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Trends in Chinook salmon spawner abundance and total run size highlight linkages between life history, geography and decline

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Abstract

Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) are foundational to social-ecological systems of the Northeast Pacific Rim and exhibit a rich diversity of life histories including in their adult migration timing, age at critical life-history transitions and marine feeding distributions. In recent decades Chinook have experienced declines across much of their native range; however, changes in productivity and abundance have rarely been evaluated in relation to life-history variation. To understand trends in Chinook salmon production, and how they are related to life history, we compiled time series data from the Fraser River to the Sacramento River on total run size (pre-fishery abundance) and escapement (post-fishery spawner abundance) and fit time series models to estimate trends across this bioregion. Our analysis revealed that most Chinook populations are declining, with negative trends in escapement (57 of 79) and total run (16 of 23) size. Trends were most acutely negative for interior spring Chinook in the Fraser, Columbia and Snake Rivers and most populations in California. Summer and fall Chinook had mixed trends, with several summer and fall upriver bright populations in the interior Columbia and Fraser exhibiting increases in abundance from the 1990s to 2019. Our research reveals widespread declines of this important species, but local complexity in trends that are mediated by population-level life history, migratory behaviours and watershed-scale restoration actions. Understanding linkages between life histories and resilience should inform rebuilding efforts for Chinook salmon and highlight the need to conserve intraspecific biodiversity.

KEYWORDS
endangered species, fisheries management, life history diversity, mixed-stock fisheries, *Oncorhynchus tshawytscha*, time series analysis

1 | INTRODUCTION

Migratory animals traverse diverse and often distant habitats to exploit spatial and temporal variability in climate and ecosystem productivity and to fulfil the distinct needs of each of their life stages. Many migratory species are also keystones of ecosystems, cultures and economies, and their predictable arrival sustains rich ecological and human communities (Lundberg & Moberg, 2003; Schindler et al., 2013). Migration routes traversing multiple governmental jurisdictions create unique challenges for conservation and management across of these species (López-Hoffman et al., 2017; Runge et al., 2014; Vierros et al., 2020), when natural or anthropogenic impacts on habitats and species survival rates may be felt hundreds or thousands of kilometres away (e.g. Springer et al., 2018). Climate change is also creating unique challenges among migratory species for whom timing can be a matter of life and death, and well documented climate-driven changes in the phenology of key ecological events are already impacting survival and reproductive success for some species (Dingle, 2014; Rand et al., 2006; Robinson et al., 2009; von Biela et al., 2022).

Highly mobile species often exhibit diverse life histories, phenology and reproductive strategies that have evolved in response to the range of physical and biological conditions they confront during different stages of their lives. All told, this diversity can stabilize population and ecosystem dynamics, providing more reliable ecological, cultural and economic benefits in social-ecological systems (Moore et al., 2014; Oken et al., 2021; Schindler et al., 2010). However, life histories may also influence the exposure, and thus vulnerability, of specific populations to different stressors. Effective conservation of migratory species is, therefore, contingent on understanding and protecting their diversity and on cooperation across jurisdictional boundaries to protect habitats and vulnerable populations.

Pacific salmon (*Oncorhynchus* spp.) are among the most widely distributed, abundant and diverse migratory animals on the planet and play a foundational role in ecosystems and cultures across their native range (Earth Economics, 2021). Their long-distance, anadromous migrations link the distant and productive marine habitats of the North Pacific to watersheds draining the Asian and North American continents. Salmon exhibit tremendous intraspecific life-history diversity, including diversity in age and size at key life-history transitions (e.g. seaward migration, maturity), and spatiotemporal variation in their distribution at sea, migration timing and behaviour, spawn timing and relative reproductive investment (Groot & Margolis, 1991). Driven be the selective pressures of local adaptation and the interplay between homing and straying, genetic and life history diversity is shaped by the successive demands of freshwater spawning migrations, juvenile rearing and multi-year marine feeding migrations (Quinn, 2005). This diversity promotes resilience within populations and the social-ecological systems they support, since it encompasses evolutionary adaptations and portfolio effects that stabilize population responses to climate and habitat variability, lengthen the annual duration of harvest opportunities for salmon predators (including humans), and spread risks and opportunities
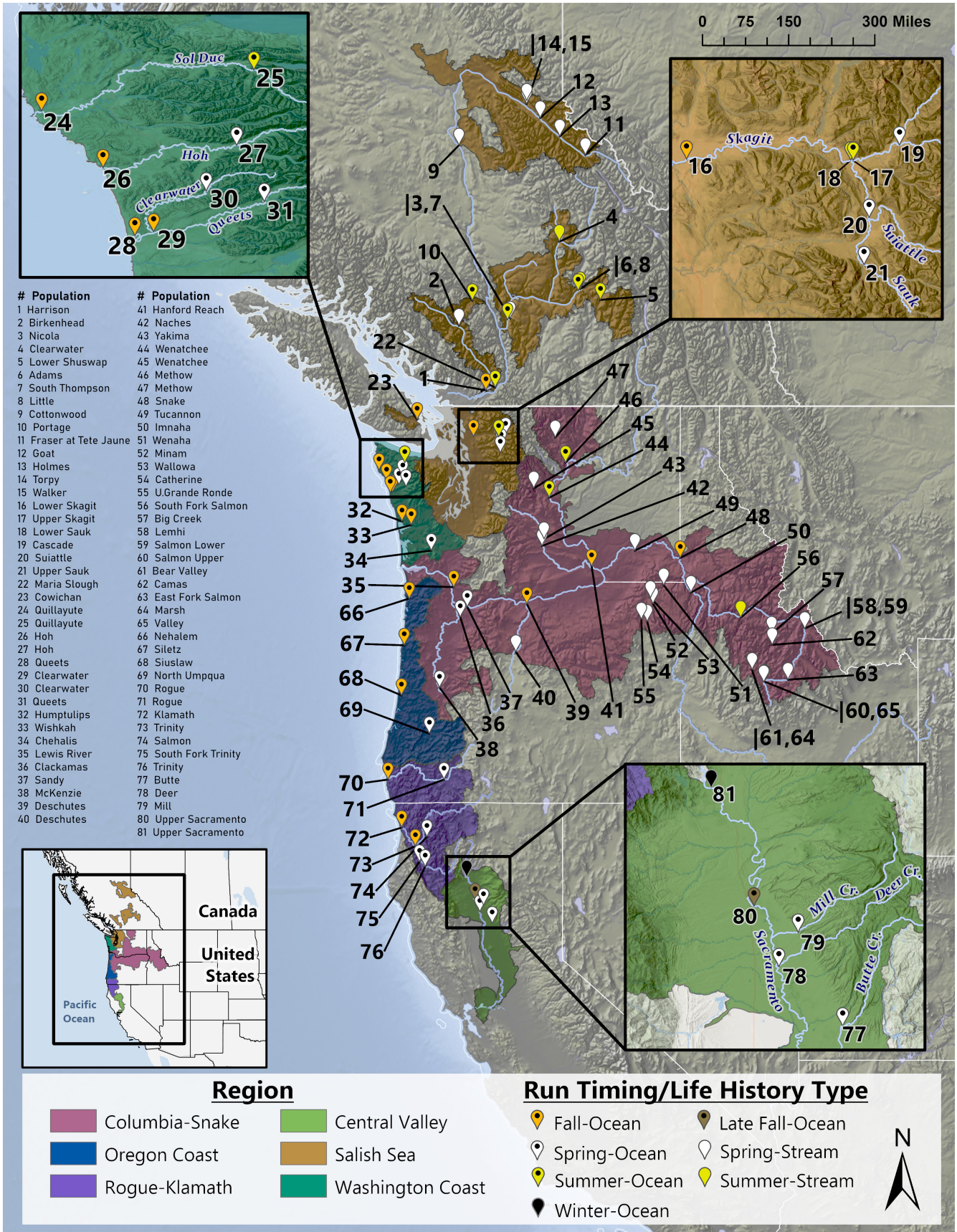
across multiple comigrating cohorts of salmon (Moore et al., 2014; Nesbitt & Moore, 2016; Schindler et al., 2010). However, different aspects of diversity also likely influence the vulnerability or exposure of populations to the many stressors they encounter across their range.

Among Pacific salmon, Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) are highly diverse and are perhaps the most prized species for fishers and salmon predators alike. Chinook have exceptionally high food value due to their large size and fatty flesh. They are the preferred food source for marine apex predators like Southern Resident Killer Whales (SRKW) (*Orcinus orca*, Delphinidae) whose health and demographic productivity is linked to the availability of Chinook as prey (Ford et al., 2009, 2016; Stewart et al., 2021; Williams et al., 2011). Some the most important and productive fishing areas for West Coast Indigenous communities are those with abundant Chinook runs (Swezey & Heizer, 1977; Fisher, 2004; Nesbitt & Moore, 2016). Chinook also support major US and Canadian commercial and recreational fisheries with an annual economic contribution to both countries measured in the hundreds of millions of dollars annually (The Research Group, 2009; Gislason, 2017). However, Chinook have recently exhibited declining size, productivity and abundance throughout much of their North American range (Dorner et al., 2018; Ohlberger et al., 2016; Welch et al., 2021), and Chinook fisheries have also declined dramatically in response to these changes ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020; Walters et al., 2019).

The availability of Chinook salmon for both predators and human fisheries is driven in part by their adult migration timing (also called run timing), which is highly diverse across their extensive North American range from Alaska and the Yukon to California (Healey, 1991; Parken et al., 2008; Quinn et al., 2016). In particular, the species exhibits exceptionally high run timing diversity in populations from the Salish Sea south to California's Central

Valley (Figure 1), with Chinook freshwater entry timing ranging from late-winter entry among reproductively immature fish to early-winter entry among reproductively mature fish. In contrast with more northerly watersheds, in this part of their range multiple distinct Chinook salmon runs are observed, even within the same watershed and are commonly named based on their season of river entry (e.g. spring, summer, fall, late fall, winter). Run timing groups are also classified as 'early' and 'late' migrators based on their timing of river entry in relation to maturation and spawn timing. For example, spring Chinook are considered early migrators because they enter freshwater in a relatively immature state many months before fall spawning and undergo final maturation in rivers. Fall and late-fall Chinook salmon are considered late migrators because they enter rivers just prior to spawning and after most of their reproductive maturation process has already occurred in the ocean (Healey, 1991; Quinn et al., 2016). Summer Chinook salmon are intermediate to spring and fall runs in their run timing and state of maturity at river entry. Winter Chinook salmon migrate in the winter and spawn in late spring and summer, a unique pattern of early entry and spawn timing found only in the Sacramento River system in California (Healey, 1991).

