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OVERVIEW AND SYNTHESIS: EARLY MIGRATION AND PREMATURE MORTALITY IN FRASER RIVER LATE-RUN SOCKEYE SALMON

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INTRODUCTION

A fascinating biological situation, a vexing management issue, and a conservation crisis are all apt descriptors for a phenomenon that has been on-going for at least the past 14 years involving adult Late-run Fraser River sockeye salmon (*Oncorhynchus nerka*). These stocks make up the dominant run of Fraser River sockeye in some years, and are one of the most valuable and important groups of salmon in Canada. They are unique among sockeye populations anywhere, and perhaps among Pacific salmon in general, in that following their directed migration from the ocean they 'hold' or 'delay' in the estuary (i.e., the Strait of Georgia) for several weeks (i.e., 3–6) prior to migrating into the mainstem of the Fraser River and onward to spawning areas. Beginning in 1995 and continuing through 2008 this delay period shortened substantially—in several recent years it was 5 days or less (Lapointe, p.15 these proceedings) [6]. The pattern of early migration appears to be occurring in all Late-run populations, including Cultus sockeye for which fence data suggest that the normal migration pattern was observed consistently back into the 1940s. Other salmon species for which delay behaviour in the estuary is not well understood are also migrating into the Fraser River earlier than usual (Lapointe, p.15 these proceedings). Early river entry is not by itself necessarily a large concern; however it is associated with 'en route' mortality during upstream migration and 'pre-spawning' mortality after arrival at spawning areas in sockeye (Lapointe, p.15 these proceedings). In years of the most extremely early entry (e.g., 2000, 2001), total freshwater mortality has exceeded 90% (Lapointe, p.15 these proceedings) meaning less than 10% of some populations have reached natal areas and successfully reproduced.

The early migration / high mortality phenomena pose risks to the perpetuation of these fisheries resources. Prior to 2003, there were few tested hypotheses about potential mechanisms that may underlie these phenomena and no predictive tools to identify when or how they may occur. Such uncertainty challenged fisheries managers and has led to a precautionary approach to harvest decisions. This proceedings document contains a considerable level of new and emerging results and several recommendations are made by individual presenters on what the next research steps should be. The following summary overviews the biological studies conducted to date, the current thinking on causes of early migration and high mortality, potential management uses of this information, and future research needs.

[6] Page numbers referring to articles in these proceedings indicate the first page of the article.

OVERVIEW OF SCIENTIFIC RESULTS

Why Does Early Migration Occur?

This abrupt shift in behaviour has resulted in almost all Late-run fish since 1995 entering the river prior to the historical median upstream date. As a consequence, research examining causal factors for the change in behaviour is hampered by the lack of an experimental control. Thus, the causes of the shortening or complete elimination of the estuarine delay period are still not completely understood but a picture is emerging which illustrates complex links between physiology, environment and behaviour. Reproductive advancement is a key feature in coastal migration speed and in reduced estuarine holding (Cooke *et al.,* p.37 these proceedings; Crossin *et al.,* p.41 these proceedings), and because the physiological changes that initiate reproductive maturation occur prior to fish reaching the coast during their homeward migration (Patterson and Hills, p.31 these proceedings; Miller *et al.,* p.33 these proceedings) the estuarine behavioural change may have its roots in the open ocean. Early entering fish are also not healthy. Their gene array profiles reveal disease, viral, pathogen, and stress responses (Miller *et al.,* unpublished analyses conducted since conference). The fact that 50% of the fish sampled at the Queen Charlotte Islands carried the same disease signatures identified later in the migration at coastal sites and in the lower Fraser River suggests that segments of fish populations may become ill and/or susceptible to diseases while in the high seas (Miller *et al.,* p.77 these proceedings; Miller *et al.,* unpublished analyses conducted since conference). The disease state appears to alter the osmoregulatory physiology of migrants making them osmotically similar to freshwater fish. The physiological processes regulating reproductive maturation and osmoregulation are tightly linked in migrating salmon (Cooperman *et al.,* p.52 these proceedings) so it is possible that the disease state is also responsible for the advanced maturation observed in early-migrating Late-runs. The cause of the disease and/or early maturation and whether these characteristics are driving fish to migrate upstream earlier than normal are unknown. Interannual variation in open-ocean wind speed correlates over the past two decades with interannual variation in river entry timing—suggesting an environmental link (Thomson and Hourston, p.46 these proceedings). How this variable, or others it affects or which affect it, alters the maturation process or disease state of a segment of all Late-run populations is not clear. Further, because genomic and plasma assay analyses have only been conducted in a few recent years on high seas departing migrants (e.g., those sampled at the Queen Charlotte Islands), there is no historic baseline for comparisons and hence only a limited means to argue that some physiological patterns are ‘abnormal’ (conference comments submitted by J. Woodey, p.111 these proceedings).

