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Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*

S. G. Hinch*†, S. J. Cooke‡, A. P. Farrell§, K. M. Miller‖, M. Lapointe¶ and D. A. Patterson**

**Pacific Salmon Ecology and Conservation Laboratory, Centre for Applied Conservation Research and Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia, V6T 1Z4 Canada, ‡Fish Ecology and Conservation Physiology Laboratory, Ottawa-Carleton Institute of Biology and Institute of Environmental Science, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, K1S 5B6 Canada, §Department of Zoology and Faculty of Land and Food Systems, University of British Columbia, 3325–6270 University Blvd, Vancouver, British Columbia, V6T 1Z4 Canada, ‖Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Rd, Nanaimo, British Columbia, V9R 5K6 Canada, ¶Pacific Salmon Commission, 600–1155 Robson Street, Vancouver, British Columbia, V6E 1B5 Canada and **Cooperative Resource Management Institute, Fisheries and Oceans Canada, School of Resource and Environmental Management, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6 Canada*

Adult sockeye salmon *Oncorhynchus nerka* destined for the Fraser River, British Columbia are some of the most economically important populations but changes in the timing of their homeward migration have led to management challenges and conservation concerns. After a directed migration from the open ocean to the coast, this group historically would mill just off shore for 3–6 weeks prior to migrating up the Fraser River. This milling behaviour changed abruptly in 1995 and thereafter, decreasing to only a few days in some years (termed early migration), with dramatic consequences that have necessitated risk-averse management strategies. Early migrating fish consistently suffer extremely high mortality (exceeding 90% in some years) during freshwater migration and on spawning grounds prior to spawning. This synthesis examines multidisciplinary, collaborative research aimed at understanding what triggers early migration, why it results in high mortality, and how fisheries managers can utilize these scientific results. Tissue analyses from thousands of *O. nerka* captured along their migration trajectory from ocean to spawning grounds, including hundreds that were tracked with biotelemetry, have revealed that early migrants are more reproductively advanced and ill-prepared for osmoregulatory transition upon their entry into fresh water. Gene array profiles indicate that many early migrants are also immunocompromised and stressed, carrying a genomic profile consistent with a viral infection. The causes of these physiological changes are still under investigation. Early migration brings *O. nerka* into the river when it is 3–6° C warmer than historical norms, which for some late-run populations approaches or exceeds their critical maxima leading to the collapse of metabolic and cardiac scope, and mortality. As peak spawning dates have not changed, the surviving early migrants tend to mill in warm lakes near to spawning areas. These results in the accumulation of many more thermal units and longer exposures to freshwater diseases and parasites compared to fish that delay freshwater entry by milling in the cool ocean environment. Experiments have confirmed that thermally driven processes are a primary cause of mortality for early-entry migrants. The Fraser River late-run *O. nerka* early migration

†Author to whom correspondence should be addressed. Tel.: +1 604 822 9377; email: scott.hinch@ubc.ca

phenomenon illustrates the complex links that exist between salmonid physiology, behaviour and environment and the pivotal role that water temperature can have on population-specific migration survival.

Key words: climate warming; harvest management; high temperatures; maturation and osmoregulation; physiological biopsy; telemetry.

INTRODUCTION

Abundant and sustainable Pacific salmon *Oncorhynchus* spp. populations have economic, ecological, cultural and political importance to Canada. The five species of *Oncorhynchus* contribute to some of Canada's and the world's last remaining large commercial fisheries on wild fishes. The commercial *Oncorhynchus* spp. fishery and its subsidiary industries are a major economic driver in the province of British Columbia (2003–2005; BCMOE, 2006) and recreational *Oncorhynchus* spp. fishing enormous economic benefits including supporting >10 000 jobs in communities throughout the province (Anon, 1995; Kristianson & Strongitharm, 2006). Ecologically, salmonids are important components of food chains in both freshwater and marine environments (Cederholm *et al.*, 2000) and are considered keystone species in aquatic ecosystems providing marine-derived nutrients for stream and riparian forest ecosystems in coastal Pacific catchments (Helfield & Naiman, 2001). Culturally, salmonids are integral to the mythology, spiritual integrity and livelihoods of Pacific First Nations (Jacob *et al.*, 2010). Politically, *Oncorhynchus* spp. fisheries have been a large source of conflict in federal–provincial and federal–First Nation relations and internationally between Canada and the U.S.A. To the general public, *Oncorhynchus* spp. are icons with abundant fishes confirming a healthy and productive environment.

The migrations of *Oncorhynchus* spp. are truly remarkable among the animal kingdom. Sockeye salmon *Oncorhynchus nerka* (Walbaum 1792), for example, travel thousands of kilometres during their 2 years in the high seas, and as they mature reliably re-locate to their natal freshwater habitats for a single spawning event. This upstream migration can add up to 1200 km over just a 3–4 week period and is undertaken without feeding. Equally remarkable is that for any given population, upriver spawning migrations by mature adults usually commences within the same week each year (Woodey, 1987; Gilhousen, 1990). Indeed, the migratory behaviour of *O. nerka* is so precise that, for generations, First Nations have planned food fisheries and traditional ceremonies to within a matter of days because of timely return of fish to natal streams. Yet, despite the fact that abundant and sustainable fish populations are so important, knowledge of how returning adults achieve these remarkable feats of navigation and timing is rudimentary (Hinch *et al.*, 2006). It was not until large numbers of *O. nerka* started to radically alter their migration timing in 1995 (Cooke *et al.*, 2004), and in association with this, began to die prematurely at high levels, did researchers truly appreciate how little was known and how the consequences of this knowledge gap would affect the management and conservation of this resource. The purpose of this article is to review the early migration and high mortality issue that continues to date within one large group of *O. nerka*. This topic shall be addressed by an overview of the results from a large and on-going interdisciplinary research programme investigating the causes of the early migration phenomenon, highlighting how fisheries managers can utilize the scientific results. The interdisciplinary framework and novel study approaches described here can serve as examples for how large-scale field science could be used to address conservation and management issues on other migratory fishes (Cooke *et al*., 2008*a*).

OVERVIEW OF THE EARLY MIGRATION AND HIGH-MORTALITY PHENOMENON

The Fraser River is the largest producer of *Oncorhynchus* spp. in Canada. Of its five species, *O. nerka* is most commercially valued and the second most numerically abundant. About 150 genetically distinguishable and geographically isolated populations spawn throughout the catchment in locales ranging from 50 to 1200 km from the ocean. Before entering the river, fish cease feeding and have early stages of developing gonads, but no secondary sexual characteristics. Males and females are distinguished only by biopsies (sex hormones), necropsy or molecular techniques. Populations are distinguished only by scales and DNA analyses (Beacham *et al*., 2004, 2006). Upriver adult spawning migrations commence in July with the early-run populations. Summer-run populations follow in August, and late-run populations enter in September and October (Woodey, 1987). River water flows decrease from the peak freshet, whereas the river reaches its peak summer temperature around the timing of the summer run (hence the name). Curiously, while late-run and summer-run population aggregates arrive off shore near the Fraser River at approximately the same time, late-run populations historically display milling behaviour offshore in the southern Strait of Georgia (see Fig. 1) for 3–6 weeks before starting their upriver migration. The arrival of the different population aggregates into the Strait of Georgia is determined through test fisheries that take place in the same marine locales each year. River-entry timing and abundance of adult *O. nerka* entering the river has been quantitatively assessed since 1977 by the Pacific Salmon Commission (PSC), situated at Mission B.C., *c*. 50 km upstream of the estuary. These data are collected through various hydroacoustic methods in combination with scale and DNA analyses used for population identification.

