# A hypothesis-driven statistical approach for identifying ecosystem indicators of coho and Chinook salmon marine survival

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## ABSTRACT

Efforts to understand causes of declines in productivity of species of concern often involve retrospective evaluation of multiple possible causes based on trends in relevant ecological indicators. We describe a hypothesis testing framework for examining declines in marine survival for coho and Chinook salmon in the Salish Sea. Independent populations of both anadromous species have declined over the last 50 years, prompting extensive examination of mortality in different life stages. Previous studies have identified declining trends in marine survival, and we re-evaluated these trends in light of a number of possible hypotheses for declines. We laid out seven potential explanations for declines: changes in predator buffering related to abundance and timing, density-dependent or -independent food availability, water quality, timing of freshwater delivery to Puget Sound, and anthropogenic impacts. We compiled ecosystem indicators relevant to these hypotheses and used generalized additive models (GAMs) to examine multivariate relationships with survival from multiple coho and Chinook salmon stocks. We also developed additional models using the most informative indicators based on variable importance weighting (VIW) from the seven hypothesis groups. We examined how these models explained overall trends in marine survival, as well as survival in three temporal stanzas (before, during, and after a major decline, based on statistical breakpoint analysis). Across the entire time series, best fitting models explained 30–40% of the variation in the survival data. Best fitting models were from multiple hypotheses, including predation (abundance and timing), competition, water quality, and anthropogenic impacts; the freshwater delivery hypothesis was the least supported. Different models performed best (lowest error) during different stanzas of the coho salmon marine survival time series and the two VIW models were generally the top performing models, but performance varied in different years. Indicators with the strongest support included seal abundance, herring abundance, timing of hatchery salmon releases, and indicators related to water properties like stratification and temperature. These findings suggest that multiple processes embedded in several of our hypotheses influence marine survival but that an ecological "smoking gun" for Salish Sea salmon declines will remain elusive.

## 1. Introduction

Following fields like economics and human health where experts have sought indicators with which to measure current performance and make predictions about future responses, population biologists seek to identify indicators of ecosystem processes to understand past observations, to establish the relative status of current biological communities, and to forecast future trends (Link et al., 2010; Large et al., 2015; Dietze et al., 2018; Olmos et al., 2020). But indicators must reflect an understanding of the ecosystem components regulating productivity of

organisms, and for many marine species, this is often largely unknown and increasingly impacted by humans (Levin et al., 2010; Large et al., 2015). For species like salmon that have undergone large declines in abundance, survival, and/or productivity, understanding how disparate environmental and anthropogenic factors have led to declines is especially relevant to reversing declining trends. Here we developed multiple hypotheses and associated ecosystem indicators and used statistical models in a retrospective analysis to better understand causes of declines in Puget Sound salmon marine survival.

Ecosystem constraints are magnified for anadromous species such as Pacific salmon, which by nature of their life cycle, are exposed to stressors in freshwater, estuarine, and marine habitats. Each habitat has unique physical and biological constraints and is influenced by humans to varying degrees. In the Salish Sea, a semi-enclosed body of water encompassing the Strait of Georgia, British Columbia, Canada and Puget Sound, Washington, USA, large ecosystem changes have occurred over the past two centuries. These changes include human population growth, subsequent land use change, and estuarine habitat loss due to agriculture and development, among other factors. The ecosystem has continued to change in new ways in recent decades due to increasing urbanization and climate change (Ruckelshaus and McClure, 2007; Elsner et al., 2010; Mantua et al., 2010; Bond et al., 2015) and the impacts to salmon remain multifaceted and cumulative (Jacobson et al., 2003). Increasingly, climate change threatens freshwater and marine ecosystems (Bond et al., 2015; Ward et al., 2015; Mauger et al., 2015; NWIFC, 2016) and the species that reside within. Identifying ecosystem constraints—biological, environmental, anthropogenic, and/or management-related—on salmon productivity is critical to restoring productive populations and understanding trends in critical factors governing mortality will aid decision-makers in conservation strategies.

In addition to overall declining salmon population trends in the Pacific Northwest (Ford et al., 2011), there is evidence for declines in marine survival in some salmon species over the last 40 years within the Salish Sea. Chinook salmon (*Oncorhynchus. tshawytscha,* Ruff et al., 2017), coho salmon (*O. kisutch,* Zimmerman et al., 2015), and steelhead trout (*O. mykiss*; Kendall et al., 2017) have all shown evidence of declines in marine survival, although the trends vary by species and population. We define marine survival as survival from river outmigration of juveniles to returning adults, across the mosaic of habitats salmon occupy in the estuarine and marine seascape. Marine survival of Chinook salmon in the Strait of Georgia, Canada declined from 1980 to 1990, whereas for Puget Sound populations, survival declined prior to 1980 and has remained persistently low, with no apparent temporal trend since the 1980s (Ruff et al., 2017). Chinook salmon in Puget Sound are listed as threatened under the US Endangered Species Act (ESA). Both steelhead trout and coho salmon exhibited marked declines starting in the 1980s and have remained low (Zimmerman et al., 2015; Kendall et al., 2017). These trends differ from coho salmon and steelhead trout stocks from outside of the Salish Sea (Oregon, Washington, and BC coastal stocks), which exhibited lower marine survival than Salish Sea populations during the 1980s, a subsequent decline in survival, and a rebound in survival more recently. The causes for increased marine mortality 30–40 years ago and the subsequent failure of Salish Sea salmon stocks to rebound are still unknown.

Puget Sound is highly populated, and both natural and anthropogenic impacts have likely contributed to declining salmon populations and decreases in marine survival in this region. Ecologists and salmon managers have pointed to a number of possible causes including bottom-up based limitations on food resources (Beamish et al., 2012a, 2012b), top-down trophic impacts caused by increasing numbers of predators (Berejikian et al., 2016; Nelson et al., 2019a, 2019b; Allegue et al., 2020), and multiple anthropogenic impacts from habitat loss to contaminants (National Research Council, 1996; Bradford and Irvine, 2000; Meador, 2014) the cumulative effects of which are likely to be significant (Sobocinski et al., 2018). While much work on understanding salmon survivorship has focused on ocean conditions in regulating

marine survival (Mantua et al., 1997; Sharma et al., 2012; Kilduff et al., 2015), less attention has been paid to a diversity of drivers across the seascape the fish occupy during their entire life histories, including inshore marine waters.

To understand factors governing marine species, scientists have turned to a variety of modeling tools. Ecosystem models are powerful tools for documenting scenarios through which natural and anthropogenic drivers can influence change in populations (Fulton et al., 2003; Rose et al., 2010; Samhouri et al., 2010). While these models are unlikely to be useful on a tactical basis because they can rarely pinpoint specific causes of change (Plagányi et al., 2014; Schindler and Hilborn, 2015), they can assess multiple factors simultaneously and simulate changes through space and time (Rose et al., 2010). Even simple models, like qualitative network models or conceptual models, are helpful in articulating dominant ecosystem processes (Harvey et al., 2016; Sobocinski et al., 2018). Alternately, retrospective analyses of long time series, when paired with putative mechanistic drivers, may yield information about ecological processes that have influenced change (Cottingham and Carpenter, 1998; Blanchard et al., 2010). In forecasting salmon returns, identifying multiple ecosystem drivers of salmon productivity (or mortality) is one approach for explaining historical trends that may in turn inform forecasts (Mills et al., 2013; Satterthwaite et al., 2019). Time series approaches allow for improved understanding of ecological history relevant to species declines and can inform more integrated ecosystem approaches (Plagányi et al., 2014) as well as needed near-term forecasting (Dietze et al., 2018), making them an important tool for ecologists and managers.

Ecosystem indicators show promise for providing insight into Pacific salmonid trends and environmental and anthropogenic constraints that shape these trends (Logerwell et al., 2003; Burke et al., 2013; Sobocinski et al., 2020). Ecosystem indicators are defined as quantitative measurements that reflect the structure, composition, or functioning of a complex system (Niemeijer and de Groot, 2008; Kershner et al., 2011; Otto et al., 2018). Ecosystem indicators have become important tools for bringing together information about environmental conditions, and then assessing how those conditions may be related to species' population or biomass trends (Large et al., 2013; Otto et al., 2018). Such indicators are important where direct measurements of specific conditions that impact population trends are challenging to collect. Thus, indicators of salmon survival must summarize complex mechanisms and processes related to salmon life-history. Indicators should be theoretically sound, respond predictably to ecosystem change, be integrative, and be relevant to management concerns—in this case, marine survival of salmon and subsequent population sustainability (Link et al., 2010; Shin et al., 2010). Selecting the best indicators is a function of ecological understanding, available data, and continued capacity for monitoring (Rice and Rochet, 2005). For anadromous species, relevant indicators can include freshwater, estuarine, and ocean conditions; ecological interactions (food webs); salmon management actions; and the human footprint on the environment.

Given the declines in Salish Sea coho and Chinook salmon marine survival and the numerous potential reasons for these declines, we developed a framework of hypotheses and associated indicators for retrospectively assessing marine survival using a ~ 40-yr time series of survival. We built on the previous work establishing trends in coho and Chinook salmon marine survival (Zimmerman et al., 2015; Ruff et al., 2017) and identified potential drivers of change in the marine survival time series for Puget Sound, WA, USA stocks. We evaluated candidate indicators of marine survival in the context of the hierarchical framework, with functional hypotheses incorporating data at local, regional, and global (Pacific Ocean) scales. We fit models with indicators for each hypothesis and compared overall model performance among hypotheses to identify which ecological processes contributed the most to understanding declines in marine survival. We also built composite models using the most supported indicators arising from each hypothesis. We examined models in the context of changing survival during different

historical stanzas identified by change point analysis to determine if indicator performance varied during different periods. We sought to identify indicators of marine survival of Salish Sea coho and Chinook salmon, keystone species in an urbanizing, highly impacted inland sea.

## 2. Methods

### 2.1. Marine survival indices

The response variable of interest for developing ecosystem indicators was smolt-to-adult return rate (SAR), which is the ratio of smolts (juveniles released from hatcheries or captured in river mouths) to adults returning from the ocean to spawn. SAR is the best available long-term estimator for survival during the marine phase for coho and Chinook salmon. Salmon originating from Puget Sound stocks are harvested extensively in mixed-stock fisheries along the Pacific Coast. We primarily used coded wire tag (CWT, a small numerically coded metal tag) data from releases and recoveries downloaded from the Pacific States Marine Fisheries Commission's (PSMFC) Regional Mark Information System (RMIS) to estimate marine survival. In general, stock-specific survival indices form the basis for this study but the methods were different for coho and Chinook and followed earlier work; differences in methods are highlighted below. We refer to the estimates of marine survival as Marine Survival Indices (MSI) to account for the varying methods (Appendix A). The quality of MSI derived from CWT recovery data can vary substantially (especially during the early part of the time series) by population and year, due to poor fishery and escapement sampling coverage (PSCCWTWG 2008). Nevertheless, we have included all stocks with>5 years sampled, even if noncontiguous.

Estimates for 18 populations of coho salmon marine survival (Fig. 1, Appendix A) were made using two methods, the first using CWT releases and recaptures and the second using estimates of wild smolt outmigration, adult immigration, and estimated exploitation rates (collectively termed "smolt survival" in Zimmerman et al., 2015). Thus, coho marine survival estimates include both hatchery and natural origin stocks. Smolt survival was the estimated number of 3-year-old coho salmon caught in all fisheries plus the number of 3-year-old coho salmon escaping fisheries to return to the rivers or hatchery to spawn divided by the number of smolts that produced these adults. Coho typically return at age 3 in this region (Sandercock, 1991). For both methods, data included ocean entry years 1977 to 2015, although not all years were available for all stocks.

