

The cumulative impacts of climate change on Fraser River sockeye salmon (*Oncorhynchus nerka*) and implications for management

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Abstract: Anadromous Pacific salmon (*Oncorhynchus* spp.) are vulnerable to climate change in both freshwater and marine habitats. I use a qualitative model to assess the cumulative effects of climate change across life stages and generations of Fraser River sockeye salmon (*Oncorhynchus nerka*) and other salmon species. The effects of climate change most relevant to Fraser River sockeye include warming of freshwater and marine habitats, altered hydrology in spawning rivers, reduced productivity in nursery habitats, and changed distribution and phenology of predator and prey species. The weight of evidence indicates that these changes will negatively affect growth and survival of Fraser River sockeye at all life stages. Effects on one life stage will also carry forward to heighten adverse effects at subsequent life stages and across generations so that the cumulative impact is greater than the impact on individual stages. Salmon can adapt to climate change but probably not enough to sustain productivity. In the south, focus of policy and management on conserving and enhancing resilience is needed to retain some salmon production. At the same time, Arctic habitats are becoming accessible to salmon. Management in the Arctic should protect potentially productive habitats from development and facilitate their colonization by Pacific salmon.

Résumé : Les saumons du Pacifique (*Oncorhynchus* spp.) sont vulnérables aux changements climatiques, à la fois en milieu d'eau douce et en milieu marin. Un modèle quantitatif permet d'évaluer les effets cumulatifs des changements climatiques durant les stades du cycle biologique et au cours des générations chez le saumon rouge (*Oncorhynchus nerka*) du fleuve Fraser et chez d'autres espèces de saumons. Les effets des changements climatiques les plus pertinents pour les saumons rouges du Fraser incluent le réchauffement des habitats d'eau douce et de mer, une modification de l'hydrologie des rivières de fraie, une réduction de la production dans les habitats de nurserie et un changement dans la répartition et la phenologie des espèces de proies et de prédateurs. Les données actuelles indiquent que ces changements vont affecter négativement la croissance et la survie du saumon rouge du Fraser à tous les stades de son cycle biologique. Les effets sur un stade du cycle vont se répercuter sur les stades subséquents et sur les générations suivantes en augmentant les effets négatifs, si bien que l'impact cumulatif sera plus important que l'impact sur les stades individuels. Les saumons peuvent s'adapter aux changements climatiques, mais probablement pas assez pour maintenir la productivité. Dans le sud, les politiques et la gestion devront cibler la conservation et l'augmentation de la résilience afin de sauvegarder une partie de la production de saumons. Au même moment, les habitats arctiques vont s'ouvrir au saumon. La gestion dans l'arctique devrait protéger les habitats productifs potentiels du développement et faciliter leur colonisation par les saumons du Pacifique.

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Introduction

The species of Pacific salmon (*Oncorhynchus* spp.) are economically, culturally, and ecologically important throughout their North Pacific range (Healey 1993; Johnsen 2001; Naiman et al. 2002). Because of this, the effects of climate change on Pacific salmon are of major concern to resource managers (Mote et al. 2003; Mantua and Francis 2004; Schindler et al. 2008). The freshwater and marine habitats of salmon are expected to warm by 2–5 °C or more over the next century, perhaps earlier (Henderson et al. 1992; Ficke et al. 2007; Mackas et al. 2007). This degree of warming will have uncertain but potentially devastating effects on salmon and their ecosystems (Beaugrand and Reid 2003; Beamish 2008; Barange and Perry 2009). In addition, precipitation

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patterns, storm frequency and severity, distribution and phenology of food organisms and predators, and many other factors affecting salmon are expected to change with uncertain but potentially serious consequences for the species (Richardson 2008; Bryant 2009; Schwing et al. 2010).

The Fraser River in British Columbia is the most important salmon-producing river in Canada and one of the most important in North America (Northcote and Larkin 1989). Salmon have spawned in the Fraser River for thousands of years, and their annual spawning run has provided an abundant harvest for aboriginal and, more recently, commercial fishers (Johnsen 2001). Sockeye salmon (*Oncorhynchus nerka*) is the most valuable species in the Fraser River, and the sockeye harvest is shared with fishers from the USA under the terms of the Pacific salmon treaty (Roos 1991). Aboriginal communities along the Fraser River also depend on the sockeye runs to provide salmon for food and ceremonial purposes. Because of their commercial and cultural importance, sockeye salmon in the Fraser River are among the best studied of Pacific salmon. The wealth of information on this species allows me to make relatively informed judgments about the likely effects of climate change. Fraser River sockeye are thus a useful model species for understanding the effects of climate change.

Over the past century, Fraser River sockeye runs have ranged from highs of 20–30 million to lows of a few million fish (Roos 1991). Returns during the 1980s and 1990s were particularly strong owing to favourable ocean conditions (Beamish et al. 1997). In the past decade, however, some of the major sockeye runs to the Fraser River have shown anomalous timing and unusual mortality (Cooke et al. 2004). In the past few years, ocean returns have collapsed, prompting a judicial inquiry (Prime Minister's Office 2009). Paradoxically, the 2010 sockeye return to the Fraser River is one of the largest on record (CBC news: www.cbc.ca/news/canada/british-columbia/story/2010/08/25/bc-sockeye-salmon-fraser-river.html, accessed 17 March 2011). The causes of these events are unknown, but the multifaceted and cumulative effects of climate change offer one explanation (Hinch and Gardner 2009; Hague et al. 2010). An examination of the effects of climate change is timely, therefore, in terms of the ongoing management of salmon fisheries.

Various authors have examined the potential effects of global warming on parts of the salmon life cycle (Henderson et al. 1992; Hinch et al. 1995a; Rand et al. 2006), as well as on overall production rates (Klyashtorin 1998; Levin 2003; Beamish 2008). Crozier et al. (2008) examined the potential for phenotypic and genetic responses to climate warming among different life history stages of Chinook salmon (*Oncorhynchus tshawytscha*). To date, however, no one has explored the way changes at one life stage propagate through the life cycle to affect other stages or accumulate across generations. Here I develop such a qualitative model, emphasizing the cumulative effects of climate change on successive stages in the life cycle of Fraser River sockeye salmon. Although I develop the model in detail for sockeye salmon, it is easily adapted to other salmon species and, potentially, to other marine and freshwater fishes. I also explore the implications of the model for future salmon production and management. The paper is organized into four sections: the

effects of climate change on the habitats of different life stages; biological responses by each life stage to habitat change; synthesis of cumulative effects; and potential for mitigation. I summarize life stage responses to climate change and potential for mitigation in Table 1. Although any forecast of the effects of climate change has high uncertainty, the prognosis for salmon in the southern part of their range is not good. However, there are some positive notes for salmon productivity in the northern half of their range, at least for a number of decades, and new habitats are emerging in the Arctic that may provide future opportunity if they receive the right kind of management.

Climate warming and sockeye habitats

Pacific salmon are anadromous, spawning and spending a portion of their juvenile life in fresh water but migrating to sea to complete the majority of their growth before maturity. In the Fraser River, female sockeye deposit their eggs in the late summer and autumn in gravel spawning beds distributed throughout the basin, the eggs incubate over the winter in the spawning nest, and the fry emerge in spring and typically migrate to a nearby nursery lake. After 1 or sometimes 2 years feeding and growing in the lake, fry transform to smolts in spring and migrate to sea (Burgner 1991). In a few (mainly very small) populations, fry do not migrate to a nursery lake but reside for a few months in their natal stream or nearby river delta and migrate to sea in late summer. The Harrison River population of sockeye in the Fraser River shows this behaviour pattern (Gustafson and Winans 1999). When they reach the ocean, juveniles migrate north and west in continental shelf waters until autumn, then move offshore into the Gulf of Alaska. They mature after 2 or more years at sea and return to the Fraser River to spawn (Foerster 1968; Burgner 1991). Over their life cycle, therefore, Fraser River sockeye (and other anadromous salmon species) integrate the effects of climate change across a number of freshwater and marine habitats; climate effects on one stage can carry forward to influence effects at another stage. The consequences of changes in habitat for one generation can also carry forward to influence success in subsequent generations. For the purposes of this paper, I assess climate effects on eight stages in the life of sockeye: (1) egg and alevin; (2) fry: emergence to lake entry; (3) fry: lake entry to first winter; (4) fry: first winter; (5) smolting and seaward migration; (6) postsmolts: estuary and coastal; (7) immatures in the ocean; (8) returning adults. I chose these stages to illustrate the impact of different sets of climate change factors across the life of salmon.

