

Supplement 1

From diatoms to killer whales: impacts of pink salmon on North Pacific ecosystems

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Text S1 Pacific Salmon

Trophic level of maturing pink salmon

Based on stable isotope research, some investigators and managers have discounted competition for prey between pink salmon and "higher trophic level" Chinook and coho salmon as a likely cause of the decline in average age and size-at-age in Chinook salmon and coho salmon (e.g., Johnson & Schindler 2009, Ohlberger et al. 2018). Their findings suggested that Chinook and coho salmon feed at a higher trophic level and presumably on different prey species than pink, sockeye and chum salmon.

This simplified conclusion, however, overlooks extensive direct evidence of dietary overlap among maturing pink salmon and larger salmon species on the high seas. Field studies indicate that diets can be remarkably similar across species, including a substantial squid component, except in chum salmon which rarely consume maturing squid (Percy et al. 1988, Kaeriyama et al. 2004, Davis 2003, Aydin 2000, and others). Several studies from across the subarctic North Pacific and Bering Sea indicate that maturing pink salmon have an important influence on squid populations that comprise the most important component of the offshore diets of coho, steelhead, and Chinook salmon (Ito 1964, Davis 2003, Jorgensen 2011, Atcheson et al. 2012, Shaul and Geiger 2016). The reason for the discrepancy between direct observation and stable isotope analysis lies in the brief period of about 2-3 months when rapidly growing pink salmon are of sufficient size (≥ 1 kg) to be effective predators on maturing *B. anonychus* (Aydin 2000, Davis 2003, Shaul and Geiger 2016).

This late ontogenetic dietary shift by pink salmon from zooplankton to squid and small fishes is not accurately reflected in adult pink salmon muscle tissue because it takes months to years for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to be incorporated into muscle tissue of fish. For example, in a controlled laboratory experiment with California yellowtail (*Seriola dorsalis*), it took 520 days after switching from 100% pellet diet to 100% mackerel and squid diet for Bayesian mixing models to accurately predict the 100% mackerel and squid diet (Madigan et al. 2021). After 160 days of a 100% fish/squid diet, yellowtail muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values resulted in mixing model estimates of 50% pellets and 50% fish/squid. Studies using other fish species have also shown that months to years are needed before stable isotope analyses capture a dietary switch (MacNeil et al. 2006, Madigan et al. 2012). Therefore, diet of maturing pink salmon is a more accurate indicator of potential competition with species such as Chinook and coho salmon and steelhead trout.

Chinook salmon

Offshore distribution of Chinook salmon

Researchers sometimes characterize Chinook salmon as a coastal species remaining on the continental shelf, but we suggest this generalization is not justified because many Chinook salmon also inhabit oceanic regions after their first year at sea. For example, during 1960 to 1980, the Japanese offshore mothership and land-based drift net salmon fisheries caught 390,000 Chinook salmon per year, on average, or 2.4 times more Chinook salmon than caught in Russian coastal fisheries during this period (INPFC 1979). The high seas fisheries were west of 175°W in both the North Pacific and Bering Sea, yet many Chinook salmon originated from western and central Alaska, and British Columbia to a lesser extent (Major et al. 1978, Rogers et al. 1984). Genetic stock identification during 2005-2010 indicated 11-38% of immature Chinook salmon sampled in the southeastern Bering Sea and 10-12% of Chinook salmon sampled along the southern Alaska Peninsula originated from the lower United States, highlighting the long distances that Chinook salmon travel at sea (Larson et al. 2013).

Research surveys on the high seas also catch Chinook salmon, but the catchability of Chinook salmon by research and commercial gear is low because Chinook salmon are typically much deeper in the water column and larger than other salmon species that are targeted by surface gillnets, trawls, and seines (Mason 1965, Major et al. 1978, Courtney et al. 2021). Relatively high ¹³C isotope levels suggest a coastal presence relative to other salmon species (Johnson and Schindler 2008), but high ¹³C also reflects feeding in coastal waters during their first year at sea and during their homeward migration (Trudel et al. 2009, Tucker et al. 2012). Furthermore, even though maturing ocean-type Chinook salmon (subyearling smolts) migrate southward along the Southeast Alaska and British Columbia coasts whereas stream-type Chinook salmon (yearling smolts) tend to remain offshore before returning to natal rivers, size-at-age of both ocean- and stream-type Chinook salmon in Southeast Alaska fisheries are highly correlated and has declined over time even though biomass of herring, a primary prey in coastal areas, increased after the mid-1990s (Hebert 2020; Fig. S1.1).

This supports our assessment in the main text that the decline in Chinook size is related in part to feeding in offshore regions where pink salmon affect key prey such as squid and forage fishes. In support of this view, length of ocean age-4 Chinook salmon caught in the Southeast Alaska troll fishery, 1982-2018, was negatively correlated with the biomass of North American pink salmon and positively correlated with the Pacific Decadal Oscillation Index (PDO), based on the modelling approach developed by Shaul and Geiger (2016) for Southeast Alaska coho salmon (Fig. S1.1). Approximately 75% of the variability in Chinook salmon size during the past 37 years was explained by pink salmon abundance and the PDO.

The consistency in the decline in size at age of Chinook salmon throughout Alaska in relation to pink salmon (Table S1, Fig. S1.1), the decline in annual scale growth of western Alaska Chinook salmon at sea (Section 3.4.4, Supplement 2), and the biennial variability and declining size of coho salmon in Southeast Alaska in relation to pink salmon abundance (Shaul & Geiger 2016,

Section 3.4.3) support the pink salmon hypothesis. Resident killer whales have also been hypothesized to drive the declining size of Chinook salmon through size-selective predation (Ohlberger et al. 2018, 2019), but killer whales are unlikely to have caused the decline in annual scale growth at sea or the steep decline in coho size over time, because coho salmon mature after only one winter (or none) at sea and they are consumed less frequently by killer whales. Size of all other species of salmon have declined over time and in relation to the biennial pattern of pink salmon abundance, which has reached record levels in recent years (Section 3.4). The declining size of all species of salmon across most of their range is strong evidence that prey availability is limiting their growth at sea, especially in the warming ocean. The evidence indicates pink salmon has affected prey availability for all species of salmon in the open ocean.