Importantly, Chinook salmon populations also exhibit differences in their juvenile life histories, migration routes and distributions at sea, which differentially expose them to environmental variation affecting freshwater and marine survival, as well as exploitation in mixed-stock commercial fisheries. Chinook populations are generally predominated by one of two primary types of juvenile life histories: (a) 'stream-type', characterized by a year or more of stream rearing prior to outmigration; and (b) 'ocean-type', characterized by migration to sea during their first year of life (Taylor, 1990; Healey, 1991; Waples et al., 2004). These juvenile life histories result in differential exposure to freshwater stressors, such as low summer flows and warm temperatures (Jones et al., 2020; Warkentin et al., 2022). Further, differences in the timing and body size at outmigration and in their oceanic distributions can have carryover effects on marine survival. For example, interior stream-type Chinook from the Snake and Columbia basins undertake lengthy northward migrations in their first year of marine life before moving offshore and are rarely intercepted in coastal fisheries (Weitkamp, 2010). In contrast, many ocean-type fall Chinook salmon from populations in the Salish Sea are more locally distributed, with most fishery interceptions occurring in the Salish Sea and along the West Coast of Vancouver Island ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020; Freshwater et al., 2021; Riddell et al., 2013; Weitkamp, 2010). These population and life-history-specific distributional differences are generally consistent across years, which may expose populations to different physical and biological conditions during their marine lives (Shelton et al., 2019). Consequently, populations of Chinook in the Northeast Pacific exhibit both synchronous and unique responses to climate variability, food availability and fisheries exploitation (Braun et al., 2016; Sharma et al., 2012; Shelton et al., 2021; Tucker et al., 2012).

Despite the potential for life-history variation to influence the exposure of different populations to environmental stressors and fisheries, Chinook salmon population trends have not been evaluated to understand how life-history traits influence abundance trends across different regions. We, therefore, sought to quantify trends for Chinook salmon populations across the southern half of their Northeast Pacific range, which is home to rich intraspecific biodiversity in Chinook salmon (Figure 1) and to compare trends in stocks exhibiting different adult and juvenile life histories. Among the populations we assessed are many of North America's largest and most important Chinook salmon stocks ([PFMC] Pacific Fishery Management Council, 2021; [PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020), which have supported productive fisheries and ecosystems for thousands of years (Yoshiyama, 1999; Butler et al., 2010; Carothers et al., 2021; Atlas et al., 2021).

We quantified trends in escapement and total run size (escapement+harvest) for individual populations of natural-origin Chinook salmon in two separate analyses to (1) describe regional trends in spawner escapement for Chinook salmon populations, (2) quantify trends in total run sizes for a subset of populations where both escapement and harvest information was available and (3) qualitatively evaluate how these changes vary among regions and life histories, including variation in run timing, juvenile age at outmigration and oceanic migration routes. Spawner escapement data are more broadly available than total run size information and escapement is a direct measure of fish on the spawning grounds, providing a valuable metric for the services Chinook provide in freshwater systems, as prey for terrestrial and freshwater predators and as long-distance transporters of marine derived nutrients and energy. Total run size data rely on harvest rate estimates, which are often uncertain and unavailable for many stocks but nonetheless provide insight into the total production from individual Chinook populations, the influence of changing harvest regimes on population trends and the overall contribution of natural-origin Chinook salmon to North American fisheries. Our analyses addressed the two questions: (1) how have changes in the escapement and total run sizes of Chinook salmon manifested across different life histories and regions and (2) have certain Chinook life-history groups been more resilient to recent natural and anthropogenic changes than others? Taken together these findings can clarify conservation risks and population trajectories for Chinook salmon populations around the southern half of their eastern-Pacific range, informing fishery management for both productive and weak stocks, and guiding restoration activities that can bolster long-term prospects for protecting the rich intraspecific biodiversity exhibited by this iconic species.

2 | METHODS

We assembled and analysed spawner escapement data as well as information on total run size (pre-fishery abundance: escapement+harvest) to better understand key features in West Coast

#	Population	#	Population
1	Harrison	41	Hanford Reach
2	Birkenhead	42	Naches
3	Nicola	43	Yakima
4	Clearwater	44	Wenatchee
5	Lower Shuswap	45	Wenatchee
6	Adams	46	Methow
7	South Thompson	47	Methow
8	Little	48	Snake
9	Cottonwood	49	Tucannon
10	Portage	50	Imnaha
11	Fraser at Tete Jaune	51	Wenaha
12	Goat	52	Minam
13	Holmes	53	Wallowa
14	Torpy	54	Catherine
15	Walker	55	U.Grande Ronde
16	Lower Skagit	56	South Fork Salmon
17	Upper Skagit	57	Big Creek
18	Lower Sauk	58	Lemhi
19	Cascade	59	Salmon Lower
20	Suiattle	60	Salmon Upper
21	Upper Sauk	61	Bear Valley
22	Maria Slough	62	East Fork Salmon
23	Cowichan	63	East Fork Salmon
24	Quillayute	64	Marsh
25	Quillayute	65	Valley
26	Hoh	66	Nehalem
27	Hoh	67	Siletz
28	Queets	68	Siuslaw
29	Clearwater	69	North Umpqua
30	Clearwater	70	Rogue
31	Queets	71	Rogue
32	Humptulips	72	Klamath
33	Wishkah	73	Trinity
34	Chehalis	74	Salmon
35	Lewis River	75	South Fork Trinity
36	Clackamas	76	Trinity
37	Sandy	77	Butte
38	McKenzie	78	Deer
39	Deschutes	79	Mill
40	Deschutes	80	Upper Sacramento
		81	Upper Sacramento

Region

- Columbia-Snake
- Oregon Coast
- Rogue-Klamath
- Central Valley
- Salish Sea
- Washington Coast

Run Timing/Life History Type

- Fall-Ocean
- Spring-Ocean
- Summer-Ocean
- Late Fall-Ocean
- Spring-Stream
- Summer-Stream
- Winter-Ocean

FIGURE 1 A map depicting the regional groupings, specific population locations, run timing, and dominant juvenile life history for each of the 81 Chinook populations included in our analysis. Among these populations 79 were included in analyses of escapement trends, and two populations (Hanford and Snake Fall) were only included in the total run size analysis due to their shorter time series.

Chinook salmon population trends. We limited our analyses to populations and years where hatchery- and natural-origin fish could be reliably separated, and further compiled information on the run timing, juvenile life history and marine distributions for these populations.

Chinook population trends were analysed using a time series modelling approach, implemented in the R-package MARSS (Holmes et al., 2012). Using these time series models we evaluated temporal trends in both individual populations and populations grouped by conservation units (i.e. ESUs or CUs) and then compared populations trajectories across three key axes of life-history variation: adult run timing (e.g. spring v. fall), age at marine entry and migratory distribution in the marine phase.

2.1 | Data compilation

We compiled data on spawner escapement and harvest of Chinook populations from multiple sources. Fraser River escapement data came from Fisheries and Oceans Canada (Chuck Parken – *unpublished* data). Escapement and harvest for some populations in British Columbia, Washington and Oregon came from the Pacific Salmon Commission (PSC) escapement and harvest analysis reports ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020). Escapement data for Washington watersheds was downloaded from the Washington Department of Fish and Wildlife (WDFW) Salmonid Conservation and Reporting Engine (SCoRE) website ([WDFW]Washington Department of Fish and Wildlife, 2021) and for Columbia Basin populations from the StreamNet coordinated assessment website (StreamNet, 2021). Data on Oregon Chinook escapements came from the Pacific Fishery Management Council annual reports on salmon fisheries and escapement ([PFMC] Pacific Fishery Management Council, 2021) and from the Oregon Department of Fish and Wildlife dam passage website ([ODFW] Oregon Department of Fish and Wildlife, 2021). Additional data on Columbia Basin stocks in Oregon came from the coordinated assessments data portal (StreamNet, 2021), and escapement data for Deschutes spring and fall Chinook were provided by the US Fish and Wildlife Service (David Hand – *unpublished data*). Abundance information for California populations was drawn from the Sacramento and Klamath escapement tables accessed on the California Department of Fish Wildlife website ([CDFW] California Department of Fish and Wildlife, 2021a, 2021b, 2021c) and from Pacific Fishery Management Council (PFMC) online reports ([PFMC] Pacific Fishery Management Council, 2021).

In total, we compiled escapement time series for 231 populations of Chinook salmon and refined this dataset to a final set of escapement time series comprising 79 populations. Populations were selected based on (1) the ability to differentiate hatchery and natural-origin spawners or the ability to make strong inference that hatchery influence was low, (2) time series continuity with no or few (<4) missing years of data and (3) data quality based on the professional judgement of the authorship group. The population time series that were included in our analysis ranged in length from 27

to 89 years. Generally, estimates of escapement are reported as a single point estimate of total spawner abundance with a breakout of hatchery and natural-origin spawner totals or an estimate of percent hatchery contribution. In total our data set encompassed 4007 river-specific annual observations of spawner abundance, and these estimates were derived using a wide variety of methods. Most often escapement estimates were derived from visual surveys of spawning salmon or redds (nests), but in some locations and years mark-recapture, dam counts, weir census counts, carcass surveys and expansions from in-river test fisheries were used. In several locations escapement estimates from visual counts have been calibrated with mark-recapture or dam counts and we analysed these calibrated datasets (e.g. [PSC] Pacific Salmon Commission Sentinel Stocks Committee, 2018). Likewise, in locations where enumeration methods have shifted over time, we analysed calibrated datasets. Accordingly, we do not expect methodological differences in monitoring design to create any systematic bias in the overall trends observed in Chinook abundance (e.g. Parken et al., 2003). Where counts of jacks and large adult Chinook are kept separately, we excluded jack counts and analysed data on large adult Chinook abundance, since jacks are predominantly male and, therefore, contribute minimally to the regulation of population growth rates. In addition, jacks are often not recorded in overflights and other visual surveys, so counts of large adult Chinook were most immediately comparable between populations (Table S1). All data and code used in our analyses are freely available online and stored in a public GitHub repository (https://github.com/willatlas/ChinookEscapement-RunSize).

