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Global climate change and potential effects on Pacific salmonids in freshwater ecosystems of southeast Alaska

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Abstract General circulation models predict increases in air temperatures from 1°C to 5°C as atmospheric CO_2 continues to rise during the next 100 years. Thermal regimes in freshwater ecosystems will change as air temperatures increase regionally. As air temperatures increase, the distribution and intensity of precipitation will change which will in turn alter freshwater hydrology. Low elevation floodplains and wetlands will flood as continental ice sheets melt, increasing sea-levels. Although anadromous salmonids exist over a wide range of climatic conditions along the Pacific coast, individual stocks have adapted life history strategies—time of emergence, run timing, and residence time in freshwater—that are often unique to regions and watersheds. The response of anadromous salmonids will differ among species depending on their life cycle in freshwater. For pink and chum salmon that migrate to the ocean shortly after they emerge from the gravel, higher temperatures during spawning and incubation may result in earlier entry into the ocean when food resources are low. Shifts in thermal regimes in lakes will change trophic conditions that will affect juvenile sockeye salmon growth and survival. Decreased summer stream flows and higher water temperatures will affect growth and survival of juvenile coho salmon. Rising sea-levels will inundate low elevation spawning areas for pink salmon and floodplain rearing habitats for juvenile coho salmon. Rapid changes in climatic conditions may not extirpate anadromous salmonids in the region, but they will impose greater stress on many stocks that are adapted to present climatic conditions. Survival of sustainable populations will depend on the existing genetic diversity within and among stocks, conservative harvest management, and habitat conservation.

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1 Introduction

Global temperatures are increasingly driven by greenhouse gas accumulation over the last 50 years (IPCC 2007). The response of Pacific salmon in Alaska to climate change is of ecological and social consequence. Alaska supports the greatest proportion of salmon harvested along the west coast of North America (Clark et al. 2006; Meacham and Clark 1994; Howe et al. 2001; Shaul et al. 2003). In contrast to most salmon stocks along the west coast of the US, most stocks in southeast Alaska maintain sustainable harvests and escapements (Baker et al. 1996; Halupka et al. 2000). The condition of salmon stocks in Alaska can be attributed largely to the absence dams, agriculture, and urbanization that have contributed to the decline of salmon stocks elsewhere (Nehlson 1997). Over-harvest has been an issue in the past in southeast Alaska (Meacham and Clark 1994) and in some watersheds and timber harvest has been and is still a concern (Koski et al. 1966; Murphy et al. 1986; Thedinga et al. 1989). However, the large land base, low human population, and numerous intact watersheds throughout southeast Alaska mitigate these effects on a region-wide scale (Bryant and Everest 1998). Furthermore, the large number of stocks in southeast Alaska represents an immense genetic reservoir that provides resiliency across the region for anadromous salmonid stocks (Halupka et al. 2003). The genetic diversity is manifested in a wide range of phenotypic adaptations to both small and large scale features. This biocomplexity is an important factor in the resilience of salmon stocks to a range of natural and anthropogenic disturbances (Hilborn et al. 2003).

The genetic and phenotypic diversity represents stocks that have adapted over centuries to environmental conditions particular to geographic location—north to south, mainland to island, east to west—and watershed conditions (Halupka et al. 2000). The physical geometry of watersheds and landscapes provides a template for some of these differences as does stock separation and isolation (Waples 1991). In addition to these, climatic factors play an important role in the development of specific stock characteristics. Temperature and hydrology control several critical stages in the life cycle of salmonids. During periods of rapid climate change, these can have significant effects on anadromous salmonid populations.

Southeast Alaska supports a diverse set of salmonids that depend on freshwater ecosystems. The five Pacific salmon include pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), sockeye (*O. nerka*), and chinook (*O. tshawytscha*) salmon. These form the basis of a significant commercial, sport, and subsistence fishery. Steelhead and rainbow trout (*O. mykiss*), cutthroat trout (*O. clarki*), Dolly Varden (*Salvelinus malma*) are important in varying degrees to both sport and subsistence fisheries. These fish employ a wide range of life histories and their response to climate change will be complex and differ among species.

Life history strategies of anadromous salmonids in Alaska separate into two groups on the basis of how they use the freshwater environment (Groot and Margolis 1991). Pink and chum salmon spawn in freshwater and the fry emerge from the gravel from April through May and migrate to the ocean in a few weeks (Fig. 1). Pink and chum salmon often spawn in the lower reaches of rivers; however, some chum salmon may migrate considerable distances upstream in rivers such as the Yukon and Frazier (Salo 1991). Sockeye, Chinook, and coho salmon spawn in freshwater, but the fry typically spend one or more years in freshwater after they emerge from the gravel.

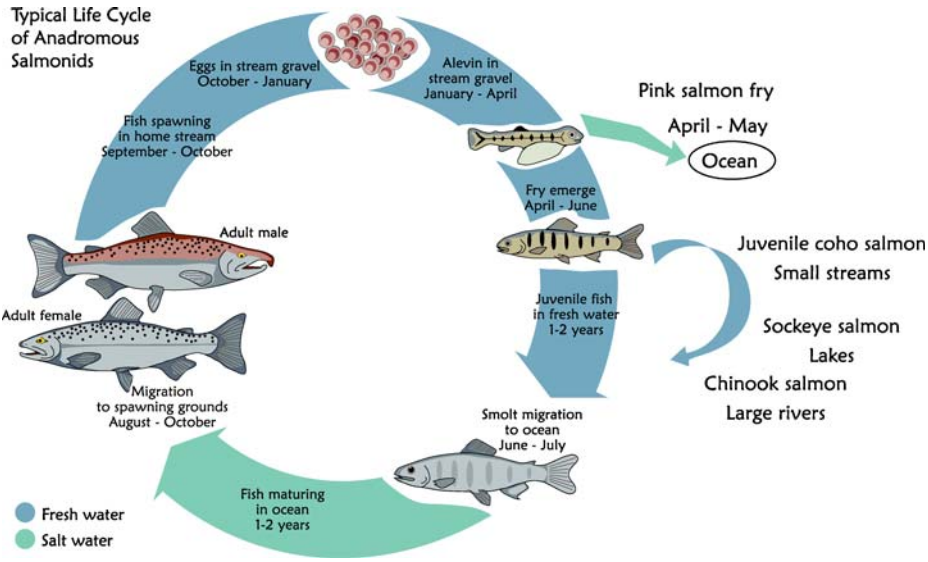


Fig. 1 Life cycle strategies of the five species of salmon (*Oncorhynchus*) found in southeast Alaska with those that rear in freshwater and those that migrate directly to the ocean

As a general pattern, Chinook salmon spawn in large rivers, coho salmon use small streams and sockeye salmon spawn in streams associated with lakes and to a lesser degree along lake margins. Juvenile sockeye salmon usually rear in lakes from 1 to 2 years (Burgner 1991; Quinn 2005).

