Impact and Adaptation Responses of Okanagan River Sockeye Salmon (*Oncorhynchus nerka*) to Climate Variation and Change Effects During Freshwater Migration: Stock Restoration and Fisheries Management Implications

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ABSTRACT

We summarized existing knowledge on behavioural and physiological responses of Okanagan sockeye salmon (*O. nerka*) adults to annual and seasonal variations in aquatic thermal regimes during migration. This enabled us to identify an underlying set of ‘decision rules’ as a biophysical model of how temperature mediates en–route delays as a specific element of annual migrations by sockeye salmon. Several sets of results indicate that adult sockeye migrations stop as seasonal water temperatures increase and exceed 21°C and then restart when temperatures decrease and fall below 21°C. Model predictions of annual variations in the duration of migratory delay exhibited close agreement with independent estimates of observed delays available from a subset of years (predicted delay = 1.23 observed delay + 2.08, $r^2 = 0.92$, $p < 0.001$, $n = 10$). We applied the model in a retrospective analysis of the likely impacts of climate variation and change events on adult sockeye migrations in freshwater over the 70 plus year interval between 1924 and 1998. Results indicate that migration delays for a significant portion of the sockeye population averaged 29 days per year (range 0–55). Average annual migration delays roughly equal the 33 day estimate of time required, given continuous migration, to traverse the 986 km distance from the Columbia River mouth to terminal spawning grounds near Osoyoos Lake, BC. Alternating intervals of above–average and below–average migration delays corresponded closely with ‘warm–phase’ and then ‘cold–phase’ periods of the Pacific Interdecadal Oscillation. Circumstantial evidence suggests alternating periods of sub–average and above–average productivity for salmon on the southern end of their range are linked to climate variation and change events in both freshwater and marine environments. Climate impact and adaptation responses that register first at the level of salmon, propagate rapidly through both salmon resource users and fisheries managers. Consequently, future climate warming episodes will complicate the manageability and threaten the sustainability of many salmon populations in the southern end of their range (Georgia Basin and the Pacific Northwest). This requires strategies that minimize the impact of uncertain

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climate variability and change scenarios on the resilience of the salmon resource, and maximize our adaptive capacity for both short– and long–term fisheries planning and management decisions.

RÉSUMÉ

Nous avons résumé les connaissances actuelles au sujet des réactions comportementales et physiologiques du saumon sockeye adulte *(O. nerka)* dans l'Okanagan face aux variations annuelles et saisonnières dans les régimes thermiques aquatiques pendant la migration. Cela nous a permis de cerner et de déterminer un ensemble de règles de décision comme modèle biophysique de la façon dont la température modifie légèrement les délais de parcours en tant qu'élément spécifique des migrations annuelles du saumon sockeye. Plusieurs séries de résultats indiquent que les migrations du saumon sockeye adulte cessent lorsque les températures saisonnières de l'eau augmentent et dépassent 21 °C puis reprennent ensuite lorsque les températures baissent pour tomber sous la barre des 21 °C. Les prédictions de modèle des variations annuelles dans la durée des délais de migration ont révélé une concordance étroite avec les estimations indépendantes des délais observés disponibles pour un sous-ensemble d'années (délai prédit = 1,23 délai observé + 2,08, $r^2 = 0{,}92$, $p < 0{,}001$, $n = 10$). Nous avons appliqué le modèle dans une analyse rétrospective des incidences probables de la variation et du changement climatiques sur les migrations du saumon sockeye adulte en eau douce au cours de la période de plus de 70 ans entre 1924 et 1998. Les résultats indiquent que les délais de migration pour une importante partie de la population de saumon sockeye étaient d'en moyenne 29 jours par année (échelle de 0 à 55). Les délais de migration annuels moyens correspondent plus ou moins à l'estimation de 33 jours nécessaires, en supposant une migration continue, à la traversée des 986 km de distance depuis l'embouchure du fleuve Columbia jusqu'aux lieux de frai près du lac Osoyoos, en Colombie-Britannique. Les intervalles alternants des délais de migration au-dessus de la moyenne et en deçà de la moyenne correspondaient étroitement aux périodes de la phase chaude puis ensuite de l'ère de refroidissement de l'oscillation inter-décennale du Pacifique. Les preuves circonstancielles semblent indiquer que les périodes alternantes de productivité sous la moyenne et au-dessus de la moyenne pour le saumon dans l'extrémité sud de son aire de distribution géographique sont liées à la variation et au changement climatiques à la fois en eau douce et dans les milieux marins. Les mécanismes d'adaptation possibles à l'incidence du changement climatique, d'abord adaptés au niveau du saumon, s'étendent rapidement à la fois chez les utilisateurs de ressources en saumon et chez les gestionnaires des pêches. Les épisodes futurs de réchauffement climatique compliqueront donc la capacité à gérer la ressource et menaceront la durabilité de nombreuses populations de saumon dans la partie sud de leur aire de distribution géographique (bassin de Géorgie et nord-ouest du Pacifique). Cela appelle des stratégies qui permettront de réduire au minimum l'incidence des scénarios de variabilité et de changement climatiques incertains sur la résilience de la ressource en saumon et de maximiser notre faculté

d'adaptation pour la planification des pêches et les décisions en matière de gestion tant à court terme qu'à long terme.

INTRODUCTION

Okanagan sockeye salmon (*O. nerka*) are part of a species complex that occupies hundreds of freshwater lakes and rivers scattered throughout the eastern and western rims of the North Pacific Ocean (Groot and Margolis, 1991). Sockeye salmon populations support important subsistence and commercial fisheries in both fresh and marine waters throughout their geographic range (Foerster, 1968). However, Okanagan sockeye salmon, like many salmon populations located at the southern end of their range, exhibit a time–weighted trend of declining numbers over the past 50 years (Hyatt and Rankin, 1999; Nehlsen *et al.,* 1991; Slaney *et al.,* 1996). Most of the declines have been attributed to overexploitation and habitat degradation by rapidly growing human populations in the southern portions of the range of salmon (Lackey, 1999). Okanagan sockeye fit this pattern as they constitute the last persistent population of more than a dozen now extirpated salmon stocks that originated in Canadian portions of the Columbia River and its tributaries prior to its intensive development to meet hydroelectric power and irrigation needs (Slaney *et al.,* 1996). The depressed state of Columbia River salmon stocks and associated listings of multiple populations under the United States *Endangered Species Act* (ESA) has promoted a massive effort to 're–engineer' the management of habitat, water supplies and the role of fish production facilities to facilitate the long–term restoration of these stocks (National Research Council, 1996; McClure *et al.,* 2003). Similarly, in Canada, concerns on the part of the 'three party' Okanagan Basin Technical Working Group (COBTWG representing Fisheries and Oceans Canada, the Okanagan Nation Alliance, and BC Ministry of Water, Land and Air Protection) have resulted in stock restoration efforts to rebuild Okanagan sockeye salmon to historic levels of abundance capable of supporting First Nations food, ceremonial and societal fisheries entitlements.

More than seventy years after the initiation of Columbia River hydroelectric development (NRC, 1996) hundreds of studies have documented the complexities and difficulties and have resulted in only limited success of wild salmon population restoration. Many studies have identified the importance of changes to annual and seasonal variations in riverine temperature (Quinn and Adams, 1996; Quinn *et al.,* 1997; McCullough, 1999) and flow (Williams *et al.,* 1996) in controlling migration, spawning, incubation and rearing success of various life history stages of salmon under the highly regulated conditions now found in the Columbia River and its tributaries. Adding to this complexity are observations that climate conditions in both Canadian and U.S. portions of the Columbia Basin exhibit signs of directional change that support the notion that global climate warming is under way (Leith and Whitfield, 1998; Hamlet and Lettenmaier, 1999; Anonymous, 2002). Thus, future climate change effects are likely to become increasingly important determinants of the success of salmon population management and restoration in this region.

