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REVIEWS

Climate effects on growth, phenology, and survival of sockeye salmon (*Oncorhynchus nerka*): a synthesis of the current state of knowledge and future research directions

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Abstract Sockeye salmon (*Oncorhynchus nerka*) is one of the most iconic and valued species of Pacific salmon. Various studies have examined the potential effects of future climate change on sockeye salmon, but there is currently no synthesis of the documented effects of climate on this species. In this paper, we present a synthesis of 80 peer-reviewed publications in the English language evaluating the effects of climate on sockeye salmon growth, phenology, and survival. The great majority of studies examined have been conducted with stocks from North America (90 % of studies). Survival (55 %) has been the most frequently studied aspect of the sockeye salmon life history in relation to climate, followed by growth (45 %) and phenology (30 %), with temperature (83.4 %) being the climate-related variable most frequently examined in such studies. Across life stages, the effects of climate-related variables have been most frequently studied on fry (36.3 %) and least studied on spawners (7.5 %). Our synthesis revealed that associations between temperature and growth, phenology, or survival have been uncovered for all the life stages of sockeye salmon, whereas relationships with other climate-related variables have been sparse. There is substantial evidence that sockeye salmon are influenced by thermal conditions experienced at regional, rather than ocean- or continental-wide scales, and that responses to temperature vary among and within stocks. The mechanisms by which climate affect sockeye salmon during the early stages in freshwater and while at sea are still poorly understood and warrant future research. More research on the effects of non-temperature, climate-related variables (e.g. stream flow, ocean pH), inter-generational and carry-over effects of climate, interaction between climate and non-climate stressors, and adaptation to climate change are also needed. Such information will be critical to advance our understanding of how sockeye salmon stocks will fare with future climate change.

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Introduction

Abundant and sustainable Pacific salmon (*Oncorhynchus* spp.) stocks are important economically, ecologically, culturally, and politically along the Northern Pacific Rim. In Canada and in the United States, Pacific salmon species support valuable commercial and recreational fisheries, generating hundreds of millions of dollars in revenues annually and supporting thousands of jobs throughout communities (BCMOE 2008; Kristianson and Strongitharm 2006; Schindler et al. 2010). Ecologically, Pacific salmon are important components of food chains in both freshwater and marine environments and their carcasses are important sources of nutrients for estuaries, streams, and riparian forests (Field and Reynolds 2011; Helfield and Naiman 2001; Naiman et al. 2002). Culturally, Pacific salmon are integral to the mythology, spiritual integrity, and livelihoods of Pacific First Nations (Augerot 2005; Jacob et al. 2010). Politically, Pacific salmon fisheries have been a large source of conflict in federal-provincial and federal-First Nations relations and internationally between Canada and the United States (Miller 2000; Rogers and Stewart 1997). To the general public, Pacific salmon are icons with abundant salmon indicating a healthy and productive environment.

Sockeye salmon (*O. nerka*) are one of the most iconic and valued species of Pacific salmon throughout the species range from Washington to Western Alaska in the eastern Pacific, and from northern Hokkaido to eastern Siberia in the western Pacific (Augerot 2005). It is the only anadromous Pacific salmon species for which a global assessment of population status has been conducted and incorporated into the IUCN Red List of Threatened Species™. Although the assessment concluded that sockeye salmon are of least concern at the global level, 31 % of the 62 populations for which data were available were classified as threatened, most of which are located in the southern end of the species distribution in North America (Rand 2011). Indeed, in the past 20 years, the abundance and productivity of many sockeye salmon stocks (i.e. populations or groups of different populations) from Washington to southeastern Alaska have declined (Peterman and Dorner 2011). In the Fraser River, one of the world's largest producers of sockeye salmon, such declines have prompted a federal judicial inquiry (Cohen 2010). Hypotheses have been put forward to explain the declines in several stocks of sockeye salmon, including climate change (McDaniels et al. 2010; Peterman et al. 2010).

The dynamics of sockeye salmon (and Pacific salmon in general) abundance and productivity is thought to be particularly sensitive to changes in climate because their anadromous life cycle exposes them to a variety of climate-related stressors in both marine and freshwater environments (Fleming and Jensen 2002). Indeed, paleolimnological records of δ^{15}N (a salmon-derived nutrient) taken from sediment cores of Alaskan lakes have revealed that large shifts in sockeye salmon abundance over the past 2,200 years occurred during major changes in the climate of the northeastern Pacific Ocean (Finney et al. 2002). Furthermore, these records have shown that the abundance of sockeye salmon closely tracked decadal-scale fluctuations in sea surface temperature (SST) over most of the past 300 years (Finney et al. 2000; Hill et al. 2009). In fact, fluctuations in the abundance of Pacific salmon over decadal-scales have been well documented during the past century and linked to major climate-driven changes in the marine environment occurring every 20–30 years (Beamish and Bouillon 1993; Beamish et al. 1997, 1999, 2004; Beamish and Noakes 2002; Irvine and Fukuwaka 2011; Mantua et al. 1997).

Various authors have examined the potential effects of future climate change on particular life stages of sockeye salmon, with much of the analysis done on Fraser River stocks (e.g. Bryant 2009; Hague et al. 2011; Healey 2011; Henderson et al. 1992; Hinch et al. 1995; Levy 1992; Martins et al. 2011; Rand et al. 2006). However, there is currently no synthesis of the documented effects of climate-related variables (i.e. climate variables and other physical variables influenced by climate) on sockeye salmon. In this paper, we present a review of the literature evaluating the effects of climate-related variables on three fundamental aspects of the life history of sockeye salmon—growth, phenology, and survival. Specifically, our objectives were to: (1) make an assessment of trends in the peer-reviewed literature linking sockeye salmon growth, phenology, and survival to climate-related variables; (2) synthesize the current state of knowledge on the effects of climate-related variables on growth, phenology, and survival of all life stages of sockeye salmon; and in view of our synthesis (3) identify critical knowledge gaps that warrant future research.

Literature compilation

We conducted a systematic literature search for peer-reviewed articles published in the English language that examined the effects of climate-related variables on sockeye salmon growth, phenology, and (or) survival. A keyword-based search was conducted using two academic search engines: ISI Web of Knowledge and Aquatic Sciences and Fisheries Abstracts. In both search engines, we used combinations of:

1. keywords for climate variables and physical variables potentially influenced by climate (climat* OR temperature$ OR precipitation OR rain* OR wind OR pressure OR flow$ OR discharge OR ice OR pH OR acid* OR salinity OR current$ OR "sea level" OR upwelling OR "global warming");
2. keywords related to the biological variables of interest (surviv* OR mortality OR productivity OR growth OR size OR weight OR energy OR phenology OR tim*);
3. the keywords sockeye and *Oncorhynchus nerka*.

The individual keywords were formatted before the search to represent various spellings of terms and forms of the word. For example, we used descriptors (popularly known as 'wild cards') such as an asterisk after a search term (e.g. surviv*) so that the search engines would then search for all words beginning with that term (e.g. 'survival' and 'survivorship'). Weekly publication alerts were set up in each search engine so that relevant papers matching the above keywords and published after the search date (June 2, 2011) could be included in our review prior to its submission.

All publications found were included into a database, after which duplicates were excluded. We then read the abstracts of all papers and kept in our database only those that were peer-reviewed, original research examining the effects of climate-related variables on growth, phenology, and (or) survival of sockeye salmon. We screened the reference section of the relevant papers to look for additional peer-reviewed publications not captured by our keyword-based search as well as for relevant grey literature (i.e. reports and theses). Additional grey literature dealing with the effects of climate-related variables on sockeye salmon growth, phenology and (or) survival was obtained from the Fisheries and Oceans Canada's (DFO) WAVES database and by browsing documents on the website of several organizations involved with the assessment and management of fisheries resources, particularly Pacific salmon, such as the Pacific Salmon Commission (PSC), the North Pacific Anadromous Fish Commission (NPAFC), the Pacific Fisheries Resource Conservation Council (PFRCC), and the North Pacific Marine Science Organization (PICES). Since we did not conduct a systematic and comprehensive search for grey literature, only peer-reviewed papers were used in our assessment of research trends. However, we did consider the grey literature in our synthesis of the current state of knowledge if the findings reported in them had not been published in the peer-reviewed literature.

