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Climate Change and a Dynamic Ocean Carrying Capacity: Growth and Survival of Pacific Salmon at Sea

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Abstract.—Studies have documented reduced growth of salmon in response to competition with conspecific salmon and with other salmon species during early and late marine life stages. However, key questions remain as to whether density-dependent growth translates to reduced survival of salmon at sea and whether changes in ocean regimes, similar to that of 1976/1977, can alter this relationship. These questions are particularly important with respect to annual releases of numerous hatchery salmonids into the ocean. Few studies have tested these questions because the capacity of the ocean to support salmon is dynamic and reduced growth in Pacific salmon is often associated with great abundance of smaller fish which infers a higher overall survival rate, thereby confounding traditional statistical fisheries harvest modeling efforts. We review evidence from several recent studies suggesting that, when the density-dependent effect on growth at sea is large, salmon survival is lower with lower reproductive potential from survivors, and that the salmon carrying capacity of the ocean is influenced by climate change. We conclude that salmon growth and survival responses to oceanic changes can vary with season and life stage and that density-dependent growth at sea is an important, yet often elusive, mechanism affecting salmon survival. Pacific salmon life history models should account for these relationships.

Introduction

Impacts of climate change on salmonid fishes have been characterized in recent decades by their significant effects on interrelated biological and physical relationships including growth, survival, and abundance of salmon in the North Pacific Ocean. Transitions from one climatic state to another are called regime shifts, and there is significant literature linking such shifts in ocean condition to the distribution and abundance of aquatic organisms (Francis et al. 1998; Anderson and Piatt 1999; Hare and Mantua 2000 and 2001; Welch et al. 2000; Benson and Trites 2002; Clark and Hare 2002; Zamon and Welch 2005). There is still controversy on the true nature of "regime shift" in the North Pacific Ocean even though there is substantial support for regime-like behavior in these marine ecosystems (Hsieh et al. 2005; Mangel and Levin 2005). Pacific salmon in marine environments have faced changes in sea surface

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temperature and ocean condition associated with shifts in the Pacific Decadal Oscillation (PDO), Arctic Oscillation Index, and the El Nino-Southern Oscillation (ENSO) (Mantua et al. 1997; Hare and Mantua 2000; Minobe 2000). A well-documented climatic regime shift altered conditions in the North Pacific Ocean in 1976–1977 (Minobe 1997). A less pervasive regime shift occurred again in 1989 (Hare and Mantua 2000). Ocean conditions can significantly affect salmon growth and survival (Holtby et al. 1990; Friedland 1998; Beamish et al. 2004). Abundances of all species of Pacific salmon in the North Pacific Ocean and the Bering Sea increased after the marine climate shift during the mid-1970s (Figure 1; Rogers 1984; Beamish and Bouillon 1993; Hare et al. 1999; Mueter et al. 2007). Salmon production in the period from 1951 to 1976 averaged approximately 280 million salmon per year; after the mid-1970s climate shift, adult runs nearly doubled to approximately 520 million salmon per year (Rogers 2001; Eggers et al. 2005). Hatchery production of Pacific salmon also increased dramatically during this period contributing to confounding impacts among species, populations at sea, and recruitment (Beamish and Noakes 2002; Orsi et al. 2004; Ruggerone and Goetz 2004; Beamish et al. 2004; Spies et al. 2007).

Salmon from different regions or continents of origin can overlap at their ocean feeding grounds in the North Pacific Ocean, but the extent of overlap among species is not easily determined (McKinnell 1995; Myers et al. 1996). Density-dependent growth has been observed in Pacific salmon (Peterman 1984; Rogers and Ruggerone 1993; Bigler et al. 1996). Competition for limited resources in marine habitats has been recognized as an important factor in growth of Pacific salmon at sea (McKinnell 1995; Ishida et al. 2002; Ruggerone and Nielsen 2004; Holt and Peter-

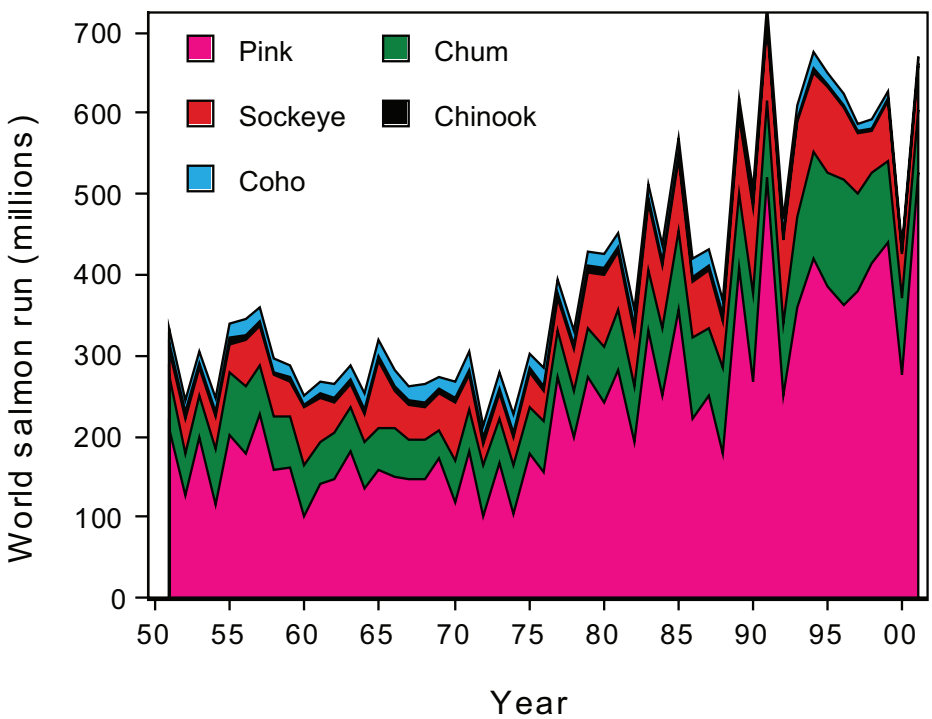

FIGURE 1. World salmon run size 1951–2001 (adapted with permission from Rogers 2001).

