Preparatory Physiological Adaptations for Marine Life of Salmonids: Osmoregulation, Growth, and Metabolism

STEPHEN D. MCCORMICK[1] AND RICHARD L. SAUNDERS

Department of Fisheries and Oceans, Biological Station
St. Andrews, New Brunswick E0G 2X0, Canada

Abstract.—Atlantic salmon *Salmo salar*, steelhead *S. gairdneri*, and several species of Pacific salmon *Oncorhynchus* spp. undergo transformation from stream-dwelling parr to seaward-migrating smolts. Physiological, behavioral, morphological, and biochemical changes occur in fresh water in preparation for marine life. The preparatory nature of these adaptations is reviewed and discussed with particular emphasis on osmoregulation, metabolism, and growth. Functional changes in gill, kidney, gut, and urinary bladder result in increased salinity tolerance and hypoosmoregulatory ability. Some or all of these preparatory physiological changes may reverse in the absence of exposure to seawater. Changes in lipid, protein, and carbohydrate metabolism, oxygen consumption, and aerobic respiratory enzyme activity suggest increased catabolism during parr–smolt transformation. These transient changes in catabolism may reflect energetic demands of the extensive differentiation occurring during transformation. Although there is increased growth during parr–smolt transformation, evidence for a hypothesized increase in scope for growth after transformation is not convincing. We suggest that different aspects of the transformation have different developmental patterns, the timing of which is species-dependent and responsive to environmental change. Phylogenetic comparison of the differentiation of salmonid hypoosmoregulatory mechanisms and migratory behavior suggests that their evolution has occurred through heterochrony.

Transformation of the stream-dwelling parr to the seaward-migrating smolt is a significant life history event in many salmonids. Various morphological, physiological, and behavioral changes occur seasonally (usually in spring), develop over a period of 1–2 months, and are presumably adaptive for downstream migration and residence in the marine environment (see Table 1 and reviews by Hoar 1976; Folmar and Dickhoff 1980; Wedemeyer et al. 1980). Parr–smolt transformation has for some time been of interest as a developmental process (Hoar 1939; Bern 1978) and recently has come under more intense scrutiny as an important factor in the performance of hatchery-reared salmonids in ocean ranching and intensive aquaculture (Wedemeyer et al. 1980).

In the present undertaking, we review changes in osmoregulation, metabolism, and growth that occur during the parr–smolt transformation and that are to some degree interrelated. Substantial information exists concerning changes in salinity tolerance and metabolism, though much remains to be done in this area. Less is known concerning growth, and our discussion centers on what is not known. By stating hypotheses concerning the interrelationships of physiological changes during

the parr–smolt transformation, we hope to spur more focused research in this most fascinating and important area. In reviewing each of these areas we develop a common hypothesis: physiological changes during the parr–smolt transformation are preparatory adaptations, preparatory because they anticipate a change in environment and adaptive because they increase survival and fitness in a new environment.

Experiments conducted on the parr–smolt transformation have, of necessity, examined isolated aspects of development. Evidence for developmental changes are then unified under the single term "smoltification." This has often led to two disparate views that are equally wrong: that the transformation is a single and common process, or that it is a series of unconnected changes. Simpson (1985) stated the problem the following way:

> Perhaps we should also be concerned lest our use of the term "smoltification" encourages a predilection to the belief that the process is a single one with a single or organically linked set of effectors. Smolting ought rather to be seen as the result of a large number of distinct processes—the change to particular patterns of growth, the elaboration of neurons associated with long-term memory, the development of different patterns of behaviour, major changes in metabolism and, finally, those changes in gill structure which permit the fish to pass from a hypo- to a hypertonic

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[1]Present address: Department of Zoology, University of California, Berkeley, California 94720, USA.

environment. There seems to me no *a priori* reason for supposing that these processes evolved simultaneously, or for supposing that they are linearly interdependent or have functionally linked endocrine mediators.

If we are successful in this review, we shall have shown or suggested both the distinction between these processes and their interrelations. By adopting a comparative view, we hope to establish that different aspects of the parr–smolt transformation are present in different salmonid species and that their presence and developmental pattern are related to the timing and duration of anadromy of a population or species.

Osmoregulation

Ontogeny of Salinity Tolerance

Ontogenetic changes in salinity tolerance (defined here as the ability to survive seawater >30‰) have been found in virtually all salmonid species investigated. Whereas salmonid eggs cannot survive more than a few days in seawater, the posthatch alevin has even poorer survival, presumably due to loss of the chorion (Weisbart 1968). Salinity tolerance of Atlantic salmon *Salmo salar* alevins decreases as the water-impermeable vitelline membrane decreases in favor of a water-permeable epithelium (Parry 1960; Talbot et al. 1982). In contrast, salinity tolerance of chum salmon *Oncorhynchus keta* increases during development of the alevin (Kashiwagi and Sato 1969).

After resorption of the yolk sac, salinity tolerance of all salmonids increases with size and age, and is closely tied to, and probably caused by, increased ability to regulate plasma ions and osmolarity following exposure to seawater[2] (Parry 1958, 1960; Houston 1961; Conte and Wagner 1965; Conte et al. 1966; Wagner 1974b; McCormick and Naiman 1984b; Ouchi 1985). Conte and Wagner (1965) and McCormick and Naiman (1984b) concluded that size, not age, is the primary determinant of increased seawater survival for steelhead *Salmo gairdneri* and brook trout *Salvelinus fontinalis*, respectively. Size-dependent salinity tolerance may be due to a more

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[2]Chinook salmon *(O. tshawytscha)* are an apparent exception to this rule. Whereas other *Oncorhynchus* species develop increased salinity tolerance through increased ability to regulate plasma ions, chinook salmon develop an increased tolerance of elevated plasma ions (Weisbart 1968).

favorable surface-area-to-volume ratio for larger fish, or to a progressive development of hypoosmoregulatory mechanisms with size, or to both. By comparing studies of similar design, McCormick and Naiman (1984b) concluded that salinity tolerance was also related to genus: the size at which seawater survival occurs is smallest for *Oncorhynchus* species, larger for *Salmo* species, and largest for *Salvelinus* species. This phylogenetic relationship follows closely the duration of marine residence (shortest for *Salvelinus* species) characteristic of each genus, as pointed out by Rounsefell (1958) and Hoar (1976).

There is substantial evidence indicating that size-dependent changes in salinity tolerance are distinct from the more rapid, seasonally occurring changes in salinity tolerance associated with the parr–smolt transformation. Salinity tolerance of seasonally migrating Atlantic salmon, rainbow trout *Salmo gairdneri* and coho salmon *Oncorhynchus kisutch* increases rapidly over a period of 1–2 months, coinciding with the normal period of migration and visible smolt characteristics (Conte and Wagner 1965; Komourdjian et al. 1976; Clarke et al. 1978; Saunders et al. 1983, 1985; McCormick et al. 1987). These changes are independent of temperature (except as it affects developmental rate), and are responsive to photoperiodic cues (Saunders and Henderson 1970; Wagner 1974a; Komourdjian et al. 1976; Clarke et al. 1978; Johnston and Saunders 1981; Clarke et al. 1985; Saunders et al. 1985; McCormick et al. 1987).

Although some seasonal periodicity in salinity tolerance may occur at all life stages (Hoar 1965; Wagner 1974a), the ability to manifest large seasonal changes in salinity tolerance is size-dependent. Rainbow trout do not respond to seasonal cues with increased salinity tolerance until they are at least 10 cm long (Conte and Wagner 1965). Similar size-related limitations in the expression of parr–smolt transformation have been found for coho salmon (Clarke et al. 1978) and Atlantic salmon (Elson 1957; Parry 1960).

In distinguishing between size-dependent changes in salinity tolerance and the size-dependent parr–smolt transformation, the *degree* of salinity tolerance becomes important. Atlantic and coho salmon parr of 10–12 cm can routinely tolerate (i.e., survive for many days) a salinity of 30‰ (Saunders and Henderson 1969; Clarke and Nagahama 1977). These fish may begin to die after several weeks, however, and growth is inevitably poor. Such differences in the degree of salinity

tolerance are not limited to the parr stage. Smolt-size (14–17 cm) Atlantic salmon that are denied seasonal cues through exposure to continuous light can adapt to 30‰ seawater, but cannot survive in 40‰ as can normal smolts, and exhibit poor feeding and growth in seawater (Saunders et al. 1985; McCormick et al. 1987). This distinction between the merely adequate or short-term sea-water survival of parr and the complete adaptability of smolts is an important one. Its basis lies in the increased hypoosmoregulatory ability of smolts (Parry 1960; Conte and Wagner 1965; Clark et al. 1978; Boeuf et al. 1978; Saunders and Henderson 1978; Hogstrand and Haux 1985) and perhaps other transport-related phenomena such as food conversion efficiency. Since parr can survive in seawater for extended periods of time, however, one can justifiably ask what the adaptive basis of increased salinity tolerance is at the time of smolting. Rapid acclimation to higher salinities with fewer osmotic perturbations may permit rapid movement through estuaries (Chernitsky 1983; McCormick et al. 1985), and immediate resumption of physiological and behavioral processes that might otherwise result in increased predation and interrupted feeding and growth.

The developmental processes that result in seasonally increased salinity tolerance and hypoosmoregulatory ability are apparently reversible if fish remain in fresh water. Rapid summer decreases in salinity tolerance have been observed in rainbow trout (Conte and Wagner 1965), coho salmon (Mahnken et al. 1982), and Atlantic salmon (Evropeytseva 1962). Generally known as "desmolting," this process may also result in reversion to a parr-like appearance (see Folmar et al. 1982). Whether or not "desmolting" results in a reversal of all physiological changes associated with the parr–smolt transformation will be discussed below.

Functional Changes in Osmoregulatory Organs

Teleosts normally maintain their plasma osmolarity within a narrow range (290–340 mOsmol/L) irrespective of the salinity of the external medium, and failure to do so for prolonged periods results in death. The transition from fresh water to seawater requires a reversal from net ion influx to net ion efflux which is regulated primarily by the gills but also involves the kidney, gut and urinary bladder (for a review of osmoregulation in teleosts, see Evans 1979; Foskett et al. 1983). In most teleosts this reversal is initiated by exposure to a hyperosmotic environment. As the following discussion should demonstrate, seasonal changes in structure or function (differentiation) of the osmoregulatory machinery, which occur prior to and in anticipation of exposure to seawater, are responsible for increased salinity tolerance during the parr–smolt transformation. This seasonal differentiation is likely to be the result of qualitative and quantitative changes in gene expression, the hormonal control of which has yet to be elucidated (Dickhoff and Sullivan 1987, this volume).

