DETERMINING THE EFFECTS OF ASIAN PINK AND CHUM SALMON ON WESTERN ALASKA CHUM SALMON GROWTH

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Abstract

Increased hatchery production and favorable ocean conditions have resulted in historically high abundances of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. Despite these conditions, chum salmon (*O. keta*) have experienced reductions in growth, body size, and increases in age at maturity throughout their range. In western Alaska, dramatic declines in the abundance of chum salmon between 1997-2001 resulted in numerous fishery and economic disasters among commercial and subsistence users. Chapter 1 reviews existing data on salmon diet and ocean distribution to address the potential for competition between western Alaska chum salmon and Asian pink (*O. gorbuscha*) and chum salmon in the Bering Sea. Western Alaska chum salmon reside in the Bering Sea during their summer foraging months where they overlap with abundant populations of Russian pink salmon (primarily wild origin) and Japanese chum salmon (primarily hatchery origin). Chum and pink salmon occupy a similar feeding niche, and during years of high pink salmon abundance chum salmon have been observed to alter their ocean distribution and rely more heavily on gelatinous zooplankton species as a primary food source. This spatial and diet overlap suggests that inter- and intra-specific competition might contribute to reduced growth and increased age at maturity of western Alaska chum salmon. Chapter 2 uses retrospective scale analysis coupled with linear mixed-effects modeling to investigate the potential for such competition between Asian pink and chum salmon abundance and the growth of chum salmon that rear in the Bering Sea. Chum salmon scale samples were collected through in-river fisheries on the Kuskokwim River during 1973-2014 and from incidental catches of chum salmon in the Bering Sea Aleutian Island walleye pollock (*Gadus chalcogrammus*) fishery during 2001-2016. Linear mixed-effects models demonstrated a strong negative relationship between Bethel chum salmon growth and the abundance of Japanese hatchery chum salmon. Chum salmon intercepted in the Bering Sea did not exhibit increased growth during 2012-2014 despite reductions in Japanese hatchery releases of chum salmon in 2011 as a result of the Tōhoku Earthquake and tsunami. We did not observe a relationship between Bethel chum salmon growth and the abundance of wild Russian pink salmon. Understanding how salmon populations interact while at sea will assist fishery managers in conserving threatened salmon stocks, particularly as Pacific Rim nations consider increasing production of hatchery salmon.

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Introduction

Favorable ocean conditions for survival and a 200,000% increase in the production of hatchery salmon (*Oncorhynchus* spp.) from Pacific Rim countries between 1952 and 2016 have resulted in historically high abundance of Pacific salmon species in the North Pacific Ocean (Irvine and Ruggerone 2016). Concurrent with increased salmon abundance, chum salmon (*O. keta*) have experienced decreases in fork length and growth rates and increases in age at maturity throughout their spawning range (Helle and Hoffman 1995; Bigler et al. 1996; Kaeriyama 1998). These synchronous changes in chum salmon life history suggest that a shared variable may responsible. Although the mechanisms underlying these changes are not well understood, density-dependent effects, specifically competition with abundant Asian pink (*O. gorbuscha*) and chum salmon populations in the Bering Sea, is a primary hypothesis (Ishida et al. 1993; Ruggerone et al. 2011).

While at sea, chum salmon exhibit a large geographical distribution, inhabiting areas from Japan to the west coast of the United States (Salo 1991). Research on salmon distribution using tagging studies and genetic stock identification has identified general ocean migration patterns by stock of origin. These studies suggest that western Alaska and Japanese chum salmon follow similar migration patterns while at sea, inhabiting the Bering Sea during summer and the Gulf of Alaska in winter (Myers et al. 2007; Urawa et al. 2009). Chum salmon originating from Japan are assumed to be entirely of hatchery origin and are one of the dominant chum salmon stocks in the Bering Sea (Urawa et al. 2009; Irvine and Ruggerone 2016). Chum salmon growth has been demonstrated to decline significantly with increasing abundance of Japanese hatchery chum salmon for chum salmon stocks returning to areas in Russia, Japan, and Alaska, potentially as a result of density dependence (Ishida et al. 1993; Ruggerone et al. 2011; Yasumiishi et al. 2016).

Pink salmon are the most abundant salmonid in the North Pacific Ocean, accounting for 63% of commercial catches in 2015 (data from http://www.npafc.org/new/science_statistics.html). Pink salmon grow rapidly and exhibit a fixed two-year life cycle that can result in significant differences in pink salmon abundance between even- and odd-numbered years. Pink salmon originating from eastern Kamchatka represent the dominant stock of pink salmon in the Bering Sea and are more abundant during odd-numbered years (Takagi et al. 1981; Ruggerone and Nielsen 2004). Researchers have taken advantage of the natural even- and odd-year cycles of pink salmon abundance to measure their potential competitive effects on other salmon species, as pink salmon are efficient foragers and can significantly reduce prey weight during years of high abundance (Sano 1963; Davis 2003; Ruggerone and Nielsen 2004). Although chum and pink salmon occupy a similar feeding niche, chum salmon are the only salmonid observed to feed on gelatinous zooplankton species due to specializations in their gut morphology (Welch 1997; Davis 2003). This trait may be a result of past selective pressure that evolved to minimize competition by exploiting a unique branch of the food web (Welch 1997). In the Bering Sea, chum salmon have been shown to alter their diets during odd-numbered years by foraging more heavily on gelatinous zooplankton species (Tadokoro et al. 1996; Davis 2003). Although this unique feeding adaptation allows chum salmon to take advantage of this feeding niche, gelatinous zooplankton species are low in calorie and lipid content compared to other prey items, such as squid and fish (Davis 2003). As a result, chum salmon lipid content in the Bering Sea has been shown to be lower during odd-numbered years, which can have adverse effects on growth, fecundity, and overwinter survival (Nomura et al. 2002; Kaga et al. 2013).

This thesis investigates the relationship between western Alaska chum salmon growth and the abundance of Asian pink and chum salmon in the Bering Sea. Pacific salmon stocks from the Arctic-Yukon-Kuskokwim (AYK) region of western Alaska play a crucial role in the economic and food security of many rural Alaskan communities through commercial and subsistence fisheries (Krueger et al. 2009). Substantial decreases in the abundance of AYK chum and Chinook (*O. tshawytscha*) salmon runs from 1997-2002 resulted in 15 disaster declarations from state and federal agencies throughout the region (AYK SSI 2006). The AYK region includes the Norton Sound and Yukon and Kuskokwim River watersheds, which collectively encompass 40% of the State of Alaska and were all affected by fisheries disasters. Subsistence fishing in western Alaska has provided food to indigenous peoples for centuries and is an integral part of Alaska Native culture through the passage of traditional ecological knowledge to younger generations (Wolfe and Spaeder 2009). Commercial fishing in the region began gaining momentum in the 1970s and quickly became an important source of monetary income (Hilsinger et al. 2009; Wolfe and Spaeder 2009). Fishery closures in this region have had detrimental economic, food security, and cultural impacts on rural Alaska natives and highlight the need to understand what is driving changes in chum salmon life history.

Retrospective analysis of chum salmon scales collected through commercial fisheries in western Alaska and as incidental catches in the Bering Sea Aleutian Island (BSAI) walleye pollock (*Gadus chalcogrammus*) fishery allows us to examine growth accrued during ocean residence (Yasumiishi et al. 2015). Western Alaska chum salmon scales from the Kuskokwim River were collected and analyzed by the Alaska Department of Fish and Game through in-river harvest during 1968 and 1973-2014. In-river harvest represents fish that survived their ocean residence and provides stock-specific information on temporal trends in chum salmon growth. Chum salmon scales collected through the BSAI pollock fishery were intercepted in the Bering Sea during 2001-2016 and represent both mature and immature chum salmon from a mixture of stocks that might or might not have survived their ocean residence.

Chapter 1 provides a synthesis of data regarding the extent of spatial and diet overlaps among salmon stocks in the Bering Sea and North Pacific Ocean. Data from previously published research on stock-specific distribution patterns, including high-seas tagging, genetic stock identification (GSI), and size distribution were synthesized to determine where, when, and to what extent western Alaska chum salmon populations overlap in space and time with Asian pink and chum salmon. GSI from chum salmon caught incidentally in the BSAI pollock fishery provides information on the origin of chum salmon that reside in the Bering Sea during July and August. Distribution data was used to assess when overlaps between Asian pink and chum salmon and western Alaska chum salmon populations are most likely to occur by season and age class. To evaluate the potential for intra- and inter-specific competition due to diet overlap, information on seasonal and age-specific chum and pink salmon distribution was used to assess when diet overlaps are most likely to occur. Collaboration with Dr. Nancy Davis allowed me to examine food habits and feeding ecology of Pacific salmon in the Bering Sea from 1991-2000. Davis's study was the first to capture temporal trends in salmon feeding ecology in both the central Bering Sea and central North Pacific Ocean over a ten-year period, allowing us to observe how chum salmon diet changes by region and during years of high and low pink salmon abundance.

Chapter 2 uses linear mixed-effects models to determine the relationship between western Alaska chum salmon growth and Asian pink and chum salmon abundance. Stock-specific abundance estimates of pink and chum salmon were obtained from Irvine and Ruggerone (2016) to assess how western Alaska chum salmon growth changes with the abundance of Asian pink and chum salmon. Sea-surface temperature was also included in the analysis to capture environmental effects on chum salmon growth. While pink salmon have been demonstrated to affect other salmon species (Ruggerone and Nielsen 2004), interactions between pink and other salmon species may simply be easier to identify due to biennial cycles of pink salmon abundance. Understanding how the abundance of conspecifics affects western Alaska chum salmon is more difficult, as chum salmon exhibit variation in age at maturity and Japanese hatchery chum salmon abundance has remained largely unchanged from year to year. However, in 2011 the Tōhoku earthquake occurred off the east coast of Japan, triggering a large tsunami that struck and destroyed 26 salmon hatcheries (North Pacific Anadromous Fish Commission Newsletter 32, www.npafc.org; North Pacific Anadromous Fish Commission Newsletter 37, www.npafc.org). This resulted in a 37% decrease in Japanese hatchery chum salmon releases in 2011, representing the lowest year of Japanese hatchery chum salmon production since 1978 (data from http://www.npafc.org/new/science_statistics.html). Although many of the hatcheries were rebuilt by the following year, this temporary decrease in hatchery chum salmon production provided a means to test for density dependence between western Alaska chum salmon and Japanese hatchery chum salmon in the Bering Sea.

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Chapter 1: Chum (*Oncorhynchus keta*) salmon in the Bering Sea: a review of diet and ocean distribution

1.1 Abstract

Increased hatchery production and favorable ocean conditions have resulted in historically high abundances of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. Although many salmon populations in the North Pacific increased following the 1976-77 climate regime shift, there have been reductions in chum salmon (*O. keta*) growth and body size and increases in age at maturity throughout their range. In western Alaska, Yukon River subsistence fall chum salmon harvests decreased by 89% between 1990 and 2000, and Kuskokwim River chum salmon subsistence harvests fell by 63.3% between 1989 and 2007. The Alaska Board of Fisheries has since labeled numerous stocks as stocks of yield concern, with important implications for rural Alaskans who rely on salmon for food. The mechanisms underlying these changes in chum salmon body size are not well understood, although density dependence, specifically competition with abundant Asian pink (*O. gorbuscha*) and chum salmon in the Bering Sea, is a primary hypothesis. This review synthesizes existing data on salmon diet and ocean distribution to address the potential for competition among salmon stocks in the Bering Sea. Asian pink and chum salmon and western Alaska chum salmon occupy a similar feeding niche and exhibit similar ocean migration patterns after the first year at sea, which may result in competition when food is limited. Understanding the degree of diet and distribution overlap between western Alaska chum salmon and distant salmon stocks is critical, especially as Pacific Rim countries consider increasing their hatchery salmon production.

1.2 Background

Increased hatchery output and favorable ocean conditions for survival have resulted in historically high abundances of Pacific salmon species (*Oncorhynchus* spp.) in the North Pacific Ocean (Irvine and Ruggerone 2016; Fig. 1.1). Pink (*O. gorbuscha*) and chum (*O. keta*) salmon are the most abundant salmonids, collectively accounting for 84% of commercial salmon catches in the North Pacific in 2015. Despite favorable ocean growing conditions and increased catches, researchers began observing a decline in chum salmon body size, growth rate, and an increase in age at maturity throughout their range beginning in the 1980s (Ishida et al. 1993; Azumaya and Ishida 2000; Irvine and Ruggerone 2016). Declines in chum salmon body size have been attributed to increased salmon abundance, whereby 35% of the variability in chum salmon body weight may be attributable to density dependence (Ruggerone et al. 2011; Irvine and Ruggerone 2016). In the Arctic-Yukon-Kuskokwim (AYK) region of western Alaska, declines in the abundance of Chinook (*O. tshawytscha*) and chum salmon have led to reductions in commercial, sport, and subsistence fisheries, threatening the traditional way of life of rural and native Alaskans who have relied on the subsistence harvest of salmon for thousands of years (Krueger et al. 2009). The objective of this paper is to review the potential factors that may be driving the observed changes in chum salmon life history. Catch statistics provided by the North Pacific Anadromous Fish Commission (NPAFC; http://www.npafc.org/new/science_statistics.html) and abundance estimates from Irvine and Ruggerone (2016) are used to quantify the proportion of wild and hatchery chum and pink salmon by region. Data on the extent of spatial and dietary overlap between chum and pink salmon populations in the Bering Sea and North Pacific is synthesized to determine the potential for competition among stocks. Understanding the diet and ocean distribution of potentially competing salmon stocks can assist fishery managers in understanding how at-sea interactions affect the growth, body size, and age at maturation of western Alaska chum salmon populations.

1.2.1 History of wild salmon abundance

Pink salmon are the most abundant salmonid in the North Pacific, accounting for 63% of commercial catches in 2015 (data from http://www.npafc.org/new/science_statistics.html). Pink salmon are mostly of wild origin, with wild fish accounting for 81% of total pink salmon abundance in 2015 (Irvine and Ruggerone 2016). During 1990-2015, wild pink salmon in the North Pacific originated primarily from regions of Russia (57%), including Kamchatka, Sakhalin, and the Kuril Islands; followed by Alaska (34%), primarily southeast Alaska (22%); and Canada (6%; Fig. 1.2; Table 1.1).

Chum salmon constituted 21% of commercial salmon catches in the North Pacific in 2015 (data from http://www.npafc.org/new/science_statistics.html; Fig. 1.1) with wild fish comprising 55% of total chum salmon abundance (Irvine and Ruggerone 2016; Fig. 1.3). Although dramatic increases in abundance were observed for pink and sockeye (*O. nerka*) salmon following the 1976/77 ocean regime shift, wild chum salmon abundance did not increase, and from 1980-2005 wild chum salmon abundance was lower than the estimated abundance in the 1950s (Ruggerone et al. 2010). During 1990-2015, the average contribution of wild chum salmon populations from Pacific Rim countries was largely from Russia (52%); followed by Alaska (34%), primarily western Alaska (15%); and Canada (12%; Irvine and Ruggerone 2016; Fig. 1.3; Table 1.2).

1.2.2 History of hatchery salmon abundance

Hatchery salmon releases into the North Pacific were first recorded beginning in 1952 (data from http://www.npafc.org/new/science_statistics.html). Releases have since increased from 2.7 million salmon in 1952 to over 5.1 billion salmon in 2016 (Fig. 1.4). The 1970s marked the beginning of steadily intensifying hatchery production, with outputs increasing from an average of 1.7 million juvenile salmon releases per year from 1952-1970 to over 1 billion juveniles per year on average from 1990-2016. Hatchery salmon production peaked in 2014 when more than 5.3 billion juvenile salmon were released from hatcheries in Canada, Japan, Korea, Russia, and the United States. Japan is the leader in hatchery chum salmon production, accounting for 80% of total hatchery chum salmon releases on average from 1990-2015 (Fig. 1.3). Alaska is the largest producer of hatchery pink salmon, accounting for 70% of hatchery pink salmon releases from 1990-2015, with a majority of hatchery pink salmon being released from Prince William Sound (65%; Fig. 1.2).

Hatchery-origin salmon represented 58% of total chum salmon and 14% of total pink salmon abundance in the North Pacific on average from 1990-2015 (Irvine and Ruggerone 2016). Hatchery chum salmon were more abundant than wild chum salmon from 1984-2013, accounting for 62% of total chum salmon abundance in 2005. However, a 264% increase in the abundance of wild Russian chum salmon between 2005-2015 resulted in wild chum salmon outnumbering hatchery chum salmon beginning in 2014 (Fig. 1.5). By 2015, wild chum salmon accounted for 55% of total chum salmon abundance. During 1990-2015, hatchery origin salmon represented 38% and 25% of U.S. and 15% and 7% of Russian chum and pink salmon (Fig. 1.6; Tables 1.1 and 1.2). In Japan, 100% of chum salmon are assumed to be of hatchery origin compared to only 20% of pink salmon.

1.2.3 History of western Alaska chum salmon

The Arctic-Yukon-Kuskokwim (AYK) region of western Alaska constitutes over 40% of the State of Alaska's land area and includes the watersheds of Norton Sound, the Yukon and Kuskokwim Rivers, and the Bering Sea and North Pacific ecosystems (Krueger et al. 2009; Fig. 1.7). Wild chum salmon stocks from the AYK region play a crucial role in the economic and food security of many rural Alaskan communities through commercial and subsistence fisheries. While subsistence fishing in western Alaska has provided food to indigenous peoples and their dog teams for centuries, commercial fishing in the region began gaining momentum in the 1970s and quickly became an important source of monetary income in otherwise cash-poor villages (Hilsinger et al. 2009; Wolfe and Spaeder 2009). Money generated through commercial fishing is used to mend nets and purchase goods required for subsistence fishing, thereby strengthening core village subsistence activities (Wolfe and Spaeder 2009). Village residents traditionally have high wild-food harvests and low monetary incomes, as villages are geographically dispersed throughout the region and usually have less than 500 residents. During the 1990s, wild-food harvests for the AYK region averaged 670 pounds per person per year, compared to only 19 pounds per person per year in Anchorage. This difference in harvest between village and city residents highlights the importance of fish returns in western Alaska. Here, salmon serve as a protein source for people who are otherwise isolated from the conveniences of larger cities and enable the passage of traditional ecological knowledge from one generation to the next through the practice of subsistence fisheries.

Dramatic declines in Pacific salmon runs throughout the AYK region between 1997-2001 resulted in numerous fishery and economic disasters among commercial and subsistence users (Krueger et al. 2009). Declines in AYK commercial fishing in the 1990s caused the total ex-vessel value of the Yukon, Kuskokwim, and Norton Sound-Port Clarence areas to decrease from $15.7 million in 1998 to $2.0 million in 2002 (Wolfe and Spaeder 2009). Subsistence harvests fell by 89% between 1990 and 2000 for Yukon River fall chum salmon and by 63.3% between 1989 and 2007 for Kuskokwim River chum salmon. Consequently, the Alaska Board of Fisheries (BOF) has designated numerous stocks as "stocks of yield concern" intermittently since the 2000s (Bue et al. 2006; Linderman and Bergstrom 2006; Schindler et al. 2013). A stock of yield concern is defined as "a concern arising from a chronic inability, despite the use of specific management measures, to maintain expected yields, or harvestable surpluses, above a stock's escapement needs" (5 AAC 39.222(f)(42)), where chronic inability is defined as "the continuing or anticipated inability to meet expected yields over a 4 to 5 year period." Closures and reductions in both commercial and subsistence harvest of Chinook and chum salmon have negatively affected rural Alaska native communities in regards to economic and cultural impacts and food security concerns (Loring and Gerlach 2010). Although many AYK chum salmon stocks have increased in abundance since the 2000s, rural Alaskans rely more heavily on chum salmon harvests when AYK Chinook salmon runs are poor. Understanding the mechanisms behind the decline of chum salmon returns to the AYK region and changes to their life history is critical for rural Alaskans who rely on salmon as a food source.

1.3 Observed changes in chum salmon life history

Decreases in adult chum salmon body size have been concurrent with an increase in age at maturity throughout the species' range (Ishida et al. 1993; Helle and Hoffman 1998; Morita et al. 2005; Zavolokin et al. 2009). While specific changes in chum salmon growth and maturity vary by stock, regional responses of chum salmon returning to Alaska, Japan, and Russia have led researchers to investigate high-seas interactions between potentially competing salmon stocks in the Bering Sea and North Pacific. While this review will focus on potential factors underlying changes in growth and age at maturity of AYK chum salmon stocks, these trends are occurring in chum salmon stocks throughout the North Pacific and Bering Sea. In Alaska, declines in body size and increases in age at maturity have been observed in Norton Sound (Ruggerone et al. 2011), Bristol Bay and the Yukon River (Agler et al. 2013), and southeast Alaska (Yasumiishi et al. 2016).

1.3.1 Eastern North Pacific

Helle and Hoffman (1998) observed decreasing body size and increasing age at maturity for two populations of North American chum salmon beginning as early as the 1970s. Mean body length of age-0.3 chum salmon decreased by 11.6% and 8.6% for fish returning to Fish Creek in southeast Alaska and the Quilcene National Fish Hatchery in Washington State, respectively (Helle and Hoffman 1998; Yasumiishi et al. 2016). Although body size did increase from the early 1990s to 2000, changes were relatively small and neither population rebounded to body sizes observed in the 1970s. Declines in body size can influence reproductive success due to effects on fecundity, competition on the spawning grounds, and the scour resistance of redds (Schoener 1982; Helle 1989; Montgomery et al. 1996).

