

- Neyman, J., T. Park, and Elizabeth L. Scott. 1956. Struggle for Existence—the Tribolium Model: Biological and Statistical Aspects. in J. Neyman, ed., Proceedings of the Third Berkeley Symposium on Mathematical Statistics and Probability. vol. IV, pp. 41-79. Berkeley, University of California.
- Park, T. 1934. Observations on the General Biology of the Flour Beetle, *Tribolium confusum*. Quart. Rev. Biol. 9: 36-54.
- . 1937. The Culture of *Tribolium confusum*. in J. G. Needham, ed., Culture Methods for Invertebrate Animals. Comstock.
- , B. Ginsburg, and Shirley Horwitz. 1945. Ebony: a Gene Affecting the Body Color and Fecundity of *Tribolium confusum*. Physiol. Zool. 18: 35-52.
- , and Nancy Woolcott. 1937. Studies in Population Physiology VII: The Relation of Environmental Conditioning to the Decline of *Tribolium confusum* Populations. Physiol. Zool. 10: 197-211.
- Rich, E. R. 1956. Egg Cannibalism and Fecundity in *Tribolium*. Ecology 37: 109-120.
- Roth, L. M. 1943. Studies on the Gaseous Secretion of *Tribolium confusum* II. The Odoriferous Glands. Ann. Ent. Soc. Amer. 36: 397-424.
- Salt, G. 1937. The Sense Used by *Trichogramma* to Distinguish between Parasitized and Unparasitized Hosts. Proc. Roy. Soc. B 122: 57-75.
- , and F. S. Hollick. 1946. Studies of Wireworm Populations II. Spatial Distribution. J. Exp. Biol. 23: 1-46.

## FLOW, TEMPERATURE, SOLAR RADIATION, AND ICE IN RELATION TO ACTIVITIES OF FISHES IN SAGEHEN CREEK, CALIFORNIA

PAUL R. NEEDHAM AND ALBERT C. JONES

Department of Zoology, University of California, Berkeley, California

As pointed out by Hubbs and Trautman (1935), Maciolek and Needham (1952), and Benson (1953), a study of winter conditions in streams is a badly neglected phase of freshwater ecology. Most stream surveys and studies are conducted in summer when weather is hospitable. However, a fundamental characteristic of high mountain trout waters is the possession of a relatively short, pleasant summer season while, over the rest of the year, generally severe conditions prevail with low temperatures, floods, ice, and snow.

It is well known that severe winter conditions cause extremely high mortalities of trout, as indicated by the work of Needham and Slater (1945), Needham, Moffett and Slater (1945), Maciolek and Needham (1952), Nielson *et al.* (1957), and Miller (1958). Tack (1938) reports that ice crystals plugged the mouths and gills of trout in ponds and killed them by suffocation. Reimer's (1957) work indicates that such heavy winter mortalities are due more to adverse and exhaustive physical conditions than to food conditions at this season. Despite these observations, the factors that actually cause heavy mortalities of stream-dwelling animals remain to be clearly defined and measured. It is the purpose of this paper to present the effects of certain of these physical factors on stream conditions and on the activities and well-being of fishes during winter periods. These studies were conducted at the Sagehen Creek Project operated under the University of California. This project is located at an elevation of 6,337 feet on the east slope of the

Sierra Nevadas in the Tahoe National Forest, 12.8 miles north of Truckee, California.

Sagehen Creek is a tributary of the Little Truckee River which flows into the main Truckee River near the California-Nevada state line. Averaging around 15 feet in width, it is fed by springs and melting snow and fluctuates from around 50 cubic feet per second during spring run-off to about 2.0 c.f.s. in September. It rises at an elevation of around 7,000 feet and after passing over its 10 mile course, enters the Little Truckee at an elevation of 5,000 feet. The winter studies described here were all conducted within a half mile of the station headquarters. The facilities provided there have been described by Needham (1956).

Sagehen Creek basin is entirely forested except for scattered meadows along the stream. The dominant trees consist of Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), red fir (*Abies magnifica*), and lodgepole pine (*Pinus contorta*) which dominates the wetter areas. The average winter snow pack is roughly 44 inches. Severe winter conditions usually prevail from mid-December to the end of March with intermittent periods of clear weather occurring for short intervals.

The only native salmonid fish in Sagehen Creek was the Lahontan cutthroat trout, *Salmo clarki henshawi*, but these have long since been replaced by introduced forms: eastern brook trout, *Salvelinus fontinalis*; rainbow trout, *Salmo gairdneri*; and brown trout, *Salmo trutta*. These 3 species all occur in the area of the station and the only

other species of fish that is present in this area is the sculpin *Cottus beldingi*.

Of the salmonids, rainbow trout are most abundant, followed by eastern brook, with brown trout being relatively scarce. The last is the dominant species, however, in the beaver ponds on the lower portions of the stream.

#### FACILITIES AND METHODS

In order to make outdoor observations for fairly long periods of time in cold weather, one of the first essentials is shelter for the observer. At Sagehen Creek this was provided in an underwater observation tank. This was fitted with four, 15 × 23 inch plate glass windows, two to a side, for viewing the hydrohabitat below the stream surface (Needham 1956).

A series of thermocouple stations was established around the tank in various positions for recording both air and water temperatures. Air temperature was measured in the shade of the roof eave on the north side of the tank about 12 feet above the water. Surface-water temperatures were measured from one inch to about 16 inches below the water surface. No differences were found in these measurements because of the turbulence of the stream in this area. Ground-water temperatures were measured at the downstream end of the tank where a relatively large volume of water upwelled from the gravel stream bottom beneath the tank.