Brett (1971) considered temperature to be an "ecological master factor" for fish because so many elements of their behaviour and physiology are controlled by it. Okanagan sockeye salmon occupy the most southerly range for this species in North America (Foerster, 1968). Consequently, climate variability and change (CVC) effects pose a challenge for life history adaptation by Okanagan sockeye to both historic and future variations in seasonal thermal regimes of aquatic ecosystems in the Columbia and Okanagan basins. In this paper we begin a systematic exploration of potential linkages among CVC events, life history responses of Okanagan sockeye salmon, and management steps for their conservation and restoration. Although our intent is eventually to examine and model the impact of cumulative, CVC effects across several life history stages for this and other populations, our focus here is restricted to an assessment of temperature CVC effects on freshwater migration of adult sockeye in the Columbia and Okanagan Rivers.

METHODS

General Approach

The general approach taken here has been to: (1) summarize existing knowledge on behavioural responses of Okanagan sockeye to variations in aquatic thermal regimes during migration; (2) identify an underlying set of 'decision rules' as a biophysical model of how temperature mediates a given life history outcome; (3) utilize the 'model' to assess either historic or future responses of sockeye to temperature CVC effects; and (4) consider the implications of our analysis for future conservation and restoration activities focused on Okanagan sockeye salmon.

Data Sources

Sockeye Migration

There is a rich literature documenting the general patterns of migration by sockeye salmon in both freshwater and marine environments (Groot and Margolis, 1991). Of particular relevance here, several major studies have been completed on annual associations among temperature, flow and migratory behaviour of adult sockeye salmon negotiating passage at several dams and through intervening stretches of water on the Columbia and Okanagan Rivers (Major and Mighell, 1967; Quinn and Adams, 1996; Quinn *et al.,* 1997; Alexander *et al.,* 1998). Therefore, our first step was to review these studies as a source of information regarding the general pattern of seasonal migration exhibited by Okanagan sockeye. Next, we identified sets of observations that served as a basis for specifying the 'decision rules' that adult sockeye employ concerning where, when and under what conditions to either delay or resume migration. We utilized both published and unpublished data sets on annual and seasonal passage of adult sockeye at Wells Dam on the Columbia River as well as at Zosel Dam located immediately downstream of Osoyoos Lake on the Okanagan River (Figure 1) as all sockeye observed at these locations are of Okanagan origin. Enumeration methods at these locations usually involved direct visual counts of individual salmon passing through fishways or gates at each facility.

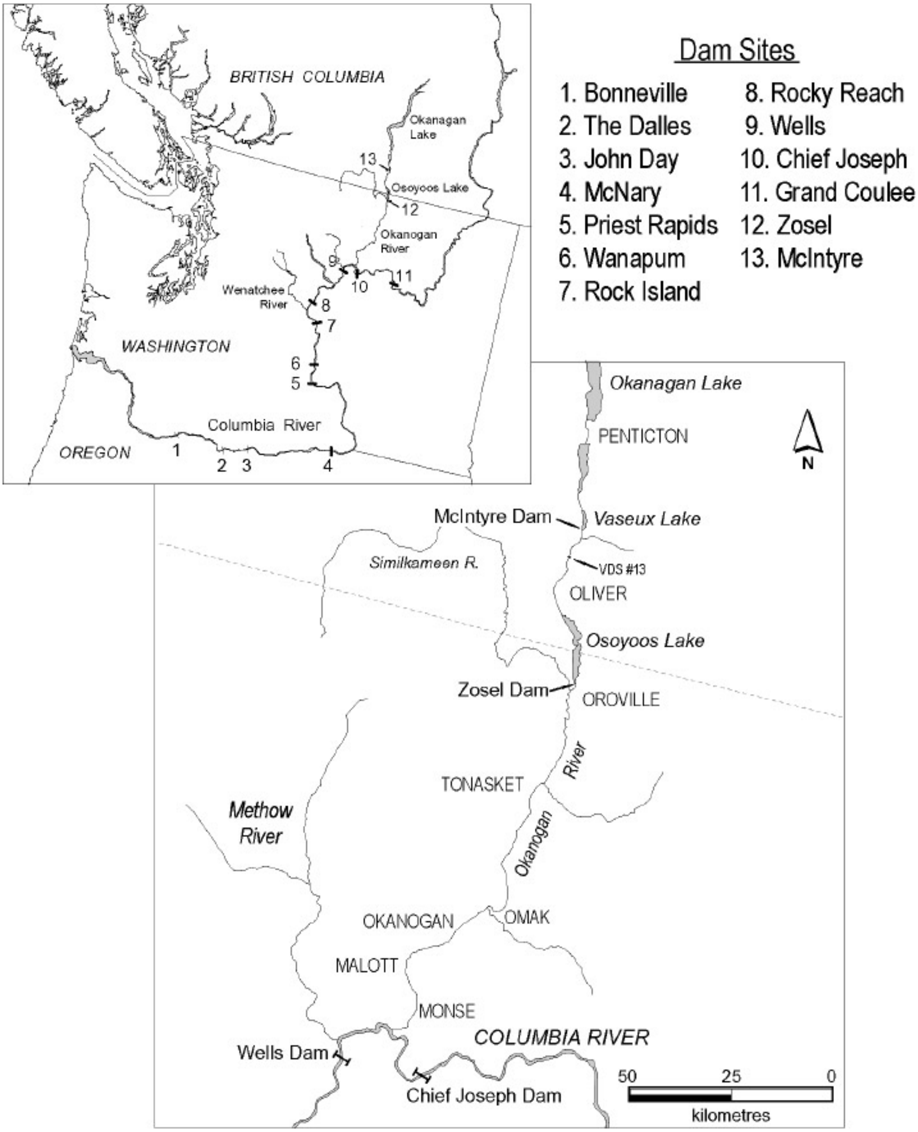


Figure 1. General Location of the Canada–U.S. Study Area, Dams and Other Sites Along the Migration Route of Okanagan Sockeye.

Unpublished observations of sockeye passage at Wells Dam were provided by personnel at Douglas County Public Utility Division No. 1 in Wenatchee, Washington (Rick Klinge, pers. comm.). Data regarding sockeye passage at Zosel Dam were extracted as follows: migration years 1937, 1944, 1952, 1953, 1954, 1962 and 1963 (Major and Mighell, 1967), migration year 1992 (Hatch *et al.*, 1992), migration year 1993 (Sullivan and Dawson, 1994), and migration year 1997 (Alexander *et al.*, 1998). As a third step, we assembled supplementary observations from migrations of radiotagged adult sockeye (Alexander *et al.*, 1998) and from annual spawning ground surveys in the Okanagan River (Hyatt and Rankin, 1999) to verify the repeatability of the inferred decision rules for migration under carefully monitored field conditions during the summer and fall of 1997 and 2000, respectively. General methods for annual spawning ground surveys are described in Hyatt and Rankin (1999). Spawner abundance observations by date, river segment and year are summarized in Stockwell and Hyatt (2003). However, relevant methodological details associated with observations of adult migratory behaviour in the upper Okanagan River in 1997 and 2000 will be reported along with specific results below.

