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ENDOCRINE AND OTHER PHYSIOLOGICAL FACTORS
ASSOCIATED WITH THE SPAWNING MIGRATION OF PACIFIC SALMON
(ONCORHYNCHUS SPP.) AND THE STEELHEAD TROUT (SALMO GAIRDNERI)

by

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Two genera of fishes in the family Salmonidae have stimulated considerable biological interest on the Pacific coast of North America. The anadromous life histories of both the Pacific salmons (Oncorhynchus spp.) and the migratory rainbow trout (Salmo gairdneri) have provided many research opportunities during the past several decades. Although the life histories of these two genera of fishes are quite similar, a basic difference is reflected in their post-spawning mortalities. While the universal post-spawning mortality of adult Pacific salmon restricts them to a single spawning, some of the anadromous trout may spawn repeatedly, but post-spawning mortality may amount to as much as 50%. The ability of the steelhead trout to survive under the same environmental stresses that result in the death of Pacific salmon represents a still somewhat puzzling species difference of vertebrate physiological uniqueness. This paper will attempt to review current and past work on this question of survival vs. death in these anadromous fishes which comprise one of our most valuable local natural resources.

EARLY LIFE HISTORY

The life of salmonid fishes begins in the headwaters of fresh water streams. Steelhead trout and Pacific salmon normally spawn during the winter and spring, often in the same stream. A coho salmon (Oncorhynchus kisutch) of average size, i.e., 70 cm, will produce approximately 3000 eggs. A steelhead trout of comparable size may produce 7500 eggs (Shapovalov and Taft, 1954). The eggs of the coho are larger, the average volume being approximately .21 cc, while the eggs of the steelhead average less than .10 cc.

Smoltification includes one of the first major physiological events that occurs in the lives of anadromous salmonids. Although the exact environmental cues which trigger smoltification are not completely understood, photoperiod and water temperature appear to be foremost. The size of the juvenile fish appears to be one of the most important factors correlated with time of smoltification. The amount of time spent in fresh water, food supply and water temperature, and inherent growth rates all influence the size of the fish. Hoar and Bell (1950) have shown that smoltification is accompanied by an increase in thyroid activity.

OCEANIC LIFE

Anadromous salmonids spend the greater part of their life in the ocean. This phase of their life is characterized by vigorous feeding and rapid growth. The great majority of Pacific salmon live in the ocean for 2 or 3 years (Table I). Small male chinook salmon (Oncorhynchus tshawytscha), referred to as "jack salmon", make a spawning journey after 2 years of ocean residence. All of the coho salmon (Oncorhynchus kisutch) which returned to spawn after 1 year in the ocean were small males (i.e., 40 cm) (Shapovalov and Taft, 1954).

Table I. Length of seawater residence of salmonid fishes.

Species	Average seawater residence (yrs)	Range (yrs)
*Pink salmon (Oncorhynchus gorbuscha)	2	2
'Coho salmon (Oncorhynchus kisutch)	2	1-3
*Sockeye salmon (Oncorhynchus nerka)	2	1-4
*Chum salmon (Oncorhynchus keta)	3-5	2-7
*Chinook salmon (Oncorhynchus tshawytscha)	2-4	2-7
'Steelhead trout (Salmo gairdneri)	1	1-5

* Hart (1973)

' Shapovalov and Taft (1954)

A large percentage of the steelhead trout which are spawning for the first time spend 1 year in the ocean before undertaking the spawning migration. Steelhead which have spent 2 years in the ocean make up a significant portion of the spawning population. A steelhead trout may spend as much as 5 years total time in saltwater, but this is interrupted by spawning migrations. The majority of repeat spawners are fish which spend a year in the ocean between spawning migrations.

ADULT MIGRATION OF PACIFIC SALMON

During the last year of their life, Pacific salmon commence the migration for which they are noted, from the oceanic realm into fresh water. A variety of physiological and histological changes take place which may be responsible for the post-spawning death of these fishes. Endocrine influences appear to play a major role in promoting these physiological and histological alterations.

Pituitary activity regulates many processes necessary for the physiological integrity of the salmon. A brief summary of pituitary structure may aid in interpretation of the histological changes which occur during the spawning migration. The salmonid pituitary consists of four well-vascularized divisions or lobes. The following description applies to the sexually immature adult salmon (Robertson and Wexler, 1962b, van Overbeeke and McBride, 1967). The dorsal lobe or meso-adenohypophysis (caudal pars distalis) consists of acidophilic cells arranged in columns. Basophilic cells are rare or absent. A few undifferentiated cells may be found in the lateral portions of this lobe, which is the smallest lobe of the immature salmon pituitary. A curtain-like anterior lobe or pro-adenohypophysis (rostral pars distalis) covers the anterior portion of the dorsal lobe. A few basophilic cells may be present, but columnar acidophils arranged in follicles comprise the majority of the anterior lobe. The ventral lobe (meta-adenohypophysis, pars intermedia) occupies the ventral half of the pituitary and consists of columns and masses of acidophilic cells delimited by basement membranes. The neural lobe (neurohypophysis) consists of neural elements interspersed in a connective tissue framework. A few large ovoid nuclei with or without cytoplasm may be present in the neural lobe. This general pituitary condition, found as late as the early stages of the upstream migration, reflects generally low activity, but mitotic activity is common in all parts of the gland.

As the salmon matures sexually, several histological changes (primarily differences in the relative proportions of different cell types) occur in the pituitary. Most significant is the increase in size of the dorsal lobe, which begins to form a wedge between the anterior and ventral lobes. The acidophils and particularly the basophils increase in number (Robertson and Wexler, 1962b). The basophilic cells probably are gonadotrophs (van Overbeeke and McBride, 1967). The gonadotropic cells begin to actively produce gonadotropin, resulting in a progressive sexual maturation of the salmon (Crim, et. al., 1973). The ventral lobe shows signs of fibrosis and disintegration of the basement membranes. Some of the cells with a high degree of degeneration (cytoplasmic vacuolization, shrinkage of cytoplasm and nuclei) appear to break away from disrupted cell columns and "migrate" into the neural lobe.

Advanced gonad development results in a progressive degeneration of the dorsal lobe, characterized by open spaces, vesicles, and cysts. An increasing number of chromophobes appear as the basophils become degranulated (depleted of hormone).

The pituitary of the spent salmon exhibits further degeneration and occasional hemorrhages may be present (McBride and van Overbeeke, 1969a). The follicles of the anterior lobe increase in size, and limited focal cytolysis sometimes takes place. Cyst-like structures are occasionally found in this lobe. The greatest degeneration occurs in the dorsal lobe, where first the basophils, and then the acidophils undergo vacuolization, nuclear pycnosis, and cytolysis. Increasing fibrosis follows and cysts form. The cells of the ventral lobe exhibit degranulation, followed by pycnosis, loss of cytoplasm, and cytolysis. In the neural lobe, large degenerating nuclei appear. Robertson and Wexler (1962b) called these "ghost cells". These nuclei may be the remnants of degenerating cells which have migrated into the coarse fibrous connective tissue which has penetarted into all portions of the pituitary. No significant sex differences in pituitary degeneration was found in either chinook salmon (*Oncorhynchus tshawytscha*) (Robertson and Wexler, 1962b) or sockeye salmon (*Oncorhynchus nerka*) (van Overbeeke and McBride, 1967).