In 1995, a proportion of individuals in all late-run populations (*e.g*. Lower Adams, Lower Shuswap, Weaver, Harrison, Portage and Cultus; Fig. 1), which comprise the majority of *O. nerka* in the Fraser River run in many years, commenced their river entry *c*. 3 weeks earlier, although they arrived off the Fraser River at a normal time. This aberrant behaviour has continued with variable proportions (up to 90%) of late-run fish (early-entry late-runs) entering the river 2–6 weeks earlier than historical norms (Fig. 2). Historical data from a counting fence situated on the migratory route of late-run Cultus Lake *O. nerka* indicate that the normal milling behaviour and delayed river entry (normal-timed late-runs) was observed consistently from the 1940s to 1995 (Bradford *et al*., 2010*a*), implying the early migration behaviour is indeed relatively recent. The abrupt shift in migration behaviour has resulted in segments of all late-run fish populations since 1995 entering the river prior to the historical median upstream date (Fig. 2). Unfortunately, this has dramatic negative consequences in terms of extremely high freshwater mortality.

The PSC and Fisheries and Oceans Canada (DFO, the federal agency responsible for the management and conservation of *Oncorhynchus* spp.) use the term

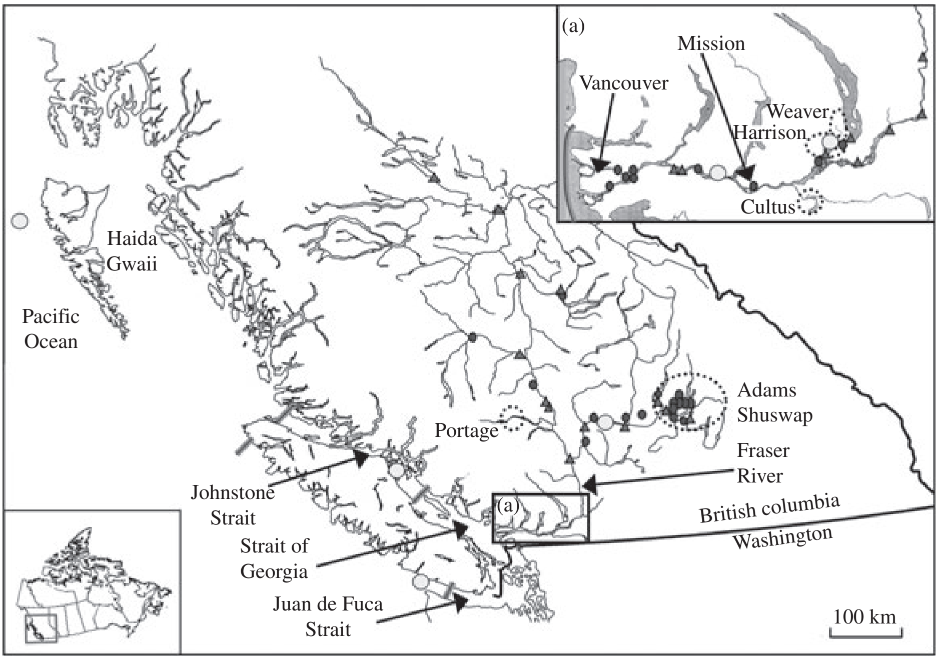

FIG. 1. Map of southern half of British Columbia, with an inset of Canada, and an inset (a) showing the lower Fraser River. The Fraser River main stem and its main tributaries and lakes are indicated. Circled and labelled are spawning areas (by name) for late-run *Oncorhynchus nerka* populations. Shown are *O. nerka* tagging and release locales (○), acoustic receiver curtain lines (▬, associated with the Pacific Ocean Shelf Tracking project (P) and other groups, sentinel acoustic receivers (●, maintained by Kintama Ltd and the University of British Columbia), and sentinel radio receivers (▲, maintained by LGL Ltd) that existed with various modifications during most of the studies that are reviewed. Acoustic receiver locations are shown in inset map (a) represent pairs of receivers.

'escapement discrepancies' for the difference in population abundance estimates at the Mission site and that obtained at spawning grounds (made either through direct counts at weirs or through mark–recapture of spawners), after accounting for reported in-river harvest upstream of Mission. Escapement discrepancies are therefore an indirect assessment of fish not accounted for during the migration, which when expressed as a percentage of the run is termed '*en route* loss' (Macdonald *et al*., 2010) or '*en route* mortality' (Cummings *et al*., 2011). High e*n route* losses began to be reported in 1996 for late-run populations (Fig. 3). Of particular note is that *en route* losses have been increasing, with most years exhibiting at least 30% losses and in some years it is the dominant component of the fate for late-run fish (Fig. 3).

Although *Oncorhynchus* spp. are semelparous and die shortly after spawning, what is unusual with late-run *O. nerka* is the scale of the premature mortality that has occurred *en route* (Fig. 4) as well as on spawning grounds prior to spawning (termed pre-spawn mortality or PSM; Fig. 5) associated with early migration. Total freshwater mortality (excluding harvest) in several populations has ranged from 40 to 95% for most populations each year since the early migration phenomenon began. In contrast, when *O. nerka* milled along the coast prior to 1995, total freshwater mortality for late-run populations rarely exceeded 20%. While other *Oncorhynchus* species, for

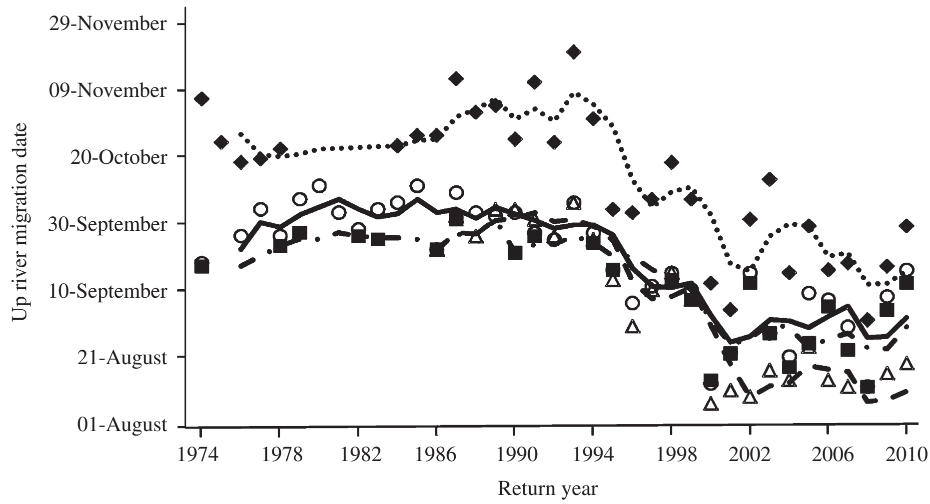

FIG. 2. Median upriver migration date (50% of the run has passed a hydroacoustic facility near Mission BC, see Fig. 1) from 1974 to 2010 for four populations [Weaver (○), Adams (■), Harrison (△) and Cultus (◆)] of late-run *Oncorhynchus nerka*. Lines are based on running 3 year averages.

which estuarine behaviour is not well understood, are also migrating into the Fraser River earlier than usual, including pink salmon *Oncorhnchus gorbuscha* (Walbaum 1792) (whose change to earlier migration occurred coincident with the change in *O. nerka*), chum salmon *Oncorhynchus keta* (Walbaum 1792) and white-fleshed Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (Lapointe *et al.*, 2004), there has been little research into whether mortality rates have been elevated as a result.