man 2004). Over the last quarter century, the apparent abundance of salmon in the ocean has doubled with a large component of that productivity based on artificial propagation from hatcheries with approximately 5 billion salmon fry released annually into the Pacific Ocean (Mahnken et al. 1998). In Japan, hatchery release programs for pink salmon have been credited with a significant increase in the Japanese commercial salmon harvest at sea (Hiroi 1998; Kaeriyama 1999), but Morita et al. (2006b) question their benefits in relation to loss of wild salmon production.

The ability of natural ocean systems to sustain large numbers of fish and the concept of an ocean carrying capacity for salmon remains controversial (Shuntov and Temnykh 2005). However, few studies have looked at the actual increase in net population growth for adult salmon at sea when the effects of density dependence and climate change are taken into account (Hilborn 1999; Morita et al. 2006a). Environmental and oceanic conditions at various sea-ages have been correlated with patterns in growth and survival in juvenile salmon (Mason 1974, Holtby et al. 1990; Pearcy 1992; Farley et al. 2007) and in later marine life stages where growth-related mortality appears less important (Rogers and Ruggerone 1993; Ruggerone et al. 2003).

Several life history models have been published on the impacts of climate change on marine species (Giske et al. 1992; Nonacs et al. 1994; Mangel 1994; Hilborn and Mangel 1997; Tian et al. 2004). Although many excellent papers have associated variation in Pacific salmon growth and abundance with climate change (Mantua et al. 1997; Hare et al. 1999; Beamish et al. 1999 and 2000; Wells et al. 2005), few have directly focused on the implications of a changing marine environment on salmon life history characteristics. Climate change may influence the important trade off between somatic growth and reproductive investment since salmonid life history variation is a trade off between the optimal allocation of resources to maximize growth during early life stages and facilitate reproduction in later life stages (Fleming and Gross 1989; Thorpe 1990). Marine growth has been associated with age-at-maturity in Pacific salmon (Bigler et al. 1996; Pyper and Peterman 1999; Pyper et al. 1999; Morita et al. 2005). Older, maturing salmon are usually larger adults (Friedland and Haas 1996; McGurk 1996: Hobday and Boehlert 2001); fish size has been directly correlated with egg number and size (Fleming and Gross 1990; Mangel 1994; Quinn et al. 2004) and reproductive success (Gross 1991; Beacham and Murry 1993; Quinn et al. 1995). Therefore, salmon that are impacted by climate variation and/or density-dependent factors, leading to reductions in growth and development, may lose individual reproductive potential despite increases in total abundance. In this paper we review 1) the productivity-climate change relationship documented for salmon in the North Pacific Ocean in relation to growth-at-sea for different life stages, and 2) the effects of the mid-1970s regime shift on salmon growth and abundance. We explore potential causes of density-dependent salmon growth in marine habitats and discuss the implications that reduction of growth-at-sea may have on life history trade offs.

Early Growth and Movements at Sea

Anadromous Pacific salmon typically spend 1–5 years at sea where the majority of their growth and development takes place (Groot and Margolis 1991). Some salmon migrate over great distances to feed in the ocean while others remain relatively close to shore during their whole ocean cycle (Quinn and Myers 2005). Survival during the first year at sea is most difficult for Pacific salmon, and growth and survival appear to be linked (Pearcy 1992; Beamish and Mahnken 2001; Farley et al. 2005, 2007). During their early

weeks at sea, growth-mediated survival may define year-to-year variability and patterns of recruitment in salmon populations (Friedland 1998; Welch et al. 2000; Beamish and Mahnken 2001).

Physiological adaptation to the marine environment, the need to discover previously unknown food resources, and a gauntlet of active predators take their toll on young marine salmon. Changes in climate can affect survival during any of these activities. Although salmon species have feeding tendencies, salmon select a variety of prey at different life stages which may represent several trophic levels (Kaeriyama et al. 2004). Significant changes in chlorophyll and zooplankton abundance and distribution have been associated with patterns of climate change (Napp and Hunt 2001; Gregg 2002; Zamon and Welch 2005). Major zooplankton assemblages have shifted their composition since the early 1990s (Kang et al. 2002). Recent increases in gelatinous zooplankton in the Bering Sea have been linked to climate change (Brodeur et al. 1999). Anomalous blooms of coccolithophores *Emiliania huxeyi* in the Bering Sea have been suggested as disruptive ecosystem components affecting the distribution and abundance of marine fauna (Napp and Hunt 2001). Large oceanographic models such as PICES' Carrying Capacity and Climate Change BAsin Scale Studies (CCCC BASS; Aydin et al. 2003) have been developed to facilitate understanding of the impacts of climate change and climate variability on physical and lower trophic level biological processes in the North Pacific Ocean, but these models are not yet connected to upper trophic level fishes. Also, in some regions, such as the Bering Sea, the mid-1970s climate shift did not lead to a significant change in zooplankton biomass (Napp et al. 2002).

Significant changes in the distribution and abundance of predators such as marine birds, sea lions, baleen whales, walleye pollock, and Pacific salmon have recently been recorded in the eastern Bering Sea, most likely linked to changes in the availability of different prey (Merrick 1997; Hunt et al. 2002). Empirical data show that ocean regime shifts influence the composition and productivity of both higher and lower tropic levels in marine habitats (Francis and Hare 1994; Francis et al. 1998; Anderson and Piatt 1999; Gregg 2002). Our own studies indicate that sockeye growth during their first two years at sea tended to be greater after the mid-1970s (Ruggerone et al. 2005). Greater growth in the first year at sea was most pronounced in salmon from Bristol Bay which occupy the Bering Sea, while growth in the second year at sea was greatest in salmon from the Chignik River which inhabit the North Pacific Ocean (Figure 2).

