Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia

ABSTRACT

Since 1995, several stocks of Fraser River sockeye salmon (*Oncorhynchus nerka*) have begun upriver spawning migrations significantly earlier than previously observed. In some years, the timing of peak migration has shifted more than 6 weeks. Coincident with this early migration are high levels of en route and pre-spawning mortality, occasionally exceeding 90%. These phenomena pose risks to the perpetuation of these fisheries resources. At present, although there are many competing hypotheses (e.g., energetics, osmoregulatory dysfunction, oceanic conditions, parasites) that may account for early migration and high mortality, there are no definitive answers, nor any causal evidence that link these issues. With poor predictive ability in the face of uncertainty, fisheries managers have been unable to effectively allocate harvest quotas, while ensuring that sufficient fish are able to not only reach the spawning sites, but also successfully reproduce. If trends in mortality rates continue, several important sockeye salmon fisheries and stocks could collapse. Indeed, one sockeye stock has already been emergency listed as endangered under Canadian legislation.

Introduction

The migrations of Pacific salmon (*Oncorhynchus* spp.) are remarkably precise geographically and temporally. Although they travel thousands of kilometers in high seas, almost all maturing salmon return to their natal freshwater streams to spawn and, for any given stock, upriver spawning migrations usually commence within the same week each year (Groot and Margolis 1991). Our knowledge of how Pacific salmon achieve these feats of navigation and timing is rudimentary, despite the fact that abundant and sustainable salmon stocks are important economically, ecologically, and culturally to Canada. Economically, the British Columbia (BC) commercial fishery for salmon is valued at $85–250 million CAD annually (1990–95; Anon 2002) and the recreational fishery at over $1 billion CAD (1995 National Survey; Anon 1995a). Approximately $40 million CAD in tax dollars are spent annually on salmon management and habitat conservation in Canada. Ecologically, salmon are important components of food chains in both freshwater and marine environments (Naiman et al. 2002; Schindler et al. 2003). Also, adult salmon carcasses are fundamental sources of nutrients for stream and riparian forest ecosystems in coastal Pacific watersheds (Helfield and Naiman 2001). Culturally, salmon are integral to the mythology and spiritual integrity of Pacific coast First Nations. Indeed, the migratory behavior of Pacific salmon 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 salmon to natal streams. The economic and cultural value of salmon has led to serious political conflicts in federal-provincial, federal-First Nations, and U.S.-Canada relations.

The Fraser River (Figure 1) is the largest producer of wild salmon in Canada. Of its five salmon species, sockeye salmon (*Oncorhynchus nerka*) is the most commercially valuable and the second most numerically abundant. Over a dozen large stocks and several dozen smaller stocks occupy more than 150 natal areas

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throughout the watershed, distributed from as little as 100 km to as far as 1,200 km from the ocean. In the Fraser, juvenile sockeye salmon usually spend one or two years in freshwater lakes before migrating to the ocean where they spend the next two to four years gaining >98% of their mature weight (Healey 1986; Burgner 1991). When adult sockeye return, near-shore and river navigation clearly involves olfactory cues (reviewed in Ueda et al. 1998). However, our understanding of the physiological and environmental cues that enable salmon to return so precisely, in time and space, from the high seas to their natal freshwater is rudimentary (reviewed in McKeown 1984; Quinn 1990). Early telemetry studies in the open ocean show that the return to the coast is not a random event. Computer modeling suggests that maturing sockeye salmon find their way from high seas to coastal rivers using a combination of "assists" by ocean currents and environmental cues (e.g., celestial bodies, amount/angle of daylight, magnetic fields) that permit compass-orientation (Thomson et al. 1992; Dat et al. 1995). A high seas telemetry study on a small number of maturing chum salmon (*O. keta*) supports the compass-orientation theory (Ogura and Ishida 1995). Furthermore, work with experimentally "blinded" sockeye salmon carrying acoustic transmitters in Lake Toya, Japan, revealed that vision is paramount for fish to navigate successfully from open water to coastal areas (Ueda et al. 1998).

