SEX CHROMOSOMES IN THE SOCKEYE SALMON: A Y-AUTOSOME FUSION

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Chromosomes of 21 sockeye salmon [*Oncorhynchus nerka* (Walbaum)] from three locations in Washington state were examined. All males had 57 chromosomes, while all females had 58 chromosomes. Both sexes had 104 chromosome arms. It appears that in males of this species the Y chromosome and an autosome have fused to form a metacentric chromosome.

On a étudié le complément des chromosomes chez 21 saumons rouges [*Oncorhynchus nerka* (Walbaum)] échantillonnés à trois sites dans l'état de Washington, Etats-Unis. Tous les mâles portaient 57 chromosomes tandis que toutes les femelles en avaient 58. Les deux sexes ont démontré 104 bras chromosomiques. Il semble que les mâles portent un chromosome métacentrique résultant d'une fusion entre un chromosome autosomique et le chromosome Y.

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Introduction

Although morphologically distinguishable sex chromosomes recently have been found in a number of fish species (Ebeling and Chen, 1970; Ohno, 1974; Gold, 1978), both sexes have similar karyotypes in most species which have been examined. Among salmon and trout, the only report of a chromosome difference between males and females is in the rainbow trout (Thorgaard, 1977).

Previous studies of the chromosomes of sockeye salmon have reported individuals with 56 (Simon, 1963), 56-58 (Chernenko, 1971 in Chernenko, 1976), 57 and 58 (Fukuoka, 1972), and 58 chromosomes (Sasaki *et al.*, 1968; Muramoto *et al.*, 1974). Chernenko and Fukuoka reported Robertsonian differences between individuals.

I have found that there is a Robertsonian rearrangement difference between male and female sockeye salmon, resulting in males having 57 and females 58 chromosomes. The Y chromosome of males appears to have fused with an autosome.

Materials and Methods

Chromosomes of 21 sockeye salmon from three locations in Washington state were examined following white-blood-cell culture. Fish studied were caught in gill nets in the Straits of Juan de Fuca near Port Angeles, and in the Quinault River. The salmon from the Straits were probably returning to the Chilko River, British Columbia, to spawn (Larry Lawson, personal communication). One angler-caught fish from Lake Washington was also studied.

Heart blood samples were taken, white blood cells cultured, and chromosome preparations made as previously described (Thorgaard, 1976). The $Ba(OH)_2$ procedure of Salamanca and Armendares (1974) was used for C-banding.

Results and Discussion

Chromosome counts from white-blood-cell cultures of the 21 sockeye salmon are shown in Table I. The modal chromosome are number (NF) was 104 in all individuals. In all 13 males the modal chromosome number was 57; all eight females had a modal number of 58. Counts with less than the modal number were probably the result of broken cells and occasional aneuploid cells. Because the position of the centromere was not always easy to determine, I believe that the cells with the modal chromosome number which did not have 104 arms were probably the result of errors in the

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TABLE I

Chromosome Counts of 21 Sockeye Salmon

Location sampled (Date)	Fish #	Sex	Chromosome number: Cells with NF=104*: 56 (8)	57 (10)	58 (12)	59 (14)	Cells with NF≠104: <56	56	57	58	59
Straits of Juan de Fuca (July 1976)	243	F	–	–	6	–	1	1	2	8	1
	245	F	–	1	4	–	6	3	1	1	–
	248	F	–	–	5	–	2	2	–	2	–
	229	M	–	6	1	–	1	–	2	–	–
	230	M	–	5	–	–	1	4	4	1	1
	231	M	–	5	–	–	2	–	5	–	–
	232	M	–	5	–	–	1	1	4	–	–
	233	M	–	5	–	–	–	–	1	–	–
	234	M	–	5	–	–	–	1	2	–	–
	235	M	–	5	–	–	1	–	2	–	–
	236	M	–	5	–	–	1	3	4	2	–
	237	M	–	7	–	–	1	1	2	–	–
	239	M	–	5	–	–	2	1	2	1	
Quinault River (June 1976)	215	F	–	–	5	–	–	2	4	4	–
	216	F	–	–	5	–	2	2	2	–	–
	217	M	–	5	–	–	3	4	4	–	–
Quinault River (June 1977)	672	F	–	–	5	1	2	–	4	3	1
	673	F	–	–	5	–	–	2	2	2	–
	674	F	–	–	5	–	1	3	3	2	–
	666	M	1	4	–	–	5	3	5	–	–
Lake Washington (August 1977)	729	M	1	5	–	–	5	2	4	–	–

*Number of acrocentric chromosomes shown in brackets.

determination of arm number. The extensive intra-individual Robertsonian variation reported in other salmonid species (Ohno *et al.*, 1965; Roberts, 1968, 1970; Davisson *et al.*, 1973; Gold and Gall, 1975; Zenzes and Voiculeseu, 1975) was not observed in this study; only five of 112 cells with NF = 104 had a nonmodal chromosome number.

Karyotypes of female and male sockeye salmon are shown in Figs. 1 and 2, respectively. Chromosomes are arranged in the figures on the basis of size and centromere position. There were 44 metacentric and submetacentric, 2 subtelocentric, and 12 acrocentric chromosomes in the female, and 45 metacentric and submetacentric, 2 subtelocentric, and 10 acrocentric chromosomes in the male. Thus, compared to females, the male sockeye had one additional metacentric or submetacentric chromosome and two less acrocentric chromosomes. This chromosome difference between males and females is apparently the result of the fusion of the Y chromosome with an autosome. Similar rearrangements (termed X_1X_2Y sex determination systems) have been observed in other fish species (Uyeno and Miller, 1971; Uyeno and Miller, 1972), and in a number of other animals (White, 1973; Vorontsov, 1973).

The sex chromosomes are not identifiable in the karyotypes. The presumed Y-autosome fusion chromosome is one of the 45 metacentric or submetacentric chromosomes in males; the unpaired metacentric shown in Fig. 2 (No. 17) was chosen arbitrarily. The X chromosome (designated X_1) and the autosome involved in the fusion (designated X_2) are acrocentric. The female karyotype (Fig. 1) has six pairs of

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KOKANEE IN CALIFORNIA

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The "kokanee" (*Oncorhynchus nerka kennerlyi*) was first planted in California waters in 1941. This is a landlocked form of the Pacific sockeye or red salmon. It is native to the Pacific Northwest, where it is also called "little redfish" and "silver trout." Under highly favorable conditions it may reach a size of five pounds. Twelve to fourteen inches is average, and under poor conditions it never exceeds eight inches.

It is preeminently a lake resident, and may spawn on gravelly lake shores as well as in streams connecting with lakes. It matures and spawns at the end of its third or its fourth year, and like all Pacific salmons dies after spawning. It prefers cool waters, and therefore goes deeper as temperatures rise in summer. Although its food is made up largely of plankton, the minute animals which drift in the water, it can be easily taken in some lakes on hook and line in spring and autumn. In summer it is harder to catch. Trolling with flashers and baited hook, and still-fishing a few feet off bottom, are favored methods; fly-fishing can be successful in the late afternoon in spring or fall when the fish are near the surface. The kokanee puts up a good fight, but has a tender mouth and is hard to land. It is excellent eating. In its native regions it has furnished abundant fishing and is looked upon as a valuable element in the angling resources.

The decision to introduce it to California was based in part on its popularity in certain sections of the northwest, and in part on its plankton feeding habits, which suggested that it might do well in reservoirs where fluctuations made for poor production of bottom food. Salt Springs Reservoir on the North Fork of the Mokelumne River off the Carson Pass Road was selected for the initial test; its level fluctuates extensively, and it is so located that little harm could be done if the kokanee turned out to be an undesirable citizen. One hundred thousand eggs obtained in late 1940 from Idaho through the U. S. Fish and Wildlife Service were hatched at the Basin Creek State Fish Hatchery near Sonora, and 67,000 fingerlings were planted in July of 1941 at a length of a little under two inches. (In the State of Washington, incidentally, where great numbers of this species are produced, planting at a very small size is favored.) The Salt Springs area was closed shortly thereafter as a war measure, but tests in the spring of 1943 showed the kokanee to be abundant and easily caught, at a size of about 10 inches. In November of 1943, at the end of their third year, and at a length of 11 to 12 inches, they were ready to spawn, and some 300,000 eggs were taken from 626 females. A total of over 3,000 fish were caught in seines at this time, 4½ percent of the number planted, and since many more were present than were netted, a good survival was indicated.

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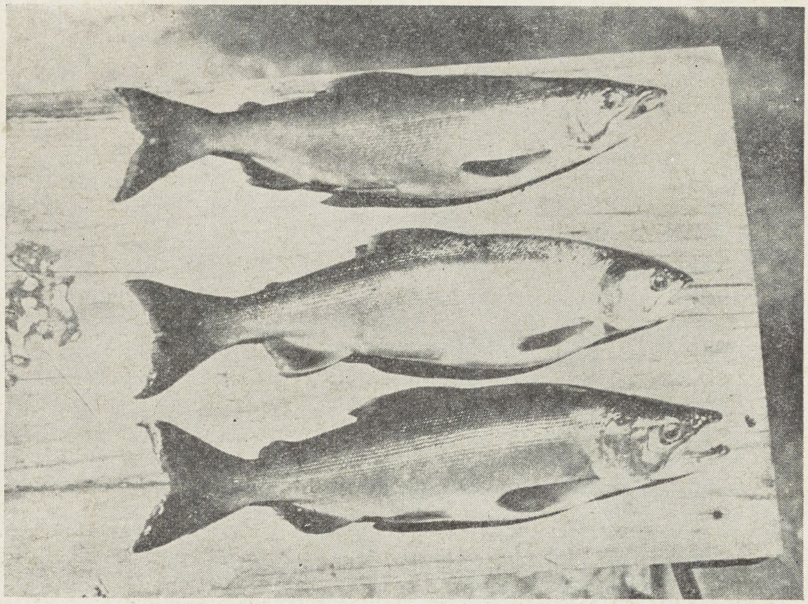

FIGURE 37. Kokanee from Salt Springs Reservoir, November, 1943. Female in center, male below and above. Photograph by Malcolm Wilson

These results were sufficiently encouraging to warrant further stocking, which has been carried out as shown in the following table:

STOCKING OF KOKANEE IN CALIFORNIA

Name of water	*Date of planting*	*Source of eggs*	*Number planted*	*Size in numbers per oz.*
Salt Springs Reservoir, Amador County	1941—7/12–16	Idaho	67,000	27
Strawberry Lake (also called Pinecrest), Tuolumne County	1944—8/12–19	Salt Springs	106,000	22–32
	1945—7/28 8/6	Montana	99,000	25–40
	1947—5/28 6/16	Washington	284,000	140–265
Waterhouse Lake, Tuolumne County	1944—8/3	Salt Springs	700	32
Echo Lake, El Dorado County	1944—7/5–20	Montana	69,000	51–72
	1945—8/2–7	Montana	79,000	52
Donner Lake, Nevada County	1944—6/22 7/19	Montana	83,000	270–280
	1945—8/3–8	Montana	74,000	52
	1947—5/28	Washington	100,000	265

NOTE:

Average lengths of fish are approximately:
$1\frac{3}{4}$ inches at 25 per ounce.
$1\frac{1}{4}$ inches at 50 per ounce.
1 inch at 100 per ounce.