To assess changes in body size and age at maturity, Bigler et al. (1996) investigated 10 chum salmon populations in Alaska, Washington, and British Columbia. The authors observed a decrease in body weight for all stocks examined, including populations from Bristol Bay, the Kuskokwim and Yukon Rivers, and Kotzebue Sound. Yukon River summer chum salmon body weight declined by an average of 0.003 kg/year. Length at age also decreased for all age groups of summer and fall Yukon River chum salmon stocks by 2-4% from 1975-1993. Age at maturity increased from 3.0 to 3.8 years for summer run, and 2.9 to 3.4 years for fall run Yukon River chum salmon. In Norton Sound, decreases in body size, productivity, and abundance, and increases in age at maturity have been observed for Kwiniuk River chum salmon (Ruggerone et al. 2011). Decreases in third and fourth-year ocean growth of age-0.3 and age-0.4 chum salmon were also observed for Bristol Bay and Yukon River populations (Agler et al. 2013). AYK chum salmon growth was correlated with Asian pink and chum salmon abundance and climate indices (Ruggerone et al. 2011; Agler et al. 2013).

1.3.2 Western North Pacific

Asian chum salmon stocks are experiencing changes in body size, growth, and age at maturity similar to those observed in North American stocks (Ishida et al. 1993; Azumaya and Ishida 2000; Zavolokin et al. 2009). Mean body weight of age-0.3 Japanese and Russian chum salmon declined significantly with increasing density (measured as catch per unit effort, CPUE) during summer in the central North Pacific from 1972-1988 (Ishida et al. 1993). Significant decreases in scale radius for Ishikari and Bolshaya chum salmon and third-year growth of chum salmon from the Ishikari, Amur, Bolshaya, and Kamchatka rivers were also observed after 1970. Body size and growth of Hokkaido chum salmon declined significantly with population abundance, while the average age at maturity increased from 3.7 to 4 years between 1972 and 1980 (Kaeriyama 1998). Third-year growth of age-0.3 and age-0.4 Hokkaido chum salmon was reduced by 26.4% and 29.9%, respectively, while body weight declined significantly as well. Increases in the proportion of age-0.3 and older chum salmon in the Ishikari River, and of age-0.4 and older chum salmon in the Amur, Bolshaya, and Kamchatka rivers were also observed after 1970 (Ishida et al. 1993).

1.4 Factors influencing changes in size and age of chum salmon

Although changes in chum salmon body size and age at maturity have been observed throughout the species' range, the mechanisms behind these changes are less clear. Previous research suggests that ocean carrying capacity may contribute to reductions in salmon growth due to competition for prey resources (Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996; Kaeriyama 1998; Ruggerone et al. 2003). Researchers debate whether chum salmon growth is more influenced by interspecific competition (Ruggerone et al. 2003, 2005; Ruggerone and Nielsen 2004) or intraspecific competition (Peterman 1984; Kaeriyama 1998; Pyper and Peterman 1999; Helle et al. 2007). Understanding the degree to which salmon stocks overlap in their diet and ocean distribution can assist fishery managers and scientists in predicting how increases in salmon abundance will affect local stocks.

1.5 Ocean distribution

Since the 1950s, researchers have employed a variety of methods to assess ocean distribution patterns, including collaborative studies conducted by the International North Pacific Fisheries Commission (INPFC), 1955-1992, and the North Pacific Anadromous Fish Commission (NPAFC), 1993-present (Takagi et al. 1981; Heard 1991; Salo 1991; Urawa 2004; Urawa et al. 2004; Myers et al. 2007; Sato et al. 2009). Initial models of salmon distribution suggested a counter-clockwise movement while at sea (Royce et al. 1968), with Asian stocks occupying waters largely west of 180° and North American stocks being mostly east of 180° (Myers et al. 2007). Advances in stock identification methods, including genetic analysis, otolith marking, and coded-wire tagging, indicate broader movements while at sea than previously thought. Salmon exhibit seasonal patterns, moving south and east in winter and spring and north and west in summer and fall (Takagi et al. 1981; Beamish and Bouillon 1993; Seeb et al. 2004; Myers et al. 2007; Urawa et al. 2009). While past research suggests that salmon migration routes are under partial genetic control (Brannon 1984), evaluation of lineage-specific migration routes suggests that chum salmon stocks located in close proximity to each other are likely to exhibit similar ocean migration patterns, regardless of their genetic similarities (Seeb et al. 2004). Defining specific migration routes can be confounded by changes in ocean attributes, year-class strength, and individual variation. Despite this interannual variability, we can obtain an overall picture of where salmon are moving in the open ocean at different times of the year by amalgamating individual distribution studies and agency reports.

1.5.1 Chum salmon distribution

Chum salmon are broadly distributed throughout the Pacific Rim, inhabiting areas from Japan to the west coast of the United States (Salo 1991). Chum salmon spend minimal time in freshwater, migrating directly downstream as fry after emergence. Chum salmon fry rear in estuaries where they undergo smoltification and migrate into the ocean when early marine survival is maximized. Juvenile chum salmon move from coastal areas in the spring and early summer to deeper waters in late fall or early winter, and exhibit stock-specific migration patterns thereafter (Myers et al. 2007).

Chum salmon from western Alaska are entirely of wild origin, constituting ~ 15% of wild chum salmon abundance in the North Pacific on average during 1990-2015 (Irvine and Ruggerone 2016). General migration patterns of western Alaska chum salmon indicate a move from shallow, coastal waters during their first summer at sea, to overwintering grounds in the Gulf of Alaska (GOA), followed by a return to their summer feeding areas in the Bering Sea and North Pacific (Urawa et al. 2009; Fig. 1.8). In the Bering Sea, North American stocks constituted 20-37% of maturing chum salmon in June and July, and 23-31% of immature chum salmon in August and September (Urawa et al. 2009). These results are supported by NOAA agency reports from the Bering Sea Aleutian Island (BSAI) walleye pollock (*Gadus chalcogrammus)* fishery, where chum salmon caught incidentally are genotyped for management purposes (https://www.npfmc.org/bsai-salmon-bycatch/). From 2005-2014, western Alaskan chum salmon constituted 13-25% of total chum salmon bycatch (e.g., Gray et al. 2010, 2011; Kondzela et al. 2012, 2013); however, stock composition estimates are highly variable by location, season, and year. During summer 2004, stock composition of North American chum salmon was observed to be approximately 9-16% in the southern Bering Sea, 4-21% in the central Bering Sea, 6-31% in the eastern Bering Sea, and 27-70% in the western Bering Sea (Sato et al. 2009).

Distribution patterns are also influenced by ocean attributes, including temperature, salinity, dissolved oxygen, depth, and pH. Echave et al. (2012) examined the influence of sea-surface temperature (SST), sea-surface salinity (SSS), and bottom depth on salmon migration and habitat use within the Alaska Exclusive Economic Zone (EEZ), located 0-200 nautical miles offshore. The authors observed that 75% of juvenile chum salmon surveyed off of western Alaska were distributed north of latitude 55.3°N, with the northernmost distribution reaching as far as 70.1°N. Preferred habitat conditions for juvenile chum salmon within the Bering Sea were observed in areas off of the western coast of Alaska between 70.1°N and 58.5°N in areas of 50-100m in depth. Immature chum salmon were found in deeper waters than juveniles but were still distributed from as far north as latitude 64°N to the southern portion of the Alaska EEZ. Immature chum salmon were observed further offshore than juveniles, with 75% of immature chum salmon occupying waters west of longitude 166°W. Mature chum salmon were found in areas off the Alaska coast out to longitude 173.2°W and were distributed in relation to SST, SSS, and water depth, preferring a small range of salinities but a broad range of water depths. Although some patterns emerged, catch was not significantly related to SST, SSS, or bottom depth for all age classes.

Japanese chum salmon (assumed to be entirely of hatchery origin) comprise more than 60% of chum salmon found in the western Bering Sea by August (Seeb et al. 2004). Japanese chum salmon spend their first winter in the western North Pacific and all subsequent winters in the GOA (Urawa 2004; Fig. 1.7). Like western Alaska chum salmon, Japanese chum salmon migrate between their summer feeding grounds in the Bering Sea to their overwintering grounds in the GOA. Japanese chum salmon abundance has been shown to increase with latitude and they are the dominant stock in the central and northern regions of the Bering Sea (Sato et al. 2009, 2012). During summer 2004, Japanese chum salmon constituted approximately 33-48% of chum salmon in the southern Bering Sea, 60-67% in the central

Bering Sea, 26-66% in the eastern Bering Sea, and 14-19% in the western Bering Sea (Sato et al. 2009). While many Japanese chum salmon will stay north of 60°N in the Bering Sea during the summer months, chum salmon migrate back to their overwintering grounds in the GOA by late November when sea surface temperatures are less than 4°C (Urawa et al. 2009; Sato et al. 2012).

Russian chum salmon have been shown to overlap with North American stocks, although their westward distribution into the central and eastern regions of the GOA can be more limited due to spawn timing for summer stocks (Urawa et al. 2009). Russian chum salmon are found predominantly in the western and southern Bering Sea; however, stocks will inhabit the northern and eastern Bering Sea and the North Pacific (Urawa et al. 2009; Sato et al. 2012; Fig. 1.7). Sato et al. (2012) observed a higher abundance of Russian stocks compared to Japanese stocks of chum salmon in the southern and western Bering Sea during May and June, constituting over 60% of sampled chum salmon (Seeb et al. 2004). During summer 2004, Russian chum stock composition was approximately 37-58% in the southern Bering Sea, 19-36% in the central Bering Sea, 16-61% in the eastern Bering Sea, and 14-54% in the western Bering Sea (Sato et al. 2009). As the abundance of wild and hatchery Russian chum salmon populations continues to increase, it is likely that overlaps in ocean distribution will become more pronounced.

1.5.2 Pink salmon distribution

Pink salmon are broadly distributed within a given area but have little overlap with distant populations due to their limited time at sea (Ruggerone and Nielsen 2004). Pink salmon can travel up to 7,400 km in their 14- to 16-month ocean residence and occupy the southern part of their ocean distribution during late autumn and winter, moving northward in spring and returning to their spawning rivers by late summer (Takagi et al. 1981; Ruggerone and Nielsen 2004; Myers et al. 2007; Fig. 1.7). Tagging studies in the North Pacific conducted by the INPFC during 1956-1971 were compiled by Takagi et al. (1981). Tag recoveries indicate that pink salmon distributed in the GOA primarily belong to stocks from southwest, southeast, and central Alaska, as well as northern and southern BC. Pink salmon originating from western Alaska produce relatively small runs and are abundant during even-numbered years, while pink salmon from central and southeast Alaska produce large runs that are usually more abundant during odd-numbered years (Ruggerone and Nielsen 2004).

Japanese pink salmon constitute 2% and 4% of total wild and hatchery pink salmon abundance, respectively (Irvine and Ruggerone 2016; Table 1.1). Pink salmon stocks returning to Hokkaido, Japan are distributed in the western North Pacific (Takagi et al. 1981); however, little is known about the ocean distribution of other Japanese pink salmon stocks. Pink salmon originating from eastern Kamchatka travel the furthest east during their ocean migration compared to all other Asian pink salmon stocks, ranging to 155°W and 44°N into the Bering Sea and North Pacific (Ruggerone and Nielsen 2004). Pink salmon originating from eastern Kamchatka are odd-year dominant, compared to a small percentage from western Kamchatka that are even-year dominant. Eastern Kamchatka pink salmon enter coastal waters in early spring after emergence and travel counter-clockwise along the coast of Kamchatka and Japan, moving into the North Pacific and Bering Sea (Heard 1991; Ruggerone and Nielsen 2004). Pink salmon stocks originating from other areas in Russia, including west Kamchatka, Sakhalin, Primoye, and the Kuril Islands, are distributed primarily in the western North Pacific and Sea of Okhotsk (Takagi et al. 1981).

1.6 Salmon diet

Salmon diet composition is determined by prey availability and ocean distribution patterns, which can influence salmon diets through inter- and intra-specific prey competition. Salmon diets vary by species, age class, region, year, water depth, and relative sea surface temperature, among other variables (Davis et al. 2009). Previous research suggests that chum and pink salmon occupy a similar feeding niche (Andrievskaya 1966; Tadokoro et al. 1996; Davis 2003; Davis et al. 2005), leading to the expectation that they will compete for prey resources when food is limited (Schoener 1982). Pink salmon are considered more efficient foragers than chum salmon (Ruggerone and Nielsen 2004) and can significantly reduce total prey weight and zooplankton biomass in the North Pacific during years of high abundance (Tadokoro et al. 1996; Davis et al. 2000, 2009). Abundant stocks of western Alaska chum salmon and Japanese hatchery chum salmon also interact after the first year at sea, with both populations occupying summer feeding grounds in the Bering Sea and overwintering grounds in the Gulf of Alaska (Urawa 2004; Urawa et al. 2009). Understanding the degree of diet overlap between species, stocks, and by location is critical to understand how western Alaska chum salmon are affected by competition for food resources in the Bering Sea.

To assess how salmon diet varies by species, location, and over time, Davis (2003) investigated the feeding ecology of Pacific salmon in the central North Pacific (41°-44°N, 45°-51°N) and in the central Bering Sea (52°-58°N) during June and July, 1991-2000. Fish stomachs were collected, weighed, and examined to determine stomach fullness and prey composition. A stomach content index (SCI) was calculated by standardizing prey weight (stomach fullness) with fish body weight (prey weight/body weight *100). Prey composition was separated by prey quality, where high- and low-quality prey items were differentiated based on caloric density per individual food item. For chum and pink salmon, high-quality prey consists of euphausiids, copepods, squid, and fish, while low-quality prey consists of amphipods, pteropods, and, for chum salmon, gelatinous zooplankton and unidentified material. This ten-year time series is the most comprehensive salmon diet study to date and enables researchers to observe chum and pink salmon food habits in years of high and low pink salmon abundance and prey availability. All salmon diet data reported below were collected and analyzed by Davis (2003).

1.6.1 Chum salmon diet

In the central North Pacific, chum salmon had a more versatile diet compared to other salmon species and fed on euphausiids, hyperiid amphipods, squid, pteropods, fish, appendicularians, ostracods, heteropods, and a large amount of gelatinous zooplankton (medusae, ctenophores, and salps). Salps were the most common gelatinous zooplankton consumed in this area, and fish were only consumed as prey by chum salmon larger than 2500 g. Prey weight from chum salmon stomach contents averaged 9.8 g (1.00% body weight; 41°-44°N) and 9.35 g (0.90% body weight; 45°-51°N). Small chum salmon (< 500 g) were able to consume more prey relative to their body weight (0.88% body weight) than larger chum salmon (> 2500 g, 0.70% body weight). Higher SCIs were also observed for age-0.1 and age-0.2 chum salmon and decreased with fish age. There was no significant difference in prey quality between even- and odd-numbered years in this region.

Chum salmon consumed more prey relative to their body weight (15.5 g; 1.10% body weight) in the central Bering Sea (52°-58°N) compared to the central North Pacific, consuming more euphausiids and fish and less gelatinous zooplankton in this region than further south. Chum salmon diet in the central Bering Sea consisted of primarily euphausiids, copepods, amphipods, squid (juveniles), pteropods, fish, and gelatinous zooplankton (medusa and ctenophores, Fig. 1.9). Small chum salmon (< 500 g) were able to consume more prey relative to their body weight (1.39% body weight) than large chum salmon (> 4000 g, 0.62% body weight). Small chum salmon (< 500 g) also relied more heavily on amphipods while large chum salmon (> 1000 g) consumed more fish. While all size classes of chum salmon consumed gelatinous zooplankton, large chum salmon (> 3000 g) consumed more relative to their more weight (36%) than small chum salmon (< 500 g, 12%). Percent prey composition of juvenile fish, pteropods, and small squid was similar across chum salmon weight classes.

1.6.2 Pink Salmon Diet

Pink salmon consumed more prey relative to their body weight than chum salmon in both the central North Pacific and central Bering Sea. Prey weight of pink salmon stomach contents in the central North Pacific (41°- 45°N) averaged 14.8 g (1.37% body weight), and increased with body weight (500-999 g, 1.18% body weight; > 1500 g, 1.39% body weight). Pink salmon in this area fed heavily on large squid. Larger pink salmon consumed more squid and euphausiids compared to smaller pink salmon, which foraged more heavily on copepods and pteropods.

In the central Bering Sea, the mean prey weight of pink salmon was 15.2 g (1.29% body weight), and pink salmon consumed more small squid and fish compared to the central North Pacific (Fig. 1.8). Pink salmon abundance was negatively correlated with stomach fullness and quality of prey, presumably due to density dependence. Pink salmon abundance was also negatively correlated with euphausiid, copepod, squid, and fish abundance in stomach contents. Similar to the central North Pacific, average prey weight increased with fish size (< 500 g = 1.10% body weight; > 2000 g = 1.29% body weight). Pink salmon consumed more juvenile fish in the central Bering Sea than in the central North Pacific, with smaller pink salmon foraging more heavily on euphausiids. Smaller pink salmon also relied more heavily on juvenile fish species (64%) and less on squid compared to larger pink salmon, which foraged on similar amounts of both prey items.

1.6.3 Interannual variability in salmon diet

Researchers have used the natural even/odd cycle of pink salmon abundance to measure their potential competitive effects on other species by assessing changes in salmon diet between even- and odd-numbered years (e.g., Sano 1963; Tadokoro et al. 1996). The food habits and feeding ecology data collected and analyzed by Davis (2003) was the first to capture temporal trends in salmon feeding ecology in both the central Bering Sea and central North Pacific over a ten-year period and examined changes in prey quantity and quality between even- and odd-numbered years. While no difference in the stomach fullness of chum salmon was observed in the central Bering Sea, there was a significant difference in the weight of high- and low-quality prey. Chum salmon averaged 38% less high-quality prey and 19% more low-quality prey during odd-numbered years when pink salmon abundance was high (Fig. 1.10). For chum salmon, high-quality prey consists of euphausiids, copepods, squid, and fish, while low-quality prey consists of pteropods and gelatinous zooplankton species. Interannual differences in diet were more pronounced in pink salmon, which exhibited a 23% decrease in stomach fullness during odd-numbered years. Prey quality also decreased significantly when pink salmon abundance was high, owing to a 32% decrease in the proportion of high-quality prey (euphausiids, copepods, squid, and fish) and a 72% increase in the proportion of low-quality prey (amphipods and pteropods) during odd-numbered years.

1.7 Climate variability

Different environmental conditions have been shown to affect salmon growth and survival, including those indexed by the Pacific Decadal Oscillation (PDO), sea surface temperature (SST), and date of sea-ice retreat (Mantua et al. 1997; Hunt et al. 2002; Mueter et al. 2002; Agler et al. 2013). While climatic influences are more difficult to decipher due to regional differences in salmon responses, researchers have identified changes in ocean patterns that may affect chum salmon throughout their range.

1.7.1 Pacific Decadal Oscillation

Patterns of climate variability in the North Pacific occurring on an interdecadal timescale are referred to as the Pacific Decadal Oscillation (Mantua et al. 1997). The PDO can be described as a pattern of SST variability having distinct spatial and temporal characteristics that alternate between positive and negative phases every 20-30 years (Hare et al. 1999; Mantua and Hare 2002). Reversals in the polarity of the PDO correspond to changes in ocean temperatures between warming and cooling periods and are described as ‘regime shifts’ (Mantua et al. 1997; Hare et al. 1999). Major regime shifts have been recorded in 1925, 1947, and 1977, where cool PDO regimes occurred from 1890-1924 and 1947-1976, and warm PDO regimes prevailed from 1925-1946 and 1977 through the mid-90s (Mantua et al. 1997; Mantua and Hare 2002). The marine environment is affected by climate variability characterized by the PDO through bottom-up responses due to changes in sea level pressure and wind mixing (Hare et al. 1999; Mantua and Hare 2002).

Juvenile salmon experiencing high annual variability in marine survival rates may be a result of fluctuations in climate patterns and the PDO (Hare et al. 1999). Pacific salmon catch is strongly related to the El Nino Southern Oscillation (ENSO) and the winter Aleutian Low (AL) pressure index, which closely resemble the PDO but operate on shorter timescales. While changes in the PDO occur on a decadal scale and represent low-frequency changes in atmospheric circulation and ocean properties, changes in the ENSO and AL occur every 2-7 years and are related to SST and wind stress in the North Pacific. Positive PDO phases characterize a cool SST anomaly in the central North Pacific with warmer than average SST along the west coast of North and South America (Mantua and Hare 2002). During winter and spring (November-March), low sea-level pressure anomalies over the North Pacific cause strong counterclockwise winds which results in more advection of zooplankton species into nearshore habitats for downwelling regions, creating better feeding condition for Alaskan salmon stocks (Brodeur and Ware 1992; Mantua and Hare 2002; Mueter et al. 2002). In the upwelling domain along the west coast of the U.S., positive PDO phases are associated with increased stratification, decreased upwelling, lower primary production and zooplankton prey availability, and poor feeding conditions for west coast salmon stocks (Ware and McFarlane 1989; Ware and Thomson 1991; Mueter et al. 2002). The opposite trend is observed during negative PDO phases, characterized by a warm SST anomaly in the central North Pacific. Cooler than average SST along the west coast of North America results in poor feeding conditions for Alaskan salmon and good feeding conditions for west coast salmon stocks.

1.7.2 Sea-surface temperature

While the PDO has been used to describe large-scale ocean temperature patterns, Mueter et al. (2002) suggested that local SST is a better indicator of salmon survival than large-scale indices such as the PDO. Local SST can serve as a proxy for the indirect effects of SST on salmon survival, such as prey availability and the relationship between SST and chum salmon body size (Mueter et al. 2002; Helle and Fukuwaka 2009). Mueter et al. (2002) observed regional responses to SST in 120 Pacific salmon stocks in the northern and southern regions of their range. Survival rates of pink, sockeye, and chum salmon were associated with regional SST during early-ocean residence, suggesting that salmon survival rates are closely related to local environmental conditions. The authors observed opposite responses in salmon survival between northern and southern stocks and suggested that SST is a proxy for the indirect effects on salmon survival due to differences in ocean conditions between northern and southern regions. Oceanographic conditions seem to diverge at the convergence point between the downwelling domain, located along the coast of Southeast Alaska, and the upwelling domain, which begins along the B.C. and Washington border and continues along the west coast of the U.S (Ware and McFarlane 1989). The upwelling domain in southern waters results in increased SST, which reduces prey availability due to decreased upwelling, increased stratification, and therefore decreased primary and secondary production (Ware and McFarlane 1989; Ware and Thomson 1991; Mueter et al. 2002).