We developed a model to characterize trends in natural-origin Chinook salmon spawner abundance across 79 of these populations. Hatchery spawners were excluded from our analysis or presumed to make negligible demographic contributions where the abundance of hatchery fish is not regularly estimated but a preponderance of evidence suggests they are uncommon. Given the variety of methods and associated assumptions used to derive estimates of escapement in our study area (e.g. spawner or redd counts expanded to abundance, hatchery proportions estimated from carcass recoveries), annual estimates of natural-origin Chinook spawner abundance are prone to error stemming from uncertainty in the true number of fish. We, therefore, treated each estimate of spawner escapement as an imperfect observation of a true underlying state—in this case natural-origin spawner abundance—and modelled both natural variability in abundance (process error) and observation errors using a state-space approach (see *Data Analysis* below).

Estimates of harvest were also compiled for a subset of hatchery and natural populations where Chinook are tagged with coded wire tags (CWTs), and where these tag recovery data are routinely used by the PSC and PFMC to estimate exploitation rates (ERs). These estimates of annual ERs are reported by both the PSC Chinook Technical Committee (CTC) and the PFMC ([PFMC] Pacific Fishery Management Council, 2021; [PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020). Historical harvest rates for Sacramento winter Chinook prior to 2000 were reconstructed by O'Farrell and Satterthwaite (2015), and fall Chinook harvest rates

were estimated as described in O'Farrell et al. (2013). Harvest estimates derived from a limited number of CWT recoveries are inherently uncertain and have become more uncertain over time owing to reduced harvest rates in marine fisheries (Jensen et al., 2022; PSC CTC, 2020; PSC CWT Work Group, 2008); harvest data are also reported as point estimates and do not reflect uncertainty in ERs. While these estimates reliably capture long-term changes in harvest management, annual estimates of harvest should be interpreted with caution. We, therefore, adopted a similar state-space modelling approach for estimating harvest trends over time, partitioning variability in total run size estimates into observation error stemming from uncertainty in harvest estimates and the level of process variability underlying the true pre-fishery run size. In total, harvest estimates were available for 23 populations, including two populations (Hanford and Snake Fall) where data have been collected since the early-1990s. Accordingly, we analysed total run size trends between 1990 and 2019.

In some instances, the recent adoption of mark-selective fisheries necessitated assumptions be made about the relationship between harvest rates observed in adipose fin-clipped salmon tagged with a CWT and unmarked natural-origin Chinook. Estimated harvest rates are reported by the PSC for each fishery and gear type that encounters Chinook salmon from Southeast Alaska to the South of Falcon region on the Oregon Coast; in most of these areas Chinook salmon fisheries remain non-selective. For fishing areas where mark-selective fishing has been implemented we assumed that harvest impacts were zero for unmarked wild fish; this assumption is likely a modest underestimate of fishery impacts since unmarked fish that are released in the fishery experience post-release mortality (Conrad & McHugh, 2008; Warkentin et al., 2022). In addition, at the time of our analysis some harvest estimates had not been reconstructed through 2019; in these few cases, we took the stock-specific average harvest rate in the previous 10 years and applied it to the 2019 cohort with missing harvest data. For a full summary of exploitation rate estimates and information on the sources see the (Table S2).

2.2 | Escapement trend analysis

For the first set of time series analyses Chinook salmon populations were divided into six groups corresponding to their geographic location: (1) Salish Sea, (2) Washington Coast, (3) Columbia River, (4) Oregon Coast, (5) Rogue and Klamath rivers and (6) Sacramento River (Figure 1). Columbia River stocks were further divided into three trend groups corresponding to the length of their escapement time series: (i) Snake River spring and summer runs where populations have been consistently monitored since at least 1957, (ii) Columbia River stocks with data beginning around 1967, (iii) Columbia River stocks with data beginning after 1982. Each of these analysis groups for the Columbia and Snake watersheds included some populations from analyses, which started earlier, for example in our analysis, which spanned from 1967 to 2019, 11 populations from the Snake

River were analysed alongside four populations from the Columbia (Lewis, Wenatchee spring, Methow spring and Methow summer). Trends in escapement were evaluated for an additional 8 populations in the Columbia River with data starting in 1982. Information on the populations and their respective time periods included in each group examined in our trend analysis is presented in Table 1.

2.3 | Total run size analysis

In addition to evaluating trends in spawner escapement, we examined trends in total run size (escapement + total harvest) for populations where data on harvest rates were available, or where estimates of harvest from a nearby population are believed to reflect harvest impacts on the stock of interest ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020) (Table 2). Harvest data were available for a much smaller subset of populations ($n = 17$) and were applied to an additional six geographically proximate stocks. These harvest monitoring programs generally began in the mid-1980s when widespread CWT tagging of Chinook salmon and sampling of fisheries and escapements were initiated. Accordingly, our analysis of run size covers a smaller geographic and temporal (1990–2019) scope but provides greater clarity on the magnitude of variability in recruitment, harvest and population status.

These 23 populations with total run size data were divided into four separate regional analysis groups to enable time series model convergence and limit the number of parameters being estimated in each model: (1) the Salish Sea group included seven populations from British Columbia and Washington State; (2) the Columbia River analysis group, which included eight populations; (3) the five populations on the Washington and Oregon Coast; and (4) the three Klamath and Sacramento stocks (Table 2). In addition, harvest data (CWT tagging) were not available for Skagit summer Chinook until 1998, so we fit a separate time series model to the estimated harvest rates for Washington State stocks beginning in 1990, including correlations between the Skagit summer stock and other regional populations falling under the same management to produce a derived estimate of harvest rate for this specific population (details in Appendix S1; Table S3).

In many locations harvest rates have declined alongside total run sizes, meaning that spawner escapement in many cases does not capture the full magnitude of the population decline. Accordingly, failing to account for the effects of harvest on the observed escapement over time will often underestimate the level of conservation risk. Total run size is more relevant to the provisioning of some of the ecosystem services supported by Chinook salmon, including what opportunities exist for the fishers and marine predators who depend on Chinook salmon for their livelihoods, culture or sustenance.

2.4 | Time series modelling approach

To quantify changes in natural-origin Chinook salmon spawner escapement and total run size we fit 12 regionally grouped state-space

TABLE 1 Estimated spawner escapement states ($x_{i,t}$) and trends for 79 Chinook stocks from Northern California to the Salish Sea. Trend (u_i) and percent change per year are estimated for the full time series (Start year to 2019). Mean spawner escapements from the start year to 2019 are also reported, as well as the relative magnitude of the 15-year and 5-year average escapements.

Group	Start year	Population	Pop no.	Run timing	Mean spawn	5-year % of mean	15-year % of mean	U trend	Median % change per year
Columbia	1967	Lewis River	35	fall	9753	104.8%	96.9%	0.003	0.25%
		Methow	47	spring	839	26.7%	41.5%	−0.052	−5.08%
		Methow	46	summer	1266	104.0%	107.4%	−0.018	−1.75%
		Wenatchee	45	spring	1423	32.1%	39.7%	−0.055	−5.39%
Columbia	1982	Clackamas	36	spring	1713	205.5%	137.4%	0.024	2.44%
		Deschutes	39	fall	10,092	112.4%	121.0%	0.035	3.55%
		Deschutes	40	spring	1012	39.0%	61.5%	−0.055	−5.38%
		McKenzie	38	spring	1918	99.5%	91.3%	0.035	3.57%
		Naches	42	spring	1096	65.6%	86.4%	−0.014	−1.40%
		Sandy	37	spring	1306	244.0%	165.7%	0.050	5.15%
		Wenatchee	44	summer	6999	69.3%	77.6%	−0.004	−0.35%
		Yakima	43	spring	2341	69.3%	98.3%	−0.032	−3.16%
Oregon coast	1975	North Umpqua	69	spring	5077	82.7%	95.1%	−0.009	−0.88%
		Nehalem	66	fall	8773	101.4%	90.2%	0.003	0.30%
		Siletz	67	fall	5109	117.3%	92.2%	0.016	1.66%
		Siuslaw	68	fall	19,877	74.9%	92.5%	0.001	0.14%
Rogue & Klamath	1978	Klamath	72	fall	24,006	71.5%	104.9%	−0.024	−2.33%
		Rogue	70	fall	63,293	63.3%	75.8%	−0.039	−3.82%
		Rogue	71	spring	12,313	67.4%	64.3%	−0.041	−4.03%
		Salmon	74	spring	511	47.0%	131.7%	−0.014	−1.43%
		South Fork Trinity	75	spring	199	16.6%	79.9%	−0.070	−6.75%
		Trinity	73	fall	19,940	41.2%	79.5%	−0.032	−3.12%
		Trinity	76	spring	9478	28.9%	62.4%	−0.036	−3.57%
Sacramento	1960	Butte	77	spring	2438	95.0%	165.2%	0.000	0.03%
		Deer	78	spring	1259	19.0%	48.1%	−0.054	−5.25%
		Mill	79	spring	735	29.1%	63.1%	−0.037	−3.67%
		Upper Sacramento	80	late fall	17,755	15.8%	23.1%	−0.063	−6.08%
		Upper Sacramento	81	winter	34,393	7.0%	10.5%	−0.079	−7.61%
Salish	1979	Lower Adams	6	summer	3165	197.1%	174.1%	0.056	5.78%
		Birkenhead	2	spring	440	67.3%	130.9%	−0.013	−1.24%
		Cascade	19	spring	264	78.4%	112.1%	−0.016	−1.58%
		Clearwater	4	summer	3265	37.3%	69.0%	−0.021	−2.07%
		Cottonwood	9	spring	1104	29.5%	42.6%	−0.023	−2.30%
		Cowichan	23	fall	4961	205.9%	93.8%	0.016	1.63%
		Fraser at Tete Jaune	11	spring	2892	44.4%	57.3%	−0.054	−5.22%
		Goat	12	spring	159	36.5%	74.8%	−0.063	−6.09%
		Harrison	1	fall	79,834	56.0%	75.0%	−0.024	−2.34%
		Holmes	13	spring	1467	34.3%	50.4%	−0.063	−6.06%
		Little	8	summer	5448	330.4%	234.9%	0.100	10.46%
		Lower Sauk	16	summer	722	83.9%	75.3%	−0.046	−4.53%
		Lower Shuswap	5	summer	20,527	100.2%	109.7%	0.007	0.72%
		Lower Skagit	16	fall	2176	100.5%	95.0%	−0.035	−3.45%

TABLE 1 (Continued)