The survival estimates for Chinook salmon stocks (25 total stocks, Fig. 1, Appendix A) were made using CWT releases for ocean entry years 1975–2012. Population- and brood-specific early marine survival rates were estimated using backwards cohort reconstruction as described in Ruff et al. (2017). The estimated cohort size is determined by reconstructing population-specific cohorts based on CWT recoveries in pre-terminal ocean fisheries, terminal freshwater fisheries, and escapement to spawning areas. An assumed natural mortality rate for each age-class, ranging from 40% for age-2 fish to 10% for age-5 fish (Chinook Technical Committee, 1988; Ruff et al., 2017) is then applied. Survival includes sources of post-release mortality of CWT fish to age-2 for Chinook salmon released as subyearlings (migrating to the ocean in their first year) and to age-3 for Chinook salmon released as yearlings (migrating to the ocean after a year in fresh water); thus, for both life-history types returning individuals were captured after 1 ocean year).

All Chinook survival estimates included in this analysis are from hatchery stocks and include both subyearling and yearling life histories. MSI for Chinook salmon was modeled separately for subyearling and yearling runs on the basis that predator/prey interactions, physiological optimums, and outmigration timing differ based upon the average fish body size among these life-history types. We used time series data from the mid-1970s, whereas the Ruff et al. (2017) analysis only included
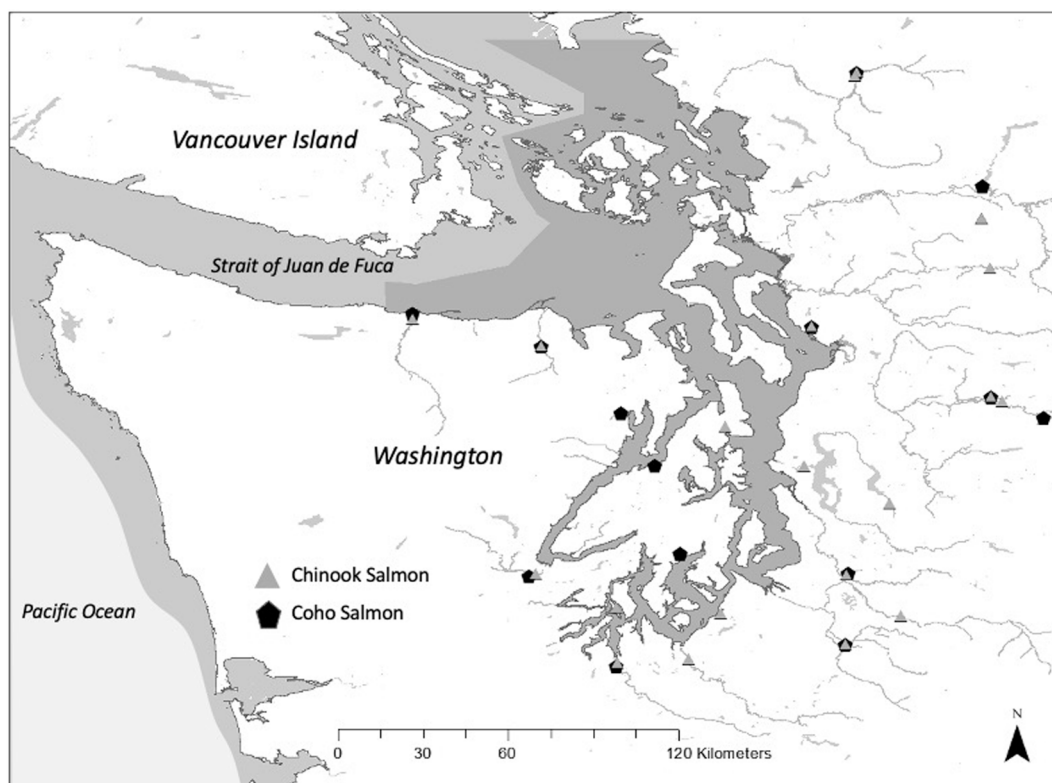


**Fig. 1.** Map of the Salish Sea with origins of Chinook and coho salmon stocks from Puget Sound. Chinook salmon stocks are depicted with gray triangles; coho salmon stocks are depicted with black pentagons. The scales considered in the analysis include Puget Sound subbasins (local scale) in darkest gray, Strait of Juan de Fuca, Strait of Georgia and the near coastal waters (regional scale) in the medium gray, and Pacific Ocean (global scale) in the lightest gray. The salmon stocks used in this analysis migrate to the North Pacific Ocean toward the Gulf of Alaska, beyond the scale of this map.

data from 1980 onward due to sparse data earlier in the time series and the modeling framework they employed.

For the analysis herein, we limited our dataset to stocks originating in Washington, USA rivers and entering Puget Sound, the Strait of Juan de Fuca, and the Southern Strait of Georgia, Canada. The data were provided by Washington Department of Fish and Wildlife (WDFW). Full methods are provided in two previous papers, Zimmerman et al., 2015 (coho salmon) and Ruff et al. (2017) (Chinook salmon); values from more recent brood years were updated in a Salish Sea Marine Survival Project technical report (M. Alexandersdottir, unpublished report to *Long Live the Kings*, Seattle, WA).

### 2.2. Hypotheses for Indicators

We developed multiple hypotheses related to potential mechanisms for coho and Chinook salmon marine survival (Table 1) building off of the approach developed by Sobocinski et al., (2020) for steelhead trout and informed by other salmon indicators efforts (Burke et al., 2013; Mills et al., 2013; Peterson et al., 2014; Litzow et al., 2018; Satterthwaite et al., 2019). We posited seven overarching explanations for declines in salmon marine survival, capturing a variety of ecosystem processes; we summarize these below. Two hypotheses involve predation: for H1 we posit that predators are buffered by abundance of conspecifics, congeners, and alternative prey from increasing numbers of predators; H2 is similar, but deals specifically with the variable timing of outmigrating salmon. Two hypotheses incorporate indicators of prey availability: for H3 we examine the density-dependent component (competition) and for

**Table 1**
Hypotheses related to declines in salmon marine survival, short descriptions, and supporting literature for each.

| Hypothesis | Description | Supporting References |
|---|---|---|
| H1: Predator Buffering (Abundance) | Abundance of potential prey fish in the system mitigates predation impacts | Weitkamp et al., 2011; Berejikian et al., 2016; Chasco et al., 2017; Wells et al., 2017 |
| H2: Predator Buffering (Timing) | Twofold: 1) release timing of hatchery fish mitigates predation impacts (positive relationship) or 2) release timing of hatchery fish attracts predators (negative relationship) | Thomas et al., 2016; Chasco et al., 2017; Nelson et al., 2019a, 2019b; Allegue et al., 2020 |
| H3: Food Availability and Competition (Density-dependent) | A scarcity of prey and an abundance of competitors (salmon and forage fishes) results in low marine survival | Ruggerone and Goetz, 2004; Ruggerone and Nielsen, 2004; David et al., 2016; Cline et al., 2019; Kendall et al., 2020; Claiborne et al., 2020 |
| H4: Food Availability Timing (Density-independent) | Production of prey is driven by physical conditions and a mismatch in timing of prey production and salmon outmigration leads to low marine survival | Cushing, 1990; Beamish et al., 2012a, 2012b; Satterthwaite et al., 2014 |
| H5: Water Quality | Salish Sea and ocean conditions are unfavorable leading to poor marine survival | Mantua et al., 1997; Logerwell et al., 2003; Trudel et al., 2009; Kilduff et al., 2015 |
| H6: Freshwater Delivery Timing | The timing of freshwater delivery to the nearshore influences marine survival (relationship unknown, but freshwater flow during spring may influence year class success) | Jensen and Johnson, 1999; Greene et al., 2005; Bradford and Heinonen, 2008; Michel, 2019; Morrice et al., 2020 |
| H7: Anthropogenic Impacts | Impacts of human population negatively impact survival | Magnusson and Hilborn, 2003; Meador, 2014; Greene et al., 2015; Khangaonkar et al., 2018 |

H4 the density-independent food availability. For H5, we evaluate water quality in the Salish Sea and the Pacific Ocean and for H6 the timing of freshwater delivery to Puget Sound. Lastly, for H7 we evaluate anthropogenic impacts. We describe these hypotheses briefly below (we refer readers to Sobocinski et al., 2020 for additional background), with supporting references in Table 1.

The predator buffering hypothesis (H1) includes predation on salmon from predators and the abundance of alternative prey such as forage fishes and other salmon species such as pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*). We hypothesize that the abundance of alternative prey will mitigate predation on the focal salmon species. The predators primarily include harbor seals, *Phoca vitulina,* which have increased in abundance during the period of marine survival declines (Chasco et al., 2017), and to a lesser extent, orcas (*Orcinus orca,* Ford et al., 2016), which have experienced variable abundance in our study period. The second predation hypothesis (H2) is related to timing of prey, driven primarily by hatchery release timing. Under this hypothesis we propose two potential yet conflicting mechanisms: a) a pulse of prey (release of hatchery fish over a short time period) might mitigate predation by dispersing the impact across more individuals (as in H1) resulting in increased marine survival and b) a pulse of prey available in nearshore marine habitats could attract predators (resulting in reduced marine survival). We used hatchery release dates and variation in release dates (coefficient of variation, CV, of release timing within each year) to explore the effects of pulses.

In hypotheses 3 and 4 we indirectly investigate prey availability and competition. H3 is the density-dependent component, hypothesizing that outmigrating hatchery Chinook and coho are limited by available food and habitat within estuarine areas (David et al., 2014), competition for prey with other small-bodied fish (forage fishes and other salmon, Brodeur et al., 1990), and conspecifics in the ocean (Ruggerone and Goetz, 2004; Ruggerone and Nielsen, 2004). For H4 we hypothesize that food web changes driven by environmental conditions (density-independent factors) have created a bottom-up driven food shortage and increased competition in the inland marine waters and ocean (Beamish et al., 2012a, 2012b; Preikshot et al., 2013).

H5 is concerned with water quality in the Salish Sea and the ocean. Here we use "water quality" as a general term to describe physical conditions within the inland waters and large-scale climate indicators reflective of conditions in the Pacific Ocean (Logerwell et al., 2003; Teo et al., 2009; Kilduff et al., 2015). H6 specifically addresses variable freshwater discharge to the estuarine waters of Puget Sound and the Strait of Georgia. Freshwater outflow drives much of the estuarine circulation in Puget Sound (MacCready and Banas, 2011) and also influences the proximal habitats of salmon as they enter estuarine waters. We evaluated variation in river discharge (volume, timing, and seasonal averages and peaks) from stations nearest the saltwater boundary and physical characteristics, like stratification, that result from changes in freshwater discharge-driven estuarine circulation.

Researchers have documented the impacts of contaminants (O'Neill et al., 2019; Meador, 2014; Meador et al., 2016; O'Neill et al., 2008) and disease (Chen et al., 2018) on salmon in this region, but few studies have spanned the time span of our inquiry. In the absence of time series data related to many anthropogenic impacts, we primarily used human population abundance as the indicator for H7, following Greene et al., (2015), which provided the foundation for understanding negative associations between Chinook salmon abundance and anthropogenic stressors along the west coast (Toft et al., 2018).