One station set up on the stream bank to measure solar radiation, used a Gier and Dunkle flat-plate radiometer. Because of difficulties encountered in making an underwater solarimeter watertight, no measurements were made of the penetration of solar radiation through water. The copper-constantan thermocouples were attached to a selector switch and an ice bath standard inside the tank. A lead-covered cable was run from this some 400 feet to the laboratory where it was connected to a Leeds and Northrup No. 8662 potentiometer. Thus, two workers were required: one in the tank to select the stations where temperatures were being taken, and the other in the laboratory to record the readings on the potentiometer. Telephones connected the tank with the laboratory.

The observer in the tank, aside from selecting the stations for temperature measurements, also made observations on the behavior of any fishes seen. In subzero weather this was a rigorous task to say the least, and during the 24-hour diurnal studies reported here, this job was rotated between two or more workers. Students quickly dubbed this work "the deepfreeze." The bottom

of the tank was floored with wood. On this, Air Force litter blankets and air mattresses were placed to reduce the hardship. Even though heavily clothed, an observer could not usually stand more than about 45 minutes lying in the tank before he would have to return to the station headquarters to warm up.

Lights were provided for night observations. Strong white light invariably disturbed or drove away fish in areas adjacent to the tank windows but subdued red or violet light modified their behavior only slightly. However, any light that was strong enough to permit the observer to see clearly, usually frightened or drove fishes away. The use of infra-red light was considered but abandoned because of its rapid absorption in water.

A second series of thermocouple stations was set up at a location 500 yards downstream from the tank site. This location will be referred to subsequently as the truck-crossing site.

Water levels were measured with a Leopold-Stevens water-stage recorder (type A35), installed about 200 yards below the truck crossing. A rating curve established for this station permits conversion of gage heights into discharge in cubic feet per second.

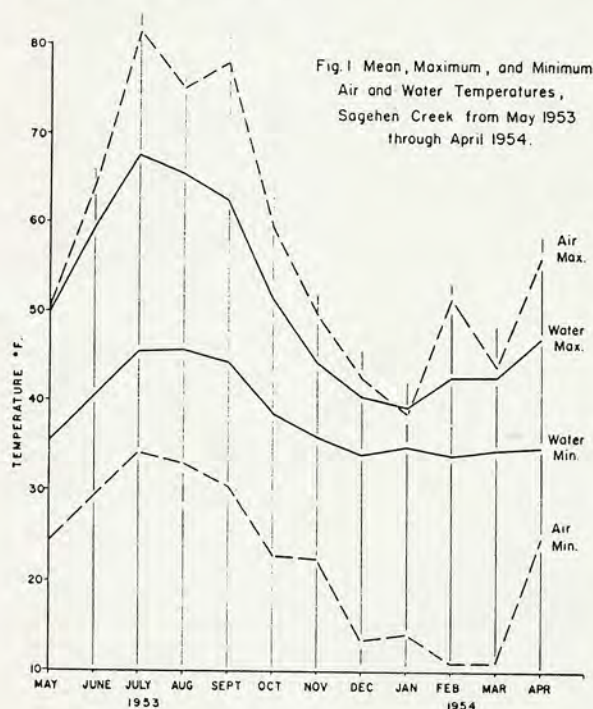
Air and water temperatures at the station headquarters were taken constantly with a two-pen recording Bristol thermograph, using 12-inch charts and operated the year round. The bulb recording air temperatures has a 10 foot lead and is mounted on the north side of a tree about 3 feet above the instrument in a small cupola to protect it from direct rays of the sun. The water lead is 50 feet long and is buried in the ground from the tree into the stream. There the bulb is placed in an iron pipe in swift water about 3 feet from the bank and at a depth of about one foot at normal flows.

#### RESULTS

##### *Seasonal Characteristics of Air and Water Temperatures*

Sagehen Creek is characterized by a marked seasonal variation in temperature. Temperature records show that the most stable period, temperature-wise, is in winter and that the least stable period is in summer. Water temperatures, obviously, are strongly influenced by air temperatures. Daily thermograph charts show that air and water temperature curves have similar shapes but the latter show a smaller range between maximum and minimum temperatures and the temperature fluctuations lag several hours behind those of the air.

The greatest differences between mean monthly maximum and minimum water temperatures occur in July and August. In the former month the difference was 21.5°F and in the latter, 14.4°F (Figure 1). The smallest differences occurred in December and January and were 6.2°F and 4.3°F respectively. These small winter differences may be accounted for, in part at least, by the much smaller amounts of solar energy reaching the stream and its environment in the winter than in the summer. Also, during the winter much heat may be stored as latent heat of fusion during ice formation without further lowering of the water temperature.



In terms of actual, daily minimum water temperatures, 32°F was first recorded on October 26, 1953, when the air temperature dropped to 18°F. In November, 32°F was recorded on 4 days; December 6 days; January 2 days; February 5 days; and March 3 days. Daily minimum water temperatures never dropped to 32°F during the months of April through September.

The maximum daily water temperature recorded during the period covered was 70°F on August 11, 1953. The mean maximum for this month was 65.2°F. In July a maximum of 69.0°F was recorded on 8 days while the mean maximum for this month was 67.3°F or 2.1°F warmer than the mean for August.

