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The importance of smolt development to salmon conservation, culture, and management: perspectives from the 6th International Workshop on Salmonid Smoltification

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Abstract

The 6th International Workshop on Salmonid Smoltification was held in Westport, Ireland, during September 3–7, 2001. Perhaps more so than at past workshops, this meeting took a 'salmon life cycle' approach to smoltification. Results presented at the workshop illustrated the variation in the smoltification process among species, populations and individuals, suggesting that within-species variation can be of adaptive significance. Workshop presentations also demonstrated the importance of environmental factors and culture conditions. Salmon conservation and restoration programs should work to restore aquatic systems that allow for the full suite of smolt phenotypes, ensuring their full range of adaptations. A future challenge to anadromous salmonids, which depend on both marine and freshwater ecosystems, is global warming. The rate of change in, e.g., temperature, rainfull, runoff, and ocean climate is critical to the performance of smolts and their ability to cope with change. It is essential to ensure that the genetic variation and diversity in wild stocks are not reduced, so that the capacity to adapt remains. Climatic changes will likely further compound the

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adverse effects stemming from anthropogenic sources such as dams, pollution, water diversion and riparian deforestation.

An important question raised at the workshop is whether smolting is completed under artificial rearing conditions, which again brings us back to the question of *what is a smolt?* While the basic physiological blueprint associated with smoltification in hatchery and wild fish tends to be similar, cultured fish have less intense changes and differ in timing compared to smolts in the wild. Although the fundamental genetic basis for smoltification remains, a concern is that the population-level variation in smolt phenotypes is being reduced.

Enhancement operations have been initiated in most salmon-producing regions to compensate for loss of natural production. While the interests of salmon conservation and exploitation are superficially similar, i.e., to ensure a viable population with a good adult run, obvious differences are emerging. Workshop presentations and discussions focused on ways of combining the interests of conservation and exploitation. Local adaptation should be maintained in hatchery-enhanced stocks and combined with a move towards a more natural rearing environment. This is likely to benefit both conservation efforts and fisheries interests.

Current advances in biology are likely to have a major influence on our approach to smolt research. Still, the 'traditional' ecological, physiological, behavioral and environment–fish interaction studies at the organismal level will be critical for interpretation of findings at the molecular, cellular and organ levels, and are vital as input for the management of our wild and reared salmon stock. Perhaps once all of this has been accomplished we will have come to terms with the vexing question: what is smolt? However, even if this question remains unanswered, our increased understanding of smolts as a critical stage in the life history of salmon will improve our ability to conserve, enhance and enjoy this vital natural resource.

Keywords: Salmon; Smolt development; Salmonid smoltification

1. Preface

This International Workshop on Salmonid Smoltification is the 6th in a series of international meetings dedicated to studies of salmonid smolting from a wide range of perspectives including ecological, physiological, behavioural, and genetic, with papers and discussions spanning all levels of biological organization from molecular to environmental. Past meetings have been held in LaJolla, California, Stirling, Scotland, Trondheim, Norway, St. Andrews, Canada, with the 5th workshop held in Muonio, Finland during December 1996. A scientific organizing committee was selected in Muonio consisting of Björn Thrandur Björnsson, Stephen D. McCormick, Carl Schreck and Sigurd O. Stefansson. That committee was charged with exploring various options for the 6th workshop, propose a location, formulate a venue, and invite participants. The group soon came up with the idea of having the meeting in Ireland. It was felt that Ireland would make an excellent setting for the next meeting, being one of the most important strongholds for wild salmon in Europe and having developed a recent aquaculture industry. Through contacts between Sigurd Stefansson, Tom Cross and Phil McGinnity, the town of Westport in County Mayo was quickly identified as the place for the meeting. In addition to being the town closest to Ireland's famous salmon research facility on the Burrishoole River at

Furnace, near Newport in Co. Mayo, Westport also has a great selection of pubs, restaurants, and cultural activities, and is located in the spectacular scenery of Co. Mayo.