Within each hypothesis, we identified indicators that would be theoretically relevant based upon previous work in the region or on salmon more broadly (Tables 1 and 2 and Appendix C). Based upon available data (i.e., quantitative metrics spanning our study period, 1975–2015) we selected time series that described aspects of ecological structure, relationships (e.g., competition, predation), environmental conditions or other potential mechanisms related to survivorship for each hypothesis. Some indicators are included under more than one

**Table 2**

Hypotheses relating to Chinook and coho marine survival and indicators associated with each. Scale refers to the spatial scale at which data are applicable, where local refers to subbasin scale, regional to Salish Sea scale, and global to N. Pacific Ocean (see Fig. 1). The hypothesized relationship to MSI refers to the hypothesized direction of the effect. Indicators may have both positive and negative hypothesized effects depending upon the mechanisms in question.

| Hypothesis | Indicators | Scale | Hypothesized Relationship to MSI |
|---|---|---|---|
| H1: Predator Buffering (Abundance) | Seal Abundance | Regional | Negative |
| | Orca Abundance | Regional | Negative |
| | SOG Herring Abundance | Regional | Positive |
| | PS Herring (all) | Regional | Positive |
| | Fraser Pink Salmon Abundance (Outmigrating) | Regional | Positive |
| | PS Pink Salmon Abundance (Outmigrating) | Local | Positive |
| | Herring SSB (by subbasin) | Local | Positive |
| | Yearling Chinook Hatchery Release Abundance | Local | Positive |
| | Subyearling Chinook Hatchery Release Abundance | Local | Positive |
| | Yearling Coho Hatchery Release Abundance | Local | Positive |
| | Index of Ocean Salmon | Global | Positive |
| H2: Predator Buffering (Timing) | Seal Abundance | Regional | Negative |
| | Orca Abundance | Regional | Negative |
| | Yearling Chinook Hatchery Release Date | Local | Parabolic |
| | Subyearling Chinook Hatchery Release Date | Local | Parabolic |
| | Yearling Coho Hatchery Release Date | Local | Parabolic |
| | Subyearling Coho Hatchery Release Date | Local | Parabolic |
| | CV of Subyearling Chinook Hatchery Release Date | Local | Positive |
| H3: Food Availability and Competition (Density-dependent) | SST | Local | Positive |
| | Salinity | Local | Negative |
| | PS Herring Spawning Stock Biomass | Local | Positive |
| | PS Pink Salmon Abundance (Out) | Local | Negative |
| | Fraser Pink Salmon Abundance (Out) | Regional | Negative |
| | Index of Ocean Salmon | Global | Negative |
| | Fraser River Flow (Spring) | Regional | Unknown |
| | PS River Flow (Apr.-May) | Local | Unknown |
| | Chl $a$ (JDF Strait) | Regional | Positive |
| | SOG Wind Index | Regional | Positive |
| | Upwelling Index | Global | Positive |
| | Yearling Chinook Hatchery Release Abundance | Local | Negative |
| | Subyearling Chinook Hatchery Release Abundance | Local | Negative |
| | Yearling Coho Hatchery Release Abundance | Local | Negative |
| | Precipitation (Spring) | Regional | Negative |
| | Stratification Index at Race Rocks | Regional | Negative |
| | Max Air Temp (Spring) | Regional | Negative |
| H4: Food Availability Timing (Density-independent) | Cumulative Degree Days | Regional | Negative |
| | Date of 75% Cumulative Flow | Local | Positive |
| | Duration between 25% and 75% Cumulative Flow | Local | Unknown |
| | Spring Transition Date | Global | Negative |
| | Yearling Chinook Hatchery Release Date | Local | Negative |
| | Subyearling Chinook Hatchery Release Date | Local | Negative |
| | Yearling Coho Hatchery Release Date | Local | Negative |
| | Subyearling Coho Hatchery Release Date | Local | Negative |
| | CV of Subyearling Chinook Hatchery Release Date | Local | Positive |
| H5: Water Quality | SST | Local | Positive |
| | Salinity | Local | Unknown |
| | PS River Flow (Apr-May) | Local | Unknown |
| | Sea Level Height | Global | Positive |
| | Precipitation (Spring) | Regional | Unknown |
| | Stratification Index at Race Rocks | Regional | Negative |
| | Max Air Temp (Spring) | Regional | Negative |
| | SOG Wind Index | Regional | Positive |
| | PDO | Global | Negative |
| | PNI | Global | Unknown |
| | NPGO | Global | Positive |
| | NPI | Global | Unknown |
| H6: Freshwater Delivery Timing | Cumulative Degree Days | Regional | Negative |
| | Date of 75% Cumulative Flow | Local | Positive |
| | Duration between 25% and 75% Cumulative Flow | Local | Unknown |
| | Date of Max. Freshwater Flow | Local | Unknown |
| | Spring Transition Date | Global | Negative |
| H7: Anthropogenic Impacts | Population | Local | Negative |
| | Yearling Chinook Hatchery Release Abundance | Local | Negative |
| | Subyearling Chinook Hatchery Release Abundance | Local | Negative |
| | Yearling Coho Hatchery Release Abundance | Local | Negative |
| | Coho/Chinook Harvest | Regional | Positive |
| | Total Salmon Harvest | Regional | Positive |

hypothesis, as that indicator is functionally applicable to multiple hypotheses. For example, harbor seals appear in both hypotheses related to predation; although the two hypotheses address separate mechanisms (abundance of predators and timing of predators and alternate prey), the presence of seals is an important component of our hypotheses regarding predation. It is possible that this duplicity may limit our ability to discriminate among the hypotheses, but by including all relevant variables in our models and using model selection, the indicators that have strong support should emerge.

### 2.3. Relevant spatial scale for indicators data

Within our hypothesis-driven framework is the assumption that processes influencing survival act at different temporal and spatial scales. Understanding variation in the marine survival index data was important for aggregating data at the proper scale and defining the correct model form in our statistical analysis. Puget Sound has multiple subbasins that differ in oceanography (Khangaonkar et al., 2018) and river inputs, as well as degree of human footprint. Following the work of Zimmerman et al., 2015 and Ruff et al., 2017, where coherence in survival trends was evident at both subbasin and regional (Puget Sound-wide) scales, but with overall coherence at the Puget Sound (regional) scale, we investigated further whether subbasin differences were evident in the datasets. Zimmerman et al., (2015) found some evidence for differences at the subbasin scale, but low statistical power limited inference. Here, with a longer time series and additional data in recent years, we used Dynamic Factor Analysis (DFA, Zuur et al., 2003), to investigate whether one or more common underlying but unobserved (latent) trends best explained the MSI data from the time series of coho and Chinook from Puget Sound. Our aim in conducting these analyses was to determine if there was a shared trend among all stocks of one species within Puget Sound or if there was subbasin-scale variability that would need to be accounted for with our indicators models. As one latent (shared) trend had the most statistical support, we found little evidence for subbasin scale variation needed for Chinook or coho and models. Full methods and results are provided in Appendix B.

We further investigated scale dependence by developing indicators at local (subbasin), regional (Puget Sound and the Strait of Juan de Fuca), and global (North Pacific Ocean) scales. For each hypothesis, we included potential indicator data at relevant spatial scales and at the highest resolution available. For example, sea surface temperature in Puget Sound was aggregated by subbasin and considered local scale, while Fraser River flow (the dominant freshwater input to the region) was considered regional because its value was not unique at the subbasin spatial scale. The potential indicators associated with each hypothesis (Table 2) ranged from local to global scales and varied from 5 to 17 candidate indicator datasets per hypothesis. It should be noted that some potential indicators provide a more direct link to salmon marine survival (e.g., seals via predation and hatchery conspecifics via competition) than others (e.g., water delivery timing, index of chlorophyll *a*, and date of spring transition), which serve as proxies for larger scale processes that are not easily measured.

### 2.4. Identifying temporal scale for Indicators Data

Data for potential ecosystem indicators were gathered from local, state, and federal agencies and collaborators (Table 2, Appendix C). Given that our focus was on marine survival, each potential indicator was indexed to salmon ocean entry year, spawning (brood) year + 1 for subyearling runs that enter the ocean in their first year and spawning year + 2 for yearling runs that enter the ocean after a year rearing in freshwater. In cases where lagged climate indicators have been previously shown to be important (e.g., Pacific Decadal Oscillation, PDO, and North Pacific Gyre Oscillation, NPGO), we generated 1–2 year lagged and led versions of the indicator for exploration, and selected the best fitting version (using Akaike's Information Criterion corrected for small

sample size, $AIC_c$, in preliminary univariate models) for inclusion in the indicators dataset associated with each hypothesis. We also aligned the time period of the aggregated data to that reflective of the salmon life history stage. For example, for local indicators (such as temperature and salinity in Puget Sound waters), we aggregated data over the out-migration period (March-June), when outmigrating fish would be in the system. For regional level indicators, we used a later time period of May-September to account for movement through Puget Sound out toward the Pacific Ocean. All metadata and time series sources and time periods of aggregation are provided in Appendix C.

### 2.5. Ecosystem indicators models

To test the descriptive power of each hypothesis, we used generalized additive models (GAM) with an information theoretic approach. GAM utilizes a smoothing function on selected terms and allows for nonlinear relationships between response and explanatory variables. The general form of the model is: $Y_i \sim \beta_0 + f_1(x_i\beta_1) + f_2(x_i\beta_2) + \ldots f_n(x_i\beta_n) + \varepsilon_i$, where the functions $f_i$ are the non-parametric smoothing terms. This approach is useful in indicators development because it allows for associations where the response (MSI) varies non-linearly across the values of the indicators and where the exact relationship is unknown (Zuur, 2012; Wood, 2017); it can be used to illustrate threshold effects as well (Hunsicker et al., 2016; Samhouri et al., 2017; Satterthwaite et al., 2019). We used the beta distribution with a logit link to account for the proportional nature of the survival data (the ratio of returning fish to outmigrating smolts), where the response values are neither 0 nor 1 (Ferrari and Cribari-Neto, 2004). The error term ($\varepsilon$) was assumed to be independent and identically distributed (Zuur, 2012). The models were fitted using restricted maximum likelihood (REML) in the *mgcv* package in R (Wood, 2017; R Core Team, 2020). The outputs of all best models were assessed using the function *gam.check* (Wood, 2017), which plots residuals and presents diagnostic measures related to model fit and the appropriateness of the smoothing parameter.

For model selection we used $AIC_c$, based upon a full subsets approach (Symonds and Moussalli, 2011; Fisher et al., 2018). Full subsets selection is an information theoretic approach that allows all good candidate models to be compared. This approach is more transparent than backwards selection approaches because all non-collinear combinations of predictors can be identified and evaluated without risk of inadvertently excluding important variables, as can happen with step-wise forward/backwards selection (Fisher et al., 2018). Full subsets selection accommodates our hypothesis-driven framework, while enabling evaluation of a large set of potential indicators without overfitting. We used the R package *FSSgam* (Fisher et al., 2018) to generate the best fitting model(s) for each hypothesis across local, regional, and global scales.

Within each hypothesis, models with ΔAICc < 3 were considered supported. To minimize overfitting given our large set of potential covariates, we limited the maximum number of explanatory variables to 5 (with all combinations tested) and restricted the knots for each parameter within a given model to 4. Knots indicate the general nonlinearity of the spline within a GAM, with fewer knots allowing for less bends in the curve (sometimes referred to as "wiggliness"). Prior to model fitting, we evaluated all potential explanatory indicators for collinearity, removing any that had r > 0.6 and maintaining the indicator with better univariate explanatory power. In addition to models fit with the covariates for each hypothesis, for each set we also included an intercept only model (null model) for comparison.

We calculated the relative importance of different variables within a hypothesis by summing model weights for each variable (Burnham and Anderson, 2002; Fisher et al., 2018). This allowed for evaluation of the full set of indicators within a hypothesis to arrive at those occurring most frequently within the supported candidate models. To compare the predictive abilities among hypotheses, we used deviance explained for the best fitting models for a given hypothesis to demonstrate explanatory power. We compared these values among the hypotheses.

Lastly, we developed an additional candidate model set: all variables with the highest variable importance weightings (VIW Model) within each of the 7 hypotheses. By doing this we arrived at a model that integrated our theoretical assumptions (hypotheses) and the most probable factors impacting coho and Chinook marine survival by using the best predictors from each individual hypothesis. In this way, we built a portfolio of ecosystem indicators based upon model fits (Greene et al., 2010; Schindler et al., 2015). We preferred this approach to model averaging (Dormann et al., 2018) as it leverages information provided by our theoretically-grounded analysis of individual hypotheses using probable indicators and results in a more interpretable model (through evaluation of component smooth function plots for each indicator) than a composite model resulting from averaging.

Within each hypothesis, AIC$_c$ was used to identify the most supported models, VIW was used to identify the indicators that appeared most frequently in the supported models, and deviance explained was used to demonstrate the ability of any given model to explain the variation in marine survival. In combination, these three metrics provided a weight of evidence in identifying indicators with the strongest explanatory power.