Group	Start year	Population	Pop no.	Run timing	Mean spawn	5-year % of mean	15-year % of mean	U trend	Median % change per year
		Maria Slough	22	summer	293	90.4%	164.8%	0.039	3.93%
		Nicola	3	spring	4087	39.8%	57.6%	−0.009	−0.94%
		Portage	10	summer	107	68.2%	83.2%	0.019	1.90%
		South Thompson	7	summer	29,826	203.7%	196.0%	0.067	6.91%
		Suiattle	20	spring	455	144.0%	98.0%	0.013	1.30%
		Torpy	14	spring	1424	39.0%	64.9%	−0.099	−9.42%
		Upper Sauk	21	spring	666	245.8%	152.6%	0.046	4.72%
		Upper Skagit	17	summer	8452	105.3%	106.8%	−0.024	−2.39%
		Walker	15	spring	231	39.8%	61.5%	−0.070	−6.71%
Snake	1957	Bear Valley	61	spring	681	44.2%	70.8%	−0.051	−4.94%
		Big Creek	57	spring	262	45.4%	71.4%	−0.060	−5.85%
		Camas	62	spring	142	38.0%	33.8%	−0.048	−4.65%
		Catherine	54	spring	430	26.7%	43.7%	−0.078	−7.49%
		East Fork Salmon	63	spring	750	29.7%	47.2%	−0.079	−7.60%
		Imnaha	50	spring	1039	32.9%	43.4%	−0.059	−5.70%
		Lemhi	58	spring	543	46.6%	37.9%	−0.037	−3.58%
		Marsh	64	spring	460	58.0%	72.2%	−0.043	−4.21%
		Minam	52	spring	501	72.9%	103.4%	−0.049	−4.82%
		Salmon Lower	59	spring	260	20.8%	39.2%	−0.094	−9.01%
		Salmon Upper	60	spring	775	28.8%	50.3%	−0.056	−5.41%
		SF Salmon	56	summer	1007	20.4%	57.5%	−0.072	−6.96%
		Tucannon	49	spring	421	15.4%	54.4%	−0.091	−8.66%
		U.Grande Ronde	55	spring	210	35.2%	37.1%	−0.037	−3.63%
		Valley	65	spring	261	34.9%	48.7%	−0.062	−5.97%
		Wallowa	53	spring	528	72.5%	114.2%	−0.050	−4.83%
		Wenaha	51	spring	588	60.7%	71.4%	−0.047	−4.55%
WA coast	1980	Chehalis	34	spring	1708	69.4%	90.5%	0.022	2.19%
		Clearwater	29	fall	1248	76.8%	85.3%	−0.004	−0.36%
		Clearwater	30	spring	84	90.5%	65.5%	−0.057	−5.56%
		Hoh	26	fall	2591	71.6%	74.8%	−0.007	−0.75%
		Hoh	27	spring	1356	75.5%	67.3%	−0.005	−0.51%
		Humptulips	32	fall	3172	85.9%	104.1%	0.016	1.66%
		Queets	28	fall	4178	72.4%	75.7%	−0.006	−0.60%
		Queets	31	spring	677	84.2%	66.3%	−0.025	−2.45%
		Quillayute	24	fall	5801	71.8%	69.5%	−0.006	−0.57%
		Quillayute	25	summer	974	100.7%	81.5%	0.008	0.78%
		Wishkah	33	fall	650	53.2%	77.1%	0.001	0.13%

time series models to the natural log of Chinook spawner abundance. These state-space time series models allowed us to partition annual variability in salmon escapement into observation and process errors. Observation errors are random and accounting for uncertainty stemming from imperfect observations, while process error is systematic and tracks the underlying variability in the process of interest, in our case changes in Chinook spawner escapement and total run size.

This time series model took the form:

$$x_{i,t} = x_{i,t-1} + u_i + w_{i,t}; w_{i,t} \sim MVN(0, \mathbf{Q}), \tag{1}$$

$$y_{i,t} = x_{i,t} + v_{i,t}; v_{i,t} \sim N(0, r_i) \tag{2}$$

where Equation 1 describes the unobserved state process x_t, in our case the true spawner escapement or total run size for a population

TABLE 2 Estimated total run size states ($x_{i,t}$) for 23 Chinook populations with both escapement and harvest data. The source of coded wire tag harvest data used to infer harvest rates and total run size for each population are also presented, as well as the 1990–2009 and the 10-year average exploitation rates (ER) for each indicator stock. In cases where another population's ER has been applied to a population, mean ER values are left blank. Mean run sizes are for the years 1990–2019 and the relative magnitude of 5-year and 15-year run sizes are compared each population's 1990–2019 average. Median estimates for percent yearly change are reported in the rightmost column.

Group	Pop no.	Population	CWT indicator	Run timing	Mean total run size	5-year % of mean	15-yr % of mean	1990–2009 ER mean	10-yr ER mean	Median yearly % change
Salish	1	Harrison	Harrison	fa	147,655	46.4%	59.0%	43.7%	27.2%	-6.11%
	3	Nicola	Nicola	sp	4651	41.1%	80.1%	29.9%	17.3%	-5.32%
	5	Lower Shuswap	Lower Shuswap	su	46,008	55.6%	79.2%	53.8%	39.6%	-3.45%
	7	South Thompson	Lower Shuswap	su	88,143	128.9%	139.9%	-	-	3.96%
	16	Skagit su/fa	Skagit summer	su/fa	19,765	127.0%	110.7%	40.6%	45.0%	-1.86%
	19	Skagit spring	Skagit spring	sp	2356	142.9%	101.1%	43.9%	35.5%	-2.01%
	23	Cowichan	Cowichan	fa	16,678	146.1%	68.4%	66.5%	58.4%	-1.57%
WA/OR coast	24	Quillayute	Queets fall	fa	11,914	89.3%	90.3%	-	-	-0.92%
	26	Hoh	Queets fall	fa	5407	87.4%	92.8%	-	-	-1.41%
	28	Queets	Queets fall	fa	8316	86.4%	94.0%	51.6%	60.1%	-2.71%
	66	Nehalem	Salmon River	fa	19,942	100.8%	94.9%	59.8%	53.7%	1.00%
	67	Siletz	Salmon River	fa	13,975	77.7%	81.9%	-	-	-1.42%
Columbia & Snake	35	Lewis River	Lewis	fa	16,299	108.2%	111.9%	38.2%	45.0%	-0.72%
	36	Clackamas	Willamette spring	sp	2609	166.9%	114.1%	41.2%	23.0%	-0.57%
	38	McKenzie	Willamette spring	sp	3079	80.3%	73.4%	-	-	-4.07%
	39	Deschutes	Columbia URB	fa	21,786	96.0%	112.8%	52.5%	49.4%	1.92%
	41	Hanford Reach	Hanford Wild	fa	163,256	137.3%	133.5%	56.7%	61.7%	0.88%
	44	Wenatchee	Columbia su	su	15,297	84.0%	90.7%	49.3%	60.4%	-3.59%
	46	Methow	Columbia su	su	3160	118.7%	117.1%	-	-	1.75%
	48	Snake	Columbia URB	fa	10,448	191.4%	166.8%	-	-	8.74%
California	72	Klamath	Klamath fall	fa	80,019	55.1%	97.2%	39.4%	40.7%	-1.62%
	80	Upper Sacramento	O'Farrell & Satterthwaite, 2015	late-fa	21,783	18.7%	40.4%	60.1%	52.8%	-8.97%
	81	Upper Sacramento	PFMC tables	win	3652	82.5%	107.0%	25.6%	16.0%	6.82%

(*i*) at time (*t*), expressed in log space. This state process takes an autoregressive form, relating the state $x_{i,t}$ to the estimated state in the previous time step $x_{i,t-1}$. Each $x_{i,t}$ is a realization of the state process at time *t* with a population-specific slope (trend) parameter u_i controlling the overall trend in the population-specific state, where each population had its own hidden state trajectory. $y_{i,t}$ is the observed quantity (the natural log of escapement or total run) for each population in each timestep. Process errors $w_{i,t}$, the true underlying variability in Chinook escapement, are drawn from a multivariate normal distribution with a mean of zero and a covariance matrix of **Q** (an *m* x *m* matrix where *m* is the number population of trends), with the diagonals representing the process error variance, and the off diagonals the covariance among process errors. We estimated unique process errors for each population, and these population-specific process errors were related to one another via unique covariance terms estimated between each population. Observation errors ($v_{i,t}$) were also estimated as a multivariate normal distribution with a mean of zero and a population-specific observation error variance r_i such that each population had its own independent observation error.

Previous research has demonstrated that salmon population trends are correlated among regionally proximate stocks (e.g. Mueter et al., 2005). For each regional grouping preliminary data analysis AIC scores (i.e. lower AIC values) revealed greater support for models with correlated process errors. We, therefore, modelled pairwise correlations among population-specific process errors in all of our regional analyses. Parameter identifiability for process and observation errors is challenging when simultaneously estimating variance–covariance matrixes for both sources of error. We, therefore, restricted our models to include only process error covariation. Observation errors were estimated independently for each population and off diagonals of **R** related to the covariance between observer errors were set to zero. For four populations where spawner abundance was derived from dam counts (North Umpqua, Clackamas, Yakima and Naches) we set observation error to zero.

Specific details of model parameterization and fitting, as well as parameter estimates associated with each regional escapement trend models and total run size model are reported in the (Appendix S2; Tables S4–S15).

2.5 | Interpreting trends

To quantify changes in natural-origin Chinook salmon escapement we interpreted the state $x_{i,t}$ values for each population over time and the u_i parameter as an indication of the overall trend across the time series. Generally, u_i values had high uncertainty owing to the sensitivity of the trend parameter to the initial population size (x_0) and the most recent values. We therefore interpreted the median value

of the u_i parameter and converted these median values into annual growth rate (AGR) expressed as a percent change per year over the course of the time series we analysed, where $AGR = 100(e^{u_i} - 1)$.

In addition to quantifying the overall trend, we back-transformed the log(escapement) states to estimate mean escapement and total run size states ($\bar{x}_i$) for the entirety of each time series and compared them to estimated escapement or total run size state in the last 5- and 15-years (2015–2019 and 2005–2019, respectively). We then calculated the percent change from the long-term mean at these time horizons (5 and 15 years) and the number of recent years when escapement or total run size state fell below the long-term mean value. These trend values were summarized for individual stocks, regional groupings and across life-history groups to understand recent population trajectories across geographic and biologically important constellations of Chinook salmon production and biodiversity.