Hypophyseal levels of cholinesterase decline in pink salmon (*Oncorhynchus gorbuscha*) during the spawning migration. Trams (1969) suggested that decreasing levels of neurotransmitters may result in poor hypothalamic control of the pituitary.

Gonadotropin stimulates the sex organs to mature, produce gametes, and produce gonadal hormones. Although there may be two different types of gonadotrophs present in the salmon pituitary (van Overbeeke and McBride, 1967), considerable evidence suggests that there is only one teleost gonadotropin (Chester Jones, *et. al.*, 1974). Crim, *et. al.*, (1973), through the use of radioimmunoassay techniques, demonstrated that plasma gonadotropin levels in *Oncorhynchus gorbuscha* are low during summer and early fall, but the levels progressively increase up to the time of spawning. While plasma levels reach a plateau in the male after the emission of spermatozoa, females exhibit variable levels with average plasma gonadotropin concentrations higher than the male. The range of concentrations in the female pink salmon is quite variable, however (76-304 ng/ml plasma).

Increasing gonadotropin levels and subsequent gonad maturation result in increasing gonosomatic indices (gonad wt./body wt. X 100). Robertson and Wexler (1959) give the average GSI of the mature Pacific female salmon as 21-25.

In the hope of elucidating pituitary-gonad regulation, McBride and van Overbeeke (1969a) gonadectomized sockeye salmon (Oncorhynchus nerka). They reported that gonadotrophs were absent in the immature fish. Gonadectomy of the mature fish resulted in degranulation of the gonadotrophs. In the subsequent study (van Overbeeke and McBride, 1971), androgen injections into a gonadectomized fish caused the gonadotrophs to increase in size and become filled with granules of gonadotropin.

Gonadal hormones are normally grouped in two classes: estrogens and androgens. Although the primary function of these hormones is the control of production and maturation of gametes, they also elicit important secondary effects. These effects have been convincingly demonstrated by Donaldson and Fagerlund (1969), through the use of gonadectomy followed by injections of hormones. Gonadectomy of a mature sockeye salmon (Oncorhynchus nerka) results in a return to the silvery coloration of the immature fish. Administration of androgens to the same fish results in the reddish external coloration, hooked snout, and premaxillary teeth characteristic of the spawning male sockeye salmon. Estrogens are responsible for the equivalent changes inthe female sockeye salmon. In addition, the same workers (Fagerlund and Donaldson, 1969) have concluded that androgens in sockeye salmon of either sex appear to be responsible for the loss of pink flesh color during the spawning migration, since estrogens failed to bring about this change in either male or female gonadectomized sockeye salmon.

The diffuse interrenal tissue scattered throughout the head kidney of the salmon is analogous to the mammalian adrenal cortex. The catabolic group of steroids called 17-hydroxycorticosteroids are produced in this tissue. The migration of Pacific salmon is accompanied by significant changes in the interrenal tissue, the most important of which may be massive hypertrophy, resulting in a rise in plasma 17-hydroxycorticosteroid concentration, as much as a sevenfold increase in chinook salmon (Oncorhynchus tshawytscha) (Robertson and Wexler, 1960). The immature salmon has adrenal tissue arranged in narrow collars around the cardinal vein. As the fish matures (i.e., gonad wt. is greater than or equal to 10% of mature gonad wt.), these adrenal cells begin to hypertrophy and mitoses are frequently observed. By the time the salmon has matured and spawned, a marked hypertrophy has occurred and the adrenocortical cells become arranged in large lobules or cords (Hane, et. al., 1966). However, mitoses have become rare (Robertson and Wexler, 1959). New patterns of vascularization break up the cords of cells, and nuclear and cytoplasmic vacuolization commence. Hemorrhages are not uncommon. Degeneration (nuclear pycnosis and cytolysis) characterizes the interrenal tissue of the spent salmon.

The hypertrophic cells are actively secreting cortical steroids, the most common being cortisol and cortisone in sockeye salmon (Fagerlund and McBride, 1969) and hydrocortisone in chinook salmon (Hane and Robertson, 1959). Where immature sockeye salmon may have plasma cortisol concentrations of less than 5 μg/100 ml plasma, a moribund fish may have plasma concentrations approaching 200 μg/100 ml plasma (Fagerlund, 1967). Females normally have higher concentrations than males (Hane and Robertson, 1959, Donaldson and Fagerlund, 1970). This appears to be partly due to differences in metabolic clearance rates. Male sockeye salmon have a higher metabolic clearance rate (MCR) of cortisol (Donaldson and Fagerlund, 1970) and cortisone (Fagerlund and Donaldson, 1970) than female sockeye salmon.

In the spent fish, however, the plasma concentrations of adrenocortical steroids may drop down to levels similar to those of the immature fish (Fagerlund, 1967). Species differences do exist. Chinook salmon normally have higher plasma concentrations of adrenal steroids than sockeye salmon, yet Hane and Robertson (1959) reported a decrease in plasma 17-hydroxycorticosteroid concentrations in the spent male chinook salmon. As will be discussed in more detail later, high plasma concentrations of 17-hydroxycorticosteroids result in a general body catabolism.

One of the major excretory sites of the salmon's body, the kidney, undergoes considerable degeneration during the spawning migration of the Pacific salmon. A progressive glomerulosclerosis (Hane, et. al., 1966) and thickening of Bowman's capsules keeps pace with sexual maturation (McBride, 1967). Edematous glomeruli and vacuolated tubule cells further hinder the excretory mechanisms of the spawning salmon (Robertson and Wexler, 1960). Scattered hemorrhages contribute to this deteriorating kidney condition. Since the kidney seems to be a major site of cortisol excretion (Donaldson and Fagerlund, 1972), these deteriorative changes will have a significant negative effect on the adrenocortical steroid MCR and result in high plasma concentrations of 17-hydroxycorticosteroids. In addition, the kidney assists in regulation of sodium balance in euryhaline fishes. The advancing kidney degeneration could interfere with osmoregulation.

Deterioration also affects the liver, another important site of metabolic clearance processes (Donaldson and Fagerlund, 1972). Until the salmon is mature, the degeneration consists primarily of fat depletion. By the time the salmon spawns, general hepatic degeneration, characterized by nuclear and cellular dissolution, has affected the liver (Robertson and Wexler, 1960).