Mechanisms supporting marine growth and survival for young salmon are poorly understood in part because stock-specific salmon distributions span exceptionally broad areas that include multiple ocean habitats. Therefore, it is understandable that the concept of a food competition-related ocean carrying capacity has long been controversial (Cushing 1975; Joyner 1975; Aydin 2000; Azumaya and Ishida 2000; Achord et al. 2003; Ruggerone and Nielsen 2004; Shuntov and Temnykh 2005). Evidence is growing that greater prey availability during early marine life of salmon contributed to greater salmon abundance following the 1977 regime shift in the North Pacific Ocean (Brodeur and Ware 1992; Ruggerone et al. 2005). In Puget Sound, salmon prey availability was greater prior to the 1982/83 El Niño. The 1982/83 El Niño and subsequent events appeared to reduce prey abundance, thereby enhancing competition between juvenile pink salmon *Oncorhynchus gorbuscha* and juvenile Chinook salmon *O. tshawytscha*, which experienced significantly reduced growth and a 62% reduction in survival when pink salmon were present during 1984–1997 (Ruggerone and Goetz 2004).

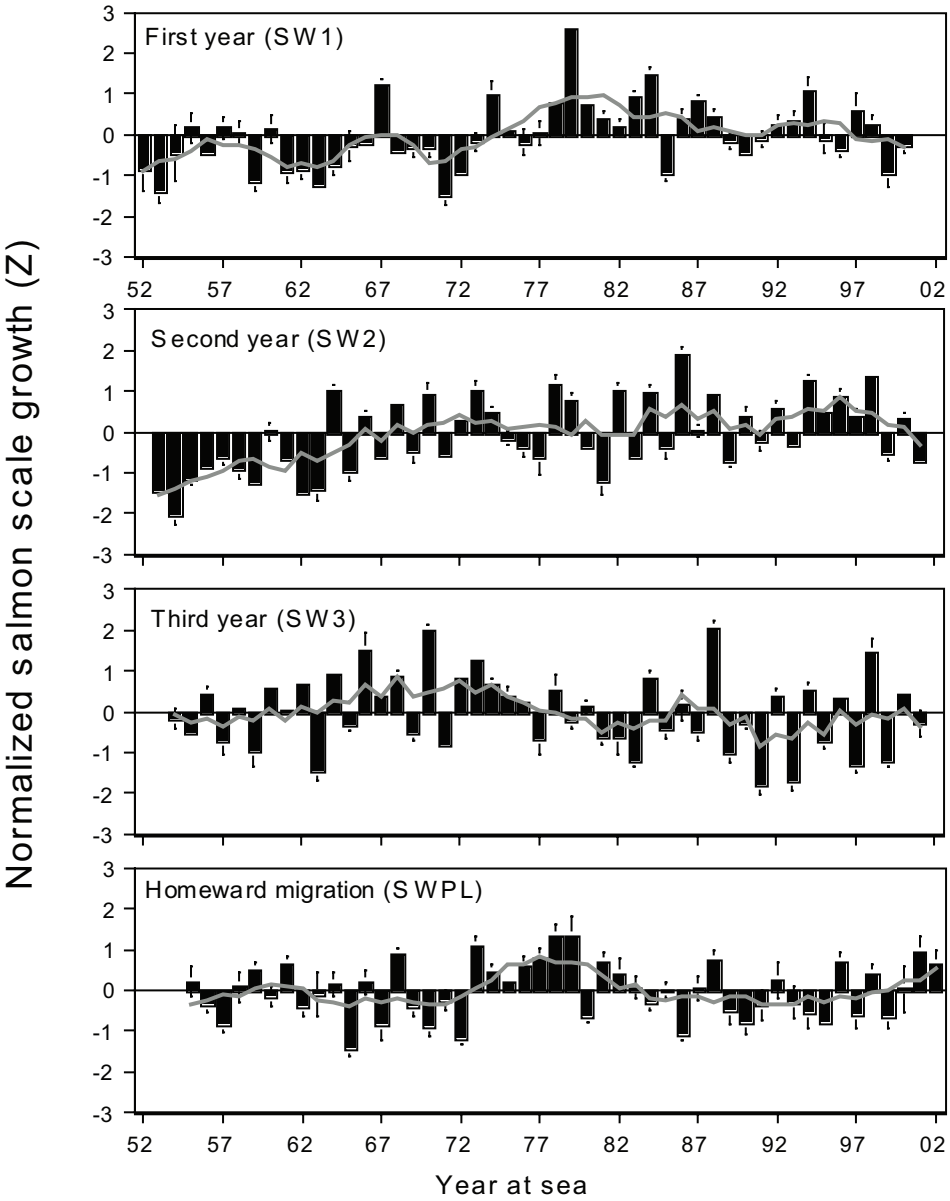

FIGURE 2. Trends in sockeye salmon *O. nerka* scale growth 1952–2002 in: a. Bristol Bay sockeye and b. Chignik River sockeye populations (with permission Ruggerone et al. 2007). Growth is normalized to the population mean.

