weight of trout in the pond was more than five times greater than that for the stream. Pond fish averaged 117 g. in weight while stream fish averaged only 22 g. The 4-yr. average total weight of all trout in the pond was 10.7 lb. (193 lb./a.) as contrasted to only 2.0 lb. (32 lb./a.) in an equal length of the combined stream sections. All weight differences are significant at the 1 percent level.

During the 4 study years, the standing crop of trout in the pond showed a general decline (Fig. 6). The sharp decline in 1956 also occurred in the stream and was doubtless due largely to the devastating flood of December 1955. The relatively greater decrease in total weight of trout in the pond

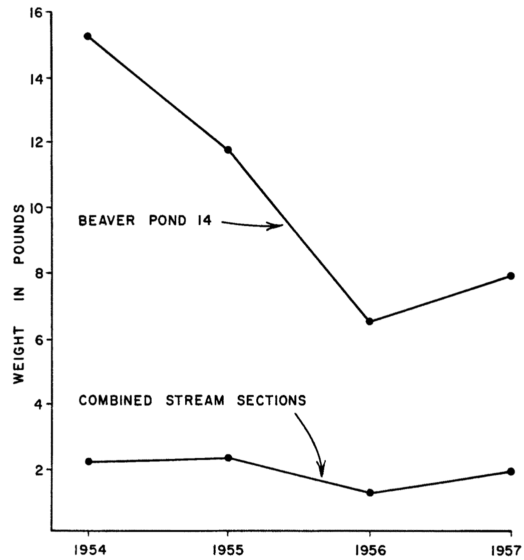

FIG. 6. Total weights of trout in equal lengths of beaver pond and stream sections of Sagehen Creek.

as compared to the stream was due to the exclusion of fishing from the stream section at the Sagehen Creek Project during the latter 2 years and to the fact that the pond was aging. It has often been noted that beaver ponds age and become less productive in time.

Removal by angling.—The greater number of larger sized trout in the ponds was reflected by a greater relative take of pond fish by anglers. A creel census of the upper 6 mi. of Sagehen Creek, including the Rockslide and Upper Beaver Colonies, was taken on randomly selected days during each fishing season. This survey revealed that 31 percent of the 4-yr. catch was taken from the two beaver colonies which occupied only 10 percent of the length of the census area. Certainly, the relatively higher catch from the ponds is at least in part the result of the larger trout populations there, although differential fishing pressure between pond and stream may also be involved. Bailey and Stephens (1951) report a situation in a West Virginia stream where over 4 times as many trout were caught after the stream had been ponded by beavers.

Differential removal of pond and stream trout means that the weight comparisons

TABLE 5.—TOTAL NUMBERS AND WEIGHTS OF SCULPINS PRESENT IN BEAVER POND 14 AND IN THE COMBINED STREAM SECTIONS OF SAGEHEN CREEK (221 ft. of each habitat compared)

Year	Pond 14		Combined Stream Sections	
	Numbers	Pounds	Numbers	Pounds
1954	366	1.85	695	4.28
1955	225	1.28	381	2.66
1956	264	1.31	370	2.51
1957	444	1.69	604	3.93
Average	325	1.53	513	3.35

in Fig. 6 would show even more contrast in the absence of angling.

Sculpin Populations

The standing crop (numbers and weights) of sculpins (*Cottus beldingii* Eigenmann and Eigenmann) in the stream was significantly higher than that in the pond at the 5 percent level (Table 5). This situation is consonant with the known preference of sculpins for riffles.

Relatively high sculpin populations in 1954 were followed by a low in 1955 (pond) or 1956 (stream) and a marked increase in 1957. Seemingly the flood of 1955 had an adverse effect on sculpins as well as on trout.

Dietsch (1958) found that both sculpins and brook trout in Sagehen Creek eat considerable amounts of immature Diptera, Trichoptera, Ephemeroptera, and Plecoptera. The present investigation indicates that rainbow and brown trout also rely heavily on the same insect orders for food. Large trout eat sculpins (Table 3) and sculpins eat some trout eggs (Dietsch, 1958), but food competition is probably the most important interaction.

EFFECTS OF POND REMOVAL UPON TROUT HABITAT, FOOD, AND POPULATION

The flood of December 1955 washed out most of the Rockslide beaver dams and provided an excellent opportunity to assess the effects of dam removal upon trout foods and populations.

Post-flood sampling was delayed 1½ yr. to permit the Rockslide area to re-establish itself as a typical stream. In July 1957, two 1-sq.-ft. samples of the bottom faunas at B3, B4, and B5 were taken with a Surber sampler and analyzed in the fashion already described. It will be recalled that Stations B3 and B4 were sampled with an Ekman dredge in July 1954, when the dams were intact.

