FEATURE ARTICLE: REVIEW

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

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ABSTRACT: In response to a climate regime shift in 1977 and general heating of the North Pacific Ocean, pink salmon *Oncorhynchus gorbuscha* abundance reached record highs during 2005–2021, comprising 70% of all Pacific salmon. Pink salmon are approximately 25 times more numerous in odd- than even-numbered calendar years in some major North Pacific ecosystems, a unique demographic pattern analogous to repeating whole ecosystem treatment–control experiments. We found compelling examples indicating that in odd years, predation by pink salmon can initiate pelagic trophic cascades by reducing herbivorous zooplankton abundance sufficiently that phytoplankton densities increase, with opposite patterns in even years. Widespread interspecific competition for common-pool prey resources can be dominated by pink salmon, as indicated by numerous biennial patterns in the diet, growth, survival, abundance, age-at-maturation, distribution, and/or phenology of ecologically, culturally, and economically important forage fishes, squid, Pacific salmon and steelhead trout *Oncorhynchus* spp., seabirds, humpback whales *Megaptera novaeangliae*, and endangered southern resident killer whales *Orcinus orca*. In aggregate, the evidence indicates that open-ocean marine carrying capacity in the northern North Pacific Ocean and Bering Sea can be mediated by top-down forcing by pink salmon and by ocean heating, and that large-scale hatchery production (~40% of the total adult and immature salmon biomass) likely has unintended consequences for wild salmon, including Chinook salmon *O. tshawytscha*, and many other marine species. Further investigation of the effects of pink salmon on other species will increase our knowledge of ecosystem function and the important role top-down forcing plays in the open ocean

Pink salmon returning to Prince William Sound, Alaska hatcheries have contributed to record-setting abundances in recent years and to impacts on other marine species.

*Photo: Preston and Teresa Cole,
https://taps-photography.pixels.com/*

1. INTRODUCTION

Some upper trophic level species play crucial roles in the natural histories of other species and the structure and function of ecosystems. Such interactions have been well documented in terrestrial (Carpenter et al. 1995, Painter et al. 2015), freshwater (Carpenter

et al. 1985, Naiman et al. 1988, Ellis et al. 2011, Beschta & Ripple 2019), and nearshore marine environments (e.g. Paine 1977, Estes et al. 1998, Christianen et al. 2023), primarily from treatment–control experiments. This has been poorly documented in the open ocean, where experiments are generally impractical because of the great spatial scales, challenging logistics, and expense. Although considerable progress has been made in identifying top-down effects in ocean ecosystems (e.g. Baum & Worm 2009), most inferences have been based on before–after comparisons of change following predator removals or additions. Examples include the slaughter of great whales in the 19th and 20th centuries in the North Pacific and Southern Oceans (Springer et al. 2003, 2006, Roman et al. 2014), the collapse of cod *Gadus morhua* stocks in the NW Atlantic (Frank et al. 2005), and the invasion of killer whales *Orcinus orca* into the eastern Canadian Arctic (Breed et al. 2017, Matthews et al. 2020).

Pink salmon *Oncorhynchus gorbuscha* in the North Pacific Ocean (NPO) exhibit a unique, exaggerated biennial alternation between high and low abundance that can be viewed as a simple, natural treatment–control 'experiment' (Ruggerone & Nielsen 2004), even though all variables cannot be controlled. Many pink salmon populations are predictably much more abundant in odd-numbered calendar years than in even-numbered years (Irvine et al. 2014), thus in this analogy, odd years are equivalent to treatment years and even years are equivalent to control years. The biennial cycles repeat over many decades (Fig. 1), creating reliable replication that can be used to identify effects of pink salmon on the ecosystem. A growing body of evidence suggests that biennial patterns in the biology of many marine species in the NPO can be linked directly and indirectly to pink salmon, and that pink salmon can initiate pelagic trophic cascades.

Our goal here is to synthesize information on those biennial patterns and evaluate evidence that they are caused by direct and indirect effects of pink salmon. Such evidence provides novel information about the influences of top-down predation on the structure and function of open ocean ecosystems, and has important biological and policy value for understanding the ocean's carrying capacity. If, for example, the forage demand of billions of additional salmon released from industrial-scale hatcheries pushes closer to the ocean's carrying capacity, this may have deleterious effects on wild salmon as well as non-salmon species, such as decreased survival rate, productivity, and body size (e.g. Cooney & Brodeur 1998, Perry et al. 1998). Governments and managers often assume hatchery and wild populations do not compete for prey (Holt et al. 2008), or with other species in pelagic food webs, yet the overall benefits and costs of hatchery production to ecological and societal well-being is a matter of considerable debate (e.g. Kaeriyama & Edpalina 2004, Harrison & Gould 2022).

We show that pink salmon can have major top-down impacts on species and food webs that include 5 major taxa — phytoplankton, zooplankton, fishes, marine birds, and marine mammals — over vast regions of the NPO, and through a transhemispheric teleconnection on terrestrial ecosystems in the southern hemisphere (Table 1). In aggregate, the weight of evidence leads to a robust conclusion: pink salmon can exert strong top-down effects on a common pool of prey resources that affect many other species and influence pelagic ecosystems of the NPO. These effects, in turn, may affect human subsistence and cultural, recreational, and economic values in both the northern and southern hemispheres. The examples of direct and indirect effects of pink salmon presented here are likely not the only ones that exist, and other researchers with multi-year data sets might seek additional biennial patterns waiting to be found, and explanations for them.

2. BACKGROUND

Pink salmon life history characteristics are uniquely suited for testing hypotheses about top-down interactions with other marine species. These fish are widely distributed throughout epipelagic waters of the NPO; e.g. those from eastern Kamchatka, Russia, migrate eastward to approximately 150° W (Radchenko et al. 2018), suggesting that they have the potential to interact with species across the Bering Sea (BS) and Gulf of Alaska (GOA), including North American salmon. Major populations spawn in Alaska, British Columbia (BC), Puget Sound (WA), the Russian Far East, and northern Japan (Takagi et al. 1981). Their overall abundance increased steadily after the mid-1970s, reaching unprecedented levels during 2005–2021, when annual abundance averaged 522 million adults, or nearly 70 % of all Pacific salmon (Fig. 1). Approximately 82 million adult pink salmon per year (16 % of total) originated from hatcheries during 2005–2015 (Ruggerone & Irvine 2018).

Pink salmon have benefited from climate change, beginning with a major climatological regime shift in 1977 (Mantua et al. 1997) and heating of the NPO, as indicated by a strong positive correlation between

Table 1. Evidence for interactions between pink salmon and plankton, forage fishes, squid, Pacific salmon, seabirds, and whales. Evidence includes biennial or cyclic patterns, and positive (+) and negative (−) correlations (Pearson's correlation or linear regression) when available. Biennial patterns without correlation analyses indicate negative effects of pink salmon on other species. For seabirds, biennial patterns with correlation analyses apply only to omnivores; biennial patterns in Births, Productivity, and Phenology indicate positive correlations with pink salmon. See Section 3 and Supplement 2 at www.int-res.com/articles/suppl/m719 p001_supp2.xlsx for details. SH: southern hemisphere; NH: northern hemisphere; NP: North Pacific; AI: Aleutian Islands; BS: Bering Sea; GOA: Gulf of Alaska; PWS: Prince William Sound; SOG: Strait of Georgia; AK: Alaska; BC: British Columbia; OR: Oregon; WA: Washington; WC: West Coast; R: river; I: island

| Species	Diet	Growth	Fecundity	Births	Productivity	Abundance	Age-at-maturation	Distribution	Phenology	Body condition	Ecosystem	Population location
Plankton												
Phytoplankton						Biennial, +					BS, AI, central NP	
Zooplankton		Biennial, +				Biennial, −					BS, AI, central NP	
Forage fishes and squid												
Herring		Biennial, −				—					PWS, Sitka Sound	PWS, Sitka Sound
Atka mackerel		Biennial, −									AI	AI
Sand lance						Biennial					Salish Sea	Salish Sea
Pacific Ocean perch						Biennial, −					GOA	GOA
Squid spp.						Biennial					BS, W NP	BS, W NP
Berryteuthis anonychus						Biennial, − and cyclic					BS, GOA	BS, GOA
Pacific salmon												
Sockeye	Biennial	Biennial, −	Assumed −		Biennial, −	Biennial, −	Biennial, +				NP, BS, Salish Sea	Kamchatka, AK BC, WA, PWS
Chum	Biennial, −	Biennial, −	−		Biennial, −	Biennial, −	Biennial, +	Biennial, −		−	NP, BS, Kuril I, Salish Sea	Japan, Russia, Norton Sound, Kuskokwim R, Yukon R, Bristol Bay, SE AK, BC, Salish Sea, WC
Coho	Biennial	Biennial, −	Biennial, −		Biennial, −	Biennial, −					W NP, GOA, Salish Sea	SE AK, Kuskokwim R, Russia, SOG
Chinook	Biennial	Biennial, −	−		Biennial, −	Biennial, −	−				NP, BS, Salish Sea	Kamchatka R, Yukon R, Kuskokwim R, Nushagak R, Columbia R, Central AK, SE AK, Salish Sea, AK, BC, WA, OR
Steelhead	−	−			−	Biennial, −					NP	Thompson R, Keogh R, Chilcotin R (BC), Columbia R
Pink	Biennial					Biennial and cyclic					NP, BS, Salish Sea, PWS	Russia, Japan, AK BC, WA
Seabirds												
NH Seabirds	Biennial		Biennial, −	Biennial, −	Biennial, −				Biennial, −	Biennial, −	BS, AI, GOA, PWS	Buldir I, Chowiet I, Pribilof Is, PWS
SH Seabirds						Long-term, −				Biennial, −	BS	Australia, Tasmania
Whales												
Humpback whale				Biennial	Biennial						SE AK	SE AK
Killer whale				Biennial						Biennial	Salish Sea	Salish Sea / WC
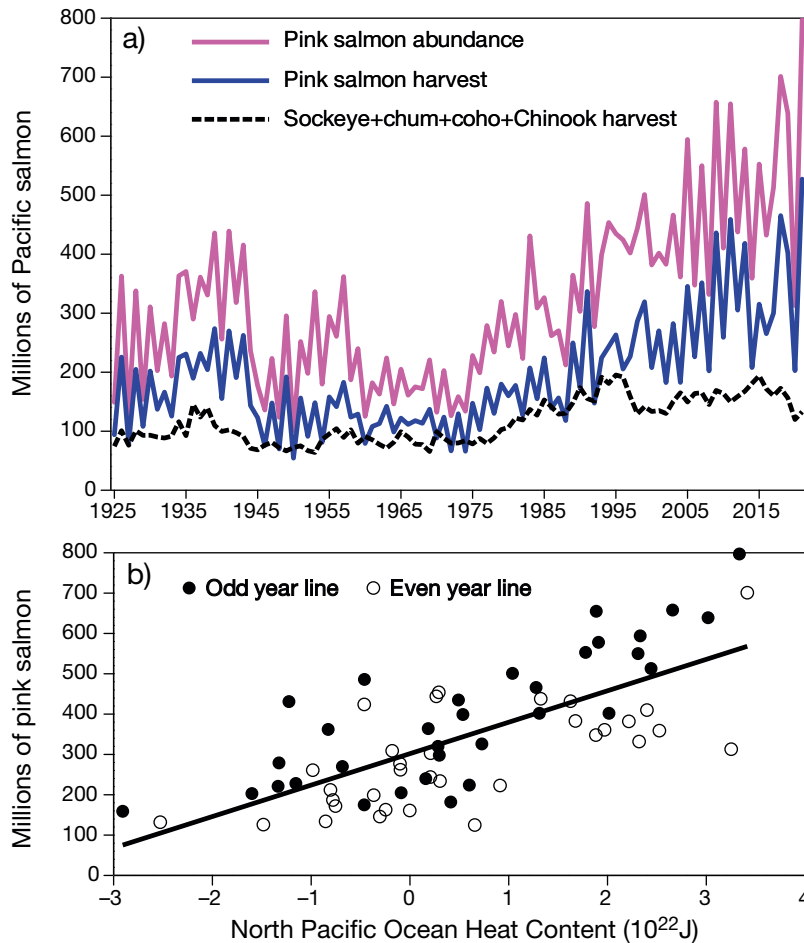
Fig. 1. (a) Annual abundance of adult pink salmon (catch plus spawners) returning from the North Pacific Ocean; commercial harvest of pink salmon; and the combined commercial harvest of sockeye, chum, coho, and Chinook salmon in Asia and North America, 1925–2021 (Ruggerone & Irvine 2018, Ruggerone et al. 2021, NPAFC 2022a). (b) Relationship between pink salmon abundance (odd and even years combined) and annual heat content for the North Pacific Ocean (0–700 m) during the year of juvenile pink salmon entry to the ocean, 1955–2021 (linear regression, df = 1, 65, p < 0.001, R^2 = 0.51; updated from Radchenko et al. 2007, NOAA 2022)

the Ocean Heat Index in the year they go to sea and adult abundance in the following year (Fig. 1b), and the use of ocean temperature to forecast adult returns (Radchenko et al. 2007, Krovnin et al. 2021, Bugaev et al. 2022). Pink salmon numbers are increasing in the Arctic (Dunmall et al. 2016, Farley et al. 2020), and they recently colonized the North Atlantic Ocean and Barents Sea following intentional stocking by Russia in the White Sea region (Sandlund et al. 2019, Diaz Pauli et al. 2023, Lennox et al. 2023).

Pink salmon have a fixed 2 yr anadromous life cycle in which they spawn in rivers during summer and fall, emerge as fry and emigrate to sea in spring, migrate over 5500 km, and then return to spawn and die after 1 winter at sea (Heard 1991). Odd- and even-year lines are separate, genetically isolated populations. Most notably, they have a unique, exaggerated biennial pattern of abundance in many regions of the NPO. For example, pink salmon sampled in the central BS were approximately 25 times more abundant in odd years than in even years during 1990–2010 (Davis 2003, Morita & Fukuwaka 2020). Potential mechanisms supporting the biennial fluctuations include negative interactions between odd- and even-year lines at sea and in fresh water (Heard 1991), and genetic adaptations of the odd-year line to warmer spawning temperatures (Beacham & Murray 1988).

Growth of pink salmon is relatively slow during the first 8 mo at sea but accelerates after winter, leading to prodigious consumption to fuel a rapid 5-fold increase in body weight by the time they spawn in summer to early fall (Heard 1991, Karpenko & Koval 2012). In the ocean, young pink salmon feed on various zooplankton species, primarily large calanoid copepods and euphausiids, and increasing amounts of squids and forage fishes as they grow (Brodeur 1990, Karpenko et al. 2007, Davis et al. 2009, Graham et al. 2021). Pink salmon <500 g consume zooplankton and small fishes; those >500 g consume zooplankton, fishes, and juvenile squid; and those >1000 g also consume adult squid (*Berryteuthis anonychus*) in spring and summer after overwintering at sea (Davis 2003, Aydin et al. 2005, Shaul & Geiger 2016). Their forage demand during 2005–2021 averaged approximately 4.35 × 10^6 Mt yr^{-1}, based on the methodology of Cooney & Brodeur (1998) and updated abundance values. About 90% of the forage demand occurs in oceanic rather than coastal habitats, especially during their second spring/summer at sea when they consume squid and small fishes and grow rapidly. A key question given such high consumption is whether the bottom-up processes supporting pink salmon are sufficient to also support other marine species.

Scientists have searched for biennial patterns in atmospheric and physical oceanographic variables

that might underpin the biennial patterns observed and summarized here, but none have been found. Physical variables that have been associated with interannual and decadal-scale changes in primary, secondary, and/or tertiary production — Northern Hemisphere Zonal Index, solar radiation flux, surface wind speed, sea surface temperature (SST), salinity, density, nutrient levels, integrated mean water column temperature, average winter sea ice extent in the BS, vertical stability index, North Pacific Index, North Pacific Gyre Oscillation, Pacific Decadal Oscillation, and Southern Oscillation Index — have displayed no systematic biennial variability (e.g. Polovina et al. 1995, Mantua et al. 1997, Shiomoto et al. 1997, Sugimoto & Tadokoro 1997, Kobari et al. 2003, Brown et al. 2011, Jorgensen 2011, Litzow et al. 2020a, Thoman et al. 2020, Belkin & Short 2023). Recently, Ohlberger et al. (2023, their Fig. 5g) presented a time series of average summer SST in the BS between 1962 and 2020 that revealed a weak biennial pattern in 1976–1998. Since then, summer SST has been highly irregular between years, unlike the highly regular biennial patterns in biological variables we summarize here.

3. THE EVIDENCE

3.1. Pelagic trophic cascades

Evidence of trophic cascades in open ocean ecosystems is uncommon, although here we document 5 compelling examples, linked to pink salmon, from the NPO and BS spanning multiple decades. The cascades flow downward from pink salmon to large copepods to diatoms: diets of pink salmon include large copepods, primarily *Neocalanus* spp., that consume diatoms in the BS (Davis et al. 2005, Karpenko et al. 2007, Campbell et al. 2016).

In the most recent example, Batten et al. (2018) used continuous plankton recorder data to develop indices of abundance of phytoplankton (primarily large diatoms) and zooplankton (primarily large calanoid copepods) in the BS and Aleutian Islands region during summer, 2000–2014. Three lines of evidence suggested that predation by maturing pink salmon during spring and summer altered the abundance of large copepods, which in turn altered the abundance of diatoms. First, copepods were less abundant and diatoms more abundant in odd years of higher pink salmon abundance (Fig. 2a–c). Second, diatom abundance was negatively correlated with copepod abundance, and copepod abundance

was negatively correlated with adult pink salmon abundance (Fig. 2d–f). Third, in 2013, when pink salmon abundance was exceptionally low for an odd year, copepod abundance rebounded to high levels that year and diatom abundance was low (Fig. 2a–c). Evidence for a trophic cascade was strong in both the southcentral BS and eastern Aleutian Islands region, although reduced or absent in the western Aleutian Islands. These findings illustrate the importance of variability in pink salmon abundance and its effects across the ecosystem, which in that study was greater than physical oceanographic variability, according to the authors.

Earlier studies also found evidence of direct effects of pink salmon on summer plankton standing stocks in the central subarctic NPO and the eastern BS. Sugimoto & Tadokoro (1997) reported negative correlations between zooplankton biomass anomalies and Asian pink salmon abundance, and between chlorophyll *a* (chl *a*) concentration (a proxy for phytoplankton biomass) and zooplankton, during 1954–1981. They suggested that top-down predation by pink salmon increased interannual variations in zooplankton and in turn phytoplankton, whereas bottom-up factors were more important at decadal or longer scales. Toge et al. (2011) also reported a positive correlation between chl *a* concentration in the central BS and regional pink salmon abundance during 2002–2008 while noting the apparent trophic cascade through zooplankton.