In considering the mechanisms of osmoregulatory change (as well as metabolism and growth), we shall consider only those salmonid species which show a rapid (1–2 month), reversible, seasonally cued increase in salinity tolerance. In this group, Atlantic, coho, and masu salmon *Oncorhynchus masou* and steelhead have received the greatest attention. There are, however, inherent difficulties in conducting and comparing studies on a developmental phenomenon that occurs over many weeks but which has no absolute morphological criterion (Gorbman et al. 1982). Many researchers have used appearance (often the degree of silvering or fin darkening) as a sole criterion to distinguish smolts from nonsmolts. In addition to the subjective nature of this criterion, it has proved to be highly variable under artificial culture conditions and is often "uncoupled" from other aspects of the parr–smolt transformation (Wedemeyer et al. 1980). Seasonal changes in temperature may introduce physiological changes independent of developmental phenomena (Virtanen and Oikari 1984). Differences in methodology, species, and size further increase the difficulties of assessing experimental results. In most cases, the developmental process is clear enough (or the experimental condition controlled enough) in spite of these confounding factors. We shall attempt to point out the exceptions, particularly when conflicting results are apparent.

Gills.—For a variety of euryhaline teleosts, gill Na^+,K^+-ATPase activity increases after transfer from fresh water to seawater (Epstein et al. 1967; Kirschner 1980). Ionic and electrical gradients generated by this enzyme are central to current models of branchial ion fluxes (Maetz and Garcia-Romeau 1964; Silva et al. 1977). Increases in gill Na^+,K^+-ATPase occur in several salmonid species in freshwater *prior* to seawater entry. Such increases in coho salmon (Zaugg and McLain 1970; Giles and Vanstone 1976a; Lasserre et al. 1978), chinook salmon (Hart et al. 1981; Buckman and Ewing 1982), rainbow trout (Zaugg and Wag-

ner 1973), and Atlantic salmon (McCartney 1976; Saunders and Henderson 1978; Boeuf et al. 1985; McCormick et al. 1987) occur seasonally and in phase with migration and increased salinity tolerance (Figure 1). Most of the gill Na^+,K^+-ATPase activity and ion transport capacity resides in mitochondria-rich chloride cells (Epstein et al. 1980; Foskett and Scheffey 1982). Chloride cells increase in number in gill opercular epithelium (Loretz et al. 1982) and change morphology in gill filaments (Richman 1985) of freshwater coho salmon smolts. Langdon and Thorpe (1985) found increased size and number of chloride cells in Atlantic salmon in early spring just before attainment of maximum salinity tolerance.

D. R. N. Primmett, F. B. Eddy, M. S. Miles, C. Talbot, and J. E. Thorpe (personal communication) measured whole-body Na^+ fluxes in juvenile Atlantic salmon; these fluxes are generally assumed to reflect the function of gill epithelium. During parr–smolt transformation, Na^+ flux changed from net influx (characteristic of freshwater teleosts) to net efflux. However, net Na^+ efflux is not an absolute requirement for increased salinity tolerance since maximum salinity tolerance was achieved after Na^+ flux had returned to a net influx. Iwata et al. (in press) found developmental changes in whole-animal transepithelial potential (TEP) of coho salmon. The TEP of coho

salmon in fresh water decreased gradually from 6 mV in early February to -12 mV in mid-April. In fish transferred to seawater for 12 h, TEP was 5 mV in February and increased to 16–18 mV in April through August. Taken together, these results indicate that developmental changes in mechanisms for ion transport found in freshwater-adapted smolts are important for seawater adaptation.

Kidney and urinary bladder.—The urine flow and water excretory rates of rainbow trout smolts in fresh water decrease relative to those in both pre- and postsmolts and are due entirely to a reduction in glomerular filtration rate (Holmes and Stainer 1966). Urine excretory rates of sodium and potassium and total osmolarity are also reduced in smolts. (Decreased urine flow and glomerular filtration occur in euryhaline teleosts after exposure to seawater [Hickman and Trump 1969], and the results of Holmes and Stainer may be interpreted as a preparatory adaptation.) However, the "seasonal" temperatures, variable timing of measurements, and use of appearance as the sole smolt criterion make it difficult to interpret these results. Recent work by Eddy and Talbot (1985) indicates that urine production by juvenile Atlantic salmon (>15 cm) increases during spring coincident with increasing gill Na^+,K^+-ATPase activity. These conflicting results con-
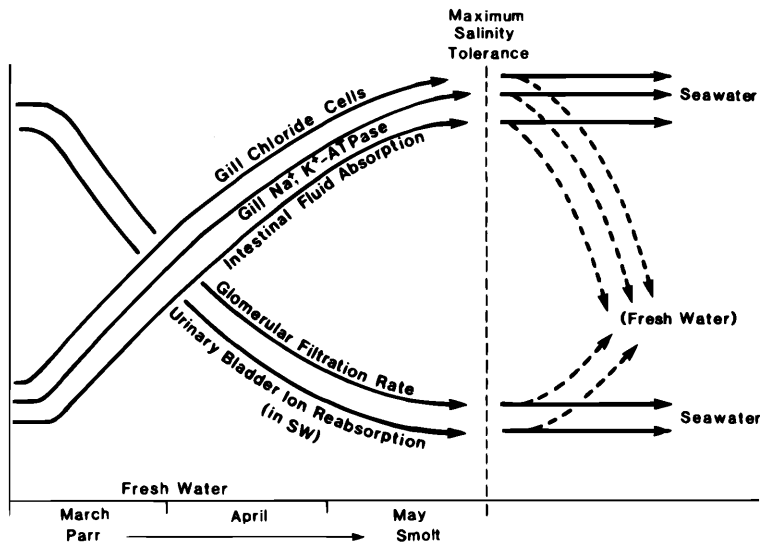

FIGURE 1.—Functional changes in osmoregulatory organs during the parr–smolt transformation. Functional changes normally associated with osmoregulation in seawater occur in fresh water and result in increased hypoosmoregulatory ability and salinity tolerance. In the absence of exposure to seawater, these changes are reversible.

cerning alteration of kidney function during parr–smolt transformation are, at present, unexplained.

Declines in kidney Na$^+$,K$^+$-ATPase activity in juvenile Atlantic salmon in spring were reported by McCartney (1976). Virtanen and Soivio (1985) reported that kidney Na$^+$,K$^+$-ATPase activity of juvenile Atlantic salmon raised in brackish water fluctuates considerably during spring, falling in early spring then rising to high levels in mid spring and falling again in late spring. S. D. McCormick and R. L. Saunders (unpublished data) found no seasonal change in kidney Na$^+$,K$^+$-ATPase activity in freshwater-reared Atlantic salmon, nor was the activity level of this enzyme different from that in fish exposed to continuous light (conditions that inhibit physiological changes associated with transformation). It should be noted that, unlike gill Na$^+$,K$^+$-ATPase activity, kidney Na$^+$,K$^+$-ATPase activity of Atlantic salmon changes slightly or not at all following increases in environmental salinity (Virtanen and Oikari 1984; McCormick et al., unpublished data).

Loretz et al. (1982) found that Na$^+$ and Cl$^-$ reabsorption by the urinary bladder of freshwater-adapted coho salmon did not change between March and June. However, developmental changes in the urinary bladder were detected when coho salmon were experimentally adapted to seawater over this same period. In May, when seawater survival was low, Na$^+$ and Cl$^-$ reabsorption by the urinary bladder of seawater-adapted fish was at high levels characteristic of salmon in fresh water. In June, when seawater survival was high, Na$^+$ and Cl$^-$ reabsorption was abolished. While no functional differentiation of the urinary bladder was apparent in fresh water, a clear increase in its capacity to respond to sea water had occurred.

Gastrointestinal tract.—Increased drinking rate and absorption of water and salts across gut epithelia occur following adaptation of euryhaline telosts to seawater. Collie and Bern (1982) found that the capacity for net fluid absorption of the intestine increased twofold in freshwater-adapted juvenile coho salmon between March and May, and that high values in May were similar to those of salmon adapted to seawater. Reversion of intestinal net fluid absorption to prespring levels occurred in early autumn in fish held in fresh water. Developmental changes in drinking rate associated with the parr–smolt transformation have yet to be investigated.

Consequences of Developmental Changes on Osmoregulation in Fresh Water

The previous section has established that seasonal increases in salinity tolerance and hypoosmoregulatory ability occur in conjunction with increases in gill Na$^+$,K$^+$-ATPase activity, quantity of gill chloride cells, intestinal net fluid absorption and other osmoregulatory changes that are characteristic of seawater-adapted teleosts but which occur prior to seawater entry (Figure 1). If these mechanisms are detectable in smolts in fresh water, are they also fully functional in vivo, and do they, therefore, produce osmoregulatory difficulties (water gain and ion loss) for smolts in fresh water? D. N. R. Primmett, F. B. Eddy, M. S. Miles, C. Talbot, and J. E. Thorpe (personal communication) have recently argued that increases in ion fluxes across the body surface, which are presumably hormone-induced, precede and are responsible for increases in gill Na$^+$,K$^+$-ATPase activity and other osmoregulatory changes during transformation. Whereas we have stressed the adaptive nature of these changes, these researchers suggest they are primarily a consequence of the loss of freshwater osmoregulatory capacity (see also Langdon and Thorpe 1985; Simpson 1985). It should be stressed, however, that in each of these scenarios a seasonal differentiation occurs that results in increased salinity tolerance, which is clearly adaptive for a seaward-migrating fish. It is still unclear that all the osmoregulatory changes portrayed in Figure 1 are functional in the freshwater smolt (e.g., Na$^+$,K$^+$-ATPase increases may be demonstrable by enzymological assay of gill homogenates but the enzyme may not be functionally active in vivo), or whether they require induction by exposure to seawater. In either event, we emphasize that the physiological mechanisms necessary for long-term survival in seawater take several days to develop in euryhaline species (Foskett et al. 1983); in smolts, these adaptations are already in place and may be rapidly induced to become functional upon exposure to seawater.

Decreases in plasma chloride (in the late parr stage: Houston and Threadgold 1963) and muscle chloride (in migrating smolts: Fontaine 1951) occur in Atlantic salmon in fresh water. Plasma osmolarity has been reported to decrease during smolting of masu salmon (Kubo 1953), to be more variable in smolting Atlantic salmon (Koch and Evans 1959), and to increase absolutely in post-smolt Atlantic salmon (Parry 1961). On the other

hand, a number of studies failed to find significant changes in plasma or muscle ions coincident with the parr–smolt transformation (see Folmar and Dickhoff 1980).

