Environmental Factors Affecting Smoltification and Early Marine Survival of Anadromous Salmonids

GARY A. WEDEMEYER, RICHARD L. SAUNDERS,
and W. CRAIG CLARKE

Gary A. Wedemeyer is with the U.S. Fish and Wildlife Service, National Fisheries Research Center, Bldg. 204, Naval Support Activity, Seattle, WA 98115. Richard L. Saunders is with the Fisheries and Environmental Sciences Biological Station, Department of Fisheries and Oceans, Canada, St. Andrews, New Brunswick, Canada E0G 2X0. W. Craig Clarke is with the Pacific Biological Station, Resource Services Branch, Department of Fisheries and Oceans, Nanaimo, B.C., Canada V9R 5K6.

Introduction

A perennial problem in the efficient use of artificially propagated juveniles in salmon enhancement programs and in aquaculture is that ocean survival often has been below estimated survival of naturally produced smolts even though hatcheries can consistently outperform nature in survival through the hatching and early developmental stages. For example, Saunders and Allen (1967) estimated that survival to adults of wild, unmarked Atlantic salmon, *Salmo salar,* smolts in the Miramichi River, New Brunswick, was no less than 8 percent and possibly as high as 32 percent. Allowing for the detrimental effects of tagging, few plantings of hatchery Atlantic salmon have come close to these values, although survival of hatchery coho salmon, *Oncorhynchus kisutch,* to adults can be as high as 45 percent under optimal conditions;[1] however, it is more often less than 10 percent. Experience in both Europe and North America shows that, within limits, survival through to adult returns tends to be directly proportional to size-at-release (Carlin, 1969; Ritter, 1972; Peterson, 1973). Accordingly, most hatcheries release large smolts in an attempt to increase contribution to the fishery and returns to the hatchery. However, Bilton (1978) has shown that release of very large coho smolts caused an increased incidence of precocious males and reduced adult returns.

ABSTRACT—An important requirement in the efficient use of artificially propagated juveniles for salmon enhancement programs is that the resulting smolts be fully prepared behaviorally and physiologically to migrate to sea and continue to grow and develop normally. In this paper, physiological criteria for identifying fully functional smolts are presented and environmental factors are identified which will influence smoltification, and thus early marine survival. Methods are described for optimizing time, age, and size at release, and data are presented on methods of environmental manipulation to alter smoltification to fit specific resource management needs. On the basis of our present understanding of the physiology of the parr-smolt transformation and of the influence of environmental alterations during rearing, guidelines are presented for management strategies to improve survival of Pacific, Oncorhynchus *sp., and Atlantic salmon,* Salmo salar, *and anadromous (steelhead) rainbow trout,* Salmo gairdneri.

There is reason to suspect that in many cases apparently healthy hatchery fish, though large and silvery, are not actually functional smolts and their limited contribution to the fishery, even when stocked into the same rivers from which their parents were taken, results from their being unprepared to go to sea. This failure to produce good quality smolts probably arises from an incomplete understanding of exactly what constitutes a smolt, as well as from a lack of understanding of the environmental influences that affect the parr-smolt transformation and which may lead, as a long term consequence, to reduced ocean survival. There are many case histories describing poor performance following release of juveniles which, although clinically healthy and large enough to be smolts, apparently did not have complete smolt physiology and behavior. Gudjonsson (1972) reported that initial attempts to produce yearling Atlantic salmon in an Icelandic hatchery supplied with heated (geothermal) water resulted in the release of large healthy juveniles but no adult returns. Many remained in the stream during the summer following release. These ''smolts'' had been reared indoors under a constant, artificial light photoperiod and did not show normal migratory behavior. However, a similar group that had been held outside the hatchery under a natural (increasing) photoperiod showed normal migratory behavior and good adult returns. Subsequent work with natural or artificial light under a simulated natural photoperiod resulted in normal migration and adult returns (Isaksson, 1973, 1974, 1976).

A second case history report of detrimental environmental effects occurred at the Craig Brook (Maine) National Fish Hatchery.[2] In this case, Atlantic salmon in open, shallow raceways became silvery and showed smolt behavior as early as February. Subsequently many fish developed dorsal epidermal lesions and died. This condition is often referred to as ''sunburn.'' Releasing the surviving fish in late May, the usual smolt release time, gave few adult returns. This problem was overcome by shielding the raceways from direct sunlight.

In these two examples involving Atlantic salmon, poor smolt development probably resulted from an unnat-

---

[1] H. T Bilton and T. Alderdice, Research Scientists, Pacific Biological Station, Nanaimo, B.C., Canada, pers. commun. June 1979.

[2] Roger Dexter, Fishery Biologist, U.S. Fish and Wildlife Service, Craig Brook National Fish Hatchery, Orland, Maine, pers. commun. February 1979.

ural day length (photoperiod) and from high light intensity, respectively.

This review paper will describe the physiological and behavioral criteria used to distinguish Atlantic and Pacific (*Oncorhynchus* sp.) salmon, and steelhead trout, *Salmo gairdneri*, smolts from parr; discuss the influences of environmental conditions on smoltification and subsequent early marine survival; and conclude with guidelines for management strategies to maximize survival and potential contribution to the fishery.

Physiological and Behavioral Criteria for Smolt Status

Body Silvering, Fin Darkening

A summary of the physiological changes occurring during the parr-smolt transformation of anadromous salmonids is given in Table 1. Among the many changes which occur, the external body silvering, and fin margin blackening (in Atlantic salmon, coho salmon, and steelhead trout) are among the most dramatic characteristics used to distinguish smolts from parr. The silvery color results from deposition of guanine and hypoxanthine crystals in the skin and scales. These are products of protein catabolism and their seasonal appearance reflects changes in the dynamics of protein metabolism. Early studies showed that thyroid hormone was somehow involved in the silvering process (Landgrebe, 1941). Piggins (1962) found that feeding beef thyroid gland resulted in body silvering of Atlantic salmon parr. Dodd and Matty (1964) reported that alevins (Atlantic salmon) would become silvery if thyroxine was added to the water. Cortisol has also been demonstrated to cause silvering in the eel, *Anguilla anguilla* (Epstein et al., 1971; Olivereau, 1972). Johnston and Eales (1970) found that silvering during smoltification of Atlantic salmon is greater on large than on small parr and that water temperature influences silvering more than photoperiod. In naturally produced Atlantic salmon smolts, particularly, the caudal and pectoral fin margins become black. This characteristic helps to differentiate silvery parr, often seen in the early part of the out-migrant run, from true smolts. However, coloration by itself is not an adequate criterion for smolting in either Atlantic or Pacific salmon, especially in hatchery fish. Though silvering and fin blackening may be a good indication of smolt status in wild fish, these colors often develop in hatchery parr when the fish are not otherwise smoltlike. Clearly, additional physiological criteria are necessary.

Table 1.—Physiological changes occurring during the parr-smolt transformation of Pacific (*Oncorhynchus* sp.) and Atlantic salmon, *Salmo salar*, and steelhead trout, *Salmo gairdneri*. All of these changes must be properly coordinated to ensure adequate smolt functionality and health.

Physiological characteristics	Level in smolts compared with parr
Body silvering, fin margin blackening	Increases
Hypoosmotic regulatory capability	Increases
Salinity tolerance and preference	Increases
Weight per unit length (condition factor)	Decreases
Growth rate	Increases
Body total lipid content	Decreases
Oxygen consumption	Increases
Ammonia production	Increases
Liver glycogen	Decreases
Blood glucose	Increases
Endocrine activity	Increases
Thyroid (T_4)	
Interrenal	
Pituitary growth hormone	
Gill microsome, Na^+, K^+-ATPase enzyme activity	Increases
Ability to grow well in full-strength (35‰) sea-water	Increases
Buoyancy (swim bladder, Atlantic salmon)	Increases
Migratory behavior	Increases

Hypoosmotic Regulatory Capability, Salinity Tolerance, and Preference

Perhaps the major physiological process of the smolting phenomenon is the increase in hypoosmoregulatory ability which preadapts the fish to life in seawater (Folmar and Dickhoff, in press). Associated ionoregulatory changes have long been recognized to occur in fresh water and include a decrease in plasma and tissue chloride (Fontaine, 1951; Houston, 1960; Houston and Threadgold, 1963), a decrease in glomerular filtration rate (Holmes and Stainer, 1966), and, more recently, a dramatic increase in gill Na^+, K^+-ATPase activity (Zaugg and McLain, 1970; McCartney, 1976; Saunders and Henderson, 1978). However, salinity tolerance or ability to survive in seawater cannot by itself be used to distinguish smolts from parr. Juvenile steelhead trout and coho and Atlantic salmon develop seawater tolerance before the smolting process is complete (Conte and Wagner, 1965; Conte et al., 1966; Wagner, 1974b; Farmer et al., 1978). Nevertheless, the hypoosmoregulatory ability of parr can be distinguished, physiologically, from that of true smolts during the process of adaptation to seawater (Parry, 1960; Houston, 1959, 1961; Clarke and Blackburn, 1977, 1978). Recently, Komourdjian et al. (1976a) and Saunders and Henderson (1978) showed that a challenge with high salinity (40‰) reveals a degree of salinity tolerance in Atlantic salmon smolts that is undeveloped before smoltification and which is an excellent indication of smolt status and preparedness for hypoosmotic regulation.

Salinity tolerance is also influenced by size (Parry, 1960). In species such as Atlantic salmon, steelhead trout, and coho salmon, hypoosmoregulatory capacity increases with growth until smolting occurs. However, if the smolts are prevented from entering seawater, their ability to adapt to it then decreases, despite continued growth (Evropeitseva, 1957; Koch, 1968; Zaugg and McLain, 1970). This phenomenon (designated as desmoltification in freshwater, parr-reversion in salt water) has been suggested as one reason for the frequently lower growth rates of landlocked compared with sea-run salmon (Koch, 1968; Saunders and Henderson, 1969). However, Saunders and Henderson (1969) observed a growth rate inversely related to salinity and no increased mortality of Atlantic salmon held past the smolt stage in freshwater. They concluded that stunting of landlocked Atlantic salmon was more likely due to inadequate food supply in fresh water than to salinity per se. In "non-smolting" species such as nonanadromous rainbow trout, *Salmo gairdneri*, continued growth appears to confer increased seawater adaptive efficiency (Houston, 1961; Landless and Jackson, 1976).