*2.6. Model performance relative to time stanzas*

Previous research noted that marine survival exhibited changes in trend and variability over the last 40 years (Zimmerman et al., 2015). During our model development and testing we also noted variation in model performance relative to the time period in which predictions were assessed (i.e., models for some hypotheses performed better at the beginning or end of the time series but had more error in other time periods). Model stability, including time-invariance of the regression coefficients, is important in developing accurate model predictions and is a central concern in many applications of linear regression where temporal change occurs. The variable performance we observed indicated that different mechanisms might be driving marine survival during different periods of our time series and led to an additional model assessment for each hypothesis by time period.

Given the differential model performance we observed and the differences in slope in the MSI time series (sharp declines followed by persistent low survival), we sought to identify the time point at which the slope changed (Zeileis, 2006). To determine if there were in fact structural breaks (stanzas) within the MSI time series and to identify the appropriate time periods, we used structural change analysis with the R package *strucchange* (Zeileis et al., 2002). We evaluated structural change to determine a) if breakpoints (changes in trend) existed within each species' MSI and b) to identify in which year(s) those changes occur. For this analysis we used mean MSI among all stocks for each year and calculated the most likely breakpoints (0–5) within the time series. A breakpoint was considered to be a step change in the parameters of the generating model and was tested using the *F* test approach, whereby we tested the null hypothesis of "no structural change," using *F* test statistics (Zeileis et al., 2002). We used two metrics of model performance: residual sums of squares (RSS) and Bayesian Information Criterion (BIC) to determine the best number of breakpoints in the data. We used the resulting breakpoints to define the stanzas in which we evaluated our indicator model performance.

For each stanza, we calculated the difference between the observed and predicted MSI from the best fitting model for each hypothesis. From this we determined which hypotheses were most accurate in predicting MSI during specific time periods. We describe differences in performance among the models related to each hypothesis for each stanza, defined using the break point analysis.

## 3. Results

### 3.1. Marine survival estimates

MSI values used in this analysis are provided in Appendix A. Coho salmon MSI ranged from 0.0003 to 0.2552, with a median value of 0.05 across 18 populations. Chinook salmon MSI ranged from 0.0002 to 0.1769, with a median value of 0.01 across 25 populations. The Chinook MSI time series included both subyearling and yearling life history types and MSI varied among life history types (Fig. 2), but MSI was, in general, lower than that for coho salmon. For both species (and both life history types within Chinook salmon), the latter part of the time series revealed lower MSI and less variation within the data, reflecting in part more complete datasets with estimates for additional stocks within a year.

## 4. GAM for ecosystem indicators

### 4.1. Coho salmon

For each of the seven hypotheses (Tables 1 and 2) we used AIC$_c$ to determine supported candidate models (Table 3). It should be noted that for many hypotheses, multiple models were supported. With the exception of Hypothesis 7 (anthropogenic impacts) which had a single model with $\Delta$AIC$_c$ < 3, models ranged from 2 candidate models (H4) to 12 supported models (H1). Models with the lowest AIC$_c$ scores were not necessarily those that explained the most variation in the model subset (highest r$^2$), although they tended to be within 1 AIC unit of the models with the most variance explained.

Among the 7 hypotheses for coho salmon MSI, hypotheses 1, 2, 5, and 7 (the two predator buffering hypotheses, the water quality hypothesis, and the anthropogenic impacts hypothesis) each explained about 35% of the variation in the data. The worst performing hypothesis was that for water delivery timing (H6), where the best model in the subset explained < 6% of the variation in the data. When model predictions were plotted with observed MSI data, most of the models underpredicted MSI in the early part of the time series and overpredicted MSI in the middle and latter part of the time series (Fig. 3a). In other words, the models also underestimated the magnitude of the decline in survival.

The variables with the highest weightings across the 7 hypotheses included a diverse suite of indicators, ranging from predator abundance (seals) to abundance of other small fishes in the system (e.g. outmigrating pink salmon, herring, and hatchery salmon releases) to Salish Sea and ocean conditions (e.g., stratification index, NPI, and NPGO). When the variables with the strongest weighting scores (VIWs from H1-H7) were evaluated as a set, two models showed strong support (Table 3, Best VIW), explaining > 40% of the variation in the data. These were the only 2 VIW models with $\Delta$AIC$_c$ < 3 and the variables included in each were not overlapping, suggesting that multiple mechanisms influence MSI (Fig. 3b). Best VIW Model 1 was driven by water quality drivers like precipitation and stratification and included variation in subyearling Chinook release timing; Model 2 captured predation and predation buffering indicators like seal abundance and herring abundance in addition to ocean conditions (NPGO) and harvest (Fig. 4). Additionally, while the prediction error for VIW models was lower than for models H1-H7 (i.e., the VIW predictions better fit the data overall), it was not systematic by stanza within the time series (Fig. 3b, see explanation of stanzas below).

### 4.2. Chinook salmon

While we modeled subyearling and yearling life history types separately, for none of the 7 hypotheses did the best models include the same variables for both life-history types (Appendix D, Table 1). For Hypothesis 2, the majority of indicators were the same for both yearling and subyearling runs (common indicators included seals, hatchery
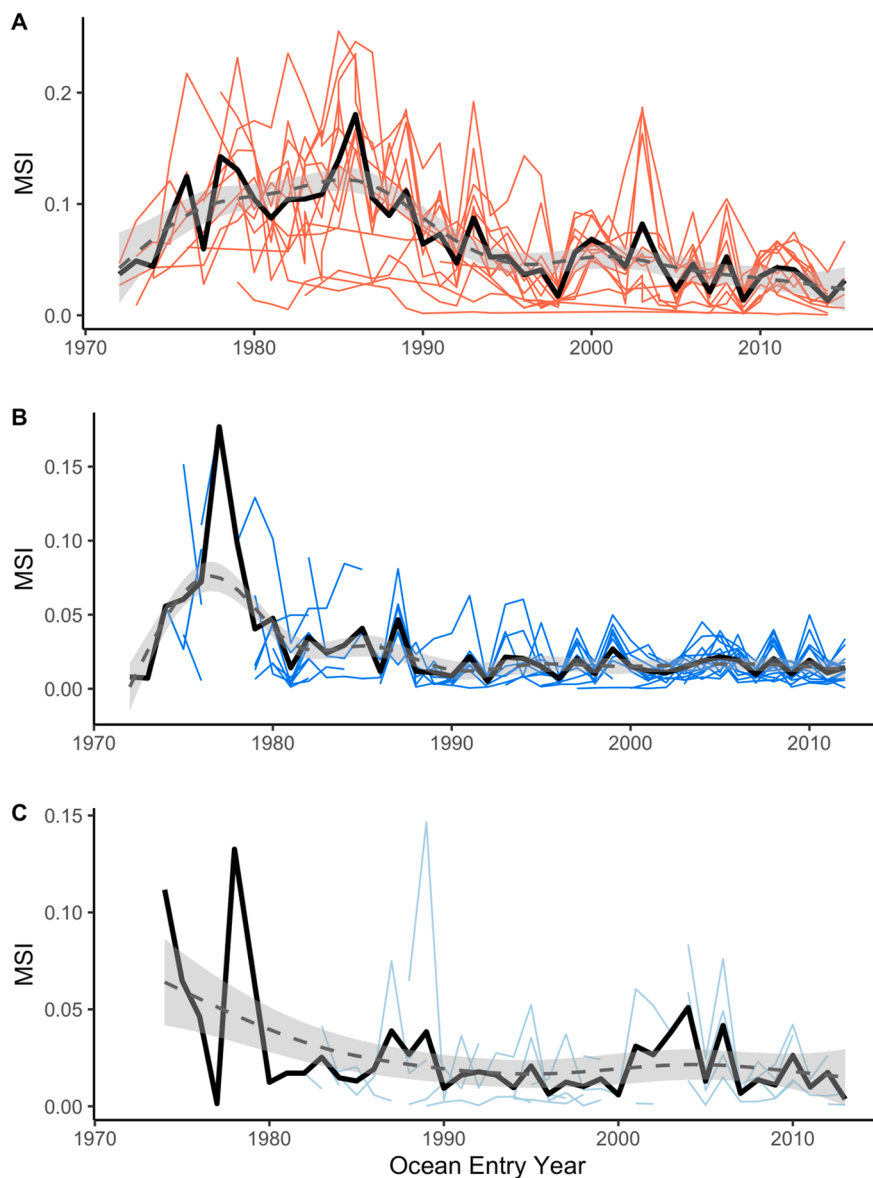
**Fig. 2.** Marine Survival Index for a.) coho salmon b.) subyearling Chinook salmon and c.) yearling Chinook salmon from mid-1970s to 2010s (start and end years are variable by species and life history type). Thick solid black line represents mean for a given year with individual stocks represented by the thin colored lines. A smoothing function (dashed black line and gray envelope showing 95% confidence interval, GAM, where MSI ~ Ocean Entry Year) has been added to illustrate general trends.

subyearling Chinook salmon release date, and hatchery yearling coho salmon release date) but the explanatory power was different, with the yearling model explaining 19% of the variation in the time series of MSI and the subyearling model explaining 27%. In general, model performance was quite poor for yearling Chinook salmon, with most hypotheses explaining < 10% of the variation in the data. There were 2 occurrences (H5 and H6) where the intercept-only model occurred in the best subset of models within each hypothesis due to overall poor fit. Even the best VIW models for yearling Chinook explained < 30% of the variation in the data. We believe the sparseness of the data set and the relative lack of data in some years resulted in poorly fit models. For this reason, the remainder of the results will focus on subyearling Chinook salmon, which was more robust in terms of data completeness.

As in the coho salmon analysis, Hypotheses 1, 2, and 7 (the two predator buffering hypotheses and the anthropogenic impacts hypothesis) were best at predicting subyearling Chinook salmon marine survival, explaining between 25 and 30% of the variation in the data (Appendix D, Table 2, Fig. 5a). Also, similar to coho salmon, Hypothesis 6 (the water delivery timing hypothesis) was the poorest performing hypothesis, with very low explanatory power; for this hypothesis, the intercept-only model was included in the set of best models illustrating

the lack of fit of the covariates. Also, similar to coho salmon, for Hypothesis 7 (anthropogenic impacts) a single model was supported (total salmon harvest + population, 29% deviance explained).

Three variables, Puget Sound sea surface temperature, hatchery yearling coho salmon release date, and seal abundance, had variable importance weightings over 0.95 in the Best VIW models, indicating their consistency in explaining MSI (Table 4, VIW models only). The relationship between MSI and seal abundance was strongly negative, suggesting a predation effect, while that with temperature was positive. It should be noted that the sea water temperatures included in the data set were all within an optimal range for salmon (mean = 11.6 °C, max = 15.9 °C, Brett et al., 1982; Hinke et al., 2005; Hayes et al., 2011) although locally temperatures likely varied from the buoy data we used. Subyearling Chinook salmon MSI was negatively influenced by hatchery coho salmon release date (lower survival when coho were released later in the season) but the mechanism for reduced MSI is not clear. All of the Best VIW models (6 total) included these three variables.

Predictions for subyearling Chinook salmon MSI for all hypotheses missed the peak in the early part of the time series but fit better in more recent years, where there was little contrast in the time series and persistently low MSI values (Fig. 5b).

**Table 3**

Supported GAMs for each coho salmon hypothesis. All potential indicators for each hypothesis and their associated icons are in left panel. The other columns in the left panel show VIW = Variable Importance Weighting and Direction of Relationship, which refers to the direction of the relationship between Marine Survival Index value and the indicator, described as general curves (these are not model outputs). In the right panel are model outputs. Best Models, with indicators shown as icons, include all models in the set with with ΔAICc < 3. Also in the right panel are ΔAICc, the difference in AICc between the best model and the given model; ωiAICc, the weighted value of the given model in relation to all models in the set; and $r^2$, the proportion of deviance explained by a given model. Best VIW model includes variables with the highest weightings (VIW > 0.5) from each hypothesis subset.