The variety and conflict of results in the investigations cited above suggest that environmental, experimental, and species differences may have influenced the results. Indeed, regulation of plasma and cellular ions of salmonids in fresh water can be affected by temperature (Kubo 1955), size (McCormick and Naiman 1984a), activity (Wood and Randall 1973), water quality (Eddy 1982), pH (Saunders et al. 1983), and stress (Schreck 1982). We have recently conducted a study in which rearing temperature for Atlantic salmon was held constant (5–8°C) from February to August (McCormick and Saunders, unpublished data). The interaction of seasonal and developmental phenomena was controlled by examining fish under both a simulated natural photoperiod and continuous light. (Atlantic salmon raised under continuous light grow normally but do not undergo a parr–smolt transformation: Saunders et al. 1985; McCormick et al. 1987.) A slight (<5%) decrease in plasma Na$^+$, Cl$^-$, and osmolarity occurred in each group between March and April. No change in plasma Na$^+$, Cl$^-$, Mg^{++}, K$^+$, or osmolarity occurred during the period when salinity tolerance and gill Na$^+$,K$^+$-ATPase activity increased (May and June) and subsequently decreased (August) in Atlantic salmon reared under natural photoperiod; nor were the levels of plasma ions and osmolarity different from those in fish reared under continuous light, in which increases in gill Na$^+$,K$^+$-ATPase activity and salinity tolerance did not occur. These results indicate that changes in plasma ions are not a necessary consequence of differentiation in osmoregulatory organs during the parr–smolt transformation.

The above conclusion does not imply, however, that changes in plasma or muscle ions do not occur *in response to* environmental change during the parr–smolt transformation. Several authors have suggested a direct connection between downstream migration and osmoregulatory dysfunction in fresh water caused by preparatory differentiation (Fontaine 1975; D. R. N. Primmett, M. S. Miles, C. Talbot, and J. E. Thorpe, personal communication). We suggest that preparatory physiological changes followed by environmental change (such as increased temperature or water flow) may be required for osmoregulatory perturbation, which may, in turn, be connected to migratory behavior. Strong correlations exist be-

tween downstream migration and water temperature for Atlantic salmon (Fried et al. 1978; Jonsson and Rudd-Hansen 1985). Kubo (1955) found that depression of plasma osmolarity during the parr–smolt transformation of masu salmon closely paralleled increases in water temperature.

Since a variety of other physiological and behavioral changes such as buoyancy, swimming ability, and orientation also occur during the parr–smolt transformation (Table 1), it seems likely that a variety of factors will be important in initiating migration. While we have supplied some suppositions, it is clear that the primary cue(s) of downstream migration and their relationship to osmoregulatory differentiation have yet to be established. In salmonid populations which undergo prolonged downstream migration there is evidence that migratory behavior and osmoregulatory differentiation do not occur together (Ewing et al. 1980; Bradley and Rourke 1984). This phenomenon may be due to the length and variability of migration, which might preclude accurate anticipation of seawater entry.

Metabolism

There is substantial evidence of a metabolic reorganization during the parr–smolt transformation. This evidence is derived primarily from

TABLE 1.—Some behavioral and physiological changes coincident with the parr–smolt transformation in salmonids.

Behavioral or physiological change	Reference
Increased deposition of guanine and hypoxanthine in skin and scales (silvering)	Johnston and Eales (1967)
Increased buoyancy due to increased air volume of swimbladder	Saunders (1965); Pinder and Eales (1969)
Alterations in blood hemoglobins (rapid increase in adult forms)	Vanstone et al. (1964); Giles and Vanstone (1976b); Koch (1982); Sullivan et al. (1985)
Increased schooling behavior	Kalleberg (1958)
Increased salinity preference	Baggerman (1960); McInerney (1964)
Negative rheotaxis	Wagner (1974b); Eriksson and Lundqvist (1982); Lundqvist and Eriksson (1985)
Decreased swimming ability	Glova and McInerney (1977); Smith (1982)

observations on changes in body composition, oxygen consumption, and mitochondrial enzyme activity. We wish to address two general hypotheses during the review of this evidence. First, does a metabolic increase occur during the parr–smolt transformation? Second, is such a metabolic increase due to energetic requirements of differentiation or to increased anabolism associated with growth or to both (Figure 2)?

Changes in Body Composition

Several changes in carbohydrate metabolism are concurrent with the parr–smolt transformation. Reduction of liver and muscle glycogen occurs in spring in Atlantic and coho salmon in both the presence and absence of migratory activity (Fontaine and Hatey 1953; Malikova 1957; Wendt and Saunders 1973; Woo et al. 1978). Blood glucose has been reported to increase in Atlantic salmon (Wendt and Saunders 1973) and to decrease in coho salmon (Woo et al. 1978) at

FIGURE 2.—Possible causes of metabolic increase during the parr–smolt transformation. Increases in metabolic rate due to differentiation and growth can be associated with catabolism and anabolism, respectively. Increased growth rate (which occurs in both parr and smolts in spring) will, a priori, result in increased metabolic rate. There also is evidence for increased metabolic rate due to differentiation. Arrows suggest the magnitudes of the influence on metabolic rate exerted by differentiation (D) and growth (G) acting separately or together.

the time of the parr–smolt transformation. Fontaine et al. (1963) reported that the powerful hyperglycemic agents adrenaline and noradrenaline are at their highest levels in Atlantic salmon during the final stages of smolting in April–May.

With the exception of decreased blood glucose, the above changes are often associated with short-term stress (Schreck 1981). The increased susceptibility of smolts to stress has been noted by several authors (Wendt and Saunders 1973; Schreck 1982). Seasonal changes in enzyme activity associated with glycogenolysis and glycogenesis, however, suggest a more permanent change that is unrelated to stress. Sheridan et al. (1985b) found that liver phosphorylase-a activity (glycogenolysis) of coho salmon increases by 64% between March and April, while uridine phosphate formation (glycogenesis) decreases by 54% from March to June.

Total body protein decreased by 10% between February and April in large (>14 cm) juvenile rainbow trout, but not in smaller fish under the same conditions (Fessler and Wagner 1969). In contrast, Woo et al. (1978) found no change in liver and muscle protein content of coho salmon parr and smolts. Serum protein content of coho salmon smolts was 15% lower than in parr or postsmolts (Woo et al. 1978). Cowey and Parry (1963) found a 30% increase in muscle content of nonprotein nitrogenous constituents of smolts over that in parr, due almost entirely to increased creatine content. The authors suggested that increased creatine may be due to greater availability of N-phosphoryl creatine for endergonic reactions or to increased metabolism of several amino acids for which creatine is an end product.

Cowey and Parry (1963) and Fontaine and Marchelidon (1971) could find no differences in total amino acid content of the brain or muscle between Atlantic salmon parr and smolts (they were able to sample both laboratory-reared and wild fish). The levels of particular amino acids did change, however. Threonine and glutamine contents of the brains of smolts increased, while muscle glycine and taurine decreased (Fontaine and Marchelidon 1971). Decreased muscle taurine content of Atlantic salmon smolts was also found by Cowey and Parry (1963). Fontaine and Marchelidon (1971) explained these changes as ramifications of several physiological changes during the parr–smolt transformation. Glycine (a precursor of purines) may be involved in events leading to deposition of guanine and hypoxanthine in skin and scales, which results in silvering (Johnston and Eales
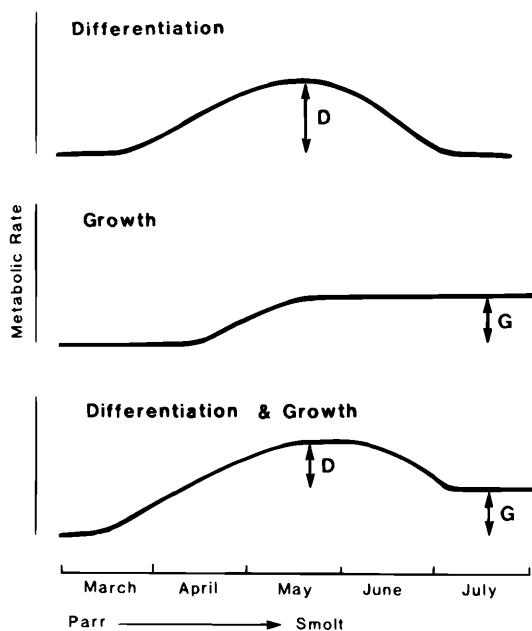
1967). Taurine is important for intracellular isosmotic regulation in teleosts (increasing when plasma osmolarity increases: King and Goldstein 1983) and may be lowered in response to osmoregulatory changes in fresh water or be distributed to other more sensitive tissues in preparation for hyperosmotic regulation. Increases in threonine in the brain, which is under insulin control in mammals (Okumura et al. 1959), may be a byproduct of increased insulin concentration resulting from glycemic fluctuations. While these intriguing suppositions have yet to be given experimental support, they underline the importance of distinguishing cause and effect in this complex developmental process.

Total body and muscle lipid decreases markedly in spring in juvenile Atlantic, coho, and masu salmon and in rainbow trout coincident with other parr–smolt changes (Vanstone and Markert 1968; Fessler and Wagner 1969; Saunders and Henderson 1970, 1978; Ota and Yamada 1974a, 1974b; Komourdjian et al. 1976; Farmer et al. 1978; Woo et al. 1978; Sheridan et al. 1983). These changes do not occur in small juveniles (parr), are not dependent on changes in activity or temperature, and return to prespring levels by late summer when fishes are retained in fresh water (Malikova 1957; Fessler and Wagner 1969; Ota and Yamada 1974a, 1974b; Farmer et al. 1978; Saunders and Henderson 1978; Woo et al. 1978). Moisture content of muscle varies inversely with lipid content (Farmer et al. 1978; Saunders and Henderson 1978; Woo et al. 1978) though this appears to be a common feature of teleosts and not peculiar to the parr–smolt transformation (Phillips 1969).

Sheridan and co-workers (Sheridan et al. 1983, 1985a, 1985b; Sheridan and Allen 1983) have examined lipid dynamics of coho salmon and rainbow trout in some detail. Lipid content of serum, liver, and muscle (white and red) is depleted by up to 60% in spring. Mesenteric fat does not fluctuate. Large amounts of triacylglycerol (normally used as energy storage) in muscle and liver are reduced more than other lipid classes. A reorganization of the fatty acid composition also occurs. Increased amounts of long-chain polyunsaturated fatty acids and decreased linoleic acid, characteristic of marine teleosts, occur in fresh water during the parr–smolt transformation. Similar changes in lipid composition coincident with the migratory period were observed in juvenile Atlantic and masu salmon (Lovern 1934; Ota and Yamada 1974a, 1974b). The adaptive value of these changes is as yet unknown, though suggestions for a role in osmoregulation have been made (Sheridan et al. 1985a).