Assessment of research trends in the peer-reviewed literature

To make an assessment of research trends in the peer-reviewed literature, we extracted several variables from each of the relevant papers. The variables were chosen as a means to detect temporal and spatial trends in publication, the range of life stages and variables assessed in the studies, and whether the studies were focusing on correlational or mechanistic (determined from results obtained in experimental manipulations in the laboratory and field, physiological sampling or from tracking of fish carrying electronic tags) associations between climate-related variables and sockeye salmon growth, phenology, and survival. Specifically, the variables extracted were:

1. publication decade;
2. country and region (or river) of stock origin (the latter was adapted from Hodgson and Quinn 2002; Hodgson et al. 2006);
3. life stage studied (for the purposes of this paper, we distinguish among nine stages in the sockeye

salmon life cycle: egg, alevin, fry, smolt [freshwater], post-smolt [marine], immature [open-ocean], returning adult [marine], returning adult [freshwater], spawner; adapted from McDaniels et al. 2010);

4. biological variable investigated (i.e. growth, phenology, and survival—the latter was estimated in the examined papers either indirectly [i.e. using productivity indices, which are a surrogate for survival during the life cycle; Peterman and Dorner 2011] or directly [i.e. through direct observation in the laboratory or the analysis of tagging data]);
5. climate-related variable investigated as to its effects on the biological variables (e.g. climate index [e.g. ocean regime, Pacific Decadal Oscillation or PDO, Aleutian Low Pressure Index or ALPI], temperature, precipitation, etc.);
6. type of study (i.e. correlational [including descriptive studies] or experimental);
7. whether the effect of climate-related variables on the fish physiology was investigated (i.e. yes, no);
8. whether electronic tags were used (i.e. yes, no).

Studies using productivity as a surrogate for survival during the life cycle associated it to climate-related variables at different time lags. For these studies, we considered the life stage investigated those that corresponded to the time lags used. Unless otherwise specified, all percent occurrences reported below refer to the total number of peer-reviewed publications examined.

Research trends

We found 1779 peer-reviewed publications as of June 2, 2011, using the aforementioned search keywords and criteria. After the removal of duplicates and other documents that did not aim to assess the relationship between a climate-related variable and sockeye salmon growth, phenology and (or) survival, only 72 papers remained in our database. Since our literature search was conducted, we have included eight additional papers in our database (eight papers found in weekly publication alerts received until February 3, 2012), for a total of 80 papers (Table 1). The earliest publication in this subset of publications appeared in the 1930s (Foerster 1937). In the subsequent three decades, only a few publications on the effects of climate-related variables on sockeye salmon growth, phenology, and (or) survival appeared in the peer-reviewed literature and virtually all of them dealt with freshwater life stages (Fig. 1). It was not until the 1970s that the number of publications started to increase considerably until the current decade, when in only three years the number of publications dealing with freshwater life stages is nearly the same as that published in the 2000s (Fig. 1). Publications dealing with marine life stages started to increase in number by the 1990s but overall they still lag behind those dealing with freshwater life stages (Fig. 1).

Among the biological variables of interest in this review, survival (55 %) has been the most frequently studied aspect of sockeye salmon life history in relation to climate, followed by growth (45 %) and phenology (30 %). The publications examined presented research findings for sockeye salmon stocks from Canada (57.5 %), United States (42.5 %), and Russia (3.8 %), while the country of stock origin was not specified in five publications (6.2 %). At a regional scale, sockeye salmon stocks from the Fraser River have been the most frequently studied, while those from Norton Sound (Western Alaska), Vancouver Island, the Yukon Territory, and Kamchatka Peninsula have been the least studied (Table 2). We only found three (3.8 %) peer-reviewed publications in the English language on sockeye salmon stocks from the western Pacific. The study of the effects of climate-related variables is biased towards survival in stocks of the Fraser River and Washington Coast, towards growth in Bristol Bay and Central B.C. Interior, and towards phenology in stocks of the Columbia River. In contrast, the number of studies is more evenly distributed across growth, phenology, and survival in stocks of the other regions (Table 2).

The effects of climate-related variables have been most frequently studied on fry and least studied on spawners (Table 3). Within each life stage, survival has been the biological variable most frequently investigated in relation to climate-related variables, with the exception of fry, immatures, and returning adults (marine) for which growth has been most frequently studied (Table 3). Approximately one-third (n = 29) of all studies were on marine life stages, but 97 % of those studies were largely correlational; that is, the authors were simply relating a biological variable (e.g. productivity, growth) measured upon the return migration to a climate-related variable lagged

Table 1 Characterization of 80 peer-reviewed papers investigating associations between climate-related variables and sockeye salmon growth, phenology, and (or) survival

Reference	Country	Region or river	Life stage	Biological variable	Climate variable	Study type	Physiology	Telemetry
Foerster (1937)	Canada	Fraser River	Smolt	Phenology	Temperature	Correlational		
Donaldson and Foster (1941)	USA	Columbia River	Fry	Growth, survival	Temperature	Experimental		
Brett (1952)	USA	Coastal Washington	Fry	Survival	Temperature	Experimental		
Tully et al. (1960)	Canada	Fraser River	Returning adult (SW)	Phenology	Temperature, ocean current	Correlational		
Hartman et al. (1967)	Canada, USA	Alaska Peninsula, Coastal B.C., Bristol Bay, Central B.C. Interior, Kodiak Island, Prince William Sound, SE Alaska Coast	Fry, smolt	Phenology	Ice break-up, temperature, wind	Correlational		
Major and Mighell (1967)	USA	Columbia River	Returning adult (FW)	Phenology	Temperature	Correlational		
Bjornn et al. (1968)	USA	Columbia River	Smolt	Phenology	Flow, ice break-up, temperature	Correlational		
Brett et al. (1969)	Canada	Coastal B.C.	Fry	Growth	Temperature	Experimental	*	
Sylvester (1972)	NA	NA	Fry	Survival	Temperature	Experimental		
Rogers (1973)	USA	Bristol Bay	Fry	Growth	Temperature	Correlational		
Shelbourn et al. (1973)	Canada	Central B.C. Interior	Fry	Growth	Temperature	Experimental		
Goodlad et al. (1974)	Canada	Fraser River	Fry	Growth	Temperature	Correlational		
Brett (1976)	Canada	Central B.C. Interior	Fry	Growth	Temperature	Experimental	*	
Ginetz and Larkin (1976)	Canada	Central B.C. Interior	Fry	Survival	Flow	Experimental		
Clarke et al. (1978)	Canada	Central B.C. Interior	Fry, smolt	Growth, phenology	Temperature	Experimental	*	
Biette and Geen (1980)	Canada	Central B.C. Interior	Fry	Growth	Temperature	Experimental		
Clarke et al. (1981)	Canada	Central B.C. Interior	Fry, smolt	Growth, phenology	Salinity, temperature	Experimental	*	
Ricker (1981)	Canada	Central B.C. Interior, Coastal B.C., Fraser River	Immature, returning adult (SW)	Growth	Salinity, temperature	Correlational		

Table 1 continued

Reference	Country	Region or river	Life stage	Biological variable	Climate variable	Study type	Physiology	Telemetry
Bower and Margolis (1985)	Canada	Central B.C. Interior	Fry, smolt	Survival	Salinity, temperature	Experimental		
Thorne and Ames (1987)	USA	Coastal Washington	Egg, alevin	Survival^{P}	Flow	Correlational		
Murray and McPhail (1988)	Canada	Fraser River	Egg, alevin, fry	Growth, phenology, survival	Temperature	Experimental		
Beacham and Murray (1989)	Canada	Fraser River	Egg, alevin, fry	Growth, phenology, survival	Temperature	Experimental		
Beacham and Murray (1990)	NA	NA	Egg, alevin, fry	Growth, phenology, survival	Temperature	Experimental		
Markevich and Bilenskaya (1991)	Russia	Kamchatka Peninsula	Egg, alevin	Growth, survival	Temperature	Experimental		
Henderson et al. (1992)	Canada	Fraser River	Spawner	Survival	Temperature	Correlational		
Hsieh et al. (1991)	Canada	Fraser River	Post-smolt, immature, returning adult (SW)	Growth, phenology, survival	Temperature, wind, ocean current	Correlational		
Rogers and Ruggerone (1993)	USA	Bristol Bay	Post-smolt, immature, returning adult (SW)	Growth	Temperature	Correlational		
Hinch et al. (1995)	Canada	Fraser River	Post-smolt, returning adult (SW)	Growth, survival^{P}	Temperature	Correlational		
Adkison et al. (1996)	Canada, USA	Bristol Bay, Fraser River	Egg, alevin, fry, smolt, post-smolt, immature, returning adult (SW, FW), spawner	Survival^{P}	Climate index, temperature	Correlational		
Quinn and Adams (1996)	USA	Columbia River	Returning adult (FW)	Phenology	Flow, temperature	Correlational		