Salmon ocean distribution is associated with SST, which influences salmon growth due to prey availability (Davis et al. 2005; Fukuwaka et al. 2007). In the Bering Sea and North Pacific, SST influenced the ocean distribution of juvenile and immature chum salmon more so than that of older chum salmon cohorts (Fukuwaka et al. 2007). Fukuwaka et al. (2007) also observed that age-0.1 and age-0.2 chum salmon were more prevalent in the Bering Sea when SST in the central North Pacific was high, but were more equally distributed between the two areas when SST was low. Age-0.3 and age-0.4 chum salmon were found mainly in the Bering Sea and their distribution was not correlated with SST in the central North Pacific. Because SST influences salmon growth and feeding, immature salmon may be more selective in their ocean distribution and will occupy an area with a thermal regime that maximizes somatic growth (Rand 2002; Fukuwaka et al. 2007).

1.7.3 Sea-ice extent

Sea-ice extent in the Bering Sea indirectly affects salmon growth through the relationship between the timing of sea-ice retreat and the spring phytoplankton bloom. Initially proposed in 2002 to explain recruitment variability in walleye pollock, the Oscillating Control Hypothesis predicts that late sea-ice retreat (mid-March or later) results in algae blooms beneath the ice causing thermal limitations to zooplankton production (Hunt et al. 2002). Warm May SST results in the opposite trend, where early sea-ice retreat caused a delay in algae blooms due to insufficient light. Late blooms, occurring in May or June, promote rapid growth of zooplankton that are consumed by salmon. However, while the annual net primary production in the southeastern Bering Sea was enhanced by 40-50% during years with early sea-ice retreat (warmer springs), zooplankton were lipid-poor, and consequently the amount of energy available to higher trophic levels was reduced (Coyle and Pinchuk 2002; Coyle et al. 2011; Hunt et al. 2011; Brown and Arrigo 2013). Years with late sea-ice retreat (cooler springs) experienced lipid-rich zooplankton blooms, allowing more energy to be available to pelagic fish species through prey capture.

Energy obtained by salmon through the consumption of zooplankton species is allocated towards growth or stored for periods of low food availability (Nomura et al. 2002; Davis 2003). During warm years in the eastern Bering Sea, whole body energy content of pink and chum salmon is lower while body length is longer (Andrews et al. 2009; Wechter et al. 2017). Increases in fork length are beneficial to reduce the chances of size-selective mortality, but decreased energy reserves can lead to increased overwintering mortality during periods of food limitation (Nomura et al. 2002).

1.8 Effects of competition on chum salmon diet and ocean distribution

Research suggests that salmon are food limited in the North Pacific and Bering Sea (Rogers and Ruggerone 1993; Ruggerone et al. 2003; Kaeriyama et al. 2004; Aydin et al. 2005). Ocean carrying capacity may be contributing to observed changes in chum salmon growth and maturation due to density dependence (Ishida et al. 1993; Helle and Hoffman 1995; Bigler et al. 1996; Ruggerone et al. 2003). Growth rate slows when salmon are not consuming prey near their daily maximum physiological consumption rate, and even small decreases in feeding can have substantial impacts on growth (Davis et al. 1998). Reduced growth can adversely affect salmon through increased predation, decreased fecundity and reproductive success, reduced lipid reserves, and higher susceptibility to parasites and disease (Bigler et al. 1996; Myers et al. 2004; Kaga et al. 2013). What remains unclear is the degree to which chum salmon are affected by inter- and intra-specific competition. To answer this question, researchers have examined chum salmon growth rates in the Bering Sea and North Pacific as a function of prey availability and species abundance.

1.8.1 Interspecific competition

Due to the fixed two-year life history of pink salmon, overlaps in species distribution between eastern Kamchatka pink salmon and western Alaska chum salmon do not occur until after the first winter at sea (Tadokoro et al. 1996; Myers et al. 2007). In Russia, decreases in the growth rate of age-0.3 and age-0.4 Anadyr chum salmon were observed from the second through the fourth year at sea (Zavolokin et al. 2009). Length, weight, and scale growth of Anadyr chum salmon declined significantly with total salmon catches in the North Pacific, but were not related to Anadyr chum salmon abundance, suggesting that Anadyr chum salmon growth is a function of the abundance of high-density species such as pink salmon. Retrospective scale analysis of chum salmon intercepted near the Aleutian Islands demonstrated a negative relationship between growth accrued during the year of capture and the abundance of Asian pink and chum salmon (Walker et al. 1998). Decreases in growth rate of age-0.3 chum salmon from southeast Alaska and Washington State was observed during the second, third, and fourth ocean year, and was negatively correlated with pink and chum salmon abundance (Yasumiishi et al. 2016).

High pink salmon abundance in the North Pacific may also indirectly affect chum salmon growth due to changes to their diet and ocean distribution. Chum salmon in the Bering Sea have been observed to shift their ocean distribution during years of high pink salmon abundance by migrating to the North Pacific where pink salmon are less abundant (Azumaya and Ishida 2000). Shifts in chum salmon ocean distribution from their preferred feeding grounds in the Bering Sea to an area with potentially less abundant or less nutritious prey may adversely affect their growth. Chum salmon also exhibit feeding plasticity in years of high pink salmon abundance by foraging more heavily on gelatinous zooplankton (Andrievskaya 1966; Tadokoro et al. 1996; Davis 2003; Davis et al. 2005). Increases in the consumption of micronekton and crustacean species and decreases in the consumption of gelatinous zooplankton species were observed by Tadokoro et al. (1996) in the Bering Sea between the summers of 1991 and 1992. Here, the consumption of high-quality prey increased from 20% of chum salmon diet in 1991 to 74% in 1992. The consumption of low-quality prey also decreased from 81% of chum salmon diet in 1991 to 25% of chum salmon diet in 1992 when pink salmon abundance was low. Foraging on gelatinous zooplankton is helpful in maintaining stomach fullness and expanding the chum salmon's feeding niche (Dulepova and Dulepov 2003). However, considering both prey quality and prey quantity is important when assessing how interspecific competition affects chum salmon growth (Davis 2003). Switching from high-lipid to low-lipid prey results in lower energy acquisition through prey capture and is evident when analyzing chum salmon lipid content, which has been observed to decrease significantly when pink salmon abundance is high (Kaga et al. 2013).

Lipids are considered a primary energy source for salmonids and lipid concentration in salmon muscle can serve as a proxy for salmon prey availability (Nomura et al. 2000). Salmonids rely on lipid and protein storage as their main energy sources during periods of low food supply, particularly in winter (Parker and Vanstone 1966). Nomura et al. (2002) assessed chum salmon lipid levels by age group within areas of the Bering Sea and GOA to estimate trophic condition and growth of salmon during their high-seas migration. Despite high consumption rates, the authors observed significantly lower lipid levels in age-0.1 chum salmon compared to older age classes, concluding that younger chum salmon may be allocating more energy towards growth during the summer months as opposed to lipid storage. Total lipid content increased significantly with fish age, suggesting that older chum salmon are allocating energy acquired into lipid storage over somatic growth. Stored lipids are used by young salmon to aid in overwinter survival and by older salmon in maturation potential (Morita et al. 2005; Morita and Fukuwaka 2006). Research by Morita and Fukuwaka (2006) found that the “decision” to mature in chum salmon was influenced by the most recent growth condition, where individuals that did not grow enough during a critical period delayed maturation due to decreased energy reserves. Delayed maturation may represent adaptive phenotypic plasticity for salmon with inadequate lipid reserves required for gamete production or homing migration. Reduced growth may also adversely affect chum salmon fecundity and reproductive success (Helle 1989; Bigler et al. 1996; Morita et al. 2005), as optimal ocean feeding conditions result in higher energy reserves, which can be beneficial on the spawning grounds for courtship, redd construction, and nest guarding (Helle 1989). Larger adult spawner size resulted in a significantly higher survival rate of progeny to adulthood for chum salmon returning to Olsen Creek in Prince William Sound, Alaska. Larger fish tend to have larger eggs and can dig deeper redds, which protects eggs from scour and redd superimposition (Helle 1989; Montgomery et al. 1996).

1.8.2 Intraspecific competition

While pink salmon have been demonstrated to be strong competitors with other salmon species (Ruggerone and Nielsen 2004), interactions between pink and chum salmon may be easier to identify due to biennial cycles of pink salmon abundance. Understanding how the abundance of conspecifics affects western Alaska chum salmon is more difficult, as chum salmon exhibit variation in spawning age (Salo 1991). Previously reviewed studies have demonstrated the effects of interspecific competition between pink and chum salmon (e.g., Walker et al. 1998; Zavolokin et al. 2009; Yasumiishi et al. 2016). However, research suggests that conspecifics may have a larger impact on chum salmon growth (e.g., Azumaya and Ishida 2000; Helle et al. 2007; Agler et al. 2013).

In western Alaska, third-year growth of age-0.3 Bristol Bay and age-0.4 Bristol Bay and Yukon River chum salmon decreased significantly with increasing abundance of Asian chum salmon, and to a lesser extent, Asian pink salmon (Agler et al. 2013). Asian hatchery chum salmon abundance had a larger impact on age-0.3 Bristol Bay chum salmon growth than age-0.4 Bristol Bay chum salmon growth. Age-0.3 is the dominant age of Asian hatchery chum salmon and may result in greater competition for prey items between conspecifics of the same age class, as they are likely to exhibit similarities in prey choice and ocean distribution patterns (Kaeriyama 1998). The third year of ocean residence is also a time of high potential growth rates, and therefore the effects of competition during the third ocean year may be greater than during forth ocean year when growth rates are lower (Agler et al. 2013).

In Norton Sound, located in the northern region of western Alaska, Ruggerone et al. (2011) investigated changes in productivity, body size, and age at maturity of Kwiniuk River chum salmon populations from 1974-2005. The authors observed that 50% of the variability in Kwiniuk chum salmon productivity during 1965-2001 was explained by Asian chum salmon abundance, Kamchatka pink salmon abundance, and the number of parent spawners. Asian hatchery chum salmon constituted approximately 68% of total chum salmon abundance in the area after 1980, and accounting for the abundance of western Alaska chum salmon populations did not improve the model fit. The abundance of Kwiniuk chum salmon decreased on average by 60% during a period when hatchery chum salmon production increased by 190%. Average age at maturity also increased significantly with Asian hatchery chum salmon abundance, from 3.9 to 4.8 years.

In Asia, growth of age-0.4 Hokkaido chum salmon demonstrates density dependence, particularly during the third year at sea (Kaeriyama et al. 2007). Density dependence also negatively affected body weight, scale radius, age at maturity, and third year growth of age-0.3 Russian and Japanese chum salmon in the Bering Sea, where 35% of the variability in mean body weight of chum salmon in the central North Pacific was a result of density dependence (Ishida et al. 1993). Azumaya and Ishida (2000) observed a shift in chum salmon distributions during odd-numbered years, possibly in response to competition with pink salmon, but they did not detect a significant relationship between chum salmon growth and pink salmon abundance. In contrast, the authors observed a significant negative relationship between chum salmon abundance and growth rate of age-0.2 and age-0.3 chum salmon in the eastern Bering Sea. Based on their study, it is likely that pink salmon indirectly affect chum salmon growth by altering their distribution and diet, while chum salmon directly compete with conspecifics for food resources in the Bering Sea.

1.9 Conclusion

This review provides evidence that the ocean distribution and diet of western Alaska chum salmon overlaps with that of distant pink and chum salmon stocks in the Bering Sea. Overlaps in ocean distribution may contribute to observed decreases in chum salmon growth rate and increases in age at maturity. Pink and chum salmon occupy a similar feeding niche and may affect western Alaska chum salmon growth through interspecific competition or changes to their ocean distribution. Highly abundant Japanese chum salmon stocks may influence western Alaska chum salmon growth through intraspecific competition. Understanding the degree of diet and distribution overlap, as well as the cumulative effects of competition between potentially competing salmon stocks, will assist managers in conserving threatened salmon stocks throughout Alaska and will contribute to greater understanding of the ocean phase of salmon life history.

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1.12 Figures

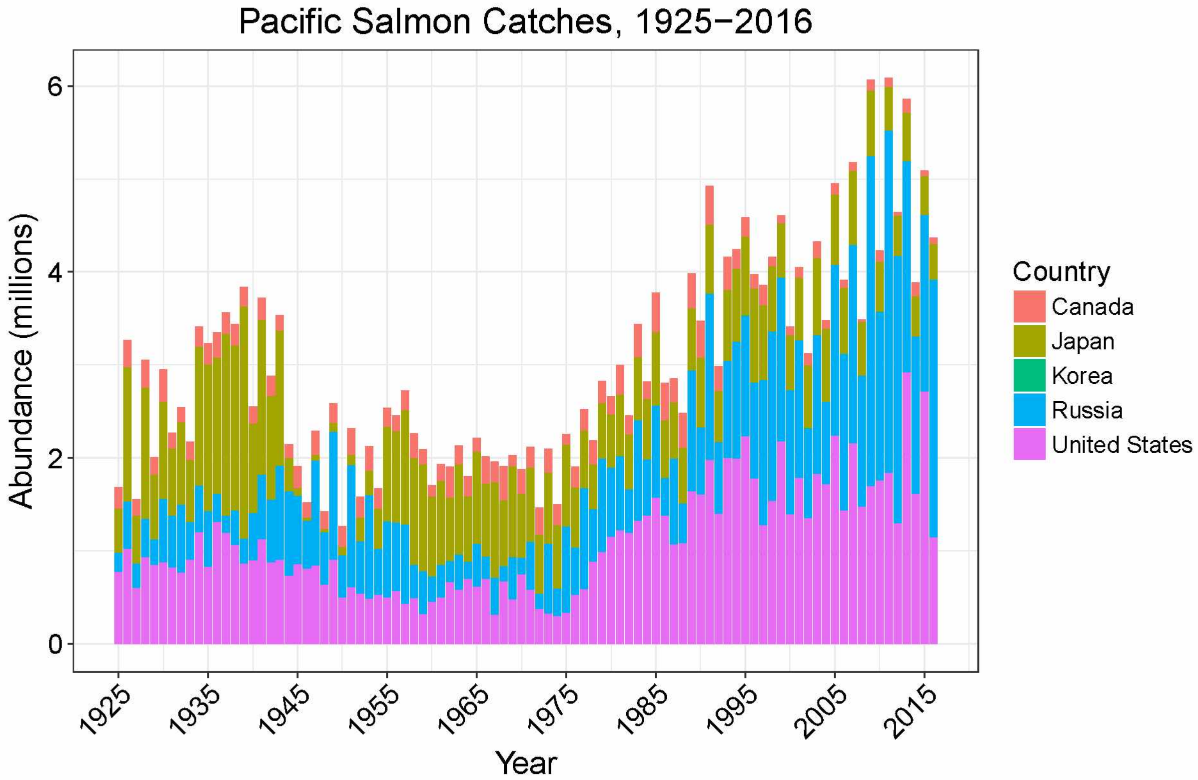


Figure 1.1. Pacific salmon catches by country, 1952-2016. Data from North Pacific Anadromous Fish Commission (http://www.npafc.org/new/science_statistics.html).

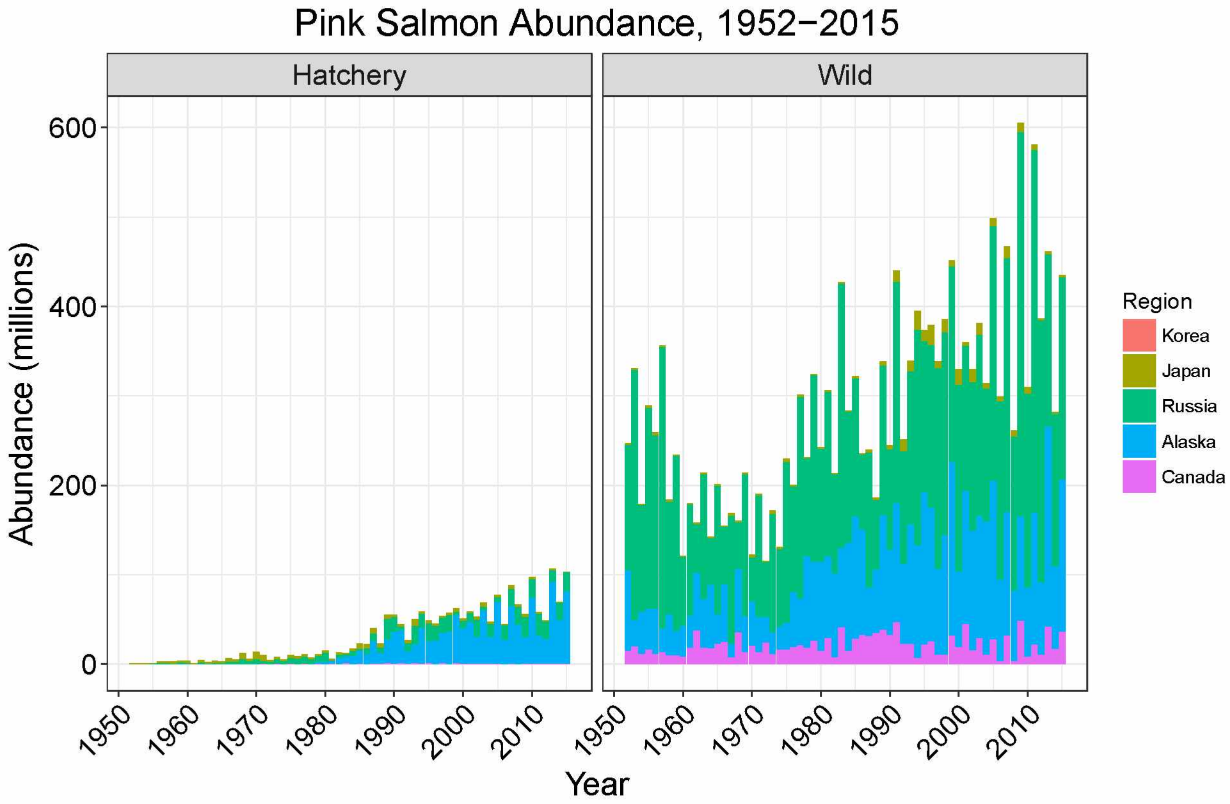


Figure 1.2. Total hatchery and pink salmon abundance by country, 1952-2015. Data from Irvine and Ruggerone (2016).

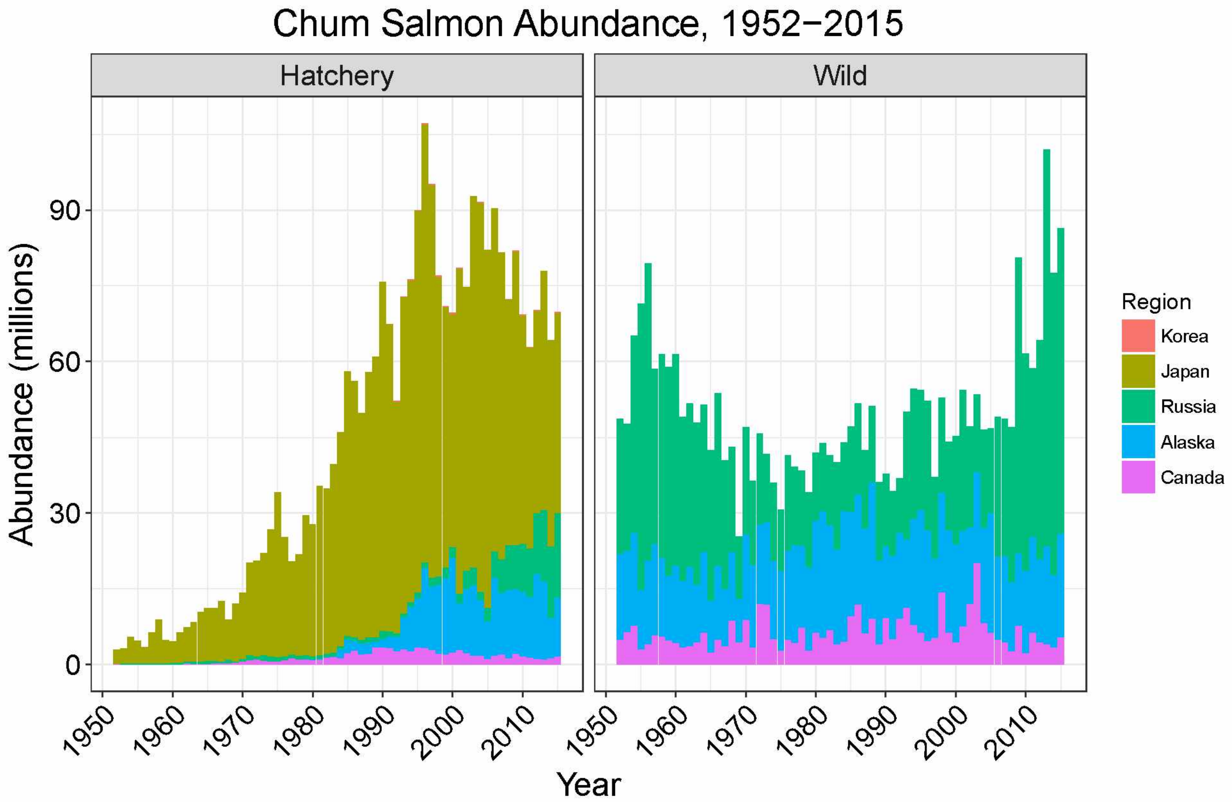


Figure 1.3. Total hatchery and wild chum salmon abundance by country, 1952-2015. Data from Irvine and Ruggerone (2016).