## H1: Predator Buffering (Abundance)

| Indicators | VIW | Direction of Rel. | Best Models | ΔAICc | ωiAICc | $r^2$ |
|---|---|---|---|---|---|---|
| Seal Abundance | 0.82 | | PS Pink — Seal — SOG Herring | 0 | 0.142 | 0.353 |
| SOG Herring Abundance | 0.57 | | PS Pink — Seal | 0.500 | 0.111 | 0.340 |
| PS Pink Abundance (outmigrating) | 0.49 | | SY Chinook — FR Pink — Orca — SOG Herring — PS Herring | 1.212 | 0.077 | 0.342 |
| Y Chinook Hatch Release Abundance | 0.32 | | Seal | 1.436 | 0.069 | 0.339 |
| Fraser Pink Abundance (outmigrating) | 0.25 | | PS Pink — Seal — SOG Herring — PS Herring | 1.726 | 0.060 | 0.355 |
| PS Herring Abundance (total) | 0.23 | | Y Chinook — PS Pink — Seal — SOG Herring | 1.784 | 0.058 | 0.359 |
| PS Herring Abundance (by subbasin) | 0.09 | | Seal — SOG Herring | 1.989 | 0.052 | 0.349 |
| Orcas Abundance | 0.09 | | Y Chinook — Seal | 2.349 | 0.044 | 0.345 |
| SY Chinook Hatch Release Abundance | 0.08 | | Y Chinook — PS Pink — Seal | 2.388 | 0.043 | 0.345 |
| Y Coho Hatch Release Abundance | 0.00 | | Y Chinook — Seal — SOG Herring | 2.513 | 0.040 | 0.357 |
| Ocean Salmon Abundance | 0.00 | | PS Pink — Seal — SOG Herring | 2.591 | 0.039 | 0.341 |
| | | | FR Pink — Seal | 2.804 | 0.035 | 0.342 |

## H2: Predator Buffering (Timing)

| Indicators | VIW | Direction of Rel. | Best Models | ΔAICc | ωiAICc | $r^2$ |
|---|---|---|---|---|---|---|
| Seal Abundance | 1.00 | | Seal — Y Coho Date | 0 | 0.246 | 0.350 |
| Y Coho Hatch Rel Date | 0.50 | | Seal | 0.237 | 0.219 | 0.339 |
| SY Chinook Hatch Rel Date | 0.37 | | SY Chk Date — Seal | 1.023 | 0.148 | 0.338 |
| SY Coho Hatch Rel Date | 0.26 | | SY Chk Date — Seal — Y Coho Date | 1.341 | 0.126 | 0.348 |
| Y Chinook Hatch Rel Date | 0.00 | | Seal — Y Coho Date — SY Coho Date | 2.085 | 0.087 | 0.350 |
| CV SY Chinook Hatch Rel Date | 0.00 | | Seal — SY Coho Date | 2.297 | 0.078 | 0.339 |
| Orca Abundance | 0.00 | | | | | |

*(continued on next page)*

**Table 3** (*continued*)

## H3: Food Availability and Competition (Density-dependent)

| | Indicators | VIW | Direction of Rel. | | Best Models | | | | | ΔAICc | ωiAICc | r² |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Precipitation (Spring) | 1.00 | ↘ | Salinity | Max Air Temp | Precipitation | Chl a | | | 0 | 0.167 | 0.300 |
| | Max Air Temp (Spring) | 0.74 | ↘ | Salinity | Max Air Temp | Precipitation | Chl a | PS Pink | | 0.513 | 0.129 | 0.303 |
| | Chl *a* (JDF Strait) | 0.73 | ↘ | Salinity | SOG Wind | Precipitation | Stratification | PS Pink | | 1.305 | 0.087 | 0.299 |
| | Salinity | 0.63 | ↘ | Salinity | Max Air Temp | Precipitation | Chl a | Y Chinook | | 1.384 | 0.084 | 0.307 |
| | PS Pink Abundance (outmigrating) | 0.40 | ↘ | | Max Air Temp | Precipitation | Chl a | Ocean Salmon | | 1.573 | 0.076 | 0.304 |
| | SOG Wind Index | 0.27 | ↘ | SST | SOG Wind | Precipitation | Stratification | PS Pink | | 1.690 | 0.072 | 0.296 |
| | Stratification at Race Rocks | 0.27 | ↘ | Salinity | Max Air Temp | Precipitation | Chl a | FR Pink | | 1.694 | 0.072 | 0.301 |
| | Y Chinook Hatch Release Abundance | 0.15 | ⌒ | Salinity | Max Air Temp | Precipitation | Chl a | SB Herring | | 1.783 | 0.069 | 0.299 |
| | Ocean Salmon Abundance | 0.13 | ↘ | | SOG Wind | Precipitation | Stratification | PS Pink | | 2.406 | 0.050 | 0.288 |
| | PS Herring Abundance (by subbasin) | 0.12 | ↗ | Y Chinook | Max Air Temp | Precipitation | Chl a | Ocean Salmon | | 2.862 | 0.040 | 0.310 |
| | Fraser Pink Abundance (outmigrating) | 0.11 | ↘ | | | | | | | | | |
| | SST | 0.08 | ↗ | | | | | | | | | |
| | Fraser River Flow (Spring) | 0.0 | | | | | | | | | | |
| | PS River Flow (Apr.-May) | 0.0 | | | | | | | | | | |
| | Upwelling | 0.0 | | | | | | | | | | |
| | SY Chinook Hatch Release Abundance | 0.0 | | | | | | | | | | |
| | Y Coho Hatch Release Abundance | 0.0 | | | | | | | | | | |

**Table 3** (*continued*)

## H4: Food Availability Timing (Density-independent)

| Indicators | | VIW | Direction of Rel. |
|---|---|---|---|
| CV SY Chk Date | CV of SY Chk Hatch Rel Date | 1.00 | ～〰 |
| Spring Tran Date | Spring Transition Date | 1.00 | ＼ |
| Y Coho Date | Y Coho Hatch Rel Date | 0.93 | ∪ |
| Y Chk Date | Y Chinook Hatch Rel Date | 0.78 | ∪ |
| Flow Date 75% | Date of 75% Cumulative Flow | 0.56 | ／ |
| Flow Duration 25%-75% | Duration 25% -75% Cumulative Flow | 0.33 | ／ |
| SY Chk Date | SY Chk Hatch Rel Date | 0.10 | |
| SY Coho Date | SY Coho Hatch Rel Date | 0.07 | |
| Cumulative Days | Cumulative Degree Days | 0.0 | |

| Best Models | | | | | ΔAICc | ωiAICc | r² |
|---|---|---|---|---|---|---|---|
| Y Chk Date | Y Coho Date | CV SY Chk Date | Spring Tran Date | Flow Date 75% | 0 | 0.405 | 0.285 |
| Y Chk Date | Y Coho Date | CV SY Chk Date | Spring Tran Date | Flow Duration 25%-75% | 1.129 | 0.231 | 0.277 |

## H5: Water Quality

| Indicators | | VIW | Direction of Rel. |
|---|---|---|---|
| Stratification | Stratification Index at RR | 0.98 | ∩ |
| NPI | NPI | 0.95 | ＼／ |
| Precipitation | Precipitation (Spring) | 0.94 | ＼ |
| Salinity | Salinity | 0.70 | ＼ |
| NPGO | NPGO | 0.54 | ／ |
| Max Air Temp | Max Air Temp (Spring) | 0.35 | ＼ |
| SOG Wind | SOG Wind Index | 0.32 | ― |
| PDO.2 | PDO.2 | 0.06 | |
| Fraser Flow | Fraser River Flow (Spring) | 0.03 | |
| PS Flow | PS River Flow (Apr-May) | 0.02 | |
| SST | SST | 0.02 | |
| PNI | PNI | 0.0 | |
| PDO.Out | PDO.Out | 0.0 | |
| Sea Level | Sea Level Height | 0.0 | |

| Best Models | | | | | ΔAICc | ωiAICc | r² |
|---|---|---|---|---|---|---|---|
| Salinity | NPGO. Out | Precipitation | Stratification | NPI | 0 | 0.514 | 0.345 |
| Max Air Temp | SOG Wind | Precipitation | Stratification | NPI | 1.559 | 0.236 | 0.349 |

**Table 3** (*continued*)

## H6: Water Delivery Timing

| Indicators | | VIW | Direction of Rel. |
|---|---|---|---|
| Spring Tran Date | Spring Transition Date | 0.97 | |
| Flow Date 75% | Date of 75% Cumulative Flow | 0.72 | |
| Max Flow Date | Date of Max River Flow | 0.50 | |
| Flow Duration 25%-75% | Duration 25% - 75% Cumulative Flow | 0.26 | |
| Cumulative Days | Cumulative Degree Days | 0.0 | |

| Best Models | | | ΔAICc | ωiAICc | r² |
|---|---|---|---|---|---|
| Flow Date 75% → Spring Tran Date | | | 0 | 0.438 | 0.058 |
| Max Flow Date → Flow Date 75% → Spring Tran Date | | | 0.677 | 0.312 | 0.062 |
| Max Flow Date | Spring Tran Date | Flow Duration 25%-75% | 2.498 | 0.126 | 0.063 |

## H7: Anthropogenic Impacts

| Indicators | | VIW | Direction of Rel. |
|---|---|---|---|
| Density | Population | 1.00 | |
| Salmon | Total Salmon Harvest | 0.91 | |
| SY Chinook | SY Chinook Hatch Release Abundance | 0.0 | |
| Y Chinook | Y Chinook Hatch Release Abundance | 0.0 | |
| SY Coho | SY Coho Hatch Release Abundance | 0.0 | |
| Y Coho | Y Coho Hatch Release Abundance | 0.0 | |
| Coho Chk | Coho/Chinook Harvest | 0.0 | |

| Best Models | | ΔAICc | ωiAICc | r² |
|---|---|---|---|---|
| Density → Salmon | | 0 | 0.909 | 0.347 |

## Best VIW

| Indicators | | VIW | Direction of Rel. |
|---|---|---|---|
| NPI | NPI | 0.74 | |
| Precipitation | Precipitation (Spring) | 0.66 | |
| Stratification | Stratification Index at RR | 0.66 | |
| CV SY Chk Date | CV of SY Chk Hatch Rel Date | 0.66 | |
| Max Air Temp | Max Air Temp (Spring) | 0.53 | |
| Salmon | Total Salmon Harvest | 0.39 | |
| Seal | Seal Abundance | 0.34 | |
| NPGO. Out | NPGO.Out | 0.34 | |
| SOG Herring | SOG Herring Abundance | 0.34 | |
| Y Coho Date | Y Coho Hatch Rel Date | 0.09 | |
| Flow Date 75% | Date of 75% Cumulative Flow | 0.05 | |
| PS Pink | PS Pink Abundance (outmigrating) | 0.04 | |
| Salinity | Salinity | 0.0 | |
| Chl a | Chl *a* (JDF Strait) | 0.0 | |
| Spring Tran Date | Spring Transition Date | 0.0 | |
| Density | Population | 0.0 | |

| Best Models | | | | | ΔAICc | ωiAICc | r² |
|---|---|---|---|---|---|---|---|
| Max Air Temp | CV SY Chk Date | Precipitation | Stratification | NPI | 0 | 0.524 | 0.417 |
| NPGO. Out | Seal | SOG Herring | Salmon | | 2.613 | 0.142 | 0.411 |

**Fig. 3.** Coho salmon GAM model predictions for a) models H1-H7 (colored lines) and b) Best VIW Models 1 (red) and 2 (teal), with 95% confidence intervals for the predictions from each shown by the respective colored envelope. Black line shows average observed coho salmon MSI in both plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*4.3. Structural change analysis for time stanzas and associated model error*

*4.3.1. Coho salmon*

Given the systematically variable performance of the GAMs with relation to time periods in our coho salmon model predictions, we investigated the coho MSI dataset for structural breaks (changing slopes in the regression). Using the *F*-stats approach, a model with two breakpoints was optimal. These points occurred in 1989 and 2004 (Fig. 6a) with the slope of the initial segment positive (0.02), and the middle and last segments negative (-0.02 and −0.03). The 95% confidence intervals for all slopes included 0, indicating that these were not robust breakpoints. However, this method seemed an objective approach for determining discrete changes in the time series with which to analyze GAM performance. For subsequent post-hoc analysis of GAM performance, we used the 3 time stanzas defined by the structural change analysis as the periods in which to evaluate model performance.

