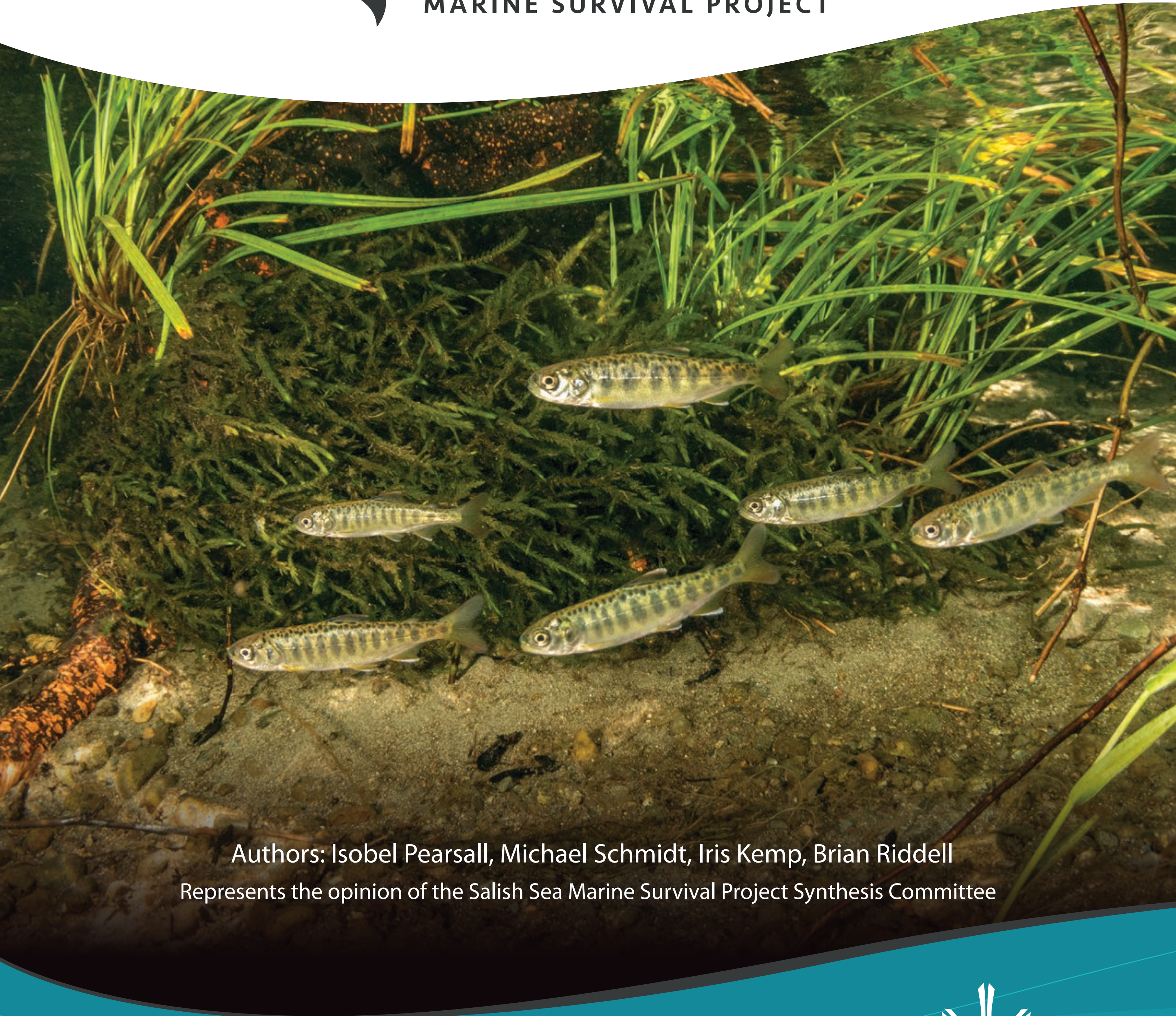
FACTORS LIMITING SURVIVAL OF JUVENILE CHINOOK SALMON, COHO SALMON AND STEELHEAD IN THE SALISH SEA: SYNTHESIS OF FINDINGS OF THE

SALISH SEA
MARINE SURVIVAL PROJECT



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Represents the opinion of the Salish Sea Marine Survival Project Synthesis Committee

LONG LIVE THE KINGS

PACIFIC SALMON FOUNDATION

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TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

EXECUTIVE SUMMARY

Our northwest culture, economy, tribal treaty rights, and natural ecosystems are all suffering from declines in abundance of Pacific salmon, with many populations of Chinook salmon (Oncorhynchus tshawytscha), Coho salmon (Oncorhynchus kisutch) and steelhead trout (Oncorhynchus mykiss) considered at risk of extinction. We have heavily invested in habitat restoration, significantly reduced harvest, and improved the way we manage hatcheries; yet we are still struggling to recover salmon in Puget Sound and the Strait of Georgia, the two primary marine basins of the Salish Sea.

In 2013, the Pacific Salmon Foundation (PSF) and Long Live the Kings (LLTK) launched the Salish Sea Marine Survival Project (SSMSP): a US-Canada research collaboration to identify the primary factors affecting the survival of juvenile Chinook, Coho, and steelhead in the Salish Sea marine environment.[1] From 2014-2018, this international collaborative of over 60 federal, state, tribal, nonprofit, academic, and private entities implemented a coordinated research effort that encompassed all major hypothesized impacts on Chinook, Coho, and steelhead as they entered and transited the Salish Sea. Ultimately, several hundred scientists collaborated to implement over 90 studies. Some of the research continues today.

This report synthesizes the work to date and provides our perspectives regarding the primary factors affecting survival and the next steps in research and management. While the findings represent important progress towards understanding salmon in the Salish Sea ecosystem, our understanding will undoubtedly continue to evolve. In this vein, we treat this report as a living document to be updated over time.

Survival Declines and the Critical Period

The Salish Sea was previously a productive environment for Pacific salmon but Chinook, Coho, and steelhead abundance and their marine survival[2] rates have declined since the late 1970s to present and differ from coastal and Columbia River populations (Figure 1). Patterns of marine survival rates vary significantly between Salish Sea Chinook populations with Strait of Georgia populations exhibiting more synchronous declines among populations (Ruff et al. 2017). Coho had more synchronous marine survival declines among populations throughout the Salish Sea (Zimmerman et al. 2015). This is consistent with salmon distribution patterns in the Salish Sea that suggest different Chinook populations rear in specific areas of the Salish Sea whereas Coho are more widely distributed and mixed (Neville pers. comm.). Like Coho, steelhead marine survival declined across Salish Sea populations although the strength of synchrony was slightly less (Kendall et al. 2017).

Biologists refer to a "critical period" for fish as a time during early life when mortality is unusually high and a stage when longer-term survival rates are determined (Hjort 1914). For salmon and steelhead, the time following saltwater entry (also called the early marine phase) is commonly considered a critical period. The 'critical' aspect of the early marine phase for individuals may be to achieve a growth threshold or specific condition in their first summer at sea in order to avoid size-selective predation and build up enough fat to survive the subsequent fall/winter period (Beamish and Mahnken 2001, Tomaro et al. 2012, Tovey 1999, Holtby et al. 1990) Alternatively, direct mortality during the early marine phase may signify the importance of the critical period. Juvenile steelhead experience high mortality during their rapid migration through the Salish Sea, irrespective of size (Moore et al. 2015, Moore and Berejikian 2017). For Chinook and Coho, growth during the first summer in the Salish Sea is likely a greater determinant of overall marine survival (Duffy and Beauchamp 2011, Claiborne et al. 2020, Beamish et al. 2008). That said, during this early marine phase there are signs of high juvenile Chinook and Coho mortality due to seal predation (Chasco et al. 2017, Nelson et al. 2019b, Nelson in prep, Nelson in press) and little evidence that size-selective mortality is occurring on Chinook (Gamble et al. 2018, Pellett pers. comm.).

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[1] www.marinesurvivalproject.com

[2] Marine survival covers the period from release in freshwater at hatcheries or, for wild fish, from their downriver migration as juveniles and through their ocean phase to the point where these fish are either captured as adults in fisheries or return to rivers and hatcheries to spawn.

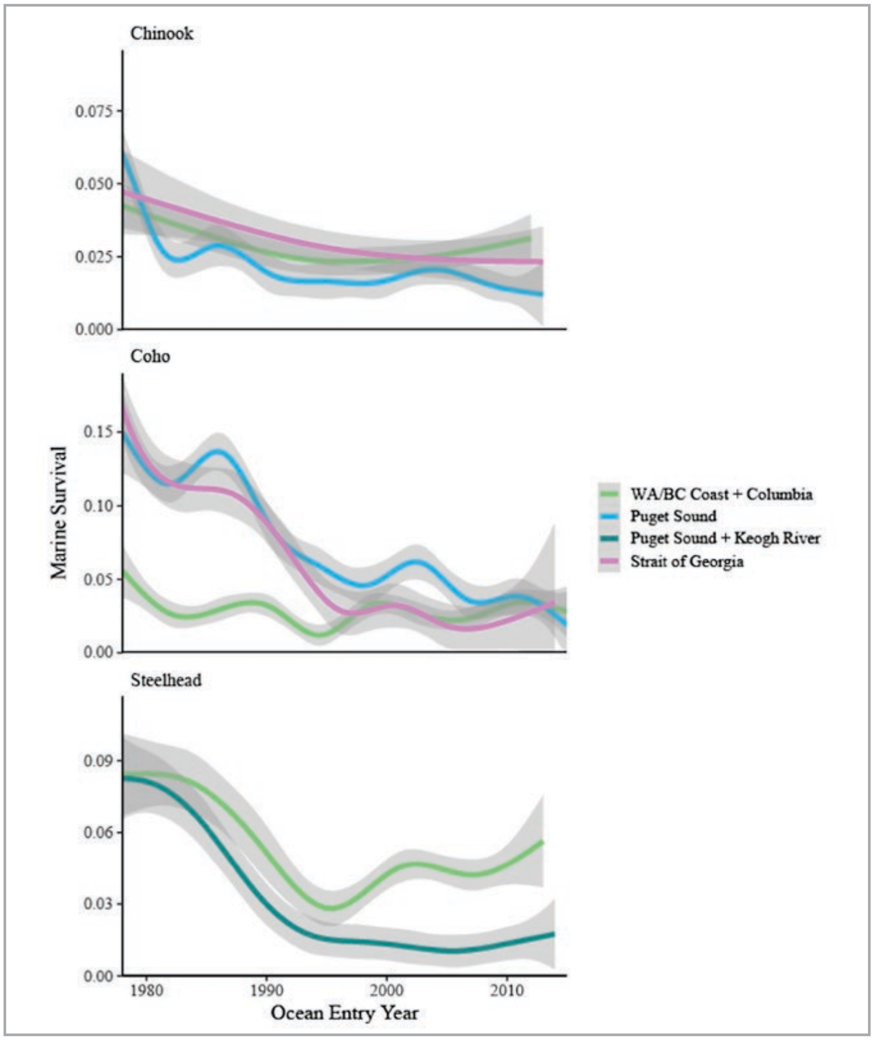

Figure 1. *Marine survival trend for Chinook (top panel) and Coho (middle panel) in Puget Sound (blue), Strait of Georgia (pink), and WA/BC Coast and Columbia River (green) and for steelhead (bottom panel) in Puget Sound + Strait of Georgia's Keogh River (teal). A smoothing function (colored line and gray envelope showing confidence interval, generalized additive model (GAM), survival ~ year) was applied to illustrate trend. All panels span ocean entry years 1978-2015. Underlying data as described in Zimmerman et al. 2015, Ruff et al. 2017, Kendall et al. 2017, and Sobocinski et al. 2021. See Appendix B for the stock list and any discrepancies between this graph and the papers.*

Factors Affecting Marine Survival During the Salish Sea Critical Period

Numerous factors can affect salmon survival during the early marine phase. Broadly, the primary hypotheses were:

1. Early marine survival is determined by bottom-up ecological processes: **weather, water conditions, and productivity that determine the food supply for salmon and result in variation in size and growth rate.** Salmon may also compete among themselves or with other fishes for food.

2. Early marine survival is determined by top-down ecological processes. **Predation is likely the direct cause of mortality**, but salmon may be affected by other biological factors (e.g., disease and contaminants), increasing their susceptibility to predation, directly killing them, or affecting their condition such that overall marine survival is reduced.

3. **Multiple factors may interact and have cumulative effects** in determining early marine survival. These may be additive, synergistic, or dampening.

Humans may have also changed the natural forces determining annual variation in salmon production through our impact on habitats and related losses of life history diversity in salmon.

Categorizing factors as having top-down or bottom-up influence is overly simplistic. This report attempts to address this issue by describing the multiple pathways of impacts to salmon and each factor's interrelationships with other factors and by illustrating the results of comprehensive ecosystem modelling. The primary hypotheses were broken down to focus on specific factors for the purposes of investigation (Table 2 and Appendix A).

Synthesis Committee's Review of the Findings

Salish Sea-wide, factors affecting food supply and predation appear most critical to determining Chinook, Coho, and steelhead marine survival, while at local population or sub-basin levels, other factors are also significant. Findings of the SSMSP clearly illustrate that changes in annual environmental conditions influence zooplankton and forage fish production, which, in turn, regulate salmon growth and survival (Greene et al. 2020, Keister et al. 2019, Keister and Herrmann 2019, Perry et al. 2021, Chamberlin et al. 2017, Duguid et al. in review, Morzaria-Luna in prep, Beauchamp et al. 2018, Gamble 2016, Connelly et al. 2018, Costalago et al. 2020, Weil et al. 2019). Also, populations of harbour seals have increased concomitantly with declines in salmon marine survival, seal diet data show consumption of salmon, and bioenergetic models and other analyses suggest seal predation contributes significantly to steelhead mortality (Berejikian et al. 2016, Moore et al. 2021) and to increased mortality of Coho and Chinook (Nelson et al. in prep, Nelson et al. in press, Chasco et al. 2017, Thomas et al. 2017). Other contributing factors include habitat loss, contaminants, and disease, which limit growth and/or cause sub-lethal stress in some populations (Campbell and Claiborne 2017, PSP 2021, Bass et al. in prep, Teffer et al. in prep).

In all, empirical findings and modelling efforts suggest multiple interacting causes of declines in marine survival. Further, there is substantial concern about the role of climate change in both the Salish Sea and North Pacific Ocean and how changing conditions will further impact salmon. The difficulties in isolating climate change impacts are considerable, especially in inland waters where numerous other factors are at play. Climate change may influence prey availability for salmon by changing spring bloom timing (Allen and Wolfe 2013, Banas et al. 2019) or affecting plankton composition. It can also affect salmon and the ecosystem through many other pathways, including more acidic waters (Busch et al. 2013, Feely et al. 2009) and larger and more frequent harmful algae blooms (Tatters et al. 2013, Hallegraeff et al. 2003, Lewitus et al. 2012) that can impact salmon and their prey (Chittenden et al. 2018, Hallegraeff et al. 2004, Sunda et al. 2006). Increased temperatures can also increase susceptibility to disease and contaminant impacts (Ray et al. 2012, Gouin et al. 2013).

Table 1, below, summarizes the SSMSP Synthesis Committee's[3] perspective regarding the extent to which specific factors affect marine survival. The Committee assessed the role of each factor relative to trends over the period of declines in marine survival (late 1970s to 2015) and to recent patterns in marine survival (past 5 to 10 years). They ranked each factor's level of impact, from **substantial to none.** Substantial meant available evidence was consistent with the factor contributing significantly to changes in marine survival, whereas none meant there was no evidence that the factor affected marine survival or, in some cases, there was evidence that the factor likely did not impact marine survival. Finally, an **unknown** category was included for factors which the Committee was unable to rank due to limited information.

The Committee also assessed the strength of evidence supporting their assessment, ranked from **strong to weak** based on the quantity and quality of data available. Rankings were done separately for Chinook, Coho, and steelhead. The results are presented for the Salish Sea in Table 1, and further broken down between Puget Sound and Strait of Georgia in the body of the report.

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[3] The Synthesis Committee, which was made up of the primary SSMSP scientists from each discipline, convened in 2018-2020 to evaluate hypotheses relative to the evidence collected via the SSMSP and other studies.

Table 1. *Synthesis Committee perspectives on the significance of the different SSMSP hypotheses to explain the changes in marine survival for Chinook, Coho, and steelhead in the Salish Sea.*

Hypotheses	Salish Sea								
	Chinook			Coho			Steelhead		
	Trend since late 1970s	Recent Patterns	Strength of Evidence	Trend since late 1970s	Recent Patterns	Strength of Evidence	Trend since late 1970s	Recent Patterns	Strength of Evidence
Decline in marine survival	1	NA	M	1	NA	H	1	NA	H
Critial Period - Growth	U	2	M	U	2	M	6	6	H
Critical Period - Instantaneous Mortality	U	3	L	U	2	M	U	1	H
Salmon Behavior and Physical Habitat									
Outmigration Timing*	2	1	H	4	4	H	U	U	H
Distribution & Migration Pathways	5	2	L	6	6	L	6	6	H
Residency	5	3	M	2	2	L	6	6	H
Physical Habitat	3	3	M	5	5	L	6	6	M
Bottom up - Food Supply									
Prey availability	1	1	M	1	1	M	6	6	L
└ Water quality/Biogeochemistry	2	2	L	2	2	L	3	3	L
└ Mismatch	3	3	L	3	3	L	6	6	H
└ Competition	4	3	M	4	3	L	6	6	H
Ocean Acidification**	5	5	NA	5	5	NA	6	6	H
Harmful Algae**	5	5	NA	5	5	NA	6	6	H
Top down - Predation									
Predator abundance	2	2	M	2	3	M	2	1	M
Specialization	6	5	L	6	5	L	6	6	L
Pulse prey abundance	4	4	L	4	4	L	4	5	L
Buffering/Prey switching	3	U	L	3	U	L	2	2	M
Top down - Disease and contaminants									
Disease	U	1	M	U	2	M	5	5	H
Contaminants	3	2	M	U	4	L	U	U	NA

** Rankings reflect the finding of a reduction in variability and change in mean of hatchery Chinook release times, some change in Coho hatchery release times, and correlations with survival in multi-factor models (Sobocinski et al. 2021). Outmigration timing in and of itself may not affect survival. Rather, it may interact with other ecosystem factors (e.g., mismatch with prey availability, competition, and pulse prey abundance).*

***Ocean acidification and harmful algae likely have minimal impact now but are a substantial concern into the future as climate change increases the potential impact of these factors.*

Legend

Level of Impact	
Substantial-Moderate	1-2
Some	3-4
Minimal - None	5-6
Unkown	U

Strength of Evidence	
Strong	H
Moderate	M
Weak	L
Not Applicable	NA

Summary of Findings and Perspective on Impact to Marine Survival

The following summarizes the research findings and the Synthesis Committee's perspective for each factor. These are the basis for the rankings in Table 1.

Outmigration Timing — There has been a substantial reduction in variability of release dates, and therefore outmigration timing, of hatchery-produced Chinook over the period of marine survival declines (Nelson 2019a). Most hatchery Chinook are now released into the Salish Sea around the third week of May. Ecosystem indicators modelling suggests this could, in concert with environmental changes, be contributing to declines in marine survival (Sobocinski et al. 2021). However, the mechanisms are unclear. Changes to hatchery Coho release times may be less influential (Irvine et al. 2013), but are also included in best models for explaining Chinook and Coho declines (Sobocinski et al. 2021). There is no evidence for changes to wild Chinook, Coho, or steelhead outmigration timing.

Distribution, Residency, and Migration Pathways — Chinook smolts from different Strait of Georgia populations were found to consistently rear in distinct locations in the Strait of Georgia and exhibit different marine survival trend patterns (Neville pers. comm., Ruff et al. 2017). However, it is unclear whether location-specific rearing in the Strait of Georgia contributed to long-term declines. Some Chinook also rear to maturity in the Salish Sea rather than migrating to the open Pacific Ocean (Chamberlin et al. 2011, O'Neill and West 2009). Study results did not find consistent patterns between this "residency" behaviour and marine survival trends among Chinook populations (Chamberlin et al. 2020). Unlike Chinook, Coho populations are found to be more widely distributed in the Strait of Georgia, which may explain why their marine survival trends are more synchronous (Neville pers. comm., Zimmerman et al. 2015). Coho also appear to be spending a larger portion of their early marine phase in the Strait of Georgia in recent years. The speculation is that this change in behaviour is related to improved rearing conditions (Neville and Beamish 2018). Juvenile steelhead only spend a couple of weeks migrating through the Salish Sea from their natal rivers to the ocean (Moore et al. 2015, Welch et al. 2011). However, differences in survival occurred: 1) based on different migration pathways chosen by steelhead migrating through and out of the Strait of Georgia (Furey et. al. 2015, Healy et al 2017), and 2) based on distance traveled through Puget Sound: steelhead populations migrating from natal rivers located farther from the ocean experience higher mortality rates (Moore at al. 2015, Berejikian and Moore 2017).

Physical and Biogenic Habitat — The Synthesis Committee could not reach consensus regarding the role of physical or biogenic habitat in declines in marine survival. Degraded habitat is likely limiting the survival of some salmon populations, in particular the loss of estuary habitat for wild subyearling Chinook (Beamer et al. in revision, Chalifour et al. 2019). SSMSP studies found that fewer Chinook fry[4] out-migrating from watersheds with degraded estuaries survive to adulthood (Campbell and Claiborne 2017). Further, there may be linkages between lost kelp habitat (Lamb et al. 2011, Calloway et al. 2020, Berry et al. 2020, Heath pers. comm.), increased patchiness of eelgrass habitat (Nahirnick et al. 2018), and salmon prey, such as herring and larval crab, which could be contributing to broader survival declines. While data are insufficient to draw conclusions, it is certainly tenable that cumulative habitat losses/changes contributed to loss of life history diversity and survival declines.

Prey Availability — The evidence for links among food quality and quantity and recent marine survival patterns for both Coho and Chinook is substantial throughout the Salish Sea. Relationships between zooplankton and Coho and Chinook marine survival rates were identified (Keister et al. 2019, Keister and Herrmann 2019, Perry et al. 2021), and evidence points to strong links between herring availability and Chinook growth (Chamberlin et al. 2017, Duguid et al. in review). There is also a positive relationship between herring abundance and Chinook and Coho survival in linear models (Sobocinski et al. 2021), and ecosystem models suggest reduced herring abundance could have a substantial impact on Chinook and Coho productivity (Morzaria-Luna in prep). Of particular concern is the status of age-0 herring. Larval crab (Beauchamp et al. 2018, Gamble 2016, Connelly et al. 2018) and amphipod (Costalago et al. 2020, Weil et al. 2019) availability may also be important given the abundance of these prey in Chinook and Coho diets.

While juvenile salmon diet and plankton datasets do not go far enough into the past to relate to the declines in marine survival, the strength of recent correlations between prey availability and Coho and Chinook survival (Keister et al. 2019, Keister and Herrmann 2019, Perry et al. 2021) and known changes in the plankton assemblage over time

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[4] **Fry** are small salmon that are just after they hatch from eggs and in the wild begin to come out of their gravel nest also known as redd. As fry grow, they become juvenile fish known as **parr** because of the vertical parr marks on their sides. Juvenile salmon then lose their parr marks and become silvery as they transition to "**smolt**" stage and migrate to sea.

(Bornhold 1996, Chiba et al. 2006, Batten and Mackas 2009, Mackas et al. 2013, Kemp and Keister 2014, Li et al. 2013) suggest a relationship. Overall, the Committee concluded that prey availability, either in terms of quantity or quality, is an important factor operating in tandem with other factors such as prey distribution, fish condition, fish health, and ocean conditions to impact marine survival. Whether there is a direct relationship, or if there is a common driver impacting both plankton and salmon, is as yet unknown. For steelhead, data are insufficient to address recent and long-term patterns in marine survival. However, steelhead migrate quickly and directly to the ocean, suggesting they are not foraging within the Salish Sea and prey availability is less important (Moore et al. 2015, Welch et al. 2011).

Water Quality/Biogeochemistry — There is substantial evidence that Salish Sea water quality or biogeochemistry[5] of the Salish Sea has changed over the period of declines in marine survival. Water temperatures have increased (Riche et al. 2014, Martins et al. 2020), more freshwater is entering the Salish Sea earlier from rivers (Gower 2002, Morrison et al. 2002, Cuo et al. 2009), hypoxia is more common (Brandenberger et al. 2011), and nutrient concentrations may have increased (Pool et al. 2015). There are signs of impacts to the nutrient value of the food web, with changes to the plankton community (see above) including increases in the abundance of jellyfish, which prey on young salmon and can deplete areas of plankton (Greene et al. 2015, Perry et al. 2021, Mackas et al. 2001, Rice et al. 2012, Purcell et al. 2007). Major climate events[6] also occurred over the period of declines in marine survival. There is conflicting evidence regarding shifts in primary productivity, with one SSMSP study suggesting no change occurred over the period of declines in marine survival (Johannessen et al. in press) and another suggesting chlorophyll concentration has increased since the 1980s (Greene et al. in revision). While increases in chlorophyll concentration are often a sign of a more productive environment, Greene et al. (in revision) suggest that ecosystem decoupling could have occurred, with a decline in zooplankton quality/availability due to some phenological shift in edible phytoplankton.

While the Synthesis Committee agreed that water quality changes in Salish Sea have likely contributed to marine survival declines and to recent survival patterns, the amount of supporting evidence is weak. Currently, the evidence linking changes in biogeochemistry to salmon prey to salmon survival in the Salish Sea is predominantly correlational, with few to no understood mechanistic links. Limited amounts of long-term data are part of the problem (e.g., there are no adequate time series of zooplankton and limited time series of forage fish within the Strait of Georgia prior to the 1990s). However, with more recent data, Greene et al. (2020) found strong evidence for connections among abiotic variables, primary and secondary production, and salmon growth, individual condition, and marine survival.

SSMSP efforts to link abiotic changes to plankton productivity suggest that sea surface temperature, salinity, winds, and light/cloud cover are important to driving marine survival in the Salish Sea via their impact on the food web (Banas et. al. 2019, Allen and Wolfe 2013, Greene et al. 2020, Sobocinski et al. 2021). Notably, recent modelling suggests changes in light attenuation during the transition from winter storminess to spring could strongly affect spring bloom timing, and thus the timing and magnitude of prey available to salmon (Banas et. al. 2019, Allen and Wolfe 2013). In light of these findings, there are substantial concerns about the role of climate change in salmon survival. However, the impact of warming waters on salmon in the Salish Sea is far from clear. For example, Puget Sound surface water temperature in April-July (when many Chinook and Coho are out-migrating) has declined alongside Chinook and Coho marine survival since the late 1970s (Sobocinski et al. 2021). Further, Chinook growth and survival increased in recent years where Puget Sound sea surface temperatures were warmer than average (Greene et al. 2020).

While relationships may exist between water quality and juvenile Chinook and Coho growth and early marine survival via the impact of water properties on their prey, relationships between juvenile steelhead and water quality may be more indirect. Steelhead migrate quickly through the Salish Sea (Moore et al. 2015), suggesting foraging opportunities are less important. However, correlational analyses over the recent past suggest that warmer Puget Sound and coastal marine waters promoted increased anchovy abundance in the Salish Sea which provided an alternative prey resource for steelhead predators and led to a reduction in steelhead mortality (Moore et al. 2021).

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5. Biogeochemistry is the cycle in which chemical elements are transferred between the environment and living organisms. This includes the physical and chemical properties of the Salish Sea as well as phytoplankton.
6. For example, the Pacific Decadal Oscillation shifted in 1976-77, 1988-89, and 1997-98, and major El Niños occurred in 1982-83, 1997-98, and 2014-2106 (https://climate.ncsu.edu/climate/patterns/pdo, https://en.wikipedia.org/wiki/El_Ni%C3%B1o).

Mismatch — It is difficult to determine whether there has been a disconnect between the outmigration timing of juvenile Chinook, Coho, and steelhead and availability of their prey. However, the Committee believes a timing mismatch could be having some level of impact on salmon growth and survival. While there is no linear trend, it appears that spring bloom timing began occurring earlier more frequently after 1990 compared to before (Allen and Wolfe 2013). Further, as indicated previously, hatchery release times for Chinook (Nelson 2019a) and Coho (Irvine et al. 2013) have changed or become less variable and these changes are included in best models for explaining Chinook and Coho marine survival trends (Sobocinski et al. 2021). This may mean Chinook and Coho are now more susceptible to variation in prey availability. For example, juvenile Chinook were found to be sensitive to changes in larval crab size over only a couple of weeks (Beauchamp et al. 2019). Access to young herring is also important given that eating fish and plankton results in higher growth rates for Chinook compared to eating only plankton. Changes in juvenile Chinook diets suggest lower contributions of herring since the 1970s and two studies found relationships between size of herring available and quantity in diets (Duguid 2020 and Chamberlin et al. 2017). The rapid outmigration of juvenile steelhead during a narrow time window (Moore et al. 2015, Welch et al. 2011) suggests foraging opportunities may be less important to their early marine survival.

Competition — The Committee concluded that competition may have some role in explaining long-term trends and recent patterns in Chinook and Coho marine survival. Study results are mixed and require further investigation. There is a strong negative correlation between Salish Sea hatchery Coho survival and the number of hatchery Coho released, but the presence/absence of juvenile Pink salmon (which are abundant only in even years) during juvenile Coho ocean entry has no effect (Kendall et al. 2020b). Central and southern Puget Sound Chinook marine survival was negatively correlated with abundance of hatchery Chinook released and the presence of Pink salmon between 1983 and 2012 (Kendall et al. 2020); however, ongoing analyses suggest this relationship may have only existed in Puget Sound until 2000, then switched to a positive correlation when Pink salmon were very abundant (Haggerty pers. comm.). Haggerty (pers. comm.) found similar even/odd year survival patterns for Chinook from some coastal streams where no juvenile Pink salmon are present, suggesting Chinook survival variability may be due to prey availability rather than direct competition with Pink salmon. Further, this relationship does not exist for wild Chinook (Kendall et al. 2020, Beamish et al. 2010) and there is a weakly positive relationship between Strait of Georgia hatchery Chinook survival and release numbers (Nelson 2019b). Density-dependent effects were found among Chinook in Puget Sound estuaries; however, this seemed to be largely a function of habitat condition and not hatchery/wild competition (Greene et al. 2020). There have been concerns regarding the potential for competition between herring and juvenile Chinook and Coho when they comingle at similar sizes. However, recent evidence suggests that patterns in juvenile Chinook, Coho, and age-0 herring abundance in the Strait of Georgia correlate and are driven by bottom-up processes (Boldt et al. 2018). Juvenile steelhead abundance is very low relative to other salmon and they migrate out of the Salish Sea quickly (Moore et al. 2015); therefore, competition is not likely a factor.

Ultimately, if inter- or intraspecies competition is occurring in the Salish Sea, it is most likely an exacerbating factor in situations or places where food supply and/or habitat are limited.

Predator abundance, specialization, pulse prey abundance, buffering/prey switching — Predator studies largely focused on harbour seals. Increased seal abundance has likely reduced the marine survival of Chinook, coho, and steelhead. Correlative analyses indicate a stronger relationship between increased seal abundance and marine survival declines for Coho and steelhead than for Chinook (Sobocinski et al. 2020, Sobocinski et al. 2021, Trites and Rosen 2019). Consumption estimates, bioenergetic modelling and the population size of seals suggest there is significant mortality of out-migrating Chinook and Coho (Nelson et al. in prep, Nelson et al. in press, Chasco et al. 2017). However, ecosystem modelling suggests smaller impacts (Morzaria-Luna in prep). The Committee also noted contraindications for Chinook salmon. The number of adult Chinook returning to Cowichan, Puntledge, and Big Qualicum rivers has improved recently, regardless of significant seal predation when they were out-migrating as juveniles (Trites pers. comm.). Steelhead are larger and therefore have fewer potential predators. Of those, only harbour seals and porpoises have significantly increased in abundance since the late 1970s (Pearson 2015). Further, steelhead mortality is greater near seal haulouts in years of high early marine mortality in Puget Sound (Berejikian et al. 2016, Moore et al. 2021).

A critical uncertainty in ecosystem models is whether predation is additive or not (Trites and Rosen 2019, Walters and Christensen 2019).[7] Additional uncertainty in the consumption estimates results from the limited spatiotemporal coverage of seal diet data and whether the variation of fish size in seal diets is appropriately represented (Nelson et al. in press). However, additional observational data may not substantially improve our confidence in our estimates of the impact seals have on salmon. The Committee notes direct experiments may be necessary to adequately assess the impact of any one predator.

The Committee concluded that specialization by seals (i.e., seals selectively eating juvenile salmon) cannot account for the bulk of the mortality; instead, predation of juvenile salmon primarily occurs by many seals throughout the Salish Sea in the summer (Thomas et al. 2017), likely as a byproduct of targeted feeding on Pacific herring, a primary food source that salmon often co-locate with.

While predation may be occurring on pulses of out-migrating salmon, the Committee was divided on whether predators targeting these pulses could be a primary driver of marine survival. One SSMSP study found a few seals respond to Coho migrating downstream and into the Strait of Georgia soon after release from a hatchery, but not Chinook. This may be because Coho are larger than Chinook at the time of release and within a seal's targeted prey size. (Allegue et al. 2020). However, many studies document predators changing their behaviour to take advantage of hatchery releases (Wood 1987, Beamish 1992).

The Committee concluded that data were insufficient to state whether prey switching was occurring and affecting marine survival; however, the relationship between increased anchovy abundance and decreased juvenile steelhead early marine mortality is compelling (Moore et al. 2021).

Additional predation studies found higher predation rates by raccoons, herons, and other animals in the Cowichan River when river flows were at extreme lows (Sherker 2020, Pellett pers. comm.).

Pathogens and Disease — Disease impacts are likely highly relevant to marine survival of Chinook and Coho (and Sockeye salmon) in the Salish Sea, at least in more recent years. Our strongest evidence for impact is in Chinook, where sampling, pathological investigations, and modelling efforts have been concentrated; Chinook also carry the highest diversity of disease agents of the three species. Although there is no historic evidence to determine whether disease was related to long-term trends in survival, relationships between increased temperatures (Laufkötter et al. 2020) and disease susceptibility (Teffer et al. 2018, Stocking et al. 2006, Ewing et al. 1986, Crossin et al. 2008, Ray et al. 2012) as well as evidence of recent disease relationships with salmon survival (Bass et al. in prep; Teffer et al. in prep) are cause for concern. The southern Strait of Georgia has been identified as an infection hotspot in summer months, with more infection overall in the Strait of Georgia as compared to the outer Pacific coast (Bass et al. in prep). SSMSP scientists concluded that the length and intensity of exposure to disease agents are major determinants of impact on Pacific salmon, with highest loads associated with residency in specific areas of the Strait of Georgia (Bass et al. in prep). Strategic Salmon Health Initiative (SSHI) studies focused on the Strait of Georgia; less is known about the distribution of disease impacts in Puget Sound. There is less concern regarding disease impacts to Puget Sound steelhead. An expert review suggested only a few disease agents could result in the early marine mortality patterns exhibited by steelhead, with the Nanophyetus salmincola parasite being the most likely (Puget Sound Steelhead Marine Survival Workgroup 2014). SSMSP studies found high infection loads of N. salmincola in some streams (Chen et al. 2018) but no association between infection loads and early marine mortality (Hershberger and Schmidt 2020).

Contaminants — While Meador (2014) suggested that contaminant exposure may result in variation in marine survival among Chinook populations in Puget Sound, it is not known if contaminants were a primary contributor to declines in Chinook marine survival across the Salish Sea since the late 1970s. The Synthesis Committee agreed that there is evidence that current contaminant loads could be preventing or limiting the recovery of many Chinook populations in the Salish Sea. Juvenile Chinook are exposed to PCB levels above adverse effects thresholds in urban rivers (PSP 2021), and PCBs accumulate in all juvenile Chinook that enter and rear in the marine waters of Puget Sound (O'Neill and West 2009, PSP 2021). PCB impacts are greatest on Chinook residing in central and southern Puget Sound for most of their lives (PSP 2021, Osterberg and Pelletier 2015). Further, there are very high levels of PBDEs in

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[7] Additive mortality is when all predation mortality rates are independent, so that total predation rate decreases when any one predator's mortality component is eliminated or reduced. Mortality is not additive when the prey of a predator that is removed from the system will die anyway due to another factor (e.g., disease) that made the prey vulnerable to the predator in the first place.

juvenile Chinook in the Snohomish River estuary, well above adverse effects thresholds, and high levels of PBDEs in juvenile Chinook in the Puyallup River that are of concern (PSP 2021, O'Neill et al. 2020a). Insufficient data exist regarding the impacts of PCBs and PBDEs on juvenile Coho, and there are limited data for steelhead. PBDE levels are above adverse effects thresholds in juvenile steelhead in the Nisqually River (Chen et al. 2018, O'Neill et al. 2020b). Given their susceptibility to urban runoff mortality syndrome (URMs), the exposure of juvenile Coho to tire dust in road runoff, especially in urban areas where traffic is high, warrants further investigation (McIntyre et al. 2018, McIntyre et al. 2015, Chow et al. 2019, Tian et al. 2020). Steelhead may also be adversely affected and should be included in future URMs investigations (McIntyre et al. 2018, French et al. 2020).

Insufficient contaminant data currently exists for the Strait of Georgia given historic lack of a focused contaminant program in this region. Recent investments in contaminant assessments of Strait of Georgia Chinook and southern resident orcas by Canada Department of Fisheries and Oceans and others may begin to fill this gap (O'Neill pers. comm.). The Committee speculates that Chinook originating from the Fraser River and rearing in the lower Fraser River or the southern Strait of Georgia (near Vancouver) could be similarly impacted, as might some Harrison/Chilliwack populations that rear in Puget Sound. Finally, the Committee noted that there are insufficient data regarding the impacts of Chemicals of Emerging Concern (CECs), but CECs are of concern especially in urban areas (Meador et al. 2016, 2017, 2018, 2020). Synergistic impacts driven by climate change—the compounding effect of contaminants with increased water temperatures, pathogens, and disease—is also of substantial future concern.

Harmful Algae — The Synthesis Committee concluded that there are recent signs of harmful algae impacts to juvenile Chinook; however, it is unlikely harmful algae contributed to the decline in Chinook, Coho, and steelhead marine survival since the late 1970s. Harmful algae impacts are typically localized and sporadic, unlikely to result in basin-wide marine survival declines. No studies were performed during the SSMSP to assess the relationship between harmful algae blooms and Chinook, Coho, or steelhead marine survival patterns. However, Rensel (2000) suggested a relationship between Sockeye productivity and harmful algae blooms. During the SSMSP, Esenkulova (2014) observed that presence of the harmful algae Heterosigma akashiwo was related to reduced Chinook feeding, gill damage, and higher mortality during PIT tagging operations in Cowichan Bay. Broadly, indirect effects of harmful algae on plankton composition and overall nutrition are poorly understood but a significant concern, especially if temperatures increase with climate change (Hallegraeff 2010). Patterns of several harmful algae species were tracked from 2015-2017 to develop relationships with water quality parameters and improve prediction ability for bloom events (Esenkulova et al. in prep).

Ocean Acidification — As an inland sea, the Salish Sea may be particularly vulnerable to impacts of ocean acidification (Ianson et al. 2019, Feely et al. 2010). However, participating scientists stated they are more concerned about future impacts of ocean acidification given that changes in acidification since the 1980s do not appear to be significant enough to impair salmon behaviour (Williams et al. 2018, Frommel et al. 2020) or impact salmon prey (Bednarsek et al. 2017, McLaskey et al. 2016, Haigh et al. 2015).

Cumulative effects — In combination, factors can have additive, synergistic, or dampening effects on juvenile salmon survival. The Committee strongly believes that no one factor caused the decline in Salish Sea marine survival. This report qualitatively describes the potential interrelationships among the factors that may impact survival; however, assessing cumulative effects is notoriously difficult and limited work has been done in a combined, holistic fashion. A qualitative network model produced by Sobocinski et al. (2018) suggests that anthropogenic impacts result in the strongest negative responses in salmon survival and abundance. Additionally, feedbacks through the food web were strong, beginning with primary production, suggesting that several food web variables may be important in mediating effects on survival within the system. Multi-factor analyses to explain Puget Sound Chinook and Coho (Sobocinski et al. 2021) and steelhead (Sobocinski 2020) marine survival trends found support for various combinations of factors, from hatchery release practices to unfavorable climate conditions to increased predation, reinforcing the perspective that no one factor has been driving survival independently. The authors noted that a lack of data for some potentially important ecological variables (for example, age-0 forage fishes and plankton prey indices) limit the explanatory power of their models related to marine survival. Two ecosystem models are under development that may help further assess cumulative effects. These are described in the next section.

Management Implications and Next Steps in Research

While we must continue scientific research to address key questions, that does not preclude testing management actions in response to these findings. Any actions should be tailored to specific populations and regions, and an adaptive management approach should be applied where actions are treated like experiments given the uncertainty of outcomes (monitor, analyze, adjust). While a formal management analysis was not done, financial, social, and political constraints were considered. Several recommendations for actions are included in this report, and the following were selected for this summary:

- Recognize the role and impact of climate and oceanic changes to salmon prey in recovery plans and state and province-wide climate initiatives. Develop monitoring plans and tools to measure changes in our marine waters.
- Reduce damage to and restore estuary and nearshore habitat (e.g., kelp and seagrass) for salmon, Pacific herring, sand lance, and crab. Ensure connectivity of marsh, eelgrass, and kelp habitats is maintained. Support soft-shore initiatives to minimize habitat loss.
- Recover, protect, and maintain diversity in herring populations. Better understand early year class dynamics.
- Support salmon life history variability through habitat restoration, population management, and experimentation with hatchery rearing and release strategies. This may build resilience to variation in food supply driven by changes in climate and ocean conditions and may reduce the potential for density-dependent impacts including competition, disease, and predation.
- Investigate approaches to reducing predation by seals including: facilitating passage at migration barriers where predation is an issue, obstructing or removing log booms and other haulouts, using predator deterrents, and, if necessary, performing experimental removals. Consider seal predation from an ecological perspective and account for the role of changes in abundance/timing of their primary prey (forage fish and gadids).
- Take targeted actions to reduce contaminant burdens in juvenile salmon and steelhead where those impacts are greatest (e.g., PBDEs affecting Chinook in the Snohomish estuary). Focus larger-scale remediation efforts on PCB hotspots to reduce impacts to Chinook residing in Puget Sound.
- Optimize fish health (disease and smolt readiness) in hatcheries, especially as increasing temperatures associated with climate change continue to be a concern. Applying new genomic technologies (e.g., Fit-chip[8]) and research within facilities may significantly improve our understanding of hatchery effects and interactions with wild salmon.
- Where possible (e.g., Cowichan River), protect and manage flows to reduce predation-based mortality of out-migrating salmon smolts (e.g., under BC Water Sustainability Act, 2014).
- Use newly compiled environmental data to improve adult return forecasting and harvest management and new ecosystem models to guide ecosystem recovery actions.

We acknowledge there are still uncertainties to address. In particular, we have substantial evidence that impacts to the food supply of Chinook and Coho are occurring, but mechanisms are poorly understood. This includes understanding the relative impact of temperature, nutrients, winds, shifts in primary productivity (e.g., diatoms versus dinoflagellates), and conditions that affect light attenuation underwater. It also includes a more refined understanding of salmon rearing locations, as SSMSP results suggest different rearing locations may be associated with variation in survival. This information is critical for improving our ability to predict adult returns for fisheries management and recovery and refining our recovery actions for resilient salmon and their ecosystems.

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[8] Fit-chips are a genomic technology developed via the Strategic Salmon Health Initiative to evaluate the health of salmon https://www.dfo-mpo.gc.ca/science/rp-pr/grdi-irdg/projects-projets/007-eng.html.

Additional priority research needs include:

- Assess what happens to juvenile Chinook and Coho during their first winter to determine the outcomes of different growth trajectories during their first summer in the Salish Sea. Continue to separate mortality across life history stages in the process.
- Continue to analyze historical datasets (e.g., plankton surveys, archived otoliths) to assess historical conditions for salmon prey and growth.
- Improve our understanding of migration timing and nearshore marine conditions relevant to survival. Better assess nearshore habitat use, value, and connectivity throughout major juvenile migration routes.
- Evaluate population-specific herring (and other forage fish) distribution and movement patterns in the Salish Sea, most notably with respect to age-0 herring. Integrate local citizen science and First Nation and tribal knowledge to improve our understanding of spawn timing and locations. In general, responsible agencies should improve assessments of forage fish given their critical role as both prey for salmon and for salmon predators.
- Examine the hypothesis that feeding by juvenile Pink, Chum, and herring before Chinook and Coho enter the Salish Sea marine environment deplete the availability of edible crab larvae (or other prey) for Chinook and Coho.
- Improve our understanding of seal predation. Assess potential hotspots, diet variation within seal populations, the impact of prey size, and whether mortality is additive or non-additive. Also, assess predator behaviour in relation to pulses of out-migrating salmon and impacts of prey switching.
- Assess synergistic relationships and the impact of cumulative stressors associated with disease (e.g., contaminants, harmful algae, predation, ocean acidification, etc.). Test the utility of Fit-chips developed by the SSHI to evaluate the physiological fitness of Pacific salmon under climate change.
- Assess contaminant inputs and impacts in the Strait of Georgia. Prioritize the lower Fraser.
- Determine the contaminant pathway for PCBs in Puget Sound marine waters and assess the impact of CECs.
- Continue to assess ocean acidification and harmful algae since these could become significant issues for salmon and their ecosystem under future climate change scenarios.

To integrate multiple environmental changes within the Salish Sea and assess their impacts on salmon, the development of computer models that simulate the entire marine ecosystem from physical properties through the food web is an ongoing effort within the SSMSP. These include an Ecopath with Ecosim model being developed by University of British Columbia and an Atlantis model developed by the National Oceanic and Atmospheric Administration (NOAA) and LLTK. These models are a critical part of the toolbox for supporting ecosystem-based management of fisheries and marine resources. Due to the uncertainty in understanding complex natural systems with limited data, using multiple models to evaluate and inform policy choices and management decisions is an emerging best practice.

The accuracy of these models and other analyses of ecosystem change are tied to the quality and quantity of data available. Therefore, we must continue to collect and improve upon the empirical data available. This includes:

- Maintaining and improving upon the expanded oceanographic and zooplankton monitoring efforts initiated via the SSMSP.
- Implementing juvenile salmon and herring midwater sampling throughout the Salish Sea, especially in Puget Sound where no consistent program exists.
- Improving our ability to assess stage-specific growth and mortality of juvenile salmon.
- Expanding our pinniped demographics and diet sampling in space and time.
- Expanding contaminants sampling throughout the Salish Sea.

Several new tools and research strategies were created via the SSMSP to improve Salish Sea ecosystem monitoring and research including: microtrolling for juvenile salmon, PIT tag strategies to develop segment-specific survival estimates, using geoduck shells to assess primary productivity trends, improved use of remote sensing, satellite, and aerial imagery to assess ecosystem changes, and new genomic tools for assessing disease and hatchery/wild salmon interactions. Further, the PSF created numerous citizen science efforts to broadly collect ecosystem data throughout the Strait of Georgia at a fraction of the cost of what it would take for public entities to do the same. A detailed overview of these new tools and research strategies, as well as the specific recommendations for continued monitoring, are described in the associated paper titled, "Novel Assessment Techniques, Monitoring Recommendations, and New Tools for Ecosystem-Based Management Resulting from the Salish Sea Marine Survival Project" available at www.marinesurvivalproject.com.

An Achievement in Science and Transboundary Collaboration

The SSMSP has been influential throughout the region. In the Strait of Georgia, DFO has expanded zooplankton, harmful algae, and biotoxin monitoring; nearshore habitat restoration and monitoring has increased; citizen science has been broadly adopted; and partnerships with groups such as BC Ferries have been formed to improve oceanographic monitoring. Further, the PSF is expanding their PIT tag study of segment-specific mortality to several major salmon-bearing watersheds in the Strait of Georgia; implementing novel approaches to kelp, nearshore, and estuary restoration; implementing a study to assess the winter ecology of Chinook in the Strait of Georgia; and embarking on a thorough review of hatchery effectiveness in the Strait of Georgia. In Puget Sound, LLTK and SSMSP collaborators continue to evaluate seal predation and test predation deterrents at hotspots; assess Coho diets and growth; test approaches to recover herring; more broadly assess Chinook survival relative to estuary conditions; and further examine Chinook survival trends. LLTK and PSF are also working with federal, tribal, and state hatchery managers throughout the Salish Sea to assess the effectiveness of various Chinook and Coho rearing and release strategies on improving survival. The SSMSP also led to the development of PSF's Strait of Georgia Data Centre, the Strategic Salmon Health Initiative, and the Hood Canal Bridge Ecosystem Impact Assessment.[9] Finally, findings of SSMSP studies have already begun to guide recovery planning. Over 20% of recommended recovery actions from the Washington State Governor's Southern Resident Orca Task Force were influenced by SSMSP findings, as well as many proposed actions in NOAA's Puget Sound Steelhead Recovery Plan. LLTK is also working with the Puget Sound region to incorporate SSMSP findings into Chinook recovery plans.

One of the greatest achievements of the SSMSP has been the development of an integrated and broad community of researchers across disciplines and borders. This network of professional and citizen scientists was necessary to undertake the most comprehensive study of salmon in the Salish Sea ecosystem conducted to date. Strong transboundary collaboration among researchers in government, academia, and nonprofits was facilitated through program funding, annual workshops, and working groups. For more information regarding the approach, see the affiliated paper titled "The Salish Sea Marine Survival Project: how collaborative ecosystem research addressed a major impediment to salmon recovery" available at www.marinesurvivalproject.com.

In summary, the Salish Sea Marine Survival Project has made a significant contribution to our understanding of Pacific salmon and coalesced an active research and management community in the process. Our findings support the implementation of management actions that benefit Chinook, Coho, steelhead and the orca whales, Tribes, First Nations, and other people who depend on and value Pacific salmon. We at LLTK and the PSF will continue to work with our SSMSP collaborators to address research gaps, integrate findings into recovery plans, and test management actions.

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[9] www.sogdatacentre.ca, www.psf.ca/what-we-do/strategic-salmon-health-initiative, https://lltk.org/project/hood-canal-bridge/.

INTRODUCTION

The salmon life cycle takes fish from riverbeds to estuaries and through thousands of miles of marine habitat before returning to their natal rivers as adults to reproduce and start the process all over again. Survival during the marine phase plays a critical role in determining the number of salmon that annually return for fisheries or as spawners for the next generation (Pearcy 1992). In this report, the Salish Sea is the marine habitat of focus.

The Salish Sea is defined as the combined waters of Puget Sound, the Strait of Georgia, and the Strait of Juan de Fuca (Figure 2 and BC Geographical Names 2020). Chinook salmon (Oncorhynchus tshawytscha), Coho salmon (Oncorhynchus kisutch), and steelhead trout (Oncorhynchus mykiss) abundance has declined substantially in the Salish Sea (Coronado and Hilborn 1998b, Scott and Gill 2008, Beamish et al. 2010, Irvine and Fukuwaka 2011), in some cases leading to federal protections under the Endangered Species Act in the US and the Species at Risk Act in Canada. Salmon recovery efforts that began in the late 1990s focused on understanding and addressing harvest, freshwater habitat, hydroelectric operations, and hatchery impacts; little emphasis was put on impacts in the marine environment.

