Ecological implications of changing hatchery practices for Chinook salmon in the Salish Sea

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Abstract. For over a century, hatchery programs have been used to subsidize natural salmon populations in order to increase fisheries opportunities and, more recently, to conserve declining natural populations. While an extensive literature has described the impacts of large-scale hatchery operations on freshwater ecosystems, less attention has been given to ecosystem interactions within the marine environment. We analyzed records of hatchery-released Chinook salmon in the Salish Sea to assess temporal and spatial changes in hatchery practices since 1950, with the goal of identifying potential implications for ecosystem dynamics and conservation efforts in the region. Over the past 65 yr, we found significant changes in the size and time at which juvenile salmon are released, resulting in decreased diversity of these traits. Research suggests that predation on juvenile salmon by other fish, avian, and marine mammal species could be size-dependent, and our results indicate that current hatchery practices are releasing Chinook salmon in the size range preferred by these predators. With current marine survival rates at chronically low levels, and increasing demand for hatchery subsidies, it is important to consider how modifying existing hatchery programs intended to reduce homogenization may promote more natural marine food web dynamics, with potential benefits to both hatchery and natural Chinook populations.

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INTRODUCTION

Hatcheries and fish stocking programs can provide both ecological and economic benefits. For depleted fish populations, hatcheries may be used to enhance population size and maintain the genetic diversity of natural-origin individuals (Hedrick et al. 2000, Fraser 2008). Simultaneously, many hatcheries exist to increase opportunities for both commercial, recreational, and indigenous fishers (Waples et al. 2007). Downstream industries, such as aquaculture facilities and fish farms, also rely on hatcheries for providing juvenile fish. As levels of human fish consumption increase worldwide, there will be a growing demand for hatcheries and associated industries to provide food security (Gentry et al. 2017).

A range of concerns have been identified about the genetic (Fraser 2008) and ecological consequences hatcheries may have for natural fish populations (Rand et al. 2012). Hatchery-raised fish may introduce density-dependent effects on

natural populations (Bohlin et al. 2002) and can also negatively affect natural fish through inter-breeding (Bourret et al. 2011). If hatchery-origin fish have reduced fitness, allowing hatchery individuals to breed with natural fish can have negative impacts on those natural populations (Hindar et al. 1991, Araki et al. 2007, Tillotson et al. 2019). Further, recent research suggests that high abundances of hatchery-raised salmon may alter life-history strategies of wild populations, possibly through increased competition (Cline et al. 2019). Therefore, understanding the cumulative historical effects of hatcheries on ecosystems is essential for improving future hatchery practices and ensuring sustainable management.

In the marine environment, hatchery programs may have bottom-up or top-down effects on food webs (Rand et al. 2012). For example, large populations of pink salmon (*Oncorhynchus gorbuscha*) are thought to reduce zooplankton biomass and may affect the success of more economically valuable sockeye salmon (*Oncorhynchus nerka*; Ruggerone and Connors 2015). Juvenile or adult hatchery fish may also provide reliable prey subsidies for predators. For example, predation by birds or mammals at or near hatcheries has been researched for nearly a century (Lagler 1939, Parkhurst et al. 1987). Much of this published literature has focused on effective solutions for predator control, rather than investigating potential strategies to minimize interactions between hatchery fish and potential competitors or predators.

Some of the most studied hatchery fishes in the world are Pacific salmon raised and released by hatcheries into the northeast Pacific Ocean (USA, Canada). Salmon are anadromous, typically migrating to the ocean in their first or second year of life, and returning to spawn as adults 1–6 yr later. Understanding the role of hatchery-produced salmon in this ecosystem is important for economic, conservation, and ecological reasons. Ecologically, salmon provide prey subsidies to marine and terrestrial predators, including grizzly bears and killer whales (Schindler et al. 2013). Populations of avian (e.g., cormorants, Collis et al. 2001, and gulls, Osterback et al. 2013) and marine mammal predators (e.g., seals, Lance et al. 2012) are also supported by migrations of juvenile salmon from rivers to the ocean. As the primary target for both commercial, recreational, and treaty fisheries in

southern British Columbia and the states of Washington, Oregon, and California, Chinook salmon (*Oncorhynchus tshawytscha*) represent the majority of hatchery production in this region (Naish et al. 2007, Flagg 2015). Chinook salmon are also iconic species throughout their range, with profound cultural significance to indigenous North Americans.

Most natural Chinook salmon populations in Washington, Oregon, and California are depleted relative to historical abundances and are of high conservation concern (nine population segments are protected under the U.S. Endangered Species Act; Good et al. 2005). The primary causes of these declines are still debated and likely vary regionally, but there is evidence that changing climate, large-scale habitat loss/degradation, and increases in some predator populations are major contributing factors (Battin et al. 2007, Kilduff et al. 2015, Chasco et al. 2017, Nelson et al. 2018). The ecological and economic benefits conferred by abundant salmon populations, regardless of origin, have been increasingly difficult to maintain while preserving the genetics, life histories, and population dynamics of natural populations.

Here, we analyze 65 yr of data on hatchery-origin Chinook salmon in Washington State (USA) and British Columbia (Canada) to examine long-term changes in hatchery release characteristics. We focus geographically on the Salish Sea (Fig. 1), both because there is an opportunity to compare hatchery characteristics across international boundaries, and because this inland sea encompasses a unique marine environment, with consequences for salmon survival dynamics (Zimmerman et al. 2015*a*). We present estimates of changes in average time and size at release, as well as changes in variability of these traits over time. Additionally, we compare these characteristics with natural Chinook populations and examine changes in the spatial distribution of juvenile salmon as a result of hatchery supplementation. Finally, we consider the potential ecological and conservation implications of long-term changes to hatchery practices.

Materials and Methods

Study species

Though life-history strategies exist along a continuum, there are two dominant life-history

Fig. 1. Study area showing the approximate locations of sub-basins (dashed lines) included in the analysis, and the location of fish trapping operations (red triangles) on Puget Sound rivers (Skagit [North Puget Sound, NPS], Green [Middle Puget Sound, MPS], Dungeness [Juan de Fuca, JUAN]). The Thompson and upper-Fraser sub-basins are not shown on this figure.

types of Chinook salmon (Healey 1991). Juveniles that migrate to the sea after a relatively short time in fresh water (<1 yr) are known as sub-yearling fish, while those with extended fresh water residency (>1 yr) are termed yearling fish. Chinook salmon with sub-yearling life histories are often associated with fall migration timing of adults, while yearling juvenile migration is

often associated with spring returns. Fall Chinook and sub-yearling releases currently outnumber spring and yearling types among both natural and hatchery populations (Appendix S1: Figs. S1, S2).