Chinook salmon harvest trends in Alaska and British Columbia

We compared Chinook salmon harvest trends in Alaska and British Columbia with pink salmon abundance (catch and escapement) in the North Pacific Ocean (NPO) from 1952-2021 (NPAFC 2022a, Ruggerone et al. 2021). Most Chinook salmon in this region spend three or four winters at sea, but they are less likely to be directly influenced by pink salmon foraging during their spring migration back to the spawning grounds. Given the potential for direct and indirect (food web) interactions between pink salmon and Chinook salmon, and the effect of reduced size and fecundity on future production of Chinook salmon (Ohlberger et al. 2020), we compared Chinook salmon harvests with mean pink salmon abundance one to four years earlier. This lag, modified to account for older ocean age in Chinook salmon, is consistent with lags involving pink salmon catch biomass along even- and odd-year lines that explained a large proportion of interannual variation in Southeast Alaska coho salmon weight and Chinook salmon length (Fig. S1.1), and are inferred to reflect the cumulative impact by maturing pink salmon across multiple generations of squid (*B. anonychus*), key offshore prey of coho, Chinook, and pink salmon (Shaul and Geiger 2016).

Chinook salmon catch from 1952 to 2021 was highly negatively correlated with pink salmon abundance (see Fig. 10a and text in manuscript) but autocorrelation of the model residuals was high, as expected, because multiple year classes of pink salmon can affect a single year of Chinook salmon harvest and because pink salmon can 1) alter the food web, 2) compete directly for shared prey such as squid, small fishes, and some zooplankton species, and 3) reduce body size and reproductive potential of Chinook salmon. As noted in the main text, we caution that fishery regulations and oceanographic factors may also influence Chinook salmon abundance and harvests in this region.

Fig. 10a in the main text shows that Chinook salmon harvests in Alaska and British Columbia were relatively high during 1952 to 1982 (~1.5 to 2 million fish per year), then declined steadily over time—just the opposite of pink salmon abundance. Harvests in Alaska could have been higher during the period of low pink salmon abundance if the Japanese high seas salmon fishery had not captured an average of 330,000 Chinook salmon per year during 1955-1982, declining to 145,000 Chinook salmon per year through 1991 when the fishery was terminated. Scale

pattern analyses during the 1970s and 1980s indicated approximately 85% of the Chinook salmon had originated from Alaska (Rogers et al. 1984). Pink salmon harvests in the high seas fishery (adult equivalent values) were included in the abundance values (Ruggerone and Irvine 2018).

Chinook salmon are also captured as bycatch in groundfish fisheries, and these mortalities would also influence Chinook salmon harvests in Alaska and British Columbia, though total annual bycatch was typically smaller than harvests in the Japanese high seas salmon fishery. An estimated 37,000 Chinook salmon were caught per year by the United States pollock fishery in the Bering Sea during 1991 to 2013 (Ianelli and Stram 2014). During 1977 to 1986, an estimated 38,700 Chinook salmon per year were captured in the foreign groundfish and joint venture fisheries within the US exclusive economic zone (Myers & Rogers 1988). Foreign groundfish fisheries took undocumented numbers of Chinook salmon prior to 1977.

Chinook salmon length-at-age in relation to pink salmon abundance

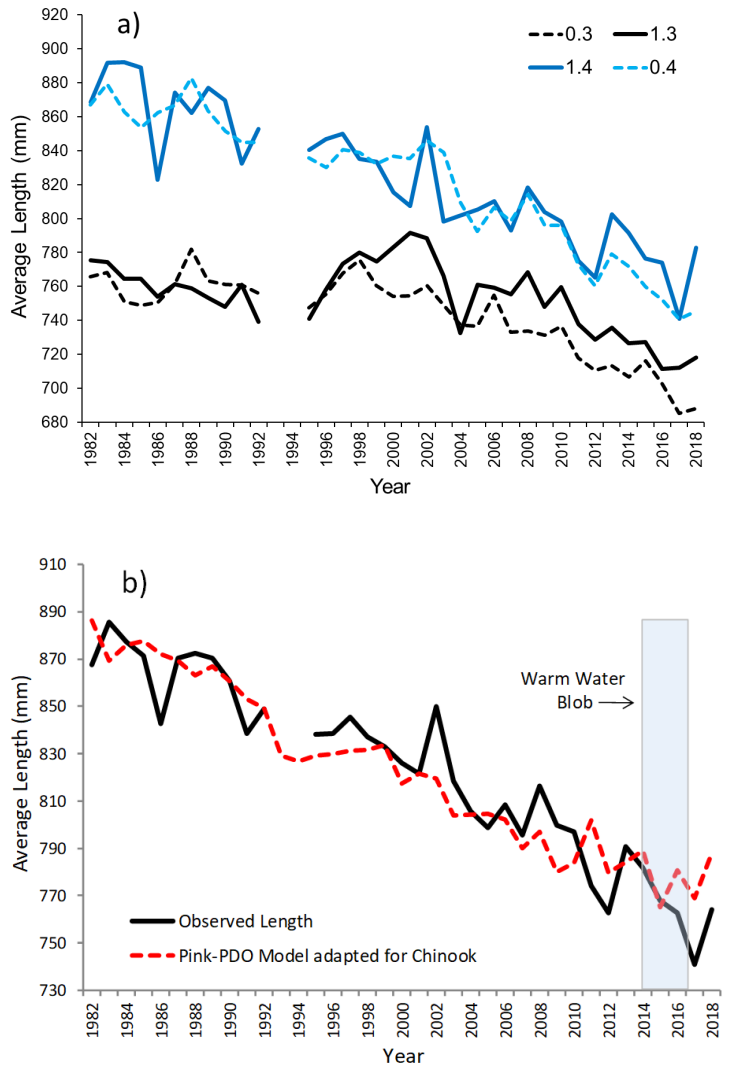


Fig. S1.1. (a) Trend in average length-at-age of Chinook salmon caught in the Southeast Alaska commercial troll fishery during July, 1982-2018, indicating that the downward trend in size-at-age is similar for subyearling (age-0.3, age-0.4) and yearling Chinook salmon (age-1.3, age-1.4). (b) Average observed length-at-age of Southeast Alaska Chinook salmon spending four winters at sea (mean for ages 0.4 and 1.4) and the predicted length of these Chinook salmon based on the pink salmon/PDO multiple regression model developed for Southeast Alaska coho salmon (Shaul and Geiger 2016) and adapted for Chinook salmon ($p < 0.001$, adjusted $R^2 = 0.75$ after accounting for autocorrelation). Pink salmon biomass in the model averaged 2-5 years before the Chinook salmon return and the April-March PDO index was averaged 0-5 years before the return, corresponding to the period of expected influence on Chinook salmon in their third and fourth years at sea, based on the coho weight model. L. Shaul, unpublished analysis. Data source: Alaska Department of Fish and Game Oceanic database.