Although the genesis of the early migration phenomenon seems to, in part, be in the open ocean, coastal processes appear to further influence migration timing. Specifically, there are several lines of evidence that coastal salinity and osmoregulatory preparedness play important roles: 1) historical correlations show that in years with lower coastal salinity some stocks of Late-run fish entered the river earlier (Thomson and Hourston, p.46 these proceedings); 2) physiological systems of some coastally sampled fish are clearly ‘freshwater prepared’ and these fish enter the river early (Crossin *et al.,* p.41 these proceedings); 3) estuarine captured Late-runs which were experimentally exposed to freshwater, tagged and released migrated in-river earlier than saltwater exposed fish (Cooperman *et al.,* p.52 these proceedings); and, 4) in that same year, fish which migrated the fastest from estuarine capture sites into the river were associated with the lowest salinity concentration at the capture and tagging site (Olsson *et al.,* p. 44 these proceedings). These more recent findings are consistent with earlier work by Phil Gilhousen decades ago with the Pacific Salmon Commission who found that even in years prior to the beginning of the early upstream migration phenomenon, shorter durations of upstream migration in Adams River sockeye were related to higher Fraser River flows. The other coastal issue that may be important in terms of migration timing of Late-runs is the correlation observed between river entry timing and the proportion of Summer to Late-runs in the Strait of Georgia (English and Robichaud, p.49 these proceedings), which may represent a contributing process responsible for early entry. However, adopting a radically different behaviour that is seemingly non-adaptive (e.g., entering the Fraser River early) would likely not occur without some physiological basis. Early migrating Late-run fish are not in physiological homeostasis during their coastal migration (Farrell, p.28 these proceedings). Early migrants are relatively more reproductively prepared, less osmotically prepared for marine holding, and stressed. These factors could be enough to motivate these potentially 'unhealthy' fish to migrate in-river early. However, additional motivation might come from sensing high abundances of Summer-runs also migrating into the river. It is impossible to determine if the Summer-run mechanism is merely correlative with, or complementary to, the physiological ones because it was not possible to examine the relative physiological states of fish in terms of their local experiences with differing abundances of Summer-runs. There is little evidence that water chemistry or known environmental chemicals (Herunter, p.56 these proceedings; Addison, p.107 these proceedings appendix) are likely triggers or enticements for early migrations. Time-series data are lacking for some therapeutic drugs that possibly could play a role.

Causes of High Enroute Mortality—'Dead Fish Swimming'

Multi-year telemetry and conventional disk tagging studies have confirmed that early river-entering Late-run sockeye perish at relatively high rates during their river migration compared to fish which enter during more 'normal' times (English and Robichaud, p.65 these proceedings; Cooke *et al.,* p.68 these proceedings). Early-timed fish encounter much warmer river conditions and accumulate more thermal units than normal timed fish (Patterson *et al.,* p.61 these proceedings). During their estuarine holding, Late-run sockeye are undergoing reproductive development so they can be prepared to reproduce shortly after arrival at spawning sites. Because adult salmon stocks in the Fraser River appear to be adapted to their historical migration temperatures, early migrants are physiologically stressed during migration (Farrell *et al.,* p.74 these proceedings). Because additional maturation is still required when they get near spawning areas, survivors hold in nearby lakes, instead of holding in the estuary. Spawning times in sockeye salmon are known to be adapted to the thermal regimes in their natal streams that maximize survival of their offspring (i.e., to ensure that eggs incubate and fry emerge at a time when plankton food items are available in nursery lakes), and spawning times have changed very little during this period of early upstream migration (Patterson *et al.,* p.61 these proceedings). Early-timed fish are therefore exposed to freshwater diseases and parasites (i.e., *Parvicapsula minibicornis,* and others) for longer periods of time with disease development being accelerated by higher than normal river temperatures due to early river entry and climate warming, and greater degree days due to earlier summer migrations (Hinch *et al.,* p.70 these proceedings). The evidence suggests that a combination of factors including premature senescence, elevated stress, ionoregulatory dysfunction and disease (Farrell *et al.,* p.74 Hinch *et al.,* p.70 Cooke *et al.,* p.68 Miller *et al.,* p.77; these proceedings) kills many of these fish in freshwater before they reach spawning grounds. These results provide some insights into the selective forces at play that may have originally contributed to the evolution of their estuarine holding, a behaviour which minimizes their freshwater residency times prior to spawning and reduces contact with freshwater diseases and parasites and high migratory temperatures in-river, yet ensures that spawning occurs at a time that maximizes survival of offspring. In some recent years, Late-run fish have experienced temperatures that are acutely lethal so some Late-run fish are likely dying due to cardiorespiratory collapse (Farrell *et al.,* p.74 these proceedings). Lastly, genomics results point towards a further issue—early-timed migrants appear to be 'unhealthy' when they depart the ocean, possibly the result of a viral disease (Miller *et al.,* p.77 these proceedings). Thus, early migrants are physiologically compromised prior to freshwater entry. This would likely increase the lethality of freshwater diseases and exacerbate thermal stressors affecting these fish. All studies emphasized the pivotal role of water temperature, both as an acute and chronic stressor, on the behaviour and survival of Late-run sockeye salmon.