Extreme variation occurs within the group, for example, some coho salmon juveniles may use lakes (Bryant et al. 1996). Some Chinook and sockeye stocks have subgroups that may migrate to the ocean shortly after emergence (Groot and Margolis 1991). Small populations of Chinook salmon are found in some small streams on Admiralty Island (Halupka et al. 2000). Scott and Crossman (1973) and Mecklenburg et al. (2002) describe the various life histories for each group. These variations are significant in as much as they illustrate the plasticity of salmonids to adapt to a range of environmental conditions and may be important in an environment of rapidly changing climatic conditions.

Salmon populations respond to variation in climate patterns in the marine environment (Beamish et al. 1999). Ocean temperatures driven by the Pacific Decadal Oscillation (PDO) have been shown to affect their survival (Hare and Mantua 2000; Mueter et al. 2002). Among other things, their results indicated that northern stocks, including Alaska, had higher survival rates during warmer periods, whereas, the southern stocks had lower early marine survival during warm periods. Similar results are reported by Hare et al. (1999). Sockeye salmon average length appeared to decrease with increasing temperatures (Pyper and Peterman 1999). However, ocean surveys of salmon populations suggest that thermal boundaries limit southern feeding areas in the Pacific Ocean. As the warm thermal boundary moves northward with global warming, ocean foraging area will decrease (Welch et al. 1998a, b).

Similar studies of the effects of changes in temperature regimes on Pacific salmon populations in the freshwater environment are limited.

This assessment examines potential responses of the five species of Pacific salmon found in southeast Alaska to climate change. The focus is on the freshwater phase of the life cycle of each species and potential effects of climatic changes. The three major climate change variables are temperature, precipitation (hydrology), and sea level. The purpose of this assessment is to identify potential effects and responses by each species, and to propose questions that can be used to quantitatively evaluate some of the effects and responses. Although the emphasis of the assessment and examples of potential effects are drawn from Pacific salmon stocks in southeast Alaska, the responses and effects may apply to stocks throughout their range. In regions where stocks are stressed potential responses may be more severe.

2 Climate change scenarios

Most assessments of the effects of climate change on both marine and freshwater ecosystems are based on general circulation models (GCM) that are large scale and complex (Smith and Tirpak 1989; Kalkstein 1991; IPCC 2007). Hauer et al. (1997) discuss the limitations of these models in their examination of climate change and freshwater ecosystems of the Rocky Mountain region of the USA. They use a methodology that nests GCMs into regional climate models (RCM) to simulate climate changes for their assessment of freshwater ecosystems of the Rocky Mountain region. In all scenarios commonly used in GCMs, increasing concentrations of CO_2 in the atmosphere result in increased atmospheric temperatures (Magnuson et al. 1990; Hauer et al. 1997; Schindler 1997). A RCM specific for Southeast Alaska is needed, but GCMs generally predict an increase from 1°C to 4.5°C during the next 100 years and that the effect will be greater near polar regions (Hengeveld 1990).

Three major effects are likely from increasing atmospheric temperatures. Temperatures in ocean and freshwater habitats will increase, precipitation intensity and distribution will change, and sea level will rise. The response of precipitation depends on location and season. Inland regions may experience increased drought, whereas, coastal regions may receive more rain during the fall and winter. One scenario suggests that intensity of rainfall is likely to increase (Trenberth 1999). Changes in winter snow pack and the time of spring melt will also occur (Stewart et al. 2004). As ocean temperatures increase, sea level is projected to increase (Wigley and Raper 1993). However, the increase of sea level relative to land is complicated by isostatic rebound (Peltier 2001).

Changes in temperature and precipitation are likely to have important consequences in freshwater ecosystems. In their systematic assessment of the effects of climate change in freshwater ecosystems of the Rocky Mountains, USA, Hauer et al. (1997) identify changes in community structure as temperatures increase in both streams and lakes with elimination or isolation of cold water fish species. They also point to the intensification of anthropogenic effects that include habitat degradation and introduction of non-native species. Eaton and Scheller (1996) estimate that habitat for cold and cool water fish could be reduced by about 50% under most scenarios in US streams. Using a bioenergetics model, McDonald et al. (1996) predicted a substantial decrease in lake trout in a lake in northern Alaska resulting from increased metabolic demands from higher temperatures accompanied by either reduction or no increase in food supply available to young of the year trout. In streams, increases in thermal regimes may reduce or eliminate cold water pool refuges important during the summer for cold water fish (Bagiun et al. 2000).

Various GCMs predict that mean temperatures will increase and most studies that examine fish response to an increase in temperatures within the predicted ranges show a trend of decreasing thermal habitat for cold water fish in both lakes and streams (Hauer et al. 1997; McDonald et al. 1996; Meisner 1990; Schindler 1997). In southeast Alaska, stream water temperatures range from freezing to about 20°C and generally are less than 10°C in most streams during most of the year (Fig. 2). Anadromous salmon in southeast Alaska are cold water species and have spawning, incubation, and growth characteristics that are tuned to these temperature ranges (e.g. Hodgson and Quinn 2002).

Precipitation directly influences hydrology, and stream and river discharges respond to precipitation. Salmonid life histories are intimately connected to discharge timing and stage in streams and rivers. Spawning generally occurs during periods of high flows for most species and changes in discharge patterns can adversely affect spawning success (Moscrip and Montgomery 1997). Coho salmon production has been shown to be related to discharge (Smoker 1955). Timing of high flows is critical both to spawning migration and to emigration of smolt in the spring and spring discharge regimes are often highly dependent on snow accumulations during the winter (Mote et al. 2003; Lawson et al. 2004; Stewart et al. 2004). Summer habitats are maintained by suitable flow regimes for stream rearing species and fall freshets provide access to off-channel refuges for over-winter habitats (Peterson 1982). Poff and Allan (1995) found ecological relationships between fish assemblages and stream flow variability, which would be modified with changes in hydrological regimes induced by climate change. Alterations in stream flows may also affect lake catchments. Schindler (1997) suggests that acidification may occur in streams accompanied by alkalization of lakes with decreasing discharge regimes, depending upon the surrounding geochemistry of the land base.