The productivity of the workshop was certainly enhanced by the stimulating scientific venue complemented with evening activities including Guinness, socializing at Matt Moloy's and other local establishments. On the last day, a tour was organized that included the Marine Institute on the Burrishoole, the River Moy (one of the most productive salmon angling fisheries in the world), peat bog-influenced salmon habitats, as well as excavations of early farming settlements in Ireland. All participants found that the reputation of the Irish people for hospitality and good cheer was no myth and truly well deserved.

Perhaps more so than at past smolt workshops, this meeting took a 'salmon life cycle' approach to provide an understanding of smoltification (also referred to as 'parr–smolt transformation' or 'smolting') as a critical stage for the species. Wild salmonids are facing a wide range of challenges throughout most of their distribution, including climate change (global warming), habitat degradation (man-made or natural), over-harvesting and pollution, to name some of the most important (see Parrish et al., 1998 for review of human factors affecting salmon populations). The growth of salmon aquaculture and ranching operations in Europe, North America and Asia represents yet another challenge to the wild stocks of anadromous salmonids. While much of the research on smoltification is directed at aquaculture, it is now becoming recognized that hatchery stocks and aquaculture operations can affect wild stocks of Atlantic salmon (*Salmo salar*), sea trout (*S. trutta*) and Pacific salmon (*Oncorhynchus* spp.) in a variety of ways. Recent examples of such potential interactions are the spread of salmon lice (*Lepeophtheirus*, *Caligus*) between farmed and wild Atlantic salmon and sea trout in Norway, Scotland and Ireland, and genetic interactions as farmed salmon escape or stray and interbreed with wild fish.

Although the anadromous life strategy has proven to be very successful throughout the evolution of salmonid species, new challenges are facing these species that are dependent on the health of both marine and freshwater ecosystems for their survival. Smolts may be a particularly vulnerable life history stage, as the juvenile salmon must complete a wide range of morphological, physiological and behavioral changes as they prepare to undertake an extended migration and enter the ocean. During this transformation and transition from freshwater to seawater, the smolts are exceptionally vulnerable to environmental disturbances such as habitat degradation involving altered flow and temperature regimes, reduced water quality including pollution, dams and impoundments, and altered estuarine habitat (McCormick et al., 1998). Thus, factors that may not have affected earlier fresh water life stages may have large impacts during the short time that salmon use the main stem of rivers and estuaries to migrate downstream and enter the ocean.

2. Workshop synthesis and summary

2.1. Introduction

The anadromous life cycle is widespread among salmonids, and includes species of the genera *Oncorhynchus*, *Salmo* and *Salvelinus*. This life history strategy that combines the benefits of reproduction and juvenile development in the freshwater environment with a rapid adult growth phase in the marine environment has allowed anadromous salmonids to dominate watersheds in the temperate and arctic regions of the Northern Hemisphere. It is not our intention to give an in-depth review of the wide range of salmonid life history strategies, as such information can be found elsewhere (see, e.g. Hoar, 1988), but rather point to the smolt as the critical link between the freshwater and marine environments in the context of species and population management and conservation efforts, in salmon aquaculture operations and in enhancement programs aimed at restoring or enhancing salmon populations. The following conclusions and syntheses are cantered on the workshop and are based on our interpretations of the papers presented and/or on the topical discussion sessions that were held at the workshop; we make no attempt to cite these or other specific papers. Hence, any inaccuracies or misrepresentations are ours, not the authors'. Only a few citations to the more general literature are offered to help establish the perspective for our comments. In the spirit of the workshop we have also attempted an untraditional twist to our understanding of why salmonids smoltify by describing some key characteristics of smolt development (Table 1).

2.2. Salmon conservation and freshwater habitat

Results presented and discussed during this workshop, as in prior workshops, have amply illustrated the great variation in the smoltification process among salmonid species, populations, and individuals and subsequently the huge variation in physiological state among animals we collectively refer to as smolts (see Healey and Prince, 1995, for a discussion of salmon life history tactics and conservation). It is probably appropriate to once again bring up the classical question raised at all previous smolt workshops: *what is a smolt*?