Study area and RMIS database

In the Salish Sea, over 50 million Chinook salmon are released by hatcheries annually (Fig. 2), primarily to support a large mixed-stock fishery off the west coast of North America. Decades of extensive tagging records (coded-wire tags) have been compiled in a centralized database (Regional Mark Information System database; RMIS) maintained by the Regional Mark Processing Center (www.rmpc.org). For this study, hatchery release data for Chinook salmon were compiled

Fig. 2. Annual releases (top) and biomass (bottom) of hatchery Chinook salmon in the Puget Sound (green) and Strait of Georgia (purple), from 1950 to 2016.

from the three regions of the Salish Sea: Puget Sound, Strait of Juan de Fuca, and Strait of Georgia; all records from these regions were downloaded from the RMIS database (http://www.rmpc.org). Individual entries in the RMIS database describe the total number of fish released in each group, along with the date and location of the release, origin of the brood stock, developmental stage (fry, smolt, etc.), and average size (length and/or weight) of fish in the release group. For this study, we excluded groups whose developmental stage was classified in the database as eggs or adults.

To examine spatio-temporal variation in hatchery releases, we divided our study area into two large basins, Puget Sound (including the Strait of Juan de Fuca) and the Strait of Georgia, and then divided each basin into six geographical sub-basins (Fig. 1). In the Puget Sound, these sub-basin classifications are nearly identical to those defined within the RMIS database. However, here we included the Skagit River with the North Puget Sound (NPS) sub-basin. We separated the Strait of Georgia basin into six sub-basins: the upper-Fraser (UPFR), Thompson River (TOMM), lower-Fraser (LWFR), east Vancouver Island (GSVI), Strait of Georgia mainland (GSMN), and Strait of Georgia lower-mainland (GSMS; Fig. 1).

Because of the potential for inaccuracies in entered release size and release date in RMIS, we filtered/searched the dataset for obvious errors (e.g., unfeasible length–weight combinations). We modified 51 of 52,380 entries for Chinook salmon (<0.1%) based on obvious discrepancies in the length–weight relationships. In addition, we estimated missing release size (length or weight) for groups missing one of these metrics (Appendix S1).

Changes in release size and timing

To quantify temporal changes in variability and diversity of release size and release date of hatchery Chinook salmon, we calculated annual means (weighted by release group size) for both characteristics in both basins (Puget Sound, Strait of Georgia), and in the entire Salish Sea. The among-sub-basin [weighted] standard deviations were calculated at both the basin (Puget Sound, Strait of Georgia) and ecosystem (Salish Sea) scales. We combined entries in the Strait of Georgia Mainland (GSMN) and Strait of Georgia
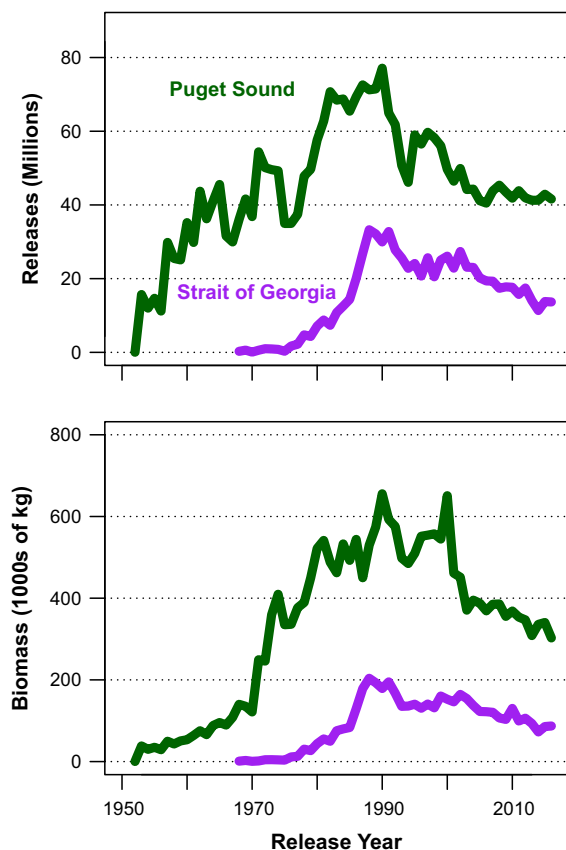
Lower-Mainland (GSMS) sub-basins, and the Upper-Fraser (UPFR) and Thompson River (TOMM) sub-basins, in order to extend the time series (i.e., to prevent missing years). We estimated temporal trends in annual mean release size and release date, and the annual standard deviations of these two characteristics by fitting linear regression models to each time series. Temporal autocorrelation in the data was accounted for by assuming error residuals followed a lag-1 autoregressive process (AR[1]). We assumed a log-normal error structure for both release date and release size, and used maximum likelihood to fit the models to data with the nlme package in the R Programming Environment (R Core Team 2017).

Comparison of hatchery and natural populations

To examine whether hatchery-produced juvenile salmon were similar to their natural counterparts, we compared out-migration size and timing of both populations in several major salmon-producing rivers in the Puget Sound. Data on the size and migration timing of juvenile Chinook salmon were collected by Washington Department of Fish and Wildlife (WDFW) on the Green, Skagit, and Dungeness rivers using rotary screw traps (Fig. 1). Assuming adult escapement is proportional to relative juvenile production, these three systems combined produce nearly 60% (Skagit, 50%) of the natural Chinook in the Puget Sound (Appendix S1: Table S2). We compared hatchery and natural populations using trap data from all three rivers, in addition to RMIS data from the same periods. Specifically, trap data were used to compare migration timing of both natural- and hatchery-origin Chinook in the Skagit and Dungeness rivers, and a combination of trap and RMIS data was used to compare fish size on the Skagit and the Green. Juvenile salmon data from traps include both day and night records from February through July on all three rivers. Sampling methods for the rotary screw traps are described in detail in Anderson and Topping (2018), and Zimmerman et al. (2015b). Because no consistent systematic trapping operations exist for Strait of Georgia tributaries, we were not able to perform a comparable analysis for that basin. Methods used to describe differences in size of natural and hatchery populations are described in Appendix S1.

Hatchery subsidies by sub-basin

To measure the extent to which each sub-basin is subsidized with hatchery Chinook salmon, we compared each sub-basin's contribution to the total hatchery population $p_i^{\text{Hatch}} = N_i^{\text{Hatch}}/N_{\text{Total}}^{\text{Hatch}}$ with the current and historical natural contribution of the sub-basin (1): $p_i^{\text{Wild}} = N_i^{\text{Natural}}/N_{\text{Total}}^{\text{Natural}}$. In sub-basins where the hatchery contribution is comparable to its contribution to the overall natural population, the ratio $p_i^{\text{Hatch}}/p_i^{\text{Natural}}$ is close to 1.0, while in sub-basins where hatchery fish are over-represented relative to the current and historical natural contribution, that ratio is >1.0. Sources of current and historical natural Chinook abundance estimates are listed in the Appendix S1: Table S2. While estimates of current spawner abundance are provided for each river, estimates of historical abundance are missing for several populations. To estimate the approximate historical spawning abundance for those populations, based on their current abundance, we fit a linear regression (nlme package; R Core Team 2017) to data for rivers where estimates for both were available, thereby assuming that the magnitude of abundance decline from historical to current was comparable across populations. Both dependent and independent variables were log$_e$-transformed, which resulted in a very good fit to the data ($R^2 = 0.90$; Appendix S1: Fig. S4).