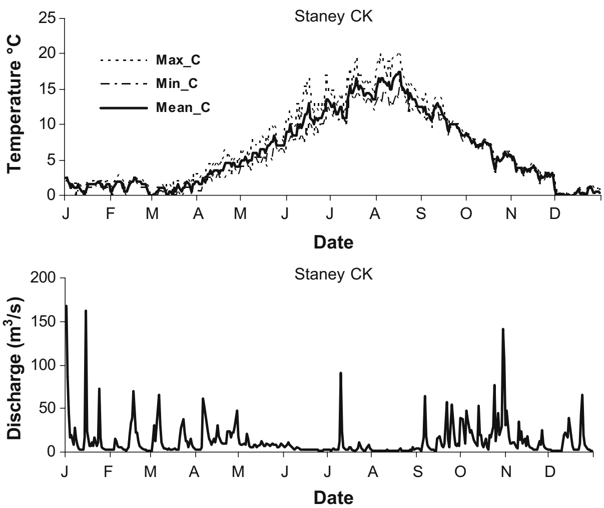


Fig. 2 The average daily mean, maximum, and minimum temperature and discharge for Staney Creek, Prince of Wales Island for 2007 (USGS)

Shifts in the amount, intensity, and form (snow vs. rain) of precipitation will alter the hydrological regimes of streams in southeast Alaska. Warming trends will also affect streams and rivers fed by glaciers. Most aspects of the life history of salmon are linked to hydrological patterns and seasonal freshets. Pacific salmon spawn during periods of high flows during the fall and fry migrate to the ocean as spring flows increase with snowmelt. Species rearing in fresh water depend on maintenance flows during the summer that may be sustained by snow melt and ground water sources that depend on snow melt at higher elevations (Hauer et al. 1997; Harr and McCorison 1979). The terrain in southeast Alaska is mountainous and weather patterns can be highly localized; however, stream and river discharge patterns are linked to precipitation and climatic events (Neal et al. 2002). Neal et al. (2002) observed lower summer flows and higher winter flows in an old-growth river in southeast Alaska for warmer periods than colder periods during Pacific Decadal Oscillations (PDO). A similar response could be expected with warmer atmospheric temperatures as a result of global climate change.

Sea level is linked to climate change and is projected to increase with global warming (Warrick et al. 1993; Douglas et al. 2001). A wide range of factors can influence sea level and historical evidence reviewed by Gornitz (1993) shows substantial variation in mean sea level during the past 200 years. Predictions of net increase in sea level vary widely and are likely to vary locally with glacio-isostatic and tectonic activity (Gornitz 1995). Most of the increase in sea level is expected to occur from melting of the large land-based ice sheets in Greenland and Antarctica (Alley et al. 2005). They predict an increase of about 70 m if these completely melted; however, more common ranges are from no change to slightly more than 1 m by 2100 (Neumann et al. 2000). More recent models indicate that sea-level may increase between 0.5 and 1.4 m by 2100 (Rahmstorf 2007). The response of sea-level to atmospheric temperature increase is complex and may exceed current projections.

Neumann et al. (2000) cite assessments that estimate flooding of 18,000 km^2 of coast land in the US with an increase in sea level of 0.5 and 35,000 km^2 with an increase of 1.0 m of sea level. The social and economic consequences are huge and the effects on wetlands and associated ecosystems are substantial (Titus 1990). Galbraith et al. (2002), using a series of rates of increase in sea level over 100 years, predicted a loss of 20% to 70% of habitat for shore birds at four sites along the coast of the US. In coastal freshwater ecosystems, changes in mean sea level can affect salmonids in freshwater habitats. A large proportion of both spawning and rearing habitat for anadromous salmonids occurs in low elevation flood plains that could be flooded by rapid increases in mean sea level.

Rising sea levels will flood low elevation habitats converting freshwater habitats into brackish or saline environments (Titus 1990). Habitats above the immediate effects of flooding will become inter-tidal and subject to periodic tidal flooding and pulses of saline water. Habitats not directly affected by incursion of salt water and tides are likely to be affected by channel readjustment resulting from changes in sediment deposition or scour (Blum and Tornqvist 2000). In other geographic locations, loss of wetlands through rising sea level may be compensated by conversion of low gradient uplands (Titus 1990). Throughout most of southeast Alaska, the terrain is precipitous and rises rapidly to elevations above 1,000 m from coastal margins (Nowacki et al. 2001) and replacement of low gradient habitats along coastal margins is not likely to compensate for habitats lost to marine incursions (Fig. 3).