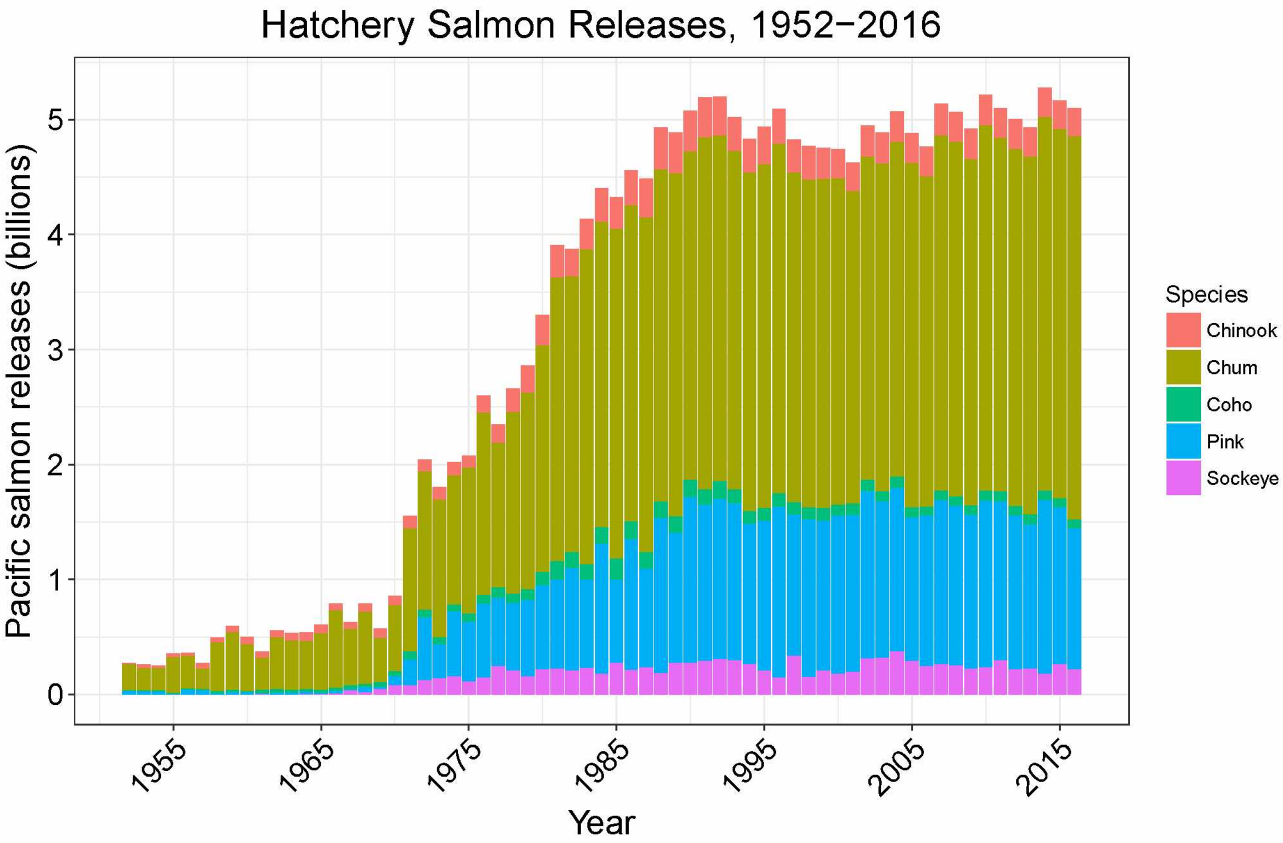


Figure 1.4. Hatchery salmon releases by species, 1952-2016. Data from North Pacific Anadromous Fish Commission (http://www.npafc.org/new/science_statistics.html).

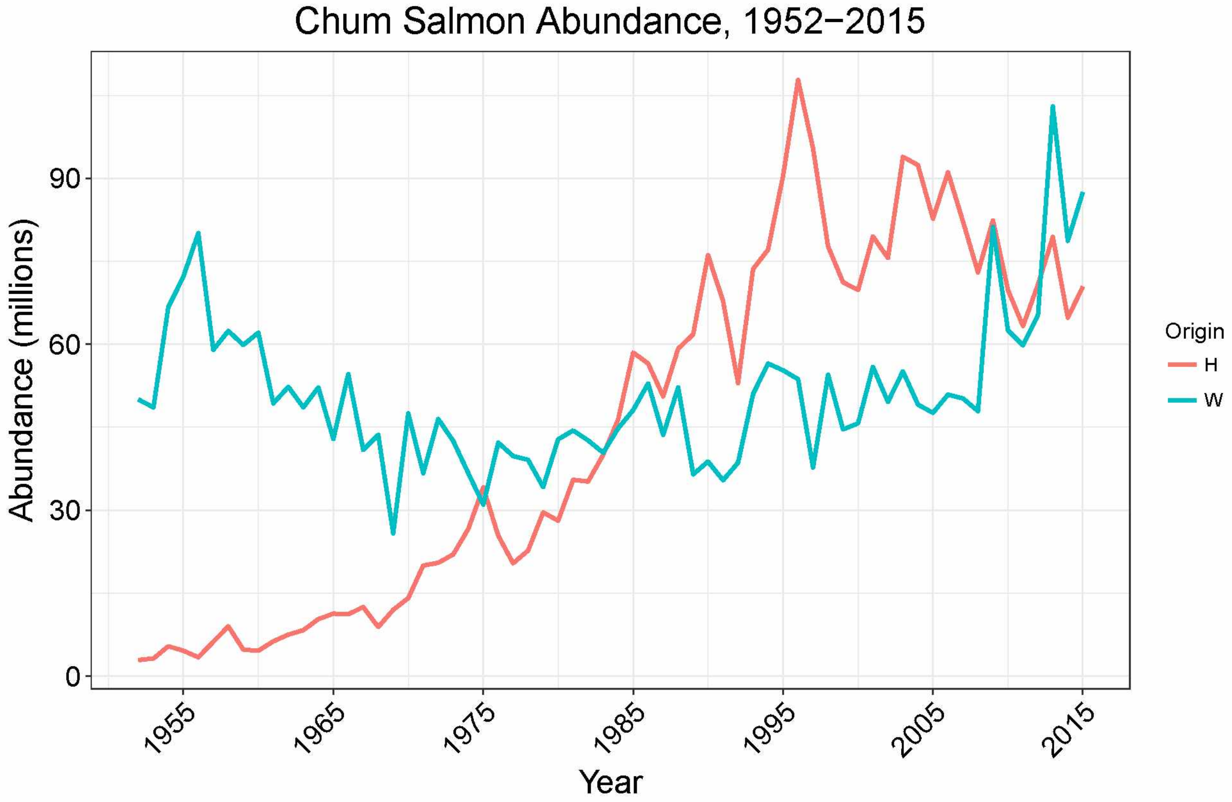


Figure 1.5. Total abundance of hatchery (H) and wild (W) chum salmon in the North Pacific Ocean, 1952-2015. Data from Irvine and Ruggerone (2016).

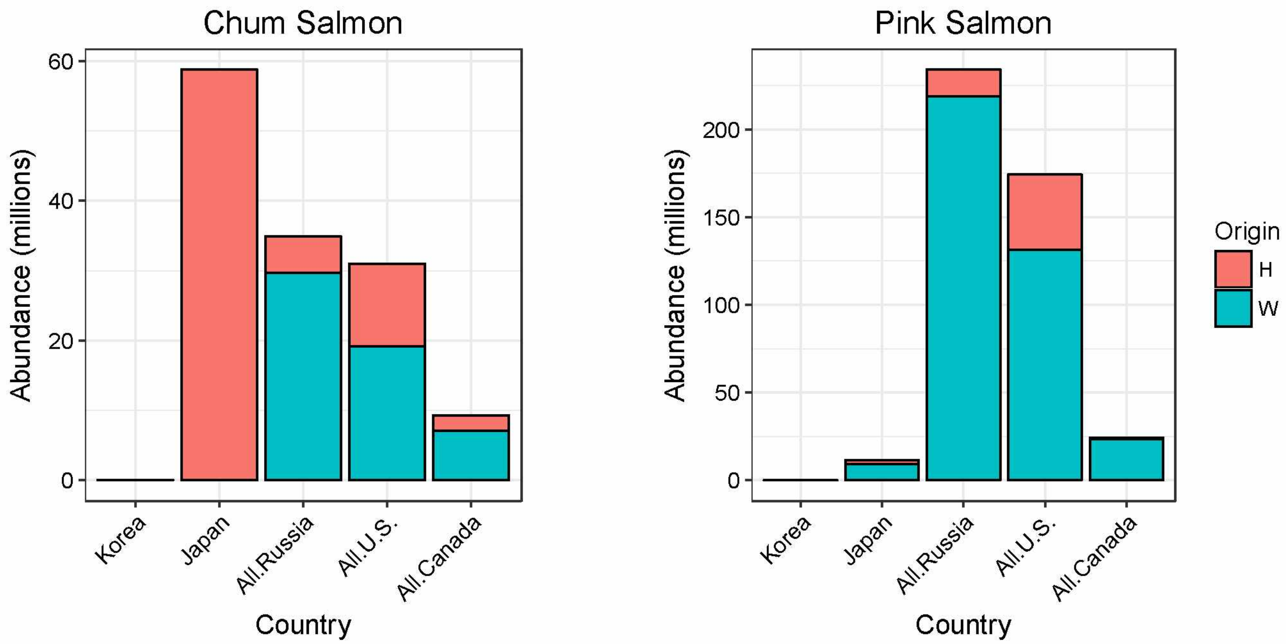


Figure 1.6. Average contribution of hatchery (H) and wild (W) chum and pink salmon in the North Pacific Ocean, 1990-2015. Data from Irvine and Ruggerone (2016).

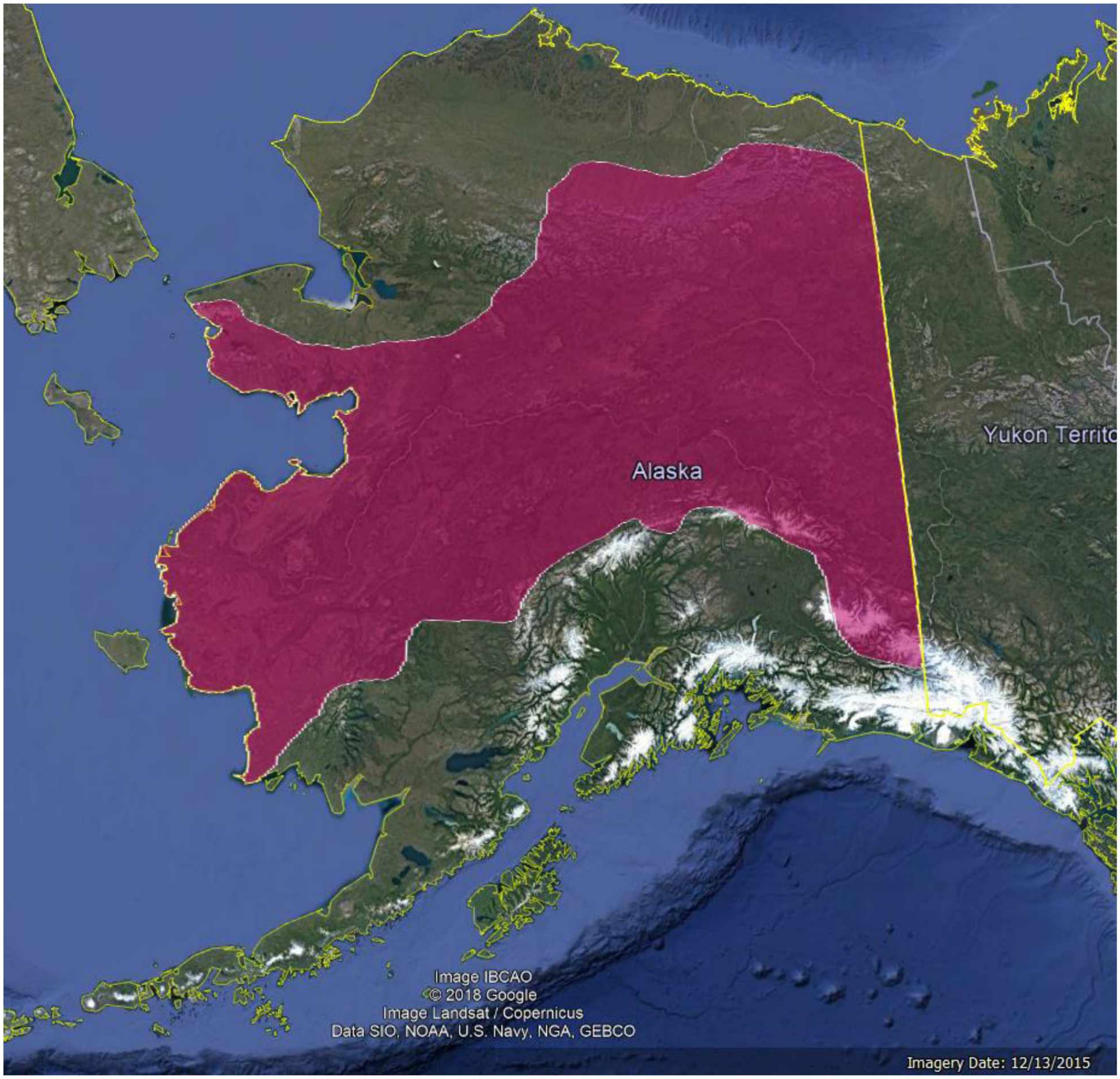


Figure 1.7. The Arctic-Yukon-Kuskokwim (AYK) region in western Alaska, highlighted in red.

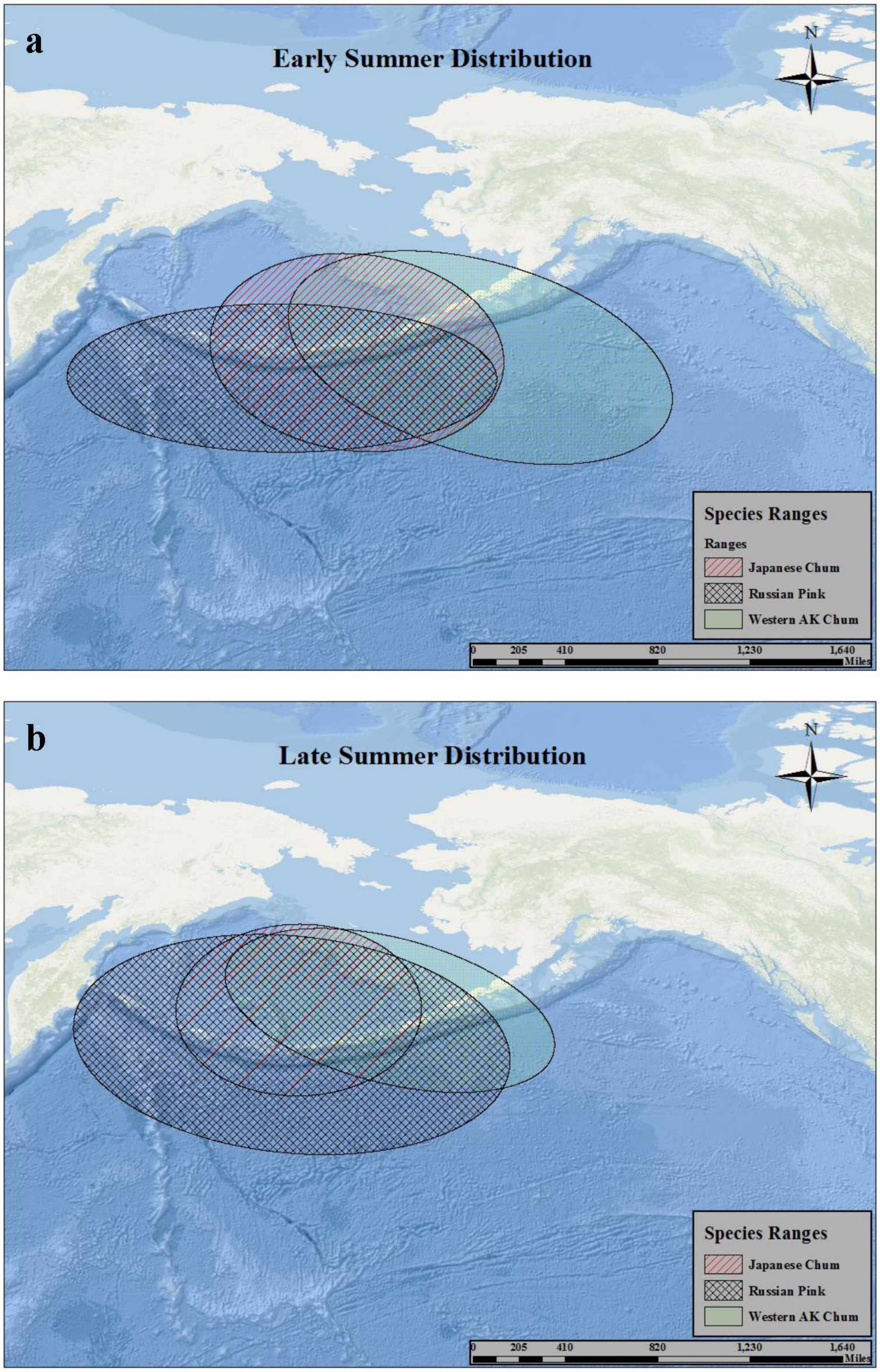
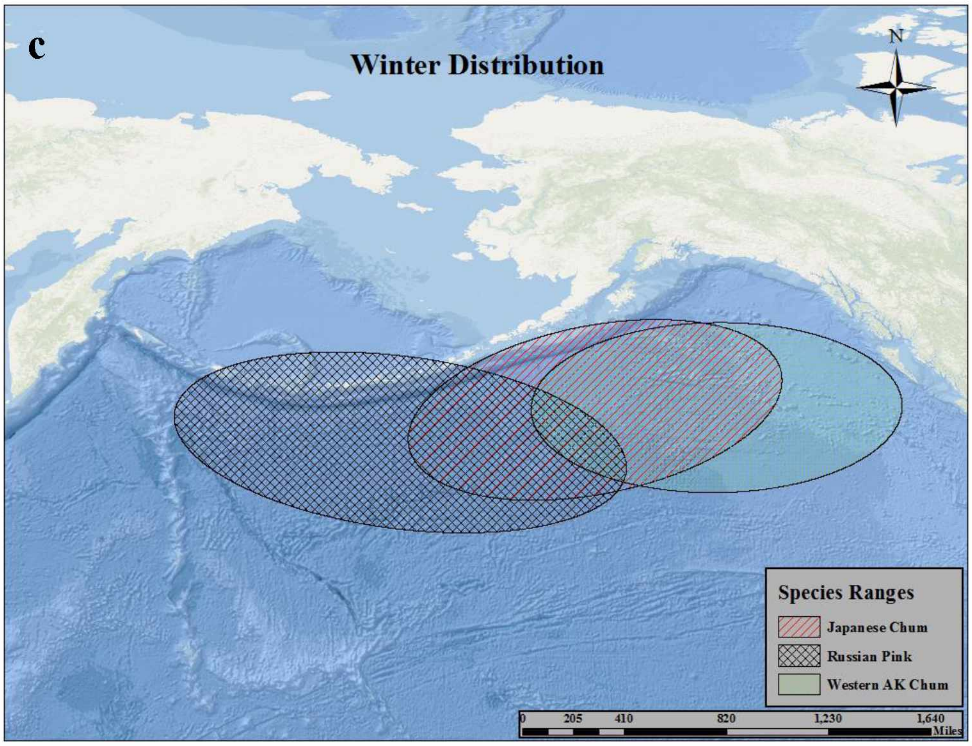


Figure 1.8. Distribution of Japanese chum salmon (red), western Alaska chum salmon (green) and Russian pink salmon (black) stocks in the Bering Sea and North Pacific Ocean during early summer (a), late summer/fall (b) and winter (c) months. Maps by Evan Fritz.

Figure 1.8 cont.



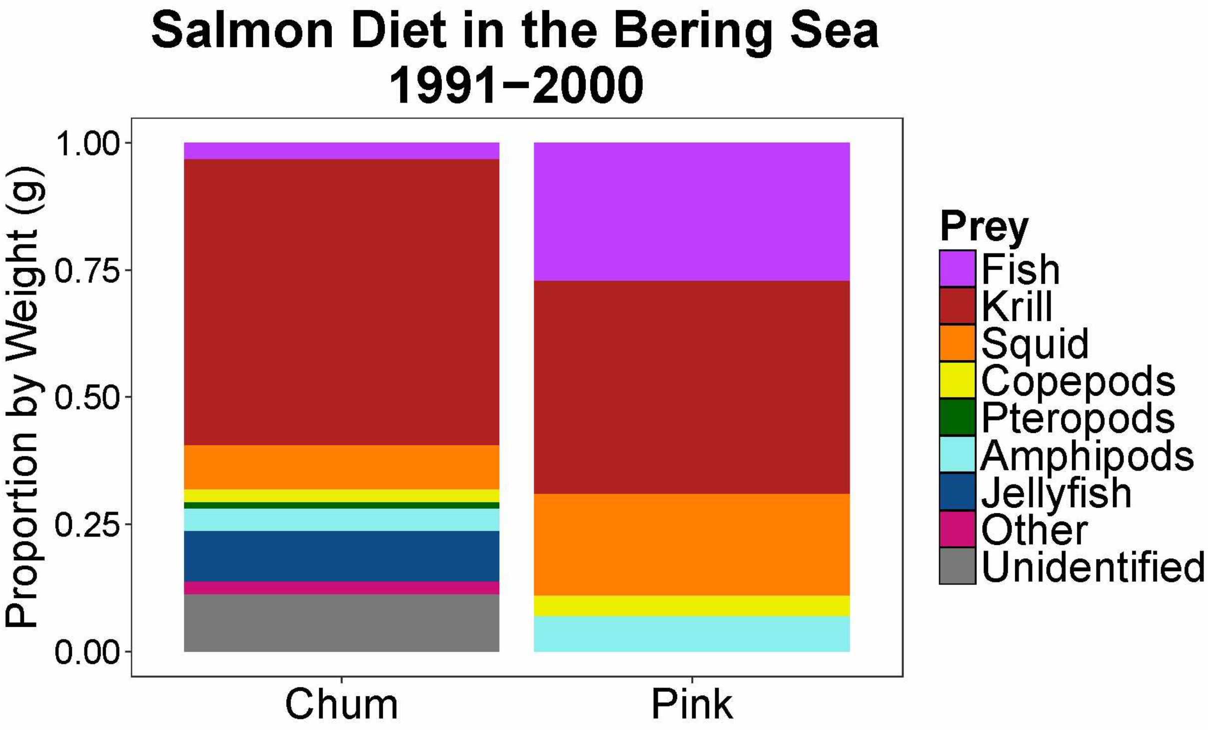


Figure 1.9. Chum and pink salmon diet in the Bering Sea, 1991-2000. Data from Davis (2003).