Comparing predation vulnerability and release size

It is well documented that avian species are a significant source of predation for young salmon shortly after marine entry (Collis et al. 2001), and multiple studies in the eastern Pacific have documented size selectivity of forage fish and juvenile salmon (Schrimpf et al. 2012, Tucker et al. 2016). This is also the case with fishes that prey on juvenile salmon (Beamish et al. 1992, Emmett and Krutzikowsky 2008), including larger individuals of the same species (Beauchamp and Duffy 2011). Additionally, research describing harbor seal (*Phoca vitulina*) predation on juvenile fish provides further evidence of size-selective predation (Tollit et al. 1997, Allegue 2017, Thomas et al. 2017). We evaluated the potential implications of current hatchery practices for predation on juvenile Chinook, given the existence of a predation window implied by existing studies of these known
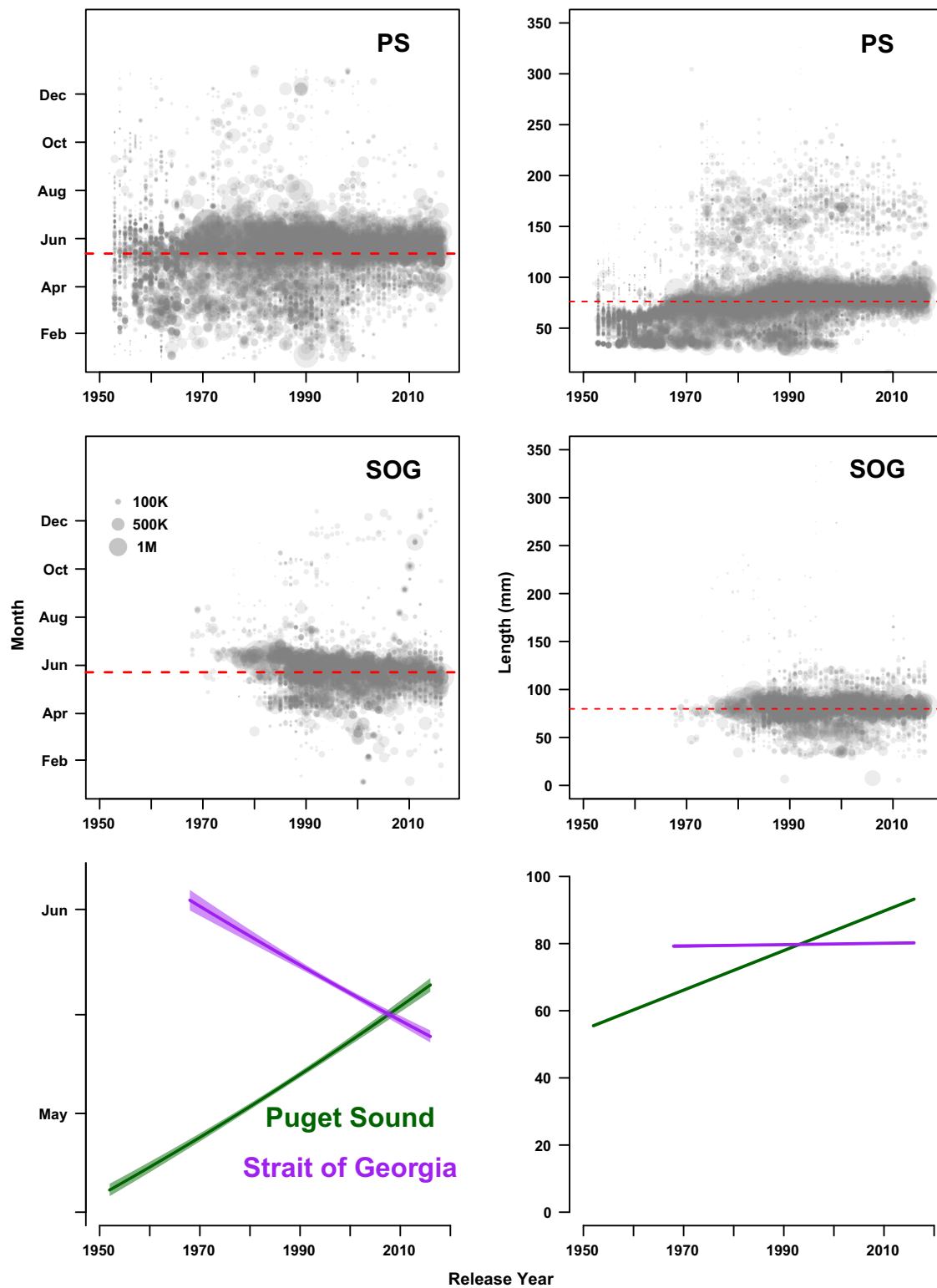
Fig. 3. Changes in date (left) and size at release (right) for Chinook salmon in the Puget Sound (PS) and Strait

(Fig. 3. *continued*)
of Georgia (SOG). Gray circles in the top two rows are individual release groups from the Regional Mark Information System database. Sizes of the circles are proportional to number of fish in each release group. Red dashed lines are the weighted average for the entire time series. Plots on the bottom row show convergence of mean release date and size in the Puget Sound (green) and Strait of Georgia (purple). Solid lines are the regressions, and the shaded bands are the 95% confidence intervals.

predators. Measures of central tendency were summarized for preferred prey size in harbor seals (Tollit et al. 1997, Lance et al. 2012, Thomas et al. 2017), fish predators (Duffy and Beauchamp 2008, Emmett and Krutzikowsky 2008, Beauchamp and Duffy 2011), and avian predators (Collis et al. 2002, Schrimpf et al. 2012, Tucker et al. 2016). We compared these preferences to size distributions of natural- and hatchery-origin salmon to qualitatively assess overlap with predators' preferred prey sizes, as well as any disparities in overlap between natural and hatchery populations.

RESULTS

Since 1950, 3.7 billion Chinook salmon were released into Salish Sea tributaries from hatcheries in the United States and British Columbia (Fig. 2; Appendix S1: Table S4). The total biomass of these releases equates to approximately 26.4 million kg. In the Puget Sound (USA), annual releases of Chinook salmon peaked in 1990 (77.1 million), while releases in the Strait of Georgia (Canada) peaked in 1988 (33.2 million; Fig. 2). Peak biomass (abundance multiplied by mean release weight) coincided with peak abundance in both regions (Fig. 2), with hatcheries in the United States producing more Chinook than those in Canada (both numbers and biomass; Fig. 2). Within both basins, hatchery releases were unevenly distributed among sub-basins. In the Puget Sound, the Middle Puget Sound and South Puget Sound sub-basins produced the most Chinook releases in each decade (Appendix S1: Table S4). Vancouver Island released the highest proportion of total Chinook in every decade since the inception of major hatchery programs in the Strait of Georgia (Appendix S1: Table S4).