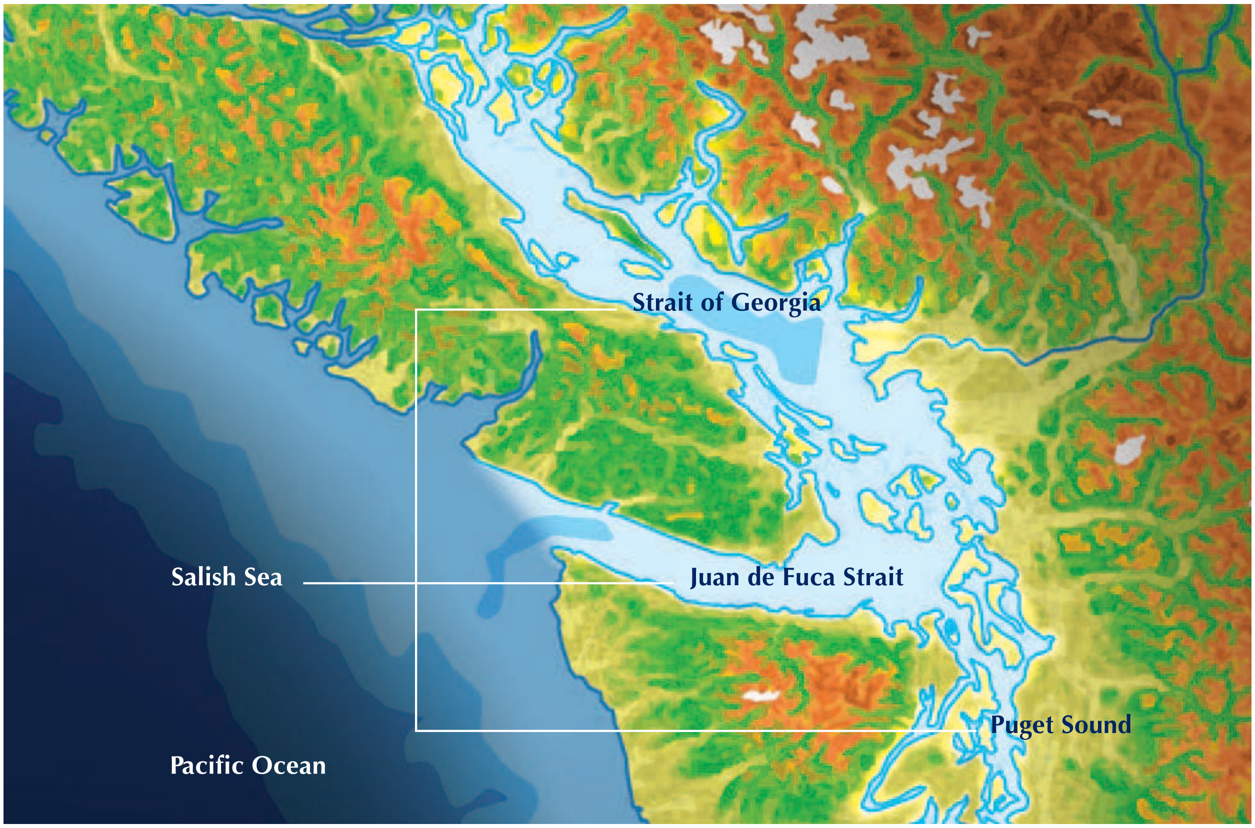

Figure 2. *Map of the Salish Sea.*

Concerns regarding the limited focus on salmon in the marine environment escalated between the mid-1990s and 2010 as studies showed significant impacts to salmon productivity (Beamish et al. 1995, Beamish et al. 1997, Kareiva et al. 2000, Beamish and Mahnken 2001, Welch et al. 2011). In the Salish Sea, relationships between Puget Sound Chinook early marine growth and marine survival (Duffy and Beauchamp 2011) and declines in Strait of Georgia Coho marine survival since the 1980s were documented with early marine survival a particular concern (Beamish et al. 2010, Beamish 2000), while more recent studies show high mortality of juvenile steelhead as they migrate through the Puget Sound marine environment (Moore et al. 2015). Further, the Strait of Georgia Ecosystem Research Initiative documented substantial changes in the Strait of Georgia marine environment since the late 1970s, associated with climate and oceanographic changes (Masson and Perry 2013). Seawater and river water temperatures have increased, deep water oxygen has declined, sea level has risen, and timing of the Fraser River freshets has changed (Riche et al. 2013). These resulted in major regime shifts in the late 1970s and mid-1990s (Perry and Masson 2013), including a shift in the zooplankton community in 1998–1999 (Li et al. 2013) and a decrease in the mean vertebrate trophic level since the 1980s (Preikshot et al. 2013).

The Pacific Salmon Foundation (PSF, Vancouver, BC) and Long Live the Kings (LLTK, Seattle, WA) initiated the Salish Sea Marine Survival Project (SSMSP) in 2013 to identify the primary factors affecting the survival of juvenile Chinook salmon , Coho salmon , and steelhead [3] trout in the Salish Sea marine environment.

The SSMSP was established in response to loss of catch in local fisheries, unique declining patterns of marine survival of these species in the Salish Sea (see Declines section), and other observed ecological changes. Research on salmon was focused on the critical period hypothesis that survival is largely determined by growth in the first few months after marine entry (Beamish and Mahnken 2001) and the general belief that the overall marine survival of salmon is associated with larger size (Ward et al. 1989; Henderson and Cass 1991; Mortensen et al. 2000) and faster growth (Duffy and Beauchamp 2011, Tovey 1999; Beamish et al. 2004; Cross et al. 2008). The SSMSP focused primarily on Puget Sound and the Strait of Georgia and to a lesser extent on the Strait of Juan de Fuca which largely functions as a migratory corridor for juvenile and adult salmon and has conditions more like the outer coast.

The SSMSP was designed as an intensive five-year (2014-2018) ecosystem-based, interdisciplinary research effort involving over 60 government agencies, universities, private consultants, local communities, and nonprofit groups. Unlike most previous work, the SSMSP endeavored to concurrently study Bottom-up and Top-down ecological controls [10] through a coordinated research effort that encompassed all major hypothesized impacts on Chinook, Coho, and steelhead. The Project operated under one overarching research framework with shared hypotheses and aligned sampling and analytical strategies. The Project aimed to determine the extent to which Chinook, Coho, and steelhead survival is driven by local factors, global processes, or, most likely, some cumulative combination thereof. Ultimately, local impacts would result in management recommendations to improve the Salish Sea ecosystem and globally-driven impacts may require adaptation to a changing environment.

In this document, we synthesize results from 90+ studies implemented during the SSMSP, plus other related studies. We illustrate progress made toward addressing hypotheses that served as the framework, first describing the science supporting the overarching hypotheses homing in on principal factors affecting survival and recommending next steps in research and management. While the findings represent important progress towards understanding salmon in the Salish Sea ecosystem, our understanding will undoubtedly continue to evolve. We treat this as a work in progress and a living document. The SSMSP Synthesis Committee will continue to review progress in research and update this document. The studies are available via the SSMSP website at www.marinesurvivalproject.com.

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[10] See "Hypotheses Assessed" section for how bottom-up and top-down ecological processes are defined in this report.

PROJECT HISTORY

In 2009, the PSF developed a scientific program (Riddell et al. 2009) to determine what presently limited the production of Chinook and Coho salmon and what mitigation actions may be undertaken to increase production.[11] The catch of Chinook and Coho salmon within the Strait of Georgia crashed during the 1990s and had not recovered (Figure 3), and no studies had been undertaken to explain this. Strait of Georgia fisheries were once amongst the most valuable in Canada. Catches that annually had numbered in the hundreds of thousands to a million fish decreased to a mere tenth or less and had not recovered despite continued investments in hatchery programs and significant reductions in fishing pressures. Monitoring of released hatchery salmon clearly demonstrated a significant decrease in the survival rate of these fish but the cause of the decline had not been assessed.

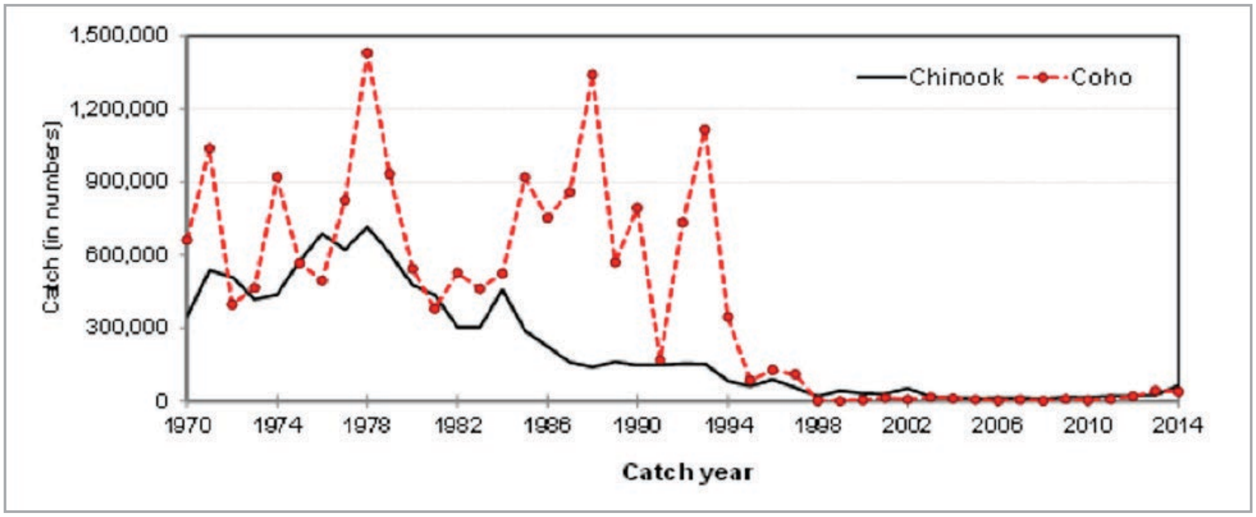

***Figure 3.** Landed catch of Chinook and Coho salmon in the Strait of Georgia and Strait of Juan de Fuca, 1970 to 2014. Prior to 1995, catches included recreational fishing and commercial troll; after 1995, catch is limited to recreational catch as troll gear is prohibited for Chinook and Coho in this region.*

The Strait of Georgia is only one part of the Salish Sea's larger ecological zone (Figure 2). The American portion of the Salish Sea, Puget Sound, is also a human population center with extensive development and many similar problems for Pacific salmon. In 2010, LLTK facilitated a Salish Sea-focused session at the State of the Salmon Conference in Portland, Oregon, where attendees highlighted the need for a broader, more coordinated effort to address how salmon originating in the Salish Sea are adversely impacted in the marine environment compared to salmon from other regions. In response to this, LLTK and PSF combined efforts to create one international endeavor.

In 2012, LLTK and PSF held the first Salish Sea Marine Survival Workshop with 90 U.S. and Canadian participants and a 15-member advisory panel to present the state of science and receive feedback from the broader scientific community regarding critical elements of a transboundary research project. The workshop resulted in initial research recommendations, fundraising, and research planning. In October 2013, an endowment fund under the Pacific Salmon Treaty[12] agreed to provide $5 million for an international research program named "The Salish Sea Marine Survival Project (SSMSP)".

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11. The original focus in Canada was on the loss of Chinook and Coho catches, but in Puget Sound, Steelhead trout are also a significant concern. Production of Steelhead trout in southern BC has also declined in recent decades but has not received the attention of Chinook and Coho salmon.

12. Many fisheries in these joint waters are managed under the Pacific Salmon Treaty (1985) between the United States and Canada (www.psc.org).

ENVIRONMENTAL CONDITIONS DURING THE PROJECT PERIOD

Every research program in the natural environment is subject to the variability of weather and intensive short-term studies are more vulnerable. With most of the field research implemented from 2014-2018, the SSMSP was exposed to the influence of marine heat waves in the North Pacific Ocean (Di Lorenzo and Mantua 2016). These events had major impacts in the North Pacific Ocean as well as within the Salish Sea. In late 2013, scientists started to notice unusually warm sea surface temperatures in the Gulf of Alaska; by the fall of 2014, these warmer waters extended along vast portions of the Canadian and US coasts. Warming persisted during most of 2015 and into 2016 (Figure 4). This mass of warm water was named the "Blob" and resulted in sea surface temperatures up to 2.5 degrees Celsius above the 1981-2010 average, an unprecedented observation (Bond et al. 2015).

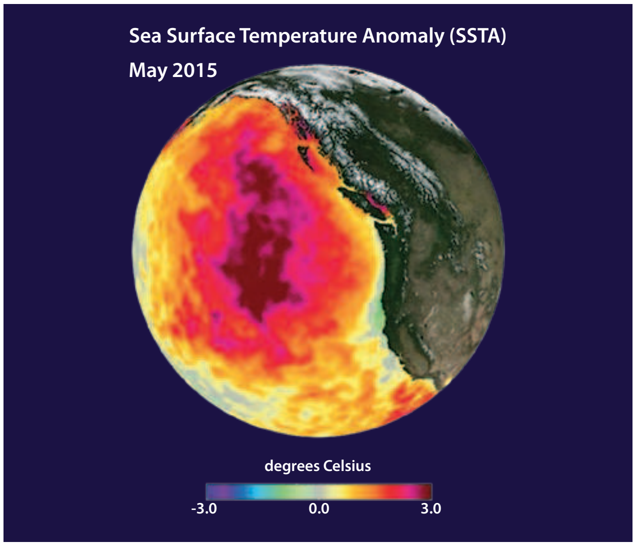

Figure 4. *Image showing unusually high sea surface temperatures in the Pacific Ocean in May 2015 as compared to the 2002-2012 average. (Source: American Geophysical Union)*

The development of this warm water has been attributed to a higher-than-normal ridge of pressure over the ocean. The number and intensity of storms reaching land resulted in reduced precipitation along the west coast and diversion of cold Arctic air into the middle and eastern parts of Canada and the US. Increased temperatures on the surface of the ocean caused the air just above to heat up and stagnate, resulting in greatly weakened coastal winds which were no longer able to push the warm top layer of the Pacific Ocean away from the shoreline. The result was a greatly reduced rate of heat transfer from the ocean to the atmosphere and slower movement of cooler water into the area of the Blob. This situation was exacerbated by an El Niño event in 2015-2016. The initial cause of this high pressure ridge is still under some debate; using climate modelling, researchers recently concluded that this climate event was 53 times more likely to have happened as a result of human-induced climate change, particularly in the Arctic (Oliver et al. 2017, Herring et al. 2018).

There was general concern that these conditions would result in widespread salmon recruitment failures, but this did not appear to occur, at least not immediately. Unusually high winter flows and/or temperatures in freshwater systems led to variable impacts, while the subsequent summer droughts combined with record-breaking summer temperatures resulted in widespread losses of salmon adults migrating upriver and rearing juveniles for many populations. Summer droughts also led to high mortalities for "summer-run" adult Sockeye returning to spawning grounds in the Okanagan River (> 90% en route mortality), Vancouver Island's Sproat River (hundreds of pre-spawn losses) and the Fraser River (various populations exhibiting 20%-50% pre-spawn losses) (Grant et al. 2019, Hyatt pers. comm.).

During 2017, physical oceanographic processes associated with the marine heat wave reverted to more normal conditions. Most SSMSP field programs occurred between 2014 and 2017, and thus data collection occurred during the warm years associated with the Blob (2014-2016) and during a more "normal" year in 2017. Impacts of the Blob were apparent within the Salish Sea as early freshets, increased ocean temperatures, warming at depth, droughts, and reduced river flows, most notably in 2015 and 2016 (Grant et al. 2019). Conditions within the Salish Sea have been variable since SSMSP; however, marine heat waves in the Northeast Pacific Ocean have continued, occurring in 2019 and 2020. Recent climate modeling at NOAA and the Pacific Climate Impacts Consortium (PCIC) are providing evidence that the frequency of such marine heat waves may be increasing as our climate continues to warm, indicating that SSMSP research may provide insight into the types of ecological changes that we may expect to become more of the norm.

Environmental changes associated with the period of declines in Chinook, Coho, and steelhead marine survival, the late 1970s through the 2000s, are explored in subsequent sections.

HYPOTHESES ASSESSED

The Salish Sea Marine Survival Project research was structured around a suite of hypotheses about the factors that could contribute to the decline in marine survival. Given the broad scope of the effort, we created hypotheses that act more as general guidance than are directly testable. These hypotheses are not considered mutually exclusive, and interrelationships were considered likely.

Broadly, the primary hypotheses were:

1. Early marine survival is determined by bottom-up ecological processes: **weather, water conditions, and productivity that determine the food supply for salmon and result in variation in size and growth rate.** Salmon may also compete among themselves or with other fishes for food.
2. Early marine survival is determined by top-down ecological processes. **Predation is likely the direct cause of mortality**, but salmon may be affected by other biological factors (e.g., disease and contaminants) increasing their susceptibility to predation, directly killing them, or affecting their condition such that overall marine survival is reduced.
3. Multiple factors may interact and have cumulative effects in determining early marine survival. These may be additive, synergistic, or dampening.

Humans may have also changed the natural forces determining annual variation in salmon production through our impact on habitats and related losses of life history diversity in salmon as will be evident in some studies presented.

Categorizing factors as having top-down or bottom-up influence is overly simplistic. For example, predation, contaminants, ocean acidification, and harmful algae all can either impact salmon directly or affect their food supply. The report attempts to address these intricacies by describing the multiple pathways of impacts to salmon, each factor's interrelationships with other factors, and illustrating the results of comprehensive ecosystem modelling approaches.

The hypotheses were configured operationally as shown in Table 2. Explanations and predictions are included in Appendix A. The suite of hypotheses was developed in 2012 and refined over the course of the Project.

Table 2. *SSMSP hypotheses. Explanations and predictions are in Appendix A.*

A.	Salish Sea marine survival trends are unique to the region	
B.	Early marine growth or mortality in the Salish Sea determines marine survival (critical period)	
C.	Factors that may affect early marine survival are:	
	1. Salmon Behaviour and Physical Habitat • Outmigration Timing • Distribution and Migration Pathways • Residency • Physical Habitat • _Metabolic effect_*	**2.** Bottom up — Food Supply • Prey availability • Water quality/Biogeochemistry • Mismatch • Competition • Ocean Acidification* • Harmful Algae**
	3. Top down — Predation • Predator abundance • Specialization • Pulse prey abundance • Buffering/Prey switching • Ocean acidification** • Visibility*	**4.** Top down — Disease, contaminants, harmful algae • Disease • Contaminants • Harmful Algae**

*Hypotheses that received less attention by investigators and are not discussed in this report are in italics.

**While top-down and bottom-up effects are described for ocean acidification and harmful algae, their sections are categorized with bottom-up effects.

The PSF and LLTK established several multidisciplinary science workgroups to execute the SSMSP and held several workshops over the course of the SSMSP to facilitate strong collaboration. The Synthesis Committee, which was made up of the primary SSMSP scientists from each discipline, convened in 2018-2020 to evaluate hypotheses relative to the evidence collected via the SSMSP plus recent external studies. For each hypothesis, we asked:

1. How extensive is the impact? Is it species- or population-specific, Puget Sound or Strait of Georgia-specific, or Salish Sea-wide?
2. How significant of a role do we think it has in driving declines in marine survival since the late 1970s and/or recent marine survival patterns over the past 5-10 years?
3. How strong is the evidence?
4. Are there interrelationships that make this factor more or less significant?

Similar questions were asked in series of workshops in 2019 and 2020 with a larger subset of scientists participating in the SSMSP. We use the results of these workshops and the Synthesis Committee review as the basis for describing the findings in this report. The three focal species of the SSMSP are addressed separately given their different life histories and behaviour.

WHERE ARE WE? A STATE OF KNOWLEDGE SNAPSHOT

The Synthesis Committee assessed the role of each factor relative to long-term trends (late 1970s to 2015[13]) over the period of decline in overall marine survival and relative to recent (past 5 to 10 years) patterns in marine survival (Table 3 on next page). They ranked the level of impact each factor may be having on marine survival, from **substantial** to **none**. Substantial meant available evidence was consistent with the factor contributing significantly to changes in marine survival, whereas none meant there was no evidence that the factor affected marine survival, or, in some cases, there was evidence that the factor likely did not impact marine survival. Finally, an **unknown** category was included for factors which the Committee was unable to rank due to limited information.

They Committee also assessed the strength of evidence supporting their position, ranked from **strong** to **weak** based on the quantity and quality of data available. Rankings were done separately for Chinook, Coho, and steelhead in Puget Sound and in the Strait of Georgia. The rationale for each ranking is supported by the findings and the "Synthesis Committee Perspective" as described in the "What we know about each factor's influence on survival" below.

Note that other than a study of survival trends and some examination of mortality relative to different migration pathways through acoustic tagging programs, Strait of Georgia steelhead were not assessed and therefore are left out of this table.

Further, the Committee concluded that it is likely that no single factor has driven the declines in marine survival. Rather, factors are likely working in an additive or synergistic manner.

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[13] Puget Sound Chinook include the late 1970s because data suggest marine survival declines may have occurred then (see "Declines in marine survival and early marine critical period" section).

Table 3. *Synthesis Committee perspectives on the significance of the different SSMSP hypotheses to explain the changes in marine survival for Chinook, Coho, and steelhead in Puget Sound and Strait of Georgia.*

Hypotheses	Strait of Georgia						Puget Sound								
	Chinook			Coho			Chinook			Coho			Steelhead		
	Trend since late 1970s	Recent Patterns	Strength of Evidence	Trend since late 1970s	Recent Patterns	Strength of Evidence	Trend since late 1970s	Recent Patterns	Strength of Evidence	Trend since late 1970s	Recent Patterns	Strength of Evidence	Trend since late 1970s	Recent Patterns	Strength of Evidence
Decline in marine survival	1	NA	H	1	NA	H	1	NA	M	1	NA	H	1	NA	H
Critial Period - Growth	U	2	M	U	2	M	U	2	M	U	U	NA	6	6	H
Critical Period - Instantaneous Mortality	U	3	L	U	2	M	U	3	L	U	U	NA	U	1	H
Salmon Behavior and Physical Habitat															
Outmigration Timing*	2	1	H	4	4	H	2	1	H	4	4	H	U	U	H
Distribution & Migration Pathways	5	2	M	6	6	M	5	3	L	6	6	L	6	6	H
Residency	5	3	L	2	2	L	5	3	M	U	U	NA	6	6	H
Physical Habitat	3	3	M	5	5	M	3	3	M	5	5	L	6	6	M
Bottom up - Food Supply															
Prey availability	2	2	M	1	1	M	1	1	M	2	2	L	6	6	L
└ Water quality/Biogeochemistry	2	2	L	2	2	L	2	2	L	2	2	L	3	3	L
└ Mismatch	3	3	L	3	3	L	3	3	L	3	3	L	6	6	H
└ Competition	4	4	L	4	3	L	4	3	M	4	3	L	6	6	H
Ocean Acidification**	5	5	NA	5	5	NA	5	5	NA	5	5	NA	6	6	H
Harmful Algae**	5	5	NA	5	5	NA	5	5	NA	5	5	NA	6	6	H
Top down - Predation															
Predator abundance	2	2	M	2	2	M	3	2	M	2	4	M	2	1	M
Specialization	6	5	L	6	5	L	6	6	L	6	6	L	6	6	L
Pulse prey abundance	4	5	L	4	5	L	4	4	L	4	4	L	4	5	L
Buffering/Prey switching	4	U	L	4	U	L	3	U	L	3	U	L	2	2	M
Top down - Disease and Contaminants															
Disease	U	1	M	U	2	M	U	U	NA	U	U	NA	5	5	H
Contaminants	U	U	NA	U	U	NA	3	2	M	U	4	L	U	U	NA

** Rankings reflect the finding of a reduction in variability and change in mean of hatchery Chinook release times, some changes with Coho hatchery release times, and correlations with survival in multi-factor models (Sobocinski et al. 2021). Outmigration timing in and of itself may not affect survival. Rather, it may interact with other ecosystem factors (e.g., mismatch with prey availability, competition, and pulse prey abundance).*

***Ocean acidification and harmful algae likely have minimal impact now but are a substantial concern into the future as climate change increases the potential impact of these factors.*

Legend

Level of Impact	
Substantial-Moderate	1-2
Some	3-4
Minimal - None	5-6
Unkown	U

Strength of Evidence	
Strong	H
Moderate	M
Weak	L
Not Applicable	NA

DECLINES IN SALISH SEA MARINE SURVIVAL AND THE EARLY MARINE CRITICAL PERIOD

Marine survival covers the period from release in freshwater at hatcheries or, for wild fish, from their downriver migration as juveniles and through their ocean phase to the point where these fish are either captured as adults in fisheries or return to rivers and hatcheries to spawn. The SSMSP originated from two shared overarching hypotheses. First, populations of Chinook, Coho, and steelhead originating in the Salish Sea experienced unique declines in marine survival between the late 1970s and the present relative to populations of salmon from other regions. Second, overall marine survival rates are largely determined by a **critical period:**[14] when juvenile Chinook, Coho, and steelhead first enter and then migrate through the Salish Sea.

DECLINES IN MARINE SURVIVAL

The initial analyses of marine survival trends to justify the Project were limited, unpublished, and the data were insufficient to use as metrics for performing correlative analyses to assess impacts to marine survival. Three studies (Zimmerman et al. 2015, Ruff et al. 2017, Kendall et al. 2017) were completed early in the Project to further investigate trends in marine survival (referred to as "smolt survival"[15] in these papers) of Chinook, Coho, and steelhead populations from the Salish Sea and Washington and BC coast, for between the late 1970s and 2011. Other studies including complimentary marine survival data are also referenced in this section.

Most of the salmon populations assessed for the three primary studies of marine survival rates were hatchery origin because the data to assess smolt survival are more robust, with very large tag groups consistently released and monitored over long time periods; however, wild populations were included where possible. Data from coded-wire tags implanted in juvenile salmon and later recovered in fisheries or in freshwater collections were primarily used for estimating Chinook and Coho survival (Ruff et al. 2017, Zimmerman et al. 2015). These data were downloaded from the coast-wide Regional Mark Information System (RMIS) database (www.rmpc.org). Steelhead survival was estimated based upon the number of juveniles released from hatcheries or out-migrating downriver compared to the number of adults returning to the rivers or hatcheries (Kendall et al. 2017).

Assessing patterns of marine survival among salmon populations from a broad geographic region and over extended periods provides insight into the factors affecting their survival. If marine survival patterns are similar among populations over a broad range, this suggests primary influence from large-scale drivers like climate conditions (Mantua et al. 1997, Beamish et al. 1999b). However, when marine survival patterns are synchronized over a smaller geographic range, or not synchronized at all, this suggests regional factors are having greater influence than large-scale drivers. When marine survival varies by population, this suggests in-river/estuary factors and/or population traits have the strongest influence (Zimmerman et al. 2015). Changes in synchrony in marine survival among populations over time can also elucidate whether the influence of specific factors changes.

The average annual marine survival rates for Chinook, Coho, and steelhead from ocean entry year[16] 1978 through 2015 are illustrated in Figure 4, below. Individual survival rates for stocks are aggregated by species and location (Puget Sound, the Strait of Georgia, and Washington/British Columbia Coast and Columbia River). As illustrated, Chinook, Coho, and steelhead show declining marine survival trends unique to the Salish Sea (Figure 4), and the changes in marine survival rates over time suggest the Salish Sea may have supported higher productivity compared to the coast in the 1970s and 80s. The complete stock list with years of data used in Figure 4 is in Appendix B. These data are largely the same as used in Zimmerman et al. 2015, Kendall et al. 2017, and Ruff et al. 2017. Note that data from the 1970s was included for Chinook in this figure, whereas it is not included in the Ruff et al. 2017 analysis. The reasons are explained below.

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14. A "critical period" for fish is a time during early life when mortality is unusually high and a stage when longer-term survival rates are determined (Hjort 1914).
15. A "smolt" is the stage of a juvenile salmon's life when it is physiologically capable of adapting to saltwater. In this stage, the juvenile becomes silvery (losing its dark bars) and begins migration out of freshwater habitats.
16. Ocean entry year is the year that juvenile salmon or steelhead left the freshwater environment and entered the marine environment, such as the Salish Sea or, if a coastal stock, directly into the Pacific Ocean.

The three individual studies of each species, Coho = Zimmerman et al. 2015, Steelhead = Kendall et al. 2017, and Chinook = Ruff et al. 2017, provided a more refined understanding of these trends. The results of these studies are described below.

The Zimmerman et al. (2015) Coho analysis of ocean entry years 1977-2010 strongly suggests that early marine conditions influence marine survival and that Salish Sea conditions supporting higher marine survival have diminished (Figure 5). Coho populations from the Salish Sea generally exhibited declining patterns in marine survival over the time period assessed, with declines occurring faster in the Strait of Georgia compared to Puget Sound in the 1980s but both groups continuing to decline until the late 1990s. Coastal populations did not show this decline, instead initially having a much lower and then slightly increasing survival trend over the same period (Zimmerman et al. 2015). Marine survival among Salish Sea populations became more synchronous after much of their decline, following the climate regime (Pacific Decadal Oscillation) shift in the late 1980s. Marine survival among Coho populations was synchronized at a more local scale (exponential decay model e-folding scale estimate of 294 km) compared to Chinook, Pink, and Chum salmon. Sub-basin differences in survival were small when compared to basin scale differences. However, at a sub-basin scale, populations in South Puget Sound went from having high marine survival relative to other sub-basins to the lowest survival relative to other sub-basins over time; whereas the reverse occurred for Hood Canal and southern Strait of Georgia.

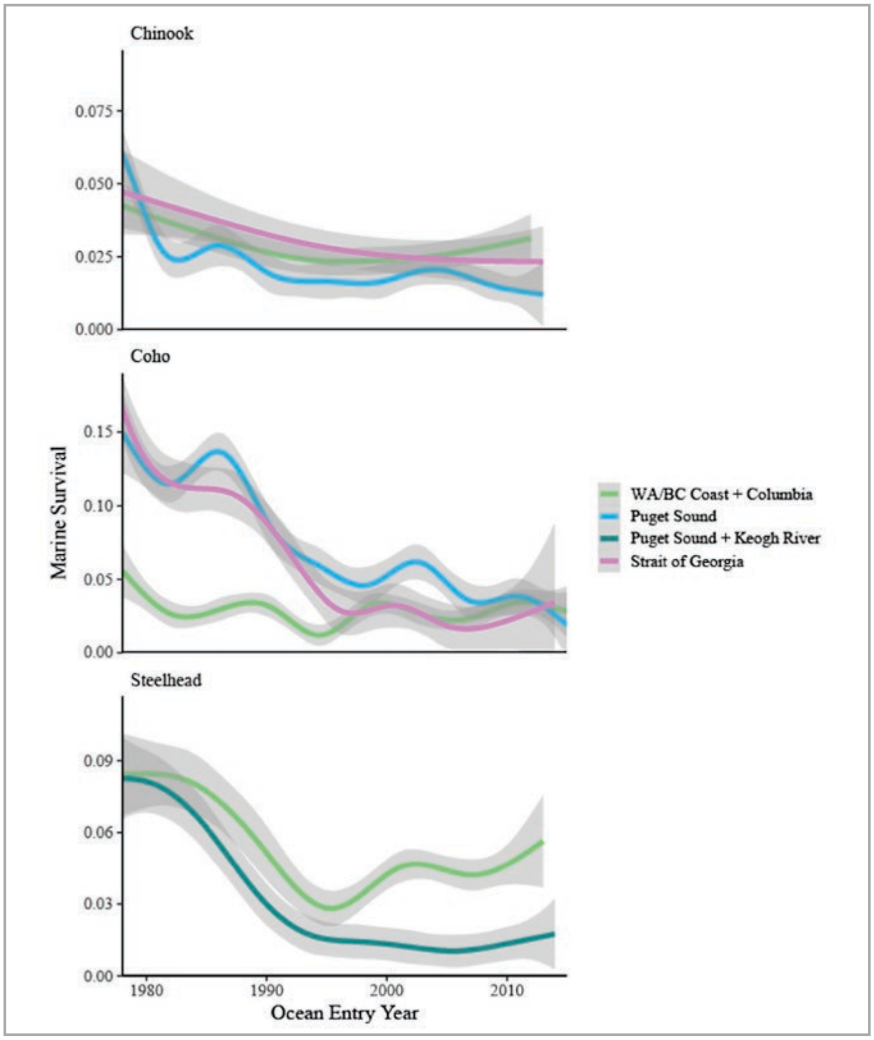

Figure 5. *Marine survival trend for Chinook (top panel) and Coho (middle panel) in Puget Sound (blue), Strait of Georgia (pink), and WA/BC Coast and Columbia River (green) and for steelhead (bottom panel) in Puget Sound + Strait of Georgia's Keogh River (teal). A smoothing function (colored line and gray envelope showing confidence interval, generalized additive model (GAM), survival ~ year) was applied to illustrate trend. All panels span ocean entry years 1978-2015. Underlying data as described in Zimmerman et al. 2015, Ruff et al. 2017, Kendall et al. 2017, and Sobocinski et al. 2021. See Appendix B for the stock list and any discrepancies between this graph and the papers.*

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17. The e-folding scale is the distance apart at which population correlation coefficients would be reduced to 37% (i.e., e–1 × 100%) of the expected mean correlation at a distance of 0 km, 0 (the intercept). The e-folding scale is an arbitrary measure but provides a common metric to compare the scale of spatial synchrony in smolt survival with that in other studies (from Kendall et al. 2017. E.g., Kendall et al. 2017, Kilduff et al. 2014; Ruff et al. 2017; Teo et al. 2009; Zimmerman et al. 2015).
18. 294 km (95% CI D 246–354 km, Intercept = 0.84), approximately one-third the value for Chinook Salmon (1,069 km; Kilduff et al. 2014) and one-half to three quarters the values for Pink Salmon (431 km; Pyper et al. 2001) and Chum Salmon (564 km; Pyper et al. 2002).

Like Coho, the steelhead analysis (Kendall et al. 2017) of ocean entry years 1977-2011 suggests early marine conditions influence marine survival and that Salish Sea conditions supporting higher marine survival have diminished. Both adult abundance and marine survival trends were analyzed for steelhead. Across the entire time series, marine survival among steelhead populations was synchronized at a more local scale compared to other salmon species; however, the strength of synchrony was less than for Coho (steelhead exponential decay model e-folding scale estimate of 248 km).[19] All steelhead populations assessed declined in abundance and survival including Puget Sound and Strait of Georgia populations.[20] Abundance also declined for all but a couple of Lower Columbia River steelhead populations, with Puget Sound populations having the greatest change in abundance between the 1980s and 2000s. Marine survival for steelhead populations from Puget Sound and Keogh River[21] declined dramatically until 1996, then leveled off until slightly increasing after 2006. Marine survival from the coast, lower Columbia, and Puget Sound/Keogh steelhead all exhibited declines and then breakpoints in the late 1990s, consistent with the timing of a climate regime shift in the North Pacific Ocean (Overland et al. 2008, Peterson and Schwing 2003). No sub-basin analysis of the Salish Sea was performed.

The results of the Chinook analysis of ocean entry years 1980-2008 (Ruff et al. 2017) also illustrated a decline in marine survival, calculated to ocean age-2 or -3, for Strait of Georgia Chinook and generally illustrated that factors affecting survival at more local scales (e.g., individual population level) are more pronounced for Salish Sea as compared to coastal populations. Overall, there was high variability in marine survival among populations, with weaker coherence in survival trends among populations within the Salish Sea as compared to those outside of the Salish Sea. Further, spatial coherence among populations of Salish Sea Chinook was generally weaker compared to all Coho and steelhead populations assessed (exponential decay model e folding scale estimate of 292km).[22] Unlike Coho, there was no increase in spatial synchrony among Salish Sea populations after 1990, while there was for coastal populations. Regional-scale differences in survival trends were identified for northern coastal (Northern BC and Southeast Alaska), southern coastal (Oregon and Washington Coast and Lower Columbia River), Strait of Georgia, and Puget Sound Chinook salmon populations. Marine survival declined for all four Northeast Pacific population groups between the 1980s and early/mid 1990s, with the trend most pronounced in Strait of Georgia and least pronounced in Puget Sound. Marine survival of Puget Sound populations was generally lower than Chinook populations from other regions over the time series (Ruff et al. 2017). Further, geography more strongly influenced survival trends compared to release strategy (yearling versus subyearling) and run timing (spring, summer, fall). Finally, survival of southern coastal populations was correlated with the North Pacific Gyre Oscillation, a large-scale ocean circulation pattern, whereas survival of Salish Sea populations was not. No sub-basin analysis of the Salish Sea was performed as part of this study due to the limited number of populations from each basin.

It is worth noting that five Strait of Georgia Chinook populations clustered together within the Salish Sea cluster, whereas four other Strait of Georgia populations did not. Recent work suggests these populations consistently rear in different areas of the Salish Sea, which could help explain the survival differences (see Distribution section). Coho salmon, which have more synchronous marine survival patterns throughout the Strait of Georgia, are more widely distributed and intermixed (Neville and Beamish pers. comm.).

The Ruff et al. (2017) Chinook survival assessment used data beginning with ocean entry year 1980 due to concerns about data quality associated with incomplete sampling, and limited data in general, during the 1970s when coded-wire tag programs began. However, excluding the 1970s was strongly debated among participating scientists because, while limited, the data suggest significantly higher marine survival rates for Puget Sound Chinook before ocean entry year 1980 (Sobocinski et al. 2021, Ruggerone and Goetz 2004, Welch et al. 2020). Further, the limited sampling and recovery of coded-wire tags in returning adults prior to the 1980s likely resulted in underestimates of marine survival during that time period (M. Crewson pers. comm.). In a subsequent study of Puget Sound marine survival, Sobocinski et al. (2021) included all data available. When doing so, it was shown that Puget Sound Chinook populations did exhibit significant declines in marine survival from late 1970s to the early 1980s. Ongoing work by Haggerty et al. (pers. comm.) analyzing all Chinook survival data available in the RMIS database from 1970 to present also indicates a significant decline in marine survival in nearly all Puget Sound and Strait of Georgia Chinook salmon stocks by the mid-1980s. Welch et al. (2020) also found a pronounced decline in Puget Sound Chinook survival (2% in the 1970s to less than 0.5% in 2010).

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[19] 248 km: 95% CI = 200–310 km. Intercept = 0.42.

[20] Only Keogh River steelhead were included in the survival analysis. Other Strait of Georgia steelhead were included in the abundance analysis.

[21] In Johnstone Strait at the northern end of Strait of Georgia.

[22] 292km: 95% CI= 151-1,916km; Intercept = 0.28.

Welch et al. (2020) contended that the marine survival of many Chinook populations along the northeast Pacific coast has declined, suggesting that a broader oceanic (or climate) factor is at play. Finally, Ruggerone and Goetz (2004) found a decline in marine survival of Puget Sound Chinook when comparing the mean rates from 1972-1983 (0.88%) to 1984-1997 (0.44%). The decline in marine survival corresponded with one of the biggest El Niño events on record (1982–1983; Wolter and Timlin 1998) and subsequent relatively frequent El Niño events (Wolter and Timlin 1998). Both Welch et al. (2020). Ruggerone and Goetz (2004) estimated survival through adult return for all ages instead of estimating survival to age-2 based on coded-wire tagged salmon recoveries and assumptions of natural mortality in the older age classes as done in Ruff et al. (2017) and Sobocinski et al. (2021). Due to the quantity of published data on the matter, we concluded that Chinook marine survival data prior to 1980 is relevant and included it in figure 4, above.

Isolating decadal or other relevant ecological stanzas[23] is a critical step toward evolving our understanding of the relationship between salmon and their ecosystem. Some studies have shown strong even versus odd year variation in Puget Sound Chinook marine survival rates (Ruggerone and Goetz 2004, Kendall et al. 2020a, Haggerty pers. comm.), and that the relationship between marine survival and year switches at specific points over the 43 years of data available (ocean entry year 1972-2015) (Ruggerone and Goetz 2004, Haggerty pers. comm.) Ruggerone and Goetz (2004) describe a flip that occurred somewhere between 1983-1985 from higher even-ocean entry year marine survival for 1972-1985 (Period 1) to higher odd-ocean entry year marine survival in the next period (1986-1999, Period 2). Haggerty (pers. comm.) extended the Ruggerone and Goetz assessment and found a third shift back to higher even-ocean entry year survival 2000 (2000-2012, Period 3). Haggerty's findings are illustrated in figure (Figure 6), below. They suggest these patterns and their shifts are indicators of major ecological shifts or stanzas. The findings of Ruggerone and Goetz 2004, Kendall et al. 2020a and Haggerty (pers. comm.) are discussed in greater detail in the competition section below.

Instead of changes to even versus odd year variation in Chinook survival, Sobocinski et al. (2021) used the periods of before, during, and after declines in marine survival of Chinook and Coho as temporal stanzas to model separately with ecological factors that may affect survival. In their work, the influence of specific suites of ecological factors varied by stanza for Coho but not for Chinook. The findings of this study are described in greater detail in subsequent sections of this report.

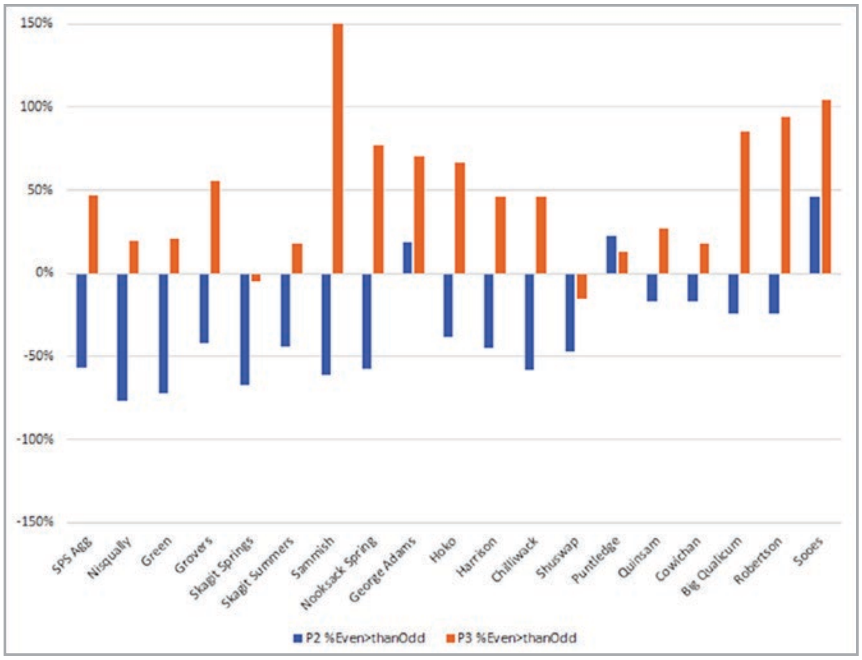

Figure 6. *Proportions of Salish Sea Chinook marine survival rates on even ocean entry years greater than on odd ocean entry years for two time periods (1986-1999 in blue and 2000-2012 in orange), illustrating a regime shift that occurred around the year 2000 (Source: M. Haggerty)*

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[23] The term ecological stanzas refers to time periods where the ecology of the system dramatically differs from one period to another. A switch is typically caused by some sort of dramatic event.

IS THERE A CRITICAL PERIOD DETERMINING THE ABUNDANCE OF SALMON IN THE SALISH SEA?

A critical period refers to a portion of the salmon life cycle that largely accounts for the total adult abundance of returning salmon. There are two prevailing hypotheses about the mechanisms that determine these outcomes.

1. Early marine **growth** through the first summer regulates survival over summer and at later life stages.
2. Total marine survival is heavily influenced **by mortality** during the first spring/summer, irrespective of fish size.

Early marine growth

Hypothesis 1 is consistent with the critical size–critical period hypothesis (Beamish and Mahnken 2001) that proposes that Pacific salmon experience two size-related survival bottlenecks—one due to predation during their first marine summer and the second due to starvation during their first marine winter. Energy allocations by juvenile salmon may shift between somatic growth, activity, and storage of lipids depending on the pressures during these two critical periods: the former most impacted by predation mortality and the latter by mortality due to energy or nutrient depletion. Beauchamp et al. (2007) suggest that juveniles that achieve a faster growth rate can reach a critical size (a larger body size but with low energy content) resulting in reduced predation risk as they outgrow the mouth gape of predators. Beamish et al. (2008) found that length increase of juvenile Coho between July and September was inversely related to marine survival. These authors suggested that the larger Coho in July allocated less energy to somatic growth and more energy to lipid storage through September, resulting in better survival over winter. This finding led to further development of the critical period hypothesis to include the importance of lipid storage, and the concept that absolute size may be of lower importance than early marine growth followed by energy diversion into reserves needed for migration and overwinter survival.

Relationships between early marine growth, size, and marine survival of Chinook from the Salish Sea and beyond has been documented in several studies (Tomaro et al. 2012, Miller et al. 2014, Holtby et al. 1990). Recent work by Claiborne et al. (2020) illustrates a relationship between growth in the first year at sea and survival for both Puget Sound and coastal Chinook populations. First ocean year growth was assessed for 5 populations via scale analysis (measuring the distance between ocean entry and ocean age-1 circuli) for 1992, 1998, 1999, 2002, 2005, and 2008: a range of years that included wide variation in marine survival (survival rates ranging from 0.11% to 9.5%). Generally, when Chinook growth in the first ocean year was above average, fish experienced higher overall marine survival. Three of the five populations assessed showed positive, statistically significant relationships [Skagit ($r = 0.88$, $n = 5$, $p = 0.05$) and Green ($r = 0.89$, $n = 7$, $p < 0.01$) from Puget Sound, Willapa ($r = 0.91$, $n = 5$, $p = 0.03$) from Washington coast], and the two others showed positive relationships but were not statistically significant [Puyallup ($r = 0.51$, $n = 7$, $p = 0.24$) from Puget Sound, Quillayute ($r = 0.66$, $n = 6$, $p = 0.15$) from the coast].[24]

Focusing on growth in Puget Sound, Duffy and Beauchamp (2011) demonstrated a strong relationship between size in July—while juvenile Chinook are rearing in Puget Sound within the first two months following ocean entry—and marine survival (10 populations from throughout Puget Sound, years 1997, 1999, 2000, 2001). Fish size at hatchery release was not found to be statistically related to survival for the populations examined in those years, reinforcing the role of growth through July (Duffy and Beauchamp 2011).

However, in a larger meta-analysis that compared size and time at release to all available marine survival rate data (hatchery tag groups) for U.S. Chinook releases into tributaries to the Salish Sea, Haggerty (pers. comm.) found a very strong positive relationship between size at release ($R2= 0.85$, $n = 980$) and marine survival and, conversely, a strong negative relationship ($R2 = 0.71$, $n = 1,286$) between time of release and marine survival. Over time, hatchery operators found a "sweet spot" by releasing large, fast-growing and smolting, subyearling Chinook as early as possible (April-May) to optimize survival benefits of earlier outmigration. Hatchery release times have also been adjusted to reduce ecological interactions with ESA-listed natural-origin fish (Crewson pers. comm.)

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[24] It is worth noting that a relationship between faster early marine growth and higher marine survival may be a consequence of changing environmental conditions. Slower growth is typically associated with later maturation in Chinook (Groot and Margolis 1991). In recent times, size and age of maturity in Chinook has declined (Ohlberger et al. 2018, Jeffrey et al. 2015).

Another study suggests that growth rates for wild and hatchery juvenile Chinook were highest in Puget Sound offshore regions compared to nearshore and estuary habitats; there was little evidence of size-selective mortality throughout the first summer across nearshore, estuary, and offshore habitats (Gamble et al. 2018). Pellett (pers. comm.) also found little evidence of size-selective mortality occurring during the first summer for hatchery and wild Cowichan Chinook rearing in the Strait of Georgia. These results suggest that Chinook growth- or size-related mortality is likely occurring later, possibly over the first winter.

Similarly, Coho early marine growth has been correlated with marine survival (Holtby et al. 1990, Beamish 2007, Beamish et al. 2008). Within the Strait of Georgia, it has been proposed that growth to a critical size during the early marine period regulates the marine survival of Coho salmon (Beamish and Mahnken 2001, Beamish et al. 2004). Further, the positive relationship between fork length and abundance in July might suggest that rapid growth immediately following entry into the Strait of Georgia improves early marine survival (Beamish et al. 2008). Insufficient data exist to assess relationships between Puget Sound Coho early marine growth and survival, due to limited offshore sampling in Puget Sound and a hypothesized faster migration of Coho salmon out of Puget Sound versus Strait of Georgia (Beamish and Mahnken 2001).

It is difficult to determine whether the capacity for faster early marine growth in the Salish Sea declined over the period when the overall marine survival of Salish Sea Coho and Chinook declined. Summer fish length data were not consistently collected until the mid-1990s, after the period of decline (Beamish 2007). However, as noted in (Ruggerone and Goetz 2004).unpublished data suggest the first-year marine growth of Puget Sound Coho may have been higher prior to 1983.

Recent data suggest the capacity for early marine growth in the Salish Sea may have improved over the past decade. From 1999 through 2008, there was a declining trend in Strait of Georgia Coho catch per unit effort (CPUE), which shifted to an increasing trend from 2009 to 2018. Average Coho length in September concomitantly increased (Neville and Beamish 2018; see Distribution, Migration Pathways, and Residency section of this report for more information). Higher early marine growth and lower early marine mortality could result in higher overall marine survival of Strait of Georgia Coho. However, Puget Sound Coho marine survival has not increased in recent years (Sobocinski et al. 2021).

Mortality in first summer

Hypothesis 2 suggests mortality occurs in the first summer, regardless of size, likely due to predation.

There is sparse evidence to evaluate the relationship between mortality in first summer and total marine survival. Midwater trawl data from the Strait of Georgia (1997-2006) suggests a relationship between juvenile Coho mortality through September and overall marine survival (Beamish et al. 2010). A Strait of Georgia Chinook acoustic tagging study and the low number of Strait of Georgia Chinook stocks captured on the west coast in the summer and fall suggest that mortality during the first summer/early marine period in the Strait of Georgia is significant (Neville et al. 2015). Relationships between size and survival were not assessed in Beamish et. al. 2010 or Neville et al. 2015; therefore, we cannot determine whether early marine mortality was size-selective. Further, initial results from one year (2015 outmigrants) of a Passive Integrated Transponder (PIT) tag study of Cowichan River hatchery and wild Chinook suggested 78 and 80% mortality, respectively, over the first summer with little evidence of size-selective mortality (Pellett pers. comm.). Mortality rates were also high (97% and 93% for hatchery and wild, respectively) for the much longer period between the end of the first summer to adult return, but it is uncertain at what point in the life cycle and at which locations later mortality occurred (Pellett pers. comm.). In Puget Sound, there was little evidence of size-selective mortality throughout the first summer across nearshore, estuary, and offshore habitats (Gamble et al. 2018). A follow up telemetry study to Pellett's work found that only 50% of Cowichan Chinook tagged in mid-September survived to mid-October in the Cowichan Bay area, supporting the idea that high mortality continues beyond the summer for fish that reside in the Salish Sea as juveniles (Rechisky et al. in prep). In Puget Sound, midwater trawls have not been performed consistently enough nor at the scale required to draw associations between late summer juvenile Chinook and Coho abundance and overall marine survival.

Unlike Chinook and Coho which may reside in the Salish Sea for extended periods, steelhead migrate quickly to the ocean, which facilitates the use of acoustic telemetry to measure early marine mortality (Moore et al. 2010, Moore et al. 2013, Moore et al. 2015, Moore and Berejikian 2017, Berejikian et al. 2016). Generally, early marine survival of Puget Sound steelhead was low for the years studied between 2006-2014, increased substantially in 2016-2017, then decreased slightly in 2018 and 2019. From 2006 to 2009, early marine survival rates, defined here as survival from river mouth to western portion of the Strait of Juan de Fuca, from eight Puget Sound rivers ranged from 0.8% to 39.3%, and averaged 16.0% for wild smolts and 11.4% for hatchery smolts (Moore et al. 2015). In 2014, early marine survival rates remained low (5.9 ± 4.2% and 17.4 ± 7.1%) for wild steelhead released from the Nisqually and Green rivers, respectively (Moore and Berejikian 2017). In 2016 and 2017, early marine survival rates for Nisqually wild steelhead increased substantially, to 37.2% and 38.6%, respectively (Moore et al. 2021). Data to calculate the contribution of early marine survival to overall marine survival by population and ocean entry year are limited; however, modelling suggests that early marine survival rates under 14-16% through Puget Sound prevents population growth (Puget Sound Steelhead Recovery Team 2019).[25] No relationship has been found between early marine mortality in Puget Sound and steelhead smolt size (Moore et al. 2015, Moore et al. 2021).

