

Ontogeny and Evolution of Salinity Tolerance in Anadromous Salmonids: Hormones and Heterochrony

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ABSTRACT: Use of estuaries and oceans by salmonids varies greatly, from no use in nonanadromous species, to movement toward the sea soon after hatching and emergence in some Pacific salmon. This variation is accompanied by large differences in the ontogeny of salinity tolerance among salmonids. Some species acquire increased salinity tolerance early in development, whereas others develop this characteristic much later, indicating there is a heterochrony (change in timing) in the development of salinity tolerance in salmonids. The basic physiological mechanisms for ion regulation in seawater (such as increased gill chloride cells, gill Na^+/K^+ -ATPase activity, membrane permeability, and drinking rate) are common to all salmonids. What determines the differences in salinity tolerance among the salmonids is not the basic mechanisms for salt secretion but the environmental and ontogenetic control of these mechanisms. In salmonids such as pink and chum salmon that enter seawater soon after emergence, acclimation to seawater may be controlled largely by internal (ontogenetic) information. In smolting salmonids that acquire increased salinity tolerance 1-2 yr after hatching, photoperiod is the dominant environmental cue. In nonsmolting species that migrate 2-3 yr after hatching, salinity itself may be the primary stimulus for salt secretory mechanisms. Physiological changes triggered by developmental and environmental cues are mediated by endocrine factors. Treatments with cortisol, growth hormone, and insulin-like growth factor I have been shown to increase seawater tolerance of salmonids, whereas prolactin is inhibitory. Differences in developmental patterns of endocrine activity (such as secretion, binding proteins, and receptors) are hypothesized to be responsible for the differences in timing (heterochrony) of increased salinity tolerance among and within salmonid species.

Variations in Salmonid Life History

Life history characteristics vary greatly among and within salmonid species. This diversity and plasticity are seen not only in the migratory behavior that characterizes anadromy but in many other critical aspects such as size and age at maturation, semelparity versus iteroparity (single versus repeat spawning), and many others. In spite of this variation, some patterns in anadromy among the salmonids are clear. Rounsefell (1958) used six characteristics of the anadromous life cycle (geographical length of migration, duration at sea, state of maturity at sea, spawning habits, mortality after spawning, and occurrence of freshwater forms) to rank the "degree of anadromy" among salmonid species. This comparison indicated that anadromy in the salmonids was least developed in char (*Salvelinus* sp.), more developed in *Salmo*, and most developed in Pacific salmon (*Oncorhynchus* sp.).

A critical component of the variation in anadromy among salmonids is the variability in developmental stage at the onset of seaward migration. Three general (but not completely exclusive) patterns of migratory stage and pattern can be distinguished among salmonids. Pink (*Oncorhynchus gor-*

buscha) and chum (*O. keta*) salmon leave fresh water as fry within a month or two of emergence (Hoar 1988, and references in Fig. 1 for details). Coho (*O. kisutch*), masu (*O. masou*), steelhead (anadromous rainbow trout, *O. mykiss*), and Atlantic salmon (*Salmo salar*) spend at least 1 yr in fresh water, emigrate in spring as smolts, and spend at least 1 yr at sea. Seaward migration of these fishes is a size-dependent or size-related phenomenon; size at migration is remarkably uniform within species, and age at migration has clinal (latitudinal) variation. Brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*), and brook trout (*Salvelinus fontinalis*) usually spend three or more years in fresh water before migrating, when they are larger than 17 cm. Migration of these species is generally in the spring and is limited to the coastal environment for 2-5 mo.

Many salmonids show a marked increase in salinity tolerance that coincides with the period of downstream migration (Hoar 1988). There is a strong correlation between the age at migration and the size at which a species develops the capacity to move directly into seawater (Fig. 1). Like the degree of anadromy outlined by Rounsefell