Table 1 continued

Reference	Country	Region or river	Life stage	Biological variable	Climate variable	Study type	Physiology	Telemetry
Beamish et al. (1997)	Canada	Fraser River	Post-smolt, immature, returning adult (SW)	Survival^{P}	Climate index	Correlational		
Cox and Hinch (1997)	Canada	Fraser River	Immature	Growth	Temperature	Correlational		
Quinn et al. (1997)	USA	Columbia River	Returning adult (FW)	Phenology	Flow, temperature	Correlational		
Hendry et al. (1998)	USA	Coastal Washington	Egg, alevin, fry	Growth, phenology, survival	Temperature	Experimental		
Pyper and Peterman (1999)	Canada, USA	Bristol Bay, Central B.C. Interior, Cook Inlet, Fraser River	Immature, returning adult (SW)	Growth	Temperature	Correlational		
Edmundson and Mazumder (2001)	USA	Cook Inlet, Kodiak Island, Norton Sound, Prince William Sound, SE Alaska Coast	Fry	Growth	Temperature	Correlational		
McKinnell et al. (2001)	Canada	Coastal B.C.	Post-smolt	Survival^{P}	Wind	Correlational		
Hodgson and Quinn (2002)	Canada, USA	Alaska Peninsula, Bristol Bay, Central B.C. Interior, Coastal B.C., Columbia River, Cook Inlet, Fraser River, Kodiak Island, Prince William Sound, SE Alaska Coast, Vancouver Island, Coastal Washington, Yukon Territory	Returning adult (FW), spawner	Phenology	Temperature	Correlational		
Ishida et al. (2002)	NA	NA	Immature, returning adult (SW)	Growth	Climate index, temperature	Correlational		
Mueter et al. (2002a)	Canada, USA	Alaska Peninsula, Bristol Bay, Central B.C. Interior, Coastal B.C., Cook Inlet, Fraser River, Kodiak Island, Prince William Sound, Coastal Washington	Post-smolt	Survival^{P}	Climate index, temperature	Correlational		
Ostrovskii and Semenchenko (2002)	Russia	Kamchatka Peninsula	Fry	Growth	Temperature	Correlational		
Parensky et al. (2002)	Russia	Kamchatka Peninsula	Alevin, fry	Growth, phenology	Temperature	Correlational		
Rand (2002)	NA	NA	Immature	Growth	Temperature	Correlational		

Table 1 continued

Reference	Country	Region or river	Life stage	Biological variable	Climate variable	Study type	Physiology	Telemetry
Hyatt et al. (2003)	Canada, USA	Columbia River	Returning adult (FW)	Phenology	Climate index, temperature	Correlational		
Beamish et al. (2004)	Canada	Fraser River	Post-smolt	Survival^{P}	Climate index	Correlational		
Crossin et al. (2004)	Canada	Fraser River	Immature, returning adult (SW)	Growth	Climate index, temperature	Correlational		
Patterson et al. (2004)	Canada	Fraser River	Spawner	Phenology, survival	Flow	Experimental	*	
Mueter et al. (2005)	Canada, USA	Alaska Peninsula, Bristol Bay, Central B.C. Interior, Coastal B.C., Cook Inlet, Fraser River, Kodiak Island, Prince William Sound, Coastal Washington	Egg, alevin, fry, smolt, post-smolt, immature	Survival^{P}	Climate index, salinity, temperature, upwelling	Correlational		
Naughton et al. (2005)	USA	Columbia River	Returning adult (FW)	Survival	Flow, temperature	Correlational		*
Schindler et al. (2005)	USA	Bristol Bay	Fry	Growth	Ice break-up	Correlational		
Hodgson et al. (2006)	Canada, USA	Alaska Peninsula, Bristol Bay, Central B.C. Interior, Coastal B.C., Columbia River, Cook Inlet, Fraser River, Kodiak Island, Prince William Sound, SE Alaska Coast, Coastal Washington, Yukon Territory	Returning adult (SW, FW)	Phenology	Flow, temperature	Correlational		
Rand et al. (2006)	Canada	Fraser River	Returning adult (FW)	Survival	Flow, temperature	Correlational		
Farley et al. (2007)	USA	Bristol Bay	Post-smolt	Growth	Temperature	Correlational		
Newell et al. (2007)	USA	Coastal Washington	Spawner	Survival	Temperature	Correlational		*
Quinn et al. (2007a)	USA	Bristol Bay	Spawner	Survival	Temperature	Correlational		
Quinn et al. (2007b)	USA	Bristol Bay	Returning adult (SW)	Phenology	Temperature	Correlational		
Ruggerone et al. (2007)	USA	Bristol Bay, Alaska Peninsula	Post-smolt, immature, returning adult (SW)	Growth, survival^{P}	Climate index, temperature	Correlational		
Crossin et al. (2008)	Canada	Fraser River	Returning adult (FW)	Survival	Temperature	Experimental	*	*

Table 1 continued

Reference	Country	Region or river	Life stage	Biological variable	Climate variable	Study type	Physiology	Telemetry
Keefer et al. (2008)	USA	Columbia River	Returning adult (FW)	Survival	Flow, temperature	Correlational		*
Martinson et al. (2008)	USA	Kodiak Island	Post-smolt, immature, returning adult (SW)	Growth	Climate index	Correlational		
McKinnell (2008)	Canada	Fraser River	Fry, smolt, post-smolt, immature	Survival^{p}	Climate index	Correlational		
Farley and Trudel (2009)	NA	NA	Post-smolt	Growth	Temperature	Correlational		
Martinson et al. (2009)	USA	Kodiak Island	Post-smolt, immature, returning adult (SW)	Growth, survival	Climate index, precipitation, temperature, upwelling	Correlational		
Rich et al. (2009)	USA	Bristol Bay	Fry	Growth	Temperature	Correlational		
Cooperman et al. (2010)	Canada	Fraser River	Returning adult (SW, FW)	Survival	Salinity	Experimental	*	
Macdonald et al. (2010)	Canada	Fraser River	Returning adult (FW)	Survival	Flow, temperature	Correlational		
Mathes et al. (2010)	Canada	Fraser River	Returning adult (FW)	Survival	Temperature	Correlational	*	*
Nadeau et al. (2010)	Canada	Fraser River	Returning adult (FW)	Survival	Flow	Experimental	*	
Reed et al. (2010)	USA	Prince William Sound	Fry, smolt, post-smolt, immature, returning adult (SW, FW)	Growth, phenology, survival	Temperature	Experimental, correlational		
Ainsworth et al. (2011)	Canada	Coastal B.C.	Smolt	Survival^{p}	Flow	Correlational		
Crozier et al. (2011)	USA	Columbia River	Returning adult (FW)	Phenology, survival	Climate index, flow, temperature, upwelling	Correlational		*
Farley et al. (2011)	USA	Bristol Bay	Post-smolt	Growth	Temperature	Correlational		

Table 1 continued

Reference	Country	Region or river	Life stage	Biological variable	Climate variable	Study type	Physiology	Telemetry
Gale et al. (2011)	Canada	Fraser River	Returning adult (FW)	Survival	Temperature	Experimental	*	
Griswold et al. (2011)	USA	Columbia River	Smolt	Survival	Flow	Correlational		*
Martins et al. (2011)	Canada	Fraser River	Returning adult (FW)	Survival	Temperature	Correlational		*
Rogers and Schindler (2011)	USA	Bristol Bay	Egg, alevin, fry, smolt, post-smolt, immature	Survival^{P}	Climate index, ice break-up, temperature	Correlational		
Thomson and Hourston (2011)	Canada	Fraser River	Returning adult (SW, FW)	Phenology	Flow, ocean current, salinity, temperature, wind	Correlational		
Burt et al. (2012)	Canada	Fraser River	Egg, alevin, fry	Growth, phenology, survival	Temperature	Experimental		
Jeffries et al. (2012)	Canada	Fraser River	Returning adult (FW)	Survival	Temperature	Experimental	*	
Martins et al. (2012)	Canada	Fraser River	Returning adult (FW)	Survival	Temperature	Correlational		*