Spawning Ground Fish and Their Offspring—Legacy Effects of Early Migrations?

Spawning ground arrival dates and peak spawning periods of Late-run sockeye have varied within the normal historical range since the onset of the early migration phenomenon (Patterson *et al.,* p.61 these proceedings). Historically, pre-spawn mortality (termed PSM; e.g., dying unspawned) in most stocks was correlated with upstream migration timing and temperature, with higher levels in the earliest arriving fish. Though PSM is still observed in Late-run fish, it does occur throughout their entire spawning period and in some recent years has been as high in the both the earliest and latest arrivals at spawning areas (Patterson *et al.,* p.61 & 81 these proceedings). On average early river migrants are more likely to be the first to arrive on the spawning grounds, however diminishing proportions still continue to arrive throughout the entire spawning period and may contribute to elevated pre-spawn mortality in later time periods. Early entering Late-runs encounter relatively high temperatures and flows in the Fraser River compared to normal-timed Late-runs, and they are on average more reproductively advanced at river entry than fish delaying; therefore, faced with a more difficult migration condition it was reasonable for investigators initially to assume that Late-runs would arrive on spawning grounds with less body energy and thus be more at risk to PSM. However, first arrivals on spawning grounds actually have the highest energy reserves (Patterson *et al.,* p.61 & 81 these proceedings), suggesting that energy exhaustion on spawning grounds is not a factor affecting spawning success in early migrating Late-runs. Results from experiments which have altered energy reserves and physiological stress levels towards the end of river migration in Fraser sockeye support this (K. Hruska, UBC, PhD thesis unpublished. data). The physiology and histopathology of PSM fish indicates gill and kidney diseases play a significant role in mortality, in particular those caused by *Parvicapsula minibicornis,* though also *Loma, Columnaris* and *Saprolegnia* (Patterson *et al.,* p.82 these proceedings). The search for a single cause or suite of casual agents of PSM has been difficult—PSM appears to be complex and can likely result from a multitude of factors whose efficacy can change both annually and seasonally. Most, if not all, of the causal factors are accentuated by increases in temperature and freshwater residency times. Thus once fish enter freshwater it is a race against time for early migrants to be able to spawn prior to succumbing to various disease agents. Considering that the primary determinant of spawning success is longevity on spawning grounds (K. Hruska, UBC, PhD thesis unpublished data), early migrants that are already compromised by their thermal history which reach spawning grounds are at a clear disadvantage to spawn successfully, so they probably have reduced spawning success though there are few data available to test this hypothesis.

There is no evidence that egg quality varies with time of arrival onto spawning grounds, and eggs from PSM females produce highly viable offspring in experiments (Patterson *et al.,* p.84 these proceedings). These findings indicate that gamete quality is highly preserved even at the expense of parental health and survival. Individual variability among spawning ground adults in some physiological characteristics had intergenerational consequences in that it affects egg and offspring survival but it is not clear how much of that variability was caused by an individual's migration experience and/or its genotype (or both) (P. Nadeau, UBC, MSc thesis; K. Hruska, UBC, PhD thesis in progress).