Before the spawning migration, the bright silver immature salmon spends several months actively feeding in the ocean. The resulting liver and muscle glycogen deposition provide energy for the spawning migration. These fat and protein stores are made available through the gluconeogenic action of the

17-hydroxycorticosteroids. High concentrations of these steroids result in a progressive hyperglycemia during the migration (Robertson, et. al., 1961b).

Pancreatic insulin-producing beta cells hypertrophy and increase in number probably to compensate for the hyperglycemia. The resulting high levels of insulin may overcompensate because urinary glucose is near zero in the spawning fish. The pancreatic islet cells exhibit a progressive deterioration (which may represent a functional exhaustion) during the migration (McBride, 1967). In the spent salmon, beta cells may outnumber the alpha cells in the pancreatic islets. Atrophied cells with nuclei in various states of dissolution are found in the exocrine tissue as well as the islet cells. In addition, the fat stores in the pancreas have become depleted during the migration(Robertson and Wexler, 1960).

Since Pacific salmon cease feeding on the spawning run, energy requirements must be met by body tissues. Patton, et. al., (1970) reported that a pink salmon (Oncorhynchus gorbuscha) may utilize 90-95% of stored fat in the duration of a spawning migration. A mature salmon may lose up to 30% of its muscle tissue by the time it spawns (Robertson, et. al., 1961b). The nearly totally depleted muscle fat and protein is replaced by water and increased amounts of sodium (Tomlinson, et. al., 1967). Starvation is accompanied by a general atrophy of the gastrointestinal system. The change in gastrointestinal weight in a sockeye salmon (Oncorhynchus nerka) was from 90.5 g in the immature fish to 12 g in the spent fish (Berdyshev and Protsenko, 1972). The stomach contracts considerably, and loss of villi and degeneration of the muscle layers is widespread (Robertson and Wexler, 1960). Circular muscles atrophy, while the longitudinal muscles exhibit thickening and shrinkage. Pyloric caeca and the intestine also undergo shrinkage and the omentum shows almost total fat depletion (McBride, 1967).

The diffuse thyroid tissue scattered along the ventral aorta assists in the regulation of the basal metabolic rate (Lagler, et. al., 1962). During the spawning migration the follicular cells decrease in size, yet the follicles increase in size (Robertson, et. al., 1961a, McBride, 1967). Although a progressive vacuolization of the follicular colloid indicates high initial activity due to the profound metabolic changes in the salmon's body, a progressive decrease in activity parallels sexual maturation. Atrophic follicles, degeneration of the follicle walls, and loss of cytoplasm characterize the thyroid gland of the spent Pacific salmon (Robertson and Wexler, 1960). These degenerative changes coupled with decreasing activity may represent some type of functional exhaustion.

The spleen and the thymus tissue produce lymphocytes necessary for the immune system. Adrenal steroids have been shown to have a significant "anti-inflammatory effect" in mammals (Turner and Bagnara, 1971). The same may also be true for fishes (Chester Jones, et. al., 1969). This effect could possibly contribute to the very large decrease in the number of lymphocytes in the spleen and the involuting thymus gland which accompanies sexual maturation in the Pacific salmon. Lymphocytes may be nearly absent in these tissues in the spawning fish (Robertson and Wexler, 1960). Increasing fibrosis parallels the disappearance of lymphocytes from the spleen and thymus tissue.

The gonads of the spent Pacific salmon may exhibit deterioration. Nearly all the ova of chinook salmon mature at the same time (Robertson, et.al., 1961a), so there are only a few residual ova in the spent female. However, degenerating granulosa cells are found in the remaining ova of the spent female chinook salmon. Although spawning does not reduce the size of the testes to any appreciable extent (Donaldson and Fagerlund, 1970), vacuolization, loss of cytoplasm and disintegration occur in the cells lining the lobule walls of the testes (Robertson and

Wexler, 1960).

The skin thickens during maturation and the scales become absorbed. Epidermal thickening and scale absorption are normally 25% greater in males than in females. These changes seem to be associated with androgens. Through the use of methyltestosterone treatments, Yamazaki (1972) was able to produce skin changes in juvenile pink salmon (Oncorhynchus gorbuscha) and chum salmon (Oncorhynchus keta) similar to those found in adults. In addition to reddish-yellow skin coloration, the androgens resulted in mucous cell hypertrophy.

The heart muscle and vascular system show a moderate but progressive sclerosis as the fish matures (Robertson and Wexler, 1960). The number of red corpuscles decreases, but the remaining red blood cells hypertrophy and have a higher hemoglobin content than the immature fish (Robertson, et. al., 1961b). The sodium and potassium concentrations in the blood decrease significantly. Cholseterol levels show a moderate decrease. Triglycerides and total blood proteins (Donaldson and Fagerlund, 1969) show a similar drop to low levels. Patton (1970) suggested that the low triglyceride levels found in spawning pink salmon may indicate little available energy for muscles and vital organs.

The male Pacific salmon, like the pink salmon (Hart, 1973), develops a hooked snout and often a humped back as he becomes sexually mature. Calcitonin, produced in the ultimobranchial glands (Keutman, Parsons, and Potts, 1970), may be related to calcium regulation in the salmon. Watts, et. al., (1975) reported that the female sockeye salmon shows a slight progressive increase in plasma calcitonin and plasma calcium concentrations up to the time of spawning, at which time calcitonin levels drop. Males, however, show a steady decrease in plasma concentrations of both calcitonin and calcium. Before spawning, the calcitonin and calcium concentrations rapidly increase. The same workers hypothesized that the unusual morphological changes in the snout and the spine may be related to plasma calcitonin concentration changes.

ADULT MIGRATION OF STEELHEAD TROUT

The steelhead trout (Salmo gairdneri) makes a spawning journey comparable to that of the Pacific salmon and experiences similar morphological and physiological changes. Probably 50% of the steelhead survive their first spawning and undertake a migration back to the ocean. However, the percentage of repeat spawners is normally fairly low (Robertson and Wexler, 1962a), although in individual stream populations it may approach 35% in a particular year (Withler, 1966).

The pituitary gland of the steelhead trout has essentially the same structure as that of the Pacific salmon, but some differences are apparent (Robertson and Wexler, 1962a). Numerous acidophils arranged in columns, numerous undifferentiated cells, and very few basophils characterize the dorsal lobe of the immature steelhead trout. However, the ventral lobe is relatively larger than in salmon and occupies about 2/3 of the gland of the sexually immature fish. In addition, the pro-adenohypophysis covers the anterior portion of the ventral lobe. Thus the dorsal lobe in the immature steelhead is proportionately smaller than that of the salmon.

As the steelhead matures, the dorsal lobe enlarges and increased vascularization occurs. The basophilic gonadotrophs and acidophils increase in number, but undifferentiated cells are absent. The follicles in the dorsal lobe enlarge and some colloidal material, suggesting secretory activity, may be present in the follicles. The columnar structure of the ventral lobe changes to a new follicular structure and the entire lobe decreases in size.