We have known for a long time that Pacific salmon (*Oncorhynchus*) smolts are generally smaller and younger than Atlantic salmonid (*Salmo*, *Salvelinus*) smolts. We also know that the environment has a major impact on size and age at smolting in all species. There is an accumulating body of evidence, including results presented at the workshop, suggesting that populations within a species differ in the process of smolting, and that this within-species variation can be of adaptive significance. Considering the large variation among populations in a wide range of characteristics like growth rate, age at maturity or smolting, run timing, etc., these suggested differences in smolting character-

Table 1
The top ten reasons for why salmonids smoltify

10.	Foreign travel is such a big part of the family tradition.
9.	I'm a big fish now; I want to go to school.
8.	Because my hypothalamus told me to.
7.	I need to get this strong smell of home out of my head.
6.	My little brother is chasing females all the time, I don't understand it.
5.	I've been feeling irritable and stressed lately; I've just got to get out of here.
4.	I've got this new set of shiny clothes that I want to show off.
3.	I get to play with my magnetic navigation system.
2.	I really like these all-you-can-eat seafood places.
1.	I don't have to go to the toilet all of the time.

istics may not come as a surprise. They do, however, require attention from a management point-of-view, as they further emphasize the importance of maintaining population-specific adaptive characters and within-species variability as a long-term objective in salmon conservation efforts. Further research should be directed towards understanding this variability, its adaptive value and the relative contribution from genetic vs. nongenetic sources in shaping the different life-history phenotypes.

The debate about whether it is indeed possible to sustain wild salmon stocks through hatchery releases has gone on for decades, and is likely to go on for many years to come. As our rivers are changing, mainly as a consequence of human impact, stocks have generally shown a decline, sometimes severe in cases where spawning habitat is lost, populations are overexploited, and/or adults and smolts are prevented from completing their migrations. In some cases, such as where stocks have already been lost or spawning grounds are no longer accessible or suitable, a hatchery/smolt rearing facility could be the only viable option to replace the lost natural production. Several presentations during the workshop have demonstrated the critical importance of environmental factors and culture conditions for the development of smolt characters. Smolting is rightly considered a complex integration of a range of independent processes influencing most aspects of the juvenile salmon's morphology, physiology and behaviour, and the timing and intensity of these changes is clearly under environmental control. Major challenges to salmon conservation and restoration programs will therefore be to restore or rehabilitate aquatic systems that allow for the full suite of smolt phenotypes that were extant historically, ensuring their full range of adaptations (see further discussion below).

An increasingly evident challenge that will face anadromous salmonids, as most other species and ecosystems, is global warming (Wood and McDonald, 1997). While various scenarios have been described, it is most likely that changes will take place that affect the freshwater phase as well as the marine phase of the anadromous salmonid life cycle. Climate changes are rapidly reflected in changes in freshwater temperatures, which will have direct and specific effects on smolting. Temperature has been shown to increase the rate of smolt development, and decrease the time during which smolts are prepared to enter seawater. Thus, the distribution range of salmon species is likely to be altered northwards (or southwards for salmonids introduced into the Southern Hemisphere). There are also predictions for long-term changes in oceanic current flows (increased occurrence of the Pacific El Niño phenomenon and weakening of the Atlantic Gulf stream). Climatic changes will likely compound the adverse effects stemming from anthropogenic sources such as dams, pollution, water diversion and riparian deforestation. On the other hand, Arctic rivers, which are presently unsuitable or marginally suitable for salmonids, may become habitable to sustain new populations of anadromous salmonids. Such changes in distribution of salmonid species have undoubtedly taken place during periods of climatic change in the past, but this will be small comfort to those in the southern distribution of salmonids that experience local extirpation over the coming decades. The rate of change in factors like temperature, rainfall and runoff is surely also critical to the performance of smolts and their ability to cope with change. Anadromous salmonids are quite robust in their capacity to adapt to environmental conditions within the range of their physiological tolerance limits. It is incumbent on managers to ensure that the genetic variation and diversity in wild stocks is not reduced, so that the capacity to adapt remains.