Table S1. Correlation of mean annual adult Chinook salmon length-at-age with the average abundance of pink salmon returning from the North Pacific Ocean one to four years earlier, and the correlation of Chinook salmon mean age-at-maturation with the average abundance of pink salmon one to four years after the brood year of Chinook salmon. Values adjusted for autocorrelation in the linear regression model (Durbin-Watson test), if present, using the Cochran-Orcutt transformation. Bold text shown when $p < 0.05$. See Section 3.4.4 of main text. Data source for Chinook salmon: Lewis et al. 2015.

Region	Population	n	Correlation (r)	p-value
Age 1.4 Chinook salmon length, 1983-2012				
Bering Sea	Yukon R	27	-0.51	0.007
	Kanektok R	28	-0.59	<0.001
	Goodnews R	25	-0.41	0.036
	Kuskokwim R	22	-0.72	<0.001
	Kogrukluk R	30	-0.62	<0.001
	Nushagak R	28	-0.41	0.022
Central Alaska	Copper R	29	-0.01	0.970
	Deshka R	18	-0.53	0.020
	Kenai R	30	-0.21	0.27
Southeast Alaska	Unuk R	28	-0.70	<0.001
Age 1.3 Chinook salmon length, 1983-2012				
Bering Sea	Yukon R	27	-0.18	0.38
	Kanektok R	28	-0.12	0.55
	Goodnews R	24	-0.03	0.89
	Kuskokwim R	22	-0.49	0.021
	Kogrukluk R	30	-0.07	0.72
	Nushagak R	26	-0.76	<0.001
Central Alaska	Copper R	29	-0.45	0.014
	Deshka R	18	-0.37	0.13
	Kenai R	29	0.23	0.23
Southeast Alaska	Unuk R	28	-0.54	0.003
Average age of mature Chinook salmon, brood years 1980-2005				
Bering Sea	Kuskokwim R	26	0.01	0.98
	Nushagak R	26	-0.53	0.005
Central Alaska	Copper R	26	-0.90	<0.001
	Deshka R	23	-0.70	<0.001
Southeast Alaska	Unuk R	26	-0.21	0.290

Chinook salmon harvest trends in the Japanese high seas salmon fishery

We analyzed annual catch of Chinook salmon in the Japanese high seas salmon fishery in relation to pink salmon catch during 1955 to 1981. The high seas fishery involved gillnets (mostly 130 mm mesh) fished from motherships in the western/central Bering Sea and NPO, and gillnets (mostly 115 mm mesh) and longlines fished from offshore land-based vessels in the western/central NPO (Major et al. 1978). Approximately 69% of the catch was from the mothership fishery (mostly in the Bering Sea), where 73% and 25% of all Chinook salmon were ocean age-2 and age-3, respectively. Few ocean age-1 and relatively large age-4 and age-5 Chinook salmon were captured in the gear, which targeted smaller salmon species. Most Chinook salmon were immature fish. Scale pattern analysis revealed that Chinook salmon captured in the Bering Sea were predominantly from western Alaska (especially the Yukon R), followed by central Alaska, Asia, and Southeast Alaska/British Columbia (Rogers et al. 1984). Chinook salmon captured in the NPO were predominantly from central Alaska, followed by western Alaska, Asia, and Southeast Alaska/British Columbia.

We found a biennial pattern of Chinook salmon catch during 1955-1981 (Fig. S1.2a). Annual catches averaged 39% lower in odd years ($254,000 \pm 40,000$ fish [SE]) compared with even years ($417,000 \pm 60,000$ fish; t-test, $n = 27$, $p = 0.03$). Chinook salmon catch was negatively correlated with pink salmon catch (Fig. S1.2b; linear regression: $r = -0.63$, $p < 0.001$). We suspect the biennial pattern was revealed because the sampling gear targeted a single age group, i.e., ocean age-2 Chinook salmon: age-specific catch data may have shown a stronger biennial pattern. Also, while high numbers of pink salmon in a gillnet might cause some Chinook salmon to avoid capture in odd years, we note that catches of sockeye salmon tended to be higher in odd years, not lower. Thus, the evidence indicates fewer Chinook salmon were available to be captured in odd years in the western/central Bering Sea and North Pacific Ocean, and this pattern was likely related to competition with pink salmon.

We note that the unusually large Chinook salmon catch in 1969 (640,000 fish, Fig. S1.2a) was associated with the smallest fish weight in the series (2.4 kg), or 31% below the annual mean weight. We suspect that this large catch resulted from an unusual number of ocean age-1 Chinook salmon in addition to the typically dominant ocean age-2 salmon.

Our analysis spans 27 of the 40 years in which the Japanese high seas fishery was operational. We excluded values from 1952-1954 because the fishery was just beginning and small. We also excluded data from 1982 to 1991 because most harvests had shifted from the mothership fishery in the Bering Sea to the land-based fishery in the NPO in response to international agreements (Rogers et al. 1984), harvest levels were declining, and the magnitude of the biennial pattern of both pink and Chinook salmon was less (Fig. S1.2a).