Pink salmon are usually, but not always, more abundant in odd than even years, and plankton communities reflect those shifts in abundance. Shiomoto et al. (1997) quantitatively sampled pink salmon in the BS, and macrozooplankton (mostly copepods) and chl *a* just south of the central Aleutian Islands during 1985–1994. Early in their research (1985–1988), few differences existed between even- and odd-year pink salmon numbers, macrozooplankton biomass, or chlorophyll concentrations. However, beginning in 1989, odd-year pink salmon abundance and chl *a* notably increased while odd-year macrozooplankton biomass declined. We found negative correlations between the estimates of Shiomoto et al. (1997) of maturing pink salmon abundance and macrozooplankton biomass (Pearson's correlation, p = 0.040), and between their macrozooplankton biomass and chl *a* levels (p = 0.086). The authors also reported that zooplankton biomass in the central NPO remained low throughout summer of odd years after maturing pink salmon had migrated into the BS, an observation that is consistent with relatively low summer/fall marine scale growth of Bristol Bay sockeye salmon *Oncorhynchus nerka* in odd years (Ruggerone et al. 2005).
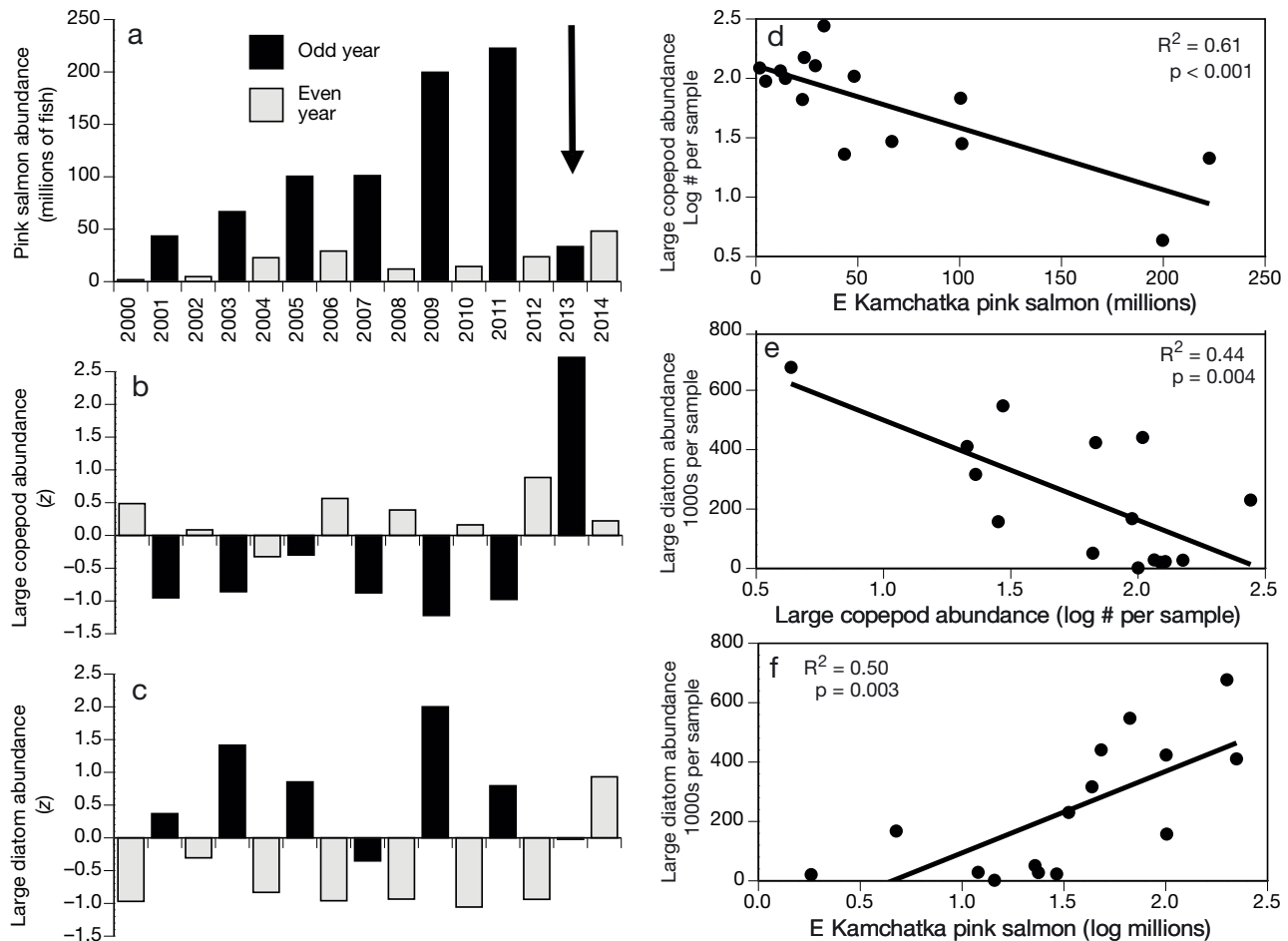
Fig. 2. Three lines of evidence supporting the pink salmon trophic cascade hypothesis in the southern Bering Sea and Aleutian Islands. (a) Biennial pattern of eastern Kamchatka pink salmon, the primary population in this region. (b) Normalized abundance of large copepods. (c) Normalized abundance of large diatoms. (d) Relationship between abundances of eastern Kamchatka pink salmon and large copepods. (e) Relationship between abundances of large copepods and diatoms. (f) Relationship between abundances of eastern Kamchatka pink salmon and large diatoms in 2000–2014. In 2013 (arrow in panel a), pink salmon abundance declined sharply, zooplankton abundance increased substantially, and diatom abundance declined. In 2014, diatom abundance was high for an even year, possibly in response to the marine heatwave that was occurring at the time (DiLorenzo & Mantua 2016). Redrawn from: Batten et al. (2018)

The trophic cascade described here requires tight coupling between phytoplankton and zooplankton, such that changes in the standing stock and grazing pressure by the herbivorous zooplankton have measurable effects on phytoplankton abundance. It then would be expected that in even years of relatively low pink salmon abundance, and thus higher copepod abundance, food limitation might have consequences for copepod growth and body size. A 20 yr study from 1979 to 1998 identified biennial patterns in the abundance of *Neocalanus cristatus*, *N. plumchrus*, and *N. flemingeri* in the central subarctic Pacific and attributed them to pink salmon predation (Kobari et al. 2003). Notably, they also documented biennial patterns in the growth of those copepods, with growth higher in odd years of lower copepod abundance. In addition, they found a

positive correlation between body size of *N. cristatus*, the largest of the 3 species, and chl *a* concentration.

3.2. Forage fishes

3.2.1. Pacific herring

As with many forage fishes, Pacific herring *Clupea pallasii* are widely distributed and highly important to marine ecosystems (Surma et al. 2018). Herring are also important to Indigenous people and subsistence fishermen (Thornton & Moss 2021), and they support commercial fisheries.

Sitka Sound, Alaska, has one of the largest herring populations in North America. We found that herring

growth (proportional increase in mean annual body weight) was lower in 5 adult herring age groups when emigrating from Sitka Sound in the spring of odd years and returning in the following even years compared with those emigrating in even years, 1996–2018 (Fig. 3a). The magnitude of year-to-year variation in herring growth was negatively correlated with that of adult pink salmon abundance (Prince William Sound [PWS], Southeast Alaska (SEAK), and BC stocks) for each herring age group, especially younger fish (Fig. 3b). Adult herring emigrate from Sitka Sound in spring after spawning and feed in offshore continental shelf waters, possibly from PWS to BC (D. Hay pers. comm.), where in odd years they may encounter fewer zooplankton prey during spring, summer, and fall as a result of
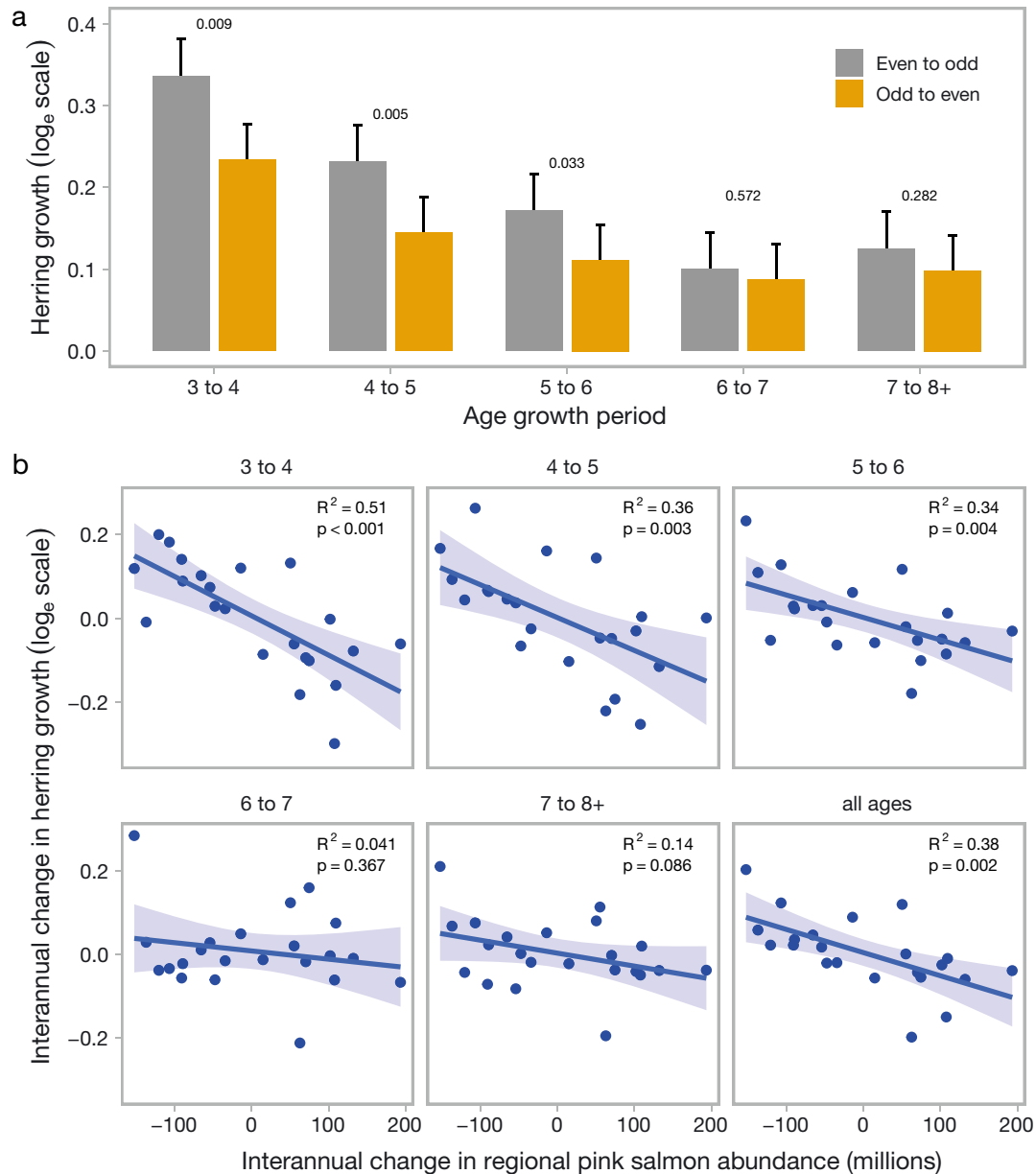

Fig. 3. (a) Biennial pattern in age-specific annual proportional increase in mean weight (growth index, ±95% CI) of adult herring returning to Sitka Sound, Alaska, from 1996 to 2018; and (b) relationships between the magnitude of year-to-year variation of age-specific mean growth of herring and the magnitude in year-to-year variation in abundance of pink salmon returning to North America, where interannual change (G) in year i = G_i − avg. (G_{i-1}, G_{i+1}). In panel (a), 'Even to odd' refers to proportional growth from even to odd years (e.g. $\log_e$[weight-at-age in year t+1/weight-at-age in year t]); t-test p-values are shown above each growth period in (a), and linear regression statistics are shown in panel (b). Herring weight-at-age measured in the commercial fishery prior to spawning. Data sources: S. Dressel unpubl. data, Hebert (2019), Ruggerone & Irvine (2018)

numerous maturing pink salmon. These relation-
ships were weaker during the previous 16 yr period
(not shown), possibly because several year classes
failed to produce many herring and because the
magnitude of variation in pink salmon abundance
was smaller.

In PWS, herring recruitment declined sharply after
the 'Exxon Valdez' oil spill in 1989, and the popula-
tion has yet to recover, leading to several studies of
factors inhibiting recovery. A statistical examination
of 19 hypotheses for the lack of recovery and subse-
quent analyses found competition with hatchery pink
salmon (up to 600 million released per year) had the
greatest support (Deriso et al. 2008, Pearson et al.
2012). This conclusion was based on the large reduc-
tion in herring spawning biomass associated with
hatchery releases, sympatry of pink salmon fry and
age-1 herring in nearshore habitats during late
spring and summer, diet overlap, and field studies
indicating reduced food intake by juvenile herring in
the presence of juvenile pink salmon. Other studies
have found equivocal support for this hypothesis, but
recommended further study of pink salmon effects
on the PWS food web (Cooney 1993,
Ward et al. 2017, 2018).

3.2.2. Sand lance

Sand lance *Ammodytes personatus*
recruitment and abundance in the Sal-
ish Sea were 13 times higher in odd
versus even years, corresponding with
the strong biennial pattern of pink
salmon (Baker et al. 2019). In this
region, maturing pink salmon are ap-
proximately 45 times more abundant
in odd years, leading to exceptionally
high abundances of juvenile pink
salmon in the following even year that
may reduce sand lance prey (Osgood
et al. 2016, Sisson & Baker 2017).

3.2.3. Atka mackerel

Atka mackerel *Pleurogrammus mon-
opterygius* are important prey of Pacific
salmon and other fishes, marine birds,
and marine mammals and the target of
a commercial fishery in the Aleutian
Islands (Davis 2003, Lowe et al. 2018).
Atka mackerel feed heavily on *Neo-*

calanus spp. and euphausiids (Yang 1999, 2003, Rand
et al. 2010), a diet that overlaps extensively with that
of pink salmon.

Matta et al. (2020) found a conspicuous biennial
pattern in the growth of Atka mackerel otoliths (an
index of annual body growth; Fig. 4): a Pearson's
negative correlation between otolith growth and the
abundance of eastern Kamchatka pink salmon (p =
0.005), and a positive correlation between otolith
growth and the abundance of large copepods (p =
0.023). The abundance of large copepods in the
region of their study was negatively related to pink
salmon abundance (p = 0.002).

3.2.4. Pacific Ocean perch

Pacific Ocean perch (POP) *Sebastes alutus* is a
long-lived, commercially important rockfish that
mainly occupies continental slope and shelf habitats
from California to Japan (Hulson et al. 2021). POP
are considered to be semi-demersal, but limited sam-
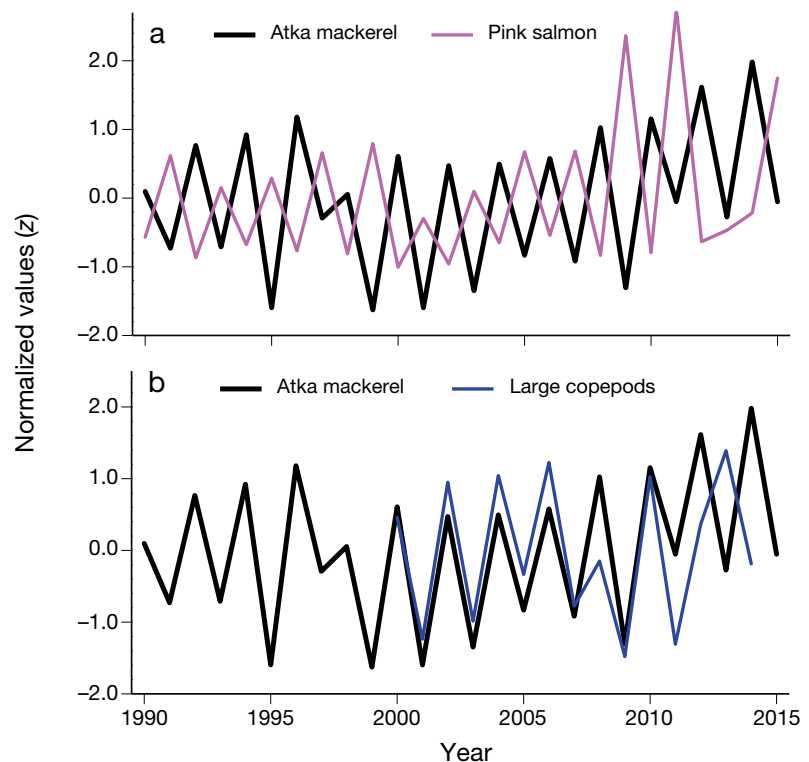pling at sea indicates larvae and juveniles inhabit

Fig. 4. Relationships between anomalies in otolith growth of Atka mackerel
and (a) the normalized abundance of eastern Kamchatka pink salmon (nega-
tive), and (b) the abundance of large copepods (positive) in the central Aleu-
tian Islands. Pink salmon data from Ruggerone & Irvine (2018); Atka mackerel
and large copepod data from Matta et al. (2020) and M. Matta and S. Batten,
with permission

epipelagic waters far from adult habitats (Kendall et al. 2007, Boldt & Rooper 2009). Juvenile POP primarily consume copepods.

We analyzed age-2 POP recruitment estimates from the GOA (Hulson et al. 2021) and found a pronounced biennial pattern from 1999 through 2019, corresponding to a period of relatively high POP abundance and high interannual variation in numbers of pink salmon returning to North America (Fig. 5). Age-2 POP recruits (typically <160 mm) averaged 45% fewer fish in odd (101 million fish) versus even years (183 million fish) during 1999–2019, suggesting a negative interaction with pink salmon during the growing season (Fig. 5), even though abundances of both species increased after 1977. Over the 43 yr period 1977–2019, approximately 50% of the interannual variability in age-2 POP abundance was explained by interannual variation in the abundance of pink salmon, which also consume copepods, and POP female spawning biomass 2 yr earlier (Fig. 5). Ortiz & Zador (2022) also reported that POP recruitment in the Aleutian Island region exhibited a biennial pattern; abundances of age-3 POP were often higher in odd years.

3.3. Squid

Subadult and adult squid are highly important prey of many fishes, birds, and marine mammals in the NPO (Aydin 2000). For example, large proportions of salmonid diets were squid (subadult and adult *Berryteuthis anonychus*, <150 mm) in the Subarctic Current region of the GOA during 1994–1998: e.g. pink (40–80% of prey weight), sockeye (>85%), coho *O. kisutch* (>95%), and Chinook salmon *O. tshawytscha* (100%), and steelhead *O. mykiss* (50–100%) (Kaeriyama et al. 2004). Bioenergetic modeling indicated a substantial increase in salmon growth when consuming high-energy *B. anonychus*, which is especially important to maintaining growth as temperature increases (Aydin 2000), particularly among larger salmon

(Beauchamp 2009). *B. anonychus* is the most abundant squid in the GOA and is distributed primarily south of 53° N and west from North America to about 160° W.

