Movement, migration, and smolting of Atlantic salmon (*Salmo salar*)

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Abstract: A variety of movements characterize the behavioral plasticity of Atlantic salmon (*Salmo salar*) in fresh water, including movements of fry from redds, establishment of feeding territories, spawning movements of sexually mature male parr, movement to and from winter habitat, and smolt migration in spring. Smolting is an adaptive specialization for downstream migration, seawater entry, and marine residence. While still in fresh water, smolts become silvery and streamlined, lose their positive rheotaxis and territoriality, and begin schooling. Physiological changes include increased salinity tolerance, olfactory sensitivity, metabolic rate, scope for growth, and altered hemoglobin and visual pigments. Through their impact on the neuroendocrine system, photoperiod and temperature regulate physiological changes, whereas temperature and water flow may initiate migration. Smolt survival is affected by a limited period of readiness (a physiological “smolt window”) and the timing of seawater entry with environmental conditions such as temperature, food, and predators (an ecological “smolt window”). Smolt development is adversely affected by acidity, pollutants, and improper rearing conditions, and is often more sensitive than other life stages. Unfortunately, the migration corridor of smolts (mainstems of rivers and estuaries) are the most heavily impacted by pollution, dams, and other anthropogenic activities that may be directly lethal or increase mortality by delaying or inhibiting smolt migration.

Résumé: Une grande variété de déplacements caractérise la plasticité comportementale du saumon de l’Atlantique en eau douce, notamment le départ des alevins qui quittent le nid, l’établissement de territoires d’alimentation, les déplacements génésiques des tacons mâles sexuellement matures, les allers-retours vers les zones d’hivernage, et la dévalaison des smolts au printemps. La smoltification est une spécialisation adaptative enn vue de la dévalaison, de l’entrée dans l’eau salée, et du séjour océanique. Alors qu’ils sont encore en eau douce, les smolts prennent leur livrée argentée et leur forme devient plus hydrodynamique, ils perdent leur rhéotaxie positive et leur territorialité, et commencent à se rassembler en bancs. Ils subissent des changements d’ordre physiologique : tolérance accrue à la salinité, sensibilité olfactive, métabolisme, potentiel de croissance et modification de l’hémoglobine et des pigments visuels. Par leur impact sur le système neuroendocrinien, la photopériode et la température régulent les changements physiologiques, tandis que la température et le débit peuvent déclencher la migration. La survie des smolts est affectée par l’existence d’une période limitée de condition optimale (une « fenêtre physiologique ») et par la synchronisation de l’entrée en eau salée avec des conditions environnementales comme la température, la nourriture, et la présence de prédateurs (une « fenêtre écologique »). Le développement des smolts est négativement affecté par l’acidité, les polluants, et les mauvaises conditions de grossissement, et ce stade est souvent plus vulnérable que les autres. Malheureusement, le corridor de migration des smolts (cours principal des cours d’eau et estuaires) passe par les eaux les plus fortement touchées par la pollution, les barrages, et d’autres activités humaines qui peuvent avoir un effet létal direct ou accroître la mortalité en retardant ou en empêchant la migration des jeunes saumons.

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Introduction

Migration is the hallmark of salmon life history. When juvenile Atlantic salmon (*Salmo salar*) reach a certain size-related developmental stage in fresh water, they leave their rearing tributaries in spring and begin a journey that will take them downriver, through estuaries, and hundreds or thousands of kilometres to ocean feeding areas. Prior to and during this downstream movement, they display many complex physiological, behavioral, and morphological adaptations for seaward migration and life at sea. Along with these complex changes, smolts face other challenges: new food sources, diseases, parasites, and predators, which make the smolt stage a critical one in which mortality can be high and variable. Growth opportunities for salmonids are generally better at sea than in fresh water, but natural mortality may be

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higher in the marine environment. The “decision” as to whether the population or individual gains greater advantage from migration or residence depends on the balance of these two factors (see Jonsson and Jonsson 1993; Thorpe 1994). The much greater fecundity of anadromous females and reduced mortality of eggs and fry in fresh water are the apparent rewards for undertaking the risks of anadromy (Gross 1987).

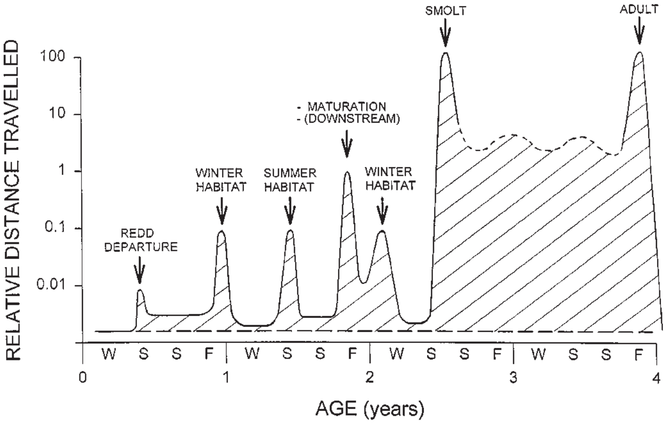
In addition to the smolt migration, Atlantic salmon make other movements in fresh water that are important to their survival (Fig. 1 and next section), including movements to winter habitat and spawning movements of mature parr. Because smolting, winter survival, and sexual maturation require high levels of stored energy, feeding and growth are of prime importance during freshwater residence. Movements, then, are mainly associated with attaining the maximum amount of food or a suitable habitat while avoiding predation or other sources of mortality.

The downstream movement of smolts is a “true” migration, being highly directed, temporally synchronous, and occurring in virtually all individuals of the appropriate developmental stage. It is less clear whether the movements made by Atlantic salmon before smolting are migrations and no single definition of this term is accepted by all or even most biologists. Dingle (1996) defined migratory behavior as “persistent and straightened-out movement effected by the animal’s own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence.” He also considered that migration is persistent, straightened-out (directed), undistracted by resources that would ordinarily halt it, has distinct departing and arriving behavior, and requires a special allocation of energy. Under these terms, salmon movements in fresh water would not be considered migrations unless they were directed (e.g., upstream or downstream) and could not be stopped by encountering a particular resource (e.g., habitat or food). We do not know whether all Atlantic salmon movements fulfill this definition, but in many cases they clearly do not. While it is beyond the scope of the present undertaking to classify salmon movements, we will conservatively interpret most (but not all) nonsmolt movements in fresh water as meeting the more general criteria of “movement” rather than the more restrictive “migration.” Although some of these considerations are semantic, they facilitate our understanding of the external stimuli and internal motivation that underlie the initiation and cessation of juvenile salmon movements.

We also note that salmon can successfully complete their life cycle without migrating. Maturation of male as parr is common in many Atlantic salmon populations and there are also several populations of “dwarf” Atlantic salmon in Newfoundland in which both females and males mature in streams (Sutterlin and Maclean 1984). There are also many “land-locked” populations in which smolts migrate downstream but reside in lakes rather than the sea (Berg 1985). This capacity to complete their life cycle without anadromy further demonstrates the plasticity of salmon life history traits.

This paper reviews the movements and migrations of juvenile Atlantic salmon in fresh water from “swim up” fry to the smolt stage and discusses possible motivations for these behaviors. We also describe the smolting process in terms of physiology, morphology, and behavior and discuss the possible role of olfactory imprinting in relation to these factors. Finally, some factors affecting the mortality of smolts during downstream migration and the transition from fresh to salt water are reviewed and fruitful areas of future research are presented.

Fig. 1. Movement patterns of Atlantic salmon. Filled area represents the range of estimated distances travelled for a given life history stage. A representative 4-year life cycle (2-year-old smolt) is shown on the x-axis (W = winter, S = spring and summer, F = fall). Relative values for distance travelled are approximate and taken from literature discussed in section on “Fry and parr movement.” Smolt migration distance includes both river and initial ocean migration.



Fry and parr movement

We have divided the movements of juvenile Atlantic salmon prior to the smolt transformation into five phases: (1) movement of fry from the vicinity of their redds; (2) establishment and occupation of feeding territories; (3) spawning movements of sexually mature male parr; (4) shifting from summer feeding territories to winter habitat; and (5) descent from nursery streams to lower reaches of some rivers in late autumn as a forerunner or component of smolt migration.

Movement of fry from redds

Spawning areas are typically gravel beds with moderate current velocity and depth (Fleming 1996). When their yolk is largely or entirely absorbed, the fry emerge from the gravel, mainly at night (Gustafson-Marjanen and Dowse 1983; Crisp and Hurley 1991*b*). Crisp and Hurley (1991*a*) noted that fry disperal rates were low at water velocities similar to their preferred velocities (25–70 cm@s^{-1}) and that dispersal rates were higher at lower water velocities. There is, then, a tendency for the newly emerged fry to seek areas with moderate current velocity rather than calm water. R.L. Saunders (unpublished observations) noted that fry that had recently completed yolk absorption delayed first filling of their swimbladders in high water velocities. In their study of movements of underyearling fry in a small coastal stream during August–September, Saunders and Gee (1964) observed that most fry were found in shallow riffles with more moderate current velocity compared to the faster riffles and coarse substrate occupied by older, larger parr. In their first summer, fry tended to remain in the area of their initial capture; those recaptured in adjacent areas were near where they were first observed. In early December fry had moved into nearby parr habitat. However, the sensitivity of many studies of stream-dwelling fishes to movement outside the study area is low and there is good reason to question the assumption of limited movement (Gowan et al. 1994).

The apparent tendency of fry to remain in localized areas is important in several respects. First, juvenile salmonids are incubated with full-siblings and maternal half-siblings (same mother and different fathers) and the general tendency of salmonids to associate with siblings (reviewed by Brown and Brown 1996) suggests that families might remain together for some time after emergence. Such nonrandom distribution patterns could result in marked variation in family-specific growth and survival. Second, limited movement by juveniles, regardless of family, has important management implications. Hatchery-reared fry may not move far from release sites; hence, releases should be in small groups, widely dispersed in suitable shallow riffles (Crisp 1995; McMenemy 1995).

Movements of parr

Parr, in their second or succeeding juvenile years, are typically found in fast flowing riffles in association with rough gravel substrate and they defend feeding territories against other parr and heterospecifics. (Kalleberg 1958; Keenleyside and Yamamoto 1962; Gibson 1966, 1993). The size of the territory depends on the size and density of parr, food availability, the size and roughness of the substrate, and current velocity (Kalleberg 1958; Grant et al. 1998). Territorial and efficient position-holding behaviors (Arnold et al. 1991) enable parr to maximize their opportunity to capture floating aquatic and terrestrial invertebrates (Godin and Rangeley 1989; Gotceitas and Godin 1992). This positioning is facilitated by a reduced swimbladder volume and resulting increased density of parr at high-water velocity (Saunders 1965).

Atlantic salmon are not confined to stream riffles at the parr stage but may also be in slow-moving water such as pools (e.g., Saunders and Gee 1964). Parr tended to remain in the type of habitat where they were first observed but moved from riffles to pools during periods of low water, usually returning to riffles when water level rose again. Parr displaced up- or down-stream were subsequently observed at their original capture sites within 14–39 days (Saunders and Gee 1964). Saunders (1960) noted that where brook trout (*Salvelinus fontinalis*) were abundant in pools, their preferred habitat, salmon parr were absent from these pools whereas in allopatry salmon occupied pools.