Synthesis Committee Perspective

The Synthesis Committee concluded that, based on available data, juvenile salmon growth was a more influential determinant of overall marine survival for Chinook and Coho than mortality during their first summer in the Salish Sea. However, the rapid migration of steelhead through the Salish Sea and high early marine mortality observed during that relatively brief period suggests mortality is a more influential determinant of overall marine survival than size/growth for steelhead during their first summer. Early marine growth and survival data to assess the critical period hypothesis are only available for Strait of Georgia Coho, and the data do not extend back into the 1980s; therefore, the Committee could not determine whether there has been a change in first summer growth or mortality over the period of marine survival declines.

HATCHERY VERSUS WILD SURVIVAL

While the intent of the SSMSP was to assess determinants of production and early marine survival of both hatchery and wild juvenile salmon; the vast majority of the data used to assess marine survival rates comes from hatchery fish. Coded-wire tags, the basis for marine survival trend data for Coho and Chinook, have been deployed in many hatchery populations but few wild populations since the 1970s. Further, sampling of mixtures of hatchery and wild salmon has led to concerns regarding whether these data are representative of wild populations.

Generally, hatchery and wild marine survival trends over time are similar. In the Coho marine survival trends analysis, populations of hatchery and wild Coho clustered together by region, suggesting similar regional trends in survival (Zimmerman et al. 2015). However, across all regions, wild marine survival was higher than hatchery Coho survival, with minimums and maximums as much as double that of their hatchery counterparts. Origin (hatchery or wild) was statistically significant in analytical models of factors contributing to marine survival. The models predicted similar trends for hatchery and wild Coho, but at different magnitudes (Zimmerman et al. 2015). A recent study by Irvine et al. (2021) suggests that Strait of Georgia hatchery Coho marine survival estimates may be biased low because they are coded-wire tagged months before release and could experience some freshwater mortality prior to release, whereas wild Coho are tagged during their seaward migration. However, that bias is likely not enough to explain the published differences in marine survival of hatchery and wild salmon (Irvine et al. in review).

25. https://pugetsoundlcm.shinyapps.io/Steelhead/ - Model created by Joseph Anderson and Phil Sandstrom, Washington Department of Fish and Wildlife, for Puget Sound steelhead recovery planning. An average of open ocean survival over a 35-year period was used to isolate the effects of early marine mortality. Open ocean survival was estimated using Washington and Oregon coastal steelhead populations where smolt-to-adult survival and downriver survival data were both present (Romer et al. 2013 and Johnson et al. 2010). Downriver survival was deducted from smolt-to-adult survival, leaving estimates of open ocean survival (20.7%). See Appendix 3 of the Puget Sound Steelhead Recovery Plan, https://www.fisheries.noaa.gov/resource/document/esa-recovery-plan-puget-sound-steelhead-distinct-population-segment-oncorhynchus.

Models of steelhead marine survival patterns did not support separating hatchery and wild populations, suggesting no significant difference in trends or magnitude (Kendall et al. 2017). However, this may be due to the limited amount of wild steelhead marine survival data available. In a study of Puget Sound steelhead early marine mortality, wild steelhead smolts survived the early marine period better than hatchery steelhead; however, the difference between hatchery and wild early marine survival rates varied greatly based upon hatchery program, region, and other factors (Moore et al. 2015). No differences were found between wild and hatchery early marine survival in a similar study of steelhead in the Strait of Georgia (Welch et al. 2011).

A broad comparison of hatchery and wild Chinook survival trends was not pursued due to limited availability of wild Chinook marine survival data. However, a study on segment-specific survival of Cowichan River Chinook suggests that, although hatchery and wild Chinook survival rates do not differ during early marine residency through their first summer at sea, hatchery Chinook have 60% lower survival after their first summer in the southern Strait of Georgia to the time they return as adults (Pellet pers. comm.).[26]

The Synthesis Committee considered the potential impacts of hatchery practices on hatchery and wild marine survival in the sections pertaining to outmigration timing and competition.

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[26] Losee et al. (2019) recently reported an increasing trend in smolt survival for Puget Sound hatchery Chinook salmon. While this work assesses a long period (1970-2015) for hatchery and naturally produced Chinook salmon, the analyses do not account for changes in ocean fisheries. The resulting survival estimates are not comparable to survival rates estimated from coded-wire tag data used in the SSMSP assessments. Therefore, Losee et al.'s (2019) survival analyses are not included here.

WHAT WE KNOW ABOUT FACTORS AFFECTING MARINE SURVIVAL: FINDINGS, NEXT STEPS IN RESEARCH, AND MANAGEMENT IMPLICATIONS

The following summarizes what we know about the factors affecting the survival of Chinook, Coho, and steelhead in the Salish Sea marine environment. These factors are listed in Table 2 and their level of impact ranked by the Synthesis Committee in Table 3. This is not an exhaustive review. Rather, it focuses primarily on illustrating the findings of the work implemented via the SSMSP as well as other recent work supporting or refuting the hypotheses that served as the basis for the Project. Descriptions of recommended next steps in research and potential management actions/implications for consideration are also included.

1. Salmon Behaviour and Physical Habitat

Changes to outmigration timing and interrelationships with other factors

Outmigration timing of Chinook, Coho, and steelhead may have changed; if so, it could influence the magnitude of predation, competition, or result in a timing mismatch between the presence of juvenile salmon and their prey. Outmigration timing may be influenced by hatchery practices and/or reduced diversity in salmon populations. The key predictions associated with this hypothesis were: a) outmigration timing of Chinook, Coho and steelhead has contracted or the peak outmigration time has shifted, and b) changes in outmigration timing correlate with changes in marine survival. Hypotheses that address how changes in outmigration timing in concert with environmental changes could contribute to changes in marine survival — mismatch, competition, pulse prey abundance — are addressed in subsequent sections.

Most Chinook are currently released from hatcheries into the Salish Sea around the third week of May; the variability of release dates has declined significantly since the 1970s (Figure 7; Nelson et al. 2019a). Synchronized, short-duration hatchery releases differ substantially from wild Chinook which typically exhibit prolonged, bi-modal downstream migration periods with peaks for fry in February-March and for parr in May-June (Nelson et al. 2019a), though it is understood that smaller Chinook generally rear in estuaries to achieve a minimum size of ~70mm before emigrating to the marine area (Healey 1978, 1980, Levings 2016). This shift in hatchery release practices in Puget Sound was driven by adaptive management efforts to maximize survival rates and minimize ecological interactions with wild Chinook by releasing hatchery fish when they undergo smoltification and are prepared to rapidly out-migrate (see Critical Period section).

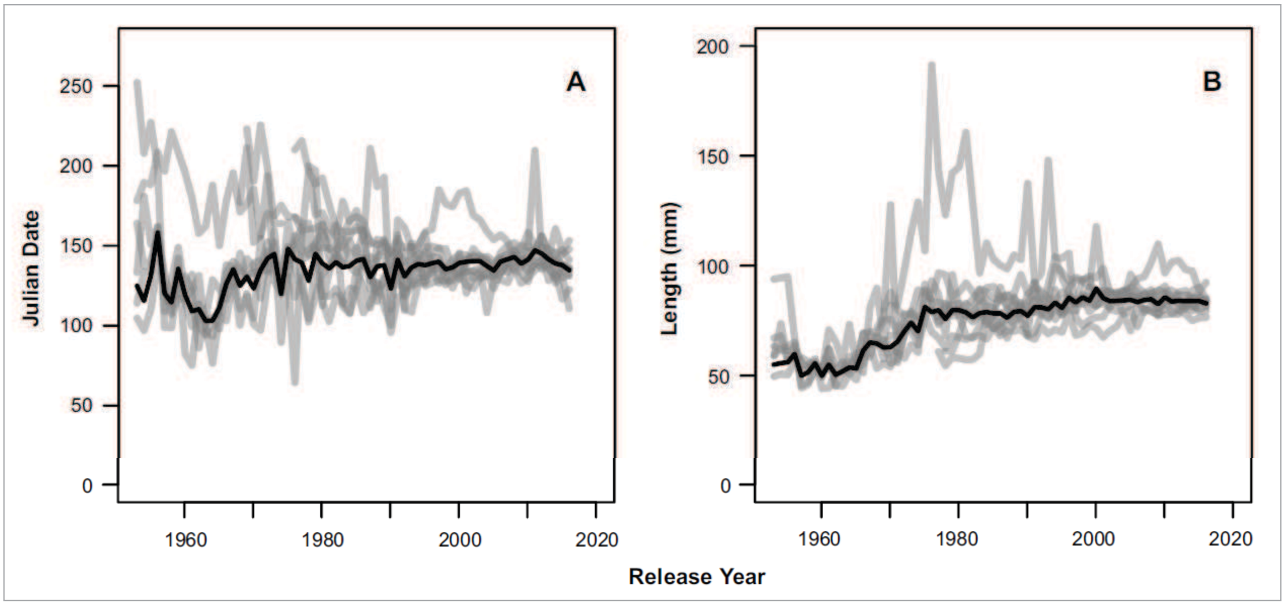


Figure 7. *Annual mean and standard deviation of release date and release size (length) for hatchery Chinook in the Salish Sea from 1950 to 2016. Panels display annual mean release date (A) and size (B) for the entire Salish Sea (black lines), and for individual sub-regions (gray lines) (Adapted from Nelson et al. 2019a).*

Coho hatchery release timing has also become less variable in the Strait of Georgia since the 1970s; however, changes in survival do not appear to be related to release timing (Irvine et al. 2013). Overall, ocean entry year had a much greater impact, with survival declining significantly since the 1980s (Irvine et al. 2013, Zimmerman et al. 2015). However, changes in the variability and mean timing of Puget Sound Chinook and Coho release dates were included in best models for explaining Puget Sound Chinook, Coho, and steelhead marine survival trends (Sobocinski et al. 2020, Sobocinski et al. 2021). Further, South Thompson Chinook, which enter the Strait of Georgia later than most other Fraser Chinook, appear to have had higher survival over the period of marine survival declines (Beamish pers. comm.).

Synthesis Committee Perspective

The Synthesis Committee concluded that there has been a reduction in the variability of hatchery release dates and thus a contraction in outmigration timing of hatchery Chinook. Ecosystem indicators models suggest this timing change, in concert with environmental changes, could be contributing to declines in marine survival. However, the mechanisms are not clear. There is no evidence for changes to wild Chinook, Coho, or steelhead outmigration timing.

Interrelationships with other factors

Changes to the outmigration timing of Chinook, Coho, and steelhead could result in a mismatch between the presence of juvenile salmon and their prey, influence the magnitude of predation, increase competition, or exacerbate density-dependent processes such as changes in movement or distribution. These are discussed in the food supply and predation sections that follow.

Management implications and next steps

Hatcheries provide opportunity for testing whether differences in outmigration timing affect marine survival relative to environmental changes. Chinook and Coho hatchery release timing experiments are now underway at 10 different hatcheries throughout the Salish Sea. In the Strait of Georgia, Coho studies indicate survival of a late June release in 2014-2016 was two to three times greater than that of the standard early/mid-May release for rivers on East Coast Vancouver Island, but not for Fraser systems (Willis pers. comm.). Recent data from Chinook release studies in 2014-2016 on the East Coast of Vancouver Island suggest higher survival from late June/early July releases as compared to the traditional early/mid-May releases; however, the studies have not been replicated in the Fraser (Willis pers. comm.). In Puget Sound, these programs have just begun and are testing release strategies ranging from early (March) to late (October). We recommend continued support for these studies and continued research to determine whether release timing changes improve access to prey, impact predation rates, or reduce competition or other density-dependent processes. Further, increasing the quality and amount of freshwater and estuary habitat could improve fry survival (Campbell and Claiborne 2017) and support greater life history diversity and variability in outmigration timing for wild and hatchery Chinook.

Distribution, Migration Pathways, and Residency

The main hypothesis associated with distribution was that Coho and Chinook rearing locations within the Salish Sea affect marine survival outcomes. The key predictions associated with this hypothesis were that a) populations of Chinook and Coho rear in distinct locations in the Salish Sea, and b) marine survival or growth are related to rearing location. Regarding residency, the key hypothesis was that resident-type behaviour and duration of residence influence marine survival in the Salish Sea.

Trawl surveys within the Strait of Georgia since 1997 (Beamish 2007) indicate that there are often similar abundances of juvenile Chinook in the Strait of Georgia in the early summer and fall (Figure 8). However, DNA analysis indicates that stock composition within the Strait of Georgia changes over the summer. Stocks present in June catches remain present in September, but South Thompson Chinook dominate September catches (50-70%), perhaps because they enter the Strait later (July-August). Neville and Beamish (pers. comm.) suggest that reduction in number of the early ocean entry Chinook stocks between summer and fall is a combination of mortality and migration out of the Strait of Georgia; Pellett (pers. comm.) suggests that migration within the region resulting in lower catchability by the trawl survey could also play a role. Earlier results from an acoustic tagging study and surveys capturing low numbers of these stocks on the west coast in the summer and fall suggested that mortality during the early marine period in the Strait of Georgia was the primary factor (Neville et al. 2015); however, acoustic telemetry of Cowichan Chinook found that partial migration occurred, and that many of the Cowichan Chinook surviving to return as adults remained resident in the Strait of Georgia over the winter (Kintama Research Services Ltd. 2019). Additionally, if early ocean entry stocks migrate northwards towards Queen Charlotte Sound, they would not necessarily be caught in any of the DFO trawl surveys, either in the Strait or on the West Coast.

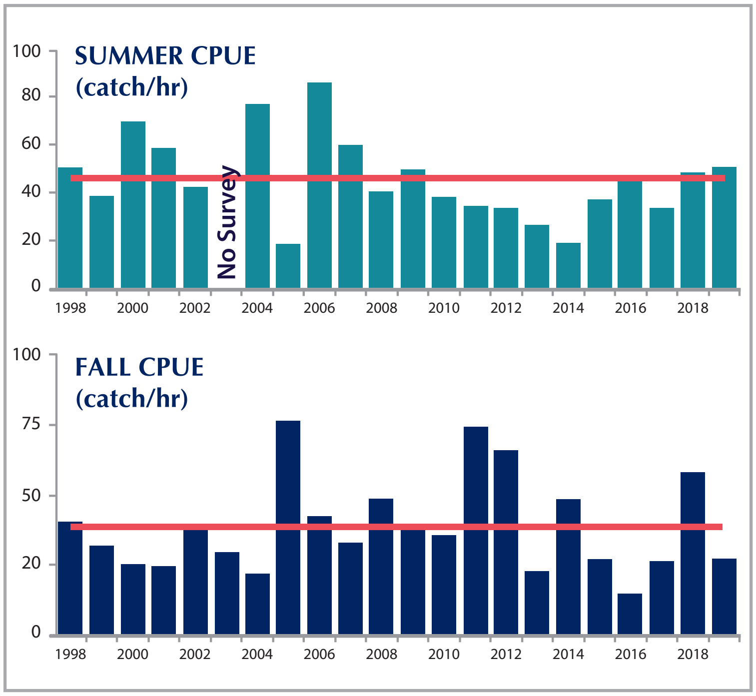


Figure 8. *CPUE (catch per hour) of juvenile Chinook salmon captured in trawl surveys 1998-2017. Top panel shows summer CPUE; bottom panel shows fall CPUE. (Source: C. Neville, DFO)*

??. Footnote

Stock-specific cohesion in juvenile distribution has been observed in Strait of Georgia (Figure 9). About 70-80% of Chinook salmon are captured near their natal streams. Hatchery Chinook from Big Qualicum River and Puntledge River are caught along the east coast of Vancouver Island, Cowichan River fish are caught in Gulf Islands and fish from the South Thompson are primarily caught in Howe Sound. In September, the distribution of Chinook remains consistent with that seen in July, although there are now far more South Thompson fish in the Strait of Georgia (Figure 9). Distributions of Puget Sound Chinook in Puget Sound appeared to show similar behaviour, with stocks primarily rearing in basins near their natal streams through August (Rice et al. 2011).

Surprisingly low numbers of Harrison/Chilliwack Chinook salmon were captured in the Canadian survey area. This stock is the dominant Fraser Chinook stock and historically one of the most productive Fraser River populations. It would normally be expected to represent about 40% of the Chinook captured; however, it represented only about 5% of the catch during trawl surveys for the SSMSP. Associated US surveys indicate these Chinook rear around the San Juan Islands and in Puget Sound.

When comparing stock-specific distributions to an analysis of historical Salish Sea Chinook marine survival data: Big Qualicum, Puntledge, Chilliwack, and Harrison populations clustered together with similar marine survival trends to other Salish Sea populations, whereas Nicola and Lower Shuswap populations (tributaries of the Thompson River) and the Cowichan population did not cluster with the Salish Sea populations (Ruff et al. 2017). **This suggests that locations where Chinook rear in the Strait of Georgia could influence their overall marine survival.**

One acoustic telemetry study provided evidence that some juvenile Cowichan Chinook show residency behaviour: tagged Cowichan Chinook moved from the southern Gulf Islands in fall and resided in the Strait of Juan de Fuca and/or greater Salish Sea over winter. Some fish appeared to reside in the southern Gulf Islands at least into the spring of their second ocean year (until tag batteries died; Kintama Research Services Ltd. 2019). These fish were also tagged with PIT tags and thus far one jack and two adults have returned to the Cowichan River. Interestingly, these three fish were detected in the Salish Sea in their second ocean year; none of the non-detected fish or those that were assumed to have emigrated from the Strait of Georgia survived to return as adults, again suggesting that different rearing areas may influence survival.

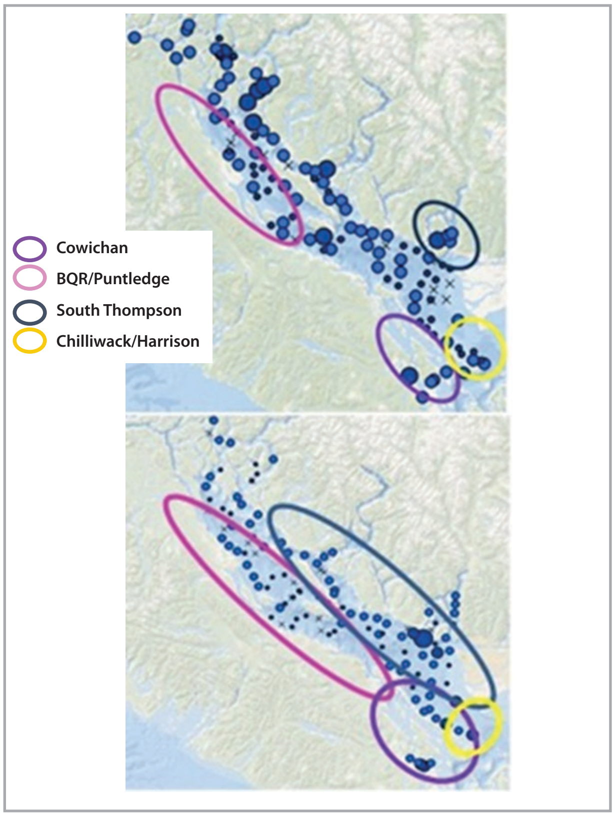


***Figure 9.** Catch distributions of juvenile Chinook salmon in trawl surveys 1998-2017. Top panel shows summer catches and bottom panel shows fall catches. (Source: Chrys Neville, DFO).*

Puget Sound Chinook resident behaviour was also assessed. Up to 30% of hatchery-origin Chinook spend most of their lives in Puget Sound instead of migrating to the Pacific Ocean (Chamberlin et al. 2011, O'Neill and West 2009). An analysis of the relationship between survival and residency of 32 Puget Sound and Strait of Georgia stocks revealed some stock-specific patterns but did not suggest a cohesive, regional pattern or relationship between the two metrics (Chamberlin et al. 2020). In resident recoveries[27] from all regions in the Salish Sea, half the stocks showed a weakly positive and the other half a weakly negative relationship between survival and residency. There was no regional pattern for the direction of the relationship. Of the four stocks that had statistically significant relationships, three of them (all originating from Canada) were driven by a few highly influential data points and thus the relationships were determined to be inconclusive. The remaining stock with a significant relationship was Squaxin Pass, a South Puget Sound stock, which showed a relatively strong negative relationship suggesting decreased marine survival when a higher proportion of the stock remained resident (Chamberlin et al. 2020).

[27] Resident recoveries = coded-wire tagged Chinook salmon recovered in the Salish Sea in November-April of each year, when only resident fish are expected to be in Salish Sea waters (Chamberlin et al. 2020).

Unlike Strait of Georgia Chinook, Coho stocks are widely distributed and mixed throughout the Strait of Georgia (Neville and Beamish pers. comm.). This may explain why their marine survival patterns are more synchronous than Chinook.

The CPUE of juvenile Coho salmon in September trawl surveys in the Strait of Georgia has increased since 2009 (Figure 10). The size and condition of the juveniles has improved, and residency behaviour of Coho salmon in the Strait has changed (Neville and Beamish 2018). Coho salmon smolts enter the marine environment in April-May and rear within the Strait of Georgia until October or November (Chittenden et al. 2009, Beamish et al. 2010). Historically, Coho salmon originating from rivers flowing into the Strait of Georgia were caught within the Strait and off the southwest portion of Vancouver Island. Prior to 1994, the proportion captured within the Strait or outside of the Strait varied among years. When catches were greater outside the Strait of Georgia, the year was classified as an "outside year" versus "inside years" when the catches were greater within the Strait (Beamish et al. 1999). From the mid-1970s through to the early 1990s, there was no trend in inside or outside catches.

Beginning in 1995, virtually all juvenile Coho salmon left the Strait of Georgia late in their first ocean year and did not return until their spawning migration later in their second ocean year (Beamish et al. 1999), though it is also possible that the loss of Coho within the Strait may have been the result of mortality rather than migration. This behavioural change was also coincident with the decline in marine survival from about 10-25% in the late 1970s to about 1% in the 1990s (Beamish et al. 2010, Zimmerman et al. 2015). Neville and Beamish (2018) suggest this outmigration behaviour continued until 2013.

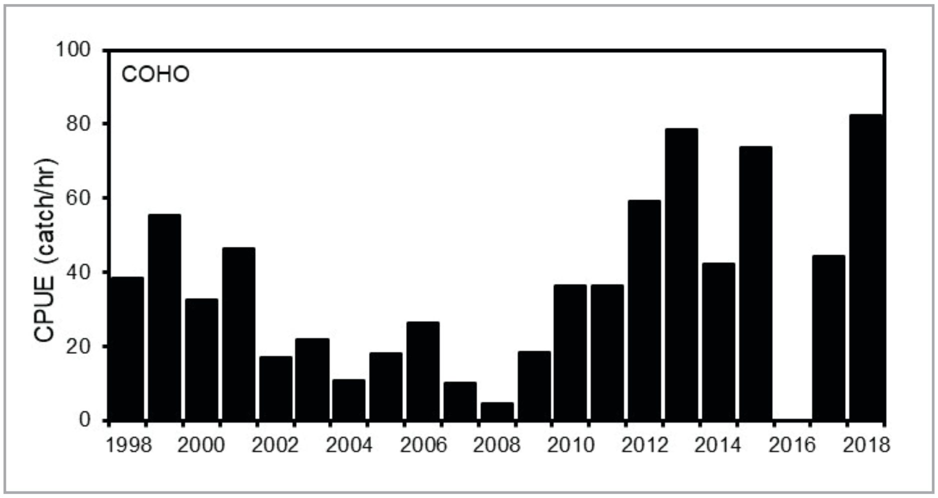


__Figure 10.__ CPUE for juvenile Coho salmon in the Strait of Georgia in September. (Source: C. Neville, DFO)

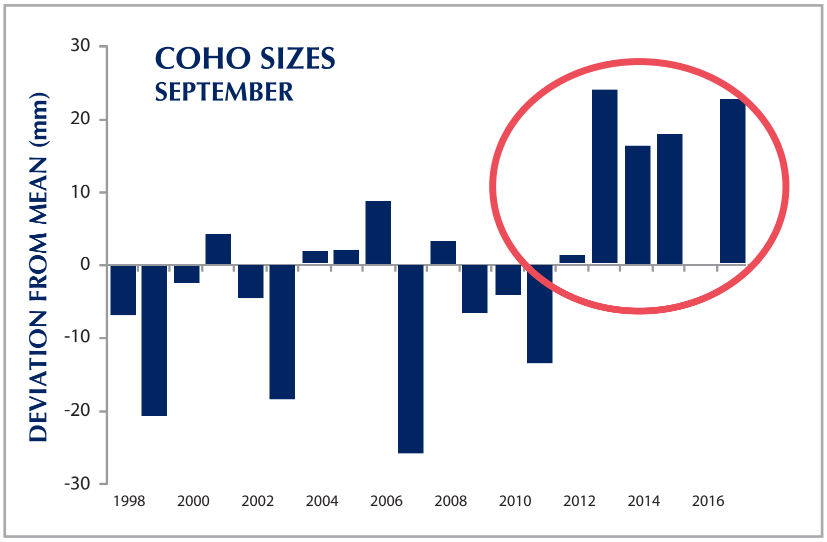


Figure 11. *Deviation from mean length of Coho juveniles in the Strait of Georgia in September. Positive deviations from the mean indicate larger fish. Juveniles have been generally larger since 2013. (Source: C. Neville, DFO)*

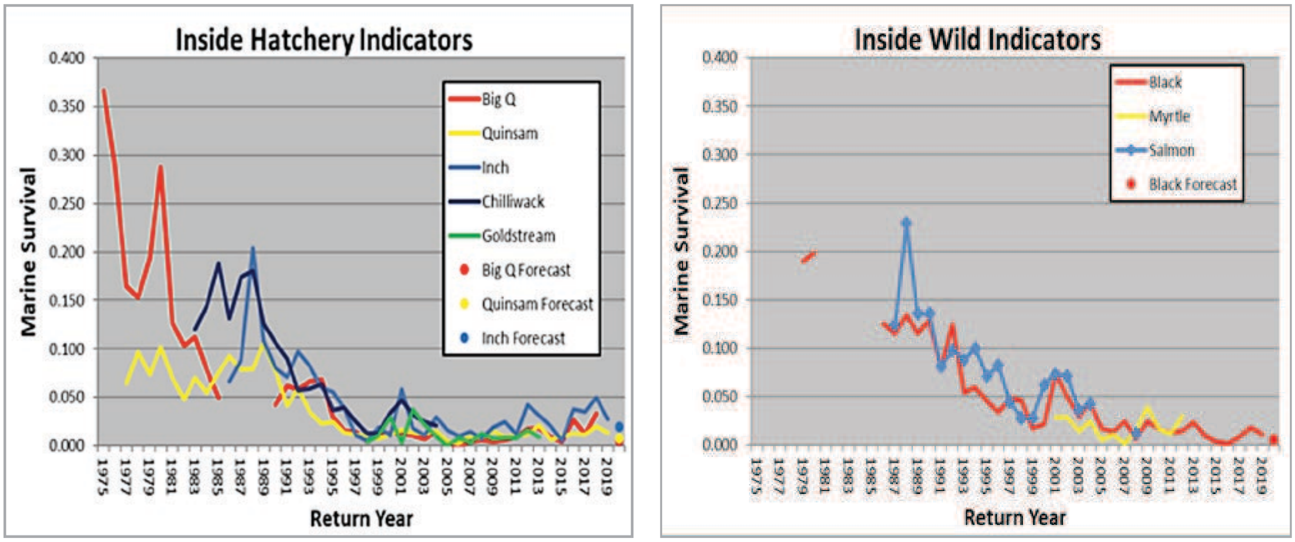


Figure 12. *Marine survival rates of hatchery and wild Coho salmon indicator populations entering the Strait of Georgia (Source: K. Pellett, DFO).*

Beginning in about 2013, based on recreational fishermen reports, Strait of Georgia creel survey data, and CWT data, Coho salmon were present in the Strait of Georgia in the late spring when the recreational fishery opened. This was attributed to to Coho overwintering in the Strait or returning to the Strait in the late winter. Since 2013, Coho juveniles have been larger in September of their first ocean year (Figure 11). In 2017 and 2018, Coho salmon remained in the Strait of Georgia over the winter. Neville and Beamish (2018) suggest this was the first time in over 20 years that there was an abundance of Coho salmon in the Strait of Georgia in the winter. A relationship between this potential increase in Coho residency in the Strait of Georgia and marine survival has not been formally investigated; however, a brief look at marine survival rates for Strait of Georgia hatchery and wild indicator stocks shows no significant change in marine survival (Figure 12, Pellett pers. comm.).

Results of acoustic telemetry studies have shown that steelhead migrate quickly out of both the Strait of Georgia and Puget Sound, suggesting residency does not play a substantial role in mortality (Welch et al. 2011, Moore et al. 2015). However, those steelhead that must travel longer distances from river mouth through Puget Sound experience higher early marine mortality rates (Moore et al. 2015, Moore and Berejikian 2017, Connor et al. as reported in Puget Sound Steelhead Marine Survival Workgroup 2015). Further, the migration route chosen can affect steelhead survival. Furey et al. (2015) found that juvenile steelhead were twice as likely to survive their journey out of the Strait of Georgia via Malaspina Strait on the eastern side of Texada Island as compared to travelling up the Strait of Georgia on the western side. Healy et al. (2017) determined route-specific survival in the Discovery Islands region, as fish exited the Strait of Georgia via various routes to Johnstone Strait. They found that most smolts (~77%) used the westernmost route (Discovery Passage), and those smolts had twice the survival to Johnstone Strait than smolts migrating through Sutil Channel. These differences in survival could be the result of variable impacts of predators along different migration routes.

Interrelationships with other factors

Changes to residency and distribution may be associated with prey availability. If more prey are available in the Salish Sea, fish may reside there longer. Salmon that reside longer in the Salish Sea could also be more susceptible to pinniped predation or impacts from contaminants and disease. Rohde et al. (2014) reported smaller size at maturity for Puget Sound Coho residents, suggesting that there may be tradeoffs to this life history strategy. No clear, consistent relationship has been found between residency and marine survival across populations where data are available.

Management implications and next steps including Synthesis Committee perspective

Given the uncertainties regarding the impacts of residency and distribution, there are no recommendations for specific management actions. The Synthesis Committee instead recommends year-round, seasonal evaluation of behaviour, stock-specific distribution, and growth rates of Chinook (and possibly Coho) via scale, otolith, stable isotope, and genetic analyses.

Physical and Biogenic Habitat

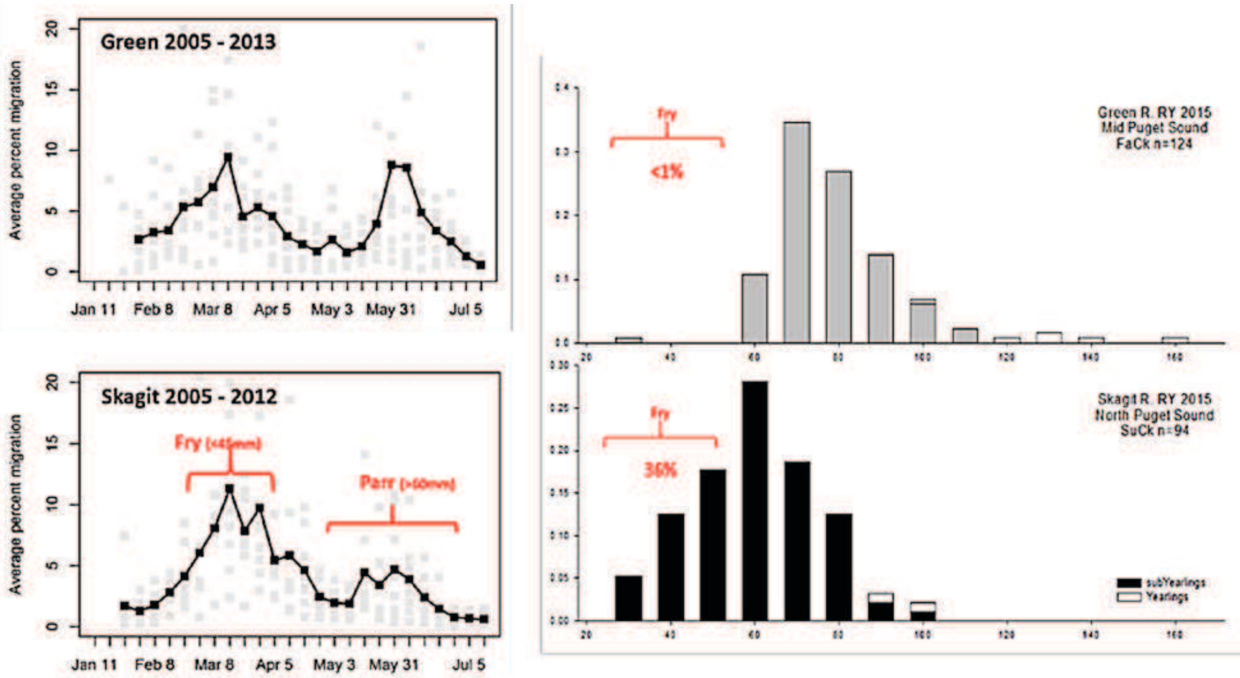
Estuaries and nearshore vegetation like eelgrass meadows and tracts of bull kelp are some of the most productive and sensitive marine habitats, and they provide shelter and food to numerous species including Pacific salmon and forage fish such as sand lance and herring (Fresh 2006, Leaman 1980, Duggins 1988, Simenstad et al. 1982, Healey 1982, Macdonald et al. 1988, Thorpe 1994). The SSMSP hypothesis related to critical habitat is that reduced habitat availability has affected the behaviour and reduced the diversity of juvenile salmon while in the Salish Sea. The main predictions associated with this hypothesis were a) the amount of estuary and nearshore habitat has declined and b) reductions of estuary, eelgrass, and/or kelp habitat in specific sub-basins correlates with lower survival or reduced growth.

There were no analyses done during SSMSP to determine an overall relationship between basin-scale marine survival and degree of loss or degradation of nearshore or estuarine habitats. However, numerous studies were carried out in Canada during SSMSP to assess the use of kelp, eelgrass, and other estuarine habitats by juvenile salmon, the importance of intact estuarine habitat for juvenile Chinook life history diversity, and the environmental factors most important for re-establishment and restoration of these important habitats (SeaChange pers. comm., Iacarella et al. 2018, Schroeder et al. 2020, Campbell and Claiborne 2017, Nahirnick et al. 2020, Chalifour et al. 2019, Chalifour et al. 2020). There is also a wealth of information from non-SSMSP studies that are ongoing in Puget Sound, including Washington Department of Fish and Wildlife (WDFW)'s Estuary and Salmon Restoration Program.

In the Cowichan River, SSMSP studies confirmed the importance of the estuary, especially to smaller fry as compared to stream-rearing Chinook that left the river later and at a larger size (Craig 2015, Campbell and Claiborne 2017, Chittenden et al. 2018). Similarly, Chalifour et al. (2019) found high residency and dependence on estuarine habitats, particularly brackish marsh channels, for growth by small yearling Harrison Chinook in the Fraser estuary. They also found that Pacific herring (Clupea pallasii) and surf smelt (Hypomesus pretiosus) utilized eelgrass as their primary habitat type. Chalifour et al. (2019) emphasized the importance of interconnected estuarine habitats in the Fraser estuary across Roberts and Sturgeon banks, finding that, while eelgrass habitats housed the highest total abundance and diversity of fish, many species also depended on the interconnected salt flats and brackish marsh habitats. Harrison Chinook spent an average of 42 days in the estuary, with a gradual ontogenetic shift from the brackish marsh to more saline habitats and similar daily growth rates to yearling Chinook in non-Salish Sea estuaries (Chalifour et al. 2020, 2021).

Other studies highlighted the value of eelgrass in providing nearshore foraging opportunities for juvenile salmon: eelgrass-associated prey species, particularly harpacticoid copepods, made up a large portion of prey species for juvenile Chum (93%) and Chinook (83%) salmon (Kennedy et al. 2018). Additionally, stable isotope analysis for juvenile Chum salmon showed that approximately 80% of their diets consisted of eelgrass-associated invertebrates (Kennedy et al. 2018).

Campbell and Claiborne (2017) found that small juvenile Chinook migrating out of North Puget Sound rivers (Nooksack and Skagit) and from the Cowichan River early in the season have a much greater chance of surviving to return as adults when compared to populations from Central and South Puget Sound rivers (Cedar, Green, Puyallup), and suggested that survival differentials are related to the health and quality of estuary habitats (Figure 13). Craig (2015) noted that estuary-reared fry could be an important component of annual Chinook production, particularly during low flow years when river-reared smolts experience high mortality, suggesting that the presence of an intact estuary would allow for a greater diversity of rearing strategies. Pellett (pers. comm.) noted that estuary-reared smolts were more likely to return at age-2 (jacks) than the river-reared smolts, which may be a result of faster growth for juveniles with earlier entry to marine habitats. Evidence from long-term monitoring in four estuaries in Puget Sound supports the idea that rearing habitat in these systems is limiting for portions of the outmigration, which could result in density-dependent changes to growth, outmigration size, timing, and early mortality (Greene et al. 2020).



Lance Campbell (Washington Department of Fish and Wildlife), unpublished 2016.
Juvenile Chinook salmon migration timing data courtesy of WDFW Wild Salmon Evaluation Unit

Figure 13. *Chinook smolts leave both the Green and Skagit Rivers early as small fry and later as larger parr. However, returning adults to the urbanized, developed Green River are only derived from those smolts that left as larger parr. The fry component did not appear to survive. Similar results were apparent in a number of other degraded estuaries. (Source: L. Campbell, WDFW)*

The amount of estuary and nearshore habitat has declined

Globally, seagrass ecosystems are declining in area by about 7% per year due to anthropogenic stresses, including decreased water quality and increased water temperatures (Cullen-Unsworth and Unsworth 2013). These habitats are threatened by human activities and have been documented as decreasing throughout many areas of the Strait of Georgia (SeaChange Marine Conservation Society pers. comm.). Despite their high growth and reproductive capacity, bull kelp populations also have been in steady decline within central Strait of Georgia (northern Salish Sea), including Lambert Channel and Baynes Sound (Lamb et al. 2011). Throughout Puget Sound, the extent and density of bull kelp forests have declined (Calloway et al. 2020): one study of South Puget Sound suggests a decline of 62% since the 1870s, with particularly high losses in the central and western areas of the basin (Berry et al. 2020). Since eelgrass monitoring began in Puget Sound in 2000, the total area occupied by eelgrass has remained relatively stable; however, site-level research has indicated that declines have been more frequent than increases (Gaeckle et al. 2009). Shelton et al. (2017) noted a lack of geographic coherence in these losses, concluding that local drivers rather than large-scale climatic drivers were likely most important in determining eelgrass persistence. Factors that may have had an influence on the disappearance of bull kelp and eelgrass beds include coastal development, rising ocean temperatures, local changes in oceanographic conditions (e.g., salinity, increased turbidity, and sedimentation), intensified herbivore grazing, or a combination of these (Steneck et al. 2002).

During SSMSP, Heath (pers. comm.) identified reductions or loss of kelp beds in many regions of the Strait of Georgia, particularly in the northern and central Salish Sea, while other beds appear to persist, e.g., in Sansum Narrows, Dodds Narrows, Mayne Island, Saratoga Beach, and Burrard Inlet side of Stanley Park. Satellite imagery techniques showed that areas of kelp around Cowichan Bay have not varied greatly since 2004 (Schroeder et al. 2020). Grazing by sea urchins and rising ocean temperatures are thought to be a major contributor to kelp declines. Schiltroth (2021) found that bull kelp spore density and germination is reduced at sites with sea surface temperatures over 17°C. Studies are currently underway at the University of Victoria to fully assess the changes in kelp coverage over the past 30 years throughout the entire Strait of Georgia.

Nahirnick et al. (2018) found increasing fragmentation and an average loss of 41% in eelgrass beds at three sites in the southern Gulf islands between 1932-2016, which were associated with shoreline activities (boats, docks, log booms, and armouring) and increased housing density. Similarly, Iacarella et al. (2018) found evidence for decreased species richness and increasing simplicity of eelgrass fish communities in highly disturbed regions (e.g., sites within Fraser Estuary, Comox Estuary, southern Vancouver Island).

Although nearshore habitats may be present, there is increasing evidence of degradation in many areas. The Fraser River estuary, the largest delta in the Salish Sea, has been heavily impacted by historic and ongoing urban, agricultural, and industrial development (Kehoe et al. 2020). Continued log-booming activities in the northwestern part of Cowichan Bay and the Cowichan River estuary (as well as many other Salish Sea estuaries) have altered the substrate; the constant shedding from logs and lack of sunlight make the substrate inhospitable to eelgrass and the many organisms that live in eelgrass ecosystems including harpacticoid copepods, a favoured prey of Chinook salmon smolts (Chittenden et al. 2018). Decomposing bark and wood on the bottom of the ocean also release toxins, such as log leachates, which are lethal to fish.

Synthesis Committee Perspective

The Synthesis Committee could not reach consensus regarding the relative importance of physical or biogenic habitat in the decline of marine survival of salmonids in the Salish Sea. However, degraded habitat is likely limiting the survival of salmon populations and impacting life history diversity for wild subyearling Chinook. Further, there are linkages between habitat degradation and impacts to salmon prey, such as herring and larval crab, which could be contributing to broader survival declines. While data are insufficient to draw any conclusions regarding changes over the period of marine survival declines, it is tenable that cumulative losses/changes in habitat contributed to loss of life history diversity and survival.

Interrelationships with other factors

As spawning adult numbers decrease, density dependence of juveniles rearing in freshwater environments would also be expected to decrease (Zimmerman et al. 2015, Hall et al. 2018), potentially reducing estuarine and nearshore habitat use by early life history types of Chinook and Coho salmon rearing there because of density-dependent migration

(Reimers 1970, Greene and Beechie 2004). Hence, the impact of habitat losses in estuary and nearshore environments on juvenile life history stages may be masked by reduced adult spawners in many rivers. Conversely, if adult returns begin to increase, then habitat loss and degradation in estuaries and the nearshore may become limiting factors to the successful restoration of salmon.

Eelgrass and kelp also provide refuge, spawning habitat, and foraging resources for forage fish, including herring, linking this hypothesis with other hypotheses addressing bottom-up relationships with food availability and top-down effects of alternative prey. Shaffer et al. (2020) has shown that kelp habitat contains more structure-associated zooplankton taxa than open water habitats, suggesting a possible preference due to greater resource availability. Harpacticoid copepods, an important and common prey item for juvenile salmon, comprised most of the taxa found in kelp (Shaffer et al. 2020). Further, Shaffer et al. (2020) posit that detection of juvenile Pacific herring by juvenile salmon may be another benefit of kelp forests: the visual contrast between the color of Pacific herring against the dark backdrop of the kelp provides greater opportunities for juvenile salmon to corner, capture, and consume herring. Although initially driven to kelp for prey availability and shelter due to its structure and complexity, Pacific herring shoals may also be disrupted in kelp forests, possibly providing increased opportunities for foraging by juvenile salmon (Shaffer et al. 2020).

In addition to providing prey resources for juvenile salmon and forage fish, eelgrass beds and kelp forests likely provide additional support as refuge from predation and likely function as a migratory corridor throughout the outmigration period (Shaffer et al. 2020), suggesting another link to the top-down hypotheses regarding predation risk for both juvenile and adult salmonids.

Management implications and next steps

Estuarine and nearshore coastal habitats create a mosaic and linkage of habitats that support Pacific salmon. In general, research addressing the importance of habitat connectivity has been lacking (Flitcroft et al. 2019), though studies are beginning to emerge. SSMSP researchers such as Kennedy et al. (2018) emphasized the importance of nearshore ecosystems and their integrity in being able to support anadromous juvenile Pacific salmon through critical stages, supporting them in a variety of habitat types at various life stages. Similarly, Chalifour et al. (2019) support this notion and suggest that managing estuaries through a seascape lens, thus supporting the connectivity of various habitat types, will ultimately support greater biodiversity and productivity. Pacific salmon represented five of 102 species recently assessed for extinction risk in the Fraser River estuary, and a suite of management strategies to revitalize this important estuary and support salmon persistence was identified by Kehoe et al. (2020).

Anthropogenic stressors are negatively impacting these critical habitats and influencing the availability, integrity, and resilience of these ecosystems. Novel approaches are needed to manage them holistically to support Pacific salmon in our changing climate.

SSMSP researchers agreed upon a series of next steps for both research and restoration including the following:

1. Estuary and shoreline rehabilitation and protection in the Salish Sea is deemed highly critical.
2. Removal of marine debris from major estuaries is required for successful restoration. Eliminating log booming in estuaries and shallow marine environments and restoring eelgrass beds would improve salmon habitat quality in the Salish Sea.
3. Signage providing boater information (e.g., with the Navionics app) would reduce anchorage damage to eelgrass and kelp.
4. Studies are required to determine effective strategies to mitigate high levels of contaminants, including hydrogen sulfide, in estuarine sediments otherwise suitable for eelgrass productivity.
5. Research is needed to find possible genetic strains of eelgrass resistant to wasting disease (*Labyrinthula zosterae*), a mold disease related to increased sea surface temperatures.
6. Research is needed to fully map the extent and state of eelgrass and kelp throughout the entire Salish Sea and to determine spatiotemporal changes across human-impacted areas and remote regions.
7. Studies using sea urchin exclusion pens have been suggested to assess whether pens protect and increase success of local kelp restoration initiatives. Other suggestions for successful restoration of kelp include use of locally identified resilient kelp stocks, i.e., those that have persisted over time and display thermo-tolerant characteristics, as well as trials to pre-adapt spores/gametophytes to stressful conditions.

2. Food Supply

Prey availability

The overarching hypothesis states that variation in food supply is linked to juvenile salmon growth and survival. The main prediction associated with this hypothesis is that the timing, duration, quantity, spatial extent, and/or composition/quality of prey influence juvenile salmon growth and survival.

The Beamish and Mahnken (2001) critical size hypothesis stimulated many investigations of the factors influencing diet and growth of juvenile Chinook during their first summer in the Salish Sea (e.g., Duffy et al. 2010, Ferriss et al. 2014, Hertz et al. 2015, Journey et al. 2018), including many carried out during SSMSP (Gamble 2016, Beauchamp et al. 2018, Chamberlin et al. 2017, Chittenden et al. 2018, Gamble et al. 2018, Davis et al. 2020, Chamberlin et al. 2020, Chamberlin et al. in review, Duguid et al. in review).

The diets of both Chinook and Coho salmon during their early marine residence in the Puget Sound are composed of euphausiids, crab larvae, hyperiid and gammarid amphipods, and large copepods, with an increasing proportion of small fish as they grow (Simenstad 1982, Daly et al. 2009, Duffy et al. 2010). Individuals in offshore (greater than 30 m bottom depth) habitats of Puget Sound consume more decapod larvae and fish (Duffy et al. 2010) and grow more rapidly (Gamble et al. 2018) than those in estuarine or nearshore habitats. Similarly, juvenile Chinook and Coho salmon in the Strait of Georgia feed upon larger zooplankton, such as euphausiids, amphipods, larval decapods, and larval and juvenile fish (Neville and Beamish 1999, Daly et al. 2010). In nearshore areas, terrestrial insects may also contribute significantly to juvenile salmon diets (Gamble 2016).

Changes in the quality and quantity of food available are likely to affect salmon diets and survival (Hertz et al. 2016). Daly et al. (2009, 2013) noted that Chinook consumed less food and had more empty stomachs during years of lower survival and that much of the variance in marine survival of Columbia River Chinook and Coho salmon was related to the biomass of ichthyoplankton off the coast of Oregon. In the California Current, zooplankton communities show interannual and multiyear shifts in species dominance that are tracked by survival of salmon populations (Keister et al. 2010). These zooplankton community changes correlate with the Pacific Decadal Oscillation (PDO) index: a 'warm-water' copepod species group is more abundant during warm (positive) phases of the PDO and less abundant during cold (negative) phases; the reverse occurs for a 'cold-water' species group.

Wells et al. (2012) found a positive relationship between the abundance of krill off the coast of California, the physical condition of Chinook salmon juveniles, and returns of Chinook jacks. Beauchamp and Duffy (2011) and Duffy and Beauchamp (2011) found that feeding rate of juvenile Chinook influenced growth more than prey energy content and that variability in growth, feeding, and survival can largely be accounted for by the variable contribution of larval crab to the energy budget of juvenile Chinook during the critical growth period during June- July, likely due to very high abundances of larval crab during that period in most years. On the other hand, bioenergetics modelling showed that juvenile salmon growth was more closely related to the energy density of available prey than to feeding rate off the west coast of B.C. (Trudel et al. 2002).

With respect to prey quality, diets rich in essential fatty acids (EFAs) are critical for the nutritional requirements of salmon, particularly during their juvenile life stages. Diets with low DHA or low DHA/EPA[28] ratios can lead to visual maldevelopment (Sargent et al. 1999), which is expected to impact foraging efficiency and growth, as well as predator avoidance. EFAs can be limiting in marine food webs because they are only synthesized by phytoplankton and therefore must be assimilated by zooplankton and benthic invertebrates to be transferred up the food chain (Fraser et al. 1989, Tocher et al. 1998, Ravet et al. 2010, Strandberg et al. 2015). Thus, environmental changes that impact phytoplankton could impact food quality higher up the food web (Fraser et al. 1989, St. John and Lund 1996, Rossi et al. 2006, Daly et al. 2010, Vargas et al. 2010). Salmon are rich in EFA and have high dietary fatty acid requirements, so they may be particularly sensitive to changes in diet quality (Sargent et al. 1999).

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[28] Eicosapentaenoic acid + docosahexaenoic acid.

Plankton communities in the northern Pacific Ocean have changed over the last fifty years in terms of species composition, as well as the number, size, timing, and duration of blooms; similar changes have been seen in the Strait of Georgia since the 1990s when plankton sampling efforts began (Bornhold 1996, Chiba et al. 2006, Batten and Mackas 2009, Mackas et al. 2013). Colder-water species of copepods have been declining in the southern part of their range, while warming waters are host to increasing numbers of jellyfish and crab larvae (Mackas et al. 2013). In the Strait of Georgia, a strong decline in the total zooplankton biomass occurred in the mid-2000s but since 2011, total zooplankton biomass has been near, or above, average levels (Perry et al. 2021). Historically, copepods were important prey for Strait of Georgia Chinook salmon (Barraclough 1966a, 1966b, Barraclough and Fulton 1967, Robinson et al. 1968a, 1968b). Both species composition and quality of copepods in the Salish Sea may have changed over time (El-Sabaawi et al. 2009, Perry et al. 2021).

No long time series for zooplankton exist in Puget Sound apart from qualitative data collected between 1974 and 1994 at Cherry Point and Squaxin (Kemp and Keister 2014) which found increases in gelatinous organisms (jellyfish, ctenophores, siphonophores) and concurrent declines in forage fish. This may indicate an altered food web structure and a transition towards a truncated food web, as described in the next paragraph (Pentilla 2007, Greene et al. 2015). Kemp and Keister (2014) also noted changes in other zooplankton taxa such as chaetognaths (decline), amphipods (decline), crab larvae (decline), and barnacle larvae (increase), all common prey items for several fish species in Puget Sound (e.g., Chinook salmon, Coho salmon, Chum salmon, and herring; Duffy et al. 2010, Kemp 2014).

Warming oceans polluted with nitrates and phosphates are supporting higher abundances of jellyfish and harmful algae (Brodeur et al. 2002, Landsberg 2002, Hallegraeff et al. 2003, Chittenden et al. 2018). In South and Central Puget Sound, Greene et al. (2015) found evidence of 3-9-fold increases in jellyfish-dominated surface trawls over the period from the 1970s to 2011. Similarly, Perry et al. (2021) identified recent increases in jellyfish in the Strait of Georgia. Increased populations of ctenophores and cnidarians may have a detrimental effect on young salmon through competition and predation on salmon prey: they feed on the same zooplankton as young salmon and deplete surface waters of food (Mackas et al. 2001, Brodeur et al. 2002, Rice et al. 2012). Jellyfish are typically generalist predators and can feed continuously without satiation, can reproduce sexually or asexually, and have short generation times (Purcell et al. 1999). Some jellyfish may prey directly upon fish eggs and larval or juvenile fishes (Lebour 1922, Purcell and Arai 2001, Pauly et al. 2009). For these reasons, as well as the fact that few predators can derive nutritional benefits by preying on them, jellyfish are often considered trophic "dead ends" (Purcell et al. 2007, Richardson et al. 2009).