In Fig. 1, it is of interest to note that mean monthly minimum air temperatures of less than

32°F occurred in 10 months of the year (September through June). Individual daily minima below 32°F are encountered each month of the year. In July, 1953, the air temperature dropped to 32°F or below on 15 days. Similarly, August produced 18 days below 32°F.

#### Acclimation

The observed water temperature pattern is one of gradually decreasing temperatures in October and November with the reverse occurring in April, May and June. In relation to survival of fishes, these observations clearly indicate that 2 long periods of temperature acclimation are provided, one in fall and one in spring. The former gradually prepares fish for adjustment to the low water temperatures of December through March and the latter to the high temperatures of June through September.

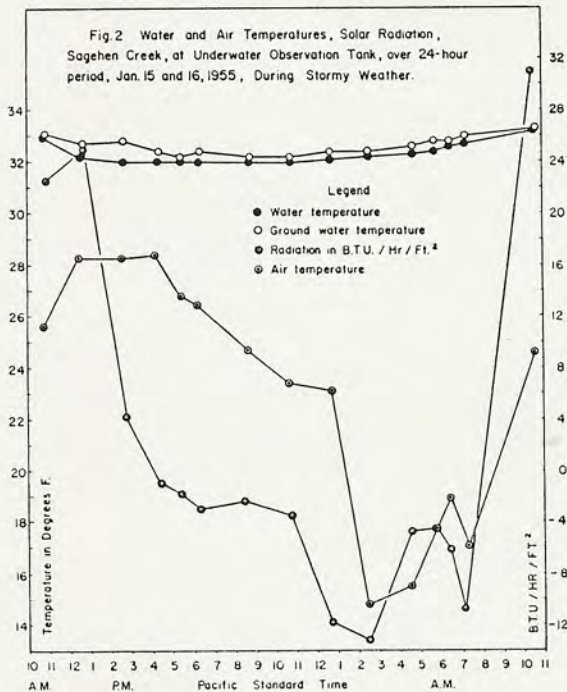
Trout are relatively stenothermal animals but the temperatures recorded for Sagehen Creek are all well below the maximum tolerance limit of 78°F reported for eastern brook trout by Embury (1921) and Fry *et al.* (1946).

The senior author observed a kill, estimated at 50%, when 15,000 3 to 4 inch rainbow trout were planted in Convict Lake in eastern California. The water temperature of the lake was 45°F whereas the fish had been reared for approximately 6 months in a hatchery at a water temperature of 63°F. From this and other observations, it is concluded that acclimation must be a continuous and necessary process under natural conditions, one that is essential for the continual readjustment to changing thermal conditions from month to month and season to season. Lack of a thorough acclimation process may provide one answer at least to the extremely heavy losses of hatchery-reared trout following planting as reported by Needham (1949), Miller (1958), and other workers.

#### Diurnal Cycles in Air and Water Temperatures and Solar Radiation

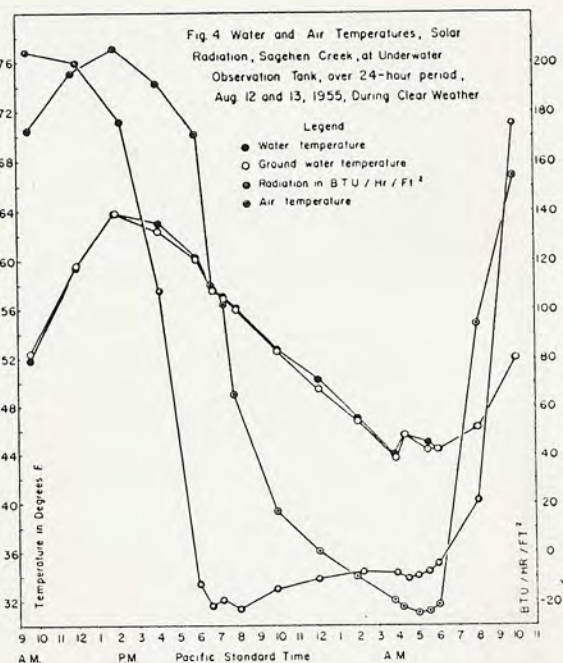
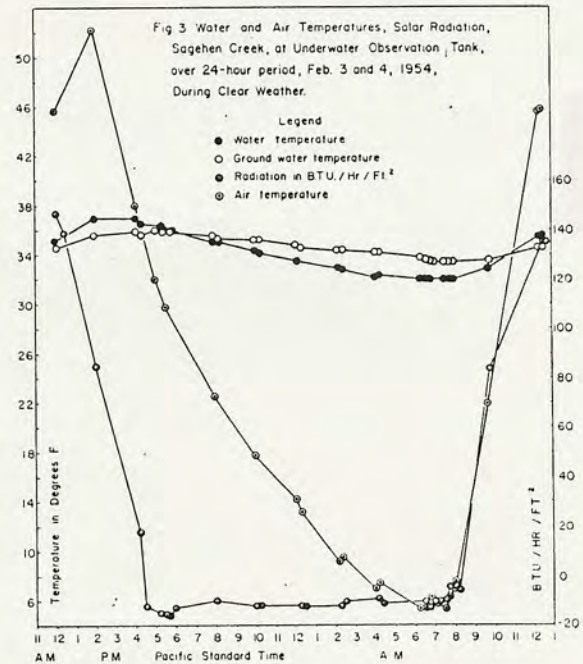
Twenty-four hour temperature and solar radiation patterns were measured for 4 different periods of the year. Three of these were taken in clear weather in February, August, and October. Only one was taken in stormy weather in January. These periods were selected because they provide data typical of the behavior of these factors in relation to seasons and weather conditions. Clear weather usually prevails during summer periods while intermittent storms may occur at other seasons of the year. All of these observations were made manually without the use of a constant recorder.