In addition to movements within the natal stream, salmon may move to other rearing sites. For example, in a large Finnish river (the Teno), fry left the main river and entered tributaries too small for spawning, where they grew faster and attained a larger size as smolts than in the main (spawning) stream (Erkinaro and Niemelä 1995). Parr often move into the small tributaries during summer and remain there until they leave as smolts one or more years later. The small tributaries have much rougher substrate than the spawning stream, not only producing more food organisms but also better winter habitat. In some instances parr may move to cooler tributaries to avoid high temperatures (R.A. Cunjak, personal communication). Armstrong et al. (1997) observed that a few 1-year-old and older fish moved into an area that had been depleted of juvenile salmon but that most fish did not move far from their small territories. Thus, fish that colonize new areas may represent a small number of highly mobile individuals. It is unclear whether all fish have a weak tendency to move and movement is influenced primarily by environmental factors, or whether there are mobile and sedentary individuals in each population as reported for chinook salmon (*O. tshawytscha*; Bradford and Taylor 1997). We currently have a very limited understanding of the risks associated with parr movements and the rewards of colonizing new areas.

In many Newfoundland streams, parr move up or downstream to lakes within the stream system (Chadwick 1982; Hutchings 1986), where parr are observed singly or in small schools. Salmon parr from some streams may also spend weeks or months in estuaries during the summer (Cunjak et al. 1989, 1990; Power and Shooner 1966). Cunjak et al. (1989) reported that the larger parr in estuaries apparently went to sea as smolts whereas the smaller ones probably returned to their natal stream in autumn. Thus, although salmon parr generally have territories and a rather limited home range, they can occupy habitats ranging from riffles to pools and lakes within the stream system and even to estuaries. The extent to which population pressure influences the movement from riffles to other habitats is a subject needing further investigation.

Movements of mature male parr

Apart from the habitat choices of parr rearing in streams, some males become sexually mature and move up or down stream to spawning sites (Buck and Youngson 1982; Youngson et al. 1983). It was believed for some time that mature male parr were incapable of stimulating large anadromous females to spawn and that the male parr served only as satellite spawners, dashing in at the last second to contribute their milt (Jones and King 1952). During courtship, the large anadromous males repeatedly chase away the parr but cannot do so during the crucial moment when the large fish release their spawn. However, Hutchings and Meyers (1985) reported that sexually mature male parr are capable of spawning with anadromous salmon (grilse) in the absence of large anadromous males. Mature parr eat salmon eggs (Cunjak and Therrien 1996), which could have an important function in providing energy to replace that expended in the production of gonads and participation in spawning.

Movements to winter habitat

Juvenile Atlantic salmon take advantage of seasonally warm water to maximize food intake and growth but they must conserve energy during winter when food is less available and maintaining station in rapidly flowing water would have a high energy cost. Usually they enter spaces under or between stones, sometimes in excavations associated with redds made the previous autumn (Cunjak 1988; Erkinaro et al. 1994). The size of the “home stone” is usually correlated with the size of the parr (Cunjak 1988). Winter sites are often in the same area as summer feeding territories (Saunders and Gee 1964; Rimmer et al. 1983) but there is some movement, probably in response to changing physical and chemical conditions and the availability of food (Cunjak and Randall 1993; Cunjak 1996). Smirnov et al. (1976), Riddell and Leggett (1981), and Cunjak (1988) emphasized that parr have reduced daytime activity during winter, leaving their hiding places at night to feed. This is in keeping with the observation that salmon parr become negatively phototactic in winter (Rimmer 1980). Daytime hiding behavior in winter allows parr to maintain position without great expenditure of energy and may make them less vulnerable to predation at a time when they have a reduced escape response. Hiding in the stream bed does not entirely preclude salmon from feeding during winter. Riddell and Leggett (1981) and Cunjak (1988) observed that overwintering parr consume some food but the rates of consumption and digestion are probably quite low because low temperatures are only slightly above freezing in most salmon nursery streams during midwinter. Cunjak (1988) discussed the importance of winter feeding to maintain energy reserves in dealing with stresses associated with drastic physical and chemical conditions as well as those resulting from human activity.

Autumn downstream movement of presmolts

In some headwater tributaries the large parr, those likely to become smolts the following spring, depart their summer rearing areas and move downstream for some unknown distance, not necessarily entering an estuary or the sea (e.g., Meister 1962). R.L. Saunders (unpublished observations) marked large parr moving downstream past a counting weir on the headwaters of the Northwest Miramichi River, New Brunswick in the early 1960s. A few of these marked fish were recaptured the following spring at a counting weir farther down river, 12 km above head of tide. It was assumed that the marked fish spent the winter at some location between the two counting fences. Riddell and Leggett (1981) found large numbers of parr moving downstream and out of Rocky Brook (an upriver tributary of the Southwest Miramichi River) in autumn and that there was no smolt migration in Rocky Brook the following spring. Youngson et al. (1994) described a similar autumn migration of parr and their contribution to the fishery from Girnock Burn, an upriver tributary of the River Dee in Scotland. Such movement to larger, downriver habitats in winter may reflect a need for appropriate physical habitat or greater energy input than is available in the nursery stream. Riddell and Leggett (1981) suggested that the habitat which is suitable in summer and winter for smaller parr is unsuitable for larger parr because the gravel substrate is too small to provide refuge. In such salmon populations, one might view the smolt run as beginning with the downstream migration of large parr in late autumn. If salmon become imprinted to the odors of their nursery stream and this is the mechanism by which they return to that stream, imprinting in such stocks must take place no later than the autumn when they emigrate from their natal stream (Dittman and Quinn 1996).

Researchers and management agencies should consider these movements by juvenile salmon at various life stages. It is important to understand both the “typical” movement of juveniles and the full range of possible movements (Fig. 1). In addition, differences in behavior attributable to distinct populations or river habitats will be important to conservation of populations (Saunders 1981).

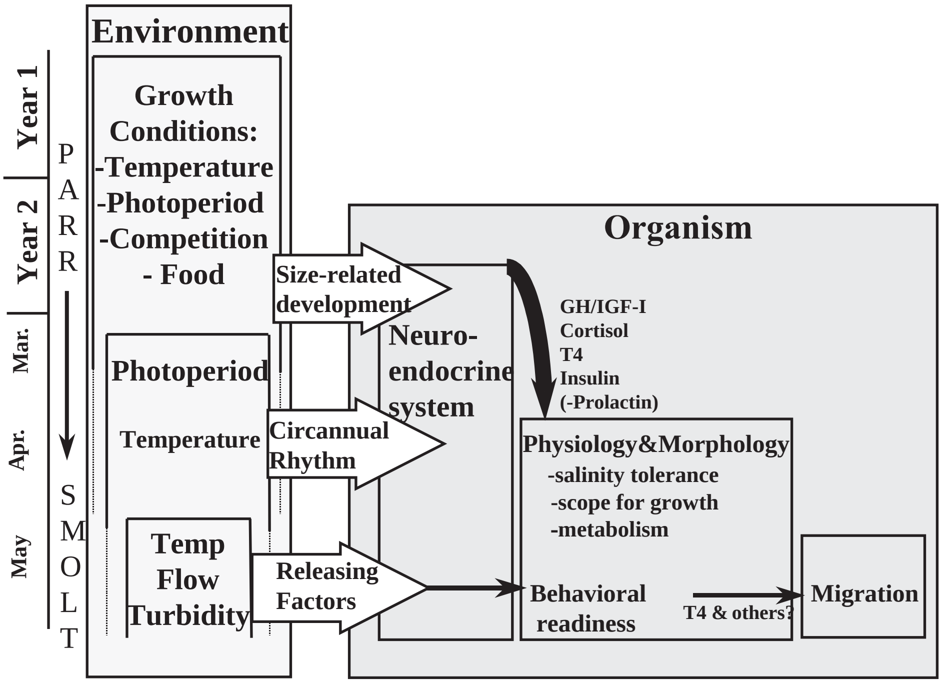
Smolt physiology

Extensive research on the physiology of smolting has been conducted over the last 20 years, due in part to the demands of the salmon culture industry and government enhancement programs that release billions of salmonid smolts annually. The extent of this research is exemplified by the five International Smolt Workshops that have been held since 1982, the proceedings of which have been published in the journal *Aquaculture* (Volumes 28, 45, 82, 121, and 168). Rather than comprehensively review this material (as has been done by McCormick and Saunders 1987, Hoar 1988, and Boeuf 1993), we will present an overview of smolt physiology that emphasizes factors that are relevant to our understanding of the population biology of Atlantic salmon and future research efforts.

Several morphological changes are obvious during smolting. The deposition of guanine and hypoxanthine in the skin and scales covers the parr marks and results in the external silvering that is characteristic of smolts. Reflective silvering is common to many pelagic fishes and is presumably adaptive for predator avoidance. Darkened fin margins also characterize Atlantic salmon smolts. Smolts grow more in length than weight, resulting in reduced condition factor (weight relative to length) (S.D. McCormick, unpublished results). Loss of total body lipid during smolting also reduces condition factor (Wedemeyer et al. 1980). It is unclear whether lower condition factor is part of an adaptive change in morphology during smolting (e.g., to increase swimming performance in open water) or if it results from the energetic demands of smolt transformation. The emergence of teeth and changes in body shape that have been found in coho salmon, *Oncorhynchus kisutch* (Gorbman et al. 1982) have not been demonstrated in Atlantic salmon.

Many of the physiological changes that occur in Atlantic salmon smolts in fresh water are adaptive for seawater entry. These include development of a high level of salinity tolerance, increased scope for growth in seawater, shift in visual pigments from porphyropsin to rhodopsin (the latter characteristic of ocean fishes, Alexander et al. 1994), change in hemoglobin to the adult isoforms (Koch 1982), and increased buoyancy (Saunders 1965). The development of salinity tolerance is obviously important to seaward migrants and has been the most widely studied physiological change that occurs during smolting. The mechanisms for increased hypoosmoregulatory ability include differentiation of the gill, gut, and kidney (McCormick and Saunders 1987). Increased gill Na^+, K^+-ATPase activity, number and size of gill chloride cells, and intestinal water permeability have been strongly linked to increased salinity tolerance during smolting (Boeuf 1993). Although parr can survive gradual acclimation to seawater (Duston 1994), smolts can directly enter seawater with minimal ionic disturbance (Hoar 1988). This heightened hypoosmoregulatory ability permits uninter-

Fig. 2. Multiple interactions between the environment and the organism that lead to smolt development. Growth conditions such as temperature, food, photoperiod, and competition determine growth of Atlantic salmon parr. A critical size (or size-related development stage) is necessary for smolting to proceed and thus environmental conditions determine the age at which smolting occurs. Once this developmental stage has been reached photoperiod and to a lesser degree temperature regulate neuroendocrine changes that bring about physiological changes in spring. Releasing factors such as temperature, flow, and turbidity may have rapid effects (dashed arrows) to initiate downstream migration. Development of the smolt physiological condition (which presumably includes a behavioral readiness or a migration disposition), induced by prior development, photoperiod, and temperature, is necessary for releasing factors to initiate downstream migration (see also Baggerman 1960). The possible neuroendocrine or physiological mediators of these rapid effects are not currently known.



rupted feeding after seawater transfer, whereas nonsmolts experience high plasma ion concentrations and delayed feeding for several days (McCormick 1994). The increased salinity tolerance of smolts also permits decreased estuarine residence time (Tytler et al. 1978; McCormick et al. 1985) and improved swimming performance in seawater (Jarvi 1989), both of which may reduce exposure to estuarine predators. Smolts are adapted not just to survive in seawater, but to thrive there.