HETEROCHRONY IN SALINITY TOLERANCE OF SALMONIDS

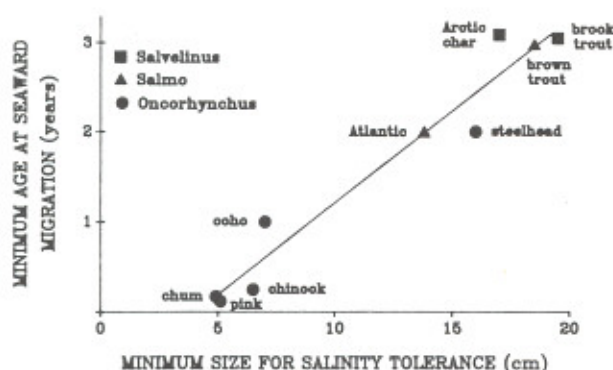


Fig. 1. Relation between minimum age at migration and minimum size at salinity tolerance in several anadromous salmonids. This relation suggests that a heterochrony (change in timing of a developmental event) in salinity tolerance occurred during salmonid evolution. To arrive at comparable ages at migration, southern populations of wide-ranging species were excluded from consideration (e.g., 1-yr-old migrant Atlantic salmon below 35°N latitude in Europe). Physiological measures of salinity tolerance used a direct transfer from fresh water to seawater (>28‰), except the studies on brook trout, which used a stepwise exposure to 30‰. Determination of the size at salinity tolerance were from Parry (1960), Conte and Wagner (1965), Conte et al. (1966), Wagner et al. (1969), Weisbart (1968), Johnston and Saunders (1981), McCormick and Naiman (1984b), Arnesen et al. (1992), and age at migration from Scott and Crossman (1973), Salo (1991), and Kato (1991).

(1958), a general pattern in the development of salinity tolerance exists among salmonid genera, with *Oncorhynchus* having the earliest development of salinity tolerance, followed by *Salmo*, and then *Salvelinus*.

The difference in the developmental stage at which salinity tolerance and migratory behavior occurs in salmonids is a heterochrony, a change in the timing of a developmental event in closely related species. Changes in salinity tolerance (and perhaps other physiological and behavioral changes associated with migration) are an example of a dissociated heterochrony, in which a limited growth field (the cells and tissues responsible for a developmental event, in this case those involved in seawater acclimation) undergoes change independent of other organs (see McKinney and McNamara 1991 for review and terminology used in this section). Systematic analysis and fossil evidence indicate a freshwater origin of salmonids, with *Salvelinus* and related genera occupying a primitive position relative to *Salmo* and *Oncorhynchus* (Fig. 2). Assuming a primitive status of the char, an earlier appearance of salinity tolerance in ontogeny (peramorphosis) has occurred. Because age at maturation is not strongly correlated with

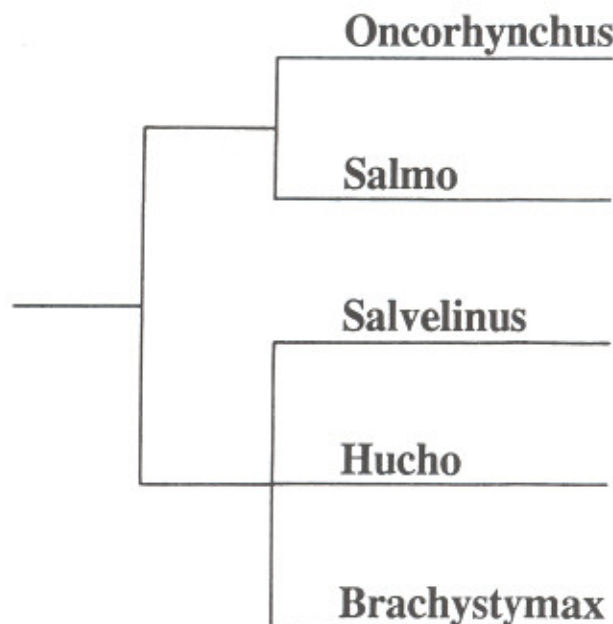


Fig. 2. Phylogeny of extant salmonid genera in the subfamily salmoninae, based on morphological and genetic characters (Norden 1961; Kendall and Behnke 1984; Grewe et al. 1990). The genera *Hucho*, *Brachystymax*, *Salvelinus* lineage is generally regarded as the most primitive (the genera *Parasalmo* and *Salmothymus* are not included due to lack of consensus for their existence and affiliation). Although the family salmonidae contains two additional subfamilies (Coregoninae and Thymallinae), only those genera whose migratory physiology and behavior have been sufficiently investigated are included in the present analysis (*Salvelinus*, *Salmo*, and *Oncorhynchus*). Two major points argue in favor of a freshwater origin for salmonids. First, all extant salmonids can spend their entire life cycle in fresh water, whereas none are wholly marine. Second, the oldest known salmonid in the fossil record is *Eusalmo driftwoodensis* (morphologically intermediate between Thymallinae and Salmoninae), found in freshwater sediments of the Middle Eocene (50 million years before present; Wilson 1977).