The seasonal increase in salinity tolerance of salmonids is well known, and peak hypoosmotic regulatory capability generally is thought to coincide with smolt migratory behavior. Periodic seawater challenge tests have demonstrated that the hypoosmoregulatory ability of juvenile Atlantic, as well as coho salmon, peaks at the time of smolting (Komourdjian et al., 1976b; Boeuf et al., 1978; Clarke and Blackburn, 1978). On the other hand, certain populations of anadromous salmonids may initiate migration before they are able to adapt to full strength seawater (Clarke and Blackburn, 1978). However, smolting is a necessary prerequisite for juvenile salmon to continue to grow well after conversion to seawater. Saunders and Henderson (1970) observed supressed feeding behavior and growth of juvenile Atlantic salmon transferred to seawater after being exposed to an unnatural photoperiod regimen, which disrupted the smolting process. Similarly, transfer of juvenile coho salmon to seawater before they are fully smolted causes dramatic suppression of growth; these stunted fish also show a number of endocrine abnormalities (Clarke and Nagahama, 1977).

Houston (1960) reported reduced tissue Na^+ concentrations in Atlantic salmon at the time of smolting. Fontaine (1951) found low tissue Cl^- levels, while Houston and Threadgold (1963) noted increased tissue water content at smolting; both indicative of a shifting pattern of water and ion regulation. These observations suggested that a Na^+,Cl^- pump had begun operation while the fish were still in fresh water. Houston and Threadgold (1963) noted an increase in number and apparent activity of the Keys-Willmer (chloride) cells of salmon in seawater. Van Dyck (1966) found increased activity of Keys-Willmer cells during smolting and decreased activity during desmoltification if the salmon were not allowed to migrate. Hoar (1951) reported that injection of mammalian anterior pituitary extract in Atlantic salmon parr resulted in stimulation of these supposed Cl^- secretory cells.

Growth Rate, Condition Factor

Two other features which have proven to be helpful indicators of smolt status are growth rate and condition factor. Saunders and Henderson (1970) and Komourdjian et al. (1976b) showed that Atlantic salmon smolts, whether naturally smolted or induced to smolt by manipulation of photoperiod, have a higher growth rate than nonsmolts. Komourdjian et al. (1976a) also showed that salmon parr which had received injections of porcine growth hormone every other day for 4 weeks showed both increased growth rates and greater salinity tolerance than placebo injected controls. The use of condition factor as an indicator of smolt status is based on the fact that the length-weight relation is typically low in wild smolts; that is, smolts typically weigh less per unit length than do parr. Wagner (1974a) has successfully used decreased condition factor as a criterion of smolting in steelhead trout. Saunders and Henderson (1970) and Komourdjian et al. (1976a) found that the condition factor of Atlantic salmon also decreased at the time of smolting or as a result of growth hormone injection.

Body Composition, Lipid-Moisture Dynamics, Carbohydrate Metabolism

Another physiological change during smoltification, which has long been used as a criterion, is the reduction in total body lipid. This is undoubtedly related to the other metabolic parameters which show characteristic alterations during the parr-smolt transformation. Recently, Komourdjian et al. (1976b) have demonstrated this effect in Atlantic salmon induced to smoltify during winter by artificially increased day length. Total lipid content was significantly lower than in the nonsmolted controls held under a simulated natural photoperiod. The criteria of smolting used were silvering, growth rate, salinity tolerance, and increase in number and apparent activity of pituitary growth hormone cells as revealed by histological examination. Coincident with falling lipid levels, total moisture content increases during smoltification (Komourdjian et al., 1976b; Farmer et al., 1978; Saunders and Henderson, 1978). Reduced lipid and increased moisture content probably reflect metabolic changes that accompany smolting. Withey and Saunders (1973) confirmed experimentally that photoperiod manipulation to retard smoltification resulted as well in lower standard oxygen consumption rates, compared with fish of similar age under natural photoperiods.

An altered carbohydrate metabolism is also characteristic of the parr-smolt transformation. Early work by Fontaine and Hatey (1950) and Malikova (1957) showed that reduced liver glycogen accompanied an accelerated protein and lipid catabolism. More recently, Wendt and Saunders (1973) found both reduced liver glycogen and elevated blood glucose levels in hatchery reared Atlantic salmon during smoltification. At the same time of year, the salmon parr had high liver glycogen levels, low blood glucose, and, unlike smolts, survived transport without sharp reverses in these carbohydrate levels. Wedemeyer (1972) showed that the stress of handling smolting coho salmon caused severe hyperglycemia, hypochloremia, and the activation of subclinical kidney disease infection. Carbohydrate metabolism of coho parr was much less affected by the stress of hatchery practices.

Endocrine Control

A number of endocrine changes have been observed during the parr-smolt transformation; chiefly, an activation of thyroid, interrenal, and pituitary growth hormone cells. Hoar (1939) first observed increased thyroid cell activity (by histological examination) in Atlantic salmon at the time of smolting and this has since been confirmed in other anadromous salmonids (Robertson, 1948; Baggerman, 1960). Recently, Dickhoff et al. (1978) and Folmar and Dickhoff (1979) have measured very high plasma thyroid hormone concentrations in coho smolts. As a practical application, oral administration of thyroidal materials, particularly triiodothyronine, shows considerable promise as a technique for stimulating growth and smolting of cultured salmon (Piggins, 1962; Higgs et al., 1977).

The pituitary-interrenal axis, as judged by histological evidence, is also known to be activated at the time of smolting in Atlantic and Pacific (coho) salmon (Fontaine and Olivereau, 1959; Olivereau, 1962, 1975; McLeay, 1975; Komourdjian et al., 1976b). Evidence for an involvement of pituitary growth hormone in the smolting process is derived from both physiological and histological studies. First of all, it has long been recognized that a period of rapid growth accompanies the smolting process and secondly, that there is a strong correlation between growth rate and smolting tendency (Parry, 1958; Houston and Threadgold, 1963; Conte, 1969; Saunders and Henderson, 1970; Komourdjian et al., 1976b; Ewing et al., in press).

The first direct evidence for an effect of growth hormone was provided by Smith (1956) who reported that injections of mammalian growth hormone enabled brown trout, *Salmo trutta,* to survive in seawater. Since then, Komourdjian et al. (1976a) have demonstrated that injections of porcine growth hormone enable Atlantic salmon parr to survive in seawater. Similarly, Clarke et al. (1977) demonstrated that injections of either bovine or teleost growth hormone improve the hypoosmoregulatory performance of underyearling sockeye salmon. Histological changes in the pituitary growth hormone cells were first described in Atlantic salmon smolts by Olivereau (1954). More recently, Komourdjian et al. (1976b) demonstrated experimentally that holding Atlantic salmon parr under a long photoperiod during winter promoted growth, and accelerated the development of smolt characteristics, including an increase in the number and granulation of pituitary growth hormone cells. In coho smolts, hypertrophy as well as hyperplasia of the growth hormone cells has been observed (Clarke and Nagahama, 1977).

Further studies are needed to clarify the functions of growth hormone and other hormones in coordinating the smolting process (Bern, 1978). Particularly intriguing is the possible role of prolactin, which is known to influence the osmoregulatory capability of salmon in freshwater; however, little is known about its function in smolts (Ball, 1969). Zambrano et al. (1972) observed a decrease in the activity of the pituitary prolactin cells in smolting Pacific salmon (*O. masou*) in freshwater but no similar changes have been observed in smolting Atlantic salmon prior to seawater entry (Komourdjian et al., 1976b). The activity of the prolactin cells in coho salmon also appears considerably lower after acclimation to seawater (Clarke and Nagahama, 1977; Nagahama et al., 1977).

Na$^+$, K$^+$-ATPase Activity

One of the important changes taking place during salmonid smolting is an increase in the Na$^+$, K$^+$-activated ATPase enzyme activity of the gill microsomal system (Zaugg and McLain, 1970; Zaugg and Wagner, 1973; McCartney, 1976; Giles and Vanstone, 1976; Saunders and Henderson, 1978). The gill ATPase system is involved, directly or indirectly, in excretion of monovalent ions from the blood. Salmonids and other euryhaline fishes typically show increased ATPase and ion pump activity prior to and following adaptation to seawater (Epstein et al., 1967; Kamiya and Utida, 1969; Kamiya, 1972). The increase in ATPase activity begins in salmonids during smoltification, prior to their entry into seawater and peaks near the time they show typical "smolt behavior" in a hatchery, or the most active migratory behavior in a stream (Fig. 1). If the smolts are allowed entry to seawater, ATPase activity continues to rise and stabilizes at an elevated level (Folmar and Dickhoff, 1979). If the smolts are not allowed to migrate, enzyme activity will gradually decline to initial levels as desmoltification occurs.

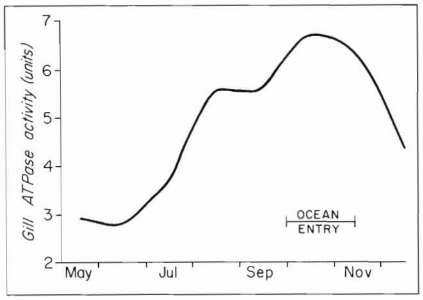

Figure 1.—Gill Na$^+$, K$^+$-ATPase activity in juvenile spring chinook salmon over a 2-year period. This chinook salmon race normally enters the ocean from the Rogue River (Oregon) in September-October (redrawn from Ewing et al., in press).