It should be emphasized that smolting is fundamentally a developmental phenomenon; juvenile Atlantic salmon must be of an appropriate size-related developmental stage or they will not smolt in response to environmental cues (Fig. 2). In the wild this translates to a lower age at smolting in southern latitudes with long growing seasons (1-year-old smolts in Spain, France, southern British Isles, and New England) and increasing smolt age with increasing latitude (usually 2–4 year old smolts; Wedemeyer et al. 1980; Hutchings 1998; Metcalfe 1998). The precise nature and proximate (neuroendocrine) regulators of this size-related development in smolting are unknown.

Of the environmental factors that regulate physiological development during smolting, photoperiod has the greatest influence. Seasonally advanced increases in daylength or out-of-phase photoperiod can advance smolting by many months (Duston and Saunders 1995). Although there is some evidence for an endogenous rhythm of smolting (Eriksson and Lundqvist 1982; Duston and Saunders 1990; McCormick et al. 1995*a*), increased daylength is probably necessary for complete smolting to occur. The capacity of photoperiod to affect smolting may be restricted at low temperatures (<3°C, McCormick et al. 1995*b*), indicating that temperature may be a controlling factor in smolting (Fry 1971). Temperature also has a role in the timing of smolt development that may be more direct and of particular importance in wild fish. Several laboratory studies indicate that increasing mean daily rearing temperatures from 2 to 10°C can advance smolting (as judged by peak gill Na$^+$, K$^+$-ATPase activity) by up to a month. In reviewing the influence of temperature on smolt development, McCormick et al. (1996) concluded that although increased temperature was not necessary for the completion of smolting, it acted with photoperiod to advance smolting and could act as a directive factor in the absence of photoperiod cues. High temperature increases the rate of loss of physiological smolt characteristics (Duston et al. 1991; McCormick et al. 1996) and has serious implications for smolt survival in the wild (discussed below).

The neuroendocrine system is the primary means of transmitting environmental change to physiological response and there is strong evidence that smolting involves the coordination of several endocrine systems (Bern 1978). This can be contrasted with metamorphic events in flounders and amphibians that are primarily stimulated by thyroid hormones, although other endocrine systems are certainly involved. Growth hormone, insulin-like growth factor I (IGF-I), cortisol, and thyroxine have all been implicated in the development of salinity tolerance in smolting and these hormones all increase during smolting (Hoar 1988). Increased daylength has a strong positive effect on growth hormone levels in smolts (Björnsson et al. 1989; McCormick et al. 1995*a*) and, to a lesser extent, stimulates plasma levels of IGF-I, cortisol, and thyroxine (McCormick et al. 1995*b*). Relatively little is known about the possible influence of temperature on these hormones during smolting of Atlantic salmon. Prolactin has a negative influence on salinity tolerance, perhaps through its antagonism of the action of growth hormone (Madsen and Bern 1992). Most of the evidence for the involvement of hormones in smolting has been in relation to their effects on salinity tolerance. Although thyroid hormones influence silvering, hemoglobin forms, and retinal pigmentation (Hoar 1988; Alexander et al. 1994), endocrine control of other aspects of smolting have not been widely examined. The influence of hormones on migratory behavior would be especially interesting but has not been widely examined in fishes.

Maturation of male parr reduces but does not eliminate the probability of later smolting (Saunders et al. 1982; Hansen et al. 1989; Berglund et al. 1991). Previously mature parr released into the River Imsa in spring were 30% less likely to migrate than immature parr (Hansen et al. 1989). Large mature parr can smolt the following spring (Saunders et al. 1994) and it is possible to increase the proportion of the mature males that smolt by keeping them in heated water during winter (Berglund et al. 1991) or by stripping the mature parr in the autumn (Hansen et al. 1989; Greenstreet 1992). Sex steroids have a negative effect on several aspects of smolt development including salinity tolerance and migratory behavior (Lundqvist et al. 1989; Berglund et al. 1994). However, sex steroids in previously mature salmon parr have returned to low levels well before completion of smolting in spring (Mayer et al. 1990; Shrimpton and McCormick, unpublished data) indicating that the negative influence of maturation on smolting may be part of developmental decisions determined well in advance of spring changes in smolt physiology (Metcalfe 1998). Although increased size results in greater incidence of mature male parr, maturation has a negative effect on growth in autumn (Berglund 1992). Maturation may therefore affect the probability of smolting simply by influencing fish size, causing some fish to fall below the size threshold for smolting. It remains to be seen whether other mechanisms are also invovled.

Although the patterns of smolt development vary among populations, the genetics of smolting have not received much research attention and there is conflicting information. Birt et al. (1991) found substantial differences between anadromous and nonanadromous populations of Atlantic salmon in Newfoundland. The anadromous stock had higher gill Na^+, K^+-ATPase activity, more and larger gill chloride cells, and greater silvering than a nonanadromous stock. Although no difference in salinity tolerance was found, the authors suggested this may have been due to the low salinity (32 ppt) used in these tests (other studies have used 35–40 ppt). Reduced salinity tolerance has been found in other nonanadromous stocks in Newfoundland (Burton and Idler 1984). In contrast, Staurnes et al. (1992) found no difference in gill Na^+, K^+-ATPase activity and silvering between anadromous and nonanadromous strains in Norway. Orciari and Leonard (1996) found that fish that originated from the Penobscot River, Maine, and from Icelandic rivers developed differently when transplanted in a tributary of the Connecticut River as fry; smolts from Icelandic stocks were smaller and migrated earlier than Penobscot or Connecticut river strains. These studies indicate that genetic factors are important in size at smolt development, intensity of physiological changes, and timing of migration. Population-specific differences in smolt development could be very important to conservation and restoration and deserve much more attention. For instance, the trajectory of smolt development and migratory behavior may be quite different in fish from long rivers (where physiological development may follow initiation of migration) compared to fish in short rivers where physiological development may precede migration. Extinction of stocks, as has occurred in southern New England, may make restoration difficult due to the loss of adaptive features characteristic of regions or watersheds.

Smolt migration

Behavioral changes during smolting

Numerous behavioral changes occur during downstream migration of smolts, including increased negative rheotaxis (i.e., downstream orientation) and schooling, decreased agonistic and territorial behavior, and increased salinity preference (Hoar 1988; Iwata 1995). Although endogenous rhythms in smolt-related behavior may occur, the studies described below strongly indicate that behavioral changes during smolting are dependent on environmental change. For instance, Gibson (1983) found that Atlantic salmon parr and smolts in artificial streams had similar agonistic behaviors that did not change in spring and concluded that smolt-related increases in buoyancy and seasonal increases in water velocity were necessary to cause decreased agression and downstream migration. Findings such as these also underscore the interelation between physiological and behavioral changes during smolting. Baggerman (1960) suggested that “migration occurs only when the animals are in the proper physiological condition (migration disposition) and at the same time under the influence of appropriate external stimuli which act as releasers.” The interaction of internal developmental events, environmental “priming” factors (which bring about “migration disposition”) and “releasing” factors is shown in Fig. 2. The importance of light, temperature, and water flow as releasing factors that act to initiate downstream migration of smolts is discussed below. It should be noted that most of these studies rely on correlations and there is little experimental evidence establishing the environmental factors that initiate migration. In addition to these environmental factors, other factors such as social cues (i.e., the presence of other migrants) may play a role in initiating downstream migration (Hansen and Jonsson 1985). The synchronous nature of smolt migration (occurring over a 3–6 week period in most populations) is due to the individual smolts reaction to these releasing factors and may have the adaptive value of overwhelming predators by sheer numbers.

Light

As discussed above, photoperiod is the seasonal "zeitgeber" that triggers a complex series of physiological events that prepare salmon for migration. Although photoperiod influences migratory behavior of Pacific salmon smolts (see Hoar 1976), there has been no direct investigation of the role of photoperiod in regulating behavioral changes in Atlantic salmon smolts. By analogy to other vertebrate migrations, photoperiod may act to increase activity (migratory restlessness or Zugunruhe) and make fish sensitive to other factors (releasing factors) that initiate migration. Thus, photoperiod may determine the range of dates during which migration may occur but other factors such as water temperature, flow, and turbidity may act as releasing factors.

Smolt migration usually takes place during the night, but towards the end of the migration period smolts are also observed during the day (e.g., Osterdahl 1969; Thorpe and Morgan 1978). The fact that smolts move downstream at night may be an adaptation to avoid potential predators (Solomon 1982). At high latitudes in areas with midnight sun, Atlantic salmon and brown trout (*Salmo trutta*) smolts migrate during hours of strong sunlight (see Thorpe and Morgan 1978 for review). In a Swedish river at 64°N, Osterdahl (1969) observed a change from nocturnal migration in late May and early June to a diurnal pattern in late June. There was no information on the length of the night during the smolt run, but at this latitude in May and June the nights are short and there is no period of real darkness. Daytime migration may also occur farther south; in the River Piddle, U.K., many Atlantic salmon smolts migrated in bright sunlight, whereas brown trout smolts migrated primarily in the early hours of the night (Solomon 1978). Moreover, Fraser et al. (1993) maintained that late descending smolts tended to migrate during daytime because the higher water temperature increases their ability to avoid endothermic predators such as birds.

Temperature

Water temperature is one proximate factor initiating downstream migrations in fish (Jonsson 1991). Several studies have shown that increasing water temperature in the spring is strongly correlated with the initiation of the smolt run (e.g., White 1939; Mills 1964; Osterdahl 1969; Bagliniere 1976; Solomon 1978; Jonsson and Ruud-Hansen 1985). Several authors have reported that downstream migration of smolts of Atlantic salmon and brown trout occurs at about 10°C or slightly above (White 1939; Mills 1964; Osterdahl 1969; Solomon 1978). Jonsson and Ruud-Hansen (1985) reported that only water temperature, not water flow, turbidity, or lunar cycle influenced the timing of Atlantic salmon smolt migration in the River Imsa. The increase in water temperature between 9 April and 16 May explained 91, 95, and 89% of the yearly variance in the date of 25, 50, and 75% yearly cumulative smolt descent, respectively. Smolts began to descend at temperatures between 5.8–11.2°C and the smolt run started early in years when the water temperature was high or when the increase in temperature was rapid, indicating that for the River Imsa the timing of smolt descent was controlled by a combination of temperature and temperature increase during spring rather than by a specific water temperature or by degree-days. Direct experimental evidence would help determine whether these correlations are causally related to the initiation of smolt migration.