The results have been uneven. Echo Lake has been the most disappointing. In this high, rocky basin it has been very difficult to produce good fishing, and it was hoped that the plankton-eating kokanee would solve the problem. However, growth has been poor here, the fish not exceeding eight to nine inches at maturity, and anglers have shown little interest in them. Strawberry Lake has provided the best fishing, especially when it was drawn down in late summer of 1946; large catches were made at this time, with the kokanee reaching a size of 10 inches. Donner Lake has produced the largest fish, the spawners running from 12 to 16 inches. The kokanee aroused little angler interest here at first, but their popularity seems to be growing, and more are being caught every season.[2]

Kokanee have appeared in other waters than those in which they were planted. About 100 were found in December, 1946, spawning in the small stream formed by the water running from the Tahoe Hatchery into the lake. These had evidently escaped in 1944 from the hatchery troughs where they were reared, and were returning to the "home stream." In the Truckee River spawning kokanee appeared just below the Tahoe Dam in the winter of 1947-1948; these are presumed to have migrated out of Donner Lake. And in 1946 a number of Kokanee went out of Strawberry with the declining water and down to Lyons Reservoir. In no case has any harm come from the escape of kokanee into other waters, nor is any possibility of harm foreseen.

In California all kokanee so far observed have matured at the end of their third year. Kokanee were seen spawning by the junior author in Donner Lake in November of 1947, in water varying in depth from one-half to three feet, and from right along the shore-line to 20 feet out. Concentrations of fish were found near the mouths of the small inlet streams on the north side where the lake bottom was sandy with some pebbles and a few rocks, and many also spawned along the north shore where water trickled in from the road culverts. Water temperature was 45 degrees Fahrenheit.

The spawning pattern insofar as it could be observed resembled that described by Schultz (1937), with such differences in detail as might be attributable to stream spawning in Schultz's report as against lake spawning here. Only one female was seen in the process of building a nest, and unfortunately she was in the center of a group of fish where it was impossible to follow her actions closely, or those of any males involved. She apparently rolled over on her side and dug vigorously with the posterior part of her body for a few seconds, then circled away from the nest; occasional interruptions would be caused by a general milling around of all the fish in the vicinity. Actual pairing of fish seemed to be the rule.

Spawning activity began by male and female circling the nest, one behind the other. Eventually the female would pass over the center of the nest, and come to a stop there—sometimes on the first pass, and sometimes on the second or third. The male would then join her, and both would vibrate at which time it is presumed that the sex products were deposited. The female invariably dug into the sand near the end of the vibrations, raising a small cloud of fine particles. All of this took about

[2] Reports from Donner Lake received after this paper went to press tell of excellent fishing in May, 1948, with many limit catches of kokanee weighing about one pound each.

10 seconds, after which circling was resumed. Individual pairs were seen to repeat this process four or five times over the same nest, presumably with deposition of eggs each time. Covering of the eggs was apparently accomplished by the digging action of the female at the end of each period of vibrations, but it is possible that a further and final covering took place after the completion of egg deposition in any particular nest.

Unfortunately Donner Lake was drawn down very heavily in January and February, and all of these spawning beds were left high and dry in frozen ground.

Reference

Schultz, Leonard P.
1937. The Breeding Habits of Salmon and Trout. Report of the Smithsonian Institution for 1937, pp. 365-376.

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The Resources Agency of California
Department of Fish and Game

A REVIEW OF KOKANEE IN CALIFORNIA[1]

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SUMMARY

Kokanee salmon, Oncorhynchus nerka, the freshwater form of the sockeye salmon, were introduced into California in 1941. They are increasing in importance, having been stocked in 35 lakes by 1963.

This report summarizes the available information about kokanee, including origin and distribution, age and size at maturity, temperature preference, spawning requirements, fecundity, growth rate, homing, food habits, and management.

The kokanee life cycle varies from two to seven years. Habitat requirements resemble those of trout, although kokanee all die after spawning.

California kokanee fall into two groups: one spawning from August to October; the other, from late October to February. Early spawning is associated with the British Columbia strain; late spawning with kokanee from other areas. In California, both groups may produce many two-year-old spawners, predominantly males, of little benefit to the fishery. The British Columbia strain appears to do this more commonly than others. They are clearly less desirable for California lakes than other strains because they spawn earlier in the year, and at a younger age than kokanee from other sources.

Kokanee spawn and reproduce successfully in streams or in spring areas along lake shores.

Kokanee feed primarily on pelagic zooplankton throughout most of their lives. The growth rate in most California waters is quite rapid, enhancing their value as a sport fish.

Kokanee have not provided significant forage for trout in California lakes. Substantial evidence suggests that they may adversely affect trout in smaller lightly fished lakes, through direct competition for food. Moreover, in such waters, they may not be harvested adequately, whereas the trout are more readily caught. Hence, their use in smaller lakes with natural trout populations, or those stocked with fingerlings, is highly questionable.

In California, kokanee planted as "swimup" fry have supplemented stocked, "catchable-sized" trout in several heavily fished waters in a substantial way at little cost. The late-spawning strains are most suitable for this purpose.

Kokanee also hold promise for certain problem waters. Pardee Reservoir, for example, a 2,000-surface-acre, low elevation reservoir of unusually low fertility, has never provided much fishing since the initial bloom after construction. It has a deep, well-aerated, cool hypolimnion. The usual assemblage of warmwater species is present. This lake was stocked with 175,000 kokanee fry from a Colorado source at 175 per ounce in 1961. During 1963, kokanee fishing was fairly good over an extended period, substantially augmenting the usual fishery.

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[2] Now with Region 2, Water Projects.

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A REVIEW OF KOKANEE IN CALIFORNIA

Kokanee salmon, the nonanadromous form of the sockeye salmon (Oncorhynchus nerka), were first introduced into California in 1941, when 67,000 fingerlings from eggs taken in Idaho were planted in Salt Springs Reservoir, Amador County, on the North Fork of the Mokelumne River (Curtis and Fraser, 1948). This introduction succeeded. In November, 1943, several hundred thousand kokanee eggs were taken at the reservoir from fish maturing at the end of their third year.

This success aroused interest in the species. In 1944, it was stocked in Donner, Strawberry, Lower Echo, and Waterhouse lakes, and accidentally into Lake Tahoe, when fry escaped from Tahoe Hatchery.

Following an introduction into Upper Echo Lake in 1945, new introductions ceased for several years, although maintenance stocking of some previously planted waters, primarily Donner Lake, continued. An important sport fishery for kokanee had developed in Donner Lake by 1948.

In 1951, kokanee from Pennask Lake, British Columbia, were planted in Shasta Lake in an effort to establish a forage fish for recently stocked Kamloops rainbow trout (Salmo gairdnerii kamloops). A large, self-sustaining kokanee population, developed rapidly.

Renewed interest in the possibilities of kokanee as a game fish in large, cool lakes resulted from their success in Shasta Lake.

From 1951 through June 1963, 27 additional waters were planted with kokanee, 16 of these from 1959 through the first half of 1963. More introductions would probably have been made if more eggs had been available. A complete history of kokanee stocking in California is included in the Appendix.

The accelerated construction of large, cool reservoirs in California has focused interest on game fish such as kokanee which might develop large populations in such waters through natural reproduction or inexpensive stocking.

There are different strains or races of kokanee, each with different characteristics. It is important, therefore, to understand these characteristics in order to match strains with the waters stocked.

This report summarizes the available information bearing on the use of kokanee in California lakes. We hope that it will help field personnel plan future stocking programs.

GENERAL LIFE HISTORY

Origin and Distribution

The kokanee completes its life cycle entirely in fresh water. It presumably evolved from "residual" sockeye of anadromous stock that matured in a lake (Ricker, 1959). Conditions unfavorable to the anadromous type, such as natural barriers to the upstream migration of adults or the downstream migration of smolts (e.g., a deep epilimnion of warm water that would present a physiological barrier to downstream migration), would favor the evolution of a permanently freshwater variety.

Under certain conditions, kokanee may revert to their ancestral habits and become anadromous. In both British Columbia and Washington, experimental releases of marked kokanee have resulted in returns of a few sea-run adults (Rounsefell, 1958). Whether this anadromous habit survives in all strains is uncertain. Mature "sockeye" salmon occasionally captured in the Sacramento River may represent returning kokanee escapees from Shasta Lake, or they may be strays from other runs.

It is commonly believed that each kokanee population evolved independently from a specific sockeye run. Genetic variations in some races support this hypothesis, although many apparent racial characteristics may stem from environmental differences.

Kokanee originally occurred in lakes of the Pacific Coast drainages of North America, Siberia, and Japan. Almost all major drainages with large sockeye runs have kokanee populations except in Alaska. In recent years, kokanee have been transplanted to Oregon, Nevada, California, Arizona, Colorado, Wyoming, and some eastern states, augmenting natural populations in Washington, Idaho, and Montana. The largest number of native North American populations occurs in British Columbia.

Age and Size at Maturity

The life cycle of kokanee varies from two to seven years. In their original range in North America, a four-year cycle predominates. However, in the Skeena Trench of northern British Columbia, maturity is not usually reached until the fish are five years old (letter from P. A. Larkin to Henry Clineschmidt, Sept. 15, 1952). In contrast, certain discrete subpopulations in lakes of the Upper Columbia Trench in southeastern British Columbia commonly mature in three years from the time the egg is fertilized, and some precocious males in these populations mature in two years.

The variability in age at maturity is illustrated in Kootenay Lake, British Columbia, which has three distinct races. Two of these spawn at three years and one at four years (Vernon, 1957). The introduced kokanee in Upper Priest Lake in Idaho mature at five years rather than the four years typical of Priest Lake and most other Idaho waters (Bjornn, 1956).

With some apparent exceptions, age at maturity decreases with decreasing latitude and elevation over their original range. There is some evidence that this trend has been extended in California, where maturity is attained in two to five years. Information about the age at maturity in many California lakes is clouded by the past practice of stocking different strains in the same waters because eggs from the same source were not always available. Strains from northern latitudes that originally matured in four years are maturing in three years in some California waters. It is not yet clear whether this is a permanent change caused by higher temperature and more light or a temporary adjustment to abundant food during the early stages of population growth.

Until fish from British Columbia were stocked in Shasta Lake (elevation 1,000 feet) in 1951, kokanee populations in California matured in either three or four years. However, in Shasta Lake substantial numbers matured in less than two years (20 months). Since then, this strain has been stocked in several other California waters already having other strains.