Buoyancy Adjustment

In addition to the physiological aspects of smolting, several behavioral changes distinguish smolts from parr. Atlantic salmon parr are territorial and live on or near the stream bottom, whereas smolts tend to develop schooling behavior and swim at middepth (Kalleberg, 1958). The physiological basis of this difference is not fully understood. However, salmonids are physostomous and fill their swim bladder by swallowing air. Saunders (1965) and Pinder and Eales (1969) demonstrated that smolts maintain larger volumes of air in their swim bladders than do parr, and therefore are more buoyant despite their reduced lipid content. Increased buoyancy could result in more difficulty maintaining a position on a stream bottom, and may have some influence in initiating downstream movement. This behavioral response is probably at least one of the factors involved in the change from a predominantly bottom living existance to a pelagic one (Saunders, 1965).

Another behavioral pattern is the development of preference for increased salinities. Baggerman (1960) and McInerney (1964) first reported seasonal changes in salinity preference of juvenile Pacific salmon presented with a horizontal salinity gradient. Baggerman also demonstrated that salinity preference was affected by photoperiod, and suggested that endocrine activity, controlled by environmental priming factors, was involved.

Migratory Activity

Perhaps the most dramatic behavioral change shown by smolts is downstream migration. Migratory activity has long been used as an index of smolt status. However, as with the other criteria, it has limitations. Baggerman (1960) originally developed the model of diadromous fish migrations in which environmental ''priming'' factors such as day length and temperature condition the smolts physiologically, mainly through the pituitary, to prepare for migration. External ''releasing'' factors such as light intensity and river flow rates finally trigger migrations. In the George and Koksoak Rivers at the northern end of the Atlantic salmon range in Labrador, salmon sometimes ''smoltify'' during several successive years before finally leaving the rivers (Power, 1959). The seawater migrating smolts are commonly 6 years old and longer than 20 cm. They may represent an incipient landlocked population. On the other hand, it is entirely possible that, under the extreme environmental conditions at the northern end of the Atlantic salmon range, coordination of the several physiological and behavioral processes that constitute smoltification is imperfect, particularly with the slow growth that occurs. In this area of Labrador, the ice persists well into the summer, and seawater temperatures remain low. From this and other case history observations, Koch (1968) concluded that smoltification and migration may have separate causes.

A practical application of the relation between smolting and migratory behavior has been the use of delayed smolt releases from hatcheries to obtain ''non-migrating'' populations of Pacific salmon in Puget Sound (Mahnken and Joyner, 1973). It was first observed that coho salmon that escaped from saltwater net pens in late summer did not leave the general area. More recently, chinook salmon as well have been induced to form residual populations by delaying release until after the usual migration time.

Size Threshold

A final criterion to consider is the influence of body size on smolting. Allen (1944) and Elson (1957) early emphasized the importance of size in Atlantic salmon smoltification. Pinder and Eales (1969) and Johnston and Eales (1970) found that buoyancy development and silvering both proceeded faster and to a greater degree in larger than in smaller parr. Conte and Wagner (1965) noted a significant size dependence in salinity tolerance in Pacific salmon and steelhead trout. In wild Atlantic salmon, the minimum size threshold for smolting appears to be 12-13 cm, although most smolts are in the 14-17 cm range. However, they may range in age from 2 to as much as 5 years. Although smaller salmon may be silvery, have a certain degree of salinity tolerance, and show increased buoyancy at smolting time, other aspects, especially migratory behavior, do not develop until the following year after the threshold size has been reached. It appears that, although several of the components of smolting exist in very small salmon, the needed physiological coordination is lacking.

In summary, considerable progress has been made, but much additional information is still needed if biologists are to be able to explain fully the phenomenon called smolting and control it to increase efficiency in the use of artificially propagated juveniles in salmon enhancement programs.

The word ''smolting'' has been used to describe the physiological and behavioral preadaptation of salmonids for movement between the nursery rivers and the sea. However, it is perhaps unfortunate that the term is used in this sense. The result has been to encourage the belief that several separate physiological processes must take place before smolting is complete.

A more functional view is that smolting is the coordination of several, separate, physiological and behavioral processes, including downstream migration, resulting in the ability to continue to grow and develop normally in the ocean. For example, in Atlantic salmon these processes allow the change, from a bottom dwelling territorial fish in freshwater to a pelagic, loosely schooling fish in the sea. Some of these changes are in progress well before smolting time, some are in response to recognizable environmental stimuli, and perhaps all of them have an endogenous rhythm. In Atlantic and Pacific salmon, photoperiod has been identified as the major environmental priming factor and coordinator which brings these endogenous physiological processes together on a temporal basis. There are ample experimental data to show that body silvering, fin darkening, salinity tolerance and preference, growth rate, growth hormone cell activity, gill ATPase activity, and lipid metabolism can be activated, postponed, advanced, or coordinated by photoperiod manipulation. Water temperature acts as the major controlling factor setting the range within which these processes can go on and, within these limits, determining their rates of reaction (Clarke, Shelbourn, and Brett, 1978).

Environmental Factors Affecting the Parr-Smolt Transformation

Contaminant Exposure

It has recently been shown that alterations of water chemistry can have a major deleterious effect on smoltification and early marine survival. One example of this phenomenon, which has particularly serious resource management consequences, is the effect of trace heavy metal exposure during rearing; normally due to mineral deposit drainage or to non-point-source industrial pollution (Lorz and McPherson, 1976). Unfortunately, the gill ATPase enzyme system of smolts and pre-smolts is sensitive to levels of dissolved heavy metals currently considered to be within the maximum safe exposure limits for freshwater fish populations. For example, wild coho salmon juveniles normally become migratory during the spring of their second year but are euryhaline somewhat before this time if they have reached a threshold size of about 9 cm (Conte et al., 1966). Chronic copper exposure during the parr-smolt transformation, at only 20-30 μg/l, partially or completely inactivates the gill ATPase system (Lorz and McPherson, 1976). The biological damage is not apparent unless the fish are moved into saltwater, at which time severe mortalities begin. A more subtle but equally devastating consequence is that normal migratory behavior is also suppressed. Similar results were obtained by Davis and Shand (1978) using sockeye salmon. Laboratory exposure of smolts for 144 hours to copper at 30 μg/liter impaired hypoosmoregulatory performance, as revealed by a seawater challenge test, and resulted in some mortality.

Cadmium levels of more than 4 μg/liter in freshwater also result in a dose-dependent mortality if exposed coho smolts are transferred directly into 30‰ seawater (Lorz, Williams, and Fustish, 1978). However, if a 5-day freshwater recovery period is allowed before saltwater challenge, survival returns to normal. In contrast to copper, sublethal cadmium or zinc exposure during rearing apparently does not adversely affect migratory behavior. However, if even very low levels of copper (10 μg/l) are simultaneously present, downstream migration is reduced, and normal gill ATPase activity is suppressed. Unfortunately, few apparent alterations in growth or in feeding behavior occur to act as a warning and the smolts appear to be ''normal'' when released.

Nickel or chromium exposure at up to 5 mg/liter for 96 hours in freshwater apparently does not compromise migratory behavior or capability for ocean survival but sublethal mercury exposure results in a dose-dependent seawater mortality (Lorz, Williams, and Fustish, 1978). The fact that coho smolts would be unable to migrate directly into the ocean would probably tend to increase their residence time in the river and estuary—with consequent exposure to predation and diseases such as *Vibrio* and viral erythrocytic necrosis (VEN).

Less is known about the effects of low-level heavy metal exposure on smoltification and migration of salmon such as sockeye, pink, chum, or fall chinook, which have much different freshwater behavior patterns. However, Servizi and Martens (1978) reported that mortality, hatching, and growth of sockeye salmon during the egg to fry stage were not affected by continuous exposure to 5.7 μg/liter cadmium. However, the 168 hour LC_{50} decreased from 4,500 to 8 μg/liter as development from the alevin to fry stage occurred. For copper, the incipient lethal level during the egg to fry stage was within the range of 37 to 78 μg/liter for sockeye salmon and 25 to 55 μg/liter for pink salmon. Copper inhibited egg capsule softening, but hatching mortality occurred only at concentrations also lethal to eggs and alevins. Dissolved copper was concentrated by eggs, alevins, and fry in proportion to exposure concentrations. For pink salmon, mortalities of eyed eggs and fry occurred when tissue copper concentrations reached levels of 105 and 7 mg/kg, respectively.

For (inorganic) mercury exposure, concentrations of only 2.5 μg/liter caused development of malformed embryos. Hatching success, fry mortality, and growth were less sensitive to mercury exposure than was malformation. Mercury was also concentrated by sockeye and pink salmon eggs, and embryo abnormalities occurred when concentrations reached about 1.9 mg/kg.

In addition to trace heavy metal exposure, normally due to drainage from mineral deposits, or to non-point-source industrial pollution, increasingly intensive forest, range, and agricultural practices are resulting in chronic low-level herbicide concentrations in many juvenile salmon rearing waters. Coho salmon smolts exposed for only 96 hours to the herbicide Tordon 101[3] at 0.6-1.8 mg/liter just prior to release did not migrate as successfully as the control group (Lorz, Glenn, Williams, Kunkel, Norris, and Loper, 1978). Tordon 101 is a formulation of picloram and the dimethylamine salt of 2,4-D used for brush, weed, and vine control on noncrop lands, including rights of way. Other 2,4-D and 2,4,5-T formulations, such as the esters used for Eurasian water milfoil control, may also inhibit smolt function and migratory behavior. Low level 2,4-D exposure is known to cause an avoidance response in nonanadromous steelhead trout (Folmar, 1976). The potential for such deleterious effects should be ruled out before extensive herbicide applications are made.