The spawning steelhead trout exhibits a further increase in the size of the dorsal lobe, due to greater numbers of acidophils, basophils, and chromophobes. Vacuolization, degranulation, pycnosis, and cytolysis are found in many of the basophils of the dorsal lobe. Acidophils show similar but less pronounced alterations. The anterior lobe also may increase in size. The acidophils of the anterior lobe and the ventral lobe may exhibit changes similar to the acidophils of the dorsal lobe. Fibrosis of the ventral lobe was found in about 2/3 of the pituitaries of spawning steelhead (Robertson and Wexler, 1962a). However, "ghost cells" are not found in the neural lobe (Robertson and Wexler, 1962b). As in salmon, no sex differences were found in the amount of pituitary degeneration of steelhead trout (Robertson, et. al., 1961a).

The adrenal cortical tissue of the sexually maturing steelhead trout exhibits a hypertrophy similar to that of the salmon (Robertson and Wexler, 1959, Robertson, et. al., 1961a). The degree of degeneration in the spent steelhead is quite variable, but there appear to be no sex differences in the amount of degeneration (Hane and Robertson, 1959). Some fish exhibited very little degeneration, and mitoses were occasionally found in the interrenal tissue of the sexually mature steelhead (Robertson and Wexler, 1959). Plasma 17-hydroxycorticosteroid concentrations follow the same general pattern as in Pacific salmon, but lower concentrations are found in the steelhead trout (Hane and Robertson, 1959).

The kidneys may undergo moderate degeneration during the spawning migration. The primary deteriorative change seems to be degeneration of the tubular epithelium. Some edema of the glomeruli may also affect the kidneys. However, this degeneration is moderate compared to the changes taking place in the salmon (Robertson, et. al., 1961a).

Pycnosis, loss of cytoplasm, and disintegration of hepatic cells occur in focal patches in the liver of spawning steelhead. Again, the degeneration is less than in the spent Pacific salmon (Robertson, et. al., 1961a).

Possibly due to high glucose levels caused by high plasma 17-hydroxycorticosteroid concentrations, pancreatic islet cells hypertrophy in steelhead trout to about the same degree as in salmon. Beta cells normally outnumber the alpha cells in the spawning fish. Some degranulation of cells and degeneration may be present.

While salmon cease feeding during the spawning migration, steelhead have been known to feed occasionally. The gastrointestinal system undergoes shrinkage in the steelhead, but to a lesser degree than in salmon. The stomach of the spawning steelhead is characterized by loss of villi, but the epidermal cells do not show degeneration.

Although the thyroid tissue consists of large follicles during the migration, its activity remains at a low level. Basically, the thyroid undergoes no changes and can be considered normal for the duration of the migration (Robertson, et. al., 1961a).

The spleen of the steelhead trout undergoes changes nearly identical to those in migratory salmon. Lymphocytes are nearly absent and fibrosis of the spleen is general and quite severe. The thymus gland likewise shows a decrease in the number of lymphocytes, but the decrease is moderate compared to that in salmon.

Histological changes in the gonads of the steelhead differ with sex. The testes do not degenerate and appear normal in all respects. In more than 50% of the ovaries examined, degeneration of ova was present (Robertson, et. al., 1961a). Similar ovarian degeneration is noted in salmon.

An epidermal skin thickening and consequent scale absorption develops in the sexually mature steelhead trout in a manner similar to that of salmon. In addition, patches of fungus become established in the skin of both spent salmon and steelhead trout.

Cardiac muscle fibers exhibit vacuolization in the spawning steelhead trout. Occasional small hemorrhages or edema may be present. Although the degree of cardiac muscle degeneration is not as severe as in the salmon, lesions are common in the pancreatic arteries of the steelhead. This condition may be pronounced.

Changes in the blood of the spawning steelhead trout are similar to those in salmon. While the Pacific salmon shows higher plasma concentrations of 17-hydroxycorticosteroids and glucose, the steelhead has higher plasma levels of potassium and much higher levels of protein bound iodine. Female steelhead trout have the lowest cholesterol levels. Total blood proteins and red blood cell volume are very similar in both steelhead and salmon (Robertson, et. al., 1961a).

DISCUSSION

An examination of differences and similarities in the life histories and physiological changes taking place in salmon and steelhead trout may be useful in attempting to solve the problem of differences in post-spawning mortality in these two genera of fishes. The larger number of eggs produced by the steelhead poses an interesting question. For many different types of fishes, there exists an inverse correlation between the number of eggs laid and the probability of survival of the juvenile fish. If this relationship holds for salmonids, it would indicate slightly better chances of survival for the salmon than the steelhead. The percentages of egg fertilization and subsequent successful emergence from gravel are very similar for both types of fishes (Shapovalov and Taft, 1954). Size at time of

Table II. Length of fresh water residence of salmonid fishes.

Species	Average freshwater residence
* Chum salmon (*Oncorhynchus keta*)	Migrate almost immediately
* Pink salmon (*Oncorhynchus gorbuscha*)	1 to 2 months
' Coho salmon (*Oncorhynchus kisutch*)	1 year
* Chinook salmon (*Oncorhynchus tshawytscha*)	Several months to greater than 1 year
* Sockeye salmon (*Oncorhynchus nerka*)	1 to 2 years
' Steelhead trout (*Salmo gairdneri*)	1 to 4 years

* Hart (1973)

' Shapovalov and Taft (1954)

smoltification may be one of the most important factors related to subsequent survival. The amount of time spent in fresh water by salmonids (Table II) appears to be correlated with their size at smoltification. Although the length of fresh water residence varies greatly in steelhead, they are often larger than salmon smolts. The greater size seems to be related primarily to a longer fresh water residence, because the majority of steelhead undergo smoltification at 2 years of age. Growth rates are similar in steelhead and coho salmon (*Oncorhynchus kisutch*). Shapovalov and Taft (1954) reported that 1 year old steelhead and coho salmon smolts were comparable in size. The same workers suggested that larger size may be an advantage in escaping predators. This same study also revealed that the great majority of steelhead spawning for the first time and almost all of the repeat spawners were fish which had spent 2 years in fresh water prior to smoltification.