The amount of solar energy reaching the stream shows a characteristic pattern for each season. On January 15-16, 1954 (Figure 2), the weather was stormy and maximum solar radiation reached only 31 BTU/hr/ft.<sup>2</sup> The air temperature over the same period fluctuated only between 28.4°F and 14.8°F. Water temperatures were between 32.0°F and 33.3°F. Surface-water temperatures remained slightly below those of the ground water throughout the period.



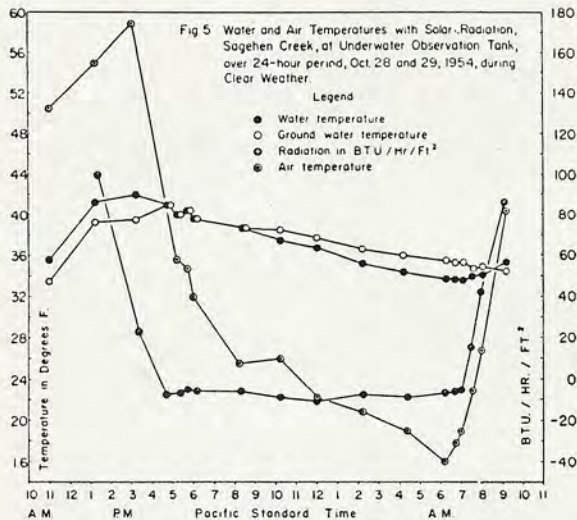
In contrast, periods of clear weather in winter produced larger fluctuations in radiation and temperature but the variations still are moderate compared to other seasons of the year. On February 3-4, 1954 (Figure 3), radiation reached a maximum of 147 BTU/hr/ft.<sup>2</sup>, and a minimum of -16 BTU/hr/ft.<sup>2</sup>. Air temperature varied between 52.3°F and 5.4°F. However, the water temperature varied only between 37.0°F and 32.0°F. The ground-water temperature again exerted a modifying influence on the temperature of the surface water. During the day, when air temperature was high, the surface-water temperature was higher than that of the ground water. However, from 6:15 PM to 10:30 AM the surface-water temperature fell to below that of the more stable ground-water temperature.

As indicated above, extremes in temperature fluctuations occur during the summer period as is shown on August 12-13, 1955 (Figure 4). Air temperatures varied from 77.2°F to 31.0°F. Solar radiation varied from 204 to -23 BTU/hr/ft.<sup>2</sup>.



The temperatures of ground water and surface water were almost identical at all times and varied between 43.9°F and 63.8°F.

Conditions in autumn were intermediate between those of summer and winter. On October 28-29, 1954 (Figure 5), solar radiation varied from 100 to -10 BTU/hr/ft.<sup>2</sup>. Air temperature fluctuated between 58.9°F and 16.0°F. Water temperature varied between 41.0°F and 33.5°F.



The effect of ground water in exerting a modifying influence on the temperature of the surface water was again noticeable. During the day surface water was warmer than ground water but during the night it was cooler. Nightly reversal of the relationships between surface-water and ground-water temperatures during clear cold weather are clearly illustrated in Figures 3 and 5. When the radiation and air temperature fall rapidly in the late afternoon, the surface water slowly cools and usually drops below the temperature of the ground water between 7:00 and 9:00 P.M. With the advent of daylight, increasing radiation and higher air temperatures cause the surface water to warm slowly, and its temperature rises above that of the ground water usually between 8:30 and 11:00 A.M. During stormy periods, as indicated above for January (Figure 2), the temperature of the surface water may consistently run below that of the ground water for full 24-hour periods.

It is evident from the above that both temperature and solar radiation show pronounced differences between summer and winter and between stormy and clear weather periods. The air temperature and radiation curves, in general, parallel each other. In summer, maximum radiation is usually reached between 9:00 and 10:00 A.M. Standard time, after which for the remainder of the day the amount of energy falls away sharply, becoming negative around 6:00 P.M. when more heat is being lost than is being gained. In winter, in both clear and stormy weather, solar radiation usually peaks between 12:00 noon and 1:00 P.M., after which it falls away rapidly and becomes negative between 4:00 and 5:00 P.M.

### Effect of Anchor Ice on Stream Flow

Anchor ice is a type of underwater ice that forms on the bottom of streams and on objects under water. In contrast, frazil ice particles are very small crystals and discs of underwater ice which are distributed throughout a turbulent flowing stream. Underwater ice forms only when the water temperature falls below 32.0°F. A temperature gradient from the ice to the water is required in order to carry away the latent heat of fusion. Thus, supercooling of the water and the rapid transfer of heat work together to cause the formation of underwater ice (Mantis 1951). Anchor ice is formed in riffles where it first appears as small white masses on the substrate. It is soft and mushy in consistency since it is a mixture of both liquid phase and ice particles. Key points of beginning formation are the upstream points of stones, where the current is split to each side and where the current velocity is reduced nearly to zero. Although the reasons have not been definitely established, Dorsey (1948) suggests a purely mechanical action in which the motion of the water molecules is slowed sufficiently to enable them to orient themselves as required for crystallization. There is also an extension of growth by accumulation and adhesion of fine frazil-ice particles which are always found in supercooled water. In riffles the presence of turbulence and of irregular surfaces from which heat may be conducted away faster, often causes anchor ice to form to such an extent that it dams up the stream. At times anchor-ice dams will almost completely block all flow of water and will even extend some distance into pool bottoms above and below the riffles.