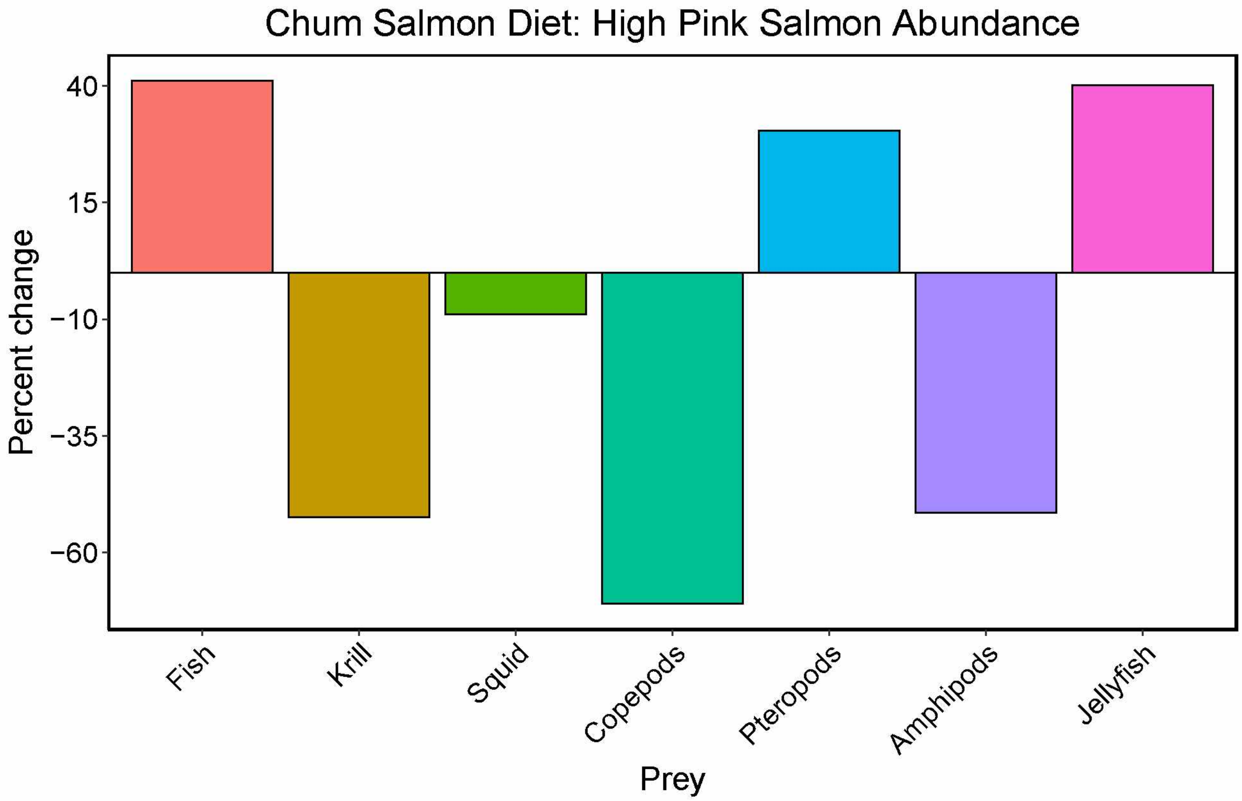


Figure 1.10. Percent change in prey composition of chum salmon diet in the Bering Sea during years of high pink salmon abundance (odd-numbered years). Data from Davis (2003).

1.13 Tables

Table 1.1. Average proportion of wild and hatchery pink salmon by region, 1990-2015. Data from Irvine and Ruggerone (2016).

Country	*Region*	*Percent Wild*	*Percent Hatchery*	*Percent Total*
Korea				
	Whole Country	0%	0%	0%
Japan				
	Whole Country	2%	4%	3%
Russia				
	Mainland and Islands	30%	25%	29%
	Western Kamchatka	11%	0%	9%
	Eastern Kamchatka	16%	0%	14%
	Whole Country	57%	25%	53%
United States				
	Western Alaska	< 1%	0%	1%
	Southern Alaska Peninsula	3%	0%	3%
	Kodiak	5%	9%	5%
	Cook Inlet	< 1%	2%	1%
	Prince William Sound	3%	56%	10%
	Southeast Alaska	22%	3%	19%
	Washington State	< 1%	1%	5%
	Whole Country	34%	70%	39%
Canada				
	Northern British Columbia	4%	0%	3%
	Southern British Columbia	3%	1%	2%
	Whole Country	0%	0%	0%

Table 1.2. Average proportion of wild and hatchery chum salmon by region, 1990-2015. Data from Irvine and Ruggerone (2016).

Country	*Region*	*Percent Wild*	*Percent Hatchery*	*Percent Total*
Korea				
	Whole Country	0%	0%	0%
Japan				
	Whole Country	0%	80%	37%
Russia				
	Mainland and Islands	40%	5%	24%
	Western Kamchatka	5%	0%	3%
	Eastern Kamchatka	7%	0%	4%
	Whole Country	52%	5%	30%
United States				
	Western Alaska	15%	0%	8%
	Southern Alaska Peninsula	4%	0%	2%
	Kodiak	2%	0%	1%
	Cook Inlet	3%	0%	2%
	Prince William Sound	2%	2%	2%
	Southeast Alaska	8%	8%	8%
	Washington State	2%	1%	1%
	Whole Country	36%	11%	24%
Canada				
	Northern British Columbia	5%	0%	3%
	Southern British Columbia	8%	3%	5%
	Whole Country	12%	3%	8%

Chapter 2: Effects of Asian pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon on western Alaska chum salmon growth[1]

2.1 Abstract

Poor returns in western Alaska chum salmon (*Oncorhynchus keta*) stocks followed by varying levels of recovery have been accompanied by reductions in chum salmon growth, body size, and increases in age at maturity throughout their range. We used retrospective scale analysis coupled with linear mixed-effects modeling to investigate the relationship between Asian pink (*O. gorbuscha*) and chum salmon abundance and the growth of chum salmon that rear in the Bering Sea. A 37% decrease in Japanese hatchery chum salmon releases in 2011 following the Tōhoku earthquake and resulting tsunami allowed us to observe Bering Sea chum salmon growth during a period of reduced Japanese hatchery chum salmon production. Chum salmon growth decreased significantly with increasing Japanese hatchery chum salmon abundance, but did not increase during 2012-2014 despite a reduction in Japanese hatchery chum salmon releases. Western Alaska chum salmon growth was not correlated with Asian pink salmon abundance, but this does not rule out interactions that may indirectly affect chum salmon growth through changes in chum salmon diet. Understanding how distant salmon populations interact while at sea will assist fishery managers and scientists in protecting salmon stocks with conservation concerns, particularly as Pacific Rim nations consider increasing production of hatchery salmon.

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[1] Minicucci, T.J., Yasumiishi, E.M., Adkison, M.D., and M.V. McPhee. 2018. Effects of Asian pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon abundance on western Alaska chum salmon growth. Manuscript prepared for submission to the Canadian Journal of Fisheries and Aquatic Sciences.

2.2 Introduction

The abundance of Pacific salmon (*Oncorhynchus* spp.) has been increasing in North America and Asia since the late 1970s, with record catches of pink (*O. gorbuscha*) and chum (*O. keta*) salmon from the Pacific Rim beginning in the 1990s (Ruggerone et al. 2010). Increases in salmon abundance are attributed to favorable ocean growing conditions and increased hatchery output, resulting in nearly twice as many salmon in the North Pacific Ocean during 1990-2005 as compared to 1952-1975. Despite favorable ocean conditions, decreases in chum salmon body size, growth rate, and an increase in age at maturity have been observed throughout the chum salmon's range (Ishida et al. 1993; Ruggerone et al. 2011). While the mechanisms underlying these changes are not well understood, highly abundant Asian pink and chum salmon populations in the Bering Sea may result in density-dependent processes.

Chum salmon are widely distributed in the North Pacific Ocean, and their range can overlap with other salmon species and stocks during their ocean residence (Seeb et al. 2004; Urawa et al. 2004; Myers et al. 2007, 2009; Sato et al. 2009). Chum salmon head directly out to sea after emergence and exhibit variability in age at maturity, returning to spawn at between two and five years of age (Salo 1991). Western Alaska chum salmon migrate between their summer feeding grounds in the Bering Sea and overwintering grounds in the Gulf of Alaska (Urawa et al. 2009). Japanese chum salmon exhibit a similar migration pattern, with the exception of their first winter at sea which is spent in the western North Pacific Ocean (Urawa 2004). The similarity in migration patterns between Japanese and western Alaska chum salmon may lead to intra-specific competition when prey resources are limited (Ishida et al. 1993).

Pink salmon are the most abundant salmonid, accounting for ~ 60% of anadromous Pacific salmon (Heard 1991; Ruggerone et al. 2003). Pink salmon grow rapidly and exhibit a fixed two-year life cycle, leading to genetically distinct even- and odd-year brood lines that exhibit biennial cycles of abundance (Ruggerone and Nielsen 2004). The Russian Far East supports the world's largest pink salmon runs, and pink salmon abundance can be up to 2500% greater during odd- than even-numbered years in the central Bering Sea (Ruggerone et al. 2003; Ruggerone and Nielsen 2004). Pink salmon originating from eastern Kamchatka are the dominant pink salmon stock in the Bering Sea, entering coastal waters in early spring after emergence and traveling counter-clockwise along the coast of Asia (Takagi et al. 1981; Ruggerone and Nielsen 2004). Due to their fixed life history, pink salmon spend their only winter in the North Pacific Ocean before homing through the Bering Sea (Takagi et al. 1981; Heard 1991; Ruggerone and Nielsen 2004).

Significant differences in pink salmon abundance between odd- and even-numbered years provide a natural experiment to measure their potential competitive effects on other salmon species. Chum and pink salmon occupy a similar feeding niche and exhibit a 58% diet overlap in the Bering Sea when pink salmon abundance is low (Davis et al. 2005). Chum salmon have a more diverse diet than pink salmon, possessing stomachs specially adapted to feed on gelatinous zooplankton species (Welch 1997; Davis et al. 2004, 2005; Myers et al. 2004). This trait may have evolved to minimize competition during years of high pink salmon abundance by exploiting a unique branch of the food web (Welch 1997); for example, gelatinous zooplankton constituted 25% of chum salmon diet in the Bering Sea when pink salmon abundance was low, but 81% of chum salmon diet when pink salmon abundance was high (Tadokoro et al. 1996). While foraging on gelatinous zooplankton is helpful in maintaining stomach fullness, these species are calorie and lipid poor compared to other prey, which may adversely affect growth rate, maturation, and energy reserves (Davis 2003; Morita and Fukuwaka 2006; Kaga et al. 2013). Understanding the spatial, temporal, and dietary overlap of distant salmon stocks may provide information about competition-driven abundance trends.

Salmon growth and survival is also influenced by interannual variability in environmental conditions and can be indexed by sea surface temperature (SST), the Pacific Decadal Oscillation (PDO), and date of sea-ice retreat (Hunt et al. 2002; Mueter et al. 2002; Agler et al. 2013). While the PDO has been used to describe large-scale ocean temperature patterns, Mueter et al. (2002) and other researchers have found that local SST is a better indicator of salmon survival than large-scale indices such as the PDO. Local SST can serve as a proxy for the indirect effects of SST on salmon survival, such as prey availability and the relationship between SST and chum salmon body size (Mueter et al. 2002; Helle and Fukuwaka 2009). Date of sea-ice retreat in the eastern Bering Sea is also associated with salmon growth due to the relationship between the timing of the spring bloom and chum salmon prey energy densities (Wechter et al. 2017). Years with late sea-ice retreat, or “cold” years, support lipid-rich zooplankton blooms and result in more energy being available to pelagic fish species compared to years with early sea-ice retreat, or “warm” years (Coyle and Pinchuk 2002; Andrews et al. 2009; Coyle et al. 2011; Hunt et al. 2011; Wechter et al. 2017).

This study focuses on chum salmon stocks originating from the Arctic-Yukon-Kuskokwim (AYK) region of western Alaska, which constitutes over 40% of the State of Alaska by land area and includes the watersheds of Norton Sound and the Yukon and Kuskokwim Rivers (Krueger et al. 2009). Sharp declines in Chinook (*O. tshawytscha*) and chum salmon runs in western Alaska between 1997-2002 prompted the Alaska Board of Fisheries to declare a “fisheries disaster” and left fisheries managers and scientists puzzled over the potential causes (AYK SSI 2006, Krueger et al. 2009). Closures and reductions in both commercial and subsistence harvest of Chinook and chum salmon in western Alaska have had detrimental economic, food security, and cultural impacts on rural Alaska native communities (Loring and Gerlach 2010). Understanding the mechanisms behind the decline of chum salmon returns to the AYK region is critical for fishery managers and rural Alaskans.

Here, we investigated the relationship between western Alaska chum salmon growth and Asian pink and chum salmon abundance using retrospective scale analysis. The relationship between scale radius and fish length allows us to examine growth during specific periods of ocean residence (Yasumiishi et al. 2015). Growth has a strong influence on age at maturity in salmon, where the timing of maturation is a trade-off between increased ocean foraging time and increased risk of mortality (Morita et al. 2005). Longer ocean residence leads to increased body size, resulting in increased fecundity and larger egg size for females, thus increasing their reproductive success. Research suggests that the "decision" to mature in chum salmon is influenced by the most recent growth condition, where individuals that did not grow enough during a critical period may delay maturation due to decreased energy reserves (Morita and Fukuwaka 2006). Decreases in chum salmon growth during specific periods of marine residence may explain observed increases in age at maturity for western Alaska chum salmon populations.

Interactions between pink and chum salmon manifest as interannual variability in chum salmon diet due to biennial cycles of pink salmon abundance. Determining how the abundance of conspecifics affects chum salmon growth and maturity is more difficult, as chum salmon are longer-lived species and exhibit variability in age at maturity (Salo 1991), and thus exhibit less variability in abundance from year to year. Chum salmon growth has been observed to decline significantly with the abundance of Japanese hatchery chum salmon (Ishida et al. 1993, Ruggerone et al. 2011, Agler et al. 2013). However, it is difficult to distinguish whether this negative relationship is due to causation or correlation due to steady increases in Japanese hatchery chum salmon production through the 1990s, followed by little variation in releases since (Irvine and Ruggerone 2016). Japan is the single largest producer of hatchery chum salmon, releasing approximately 2 billion chum salmon fry from hatcheries each year since 1980 (data from http://www.npafc.org/new/science_statistics.html) and accounting for 80% of total hatchery chum salmon releases on average during 1990-2015 (Irvine and Ruggerone 2016). In 2011, the Tōhoku earthquake occurred 80 miles east off the Pacific coast of Japan, triggering a large tsunami that struck and destroyed 26 salmon hatcheries; chum salmon fry reared at these facilities were considered a total loss (North Pacific Anadromous Fish Commission Newsletter 32, www.npafc.org; North Pacific Anadromous Fish Commission Newsletter 37, www.npafc.org). This resulted in a 37% decrease in Japanese hatchery chum salmon releases in 2011 and was the lowest year of Japanese hatchery chum salmon production since 1978 (data from http://www.npafc.org/new/science_statistics.html). Although many of the hatcheries were rebuilt by the following year, this temporary decrease in hatchery chum salmon production provides a means to test for density dependence between western Alaska chum salmon and Japanese hatchery chum salmon in the Bering Sea.

The first objective of our study was to determine if growth of western Alaska chum salmon varies with the abundance of Asian pink and chum salmon in the Bering Sea. Overlaps in ocean distribution and diet among salmon stocks may result in decreased growth of western Alaska chum salmon during periods of low food availability or poor ocean conditions. Our second objective was to test the hypothesis that the reduction in Japanese hatchery chum salmon releases in 2011 resulted in increased growth of Bering Sea chum salmon. Chum salmon residing in the Bering Sea during 2012-2014 may have experienced increased growth during their second, third, and/or fourth ocean year due to decreased intraspecific competition.

2.3 Methods

2.3.1 Study populations

We analyzed fish scales in two groups of chum salmon that rear in the Bering Sea during their marine residence. The Kuskokwim dataset consists of scales collected by the Alaska Department of Fish and Game (ADF&G) from Kuskokwim River commercial and test fisheries in district W-1 near Bethel, Alaska in the lower 137 miles of the river (Bue 2005; Fig. 2.1). Set and drift gillnets are used to intercept fish with mesh sizes restricted to 15 centimeters (6 inches) or smaller. The Kuskokwim dataset represents maturing fish that survived their ocean residence and provides stock-specific information on temporal trends in chum salmon growth. The Bering Sea dataset is comprised of chum salmon caught incidentally in the Bering Sea Aleutian Island (BSAI) commercial trawl fishery for walleye pollock (*Gadus chalcogrammus*). Scales were collected by fishery observers deployed by the National Oceanic and Atmospheric Administration (NOAA) to collect biological samples and information from commercial fishing, processing, receiver ships, and land-based processing plants (Chilton 2016). The Bering Sea dataset represents both maturing and immature chum salmon from a mixture of populations, including hatchery-origin fish, that were intercepted in the Bering Sea before their homeward migration.

2.3.2 Scale sampling and processing

Kuskokwim chum salmon scales were collected during years 1968 and 1973-2014 (*n* = 3 742, Appendix Table A.2-1) and measured using procedures described by Hagen et al. (2001). Kuskokwim scales were scanned and measured by ADF&G personnel following methods described by Agler et al. (2013). Images of salmon scales were scanned from the acetate impressions using an Indus 4601-11 Screen Scan microfiche reader and measured using Image-Pro Premier 9.0 software with a customized application. Bering Sea chum salmon scales (*n* = 1 845, Appendix Table A.2-2) were collected during July 16-31 for years 2001-2016 (52°N-60°N, 160°W-175°W, Fig. 2.1) using procedures described by

AFSC (2016). Acetate impressions made of scales mounted on gummed cards were scanned at 24x magnification using Z Scan 46-II Image Scanner through NOAA's imaging lab and a scanner by a private contractor and were digitized using Image-Pro Plus 7.0 software with a customized application, ring structure macro.

Fish ages were recorded using European notation (Koo 1962) where numbers preceding the decimal represent the number of winters spent in freshwater and numbers following the decimal represents the number of winters spent in marine water. As chum salmon migrate to sea during their first spring (Salo 1991), we followed the growth-zone notation of Morita and Fukuwaka (2006) where the numerical subscript indicates the year of ocean residency (e.g., g_1 indicates growth during the first year at sea, g_2 describes growth accrued during the second year at sea, and so on). A scale was used for measurement if (1) the scale came from the "preferred" zone; (2) age, sex, and length data could be matched to the scale; (3) the annuli were clearly defined; (4) the scale could be measured on the longest axis; (5) scales were collected through the test or commercial fishery (Kuskokwim dataset); and (6) scales were collected during July 16-30 (Bering Sea dataset). Scales were discarded if: (1) the scale was regenerated; (2) the scale impression was too poor for the reader to measure with confidence; or (3) the scale did not meet the aforementioned criteria. A reference line was drawn along the longest axis from the scale origin to the scale margin and annuli were identified by visual inspection (Fig. 2.2). The width of each growth zone was measured as the distance between adjacent annuli (e.g., size of g_2 was the distance between the outer edge of the annulus ending g_1 to the outer edge of the annulus ending g_2). This method was repeated until the edge of the scale was reached. Measurement data were stored in a database and linked to the age, sex, and length data by an image name.

Target sample size for Kuskokwim scales was 25 samples for each sex (male, female) and age (age-0.3, age-0.4). Bering Sea chum salmon scales were collected opportunistically when intercepted in the pollock fishery. All Bering Sea scales were measured by a single reader and most Kuskokwim scales were measured by two readers and their measurements were comparable. A randomly selected set of Kuskokwim scales (n = 50) were re-measured by an independent reader to test for a reader effect using multiple analysis of variance (MANOVA) with independent variable reader with multiple response variables (growth measurements). No reader effect was found; measurements by the independent reader were not significantly different from the original measurements over the entire scale (MANOVA, p = 0.97) or for each growth zone when compared separately (ANOVA, $p > 0.5$ for all).

2.3.4 Sea-surface temperature

To account for changes in chum salmon growth due to SST, we developed seasonal indices for spring and summer SST in the Bering Sea. Temperature data were obtained from NOAA's Earth System Research Laboratory's Physical Sciences Division website (available from https://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl), based on National Centers for Environmental Prediction/National Center for Atmospheric Research gridded reanalysis data (Kalnay et al. 1996). Summer SST was averaged across July and August (the two warmest months) in the central Bering Sea (54.3°-60.0°N, 170.6°-178.1°W; Fig. 2.3). This spans an area used by immature chum salmon during their summer feeding months (Echave et al. 2012) and encompasses both shelf and slope habitats. Spring SST was based on average SST during April and May at the M2 mooring buoy in the southeastern Bering Sea (56°N, 164°W; Fig. 2.3).