The ultimate survival of adult fish may depend on the development of particular physiological features during the juvenile phase of the life history. Proper functioning of the osmoregulatory mechanisms throughout a wide range of salinities could be of crucial importance to anadromous fishes. In addition to stimulating growth and increased utilization of fats, the increased thyroid activity noted during smoltification may be involved in chloride metabolism (Hoar and Bell, 1950). These same workers did not speculate on the mechanisms involved in these processes, but they did show a rough parallel between the degree of thyroid activity and the amount of time spent in fresh water by the juvenile fish. Smoltification presents greater energy demands and this results in increased adrenocortical steroid production. Holmes, et. al., (1963) have shown that an important effect of cortisol in rainbow trout involves sodium concentration regulation, primarily through extrarenal sodium excretion. An anadromous fish such as the steelhead trout which spends more time in fresh water than the juvenile Pacific salmon may be able to develop a more stable osmoregulatory system. During the spawning migration, adult Pacific salmon show several physiological changes which might be interpreted as some type of "osmoregulatory stress". Sodium levels decrease in the blood, but increase in the muscle tissue. Potassium levels decrease significantly in both the blood (Robertson, et. al., 1961b) and skeletal muscle (Tomlinson, et. al., 1967). The degree of variation from normal of these plasma constituents is much greater in Pacific salmon than in steelhead trout (Robertson, et. al., 1961a). Fagerlund (1967) reported that the highest cortisol concentrations were found in salmon with diseased gills. Since the gills are a major site of osmoregulation, these very high cortisol concentrations may be necessary to achieve normal osmotic balance. The acidophilic cells of the anterior lobe of the pituitary may be responsible for the production of prolactin (van Overbeeke and McBride, 1967). Although prolactin plays a major osmoregulatory role in many fishes, it appears to be secondary to adrenal steroids in salmonids. The acidophils of the dorsal lobe of salmon may exhibit moderate degeneration (greater than in steelhead) during the migration (Robertson and Wexler, 1962a), or they may undergo few cytoplasmic changes (Schreibman, Leatherland, andMcKeown, 1973). This suggests low activity for these cells, and a minor influence of prolactin in salmonid osmoregulation. Thyroxine may assist in osmoregulation (Gorbman, 1969). The degenerative histological changes and decreasing activity in the thyroid of the migrating Pacific salmon suggest a gradual loss of metabolic regulation and lessened osmoregulatory capabilities. While the thyroid may have a subordinate function in osmoregulation, the kidneys are important sites of sodium concentration regulation. The advancing kidney degeneration results in impaired osmoregulation. The changes in the Pacific salmon during the spawning migration suggest a decrease in the ability of the fish to achieve normal osmotic balance. However, a main argument against this line of reasoning comes from Robertson and Wexler (1960). They cite the case of the kokanee salmon (Oncorhynchus nerka kennerlyi). Although the kokanee spends its entire life in fresh water, it has a life history nearly identical to the sockeye salmon. The kokanee spends its adult life in a lake instead of the ocean. The histological changes which occur during the spawning migration in kokanee are identical to those in other salmon. In some cases (i.e., liver deterioration), the changes may be even more pronounced.

The massive pituitary degeneration in Pacific salmon may contibute substantially to their post-spawning mortality. Although about 2/3 of the steelhead trout exhibit pituitary degeneration, it is usually less pronounced than in mature salmon (Robertson, et. al., 1961a). The varying amount of pituitary degeneration appears to parallel the general physical condition of the steelhead. Degranulation (depletion of hormone) of the pituitary cells usually precedes the advancing degeneration (McBride and van Overbeeke, 1969). The dorsal lobe, which undergoes the greatest amount of deterioration, may be indicative of the general body condition. Some of the acidophils may produce a hormone similar to mammalian somatotropin, the growth hormone, while other acidophils are responsible for TSH production (van Overbeeke and McBride, 1967). The degenerative changes in these cells and the basophilic gonadotrophs suggest functional exhaustion. Perhaps the life history strategy of Paicfic salmon dictates that the final stage of life be characterized by a short period of intense pituitary secretory activity resulting in an outpouring of growth and gonad maturation hormones. The acidophils of the ventral lobe exhibit degeneration similar to those of the dorsal lobe. Although the function of these cells is not completely understood, van Overbeeke and McBride (1967) suggest that the ventral lobe may be involved in chromatophore regulation. Since Pacific salmon undergo extensive coloration changes during the spawning migration, these cells may deteriorate from hypersecretion. The chromophobes in the dorsal lobe present an interesting problem. Robertson and Wexler (1962b), on the basis of decreasing affinities for stains, regard them to be degranulated basophils. However, McBride and van Overbeeke (1969a) have suggested that some of them may be ACTH-producing adrenocorticotrophs.

Robertson and his co-workers (1959, 1960. and later studies) have proposed that the increasing 17-hydroxycorticosteroid concentrations are in the main responsible for the death of Pacific salmon. Due to their catabolic actions, cortisol and other adrenal steroids provide energy to the fish in situations of stress. The adrenocortical tissue of stressed immature salmon and steelhead trout undergoes rapid hypertrophy with a subsequent rise in plasma 17-hydroxycorticosteroid concentrations (Hane, et. al., 1966). The spawning migration creates intense energy demands in the form of production of eggs and spermatozoa, body metabolism, and the physical stress of migration. Since the salmon cease feeding during the migration, and steelhead feed only sporadically, these energy demands must be met by fat and protein reserves. Thus lack of food may be one of the major factors underlying increased 17-hydroxycorticosteroid levels. Spawning salmon may have lost 1/3 of their body weight (Patton, et. al., 1970). If this weight loss and other deteriorative changes are due to starvation, then feeding should prevent these changes. McBride, et. al., (1963) reported that fed sockeye salmon survived several months past the time when they normally would have died. The fish gained weight and exhibited the silvery green coloration characteristic of the immature fish, even though these were mature fish. However, feeding had no effect on other secondary sexual characteristics, such as the hooked snout of the male. Tomlinson, et. al., (1967) also showed that fed salmon survived longer, but muscle changes still occurred, primarily an increase in sodium and water content. In another study, McBride (1967) showed that feeding delayed or lessened some of the deteriorative changes that normally take place in the migrating salmon, but it did not prevent them. Muscle deterioration, pancreatic islet degeneration, and fat depletion of the omentum were nearly identical to unfed fish. The degeneration of pancreatic exocrine tissue and shrinkage of pyloric caeca were less drastic than in normal fish. Glomerulosclerosis of the kidney was delayed but not prevented. The thyroid tissue was the only site where degeneration was prevented, although the follicular colloid sometimes appeared vacuolated. Robertson, et. al., (1961a) showed that the nonmigratory rainbow trout, which feeds continually before and after spawning, exhibits adrenal hypertrophy and degeneration, although this is quite mild in comparison with that of the salmon or the steelhead. This would suggest that starvation may only accelerate interrenal hypertrophy, but it is probably not the main causative agent.

A definite difference of opinion exists as to what factors control the production of adrenal steroids. ACTH may regulate interrenal tissue through a negative feedback process (Fagerlund and McBride, 1969). Donaldson and McBride (1967) removed the pituitary from rainbow trout and reported a marked decrease in cortisol concentrations one day after the operation. This decrease paralleled interrenal cell atrophy. Hane, et. al., (1966) injected ACTH into steelhead trout at various times during the spawning migration. The response (measured by plasma 17-hydroxycorticosteroid concentrations) was very high during all phases of the migration. Immature salmon also have a very high response (Fagerlund, 1970), but the response progressively decreases as sexual maturation progresses. The spawning male salmon shows no response to ACTH. Donaldson and McBride (1974) injected ACTH from chinook salmon into gonadectomized sockeye salmon. Stimulation of the interrenal tissue followed. These studies suggest that adrenal cortical steroid production may be under pituitary control in the steelhead trout, but pituitary regulation declines in salmon as the spawning migration progresses.