The biochemical bases of changes in lipid metabolism have also been investigated (Sheridan et al. 1985b). Lipolytic rate (measured by the release of ^{14}C-oleic acid from ^{14}C-triolein) increases one- to three-fold in liver, red muscle, and mesenteric fat in coho salmon over a 4-month period in spring. During this same period ^3H_2O incorporation into fatty acids of liver and mesenteric fat was halved, though no difference in lipogenesis of neutral lipids was detected. These results suggest both a reorganization of lipid composition for a marine existence and increased catabolism associated with the parr–smolt transformation.

Oxygen Consumption

Direct measurement of oxygen consumption is difficult to assess because of the relatively high individual variation, dependence on temperature and size (often requiring use of regressions, which can obscure data), effects of various activity levels, and differential response to handling stress or confinement. Baraduc and Fontaine (1955) found resting, weight-specific oxygen consumption of wild Atlantic salmon parr at 8°C was 25% lower than for wild smolts. Power (1959), working with Atlantic salmon from an Arctic environment, found a temperature divergence in oxygen consumption: smolts had lower oxygen consumption than parr below 13.5°C, but higher oxygen consumption above this temperature. This may be the result of increased activity in response to temperature. Higgins (1985) reported oxygen consumption as a function of differential growth and the parr–smolt transformation in Atlantic salmon. When oxygen consumption per animal was regressed to a common size, rapidly growing fish had higher oxygen consumption at 7.5°C than slower growing fish. Smolts (based on external appearance), however, had lower weight-specific oxygen consumption than nonsmolts. In one of the few reported studies in which activity levels were taken into account, Withey and Saunders (1973) found that postsmolt Atlantic salmon had higher rates of oxygen consumption than nonsmolts. Without more critical studies taking activity level into consideration, it is difficult to arrive at a firm conclusion concerning changes in oxygen consumption during the parr–smolt transformation.

Respiratory Enzymes

Mitochondrial enzyme activities are indicative of tissue respiratory rate or respiratory potential,

though some enzymes are more representative than others (Ericinska and Wilson 1982). Succinate dehydrogenase (Chernitsky and Shterman 1981; Langdon and Thorpe 1985), citrate synthase and cytochrome-*c* oxidase activities (S. D. McCormick and R. L. Saunders, unpublished data) increase in gill homogenates of Atlantic salmon concurrent with the parr–smolt transformation. At first glance, these results would appear to coincide with the observed increase in numbers of mitochondria-rich chloride cells discussed earlier. Although chloride cells have greater respiratory enzyme activity than other gill cells (Sargent et al. 1975), whole-gill homogenates of fish which are acclimated to seawater do not have different respiratory enzyme activities (Epstein et al. 1967; Conte 1969; McCormick et al., unpublished data; for exceptions, see Sargent et al. 1975; Langdon and Thorpe 1984). Increases in gill respiratory enzyme activity observed during the parr–smolt transformation appear to go beyond what may be required for steady-state osmoregulation once seawater acclimation has occurred. The increase may be required for preparatory differentiation of the gills, or perhaps may aid in seawater adaptation during initial acclimation.

Blake et al. (1984) found up to 50% increases in mitochondrial concentration, and in the activities of succinate dehydrogenase and cytochrome-*c* oxidase, in the livers of large (>16 cm), silvery Atlantic salmon relative to those of parr. Similarly, McCormick and Saunders (unpublished data) found that liver citrate synthase activity of smolt-size Atlantic salmon increased 25% between March and June (coincident with increases in gill Na^+,K^+-ATPase activity) and subsequently declined to basal levels in August. These results, in combination with increased lipolytic and glycogenolytic enzyme activities in coho salmon livers, suggest that increased catabolism occurs in the liver during the parr–smolt transformation.

The evidence summarized here indicates that there is both reorganization and enhancement of metabolic activity during the parr–smolt transformation. Unfortunately, there is relatively little information on the reversibility of these changes. Metabolic alterations which are adaptations for seawater entry, such as changes in lipid composition, are analogous to preparatory osmoregulatory changes and are probably lost if the animals are maintained in fresh water. Metabolic increases appear to be at least partly catabolic, owing possibly to the energetic demands of differentiation. Recovery of pretransformation body

composition (Malikova 1957; Woo et al. 1978) and return of liver respiratory enzyme activity to presmolt level in summer indicate that increased catabolism subsides after the transformation, irrespective of the environmental salinity.

Growth

The apparent size threshold of the parr–smolt transformation may rule out growth rate as the primary stimulus for differentiation. Yet patterns of growth will undoubtedly affect the year of occurrence of the parr–smolt transformation and perhaps also its timing and intensity (Clarke 1982). The bimodal growth pattern of Atlantic salmon is a good example of the complex relationship between growth and transformation. Bimodal length-frequency distributions of laboratory-reared Atlantic salmon can be distinguished during the first autumn following hatching and have been attributed to an increase in growth rate of upper-mode fish (Kristinsson et al. 1985) and to a decline in growth rate owing to reduced appetite of lower-mode fish (Thorpe et al. 1982; Higgins 1985; Thorpe 1987a). Though these distinctions are controversial, it is clear that upper- and lower-mode fish do not further subdivide even after the fish in each mode are placed in separate tanks (Thorpe 1977). Upper-mode fish invariably become smolts in 1 year, while lower-mode males undergo a high rate of sexual maturation during their first autumn and normally require another year to achieve smolt size. Existence in the lower mode, however, does not preclude undergoing transformation; elevated early winter temperature resulting in higher growth and a greater size in early spring will result in normal smolt appearance and performance (Saunders et al. 1982; Kristinsson 1984). The relationship between high growth rates of upper-mode fish and the parr–smolt transformation may be indirect, coupled only by the size dependence of the transformation (Thorpe et al. 1982). Alternatively, bimodality may be an early manifestation of parr–smolt transformation such that changes taking place in spring are the climax of processes which have been proceeding since the previous autumn (Thorpe 1986).

Under natural conditions, juvenile Atlantic salmon may begin seaward migration at 2–4 years of age, and at weights of 30–50 g. They frequently attain weights of 1.5–2.5 kg in their first year at sea. Increased growth is undoubtedly due in large part to increased quantity and quality of food and more favorable year-round temperatures (Gross

1987, this volume). It is presently unclear whether smolts undergo a physiological change resulting in increased scope for growth (maximum food intake minus that necessary for maintenance: Brett 1979) at temperature and ration levels characteristic of the marine environment.

Increased growth of juvenile salmon occurs in spring concurrent with other transformation-related changes and in direct response to increasing photoperiod (Saunders and Henderson 1970; Knutsson and Grav 1976; Komourdjian et al. 1976; Clarke et al. 1978; Johnston and Saunders 1981; Higgins 1985). Though evidence for a common growth response of all salmonids to increasing photoperiod is lacking (Brett 1979), increased growth under increasing photoperiod also occurs in Atlantic salmon parr (Higgins 1985). One peculiar aspect of growth during the parr–smolt transformation is a decrease in condition factor (100 · weight/length^3; see Wedemeyer et al. 1980). This may be the result of a relative weight loss due to catabolism, or to an increased growth in length, such that increase in length outstrips growth in weight. Several authors have suggested an adaptive change in morphology to explain the latter hypothesis (Thorpe 1982).

In the absence of salinity effects, are parr and smolt distinguishable in their scope for growth either during or after the parr–smolt transformation? Higgins (1985) found that, at maximum ration and identical thermal regimes, Atlantic salmon in the upper size mode (incipient smolts) had a higher instantaneous growth rate in spring than lower-mode fish (parr), despite the smaller size of lower-mode fish which would, other things being equal, result in higher instantaneous growth rates (Brett 1979). It is unclear, however, whether this result is a function of the bimodal-growth pattern, the parr–smolt transformation, or both. We have recently compared the summer growth in fresh water of Atlantic salmon smolts (50 g) with juveniles (50 g) exposed to continuous light that inhibited at least the osmoregulatory aspects of the transformation (McCormick et al. 1987). Instantaneous growth rate of smolts and of fish in continuous light over a 6-week period at constant temperature (13°C) was the same (1.8%/d). We have concluded that either continuous-light treatment does not inhibit all aspects of the parr–smolt transformation, or that an increase in scope for growth (at maximum ration and at 13°C) does not accompany transformation in Atlantic salmon.

This limited evidence does not favor either acceptance or rejection of an increased scope for growth accompanying the parr–smolt transformation. If it does indeed occur, it is likely to be large and more easily detected in species such as Atlantic salmon which spend longer periods (2–5 years) in fresh water. Environmental effects on growth and scope for growth may also change after transformation. There is indirect evidence that the optimum temperature for marine growth of Atlantic salmon is lower than that for presmolt growth in fresh water (Reddin and Shearer 1987, this volume; Saunders 1987). Many fishes show reduced thermal optima for growth after the early juvenile stage (Hokanson 1977; Brett 1979; Mc-Cauley and Huggins 1979; Jobling 1981). Photoperiodic response may also change. Whereas growth of Atlantic salmon parr drops sharply in early autumn (decreasing photoperiod), despite favorable temperature and ration levels (R. L. Saunders, unpublished data), postsmolts in sea cages appear to continue growing rapidly in autumn until temperatures fall below 4°C (Sutterlin et al. 1981). Such an alteration in growth response to photoperiod has been observed in the bimodal growth pattern of juvenile Atlantic salmon (Kristinsson 1984; Higgins 1985; Kristinsson et al. 1985; Thorpe 1987a). Substantiation or rejection of these suppositions could greatly increase our understanding of ontogenetic and environmental influences on growth in teleosts.