While debate on global warming is beyond the scope of this workshop, the workshop considered whether or not there are actions that can be taken that could reduce the risk to, or improve the survival of, smolts as they enter seawater. The workshop identified factors that can be controlled and used to counter some of the adverse effects of global warming. One of the most obvious is to maintain or re-establish a healthy riparian zone to provide both cooling effects of endorheic flow and shade (see Naiman and Bilby, 1998 for discussion of river ecology). Such projects can be initiated and managed locally and studies have documented a reduction in temperature by riparian enhancements, with positive effects on salmonids. On a larger scale, the hydrographic conditions of regulated rivers can be managed to better meet the needs of salmon throughout their life cycle. For smolts in particular this would generally mean an increased runoff during migration. Management scenarios concerning water abundance are often controversial. It is difficult from a science perspective to definitively determine the biological benefits from any particular proposed flow-augmentation, making it difficult for decision-makers to resolve the conflict between differing demands made on water allocation. As the annual cycle of water flow is expected to change, additional environmental stressors such as pollution will probably have greater effects during dry periods.

The anadromous strategy adopted by salmonid species is dependent also on a suitable marine ecosystem in which the post-smolts and adults can feed and grow. Concurrent with the changes expected in the freshwater ecosystems, salmonids are facing new challenges as global warming is expected to shift the oceanic climate and the distribution of key marine prey species. These are global changes with major consequences expected in the temperate and arctic regions, coinciding with the distribution range of anadromous salmonids. Solutions to such challenges must be found on a global scale, again beyond the scope of this workshop. What salmon biologists can contribute, however, would be to enhance our knowledge about the marine phase of the salmonids and critical factors involved in adaptations to marine water, temperature preferences, migration, feeding, predator/prey interactions, diseases/parasites, etc. Such knowledge would be important from a management perspective, e.g. in predicting marine survival, year-class strength, spawning return and harvesting quotas.

2.3. Impact of dams

Although dams have their most obvious impact on blocking access of adult salmon to spawning grounds, there is increasing evidence that they have substantial negative impacts on smolt survival (Gregory et al., 2002). Passage at just one dam can lead to direct mortality of anywhere between 5% and 15%. It appears that survival to adulthood of smolts that pass a dam via spill is greater than that of fish that go through the turbines of hydroelectric projects. Dams can also cause gas supersaturation resulting in gas bubble trauma in smolts. Delays in migration caused by dams or the altered hydrographic conditions they impose may alter the timing of smolt migration, which may result in loss of smolt characteristics and/or poor timing of migration to optimal ocean conditions. Dams may serve to concentrate predators, and smolts spilled over or bypassed around dams may be particularly vulnerable to predation. It is possible that effects of passage through multiple dams may result in cumulative effects resulting in delayed (i.e. in the lower rivers or ocean) mortality. As an example, to help minimize adverse effects of dams, the majority of smolts migrating in the Snake–Columbia River system are collected at upper dams and transported in barges or trucks for liberation below the lowermost dam. It appears that this practice also results in delayed mortality.

2.4. Impact of pollution

While smolts are highly adapted for downstream migration and ocean entry, these adaptations may make them sensitive to external environmental changes such as pollutants. Previous work has shown that transitional states during development, including smoltification, are more sensitive than other life stages to a variety of contaminants (DiGiulio and Tillitt, 1999). Specific aspects of smolt development may also be affected by contaminants. For example, exposure to sublethal acid and aluminium can block normal development of seawater tolerance without affecting other aspects of growth, survival or physiology in fresh water. Recent research also indicates that contaminants that act as endocrine disruptors can affect key endocrine axes involved in smolt development (Kime, 1998). Endocrine disruptors may affect many aspects of smolt development, and mixtures of compounds may have synergistic actions. The combination of a higher sensitivity of smolts and high concentrations of pollutants encountered during their downstream migration may make them particularly susceptible to anthropogenic chemicals. Demonstrating these effects in nature is particularly problematic due to the difficulties inherent in determining causes of mortality in species with highly migratory life history stages. Local, regional, national, and even international action is required to reduce or remove sources of pollution that could adversely affect smolts.