Changes in date of release

Our summaries of Chinook salmon release dates suggest that hatcheries in the United States and Canada have trends that are moving the opposite direction (Fig. 3) and are becoming less diverse—both within and between countries (Fig. 4; Appendix S1: Table S6). In Puget Sound (USA), the date of release for hatchery Chinook salmon became significantly later since the 1950s and 1960s (Fig. 3; Appendix S1: Tables S5, S6), with the mean release date shifting several weeks (from late April or the first week in May to the third week of May in the 2000s, at a rate of 1.7 d per decade). In the Strait of Georgia (Canada), the mean date of release became significantly earlier since the 1960s and 1970s, shifting from mid-June to the third week of May (at a rate of 3.8 d per decade; Fig. 3; Appendix S1: Table S6). Diversity of release dates from hatcheries has decreased significantly since the 1970s among sub-basins and among all releases in the Salish Sea (Fig. 4; Appendix S1: Table S6).

Changes in size at release

Chinook salmon released from hatcheries in the Puget Sound increased significantly in size from the 1950s to the 2010s (Fig. 3), with juveniles released from 2010 to 2016 being 50% larger (by length) than those released during the 1960s (about 3.6 mm per decade; Appendix S1: Table S6). Unlike hatchery-origin Chinook salmon in the United States, Chinook salmon produced by Canadian hatcheries saw no significant change in size at release between the late 1960s and 2016 (Fig. 3; Appendix S1: Table S6). However, diversity in size at release has significantly decreased since 1970 among sub-basins, and for the aggregate of releases in the Salish Sea (Fig. 4; Appendix S1: Table S6).

Comparison of hatchery and natural populations

Downstream migration dynamics of juvenile Chinook differed between natural and hatchery populations in both Skagit and Dungeness rivers. Peak migration dates for natural Chinook salmon in the Skagit River over a 20-yr period occurred in February and March, while peak abundance
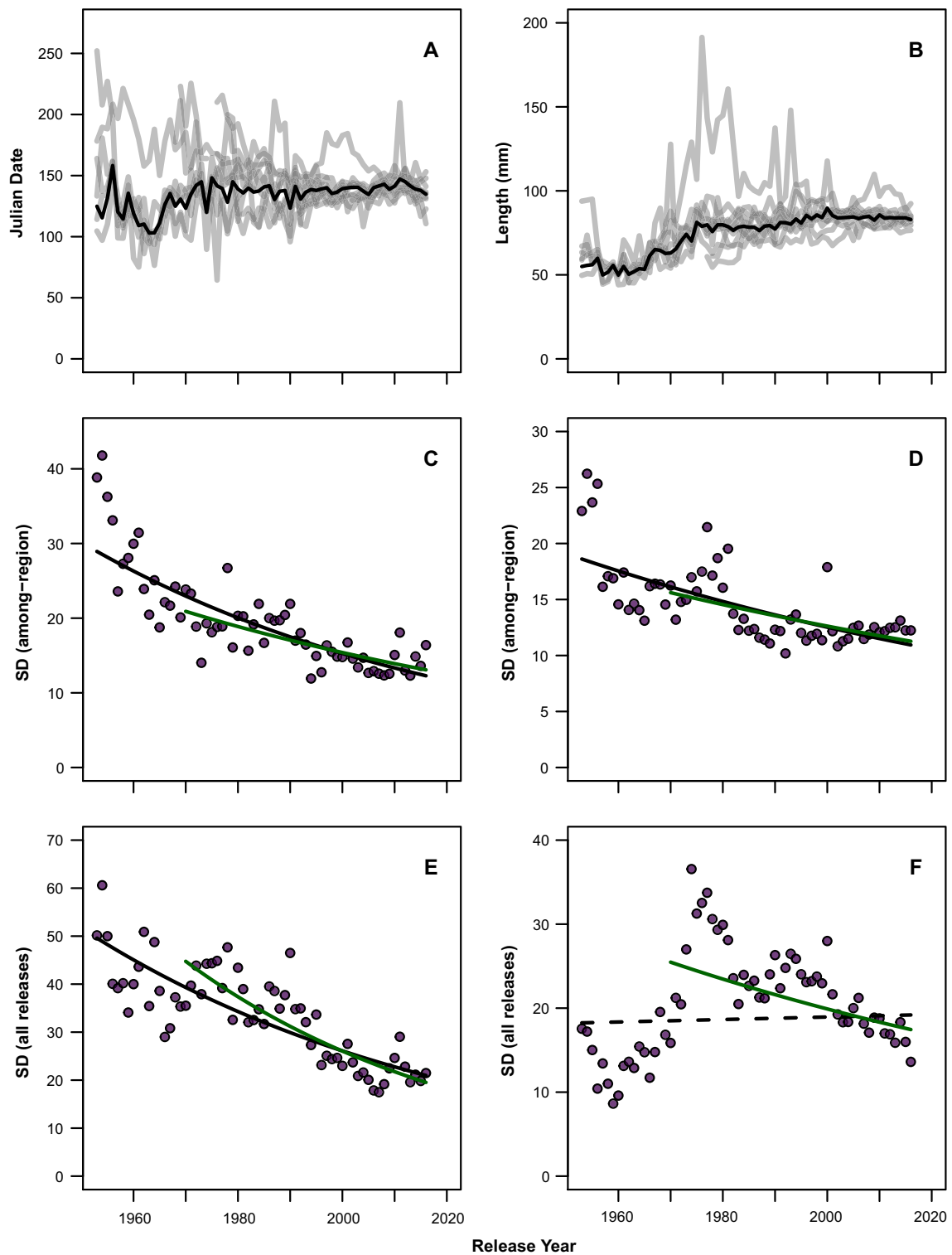
Fig. 4. Annual mean and standard deviation of release date and release size (length) for Chinook in the Salish

(Fig. 4. *continued*)

Sea from 1950 to 2016. Top panels (A and B) display annual mean release date and size for the entire Salish Sea (black lines), and for individual sub-regions (gray lines). Middle panels (C and D) show the standard deviation among all regions for both characteristics for the entire time series (black lines) and after 1970 (green lines). Bottom panels (E and F) show the annual standard deviation in release date and size for all releases in the Salish Sea. Solid trend lines represent regressions where the slope is significantly different from zero, while dashed trend lines depict regressions where it is not.

for (trapped) hatchery fish during 2010–2014 occurred in a relatively narrow window in May–June (Fig. 5). In the Dungeness River, peak out-migration occurred in June, along with a secondary peak in March (Fig. 5). Like the Skagit, the peak migration of hatchery-origin Chinook occurred in June. While peak migrations of natural Chinook in the Skagit and Dungeness rivers occurred in different months, both natural populations had a prolonged, bi-modal out-migration period that was considerably different than the abrupt migration of hatchery-origin fish (Fig. 5).

Chinook salmon released from hatcheries were larger (on average) than their natural counterparts in both Skagit and Green rivers, and less variable in size (Fig. 6; Appendix S1: Table S3). In both rivers, the most abundant size of natural juvenile Chinook was consistently between 40 and 60 mm, while the mean size of hatchery-origin Chinook in each river, and the Puget Sound, was typically >80 mm, and often near 100 mm in length. The size of natural Chinook out-migrants in both rivers was very similar (Fig. 6). It should be noted that the size of hatchery-origin fish was measured prior to their release, unlike natural Chinook that are measured upon capture at a trap. Thus, the disparity in size between natural- and hatchery-origin Chinook documented here would only be exacerbated, due to any growth between hatchery release and the trap location where natural fish were captured.