Comparative Aspects of the Parr–Smolt Transformation

The variety of differentiative processes which occur and their responsiveness to photoperiodic cues underline the developmental nature of the parr–smolt transformation. This development has often been viewed as a single, size-related event which occurs seasonally and is reversible in the absence of sea water (Figure 3A). Although this may be true for some aspects of the transformation, other aspects, such as silvering, salinity tolerance, and gill Na^+,K^+-ATPase activity, often display slight but significant seasonal rhythms in the absence of "real" or "total" changes associated with transformation (Hoar 1965, 1976; Saunders and Henderson 1978; Langdon and Thorpe 1985; McCormick et al. 1987). Perhaps we can more correctly view these developmental processes as an interaction or synergism (Figure 3D) between prior development (Figure 3B) and seasonal rhythms (Figure 3C) which manifests itself in a critical size and season for transformation. Each component of the parr–smolt transformation may possess a different gradient of these develop-

mental types. The existence of different developmental patterns emphasizes the adaptive value of temporal orchestration of the many changes that occur during the transformation. Otherwise, they may occur as isolated events or physiological developments which fall short of the attributes required for long-term marine residence.
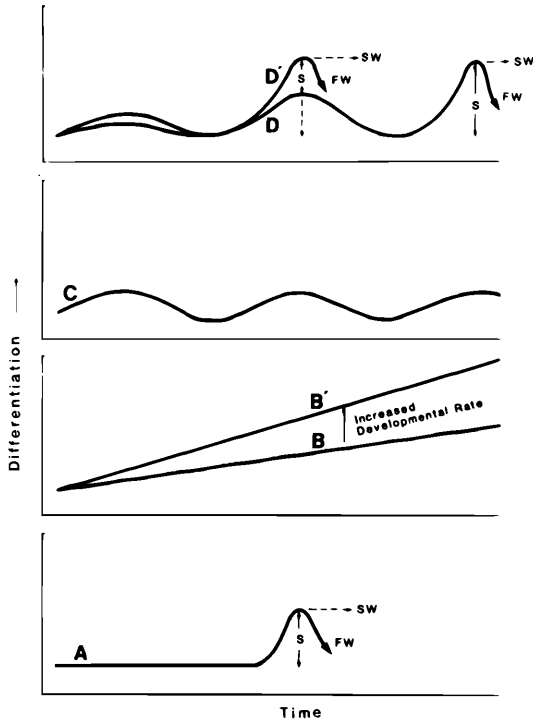

FIGURE 3.—Developmental patterns that may occur for different aspects of the parr–smolt transformation. A: Seasonal occurrence of physiological change that is dependent on seasonal cues and prior development (a critical size). B: Differentiation that is independent of season. A change from B to B′ may represent a change in ontogeny (i.e., increased growth rate resulting in increased differentiation at any time) or phylogeny (i.e., a different rate of differentiation relative to size resulting in increased salinity tolerance at any given size). C: Seasonal change that is independent of size, such as a photoperiod-cued increase in growth rate. D: Interaction of season and developmental rate. In this pattern, aspects of the parr–smolt transformation are an intensification and synchronization of seasonal changes that are also dependent on prior development. D and D′ represent, for instance, segments of a population that will undergo the parr–smolt transformation in the years *n* and *n* + 1, respectively. Analogous changes in developmental timing may have occurred in the course of salmonid evolution (see Figure 4). S represents physiological differences between parr and smolt; SW is seawater and FW is fresh water.

Analysis of the parr–smolt transformation as a developmental process consisting of numerous components can facilitate comparisons among salmonid species. Osmoregulatory physiology has received the most attention and can be more thoroughly explored. Brook trout, a member of the genus *(Salvelinus)* that has the least-developed capacity for marine residence in the subfamily Salmoninae (Rounsefell 1958; Hoar 1976), migrates into seawater at a relatively large size (>17 cm) and shows variability in the season of migration (White 1940; Wilder 1952; Castonguay et al. 1982; Montgomery et al. 1983). The development of salinity tolerance and hypoosmoregulatory ability in brook trout occurs at a larger size than in species of *Salmo* or *Oncorhynchus* (e.g., Figure 3, B versus B′; see also McCormick and Naiman 1984b). The osmoregulatory aspect of the parr–smolt transformation, as characterized by seasonal differentiation of osmoregulatory organs resulting in increased salinity tolerance, is undeveloped in brook trout (McCormick and Naiman 1984b; McCormick et al. 1985a). It should be noted, however, that seasonal silvering occurs in anadromous brook trout populations (though this is not necessarily associated with seawater entry: Black 1981), indicating that different physiological changes associated with the parr–smolt transformation can occur independently of one another.

Pink salmon *Oncorhynchus gorbuscha* and chum salmon represent the opposite end of the salmonid spectrum, often spending as little as a month or two in fresh water after hatching before migrating to sea. Salinity tolerance in these two species is incomplete in the posthatch alevin stage but increases rapidly, permitting survival in sea water at sizes less than 5 cm long (Weisbart 1968). It seems probable that such a rapid attainment of salinity tolerance will preclude a photoperiodically cued differentiation typical of other *Oncorhynchus* and *Salmo* species which undergo transformation and migrate at larger sizes. With the exception of changes in gill Na^+,K^+-ATPase activity (Sullivan et al. 1983) and kidney morphology (Ford 1958), little is known of the differentiation of osmoregulatory organs in pink and chum salmon. As in seasonally transforming salmonids, prolonged rearing of pink and chum salmon in fresh water results in substantial loss of salinity tolerance (Kashiwagi and Sato 1969; Iwata et al. 1982).

A phylogenetic comparison of the minimum size at which seawater entry occurs in salmonid species is presented in Figure 4. The developmen-
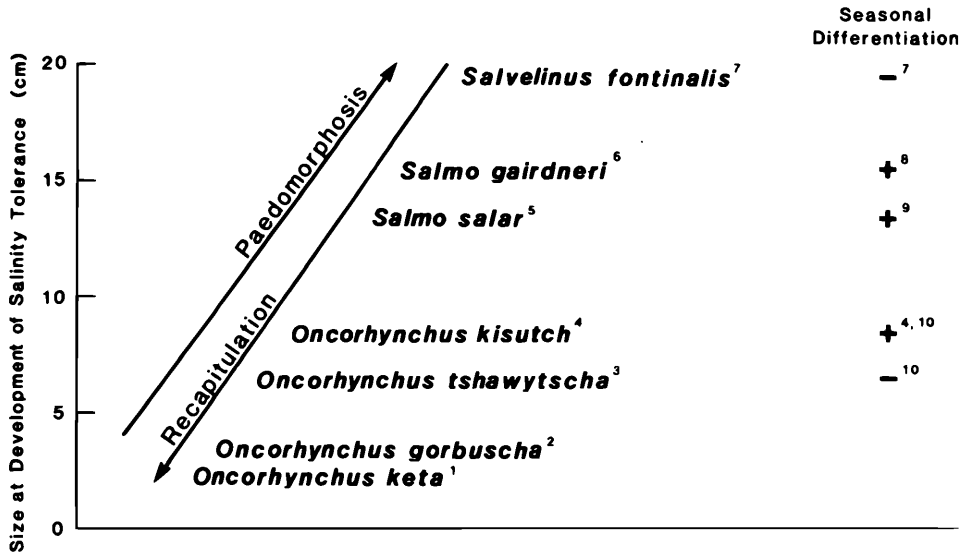
FIGURE 4.—Phylogenetic comparison of the minimum size at which the development of salinity tolerance occurs in the subfamily Salmoninae. Salinity tolerance is defined as greater than 75% survival in seawater (29‰ for at least 14 d. Seasonal differentiation (+) is defined as a photoperiod-controlled differentiation of osmoregulatory organs resulting in increased salinity tolerance. With the exception of brook trout, reversible ontogenetic differentiations have been shown to occur in the depicted species. Phylogenetic relationships suggest that heterochrony has occurred either through paedomorphosis (increasing size at differentiation) or recapitulation (decreasing size at differentiation). This hypothesis should not imply existence of a linear salmonid lineage but rather that, in the course of salmonid evolution, heterochrony has occurred in differentiation of osmoregulatory organs. References (superscripts): 1, Kashiwagi and Sato (1969); 2, Weisbart (1968); 3, Wagner et al. (1969); 4, Conte et al. (1966); 5, Johnston and Saunders (1981); 6, Conte and Wagner (1965); 7, McCormick and Niaman (1984a, 1984b); 8, Wagner (1974b); 9, Saunders and Henderson (1970); 10, Clarke et al. (1978).

tal nature of the attainment of salinity tolerance and the correspondence of this phylogeny to morphometrically and genetically based phylogenies of the subfamily Salmoninae (especially in that *Salmo* is intermediate between *Salvelinus* and *Oncorhynchus;* see Neave 1958 for review) leads us to conclude that heterochrony[3] in differentiation of hypoosmoregulatory capacity (and its underlying physiological mechanisms) has occurred during the evolution of these species (Figure 4; see Balon 1979, 1980 and Thorpe 1982 for earlier discussions of heterochrony in salmonids). The direction of heterochrony, either paedomorphic (increased size at attainment of salinity tolerance with advancing phylogeny) or recapitulatory (decreased size at attainment of salinity tolerance) has yet to be established. It seems likely that paedomorphosis would be associated with an ancestral seawater origin for salmonids,

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[3]Heterochrony is defined as changes in the timing of development, following the terminology of Gould (1978).

and recapitulation with a freshwater origin. Arguments based on fossil and extant species have been given for freshwater (Tchernavin 1939; Hoar 1976) and seawater (Day 1887; Regan 1911; Balon 1968; Thorpe 1982) origins of salmonids. Developmental conflict between transformation and maturation, argued by Thorpe (1987, this volume) underlines the importance of changes in the timing of development in establishing a life history pattern. Viewing the parr–smolt transformation as a developmental process subject to changes in timing during the course of salmonid evolution should facilitate species comparison and help generate hypotheses concerning the adaptive mechanisms for seawater entry and their hormonal control. Indeed, it seems likely that changes in the timing of expression of endocrine mechanisms controlling the transformation are responsible for the observed heterochrony.

In a "common strategies" symposium, a final statement on comparative physiological tactics may seem inappropriately brief, yet a longer one is precluded by the limited state of our knowledge

concerning the osmoregulatory physiology of diadromous fishes which, with the exception of salmonids and anguillids, have been little studied. The seaward migration of salmon and eels, despite the many differences between these fishes, is accompanied by morphological change (such as silvering) and increases in salinity tolerance and gill Na^+,K^+-ATPase activity (Fontaine 1975; Thomson and Sargent 1977). The common "strategy" of these two groups is to make a single, seasonal seaward migration during their lifetime, and they display a "tactic" of undergoing preparatory physiological adaptations. This is in contrast to euryhaline species (such as *Fundulus* spp.) which make repeated, less predictable movements into seawater. These fishes must have the capacity to alter osmoregulatory physiology more frequently, and it is generally believed that these changes are induced by environmental salinity (Karnaky 1986). One might predict, therefore, that preparatory physiological adaptations for seawater entry entailing ontogenetic differentiation would occur in species which make a single seaward migration. Conversely, diadromous or nondiadromous fishes which make repeated seawater entries seem less likely to display such a tactic and may rely more heavily on induction by external salinity of a perpetual hypoosmoregulatory capacity.

Acknowledgments

References

Baggerman, B. 1960. Salinity preference, thyroid activity and the seaward migration of four species of Pacific salmon *(Oncorhynchus)*. Journal of the Fisheries Research Board of Canada 17:295–322.

Balon, E. K. 1968. Notes to the origin and evolution of trouts and salmons with special reference to the Danubian trouts. Vestnik Ceskolovenske Spolecnosti Zoologicke 32:1–21.

Balon, E. K. 1979. The juvenilization process in phylogeny and the altricial to precocial forms in the ontogeny of fishes. Environmental Biology of Fishes 4:193–198.

