

elegance. Although much more precision could be added to the system, it is doubtful whether the purely qualitative aspects could ever be removed. The shape of the generating curve, for example, is generally irregular enough to greatly hinder mathematical description. Furthermore, the complete generating curve, as a closed curve, can rarely be seen, and thus its position relative to the axis of coiling is difficult to define mathematically. Finally, the departures from regularity observed in ontogeny discourage completely rigorous analysis of gastropod geometry.

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¹ Réamur, R. A. de, *Mém. Acad. Roy. des Sci.*, 475-520 (1709).

² Mosely, H., *Trans. Roy. Soc. (London)*, part 1, 351-370 (1838).

³ Mosely, H., *Phil. Mag.*, (ser. 3), 21, 300-305 (1842).

⁴ Naumann, C. F., *Abh. k. sächs. Ges.*, 153-196 (1846).

⁵ Blake, J. F., *Phil. Mag. (ser. 5)*, 6, 241-263 (1878).

⁶ Thompson, D'A., *On Growth and Form* (New York: Macmillan Co., 1942), pp. 748-849.

⁷ Thompson, *ibid.*, p. 812. The defining characteristic of this spiral (as a plane figure) is that the angle formed by a tangent to the spiral and a radius (at the point of tangency) is constant. The size of the constant angle controls, therefore, the shape of the spiral.

⁸ The reader is referred to Thompson (*ibid.*, pp. 798-805) for a fuller discussion of the angle of retardation.

⁹ Lister, M., *Historia sive synopsis methodicae Conchyliorum* (London, 1685), Plate 1059, Figure 2.

¹⁰ Martin, G. C., *Maryland Geological Survey*, Miocene Volume, Plate 52, Figure 1 (1904).

*PROLONGATION OF THE LIFE SPAN OF KOKANEE SALMON
(ONCORHYNCHUS NERKA KENNERLYI) BY CASTRATION BEFORE
BEGINNING OF GONAD DEVELOPMENT**

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The present investigation was undertaken as an initial approach to the problem of the nature of the post-spawning death of Pacific Coast salmon. The regularity with which all five species of this salmon die after their first reproduction, no matter whether the normal life cycle of the species is 2, 3, or 4 years, strongly suggests a causal relationship between the spawning act and subsequent death. However, it is also possible that the life span of each species is biologically fixed and that spawning constitutes the final phase. Would prevention of spawning extend the salmon's life cycle? An attempt to answer this question was made by castrating a number of sexually immature kokanee and observing them over a period of years. Unoperated controls of the same hatch were maintained under the same environmental conditions.

Since the beginning of this experiment in 1954 much has been learned about the changes that take place in migrating and spawning salmon. The sexually mature fish exhibits extensive histological alterations in its organs and tissues, degenerations and hyperplasias¹⁻³ accompanied by marked physiological disturbances,⁴ most significant of which is a greatly increased concentration of 17-hydroxycorticosteroids (17-OHCS) in the blood.⁵ This is associated with pronounced hyperplasia of the adrenal cortical tissue.² These physiological and histological changes begin during the spawning migration some time before full sexual maturation. It seems probable that the catabolic action of high levels of plasma 17-OHCS over prolonged periods, combined with the starved state of the migrating and spawning salmon, could cause the deterioration present at the termination of the life cycle. Yet lacking information as to whether or not changes of a similar nature would take place in the absence of sexual maturation this explanation until now has been entirely presumptive. The results of the present study, on which three brief preliminary reports have already been published,^{6, 7} show that castrated kokanee salmon do not deteriorate and die at the time at which the life cycle of this species normally ends.

Materials and Methods.—Kokanee: The kokanee, a variant of the blue back (sockeye) salmon (*O. nerka nerka*), has become landlocked, lives in lakes and spawns either in tributary streams or in the lake itself. The kokanee's normal life cycle is the same as that of its kindred form *nerka nerka*; namely, 4 years. It is a convenient experimental salmon not only because it lives in fresh water but also because of its small size: the full grown adults of most well established populations seldom reach more than 15 to 16 in. in length.

The kokanee employed in the present experiment were hatched at the Lake Tahoe fish hatchery of the California Department of Fish and Game from eggs obtained at Park Fork, Idaho. Hatching was completed by April 19, 1952. Until a year of age the fish were held in a wooden trough approximately 15 × 4 × 4 ft., supplied by an abundant flow of spring water with winter Fahrenheit temperatures in the low 40's and summer temperatures in the mid 40's to mid 50's. Water was kept at a depth of 2 ft. They were then transferred to a small dirt pond about 25 × 10 ft. with the same supply of water at a depth of about 18 in. A wooden platform shelter 4 × 4 ft. was placed at the intake end of the pond. During the winter deep snow not infrequently made the pond inaccessible for considerable periods of time. The kokanee were fed a mixture of liver and sea fish. During the last three years of the experiment at Crystal Lake, where they had been transferred as will be described later, they were given mostly sea fish-rock cod. How much of this diet the kokanee ate is not known since they apparently preferred snails brought in by the water supply.