The electric-shocking method, described by Haskell (1940), was used to determine the trout populations present in the area occupied by ponds 6N, 6S, 7N, and 7S in July of 1955 and 1957. A portable generator delivering 110 v. and 18.2 amp. of direct current was used to supply electricity. Two separate drives were made with the shocker during each sampling period.

Before the electro-fishing method was used, it was compared to the diversion and draining method to appraise its effectiveness. After the 1954 fish census of Pond 14, the stop nets were left in position. The trout population was then sampled with the shocker. Forty-two of the 61 trout replaced in the pond were taken with the shocker, a 69 percent recovery. Nearly all the trout missed by the shocker were small, since only 1 trout over 150 mm. long was not recaptured. Other reports show that shocking success is greater with larger than with smaller trout (Huey and Wolfrum, 1956).

Changes in Habitat and Bottom Fauna

Several physical changes in the habitat occurred after the dams washed away. The aquatic environment shrank in depth, width, volume, and area but water velocity increased from almost none to an average of 1.8 ft./sec. at B3 and B4. Most of the silt in the ponds washed downstream and left a rubble and gravel stream bed.

With the change to a stream habitat came a sevenfold average reduction (2.29 to 0.31 g./sq. ft.) in weight of bottom organisms at Stations B3 and B4. This difference is significant at the 1 percent level. That this decrease was due to dam removal and not merely to changing conditions between years is indicated by a stream station (B5) which had similar weights (0.40 and 0.43 g./sq. ft.) of bottom organisms at

TABLE 6.—NUMBERS OF TROUT PRESENT IN THE AREA ENCOMPASSED BY FOUR ROCKSLIDE BEAVER PONDS ON SAGEHEN CREEK BEFORE AND AFTER THE REMOVAL OF THE DAMS

Trout Species	Before Dam Removal		After Dam Removal	
	Number	Percentage	Number	Percentage
Brown trout	76	74	6	31
Brook trout	24	23	3	16
Rainbow trout	3	3	10	53
Totals	103	100	19	100

each period. Decrease in total standing crop at the areas occupied by ponds 6N and 8 was computed to be 22-fold. The difference here is much greater than that for weight per unit area since there was a notable decrease in water area after the dams washed out.

Changes in Trout Populations

A marked change in the species composition and standing crop of trout inhabiting the area encompassed by Rockslide Ponds 6N, 6S, 7N, and 7S occurred after the removal of the dams. These ponds supported mostly brown trout, but after the washout, rainbow trout replaced brown trout as the dominant form and brook trout became least abundant (Table 6). A pre-flood population of 103 trout totaling 8.3 lb. decreased drastically to only 19 trout totaling 2.7 lb. after the washout changed ponds to a stream (Fig. 7). Neff (1957) reported a large number of brook trout in an active Colorado beaver colony and only a few trout in beaver-abandoned streams where the ponds had drained.

A stream section, little affected by the flood, had been sampled concurrently with the Rockslide site and was used as a control. In this section, 104 trout were shocked in July 1955 and a nearly equal number (108) was taken in July 1957. Therefore, the decrease in the trout population in the four Rockslide ponds must be attributed to the removal of the dams and not merely to yearly fluctuation.

BEAVER DAMS AND TROUT MIGRATIONS

Many publications on beaver-trout relationships mention the possible blocking of migrating trout by beaver dams, but most of these discussions are of a speculative nature. In order to determine to what extent beaver dams affected trout spawning success in Sagehen Creek, a study of migrating trout was undertaken.

Critical locations throughout the Rockslide Colony were selected for the placement of fish weirs, which were installed in October of 1954. One weir was located at each end of the colony and five others were placed among the ponds where the topography permitted (Figs. 1 and 2). The weirs consisted of a picket fence with half-inch openings bordered by box-type traps with V-shaped entrances. Daily visits were made to the weirs during the fall and captured trout were measured, jaw-tagged, and placed on the side of the weir toward which they were headed. Electric shocking and a creel census were also carried out in the Rockslide area between October 1954 and September 1955 to expedite tagging and to determine movements.

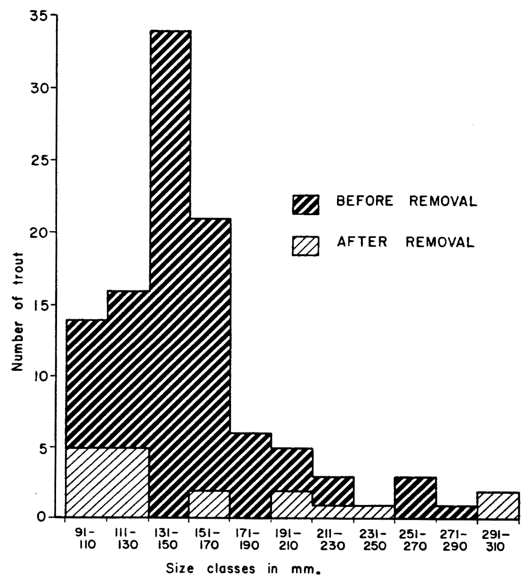

FIG. 7. Numbers of trout in four Rockslide beaver ponds on Sagehen Creek before and after the dams were washed out.