the degree of anadromy (Hutchings and Morris 1985), it seems likely that an earlier onset of salinity tolerance, rather than relative alteration in other developmental events has occurred. However, this speculation needs to be examined more thoroughly.

Although the phylogeny in Fig. 2 is consistent with a freshwater origin of salmonids (with *Oncorhynchus* being the most recent and "advanced"), several authors have argued for a seawater origin of salmonids (see Thorpe 1982). A seawater origin would suggest that a delayed development (hypermorphosis) in salinity tolerance has occurred in salmonid evolution. Further research into systematics and paleontology are necessary to answer this question. However, one important and recurring feature is the existence of nonanadromous forms within almost all species of anadromous salmonids

(Rounsefell 1958). The abandonment of anadromy is apparently not, at least in an evolutionary context, a difficult behavioral or physiological constraint. The existence of the many landlocked forms of salmonids suggests that hypermorphosis in seaward migration and perhaps salinity tolerance has occurred in salmonid species.

The analysis of minimum age and size for salinity tolerance (Fig. 1) emphasizes the variation in ontogeny primarily as a function of size. This ignores the important fact that ontogeny acts along with environmental change in several species (discussed in some detail in the next section). Furthermore, hypoosmoregulatory ability increases with size in most salmonids, perhaps because of a more favorable surface area-to-volume ratio. This size-dependent increase in salinity tolerance is distinct from the more rapid, seasonal increase in salinity tolerance in smolts. These seasonal changes are themselves size-related because a critical size must be reached for this development to occur (Wedemeyer et al. 1980; Johnston and Saunders 1981; McCormick et al. 1987).

Physiological Mechanisms for Seawater Adaptation

The basic strategy for maintaining salt and water balance in seawater are similar for all teleosts (Evans 1979). Plasma osmolality is maintained at about one third that of seawater. Fish ingest seawater and absorb ions and water across the gut. The kidney and bladder produce an isosmotic urine with high concentrations of divalent ions; excess monovalent ions are secreted primarily from the gills through cells on the primary filaments known as chloride secretory cells. Both chloride and sodium excretion are dependent on the generation of ionic and electrical gradients by Na^+, K^+ -ATPase that is present in very high concentration in chloride secretory cells (10^8 molecules per cell; Karnaky 1986).

In most euryhaline teleosts, the full complement of these physiological mechanisms are induced after exposure to seawater (Evans 1979). However, in some salmonids these changes are induced before entry into seawater. For instructive rather than exhaustive comparisons, three species (brook trout, *Salvelinus fontinalis*; Atlantic salmon, *Salmo salar*; and chum salmon, *Oncorhynchus keta*) representative of the continuum (Fig. 1) will be used to compare the physiological mechanisms for acclimation to seawater and their regulation.

BROOK TROUT

The brook trout is probably the least anadromous of all riverine salmonids. Most populations remain in fresh water, but anadromous popula-

tions exist from Cape Cod, Massachusetts, north (see Naiman et al. 1987 for review). The timing of migration is variable but generally occurs in spring in northern latitudes. Seaward migrants are usually larger than 16 cm and spend at most 3 mo in coastal seawater. Residence time in brackish water is highly variable and size-dependent, ranging from 1 d to 60 d (Montgomery et al. 1990; see Thorpe 1994 for a review of salmonid behavior in estuaries).

Brook trout display little if any of the changes in gill physiology in fresh water that characterize smolting salmonids. There is no seasonal cycle of gill Na^+, K^+ -ATPase activity in brook trout reared at constant temperature and under simulated natural photoperiod (McCormick and Naiman 1984a). There is no significant difference in gill Na^+, K^+ -ATPase activity between anadromous and nonanadromous brook trout sampled in fresh water in the wild (McCormick et al. 1985). Gill Na^+, K^+ -ATPase activity decreases in both wild and captive stocks of brook trout in late summer as water temperatures increase (McCormick et al. 1985; Besner and Pelletier 1991); whether this reflects a circannual cycle or simply a response to temperature change is unclear.