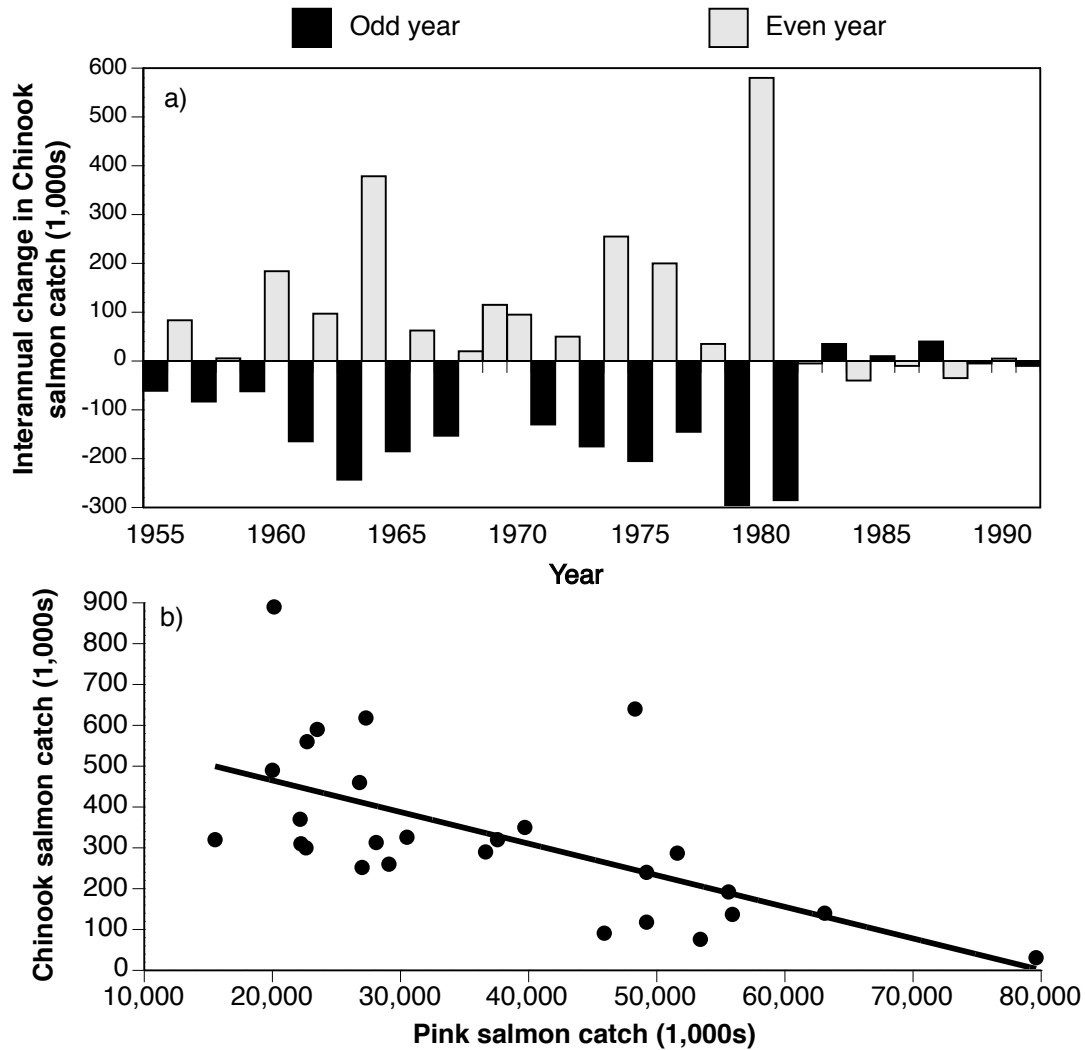


Fig. S1.2. Interannual change in Chinook salmon catch during 1955 to 1991 (a), and the linear regression relationship between Chinook salmon catch and pink salmon catch in the Japanese high seas fishery during 1955 to 1981 (b). Interannual change in catch (C) in year $i = C_i - \text{avg.}(C_{i-1}, C_{i+1})$. Data source: NPAFC (2022a).

Juvenile Chinook salmon growth in the Salish Sea

Growth of subyearling Chinook salmon was examined in the Salish Sea to test whether the observed biennial pattern of survival at sea was related to early marine growth in addition to biennial lengths of age-2 and age-3 Chinook salmon returning to the Salish Sea (Ruggerone and Goetz 2004). Scales from up to 50 age-0.3 salmon per year (avg. 44 fish per year) were measured from adults returning to Skagit Bay and Skagit River during 1961-2000. The scales were measured by N. Davis, University of Washington, using equipment and methods previously described (Davis et al. 1990, Ruggerone et al. 2005). The growth analysis used measurements of cumulative growth from circuli 11 to circuli 34, corresponding to residence in the Salish Sea. Early marine scale measurements of Skagit River Chinook salmon were 7% less wide, on average, during even years when juvenile pink salmon were abundant than in odd years when few juveniles were present, 1961-2000 (t-test, $p < 0.01$, $df = 35$). Mean scale growth in 15 of 19 even-years was lower than growth in both adjacent odd years (Fig. 11b in main text).

Steelhead survival

We examined marine survival estimates for Thompson and Chilcotin river steelhead (Fraser River watershed, British Columbia) and productivity estimates for Keogh River steelhead (Vancouver Island, British Columbia) in relation to pink salmon biomass. Survival indices of Thompson and Chilcotin river steelhead were estimated as adult recruit-per-spawner anomalies based on numbers of spawning steelhead and pre-harvest adult recruits provided by R. Bison (Province of British Columbia, Fish & Wildlife Branch). Recruitment values include harvests in the terminal fishery in addition to bycatch estimates in salmon fisheries. Our analysis followed that by J. Korman and R. Bison, who conducted an unpublished Recovery Potential Assessment for Thompson and Chilcotin river steelhead in 2018. Recruits-per-spawner anomalies are the residual \log_e Recruits per Spawner from a fitted stationary Ricker recruitment curve, brood years 1978-2012 (Thompson River) or 1972-2011 (Chilcotin River), thereby removing spawning density effects on the recruitment rate. Smolt to adult survival of Keogh River steelhead, 1977-2018, was available from the Province of British Columbia, Fish & Wildlife Branch (2021). We regressed the steelhead survival indices on the average of NPO pink salmon biomass corresponding to the two or three years of overlap (Fig. 12 in main text).

Both Thompson River and Keogh River steelhead metrics were negatively related to pink salmon biomass. Productivity of Chilcotin River steelhead, 1972-2011, also exhibited a strong negative correlation with pink salmon abundance, but autocorrelation in the residuals was high. See the main text.

Predation by local populations of seals on adult and post-smolt steelhead is also considered a key factor in the decline of these steelhead populations (COSEWIC 2020, Wilson et al. 2021). We found that seal and NPO pink salmon abundances are highly correlated, so it is not possible to quantify their relative influence on the decline of steelhead.

However, in support of the pink salmon hypothesis described in the main text, Friedland et al. (2014) reported that smolt-to-adult survival of Keogh River steelhead (1977-1999) was correlated with their scale growth during the first year at sea, especially during summer and fall. They hypothesized that slower growth led to longer vulnerability to predators and therefore lower survival. Given the rapid offshore movement of young steelhead (Myers 2018), the summer/fall period corresponds with increasing overlap with abundant pink salmon in the north and less overlap with local seal populations. Steelhead survival was weakly negatively correlated with sea surface temperature. Friedland et al. (2014) did not test for the effect of pink salmon, but the declining growth of steelhead scales over time was opposite in sign from the 58% increase in pink salmon biomass from 1977 to 1999 (e.g., see Fig. 1 of main text).