British Columbia, Washington, Idaho, Montana, and Colorado have all been utilized as egg sources for kokanee stocking in California. The strain of fish planted in any one season has usually been dependent upon the availability of eggs. As a consequence, a variable pattern of maturity among kokanee in California has resulted from this "mixing" of fish of different geographical origins. Although two or more strains may be present in the same water at the same time, there is no evidence that genetic mixing has occurred.

The largest fish are most often recorded from waters with relatively low populations of kokanee, particularly larger lakes and reservoirs.

In Donner Lake (elevation of 5,900 feet) most of the late-run spawners are four-year-olds, although a few fish mature precociously in three years. Donner is a medium-size, deep, cold lake. Apparently it would be ideal for kokanee, except that spawning tributaries are lacking and otherwise suitable shore spawning areas are of little value because they are exposed by winter drawdown. The egg source for the original introduction in 1944 was Montana; however, eggs from Washington, Idaho, and British Columbia, in addition to eggs taken at Shasta Lake, Twin Lakes and Donner Lake itself, have since been used for maintenance stocking. Most mature late-spawning fish in Donner now average about 15 inches (all body lengths in this report are fork lengths). Kimsey (1951) observed 18-inch spawners there in 1949, measured one 20-inch specimen, and estimated another to be 24 inches. Early-run spawners, in September, 1962, resulted from the 1959 plant of the British Columbia strain and the 1960 plant of the Shasta Lake strain. They ranged from 9 to 16 inches in length, averaging about 12 inches. None of these fish had completed their fourth year of life and probably most were in their second and third years.

Lake Tahoe is an immense lake with an insignificant kokanee population and anglers rarely catch a kokanee. J. H. Wales (memorandum to Leo Shapovalov, Feb. 12, 1959) reported three males averaging 21.7 inches and three females averaging 19.5 inches. These fish were found among dead spawners in Taylor Creek, a tributary of Tahoe. Male and female spawners in this creek in 1960 averaged 17.6 and 15.8 inches, respectively, while in 1961 they measured 18.7 and 16.7 inches (Cordone and Frantz, 1962). All Tahoe kokanee are late fall spawners which probably mature at three and four years, although their age has not been determined because of extensive scale erosion in mature fish.

Size records from Lake Millerton and Shasta Lake are of unusual interest, since both are so-called "warmwater reservoirs" which have substantial amounts of cold water in their depths all summer.

At Millerton, fish from the initial introduction in 1956 matured in 1958 and averaged 15 inches in length. These were of Donner Lake stock.

Few size measurements were recorded at Shasta during the first few years following their introduction but reportedly kokanee were about the same size as those at Millerton.

For the past few years the largest run at Shasta has been the early run, which spawns in August and September. These fish now average about 9 to 11 inches in length and are two- and three-year-olds. (The relative proportion of each has not been established.) A late run, which originated with fish stocked in 1952 and 1953, presumably from Montana, has diminished somewhat in recent years. This run is composed of fish which reportedly are smaller than the early-run fish and differ somewhat in color (Wales, 1957). Their age has not been determined.

Bucks Lake, a 2,100-acre lake in Plumas County, was stocked in 1954 with only 8,000 fry from late-run Donner fish. It now has a large annual spawning run of kokanee averaging between 15 and 16 inches and probably three years old.

In most other waters the mature fish are typically smaller. Three-year fish averaged about 11½ inches at Salt Springs Reservoir, Amador County, in 1943. This is a 725-acre power reservoir which fluctuates severely.

In 1955, kokanee fry from Donner Lake were stocked in Lake Arrowhead, a 782-acre reservoir with a maximum depth of 180 feet, which is located in the San Bernardino Mountains in southern California at an elevation of 5,106 feet. No kokanee spawners were observed in 1956, but in 1957 and 1958 large numbers of fish formed spawning runs. Kokanee maturing as three-year-olds in 1957 had a mean length of 12.3 inches, while those maturing as four-year-olds in 1958 averaged about 14 inches. No estimates are available regarding either the number of fish in each run or the sex ratios. In 1958, fry from Lake Arrowhead parentage and fry from Donner Lake parentage were stocked in approximately a 2:1 ratio. In December, 1959, two size groups of maturing fish were captured: 253 kokanee averaging 8.8 inches in length and 13 kokanee averaging 13.7 inches. The larger fish were remnants of the 1955 year class maturing in their fifth year while the smaller were members of the 1958 year class maturing as two-year-olds. A second group of 1,600 mature kokanee, captured in February, 1960, contained 98 percent two-year-old fish and 2 percent five-year-old fish. However, only about 8 percent of the two-year-olds were females (Beland, 1961).

Echo Lakes, El Dorado County, which were chemically treated in 1960 to remove the existing fish population, have been notably unproductive waters. Prior to 1960, maturing three-year-old kokanee averaged between 8 and 9 inches in length. These lakes lie at an elevation of about 7,500 feet, have a total surface area of slightly over 315 acres, and a maximum depth of 145 feet.

Twin Lakes, Mono County, situated at an elevation of 7,000 feet, consist of 400-acre Upper Lake, with a maximum depth of 108 feet, and 375-acre Lower Lake, with a maximum depth of 149 feet. Both lakes were intially stocked in 1958 with a late-spawning strain of kokanee.

Two-year-old spawners, nearly all males, were observed in December, 1959. Twenty-three fish had a mean length of 9.7 inches, with a range of 8.0 to 10.5 inches. In 1960, three-year-old fish ranged from 10½ to 12 inches, while fish from an early-run British Columbia strain which had been planted in 1959 matured as two-year-olds 7 to 8 inches long. In 1961, the late-run fish were again composed of 10- to 12-inch adults, primarily three years old, while the early-run fish ranged in length from 9 to 11 inches and were made up of both two- and three-year-old fish. Two-year-old males made up approximately 20 percent of the early run in 1961.

Information about the many kokanee introductions into California and their subsequent histories is too fragmentary to contribute much to our understanding of the comparative growth potentials of different strains under the same conditions. This is unfortunate, since such information would be invaluable in planning future programs.

Temperature Preference

Water temperatures close to 50 degrees F. are preferred by kokanee. Temperatures above 60 degrees F. lead to severe mortalities, at least among young fish. William A. Dill, in a letter to the Bureau of Fish Conservation (August 22, 1947), relates a conversation with Dr. Lauren Donaldson and states that "... a typical lake suitable for both kamloops and kokanee is deep, with much shore area, with a thermocline. In some such lakes, the kokanee will lie in a band not more than 10 feet wide and not rising above a zone warmer than 50° F." Such behavior may explain anglers' observations in California that during the early spring and late fall, when surface temperatures are cool, kokanee are often easily caught in the upper water levels, while in the summer they are taken, if at all, only by fishing relatively deep.

An apparent example of this preference for a particular stratum of water was found in Pine Flat Reservoir in 1960. Kokanee were collected in the Kings River about 10 miles below Pine Flat Dam during one period in the spring and another in the summer. In both instances, the fish had escaped from the reservoir when water was withdrawn from a level 60 feet below the surface. During the spring the lake level had been rising, while in the summer it was falling (personal communication from Charles von Geldern).

Lake Almanor, Plumas County, is a large (26,000 surface acres) reservoir which stratifies thermally and chemically during the summer months. Large numbers of kokanee were reported dead and dying in this lake during the summer of 1960. Surface water temperatures during the first three days of August ranged from 66 to 72 degrees F. The fish were concentrated around an underground spring area where the water temperature was 46 degrees F., but this water, though cool enough for kokanee, was probably deficient in dissolved oxygen.

Kokanee, if they are to do well in any lake, must have a cool, well-oxygenated layer of water available to them during the critical summer months. Lakes and reservoirs which stratify thermally or chemically so that no such layer exists are obviously unsuitable for them.

Spawning Period

Like their anadromous ancestors, most kokanee spawn in late summer and early winter--between August and January. The exact time appears to depend upon both the race of fish and the lake environment.

In California, kokanee fall into two distinct groups on the basis of spawning times. One spawns in August, September, and early October. Mature adults of this form may begin migrating upstream in late July. The second group spawns from late October into February. An exception to this grouping occurred in lower Echo Lake, El Dorado County, where a few spawning fish were trapped as late as mid-April in 1951. These fish averaged about two inches longer than the usual Echo Lake kokanee, which spawned in November.

Among the forms of O. nerka native to Cultus Lake, British Columbia, there are two main spawning periods. Both the residual sockeye (those that never go to sea) and the anadromous population spawn from October to December. The residuals remain a dull olive-gray at maturity and are predominantly males. The kokanee, on the other hand, spawn early in August and September and at maturity show the bright red body and green head characteristic of the mature anadromous form (Rounsefell, 1958).

Early-spawning kokanee populations in California are of British Columbia lineage. Fry from eggs imported directly from British Columbia have been planted in 16 California lakes. Shasta Lake, the first one planted with the British Columbia strain, has been a source of eggs for 10 other lakes. The California waters which are known to possess early-spawning kokanee have been planted with fish from either or both of these two sources.

Late-spawning strains of kokanee have been stocked in 33 California lakes, 17 of which have also received plants of early-spawning fish. Early-spawning runs of mature adults have been recorded in six of the latter.

There is little doubt that spawning time is affected by environment. Progeny of early-run kokanee spawning in Chatterdown Creek (tributary to the McCloud River and thence Shasta Lake) were planted in Trinity Lake in 1961. In 1962, kokanee spawning activity did not occur in Trinity Lake until nearly two weeks after it had begun in Chatterdown Creek. However, data are inadequate at present to separate the factors responsible for this difference.

Spawning Temperatures

Kokanee require cool water for spawning, from 42 to 55 degrees F. Spawning usually occurs between 44 and 54 degrees F. In Donner Lake, kokanee have been observed spawning at water temperatures of 45 degrees (Curtis and Fraser, 1948) and 51 degrees (Kimsey, 1951). Early-spawning kokanee in Shasta Lake will enter spawning tributaries when water temperatures drop below 60 degrees but begin spawning only when temperatures fall to around 55 degrees (personal communication from Harold Hewitt to Seeley, September 19, 1962). The general deterioration of early-spawning runs of kokanee in tributaries at Shasta Lake outside the McCloud River system is probably due to high stream temperatures.

At Bucks Lake in 1962, kokanee were observed spawning in Bucks Creek when water temperatures ranged from 42 to 44 degrees F.

Boyd (1959), reporting on SCUBA investigations of anadromous sockeye salmon in Great Central Lake, Vancouver Island, recorded spawning only within a temperature range of 43 to 56 degrees F.

Almo Cordone (personal communication to Seeley) observed spawning activity in the Truckee River in September, 1962, when water temperatures exceeded 65 degrees F.

Fecundity

The mathematical relationship between egg number and body length has not been determined for kokanee. Small increases in length usually reflect substantial increases in egg number.

For the anadromous sockeye the relationship for mature fish is generally linear. The number of eggs for any given length as well as the size of the eggs, however, may vary with such factors as race of fish, time spent in the ocean, latitude, water temperature, and age of the fish (Rounsefell, 1957). Quite likely, kokanee exhibit similar variations, dependent upon race and local conditions.