In the early 2000s, dozens of scientists with backgrounds in fish ecology, physiology, immunology, oceanography and animal behaviour from academic, government and private organizations began meeting to identify hypotheses responsible for *O. nerka* early migration and high mortality in order to formulate an integrative research programme. Working under the premise that early migration was caused by something that had changed in the environment and in the fish, which then affected migratory cues or their perception, or affected biological clocks, and that high mortality was caused by changes in these factors, the group advanced numerous hypotheses (Cooke *et al.*, 2004). Early in this process, it became abundantly clear that little was known of what the baseline physiological conditions and migration behaviours were for ocean and coastal migration adult *O. nerka* prior to early migration starting. On a broader scale, these same knowledge gaps exist for *O. nerka* in general, as well as for most other species of *Oncorhynchus*. Specifically, what are the physiological and associated environmental and behavioural factors responsible for initiating upriver migrations, what is different in early-entry late-run *O. nerka*, and are these factors also responsible for the high levels of migration mortality?

Because escapement discrepancies and run-timing estimates can have large error associated with them at the population-level, it was important to have independent approaches for examining river-entry timing and migration survival. This data gap triggered large-scale telemetry programmes starting in 2002, which involved tagging

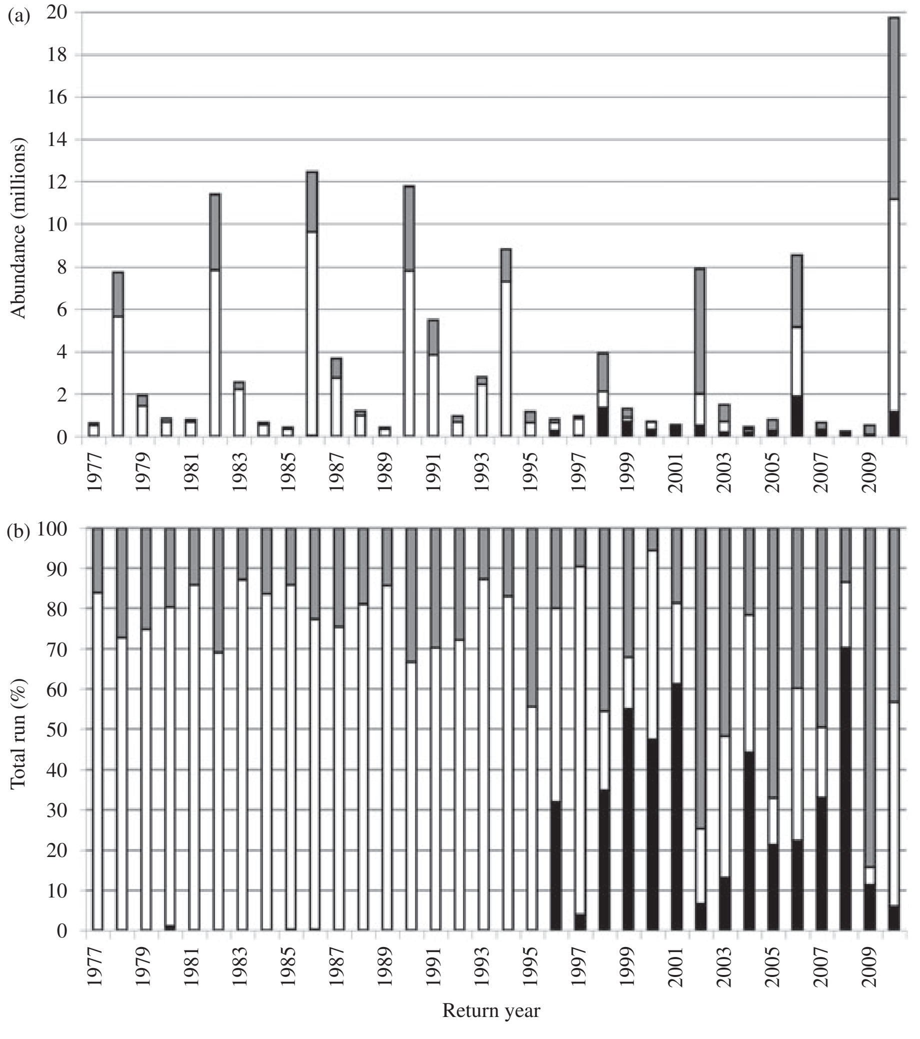

FIG. 3. Returns of later-run *Oncorhynchus nerka* from 1977 to 2010 showing fish fate categorized into total catch (□), *en route* loss (■) and spawning escapement (■). (a) Total run size (abundance) for each year and (b) the fate categories more clearly expressed as percentages of the total run size (abundance). Data source: Sockeye Salmon Stock Production Files, Fisheries and Oceans Canada and Pacific Salmon Commission, unpubl. data.

fish in both ocean and river to assess population-specific behaviour and survival. In several years, biopsy, which involved taking a sample of plasma, gill tissue and muscle tissue, was added to telemetry (Cooke *et al*., 2008*a*) to link initial physiological condition with behaviour and fate. Biotelemetry indeed confirmed that large proportions of late-run populations migrated early, and it was the early-entry migrants that perished at high levels during the river migration (English *et al*., 2005; Cooke *et al*., 2006; Crossin *et al*., 2009*a*; Mathes *et al*., 2010). Biotelemetry also revealed that the early-entry migrants that reached the natal spawning catchment held in natal lakes for about the same amount of time they would have spent in the Strait of

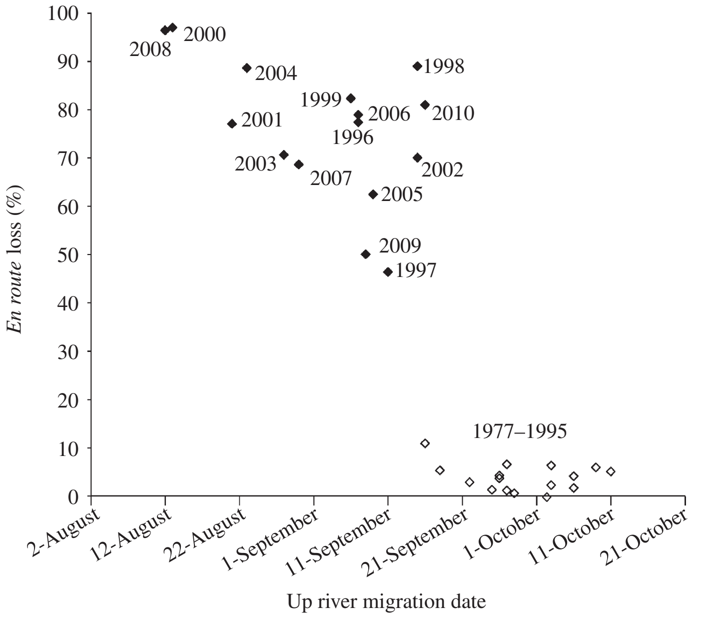

FIG. 4. Relationship between *en route* loss (as a per cent of the total run) and the median upriver migration date (50% of the run passed the Mission hydroacoustic facility) for Weaver Creek *Oncorhynchus nerka*. ◆, years since the early-migration phenomenon began for this population (1996–2010); ◇, years prior to major change in river-entry behaviour but after the start of the Mission hydroacoustic facility (1977–1995). Estimates of absolute levels of *en route* mortality are very large in some years (*e.g.* 2000, 270 000 fish; 2001, 165 000 fish; 1998, 490 000 fish).