2.5. Aquaculture

The current workshop, as those in the past, emphasized the potential pitfalls in drawing overly broad conclusions from studies on the physiology and other aspects of smolt development in hatchery-raised, aquaculture-selected strains of salmonids. Presentations and discussions throughout the workshop pointed out differences as well as similarities in salmonid smoltification in an aquaculture setting compared with fish in the wild. Even criteria by which smolts for aquaculture are assessed differ to some extent from those used to assess smolt status of wild fish. A critical factor of smolting in nature is the behavioral shift from the stationary, territorial parr to the downstream migrating, schooling smolt. These natural behavioral patterns have largely been ignored by the aquaculture industry as being of no practical consequence. However, as parr are forced into schooling behavior in the confined, high-density aquaculture environment, this may have consequences for the whole process that have been largely ignored. However, downstream orientation does occur in aquaculture, and is sometimes used as an indication of completion of smolting. As such, it may be a useful index to predict the time of seawater transfer. Further, results from studies on Atlantic salmon suggest that schooling and active swimming stimulates marine growth and reduces early maturation (grilsing), suggesting that the schooling component of smolting is important even in intensive salmonid culture.

An important question raised by these observations is whether the completion of smolting does indeed take place under artificial rearing conditions. It thus brings us back to the question of 'what is a smolt', and whether intensively reared smolts for aquaculture have reached the same physiological, morphological and behavioral state as their wild counterparts. Results from enhancement operations (see below) have demonstrated that intensively reared smolts may not return at the same rate as wild smolts. As the intensive rearing environment is generally uniform, protected and controlled in terms of most abiotic and biotic factors, it appears likely that the juvenile salmonids will assume a more limited behavioral repertoire that is sufficient for a life in culture, but likely to be insufficient for optimally coping with predation, feeding and migration under natural conditions. Recent work suggests that more complex artificial rearing habitat in terms of structure and cover may produce a phenotype in hatchery fish that is more similar to their wild counterparts. While the basic physiological blueprint associated with smoltification in hatchery and wild fish tends to be similar, comparative studies are scarce though evidence of differences is emerging. It appears that cultured fish have less intense changes and differences in timing compared to smolts in the wild. Clearly, the fundamental genetic basis for smoltification remains after many generations of domestication and selection in the hatchery. However, a concern for conservation biology is that the population-level variation in smolt phenotypes (such as fall and spring smolts, or run timing in response to environmental cues) is perhaps being lost. The workshop recognized the importance of further studies comparing smolting under natural and controlled conditions and in wild and selected strains, both to monitor potential effects of breeding programs and to provide critical input to management practices when smolts are reared for release into the wild.

Commercial salmon aquaculture is based almost exclusively on intensive rearing of smolts that are transferred to sea-cages at various times of the year, depending on species and region. A critical question in culture as in nature concerns the timing of seawater entry in relation to smolt development. In aquaculture, the prediction of this has traditionally been based on morphological characters (silvering, fin margins, reduced condition). However, while these criteria may still be valid, it should be recognized that as rearing methods have changed (e.g. smolt production at a time and/or age that is atypical for that species), other characteristics represent better indicators of fish quality and the time when they can be transferred to seawater. Various tests for seawater performance have been adopted by the aquaculture industry, including seawater challenge tests and gill Na^+, K^+-ATPase activity, both of which have provided important information about smolt quality and seawater transfer. The workshop recommended further studies linking the freshwater rearing environment, smolt quality criteria and seawater performance as important contributions to our insight into the physiology of smolting, as well as new predictors of smolt performance for the aquaculture industry and smolt release programmes.