Global climate change is expected to result in higher average temperatures and altered precipitation and storm patterns (Mote et al. 2003; Beamish 2008; Barange and Perry 2009). Absorption of CO₂ by the ocean is also reducing the pH of oceanic waters (Fabry et al. 2008). The degree of future change in these variables is uncertain, but under a "Business As Usual" scenario over the next century, air temperatures in the Fraser basin will increase between 2 and 5 °C. Increases will be greater in winter than in summer and greater further north and at higher elevations (Melack et al. 1997; McDaniels et al. 2010). Sea surface temperature (SST) in the Gulf of Alaska will increase by 2–4 °C, and the increase will be greater near the coast than offshore (Mackas et al. 2007). In

Table 1. Effects of global warming and the potential for mitigation–adaptation (in terms of the biological response of the fish, direct management action, or modification of policy) among life cycle stages of sockeye salmon.

High temperature, changing weather effects	Mitigation–adaptation possibilities
Stage 1. Egg and alevin	
<ol style="list-style-type: none"> 1. Increased maintenance metabolism → smaller fry. 2. Lower disease resistance → lower survival. 3. Changed thermal regime during incubation → lower survival. 4. Faster embryonic development → earlier hatching–emergence. 5. More intense fall storms → redd scour and egg loss. 	<p><i>Biological:</i> Developmental program is probably labile and fairly rapid selection for successful development under altered regime is possible, up to a point.</p> <p><i>Management:</i> Cool water release from reservoirs upstream of spawners could ameliorate climate effects and (or) reduce scour. Protect spawning areas with cool groundwater discharge.</p> <p><i>Policy:</i> Reserve flow of spawning rivers for fish to minimize thermal changes.</p>
Stage 2. Fry: emergence to lake entry	
<ol style="list-style-type: none"> 1. Faster yolk utilization → early emergence. 2. Smaller fry → lower survival rates. 3. Early emergence → mismatch with spring bloom. 4. Higher maintenance metabolism → greater food demand – slower growth – higher predation risk while foraging. 5. Smaller weaker fry → potential problems emerging. 	<p><i>Biological:</i> Development program may adjust through selection so that emergence timing remains linked to zooplankton blooms.</p> <p><i>Management:</i> Cool water release from reservoirs upstream of inlet spawners could ameliorate climate effects.</p> <p><i>Policy:</i> Reserve flow of spawning rivers for fish to minimize thermal changes.</p>
Stage 3. Fry: lake entry to first winter	
<ol style="list-style-type: none"> 1. Warmer lake waters → higher maintenance metabolism → greater food demand – slower growth – higher predation risk while foraging. 2. Changing plankton phenology → disruption of lake food web – changed plankton community → poorer growth of fry. 3. Mismatch of lake entry to spring bloom → lower survival rate. 4. Earlier and stronger stratification → shallower thermocline → longer and stronger nutrient deficit in epilimnion during summer → lower plankton production → reduced food supply in midsummer → slower fry growth. 	<p><i>Biological:</i> Fry may adjust vertical migration behaviour to take maximum advantage of energy saving in cool hypolimnion while foraging in epilimnion. Probable trade-off with predation risk because of the need to forage more in a warmer lake environment.</p> <p><i>Management:</i> Fertilization of epilimnion during summer may mitigate effects of midsummer nutrient deficit. In smaller lakes, pneumatic mixing may help slow thermocline development. Enhanced harvest of predatory game fish may reduce predation pressure.</p> <p><i>Policy:</i> Policies regarding predator management and bag limits for trout and other large fish may be revised to help keep predator populations low.</p>
Stage 4. Fry: first winter	
<ol style="list-style-type: none"> 1. Smaller size at start of winter → lower winter survival. 2. Warmer winter → higher metabolic demands → lower winter survival. 3. Warmer winter → increased predator activity – hunger → lower winter survival. 	<p><i>Biological:</i> Winter has some of the greatest conflicting possibilities and unknowns. Situation will probably differ depending on lake type.</p> <p><i>Management:</i> Take steps above to improve summer growth so fry enter winter at larger size. Take steps above to keep predator populations low.</p> <p><i>Policy:</i> As above.</p>

Table 1 (continued).

High temperature, changing weather effects	Mitigation–adaptation possibilities
Stage 5. Smolting and seaward migration	
<ol style="list-style-type: none">1. Smaller fry enter winter → smaller potential smolts → lower survival of smolts.2. Smaller fry at end of first summer → delay of smolting 1 year → fewer smolts.3. Earlier smolting → reduced marine survival.4. Smaller smolts → poorer marine survival.	<p><i>Biological:</i> Timing of smolt migration is labile; population would probably adjust migration time fairly quickly.</p> <p><i>Management:</i> Measures to ensure good fry growth above would also carry forward to winter survival and smolt size.</p> <p><i>Policy:</i> If winter survival is mainly a matter of energy reserves, then there is probably not a policy response. If winter survival is predator driven, then policies affecting predator control apply here as well.</p>
Stage 6. Postsmolts: estuary and coastal	
<ol style="list-style-type: none">1. Smolt migration timing → timing mismatch with estuarine – nearshore productivity → lower growth–survival.2. Altered coastal predator populations → greater mortality.3. Altered prey populations → poorer growth → reduced survival during critical first summer.4. Higher coastal water temperatures → greater maintenance metabolism → greater food demand → slower growth – lower survival.5. Advection of acidified ocean waters onto continental shelf → impairment of shell-building plankton → poorer feeding for salmon.6. Poorer growth in coastal waters → delayed transition to larger prey → poorer oceanic growth → smaller adult size.	<p><i>Biological:</i> Time of ocean entry, coastal migration tactics, predator avoidance tactics are labile behaviours, and in time fish might adapt somewhat, but it is doubtful that coastal habitats will be as productive for juvenile salmon under global warming.</p> <p><i>Management:</i> Ensure minimum anthropogenic stressors during ocean entry phase (low tolerance for pollution, maintenance of physical habitats).</p> <p><i>Policy:</i> “Salmon first” policy for estuarine and other critical nearshore habitats.</p>
Stage 7. Immatures in the ocean	
<ol style="list-style-type: none">1. Warmer surface temperatures → higher maintenance metabolism → higher food demand – slower growth.2. Warmer temperatures → reduced suitable thermal habitat → greater competition for food → reduced growth.3. Acidification of surface layer → lower plankton production → poor feeding conditions for salmon → reduced growth.4. Changed structure and seasonality of forage organisms → changed foraging conditions → slower growth – higher predation risk.	<p><i>Biological:</i> Possible greater use of cool, deep water to offset higher metabolic rates in warmer surface waters and greater movement into the Bering Sea. However, these adaptations will also impose costs.</p> <p><i>Management:</i> Ensure remaining high seas habitats are protected from fishing. Facilitate invasion of Arctic waters by salmon (by transplants or management of freshwater nurseries).</p> <p><i>Policy:</i> Develop anticipatory policy to protect suitable salmon habitats in the Arctic and to facilitate the natural colonization that has already begun.</p>

Table 1 (concluded).

High temperature, changing weather effects	Mitigation–adaptation possibilities
Stage 8. Returning adults	
<ol style="list-style-type: none"> 1. Reduced quality of marine nursery habitats → fewer and smaller adults with lower energy reserves returning to Fraser River → increased risk of en route and prespawning mortality. 2. Higher river temperature during upstream migration → greater energy cost – lower scope for activity during migration → higher risk of en route and prespawning mortality. 3. Higher temperatures during migration and spawning → greater risk of disease outbreak → greater risk of prespawning mortality. 4. Smaller adults → fewer smaller eggs → shorter development times, smaller fry, mistimed emergence. 5. Delayed maturation in ocean → lower marine survival → fewer adults returning. 	<p><i>Biological:</i> Adaptive adjustments to ocean migration and maturation schedules are possible to improve potential for successful migration. Adaptive adjustments of optimal and critical temperatures for activity are also possible.</p> <p><i>Management:</i> In the short term, rates of return, growth, etc. will be highly uncertain. Managers will need to reduce interception fisheries to ensure sufficient salmon reach spawning grounds. Commercial fisheries will need to be greatly reduced in capacity and perhaps eliminated altogether at some point.</p> <p><i>Policy:</i> Reemphasize policy hierarchy of allocating salmon for spawning escapement first, then for aboriginal food and ceremonial purposes, before any commercial harvest. Make identification and protection of habitats that may still support salmon under global warming a policy priority.</p>
Intergenerational effects	
<p>Cumulative effects across life history stages and generations suggests the possibility of a downward spiral of size and productivity.</p>	<p><i>Biological:</i> A multifaceted and uncertain set of adaptive responses is to be expected. Short-term adjustments will be within existing reaction norms. Longer term adjustments will involve genetic change. Overall capacity of the species to adjust is uncertain and will change as global warming proceeds.</p> <p><i>Management:</i> Protect the species' opportunity to adjust and encourage it to invade new suitable habitats as they come available.</p> <p><i>Policy:</i> Have a policy focus on maintaining and expanding the species' natural resilience.</p>