The primary effect of pink salmon on *B. anonychus* abundance appears to be via predation on subadults and adults, rather than competition with juveniles for prey (Shaul & Geiger 2016). In the northwestern GOA, the abundance of *B. anonychus* paralarvae
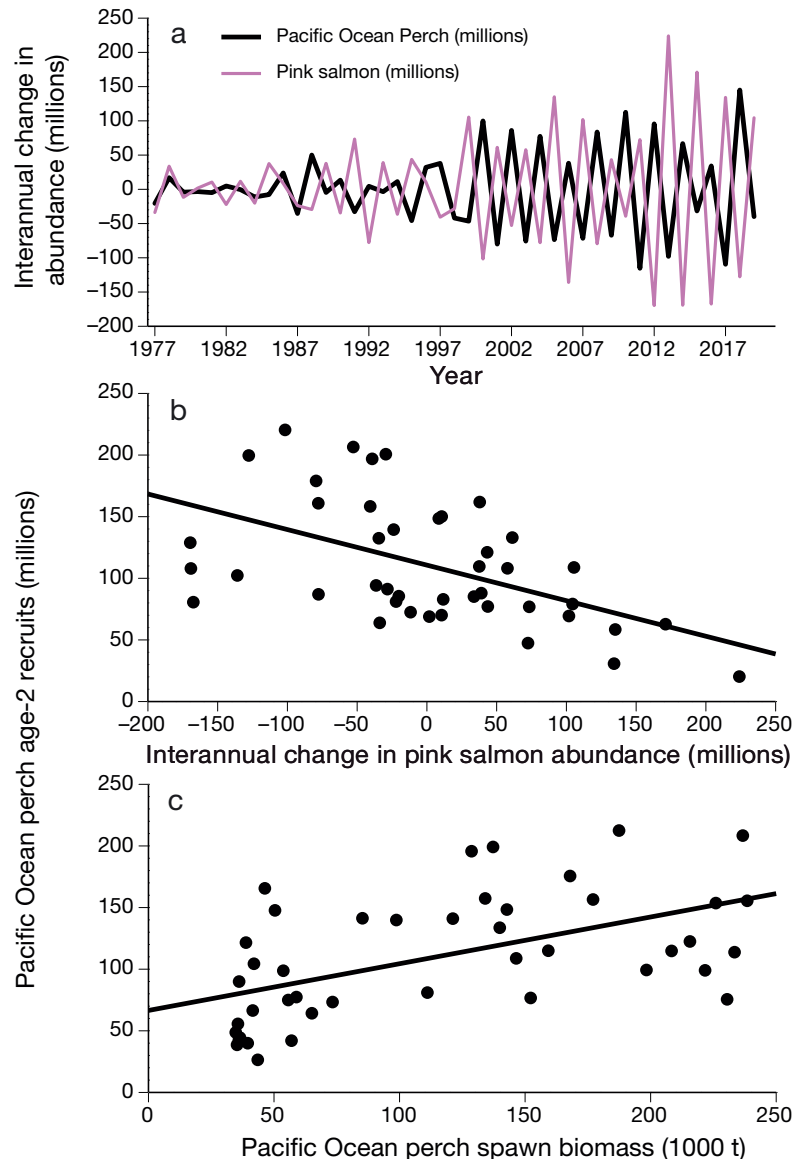

Fig. 5. (a) Interannual change in abundances of age-2 Pacific Ocean perch (POP) in the Gulf of Alaska and pink salmon returning to North America during 1977–2019; and regression-corrected plots of (b) age-2 POP recruits in relation to interannual change in abundances of North American pink salmon (p < 0.001) and (c) age-2 POP recruits in relation to the parent spawning biomass (p = 0.019). Cochrane-Orcutt multiple regression accounted for autocorrelation (R^2 = 0.50; overall df = 2, 39; p < 0.001). Interannual change in abundance (*A*) in year i = A_i − avg. (A_{i-1}, A_{i+1}). Data source: Hulson et al. (2021)

was negatively correlated with maturing pink salmon abundance during the previous year, as expected from predation by maturing pink salmon on the parent squid (r = −0.55, p = 0.009, Jorgensen 2011). Over a 19 yr period, paralarvae were 95% less abundant in even versus odd years, leading to fewer adult squid in the following odd year (Jorgensen 2011). Jorgensen (2011) could not explain the biennial pattern using oceanographic variables. *B. anonychus* appears to have a 2 yr life cycle, which leads to a strong and consistent biennial cycle when combined with predation by biennial pink salmon. In odd years when pink salmon are highly abundant, squid are less common in diets of all salmon species in the BS (Fig. 6) and the Alaska Gyre in the GOA (Aydin 2000, Kaeriyama et al. 2004).

B. anonychus are critical prey for marine fishes, birds, and mammals, such that substantial predation by pink salmon on squid, as in spring and summer of odd years, can reverberate through the offshore ecosystem (Aydin 2000). Furthermore, the 2 yr lifespan of *B. anonychus* and predation on them by biennially-abundant pink salmon sustains

and perhaps exacerbates biennial patterns in squid abundance.

3.4. Pacific Salmon

Biennial variation in the abundance of pink salmon may lead to biennial feeding patterns by other species of Pacific salmon if they are out-competed for common prey, as detailed below. For example, in odd years when pink salmon are typically most abundant, Davis (2003) found that over a 10 yr period, Chinook, sockeye, and pink salmon in the BS consumed fewer nutritionally valuable prey such as squid, fishes, and euphausiids, and all salmon species consumed more low-calorie prey than in even years (Fig. 6). Those high-quality prey are among the principal conduits of energy flow through pelagic food webs that include zooplankton, forage fishes, squids, salmon, seabirds, and marine mammals (Brodeur et al. 1999, Aydin 2000).

Stable isotope signatures of Chinook and coho salmon and steelhead have been used as evidence that they typically feed on higher trophic level prey than pink salmon, and thus there is little direct competition between them (Welch & Parsons 1993, Kaeriyama et al. 2004, Johnson & Schindler 2009). However, diet composition of pink salmon during the second year at sea is more accurate for identifying potential competition with salmon species that consume squid and fishes than stable isotope signatures, which fail to reflect the consumption of squid and fishes by pink salmon during their second year at sea when forage demand is especially great. Muscle isotope signatures require many months after a diet shift from plankton to fish and squid to be partially detected, and years to accurately reflect the new diet (e.g. Madigan et al. 2021; see Text S1 in Supplement 1 at www.int-res.com/articles/suppl/m719p001_supp1.pdf).
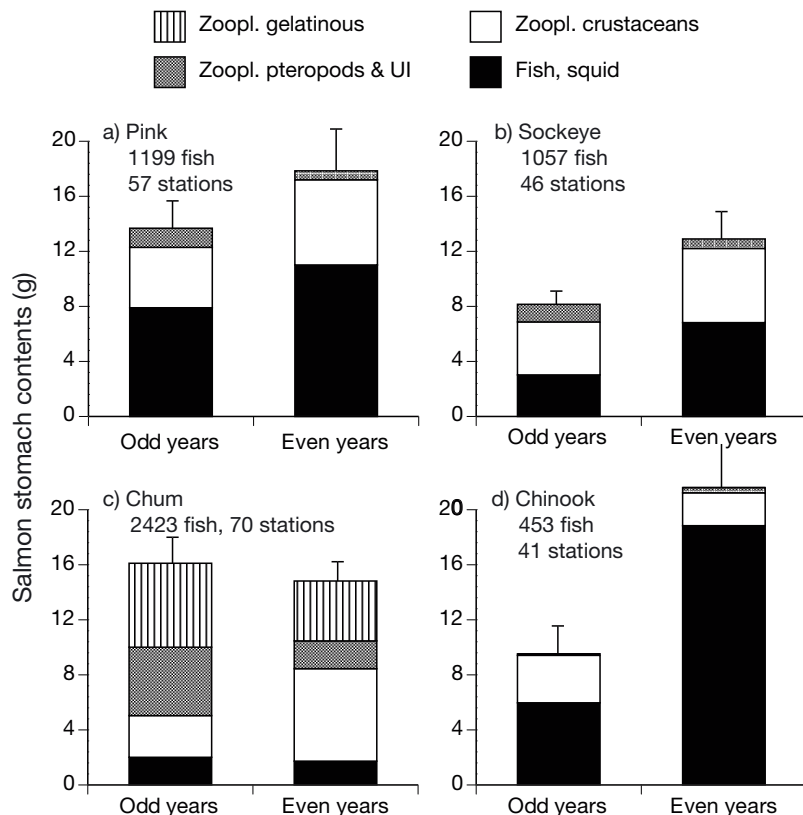

Fig. 6. Mean weights of stomach contents from (a) pink, (b) sockeye, (c) chum, and (d) Chinook salmon sampled in the central Bering Sea during odd and even years, 1991–2000 (UI = unidentified). Error bars: SE. Data source: Davis (2003)

3.4.1. Sockeye salmon

Sockeye salmon migrate long distances during their 2 or 3 yr at sea where they can interact with nearby and distant populations of pink salmon. For example, Bristol Bay sockeye

salmon range from the Kamchatka Peninsula to Kodiak Island (Myers et al. 2007, Habicht et al. 2010, Espinasse et al. 2020), and ocean age-1 Fraser River, BC, sockeye salmon have been observed in the central NPO (176.2° E) approximately 4000 km from their natal river (Neville & Beamish 2022).

Among Pacific salmon species, sockeye salmon have the greatest diet overlap with pink salmon (Brodeur 1990, Kaeriyama et al. 2000, Qin & Kaeriyama 2016). Both species are primarily planktivores, but each can switch to higher trophic level prey such as small fishes and squid as they grow in their second season at sea. During a 10 yr study in the central BS (52–58° N), the diet of sockeye salmon averaged 47 % fish and squid, 44 % zooplankton, and 9 % other prey by weight (Fig. 6). However, in odd years, when pink salmon were approximately 40 times more abundant, total prey weight consumed per sockeye salmon declined 36 % versus only 23 % among pink salmon. In odd years, the consumption of energy-rich fishes and squid declined 50 to 58 % in sockeye salmon, respectively, but only 25 to 32 % in pink salmon (Fig. 6; Davis 2003). Likewise, in odd years, consumption of higher caloric-value euphausiids and copepods declined 46 to 50 % in sockeye salmon compared with only 37 to 48 % in pink salmon, respectively. In contrast, lower caloric-value pteropods and amphipods increased in diets of both sockeye (13 %) and pink salmon (72 %) in odd years. These data suggest that pink salmon were able to consume fishes, squid, and energy-rich zooplankton more effectively than sockeye salmon when availability of these key prey was limited (Ruggerone et al. 2003).

In the western NPO, only trace amounts of squid were observed in the stomachs of sockeye and pink salmon during odd years, whereas both species contained 50 times more squid by weight in even years during 1956–1963 (Ito 1964). This observation, which preceded the large increase in pink salmon abundance after the 1977 regime shift, occurred when Asian pink salmon abundance averaged 67 % more fish in odd (200 million) versus even years (120 million; Ruggerone & Irvine 2018).

Despite the tremendous amount of research on sockeye salmon over the past 75 yr, and the odd–even year differential in consumption of squid noted above, interactions between them and pink salmon were largely unknown until the early 2000s (Peterman 1982, Bugaev et al. 2001, Ruggerone et al. 2003). In the past 20 yr, however, a growing body of evidence indicates that pink salmon influence the growth, age, survival, and abundance of sockeye salmon throughout their range in North America.

A quantitative analysis of 47 sockeye salmon populations, representing approximately 90 % of all sockeye salmon ranging from the Fraser River in southern BC to the Kuskokwim River region in southwestern Alaska, found strong associations between sockeye salmon productivity ($\log_e$ recruits per spawner) in brood years 1976–2009 and NPO pink salmon abundance and SST during early life at sea (Connors et al. 2020). Based on these relationships, it was estimated that a 119 million increase in pink salmon abundance (i.e. 1 SD above the mean) was associated with a 9 % decline in sockeye salmon productivity in the BS and the GOA, and a 21 % decline in productivity in BC and SEAK (Fig. 7a), whereas a 1.5°C increase in SST (1 SD) was associated with a 23 % increase in sockeye salmon productivity in the BS and a 9 % increase in the GOA, but with a 12 % decline in BC and SEAK. The mean annual return of approximately 82 million hatchery pink salmon during 2005–2015 was estimated to reduce sockeye salmon productivity by 5 % in the BS, 6 % in the GOA, and 15 % in BC and SEAK.

Sockeye salmon have a diverse life history, especially in northern areas, that can mask detection of biennial pink salmon effects. Sockeye salmon typically enter the ocean after spending 1 or 2 winters in freshwater, then return to their natal rivers to spawn after 2 or 3 winters at sea, thereby encountering both odd-year (abundant) and even-year (few) pink salmon. Therefore, age-specific analyses of sockeye salmon are often needed to unravel the apparent effects of pink salmon on sockeye salmon growth, age-at-maturation, survival, and abundance.

Analyses of annual and seasonal sockeye salmon scale growth at sea revealed strong interactions with pink salmon. For example, over a 43 yr period, odd-year scale growth of Bristol Bay sockeye salmon averaged 6.2 and 10 % less than adjacent even-year growth during the second and third years at sea, respectively (Fig. 8a; Ruggerone et al. 2003, 2016a). Scale growth declined with increasing abundances of pink salmon returning to Russia (the primary overlapping population), explaining 33 and 58 % of second- and third-year scale growth variability, respectively, during 1965–2009 (Fig. 8b; Ruggerone et al. 2016a). Analysis of seasonal scale circuli measurements indicated that the biennial divergence in sockeye salmon growth began in early spring (third season at sea) or late spring (second season at sea) and continued through summer and fall; no biennial pattern was detected during winter when most pink salmon were distributed farther south than
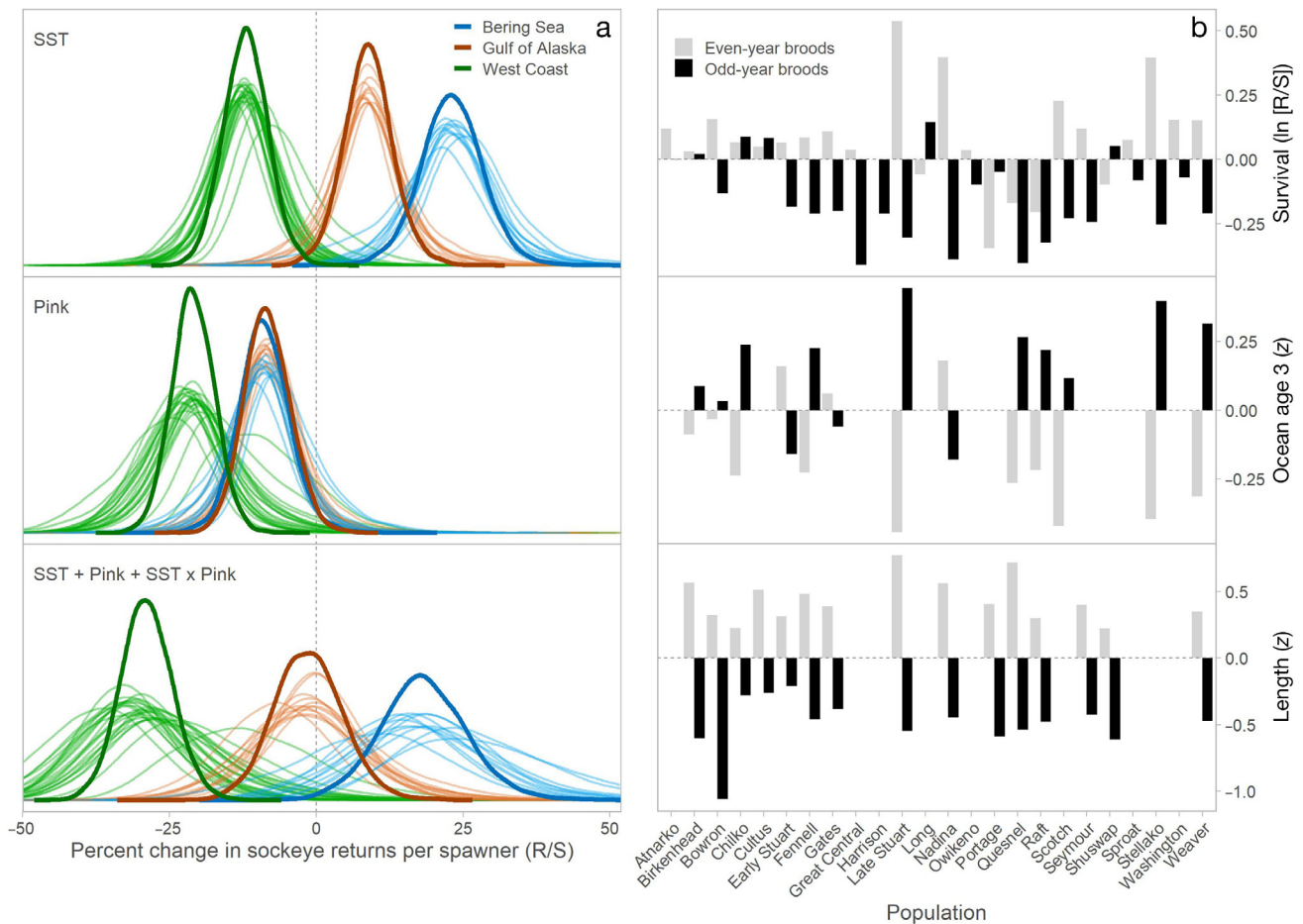
Fig. 7. (a) Posterior probability distributions of the predicted effect of sea surface temperature (SST; top), pink salmon competitors (middle), and the combined effect from all covariate terms (bottom), on survival of 47 sockeye salmon populations originating from the Bering Sea, Gulf of Alaska, and west coast of North America (Southeast Alaska and British Columbia). Posterior hyperdistributions of the covariate effects are in bold lines, with individual stock-specific posterior distributions illustrated by the thin lines. Covariate effects are standardized (i.e. per standard deviation unit increase in each covariate), which equates to 1.5°C SST and 119 million pink salmon above the mean. (b) Mean survival (top), proportion of ocean age-3 sockeye salmon in the adult return (middle), and length-at-age of 24 sockeye salmon populations from British Columbia and Washington state during odd- versus even-numbered brood years, 1978–2005 (bottom). Values are normalized (z) relative to the entire data time series, except survival, which is the mean residual ($\log_e$ recruits per spawner) from the recruitment relationship. Data sources: Ruggerone & Connors (2015), Connors et al. (2020)

sockeye salmon (Ruggerone et al. 2005). Biennial patterns in sockeye salmon scale growth were not observed during the first year at sea or during the homeward migration, presumably because abundance of pink salmon is low in Bristol Bay (Ruggerone & Irvine 2018). Biennial scale growth of sockeye salmon returning to watersheds in the GOA region (Chignik, Cook Inlet, PWS, Copper River, and SEAK) was also observed during the second and third years at sea (low growth in odd years), but not consistently during the first year at sea (P. Rand & G. Ruggerone unpubl. data).