Water Temperature

The U.S. Army Corps of Engineers annual fish passage reports provide a long–term (1938–present) source of data on daily temperature and flow conditions experienced by Okanagan sockeye as they migrate from near the mouth of the Columbia River (Bonneville Dam) to Wells Pool located at the confluence of the Okanagan River and immediately upstream of Wells Dam (Figure 1) on the Columbia River (Quinn *et al.*, 1997). By contrast, Stockwell *et al.* (2001) were unable to identify any source of long–term, continuous records (greater than five years) of daily water temperature for any locations along the Okanagan River in either the U.S. or Canada. Hyatt and Stockwell (2003) investigated the feasibility of employing long–term, air temperature records and regression analysis of air–to–water temperature associations to reconstruct historic seasonal thermal regimes for selected aquatic sites in the Okanagan Basin. They concluded that simple air–to–water relationships were sufficient to explain most of the seasonal variations in water temperature at selected sites. Accordingly, in the current paper, both direct and 'reconstructed' observations of mean daily water temperature at specific sites in the Columbia and Okanagan Rivers, respectively have been used to gauge responses of Okanagan sockeye adults to seasonal or annual variations in water temperature associated with site–specific, migration and spawning activities.

RESULTS

General Pattern of Sockeye Migration

Detailed studies or reviews by Major and Mighell (1967), Fryer (1995), Quinn and Adams (1996), Quinn *et al.* (1997) and Alexander *et al.* (1998) have provided results from which to infer the general seasonal pattern of migration by Okanagan sockeye adults from the mouth of the Columbia River near Astoria, Washington to their spawning area in the Okanagan River near the town of Oliver in British Columbia's southern interior (Figure 1). The following general account is based largely on results from these authors who are not cited further except where details of specific results recommend it.

Maturing sockeye salmon arrive at river km (rkm) 234 at Bonneville Dam by early summer (primarily June and July) on the way to distant spawning areas in tributaries to either Wenatchee (rkm 842) or Osoyoos (rkm 986) lakes (Figure 1). Elapsed travel times between Bonneville (rkm 234) and McNary Dam (rkm 470) average approximately seven days (range 5–11 days) and between McNary and Rock Island Dam (rkm 725) 8.5 days (range 6–13 days). Wenatchee system adult sockeye leave the Columbia River to enter the Wenatchee River after clearing Rock Island Dam but Okanagan sockeye salmon continue migration on average for another 5–7 days during which they pass through Rocky Reach Dam, then Wells Dam to enter Wells Pool located at the confluence of the Columbia and Okanagan Rivers. Completion of the final leg of the journey from Wells Pool to Zosel Dam and Osoyoos Lake takes an additional 5–7 days on average. Thus, the elapsed time for Okanagan sockeye to travel from the mouth of the Columbia River (rkm 0) to Osoyoos Lake is approximately 33 days of 'active migration' during which they maintain an average velocity of 30 km/day.

Studies involving observations of sockeye migration over intervals of only a few years (Major and Mighell, 1967) or alternately over several decades (Quinn *et al.*, 1997) have highlighted the influence of temperature and/or water flow variations on sockeye migrations through the Columbia and Okanagan Rivers. These environmental indicators exhibit large seasonal to annual fluctuations and although both will reflect future CVC events and affect salmon populations, the focus here is principally the influence of temperature on migration events for Okanagan sockeye.

Annual and Seasonal Effects of Temperature on Sockeye Migration

Detailed analysis by Quinn *et al.* (1997) related the median date of arrival (i.e. time to 50%) of all adult sockeye for a given year at specific dams on the Columbia River (Bonneville, McNary and Rock Island) and Snake River (Ice Harbor) to temperature and flow variations over several decades. These authors found adult sockeye travel rates increased and time to 50% passage at dams decreased significantly ($p < 0.05$ in all cases) as river temperatures increased and flows decreased over several decades. Thus, recent–year (1994), times to 50% passage of sockeye adults at McNary and Rock Island Dams were 11–14 days earlier than in 1954 or 1933, respectively. However, strong correlation between diminished flow and increased river temperatures, associated with hydroelectric development and river regulation, made it impossible to separate the effects of temperature versus flow on sockeye salmon travel rates and passage dates.

Sockeye adults migrating through the Columbia and Snake River mainstem were generally exposed to temperatures that exceeded their assumed 15°C optimum for physiological and swimming performance (Brett, 1995; Lee *et al.,* 2003). However, temperature observations at several dams indicate that sockeye never encountered lethal temperatures (>24°C, Servizi and Jensen, 1977). Quinn *et al.* (1997) noted a bimodal frequency distribution of sockeye passage at Ice Harbor Dam in some years as evidence of migration delay there. Inspection of yearly temperature curves suggested adult sockeye migration at this dam usually ceased at temperatures >21°C. These observations are consistent with those obtained from an earlier tagging program (Major and Mighell, 1967) that documented travel rates of Okanagan sockeye salmon adults between Rock Island Dam on the mid–Columbia River and Zosel Dam on the Okanagan River near Osoyoos Lake (Figure 1). Major and Mighell (1967) noted that annual sockeye salmon migrations between Rock Island and Zosel Dams are marked by movements from the larger cooler Columbia River to the smaller warmer Okanagan River. Evidence presented by these authors indicated that annual variations in this temperature difference are sufficient to produce long delays of adult sockeye entry from Wells Pool into the Okanagan River in some years but not others.

Tagging data indicated that July travel times between Rock Island and Zosel Dams ranged between 6–12 days (mean 8.3) in the years 1953, 1954 and 1963 but spanned 12–26 days (mean 18.8) during 1962. The key difference between the former and the latter years appeared to be the occurrence of Okanagan River temperatures >20–21°C in 1962 that served to delay entry by adult sockeye into the Okanagan from the Columbia River. Moreover, comparisons of seasonal arrival timing distributions of sockeye at mid–Columbia River (Rock Island) versus Okanagan River (Zosel) dams indicated that highs and lows in counts at Zosel Dam often followed falling and rising river temperatures in the Okanagan River but not in the Columbia. Again, the key difference for several years of observation appeared to be the occurrence of seasonal temperature increases that regularly exceeded 21°C in the Okanagan River but that remained below 18.5°C in the Columbia River. Accordingly, Major and Mighell suggested a threshold of 21°C below which migratory progress is not affected, but above which rising or stable temperatures inhibit migration. Migrations delayed in this way resume coincident with or immediately after sharp declines in Okanagan River temperature (details in Major and Mighell, 1967).

Recent Evidence of Temperature Effects on Migrations of Okanagan Sockeye Salmon

Three data sets generated in 1992, 1993 and 1997 permit comparison of the distributions of sockeye passage at Wells Dam on the Columbia mainstem versus Zosel Dam on the Okanagan River more than 30 years after the study executed by Major and Mighell (1967) (Figure 2). As noted above, once initiated, migration of Okanagan sockeye on the Columbia River mainstem tends to be continuous (e.g. at