A large body of evidence indicates that the gonadal hormones may be responsible for the interrenal hypertrophy and subsequent drastic increase in plasma 17-hydroxycorticosteroid concentrations. When Donaldson and McBride (1974) injected gonadotropin into the gonadectomized sockeye salmon, there was no stimulation of the interrenal tissue. This is to be expected, since there was no possibility of gonadal influence in this experiment. Hane, et. al., (1966) noted that increased adrenal cortical activity in salmon and steelhead appeared only after the gonads began to develop. Gonadectomy of the mature female sockeye salmon results in an involution of the interrenal tissue (McBride and van Overbbeke, 1969b). Adrenal cortical steroid levels are similar to those of the immature fish, i.e., 1/4 that of the spawning fish (Fagerlund and Donaldson, 1970). Injection of androgens into a gonadectomized male sockeye salmon leads to a general interrenal hypertrophy with frequent hemorrhaging and nuclear pycnosis. Estrogens may have a more potent effect than androgens. The spawning female may have concentrations twice that of the spawning male (Fagerlund and Donaldson, 1970). Estrogens may affect the metabolism and excretion of corticosteroids (Hane, et. al., 1966). Although females have lower secretion rates, the slower MCR of adrenal steroids in females results in higher plasma concentrations. A gonadectomized sockeye salmon has a lower cortisol MCR than an intact fish (Donaldson and Fagerlund, 1972). Androgens may increase the MCR of adrenal steroids. Fagerlund and Donaldson (1969) noted a definitive increase in the metabolic clearance rate of cortisol after injections of androgens into the gonadectomized sockeye salmon.

Although nonmigratory rainbow trout normally feed duing sexual maturation and spawning, Hill and Fromm (1968) have shown that cortisol maintains normal glycogen levels and energy if the fish is forced to fast. Adrenocortical tissue in the immature rainbow trout is similar to that of the immature salmon. Maturation results in a mild hypertrophy with occasional vacuolated nuclei, but plasma concentrations of 17-hydroxycorticosteroids remain low. Robertson, et. al., (1963) treated fasting immature rainbow trout with hydrocortisone. The administered doses were comparable to those found in mature Pacific salmon. The resulting histological changes were very similar to those in maturing salmon. In some cases, such as loss of muscle fibrils, the changes were more pronounced than in salmon.

These studies give support to the idea that starvation aggravates the general catabolic action of adrenal cortical steroids which result in massive histological alterations in maturing Pacific salmon (Donaldson and Fagerlund, 1969, McBride and van Overbeeke, 1969b, Robertson and Wexler, 1962a, Robertson, et. al., 1963). The increasing plasma concentrations of 17-hydroxycorticosteroids rapidly deplete the energy stores of the migrating salmonids. An impaired metabolism of adrenal steroids may contribute significantly to this condition. In normal steroid metabolism, cortisol is rapidly converted to cortisone (Donaldson and Fagerlund, 1968). Although the primary function of the kidney of the migrating salmon is involved with salt conservation and water excretion (Miles, 1970), it may also be a major excretory site of cortisol, while the liver may be important in cortisone excretion (Donaldson and Fagerlund, 1972). Both of these tissues undergo extensive degeneration during the spawning migration, and this will hinder their ability to function properly. Idler, et. al., (1963) suggested that an impaired metabolic clearance rate of adrenal steroids may be a sign of approaching mortality.

Gonadectomy of the mature sockeye salmon results in a return to an immature condition. Robertson (1961) was able to double the life span of kokanee salmon by gonadectomizing them when they were immature. These fish continued to gain weight and showed neither adrenal hypertrophy nor scale absorption when they reached the age where the controls had matured and died. Gonadectomy of mature fish had little effect on prolonging life span. In an earlier study, Robertson (1957) reported that sexually precocious male chinook salmon are able to survive spawning. These fish were approximately 10 months of age and exhibited normal spermatogenesis and produced viable spermatozoa. However, they differed markedly from the majority of the adult spawners, which normally mature at 3-5 years of age. First, these mature parr were observed actively feeding before and after spawning. In addition, the usual secondary sexual characteristics were absent. The only major histological alteration was a fibrosis resembling scar tissue in the septa of the testes lobules. General pituitary activity was low, although there were many more basophils than in the adult (Robertson and Wexler, 1962b). No pituitary degeneration occurred before or after the artificial spawning to which these fish were subjected. These studies indicate that a combination of gonadal maturation and age are probably quite important in the post-spawning mortality of Pacific salmon. Pituitary changes in maturing salmon are very similar to those in aging mammals (Robertson and Wexler, 1962b). Rapid aging and the histological alterations taking place during the migration may be responsible for the death of Pacific salmon (Robertson and Wexler, 1960).

McBride (1967) noted that the mature salmon readily ate euphausids. This observation leads to the question of why Pacific salmon cease feeding during their spawning migration. They readily took food normally found in a marine environment. Cessation of feeding in fresh water may reflect an inadequate food supply. The life history strategy of one spawning is unusual and could be detrimental. Several consecutive years of unfavorable environmental conditions could lead to poor juvenile survival and virtually abolish future migrations. However, the salmon seem to have evolved in a direction of putting all their energy into the production of vigorous eggs. Thus, it seems that for Pacific salmon, the production of eggs and juveniles tolerant to fluctuating environmental conditions is more advantageous than post-spawning survival of adults.

CONCLUSION

The spawning migration of Pacific salmon is characterized by profound histological and physiological alterations. Similar changes occur in the steelhead trout, although many of these are less drastic than those in salmon (Table III). None of these alterations are necessarily fatal in themselves, but the combination of all them together is probably sufficient to cause death. Survival of steelhead may be proportional to the intensity of these changes. The small percentages of repeat spawners indicates high mortality during downstream migration or in the ocean. It is quite possible that, even though these fish survived spawning, the histological and physiological changes taking place during the migration leave the fish in such a weakened state that they are unable to survive for an extended period of time.

The pituitary, kidney, and liver degeneration of Pacific salmon are probably the most serious combination of detrimental factors leading to their death. Although the exact cause for this degeneration is unknown, the very high 17-hydroxycorticosteroid concentrations appear to be the primary factor. In addition to general catabolic actions, the adrenal steroids, particularly cortisol, are important in osmoregulation. The abnormally high levels of cortisol in salmon may result in a hyperactive osmoregulation system which eventually breaks down. The degenerating kidney will contribute to this condition.