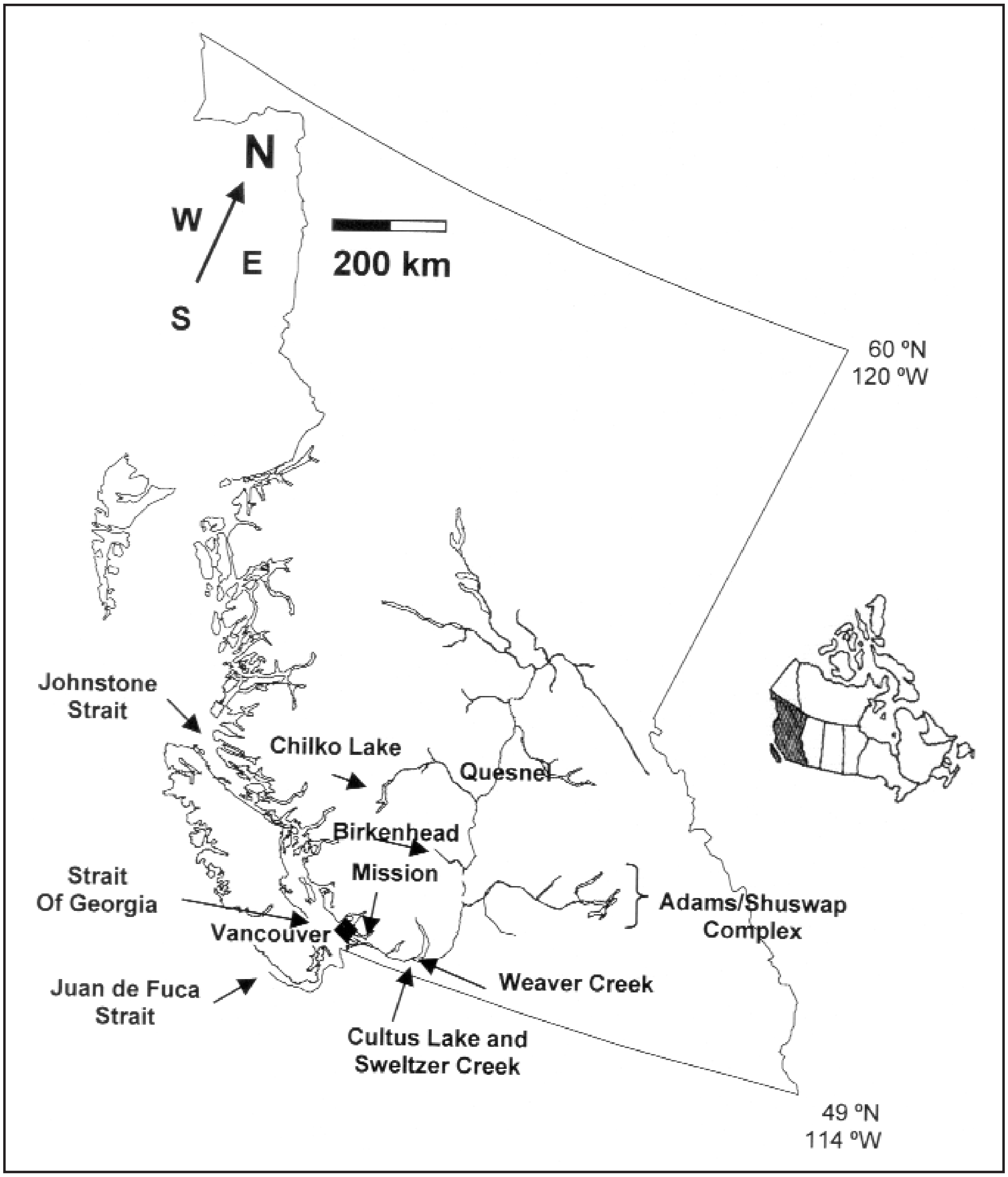


Figure 1. Map of the Fraser River watershed indicating locations of relevanat spawning grounds, coastal migration routes, and cities in British Columbia. The inset shows the location of British Columbia in Canada.

Upriver Migration Timing: Normal and Abnormal

Salmon migrate up rivers as a cohesive group (termed a "run") and each run enters and migrates through the river on specific dates, with very little overlap of the peak abundance between these groups. So precise is this timing that stocks can be roughly identified by the sequence of their appearance in the Fraser River, as was done before stock identification using scale analysis and, more recently, DNA analysis. At present, the Fraser River sockeye migration is divided into four main run timing groups for management purposes: the "early Stuart run" in June, the "early run" in July, the "summer run" in August, and the "late run" in September/October (Burgner 1991; Figure 2). Each run is comprised of multiple stocks that overlap in timing. Early and summer-run stocks migrate quickly through the estuary and upstream whereas late-run stocks usually "hold" in the estuary or the marine areas of the Strait of Georgia in the vicinity of the river mouth for several weeks before initiating up-river migration. However, in 1995/1996, many late-run stocks (including the "famous" Adams River stock) arrived in the estuary at the normal time, but commenced their river migration about 3 weeks earlier than normal (Lapointe 2002). Since then, these late-run stocks have generally entered the river progressively earlier each year, and in 2000 and 2001, entered the river at the same time as the summer-runs. The shift in river entry timing of late-run stocks is well illustrated by Weaver Creek sockeye (Figure 1), which during 1995-2002 began upriver migration up to 6 weeks earlier than historically recorded (Figure 3). Not all late-run stocks have changed their time of river entry. A few, such as the Birkenhead stock (Figure 1), have retained their historic timing.

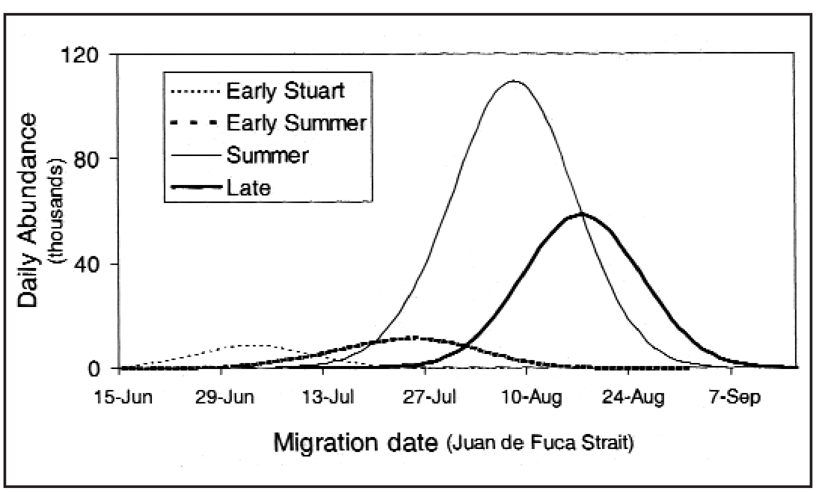
High Mortality Associated with Abnormal Migration Timing

Associated with this abnormal migratory behavior has been an extraordinarily high en route and pre-spawning mortality rate (See Box 1), which has generally increased since 1996. By 2001, mortality during the up-river migration prior to reaching their spawning grounds (termed "en route mortality") ranged from 90-96% in many stocks. Mortality of the migrants that successfully reached the spawning grounds but died without spawning (termed "pre-spawning mortality") ranged from 10-30% (Lapointe 2002). In contrast, prior to 1995, total en route and pre-spawning mortality for late-run stocks rarely exceeded 20%. In 2001, "early" migration behavior also was observed for the first time in other salmon species with late runs including pink (*O. gorbuscha*), chum, and chinook (*O. tshawytscha*) (Lapointe 2002), indicating that the phenomenon may not be restricted to sockeye. In 2003, this phenomenon was clearly observed in pink salmon which entered the Fraser River 3 weeks earlier than normal (PSC, unpublished data). Whether mortality rates were elevated in these other species is unknown as en route and pre-spawning mortality is not routinely measured for these other species. Those late-run sockeye stocks that have retained their historic timing have not shown increased en route or pre-spawning mortality.