Castration: In May 1954, at the age of 2 years 1 month, 175 kokanee 6-7 in. long were castrated. The details of the technique employed have been described in a former publication.⁸ Briefly, the fish were anesthetized in a 1:20,000 dilution of tricaine methanesulphonate (MS222-Sandoz) and then placed on an operating board with the head submerged in a 1:25,000 dilution of the same anesthetic. The gonads were removed through a midline abdominal incision, the attempt being made to excise the cephalic pole completely and as much of the posterior portion of the gonad as possible by pulling the gonad taut and cutting it off well down toward the caudal attachment. A few milligrams of penicillin⁹ were placed in the peritoneal cavity before closing the wound with absorbable chromic gut. Average weights of testes were 59 mg, and of the ovaries, 80 mg. Histological examination showed them to be in the infantile stage.

Males were marked by clipping the right pelvic and adipose fins; females, by clipping the left pelvic and adipose fins. The operated kokanee were kept in the hatchery for 3 weeks in covered troughs to permit healing of the incision before transferring to the pond, which also contained 305 control unoperated fish.

Because of the distance of the Lake Tahoe hatchery, and later the Crystal Lake hatchery, from Stanford, population counts, quantitative observations on growth, photography, and the like

could be made only at infrequent intervals. However, the hatchery personnel took unusual interest in these experimental kokanee and inspected them twice a day or more frequently in the fall when the controls were maturing and dying. They performed autopsies on all dead fish, recording length, changes in morphology and skin, presence and state of gonads, size of eggs, and other pertinent data.¹⁰ The attempt was made to secure fish immediately after death, or if possible in a moribund state in order to obtain tissues satisfactory for histological study. Post-mortem fish tissues deteriorate rapidly.

The live fish were handled as little and as infrequently as possible since kokanee seem to be more sensitive to trauma than other hatchery salmonids and are distinctly more difficult to rear in captivity.

For weighing, measuring and photographing, the kokanee were anesthetized in a 1:20,000 solution of MS222. After the fifth year some of the fish developed fungus infection, which was kept under control by means of a malachite green bath given twice a week.

Survival.—One hundred sixty eight kokanee, 125 males and 43 females, survived operation. Figure 1 shows the typical appearance of the fish at the time of

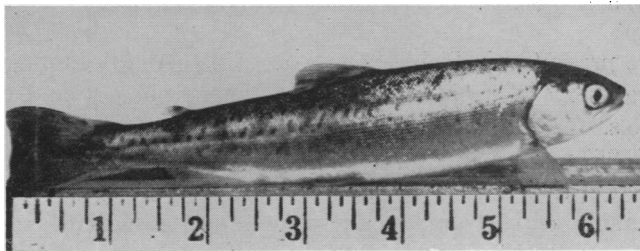


FIG. 1.—Kokanee at time of castration. Age 2 years 1 month, length 6-7 in. Gonads were infantile.

operation.²⁸ By the fall of 1954 some of the control males, now well along in their third year but still only 7-8 in. long, became sexually mature and died as did one of the castrated males in which a small piece of regenerated testicular tissue was found at autopsy. During the winter of 1954-55 observed deaths were few and almost entirely among the control population. However, a large loss from predation (principally raccoons) occurred. By June, 1955, the census showed that 13 castrated males, 11 castrated females, and 135 unoperated controls had been lost.¹¹

TABLE 1
NUMBERS OF SURVIVING KOKANEE AT SUCCESSIVE YEARS

Year of life	Date of population count	Age		Number of castrated		Un-operated controls	Other data
		Yrs.	Mos.	males	females		
3rd	5/13/54	2	1	125	43	305	Start of experiment
	10/22/54	2	6	122	37	302	
4th	6/ 7/55	3	2	108	30	161	Including loss from predation
	10/24/55	3	6	103	29	141	
5th	5/23/56	4	1	22	21	25	Including loss from predation
	11/ 4/56	4	7	11	18	18	
	3/ 3/57	4	11	6	15	0*	
6th	5/15/57	5	1	3	11	--	No predation
	10/28/57	5	6	2	8	--	
7th	8/13/58	6	4	2	7	--	No predation
	2/24/59	6	10	2	5	--	
8th	5/20/59	7	1	2	5	--	No predation
	10/21/59	7	6	1	5	--	
9th	4/14/60	8	0	1	1	--	No predation
	7/27/60	8	3	0	1	--	
	10/21/60	8	6	0	0†	--	

* Last control died on this date.
† Last castrated fish died on this date.

TABLE 2
DEATHS AND LOSSES OF KOKANEE AT SUCCESSIVE YEARS

Year of life	Castrated								Predation and other unobserved deaths during winter		
	With regeneration of gonads		Observed Deaths				Unoperated controls with sexual maturation			Castrated	Controls
	♂	♀	♂	♀	♂	♀	♂	♀			
3rd	1 (K)*	0	1 (K)	1 (K)	6 (2K)	3 (3K)	15	12	135		
4th	46 (2K)	0	2 (1K)	2	27 (3K)	37 (1K)	38	7	69		
5th	9	1	7	5	8 (2K)	18 (1K)	0	0	3		
6th	0	8	1	2	0	0	0	0	0		
7th	0	0	0	2	0	0	...		
8th	0	0	1 (K)	4	0	0	...		
9th	0	1	1	0	0	0	...		