Note: See appropriate text section on life history stages for more detail and references. Symbol “→” means “leads to”. Note how effects at one stage affect performance at subsequent stages.

the Bering Sea, temperature may increase 3–7 °C (Mackas et al. 2007). There will be less precipitation as snow in the Fraser basin and more as rain. Coastal precipitation will increase but interior precipitation may decrease. Winter storm intensity will increase. Ocean surface waters will become less saline, stratification will intensify, and the thermocline may shoal. pH values low enough to affect calcification in marine organisms will rise into the surface layer in the North Pacific (Feely et al. 2008). The detailed effects of global change on freshwater and marine habitats of salmon remain very uncertain. However, current literature suggests the following.

Spawning streams during migration, spawning, and incubation

The majority of sockeye populations spawn in river systems that have a hydrograph dominated by snowmelt (a freshet in spring or early summer but with stable or declining

flows during the late summer and winter spawning and incubation period; Mote et al. 2003). As climate warming proceeds, spring freshet will become earlier, smaller, and of shorter duration because of warmer temperatures and the decrease in seasonal snow pack (Morrison et al. 2002; Stewart et al. 2004). The rivers that sockeye use to access their spawning streams (e.g., Fraser, Thompson, Nechako) will be warmer and have lower discharge. Morrison et al. (2002) predict that by the end of the century, peak discharge in the Fraser River will decrease 18%, the peak will occur 26 days earlier (although in some years it may occur later because of heavy summer and fall rains), and the likelihood of migrating adult sockeye encountering temperatures greater than 20 °C will increase by a factor of ten. Spawning streams themselves will be warmer and discharge may be lower during the normal late summer – autumn spawning time and through the incubation period as permanent snow and glaciers disappear (Hauer et al. 1997; Melack et al. 1997). Not only will spawn-

ing streams be warmer on average but the schedule of temperature change during the incubation period may also change. Precipitation as rain rather than snow during late autumn and early winter may cause freshets large enough to scour spawning gravels (Melack et al. 1997; Stewart et al. 2004). Many spawning streams are ice-covered during winter months, and this ice cover will gradually disappear as winter temperatures increase. Coastal spawning streams will be warmer and may be subject to stronger winter freshets and greater scouring of spawning gravels as winter storms intensify (Melack et al. 1997). Temperatures in summer will be higher and base flows lower, particularly in smaller streams, which may cause stress for stream resident species like coho (*Oncorhynchus kisutch*) and Chinook but will be less important for sockeye (Mote et al. 2003; Ficke et al. 2007).

Nursery lakes

Sockeye nursery lakes in the interior of British Columbia are typically ice-covered or partially ice-covered during the winter. As global warming proceeds, these lakes will lose ice cover earlier in the year (or may not be ice-covered at all), will stratify thermally earlier and remain stratified longer, and will have higher summer epilimnion temperatures (Ficke et al. 2007). In interior lakes, nutrient depletion in surface waters will be more intense and last longer because of the strengthened and extended period of stratification (Henderson et al. 1992). Coastal nursery lakes will also stratify longer and have higher summer temperatures, but increased summer precipitation near the coast may moderate temperature increases somewhat and deliver nutrients to lake surface waters (Hauer et al. 1997; Melack et al. 1997).

Coastal marine habitats

Coastal waters of British Columbia will be warmer. In fact, coastal SST has increased about 1 °C over the past century (Roemmich and McGowan 1995; Mackas et al. 2007; Schwing et al. 2010). River discharge, which drives estuarine circulation, will be lower during spring freshet but higher during winter (and somewhat higher overall). The subarctic current system will move north so that more of southern British Columbia will be within the California Current system (Mackas et al. 2007). The spring transition from predominantly southeastern winds (which drive the poleward flowing, downwelling Davidson Current along the coast) to predominantly northwestern winds (which drive the equatorward flowing, upwelling California Current) will occur earlier in the spring (Mackas et al. 2007). Bakun (1990) suggested that alongshore winds may be stronger in summer, enhancing coastal upwelling, and there is some empirical support for this conjecture. However, modeling by Hsieh and Boer (1992) suggests that alongshore winds will be weaker and there will be a modest decrease in upwelling. McGowan et al. (1998) found that as the California Current has warmed over the second half of the 20th century, upwelling has drawn shallower, less nutrient-rich water to the surface. The Aleutian low will deepen and winter freshwater discharge from Alaska will increase so that the Alaskan gyre will speed up and buoyancy-driven flow along the coast of Alaska will be greater (Royer and Grosch 2006; Mackas et al. 2007; Schwing et al. 2010). Low pH waters will be drawn onto the coast by upwelling processes (Feely et al. 2008).

Gulf of Alaska

Climate variability in the North Pacific has been dominated by the Pacific Decadal Oscillation (Mantua et al. 1997), making it difficult to detect persistent trends in temperature; however, recent data show that the North Pacific has been warming for at least 60 years. Overland and Wang (2007) suggest that temperature increases due to anthropogenic climate change will exceed natural variation by about 2050, and temperature increases are expected to be 2–4 °C by the end of the century (Mackas et al. 2007; Barange and Perry 2009). Decadal variation will continue around the higher thermal mean. Salinity has also been declining in the North Pacific because of increasing precipitation over the ocean and coastal areas (Freeland et al. 1997). The precipitation increase over the ocean is expected to be about 100 mm·year⁻¹ by the end of the century. Stratification has strengthened in the Gulf of Alaska and the thermocline has shoaled (Freeland et al. 1997). Upwelling of nutrients has declined at Station P (nitrate and silicate by about 25%), but concentrations are still greater than phytoplankton can utilize (production in the Gulf of Alaska is limited by iron) (Freeland et al. 1997; Mackas et al. 2007).

The surface layer in the North Pacific is expected to become sufficiently acidic to affect shell construction by plankton and benthos that build calcareous skeletons by mid-century (Fabry et al. 2008).