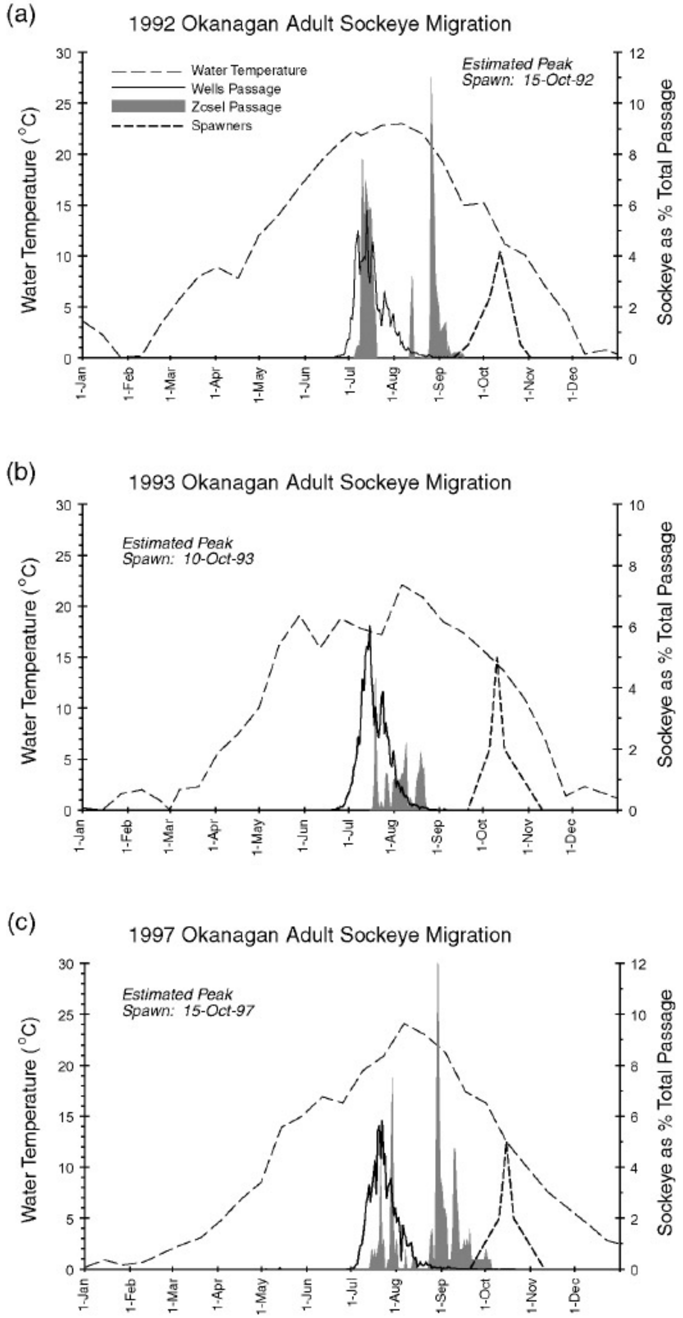


Figure 2. Seasonal Patterns of Migration by Okanagan Sockeye Salmon Adults at Wells Dam (Columbia River), Zosel Dam (Okanogan River), and to the Spawning Area near Oliver, BC. Water Temperatures at McIntyre Dam are Interpolated from All–Year 10–Day Mean Air–to–Water Temperature Relation (Hyatt and Stockwell, 2003). Peak Spawning Dates are from Data Summarized in Stockwell and Hyatt (2003).

Wells Dam, Figure 2a–c). Continuous migrations of sockeye adults past Wells Dam are associated with mainstem river temperatures that consistently remain <20°C. In addition, distributions of Okanagan sockeye passage at Wells Dam are relatively unimodal by comparison with the polymodal distributions exhibited by sockeye adults passing Zosel Dam. Although the first peaks in passage at Zosel follow shortly after the first peaks observed at Wells Dam, significant intervals of virtually zero migration, followed by one to several secondary peaks of fish, are evident in all three years of results from Zosel Dam. These patterns are especially clear in 1992 and 1997 (Figures 2a and c) and are consistent with earlier suggestions that adult sockeye migrations into the Okanagan River are blocked as water temperatures are >21°C, and migrations restart, following an interval of delay, when temperatures decrease <21°C. Results from 1997 suggest that migration delays rather than losses due to mortality determined timing distributions as all observations in that year were derived from hundreds of adult sockeye carrying individual radio–tags that were actively tracked from release points in the Columbia mainstem to their final destination in either Osoyoos Lake or spawning areas in the Okanagan River (Alexander *et al.*, 1998).

Sockeye Migration Pattern at McIntyre Dam

McIntyre Dam, immediately below Vaseux Lake (Figure 1), marks the generally accepted upstream limit of adult sockeye migration because it is impassable at most water levels. During the summer of 2000, field crews involved in extensive habitat assessment work, were able to conduct index counts of adult sockeye holding immediately downstream of McIntyre Dam on a daily basis. The procedure consisted of enumerating all adult sockeye at the downstream face of McIntyre Dam that were visible from a vantage point on a catwalk near the face of the dam. Daily observations involved constant effort and were carried out at approximately the same time each day when water temperatures were recorded at the dam face. Because of the relatively small numbers of fish involved on a given day, total counts for each successive week of observation are presented here (Figure 3a).

Few adult sockeye were observed at McIntyre Dam prior to July 9. During the following two weeks, sockeye numbers at the dam increased dramatically while maximum daily water temperatures remained <20°C. Numbers of adult sockeye holding at the face of McIntyre Dam decreased precipitously the week of July 23 as mean water temperatures were >21°C (Figure 3a). From August 6–19, mean daily water temperatures were >23°C at McIntyre Dam during which time no adult sockeye were observed holding there. However, adult sockeye reappeared at the face of McIntyre Dam the week of August 20 just as weekly mean water temperatures declined <21.3°C. Numbers of adult sockeye holding at the face of the dam then declined slowly to zero over the next several weeks in association with increasing spawning activities at downriver sites (Figure 3b). Thus, a threshold of 21°C appears to be associated with not only delays of entry by adult sockeye from the cooler Columbia to the warmer Okanagan River but also with 'decisions' by adult sockeye to vacate an upriver site (McIntyre Dam) in favour of dropping back into the cooler waters available in Osoyoos Lake less than 25 km downstream of the dam.