Text S2a – Seabirds 1

The omnivorous seabirds considered here include fork-tailed storm-petrels (*Hydrobates furcata*), black-legged kittiwakes (*Rissa tridactyla*), red-legged kittiwakes (*R. brevirostris*), glaucous-winged gulls (*Larus glaucescens*), ancient murrelets (*Synthliboramphus antiquus*), thick-billed murres (*Uria lomvia*), horned puffins (*Fratercula corniculata*), and tufted puffins (*F. cirrhata*). As a group they are widely distributed in the Subarctic North Pacific Ocean, with all species nesting on offshore islands and several nesting on or near the mainland in the Bering Sea (ADEC 2020). The exception is the red-legged kittiwake, which nests in large numbers at only five locations in the Bering Sea—St. Paul and St. George islands in the Pribilof Islands, Bogoslof and Buldir islands in the Aleutian Islands, and in the Commander Islands.

Diets of omnivores include, but are not limited to, walleye pollock (*Gadus chalcogrammus*), sand lance (*Ammodytes* spp.), Atka mackerel (*Pleurogrammus monopterygius*) and other greenlings (Hexagrammidae), myctophids, particularly northern lampfish (*Stenobrachius leucopsarus*), northern smoothtongue (*Leuroglossus schmidtii*), and gonatid squids. Planktonic prey includes primarily euphausiids (*Thysanoessa* spp.) and occasionally large calanoid copepods (*Neocalanus* spp.) (e.g., Hunt et al. 1981, Springer et al. 1986, 1996a, Higgins et al. 2022, A. Springer unpubl. data).

The planktivores include least auklets (*A. pusilla*), crested auklets (*A. cristatella*), whiskered auklets (*A. pygmaea*), and parakeet auklets (*A. psittacula*). Large calanoid copepods (*Neocalanus cristatus*, *N. plumchrus/flemingeri*, *Calanus marshallae/glacialis*), and euphausiids (*Thysanoessa* spp.) are primary prey of least, crested, and whiskered auklets, although hyperiid amphipods, pteropods, and decapods can at times also be important e.g., Bedard 1969, Hunt 1981, Springer and Roseneau 1985, Higgins et al. 2022). Parakeet auklets typically consume fewer copepods and euphausiids and more of the other taxa, and notably significant amounts of gelatinous zooplankton (Harrison 1990). Nesting colonies of these species occur at island locations in close proximity to abundant stocks of zooplankton, including particularly *Neocalanus* spp., *Calanus* spp., and euphausiids (*Thysanoessa* spp.) In the Bering Sea, colonies are located primarily in the Aleutian and Pribilof islands that lie adjacent to the deep basin and the source of *Neocalanus*; and St. Lawrence Island and the Diomed Islands in the northern Bering Strait region that receives a vast advected biomass of *Neocalanus* and other zooplankton entrained in the flow of the Anadyr Current (Coachman et al. 1975, Springer and Roseneau 1985, Springer et al. 1989, 1996b).

Text S2b – Seabirds 2

St. George Island, Pribilof Islands, Bering Sea

Thick-billed murres (*Uria lomvia*) in the Pribilof and Aleutian islands, were found to exhibit few differences in elements of their breeding parameters between even and odd years, and none were correlated with pink salmon abundance (Springer and van Vliet 2014). Hatching phenology averaged slightly earlier in even years at Buldir I. (Aleutian Is.) and St. George I. (Pribilof Is.), but slightly later at St. Paul I. (Pribilof (Is.)), and fledging success was slightly lower in even years at Buldir I. (t-test, all $p \leq 0.10$). Murres are able to buffer effects of variability in prey availability by behavioral adaptations much better than most other species of seabirds (Burger and Piatt 1990), so little variation was not surprising.

Yet, corticosterone (CORT) concentration, an indicator of physiological stress, in plasma of thick-billed murres at St. George I. was typically lower in even years than in odd years—only in 2004 was the mean concentration higher than in the two adjacent odd years, which were very low compared to all other odd years (Fig. S2.1). Overall, the mean CORT concentration in even years was somewhat lower than in odd years (3.5 ± 0.55 v 5.2 ± 0.92 ng ml⁻¹, t-test, $p = 0.15$).

CORT was correlated with the abundance of eastern Kamchatka pink salmon across all years (linear regression: $R^2 = 0.22$, $p = 0.12$), and it was very highly correlated when four outlying years (2004, 2008, 2010, and 2013) were excluded from the calculation (Fig. S2.1). Three of those years (2004, 2008, 2010) were even years of very low pink salmon abundance, and one (2013) was an odd year of anomalously low pink salmon abundance for an odd year. Also, only one year (2004) was an environmentally warm year, while three (2008, 2010, 2013) were cold years (Kokubun et al. 2018). Among the other years in the series, only two (2009 and 2011) were cold, while the rest (2003-2005, 2014-2017) were warm.

Stress in thick-billed murres at St. George I. tends to be elevated in cold years (Kokubun et al. 2018). For example, CORT concentrations averaged 6.0 ± 0.84 ng ml⁻¹ in the five cold years, but only 3.9 ± 0.69 ng ml⁻¹ in the seven warm years (t-test, $p = 0.086$). This might explain the high values in cold years 2008, 2010, and 2013 despite low abundances of pink salmon, and the similarly high values in cold years 2009 and 2011, regardless of the abundance of pink salmon. CORT concentration in the cold years varied by a factor of 2.1 (4.1-8.8 ng ml⁻¹), however in warm years it varied by a factor of 3.6 (range 1.9-6.9 ng ml⁻¹), suggesting that something other than water temperature might have been driving the variability. We hypothesize that it was pink salmon.