Balon, E. K. 1980. Comparative ontogeny of charrs. Pages 703–720 *in* E. K. Balon, editor. Charrs:salmonid fishes of the genus *Salvelinus*. Dr. W. Junk, The Hague, The Netherlands.

Baraduc, M. M., and M. Fontaine. 1955. Etude comparée du métabolisme respiratoire du jeune saumon sédentaire (parr) et migrateur (smolt). Compte Rendu des Seances de la Société de Biologie Paris 149:1327–1329.

Bern, H. A. 1978. Endocrinological studies on normal and abnormal salmon smoltification. Pages 77–100 *in* P. J. Gaillard and H. H. Boer, editors. Comparative endocrinology. Elsevier/North-Holland Biomedical Press, Amsterdam, The Netherlands.

Black, G. A. 1981. Metazoan parasites as indicators of movements of anadromous brook charr *(Salvelinus fontinalis)* to sea. Canadian Journal of Zoology 59: 1892–1896.

Blake, R. L., F. L. Roberts, and R. L. Saunders. 1984. Parr–smolt transformation of Atlantic salmon *(Salmo salar)*:activities of two respiratory enzymes and concentrations of mitochondria in the liver. Canadian Journal of Fisheries and Aquatic Sciences 41:199–203.

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 seawater. Aquaculture 15:35–52.

Boeuf, G., A. LeRoux, J. L. Gaignon, and Y. Harache. 1985. Gill (Na^+,K^+)-ATPase activity and smolting in Atlantic salmon *(Salmo salar)* in France. Aquaculture 45:73–81.

Bradley, T. M., and A. W. Rourke. 1984. An electrophoretic analysis of plasma proteins from juvenile *Oncorhynchus tshawytscha* (Walbaum). Journal of Fish Biology 24:703–709.

Brett, J. R. 1979. Environmental factors and growth. Pages 599–677 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8. Bioenergetics and growth. Academic Press, New York, New York, USA.

Buckman, M., and R. D. Ewing. 1982. Relationship between size and time of entry into the sea and gill (Na^+-K^+)-ATPase activity for juvenile spring chinook salmon. Transactions of the American Fisheries Society 111:681–687.

Castonguay, M., G. J. Fitzgerald, and Y. Côté. 1982. Life history movements of anadromous brook charr, *Salvelinus fontinalis,* in the St. Jean river, Gaspé, Québec. Canadian Journal of Zoology 60: 3084–3091.

Chernitsky, A. G. 1983. Adaptive significance of smoltification in the Atlantic salmon, *Salmo salar.* Journal of Evolutionary Biochemistry and Physiology 19:186–190.

Chernitsky, A. G., and L. Ya. Shterman. 1981. Peculiarities of osmoregulation in the migrating juvenile Atlantic salmons. Voprosy Ikhtiologii 21:497–502.

Clarke, W. C. 1982. Evaluation of the seawater challenge test as an index of marine survival. Aquacul-

ture 28:177–183.

Clarke, W. C., H. Lundqvist, and L.-O. Eriksson. 1985. Accelerated photoperiod advances seasonal cycle of seawater adaptation in juvenile Baltic salmon, *Salmo salar* L. Journal of Fish Biology 26:29–35.

Clarke, W. C., 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).* Canadian Journal of Zoology 54: 1620–1630.

Clarke, W. C., J. E. Shelbourn, and J. R. Brett, Jr. 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 daylength. Canadian Journal of Zoology 56:2413–2421.

Collie, N. L., and H. A. Bern. 1982. Changes in intestinal fluid transport associated with smoltification and seawater adaptation in coho salmon, *Oncorhynchus kisutch* (Walbaum). Journal of Fish Biology 21:337–348.

Conte, F. P. 1969. The biochemical aspects of salt secretion. Pages 105–120 *in* O. W. Neuhaus and J. E. Halver, editors. Fish in research. Academic Press, New York, New York, USA.

Conte, F. P., and H. H. Wagner. 1965. Development of osmotic and ionic regulation in juvenile steelhead trout *Salmo gairdneri.* Comparative Biochemistry and Physiology 14:603–620.

Conte, F. P., H. H. Wagner, J. Fessler, and C. Gnose. 1966. Development of osmotic and ionic regulation in juvenile coho salmon *(Oncorhynchus kisutch).* Comparative Biochemistry and Physiology 18:1–15.

Cowey, C. B., and G. Parry. 1963. The non-protein nitrogen constituents of the muscle of parr and smolt stages of the Atlantic salmon *(Salmo salar).* Comparative Biochemistry and Physiology 8:47–51.

Day, F. 1887. British and Irish salmonidae. Williams and Norgate, London, England.

Dickhoff, W. W., and C. Sullivan. 1987. Involvement of the thyroid gland in smoltification with special reference to metabolic and developmental processes. American Fisheries Society Symposium 1:197–210.

Eddy, F. B. 1982. Osmotic and ionic regulation in captive fish with particular reference to salmonids. Comparative Biochemistry and Physiology B, Comparative Biochemistry 73:125–141.

Eddy, F. B., and C. Talbot. 1985. Urine production in smolting Atlantic salmon, *Salmo salar* L. Aquaculture 45:67–72.

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

Epstein, F. H., 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 (Washington, D.C.) 156:1245–1247.

Epstein, F. H., P. Silva, and G. Kormanik. 1980. Role of Na-K-ATPase in chloride cell function. American Journal of Physiology 238:R246–R250.

Ericinska, M., and F. F. Wilson. 1982. Regulation of cellular energy metabolism. Journal of Membrane Biology 70:1–14.

Eriksson, L.-O., and H. Lundqvist. 1982. Circannual rhythms of growth and smolting in Baltic salmon. Aquaculture 28:113–122.

Evans, D. H. 1979. Fish. Pages 305–390 *in* G. M. O. Maloiy, editor. Osmotic and ionic regulation in animals, volume 1. Academic Press, London, England.

Evropeytseva, N. V. 1962. [Comparative analysis of the desmoltification process among the young of different ecological forms of Atlantic salmon.] Uchenye Zapiski Leningradskogo Gosudarstrennogo Universiteta 311:46–76. Translated from Russian: Fisheries Research Board of Canada Translation Series 431, Ottawa, Canada.

Ewing, R. D., C. A. Fustich, S. L. Johnson, and H. J. Pribble. 1980. Seaward migration of juvenile chinook salmon without elevated gill (Na+K)-ATPase activities. Transactions of the American Fisheries Society 109:349–356.

Farmer, G. J., J. A. Ritter, and D. Ashfield. 1978. Seawater adaptation and parr–smolt transformation of juvenile Atlantic salmon, *Salmo salar.* Journal of the Fisheries Research Board of Canada 35:93–100.

Fessler, J. L., and H. H. Wagner. 1969. Some morphological and biochemical changes in steelhead trout during the parr–smolt transformation. Journal of the Fisheries Research Board of Canada 26: 2823–2841.

Folmar, L. C., and W. W. Dickhoff. 1980. The parr–smolt transformation (smoltification) and seawater adaptation in salmonids. A review of selected literature. Aquaculture 21:1–37.

Folmar, L. C., W. W. Dickhoff, C. V. M. Mahnken, and F. W. Waknitz. 1982. Stunting and parr-reversion during smoltification of coho salmon *(Oncorhynchus kisutch).* Aquaculture 28:91–104.

Fontaine, M. 1951. Sur la diminution de la teneur en chlore du muscle des jeunes saumons (smolts) lors de la migration d'avalaison. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 232:2477–2479.

Fontaine, M. 1975. Physiological mechanisms in the migration of marine and amphihaline fish. Advances in Marine Biology 3:241–355.

Fontaine, M., and J. Hatey. 1953. Contribution à l'étude du métabolisme glucidique du saumon *(Salmo salar* L.) à diverses étapes de son dévelopment et de ses migrations. Physiologia Comparata et Oecologia 3: 36–52.

Fontaine, M., and J. Marchelidon. 1971. Amino acid contents of the brain and the muscle of young salmon *(Salmo salar* L.) at parr and smolt stages. Comparative Biochemistry and Physiology A, Comparative Physiology 40:127–134.

Fontaine, M., M. Mazeaud, and F. Mazeaud. 1963. L'adrénalinémie du *Salmo salar* L. à quelques étapes de son cycle vital et de ses migrations. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 256:4562–4565.

Ford, P. 1958. Studies on the development of the kidney of the Pacific pink salmon (*Oncorhynchus gorbuscha* (Walbaum). II. Variation in glomerular count of the kidney of the Pacific salmon. Canadian Journal of Zoology 36:45–47.

Foskett, J. K., H. A. Bern, T. E. Machen, and M. Conner. 1983. Chloride cells and the hormonal control of teleost fish osmoregulation. Journal of Experimental Biology 106:255–281.

Foskett, J. K., and C. Scheffey. 1982. The chloride cell: definitive identification as the salt-secretory cell in teleosts. Science (Washington, D.C.) 215:164–166.

Fried, S. M., J. D. McCleave, and G. W. LaBar. 1978. Seaward migration of hatchery-reared Atlantic salmon, *Salmo salar*, smolts in the Penobscot River estuary, Maine:riverine movements. Journal of the Fisheries Research Board of Canada 35:76–87.

Giles, M. A., and W. E. Vanstone. 1976a. Changes in ouabain-sensitive adenosine triphosphatase activity in gills of coho salmon (*Oncorhynchus kisutch*) during parr–smolt transformation. Journal of the Fisheries Research Board of Canada 33:54–62.

Giles, M. A., and W. E. Vanstone. 1976b. Ontogenetic variation in the multiple hemoglobins of coho salmon (*Oncorhynchus kisutch*) and the effect of environmental factors on their expression. Journal of the Fisheries Research Board of Canada 33:1144–1149.

Glova, G. J., and J. E. McInerney. 1977. Critical swimming speeds of coho salmon (*Oncorhynchus kisutch*) fry to smolt stages in relation to salinity and temperature. Journal of the Fisheries Research Board of Canada 34:151–154.

Gorbman, A., W. W. Dickhoff, J. L. Mighell, E. F. Prentice, and F. W. Waknitz. 1982. Morphological indices of developmental progress in the parr–smolt coho salmon, *Oncorhynchus kisutch*. Aquaculture 28:1–19.

Gould, S. J. 1978. Ontogeny and phylogeny. Harvard University Press, Cambridge, Massachusetts, USA.

Gross, M. A. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14–25.

Hart, C. E., G. Concannon, C. A. Fustish, and R. D. Ewing. 1981. Seaward migration and gill (Na+K)-ATPase activity of spring chinook salmon in an artificial stream. Transactions of the American Fisheries Society 110:44–50.