For example, the abnormally early migration of Weaver Creek sockeye (Figure 3) was coincident with unprecedented mortality prior to spawning (included both en route and pre-spawning mortality). Between 1995 and 2001, such rates have ranged between 46% and 94% (Figure 4), and were correlated positively with early migration (See Box 1 for discussion of mortality calculations; see Gilhousen 1990). Recent mortality rates of the Weaver Creek stock grossly exceed levels observed for the same stock between 1974 and 1994 (0% to ~22%). Similar patterns have been observed in other large stocks including the Adams River/Late Shuswap stock complex (mean run size of 13.01 million fish from 1948-1987; Anon 1995b), as well as in smaller stocks. For example, the smaller Cultus Lake sockeye stock have begun to migrate progressively earlier than historically noted and are exhibiting very high pre-spawning mortality (Figure 5). Very little successful spawning was thought to occur during 1999 and 2001 as evidenced by no observed spawning and only limited smolt production (Schubert et al. 2003). These unprecedented losses to the breeding populations have brought small stocks (e.g., Cultus Lake) to the point of collapse, and even impacted abundant stocks (e.g., Weaver Creek, mean run size of 0.36 million fish from 1948-1987; Anon 1995b).

Although the Cultus Lake stock has been declining for more than 20 years, the recent increase in mortality and reduction in spawning success coincident with the early migration phenomenon has served to push this stock to critical levels, even in dominant year classes, despite a reduction in the exploitation rate to ~17% in 2001 (Figure 6). Projections for the next three generations under different mortality scenarios for pre-spawning and exploitation suggests that the effective spawning population will decline by more than 75% if pre-spawning mortality exceeds 90%, with no exploitation. It may decline over 80% if the exploitation rate exceeds 10% (Schubert et al. 2003). The Committee for the Status of Endangered Wildlife in Canada (COSEWIC) emergency listed the Cultus Lake Stock as endangered on 25 October 2002, representing only the second time in the past decade that COSEWIC has made such a designation. Emergency listings are reserved for instances when the risk of extinction is imminent and COSEWIC determines that there is insufficient time for a normal assessment process. In May 2003, COSEWIC confirmed the emergency listing. A number of factors contributed to this decision, but COSEWIC identified two main factors: unsustainable harvest practices in most years from 1952 to 1995, and unprecedented levels of pre-spawning mortality observed since 1995 (COSEWIC 2002). The plight of the Cultus Lake sockeye exemplifies the additional risk to the stock imparted by the recent phenomenon of early migration, high mortal-

Figure 2. Generalized schematic of sockeye run timings prior to 1995. Note the distinct lack of overlap in the modal abundance of sockeye salmon in the Juan de Fuca Strait.



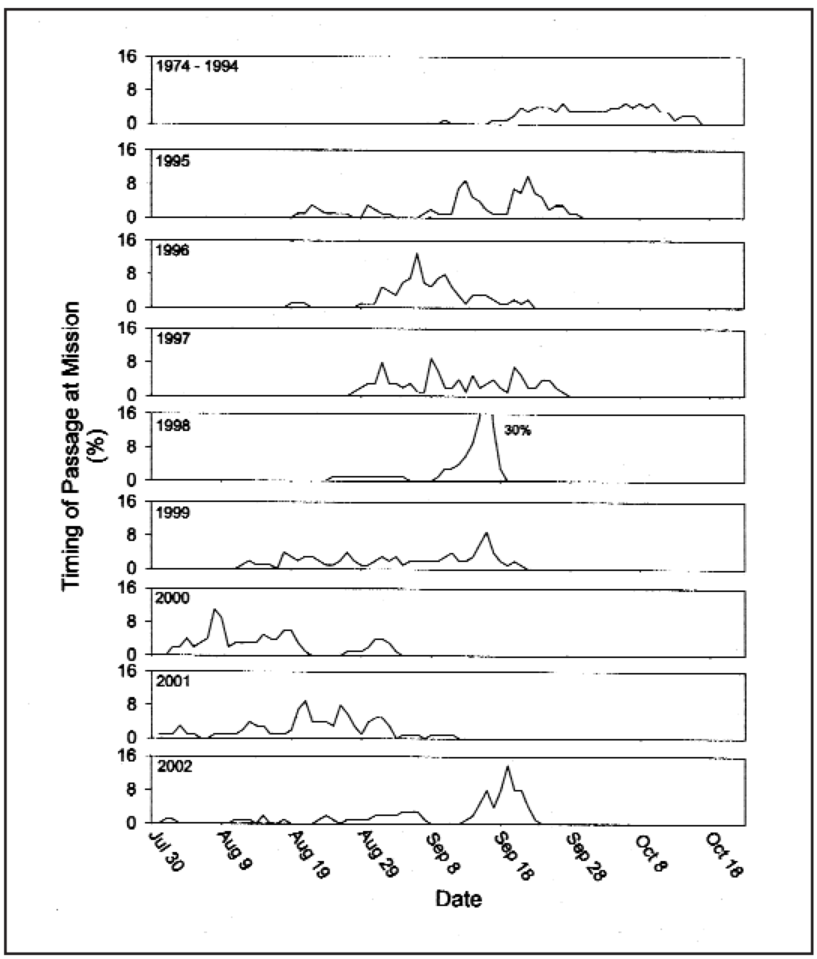
ity, and general uncertainty, in addition to other sources of mortality such as harvest.

Box 1. How is mortality estimated? There are two estimates of in-river migration mortality determined for Fraser River sockeye; en route mortality (those that die between Mission and spawning grounds) and pre-spawning mortality (those that reach the spawning grounds but die prior to spawning). Estimates of en route mortality are generated using two estimates of abundance. The first estimate of abundance is made primarily using a hydroacoustic counting facility during the commercial fishing season as the fish pass beyond Mission in the lower river (Fig. 1; Banneheka et al. 1995). The second estimate is based upon a combination of the estimates of catch in fisheries operating upstream of Mission and the estimates of abundance on the spawning grounds. These two estimates are rarely the same (Alexander 1999) which complicates a management system that allocates catch in commercial, First Nations, and recreational fisheries to achieve spawning ground escapement targets. The Mission estimate often exceeds the estimate from the spawning grounds, but the reverse may also occur. The disparity is prevalent for the less abundant early-migrating stocks (Early Stuart and early summer-run groups) and a relatively recent phenomenon for the summer-run (e.g., Chilko and Quesnel) and late-run stocks (e.g., Adams and Weaver but excluding Birkenhead). The difference in estimates is often attributed to mortality during years with extreme migration conditions, or in the case of this article, mortality arising from undetermined reasons. However, errors in lower river and spawning ground escapement estimates, and in estimates of First Nations and recreational catches above Mission, may have an annual bias that confounds the determination of accurate estimates of in-river migration mortality. We are unable to objectively apportion the difference between estimates into component sources and must assume an unbiased error in the combined fish enumeration efforts when using the differences in estimates of abundance as a measure of en route mortality. Pre-spawning mortality is generally determined more easily as it only requires as single estimate. This is done by estimating the total abundance of spawners that reach the spawning grounds and the proportion of fish that actually die without spawning.