Georgia (Fig. 6). Hence, early-entry migrants do not spawn any earlier (Fig. 7), but spend more time in fresh water that is typically much warmer than the sea that they historically milled in before river entry.

CAUSES OF EARLY MIGRATION

Why the offshore milling period has been abbreviated or eliminated is still not completely understood, but a picture is emerging that illustrates the complex links between physiology, environment and behaviour. To examine the relationship between physiological status and migration behaviour (early-entry or normal-timed entry into the Fraser River), in 2003 and 2006, late-run *O. nerka* were intercepted at ocean locales (Fig. 1) to obtain a non-lethal blood and gill biopsy, evaluate energy status with a microwave meter, and implant either radio or acoustic transmitters prior to releasing fish to complete spawning migration (Cooke *et al.*, 2005). Indicators of osmoregulatory function (*i.e.* plasma ions and gill Na^+/K^+-ATPase activity) were used to examine the possible linkage between early river-entry behaviour and physiological preparedness for the transition to fresh water. In 2003, osmoregularoty preparedness at the release site provided little insight into migration timing aside from greater variation in Na^+/K^+-ATPase activity in early migrating fish (Cooke *et al.*, 2008*b*). In 2006, a year with much larger sample sizes, however, early migrants

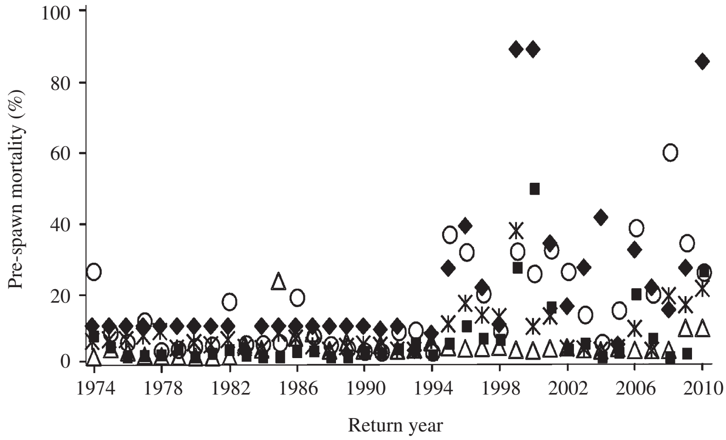

FIG. 5. Pre-spawn mortality (percentage of total spawners) by year for five late-run *Oncorhynchus nerka* populations from 1974 to 2010: Weaver (○), Adams (■), Harrison (△), Cultus (◆) and Portage (✳).

had much higher levels of Na^+/K^+-ATPase activity than normal timed migrants (*c*. 4 *v*. 2 µmol ADP mg^{-1} protein h^{-1}; Crossin *et al*. 2009*a*). As 1–2 µmol ADP mg^{-1} protein h^{-1} is a range indicative of fish that are entering fresh water (Hinch *et al*., 2006), these early migrants had not yet begun to modify their osmoregulatory systems for their impending freshwater entry.

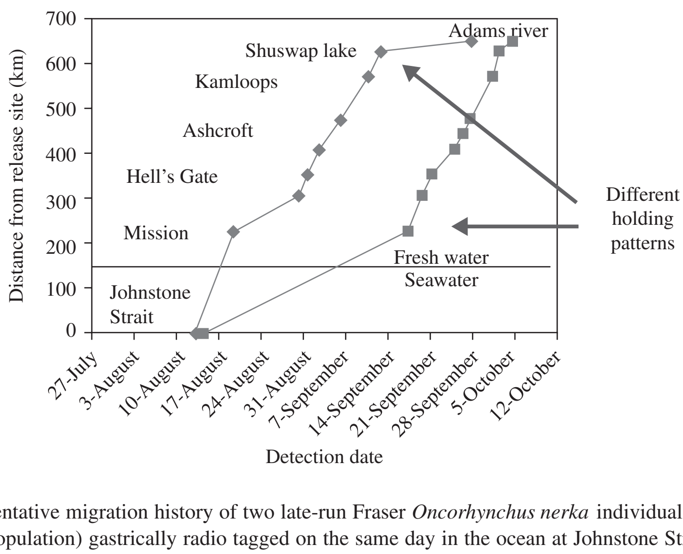

FIG. 6. Representative migration history of two late-run Fraser *Oncorhynchus nerka* individuals (both from the Adams population) gastrically radio tagged on the same day in the ocean at Johnstone Strait (see Fig. 1). Movement was monitored with an array of radio receivers that detected migrants as they moved upriver towards spawning grounds on the Adams River (see Fig. 1). One individual fish exhibits the typical holding period (2–3 weeks) in the estuary prior to entering the river (bottom line). The other individual enters the Fraser River within a few days of tagging and migrates upriver, however, this individual holds in their natal Shuswap Lake for 2 weeks prior to reaching the Adams River spawning ground (upper line). The actual spawning date does not differ appreciably between these two very different migration strategies. Adapted from Cooke *et al*. (2008*a*).

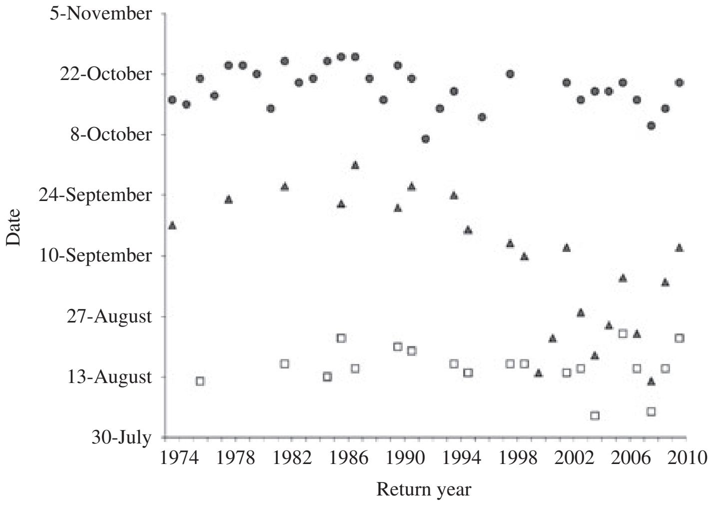

FIG. 7. Timing of three key migration stages for adult Adams River *Oncorhynchus nerka* collected from 1974 to 2010: peak abundance (□) in Juan de Fuca Strait (a coastal area late-runs migrate through *en route* to their Strait of Georgia milling areas), peak Fraser River entry at Mission (▲), and peak spawning at the Adams River (●). Note, only river-entry timing has changed substantially since 1996. Data provided by Pacific Salmon Commission and Fisheries and Oceans Canada. Refer to Fig. 1 for locations.

