

Taking It with You When You Go: How Perturbations to the Freshwater Environment, Including Temperature, Dams, and Contaminants, Affect Marine Survival of Salmon

STEPHEN D. McCORMICK*

*U.S. Geological Survey, Conte Anadromous Fish Research Center
Turners Falls, Massachusetts 01376, USA*

*Program in Organismic and Evolutionary Biology, University of Massachusetts
Amherst, Massachusetts 01003, USA*

DARREN T. LERNER, MICHELLE Y. MONETTE, AND
KATHERINE NIEVES-PUIGDOLLER

*U.S. Geological Survey, Conte Anadromous Fish Research Center
Turners Falls, Massachusetts 01376, USA*

*Program in Organismic and Evolutionary Biology, University of Massachusetts
Amherst, Massachusetts 01003, USA*

JOHN T. KELLY

*U.S. Geological Survey, Conte Anadromous Fish Research Center
Turners Falls, Massachusetts 01376, USA*

*Department of Natural Resource Conservation, University of Massachusetts
Amherst, Massachusetts 01003, USA*

BJÖRN THRANDUR BJÖRNSSON

Department of Zoophysiology, University of Göteborg, Göteborg 405 30, Sweden

Abstract.—Most anadromous fish undergo physiological and behavioral changes that are preparatory and adaptive for seawater entry. In anadromous salmonids, these preparatory changes are collectively known as smolting. Smolt development is regulated by environmental factors such as photoperiod and temperature and mediated by the neuroendocrine system. In this paper, we review evidence that a variety of anthropogenic factors can influence smolt development and affect marine survival. Hatchery rearing can affect the size of smolts and the extent and timing of smolt development. Smolt development is reversible, and the period of peak physiological preparedness in salmon smolts is limited by time and temperature. By influencing temperature and the duration of the migratory period, climate change and dams will have negative effects on smolt survival beyond direct lethal impacts. Contaminants acting on developmental physiology or underlying endocrine control mechanisms can also reduce marine survival. Exposure to estrogenic compounds prior to or during smolt development can reduce seawater tolerance and preference. Acid and aluminum exposure can reverse the development of seawater tolerance and reduce adult return rates. We conclude that environmental conditions in freshwater can affect physiological development, estuarine and ocean behavior, early seawater survival, and long-term seawater growth and homing, thus having influences on adult returns and long-term population sustainability of anadromous fishes.

* Corresponding author: steve_mccormick@usgs.gov

Introduction

The freshwater and marine survival of anadromous fishes is critically intertwined, though our understanding of the relationship between the two is limited. Availability of favorable freshwater habitat can affect the number of juvenile anadromous fish that enter seawater from any given river. The number of emigrating juveniles will thus be determined by both the number of spawning adults and the ability of the freshwater habitat to produce and sustain the entire freshwater life cycle (Jonsson et al. 1998; Pess et al. 2002). In addition to the number of fish that leave the freshwater environment, the quality of these fish and their capacity to enter the marine environment will also be important. In this paper, we review the adaptive value of smolt development in salmon and its relation to marine survival. We also examine the environmental factors, both natural and anthropogenic, that influence smolt development and seawater performance. Although most of the information on preparatory physiological adaptations for seawater entry and residence comes from research on salmonids, we hypothesize that similar environmental influences will affect the seawater performance of other anadromous species, particularly those in which preparatory physiological adaptations also occur. The effect of environmental factors in freshwater on seawater performance may have far-reaching impacts on the long-term sustainability of anadromous fish populations.

Smolt Development and the Adaptive Value of Smolting

Smolts are the juvenile downstream-migratory stage of salmon. In addition to the behavioral changes that are required for downstream migration, the transition from parr to smolt is accompanied by physiological and morphological changes that are generally recognized to be adaptive for migration and seawater entry. Although there are some variations in smolt development among salmon, particularly with regard to the timing of the event, most species share many common features. Several excellent reviews have summarized the major features of smolt development (Hoar 1988; Boeuf 1993; McCormick et al. 1998), and we will limit this review to those that are likely to have the greatest influence on seawater performance.

There is substantial variation in the timing of downstream migration and seawater entry among anadromous salmonids (Rounsefell 1958; Hoar 1988; McCormick 1994). Pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta* enter seawater soon after hatching, whereas Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, steelhead *O. mykiss*, and Atlantic salmon *Salmo salar* spend more substantial periods in freshwater as parr. The earliest life history stages (eggs and yolk sac larvae in the case of pink and chum salmon; eggs, yolk-sac larvae, and parr in the others) have relatively poor salinity tolerance (Weisbart 1968). In contrast, smolts have the capacity to withstand a direct transfer to seawater (30–35 parts per thousand [ppt]), with little perturbation in plasma ions (Figure 1). This feat is accomplished through a preparatory reorganization of the osmoregulatory tissues: the gill, gut, kidney, and urinary bladder. The gill is the site of sodium and chloride uptake in freshwater and secretion in seawater (Evans et al. 2005), involving specialized cells known as chloride cells or mitochondrion-rich cells. Both the number and size of chloride cells increase during smolt development, and this is accompanied by an increase in the amount and activity of Na⁺,K⁺-ATPase (NKA; Figure 1). As the key enzyme for salt secretion by the gill, its branchial activity has been widely used as a marker for the acquisition of salinity tolerance and smolt development in salmon.

An inherent challenge facing smolts is that while the mechanisms for salt secretion develop and the hypoosmoregulatory capacity of the fish increases, the capacity to osmoregulate in freshwater can be compromised. This makes smolts vulnerable to external factors that may perturb ion regulation in freshwater. Although loss of plasma ions does not appear to be a necessary feature of smolt development or migration (McCormick and Saunders 1987), ion flux rates in freshwater are greater in Atlantic salmon smolts than in parr (Primmitt et al. 1988), and decreased plasma osmolality has been observed during coho salmon smoltification (Björnsson et al. 1987). The respiratory function of the gill requires increased blood flow and decreased diffusion distance in the face of increased oxygen demand (for instance during prolonged swimming), which results in a net loss of plasma ions (Nilsson and Sundin 1998). Known as the “osmoregulatory compromise,” this may be part of the reason that smolts in freshwater experience greater decreases in plasma ions in response to