Size-at-age of returning Bristol Bay sockeye salmon was negatively correlated with both abundance of

Russian pink salmon during the year prior to return and abundance of Bristol Bay sockeye salmon during the year of return, 1958–2003 (Ruggerone et al. 2003, 2007). Eight sex- and age-specific statistical models explained on average 45% of the variability in adult sockeye salmon length. The models indicated that competition with pink salmon reduced the length of female sockeye salmon more than that of males, suggesting a possible adverse effect on future abundance because salmon fecundity is associated with body size (Quinn 2005). A recent analysis of Bristol Bay sockeye salmon size-at-age over a 60 yr period, which considered SST, also found that pink and sockeye salmon abundance had the greatest ex-
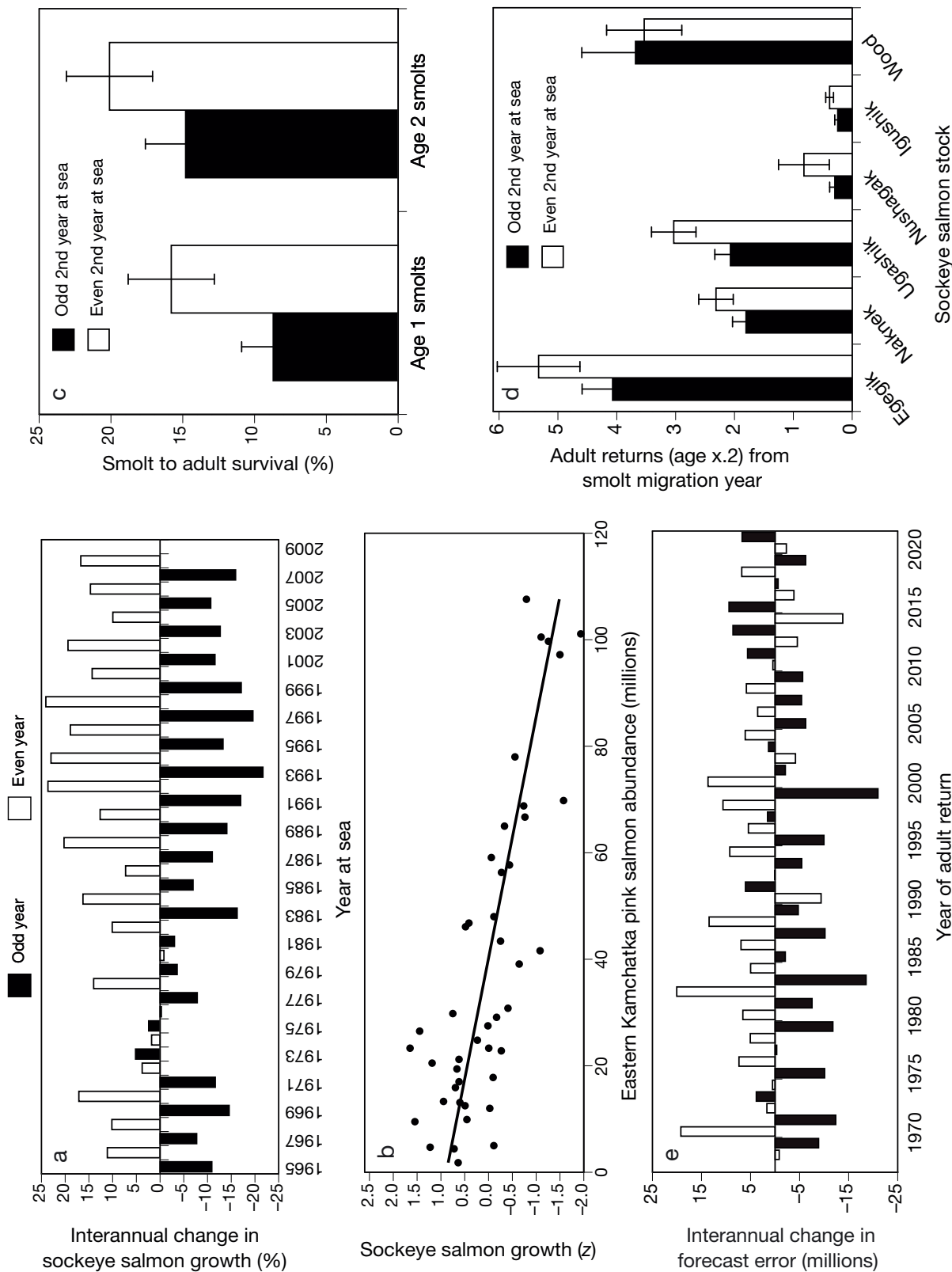
Fig. 8. Examples of biennial patterns and correlation analyses among Bristol Bay sockeye salmon (a,b) testing the hypothesis that pink salmon affect sockeye salmon growth at sea, (c) smolt to adult survival, (d) adult returns from smolt migrations, and (e) adult sockeye salmon forecast error, 1968–2021. Interannual change in scale growth or forecast error (G) in year $i = G_i$ − avg. (G_{i-1}, G_{i+1}). Mean scale growth values in (a,b) represent Kvichak, Egegik, Naknek, Ugashik, and Wood River stocks during the third year at sea, 1965–2008. Second-year growth shows similar patterns (not shown). Smolt-to-adult survival (c) is the annual mean for Kvichak, Egegik, and Ugashik stocks, 1977–1997. Mean annual adult returns of ocean age-2 salmon (d) are from odd- or even-year smolt migrations, 1977–2019, excluding 1999 as an extreme outlier. Error bars are ±1 SE. Updated from Ruggerone et al. (2003, 2016a)

planatory power (Ohlberger et al. 2023). Oke et al. (2020) reported a negative correlation between body size of sockeye salmon in Alaska (128 populations, up to 60 yr) and the abundance of pink salmon in the NPO.

Smolt to adult survival of Bristol Bay sockeye salmon was significantly lower for fish entering the southeastern BS during even years compared with odd years, 1977–1997 (Fig. 8c, p < 0.02; Ruggerone et al. 2003). Specifically, smolt survival declined 35%, on average, when they entered Bristol Bay in even years and competed with highly abundant Russian pink salmon during their second year at sea (odd year). Survival of younger age-1.2 salmon declined 59% compared with 30% among age-1.3 and age-2.2 salmon and 19% among age-2.3 salmon that interacted with pink salmon in both odd (second year) and even (third year) years at sea.

Age-specific adult sockeye salmon returns to Bristol Bay from odd- versus even-year smolt migrations also revealed apparent interactions with pink salmon (Ruggerone et al. 2003). Adult returns of ocean age-2 sockeye salmon from 6 stocks declined 21%, or 3.3 million adults per even year, on average, in 1977–2019 when they competed with abundant odd-year pink salmon during their second growing season at sea (Fig. 8d). Ocean age-2 sockeye salmon primarily interacted with pink salmon during a single second year at sea, i.e. either abundant pink salmon in an odd year or few pink salmon in an even year. Adult returns of ocean age-3 sockeye salmon declined only 6% when emigrating in even years (odd second year) because ocean age-3 sockeye salmon interacted with both even- and odd-year pink salmon. Overall, during 1977–2019, approximately 85 million fewer adult sockeye salmon returned from even-year smolt migrations that encountered abundant pink salmon in the following year than from odd-year smolt migrations that encountered fewer pink salmon.

Interannual variation in forecast error (i.e. error relative to error during the 2 adjacent years) was used to further test the hypothesis that pink salmon affect the survival and abundance of Bristol Bay sockeye salmon (Ruggerone et al. 2016a). Forecast error of southeastern Bristol Bay sockeye salmon (Kvichak, Naknek, Egegik, and Ugashik stocks) was biased high during even-numbered years (avg. 4.0 million fish yr^{-1}), and biased low during odd-numbered years (avg. −3.9 million fish yr^{-1}), 1968–2021 (Fig. 8e). High-biased forecasts in even return years reflect interaction with abundant pink salmon during the previous odd year in which sockeye salmon growth is reduced (Fig. 8a,b); seasonal scale-growth measurements demon-

strated little effect of pink salmon during the homeward migration (Ruggerone et al. 2005, 2016a). Likewise, low-biased forecasts in odd return years reflect interaction with fewer pink salmon and greater sockeye salmon growth during the previous even year (Fig. 8a,b). After standardizing forecast error relative to adjacent years, forecasts in even years were biased high in 63% of the years and biased low in 22% of the years. Interannual variation in forecast error increased with interannual variation in the abundance of eastern Kamchatka pink salmon during the previous year, 1968–2008 (linear regression, p < 0.01, r = 0.41, after accounting for autocorrelation). Forecast error was greater for ocean age-2 than for ocean age-3 sockeye salmon because age-2 sockeye salmon interact with either odd-year or even-year pink salmon, whereas age-3 sockeye salmon interact with both pink salmon lines (Ruggerone et al. 2016a). Interannual variation in forecast error shifted after 2009 (Fig. 8e), possibly reflecting an increase in the proportion of sockeye salmon spending 3 rather than 2 winters at sea in response to younger age of smolts (Nielsen & Ruggerone 2009, Cline et al. 2019) and the exceptional abundance of Bristol Bay sockeye salmon since 2014 (Ruggerone et al. 2021).

Interannual variation in forecast error of northwestern Bristol Bay sockeye salmon (Wood River, Nushagak, and Igushik stocks combined) was also biased high in even years (avg. 0.79 million fish yr^{-1}) and biased low in odd years (avg. −1.06 million fish yr^{-1}), 1968–2021. This pattern was not as consistent nor as strong as it was for the southeastern stocks, possibly reflecting the more easterly distribution of Wood River (Bristol Bay, Alaska) sockeye salmon in the NPO and less interaction with eastern Kamchatka pink salmon (Ruggerone et al. 2016a).

The annual return of sockeye salmon to Bristol Bay exceeded 50 million fish from 2015 to 2021 at the same time when pink salmon returns to Russia were exceptionally large (Ruggerone et al. 2021). We hypothesize that this counterintuitive relationship occurs because Bristol Bay sockeye salmon encounter few pink salmon during their first season at sea (Ruggerone et al. 2003, 2005, 2016a) and because both species in the north have benefited from recent marine heatwaves, especially during early life at sea (e.g. Ruggerone et al. 2005, 2007). Greater sockeye and pink salmon abundance, however, led to reduced growth during late life at sea and reduced adult size-at-age of sockeye salmon. Our findings suggest that early growth at sea is critical to salmon survival and subsequent abundance, but that reduced growth at later marine life stages can also affect survival,

although to a lesser extent. For Bristol Bay sockeye salmon, favorable early marine conditions have likely overwhelmed competition effects with pink salmon during the second and third seasons at sea (Connors et al. 2020).

This pattern of abundance is reversed among sockeye salmon in the south. Sockeye salmon in BC and SEAK have encountered unfavorable early and late marine conditions in recent decades, leading to declining survival and abundances (Connors et al. 2020). An analysis of up to 36 sockeye salmon populations from Puget Sound, WA, through SEAK during the past 55 yr revealed that high abundance of NPO pink salmon in the second year of sockeye salmon life at sea was associated with lower sockeye salmon productivity, reduced adult length-at-age, and delayed maturation (Ruggerone & Connors 2015). While accounting for SST, they predicted that an increase from 200 million to 400 million pink salmon would lead to a 39% reduction in productivity of Fraser River sockeye salmon, an estimate that is consistent with that of Connors et al. (2020). Furthermore, biennial patterns in sockeye salmon life history characteristics were significant: productivity was low, length-at-age was small, and age-at-maturation was delayed when sockeye salmon encountered highly abundant pink salmon (Fig. 7b). The greatest statistical support for models occurred when sockeye salmon were aligned to interact with immature pink salmon during their second season at sea and continued to interact with maturing pink salmon as they migrated to their natal river. Less support was found for negative interactions during the first season at sea. In contrast, McKinnell & Reichardt (2012) found some support for negative effects of juvenile pink salmon in northern BC on first-year scale growth of Fraser River sockeye salmon, but no support in the Strait of Georgia.

Several studies reported evidence for adverse effects of adult pink salmon on the growth and survival of juvenile sockeye salmon. Marine survival rate residuals of Babine Lake (Skeena River, BC) sockeye salmon were inversely related to the abundance of adult pink salmon returning to northern BC during the year of sockeye smolt emigration to sea in 1961–1977 (Peterman 1982). Sockeye salmon survival was positively correlated with juvenile pink salmon abundance in the year of outmigration. Thus, Babine Lake sockeye salmon may experience both compensatory and depensatory mortality in relation to pink salmon. In PWS, productivity of sockeye salmon returning to the Copper River, Coghill Lake, and Eshamy Lake in 1981–2011 was inversely related to abundance of returning hatchery pink salmon, but

no effects were found on wild pink, chum *O. keta*, or Chinook salmon (Ward et al. 2017, 2018). In support of the competition hypothesis, Martinson et al. (2008) reported decreased scale growth of sockeye salmon emigrating from the Karluk River (Kodiak Island, AK) during years when large numbers of adult pink salmon returned to the same area, while providing some evidence for diet overlap between juvenile sockeye salmon and adult pink salmon.

Russia produces approximately 15% of the annual sockeye salmon returns from the NPO (Ruggerone & Irvine 2018). Bugaev et al. (2001) reported that the length and weight of sockeye salmon returning to the Ozernaya River (Kuril Lake, Kamchatka) during 1970–1994 was reduced in years when the ocean abundances of Kamchatka pink salmon were high. The effect of pink salmon abundance on sockeye growth was greater than that of sockeye salmon abundance, owing to the much higher abundance of pink salmon. Additional studies provided evidence that trophic competition between pink and sockeye salmon at sea influenced the growth of Russian sockeye salmon ([Krogius 1960, Birman 1985] in Bugaev et al. 2001). Sano (1963) found that both the size of sockeye and pink salmon caught in the western NPO and the average weight of their stomach contents were smaller in odd years, when pink salmon abundance was high.

3.4.2. Chum salmon

Chum salmon are highly abundant and widely distributed in the NPO (Myers et al. 2007). Most fish (60%) are from hatcheries in Japan, Russia, and Alaska (Ruggerone & Irvine 2018). They enter the ocean as young-of-the-year fry during spring and primarily consume zooplankton while typically spending 3 or 4 yr at sea (Graham et al. 2021). Their unusually large stomach is uniquely adapted to process large quantities of low-calorie gelatinous plankton (cnidarians, ctenophores, and salps), which is thought to be an evolutionary response to reduce competition with other salmon species, especially highly abundant pink salmon (Welch 1997).

Despite this adaptation, there is evidence for competition between chum and pink salmon. For example, in odd years when maturing pink salmon are highly abundant in the BS during June and July, zooplankton abundance has been found to be negatively correlated with pink salmon abundance (Section 3.1). Consequently, in odd years, chum salmon consumed 40% more low-calorie gelatinous zooplankton and

30% more pteropods, and 40% less high-calorie prey than in even years when few pink salmon were present, 1991–2007 (Fig. 6; Tadokoro et al. 1996, Davis 2003, Kaga et al. 2013). Furthermore, in odd years, the distribution of immature chum salmon shifts southeastward from the BS (e.g. a 50% reduction in abundance in the BS) to the eastern NPO, based on Japanese research in 1972–2000, presumably to find higher densities of prey (Azumaya & Ishida 2000, Davis 2003).

Besides changes in chum salmon diet and distribution, a number of studies reported additional effects of competition between chum and pink salmon. For example, chum salmon sampled in the BS exhibited reduced second- and third-year body growth, reduced condition factor, and lower gonad weight (maturity rate index) with increasing local abundance of pink salmon in the previous year, 1971–2010 (Morita & Fukuwaka 2020); slower growth was linked to delayed maturation (Morita & Fukuwaka 2007). Lipid content of chum salmon in the BS was negatively related to local pink salmon abundance (2002–2007) after accounting for chum salmon body size; pink salmon abundance had a greater effect on lipids than chum salmon abundance (Kaga et al. 2013). In the central NPO south of the Aleutian Islands (1959–1995), third-year scale growth of chum salmon was negatively correlated with abundance of Asian pink salmon (Walker et al. 1998). In the western NPO, prey weight consumed by chum salmon was 27% lower during odd years when maturing pink salmon were abundant (Sano 1963), and feeding rates of immature chum salmon near the Kuril Islands were lower in years of high juvenile pink salmon abundance (Ivankov & Andreyev 1971). However, Shuntov et al. (2017) argued that positive correlations over time between pink and chum salmon weights and pink and chum salmon numbers in the Sea of Okhotsk and the western BS were evidence that environmental factors drove size and abundance rather than competition for prey; there is considerable debate about how applicable those results are to other geographic regions (Shuntov et al. 2017).

Likewise in western Alaska, scale growth of Kuskokwim River (1968–2010), Yukon River (1965–2006), and Bristol Bay (1965–2006) chum salmon was negatively correlated with pink salmon abundance, especially during their third and fourth years at sea; these and other studies also considered oceanographic variables (Agler et al. 2013, Frost et al. 2021). Productivity of Norton Sound chum salmon was negatively correlated with Asian pink salmon abundance in addition to chum salmon abundance (Ruggerone et al. 2012). Scale growth of chum salmon returning to SEAK (1972–2004) and to southern BC (1971–2010) was negatively correlated with the abundance of pink salmon or pink and chum salmon (Yasumiishi et al. 2016), and to the combined biomass of pink, chum, and sockeye salmon during each year at sea (Debertin et al. 2017).

In the Salish Sea, where maturing pink salmon are approximately 40 times more abundant in odd versus even years, chum salmon exhibited strong biennial variations in abundance, size, age-at-maturity, and productivity (recruits per spawner), consistent with the hypothesis of competition for food with pink salmon (Gallagher 1979, Ruggerone & Nielsen 2004, Litz et al. 2021). Overall, chum salmon returns were 32% lower in high pink salmon years (odd) compared to low pink salmon years (even) during the last 5 decades (Litz et al. 2021). This pattern was reinforced by early maturation of chum salmon produced from odd-year broods that interact with adult and juvenile pink salmon (15% more age-3 than age-4) compared with those produced from even year broods (17% more age-4 than age-3). Scale growth of Quilcene River (Salish Sea) chum salmon during the third season at sea (1973–2004) was negatively correlated with the combined abundances of pink and chum salmon while also considering the effect of climate indices (Yasumiishi et al. 2016). Likewise, scale growth of Puget Sound chum salmon (brood years 1997–2012) was negatively correlated with local pink salmon abundance during the first year at sea and with NPO pink salmon abundance during the third year (Anderson et al. 2021). In the Strait of Georgia during 1966–1969, chum salmon fry were smaller in even years when pink salmon fry were abundant versus odd years when few juvenile pink salmon were present (Phillips & Barraclough 1978), and fry-to-adult survival of Fraser River chum salmon declined 44% (from average of 1.53 to 0.85% survival) when they entered marine waters in even-numbered years with numerous juvenile pink salmon, 1961–1979 (Beacham & Starr 1982). Chum salmon on the Washington (USA) coast, where few pink salmon spawn, also exhibited biennial patterns in abundance, age, and productivity, suggesting that factors such as intra- and interspecific competition occurring in the northeast Pacific contributed to those patterns (Ruggerone & Nielsen 2004, Debertin et al. 2017, Litz et al. 2021).