Chittenden et al. (2018) noted that harpacticoid copepods were historically eaten by Chinook in nearshore areas (e.g., Healey 1980, Magnhagen et al. 2007); their sensitivity to pollution requires them to have healthy substrates and eelgrass to survive, both of which have been extensively damaged by humans during recent decades (Waycott et al. 2009). Water contaminants, log booming, and shoreline development destroy habitat for harpacticoid copepods, as well as for insects, small fish, and some gammarid amphipods, other preferred prey of Chinook smolts (Hetrick et al. 1998; Duffy et al. 2010).

Chinook salmon undergo ontogenetic diet shifts as they grow, consuming an increasing proportion of fish over zooplankton (Brodeur 1991, Keeley and Grant 2001, Schabetsberger et al. 2003, Hertz et al. 2015, 2016). This shift to piscivory may be crucial so that they can reach a critical body size to avoid predators and survive their first marine winter as postulated by Beamish and Mahnken (2001).

During SSMSP, several studies examined spatial and temporal changes in zooplankton assemblages, biomass, and abundance in the Salish Sea, and assessed the relationship between those changes and marine survival of Chinook and Coho (Keister et al. 2019, Keister and Herrmann 2019, Perry et al. 2021). Perry et al. (2021) found that in the Strait of Georgia, between 1996 and 2018, annual total zooplankton biomass was highest in the late 1990s, lowest in the mid-2000s, and near its climatological (1996-2010) average since 2011. Total zooplankton biomass was dominated by a few larger-sized taxa, such as euphausiids, large- and medium-sized calanoid copepods, and amphipods. All these groups had negative biomass anomalies in the mid-2000s, and most had recovered to their climatological (1996-2010) average by 2012. For example, large calanoid copepods made up 19% of the annual total zooplankton biomass between 1996 and 2006, but only 9% of the annual total zooplankton biomass from 2007 to 2018. In contrast, slightly over half (11 out of 20) of the zooplankton groups examined in this study had positive biomass anomalies after 2011 (e.g., hyperiid amphipods, meroplanktonic larvae of benthic animals, small calanoid copepods, ctenophores, non-calanoid copepods, crab larvae, and siphonophores).

Perry et al. (2021) also identified two trends among the 12 zooplankton groups that they studied (Figure 14). Several physical variables were significantly related to these two zooplankton trends including the Pacific Decadal Oscillation, sea surface salinity measured at Entrance Island in the central Strait of Georgia, and the (modelled) start date of the spring phytoplankton bloom in the central Strait of Georgia. The variability of both the zooplankton and physical variables clustered into two distinct time periods: 1996-2006 and 2007-2018, representing a period of declining zooplankton biomass anomalies followed by a period of increasing zooplankton biomass anomalies. The authors found that a small number of zooplankton and physical variables explained 38% to 85% of the annual variability in early marine survival rates of four Strait of Georgia salmon populations (Cowichan River Chinook (Figure 15), Puntledge River Chinook, Harrison River Chinook, and Big Qualicum Coho). Specifically, the inclusion of total zooplankton biomass in the relationship with Cowichan River Chinook, of medium-sized calanoid copepods in the relationship with Puntledge River Chinook, and of larval fish in the relationship with Harrison River Chinook resulted in strong predictive relationships with marine survival; these findings are consistent with known key prey items for Chinook salmon in these regions (Perry et al. 2021).

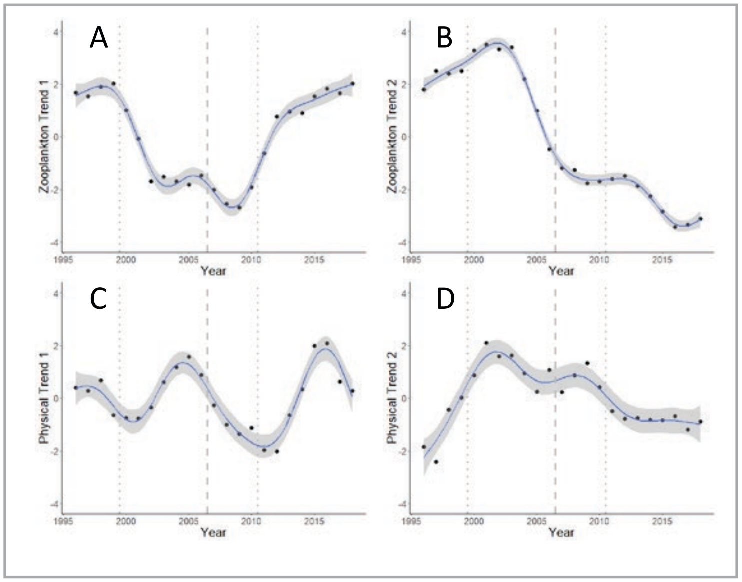

Figure 14. Underlying trends derived from 12 zooplankton taxonomic groups (top panels A, B) and 10 physical variables (bottom panels C, D) in the Strait of Georgia. Black dots and blue line and shading represent trends and their 95% confidence intervals derived for each year. Dashed and dotted lines separate groups of years which cluster together. Zooplankton trend 1 represents large- and medium-sized calanoid copepods; zooplankton trend 2 represents chaetognaths, fish larvae, and medusae. Physical trend 1 represents sea temperature and event timing (e.g., spring bloom, Fraser River peak flow); physical trend 2 represents sea surface salinity and vertical stratification. (Source: Perry et al. 2021).

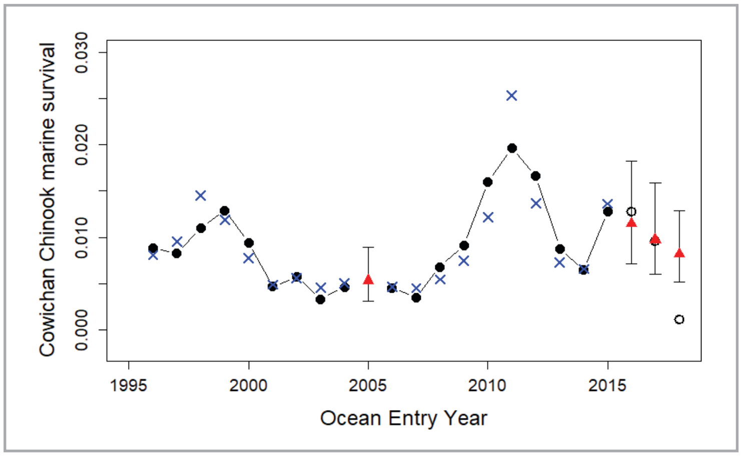

***Figure 15.** Early marine survival rates for the Cowichan River Chinook salmon stock compared with marine survival model estimates developed from biophysical variables. Black dots and line are the early marine survival data; open black circles are estimated survivals from incomplete returns. Blue crosses are the marine survival rates estimated from a regression model with sea surface salinity, sea surface temperature, and total zooplankton biomass in the Strait of Georgia; red triangles and vertical lines are predicted marine survival estimates and their 95% confidence intervals using the model for incomplete Chinook survival estimates. (Source: Perry et al. 2021)*

Large calanoid copepods were not a significant predictor of salmon early marine survival patterns in the Strait of Georgia over 1996-2018 (Perry et al. 2021). The authors suggest that vertical life cycle migrations and difficulty of capture may result in reduced importance of large calanoid copepods for juvenile Chinook and Coho marine survival.

Keister and Herrmann (2019) identified relationships between Chinook and Coho marine survival and copepod community structure in Puget Sound (Figure 16 and Figure 17). Some stocks of Coho correlated more strongly with community structure than others, but the mechanistic relationship was not clear because copepods are not a main diet item for Coho once they move offshore in Puget Sound (beyond the 30 m isobath). The marine survival of some stocks of Chinook correlated strongly with biomass of important prey items; more years of data are required to see whether the relationship persists. In general, relationships between zooplankton structure and Chinook and Coho marine survival need additional study before they can be considered good predictors of marine survival.

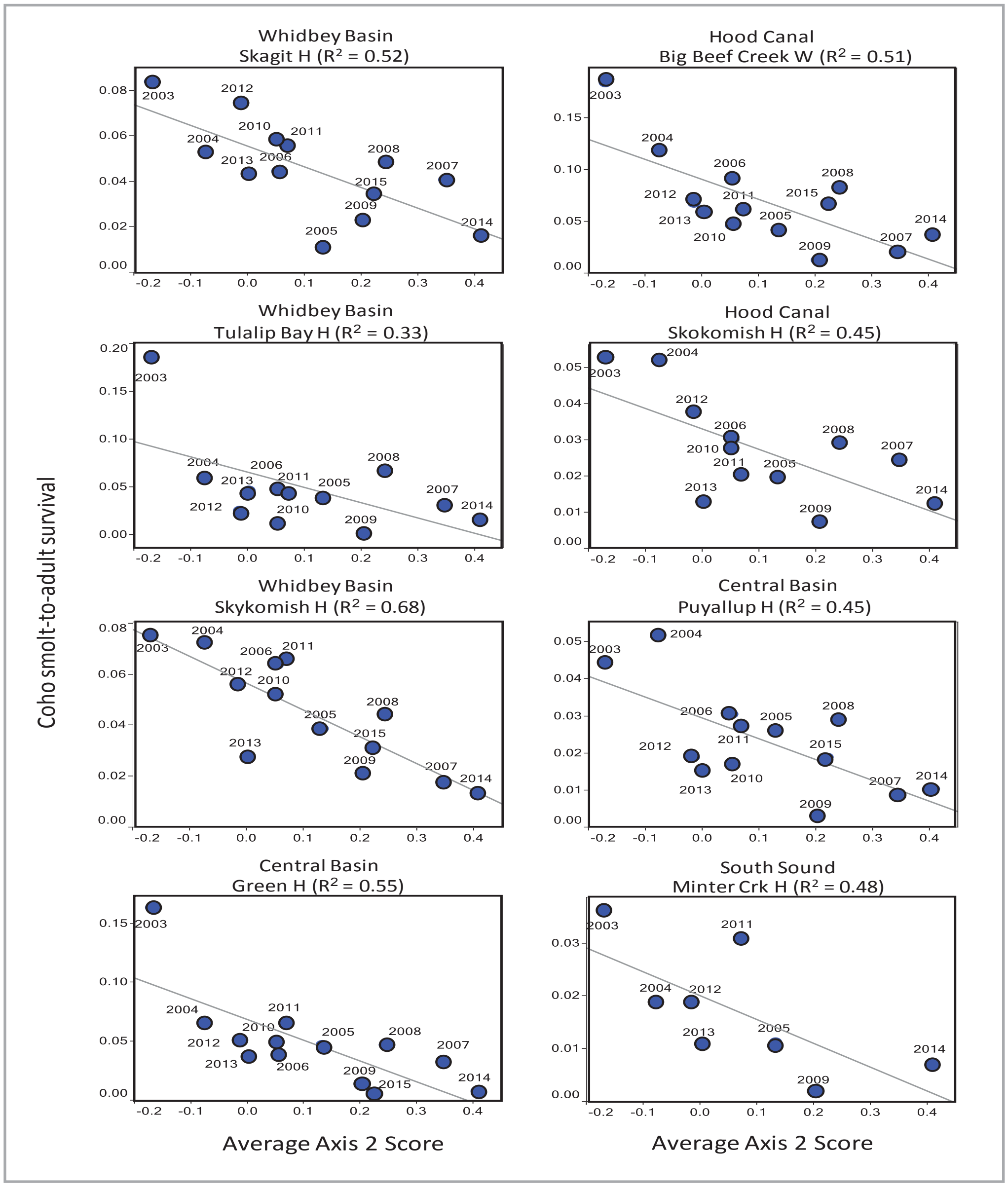

__Figure 16.__ Correlations between Coho salmon marine survival and Axis 2 scores from NMS ordination of the 2003-2018 copepod time series data from a station (JEMS) in Strait of Juan de Fuca. Axis 2 scores were averaged over May to September in each year and correlated with annual survival values. Only stocks from rivers that enter into Puget Sound or northern Washington with at least seven years of survival data available between 2003-2015 and stocks which correlated (R2 > 0.3) with the axis scores are shown. H indicates hatchery origin fish; W indicates wild stocks. (Source: Keister and Herrmann 2019).

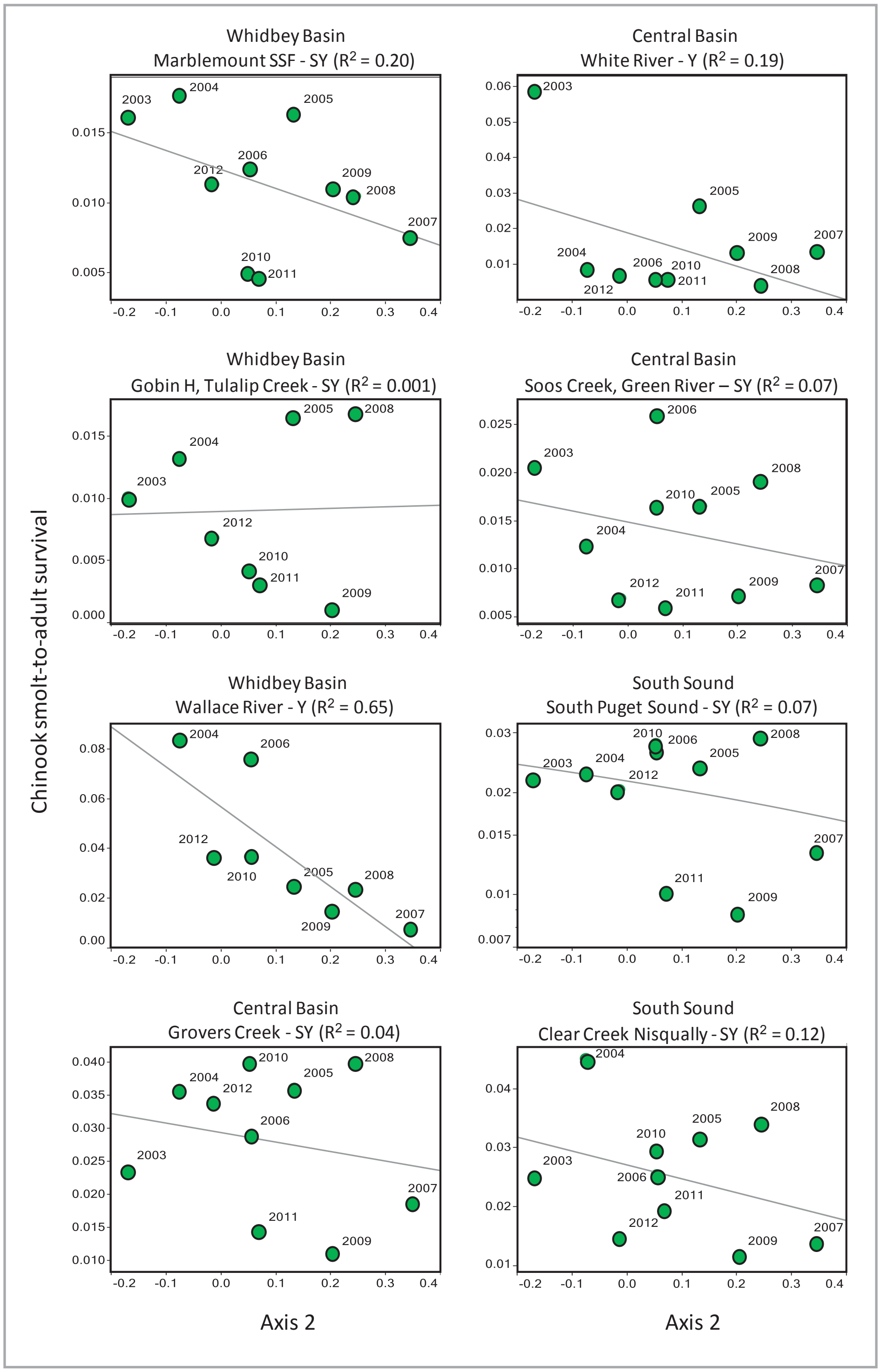

Figure 17. Correlations between Chinook salmon marine survival and Axis 2 scores from NMS ordination of the 2003-2018 copepod time series data from a station (JEMS) in Strait of Juan de Fuca. Axis 2 scores were averaged over May to September in each year and correlated with annual survival values. Only stocks from rivers that enter into Puget Sound or northern Washington are shown. All are hatchery-reared stocks. Y indicates yearling releases; SY indicate subyearling releases. Note that some regressions include < 10 years of data. (Source: Keister and Herrmann 2019).

A transboundary analysis of zooplankton abundance, biomass, phenology, and community structure (Suchy pers. comm.) found that mean abundance of total zooplankton is typically 2-3 times higher in Puget Sound compared to the Strait of Georgia; however, abundances in Canadian Gulf Islands were similar to that of Puget Sound. Additionally, crustacean community structure was very different in the Strait of Georgia and Puget Sound, with generally lower abundances of euphausiids, decapods, and copepods in the northern and central Strait of Georgia compared to other subregions. How this impacts the food web is under investigation.

Many other SSMSP projects focused on diets and prey availability in the Salish Sea. Chittenden et al. (2018) examined diets of young out-migrating Chinook salmon for four consecutive years in the Cowichan River estuary and in Cowichan Bay. They found that hatchery-reared smolts were larger than unclipped smolts (primarily naturally reared), ate larger prey, spent very little time in the estuary, and disappeared from the bay earlier. They suggested that the larger body size of hatchery smolts could be a disadvantage if it results in leaving the estuary early to meet energy needs. Gut fullness was correlated with zooplankton biomass and that decapods and cirripeds were positively selected by Chinook salmon smolts in Cowichan Bay. Copepods were abundant in the zooplankton community but were not chosen as prey. Only 24% of the fish consumed by the smolts in this study were herring; Chittenden et al. (2018) suggested that improving production of forage fish would be beneficial for production of Chinook salmon. Duguid et al. (in review) summarize evidence that herring were more important to juvenile Salish Sea Chinook salmon diets in the 1970s (Argue et al. 1986, Healey 1980) than in recent years. Finally, using an ecosystem model for Puget Sound built with the Atlantis ecosystem model framework, Morzaria-Luna et al. (in prep) found that declines in Pacific herring abundance had significant impacts on Chinook and Coho survival.

Weil et al. (2019) found that jellyfish-associated amphipods (*Hyperia medusarum*) recovered from Chinook salmon stomachs in the southern Gulf Islands contained nematocysts of their jellyfish hosts. Further, these authors found that occurrence of these amphipods in Chinook stomachs was related to abundance of jellyfish in the water column. Juvenile Chinook salmon consumed almost exclusively adult female amphipods which had significantly higher energy density than males (Weil et al. 2020). This evidence for energy flow from a large scyphozoan jellyfish back to juvenile salmon illustrates the complexity of bottom-up processes influencing salmon growth.

Beauchamp et al. (2020) found a higher-than-expected reliance on invertebrates in the diets of resident Coho and Chinook in Puget Sound during 2018-2019. All sizes of Coho salmon relied more heavily on invertebrates throughout the growing season than Chinook, which fed on large proportions of larval crab in spring, shifted to increasing fractions of gammarid or hyperiid amphipods through the summer, and transitioned to feeding on herring and sand lance in the fall. When assessing Puget Sound as a whole, predation on Pacific herring was surprisingly comparable between resident Chinook and Coho despite considerable differences in monthly diet, growth, consumption, and survival.

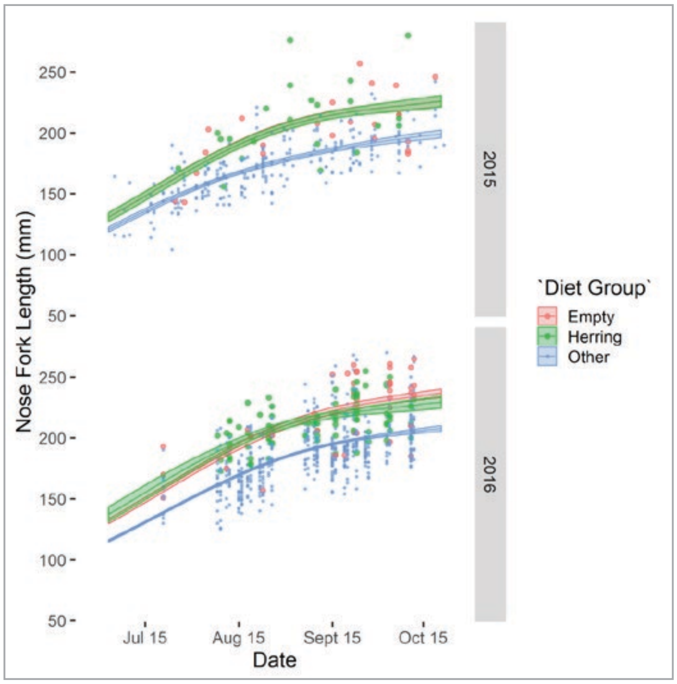

Figure 18. Actual (points) and generalized additive model (GAM) predictions (lines and ribbons) of fork lengths of juvenile ocean-type Chinook Salmon captured by microtrolling in the Southern Gulf Islands in 2015 and 2016. The GAM (Gamma distribution, log link) contained parametric terms for year and diet grouping (empty stomachs, containing Pacific Herring, and containing other prey) and a global smooth term for day of the year. The model also included separate smooth terms allowing each year and each combination of year and diet grouping to differ from the global relationship between fork length and day of the year. Application of a first derivative penalty to these latter smooth terms allowed them to be penalized out of the model (reduced to a line with 0 slope) where non-significant based on Pedersen et al. 2019. (Source: W. Duguid, U. Victoria)

Several other SSMSP studies have focused on the importance of the transition to piscivory of Chinook salmon. Duguid et al. (in review) found concomitant declines in densities of zooplankton prey and juvenile Chinook stomach fullness and growth during fall in the Gulf Islands. Meanwhile, the frequency of empty stomachs and importance of fish in diets increased. The trophic ecology of juvenile Chinook appeared to vary among sites only a few (2-23) kilometres apart, with larger and faster growing juveniles at sites where fish (generally Pacific herring) made up a larger proportion of the diet. Juvenile Chinook which had consumed Pacific herring had greater mean stomach fullness and were larger than those which had not, suggesting that age-0 Pacific herring may have been too large to be consumed by smaller Chinook. Duguid et al. (in review) did not find evidence that juvenile Chinook salmon abundance (as reflected by CPUE) was directly related to local water column stratification or zooplankton composition and abundance and suggested that differing spatial distribution of larger and smaller Chinook may have been related to distribution of forage fish prey (Figure 18) .

Similarly, Chamberlin et al. (2017) suggested that only larger juvenile Chinook salmon were able to access Pacific herring prey resources in Puget Sound, based on stronger relationships between IGF-1 concentrations (insulin-like growth factor-1, a proxy for growth rate) and length of juvenile Chinook in sub-basins where relatively small (relative to Chinook length) Pacific herring were abundant.

Another project elucidated the importance of Pacific herring to winter diets of resident Chinook in the San Juan Islands (Chamberlin et al. 2020), where Pacific herring accounted for 60-90% of total biomass and 75-98% of fish prey found in stomach contents during the winter. Chamberlin et al. (2020) found that larger individual prey fish were consumed more often by larger Chinook salmon though the difference was nearly indistinguishable for Chinook salmon over 550 mm fork length. Interestingly, it appeared that sand lance were observed more often than herring in the gut contents of Chinook salmon smaller than 550 mm fork length. Most prey fish sizes occurred within a relatively narrow size range (90-107 mm) suggesting Chinook salmon may target a single age class for both species.

Similar results were found by Davis et al. (2020), who examined how certain foraging strategies could lead to increased growth of juvenile salmon in estuarine and marine environments. Subyearling Chinook caught in northern Puget Sound ate insects in estuarine and nearshore habitats, followed by decapod larvae, euphausiids, or forage fish in the offshore zone (beyond the 30 m isobath). Fish in southern Puget Sound also ate insects in the estuary but were more likely to eat mysids and other crustaceans in the nearshore zone. As shown by Chamberlin et al. (2020), subyearlings found in marine habitats adjacent to the San Juan Islands ate forage fish, and their stomachs were as much as 1.4 to 3 times fuller than salmon captured in other regions. Scale-derived growth rates and IGF-1 levels showed distinct growth advantages for San Juan Islands fish which were strongly associated with the early adoption of piscivory. However, consumption of larger crustaceans such as mysids and euphausiids was also associated with greater relative growth regardless of where individuals were captured.

The strong relationship that Duguid et al. (in review) and Chamberlin et al. (2020) observed between juvenile Chinook salmon size and consumption of Pacific herring may have important implications: it is generally accepted that failure to reach the size threshold necessary to transition to piscivory on a dominant prey species can dramatically reduce growth of juvenile fish (Olson 1996).

There is some evidence that herring availability for juvenile Chinook salmon has changed over the past few decades in the Strait of Georgia and that consumption of age-0 herring may begin later in the year than it did in the 1970s (Duguid et al. in review). For example, although there was no overall trend in the relative abundance of Strait of Georgia age-0 herring during 1992-2018, there was a pattern of alternating high (with high associated variance estimates) and low abundances of age-0 herring, every two or three years until 2012, after which the interannual variability in mean estimates was low compared to past observations (Thompson et al. 2020). Boldt et al. (2018) found that the condition of Strait of Georgia age-0 herring increased from 2007 to 2011 and has remained high (Figure 19). An increase in condition indicates that age-0 herring are heavier for a given unit of length; an age-0 herring of a given length in 2018 may have provided more energy to predators compared to a similarly sized age-0 herring in 1995. The spawning biomass of adult herring has generally increased in the Strait of Georgia since the 1980s (DFO 2020). In contrast, spawner abundance of Puget Sound herring populations has generally declined since the 1980s, herring size at age has declined, and there has been a collapse of younger age classes, all factors which affect overall biomass (Siple and Francis 2015, Stick and Lindquist 2009, Greene et al. 2015, Landis and Bryant 2010).

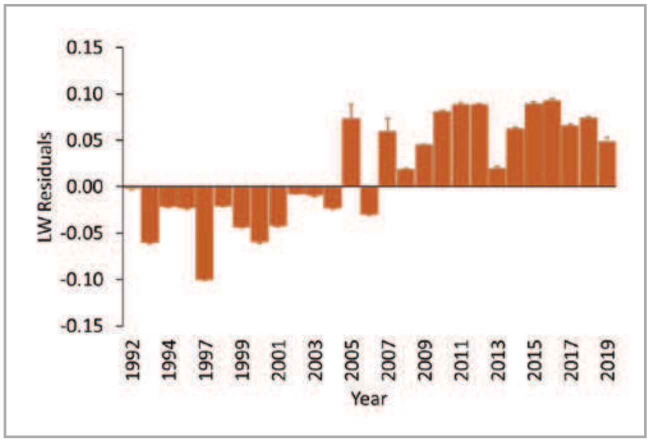

Figure 19. *Mean age-0 Pacific herring condition (length-weight (LW) residuals) from DFO's Strait of Georgia juvenile herring survey, 1992-2019 (no survey in 1995). (Source: J. Boldt, DFO).*

In Puget Sound, it has been hypothesized that juvenile Chinook salmon could be dependent on late spawning (April through June) herring due to their presumed smaller size during the Chinook early marine growth period (Chamberlin et al. 2017). The late spawning Cherry Point stock, which historically represented half of the total Puget Sound herring spawning biomass, has declined significantly (Sandell 2019, Siple and Francis 2015). However, Chamberlin et al. (in review) found that most herring found in the guts of juvenile and adult resident Chinook salmon were from March–April spawning stocks, currently the most abundant in Puget Sound. Counterintuitively, juvenile salmon captured in the summer had a significantly higher proportion of herring spawned in January–February in their diets than would be expected from estimated January-February spawn biomass. The increased proportion of January–February stocks in the stomach contents of juvenile Chinook salmon may indicate selective foraging by salmon on seasonally variable distributions of herring. This suggests Chinook salmon rely on genetic and life history diversity of herring populations to sustain growth and that movement and distribution of herring likely play important roles in supporting juvenile salmon growth. Within the Strait of Georgia, there appears to have been a contraction in the spatial diversity of herring spawning sites, with most spawning activity confined to sites along the west coast between Saltspring Island and Denman Island and concomitant losses in areas of the southern Strait, which could also impact herring availability to juvenile salmon (Hay and McCarter 2013; Therriault et al. 2009).

In Whidbey Basin (Puget Sound), the summer size of age-0 herring is dependent primarily on spring water temperature while size in fall is controlled by density dependence (Rheum et al. 2013). In the Strait of Georgia, density-dependent growth also plays a role in the size and condition achieved by age-0 herring in fall (Boldt et al. 2018). The role of density dependence suggests the possibility of positive feedback where low abundances of age-0 herring impact juvenile salmon directly by reducing encounter rates and indirectly by decreasing the proportion of individuals that are a suitable size for consumption.

Several SSMSP studies focused on the importance of food quality. Zooplankton vary widely in their EFA content, with primary differences driven by taxonomy (Costalago et al. 2020; Hiltunen et al. 2019), so variation in zooplankton species composition can affect juvenile salmon growth and development. Hiltunen et al. (2019) studied the quality of juvenile salmon prey by examining EFA content of zooplankton in Puget Sound and adjacent waters. They created an integrated measure of food quality and quantity by combining taxon-specific EFA content with data on juvenile salmon prey biomass distribution measured by quantitative net tows. They found that prey taxa differed in EFA content: gammarid and hyperiid amphipods contained the highest amount of EFA while shrimps and copepods had much lower EFA content. The availability of important EFAs varied in timing and magnitude among different regions of Puget Sound; EFA availability was highest in the northern regions and lowest in South Puget Sound, indicating better feeding conditions in the north (Figure 20). Hiltunen et al. (2019) concluded that, overall, amphipods had high lipid, EFA, and energy content and appeared to be the highest quality prey items. Crab larvae, which are among the most dominant prey by biomass of juvenile salmon in Puget Sound, had an intermediate EFA content and the lowest energy density of the studied taxa. Copepods in this study were low in EFA, indicating that their nutritional value is lower than that of the other prey taxa.

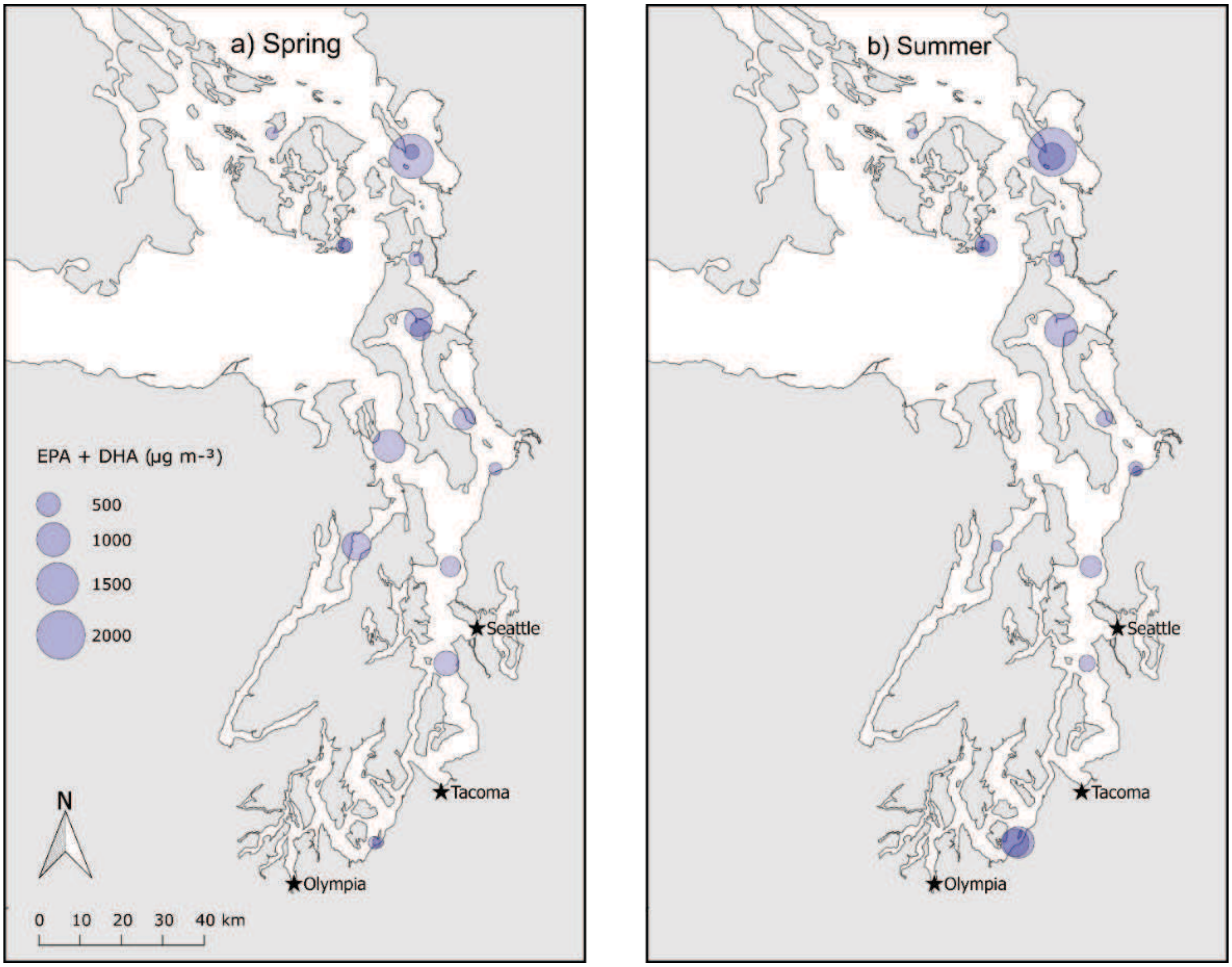

Figure 20. *Bubble chart of eicosapentaenoic acid + docosahexaenoic acid (EPA + DHA) availability in zooplankton prey to juvenile salmon in Puget Sound and adjacent waters during a) spring (April-May, left panel) and b) early summer (June-July, right panel) of 2017. Note that closely located stations show as overlapping bubbles. (Source: M. Hiltunen)*

Costalago et al. (2020) examined trophic linkages in the Strait of Georgia using biochemical tracers (i.e., fatty acids and bulk carbon and nitrogen isotopes) in plankton. Their study focused on two key fatty acids, EPA (highly retained in zooplankton, especially in larger zooplankters), and DHA (important for early development of fish, and highly retained in juvenile salmon). They found that total fatty acid content was highest in copepods, was also high in hyperiid and gamariid amphipods, but was low in crab megalopae. For salmonid prey species, the ratio of DHA:EPA only exceeded one (which is good) for fish larvae and the copepod *Paraeuchaeta* elongate and was lowest in large calanoid copepods *Eucalanus bungii*, *Calanus* species, and *Neocalanus* species. Costalago et al. (2020) compared seasonal (winter, spring and summer) differences in fatty acid composition and found that summer was the optimal period for zooplankton quality.

Other SSMSP studies looked at the relationships between prey availability and quality on performance of juvenile salmon. In Puget Sound, Beauchamp et al. (2018) examined how larval crab availability and energy density during the critical growth period for juvenile salmon related to foraging success, growth, and bioenergetics. The authors found that Z5 (a larval stage) zoea and megalopae of Red Rock crab (*Cancer productus*) and other Cancer species were the primary categories of larval crab supporting growth during the critical growth period in epipelagic habitats of Puget Sound, especially during June-July. These taxa were available in space (i.e., in the upper water column) and size relative to the gape limitations of subyearling Chinook salmon during this growth period. They hypothesized that juvenile Chinook would adopt a fast growth, low lipid storage strategy through at least the June-July critical growth period, followed by a phase of energy allocation to increase lipid stores during the latter portions of summer and autumn, but this did not appear to be the case. Instead, energy densities of salmon remained low through the end of summer with a modest increase by October rather than increasing significantly before winter. Body mass did, however, increase significantly over the entire growing season and this, together with a small increase in energy density by early October, resulted in a higher overall energy content in the bodies of the juveniles going into winter. The implications of this energy status for overwinter survival are yet to be determined. These juveniles were likely residents; different energy allocation strategies might have been employed by juveniles that had already migrated out of Puget Sound.

Gamble (2016) used bioenergetics models to examine the relative roles of prey quality, prey availability, and temperature in regulating stage-specific growth rates of juvenile Chinook salmon across stocks, habitats, and time in Puget Sound. Subyearling Chinook were larger and grew faster in offshore (beyond the 30 m isobath) than nearshore habitats. Differences in growth rates were likely due to differences in prey availability and may have been exacerbated by higher nearshore temperatures. Feeding rates were generally low across Puget Sound, suggesting that prey availability limited early marine growth.

Similarly, Connelly et al. (2018) used bioenergetics models to mechanistically link Chinook size and growth with ecological factors including diet, water temperature, and prey availability. Despite complex interactive effects among habitat, prey quality, prey availability, stock, and time, no relationship was evident between prey quality and growth or feeding in either nearshore or offshore habitats for subyearling Chinook in Puget Sound. Overall, water temperature and feeding rate (a surrogate measure of food availability) were identified as ecological drivers of growth rates. Water temperatures and prey energy densities were more variable in nearshore rearing habitats than offshore. Offshore habitats provided more reliable thermal regimes and appeared to support higher growth rates in general. However, the availability of key prey like crab megalopae can vary considerably among regions, months, and years. In summary, the authors suggested that conditions with adequate prey supply and temperatures confer higher growth rates and may lead to higher marine survival rates.

Synthesis Committee Perspective

The Synthesis Committee noted that the evidence for links between food quality and quantity and inter-annual variation in survival for both Coho and Chinook is substantial throughout the Salish Sea, but data are likely insufficient to relate to longer-term (pre-2000) changes in marine survival. For steelhead, data are deemed insufficient to address both recent and long-term changes in marine survival.

Relationships have been found between zooplankton and Coho and Chinook marine survival rates, and evidence points to strong links between herring availability and growth/survival. In particular, the importance of the transition to piscivory was highlighted for two key reasons: 1) a switch to piscivory is related to increased juvenile salmon growth (Litz et al. 2017, Davis et al. 2020) and growth is related to survival (Moss et al. 2005, Duffy and Beauchamp 2011) and 2) changes in the predator to prey size ratios of Chinook salmon and Pacific herring throughout the Salish Sea as a result of changes in availability and body condition of herring (in the Strait) and loss of herring diversity, particularly late spawning populations (in Puget Sound), could explain some portion of interannual variability and long-term trends in Salish Sea Chinook salmon survival.

Overall, the Synthesis Committee concluded that prey availability, either in terms of quantity or quality, is a very important factor operating in tandem with other factors such as prey distribution, fish condition, fish health, ocean conditions, etc. to impact marine survival. Whether there is a direct relationship or whether a common driver impacts plankton, forage fish, and salmon is as yet unknown.

Interrelationships and Cumulative Impacts

Key interrelationships affecting salmon growth and survival may include links between feeding behaviour, food availability and quality, and predation risk. When less food is available, a fish may use more energy to find prey and aggressive feeding behaviour may increase exposure to predators. SSMSP studies have found evidence for different behavioural strategies that are probably linked to food supply but a fuller understanding of the relative impacts of energy allocation (somatic growth versus lipid reserves, short-term versus long-term energy storage) is still needed. Further, behaviour with respect to migration out of the Salish Sea or residency within the Salish Sea is also likely related to food supply affecting growth/distribution/survival patterns. The observation that Chinook salmon from the Strait of Georgia and Fraser use stock-specific feeding areas within the Canadian Salish Sea was an important new finding of the SSMSP.

Observations from lab feeding experiments suggests that food quality impacts feeding behaviour. Fish fed lower quality food behave more aggressively and spend more time foraging (Hunt pers. comm.). Such behavioural changes may lead to a change in predation risk. Duguid (2020) found that diets and growth in juvenile Chinook belonging to a single stock (Cowichan River) varied at small spatial scales and that larger, faster growing individuals appeared to spatially associate with age-0 herring, possibly increasing predation risk from seals but improving food quality. Analysis of scale circulus spacing suggested that larger, faster growing fish had been faster growing prior to ocean entry and may have entered the ocean later than slower growing fish. These results suggest that either environmental or intrinsic control of freshwater or estuarine growth and ocean entry phenology may influence subsequent marine behaviour, distribution, diet, growth potential, and predation exposure.

Duguid (2020) postulated the existence of feedback loops in the complex relationship between age-0 herring and juvenile Chinook. Lower densities of herring **1)** may lead to larger herring that are only accessible to the larger juvenile Chinook and **2)** may lead to greater search and handling times by juvenile Chinook, increasing predation risk by seals. If low age-0 Pacific herring density was a consequence of mechanisms which also impact abundance or growth of juvenile Chinook salmon (i.e., low prey availability for both herring and Chinook) (Beamish et al. 2012), these feedback loops could be superimposed on already poor recruitment prospects. Similarly, the complex relationships between gelatinous zooplankton, which are increasing throughout the Salish Sea, and juvenile salmon and their forage fish prey need to be investigated.

Management Implications and Next Steps

The SSMSP studies described above have led to several recommendations.

The results of Perry et al. (2021) and Keister and Herrmann (2019) highlight that a consistent zooplankton monitoring program in the Salish Sea could identify important changes in the ecosystem and establish relationships between oceanographic conditions, zooplankton production and composition, and salmon and forage fish growth and survival. Zooplankton data can also assist with projections of future abundances of salmon. Information on size, duration, and predictability/consistency of plankton blooms could shed considerable light on what constitutes "functional prey availability."

Costalago et al. (2020) noted the need for a mechanistic understanding of plankton food webs and the nutritional support that they provide for planktivorous fish, and for more research to examine the links between zooplankton and oceanographic conditions in the Strait of Georgia. Hiltunen et al. (2019) also suggest that indicators of salmon survival could be more robust if they were to incorporate both zooplankton species composition and the fatty acid composition of important prey taxa.

Beauchamp et al. (2018) noted that little is known about how the spatiotemporal availability of larval crab relates to feeding and growth of juvenile Chinook salmon, but this knowledge could become a fundamental element in the recovery of these stocks by identifying important functional components for habitat restoration and informing water quality and quantity management. Beauchamp (pers. comm.) also emphasized the need for more studies of circulation features that concentrate and retain zooplankton prey species.

Insect populations have exhibited huge (75%) declines in some regions of the world over the past ~30 years (Hallman et al. 2017), yet represent an important terrestrial subsidy to salmon diets in estuary, nearshore, and even marine environments. As noted above, insects are high energy density prey and can greatly facilitate salmon growth at early marine life stages; long-term studies of changes in nearshore insect availability, fish diets, and growth rates could help determine whether loss of insects from diets (e.g., via pesticides or shoreline habitat loss) has reduced early growth over time.

Chamberlin et al. (2020), Duguid et al. (in review), Atlantis modelling by Morzaria-Luna et al. (in prep), and other studies reinforce the value of protecting herring and sand lance for the benefit of Chinook recovery. Chamberlin et al. (in review) note that population-specific distribution and movement patterns of herring in the Salish Sea remain a critical information gap, especially with respect to age-0 herring. Duguid et al. (in review) suggest that further research is necessary to determine whether fine-scale distribution of larger, piscivorous juvenile salmon is linked to forage fish prey distribution and to understand the role of prey to predator size ratios in limiting the ability of juvenile salmon to transition to piscivory. In sum, results from SSMSP studies highlight the importance of maintaining herring abundance and diversity in the Salish Sea as well as supporting Pacific sand lance and other forage fish, and the authors suggest that any recovery efforts aimed at these forage fish species would benefit Chinook salmon.

Chittenden et al. (2018) and many others have noted numerous factors impacting nearshore and marine habitats which support important diet items of juvenile salmonids, including shoreline development, boat traffic, log-booming activities, agricultural runoff, and sewage outflows. They suggest that eliminating log booming, sources of pollution, and restoring riparian cover and eelgrass beds would improve salmon habitat quality and allow salmon prey to flourish as well as provide habitat for herring populations. They also emphasize the importance of carefully managing fisheries on salmon prey (e.g., euphausiid and herring).

A key next step in examining the role of prey availability to survival of Chinook and Coho salmon is food web modelling. Models that incorporate Salish Sea food web ecology, such as the Puget Sound Atlantis model (Morzaria-Luna et al. in prep) and the Salish Sea Ecopath with Ecosim model (Oldford pers. comm.), will shed additional light on dynamic interactions of various predator-prey and competitive relationships that affect salmon. These models are capable of testing individual and cumulative hypotheses of how juvenile salmon interact with a range of prey types and account for top-down forces (e.g., predation, fishing) that further influence relationships between salmon and different prey resources.

Water quality/Biogeochemistry

The key hypothesis related to water quality and biogeochemistry impacts on food supply addressed by SSMSP studies was that changes in circulation and water properties have altered phytoplankton and zooplankton production resulting in degraded salmon food-webs in the Salish Sea. The main prediction associated with this hypothesis was that the timing, duration, quantity, spatial extent, and/or composition/quality of salmon prey has declined due to a different state of circulation, water properties (e.g., temperature, nutrients), and boundary forces (wind, temperature, open ocean conditions, river inputs) in the 2000s versus the 1970s/early 1980s.

Numerous studies have provided information on biogeochemistry changes within the Salish Sea. Riche et al. (2014) reviewed available time series for the Strait of Georgia and found that that both surface and deep seawater in the Strait has been warming at over 1°C per century, as has the freshwater entering from the Fraser River, and the freshet is occurring earlier in the year (Gower 2002, Morrison et al. 2002). Sea surface temperatures increased from 10.5°C to 12°C over 1971-2007, and the amount of time Fraser River temperature exceeds the 18°C threshold for salmon migration has increased over the last 50 years (Martins et al. 2010, Rand et al. 2006). Decadal-scale changes in wind are evident within the Strait (Tuller 2004). In Puget Sound, Moore et al. (2015) documented long-term trends in Puget Sound hydrology, with increased river flow in spring and decreased flow in summer over the course of the data series (Cuo et al. 2009, 2011), and suggested that this might affect phytoplankton dynamics by modulating stratification. Johannessen et al. (2014) analyzed 58 years of dissolved oxygen (DO) concentrations in deep waters of the Strait of Georgia and noted a decline at a rate of 0.010 – 0.029 ml L—1 yr—1 (0.45 – 1.3 μmo L—1 yr—1); DO levels seasonally approached biological tolerance thresholds. The authors suggested the decline was mostly due to increasing hypoxia of upwelled Pacific Ocean water and that extrapolation of the long-term trend indicated that parts of the Strait could become episodically hypoxic as early as 2042. Similarly, hypoxia has been observed in Puget Sound's Hood Canal since the 1970s. Brandenberger et al. (2011) suggested that climate oscillations may influence the ventilation and/or productivity of deep water in Puget Sound, particularly in poorly mixed regions.

Many other studies have shown that large-scale climate variability in the North Pacific can affect salmon prey production in the Salish Sea by altering water temperature, nutrient levels, the production and composition of phytoplankton and zooplankton communities, and the degree of timing match/mismatch between consecutive trophic levels. Pacific salmon population trends track decadal patterns in the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997, Rupp et al. 2012) and El Niño Southern Oscillation (ENSO) (Rupp et al. 2012), upwelling conditions (Scheuerell and Williams 2005), and North Pacific Gyre Oscillation (NPGO) (Kilduff et al. 2015). These climate and upwelling patterns have been linked to changes in the salmon prey community (Hooff and Peterson 2006, Araujo et al. 2013), as well as size and growth of the salmon themselves during early residence in the ocean (Beckman et al. 1999).

Climate variability in the North Pacific affects water properties and surface currents in the Salish Sea via physical processes such as changes in sea level pressure and atmosphere-ocean interactions (Masson and Cummins 2007, Mackas et al. 2013). Changes in sea level pressure are closely linked to changes in surface winds, which directly result in variability in sea surface temperature, upper ocean temperature, mixed layer depth, and direction and strength of near-surface wind-driven currents in the Salish Sea (Schwing et al. 2002). Changes in the strength of trade winds and winds favourable for coastal upwelling affects the intensity of upwelling offshore, which results in changes in nutrient levels due to deep estuarine inflow to the Strait of Georgia via the Strait of Juan de Fuca (Guan et al. 2017). Variation in the intensity of local wind strength and cloud cover can modify the timing of the Strait of Georgia spring phytoplankton bloom (Allen and Wolfe 2013). Collins et al. (2009) noted that high winds cause late blooms whereas weak winds result in early blooms; given that mean spring wind speed has decreased over the last 35 years in the Strait of Georgia, the likelihood of early blooms may have increased.

Additionally, climate-associated fluctuations in the timing and amount of precipitation and snowmelt influence Fraser River discharge and the timing and magnitude of the summer freshet which, in turn, influence nutrient entrainment and the magnitude of phytoplankton production (Yin et al. 1997), as well as hydrodynamic features of estuarine circulation. The composition of the phytoplankton community can be affected by entrained nutrients. Survival and growth of zooplankton in the Strait are impacted by all these factors (El-Sabaawi et al. 2009).

Species composition, timing, size, and duration of zooplankton blooms in the Strait of Georgia and northern Pacific Ocean have changed over the last fifty years (Bornhold 1996, Chiba et al. 2006, Batten and Mackas 2009, Mackas et al. 2013). Colder-water species of copepods have been declining in the southern part of their range, while warming waters are associated with increasing numbers of jellyfish and crab larvae (Mackas et al. 2013). In the 1990s and 2000s, dramatic shifts in the relative abundances of copepods, euphausiids, and amphipods were observed in the Strait (Johannessen and McCarter 2010; Mackas et al. 2013). Mackas et al. (2013) noted that the zooplankton signal correlated positively with the NPGO climate index, negatively with temperature anomalies throughout the water column, and positively but less consistently with survival anomalies of Strait of Georgia salmon and herring (Mackas et al. 2013). Another synthesis of zooplankton data from the Strait of Georgia suggested an abrupt decline in the total biomass of several species of zooplankton in 1999 (Li et al. 2013). This decline was most pronounced for euphausiids and calanoid copepods, and the best indicator of zooplankton community change was the spring extratropical-based Southern Oscillation Index, with a one-year lag. Correlations were weaker for local variables; the best single local indicator was the day of the peak flow of the Fraser River.

Within-year patterns in the abundance and composition of larval fish assemblages have been closely associated with chlorophyll variability in the Strait (Guan et al. 2017). Guan et al. (2015) noted that the concentration and composition of the larval fish assemblage in the Strait of Georgia changed between the early 1980s and late 2000s. Larval Pacific hake, walleye Pollock, rockfish species, and northern smoothtongue declined, while Pleuronectidae and several other demersal fish taxa increased. The most prominent changes among pelagic species in the Strait were decreases in absolute and relative concentration of hake and corresponding relative increases of Pacific herring. A food web model developed by Preikshot et al. (2013) showed a reduction in the mean trophic level of vertebrates over the period 1990 to 2009.

Puget Sound's water quality has experienced long-term nutrient increases. Excessive phytoplankton blooms in response to human influences have been well-documented (Pool et al. 2015). These authors note that *Noctiluca scintillans* "orange-tide" blooms have been observed in Puget Sound since at least 1946. *Noctiluca* is a heterotrophic dinoflagellate that blooms late spring to early summer and is a potential indicator of eutrophication in coastal environments (Vasas et al. 2007). *Noctiluca* has a strong grazing impact on diatoms and excretes ammonium into the water (Faust and Gulledge 2002, Vasas et al. 2007). *N. scintillans* does not appear to be a preferred food source for common mesozooplankton. It is too large to be grazed by copepods; instead, it is generally consumed by jellyfish and salps. Thus, in addition to causing shifts in diatom abundance and plankton communities, *N. scintillans* can alter trophic interactions via carbon transfer to salps and jellyfish. Increased prevalence of this species can produce a trophic "dead end" (Gomes et al. 2014).