In contrast to the limited changes that occur in fresh water during ontogeny, exposure of brook trout to intermediate or high salinity results in substantial (3- to 4-fold) increases in gill Na^+, K^+ -ATPase activity (McCormick and Naiman 1984b; Besner and Pelletier 1991), which presumably result from chloride cell proliferation and/or differentiation. Acclimation of brook trout to intermediate salinity prior to transfer to high salinity significantly improves survival (McCormick unpublished observation). McCormick et al. (1985) found that brook trout in estuaries have higher gill Na^+, K^+ -ATPase activity and higher salinity tolerance than brook trout in fresh water, and suggested that estuarine residence was important to the physiological acclimation of brook trout to entry into full-strength seawater. These results indicate that seawater acts as a major stimulant for the induction of mechanisms for salt secretion in brook trout (Fig. 3). It should be noted that stimulation of salt secretory mechanisms by salinity is probably present in *Salmo* and *Oncorhynchus* species as well (Hoar 1988), possibly reflecting the early evolution and retention of this feature.

ATLANTIC SALMON

Anadromy is a more characteristic life-history event of Atlantic salmon than of brook trout. Spring emigration of anadromous Atlantic salmon juveniles 13–16 cm is highly synchronous. Although their estuarine residence is short (1–5 d),

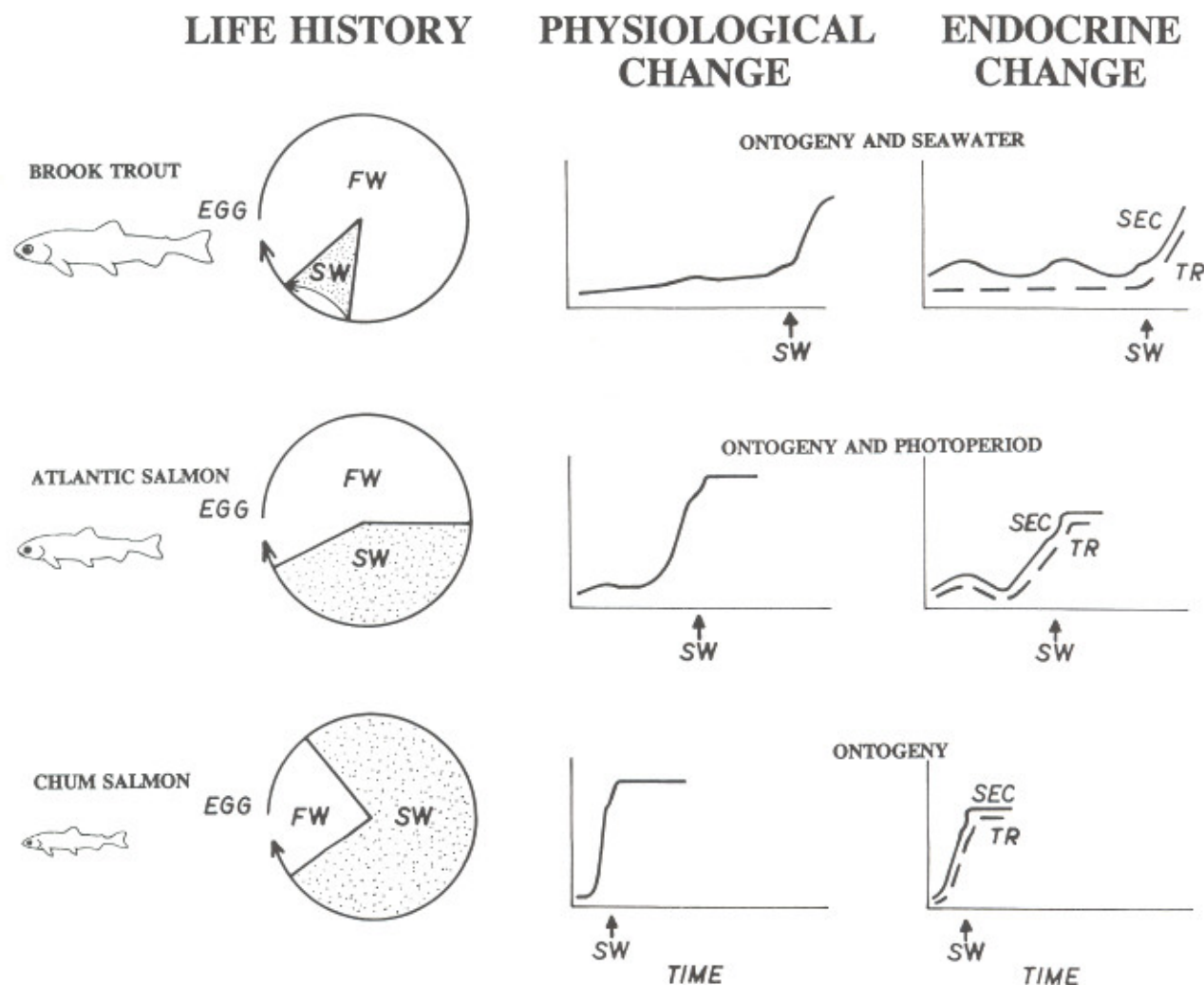


Fig. 3. Comparison of life-history, anadromy, and ontogeny of physiological changes (largely known) and endocrine changes (hypothesized) associated with ontogeny of salinity tolerance in three representative species of anadromous salmonids (brook trout, *Salvelinus fontinalis*; Atlantic salmon, *Salmo salar*; and chum salmon, *Oncorhynchus keta*). The analysis indicates that the ontogeny of salinity tolerance occurs late in development in brook trout, earlier in Atlantic salmon, and earlier still in chum salmon. The factors regulating physiological and endocrine change have shifted from primarily salinity in brook trout, to photoperiod in Atlantic salmon, to ontogeny (genetic developmental program) in chum salmon. Salinity retains at least some function in differentiation of salt secretory mechanisms in all species.