At Lake Pend Oreille, in 1955, a small sample of immature females which averaged 10.2 inches in length had a mean egg count of 395 (Jeppson, 1956). Counts varied from 297 from a 10.0-inch fish to 499 from a 10.7-inch fish.

Lloyd C. Hume (personal communication to McCammon) stated that in 1960 females 10.5 to 12 inches long from Twin Lakes, Mono County, averaged 400 eggs. At Salt Springs Reservoir in 1943, 626 females 11 to 12 inches long yielded some 300,000 eggs, an average of 479 eggs per fish (Curtis and Fraser, 1948). Beland (1961) reported that in 1957 Lake Arrowhead females averaging 12.2 inches in length produced a mean of 534 eggs. Fifteen-inch Donner Lake females average about 1,174 eggs. Seven females averaging 15.3 inches in length from Lake Granby, Colorado, contained an average of 1,676 eggs per fish (Bassett, 1957). In Bucks Lake, Plumas County, in 1961, 154 females yielded a total of 271,720 eggs, an average of 1,764 per fish. No measurements were taken, but the fish were said to have averaged about 16 inches in length (personal communication from Alan F. Pollitt to Seeley, 1962). In 1962, spawning females with a mean length of 15.3 inches yielded an average of 1,280 eggs. These egg counts were obtained during artificial spawning operations and represent the average number of eggs stripped from a female.

Whitt (1957) estimated that about 93 percent of the eggs within the ovaries are deposited during spawning, while the remainder are retained within the dying fish.

Spawning Habitat

Kokanee spawn in tributaries and outlets to a lake or in suitable shoreline gravels in the lake itself. It is suspected that strains may differ in their ability to spawn in lakes, although this has not been demonstrated.

Few close observations of spawning site selection and redd construction in streams have been recorded. Schultz and students (1935) observed spawning activities in Swamp Creek in Washington. Behavior resembled that of other Pacific salmon. Spawning gravels ranged from less than ½ inch to 4 inches in diameter. Redds, from 18 to 24 inches up to 2 by 4 or 5 feet in size, were located in 3 to 10 inches of water, with a current of less than 2.5 feet per second. Delisle (1962), reporting on kokanee spawning in the stream below Bucks Lake, Plumas County, found spawning activities confined to locations where water velocites, measured 0.2 feet above the stream bottom, were below 2.0 feet per second.

Richard (1954) noted that in Taylor Creek (tributary to Lake Tahoe) most spawning activity occurred in areas of small- and medium-sized gravel, in both riffles and pools. In the lower, meandering section of this stream a few fish spawned in coarse sand. Richard collected numerous eggs from redds in sandy areas of nearby Trout Creek but found none alive. In California, successful stream spawning occurs in tributaries of the McCloud River (a major tributary of Shasta Lake); Taylor Creek, tributary to Lake Tahoe; Robinson Creek, tributary to Twin Lakes, Mono County; Bucks Creek, tributary to Bucks Lake, Plumas County; and tributaries of Lake Almanor, Plumas County.

Observations in California indicate that migrating kokanee are weak swimmers or else lack the strong urge to swim upstream, characteristic of many anadromous salmonids. Low falls and dams of the sort easily negotiated by anadromous salmon or by steelhead effectively bar upstream movement. During the 1952-53 spawning season in Taylor Creek, an 18-inch dam located about one mile above the mouth was evidently a complete barrier. Following removal of this structure, kokanee moved above the old dam site. In the McCloud River, spawning kokanee are stopped by rapids about 9 miles above the mouth. The greatest distance traveled by kokanee on a spawning migration in California has been the 30 miles up the Sacramento River from Shasta Lake to Mears Creek.

Kokanee have been observed spawning in the outlets of some lakes, especially in the absence of suitable inlet streams. Kimsey (1951) and Almo J. Cordone (personal communication to Seeley, 1962) both noted spawning fish in Donner Creek below Donner Lake. Spawners have also been reported in the Truckee River immediately below the outlet of Lake Tahoe. Fish apparently migrate out of Donner Lake via Donner Creek and move up the Truckee River. In Gold Lake, Sierra County, fish screens were installed in the outlet stream to keep kokanee from moving downstream to spawn, where the resulting fry would be lost. As mentioned earlier, Delisle (1962) observed kokanee spawning in the stream below Bucks Lake.

Lake-spawning kokanee usually select gravels near shore, over spring seepage. Redds have been observed at depths from $\frac{1}{2}$ foot to 25 feet. Jeppson (1956) found a few redds in Lake Pend Oreille at depths to 20 feet, but most were between 7 and 11 feet. Boyd (1959) reported that sockeye salmon spawned successfully at depths to 70 feet.

Kokanee in Donner Lake were seen spawning in a spring seepage area with a bottom of mixed sand, gravel, and cobbles on a clay substrate. Water depths ranged from 1 to 3 feet. Dropping water levels subsequently exposed the redds and the eggs were found buried under 4 to 7 inches of gravel (Kimsey, 1951).

The extent of successful lake reproduction in Donner Lake remains unknown, since annual plants of large numbers of fry mask naturally produced fish in the catch.

Successful shore spawning and reproduction are also known to occur in Gold Lake, Sierra County (personal communication from Hallet D. Boles to Seeley, 1962), and in Lake Tahoe (Cordone and Frantz, 1962). Small sacks of eyed kokanee eggs were planted along the shore of Lake Tahoe near Chambers Lodge, Tahoma, and Dollar Cove in January and February, 1962, where kokanee had been observed spawning in the past, as well as in several other likely looking areas. Survival was nil except at these three locations, where it ranged as high as 50 percent. Spring seepage and dissolved oxygen content of the water within the substrate are, without a doubt, important factors.

Incubation

The temperatures at which incubation has been reported range from 32 degrees through 55 degrees (memo from Lloyd C. Hume to Robert M. Macklin, June 12, 1963). Water temperatures of 38 degrees seem to be the lower limit at which green eggs will eye (letter from Harry R. Woodward, Colorado Department of Game and Fish, to David L. Ward, December 26, 1961). At Hot Creek Hatchery, Mono County, a few eyed eggs have been hatched in 55-degree water, but mortality in the sac stage was quite high. The period of time between hatching and feeding at this temperatue was approximately 10 to 12 days.

In Donner Lake in 1949, Kimsey reported that eggs spawned in shoreline gravels developed normally at temperatures ranging from 44 to 48 degrees F. Spawning activity was first observed on November 4. Nine kokanee nests were marked on November 15 and 29. Eggs began hatching in these nests about January 20. Ninety eggs from frozen nests along the shore and 30 eggs from nests in seepage areas had been collected and taken to Tahoe Hatchery to hatch in troughs. Eggs removed from nests which had experienced occasional freezing began hatching March 15, while eggs from seepage areas began hatching on February 12 at a water temperature of 43 degrees.

In Lake Pend Oreille, "kokanee eggs hatch in three to five months depending upon water temperature; the fry live on the yolk sac for 30 to 45 days, after which they emerge from the gravel and migrate to the lake where they remain until mature". (Jeppson, 1955).

Growth Rate

The most complete age and growth studies of kokanee thus far have been carried out at Lake Pend Oreille in Idaho. The following information, based on scale analyses, was reported by the Idaho Fish and Game Department, (Whitt, 1958).

Back calculated body lengths at the end of the first and second years of growth were made for 160 kokanee from four age classes (40 fish each from the 3-, 4-, 5-, and 6-year age classes taken in 1956). The average length at the end of the first year was 2.4 inches while that at the end of the second year it was 6.4 inches.

An age and length frequency distribution constructed for 645 angler-caught kokanee taken from February through October, 1956, results in the following:

Age class	Average length (total) in inches	Total fish in sample	Percentage of total
3-year	6.9	75	11.63
4-year	8.7	217	33.64
5-year	9.1	254	39.38
6-year	9.1	97	15.04
7-year	9.0	2	0.31

The total 1961 harvest of kokanee from this lake was about 993,000 fish which weighed 140 tons. Length frequency studies at this time showed that 82 percent were in their fifth year of life, 11 percent in their fourth year, and 7 percent in their third year.

The growth and ultimate size of kokanee in Lake Pend Oreille depend largely on the fall zooplankton abundance and on the numbers of kokanee and other species competing for the available food. Very little growth occurs during the winter and spring (Idaho Department of Fish and Game, 1961).

Elsewhere, little is known of the growth of kokanee from the time of hatching to maturity. The available California data support the general belief that size at maturity is controlled by both racial characteristics and environmental factors such as population density, interspecific competition, lake productivity, and water temperature. In California, mature kokanee have ranged in body length from 8 inches at Twin Lakes, Mono County, to 24 inches at Donner Lake.

Homing

Homing is apparently highly developed. Vernon (1957) found that only 3 percent of the maturing kokanee in Kootenay Lake, British Columbia spawned in streams other than those in which they had been hatched. Curtis and Fraser (1948) note that in December, 1946, two years after kokanee fingerlings had escaped from Tahoe Hatchery, adults spawned in the small stream immediately below the hatchery. In Shasta Lake, large numbers of spawners appeared in streams which had been planted during the initial introduction.

Good evidence of homing among shore-spawning kokanee has been found in Donner Lake. Following the first few years of stocking, mature kokanee congregated in areas where fry had been released. Spawning took place in suitable areas. At other points of release, however, where conditions were not satisfactory, groups of mature kokanee dispersed and presumably spawned elsewhere (personal communication from Alan F. Pollitt to Seeley, September 27, 1962).

Mature adults in Millerton Lake have been seined from shoreline sites where fry had been released from trucks (personal communication from Earle Mitchell to Seeley, 1962). Conversely, at Donner Lake seining of mature fish planted as fry from an airplane has not been feasible. Although large numbers of spawners were observed, they were scattered about the entire shoreline, and congregations large enough for economical seining were not present.

At Bucks Lake in 1954, fry were air planted near the mouths of four streams: Bucks Creek, Left Hand Creek, Right Hand Creek, and Mill Creek. As noted earlier, a large run is now established in Bucks Creek, the largest tributary. It is not known if runs have become established in the other three creeks but spawning kokanee have been seen in Haskins Creek, which has never been planted. No shore spawning has been reported but such activity may go undetected, since few people visit this isolated area when the fish are spawning.

Food Habits

Kokanee feed primarily on pelagic zooplankton throughout most of their lives. Entomostraca are utilized most heavily. Phytoplankton apparently is little used. Beland's (1961) report on kokanee in Lake Arrowhead supports this contention. They are well adapted to such a diet by virtue of their high gill raker count (28 to 40 on the first gill arch) and because these gill rakers are relatively long, slender, rough, and closely set (Clemens and Wilby, 1961). Presumably, this enables the kokanee to capture zooplankters more effectively than rainbow (17 to 21 gill rakers on the first gill arch), and may place the latter at a decided disadvantage in waters where both species must compete for zooplankton. Platts (1958) observed that in Lake Pend Oreille kokanee fry, starting life out as insect feeders in streams, enter the lake and switch to a primarily plankton diet.