2.6. Enhancement/hatcheries

With all too few exceptions, Atlantic and Pacific salmon stocks have been declining worldwide over the last several decades. Reasons for this decline are complex and still under intense debate, as explanatory models include multiple variables in both the freshwater and marine habitats, as well as variables affecting the smolt and the adult migration (Parrish et al., 1998). It is well known that the degradation of freshwater habitats, interruption of smolt and adult migrations in rivers, and over fishing have led to significant declines in salmon stocks. Under the assumption that the ocean can sustain more wild salmon than is presently the case, enhancement operations have been initiated in most salmon-producing regions to compensate for the loss of natural production. Enhancement programs have frequently been initiated to address objectives differing form those necessary to achieve restoration goals (e.g., conservation versus harvest); these objectives are often conflicting. Hatcheries were generally established to mitigate for loss of spawning habitat and overall production in rivers as a consequence of human impact. For this purpose, juveniles at various stages of development from yolk-sac larvae to smolts were released. The goals were usually to maintain the salmon stock of a particular river, securing an adult return to sustain a commercial or a recreational fishery. Thus, while the interests of salmon conservation and exploitation were superficially similar, i.e., to ensure a viable population with a good run of adult salmon, the differences are becoming increasingly obvious, particularly if hatchery fish have a deleterious effect on fish produced in the wild.

While hatcheries and smolt rearing units may produce large numbers of smolts under controlled conditions, these fish may differ significantly in phenotype from wild smolts of the same population. Studies suggest irreversible differences in the central nervous system controlling development, behaviour and reproduction, and their percentage return is invariably lower than that of wild smolts. Compounding the rearing habitat effects of hatcheries, other aquaculture practices can result in domestication selection. Broodstock are often collected without concern for representation of the genetic diversity present in the wild donor stock (e.g., smolt or adult run timing); rather criteria concerning large size or high growth rate have been favored. The hatchery offspring are also frequently derived from a very limited number of parents, reducing genetic variation because of the small effective population size. The selective forces in aquaculture over the periods of hatching and swim-up, acting on competitive behavior of parr, or affecting growth and smoltification, differ from those imposed on wild fish. This potentially can result in genetic differentiation that could affect the performance of fish at later life stages when fish are released into the wild. Often while a fishery may remain strong for a considerable time, buoyed by hatchery fish, abundance of a sympatric wild stock may become in jeopardy of extinction, its decline unrecognized amongst the harvest of the much larger domesticated stock.

Against this background, many workshop presentations and discussions focused on ways of combining the interests of conservation and exploitation. There was a general consensus that a long-term objective should be to maintain local adaptation in hatchery-enhanced stocks, where such stocks are necessary. It was further argued that this is best achieved through a combination of strategies. Reducing the time juveniles spend in the hatchery by release at the fry age, in cases where there is sufficient juvenile habitat left to sustain good smolt production, could potentially minimize the impact of the hatchery environment and help maintain the wild phenotype and perhaps even reduce negative impact on any natural reproduction in an underseeded river. Combining this approach with a move towards a more natural rearing environment would further reduce the negative impact of the artificial rearing environment on smolt physiology, morphology and behavior. As discussed above, ensuring the development of a natural behavioral repertoire would greatly increase the chances of a successful smolt migration, predator avoidance and marine feeding, factors that are likely to contribute to increased survival and adult returns. Identifying critical abiotic and biotic environmental factors for the development of normal behaviour, critical periods of ontogeny of the central nervous system when the salmon are sensitive to learning the appropriate behaviour and designing rearing systems to integrate this information is a major challenge. However, each small step in the right direction is likely to benefit both conservation efforts and fisheries interests, and contribute to bridging the gap between the two objectives.

2.7. Atlantic salmon and smoltification—an Irish perspective

Atlantic salmon and sea trout occur in almost every river system in Ireland. Examination of long-term survival and productivity trends would suggest that many populations of both species are undergoing chronic and in many instances acute decline. As in other areas where these species occur, there have been major changes in both freshwater and marine environments. Climate changes in Irish fresh water and marine environments presently are of a greater magnitude and occurring at a faster rate than at any time over the last thousand years as evidenced from the dendro-chronological record (study of tree rings). Forecasts suggest that air temperature will increase by an estimated 3 to 5 °C in the next 50 years (Hulme and Jenkins, 1998) and with an increase in air temperature will come an increase in water temperature. Also the type and rate of change that is occurring in freshwater (Water Temperature Record 1960–2001, Lough Feeagh – Burrishoole River system) is different from the changes happening at sea (Water Temperature Record 1960–2001, Malin Head Marine Station). Consequently, the stress on an organism that depends on both environments and undergoes significant physiological preparatory changes is great, and is likely to increase vulnerability to disease and predation. Successful smoltification is an essential prerequisite to marine survival of both salmon and trout. Thus in an Irish context the protection, conservation and management of these species will rely on identifying and addressing anything potentially perturbing the smoltification process.