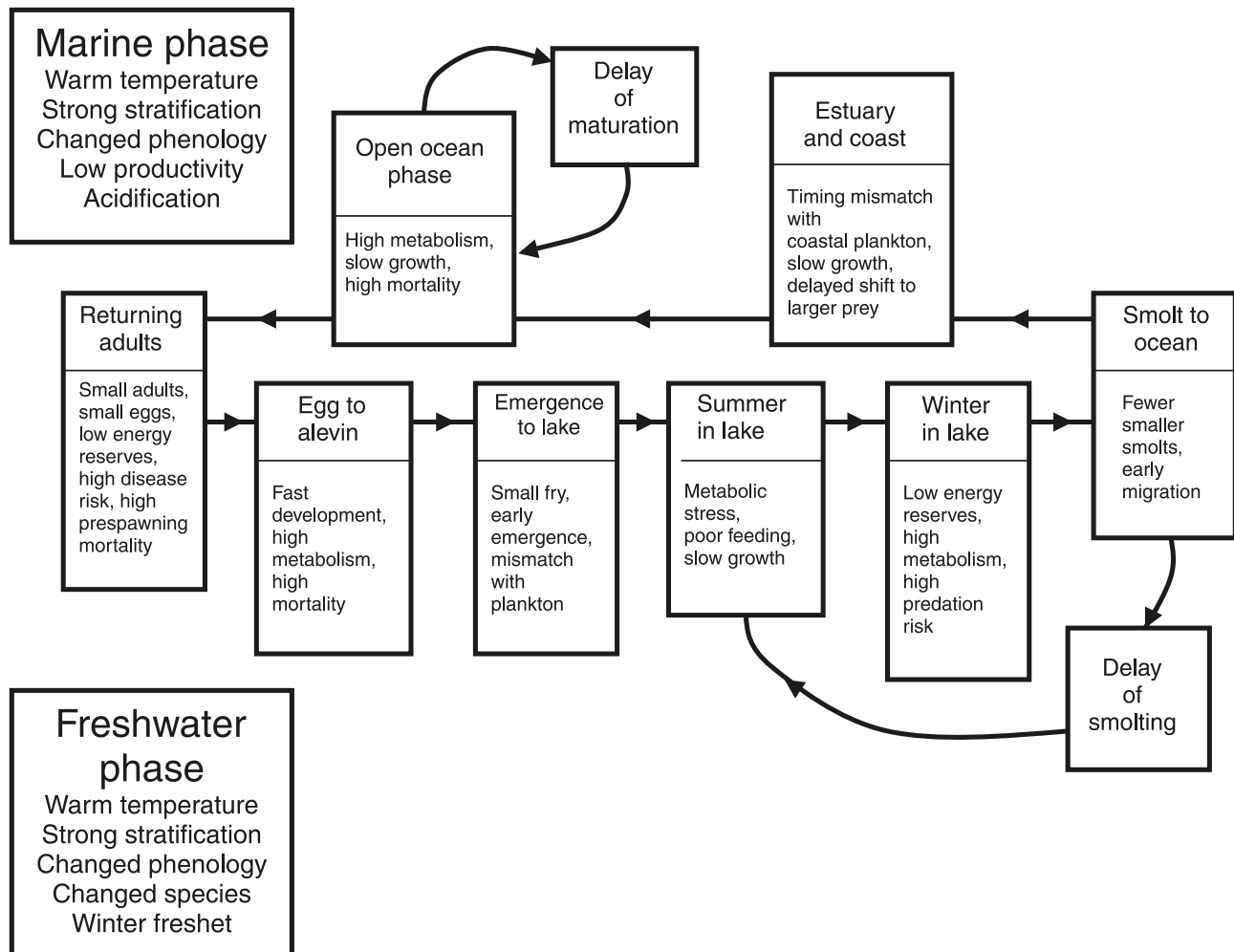
Responses of sockeye to changing freshwater and marine habitats

The responses of sockeye (and other species) to climate change will be complex and multifaceted. Freshwater and marine habitats will not all change in exactly the same ways or at the same times. For some populations and life stages, conditions may improve at first, while for others they deteriorate. Over time, however, all evidence points to a progressive decline in productive capacity of all stocks. Particularly important are the cumulative effects of change across life stages and habitats and across generations (Fig. 1; Table 1, columns 1 and 2). Below I provide details on life stage effects of climate change and their interstage and intergenerational consequences. Although specific counter examples to the general patterns I describe can certainly be found, the descriptions below represent, in my opinion, the most likely overall response of Fraser River sockeye (and other salmon species in the southern half of their geographic range) to climate change.

Stage 1. Egg and alevin

Embryonic development of sockeye eggs is temperature sensitive (Alderice and Velsen 1978; Murray and McPhail 1988; Beacham and Murray 1990). Individual spawning populations appear to have specific development rate adaptations to conditions in their spawning stream (Tallman 1986; Beacham and Murray 1990). These adaptations ensure that sockeye fry emerge in the spring at the optimal time to take advantage of the spring zooplankton bloom in their nursery lake (Brannon 1987). Synchronized emergence from nearby spawning areas may also help swamp predator responses to fry, increasing survival probability (Tallman and Healey 1994). Under warmer incubation conditions, development

Fig. 1. Diagram of the conceptual model of the cumulative effects of climate change on Fraser River sockeye salmon. The diagram shows the eight life stages of sockeye salmon examined in the paper (boxes intersecting the life cycle loop), with freshwater stages below and marine stages above. Major effects of climate change are shown for each life stage. Major climate and ecosystem changes affecting salmon are shown in the boxes labeled “Freshwater phase” and “Marine phase”. Salmon responses to climate change at one stage carry forward to affect performance at the next stage and between generations.



will be accelerated and the embryo will use more of its fixed store of yolk in maintenance metabolism. As a result, fry will be smaller and emergence timing will be earlier and may no longer coincide with development of the fry's food supply (Walther et al. 2002; Winder and Schindler 2004a). As discussed later, cumulative effects of climate change are likely to lead to smaller adults that will produce smaller eggs, which develop more quickly, exacerbating any problems of small size and early emergence of fry. Small eggs have also been shown to have reduced survival compared with large eggs in brown trout (*Salmo trutta*) and Chinook salmon (Bagenal 1969; Heath et al. 1999). Other studies, however, have not found a similar relationship (Beacham and Murray 1985; Hutchings 1991). Eggs subject to altered thermal regimes during development may also suffer high mortality (Tallman 1986).

Fall rainstorms (that previously would have fallen as snow) may scour embryos from spawning nests (Cunjak et al. 1998; Steen and Quinn 1999). Montgomery et al. (1996) suggest that even a small increase in scour depth could have a big

impact on embryo survival. Smaller adults resulting from global warming (see later discussion of marine growth) will construct shallower redds, increasing the probability of scour (Steen and Quinn 1999). Autumn storms are also likely to be more intense, increasing the probability of scour. Because of more variable fall and winter discharge, sockeye may spawn in marginal areas that dry up when water levels fall. Changes in winter temperatures can affect the likelihood that frazil or anchor ice will form in spawning beds that can penetrate redds and freeze or smother embryos (Reiser and Wesche 1979; Cunjak and Therrien 1998). In the long term, the mortality risk from this factor will go down, but as very cold winters warm up, the risk will at first increase as areas of open water encourage the formation of frazil ice (Bisaillon et al. 2007).

In summary, incubation at higher temperatures and under more variable flow regimes is likely to result in fewer, smaller fry surviving to the time of emergence. Fry will also reach the emergence stage earlier, a change in phenology that may be maladaptive (Fig. 1; Table 1).

Stage 2. Fry: emergence to lake entry

Emergence from the gravel spawning nest can be a difficult time for salmon fry, particularly if sediment plugs gravel during incubation (Phillips et al. 1975; Mackenzie and Morring 1988; Pauwels and Haines 1994). Autumn storms falling as rain rather than snow have the potential to wash fine sediments into spawning streams, partially plugging interstitial spaces and making fry emergence more difficult. Any factors that reduce fry competence, such as reduced energy reserves or incomplete development, are likely to increase mortality at this time. Predators also cue onto emerging fry so that smaller fry with reduced swimming competence will be subject to higher predation risk (Taylor and McPhail 1985).

Once fry emerge from the gravel nest, they migrate to a nursery lake. When the nursery is downstream from the spawning location, fry need only drift to the lake. However, when the nursery lake is upstream, fry must migrate against the current. Smaller fry may be less able to make such an upstream migration successfully (Taylor and McPhail 1985). Patterson et al. (2004) found that sockeye spawning in outlet streams had larger eggs and produced larger fry that had greater swimming capability than sockeye spawning in inlet streams. This suggests that the smaller fry expected under global warming will find it more difficult to reach their nursery lake. Smaller fry may also expend more energy to reach the nursery lake, particularly if the water is warmer, so that their need for abundant food may be even greater than under present circumstances. This difficulty may be somewhat mitigated if spring discharge is reduced so that the velocities fry encounter are lower.

Once in the nursery lake, fry feed and grow on limnetic zooplankton. Under natural conditions, fry entry into the nursery lake is timed to coincide with the spring bloom of lake zooplankton (Brannon 1987). Changes in the phenology of fry emergence may mean that the time of lake entry no longer coincides with the spring zooplankton bloom. Changes in phenology of phytoplankton and zooplankton in the nursery lake could accentuate this problem. Changes in phenology leading to mismatch between predators and prey are a frequently observed consequence of climate change (Parmesan and Yohe 2003; Edwards and Richardson 2004; Hays et al. 2005). Winder and Schindler (2004a, 2004b) have shown that as Lake Washington has become warmer, the spring bloom of zooplankton has become uncoupled from the spring phytoplankton bloom, resulting in lower spring zooplankton densities and poorer feeding conditions for sockeye fry. As warming continues, zooplankton composition in Lake Washington may also change from large *Daphnia* to smaller *Bosmina* and copepods, providing a less valuable food for sockeye fry.

Hutchings (1991) found that size and survival of brook trout (*Salvelinus fontinalis*) fry was positively correlated with egg size over the first 50 days after emergence regardless of feeding conditions. Under reduced feeding conditions, however, fry from smaller eggs had much higher mortality, whereas mortality of fry from larger eggs did not change. If similar relationships exist for sockeye, any reduction in egg size and (or) mismatch between fry emergence and food production could dramatically reduce survival from emergence to lake entry, particularly in outlet spawning populations.