In 2002, risk-averse fisheries management tactics were adopted to ensure the viability of late-run stocks resulting in the early closure of some fisheries and enhanced escapement of sockeye. As in past years, late-run sockeye exhibited early migration timing in 2002. However, the stock as a whole exhibited three distinct pulses of river entry. The last of these pulses, which contained the largest number of fish, behaved "normally" and delayed in the Strait of Georgia (Figure 1). Nonetheless, timing for late-run stocks was still 2 weeks earlier than the long-term average (PSC 2003), and as indicated below, the high mortality phenomenon was again evident and more prevalent among the fish that entered the river in the first two pulses than those that delayed longer in the Strait of Georgia.

In 2002 the agencies responsible for salmon management (Pacific Salmon Commission and Canadian Department of Fisheries and Oceans) funded and conducted two studies designed to independently assess in-river survival of late-run sockeye: a radio tagging study, in which large numbers of fish were tracked from the ocean to spawning grounds; and a Peterson disc tagging study near the spawning grounds of the Adams/Shuswap stock complex. The radio tagging study revealed that about 51% of late-run sockeye entered the river without holding in the Strait of Georgia (Karl English, LGL Inc., unpublished data). In-river survival was very low for these fish—89% of tagged late-run fish that passed Mission, B.C., prior to 18 August 2002 died before getting to spawning grounds. After 11 September 2002, mortality rates fell to only 8%. The Peterson disc tagging study showed that early arrivals to spawning regions experienced 70% mortality whereas, later arrivals experienced less than 3% mortality (Timber Whitehouse, Fisheries and Oceans Canada, unpublished data). When the results of these two studies are combined to estimate overall survival from river entry to spawning for the Adams late-run sockeye, 96% of fish that passed Mission before 18 August 2002 died, whereas after 11 September 2002, only 10% of

Figure 3. Annual migration timing for Weaver Creek sockeye salmon for the period of 1974–1994 as mean values for the individual years from 1995 through 2002. The passage of fish past a hydroacoustic counting facility at Mission, B.C. was used to assess timing.



sockeye died. This latter summary point somewhat obscures the fact that the early migration/high mortality phenomenon did indeed occur in 2002. In early August 2003, there are indications that segments of late-run sockeye are again entering the Fraser River early without holding in the Strait of Georgia.

Clearly the high mortality associated with earlier entry of the late-run sockeye salmon is an important management issue. In 2002, nearly 6 million late-run sockeye salmon entered the Fraser River and had the overall mortality for the stock been as high as in the previous year, the loss of fish would have been unprecedented. Neither fisheries managers nor scientists understand why these fish are entering the Fraser River early and experiencing such high levels of premature mortality. In this article we provide an overview of some of the possible factors that are associated with this problem and conclude by presenting the management and conservation concerns. These carry a large degree of uncertainty surrounding the future of the late-run Fraser River sockeye salmon and associated fisheries.

Possible Causes of Early Migration/High Mortality Phenomenon

A number of key decisions and events, which likely are tied to biological clocks and environmental cues, are involved in the initiation, progress, and success of a salmon's spawning migration. These decisions and events become the focus for the possible causes of early migration and high mortality. Salmon likely use a number of biological clocks and cues to time the: (1) initial departure from the open ocean, (2) onset of gonad development, (3) switch from hyperosmotic to hypoosmotic regulation, (4) metering out of energy reserves, (5) final gonadal maturation and development, (6) migratory and mating behaviors, and (7) senescence. Behavioral and physiological aspects of the first two points are "high-seas" issues, whereas the last five points are more pertinent to the early migration phenomenon, which is related to early entry into the river and not early arrival at the river (Lapointe 2002). Late-run sockeye arrive at the mouth of the Fraser River at the same time as they always have historically, but are not "holding" as they used to do. Below we explore possible causes responsible for early migration (points 3 to 7) and mortality. Some factors may only affect timing or mortality, so both are not discussed in all cases.

Migration Timing

Energy Status

Sockeye salmon, indeed all anadromous fish, do not actively feed during upriver migrations. Late-run sockeye do not generally feed during their "holding" pattern in the Strait of Georgia (Figure 1). Because salmon have limited energy and time to complete their migration and spawn, unusually low energy reserves could be a trigger that prompts late-run sockeye to initiate freshwater migrations earlier than usual but this is speculative. In recent years, body energy densities in Fraser River sockeye stocks have been significantly lower (Crossin 2003) than that observed during the 1950s, the only other time it was measured (Gilhousen 1980). However, unlike earlier runs, the late-run sockeye salmon

Figure 4. Relationship between the annual 50% upstream migration date at Mission B.C. and annual pre-spawning mortality levels for Weaver Creek sockeye salmon. Data for the years 1974–1994 are plotted in black, 1995–2001 in open circles. Mortality data for 2002 were unavailable due to problems with the terminal count.