Atlantic salmon apparently do not move directly into seawater but stay in the estuary for at least one tidal cycle (Tytler et al. 1978). The potential importance of this brief estuarine residence to physiological adjustments to salinity should not be overlooked and has yet to be fully investigated. An extensive oceanic migration (>1,000 km) occurs and fish reside at sea for 1–3 yr before returning to spawn.

Coincident with the time of spring migration, captive Atlantic salmon substantially increase salinity tolerance during a 6- to 8-wk period. The physiological mechanisms that permit this increased hy-

poosmoregulatory ability have been investigated in Atlantic salmon and other smolting salmonids with large preparatory changes in fresh water. These changes include increases in chloride cell number and size, gill Na^+/K^+ -ATPase activity, and intestinal absorption, and decreases in glomerular filtration rate (reviewed in McCormick and Saunders 1987; Hoar 1988; Boeuf 1993). These salt secretory mechanisms not only increase the ability of Atlantic salmon to survive direct transfer to seawater but permit smolts to rapidly enter seawater with a minimum of ionic disequilibrium (Fig. 4). This may be adaptive in two ways. First, it permits rapid move-

EXPOSURE OF ATLANTIC SALMON TO 30 ppt SEAWATER

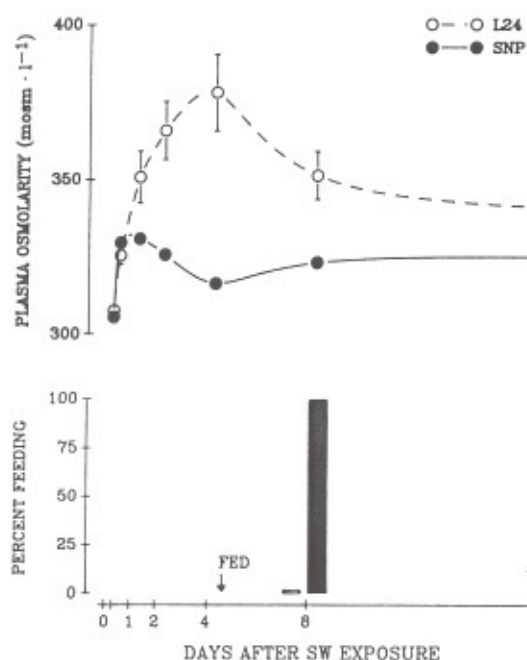


Fig. 4. Plasma osmolarity and percent of Atlantic salmon feeding after transfer to 30‰ seawater. Fish had previously been exposed to either continuous light (L24, nonsmolts) or simulated natural photoperiod (SNP, smolts). Number of fish feeding was determined by examination of gut contents. Details of experimental design can be found in McCormick et al. (1989), where data from upper half of figure originally appeared.