As kokanee mature, insect larvae or nymphs may again become increasingly important in some waters; however, they never replace zooplankton as the principal food.

Large kokanee will occasionally prey on small fish.

Forage Value

Kokanee have been heralded as a nearly ideal forage fish for large trout. This may be true in certain waters of British Columbia, Washington, and Idaho. Comments solicited from biologists in these areas indicate that kokanee provide the major source of food for large lake trout (Salvelinus namaycush), Dolly Varden trout (S. malma), and rainbow trout (Salmo gairdnerii) in many of their lakes. It is important to note, however, that such predator-prey relationships are nearly always restricted to very large lakes in areas where kokanee are relatively slow growing. Kokanee are quite important in the diet of large trout in lakes such as Kootenay Lake and Shauswap Lake in British Columbia, Loon Lake and Deer Lake in Stevens County and Mountain Lake on Orcas Island in Washington, and Priest Lake and Lake Pend Oreille in Idaho.

In other areas, kokanee are not highly regarded as a forage species. Their presence in some fisheries may, in fact, be detrimental to other species of salmonids. This is discussed more fully in a subsequent section.

The potential value of the kokanee as a forage species was one of the primary reasons for introducing it into California, especially into Shasta Lake, already mentioned. However, in spite of widespread distribution within the State, there is no evidence that it is providing significant forage for trout anywhere.

Kokanee as a Game Fish

In many lakes in western North America kokanee furnish a considerable amount of sport fishing. Indeed, in some lakes such as Priest Lake and Lake Pend Oreille in Idaho, they may dominate the catch. Elsewhere, their chief value seems to be in supplementing rainbow trout fisheries. Examples of their worth as a game species are numerous throughout their present range. In California, angler satisfaction has generally been good and appears to be increasing as anglers become more familiar with them.

Since they are commonly planted at a very small size, they can sometimes augment an existing fishery quite cheaply. They are tasty, provide good sport, and often are easy to catch at certain times of the year on flies, bait, and artificial lures.

In California, kokanee have contributed significantly to the fisheries of Donner Lake; Shasta Lake; Millerton Lake; Twin Lakes, Mono County; Lake Arrowhead; Gold Lake, Sierra County; Trinity Reservoir, Trinity County; Pardee Reservoir, Amador County; and Lake Almanor, Plumas County.

Under some circumstances, however, kokanee may be present in large numbers without adding significantly to a fishery. Such was the case at Echo Lake, El Dorado County. Fishing for all species had been notably poor, yet the 1960 chemical treatment revealed a very large kokanee population. Similarly, studies during 1961 at Ashurst Lake in Arizona (Bassett, 1962a, 1962b, 1962c) showed kokanee to be relatively unaffected by angling. Limited gill netting in the spring and summer resulted in catches of kokanee (planted in 1959) outnumbering planted rainbow trout of comparable size. According to periodic creel checks throughout the fishing season, however, anglers caught the two species at a rate of 190 trout to one kokanee.

Kokanee may escape harvest because of their schooling habits, because of their preference for rather restricted layers of water during most of the fishing season, or because most anglers are simply unfamiliar with methods of fishing for them. Additionally, kokanee which mature, spawn, and die at a small size or at a young age are available to anglers for only a very brief period before they pass out of the picture in the fall.

Competition with Other Species

To more clearly understand the relationships between kokanee and other species, it is helpful to examine the food chains and trophic structures which exist in the waters in which kokanee and trout occur.

A food chain in a lake or reservoir is based almost entirely on the numbers and kinds of producer organisms (chiefly green plants) found in that particular body of water. Through photosynthesis these organisms utilize the sun's energy and convert water, carbon dioxide, and various nutrient materials into foods which can be used by primary consumer organisms. In many California lakes and in the majority of fluctuating reservoirs most of this photosynthetic activity is carried out by phytoplankton. Herbivorous primary consumer organisms provide a food source for carnivorous secondary consumers. Tertiary and quarternary consumers, each a potential source of energy for the next higher level, may extend the food chain upwards. Each of these levels, from producer to top consumer, represents a trophic or energy level. This interrelated organization or food chain of plants and animals forms what has been called a pyramid of energy. Figure 1 illustrates a simplified diagram of such a pyramid.

At each level of the pyramid, energy is taken from the underlying trophic level and is used in basic metabolism, growth, reproduction, and movement - in short, in all life processes. It is significant that about 90 percent of the energy is lost at every level, so that only about 10 percent of the energy which was taken from the underlying level is available to the next higher group of organisms. As a result, the biomass (total protoplasmic mass produced over a period of time) of any kind of organism is directly related to its position in the pyramid: the closer the organism is to the bottom, the greater will be its biomass and the less will be the energy loss. Also, the number of consumer levels in any natural situation (ecosystem) is usually limited to four or five (Odum, 1953).

Some kinds of organisms often occupy more than one level in the pyramid. Kokanee are ordinarily secondary consumers, since their diet consists almost exclusively of zooplankton. Trout more frequently occupy two levels, that of secondary consumer in competition with kokanee, and that of tertiary or top consumer in instances in which large trout prey on smaller fish. Zooplankters and insects which feed on herbivorous organisms could be termed secondary consumers, so that trout or kokanee feeding on them would become tertiary consumers.

In most situations, trout will utilize food sources in addition to zooplankton in lakes and reservoirs with low littoral food production. Bottom foods, such as chironomids and snails, are often quite important, as are terrestrial insects. The presence of a large kokanee population, however, would inhibit trout production, since trout also feed on zooplankton. This would be true in any water in which both trout and kokanee occur, but in waters in which a limited zooplankton supply is the primary food source, competition for it could become serious for trout if the kokanee population were very large.

As mentioned earlier, there are no food habits data which show that kokanee in California provide appreciable forage for trout, despite considerable evidence of such a role in other areas. It is unlikely that a small kokanee passing in front of a large, hungry trout would be refused as food. Nevertheless, rapid growth rates, pelagic schooling habits, and a narrow range of temperature preferences probably make kokanee less available than comparable-sized trout as potential food for larger fish in California waters. Because fish become increasingly important in the diet of large trout, the displacement of trout or more suitable forage species by kokanee as secondary consumers may well lead to a lowered production of large trout in California waters in which both trout ahd kokanee occur.

S. B. Smith (letter to Robert C. Sumner, March 3, 1960), while acknowledging the beneficial forage value of kokanee in large British Columbia lakes, stated emphatically that "We have found almost invariably in our smaller lakes, regardless of productivity type, that introduction of kokanee will sound the death knell even of strongly established populations of rainbow trout". R. G. McMynn (letter to Almo J. Cordone, March 30, 1962) expressed the opinion that kokanee introductions into small lakes (less than one or two square miles in surface area) appeared to adversely affect young rainbow trout because of increased competition. Such competition apparently offsets any advantages of the desired predator-prey relationship between trout and kokanee.

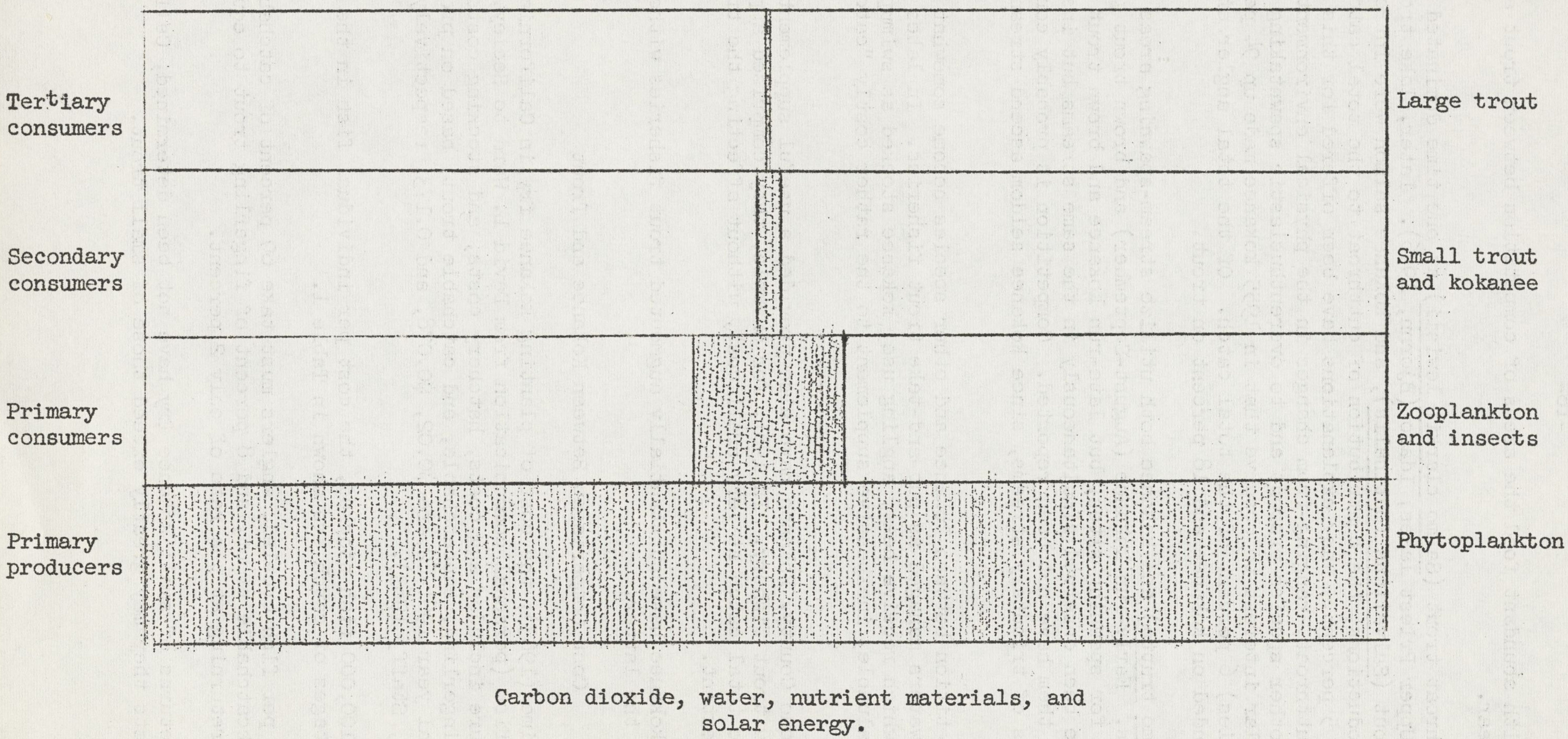

FIGURE 1. Pyramid of energy in a trout lake.

In rich waters with abundant food the areas of competition between trout and kokanee are much less clear.