3.4.3. Coho salmon

Coho salmon typically spend approximately 16 mo at sea, and many individuals from North America

migrate into the GOA and the eastern NPO (Godfrey et al. 1975, Myers et al. 1996). Coho salmon occupy a somewhat higher trophic level than pink salmon because they eat more fishes and squid throughout their life (Welch & Parsons 1993, Kaeriyama et al. 2004, Johnson & Schindler 2009). However, diet overlap between them increases during the second season at sea as pink salmon grow and begin to capture small fishes and squid (Ito 1964, Pearcy et al. 1984, Brodeur et al. 2007). Consumption of squid by pink salmon becomes more pronounced during their final 2 or 3 mo at sea, especially after they reach 1 kg (Davis 2003, Aydin et al. 2005). Maturing coho salmon also consume some zooplankton, but depend primarily upon energy-rich squid.

Over a period of 50 yr (1970–2019), the average weight of coho salmon caught in the SEAK troll fishery declined with increasing biomass of pink salmon harvested in North America (an index of abundance) and increased with broad-scale SST, as indexed by the Pacific Decadal Oscillation (PDO; Shaul & Geiger 2016). An updated version of the statistical model used by Shaul & Geiger (2016) explained 68% of the variability in average annual coho salmon weight, which exhibited a strong biennial pattern that was opposite of adult pink salmon abundance (Fig. 9). Interannual variation in coho salmon weight explained by adult pink salmon biomass was slightly greater (55%) than variability explained by the PDO (45%).

The most likely mechanism responsible for those relationships involves predation by maturing pink salmon on squid (*B. anonychus*), a key prey of maturing coho salmon. The biennial life cycles of pink salmon and squid contribute to distinct biennial abundances of maturing squid that are consumed by a single cohort of ocean age-1 coho and pink salmon (Jorgensen 2011, Shaul & Geiger 2016). Thus, evidence indicates that predation by abundant odd-year pink salmon leads to fewer squid available to maturing coho salmon in odd years (Kaeriyama et al. 2004, Jorgensen 2011) and to their reduced growth and body size (Shaul & Geiger 2016). Adult coho salmon weight was explained by average North American pink salmon biomass 2 and 4 yr earlier, owing to a long-term influence of distinct even- and odd-year
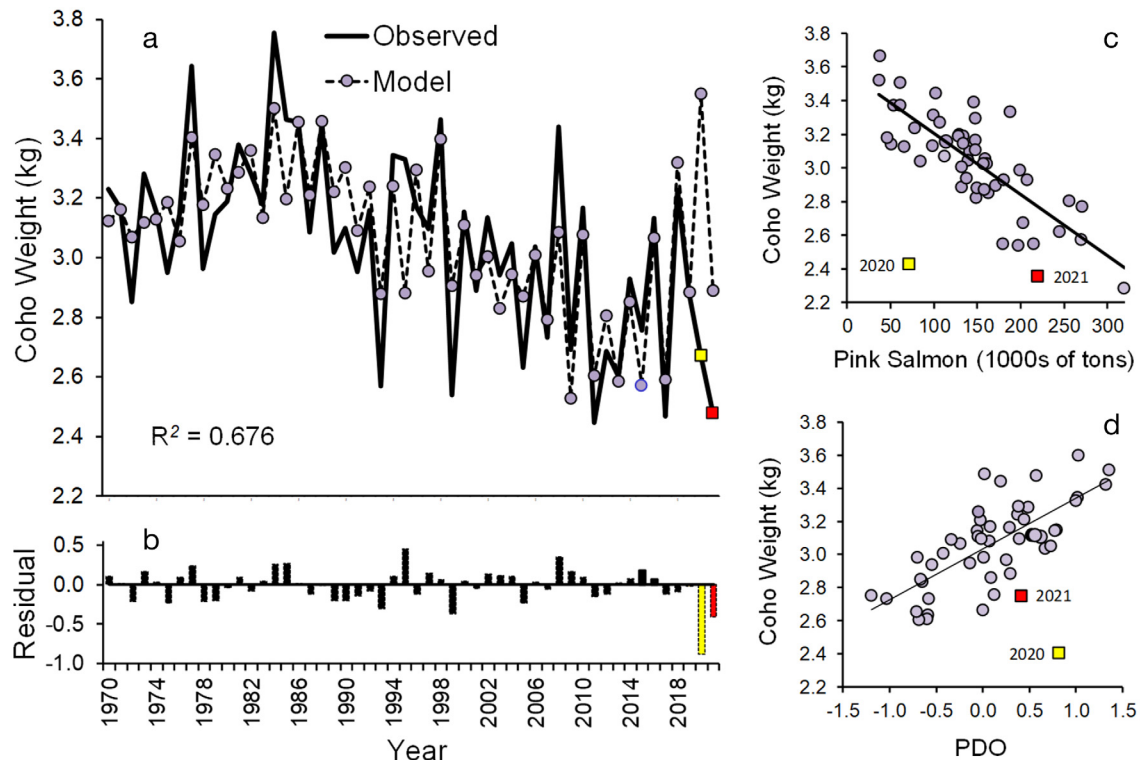

Fig. 9. Southeast Alaska troll-caught coho salmon average dressed weight (ocean age-1) compared with (a) predicted weight based on a multiple regression model with 2 variables: the standardized April–March Pacific Decadal Oscillation (PDO) Index (average for lag 0, 2, and 4 yr) and the standardized average commercial catch of pink salmon in North America (excluding the Bering Sea and Aleutian Islands) lagged by 2 and 4 yr. (b) Model residuals. Also shown are partial residual plots for (c) pink salmon abundance and (d) the PDO index. The multiple-regression model developed by Shaul & Geiger (2016) using 1970–2014 data was refitted for 1970–2019, with 2020 and 2021 values indicated on the partial residual plots by yellow and red squares, respectively

pink salmon lines preying on even- and odd-year lines of maturing squid. In the season of coho maturation, it is possible that pink salmon were too small (<1 kg) to strongly influence squid abundance during winter through late spring when coho salmon began intensive feeding on squid. High average PDO values during the year of maturation and 2 and 4 yr earlier were positively correlated with coho salmon weight, presumably through increased abundance of squid in response to warmer conditions associated with positive PDO index values.

Pink salmon biomass was linked to additional population characteristics of coho salmon in SEAK. Coho salmon survival at sea (1990–2014) was negatively correlated with both pink salmon biomass (r = −0.58, p < 0.05) and coho salmon body length (r = −0.67, p < 0.05), which was influenced by pink salmon abundance (Shaul & Geiger 2016). The ratio of female to male coho salmon was lower in odd years (p = 0.012), and the per capita egg biomass of maturing coho salmon, which provides an index for the reproductive potential of the spawning coho salmon population, was negatively correlated with pink salmon biomass (r = −0.60, p < 0.05). The investigators provided evidence that coho salmon body size and survival were primarily influenced during late marine life when coho salmon are offshore. These findings suggest that pink salmon adversely affect both coho salmon survival and future coho salmon abundance by reducing the reproductive potential of the survivors through a combination of lower egg biomass and lower survival of female versus male coho salmon in odd years (Shaul & Geiger 2016).

After 50 yr of strong correlation, the pink salmon–climate statistical model of Shaul & Geiger (2016) failed to predict the extremely low body size of SEAK coho salmon in 2020 (2.67 kg) and 2021 (2.48 kg), both of which followed warm conditions during 2016–2020 and poor GOA pink salmon returns on the even-year line in 2016 and 2018 (Fig. 9). However, total pink salmon returns to North America and Asia in 2018 and 2019 (avg. 670 million fish) were the largest consecutive years on record since 1925 when records were first kept (Ruggerone et al. 2021), raising the question of whether Asian pink salmon, which are typically west of most SEAK coho salmon, may have contributed to the small size of coho salmon in 2020 and 2021. Lastly, the PDO index covers a large region of the NPO and may not have reflected mesoscale effects of marine heat waves in the GOA region.

Studies in other regions are consistent with the findings of Shaul & Geiger (2016), indicating an adverse effect of pink salmon on coho salmon growth,

survival, and abundance. Ogura et al. (1991) also reported that final-year growth rates of coho salmon in the western NPO, 1978–1987, were lower in odd years when maturing pink salmon were highly abundant. In the Kuskokwim River in western Alaska, commercial coho salmon harvests in odd years averaged 33% less (avg. 225 000 coho salmon) compared with even years (avg. 336 000 coho salmon) during 1965–2007 (t-test, p < 0.001, Ruggerone & Nielsen 2009). Further south in the Strait of Georgia, where diet overlap of juvenile coho and pink salmon was high during 1998–2009, the proportion of coho salmon with empty stomachs increased approximately 37%, and the abundance and survival of hatchery coho salmon by September declined approximately 73 and 80%, respectively, in even years when juvenile pink salmon were highly abundant (Beamish et al. 2010).

3.4.4. Chinook salmon

Subadult Chinook salmon have been found extensively in offshore areas of the NPO and BS, where they overlap with pink salmon (Major et al. 1978, Myers et al. 1996; Text S1). Diet overlap between Chinook and pink salmon can be considerable, especially during the second season at sea for pink salmon, when they are large enough to consume squid and small fishes. The small energy-rich squid *B. anonychus* is a major component in the diet of Chinook salmon (and other salmon species) in the GOA, central NPO, and central BS, and is also consumed heavily by maturing pink salmon in these same waters. For example, during a 10 yr study in the central BS (52–58° N), the diet of Chinook salmon averaged 80% fish and squid, 19% zooplankton, and 1% other prey by weight, and the diet of pink salmon averaged 60% fish and squid, 34% zooplankton, and 6% other prey (Fig. 6; Davis 2003). In odd-numbered years, when pink salmon were approximately 40 times more abundant than in even years, total prey weight consumed per Chinook salmon declined 56% versus only 23% among pink salmon (Fig. 6). In odd years, Chinook salmon consumed 72% less squid and 44% less fish, but 44% more euphausiids compared with even years (Fig. 6). In odd years, pink salmon consumed 32% less squid, 25% less fish, and 29% less zooplankton compared with even years (Fig. 6). These data suggest that pink salmon consumed fishes and squid more efficiently than Chinook salmon when availability of key prey was low. Other studies indicate that the degree of overlap in

the consumption of squid, small fishes, and euphausiids varies with region (Davis et al. 2009, Qin & Kaeriyama 2016). Collectively, this evidence suggests that pink salmon may directly and indirectly affect Chinook salmon growth and survival by consuming the same prey and by altering the food web that supports small fishes, squid, and zooplankton consumed by Chinook salmon.

Chinook salmon harvests, abundances, and average body sizes in northern regions where freshwater habitat is mostly intact have been declining for several decades (Bigler et al. 1996, Lewis et al. 2015, Ohlberger et al. 2018, Welch et al. 2021), and several studies have suggested Chinook survival and growth may be inversely related to pink salmon abundance at sea (e.g. Cunningham et al. 2018, Oke et al. 2020). We examined the time series of annual Chinook salmon commercial harvests in Alaska and BC from 1952 to 2021. Commercial harvests reflect fishing effort, based on abundance predictions and fishery regulations (PSC 2022), and can provide a first-order approximation of abundance, although they can also be confounded by changes in fishery regulations and effort over time. Consistent with the hypothesis that pink salmon affect Chinook salmon, we found that harvest trends during the 70 yr period were opposite those of pink salmon abundance trends (Fig. 10a).

Body size of adult Chinook salmon in Alaska also declined with increasing abundance of pink salmon since 1952. Average weight of commercially caught Chinook salmon was relatively stable over time when abundance of pink salmon was low during 1952 to 1975 (Fig. 10b). Immediately after the 1977 ocean regime shift, body size of Chinook salmon reached its maximum (9.3 kg) and then declined steadily over time as pink salmon abundance increased (Fig. 10b). Chinook salmon body size reached the long-term minimum during 2015–2021 (avg. 5.7 kg) when pink salmon abundance was peaking (564 million yr^{-1}) and when marine heat waves became more frequent (Ross et al. 2021). We note, however, that these trends in size and commercial harvest can be confounded with other long-term trends in oceano-

graphic and freshwater processes, and so should be interpreted with caution. Also, the Japanese salmon fishery on the high seas removed, on average, 334 000 Chinook salmon per year from 1955 to 1980, then harvests declined steadily until its termination in 1991 (NPAFC 2022a). Most of the Chinook salmon had originated from western and central Alaska (Rogers et al. 1984; Text S1), suggesting that Chinook salmon harvests in Alaska would have been even higher during the period when pink salmon abundance was low. Other factors contributing to long-term declines in catch and size of North American Chinook salmon have been hypothesized, including size-selective predation by resident killer whales (Ohlberger et al. 2018, 2019; Text S1).

Lewis et al. (2015) demonstrated a consistent decline in Alaskan Chinook salmon length-at-age and age-at-maturation over a 30 yr period while noting the potential influence of competition for prey with other salmon species. Our analyses of these data
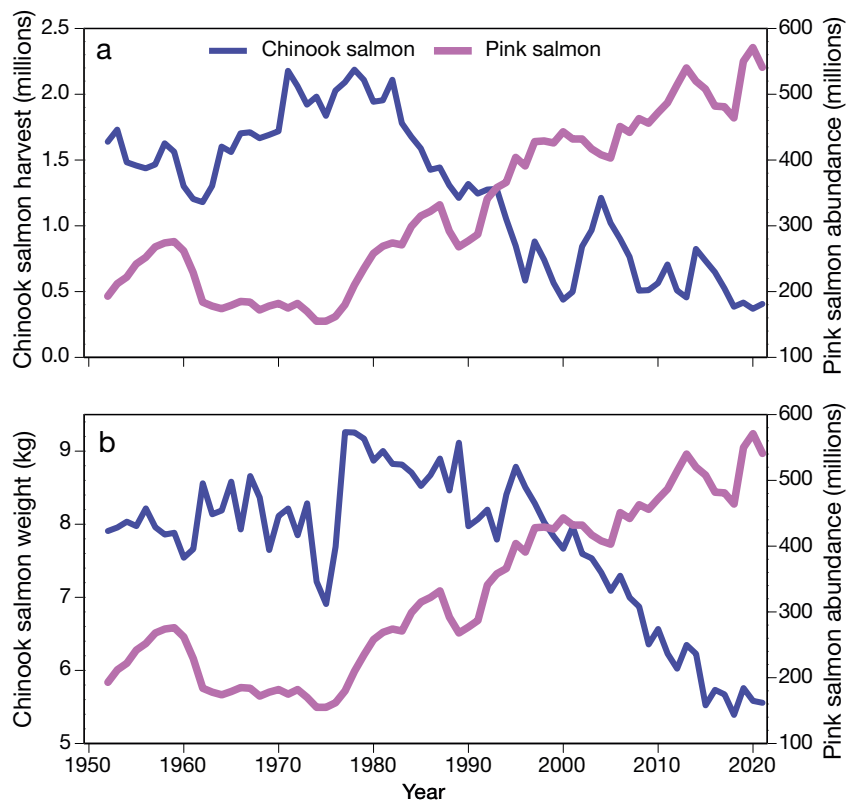

Fig. 10. Time series of (a) Chinook salmon commercial harvests in Alaska and British Columbia, and (b) average weight of Chinook salmon in Alaskan harvests in relation to average pink salmon abundance returning from the North Pacific Ocean 1 to 4 yr prior to the Chinook salmon harvest during 1952–2021 (e.g. harvest in year 2000 was related to average pink salmon abundance during 1996–1999, corresponding to the period of species overlap and potential direct and indirect effects of pink salmon). Data sources: Ruggerone et al. (2010, 2021), Ruggerone & Irvine (2018), NPAFC (2022a)

and the aggregate length of troll-caught Chinook salmon reveal that mean length of age-1.4 Chinook salmon from all 11 populations declined coincident with increasing pink salmon abundance, although the relationship was weak in 2 populations (Table S1, Fig. S1.1). The populations ranged from the Yukon River in the northeastern BS to the Copper River in the northeastern GOA, and the Unuk River in SEAK. Likewise, average length of 9 of 10 age-1.3 populations of Chinook salmon declined with increasing pink salmon abundance, including 4 weak relationships (Table S1). Average age of 4 of 5 Chinook salmon populations declined with increasing abundance of pink salmon, including 1 weak relationship (Table S1). In the Yukon River, the decline in body size led to a 24–35% reduction in the reproductive potential of female Chinook salmon since the 1970s (Ohlberger et al. 2020). In the Kamchatka River, Russia, scale analysis of Chinook salmon revealed biennial growth patterns during the first and second years at sea, 1935–1955, that may have been related to pink salmon (Grachev 1967).

Analyses of survival across the entire life cycle of Chinook salmon found support for the adverse effect of pink salmon on 2 Yukon River populations using a Bayesian life-cycle model (Cunningham et al. 2018), but no support using dynamic factor analysis of data from 15 populations throughout Alaska (Ohlberger et al. 2016); those studies also considered a number of other variables. Both studies aligned pink salmon abundance with the second season at sea (brood year plus 3 yr) of Chinook salmon rather than each year in which Chinook salmon interact with pink salmon. In contrast, while also considering the effect of oceanographic variables, moderate to strong support was found for an adverse effect of Russian pink salmon abundance on annual scale growth of Yukon, Kuskokwim, and Nushagak Chinook salmon during the third and fourth years at sea over a period of 30 yr or longer (Ruggerone et al. 2016b; Supplement 2 at www.int-res.com/articles/suppl/m719 p001_supp2.xlsx). Survival of 2 of the 3 major stocks of Chinook salmon in western Alaska declined with the running 2 yr abundance of Russian pink salmon during the third and fourth years at sea. The percentage of age-6 (age-1.4) and older Chinook salmon in each stock declined with increasing abundance of pink salmon, but support was weak in 1 stock. The decline over time in abundance, growth at sea, and the proportion of older Chinook salmon led the investigators to hypothesize that mortality during late marine life had increased in response to competition with pink salmon and to predation by salmon sharks and other marine predators (Manishin et al. 2021).

Lastly, in the Japanese high seas salmon fishery in the western/central BS and NPO, we found a biennial pattern in the catch of Chinook salmon during 1955–1981. The mean catch in odd years (254000 ± 40000 fish [SE]) was 39% lower than the catch in even years (417000 ± 60000 fish, *t*-test, p = 0.03). Chinook salmon catch was negatively correlated with pink salmon catch (linear regression, r = −0.63, p < 0.001; Text S1, Fig. S1.2). Scale pattern analysis indicated that most of the Chinook salmon originated from western and central Alaska.