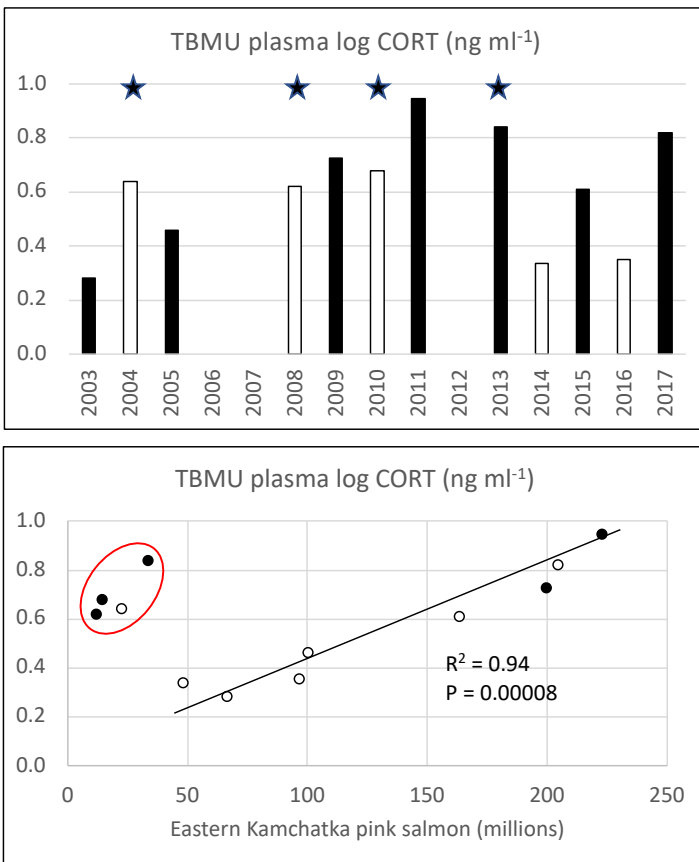


Fig. S2.1. a) Plasma corticosterone (CORT) concentrations in thick-billed murres (*Uria lomvia*) at St. George Island, and b) relationship of CORT to eastern Kamchatka pink salmon. The first four years in the linear regression (years with stars above them in (a), red circle in (b)) were not included. Panel (b): open circles = warm years, closed circles = cold years. Murre data are from Kokubun et al. (2018) and Will et al. (2020); pink salmon data are from Ruggerone and Irvine (2018) and G. Ruggerone (unpubl. data).

Gulf of Alaska (GOA)

Black-legged kittiwake (Rissa tridactyla)

The productivity of black-legged kittiwakes has been monitored at Chowiet Island (Semidi Islands, northwestern GOA) in 25 years between 1979 and 2021 (e.g., Bode et al. 2021). Beginning in 2004, data were collected over 16 nearly-consecutive years (with only two 1-y gaps), allowing robust comparisons of productivity to be made in a series of alternating even and odd years. Between 2004 and 2021, productivity exhibited a pronounced biennial pattern that was negatively correlated with Prince William Sound (PWS) pink salmon abundance (Fig. S2.2): the at-sea distribution of PWS pink salmon extends west in the Gulf of Alaska well beyond the Semidi Islands (Takagi et al 1981). The correlation was weak when all years were included in the calculation (linear regression: $R^2 = 0.13$, $p = 0.18$), but very strong when four seemingly

anomalous years were excluded. Those years were characterized by little or no production, although they were not the only such years in the overall record.

Kittiwake productivity at Chowiet I. can be influenced by weather and prey availability unrelated to pink salmon. For example, a major storm in 2009 caused many nest failures, and the failure in 2015 was associated with the Pacific Marine Heat Wave that broadly disrupted patterns of energy flow throughout most of the GOA (Arimitsu et al. 2021; B. Drummond, US Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge *in litt.*). Elsewhere in the northwestern GOA, avian predators at Kodiak Island may be very influential to nesting success of black-legged kittiwakes (Kildaw et al. 2005) and are thought to be potentially important in the Barren Islands (A. Kendall, US Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge *in litt.*). They are a major factor in PWS, as discussed in the main text. Differential direct and indirect environmental effects, and predation, between years could explain the apparent anomalies between kittiwake productivity at Chowiet I. and pink salmon abundance.

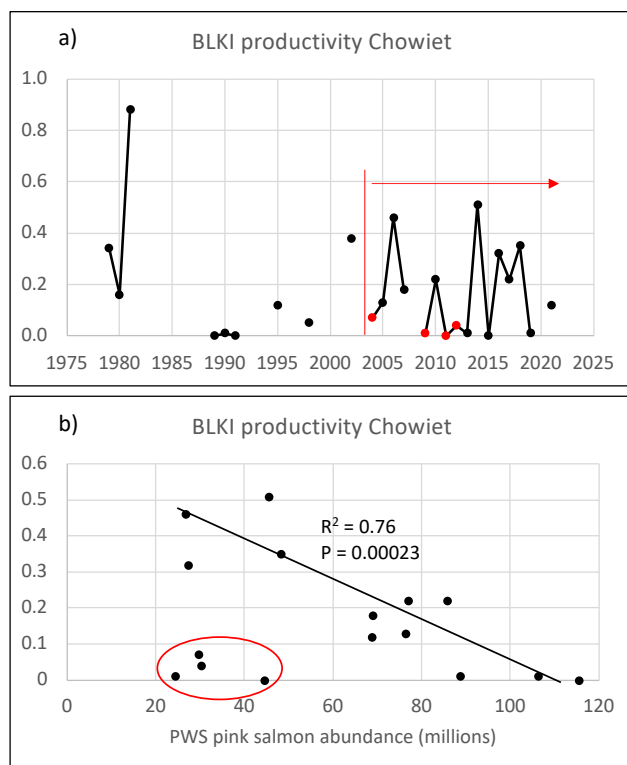


Fig. S2.2. a) Productivity of black-legged kittiwakes (*Rissa tridactyla*, BLKI) at Chowiet Island (western Gulf of Alaska), and b) relationship to Prince William Sound pink salmon abundance. Years in red (a) and in red circle (b) are considered to be outliers from the relationship between productivity and pink salmon in 2004-2021. Productivity estimated as number of nests with chicks fledged/total nest starts. Kittiwake data are from Bode et al. 2021; pink salmon data are from Ruggerone and Irvine (2018), G. Ruggerone (unpubl. data).

Tufted puffin (Fratercula cirrhata)

Tufted puffin nesting biology also was monitored at Chowiet I. in all but two years in 2005–2021 (Bode et al. 2021). Phenology (mean hatch date of eggs) varied little between even and odd years in 2006–2013 (Fig. S2.3). However, in 2013–2019 phenology exhibited a pronounced biennial pattern, with hatch dates about 1–2 weeks earlier in even years than in odd years. The change corresponded with the beginning of a biennial pattern of PWS pink salmon abundance after 2012 (Fig. S2.3). There was no correlation between phenology and pink salmon abundance in 2005–2012 (Pearson correlation: $p = 0.85$), but there was a very strong correlation between the two in 2013–2021 (Fig. S2.3). This relationship is the same as that between tufted puffins at Buldir I. (western Aleutian Islands) and eastern Kamchatka pink salmon abundance as described in the main text.