Hickman, C. P., and B. F. Trump. 1969. The kidney. Pages 91–239 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume 1. Excretion, ionic regulation, and metabolism. Academic Press, New York, New York, USA.

Higgins, P. J. 1985. Metabolic differences between Atlantic salmon (*Salmo salar*) parr and smolts. Aquaculture 45:33–54.

Hoar, W. S. 1939. The thyroid gland of the Atlantic salmon. Journal of Morphology 65:257–295.

Hoar, W. S. 1965. The endocrine system as a chemical link between the organism and its environment. Transactions of the Royal Society of Canada 3: 175–200.

Hoar, W. S. 1976. Smolt transformation:evolution, behavior and physiology. Journal of the Fisheries Research Board of Canada 33:1233–1252.

Hogstrand, C., and C. Haux. 1985. Evaluation of the seawater challenge test on sea trout, *Salmo trutta*. Comparative Biochemistry and Physiology A, Comparative Physiology 82:261–266.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34:1524–1550.

Holmes, W. N., and I. M. Stainer. 1966. Studies on the renal excretion of electrolytes by the trout *Salmo gairdneri*. Journal of Experimental Biology 44: 33–46.

Houston, A. H. 1961. Influence of size upon the adaptation of steelhead trout (*Salmo gairdneri*) and chum salmon (*Oncorhynchus keta*) to sea water. Journal of the Fisheries Research Board of Canada 18:401–415.

Houston, A. H., and L. T. Threadgold. 1963. Body fluid regulation in smolting Atlantic salmon. Journal of the Fisheries Research Board of Canada 20: 1355–1369.

Iwata, M., S. Hasegawa, and T. Hirano. 1982. Decreased seawater adaptability of chum salmon (*Oncorhynchus keta*) fry following prolonged rearing in freshwater. Canadian Journal of Fisheries and Aquatic Sciences 39:509–514.

Iwata, M., R. S. Nishioka, and H. A. Bern. In press. Whole animal transepithelial potential (TEP) of coho salmon during the parr–smolt transformation and effects of thyroxine, prolactin and hypophysectomy. Fish Physiology and Biochemistry.

Jobling, M. 1981. Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. Journal of Fish Biology 19:439–455.

Johnston, C. E., and J. G. Eales. 1967. Purines in the integument of the Atlantic salmon (*Salmo salar*) during parr–smolt transformation. Journal of the Fisheries Research Board of Canada 24:955–964.

Johnston, C. E., and R. L. Saunders. 1981. Parr–smolt transformation of yearling Atlantic salmon (*Salmo salar*) at several rearing temperatures. Canadian Journal of Fisheries and Aquatic Sciences 38: 1189–1198.

Jonsson, B., and J. Rudd-Hansen. 1985. Water temperature as the primary influence of timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. Canadian Journal of Fisheries and Aquatic Sciences 42:593–595.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Institute of Freshwater Research Drottningholm Report 39: 55–98.

Karnaky, K. J. 1986. Structure and function of the chloride cell of *Fundulus heteroclitus* and other teleosts. American Zoologist 26:209–224.

Kashiwagi, M., and R. Sato. 1969. Studies of the osmoregulation of chum salmon, *Oncorhynchus*

keta (Walbaum). I. The tolerance of eyed period of eggs, alevins and fry of the chum salmon to seawater. Tohoku Journal of Agricultural Research 20: 41–47.

King, P. A., and L. Goldstein. 1983. Organic osmolytes and cell volume regulation in fish. Molecular Physiology 4:53–66.

Kirschner, L. B. 1980. Comparison of vertebrate salt-excreting organs. American Journal of Physiology 238:R219–R223.

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

Koch, H. J. 1982. Hemoglobin changes with size in the Atlantic salmon *(Salmo salar* L.). Aquaculture 28: 231–240.

Koch, H. J., and J. C. Evans. 1959. Sodium regulation in the blood of parr and smolt stages of the Atlantic salmon. Nature (London) 184:283–284.

Komourdjian, M. P., R. L. Saunders, and J. C. Fernwick. 1976. Evidence for the role of growth hormone as a part of a 'light-pituitary axis' in growth and smoltification of Atlantic salmon *(Salmo salar).* Canadian Journal of Zoology 54:544–551.

Kristinsson, J. B. 1984. Factors influencing the growth of juvenile Atlantic salmon. Doctoral dissertation. University of New Brunswick, Fredericton, Canada.

Kristinsson, J. B., R. L. Saunders, and A. J. Wiggs. 1985. Growth dynamics during the development of bimodal length-frequency distribution in juvenile Atlantic salmon *(Salmo salar* L.). Aquaculture 45: 1–20.

Kubo, T. 1953. On the blood of salmonid fishes of Japan during migration. I. Freezing point of blood. Bulletin of the Faculty of Fisheries Hokkaido University 4:138–148.

Kubo, T. 1955. Changes of some characteristics of blood of smolts of Oncorhynchus masou during seaward migration. Bulletin of the Faculty of Fisheries Hokkaido University 6:201–207.

Langdon, J. S., and J. E. Thorpe. 1984. Response of the gill Na$^+$–K$^+$ ATPase, succinic dehydrogenase activity and chloride cells to saltwater adaptation in Atlantic salmon, *Salmo salar* L., parr and smolt. Journal of Fish Biology 24:323–331.

Langdon, J. S., and J. E. Thorpe. 1985. The ontogeny of smoltification:developmental patterns of gill Na$^+$/K$^+$-ATPase, SDH, and chloride cells in juvenile Atlantic salmon, *Salmo salar* L. Aquaculture 45:83–96.

Lasserre, P., G. Boeuf, and Y. Harache. 1978. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. I. Seasonal variations of gill Na$^+$–K$^+$ ATPase activity in coho salmon, 0+-age and yearling, reared in freshwater. Aquaculture 14:365–382.

Loretz, C. A., N. L. Collie, N. H. Richman, and H. A. Bern. 1982. Osmoregulatory changes accompanying smoltification in coho salmon. Aquaculture 28: 67–74.

Lovern, J. A. 1934. Fat metabolism in fishes. V. The fat

of the salmon in its young freshwater stages. Biochemical Journal 28:1961–1963.

Lundqvist, H., and L.-O. Eriksson. 1985. Annual rhythms of swimming behavior and seawater adaptation in young Baltic salmon, *Salmo salar,* associated with smolting. Environmental Biology of Fishes 14:259–267.

Maetz, J., and F. Garcia-Romeau. 1964. The mechanism of sodium and chloride uptake by the gills of a freshwater fish, *Carassius auratus.* II. Evidence for NH$_4$$^+$/Na$^+$ and HCO$_3$$^-$/Cl$^-$ exchanges. Journal of General Physiology 47:1209–1227.

Mahnken, C., E. Prentice, W. Waknitz, G. Moran, C. Sims, and J. Williams. 1982. The applicability of recent smoltification research to public hatchery releases:an assessment of size/time requirements for Columbia River hatchery coho salmon *(Oncorhynchus kisutch).* Aquaculture 28:251–268.

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. Trudy Latviiskovo Otdeleniia VNIRO 2:241–255.

McCartney, T. H. 1976. Sodium–potassium dependent adenosine triphosphatase activity in gills and kidneys of Atlantic salmon *(Salmo salar).* Comparative Biochemistry and Physiology A, Comparative Physiology 53:351–353.

McCauley, R. W., and N. W. Huggins. 1979. Ontogenetic and non-thermal seasonal effect on thermal preferenda of fish. American Zoologist 19:267–271.

McCormick, S. D., and R. J. Naiman. 1984a. Osmoregulation in the brook trout, *Salvelinus fontinalis.* I. Diel, photoperiod and growth related physiological changes in freshwater. Comparative Biochemistry and Physiology A, Comparative Physiology 79: 7–16.

McCormick, S. D., and R. J. Naiman. 1984b. Osmoregulation in the brook trout, *Salvelinus fontinalis.* II. Effects of size, age and photoperiod on seawater survival and ionic regulation. Comparative Biochemistry and Physiology A, Comparative Physiology 79:17–28.

McCormick, S. D., R. J. Naiman, and E. T. Montgomery. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout *(Salvelinus fontinalis)* and Atlantic salmon *(Salmo salar).* Canadian Journal of Fisheries and Aquatic Sciences 42:529–538.

McCormick, S. D., R. L. Saunders, E. B. Henderson, and P. R. Harmon. 1987. Photoperiod control of parr–smolt transformation in Atlantic salmon *(Salmo salar):* changes in salinity tolerance, gill Na$^+$,K$^+$-ATPase and plasma thyroid hormones. Canadian Journal of Fisheries and Aquatic Sciences 44:1462–1468.

McInerney, J. E. 1964. Salinity preference:an orientation mechanism in salmon migration. Journal of the Fisheries Research Board of Canada 21:995–1018.

Montgomery, W. L., S. D. McCormick, R. J. Naiman, F. G. Whoriskey, and G. A. Black. 1983. Spring migratory synchrony of salmonid, catostomiol and

cyprinid fishes in Rivière a là Truite, Québec. Canadian Journal of Zoology 61:2495–2502.

Neave, F. 1958. The origin and speciation of *Oncorhynchus*. Transactions of the Royal Society of Canada, Section 5:Biological Sciences 52:25–39.

Okumura, N., S. Otsuki, and H. Nasu. 1959. The influences of hypoglycaemic coma, repeated electroshocks and chlorpromazine or β-phenylisopropylmethylamine administration on the free amino acids in the brain. Journal of Biochemistry 47:207–247.

Ota, T., and M. Yamada. 1974a. Lipids of masu salmon. II. Seasonal variations in the lipids of masu salmon parr during the life in freshwater. Bulletin of the Japanese Society of Scientific Fisheries 40:699–706.

Ota, T., and M. Yamada. 1974b. Lipids of masu salmon. III. Differences in the lipids of residual type and seaward migration type of masu salmon parr during the period of seaward migration. Bulletin of the Japanese Society of Scientific Fisheries 40:707–713.

Ouchi, K. 1985. Effect of cortisol on the salinity tolerance of masu salmon *(Oncorhynchus masou)* parr adapted to different salinities. Bulletin of the National Research Institute of Aquaculture 7:21–27.

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

Parry, G. 1960. The development of salinity tolerance in the salmon, *Salmo salar* (L.), and some related species. Journal of Experimental Biology 37:425–434.

Parry, G. 1961. Osmotic and ionic changes in blood and muscle of migrating salmonids. Journal of Experimental Biology 38:411–427.

Phillips, A. M. 1969. Nutrition, digestion and energy utilization. Pages 391–432 *in* W. S. Hoar and D. J. Randall, editors. Fish Physiology, volume 1. Excretion, ionic regulation, and metabolism. Academic Press, New York, New York, USA.