Chinook salmon growth and survival may also be affected by pink salmon in coastal seas. In the Salish Sea, subyearling ocean-type Chinook salmon smolts released from 13 hatcheries experienced a 59% decline in marine survival, on average, when released during even years compared with those released during odd years, 1984–1997 (Fig. 11a; Ruggerone & Goetz 2004). Juvenile pink salmon were highly abundant in even years (avg. ~8 million odd-year spawners, 1983–1996) but rare in odd years (<0.5 million even-year spawners). Additional analyses of over 53 million coded-wire-tagged Chinook salmon indicated that the biennial mortality pattern was established during the first year at sea, i.e. within the Salish Sea. No biennial pattern in Chinook salmon survival was observed along the Washington coast and southern Vancouver Island, where few pink salmon spawn. During 1972–1983, overall survival of juvenile Chinook salmon was high and tended to be highest when emigrating with juvenile pink salmon in even years, a change from 1984–1997 possibly related to the 1982–83 El Niño and a shift from predation- to competition-based mortality (Ruggerone & Goetz 2004). Subsequent analyses of subyearling and yearling hatchery Chinook salmon from 1983 to 2012 found lower density-dependent survival and fewer adult returns of hatchery Chinook salmon when released into the Salish Sea during even years when juvenile pink salmon were abundant (Kendall et al. 2020). In odd years, when few juvenile pink salmon were present, density-dependent survival of Chinook salmon was not apparent and survival was higher. From 1970 to 2015, abundance and size of adult natural-origin Chinook salmon in the Salish Sea were negatively correlated with pink salmon abundance (Losee et al. 2019).

Diet overlap between juvenile pink and Chinook salmon in the Salish Sea is relatively low, and researchers hypothesized that pink salmon indirectly influenced Chinook salmon growth and survival (Ruggerone & Goetz 2004, Kendall et al. 2020). Several lines of evidence support a hypothesis of trophic
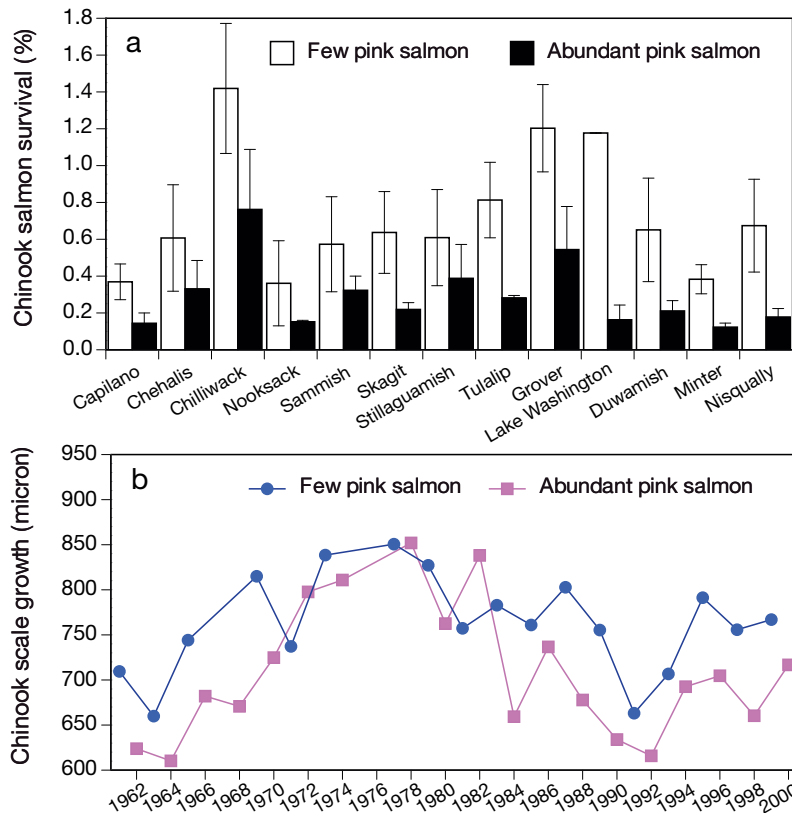
Fig. 11. (a) Mean smolt to adult survival (±1 SE) of subyearling Chinook salmon (tagged ocean type) released from 13 hatcheries in the Salish Sea (Washington and British Columbia) during even years (numerous juvenile pink salmon) and odd years (nearly zero juvenile pink salmon), 1984–1997, and (b) mean early marine scale growth (circuli 11 to 34) corresponding to residence in the Salish Sea of adult Skagit River Chinook salmon (ocean type) during even and odd years, 1961–2000. Data sources: Ruggerone & Goetz (2004); Text S1

interaction. (1) Juvenile pink salmon enter the Salish Sea approximately 2 mo before subyearling Chinook salmon. (2) We found that first-year marine scale circuli measurements of surviving adult Skagit River Chinook salmon were 7% narrower, on average, during even years than odd years, 1961–2000 (*t*-test, p < 0.01, df = 35, Fig. 11b; Text S1). (3) During 1983 to 1997, returning coded-wire-tagged Chinook salmon were smaller at age and tended to delay maturation when released into Salish Sea watersheds in even years when juvenile pink salmon were abundant (Ruggerone & Goetz 2004). (4) Early marine growth and survival of Salish Sea Chinook salmon increased with fewer juvenile pink salmon (Claiborne et al. 2021).

Approximately 11–38% of Chinook salmon sampled for genetic stock identification in the southeastern BS during 2005–2010 originated from the Pacific Northwest, raising concern that climate warming may be shifting salmon from the Pacific Northwest

into a crowded BS where temperatures are cooler (Larson et al. 2013). In support of this hypothesis, Buckner et al. (2023) analyzed the growth of 48 stocks of Chinook salmon returning to hatcheries and spawning grounds in the Columbia River Basin, Oregon coast, and Washington coast (brood years 1976–2013), and found that growth of subyearling and yearling far-north migrating Chinook salmon was negatively associated with pink salmon abundance. The effect of pink salmon on Chinook salmon growth was stronger than that of the tested oceanographic variables (see their Fig. 4). Growth of subyearling Chinook salmon populations that did not migrate as far north was also negatively associated with pink salmon abundance, but to a lesser extent; growth of yearling Chinook salmon in the southern distribution area was not associated with pink salmon abundance.

3.4.5. Steelhead

Steelhead migrate long distances during their typical 1 to 3 winters at sea, leading to a broad distribution across the NPO. Ocean age-0 steelhead migrate farther offshore than other salmonids in their first year at sea, and many immature steelhead from North America have been sampled west of 180° and off the Kuril Islands, Russia (Myers 2018). Steelhead in the open ocean are opportunistic foragers, but they specialize to some degree on a few species of micronekton, including cephalopods (especially *B. anonychus*) and small mesopelagic fishes, and zooplankton such as adult euphausiids, pelagic decapods, amphipods, and pteropods (Myers 2018).

Steelhead feed at a somewhat higher trophic level than pink salmon, but they also share many common prey, leading Atcheson et al. (2012a) to conclude that ocean age-0 and older steelhead may compete with maturing (ocean age-1) pink salmon. In the central NPO, consumption of highly energy-dense mesopelagic forage fishes and squids was negatively correlated with abundance of eastern Kamchatka pink salmon, whereas the percentage of empty stomachs increased with increasing pink salmon abundance

(Atcheson et al. 2012b). These researchers recognized that pink salmon are less abundant in the central NPO than in the central BS, but suggested that large runs of adult pink salmon may deplete prey resources as they migrate through broad North Pacific regions from winter to spring (Myers 2018). They also hypothesized that the surface orientation of foraging steelhead may be a mechanism to reduce trophic interactions with pink salmon.

Steelhead survival indices in BC provide evidence that pink salmon may adversely affect their survival at sea. Adult recruit per spawner anomalies of critically endangered Thompson River summer-run steelhead in the interior of the Fraser River watershed were negatively correlated with the biomass of NPO pink salmon that overlapped their final 2 yr at sea during 1978–2012 (Fig. 12a; Text S1). Smolt-to-adult survival of Keogh River (northeast Vancouver Island) winter-run steelhead was negatively correlated with pink salmon biomass in 1977–2018 (Fig. 12b). Approximately 46 and 49%, respectively, of the annual variability in the Thompson River and Keogh River steelhead survival indices were explained by pink salmon abundance. In the Chilcotin River (interior Fraser River), steelhead recruit per spawner anomalies were negatively correlated with pink salmon abundance (r = −0.65), but autocorrelation was high and reduced the significance of the relationship (linear regression, df = 1, 38, p = 0.14). 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. 2022). 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, 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

when they overlap with abundant pink salmon in the north (Myers 2018; Text S1).

In the Columbia River Basin, we found that B-run summer steelhead exhibit a pronounced biennial pattern of abundance, suggesting strong interactions with pink salmon at sea (Fig. 12c). These fish are
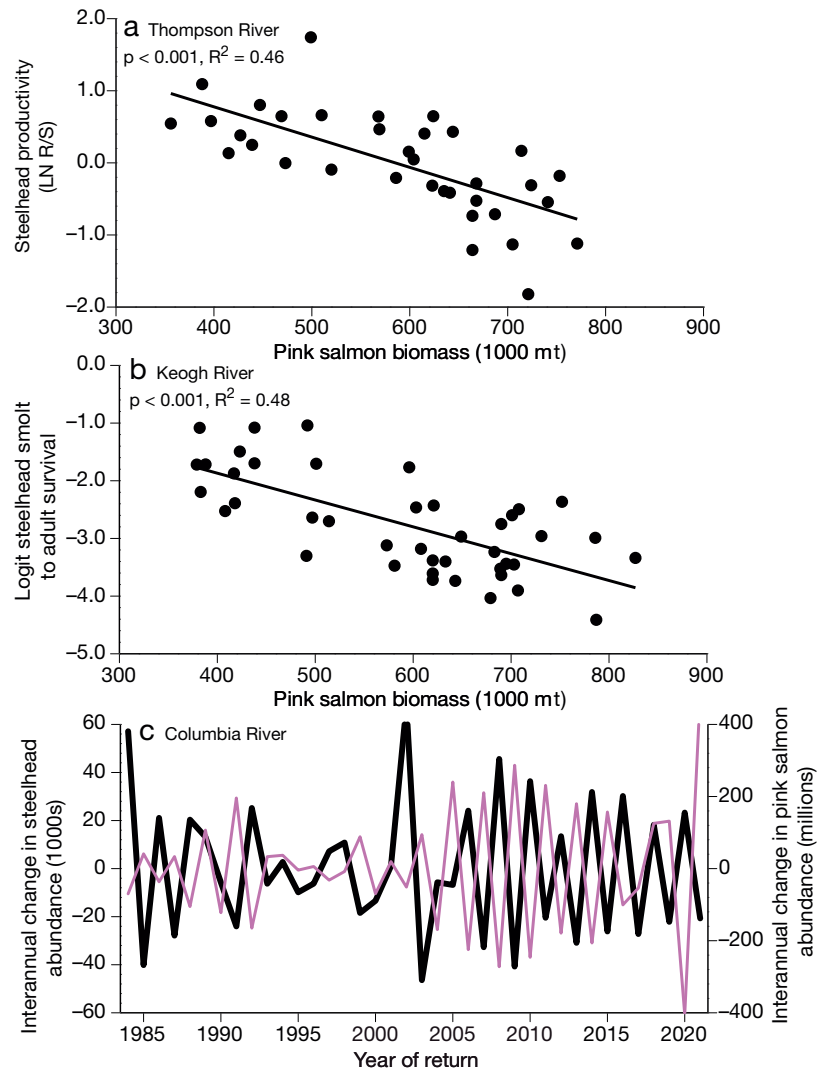

Fig. 12. Potential influence of North Pacific Ocean (NPO) pink salmon abundance on (a) the productivity (return per spawner, R/S) of Thompson River summer-run steelhead (Fraser River watershed, BC), brood years 1978–2012, and (b) smolt to adult survival of Keogh River winter-run steelhead (NE Vancouver Island), smolt years 1977–2018. (c) Interannual change in abundances of Columbia River B-run summer steelhead (black line) and North Pacific pink salmon (pink line) during 1984–2021, where interannual change in abundance (A) in year $i = A_i −$ avg. ($A_{i−1}, A_{i+1}$). Pink salmon biomass is the average biomass 3 and 4 yr after the brood year for Thompson steelhead (mostly 5 yr old fish that spend 2 winters at sea and the last winter in freshwater), and average biomass 1 to 3 yr after the smolt migration of Keogh River steelhead (up to 3 winters at sea), accounting for overlap at sea and different age composition of the 2 steelhead populations. Autocorrelation in the linear regressions was inconclusive (a) or non-significant (b). Data sources for our analyses: Ratzburg (2021), WDFW/ODFW (2022), R. Bison unpubl. data

listed as 'threatened' under the US Endangered Species Act. Returning B-run steelhead counted at Bonneville Dam were 38% less abundant in odd versus even years during 1984–2021 (*t*-test, p = 0.014, n = 38). Furthermore, odd-year pink salmon have become more dominant in recent years (Irvine et al. 2014), and this is reflected in the negative correlation between interannual change in abundances of B-run steelhead and NPO pink salmon over the past 38 yr (Fig. 12c; linear regression, p = 0.014 after accounting for autocorrelation).

In contrast to B-run steelhead, A-run summer steelhead abundance did not differ between odd and even years (*t*-test, p = 0.24, n = 38). B-run steelhead typically spend 2 yr at sea and migrate farther north and west and potentially interact with more abundant pink salmon than A-run steelhead, which spend only 1 yr at sea (Myers 2018). Importantly, the biennial abundance pattern shown by B-run, but not A-run, steelhead suggests substantial mortality after the first year at sea, consistent with late marine mortality observed in other salmon species described here.

3.4.6. Pink salmon

In comparison with other Pacific salmon, pink salmon appear to be well-adapted to foraging in a warming ocean given that the ocean supports more pink salmon now than at any other time since detailed record keeping began in 1925. Pink salmon stomachs are often much fuller than those of other salmon species, they typically consume higher caloric prey than chum and sockeye salmon, and they have high daily rations (Fig. 6; Davis 2003, Karpenko et al. 2007, Karpenko & Koval 2012, Shuntov et al. 2017, Radchenko et al. 2018). Bioenergetic analyses show that body growth declines less in pink salmon (−31%) than in chum (−52%), sockeye (−43%), and coho salmon (−33%) when ocean temperature increases from 5 to 9°C and daily ration is constant (Davis et al. 1998). Growth of smaller salmon is more efficient than growth of larger salmon as temperature rises (Beauchamp 2009). These studies suggest that the strength of density-dependence at sea among pink salmon may be weaker than within other salmon species.

Intraspecific studies of pink salmon at sea often examine interactions between hatchery and wild fish because approximately 1.35 billion juvenile pink salmon are released into the NPO each year, 1990–2021, of which 66% are released in Alaska, primarily in PWS (NPAFC 2022b). Multiple studies reported that adult run size and returns per spawner of PWS wild pink salmon declined in response to increased hatchery production (Hilborn & Eggers 2000, 2001, Amoroso et al. 2017). In contrast, abundances of wild pink salmon in adjacent regions of Alaska increased during this period, further indicating increased hatchery production of pink salmon influenced the decline of wild pink salmon in PWS.

Increased intraspecific competition for prey in PWS and at sea was identified as a key mechanism affecting wild PWS pink salmon. In support of the competition hypothesis, the food demand of juvenile pink salmon in PWS reportedly exceeded the standing stock of preferred prey during July when salmon densities were high (Cross et al. 2005), resulting in reduced growth, greater size-dependent predation, and higher mortality (Willette et al. 2001), although a bioenergetic model approach suggested prey availability may be adequate (Boldt & Haldorson 2002). Adult body size of wild PWS pink salmon also declined with greater releases of hatchery pink salmon, leading to reduced fecundity and a loss of approximately 1 million wild adult pink salmon per year (Wertheimer et al. 2004). More recently, using 60 yr of data on wild pink salmon abundances, hatchery releases, and ecological conditions in the ocean, Ohlberger et al. (2022) provided evidence that hatchery pink salmon releases into PWS (i.e. 700 million fish yr^{-1}) reduced productivity of wild pink salmon by 55%. That study also provided evidence that productivity of emigrating juvenile pink salmon declined with increasing numbers of returning pink salmon, thereby supporting the hypothesis that biennial patterns in adult pink salmon are partly related to brood interactions at sea (Ruggerone & Nielsen 2009, Krkosek et al. 2011, Irvine et al. 2014).

Analyses of scale growth of pink salmon sampled in the GOA and adult pink salmon returning to PWS hatcheries indicated significant size-selective mortality of juvenile pink salmon during and after the first growing season — slower-growing salmon experienced reduced survival (Cross et al. 2008, 2009). A potential bottleneck for growth during early to mid-July was observed, corresponding with fewer zooplankton. The authors concluded that the large influx of juvenile pink salmon into the GOA, in conjunction with the seasonal dynamics of zooplankton prey, could create localized prey depletions, density-dependent growth, and reduced survival (see Section 3.1).

Most, but not all, studies have observed density-dependent growth of pink salmon at sea. Body length and scale growth of pink salmon sampled in the central BS and in the western NPO during 1972–1998 were negatively correlated with catch per

unit effort of pink salmon in the non-selective research gillnets (Ishida et al. 1995, Azumaya & Ishida 2000), consistent with a 23% decline in pink salmon stomach fullness in odd- compared with even-years, 1991–2000 (Davis 2003). Body weight of maturing Fraser River pink salmon declined as zooplankton availability declined at Ocean Station P, 1957–1977 (odd years only, $r = -0.86$, $p < 0.001$; Peterman 1987). In BC (1951–1993) and Puget Sound, Washington (1959–1999), weight of odd-year adult pink salmon declined up to 40% with increasing pink salmon abundance (Welch & Morris 1994, Ruggerone & Nielsen 2004, Jeffrey et al. 2017). In Russia, size of pink salmon migrating through the Kuril Islands and returning to the Sea of Okhotsk region was negatively correlated with pink salmon biomass, 1991–2003 (Shuntov & Temnykh 2005). Throughout Asia and North America overall, the combined average weight of adult pink salmon declined with increasing pink salmon abundance, 1925–2015 (Ruggerone & Irvine 2018).

Density-dependent growth was not observed in other studies. For example, second-year scale growth of pink salmon sampled south of the central Aleutian Islands was positively correlated with Asian pink salmon abundance after the 1977 regime shift (1983–1995), but negative prior to the 1977 shift (Walker et al. 1998). Size of pink salmon returning to eastern Kamchatka was not related to Kamchatka pink salmon abundance, 1971–2001 (Shuntov & Temnykh 2005).

3.5. Seabirds

Most species of seabirds in the subarctic NPO fall into a functional planktivore or omnivore trophic guild (Text S2). Overlap in diet between guilds does occur, and the guilds are separated by somewhat less than one trophic level. Diets in both guilds overlap extensively with diets of pink salmon, which prey on the same species and taxa of zooplankton and fishes (Text S2). Evidence of interactions between resident seabirds and pink salmon can be found across a broad region from the western Aleutian Islands to the eastern GOA, and in 1 migrant species from the southern hemisphere that spends the austral summer primarily in the BS and Chukchi Sea.