There have been few studies on the effects of adrenal steroids on blood cells in fish. Whether the breakdown in resistance to bacterial and fungal attacks during the spawning migration is due to skin changes, some type of "anti-inflammatory" effect of adrenal steroids, or a combination of these is undetermined at present. Spawning salmon are often covered with fungal patches and the gills may be heavily

Table III. Comparison of histological alterations in spawning rainbow trout, nonmigratory and migratory, and spawning salmon.

	Rainbow trout		
	Nonmigratory	Migratory (steelhead)	Salmon*
Post-spawning mortality	low	circa 50%	100%
Pituitary degeneration	slight	moderate	marked
Adrenocortical tissue			
a. hyperplasia	mild	marked	marked
b. degeneration	mild	moderate	marked
Skin increased thickness	moderate	marked	marked
Scales absorption	present	present	present
Stomach	normal	loss of villi only	atrophy and degeneration
Liver degeneration	slight	moderate	marked
Spleen			
a. lymphocyte depletion	moderate	marked	marked
b. increased connective tissue	marked	marked	marked
Thymus lymphocyte depletion	moderate	moderate	marked
Kidney degeneration	none	moderate	marked
Pancreas islet hypertrophy	marked	marked	marked
Thyroid	normal	normal	atrophy and degeneration
Testis degeneration	none	none	marked
Ova degeneration	none	present	present (few residual ova)
Cardiovascular degeneration	mild	moderate	marked

Robertson, et. al., (1961a)

* Robertson and Wexler (1960)

diseased. This could result in suffocation of individual fish.

The factors causing an increase in 17-hydroxycorticosteroid concentrations may be varied. If starvation is not the major cause, it certainly contributes to the general deterioration of the anadromous salmonids. Hormones are known for a variety of effects and endocrine interrelationships are most complex. However, these studies indicate gonadal maturation may be the prime stimulus for adrenal hypertrophy. If the effect is direct, this could help to explain the higher plasma concentrations found in salmon, since female salmon have an average gonosomatic index of over 20, and the female steelhead trout have an average gonosomatic index less than 20. Gonosomatic indices are comparable in males. The difference in the resulting adrenal steroid levels could represent the maximum tolerance limit of cells to adrenal steroids.

Since the effects of adrenal steroids are so varied, the method of action at the cellular level remains unsolved (Turner and Bagnara, 1971). Berdyshev and Protsenko (1972) suggested that the steroids may increase the permeability of lysosomal membranes, allowing DNAase to escape into the cell. This could explain the nuclear pycnosis so commonly observed in degenerating cells. Loss of cellular control and cytolysis would follow destruction of the DNA. The ability of the cell to withstand these deteriorative changes could be dependent upon adrenal cortical steroid levels. Very high levels, such as found in the Pacific salmon, may lead to marked degeneration, while levels somewhat lower, found in steelhead trout, may not preclude cellular integrity and subsequent regeneration. Complete elucidation of this problem rests on studies involving: (a) the method of action of steroid hormones on individual cells, and (b) the relationships and actions of androgens and estrogens on salmonid adrenocortical cells.

BIBLIOGRAPHY

Berdyshev, G. D., and N. A. Protsenko. (1972). Current theories on the mechanisms of the post spawning death of Pacific salmon. Hydrobiol. J., 8(4): 85-94.

Chester Jones, I., D. K. O. Chan, I. W. Henderson, and J. N. Ball. (1969). The adrenocortical steroids, adrenocorticotrophin, and the corpuscles of Stannius, pp. 321-376. In "Fish Physiology" (W. S. Hoar and J. D. Randall, eds.). Vol. 2. Academic Press, New York.

Chester Jones, I., J. N. Ball, I. W. Henderson. T. Sandor. and B. I. Baker. (1974). Endocrinology of fishes, pp. 523-593. In "Chemical Zoology" (M. Florkin and B. T. Scheer, eds.). Vol. VIII, Academic Press, New York.

Crim, L. N., R. K. Meyer, and E. M. Donaldson. (1973). Radioimmunoassay estimates of plasma gonadotropin levels in spawning pink salmon. Gen. Comp. Endocrinol., 21: 69-76.

Donaldson, E. M., and U. H. M. Fagerlund. (1968). Changes in the cortisol dynamics of sockeye salmon (Oncorhynchus nerka) resulting from sexual maturation. Gen. Comp. Endocrinol., 11: 552-561.

Donaldson, E, M., and U. H. M. Fagerlund. (1969). Cortisol secretion rate in gonadectomized female sockeye salmon (Oncorhynchus nerka): effects of estrogen and cortisol treatment. J. Fish. Res. Bd. Canada, 26: 1789-1799.

Donaldson, E. M., and U. H. M. Fagerlund. (1970). Effect of sexual maturation and gonadectomy at sexual maturity on cortisol secretion rate in sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada, 27: 2287-2296.

Donaldson, E. M., and U. H. M. Fagerlund. (1972). Corticosteroid dynamics in Pacific salmon. Gen. Comp. Endocrinol., Supplement 3: 254-265.

Donaldson, E. M., and J. R. McBride. (1967). The effects of hypophysectomy in the rainbow trout (Salmo gairdneri Rich.) with special reference to the pituitary-interrenal axis. Gen. Comp. Endocrinol. 9: 93-101.

Donaldson, E. M., and J. R. McBride. (1974). Effect of ACTH and salmon gonadotropin on interrenal and thyroid activity of gonadectomized adult sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada, 31: 1211-1214.

Fagerlund, U. H. M. (1967). Plasma cortisol concentrations in relation to stress in adult sockeye salmon during the fresh water stage of their life cycle. Gen. Comp. Endocrinol., 8: 197-207.

Fagerlund, U. H. M. (1970). Response to mammalian ACTH of the interenal tissue of sockeye salmon (Oncorhynchus nerka) at various stages of sexual maturation. J. Fish. Res. Bd. Canada, 27: 1169-1172.

Fagerlund, U. H. M., and E. M. Donaldson. (1969). The effects of androgens on the distribution and secretion of cortisol in gonadectomized male sockeye salmon (Oncorhynchus nerka). Gen. Comp. Endocrinol., 12: 438-448.

Fagerlund, U. H. M., and E. M. Donaldson. (1970). Dynamics of cortisone secretion in sockeye salmon (Oncorhynchus nerka) during sexual maturation and after gonadectomy. J. Fish. Res. Bd. Canada, 27: 2323-2331.

Fagerlund, U. H. M., and J. R. McBride. (1969). Suppression by dexamethasone of interrenal activity in adult sockeye salmon (Oncorhynchus nerka). Gen. Comp. Endocrinol., 12: 651-657.

Gorbman, A. (1969). Thyroid function and its control in fishes, pp. 241-274. In "Fish Physiology" (W. S. Hoar and J. D. Randall, eds.). Vol. 2. Academic Press, New York.