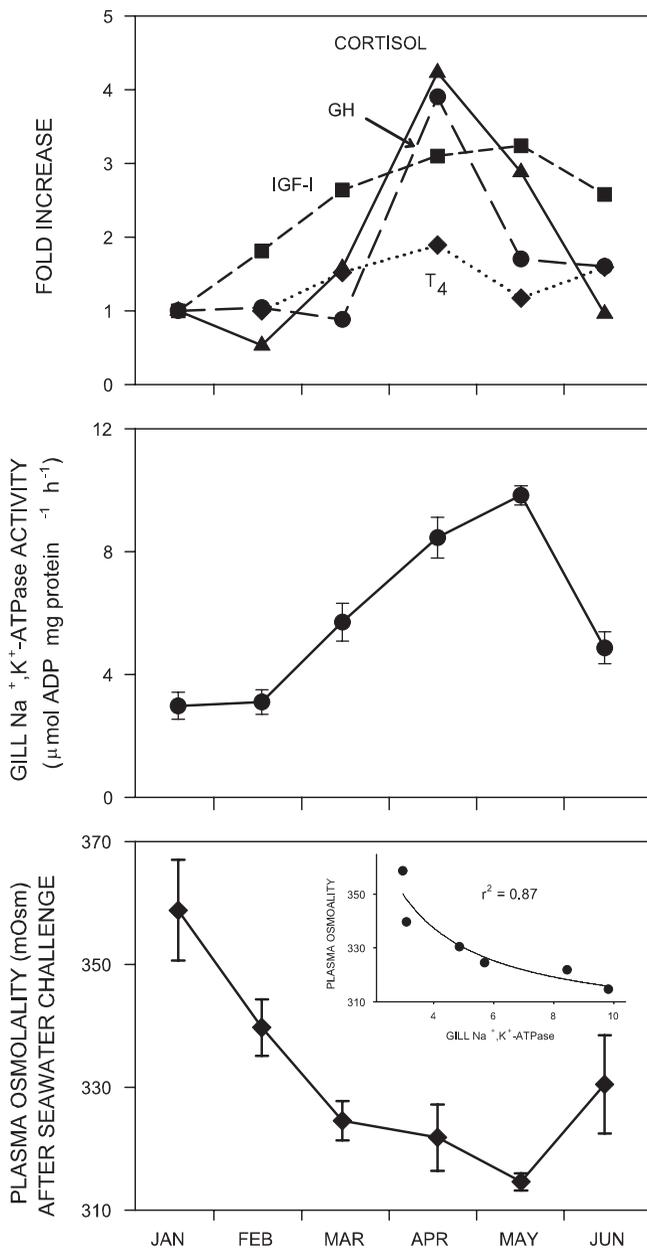


Figure 1.—Plasma hormone levels, gill Na⁺,K⁺-ATPase activity, and salinity tolerance of Atlantic salmon during the parr–smolt transformation. Abbreviations: GH = growth hormone, IGF-I = insulin-like growth factor I, T4 = thyroxine. Increase in hormone levels were expressed by setting the mean value of the January sample (February in the case of thyroxine) to 1 and expressing all subsequent changes relative to that value. Details of rearing regime and analytical methods used can be found in McCormick et al. (2000).

a handling stress than do parr (Carey and McCormick 1998).

Although there have been no direct comparisons of maximum growth rate or scope for growth in seawater between parr and smolt, Brett (1979) reviewed several different studies and species and concluded that smolts had a greater maximum growth capacity in seawater than parr. It should be noted that these conclusions are circumstantial and are confounded by the inherent size difference between parr and smolt. McCormick et al. (1987) found that continuous light (L24) applied at the time of first feeding in May resulted in good growth compared to fish on natural photoperiod, but prevented normal development of gill NKA activity and salinity tolerance the following spring. These L24 fish grew to the same size as smolts reared under normal photoperiod but, when transferred to sea cages of 28–30 ppt seawater for 3 months, had a 60% lower linear growth rate. Similarly, (Handeland and Stefansson 2001) found that juvenile Atlantic salmon maintained under continuous light had increased growth in freshwater, lower gill NKA activity and salinity tolerance, and reduced growth rates following transfer to seawater when compared to fish reared under normal photoperiod. Further, a number of studies indicate that the growth hormone system, involved both in promoting growth and hypoosmoregulatory capacity, is activated following exposure of salmonids to seawater (see Björnsson 1997). Thus, there is strong indirect evidence that smolt development is accompanied by an increase in the capacity for growth in seawater.

Other physiological and behavioral changes that occur during smolt development are also likely to be adaptive for marine conditions. Loss of parr marks, increased silvering, and darkened fin margins of smolts may be important to the development of schooling behavior (Johnston and Eales 1967), which itself may be adaptive for food acquisition and predator avoidance. Increased muscle phosphofructokinase (Leonard and McCormick 2001) and buffering capacity (Ogata et al. 1998) of smolt relative to parr may provide the former a greater capacity for repeated sprint performance necessary in an open ocean environment. Peake and McKinley (1998) have dispelled the notion that smolts have reduced swimming capacity relative to parr, indicating that initiation of downstream migration is unlikely to be a passive response to increased flow. Additionally, although some aspects of imprinting may occur

throughout the juvenile phase, there is a critical period of imprinting during smolting that can override previous experience (Dittman and Quinn 1996). It should be noted, however, that relatively little is known about the behavior of smolts once they enter seawater.

It is likely that virtually all of the features of smolt development are under the control of the neuroendocrine system (see reviews by Hoar 1988; McCormick et al. 1998). Although hormonal control of salinity tolerance has received substantial attention, relatively little is known about the hormonal control of other physiological and behavioral changes during smolting. Changes in circulating levels (Figure 1) and exogenous treatment with hormones indicate that salinity tolerance is under the positive control of cortisol, growth hormone (GH), and insulin-like growth factor I (IGF-I) (McCormick 2001). Given its importance in maintaining ion uptake in freshwater fish (Pickford and Phillips 1959), prolactin is likely to have a negative affect on smolt development (Thorpe 1982; Young et al. 1989), though surprisingly little research has been done in this area. Thyroid hormones (thyroxine and triiodo-L-thyronine) may play only a supportive role in development of salinity tolerance, but are more directly involved in the morphological changes (such as silvering and retinal pigmentation), behavioral changes, and imprinting (Dickhoff and Sullivan 1987; Dittman and Quinn 1996). Given the known role of the GH-IGF-I system in regulating growth and salt secretion in fish, and their increase during smolting and seawater entry, it seems likely that this endocrine axis will play a key role in the increased capacity for growth in seawater, though to date, this has not been substantiated. It has been suggested that early growth in seawater is a critical factor in determining overall seawater survival (Friedland et al. 1996).