Tufted puffins also were monitored at Middleton Island (north-central GOA, Shoji et al. 2023) in 2016–2019, and a similar index of nesting phenology (date when the first chick was observed) exhibited a biennial pattern across the four years of observations—early in even years and late in odd years (Fig. S2.4). Moreover, four indices of nesting success also exhibited biennial patterns (Fig. S2.4). Phenology at Middleton I. was correlated with PWS pink salmon abundance (linear regression: $R^2 = 0.82$, $p = 0.092$), as was the number of eggs they laid ($R^2 = -0.76$, $p = 0.13$). The other three indices of productivity were not correlated with PWS pink salmon abundance (all $p \geq 0.30$) despite the exaggerated biennial patterns.

The apparent relationships between pink salmon and tufted puffins in the western Aleutian Islands (Buldir I.), the northwest GOA (Chowiet I.), and the northcentral GOA (Middleton I.) span a broad swath of the subarctic North Pacific Ocean. They further highlight how pink salmon of different stocks appear to similarly affect other species, in this case tufted puffins.

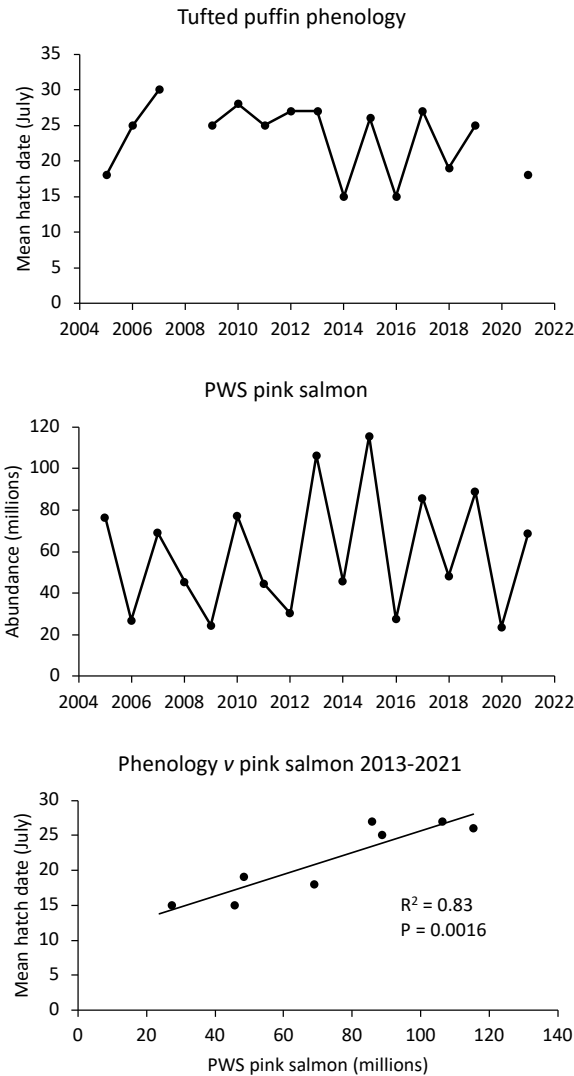


Fig. S2.3. Tufted puffin (*Fratercula cirrhata*) phenology (mean hatch date) at Chowiet Island, Prince William Sound pink salmon abundance, and the relationship between the two in 2013-2021 (no data in 2020). Tufted puffin data from Bode et al. (2021); pink salmon data from Ruggerone and Irvine (2018) and G. Ruggerone (unpubl. data).

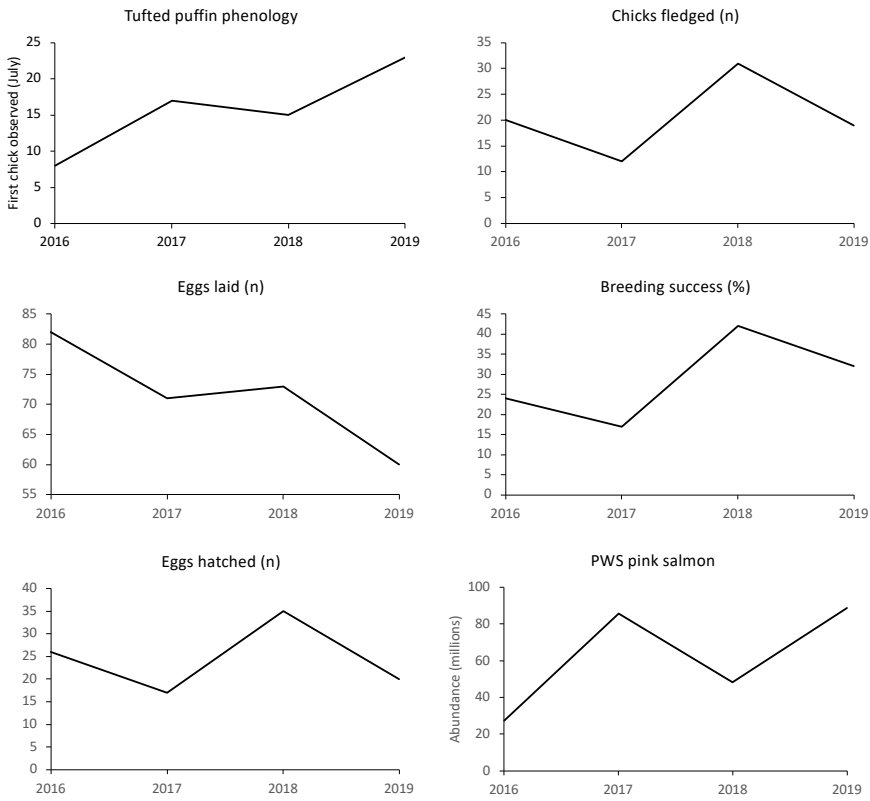


Fig. S2.4. Nesting parameters of tufted puffins (*Fratercula cirrhata*) at Middleton Island in the northcentral Gulf of Alaska. Data from Shoji et al. (2023).

Text S3 Pink Salmon Impacts Model

Strong biennial variability in pink salmon abundance (odd-calendar-year stocks are typically much more abundant than even-year stocks) and resulting differential effects on other species have been observed for as long as ~70 years despite multiple climatological regime shifts. Based on those patterns, we developed a conceptual model (see Fig. 16 in main text) that synthesizes our hypotheses about how pink salmon in northern regions of the NPO affect other species, as well as food webs and ecosystem function, based on evidence in Section 3 of the manuscript. This conceptual model expands upon the Trophic Triangle conceptual model presented by Aydin (2000) and Shaul & Geiger (2016), who emphasized the importance of predation by pink salmon on *B. anonychus*. The following points highlight key dynamics implied by what we refer to as the Pink Salmon Impacts Model. Please see Section 3 of the main text for additional supporting evidence.