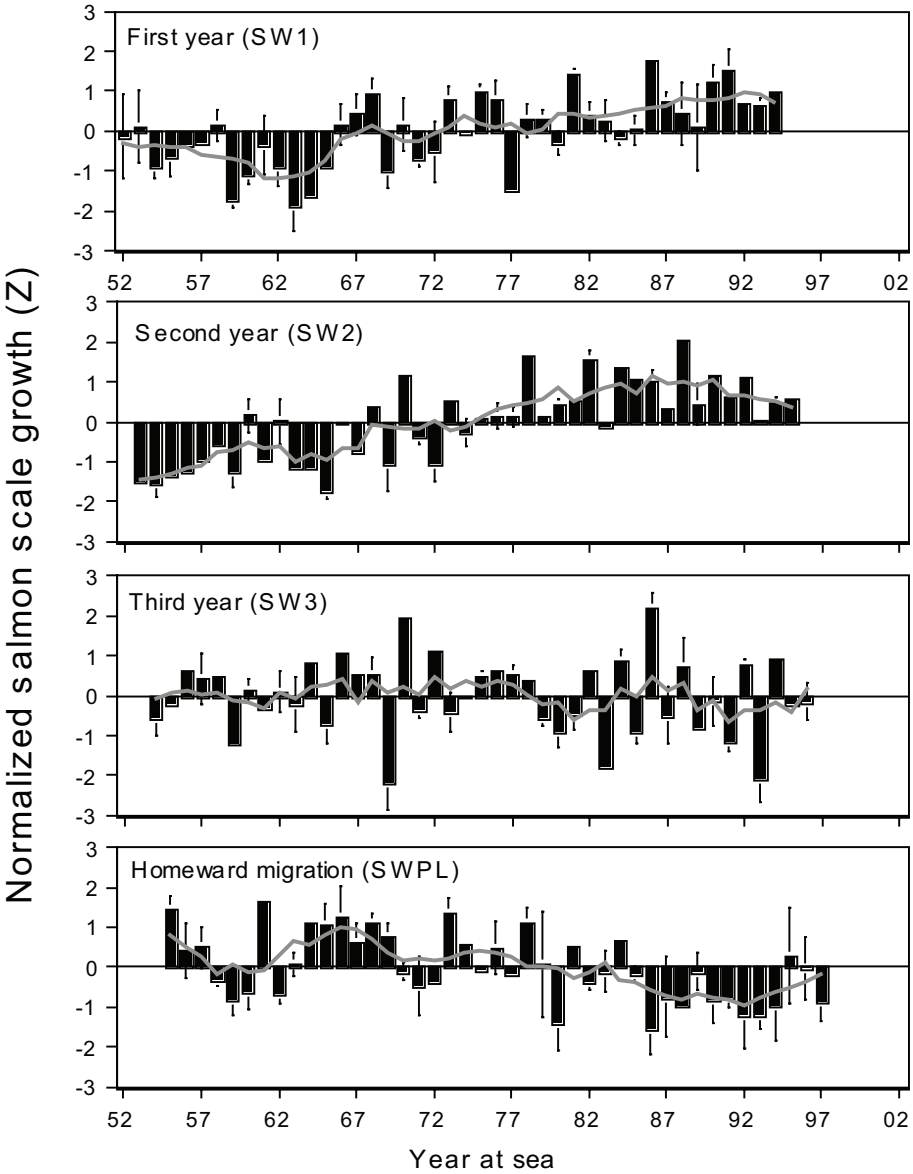

FIGURE 2. Continued.

Most studies of early-marine salmon responses to climate change have focused on bottom-up control of salmon abundance. However, some evidence suggests predation by salmon sharks *Lamna ditropis*, North Pacific daggertooth *Anotopterus nikparini* and other predators may influence juvenile salmon abundance in oceanic habitats (Welch et al. 1991; Yodzis 2001; Nagasawa 1998). Beamish and Neville (1995) reported that river lamprey *Lampetra ayresii* attack and kill a significant portion of Chinook and coho salmon *O. kisutch* in the Fraser River plume. In Puget Sound, abundances of most salmon predators were much greater prior to the series of El Nino events beginning in 1982/83 and predation rather than competition appeared to be the primary mechanism of mortality affecting Chinook salmon during 1972–1983 (Ruggerone and Goetz 2004). Changes in salmon predator abundances in the North Pacific Ocean have not been directly linked to climate change, although salmon shark abundance increased sharply in 1996 and thereafter compared with 1984 to 1993 (Nagasawa et al. 2002). Size-dependent predation has been suggested as a key mechanism linking climate change and salmon growth to salmon survival and abundance, but few data are available on size-dependent predation after salmon leave nearshore marine areas (Holtby et al. 1990). Ultimately, the relative importance of mechanisms leading to mortality of salmon at sea, such as predation, delayed density-dependent effects, starvation, or disease, are rarely quantified.

Salmon Maturation at Sea

Life at sea for anadromous salmonids serves two purposes—one to grow rapidly and survive in marine habitats; the other to develop gonadal material for reproduction. Aquaculture has provided a large literature on the growth/reproductive trade offs measured in terms of the gonosomatic index (GSI) necessary for salmonid reproduction (Hoar et al. 1983). In general, age at maturity in Pacific salmon has been linked to marine growth with faster growing progeny generally maturing at younger ages (Hankin et al. 1993; McGarvey et al. 2007). Somatic growth rates in apparently similar individuals, however, often vary widely producing dynamic effects in reproductive potential (Sebens 1987; Bacon et al. 2005). At a specific point in adult development, most energetic inputs cease to contribute to somatic growth and, instead, begin to contribute to reproductive development. However, the turning point in the trade off between these two physiological processes has not been well described for adult Pacific salmon at sea. A smooth progression through reproductive cycles at sea depends on the continuing interplay between an individual endrocrine system and the environment (Lam 1983). We can therefore assume that hormonal, environmental, and behavioral aspects of salmonid gametogenesis may be influenced by climate change.