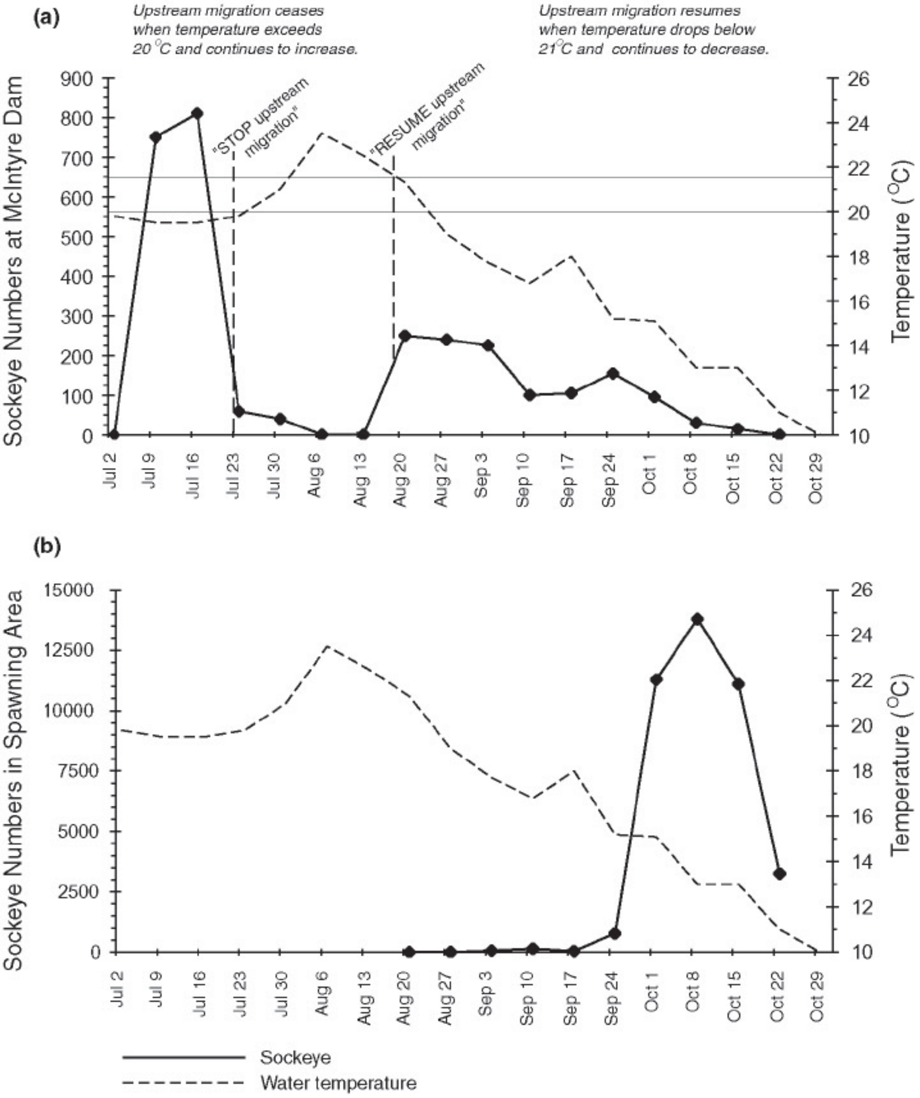


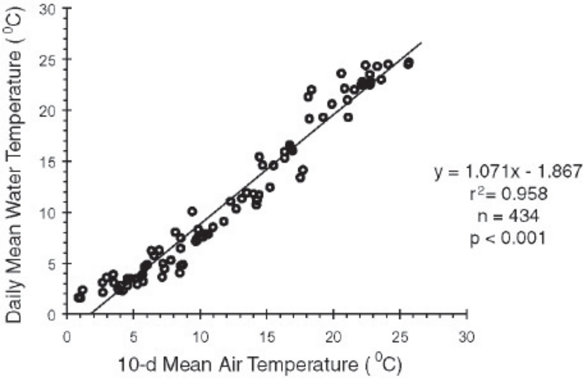
Figure 3. (a) Weekly Numbers of Adult Sockeye and Maximum Water Temperatures Observed at McIntyre Dam in 2000. (b) Weekly Numbers of Adult Sockeye in the Main Spawning Area (Stockwell and Hyatt, 2003) and Maximum Water Temperatures Observed at McIntyre Dam in 2000.

Retrospective Analysis of Annual Migration Delays

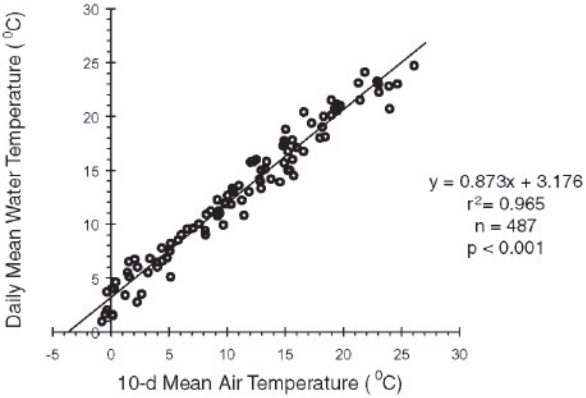
Results presented above suggest that adult sockeye follow repeatable ‘decision rules’ that govern whether they will delay or even reverse upstream migrations in the face of seasonal changes of water temperature. Consequently, it should be possible to assess the frequency and the duration of seasonal and annual migration delays displayed by adult sockeye entering the Okanagan River from the Columbia River given time series observations of daily temperature for the Okanagan River. Because the latter have not been routinely recorded, we employed regression relationships for air–to–water temperature, developed by Hyatt and Stockwell (2003), to reconstruct water temperature at several sites in the Okanagan River. These authors found that, in general, mean daily–temperature reconstructions were possible based on season and site–specific regression functions (Figure 4a–c) that represented: a spring–summer, rising–limb function starting the week that the 10–day–mean air temperature was >4°C and ending the week that the 10–day–mean air temperature is at a maximum (Figure 4a); a summer–fall, descending–limb function starting the week that the 10–day–mean air temperature is at a maximum and ending the week that the10–day–mean air temperature reaches −4°C (Figure 4b); and a relatively ‘flat–limb’ function for ‘winter’ initiated when the 10–day–mean air temperature is <−4°C and ending when it is >4°C the following spring (Figure 4c).

Temperatures associated with adult sockeye migration delays for entry into the Okanagan River have been more commonly available from upriver sites (Oroville, Zosel Dam) near Osoyoos Lake on the Okanagan River rather than sites such as Monse or Malott (Figure 1) near the confluence of the Okanagan and Columbia Rivers. Comparisons of water temperatures between upriver and downriver sites suggest that water temperatures at McIntyre Dam are indistinguishable from those observed at Malott while temperatures at Zosel Dam are biased high relative to Malott over most of the range of interest 10–21°C (Figures 5a and b). Further, temperatures recorded at McIntyre Dam do not track temperatures at Malott very closely >21°C. Reductions of covariance of temperatures between upper and lower river sites >21°C appear to be driven by increasing volumes of cold, meltwater flowing from the Similkameen River into the lower Okanagan below Oroville (Hyatt and Stockwell, 2003). These cooler flows serve to moderate mid–summer temperature increases at lower river sites such as Malott but not at upriver sites that receive most of their flow from the epilimnial spill of large headwater lakes. Accordingly, site–specific observations used to interpret adult sockeye migratory responses to temperature variations must be chosen carefully. We chose the spring air–to–water relationship (Figure 4a) for reconstruction of water temperatures at McIntyre Dam because the latter location is more representative of temperatures that adult sockeye will encounter at the Okanagan and Columbia confluence near Malott. However, it should be noted that when adult sockeye encounter 20–21°C temperatures at Malott, it is certain that they will encounter either the same or even higher temperatures at upriver locations on their return to Osoyoos Lake (Figure 5a). Daily temperature reconstructions were completed for all years at McIntyre Dam between 1924 and 1998.

(a) Spring



(b) Fall



(c) Winter

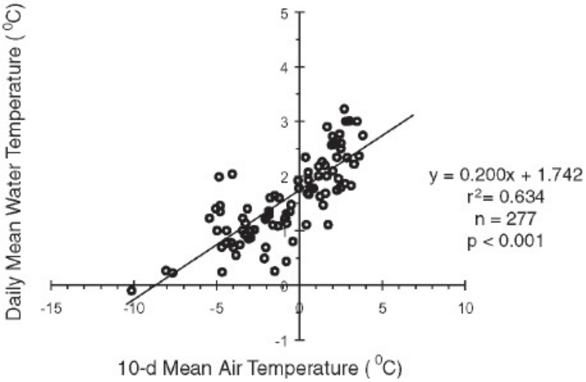


Figure 4. Relationship Between the 10–Day–Mean of Air Temperature at Oliver and Daily Mean, Water Temperatures Recorded at McIntyre Dam for (a) Spring, (b) Fall and (c) Winter Intervals. Data Sources are Fully Documented in Stockwell *et al.* (2001). For Clarity, Every 5th Point has been Plotted for Spring and Fall; Every 3rd Point for Winter.