Global climate change is also affecting the way water is delivered into Irish rivers. Heavy, convectional-type precipitation events occur with increasing frequency (Jones et al., 1997). These events are interspersed by periods of prolonged drought. These droughts often occur during critical times for smolt migration and can have drastic effects on marine survival of delayed smolts presumably by preventing migration during the optimal smolt "window" (McCormick et al., 1998). As a consequence of the changes in land and water use and of changes in weather patterns, Irish salmon and trout grow, develop and smoltify in freshwaters that are warmer than in the past. Many are organically enriched, some are acidified, others burdened with sediment, and a few may be receiving environmental contaminants (organo-phosphates, estrogenic compounds), the effects of which are poorly understood but have the potential to disrupt the parr–smolt transformation.

At the scale of the Irish catchment, particularly since the 1970s, there has been a substantial increase in the amount of land that is planted for commercial forestry (from 2% to a current 9% of the land surface) and that is intensively farmed (e.g. 3 million sheep to 8 million sheep). Land is developed to accommodate an expanding human population with the water, waste treatment, road infrastructure and industry requirements of a demanding modern global economy. There is also a legacy from the 1940s and 1950s of the impoundment of certain large rivers for the generation of electricity. These changes affect smolt biology and ultimately performance.

In those Irish rivers where long-term biological data exist (1960 to present), the rivers Bush and Burrishoole, changes in smolt quality and performance have been observed and measured, concurrent with changes in the freshwater environment. These studies indicate that salmon and sea trout smolts are entering the sea earlier in spring than they have done since monitoring of these rivers began, but are also migrating at a smaller size and at a younger age and perhaps in consequence are surviving less well at sea. Freshwaters warm more rapidly than the sea. As a consequence, Irish smolts that formerly migrated from rivers that were cooler than the sea now enter a marine environment that is substantially colder than the contributing rivers and lakes. The thermal shock experienced likely has developmental and growth implications.

There are also other significant changes in the marine environment. A large salmon farming industry has grown up in the inshore marine environment particularly on the West Coast, with a current production of approximately 30,000 tonnes. There are a number of associated factors, with potential direct and indirect effects, which can impact on fitness of migrating salmon and sea trout smolts. Direct effects include diseases and parasites that cause increased mortality. Indirect consequences include farm escapes impinging on the genetic integrity of natural populations (McGinnity et al., 1997). In the latter case there are two possible mechanisms that may lead to genetic changes in wild populations. One is the hybridisation of cultured and wild fish through the deliberate (as in the case of stocking and ranching) and inadvertent (as in farm escapes) release of reared salmonids. The second is through disease transmission from aquaculture strains to wild populations. In Ireland, a drastic increase in marine mortality of sea trout post-smolts has occurred in bays where salmon farms are sited, particularly in the mid-western area. The history of this collapse and subsequent events has been well-documented (Poole et al., 1996). Sea lice from marine salmon farms are a major contributory factor in the sea trout collapse, with a strong statistical relationship being evident between lice infestation on sea trout post smolts, and the distance to the nearest salmon farms. The highest infestations, many of which prove lethal, are seen close to the fish farms.

Farm salmon can escape and breed in the wild, and as a consequence can change quantitative genetic life history traits. Studies carried out in Ireland by McGinnity et al. (1997) have shown that changes in life history traits could undermine the adaptive basis of smoltification by affecting developmental and behavioural processes that have a strong element of genetic control, such as growth rate. In these studies nonnative fish were invariably shown to do less well than native ones. Hybrids between native and nonnative fish are generally intermediate between the parents, but occasionally do less well than either of the parent stocks.