* (K) = killed for tissue specimens.

These data are presented in Tables 1 and 2. Up to the beginning of the fourth year the castrated fish were indistinguishable in morphology and rate of growth from the controls.

In the fall of 1955 many control kokanee were maturing and dying. They were now in the latter part of their fourth year, when most kokanee spawn in the wild state. Likewise a number of castrated males were showing signs of sexual maturity: prolonged snout, hooked jaws, humped back and eroded skin (Fig. 2). The mor-

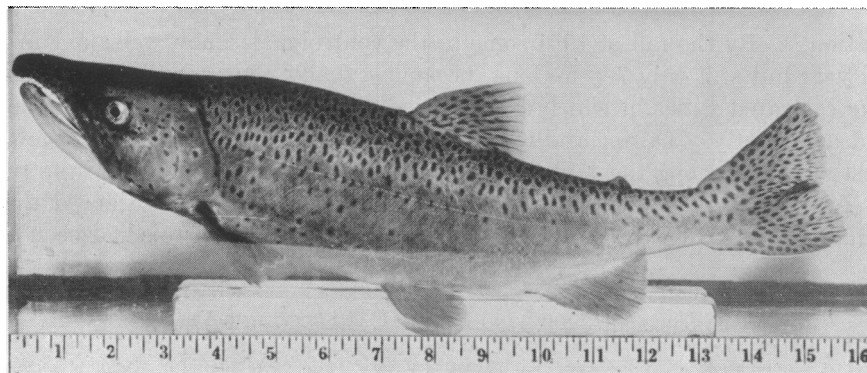


FIG. 2.—Castrated male kokanee showing characteristic morphological changes of normal spawning male—elongated snout, hooked jaws, and hump back. Small fragments of regenerated testes present. Age 4 years 7 months, length 16 inches, at death.

phological changes in these fish were exactly like those occurring in the sexually mature control males. When the castrated male kokanee were examined after death, all but two (Table 2) were found to have regenerated testicular tissue, frequently at the anterior pole of testis attachment but more often in the caudal region adjoining the spermatic duct. Obviously gonadectomy had been incomplete in these fish. In many instances the mass of regenerated testicular tissue was very small, 200 mg or less, whereas the normal mature testes of the control kokanee weighed 9 grams or more. Two castrated females died during their fourth year without regeneration of ovaries. No apparent cause for death was found in these females or in the two completely castrated males which died.

During the winter of 1955-56 the loss from predation was again high (Table 2) despite all preventive measures. By the beginning of their fifth year of life the kokanee population had been reduced principally as the result of sexual maturation plus predation to 22 castrated males, 21 castrated females, and 25 controls. At this time three of the control fish were killed for examination. One was a female with very small eggs, one was an immature male, and the third had no gonads. The number of experimental fish was now sufficiently small so that it was possible to place them in a large outdoor wooden trough 15 × 4 × 4 ft. completely screened to prevent any further predation. The water flow that had supplied the pond was now diverted into the trough.

In November, 1956, it was necessary to transfer the kokanee to another location since the Tahoe hatchery was being closed. The remaining population of 47 fish (see Table 1, Nov. 4, 1956) were taken by tank truck to Crystal Lake hatchery just north of Mt. Lassen some 350 miles distant. The transfer was accomplished without loss and the experimental kokanee were placed in a large screened trough of the same size to which they had been accustomed, and supplied with water at essentially the same temperatures as those at Lake Tahoe. The water flow was 50-60 gallons a minute, and the water depth was kept at 26 in.

During the fall and winter of their fifth year all the remaining control kokanee died—the last one, a maturing bisexual fish, succumbed on March 3, 1957, at the age of 4 years 11 months. Autopsies on 143 of the controls showed that the ratio of males to females was 1:3.5, just the reverse of the sex ratio of the castrated population. Twenty-one castrated fish died during this period; all but 2 of the males showed regeneration of testicular tissue, but 5 of 6 females were found to be completely castrated. This left 6 male and 15 female castrated survivors, all of which had a juvenile appearance.

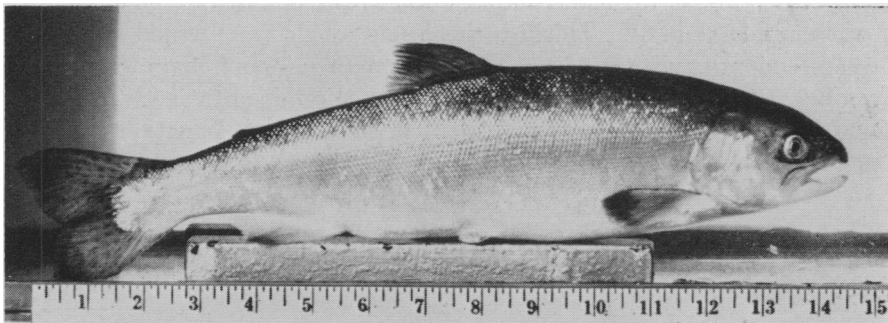


FIG. 3.—Castrated male 5 years and 6 months of age and 14½ inches in length. Silvery color and juvenile appearance.