The timing of the spring phytoplankton bloom in the eastern Bering Sea is strongly correlated with sea-ice extent, where the presence or absence of sea ice after March 15 is an indicator of early or late sea-ice retreat (Sigler et al. 2014). NOAA's ice retreat index (IRI; available from https://www.beringclimate.noaa.gov/data/index.php) at the M2 buoy provides data on the number of days with ice after March 15 but does not span the entire study period, 1973-2016. We used the Spring SST index as a proxy for the date of sea-ice retreat based on the relationship between IRI and mean April and May SST at the M2 mooring buoy ($R^2 = 0.72, p < 0.001$).

2.3.5 Indices of Asian pink and chum salmon abundance

Genetic stock identification (GSI) of salmon caught incidentally in federally managed fisheries provides important information regarding the effects of fishing on chum salmon stocks with conservation concerns (Stram 2012; Kondzela et al. 2016). In 2005, GSI determined that approximately 50-60% of chum salmon caught in the Bering Sea pollock midwater trawl fishery originated from Asia, while western Alaska stocks represented 23% of the catch, with the remaining stocks originating from southeast Alaska, Washington, and British Columbia (Guyon et al. 2010). Our analysis focuses on interactions in the Bering Sea between western Alaska chum salmon and the dominant stocks of pink and chum salmon during the study period. These stocks include Japanese chum salmon, which are assumed to be entirely of hatchery origin, and eastern Kamchatka pink salmon, which are of wild origin (Urawa et al. 2004, 2009; Myers et al. 2007; Irvine and Ruggerone 2016).

Abundance estimates of Japanese chum salmon and eastern Kamchatka pink salmon abundance were obtained from Irvine and Ruggerone (2016) and include maturing and immature fish by region.

Japanese hatchery chum salmon release data were obtained from the North Pacific Anadromous Fish Commission (NPAFC; http://www.npafc.org/new/science_statistics.html). The NPAFC was established by international convention to promote conservation of Pacific salmon and steelhead trout in the North Pacific Ocean. NPAFC has collected and reported salmon hatchery releases numbers for Canada, Japan, Korea, Russia, and the United States since 1993.

2.3.6 Statistical analysis

All explanatory variables were standardized (mean=0, standard deviation=1) to allow for comparability of the coefficients among variables (Fig. 2.4). Each growth zone was standardized separately, as were the growth zone data for each dataset. The models described below were fit in R version 3.4.0 (R Core Team 2017) using the nlme package (version 3.1-131; Pinheiro et al. 2018) for linear mixed-effects models.

To determine if growth of western Alaska chum salmon varied with Asian pink and chum salmon abundance, a linear mixed-effects model was fit separately to each growth zone g_2 - g_4 to examine the influence of predictor variables on interannual variability in growth. The model was:

$$(1) \qquad g_{i,y,s} = Sex_s + OceanAge + \beta_1 SpringSST_y + \beta_2 SummerSST_y + \beta_3 JapanChum_y + \beta_4 EKamPinks_y + \beta_5 (JapanChum * EKamPinks)_y + a_y + \varepsilon_{i,y,s}$$

Where $g_{i,y,s}$ is the anomaly in growth at growth zone *i* for sex *s* during calendar year *y*. *JapanChum* is a covariate for Japanese chum salmon abundance, *EKamPink* is a covariate for eastern Kamchatka pink salmon abundance, *Sex* is included as a factor to allow for differences in growth between males and females, *OceanAge* is a factor included to allow for differences in growth of fish that matured at different ages, the β coefficients describe linear changes in growth with temperature and Asian pink and chum salmon indices, and a_y is a random effect to allow for interannual variability in the average growth index by calendar year *y*. The random intercepts a_y and the residuals $\varepsilon_{i,y,s}$ are assumed to be independent and normally distributed with means 0 and variances σ_a^2 and σ_ε^2, respectively.

To determine if a reduction in Japanese hatchery chum salmon releases in 2011 resulted in increased growth of Bering Sea chum salmon, a linear mixed-effects model was fit separately to each growth zone g_2 - g_4 to examine the influence of predictor variables on interannual variability in growth. Because the decrease in Japanese hatchery outputs was only observed in 2011, its effect was expressed as a factor by use of a dummy variable (equal to 1 for calendar years expected to be impacted by the earthquake, i.e., 2012-2014; and equal to 0 otherwise), allowing us to estimate the effect of decreased hatchery production on growth of chum salmon that were in the ocean during 2012-2014. The model was:

$$(2) \qquad g_{i,y,s} = Sex_s + \delta EQ_y + \beta_1 OceanAge + \beta_2 SpringSST_y + \beta_3 SummerSST_y + a_y + \varepsilon_{i,y,s}$$

Where *EQ* is a dummy variable (0, 1) for years affected by decreased hatchery chum salmon releases, δ is the incremental change in growth due to the earthquake effect, and *OceanAge* is a covariate to allow for differences in growth among different age-classes of fish, and other terms are the same as in Equation 1. We compared models with ocean age as an integer and as a factor using Akaike's Information Criteria (AIC) to determine the best model fit with growth and ocean age.

2.4 Results

2.4.1 Study populations

Sample size varied by population, sex, age class, and growth zone (Appendix Tables 2.A-1 and 2.A-2). Target sample size was generally achieved for Kuskokwim chum salmon, except for the 1963 and 1969 brood years, which were represented by fewer than 20 individuals each. Bering Sea sample sizes were more variable, with g_4 tending to have fewer samples than g_2 and g_3. Mean width of all growth zones declined over time in Kuskokwim (Figs. 2.5*a* and 2.5*b*) and Bering Sea (Fig. 2.5*c*) samples, except in g_2 for Bering Sea chum salmon. Male chum salmon exhibited higher growth than female chum salmon in all growth zones for both populations (Tables 2.1 and 2.2), except in g_4 for Bering Sea chum salmon. Within-year variability in growth among individuals was larger than the among-year variability captured by the random year effect (Table 2.3) for both chum salmon populations.

The width of all growth zones decreased with age for Bering Sea (Table 2.2) and Kuskokwim chum salmon (Table 2.1). Younger fish (Bering Sea samples) and fish that matured as age-0.3 (Kuskokwim samples) grew significantly more during each growth zone compared to older fish and fish that matured as age-0.4. Linear mixed model regression with ocean age as an integer had a lower AIC value than an alternative model allowing for ocean age as a factor (ΔAIC = 8), suggesting that growth decreases linearly with ocean age for Bering Sea chum salmon that may not be returning to spawn.

2.4.2 Sea-surface temperature

Spring and Summer SSTs were not significantly related to growth of Kuskokwim chum salmon for any of the growth zones examined (Table 2.1). Pearson's pairwise correlation test found that Spring and Summer SSTs were correlated ($r = 0.53$), but this correlation was low enough that we chose to retain both metrics in the model. Over the shorter time series of the Bering Sea dataset, the Pearson's correlation coefficient between Spring and Summer SST coefficients was higher ($r = 0.72$). We chose to retain Spring SST in the model despite the lack of statistical significance because of the documented relationship between date of sea-ice retreat and primary production in the Bering Sea (Brown et al. 2011; Hunt et al. 2011). A linear effect of SST was considered adequate because including SST as a second-order polynomial did not improve the model fit (ΔAIC = 1). Overall, Spring SST had a marginally significant effect on chum salmon growth during g_2 (Wald's t-test for coefficient δ: $t = 1.903$, $p = 0.081$) but not for other growth zones.

2.4.3 Asian pink and chum salmon abundance

Kuskokwim chum salmon growth was not related to eastern Kamchatka pink salmon abundance for any growth zone examined (Fig. 2.6; Table 2.1). Kuskokwim chum salmon growth during g_4 exhibited the largest negative relationship with eastern Kamchatka pink salmon abundance, but this relationship was not significant ($t = -1.760$, $p = 0.087$). Kuskokwim chum salmon growth declined significantly with the abundance of Japanese hatchery chum salmon for all growth zones examined (Fig. 2.6; Table 2.1). This relationship was strongest during g_2 and g_4. Interactions between Japanese hatchery chum and Kuskokwim chum salmon growth during g_3 are likely influenced by the decision to mature. Decreased Japanese hatchery chum salmon releases in 2011 were not associated with increased growth of Bering Sea chum salmon for any growth zone examined (Fig. 2.7; Table 2.2). Additionally, the model fit without the earthquake effect had a lower AIC (ΔAIC = 2), further suggesting that decreased Japanese hatchery chum salmon outputs had no significant effect on Bering Sea chum salmon growth.

2.5 Discussion

This study assessed how Kuskokwim and Bering Sea chum salmon growth is affected by Asian pink and chum salmon abundance. Our results indicate that Kuskokwim and Bering Sea chum salmon have experienced significant decreases in growth over the study period as assessed by scale annulus width of each growth zone. These findings have been observed in chum salmon populations throughout the

Pacific Rim, including Russia, Japan, Canada, and the United States (Ishida et al. 1993; Bigler et al. 1996; Kaeriyama 1998; Zavolokin et al. 2009, 2011; Ruggerone et al. 2011; Yasumiishi et al. 2016; Debertin et al. 2017). Because changes in growth do not appear to be constrained to specific chum salmon stocks or countries, factors occurring during the ocean phase of chum salmon life history are likely driving these changes.

Our results support previous studies that provide evidence of density dependence between western Alaska chum salmon growth and Japanese hatchery chum salmon abundance in the Bering Sea (Ruggerone et al. 2011; Agler et al. 2013). Western Alaska chum salmon growth during g_2 - g_4 exhibited a negative relationship with the abundance of Japanese hatchery chum salmon (Fig. 2.6), and this relationship was strongest during g_2. This relationship has been observed for chum salmon populations in Asia (Ishida et al. 1993; Zaporozhets and Zaporozhets 2004) and North America (Helle et al. 2007; Ruggerone et al. 2011; Agler et al. 2013). In western Alaska, increased production of Asian hatchery chum salmon was significantly related to reduced adult length at age, productivity, and delayed age at maturity of Norton Sound chum salmon (Ruggerone et al. 2011). The reduced growth of Kuskokwim chum salmon we observed during g_2 may contribute to increases in chum salmon age at maturity, as slower growing salmon tend to mature at an older age compared to fast-growing salmon (Morita et al. 2005; Siegel et al. 2017). While age at maturity has been shown be heritable in some salmon populations (Hankin et al. 1993), research assessing growth trajectories and optimal maturation timing found that reduced growth rates alone could explain increased age at maturity and reduced size at age in Japanese chum salmon, without a genetic change taking place (Morita et al. 2005). Reductions in growth may therefore result in smaller length at age and increased age at maturity if chum salmon are not able to grow enough during critical periods of ocean residence (Hankin et al. 1993).

While the results of our analysis suggest that Kuskokwim chum salmon growth is inhibited by Japanese hatchery chum salmon abundance, a steady increase in Japanese hatchery chum salmon production through the 1990s followed by little variation since makes it difficult to quantify the extent to which growth of overlapping chum salmon stocks is reduced. To estimate this relationship, we used a decrease in Japanese hatchery chum salmon production in 2011 resulting from earthquake-related damage to hatcheries to contrast growth of chum salmon intercepted in the Bering Sea during periods of normal (2001-2011, 2015-2016) and low (2012-2014) Japanese hatchery chum salmon releases. Chum salmon did not experience increased growth due to the earthquake-induced reduction in Japanese hatchery chum salmon production (Fig. 2.7). Although this was contrary to our expectations, the reduction in Japanese hatchery chum salmon outputs may have been too small to cause a significant impact on growth of chum salmon in the Bering Sea. While the 37% decrease in hatchery chum salmon outputs is the largest reduction in hatchery chum salmon releases in the last 39 years, from 1.9 billion chum salmon released in

2010 to 1.2 billion chum salmon released in 2011 (data from http://www.npafc.org/new/science_statistics.html), rebuilding efforts in Japan resulted in most damaged hatcheries being rebuilt by August 2011 and chum salmon fry releases resumed the following year (North Pacific Anadromous Fish Commission Newsletter 37, www.npafc.org). Additionally, decreased intraspecific competition may have been counteracted by other variables not included in the analysis, including environmental indices such as the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation, among others (Debertin et al. 2017). Because the goal of this analysis was to describe growth of Bering Sea chum salmon during a period of reduced Japanese hatchery chum salmon production, the relationship between chum salmon growth and large-scale climate indices were not examined but may warrant consideration in future analyses. We also observed a substantial increase in the abundance of wild chum salmon over the study period, 2001-2016. From 1984-2013, hatchery chum salmon abundance exceeded wild chum salmon abundance in the North Pacific Ocean and accounted for 62% of total chum salmon abundance by 2005 (Irvine and Ruggerone 2016). However, a 264% increase in the abundance of wild Russian chum salmon from 2005-2015 reduced the proportion of hatchery chum salmon to 45% of total chum salmon abundance by 2015. Russian chum salmon follow a similar ocean migration pattern as Japanese and western Alaska chum salmon (Urawa et al. 2009) and may have negated any effect of decreased Japanese hatchery chum salmon production on Bering Sea chum salmon growth. Future analyses of chum salmon growth should account for the abundance of Russian chum salmon populations in addition to Japanese chum salmon.

We did not observe a relationship between Kuskokwim chum salmon growth and eastern Kamchatka pink salmon abundance (Fig. 2.6). Although chum and pink salmon occupy a similar feeding niche, the specialized gut morphology of chum salmon enables them to exploit gelatinous zooplankton species as a prey source. This trait likely evolved in response to past selective pressure as a way to mitigate interspecific competition. Data collected by Davis (2003) on the Pacific salmon feeding ecology in the central Bering Sea during 1991-2000 observed no difference in chum salmon stomach fullness between even- and odd-numbered years. However, both prey quantity and prey quality are important to examine when considering interactions between pink and chum salmon. Davis (2003) observed that the quality of chum salmon prey decreased significantly when pink salmon abundance was high, whereby the weight of low-quality prey items increased by 19% and the weight of high-quality prey items decreased by 38% during odd-numbered years. The quality of prey items is based on caloric density and lipid content, where high-quality prey items consist of euphausiids, squid, and fish species, and low-quality prey items refer to gelatinous zooplankton species. This suggests that while chum salmon are still able to maintain stomach fullness when pink salmon abundance is high, the calorie and lipid content of the prey consumed is significantly lower. Interactions between pink and chum salmon may therefore not be expressed in scale growth, as maintaining stomach fullness allows salmon to invest energy acquired into somatic growth, but the consumption of low-lipid prey may result in decreased energy and lipid storage. Chum salmon lipid content, which serves as a proxy for body condition, has been observed to decrease significantly when pink salmon abundance is high (Kaga et al. 2013). Lipids are the primary energy source for salmonids and are consumed during periods of low prey availability as a primary energy source (Parker and Vanstone 1966). Observed changes in chum salmon diet when pink salmon abundance is high could result in decreased lipid storage and may indirectly affect chum salmon growth, reproductive potential, and overwinter mortality (Morita et al. 2005; Kaga et al. 2013). Because chum salmon scales collected from the Kuskokwim dataset represent fish that survived their ocean residence, the relationship between eastern Kamchatka pink salmon abundance and Kuskokwim chum salmon growth may be confounded by growth processes at sea that negatively affect ocean survival.

The relationship between chum salmon growth and Spring and Summer SST in the Bering Sea was smaller than expected. However, previous research has shown that the effects of SST on chum salmon growth are variable. In southeast Alaska, Yasumiishi et al. (2016) observed a positive relationship between growth during g_2 and cooler summer and fall SST. But after accounting for density-dependent effects, growth was more strongly correlated with population abundance and was positively associated with SST. In contrast, Agler et al. (2013) observed a negative relationship between western Alaska chum salmon growth and Gulf of Alaska SST. An analysis of Kwiniuk chum salmon in Norton sound found no correlation between g_2 - g_4 scale growth of age-0.3 and age-0.4 chum salmon and SST in the North Pacific Ocean during winter, spring, or summer (Ruggerone and Agler 2008). These contradictory responses suggest that the relationship between salmon growth and SST is not straightforward and may vary by population.

Our study examined the growth effects of the dramatic decrease in Japanese hatchery chum salmon releases in 2011 to illuminate interactions between potentially competing chum salmon stocks in the Bering Sea. Although western Alaska chum salmon growth generally decreased significantly with increasing abundance of Japanese hatchery chum salmon during g_2 - g_4, we did not observe an increase in Bering Sea chum salmon growth when the production of Japanese hatchery chum salmon was decreased due to the Tōhoku earthquake. This may be because decreases in Japanese hatchery chum salmon outputs were too small and too short-lived to detect a difference in growth, or because the recent increase in wild Russian chum salmon abundance overwhelmed any changes in Japanese chum salmon abundance. Testing for density dependence in the open ocean is difficult, but our analysis may provide some insight into whether additional hatchery salmon outputs would adversely affect wild chum salmon growth in the Bering Sea.

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2.8 Figures

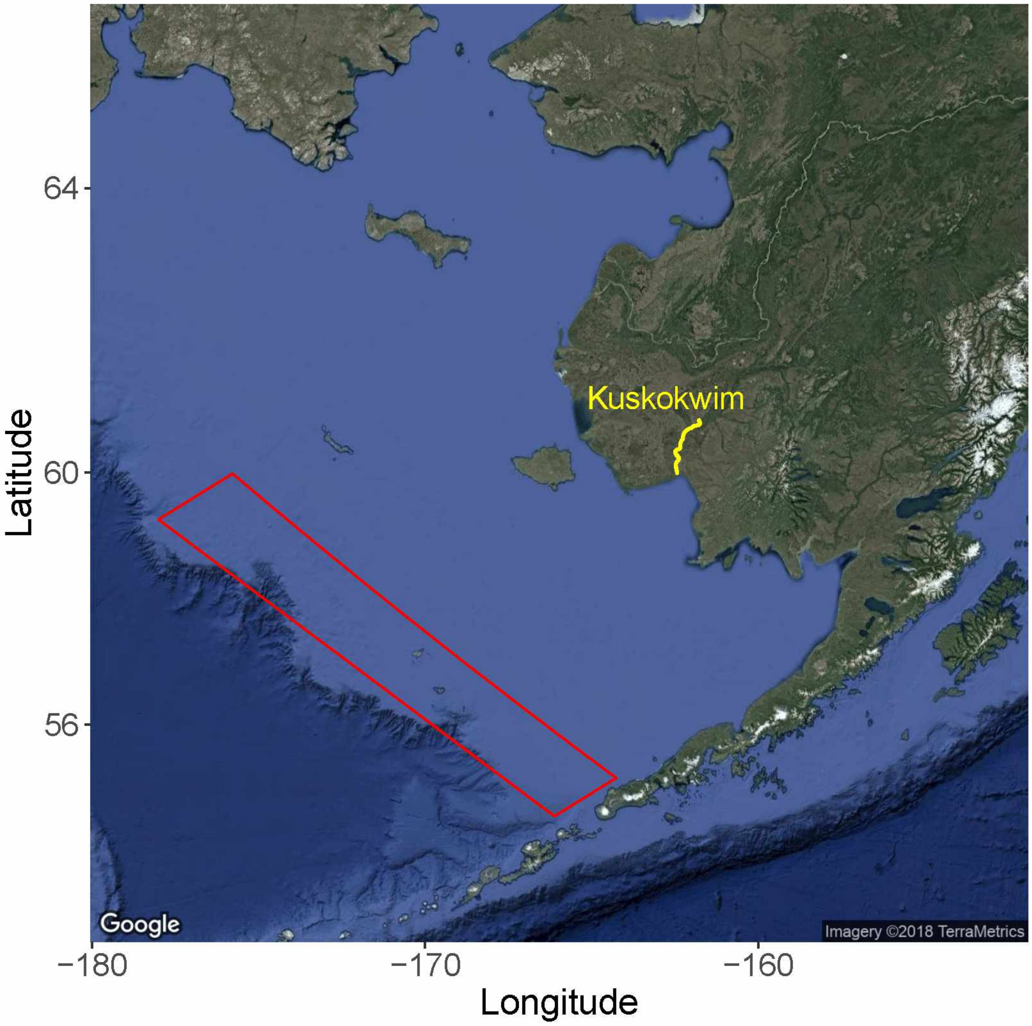

Figure 2.1. Locations of chum salmon samples from the Kuskokwim (yellow) and the Bering Sea (red) datasets. Maps generated using ggmap package in R (Kahle and Wickham 2013).