The Physiological Smolt Window

For all anadromous salmonids, the salinity tolerance and other aspects of development that occur during smolting (or as fry in the case of pink and chum salmon) are lost if fish remain in freshwater (Figure 1; Hoar 1988). Smolting is therefore a reversible process, and there is a limited period of time during which the fish are at peak preparedness for seawater entry, known as the “physiological smolt window.” The temporal limits of the physiological smolt win-

dow will be determined by the environmental factors that control both the stimulation and loss of smolt characters. By way of example, smolt development in Atlantic salmon occurs in the spring and is stimulated primarily by photoperiod and secondarily by temperature (Björnsson 1997). Both the timing of development and the factors that control it differ among salmonids, driven by the evolution of their life histories (McCormick 1994). Smolt development in coho salmon and steelhead are also driven by changes in increased day length, but photoperiod may be less important in pink and chum salmon that develop salinity tolerance soon after hatching.

In Atlantic and coho salmon and steelhead, it appears that the loss of salinity tolerance and other aspects of smolt development are driven primarily by temperature and time (Zaugg and McLain 1976; Duston et al. 1991). This relationship has been investigated in detail in Atlantic salmon, where there is a dome-shaped relationship between degree-days (summation of average daily temperatures experienced after the peak of smolt development) and the loss of salinity tolerance and/or gill NKA activity (Figure 2). After peak smolt development is reached, fish that experience 500 degree-days will have completely reverted to presmolt or parr levels (Figure 2). It also appears that the regulation of smolt behavior is similar to salinity tolerance in that higher temperatures lead to an earlier cessation of downstream migratory behavior (Wagner 1974; Zydlewski et al. 2005).

Many studies have shown that adult return rates—perhaps the most important index of seawater performance—of hatchery-reared salmon smolts are strongly dependent on the timing of release. Hatchery-reared Atlantic salmon released in late May during the normal migratory period of wild fish have higher adult return rates than fish released in April and June (Staurnes et al. 1993b; Lundqvist et al. 1994). Similarly, Bilton et al. (1982) found substantially higher return rates in hatchery-reared coho salmon released in April and May than in June and July. In the studies where it was measured, the peak of physiological smolt development corresponds with the timing of release that yielded the highest adult return rates (Virtanen et al. 1991). This correspondence is likely dependent on both the physiological smolt window and coincidence of release with optimum environmental conditions for smolt survival (ecological smolt window) (McCormick et al. 1998). It seems likely that natural selection will have shaped

the physiological smolt window to coincide with the ecological smolt window. Stock-specific differences in the timing of downstream migration (Orciari and Leonard 1996) or increases in salinity tolerance (Handeland et al. 2004) under the same environmental cues are a likely example of selection acting on the timing of smolt development.

In addition to the timing of release, freshwater rearing conditions in hatcheries will affect the overall seawater performance of smolts. Beckman et al. (1999) found that the same strain of spring-run Chinook salmon reared at three different hatcheries had different smolt-to-adult return rates and that these were most strongly correlated with spring growth, plasma IGF-I levels, and gill NKA activity. Fish density and raceway flows experienced by juveniles in freshwater affect the adult return rates of spring-run Chinook salmon (Banks 1994). Several studies have found a positive correlation between size of released smolts and smolt survival and adult return rates (Miyakoshi et al. 2001; Connor 2004). The effect of size appears to be more pronounced in years with poor overall marine survival (Saloniemi et al. 2004). These effects are generally smaller than the effects of time of release and some other factors discussed, but nonetheless indicate that growth conditions in freshwater will influence marine survival. While these studies have focused on hatcheries, they underscore the principal that variations in environmental conditions in freshwater impact smolt development and seawater performance.

The mechanisms through which smolt development affects seawater survival and growth are likely to be more complicated than that of simple acute mortality, due to osmoregulatory failure following seawater entry. Minor compromises to physiological and/or behavioral preparations that are sublethal in the laboratory may have dire consequences in the wild. For example, Dieperink et al. (2001) reported daily predation rates as high as 34% percent in brown trout *S. trutta* smolts during the first 2 d of seawater entry. Atlantic salmon smolts directly transferred to seawater suffered greater experimental predation in seawater than smolts that had been acclimated to seawater for 30 d (Jarvi 1990). Similarly, Handeland et al. (1996) determined that the greatest predation rates on smolts occurred during the first days of exposure to seawater when osmotic perturbations were greatest. We have observed that smolts that perform poorly in seawater challenge tests often swim at the