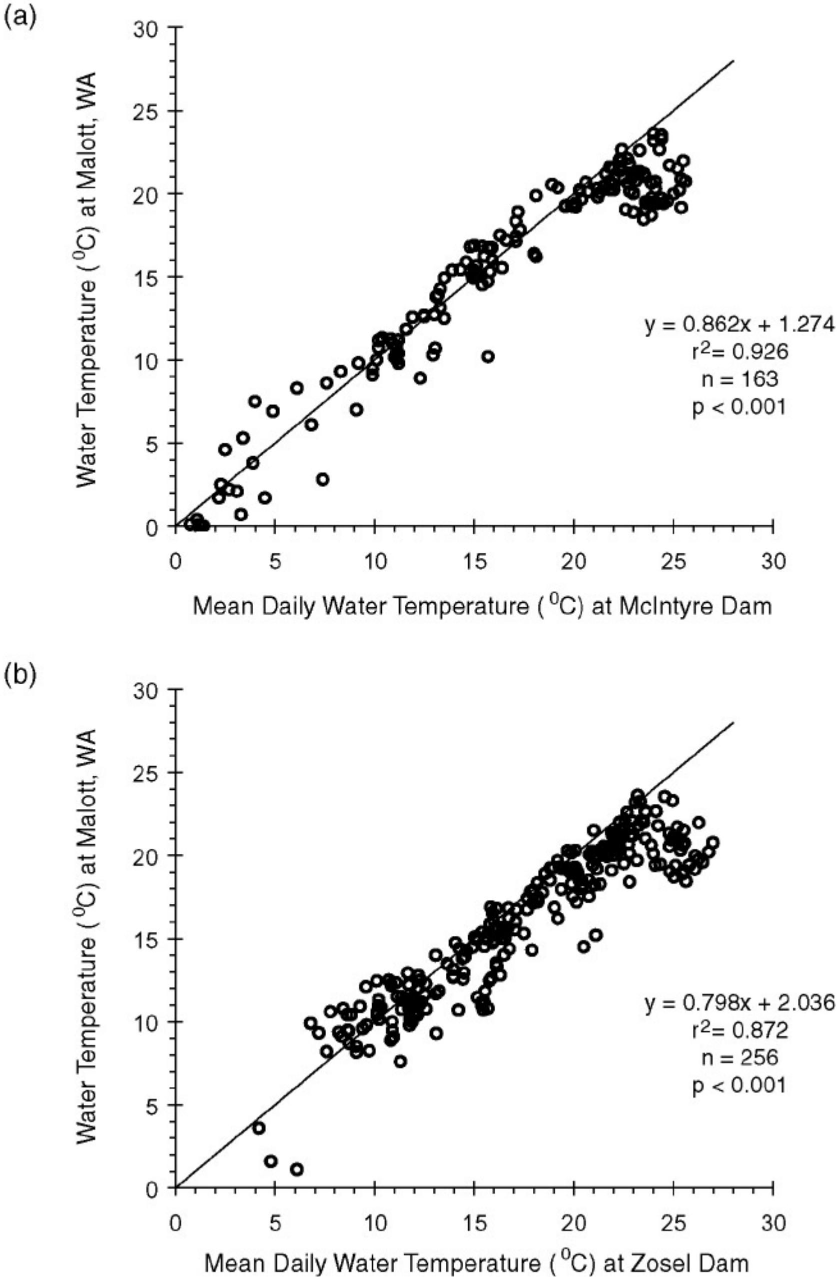


Figure 5. Relationship Between Daily Mean, Water Temperatures for the Okanagan River Mainstem at (a) McIntyre Dam, BC Versus a Location Approximately 120 km Downstream at Malott, WA, and (b) at Zosel Dam Versus Malott, WA. The 1:1 Lines are Shown on Figure Panels While the Equations Describe the Lines of Best Fit to the Data.

Multiyear observations of the timing of sockeye passage at either Wells or Rocky Reach Dams suggested that sockeye are generally available to enter the Okanagan River no later than the first week of July (Figure 2). Similarly, because the all–year average date of peak spawning in the Okanagan River is October 17 (Hyatt and Stockwell, unpublished data) we assumed sockeye could continue migration to at least the middle of October of a given year. We determined the likely magnitude of annual delays of sockeye entry into the Okanagan River (i.e. 'predicted' days of little or no migration) for the entire period of record (1924–1998) by inspection of each year's seasonal temperature regime in concert with the application of the 'stop' and 'restart' migration rules, identified above (sockeye migrations stop when water temperatures are >21°C and restart when temperatures are <21°C). Ten years of seasonal enumerations at Zosel Dam (1937, 1944, 1952, 1953, 1954, 1962, 1963, 1992, 1993, 1997) also allowed us to estimate the actual magnitude of annual delays of sockeye entry into the Okanagan River by determining the number of days during the main migration period (July–October) when Okanagan River temperatures were >21°C and there was little to no migration activity there. During the main migration interval, days of little to no passage were defined as those accounting for passage <1% of the annual total.

Model predictions of annual variations in the duration of migratory delays for adult sockeye exhibit a highly significant level of agreement ($r^2 = 0.92$, $p < 0.001$) with independent estimates of observed delays during the main migration interval (Figure 6). Although there is some indication that the model overestimates the magnitude of annual migration delay by approximately 25%, we conclude that the model is sufficiently reliable to generate a useable index of the relative magnitude of annual migration delays experienced by sockeye over the multi–decadal period of record. Results from the latter analysis, adjusted to eliminate the high bias in delay predictions, indicate that delay of entry into the Okanagan River likely occurs for an average of 29 days per year (range 0–55 days) over the period of record (1924–1998) for some portion of the adult sockeye run (Figure 7). Thus, the average migration delay that Okanagan sockeye experience is approximately equal to the average total time (approximately 33 days at an average travel rate of 30 km per day) taken to travel from the mouth of the Columbia River to Osoyoos Lake under conditions of no delay (e.g. especially cool years such as 1948, 1954, 1957 and 1976). Our results suggest delays >50 days may occur in especially warm years (e.g. 1924, 1938, 1967 and 1998). Further, the magnitude of delays appears to have been steadily increasing from the early 1970s to present.

Decadal Climate Cycles and Okanagan Sockeye Salmon Migration

Given the close dependence of our index of Okanagan sockeye migration delay on seasonal and annual changes in regional temperature, it should not be surprising that the all–year records of migration delay exhibit 'cyclic' patterns. Thus, average delays are much longer for Okanagan sockeye during the 1924–1946 and 1977–1998 'warm' intervals (average delays of 38 and 30 days, respectively) than during the relatively 'cool' interval of 1947–1976 (average delay of 21 days, Figure 7). Ebbesmeyer and

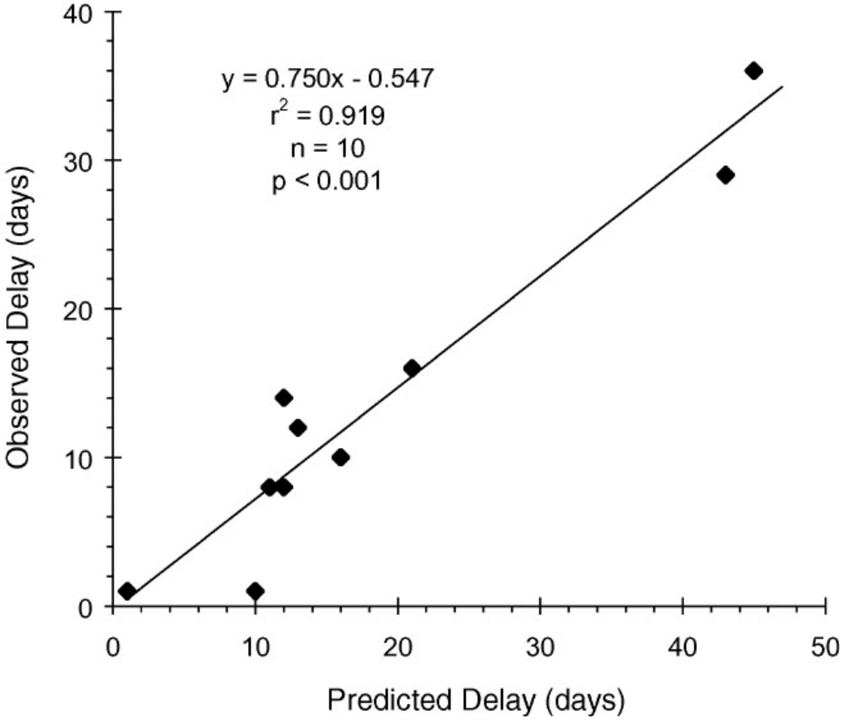


Figure 6. A Comparison of Predicted Versus Observed Migration Delays Exhibited by Adult Sockeye (see text for details). A Single Day has been Added to All Predicted and Observed Values to Offset Zero Values from the Plot Axes. Note, we have treated observed delays as the independent variable here in order to apply this relationship to adjust annual predictions of delay to 'observed' equivalents summarized in Figure 7.