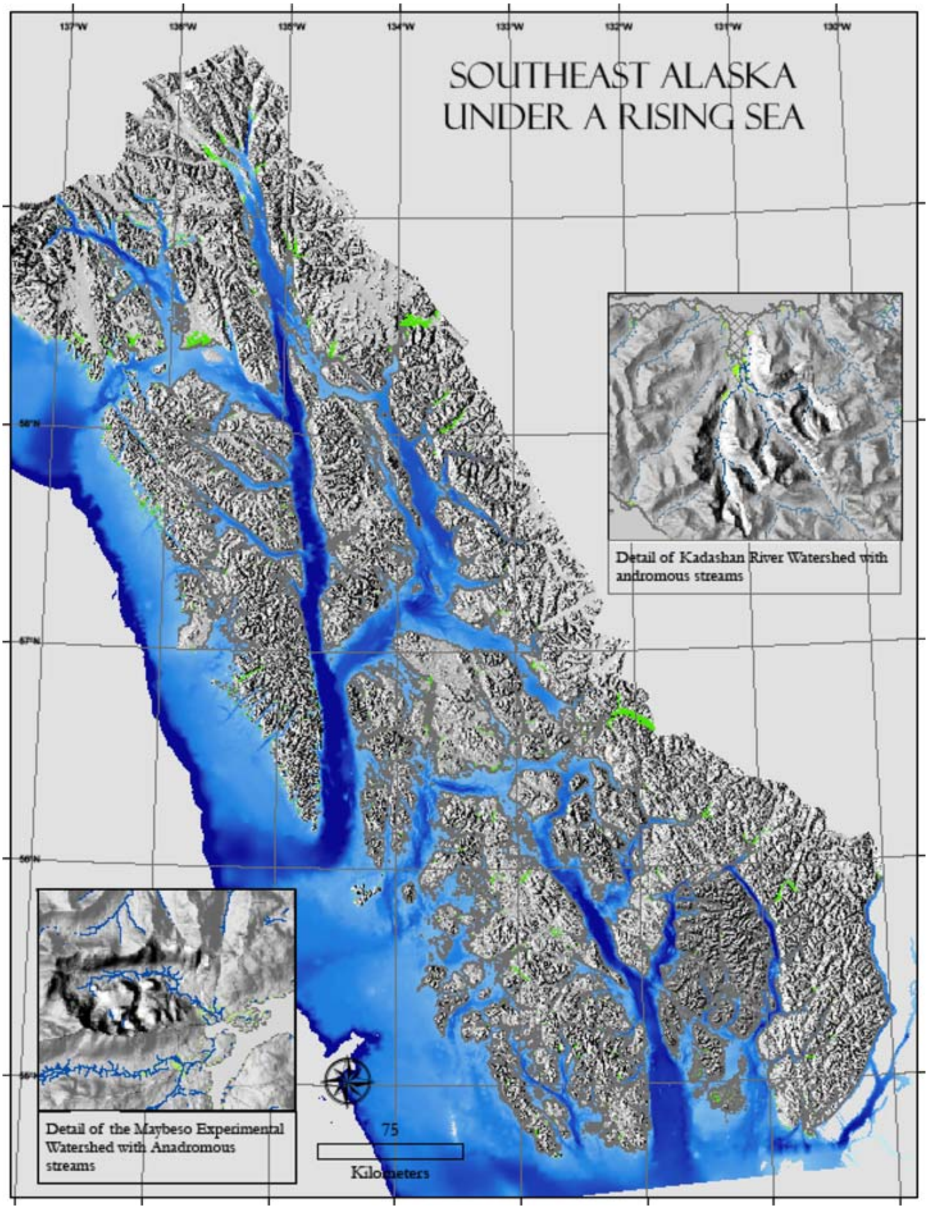


Fig. 3 Southeast Alaska topography from shuttle radar topography with elevations 20 m (best DEM resolution for all of southeast Alaska is 20 m) *shaded dark gray* and intertidal area *shaded light gray*

In Alaska, the amount of increase relative to the present land mass is complicated by glacio-isostatic rebound and tectonic activity such as the 1964 earthquake. Glacio-isostatic rebound also varies from location to location throughout southeast Alaska (Larsen et al. 2005). In recently de-glaciated areas such as Glacier Bay, land emergence with respect to sea-level has been reported at 3.96 cm/year (Hicks and Shofnos 1965). Recent observations show uplift of 10 mm/year near Glacier Bay decreasing southward to 2 mm/year, varying from location to location (Larsen et al. 2005). Therefore, prediction of the actual increase (or decrease) of sea level in relation to land is difficult.

Each salmon species in southeast Alaska has a unique life history that can be affected in different ways and intensity by rapid changes in environmental conditions. Some effects are likely to be common across two or more species and some effects may be more severe on one species than another.

3 Potential consequences of climate change on salmonids

3.1 Pink and chum salmon

Pink and chum salmon enter freshwater to spawn during the late summer when stream temperatures are close to the maximum for the season. Mean run times (approximately the peak time of entry into freshwater) range from July 25 through September 10 (Halupka et al. 2000). Usually the highest temperatures occur during August and begin to decrease in September. In more southern streams such as Staney Creek temperature can exceed 20°C (Fig. 2). They enter streams in large numbers over several weeks where they often hold in deep pools and move upstream following periods of rain and pulses in stream flow. The consequences of increasing temperatures are inter-related with decreases in summer precipitation and low flow. Low flows will delay migration and fish will hold in pools at various locations in freshwater and inter-tidal areas. Low flows and high temperatures usually coincide in August (Fig. 2). During periods of low flows extending for several weeks, the combination of high temperatures, low flows, and high fish density rapidly depletes dissolved oxygen content of stream water leading to high pre-spawning mortality (Murphy 1985; Pentec Environmental 1991). Under present temperature regimes, large pre-spawner mortality events are not common occurrences and generally occur in the southern region of southeast Alaska. As temperatures increase and summer flows decrease, these events are likely to become more common and occur in more northern watersheds of southeast Alaska.

Pink and chum salmon fry migrate to the ocean shortly after they emerge from the gravel (Heard 1991; Salo 1991). Time of emergence is related to temperature during incubation (see references in Heard 1991 and Salo 1991) and changes during the early part of incubation can affect time of emergence. Fry of both species migrate to the ocean in large schools, particularly pink salmon, at small size (<50 mm). Timing of their migration is generally thought to be related to food resources in inter-tidal areas (Mortensen et al. 1999 and references cited therein). As temperatures increase, egg incubation rates will increase and time to emergence and migration will decrease for both species and entry into the ocean will occur earlier in the season. Presently, both species enter the near shore marine environment beginning in late March and continuing through May when productivity is higher than in January or February. Early entry into the marine environment when food resources are low or absent will decrease growth and survival. Spawning later in the season may compensate for shorter incubation times.

Landslides, debris avalanches, and mass soil movement can have severe consequences on salmon eggs and embryo during their residence in streambeds (Everest and Meehan 1981; Tripp and Poulin 1986a; Swanson et al. 1987). In southeast Alaska, these events are closely associated with intense rainfall on saturated soils (Swanston 1970; Johnson et al. 2000). A frequent outcome of several global climate change models is a shift to more frequent high intensity precipitation events where precipitation increases (Hauer et al. 1997; Melack et al. 1997; Trenberth 1999). In erosion prone landscapes, landslides and mass failures are likely to increase, which will increase egg and embryo mortality as landslides scour redds where they run through spawning locations and deposit fine sediment on downstream locations (Lisle 1989; Swanson et al. 1987; Tripp and Poulin 1986a, b).

Pink and chum salmon that spawn in low salinity inter-tidal reaches of rivers or in the lower reaches of rivers and streams will be susceptible to changes in sea level and tidal influence even with relatively small changes. As sea level rises the deposition zones for sediment at the river outfall will change (Blum and Tornqvist 2000). The response is complicated by basin morphology, upslope sediment supply, and local rates of isostatic rebound or subsidence (Blum and Tornqvist 2000). These processes will affect spawning locations used by pink and chum salmon that spawn in the lower reaches of rivers.

3.2 Sockeye salmon

Small populations, relative to those in western Alaska, of sockeye salmon occur throughout southeast Alaska in watersheds with lakes of varying sizes. They usually enter freshwater to spawn from late summer through early fall. However, they usually enter and hold in lakes before they spawn in streams. Some may spawn along lake margins. Mean summer temperatures in lakes throughout Alaska seldom rise above 14°C and are below 10°C most of the time (Cartwright et al. 1998; Rogers and Rogers 1998; Westley and Hilborn 2006). Changes in temperature and discharge regimes may shift spawning timing and time of emergence of sockeye fry with unknown effects on growth and survival. Low flows may impede access to lakes and spawning locations. Higher water temperatures in lakes can also increase stress on adult sockeye holding in lakes. More high intensity rainfall events in the fall that increase the number of landslides in upstream high gradients streams will increase sediment deposition in both spawning streams and in lakes where sockeye rear.

Temperature increases are likely to affect growth and survival of sockeye fry that rear in lakes for one to two summers. Increasing temperature in the epilimnion zone may increase growth rates for juvenile salmonids. McDonald et al. (1996) found that food requirements for young-of-the-year lake trout increased as metabolic requirements increased with temperature in a lake in interior Alaska. However, food resources (zooplankton) did not increase and their model predicted a decline in lake trout populations with increasing temperature. Similar studies have not been done for lake rearing sockeye salmon. Climate changes can also affect the trophic structure of lakes. Winder and Schindler (2004) observed shifts in the time of vernal and autumnal mixing and the length of summer stratification associated with PDOs. The time of stratification increased and vernal mixing occurred earlier with increasing temperature in PDO cycles. Spring peak in phytoplankton and zooplankton shifted with changes in the thermal dynamics of Lake Washington.