Hatchery subsidies of Chinook by sub-basin

Hatchery production has changed the spatial distribution of juvenile Chinook salmon production in both Puget Sound and Strait of Georgia (Fig. 7; Appendix S1: Table S7). For example, Chinook populations in the South Puget Sound historically made up only 4% of total natural production in the Puget Sound, but now account for a nearly a quarter of hatchery production (Fig. 7; Appendix S1: Table S7). Overall, hatchery produc-

tion in Puget Sound is more evenly distributed among sub-basins than historical or current natural Chinook salmon production (Fig. 7; Appendix S1: Table S7). Since 2010, hatchery contributions from northern Washington, Hood Canal, and the Juan de Fuca Strait sub-basins are higher than their natural contributions to the Puget Sound, while north Puget Sound is underrepresented by its current hatchery production (Fig. 7).

In the Strait of Georgia, we lack reliable historical estimates of Chinook production. However, in recent years, the ratios of hatchery to natural contribution in the Strait of Georgia suggest large differences in the spatial distribution of hatchery subsidies (Fig. 7; Appendix S1: Table S7). For example, the non-Fraser sub-basins of the British Columbia mainland (GSMN and GSMS) currently produce less than 1% of the natural Chinook in the Strait of Georgia, but account for approximately 15% of the entire basin's hatchery releases (Fig. 7). Similarly, hatchery operations on east Vancouver Island release the majority (~60%) of hatchery Chinook in the Strait of Georgia, but its tributaries are responsible for less than 5% of the natural spawners. The upper-Fraser River (including the Thompson River) is not heavily subsidized by hatchery fish, while in the LWFR contribution from hatcheries is comparable to its natural production (Fig 7; Appendix S1: Table S7).

Predation analysis

Hatchery-origin Chinook salmon tend to be larger and less variable in size than their natural counterparts (Figs. 6, 8; Appendix S1: Table S3). When compared to avian, fish, and marine mammal predator size preferences, hatchery Chinook in the Puget Sound overlap with the preferred prey size windows to a greater extent than Chinook of natural origin (Fig. 8). Hatchery Chinook from the Strait of Georgia are similarly sized to fish from Puget
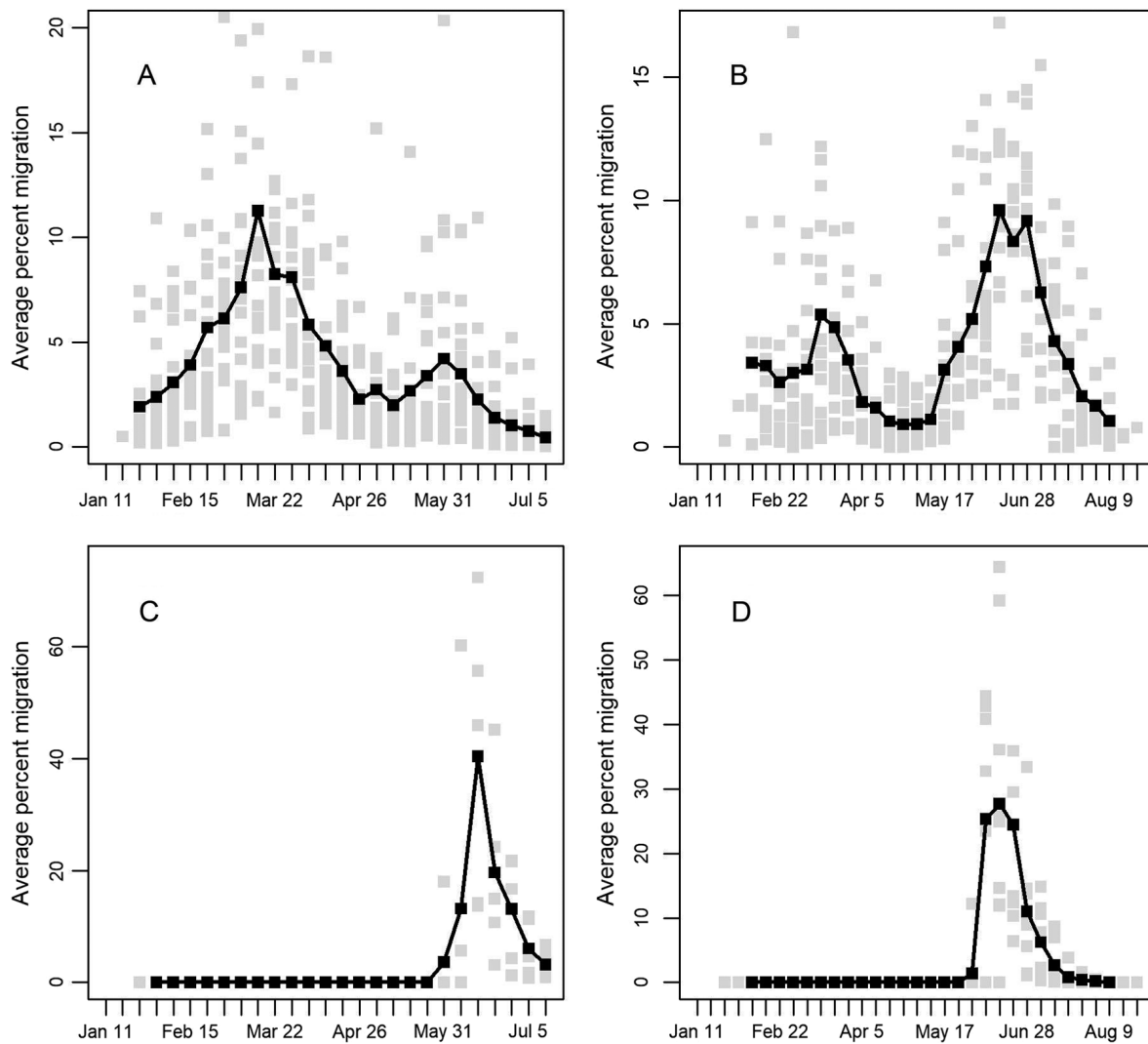
Fig. 5. Migration timing of juvenile sub-yearling Chinook salmon encountered at fish traps, including (A) Skagit River natural-origin 1998–2017; (B) Dungeness River natural-origin 2005–2018; (C) Skagit River hatchery-origin 2010–2014; and (D) Dungeness River hatchery-origin 2010–2018. In each panel, the gray boxes represent weekly estimates for individual years whereas the black line and black boxes represents average weekly estimates across all years. Hatchery fish were identified by marks (adipose clip and/or presence of coded-wire tags). In some panels, a small number of individual year weekly estimates (gray boxes) are not shown because they exceed the maximum *y*-axis value.

Sound (Fig. 8) and show a comparable degree of size overlap with the predation window with Puget Sound hatchery Chinook. Trawl survey data from the Strait of Georgia suggest that natural Chinook are significantly smaller than hatchery fish shortly after marine entry (Beamish et al. 2012), so it is likely the disparity in overlap with the predation window (between natural and hatchery) is similar to Puget Sound Chinook.