Photoperiod and/or temperature are generally recognized as the most important cues in the timing of gametogenesis in temperate fishes. Typically, oocytes progress into early vitellogenesis when a fish is exposed to low temperatures and short photoperiod, but warmer temperatures are required for final oocyte maturation and spawning (Scott 1990). In addition to temperature cues, the primary growth phase of oocytes in salmonid females, i.e. yolk vesicle formation and endogenous vitellogenesis, requires significant exogenous input of energy for lipid development. Viable salmon eggs contain over 80% lipid stores in the form of yoke material (Lam 1983). Gonadal development in marine environments—in females particularly—requires significant energy which in turn is linked to the availability and quality of food at sea (Aydin 2000).

Neutral lipids (as opposed to cellular or polar lipids) are used by salmon as an energy source while at sea (Davis et al. 1998; Nomu-

ra et al. 1999; Myers et al. 2000). Lipid levels can vary from 3% to 23% during spring and summer in chum and pink salmon (Nomura et al. 2000), and significant differences in lipid levels have been found between younger (lower) and older (higher) chum salmon white muscle tissues (Nomura et al. 2001). Lipid-rich squid provide an important resource for salmon at sea (Lordan et al. 1998; Yatsu et al. 2000; Davis et al. 2001). Changes in lower trophic levels, i.e. zooplankton biomass and composition, have been positively associated with squid production (Nesis 1997; Kang et al. 2002). Therefore, we speculate that variation in bottom-up ocean conditions resulting from climate change (Brodeur and Ware 1992; Sakurai et al. 2000) may have a significant effect on salmonid development and subsequent reproductive success.

We examined age at maturation of Bristol Bay salmon in relation to climate shifts during 1952 to 1998. Total age at maturation of westside and eastside Bristol Bay sockeye salmon stocks remained relatively constant throughout three climate regimes (Figure 3, bottom panel). However, the number of

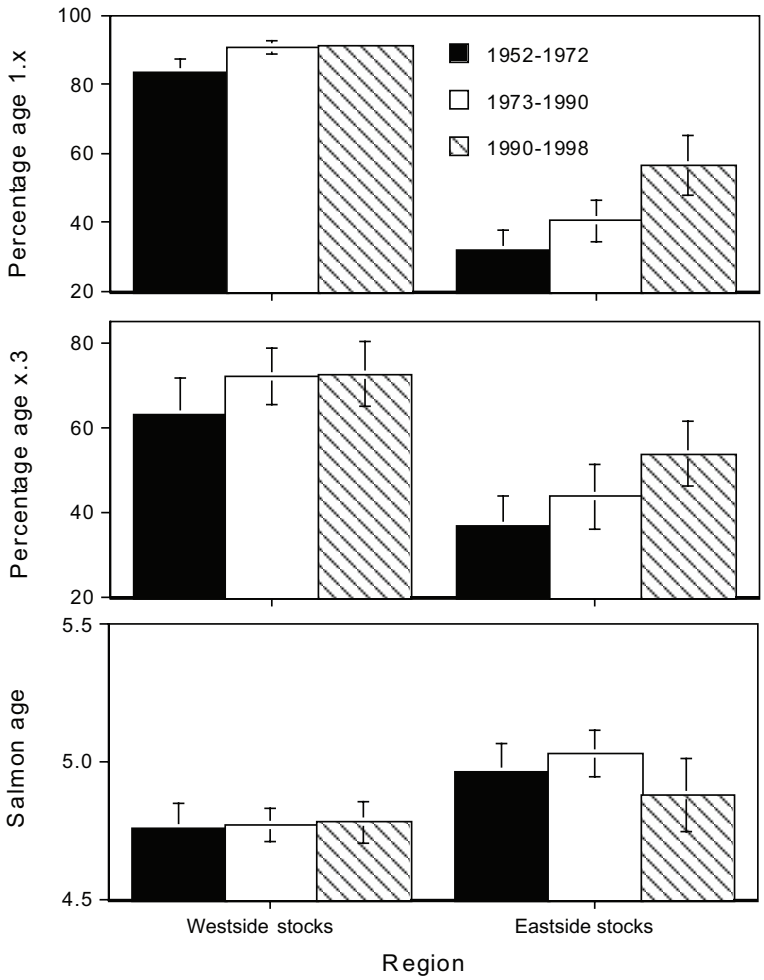

FIGURE 3. Freshwater and marine age composition and total mean age of eastside and westside Bristol Bay sockeye salmon *O. nerka* stocks during three climate regimes, 1952–1998. Values are mean ± 1 SE (with permission Ruggerone and Link 2006).

years spent in freshwater versus marine areas changed markedly between each regime, except for westside stocks during the recent 1989 climate shift. Among eastside sockeye salmon stocks, the percentage of freshwater age 1 (1.x) and ocean age 3 (x.3) salmon increased over time and during each regime (Ruggerone and Link 2006). Reduced salmon residence time in freshwater (in likely response to increasing temperature during the past 45 years) was associated with increased time in the ocean, leading to little change in total age at maturation (Peterman et al. 2003; Ruggerone and Link 2006). Thus, Bristol Bay sockeye salmon have tended to experience a relatively fixed age at maturation, which is achieved through trade offs of residence in freshwater versus marine environments (Rogers 1987). Warming temperatures can have a marked effect on residence in lakes and the ocean, especially among populations such as those on the eastside of Bristol Bay where fish formerly tended to spend two winters in freshwater and two winters at sea. Changes in the ocean age may affect reproductive potential and success of salmon through changes in fecundity or by affecting the ability of salmon to successfully spawn in habitats where size affects reproductive success, e.g., large rivers, shallow creeks, and areas with size-dependent predation by bears.