Water flow

High water flow in rivers may stimulate downstream movement in a large number of fish species (Jonsson 1991) and the downstream migration of smolts has been linked to increased water flow (e.g., Berry 1932, 1933; Allen 1944; Osterdahl 1969; Hesthagen and Gärnäs 1986). In the River Orkla, Norway, Hesthagen and Gärnäs (1986) observed that migration of Atlantic salmon smolts was initiated by the first spring peak in water discharge when the water temperature was above 2–3°C. It has been hypothesized that smolt migration is a result of a passive displacement (Tytler et al. 1978; Thorpe et al. 1981), although this hypothesis has gained little general support (Thorpe and Morgan 1978; Solomon 1978; Kennedy et al. 1984; Bourgeois and O'Connell 1988). It is clear, however, that smolts migrate more quickly at high water flow than low (Youngson et al. 1989). Smolts appear to move actively out into the main current of the river to avoid being caught in backwaters and sloughs (Hansen and Jonsson 1985), indicating that the descent is not purely passive. Similarly, smolts migrating through lakes move faster than the downstream current velocity (Groot 1965; Bourgeois and O'Connell 1988), suggesting that local adaptations in this trait may occur in salmonids reared above lakes (but see Thorpe et al. 1981 for evidence to the contrary). In both the rivers Gaula and Surna, the survival of hatchery-reared smolts improved significantly when they were released at high water discharge within the normal period of migration (Hvidsten and Hansen 1988), as was also observed in rivers in Maine, U.S.A. (Hosmer et al. 1979). This may be because they migrated at a faster speed and were closer to the water surface, using high turbitidy to make them less visible to predators.

Estuaries and fjords

Knowledge of salmonids in the early marine phase is relatively scarce and has been reviewed by Thorpe (1994). The estuarine residence time of Atlantic salmon is relatively brief, generally lasting only one or two tidal cycles (Tytler et al. 1978). In estuaries schools of postsmolts reside in and are displaced with the surface current and movement is influenced by the tide and the direction of the water flow (Carlin 1969; LaBar et al. 1978; Thorpe 1988; Pethon and Hansen 1990; Jonsson et al. 1993). Several authors have concluded that smolts in the upper estuary move by selective ebb tide transport (Fried et al. 1978; Moore et al. 1995) but display active swimming in the lower estuary or bays (Moore et al. 1995; Lacroix and McCurdy 1996). Tytler et al. (1978) found that hatchery fish spent less time in the estuary than wild fish, although the possibly greater effect of the stress of tagging on wild fish cannot be ruled out. The marine migration of Atlantic salmon has recently been reviewed by Hansen and Quinn (1998).

Olfactory imprinting

The differentiation of conspecific populations of Atlantic salmon and other salmonids, which makes their management complex, arises in part from their tendency to learn site-specific odors during freshwater residence and seaward migration and seek these odors when they mature years later. This homing behavior isolates populations which, under the pressure of natural selection in different habitats, adapt to their local environment (Saunders 1981; Taylor 1991). The patterns of olfactory learning that enable the salmon to home are thus critical aspects of their freshwater lives.

Although it is widely known that salmon usually return to their river of origin to spawn, two important issues remain unresolved for Atlantic salmon and their Pacific relatives. First, do salmon learn the site-specific odors at a single, critical period (“imprinting”) or do they learn odors in sequence during all or part of their lives? Second, what is the interplay between homing and spawning site selection in determining the distribution of spawning adults? Both questions pertain to the spatial precision of homing, hence the potential for genetic isolation among progressively small local groups; however, only the first of these two issues will be discussed here.

Experimental studies on the spatial and temporal aspects of olfactory imprinting have generally taken one of two forms: displacement of salmon from their rearing site for release elsewhere and exposure of juvenile salmon to artificial odors at selected developmental stages. Displacement experiments, such as those conducted by Donaldson and Allen (1958) with coho salmon (*O. kisutch*), revealed that almost all salmon returned to their release site, not to the site where they were reared. Similar results have been obtained with Atlantic salmon (e.g., Carlin 1969; Potter and Russell 1994). Not only do salmon generally return to the river where they were released but they also tend to return to a particular section of the river rather than other sections (Atlantic salmon: Hvidsen et al. 1994; steelhead trout, *O. mykiss*: Wagner 1969; Cramer 1981). Atlantic salmon are particularly sensitive to olfactory learning during smolting (Morin et al. 1989*a*, 1989*b*). Salmonids exposed to morpholine or phenylethyl alcohol at the smolt stage were decoyed to sites containing the odor as mature adults (e.g., coho salmon, Scholz et al. 1976; steelhead trout, Scholz et al. 1978*a*; brown trout, Scholz et al. 1978*b*; Atlantic salmon, Sutterlin et al. 1982). Parr induced to undergo smolting by application of hormones imprinted on odors whereas controls did not (coho salmon, Hasler and Scholz 1983). Displacement, odor exposure, and hormone treatment studies all support the hypothesis that substantial imprinting occurs during the parr–smolt transformation.

Despite the large body of experimental evidence that olfactory imprinting takes place during smolting, other lines of evidence indicate that odors are learned much earlier and that homing is a more complex process (Riddell and Leggett 1981; reviewed by Dittman and Quinn 1996). First, many salmonids move away from their incubation site during their residence period in fresh water (as discussed above) and undergo smolt transformation farther down the river system, yet they home to natal sites, not to sites where they smolted. Second, close examination of the displacement studies reveals that when the release site is near the rearing site, many salmon return to the rearing site, especially if it is in the same river system (reviewed by Quinn 1993). Third, experiments have shown that salmon alevins and newly emerged fry learn and respond to the odors of a stream (Brannon 1972), conspecifics (Quinn and Hara 1986), and artificial substances (Courtenay 1989).

It has been hypothesized that salmon imprint or learn a sequence of odors during their period of freshwater residence and seaward migration (Harden Jones 1968; Brannon 1982) and that they reverse this sequence during their homing migration. This may explain why salmon displaced from their rearing sites as juveniles home to their release site as adults, especially if it is in a different drainage area than the rearing site. Once such salmon have located the release site, the rearing site is not detectable and there is no stimulus for further migration (Dittman and Quinn 1996). However, if they were able to detect odors experienced earlier in their lives as juveniles, they might continue migrating. The imprinting process, even at the smolt stage, seems to involve more than mere exposure to odors of a river or hatchery, as the date of release affects homing performance (Hansen and Jonsson 1991). In support of a sequential learning hypothesis, Hansen et al. (1983) have shown that smolts deprived of the experience of part of their migration route failed to return to their home river.

The act of migration itself may stimulate olfactory learning, as exposure to new odors can stimulate the thyroid hormones associated with smolt transformation and imprinting (Dittman and Quinn 1996). To the extent that this is true, salmon may learn new odors as often as their movements bring them into contact with such stimuli, although exposure to novel waters does not always increase thyroid hormone levels and successful imprinting does not depend on high or rapidly rising levels (Dittman et al. 1994).

Factors affecting smolt survival

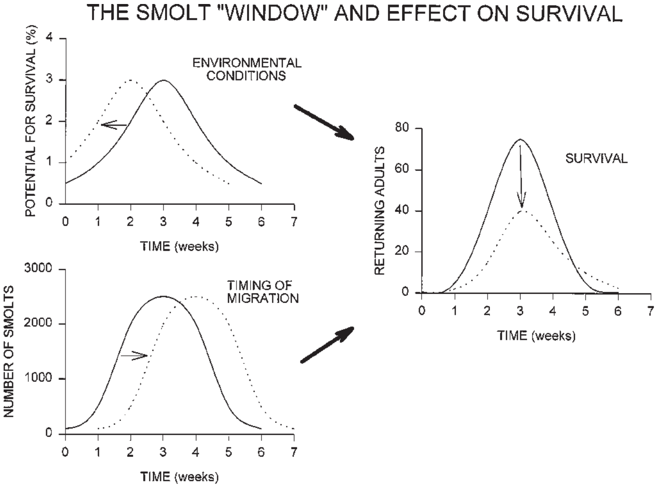
The smolt window: physiology, behavior, and predation

Many factors affect smolt survival and return of adult salmon, although they are poorly known (e.g., Saunders 1981). Factors related to predation and processes in the open sea are beyond the scope of this paper and we will emphasize physiological factors operating at the parr–smolt transformation (smolting) and the postsmolt stage (the period just after the smolts have left the rivers). These periods are of particular interest in salmon ranching because they strongly influence overall marine survival (Thorpe 1994). The timing of smolt migration seems to be crucial for survival of Atlantic salmon (Hansen 1987) and the migratory timing of wild smolts is presumably an adaptation to the area’s prevailing environmental conditions. When hatchery-reared salmon smolts are retained in fresh water they will “desmolt,” losing many of the physiological and behavioral characteristics of smolts (Lundqvist and Fridberg 1982). (Desmolt may be an unfortunate term in that it implies a complete loss of smolt characters; although some critical aspects such as salinity tolerance and migratory urge are lost, elevated metabolic rate and scope for (freshwater) growth are not.) Duston et al. (1991) have shown that higher temperatures result in a more rapid loss of gill Na^+, K^+-ATPase activity and salinity tolerance. After analyzing data from several studies, McCormick et al. (1996) found that the decrease in gill Na^+, K^+-ATPase activity was directly related to the number of degree days (cumulative daily temperature) experienced by smolts; there is an 80% loss in enzyme activity (equivalent to parr levels) 400 degree-days after the peak in gill Na^+, K^+-ATPase activity. These results under controlled conditions indicate that the physiological smolt window will be narrower in warmer water. Recent work on the Connecticut River, which is near the historical southern limit of Atlantic salmon in North America, indicates that late migrants have lower gill Na^+, K^+-ATPase activity and salinity tolerance than early migrants and that increasing numbers of fish are affected in warmer years (S.D. McCormick, R.A. Cunjak, B. Dempson, M.F. O'Dea, and J.B. Carey, unpublished data). A temperature-related smolt window indicates that delays in migration (such as those that occur at dams) will decrease smolt survival and that these negative consequences will be greater in warmer, southern rivers.

In addition to the change in physiological state of smolts, it is likely that there are other mechanisms behind the observations that there is an optimal time for smolt migration. These are less well understood, but predators, diseases, parasite abundance, and food conditions clearly affect smolt survival. Atlantic salmon smolts are subjected to heavy predation (see Mather 1998) from birds such as gulls, cormorants, herons, and mergansers (Huntsman 1941; White 1957; Reitan et al. 1987; Kennedy and Greer 1988), and fishes such as Atlantic cod, saithe, pollack, striped bass, and sea trout (Hvidsten and Mokkelgjerd 1987). There may be an interaction between migration timing, physiological readiness, and predation. Under laboratory conditions the risk of predation is greater during acclimation of smolts to seawater and osmotic imbalance during seawater acclimation is greater in the presence of predators (Jarvi 1990; Handeland et al. 1997). Thus, even if smolts with reduced salinity tolerance (such as those migrating too early or too late in their development) survive when they enter seawater, they are less likely to escape predation due both to their greater susceptibility and the increased time they need to spend in an estuary for gradual acclimation. When smolts are retained in saltwater pens or cages from spring to late summer and autumn, they survive poorly when released despite their larger size (Hansen and Jonsson 1986, 1989). This is not the case, however, in Baltic salmon where experiments with delayed release have demonstrated greater survival from late summer and fall releases than spring releases (Eriksson 1988). Low salinity of the Baltic may release smolts from their normal dependence on spring increases in salinity tolerance.