Strickland (1995) and Mantua *et al.* (1997) have noted that the Pacific Northwest Climate Index (PNI) and the Pacific Interdecadal Oscillation (PDO) indices, both identify 1925, 1947 and 1977 as the starting points for three major climate regime shifts that have occurred in this region over the last hundred years. Our results provide persuasive evidence that CVC events associated with these regime shifts are likely to have a profound influence on Okanagan sockeye migration events over decades of time.

DISCUSSION

Climate impact and adaptation responses register first at the level of a given biological resource (e.g. Okanagan sockeye salmon), after which they propagate through the users and the managers of the resource. Effects at all three levels are considered here first for Okanagan sockeye salmon and then for their relevance to salmon 'fisheries' in the Georgia Basin and Puget Sound area.

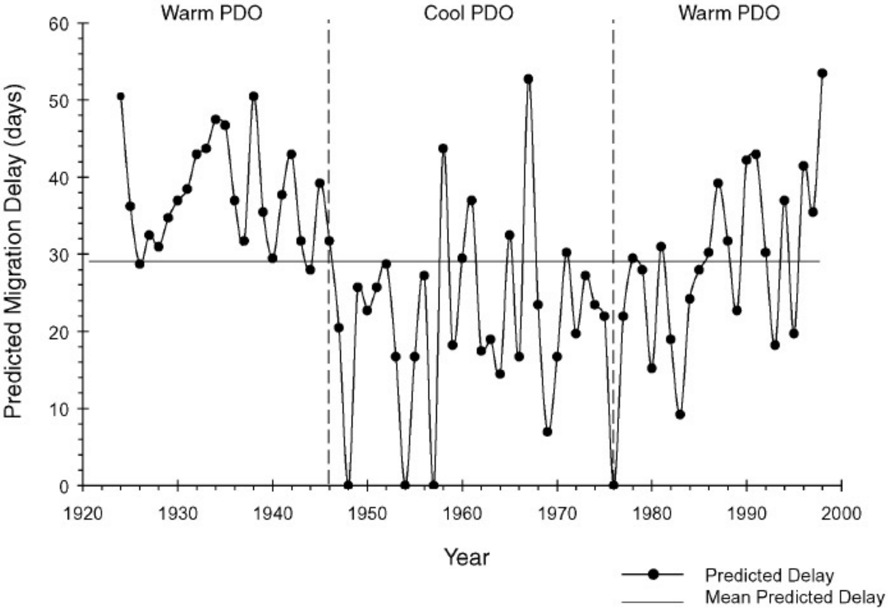


Figure 7. Predicted Migration Delays for Adult Sockeye Based on Application of Migration 'Rules' Relative to Reconstructed Temperatures at McIntyre Dam for the Interval 1924–1998. Predicted Delays have been Adjusted to 'Observed Delay Equivalents' as per the Relationship in Figure 6. Multidecadal Migration Delays are Above Average during the 1924–1946 Warm–Phase of the PDO (Mean Delay = 38 days), Generally Below Average During the 1947–1976 Cold Phase of the PDO (Mean Delay = 21 days) and Then Above Average for the Latter Portion of the 1977–1998 Warm–Phase PDO (Mean Delay = 30 days).

Impact and Adaptation Responses of Sockeye Salmon

Results on salmon migration patterns presented above suggest that freshwater migrations of Okanagan sockeye adults are influenced significantly by CVC events that occur on both local and regional scales. Thus, average travel rates for adult sockeye have increased and the average time of arrival in upriver locations has advanced to earlier in the summer in association with several decades of hydroelectric development and flow regulation in the Columbia River (Quinn and Adams, 1996; Quinn *et al.*, 1997). However, contrary to the suggestion of Quinn *et al.* (1997), earlier dates of arrival to upriver locations in the Columbia have not necessarily meant earlier dates of arrival for adult sockeye at their final destinations in either Osoyoos Lake or the upper Okanagan River. Average arrival dates in the latter locations will be influenced by a higher frequency of prolonged migratory delays at the mouth of the Okanagan River during warm–phase (1925–1946, 1977–1998) relative to cool–phase (1948–1976) PDO–PNI intervals such that average annual arrival dates will be later in warm PDO–PNI intervals. Similarly, arrival dates will be later than average for any year in which summer temperatures in the Okanagan River are above average regardless of the PDO–PNI phase they fall within.

Although the consequences of prolonged migration delays for Okanagan sockeye are not well known, various studies suggest that delays associated with temperatures >17°C may be accompanied by increased susceptibility to disease, impaired maturation processes, increases to stress parameters, reduced swimming performance, reduced efficiency of energy use during migration or spawning and reduced viability of gametes (references in review by MacDonald *et al.,* 2000). Moreover, exposure to temperatures >20–21°C for more than a few days may trigger complex physiological and biochemical changes associated with poor spawning success, poor egg quality and senescent death prior to spawning as observed for some populations of Somass River (K. Hyatt, unpublished data) and Fraser River sockeye (MacDonald *et al.,* 2000) during high temperature and low discharge years in 1992 and 1998. In this context, 'decisions' taken by adult sockeye to delay migration when confronted by high seasonal temperatures at the mouth of the Okanagan River would appear to be an adaptation that reduces the biological consequences of clearly adverse environmental conditions. However, the level of success that this confers is still open to debate because adult sockeye numbers in terminal spawning areas routinely account for only 45–65% of the numbers observed passing through Wells Dam each year (Alexander *et al.,* 1998; Hyatt *et al.,* unpublished data). Thus, migration delays and the associated stress of exposure to temperature extremes have commonly been considered by salmon managers to inflict poorly quantified but significant levels of prespawn mortality on Okanagan sockeye salmon (Rosenberger, Fisheries and Oceans Canada, pers. comm.).

A bewildering array of subtle interactions among anthropogenic and natural causal factors is involved in determining abundance variations of Columbia River salmon (NRC, 1996), including Okanagan sockeye salmon. However, evidence for some involvement of CVC events and climate cycles that favour 'boom' and 'bust' periods of productivity has been building (Anderson, 2000). The latter author linked variations in biophysical conditions in both freshwater and marine environments to alternating periods of above and then below average productivity of Columbia River salmon during 'cold–phase' and then 'warm–phase' PDO–PNI intervals, respectively. Impact and adaptation responses of Okanagan sockeye to stressful thermal regimes during migration provide at least circumstantial evidence for specific mechanisms operating on adult sockeye to support such an outcome. Thus, although the cumulative impacts of dams, water regulation, over fishing, irrigation and intensive land use have undoubtedly driven salmon stock declines, salmon responses to cyclic CVC events likely also play an important role. Indeed, some authors have concluded that strong interactions between cyclic natural and cumulative anthropogenic variations combine to induce a pattern of 'ratchet–like' declines in salmon stocks. Thus a given stock will exhibit increases and decreases with the periodicity of the natural cycles but over a number of cycles will exhibit a time–weighted trend to decline (Lawson, 1993). These observations are consistent with long–term patterns of abundance observed for both ESA listed Redfish Lake (Gustafson *et al.,* 1997) and unlisted Okanagan sockeye salmon (Hyatt and Rankin, 1999).