Climate Change and Late Ocean Life Stages

Marine fish populations have been shown to be responsive to climate variability with strong regional and local patterns (Mueter et al. 2002; McGinn 2002 and literature therein). Since adult salmon at sea are influenced by climate on multiple temporal and spatial scales, it is important to link questions and data to the same scale. Climate drivers have large-scale regional footprints. Data collected from sediments in sockeye-bearing lakes suggest that climate and salmon runs may have a long correlated history (Finney et al. 2000). Several studies have shown that the distribution and abundance of anadromous salmon returning to freshwater to spawn are vulnerable to the influences of climate change on a more local scale (Beamish and Bouillon 1993; Clark and Hare 2002; Meuter et al. 2002; Beamish et al. 2004; Pyper et al. 2005). Changes in ocean temperature may affect the migration timing and behavior of locally adapted spawning stocks (Bernatchez and Dodson 1987; Hodgson and Quinn 2002; Ruggerone 2004). However, inter-decadal and even shorter patterns in climate variation have had associated fisheries impacts (McGinn 2002).

Several recent climate simulation models and empirical models predicted a phase shift in fisheries productivity from northern to southern Pacific Ocean habitats based on cyclical climatic fluctuations (Francis and Sibley 1991; Peterson et al. 1993; Peterman et al. 1998; Francis et al. 1998; Anderson and Piatt 1999; Hare and Mantua 2001; Botsford et al. 2002). Under this concept, salmon in northern British Columbia and Alaska are thought to be on an alternate trajectory of abundance compared with southern stocks (Hare et al. 1999; Pyper and Peterman 1999). Furthermore, productivity of salmon populations tends to be more correlated among nearby compared with distant stocks, implying that regional climate affects salmon populations in addition to large-scale effects (Pyper et al. 2005).

Although large scale and regional oceanographic features are important to salmon production, the interactions between species originating from distant regions is also important. For example, multivariate time series analyses indicated that Bristol Bay sockeye growth during the second year at sea was negatively related to abundance of Eastern Kamchatka pink salmon and positively related to winter sea-surface temperature in the North Pacific Ocean (Ruggerone and Nielsen 2004).

Additionally, McKinnell (1995) reported that growth of northern British Columbia sockeye salmon during their last year at sea may be negatively influenced by abundance of Bristol Bay sockeye salmon.

Fisheries harvest data supporting negative sockeye growth at sea in relationship to abundance, however, remain controversial. A PDO phase shift thought to contribute to this effect was documented in 1998, but recent recruitment to Pacific salmon stocks in different geographic regions has been mixed (Beamish et al. 2004). Significantly larger runs of salmon have been reported in recent years in some Pacific Northwest rivers, but not in others (Keefer et al. 2004). Salmon in Alaska have also experienced variable productivity with declines in some Bristol Bay stocks, but not in other geographically proximate rivers (Ruggerone and Nielsen 2004; Ruggerone and Link 2006). Local variations in natural productivity or effects of fisheries are likely superimposed on broad-scale, climate-driven production variations. Little data are available for salmon growth at sea throughout each life stage. Our studies concluded that Bristol Bay and Chignik River sockeye salmon *O. nerka* growth declined during their third year at sea and during their homeward migration after the mid-1970s (Ruggerone et al. 2007). Reduced growth during their third year at sea was especially great during odd-numbered years when Asian pink salmon were most abundant (see below).

Local, fine-scale environmental conditions in both near-shore marine and freshwater outflow habitats may play an important role in the climate-salmon relationship (Mueter et al. 2002). Global change effects may impact estuarine migration patterns and oxygen consumption requirements for migrating salmon (Stevenson et al. 2002; Roessig et al. 2004). Additional research is needed on salmon life histories at the freshwater-marine interface during upstream and downstream migrations under different patterns of climate change.

Climate Change and Population Distribution

The most abundant North American salmonid populations in the Pacific Ocean are thought to have colonized freshwater habitats from more southern refugia populations since the end of the last ice cover, less than 10,000 years before present (Macdougall 2004). Warming climate may increase or accelerate the movement of aquatic species including spawning salmon populations further north (Welch et al. 1998; Rahel 2002; Roessig et al. 2004; Perry et al. 2005; Wing 2006). All five Pacific salmon species have been recently reported in previously unoccupied riverine habitats in the Canadian arctic (Babluk et al. 2000; Beamish and Noakes 2002). Incidental reports of coho, pink and chum salmon *O. keta* are available from rivers draining into the North Bering and Chukchi seas in Alaska, north of the current limits of each species' range (Craig and Haldorson 1986; Beamish and Noakes 2002). In 2004 and 2005, unprecedented numbers of pink salmon returned to the Norton Sound region, apparently in response to warm ocean temperatures in recent years (G. Sandone, Alaska Department of Fish and Game, personal communication) and the most northerly sockeye population in Port Clarence has expanded dramatically over the past five years (E. Knudsen, C. Lean, K. Dunmall and G. Sandone, personal communications). Natural colonization of novel habitats by Pacific salmon has been facilitated in Alaska by glacial retreat (Milner et al. 2000). Novel colonizations of new glacial streams have resulted in highly variable ecosystem structure and research has shown that colonization pathways can differ significantly across ecosystems (Milner and Bailey 1989; Burger et al. 2000; Milner et al. 2000; Pavey 2004; Quinn and Myers 2005). There is a clear need to study shifts in life history characteristics of salmon in relation to climate change and colonization of new habitats (Field and Francis 2002; Pavey 2004).