In recent years, Ireland has moved towards a proactive regime for the management of Atlantic salmon stocks, based on the provision of scientifically determined stock escapement targets or conservation limits. These determinants depend on the ability of managers to quantify the numbers of smolts leaving freshwater and entering the sea. However, as indicated above, it may not be sufficient to count the smolts but also equally important to assess the quality of those smolts in terms of their ability to survive in the sea. Research to achieve this goal is a high priority.

2.8. Future research directions and new approaches

Recent scientific progress concerning other taxa of anadromous species, e.g. shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*, see Dadswell et al., 1987, for a discussion of anadromous species), has raised the question of whether the parr–smolt transformation is unique to salmonids, or whether similar processes can be found among other families of teleosts. The preparatory nature of the smolting process sets it apart from the widespread capacity among euryhaline teleosts to adapt to gradual changes in salinity. Recent evidence in shad, however, suggests that these fish develop salinity tolerance while still in freshwater, with a loss of freshwater adaptations during migration, akin in many ways to the osmoregulatory changes occurring in smolts. Further studies comparing preparatory adaptations to seawater in various anadromous and euryhaline species are needed to determine whether the parr–smolt transformation is indeed unique to salmonids and to provide a better understanding of the various physiological mechanisms used among teleosts in seawater adaptation.

Throughout our workshop discussion, specific research needs (traditional and novel) were highlighted that would be particularly fruitful at increasing our understanding of the smoltification process and/or benefiting the management of wild salmon, aquaculture and enhancement efforts. These suggestions include a better understanding of the variability in smolting between and within strains, the importance of local adaptation for smolt quality and migration, challenges and actions under a global warming scenario, parameters defining and predicting smolt quality, and perspectives for improving hatchery smolt production.

Research on smolting at the level of the central nervous system emerged from a few workshop papers and discussion as an important, rather new study direction. Studies on smolt-related changes in brain structure and function, and neuroendocrine activity, can hopefully be correlated with 'downstream' changes in physiology, morphology and behavior, helping identify the various brain–pituitary–periphery axes that regulate smolting. Many technical and practical hurdles will need to be cleared to advance in this area. It is notable that such studies on the nervous system of various vertebrates (including fish, and mainly concerning stress and reproduction) have had a major impact on overall understanding of these processes, and future perspectives are therefore fascinating.

Functional genomics is another 'novel' approach quickly making its way into smolt research. Large-scale gene expression/identification studies are likely to describe, on a very basic level of biological organization, the control of smoltification. As more genes are identified in salmonids and other species and their products tied to specific functions (proteomics), an understanding of the biochemical and physiological processes involved in smolting should emerge. Indeed, as we have pointed out above, integrating information from other teleost models or target species will allow us to make rapid progress in traditional behavioral and physiological studies, as well as in functional genomic approaches to smolting. Such work will hopefully also lead to development of useful tools such as microarrays for use in staging smolt development.

Much smolt research has focused on developmental changes in osmoregulatory physiology, and we have clearly achieved a greater (though incomplete) understanding in this area. Other areas that have received some attention include changes in visual pigmentation and muscle physiology, though much more work is needed in these areas. Clear understanding of the environmental 'releasers' for migratory behavior is still lacking. Although there is evidence to support the development of imprinting during smolting, little is known of how this process occurs and what factors control it. As mentioned previously, most of our understanding in all of these areas is based on laboratory studies, and more work is required to understand the physiological and behavioral changes that occur in smolts in the wild and how these relate to survival and population dynamics.

We would like to close this short summary by restating the importance of maintaining and strengthening the 'traditional' ecological, physiological, behavioral and environment-fish interaction studies at the organismal level. Such studies are critical for interpretation of findings at the molecular, cellular and organ levels, and are vital as input for the management of our wild and reared salmon stock. Perhaps once all of this has been accomplished we will have come to terms with the vexing question: what is a smolt? But even if this question remains unanswered, our increased understanding of smolts as a critical stage in the life history of salmon will improve our ability to conserve, enhance and enjoy this vital natural resource.

The progress that has been reported at this workshop would not have been achieved without us standing on the shoulders of giants such as Howard A. Bern, Aubrey Gorbman, Tetsuya Hirano, William Hoar, Richard Saunders, John Thorpe and Harry Wagner.

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