MANAGEMENT USE OF LATE-RUN SOCKEYE SCIENCE

Overview

A primary goal of the presentations at this conference was to provide fisheries managers with information that could be used to change harvest regulations and policy, and, if possible, consider mitigation or adaptation strategies to help prevent the collapse of fisheries and extinction of some stocks. It was hoped that a better understanding of the immediate and intergenerational fitness consequences will provide valuable information for developing pre-season prediction tools, aid in-season decisions, and improve future season prediction models for harvest and stock sizes. Indeed the high rates of en-route and pre-spawn mortality documented during some years have caused managers to take a precautionary approach and prohibit fisheries targeting Late-run sockeye, and limit harvesting to by-catch in fisheries directed at other healthy sockeye stocks. In years of larger Late-run abundances, exploitation rates have been adjusted based on river entry timing predictions that are based on the fraction of fish migration upstream at any given point in time. However, fisheries managers at the conference expressed mixed opinions on whether the research results could convert directly into management actions. Some advocated concentrating more fishing with the Fraser River in early to mid-August when the prospects for survival of Late-run sockeye were particularly poor. Such a tactic could increase harvests of healthier stocks while minimizing short-term impacts on Late-run stocks. However, others suggested that if some of the earliest upstream migrants were able to successfully reach the natal areas and spawn, they would be amongst the most valuable to protect in a long term evolutionary sense (see Management Panel Discussion, p.89 these proceedings).

Early River Entry Phenomenon—Can It Be Predicted?

The inability of the management agencies to predict river entry timing of Late-run sockeye in the past has resulted in hundreds of millions of dollars in foregone harvest. Identifying the causes of early migration would hopefully provide some level of mechanistically based predictability of the behaviour, based on physiological and/or environmental conditions along adult sockeye coastal migratory routes. It should be first noted that the marine approach timing into the Strait of Georgia has not changed—early entry into the Fraser River means early departure from the Strait. There were over a dozen hypotheses proposed when the early entry phenomenon was first realized. Conference presenters have reduced that list substantially and have a much better understanding of the factors affecting early migration. A conceptual model that involves both open ocean and coastal ocean processes is proposed (see above; and Science Panel Discussion, p.93 these proceedings). However, there is still no 'silver bullet' factor that managers desire for pre-season prediction as it appears this is a complex, multi-factor phenomenon. Regardless, there are several indices that managers can presently turn to for aid in predicting river entry timing both pre-season and in-season. Specifically, open-ocean wind stress strongly correlated with river entry date for the Adams stock and coastal salinity strongly correlated for the Weaver stock. These relationships could give managers insights into river entry timing several weeks in advance of fish reaching the Fraser River. Summer-run abundance can be estimated pre-season which may give managers several months' advance insights into Late-run entry timing. During the season, managers have developed models that predict the median date of upstream migration from the fraction of the total run that has migrated upstream to date. While the inputs to these models are subject to assessment error and they do not provide much advanced warning of early entry, the models have allowed managers to react to changes in-season, particularly in years of large Late-run abundances.

As investigators have not discovered any single process that appears to govern entry timing, prudence dictates that managers use multiple sets of information to develop the broadest picture possible for pre- and in-season forecasting. Because behavioural changes are largely driven by physiological processes, physiological indicators that can be readily collected and rapidly processed in real-time during coastal migration could guide future management decisions. Genomic biomarkers (small sets of genes that when expressed may be predictive of a behaviour), which are currently being researched and developed for Late-run entry timing (and river migration fate), may provide such a system, particularly if it turns out that the early migration Late-run phenomenon is being driven by an ocean disease state as some preliminary results suggest.

High River Migration Mortality Phenomenon—It Can Be Predicted

Managers need to know how many fish are likely to perish during river migration in order to adjust harvest levels in the ocean and lower Fraser River to ensure spawning ground escapement targets are achieved. Presently, managers use models based on associations among historic differences between lower and upper-river escapement estimates and environmental conditions and/or entry timing for this purpose. These models are then used to increase escapement targets to compensate for anticipated mortality or differences resulting from adverse river conditions (flows or temperatures) or early river entry. Current adjustment models do not explicitly use much of the mechanistic knowledge presented at the conference, though future adjustment models could benefit from it (Hague and Patterson, p.85 these proceedings). Investigators made considerable progress in understanding the mechanisms, and predicting the levels, of river migration mortality experienced by Late-run sockeye. As with the early migration issue, high mortality is complex and caused by several factors. Nonetheless, the research conclusively demonstrated that physiological factors and higher than normal temperatures kill early migrating fish before reaching spawning areas in expected ways. Managers could use specific water temperature metrics to predict migration mortality (e.g., critical thermal limits, or degree day accumulation). For example, encountering migration temperatures > 20ºC resulted in 90–100% enroute mortality of Weaver Creek sockeye because of collapse of metabolic scope. At less extreme temperatures (i.e., 18–19ºC) where the processes of disease and stress were paramount, levels of migration mortality were correlated to specific levels of degree day accumulation during migration. Hague and Patterson (p.85 these proceedings) overviewed how environmental variables, which may be surrogates for physiological processes, could be integrated into management adjustment models in order to increase their biological realism. For example in addition to river entry timing, average or extreme river temperatures or flows, weighted temperatures, or degree day accumulation were all suggested as candidate variables. The largest challenge for incorporating environmental variables into adjustment models is the need for spatially and temporally explicit migratory information, which is difficult to obtain and integrate into model predictions on the time scales needed for in-season forecasting. Post-season estimates of en route mortality, independent of differences between estimates, can now be estimated based on these biological relationships explored at this conference to generate better total return size estimates for recruitment curves. These environmental variables can also be used in future-scenario modeling in order to examine how climate change predictions will influence migration survival and escapement.