Yellowstone cutthroat trout (Salmo clarkii lewisii) at one time dominated the catch from Priest and Upper Priest lakes, Idaho (Bjornn, 1956). Later, lake trout, eastern brook trout (Salvelinus fontinalis), and kokanee salmon were introduced. After these introductions, the contribution of cutthroat to the total catch dwindled to approximately 5 percent. Many explanations have been offered for this gradual decline of the cutthroat, ranging from changes in the physical environment to competition with the other species present and to overenthusiastic spawntaking operations. It is of particular interest to observe that in 1955 kokanee made up 94 percent and trout (four species) 6 percent of the total catch. Of the total angler effort, 82 percent was expended on kokanee and 18 percent on trout.

Brown trout (Salmo trutta) and kokanee both utilize stream-spawning areas and both are fall spawners. Early-run kokanee (August-September) and brown trout probably do not compete much for spawning sites, but late-run kokanee and brown trout may do so. Both species have been observed simultaneously in the same streams but instances of fighting between them have not been reported. Competition is probably confined to the lower reaches of tributary streams, since kokanee seldom ascend streams great distances.

Problems of competition between kokanee and other species become somewhat academic when related to waters managed as put-and-take trout fisheries. In lakes such as Lake Arrowhead, which receive heavy angling use, kokanee stocked as swimup fry have proved to be a valuable, inexpensive supplement to the rather costly "catchable" trout program.

In Twin Lakes, Mono County, kokanee have also provided a useful supplement to a catchable rainbow trout fishery. In 1961, for example, they comprised approximately 35 percent of the total catch at very small cost, without affecting the trout fishery to any apparent extent.

In Idaho, also, kokanee have substantially augmented trout fisheries without apparent ill effects upon the latter.

Cost Comparisons Between Kokanee and Trout

At the present time (1963), the cost of planting kokanee fry in California is less than $0.005 per fish (personal communication from David L. Ward to Seeley, April 29, 1963). This figure includes egg costs, hatchery costs, and stocking costs. Comparable costs for fingerling, subcatchable, and catchable trout, based on production figures for fiscal year 1961-62,are $0.02, $0.078, and 0.173, respectively (Inland Fisheries Branch, Staff, 1963).

On the basis of 100,000 fish stocked, the cost per individual fish in the creel at different percentages of catch are shown in Table 1.

In terms of cost per fish creeled, anglers must take 69 percent of catchable trout, 31 percent of subcatchable trout, and 8 percent of fingerling trout to equal the cost of kokanee returning at the rate of only 2 percent.

Although exact returns of small kokanee fry have not been determined, California's experience suggests they may greatly exceed those of small trout.

TABLE 1

Cost of Each Fish in Creel

Percentage caught	100,000 kokanee fry at $0.005 each	100,000 fingerling trout at $0.02 each	100,000 subcatchable trout at $0.078 each	100,000 catchable trout at $0.173 each
1	$0.50	$2.00	$7.80	$17.00
2.	0.25	1.00	3.90	8.50
5	0.10	0.40	1.56	3.40
		8% = 0.25		
10	0.05	0.20	0.78	1.70
20	0.03	0.10	0.39	0.85
30	0.02	0.07	0.26	0.57
			31% = 0.25	
50	0.01	0.04	0.16	0.35
60			0.13	0.28
				69% = 0.25
70			0.11	0.24
80			0.10	0.21

Management Considerations

The record of kokanee in California reveals a varied picture of success and failure. Success includes such waters as Lake Arrowhead, Twin Lakes, Donner Lake, and Gold Lake. Significantly, they are all subject to moderate to high angling pressures, are good trout lakes, and usually are rather heavily stocked with catchable trout. Kokanee have formed sizeable portions of the total catch from each of these waters at a relatively low cost, with no apparent deleterious effects on the trout fisheries.

In the absence of accurate inventories of catch or population, we must depend upon the more or less casual observations of wardens, biologists, and anglers regarding the quality of most kokanee fisheries. We know that Shasta Lake, Pardee Reservoir, Lake Almanor, Bucks Lake, Icehouse Reservoir, Independence Lake, Trinity Reservoir, Huntington Lake, Millerton Lake, and Strawberry Reservoir have provided kokanee fishing ranging from poor to good, but little more is known about them. Shasta Lake, for example, is known to furnish good kokanee fishing for a limited number of anglers during the spring and again during the fall, but we know nothing regarding the actual number of kokanee taken, the total number of kokanee in the lake, or the proportion of kokanee taken in relation to other game species.

At Icehouse Reservoir in 1962, a biweekly creel census indicated the ratio of kokanee to rainbow trout in the total catch to approximate 2:9.

Several lakes have been stocked with kokanee with negative results. Merced Lake, Kent Lake, Lake Mendocino, Eagle Lake, Lake Pillsbury, Florence Lake, Don Pedro Reservoir, Pleasant Valley Lake, and Waterhouse Lake fall into this category.

General Considerations

Any evaluation of kokanee at this time is subject to revision as more facts come to light and our experience increases. Nevertheless, such an evaluation based on what we know presently is necessary if we hope to utilize this species more efficiently than in the past. Before starting new management programs which include kokanee it seems appropriate to review some of the more salient aspects of our present knowledge and experience.

On the positive side, we have found that:

1. Kokanee have functioned as an additional game fish in catchable trout waters, as well as in some larger lakes and reservoirs which support both warmwater fish and trout. No detrimental effects have thus far been indicated.

2. They have often provided good angling in waters of the types mentioned above at a relatively low cost.

3. Angler satisfaction has generally been high.

4. Their growth rate in most California waters is quite rapid so that they often become available to the angler within two years after stocking.

5. They are primarily plankton feeders and competition with other species for this food source is generally limited to the more open waters of a lake or reservoir.

6. In suitable waters they may establish self-perpetuating populations.

7. In many waters, the lack of natural reproduction is a definite advantage in that the maximum size of the population can be easily controlled by adjusting the size of the plant.

8. Angler harvest will increase as more efficient fishing techniques are evolved.

9. Kokanee appear to achieve their maximum size in large lakes and reservoirs.

10. When stocked as very small fry, they may survive to the creel in substantial numbers.

On the other hand:

1. In some lakes, both large and small, they have not contributed to the fishery despite heavy stocking. These have often been waters without a deep, cool, well-aerated hypolimnion.

2. Though conclusive evidence within California is lacking, in other areas they are sometimes serious competitors with trout and actually depress trout populations, particularly in smaller lakes.

3. Although they may contribute appreciably to the catch for brief periods in the spring and fall, they are usually taken in small numbers, if at all, during the intervening portion of the fishery season. Pardee Reservoir, Amador County, however, provides an exception. During the 1963 season, kokanee were caught in relatively large numbers throughout the summer.

4. Their value as forage for large trout, one of the reasons for their introduction into California, has never been established.

5. A large proportion of the population may mature, spawn, and die within a two-year period, resulting in only a brief exposure to the fishery.

6. Kokanee may compete with brown trout for spawning areas in tributary streams.

7. Large populations may be relatively unaffected by angling.

8. Although smaller lakes and reservoirs typically have smaller kokanee, large waters may also produce relatively small fish (Shasta Lake).

The question of whether or not a particular fishery will benefit from the addition of kokanee should be answered in specific terms insofar as possible. The physical and biological requirements of kokanee have been discussed in earlier sections of this paper. Undoubtedly they could be introduced into several additional lakes and reservoirs with a reasonable chance of survival. In some, they would probably establish self-sustaining populations. More important than the probability of their survival, however, are two questions concerning the role they will play in the overall management of the fishery. Will they provide satisfactory angling? How will they affect the present and future fishery? Kokanee should never be planted in a lake or reservoir merely because fish are available and the water appears capable of supporting a population.

To Stock or Not To Stock?

In California, the success or failure of kokanee in any reservoir or lake is closely related to maximum summer water temperatures and to minimum oxygen content. The inability of kokanee to withstand high water temperatures rules out stocking them in most lowland waters.

Kokanee should not be introduced into rainbow trout waters maintained by adequate natural reproduction or by fingerling or subcatchable trout plants, particularly if they can become self-sustaining. Serious consequences to a rainbow trout population because of competition are a definite possibility. Judging from information from British Columbia, as well as from past experience at Echo Lakes, the smaller the lake the greater the danger to trout.

Kokanee should never be stocked with the expectation that they will provide appreciable forage for other game species. In waters in which lack of forage appears to be the factor limiting trout production, kokanee could conceivably do more harm than good in that they might inhibit a suitable forage organism (fish or invertebrate) from becoming established.

Careful evaluation of stream spawning areas should be made before kokanee are planted in waters which support important brown trout fisheries. Competition for these spawning areas could be detrimental to the brown trout. If these spawning areas appear equally suitable for both species, the late-spawning strain of kokanee should not be planted.

The merits of kokanee in fisheries which support both trout and warmwater species cannot be evaluated satisfactorily on the basis of present information. In some waters, e.g., Shasta Reservoir, Pardee Reservoir, Lake Almanor, and Huntington Lake, they have added to the total sport catch to an unknown degree. In others, such as Lake Pillsbury and Lake Britton, introductions were unsuccessful and few, if any, fish were ever taken by anglers. In the absence of valid information, logical arguments for and against their use in similar waters can be presented with little hope of resolution. Until we definitely know that kokanee are not detrimental in such waters and that they actually add to the total catch, kokanee plants should be restricted to waters where self-propagation will not occur. The possibility of establishing a species which may turn out to be unwelcome would thus be avoided.

In a lake or reservoir which provides poor trout fishing despite intensive management efforts to improve it, kokanee might be tried on a trial basis if physical and chemical conditions appear suitable.

The utilization of kokanee in California as a cheap means to augment catchable trout in heavily fished waters appears to be their best use to date and is definitely recommended. In such waters, kokanee will utilize the basic productivity of the water far more effectively than do the catchable trout, which are harvested within a short time. Their use in such fisheries can often provide a better fishery at a minimum cost with little or no risk.

Which Strain of Kokanee Should be Planted?

Once the decision has been reached to plant kokanee in a particular water, the manager must decide which strain will prove most satisfactory. Over the past few years, the choice has been dictated largely by the availability of kokanee eggs. Generally, this has resulted in widespread stocking of the early spawning British Columbia strain.

For general use, the early-spawning strain is less desirable than the late-spawning strain. Although two-year-old spawners have been reported from both early- and late-spawning strains, it appears that the greater proportion of early-maturing fish can be expected from the early-run strain. As pointed out earlier, fish which spawn in two years will have only a minimal exposure to the fishery.

Attempts to establish a self-sustaining population will stand a better chance of success in most instances if late-spawning fish are planted. High water temperatures in most California waters during August, September, and early October would undoubtedly prevent early-spawning strains from becoming established. Conversely, if a permanent population is not desired, early-run fish may be preferable despite their tendency toward early maturation.

Egg-taking operations for fish cultural needs are generally more successful at low water temperatures. This implies that the late-spawning strain is more desirable if in-state egg sources are needed.