References are ordered by year of publication and first author. For studies using productivity as a measure of survival (denoted by survival^{P} under Biological variable), the life stages investigated were determined based on the time at which the climate-related variable was lagged for in correlation-type analyses. The only exception was Reed et al. (2010), for which the effect of lake conditions, including temperature, was assumed to have affected the smolt-to-adult survival (i.e. a carry-over effect). In studies dealing with multiple life stages, not all biological or climate-related variables were necessarily investigated for all stages. The asterisk under Physiology indicates whether the study assessed the effect of a climate-related variable on the fish physiology, and under Telemetry indicates whether electronic tags were used to track fish

SW saltwater, *FW* freshwater

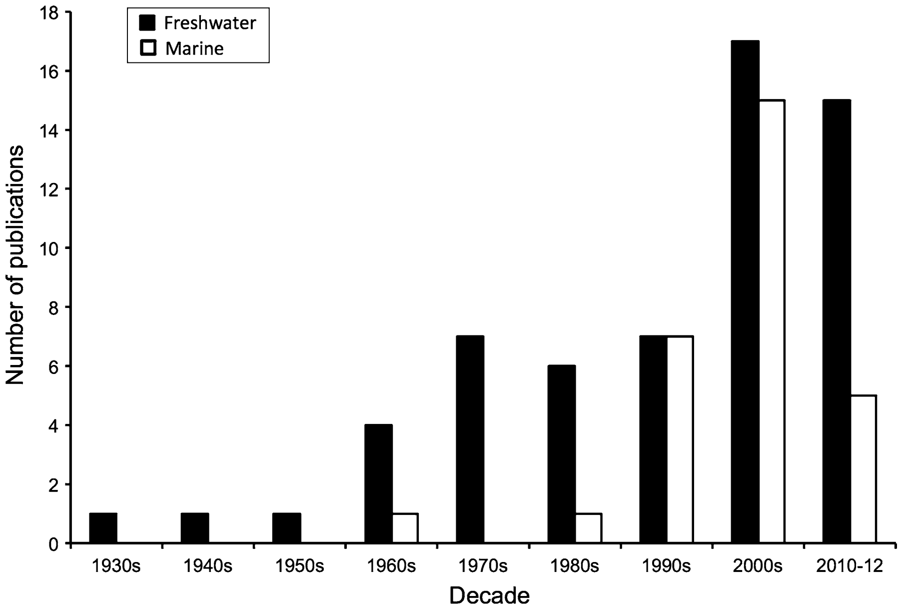

Fig. 1 Number of publications on the effects of climate-related variables on sockeye salmon growth, phenology, and (or) survival by decade and environment where life stage studied occurs

Table 2 Number (% of 80 publications reviewed) of peer-reviewed publications that investigated the effects of climate-related variables on sockeye salmon growth, phenology, and (or) survival by country and region or river of stock origin

Country and region or river of stock origin	Number of publications (%)			
	Growth	Phenology	Survival	Total
Canada				
B. C. Coast	2 (2.5)	2 (2.5)	4 (5)	8 (10)
Central B. C. Interior	7 (8.8)	5 (6.3)	4 (5)	14 (17.5)
Fraser River	10 (12.5)	10 (12.5)	23 (28.8)	33 (41.3)
Vancouver Island	0 (0)	1 (1.3)	0 (0)	1 (1.3)
Yukon Interior	0 (0)	2 (2.5)	0 (0)	2 (2.5)
Russia				
Kamchatka Peninsula	3 (3.8)	1 (1.3)	1 (1.3)	3 (3.8)
USA (Alaska)				
Alaska Peninsula	1 (1.3)	3 (3.8)	3 (3.8)	6 (7.5)
Bristol Bay	8 (10)	4 (5)	6 (7.5)	17 (21.3)
Cook Inlet	2 (2.5)	2 (2.5)	2 (2.5)	6 (7.5)
Kodiak Island	3 (3.8)	3 (3.8)	3 (3.8)	8 (10)
Norton Sound	1 (1.3)	0 (0)	0 (0)	1 (1.3)
Prince William Sound	2 (2.5)	4 (5)	3 (3.8)	7 (8.8)
Southeast Alaska Coast	1 (1.3)	3 (3.8)	0 (0)	4 (5)
USA (Pacific Northwest)				
Columbia River	1 (1.3)	8 (10)	5 (6.3)	12 (15)
Washington Coast	1 (1.3)	3 (3.8)	6 (7.5)	8 (10)
Not specified	4 (5)	1 (1.3)	2 (2.5)	5 (6.3)

Country and region or river of stock origin are ordered alphabetically. The values under column Total do not always equal the sum of the values in the other columns because some studies investigated the effects of climate-related variables on more than one biological variable

by a time when sockeye salmon would be in one of their marine life stages. In contrast, a larger proportion of the studies on the freshwater life stages were experimental (40.7 % of the studies on freshwater life stages, n = 59). Furthermore, tracking of fish (particularly adults) equipped with electronic transmitters or

Table 3 Number (% of 80 publications reviewed) of peer-reviewed publications that investigated the effects of climate-related variables on sockeye salmon growth, phenology, and (or) survival by life stage

Life stage	Number of publications (%)			
	Growth	Phenology	Survival	Total
Egg	NA	NA	10 (12.5)	10 (12.5)
Alevin	7 (8.8)	6 (7.5)	9 (11.3)	11 (13.8)
Fry	18 (22.5)	6 (7.5)	11 (13.8)	29 (36.3)
Smolt	0 (0)	6 (7.5)	8 (10)	13 (16.3)
Post-smolt	9 (11.3)	0 (0)	13 (16.3)	19 (23.8)
Immature	11 (13.8)	0 (0)	8 (10)	17 (21.3)
Returning adult (marine)	10 (12.5)	5 (6.3)	6 (7.5)	18 (22.5)
Returning adult (freshwater)	NA	8 (10)	15 (18.8)	22 (27.5)
Spawner	NA	2 (2.5)	5 (6.3)	6 (7.5)

Life stages are ordered as they occur in the sockeye salmon life cycle. Growth is not applicable for eggs, returning adults in freshwater, and spawners. Time of hatching was considered a phenological attribute of alevins, instead of eggs. Spawner survival refers to pre-spawn mortality in this semelparous species. The values under column Total do not always equal the sum of the values in the other columns because some studies investigated the effects of climate-related variables on more than one biological variable

physiological sampling and evaluation, which can both provide a better understanding of the mechanisms through which climate-related variables affect fish biology and ecology (Cooke et al. 2004b, Cooke et al. 2008), were conducted predominantly on freshwater life stages (telemetry: 15.3 %; physiological sampling/evaluation: 18.6 %, of the studies on freshwater life stages), whereas no study on marine life stages used telemetry and only one (3.4 % of studies on marine life stages) investigated the fish physiology. Among the climate-related variables, the most frequently investigated as to its effects on sockeye salmon was temperature (83.4 %), followed by flow (20 %), various climatic indices (17.5 %), date of ice break-up (6.3 %), salinity (6.3 %), wind (5 %), oceanic currents (3.8 %), upwelling (3.8 %), and precipitation (1.3 %).

Synthesis of the documented effects of climate on sockeye salmon life stages

Eggs and alevins

The growth, phenology, and survival of sockeye salmon eggs and alevins have been examined at a broad range of temperatures in the laboratory (1–16 °C). The relationship between egg survival (i.e. fertilization to hatch) and temperature is variable among studies but point to a maximum around 8 °C, with survival decreasing faster towards the upper than the lower end of the range of incubation temperatures (Beacham and Murray 1989, 1990; Burt et al. 2012; Hendry et al. 1998; Markevich and Bilenskaya 1991; Murray and McPhail 1988). In contrast, alevins (i.e. hatch to emergence from the gravel) are tolerant to the wide range of tested temperatures (Beacham and Murray 1989, 1990; Murray and McPhail 1988). Burt et al. (2012) have found that, despite post-hatching rearing at a common cool temperature (6.9 °C), alevins and fry that had been incubated at warm temperatures (14–16 °C) persisted suffering higher mortality than those that had been incubated at a cool temperature (12 °C).