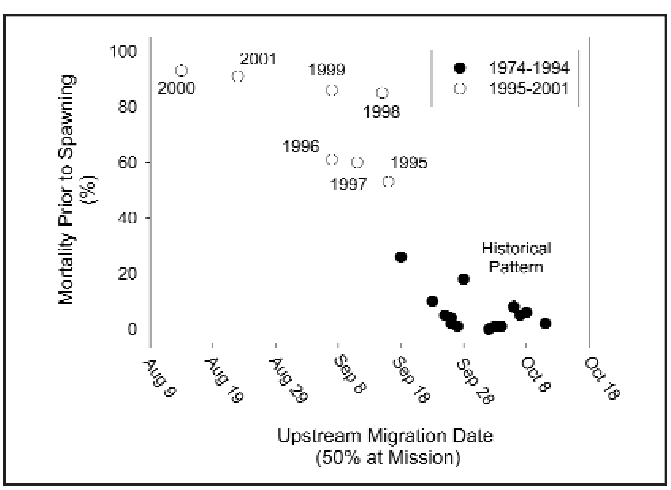
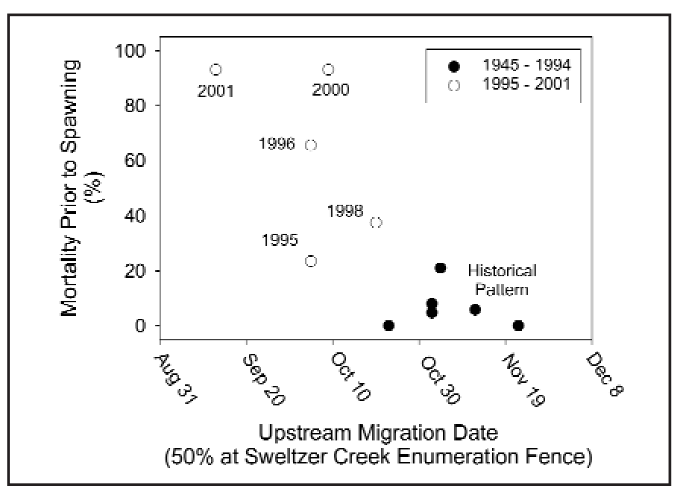


Figure 5. Relationship between the annual 50% upstream migration date at Sweltzer Creek counting fence and annual pre-spawning mortality levels for Cultus Lake sockeye salmon. Data for the years 1945–1994 are plotted in black, 1995–2001 in open circles.

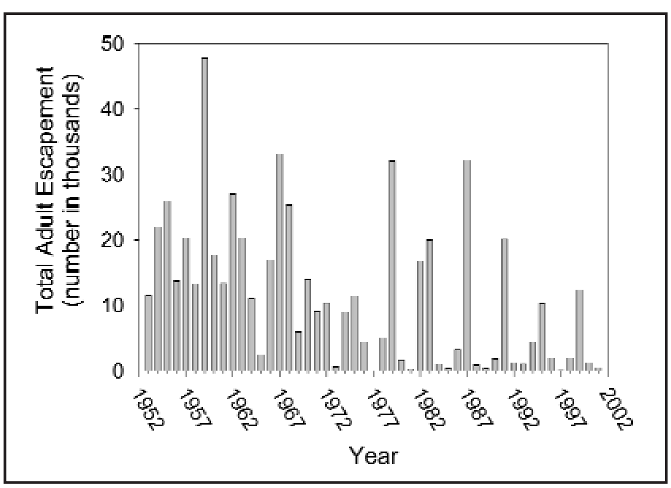


tend not to be energy limited as they generally don't use all of their reserves to reach their spawning grounds.

Osmoregulatory Dysfunction and Photoreception Impairments

Salmon must adjust their osmoregulatory (and ionoregulatory) systems before moving from the sea to freshwater. In seawater, fish constantly gain ions and lose water across the gills, but remain in osmotic and ionic balance by drinking seawater and excreting excess ions (Clarke and Hirano 1995). In freshwater, fish face the opposite problem because they gain water and lose ions across the gills, but remain in balance by producing dilute urine and actively taking ions up at the gills. We do not know either when or what cues adult migratory salmon to reorganize the gill and kidney transport mechanisms (Wood and Shuttleworth 1995). Sockeye salmon, as they approach the Fraser River, move higher in the water column. Ultrasonic telemetry studies of sockeye salmon as they approach the Fraser River from Johnstone Strait (Quinn and terHart 1987) have shown behavioral selection of water depths where temperature and salinity gradients were the largest in waters with more distinct vertical structure, in addition to the known diurnal (dusk and dawn) vertical migrations. This means that fish may be exposed to, or even sampling, water of lower salinity and different light quality. Photoperiod has been suggested as a cue affecting migratory timing in sockeye (Quinn and Adams 1996). Also, ultraviolet (UV) cone densities or their visual pigment properties, which are elevated in freshwater juvenile salmon, decline upon seawater entry (McKeown 1984; Novales Flamarique 2001). They may elevate again as homing adults mature. Endocrine factors such as thyroid hormone, cortisol, prolactin, and growth hormone control the remodeling of visual pigments and the osmoregulatory transition from seawater to freshwater. An uncoupling of the endocrine signals that prepare adults to migrate upstream may cause early freshwater entry. The exact mechanisms that would lead to such uncoupling are unclear, but documentation of the progression of osmoregulatory and photoreception alteration associated with different phases of migration in early and normal timed migrants would allow this hypothesis to be tested.

Figure 6. Annual escapement for Cultus Lake sockeye salmon between the years 1953 and 2001. Figure adapted from Schubert et al. (2003).



Endocrine Disturbance

Reproductive hormone titres play a critical role in gonad maturation and spawning behaviors during salmon migration (McKeown 1984), and may play a role in migratory timing (Ueda et al. 1998). The gonadotropin-releasing hormone (GnRH) triggers the initiation of gonad growth. Sockeye implanted with artificial GnRH ceased feeding in Lake Toya, Japan and prematurely migrated homewards (Kitahashi et al. 2000). The trigger for GnRH release is not well understood, but disruption of GnRH release could impact timing of freshwater entry. Furthermore, if there are disruptions to the normal cycle of reproductive hormones, through either exposure to waterborne toxicants that are known endocrine disruptors or other stressors, salmon could begin to senesce prior to reaching full reproductive maturity (See contaminants section).