3 | RESULTS

3.1 | Trends in spawner escapement

Our analysis included 47 spring-run, 20 fall-run, 13 summer-run Chinook populations, as well as one population – in the Upper Sacramento – with winter-run timing. The largest number of populations with suitable time series for analysis came from the Columbia and Snake River watersheds, with 13 populations from the Columbia and 17 from the Snake. Salish Sea populations from both Washington State and British Columbia comprised another large group of stocks with suitable time series for analysis (*n* = 23). In Canadian areas of the Salish Sea, all populations that were in the Fraser River watershed, except for the Cowichan River on southern Vancouver Island. Unfortunately, other populations in southern BC were excluded from our analysis because of a lack of information on the contribution of hatchery-origin spawners. Likewise, limited time series of data on hatchery contributions led to the exclusion of other Puget Sound Chinook stocks in Washington State. Data for the Klamath system was readily available, and we included five populations in the basin in our analysis. The availability of suitable data on hatchery contributions was notably limited for the Sacramento and San Joaquin watersheds, where a majority of populations were excluded from the analysis due to a lack of information on the contribution of hatchery fish, including among almost all major fall Chinook populations. Data availability or quality also limited the inclusion of any California coastal populations south of the Klamath River (Figure 1).

A substantial majority of Chinook populations we analysed showed evidence of declining trends in escapement (57 of 79), with many populations declining to their lowest levels on record in recent years. Median estimates for long-term escapement trends ranged

FIGURE 2 Spawner escapement trends estimated as the percent change per year for 79 Chinook stocks arranged from north to south and denoted by their population number. Points represent median trend estimates, and whiskers are 95% confidence bounds. Time series length varied by regional grouping and is reported in Table 1.
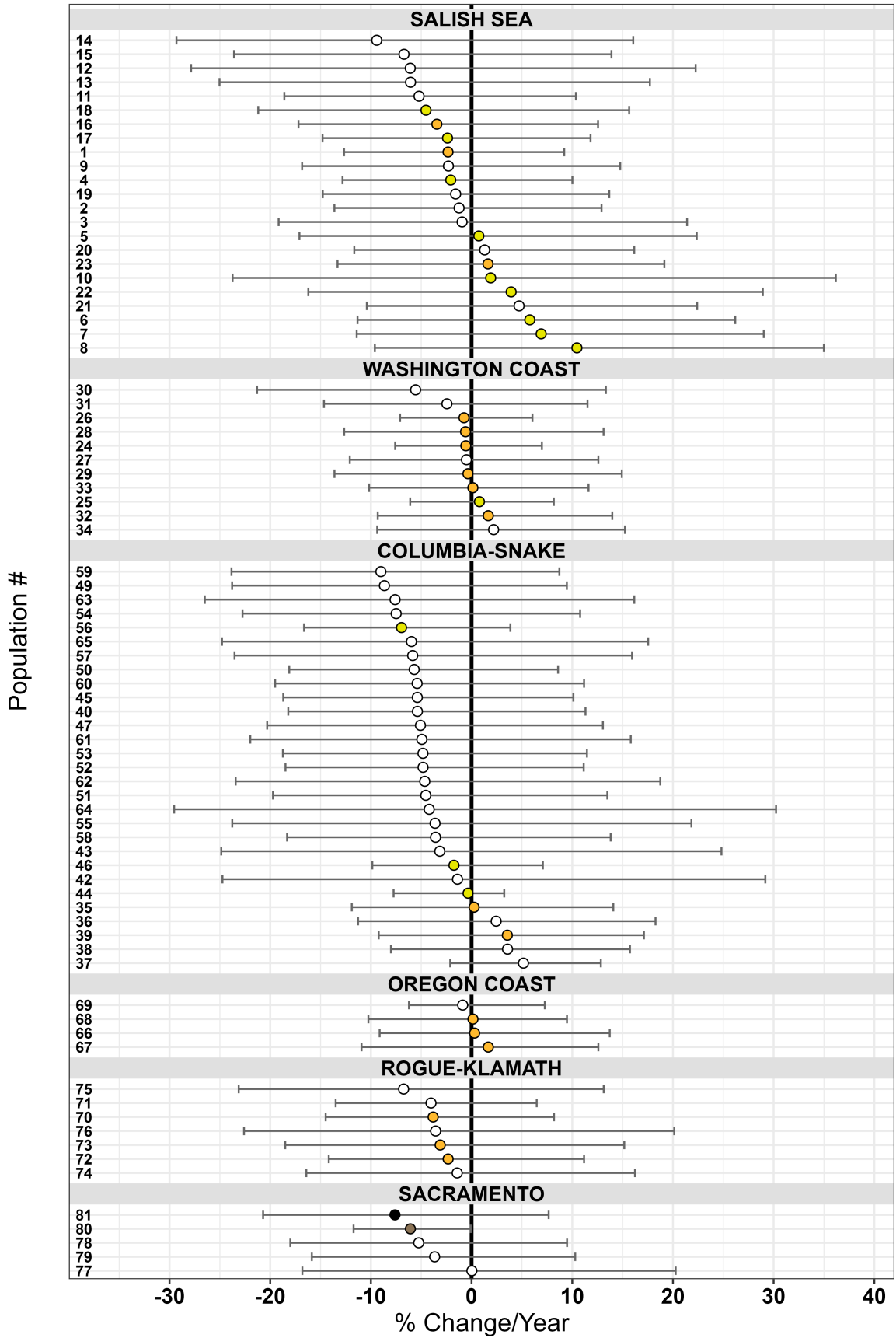
from +10.4% per year for summer Chinook returning to the Little River in the Thompson River to −9.4% per year for Torpy River spring Chinook in the Upper Fraser; however, these median estimates were bounded by significant uncertainty owing to the high level of natural variation in salmon abundance and the influence of the starting and ending values on the estimated trends (Figure 2).

Across the 79 populations we evaluated, escapement trends varied in relation to both geographic location and life history. In general, early-migrating spring Chinook populations, especially those with obligate stream-type juvenile life histories, experienced greater declines in spawner abundance than later-migrating fall Chinook and populations with ocean-type juveniles within the same regions. A total of 85% (40/47) of the spring Chinook stocks we evaluated had negative coefficient estimates for u_i. Even among populations that experienced substantial declines in abundance 95% confidence intervals for u_i all overlapped zero (Table 1; Figure 2). These declines among spring-run populations were evident in both recent cohorts (5-year spawner abundance was −37% below long-term average levels) and in the most recent three generations (15-year average spawner abundance −24% below the long-term average) (Table 1). Five- and 15-year changes in average spawner abundance were particularly negative for interior spring Chinook in the Fraser (5-year: −56%; 15-year: −28%), Columbia (5-year: −54%; 15-year: −35%) and Snake rivers (5-year: −59%; 15-year: −42%), where spring Chinook have obligated stream-type juvenile life histories. Coastal spring Chinook stocks, which express predominantly ocean-type juvenile life histories fared comparatively better, with 50% (6/12) of coastal spring Chinook populations north of the Rogue River experiencing positive trends in escapement across their time series. More southerly spring Chinook populations in the Rogue, Klamath and Sacramento watersheds fell below their mean long-term escapement levels by an average of 57% in the most recent 5 years, with the Butte Creek spring Chinook population being a notable exception (Table 1).

Estimated correlations between population-specific process errors provide further evidence for shared trends among interior spring Chinook, both in the Fraser and the Columbia watersheds. For example, among interior spring Chinook populations in the Upper Fraser River process errors showed strong positive correlations but had negative correlations with ocean-type summer and fall Chinook populations in the Fraser and relatively neutral correlations with other Salish Sea populations (Figure S1). Likewise, interior migrating Snake River spring Chinook populations showed consistently positive process error correlations (Figure S3) but had neutral or negative correlations with fall and summer Chinook in the Lewis and Methow Rivers (Figure S4). Even geographically proximate populations of spring and fall Chinook showed evidence of negative correlations in their interannual variability. For example, in the Mid-Columbia region, fall Chinook in the Deschutes River had negative correlations with nearby spring Chinook populations in the Yakima and Naches Rivers, while Deschutes spring Chinook were positively correlated with both (Figure S5).

Fall and summer Chinook populations experienced a mix of escapement trends: 56% (10/18) of fall Chinook and 46% (6/13) of summer Chinook populations that we analysed had negative coefficient estimates for their overall trend (u_i) (Table 1; Figure 2). On average, escapement among fall Chinook populations in our analysis declined at both 5-year (−18%) and 15-year (−15%) time horizons and median trend estimates ranged from −3.8% per year for Rogue fall Chinook to +3.5% per year for Deschutes fall Chinook. On average, summer Chinook populations in our analysis experienced modest increases in spawner escapement at both 5-year (+16%) and 15-year time horizons (+18%). Trends among summer Chinook were buoyed by large increases in escapement among three stocks in the South Thompson River, where average Chinook spawner abundance in the most recent 5 years exceeded their long-term average by +243% (Table 1; Figure 3; Figure S13).

A more complete description of escapement trends among populations in each region is presented in Appendix S3, and escapement trends and data for each regional group are visualized in Figures S13–S19.