Relationships between incubation temperature and alevin growth, as estimated from the length and body mass of fry upon emergence, showed that maximum sizes are normally attained between 4 and 8 °C (Beacham and Murray 1989, 1990; Hendry et al. 1998; Markevich and Bilenskaya 1991; Murray and McPhail 1988). All studies consistently showed that time to hatch and emergence from the gravel is inversely related to temperature (Beacham and Murray 1989, 1990; Burt et al. 2012; Hendry et al. 1998; Murray and McPhail 1988; see also Parensky et al. 2002). In the field, emergence of fry has been observed to begin when temperatures reach 3.3–4.4 °C in Fraser River streams (Brannon 1972).

Laboratory studies also showed that the effects of temperature on growth, phenology, and survival of eggs and alevins vary among stocks. For example, in the Fraser River, eggs from the interior-spawning Adams River stock had higher survival at low incubation temperature (2 °C) than the coastal-spawning Weaver Creek stock, but lower alevin survival at a high temperature (15 °C). Moreover, eggs from the Adams River stock developed faster at all temperatures and hatched proportionally larger alevins at low temperature than did eggs from the Weaver Creek stock. Interestingly, Adams River sockeye salmon incubate their eggs at colder temperatures in the wild when compared to Weaver Creek fish (Beacham and Murray 1989). Such a close correspondence between the developmental biology of sockeye salmon eggs and local incubation temperatures is well documented for spatially-separated populations (Brannon 1987), but this phenomena occurs even at more localized spatial scales among different run-timing groups spawning in the same stream. Hendry et al. (1998) showed that, in the Cedar River, eggs collected from fish spawning in October survived and grew better at a incubation temperature of (12.5 °C) than those collected from fish spawning in the colder months of November and December.

Assessments of the relationships between productivity and climate-related variables at a lag corresponding to incubation time have indicated no relationship between egg and alevin survival and the value of the ocean-wide scale PDO index (Mueter et al. 2005; Rogers and Schindler 2011). At regional scales, there is a negative association between SST and survival towards the end of the winter in stocks from Washington and British Columbia, but a positive association in stocks from Alaska (Mueter et al. 2005). At the stream level, there is an exponential decrease in survival with increasing discharge, as measured during the entire incubation period (Thorne and Ames 1987). Such a relationship is likely a reflection of increased scouring mortality caused by high discharge during periods of increased rainfall (Steen and Quinn 1999). At finer temporal scale, it has been suggested that increased rainfall during spawning time improves egg survival by increasing the wetted area available for spawning, presumably because it reduces mortality caused by superimposition of eggs (Brett 1951) and predation risk. Collectively, these findings suggest that fine spatial and temporal scales and regional climate conditions are more important in determining egg and alevin survival than large-scale, ocean-wide climate conditions.

Fry

The observation that sockeye salmon fry migrations from the spawning streams to rearing lakes occur later in the spring after colder incubation periods (Hartman et al. 1967; Macdonald et al. 1998) is consistent with the slower rate of egg and alevin development under low temperatures. Experiments conducted in artificial streams have revealed that predation mortality of migrating fry is increased at low water velocity (Ginetz and Larkin 1976), while bioenergetic modeling indicated that predation on migrating fry is increased at warm temperatures (Beauchamp 1995). Once fry reach their rearing lakes, they typically spend one or two years growing before migrating to sea (Burgner 1991; Quinn et al. 2009). In the laboratory, the single optimum temperature for growth of lake fry fed ad libitum is 15 °C, but this optimum decreases with reduced food rations (Donaldson and Foster 1941; Biette and Geen 1980; Brett et al. 1969; Brett 1976; Burgner 1987; Shelbourn et al. 1973). However, observations that fry undergo daily vertical movements wherein they move to the warm surface waters of lakes at dusk and dawn to feed and return to cooler depths at other times suggest that they do not have a single optimum temperature (Brett 1971). In fact, it has been shown that fry subjected to a diel temperature cycle in the laboratory similar to that experienced during their vertical movements in the wild (i.e. 4.5–17 °C) grew better than those subjected to constant temperatures (Biette and Geen 1980; Clarke 1978). Nonetheless, sockeye salmon fry vertical migrations cannot be fully explained by a foraging or bioenergetics advantage (Clark and Levy 1988), and it also seems to serve as an predator avoidance strategy (Scheuerell and Schindler 2003).

In the Fraser River, comparisons of fry growth during the rearing period among lakes of different mean water temperature suggest that growth is enhanced in warmer lakes (Goodlad et al. 1974). Consistent with this finding, Reed et al. (2010), using a reverse common-garden experiment (i.e. releasing sockeye salmon fry from a single population into two different Alaskan lakes—Summit Lake and Crosswind Lake), showed that fry grew better at the warmer, more productive Crosswind Lake. Furthermore, analyses of inter-annual relationships between growth and temperature (or date of ice break-up) have generally revealed that fry growth is positively related to temperature (or negatively related to date of ice breakup) during lake residence (Edmundson and Mazumder 2001; Ostrovskii and Semenchenko 2002; Rich et al. 2009; Rogers 1973; Schindler et al. 2005; but see Goodlad et al. 1974). This relationship in northern lakes likely results from an increase in fry metabolic rates (Edmundson and Mazumder 2001) and food availability (Schindler et al. 2005), both incurred by warm temperatures. For example, the warming trend of Lake Aleknagik was accompanied by increased zooplankton density, particularly *Daphnia* spp., which is the main prey of sockeye salmon fry. Concomitant with these changes was an increase in fry growth during their first year of lake residence (Schindler et al. 2005). A similar effect of warming trends on fry growth was observed in Lake Iliamna where temperatures were positively associated with fry size, suggesting that the length of the growing season and (or) the density of zooplankton have increased (Rich et al. 2009). In contrast, warming trends in a southern lake that does not freeze (Lake Washington) were associated with a decline in *Daphnia* spp. density (Winder and Schindler 2004a, b). Moreover, it has been taking longer for the most valuable prey *D. pulicaria* to reach a threshold density at which fry start feeding on them. Consequently, fry have had to rely on less valuable prey for longer periods, which has possibly reduced their growth (Hampton et al. 2006).

In general, survival has been found to increase with increasing temperature experienced by fry in stocks examined in Alaska, though there is substantial variability among stocks in such a relationship (Adkison et al. 1996; Mueter et al. 2005; Reed et al. 2010; Rogers and Schindler 2011). In contrast, there is some indication that survival of fry from Washington and British Columbia stocks decreases in warm years (Adkison et al. 1996; Mueter et al. 2005). Although the direct effects of temperature are unlikely the cause of mortality in these southern regions, as fry are able to move to cooler lake depths to avoid stressful temperatures (Brett 1971), increased mortality due to higher predation rates is possibly implicated. Sylvester (1972) showed that fry exposed to juvenile coho salmon (*O. kisutch*) in the laboratory suffered significantly more predation mortality at a warm (17 °C) than at a cool temperature (7 °C). Moreover, bioenergetic models have indicated that predation of the northern pikeminnow (*Ptychocheilus oregonensis*) on salmonid fry in the Columbia River would have been 26–31 % higher during historically warm climate periods (1–2 °C difference between warm and cool periods). Similar predation rate estimates on salmonid fry during warm and cool climate periods were also found for other fish predators such as smallmouth bass (*Micropterus dolomieu*) and walleye (*Stizostedion vitreum*) (Petersen and Kitchell 2001).

Parasites and associated diseases may also play a role in temperature-related mortality of sockeye salmon fry. Bower and Margolis (1985) showed that fry inoculated with the haemoflagellate parasite *Cryptobia salmositica* had higher mortality rates when held at 13 °C than at 5 °C. However, fish held at 20 °C did not develop heavy infections and no mortalities were observed possibly because such a high temperature was suboptimal for development of the parasite. No relationship between temperature (over a range of 11–14 °C) and infestation rates with the tapeworm *Triaenophorus crassus* have been found in a recent study on sockeye salmon fry from Alaska (Bentley and Burgner 2011).

Smolts and post-smolts

Photoperiod is regarded as the primary cue to initiate the smoltification process and downstream migration in sockeye salmon, with temperature acting as a modifying factor by influencing growth and the rates of physiological change related to the development of saltwater tolerance (Ban 2001; Clarke et al. 1978, 1981). Indeed, warm temperatures during the months preceding seaward migration have been generally associated with an advance in the timing of downstream movement in several stocks across the northeastern Pacific, though in some cases modifying effects of wind strength, flow, and precipitation have also been implicated (Bjornn et al. 1968; Foerster 1937; Hartman et al. 1967; Reed et al. 2010). Some studies have indicated that high survival during downstream migrations is associated with low discharge in the spring (Ainsworth et al. 2011), whereas others have suggested that survival is higher if the smolts encounter high discharge (Griswold et al. 2011).