The effects of changes in precipitation and hydrology on lake rearing sockeye are likely to be less direct, but may affect nutrient dynamics, turbidity, and temperature regimes which in turn will affect productivity. Carpenter et al. (1992) discuss the effects of water renewal on lake ecosystems. Increased precipitation can increase nutrient inputs and amplify anthropogenic disturbances such as urban and agricultural runoff. Decreased precipitation and increased evaporation may increase concentrations of chemicals and nutrients resulting in increased primary production. Coupled with decreased water turn-over, this could lead to severe reductions in hypolimnetic oxygen. Although most of the severe anthropogenic effects are absent in southeast Alaska, greater evaporation and lower water replacement can magnify acidification in lakes. This could have significant consequences for sockeye salmon rearing in lakes located in watersheds of southeast Alaska with large areas of acidic wetlands.

Predation can have a substantial effect on juvenile sockeye salmon in lakes (Cartwright et al. 1998). Alterations in the trophic status of lakes may also change dynamics of other species. The effect of higher temperatures in Alaskan lakes on cutthroat trout is not known; however, higher temperatures may increase metabolic requirements for cutthroat trout and increase predation rates on juvenile sockeye salmon.

Small lakes throughout southeast Alaska that support populations of sockeye salmon are located near salt water and are often connected to salt water by short streams. As the sea level rises, lakes at lower elevations may be subject to salt water intrusion as higher tidal cycles push salt water into the lake. As heavier salt water enters these lakes, it will sink to the bottom creating a layer of salt water. This will create a stable chemocline in the bottom layer of water that will effectively isolate the bottom surface of the lake from mixing during vernal and autumnal isothermal periods (Hutchinson 1957). The result will decrease productivity of the lake as nutrients are isolated in bottom sediments and are not released when vertical mixing occurs in the spring and fall (see Winder and Schindler 2004).

3.3 Chinook salmon

Most populations of Chinook salmon that spawn in southeast Alaska are less than 1,000 fish (Halupka et al. 2000). Larger numbers migrate through the large transboundary rivers, such as the Taku, Stikine, and Alsek and spawn in the interior in Canadian territory (Halupka et al. 2000). Climatic conditions in the interior are different from those in coastal Alaska and the manifestations of climate change will be different as well (Rouse et al. 1997). For example, it is possible that warmer drier conditions may occur in interior habitats than those in coastal habitats. Juvenile Chinook salmon from upstream spawning locations migrate into coastal river habitats where they will be exposed to changes imposed on the coastal climate (Murphy et al. 1989; Pahlke 1995). However, in both locations the general trend is expected to be warmer. Chinook salmon travel long distances to spawning grounds and increased temperatures will increase metabolic costs during migration (Berman and Quinn 1991; Torgersen et al. 1995).

As with most salmonids, Chinook salmon egg development responds to temperature changes and an increase in incubation temperature will decrease the amount of time to hatch and subsequently fry emerge from the gravel earlier (Alderdice and Velsen 1978; Beer and Anderson 2001). Higher temperatures and early emergence may affect feeding and growth (Heming et al. 1982) with subsequent effects on survival and time of smoltification (Berggren and Filardo 1993; Taylor 1990). Early emergence may alter life history patterns.

Life history strategies of Chinook salmon appear to be related to geographic location, distance from saltwater, and growth. Chinook salmon display two life history strategies in freshwater that occur in southeast Alaska (Healey 1991; Halupka et al. 2000). Ocean-type fish migrate to sea after 2–3 months in freshwater; stream-type fish remain in fresh water for one or more years. The fish with the stream-type life cycle tend to rear further upstream, experience slower growth and are located in more northern locations (Taylor 1990). In southeast Alaska, both strategies often occur in the same river system from apparently similar stocks (Murphy et al. 1989). Increasing temperatures may increase the occurrence of ocean-type fish in these rivers. Beechie et al. (2006) observed that life history strategies of Chinook salmon in Puget Sound responded to hydrologic regimes. They reported that stream-type fish were more common in watersheds dominated by snowmelt and suggest that their numbers would decline with decreasing snowmelt with global warming. It is unclear if this would be the case for populations in southeast Alaska, but it does indicate that temperature changes may cause a shift in life history strategies for Chinook salmon. In most cases, higher marine survival may be expected from stream-type smolt that migrate to the ocean at a larger size. However, there is a trade-off with survival probabilities in fresh water.

The effects on fish rearing in the large trans-boundary rivers will be complex as the effects from weather patterns in the interior interact with changes in coastal environments. Warmer drier weather in the interior may increase temperatures in rearing habitats for Chinook salmon in large rivers and their tributaries. Increases in temperature have been shown to affect juvenile salmon growth. In a watershed in California, Sommer et al. (2001) observed higher growth rates for Chinook salmon juveniles that reared in floodplain habitats that were 5°C higher than those in an adjacent river reach. They attribute the higher growth rates in the floodplain to higher food consumption. Beckman et al. (1998) found that Chinook grew faster at higher temperatures, but Bisson and Davis (1976) found that Chinook in artificial channels with elevated temperatures did not grow as fast as those in control channels. Many of the rivers used by Chinook salmon are fed by glaciers which would moderate potential increases in temperatures.

Dry conditions during the summer in the interior will reduce flows. Lower flows during the summer may reduce rearing habitat; however, in larger glacial rivers increased temperature during the summer may increase flows as glacial melting increases. Migration of both adult and fry may be affected by changes in flows. Healey (1991) proposed that downstream migration was initiated by spring freshets; however, the relationship is not clear in other studies. Low flows may also affect upstream migration timing (Berggren and Filardo 1993). Juvenile Chinook salmon respond to alterations in discharge regimes; however, it is unclear if it will be positive or negative with respect to survival in Southeast Alaska.