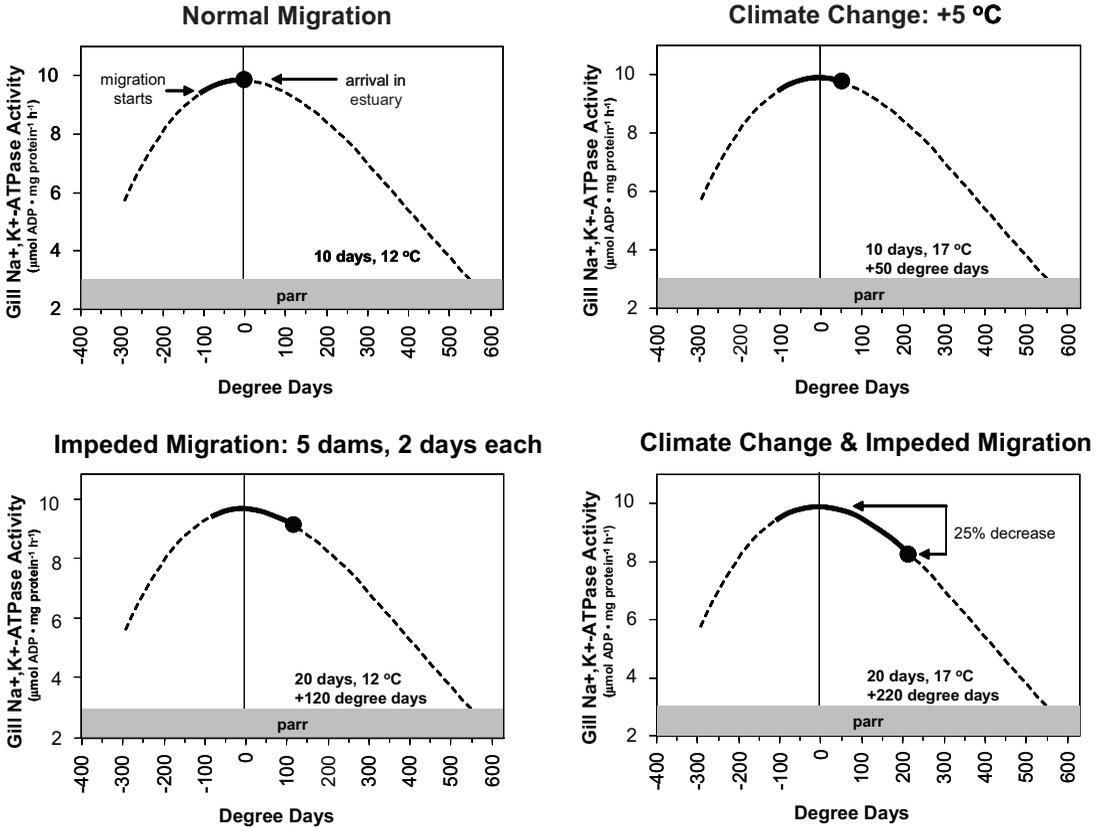


Figure 2.—Hypothetical impacts of increased spring temperature and dams on seawater preparedness of Atlantic salmon smolts. The dashed line in each panel is the response of gill Na⁺,K⁺-ATPase (NKA) activity (μmol ADP mg/protein/h) to degree-days (cumulative daily temperature) since March 30 (McCormick et al. 1997; Handeland et al. 2004). Gill NKA and salinity tolerance are tightly correlated (Figure 1). Degree-days initially increased gill NKA activity (and salinity tolerance) and then caused a decline. Vertical line represents the peak levels of gill NKA activity. In this model, the average fish (bold line, upper left graph) has a 10-d migratory period at 12°C and arrives at the estuary (dot symbol) with peak levels of gill NKA activity (i.e., highest seawater preparedness). An increase in average temperature of 5°C (upper right) may be due to annual differences in spring temperature, global climate change, or a combination and results in slight (1.4%) decreases in gill Na,K-ATPase (a 100% decrease would be reversion to parr levels of 2–3 μmol ADP mg/protein/h, shown in the gray area). Imposition of delays in migration of 10 d (e.g., five dams with 2 d of migratory delay each; lower left) also results in minor decreases (8.3%). Combined temperature increases (5°C) and delay in migration (10 d) result in synergistic decreases in seawater preparedness of 25% (lower right). It should be noted that this represents the average individual and that late migrants or smolts in river systems with warmer temperatures will likely experience even greater impacts (McCormick et al. 1999).

surface of a tank and are less responsive to external stimuli such as netting. In the wild, Chinook salmon smolts subjected to a handling stress spent more time in the upper, freshwater layers of a simulated estuary than did unstressed fish (Price and Schreck 2003), which the authors suggest would expose them to

greater avian predation. Furthermore, lower levels of gill NKA activity are associated with greater levels of avian predation in estuaries during downstream migration of Chinook salmon (Schreck et al. 2006). Osmotic and other stressors may also result in increased susceptibility to diseases that reduce estuarine and

marine survival (Loge et al. 2005). Adult return rates of coho salmon subjected to transportation stress just prior to release were reduced compared to fish released directly from the hatchery or those allowed 6 weeks to recover from transportation stress (Schreck et al. 1989). These studies indicate that factors negatively influencing the physiological and behavioral capacity of smolts to make the transition from freshwater to seawater are likely to result in an overall decrease in marine survival, even if final cause of mortality is predation or disease rather than osmoregulatory failure.

Climate Change, Dams, and the Smolt Window

As outlined above, laboratory and hatchery studies indicate that increased temperature and time in freshwater decrease the amount of time that smolts are at the highest levels of seawater preparedness. Global climate change scenarios suggest that an increase in temperature will occur in many temperate and arctic regions, the natural distribution zone of anadromous salmonids (Battin et al. 2007; Hayhoe et al. 2007). Such an increase in temperature is likely to decrease the width of the smolt window and thus have negative impacts on overall seawater preparedness of many smolt populations. Populations already close to the upper temperature tolerance limit should be especially vulnerable, as demonstrated by McCormick et al. (1999), who found that decreased gill NKA activity of smolts at the end of the migratory period was seen only in southern populations that experienced warm spring temperatures and not in northern populations that experienced cool spring temperatures. Furthermore, the proportion of the smolt population with reduced gill NKA activity was greater in years with warmer spring temperatures. Temperature increases associated with global climate change are likely to result in more years with high numbers of smolts that experience loss of seawater preparedness (Figure 2). Higher freshwater temperatures may also result in asynchrony between migration timing and ocean conditions, which could decrease marine survival (McCormick et al. 1998). Recent comprehensive assessment of the geographical distributions of all *Oncorhynchus* species (Augerot 2007) and Atlantic salmon (Parrish et al. 1998) shows that stock disappearances have largely taken place at the southern-most edge of their natural distribution. To

what extent these are due to climate change or other anthropogenic disturbances changes, such as habitat loss, dams, and pollution, remains unclear.

Global climate change may have other effects beyond the impact of temperature. Both the amount of rainfall and its seasonal distribution are likely to change, though impacts will vary by region (Hayhoe et al. 2007). Areas with reduced snowmelt or spring rain will have lower water velocity and water levels in spring, which may have profound impacts on in-river smolt mortality. Given the variation that exists in the timing of migration especially among Pacific salmon, the importance of flow and seasonal hydrographs is likely to vary among species. Although a full review is outside the scope of this paper, there is evidence that flow has a substantial impact on smolt survival both in river and after fish reach the ocean. A relation between freshwater discharge and adult survival has been shown for hatchery-reared Atlantic salmon, with greatest survival occurring when smolts are released into high levels of freshwater discharge (Hvidsten and Hansen 1988). Flow has been shown to be a positive factor for in-river survival of steelhead and spring-migrating sockeye salmon, but less important for yearling and summer-migrating Chinook salmon in the mid-Columbia River basin (Giorgi et al. 1998). In the Snake River, the in-river survival of migrating juvenile fall Chinook salmon increases with increasing flow and decreasing temperature (Connor et al. 2003). In addition to providing correlative evidence of a link between flow during out-migration and marine survival of coho salmon, Lawson et al. (2004) demonstrate that annual variations in climate that improve freshwater survival also improve marine survival. In addition to the direct effects of reduced flow on in-river survival, by reducing the speed of migration, reduced water flow may affect smolt survival through loss of smolt development or altered timing of seawater entry (Budy et al. 2002). There are other climate change issues that may have profound effects on seawater entry and marine performance of anadromous fish, including increased salinity intrusion in estuaries due to higher sea levels, as well as a projected decrease of seawater pH (Orr et al. 2005).