During the sixth year 10 castrated females died, 8 with regeneration of ovarian tissue (Table 2). In most of them very few eggs were present. One had approximately 400 eggs.¹² Following the death of this female only one of the remaining fish revealed any regeneration of gonadal tissue. Figure 3 shows a castrated male 5½ years old still exhibiting juvenile morphology and a silvery color.

In the seventh year of their lives 2 of the females and 1 male began to develop changes in the shape of the head. One female (Fig. 4) showed a blunting of the nose, and the other, a slight hooking of the jaw, as did the male. The female of

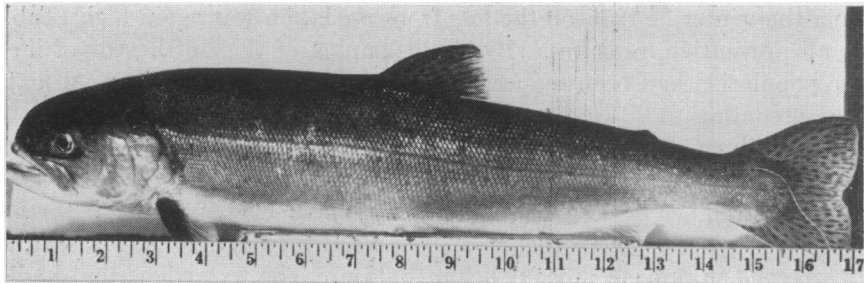


FIG. 4.—Castrated female. Age 6 years 4 months, length 17 inches, weight 880 grams. Shows blunting of nose, projection of lower jaw, and loss of silvery color. Died 4 months later, growth to $17\frac{3}{4}$ inches. No regeneration of ovaries.

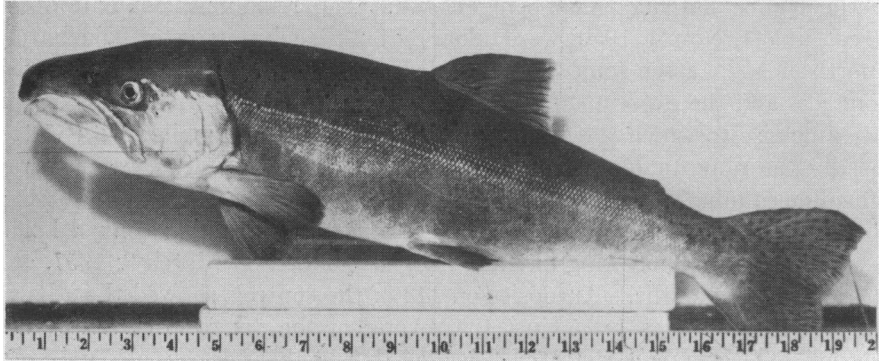


FIG. 5.—Castrated male. Age 6 years 10 months, length 19 inches, weight 1,195 grams. Has appearance of spawning male salmon. Sacrificed at 7 years of age as fish was losing weight. No regeneration of testes.

Figure 4 died 4 months after the date of photo, at the age of 6 years 8 months. Hooking of the jaws of the male continued to increase and by the end of the seventh year was marked (Fig. 5). This fish was losing weight rapidly and was sacrificed at 7 years 1 month. Not a vestige of testicular tissue was found at autopsy.

Even in their eighth year several of the kokanee retained their silvery color and juvenile form (Fig. 6). The others began to show some elongation of the jaws,

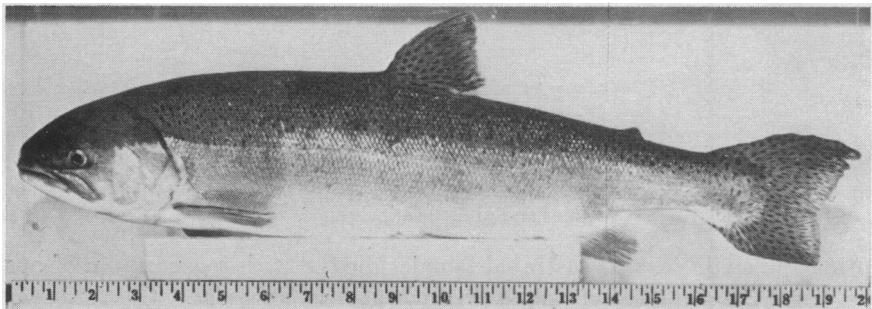


FIG. 6.—Castrated female. Age 7 years, length $19\frac{1}{2}$ inches, weight 1,420 grams. Silvery color and juvenile appearance.

blunting of the nose and darkening of the skin. Four of the 5 remaining females died during this year.