3.4 Coho salmon

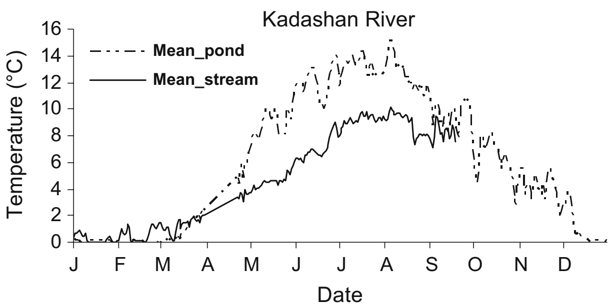
Coho salmon spawn over an extended period of time in southeast Alaska. Summer run stocks may enter freshwater in late July (Bryant et al. 1999; Halupka et al. 2000). Most coho salmon migrate into freshwater spawning areas from September through

November, although some stocks may spawn as late as December (Halupka et al. 2000). During the fall, freshwater temperatures rapidly decline and flows tend to be high. Increasing stream temperatures during the fall and winter are not likely to substantially increase mortality of spawning fish; however, as with other species alterations in the temperature regime during incubation may affect development rates and emergence timing (Tang et al. 1987). In an analysis of temperature effects of clear cut logging, Holtby et al. (1989) observed that coho salmon fry emigrated from spawning locations earlier as temperatures increased; however, they did not observe a significant relationship between smolt emigration and temperature.

In southeast Alaska, most juvenile coho salmon spend two summers in freshwater (Halupka et al. 2000). Although not well documented, the 2 year freshwater residence may be attributable to the cool temperatures of most rearing habitats used by juvenile coho salmon. In most streams in old-growth watersheds, mean daily temperatures usually do not exceed 5°C until late May and by mid September are below 6°C (Figs. 2 and 4). Throughout southeast Alaska, most fry are less than 60 mm fork length by fall of their first year of freshwater residence (Thedinga et al. 1989; Bramblett et al. 2002; Bryant et al. 2004). A combination of increased temperatures and a longer period where temperatures are within physiological growth boundaries may lead to increased growth and potentially a shift from a two-summer life cycle to a one-summer freshwater life cycle. The ultimate effect on survival may depend in part upon the size of the smolt as they migrate to the ocean (Holtby et al. 1990). If one-summer smolt are smaller than two-summer smolt, marine survival may be less for one summer smolt than for two summer smolt.

Although small streams are important rearing areas for juvenile coho salmon, a substantial but largely undocumented number use off-channel habitats such as beaver ponds and sloughs (Bryant 1984b; Murphy et al. 1989; Swales and Levings 1989; Bryant 1991; Pollock et al. 2004). These are often used as over-winter habitat, but substantial numbers remain in the ponds during the summer (Bryant 1984b; Sampson 1994). Fish in the ponds tend to be larger than those in adjacent stream reaches and most are parr (age 1+) fish. Temperatures in these ponds may be 2° to 4°C warmer than the adjacent free flowing stream during the summer (Fig. 4). The response to warmer temperatures in these habitats may become less favorable as summer temperatures approach or exceed physiological limits for growth. With increasing temperatures, water quality may decrease as biological oxygen demand increases with temperature.

Fig. 4 Mean daily temperatures for the Kadashan River and an adjacent beaver pond for 2000



Alterations to seasonal flow regimes caused by shifts in precipitation patterns are most likely to affect the freshwater residence of juvenile coho salmon. In southeast Alaska, the summer season is short and coho salmon fry grow relatively slowly (Wright and Bryant unpublished manuscript[1]). Reduced flows during the summer restrict pool habitats and may increase density and competition among coho fry (Nickelson et al. 1992; Rosenfeld et al. 2000). Low flows that reduce the size and depth of pools accompanied by increases in temperature will impose higher mortality and reduced growth rates among coho fry. Lower flows will also decrease the amount of invertebrate drift further reducing growth (Wilzbach and Hall 1985; Hetrick et al. 1998; Hughes 1998).

Most coho salmon spawn during the fall and are not likely to be affected by reduced summer flows. However, a few stocks move into fresh water during the summer and may encounter barriers to upstream migration at low flows (Halupka et al. 2000). Spawning success may be adversely affected by intensification of precipitation events that trigger landslides, which will scour spawning areas in low gradient headwater streams often used by spawning coho salmon. Downstream locations would be subject to increased sedimentation resulting from landslides (Tripp and Poulin 1986a).

Landslides induced by high intensity rainfall events will scour streambeds and remove habitat in small streams commonly used for rearing by juvenile coho salmon (Tripp and Poulin 1986b; Cederholm and Reid 1987; Hogan 1987; Benda 1990; Tripp 1998) and remove alcoves and dammed pools may also limit over-winter survival (Nickelson et al. 1992). However, in some Oregon watersheds, landslides can be significant sources of large wood to streams (Reeves et al. 2003). In the U-shaped valleys of southeast Alaska, most landslides and debris flows deposit large wood in the moderate (4–7%) gradient zones of small tributaries and do not enter larger third and fourth order streams (Johnson et al. 2000). In most cases landslides and mass wasting events will have a deleterious effect on winter survival of juvenile coho and if they become a chronic occurrence, they will have long term effects on populations.

Juvenile coho salmon use a wide range of habitats that are common in small low elevation streams that may be affected by rising sea levels (Elliott and Reed 1974; Bryant 1984a). Habitats within 1 to 5 m of existing sea level include small tributaries in the lower reaches of watersheds (Bryant 1984a), off-channel and main stream habitats near the inter-zone (Murphy et al. 1989), and flood plain habitats in large river deltas (Bryant 1991; Schaberg 2006). Some of these areas are extensive such as the Copper River Delta and the Yakutat Forelands located a few hundred miles north of southeast Alaska (Bryant 1991; Schaberg 2006). Numerous other low elevation river delta and intertidal areas that support large numbers of several species of anadromous salmon are scattered throughout southeast Alaska (Fig. 3). The Kadashan River watershed (see inset in Fig. 3) is one example of a low level alluvial floodplain associated with an extensive intertidal area that would be susceptible to a relatively small (<1 m) increase in sea level (Fig. 5). Rising sea level will increase salinity in the lower reaches and increase sediment deposition as flows are altered by tidal effects (Blum and Tornqvist 2000). Rising sea level as a result of global warming

[1] Wright, B. E., and Bryant, M. D. Unpublished. How Wild Steelhead Win the Summer Growth Race in Southeast Alaska. Unpublished manuscript, Juneau Forestry Sciences Laboratory, USDA Forest Service, 2770 Sherwood Ln 2A., Juneau, AK 99801, USA.

Fig. 5 The lower watershed and intertidal area of the Kadashan River showing area that would be affected by an increase in sea level of 1 m

may be compensated by isostatic rebound as result of recent de-glaciation in many areas of Southeast Alaska.

4 Discussion

Many of the predicted outcomes from scenarios for climate change are not favorable for anadromous salmonids (Table 1). However, some may be positive. In several instances the outcome is not known and may depend on interacting events. In all cases, the magnitude is speculative. It is highly unlikely that there will be a wholesale extirpation of salmon stocks in southeast Alaska. All anadromous species found in southeast Alaska are also found in more southern locations with thermal regimes that might be expected in southeast Alaska under most predictions of climate change. Nonetheless, stocks with small numbers or unique habitat requirements may be lost. The small run of Chinook salmon in two streams on Admiralty Island are examples of "at risk" stocks (Halupka et al. 2000). Other examples are stocks of summer run coho salmon and small populations of sockeye salmon in small lakes.