Hane, S., and O. H. Robertson. (1959). Changes in plasma 17-hydroxycorticosteroids accompanying sexual maturation and spawning of the Pacific salmon (Oncorhynchus tshawytscha) and rainbow trout (Salmo gairdneri). Proc. Nat. Acad. Sci., 45: 886-893.

Hane, S., O. H. Robertson, B. C. Wexler, and M. A. Krupp. (1966). Adrenocortical response to stress and ACTH in Pacific salmon (Oncorhynchus tshawytscha) and steelhead trout (Salmo gairdneri) at successive stages in the sexual cycle. Endocrinology, 78: 791-800.

Hart, J. L. (1973). Pacific fishes of Canada. Fish. Res. Bd. Canada, Bulletin 180: 740 pp.

Hill, C. W., and P. O. Fromm. (1968). Response of the interrenal gland of rainbow trout (Salmo gairdneri) to stress. Gen. Comp. Endocrinol., 11: 69-77.

Hoar, W. S., and G. Mary Bell. (1950). The thyroid gland in relation to the seaward migration of the Pacific salmon. Can. J. Zool., 28: 126-136.

Holmes, W. N., J. G. Phillips, and I. Chester Jones. (1963). Adreonocortical factors associated with adaptation of vertebrates to marine environments. Rec. Prog. in Hormone Res., 19: 619-672.

Idler, D. R., B. Truscott, et. al., (1963). In vivo metabolism of steroid hormones by sockeye salmon. Can. J. Biochem. Physiol., 41: 875-887.

Keutman, H. T., J. A. Parsons, and J. T. Potts, Jr. (1970). Isolation and chemical properties of two calcitonins from salmon ultimobranchial glands. J. Biol. Chem., 245: 1491-1496.

Lagler, K. F., J. E. Bardach, and R. R. Miller. (1962). Ichthyology. John Wiley and Sons, Inc., New York.

McBride, J. R. (1967). Effects of feeding on the thyroid, kidney, and pancreas in sexually ripening adult sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada, 24: 67-76.

McBride, J. R., and A. P. van Overbeeke. (1969a). Cytological changes in the pituitary gland of the adult sockeye salmon (Oncorhynchus nerka) after gonadectomy. J. Fish. Res. Bd. Canada, 26: 1147-1156.

McBride, J. R., and A. P. van Overbeeke. (1969b). Hypertrophy of the interrenal tissue in sexually maturing sockeye salmon (Oncorhynchus nerka) and the effect of gonadectomy. J. Fish. Res. Bd. Canada, 26: 2975-2985.

McBride, J. R., U. H. M. Fagerlund, M. Smith, and N. Tomlinson. (1963). Resumption of feeding by and survival of adult sockeye salmon (Oncorhynchus nerka) following advanced gonad development. J. Fish. Res. Bd. Canada, 20: 95-100.

Miles, H. McC. (1970). Renal function in migrating adult coho salmon. Diss. Abstr. Int., 30B: 5213.

Patton, S., G. F. Crozier, and A. A. Benson. (1970). Serum lipids and the death of spawning Pacific salmon. Nature (London), 225: 754-755.

Robertson, O. H. (1957). Survival of precociously mature King Salmon male parr (Oncorhynchus tshawytscha juv.) after spawning. California Fish and Game, 43: 119-130.

Robertson, O. H. (1961). Prolongation of the life span of kokanee salmon (Oncorhynchus nerka kennerlyi) by castration before beginning of gonad development. Proc. Nat. Acad. Sci., 47: 609-621.

Robertson, O. H., and B. C. Wexler. (1959). Hyperplasia of the adrenal cortical tissue in Pacific salmon (Genus Oncorhynchus) and rainbow trout (Salmo gairdneri) accompanying sexual maturation and spawning. Endocrinology, 65: 225-238.

Robertson, O. H., and B. C. Wexler. (1960) Histological changes in the organs and tissues of migrating and spawning Pacific salmon (genus Oncorhynchus). Endocrinology, 66: 222-239.

Robertson, O. H., and B. C. Wexler. (1962a). Histological changes in the pituitary gland of the rainbow trout (Salmo gairdneri) accompanying sexual maturation and spawning. J. Morphol., 110: 157-169.

Robertson, O. H., and B. C. Wexler. (1962b). Histological changes in the pituitary gland of the Pacific salmon (genus Oncorhynchus) accompanying sexual maturation and spawning. J. Morphol., 110: 171-185.

Robertson, O. H., et. al. (1961a). Hyperadrenocorticism in spawning migratory and non-migratory rainbow trout (Salmo gairdneri); comparison with Pacific salmon (Genus Oncorhynchus). Gen. Comp. Endocrinol., 1: 473-484.

Robertson, O. H., et. al. (1961b). Physiological changes occurring in the blood of the Pacific salmon (Oncorhynchus tshawytscha) accompanying sexual maturation and spawning. Endocrinology, 68: 733-745.

Robertson, O. H., et. al. (1963). The effect of hydrocortisone on immature rainbow trout (Salmo gairdneri). Gen. Comp. Endocrinol., 3: 422-436.

Schreibman, M. P., J. F. Leatherland, and B. A. McKeown. (1973). Functional morphology of the teleost pituitary gland. Amer. Zool., 13: 719-742.

Shapovalov, L., and A. C. Taft. (1954). The life histories of steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch). Calif. Dept. Fish. Game. Bull., 98: 373 pp.

Tomlinson, N., J. R. McBride, and S. E. Geiger. (1967). The sodium, potassium, and water content of the flesh of sockeye salmon (Oncorhynchus nerka) in relation to sexual development and starvation. J. Fish. Res. Bd. Canada, 24: 243-248.

Trams, E. G. (1969). Neurochemical observations on spawning Pacific salmon. Nature, 222: 492-493.

Turner, C. D., and J. T. Bagnara. (1971). General Endocrinology. W. B. Saunders Company, Philadelphia.

van Overbeeke, A. P., and J. R. McBride. (1967). The pituitary gland of the sockeye (Oncorhynchus nerka) during sexual maturation and spawning. J. Fish. Res. Bd. Canada, 24: 1791-1809.

van Overbeeke, A. P., and J. R. McBride. (1971). Histological effects of 11-ketotestosterone, 17α-Methyltestosterone, Estradiol, Estradiol cypionate, and cortisol on the interrenal tissue, thyroid gland, and pituitary gland of gonadectomized sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Canada, 28: 477-484.

Watts, E. G., D. H. Copp, and L. J. Deftos. (1975). Changes in plasma calcitonin and calcium during the migration of salmon. Endocrinology, 96: 214-218.

Withler, I. L. (1966). Variability in life history characteristics of steelhead trout (Salmo gairdneri) along the Pacific coast of North America. J. Fish. Res. Bd. Canada, 23: 365-393.

Yamazaki, F. (1972). Effects of Methyltestosterone on the skin and gonads of salmonids. Gen. Comp, Endocrinol., Supplement 3: 741-750.