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

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Abstract.—Atlantic salmon Salmo salar, steelhead S. gairdneri, and several species of Pacific salmon Oncorhyncus 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
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 (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 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 normally lead to a selective advantage for larger fish in anadromous environments. The ability to tolerate a high salinity is therefore of great importance in anadromous environments, where seawater survival may be critical for the survival of the species.
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 seawater 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 silverying 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 (Virrankari 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-
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-
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 seawater had occurred.

Gastrointestinal tract.—Increased drinking rate and absorption of water and salts across gut epithelia occur following adaptation of euryhaline teleosts 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 postsmolt 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. Primnett, 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 between 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>
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<tr>
<th>Behavioral or physiological change</th>
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<tr>
<td>Increased deposition of guanine and hypoxanthine in skin and scales (silvering)</td>
<td>Johnston and Eales (1967)</td>
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<tr>
<td>Increased buoyancy due to increased air volume of swimbladder</td>
<td>Saunders (1965); Pinder and Eales (1969)</td>
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<td>Alterations in blood hemoglobins (rapid increase in adult forms)</td>
<td>Vanstone et al. (1964); Giles and Vanstone (1976b); Koch (1982); Sullivan et al. (1985)</td>
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<td>Increased schooling behavior</td>
<td>Kalleberg (1958)</td>
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<td>Increased salinity preference</td>
<td>Baggerman (1960); McInerney (1964)</td>
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<td>Negative rheotaxis</td>
<td>Wagner (1974b); Eriksson and Lundqvist (1982); Lundqvist and Eriksson (1985)</td>
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<tr>
<td>Decreased swimming ability</td>
<td>Glova and McInerney (1977); Smith (1982)</td>
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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 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...

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**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.
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 by-product 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 14C-oleic acid from 14C-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 3H2O 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 glycolytic 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/length²; 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; McCauley 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 silverying, 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.

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 seawater 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 salmonoids, 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 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.
Seasonal Differentiation

**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 (1969); 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).

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

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