The most pervasive anthropogenic effect on the landscape throughout southeast Alaska is timber harvest and the effects of poor management practices in the past (Heifetz et al. 1986; Murphy et al. 1986; Thedinga et al. 1989); however, a large number of intact watersheds with little or no anthropogenic disturbance on the habitat remain throughout southeast Alaska (Bryant and Everest 1998). These are important buffers to many of the effects that may be imposed by climate change. Although the harvest of salmon by commercial, sport, and subsistence fisheries appears to be sustainable under current management practices, a substantial portion

Table 1 Summary of potential effects of climate change on anadromous salmonids in freshwater habitats of southeast Alaska

Pink salmon and chum salmon		
	Increased frequency and extent of pre-spawner mortality resulting from increasing temperatures and decreasing summer flows	
	Earlier emergence time and entry into the marine environment with less favorable conditions for early feeding and growth	
	Deterioration of spawning habitats	
		Greater upslope landslide activity increasing scour and sediment infiltration
		Incursion of saltwater from rising sea levels into spawning areas
		Alterations in sediment dynamics with changes in sea level
	Alterations in run timing as a result of shifts in temperature and discharge	
Sockeye salmon		
	Shifts in spawning time with subsequent changes in time of emergence of fry	
	Spawning habitat deterioration from upslope landslides induced by increased rainfall intensity	
	Changes in growth and survival resulting from alteration of trophic status of lakes	
		Shifts in zooplankton availability
		Changes in lake physical and chemical dynamics resulting from either increases or decreases in water recharge
		Decreasing rearing capacity and secondary production from saltwater intrusion
	Increased predation as thermal characteristics become more favorable for natural or introduced predators	
Chinook salmon		
	Changes in run timing forced by temperature and/or discharge regimes	
	Increased stress and mortality during spawning migration resulting from loss of thermal refuges in large pools	
	Deterioration of spawning habitat caused by increased frequency of upslope landslides	
	Loss of rearing habitat as thermal refuges are lost	
Coho salmon		
	Deterioration of spawning habitat from landslides that scour spawning beds and deposit sediment on downstream spawning areas	
	Changes in fry emergence timing and emigration	
	Effects of climate change induced temperatures on growth and survival of juvenile coho salmon	
		Increased growth as temperatures in streams increase above 10°C but remain below 18°C
		Decreased survival as metabolic demands increase but food supplies become limited
	Loss of rearing habitats	
		Decrease in summer rearing habitats as flow decreases and pool abundance and quality decrease
		Deterioration of off-channel habitats as temperatures exceed optimum ranges
		Loss of off-channel habitats through more frequent high intensity rainfall events that remove instream structure and beaver dams during fall and winter
		Intrusion of salt water into low elevation rearing areas

of a run for a given stock may be harvested depending on the run size and the escapement goals (Clark et al. 2006; Eggers 2007). High harvest rates are a significant anthropogenic disturbance with unknown results in an environment of rapid climate change. Rapid and sustained changes in climate regimes occurring over a period of decades are likely to impose increased stress on stocks that have adapted over centuries to specific environments (Halupka et al. 2003).

A favorable outcome for Alaskan salmon depends upon a few assumptions. The first is that they can acclimate to the rapid (i.e. decades rather than centuries) changes in temperature regimes that are likely to occur with climate change. The ability of individual stocks to adapt to and withstand the effects of precipitation and sea-level will also influence the outcome. The issue of climate change and ocean conditions and its effects on salmon populations is not directly addressed in this analysis. Recruitment to freshwater ecosystems depends on oceans conditions which may also influence the response in freshwater.

Ocean conditions impose another element of complexity to potential effects of climate change on salmon in freshwater (Beamish 1995). Beamish and Bouillon (1993) identified trends in catch associated with weather patterns for pink and chum salmon in the northern Pacific Ocean using historical catch and weather data. Recent studies have shown that the abundance of salmon production responds to ocean temperature cycles associated with PDO and El Niño (ENSO) events (Beamish et al. 1999; Hare et al. 1999; Hollowed et al. 2001). Temperature increases appear to have contradictory effects on salmon production with increasing survival rates for northern stocks and decreasing rates for southern stocks (Hare et al. 1999; Mueter et al. 2002). Ocean surveys by Welch et al. (1998a) suggest that as thermal boundaries move northward, the ocean rearing area available for sockeye will decrease with increasing ocean temperatures. The response of salmon to climate change in the ocean is complex and is likely to differ by geographic region and is likely to have a bearing on freshwater populations.

The combination of the three outcomes—positive, negative, or neutral—for the freshwater and ocean environments results in nine combinations of outcomes when the responses in each environment are considered. Three may be considered as positive outcomes, a positive outcome in both environments and a positive in one and a neutral in the other. Neutral outcomes in each are possible. It is uncertain if a positive outcome in one environment would “cancel out” a negative outcome in the other environment. The remaining outcomes are negative. All of this assumes equal weighting for each outcome. A qualitative evaluation of the evidence suggests that the probability for negative outcomes is greater than that for positive outcomes with respect to salmon response to global climate change. Furthermore, negative outcomes are more likely where salmon stocks are already stressed or are at the more southern range of their distribution than those in regions where they tend to have robust populations.

Pacific salmon as a group occupy habitats that range from the Beaufort Sea where they occur in relatively small numbers to San Francisco Bay where they are nearly extirpated (Craig and Haldorson 1986; Nehlson 1997; Groot and Margolis 1991). Furthermore, they have been introduced to diverse geographic locations in both the northern and southern hemispheres (Quinn et al. 2001; Hansen and Holey 2002). They readily exploit new habitats opened with fish ladders and major changes in watersheds (Hendry et al. 1998, 2000; Bryant et al. 1999). These characteristics suggest that Pacific salmon in southeast Alaska may be fairly resilient in the face of global temperature increases. If the temperatures in southeast Alaska increase by 2–4°C, then the climate might be similar to that in southern British Columbia or Washington State. Both locations have climates that are generally favorable to Pacific salmon and have or had robust salmon stocks.