3.2 | Trends in total run size and management responses

Total run size declined over our study period for 16 of 23 stocks with sufficient data (Figures 3 and 4). These declines have been met with a mix of management responses and varied success at arresting declines. For example, on the Harrison River, a tributary of the lower Fraser, fall Chinook have declined by approximately 6% per year for the last 35 years (Table 2; Figures 3 and 5), with escapements falling below a minimum stock size threshold (MSST) in 11 of the most recent 15 years with data (Figure S13). In response, managers have restricted fisheries and reduced harvest rates from a long-term (1985–2008) mean of 51% (range: 14%–79%) to a mean of 29% from 2009 to 2019 (range: 16%–58%) (Table 2). Run sizes for natural-origin Upper Sacramento fall Chinook have also declined sharply, particularly since 2007, and total run sizes have never recovered to levels observed in the 1980s and 1990s (Figure 5). Harvest rates have remained relatively high for Upper Sacramento fall Chinook in most years, averaging 62.3% (range: 0.7%–86.5%) between 1983 and 2011, and 58.6% (range: 52.1%–67.7%) from 2012 to 2019 when new harvest control rules were implemented ([PFMC] Pacific Fishery Management Council, 2011) (Tables 2; Table S2). In contrast, harvest rates for Sacramento winter Chinook have been reduced substantially since winter Chinook were ESA listed, contributing to an estimated 6.8% annual increase in total run sizes between 1990 and 2019 (Tables 2, Table S15; Figures 3 and 5). Harvest rates on Skagit River spring Chinook were reduced in recent decades from a peak of 75% (range: 48%–84%) between 1986 and 1992, to a recent 10-year mean of 36% (range: 16%–58%). This reduction in harvest was accompanied by modest improvements
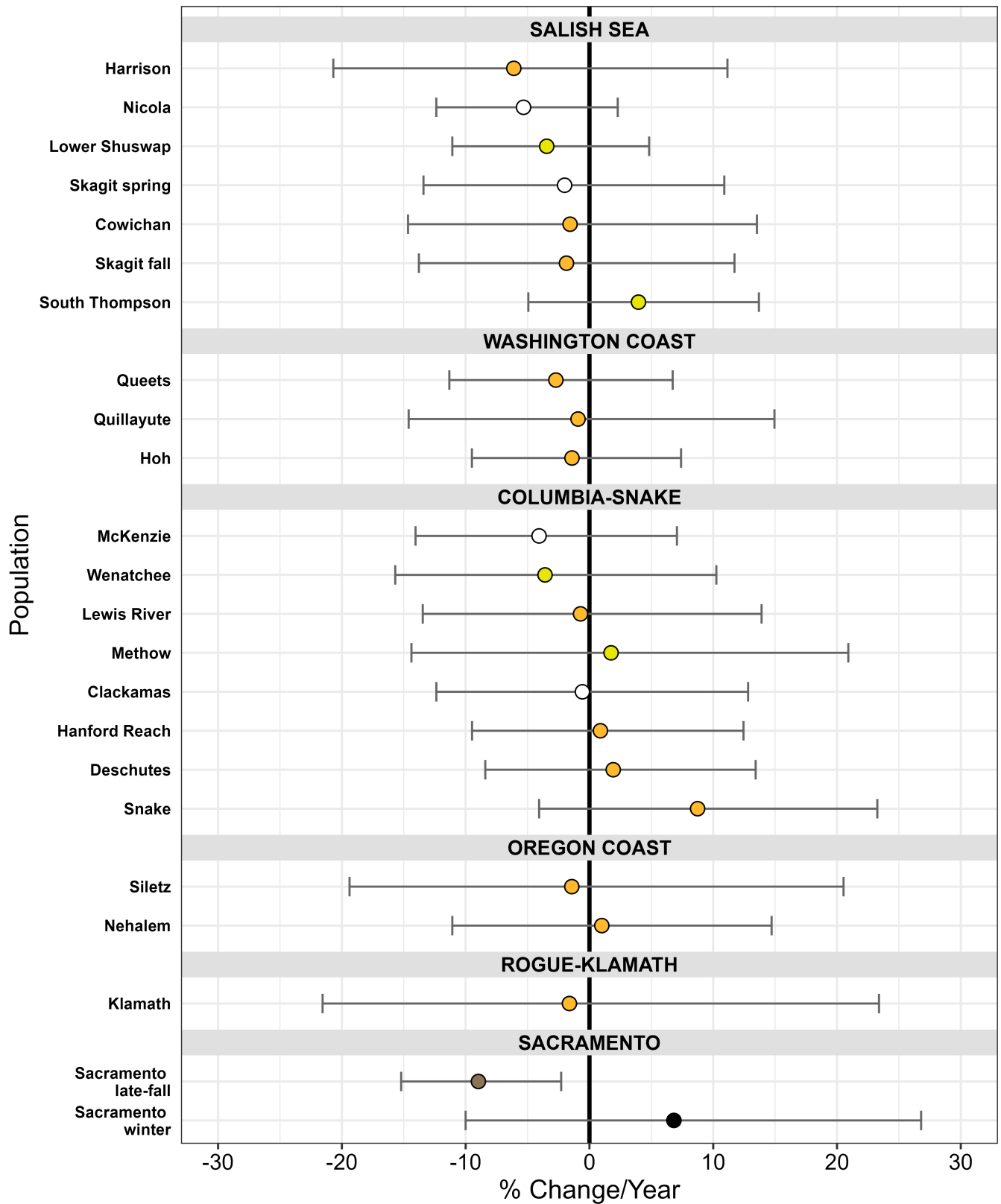
FIGURE 3 Estimated population trends, estimated as the percent change per year trend parameter (u_i) from 1990 to 2019 for total run size (escapement + harvest) in 23 Chinook stocks by population number (Table 2), ranging north from the Salish Sea south to California's Central Valley.

in escapement and the stock has met or exceeded its ESA recovery target of 2000 spawners in 5 years during that period (Figures 5, Figure S13; Tables 2, Table S2). In contrast, Skagit summer/fall Chinook continue to experience harvest rates above 50% in many years, with a 10-year average of 45% (range: 24% to 66%). Since 2012, total pre-fishery abundance of Skagit summer/fall Chinook has exceeded their ESA recovery goal of 14,500 fish in each year (mean run size state: 24,229) but fishery removals have contributed to the stock failing to meet its recovery escapement goal in every year but 2016 (Figure 5, Figure S13; Table 2,Table S2).

In a smaller number of instances (5/21), total run sizes increased across the time series. South Thompson summer Chinook have been increasing in abundance since the late-1990s and between 2000 and 2019 the population surpassed its long-term average run size of 88,140 Chinook in 14 years and experienced strongly positive trend in total run size (+4.0% per year) (Figure 3; Table S12). Some stocks have experienced stable or increasing abundance even while supporting harvest rates in excess of 50%. For example, Cowichan River Chinook have also recently experienced an increasing trend after persistent low abundance lasting from the late 1990s to about 2015. Prior to their collapse, between 1989 and 1994, CWT-tagged Chinook from the Cowichan were harvested at an average annual rate of 83%. Since 1995, harvest rates have been reduced modestly but remain among the highest among Canadian Chinook stocks (1995–2019 mean: 60%). In the most recent 2 years in our analysis, Cowichan Chinook showed strong signs of increasing abundance, with the pre-fishery abundance of Cowichan Chinook surpassing their 1990–2019 mean total run size (16,678 fish) by an average of 46% (Figure 3; Table 2, Table S12, Figure 4). Likewise, Both Hanford and Snake River Fall chinook had strongly positive trends in total pre-fishery abundance, with 1990–2019 abundance peaking for both stocks between 2013 and 2015 (Figure 3; Table S2). For the four Northern Oregon coastal stocks with long-term estimates of total run size, trends in total run sizes since 1990 have been relatively flat (Nehalem: +1% per year) or have declined modestly (Siletz: −1.4% per year) (Table 2; Table S14; Figure 3). Harvest rates for Oregon Coast fall Chinook averaged 59% (range: 41%–85%) between 1985 and 2019 (Table 2; Table S2).

4 | DISCUSSION

We evaluated regional trends in spawner escapement and total run size for Chinook salmon populations from the Fraser River to the Sacramento River, a region that is home to a diverse range of locally adapted Chinook runs, to understand how changes in Chinook salmon abundance varied across geographic and life histories groups. Overall, we found that the escapement of Chinook salmon declined in 57 of 79 populations we assessed, with many populations experiencing especially poor returns in the last 5 years. Total run size data sampled a relatively shorter temporal window (1990–2019) and revealed similarly negative trends in abundance for many populations,

but also shed light on some of the notable bright spots for Chinook. These trends also highlight the degree to which population-specific harvest histories have contributed to survival and abundance trends over time, and how fisheries targeting these stocks have or have not responded to changes in their productivity. Despite numerous individual cases of declining abundance and survival, we found that the 23 Chinook stocks with total run size data continue to be harvested at rates >50% in many years, contributing an estimated 3.8 million natural-origin adult Chinook salmon to fisheries catches between 2010 and 2019 (PSC CTC, 2020; PFMC, 2020).

Chinook salmon escapement trends appear to be responding to the combined drivers of management and shifting environmental conditions. Many of our study populations had low escapements from the 1970s to the 1990s, when harvest rates in mixed-stock marine fisheries were very high (e.g. 60–80%. Morishima & Henry, 2001; PSC CTC, 2020). Although the risks posed by mixed-stock fishery impacts were known during that time (e.g. PFMC, 1978; Fraidenburg & Lincoln, 1985), widespread changes in fisheries management were not initiated until the last decades of the 20th century, when several Chinook population units were listed as threatened or endangered under the US ESA (e.g. Columbia, Puget Sound, Sacramento ESUs), and an updated Pacific Salmon Treaty was ratified in 1999 (Myers et al., 2018). Reductions in harvest rates and a period of relatively favourable environmental conditions led to variable but generally increased Chinook run sizes and escapements from Northern California to the Salish Sea from about 2000. In the last decade, most but not all populations experienced increasing variability and a general pattern of declining spawner abundance and total run sizes. These findings align with other recent research documenting declining trends in freshwater and marine survival, as well as increasing synchrony in survival across large swaths of their Northeastern Pacific range (Kilduff et al., 2015; Dorner et al. 2019; Crozier et al., 2021; Welch et al., 2021).