ment through estuaries with a reduction in exposure to predators in the estuary. Second, it permits smolts to avoid the harm from high plasma ions that reduce aerobic capacity, swimming ability, feeding, and growth (Fig. 4; Randall and Brauner 1991), all of which influence the ability of fishes to avoid predators and capture prey in their new environment (Jarvi 1990).

Increases in salinity tolerance in spring and the underlying physiological mechanisms are under photoperiodic control. Atlantic salmon exposed to continuous light soon after hatching do not develop spring increases in salinity tolerance and gill Na^+, K^+ -ATPase activity (Saunders et al. 1985; McCormick et al. 1987). Exposure of Atlantic salmon juveniles on short daylength to increased daylength accelerates the development of salinity tolerance (Clarke et al. 1985; Duston et al. 1991). The response to increased daylength is ontogenetically controlled; fish smaller than 12 cm do not respond to increased daylength with increased salinity tol-

erance or gill Na^+, K^+ -ATPase activity (Wedemeyer et al. 1980; McCormick et al. 1987).

CHUM SALMON

Only a small portion of the life cycle of chum salmon is spent in fresh water (Fig. 3). Within 2–3 mo of hatching and at 3–6 cm in size, chum salmon fry begin their downstream movement. Estuarine residence is variable (1–18 d) and seemingly dependent on the physical, chemical, and biological characteristics of the estuary (Salo 1991). Chum salmon make an extensive oceanic migration of 2 yr before returning to fresh water.

Chum salmon develop remarkable salinity tolerance as fry, coincident with the time of downstream migration (Weisbart 1968). This early development of salinity tolerance is shared by pink salmon (which also migrate at the fry stage), but is clearly absent in salmonids that migrate later. Little is known of the physiological changes that accompany increased salinity tolerance in the fry stage. Sullivan et al. (1983) found slight increases in gill Na^+, K^+ -ATPase activity in pink salmon during early development. Gill Na^+, K^+ -ATPase activity is twice as high in chum salmon fry as in Atlantic, chinook, or coho salmon (McCormick et al. 1991). Salinity tolerance in chum salmon seems to be independent of photoperiod (Clarke et al. 1989), indicating that ontogenetic information rather than environmental stimuli may be responsible for the changes in salt secretory mechanisms in fresh water.

The strategies for acclimation to seawater exemplified by the three species illustrated here represent a continuum of strategies among salmonids. Some species may show more preparatory changes than brook trout, but still use the estuary for acclimation during a period of weeks. Even in species with well-developed salinity tolerance, movement through the estuary over one or two tidal cycles may bring about important physiological adjustments. The existence of such a continuum that involves a suite of adaptations present in varying degrees underscores the difficulty of defining a single set of characters that will apply to all species of smolting salmonids.

Hormones and Heterochrony

The endocrine control of smolting and acclimation to seawater in salmonids has been reviewed in more detail than is possible here (Hoar 1988; Sakamoto et al. 1993). Thyroid hormones (and perhaps other hormones as well) play at least a permissive role in salinity tolerance, and may be more directly involved in other aspects of smolting (e.g., silvering, behavioral and metabolic changes). Three major lines of evidence suggest that growth

hormone and cortisol are primarily responsible for the differentiation of salt secretory mechanisms. First, exogenous treatment with growth hormone or cortisol can increase chloride cell density, gill Na^+, K^+ -ATPase activity, and salinity tolerance. Growth hormone may act directly on osmoregulatory organs or indirectly through insulin-like growth factor I (IGF-I), which can also increase salinity tolerance of salmonids. Cortisol has been shown to act directly on gill tissue to increase gill Na^+, K^+ -ATPase activity and cause differentiation of chloride cells. Second, circulating levels of growth hormone and cortisol usually increase in salmonids during smolting and seawater acclimation, though this finding is not universal (see Sakamoto et al. 1993). Metabolic clearance rate (a putative indicator of tissue uptake) of growth hormone increases in rainbow trout after seawater exposure, as does IGF-I mRNA in gill and kidney. Finally, specific receptors for growth hormone and cortisol are present in the major osmoregulatory organs: gill, kidney, and intestine. It should be emphasized that the ontogeny of salinity tolerance is controlled by several hormones, and probably involves both stimulatory hormones (growth hormone, IGF-I, cortisol, and thyroid hormones) and inhibitory factors (such as prolactin).