These above findings indicate that there may be two interacting aspects of migration timing that affect smolt survival (Fig. 3). First, there is a physiological smolt window, controlled by photoperiod, temperature, and flow, that determines the physiological and behavioral readiness of smolt for migration and seawater entry. The importance of physiological readiness to survival is indicated by the correlation of adult return rates with the physiological condition of hatchery fish at the time of release (Virtanen et al. 1991; Staurnes et al. 1993). Second, there is an environmental smolt window, in which seasonal changes in environmental conditions in rivers, estuaries, and the coastal environment are appropriate for high smolt survival. In the simple population simulation shown in Fig. 3, when migration timing and optimum environmental conditions coincide, adult returns are high. When migration timing and optimum environmental conditions are out of phase, adult returns are substantially lower. Results of this hypothetical simulation indicate that even when the magnitudes of migration and environmental conditions remain the same, alterations in their timing can have significant effects on adult returns.

Fig. 3. Simple mathematical model of the interaction of migration timing and environmental conditions and their effect on adult survival. Migration timing and survival estimates are typical for Atlantic salmon (e.g., Jonsson and Ruud-Hansen 1985; Hvidsten et al. 1995), but the temporal changes in environmental conditions are largely hypothetical. Values for migration timing are migrants per week. Adult returns are calculated from the weekly number of migrants and weekly survival rates. When migration timing and optimum environmental conditions coincide (solid lines), adult returns are high (total returns = 166). When migration timing and optimum environmental conditions are out of phase by 2 weeks (dashed lines), adult returns are lower (total returns = 94). Results of this simulation indicate that even when the magnitudes of migration and environmental conditions remain the same alterations in their timing can have significant effects on adult returns.



Pollution and stress

The physiological specializations that characterize smolts may make them susceptible to a variety of external stressors including pollutants. Although the greater capacity of smolts to respond to acute stress may be adaptive for migration and predator avoidance (Carey and McCormick 1998), it may have negative consequences under many natural and unnatural (anthropogenic) circumstances. One important example is the effect of acidity on smolt development. It has been known for some time that acid (and acid plus aluminum) exposures that have little effect on survival and growth of parr or smolts in fresh water can completely eliminate the development of gill Na^+, K^+-ATPase activity and salinity tolerance (Saunders et al. 1983). Recent work suggests that exposures as short as 12 h to relatively mild acidity (pH 5.2, 31 $\mu g \cdot L^{-1}$) aluminum) can compromise salinity tolerance (Staurnes et al. 1996*a*). The timing of exposure is also important; acid conditions that have little effect on smolts in April can greatly reduce salinity tolerance in May. Acid exposures at the smolt stage have devastating effects on adult return rates. Fish released in an acidic river in Norway often have no adult returns and have an average of one-tenth the returns of fish released at the mouth of the river or in a neighboring limed river (Staurnes et al. 1996*b*). These return rates were strongly correlated with the effect of acidity on gill Na^+, K^+-ATPase activity and osmotic balance of fish held in cages at the different release sites. These results illustrate two important points. First, the smolt stage may be particularly sensitive to acid rain (or run-off) and other pollutants. Second, by affecting the development of salinity tolerance, these detrimental effects may not be apparent until fish reach seawater. They may thus be difficult to distinguish from other marine mortality agents without experimental studies.

In addition to acidity, heavy metals and organic pollutants may also affect smolt development, although very few studies have specifically examined smolts. Heavy metals often exert lethal and sublethal effects on ion transport functions of the gill (Wendelaar Bonga and Lock 1992). Coho salmon are more sensitive to copper and zinc toxicity as smolts than as parr (Lorz and McPherson 1976). The numerous endocrine changes that occur during smolting may make smolts susceptible to environmental pollutants that act as endocrine disruptors (Kavlock et al. 1996). The smolt “habitats,” the mainstem of rivers and estuaries, are more heavily impacted by pollutants than high elevation tributaries where fry and parr reside. The combination of potentially greater sensitivity of smolt and greater exposure to pollutants during migration may be important factors in smolt survival in many areas. Much more laboratory and field work needs to be done to examine the importance of pollutants in affecting migrating smolts.

Pollutants may also interfere with the development of olfactory imprinting by juveniles and its expression (homing by adults), though this has not been widely examined. Royce-Malmgren and Watson (1987) reported that the responses of juvenile Atlantic salmon to amino acids varied with pH and they hypothesized that straying might be greater in acidified rivers. We are not aware of evidence that straying and pollution are correlated and the olfactory imprinting process seems to be remarkably capable of separating ephemeral from essential chemical characteristics of rivers. Experiments and field data with Pacific salmon indicated that adults avoid contaminated water (e.g., by volcanic ash from Mt. St. Helens; Whitman et al. 1982; Leider 1989) but that adults exposed to pollution from ash or crude oil could subsequently home successfully in clean water (Whitman et al. 1982; Brannon et al. 1986).

Smolts are more sensitive to handling and swimming stresses than parr (Wendt and Saunders 1973; Carey and McCormick 1998). Although this may not be relevant for many wild populations, it may be important for hatchery smolts and smolts that must move over or around dams. The impact of handling at, or movement through, dam bypass structures or falling from great heights over dams has not been thoroughly examined. It is important to note that stresses may interact with one another or act additively to the detriment of smolt survival (Barton et al. 1986). As noted above, factors that may not be directly lethal (but have physiological effects) may increase susceptibility to predation.

Hatchery-rearing

Experiments carried out in the River Imsa show that the average survival rate of hatchery-reared smolts was only half that of wild fish (Jonsson et al. 1991). This deficit may be due to genetic changes related to the selection regimes in hatcheries and nature, behavioral differences induced by culture conditions, and differences in smolt quality (such as physical condition, physiological development, disease resistance, and coloration), and time and method of release. Survival may be 30 times higher in hatcheries than in nature, so inferior fish may survive in hatcheries that would have been culled in a river. Moreover, the physical fitness of hatchery fish at release may be lower than that of wild conspecifics. Poor fin condition is more frequent in hatchery populations than in the wild, but studies to date have yielded conflicting results as to the importance of fin condition to adult returns. Virtanen et al. (1991) and Vehanen et al. (1993) found no correlation between fin condition and return rate, whereas Farmer (1994) found that an index of smolt quality that included fin condition was correlated with return rates. Hatchery fish may also be at a disadvantage because of lower physical activity in hatchery tanks and ponds than in the wild. There may also be differences in timing of smolt development in hatchery fish that may be inherent in artificial rearing or related to specific hatchery conditions (e.g., photoperiod, temperature, and growth rate). The endocrine status of wild and hatchery fish can be very different (McCormick and Björnsson 1994), which in turn may affect the rate of physiological development, migratory timing, and return rates (Virtanen et al. 1991; Staurnes et al. 1993). Hatchery fish have little experience in catching natural food and avoiding predators but they may be able to learn very quickly (Stradmeyer and Thorpe 1987). Maynard et al. (1997) have recently reviewed hatchery performance in salmonid enhancement and concluded that “seminatural” culture conditions has the potential to increase smolt survival.

Summary and future research

Movement among habitats is very important in Atlantic salmon populations. There is no single sequence of movements that characterizes all populations from fry to smolts but rather there is an array of responses to the different environments of salmon populations. These include movements of fry from their redd sites, establishment and occupation of feeding territories, spawning movements of sexually mature male parr, shifting from summer feeding territories to winter habitat, descent of large parr from nursery streams to lower reaches of certain rivers in late autumn, and smolt migration in spring. Failure to protect these habitats and the capacity of fish to move freely among them may have detrimental effects on many populations.

Smolting is a highly adaptive specialization for downstream migration, seawater entry, and marine residence; it is controlled by several hormones and is characterized by numerous physiological and behavioral changes in fresh water which prepare smolts for an ocean existence. While still in fresh water, smolts become silvery and streamlined, lose their positive rheotactic behavior and territoriality and adopt downstream orientation and schooling tendencies, and undergo several physiological changes including increased salinity tolerance, metabolic rate, and scope for growth. Smolting is a critical stage for imprinting to odors used for homing, though some learning may also occur earlier. Photoperiod and, to some degree, temperature regulate physiological changes, whereas temperature and water flow seem to be key factors initiating downstream migration. The apparent existence of a smolt window may be due to a limited period of physiological and behavioral readiness of smolts for seaward migration and the timing of downstream movement into rivers, estuaries, and seawater with ecological conditions such as food resources and predators. Interaction among these factors is likely and makes both study and prediction of smolt mortality difficult.

Smolt development is adversely affected by acidity, unsuitable rearing conditions, and pollutants. In many cases (such as acid exposure) smolting is more sensitive than other life history stages. High temperature in spring will shorten the period of physiological preparedness of smolts. Unfortunately the migration habitat of smolts (the mainstems of rivers and their estuaries) are often the most heavily impacted by pollution, dams, temperature changes, altered hydrographs, and other anthropogenic changes. These factors may be directly lethal or may increase mortality rates by delaying or inhibiting smolt migration and making smolts more likely to encounter or be susceptible to predators.

The declines in Atlantic salmon populations in many geographic areas have made an increased understanding of salmon movement and migration imperative. Although salmon are well known for their accurate homing, they are also colonizers of previously uninhabited rivers and of new habitats within rivers systems. We currently have limited knowledge of the proximate factors (genetic and environmental) that regulate homing versus straying and the costs and rewards of exploring and colonizing new rivers or habitats within rivers. Are highly mobile individuals genetically different from the territorial residents? Are there stock-(river-)specific migratory traits and are these adaptive?

Atlantic salmon research should move toward a greater integration of physiology and behavior, which until recently have been examined separately. What are the environmental and neuroendocrine factors that initiate and maintain smolt migration and how do these relate to the physiological changes that occur during smolting? What are the energetic demands of migration and are they important to smolt survival? Is the altered growth pattern of mature parr the only factor affecting subsequent smolting or are there other mechanims by which maturation affects the individual's "decision" to smolt? What are the physiological triggers for movements of fry and parr in fresh water?

Human activity has dramatically affected salmon populations, particularly where industrial activity is high (Parrish et al. 1998). We do not yet know the factors that affect smolt survival during river, estuarine, and early ocean migration. How important are barriers to migration (such as dams) and pollution affecting smolt survival? Fisheries have altered the suites of predators in the coastal and ocean environment and these changes could significantly affect smolt survival. We have relied on laboratory experiments and hatchery-reared fish for much of our understanding of smolting and migration. We must know more about wild fish, understand the differences between hatchery and wild fish, and appreciate the potential impact of hatchery releases on wild fish.