At the beginning of the ninth year only 1 male and 1 female survived. The male was still quite silvery with only a little blunting of the nose but no elongation

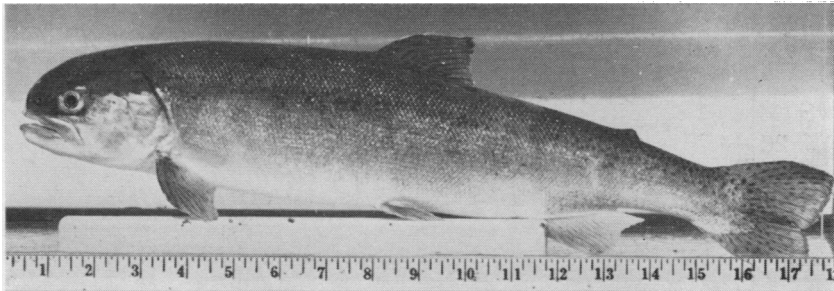


FIG. 7.—Castrated male. Age 8 years, length $17\frac{1}{2}$ inches, weight 845 grams. Still moderately silvery in color. Blunting of nose. Died at 8 years and 2 months, length 18 inches. No testicular tissue found at autopsy.

or hooking of the jaws (Fig. 7). This fish died at 8 years and 2 months of age. No testicular tissue was found. The female was of a grayish color, had well marked prolongation and hooking of the jaws as shown in Figure 8 taken at 8 years 4

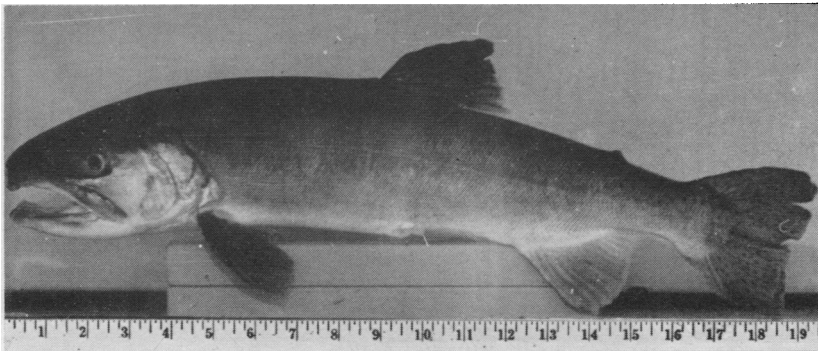


FIG. 8.—Castrated female. Age 8 years 4 months, length $19\frac{3}{4}$ inches, weight 1,200 grams. Grayish color, elongated, and hooked jaws. Died at 8 years and 6 months. Two small clusters of immature eggs found at autopsy.

months. This fish had been losing weight for the past few months, had sunken eyes and died at 8 years and 6 months of age. A small cluster of regenerated eggs 3 mm. in diameter was present at each upper pole of ovary attachment: 6 eggs in the left and 22 in the right.

Growth.—Increase in length of the experimental fish is shown in Figure 9. The castrated fish, males in particular, grew more rapidly than did the controls. The last 22 control fish at death averaged 11.7 in. in length, whereas 4 castrated males dying at this time averaged over 14 in. Among more than 100 sexually mature unoperated controls, only one reached the length of 14 in. After the 6th year of life the castrated females were slightly longer than the males and continued to grow more rapidly. Both sexes appeared to reach a maximum length in the eighth year of age. Two fish showed continuous increase in length up to the time of death. One, dying at 6 years 8 months, grew $\frac{3}{4}$ in., even though during the last 4 months it lost 75 grams in weight. The other, which died at 8 years 1 month, grew $\frac{1}{2}$ in. during the last 6 weeks of life while losing 45 grams. The remaining 5 kokanee living beyond 6 years of age showed cessation of growth several months before death.

The castrated fish of both sexes gained more weight than did the controls (Fig.

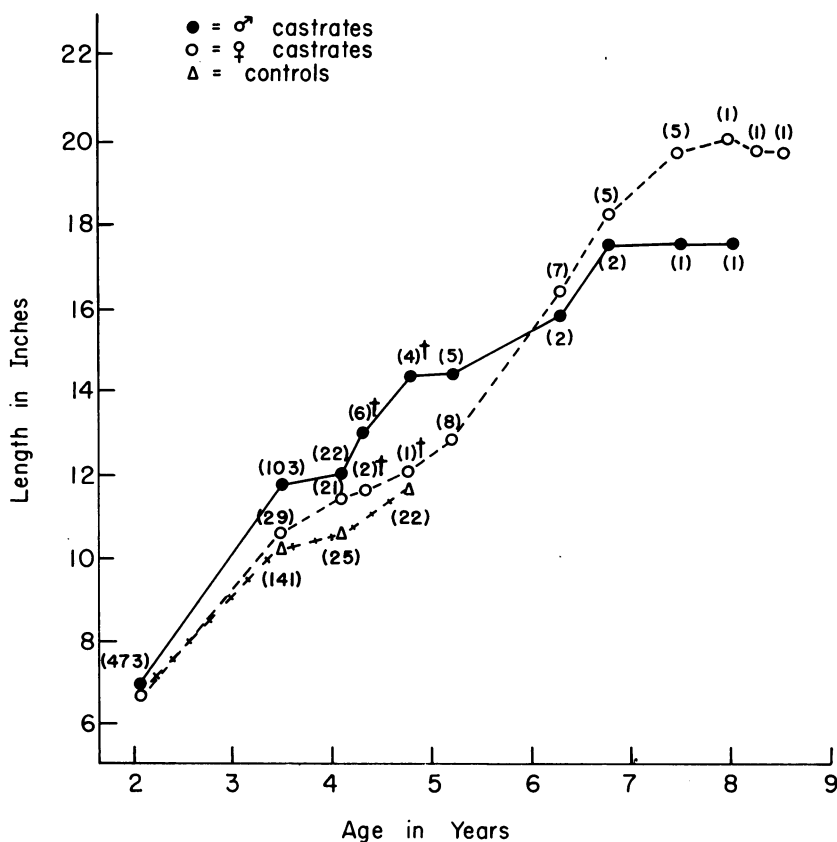


FIG. 9.—Growth in length of experimental kokanee. † = died on or about this date. Others died at irregular intervals.