Dams and associated hydropower facilities are known to have direct negative impacts on smolt survival. Turbines and spillways can be directly lethal to smolts, with mortality rates of 6–20% for passage through a single turbine or deep plunge spillway (Bickford and Skalski 2000). Dams may also have in-

direct effects by delaying migration and altering the migratory paths of smolts, often funneling them into narrow corridors with substantial numbers of predators (Venditti et al. 2000). As noted above, there is generally a positive relationship between flow and survival of salmon; dams that decrease or substantially alter flow are therefore likely to decrease smolt survival. The long reservoirs and/or highly altered hydrographs caused by dams can impose substantial delays in migration (Bentley and Raymond 1976) that will affect whether the physiological smolt window is still open by the time fish arrive at the estuary. There is surprisingly little information on the impact of physical stressors, such as those that might occur during passage through turbines, spillways, or over dams on salinity tolerance or other aspects of smolt performance. Experimental descaling, similar to that which occurs during passage through turbines, can decrease salinity tolerance of Atlantic salmon smolts (G. Zydlewski, University of Maine, Orono, personal communication). Pinpointing the specific impacts of dams on delayed mortality or overall seawater performance of smolts in a "natural" setting is difficult. Because the impact of stress and delays in migration are cumulative and often delayed (Barton et al. 1986), measurement of the impact of a single dam will underestimate the impacts of multiple dams. For instance, Budy et al. (2002) concluded that the accumulated stress and altered timing of moving through multiple dams on the Snake and Columbia rivers result in higher delayed (marine) mortality than would occur in this river system without dams. Changes in management of hydropower systems that reduced in-river mortality for Chinook salmon did not improve adult returns (Williams et al. 2001). Although this could be due to a variety of factors, including variation in ocean conditions, one possibility is that dams continued to have an impact on delayed or early marine mortality.

A hypothetical scenario of the impact of the interaction between increased temperature experienced by smolts under global climate change and delays in migration due to dams is shown in Figure 2. Temperature increases associated with global climate change are likely to result in more years with increasing numbers of smolts that have experienced loss of seawater preparedness. Delays in migration appear to have a greater impact than temperature increases, though it should be noted that the effect of temperature does not take into account those river systems in which

temperature will rise above the levels that are lethal to smolts. Perhaps most importantly, there is likely to be a synergistic interaction with global climate change, such that the presence of dams and increased temperature will have more than an additive negative effect on seawater performance (Figure 2).

Acid Rain and Aluminum Impacts

Acid rain resulting from sulfur and nitrogen oxide emissions from coal-burning power plants is a known cause of the decline of Atlantic salmon in eastern Canada (Watt 1987; Lacroix 1989) and southern Norway (Hesthagen 1989; Hesthagen and Hansen 1991). As a result of their underlying geology, rivers and streams in these regions have poor buffering capacity and are thus vulnerable to chronic (year-round) acidification. As a consequence of acidification, aluminum (Al), one of the most abundant elements in the soil, is leached into the surrounding watershed (Driscoll 1984). In addition, the solubility of Al increases as a direct result of decreased pH leading to the increased presence of inorganic Al (Al₃), the form most toxic to fish (Gensmer and Playle 1999). Recently, episodic (days to weeks) acidification and its associated Al toxicity has been identified as a possible cause of salmon decline in the northeastern United States, including Maine, where many salmon rivers have been listed as federally endangered (National Academy of Science 2004). In this region, rivers and streams are not chronically acidified, but instead experience episodic decreases in pH during acidification events such as spring snowmelts and fall storms.

During exposure to acid and aluminum (acid/Al), Al accumulates both on the surface and within the gill (Youson and Neville 1987; Wilkinson and Campbell 1993; Lacroix et al. 1993; Teien et al. 2004) damaging the branchial epithelium and ultimately leading to ion regulatory disturbance. Loss of ion regulatory ability is likely due to both an increase in branchial permeability and an inhibition of active ion uptake (Booth et al. 1988; McDonald et al. 1991). Increased permeability may be caused by the displacement of Ca²⁺ ions from anionic gill binding sites by Al, resulting in weakening of intercellular tight junctions (Booth et al. 1988; Freda et al. 1991), whereas inhibition of ion uptake may result from damage to or alteration of gill chloride cells (Jagoe and Haines 1997), and decreased NKA

activity (Staurnes et al. 1993a, 1996; Kroglund and Staurnes 1999; Magee et al. 2003).

Smolts appear to be the most sensitive of the salmon life stages to the effects of acid/Al exposure. In Atlantic salmon, smolts are more prone than parr to plasma ion losses and inhibition of gill NKA activity, and they suffer greater acute mortality during exposure to both short-term and chronic acid and aluminum (Rosseland and Skogheim 1984; Leivestad et al. 1987; Rosseland et al. 2001). Parr and smolts accumulate similar levels of aluminum in the gill following the same acid and aluminum exposure levels, indicating that increased aluminum alone is not the reason smolts are more sensitive than parr (Monette and McCormick 2008). The increased sensitivity of smolts may be due to the higher ion flux rates they experience in freshwater (Primmitt et al. 1988), putting them at greater risk of any factor that affects ion uptake.

Previous research has established that long-term (weeks–months) exposure to acid/Al during the par–smolt transformation can compromise survival, growth, and the smolting process. Thus, Atlantic salmon reared under low pH (4.2–4.7) from February to June had impaired ion regulation in freshwater, reduced seawater tolerance and lower gill NKA activity levels than control fish reared at high pH (6.4–6.7) (Saunders et al. 1983). Smolting Atlantic salmon kept for more than 1 month in soft water of pH 5.0 and 50 $\mu\text{g/L}$ Al had increased mortality, decreased condition factor, impaired ion regulation in both freshwater and seawater, and substantial declines in gill NKA and carbonic anhydrase activities (Staurnes et al. 1993a). Exposure of Atlantic salmon smolts to pH 5.5 and 158 $\mu\text{g/L}$ Al_i for ≥ 16 d significantly altered gill morphology, as indicated by changes in the number, size, and shape of chloride cells (Jago and Haines 1997).

There is an increasing body of evidence that short-term or episodic (days–week) exposure to acid/Al can also impair smolt development. Atlantic salmon smolts exposed to several episodic pulses of acid/Al (pH 5.2, 59 $\mu\text{g/L}$ Al_i) over the course of 31 d and then exposed to seawater experienced reductions in hematocrit and increases in plasma ions and suffered higher mortalities than controls (Magee et al. 2003). Staurnes et al. (1996) found that smolts placed in floating cages in the river Lygna (pH 4.7–4.9, 30–120 Al_i) for only 12 h had completely lost seawater tolerance, as indicated by 100% mortality during a 24 h,

30 ppt seawater challenge. Interestingly, during short-term exposure to acid/Al, impaired seawater tolerance can be seen in the absence of any impact on ion regulation in freshwater. Monette (2007) determined that plasma Cl⁻ levels of smolts exposed to pH 5.4, 42 $\mu\text{g/L}$ Al_i for as little as 2 d did not differ from controls in freshwater, but were significantly elevated relative to controls after 24 h in 35 ppt seawater, indicating loss of seawater tolerance in this group. Also in this study, smolts exposed to pH 5.3, 11 $\mu\text{g/L}$ Al_i for 6 d exhibited impaired seawater tolerance, demonstrating that the hypoosmoregulatory system of smolts is highly sensitive to acid and very low levels of Al_i.