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References

Alexander, G., Sweeting, R., and Mckeown, B. 1994. The shift in visual pigment dominance in the retinae of juvenile coho salmon (*Oncorhynchus kisutch*): an indicator of smolt status. J. Exp. Biol. **195**: 185–197.

Allen, K.R. 1944. Studies on the biology of the early stages of the salmon (*Salmo salar*). 4. The smolt migration in the Thurso River in 1939. J. Anim. Ecol. **13**: 63–85.

Armstrong, J.D., Braithwaite, V.A., and Huntingford, F.A. 1997. Spatial strategies of wild Atlantic salmon parr — exploration and settlement in unfamiliar areas. J. Anim. Ecol. **66**: 203–211.

Arnold, G.P., Webb, P.W., and Holford, B.H. 1991. The role of the pectoral fins in station holding of Atlantic salmon parr (*Salmo salar* L.). J. Exp. Biol. **156**: 625–629.

Baggerman, B. 1960. Factors in the diadromous migrations of fish. Zool. Soc. Symp. Lond. **I**: 33–60.

Bagliniere J.L. 1976. Étude des populations de saumon Atlantique (*Salmo salar* L., 1766) en Bretagne — Basse Normandie. II. — Activité de devalaison des smolts sur l'Elle. Hydrobiologia, **7**: 159–177.

Barton, B.A., Schreck, C.B., and Sigismondi, L.A. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile chinook salmon. Trans. Am. Fish. Soc. **115**: 245–251.

Berg, O.K. 1985. The formation of non-anadromous populations of Atlantic salmon, *Salmo salar* L., in Europe. J. Fish Biol. **27**: 805–815.

Berglund, I. 1992. Growth and early sexual maturation in Baltic salmon (*Salmo salar*) parr. Can. J. Zool. **70**: 205–211.

Berglund I., Hansen L.P., Lundqvist H., Jonsson B., Eriksson T., Thorpe J.E., and Eriksson, L.O. 1991. Effects of elevated winter temperature on seawater adaptability, sexual rematuration, and downstream migratory behaviour in mature male Atlantic salmon parr (*Salmo salar*). Can. J. Fish. Aquat. Sci. **48**: 1041–1047.

Berglund, I., Lundqvist, H., and Fangstam, H. 1994. Downstream migration of immature salmon (*Salmo salar*) smolts blocked by implantation of the androgen 11-ketoandrostenedione. Aquaculture, **121**: 269–276.

Bern, H.A. 1978. Endocrinological studies on normal and abnormal salmon smoltification. *In* Comparative endocrinology. *Edited by* P.J. Gaillard and H.H. Boer. Elsevier/North Holland Biomedical Press, Amsterdam. pp. 77–100.

Berry, J. 1932. Report of an investigation of the migrations of smolts in the river Tay during spring, 1931. Fish. Scot. Salmon Fish. **6**: 1–21.

Berry, J. 1933. Notes on the migration of salmon smolts from Loch Ness, summer 1932. Fish. Scot. Salmon Fish. **1**: 1–12.

Birt, T.P., Green, J.M., and Davidson, W.S. 1991. Contrasts in development and smolting of genetically distinct sympatric anadromous and nonanadromous Atlantic salmon, *Salmo salar.* Can. J. Zool. **69**: 2075–2084.

Björnsson, B.T., Thorarensen, H., Hirano, T., Ogasawara, T., and Kristinsson, J.B. 1989. Photoperiod and temperature affect plasma growth hormone levels, growth, condition factor and hypoosmoregulatory ability of juvenile Atlantic salmon (*Salmo salar*) during parr smolt transformation. Aquaculture, **82**: 77–91.

Boeuf, G. 1993. Salmonid smolting: a pre-adaptation to the oceanic environment. *In* Fish ecophysiology. *Edited by* J.C. Rankin and F.B. Jensen. Chapman and Hall, London. pp. 105–135.

Bourgeois, C.E., and O'Connell, M.F. 1988. Observations on the seaward migration of Atlantic salmon (*Salmo salar* L.) smolts through a large lake as determined by radiotelemetry and Carlin tagging studies. Can. J. Zool. **66**: 685–691.

Bradford, M.J., and Taylor, G.C. 1997. Individual variation in dispersal behavior of newly emerged chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. **55**: 1585–1592.

Brannon, E.L. 1972. Mechanisms controlling migration of sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Bull. **21**. 86 p.

Brannon, E.L. 1982. Orientation mechanisms of homing salmonids. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium. *Edited by* E.L. Brannon and E.O. Salo. University of Washington Press, Seattle, Wash. pp. 219–227.

Brannon, E.L., Quinn, T.P., Whitman, R.P., Nevissi, A.E., Nakatani, R.E., and McAuliffe, C.D. 1986. The homing of adult chinook salmon after brief exposure to whole and dispersed crude oil. Trans. Am. Fish. Soc. **115**: 823–827.

Brown, G.E., and Brown, J.A. 1986. Kin discrimination in salmonids. Revs. Fish Biol. Fish. **6**: 201–219.

Buck, R.J.G., and Youngson, A.F. 1982. The downstream migration of precociously mature Atlantic salmon, *Salmo salar* L., parr in autumn; its relation to the spawning migration of mature adult fish. J. Fish Biol. **20**: 279–288.

Burton, M.P., and Idler, D.R. 1984. Can Newfoundland landlocked salmon, *Salmo salar* L. adapt to sea water? J. Fish Biol. **24**: 59–64.

Carey, J.B., and McCormick, S.D. 1998. Atlantic salmon smolts are more responsive to handling and confinement stress than parr. Aquaculture, **168**: 237–253.

Carlin, B. 1969. Salmon conservation in Sweden, salmon tagging experiments, the migration of salmon. Series of lectures. The Atlantic Salmon Association, Montreal, Que. 22 p.

Chadwick, E.M.P. 1982. Dynamics of an Atlantic salmon stock in a small Newfoundland stream. Ph.D. dissertation, Memorial University of Newfoundland, St. John's, Nfld.

Courtenay, S.C. 1989. Learning and memory of chemosensory stimuli by underyearling coho salmon, *Oncorhynchus kisutch* Walbaum. Ph.D. dissertation, University of British Columbia, Vancouver, B.C.

Cramer, D.P. 1981. Effect of smolt release location and displacement of adults on distribution of summer steelhead trout. Prog. Fish-Cult. **43**: 8–11.

Crisp, D.T. 1995. Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. Ecol. Freshwater Fish. **4:** 1–8.

Crisp, D.T., and Hurley, M.A. 1991*a*. Stream channel experiments on downstream movements of recently emerged trout, *Salmo trutta* L., and salmon, *Salmo salar* L. I. Effects of four different water velocity treatments upon dispersal rate. J. Fish Biol. **39**: 347–362.

Crisp, D.T., and Hurley, M.A. 1991*b*. Stream channel experiments on downstream movements of recently emerged trout, *Salmo trutta* L., and salmon, *Salmo salar* L. II. Effects of constant and changing velocities and day and night upon dispersal rate. J. Fish Biol. **39**: 363–370.

Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Can. J. Fish. Aquat. Sci. **45**: 2156–2160.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Can. J. Fish. Aquat. Sci. **53**(Suppl. 1): 267–282.

Cunjak, R.A., and Randall, R.G. 1993. In-stream movements of young Atlantic salmon (*Salmo salar*) during winter and early spring. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci. 118. pp. 43–51.

Cunjak, R.A., and Therrien, J. 1998. Interstage survival of wild juvenile Atlantic salmon, *Salmo salar* L. Fish. Manage. Ecol. **5**: 209–223.

Cunjak, R.A., Chadwick, E.M.P., and Shears, M. 1989. Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). Can. J. Fish. Aquat. Sci. **46**: 1466–1471.

Cunjak, R.A., Saunders, R.L., and Chadwick, E.M.P. 1990. Seasonal variations in the smolt characteristics of juvenile Atlantic salmon (*Salmo salar*) from estuarine and riverine environments. Can. J. Fish. Aquat. Sci. **47**: 813–820.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, New York.

Dittman, A.H., and Quinn, T.P. 1996. Homing in Pacific salmon: mechanisms and ecological basis. J. Exp. Biol. **199**: 83–91.

Dittman, A.H., Quinn, T.P., Dickhoff, W.W., and Larsen, D.A. 1994. Interactions between novel water, thyroxine and olfactory imprinting in underyearling coho salmon (*Oncorhynchus kisutch*, Walbaum). Aquacult. Fish. Manage. **25** (Suppl. 2): 157–169.

Donaldson, L.R., and Allen, G.H. 1958. Return of silver salmon, *Oncorhynchus kisutch* (Walbaum) to point of release. Trans. Am. Fish. Soc. **87**: 13–22.

Duston, J. 1994. Effect of salinity on survival and growth of Atlantic salmon (*Salmo salar*) parr and smolts. Aquaculture, **121**: 115–124.

Duston, J., and Saunders, R.L. 1995. Advancing smolting to autumn in age 0+ Atlantic salmon by photoperiod, and long-term performance in sea water. Aquaculture, **135**: 295–309.

Duston, J., Saunders, R.L., and Knox, D.E. 1991. Effects of increases in freshwater temperature on loss of smolt characteristics in Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **48**: 164–169.

Eriksson, T. 1988. Migratory behavior of Baltic salmon (*Salmo salar* L.); adaptive significance of annual cycles. Ph.D. dissertation, Umea University, Umea, Sweden.

Eriksson, L.-O., and Lundqvist, H. 1982. Circannual rhythms and photoperiod regulation of growth and smolting in Baltic salmon (*Salmo salar* L.). Aquaculture, **28**: 113–121.

Erkinaro, J., and Niemelä, E. 1995. Growth differences between the Atlantic salmon parr, *Salmo salar*, of nursery brooks and natal rivers in the River Teno watercourse in northern Finland. Env. Biol. Fish. **42**: 277–287.

Erkinaro, J., Shchurov, L.I., Saari, T., and Niemela, E. 1994. Occurrence of Atlantic salmon parr in redds at spawning time. J. Fish Biol. **45**: 899–900.

Farmer, G.J. 1994. Some factors which influence the survival of hatchery Atlantic salmon (*Salmo salar*) smolts utilized for enhancement purposes. Aquaculture, **121**: 223–233.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon — ecology and evolution. Rev. Fish Biol. Fish. **6**: 379–416.

Fraser, N.H., Metcalfe, N.B., and Thorpe, J.E. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proc. R. Soc. Lond. B **252**: 135–139.

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

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. *In* Fish physiology. Vol. VI. Environmental relations and behavior. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 1–98.

Gibson, R.J. 1966. Some factors influencing the distributions of brook trout and young Atlantic salmon. J. Fish. Res. Board Can. **23**: 1977–1980.

Gibson, R.J. 1983. Water velocity as a factor in the change from aggressive to schooling behaviour and subsequent migration of Atlantic salmon smolt (*Salmo salar*). Nat. Can. **110**: 143–148.