In summary, the smaller fry that result from smaller eggs and warmer incubation conditions are expected to experience higher mortality from a number of factors, such as problems emerging from gravel nests, poorer swimming competence and greater vulnerability to predation, timing mismatch between fry emergence and spring zooplankton production, and changes in lake zooplankton that reduce its value as food for sockeye fry. As a consequence, fewer fry will make it into the nursery lake and their growth rate during the critical first feeding stage will be slower (Fig. 1; Table 1).

Stage 3. Fry: lake entry to first winter

Sockeye fry feed on pelagic zooplankton throughout their year or so of lake residence. Hampton et al. (2006) have shown that *Daphnia* population growth in Lake Washington has become less concordant with sockeye fry arrival. In addition, sockeye's preferred forage species, *Daphnia pulicaria*, has become relatively less abundant compared with the less preferred *Daphnia thorata*. The longer open water season in lakes under global warming will potentially provide for a longer growing season. However, as long as the lake remains stratified, nutrient concentrations and plankton production in the surface waters will be low, offering a limited feeding and growth opportunity for sockeye. The duration of stratification in Lake Washington has increased by about 4 weeks since 1962 (Winder et al. 2009). Surface waters will also be warmer, increasing energy costs and disease risk for sockeye fry. In Lake Washington, temperature of the epilimnion has increased by about 1.5 °C since 1962 (current maximum epilimnion temperatures are 18–20 °C; Arhonditsis et al. 2004). Henderson et al. (1992) suggest that in Shuswap Lake, a major sockeye nursery lake in the Fraser basin, surface temperatures in midsummer may exceed 26 °C within a few decades, lethal to young sockeye if they spend more than a few minutes above the thermocline (in 1999, epilimnion temperature was 25 °C). Not all Fraser basin nursery lakes have such high epilimnion temperatures, however. Chilko Lake, for example, seldom has epilimnion temperatures above 14 °C (Hume et al. 1996). In many nursery lakes, sockeye fry undertake daily vertical migrations to avoid warm temperatures and predators in the surface waters for much of the day. Under global warming, their vertical excursions into the surface waters to get food during dawn and dusk may have to be shortened, and the higher average temperature they experience will increase metabolic costs. Henderson et al. (1992) conclude that growth of sockeye in Shuswap Lake during their first summer will be reduced under global warming. This is likely also to be the case in many other nursery lakes in the Fraser River drainage.

West and Larkin (1987) found that growth of sockeye fry in Babine Lake was size-dependent, with smaller fry growing more slowly. The smaller fry produced under global warming may, therefore, already be at a growth disadvantage regardless of any phenological mismatch between fry and their zooplankton prey or changes in zooplankton community composition. The literature generally indicates that mortality of salmon fry in freshwater nursery habitats is size-dependent, with smaller fry suffering higher mortality (West and Larkin 1987; Sogard 1997; Einum and Fleming 2000), although under some circumstances larger fry can suffer higher mortality (Holtby and Healey 1986; Good et al. 2001).

Under global warming, therefore, Fraser River sockeye fry are likely to be smaller on average at the end of their first summer. Small size (as emergent fry facing poor growing conditions in the lake) may cause the fry to adopt risky foraging behaviour that exposes them to thermal stress, greater predation, and greater risk of disease (Eggers 1978). West and Larkin (1987) found that size-selective mortality was strongest during the late summer and autumn in Babine Lake. This may indicate that the smaller fry were risking predation to build their energy reserves sufficiently to survive the winter fasting period (see next section). It seems likely, therefore, that under global warming, fry growth during the first summer will be lower and mortality rates higher than normal. As a consequence, fewer, smaller fry will enter the winter with, on average, lower energy reserves (Fig. 1; Table 1).

Stage 4. Fry: first winter

The first winter is considered a critical time for young salmon and is often a time of high mortality (Bisaillon et al. 2007; Jonsson and Jonsson 2009). Overwinter mortality is negatively correlated with size and body energy reserves (Søgaard 1997; Biro et al. 2004; Finstad et al. 2004), so smaller, more poorly fed fry entering the winter are likely to suffer high mortality. Factors associated with winter mortality include predation, energy exhaustion, and susceptibility to extreme conditions of flow and temperature; small fry are more vulnerable to all these factors. Crozier and Zabel (2006) found that survival for Chinook salmon in 18 streams in the Salmon River basin, Idaho, was positively associated with autumn discharge, although for some populations a negative relationship with summer temperature was stronger. Cunjack et al. (1998) found that winter survival of all life stages of Atlantic salmon (*Salmo salar*) in Catamaran Brook, Newfoundland, was positively associated with winter discharge. Most data on winter survival refer to stream-dwelling salmonids, and lake-dwelling sockeye may be less susceptible during this period. Predation and energy exhaustion are likely to be the most important factors for overwinter survival of sockeye.

In summary, as global warming proceeds, sockeye fry will enter the winter at smaller size and with lower body energy reserves and will suffer greater than normal overwinter mortality. Thus, fewer fry will make up the pool of potential smolts in spring, and these fish are likely to be in poor condition (Fig. 1; Table 1).

Stage 5. Smolting and seaward migration

Smolt transformation is a critical life history stage in anadromous salmon, involving physiological and behavioural changes that allow the fish to survive in seawater (Folmar and Dickhoff 1980; McCormick et al. 1998). Salmon fry must have achieved an appropriate size and development stage to undergo successful smolting. The majority of Fraser River sockeye smolt at 1 year of age, although some smolt at 2 years of age. It appears that the decision to smolt is made well before smolting occurs, probably during the summer growth phase (Thorpe et al. 1992; Hinch et al. 2006), and is connected with growth rate. The probability that an individual fish will smolt is positively correlated with the size at which it enters the winter, and there is evidence of a minimum size for successful smolting (Folmar and Dickhoff

1980). The physiological and behavioural characteristics related to smolting develop in the early spring, rise to a maximum, and then fade away if the fish does not initiate seaward migration. Furthermore, the physiological "time window" during which successful smolting is possible is shorter under warmer conditions (McCormick et al. 1998). Smaller parr may move through this window before reaching full competence to smolt, thus forcing a 1-year delay of smolting. Fry that grow more slowly under global warming, therefore, may spend a second year in fresh water before going to sea. Or, they may decide to smolt at small size. Small fish that proceed to smolting typically show rapid growth in the spring prior to seaward migration, which brings their size closer to that of larger smolts (Eggers 1978; Nicieza and Branya 1993). Sockeye that delay smolting face a second year of mortality in the lake and increase their generation time by 1 year, both of which reduce overall productivity. Sockeye that decide to smolt at small size and feed to grow rapidly in early spring face elevated mortality risk. Davidsen et al. (2009) observed that small Atlantic salmon smolts had low survival over 11 km of river migration, and numerous authors have shown a relationship between smolt size and overall marine survival for sockeye salmon (Henderson and Cass 1991; Koenings et al. 1993).

The timing of smolt migration is cued by photoperiod but is triggered by temperature, advancing several days under warm conditions and delaying under cold conditions in the spring (McCormick et al. 1998; Jonsson and Jonsson 2009). Therefore, warmer spring temperatures may advance the smolting date. However, smaller fish also migrate somewhat later and will also be trying to put on as much spring growth as possible before migrating to sea, so that the influence of temperature on smolting phenology may not be as large as if the presmolts were of normal size (Nicieza and Branya 1993; Beckman et al. 1998). However, even small changes in migration timing can increase mortality risk (Bilton et al. 1982; McCormick et al. 1998), as there appears to be an optimal environmental window for successful smolt migration as well as an optimal physiological window. It seems unlikely that changes in smolt migration timing will match phenological shifts in estuarine and coastal ecosystems in such a way that marine growth and survival are not affected.

In summary, under global warming, yearling sockeye smolts will migrate somewhat earlier and at smaller size. More fry will delay smolting until their second year. Fewer, smaller smolts will enter the ocean, and their timing is likely to be mismatched with ocean feeding and growth opportunity (Fig. 1; Table 1).