Recent deteriorations of freshwater and ocean conditions supporting Chinook salmon production have negatively affected many populations and escapements have declined despite efforts to reduce harvest rates. These recent declining trends have coincided with warming climate conditions in the marine and freshwater habitats of Chinook salmon with no historical analogue (Lindley et al., 2021; Schoen et al., 2017); including a marine heat wave, which has impacted marine ecosystems in the North Pacific since 2014 (DiLorenzo and Mantua 2016), increasing abundances of marine mammals that prey upon juvenile and adult salmon (Chasco et al., 2017; Nelson et al., 2019), and a period when the abundance of pink salmon (*O. gorbuscha*) in the North Pacific has peaked at over 500 million fish, creating the potential for cascading effects of competition between pink salmon and other pelagic predators (Ruggerone & Nielsen, 2004; Ruggerone & Irvine, 2018). Unprecedented variability in flow and river temperatures have also impacted Chinook and other salmon species (Crozier et al., 2019; Hinch et al., 2021; Tonina et al., 2022; von Biela et al., 2022). While climate-driven disturbances and novel ecosystem conditions have likely contributed to negative trends across the regions we evaluated, California
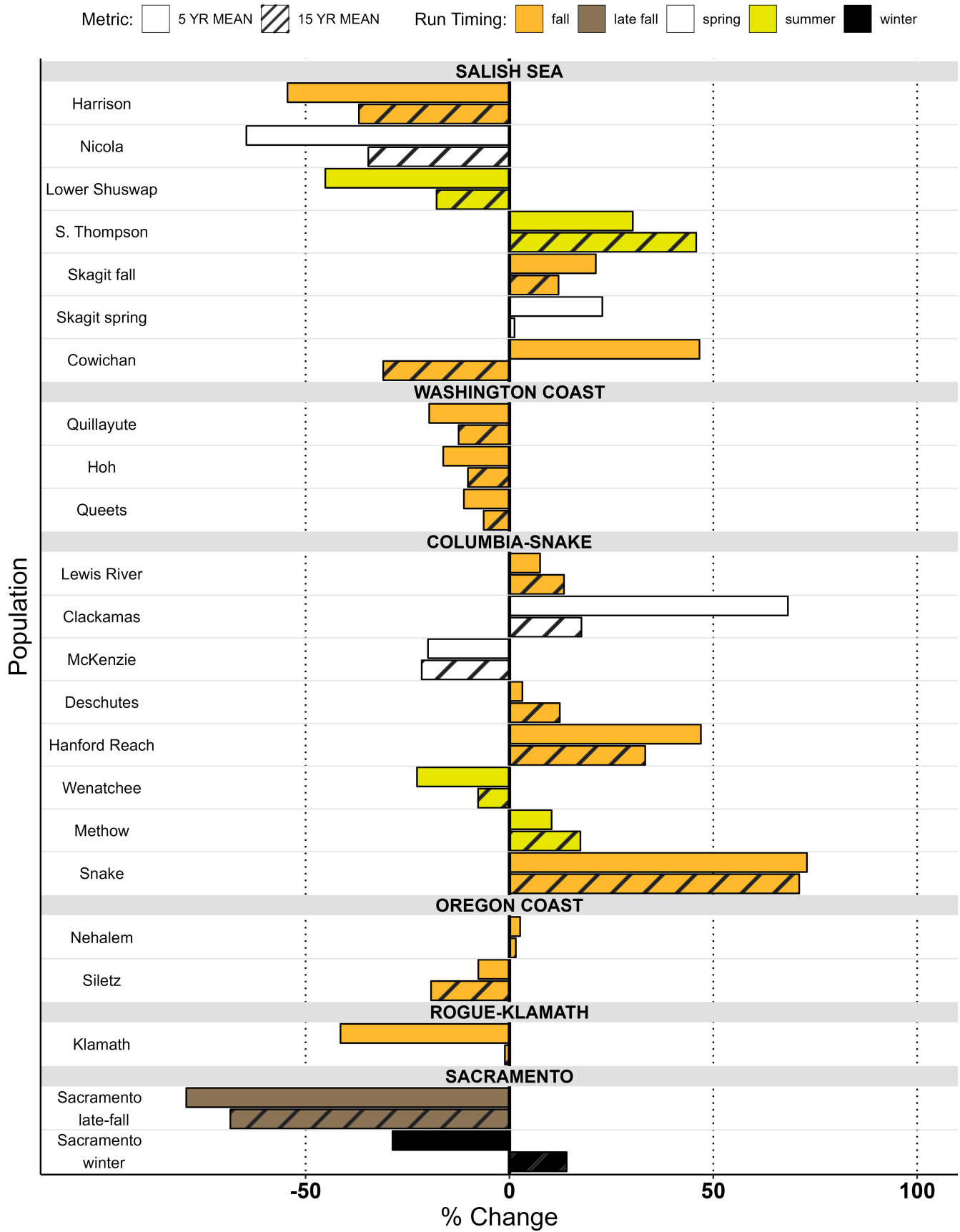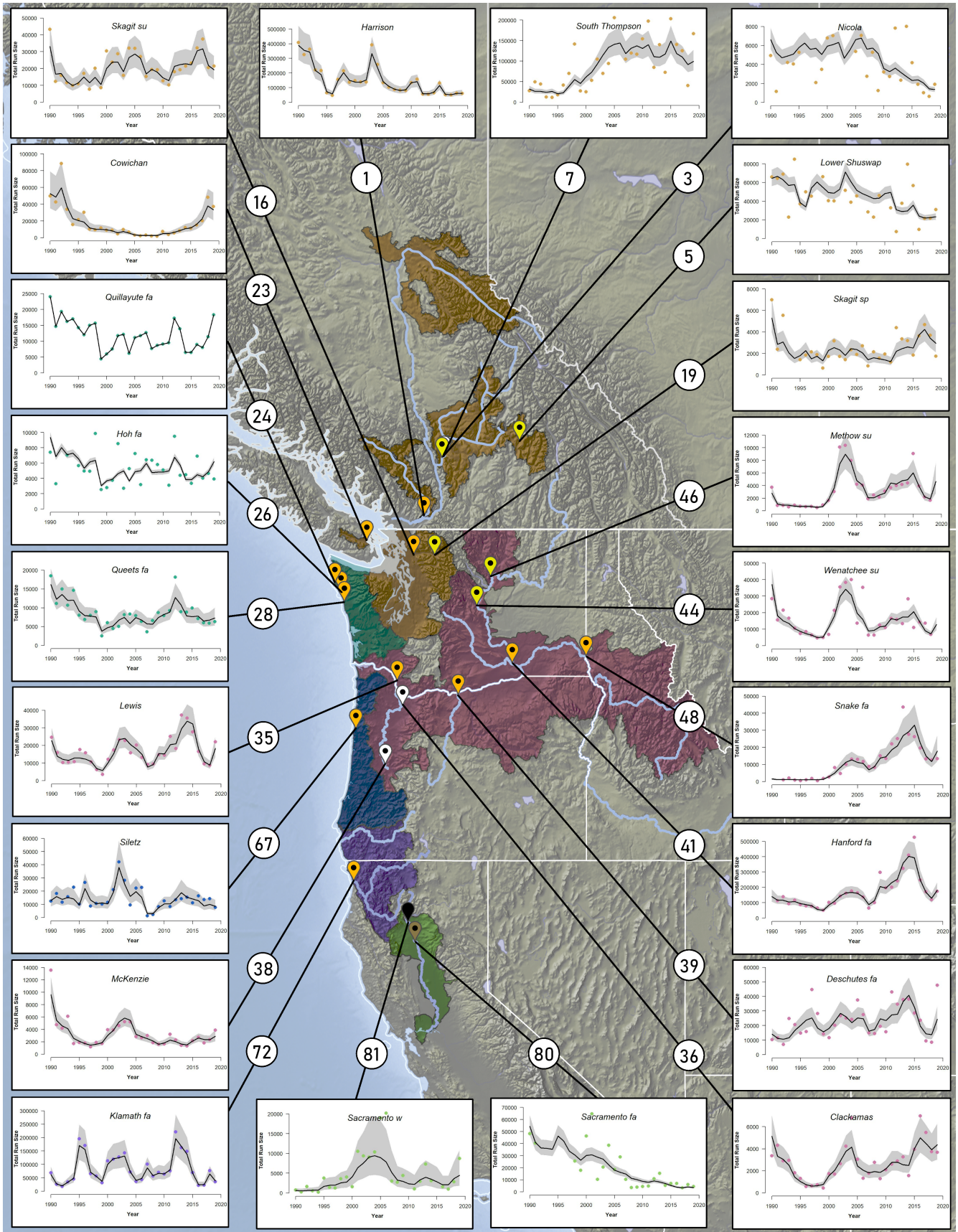
FIGURE 4 Changes in total run size relative to the 1990–2019 average estimated for 23 populations with total run size data across the most recent 5-years and 15-years in our dataset.

FIGURE 5 Median estimated total run size ($x_{i,t}$) trends (black lines) and 95% confidence intervals (grey shading), plotted alongside 5-year and 15-year changes in abundance and estimated overall trends from 1990 to 2019. Populations are mapped and colour coded by region for ease of identification.

and Southern Oregon have been further impacted by a prolonged drought affecting freshwater systems (Kogan & Guo, 2015). The negative effects of these disturbances and ecosystem shifts have been precipitated and intensified by more than two centuries of anthropogenic climate change, marine and watershed habitat alterations, and hatchery practices that have eroded the resilience and productivity of Chinook salmon (McClure et al., 2008; Satterthwaite & Carlson, 2015; Dorner et al., 2018; Beechie et al., 2021; Munsch et al., 2022). Chinook salmon are also getting smaller over time, with potentially serious implications for their demographic productivity and ability to support fisheries in the future (Ohlberger et al., 2018; Oken et al., 2021; Xu et al., 2020). These changes in size are likely driven by a multitude of factors including shifting climate and marine food webs, competition with pink salmon, and harvest; and much like survival trends these changes in size are shaped by life history, watershed of origin and marine distribution (Buckner et al., 2022). Many Chinook populations we evaluated have also experienced higher-than-average en route and pre-spawn mortality in recent years (Bowerman et al., 2021; Doutaz et al., 2021; Teffer et al., 2018; Thompson et al., 2012). Indeed, the effects of climate warming are being felt by the Chinook salmon and their associated social-ecological systems from the Yukon to California (Crozier et al., 2021; Katz et al., 2013; von Biela et al., 2022).

Life history, and in particular run timing, appears to be associated with differences in escapement and total run size trends. Our analyses revealed declines among most spring Chinook stocks (40/47), particularly those populations with stream-type juvenile life histories (e.g. interior spring Chinook in the Columbia, Snake and Fraser Rivers) but also among most of California's spring-run Chinook salmon, which have a predominantly ocean-type juvenile life history. These stocks had near-record low spawner abundances in most of the last five years of our study period and, if their current population trajectories continue, they face a high risk of extinction ([COSEWIC] Committee on the Status of Endangered Wildlife in Canada 2018, 2020; [NMFS] National Marine Fishery Service, 2016). This trend is reflected in the ESA and COSEWIC listing status of spring Chinook we assessed with 72% (34/47) of populations listed as threatened or endangered, and five more populations listed as special concern or protected under US state-level legislation.