During the winter of 1953-54 the conditions under which anchor ice formed in Sagehen Creek and the effects of such formations were observed. Warm ground water seeping up from the substrate of the stream bed prevented the formation of anchor ice near the observation tank but it formed abundantly in the riffles at the truck-crossing site some 500 yards downstream.

The two observation sites differed considerably in their ecological settings. The truck crossing was fully exposed to the elements in an open meadow with the nearest trees some 50 feet away to the south. On the north the meadow extended about 200 feet to the lodgepole pines bounding the meadow's north border. The stream winds its way through the meadow with frequent pools and riffles and except for scattered willows and a few trees here and there, represents a typical high montane meadow.

The observation-tank site was located in what might best be called a semi-exposed habitat. A group of lodgepole pine growing on the south bank partially shades it and clumps of willow are far more numerous in the general area than at the truck crossing. The only meadow present is a narrow strip on the north bank some 50 feet wide in which the radiometer station was established. The upwelling of ground water at this site may be caused, partially at least, by the fact that the valley narrows materially at this point. About a hundred yards upstream the meadow widens again and the narrowing in between the upper and lower meadows could cause a damming effect in the substrate sufficient to create the upwelling observed.

Anchor ice usually formed at minimum night-time air temperatures of from  $-9.0^{\circ}\text{F}$ , the lowest reading of the period, to  $12.0^{\circ}\text{F}$ . However, on the morning of January 15, 1954, subsurface ice, similar to anchor ice, was observed in the stream, even though the minimum air temperature of the previous night was only  $26.0^{\circ}\text{F}$ . This may be explained by the presence of high winds during the night which blew snow into the stream, super-cooled the water and resulted in a slushy snow and ice mixture which accumulated on the stream bottom.

During the course of the winter it was noticed that increasingly low temperatures were required to produce anchor ice. During the month of December anchor ice was observed on 11 out of the 15 mornings when the minimum air temperature was between  $0.0^{\circ}\text{F}$  and  $12.0^{\circ}\text{F}$ . However, in January, February and the first week of March, anchor ice was observed on only one out of the 25 mornings when the minimum temperature was in this same range. This is possibly due to an increased ice and snow cover over much of the stream, which would act as an insulator sufficient to prevent loss of heat and thus prevent underwater ice formation. Similar effects have been noted by Devik (1942, 1944) in preventing the formation of ice on underwater inlet gates. When minimum night-time temperatures were below  $0.0^{\circ}\text{F}$ , regardless of the month, anchor ice was observed each morning (a total of 7 times), with the exception of January 20 and 22, when the minimum temperatures were  $-7.0^{\circ}\text{F}$  and  $-3.0^{\circ}\text{F}$ , respectively.

As indicated above, anchor ice produces a marked effect upon stream water levels. In Figure 6, gage height and air temperature are graphed over a 72-hour period on December 28, 29, and 30, 1953, when suitable weather conditions for the formation of anchor ice prevailed. The dam

formed by anchor ice in the riffle at the lower end of the gaging station pool caused the rise in levels depicted in the graph. From this it is apparent that an inverse relationship exists between temperature and water level. As the temperature drops, anchor-ice formation commences and the water level rises. Maximum and minimum water temperatures and the length of time the minimal period lasted, are given in Table I for the periods graphed in Fig. 6.

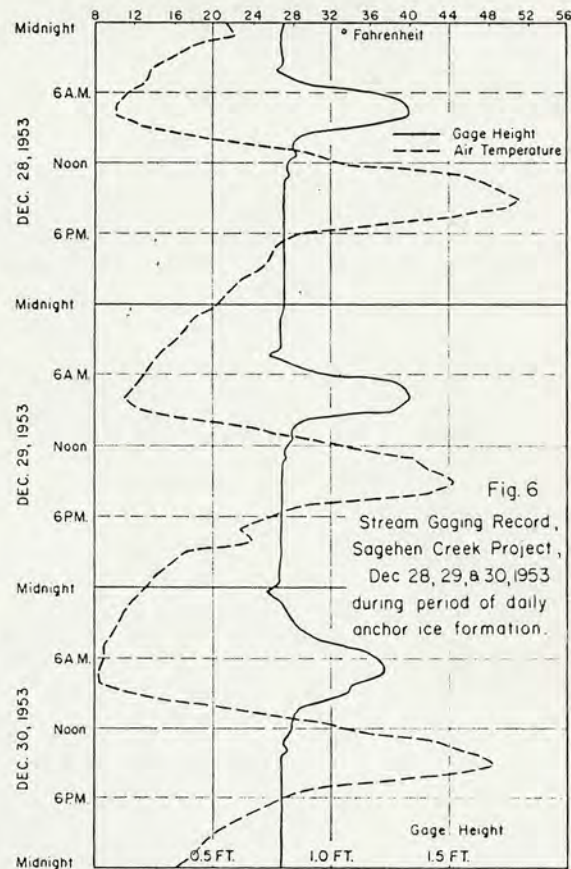


TABLE I. Water temperatures ( $^{\circ}\text{F}$ ), December 28, 29, and 30, 1953, during period of daily anchor ice formation graphed in Figure 6

Date	Max.	Min.	Duration of Minimum
Dec. 28.....	40	32	5:30-8:30 A.M.
29.....	40	32	7:00-8:00 A.M.
30.....	39	32	2:00-8:00 A.M.