Several studies have begun to make the important link between the osmoregulatory status of smolts after acid/Al exposure and overall seawater performance (Staurnes et al. 1996; Magee et al. 2001; Kroglund and Finstad 2003). Staurnes et al. (1996) Carlin-tagged over 5,000 Atlantic salmon smolts, released them into acid (Lygna) and limed (Audna) rivers in southern Norway, and monitored adult return rates over 2 years. They found a significant correlation between adult recapture rates and the osmoregulatory status of smolts held in floating cages at the respective release sites. Kroglund and Finstad (2003) determined that exposure of smolts to very low levels of Al_i (6 $\mu\text{g/L}$) impaired freshwater growth and reduced marine survival by 20–30%. Following exposure of Atlantic salmon smolts to sublethal acid/Al conditions, Kroglund et al. (2007) found a strong correlation of both gill NKA activity and salinity tolerance (plasma chloride after 24 h seawater [SW] challenge) and adult return rates. In their study, exposure of smolts to sublethal acid/Al reduced smolt-to-adult survival by 50% relative to controls. Further evidence for the impact of acid and aluminum on seawater performance is provided by the response of Atlantic salmon populations in eastern Norway to long-term liming. These programs target a pH of 6.5 in order to protect smolt development and have resulted in recoveries of Atlantic salmon populations that had been extirpated due to the effects of acid rain (Hesthagen and Larsen 2003).

To date, most research on acid impacts on salmon smolts has been done with Atlantic salmon, due to the regional nature of acidification impacts. Given the rise of industrialization in China coupled with global weather patterns, future impacts on Pacific salmon are possible, and it seems likely that Pacific

salmon smolts (and other life stages) will have sensitivity similar to Atlantic salmon. In addition, heavy metals have a similar mode of action and impact on the osmoregulatory physiology of fish as aluminum, though heavy metal impacts are not necessarily dependent on low pH. Coho salmon have a lower lethal threshold (i.e., were more sensitive) to copper and zinc in November as parr than in May as smolts (Lorz and McPherson 1976), and although zinc did not affect seawater tolerance, copper at one-tenth the lethal level was sufficient to reduce gill NKA activity and seawater tolerance.

Environmental Estrogens

Exposure to environmental estrogens can adversely affect reproductive development and overall population stability (Kidd et al. 2007). From the mid-1970s to the mid-1980s, the pesticide Maticil 1.8D, which contained the xenoestrogen nonylphenol (NP) as a surfactant, was applied to forests in the Atlantic coast watersheds of Canada to control damage from spruce budworm *Choristoneura fumiferana*. Application of this insecticide coincided with spring smolting and downstream migration of Atlantic salmon. In a retrospective study, Fairchild et al. (1999) calculated that the resulting concentrations of NP after pesticide application were within ranges found in municipal sewage outfalls and industrial effluents. Importantly, they demonstrated that for 16 rivers exposed to spraying between 1973 and 1990, the lowest adult salmon returns occurred in rivers with the largest exposure to Maticil 1.8D (Fairchild et al. 1999). These authors conclude that NP entered the aqueous environment at levels sufficient to have estrogenic actions, specifically impacting the capacity of smolts to enter seawater.

Previous research has established that administration of both androgens and estrogens are inhibitory to the development of salinity tolerance in salmonids (Ikuta et al. 1987; Schmitz and Mayer 1993). Madsen and Korsgaard (1989) found that estradiol (E_2) inhibited silvering and reduced gill NKA activity in Atlantic salmon smolts, while inducing vitellogenesis, indicated by increased total plasma calcium, hepatosomatic index and, total liver RNA. Further work by this laboratory confirmed parallels in the physiological impacts of NP and E_2 , with both compounds inhibiting smolting by reducing gill NKA activity and gill chloride cell density, as well as re-

ducing hypoosmoregulatory ability of smolts (Madsen et al. 1997). Further, E_2 and NP exposure just prior to smolting delayed smolt development and downstream migration (Madsen et al. (2004). In an effort to define the endocrine pathways involved in the physiological impairment of SW tolerance, McCormick et al. (2005) demonstrated that E_2 and NP suppressed plasma concentrations of IGF-I and thyroid hormones. Aqueous exposure of Atlantic salmon smolts to E_2 and NP also reduced gill NKA activity and plasma concentrations of IGF-I, in addition to decreasing growth and increasing stress sensitivity (Arsenault et al. 2004; Lerner et al. 2007b).

While providing useful insight into the potential impacts of estrogenic compounds on smolt development, many of the studies mentioned above have applied NP levels that were higher than those likely to be present in most salmon rivers (Kolpin et al. 2002), including those that experienced Maticil spraying in eastern Canada. It is possible that exposure to environmentally relevant concentrations at an earlier developmental stage has long term impacts on smolt development. To address this, Lerner et al. (2007c) exposed Atlantic salmon yolk sac larvae to two environmentally relevant aqueous levels of NP or E_2 for 21 d. Nonylphenol at 80 $\mu\text{g/L}$ resulted in 50% mortality during the 21-d exposure period, reaching 100% 120 d after treatment was terminated. Yolk sac larvae treated with the lower dose of NP (7 $\mu\text{g/L}$) or E_2 (2 $\mu\text{g/L}$) were not affected during the exposure period but exhibited delayed mortality (four-fold greater than controls) 31–60 d after treatment was terminated. A full year after exposure, at the peak of smolting, yolk sac larvae that had been exposed to NP or E_2 had reduced plasma IGF-I levels, gill NKA activity, and seawater tolerance. Behavioral impacts were also detected, with NP and E_2 substantially reducing behavioral preference for seawater. These studies establish that early exposure to contaminants, well before smolt development, can have long-term impacts on seawater preparedness. They also provide a possible explanation for reduced marine survival of fish exposed to nonylphenol in nature (Fairchild et al. 1999).

Environmental disruption of SW performance during smolting has been linked to negative effects of estrogenic compounds on the GH-IGF-I system. The impacts of E_2 on circulating levels of GH in fishes appear to vary among species, developmental stage, and environmental salinity (Melamed et al.