Stage 6. Postsmolts: estuary and coastal

Several authors have presented evidence that survival during the first months of marine life is critical to the abundance of returning adult salmon (e.g., Holtby et al. 1990; Friedland et al. 2000; Mueter et al. 2005). Overall marine survival is strongly related to the size of smolts entering the sea and (or) early marine growth rates (Holtby et al. 1990; Koenings et al. 1993; Friedland et al. 2000). As Mangel (1994) pointed out, growth at this stage is crucial because salmon avoid predation by growing larger than predators can easily capture. Conditions for growth of Fraser River sockeye during the

first months of marine life are, therefore, critical to overall marine survival and productivity.

Sockeye smolts from Fraser River stocks typically begin arriving in the Strait of Georgia in the latter half of April, and the migration continues through May (Groot and Cooke 1987; Tucker et al. 2009). Initially, postsmolts are concentrated in the area of the Fraser River plume but then migrate north through the Strait of Georgia, Johnstone Strait, and Queen Charlotte Strait, reaching Queen Charlotte Sound in late June or July (Groot and Cooke 1987; Tucker et al. 2009). The details of their movement beyond this point are unknown, but they continue to move north and west in continental shelf waters until sometime in the autumn when they move offshore into the Gulf of Alaska (Walter et al. 1997; Healey 2000; Tucker et al. 2009).

The precise changes in environment and feeding conditions in the coastal ocean under global warming are uncertain, but as noted earlier, coastal waters will be warmer, the spring transition to upwelling conditions on the south coast of British Columbia will be earlier, and spring freshet from the Fraser River will be lower, reducing estuarine circulation and productivity in the Strait of Georgia (Yin et al. 1997a, 1997b; Mackas et al. 2007). Mackas and Louttit (1988) showed that the copepod *Neocalanus plumchrus* (and probably other zooplankton and small fishes as well) was concentrated in the advancing plume of the Fraser River, which may enhance feeding opportunity for sockeye smolts in the estuary (Healey 1980). *Neocalanus plumchrus* is the dominant spring zooplankton in the Strait of Georgia, with an intense but short-lived peak in abundance. The timing of the *N. plumchrus* peak is responsive to temperature in the mixed layer and advances during warm years (Mackas et al. 1998). The timing of the peak at the end of the 1990s (April) was almost a month earlier than in the 1960s (May), probably due to the increase in mixed layer temperature over that period (Bornhold 2000). This degree of phenological change in the zooplankton of the Strait of Georgia is much greater than any as yet observed change in salmon smolt timing, so that even with an advance in the timing of smolt migration, there may be a big mismatch between the timing of sockeye arrival in the Strait of Georgia and the abundance of this large and dominant copepod.

Neocalanus plumchrus is, at best, a short-term forage species for Fraser River sockeye in coastal waters, and in recent years its peak abundance has become even shorter (Batten and Mackas 2009). By the time sockeye are migrating north out of the Strait of Georgia, *N. plumchrus* is returning to deep water. Coastal zooplankton are, however, the dominant food of sockeye during their period of residence in continental shelf waters (Brodeur 1990). Under warming conditions, the subarctic front is pushed northward at least to Haida Gwaii, and the plankton community off British Columbia comes to resemble that of the California Current with abundant small copepods but low biomass (Fulton and LeBrasseur 1985; Mackas et al. 2001, 2007). Under these conditions, salmon and other predators show poor survival and growth (Gaston and Smith 2001; Mackas et al. 2007). Mackas et al. (2007) described this as the “warm, unproductive” community. Presumably, under global warming, these conditions will become permanent or semipermanent off the British Columbia coast, reducing the growth and survival of young salmon.

Other changes in the coastal ocean associated with global warming will also affect growth and survival of salmon. The biological community of the Gulf of Alaska changes with changing ocean conditions, and the suite of predators that salmon will face is expected to change as marine species adjust their distributions to increasing SST (Karinen et al. 1985; see also Appendix 1 in Fulton and LeBrasseur 1985; Anderson and Piatt 1999). In addition to facing a changing predator community and reduced food supplies, foraging opportunity may be further changed by ocean acidification (Fabry et al. 2008; Feely et al. 2008). Pteropod mollusks, an important food of young salmon during the first summer, may be adversely affected by declining pH, which makes it difficult for them to construct their shells. Aydin et al. (2005) showed that this rich food source was critical for young pink salmon, allowing them to grow rapidly during early marine life and make the transition to feeding on squid. Final adult size in pink salmon was very sensitive to the timing of this ontogenetic shift in diet. Beauchamp et al. (2007) determined that higher survival of pink salmon in the Gulf of Alaska was associated with high foraging on pteropod mollusks during July–August of the first year of ocean life. In addition, phenological changes in the trophic web supporting young salmon and in the timing of salmon migrations themselves seem likely to degrade further the quality of the coastal environment as a nursery for young salmon (Edwards and Richardson 2004; Mackas et al. 2007).

In summary, the coastal ocean under global warming will change in ways that are not favourable for Fraser River sockeye and other salmon species from the region. There is a growing body of evidence that larger size at ocean entry and rapid early marine growth lead to high adult abundance and large adult size. A warmer coastal ocean supports a zooplankton community that is less valuable as food for young Fraser River salmon and an altered community of predators to which young salmon are less well adapted. In addition, an increasingly acidic ocean will affect production of important forage species such as pteropod mollusks that young sockeye should encounter as they migrate north along the coast. Couple these changes with changes in phenology of both salmon and food and the result is likely to be a coastal ocean ecosystem that is much less supportive of young salmon. As a result, the smaller smolts produced from the freshwater nurseries of the Fraser River will grow more slowly and experience higher mortality during their time in coastal marine waters (Fig. 1; Table 1).

Stage 7. Immatures in the ocean

After they leave coastal waters, the Gulf of Alaska is the primary feeding area for Fraser sockeye. Although sockeye movement patterns in the ocean are not well understood, they are probably moving so as to maximize their growth potential in a relatively unproductive environment (Healey 2000; Rand 2002). Global warming is likely to make this nursery warmer and less productive than in the past, although the degree of change is uncertain (Hinch et al. 1995b; Falkowski et al. 1998; Pierce 2004). All salmon species, and Fraser River sockeye in particular, are returning at smaller adult size (within age classes) compared with a few decades ago (Bigler et al. 1996; Cox and Hinch 1997), and these changes can be linked to warmer temperature in the Gulf of

Alaska but also to salmon density and estimates of food supply (Hinch et al. 1995a, 1995b; Cox and Hinch 1997). Returning sockeye are also older on average (Pyper et al. 1999; Morita et al. 2005), suggesting that reduced marine growth rates have caused some salmon to delay maturation. Delay of maturation will mitigate the declining size at age to some degree, but delayed maturation also means additional mortality at sea and a lengthened generation time, both of which will contribute to reduced productivity.

Welch et al. (1998) described sharp thermal limits for sockeye in the North Pacific and showed that under global warming, suitable thermal habitat for sockeye may disappear from the North Pacific. Sockeye may avoid higher temperatures in surface waters of the Gulf of Alaska by spending more time below the mixed layer or retreating north to remain within their thermal habitat preferences (Welch et al. 1998). Rand (2002) argued that salmon thermal preferences represent selection of thermal habitats where positive growth is possible rather than a response to temperature per se, as all temperatures were well within the species' tolerance. Nagasawa (2000) analyzed the winter biomass of zooplankton in the North Pacific and the distribution of salmon. Plankton biomass in winter was <10% of summer biomass, and in winter salmon were found predominantly in temperatures <8 °C. He argued that selection of low temperatures was a tactic for minimizing metabolic losses when feeding opportunity was low. Redistributing to the north and into the Bering Sea as the ocean warms will expose sockeye to higher densities of competitors, further reducing foraging efficiency. For Fraser River sockeye, such redistribution will also commit them to a much longer return migration through a warm and unproductive region of ocean at a time when they should be growing rapidly (Brett 1983).

There are many gaps in the data on ecosystem-level effects of climate on salmon in the North Pacific. The picture for Atlantic salmon in the North Atlantic is somewhat clearer. In the eastern Atlantic, Beaugrand and Reid (2003) have shown that SST has increased in recent decades, and phytoplankton productivity and the abundance of small copepods has also increased. The abundance of large copepods (e.g., *Calanus finmarchicus*) and Atlantic salmon, however, has decreased, suggesting a breakdown in the food chain supporting salmon. Edwards and Richardson (2004) have also shown divergent phenological responses among the phytoplankton, zooplankton, and zooplankton predators in the North Sea, resulting in considerable disruption of the trophic structure. In the Atlantic as in the Pacific, global warming is linked to declines in salmon production.