In both 2003 and 2006, migration speed from release site (located *c.* 250 km from the Fraser River mouth, Fig. 1) to river mouth was negatively correlated with plasma concentrations of reproductive hormones [*e.g.* 11-ketotestosterone (11-KT); 17-βoestradiol (17-βE2) and testosterone (T)] though relationships were strongest within females (Cooke *et al.*, 2008*b*; Crossin *et al.*, 2007). Furthermore, milling behaviour was reduced in the more reproductively advanced fish, with fish with higher levels of reproductive hormones leaving the estuary for the river the fastest (Cooke *et al.*, 2008*a*, *b*). These same fish also migrated faster upriver towards spawning grounds. In 2006, Fraser River *O. nerka* were also intercepted in the Gulf of Alaska as they made land-fall from the open ocean near the Haida Gwaii, *c.* 1000 km from the Fraser River, and with transmitters surgically inserted, were tracked to the first set of acoustic curtain lines (Pacific Ocean Shelf Tracking project, POST) situated along northern Vancouver Island a distance of *c.* 470 km (Fig. 1). Fish with the fastest migration speeds had high levels of plasma T and low levels of chloride suggesting that physiological systems that affect migratory behaviours were being influenced well before individuals reached the Fraser Estuary (Crossin *et al.*, 2009*b*). These results suggest that reproductive advancement is a key factor associated with both coastal migration speed and early river entry. Because reproductive maturation is initiated prior to salmonids returning to the coast (Hinch *et al.*, 2006; Miller *et al.*, 2009), the aberrant river-entry behaviour may have its roots in the open ocean or earlier in their life history.

Physiological assessments of early-entry migrants tagged in the ocean and that perished in fresh water prior to reaching spawning were characterized as having higher reproductive hormone levels, lower somatic energy (another indicator of advanced reproductive levels) and higher Na^+/K^+-ATPase activity levels than fish which survived (Cooke *et al.*, 2006; Crossin *et al.*, 2009*a*). Gene array analysis, which provides a global insight into genomic signals regulating protein manufacture, was conducted on gill tissue sampled from a subset of ocean tagged fish in 2006 (Miller *et al*., 2011). A mortality-related genomic signature, which involved the differential expression of *c*. 1600 genes, was associated with a 13·5 fold greater chance of dying in fresh water before arriving in spawning areas. Late-run fish that carried this signature also travelled more quickly both into the river and to spawning grounds. Functional analysis revealed cellular, osmoregulatory and immunosuppressive changes suggestive of a viral infection (Miller *et al*., 2011). This was the first study to suggest that a pathogen infecting *O. nerka* before they entered fresh water could be a factor both motivating early river-entry behaviour and associated with elevated pre-mature mortalities in the river. As the physiological processes regulating reproductive maturation and osmoregulation are tightly linked in migrating *O. nerka* (Cooperman *et al*., 2010), this disease state could be responsible for the advanced maturation found with the plasma studies. The causes of the disease, and advanced reproductive development and whether these characteristics are driving fish to migrate upstream earlier than normal are still under study.

Oceanographic data from the past two decades have been used to examine potential relationships between environmental conditions and the early migration phenomenon. Interannual variation in open-ocean wind speed correlates with river-entry timing of some late-run populations. Specifically, for the Adams and Shuswap populations, a strong correlation has been found between peak river-entry timing and offshore winds, such that the weaker the wind stress in the direction of the prevailing surface currents in early July, the earlier the river entry in late summer (Thomson & Hourston, 2011). How these open ocean variables, or others they affect may alter the maturation process or disease state of a proportion of all late-run populations is unclear. Further, because only limited genomic and plasma analyses have been conducted on migrants leaving the open ocean, there are few historic baselines for comparisons.

Although the genesis of the early migration phenomenon seems to, in part, be in the open ocean or even earlier in the life history, coastal processes experienced by migrating adults may still further influence migration timing. In years with lower coastal salinity, peak river entry of some populations of late-run fish (*e.g.* Weaver Creek population) was earlier (Thomson & Hourston, 2011). Furthermore, oceanographic data obtained from lightstation records in the Strait of Georgia reveal a distinct decrease in the surface salinity in the post-1995 years (excluding El Niño Southern Oscillation years of 1982 and 1983, Thomson & Hourston, 2011). To examine the role of salinity exposure and reproductive state on river-entry timing, an intervention experiment was conducted using Strait of Georgia captured late-run *O. nerka* that were taken to a nearby field laboratory. Fish were experimentally exposed to either fresh water, Strait of Georgia water, or a mixture, and half of the fish were given injections of gonadotropin releasing hormone (GnRH) to accelerate reproductive hormone development (Cooperman *et al*., 2010). After a week, fish were sampled for plasma and gill, telemetry tagged and released. As intended, reproductive hormone levels were elevated in the GnRH group (Cooperman *et al*., 2010) and genomic profiles of these fish closely resembled profiles of fish at spawning grounds (K. M. Miller unpubl. data) though few survived to enter the river supporting the notion that ocean migrating fish which have advanced maturation may not be able to osmoregulate well. Freshwater exposed fish entered the river nearly twice as fast as the saltwater exposed groups (M. Cooperman unpubl. data) supporting the hypothesis that coastal salinity exposure can modify river-entry timing in late-run fish.

The other coastal issue potentially affecting migration timing of late-runs is the abundance of summer-run Fraser *O. nerka*, which has been increasing in recent years. A positive correlation is evident between peak river-entry timing of late-run fish and the proportion of summer-run to late-run fish in the Strait of Georgia (Robichaud & English, 2007). This stay-with-the-school hypothesis suggests that relatively high abundance of summer-run fish encourages or entices late-run fish to follow them into the river. Some of the earliest river entry of late-run fish occurred in years with the highest summer-run abundances. There are some years, *e.g.* 2006, however, whereby late-run fish were dominant and still entered the river early. Moreover, adopting a radically different behaviour that is seemingly non-adaptive (*e.g.* entering the Fraser River early essentially dooms the fish to die before spawning) would probably not occur without some physiological basis. As described above, early-entry late-run fish are physiologically different from normal-timed late-run fish, and these differences could be sufficient to motivate fish to migrate in-river early. Additional motivation might come from sensing high abundances of summer-runs also migrating into the river, however, with only a few years of physiological telemetry information, it is not possible to fully examine the additional role that conspecific abundance may play. There have been several other hypotheses put forth to account for the early migration issue (*e.g.* change in coastal predator abundances, contaminants and others; Cooke *et al.*, 2004), however, these hypotheses were less frequently studied and were not supported by the evidence collected to date.

CAUSES OF *EN ROUTE* MORTALITY

Early entry exposes late-run populations of *O. nerka* to warmer river conditions (peak summer rather than a cooler fall temperatures) and as a result they accumulate more thermal units (more time in warmer fresh water) than normal-timed late-run fish (Wagner *et al.*, 2005). Furthermore, peak summer temperatures in the Fraser River have increased by 2° C over the past 60 years with 1° C of the warming occurring in the most recent 20 years (Patterson *et al.*, 2007). Early-entry late-run *O. nerka* populations thus encounter temperatures that are 3–6° C warmer on average than normal-timed late-run migrants. Normal-timed late-run *O. nerka* also mature reproductively while milling in the sea so that they are prepared to reproduce shortly after arriving at spawning sites. In early-entry late-run fish, this behaviour is replaced by maturation being completed while residing in natal lakes (Fig. 6). Spawning times in *O. nerka* 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; Brannon, 1987). As such, spawning times for late-run populations have changed very little despite the drastic shift in early upstream migration behaviour (Fig. 7). Early entry therefore exposes *O. nerka* to freshwater diseases and parasites for longer periods of time, and at river temperatures at which disease development is more rapid due to early river entry, climate warming and greater degree-days (Wagner *et al.*, 2005; Mathes *et al.*, 2010).