Although eggs from early-run kokanee are taken within the State (Shasta Lake) and imported from British Columbia at a time of year when facilities are available at most trout hatcheries, this is of slight advantage. At the time when early-run fish develop into swimup fry, many high-elevation lakes which would be suitable for them are still frozen over. As it is, their development is not greatly in advance of later-run fish because of low water temperature at most hatcheries.

No evidence has been found to indicate a preference by either strain for stream or lakeshore spawning. Nevertheless, while both strains spawn in streams, only late-spawning fish have been observed to spawn on lake shores.

What is the Size and Number of Fish That Should be Planted?

In California, successful plants have been obtained from fish ranging in size from 340 per ounce to 8.4 per ounce. In 1961, fry were planted at an average size of about 200 per ounce. Usually, they are stocked as soon as possible after the yolk sac is absorbed.

The rate of stocking has also been highly variable. It has ranged from 3-1/3 fish per acre (Bucks Lake, 1954) to over 326 per acre (Twin Lakes near Bridgeport, Mono County, 1960). Highly successful populations have developed in both cases. Currently, stocking is done at a rate of 200 to 250 fish per acre.

Neither stocking size nor rate have been evaluated satisfactorily. Probably some waters have been planted with larger numbers of fish than were needed. However, since the costs involved in planting unfed fry are quite low, this is a minor point from the viewpoint of economics if survival is appreciable. Greater insight into proper stocking size and rate may result from work underway in Oregon, where fingerling versus fry plants are currently being evaluated.

How Should Kokanee be Planted?

Successful plants have been made by truck, boat, and airplane. Of the three methods, air planting is probably the most economical for routine maintenance stocking.

If one of the objectives in planting a particular water is to provide an egg source for artificial spawning purposes, planting should be done at precisely selected locations. These locations should be picked so that future trapping or seining operations can be conducted as simply and easily as possible. The strong homing instinct of kokanee can then be utilized most effectively.

Where Do We Go From Here?

It is readily acknowledged that many important questions about kokanee and their management in California remain unanswered. Satisfactory answers will require additional information. The present wide distribution of kokanee throughout the State offers an unusual opportunity to learn much about the behavior of this species in California waters. Data on size at maturity, sex ratio, fecundity, and time of spawning in each water in which kokanee now occur can be obtained with only a little extra effort, yet would do much to complete our knowledge. Few records of this nature are available from the many waters which have been stocked, despite the number of years kokanee have been in this State.

More complex questions will be answered only by closer study than this species has thus far received. If kokanee are to be used effectively it is imperative to answer such questions as whether there is a differential return between the early- and late-spawning fish, what portion of a kokanee population is harvested by anglers and under what conditions, what is the role of kokanee in waters which presently support mixed (trout and warmwater species) fisheries, what can be done to increase angler harvest, at what size and at what rate kokanee should be stocked to achieve maximum returns, and which strain is most suitable for which type of water.

REFERENCES

Bassett, Howard M.

1957. Notes on the kokanee (Oncorhynchus nerka kennerlyi) in Lake Granby during fall, 1956. Colo. Coop. Fish. Res. Unit, Quart. Repts., vol. 3, pp. 20-22.

1962a. A summary of problems pertaining to the fishery in District II. Ariz. Game and Fish Dept., Proj. F-7-R-4, Work Plan 2, Job G-1, Completion Rept., Jan. 16, 1961 - Oct. 31, 1962, 5 pp.

1962b. A creel census of lakes in District II. Ariz. Game and Fish Dept., Proj. F-7-R-4, Work Plan 2, Job C-1, Completion Rept., Jan. 1, 1961 - Oct. 15, 1961, 6 pp.

1962c. Periodic resurvey of waters in District II. Ariz. Game and Fish Dept., Proj. F-7-R-4, Work Plan 2, Job B-1, Completion Rept., Jan. 16, 1961 - Oct. 15, 1961, 4 pp.

Beland, R. D.

1961. The Lake Arrowhead, San Bernardino County, kokanee salmon fishery, 1957-1960. Calif. Dept. Fish and Game, Inland Fisheries Admin. Rept. no. 61-7, 14 pp. (Mimeo.)

Bjornn, Ted

1956. Priest Lake fisheries investigations. Idaho Dept. Fish and Game, Ann. Prog. Rept., D-J Proj. no. F24-R-1, 31 pp. (Mimeo.)

Boyd, F. C.

1959. The use of diving gear in sockeye studies. West. Assoc. St. Game and Fish Comm., 39th Ann. Conf., Proc., pp. 327-330.

Clemens, W. A., and G. V. Wilby
1961. Fishes of the Pacific Coast of Canada. Fish. Res. Bd. Canada, Bull. no. 68, 443 pp.

Cordone, Almo J., and Ted Frantz
1962. Lake Tahoe Fisheries Study monthly report, March 1, 1962, through March 31, 1962. Calif. Dept. Fish and Game and Nevada Fish and Game Dept., 3 pp. (Typewritten)

Curtis, Brian, and J. C. Fraser
1948. Kokanee in California. Calif. Fish and Game, vol. 34, no. 3, pp. 111-114.

Delisle, Glenn E.
1962. Water velocities tolerated by spawning kokanee salmon. Calif. Fish and Game, vol. 48, no. 1, pp. 77-78.

Idaho Department of Fish and Game
1961. Fisheries management. In: Summary of operations 1961. pp. 41-42.

Inland Fisheries Branch, Staff
1963. California trout, salmon, and warmwater fish production and costs 1961-62. Calif. Dept. Fish and Game, Inland Fisheries Admin. Rept. no. 63-5, 26 pp. (Mimeo.)

Jeppson, Paul
1955. Evaluation of spawning areas in Lake Pend Oreille and tributaries upstream from Alberni Falls Dam in Idaho, April 1, 1954 - May 31, 1955, including supplemental information on the life history of the kokanee. Idaho Dept. Fish and Game, Fed. Aid in Fish and Wildl. Restoration, Ann. Summ. Rept., Investigations Proj. F-3-R-4 and F-3-R-5 (Work Plan 2), 36 pp.

1956. Evaluation of spawning areas in Lake Pend Oreille and tributaries upstream from Alberni Falls Dam in Idaho, June 1, 1955, to May 31, 1956. Idaho Dept. Fish and Game, Fed. Aid in Fish and Wildl. Restoration, Ann. Summ. Rept., Investigations Proj. F-3-R-5 and F-3-R-6 (Work Plan 2), 9 pp.

Kimsey, J. B.
1951. Notes on kokanee spawning in Donner Lake, California, 1949. Calif. Fish and Game, vol. 37, no. 3, pp. 273-279.

Odum, Eugene P.
1953. Fundamentals of ecology. Philadelphia, W. B. Saunders Co., 384 pp.

Platts, William S.
1958. A comparison of limnological data collected from Lake Pend Oreille during and after dam construction, with food habits of the kokanee. Idaho Dept. Fish and Game, Fed. Aid to Fish., Prog. Rept., Proj. F3-R-8, 73 pp.

Richard, James B.
1954. Observations of kokanee salmon spawning in the tributaries of Lake Tahoe, October 1952 to February 1953. Calif. Dept. Fish and Game, Inland Fisheries Admin. Rept. no. 54-3, 14 pp. (Typewritten)

Ricker, W. E.
1959. Additional observations concerning residual sockeye and kokanee (Oncorhynchus nerka). Fish. Res. Bd. Canada, Jour., vol. 16, no. 6, pp. 897-902.

Rounsefell, George A.
1957. Fecundity of North American salmonidae. U. S. Fish and Wildl. Serv., Fish Bull. 122, vol. 57, pp. 450-468.

1958. Anadromy in North American salmonidae. U. S. Fish and Wildl. Serv., Fish Bull. 131, vol. 58, pp. 170-185.

Shultz, Leonard P., and Students
1935. The breeding activities of the little redfish, a landlocked form of the sockeye salmon Oncorhynchus nerka. Pan-Pacific Res. Inst., Jour., vol. 10, no. 1, pp. 67-77.

Vernon, E. H.
1957. Morphometric comparison of three races of kokanee (Oncorhynchus nerka) within a large British Columbia lake. Fish. Res. Bd. Canada, Jour., vol. 14, no. 4, pp. 573-598.

Wales, J. H.
1957. Report on kokanee salmon (Oncorhynchus nerka kennerlyi) in California. Rept. to Calif. Dept. Fish and Game, 7 pp. with 2 pp. appendix. (Typewritten)

Whitt, Charles R.
1958. Age and growth characteristics of Lake Pend Oreille kokanee, 1956. Idaho Dept. Fish and Game, Ann. Prog. Rept., Fed. Aid in Fish Restoration, Proj. F3-R-6, 34 pp. (Mimeo.)

APPENDIX

A summary of kokanee plants in California through June, 1963, is contained in Tables A-1 through A-5.

TABLE A-1

Kokanee Plants in Region 1 Through June, 1963

Water	Years planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Lake Britton	1951	British Columbia	25,500	250/oz.	Truck	No
	1952	British Columbia	16,500	250/oz.	Truck	
	1953*	Unknown	25,680			
Eagle Lake	1952	Unknown	36,000	200/oz.	Truck	No
	1953	Unknown	67,000	225/oz.	Truck	
	1954	Idaho	90,750	250/oz.	Truck	
	1955	Donner Lake	450,000	200/oz.	Truck	
	1956	Idaho	243,000	200/oz.	Truck	
Shasta Lake	1951	British Columbia	162,453	250/oz.	Truck	Yes
	1952	Montana	200,930	250/oz.	Truck	
	1953*	Unknown	164,320			
Trinity Reservoir	1961	Shasta Lake	260,000	200/oz.		
	1962	British Columbia	299,880	340/oz.	Truck	
		Bucks Lake	125,000	250/oz.	Air	
	1963	Bucks Lake	305,980	270/oz.	Truck	

*California Kamloops, Inc.