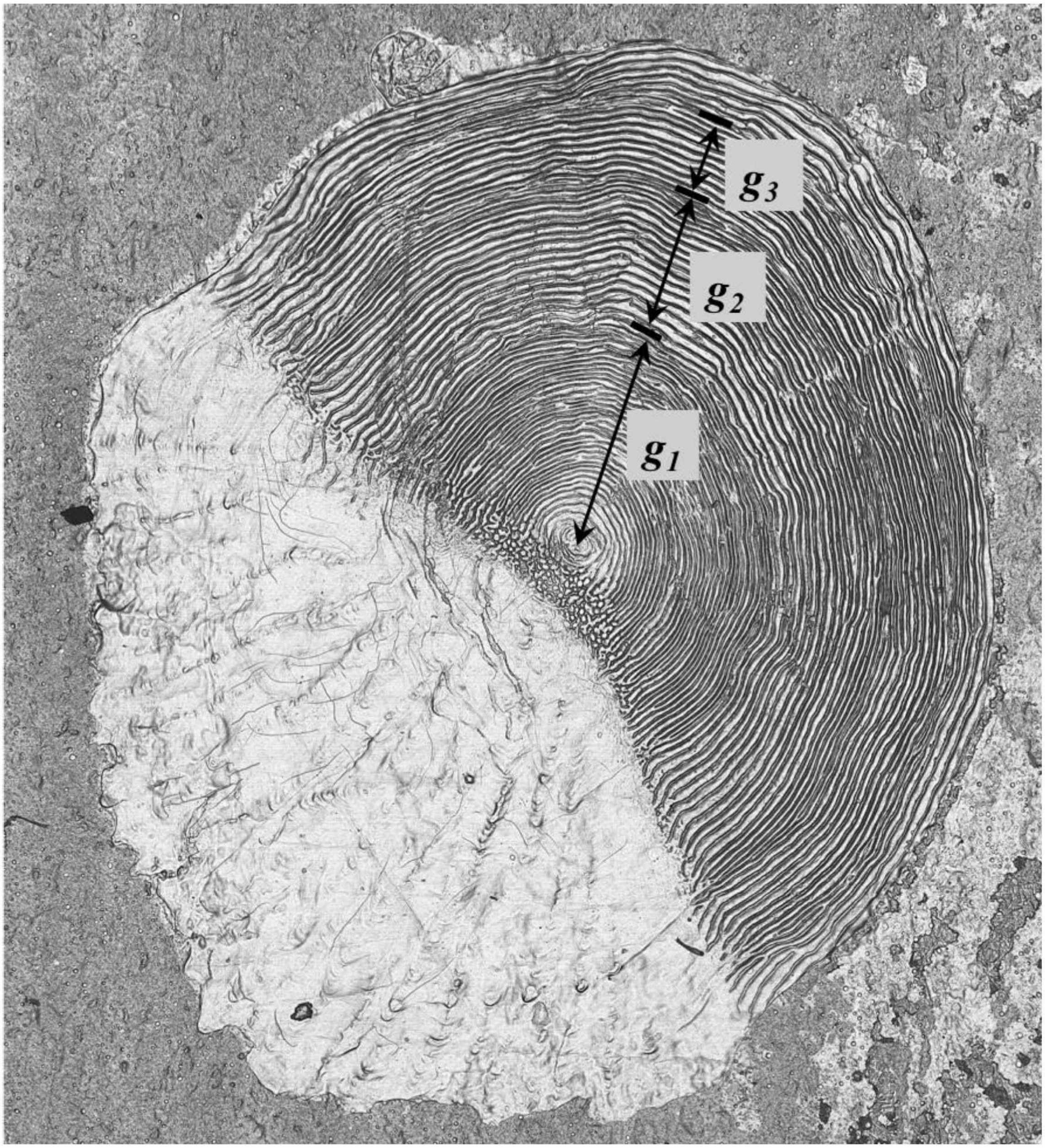

Figure 2.2. Image of a chum salmon scale showing annuli (black bars) and growth zones for a given period of ocean residence. For example, g_1 is growth accrued during the first year of ocean residence.

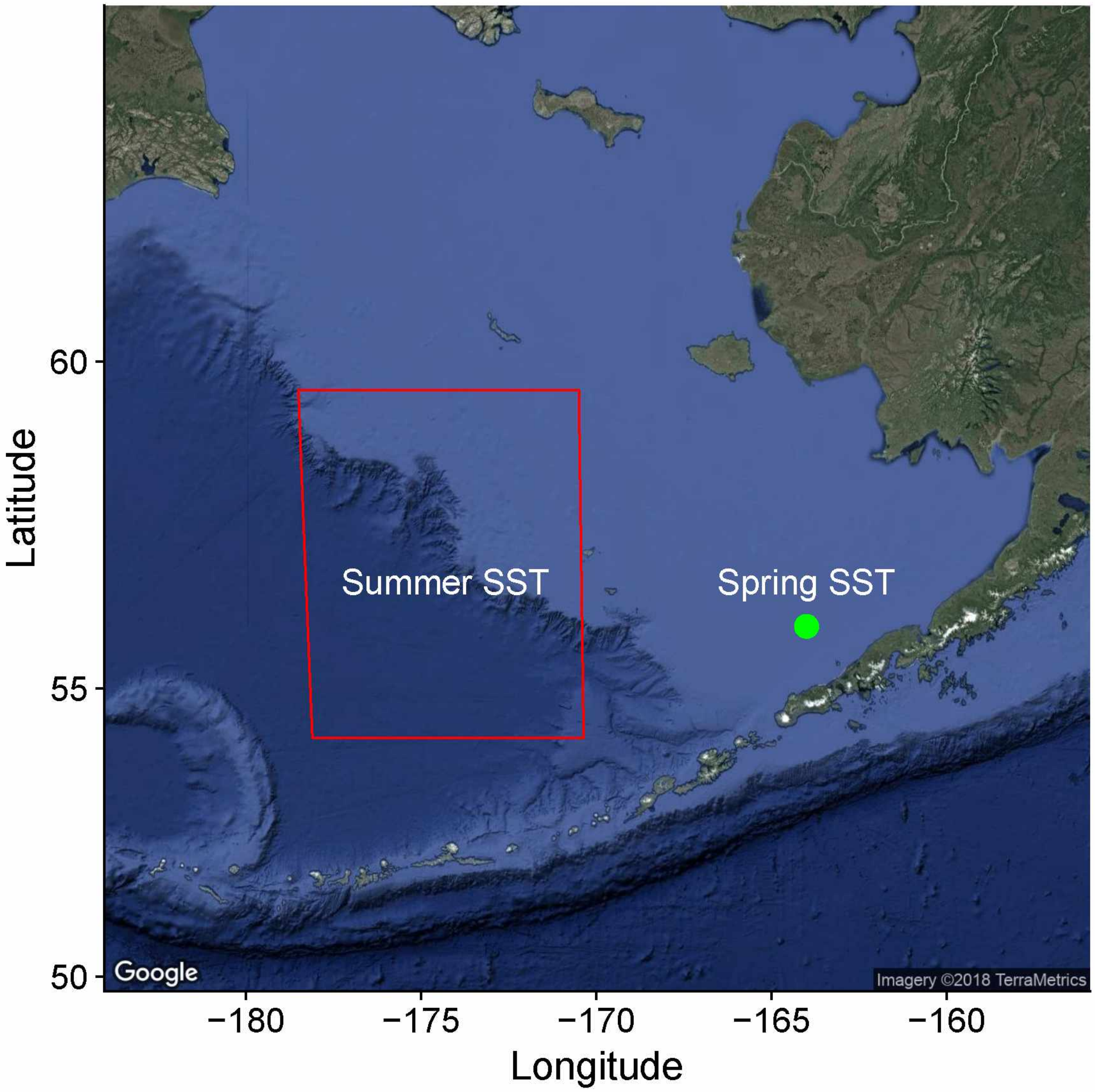

Figure 2.3. Locations of sea-surface temperatures (SST) used in our analysis. Summer SSTs were averaged across July and August in the central Bering Sea (54.3°-60.0°N, 170.6°-178.1°W). Spring SSTs were averaged across April and May in the eastern Bering Sea near the location of the M2 mooring buoy (56°N, 164°W). Maps generated using ggmap package in R (Kahle and Wickham 2013).

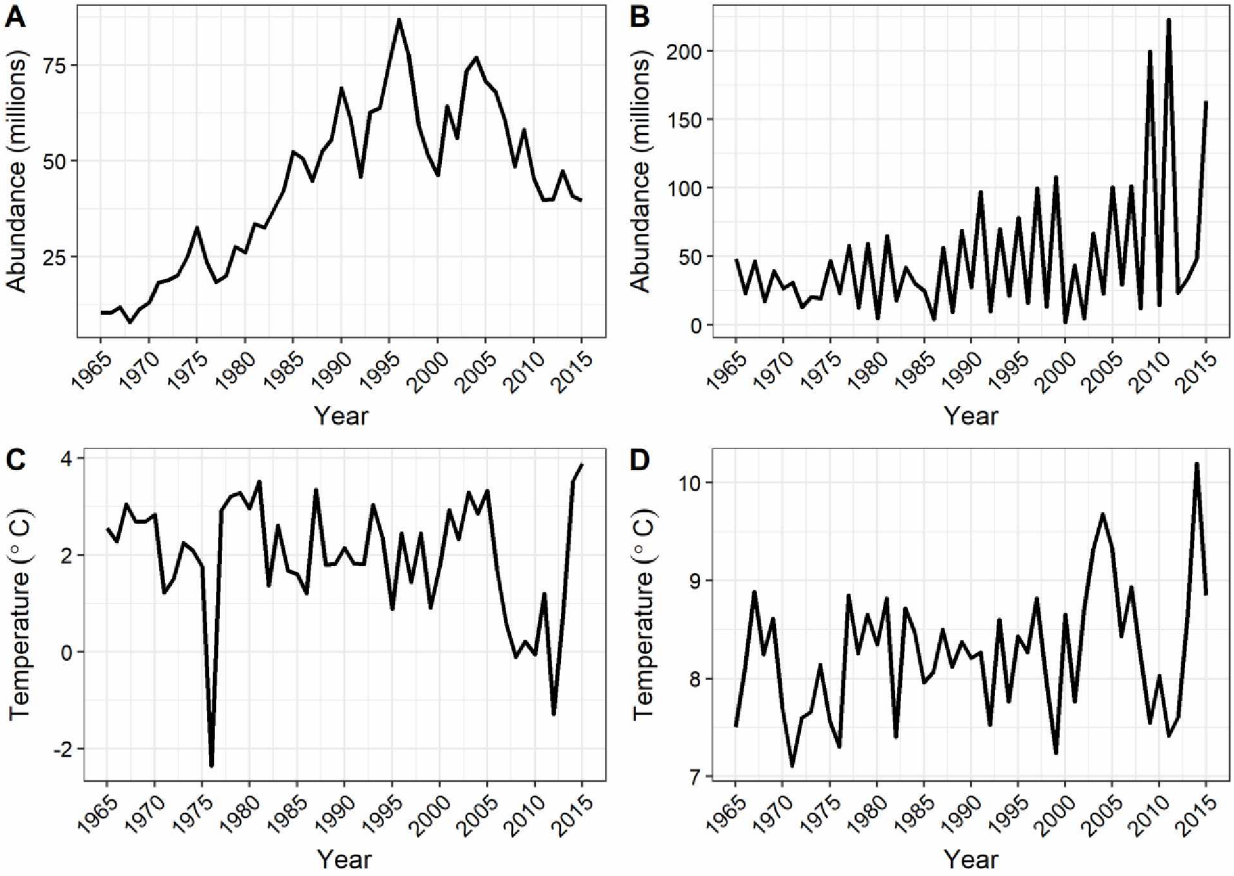

Figure 2.4. Explanatory variables of Japanese hatchery chum salmon abundance (A), eastern Kamchatka pink salmon abundance (B), spring sea-surface temperature (C), and summer sea-surface temperature (D) used in objective 1 analysis.

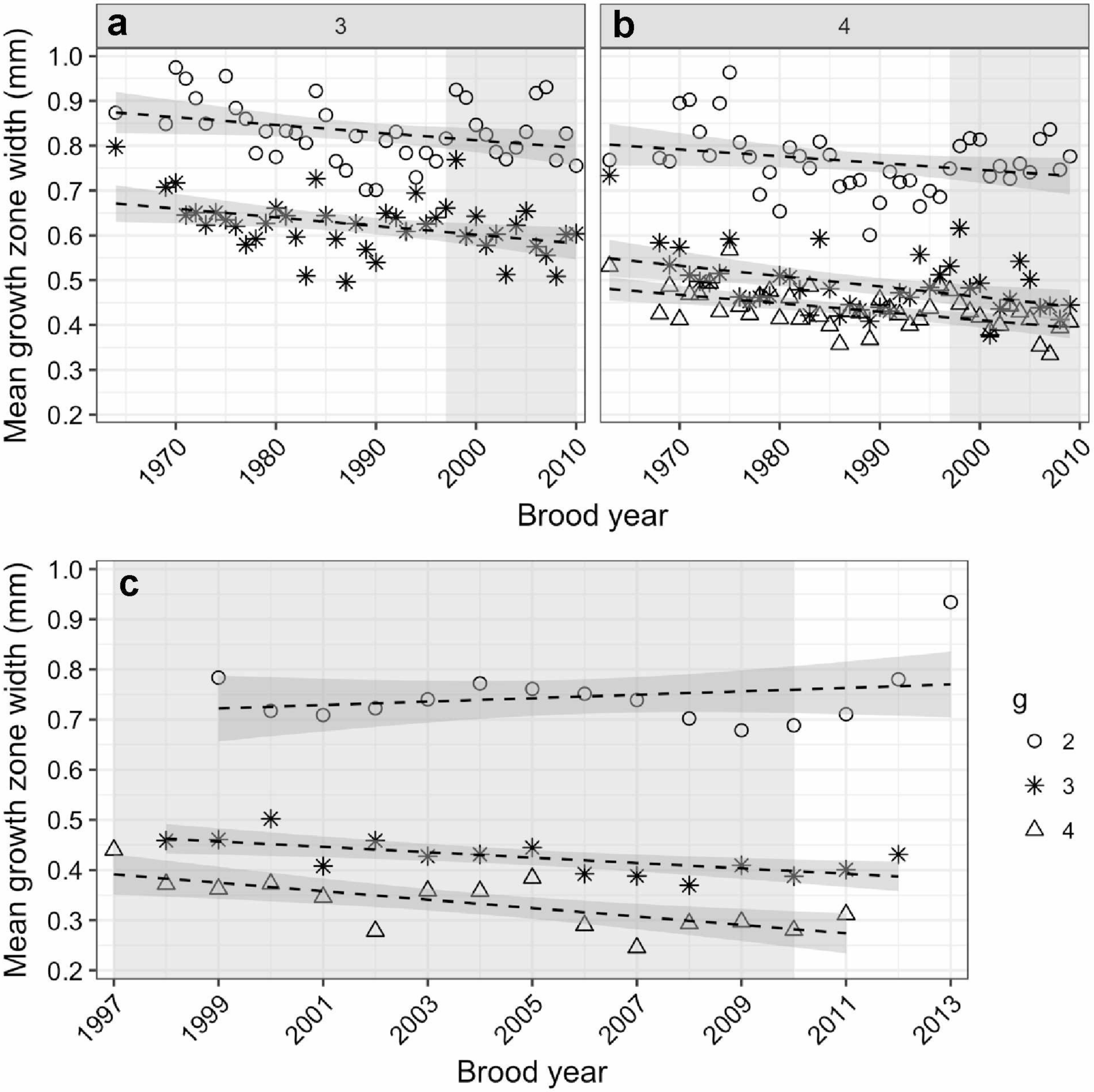

Figure 2.5. Mean growth zone width (mm) of mature age-0.3 (a) and age-0.4 (b) Kuskokwim chum salmon and (c) chum salmon collected in the Bering Sea by brood year. Ages represent age at maturity. Shaded linear regression lines represent 95% confidence intervals for each growth zone (g_2 - g_4).

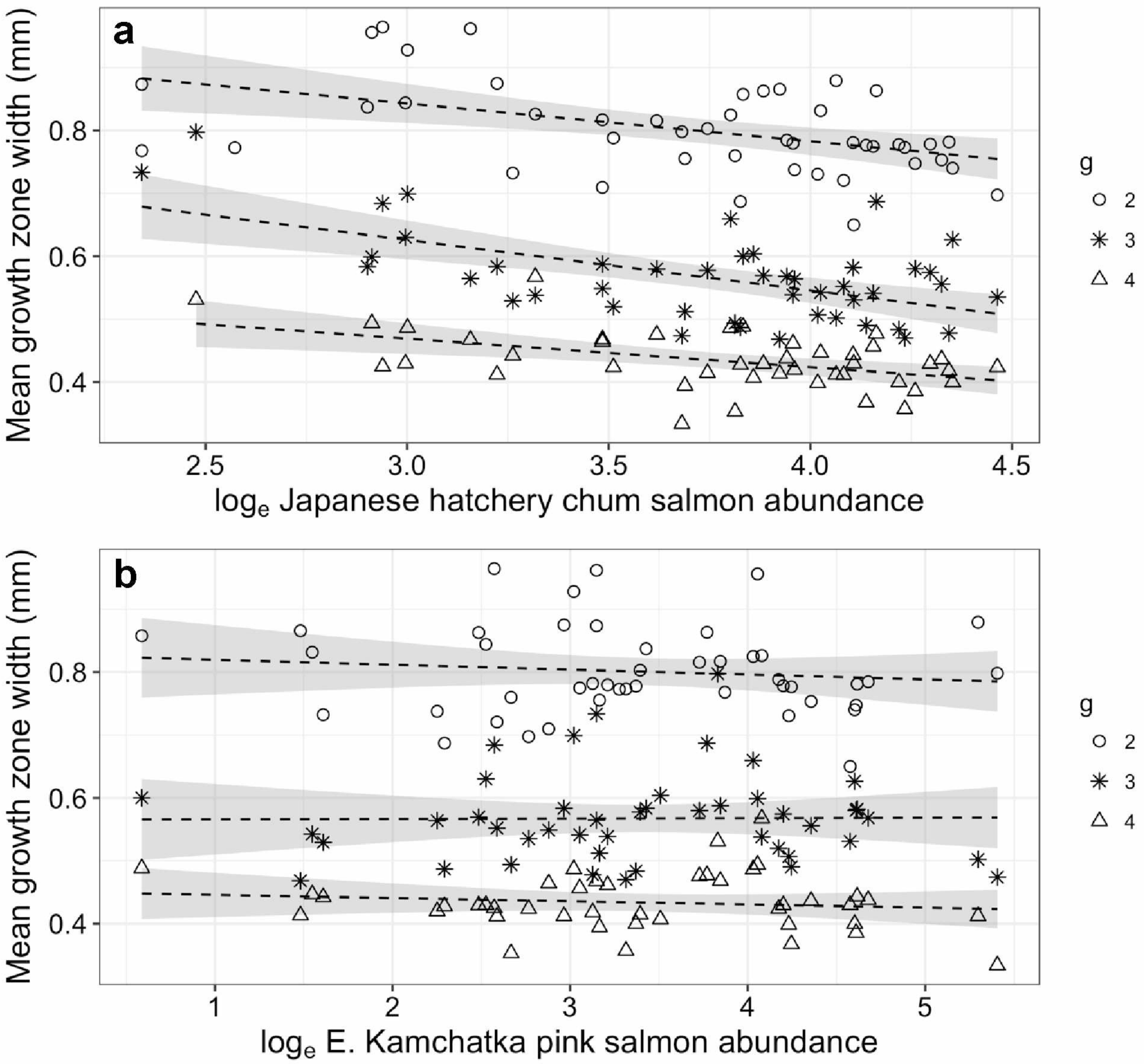

Figure 2.6. Relationship between average Kuskokwim growth zone width (mm) and log$_e$ Japanese hatchery chum salmon abundance (a) and log$_e$ eastern Kamchatka wild pink abundance (b). Linear regression lines represent 95% confidence intervals for each growth zone (g_2 - g_4).

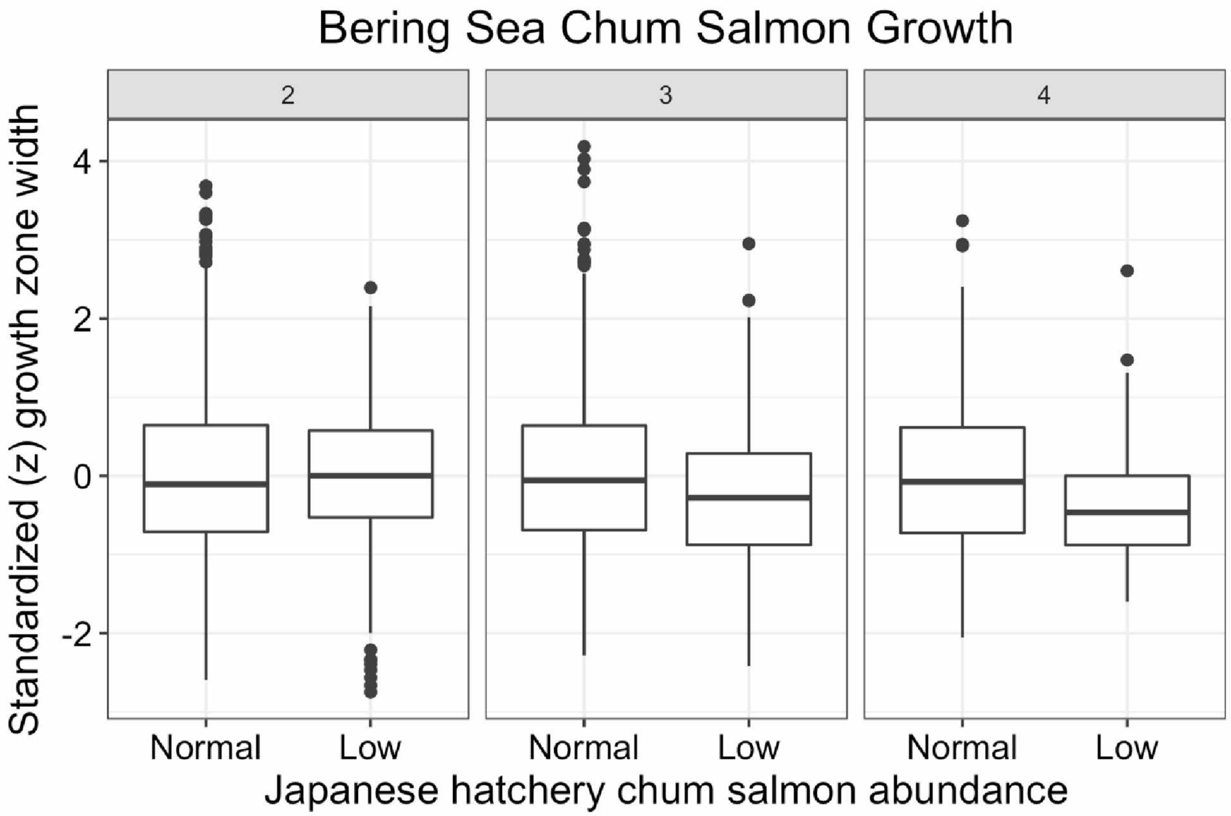

Figure 2.7. Standardized growth zone width of Bering sea chum salmon during years of normal (2001-2011, 2015) and low (2012-2014) Japanese hatchery chum salmon, by growth zone 2-4.