Oceanic and In-River Environmental Conditions

Fraser sockeye salmon spend 2 to 4 years of their lives in the Pacific Ocean where they feed and grow. Growth rates in the marine environment are influenced principally by food availability, which is in turn influenced by a suite of environmental factors. Very little is known about the biology or behavior of adult fish while at sea, so the majority of information we have is based on inference from environmental conditions and fish collections by fishers and test fisheries. Environmental conditions in the region of the Pacific where sockeye salmon grow are dynamic, responding to large-scale changes in climate. Climate changes occur on variable time scales and are caused by different phenomena. Changes to the Aleutian low pressure gradient may drive ocean productivity on 10–20 year cycles (termed regimes; Beamish et al. 1997). Abrupt changes in productivity (termed regime shifts) occurred in 1975–77 and in 1998/1999 and have been hypothesized to influence sockeye salmon migratory behavior (Beamish et al. 2002). The most recent regime (1998–2001) is regarded as exceptionally warm with poor growth and low abundance of euphausids, a primary food source for sockeye. However, the early migration phenomenon occurred during the previous regimes as well (1996–1997), suggesting that regime shifts are unlikely to be solely responsible for early migration timing. El Niño southern oscillation (ENSO) events occur every 5–7 years and can cause warmer than normal coastal temperatures and are associated with poorer coastal productivity (Beamish et al. 1997). At present there is some evidence linking ENSO events with migration timing, although these relationships require further exploration. Thomson (2002) summarized oceanographic variables (e.g., physical and chemical water properties, upwelling indices, current patterns, climate indices) for the coastal straits, continental margin, and northeast Pacific. No definitive links were established through preliminary analysis of abnormal migration behavior and conditions in the Strait of Georgia and the Juan de Fuca Strait (Figure 1). Research continues to develop integrated models to predict migration timing and in-river survival and will benefit from recent efforts to obtain real-time data on environmental conditions in the Strait of Georgia.

At present, there is little evidence to suggest that earlier than normal migration in Fraser sockeye is related to inter-annual changes in Fraser River discharge or temperature (Thomson 2002; Lapointe 2002). However, these environmental features could affect migration success and mortality, as will be discussed below.

Parasites and Disease

The migratory behavior of parasitized fish may be altered as infected fish attempt to escape coastal zones of infection. Indeed in Ireland, sea lice (*Lepeophtheirus salmonis*) infestations were associated with premature river migrations of sea trout (*Salmo trutta;* Tully et al. 1993). Although there is no evidence that sea lice infestations are responsible for the early migration of Fraser River sockeye, *Parvicapsula minibicornis*, a myxozoan parasite of the kidney, may influence cues to migrate upriver. Parasite transmission occurs as the salmon migrate through the estuary and into the lower river (Jones et al. 2003). The parasite has been identified in most stocks of upriver migrating Fraser River sockeye (St-Hilaire et al. 2002) as well as in juveniles held in cages in the lower river near the estuary (S. Jones, unpublished data). The parasite causes lesions within kidney glomeruli, which increases the opportunity for en route mortality (Raverty et al. 2000).

It is possible that the traditional “holding” behavior displayed by late-run sockeye was a tactic for avoiding premature infection with this parasite. Warm water temperatures along the spawning routes for many late-run stocks may lead to rapid development of the parasite. Delaying migration until water temperatures cool in the fall may limit the lethality of the disease. Similarly, a change in the “zone of transmission” or in parasite development rates may contribute to early migration.

Contaminants

A risk assessment conducted by Johannessen and Ross (2002) indicated that there are clearly a number of toxicants that sockeye encounter during some phase of their lives that could affect their neural, olfactory, endocrine, osmoregulatory, immunocompetence, or development. Additionally, some toxicants could act to attract fish to the Fraser River or repel fish from the Strait of Georgia. The type of contaminant that could be responsible for change in migration timing would be one that acted as an attractant (or an endocrine disruptor if the endocrine system control the timing of migration) or repellent (driving fish upstream). The researchers identified several recent trends in contaminant use in British Columbia that provide possible support to the hypothesis that contaminants may play a role in abnormal migration timing. For example, the authors noted a 77% increase in use of wood preservatives in British Columbia during 1990s while pesticide sales in B.C. increased by 19% (ENKON 2001). In addition, there have been numerous new chemicals introduced, including flame retardants, plasticizers, and surfactants. Furthermore, the Fraser River is home to more than 2.5 million human residents, most of whom contribute to the treated sewage released into the waters. Additional inputs occur from pulp and paper mill effluents and nonpoint source pollution from agriculture. Unfortunately, the lack of time-series data on in-river contaminant concentrations, and the lack of knowledge on the response of fish to many of these contaminants, or their synergistic effects, means that it’s not possible to either support or refute a causal relationship between early migration and contaminants at this time. Interestingly, most of the studies involving endocrine disruption indicate effects on either gametogenesis or development, rather than behavior.

Threat of Marine Predation

Increases in abundance or changes of behavior in marine mammals, in particular killer whales (*Orcinus orca*) and harbour seals (*Phoca vitulina*), may affect the timing of salmon river entry. Sockeye may enter freshwater prematurely in an attempt to avoid marine predators. Adult salmon are thought to comprise only 4% of the annual diet of some marine mammals, but may be an important seasonal food resource (Olesiuk et al. 1990). Recent research by Keple (2002) determined that abundance of marine mammals in the Strait of Georgia was highest in the autumn and spring, not in the summer when sockeye are holding. There is evidence of both declines and increases in population size for different species of marine mammals in the Strait of Georgia (Keple 2002), but there have not been any obvious changes in the population sizes of these mammals that coincide with the early migration.