Water Temperature

Elevated water temperatures are sometimes used to accelerate growth and shorten the normal time needed to produce smolts (Saunders, 1976). However, such artificial temperature regimes must be used with care because they can influence the smolting process itself as well as growth. Rearing temperature has a strong influence on the pattern on hypoosmoregulatory ability and gill ATPase activity development during smolting. In certain species, elevated temperature can not only accelerate the onset of smolting but also hasten the process of desmoltification so that the duration of the smolting period is shortened (Fig. 2). Coho salmon show a slow, sustained rise in gill ATPase activity at 6°C, a more normal pattern at 10°C, and a precocious development pattern at temperatures up to 20°C (Zaugg and McLain, 1976). Temperatures up to 15°C have been used to accelerate the smolting process so that juvenile coho salmon can be introduced to seawater in their first year; however, as shown in Figure 2, desmoltification is also accelerated (Novotny, 1975; Donaldson and Brannon, 1976; Clarke and Shelbourn, 1977). Juvenile fall chinook salmon also undergo a more rapid reversion to the parr condition at elevated holding temperatures (Clarke and Blackburn, 1977). The problem of accelerated desmoltification during rearing at elevated temperature can be overcome by holding sockeye, coho, or chinook salmon smolts in dilute seawater at salinities of 10-20‰ (W.C. Clarke, unpubl. data).

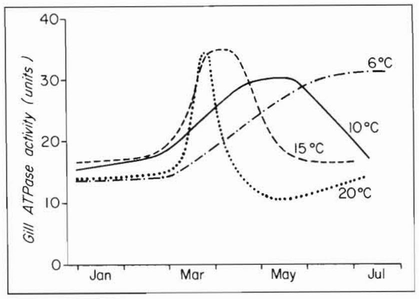

Figure 2.—Summary of the effect of water temperature on the pattern of gill Na^+, K-$^+$ ATPase activity development of juvenile coho salmon (redrawn from Zaugg and McLain, 1976).

---

[3] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

However, not all salmonids are amendable to temperature acceleration of smolting. Steelhead trout are particularly sensitive to the elevated rearing temperature sometimes used to accelerate growth (Fig. 3) and smolting can be inhibited at 13°C and above (Adams et al., 1973, 1975; Zaugg and Wagner, 1973). Laboratory experiments have shown that Atlantic salmon apparently smolt at temperatures as high as 15°C (Saunders and Henderson, 1970; Komourdjian et al., 1976b). However, until the temperature dependence of salinity tolerance development has been fully characterized, it is prudent to assume that Atlantic salmon are not unlike steelhead trout. In this regard, it may be significant that native runs of Atlantic salmon show their greatest downstream migrant activity as the temperature rises to 10°C. Smolt runs are over before the water warms to 15°C or more.

Photoperiod

Hoar's (1965) summary of the physiological and behavioral aspects of salmonid smolting cites the endocrine system as the chemical link between environmental changes and physiological changes in the fish. The seasonal cycle of growth and smolting in juvenile salmon has a strong endogenous component which is synchronized by the yearly photoperiod cycle (Hoar, 1965, 1976; Poston, 1978). This endogenous component has been demonstrated by the occurrence of asynchronous smolting under either continuous short photoperiods (Hoar, 1965) or complete darkness (Wagner, 1971). In a detailed series of experiments, Wagner (1971, 1974a) demonstrated that the photoperiod cycle synchronized the development of smolt characteristics and migratory behavior in juvenile steelhead trout. He found that the rate of change of photoperiod was an important cue, and that attempts to modify the timing of smolting were more successful if a shift in phase of the photoperiod cycle was used, rather than a change in its frequency. On the other hand, 30-day survival in seawater was not closely associated with smolting and was not influenced by photoperiod (Wagner, 1974b). In line with this, Clarke, Folmar, and Dickhoff (1978) found that presmolts held for 2 weeks under a 17-hour light, 7-hour dark photoperiod (17L:7D) had significantly higher gill ATPase and plasma thyroxine (T_4) levels, and were better able to regulate plasma Na^+ than were fish held under an 8L:16D photoperiod. However, after only 7 days in seawater, there were no differences between the groups. Experiments with juvenile Atlantic salmon have demonstrated that the spring growth acceleration, as well as smolting, can be advanced by several months if an increasing or long photoperiod is applied during winter (Saunders and Henderson, 1970; Knutsson and Grav, 1976; Komourdjian et al., 1976b). Photoperiod also has a marked effect on the growth and hypoosmoregulatory ability of underyearling sockeye and coho salmon (Clarke and Shelbourn, 1977; Clarke, Shelbourn, and Brett, 1978). Again, the most important photoperiod cues were shown to be direction and rate of change of day length, not day length per se. Prolonged exposure to a long photoperiod inhibits growth and smolting (Wagner, 1974a; Clarke, Shelbourn, and Brett, 1978). The role of temperature is to control the rate of physiological response to photoperiod such that effects are apparent sooner at elevated temperatures.

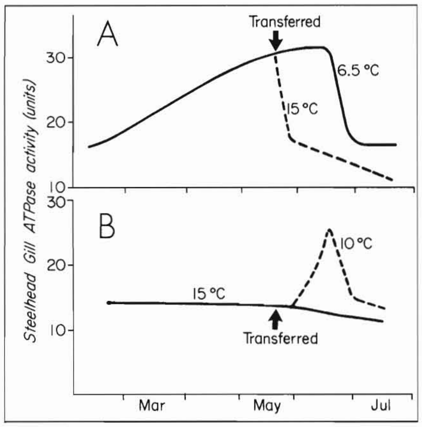

Figure 3.—Effect of water temperature on gill Na^+, K^+-ATPase activity of yearling steelhead trout. A. Held at 6.5°C, and transferred to 15°C (arrow). B. Held at 15°C and transferred to 10°C (arrow); ATPase development then occurred. (Redrawn from Zaugg et al., 1972.)

Hatchery Practices, Fish Disease Treatments

The smolt performance problems associated with the economic requirements for intensive, rather than extensive, fish culture for salmon enhancement programs have led to the widely held belief that improvements in present hatchery practices will contribute substantially to increased ocean survival and returns to the fishery. Two major areas have been identified. First, the fish cultural methods themselves. For example, a supression of normal ATPase development in juvenile chinook salmon by high population densities has recently been noted, although no data are yet available for other fishes (Strange et al., 1978). Second, certain fish disease therapeutants, including several drugs and chemicals commonly used pre-release, are now known to inhibit the seawater tolerance of smolts (Bouck and Johnson, 1979).

For clinically healthy coho salmon smolts treated and then transferred directly to 28‰ seawater for 10 days, Bouck and Johnson (1979) found low or no mortality following treatment with trichlorofon, simazine, or quinaldine. About 10 percent mortality occurred in groups treated with Formalin and nifurpirinol. High seawater mortality rates occurred following treatments with copper sulfate, hyamine 1622, potassium permanganate, malachite green, and MS-222. If a 4-day freshwater recovery period was allowed, mortality was reduced for copper sulfate, potassium permanganate, MS-222, and malachite green; much lower for hyamine 1622; and nil for the other agents. Thus the laudable effort to release fish free of external parasites and subclinical bacterial infections can potentially result in the release of disease free, but nonfunctional smolts. These findings, which are summarized in Table 2, suggest that it would be good practice to allow a 2-week freshwater recovery period when smolts are

Table 2.—Summary of seawater survival of coho salmon smolts following standard treatments with drugs and chemicals commonly used in fish culture (Bouck and Johnson, 1979).

	Treatment			Total mortality (%) during 10-days in seawater	
Chemical	Concentration of active ingredient (mg/l)	Length of daily exposure (min)	Consecutive days treatment was given	Direct transfer into seawater following treatment	Treatment, then 4-days in fresh water, then 4-hours acclimation to seawater
Controls	none	none	none	0 4	0
Copper sulfate	37	20	1	100	20
Endothal	5	60	1	100	4
Formalin	167	60	1	12	0
Hyamine 1622	2	60	4	68	4
Malachite green	1	60	1	44	12
MS-222	100	6	1	100	12
Nifurpirinol	1.5	60	4	8	0
Oxytetracycline	1	60	1	20	12
Potassium permanganate	2	60	3	80	12
Quinaldine	2.5	10	1	0	0
Simazine	2.5	60	1	4	0
Trichlorofon	0.5	60	1	0	0

given any pre-release disease treatment. For hatcheries sufficiently distant from the sea, the period of river migration might suffice.

Methods for Optimizing Time, Age, and Size at Release

Management strategies for optimizing ocean survival and total returns to the fishery must center around the production and release of functional, healthy smolts at the most favorable size, age, and time. Historically, hatchery releases have been timed to mimic the migration of resident wild salmonids in the rivers in question. However, in many waterways there have been mild to severe changes in the aquatic environment which now render historical migration times inappropriate. These include the occurrence of gas supersaturation in the spring, restrictions on stream flows due to the requirements of intensive agricultural and hydropower generation, and fluctuations in temperature and food supplies in river, estuarine, and coastal areas. In addition to these factors, the genetic composition of the hatchery fish in any particular river may have been changed significantly from that of the wild type due to the practice of importing eggs from stocks in other watersheds and the (sometimes inadvertent) genetic selection that occurs during hatchery egg taking operations. Superimposed on these problems are constantly evolving needs of resource management programs, such as the recent development of ocean ranching, or delayed releases used to establish resident salmon populations in local marine areas.

There have been relatively few studies that have separated the effects of smolt size from time of release on the number of returning adult salmon. Peterson (1973) found that 2-year-old Atlantic salmon out-migrant smolts smaller than 14 cm gave low adult returns. Greater numbers of returning adults were obtained as smolt length increased from 14 to 18 cm. Above a fish size of 18 cm, returns again tapered off. In contrast, yearling smolts showed good adult returns at release lengths of 12.5 to 14 cm (Peterson, 1973). This difference between the two age classes indicated that size is not an absolute factor in determining marine survival. Perhaps growth rate is more important.

For coho salmon, time of release, for a given smolt size, also has a profound effect on marine survival. Bilton (1978) investigated this phenomenon by releasing smolts graded into several size categories over a period of 4 months. He found that the optimal size varied with time of release and that maximum return of adult salmon resulted from the release of smolts of approximately 20 g, just prior to the summer solstice. Very large smolts were associated with more precocious males (jacks) in the population and thus a reduced total adult biomass.