TABLE 7.—NUMBERS OF TROUT KNOWN TO CROSS ONE OR MORE BEAVER DAMS DURING THE MIGRATION STUDY ON SAGEHEN CREEK

Direction of Movement	Season	Brown Trout	Brook Trout	Rainbow Trout	Total
Upstream	Fall	3	0	0	3
	Spring	8	3	1	12
	Summer	3	0	0	3
	All	14	3	1	18
Downstream	Fall	1	1	0	2
	Spring	9	1	4	14
	Summer	3	0	0	3
	All	13	2	4	19
	Total	27	5	5	37

The dams in the Rockslide Colony were constructed of willow and aspen sticks, mostly under 3 in. in diameter, and plastered with silt and sod. They ranged in height from 2.5 to 5 ft. (average, 3.5 ft.) and in length from 14 to 200 ft. (average, 63 ft.).

The Barrier Effect of Beaver Dams upon Migrating Trout

Throughout the migration study, 443 trout in the Rockslide area were tagged. Thirty-seven of these trout were known to cross one or more dams (Table 7), a fact that gave an 8 percent return. No doubt many more trout crossed dams, but were not detected. Crossing down over dams should be easier than crossing up over dams and it is interesting that almost equal numbers of trout crossed in each direction. Only 5 trout were known to cross dams during the fall, but 26 crossed dams during the winter and spring and 6 crossed during the summer. Higher waters in spring presumably permitted easier movement at that season. Four times as many trout (109) were caught moving upstream through the traps as were taken going downstream (24), a tendency that agrees with most studies.

The three kinds of trout exhibited differences in dam-crossing proclivities. Brown trout were most inclined to cross dams. This does not merely reflect the greater number of browns tagged, since the ratio of browns to rainbows and brooks tagged (247:196) is significantly less (5 percent level) than the ratio of browns to rainbows and brooks known to cross dams (27:10). Five rainbow trout, 4 brook trout, and 17 brown trout crossed dams in the spring. This was anticipated for the spring-spawning rainbows, but not for the fall-spawning brooks and browns. Rainbow trout known to traverse dams showed great facility in surmounting these obstacles since four rainbows crossed down over Dams 1 through 14 and one rainbow crossed up over Dams 7 through 14.

All dams were crossed in both directions by one or more trout except Dam 1, which was not known to be negotiated by any upward-moving trout. Salyer (1935) reported that trout did not pass upstream over ordinary beaver dams, a statement that is not supported by my data.

The question may be raised as to how trout manage to cross dams. Where present, side channels provide easy avenues along which trout may circumvent dams. Simply jumping up or down over the dam is the most obvious method. Hodgdon and Hunt (1953) suggest that this could be done most easily at the places where beavers cross dams, since small waterfalls are often present there. Trout may actually penetrate some dams by following the small trickles that percolate through them and by wiggling up through the interwoven sticks and mud. P. R. Needham (personal communication) saw a trout push upstream through a sod dam at the Sagehen Creek observation tank in such a manner.

It may be concluded that some trout can and do cross up and down over many types of beaver dams at all seasons and that the dams are not complete barriers to migration, particularly in spring. It is likely that they are partial barriers in the fall, as concentrations of trout were observed below some of the larger dams at that season.

The important question, I think, is not whether the dams are barriers to migrating trout, but whether they actually inhibit reproduction to the extent that adult populations are lowered. I cannot believe that they do because: 1) it has been demonstrated that there is at least some crossing of dams by trout; 2) many trout spawn in the short riffles between ponds; on November 6, 1954, 37 redds were observed between Dams 1 and 13, a section of almost continuous beaver dams (Fig. 2); 3) it has been shown that the ponds are well stocked with trout; and 4) it is not the number of eggs (within limits) that determines the number of adults resulting, but rather the survival rate of the eggs present.

BEAVER–TROUT RELATIONS IN DIFFERENT LOCALITIES

The effects of beaver on trout vary markedly in different geographic and ecologic situations.

In some sections of the United States, particularly on marginal trout waters of the midwest and east, beavers have been found to be detrimental to trout (Salyer, 1935; Reid, 1952; Adams, 1953). But many streams in others regions have provided better trout fishing as a result of beaver activity. Some California streams become virtually dry in summer and beaver ponds in these may be instrumental in maintaining permanent trout populations (Tappe, 1942). Most investigators in the Rocky Mountains have reported general benefits of beaver activity to trout (Rasmussen, 1941; Grasse and Putnam, 1950; Huey and Wolfrum, 1956). Beaver in the headwaters of some Missouri streams are restoring permanently flowing water and good fishing (Dalke, 1947). It is not surprising that studies from unlike areas often indicate grossly different conclusions.