10). As one would anticipate from their longer length, the males weighed more than the females until the fifth year of life. Beyond this age the females were heavier than the males. However, the number of males, 2, was too small to make a fair comparison. The largest fish, a female, weighed 1650 grams (approximately 3½ lb) at the age of 7½ years and was 20¾ in. long.

Other Changes.—Gonads: The mass of ovarian tissue found in those fish showing gonad regeneration varied from as little as 9 mg to as much as 1120 mg and the number of eggs from 5 or 6 to several score. The size of the eggs were with a single exception much smaller than the eggs of the mature control kokanee. Eggs of 29 control fish averaged 4.3 mm in diameter, whereas in 9 castrated kokanee the eggs were from 1–2 mm in 6 and 2–3 mm in 3 of them. One castrated female dying at 5 years 9 months was found to contain approximately 400 eggs measuring 5.5 mm in diameter (the same size as eggs taken from ripe kokanee in the wild state). This was the only castrated female in which the eggs of the regenerated ovary developed to a large normal size.

In contrast to the usual immature state of the eggs of regenerated ovarian tissue, the regenerated testes exhibited full sexual maturity, i.e. spermatozoa, even though the mass of the gonad tissue was very small.

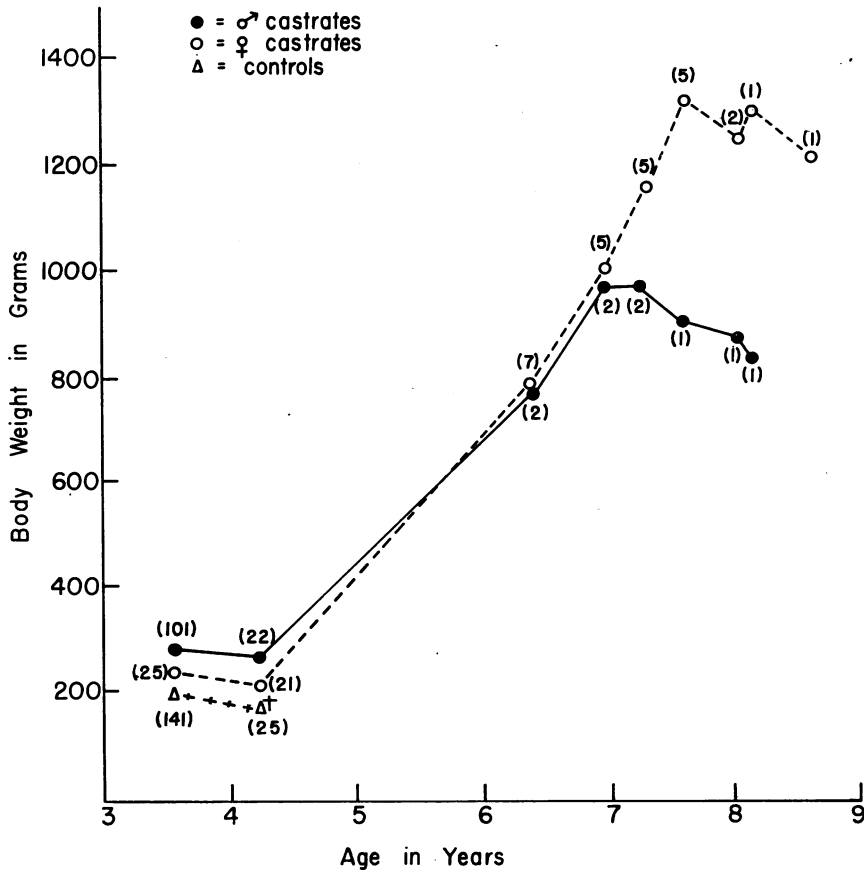


Fig. 10.—Growth in weight of experimental kokanee. † = last weighing before death of all controls in fall and winter of fifth year.

Scales: All the mature control kokanee showed absorption of the scales¹³ with one exception, that of a young female dying in the fall of the third year of life. Likewise, all but one of the castrated males showing regeneration of testicular tissue exhibited absorption of the scales equal in degree to that found in mature control kokanee (Fig. 12). On the other hand, scale absorption occurred in only one of the females with regenerated ovarian tissue; this was the fish referred to above which contained a large number of eggs. None of the castrated kokanee of either sex, dying without having regenerated gonadal tissue, exhibited absorption of their scales.