DISCUSSION

As the recovery potential of many natural salmon populations remains uncertain, and conflicting conservation objectives create potential
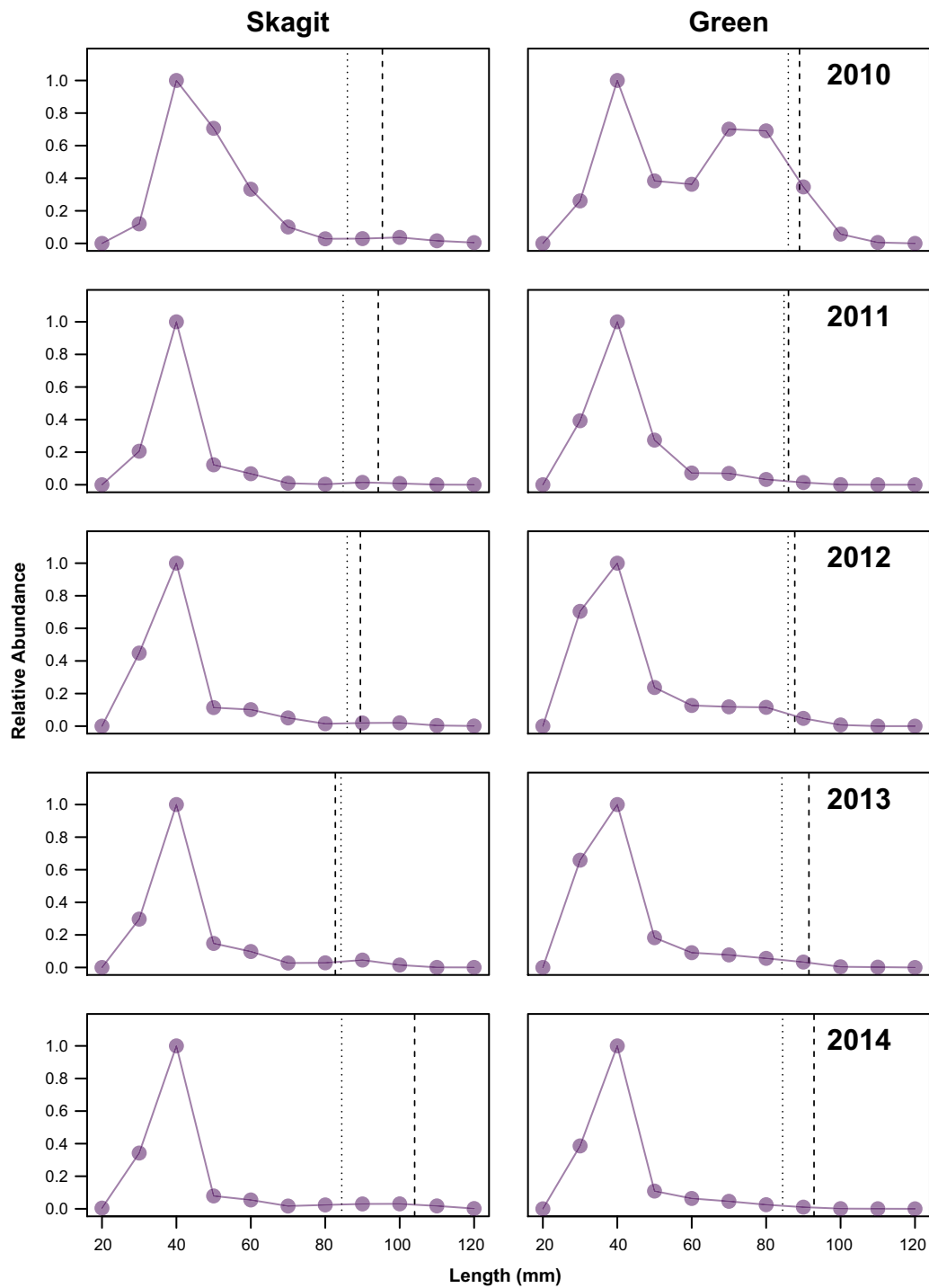
Fig. 6. Size distributions of natural-origin juvenile Chinook salmon in the Skagit and Green rivers, based on rotary screw trap data collected from 2010 to 2014. Each circle shows the relative abundance of natural Chinook at each size class (10 mm bins). Vertical lines show the mean length at release of hatchery fish in that particular river (dashed) and the Puget Sound (dotted) and are based on Regional Mark Information System data from 2010 to 2014. Abundances (*y*-axis) are scaled relative to the maximum abundance in each series.
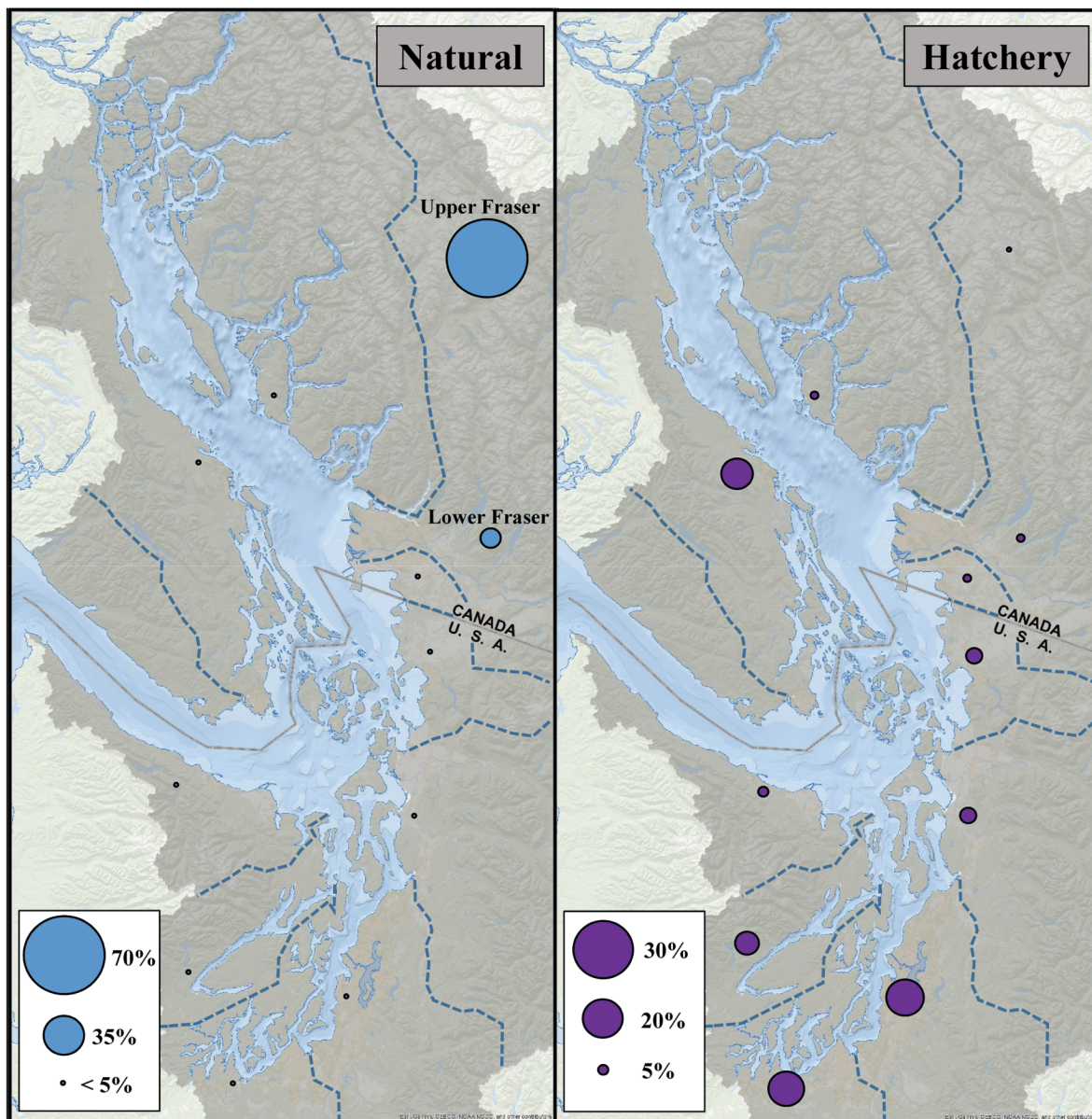
Fig. 7. Regional distributions of natural- (left) and hatchery-origin (right) juvenile Chinook salmon throughout the Salish Sea. The size of the circle in each region is proportional to the relative contribution to each population. Proportions of natural Chinook are based on recent escapement data in each region (Appendix S1: Table S2); this assumes relative regional production of natural juveniles is comparable to adult escapement. Regional proportions of the hatchery population are based on the most recent 10-yr means of releases from the Regional Mark Information System database.