There are several diseases associated with different pathogens that migrating and spawning Fraser *O. nerka* contract and that could contribute to *en route* mortality (Bradford *et al.*, 2010*b*). One pathogen that has received considerable attention with late-run Fraser *O. nerka* is the naturally occurring parasite *Parvicapsula minibicornis*. This myxosporean parasite infects kidneys and gills in all adult Fraser *O. nerka* as they migrate through the estuary (Wagner *et al*., 2005). In laboratory studies, kidney infection has been shown to start when accumulated degree days exceed 350° C days and becomes full blown at *c*. 500° C days (Wagner *et al*., 2005; Crossin *et al*., 2008). Mortality rates assessed in laboratory studies with late-run *O. nerka* closely tracks with the severity of infection in terms of accumulated degree days (Crossin *et al*., 2008).

The early-entry fish that survive upriver migration tend to hold in natal lakes for extended periods of time rather than in spawning streams (English *et al*., 2005; Mathes *et al*., 2010). This behaviour ensures that some early-entry late-run fish will spawn. Adult *Oncorhynchus* spp. are known to seek cool-water refugia during spawning migrations (Hodgson & Quinn, 2002; Hyatt *et al*., 2003; Goniea *et al*., 2006; High *et al*., 2006) and populations of *O. nerka* that migrate through lakes *en route* to spawning streams tend to do so through the hypolimnion presumably as a form of behavioural thermoregulation (Newell & Quinn, 2005; Roscoe *et al*., 2010). A telemetry study on a population of late-run *O. nerka* found that the only early-entry migrants which survived to reach spawning grounds (16% of those tagged from the early group) were those that held in a lake near the spawning stream; none of the early-entry fish which resided in the river survived to spawn (Mathes *et al*., 2010). While residing in the lake, most of the time fish were occupying the cool water below the thermocline. To access the lake migrants had to pass by the spawning stream, indicating that survivors had made an active decision to access the thermal refuge. Interestingly, the use of the lake by normal-timed migrants did not increase survival (Mathes *et al*., 2010).

Correlational studies such as those described above need support from intervention experiments to establish cause–effect relationships. Therefore, the thermal experience of a group of normal-timed late-run fish was experimentally altered and their subsequent fate assessed using biotelemetry (Crossin *et al*., 2008). Adult late-run *O. nerka* from the Weaver Creek population (Fig. 1) were captured *en route* to spawning grounds and transported to a nearby laboratory where they were held at either a warm (18° C, to simulate an early entry phenomenon) or cool (10° C) temperature for *c*. 3 weeks. At the end of the intervention, fish had accrued >450° C days in the warm treatment, and <325° C days in the cool treatment, which led to high or low, respectively, *P. minibicornis* disease expression (Wagner *et al*., 2005). Fish were released in the Fraser River a short distance upstream of the ocean, during a time when normal-timed late-run fish were still progressing upriver, and tracked to their spawning area with biotelemetry. A striking temperature effect was discovered as the warm-treated fish incurred twice the level of mortality as the cool-treated fish, both during the completion of river migration as well as during the laboratory holding phase (Crossin *et al*., 2008). Females exhibited much higher mortality rates than males. Moreover, warm-treated fish had slower migration speeds than cool-treated fish indicating strong latent effects of temperature on migration behaviour. These findings support the hypothesis that elevated water temperatures during the freshwater migration period cause high levels of *en route* mortality in late-run *O. nerka*, and that disease may play a significant role as a mortality agent.

Because adult *Oncorhynchus* spp. populations in the Fraser River appear to be thermally adapted to their historical migration conditions (Lee *et al*., 2003; Farrell *et al.*, 2008; Eliason *et al.*, 2011), thermal conditions experienced by early migrants can result in physiological stress during migration. For example, early-entry migrants that are sampled close to the completion of their migration are characterized by having relatively high levels of plasma glucose, lactate, ions, haematocrit and osmolality (Young *et al.*, 2006; Mathes *et al.*, 2010). In a controlled study, focused specifically on quantifying the physiological consequences of temperature exposure in late-run *O. nerka*, fish held in the high-temperature treatment (19° C) were characterized by, increased mortality, higher plasma chloride and osmolality, suggestive of an osmoregulatory disturbance, and reduced reproductive hormone levels, which may affect final maturation (Jeffries *et al.*, 2012*a*). In another study, directed at revealing the cellular mechanisms associated with temperature stress, a 7 day exposure to 19° C was sufficient to induce genes characteristic of a heat shock response (*e.g.* molecular chaperones) and an immune response, along with a downregulation of many genes involved in protein biosynthesis (Jeffries *et al.*, 2012*b*). Together these studies provide some of the first evidence of the mechanisms by which elevated (but not acutely lethal) temperature experienced by fish during freshwater migration may greatly contribute to increased *en route* and pre-spawn mortality.

The evidence strongly suggests that a combination of factors including high temperatures, premature senescence, elevated stress, ionoregulatory dysfunction and disease (Wagner *et al.*, 2005; Young *et al.*, 2006; Crossin *et al.*, 2008; Mathes *et al.*, 2010) kills many early-entry late-run *O. nerka* in fresh water before they reach spawning areas. These results provide some insights into the selective forces at play that may have originally contributed to the evolution of their Strait of Georgia holding, a behaviour which would minimize their freshwater residency 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 are probably dying due to cardiorespiratory collapse (Farrell *et al.*, 2008; Mathes *et al.*, 2010; Eliason *et al.*, 2011). If early-timed migrants are physiologically compromised prior to freshwater entry as recent plasma and tissue genomic assays suggest (Cooke *et al.*, 2006; Miller *et al.*, 2011), then this could increase the lethality of freshwater diseases and exacerbate thermal stressors. The freshwater research emphasizes the pivotal role of water temperature, both as an acute and chronic stressor, on the behaviour and survival of late-run *O. nerka*.

CAUSES OF PRE-SPAWNING MORTALITY

Historically, PSM in most Fraser *O. nerka* populations was correlated with upstream migration timing and temperature, with higher levels in the earliest arriving fish (Gilhousen, 1990). PSM is estimated as the proportion of egg retention from carcasses recovered on spawning grounds during carcass recovery periods by DFO. Since the early migration phenomenon began, PSM has increased in most late-run populations (Fig. 5). The search for a single cause or suite of casual agents of PSM in senescing semelparous animals is understandably difficult because premature death probably results from a multitude of factors that can change both annually and seasonally. The factors most commonly associated with PSM in Fraser River *O. nerka* are migration timing, energy depletion, stress and disease, all of which are presumed to have synergistic effects with water temperature (Gilhousen, 1990; Hruska *et al*., 2011). It is likely that PSM may simply be a continuation of mortality processes that began during the migration, *en route* sublethal factors may become lethal by the time fish are at spawning grounds. In late-run fish, PSM can occur throughout their entire spawning period being high in both the earliest and latest arrivals at spawning areas. Although early migration in late-run fish has not resulted in a change in peak spawning periods (Fig. 7), and early-entry fish that survive the migration tend to spend more time holding in natal lakes than normal-timed migrants (Fig. 6), early-entry fish are still more likely to be the first to arrive on the spawning grounds. Diminishing proportions of early-entry fish continue to arrive on spawning grounds throughout the entire spawning period. Recent evidence suggests that the primary determinant of spawning success (*i.e.* the inverse of egg retention) is longevity on spawning grounds (Hruska *et al*., 2011). Thus, in addition to being compromised by their thermal history, early-entry fish that reach spawning grounds probably have short longevity and would be at a clear disadvantage to spawn successfully.