The scales of the very old fish, those dying after the sixth year, showed distortion in shape with perhaps some absorption of the caudal end of the scale, but no obvious irregular loss of circuli such as occurs in the scales of sexually mature kokanee (Figs. 11-13). The scales of the old fish (Fig. 13) were much larger than those of the younger kokanee (Fig. 12). This finding was to be expected since the scale grows *pari passu* with the total body growth.

Lack of spawning: No evidence of spawning activity was observed among the mature control kokanee. At autopsy the females were found to be full of eggs, either loose in the body cavity or still retained in the ovary. Whether any eggs

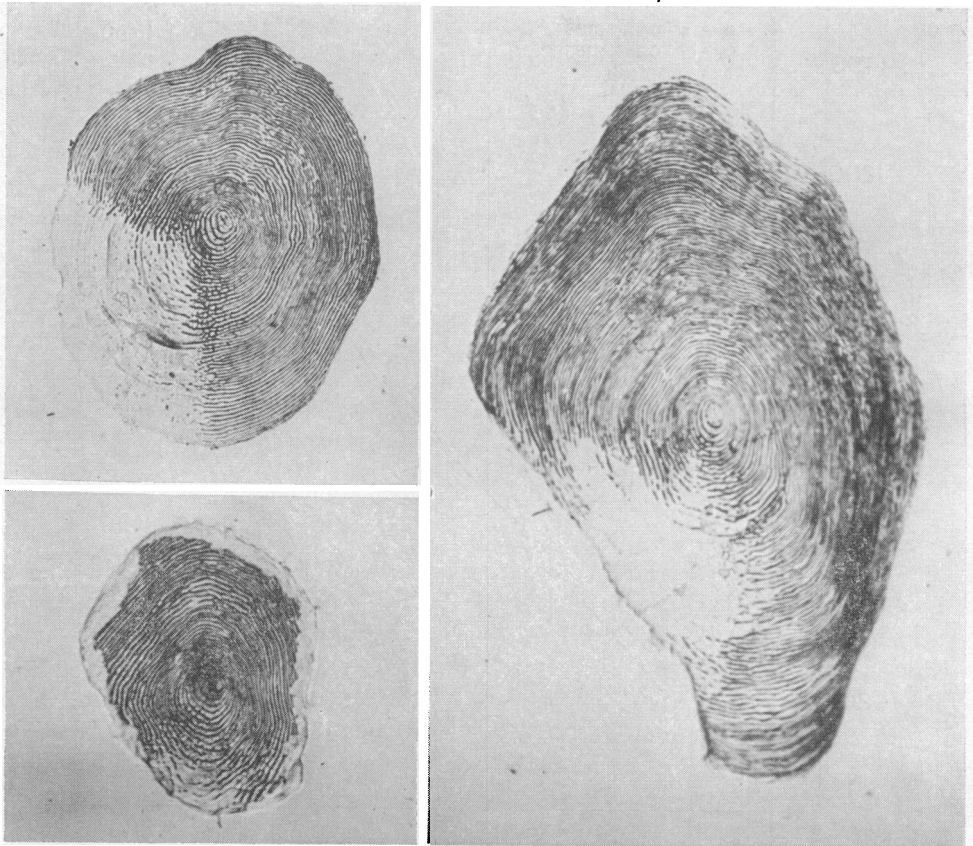


FIG. 11 (*Top left*).—Normal scale of castrated female kokanee which died at 4 years and 2 months of age without regeneration of ovaries. Length, 12 inches. $\times 16$.

FIG. 12 (*Bottom left*).—Scale of male castrated kokanee which died at 3 years and 7 months of age with regeneration of testes. Length $13\frac{1}{2}$ inches. Shows loss of peripheral circuli and loss of scale substance. $\times 16$.

FIG. 13 (*Right*).—Scale of castrated female sacrificed at 7 years of age. No regeneration of ovaries. Length $20\frac{3}{4}$ inches. Shows marked increase in size over scale of 4-year-old fish and distortion of shape. No absorption except possibly at left lower aspect. $\times 16$.

were shed was not known. The ripe males exuded milt on handling, but how much was shed before death was unknown; the presence of large testes suggested that most of the milt was retained until death. The eyes of the old fish showed no evidence of cataract formation. However, in some of them the eyes were markedly sunken in their sockets.

Histological Changes.—The histological changes occurring in spawning Pacific salmon, including the kokanee, have been described in previous communications.^{2, 3} The most striking and significant change is a marked hyperplasia of the adrenal cortical tissue. Castrated kokanee in which regeneration of gonadal tissue occurred showed hyperplasia of the adrenal tissue. In contrast, the completely castrated fish, dying or killed up to the time the last of the control kokanee matured and died, showed no detectable change in this tissue.¹⁴ A detailed account of the histological alterations which took place in the senescent kokanee will be given in a subsequent paper.¹⁵

Discussion.—The life span of kokanee under natural conditions appears to depend to a considerable extent on latitude. Curtis¹⁶ found that kokanee in California matured at the end of their third year. His observations included Donner Lake which is near Lake Tahoe and at approximately the same altitude. In the Columbia and Fraser River systems kokanee have been observed to spawn in their third, fourth, and fifth years.¹⁷ Mosher, quoted by Galligan,¹⁸ found among approximately 1,000 land-locked kokanee and sockeye salmon taken from lakes of the Northwest only a few 6-year-old and one 7-year-old fish. Farther north in Alaska, sea-run sockeye return to spawn at 3 to 8 years.¹⁹

That land-locked sockeye salmon in the wild state can survive well beyond their normal life cycle, provided they do not mature sexually, has been reported recently by Galligan.¹⁸ He secured from a lake in Connecticut a large immature female sockeye 20 in. long and weighing 3 lb whose scales showed 8 annuli and no spawning mark. Mature adults of the sockeye population of this lake spawn in the fall of their fourth year and reach a length of 14–16.5 in.²⁰ The latitude and climatic conditions of the Lake Tahoe and Crystal Lake regions are not appreciably different from those in Connecticut.