Do Managers Need to Worry About Legacy or Intergenerational Consequences?

If early entering Late-runs which arrive on spawning grounds suffer high levels of pre-spawn mortality, or if their eggs and offspring are of inferior quality, then this would mean that even higher levels of spawning ground escapement (e.g., lowered levels of harvest) may be needed to ensure stock sustainability. The implications for management of the recent research are that there is likely no need for incremental adjustments to coastal or river migration harvest strategies on early vs. normal timed migrants in terms of their ‘on-spawning ground’ fitness; compensation for en-route and pre-spawn mortality would appear to be sufficient to ensure sustainability. However, pre-spawn mortality is complex and likely results from a multitude of factors whose efficacy can change both annually and seasonally. Most, if not all, of these factors are accentuated by increases in temperature and freshwater residency times. As experiments that examine the legacy effects of high temperature exposure on adult migrants to their eggs and offspring are still in progress, management should continue to be risk averse and consider the risk of pre-spawn mortality and intergenerational effects in relation to predictable correlates such as migration temperatures and freshwater residence (e.g., accumulated degree days).

FUTURE RESEARCH—WHERE DO WE GO FROM HERE?

The integration of large-scale ocean telemetry with behavioural ecology, physiological biopsy, genomics, and experimental biology, as pioneered by several of the investigators working on the Late-run issue, has proven to be a powerful research approach. Researchers have come a long way in a short time towards identifying a short list of potential causes of the early migration phenomenon. Yet, if indeed the process is mediated through environmental factors in both high seas and coastal areas, then a single predictive explanation will be difficult to uncover without continued large-scale field research. Despite all that has been done, a better understanding is needed of how oceanographic conditions (e.g., salinity, temperature) trigger or control physiological, and hence behavioural, changes in individual migrating and maturing sockeye, and how other environmental factors (both endogenous such as disease states and exogenous such as local abundance) mediate these behavioural changes. Though a small number of manipulation experiments have been undertaken, clearly more are needed as only in this way can cause and effect truly be established. For example, holding Late-run fish in marine pens at different locales relative to the Fraser River mouth, releasing at key times, and tracking using large-scale fixed telemetry systems (e.g., POST) could help elucidate how specific local oceanographic or abundance conditions affects river entry timing by Late-run populations. Physiological interventions and individual-based tracking with mobile telemetry systems at these or other locales are needed to explore specific mechanisms which are thought to be responsible for early river entry. It will remain a challenge to assess the role of prior life history experience in any of these experiments. Some at the conference suggested that other environmental factors including biologically active contaminants and other pollutants also deserve research attention. As some other species of salmon also seem to be eliciting early migrations, the search for answers in early migrating Late-run sockeye needs to include, where possible, analogous studies in other groups of fish.

The causes of en route mortality in early migrants are now reasonably well understood. Early migrants are ‘out of synch’ with their river migration environment and are clearly not well adapted to deal with the riverine conditions they experience. Only a few Late-run stocks have been examined in detail but there is good evidence that stock-specific adaptations exist. Future work must examine the capacity for adaptation in key Fraser sockeye stocks, not just Late-runs, because as the Fraser River continues to warm from year to year there is significantly increased risk of high mortality even in normally timed Late-runs as well as in other run timing groups. The study of diseases will increase in importance, as diseases will play much larger and obvious roles as agents of en route and pre-spawning mortality in a warming Fraser River. Understanding which stocks will be able to thrive, which ones can barely survive and which ones will be extirpated in the near future is not only a purely scientific query, but also a fisheries management and policy concern.