There are other emerging problems. As with coastal waters, oceanic waters are subject to acidification from the absorption of excess CO₂. Orr et al. (2005) provide data and models to suggest that pH low enough to cause decalcification in various phytoplankton and some zooplankton that are food for salmon could occur in high latitude surface waters before the end of the century. Salmon may escape some aspects of changing ocean conditions (such as unfavourable temperatures) by changing their distribution. However, the effects of acidification are likely to be pervasive.

In summary, overall productivity of the North Pacific food web supporting salmon may decline under global warming; it seems unlikely to increase. As in the Atlantic, diverse pheno-

logical responses among the plankton and other forage species are likely to disrupt the food web supporting salmon. The subarctic front in the North Pacific, which is usually the southern boundary of sockeye distribution, will shift north, reducing habitat area. Suitable thermal habitats may even contract into the Bering Sea, driving up competition among salmon and further reducing growth. The marine phase of homeward migration for maturing Fraser River sockeye will be longer and through relatively warm, unproductive waters, further restricting growth at a time when the fish typically accumulate up to 30% of their mature biomass (Brett 1983; Hinch et al. 1995a, 1995b). In keeping with empirical trends that have already been observed, as the North Pacific continues to warm, Fraser River sockeye will return at smaller size and older average age and there will be fewer of them (Fig. 1; Table 1).

Stage 8. Returning adults

Sockeye typically mature at a number of different ocean ages, although 4-year-old fish (age 1.2, one freshwater winter and two ocean winters) are by far the most abundant in the Fraser River (Foerster 1968; Healey 1986). We can assume that a salmon must reach an appropriate size and development stage in the spring if it is to initiate maturation and homeward migration. There is, presumably, a critical size threshold and perhaps a critical growth rate threshold that triggers the maturation-migration process. Once maturation is initiated, sockeye undertake a directed migration back to their river and upstream to their natal spawning ground (Healey and Groot 1987; Burgner 1991). Genetics, maternal effects, and environment all affect the age at which a salmon matures (Bradford and Peterman 1987; Heath et al. 1994; Wood and Foote 1996). The decline in size of mature sockeye returning to the Fraser River, together with their increase in average age, suggests that some fish are reaching a sufficient size to trigger homeward migration at the usual age but others are opting to delay maturation. Not only are sockeye returning at smaller size in recent years but they also appear to be returning at lower body energy density (Crossin et al. 2004a). Energy reserves at time of river entry are critical, as salmon do not feed in fresh water and must complete their migration, complete maturation, and spawn using these reserves. Most sockeye returning to the Fraser River must undertake an arduous upstream migration of many hundreds of kilometres before reaching their spawning streams (Healey et al. 2000). Mortality occurs when sockeye reach a body energy density of about 4 MJ·kg⁻¹, so that fish must complete their migration and spawning before reaching this threshold (Crossin et al. 2004b). In recent years, some sockeye populations have been returning to the Fraser River weeks earlier than in the past, and a high proportion has died en route to the spawning grounds (Cooke et al. 2004). Others have reached the spawning grounds but died without spawning. Energetic exhaustion is one likely explanation for at least some of this mortality, although there is, as yet, little direct evidence of en route or prespawning mortality due to energy exhaustion (Rand et al. 2006). Temperature, stress, and disease are also implicated (Cooke et al. 2004; Farrell et al. 2008; Martins et al. 2011).

Problems with "missing" sockeye in the Fraser River and the unprecedented early return and high mortality of some

stocks during the past decade (Cooke et al. 2004; Williams 2005) has stimulated considerable research on the physiology and behaviour of salmon during upriver migration (e.g., Hinch and Rand 1998; Lee et al. 2003; Crossin et al. 2009). Although the precise causes of early return to the river and mortality prior to spawning remain unclear, much of this research is relevant to the potential effects of climate change on Fraser River sockeye, in particular the findings regarding temperature adaptation (Farrell et al. 2008). Fraser River sockeye from different spawning populations return to the river at various times throughout the summer, when river temperatures are near their seasonal maximum. Individual salmon populations show adaptations such that the temperature (T_{opt}) of their maximum scope for activity is the temperature they would normally encounter during their upstream migration. However, scope for activity falls off sharply at temperatures above this optimum so that the critical temperature (T_{crit}), at which there is effectively no scope for activity, is only 6–7 °C higher than T_{opt} . In very warm years, such as 2004, migration can be stalled and high en route or pre-spawning mortality can occur because temperatures approach T_{crit} (Williams 2005; Farrell et al. 2008). One experiment with Weaver Creek sockeye showed that sockeye exposed to 18 °C (about 4 °C above T_{opt} for this population) for 24 days and released back into the river suffered higher mortality and showed greater expression of the parasite *Parvicapsula minibicornis* than a second group exposed for the same period to 10 °C or an untreated control group (Crossin et al. 2008). The narrow temperature spread between T_{opt} and T_{crit} means that even a modest increase in river temperatures can compromise migration and reproductive success, especially in fish that may be experiencing other stressors.

Maximum summer temperatures in the Fraser River have increased by an average of 1.8 °C since 1950; whereas these temperatures used to range from 16 to 20 °C, they now range from 18 to 22 °C (Patterson et al. 2007; Farrell et al. 2008). Hyatt et al. (2003) suggested that 21 °C was a critical temperature for migration of Okanagan River sockeye: migration stopping as temperature rose above 21 °C and resuming when temperature fell below 21 °C. Presumably, the critical temperature blocking migration will differ according to the temperature adaptation of the salmon population. The experiment of Crossin et al. (2008) indicates that exposure even to relatively moderate temperatures can have a serious effect on migration success. The 1.8 °C increase already observed in maximum river temperatures means that migration capacity of sockeye may already have been reduced by an average of 25%. Coupled with the greater metabolic costs and risk of disease that come with higher temperatures, it is perhaps not surprising that Fraser River sockeye have been experiencing high en route and pre-spawning mortality, especially in warm years.

Fish that die without spawning are completely lost in terms of contributions to the next generation. However, smaller females also lay fewer, smaller eggs, so that even the fish that spawn make a lower per individual contribution to the next generation (Healey 1987).

In summary, under global warming sockeye will return to the Fraser River at smaller size and with lower body energy reserves, which may compromise their ability to complete migration and spawning. In addition, higher temperatures

during upstream migration may cause migration delays or stop migration altogether. Stressed fish in the warmer river will be subject to greater risk of disease. High mortality during upstream migration and prior to spawning is the likely result. Those fish that do spawn will lay fewer and smaller eggs, thus compromising productivity of the next generation (Fig. 1; Table 1).

Synthesis – cumulative effects

Any forecast of the effects of climate change has high uncertainty; however, the evidence presented above shows that global warming will likely have negative effects on productivity of Fraser River sockeye at every life history stage. Although not all environmental and ecological change with global warming will be negative for Fraser River sockeye (warmer temperatures will enhance lake and ocean productivity in some regions, for example, and lower spring and summer discharge may make upstream migration easier), the weight of evidence supports the conclusion that effects at each stage will be predominantly negative. Furthermore, the effects at one stage carry forward to the next.

The cumulative effects model can be described as follows in relation to historic norms (see also Fig. 1; Table 1): (1) Warmer incubation temperatures will result in fewer, smaller fry emerging from the gravel nests. More variable autumn and winter flows may also result in substantial scour of spawning nests. Fry from outlet spawning beds will have more difficulty reaching the nursery lake. Overall, fewer and smaller fry will enter the nursery lake earlier in spring. (2) Smaller fry will enter a warmer nursery lake where phenological changes in plankton communities have disrupted trophic relationships. As a consequence, fry will grow more slowly in the lake and will experience higher mortality. (3) Fry will enter the critical first winter at smaller size with lower energy reserves and will experience higher mortality as a result. (4) Fewer fry will have achieved the size – life stage threshold to smolt after 1 year so that a higher percentage of fry will delay smolting, experiencing a second year of freshwater mortality. Fry that do smolt after 1 year will be smaller than normal. Overall, fewer, smaller smolts will be produced from the nursery lake, and they are likely to migrate somewhat earlier. (5) Smolts will enter a warmer, less productive coastal ocean where trophic relationships have been disrupted by phenological changes that will likely not match the phenological change in smolt migration timing. Dominant zooplankton in the warmer ocean will be less suitable as prey for salmon. As a result, postsmolt growth will be slower, further compromising an already low survival rate because of their small size at ocean entry. Ocean acidification may also compromise the abundance of important prey such as pteropod mollusks. Ontological transition to feeding on larger, energy-rich prey, like squid, will be delayed. (6) Poor growth in coastal waters will carry forward into the oceanic phase. Suitable thermal habitats in the North Pacific will be pushed north by global warming so that fish will be concentrated into a smaller area of ocean and feeding competition will be greater. As a result, fish will be smaller at their normal maturation age, and a higher proportion of any year class will delay maturation by an extra year. Fewer, smaller adults will make the spawning migration each year. (7) Smaller adults