- 1) Warming in the north increases pink salmon abundance: Pink salmon abundance increases in relation to the general heating of the NPO (Fig. 1 of main text, Mueter et al. 2002), possibly in response to earlier spring bloom timing (Malick et al. 2015) and their ability to efficiently utilize prey, which initially increased in northern regions after the 1977 ocean regime shift (e.g., Brodeur et al. 1996, Francis et al. 1998, Mackas et al. 2007, Kimmel & Duffy-Anderson 2020). Warming benefits odd- more than even-year adult pink salmon, but both lines have increased over time (Sections 2 and 3.4.6).
- 2) Biennial variability in pink salmon predation drives biennial fluctuations of squid abundance: *B. anonychus* has a two-year life cycle and evidence suggests predation by maturing pink salmon on maturing squid leads to strong biennial patterns of adult squid abundance, their progeny, and subsequent generations (Table 1, Section 3.3 of main text). *B. anonychus* primarily consumes copepods that are also prey for pink salmon (Uchikawa et al. 2004). Relatively abundant juvenile squid in odd years and maturing squid in even years may compete with juvenile and maturing pink salmon, contributing to biennial variability in pink salmon abundance (Aydin 2000, Uchikawa et al. 2004), but subsequent analyses indicated predation by pink salmon on squid has a greater effect than competition between them (Shaul & Geiger 2016). Squid abundance data are not available but the declining size of Chinook and coho salmon, which depend on squid, indicates predation by increasing abundances of pink salmon has contributed to declining abundances of squid (Jorgensen 2011).
- 3) Pink salmon can initiate pelagic trophic cascades through predation on large herbivorous copepods, lowering their abundance which leads to greater standing stocks of phytoplankton (Section 3.1). Batten et al. (2018), Shiomoto et al (1997), and Sugimoto & Tadokoro (1997) documented strong negative correlations between the abundance of pink salmon and the abundance of copepods in the Bering Sea and central NPO, and positive relationships with indices of phytoplankton abundance. Kobari et al. (2003) documented biennial patterns in the growth of three species of *Neocalanus*, with growth higher in odd years of lower copepod abundance. They also found a positive correlation between body

size of *N. cristatus* and chlorophyll-a concentration. *Neocalanus* spp. are principal conduits of energy transfer from phytoplankton to higher trophic levels.

- 4) Abundant odd-year pink salmon reduce prey availability for other salmon species and seabirds: In odd years, predation by abundant maturing pink salmon reduces the density of zooplankton and squid, leading to reduced feeding, growth, survival, and abundance of Pacific salmon; and lower body condition of some seabirds (Table 1, Supplement 2). Growth of older salmon (e.g., ocean age-1 coho salmon and ocean age-2 and older Chinook and sockeye salmon) are especially affected by fewer squid, a high calorie prey needed to sustain growth of larger/older salmon in a warming ocean (Section 4.2). For example, smaller body size and lower productivity of Fraser River sockeye salmon in odd years (Ruggerone & Connors 2015) may be related to their homeward migration through the Subarctic Current region where abundance of *B. anonychus*, a main prey item, is reduced in odd years (Aydin 2000). Evidence indicates pink salmon are more successful at utilizing prey compared with other salmon when their densities are high (Section 3).
- 5) Forage fishes exhibit biennial patterns in response to biennial pink salmon abundance (not shown in Fig. 16). Biennial patterns and/or negative correlations with pink salmon abundances appear in the growth of herring and Atka mackerel, and in the abundance of herring, sand lance, and Pacific Ocean perch in relation to pink salmon predation on common prey resources (see Table 1 and Section 3.2). Fewer forage fishes were consumed by Chinook, sockeye, and pink salmon in the Bering Sea in odd than even years. Forage fishes also are highly important to many seabirds (Text S2).
- 6) Depleted populations of Pacific salmon in southern regions experience less favorable foraging conditions as they migrate north and interact with abundant wild and hatchery pink salmon: Our conceptual model does not specifically address early marine life of salmon in southern regions, such as in the Pacific Northwest or Japan, where climate warming generally leads to less favorable conditions for salmonids during early marine life (e.g., Hare et al. 1999, Mueter et al. 2002, Mackas et al. 2007, Bi et al. 2011, Keister et al. 2011, Malick et al. 2017a). However, many southern populations of each species migrate north into the Gulf of Alaska and some to the Bering Sea and beyond, including Chinook salmon (Larson et al. 2013) that have experienced substantial declines in size, survival, and abundance (Welch et al. 2021). We hypothesize that these north-migrating salmonids from the Pacific Northwest and Japan have low survival due to less favorable conditions during early marine life, and reduced foraging opportunities after the first winter at sea, especially for energy-rich squid and small fishes needed to sustain larger and older salmon. Also, northward-migrating salmonids encounter not only highly abundant wild pink salmon, but also record-high levels of hatchery pink and chum salmon that compete for common-pool prey resources (Ruggerone & Irvine 2018). See Section 3.4.
- 7) Southern Resident Killer Whales (SRKW) and humpback whales exhibit biennial patterns in demographic attributes: SRKW experience reduced body condition in odd years (L pod; Stewart et al. 2021), which may lead to fewer successful births and greater mortality in the

following even year (Ruggerone et al. 2019). Humpback whales experience lower birth rates in odd years. Pink salmon, which are not consumed by SRKW, may interfere with foraging of SRKW, and may reduce prey available to humpback whales. See sections 3.6 and 3.7 of main text.

- 8) Intensity of species interactions and the magnitude and regularity of biennial patterns vary across time and ecosystems: For example, higher abundance of zooplankton in the western NPO than central and eastern regions may reduce competition for prey (Batten et al. 2018, Naydenko & Somov 2019), which may help explain the view of some Russian scientists that competition for prey among salmon is minimal (e.g., Shuntov et al. 2017, 2019). Additionally, several examples of interrupted and emergent biennial patterns suggest interactions between pink salmon, weather, climate and/or other drivers. The strength of competition in the shared resource space and the strength of physical drivers would not be expected to be equal across all species, locations, and years, thus interrupted and emerging biennial patterns should not necessarily be expected to share common time frames.

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