A common concern in several assessments of the effect of climate change on aquatic ecosystems is the interaction with existing effects of anthropogenic disturbance (Magnuson et al. 1990; Hauer et al. 1997; Schindler 1997; Mote et al. 2003). Among these effects are chemical and thermal pollution, dams, habitat deterioration, and introduced species. These effects are not widespread in southeast Alaska and where they do occur they tend to be localized near urban areas that are considerably smaller than the large urban areas of the west coast. Nearly all of the landscapes where Pacific salmon are found along the west coast of the US are exposed to one or more of these stressors. Most of the effects on the salmon stocks of southeast Alaska are likely to be similar for stocks in more southern parts of North America; however, they are likely to be exacerbated by existing stressors described by Hauer et al. (1997). Furthermore, depleted and extirpated stocks combined with introgression of hatchery stocks are likely to have altered the genetic structure of existing stocks. The potential effects described for salmon in southeast Alaska may be more acute for stressed stocks elsewhere; therefore, their ability to respond to rapidly changing environmental conditions imposed by climate change bears considerable attention.

The preponderance of evidence supports a scenario of increasing temperatures globally (Hauer et al. 1997; Mote et al. 2003; Schindler 1997; Smith and Tirpak 1989). The potential effects of climate change and management responses for salmonid populations in Southeast Alaska (as well as elsewhere along the Pacific coast) are to a large degree speculative and based on studies that address many of the issues indirectly (e.g. Levy 1992; Mote et al. 2003; Winder and Schindler 2004). Most management practices for salmonids in southeast Alaska are designed to sustain salmon populations under present climatic conditions. Given that rapidly changing climatic conditions will impose additional stress on populations, a more conservative management strategy may be appropriate (Halupka et al. 2003). In general, these include land management practices that preserve thermal refugia, critical habitats, and intact watersheds. More intense monitoring of harvest rates that focus on specific stocks will allow managers to respond rapidly to changes in productive capacity of watersheds that may be most susceptible to potential changes in climate conditions. Development of effective management guidelines is greatly restricted by a lack of quantitative information with respect to the potential changes and the response salmonid populations in southeast Alaska.

5 A set of questions

The set of questions proposed in Table 2 provide a starting point for research to predict and anticipate how anadromous salmonids may respond to climatic changes. Most require the development of predictive models; however, models require reliable quantitative information. Some is available. For example, the relationship between rates of development, rate of embryos and temperature (Alderdice and Velsen 1978; Tang et al. 1987). Use of GIS databases can provide estimates of the amount of area affected by changing climatic conditions. Bioenergetics models such as the one applied by McDonald et al. (1996) may provide useful estimates of growth rates for specific species, such as juvenile coho salmon.

The outline in Table 2 presents a set of topics that can provide useful information that will contribute to the understanding of how salmon species may respond to changing climatic conditions in southeast Alaska. The format begins with a major question to be addressed (1) followed by a brief statement of a general hypothesis (a) under the question. The last element in the outline (i) is a one sentence description of a proposed line of research. Each in turn may be developed into a detailed study

Table 2 Questions, hypotheses, and study topics

1. How will temperature and flow interact to affect spawning conditions for pink salmon?
   (a) Predicted changes in the global climate will increase frequency and extent of pre-spawner mortality in southeast Alaska streams
      (i) Develop a model based on current and predicted ranges of temperature and discharge to predict potential mortality of pre-spawner pink salmon
   (b) Pink salmon fry will emerge earlier as stream temperatures increase and enter the marine environment during periods of low food availability
      (i) Determine the effects of increasing temperatures on development and emergence of pink salmon in Southeast Alaska streams and relationships to near-shore marine productivity on early life history survival
2. How will increasing stream temperature affect growth of juvenile coho salmon?
   (a) Atmospheric warming will lengthen growing season for juvenile coho salmon and increase temperatures that can increase growth rates
      (i) Construct a bioenergetic model to examine growth rates in southeast Alaska streams and associated habitats to determine growth under varying temperatures and food conditions
3. How will changes in lake trophic conditions affect sockeye salmon rearing in southeast Alaska lakes?
   (a) Increasing temperatures will shift thermodynamics of lakes with earlier vernal mixing and later autumnal mixing with subsequent shifts in food availability (quantity and quality) to sockeye salmon and will alter growth of juvenile sockeye salmon
      (i) Establish relationships between lake thermodynamics, lake trophic conditions, and time of entry of sockeye fry into lakes of southeast Alaska
      (ii) Determine response of juvenile sockeye salmon growth to changes in temperature and food abundance and quality in southeast Alaska lakes using a bioenergetic model
4. How much area will be lost to salmonid production through elevation of sea level throughout southeast Alaska?
   (a) Global climate change will increase temperature that will result in rising sea levels that will shift freshwater spawning and rearing into marine or intertidal habitats
      (i) Determine net loss of freshwater wetlands and habitat under a series of scenarios of sea level rise using GIS models
      (ii) Estimate the potential effects on rearing habitat for juvenile salmonids with loss of freshwater wetlands and habitats
      (iii) Determine shifts in spawning habitats of pink salmon as lower reaches of spawning locations are affected by sea water

proposal. Most statements are directed at the level of a post-doctoral or Ph.D. research assignment. Although it is not listed in the table, there is a need for a Regional Climate Model for southeast Alaska and the north Pacific coast. This is not an easy task given the complex topography, severe weather patterns, and intense interaction with the marine environment.

Most of the existing studies of the response of fish to climate change tend to remain within the realm of biological response; the multidisciplinary paper by Hauer et al. (1997) is an exception. Most of the studies suggested in Table 2 tend to be narrowly focused on specific response by species or group of species. However, understanding the potential responses and underlying causes requires an interdisciplinary approach. The questions address relatively specific aspects of the life history of each species and the response to changes in its physical environment, specifically temperature and precipitation, and in some cases changes in habitat imposed by higher sea level. These interactions require a strong interdisciplinary component as a basis for all of the suggested studies. Development of a RCM for southeast Alaska and the northern Pacific Northwest coast region would be a prerequisite for realistic modeling of potential responses of salmon and other biota to climate change in the region.

As an example of the interdisciplinary nature of the studies, determination of the effects of rising sea level on salmon populations will require a complex analysis of physical, geographic, and biological responses. As a starting point it will require a GIS assessment of area that may be affected including the development of a fine scale digital elevation model (DEM). Current DEMs that cover most of southeast Alaska are 20 m. Isostatic rebound is an important process in most of coastal Alaska and varies from location to location and must be included in the assessment. Once these processes have been quantified, effects on habitat used by salmon and biological responses can be modeled. Taken as a whole, it poses as difficult question, but with an interdisciplinary approach each element has a solution.

Even under the most draconian preventative measures climate change will occur and global atmospheric temperatures will increase. Many of the corresponding effects cannot be avoided; however, with increased information on the potential effects and responses of economically and socially important resources such a salmon, management strategies may be adopted that will mitigate or reduce adverse effects on them. The studies suggested in this paper are a starting point for understanding the consequences of climate change on anadromous salmon. They are oriented toward salmon populations in southeast Alaska; however, they may be applied to salmon populations in more southern regions of the Pacific coast where current condition and stressors may be far more critical than those in southeast Alaska.

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