At sea, the thermal conditions experienced by post-smolts during their first year of marine life are related to their growth and survival. Warm temperatures have been frequently associated with increased growth (but not energy density; Farley et al. 2011) and survival in Alaskan stocks (Adkison et al. 1996; Farley et al.

2007; Farley and Trudel 2009; Martinson et al. 2009; Rogers and Ruggerone 1993; Rogers and Schindler 2011; Ruggerone et al. 2007), whereas the same conditions have been associated with poor growth and survival of Fraser River sockeye salmon (Hinch et al. 1995; Hsieh et al. 1991; Reichardt 2005). The analysis of an extensive dataset including 120 stocks from Washington, British Columbia, and Alaska provided further evidence for such opposite effects of coastal SST on the early marine survival of southern and northern stocks of sockeye salmon (Mueter et al. 2002a, 2005). Because coastal SST experienced by southern and northern stocks are within the tolerance range of sockeye salmon, it has been suggested that temperature is actually a proxy for regional mechanisms affecting early marine survival (Mueter et al. 2002a, b, 2005). For example, in southern waters, warm SST is associated with increased abundance of fish predators as well as decreased upwelling and hence low food availability for post-smolts (Hinch et al. 1995; McKinnell et al. 2001; Mueter et al. 2002a). In contrast, in northern waters, warm SST is associated with intensified cyclonic winds and downwelling, which may result in increased food availability to post-smolts along the coast (Mueter et al. 2002a).

Immatures

The relationship between climate-related variables and survival of immature sockeye salmon in the open-ocean has been explored in only a few studies. Survival of Alaskan sockeye salmon was found to be positively correlated to SST and precipitation during most of their open-ocean residence, but negatively correlated to upwelling in their last year at sea (Martinson et al. 2009; Mueter et al. 2005). In contrast, survival of Fraser River sockeye salmon was found to be negatively correlated to the intensity of the ALPI in their first winter at sea and to SST in their last few months of ocean residence (Hsieh et al. 1991; McKinnell 2008).

Growth has been the most studied aspect of the life of immature sockeye salmon in the open-ocean, with variation in growth being linked with competitor density, precipitation (Martinson et al. 2008, 2009; Ruggerone et al. 2005, 2007), and temperature (Rand 2002). Although warm SST has been linked to increased growth during the open-ocean residence in some Alaskan stocks (Rogers and Ruggerone 1993), analysis of an extensive dataset of 69 stocks from Alaska and British Columbia, whose distributions overlap in the Gulf of Alaska, revealed that warm SST in the last months of ocean residence is related to small body size at maturity (Pyper and Peterman 1999). Similarly, warm temperature in the last year of ocean residence and (or) early stages of return migration were related not only to smaller body size (Cox and Hinch 1997; Hinch et al. 1995; Hsieh et al. 1991; McKinnell 1997; Ricker 1981), but also to lower levels of energy density (Crossin et al. 2004) in sockeye salmon from British Columbia rivers.

The reduced growth exhibited by sockeye salmon experiencing warm conditions towards the end of their ocean residence, a critical period when they acquire >50 % of their final mature body mass (Brett 1983), likely results from both direct and indirect effects of temperature. For example, warm waters experienced at this time will increase metabolic rates and thus reduce energy available for growth without commensurate increases in feeding (Cox and Hinch 1997; Hinch et al. 1995). In addition, warm temperatures possibly reflect oceanographic processes leading to decreased availability and limited distribution of food for salmon in the open-ocean (Aydin et al. 2000; Mackas et al. 2007; Richardson 2008). Furthermore, under warmer oceanic conditions, the amount of thermally suitable habitat for sockeye salmon decreases (Abdul-Aziz et al. 2011; Azumaya et al. 2007; Welch et al. 1995, 1998), potentially leading to increased density of competitors for food (Ruggerone et al. 2005, 2007; Martinson et al. 2008).

Returning adults

Temperature experienced at the end of the ocean residence is closely related to the arrival timing of return migrating sockeye salmon to coastal waters. After a spring of warm SST, Alaskan stocks tend to arrive early in coastal waters, whereas those from the Fraser River tend to arrive later (Blackbourn 1987; Hodgson et al. 2006; Hsieh et al. 1991; Tully et al. 1960; but see Quinn et al. 2007b). Presumably, such arrival timing patterns occur because of the northward distribution of sockeye salmon under warm oceanic conditions (Welch et al. 1995), leading to a shorter and longer migration distance for northern and southern stocks, respectively (Hodgson et al. 2006).

The freshwater migration timing of various sockeye salmon stocks has been linked to the thermal and flow regime of their natal rivers (Hodgson and Quinn 2002; Hodgson et al. 2006). Hodgson et al. (2006) found that, for some stocks, the freshwater migration tends to start early in years when temperatures are warm and flows are low (see also Crozier et al. 2011). Furthermore, the upstream migration of sockeye salmon is interrupted when they encounter temperatures above 21 °C, as has been observed in stocks bound for the upper Columbia River, leading to substantial delays in reaching the spawning grounds (Hyatt et al. 2003; Major and Mighell 1967). Possibly as an adaptive response to long-term warming of the Columbia River, sockeye salmon have advanced their freshwater migration approximately by 6–11 days since the 1950s (Crozier et al. 2011; Quinn and Adams 1996; Quinn et al. 1997).

Recently, an unusual shift in river entry timing towards warmer periods of the summer has occurred in some stocks of Fraser River sockeye salmon (Cooke et al. 2004a). These stocks are collectively known as Late-run and are unique among Fraser River sockeye salmon in that they historically held in the estuary for a period of 3–6 weeks prior to entering the river in the late summer or early fall. However, since 1995, these stocks have shortened or completely eliminated this holding period in the estuary and now enter the river during warmer summer temperatures (Hinch and Gardner 2009; Patterson et al. 2007). Oceanographic data from the past two decades have been used to examine potential relationships between environmental conditions and the early migration phenomenon. Thomson and Hourston (2011) found that a weakening of offshore winds in the direction of prevailing currents and reduced coastal salinity were associated with early entry timing in two Late-run stocks (Adams River and Weaver Creek, respectively). How these oceanographic variables, or other variables they affect, may influence the fish behaviour is still not fully understood. However, the fact that sockeye salmon experimentally exposed to freshwater entered the Fraser River nearly twice as fast as saltwater exposed fish support the hypothesis that coastal salinity can modify river entry timing in Late-run fish (Cooperman et al. 2009, 2010).

Upriver migration survival of adults is reduced at water temperatures >18 °C (Crossin et al. 2008; Crozier et al. 2011; Jeffries et al. 2012; Keefer et al. 2008; Macdonald et al. 2010; Martins et al. 2011; Mathes et al. 2010; Naughton et al. 2005). High levels of migration mortality can be caused by a combination of temperature-mediated factors. First, warm river temperatures increase energy use in sockeye salmon and migration failure can occur if energy reserves fall below a critical threshold (Rand et al. 2006). Second, exposure to high water temperature increases the rate of development of pathogens in sockeye salmon (Crossin et al. 2008), causing physiological stress, decreased swimming performance, and disease (Bradford et al. 2010a; Wagner et al. 2005; Tierney and Farrell 2004). Finally, warm temperature (i.e. 15–18 °C, depending on the stock) reduces aerobic scope in sockeye salmon, limiting the fish's ability to allocate energy to essential tissues during the migration (Eliason et al. 2011; Lee et al. 2003). Under extreme water temperatures, aerobic scope is reduced to such an extent that continued migration can lead to anaerobic activity, exhaustion, and death by lactic acidosis or cardiac collapse (Farrell et al. 2008).