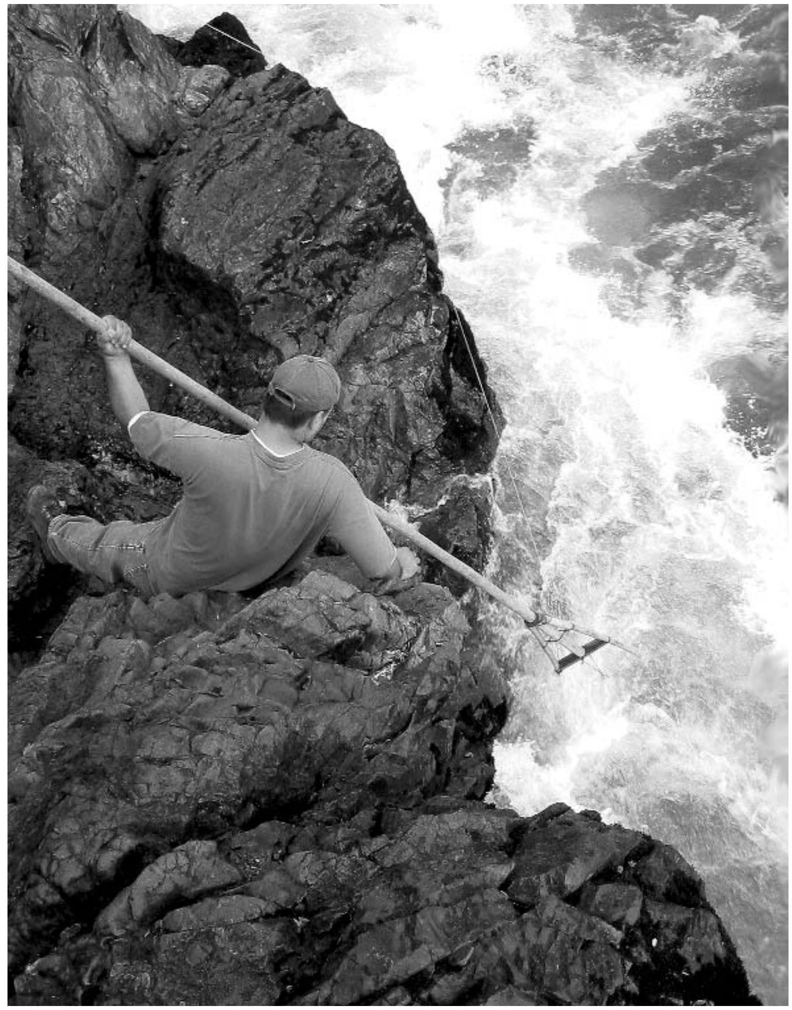
Mortality

Energy Status

Elevated temperatures accelerate energy depletion by increasing routine metabolism, but the largest energy drain is caused by fast water flows that elevate active metabolism. Physiological telemetry has shown that elevated flows force upriver migrating Fraser salmon to swim faster and for longer periods, accelerating energy use (Hinch and Rand 1998; Hinch et al. 2002; Standen et al. 2002). The prevalence of energetically costly swimming behaviors has been directly linked to migration mortality (Hinch et al. 1996; Hinch and Bratty 2000).

In the Fraser River, early summer migrations are the most difficult because river flow is high. Thus, late-run salmon tend to experience less extreme conditions than stocks that enter the river early. However, entering the river earlier than normal causes them to encounter flow conditions to which they may not be properly adapted. If fish initiate migration early and with reduced energy reserves (See Energetic Status—Migration Timing) and then encounter river conditions that are more energetically taxing than usual, it is possible that they could run out of energy prior to either reaching the spawning grounds or reproducing. Salmon do not feed after entering the river and must complete their upstream migration and spawning with the energy reserves brought from the ocean. Sockeye typically expend 50–70% of body energy in this process (Brett 1995) and seem to die when they reach a body energy density of about 4 MJ/kg (Crossin 2003). Furthermore, spawning success in sockeye is related to the extent of the energy reserves that are to be depleted on the spawning grounds (Healey et al. 2003).

Fraser sockeye begin their freshwater migrations with energy reserves that are proportional to the degree of difficulty (i.e., distance and elevation). The more difficult the migration, the greater the energy density (Crossin 2003). Furthermore, physiological telemetry (S. Hinch, unpublished data) and body energy analyses (Crossin 2003) have revealed that stocks with less difficult migrations are relatively inefficient in use of energy during migrations. The relationship between energy density upon arrival at the river mouth and difficulty of upriver migration has profound implications for the ultimate spawning success of the fish, and excessive energy depletion during migration or spawning may contribute to premature mortality (Rand and Hinch 1998; Hinch and Bratty 2000). Given these constraints, the observation that many stocks now have lower energy density on arrival at the river than in previous years (Crossin 2003) may influence migration timing and mortality.



JEFF YOUNG.

First Nations dip net fishery in the Thompson River.

Parasites and Disease

Parasitic and bacterial diseases cause stress, aberrant swimming behavior and premature mortality in migrating wild salmon (Gilhousen 1990). For example, the bacterium *Flavobacterium* that causes gill damage in migrating Fraser River sockeye is more virulent at high river temperatures and has been associated with pre-spawning mortality (Gilhousen 1990). Swimming performance of adult Atlantic salmon (*S. salar*) is reduced by sea lice infestations (Glenn Wagner, University of British Columbia, unpublished data). The pathology associated with severe *P. minibicornis* infections may interfere with the renal osmoregulatory function and increase the probability of pre-spawning mortality. However, any relationship between infection with *P. minibicornis* and migration initiation, swimming performance, and reproductive success is largely speculative. Earlier migrants may be physiologically weakened by infection, migration, and spawning, and the survivors that spawn may have been disadvantaged by the same migration challenges that killed the majority of fish.

Infections with *P. minibicornis* have not been detected before sockeye first enter the river (St-Hilaire et al. 2002; Jones et al. 2003). Transmission and development of the parasite coincide with migration of sockeye into the river. Parasitic infection is typically severe by the time salmon reach spawning grounds (Jones et al. 2003; S. Jones, unpublished data). The lack of knowledge regarding the life-history (i.e., alternate hosts) of *Parvicapsula* and the absence of historical infection data make it difficult to infer if and why this parasite has become so prevalent in recent years, and thus, its relationship to migratory behavior and/or high mortality. Manipulative and observational studies on the link between *Parvicapsula* and performance indicators such as swimming performance and survival would be particularly informative.

In-River Environmental Conditions

River flow and temperature impact both migration timing and success in adult salmonids (as discussed in Energetic Status). Increasing flows and decreasing temperatures stimulate up-river migrations in streams and small rivers, but this phenomenon is less evident in large rivers (reviewed in Quinn et al. 1997). In-river run strength models that incorporate environmental conditions including temperature and discharge are frequently used as predictive tools and decision support systems (Williams et al. 1996; Hinch and Rand 1998). Historical evidence suggests that Fraser River sockeye salmon experience passage problems in years with abnormally high discharge levels in the lower river and high water temperatures in the upper river (Macdonald 2000).

Since 1995, summer discharge or water temperatures have not consistently generated difficult migratory conditions so it is unlikely that environmental conditions, alone, are causal factors.

However, in 1997 and 1999, sockeye were impeded by high velocity regions in the Fraser Canyon. Mortality levels in the lower river were partially attributed to energetic exhaustion (Macdonald 2000). High discharge coinciding with high fish densities may create migration bottlenecks in regions of high flow. It is also possible that high densities could deplete localized oxygen concentrations and affect swimming performance and migration rate (MacDonald and Williams 1998). During periods of high discharge, suspended sediment concentrations in the Fraser River increases. Although high concentrations can be lethal (Newcombe and MacDonald 1991), moderate concentrations could harm fish by causing physical lesions and could disorient migrants (Macdonald 2000).