3.5.1. Southeastern Bering Sea and Aleutian Islands

Biennial patterns in numerous elements of the diets and breeding biology of several species of seabirds in

both guilds were conspicuous in the Aleutian and Pribilof Islands in the BS in 1988–2012 (Springer & van Vliet 2014; Supplement 2). Although biennial patterns in all nesting parameters of all species were not found at all colonies, among omnivores, nesting phenology (indexed by hatch date) was later in odd years compared to even years for as many as 6 species nesting at as many as 4 colonies (e.g. Fig. 13). Clutch sizes of the 2 species that lay more than 1 egg were smaller in odd years. Laying success, hatching success, fledging success, and productivity (chicks per nest attempt) of 3 or more species at up to 3 colonies were lower in odd years. The biennial differences indicated that foraging conditions for those species in late spring through summer were better in even years than in odd years. A biennial pattern in the stress hormone corticosterone in thick-billed murres *Uria lomvia* at St. George Island, which is rel-
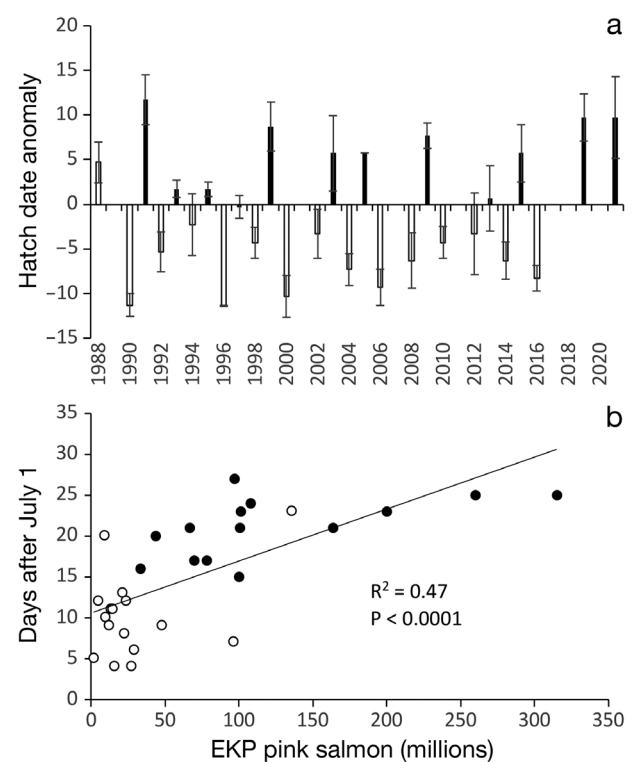

Fig. 13. (a) Phenology of tufted puffins at Buldir Island (Aleutian Islands) indexed as average hatch date each year relative to overall average hatch date across all years (no. of d relative to July 15). No data were acquired in 1989, 2017, or 2020; n = 1 nest in 2001, 2007, and 2018 and were excluded. (b) Relationship (linear regression) between eastern Kamchatka pink salmon abundance (EKP) and tufted puffin annual average hatch date (no of d after 1 July). Open bars and circles = even years; filled bars and circles = odd years. Tufted puffin data from Higgins et al. (2022); pink salmon data from Ruggerone & Irvine (2018) and Ruggerone et al. (2021)

atively high in odd years and low in even years, further supports a nutritional stress explanation for biennial variability in nesting characteristics of omnivores (Text S2).

Patterns in nesting parameters of planktivores were out of phase with those of the omnivores (Springer & van Vliet 2014). The hatching phenology of as many as 4 species at 2 locations in the Aleutian Islands and 1 species at the Pribilof Islands was earlier in odd years of higher pink salmon abundance than in even years of lower abundance. Additionally, the fledging success and productivity of 1 species at St. George Island (Pribilof Islands) were higher in odd years. Thus in contrast to omnivores, by these measures foraging conditions for planktivores apparently were better in odd years than in even years. We presently do not propose a mechanism for this observation.

In contrast, planktivorous least auklets *Aethia pusilla* at Buldir Island (western Aleutians) consumed *Neocalanus plumchrus/flemingeri*, a primary prey, in greater amounts in even years than in odd years, and consumed more of 4 out of 5 secondary prey in odd years (Springer & van Vliet 2014). Likewise, planktivorous whiskered auklets *A. pygmaea* at Buldir consumed more *N. cristatus*, a primary prey, in even years than in odd years. Those biennial dietary patterns are opposite patterns of breeding biology and suggest that even years are good relative to odd years, as in the case of the omnivorous species, and are consistent with evidence discussed above that pink salmon deplete stocks of large copepods in odd years.

Several nesting parameters of the omnivores were highly correlated with the abundance of eastern Kamchatka pink salmon (Springer & van Vliet 2014). For example, the phenology (mean hatch date of eggs) of tufted puffins *Fratercula cirrhata* at Buldir has been relatively late in odd years and early in even years since data were first acquired in 1988 (Fig. 13). In addition, annual hatch dates have been highly correlated with the abundance of eastern Kamchatka pink salmon, the dominant pink salmon population in this region. The relationship is very strong across all years, but differs between even and odd years — it is weaker in even years (linear regression, p = 0.13) and stronger in odd years (p = 0.03). As the mean abundance of pink salmon in even years since 1988 (30.4 ± 9.0 million [SE]) has been just 24% as large as in odd years (124 ± 22 million), the implication is that for the most part, only in odd years and rare even years of uncommonly high returns are pink salmon sufficiently abundant to materially alter prey fields to the detriment of tufted puffins, and by extension other seabirds. Among prey important to both tufted puffins and pink salmon are squids (Davis et al. 2005, Higgins et al. 2022), which also have been implicated as an important variable in competition for prey between pink and other species of salmon as noted above. Nesting parameters of the planktivores in the Aleutian and Pribilof Islands were not correlated with eastern Kamchatka pink salmon. We do not understand the reason for a lack of correlation, but it may be related to the even-year bad, odd-year good pattern in breeding parameters, which is opposite that of the omnivores.

3.5.2. Prince William Sound

The productivity of black-legged kittiwakes *Rissa tridactyla* in PWS has been monitored systematically since 1985 (Irons 1996, D. B. Irons unpubl. data), and since 1990, it has been positively correlated with annual returns of PWS pink salmon (wild + hatchery, linear regression, p = 0.032). Overall during that time, pink salmon returns were nearly twice as large in odd years as in even years (55 ± 7.2 vs. 34 ± 3.9 [SE] million salmon; t-test, p = 0.018). Notably, the relationship to kittiwake productivity was driven primarily by hatchery stocks (linear regression, p = 0.030) and not wild stocks (p = 0.31).

That positive relationship to pink salmon is opposite the negative relationship at Chowiet Island in the western GOA (Text S2), and in the BS as discussed in Section 3.5.1 and in Text S2. For PWS, several sources of evidence lead to the hypothesis that predation on kittiwake eggs and chicks rather than competition is the primary driver of this pattern. First, a major factor in the nesting success of kittiwakes in many PWS colonies is the level of egg and chick loss to bald eagles *Haliaeetus leucocephalus*, peregrine falcons *Falco peregrinus*, common ravens *Corvus corax*, and glaucous-winged gulls *Larus glaucescens*; the presence of these aggressive predators also causes adult kittiwakes to stay away from nests for extended periods, which allows opportunistic predators such as northwestern crows *C. caurinus* and black-billed magpies *Pica pica* to prey upon nests (Suryan et al. 2006, Robbins 2009, McKnight et al. 2020). Second, kittiwakes in PWS typically lay eggs in early June on average, which hatch in early July, and chicks leave the nest in approximately mid- to late August (Suryan et al. 2006). The PWS pink salmon run begins in mid-June and extends through late July to mid-September (ADFG 2022), thus overlapping entirely with the kittiwake nesting season. Third, McKnight et al. (2020) found that kittiwake productivity at 1 colony in PWS was higher in years

of earlier pink salmon runs than in years of later runs, i.e. more salmon throughout the full nesting season in early run years diverted avian predators. We hypothesize an analogous scenario: in odd years of high pink salmon returns, the attention of avian predators is focused more on them, which provide a much higher energetic return on investment than kittiwake eggs and chicks, and PWS kittiwakes thereby achieve higher reproductive output than in even years of low pink salmon returns.

3.5.3. Southern Hemisphere

Short-tailed shearwaters *Ardenna tenuirostris*, trans-hemispheric migrant seabirds that breed in Australia and Tasmania and spend the austral winter primarily in the BS and Chukchi Sea, also have been linked to pink salmon through diet overlap and competition for prey. They are very abundant, on the order of 25–30 million, and provide terrestrial ecosystem services by aerating soils and promoting vegetation growth in nesting colonies where they burrow. They further provide cultural and societal services to Indigenous peoples who have harvested chicks for millennia.

Short-tailed shearwaters in the BS were found to be in poorer physiological condition and to die in greater numbers in odd-year summers in 1981–1990 (Lobkov 1991); and in 2002–2008, their body mass and liver mass were negatively correlated with pink salmon biomass, which was 23 times higher in odd years than in even years (Toge et al. 2011). In the southern hemisphere beginning in 2007, major mortalities of adults occurred in every odd year (but none in even years) through at least 2013 as the birds arrived on their nesting grounds after returning from the NPO (Springer et al. 2018). Shearwaters depend upon fat reserves acquired on northern feeding grounds to carry them through their 15 000 km non-stop southward migration, and because the birds in the die-offs were emaciated, it appeared that those reserves were insufficient in odd years. Mean and median abundance indices of nesting short-tailed shearwaters at 2 well-studied colonies were consistently greater in even years than in odd years during 1976–2016 at one colony and between 1997 and 2015 at the other colony. The biennial differential at both colonies was most pro-

nounced in 2005–2016, when pink salmon abundance was exceptional, especially in odd years (Fig. 1) — in this interval, the median even:odd year ratio of nests was 1.49 at Montague Island and 1.16 at Furneaux Island (Springer et al. 2018).

3.6. Humpback whales

Humpback whales *Megaptera novaeangliae* migrate to northern SEAK to feed on forage fishes and euphausiids during spring through fall, returning south to Hawaii and Mexico in winter to breed while also fasting (Gabriele et al. 2017). Using data from Neilson et al. (2022) we calculated that from 1985 to 2013, the 'crude birth rate' was 33 % lower in odd years (7.5 ± 0.7 % [SE]) than even years (11.3 ± 1.1 %; *t*-test, df = 27, p = 0.006; Fig. 14). In 14 of 19 odd years, the crude birth rate was lower than the mean birth rate in the adjacent even years (Fig. 14). The onset of marine heat waves in 2014 may have reduced the magnitude of the biennial pattern.

The mechanism leading to this previously unreported biennial pattern is uncertain, but we hypothesize it is related to pink salmon and their effect on the prey of humpback whales in SEAK. Humpback whales feed on forage fishes, such as herring and capelin, and euphausiids (Jurasz & Jurasz 1979, Krieger 1990), all of which may be influenced by pink salmon (see Section 3). Fewer calves were observed during summer in odd than even years, based on counts reported by Neilson et al. (2022). Those whales were born the previous winter following an even-year
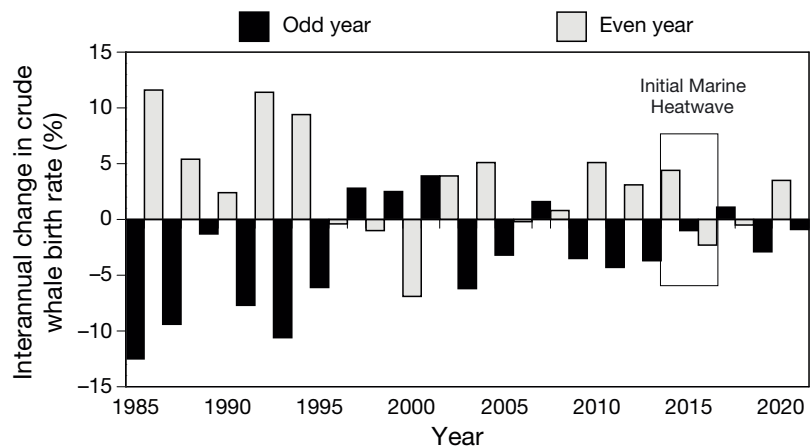

Fig. 14. Interannual change in crude birth rates of humpback whales in Southeast Alaska during even and odd years, 1985–2021. Crude birth rate is the number of unique calves divided by the total number of unique whales observed in Glacier Bay and Icy Strait from 1 June to 31 August (Gabriele et al. 2022, Neilson et al. 2022). Interannual change in birth rate (*BR*) in year *i* = BR_i − avg. (BR_{i-1}, BR_{i+1})

summer in which pink salmon were less abundant (see Fig. 5a). However, the parent breeding season was during the previous winter, following an odd year in which pink salmon were more abundant. Thus, the feeding rate and nutritional state at the end of odd years may have affected the mating and/or gestation of the parents, leading to fewer calves observed in SEAK during the following odd year.

3.7. Southern Resident Killer Whales

Southern resident killer whales (SRKWs) rarely eat pink salmon (Ford et al. 2016), yet this critically endangered population, which ranges from central California to mid-Van-couver Island and into the Salish Sea, exhibited a highly unusual biennial pattern in both successful births and mortality. From 1998 to 2020, mortality of newborn and older SRKWs was 3.1 times higher (65 versus 21 deaths) and successful births 42% lower (19 versus 33 calves) in even than in odd years as the population decreased from 92 to 74 animals (Fig. 15a; Ruggerone et al. 2019, CWR 2021). The biennial pattern was not apparent during the earlier period (1976–1997) when the population was stable or increasing, the primary prey (Chinook salmon) were more abundant, and pink salmon were less abundant. SRKWs feed primarily in the Salish Sea during spring through early fall on maturing Chinook salmon (Ford et al. 2016). Ruggerone et al. (2019) hypothesized that pink salmon, whose escapement to Salish Sea rivers increased 135% during the period of SRKW decline, interfered with the for-aging efficiency of the animals as they attempted to capture Chinook salmon. Both returning Chinook and pink salmon concentrate along the west side of San Juan Island and into Boundary Pass from late July through early September, but pink salmon are only abundant in odd years (avg. 18 million versus 0.4 million in even years). In odd years, pink salmon are approxi-mately 50 times more abundant than co-migrating Chinook salmon. Accord-ing to the hypothesis and support from

available data (Fig. 15a), reduced foraging efficiency of SRKWs in odd years when pink salmon are abun-dant would lower their nutritional status, which would be expressed in the following even year (in-creased mortality and fewer successful births) be-cause these large mammals have a strong physiolog-ical buffering capacity (Ford et al. 2010).

Body condition measurements also support the hypothesis that prey consumption by SRKWs was reduced in odd years, potentially in response to abundant pink salmon (Stewart et al. 2021). During 2008–2019, the body condition index of the L Pod of SRKWs, which was measured in September after most pink salmon have passed through the SRKW
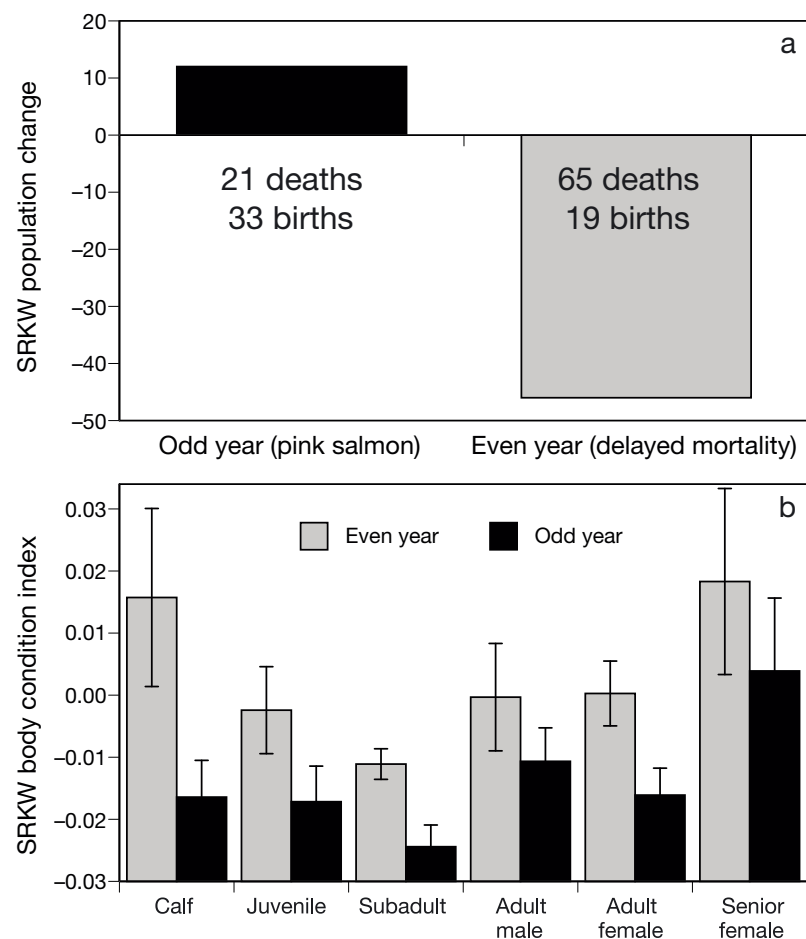

Fig. 15. (a) Southern resident killer whale (SRKW) population declined 20% from 1998 to 2020, including 46 fewer individuals in even years (19–65 ani-mals) after interacting with abundant pink salmon in the previous odd year but increased by 12 individuals in odd years (33–21 animals) due to more suc-cessful births and fewer deaths (Ruggerone et al. 2019, CWR 2021). (b) From 2008 to 2019, annual mean (±1 SE) body condition of each age class of L Pod (SRKW) in September was lower during odd years after numerous pink salmon had migrated through the Salish Sea, the primary feeding area of SRKWs during summer. Body condition measurements were taken from Fig. S6 of Stewart et al. (2021), who recognized the biennial pattern in relation to pink salmon

foraging area, was markedly lower on average during odd versus even years in each of the 6 age categories (Fig. 15b). A biennial pattern in body condition was not readily apparent in J and K pods, populations that have declined less than the L pod since 1997. From 1998 to 2020, approximately 55% of mortality and 90% of the population decline was associated with the L Pod, which exhibited strong biennial patterns in body condition, mortality, and successful births.

Understanding the mechanism of this biennial pattern is critical to the recovery of the endangered SRKW population. For example, if births and mortality during even years had been similar to those during odd years, especially within the L Pod, then the SRKW population would have substantially increased rather than decreased during the past 20 yr (Fig. 15a). In recent years, however, SRKWs have reduced foraging time in the Salish Sea (Shields et al. 2018, Ettinger et al. 2022), a behavior that may influence the extent to which the biennial pattern holds into the future.

4. DISCUSSION

Our synthesis reveals compelling evidence for top-down effects of pink salmon on numerous pelagic species, food webs, and ecosystem function spanning broad regions of the western, central, and eastern NPO, the BS, and semi-enclosed waters including PWS and the Salish Sea (Table 1; Supplement 2). Those effects were largely, but not entirely, unknown until scientists began to notice and track biennial patterns in marine organisms that coincided with the biennial patterns of pink salmon abundance. For instance, regular large interannual differences in sockeye salmon diets were documented in the 1950s (Ito 1964), long before the spectacular rise in pink salmon abundance. Overall, pink salmon apparently have interacted strongly with other species in the NPO for many decades, playing important top-down roles in structuring pelagic ecosystems.

4.1. Conceptual model

We developed a conceptual model that synthesizes our hypotheses based on evidence discussed in Section 3 (Table 1; Supplement 2). It 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 *Berryteuthis anonychus*. The following points highlight key dynamics implied by what we refer to as the 'Pink Salmon Impacts Model,' and are elaborated upon in Text S3 and Fig. 16.