Impact and Adaptation Responses of Resource Users

The complex of factors accounting for declines of Columbia River salmon, including Okanagan sockeye (Fryer, 1995), extend far beyond consideration of just impact and adaptation responses of salmon to aquatic thermal regimes during migration (NRC, 1996). However, even limited consideration of the latter events suggests the likelihood of important interactions between CVC events, the salmon resource and its availability to various fisheries. Although commercial exploitation of Columbia River sockeye is sporadic due to the generally depressed state of the stocks (Gustafson *et al.,* 1997), fisheries by tribal groups on both sides of the Canada–U.S. border still anticipate some annual harvest of Okanagan sockeye to meet a combination of subsistence and cultural needs even during intervals of low returns (Chapman *et al.,* 1995). Elders of the Okanagan Nation Alliance (ONA) have noted the virtual disappearance of 'early run' (i.e. mid–July) sockeye in recent decades from traditional fishing sites (e.g. vicinity of McIntyre Dam) in Canadian portions of the Okanagan River (Byron Louis–ONA, pers. comm.). The conventional wisdom is that the absence of early–run sockeye is attributable to the extirpation of an early returning sub–population of sockeye. However, our results suggest that the 'loss' of early–run sockeye may also be accounted for by recent decades of climate–induced increases of migratory delays of fish at the confluence of the Columbia and Okanagan Rivers along with selection of alternate holding sites (e.g. Osoyoos Lake rather than the Okanagan River in warm water years) that further reduces the availability of early–return fish to aboriginal fishermen. By contrast, harvest opportunities for the traditional aboriginal fishery located at the confluence of the Columbia and Okanagan Rivers should have experienced increases in the relative availability of sockeye salmon over the past two decades. Future adaptation to these circumstances by fishermen could involve either informal (tribe–to–tribe) or formal negotiations (through the Canada–U.S. Pacific Salmon Treaty) to share catches between tribal groups utilizing upper versus lower river fishing sites in Canada and the U.S. Alternately, the Okanagan Nation Alliance fishery could adopt new fishing methods (e.g. netting in Osoyoos Lake) to accommodate climate–induced changes in adult salmon behaviour. Observations suggest that elements of both of these responses are occurring.

Impact and Adaptation Responses of Resource Managers

Both short– and long–term changes in the status of salmon stocks have important impacts on fisheries resource managers and provoke a variety of adaptive responses. Thus, although they constitute only part of a large information–system puzzle that is assembled each year, context–dependent changes in seasonal and annual migratory timing patterns of salmon populations often provide useful information about either the likely strength of returns in a given year (Steer and Hyatt, 1987) or of the vulnerability of a given return to environmental stress and pre–spawn losses (MacDonald *et al.,* 2000). Consequently, larger–than–expected returns of salmon at lower Columbia River dams during early summer in 2000 and 2001 supported decisions by managers in both the U.S. and Canada to permit higher levels of harvest than suggested during pre–season planning. By contrast, extreme migratory delays induced by exposure of salmon adults to adverse environmental conditions have prompted actions by managers to reduce harvest levels in a given year or to plan for harvest reductions for a future return to be derived from adults in the affected year.

Over the past century, time–weighted averages for order of magnitude declines in the annual production of many Columbia River salmon stocks have provoked high levels of conflict among fisheries managers, water resource managers and resource users regarding the appropriateness of particular salmon harvest, water management or salmon restoration strategies (NRC, 1996). Okanagan sockeye salmon are no exception, as variations in their numbers over the past 50 years, are reminiscent of the pattern of 'ratchet–like' declines observed for other Columbia River salmon stocks (Lawson, 1993; Lichatowich and Mobrand, 1995; Gustafson *et al.,* 1997). Moreover, there is a perennial dialogue among water and fisheries resource managers about the maintenance of appropriate fish flow requirements through regulated water releases from a series of low–head flood control and irrigation dams on the Okanagan River (Hyatt, 2001). Possible relationships among sockeye production losses, CVC cycles and temperature–induced migratory delays warrant additional attention from fisheries managers given: (1) the chronically depressed state of Okanagan sockeye; (2) their obvious vulnerability to future climate warming effects; (3) requirements for mandatory recovery plans associated with *Canadian Species at Risk Act* legislation if Okanagan sockeye continue to decline; and (4) the recognition that there are severe constraints on readily–executable adaptation options such as reducing exploitation levels (i.e. they are generally low already) or engineering cold water releases to cool the entire Okanagan River in the face of such change.

Relevance to Salmon Fisheries of Georgia Basin and Puget Sound

Thousands of populations of several species of salmon complete their life histories by returning to freshwater rivers, lakes and streams distributed around the rim of the Georgia Basin and Puget Sound (Slaney *et al.,* 1996). There is a wealth of anecdotal information that seasonal–to–annual extremes of water flow (droughts and floods) and high temperatures influence the migratory success of many of these populations in an analogous fashion to that described above for Okanagan sockeye salmon. Chinook (*O. tshawytscha*), coho (*O. kisutch*), and steelhead (*O. gairdneri*) salmon stocks returning to rivers along the east side of Vancouver Island have encountered chronic difficulties with low flow and high temperature constraints during adult migration as well as at other life history stages in recent decades (Rosenau and Angelo, 2003). Moreover, increasing demands by expanding urban populations for limited water supplies during the summer to fall low–flow period have already exacerbated salmon and water management problems in multiple locations throughout Georgia Basin. Of particular note here, record low flow and temperature extremes during 1998 produced migration delays and multiple instances of pre–spawning mortality events among sockeye and chinook salmon populations across a broad geographic area including: interior BC (Okanagan River – this paper; Fraser River – MacDonald *et al.,* 2000); the Georgia Basin (Cowichan and Nanaimo Rivers – Ted Carter, Fisheries and Oceans Canada, pers. comm.), and the west coast of Vancouver Island, (Somass River – K. Hyatt, unpublished data). Climate–induced disruptions to customary harvest and resource management patterns occurred in several of the commercial, recreational or subsistence fisheries for these salmon stocks during 1998. Consequently, it is not difficult to imagine that future 'climate–warming' episodes of similar or greater frequency and/or magnitude than those identified here (Figure 7, 1924–1947 and 1978–1998 intervals) will complicate the manageability and threaten the sustainability of many salmon populations in the southern portions of their range. This will be particularly true in the Georgia Basin and Puget Sound area where rapid human population development has led to the creation of a complex spatial mosaic of natural resources (water, land, timber, fish) and 'built environment' assets (dams, power generating plants, fishways, hatcheries, fishing fleets, irrigation works) that are managed to meet a variety of conflicting societal objectives.

CONCLUSIONS

Natural resource managers engage in ongoing efforts to shape and respond to anthropogenic and natural processes acting on natural and 'built environment' assets both individually and collectively to generate a wide range of sustainable benefits (social, cultural, economic, environmental) for society. The weight of evidence assembled by the Intergovernmental Panel on Climate Change (IPCC) suggests that climate in the 21st Century and beyond will be substantially warmer, and significantly different from those experienced in the past millennium (IPCC, 2001). In this paper, we have clarified some important links between CVC events, environment and salmon migrations. However, this falls far short of precisely quantifying the ultimate effects that historic or future climate change effects may have on fishery productivity. Indeed, so many climate and life history links are possible that it is difficult at this stage to predict the cumulative net effect of particular sets of CVC events on salmon productivity with great certainty (see also MacDonald *et al.,* 2000). Combining the latter point with the observation that the climate record from the 20th Century may not provide a good guide for climate of the near or distant future, uncertainty about production trajectories for Pacific salmon is likely to remain large during the remainder of the 21st Century. Accordingly, we agree with Mantua and Francis (2003) that the systematic integration of CVC effects into sustainable fisheries management policies and practices will require steps to: (1) de–emphasize the role of pre–season run size predictions in management activities; (2) emphasize pre–season and in–season monitoring of both the resource and key environmental conditions that influence it (e.g. temperature, flow etc.); and (3) focus on the identification of strategies that minimize the impact of uncertain climate variability and change scenarios on the resilience of the salmon resource and that maximize our adaptive capacity for both short– and long–term fisheries planning and management decisions.

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