TABLE A-2

Kokanee Plants in Region 2 Through June, 1963

Water	Years planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Lake Almanor	1951	Washington	41,400	138/oz.	Truck	Yes
	1952	Washington	210,000	200/oz.	Truck	
	1953	Washington	180,000	300/oz.	Truck	
	1954	Idaho	100,035	195/oz.	Truck	
	1955	Idaho	89,960	260/oz.	Truck	
Bucks Lake	1954	Idaho	8,000	192/oz.	Truck	Yes
	1962	Bucks Lake	51,000	300/oz.	Air	
		Bucks Lake	75,020	110/oz.	Air	
	1963	Bucks Lake	51,000	300/oz.	Truck	
Donner Lake	1944	Montana	82,650	82/oz.	Truck	Probably; however, the contribution of lucastrine reproduction has never been measured adequately.
	1945	Montana	74,280	52/oz.	Truck	
	1947	Washington	100,000	265/oz.	Truck	
	1948	Idaho	22,400	100/oz.	Truck	
	1949	Idaho	79,980	60/oz.	Truck	
	1950	Idaho	100,000	195/oz.	Truck	
	1951	Idaho	90,090	33/oz.	Truck	
	1952	Idaho	94,000	65/oz.	Truck	
	1955	Donner Lake	149,915	75/oz.	Truck	
	1956	Idaho	75,298	100/oz.	Truck	
	1958	Donner Lake	123,280	115/oz.	Air	
	1959	British Columbia	134,880	120/oz.	Air	
	1960	Shasta Lake and Donner Lake	100,000	200/oz.	Truck and air	
	1961	Twin Lakes	35,000	49/oz.	Air	
		Twin Lakes	100,000	125/oz.	Air	
	1962	Washington	115,200	360/oz.	Air	
	1963	British Columbia	100,200	300/oz.	Truck	

TABLE A-2--Continued

Kokanee Plants in Region 2 Through June, 1963

Water	Years planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Lower Echo Lake	1944	Montana	69,270	72/oz.	Truck	Yes
	1945	Montana	43,640	52/oz.	Truck	
	1947	Unknown	75,000	275/oz.	Truck	
	1959	Millerton Lake	20,025	18,000 @ 180/oz. 2,025 @ 135/oz.	Air	
	1962	Washington	52,920	180/oz.	Air	
	1963	Colorado	40,000	80/oz.	Air	
Upper Echo Lake	1945	Montana	35,700	50-52/oz.	Truck	Yes
	1958	Lake Arrowhead	15,300	45/oz.	Air	
	1961	Twin Lakes	50,065	53/oz.	Air	
	1962	Washington	26,640	180/oz.	Air	
	1963	Colorado	16,000	80/oz.	Air	
Fallen Leaf Lake	1962	Washington	150,000	300/oz.	Air	
	1963	Bucks Lake	50,100	300/oz.	Truck	
Gold Lake	1954	Idaho	20,000	100/oz.	Air	Yes
	1955	Idaho	60,000	160/oz.	Air	
	1956	Idaho	29,580	145/oz.	Air	
	1958	Lake Arrowhead	34,560	45/oz.	Air	
	1959	Millerton Lake	50,000	100/oz.	Air	
	1960	Colorado	49,610	125/oz.	Air	
	1961	Twin Lakes	50,065	53/oz.	Air	
	1962	Washington	61,920	180/oz.	Air	

TABLE A-2--Continued

Kokanee Plants in Region 2 Through June, 1963

Water	Year planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Icehouse Reservoir	1960	Colorado	25,740	125/oz.	Air	
	1961	Colorado	100,000	125/oz.	Truck	
	1962	Washington	97,200	216/oz.	Air	
	1963	British Columbia	42,000	140/oz.	Truck	
Independence Lake	1955	Idaho	69,000	120/oz.	Truck	No
	1956	Idaho	20,010	145/oz.	Air	
	1958	Lake Arrowhead	20,250	45/oz.	Air	
	1959	Millerton Lake	24,955	1,755 @ 135/oz. 23,200 @ 160/oz.	Air	
	1960	Colorado	21,450	125/oz.	Air	
	1962	Washington	21,375	285/oz.	Air	
	1963	Colorado	29,520	180/oz.	Air	
		Colorado	40,000	80/oz.	Air	
Pardee Reservoir	1961	Colorado	175,000	175/oz.	Truck	
	1962	Washington	49,800	300/oz.	Air	
	1963	Bucks Lake	50,100	300/oz.	Truck	
		British Columbia	59,960	70/oz.	Truck	
Salt Springs Reservoir	1941	Idaho	67,365	27/oz.	Truck	No
	1955	Donner Lake	50,220	90/oz.	Truck	
	1956	Idaho	30,720	192/oz.	Truck	
	1957	Shasta Lake	12,000	200/oz.	Truck	
	1958	Donner Lake	30,820	115/oz.	Air	
	1959	British Columbia	30,030	110/oz.	Air	
	1962	Washington	49,800	300/oz.	Air	

TABLE A-2--Continued

Kokanee Plants in Region 2 Through June, 1963

Water	Year planted	Year source	Number planted	Size of fish	Planting method	Self-perpetuating?
Lake Tahoe	1944	Montana	Unknown	Unknown	Escapement from Tahoe Hatchery	Yes
(Includes plants made in tributary streams)	1949	Idaho	Unknown	Unknown	Truck	
	1950	Idaho	500,300	125-677/oz.	Truck and barge	
	1951	Idaho	418,024	100-238/oz.	Truck	
		Washington	75,000	250/oz.	Truck	
	1952	Idaho	623,585	135-285/oz.	Truck and boat	
	1953	Idaho	179,860	100-130/oz.	Truck and boat	
		Washington	46,720	73/oz.	Truck and boat	
	1954	Idaho	437,565	148-245/oz.	Truck	
Union Valley Reservoir	1963	Bucks Lake	151,200	280/oz.	Truck	

TABLE A-3

Kokanee Plants in Region 3 Through June, 1963

Water	Years planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Kent Lake	1961	Shasta Lake	100,125	225/oz.	Truck	
	1962	Colorado	100,000	340/oz.	Truck	
Lake Mendocino	1959	British Columbia	100,000	120/oz.	Truck	
North Lake Merced	1961	Shasta Lake	100,130	170/oz.	Truck	
	1962	Colorado	100,000	340/oz.	Truck	
Lake Pillsbury	1961	Shasta Lake	100,125	225/oz.	Truck	
	1962	Colorado	51,200	320/oz.	Air	
		Washington	48,600	360/oz.	Air	

TABLE A-4

Kokanee Plants in Region 4 Through June, 1963

Water	Year planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Bass Lake	1961	Colorado	50,000	40/oz.	Truck	
	1962	Bucks Lake	8,740	92/oz.	Truck	
		Bucks Lake	19,685	31/oz.	Truck	
	1963	British Columbia	50,100	300/oz.	Truck	
Don Pedro Reservoir	1953	Unknown	10,440	120/oz.	Truck	
	1954	Idaho	48,825	175/oz.	Truck	
	1955	Unknown	57,240	60/oz.	Truck	
	1956	Idaho	57,020	86/oz.	Truck	
Florence Lake	1959	Donner Lake	75,000	115/oz.	Air	No
Huntington Lake	1959	British Columbia	21,120	120/oz.	Air	
		Donner Lake	54,030	110/oz.	Air	
		Donner Lake	24,000	100/oz.	Air	
		Donner Lake	10,400	80/oz.	Air	
	1961	Shasta Lake	75,000	200/oz.	Truck	
	1962	British Columbia	75,000	265/oz.	Truck	
	1963	British Columbia	75,020	310/oz.	Truck	
Millerton Lake	1956	Donner Lake	16,320	13.6/oz.	Truck	No
		Donner Lake	70,560	8.4/oz.		
	1958	Donner Lake	202,400	115/oz.	Air	
		Lake Arrowhead	2,500	25/oz.	Truck	
	1959	British Columbia	99,840	120/oz.	Air	
		British Columbia	2,700	120/oz.	Truck	
		Donner Lake	49,935	153/oz.	Truck	
		Donner Lake	47,580	130/oz.	Truck	
	1960	Donner Lake	50,400	200/oz.	Truck	
		Donner Lake	36,600	131/oz.	Truck	
		Colorado	44,000	220/oz.	Truck	
		Shasta Lake	200,000	200/oz.	Truck	

TABLE A-4--Continued

Kokanee Plants in Region 4 Through June, 1963

Water	Year planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Pine Flat Reservoir	1960	Shasta Lake	100,050	150/oz.	Truck	
	1961	Shasta Lake	150,000	200/oz.	Truck	
	1961	Colorado	14,850	33/oz.	Truck	
	1961	Twin Lakes	37,800	56/oz.	Air	
	1962	British Columbia	300,000	265/oz.	Truck	
	1963	Bucks Lake	100,200	300/oz.	Truck	
Strawberry Lake	1944	Salt Springs Reservoir	106,000	22-32/oz.	Truck	No
	1945	Montana	99,000	25-40/oz.	Truck	
	1947	Washington	284,000	140-265/oz.	Truck	
Waterhouse Lake	1944	Salt Springs Reservoir	700	32/oz.	Truck	No

TABLE A-5

Kokanee Plants in Region 5 Through June, 1963

Water	Year planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Lake Arrowhead	1955	Donner Lake	200,000	200/oz.	Air	No
	1958	Donner Lake	151,800	115/oz.	Air	
		Lake Arrowhead	147,500	295/oz.	Air	
		Lake Arrowhead	15,252	19/oz.	Truck	
	1959	British Columbia	200,000	200/oz.	Truck	
		Millerton Lake	50,080	160/oz.	Air	
	1960	Colorado	100,440	360/oz.	Air	
		Colorado	30,000	200/oz.	Truck	
	1961	Colorado	100,000	125/oz.	Truck	
		Twin Lakes	150,000	300/oz.	Truck	
	1962	Twin Lakes	114,000	300/oz.	Truck	
		Washington	189,000	300/oz.	Truck	
	1963	Colorado	50,000	200/oz.	Truck	
		Bucks Lake	100,000	260/oz.	Truck	
Bridgeport Reservoir	1962	Twin Lakes	120,300	300/oz.	Truck	
		Twin Lakes	36,750	250/oz.	Truck	
	1963	Colorado	60,000	80/oz.	Air	
		Colorado	120,000	200/oz.	Truck	
Pleasant Valley Reservoir	1961	Twin Lakes	75,000	200/oz.	Truck	
Topaz Lake	1959	British Columbia	50,000	200/oz.	Truck	
	1961	Colorado	280,000	200/oz.	Truck	

TABLE A-5--Continued

Kokanee Plants in Region 5 Through June, 1963

Water	Year planted	Egg source	Number planted	Size of fish	Planting method	Self-perpetuating?
Lower Twin Lake	1958	Lake Arrowhead	43,100	20-40/oz.	Air	Yes
		Donner Lake	27,600	20/oz.	Air	
	1959	British Columbia	8,400	105/oz.	Truck	
		British Columbia	60,500	110/oz.	Truck	
	1960	Colorado	72,300	320/oz.	Truck	
		Colorado	50,000	200/oz.	Truck	
	1961	Colorado	52,000	200/oz.	Truck	
	1962	Colorado	90,000	300/oz.	Truck	
	1963	Colorado	60,000	80/oz.	Air	
		Colorado	90,000	200/oz.	Truck	
		Twin Lakes	37,000	200/oz.	Truck	
Upper Twin Lake	1958	Lake Arrowhead	20,240	40/oz.	Air	Yes
		Lake Arrowhead	14,700	21/oz.	Air	
	1959	British Columbia	49,875	105/oz.	Truck	
	1960	Colorado	32,640	320/oz.	Truck	
		Colorado	20,000	200/oz.	Truck	
	1961	Twin Lakes	26,000	200/oz.	Truck	
	1962	Twin Lakes	90,000	300/oz.	Truck	
	1963	Colorado	60,000	80/oz.	Air	
		Colorado	120,000	200/oz.	Truck	