A thermocouple at the truck-crossing site was installed one inch above the water surface. With the rise in water level accompanying anchor-ice formation, this thermocouple was covered by water, thus providing information as to the time and temperature when anchor ice formed. For

example, on January 22-23, 1955, anchor ice formed between 4:15 and 6:00 AM at an air temperature of between  $-3.0^{\circ}\text{F}$  and  $-4.0^{\circ}\text{F}$ . The air temperature at the thermocouple just above the water surface was usually about  $4^{\circ}\text{F}$  above the air temperature recorded on the bank, probably influenced by its proximity to water. Once anchor ice formed around the thermocouple, the temperature varied between  $29.4^{\circ}\text{F}$  and  $32.3^{\circ}\text{F}$ . When the water temperature rose above  $32.0^{\circ}\text{F}$ , the anchor ice began to melt and pool levels dropped.

Water levels in the pools above the riffles where the dams form may be raised as much as 1.7 feet. However, the average maximum height of the water level for 20 nights when anchor ice formed was 1.31 feet. The water level height during the day was nearly constant at 0.81 feet. The rise began anywhere from 9:00 PM to 5:00 AM and lasted from a minimum of 2 hours to a maximum of 12 hours. The average duration was about 4 hours.

It will be noted in Figure 6 that the rise was preceded by a slight, sudden decrease in water level which varied from 0.01 to 0.05 feet and which lasted approximately one hour. This, we believe, represents the period when the water is supercooled and much of it is rather suddenly turned into ice, thus causing a slight lowering of stream discharge.

As soon as the damming effect of anchor ice becomes apparent, the water level begins to rise although the actual flow continues to decrease. Thus the increased gage heights shown in Figure 6 were caused by anchor ice and do not represent a real increase in stream discharge. Actual discharge on the dates these observations were made averaged 3.5 cubic feet per second.

#### *Feeding of Trout in Winter*

Trout were observed to feed on numerous occasions when the water temperature was between  $32.0^{\circ}\text{F}$  and  $33.0^{\circ}\text{F}$ . The fact that trout will actively feed when the water temperature is  $32^{\circ}\text{F}$  is clearly demonstrated by the following observation made in the large underwater observation tank on January 25, 1956. About a foot of fine snow had fallen during the previous night and about 7:00 AM a strong west wind started blowing large quantities of snow into the stream, both from the banks and from adjacent pine trees. The surface of the stream was practically occluded by floating clumps of snow. From the tank windows the undersurface of the floating snow was quite irregular and at several points clumps had been pushed against the stream bottom where the cur-

rent was slack and unable to move it. That the water had been supercooled by the addition of snow blowing into it was apparent for the columns of snow touching the stream bottom appeared to grow and become larger by the addition of crystals of frazil ice during the observation period between 4:00 and 4:45 PM.

Three rainbow trout ranging from around 4 to 8 inches in length were observed actively feeding. Despite the fact that the water surface was completely covered by clumps of floating snow and that snow pressed against the bottom in places, these fish were actively swimming up to examine each food item drifting in the water. They would take particles in their mouths in a sort of "tasting" action and then either swallow or reject them. Occasionally fish were seen feeding directly off the bottom of the stream. They avoided the snow masses but ranged easily through the tunnel-like openings between the submerged snow masses. It is likely that the large masses of snow being swept downstream were dislodging aquatic insect larvae and nymphs from the stream substrate, thus offering a higher than normal quota of natural drift foods. Maciolek and Needham (1952) reported that the daily breakup of anchor ice caused it to rub over stones as it drifted downstream, thus freeing bottom food organisms which were rapidly consumed by trout.

This observation did not reveal any cause of winter mortality except to the elements composing the macrofauna. The fish seemed vigorous and fed steadily during the 45 minutes they were under observation.

These winter feeding activities must reflect a rather high metabolic rate following acclimation to temperatures at or very close to  $32^{\circ}\text{F}$ . Fry (1947, p. 16) states that an "animal can exist, often for substantial periods of time, at a temperature level beyond the zone of tolerance and may frequently do so, particularly during diurnal fluctuations." This statement refers specifically to what Fry terms the "zone of resistance" to maximum temperatures following suitable acclimation. However, from the feeding observed we can only conclude that  $32^{\circ}\text{F}$  is still within the zone of tolerance for trout and that the zone of resistance, including the lower lethal limit for this species, must fall somewhat below the freezing point (Fry *et al.* 1946). While we have no precise measure of the magnitude of the activities observed, the main difference seemed to be one of speed. In feeding observed during summer periods, the actions of the fish were more rapid and their reactions in general seemed much faster.

### *Other Activities of Fishes*

Trout observed during daylight hours were invariably seen in close proximity to shelter. This consisted of overhanging bushes, projecting snow banks, or a deep sheltered pool protected by exposed roots at the side of the underwater observation tank. This preference for cover or dark areas was reflected in the greater numbers of fish observed at night. During four 24-hour observation periods a total of 47 trout were seen at night while only 14 were seen during daylight hours. During the day trout probably moved away from the relatively shallow area surrounding the observation tank to deeper and darker areas of the stream. One 3½ inch eastern brook trout was observed intermittently for a period of 7 days close to the edge of the stream under an overhanging bank of ice and snow. This protected area was so dark even at midday that a spotlight was necessary to see the fish. At times during this period this same site was occupied by a 4½ inch eastern brook trout. However, at other times the position was vacant. During the same observation periods 25 sculpins were observed at night but only 7 during the day. However, the sculpins that were observed during the day were more likely to be found in unprotected, lighted areas of the stream than were the trout.