Warming oceans polluted with nitrates and phosphates are supporting higher abundances of jellyfish and harmful algae (Brodeur et al. 2002, Landsberg 2002, Hallegraeff et al. 2003, Chittenden et al. 2018). In South and Central Puget Sound, Greene et al. (2015) found evidence of 3-9-fold increases in jellyfish-dominated surface trawls over the period from the 1970s to 2011. Increased populations of ctenophores and cnidarians may have a detrimental effect on young salmon through competition and predation on salmon prey (Mackas et al. 2001, Brodeur et al. 2002, Rice et al. 2012, Lebour 1922, Purcell and Arai 2001, Pauly et al. 2009). Jellies are considered trophic "dead ends" as they do not provide nutrition to other organisms in the marine food web (Purcell et al. 2007, Richardson et al. 2009). Chittenden et al. (2018) found that the biomass of cnidarians and ctenophores in Cowichan Bay was similar to the Whidbey area of Puget Sound, where abundances of fish and jellyfish were negatively correlated (Rice et al. 2012).

In short, there is a lot of evidence for changes in water properties within the Salish Sea over the past 50 years, as well as for concomitant changes in lower trophic level communities. There is also a lot of evidence for impacts to Pacific salmon. Poor food availability in the Strait has been linked to the collapse of Fraser River Sockeye salmon (Beamish et al. 2012, Thomson et al. 2012, Mackas et al. 2013), while anomalies in Fraser River discharge have been closely related to interannual anomalies in the survival indices of Chinook and Coho salmon (Beamish et al. 1994). Beamish et al. (2010) concluded that declines in Coho salmon marine survival between 1970s to 2010 coincided with warming of the Strait of Georgia, where both sea surface and sea bottom temperatures have increased by approximately 1.8˚C since 1970 and the number of days with an average sustained wind strength greater than 25 km/h has increased. They suggested that links between wind strength and the timing and level of primary productivity affected salmon survival.

Work carried out as part of or during the SSMSP built upon these earlier findings.

Declining primary productivity since the 1970s has been proposed as an explanation for Coho and Chinook salmon declines in the Salish Sea. Retrospective analysis using geoduck shells and other metrics associated with annual averages of chlorophyll concentration suggested an increase in primary production in Puget Sound during the 1980s-1990s when Chinook and Coho marine survival declined (Greene et al. in revision). They used a dendrochronological approach to examine whether an index of primary production tracks growth increments in shells of long-lived (44-157 years) geoduck sampled throughout Puget Sound. Their statistical models hind-cast annual historical chlorophyll concentrations back to 1953 and indicated that chlorophyll concentrations were relatively stable until the 1980s, when they started increasing. Chlorophyll concentrations peaked in the 2000s and subsequently declined but have remained higher than historical levels. Changes were apparent not only in geoduck growth increments but also in indices of wind speed and stratification, factors which can influence primary production dynamics (Gargett and Marra 2002). These authors suggest that changes in chlorophyll concentrations were likely related to surface stability, impacted by both wind speed and stratification (Wan et al. 2010, Cummins and Masson 2014).

An increase in primary production would be expected to result in increased zooplankton, providing direct benefits to pelagic planktivores such as herring and Pacific salmon. Given that Pacific salmon marine survival declined over this same period, Greene et al. (in revision) suggest that some form of ecosystem decoupling occurred and that a decline in zooplankton quality/availability may have occurred over the period of marine survival declines. This potential decline in zooplankton may itself be related to a decline or phenological shift in edible phytoplankton.

In contrast, Johannessen et al. (in press) have concluded that total primary productivity has neither increased nor decreased in the Salish Sea since the 1970s or even over the last century. They examined marine sediments from the Salish Sea, which provide a continuous record of conditions in the overlying water, using stable isotopes of organic carbon and nitrogen from 21 sediment cores to determine the contributions and fluxes of marine-derived and terrigenous organic matter over time. The annual flux of marine-derived organic matter showed no trend for at least the last 100 years and, while there was an apparent increase in marine flux in recent years, this was a result of remineralization of organic matter as it passed through surface sediments. The flux of terrigenous organic matter has increased over the last century in the Strait of Georgia; in Puget Sound, terrigenous flux peaked in the mid-twentieth century.

Other work outside of the SSMSP by Krembs et al. (2014) showed that nutrient concentrations have significantly increased and nutrient ratios and phytoplankton biomass have steadily changed since the late 1990s in the pelagic zone of Puget Sound. Depth-integrated algal biomass declined between 1999 to 2013, but algal blooms at the surface increased, often with high abundances of autotrophic flagellates. They also documented a widespread decline in benthic community abundance. These results could indicate reduced organic material export and weaker benthic-pelagic coupling, which could explain the long-term 45% decline in specie richness in deeper-water benthic communities in Puget Sound. These trends have potential implications for marine food web structure.

Several SSMSP researchers examined influences on phytoplankton and zooplankton dynamics in the Salish Sea. Puget Sound has far fewer long-term data records than Strait of Georgia. MacCready and Banas (2016) tried to correlate Puget Sound physical drivers such as river flow and weather (which have relatively long records) to phytoplankton (for which data records are relatively short). They used chlorophyll concentrations from CTD casts over 14 years as a proxy for phytoplankton biomass, but did not find any clear univariate correlations, likely due to simultaneously active mechanisms affecting the system. To rank these mechanisms, Banas et al. (2019) integrated model simulation results and found that variation in incoming light, i.e., variation in cloud cover, is a leading climate influence on phytoplankton dynamics in Puget Sound. Collins et al. (2009) and Allen and Wolfe (2013) had similar findings regarding influences on timing of the spring bloom in the southern Strait of Georgia. Wind mixing was an important influence in the Strait, whereas river flow effects on spring stratification and mixing were more important than wind effects in Puget Sound (the two mechanisms were of comparable importance in summer). Banas et al. (2019) concluded that observed variation in light attenuation is strong enough to drive significant interannual variability and potentially long-term trends in primary production timing, magnitude, and nutrient limitation.

Suchy et al. (2019) found substantial spatiotemporal variability in phytoplankton dynamics on both intra- and interannual time scales across 2003-2016 in the Strait of Georgia. Chlorophyll-a in the northern Strait was best explained by variations in sea surface temperature and tightly coupled to large scale climate indices, whereas chlorophyll-a in the central region was best explained by Fraser River discharge and more strongly related to local factors. Satellite-derived spring bloom timing and bloom magnitude were significantly negatively related to sea surface temperature in the central Strait. Euphausiids exhibited higher abundances during "average" bloom years; none of the other dominant crustacean taxa (copepods, decapods, amphipods) had clear relationships to bloom timing. (Suchy et al, in prep). When taxa were combined in analyses, earlier spring bloom start dates and higher bloom magnitudes were associated with lower crustacean biomass, likely due to temperature effects on zooplankton body size and community composition.

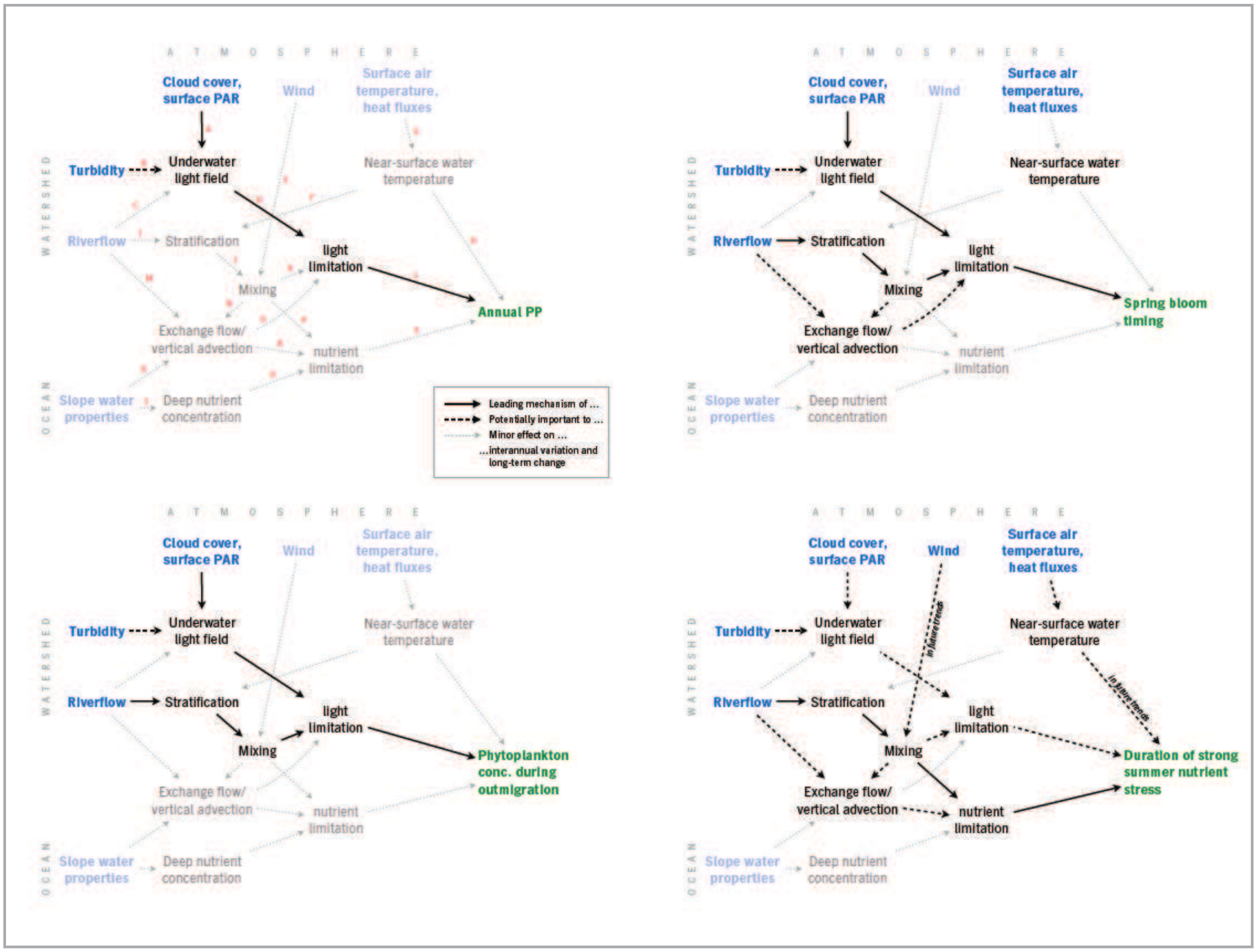

Figure 21. Final ranking of pathways of climate influence on four measures of phytoplankton dynamics. (Source: Banas et al. 2019)

Perry et al. (2021) found significant relationships between several physical variables (PDO; sea surface salinity measured at Entrance Island in the central Strait of Georgia; and the modelled start date of the spring phytoplankton bloom in the central Strait of Georgia) and zooplankton assemblages in the Strait of Georgia. Collectively, physical variables in the Strait of Georgia indicate increasing warming (although with some decadal cycling) and decreasing salinity since the early 2000s. This pattern is consistent with the observations of Chandler (2019) in DFO's annual State of the Pacific Ocean reviews.

A few SSMSP studies have directly examined the relationships between abiotic variables, the food web, and salmon marine survival. Sobocinski et al. (2018) used perturbations in a qualitative network analysis framework to test for causes of declines in marine survival, exploring both ecosystem and anthropogenic drivers. The most highly connected nodes in the model were temperature, diatoms, and salmon abundance. Results suggested that variables impacting food supply may be important in mediating effects on salmon survival in the Salish Sea (Sobocinksi et al. 2018).

Morzaria-Luna et al. (in prep) used an ecosystem model for Puget Sound built on the Atlantis ecosystem modelling framework to assess likely drivers of low salmon marine survival while accounting for food web interactions. They found that declines in herring (as mentioned above) or increases in gelatinous zooplankton (as suggested by Greene et al. 2015) could have substantial negative impacts on Chinook and Coho salmon biomass. That modelling study did not directly manipulate abiotic variables, but instead forced trends in lower trophic level biomass as a proxy for changes in water quality.

Sobocinski et al. (2021) used an ecosystem indicators approach to assess which ecosystem factors best explained variation in survival time series for salmon populations in Puget Sound. For Chinook, factors with strongest support included sea surface temperature in Puget Sound, spring river flow in Puget Sound, seal abundance, subyearling Chinook hatchery release date, and yearling Coho hatchery release date. The study did not include metrics of prey quality or availability. The relationship to marine survival was negative for all factors except Puget Sound sea surface temperature.

For Coho, factors with strongest support included the North Pacific Index in the summer (negative relationship with marine survival rates), spring precipitation (negative relationship), stratification in the Strait of Juan de Fuca (parabolic relationship), the coefficient of variation (CV) of Chinook subyearling hatchery release date (positive relationship in which greater variation in release date was associated with higher survival), maximum spring temperature (negative relationship), seal abundance (negative relationship), summer NPGO (positive relationship), and Strait of Georgia herring abundance (positive relationship). These results collectively suggest there are likely numerous causes of decreased survival for Chinook, Coho, and steelhead, from hatchery release practices to unfavourable climate conditions to increased predation. A lack of data for potentially important ecological variables (e.g., age-0 forage fishes in Puget Sound) may limit the explanatory power of models related to marine survival.

In addition to relationships between zooplankton community structure and Chinook and Coho marine survival noted in the previous section, Keister and Herrmann (2019) found clear seasonal patterns in zooplankton community structure. Both water temperatures and PDO were related to copepod community structure (Figure 22). However, there were no clear links from abiotic factors to zooplankton to salmon survival.

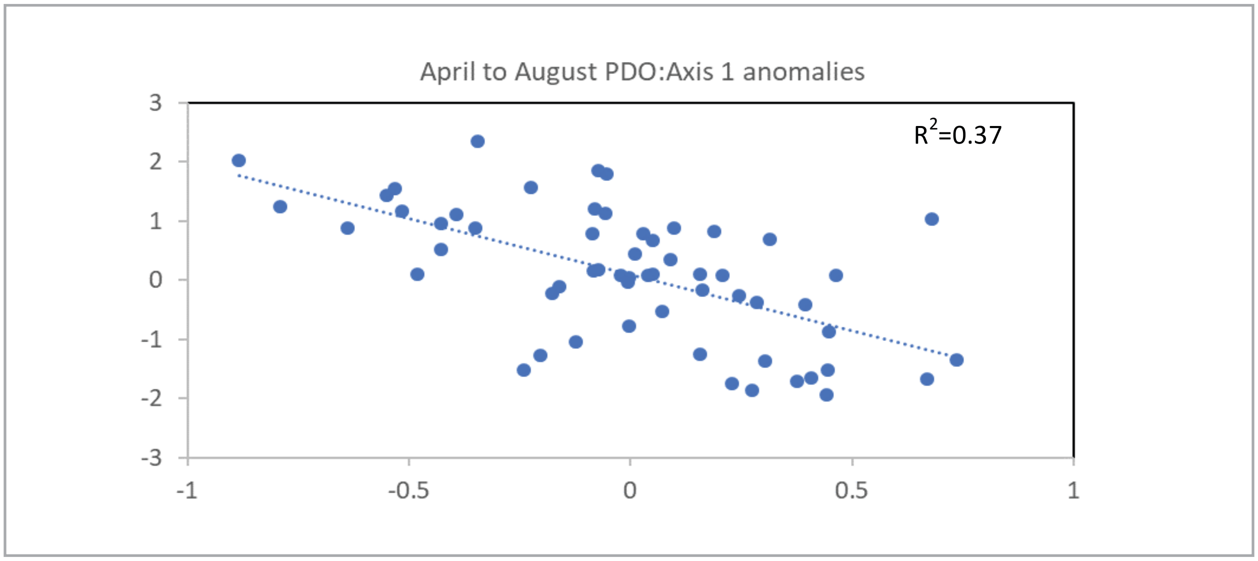

Figure 22. *Relationship between Axis 1 scores from NMS ordination of copepod species proportions and the PDO from April through August 2003-2018 samples. (Adapted from Keister and Herrmann 2019)*

Text Keister et al. (2019) found a relationship between growth of juvenile Chinook salmon from hatcheries in Puget Sound and sea surface temperature anomalies measured at Race Rocks Lighthouse, which also correlates with the Pacific Decadal Oscillation. Large interannual differences in temperature had strong effects on plankton phenology, biomass, and community structure. Local sub-basins of Puget Sound exhibited differing responses, but general patterns were evident. During warm years, zooplankton biomass and juvenile salmon growth were strongly elevated, and adult returns indicated relatively high survival: Coho salmon marine survival was higher for fish that out-migrated during the warm year of 2015 compared to cooler 2014 in nearly every stock across Puget Sound. This contrasts with observed patterns in Washington and Oregon coastal salmon populations and demonstrates the need for monitoring and indicator development within Puget Sound.

Perry et al. (2021) examined the relationship between abiotic and zooplankton variables and marine survival of specific stocks of Coho and Chinook in the Strait of Georgia. Best-fit models comparing zooplankton and physical variables with the marine survival of four salmon populations which enter the Strait as juveniles (Chinook: Cowichan River, Puntledge River, Harrison River; Coho: Big Qualicum River) all included zooplankton groups consistent with known salmon prey, and key physical variables were sea surface salinity and variables representing the flow from the Fraser River. These variables explained 38-85% of the annual variability in marine survival rates of these four salmon populations. Sea temperature was important for some relationships, but salinity was most commonly included and of high importance in the best-performing models, consistent with its influence on the hydrodynamics of the Strait of Georgia system.

Greene et al. (2020) found strong evidence for connections among abiotic variables, primary and secondary production, and growth, individual condition, and marine survival of Chinook salmon. They examined linkages between water column attributes, standing stocks of phytoplankton, epipelagic crustacean zooplankton density, and zooplankton biomass to 1) individual growth rate of juvenile Chinook salmon as reflected by IGF-1 concentrations and 2) juvenile Chinook condition factor, which integrates fish length and biomass. Over three years with contrasting environmental conditions, chlorophyll concentrations systematically varied with environmental metrics (temperature, salinity, and stratification), zooplankton biomass varied with chlorophyll concentration and environmental metrics, growth of juvenile Chinook increased with higher zooplankton biomass, higher temperature, and greater stratification, and individual size increased as a function of growth. Achieving larger size allows juvenile Chinook salmon to become piscivorous earlier in the season (Gamble et al. 2018) and, consequently, high early growth results in continued faster growth in Puget Sound (Chamberlin et al. 2016).

Greene et al.'s (2020) model predicted a positive relationship between stratification and marine survival and mixed responses of survival to temperature: a negative relationship to survival during cooler periods and positive relationship during warmer periods. Stratification facilitates osmotic transition or migration orientation (Iwata and Komatsu 1984, McInerney 1964), which may explain its positive relationship to salmon marine survival. Predicted temperature relationships contrast with observations from Pacific Coastal watersheds, where cooler marine conditions appear to facilitate better salmon growth and survival (Beckman et al. 1999, Burke et al. 2013). This may be due to the presence of fatty acid-rich boreal copepods during cooler periods (Hooff and Peterson, 2006); in the Salish Sea, cooler periods do not result in an influx of boreal copepods (Keister et al. 2017), which may explain why marine conditions on the Pacific Coast do not directly correspond with changing marine survival of Salish Sea populations (Zimmerman et al. 2015, Ruff et al. 2017).

Other findings included a unimodal relationship between chlorophyll concentrations and temperature, resulting in a prediction that chlorophyll concentrations decline as a function of temperature when temperature surpasses about 20˚C, a value that has not been observed in marine waters of Puget Sound. IGF-1 levels in Chinook increased at both the lowest and highest temperature levels. This finding is counterintuitive; growth as a function of temperature is normally treated as a unimodal relationship in bioenergetic models (e.g., Gamble 2018) with lower growth at lower and higher temperatures (Beauchamp 2009). Greene et al. (2020) suggest that this may be a result of other trophic impacts – for example, temperature may have modulated presence of forage fish, resulting in times and places with abundant forage fish prey at both lower and higher temperatures. In the Salish Sea, Pacific herring appear to prefer relatively cool temperatures (Reum et al. 2013), while pulses of high Northern anchovy abundance are associated with warmer years (Duguid et al. 2019). Conditions favoring piscivory (e.g., Chamberlin et al. 2016) deserve greater attention, as they have strong potential to modulate effects of trophic dynamics upon marine survival.

Greene et al.'s (2020) results provide strong support that bottom-up forcing can shape marine survival in Chinook salmon, especially when combined with previous analyses of size-dependent survival (Duffy and Beauchamp 2011).

Synthesis Committee Perspective

In general, the Synthesis Committee did not have enough evidence to fully assess this hypothesis: for Coho and Chinook there is some circumstantial evidence, but data are insufficient for steelhead. However, steelhead spend very little time migrating through the Salish Sea (Moore et al. 2015), suggesting that bottom-up effects may have less of an impact on their survival.

The lack of long-term datasets makes it difficult to directly test hypotheses around changes in long-term abiotic processes or associated changes in food supply. For example, there are no adequate time series of zooplankton and, although herring stock assessment data have been collected since 1951, there are very limited time series for other forage fishes within the Strait of Georgia prior to the 1990s. The synchrony in productivity shifts for salmon stocks within the Salish Sea suggests a relationship with large-scale drivers: regime changes are well-documented and well-known for the coast. However, evidence linking biogeochemistry to prey to salmon survival in the Salish Sea is weak and predominantly correlational, with almost no mechanistic links developed.

The Synthesis Committee consensus was that there is moderate evidence for impacts of changing water quality and biogeochemistry over the long-term and stronger evidence for relationships between abiotic variables and food supply in recent years. **The Synthesis Committee agreed that variables such as sea surface temperature, salinity, winds, and light/cloud cover are no doubt important to driving salmon marine survival in the Salish Sea via their impact on the food web. However, our conclusions are limited as many water properties lack long-term datasets.**

Interrelationships and Cumulative Impacts

The large number of interrelationships make it difficult to fully assess this hypothesis. For example, changes in nutrient ratios could impact zooplankton quality or availability or quantity via their impact on phytoplankton composition. As we enter a period of unknown climate regimes, we may encounter unexpected and/or new relationships between salmon populations and their environment. For example, we are beginning to see unprecedented large-scale anomalies such as marine heat waves driving short-term variation and breaking established correlational relationships. Changes in water properties under climate change are leading to increases in abundance of harmful algal blooms (HABs), changes to phytoplankton communities, and increases in abundance of jellies. In 2015, the Pacific coast experienced a massive HAB of *Pseudo-nitzschia* that was associated with the 2014-2016 Northeast Pacific marine heatwave. The HAB event delayed the opening of the lucrative commercial Dungeness crab fishery for up to five months and closed the popular recreational razor clam fishery, resulting in fishery failures and disaster declarations, causing significant sociocultural and economic impacts to coastal communities.

Management Implications and Next Steps

While it is clear the biogeochemistry of the Salish Sea has changed and is affecting salmon marine survival, we do not understand the links through the food web. It is therefore difficult to recommend specific management actions, account for biogeochemical factors in harvest management or value assessments of salmon recovery actions, or build resilience to changing biogeochemistry without additional research. Research recommendations are below. In the interim, it is strongly recommended that potential roles and impacts of climate and oceanic changes to salmon prey be recognized in recovery plans and state and province-wide climate initiatives.

Research recommendations include: improve understanding of the relationship between freshwater flows, light attenuation in the Salish Sea, and primary production; improve knowledge of historical conditions by collecting and analyzing sediment core samples to assess changes in plankton composition over time; improve modelling of zooplankton dynamics in ecosystem models; and use ecosystem models to examine tradeoffs between prey production, growth/foraging success, and predation risk including variable diatom productivity, presence/absence of *Noctiluca*, and sediment plumes. Long-term monitoring is required to better assess drivers of spring bloom timing and resulting impacts to plankton, forage fish, and salmon. This is exceedingly important as climate change continues to affect our region.

Mismatch between salmon outmigration timing and prey availability

This hypothesis states that a mismatch exists between demand (outmigrant timing and fish size) and food supply. The main predictions associated with this hypothesis were a) smolts that enter marine waters during peak prey availability grow faster, larger, and/or have higher fat content, b) peak availability of crucial prey and/or outmigration timing has shifted, decoupling supply and demand, and c) changes in peak prey availability and/or outmigration timing/fish size correlate with changes in marine survival (see Salmon Behaviour and Physical Habitat section).

The match/mismatch between juvenile salmon and their prey during this critical period can affect survival to later life stages. As noted in the Salmon Behaviour and Habitat section, there is evidence for changed Chinook and Coho outmigration timing in the Salish Sea, primarily through changes to hatchery release dates and a general reduction in wild salmon abundance. Further, changes in diversity and timing of Puget Sound Chinook and Coho hatchery release dates were included in best-fit models explaining Puget Sound Chinook and Coho marine survival trends (Sobocinski et al. 2021). The timing of prey availability may also be shifting. While there is no specific trend, it appears that spring bloom timing began occurring earlier more frequently after 1990 (Allen and Wolfe 2013). There are no sufficient zooplankton time series to assess whether changes in timing of key prey have occurred. However, previous work in the Strait of Georgia found marine survival of Coho salmon released during periods of high marine productivity was 1.5- to 3-fold greater than those released before or after high productivity periods (Chittenden et al. 2010). Further, feeding studies performed by Beauchamp et al. (2019) suggest that juvenile Chinook are sensitive to changes in larval crab size. If crab life cycles shift as little as a couple of weeks, their availability to Chinook may shift also. Pink and Chum salmon abundance, which has increased over the period of Chinook and Coho declines (Sobocinski et al. 2017), may be a signal of changes in the timing of prey availability. Pink and Chum are planktivores and enter the Salish Sea as juveniles earlier than Chinook and Coho.

Pacific herring are a key food source for juvenile Chinook as they transition to piscivory. Concerns exist regarding the match between the size of Pacific herring available for consumption and the size of juvenile Chinook that consume them. In the 1970s, juvenile Chinook consumed larval and juvenile Pacific herring throughout the spring and summer. Since then, the onset of piscivory appears to have shifted to mid-summer (Duguid et al. in review). Duguid (2020) found that predation on Pacific herring was strongly related to juvenile salmon length, suggesting that age-0 Pacific herring may have been too large to be consumed by smaller Chinook Salmon in some years. Larger juvenile Cowichan River Chinook salmon which were co-located with age-0 herring may have experienced better freshwater growth and entered the ocean later, suggesting a linkage between ocean-entry phenology and the transition to piscivory. Chamberlin et al. (2017) also found a relationship between juvenile Chinook size and the size of herring available. They suggested that the San Juan Islands are habitat for herring of suitable size as Chinook transition to piscivory. Further investigation into the relationship between herring size and juvenile Chinook diets during their first summer in Puget Sound suggests juvenile Chinook consume a significantly higher proportion of progeny from January-February Pacific herring spawners than would be expected from their estimated spawning biomass (Chamberlin et al. 2020). January-February spawners are the earliest spawning group and thus the largest-sized progeny available for consumption during the first summer for the juvenile Chinook.

Synthesis Committee Perspective

The Synthesis Committee concluded that data are insufficient to determine whether the interplay between outmigration timing and the timing of prey availability is an important driver of marine survival. Potential match/mismatch dynamics remain a concern given the sensitive relationship between juvenile salmon and their prey. This issue is of less concern for juvenile steelhead, which spend only a couple weeks within the Salish Sea on their way to the Pacific Ocean.

Interrelationships and Cumulative Impacts

Changes in timing of prey availability could be related to changes in spring bloom timing. As described in the Water Quality/Biochemistry section, spring bloom timing in the Salish Sea is sensitive to changes to light attenuation associated with the transition from winter to spring weather (Banas et al. 2019, Collins et al. 2009, Allen and Wolfe 2013). See Changes to outmigration timing and interrelationships with other factors" in the Salmon Behaviour and Physical Habitat section for more information regarding changes to outmigration timing.

Management Implications and Next Steps

It is not clear whether there is a mismatch between prey availability and juvenile Chinook and Coho prey demand; however, there are enough data to warrant testing the hypothesis. Ongoing hatchery release studies are testing the effects of different marine entry times. Environmental data should be collected in conjunction with these release studies to determine whether prey availability at release affects survival. This hypothesis will also be addressed by ongoing ecosystem modeling studies in BC and Washington (Morzaria-Luna et al. in prep, Oldford et al. in prep). Ultimately, focused sampling of salmon and lower trophic levels could be carried out in a few target regions for specific populations over the spring outmigration period to assess timing of juvenile salmon outmigration, spring bloom timing, peaks of zooplankton prey, and subsequent salmon survival.

Competition

The hypothesis related to competitive impacts on food supply was that prey availability is reduced when competition for food increases during critical periods. The main predictions associated with this hypothesis were: a) juvenile salmon growth rates are inversely rated to the abundance of conspecific or interspecific competitors and b) marine survival decreases with increasing juvenile salmon and/or forage fish abundance (e.g., Pink salmon, hatchery salmon, herring).

Salmon may experience competition at various life stages in the estuary, nearshore, and offshore rearing grounds. Juvenile Chinook and Coho competitors may include other species of Pacific salmon, hatchery salmon, and forage fish like Pacific herring. Competitive interactions may occur throughout the salmon life cycle, including in the open North Pacific, which has experienced dramatic increases in Pink, Chum, and Sockeye abundance due to changing ocean conditions and increased hatchery production (Ruggerone and Irvine 2018, Cooney and Brodeur 1998, Zaporozhets and Zaporozhets 2004, Holt et al. 2008, Walters and Juanes 1993, Ruggerone et al. 2003, 2012, 2016), and/or within the Salish Sea.

Hatchery production, Pink salmon, and Chinook salmon abundance with relation to competitive impacts on Chinook and Coho salmon

Levin et al. (2001) demonstrated a strong relationship between the numbers of hatchery Chinook produced and the survival of Snake River fall Chinook salmon; few studies have examined this in the Salish Sea. Nelson et al. (2019a) found that 3.7 billion Chinook salmon have been released into Salish Sea tributaries from hatcheries in the United States and British Columbia since 1950. Releases of Chinook peaked in Puget Sound in 1990 (77.1 million), while releases in the Strait of Georgia peaked in 1988 (33.2 million). Further increases in production of Chinook have been implemented recently for this region to increase prey for Southern Resident Killer Whales (WDFW 2019). Hatchery-wild competition within or among salmon species could occur in localized estuarine or nearshore marine habitats throughout Puget Sound. Hatchery-origin Chinook salmon tend to be larger and less variable in size than their natural counterparts. Hatchery releases can result in large pulses of fish moving into estuary and nearshore habitats over short periods of time, which may have a significant impact on demand for space and food resources. Alternatively, large numbers of juvenile Chinook entering the marine environment at once could reduce individual predation risk.

Nelson et al. (2019b) found that, although a few Salish Sea Chinook populations had moderately high probabilities of a strong negative correlation between productivity and hatchery abundance, the only statistically significant relationships found were positive. A positive relationship between productivity and hatchery abundance could possibly result from the impact of predator swamping, which has been observed for Sockeye in freshwater habitats (Furey et al. 2016). The authors concluded that these analyses did not provide clear evidence for how hatchery smolt abundance impacts wild populations at local or regional scales.

In a related effort, Greene et al. (2020) found evidence of density-dependence—competition for food and/or space—among Chinook in some Puget Sound estuaries. Frequency of density-dependent impacts varied by system (e.g., < 20% in Nisqually and > 60% in the Skagit delta) and with presence/absence of hatchery fish. However, it was clear that habitat was the primary limiting factor and not hatchery/wild competition. In the Skagit River system, Beamer et al. (in revision) found a strong stock-recruit relationship between migrant fry and juveniles in the estuary, an exponential relationship between migrant fry and fry captured in Skagit Bay (lacking estuary residence), and a negative exponential relationship between fry captured in the bay and smolt to adult return rates. The migrant fry-estuary resident transition explained 44% of the variation in smolt to adult return rates. These findings suggest competition during juvenile residency affects marine survival.

Density-dependent interactions between Pink salmon and other salmon have been documented in many studies of the North Pacific Ocean, and some studies suggest density-dependent interactions between juvenile Pink and Chinook salmon may occur in the Salish Sea (Ruggerone and Goetz 2004, Ruggerone et al. 2019, Kendall et al. 2020). High abundance of Pink salmon can impact zooplankton and, in turn, phytoplankton biomass (Sugimoto and Tadokoro 1997, Azumaya and Ishida 2000). These food web effects can result in changes in diet, food consumption, growth, and survival of salmon (Pyper and Peterman 1999, Davis et al. 2005, 2009, Ward et al. 2017). Pink salmon follow a two-year life cycle, with high numbers of juvenile Pink salmon entering the Salish Sea in even-numbered years and very low numbers entering in odd-numbered years. Most Salish Sea Pink salmon are wild, and spawner abundance has increased in the Salish Sea over the last few decades. Juvenile Chinook and Pink salmon overlap in time in the Salish Sea between April through July of even years (Duffy et al. 2005).

Ruggerone and Goetz (2004) reported a shift in even- versus odd-year variation in Chinook marine survival between two periods: ocean entry years 1972-1983 and 1984-1997. Juvenile Chinook salmon in Puget Sound had a 59% lower marine survival in even-numbered years, when juvenile Pink salmon were present, versus odd-numbered years. This pattern was evident for Puget Sound and not detectable along the coast, although coastal data were very limited. Lower survival in Puget Sound was associated with reduced growth in the first marine year and delayed maturation. Ruggerone and Goetz (2004) suggested that the shift was driven by climate-induced competition with juvenile Pink salmon in Puget Sound: prey availability for Chinook declined in Puget Sound after the 1982 El Niño and Pink salmon abundance increased. The suggestion was that Pink salmon buffered Chinook salmon from predation prior to 1982-1983 but acted as competitors thereafter, shifting mortality from predation-based to competition-based.

Kendall et al. (2020) found that the survival of hatchery Chinook salmon released into the central and southern parts of the Salish Sea between 1983 and 2012 may be associated with a combination of the number of Chinook salmon released and the presence of naturally produced Pink salmon. Consistent with Ruggerone and Goetz (2004), survival of hatchery Chinook salmon decreased in even-numbered ocean entry years (when large numbers of juvenile Pink salmon were present in the Salish Sea) but increased or remained stable during odd-numbered ocean entry years (Figure 23). This relationship was not apparent in wild Chinook salmon populations, consistent with findings by Beamish et al. (2010) in the Strait of Georgia.

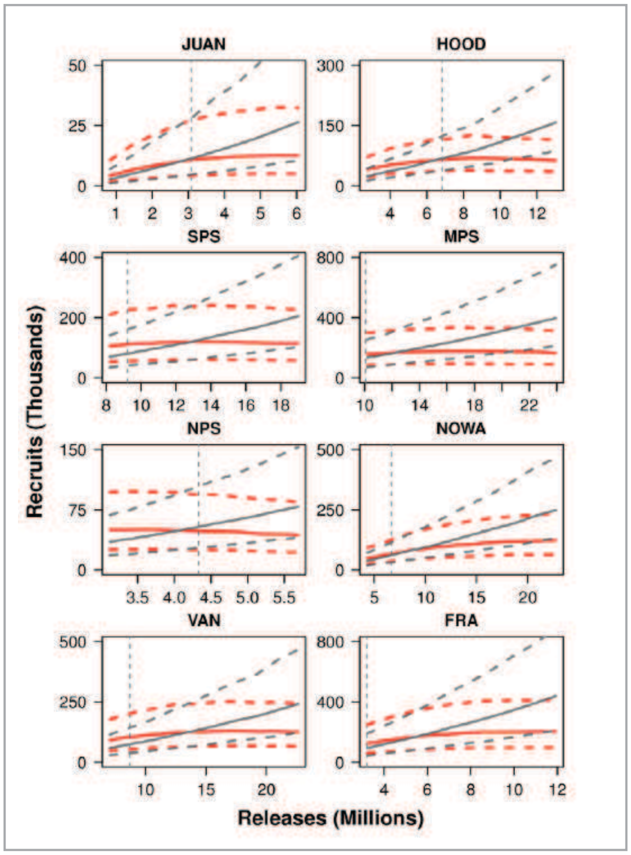

Figure 23. *Projected subyearling hatchery Chinook salmon recruits (age-2) in the ocean (y-axis) vs. the total number of juveniles released in each region (x-axis). Release number minimums and maximums on the x-axes reflect the observed range of total hatchery Chinook released in each region (Appendix S1: Fig. S5). Gray lines show projected values in non-pink (odd-numbered) years, while red lines show values in pink years. Dashed lines depict 95% posterior predictive intervals. Vertical dashed lines show average annual number of releases for the most recent five years in each region. (Source: Kendall et al. 2020)*

In a recent analysis of all available marine survival rate data available from the Regional Mark Information System (from 1970 to present), Haggerty (pers. comm.) found another shift in even versus odd year Chinook marine survival that occurred since the late 1990s through present, with even-numbered ocean entry years having higher survival rates even though juvenile Pink salmon were present (Figure 24). Haggerty (pers. comm.) found similarly strong even versus odd year Chinook survival patterns for Sooes Creek and Robertson Creek Chinook, coastal stocks where virtually no juvenile Pink salmon are present. Further, Pink salmon abundance in the Salish Sea has been much higher since the late 1990s than previous decades. This new information suggests periods of change in even versus odd year Chinook marine survival are more likely attributable to large-scale changes to prey availability for juvenile Chinook rather than competition or predation buffering by Pink salmon.

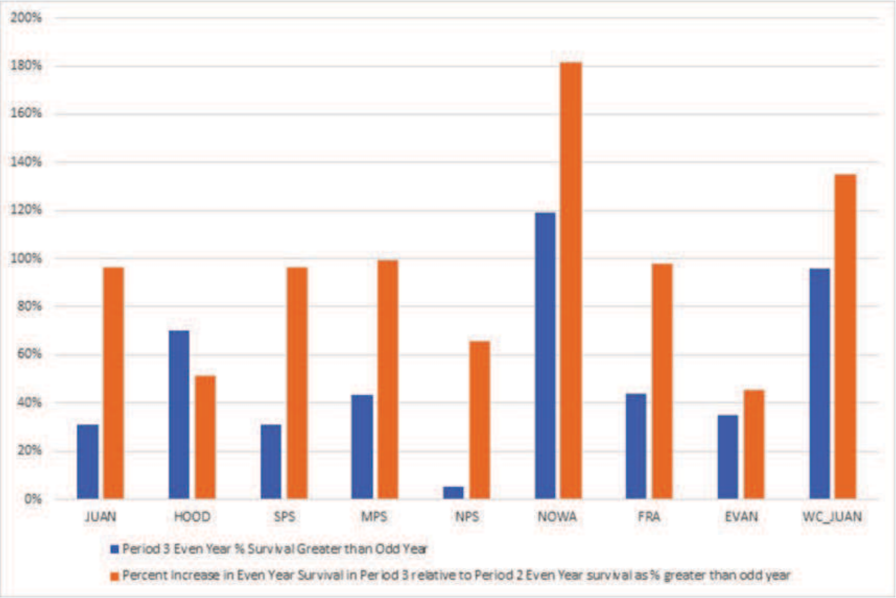

Figure 24. *The shift toward higher survival in even vs. odd years (late 1990s through present) was consistent throughout the Salish Sea, comprising 16 out of 19 stocks in Washington State and British Columbia mainland regions of the Salish Sea. The three outliers are summer-spring stocks: Wallace River Hatchery and Lower Shuswap summers, Skagit River springs. (Source: Mike Haggerty)*

Beamish et al. (2010) found that hatchery juvenile Coho had lower marine survival in years of large Pink abundance. However, initial work investigating the relationship between Salish Sea Coho marine survival and Pink salmon presence suggests there is no density-dependent Coho response to Pink salmon presence, though there is a density-dependent response to the number of hatchery Coho released (Kendall 2020b).

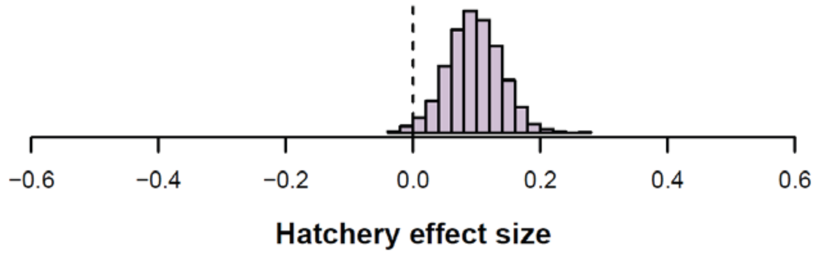

Figure 25. *Marginal posterior distributions for effect sizes relative to mortality of Salish Sea hatchery Coho abundance in the Coho salmon survival/mortality model. (Source: Kendall et al. 2020b)*

Forage fish competition with Chinook and Coho salmon

Forage fish species such as Northern anchovy and Pacific herring are both potential prey and potential competitors of juvenile Pacific salmon. Juvenile Coho salmon and Chinook salmon feed on age-0 herring during the summer and fall (Beamish et al. 2004, Duffy et al. 2010, Preikshot et al. 2013, Kemp 2014). Chamberlin et al. (2017) suggested that the impact of herring as a competitor may depend on the relative size of the co-mingling juvenile Chinook, with smaller Chinook experiencing reduced growth due to competition by abundant herring and larger juvenile Chinook salmon showing positive growth responses due to an abundant source of prey. Northern anchovy have increased in abundance since 2014 along with warming Salish Sea water temperatures (Duguid et al. 2019).

Boldt et al. (2018) found that bottom-up processes were correlated with the relative abundance and condition of age-0 herring in the Strait of Georgia. In addition, the relative abundance of age-0 herring increased with increasing juvenile salmon abundance, indicating that conditions favourable for herring were also favourable for juvenile Chinook and Coho. This corroborated previous observations of common patterns in juvenile herring and juvenile Coho salmon production in the Strait (Beamish et al. 2012). Together, these findings suggest that Pacific herring are not competing sufficiently to produce negative impacts to juvenile Chinook and Coho salmon.

Synthesis Committee Perspective

The Synthesis Committee concluded that competition may have had some role in explaining long-term trends and recent patterns in Chinook and Coho marine survival. There is weak to moderate evidence that competitive impacts could explain long-term trends in Chinook and Coho survival, and moderate to high levels of evidence in recent years suggesting impacts to marine survival for some populations.

Historically, salmon were more abundant in the Salish Sea so we might expect competition pressure among salmon to have been greater in the past. However, the relative abundance of salmon species may be changing, increasing the potential for interspecific competition. There are now twice as many Pink and Chum as Coho and Chinook within the Strait of Georgia (Neville pers. comm.). Although these species do not have the same diets, there are some signs of competition with Chinook (Kendell et al. 2020a) and it is possible that there is enough diet overlap to stress prey supply. Alternatively, Pink and Chum could be competing with herring, which are an important food source for Chinook and Coho.

Generally, the results of current studies are mixed regarding the level of impact competition may have on salmon survival. There is a strong negative correlation between Salish Sea hatchery Coho survival and the number of hatchery Coho released, but the presence/absence of abundant juvenile Pink salmon in even versus odd years of juvenile Coho ocean entry has no effect (Kendall et al. 2020b). Central and southern Puget Sound Chinook marine survival was negatively correlated with higher numbers of hatchery Chinook released and the presence of Pink salmon between 1983 and 2012 (Kendall et al. 2020); however, ongoing analyses suggest this relationship may have only occurred in Puget Sound until 2000 and switched to a positive correlation thereafter when Pink salmon were very abundant (pers. comm. Haggerty). Further, this relationship does not exist for wild Chinook (Kendall et al. 2020, Beamish et al. 2010) and there is a weakly positive relationship between Strait of Georgia hatchery Chinook survival and release numbers (Nelson 2019b). Density-dependent effects occur among Chinook in Puget Sound estuaries; this seems to be largely a function of habitat condition and not hatchery/wild competition (Greene et al. 2020). There have been concerns regarding the potential for competition between herring and juvenile Chinook and Coho salmon when they comingle at similar sizes. However, recent evidence suggests that juvenile Chinook, Coho, and age-0 herring abundance in the Strait of Georgia positively correlate and are driven by bottom-up processes (Boldt et al. 2018).

Overall, the Synthesis Committee agreed that the studies carried out to date provide some evidence of competitive impacts to marine survival of Chinook and Coho during some time periods and in some places. Juvenile steelhead abundance is very low relative to other salmon and they migrate out of the Salish Sea quickly; therefore, competition is not likely a factor. Ultimately, if inter- or intra-species competition is occurring in the Salish Sea, it is most likely exacerbating situations or places where food supply or habitat are limited.

Interrelationships and Cumulative Effects

Competition is intertwined with changes in Salish Sea productivity. If bottom-up processes lead to declines in plankton productivity, the likelihood of competition for food increases even if there is no change in the abundance of competitors. Regional differences in productivity and competitor abundance and changes to salmon distribution or movement patterns could affect the significance of competition as a mediator of survival. For example, there may be localized competitive impacts caused by large aggregations of jellyfish depleting prey supply (Greene et al. pers. comm., Greene et al. 2015). Competition may increase in local nearshore areas due to habitat loss. How variability in size and timing of hatchery releases can impact competition is another key consideration (Nelson et al. 2019a).

Finally, competition could result not only in reduced growth or survival but also changes in distribution or residency in the Salish Sea. SSMSP ecosystem modeling work (Atlantis model for Puget Sound and Ecopath with Ecosim for the Strait of Georgia) will allow testing of hypotheses related to competition for food, which will be tested at a community scale and in combination with other hypotheses in top-down and bottom-up forcing (Morzaria-Luna et al. in prep, Oldford pers. comm.).

Management Implications and Next Steps

Scientists and hatchery managers could carry out experimental studies at Salish Sea hatcheries to evaluate density-dependent effects. Larger and smaller numbers of hatchery Chinook and Coho could be released in different sub-basins throughout the Salish Sea. Impacts to size, growth, and survival of both hatchery and wild Chinook and Coho salmon could then be evaluated. Ongoing changes in hatchery production can also be perceived as natural experiments: for example, hatchery production of Puget Sound Chinook increased during 2019-2020 and Chilliwack Chinook production increased 2019-2020; Strait of Georgia Coho production was reduced about 40% in the mid-2000s.

Other potential next steps include:

1. Examine the hypothesis that feeding by Pink, Chum, and herring on earlier life stages of crab larvae deplete the availability of edible crab larvae for Chinook and Coho.
2. Investigate intra-guild predation (IGP) using 2014-2015 datasets from throughout Puget Sound to evaluate how relative size and abundance of predators influence growth of Chinook, herring, and sand lance, and identify potential size and abundance thresholds where competitors become prey.
3. Gather abundance trend data for other potential competitors such as pollock, hake, and humpback whales, and assess potential impacts in ecosystem models or correlative analyses.

Harmful Algae

Harmful algal blooms (HABs) can affect salmon survival directly through mortality or indirectly through food web impoverishment (Rensel et al. 2010). The direct mortality hypothesis was that harmful algae affects salmon survival through acute or chronic toxicity or gill damage, with a key prediction that direct mortality increases as prevalence and intensity of Heterosigma and other harmful algae increase. The hypothesis related to impacts of harmful algae on food supply was that harmful algae indirectly affects salmon survival through food web and salmon prey impoverishment. The main prediction associated with this hypothesis was that HABs impact the timing, duration, quantity, spatial extent, and/or composition/quality of zooplankton.

The prevalence and impacts of HABs on Pacific coastal communities of North America have increased greatly in frequency and distribution over the last decades (Hallegraeff et al. 2003, Lewitus et al. 2012, Rensel et al. 2010). Hypothesized reasons behind HAB increases include changes in anthropogenic nutrient loading in coastal zones, changes in sea surface temperatures due to climate change, and increasing awareness and monitoring of HABs (Heisler et al. 2008, Hallegraeff 2010). The timing of blooms is sensitive to weather and climate, and many toxic blooms are driven by warming temperatures (Moore et al. 2009).

While HABs are most often referenced as a concern for the aquaculture industry (Haigh and Esenkulova 2014a, Horner et al. 1997, Rensel and Whyte 2004, Taylor and Harrison 2002, Whyte et al. 1997), many HABs have the potential to affect wild and hatchery Pacific salmon in open marine waters. Of particular concern is *Heterosigma akashiwo*, a microflagellate HAB species that appears to have become more prevalent in the Salish Sea since 1989 and has been recorded in all basins of the Salish Sea. *H. akashiwo* is probably the most prominent fish-killing species in the world (Hallegraeff et al. 2004). *H. akashiwo* blooms have been implicated in poor survival of Fraser River Sockeye (Rensel et al. 2010). Rensel et al. (2010) found that earlier and larger spring and early summer Fraser River flows were linked to major blooms of *H. akashiwo*.

Few studies have assessed the impacts of HABs on zooplankton, although it is believed that HABs affect zooplankton grazing and reproduction and impacts are complex (Turner and Tester 1997, Sunda et al. 2006). Sunda et al. (2006) suggest that unpalatable HAB species reduce zooplankton grazing rates, thereby decreasing regeneration of nutrients. Reduced nutrient regeneration will accelerate bloom development for HAB species that are adapted to nutrient-limited environments. Zooplankton grazers may not be capable of controlling bloom formation of HAB species, and nutrient cycling dynamics in the coastal ocean may change with increases in the presence of harmful and toxic algal blooms (Saba et al. 2011).

The presence of HABs could impact food supply for juvenile fish if blooms lead to delayed entry to feeding areas in nearshore habitats and mismatches with zooplankton blooms. Studies in Cowichan Bay, BC, suggest that Chinook smolts may avoid contact with or delay entry into waters contaminated with HABs (Chittenden et al. 2018).

The SSMSP did not include assessment of relationships between HABs and Chinook, Coho, or steelhead mortality. However, SSMSP studies provided some of the first evidence for direct effects of HABs on wild juvenile salmon in the Strait of Georgia. During a 2014 juvenile salmon survey in Cowichan Bay, blooms of *H. akashiwo* were recorded and researchers observed reduced feeding in juvenile salmon (> 50% of the fish had empty stomachs) and changes in salmon diet composition during high algal biomass events. They also observed evidence of gill damage following high levels of mechanically harmful diatoms; histopathology confirmed liver damage, brain damage, and signs of starvation during moderate toxic algae levels. Chinook displayed lethargic behaviour and a dramatic increase in mortality after being PIT tagged during sampling (Esenkulova et al. 2014).

HAB patterns and composition were assessed via the PSF Citizen Science Oceanography Program. Phytoplankton and zooplankton sampling in the Strait of Georgia showed that several HAB species reached moderate levels over the course of 2015-2018, including *H. akashiwo, Dictyocha spp., Chaetoceros convolutus* and *C. concavicornis, and Rhizosolenia setigera* (See Figure 26 next page).