Gibson, R.J. 1993. The Atlantic salmon in fresh water: spawning, rearing and production. Rev. Fish Biol. Fish. **3**: 39–73.

Godin, J.J., and Rangeley, R.W. 1989. Living in the fast lane: effects of cost of locomotion on foraging behavior in juvenile Atlantic salmon. Anim. Behav. **37**: 943–954.

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

Gotceitas, V., and Godin, J.J. 1992. Effects of location of food delivery and social status on foraging site selection by juvenile Atlantic salmon. Environ. Biol. Fish. **35**: 291–300.

Gowan, C., Young, M.K., Fausch, K.D., and Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can. J. Fish. Aquat. Sci. **51**: 2626–2637.

Grant, J.W.A., Steingrímsson, S.Ó., Keeley, E.R., and Cunjak, R.A. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 181–190.

Greenstreet, S.P.R. 1992. Migration of hatchery-reared juvenile Atlantic salmon, *Salmo salar* L., down a release ladder. 2. Effect of fish development strategy on speed and pattern of movement. J. Fish Biol. **40**: 667–681.

Groot, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behaviour (Suppl.)**14**: 1–198.

Gross, M.R. 1987. Evolution of diadromy in fishes. Am. Fish. Soc. Symp. **1**: 14–25.

Gustafson-Marjanen, K.I., and Dowse., H.B. 1983. Seasonal and diel patterns of emergence from the redd of Atlantic salmon (*Salmo salar*) fry. Can. J. Fish. Aquat. Sci. **40**: 813–817.

Handeland, S.O., Jarvi, T., Ferno, A., and Stefansson, S.O. 1997. Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. Can. J. Fish. Aquat. Sci. **53**: 2673–2680.

Hansen, L.P. 1987. Growth, migration and survival of lake reared juvenile anadromous Atlantic salmon *Salmo salar* L. Fauna Norv. Ser. A**, 8**: 29–34.

Hansen, L.P., and Jonsson, B. 1985. Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L.) in the River Imsa. Aquaculture, **45**: 237–248.

Hansen, L.P., and Jonsson, B. 1986. Salmon ranching experiments in the River Imsa: effects of day and night release and of seawater adaptation on recapture rates of adults. Rep. Inst. Freshwater Res. Drottningholm, **63**: 47–51.

Hansen, L.P., and Jonsson, B. 1989. Salmon ranching experiments in the River Imsa: effect of timing of Atlantic salmon (*Salmo salar*) smolt migration on survival to adults. Aquaculture, **82**: 367–373.

Hansen, L.P., and Jonsson, B. 1991. The effect of timing of Atlantic salmon smolt and post-smolt release on the distribution of adult return. Aquaculture, **98**: 61–67.

Hansen, L.P., and Quinn, T.P. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 104–118.

Hansen, L.P., Jonsson, B., Morgan, R.I.G., and Thorpe, J.E. 1989. Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **46**: 410–415.

Hansen, L.P., Jonsson, N., and Jonsson, B. 1993. Oceanic migration in homing Atlantic salmon. Anim. Behav. **45**: 927–941.

Harden-Jones, F.R. 1968. Fish migration. Edward Arnold Press. London.

Hasler, A.D., and Scholz, A.T. 1983. Olfactory imprinting and homing in salmon. Springer-Verlag, New York.

Hesthagen, T., and Gärnäs, E. 1986. Migration of Atlantic salmon smolts in River Orkla, central Norway in relation to management of a hydroelectric station. N. Am. J. Fish. Manage. **6**: 376–382.

Hoar, W.S. 1988. The physiology of smolting salmonids. *In* Fish physiology. Vol. XIB. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 275–343.

Hosmer, M.J., Stanley, J.G., and Hatch, R.W. 1979. Effects of hatchery procedures on later return of Atlantic salmon to rivers of Maine. Prog. Fish-Cult. **41**: 115–119.

Huntsman, A.G. 1941. Cyclical abundance of birds versus salmon. J. Fish. Res. Board Can. **5**: 227–235.

Hutchings, J.A. 1986. Lakeward migrations by juvenile Atlantic salmon, *Salmo salar.* Can. J. Fish. Aquat. Sci. **43**: 732–741.

Hutchings, J.A., and Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar.* Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 22–47.

Hvidsen, N.A., Heggberget, T.G., and Hansen, L.P. 1994. Homing and straying of hatchery-reared Atlantic salmon, *Salmo salar* L., released in three rivers in Norway. Aquacult. Fish. Manage. **25**(Suppl. 2): 9–16.

Hvidsten, N.A., and Hansen, L.P. 1988. Increased recapture rate of adult Atlantic salmon, *Salmo salar* L., stocked at high water discharge. J. Fish Biol. **32**: 153–154.

Hvidsten, N.A., and Mokkelgjerd, P.I. 1987. Predation on salmon smolts (*Salmo salar* L.) in the estuary of the River Surna, Norway. J. Fish Biol. **30**: 273–280.

Hvidsten, N.A., Jensen, A.J., Vivas, H., Bakke, Ø., and Heggberget, T.G. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water tempereture, moon phase and social interaction. Nordic J. Freshwater Res. **70**: 38–48.

Iwata, M. 1995. Downstream migratory behavior of salmonids and its relationship with cortisol and thyroid hormones: a review. Aquaculture, **135**: 131–139.

Jarvi, T. 1990. Cumulative acute physiological stress in Atlantic salmon smolts: the effect of osmotic imbalance and the presence of predators. Aquaculture, **89**: 337–350.

Jarvi, T. 1989. Synergistic effect on mortality in Atlantic salmon, *Salmo salar*, smolt caused by osmotic stress and the presence of predators. Environ. Biol. Fishes, **26**: 149–152.

Jones, J.W., and King, G.M. 1952. The spawning of the male salmon parr (*Salmo salar* Linn. Juv.). Proc. Zool. Soc. Lond. **122** (Pt. III): 615–619.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Rev. Fish Biol. Fish. **3**: 348–365.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic J. Freshwater Res. **66**: 20–35.

Jonsson, B., and Ruud-Hansen, J. 1985. Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. Can. J. Fish. Aquat. Sci. **42**: 593–595.

Jonsson, N., Hansen, L.P., and Jonsson, B. 1993. Migratory behaviour and growth of hatchery-reared post-smolt Atlantic salmon *Salmo salar.* J. Fish Biol. **42**: 435–443.

Jonsson, B., Jonsson, N., and Hansen, L.P. 1991. Differences in life history and migratory behaviour between wild and hatchery reared Atlantic salmon in nature. Aquaculture, **98**: 69–78.

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

Kavlock, R.J., Daston, G.P., Derosa, C., Fennercrisp, P., Gray, L.E., Kaattari, S., Lucier, G., Luster, M., Mac, M.J., Maczka, C., Miller, R., Moore, J., Rolland, R., Scott, G., Sheehan, D.M., Sinks, T., and Tilson, H.A. 1996. Research needs for the risk assessment of health and environmental effects of endocrine disruptors — a report of the U.S. EPA-sponsored workshop. Environ. Health Perspect. **104**: 715–740.

Keenleyside, M.H.A., and Yamamoto, F. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour, **19**: 139–169.

Kennedy, G.J.A., Strange, C.D., Andersen, R.J.D., and Johnston, P.M. 1984. Experiments on the descent and feeding of hatchery-reared salmon smolts (*Salmo salar* L.) in the River Bush. Fish. Manage. **15**: 15–25.

Kennedy, G.J.A., and Greer, J.E. 1988. Predation by cormorants, *Phalacrocorax carbo* (L.), on the salmonid population of an Irish river. Aquacult. Fish. Manage. **19**: 159–170.

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

LaBar, G.W., McCleave, J.D., and Fried, S.M. 1978. Seaward migration of hatchery-reared Atlantic salmon *(Salmo salar)* smolts in the Penobscot River estuary, Maine: open-water movements. J. Cons. Int. Explor. Mer, **38**: 257–269.

Lacroix, G.L., and McCurdy, P. 1996. Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. J. Fish Biol. **49**: 1086–1101.

Leider, S.A. 1989. Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St. Helens. Environ. Biol. Fish. **24**: 219–229.

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

Lundqvist, H., Borg, B., and Berglund, I. 1989. Androgens impair seawater adaptability in smolting Baltic salmon (*Salmo salar*). Can. J. Zool. **67**: 1733–1736.

Lundqvist, H., and Fridberg, G. 1982. Sexual maturation versus immaturity: different tactics with adaptive values in Baltic salmon (*Salmo salar*) male smolts. Can. J. Zool. **60**: 1822–1827.

Madsen, S.S., and Bern, H.A. 1992. Antagonism of prolactin and growth hormone: impact on seawater adaptation in two salmonids, *Salmo trutta* and *Oncorhynchus mykiss*. Zool. Sci. **9**: 775–784.

Mather, M.E. 1998. The role of context-specific predation in understanding patterns exhibited by anadromous salmon. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 232–246.

Mayer, I., Lundqvist, H., Berglund, I., Schmitz, M., Schulz, R., and Borg, B. 1990. Seasonal endocrine changes in Baltic salmon, *Salmo salar*, immature parr and mature male parr.1. Plasma levels of 5 androgens, 17-alpha-hydroxy-20-beta-dihydroprogesterone, and 17-beta-estradiol. Can. J. Zool. **68**: 1360–1365.

Maynard, D.J., Flagg, T.A., and Mahnken, C.V.W. 1997. A review of seminatural culture strategies for enhancing the postrelease survival of anadromous salmonids. Am. Fish. Soc. Symp. **15**: 307–314.

McCormick, S.D., and Saunders, R.L. 1987. Preparatory physiological adaptations for marine life in salmonids: osmoregulation, growth and metabolism. Am. Fish. Soc. Symp. **1**: 211–229.

McCormick, S.D., and Björnsson, B.T. 1994. Physiological and hormonal differences among Atlantic salmon parr and smolts reared in the wild, and hatchery smolts. Aquaculture, **121**: 235–244.

McCormick, S.D. 1994. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. Estuaries, **17**: 26–33.

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

McCormick, S.D., Björnsson, B.T., Sheridan, M., Eilertson, C., Carey, J.B., and O'Dea, M. 1995*a*. Increased daylength stimulates plasma growth hormone and gill Na^+, K^+-ATPase in Atlantic salmon (*Salmo salar*). J. Comp. Physiol. **165**: 245–254.

McCormick, S.D., Björnsson, B.T., Moriyama, S., Carey, J.B., and O'Dea, M. 1995*b*. Plasma growth hormone (GH), insulin-like growth factor I (IGF-I), cortisol and thyroid hormones during environmental manipulation of the parr-smolt transformation of Atlantic salmon. Am. Zool. **75**: 93A (Abstract).

McCormick, S.D., Shrimpton, J.M., and Zydlewski, J.D. 1996. Temperature effects on osmoregulatory physiology of juvenile anadromous fish. *In* Global warming: implications for freshwater and marine fish. *Edited by* C.M. Wood and D.G. McDonald. pp. 279–301.