will return to the river mouth with lower body energy density, perhaps insufficient for them to complete the spawning migration and spawn in a warmer river. Upriver migration may be delayed because of reduced scope for activity in the warmer river. Mortality during upriver migration will be higher so that fewer, smaller adults arrive at the spawning grounds. (8) Smaller females with lower energy reserves will have lower capacity to construct and defend a redd so that egg burial depth will be lower and potential for superimposition higher. Eggs that are buried at shallower depth will be at greater risk of scour during autumn storms. Smaller females will also lay smaller eggs, so that development will be further accelerated in the subsequent generation, increasing the phenological change in fry emergence timing. (9) Compensatory delays in smolting and maturation will extend generation time, further reducing overall productivity. (10) Finally, as suggested in point 8 above, effects in one generation will carry forward to the next generation, potentially creating a downward spiral in size, survival, and productivity in each generation.

Though qualitative, this model is well supported by the literature, and a quantitative evaluation of salmon responses to climate change would clarify the relative importance of change at different life stages and show how change would propagate through the life cycle and across generations. Quantitative modeling would also reveal which parameters are most in need of further research. A team of researchers from Washington State and British Columbia has begun developing a model that will be a critical step toward this objective (Mantua et al. 2009).

If global warming can be stopped before a critical stage is reached, the Fraser River system will eventually settle into a new regime of production. However, on the basis of present evidence, it seems doubtful that the new regime would involve substantial commercial production of salmon. Indeed, it seems more likely that many Fraser River sockeye populations will be extirpated, and those that remain will be in a tenuous position. One critical stage would be when maximum river temperatures regularly reach T_{crit} for most populations. However, it is unlikely that temperatures would have to rise even to this level before salmon populations suffered physiological collapse (Farrell et al. 2008).

Although I developed the conceptual model for Fraser River sockeye, its main elements can easily be extrapolated to the other anadromous Pacific salmon species. All species will experience adverse changes in incubation and freshwater nursery environments in the southern portions of their ranges (higher temperature, redd scour). All species will experience coastal and oceanic environments that are warmer and reduced in productivity with changed predator species. It seems likely that by 2050 the majority of freshwater and marine habitats of Pacific salmon from the central British Columbia coast south to the limit of salmon distribution will become much less hospitable to salmon, and production in this region will be dramatically reduced. Populations in northern British Columbia and Alaska (and Russia), however, should experience improved productivity, at least for a while (see e.g., Edmundson and Mazumder 2001; Mueter et al. 2002; Schindler et al. 2005). Indeed, salmon catches in eastern Russia and Alaska are currently at all-time highs, partly because of increased hatchery production of chum (*Oncorhynchus keta*)

and pink (*Oncorhynchus gorbuscha*) salmon (Irvine et al. 2009a; Nagasawa and Azumaya 2009). Pink and chum salmon are also currently abundant in the southern part of their range (Irvine et al. 2009a). However, as global warming continues, these populations will eventually begin suffering overall negative effects, first in the south but progressing northward with time.

Mitigation and adaptation

Mitigating the effects of global warming on salmon is difficult, and it is unlikely that any mitigation will sustain salmon populations in the long run as global warming continues. However, there are some policies and practices that would slow rates of decline and help ensure continued survival of at least some southern salmon populations. The wild salmon policy (Fisheries and Oceans Canada 2005; Irvine 2009) provides a solid foundation for conservation and sustainable use under historic patterns of environmental variation. Some policy and management options for minimizing the impact of climate change are summarized (Table 1, column 3; see Nelitz et al. 2007, 2010, for a detailed discussion of policy and management options related to specific habitats and populations as well as for a conceptual model of the effects of climate change similar to the one presented here). All of these policies and practices involve foregoing other options. They also require a dramatic change in the focus of policy and management, changes that have already begun under the wild salmon policy.

To some extent, biological responses of the fish themselves will help to mitigate the effects of climate change (Table 1). Many life history characteristics have a fairly broad reaction norm, and genetic change can occur quite quickly in some instances. Crozier et al. (2008) discussed the capacity of Chinook salmon to respond phenotypically and genotypically to aspects of climate change in some detail. Presumably, other species will have similar capacity for evolutionary response. Predicting the overall pattern of change is difficult because, as Crozier et al. (2008) point out, changes at one stage can have repercussions for later stages, particularly when life stage transitions are finely tuned to conditions in radically different environments. Based on Crozier et al. (2008), traits with the greatest likelihood of an evolutionary response to climate change include heat tolerance (and perhaps T_{opt} and T_{crit} , see earlier), disease resistance, metabolic efficiency, migration timing, and spawning date. Unfortunately, it is doubtful that phenotypic or evolutionary change in these characters will be sufficient to prevent the expected decline in productivity.

Policy and management changes can also help mitigate the impacts of climate change; however, their focus must change from maximizing the potential commercial harvest to maximizing salmon resilience (Healey 2009). The wild salmon policy mandates these kinds of changes. Changes in freshwater habitats will not be uniform, and some habitats will retain capacity to support salmon much better than others. Habitats that will retain favourable characteristics longest under global warming need to be identified and conservation should target those habitats. On tributaries with reservoirs, reservoir operation to favour salmon conservation and release of deep water to cool downstream habitats should become a

priority. It may even be worth considering construction of reservoirs to provide water storage and cool water to help sustain particularly valuable stocks. Regardless, a stronger policy of reserving river flow for salmon conservation will have to be adopted. As temperatures warm, reducing other forms of anthropogenic stress on salmon will become even more important. As not everything can be protected, hard choices will need to be made about where conservation should occur. Conservation should focus on the habitats and stocks most likely to survive under global warming rather than on those where the trade-offs are easiest. For fuller discussion of these and other policy and management options, see Nelitz et al. (2007, 2010).

The most positive opportunities for sustaining salmon appear to be in the far north, where the potential exists to build new, productive salmon runs. Observations of five species of Pacific salmon in the Arctic date back a number of decades (Craig and Halderson 1986). As the Arctic warms, new habitats suitable for salmon are emerging, and salmon may already be taking advantage of them (Babaluk et al. 2000). Chum and pink salmon already have self-sustaining populations in Arctic rivers, although where they spend the ice-bound Arctic winter is unknown (Irvine et al. 2009b). It is not yet clear that the number of viable populations of salmon in the Arctic is actually increasing (Stephenson 2006), but the capacity of salmon to invade new habitats is well known (Milner et al. 2000; Anderson and Quinn 2007). Given time, salmon will naturally colonize the Arctic as conditions there become suitable (Vermeij and Roopnarine 2008). However, their rate of finding and colonizing new habitats may be too slow to keep ahead of global warming or to beat the rush to exploit mineral and other Arctic resources (e.g., Borgerson 2008). Sockeye, in particular, tend to be among the last to colonize new habitats, and their expansion into the Arctic may lag behind other kinds of development. Managers and policy makers should be thinking now about assisting salmon to colonize the Arctic and identifying suitable habitats for protection. Otherwise, this opportunity may be lost as well.

We are entering a new era of inexorable change for salmon and their habitats. Under global climate change, we cannot assume that today's most productive populations and regions will sustain that productivity into the future. Sockeye salmon in the Fraser basin, situated near the southern limit of the species' North American distribution, is highly vulnerable to the impacts of climate change. Other sockeye stocks and other species in British Columbia are also vulnerable. Research has begun to identify policy and management tools that will help mitigate the impact of climate change (Nelitz et al. 2007, 2010; Irvine 2009), and these should be implemented to the extent possible in keeping with the wild salmon policy. It is my view, however, that these measures will be insufficient to sustain salmon production in the southern part of their range through this century. If we wish to sustain options for high salmon production in Canadian river systems, we need to begin planning for the emergence of habitats capable of producing salmon in the Arctic. Given the current enthusiasm for industrial development in a warming Arctic, it will be necessary to identify and protect the potentially most productive habitats in advance of the development of abundant salmon populations. In the Arctic, salmon policy and management will need to be highly proactive.

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