Territorial behavior of trout has been described by Newman (1956). Trout occupied particular sites in the stream and it was often possible to recognize an individual fish on the basis of its size, spotting, and location.

Interspecific aggressive behavior between sculpins and trout was observed. On one occasion a 4 inch sculpin gave chase to a 2 inch trout. The sculpin made a short dash in the direction of the trout but the trout quickly swam upstream out of reach. In 2 other instances, one involving a 4 inch sculpin and a 3½ inch eastern brook trout and the other a 3 inch sculpin and a 2½ inch eastern brook trout, the trout approached from upstream to within one inch of the sculpin and veered off slightly at it passed the sculpin which apparently was not disturbed.

At night trout maintained a closer relation to the substrate than during the day. Their lower fins were often in contact with the stream bottom and it is possible that tactile cues of position were substituted for visual ones.

Trout foods and other insect life were abundant and active during the winter. On a number of occasions in January, 1954, springtails (*Collembola*) were observed crawling on the surface of the ice covering stream pools and in the air spaces between layers of ice. In addition, mayfly and

stonefly nymphs and simuliid and caddisfly larvae were seen regularly in small cavities between pebbles on the bottom of the stream. In the fall of 1955, a gravel spawning bed was constructed in shallow, swift water next to the downstream window on the south side of the tank. Sexually mature eastern brook trout of both sexes were penned inside the area with half inch mesh wire cloth. These fish proceeded to go through their courtship activities, dig their nests, and spawned within full view of the window. One redd was actually built in contact with the glass of the window and each step in the spawning process could easily be observed. Similar success in observing spawning of Atlantic salmon (*S. salar*) and Arctic charrs (*S. alpinus*) with observation chambers has been reported by Jones and King (1949) and Fabricius and Gustafson (1954).

### *Mortality of Fishes*

Reflection on the problem of over-winter survival of fishes makes it appear that when heavy mortalities do occur as a result of severe winter conditions, they must happen quickly and in localized areas subject to sudden catastrophies. On the other hand, severe floods may cause heavy damage over entire drainage areas, the effects being greatest in the lower, wider portions of streams and least in their narrower headwaters.

Needham and Slater (1945) report the loss of several hundred trout when a snowbank dropped into a rearing pond at the Hot Creek State Fish Hatchery near Bishop, California. Nielson *et al.* (1957, p. 22) report parallel effects of snow and ice. Needham (1934, p. 243) reports a reduction from 205 to 70 pounds per acre of the macrofauna in Waddell Creek near Santa Cruz, California, which was probably a direct result of a heavy flood in early February, 1933.

A heavy flood occurred in Sagehen Creek in December, 1955. Flow in the creek peaked at ca. 700 c.f.s., the highest ever recorded for Sagehen Creek. The changes wrought in the stream bed were many and drastic. Numerous new channels were cut and stream bank erosion was severe. The pool on the north side of the observation tank was partially filled by gravel washed downstream. A loose rock dam just below the station was washed completely out, as were the 3 eastern brook spawning beds that held incubating eggs from spawning in the previous fall. Apparently the force of the flood had disastrous effects on fall-spawned eggs which were incubating in stream gravels for incoming young of eastern brook and brown trout of the zero age group were almost completely missing from the population samples taken the following summer.



Evidence of the disturbance and destruction of the elements of the macrofauna by anchor ice is reported by Benson (1955). His observations, made in the Pigeon River, Michigan, showed that square foot samples of anchor ice from the stream bed contained an average of 10 organisms plus sand, gravel, and organic debris. Floating anchor ice contained similar numbers of organisms and amounts of materials. Anchor ice served as a method for downstream dispersal of bottom organisms but the number moved was so small that it "would not be great enough to deplete the bottom fauna populations" (Benson, *op. cit.*, p. 530).

The causes of winter mortality of fishes dwelling in lentic waters at high elevations subject to severe floods and winter conditions may be listed as follows:

1. Sudden collapse of snow and ice into the water may cause death by either direct crushing effect or suffocation against the stream substrate, or both.
2. Both snow and anchor-ice dams and ice jams may dewater stretches of considerable length and suffocate fish life.
3. Suffocation may occur when flooded side channels or other areas are dewatered suddenly by the breakup and dispersal of ice and snow dams.
4. Severe floods may have the following effects, all of them severe and the cause of high mortalities of aquatic organisms:

(a) Actually killing both adults and young fishes by the grinding action of huge amounts of gravel being rolled down stream beds.

(b) Stranding of fishes in side pools that later dry up or that are easily accessible to predators.

(c) Destruction of a major portion of the macrofauna that forms the bulk of fish foods.

(d) Destruction of eggs and alevins of fishes through annihilation of spawning redds.