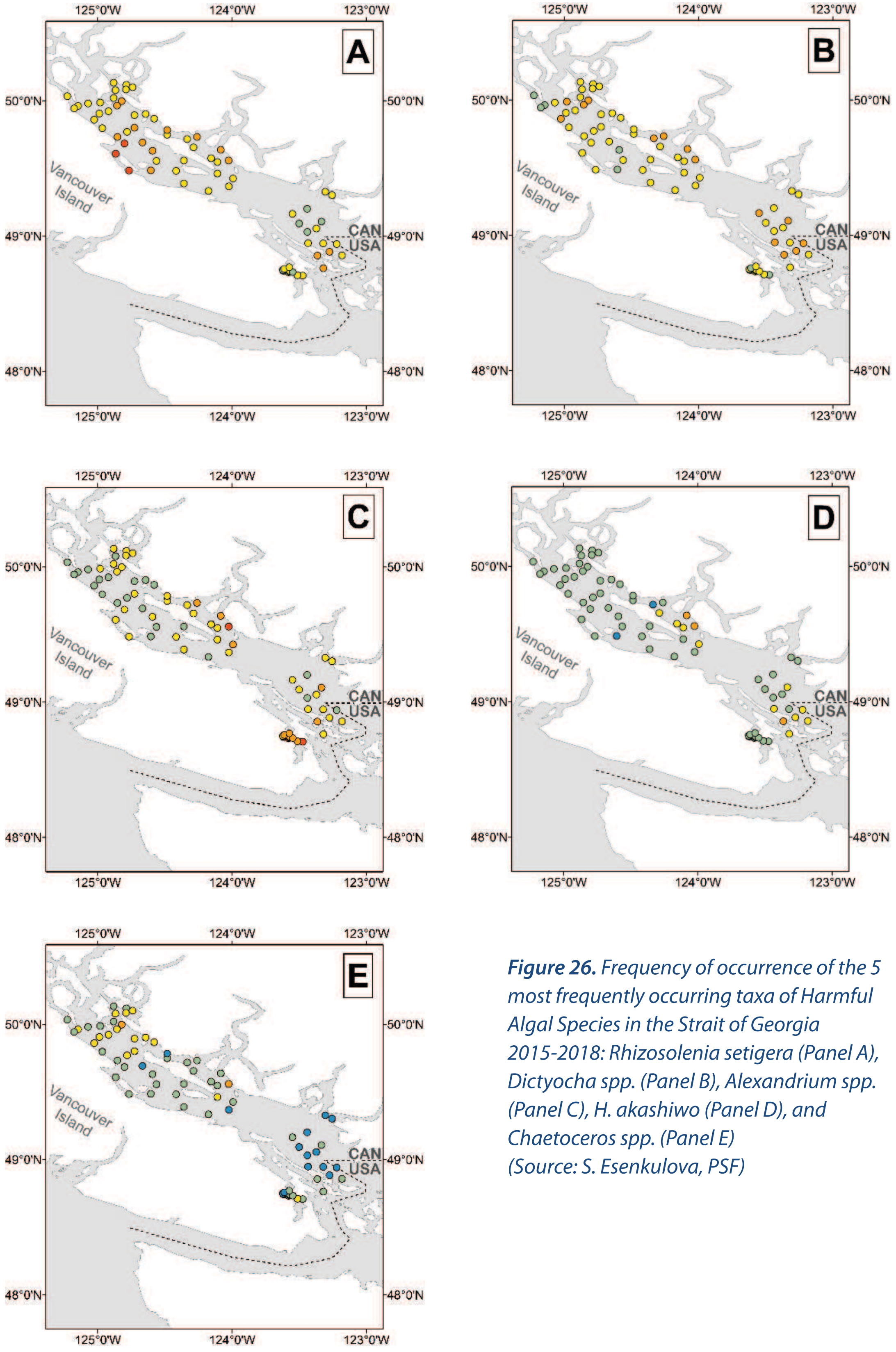

Figure 26. *Frequency of occurrence of the 5 most frequently occurring taxa of Harmful Algal Species in the Strait of Georgia 2015-2018: Rhizosolenia setigera (Panel A), Dictyocha spp. (Panel B), Alexandrium spp. (Panel C), H. akashiwo (Panel D), and Chaetoceros spp. (Panel E) (Source: S. Esenkulova, PSF)*

Cells of *Dictyocha* are toxic to salmon and very high concentrations can kill fish within minutes (Black et al. 1991, Rensel and Whyte 2004). *C. convolutus, C. concavicornis,* and *R. setigera* are mechanically harmful (Rensel and Whyte 2004); although brief exposure to high levels may not kill fish instantly, it could compromise gill function and make the fish vulnerable to infections (Albright et al. 1993, Yang and Albright 1992). Esenkulova et al. (in prep) found clear relationships between water quality parameters and HAB prevalence in the Strait, indicating that most HAB taxa have distinct environmental niches. On average, *R. setigera* was seen in nutrient-poor waters; its abundance was negatively correlated with silicates and positively correlated with salinity. Blooms of *Dictyocha* appeared to be most associated with occurrence of recent heavy rains, stratified waters, and high cloud cover. *Dictyocha*, closely followed by *Heterosigma*, appeared in the most stratified waters compared to other harmful algae. *Dictyocha* also showed a significant negative relationship with concentrations of phosphates and silicates. Both *Dictyocha* and *R. setigera* require high silica conditions to form cells; blooms of these taxa result in silica-poor waters. Similar to *Dictyocha spp*., *H. akashiwo* was present at a wide range of salinities and in highly stratified but warmer waters. *H. akashiwo* presence was statistically related to stratification, which is affected by the Fraser River flow, and silica. *C. convolutus* and *C. concavicornis* are known to cause fish kills due to gill damage in Chile and along the Pacific coast of Canada (Albright et al. 1993, Haigh and Esenkulova 2014b, Hallegraeff et al. 2004, Taylor and Harrison 2002). Overall, these species had the most unique environmental niche in the Strait and appeared to do well in cold, salty, nutrient-rich, well-mixed, unstratified waters with low light levels. Many of these conditions such as increased sea surface temperatures, early and altered freshet from the Fraser River, increased stratification, and altered geochemical cycling may become more common under ongoing climate change (Morrison et al. 2002; Johannessen and Macdonald 2009).

Spatial differences were also apparent. Most southern and northern parts of the Strait (Victoria and Campbell River) had nitrate- and nitrite-rich, turbulent waters displaying low phytoplankton cell concentrations, whereas areas of the central Strait of Georgia in close proximity to river input (Fraser River and, to a lesser extent, the Cowichan River) were silicate-rich, highly stratified, with high chlorophyll a concentrations and dense *Dictyocha* and *H. akashiwo* blooms; meanwhile, Malaspina Inlet had nitrate-, nitrite-, and phosphate-rich waters at 20 m, moderate to high stratification with high phytoplankton cell concentrations, and displayed frequent occurrence of HABs.

The variable environmental conditions over the course of SSMSP were associated with variable spring bloom composition and timing. The spring bloom of 2015 occurred very early, most likely due to warm winter temperatures and high stratification. It was unusually comprised of *Skeletonema*, and summer phytoplankton cell concentrations were low even though surface waters were not nutrient-depleted. Spring blooms in 2016-2018 occurred later and lasted longer than in 2015 and were comprised of diatoms (*Thalassiosira, Skeletonema,* and *Chaetoceros*); summer cell concentrations were high and blooms of several HAB taxa were observed. There were much higher abundances of dinoflagellates, silicoflagellates, and raphidophytes in the summers of 2016-2018 associated with high stratification and substantial freshwater input from the Fraser River and rainfall.

Synthesis Committee Perspective

In summary, the SSMSP documented direct effects of algae blooms on juvenile salmon in coastal waters, but the lack of long-term HAB occurrence data and direct tests of impacts on juvenile salmonids precluded the Synthesis Committee from forming conclusions on the role of HABS on marine survival. The frequency and magnitude of HAB occurrences are likely to increase under increasing impacts of climate change (Hallegraeff 2010). Zooplankton grazing and nutrient release processes are expected to change concurrently with phytoplankton, which may affect the behaviour, growth, and survival of salmon.

Interrelationships and Cumulative Effects

Interrelationships that increase or reduce importance of this factor to salmon include the consideration that changing climate will lead to further increases in salinity and sea surface temperatures, likely increasing the prevalence of HABs within the Salish Sea, as well as changing potential linkages salmon outmigration timing and HAB timing.

Management Implications and Next Steps

Regional studies relying on occasional, short-term phytoplankton sampling and/or neglecting taxonomic composition can be inadequate for ecosystem-based research. These challenges could be addressed with high resolution monitoring, as evident from Esenkulova et al. (in prep). Interannual variability in phytoplankton dynamics highlights the need for long-term data to capture more HAB events and establish factors influencing bloom development of certain taxa. Further studies examining impacts of HABs on productivity, carbon cycling, and physical damage and/or mortality of Pacific salmon are necessary.

Laboratory trials testing the effects of varying densities of HABs (or varying levels of the toxins they produce) on smolt behaviour and physiology would improve our understanding of field observations noted by Chittenden et al. (2018) and Esenkulova et al. (in prep). Telemetry tools, such as acoustic transmitters and receivers, could be used to examine smolt behaviour and survival around *H. akashiwo*, *Noctiluca*, and other HABs. Additionally, the new Fit Chip tool developed by the SSHI program and Dr. Miller's lab at DFO could be used to quantify HAB species and relate HABs to stressor biomarkers in salmon. Finally, a near-term action may be to access better HAB trend data by coordinating with Washington Sea Grant Sound Toxins program and assess whether there is broader correlative evidence supporting a relationship between HABs and salmon marine survival.

Ocean Acidification

The hypothesis considered was that ocean acidification affects the productivity or quality of important zooplankton invertebrate prey for salmon (and forage fish). Ocean acidification may operate alone or synergistically with low oxygen, higher temperatures, and contaminants. The main prediction associated with this hypothesis was that the timing, duration, quantity, spatial extent, and/or composition/quality of zooplankton are constrained as the Salish Sea becomes more acidic.

No direct evaluation of this hypothesis was carried out during the SSMSP, but ocean acidification (OA) has been observed throughout the global open ocean (Brewer 1978; Sabine 2004; Feely et al. 2004, 2009, Bates et al. 2014). The marine carbon dioxide system is affected by numerous processes (Evans et al. 2019), many of which make it challenging to attribute OA to anthropogenic causes in the coastal zone. However, many of the properties of the Salish Sea — which is naturally acidic due to restricted circulation, incursion of upwelled waters, and acidic river inputs — put it at high risk of impacts from OA.

Ianson et al. (2019) presented the first inorganic carbon data collected in the Strait of Georgia covering all seasons (2003 and 2010–2012) in the context of local circulation and oxygen cycles. Their results showed that the Strait of Georgia has a higher carbon content and lower pH than surrounding waters. During winter, surface pH throughout the Strait is ~7.8 ppt, similar to values reported in Puget Sound (Feely et al. 2010), and the full water column is undersaturated with respect to aragonite. Surface undersaturation only ends with the advent of the spring bloom, when pH increases rapidly, reaching 8.2 ppt in the southern Strait (Moore-Maley et al. 2016). Aragonite saturation horizons reach their deepest level in the Strait during the spring but are only 20 m in the southern and 30 m in the northern Strait. Many organisms live below these depths (Haigh et al. 2015).

A 25-year analysis of OA in Puget Sound basins found that surface seawater pH decreased significantly over time; the rate of pH decrease was, on average, about five times greater than that predicted from atmospheric CO_2 changes alone (Lowe et al. 2019). Concomitant changes in dissolved oxygen support the hypothesis that local biological processes have modulated global ocean acidification: in this case, accelerating long-term pH decline.

In Puget Sound, summer aragonite saturation horizons appear to be deeper (30 m to > 100 m) (Feely et al. 2010) than those in the Strait. However, these horizons are rarely less than 20 m on the outer BC shelf where the entire water column is often supersaturated with aragonite (Lara-Espinosa 2013). In the Strait of Georgia, less than 10–20% of the ~150–400 m water column is supersaturated. Thus, the Strait of Georgia is particularly vulnerable to OA (Ianson et al. 2019). This may be a common feature of estuarine regions with restricted exchange where tidal mixing is intense.

There are concerns about future impacts, given the predicted trajectory for atmospheric CO_2 and long-term local trends in seawater pH. Several studies have examined the seasonality of OA in the Salish Sea and predicted future conditions under global climate change. Seasonal ranges of pH are 27 times higher in Hood Canal than in adjoining areas of the North Pacific Ocean, and organisms in the Salish Sea are exposed to much greater variability in seasonal acidity than those in nearby areas in the Pacific (Fassbender et al. 2018). There is lower buffering capacity within the Salish Sea so the water is less efficient at taking up anthropogenic carbon than open waters at the same latitude. Recent work in the Strait of Georgia included continuous measurements at two sites as well as spatially- and seasonally-distributed discrete seawater samples, such as water samples collected from PSF citizen science vessels operating in the northern Strait of Georgia (Evans et al. 2019). Researchers found the northern Strait was at non-corrosive levels only during spring and summer months, and this was only in the case in the upper water column. Their study also showed that wintertime corrosive conditions were likely absent before 1900 but are projected to decline to conditions below identified biological thresholds for select vulnerable species in the coming decades.

It is generally agreed that OA will cause shifts in phytoplankton species composition, but the actual direction of these shifts is not certain (Riebesell and Tortell 2011). The harmful alga *Heterosigma akashiwo* relies on passive diffusion to obtain CO_2 and therefore responds positively to an increase in dissolved CO_2 with increased rates of growth and primary productivity (Clark and Finn, 2000) regardless of temperature (Fu et al. 2008). Climate change and increasing OA will likely increase prevalence of HABs, as well as the production of potent neurotoxins such as domoic acid by diatom species of *Pseudo-nitzschia* and *saxitoxin* by dinoflagellate species of *Alexandrium* (Hallegraeff 2010, Hwang and Lu 2000, Fu et al. 2010, Tatters et al. 2013).

The prey of all Pacific salmon may be affected by OA, and salmon populations that remain resident within the Salish Sea, or whose diet depends on species directly vulnerable to ocean acidification, would be at most risk. Increased concentrations of CO_2 in the marine environment can impede the calcification process and influence the physiology of marine organisms by changing their internal acid-base balance—potentially leading to changes in protein synthesis, growth, development, and neurophysiology—and reducing oxygen transport capacity. Invertebrate prey important to salmon and herring diets could be affected, including gammarid amphipods, harpacticoid and calanoid copepods, euphausiids, and decapod larvae (Bednarsek et al. 2020). Krill, or *Euphausia pacifica* (McLaskey et al. 2016), and the pteropod *Limacina helicina* (Bednarsek et al. 2017) may be impacted by conditions currently observed within the Salish Sea. There is experimental evidence that *E. pacifica* larval development and survival is reduced at pH levels of 7.69 (McLaskey et al. 2016), values already seen in the region (Feely et al. 2010, Fassbender et al. 2018). Finfish are likely to experience OA impacts through food web changes in BC and the main basin of Puget Sound (Haigh et al. 2015, Busch et al. 2013). In BC, OA impacts include the decline of pteropods, which are directly preyed upon by some fish (particularly Pink Salmon), and the anticipated decline of some echinoderms, which are eaten by various species of rockfish and flatfish. OA may also result in habitat changes, such as a shift from upright macroalgae to algal turf, which could have a negative impact on juvenile salmon.

Direct impacts of increased CO_2 on salmon and forage fish may also be a concern. Williams et al. (2018) found that Coho salmon exposed to elevated CO_2 can experience significant behavioural impairments likely driven by alteration in higher-order neural signal processing within the olfactory bulb. However, the levels of CO_2 tested in that study were higher than naturally occurring. Frommel et al. (2020) tested the impact of naturally occurring CO_2 levels on juvenile Pink salmon from the Strait of Georgia and found minimal effect, suggesting juvenile Pink salmon are resilient to current CO_2 levels.

Synthesis Committee Perspective

The Synthesis Committee did not review or comment on the potential impacts of ocean acidification. Participating scientists have generally stated that, while they are concerned over future impacts of ocean acidification, changes in acidification since the 1980s do not appear to be significant enough to cause direct or indirect impacts to salmon.

Management Implications and Next Steps

There was no direct assessment of this hypothesis during the SSMSP. There are few direct OA studies on Pacific salmon, nor are there studies that determine how salmon will handle cumulative impacts of increased OA and other stressors such as increased temperatures, contaminants, or reduced dissolved oxygen. The Synthesis Committee did not consider OA an important hypothesis explaining the declines in Coho, Chinook, and Steelhead in the Salish Sea, but OA impacts are flagged as an area of increasing concern given current acidification projections.

SSMSP research recommendations include concurrent monitoring of Salish Sea carbon chemistry with biological investigations of Pacific salmon, incorporating ocean acidification data into modelling exercises to evaluate synergistic and food web effects, and process studies evaluating the effects of pH/pCO_2 variability on salmon and forage fish and their invertebrate prey.

A next step to forecast future impacts of OA will be the ability to use the SalishSeaCast model developed by the Allen laboratory at the University of British Columbia which will include a fully coupled carbonate chemistry component, the Salish Sea Model, and LiveOcean[29] to predict carbonate chemistry in the Salish Sea under future climate scenarios.

3. Predation

There were several predation hypotheses guiding the SSMSP research. Four primary hypotheses are discussed here, including:

1. An increase in the abundance of predators has led to higher juvenile salmon/steelhead mortality. Predictions are a) mortality rates increase where the abundance of predators has also increased, and/or b) predation-based mortality rates account for a substantial amount of total marine mortality.
2. Certain predators specialize in consuming juvenile Coho, Chinook, and steelhead, and the number of predators that specialize has increased. Predictions are a) there is evidence that predators specialize in consuming juvenile salmon/steelhead in Puget Sound, b) proportionally, the impact of specialists on salmon is greater than generalists, and/or c) an increase in the number of harbour seal specialists correlates with lower marine survival.
3. Predation rates have increased due to large pulses of juvenile salmon/steelhead entering the marine environment. Predictions are a) mortality rates increase immediately following influxes of juvenile salmon and/or steelhead in the marine environment, and/or b) changes in outmigration timing/distribution correlate with changes in marine survival (see Salmon Behaviour and Physical Habitat section).
4. The probability of being detected/targeted by predators may decrease with increased abundance of alternative prey. Predictions are a) mortality rates decrease with increasing abundance of a predators' primary prey items (e.g., hake and forage fish for harbour seals), and/or b) a decline in predators' primary prey items is correlated with lower marine survival.

The following is a brief synopsis focused primarily on the results of work affiliated with the SSMSP. For a more thorough review of the current state of science, see the report titled "Synthesis of Scientific Knowledge and Uncertainty about Population Dynamics and Diet Preferences of Harbour Seals, Steller Sea Lions and California Sea Lions, and their Impacts on Salmon in the Salish Sea" (Trites and Rosen 2019, Trzcinski 2020).

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[29] Salish Sea Model = https://www.pnnl.gov/projects/salish-sea-model. , LiveOcean = https://faculty.washington.edu/pmacc/LO/LiveOcean.html

Predator abundance and specialization

While multiple predators were investigated in the SSMSP (Pearson 2015, Sherker 2020, Furey and Hinch 2017, Beauchamp 2020), harbour seals were the primary focus. Harbour seal abundance has increased seven-fold in the Salish Sea since seals received protection under the Marine Mammal Protection Act of 1972 (Jeffries 2003, Olesiuk 2009). Analyses suggest harbour seal abundance is negatively correlated with marine survival of Chinook, Coho, and steelhead (Nelson et al. 2019b, Sobocinski et al. 2021, Sobocinski et al. 2020). Multivariate analyses examining the influence of multiple factors on Puget Sound Chinook, Coho, and steelhead marine survival included changes in harbour seal abundance in their best models (Sobocinski et al. 2021, Sobocinski et al. 2020). An analysis of univariate relationships between each species and seal abundance suggests that for Puget Sound steelhead trout and Coho salmon, seal abundance explained more variance in the data (22% and 30%, respectively) than for Chinook salmon (< 8.6%) (Sobocinksi, as reported in Trites and Rosen 2019).

Assessments of seal diets suggest that seals preferentially target juvenile Chinook, Coho, and Sockeye salmon over juvenile Pink and Chum salmon in the spring even though Pink and Chum are more abundant (Thomas et al. 2017). This may be due to the larger size of Chinook, Coho, and Sockeye at outmigration; however, all salmon species overlap in size during residence in the Salish Sea (Thomas et al. 2017). While juvenile salmon are a minor component of the overall seal diet (< 5% juvenile salmon, and ~2% juvenile Chinook salmon in the spring diet), the high abundance of seals and their energetic demands can result in a significant overall impact (Thomas et al. 2017, Nelson et al. in prep, Nelson 2020, Nelson et al. in press, Chasco et al. 2017). Harbour seals consume an estimated 5-39% of all hatchery and wild juvenile Chinook and 3-9% of juvenile Coho migrating out of Puget Sound (Figure 27) (Nelson et al. in press). Similarly, Chasco et al. (2017) estimated that 22% of juvenile hatchery Chinook released into Puget Sound are consumed by seals.

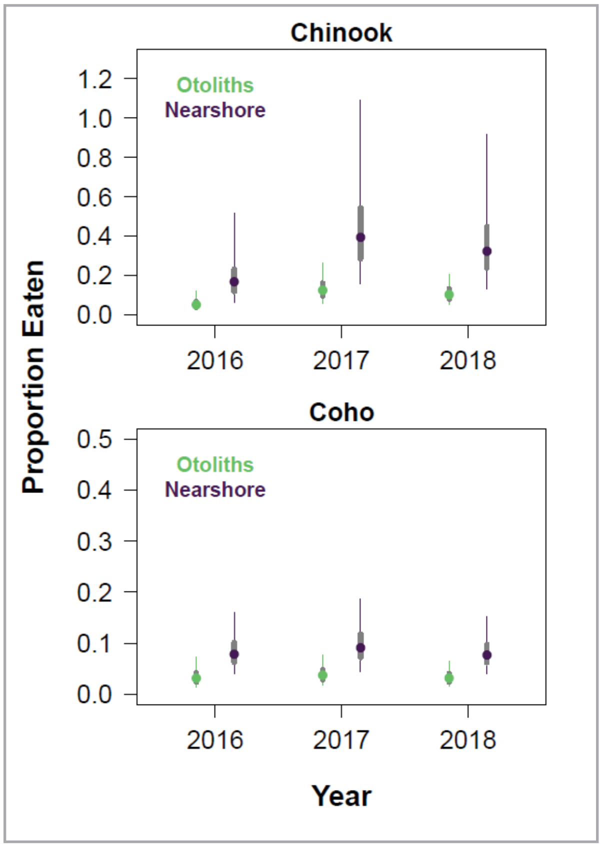

Figure 27. *Estimated proportions of ocean age-0 Chinook and coho salmon eaten by harbor seals in the Puget Sound between the months of February-August. Purple circles show estimates using size data from nearshore surveys throughout the Puget Sound, and green circles are estimates using prey size data derived from otolith measurements from structures recovered from scat samples during 2016-2018. Solid colored lines depict the 95% confidence intervals, while grey lines depict the 50% confidence intervals (Source: Nelson et al. in press)*

In the Strait of Georgia, harbour seals are estimated to consume between 37-43% of all hatchery and wild juvenile Chinook, and 47-59% of all Coho (Figure 28) (Nelson et al. in prep, Nelson 2020). Peak mortality appears to occur in June/July for juvenile Chinook smolts and April and July for juvenile Coho smolts (Thomas et al. 2017). It was estimated that 18% of the fall mortality observed in acoustic-tagged Cowichan River Chinook could be attributed to seal predation (Kintama pers. comm.). A wider range of juvenile salmon sizes were used for Puget Sound consumption estimates, illustrating the sensitivity of consumption estimates to assumptions about prey size (Nelson et al. in press). Limited seal diet sampling locations could affect the validity of generalizing site-specific consumption estimates across the entire seal population (Trites and Rosen 2019).

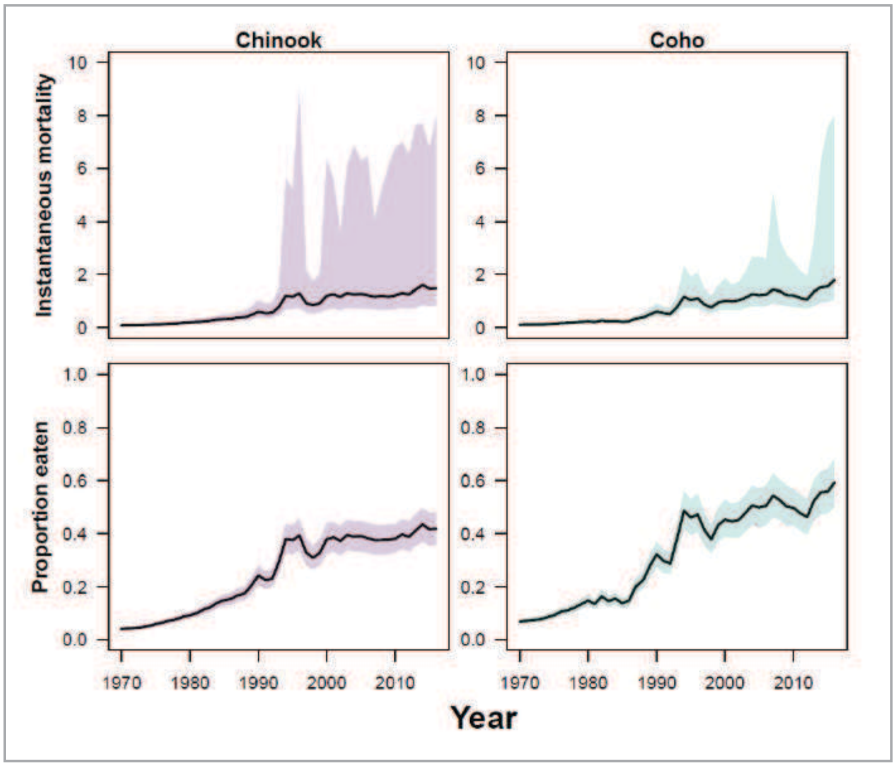

Figure 28. *Estimated annual total instantaneous mortality from seal predation during the first year at sea (top row of panels) for Chinook and Coho salmon, and the proportion of the juvenile cohort lost to seal predation (bottom row of panels) annually in the Strait of Georgia, 1970-2016. Solid black lines show maximum likelihood estimates, while colored bands depict the 95% probability intervals. Note that these projections assume production from natural-origin stocks of Chinook and Coho in the Strait of Georgia have remained stationary over time, while hatchery releases have decreased in recent years (Source: Nelson 2020).*

Based on consumption estimates expanded to the population level, Chasco et al. (2017) suggested strong potential for pinnipeds to impact Chinook abundance trends. These authors estimated the overall consumption of Chinook salmon by pinnipeds increased ~10 fold from 1970-2015, largely due to harbour seal and sea lion population recovery. Converting from juvenile Chinook salmon targeted by harbour seals to adult equivalents via assumed survival rates, by 2015, consumption by pinnipeds was twice that of resident killer whales and six times greater than fishery catches (Chasco et al. 2017). Christensen (pers. comm.) reports that the observed increases in seal abundance explain much of the change in salmon mortality based on several Ecopath with Ecosim model simulations. In contrast, Morzaria-Luna et al.'s (in prep) comprehensive Atlantis ecosystem model found minimal effects: harbour seal and other marine mammal population increases resulted in less than 2% reduction in adult salmon biomass. The two studies use different methods and metrics (energetic demands of predators in Chasco et al. versus biomass response in Morzaria-Luna et al.), and the biomass response in the Atlantis model reflects salmon survival but can also be tempered by time-varying salmon growth. A qualitative network analysis did not show strong support for marine mammal impacts (Sobocinski et al. 2018).

Predation is the most likely proximate source of early marine mortality for juvenile steelhead. Short residence times in Puget Sound coupled with high freshwater and low Puget Sound survival probabilities suggest a source of mortality that acts quickly on a large number of juvenile steelhead outmigrants in the Puget Sound marine environment (Moore et al. 2015). Further, steelhead tend to migrate near the surface (Moore and Berejikian in prep.), which may make them susceptible to bird and marine mammal predation. Evidence of smolt mortality at harbour seal haulouts during years of low steelhead survival suggest pinniped predation is an important source of mortality (Berejikian et al. 2016, Moore et al. 2021). Other potential predators based on gape size include double-crested cormorants, Caspian terns, sea lions and harbour porpoises, but only harbour seals and harbour porpoise have increased substantially in abundance and are present during the steelhead smolt outmigration (Pearson 2015, Jefferson 2016). In the Strait of Georgia, results of acoustic tagging studies suggested specific areas, such as Burrard Inlet, were mortality hotspots for out-migrating hatchery steelhead smolts from the Seymour River due to predation, possibly by seals, herons, or other predators (Healy et al. 2017). Factors such as freshwater habitat, hatchery influence, and disease likely have minimal population-level effects of predisposing steelhead to predation (Moore and Berejikian 2017, Herberger and Schmidt 2020), and relationships between steelhead early marine mortality and Puget Sound anchovy abundance (Duguid et al. 2019, Moore et al. 2021) indicate that increases in alternative prey for steelhead predators reduce predation intensity and steelhead mortality.

Population-level impacts of harbour seal predation on juvenile salmon are most likely the result of generalist feeding behaviour by a large proportion of the seal population rather than a few salmon-hunting specialists. Higher consumption of juvenile Chinook and Coho occurs during the summer when fish are broadly distributed offshore (beyond the 30 m isobath in the Salish Sea (Thomas et al. 2017, Lance et al. 2012, Nelson et al. in prep, Nelson et al. in press). Summer is also the period when Chinook are switching to piscivory and co-locate with herring prey (Duguid 2020; Chamberlin et al. in review). As herring are a primary prey for harbour seals (Lance et al. 2012, Olesiuk 1993), this behaviour likely makes Chinook vulnerable to seal predation.

Nevertheless, there is also some evidence of specialization. Broadly, male harbour seals may have a greater tendency to consume juvenile Chinook compared to female harbour seals (Schwartz et al. 2018). A portion of harbour seals (~18%) appeared to target releases of hatchery Coho at the mouth of the Big Qualicum River (Allegue et al. 2020). Further, certain animals may specialize in consuming salmon or steelhead where there are migration barriers, such as the Hood Canal Bridge (Figure 29) (Moore et al. 2010, Moore et al. 2013), the Ballard Locks (M Mahavolich pers. comm.), pinch points in estuaries (London 2006), light from overwater structures (Olesiuk 1996, Yurk and Trites 2000), and artificial pinniped haulouts or seabird roosts (Farrer and Gutierrez 2010, Scordino 2010, Kahler et al. 2000).

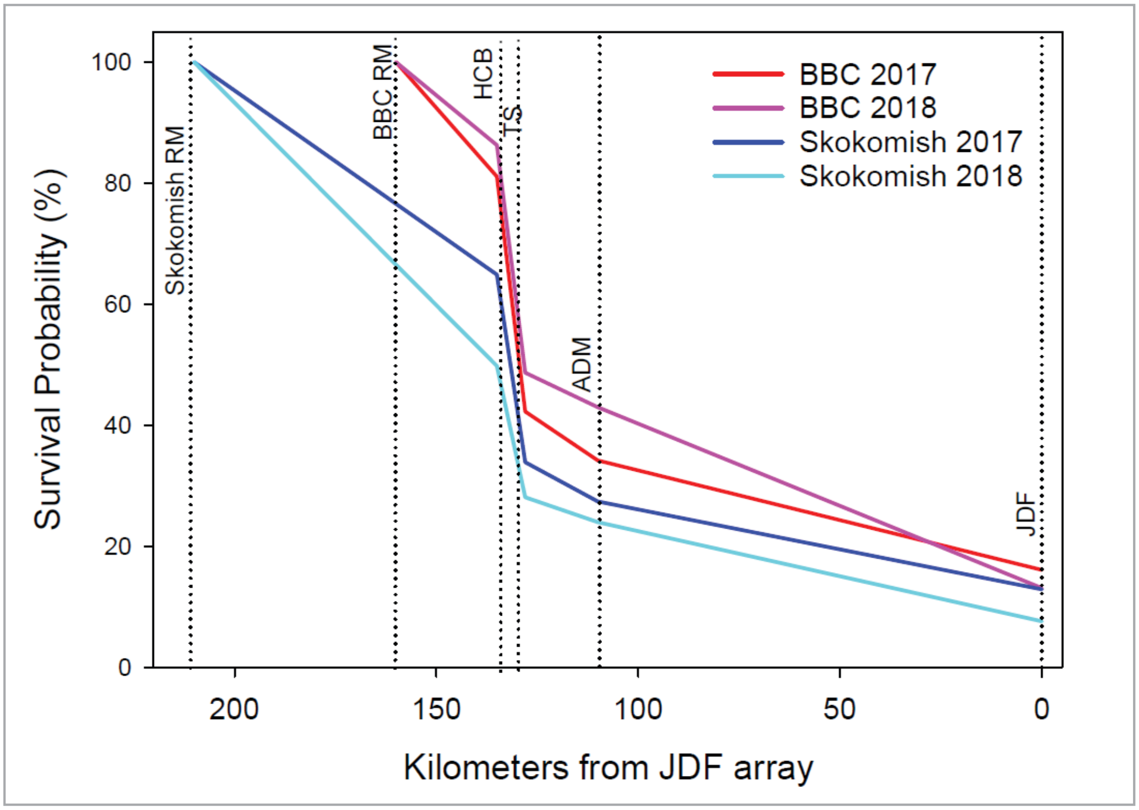

Figure 29. *The Hood Canal Bridge floats on continuous concrete pontoons that extend 4.6 m beneath the surface and span approximately 85% of the width of Hood Canal. Steelhead smolt survival probability was estimated with mark-recapture models using tagged steelhead smolt detections from the river mouths (RM) of Big Beef Creek (BBC) and the Skokomish River to the Hood Canal Bridge (HCB), Twin Spits (TS), Admiralty Inlet (ADM), and the final array at the western end of the Strait of Juan de Fuca (JDF). Survival probability per kilometre decreases steeply within the 7 km migration stretch between HCB and TS, which includes the Hood Canal Bridge (Source: Megan Moore).*

Concerns have been expressed regarding the ability to determine whether seal predation is additive or non-additive (Trites and Rosen 2019, Walters and Christensen 2019). Additive mortality is when all predation mortality rates are independent, so that total predation rate decreases when any one predator's mortality component is eliminated or reduced. Mortality is not additive when a predator consumes an individual prey item that would have died anyway due to whatever factor (like disease) made it vulnerable to the predator in the first place. The distinction is critical for predicting how an ecosystem will react to removal of a predator. Walters and Christensen (2019) developed a vulnerability exchange model to show how seal predation on Chinook and Coho may interact with sea surface temperature (SST) changes, which also correlate with Chinook and Coho survival. SST changes are a proxy for disease, metabolic responses, foraging behaviour, or prey availability impacts, all of which could increase susceptibility to predation. While there is support for interactions between SST and predation, unless Chinook and Coho are more vulnerable to changes in SST than predicted, the impacts of SST do not significantly change the outcome of reductions to the seal population: relatively large reductions in Chinook and Coho instantaneous mortality would occur with reductions in seal population abundance. However, given the complex nature of ecosystems, it is likely that the additive versus non-additive mortality question could only be answered through experimental predator removals (Trites and Rosen 2019, Walters and Christensen 2019).

Other predation relationships were investigated in the SSMSP. Low survival of out-migrating juvenile Chinook in the Cowichan River appears to be related to in-river predation, including predation by herons (Sherker 2020). Predation rates appear to be higher when freshwater flows are lower, and upriver release of hatchery Chinook may expose salmon to more predation. Hatchery managers are testing releases further downstream in an attempt to reduce this impact. In the Fraser River basin, bull trout targeted out-migrating juvenile Sockeye (Furey and Hinch 2017). In Puget Sound, there is little evidence of cannibalism by resident Chinook on juvenile Chinook (Beauchamp 2020 et al. 2020, Chamberlin et al. 2020), contrary to initial assumptions (Beauchamp pers. comm.). Lamprey have been previously cited as having a potentially significant impact (Beamish and Neville 2001); however, they were not investigated.

Prey switching and pulse prey abundance

Prey switching occurs when predators have a strong preference for prey that are more common in the environment and a weak preference for prey that are rare, such that the predator switches its diet to prey that are most abundant and then feeds disproportionately on them (Murdock 1969). Changes in the abundance of prey that would otherwise comprise a significant part of a predator's diet could increase the risk of predation on less abundant juvenile salmon and steelhead. It is unclear whether prey switching could have contributed to declines in marine salmon survival Salish Sea-wide since the 1980s.

Harbour seals primarily eat gadids and clupeids in the Salish Sea (Lance et al. 2012, Olesiuk 1993). Spawner abundance and size and age structure of Puget Sound herring populations has declined since the 1980s, affecting overall biomass (Siple and Francis 2015, Stick and Lindquist 2009, Greene et al. 2015, Landis and Bryant 2010). This includes significant declines in abundance of the later-spawning Cherry Point stock, which historically represented half of the total Puget Sound herring spawning biomass. In the Strait of Georgia, herring spawner abundance has generally increased since the 1980s, but there has been a significant contraction in spawning areas (DFO 2020). Multivariate analyses examining the influence of multiple factors on Puget Sound Chinook, Coho, and steelhead marine survival trends included changes in herring abundance in their best models (Sobocinski et al. 2020, Sobocinski et al. 2021). Harbour seals consume herring throughout the year but may not target adult herring during spawning season, possibly because this strategy is less profitable than feeding on juveniles or alternate prey species (Thomas et al. 2011). Assessing how many herring remain in the Salish Sea over the summer could improve our understanding of the relationship between herring and their predators.

Regarding gadid trends, Pacific hake are considered a species of concern in Puget Sound although trends in changes in abundance are not clear (Essington et al. 2021, NMFS 2009, Gustafson et al. 2000). However, there have been documented changes in size and age structure (Gustafson et al. 2000), which can result in a decline in overall biomass and shift in pelagic distribution. Pacific cod appear to have declined in Puget Sound prior to the mid-1970s (Essington et al. 2021, Gustafson et al. 2000). In contrast, Northern anchovies appear to fluctuate from rare to highly abundant in the Salish Sea (Duguid et al. 2019). In recent years (2006-2019), warmer Puget Sound and coastal temperatures were positively related to anchovy abundance and negatively related to early marine mortality rates of Puget Sound steelhead, suggesting that increased anchovy abundance provided an alternative prey resource for steelhead predators and led to a reduction in steelhead mortality (Figure 30) (Moore at al. 2021).

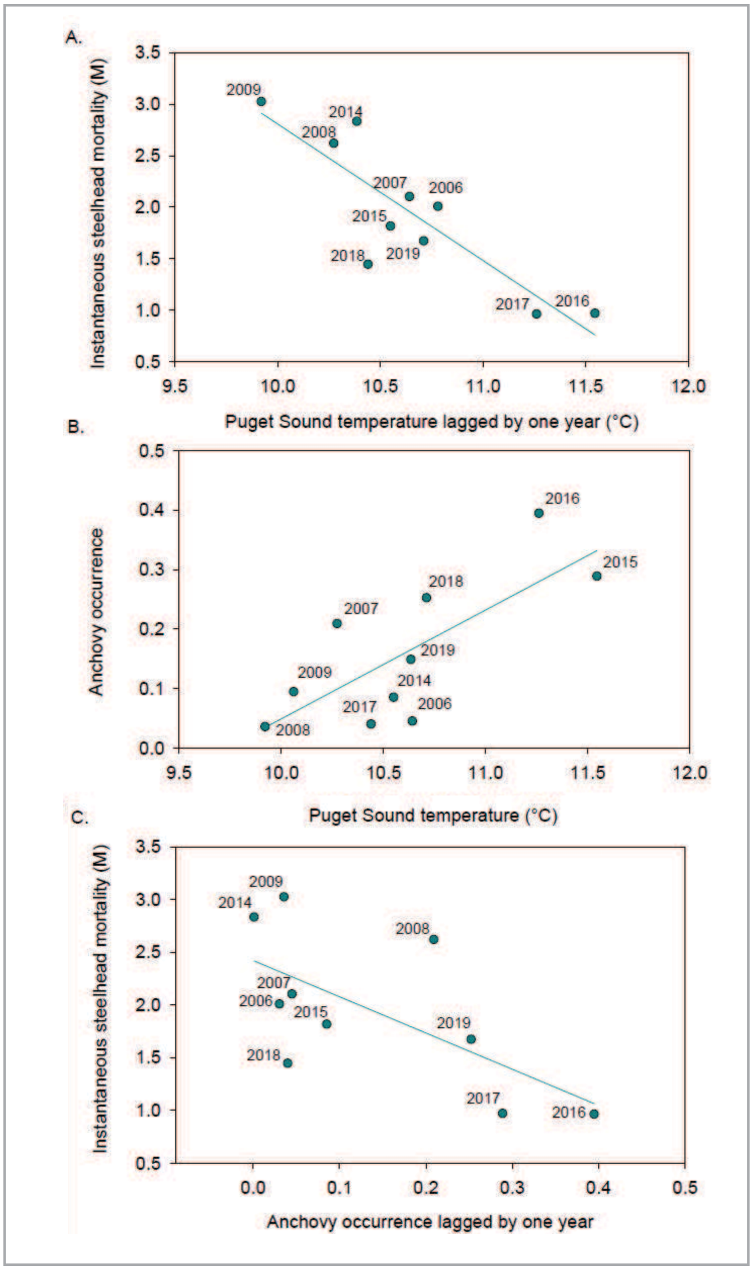

***Figure 30.** Steelhead smolt mortality from the Nisqually River mouth to the Strait of Juan de Fuca was estimated for 10 of 14 years between 2006 and 2019, including years of unusually warm Puget Sound temperatures caused by the 2014-2016 marine heat wave. Annual mortality rates were strongly and negatively related to annual mean Puget Sound temperature during the year before steelhead migration (panel A; r2 = 0.75, p = 0.001). Annual mean Puget Sound temperature was positively related to the occurrence of age-0 Northern anchovy caught in Skagit Bay townet surveys (panel B; r2 = 0.67, p = 0.004), providing evidence that warmer Puget Sound temperatures promote more successful anchovy recruitment. Steelhead mortality rate was negatively correlated with age-0 anchovy occurrence during the year prior to migration (panel C; r2 = 0.57, p = 0.01), suggesting that age-1 anchovies provided alternate prey for steelhead predators, causing reduced smolt mortality as steelhead migrated through Puget Sound. (Source: Moore et al. 2021)*

While juvenile salmon are not a primary source of prey for harbour seals and other opportunistic predators, predators may respond to consolidated releases of large numbers of hatchery fish. Examples of seal, fish, and bird predators responding to high densities of hatchery releases have been documented in the Salish Sea (Wood 1987, Beamish 1992). A targeted study found a few seals respond to Coho migrating downstream and into the Strait of Georgia soon after release from a hatchery, but not Chinook. This may be because Coho are larger than Chinook at the time of release and within a seal's targeted prey size. However, predation of Coho at the river mouth was only a small portion of all the predation events which continued offshore (Allegue et al. 2020). The diversity of hatchery Chinook release dates and sizes in the Salish Sea has decreased substantially since the 1990s, with mean release date converging around the third week of May and release size within the preferred range of seal predators (Nelson et al. 2019a). This could result in increased mortality of hatchery Chinook and increased mortality of other co-occuring salmon and steelhead. Changes in the variability and timing of Chinook and Coho release dates were included in best-fit models for explaining Chinook, Coho, and steelhead marine survival trends (Sobocinski et al. 2020, Sobocinski et al. 2021). Alternatively, high densities of juvenile salmonids can produce predator swamping effects, such as in the case of out-migrating Sockeye swamping bull trout predation in the Fraser Basin, resulting in lower mortality rates (Furey et al. 2016).

Synthesis Committee Perspective

The Synthesis Committee believes there is substantial evidence supporting the assertion that increased seal abundance has reduced the marine survival of Chinook, Coho, and steelhead. Impacts to Coho and steelhead appear consistent in correlative analyses. Recent consumption estimates from bioenergetic modelling suggest the current diet and size of the seal population can result in significant mortality to out-migrating Chinook and Coho, corroborating correlational studies. However, ecosystem modelling has shown mixed results. The Committee also noted contrasting evidence in Chinook, such as recently improved escapements of adult Chinook to the Cowichan, Puntledge, and Big Qualicum rivers and varying population trends (e.g., high Harrison Chinook abundance). Further, the Committee noted that we cannot conclude whether mortality associated with seal predation is additive or not. There are concerns given the limited spatiotemporal coverage of seal diet data and sensitivity of consumption estimates to potential variation of fish sizes in seal diets (Nelson et al. in prep). However, it is uncertain whether more observational data will substantially improve confidence. Therefore, experiments may be necessary (see management implications and next steps below).

The Committee concluded that predator specialization cannot account for the bulk of the mortality occurring and instead believe the incidental mortality of juvenile salmon associated with seal predation on other species such as Pacific herring accounts for the greatest impact. While predation may be occurring on pulses of out-migrating salmon, the Committee was divided regarding whether predators targeting these pulses could be a primary driver of marine survival. The Committee concluded that data were insufficient to state whether prey switching was occurring and affecting marine survival; however, the relationship between anchovy presence/absence and juvenile steelhead early marine mortality is compelling.

Interrelationships with other factors

In addition to changes in primary prey and hatchery release strategies, other factors can affect predation rates. Contaminants and disease can affect fish behaviour and predispose them to higher predation rates (Furey et al. 2021, Johnson et al. 2006). Fish that are having trouble finding food may take more risks when foraging, increasing susceptibility to predation (Walters and Korman 1999, van Poorten et al. 2018). Fewer herring spawning areas throughout the Salish Sea could result in patchier distribution of forage fish, longer foraging times for salmon, and greater predation risk. These connections are important but were not extensively studied in the SSMSP. In one study in the Fraser basin, bull trout selectively targeted diseased Sockeye (Furey et al. 2021). Conversely, while both contaminants and parasite loads were observed at greater levels in steelhead populations that experience higher early marine mortality in Puget Sound (Chen et al. 2018), a direct study in a single population found no difference in early marine mortality of steelhead with high or low parasite loads (Hershberger and Schmidt 2020). Higher early marine mortality of certain steelhead populations is likely related to the greater distance those fish must travel through the Puget Sound marine environment, increasing the amount of time they are susceptible to predation (Moore et al. 2017, Connor et al. as reported in Puget Sound Steelhead Marine Survival Workgroup 2015).

Management Implications and Next Steps

Pinnipeds are protected in the U.S. by the Marine Mammal Protection Act and regulated in Canada by the Fisheries Act, and the social consequences of actively managing marine mammal populations are significant. Modelling suggests that, if increased harbour seal abundance is the primary driver of salmon mortality, an initial 50% seal population reduction and continued removals of 3,000 animals per year would be required to increase numbers of returning adult salmonids (Trites and Rosen 2019).

There is a need to address uncertainty in findings, to consider the ramifications of culling, to determine whether predation by seals is additive, and to view predation impacts from an ecosystem perspective. The following recommended next steps are a general summary from various forums that occurred in 2019, including two pinniped and salmon workshops (Trites and Rosen 2019, Trzcinski 2020) and a SSMSP Synthesis Committee retreat. Both empirical studies and experiments are described. While empirical studies will increase our understanding of predation impacts, it is generally agreed that experiments are necessary to determine the extent to which seal predation is impacting salmon survival and what can be done about it. In Washington State, the "Southern Resident Orca Task Force Report" called for empirical studies, experiments, and subsequent management actions.

Empirical Studies

- Improve our understanding of sizes of salmon consumed by seals, sex and age variation in seal diet composition, seal diets in estuary versus non-estuary environments, and seal abundances, distribution, and demographics. Update correction factors for seal abundance estimates if needed.
- Assess total salmon abundance (hatchery and wild) versus proportions of salmon in seal diets to look for a functional response.
- Overlap prey (Chinook, Coho) and predator (seal) distribution data to improve our understanding of predation hot spots and focus on salmon populations of greatest concern. If possible, compare distribution of salmon populations with high versus low marine survival rates.
- Use existing and new year-round seal diet data to determine how predation on juvenile salmon co-varies with other prey species in the diet, as well as water temperatures, regions, population sizes, etc.
- Assess impact of increased presence of transient orcas on the abundance, distribution, and behaviour of pinnipeds. Transient orcas are seal predators and can have significant impact (Shields et al. 2018).
- Use models to assess seal predation and the consequences of seal population reductions from an ecosystem context and evaluate whether predation is additive or non-additive.
- Address lack of information regarding harbour porpoise impacts on juvenile salmon and steelhead and, while not a focus of this work, seal and sea lion impacts to adult salmon and steelhead.
- Maintain open-source datasets, such as the seal diet dataset published by A. Thomas (Thomas et al. in review).

Experiments

- Remove artificial haulouts and perform before/after assessment of predation rates on salmon. Account for pinniped displacement (where pinnipeds will go) in design.
- Experiment with changes in hatchery release timing to affect predation rates. Assess relationship between the timing of juvenile salmon presence in scats and the timing of hatchery releases.
- Remove pinnipeds from specific areas and compare outcome to areas where pinnipeds were not removed (treatment/control). Include substantial post-removal monitoring and design to discriminate between additive and non-additive mortality.
- Improve fish passage by modifying artificial migration barriers or pinch points where pinnipeds forage. Test whether these actions reduce predation rates.
- Test pinniped deterrents at migration barriers (e.g., Hood Canal Bridge) or pinch points and at predation hotspots.
- If the change in hatchery release location on the Cowichan does not improve downriver survival, or if wild mortality is high, test the impact of increasing flows from Cowichan Lake during outmigration in low flow years. This action may reduce observed in-river predation by herons, raccoons, and other predators.
- Instrument several haulouts/rookeries with PIT antennas and passively scan many animals (seals and sea lions) over an entire year.

4. Disease and Contaminants

Pathogens and disease

The hypothesis addressed by this set of studies was that infected fish may die from infection and/or become more susceptible to predation. Key predictions included a) infection prevalence has increased, and b) mortality increases with increasing parasite or pathogen prevalence or loads.

The Strategic Salmon Health Initiative (SSHI) specifically addressed the hypothesis that infectious disease impacts early marine survival of salmon in the Salish Sea, primarily focused on impacts on Coho, Chinook, and Sockeye salmon. The SSHI has also addressed the potential that salmon aquaculture interactions may contribute to risk of disease in migrating Pacific salmon. Associated studies with the Hinch laboratory at UBC and Kintama Research utilizing acoustic telemetry methods supported by the SSMSP (Rechisky et al. 2020) have specifically addressed the prediction that infection and disease impacts migratory speed and survival of smolt outmigrants and returning adults. Stress challenges and holding studies in adult salmon have addressed cumulative effects of fisheries handling and elevated temperature on disease development and survival in salmon. Other studies through USGS have focused on monitoring, impacts, and treatments for a digean parasite, *Nanophyetus salmincola*, infecting steelhead and Coho salmon in Washington State (Chen et al. 2018).

Researchers applied novel genomic approaches to study the presence of pathogens and associated disease expression in wild, hatchery, and net pen cultured Atlantic and Chinook salmon. Prior studies had suggested that salmon health and condition can be predictive of future survival as salmon adapt to new environments (Miller et al. 2011, Jeffries et al. 2014, Drenner et al. 2017, Bass et al. 2019). A sampling program established in 2008 facilitated collection of juvenile salmon from the time they left freshwater through their first nine months of marine residence along the coast of southern BC (Figure 31).

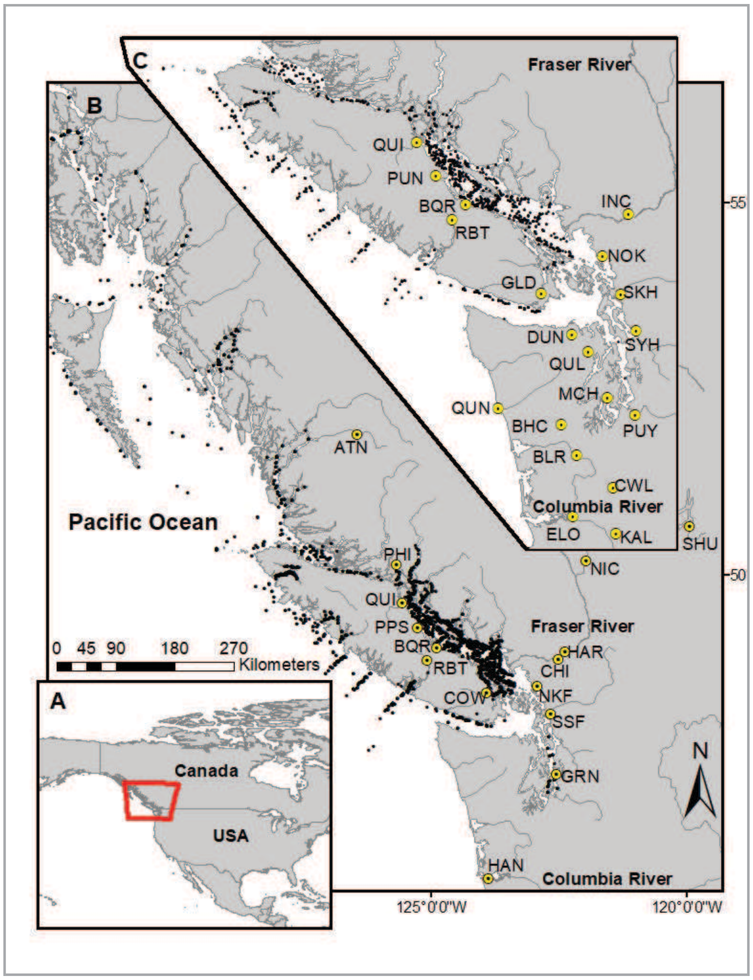

Figure 31. *Sampling locations (black points) for the Strategic Salmon Health Initiative for wild, hatchery, and aquaculture Chinook (B) and Coho (C) salmon between 2008 and 2018. Yellow circles indicate the location of hatcheries that were used in cohort survival analyses (Source: K. Miller-Saunders, DFO)*

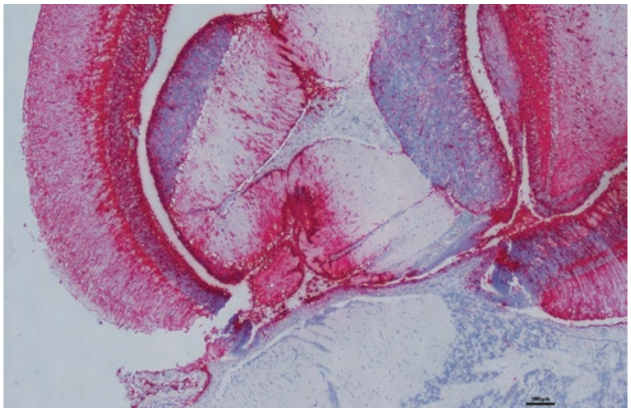

Figure 32. Investigating infectivity of a novel strain of Cutthroat trout virus (CTV-2) (red), localized to the optic lobe of an Atlantic salmon brain. (Source: E. Di Cicco, PSF)

SSHI researchers were able to assess shifts in pathogen and disease profiles within and between years for over a decade. A new technology using a high-throughput microfluidics system assessed 47 known pathogens (viruses, bacteria, and fungal and protozoan parasites) in 80 fish at once; in total, over 30,000 salmon were profiled. Host gene activity was used in some studies to detect disease-related processes associated with infection and survival (e.g., Miller et al. 2017, Teffer et al. 2018). Secondary processing of fish showing signs of viral disease but no observable viral infection led to the discovery of novel (previously uncharacterized) viruses (Mordecai et al. 2019, 2020). Histopathology and *in-situ* hybridization using special molecular "dye" to pinpoint viruses in host tissue enabled characterization of cellular damage in the host, establishment of infectivity for novel viruses, and co-localization of specific agents within damaged tissues (Figure 32) (e.g., Di Cicco et al. 2018, Mordecai et al. 2019). Molecular profiling of gill biopsy samples from acoustically tracked salmon identified pathogen and disease linkages with fate (e.g., Jeffries et al. 2014, Bass et al. 2019, Teffer et al. 2017).