We calculated standardized mean error for the best model for each hypothesis for each stanza (Fig. 7). It should be noted that there are many other models with support for each hypothesis and because the indicators used in these models vary, estimated errors would as well. Nevertheless, several generalities emerged. The first time period (stanza 1) had the greatest error and the third time period (stanza 3) had the lowest error overall. Most of the models had similar error, but the Hypothesis 6 model had the most error for stanzas one and three. Hypothesis 5 (water quality) performed the best of the 7 hypotheses in stanzas 1 and 2 but did not do as well in stanza 3. Additionally, the two

Best VIW Models (VIW1 and VIW2), which represent the portfolio of indicators that performed best overall, both had extremely low error in stanza 3; VIW2 performed better in stanza 2, but VIW1 performed better in the early part of the time series, stanza 1. Again, the variable performance of models with different covariates indicated that using a suite of indicators could best account for variation in the dominant mechanisms controlling salmon marine survival.

*4.3.2. Chinook salmon*

While Chinook salmon models did not exhibit similar temporal variation in the predictive power of different ecosystem indicators, we nonetheless performed structural change analysis on the Chinook MSI data to evaluate the time series for systematic changes in trend. For this analysis, we combined the subyearling and yearling life-history types due to the sparseness with the yearling data and the identification of one underlying latent trend in the MSI time series through our DFA analysis (Appendix B). As with coho salmon, the *F*-stats approach showed the most support for 2 breakpoints. The two breakpoints were 1980 and 1989. The slopes of the model fits were negative for all 3 time stanzas, ranging from −0.09 for the earliest period to −0.03 and −0.01 for the middle and end periods respectively, although as with coho salmon, the 95% confidence intervals for all slopes included zero (Fig. 6b). As there was no evidence of differential performance of different ecosystem indicators during different time periods, we did not evaluate model error further using stanzas.

**5. Discussion**

Our analysis of ecosystem indicators highlights the need to look broadly across the continuum of habitats—inland estuarine waters, the coastal ocean, and the open ocean—used by salmon and the processes like competition, predation, and human impacts acting upon salmon to identify promising predictors of survival. Best predictors include a combination of biotic and abiotic factors from across coastal and ocean habitats. The relative strengths of individual hypotheses were similar for coho and subyearling Chinook salmon, but no one hypothesis significantly outperformed the rest. Models associated with the hypotheses related to predators and predation buffering, both in abundance (H1) and timing (H2) of alternate prey (such as other salmon and herring), had strong support. Models related to anthropogenic impacts (H7), which was primarily driven by human population abundance also had strong explanatory power in our analysis. The hypothesis related to water delivery timing (H6) had the least support. The results for yearling Chinook salmon were considerably different, but these models had poor explanatory power and lack the MSI data to draw inference within this framework. The repeated occurrence of several indicators (e.g., seal abundance and indicators related to timing of hatchery salmon releases) for both Chinook and coho suggests further investigation of the interactions among these factors and marine survival.

Within the hypotheses we posited, models containing different indicators had similar levels of support and explained similar amounts of variation in the marine survival data. For example, within coho H3 (density-dependent food availability and competition), there were 10 supported models all explaining ∼ 30% of the variation in the data, with a total of 9 different potential predictors. This example is typical in that a few variables were included in most of the supported models, and several additional variables added to the explanatory power. Overall, the variation explained in our model set ranged from 10 to 40% and is similar to that found in other studies assessing ecosystem drivers in salmon (Satterthwaite et al., 2019; Olmos et al., 2020), although those efforts had different objectives and used different methods.

Our best VIW models included explanatory variables from across the suite of hypotheses. For coho salmon, we identified two very different VIW models. These were similarly supported and explained more variation in the data (>40%) than any of the models specific to an individual mechanistic hypothesis (<= 35%). For subyearling Chinook salmon, six
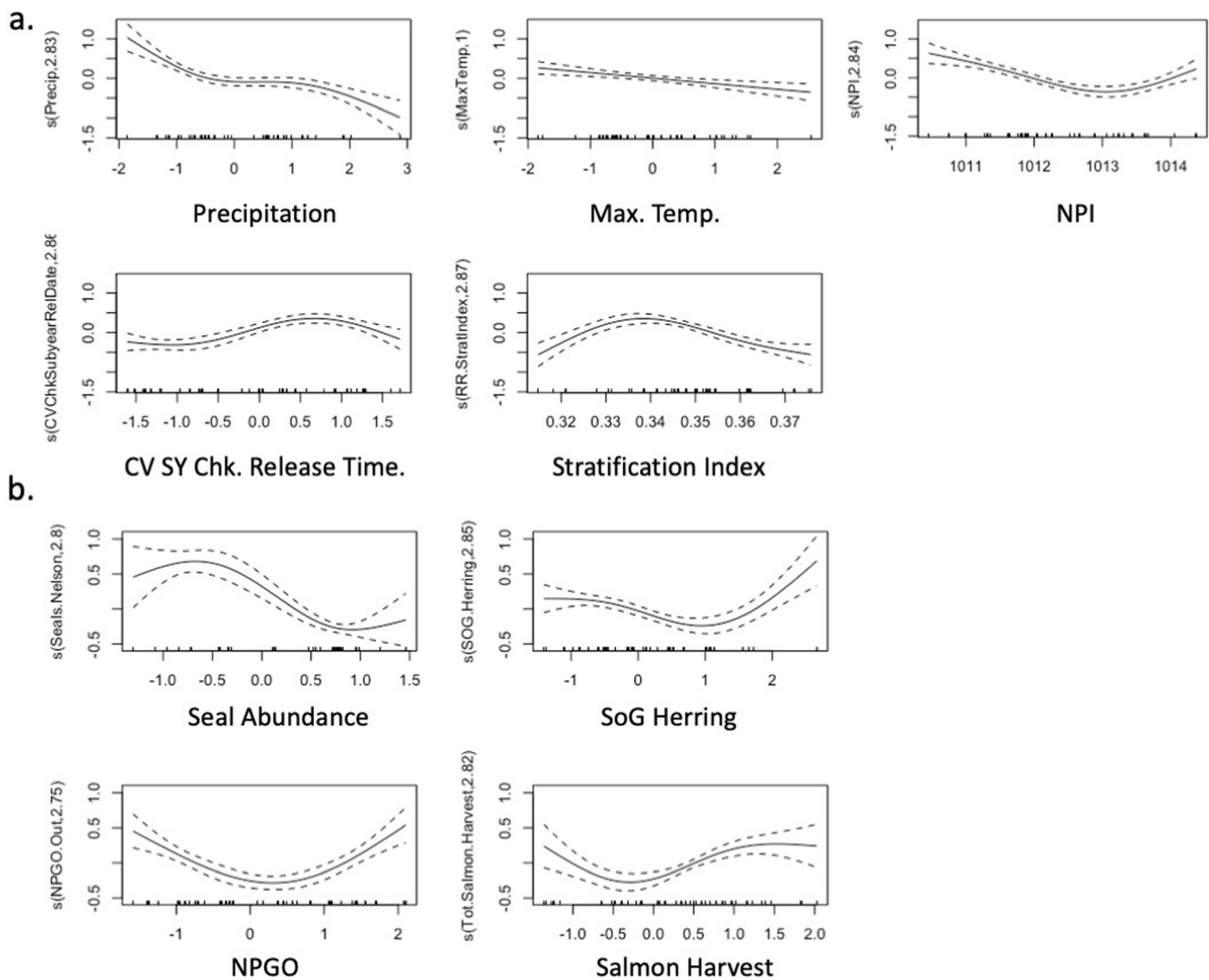
**Fig. 4.** Coho Best VIW Models 1 (a) & 2 (b) partial correlation plots showing the direction of effects for MSI for each indicator. Standardized values of indicators are along the x-axis and MSI values are represented on the y-axis. Indicators are defined in Appendix C.

VIW models were similarly supported and explained 29–30% of the variation in the data, only slightly more than the H7 models.

Together, our findings suggest that a variety of ecosystem indicators, and thus multiple mechanisms, have shaped coho and Chinook salmon marine survival, likely both within and among years over the past four decades. We did not find outsized support for any single indicator (e.g., $r^2 > 0.50$, following Satterthwaite et al., 2019), although seal abundance generally was the best predictor of survival among the candidate indicators, explaining $> 30\%$ of the variation in the MSI time series. Furthermore, in our hypothesis driven framework, the failure of any single hypothesis to dramatically outperform the rest supports our conclusion that determining a smoking gun to explain declines in Puget Sound salmon marine survival is unlikely. Even in our best models $> 50\%$ of the variation in marine survival was unexplained by all factors included here.

### 5.1. Predation and predator buffering

Our results showed strong negative correlation between seal abundance and both Chinook and coho salmon MSI, corroborating the findings of Nelson et al., (2019b). In exploratory univariate modeling, we found that seal abundance alone explained 30% of the variance in coho MSI but $< 7\%$ of the variance of subyearling Chinook MSI, indicating that the strength of the relationship is much stronger for coho. Previous work on steelhead marine survival (Sobocinski et al., 2020) also showed

seal abundance to be the strongest predictor of survival. Ongoing mechanistic work evaluating harbor seal diets, foraging behavior, and other predator–prey interactions is indicating the importance of seals in regulating early marine mortality within the Salish Sea (Berejikian et al., 2016; Chasco et al., 2017). While statistical models such as those employed here and by Nelson et al., (2019b) suggest strong predator effects, it is possible that the persistent increase in seal abundance is concomitant with other unmeasured ecosystem changes (e.g., anthropogenic impacts, changing food webs) that simultaneously affect salmon survival; combined with the correlational nature of our study, we can conclude that seal abundance and seal predation deserve further investigation. Empirical findings from field studies continue to refine our understanding of the mechanisms influencing predator abundances on salmon marine survival and will further elucidate the extent of this source of mortality.

The predation hypotheses (H1 and H2 in particular) related to abundance and timing of forage and hatchery fish include potentially opposite responses. First, for these hypotheses we posited that the abundance of prey fish in the system (be they salmonids or other forage fish, such as herring) and the temporal concentration of those fish could provide some buffering against predation. Furey et al., (2016) found that sockeye salmon smolts swamp their predators to reduce predation risk and that increased densities of co-migrating conspecifics dramatically improved survival of smolts. On the other hand, increased fish in the system, such as increased overall abundances of hatchery salmonids, a
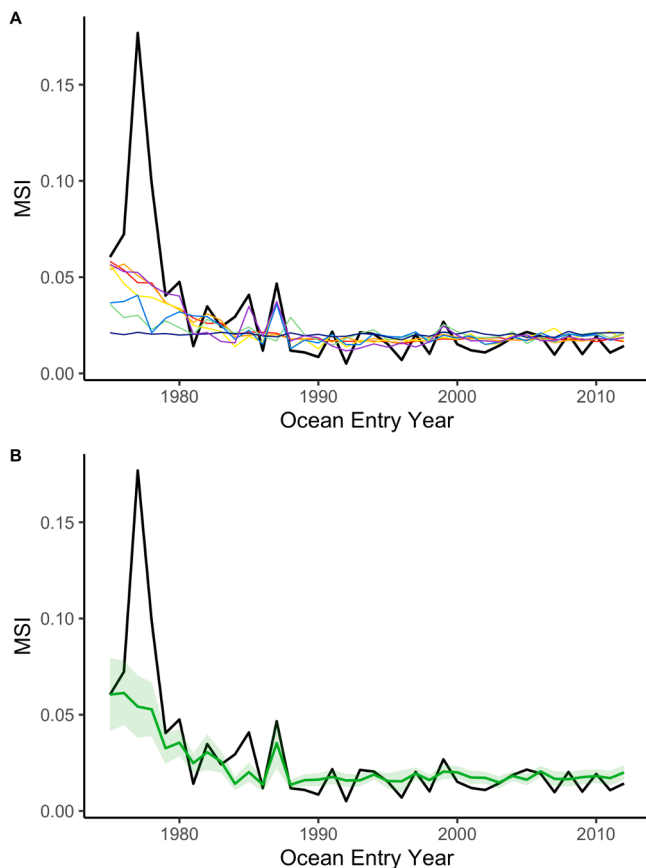
**Fig. 5.** Chinook salmon (subyearling) GAM model predictions for a) models H1-H7 (colored lines) and b) Best VIW Model with 95% confidence intervals for the predictions shown by shaded envelope. Black line shows average observed subyearling Chinook salmon MSI in both plots.

pulse of hatchery outmigrants, or forage fish appearing in nearshore waters concurrent with outmigrating salmon may also be a "call to dinner" for increasingly abundant predators. Wells et al., (2017) showed that salmon were incidentally preyed upon by a bird predator when abundances of anchovy were high, which is an example of an indirect interaction known as apparent competition (Holt and Bonsall, 2017). It is the interaction among predators (namely harbor seals) and pulses of prey (hatchery salmonids and forage fish) and their influence on salmon marine survival that we sought to address with these two hypotheses and models associated with these two hypotheses had some of the strongest support. While our analyses cannot differentiate between buffering from and attracting predators given the mixed direction of relationships among seemingly similar predictors, they emphasize the need for further work on this topic.