Contaminants

Johannessen and Ross (2002) identified several associations between the pattern of mortality and use of different contaminants while conducting a risk analysis on sockeye salmon in the Fraser River. Contaminants that could be harmful to fish include pesticides, wood preservatives, and persistent organic pollutants in addition to more recently developed contaminants that pose unknown risk. Collectively, although there has been increased application and/or use of some contaminants as discussed above, at present there is no direct evidence that any of these substances are causal agents or cofactors.

Summary and Prognosis

What is clear from this summary of possible causes is that the mechanisms responsible for these patterns may be complex, likely representing the interaction of numerous stressors (See Table 1). In this article we present a series of possible hypotheses that may be responsible for early migration, mortality, or both. Our collective subjective assessment of the relative likelihood of each of these hypotheses is presented in Table 1. However, as we know relatively little about migratory cues used by adult salmon, and even less about how the cues interact and how they control migratory behavior, the hypotheses that we present are subject to change and different interpretation.

The consequences of factors such as low energy, parasite infection, and dysfunctional osmoregulatory system on the reproductive fitness of salmon that survive to spawn are unknown. Intergeneration effects add another unknown dimension to the issue of early migration and mortality. For example, less energy allocation to egg development during difficult up-river migration could lead to smaller and/or fewer eggs. Smaller eggs could be at a survival disadvantage (van den Berghe and Gross 1989), whereas fewer eggs may reduce stock production. Because of these challenges, offspring of the few surviving early-entry spawners may be at a survival disadvantage. Recent work on egg size development during migration and cross-breeding trials (David Patterson, Fisheries and Oceans Canada, unpublished data) suggests that sockeye from normal-timed migrants exhibit 90% fertilization success. It is possible that the early arrival by late-run sockeye results in poorer mating success, egg fertilization rates, survival to larval eyed-stage, and larval swimming performance. Spawners with lower reserve energy and/or high parasite levels may exhibit impaired fitness.

The costs to the fishery of this abnormal behavior and ensuing premature mortality have been substantial. Not only have present day catches and future production of late-run stocks been reduced, catches of summer-run sockeye, which co-migrate with the late-run stocks, have also been restricted to minimize incidental by-catch of late-run stocks (Lapointe 2002). The Pacific Salmon Commission estimated that the direct cost in lost harvest was about 5 million fish in 2002 (conservatively $50 million CAD in lost revenues). When coupled with lost future production and reductions in the capture of other co-migrating stocks and species, the value in lost revenue is estimated at $72 million CAD. The greatly reduced harvest rates also have negative effects on other sectors including recreational angling, and those support industries that receive indirect economic benefits from harvest (e.g., gear manufacturers, fish packers, retail). Because overall mortality in 2002 was relatively low, there is large

Table 1. Relative likelihood of hypotheses outlined in this article relative to abnormal migration timing and mortality phenomena. We have identified where factors (and thus hypotheses) may be synergistic. Where a hypothesis is not appropriate, it is noted as not applicable (N.A.). Categorization as "unknown" is reserved for instances where there is insufficient information to assign a likelihood. Inclusion/exclusion or relative ranking of hypotheses are subject to change and reflect the current understanding by our research team.

Hypotheses	Hypothesis Code	Possible Synergistic Effects	Relative Likelihood of Hypotheses: Timing Related	Relative Likelihood of Hypotheses: Mortality Related
Energetics	A	E,F,G	More Likely	More Likely
Osmoregulation	B	D,E,G	More Likely	More Likely
Photoreception	C	B	Less Likely	N.A.
Reproductive Hormones and Sexual Maturation Alteration	D	B,H	More Likely	Less Likely
Oceanic Environment	E	A,B	More Likely	Less Likely
In-River Environment	F	A,G	Less Likely	More Likely
Parasites and Disease	G	A,B,F	More Likely	More Likely
Contaminants	H	D	Less Likely	Unknown
Marine Mammals	I	A	Less Likely	Less Likely

pressure on fisheries managers to allocate additional fish to harvest in 2003. Current policy decisions are based upon assessments of late-run abundance, in-river migration timing and associated en route mortality projections from an Environmental Management Adjustment Model. The results from 2002 highlighted the need for an in-season predictive tool to estimate mortality for real-time management decisions.

The Pacific Fisheries Resource Conservation Council (Anon 2001) warns that the exceptionally high mortality rates constitute a severe conservation risk that places the sustainability of some Fraser sockeye stocks and associated fisheries in doubt. Biological extirpation is also an imminent possibility for some stocks, impacting both fisheries and biodiversity. Indeed, Cultus Lake sockeye are now listed under Canada's new Species at Risk Act as "endangered." Currently, there is little basis for predicting long-term sustainability of Fraser River sockeye salmon stocks. A better understanding of immediate and intergenerational fitness consequences would provide valuable information for developing models to predict stock sizes for fisheries management purposes, and mitigation measures to prevent stock collapse.

The next several years will provide an opportunity to closely monitor the patterns of run timing and mortality, and to explore the relationships between these phenomena. Baseline studies that contrast normal and abnormal timing late-run individuals will facilitate testing of the hypotheses set forth in this article. The research group involved in this article is embarking on an interdisciplinary, multi-agency research program, funded largely through a Natural Sciences and Engineering Research Council of Canada Strategic Grant, to explore differences between abnormal and normal migrants and examine the intergenerational consequences of abnormal migration timing. Funding from the Pacific Salmon Commission and Canadian Department of Fisheries and Oceans is enabling complementary questions to be addressed, such as the large-scale telemetry and disc tagging program discussed earlier. As hypotheses are developed, intervention experiments can be used to study physiological variables of interest (e.g., with cortisol implants or antagonists, artificially supplementing or depleting energy stores, altering parasite loads) which will further define links between timing, mortality, and fitness. There is an urgent need to research this problem through strategic experimentation and continually monitor the physiological condition and performance of a set of representative stocks in different regions. That effort could help to identify management steps that could ultimately save millions of dollars in lost harvest opportunities while ensuring the perpetuation of the many diverse sockeye salmon populations.


STEVEN COOKE

Sockeye salmon captured by a commercial seine boat operating in Johnstone Strait.

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