The particularly severe declines experienced by spring Chinook likely stem from risk factors that are exacerbated by their early-migrating life history. Spring runs in the Columbia, Snake, Fraser, Klamath and Sacramento Rivers undertake some of the longest migrations among the populations we studied and depend on heavily industrialized and urbanized watersheds during rearing and migration. These lengthy migrations in anthropogenically altered watersheds pose considerable challenges for spring runs as both smolts and adults (e.g. Cordoleani et al., 2018; Schaller et al., 2013). Some coastal spring Chinook stocks from Washington and Oregon had qualitatively similar but less extreme declining trends, suggesting that the risk of decline may be related in part to their early-migrating life histories. Interior spring Chinook populations may experience added stress due to the predominance of yearling smolt migration stream-type life histories, which extend their dependence on freshwater rearing areas (Crozier et al., 2019; Gustafson et al., 2007; McClure et al., 2008). In addition to ongoing climate changes, these areas have suffered from the impacts of logging, grazing, forest fires and irrigation withdrawals contributing to reduced baseflow and elevated stream temperatures (e.g. Doutaz et al., 2021; Warkentin et al., 2022). Recent research has revealed distinct survival trends for stream-type and ocean-type stocks even within the same regions (Freshwater et al., 2022), and interior spring Chinook with obligate yearling life histories are also thought to undertake more offshore oceanic migrations, driving differential exposure to North Pacific-scale climate changes (Lindley et al., 2021; Weitkamp, 2010).

In some instances, spring Chinook have benefitted directly from ecosystem restoration or dam removal. Three populations of spring Chinook – in Oregon's Clackamas and Sandy rivers, and California's Butte Creek – stand out for their stable or increasing trends in abundance. These populations have all been the focus of major dam removals, fish passage improvements or ecosystem restoration efforts. Improved juvenile and adult passage at the three dams in the Clackamas watershed have contributed to a rebuilding of spring Chinook abundance in the basin, with the average 2015–2019 escapement exceeding the long-term average by 103%. On the Sandy, natural-origin spawner abundance has increased since the removal of Marmot Dam in 2011, and in the last 5 years escapement has been 144% higher than the 1982–2019 average. Butte Creek is an outlier among the spring Chinook populations we evaluated in California, with relatively strong recent escapements, which increased dramatically following watershed-scale restoration actions that included completion of the Butte Creek Fish Passage Improvement Project, and improved summertime flow and temperature regimes with imported water from a nearby basin ([ACWA] Association of California Water Agencies, 2017). Collectively, these bright spots reveal that large-scale restoration actions can have positive population-level impacts on Chinook salmon (Booth et al., 2016).

Summer and fall Chinook populations had more mixed trends, with only about half of their populations (16/31) experiencing declining escapement as indicated by a negative median trend estimate (u_i) and several populations experiencing increasing trends in abundance. The relative stability of some summer and fall Chinook populations and their ongoing ability to support social-ecological services may be due in part to differences in their life histories and habitats, which moderate their exposure to stressors and climate change impacts in freshwater and at sea. For example, these later-migrating Chinook typically undertake shorter adult spawning migrations, arrive in freshwater closer to reproductive maturity and usually depart freshwater during their first year of life (Healey, 1991; Quinn, 2005; Taylor, 1990).

In fact, most ocean-type summer and fall Chinook returning to the interior areas of the Columbia and Fraser watersheds had stable or positive trends in both escapement and total run size and continue to support major harvest in fisheries. These interior spawning ocean-type populations, colloquially referred to as *up-river brights* in the Columbia, have exhibited increasing abundance

over the last 30 years. These populations share several life-history attributes, freshwater habitat similarities and patterns of distribution at sea. In the ocean summer and fall Chinook from the interior Fraser, Columbia, Washington and Oregon Coasts typically migrate north along the continental shelf to the coastal areas of Northern British Columbia and Southeast Alaska where they feed and grow for several years before undertaking their return migrations (Weitkamp, 2010). Juveniles among these northerly migrating populations depart freshwater during their first year of life, feeding and growing in riverine habitats as they migrate downstream, and typically arriving in their estuaries in May and June, but individuals within these stocks can exhibit a high degree of variability in the timing of marine entry (Bottom et al., 2021; Chalifour et al., 2021; Scott et al., 2019). This extended seaward migration allows fish to achieve a relatively larger size at marine entry and may give these juveniles a survival advantage compared to other ocean-type populations when confronted with unpredictable marine conditions in their early marine life (Beamish et al., 2010; Duffy & Beauchamp, 2011).

Declining abundance and collapsing productivity has given fishery managers slimmer margins of error, creating trade-offs between conservation risks and harvest goals when depressed and healthy populations overlap in mixed-stock fisheries ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020; Moore et al., 2021; Parken et al., 2008). Management responses to declining Chinook salmon populations in the last several decades have included reduced harvest rates, investments in dam passage and removal, hatchery reforms to reduce the demographic and genetic influence of hatchery-origin spawners and habitat restoration. In some places these efforts have paid dividends and have either stabilized abundance or led to recovery among Chinook salmon. For example, Cowichan River fall Chinook fell below their PST-established escapement goal of 6500 spawners in every year from 1997 to 2015. During this period, fishery managers in Canada made modest reductions in the average harvest rate (1990–2009 average ER = 67%; 2009–2017 average = 58%) and changed hatchery practices by reducing the number of hatchery fish released. These management changes coupled with local investments in freshwater and estuarine habitat restoration, and improved water management were followed by a dramatic rebuilding among Cowichan River Chinook. Natural-origin spawner abundance has exceeded 6500 every year since 2016.

In other places, conservation and management actions have lagged declining trends or have been inadequate to address the scale of the challenge, contributing to the erosion of social-ecological values supported by Chinook salmon. In Washington State, some Chinook populations continue to be harvested at high rates in mixed-stock fisheries despite their declining abundance. For example, between 2009 and 2017 the average exploitation rate estimated for CWT-tagged summer Chinook returning to the Skagit River exceeded 50% (range: 24.7%–73%), and Queets River fall Chinook were subjected to average harvest rates greater than 60% (range: 46.6%–80%) ([PSC CTC] Pacific Salmon Commission joint Chinook

Technical Committee, 2020). Skagit River summer and fall Chinook met their ESA recovery goal of 14,500 spawners in 1 year between 2009 and 2019 but on average nearly half of the run was harvested (mean: 46.7%), mostly in marine mixed-stock fisheries. Spawning ground escapement and total run sizes for Queets River fall Chinook also edged downwards towards the PSC established minimum escapement goal of 2500 from 2009 to 2019 and Queets River spring Chinook fell below their PSC escapement goal in all but 4 years between 2005 and 2019. For these stock(s), where CWT-tagging programs enable estimates of harvest, about 70% of fishery impacts occurred in mixed-stock fisheries outside of Washington State waters, limiting the efficacy of local recovery actions by state and tribal management agencies and reducing access to salmon fishing opportunities for communities in these watersheds (Atlas et al., 2021; Malick et al., 2017).

We have identified trends for a subset of Chinook salmon populations in North America, but our analysis was necessarily limited in both its geographic and temporal scope. We opted to focus on the southern half of the North American range of Chinook, primarily because this region is home to the greatest variation in Chinook run timing and life-history diversity, and because data were readily available for many of these populations. Short and variable-length time series of data also create considerable uncertainty and challenge comparisons of Chinook escapement trends across regions where time series length differ. Accordingly, inter-regional comparisons of population trends should be interpreted with caution. In addition, fluctuations or stability in escapement among Chinook populations is influenced strongly by fisheries management, making escapement an imperfect indicator of the biological status of Chinook populations. However, consistent declines in Chinook escapement even after reductions in harvest rates that have corresponded with declining abundance, highlight the severity of the declines now being observed among many Chinook populations. Total pre-fishery abundance for Chinook salmon populations is a more useful indicator of biological trends. While total run size data sets were only 30 years in length (1990–2019), the fact that these populations were evaluated across the same range of dates improves our ability to draw direct comparisons in their trends.

Despite climate change headwinds, restoration actions can still contribute to increased abundance and productivity for Chinook salmon. Restoring natural hydrological and ecological processes and riverine connectivity through dam removal and floodplain reconnection are paramount for Chinook in their migratory corridors, juvenile rearing areas and headwater spawning areas (e.g. Beechie et al., 2021). Dam removal on the Snake River is among the clearest pathways to recovery for Chinook in the Columbia Basin, and recent analyses indicate that unless survival rates are improved for out-migrating Chinook smolts and returning adults extinction is likely for many of these stocks before the end of the 21st century (Crozier et al., 2021). Removing dams from migratory corridors may also boost marine survival of out-migrating smolts, since carryover effects from migration through the hydro

system including reduced condition or energy storage at ocean entry have been linked to lower smolt-to-adult returns (e.g. Gosselin et al., 2021). Dams that are complete migratory barriers to Chinook, or that inundate former spawning habitats, reduce the quantity of habitat for spawning adults and rearing juveniles for both stream- and ocean-type life histories, diminishing the productive capacity of watersheds for Chinook (Liermann et al., 2010; Parken et al., 2006) and disrupting downstream physical and ecological processes (Ward & Stanford, 1987). Dam removals have led to some of the most notable successes in wild salmon recovery (Hatten et al., 2015; Pess et al., 2008). Likewise, dam removal in the Klamath Basin holds immense promise for Chinook recovery but with spring Chinook in the basin experiencing record low returns the number of strays or colonizing salmon likely to reach newly accessible areas of the Upper Klamath may be limited without urgent action (Thompson et al., 2019).

Our analysis of Chinook abundance trends reveals clear winners and losers, even in the face of a rapidly changing climate, highlighting the importance of intraspecific diversity for stabilizing social-ecological systems (Des Roches et al., 2021). For example, ocean-type summer Chinook in the Interior Fraser, and fall upriver bright Chinook in the Columbia have increased or been stable in their abundance since the 1980s. The responses of individual populations to changes in climate can be sudden and unexpected. For example, in Alaska's Nushagak River, home to Bristol Bay's largest Chinook salmon population, the relative contribution of different spawning areas to annual returns has been shown to fluctuate in response to changing environmental regimes (Brennan et al., 2019). These changes are unforeseen and unpredictable, making the maintenance of intraspecific diversity a critical element of resilience for populations and fisheries (Moore & Schindler, 2022). A rich diversity of Chinook populations and life histories has evolved to fill a variety of niches in freshwater and ocean ecosystems, and these populations continue to evolve in response to natural and anthropogenic drivers. Protecting and rebuilding all these elements of Chinook biodiversity and maintaining the adaptive potential of populations will be essential for their future in the face of a changing climate.

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DATA AVAILABILITY STATEMENT

The data used in all analysis are presented in the supplemental materials in table form with attributions to their original source therein. Data and code are also posted on a public GitHub repository, which can accessed at https://github.com/willatlas/ChinookEscapement-RunSize

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