Asian Pink Salmon Affect Sockeye Growth and Survival at Sea

The mechanisms linking Pacific salmon growth and abundance in the ocean and climate change are very complex and often nonintuitive since most salmonid literature has focused on the freshwater phase of these fish. One aspect of the overall productivity for salmon at sea has clearly increased extensively over the last three decades, artificial propagation and release of hatchery fish into marine habitats. Salmon hatcheries across the North Pacific Ocean, in the U.S., Canada, and throughout Asia, release up to five billion salmon a year (Mahnken et al. 1998). Natural salmon production in wild riverine habitats, such as the Kamchatka Peninsula, has also increased substantially over the last three decades (Sinyakov 1998). Differentiation of hatchery and wild fish at sea is sometimes problematic since not all hatchery fish are marked at their hatchery of origin (Heard 1998). Interactions between wild and hatchery-produced salmon at sea have only recently been studied (Levin et al. 2001; Orsi et al. 2004; Wertheimer et al. 2004). However, the rapid increase in hatchery and wild salmon abundance in the North Pacific Ocean following the 1977 regime shift led to food limitations with intra-specific (Rogers and Ruggerone 1993; Bigler et al. 1996) and nonlinear inter-specific effects (Burkett et al. 2005) on salmon growth.

In northern latitudes where wild salmon have been especially abundant, the 1976/1977 regime shift appeared to enhance growth and survival of salmon during early marine stages, leading to density-dependent effects during older stages when survival is less influenced by growth (Ruggerone et al. 2002, 2007). During 1958–1999, annual growth of Bristol Bay sockeye salmon was low during odd-numbered years of the second and third years at sea (Figure 2), a pattern that was opposite from that of Asian pink salmon abun-

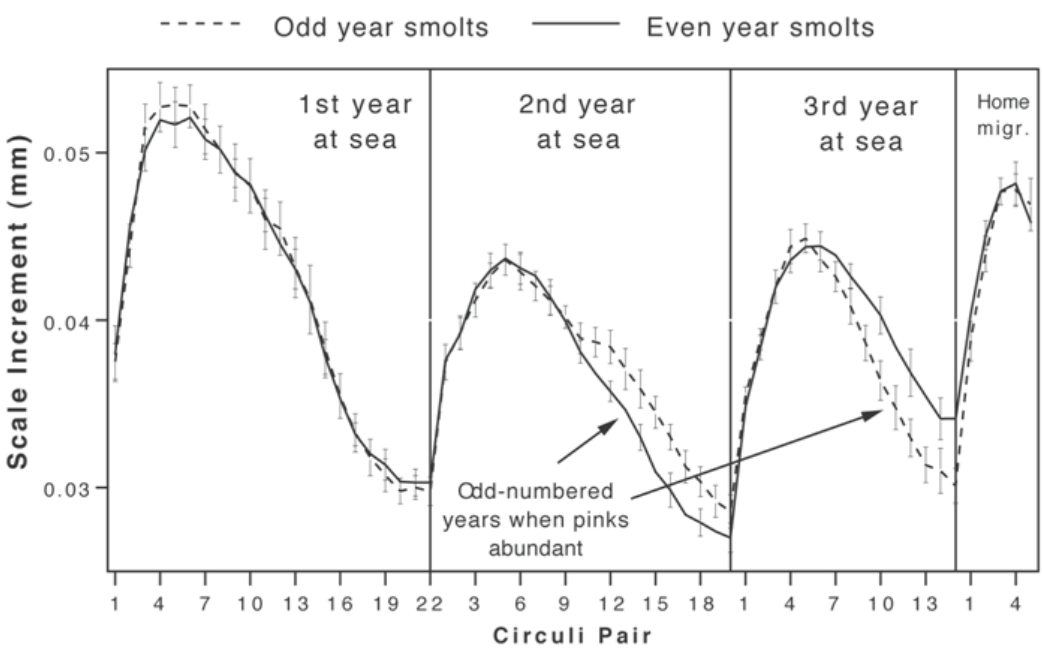

Figure 4. Seasonal growth at sea of Bristol Bay sockeye salmon during odd- and even-numbered years, based on circuli measurements from adult scales (with permission Ruggerone et al. 2005).

dance (Ruggerone et al. 2003). Competition with pink salmon occurred after peak sockeye growth in spring (Figure 4). The effect of competition on sockeye salmon growth appeared to transcend the 1976/1977 ocean regime shift because both salmon species responded similarly to the large scale climate change and increased over time (Ruggerone et al. 2005). No competition was detected during the first year at sea when there was little or no overlap with Asian pink salmon. First year competition may not be expressed in growth if all smaller fish died during their first year at sea (Farley et al. 2007). Interspecific competition was also not evident in the homeward migration of sockeye salmon when there was no overlap with Asian pink salmon.

Adult Bristol Bay sockeye length decreased in years with large Bristol Bay sockeye runs and in years following large Asian salmon runs indicative of density-dependent growth (Ruggerone et al. 2003). Sockeye salmon lengths in Bristol Bay stocks were greater in 1977–2000 compared to 1958–1976 at a given abundance of adult sockeye and pink salmon (Figure 5). However, recent evidence indicates the mid-1970s and 1989 climate shifts affected sockeye salmon size at age in addition to inter- and intraspecific competition (Ruggerone et al. 2007). The decline in size at age of Bristol Bay sockeye salmon after the 1989 climate shift may have reduced individual reproductive success of ocean age-2 sockeye salmon and contributed to the observed decline in productivity of stocks associated with a high proportion of ocean age-2 sockeye salmon (Ruggerone and Link 2006).

Recent research on species interactions in the ocean has provided evidence that competition can lead to reduced survival of salmon. During 1977–1997, sockeye salmon smolts from Bristol Bay, Alaska, experienced 26–45% lower survival at sea when migrating during even-numbered years and competing with Asian pink salmon (Ruggerone et al. 2003). Age-1 smolts experienced greater mortality compared with age-2 smolts. Adult returns from even-year smolt migrations were 22% lower, on average, leading to 482 million fewer adult sockeye salmon produced by smolts during 1977–1997 (Ruggerone and Nielsen 2004). Prior to the 1976–1977 ocean regime shift, scale growth of sockeye salmon was reduced during years of great pink salmon abundance but a reduction in sockeye salmon abundance was not detected, possibly because the high seas salmon fishery captured many Bristol Bay sockeye salmon.