1998; McCormick et al. 2005; Lerner et al. 2007b, 2007c). On the other hand, a reduction in plasma levels of IGF-I is consistent among fish treated with estrogenic compounds (Arsenault et al. 2004; McCormick et al. 2005; Lerner et al. 2007b, 2007c). Insulin-like growth factor-I is a mediator of many of the effects of GH on osmoregulatory physiology and probably includes both endocrine action (from GH binding to its hepatic receptor and release of IGF-I into circulation) and paracrine/autocrine action (GH induction of IGF-I release at the target tissue) (Duan 1998). In mammals, E_2 reduces GH receptor (GHR) density in the liver (Domene et al. 1994), and there is evidence that E_2 and some environmental estrogens reduce hepatic and branchial GHR in Atlantic salmon (Lerner 2007). Taken together, these findings suggest that modification of GH and/or IGF-I levels and their receptors may provide a likely mechanistic route for mediating the negative impacts of estrogenic compounds on the maintenance of osmoregulatory homeostasis. Exposure to estrogenic compounds also decreases the levels of thyroid hormones during smolt development (McCormick et al. 2005). Although thyroid hormones appear to have an indirect role in controlling osmoregulation in salmonids, they have a more direct role in other aspects of smolt development such as migratory behavior and imprinting (Hoar 1988). In addition to affecting seawater tolerance, estrogenic compounds may therefore inhibit other aspects of smolt development through their impact on thyroid hormones. The inhibitory effect of environmental estrogens on seawater performance may be related to the anadromous life history of salmon; endogenous sex steroids are low during early development (Sower et al. 1984), and when they increase during reproductive maturation, they may act as a signal for both migration into freshwater and the accompanying loss of hyperosmoregulatory ability (Uchida et al. 1997; Shrimpton et al. 2005; Makino et al. 2007).

Other Contaminants and Interactions

In agricultural and managed forestry areas, river contamination through rain runoff can occur due to the high application rates and water solubility of many pesticides. A number of pesticides are often present in salmon habitats, and spring pesticides ap-

plication is especially problematic because the timing of spring application of pesticides coincides with smolt development. Widely used herbicides such as hexazinone (HEX) and atrazine (ATZ), non-selective herbicides in the triazine family, are employed to control undesirable plants in crops such as corn, alfalfa, sugar cane, pineapples, and blueberries. ATZ can cause damage to gill epithelium and kidneys, increasing the renal excretion of ions and proteins of rainbow trout (nonanadromous *O. mykiss*) (Neskovic et al. 1993). Exposure of Atlantic salmon smolts to concentrations up to 100 $\mu\text{g/L}$ ATZ compromised osmoregulatory ability in freshwater (FW) and after 24 h SW challenge (Waring and Moore 2004; Nieves-Puigdoller et al. 2007). Both studies found a slight decrease in survival and growth and elevated plasma cortisol during the exposure period. Furthermore, Nieves-Puigdoller (2007) found that prior exposure to ATZ in FW resulted in reduced growth of Atlantic salmon smolts reared in clean seawater (free of any contaminants) for 1 month. Given the evidence that early growth in seawater is critical to overall marine survival (Beamish et al. 2004), this impact of contaminant exposure in freshwater on seawater growth indicates a detrimental effect on marine survival.

In salmon, the yolk sac larval stage coincides with pesticide application in the spring. Exposure of yolk sac larvae to 100 $\mu\text{g/L}$ ATZ for 21 d resulted in significantly smaller smolts 1 year after exposure (Nieves-Puigdoller 2007). This is somewhat surprising given the capacity of fish to exhibit compensatory growth and suggests that some permanent physiological effect may have occurred. Plasma cortisol levels were higher in ATZ-exposed fish a year after exposure, which suggests a permanent alteration in the hypothalamic-pituitary-interrenal axis (Nieves-Puigdoller 2007). Increased cortisol may be valuable in mobilizing energy for responding to and repairing damage caused by contaminants, but it can have negative consequences for growth and disease resistance (Wendelaar Bonga 1997).

In addition to herbicides, fungicides are widely used in numerous applications. The use of didecylmethylammonium chloride (DDAC) in wood preservation may be a problem for anadromous fish, as most lumber storage facilities are near large rivers. Exposure of coho salmon smolts to 0.75 mg/L DDAC for 24 h followed by 24 h SW challenge resulted in increased plasma cortisol, reduced gill

NKA activity, and lower salinity tolerance (Johnston et al. 1998). Chlorothalonil (CTL) is the most commonly used fungicide in the United States, but to date, there are no studies that have examined the impact of this compound on smolt development. However, Nieves-Puigdoller (2007) found that exposure of yolk sac larvae to 10 $\mu\text{g/L}$ CTL for 12 d resulted in increased whole-larvae NKA activity and Na^+ ion, which may be a compensatory response to moderate damage of ion regulatory tissues.

Organophosphate insecticides act through inhibition of acetylcholinesterase (AChE) activity, affecting normal cholinergic nerve transmission. The inhibition of AChE causes accumulation of acetylcholine in synapses and neuromuscular junctions, resulting in overstimulation of cholinergic receptors (Colombo et al. 2005). Exposure of juvenile cutthroat trout *O. clarkii clarkii* to environmentally relevant concentrations (750 $\mu\text{g/L}$) of the insecticide carbaryl for 6 h decreased brain and muscle AChE activity (Labenia et al. 2007). In trout species such as cutthroat (Labenia et al. 2007) and rainbow (Little et al. 1990), decreased AChE activity resulted in reduced swimming performance and increased experimental predation. Furthermore, decreases in AChE activity in juvenile coho salmon following exposure to another common insecticide, chlorpyrifos, were associated with reduced swimming and feeding activities (Sandahl et al. 2005). The specific impact of AChE inhibitors on seawater performance of anadromous fish has yet to be examined.

Polychlorinated biphenyls (PCBs) are highly stable anthropogenic chemicals classified as "persistent organic pollutants" (POPs). Polychlorinated biphenyls are ubiquitous in the aquatic environment and are present in significant amounts in downstream migrating smolts (Johnson et al. 2007) and adult farmed and wild salmon (Hites et al. 2004). Polychlorinated biphenyl mixtures and their parent congeners are known to reduce plasma thyroid hormone levels in mammals, which may have significant impact on brain development (Zoeller 2005). Thyroid hormones are thought to play a role in controlling downstream migratory behavior and SW preference of anadromous salmonids (Iwata et al. 1990; Iwata 1995). There is evidence that exposure to the PCB mixture Aroclor 1254 can negatively affect mechanisms involved in smolt development and migration of Arctic char *Salvelinus alpinus* (Jorgensen et al. 2002, 2004). Exposure of Atlantic

salmon smolts to 10 $\mu\text{g/L}$ aqueous PCB resulted in loss of gill NKA activity and reductions of plasma ions in freshwater (Lerner et al. 2007a). Behavioral preference for seawater was also decreased, but salinity tolerance was not detectably impacted. There is also evidence that exposure can reduce time spent in SW in striped bass *Morone saxatilis* (Zlokovitz and Secor 1999). These data indicate that exposure to sublethal, environmentally relevant concentrations of A1254 can affect critical aspects of behavior and physiology, which in turn could affect marine survival and population sustainability.