competition between fisheries and marine mammals (Williams et al. 2011, Chasco et al. 2017), hatchery production is likely to continue and possibly increase significantly in the Salish Sea and other regions (WDFW 2019). Accordingly, it is crucial that efforts to understand the ecological consequences of large-scale hatchery programs move beyond the freshwater environment and into estuarine and marine habitats (Rand et al. 2012). Here, we documented temporal and
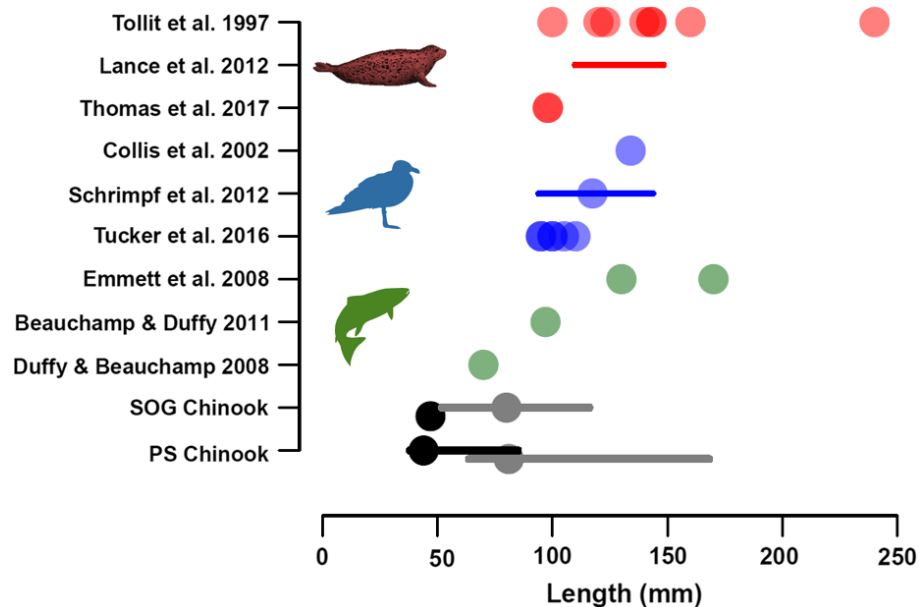
Fig. 8. Size overlap of hatchery (gray) and natural (black) juvenile Chinook salmon with hypothesized predation windows for avian (blue), marine mammal (red), and fish (green) predators, based on published studies. Circles represent measures of central tendency (mean or mode) for observed prey size in each study, while solid lines depict the range (90% quantiles or confidence intervals) reported in each study. The length distributions for hatchery Chinook are based on Regional Mark Information System data for releases between 2010 and 2017. Distributions for natural Chinook from the Puget Sound are based on trap data (see *Materials and Methods*). Mean length of natural Chinook from the Strait of Georgia is from trawl survey data reported in Beamish et al. (2012). The length range associated with Lance et al. (2012) is based on the season with the highest percentages of juvenile Chinook in the seal diet (July–September). Lengths of juvenile Chinook during that time period were estimated from survey data of the north Puget Sound reported in Beauchamp and Duffy (2011). The central tendency measures associated with Thomas et al. (2017) are based on estimated lengths during the months where their respective proportions in the harbor seal diet were the highest.

spatial changes in numbers, distribution, and important traits (size, migration timing) of hatchery-reared Chinook salmon in the Salish Sea and contrasted these patterns with natural populations. These changes may have implications for interactions between young salmon and marine mammal, avian, and fish predator assemblages in the Salish Sea, in addition to salmon of natural origin. Further, the differences between juvenile salmon of hatchery and natural origin we identify here may be helpful in explaining their disparate marine survival rates (Losee et al. 2019) and even illuminate strategies to improve hatchery performance in the future.

Our results show that in many regions of the Salish Sea—the Puget Sound, in particular—the size of hatchery Chinook has increased, making them (on average) significantly larger than natural-origin fish (Fig. 6). Although natural-origin Chinook will rear and grow in estuaries downstream from the traps we used as sampling platforms prior to marine entry, the larger size of hatchery fish persists in the marine waters of Puget Sound (Rice et al. 2011). Changes in average release size are not as apparent in Canadian waters, but diversity of release size has decreased in both countries (Fig. 4). While others have highlighted the disparity in size between natural and hatchery fish (Beamish et al. 2012), less work has evaluated the potential negative consequences of producing larger-bodied fish. The prevailing assumption that "bigger is better" may be true in many circumstances (Sogard 1997), but there is evidence that populations of

smaller juvenile salmon survive at higher rates than larger fish during their first several months at sea. For example, survival of juvenile Chinook from the South Thompson River—a composite of about 15 sub-populations in the Fraser River—appears to be increasing (Beamish et al. 2010). In addition to being smaller, juveniles from the South Thompson enter the marine environment much later (July; Beamish et al. 2011). Since 2010, the number of Chinook released after June 15 in the Salish Sea has been reduced by 63%, compared to years prior to 1990. Chinook salmon of natural origin, which are typically smaller than hatchery fish, also survive at significantly higher rates (Claiborne et al. 2014, Neville et al. 2015, Losee et al. 2019).