In the Pacific Northwest, an analysis of 53 million coded-wire-tagged Chinook salmon demonstrated that juvenile Chinook salmon survival declined 62% when entering Puget Sound and lower Strait of Georgia in even-numbered years along with the large migration of juvenile pink salmon, 1984–1997 (Ruggerone and Goetz 2004). No odd-even pattern of survival was detected among Chinook salmon released in coastal areas where few pink salmon originate. Coastal data and age-specific adult recoveries of Puget Sound Chinook salmon indicated that mortality occurred in Puget Sound and the lower Strait of Georgia during the first year at sea. Growth of Chinook salmon was significantly reduced and age at maturation was extended when competing with pink salmon. During 1972–1982, the odd-even year pattern of survival was reversed. The authors provided evidence that the mechanism of Chinook salmon mortality switched from primarily predation to competition in response to climate change and associated declines in piscivores and prey availability and an increase in pink salmon abundance.

Summary

Environmental change in critical marine habitats has had a significant impact on salmonid populations throughout the Pacific Rim. This review of studies exploring ocean

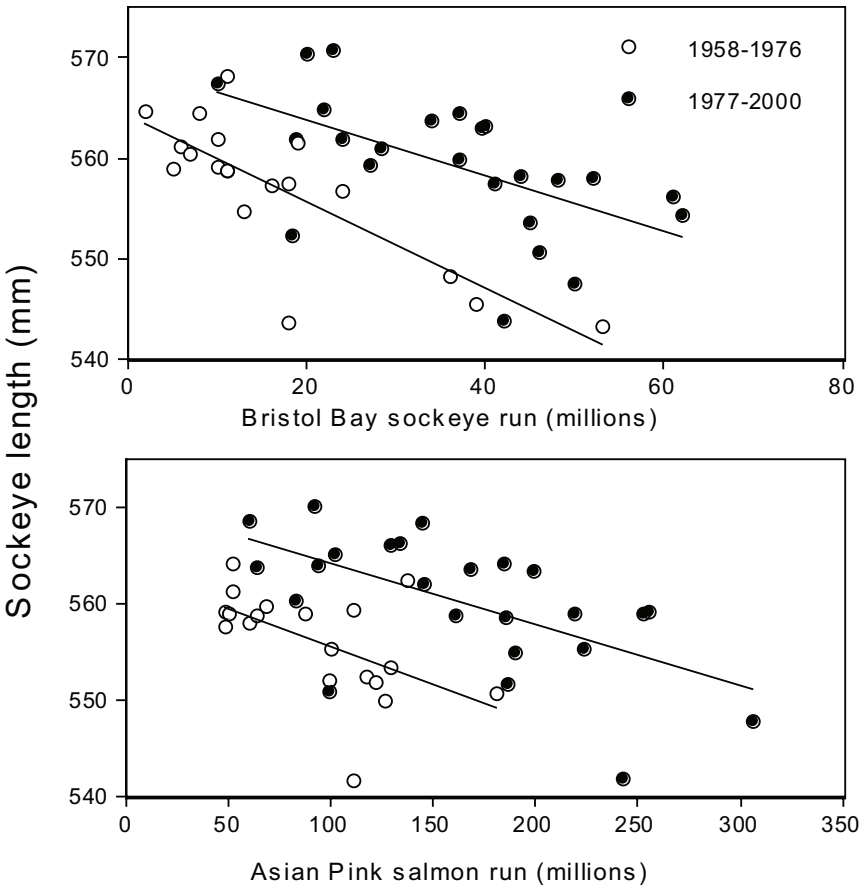

FIGURE 5. Regression-corrected plots of adult, age 1.3, female, Bristol Bay, sockeye salmon O. nerka lengths in relation to adult abundance of Bristol Bay sockeye salmon (A) and Asian pink salmon abundance during the previous year (B). Salmon lengths are partial residuals based on the following multivariate equation (adapted with permission Ruggerone et al. 2003):

Length (mm) = 571.7 – 0.0339 (sockeye run) – 0.067 (pink run) + 8.76 (period); r2 = 0.059, where period is coded as "1" after the 1976/1977 regime shift or "0" prior to 1977.

condition and physical forces that shape the North Pacific system showed significant relationships with salmon growth and productivity. However, the effects of climate change on other life history traits, such as age at maturation and fecundity, have not been well-documented and impacts of ocean regime change on community ecology are even less well known (see Mangel and Levin 2005). Anadromous salmonids demonstrate diverse behavior in their passage through coastal and marine habitats with important physiological trade offs required for survival and reproduction during these transits. Our research has shown that density-dependent growth in sockeye salmon varies with life stage and season. These patterns in marine growth can be associated with climate change and density-dependent factors that are both natural and human-induced. Greater abundance and

productivity of Alaskan salmon following the 1976/77 ocean regime shift was associated with greater salmon growth during the first two years at sea. However, density-dependent growth was significant at later life stages when growth-related mortality was less important and maturation and reproduction became primary functions affected by growth. Further research needs to be done on the relationship between growth-related changes in fecundity and maturity with total returns of North Pacific salmon in relationship to climatic variation. Hatchery and wild pink salmon production in the North Pacific Ocean has grown significantly following the 1976/77 regime shift. Our research suggests that greater pink salmon abundance has affected growth, survival, and abundance of Bristol Bay sockeye salmon over the last several decades. Salmon life history models developed for this time of dynamic ocean and climatic conditions should not ignore density-dependent growth at sea when modeling the often elusive mechanisms affecting salmon survival.

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