(1) Warming in the north increases pink salmon abundance, especially odd-year adult returns (Fig. 1).

(2) Biennial variability in predation by pink salmon drives biennial fluctuations of squid abundance (*B. anonychus*), including adult squid, their progeny, and subsequent generations as a result of the 2 yr life cycle of squid (Section 3.3).

(3) Pink salmon can initiate pelagic trophic cascades through predation on large herbivorous zooplankton, lowering their abundance, which can lead to greater biomass of phytoplankton (Section 3.1).

(4) Abundant odd-year pink salmon efficiently exploit prey (zooplankton, small fishes, squid), thus reducing prey needed by other salmon species, forage fishes, and seabirds for growth, productivity, and survival, especially in odd years (Section 3). In a warming ocean, reduced prey availability, especially energy-rich squid and fishes, is particularly harmful for larger and older salmon such as Chinook salmon (Beauchamp 2009). Most salmon evidence involves interactions after their first year at sea, indicating the importance of late marine life to growth, survival, and abundance.

(5) Forage fishes, which are critical prey for many marine species, also exhibit biennial growth or abundance patterns in relation to biennial pink salmon abundance and their predation on common prey resources (Section 3.2).

(6) Humpback whales and SRKWs exhibit biennial demographic patterns that are related to pink salmon (Sections 3.6 and 3.7, respectively).

(7) The intensity of species interactions and regularity of biennial patterns varies across time and ecosystems. The strength of competition in the shared resource spaces is not expected to be equal across all species and locations, and the effects of pink salmon may interact with those of oceanographic conditions, weather, and climate. Thus, interrupted and emerging biennial patterns would not necessarily share common time frames.

Our conceptual model does not specifically address early life stages at sea of salmon in more southerly regions, such as in the Pacific Northwest or Japan, where climate warming generally leads to less favorable conditions for them during early life at sea compared with those in the north (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 that migrate
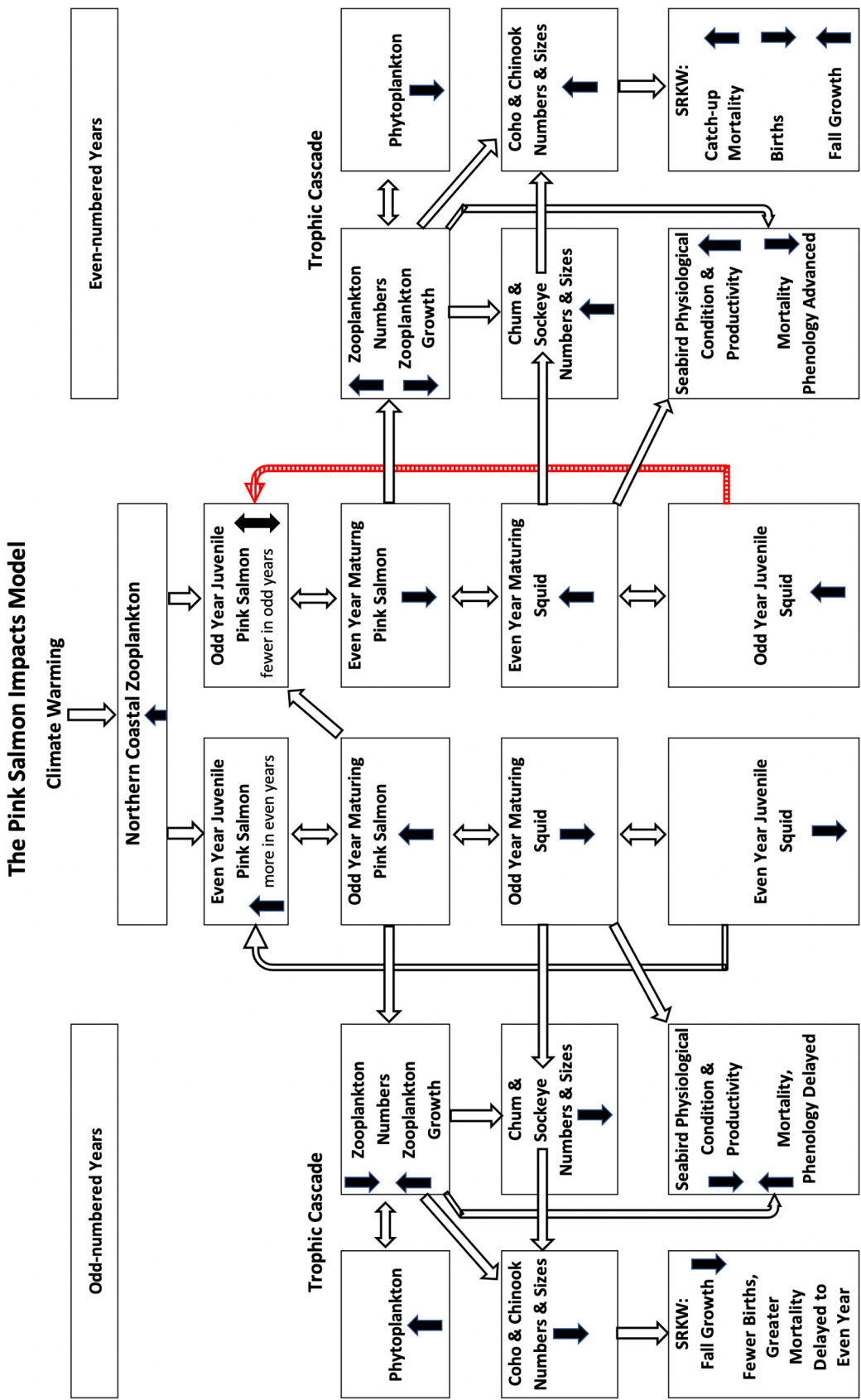
Fig. 16. The conceptual Pink Salmon Impacts Model showing how climate warming, biennial variation in pink salmon abundance, and biennial squid dynamics may influence offshore ecosystems in the North Pacific Ocean and Bering Sea. Solid arrows indicate an increase or decrease in either population abundance, growth or other variable. Hollow arrows indicate direction of influence. Red dashed arrow indicates negative competition effect of increasing juvenile squid. Although both odd and even calendar-year pink salmon abundances are currently increasing over time, odd years here reflect effects of higher pink salmon abundances relative to even years. See Section 3 for linkages to forage fishes and other species, and Text S3 for more details on the model

north into the GOA, BS, and beyond, including Chinook salmon (Larson et al. 2013), have experienced substantial declines in size, survival, and abundance (Welch et al. 2021, Buckner et al. 2023). We hypothesize that those north-migrating salmonids from the Pacific Northwest and Japan have low marine survival due to less favorable conditions during early life at sea and to reduced foraging opportunities after the first winter at sea, especially for energy-rich squid and small fishes needed to sustain larger and older Chinook salmon in a warming ocean (Section 3).

4.2. Competition exacerbated by climate warming — the case of salmon

We hypothesize that pink salmon and the warming of the NPO and adjacent seas will synergistically enhance competition between pink salmon and other marine species until continued warming leads to declines of all salmon species. Pink salmon abundance has more than doubled in the NPO since the mid-1970s ocean climate regime shift, associated warming, and increased hatchery production (Fig. 1). Pink salmon appear to have initially benefitted from increased abundance of zooplankton in northern regions (e.g. Brodeur & Ware 1992, Brodeur et al. 1996), potentially leading to faster early marine growth and improved survival compared with that prior to the mid-1970s (Ruggerone et al. 2007, Cross et al. 2009). However, warming ocean temperatures also exacerbate competition, because greater consumption of high-calorie prey is needed to offset increasing physiological demands imposed by higher temperature, especially for larger Chinook salmon (Brett 1979, Hinch et al. 1995, Beauchamp 2009, Piatt et al. 2020). Pink salmon are smaller, tend to consume prey more effectively at low densities, and more efficiently utilize food at higher temperatures than other salmon species (Davis et al. 1998), likely factors contributing to their exceptional growth in abundance in recent decades. Thus, the combined effects of greater pink salmon abundance, reduced physiological efficiency in other species at higher temperatures, and apparently fewer high-calorie prey partly in response to increasing predation by pink salmon, in addition to other oceanographic conditions (e.g. Mueter et al. 2002, 2003, Wells et al. 2008, Stachura et al. 2013, Cunningham et al. 2018, Ohlberger et al. 2019, Howard & von Biela 2023), have likely contributed to the long-term and widespread declines in growth and size of all salmon species throughout most of their range (Bigler et

al. 1996, Oke et al. 2020). Furthermore, continued warming is also projected to shrink the amount of thermally suitable marine habitat available to each species (Abdul-Aziz et al. 2011, Lindley et al. 2021) and force more salmon into an increasingly crowded BS (Larson et al. 2013, Kaeriyama 2023).

Frequent marine heat waves and high pink salmon abundance are hypothesized to have led to the largest single-year collapse in salmon abundance on record (Ruggerone et al. 2021). Heat waves in the NPO were unusually frequent during 2014–2019 (Litzow et al. 2020b). In 2018 and 2019, a combined 1.34 billion adult pink salmon returned from the NPO, the highest 2 yr abundance since at least 1925 (Fig. 1). In 2020, the combined commercial harvest of all salmon species in Asia and North America declined more relative to average catch in the previous 10 yr (187 million salmon decline) than in any previous 10 yr period since 1925; escapement information indicated that low abundance rather than the COVID-19 pandemic was responsible (Ruggerone et al. 2021). Harvests of Chinook salmon in 2020 were the lowest on record since 1925, declining 54% compared with the previous 10 yr. Chum salmon harvests in 2020 declined 42%, followed by pink (−40%), coho (−27%), and sockeye salmon (−10%). Sockeye salmon harvests beyond those in Bristol Bay declined 44%. In 2021, commercial harvests of pink salmon rebounded to a record level (527 million, or 81% of all salmon), but harvests of chum (−41%), Chinook (−33%), coho (−24%), and sockeye salmon beyond Bristol Bay (−26%) remained low relative to 2010–2019. Harvest of Chinook salmon was the fourth lowest on record (NPAFC 2022a). Thus, the combined effects of both pink salmon and ocean temperatures appear to have contributed to the sharp recent decline in Pacific salmon.

4.3. Implications for salmon hatcheries and ocean carrying capacity

Annual releases of Pacific salmon from hatcheries increased 6-fold from 1970 (0.9 billion juveniles) to 1990 (5.1 billion juveniles), producing approximately 25% of all adult salmon, or 40% of the total mature and immature salmon biomass at sea (Ruggerone & Irvine 2018). This steep rise in overall hatchery production in Asia and North America occurred in part because the primary bottleneck for increased salmon abundance was thought to be in freshwater, and managers believed hatcheries would enable a rapid return to the large harvests that occurred in the early

1900s (Larkin 1974). Also, simulation models and sampling of zooplankton at sea suggested the NPO could readily support more salmon (Sanger 1972, Favorite & Laevastu 1979, Honkalehto 1984, Shuntov et al. 2017). However, some scientists suggested that the ocean could not support large-scale hatchery production without some adverse effects on wild salmon growth and survival (Peterman 1978, 1984a,b), but evidence was somewhat limited at that time (Moberly 1983, Heard 1998, Cooney & Brodeur 1998, Pearcy et al. 1999). Furthermore, Cooney & Brodeur (1998, p. 460) warned 25 yr ago that '[t]o ignore the signals manifested in diminished size of Pacific salmon is to invite potential disaster for these and other resources.' Nevertheless, from 1990 to 2020, annual juvenile salmon released from hatcheries in relatively pristine regions of Alaska and Russia increased by 50 and 75 %, respectively, or by approximately 555 million juvenile salmon per year in each region (NPAFC 2022b).

Although hatchery salmon may lead to net gains in commercial harvests in local fisheries, these gains can come at the expense of local wild populations (Amoroso et al. 2017, Ohlberger et al. 2022) and distant populations that co-mingle with them, including depleted and at-risk wild populations from the Pacific Northwest and Alaska (Ruggerone et al. 2012, Larson et al. 2013, Cunningham et al. 2018, Frost et al. 2021). Furthermore, large-scale hatchery production can undermine the natural compensatory density-dependent response that would otherwise benefit wild salmon growth, maturation rate, and reproductive potential during periods of low abundance. For example, in the absence of hatchery salmon, wild salmon would potentially grow faster and thereby have higher reproductive potential (egg mass is proportional to female body mass) at a given age, mature at an earlier age, and therefore have greater survival at sea. The unique biennial patterns shown by salmon interacting with pink salmon provide strong evidence that large-scale hatchery production has unintended consequences and can lead to a tragedy of the commons. The latter topic is expanded upon by Holt et al. (2008).

Some scientists have argued that competition among salmon for prey at sea is limited, and that hatchery fish have little effect on wild populations (Favorite & Laevastu 1979, Shuntov et al. 2017, 2019, Radchenko et al. 2018, Naydenko & Somov 2019). This view is based on calculations suggesting a surplus biomass of prey is available to salmon — that consumption by salmon is only about 1–15 % of prey consumed by all epipelagic nekton — and because

salmon do not form dense schools that might deplete local concentrations of prey. However, those studies did not consider the nutritional value for each prey species, capture efficiency, or predation risk while foraging. Moreover, they have yet to explain widespread observations of density-dependent growth and survival of salmon, especially the unique biennial patterns of pink salmon abundance that are expressed in the growth, age, survival, and abundance of competing salmon species. Furthermore, investigators such as Shuntov et al. (2017, 2019), who argued that competition among salmon is limited, have investigated the western BS and/or western North Pacific, whereas most studies reporting evidence for competition among salmon were in other regions. Consequently, neither group of scientists has a reason to generalize too widely and deny the validity of the observations and conclusions of the other group.

Salmon typically do not form dense schools while foraging at sea, but they are often found in aggregations or groupings (Hartt & Dell 1986). Evidence collected over multiple decades of sampling salmon on the high seas indicates a significant trade-off between predation risk and foraging success in relation to group size. For sockeye, chum, coho, and pink salmon, the probability of injury (predation risk) decreased with increasing total group size (all salmon species) and conspecific group size, but the probability of consuming prey also declined for each species except pink salmon (Polyakov et al. 2022). For example, the probability of consuming prey declined approximately 20 % for sockeye salmon, 6 % for chum salmon, and 45 % for coho salmon as total group size increased (up to about 2500 salmon per seine net). These findings suggest that salmon groups can deplete local concentrations of prey (Section 3), and that competition is exacerbated by forming groups to reduce predation risk. The decline in prey consumption was greatest for the largest and oldest salmon, which is consistent with the growth decline in older salmon such as Chinook salmon in relation to pink salmon (Section 3). In contrast, pink salmon were not adversely affected by competition, and appeared to experience greater probability of consuming prey when in larger groups.

4.4. Implications of pink salmon on other marine species, ecosystem services, and society

Most of the relationships between pink salmon and other pelagic species reported here imply direct

competition between them for common-pool prey resources or indirect food web responses to pink salmon. Details of the actual mechanisms are not always known. Nonetheless, unique biennial effects have been seen in lower physiological condition, delayed nesting phenologies, lower breeding propensity, lower productivity, and higher mortality of seabirds; slower growth and lower recruitment in forage fishes; fewer births in humpback whales; and reduced body condition, higher death rate, and reduced birth rate of SRKWs (Table 1). In the case of black-legged kittiwakes in PWS, higher numbers of pink salmon appear to enhance the birds' nesting success as a result of avian predators switching from kittiwake eggs and chicks to pink salmon.

The negative effects of pink salmon on the growth, survival, and abundance of other salmon also impacts commercial, subsistence, recreational, and cultural values humans derive from them. Although climate warming has enhanced overall harvests of sockeye salmon in Bristol Bay, for example, approximately 59 million fewer sockeye salmon returned there during 1977–1997 (excluding the cyclic Kvichak population) after interacting with abundant pink salmon in odd-numbered years, and those fish would have had a value to fishermen of approximately US $310 million if they had survived (Fig. 8d; Ruggerone et al. 2003). In many regions of the Pacific Rim, especially in the Arctic–Yukon–Kuskokwim region of western Alaska, people depend on salmon for subsistence and cultural needs in addition to monetary income from commercial fisheries (Brown et al. 2022). Salmon subsistence harvests, particularly Chinook salmon, have declined over the past 25 yr, and this may partially reflect adverse interactions with pink salmon (e.g. Ruggerone et al. 2012, 2016b, Agler et al. 2013, Cunningham et al. 2018, Frost et al. 2021). Although declines in the abundance of salmon are the most obvious impact to humans, declining body size of salmon over time, which is partially linked to growing abundances of pink salmon, also has the potential to affect both humans and ecosystem services such as meals, price, eggs, and marine-derived nutrients per fish (Bigler et al. 1996, Oke et al. 2020).

Lastly, salmon are typically managed for the number of spawners or for harvest rates that rarely consider the size and fecundity of the spawning salmon and the ecosystem services they provide. Such management practices ignore the fact that decreasing body size, which is often related to increasing abundances of pink salmon, leads to fewer eggs being deposited in the spawning gravel for an equivalent number of fish (e.g. Shaul & Geiger 2016, Ohlberger et al. 2020). Declining body size and fecundity in relation to competition for prey can reduce future abundance of salmon, especially Chinook salmon, whose size, fecundity, and abundance has sharply declined over time (Section 3.4.4, Fig. 10).

5. CONCLUSIONS

The most parsimonious explanation for the many, widespread biennial patterns across the broad range of species and trophic levels in the NPO documented in this synthesis is the interaction with pink salmon. The evidence is consistent and strong that pink salmon can exert competitive dominance for common-pool prey resources shared by 4 forage fish species, all 5 species of Pacific salmon and steelhead trout, and 11 species of seabirds (Table 1; Supplement 2). It further indicates that pink salmon can have a strong influence on ecosystem structure and function by, for example, initiating pelagic trophic cascades. Whether or not it can be considered a keystone species sensu Power et al. (1996), pink salmon is clearly a very strongly interacting species in marine ecosystems of the NPO.

We cannot identify every link between pink salmon and other species. However, competing upper trophic level predators serve as proxies for the inferred direct effects pink salmon have on lower trophic level populations of food web species, including zooplankton, forage fishes, and squids. The present lack of abiotic explanations for the many biennial patterns in the natural histories of numerous species that interact with pink salmon should not be construed as evidence that physical forcing, or other biological factors, are not important to them directly or indirectly. Effects of the recent Pacific Marine Heatwave on ocean food webs and individual species are prime examples of such physical forcing (Piatt et al. 2020, Arimitsu et al. 2021).

Scientists should take advantage of the predictable biennial pattern in abundance of pink salmon, and their increasing numbers in response to ocean heating, to test these and other hypotheses about ecosystem function and species and food web interactions. Although the vast spatial scales of oceanic regions limit possibilities for true treatment–control manipulations, the biennial fluctuations fortunately create a unique natural 'experiment' that can illuminate the influence of pink salmon on their competitors and lower trophic levels. Future ecosystem models should include pink salmon as top-down drivers, in addition

to the bottom-up drivers of climate and physical oceanographic forcing. Such information is necessary for effective ecosystem-based management, especially of species harvested by humans (Malick et al. 2017b).

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