One reason why releasing larger Chinook salmon may not necessarily improve survival is greater degree of overlap with preferred prey size of predators (Fig. 8). A recent study near the most productive hatchery in the Strait of Georgia (Big Qualicum River) provides evidence for such size selectivity of salmonids by harbor seals in the Salish Sea (Allegue 2017). Seals tagged with GPS devices exhibited increased feeding behavior in the estuary shortly after releases of coho salmon (mean release size: 130 mm) but did not respond to far more abundant, smaller Chinook (release size: 80 mm) released only a few weeks later. Harbor seals do appear to target juvenile Chinook salmon, but typically in mid-summer (Lance et al. 2012, Thomas et al. 2017), when fish are larger (average size of >100 mm). Interestingly, a similar seasonal preference for Chinook of similar sizes has been documented in Caspian tern colonies near the Columbia River estuary (Collis et al. 2002). This suggests relatively smaller juvenile salmon may have lower encounter rates with certain predators shortly after marine entry. While smaller size at marine entry would obviously not keep them from eventually reaching targeted size, prolonged survival may give young salmon more time to develop predator recognition abilities (Olla and Davis 1989, Berejikian et al. 1999).

Chinook are being released from hatcheries progressively earlier in the spring in the Strait of Georgia, and later in the Puget Sound. It is unclear if this is motivated by a specific management goal, such as the segregation of natural and hatchery populations, or to maximize survival (HSRG 2014). Regardless, most hatchery releases in both basins have become constrained to relatively narrow window of time in May (Fig. 3), and diversity in release timing throughout the Salish Sea has decreased significantly (Fig. 4). For example, in 2015 over half of all hatchery Chinook in the Strait of Georgia were released between the second and third week in May. In contrast, natural Chinook from the same rivers typically migrate to the ocean earlier in the year, and over a much longer time frame (Fig. 5). Varying hatchery release timing in a way that mimics the temporal dynamics of natural-origin fish may reduce the level of competition among hatchery-origin Chinook in the spring and summer months. This may also prevent the spread of disease, which is more likely to be found in juvenile Chinook in high densities (Rhodes et al. 2011). Conversely, deliberately integrating releases of hatchery Chinook with the out-migration of wild populations may increase risk of disease transmission to wild fish, or induce predator switching to migrating salmon that were previously lower in abundance (Schindler et al. 2013).

Even in years when environmental conditions in estuaries are favorable for young Chinook, releasing large numbers of young salmon within a short time frame could make them vulnerable to opportunistic predators. Numerical responses by avian (mergansers, *Mergus merganser*) and piscivorous fish species (spiny dogfish, *Squalus suckleyi*) have been documented in the Salish Sea in response to high densities of hatchery salmonids (Wood 1987, Beamish et al. 1992). Furthermore, these predators are capable of learned behavior (Brown and Laland 2003); as hatchery releases become more predictable in time and space, we hypothesize that predators may increasingly congregate to opportunistically feed on pulsed hatchery releases and co-mingled naturally produced salmon. Alternatively, high densities of migrating juvenile salmonids have been shown to produce predator swamping effects, which result in lower mortality rates (Furey et al. 2016). It is likely that such dynamics are unique locally and vary over space and time. Thus, it would be difficult to generalize these interactions to an ecosystem level without large, replicated experiments involving multiple hatcheries. While it is unclear from our results whether earlier or later

releases would increase survival of hatchery Chinook, we found that variability in release date has generally decreased and that release dates among sub-basins in both the Puget Sound and Georgia Strait have become less diverse for Chinook (Fig. 4).

Comparing the current abundance of hatchery Chinook with their natural abundance in each sub-basin suggests the spatial distribution of the juvenile salmon in both basins is now much different relative to the historical period preceding large subsidies of hatchery salmon (Fig. 7). In regions that historically did not support high densities of juvenile salmon, density-dependent mechanisms like increased competition and predator responses could reduce survival. For example, hatchery Chinook originating from southern Puget Sound are less likely to migrate to the open ocean following their first year in the marine environment, and many will remain in the Salish Sea until maturity (Chamberlin et al. 2011). These resident types are predators of young-of-the-year Chinook and may account for up to 50% of juvenile mortality in some regions of Puget Sound (Beauchamp and Duffy 2011). Thus, it is possible that changes in the spatial distribution of Chinook (via hatchery subsidies) have increased predation risk for natural populations.

Long-term changes in hatchery practices described here should be of interest to managers seeking to understand salmon survival and interactions of hatcheries with the marine ecosystem. These potential interactions will likely vary regionally and/or locally, as suggested by previous studies of juvenile Chinook in the Salish Sea (Chamberlin et al. 2017). Inter-annual variability in ocean conditions and alternative prey availability undoubtedly modulate predator–prey interactions (Wells et al. 2017), so optimal release time and size likely vary from year to year (Mathews and Ishida 1989). The intent of this study is not to argue in favor of releasing smaller Chinook or claim that altering release dates will result in increases in marine survival of either natural or hatchery populations. However, like previous studies have suggested (Beamish et al. 1992, Irvine et al. 2013), more diverse release strategies that resemble natural stocks could be explored as a means to promote a more balanced, natural marine food web that is less

influenced by pulsed, high-density subsidies of hatchery fish. Staggering releases over several months, and coordinating releases among hatchery operations to reduce homogenization across sub-basins, could dampen numerical responses from predators and could also hedge against poor environmental conditions via increased portfolio effects (Satterthwaite and Carlson 2015). Because of the known influence that inter-annual environmental variation and regional effects have on survival, experimental approaches to hatchery releases could be replicated over space and time while being monitored systematically, along with other potentially important variables like predator densities.

The reduction in diversity of release size and timing of hatchery Chinook in the Salish Sea is similar to homogenization of hatchery Chinook salmon documented in other ecosystems, such as the California Central Valley (Huber and Carlson 2015). Reduced diversity in these stocks has likely reduced the ecosystem's hatchery portfolio, and it is hypothesized that this could have a destabilizing effect on recruitment (Sturrock et al. 2019). Maintaining diversity—and the stability it may confer—in the composite of Chinook stocks along the west coast of North America could be a critical factor for the recovery of southern resident killer whales, which depend heavily on Chinook salmon for prey (Ford et al. 2016). Thus, other regions along the west coast that provide large contributions of hatchery Chinook salmon (e.g., Columbia River, Washington, and Oregon coast) might consider the findings presented in this study relevant, as future hatchery practices are designed.

In the face of changing and unpredictable environmental conditions, understanding the interaction between hatchery strategies and the ecosystem is a major challenge for salmon management. While further data collection and modeling analyses may be helpful for clarifying objectives and priorities related to management alternatives for salmon enhancement (Walters 1994), systematic and replicated experimental approaches to hatchery releases could be a fruitful strategy to understanding the impacts of current hatchery practices on salmon survival dynamics within the marine ecosystem. Large-scale experimental and adaptive manipulations using existing infrastructure have the potential to

clarify mechanisms that affect juvenile marine survival and modulate predation and competition. Finally, deliberate ecosystem-wide manipulations could be performed to allow a concurrent assessment of potential opportunities for enhancement of prey for other endangered species (i.e., southern resident killer whales), which may help facilitate synchronized recovery of both populations (Samhouri et al. 2017).

ACKNOWLEDGMENTS

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Data Accessibility

The "cleaned" RMIS datasets for Chinook salmon releases in the Salish Sea are available on the first author's GitHub repository: https://github.com/benjaminnelson/Ecosphere_2019.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2922/full