ATPase Test

Dramatically increased gill Na^+,K^+-stimulated adenosinetriphosphatase activity has been associated with the parr-smolt transformation in salmonids for some time, and is currently being studied as a method to assess migration readiness, hypoosmoregulatory capability, and potential for ocean survival of hatchery produced anadromous fishes. In coho salmon, for example, ATPase activity in fresh water normally begins to increase in late April, peaks in late May, and then begins to decline, indicating that desmoltification is occurring. However, if the salmon are allowed to enter salt water, the gill ATPase activity continues to increase for an additional 30 days finally reaching a level three to four times that in fresh water; indicating that full osmoregulatory capability has been reached. Larger smolts do not necessarily have the highest gill ATPase activities but, at least for spring chinook salmon, there apparently is a minimum fish size which must be attained before parr can enter the gill ATPase cycle (Ewing et al., in press). For spring chinook salmon, this minimum fish size is approximately 80-90 mm (Fig. 4).

ATPase development representative of what can be expected during

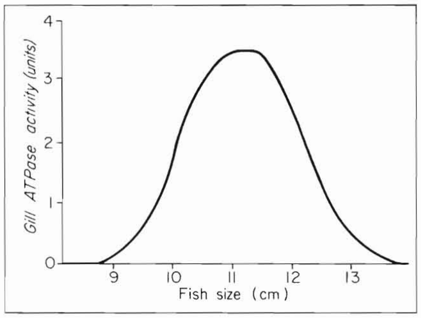

Figure 4.—The influence of fish size on changes in gill Na^+, K^+-ATPase activity, spring chinook salmon. Critical size is 8-9 cm (redrawn from Ewing et al., in press).

smolting of coho and spring chinook salmon and steelhead trout is shown in Figures 1, 2, 3, and 4. However, several fish cultural, environmental, and physiological factors must be taken into account when ATPase monitoring results are used to develop time, age, and size at release strategies for salmon enhancement programs. First, the length of the out-migration path should be considered in interpreting the data when low gill enzyme activities are obtained at the hatchery. That is, smolts with several hundred miles of downstream migration to accomplish may develop maximally elevated ATPase activity in the river rather than in the hatchery (Bjorn et al., 1978). In addition, recovery from adverse hatchery practices may occur in the river, or the act of migration itself may stimulate activity (Fig. 5). Second, certain salmonid races may have inherently lower ATPase enzyme levels than others. Finally, as mentioned earlier, crowding, pre-release disease treatments, or low-level contaminant exposure during rearing may have partially or completely inactivated the ATPase system. Significantly, this phenomenon can also be used in a positive way, as a sensitive method of biological monitoring for environmental quality.

Seawater Challenge Tests

Seawater tolerance, or ability to survive for 30 days in seawater, has long been used as a measure of smolting success (Conte and Wagner, 1965). However, as discussed earlier, this criterion fails to distinguish between large parr and true smolts in many salmonid species. For example, nonsmolting races of trout can thrive in seawater, provided that they are of sufficient size (Landless and Jackson, 1976). Also, recent aquacultural experience has shown that incompletely smolted coho salmon can survive in seawater, seemingly normally, for several months before they begin to show retarded growth (Mahnken, 1973; Kennedy et al., 1976; Clarke and Nagahama, 1977). Recently, Komourdjian et al. (1976a) and Saunders and Henderson (1978) showed that challenge with high (40‰) salinity is a good test to reveal any undeveloped salinity tolerance in Atlantic salmon and is therefore an excellent indicator of smolt status and capacity for hypoosmoregulation.

Challenge with 30‰ seawater is more common and is also an effective test of smolting if adaptation is assessed by determining the plasma sodium concentration that occurs after 24 hours (Clarke and Blackburn, 1977). True smolts suffer only a mild hypernatremia and can regulate plasma Na^+ to initial levels after abrupt transfer to seawater, as compared with the severe hypernatremia occurring in parr or postsmolts which have undergone desmoltification in fresh water (Parry, 1960; Houston, 1960, 1961; Koch, 1968; Clarke and Blackburn, 1977). This test can be run simply by taking a 10-fish blood sample for plasma sodium analyses 24 hours following transfer to seawater at their acclimation temperature (Clarke and Blackburn, 1977). Alternatively, following the plasma Na^+ profile over a 4-day period can furnish useful information.

Experience with accelerated underyearling coho salmon indicates that a plasma sodium concentration of less than 170 meq/liter after 24 hours in seawater is predictive of long term ability to grow and develop normally in the ocean. Test results obtained from wild and hatchery reared yearling coho salmon stocks of coastal British Columbia suggest that the optimal performance range for smolts is actually in the area of 150-160 meq/liter (Clarke and Blackburn, 1978). However, other stocks, such as Columbia River salmon, may not perform as well as this. In addition, it must be emphasized that the indicated performance range values will only be obtained during the first 24-48 hours in seawater, since osmoregulatory homeostasis will eventually develop even in parr, if they survive.

For example, Saunders and Henderson (1970) found that plasma chloride and osmolality were similar 3 weeks after transfer to seawater in Atlantic salmon which were smolted, and in those subjected to an unnatural photoperiod regime which had disturbed the smolting process. However, normal growth cannot be maintained, possibly because the energy costs of hypoosmoregulation in non-functional or poorly functional smolts are excessive (Woo et al., 1978). Thus, stunted coho salmon survive for several months in seawater net pens and are able to regulate their plasma sodium concentrations into the normal range but suffer poor growth, parr-reversion, and eventual mortality (Clarke and Nagahama, 1977).

Apart from coho salmon, the seawater challenge blood sodium test has been used as an indicator of smolt condition and probable ocean survival of chinook and sockeye salmon and

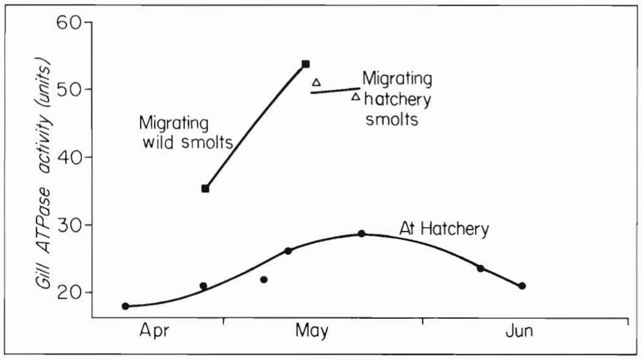

Figure 5.—Gill Na^+, K^+-ATPase activity of hatchery and wild Columbia River steelhead trout smolts. Migration itself may stimulate ATPase development to the level found in migrating wild smolts (redrawn from Bjorn et al., 1978).

steelhead trout. The degree of hypernatremia that results in smolts that are fully functional appears to be similar in all four anadromous species (Clarke and Blackburn, unpubl. data). In the case of fall chinook salmon, however, certain races may normally enter estuaries before the smolting process is fully complete (Clarke and Blackburn, 1978).

Thyroxine (T_4) Monitoring

As mentioned, there is also a substantial thyroid surge during smoltification and the monitoring of plasma T_4 holds considerable promise as an alternative method of tracking smolt development during rearing and for predicting likelihood of ocean survival (Dickhoff et al., 1978). As illustrated in Figure 6, T_4 levels in freshwater show a markedly sharper increase and decline profile than does ATPase activity, but high plasma T_4 concentrations are not sustained during saltwater residence.

Physiological Problems During Release and Emigration

Following hatchery rearing and release, downstream migrant smolts must again physiologically cope with a variety of environmental stress factors in the rivers and estuaries before their entrance into the sea. These include: dam passage problems, unfavorable stream flows and temperatures, predators, air supersaturation, activation of their own latent infections due to environmental stress, interference with saltwater adaptation in the estuary because of gill infestations by *Costia,* and, where trucking and barging around dams is employed, handling stress and descaling.

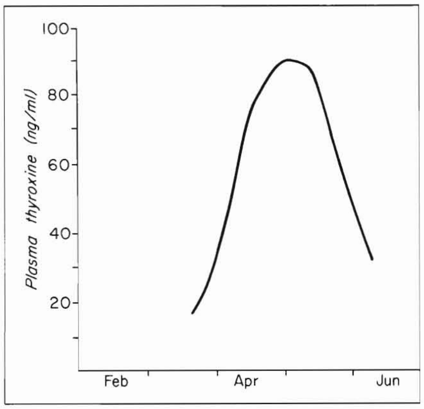

Figure 6.—Plasma thyroxine concentrations during smoltification of coho salmon (redrawn from Dickhoff et al., 1978).

The mortality pattern during emigration caused by dam passage, unfavorable temperatures and stream flows, gas supersaturation, and predation are fairly well recognized. However, many other physiological problems such as those caused by 1) scale loss, 2) the activation of latent, or subclinical, infections due to the stress of seawater conversion, or 3) effects of gill parasite infestations, have received less attention, and are briefly reviewed here.

Environmental Stress and Scale Loss

Because of the major smolt mortality problem caused by dam passage, gas supersaturation in rivers, predation, and unfavorable temperatures, smolt hauling operations are in progress in rivers such as the Columbia. However, reduced survival due to handling stress, scale loss, and subsequent disease problems have led to the necessity for stress mitigation procedures (Long et al., 1977). Mineral salt additions of several kinds are known to be useful in minimizing handling stress in general. These include NaCl at 3-5‰ (Wedemeyer, 1972; Hattingh et al., 1974) or $CaCl_2$ at 50 mg/liter (Wedemeyer and Wood, 1974). For smolt hauling, salt (NaCl) at up to 15‰ has found considerable use both for stress mitigation and for *Saprolegnia* control, a major cause of delayed smolt mortality if scale loss occurs (Long et al., 1977). Normally, some potassium is also added if NaCl at 10‰ or more is used. In addition, diluted seawater (5-15‰) can also be effective in mitigating handling stress.