Recent physiological studies on adult migrants have suggested that Fraser River sockeye salmon stocks can differ in their thermal tolerance in a manner that corresponds to temperatures experienced by each stock during historic migrations (Farrell et al. 2008; Lee et al. 2003). Indeed, the relationship between water temperature and stock-specific migration survival is consistent with their measured thermal tolerance, with more thermal tolerant stocks having higher migration survival at warm temperatures (Eliason et al. 2011; Martins et al. 2011). Furthermore, recent studies have revealed that migration survival of female Fraser River sockeye salmon is lower than that of males at warm temperatures (Crossin et al. 2008; Martins et al. 2012). This may occur because females have higher levels of cortisol compared to males at a similar level of maturation (Hruska et al. 2010; Jeffries et al. 2012; Roscoe et al. 2011; Sandblom et al. 2009), so stressful temperatures experienced during the spawning migration could have greater detrimental effects to females (e.g. increase their likelihood of being immuno-compromised and thus less resistant to pathogens). Survival during the spawning migration can substantially improve when sockeye salmon are able to behaviourally thermoregulate by making use of thermal refuges, such as deep portions of lakes and cold tributaries (Mathes et al. 2010).

Survival of adult migrating sockeye salmon in the Columbia River was found to be higher under high flow conditions, a finding that more likely reflects the inverse relationship between temperature and discharge (Naughton et al. 2005; Keefer et al. 2008). In the Fraser River, extremely high flows (>7,000 m^3/s) during the spawning migration have been implicated in reduced levels of migration survival in sockeye salmon, particularly in stocks that enter the river late in the spring (i.e. Early Stuart) and early in the summer (i.e. Early Summer stocks), when flows are the highest because of the spring freshet (Macdonald et al. 2000b, 2010). These results are consistent with bioenergetic models that indicate that energy exhaustion during upriver migrations can occur in high flow years, which can result in increased migration mortality (Rand et al. 2006). Although sockeye salmon experimentally exposed to fast (0.4 $m\ s^{-1}$) water velocities for 18 days used significantly more energy than fish exposed to low (0.1 $m\ s^{-1}$) water velocities, no differences in survival were observed between the two treatment groups (Nadeau et al. 2010).

Spawners

High temperatures encountered by sockeye salmon during the spawning migration can even affect fish after they have successfully arrived on the spawning grounds by increasing the chances that they die before successful spawn (i.e. pre-spawn mortality or egg retention). High levels of pre-spawn mortality have been reported for some sockeye salmon stocks that encountered warm temperatures during migration and (or) on the spawning grounds (Bradford et al. 2010b; Cooper 1982; Gilhousen 1990; Newell et al. 2007; Quinn et al. 2007a). In most cases, the connection between warm temperature and pre-spawn mortality is associated with increased prevalence of disease (Bradford et al. 2010b; Gilhousen 1990). Relationships between pre-spawn mortality and thermal conditions have not been detected for a Fraser River stock experiencing a range of cool temperatures (8.1–12.9 °C) on the spawning grounds from 1950 to 1989 (Henderson et al. 1992).

There is also some evidence that the effects of adverse river conditions encountered by sockeye salmon migrants may be passed on to their offspring, resulting in low progeny survival (Macdonald et al. 2000a). For example, Patterson (2004) showed that high levels of pre-spawn mortality in a stock of Fraser River sockeye salmon, presumably as a result of difficult migratory conditions (high flows), were related to low survival from egg to fry.

Discussion

Our review of the effects of climate-related variables on sockeye salmon growth, phenology, and survival identified several important aspects of the current state of knowledge. First and not surprisingly, associations between temperature and growth, phenology, or survival have been uncovered for all the life stages of sockeye salmon. This mirrors the predominance in the use of temperature as a variable in experimental and correlational studies, as revealed by our quantitative assessment of the peer-reviewed literature, and is itself a reflection of the well-known fact that temperature is the *master environmental factor* for fish (Fry 1971). Indeed, temperature governs physiological and ecological aspects of the sockeye salmon life history (Brett 1971). However, it must be noted that associations between temperature and growth, phenology, or survival revealed in correlational studies not always reflect direct effects of temperature on sockeye salmon. Temperature affects various other physical (IPCC 2007) and biological (e.g. Petersen and Kitchell 2001; Schindler et al. 2005) processes that are important for sockeye salmon and thus, in some cases, it can be just a surrogate for the effects of other factors on the fish growth, phenology, and survival.

Second, sockeye salmon seem to be more strongly influenced by climate-related variables, particularly temperature, experienced on regional rather than on large, ocean- or continental-wide scales. This has been suggested by several authors based on the observation of stronger correlations in survival and growth among geographically close stocks (i.e. <500 km apart) as well as in SST measured in coastal stations located at relatively short distances from one another (i.e. <800 km) (Mueter et al. 2002b; Peterman et al. 1998; Pyper et al. 1999). Furthermore, local and regional measures of temperature frequently explain the variability in sockeye salmon survival better than large-scale climate indices such as the PDO (e.g. Mueter et al. 2002a, 2005; Rogers and Schindler 2011). The stronger influence of regional climate conditions on processes (e.g. food productivity, predation mortality, thermal habitat) affecting sockeye salmon is consistent with the opposite effects of temperature on post-smolts growth and survival between southern and northern stocks of the northeastern Pacific (e.g. Mueter et al. 2002a, 2005; Reichardt 2005; Rogers and Ruggerone 1993).

Third, at local and regional scales, the effects of temperature on survival greatly differ among and within stocks. For example, Rogers and Schindler (2011) have shown that the relationship between survival and temperature, as well as other climate-related variables, varied in both strength and sign among several Alaskan stocks, possibly due to interactions between stock-specific life history and local environmental conditions. Indeed, among- and within-stock variability in the response of survival to temperature seems to reflect local adaptation—an evolutionary process leading to maximization of individual fitness in their local habitats (Fraser et al. 2011; Taylor 1991)—to thermal conditions their antecessors have experienced (e.g. Beacham and Murray 1989; Hendry et al. 1998; Martins et al. 2011). The best documented case comes from adult migrating Fraser River sockeye salmon, for which population specific aerobic scope is maximal at water temperatures most frequently encountered during historical river migrations, suggesting thermal adaptation. Some populations (e.g. Chilko Lake) are very resilient to high temperatures, whereas others are less able to cope (e.g. Weaver Creek) (Eliason et al. 2011). A recent field telemetry study involving Fraser River sockeye salmon confirmed that upriver migrating adults perished at temperatures that were stock-specific, and also confirmed that Chilko Lake sockeye salmon survival was the least impacted by warm river temperatures (Martins et al. 2011).

Lastly, it is likely that the effects of climate-related variables experienced by sockeye salmon in one life stage are carried over to subsequent life stages (i.e. carry-over effects; Harrison et al. 2011). For example, sockeye salmon rearing in the warmer, more productive Crosswind Lake in Alaska had better smolt-to-adult survival than fish originating from the same population but rearing in the cooler, less productive Summit Lake (Reed et al. 2010). Carry-over effects are particularly relevant in the context of recent and future climate warming as impacts on individual life stages can worsen the impacts on subsequent stages (Healey 2011). For example, the observation that sockeye salmon experiencing warm temperature at the end of their ocean residence return to the Fraser River with lower levels of somatic energy (Crossin et al. 2004) suggest that they may now have less energy available to fuel their upriver migration and to keep them alive for long enough on the spawning grounds. Moreover, sockeye salmon feeding in a warmer ocean have returned smaller than in the past (Cox and Hinch 1997). Thus, females may now be digging shallower nests (Steen and Quinn 1999), which may have increased the likelihood of egg mortality due to scouring. Furthermore, the warmer river temperatures now encountered by females during the spawning migration exacerbate their mortality (Crossin et al. 2008; Martins et al. 2012), and possibly affect the quantity and quality of their eggs (Patterson 2004; Patterson et al. 2004). Evidence for such intergenerational effects of climate is starting to accumulate, though the research on Pacific salmon is in its infancy (reviewed in Burt et al. 2011). What has been done suggests that offspring survival decreases when female encounter stressful migration conditions (Macdonald et al. 2000a; Patterson 2004).

Whether future climate change, particularly warming, will have adverse or beneficial effects on sockeye salmon will clearly depend on the geographic region. The results of several publications examined in this review suggest that southern stocks (e.g. from Washington and British Columbia) may be adversely affected by climate change, while northern stocks (e.g. from Alaska) may prosper (i.e. have better growth and survival). However, this prediction may not hold with the prospect that future warming rates will be higher in more northern latitudes (IPCC 2007; Bryant 2009). Furthermore, this expectation is based on the assumption that the physical and biological process underlying the relationships between climate-related variables and sockeye salmon growth, phenology, and survival will remain unaltered with changes in the climate (Mueter et al. 2002a).