McMenemy, J.R. (1995). Survival of Atlantic salmon fry stocked at low density in the West River, Vermont. North Am. J. Fish. Manage. **15**: 366–374.

Meister, A.L. 1962. Atlantic salmon production in Cove Brook, Maine. Trans. Am. Fish. Soc. **91**: 208–212.

Metcalfe, N.B. 1998. The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 93–103.

Mills, D.H. 1964. The ecology of young stages of the Atlantic salmon in the River Bran, Ross-shire. Freshwater Fish. Res. Scotland, **32**: 1–58.

Moore, A., Potter, E.C.E., Milner, N.J., and Bamber, S. 1995. The migratory behavior of wild Atlantic salmon (*Salmo salar*) smolts in the estuary of the River Conwy, North Wales. Can. J. Fish. Aquat. Sci. **52**: 1923–1935.

Morin, P.-P., Dodson, J.J., and Dore, F.Y. 1989*a*. Cardiac responses to natural odorants as evidence of a sensitive period for olfactory imprinting in young Atlantic salmon, *Salmo salar.* Can. J. Fish. Aquat. Sci. **46**: 122–130.

Morin, P.-P., Dodson, J.J., and Dore, F.Y. 1989*b*. Thyroid activity concomitant with olfactory learning and heart rate changes in Atlantic salmon, *Salmo salar*, during smoltification. Can. J. Fish. Aquat. Sci. **46**: 131–136.

Orciari, R.D., and Leonard, G.H. 1996. Length characteristics of smolts and timing of downstream migration among three strains of Atlantic salmon in a southern New England stream. North Am. J. Fish. Manage. **16**: 851–860.

Osterdahl, L. 1969. The smolt run of a small Swedish river. *In* Salmon and trout in streams. *Edited by* T.G. Northcote. H.R. MacMillan lectures in fisheries, University of British Columbia, Vancouver, B.C. pp. 205–215.

Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 281–287.

Pethon, P., and Hansen, L.P. 1990. Migration pattern of Atlantic salmon smolts *Salmo salar* L. released at different sites in the River Drammenselv, S.E. Norway. Fauna Norv. Ser. A, **11**: 17–22.

Potter, E.C.E., and Russell, I.C. 1994. Comparison of the distribution and homing of hatchery-reared and wild Atlantic salmon, *Salmo salar* L., from north-east England. Aquacult. Fish. Manage. **25**(Suppl. 2): 31–44.

Power, G., and Shooner, G. 1966. Juvenile salmon in the estuary and lower Nabisipi River and some results of tagging. J. Fish. Res. Board Can. **23**: 947–961.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. **18**: 29–44.

Quinn, T.P., and Hara, T.J. 1986. Sibling recognition and olfactory sensitivity in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. **64**: 921–925.

Reitan, O., Hvidsten, N.A., and Hansen, L.P. 1987. Bird predation on hatchery-reared Atlantic salmon smolts, *Salmo salar* L., released in the River Eira, Norway. Fauna Norv. Ser. A, **8**: 35–38.

Riddell, B.E., and Leggett, W.C. 1981. Evidence of an adaptive basis for geographic variation of body morphology, and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **38**: 308–320.

Rimmer, D.M. 1980. On the autumnal habitat change of juvenile Atlantic salmon (*Salmo salar* L.). Ph.D. dissertation, University of New Brunswick, Fredericton, N.B. 192 p.

Rimmer, D.M., Paim, U., and Saunders, R.L. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. Can. J. Fish. Aquat. Sci. **40**: 671–680.

Royce-Malmgren, C.H., and Watson, W.H. 1987. Modification of olfactory-related behavior in juvenile Atlantic salmon by changes in pH. J. Chem. Ecol. **13**: 533–546.

Saunders, J.W. 1960. The effect of impoundment on the population and movment of Atlantic salmon in Ellerslie Brook, Prince Edward Island. J. Fish. Res. Board Can. **17**: 453–473.

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

Saunders, R.L. 1981. Atlantic salmon (*Salmo salar*) stocks and management implications in the Canadian Atlantic Provinces and New England, U.S.A. Can. J. Fish. Aquat. Sci. **12**: 1612–1625.

Saunders, R.L., and Gee, J.H. 1964. Movements of young Atlantic salmon in a small stream. J. Fish. Res. Board Can. **21**: 27–36.

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

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

Saunders, R.L., Harmon, P.R., and Knox, D.E. 1994. Smolt development and subsequent sexual maturity in previously mature male Atlantic salmon (*Salmo salar*). Aquaculture, **121**: 79–93.

Scholz, A.T., Gross, C.K., Cooper, J.C., Horrall, R.M., Hasler, A.D., Daly, R.I., and Poff, R.J. 1978*a*. Homing of rainbow trout transplanted in Lake Michigan: a comparison of three procedures used for imprinting and stocking. Trans. Am. Fish. Soc. **107**: 439–443.

Scholz, A.T., Horrall, R.M., Cooper, J.C., and Hasler, A.D. 1978*b*. Homing of morpholine-imprinted brown trout, *Salmo trutta*. Fish. Bull. **76**: 293–295.

Scholz, A.T., Horrall, R.M., Cooper, J.C., and Hasler, A.D. 1976. Imprinting to chemical cues: the basis for homestream selection in salmon. Science (Washington, D.C.), **192**: 1247–1249.

Smirnov, Yu.A., Shastov, Yu.A., and Khrennikov, V.V. 1976. On the behavior and feeding of juvenile Onega salmon (*Salmo salar* morph *sebago*) in winter. J. Ichthyol. **16**: 503–506.

Solomon, D.J. 1982. Smolt migration in Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*). *In* Proceedings of the Salmon and Trout Migratory Behaviour Syposium. *Edited by* E.L. Brannon and E.O. Salo. University of Washington, Seattle, Wash. pp. 196–203.

Solomon, D.J. 1978. Some observations on salmon smolt migration in a chalkstream. J. Fish Biol. **12**: 571–574.

Staurnes, M., Lysfjord, G., Hansen, L.P., and Heggberget, T.G. 1993. Recapture rates ofhatchery-reared Atlantic salmon (*Salmo salar*) related to smolt development and time of release. Aquaculture, **118**: 327–337.

Staurnes, M., Lysfjord, G., and Berg, O.K. 1992. Parr–smolt transformation of a nonanadromous population of Atlantic salmon (*Salmo salar*) in Norway. Can. J. Zool. **70**: 197–199.

Staurnes, M., Kroglund, F., and Rosseland, B.O. 1996*a*. Water quality requirement of Atlantic salmon (*Salmo salar*) in water undergoing acidification or liming in Norway. Water, Air, Soil Poll. **85**: 347–352.

Staurnes, M., Hansen, L.P., Fugelli, K., and Haraldstad, O. 1996*b*. Short-term exposure to acid water impairs osmoregulation, seawater tolerance, and subsequent marine survival of smolt of Atlantic salmon (*Salmo salar* L.). Can. J. Fish. Aquat. Sci. **53**: 1695–1704.

Stradmeyer, L., and Thorpe, J.E. 1987. The responses of hatchery-reared Atlantic salmon, *Salmo salar* L., parr for pelletted and wild prey. Aquacult. Fish. Manage. **18**: 51–61.

Sutterlin, A.M., and Maclean, D. 1984. Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic salmon (*Salmo salar*) and their hybrids. Can. J. Fish. Aquat. Sci. **41**: 1139–1149.

Sutterlin, A.M., Saunders, R.L., Hendersen, E.B., and Harmon, P.R. 1982. The homing of Atlantic salmon (*Salmo salar*) to a marine site. Can. Tech. Rep. Fish. Aquat. Sci. 1058. 6 p.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture, **98**: 185–207.

Thorpe, J.E. 1988. Salmon migration. Sci. Prog. Oxford, **72**: 345–370.

Thorpe, J.E. 1994. Salmonid fishes and the estuarine environment. Estuaries, **17**: 73–93.

Thorpe, J.E., and Morgan, R.I.G. 1978. Periodicity in Atlantic salmon, *Salmo salar* L. smolt migration. J. Fish Biol. **12**: 541–548.

Thorpe, J.E., Ross, L.G., Struthers, G., and Watts, W. 1981. Tracking Atlantic salmon smolts, *Salmo salar* L., through Loch Voil, Scotland. J. Fish Biol. **19**: 519–537.

Tytler, P., Thorpe, J.E., and Shearer, W.M. 1978. Ultrasonic tracking of the movements of Atlantic salmon smolts (*Salmo salar* L.) in the estuaries of two Scottish rivers. J. Fish Biol. **12**: 575–586.

Vehanen, T., Aspi, J., and Pasanen, P. 1993. The effect of size, fin erosion, body silvering and precocious maturation on recaptures in Carlin-tagged Baltic salmon (*Salmo salar* L). Ann. Zool. Fenn. **30**: 277–285.

Virtanen, E., Soderholmtana, L., Soivio, A., Forsman, L., and Muona, M. 1991. Effect of physiological condition and smoltification status at smolt release on subsequent catches of adult salmon. Aquaculture, **97**: 231–257.

Wagner, H.H. 1969. Effect of stocking location of juvenile steelhead trout, *Salmo gairdneri*, on adult catch. Trans. Am. Fish. Soc. **98**: 27–34.

Wedemeyer, G.A., Saunders, R.L., and Clarke, W.C. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. **42**: 1–14.

Wendelaar Bonga, S.E.W., and Lock, R.A.C. 1992. Toxicants and osmoregulation in fish. Neth. J. Zool. **42**: 478–493.

Wendt, C.A.G., and Saunders, R.L. 1973. Changes in carbohydrate metabolism in young Atlantic salmon in response to various forms of stress. Inter. Atl. Salmon Fed. Publ. Ser. **4**: 55–82.

White, H.C. 1939. Factors influencing descent of Atlantic salmon smolts. J. Fish. Res. Board Can. **4**: 323–326.

White, H.C. 1957. Food and natural history of mergansers on salmon waters in the maritime provinces of Canada. Bull. Fish. Res. Board Can. 116. pp. 1–63.

Whitman, R.P., Quinn, T.P., and Brannon, E.L. 1982. The influence of suspended volcanic ash on the homing behavior of adult chinook salmon. Trans. Am. Fish. Soc. **111**: 63–69.

Youngson, A.F., Buck, R.J.G., Simpson, T.H., and Hay, D.W. 1983. The autumn and spring emigrations of juvenile Atlantic salmon, *Salmo salar* L., from the Girnock Burn, Aberdeenshire, Scotland: environmental release of migration. J. Fish Biol. **23**: 625–639.

Youngson, A.F., Jordan, W.C., and Hay, D.W. 1994. Homing of Atlantic salmon (*Salmo salar* L.) to a tributary spawning stream in a major river catchment. Aquaculture, **121**: 259–267.

Youngson, A.F., Hansen, L.P., Jonsson, B., and Nesje, T.F. 1989. Effects of exogenous thyroxine or prior exposure to raised water flow on the downstream movement of hatchery-reared Atlantic salmon smolts. J. Fish Biol. **34**: 791–797.