SSHI researchers have identified over 50 infectious agents in juvenile salmon in the Salish Sea, including 15 novel viruses and many agents never studied previously in BC salmon (Miller et al. 2014, Tucker et al. 2018, Mordecai et al. 2019). Analytical models derived from 8-10 years of infectious agent monitoring, acoustic tracking and predation studies that relate agents with fate, and physiological assessments have been applied to reveal infectious agents showing the greatest pathogenic potential during downstream freshwater migration and in the Salish Sea.

Shifts in infection prevalence over time

Thakur et al. (2018) estimated the prevalence of infectious agents in archived samples of BC return-migrating Sockeye salmon collected between 1985 and 1994, a temporal period that spanned the major expansion of the Atlantic salmon aquaculture industry in BC. Of 45 infectious agents assessed through molecular assays in 652 samples, 23 (7 bacterial, 2 viral, and 14 parasitic) were detected in liver tissue from fish sampled from spawning grounds in six regions in BC. Prevalence of agents varied significantly by region and year but showed no specific increase over the 10-year timeframe of the study. Many of the infectious agents originally characterized in farmed salmon from Europe, and documented recently in BC salmon, were found in the archived samples. One agent not detected in the Thakur et al. (2018) study, piscine orthoreovirus (PRV), has now been shown to be a relatively recent introduction onto the BC coast (Mordecai et al. in review). This SSHI phylogenetic study reveals the virus moving from the North Atlantic to the Pacific Northwest in the past 30-40 years (Mordecai et al. in review), consistent with the first repeatable detections of PRV via PCR in the early 1990s (Siah et al. 2020). The Mordecai study also revealed ongoing exchange of the virus between farmed and wild salmon in BC; in BC Chinook salmon, the likelihood of infection with PRV was higher in fish collected closer to farms. Conversely, most Columbia River Chinook, Coho, and Sockeye salmon carried a different variant of PRV-1 that was likely transmitted in freshwater but that was also shared with a small number of samples from northern BC and Alaska, consistent with findings of Purcell et al. (2018).

Due to a lack of historical samples, SSHI researchers have not been able to assess whether disease, or, more accurately, infective agent prevalence, has increased over time in Coho and Chinook. However, we do know that thermal conditions salmon experience have changed, with elevated river and coastal marine temperatures during the summer, and marine heatwaves (e.g., "The Blob") becoming increasingly common in the Northeast Pacific Ocean (Laufkötter et al. 2020). Many pathogens are positively associated with temperature, displaying higher replication rates and stronger disease impacts (Stocking et al. 2006, Ewing et al. 1986, Crossin et al. 2008, Ray et al. 2012). SSHI stress-challenge research on adult salmon, where thermal and handling effects were manipulated, has demonstrated that infection risk and disease development are closely associated with temperature (Teffer et al. 2018). Furthermore, this research has shown that if adult salmon can bypass exposure to freshwater transmitted agents, they become more robust to other stressors and survive longer under elevated thermal exposure (Teffer et al. in review).

Mortality increases with increasing pathogen prevalence

Bass et al. (2017) described the pathogen profiles of adult Chinook salmon during their return migration in southwestern British Columbia, sampling multiple populations and sites in marine and freshwater habitats. This work demonstrated sex-specific differences in infectious loads and correlated infection intensities of several agents with indices of morbidity and advanced senescence. While the authors did not directly determine the linkages between specific infectious agents and disease, comparisons of agent load to blood plasma variables (indicative of stress, osmoregulation, maturation, and senescence) revealed some positive associations between *Flavobacterium psychrophilum, Cryptobia salmositica,* and *Ceratonova shasta* and physiological indices associated with morbidity. These agents are known from previous studies to cause premature mortality of adult salmon (e.g., *C. shasta* (Hallett and Bartholomew 2012), *C. salmositica* (Woo 2012)).

In adult Chinook salmon, relative infective burden (RIB), a measure that takes into account both pathogen diversity and load (Bass et al. 2019), was associated with enhanced stress, shifts in osmoregulation and immunosuppression, earlier arrival at spawning grounds, and premature mortality (Teffer et al. 2018). In juvenile Sockeye salmon migrating through Queen Charlotte Sound, diversity of pathogens and high loads of any pathogen were associated with higher probability of predation by rhinoceros auklets (Miller et al. 2014).

Tucker et al. (2018) found that, on average, yearling Chinook from the Fraser River carried 1.3 times the level of infectious agents as subyearling salmon, noting that yearling stocks are currently in the steepest decline while subyearling stocks are generally performing better in the Strait of Georgia. The authors postulated that the differences in habitat choice and diet affecting pathogen exposure could also explain differences in survival between yearling and subyearling life history types.

Juvenile Sockeye salmon sampled in 2013, a year with very poor marine survival, had significantly higher infection burdens than in 2012, a year with average marine survival (Nekouei et al. 2018). These differences were present before fish left freshwater and were attenuated during the first few weeks of marine residence but dissipated by the time juveniles reached Johnstone Strait. This study also identified several agents first detected only after juvenile Sockeye were exposed to salmon farms in the Discovery Islands and Broughton Archipelago. Subsequent models driven by 10 years of infection data for one of these agents, *Tenacibaculum maritimum*, revealed substantially increased levels of infection associated with exposure to farms in the Discovery Islands (Bateman et al. in prep). This bacterial pathogen has been the cause of recurring outbreaks of mouth rot and associated mortality on Atlantic salmon farms throughout BC (Bateman et al. 2021). In other SSHI models depicting population-level associations between infectious agents and ocean survival, and individual-level associations with relative weight, *T. maritimum* is one of the agents most consistently associated with reduced ocean survival and low weight across salmonid species (Bass et al. in prep; Teffer et al. in prep).

The Bayesian models developed to evaluate associations between infectious agent prevalence and metrics of marine survival (coded-wire tagged smolt to adult survival for Coho and Chinook, and residuals from stock-recruitment models for Sockeye) were each fitted with 8-10 years of data (Bass et al. in prep; Teffer et al. in prep). In addition, length-mass residuals were compared to infectious agent load with the prediction that higher burdens of deleterious pathogens would be associated with leaner fish. In Chinook and Coho, species in which many stocks remain coastal for at least the first year of ocean residence, evaluations were undertaken to assess relationships with survival in both the warm spring/summer (May-August) and the cool fall/winter (September-March) periods. Because Sockeye salmon move through the study area relatively rapidly during outmigration, models were conducted for the spring-summer only. While many infectious agents were associated with survival or residual mass, a few rose to the forefront due to their consistency across the three host salmon species. The most consistent was *Ichthyophthirius multifiliis*, a freshwater ciliate not previously expected to persist in the marine environment. This could potentially represent a carryover effect, with infection in saltwater indicative of years of poorer condition fish entering the ocean (Bass et al. in prep; Teffer et al. in prep). However, there is some indication that this agent may continue to infect fish remaining in nearshore environments into the fall/winter period. While PRV was so infrequent in Sockeye that it could not be modeled, it was the pathogen most consistently negatively associated with survival and residual mass in Chinook and Coho. *Tenacibaculum maritimum* was consistently negatively associated with residual mass in Chinook and Coho and had the third strongest negative association with survival in Sockeye. While these three pathogens showed consistent patterns across host species, the single strongest negative associations varied between species, including *Candidatus* Syngnamydia salmonis (a bacteria recently identified in Norwegian aquaculture) for spring/summer sampled Chinook, *Myxobolus* arcticus (a brain parasite better known in Sockeye and previously considered benign) for fall/winter Chinook, *Loma salmonae* (a marine microsporidian parasite) in spring/summer Coho, *Nanophyetus salmincola* (see below) in fall/winter Coho, and *Paranucleospora theridion* (a microsporidian parasite better known from Norwegian aquaculture) in Sockeye. Pathological investigations are still ongoing in the SSHI, but several agents have already revealed associations with pathology in migratory juvenile salmon in the coastal marine environment.

Spatiotemporal analyses in agent profiles across Chinook, Coho, and Sockeye revealed hotspots of infection along the southern coast of BC, which varied both by agent and by season. The southern Strait of Georgia, influenced by the Fraser River freshwater plume and the convergence of water masses from Puget Sound and the outer coast through Juan de Fuca Strait, was a notable hotspot of infection from spring through the winter period. The remainder of the Strait of Georgia showed high infection intensities in spring/summer, but during fall-winter the main infection hotspot shifted to inlets off the west coast of Vancouver Island (Bass et al. in prep; Figure 33). Models identifying infectious agent spatial clusters are providing a vital tool for assessing hypotheses.

Species distribution models for infectious agents relating infection probabilities with extrinsic (e.g., temperature, sea surface salinity, distance to shore, distance from aquaculture) and intrinsic (origin—hatchery or wild, life history type, stock latitude) factors reveal that sea surface salinity in the Salish Sea is a major driver of infection (Bass et al. in prep). Sea surface temperature (SST) was also significant for a range of agents, but most of this variation could be explained by seasonal rather than annual or spatial variations in temperature. The models also show that freshwater experience (age at marine entry and hatchery as compared to wild fish) influences ocean pathogen profile, as does distance from active aquaculture and hatchery versus wild origin. Notably, in Chinook salmon, the likelihood of PRV infection was significantly higher within 30 km of active aquaculture (Mordecai et al. in review), and the likelihood of infection by the newly characterized Pacific Salmon Nidovirus (PSNV) was higher in hatchery-origin fish (Mordecai et al. 2019).

Pathogen impacts on survival may arise through direct effects, whereby fish die from disease, or indirect effects, where infection affects physiological performance and behaviour, enhancing risk of predation and susceptibility to other stressors. It is likely that the latter is more important for wild fish, where even modest compromise in performance (especially swimming and visual) can lead to death.

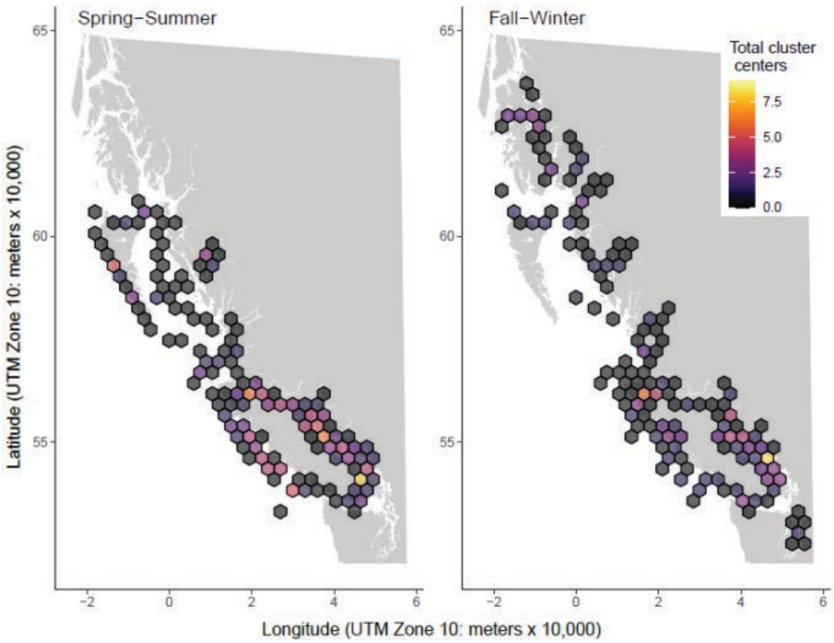

Figure 33. *Infection Hot Spot Analysis in spring/summer (left) and fall/winter (right) showing the number of overlapping cluster centers per cell for Chinook, Coho, and Sockeye salmon. The southern Strait of Georgia appears to be a hotspot for infection in both seasons (Source: K. Miller-Saunders, DFO)*

Infection leads to increased predation

Several SSHI-led studies explicitly examined the relationship between infectious agent profiles and migratory fate of both juveniles and adults. Healy et al. (2018) assessed whether infectious agents and host gene expression profiles influenced migration fate for steelhead smolts leaving Seymour hatchery and found that smolts never detected after release in the river had significantly elevated expression of two immune genes and lower expression of an osmoregulatory gene relative to other individuals. Warheit also found Puget Sound wild steelhead smolts with particular genetic expression may be predisposed to higher early marine mortality and higher parasite (*N. salmincola* loads). This may be associated with the influence of residency versus anadromy, the fishes' circadian clock, or their immune system (Warheit as reported in 2013-2017 Puget Sound Steelhead Marine Survival Summary Report). However, the power of these findings was limited. These studies demonstrate rare evidence of gene expression profiles relating to migration fate in juvenile salmonids and highlight potential mechanisms influencing fate. Stevenson et al. (2020) found that age-2 Chilko Sockeye smolts exhibited higher mortality in the first 14 km of the downstream migration and displayed elevated gene expression related to inflammation and a molecular-based mortality-related signature. Although not associated with migration failure in this study, the authors concluded that patterns of gene expression were suggestive of mortality and could have implications for smolt survival. Jeffries et al. (2014) showed that a gene expression signature indicative of viral infection was significantly correlated with migratory loss within the Chilcotin and with infection by Infectious Hematopoetic Necrosis Virus (IHNv).

Although size- or condition-based predation is well known, observing infection-based predation is rare due to the difficulties in assessing infectious agents in predated samples. In a follow-up study to the tracking study of Chilko Lake Sockeye smolts that identified linkages between IHNv and migratory survival (Jeffries et al. 2014), Furey et al. (2021) showed that in one of the two years assessed (2014 and 2015), presence of IHNv was associated with 16-25 times greater chance of predation by Bull trout in the Chilcotin; the virus was not detected in the other year. Some smolts with high IHNv loads also exhibited gene expression profiles consistent with a virus-induced disease state (VDD described in Miller et al. 2017). Another SSHI study showed that Rhinoceros auklets preferentially consumed smolts infected with *Parvicapsula* parasites (Tucker et al. 2018); one of the *Parvicapsula* species, *P. pseudobranchiocola*, is known to affect visual acuity (Karlsbakk et al. 2002). Conversely, Hershberger and Schmidt (2020) found no difference in early marine mortality rates of Puget Sound steelhead smolts heavily infected with the *N. salmincola* parasite versus those not infected. There was little evidence of a relationship between infectious agents and fate for Cowichan Chinook captured and acoustic-tagged in the fall, several months after ocean entry (Kintama, pers. comm.).

In adult Fraser River Chinook salmon, *Cryptobia salmositica* was associated with higher rates of premature mortality in both tracking and holding studies (Bass et al. 2018), suggesting that this pathogen could be contributing to pre-spawn mortality. In separate simultaneous tracking and holding studies on returning adult Chinook salmon, gill net injury enhanced infective burdens (Teffer et al. 2018). Immune and blood properties were also correlated with infection and survival. As previously mentioned, a recent study by Teffer et al. (in review) demonstrated that under a multi-stressor scenario (fisheries handling and/or high water temperatures), exposure to pathogens in-river was the tipping point for considerably enhanced mortality. The implication of these studies is that infectious disease is a significant contributor to premature mortality for adult salmon and that fisheries-related injuries and elevated temperatures can increase impacts.

Studies comparing hatchery and wild salmon

Several SSHI studies focused on differences in infectious profiles between hatchery- and wild-origin salmonids. A key question was whether hatchery-origin fish, reared in high density environments, could increase the transmission of infective agents to sympatric wild populations. Nekouei et al. (2019) carried out a study to compare prevalence, burden, and diversity of infectious agents between hatchery-reared and wild juvenile Coho collected between 2008 and 2018 in BC. The study found that infectious burden and diversity were significantly lower in hatchery smolts at the time of release than in wild counterparts sampled in freshwater drainages along mainland BC, whereas there were no significant differences in other regions. Differences were generally related to prevalence of myxozoan parasites, which require an alternate invertebrate host to complete their life cycle; myxozoans were not as commonly observed in hatchery fish due to the use of groundwater rather than river water. The authors noted that the burden of infectious agents was substantially higher for both hatchery and wild fish sampled in the marine environment than in freshwater. Thus, this study did not support the hypothesis that hatchery smolts carry higher burdens of infectious agents than conspecific wild Coho salmon.

Hatchery and wild Chinook salmon from the Cowichan River were found to carry divergent agent profiles in freshwater, with generally higher agent diversity in wild fish exposed to parasites with alternate invertebrate hosts (Thakur et al. 2018). In this system, the myxozoan *Ceratonova shasta* was observed in a higher proportion of hatchery than wild fish. Agent profiles became more similar for both hatchery and wild Chinook as they converged in the early marine environment; because hatchery fish move quickly from nearshore to inner bay environments, SSHI scientists hypothesize that they are exposed to and infected by a larger diversity of infective agents sooner after entering the marine environment than wild fish. Authors hypothesized that the impacts of higher infectious agent diversity and burdens, encountered during the critical period while smolts are adapting to their new saline environment, could account for lower levels of marine survival in hatchery fish.

Models based on 8-10 years of infectious agent data for juvenile Chinook and Coho salmon revealed differential likelihood of infection with some agents between hatchery and wild fish in the marine environment (Bass et al. in prep). Most notable was the recently discovered Pacific Salmon Nidovirus (PSNv), which is largely coming out of salmon enhancement hatcheries. As identified by Nekouei et al. (2018), freshwater myxozoans, in this case most exemplified by *M. arcticus*, were more likely to occur in wild fish than hatchery fish but some marine-transmitted myxozoans, including Parvicapsula pseudobranchicola, Parvicapsula kabatai, and *Kudoa thyrsites*, were more likely to occur in hatchery Chinook. *Candidatus* Branchiomonas cysticola infections were more likely and more intense in hatchery fish. For Coho salmon, infections with PRV were more likely to occur in hatchery-origin fish.

Relationship with Aquaculture

In aquaculture industry audit samples from farmed Chinook and Atlantic salmon, studies revealed strong divergence in infectious profiles between species, with Chinook carrying a higher diversity of agents than Atlantic salmon (Laurin et al. 2019). Divergence in primary lesion profiles were also noted, with agent and lesion distributions characterized by aquaculture management zone, time at sea, and season (Laurin et al. 2019). As a result, SSHI researchers concluded that Atlantic salmon are not a good proxy for Pacific salmon in terms of agents and diseases that may affect them. However, several agents only previously described in farmed Atlantic salmon from Europe (e.g., *P. pseudobranchicola*, *Candidatus* Syngnamydia salmonis, *Paranucleospora theridion* (also known as *Desmozoan lepeoptherii*), and Atlantic salmon calicivirus (ASCv); note the latter agent was not included in Laurin et al. 2019), were shared across farmed Atlantic and Chinook salmon and have also been observed in wild salmon.

After the discovery of HSMI (Heart and Skeletal Muscle Inflammation) on an Atlantic salmon farm in BC (Di Cicco et al. 2017), SSHI researchers began conducting further field-based studies on Pacific salmon to determine if the virus PRV-1 is associated with disease in Pacific salmon. In 2018, the SSHI provided evidence that PRV-1 is associated with differential expression of diseases in Atlantic and Chinook salmon on farms (Di Cicco et al. 2018). Analysis of Chinook salmon from farm audit data suggested a statistical and spatial (localization within tissues) association between PRV-1 and jaundice/anemia (aka. jaundice syndrome). Lesions consistent with the early stages of this disease, as well as elevated expression of genes associated with an immunological response to viruses, have been found in association with PRV infection in wild Chinook salmon (Wang et al. in prep). This disease is highly similar to diseases caused by other strains of PRV in Rainbow trout in Norway (PRV-3; Vendramin et al. 2019), and Coho salmon in Japan (PRV-2; Takano et al. 2016) and Chile (Godoy et al. 2016), and there is a linkage between co-infection by PRV-1 and infectious salmon anemia virus (ISAV) and Hemorrhagic kidney syndrome in Atlantic salmon (Ferguson et al. 2020). Moreover, research assessing host physiological associations with infective agents in wild-caught Chinook salmon revealed strong linkages between PRV, activation of a molecular viral disease response, and pathology consistent with early lesions observed in the development of jaundice/anemia on farms (Wang et al. in prep). It is important to note that PRV is far more common, and perhaps more relevant, in Chinook salmon on the west coast of Vancouver Island than in the Salish Sea, with disease manifestation (farmed and potentially wild) occurring over cool fall/winter periods. Again, PRV is among the most strongly associated with marine survival and residual mass in Chinook and Coho salmon (Bass et al. in prep).[30]

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30. As a result of conflicting reports in the scientific literature and the status and accessibility of referenced manuscripts (in prep), members were divided on the extent to which PRV impacts marine survival of Coho and Chinook salmon in the Salish Sea, with USGS and WDFW staff withholding a position until more studies are completed. Steelhead susceptibility was not evaluated.

As previously mentioned, SSHI models populated with 8-10 years of infectious data reveal associations between two agents and proximity to farm: PRV-1 for Chinook salmon (Mordecai et al. in review) and *T. maritimum* for Sockeye salmon (Teffer et al. in prep, Bateman et al. in prep). Both agents are strongly associated with variations in marine survival. A meta-analysis of species distribution model results revealed that, overall, infectious agent loads in Chinook and Coho salmon were marginally higher within 30 km of active aquaculture. An eDNA study showed that probability of detection of infectious agents was 1.76-2.72 times higher adjacent to active versus fallowed farms, with *T. maritimum* among the agents most closely associated with active farms (Shea et al. 2020).

Nanophyetus salmincola in Puget Sound steelhead

In Puget Sound, disease research focused on the impacts of *Nanophyetus salmincola*, a parasite infecting steelhead and other salmonids in freshwater from northern California to Central Puget Sound (Strong and Frest 2007). An expert review suggested only a few disease agents could result in the early marine mortality patterns exhibited by steelhead, with *N. salmincola* being the most likely (Puget Sound Steelhead Marine Survival Workgroup 2014). *N. salmincola* was found at higher loads in steelhead smolts from populations with higher early marine mortality (Chen et al. 2018). However, these populations originate farther south in Puget Sound compared to those with lower loads, and there is evidence that distance traveled through Puget Sound is more important than population condition (Moore et al. 2017). Further, Hershberger and Schmidt (2020) found no difference in early marine mortality rates of Puget Sound steelhead smolts heavily infected with the *N. salmincola* parasite versus those not infected. However, Hershberger and Schmidt (2020) indicate that infections may impact fish behaviour, as 33% of infected smolts swam upstream from a release location compared to only 7% of uninfected fish. Smoltification may have been slightly retarded in infected fish, resulting in delayed volitional emigration from the river and possibly providing a mechanism for observations by Chen et al. (2018), who noted elevated parasite densities in steelhead in the estuary at the tail end of outmigration.

While *N. salmincola* may not be contributing to early marine mortality, it remains a concern in freshwater environments. The prevalence and intensity of *N. salmincola* in Green River wild and hatchery steelhead smolts and Nisqually River wild steelhead smolts are very high (Chen et al. 2018). Unmanageable mortality from *N. salmincola* resulted in the prior closure of at least two Washington Department of Fish and Wildlife (WFDW) hatcheries in the southern Puget Sound. Further, strategies such as transferring at-risk fish to sites without the parasite are currently implemented at other facilities to mitigate impacts. Hershberger et al. (2019a) found that standard doses of formalin used for disease management in hatcheries are effective at killing *N. salmincola* cercaria. Hershberger et al. (2019b) also found that concentrations of N. salmincola increased in spring and summer and peaked in the fall when streamflow increased. A new qPCR assay that can accurately identify parasite loads in water samples was developed in the process of executing this study (Purcell et al. 2017). This information provides the tools and schedule for combating *N. salmincola* in hatcheries. The qPCR assay can also be used to characterize entire watersheds to isolate source locations of *N. salmincola*, as was done on the Nisqually River (Hershberger and Schmidt 2020). WDFW is installing a new water treatment facility at Soos Creek Hatchery on the Green River. In addition to protecting hatchery fish, this may reduce the prevalence and intensity of *N. salmincola* in the entire Green River by eliminating a large portion of the hosts in the parasite's life cycle.

Synthesis Committee Perspective

The Synthesis Committee concluded that disease impacts are highly relevant to marine survival of Chinook, Coho, and Sockeye salmon in the Salish Sea, at least in recent years. Our strongest evidence for impact is in Chinook, where sampling effort, pathological investigations, and modelling efforts have been concentrated; Chinook salmon also carry the highest diversity of agents of the three species. There is less concern regarding Puget Sound steelhead because of the lack of association between infection loads of N. salmincola and early marine mortality, although steelhead have not undergone extensive testing for other agents of disease. There is no historic evidence to determine whether disease was related to long-term trends in survival, but relationships between increased temperatures and disease susceptibility as well as recent evidence of disease make it cause for concern. To date, the southern Strait of Georgia has been identified as an infection hotspot in summer months, with more infection overall in the Strait of Georgia as compared to the outer Pacific coast. Because the SSHI studies have occurred in BC waters, less is known about the geographic distribution of disease impacts in Puget Sound.

Interrelationships and Cumulative Effects

Interrelationships among disease and other factors that may affect marine survival are not well understood, but environmental stressors and other factors are likely to amplify the impacts of disease. Climate change will likely continue to increase the prevalence of marine heat waves, increase coastal freshwater and marine temperatures, and change salinity and dissolved oxygen levels. Salmon may face increased impacts of pollutants from rapid human population growth (Tian et al. 2020), potentially exacerbating disease impacts. An example of a potential synergistic effect is the combined presence of persistent organic pollutants and high loads of the parasite *N. salmincola* in South and Central Puget Sound watersheds and their impact on juvenile steelhead (Chen et al. 2018). Disease can also increase the risk of predation (Furey et al. 2021; Miller et al. 2014).

Models are currently under development to evaluate the risks of pathogen transmission from high density salmon farms to migratory salmon. Even with a large dataset of wild and farmed salmon, this is a difficult question to answer. Early models have explored whether any agents were more commonly detected in migratory Chinook within 30 km of farms. Subsequent models have focused on Sockeye exposure to farms in the Discovery Islands, information important for decisions on continuance of licenses for farm tenures in the area. Future models will apply data from all salmon species to tackle this question and include phylogenetic data on agents showing strong transmission potential around farms. Piscine orthoreovirus and *Tenacibaculum maritimum* are the two agents currently of greatest concern.

Management implications and next steps

Key findings to date show that linkages between disease and fate vary by salmon species, season, age, and environment. One of the primary next steps will be a SSHI-hosted workshop of leading world experts to rank infective agents by their potential to cause disease in wild salmon using SSHI data and published information. The highest ranked and most understudied agents will then be tested via infection challenge studies.

Other management implications and proposed next steps are as follows:

1. Address disease risks to hatchery fish.
    - Some infectious agents correlated with marine survival come from freshwater, confirming earlier assumptions that fish condition at the time of ocean entry can impact subsequent survival (i.e., carryover effects). For example, as discussed above, differences in hatchery Chinook migratory behaviour may make them more vulnerable to infection soon after ocean entry when compared to wild fish (Thakur et al. 2018). Possible solutions could involve naturalization experiments, release of hatchery fish at similar sizes to wild fish, use of newly developed salmon Fit-Chips to ensure that fish are released at an optimal smolt readiness stage (Houde et al. 2019b), development of strategies within hatcheries to optimize health of hatchery fish, investment in estuarine and nearshore habitat restoration, and use of trickle releases rather than large pulses. Generally, managing fish health in hatcheries should be prioritized, given the potential downstream impacts on hatchery and wild fish productivity. Carefully examine agents identified in the Nekoui et al. (2019) study for pathological effects and transmission risk between farmed and wild salmon; a newly discovered Pacific salmon Nidovirus is of particular interest (Mordecai et al. 2019). Removal or management of alternate invertebrate hosts for important parasites could be carried out in freshwater.
2. Assess cumulative stressors.
    - Leverage the new molecular tool, salmon Fit-Chips, to address questions like: do harmful algal blooms, high temperatures, and low dissolved oxygen levels act synergistically with disease development to ultimately cause mortality? The Fit-Chips use validated biomarker panels of host genes to identify specific stressor and disease states in individual fish, including genes predictive of imminent mortality. Combined with comprehensive salmon surveys, the Fit-Chips can help identify environments where salmon are most compromised and likely to die.
    - Assess how disease is related to feeding/fat levels/growth, how contaminants have varied over species, time, and regions as well as with behaviour (i.e., resident or not resident) and compare to trends for marine survival rates.
    - Model cumulative effects with inclusion of infection data.

3. Conduct histopathology on agents with distributional patterns that could relate to mortality impacts, as many of these samples are already on hand and ready for analysis.
4. Carry out studies with the Trites laboratory at UBC to determine whether seals differentially predate upon juvenile salmon based on infection status, as observed with other predators. Under this pattern, predators may be consuming "dead fish swimming" which may result in healthier populations with lower infection intensities.
5. Carry out studies to link infection data with other indices relating to salmon condition and feeding to begin to explore cumulative effects *in vivo*.
6. While a greater concern for freshwater than marine survival, pursue approaches to reduce *N. salmincola* burdens in hatchery and wild steelhead and salmon in rivers with high loads like the Green and Nisqually. See "*Nanophyetus salmincola* in Puget Sound steelhead" above for additional details.

Contaminants

The key hypothesis examined relating to impacts of contaminants on Chinook, Coho, and Steelhead was that exposure to contaminants during one more parts of Chinook, Coho, and Steelhead life history in the Salish Sea slows growth, increases disease susceptibility, and/or reduces marine survival. The key prediction based on this hypothesis was that Chinook, Coho, and Steelhead populations which are exposed to contaminant loads in the river, while emigrating as juveniles, and/or while residing in the Salish Sea through adult age – at thresholds and or critical concentration ranges known to adversely affect health and/or growth rates – have lower marine survival.

The anadromous life history of salmon and steelhead exposes them to contaminants in freshwater, estuarine, and marine waters (Cullon et al. 2009, O'Neill and West 2009, Ross et al. 2013a). While transitioning from freshwater to saltwater, juvenile salmonids integrate contaminant conditions across the freshwater/saltwater interface, and water quality impairments in freshwater, estuarine, and nearshore habitats represent a significant threat to juvenile salmonids, especially Chinook salmon (Johnson et al. 2007, 2013, Lundin et al. 2019, Meador 2014, 2016, 2017, O'Neill et al. 2015, 2020a). Contaminant exposure is also a concern in some locations for Coho salmon (Chow et al. 2019, West et al. 2001, O'Neill et al. 1998), and Steelhead trout (Chen et al. 2018). During outmigration, salmon are growing rapidly and undergoing physiological changes that make them vulnerable to the deleterious effects of toxic chemicals, potentially reducing their survival. In addition to contaminant exposure as juvenile salmon are entering marine waters, salmonids continue be exposed to contaminants as they feed and grow at sea, and populations feeding in more developed regions accumulate higher concentrations than those feeding elsewhere (O'Neill and West 2009).

Contaminants of concern routinely monitored in Puget Sound include PCBs (polychlorinated biphenyls), used in commercial applications; PBDEs (polybrominated diphenyl ethers), used as flame retardants in furniture, computer monitors, and other electronics; PAHs (polycyclic aromatic hydrocarbons), associated with petroleum based products (e.g., oil spills, creosote-treated wood products, and burning of fossil fuels); and other EDCs (endocrine disrupting compounds), a wide range of compounds grouped based on their biological effects on the endocrine system (PSP 2021). PCBs, PBDEs, and PAHs are considered legacy contaminants, with known toxicity to fish. PCBs were federally banned in 1979[31] and the use of PBDEs heavily restricted in Washington in 2008[32], but both are persistent organic pollutants that bioaccumulate throughout the aquatic food web and, as such, remain active in the environment long after they enter it. In Puget Sound, PCBs declined rapidly in biota after they were initially banned (Ross et al. 2013b); however, PCBs have not declined substantially in fish over the past 20 years and remain at levels in South and Central Puget Sound high enough to cause adverse effects (West et al. 2017). PBDEs increased in biota from 1984 to 2009 (Ross et al. 2013b) but have declined substantially in Pacific herring and English sole from Puget Sound since 2005 (West et al. 2017). However, localized PBDE sources that could impact fish health remain and are cause for concern (Chen et al. 2018, O'Neill et al. 2020a, 2020b). There have historically been widespread inputs of PAHs into Puget Sound. While PAHs are still problematic for fish in some areas, a wide range of recovery actions, including removal of creosote-treated pilings and contaminated sediments, cleaning of stormwater drainpipes, and other upland source controls have resulted in substantially lower prevalence of PAH-induced liver disease in benthic fish (PSP 2021). EDCs also include CECs (chemicals of emerging concern), a broad range of compounds that are generally defined by the fact that their prevalence and toxicity

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[31] Section 6(e) of the Toxic Substances Control Act (TSCA), 15 U.S.C. 2605(e).

[32] Chapter 70A.405 RCW. Washington State Legislature. 2008.

are poorly characterized and their uses and releases to the environment are poorly managed or regulated (Diamond et al. 2011). CECs include pharmaceuticals, some flame retardants, phthalates, plasticizers, phenolic compounds, vehicle-related compounds, some highly fluorinated compounds, and personal care products (soap, lotion, sunscreen), and their release into the environment may be increasing, associated with rapid human population growth in the Salish Sea region (O'Neill pers. comm.).

Contaminants are primarily transported to the environment via stormwater, wastewater, combined sewer overflow, and atmospheric deposition (see review by James et al. 2018, summarized below). Within Puget Sound, stormwater runoff was identified as the primary pathway for PCBs, approximately 10x higher than publicly owned treatment works (POTWs) and air deposition; however, estimated loadings (kg/year) were acknowledged to be underestimates. Atmospheric deposition and POTWs were estimated to be the largest delivery pathways for PBDEs to Puget Sound; stormwater was identified a secondary pathway into some local receiving waters. Loadings of PAHs are not currently well understood, making conclusions about major pathways difficult. Loading estimates for CECs and EDCs are not available; they can be transported into the environment through stormwater runoff (e.g., from urban areas, working farms), wastewater, and combined sewer overflows. Additionally, septic systems have been shown to impact local groundwater and surface water, which can enter marine systems.

Exposure to contaminants including PCBs, PBDEs, and PAHs at levels found in urbanized estuaries and nearshore waters of Puget Sound can affect juvenile salmonid behaviour, growth, immuno-competence, disease susceptibility (Arkoosh et al. 2001, Arkoosh et al. 2010, Arkoosh et al. 1998, Arkoosh et al. 1994, Arkoosh and Collier 2002, Meador et al. 2006, Varanasi et al. 1993), and ultimately survival (Meador 2014). Further, salmon that remain in Puget Sound continue to accumulate contaminants (O'Neill and West 2009, O'Neill et al. 2018, O'Neill et al. in prep). Recently, a wide range of CECs have been measured in Puget Sound waters and aquatic species (James et al. 2020, Meador et al. 2016, Tian et al. 2019, O'Neill pers. comm.) and efforts are underway to prioritize CECs most hazardous to aquatic biota (WDOE 2020). Although there is uncertainty about the prevalence and impacts of CECs, recent evidence suggests they may be affecting the health and survival of salmonids (Meador et al. 2017, 2018, 2020). Moreover, animals exposed to multiple contaminants likely experience adverse synergistic effects (Mongillo et al. 2016, Laetz et al. 2009, Meador 2006).

Contaminants in Chinook salmon

During the SSMSP, O'Neill and colleagues carried out a synoptic assessment of contaminant exposure for major populations of juvenile Chinook salmon in estuary, nearshore, and offshore (beyond the 30 m isobath) marine habitats of Puget Sound in 2013 (O'Neill et al. 2015) and in river and estuary habitats in 2016 (O'Neill et al. 2020a, Carey et al. 2016, PSP 2021). In addition, subadult resident Chinook salmon were sampled in 2016 and 2017 (O'Neill et al. 2019, PSP 2021, O'Neill pers. comm.). Juvenile Chinook residing in urbanized and industrial estuary and nearshore habitats accumulated higher concentrations of PCBs and PBDEs and experienced higher exposure to PAHs via feeding compared to fish rearing in less developed habitats. However, the relationship between urbanization and contaminant concentrations changed after the fish moved offshore and began consuming different prey. After four months of feeding in offshore habitats, Chinook from the more developed Central Puget Sound had similar concentrations (i.e., mass per weight of fish) of PCBs and PBDEs in their bodies and PAHs in their stomach contents compared to Chinook from the less developed Whidbey Basin and South Puget Sound. However, fish continued to be exposed to and accumulate PCBs and PBDEs across all basins; the mass of contaminants per fish increased after four months of feeding in offshore habitats (O'Neill et al. 2015). These data reveal that PCBs and PBDEs from highly developed river systems and other sources reach less developed offshore habitats where juvenile salmon feed for many months (O'Neill et al. 2015, PSP 2021, Carey pers. comm.). In total, approximately one third of the juvenile Chinook salmon sampled in the 2013 study had contaminant concentrations associated with adverse effects, regardless of the degree of development of the basin they were captured in (O'Neill et al. 2015). Levels of PCBs and PBDEs in fish from the Snohomish, Green/Duwamish, and Puyallup river systems, and from offshore habitat in the Whidbey Basin and Central Puget Sound were high enough to reduce growth and disease resistance and alter hormone and protein levels, based on published adverse effect thresholds (Meador et al. 2002, Arkoosh et al. 2010, 2013, 2018).

A subset of Chinook salmon samples collected in 2013 were analyzed for the presence of CECs (O'Neill pers. comm.). Chinook migrating through Puget Sound are exposed to a variety of CECs, including pharmaceuticals and industrial contaminants, with Chinook in more urbanized areas exposed to higher number of CECs. Antibiotics, anti-depressants, and heart medications were detected at concentrations high enough to affect juvenile Chinook health (O'Neill pers. comm.). In an independent series of studies, adverse sublethal effects were observed in juvenile Chinook exposed to CECs in urbanized estuaries and nearshore habitats (Meador et al. 2016, 2017,2018, 2020)

Contaminant concentrations measured in juvenile Chinook salmon collected from the full suite of major Chinook-bearing rivers within Puget Sound in 2016 confirmed that salmon migrating through developed river estuaries are exposed to higher contaminant levels than salmon migrating through less developed river estuaries. PCB concentrations exceeded adverse effects threshold concentrations in four of the eleven Puget Sound rivers assessed (Snohomish, Duwamish, Puyallup, and Nisqually), as well as in Lake Washington, through which several Chinook salmon populations migrate to reach Puget Sound (PSP 2021). PBDEs exceeded threshold concentrations for fish health in Puyallup and Snohomish estuaries (Figure 34 next page). All five of these watersheds drain into the central and southern basins of Puget Sound where most anthropogenic development has taken place. Accumulation of PCBs and, to a lesser extent, PBDEs in seaward-migrating juvenile Chinook appears to be related to the type of land cover in their natal rivers, with those Chinook migrating through watersheds with greater than 25% impervious surface accumulating more contaminants than those migrating through less developed watersheds. For river systems where elevated contaminants in juvenile Chinook salmon were observed, evaluation of contaminant sources and pathways has been initiated or planned, including studies in the Snohomish River in 2016, the Duwamish River in 2018, and the Puyallup River in 2021. In the Snohomish River, elevated PBDE concentrations were attributed to discharges of wastewater treatment plants, whereas PCBs were attributed to stormwater, with concentrations high enough to pose a conservation threat (O'Neill et al. 2020a). Approximately 73% and 14% of the natural-origin Chinook sampled from two regions of the Snohomish estuary receiving wastewater effluent discharges had concentrations of PBDE congeners within the range that altered immune response and increased disease susceptibility in laboratory studies. In contrast, in regions of the Snohomish estuary that do not receive direct discharges from wastewater treatment plants, none of the natural-origin Chinook had PBDE concentrations high enough to alter immune response. Of note, PBDE concentrations were higher in natural-origin fish compared to hatchery-origin fish collected at the same location, likely due to their differential use of estuarine habitats (O'Neill et al. 2020a).

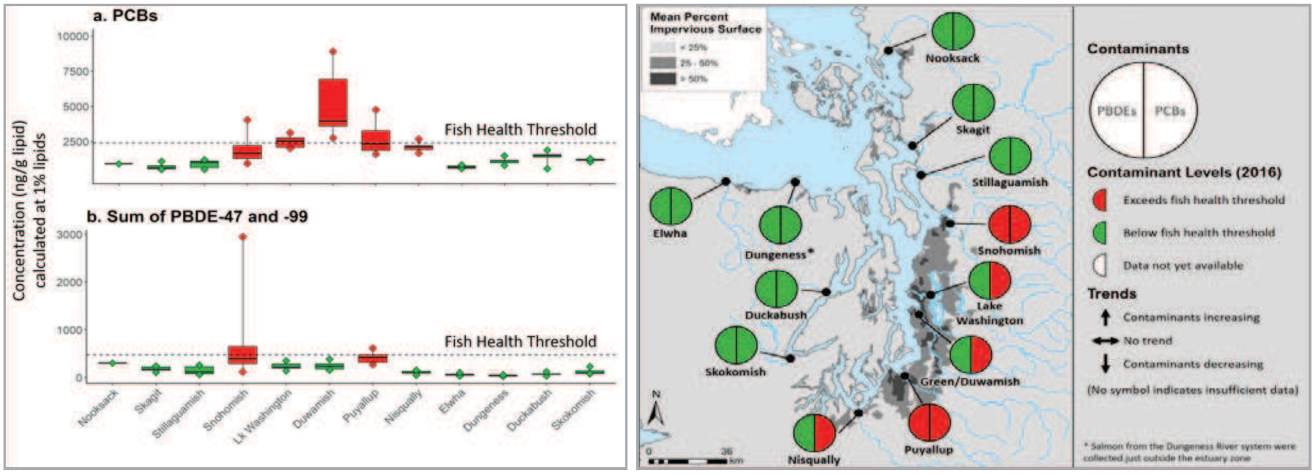

Figure 34. *Left image: PCB (a) and PBDE (b) concentrations (ng/g lipids calculated at 1% lipids) in juvenile Chinook salmon from 11 Puget Sound estuaries and Lake Washington in 2016. Solid horizontal lines inside the boxes are the median concentration. Top and bottom of boxes indicate 25th and 75th percentiles and diamonds indicate 5th (lower) and 95th (upper) percentiles. At each sampling location, the color of the box plot indicates whether the measured concentration in most of the salmon samples (i.e., the upper diamond) was below (green) or above (red) the fish health threshold concentration (horizontal dashed line) associated with adverse effects. Right image: symbols on map indicate sites where contaminants in salmon exceed (red) or remain below (green) fish health thresholds. (Source: PSP 2021: https://vitalsigns.pugetsoundinfo.wa.gov/VitalSignIndicator/Detail/49)*

Although juvenile Chinook salmon can be exposed to high levels of contaminants associated with wastewater and stormwater inputs into riverine and estuarine habitats, adult salmon acquire almost all their contaminants through bioaccumulation while in marine waters (Cullon et al. 2009, O'Neill and West 2009), where they typically acquire 99% of their final adult weight (Quinn 2018). Earlier studies documented that adult Chinook salmon originating from Puget Sound had 3-5 times higher PCB levels than Chinook salmon originating from elsewhere along the Pacific coast (O'Neill and West 2009). Moreover, O'Neill and West (2009) calculated that most of these PCBs (96%) were accumulated in marine habitats, leading to the hypothesis that residency in Puget Sound contributed to the elevated PCB levels in Puget Sound Chinook salmon populations. About 30% of Puget Sound Chinook salmon spend most of their lives in Puget Sound rather than coastal waters of the Pacific Ocean (Chamberlin et al. 2011, O'Neill and West 2009). Resident Chinook salmon are hypothesized to have higher PCB concentrations than ocean migrants because herring in Puget Sound, which are consumed by resident Chinook, are highly contaminated with PCBs (West et al. 2008, 2011).

Recent research confirmed that resident Chinook salmon have higher levels of bioaccumulated contaminants compared to ocean migrants (O'Neill pers. comm., PSP 2021). In the late fall of 2016 and winter and spring of 2017, contaminants were measured in edible muscle tissue of subadult resident Chinook collected from various fishery Marine Areas (MAs) managed by WDFW, roughly representative of Puget Sound oceanographic basins (Figure 35). Levels of PCBs measured in resident Chinook salmon from Puget Sound exceeded the recommended limits for human consumption; PBDE concentrations did not (per Washington Department of Health (DOH) screening value concentration). This suggests PBDEs have either declined in the pelagic food web (like in herring; West et al.2017) or were never elevated. Spatial variation in contaminant concentrations and patterns in resident Chinook salmon suggest higher inputs of contaminants to inner Puget Sound (MAs 10, 8-2, 8-1, and 13) and limited movement of resident salmon between inner and outer Puget Sound. Although PCB concentrations were always higher than PBDE concentrations in resident Chinook, both PCB and PBDE concentrations tended to increase with catch distance from oceanic waters, with highest concentrations observed in fish caught furthest from the ocean, in South Puget Sound (MA 13). Increasing contaminant concentrations in salmon farther into Puget Sound is consistent with increased human development. The hypothesis is supported by PCB loading studies by Osterberg and Pelletier (2015), who estimated loadings (kg/ year) of PCBs and PBDEs to Puget Sound from all major pathways was 11 times higher in inner Puget Sound than in less developed basins like Hood Canal and Admiralty Inlet (calculated based on Table 3 in Osterberg and Pelletier 2015). Furthermore, contaminant fingerprints in salmon (i.e., relative abundance of contaminant classes) varied spatially between salmon caught in the San Juan Islands (MA 7) and the Eastern Strait of Juan de Fuca (MA 6) with those caught in the rest of Puget Sound, indicating limited overlap in marine distribution consistent with previous sonic tagging studies that documented a high degree of basin fidelity, with limited movements between resident Chinook salmon caught in the Strait of Juan de Fuca and the San Juan Islands and those residing in the Central Puget Sound basin (Arostegui et al. 2017; Kagley et al. 2017).

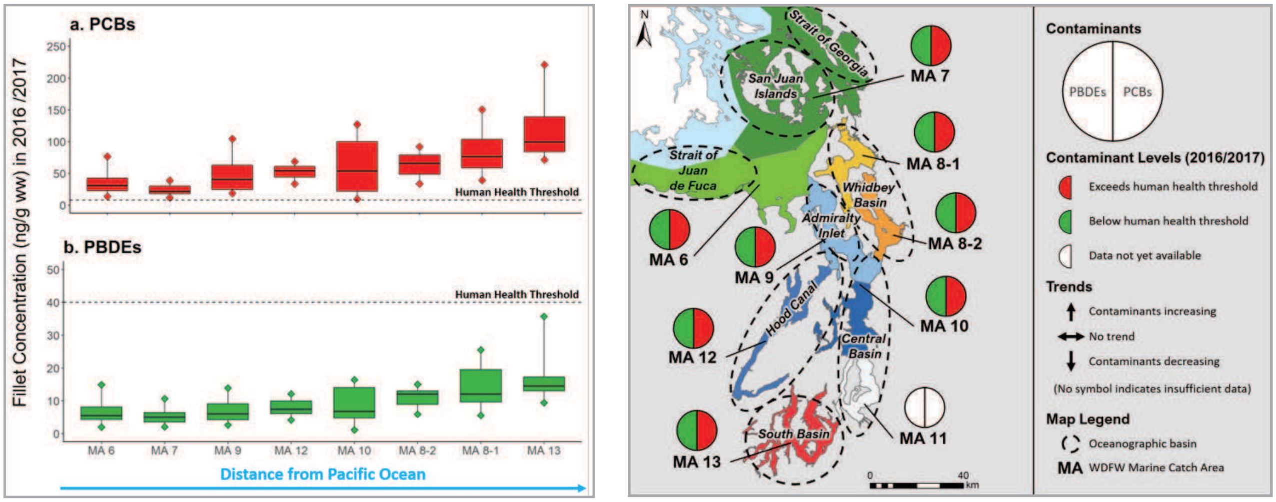

Figure 35. *Left image: current PCB and PBDE concentrations in resident Chinook salmon from eight sampling areas across Puget Sound in 2016 and 2017. Solid horizontal lines inside boxes are the median concentration. Top and bottom of boxes indicate 25th and 75th percentiles and diamonds indicate 5th (lower) and 95th (upper) percentiles. The human health threshold is met (green) if the upper diamond is below the DOH screening value for PCBs and PBDEs. Red indicates areas where the 95th percentile exceeded the screening value. Right image: symbols on map indicate sites where contaminants in salmon are exceeding (red) or are below (green) fish health thresholds. (Source: PSP 2021: https://vitalsigns.pugetsoundinfo.wa.gov/VitalSignIndicator/Detail/47)*

Resident Chinook concentrations of PCBs and, to a lesser extent, PBDEs are high enough to impair fish health, with those fish residing in inner Puget Sound most at risk. Overall, 15% of resident Chinook sampled in 2016 and 2017 (mostly sampled from inner Puget Sound) had PCB concentrations > 100 ng/g wet weight, the threshold concentration predicted to cause reproductive or growth impairments (Berninger and Tillet, 2019). Approximately 1-2% of the resident Chinook concentrations were > 220 ng/g wet weight, the threshold concentration predicted to cause mortality. Assuming laboratory PBDE exposure studies on juvenile Chinook (Arkoosh et al. 2018) are applicable to subadult resident Chinook, resident Chinook also likely experience adverse health effects associated with PBDE exposure, especially Chinook captured in inner Puget Sound. Approximately 15% of the resident Chinook had PBDE concentrations between 10.9 and 37 ng/g, concentrations associated with increased susceptibility of disease in juvenile Chinook studies conducted by Arkoosh et al. (2018). A subset of the resident Chinook salmon was evaluated for the presence of one group of CECs, per- and polyfluoroalkyl substances (PFAS), a family of more than 4,700 synthetic organic chemicals used in the manufacture of coatings, surface treatments, and specialty chemicals in cookware, carpets, food packaging, clothing, cosmetics, and in other common consumer products.