2.9 Tables

Table 2.1. Coefficients of linear mixed-effects regression of Kuskokwim chum salmon growth zone width against standardized model covariates. Separate analyses were run for each growth zone (g_2 - g_4). Abundance estimates and sea-surface temperatures correspond with growth accrued during the same calendar year. Japan:Ekam is the interaction between Japanese hatchery chum salmon and eastern Kamchatka pink salmon.

Covariate	*Estimate*	*SE*	*df*	*t*	*p*
g_2					
Sex (Male)	0.124	0.027	3695	4.570	0.000
Age (0.4)	-0.566	0.028	3695	-20.320	0.000
Japanese hatchery chum	-0.329	0.090	39	-3.655	0.001
E. Kamchatka pink	0.037	0.077	39	0.484	0.631
Japan:Ekam	0.004	0.113	39	0.031	0.975
Spring SST	-0.103	0.083	39	-1.250	0.219
Summer SST	0.109	0.092	39	1.187	0.242
g_3					
Sex (male)	0.381	0.025	3695	14.991	0.000
Age (0.4)	-0.971	0.026	3695	-37.231	0.000
Japanese hatchery chum	-0.167	0.076	39	-2.209	0.033
E. Kamchatka pink	-0.099	0.066	39	-1.486	0.145
Japan:Ekam	0.234	0.098	39	2.393	0.022
Spring SST	0.111	0.071	39	1.566	0.125
Summer SST	-0.037	0.076	39	-0.489	0.628
g_4					
Sex (male)	0.450	0.044	1748	10.323	0.000
Age (0.4)	-	-	-	-	-
Japanese hatchery chum	-0.171	0.068	37	-2.508	0.017
E. Kamchatka pink	-0.098	0.056	37	-1.760	0.087
Japan:Ekam	0.081	0.084	37	0.968	0.339
Spring SST	0.088	0.061	37	1.437	0.159
Summer SST	0.003	0.066	37	0.052	0.959

Table 2.2. Coefficients of linear mixed-effects regression of Bering Sea chum salmon growth zone width against standardized model covariates. Separate analyses were run for each growth zone (g_2 - g_4). Abundance estimates and sea-surface temperatures correspond with growth accrued during the same calendar year. Earthquake effect refers to years of reduced Japanese hatchery chum salmon releases due to the Tōhoku earthquake and resulting tsunami.

Covariate	*Estimate*	*SE*	*df*	*t*	*p*
g_2					
Sex (Male)	0.092	0.046	1714	1.993	0.046
Ocean Age	-0.273	0.038	1714	-7.117	0.000
Earthquake effect	-0.062	0.175	12	-0.356	0.728
Spring SST	0.152	0.080	12	1.903	0.081
g_3					
Covariate					
Sex (Male)	0.211	0.049	1432	4.280	0.000
Ocean Age	-0.456	0.054	1432	-8.526	0.000
Earthquake effect	-0.257	0.171	12	-1.503	0.159
Spring SST	0.106	0.076	12	1.393	0.189
g_4					
Covariate					
Sex (Male)	0.152	0.107	299	1.425	0.155
Ocean Age	-0.366	0.147	299	-2.489	0.013
Earthquake effect	-0.390	0.310	12	-1.256	0.233
Spring SST	0.049	0.135	12	0.360	0.725

Table 2.3. Residual variability of random effects in linear mixed-effects regression of Kuskokwim and Bering Sea chum salmon growth zone width against all covariates.

Variability:	g_2	g_3	g_4
		Kuskokwim	
Within-year	0.251	0.240	0.401
Among-year	0.957	0.931	0.938
		Bering Sea	
Within-year	0.453	0.388	0.303
Among-year	0.827	0.775	0.919

Conclusion

This study sought to increase our understanding regarding the extent of spatial and dietary overlap among salmon stocks in the Bering Sea and how those overlaps may affect the growth and maturation of western Alaska chum salmon. Chum salmon from the Arctic-Yukon-Kuskokwim (AYK) of western Alaska experienced sharp declines in abundance in the late 1990s, followed by varying levels of recovery. Dramatic increases in hatchery salmon production were thought to be a driving factor behind changes in chum salmon life history, which include decreases in growth and fork length and increases in age at maturity. However, increases in the abundance of wild salmon may contribute to competition in the Bering Sea when ocean or feeding conditions are poor.

The broad geographical distribution of chum salmon, as well as variation in spawning age, makes defining their ocean migration difficult. In general, both western Alaska and Japanese chum salmon have been observed to move between the Bering Sea during summer and the Gulf of Alaska in winter. It is likely that Russian chum salmon populations, which have experienced large increases in abundance, also follow these same migrations patterns, but our understanding of stock-specific movements for these populations is more limited. Pink salmon in the Bering Sea primarily hail from the eastern side of the Kamchatka Peninsula and are abundant during odd-numbered years. Eastern Kamchatka pink salmon overlap with western Alaska chum salmon during their homing migration through the North Pacific Ocean and Bering Sea.

Overlaps in species distribution may result in competition when food availability is low. Chum and pink salmon occupy a similar feeding niche and exhibit a 58% diet overlap in the Bering Sea during years of low pink salmon abundance (Davis et al. 2004). The specialized gut morphology of chum salmon facilitates a more varied diet and is manifested as changes in chum salmon stomach contents between even and odd-numbered years (Welch 1997; Davis 2003). In the central Bering Sea, chum salmon diet averaged 38% less high-quality prey and 19% more low-quality prey during odd-numbered years, where high-quality prey consists of euphausiids, copepods, squid, and fish and low-quality prey includes pteropods and gelatinous zooplankton species (Davis 2003). Diet changes from high- to low-quality prey results in less energy acquired through prey capture and can adversely affect growth and, subsequently, age at maturity (Davis et al. 1998; Morita et al. 2005).

Previous research has demonstrated a negative relationship between chum salmon growth and the abundance of Asian pink and chum salmon in the Bering Sea (Ishida et al. 1993, Walker et al. 1998, Zavolokin et al. 2009). In western Alaska, chum salmon returning to Norton Sound, Bristol Bay, and the Yukon River experienced decreased growth due to the high abundance of Japanese hatchery chum salmon, and to a lesser extent, eastern Kamchatka pink salmon abundance (Ruggerone et al. 2011; Agler et al. 2013). Our analysis in Chapter 2 supports these findings, where Kuskokwim chum salmon growth decreased significantly with Japanese hatchery chum salmon abundance during the second, third, and fourth year at sea ($g_2 – g_4$), but was not correlated with the abundance of eastern Kamchatka pink salmon.

The negative relationship between Bethel chum salmon growth and Japanese hatchery chum salmon abundance was strongest during g_2 and relatively equal during g_3 and g_4. These results differ slightly from Hokkaido chum salmon where the biggest reduction in growth was observed during g_3 (Kaeriyama 1998). Agler et al. (2013) found similar relationships between Japanese hatchery chum salmon abundance and Yukon River and Bristol Bay chum salmon growth during g_3 but did not examine growth during g_2 or g_4. Although the results of our analysis and those of others has determined that Japanese hatchery chum salmon abundance negatively affects the growth of conspecifics, steady increases in Japanese hatchery chum salmon production through the 1990s, followed by little variation in Japanese hatchery salmon production since, makes it difficult to distinguish if this observed relationship is due to causation or correlation.

In Chapter 2, we used the decrease in Japanese hatchery chum salmon releases in 2011 due to the Tōhoku Earthquake to define this relationship. If reductions in chum salmon growth are caused by high abundance of Japanese hatchery chum salmon, we hypothesized that chum in the Bering Sea during a period of reduced Japanese hatchery chum salmon production would exhibit increased growth compared to years where the abundance of Japanese chum salmon was unchanged. However, our analysis indicated that chum salmon in the Bering Sea did not experience increased growth from 2012-2014, despite reductions in Japanese hatchery chum salmon releases. Although our results were unexpected, it lends optimism to the thought that although salmon abundance is at a historic high, ocean carrying capacity may not be a limiting factor in salmon survival and growth despite contrary research (e.g. Cooney and Brodeur 1998, Kaeriyama et al. 2009). Unfortunately, our results were confounded by significant increases in the abundance of Russian chum salmon during the study period, in addition to uncertainties regarding estimates of Japanese hatchery chum salmon releases. While this makes it difficult to interpret why Bering Sea chum salmon did not experience increased growth despite reductions in Japanese hatchery chum salmon releases, it is clear that no single factor can explain observed changes to chum salmon life history.

We found that eastern Kamchatka pink salmon abundance did not significantly affect Bethel chum salmon growth; these results are supported by similar studies that found the effects of pink salmon abundance on chum salmon growth to be less than that of conspecifics (Ruggerone and Nielsen 2004; Ruggerone et al. 2012; Agler et al. 2013). Feeding plasticity in chum salmon may mitigate direct prey competition with pink salmon by enabling chum salmon to maintain stomach fullness through the consumption of gelatinous zooplankton (Davis 2003). However, decreases in chum salmon lipid content during odd-numbered years suggest that chum salmon may experience reductions in growth potential compared to when they are consuming high-lipid prey (Kaga et al. 2013). Studies assessing how interactions with pink salmon affect chum salmon growth typically evaluate changes in growth and fork length as compared to changes in body weight. However, the consequences of diet overlap between these two species may be more evident when assessing metrics other than changes in scale growth or fork length. Excess lipids acquired through prey capture are stored as energy reserves for periods of low food availability where they are used to aid with overwinter survival, and during salmon homing when energy is allocated to gamete production and the formation of secondary sexual characteristics (Nomura et al. 2002). How changes in chum salmon diet affect metrics like overwinter survival and maturation potential is difficult to quantify but may highlight the consequences of interspecific competition with pink salmon.

This study demonstrates the need for a more comprehensive understanding of how the abundance of distant salmon stocks affects Alaska chum salmon. Overlaps in diet and ocean distribution with Asian pink and chum salmon stocks in the Bering Sea may contribute to observed decreases in chum salmon growth rate and increases in age at maturity through inter- and intra-specific competition. Highly abundant Japanese hatchery chum salmon affect western Alaska chum salmon growth during $g_2 – g_4$. However, large increases in the abundance of Russian wild chum salmon should be considered in future analysis, as these stocks follow similar ocean migration patterns and may intensify density dependence. Eastern Kamchatka pink salmon did not have a direct effect on western Alaska chum salmon growth, but future studies should consider assessing changes in chum salmon body weight and lipid reserves during years of high and low pink salmon abundance to further define the relationship between these two species. Understanding the degree overlap and competition among salmon stocks in the Bering Sea and North Pacific Ocean will assist fishery managers and scientists in protecting salmon stocks with conservation concerns and in understanding the driving factors behind changes to their life history.

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Appendix

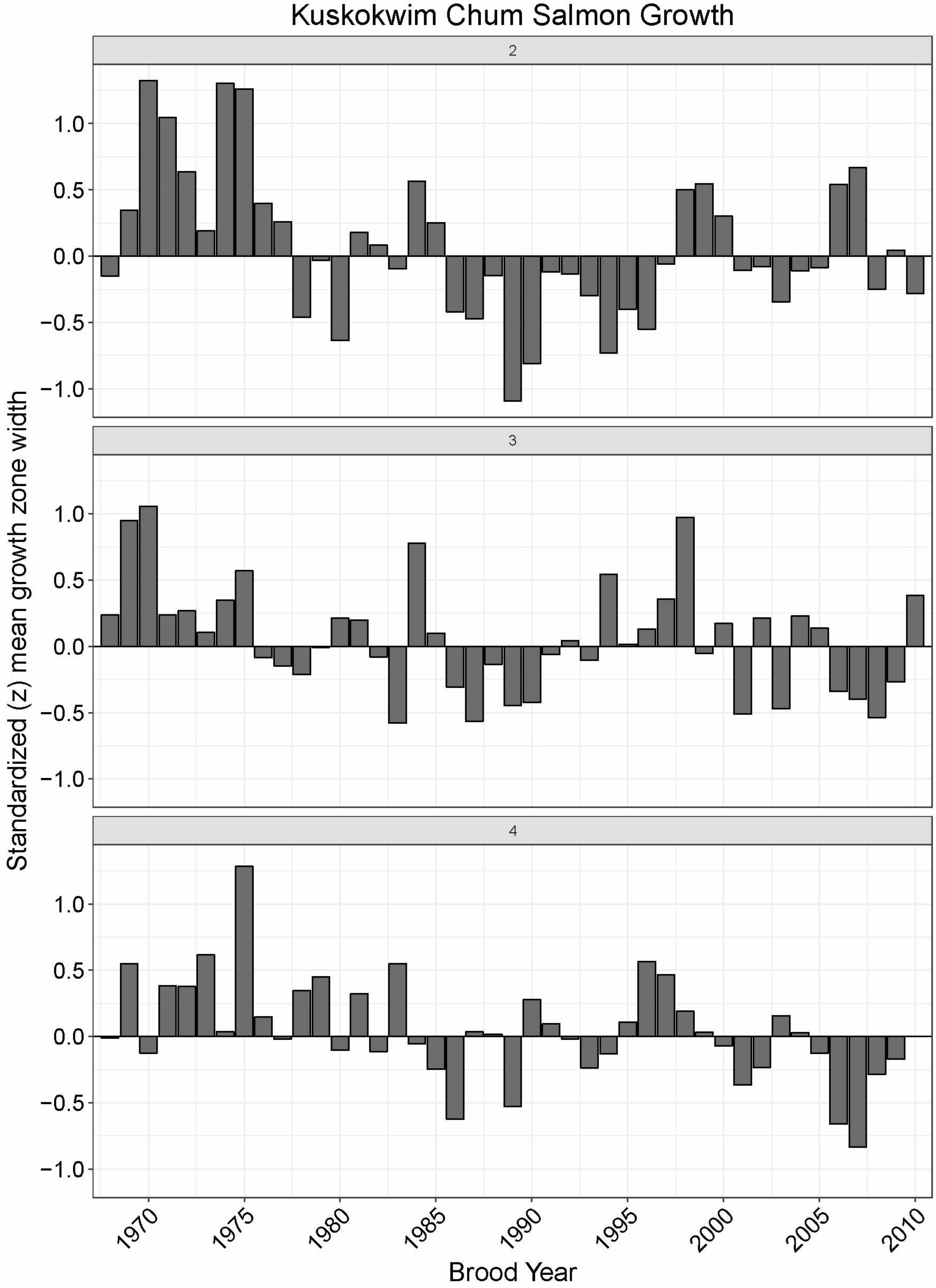

Figure 2.A-1. Standardized mean growth zone widths (mm) of Kuskokwim chum salmon collected near Bethel, Alaska, separated by brood year and growth zone (g_2 - g_4).

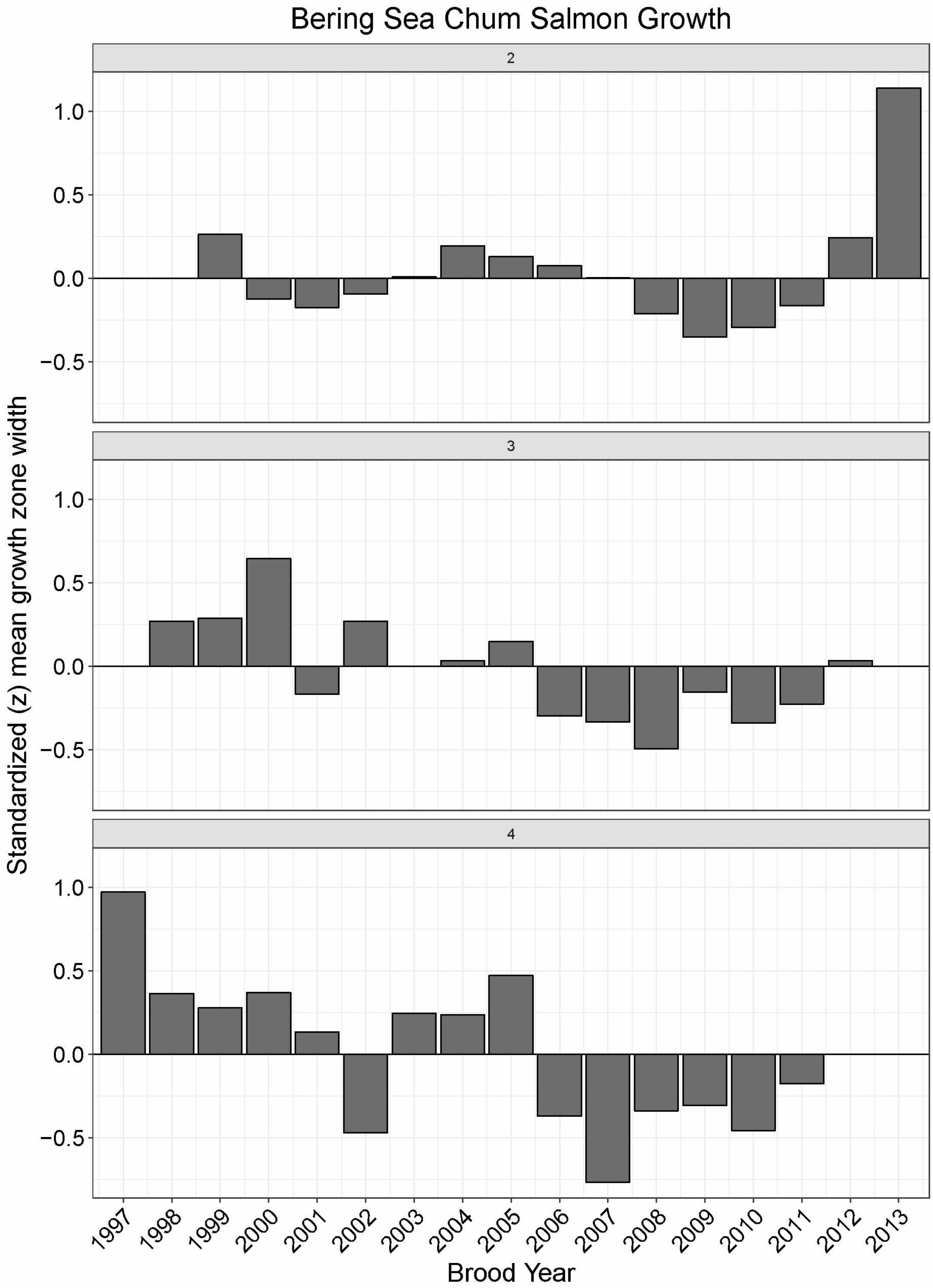

Figure 2.A-2. Standardized mean growth zone widths (mm) of chum salmon collected from the Bering Sea, separated by brood year and growth zone (g_2 - g_4).

Table 2-A.1. Number of Kuskokwim chum salmon sampled by Alaska Department of Fish and Game personnel from 1963, 1968-2010 arranged by brood year, sex, and age at maturity.

Brood year	*Male 0.3*	*Female 0.3*	*Male 0.4*	*Female 0.4*	*Total*
1963	5	1	6	3	15
1968	15	17	18	19	69
1969	2	5	1	4	12
1970	18	16	16	1	51
1971	18	22	13	13	66
1972	22	24	19	15	80
1973	21	18	5	19	63
1974	23	23	5	19	70
1976	25	21	25	25	96
1977	25	25	14	19	83
1978	21	18	24	24	87
1979	23	24	21	23	91
1980	24	25	29	28	106
1981	25	28	24	25	102
1982	26	25	25	24	100
1983	25	31	25	25	106
1984	25	25	25	25	100
1985	25	25	25	23	98
1986	25	25	24	25	99
1987	23	24	25	25	97
1988	25	25	25	24	99
1989	22	25	24	25	96
1990	25	25	25	24	99
1991	25	25	24	25	99
1992	25	25	25	25	100
1993	25	25	25	25	100
1994	23	24	23	23	93
1995	22	16	18	23	79
1996	15	22	22	25	84
1997	23	21	20	19	83
1998	18	22	22	24	86
1999	25	24	24	22	95
2000	25	25	25	17	92
2001	25	25	25	25	100
2002	25	26	6	2	59
2003	22	25	25	25	97
2004	25	25	25	26	101
2005	25	25	28	34	112
2006	25	25	31	26	107
2007	25	25	35	25	110
2008	25	28	13	17	83
2009	25	26	33	35	119
2010	33	25	0	0	58

Table A.2-2. Number of Bering Sea chum salmon samples, 1996-2014, arranged by brood year, sex, and growth zone (*g*).

	FEMALE					MALE					
Brood year	g_1	g_2	g_3	g_4	Total	g_1	g_2	g_3	g_4	Total	Total
1996	7	7	7	7	7	8	8	8	8	8	15
1997	21	21	21	6	21	22	22	22	6	22	43
1998	24	24	20	5	24	26	26	23	8	26	50
1999	57	57	49	11	57	69	69	56	10	69	126
2000	29	29	24	4	29	56	56	51	11	56	85
2001	84	84	74	23	84	91	91	81	22	91	175
2002	67	67	48	13	67	49	49	40	9	49	116
2003	32	32	29	6	32	42	42	36	8	42	74
2004	31	31	27	16	31	37	37	33	15	37	68
2005	55	55	51	4	55	72	71	71	8	72	127
2006	54	54	36	19	54	64	64	47	24	64	118
2007	80	80	76	5	80	80	79	72	10	80	160
2008	29	29	14	6	29	41	41	17	10	41	70
2009	58	57	55	8	58	57	57	54	6	57	115
2010	34	34	31	5	34	53	53	50	8	53	87
2011	66	66	57	14	66	68	68	60	16	68	134
2012	104	104	74		104	120	120	95		120	224
2013	21	21			21	36	36			36	57
2014						1				1	1