Because the development of salt secretory mechanisms is under endocrine control, the ontogeny of this control must differ among salmonids. Consequently, the onset of hormone activity and tissue responsiveness may be earlier in animals that develop salinity tolerance earlier. The cues may shift from salinity in facultatively anadromous salmonids (such as brook trout), to photoperiod in smolting salmonids (such as Atlantic salmon), to ontogenetic information in early migrators (such as chum salmon; Fig. 3). In its simplest form, this hypothesis for the hormonal control of heterochrony suggests that the involved hormones are the same for all species of salmonids, and that the ontogeny and environmental regulation of hormone secretion and tissue responsiveness differs among species. For example, growth hormone and cortisol secretion and their receptors in osmoregulatory organs may be under photoperiodic control in Atlantic salmon but under accelerated ontogenetic control in chum salmon (Fig. 3). The relative importance of hormone secretion and tissue receptors in controlling heterochrony of salinity tolerance might vary widely. For instance, amphibian metamorphosis is controlled primarily by thyroid hormones. Retention of the aquatic larval form as adults (neoteny) has evolved in at least two different ways, either by lack of secretion of thyroid hormones (as in *Ambystoma*), or by loss of tissue responsiveness

to thyroid hormones (as in *Amphiuma*; Rosenkilde 1979).

Evidence of developmental differences in responsiveness of osmoregulatory organs to hormones is limited. Atlantic salmon exposed to continuous light (in which development of salinity tolerance is suppressed) were not responsive to exogenous cortisol treatment, whereas fish under simulated natural photoperiod increased gill Na^+, K^+ -ATPase activity in response to cortisol (McCormick et al. 1991). Na^+, K^+ -ATPase activity in gill tissue of coho salmon increased in response to in vitro cortisol during the parr-smolt transformation, not prior to or at the peak. Tissue responsiveness may also differ among salmonids; at the fry stage, chum salmon gill tissue responded to high levels of cortisol with increased Na^+, K^+ -ATPase activity, whereas gill tissue from chinook, coho, and Atlantic salmon did not respond.

Although this evidence indicates that differences in gill responsiveness are at least partially responsible for the difference in ontogeny of salt secretory mechanisms in salmonids, it is clearly only one part of the puzzle. Possible differences in responsiveness to growth hormone and IGF-I and variations in ontogeny of receptors have yet to be examined. The relative importance of salinity, photoperiod, and development in controlling circulating levels of growth hormone, IGF-I, and cortisol have not been fully elucidated for anadromous salmonids. Comparisons of changes in plasma hormone levels among species and developmental stages reared under identical conditions would be valuable. Examination of endocrine changes in developmental and evolutionary contexts may focus and aid our understanding of these regulatory processes in salmonids.

Differences at the species level have been emphasized, but hopefully not at the expense of appreciation for potential differences within a species. The relative reproductive isolation of anadromous fishes in different rivers and the heterogeneity of habitat among rivers offers substantial opportunity for natural selection. And, if timing and developmental stage of migration are indeed important to survival, natural selection will act upon the ontogeny of neuroendocrine control mechanisms for regulating migration and physiological development. In this regard, Specker (1982) hypothesized that increases in circulating levels of thyroxine (due to its influence on migration) would develop earlier than peaks in cortisol (due to its influence on salinity tolerance) in populations from a long river system relative to those in a short river system. Clarke et al. (1994) provide evidence for a genetic basis of the difference in migration time between fall and spring chinook

salmon. The existence of river-specific adaptations in migratory behavior and physiology has important implications not only for the study of the ontogeny of anadromy, but also for the need to conserve river-specific stocks of anadromous salmonids.

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