Castration of mammals appears to have no significant effect on length of life.²¹ However, Korenchevski has observed various indications of accelerated senescence in castrated rats.²² Likewise, eunuchs show premature aging,^{23, 24} but there is no definite evidence that the life span of either rats or man is shortened by gonadectomy. That the effects of castration of kokanee would be other than those resulting from ablation of the gonads in mammals might be anticipated from the difference between Pacific salmon and mammals with respect to the consequences of reproduction. While only a very limited number of fishes die regularly after their first spawning²⁵ many species show a greatly increased incidence of mortality at this time.²⁶ It is possible that castration of such fishes at an early age might have the same effect as it did on kokanee.

Our studies on the nature of the post-spawning death of Pacific salmon suggest that hyperadrenocorticism is the principal cause of the fatal outcome,⁴ but what precipitates this state remains unknown. One finding in the present investigation provides a possible clue. The principal apparent stress common to both migratory and nonmigratory salmon, namely the formation of a large gonadal mass under conditions of starvation, might seem to be of sufficient intensity to produce the adrenal hyperactivity characteristic of spawning salmon. Yet the castrated male kokanee with regeneration of only a very small amount of gonadal tissue shows marked hyperplasia of the adrenal cortical tissue and dies with all the typical stigmata of the fish with normally mature testes. It is accordingly clear that the stress of gonad formation is not operating in these fish. Is the production and release of gonadotropins by the pituitary accompanied by increased ACTH production, or does some product of testicular growth stimulate the pituitary to greater ACTH secretion or perhaps act directly on the adrenal cortical cells? The possibility that hyperactivity of the adrenal cortex may be incited by factors other than ACTH is indicated by the recent finding of Hilton and co-workers.²⁷ They showed by means of direct arterial perfusion of the adrenal glands of the hypophysectomized dog that secretion of significantly increased quantities of hydrocortisone could be produced by synthetic lysine, arginine, and acetyl arginine

vasopressin.

The relationship of regeneration of gonadal tissue to death was not apparent in the castrated female kokanee. Up to and including the fifth year of life of the experimental fish, when all the controls had died, only 2 of 9 castrated females showed regeneration of ovarian tissue at the time of death while 56 of 66 dead castrated males exhibited varying degrees of testis regeneration.

Some evidence was provided by an earlier small-scale, and heretofore unpublished experiment, that castration of kokanee with well developed gonads has relatively little effect on lengthening their life span. These fish were gonadectomized when 2½ years of age, in the fall of the year. The control males began dying within a month or so after the beginning of the experiment and showed fully mature testes. The majority of the castrated males survived somewhat longer than did the male controls and died without regeneration of testicular tissue. Two of them outlived the last of the male controls by 3 months. However, no difference in length of life between female castrates and female controls was observed and the oldest survivor of the experiment was a control female.

Summary.—To ascertain whether or not there is a causal relationship between the spawning act and subsequent death of Pacific salmon, a large number of kokanee salmon (168) were castrated at 2 years of age while still completely immature. They were maintained in a rearing pond together with twice the number of unoperated controls. The castrates grew well and were indistinguishable from the controls until the fourth year when many of the males took on the morphological appearance of normally maturing salmon, exhibited degenerative changes and died. Regeneration of testicular tissue, usually very small in amount, was found to be present in these fish. The control kokanee all matured and died before the end of their fifth year. A small group of castrates (21) were alive at this time, and continued to grow. Seven of them reached the eighth year of life and two survived until the ninth year. The last, a female, died at 8 years 6 months. The results of this experiment indicate that it is the maturation of gonadal tissue and not the actual spawning (at least in males) which leads to degeneration and death and that if sexual development is prevented by castration kokanee can survive well beyond the normal life span of this species.

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⁶ Robertson, O. H., *Year Book of the American Philosophical Society*, 1956, p. 215.

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¹¹ The relatively greater loss among the controls might have been due to the fact that many of them had matured and in this state were sluggish and hence more easily caught by predators.

¹² This is less than half the number of eggs produced by the wild kokanee of Donner Lake.

¹³ Scale absorption as designated by fish biologists consists of varying degrees of loss of peripheral scale substance.

¹⁴ The author is indebted to Dr. Bernard C. Wexler, May Institute for Medical Research, Cincinnati, Ohio, for providing a number of these histological preparations.

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²⁸ I wish to record my gratitude to the late Dr. Clifford Sweet of Oakland, California, who performed many of the castrations.