### 5.2. Food availability and competition

We found that the abundance of hatchery coho and Chinook salmon released into Puget Sound were not strong predictors of coho or Chinook salmon marine survival under H3, which was related to food availability (density independent). However, we lacked spatially explicit time series data for young-of-the-year forage fish and our investigation used proxy indicators for food production, relying largely on abiotic variables. More interestingly, the timing of release of hatchery coho and Chinook salmon, including the variation in the timing, was important under H4, a hypothesis related to the density-dependent food availability and competition for juvenile Chinook and coho salmon in Puget Sound. Considerable estuarine and delta habitats have been lost over the last century (Simenstad et al., 2011) and investigations of the consequence

of this loss to salmon rearing and survival are ongoing. However, given reduced rearing habitat and much reduced carrying capacity, density dependence is a concern (Greene et al., 2005; David et al., 2016); an outmigrating pulse of fish released from a hatchery may create temporally discrete prey limitation, resulting in reduced growth and survival for fish that co-occur. Overall, for scientists and managers interested in hatchery salmon-related actions that can be taken to increase marine survival in Puget Sound, further examination of the timing and duration of release of hatchery fish and implications of density-dependence on short time scales appears to be one avenue of research and experimentation.

Four of our primary hypotheses (including predation buffering, H1 and H2, and food availability and timing, H3 and H4) are related to ecological processes that may influence early marine survival, including the abundance and/or release timing of hatchery fish, which may create resource scarcity when released as a pulse. Chinook salmon growth during the early marine phase has been previously demonstrated to influence survival (Duffy et al., 2010). A recent study by Claiborne et al., (2020) using scales to determine growth in Chinook salmon demonstrated that growth during the first year of marine residency was correlated with survival and that growth was greater when pink salmon abundance (potential competitor) was low. Our findings (H1, Table 3) also indicate a negative relationship between pink salmon abundance and survival for coho.

In Puget Sound, much of the salmon production, especially for Chinook salmon, is from hatcheries. In fact, most of our survival data come from the coded-wire tagging (CWT) program associated with hatchery production, with only a small subset of our coho salmon MSI data from wild fish. Hatchery coho salmon marine survival rates have generally been lower than those of their wild conspecifics (Zimmerman et al., 2015); while we lack comparative data for Puget Sound Chinook, evidence from British Columbia, Canada suggests the same lower survival is true for hatchery fish of this species (Beamish et al., 2012a, 2012b). Research has shown that hatchery practices that concentrate the timing of juvenile releases (which has generally coalesced to the 3rd week in May since the 1990s, Nelson et al., 2019a) can increase the synchrony of survival rates (Kilduff et al., 2014; Satterthwaite et al., 2014; Teo et al., 2009), suggesting that release timing may set the stage for response to environmental and ecological interactions after release. Additionally, hatchery fish are released at a standardized size (with much less variation than wild conspecifics) and are generally larger than wild outmigrating conspecifics (Nelson et al., 2019a). But recent research has shown that the larger size may increase exposure to predators (Nelson et al., 2019a). The consequences of these timing and size practices for salmonids during their early marine life history are unknown, and our inclusion of hatchery abundances and timing of release as potential indicators of survival was intended to further investigate these interactions. It should be noted that we did not have population-specific release dates for the subset of coho and Chinook salmon populations for which we have MSI data; thus, we used release date information from all Puget Sound hatchery coho and Chinook salmon to gauge ecosystem effects. An investigation of specific stocks and timing/abundance/size at release may yield further insights and more specific findings.

### 5.3. Abiotic factors are not strong predictors

For both species, the water delivery timing hypothesis (H6) was the poorest performing set of models. While river discharge, and specifically variation in river discharge, has been shown to be important in regulating salmon populations (Ward et al., 2015), we found little evidence of the indicators within this hypothesis explaining marine survival. For both species (and for steelhead trout also; Sobocinski et al., 2020), we found that the date at which 75% of cumulative river discharge (within a water year) was reached had a positive correlation with survival; that is, salmon benefitted from protracted duration of river flow into the springtime. While the relationship was linear and fairly strong, this

**Table 4**
Supported Best VIW GAMs for each subyearling Chinook salmon hypothesis. In the left panel, potential indicators and their associated icons are shown with VIW (Variable Importance Weighting) and Direction of Relationship. Direction of Relationship refers to the direction of the relationship between Marine Survival Index value and the indicator, described as general curves (these are not model outputs). In the right panel are the Best Models with indicators shown as icons; these include all models in the set with with ΔAICc < 3. Also in the right panel are ΔAICc, the difference in AICc between the best model and the given model; ωiAICc, the weighted value of the given model in relation to all models in the set; and r², the proportion of deviance explained by a given model. Best VIW model includes variables with the highest weightings (VIW > 0.5) from each hypothesis subset.

## Best VIW

| Indicators | VIW | Direction of Rel. |
|---|---|---|
| SST | 0.99 | (increasing) |
| Y Coho Hatch Rel Date | 0.97 | (decreasing) |
| Seal Abundance | 0.95 | (decreasing) |
| SY Coho Hatch Rel Date | 0.69 | (hump) |
| SY Chk Hatch Rel Date | 0.28 | (increasing) |
| PS River Flow (Apr.-May) | 0.27 | (decreasing) |
| PS Herring Abundance (by subbasin) | 0.22 | (increasing) |
| Population | 0.05 | |
| Total Salmon Harvest | 0 | |
| Ocean Salmon Abundance | 0 | |
| Stratification Index at RR | 0 | |
| Sea Level Height | 0 | |

| Best Models | ΔAICc | ωiAICc | r² |
|---|---|---|---|
| SST, Y Coho Date, Seal, SY Coho Date | 0 | 0.199 | 0.302 |
| SST, Y Coho Date, Seal, SY Coho Date, SY Chk Date | 0.317 | 0.169 | 0.303 |
| SST, Y Coho Date, Seal, SY Coho Date, PS Flow | 0.530 | 0.152 | 0.301 |
| SST, Y Coho Date, Seal, SY Coho Date, SB Herring | 0.961 | 0.123 | 0.305 |
| SST, Y Coho Date, Seal | 1.717 | 0.084 | 0.295 |
| SST, Y Coho Date, Seal, PS Flow | 2.521 | 0.056 | 0.294 |

factor alone was a poor predictor of marine survival. It may be important in easing the physiological transition from fresh to salt water as salmon outmigrate, but we lack a specific mechanisms for this relationship.

Many previous studies have used ocean climate indicators as predictors of salmon productivity (Beamish, 1993; Pearcy, 1997; Mantua et al., 1997; Mantua, 2009; Sharma et al., 2013; Kilduff et al., 2015). While there is little doubt that aspects of ocean conditions are important for salmon productivity, and more specifically survival, the relative importance of any one factor has been shown to be largely context-dependent, differing between Alaskan and more southerly stocks and among time periods (Kilduff et al., 2015; Mantua, 2015; Litzow et al., 2019; Gosselin et al., 2021). In our models for marine survival, NPI (North Pacific Index, a measure of Aleutian Low Pressure) and NPGO (North Pacific Gyre Oscillation, an indicator primarily referencing sea surface height) were both important predictors for coho salmon. To a lesser extent, PDO (Pacific Decadal Oscillation) had some support in explaining variation in subyearling Chinook salmon survival, as it did in previous retrospective analyses of marine survival in steelhead trout (Sobocinski et al., 2020). Emerging work from the Cowichan River in B. C., Canada is showing survival rates between hatchery and wild fish to be the same through the fall of their first year, but that fish exhibit differences in ocean survival once they return, with wild fish surviving at higher rates (K. Pellett, Department of Fisheries and Oceans Canada, personal communication). These results suggest total survival may be mediated by processes in the ocean, after the fish have left the inshore waters of Cowichan Bay, but that some pre-conditioning may be important in determining ocean survival (Gosselin et al., 2017). So, while ocean conditions remain an area of interest for Pacific salmon because they spend a large portion of their life history in the Pacific Ocean, our current work points to other stronger indicators of mortality, namely factors associated with their time of residence in the inland waters of the Salish Sea and the ecological interactions occurring there.

### 5.4. Theoretical framework is limited by data

We predicated our indicators analysis on a theoretical framework incorporating multiple hypotheses for explaining variation in salmon marine survival index. Steel et al., (2013) noted that a common analysis pitfall is the inclusion of arbitrary metrics or indicators, and by initiating our analysis with conceptual underpinnings related to marine survival, we attempted to avoid this pitfall. However, the fact remains that with a retrospective analysis such ours, any theoretical basis will be undermined by the lack of data deemed to be important to one or more of the competing hypotheses.

Within our analysis, we lacked data for some potentially important food web components, such as young-of-the-year herring and other forage fish and zooplankton (important salmonid prey, once in marine waters) and piscivorous birds and fishes on the predator side. Decapod crustaceans, insects, amphipods, and copepods, as well as herring are known to be important prey resources for juvenile salmon (Duffy et al., 2010; Beauchamp and Duffy, 2011; Kemp, 2014). To evaluate density-dependent food availability (H3), understanding the interannual abundances and distributions of these prey items is essential. Similarly, we lacked predator data with the spatial resolution necessary to fully describe interactions, and our evaluations of H1 and H2 (related to predation effects) would be strengthened with spatially-explicit data. The suite of potential indicators associated with any hypothesis therefore reflects both theoretical understanding and the reality of data availability.