Oil spills present another frequent source of aquatic pollution. Exposure of pink salmon eggs to doses of polynuclear aromatic hydrocarbon (PAHs, 1–45 $\mu\text{g/L}$) resulted in a dose-dependent decrease of growth rate in sea cages 10 months after the exposure period (Heintz et al. 2000). Furthermore, PAH-exposure of embryos that were subsequently released as downstream migrating fry decreased marine survival from 1.3% in controls to 0.8% in fish exposed to 19 $\mu\text{g/L}$ PAH. Interestingly, these authors found that the impact of PAH was greater (1.3% to 0.8%) in a year with poor marine survival, compared to a year when marine survival was high (2.0% reduced to 1.7% by PAH). The study indicates that freshwater exposure to a contaminant can have substantial impact on marine survival and suggests that the level of this impact will be greater when marine conditions are unfavorable.

Most aquatic toxicology studies have focused on single compounds. However, aquatic organisms are usually exposed to mixtures of contaminants that vary with land use. A mixture of pesticides may increase the toxicity to aquatic fauna, and only recently have efforts been made to understand the effects and mechanisms of pesticide interactions (Anderson and Lydy 2002). For example, exposure of Atlantic salmon smolts to a mixture of 4-nonylphenol and ATZ at environmentally relevant levels causes increased mortality and compromises osmoregulatory ability in SW (Moore et al. 2003); however, neither of the compounds alone affected osmoregulation in SW. In addition, Nieves-Puigdoller (2007) found that body size was smaller in yolk sac larvae exposed to a combination of pesticides than when fish were only exposed to a single compound. Moreover, exposure to contaminants and other stressors may interact with diseases to increase mortality (Loge et al. 2005).

Most studies to date have examined only a limited number of features of the preparatory adaptations for seawater entry in anadromous fish, and many have focused on the development of salinity tolerance. While this is obviously a critical factor in marine survival, other features of preparatory development may also be impacted by exposure to contaminants. Given the demonstrated sensitivity of the olfactory system to a variety of anthropogenic factors, including low pH (Leduc et al. 2007), carbofuran (Waring and Moore 1997), cypermethrine (Moore and Waring 2001), and atrazine (Moore and Waring 1998), it would not be surprising to discover that the process of imprinting is sensitive to perturbation by contaminants.

Perspectives

Developmental increases in salinity tolerance probably occur in all anadromous species; however, how this is integrated into the overall osmoregulatory capacity of the animal during its life history varies with species. In some species, such as the striped bass, the developmental acquisition of hypoosmoregulatory ability increases the osmoregulatory range of the species, leaving it highly euryhaline through most of its life cycle (Hurst and Conover 2002). In other species,

such as American shad *Alosa sapidissima*, salinity tolerance is acquired and maintained just prior to and during the downstream migratory phase, and freshwater tolerance is lost at the end of the migratory period (Zydlewski and McCormick 1997a, 1997b). While the developmental processes and strategies that govern the transition from a freshwater to marine environment varies among species, some basic aspects, such as the development of salinity tolerance (and its underlying physiology), behavioral changes during downstream migration, and the underlying neuroendocrine regulation of these changes, are likely to be shared to some degree. Thus, the environmental factors and contaminants that affect smolt performance may also affect the seawater performance of other anadromous species.

Although we are only at the beginning of focused research in this area, it appears likely that even subtle, sublethal effects during key developmental stages may have profound effects during subsequent life stages. In this review, we have presented evidence that exposure to poor environmental conditions in freshwater such as high temperature, physical obstacles (dams), and contaminants such as acid rain disrupt smolt development and salinity tolerance (Figure 3). In the wild, these impacts may compromise growth, competitive ability, migration, disease

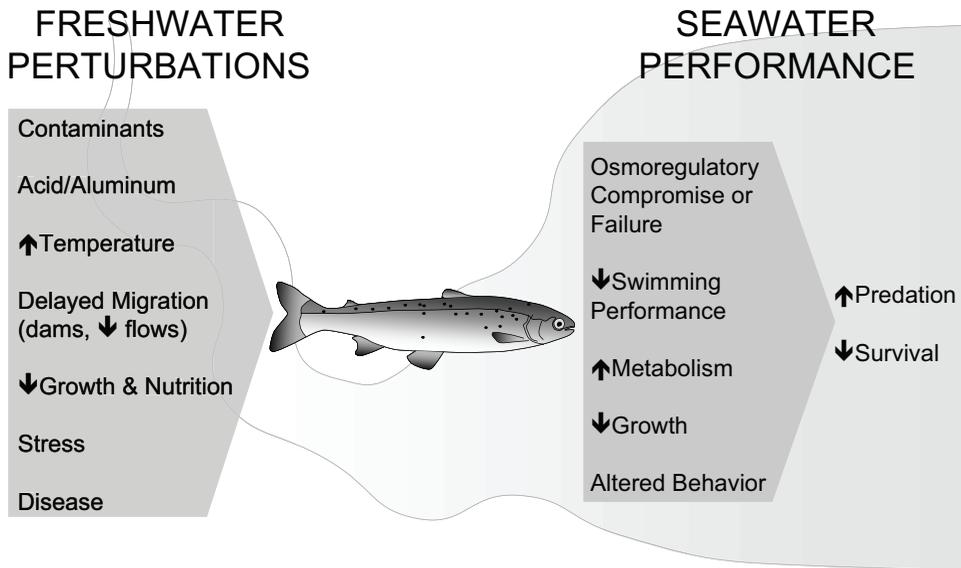


Figure 3.—Environmental impacts on salmon in freshwater and the organismal outcomes that affect survival and growth in the marine environment.

resistance, and predator avoidance of smolts, affecting their survival and population sustainability. There may also be important interactions between performance capacities affected in freshwater and their expression under various marine conditions: poor performance may be masked when ocean conditions are excellent but accentuated when marine conditions are poor. Poor conditions for salmon survival and growth in the marine environment may become more common with global warming (Friedland et al. 2003; Lawson et al. 2004), thus increasing the impacts of environmental perturbations in freshwater. The accumulated evidence summarized here indicates that decreased marine returns are due not only to changes in oceanic conditions, but are also adversely affected by anthropogenic influences during their freshwater phase. Anadromous salmonids take it with them when they go, having lasting impacts on marine survival and population sustainability.

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