A consideration of the home, foods, and spawning activities of the trout, and the trout populations themselves, can lead only to the conclusion that beaver are of decided benefit to trout in Sagehen Creek.

SUMMARY

A study of the effects of beaver on trout was conducted on Sagehen Creek, California, from 1954 to 1957. The purpose of the inquiry was to investigate several ways in which beavers and their activities influence the three species of trout present in the creek. Accordingly, comparisons were made between sections of the natural stream and sections that had been ponded by beavers, in regard to: 1) physico-chemical conditions; 2) production of trout foods; 3) feeding habits of the trout; and 4) populations of trout. Further, the consequences of beaver dam removal on trout foods and populations were assessed, as well as the ways beaver dams affect trout spawning activities.

Physical environment of the trout was altered measurably following construction of beaver dams. Most importantly, the substrate changed from gravel and rubble to silt, water velocities decreased, ice conditions became less severe, and the depth and area of the aquatic habitat increased. Water temperature extremes lessened in the ponds, but water chemistry was little affected.

These changes in physical environment resulted in profound changes in the bottom fauna. Although fewer different kinds of organisms were found to live in pond bottoms, much greater standing crops of organisms were living there than in the stream.

All trout relied heavily on bottom faunas for food. In summer, however, drift organisms also became important. Trout living in the stream ate stream fauna almost exclusively. Rainbows living in the ponds depended largely on stream organisms for food, but pond brook and brown trout were supported mainly by pond faunas. Foraging was not random; some organisms, though seemingly unavailable, were selected by trout in both habitats.

The higher standing crop of bottom fauna and the unique physical environment in the ponds were reflected in greater trout populations. These in turn resulted in a relatively higher catch in the ponds than in the stream.

A flood in 1955 removed most of the dams in one beaver colony. Following dam removal, there was a substantial decrease in surface area, trout food, and number of trout. Rainbows replaced browns as the dominant species.

Some marked trout crossed up and down

over most beaver dams at all seasons. There was no evidence that the barrier influence of dams depressed the level of adult trout populations.

It is concluded that beaver are of substantial benefit to trout in Sagehen Creek.

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LOSS OF WATERFOWL PRODUCTION TO TIDE FLOODS

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The possibility of waterfowl nesting losses of catastrophic proportions in certain Arctic areas has been recognized for 20 years or more. Cottam, *et al.* (1944), reporting a waterfowl reconnaissance of the Mackenzie River delta in 1940 by Gillham and Lynch, pinpoint the crux of the situation with the following account.

"There is, however, one grave and ever-present danger to the nesting success of the brant. . . . Storms may arise any time during the breeding season, driving sea tides over the low nesting islands. Soper (1930) mentions storms as a factor affecting populations of the blue goose. Forbush (1925) suggests that the yearly numerical fluctuations of wintering Atlantic brant denote destruction of nests and young by Arctic storms. Gillham and Lynch found the brant in the Mackenzie region to have had a favorable nesting season in 1940, but a storm had disrupted early nests of the snow goose on the islands under observation. Many "two-story" goose nests were found on low areas with one or two eggs in the bottom compartment. Numerous stray eggs were seen, some along the drift line of storm wrack, suggesting that they had been washed out of early nests. Others were dropped at random by laying females whose nests had been destroyed. These geese renested, however, and brought off a successful hatch during the first week in July. As most brant nests hatched between July 10 and 13, it was believed that the nesting season for this bird did not get under way until after the storm. Had this storm occurred when the nesting season was well advanced, wholesale destruction of brant nests and young doubtless would have resulted, because Arctic summers are too short to permit renesting when the first nests are lost late in the season. Brant nests, furthermore, are more exposed to flooding than those of snow geese. The snow goose usually nests on the highest banks of the delta islands, whereas the brant prefers to nest on low islets where usually a rise of only 6 inches in the water level will destroy many nests."

OBJECTIVES

The purpose of this paper is to summarize two field studies in Alaska where conditions comparable to the situation cited above have been under observation.

In 1951, Sigurd T. Olson conducted a waterfowl production study on the outer Yukon-Kuskokwim Delta in western Alaska. One of the objectives of his study was to determine the effect, if any, of storm tides on the production of black brant (*Branta nigricans*) and cackling Canada geese (*Branta canadensis minima*). In 1959, Charles Trainer and Peter Shepherd conducted a waterfowl production study on the Copper River Delta in southern Alaska. One of the objectives of the latter study was to determine the factors influencing production. Through an unforeseen but fortuitous circumstance, Trainer and Shepherd had an opportunity to study in detail the effect of tide floods on egg laying and incubation. It was my privilege as their supervisor to make frequent contact during