Unfortunately, various degrees of scale loss are fairly common during smolt transport operations. Bouck and Smith (1979) showed that considerable 10-day seawater mortality occurred when smolts were experimentally descaled as little as 10 percent of the body surface. The estimated 10-day TL_m was 50 percent mortality for a 10 percent scale loss on the ventral surface. These results have serious implications for the evaluation of smolt hauling programs involving stocking into seawater or of high seas tagging results, because of the delayed aspect of the mortality pattern. However, for smolt hauling involving release into rivers, the consequences would potentially be lessened by the fact that a 5-day recovery period in fresh water almost completely restored full tolerance to seawater, as judged by lack of mortality. However, partially descaled smolts released near a river mouth would probably show an avoidance reaction to salinity and would tend to remain in the estuarine area longer than normal, thus being exposed to disease and predation. Another physiological consequence of scale loss to consider is that potentially lethal amounts of Mg^{++} and K^{+} can then be absorbed from seawater or from the stress mitigating salt mixtures (Wedemeyer, unpubl. data). As little as 10 percent dorsal scale loss can result in a life-threatening hyperkalemia and hypermagnesemia in coho salmon smolts. Even if immediate mortalities do not occur, blood electrolyte imbalances of this magnitude are debilitating and would be expected to considerably reduce the ability of a smolt to survive further stress, or escape predation.

Activation of Latent Infections

There is consensus among fish disease specialists, but little published data, that latent bacterial or viral infections in smolts are probably activated by the stress of migration and saltwater adaptation resulting in substantial ocean mortality. In one documented example, coho salmon smolts undergoing a low grade bacterial kidney disease (*Corynebacterium salmonis*) epizootic at a hatchery, were divided into two groups, one transferred to another freshwater pond and the second transferred directly into 28‰ saltwater (Sanders, 1979; Sanders et al., in press). The results are summarized in Figure 7. As seen, the epizootic was exacerbated and kidney disease mortality increased dramatically in the group transferred into saltwater. These, and other case history results strongly suggest that smolts released with even subclinical infections are likely to have the disease activated by the stress of migration and conversion to saltwater and will suffer a delayed mortality in the ocean. In the experiment reported here, the majority of kidney disease deaths occurred 2 to 4 months after the fish entered saltwater. Frantsi et al. (1975) reported that bacterial kidney disease infected Atlantic salmon are generally unable to survive acclimation to seawater and suggested that few infected smolts survive to return as adults.

In the case of marine fish diseases, the recently discovered viral erythrocytic necrosis could potentially account for a portion of the so-called ''natural'' ocean mortality of anadromous fishes. Since it is a stress mediated disease, apparently contracted in estuaries, the prevention of estuarine habitat alteration offers a potential means of control. This would be especially promising for species such as chum, *O. keta,* pink, *O. gorbuscha,* or chinook salmon whose life histories include a significant amount of estuarine residence.

Gill Parasite Infestations and Seawater Tolerance

Experience gained by the Washington Department of Fisheries[4] suggests that only 15-30 *Costia necatrix* per gill arch will result in poor survival when hatchery coho and chinook salmon smolts reach seawater. This is presumably due to physical damage to gill chloride cells which results in reduced osmoregulatory competence.

Summary and Recommendations

On the basis of our present understanding and appreciation of the coordinated physiological processes called smoltification, several guidelines to be followed or precautions to be observed during the winter and spring preceeding hatchery smolt release can be recommended.

1) Temperature should follow a natural seasonal pattern. If elevated temperatures are used to promote growth, this is best done during October through December. Temperature should not be elevated too quickly or to more than about 10°C in late winter unless accelerated smolting is desired. Temperature should be held below 13°C at least 60 days prior to release of Atlantic salmon and steelhead trout. Similarly, for coho and chinook salmon, water temperatures should be held below about 12°C, if possible, in order to prevent premature smolting and desmoltification. For some anadromous fish, the temperature regimens needed to produce the most successful smolts are unknown.

2) In the absence of complicating factors such as altered river and estuarine ecology, smolt releases should be timed to coincide as nearly as possible with the historical seaward migration of naturally produced fish in the recipient stream, if genetic strains are similar. At headwater production sites, much earlier release may be called for. Planting large parr in the fall would not be unreasonable if observation shows naturally produced parr move to downriver sites at that time. The desired result is that hatchery reared smolts which are genetically similar to wild smolts enter the sea at or near the same time.

3) Proper photoperiod regulation is probably the most important environmental consideration to assure production of functional smolts. Although the facilities needed for photoperiod control are minimal, this environmental priming factor should be altered with caution, since it is easily misused with disastrous results. Unless accelerated or delayed smolting is required, the best procedure is to hold the presmolts in outdoor ponds with no artificial light. This may preclude the use of night floodlighting often needed for hatchery security. Indoor rearing should also be done under natural light if possible. Otherwise, artificial lighting should be

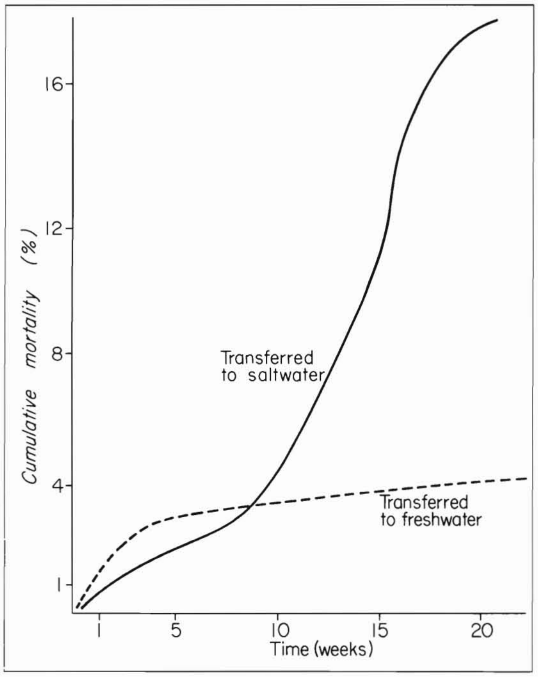

Figure 7.—Effect of transfer to saltwater on mortality from enzootic bacterial kidney disease in juvenile coho salmon (Sanders, 1979).

---

[4] Richard L. Westgard, Fish Pathologist, Washington State Department of Fisheries, Olympia, Wash., pers. commun. April 1979.

timed to simulate natural intensity and photoperiod.

4) Smolts must not be sent to sea with latent infections or gill parasite infestations. Ideally, pre-release disease treatments should be limited to medication known to have no effect on smolt performance. When this is not possible, an appropriate freshwater recovery period must be allowed.

5) In attempts to alter time, age, and size at release to fit resource management requirements, physiological testing for osmoregulatory competence should be used to track smolt development and monitor effects of hatchery practices and environmental factors. Gill Na$^+$, K$^+$-ATPase, plasma thyroxine (T$_4$), or the seawater challenge-blood sodium test are recommended.

6) Finally, in evaluating smoltification indices and hatchery performance, the major criterion should be the summation of hatchery returns and contribution to the fishery.

Acknowledgments

Many of our professional colleagues contributed judgements on technical interpretation during the preparation of this review. We especially thank H. Lorz and R. Ewing, Oregon Fish and Game Commission; R. Brett and T. Bilton, Department of Fisheries and Oceans, Canada; L. Folmar, C. Mahnken, and W. Zaugg, National Marine Fisheries Service.

Literature Cited

Adams, B. L., W. S. Zaugg, and L. R. McLain. 1973. Temperature effect on parr-smolt transformation in steelhead trout (*Salmo gairdneri*) as measured by gill sodium-potassium stimulated adenosine triphosphatase. Comp. Biochem. Physiol. 44A:1333-1339.

———, ———, and ———. 1975. Inhibition of salt water survival and Na-K-ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Trans. Am. Fish. Soc. 104:766-769.

Allen, K. R. 1944. Studies on the biology of the early stages of the salmon (*Salmo salar*) 4. The smolt migration in the Thurso River in 1938. J. Anim. Ecol. 13:63-85.

Baggerman, B. 1960. Salinity preference, thyroid activity and the seaward migration of four species of Pacific salmon (*Oncorhynchus*). J. Fish. Res. Board Can. 17:295-322.

Ball, J. N. 1969. Prolactin (fish prolactin or paralactin) and growth hormone. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology. Vol. II. The endocrine system, p. 207-240. Acad. Press, N.Y.

Bern, H. A. 1978, Endocrinological studies on normal and abnormal salmon smoltification. *In* P. J. Gaillard and H. H. Boer (editors), Comparative endocrinology, p. 97-100. Elsevier/North Holland Biomedical Press, Amsterdam.

Bilton, H. T. 1978. Returns of adult coho salmon in relation to mean size and time at release of juveniles. Can. Fish. Mar. Serv. Tech. Rep. 832, 73 p.

Bjorn, T. C., R. R. Ringe, and P. Hiebert. 1978. Seaward migration of Dworshak hatchery steelhead trout in 1976. Univ. Idaho, Forest, Wildl. Range Exp. Stn., Tech. Rep. 6.

Boeuf, G., P. Lasserre, and Y. Harache. 1978. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum II. Plasma osmotic and ionic variations, and gill Na$^+$-K$^+$-ATPase activity of yearling coho salmon transferred to sea water. Aquaculture 15:35-52.

Bouck, G. R., and D. A. Johnson. 1979. Medication inhibits tolerance to seawater in coho salmon smolts. Trans. Am. Fish. Soc. 108:63-66.

———, and S. D. Smith. 1979. Mortality of experimentally descaled smolts of coho salmon (*Oncorhynchus kisutch*) in fresh and salt water. Trans. Am. Fish. Soc. 108:67-69.

Carlin, B. 1969. Salmon tagging experiments. Swedish Salmon Res. Inst. Rep. 3, p. 8-13.

Clarke, W. C., and J. Blackburn. 1977. A seawater challenge test to measure smolting of juvenile salmon. Can. Fish. Mar. Serv. Tech. Rep. 705, 11 p.