#### SUMMARY

A study of ecological conditions in winter in relation to activity of fishes in Sagehen Creek, California, showed that there exist, temperature-wise, two long periods of acclimation, one in the fall and one in the spring. These prepare fish for both the low water temperatures of winter and the high temperatures of summer. Water temperatures show less fluctuation in winter than in summer both because of the smaller amount of net solar radiation and the storing of heat as latent heat of fusion during ice formation. Bottom macrofauna is abundant as food for trout in winter and trout were observed to feed on numerous occasions when the water temperature was between 32° and 33°F. It is concluded that 32°F

is within the zone of tolerance of trout and that trout are able to resist water temperatures below 32°F for short periods of time. Floods may act as a decimating factor to fish populations by destroying eggs and reducing bottom macrofauna.

Anchor ice was shown to be an important ecological factor since it raises the water level in pools and reduces the flow over riffles. Anchor ice formed only in those areas of the stream which had no upwelling of relatively warm ground water through the substratum. Anchor ice, when it is breaking up, melting or otherwise dispersing, dislodges considerable amounts of the bottom macrofauna, thus making more food available to trout at such times.

Trout exhibited territorial behavior, showed a strong preference to occupy sheltered locations, and in shallow water were more numerous during the night than during the day.

The high winter mortalities of trout populations which have been observed are probably not the result of lack of food or long periods of low temperatures. More likely causes are sudden catastrophes such as severe floods or suffocation under collapsed snow banks or dewatering of stream sections by ice dams.

#### ACKNOWLEDGMENTS

Our thanks are due first of all to the Max C Fleischmann Foundation of Nevada for a generous grant-in-aid of \$30,000, which permitted the employment of students and the construction and purchase of facilities and equipment used in the studies reported here. Most of the field observations were made by the authors assisted at intervals by Ray Allen, Elbert Brock, Richard Gard, and Joseph Hall.

We are indebted to the Surface Water Branch of the U. S. Geological Survey, Sacramento, California, for cooperation in installing and maintaining a stream gaging station on Sagehen Creek for the accurate and constant measurement of stream flows.

Professors Joseph Gier and R. V. Dunkle of the Engineering Department, University of California, gave much aid in instrumentation problems. We are also indebted to Dr. Ray F. Smith and Dr. R. L. Usinger of the Department of Entomology and Parasitology for helpful criticisms of this manuscript. Other colleagues and students contributed materially.

#### REFERENCES

- Benson, N. G. 1953. The importance of ground water to trout populations in the Pigeon River, Michigan. *Trans. N. Amer. Wildl. Conf.* 1953, 269-280.
- . 1955. Observations on anchor ice in a Michigan trout stream. *Ecology*, 36: 529-530.
- Devik, O. 1942. Supercooling and ice formation in open waters. *Geofys. Publ.*, 13(8): 1-10.
- . 1944. Ice formation in lakes and rivers. *Geogr. J.*, 103(5): 193.
- Dorsey, N. E. 1948. The freezing of supercooled water. *Trans. Amer. Phil. Soc.*, 38 (Part 3): 247-328.
- Embody, G. C. 1921. Concerning high water temperatures and trout. *Trans. Amer. Fish. Soc.*, 51: 58-61.

- Fabricius, E. and K. Gustafson.** 1954. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. Institute of Fresh-water Research, Drottningholm, Rept. No. 35: 58-104.
- Fry, F. E. J.** 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. 55, Publ. Ont. Fish. Res. Lab. 68.
- , **J. S. Hart,** and **K. F. Walker.** 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis*. Univ. Toronto Stud. Biol. 54, Publ. Ont. Fish. Res. Lab. 66.
- Hubbs, C. L. and M. B. Trautman.** 1935. The need for investigating fish conditions in winter. Trans. Amer. Fish. Soc., 65 (1935): 51-56.
- Jones, J. W. and G. M. King.** 1949. Experimental observations on the spawning behaviour of the Atlantic Salmon (*Salmo salar* Linn.). Proc. Zool. Soc., 119 (Part I): 33-48.
- Maciolek, J. A. and P. R. Needham.** 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. Trans. Amer. Fish. Soc., 81 (1951): 202-217.
- Mantis, H. T., ed.** 1951. Review of the properties of snow and ice. Eng. Expt. Station, Inst. of Technology, University of Minnesota, Minneapolis.
- Miller, R. B.** 1953. The role of competition in the mortality of hatchery trout. J. Fish. Res. Bd. Can., 15: 27-45.
- Needham, P. R.** 1934. Quantitative studies of stream bottom foods. Trans. Amer. Fish. Soc., 64 (1934): 238-247.
- , 1949. Survival of trout in streams. Trans. Amer. Fish. Soc., 77 (1947): 26-31.
- , 1956. The Sagehen Creek experimental wildlife and fisheries project. A.I.B.S. Bull. (Nov.): 19-21.
- , **J. W. Moffett,** and **D. W. Slater.** 1945. Fluctuations in wild brown trout populations in Convict Creek, California. J. Wildlife Mgmt., 9: 9-25.
- , and **D. W. Slater.** 1945. Seasonal changes in growth, mortality, and condition of rainbow trout following planting. Trans. Amer. Fish. Soc., 73 (1943): 117-124.
- Nielson, R. S., N. Reimers,** and **H. D. Kennedy.** 1957. A six-year study of the survival and vitality of hatchery-reared trout of catchable size in Convict Creek, California. Calif. Fish and Game, 43: 5-42.
- Reimers, N.** 1957. Some aspects of the relation between stream foods and trout survival. Calif. Fish and Game, 43: 43-69.
- Tack, E.** 1938. Trout mortality from the formation of suspended ice crystals. Fischerei-Zeitung, 41: 42. (Rev. in Prog. Fish Cult., 1937-1938, No. 37: 26.)