Rapid senescence and death on the spawning grounds have been linked to energy depletion for semelparous *Oncorhynchus* spp. (Dickhoff, 1989). The energy depletion hypothesis for PSM in late-run *O. nerka* is based on the observed positive correlation between early river-entry migration timing and PSM (Gilhousen, 1990). *Oncorhynchus nerka* that exited the marine environment early would be exposed to higher flow levels and higher temperatures, which would more rapidly drain energy reserves thereby increasing the probability of prematurely dropping below a critical energy density threshold identified for successful spawning in *O. nerka* (Crossin *et al*., 2004). Therefore, faced with an energetically more demanding migration it was reasonable for investigators to initially assume that early-entry late-run fish would arrive on spawning grounds with less body energy and thus be more at risk to PSM. First arrivals on spawning grounds, however, actually have higher energy reserves than later arrivals, and spawning females have similar energy levels to moribund but not spawned females (D. Patterson unpubl. data), both results suggesting that energy exhaustion on spawning grounds is not a factor affecting spawning success in early migrating late-run fish (Hruska *et al*., 2010). These results are supported by experiments on adult late-run *O. nerka* which have experimentally altered energy reserves and physiological stress levels towards the end of river migration (Nadeau, 2007; Nadeau *et al*., 2010).

Once *O. nerka* enter fresh water it is a race against time for migrants to be able to spawn prior to succumbing to various disease agents and the overall degenerative processes associated with senescence. The ubiquitous presence of viral (*e.g.* IHN), parasite (*e.g. P. minibicornis)*, fungal (*e.g. Saprolegnia* spp.), bacterial (*e.g. Chrondrococus columnaris)* and other pathogens that can cause disease in Fraser River *O. nerka* means that disease has always been considered central to any investigation into PSM levels in the Fraser River *O. nerka* (Colgrove & Wood, 1966; Williams, 1973; Jones *et al*., 2003). In regard to late-run fish, the fundamental problem with linking disease and PSM is determining whether pathogen presence and associated disease is the fundamental cause of PSM, or simply an effect related to other less proximate causes associated with exposure to other stressors linked to early river migration. Most, if not all, of diseases associated with pathogen presence are accentuated by increases in temperature and freshwater residency times (Crossin *et al*., 2008). Early migration exposes late-run fish to warmer temperatures for extended freshwater periods, therefore, it seems logical to view diseases associated with pathogens as both an effect of early entry and simply a proximate cause of PSM. The physiology underlying the correlations between migration temperature and PSM have been investigated with field and laboratory studies using histopathology, functional genomics and plasma analyses all indicating the functional role that gill and kidney diseases play in disturbing the homeostasis that leads to death (Bradford *et al*., 2010*a*, *b*; Jeffries *et al*., 2011).

An intriguing exception to the early migration and high PSM phenomena observed in most late-run populations is the unusual pattern of mortality observed in Cultus Lake *O. nerka* held for an artificial broodstock programme. These fish are intercepted at a fence located just prior to entry into the lake and held in a hatchery at cool hypolimnetic water temperatures until spawning time in December. Fish captured in October and November had considerable higher mortality than fish arriving at the fence to enter the lake in September (Bradford *et al*., 2010*a*). Moreover, of the fish that died prior to spawning, most had much higher levels of disease progression. The explanation for why later arrivals to the natal lake had higher mortality is speculative but points to a possible disconnect between river-entry timing and arrival at the spawning grounds. Late arrivals at the spawning ground could still have left the marine environment early but held in the much warmer Fraser River and associated tributaries downstream of Cultus Lake (Bradford *et al*., 2010*a*), thus exposing them to higher accumulations of thermal units than early lake arrivals that seek cooler hypolimnetic waters in the lake.

POPULATION TRENDS IN MORTALITY AND SPAWNER ABUNDANCE

Though segments of all late-run *O. nerka* populations have been exhibiting early migration into the Fraser River over the past 15 years, populations have differed in some years in their scale of freshwater mortality. In terms of *en route* mortality, Weaver Creek *O. nerka* have been one of the most negatively affected, in each of the past 15 brood years (brood years 1995–2010 inclusive) this population has experienced >50% mortality (1997 was slightly under) and in several years >80% mortality (Fig. 4). Similarly, Portage Creek, Harrison River and Late Shuswap and Adams populations have experienced >50% *en route* mortality in over half of these same brood years (Sockeye Salmon Stock Production Files - DFO/PSC, unpubl. data). Because of their small population size, *en route* mortality has not been assessed for Cultus Lake *O. nerka* and efforts to estimate population level PSM have been challenged by low numbers of carcass recoveries in some years (Bradford *et al*., 2010*a*). Nonetheless, nominal estimates of PSM have been high in several years (*i.e.* >70%, Fig. 5).

Since the early migration phenomenon began, a declining trend has been observed in spawner abundance in most cycle lines for all late-run populations (Sockeye Salmon Stock Production Files - DFO/PSC, unpubl. data). The one exception is the Harrison River population which, despite high levels of *en route* mortality, has had increasing levels of spawning ground escapement in recent years highlighting the complexity of links between the early migration phenomenon and population-specific productivity. Declines have been most severe in Cultus Lake *O. nerka* where the behaviour and subsequent mortality are major factors threatening that population's long-term viability, prompting assessment as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2003) and recommendations for listing under Canada's Species at Risk Act. Since 2001, Cultus Lake *O. nerka* have been supplemented using hatchery additions and protected in part by an extensive predator [northern pikeminnow *Ptychocheilus oregonensis* (Richardson 1836)] removal programme (Bradford *et al*., 2011).

MANAGEMENT ISSUES AND USE OF LATE-RUN *O. NERKA* SCIENCE

The early migration behaviour and its consequences have created a major conservation issue for the late-run populations and also management challenges. First and foremost has been the effect of variable but high levels of early migration and mortality on the numbers of fish surviving to spawn. This has led to serious concerns about long-term population viability for some populations (*e.g*. Cultus Lake; Bradford *et al*., 2011). Second, since most Fraser *O. nerka* are caught in mixed-population fisheries, restrictions to protect late-run *O. nerka* limited the magnitude of harvest of other co-migrating population aggregations like summer-run *O. nerka* which have not changed their migration behaviour and thus have not been subject to the same levels of *en route* mortality. Because of the uncertainty of the interannual levels of early migration and mortality, fisheries managers adopted a precautionary approach to harvesting decisions attempting to balance these conservation risks with the available harvests of co-migrating populations. This approach led to substantial foregone harvest of summer-run fish, and also late-run fish in a few years when the mortality was less than expected which cost the fishery a loss in revenue (Lapointe *et al*., 2004).

There were over a dozen hypotheses proposed when the early entry phenomenon was first realized to account for the behavioural change (Cooke *et al*., 2004). Though that list has been substantially reduced, there is still no silver-bullet factor that managers desire for pre-season prediction as it appears this is a complex, multi-factor phenomenon. In the face of little scientific information for the causes of early migration, beginning in 2003, models were developed by managers to predict the median upstream migration dates based on in-season estimates of the proportion of the late-run that had migrated upstream at any given point in time (Pacific Salmon Commission, 2007). These models, coupled with empirical relationships between *en route* mortality and median date of river entry for a population (*e.g*. Fig. 5), are presently used for helping to make harvest management decisions for late-runs, in years of large late-run abundance and only modest levels of early migration, exploitation rates have been set as high as *c*. 35% [*e.g*. 2006; Pacific Salmon Commission, 2011; Fig. 3(b)]. In years of relatively low late-run abundance or extremely early upriver migration, exploitation rates have been limited to 15% or lower [*e.g*. 2008 and 2009, Pacific Salmon Commission, 2008; Fig. 3(b)]. Some managers and stake-holders have advocated concentrating more fishing on early migrants given the prospects for their survival to spawning grounds were particularly poor. Others have 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 assuming surviving early entry behaviour became a necessary future adaptation.