———, and ———. 1978. Seawater challenge tests performed on hatchery stocks of chinook and coho salmon in 1977. Can. Fish. Mar. Serv. Tech. Rep. 761, 19 p.

———, S. W. Farmer, and K. M. Hartwell. 1977. Effect of teleost pituitary growth hormone on growth of *Tilapia mossambica* and on growth and seawater adaptation of sockeye salmon (*Oncorhynchus nerka*). Gen. Comp. Endocrinol. 33:174-178.

———, L. Folmar, and W. Dickhoff. 1978. Changes in gill Na$^+$K$^+$-ATPase plasma sodium, and thyroid hormone levels during adaptation of juvenile coho salmon to seawater. [Abstr.] Am. Zool. 18(3):85.

———, and Y. Nagahama. 1977. Effect of premature transfer to sea water on growth and morphology of the pituitary, thyroid, pancreas, and interrenal in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J Zool. 55:1620-1630.

———, and J. E. Shelbourn. 1977. Effect of temperature, photoperiod and salinity on growth and smolting of underyearling coho salmon. [Abstr.] Am. Zool. 17:957.

———, ———, and J. R. Brett. 1978. Growth and adaptation to sea water in 'underyearling' sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon subjected to regimes of constant or changing temperature and day length. Can. J. Zool. 56:2413-2421.

Conte, F. P. 1969. Salt secretion. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology. Vol. 1. Excretion, ionic regulation, and metabolism, p. 241-292. Acad. Press, N.Y.

———, and H. H. Wagner. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout *Salmo gairdneri*. Comp. Biochem. Physiol. 14:603-620.

———, ———, J. Fessler, and C. Gnose. 1966. Development of osmotic and ionic regulation in juvenile coho salmon (*Oncorhynchus kisutch*). Comp. Biochem. Physiol. 18:1-15.

Davis, J. C., and I. G. Shand. 1978. Acute and sublethal copper sensitivity, growth and saltwater survival in young Babine Lake sockeye salmon. Can. Fish. Mar. Serv. Tech. Rep. 847, 55 p.

Dickhoff, W. W., L. C. Folmar, and A. Gorbman. 1978. Changes in plasma thyroxine during smoltification of coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. 36:229-232.

Dodd, J. M., and A. J. Matty. 1964. Comparative aspects of thyroid function. *In* R. Pitt-Rivers and W. R. Trotter (editors), The thyroid gland, vol. 1, p. 303-356. Butterworths, Lond.

Donaldson, L. R., and E. L. Brannon. 1976. The use of warm water to accelerate the production of coho salmon. Fisheries (Bethesda) 1(4):12-16.

Elson, P. F. 1957. The importance of size in the change from parr to smolt in Atlantic salmon. Can. Fish. Cult. 21:1-6.

Epstein, F. H., M. Cynamon, and W. McKay. 1971. Endocrine control of Na-K-ATPase and seawater adaptation in *Anguilla rostrata*. Gen. Comp. Endocrinol. 16:323-328.

———, A. I. Katz, and G. E. Pickford. 1967. Sodium- and potassium-activated adenosine triphosphatase of gills: role in adaptation of teleosts to salt water. Science (Wash., D. C.) 156:1245-1247.

Evropeitseva, N. V. 1957. Transformation of smolt stage and downstream migration of young salmon. Uch. Zap. Leningrad Gos. Univ. 228. Ser. Biol. Nauk 44:117-154. (Fish. Res. Board Can. transl. ser. no. 234.)

Ewing, R. D., S. L. Johnson, H. J. Pribble, and J. A. Lichatowich. 1979. Temperature and photoperiod effects on gill (Na + K) − ATPase activity in chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 36: 1347-1353.

Farmer, G. J., J. A. Ritter, and D. Ashfield. 1978. Seawater adaptation and parr-smolt transformation of juvenile Atlantic salmon, *Salmo salar*. J. Fish. Res. Board Can. 35: 93-100.

Folmar, L. C. 1976. Overt avoidance reaction of rainbow trout fry to nine herbicides. Bull. Environ. Contam. Toxicol. 15:509-514.

———, and W. W. Dickhoff. 1979. Plasma thyroxine and gill Na$^+$-K$^+$-ATPase changes during seawater acclimation of coho salmon, *Oncorhynchus kisutch*. Comp. Biochem. Physiol. 63A:329-332.

———, and ———. In press. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids. A review of selected literature. Aquaculture.

Fontaine, M. 1951. Sur la dimunution de la teneur en chlore du muscle des jeunes saumons (smolts) lors de la migration d'avalaison. C. R. Acad. Sci. 232:2477-2479.

———, and J. Hatey. 1950. Variations de la teneur du foie en glycogène chez le jeune saumon (*Salmo salar* L.) au cours de la "smoltification." C. R. Soc. Biol., Paris 144:953-955.

———, and M. Olivereau. 1959. Interrenal antérieur et smoltification chez *Salmo salar* L. Bull. Soc. Zool. France 84:161-162.

Frantsi, C., T. C. Flewelling, and K. G. Tidswell. 1975. Investigations on corynebacterial kidney disease and diplostomulum sp. (eye fluke) at Margaree hatchery. Tech. Rep. MAR-T-75-9. New Brunswick, N.S., Canada.

Giles, M. A., and W. E. Vanstone. 1976. Changes in ouabain-sensitive adenosine triphosphatase activity in gills of coho salmon (*Oncorhynchus kisutch*) during parr-smolt transformation. J. Fish. Res. Board Can. 33:54-62.

Gudjónsson, T. 1972. Smolt rearing techniques, stocking and tagged adult salmon recaptures in Iceland. Int. Atl. Salmon Found., Spec. Publ. 4, p. 227-235.

Hattingh, J., F. LeRoux Fourie, and J. H. J. van Vuren. 1974. The transport of freshwater fish. J. Fish Biol. 7:447-449.

Higgs, D. A., U. H. M. Fagerlund, J. R. McBride, H. M. Dye, and E. M. Donaldson. 1977. Influence of combinations of bovine growth hormone, 17 α-methyltestosterone, and L-thyroxine on growth of yearling coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 55:1048-1056.

Hoar, W. S. 1939. The thyroid gland of the Atlantic salmon. J. Morphol. 65:257-295

————. 1951. Hormones in fish. Univ. Toronto Biol. Ser. 59, Publ. Ont. Fish. Res. Lab. 71, p. 1-51.

————. 1965. The endocrine system as a chemical link between the organism and its environment. Trans. R. Soc. Can. Ser. IV, 3:175-200.

————. 1976. Smolt transformation: Evolution, behavior, and physiology. J.Fish. Res. Board Can. 33:1233-1252.

Holmes, W. N., and I. M. Stainer. 1966. Studies on the renal excretion of electrolytes by the trout *Salmo gairdneri*. J. Exp. Biol. 44:33-46.

Houston, A. H. 1959. Osmoregulatory adaptation of steelhead trout (Salmo gairdneri Richardson) to sea water. Can. J. Zool. 37:729-748.

————. 1960. Variations in the plasma-level of chloride in hatchery-reared yearling Atlantic salmon during parr-smolt transformation and following transfer into sea-water Nature (Lond.) 185:632-633.

————. 1961. Influence of size upon the adaptation of steelhead trout (*Salmo gairdneri*) and chum salmon (*Oncorhynchus keta*) to sea water. J. Fish. Res. Board Can. 18:401-415.

————, and L. T. Threadgold. 1963 Body fluid regulation in smolting Atlantic salmon. J. Fish. Res. Board Can. 20:1355-1369.

Isaksson, A. 1973 The result of tagging experiments at the Kollafjordur Experimental Fish Farm from 1970 through 1972. Int. Counc. Explor. Sea Anad. Catad. Fish. Comm. C.M. 1973 /M: 26, 12 p.

————. 1974. Returns of salmon to the Kollafjordur Fish Farm 1974. Int. Counc. Explor. Sea Anad. Catad. Fish. Comm. C.M. 1974/M: 30, 6 p.

————. 1976. The results of tagging experiments at the Kollafjordur experimental fish farm from 1970 through 1972. J. Agric. Res. Iceland 8:3-13.

Johnston, C. E., and J. G. Eales. 1970. Influence of body size on silvering of Atlantic salmon (*Salmo salar*) at parr-smolt transformation. J. Fish. Res. Board Can. 27:983-987.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competiton in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Inst. Freshwater Res., Drottningholm 39:55-98.

Kamiya, M. 1972. Hormonal effect on Na-K-ATPase activity in the gill of Japanese eel, *Anguilla japonica*, with special reference to seawater adaptation Endocrinol. Jpn. 19:489-493

————, and S. Utida. 1969. Sodium-potassium-activated adenosinetriphosphatase activity in gills of fresh-water, marine and euryhaline teleosts. Comp. Biochem. Physiol. 31:671-674.

Kennedy, W. A., C. T Shoop, W. Griffioen, and A. J. Solmie. 1976. The 1974 crop of salmon reared on the Pacific Biological Station experimental fishfarm. Can. Fish. Mar Serv. Tech. Rep. 612, 19 p.

Knutsson, S., and T. Grav. 1976. Seawater adaptation in Atlantic salmon (*Salmo salar* L.) at different experimental temperatures and photoperiods. Aquaculture. 8:169-187.

Koch, H. J. A. 1968. Migration. *In* E. J. W. Barrington and C. B. Jorgenson (editors), Perspectives in endocrinology Acad. Press, N.Y., 583 p.

Komourdjian, M. P., R. L. Saunders, and J. C. Fenwick. 1976a. The effect of porcine somatotropin on growth, and survival in seawater of Atlantic salmon (*Salmo salar*) parr Can. J. Zool. 54:531-535.

————, ————, and ———— 1976b. Evidence for the role of growth hormone as a part of a 'light-pituitary axis' in growth and smoltification of Atlantic salmon (*Salmo salar*). Can. J. Zool. 54:544-551.