At a regional level, future climate change effects are likely to vary by stocks. Currently, quantitative assessments of the effects of future climate change on survival of different sockeye salmon stocks have been limited to adult migrating Fraser River fish. Martins et al. (2011) predicted that survival during the spawning migration would decrease 1–16 % (depending on the stock and river entry behaviour of Late-runs) if the summer water temperature in the Fraser River increases 2 °C over the next 100 years (Ferrari et al. 2007; Morrison et al. 2002). However, such predictions may be conservative as the models used to predict survival were not parameterized with salmonid critical temperatures (i.e. >20 °C), which are likely to occur more frequently in the future. In fact, it has been predicted that the number of days per year exceeding salmonid critical temperatures may triple in the Fraser River by the end of the century under a modest 2 °C mean warming (Hague et al. 2011). Energy depletion incurred by warm temperatures could become a significant cause of mortality during the upriver migration if a declining trend in gross somatic energy occurs in some Fraser River sockeye salmon stocks (Rand et al. 2006).

One caveat of such quantitative assessments of the effects of future climate warming on sockeye salmon, and most other fishes, is that they have rarely taken into account the potential for adaption to changes in the climate (but see Hague et al. 2011). Although there is some potential for tolerance to warm temperatures to evolve in sockeye salmon (Eliason et al. 2011), further evolutionary change may already be restricted in stocks that have historically experienced high temperatures (Carlson and Seamons 2008; Crozier et al. 2008). Phenological changes are likely to be one of the major responses of Pacific salmon to climate change (Crozier et al. 2008). One of the best examples of phenological changes in response to warming comes from the Columbia River, where sockeye salmon have started their spawning migration 6–11 days earlier than in the 1950s (Quinn and Adams 1996; Quinn et al. 1997), most likely due to an evolutionary response to thermal selection (Crozier et al. 2011). However, the rates of river warming have outpaced those of migration timing change and Columbia River sockeye salmon now experience temperatures on average 2.5 °C warmer than in the past (Quinn and Adams 1996). Similarly, recent individual-based modeling has indicated that future climate warming in the Fraser River will likely select for earlier spawning migration timing in a sockeye salmon stock (Early Stuart) and that such an evolutionary response could improve its chances for long-term persistence (Reed et al. 2011; see also Hague et al. 2011). In contrast, there are several examples of sockeye salmon stocks and other Pacific salmon species that have been shifting the onset of their spawning migration towards warmer periods (Cooke et al. 2004a; Taylor 2008). These examples illustrate the considerable uncertainty in predicting how organisms with complex life histories such as sockeye salmon will cope with or adapt to changes in the climate (Crozier et al. 2008).

Future research directions

Predicting the responses of sockeye salmon, and Pacific salmon more generally, to future climate change will require a much better understanding than we currently have of the effects of climate-related variables on this species. Perhaps the most pressing knowledge gap to remediate is how little is known on the mechanisms by which climate-related variables affect sockeye salmon at sea. It is not surprising that relatively little work has been conducted in this area due to the high costs and difficulties of tracking fish in the marine environment. However, the availability of a large-scale acoustic receiver array in the northeastern Pacific (i.e. Pacific Ocean Shelf Tracking or POST), and remarkable recent advances in electronic tagging technologies (and associated reductions in costs) over the past decade, such as the development of miniaturized tags, multi-sensor tags (i.e. which records variables related to fish behavior, physiology, and environmental conditions) and business card tags (i.e. tags applied to large marine animals that record information sent by transmitters implanted into fish and then transmit the data from themselves to satellite and underwater receivers) offer exciting opportunities for future research with sockeye salmon at sea (Cooke et al. 2004b, in press; Holland et al. 2009; Reddin et al. 2011; Welch et al. 2011; Wood et al. 2012).

Experimental manipulations are also needed to further our understanding of the effects of climate-related variables on sockeye salmon at sea. For example, smolts could be exposed to various biotic and abiotic treatments (e.g. different temperatures, food abundance and/or parasite loads) in the laboratory, acoustically tagged and released in the marine environment to investigate the impact of early marine life challenges on survival at sea (Welch et al. 2011; Wood et al. 2012). Oceans are also expected to become more acidic with future climate change (IPCC 2007) and such conditions are likely to impact fish both directly and indirectly (Ishimatsu et al. 2008; Melzner et al. 2009; Pörtner and Peck 2010). Currently, there is no empirical information on how the acidification of marine waters could affect sockeye salmon.

In freshwater, the majority of the work on the effects of temperature on the early life stages of sockeye salmon has been conducted in the laboratory, with comparatively few field studies examining how temperature, and other climate-related variables, influence their growth, phenology, and survival within streams and lakes. Field-based research on the early life stages should consider trophic-level responses with specific attention to the interaction of sockeye salmon with their prey and predators at different temperatures, given that some studies indicated that changes in temperature affect food availability (Hampton et al. 2006; Schindler et al. 2005; Winder and Schindler 2004a, b) and predation mortality (Petersen and Kitchell 2001; Sylvester 1972). Research in this area could include a long-term monitoring program of populations of sockeye salmon, prey and predators, and environmental conditions in their rearing lakes. In addition, future studies could involve experimental manipulations of nutrients, prey, and (or) predator densities at a range of temperatures in the field. Specific attention should also be directed at the effects of altered stream hydrology on egg survival since increases in precipitation patterns and associated flows during the time of incubation are expected to occur with climate change (Mote and Salathé 2010; Pike et al. 2008).

Because we specifically searched for papers published in English, the great majority of the research reviewed here was done with stocks from Canada and the United States, with greater bias towards work on stocks from only a few major systems (e.g. Fraser River, Columbia River, Bristol Bay). Since it is well known that sockeye salmon from different stocks vary substantially in their life history, habitats used, and thermal tolerance (Burgner 1991; Eliason et al. 2011), the understanding of the effects of climate-related variables on this species could greatly benefit from more information on stocks from regions in the northwestern Pacific (information that may be largely available in papers written in other languages [e.g. Russian or Japanese] but were not included in our search for papers published in English) and other less studied systems in North America. Multi-stock approaches to research on sockeye salmon have generated valuable information on stock-specific differences in their response to climate-related variables (e.g. Beacham and Murray 1989; Martins et al. 2011; Rogers and Schindler 2011), though the mechanisms underlying such variation are still poorly understood (but see Eliason et al. 2011). Such information would be important, for example, for a global-scale assessment of how different sockeye salmon populations will fare with future climate warming.

Within stock variation in response to climate-related variables should also be considered in future research programs. Recent studies of adult migrating Fraser River sockeye salmon have indicated significantly lower levels of survival in females compared to males when fish are exposed to warm temperatures (Crossin et al. 2008; Martins et al. 2012). Future research should look into the extent and physiological basis of survival differences between sexes and investigate the consequences of female-specific survival for the viability of sockeye salmon stocks in a warmer climate.

Although existing information suggest the possible occurrence of carry-over and intergenerational effects of climate-related variables on sockeye salmon, research is needed that formally verify and quantify such cumulative impacts across life stages and (or) generations for modeling stock-level impacts. Also required is research that examines the interaction of climate-related variables with other non-climate-related stressors, such as fishery activities. Sockeye salmon are typically harvested *en route* to spawning grounds, encountering different fishing gear types in both marine and river environments. Many fish are captured but escape, and some captured fish are intentionally released. It is well known that physiological and behavioural changes accompany fish capture and handling (Arlinghaus et al. 2007; Davis 2002), but the consequences of this to migration and spawning success are poorly understood for sockeye salmon or most Pacific salmon (Donaldson et al. 2011; Gale et al. 2011). There is also a growing body of evidence that fish captured under warmer temperatures are more likely to die after release (e.g. Dempson et al. 2002; Gingerich et al. 2007; Wilkie et al. 1996). With the prospect of future warming of rivers, it will be important to know how release or escape of captured fish interacts with river temperatures and affects their survival to spawning grounds (Gale et al. 2011). Finally, more research on the genetic and non-genetic mechanisms through which sockeye salmon could adapt to climate change continues to be needed (Crozier et al. 2008). Such studies will be critical to advance our understanding of how evolutionary and ecological mechanisms will interact in shaping sockeye salmon responses to future changes in the climate.

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