Indicators act as proxies for complicated processes (Link et al., 2010; Kershner et al., 2011), but some indicators more directly reflect mechanistic understanding than others. We attempted to circumvent the lack of data availability by incorporating proxy indicators, such as an index of chlorophyll *a* to represent primary productivity (within H3). But these proxy indicators are less explicitly connected to salmon marine survival, and, perhaps not surprisingly, they often did not perform well in explaining marine survival on their own.

a. Coho
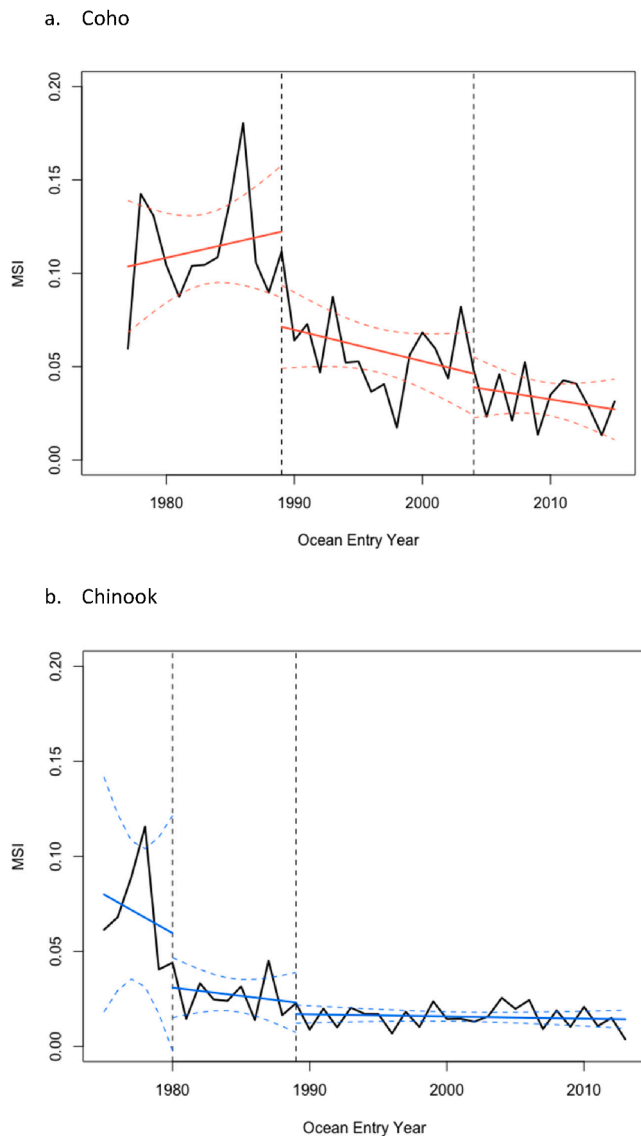


b. Chinook



**Fig. 6.** Coho (a) and Chinook (b) salmon MSI time series (1975–2015) showing changes in trend using structural change analysis. 1989 and 2004 were transition points (breakpoints) in the coho salmon data set, indicated by dashed vertical lines and change in slopes (red lines with 95% confidence intervals of predictions); 1980 and 1989 were transition points (breakpoints) in the Chinook data set, indicated by dashed vertical lines and change in slopes (blue lines with 95% CI). The Chinook dataset included both subyearling and yearling stocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

However, proxy indicators often appeared in combination with other factors in better-supported models. For example, for the coho salmon VIW models, a number of highly-ranked indicators were what we might consider proxies for larger scale processes. One of the best performing VIW models included precipitation, air temperature, index of stratification, and North Pacific Index (all abiotic factors), in addition to the coefficient of variation for subyearling Chinook salmon hatchery releases (where protracted outmigration timing of hatchery releases was correlated with higher MSI); none of these indicators is directly related to coho salmon survival. Additionally, the relationship with survival was not linear for the majority of these indicators (as seen in the evaluation of partial correlation plots for this model). Identifying an indicator that is accurate at the right scale and that best reflects the ecological process

of interest is not a simple task (Steel et al., 2013) and proxy indicators are commonly used in ecology to circumvent an absence of more direct measurement (Rozema et al., 2001; Stephens et al., 2015). Understanding causative mechanisms would strengthen the validation of these indicators as drivers of Puget Sound salmon marine survival.

Additionally, survival declined at the same time that seal and human abundance increased, and incorporating these explanatory variables into any model with survival produces significant correlation. It is also possible seal and human abundance changed simultaneously with other unmeasured ecosystem attributes. In their examination of Atlantic salmon survival, Olmos et al (2020) identified changes in primary production as possibly influencing declining survival in that species, but also acknowledged that unmeasured indirect, growth-dependent mechanisms may be contributing to the signal. Autocorrelation and a persistent downward trend in the survival data ("one way trip") offered little contrast to separate hypotheses; those covariates which also showed a persistent trend performed the best.

### 5.5. Limitations of marine survival estimates

We were able to explain more variance in the coho salmon marine survival with our modeling efforts than we were for Chinook salmon of either life-history type. This is partly attributable to the fact that the coho salmon MSI was a more robust data set than those of subyearling and yearling Chinook salmon. Additional data collection with wild populations would better refine our understanding of marine survival, especially given differential survival between hatchery and wild populations (Beamish et al., 2012a, 2012b; Zimmerman et al., 2015).

### 5.6. Ecosystem change and variation in relative importance of indicators

The Salish Sea ecosystem has changed a great deal over time (Preikshot et al., 2013), and it was important that we consider how coho and Chinook salmon marine survival may have been influenced by different factors within different periods of the last four decades. For coho salmon, most models underpredicted marine survival in the early part of the time series and overpredicted marine survival in the middle and latter parts, in essence underestimating the decline observed. Interestingly, the water quality hypothesis (H5), which explained the fourth-greatest amount of variation among the hypotheses (behind H1, H2, and H7), had the lowest amounts of error among the 7 hypotheses in stanzas 1 and 2 but did not follow the MSI trend as well in stanza 3. During this third time period, the two best VIW models fit the data well, though one VIW performed better in stanza 1 and the other better in stanza 2. For subyearling Chinook salmon, we did not see strong evidence of differential model performance, but the best supported models across all hypotheses missed the extreme peak in the early part of the time series (not uncommon in regression) and fit better in more recent years. Perhaps utilization of a distributional family that better accounts for extreme values (e.g., scaled t-distribution) could improve the model fit.

Recent work by Litzow et al. (2019) found a change in climate-salmon productivity relationships coinciding with the 1988/1989 period, with general support for a period in the late 1980s as a period of change. This period has been identified previously as a period of ecosystem change in the North Pacific (Hare and Mantua, 2000) and in other regions of the world (Mollmann and Diekmann, 2012). Litzow et al. (2019) showed distinct time periods related to the index of the Aleutian Low coinciding with periods of differing PDO–NPGO relative importance on salmon (*Onchorynchus* spp.) in the Gulf of Alaska during 1965–2012. They addressed non-stationary relationships among physical and biological variables and climate effects and found that relaxing the assumptions of stationary relationships markedly improved modelling of climate effects on salmon catches and productivity. Here we did not assume any temporal autocorrelation in our models due to the numerous predictors we were evaluating and the monotonically
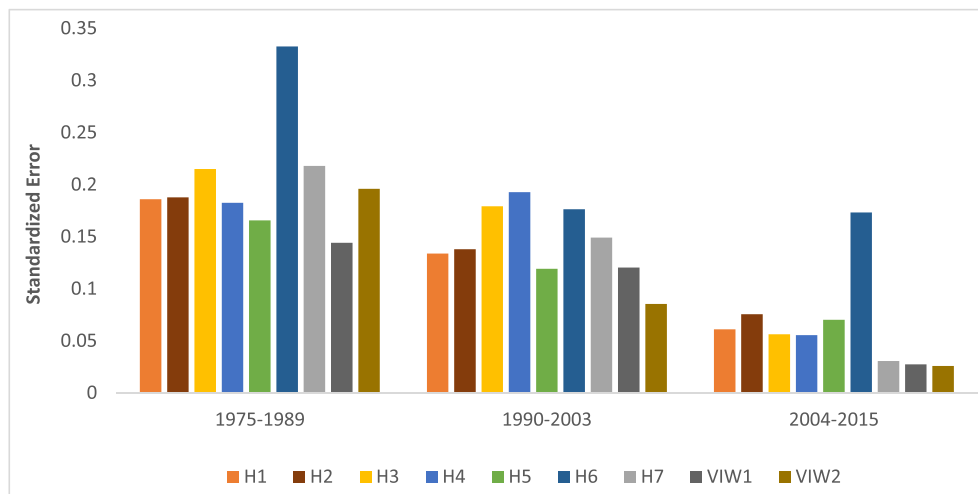
**Fig. 7.** Standardized error calculations for each coho salmon hypothesis best fit model for the three time periods, plus the two best performing variable importance weighting (VIW) models. Higher standardized error values indicate poorer model fit.

increasing trends ("ratcheting") for some of the indicators, which would confound interpretation. However, different VIW models were the top performing models in different years, suggesting that: a) a multitude of factors with differing influence drive salmon survival and b) time periods—and associated ecological regimes—may influence which of these factors is most important given other constraints. The breakpoints and stanzas we identified in the data fit well with global observations of ecosystem changes in the late 1980s, despite being weakly supported. As Litzow et al. (2019) suggest and as we have done here, treating time series data such as our MSI time series as stanzas may improve model performance.

### 5.7. A portfolio of indicators predicts MSI the best

While the hypothesis-based framework allowed comparison of competing hypotheses based on differing mechanisms, it is important to note that the suite of indicators included in each hypothesis was not unique, with several indicators being included in two or more hypotheses. Where hypotheses shared the same predictors, the best models for each hypothesis were in fact different. The differing possible combinations of factors (not all potential indicators were included in every model) allowed for comparison of models and indicators.

That said, for both species, our Best VIW models had the highest variance explained ($r^2$), suggesting that individual hypotheses relating to certain aspects of salmon ecology were not as good as a portfolio of best predictors drawn from across all hypotheses. While a portfolio approach has been commonly used in finance and investing for decades, it has only relatively recently gained use as a concept in ecology (Greene et al., 2010; Schindler et al., 2015; Wasson et al., 2016). Our modeling results show that multiple mechanisms are likely responsible for determining annual salmon survival. Even given the relatively better performance of the "portfolio" models, there remains a large amount of variation in survival that is unexplained. This uncertainty will continue to hamper efforts at prediction and forecasting, but an indicator approach with a suite of diverse indicators is more robust than any one individual indicator. This concept is important in terms of species recovery also, as our models suggest maintenance of a variety of ecosystem processes may result in higher survival.

### 6. Conclusions and next steps

Our ecosystem indicators analysis of Puget Sound coho and Chinook salmon marine survival showed commonalities in associated factors, such as seal abundance, presence of alternate prey, and various physical environmental variables, but disentangling correlational effects from mechanistic relationships remains a challenge in a statistical framework such as employed herein. It is often much easier to identify correlation than causation (Sugihara et al., 2012) and increasing mechanistic understanding of ecological interactions in the early marine phase of juvenile salmon would hone in on factors likely to be predictive. There are many factors which likely contribute to the year-class success of salmon (e.g., forage fish abundance, particularly young-of-the-year herring, Boldt et al., 2019) for which time series data are unavailable (particularly during the time period exhibiting the most change in marine survival, mid 1980s–1990s). Still, ecosystem indicators and portfolios of such indicators can suggest important impacts and guide future mechanistic research.

Moving from a retrospective analysis to a forecast approach may allow for the incorporation of other theoretically important datasets (such as zooplankton and ichthyoplankton prey abundance and other bottom-up factors, Claiborne et al., 2020) that have only recently become available (e.g., fisheries surveys from the West Coast of Vancouver Island, BC; zooplankton data from the Salish Sea; and other more recent ecological surveys). Without the time series to calibrate and test the relationships, their utility may still be limited until enough data, and data with temporal and/or spatial variation, becomes available. Our ability to recognize ongoing ecosystem changes and relate them to salmon marine survival trends may be more effective than extrapolating from past ecosystem indicators (Schindler and Hilborn, 2015).

Our findings highlight the importance of past monitoring of both Puget Sound Chinook and coho salmon MSI and ecosystem indicators. Without such data, we would not be able to identify indicators, or of greater relevance, we would only be able to speak hypothetically based on first principles about factors important to these salmon. However, it is important to note that we should continue—and, in fact, enhance—such survivorship monitoring into the future. There is great need for continued monitoring to detect and quantify ecosystem changes and thus ecosystem indicator shifts (Schindler and Hilborn, 2015). Large-scale, long-term monitoring combined with smaller-scale mechanistic studies to understand various sources of mortality, reduced fish condition, or variable growth rates can help to limit our reliance on proxies (Stephens et al., 2015; Schindler and Hilborn, 2015). Improving our understanding of the mechanisms controlling salmon marine survival will improve the management actions invoked and the forecasts needed for those actions despite uncertainty.

## CRediT authorship contribution statement

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107403.

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