Pinder, L., and J. G. Eales. 1969. Seasonal buoyance changes in Atlantic salmon *(Salmo salar)* parr and smolt. Journal of the Fisheries Research Board of Canada 26:2093–2100.

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

Reddin, D. G., and W. M. Shearer. 1987. Sea-surface temperature and distribution of Atlantic salmon in the northwest Atlantic Ocean. American Fisheries Society Symposium 1:262–275.

Regan, C. T. 1911. The freshwater fishes of the British Isles. Methuen, London, England.

Richman, N. H. 1985. Hormones and osmoregulation in developing coho salmon *(Oncorhynchus kisutch)*. Doctoral dissertation. University of California, Berkeley, California, USA.

Rounsefell, G. A. 1958. Anadromy in North American Salmonidae. U.S. Fish and Wildlife Service Fishery Bulletin 58(131):171–185.

Sargent, J. R., A. J. Thompson, and M. Bornancin. 1975. Activities and localization of succinic dehydrogenase and Na$^+$/K$^+$-activated adenosine triphosphatase in the gills of freshwater and seawater

eels *(Anguilla anguilla)*. Comparative Biochemistry and Physiology B, Comparative Biochemistry 51:75–79.

Saunders, R. L. 1965. Adjustment of buoyancy in young Atlantic salmon and trout by changes in swimbladder volume. Journal of the Fisheries Research Board of Canada 22:335–352.

Saunders, R. L. 1987. The thermal biology of Atlantic salmon:influence of temperature on salmon culture with particular reference to constraints imposed by low temperature. Institute of Freshwater Research Drottningholm Report 65.

Saunders, R. L., and E. B. Henderson. 1969. Survival and growth of Atlantic salmon parr in relation to salinity. Fisheries Research Board of Canada Technical Report 147.

Saunders, R. L., and E. B. Henderson. 1970. Influence of photoperiod on smolt development and growth of Atlantic salmon *(Salmo salar)*. Journal of the Fisheries Research Board of Canada 27:1295–1311.

Saunders, R. L., and E. B. Henderson. 1978. Changes in gill ATPase activity and smolt status of Atlantic salmon *(Salmo salar)*. Journal of the Fisheries Research Board of Canada 35:1542–1546.

Saunders, R. L., E. B. Henderson, and B. D. Glebe. 1982. Precocious sexual maturation and smoltification in male Atlantic salmon *(Salmo salar)*. Aquaculture 28:211–229.

Saunders, R. L., E. B. Henderson, and P. R. Harmon. 1985. Effects of photoperiod on juvenile growth and smolting of Atlantic salmon and subsequent survival and growth in sea cages. Aquaculture 45:55–66.

Saunders, R. L., E. B. Henderson, P. R. Harmon, C. E. Johnston, and J. G. Eales. 1983. Effects of low environmental pH on smolting of Atlantic salmon *(Salmo salar)*. Canadian Journal of Fisheries and Aquatic Sciences 40:1203–1211.

Schreck, C. B. 1981. Stress and compensation in teleostean fishes:response to social and physical factors. Pages 295–321 *in* A. D. Pickering, editor. Stress and fish. Academic Press, New York, New York, USA.

Schreck, C. B. 1982. Stress and rearing of salmonids. Aquaculture 128:241–249.

Sheridan, M. A., and W. V. Allen. 1983. Wax esters in the liver and serum of steelhead trout, *Salmo gairdneri* Richardson. Comparative Biochemistry and Physiology B, Comparative Biochemistry 74:251–253.

Sheridan, M. A., W. V. Allen, and T. H. Kerstetter. 1983. Seasonal variations in the lipid composition of the steelhead trout, *Salmo gairdneri* Richardson, associated with the parr–smolt transformation. Journal of Fish Biology 23:125–134.

Sheridan, M. A., W. V. Allen, and T. H. Kerstetter. 1985a. Changes in the fatty acid composition of steelhead trout, *Salmo gairdneri* Richardson, associated with parr–smolt transformation. Comparative Biochemistry and Physiology B, Comparative Biochemistry 80:671–676.

Sheridan, M. A., N. Y. S. Woo, and H. A. Bern.

1985b. Changes in the rates of glycogenesis, glycogenolysis, lipogenesis and lipolysis in selected tissues of the coho salmon *(Oncorhynchus kisutch)* associated with parr–smolt transformation. Journal of Experimental Zoology 236:35–44.

Silva, P., R. Solomon, K. Spokes, and F. H. Epstein. 1977. Ovabain inhibition of gill Na-K-ATPase relationship to active chloride transport. Journal of Experimental Zoology 199:419–426.

Simpson, T. H. 1985. Epilogue. Salmonid Smoltification Workshop. Aquaculture 45:395–398.

Smith, L. S. 1982. Decreased swimming performance as a necessary component of the smolt migration in salmon in the Columbia River. Aquaculture 28: 153–162.

Sullivan, C. V., W. W. Dickhoff, S. D. Brewer, and G. P. Johnston. 1983. Plasma thyroid-hormone concentrations and gill (Na+K)-ATPase activities in postemergent pink salmon. Transactions of the American Fisheries Society 112:825–829.

Sullivan, C. V., W. W. Dickhoff, C. V. W. Mahnken, and W. K. Hershberger. 1985. Changes in hemoglobin system of the coho salmon *(Oncorhynchus kisutch* during smoltification and triiodothyronine and prophthiouracil treatment. Comparative Biochemistry and Physiology A, Comparative Physiology 81:807–813.

Sutterlin, A. M., E. B. Henderson, S. P. Merrill, R. L. Saunders, and A. A. MacKay. 1981. Salmonid rearing trials at Deer Island, New Brunswick, with some projections of economic viability. Canadian Technical Report of Fisheries and Aquatic Sciences 1011.

Talbot, C., F. B. Eddy, and J. Johnston. 1982. Osmoregulation in salmon and sea trout alevins. Journal of Experimental Biology 101:61–70.

Tchernavin, V. 1939. The origin of salmon. Salmon and Trout Magazine 95:120–140.

Thomson, A. J., and J. R. Sargent. 1977. Changes in the levels of chloride cells and (Na+,K+)-dependent ATPase in the gills of yellow and silver eels adapting to seawater. Journal of Experimental Zoology 200:33–40.

Thorpe, J. E. 1977. Bimodal distribution of length of juvenile Atlantic salmon *(Salmo salar* L.) under artificial rearing conditions. Journal of Fish Biology 11:175–184.

Thorpe, J. E. 1982. Migration in salmonids, with special reference to juvenile movements in freshwater. Pages 86–97 *in* E. L. Brannon and E. O. Salo, editors. Proceedings of the salmon and trout migratory behavior symposium. University of Washington, School of Fisheries, Seattle, Washington, USA.

Thorpe, J. E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*:freshwater period influences and conflicts with smolting. Canadian Special Publication of Fisheries and Aquatic Sciences 89:7–14.

Thorpe, J. E. 1987a. Environmental regulation of growth patterns in juvenile Atlantic salmon. Pages 463–474 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth in fishes. Iowa State University Press, Ames, Iowa, USA.

Thorpe, J. E. 1987b. Smolting versus residency: developmental conflict in salmonids. American Fisheries Society Symposium 1:244–252.

Thorpe, J. E., C. Talbot, and C. Villareal. 1982. Bimodality of growth and smolting in Atlantic salmon, *Salmo salar* L. Aquaculture 28:123–132.

Vanstone, W. E., and J. R. Markert. 1968. Some morphological and biochemical changes in coho salmon, *Oncorhynchus kisutch,* during the parr–smolt transformation. Journal of the Fisheries Research Board of Canada 25:2403–2418.

Vanstone, W. E., E. Roberts, and H. Tsuyuki. 1964. Changes in the multiple hemoglobin patterns of some Pacific salmon, genus *Oncorhynchus,* during the parr–smolt transformation. Canadian Journal of Physiology and Pharmacology 42:697–703.

Virtanen, E., and A. Oikari. 1984. Effects of low acclimation temperature on salinity adaptation in the presmolt salmon, *Salmo salar* L. Comparative Biochemistry and Physiology A, Comparative Physiology 78:387–392.

Virtanen, E., and A. Soivio. 1985. The patterns of T_3,T_4, cortisol and Na^+-K^+-ATPase during smoltification of hatchery-reared *Salmo salar* and comparison with wild smolts. Aquaculture 45:97–109.

Wagner, H. H. 1974a. Photoperiod and temperature regulation of smolting in steelhead trout *(Salmo gairdneri).* Canadian Journal of Zoology 52:219–234.

Wagner, H. H. 1974b. Seawater adaptation independent of photoperiod in steelhead trout *(Salmo gairdneri).* Canadian Journal of Zoology 52:805–812.

Wagner, H. H., F. P. Conte, and J. L. Fessler. 1969. Development of osmotic and ionic regulation in two races of chinook salmon *O. tshawytscha.* Comparative Biochemistry and Physiology 29:325–341.

Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. U.S. National Marine Fisheries Service Marine Fisheries Review 42(6):1–14.

Weisbart, M. 1968. Osmotic and ionic regulation in embryos, alevins, and fry of the five species of Pacific salmon. Canadian Journal of Zoology 46: 385–397.

Wendt, C. A. G., and R. L. Saunders. 1973. Changes in carbohydrate metabolism in young Atlantic salmon in response to various forms of stress. International Atlantic Salmon Foundation Special Publication Series 4:55–82.

White, H. C. 1940. Life-history of sea-running brook trout *(S. fontinalis)* of Moser River, N. S. Journal of the Fisheries Research Board of Canada 5: 176–186.

Wilder, D. G. 1952. A comparative study of anadromous and freshwater populations of brook trout *(Salvelinus fontinalis* (Mitchell)). Journal of the Fisheries Research Board of Canada 9:169–202.

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). Journal of the Fisheries Research Board of Canada 30:1898–1900.

Woo, W. Y. S., H. A. Bern, and R. S. Nishioka. 1978. Changes in body composition associated with smolt-ification and premature transfer to seawater in coho salmon *(Oncorhynchus kisutch)* and king salmon *(O. tschawytscha)*. Journal of Fish Biology 13:421–428.

Wood, C. M., and D. J. Randall. 1973. The influence of swimming activity on sodium balance in the rainbow trout *(Salmo gairdneri)*. Journal of Comparative Physiology 82:207–233.

Zaugg, W. S., and L. R. McLain. 1970. Adenosine triphosphatase activity in gills of salmonids: seasonal variations and salt water influences in coho salmon, *Oncorhynchus kisutch*. Comparative Biochemistry and Physiology 35:587–596.

Zaugg, W. S., 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. Comparative Biochemistry and Physiology B, Comparative Biochemistry 45:955–965.