Fraser River *O. nerka* are intensively managed in that adjustments to harvest rates, both in the ocean and lower Fraser River, are made in-season and often are changed on a daily basis as managers decide if their escapement targets are being met, that is, are adequate numbers of fish arriving on spawning grounds. As river temperatures have been warming in recent decades negatively affecting all Fraser *O. nerka* populations (Martins *et al*., 2011) and late-runs have been migrating early, river environmental conditions have taken a large, though year-specific toll, on spawning ground escapement. Because *en route* river mortality can be high in some years, managers needed a way to forecast potential levels of *en route* mortality in order to adjust harvest rates during the fishing season. Managers thus developed escapement adjustment models, which are based on long-term correlations between escapement discrepancies (*i.e. en route* mortality) and environmental conditions (*e.g.* river temperature and discharge) and river-entry timing (Cummings *et al*., 2011). Discrepancies are the differences between estimates of abundance at river entry and spawning grounds, termed *en route* loss which has come to be synonymous with, and an index for, *en route* mortality (Cummings *et al*., 2011). These models thus estimate levels of *en route* mortality based on forecasted water temperature, discharge or entry timing (Macdonald *et al*., 2010), though they are relatively crude and do not explicitly use any of the physiological knowledge reviewed here. The considerable progress made by researchers in understanding mortality mechanisms, and predicting levels of *en route* mortality experienced by late-run *O. nerka via* biotelemetry, however, has been relied on extensively by managers to provide the necessary biological rationale to implement changes in harvest (M. Lapointe, pers. comm.). Specifically, research has demonstrated that physiological factors and higher than normal temperatures are responsible for killing early migrating fish before reaching spawning areas. Thus, most stakeholders (*e.g.* commercial, recreational and First Nations fishers; non-governmental environmental groups) now expect and accept that early upstream migration will result in significant *en route* mortality, that harvest restrictions are generally based in science, and they recognize that variation in the magnitude of mortality will be related to the fraction of the population migrating upstream early.

In-season and pre-season prediction of *en route* mortality could, however, be improved using water temperature metrics which are grounded in an understanding of physiological mechanisms. For example, managers could use: threshold temperature models, based on encountering migration temperatures $>20^\circ$ C, *en route* mortality of Weaver Creek *O. nerka* was 90–100% due to collapse of metabolic scope (Farrell *et al*., 2008); degree-day models, based on the accumulation of degrees above a sublethal temperatures that are associated with disease progression and cumulative stress (Crossin *et al*., 2008); metabolic or cardiac scope models, based on population-specific thermal criteria which dictate swimming performance (Eliason *et al*., 2011; Hague *et al*., 2011). Moreover, because early migration (and its concomitant mortality) has a physiological basis (Cooke *et al*., 2007; Crossin *et al*., 2009*a*), physiological indicators that can be readily collected from small tissue biopsies of fish during coastal migration and rapidly processed in real-time could assist harvest management decisions. For example, 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 (Miller *et al*., 2011).

In terms of which of these potential models might be most useful for future in-season decision-making (*i.e.* predicting levels of *en route* mortality and thus being able to adjust harvest accordingly), they all have pros and cons. Temperature threshold models are the simplest approach and most easily adaptable into the present management system, and although river temperature forecast models are currently available to link with these, they would need some refinement to more accurately predict likelihood that specific temperature thresholds would being exceeded. Metabolic-scope models are a form of temperature threshold approach but with less clearly defined thermal thresholds which are not fully biologically understood (*e.g.* the threshold is linked to when a certain percentage of maximum scope is exceeded which would thereby impair migration), until it is better understood exactly how much of maximum scope is required to migrate, these models will be difficult to apply. Degree-day models are more complex than thermal threshold ones as they require much more detailed, and longer time-scale, river temperature forecasting at multiple sites along the migratory corridor than currently exists. Such forecasting, however, is currently feasible and these models would represent the most integrative approach in terms of considering the dynamic nature of the thermal experience during the migration. Lastly, biomarker models, which would involve samples of tissue taken in high-sea or coastal areas, would offer managers the greatest potential flexibility in terms of having information available to them on estimates of river mortality the earliest of all the potential models (*e.g.* days to weeks in advance of fish reaching large marine and in-river fisheries). Biomarker development, however, is still in its infancy and more ground truthing is needed in terms of selecting a small number of powerful and relevant biomarkers before they would be accepted by managers as a means to predict *en route* mortality.

Recent work has shown that once a late-run *O. nerka* has arrived on spawning grounds, the likelihood of it successfully spawning can be predicted up to a week in advance based on arrival timing (Bradford *et al*., 2010*b*), locomotor activity (Hruska *et al*., 2011), pathogen presence (Bradford *et al*., 2010*b*), gene expression patterns (Miller *et al*., 2011) and plasma chemistry (Hruska *et al*., 2010; Jeffries *et al*., 2011). This type of information could be used by managers of artificial spawning channels (*e.g.* Weaver Creek *O. nerka*) to assist their decisions in determining how many fish, and for how long during the run, they should load channels with spawners, and for those involved with conservation broodstock programs (*e.g.* Cultus Lake *O. nerka*) to choose fish for artificial propagation.

CONCLUSIONS AND FUTURE RESEARCH

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 the phenomenon 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 and temperature) trigger or control physiological, and hence behavioural, changes in individual migrating and maturing *O. nerka*, and how other factors (both endogenous such as disease states and exogenous such as abundance of co-migrators) mediate these behavioural changes. Though a small number of manipulation experiments have been undertaken [*e.g.* temperature manipulation (Crossin *et al*., 2008; Jeffries *et al*. 2012*b*) salinity and GnRH manipulation (Cooperman *et al*., 2010)] clearly more are needed as only in this way can cause and effect 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 with large-scale fixed telemetry systems [*e.g.* POST (Crossin *et al*., 2009*a*)] 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. As some other species of *Oncorhynchus* also seem to be eliciting early migrations, the search for answers in early migrating late-run *O. nerka* needs to include, where possible, analogous studies in other groups of fishes (Crozier *et al*., 2011).

The consequences of migrating upstream early for the survival of late-run fish and the mechanisms associated with mortality are now well understood. Early migrants are out of synch with their river migration environment and cannot be expected to win the race between the competing processes of maturation, premature senescence, elevated stress, ionoregulatory dysfunction and disease needed for survival to successful spawning. While prolonged freshwater residence associated with early migration is a primary driver, the role of water temperature cannot be overlooked. Early migrants are clearly not well adapted to deal with the riverine conditions they experience. Only a few late-run populations have been examined in detail but there is good evidence that population-specific adaptations to river temperatures exist. Future work must continue to examine the capacity for physiological adaptation (Eliason *et al*., 2011) and phenological changes (Crozier *et al*., 2011; Reed *et al*., 2011) in key Fraser *O. nerka* populations, not just late-runs, because as the Fraser River continues to warm (Patterson *et al*., 2007) there is significantly increased risk of high mortality even in normal-timed late-run fish as well as in other run timing groups (Hague *et al*., 2011; Martins *et al*., 2011). The study of diseases will increase in importance, as they will play much larger and obvious roles as agents of *en route* and PSM in a warming Fraser River. Understanding which populations 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.

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