Landgrebe, F. W. 1941. The role of the pituitary and the thyroid in the development of teleosts. J. Exp. Biol. 18:162-169.

Landless, P. J., and A. J. Jackson. 1976. Acclimatising young salmon to sea water. Fish Farming Int. 3(2):15-17.

Long, C. W., J. R. McComas, and B. H. Monk. 1977. Use of salt (NaCl) water to reduce mortality of chinook salmon smolts, *Oncorhynchus tshawytscha*, during handling and hauling. Mar. Fish. Rev. 39(7):6-9.

Lorz, H., S. Glenn, R. Williams, C. Kunkel, L. Norris, and B. Loper. 1978. Effect of selected herbicides on smolting of coho salmon. U.S. Environmental Protection Agency, Grant Rep. R-804283. Oregon Dep. Fish Wildl., Corvallis.

————, and B. P. McPherson. 1976. Effects of copper or zinc in fresh water on the adaptation to sea water and ATPase activity, and the effects of copper on migratory disposition of coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33:2023-2030.

————, R. H. Williams, and C. A. Fustish. 1978. Effects of several metals on smolting in coho salmon. U.S. Environmental Protection Agency, Grant Rep. R-804283. Oregon Dep. Fish Wildl., Corvallis.

Mahnken, C. V. W. 1973. The size of coho salmon and time of entry into sea water: Part 1. Effects of growth and condition index. Proc. Annu. Northwest Fish Cult. Conf. 24:30-31.

————, and T. Joyner. 1973. Salmon for New England fisheries, Part III: Developing a coastal fishery for Pacific salmon. Mar. Fish. Rev. 35(10):9-13.

Malikova, E. M. 1957. Biochemical analysis of young salmon at the time of their transformation to a condition close to the smolt stage and during retention of smolts in fresh water. Tr. Latv. Otdel. VNIRO 2:241-255.

McCartney, T. H. 1976. Sodium—potassium dependent adenosine triphosphatase activity in gills and kidneys of Atlantic salmon (*Salmo salar*). Comp. Biochem. Physiol. 53A:351-353.

McInerney, J. E. 1964. Salinity preference: an orientation mechanism in salmon migration. J. Fish. Res. Board Can. 21:995-1018.

McLeay, D. J. 1975. Variations in the pituitary-interrenal axis and the abundance of circulating blood-cell types in juvenile coho salmon, *Oncorhynchus kisutch*, during stream residence. Can. J. Zool. 53:1882-1891.

Nagahama, Y., W. C. Clarke, and W. S. Hoar. 1977. Influence of salinity on ultrastructure of the secretory cells of the adenohypophyseal pars distalis in yearling coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 55:183-198.

Novotny, A. J. 1975. Net-pen culture of Pacific salmon in marine waters. Mar. Fish. Rev. 37(1):36-47.

Olivereau, M. 1954. Hypophyse et glande thyroïde chez les poissons. Etude histophysiologique de quelques corrélations endocriniennes en particulier chez *Salmo salar* L. Ann. Inst. Oceanogr. Monoco 29:95-296.

————. 1962. Modifications de l'interrénal du smolt (*Salmo salar* L.) au cours du passage d'eau dluce en eau de mer. Gen. Comp. Endocrinol. 2:565-573.

————. 1972. Action d'un apport de cortisol sur la cytologie de l'hypophyse chez l'anguille. Acta Zool. (Stockholm) 53:179-194.

————. 1975. Histophysiologie de l'axe hypophyso-corticosurrenalien chez le saumon de l'Atlantique (cycle en eau douce, vie thalassique et reproduction). Gen. Comp. Endocrinol. 27:9-27.

Parry, G. 1958. Size and osmoregulation in salmonid fishes. Nature (Lond.) 181:1218-1219.

————. 1960. The development of salinity tolerance in the salmon, *Salmo salar* (L.) and some related species. J. Exp. Biol. 37: 425-434.

Peterson, H. H. 1973. Adult returns to date from hatchery-reared one-year-old smolts. *In* M. V. Smith and W. M. Carter (editors), International Atlantic salmon symposium, vol. 4, p. 219-226. Int. Atl. Salmon Found., N.Y.

Piggins, D. J. 1962. Thyroid feeding of salmon parr. Nature (Lond.) 195:1017-1018.

Pinder, L. J., and J. G. Eales. 1969. Seasonal buoyancy changes in Atlantic salmon (*Salmo salar*) parr and smolt. J. Fish. Res. Board Can. 26:2093-2100.

Poston, H. A. 1978. Neuroendocrine mediation of photoperiod and other environmental influences on physiological responses in salmonids: a review. U.S. Fish Wildl. Serv., Tech. Pap. 96, 14 p.

Power, G. 1959. Field measurements of the basal oxygen consumption of Atlantic salmon parr and smolts. Arctic 12:195-202.

Ritter, J. A. 1972. Preliminary observations on the influence of smolt size on tag return rate and age at first maturity of Atlantic salmon (*Salmo salar*). Int. Counc. Explor. Sea C.M. 1972/M: 14.

Robertson, O. H. 1948. The occurrence of increased activity of the thyroid gland in rainbow trout at the time of transformation from parr to silvery smolt. Physiol. Zool. 21:282-295.

Sanders, J. E. 1979. Cell wall chemistry, deoxyribonucleic acid base composition and pathogenesis of the kidney disease bacterium in salmonid fishes. Ph.D. Thesis, Oreg. State Univ., Corvallis, 77 p.

————, D. Rowse-Eagle, and J. L. Fryer. In press. Bacterial kidney disease of salmonid fishes: A review. Oreg. State Univ. Sea Grant Rep.

Saunders, R. L. 1965. Adjustment of buoyancy in young Atlantic salmon and brook trout by changes in swimbladder volume. J. Fish. Res. Board Can. 22:335-352.

————. 1976. Heated effluent for the rearing of fry—for farming and for release. *In* O. Devik (editor), Harvesting polluted waters, p. 213-236. Plenum Press, N.Y.

________, and K. R. Allen. 1967. Effects of tagging and fin-clipping on the survival and growth of Atlantic salmon between smolt and adult stages. J. Fish. Res. Board Can. 24: 2595-2611.

________, and E. B. Henderson. 1969. Growth of Atlantic salmon smolts and post-smolts in relation to salinity, temperature, and diet. Fish Res. Board Can. Tech. Rep. 149, 20 p.

________, and ________. 1970. Influence of photoperiod on smolt development and growth of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 27:1295-1311.

________, and ________. 1978. Changes in gill ATPase activity and smolt status of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 35:1542-1546.

Servizi, J. A., and D. W. Martens. 1978. Effects of selected heavy metals on early life of sockeye and pink salmon. Int. Pac. Salmon Fish. Comm., Prog. Rep. 39, 26 p.

Smith, D. C. W. 1956. The role of the endocrine organs in the salinity tolerance of trout. Mem. Soc. Endocrinol. 5:83-101.

Strange, R. J., C. B. Schreck, and R. D. Ewing. 1978. Cortisol concentrations in confined juvenile chinook salmon (*Oncorhynchus tshawytscha*). Trans. Am. Fish. Soc. 107:812-819.

Van Dyck, M. 1966. De Keys-Willmercellen in de Kieuwen. Koninkl. Vlaam. Acad. Wetenschap., Letter. Schone Kunsten Belg., Kl. Wetenschap. 28:1-99.

Wagner, H. H. 1971 The parr-smolt metamorphosis in steelhead trout as affected by photoperiod and temperature. Ph.D Thesis, Oreg. State Univ., Corvallis, 211 p.

________. 1974a. Photoperiod and temperature regulation of smolting in steelhead trout (*Salmo gairdneri*). Can. J. Zool. 52:219-234.

________. 1974b. Seawater adaptation independent of photoperiod in steelhead trout (*Salmo gairdneri*). Can. J. Zool. 52:805-812.

Wedemeyer, G. 1972. Some physiological consequences of handling stress in the juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 29:1780-1783.

________, and J. Wood. 1974. Stress as a predisposing factor in fish diseases. U.S. Fish Wildl. Serv., Fish Dis. Leafl. 38, 8 p.

Wendt, C. A. G., and R. L. Saunders. 1973. Changes in carbohydrate metabolism in young Atlantic salmon in response to various forms of stress. *In* M. W. Smith and W. H. Carter (editors), International Atlantic salmon symposium, vol. 4, p. 55-82. Int. Atl. Salmon Found., N.Y.

Withey, K. G., and R. L. Saunders. 1973. Effect of a reciprocal photoperiod regime on standard rate of oxygen consumption of postsmolt Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 30:1898-1900.

Woo, N. Y. S., H. A. Bern, and R. S. Nishioka. 1978. Changes in body composition associated with smoltification and premature transfer to seawater in coho salmon (*Oncorhynchus kisutch*) and king salmon (*O. tschawytscha*). J. Fish. Biol. 13:421-428.

Zambrano, D., R. S. Nishioka, and H. A. Bern. 1972. The innervation of the pituitary gland of teleost fishes. *In* K. M. Knigge, D. E. Scott, and A. Weindl (editors), Brain endocrine interaction. Median eminence: structure and function, p. 50-66. Karger, Basel.

Zaugg, W. S., B. L. Adams, and L. R. McLain. 1972. Steelhead migration: potential temperature effects as indicated by gill adenosine triphosphatase activities. Science (Wash., D.C.) 176:415-416.

________, and L. R. McLain. 1970. Adenosinetriphosphatase activity in gills of salmonids: seasonal variations and salt water influence in coho salmon, *Oncorhynchus kisutch*. Comp. Biochem. Physiol. 35: 587-596.

________, and ________. 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (*Oncorhynchus kisutch*). Comp. Biochem. Physiol. 54A:419-421.

________, and H. H. Wagner. 1973. Gill ATPase activity related to parr-smolt transformation and migration in steelhead trout (*Salmo gairdneri*): influence of photoperiod and temperature. Comp. Biochem. Physiol. 45B: 955-965.