Overall, PFAS were only detected in muscle tissue of resident Chinook in two marine basins of Puget Sound (Whidbey Basin and South Puget Sound) and concentrations were low (13.3 ng/g wet weight, median = 0.99 ng/g wet weight) compared to concentrations found in more urbanized lakes (Ecology and Health 2020), suggesting PFAS are not a concern for resident Chinook. Contaminant exposure could help explain the variance in marine survival among Salish Sea Chinook salmon populations. While not part of the SSMSP, Meador (2014) assessed the relationship between marine survival rates and contaminated estuaries of Puget Sound. He found that juvenile hatchery Chinook transiting contaminated Puget Sound estuaries between 1972 and 2008 exhibited an overall rate of survival 45% lower than that of Chinook moving through uncontaminated estuaries. While the study used hatchery fish data, Meador (2014) noted that these results would have important implications for wild juvenile Chinook that spend more time in the estuary than hatchery-reared fish. In contrast, a parallel analysis of hatchery-produced Coho salmon from many of the same hatcheries did not show reduction in marine survival associated with contaminated rivers, indicating that the effects of estuarine contamination depend on species, likely because Chinook salmon spend more time in estuaries than do Coho salmon, which generally move more quickly to offshore marine waters. Meador (2014) concluded that contamination was an important factor affecting the marine survival of Chinook salmon but did not fully distinguish the impacts of contaminants from impacts of physical habitat degradation that typically accompany contamination of estuarine and nearshore marine habitats (Magnusson and Hilborn 2003).

Contaminants in Steelhead

Contaminant loads were assessed in juvenile steelhead by O'Neill and colleagues during the SSMP (Chen et al. 2018). In 2014, juvenile steelhead were collected from in-river and estuary habitats of the Skagit, Green/Duwamish, and Nisqually rivers and nearby Puget Sound marine habitats (Chen et al. 2018). Generally, steelhead did not accumulate contaminants beyond their time in the river, likely due to their rapid migration through the estuary and nearshore areas (Moore et al. 2015). Overall, PCBs measured in steelhead from Puget Sound were not high enough to exceed adverse effects thresholds for fish health. However, PBDE levels were above thresholds for increased disease susceptibility in 33% of steelhead collected from the Nisqually River basin (Chen et al. 2018). Repeat in-river sampling in 2015 confirmed these rates (O'Neill et al. 2020b). Since PBDEs were only detected in a portion of the samples, the source is likely limited to a portion of the watershed. A subsequent assessment using semipermeable membranes and biofilm (Hobbs et al. 2019) suggests the source of PBDEs is the Eatonville wastewater treatment plant located in the upper Mashel River watershed, a tributary of the Nisqually River (O'Neill et al. 2020b). Although not assessed, steelhead from the Snohomish River may also have PBDE concentrations above critical tissue levels, based on exceptionally high levels of PBDEs measured in mountain whitefish (5-37 ng/s wet weight) in that system (Mathieu and Wong 2016.).

Contaminants in Coho salmon

Contaminant exposure in seaward-migrating juvenile Coho salmon was not assessed as part of the SSMSP, and limited information is available about impacts of contaminants to juvenile Coho in freshwater or marine environments that could lead to increased marine mortality. PAH exposure in Pink salmon embryos causes cardiac edema and delayed mortality (Incardona and Scholz 2016), so it is possible that PAHs in stormwater may affect salmon species like Coho (and possibly steelhead) that reside in smaller tributaries where the effects of stormwater are likely to be greater, resulting in delayed marine mortality. However, adult Coho salmon tend to have lower concentrations of legacy contaminants (PCBs, PBDEs, PAHs) than Chinook salmon (Mongillo et al. 2016). There are abundant studies documenting high mortality in adult and juvenile Coho salmon in riverine habitats. Adult Coho salmon returning from the ocean to spawn in urban streams in Puget Sound have documented mortality before spawning due to impacts associated with contaminants in stormwater runoff from roads (Scholz et al. 2011, Spromberg et al. 2016, Feist et al. 2017, McIntyre et al. 2018). The behaviour and physiological effects associated with this acute mortality is referred to as urban runoff mortality syndrome (URMS; McIntyre et al. 2018). Severity of URMS scales with the extent of imperviousness within watersheds (Feist et al. 2011) and with the density of motor vehicle traffic near spawning habitats (Feist et al. 2017). Water collected from streams during storm events with URMS-affected Coho salmon had similar chemical composition to roadway runoff and tire tread wear particles (TWP) suggesting the toxicant source was associated with TWP (Du et al. 2017). In laboratory studies, untreated stormwater runoff from roads was lethal to juvenile Coho salmon (McIntyre et al. 2015, Chow et al. 2019), which exhibited URMS effects similar to those shown by affected adult Coho in stream environments (Chow et al. 2019). French et al. (2020) exposed juvenile Coho to an environmentally relevant range of diluted runoff (1% to 25%) from three storm events and reported that mortality increased with increasing concentration of stormwater runoff. For all three storms, nearly all the Coho survived at a concentration of 2.2%, whereas at a concentration of 25% nearly all the Coho died. Recently, Tian et al. (2020) have convincingly implicated a chemical found in automotive and truck tires, 6PPD, which ozonates to 6PPD-quinone, to be the source of acute Coho mortality. Rubber dust containing 6PPD-quinone washes from roadways into waterways at concentrations highly lethal to Coho salmon (Tian et al. 2016).

Across the salmon species, it appears that Coho salmon and, to a lesser extent, steelhead have a high susceptibility to acute mortality associated with roadway runoff to urban streams (McIntyre et al. 2018, French et al. 2020). Significant acute mortality associated with roadway runoff has not been observed in Chum salmon (McIntrye et al. 2018) or Sockeye (French et al. 2020). To date, studies of juvenile Chinook have shown minimal mortality (French et al. 2020, Scholz 2021).

URMS may have contributed to declining abundances of naturally spawning Coho salmon in Puget Sound (Losee et al. 2019) or to low abundances in developed watersheds (Pess et al. 2002, Bilby and Mollot, 2008). Moreover, modelling indicates that future urbanization, increased toxic runoff, and increased spawner mortality has the potential to drive rapid local Coho extinctions (Spromberg and Scholz 2011). However, assessment of the impact of URMS on Coho productivity has been focused on the mortality of adult Coho in freshwater. Impacts to natural spawning success due to URMS likely does not account for changes in hatchery and wild Coho marine survival. URMS primarily occurs in urban rivers and Coho show synchronicity in marine survival patterns among populations from urban and rural areas throughout the Salish Sea (Zimmerman et al.2017). That said, stormwater runoff impacts to juvenile Coho salmon and possibly steelhead in urban watersheds could contribute to changes in marine survival if sublethal effects lead to delayed mortality.

Synthesis Committee Perspective

While Meador (2014) suggested that contaminant exposure may result in variation in marine survival among Chinook salmon populations in Puget Sound, it is not known whether contaminants were a primary contributor to declines in Chinook marine survival across the Salish Sea since the late 1970s. **The Synthesis Committee agreed that there is evidence that contaminant loads could be preventing or limiting the recovery of many Chinook populations in the Salish Sea.** Juvenile Chinook are exposed to PCBs above adverse effects thresholds in urban rivers. PCBs also continue to accumulate in Chinook salmon as they rear in the marine waters of Puget Sound. This is of special concern for Chinook salmon that reside in the central and southern portions of Puget Sound for most of their lives. Further, there are very high levels of PBDEs in juvenile Chinook salmon in the Snohomish River estuary, well above adverse effects concentrations, and high levels of PBDEs in juvenile Chinook in the Puyallup River are a concern. Insufficient data exist regarding the impacts of PCBs and PBDEs on juvenile Coho, and there is limited data for steelhead. PBDEs are above adverse effects concentrations in juvenile steelhead in the Nisqually River.

Given their susceptibility to URMS, the exposure of juvenile Coho to stormwater/road runoff, especially in urban areas where traffic is high, warrants further investigation. Steelhead may also be adversely affected and should be included in future URMS investigations.

Insufficient contaminant data exists for the Strait of Georgia, which has not previously had a focused contaminant program. This may be changing, given recent investments in contaminant assessments of Strait of Georgia Chinook and southern resident orcas by Canada Department of Fisheries and Oceans and others (O'Neill pers. comm.). However, the Committee speculates that Chinook salmon originating from the Fraser River and rearing in the lower Fraser River or the southern Strait of Georgia (near Vancouver) could be similarly impacted by contaminants, as might Harrison/Chilliwack populations that rear in Puget Sound.

Finally, the Committee noted that there is insufficient data regarding the impacts of Chemicals of Emerging Concern (CECs), but it is an area of concern, especially as salmon may face increased exposure to CECs associated with rapid human population growth.

Interrelationships and Cumulative Effects

There is a strong link between contaminant loads and reduced disease resistance in juvenile Puget Sound Chinook (Arkoosh et al. 1998, Arkoosh et al. 2001, Arkoosh et al. 1994) and perhaps in other salmonids. High loads of PBDEs could exacerbate the impacts of the parasite *N. salmincola* in juvenile Puget Sound steelhead (Chen et al. 2018). We can expect synergistic effects between contaminants and increased disease risk associated with water temperatures as discussed in the pathogens and disease section. There may also be confounding or compounding effects of reduced habitat availability (Magnuson and Hilborn 2003) in watersheds with high contaminant exposure (Meador 2014). The potential for synergistic impacts driven by climate change—the compounding effect of contaminants with increased water temperatures and disease—is an area of concern (Noyes et al. 2009; Gouin et al. 2013).

Management Implications and Next Steps

Chinook salmon exposure to PCBs and PBDEs may be reduced through remediation of estuary and nearshore habitats. However, management efforts must be prescriptive to the individual river system and contaminant of concern. Further, the observation that Chinook continue to accumulate PCBs as they reside and feed throughout Puget Sound suggests that inputs from urban areas are reaching non-urbanized offshore habitats (O'Neill et al. 2015). These findings suggest that controlling initial release of contaminants to the environment may be necessary to protect offshore habitats.

A wide range of activities and actions have taken place, are underway, or are planned to address these contaminants, including usage bans, Superfund Site cleanups, sediment remediation, and source monitoring and control. An evaluation of human activities that contribute to contaminants in the environment is underway via the Stormwater Strategic Initiative coordinated by Puget Sound Partnership, and contaminant reduction actions are being prioritized for funding. See the Toxics in Fish Implementation Strategies for details.[33] In addition, recommendations to reduce chemical contamination in salmon were compiled by the Washington State Governor's Orca Task Force.[34]

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33. https://pspwa.app.box.com/s/q1rueyrajn7kgp7gfkal65k0h87cwcpx

34. https://www.governor.wa.gov/issues/issues/energy-environment/southern-resident-orca-recovery

Key suggestions for next steps include:

- Compare spatiotemporal trends in contaminants with trends in Chinook and Coho marine survival rates to build upon the Meador (2014) study and evaluate the Synthesis Committee's current perspective regarding contaminant impacts.
- Reduce the input of PBDEs from wastewater treatment plants, particularly in the Snohomish watershed for Chinook salmon and the Nisqually River watershed for steelhead. Impacts of PBDEs to Chinook salmon in the Puyallup River watershed may also warrant attention.
- Assess contaminant loads in steelhead in the Snohomish River.
- Assess the implementation of stormwater controls designed to reduce contaminants entering Puget Sound watersheds.
- Focus larger-scale remediation efforts on PCB hotspots like the Green-Duwamish River to address impacts to local Chinook salmon populations and Chinook residing throughout Puget Sound.
- Determine the contaminant pathway for PCBs in Puget Sound marine waters (e.g., through the food web or via the water itself). Use the UBC SalishSeaCast model and Ecology's Salish Sea Model to assess contaminant distributions from point sources or riverine inputs.
- Carry out a collaborative study to assess the synergistic effects of contaminants and disease.
- Compare diet, stable isotopes, and growth patterns among Chinook salmon from marine basins and with those of ocean migrants to further assess the impact of contaminants in the offshore environment.
- Include chemicals of emerging concern in future monitoring and expand the geographic scope of contaminant monitoring in Puget Sound to include other major river systems that contribute to the production of Chinook, such as Hood Canal, Nooksack, and Stillaguamish

CONCLUSIONS AND LOOKING FORWARD

The Salish Sea Marine Survival Project (SSMSP) was designed as an intensive, short-term study of the Salish Sea ecosystem to examine major components of the salmon ecosystem simultaneously, evaluate the marine survival of Chinook, Coho, and steelhead, and identify the primary determinants of marine survival of these species. With that information, we aimed to provide guidance for next steps in research and management.

As our findings accumulate, we have begun to develop a picture of what is happening to our juvenile salmon and steelhead as they traverse the Salish Sea marine environment. As a living document, this synthesis will continue to evolve as our understanding evolves.

The Salish Sea was once a uniquely productive place for Chinook, Coho, and steelhead, with higher marine survival rates in the late 1970s and 1980s declining to comparable or lower survival rates than the coast. Within the Salish Sea, Chinook rear in distinct locations resulting in differences in marine survival trends among populations, whereas Coho salmon are more distributed throughout and have more synchronous survival trends among populations. Steelhead trends are also synchronous among Salish Sea populations.

Certain periods of the salmon life cycle can be deemed critical because these periods have a disproportionately large effect on overall survival. The magnitude of a critical period reflects the condition of habitat, prey availability, competition, predation, and/or disease in that period. The "critical" aspect of the early marine phase for salmon may be the need to achieve a growth threshold/condition in their first summer at sea to survive the subsequent fall/winter conditions. Alternatively, direct mortality during the early marine phase may signify the importance of the critical period. For Chinook and Coho, growth during their first summer in the Salish Sea marine environment appears important, whereas for steelhead, which migrate quickly through the Salish Sea to the open ocean, direct mortality as smolts in the Salish Sea is important. Coho and possibly Chinook smolts may also suffer high early marine mortality, but the evidence is less clear. The lack of data from the winter months immediately following the first summer that Chinook and Coho spend in the Salish Sea is of great concern. There is some evidence of high winter mortality; data from winter months are needed to determine relationships between growth in the first summer at sea and subsequent survival/mortality.

Numerous factors can affect salmon survival during this critical period; it was the objective of the SSMSP to identify which appear most important. Salish Sea-wide, factors affecting food supply and predation are the most critical, whereas other impacts are significant at population or sub-basin levels or we lack comprehensive data with which to draw robust conclusions. Key findings of the SSMSP include:

- Fewer Chinook fry that encounter degraded estuaries survive to adulthood. There are concerns about the substantial loss of kelp and increased patchiness of eelgrass beds.
- Hatchery Chinook release times have contracted over the past 40 years, and this could influence survival in concert with environmental changes; however, mechanistic relationships are unclear.
- Changes in environmental variables (sea surface temperature, salinity, winds, and light attenuation/cloud cover) and zooplankton relate to changes in Chinook and Coho marine survival rates; however, the mechanisms by which changes in environmental variables lead to changes in marine survival are complex and currently unclear. Inter- and intra-species competition may be occurring, exacerbating situations where food supplies are limited.
- Changes in abundance and/or diversity of Pacific herring, especially age-0 herring, could be affecting the growth and survival of Chinook and Coho salmon. Larval crab and amphipod availability is also important given the abundance of these prey in Chinook and Coho diets.
- Juvenile Coho, Chinook, and steelhead mortality throughout the Salish Sea has likely increased as a result of a significant increase in seal abundance. Pulses of hatchery fish may attract or buffer predation, and changes in the availability of prey such as herring, anchovies, or other species that seals and other predators primarily eat could affect predation rates on salmon and steelhead.
- Contaminants such as PCBs and PBDEs are high in certain populations of out-migrating Puget Sound Chinook smolts, which could be resulting in slower growth and/or higher mortality in the marine environment. PCBs accumulate in Chinook as they reside in Puget Sound.

- Regarding diseases and pathogens, the southern Strait of Georgia has been identified as an infection hotspot in summer months, with more infection overall in the Strait of Georgia as compared to the outer Pacific coast. There are relationships between marine survival rates and length and intensity of exposure to disease; highest microbe loads were associated with residency in specific areas of the Strait of Georgia; and temperature was a key driver of infection.
- Although the work is not complete, initial modelling suggests that cumulative impacts are important; taking a multi-pronged approach to address factors affecting marine survival is critical.

The ultimate goal of the SSMSP was to determine the extent to which poor Chinook, Coho, and steelhead survival is driven by local factors (e.g., runoff, wastewater, marine mammal management, habitat availability, hatchery production), global processes (climate change, ocean acidification, ocean cycles), or some cumulative, synergistic combination and, based on results, to propose action-oriented research and management recommendations. It was understood that identification of local impacts would result in recommendations to improve the Salish Sea ecosystem, whereas globally-driven impacts would result in recommendations to adapt to our changing environment.

There are several potential management actions that we can try now, described throughout this document. The suite of management actions chosen will be dependent upon species, populations, and habitats targeted. Uncertainty in outcomes, particularly with respect to climate change, should be addressed through experiments or adaptive management plans. Coordinated monitoring and evaluation of actions over prolonged time periods is critical. Finally, we appreciate that we must consider what is financially, socially, and politically feasible and, while a formal management analysis was not done, these constraints were considered.

Management actions could include but are not limited to:

- Recognize the role and impact of climate and oceanic changes to salmon prey in recovery plans and state and province-wide climate initiatives. Develop monitoring plans and tools to measure changes in our marine waters.
- Reduce damage to and restore estuary and nearshore habitat (e.g., kelp and seagrass) for salmon, Pacific herring, sand lance, and crab. Ensure connectivity of marsh, eelgrass, and kelp habitats is maintained. Support soft-shore initiatives to minimize habitat loss.
- Recover, protect, and maintain diversity in herring populations. Better understand early year class dynamics.
- Support salmon life history variability through habitat restoration, population management and experimentation with hatchery rearing and release strategies. This may build resilience to variation in food supply driven by changes in climate and ocean conditions and may reduce the potential for density-dependent impacts including competition, disease, and predation.
- Investigate approaches to reducing predation by seals including: facilitating passage at migration barriers where predation is an issue; obstructing or removing log booms and other haulouts; using predator deterrents; and, if necessary, performing experimental removals. Consider seal predation from an ecological perspective and account for the role of changes in abundance/timing of their primary prey (forage fish and gadids).
- Take targeted actions to reduce contaminant burdens in juvenile salmon and steelhead where those impacts are greatest (e.g., PBDEs affecting Chinook in the Snohomish estuary). Focus larger-scale remediation efforts on PCB hotspots to reduce impacts to Chinook residing in Puget Sound.
- Optimize fish health (disease and smolt readiness) in hatcheries, especially as increasing temperatures associated with climate change continue to be a concern. Applying new genomic technologies (e.g. Fit-chip) and research within facilities may significantly improve our understanding of hatchery effects and interactions with wild salmon.
- Where possible (e.g., Cowichan River), protect and manage flows to reduce predation-based mortality of out-migrating salmon smolts (e.g., under BC Water Sustainability Act, 2014).
- Use newly compiled environmental data to improve adult return forecasting and harvest management and new ecosystem models to broadly guide ecosystem recovery actions.[35]

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[35] See the document titled "Novel Assessment Techniques, Monitoring Recommendations, and New Tools for Ecosystem-Based Management Resulting from the Salish Sea Marine Survival Project" for more information.

As indicated throughout this report, we still have many questions about what is affecting salmon survival in the Salish Sea. In particular, we have substantial evidence that impacts to the food supply of Chinook and Coho salmon are occurring, but mechanisms are poorly understood. This includes understanding the relative impact of temperature, nutrients, winds, shifts in primary productivity (e.g., diatoms versus dinoflagellates), and conditions that affect light attenuation underwater.

Additional priority research needs include:

- Assess what happens to juvenile Chinook and Coho salmon during their first winter to determine the outcomes of different growth trajectories during their first summer in the Salish Sea. Continue to separate mortality across life history stages in the process.
- Continue to analyze historical datasets (e.g., plankton surveys, archived otoliths) to assess historical conditions for salmon prey and growth.
- Improve our understanding of salmon migration timing and nearshore marine conditions relevant to survival. Better assess nearshore habitat use, value, and connectivity throughout major juvenile migration routes.
- Evaluate population-specific herring (and other forage fish) distribution and movement patterns in the Salish Sea, most notably with respect to age-0 herring. Integrate local citizen science and First Nation and tribal knowledge to improve our understanding of spawn timing and locations. In general, responsible agencies should improve assessments of forage fish given their critical role as both prey for salmon and for salmon predators.
- Examine the hypothesis that feeding by juvenile Pink, Chum, and herring before Chinook and Coho enter the Salish Sea marine environment deplete the availability of edible crab larvae (or other prey) for Chinook and Coho.
- Improve our understanding of seal predation. Assess potential hotspots, diet variation within seal populations, the impact of prey size, and whether the mortality is additive or non-additive. Also, assess predator behaviour in relation to pulses of out-migrating salmon and impacts of prey switching.
- Assess synergistic relationships and the impact of cumulative stressors associated with disease (e.g., contaminants, harmful algae, predation, ocean acidification, etc.). Test the utility of Fit-chips developed by the SSHI to evaluate the physiological fitness of Pacific salmon under climate change.
- Assess contaminant inputs and impacts in the Strait of Georgia. Prioritize the lower Fraser.
- Determine the contaminant pathway for PCBs in Puget Sound marine waters and assess the impact of CECs.
- Continue to assess ocean acidification and harmful algae since these could become significant issues for salmon and their ecosystem under future climate change scenarios.

Although many of these local-scale management responses may greatly benefit Coho, Chinook, and steelhead, it is likely that much of the variation in salmon production is driven by annual variation in climate and resulting biological oceanographic conditions in the Salish Sea. The actions discussed above may diminish the magnitude of variation but are unlikely to compensate for large-scale climate or oceanic effects. The ability to predict ecosystem consequences by understanding ecological interactions and to enact management responses is a necessary outcome of our research. For example, SSMSP results suggest that rearing locations for Chinook populations within the Strait of Georgia can impact overall marine survival. Survival issues specific to rearing locations may be improved by local-scale nearshore and estuary restoration but impacts of oceanographic conditions within different regions of the Strait could not be similarly ameliorated.

To integrate multiple environmental changes within the Salish Sea and assess their impacts on salmon, the development of food web and end-to-end models that simulate full ecosystem processes from oceanography up through trophic dynamics and fisheries is an ongoing effort within the SSMSP. These include an Ecopath with Ecosim model (Christensen and Walters 2004) being developed by University of British Columbia and an Atlantis model (Fulton et al. 2011, Audzijonyte et al. 2019) developed by NOAA and LLTK. In addition to investigating research questions about individual species or ecosystem components, end-to-end models are increasingly being used to consider cumulative impacts, evaluate fishery management options (including spatial management, harvest levels, and gear switching), quantify multi-species tradeoffs in fisheries yield, and evaluate impacts of nutrient loading, oil, and other contaminants. These types of models are now a core part of scientists' and managers' toolboxes for supporting ecosystem-based management of fisheries and marine resources. Due to the uncertainty inherent in understanding complex natural systems – especially marine systems with limited observational data – using multiple models to evaluate and inform policy choices and management decisions is an emerging best practice (Townsend et al. 2014). The two independent SSMSP models are being developed to test our understanding of mechanisms driving salmon in the Salish Sea ecosystem. Both synthesize diverse data types and represent multiple ecological processes (e.g., primary production, prey availability, growth, predation, reproduction, fishery processes). The SSMSP's definition and evaluation of hypotheses and the synthesis of related datasets has given these models a firm foundation. The models will provide forecasts of how current and future environmental conditions and management actions may affect salmon production and will be applied for hindcast (historical) tests that evaluate the set of potential drivers of salmon survival and productivity. Modelling exercises like these are one way of testing our understanding of the Salish Sea, predicting effects on salmon production, and setting future expectations.

The quality of model outputs and other analyses of the impacts of ecosystem change are intrinsically tied to the quality and quantity of data available. Therefore, we must continue to collect and improve upon the empirical data available. This includes:

- Maintaining and improving upon the expanded oceanographic and zooplankton monitoring efforts initiated via the SSMSP.
- Implementing juvenile salmon and herring midwater sampling throughout the Salish Sea, especially in Puget Sound where no consistent program exists.
- Improving our ability to assess stage-specific growth and mortality of juvenile salmon.
- Expanding our pinniped demographics and diet sampling in space and time.
- Expanding contaminants sampling throughout the Salish Sea.

Specific monitoring recommendations born from the SSMSP, as well as several new and innovative assessment techniques and tools for ecosystem management, are described in detail in the affiliated paper titled, "Novel Assessment Techniques, Monitoring Recommendations, and New Tools for Ecosystem-Based Management Resulting from the Salish Sea Marine Survival Project".

Many of our conclusions are limited due to lack of adequate long-term datasets. A significant benefit of the SSMSP has been the encouragement and provision of a foundation for long-term monitoring of the Salish Sea and salmon health, with collaboration across the international border. Some of the outcomes include:

- An augmented DFO zooplankton sampling program and new, collaborative Puget Sound zooplankton sampling program.
- Increased Washington State and DFO focus on seal and sea lion populations and their diets.
- Increased DFO focus on harmful algae and biotoxin monitoring in the Strait of Georgia.
- Extension of oceanographic and salmon studies into Johnstone Strait through collaboration with the Hakai Institute on Quadra Island.
- A significant expansion of nearshore habitat restoration, monitoring, and marine debris removal through Coast Restoration Fund support to Seachange, Project Watershed (Comox), and Raincoast Conservation in the Fraser River estuary.

Finally, the PSF Citizen Science Oceanography Program that began during the SSMSP has collected an unprecedented amount of annual oceanographic data at spatial and temporal scales not previously attainable and at a fraction of the cost of traditional research vessels. The program has also provided the framework for ongoing monitoring of the Strait's ever-changing environmental conditions impacting salmon, particularly when supplemented with innovative applications of remote sensing and ocean moorings through collaborations with BC Ferries, Ocean Networks Canada, and others. Other new PSF-supported citizen science programs include forage fish embryo sampling and habitat identification with local Shorekeepers, World Wildlife Fund, and Vancouver Island University, and a new citizen science initiative through the University of Victoria to sample adult Chinook diets in the Strait of Georgia to assess seasonal, regional, and interannual variability in herring and other forage fish availability.

The Strait of Georgia Data Centre (www.sogdatacentre.ca), a partnership between Sitka Foundation, UBC, and PSF, was developed to house and distribute existing and new data used in SSMSP studies and continues to be a vital repository of information on ecosystem management and restoration in the Strait.

LLTK, PSF, and the SSMSP collaborators continue to address research gaps, integrate findings into recovery plans, and test management actions. LLTK participated as a member of the Washington State Governor's Southern Resident Orca Task Force and its prey workgroup. Through this avenue, findings of the SSMSP influenced over 20% of the recommendations for how to proceed (Task Force 2018), including novel hatchery management approaches, a focus on estuary habitat restoration, an ecosystem approach to predation management, forage fish recovery, zooplankton monitoring, and revised NPDES permitting for wastewater treatment to include flame retardants. LLTK also participated on the Puget Sound Steelhead Recovery Team, and SSMSP findings had significant influence on recovery strategies in the NOAA Fisheries Puget Sound Steelhead Recovery Plan (NMFS 2019). Finally, LLTK is currently working to incorporate SSMSP findings into Puget Sound Chinook recovery plan updates to inform local recovery strategies.

PSF has recently embarked on a thorough review of hatchery effectiveness in the Strait of Georgia. LLTK and PSF are also working with federal, tribal, and state hatchery managers throughout the Salish Sea to assess the effectiveness of various Chinook and Coho rearing and release strategies. Significant advances in DNA-based tools (parentage-based tagging) and genomics (EPIC 4 Coho study, www.sfu.ca/epic4, and Strategic Salmon Health Initiative) can be used in combination with these hatchery studies in the future to better assess impacts to hatchery fish and interactions between hatchery and wild salmon. During the SSMSP, a novel PIT tag study was piloted in the Cowichan River to assess freshwater and marine survival. This study highlighted the importance of the link between freshwater flows and in-river predation, the timing of critical mortality periods for Chinook during both the early marine period and the first winter of marine life, and the much lower survival of hatchery-produced salmon than wild fish. These findings prompted decisions by DFO-SEP to change their hatchery release locations for Cowichan Chinook, as well as providing the impetus to address minimum ecological flows. PSF is moving forward with an expansion of the Cowichan study, deploying PIT arrays in several BC systems to provide further information on survival bottlenecks for Coho, Chinook, and steelhead. This architecture will also provide means to monitor and evaluate hatchery experiments and activities. A detailed winter ecology study of Chinook in the Strait of Georgia will be performed to assess habitat use and nutritional stress and to provide valuable information on this critical period.

PSF is continuing focused studies in Strait of Georgia nearshore environments, including studies to assess anthropogenic impacts on kelp, identification of resilient beds of kelp and thermo-tolerant varieties of kelp, studies of genetic strains of kelp best served for restoration, new monitoring methods with drones, studies of amelioration of hydrogen sulfide resulting from log booming, development of a biodiversity bank for macroalgae, marine debris clean-up, development of eco-friendly anchor chains to reduce scour of these habitats, and creation of a Climate Adaptation Strategy for Nearshore and Estuaries, including development of decision support tools for estuary restoration. PSF also continues to support citizen science groups, WWF, and Vancouver Island University in their monitoring for forage fish embryos around the Strait of Georgia. It is understood that mapping and identification of habitats for local spawning populations of surf smelt and sand lance may be the first step in protecting these vital nursery areas. PSF is supporting initiatives to encourage the adoption of soft-shore practices, which benefit forage fish populations.

LLTK is working with the Puget Sound Partnership and Puget Sound collaborators to test management actions and continue to fill research gaps. This includes evaluating seal abundance, sex ratios, and sex-specific predation, testing seal deterrents at predation hotspots, testing egg predation excluders for Cherry Point herring, assessing Coho diets, assessing Chinook survival relative to estuary conditions, and further examining Chinook survival trends and impacts to marine survival.

The SSMSP led to other major research endeavors. PSF's Strategic Salmon Health Initiative and LLTK and collaborator's Hood Canal Bridge Ecosystem Impact Assessment were formed in 2013 and 2015, respectively, to focus on specific factors affecting marine survival. The SSHI provided a huge amount of information regarding infection throughout the Strait of Georgia as well as recommendations for management actions and next steps in research described above. The Hood Canal Bridge Assessment led to development of solutions to facilitate steelhead migration past a floating marine bridge and reduce high mortality associated with the bridge.

One of the greatest achievements of the SSMSP has been the development of an integrated and broad community of researchers across disciplines and borders. The SSMSP successfully built a strong salmon network of professional and citizen scientists to undertake the most comprehensive study of salmon in the Salish Sea marine ecosystem conducted to date. The SSMSP facilitated integration and collaboration among researchers in government, academia, and nonprofits within Canada, the United States, and across international boundaries through program funding, annual workshops, and working groups. For more information regarding the approach, see the affiliated paper titled "The Salish Sea Marine Survival Project: how collaborative ecosystem research addressed a major impediment to salmon recovery".

In summary, the SSMSP has made a significant contribution to our understanding of Pacific salmon, and SSMSP findings support the implementation of a number of management actions that benefit Chinook, Coho, and steelhead and the orca whales, tribes, First Nations, and other people who depend on and value salmon.

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James A. Allard, The Aqueduct Foundation, Armstrong Family Foundation, Dick Bradshaw, Brian Denny, Judy Hager, Rivers Holdings Ltd, Tula Foundation, Rudolph North and the North Growth Foundation

Figure 36. *Donors to PSF (top panel) and LLTK (bottom panel) of $50K and above for the SSMSP.*

The SSMSP would not have been possible without the collaborative and committed network of U.S. and Canadian scientists, biologists, technicians, citizen scientists, community members, First Nations, stewardship groups, nonprofits, and researchers that became involved in the Project. Below are the names of SSMSP scientists and technicians whose work is summarized in this document. Names are provided with affiliations relevant to the duration of the SSMSP.

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APPENDIX A. COMPLETE LIST OF HYPOTHESES

NAME	EXPLANATION	PREDICTION
Overarching Hypotheses		
Critical period	Early marine **growth** through the first summer regulates survival over summer and at later life stages.	Larger body, faster growth, and/or higher fat content through late summer correlates with higher marine survival.
	Total marine survival is heavily influenced **by mortality** during the first spring/summer, irrespective of fish size.	High mortality occurs during the first spring/summer. Early marine mortality is correlated with total marine survival.
Fish – Growth, Outmigration Timing and Behavior[36]		
Outmigration timing	Outmigration timing of Chinook, Coho and steelhead influences the magnitude of predation, increase competition, or result in a mismatch between the presence of juvenile salmon and their prey. Outmigration timing may be influenced by hatchery practices and/or reduced diversity in salmon populations.	The outmigration timing of Chinook, Coho and steelhead has become more contracted or the peak outmigration time has shifted. Changes in outmigration timing/distribution correlate with changes in marine survival. (For mechanism, see affiliated hypotheses in prey and predator sections, below)
Distribution and Migration Pathways	Where Chinook and Coho rear while in the Salish Sea affects marine survival.	Populations of Chinook and Coho rear in distinct locations in the Salish Sea. Early marine survival, marine survival and/or growth is related to rearing location.
Residency	Resident-type behaviour and the duration of residence influence marine survival in the Salish Sea.	Residence time in the Salish Sea correlates with marine survival of Chinook and Coho. Reductions of estuary, eel grass, and/or kelp habitat in specific sub-basins correlates with lower survival or reduced growth.
Reduced habitat > Fish Behaviour	Reduced habitat availability has affected the behaviour (and reduced the diversity) of salmon while in the Salish Sea.	The amount of estuary and nearshore habitat has declined.
(Not directly addressed in this report) Metabolic effect	Growth is limited by the metabolic effects of temperature on juvenile salmon.	Growth decreases when outside a peak temperature window for metabolism, and we often see temperatures in the Salish Sea that are outside the peak window.

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[36] The "portfolio effect" hypothesis was removed but is broadly applicable here, and we can speak to it conceptually if it makes sense to do so.

Bottom Up - Prey availability[37]		
Prey Availability (Primary Hyp)	Variation in food supply is linked to juvenile salmon growth.	Timing, duration, quantity, spatial extent, and/or composition/quality of prey influence juvenile salmon growth.
Biogeochemistry > Prey availability	Outmigration timing of Chinook, Coho and steelhead influences the magnitude of predation, increase competition, or result in a mismatch between the presence of juvenile salmon and their prey. Outmigration timing may be influenced by hatchery practices and/or reduced diversity in salmon populations.	The outmigration timing of Chinook, Coho and steelhead has become more contracted or the peak outmigration time has shifted. Changes in outmigration timing/ distribution correlate with changes in marine survival. (For mechanism, see affiliated hypotheses in prey and predator sections, below)
Outmigration Timing > Prey Availability (match/mismatch)	There is a mismatch between demand (outmigrant timing and fish size) and food supply.	Smolts that enter during the peak of prey availability grow faster, larger and/ or have higher fat content. Peak availability of crucial prey and/ or outmigration timing/fish size has shifted, decoupling the two. Changes in peak prey availability and/or outmigration timing/fish size correlate with changes in marine survival (see "fish" section).
Competition > Prey availability	The timing, duration, quantity, spatial extent, and/or composition/quality of salmon prey has declined due to a different state of circulation, water properties (e.g., temp, nutrients), and boundary forces (wind, temp, open ocean conditions, river inputs) in the 2000s vs. the 1970s/early 80s.	Juvenile salmon growth rates are inversely rated to the abundance of competitors. Marine survival decreases with increasing juvenile salmon and/or forage fish abundance. [e.g., Pink salmon, hatchery fish, herring, etc.].
Ocean acidification > Prey availability	Ocean acidification affects the productivity or quality of important zooplankton invertebrate prey for salmon (and forage fish). Ocean acidification may operate alone or synergistically with low oxygen, higher temperatures, and contaminants.	The timing, duration, quantity, spatial extent, and/or composition/quality of zooplankton are constrained as Salish Sea becomes more acidic.
Harmful Algae > Prey availability	Harmful algae indirectly affect salmon survival through food web and salmon prey impoverishment.	The timing, duration, quantity, spatial extent, and/or composition/quality of zooplankton are constrained by competition between primary producers of high and low nutritional value.

[37] We assume the relationship to survival is through growth.

Top Down – Predation[38]		
Predator Abundance	An increase in the abundance of predators has led to higher juvenile salmon/steelhead mortality.	Mortality rates increase where the abundance of predators has also increased. Predation-based mortality rates account of a substantial amount of total marine mortality.
Specialization	Certain predators specialize in consuming juvenile Coho, Chinook and steelhead, and the number of predators that specialize has increased.	There is evidence that predators specialize in consuming juvenile salmon/steelhead in Puget Sound. Proportionately, the impact of specialists on salmon is greater than generalists. An increase in the number of harbour seal specialists correlates with lower marine survival.
Outmigration timing > Pulse prey abundance	Predation rates have increased due to large pulses juvenile salmon/steelhead entering the marine environment.	Mortality rates increase immediately following influxes of juvenile salmon and/or steelhead in the marine environment. Changes in outmigration timing/distribution correlate with changes in marine survival (see "fish" section).
Buffering/Prey Switching	The probability of being detected/targeted by predators may decrease with an increase abundance of alternative prey.	Mortality rates decrease with increasing abundance of a predator's primary prey items (e.g., hake and forage fish for harbour seals). A decline in predators' primary prey items is correlated with lower marine survival.
(not addressed in this report) Visibility	Juvenile salmon/steelhead mortality rates have increased with reduced turbidity and/or an increase in artificial light at night.	Turbidity has reduced and/or artificial increased during the outmigration period. Low turbidity and/or high artificial light correlates with lower marine survival.
(not addressed in this report) Ocean Acidification > Predation	Increased CO2 concentrations affect the nervous system and behaviour of salmon and steelhead. Chinook, Coho and steelhead mortality rates increase with increasing CO2 concentrations (cannot smell predators).	CO2 concentrations are high enough in the Salish Sea to affect the behaviour of salmon and steelhead. Mortality rates are higher in areas/at times with increased CO2 concentration.

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38. Factors that were not assessed via the SSMSP include the impacts of sound, either exacerbating predation by impacting the hearing of salmon or ameliorating predation by affecting predators who use sound to forage.

Top Down - Disease, Contaminants and Harmful Algae		
Contaminants	Exposure to contaminants during one or more parts of a salmon's Salish Sea life history slows growth, increases disease susceptibility, and/or reduces marine survival.	Chinook, Coho and steelhead populations obtain higher contaminant loads, above thresholds affecting health and/or growth rates — in the river, while out-migrating as juveniles, and/or while residing in the Salish Sea through adult age. Those fish with higher contaminant loads have lower marine survival.
Harmful algae	Harmful algae directly affect salmon survival through acute or chronic toxicity or gill damage.	Direct mortality increases as prevalence and intensity of *Heterosigma* and other harmful algae increase.
Disease	Infected fish may die from infection and/or become more susceptible to predation.	Infection prevalence has increased. Mortality increases with increasing parasite or pathogen loads.

APPENDIX B. STOCKS AND YEARS OF MARINE SURVIVAL DATA USED IN CHINOOK, COHO, AND STEELHEAD TRENDS FIGURE

Below are the stocks and years of marine survival data used in trends figure included in this report. This stock list differs slightly from those used in in Zimmerman et al. 2015, Ruff et al. 2017, Kendall et al. 2017. Strait of Juan de Fuca stocks were excluded for all three species as results are mixed there, and that represents a transition zone between the inner Salish Sea and the Pacific Ocean. Also, southern Alaska and Northern BC stocks were excluded from the Chinook analysis to ensure consistent comparisons among the three species (Coho and steelhead analyses did not include comparisons to northern stocks), and additional Chinook stocks and years were included, datasets considered too fragmented for Ruff et al. 2017, but were included in Soboncinski et al. 2021 and currently included in ongoing work by Haggerty et al. Per the description in the report, adding the other Chinook data was important as it illustrates larger declines in Puget Sound Chinook marine survival beginning in the late 1970s. Note, to improve the modeled representation of trends, the generalized additive model (GAM) included years outside of the period plotted in Figure 1 and Figure 5 in the report, prior to ocean entry year 1978.

SPECIES	STOCK	BASIN	OCEAN ENTRY YEAR
Chinook	Big Qualicum River Fall	Strait of Georgia	1978 - 2012
Chinook	Chilliwack Fall (Harrison Stock)	Strait of Georgia	1982 - 2012
Chinook	Columbia Lower River (H)	WA/BC Coast + Columbia River	1977-2012
Chinook	Columbia River Summer	WA/BC Coast + Columbia River	1976-1978, 1984-2012
Chinook	Cowichan River Fall	Strait of Georgia	1986, 1988-2004, 2006-2012
Chinook	Cowlitz Fall Tule	WA/BC Coast + Columbia River	1978 - 2012
Chinook	Dome Creek Spring	Strait of Georgia	1988-2000, 2002-2004
Chinook	Elk River	WA/BC Coast + Columbia River	1978 - 2012
Chinook	Garrison Fall Fingerling	Puget Sound	1980-1982, 1988, 1990-1992, 2003-2010, 2012
Chinook	George Adams Fall Fingerling	Puget Sound	1975-1976, 1979-1982, 1986-2012
Chinook	Green River Fall Fingerling	Puget Sound	1972-1976, 1979-1982, 1986-2012
Chinook	Grovers Creek Fall Fingerling	Puget Sound	1982 - 2012
Chinook	Hanford	WA/BC Coast + Columbia River	1987 - 2012
Chinook	Harrison Fall	Strait of Georgia	1982-2004, 2006-2007, 2009-2012
Chinook	Lake Washington (Issaquah) Fall Fingerling	Puget Sound	1979 - 1982, 1986 - 1988
Chinook	Lewis River	WA/BC Coast + Columbia River	1978-1980, 1983-1995, 1997-2012
Chinook	Lower Shuswap Summer	Strait of Georgia	1985 - 2012
Chinook	Lyons Ferry	WA/BC Coast + Columbia River	1985, 1987-1990, 1995, 1999-2000, 2002-2012
Chinook	Lyons Ferry Yearling	WA/BC Coast + Columbia River	1986, 1988-1990, 1993-2012
Chinook	Nanaimo Fall	Strait of Georgia	1980-1981, 1983, 1988-1998, 2000-2003, 2005

SPECIES	STOCK	BASIN	OCEAN ENTRY YEAR
Chinook	Nicola Spring	Strait of Georgia	1987 - 2013
Chinook	Nisqually Fall Fingerling	Puget Sound	1980 - 2012
Chinook	Nooksack Spring Fingerling	Strait of Georgia	1989-1990, 1993-2012
Chinook	Nooksack Spring Yearling	Strait of Georgia	1983 - 1984, 1986, 1988 - 1992, 1994 - 1998
Chinook	Puntledge River Summer	Strait of Georgia	1978-1995, 1997-2012
Chinook	Puyallup Fall Fingerling	Puget Sound	1972, 1979-1982, 1998, 2003-2008, 2010, 2012
Chinook	Queets Fall Fingerling	WA/BC Coast + Columbia River	1978-1984, 1986-2012
Chinook	Quinsam Fall	Strait of Georgia	1978 - 2012
Chinook	Robertson Creek Fall	WA/BC Coast + Columbia River	1974-2012
Chinook	Salmon River	WA/BC Coast + Columbia River	1977-1981, 1983-2012
Chinook	Samish Fall Fingerling	Strait of Georgia	1980, 1986-2012
Chinook	Skagit Spring Fingerling	Puget Sound	1986, 1994-2012
Chinook	Skagit Summer Fingerling	Puget Sound	1995 - 2012
Chinook	Skagit Fall Fingerling	Puget Sound	2000 - 2009
Chinook	Skagit Spring Yearling	Puget Sound	1983-1989, 1992, 1995-2012
Chinook	Skykomish Fall Fingerling	Puget Sound	2001 - 2012
Chinook	Snohomish Summer Yearling	Puget Sound	1974-1975, 1978, 1989, 1998-1999, 2004-2010, 2012
Chinook	Sooes Fall Fingerling	WA/BC Coast + Columbia River	1986-1988, 1990-2012
Chinook	South Puget Sound Fall Fingerling	Puget Sound	1972-1976, 1979-2012
Chinook	South Puget Sound Fall Yearling	Puget Sound	1980-1983, 1988-1999, 2001-2002, 2004-2010, 2012-2013
Chinook	Spring Creek Tule	WA/BC Coast + Columbia River	1973-2012
Chinook	Squaxin Net Pens Fall Yearling	Puget Sound	1988-1992, 1994-1997, 1999
Chinook	Stillaguamish Summer Fingerling	Puget Sound	1981-1984, 1987-1999, 2003-2012
Chinook	Tulalip Summer Fingerling	Puget Sound	1999, 2001-2005, 2008-2012
Chinook	University of WA Accelerated	Puget Sound	1976-1985
Chinook	Upriver Brights	WA/BC Coast + Columbia River	1976-2012
Chinook	White River Spring Yearling	Puget Sound	1976-1977, 2004-2013
Chinook	Williamette Spring	WA/BC Coast + Columbia River	1977-2012
Chinook	Willapa Bay Fall	WA/BC Coast + Columbia River	1973-1974, 1983-1988, 1997-2000, 2004-2012
Coho	Baker River	Puget Sound	1983, 1985, 1987-1988, 1991-1999, 2002-2014
Coho	Big Beef Creek	Puget Sound	1978 - 2015
Coho	Big Qualicum River	Strait of Georgia	1974-1987, 1989-2010
Coho	Bingham Creek	WA/BC Coast + Columbia River	1982 - 2015

SPECIES	STOCK	BASIN	OCEAN ENTRY YEAR
Coho	Black Creek	Strait of Georgia	1989 - 1993
Coho	Carnation Creek	WA/BC Coast + Columbia River	2001-2006, 2008-2010
Coho	Chilliwack River	Strait of Georgia	1982-1988, 1990, 1993-2004
Coho	Cowlitz River	WA/BC Coast + Columbia River	1982-1996, 1999-2007, 2009-2010
Coho	Deschutes River	Puget Sound	1979-1997, 1999, 2002, 2005, 2008, 2011, 2014
Coho	Elochoman River	WA/BC Coast + Columbia River	1985-1987, 1990-2008
Coho	Grays River	WA/BC Coast + Columbia River	1978-1987, 1990-1995, 1998-2002, 2004-2010
Coho	Green River	Puget Sound	1979-1986, 1989-2015
Coho	Inch Creek	Strait of Georgia	1984 - 2010
Coho	Kalama Creek	WA/BC Coast + Columbia River	1979, 1987-1995, 1998-2000, 2002, 2005-2014
Coho	Lewis	WA/BC Coast + Columbia River	1982-1984, 1987-1994, 1997-1998, 2000-2001
Coho	Louis Creek	Strait of Georgia	1990-1994, 1999-2007
Coho	Minter Creek	Puget Sound	1979-1985, 1996, 2001-2007, 2009, 2011-2014
Coho	Myrtle Creek	Strait of Georgia	2008 - 2010
Coho	Nooksack River	Strait of Georgia	1976, 1982-2014
Coho	Puntledge River	Strait of Georgia	1978-1999, 2001, 2003-2004
Coho	Puyallup River	Puget Sound	1979-2015
Coho	Quilcene River	Puget Sound	1979-1983, 1989-2000, 2002-2014
Coho	Quinault River	WA/BC Coast + Columbia River	1978 - 2014
Coho	Quinsam River	Strait of Georgia	1976 - 2010
Coho	Robertson Creek	WA/BC Coast + Columbia River	1978 - 2010
Coho	Satsop River	WA/BC Coast + Columbia River	1982-2015
Coho	Skagit River	Puget Sound	1991, 1995 - 2015
Coho	Skokomish River	Puget Sound	1979-2014
Coho	Skykomish River	Puget Sound	1978-1998, 2000-2015
Coho	SolDuc	WA/BC Coast + Columbia River	1978, 1982-1990, 1992-1995, 2008, 2010-2014
Coho	Sooes River	WA/BC Coast + Columbia River	1982, 1988, 1990-2014
Coho	Tulalip Bay	Puget Sound	1980-1982, 1984-2014
Coho	Washougal River	WA/BC Coast + Columbia River	1979-1986, 1990-1996, 1998-2010
Coho	Waterloo	Strait of Georgia	2002 - 2006
Coho	Willapa River	WA/BC Coast + Columbia River	1982-1988, 1995-1999, 2001-2015

SPECIES	STOCK	BASIN	OCEAN ENTRY YEAR
Steelhead	Alsea River winter	WA/BC Coast + Columbia River	1992 - 2011
Steelhead	Big Beef Creek	Puget Sound + Keogh River	2005 - 2014
Steelhead	Bingham Creek	WA/BC Coast + Columbia River	1997 - 2012
Steelhead	Coweeman River	WA/BC Coast + Columbia River	2005-2008, 2010-2011
Steelhead	Chehalis River winter	WA/BC Coast + Columbia River	1981 - 2012
Steelhead	Clackamas River	WA/BC Coast + Columbia River	1960-2011
Steelhead	Cowlitz River late winter	WA/BC Coast + Columbia River	1999 - 2010
Steelhead	Cowlitz River summer	WA/BC Coast + Columbia River	1993 - 2008
Steelhead	Cowlitz River winter	WA/BC Coast + Columbia River	1995 - 2010
Steelhead	Cowlitz River winter total	WA/BC Coast + Columbia River	1993 - 2010
Steelhead	Elochoman River winter	WA/BC Coast + Columbia River	1993-1994, 1996-2010
Steelhead	Grays River winter	WA/BC Coast + Columbia River	1998, 2000, 2003-2007, 2009-2010
Steelhead	Green River summer	Puget Sound + Keogh River	1992 - 2013
Steelhead	Green River winter	Puget Sound + Keogh River	1977-2013
Steelhead	Humptulips River summer	WA/BC Coast + Columbia River	1995-1999, 2004-2008
Steelhead	Humptulips River winter	WA/BC Coast + Columbia River	1977-2012
Steelhead	Kalama River summer	WA/BC Coast + Columbia River	1998-2009
Steelhead	Kalama River winter	WA/BC Coast + Columbia River	1992 - 2010
Steelhead	Kalama River	WA/BC Coast + Columbia River	1978-1984, 1992-1994, 1998-2012
Steelhead	Keogh River	Puget Sound + Keogh River	1977-2012
Steelhead	Lewis River summer	WA/BC Coast + Columbia River	1994 - 2009
Steelhead	Lewis River winter	WA/BC Coast + Columbia River	1993 - 2010
Steelhead	Nisqually River	Puget Sound + Keogh River	2009 - 2014
Steelhead	Nooksack River winter	Puget Sound + Keogh River	1999 - 2011
Steelhead	Puyallup River winter	Puget Sound + Keogh River	1984 - 2009
Steelhead	Queets River	WA/BC Coast + Columbia River	1981-1999, 2001-2007, 2009-2013
Steelhead	Quillayute River summer	WA/BC Coast + Columbia River	1999 - 2011
Steelhead	Quillayute River winter	WA/BC Coast + Columbia River	1982 - 2011
Steelhead	Samish River winter	Puget Sound + Keogh River	1977-1979
Steelhead	Siletz River summer	WA/BC Coast + Columbia River	1992 - 2011
Steelhead	Siletz River winter	WA/BC Coast + Columbia River	1992 - 2011
Steelhead	Siuslaw River winter	WA/BC Coast + Columbia River	1995 - 2011

SPECIES	STOCK	BASIN	OCEAN ENTRY YEAR
Steelhead	Skagit River winter	Puget Sound + Keogh River	1982 - 2013
Steelhead	Snohomish River summer	Puget Sound + Keogh River	1993 - 2013
Steelhead	Snohomish River winter	Puget Sound + Keogh River	1986 - 2014
Steelhead	Stillaguamish River summer	Puget Sound + Keogh River	1991 - 2013
Steelhead	Stillaguamish River winter	Puget Sound + Keogh River	1992 - 2013
Steelhead	Whatcom Creek winter	Puget Sound + Keogh River	1993-1996, 1998-2000, 2002-2013
Steelhead	Washougal River summer	WA/BC Coast + Columbia River	1993 - 2009
Steelhead	Washougal River winter	WA/BC Coast + Columbia River	1994 - 2010
Steelhead	Willapa River winter	WA/BC Coast + Columbia River	1994 - 2010
Steelhead	Wind River	WA/BC Coast + Columbia River	2003 - 2013
Steelhead	Wynoochee River summer	WA/BC Coast + Columbia River	1994 - 2009