

# Linking environmental and biotic variation to growth and survival of juvenile Chinook salmon in Puget Sound

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## Abstract

Marine aquatic ecosystems are often characterized by strong trophic dynamics driven by abiotic drivers that influence primary and secondary production. These “bottom-up processes” have the potential to influence productivity of planktivores through changes in individual growth, size, and survival. Using data from multiple surveys of greater Puget Sound in climatologically contrasting years of 2011, 2014 and 2015, we used linear mixed effects models to explore linkages of salinity, stratification, and temperature with chlorophyll concentrations (an index of standing stock biomass of phytoplankton), and with zooplankton biomass. We also examined whether individual growth (as measured from insulin-like growth factor plasma concentrations) in juvenile Chinook salmon as well as size and condition tracked lower trophic and abiotic measurements. The year 2011 was characterized by very cool conditions and delays in productivity, while 2015 was dominated by a coast-wide marine heatwave that strengthened starting in 2014. These large-scale conditions produced strong annual variation in all metrics we evaluated, although there were more localized differences among sub-basins of Puget Sound as well. Chlorophyll concentrations strongly tracked stratification, temperature, and salinity values, and zooplankton biomass strongly tracked temperature and stratification. Growth varied systematically as a function of zooplankton biomass, temperature, and stratification, and all size metrics were correlated with growth. Previously, Duffy and Beauchamp (2011) found that marine survival was positively correlated with average individual biomass of hatchery Chinook salmon stocks. Hence, we found strong evidence for connections among abiotic variables, primary and secondary production, and growth, individual condition, and marine survival. We also discovered that several metrics had negative or nonlinear relationships with abiotic metrics. These appear to correspond to conditions of peak productivity, but likely require further analysis of other factors, including other planktivores, to improve understanding. Likewise, the relationships suggest several pathways by which long-term changes within the Salish Sea may have influenced marine survival, but further analysis of historical datasets is warranted to confirm such changes in bottom-up pathways.

## Introduction

In marine systems, biophysical processes are well known to drive dynamics of populations and ecosystems. These “bottom-up” drivers include effects of temperature, salinity, nutrients and stratification on primary and secondary production, which in turn affect conditions favoring growth and survival of planktivores. Not surprisingly, bottom-up processes have been postulated as primary drivers of variation in recruitment dynamics of a variety of marine species with pelagic life stages. For example, Tolimieri et al. (2015) found strong patterns of recruitment in sablefish on the Pacific Coast related to summaries of temperature and pelagic transport dynamics. Similarly, Rosenkranz et al. (2001) found strong variation in year-class strength of tanner crabs related to temperature and wind dynamics in the Bering Sea. In addition to the influence of abiotic drivers, Beaugrand et al. (2003) found effects of fluctuations of zooplankton upon variation in recruitment dynamics in North Sea Atlantic Cod, and Latour et al. (2017) found mean spring surface chlorophyll *a* concentration to be important in determining fish condition across a wide variety of species in Chesapeake Bay, indicating the importance of bottom-up processes for regulating productivity.

Bottom-up dynamics have also been implicated in the context of systematic declines in abundance or survival of focal species. This concept implies that the drivers of primary and secondary production have shifted over time to less productive states. For example, Worm and Loetze (2006) used tile experiments to determine that effects of eutrophication at sites in the Baltic Sea and NE Atlantic upon macroalgae overshadowed grazing by molluscs. Using metanalyses, Micheli (1999) showed this general pattern to be true in many mesocosm studies of nutrient and predator manipulations as well as long-term monitoring of pelagic ecosystems.

These examples point to specific cases in which direct linkages can be made between changing environmental drivers and focal populations. More commonly, scientists observe declines in species and then are forced to identify potential causes of declines, which can include multiple anthropogenic impacts and predation-driven trophic cascades in addition to bottom-up processes. In these cases, understanding the plausible mechanisms for how environmental drivers link with individual attributes (such as growth, condition, or reproductive potential) is a crucial first step to understanding systematic changes in how environmental conditions regulate population status.

In the northeastern Pacific, populations of anadromous salmon (*Oncorhynchus* spp.) are excellent case studies for exploring how environmental drivers may contribute to productivity declines. Numerous studies of juvenile salmon on the Pacific coast point to bottom-up processes influencing marine survival and adult returns. 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 (Scheurell and Williams 2005), and North Pacific Gyre Oscillation (NPGO) (Kilduff et al. 2015), and these 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 during early residence in the ocean (Beckman et al. 1999).

Different species of salmon are listed as threatened or endangered under the Endangered Species Act due to huge population declines and a broad array of threats. In the Salish Sea, species of Pacific salmon have experienced increasing marine mortality over the past 40 years, and a number of hypotheses have been raised to explain these patterns. These patterns contrast with coastal stocks, which exhibit more cyclical dynamics consistent with decadal variation (Zimmerman et al. 2015, Ruff et al. 2017). One set of hypotheses for these differences focus on shifts in Puget Sound’s bottom-up processes, including water column properties and prey such as zooplankton (Keister et al. 2017) and forage fish (Greene et al. 2015, Chamberlin et al. 2016) thereby limiting growth conditions and ultimately survival.

Here we examine the underlying logic for these hypotheses (Fig. 1) in juvenile Chinook salmon (*O. tshawytscha*), a species with extended residence in Puget Sound, the southern arm of the Salish Sea, during migration to the Pacific Ocean. If bottom-up processes contribute to declines, growth and survival should track prey abundance, which should in turn track seasonal variation in environmental attributes. Hence, our goal was to address four functional linkages: 1) water column attributes to standing stock of phytoplankton, 2) water column attributes and phytoplankton to epipelagic crustacean zooplankton density, 3) water column attributes and zooplankton to individual growth and fish condition, and 4) the correlation of condition and growth with marine survival over longer time spans. To examine the first three linkages, we take advantage of multiple intensive data collection efforts in 2011, 2014, and 2015. The fourth linkage has already been verified from long-term monitoring efforts of Chinook salmon in Puget Sound (Duffy and Beauchamp 2011).



**Figure 1.** Simple logical framework for bottom-up hypotheses. Environmental conditions represent abiotic environmental conditions (e.g., light, water column attributes, nutrients) affecting primary production, zooplankton, and growth in fish. Primary producers also fuel zooplankton, which improves growth. Size increases with growth, and in turn marine survival increases with size.

## Methods

### *Study area and species*

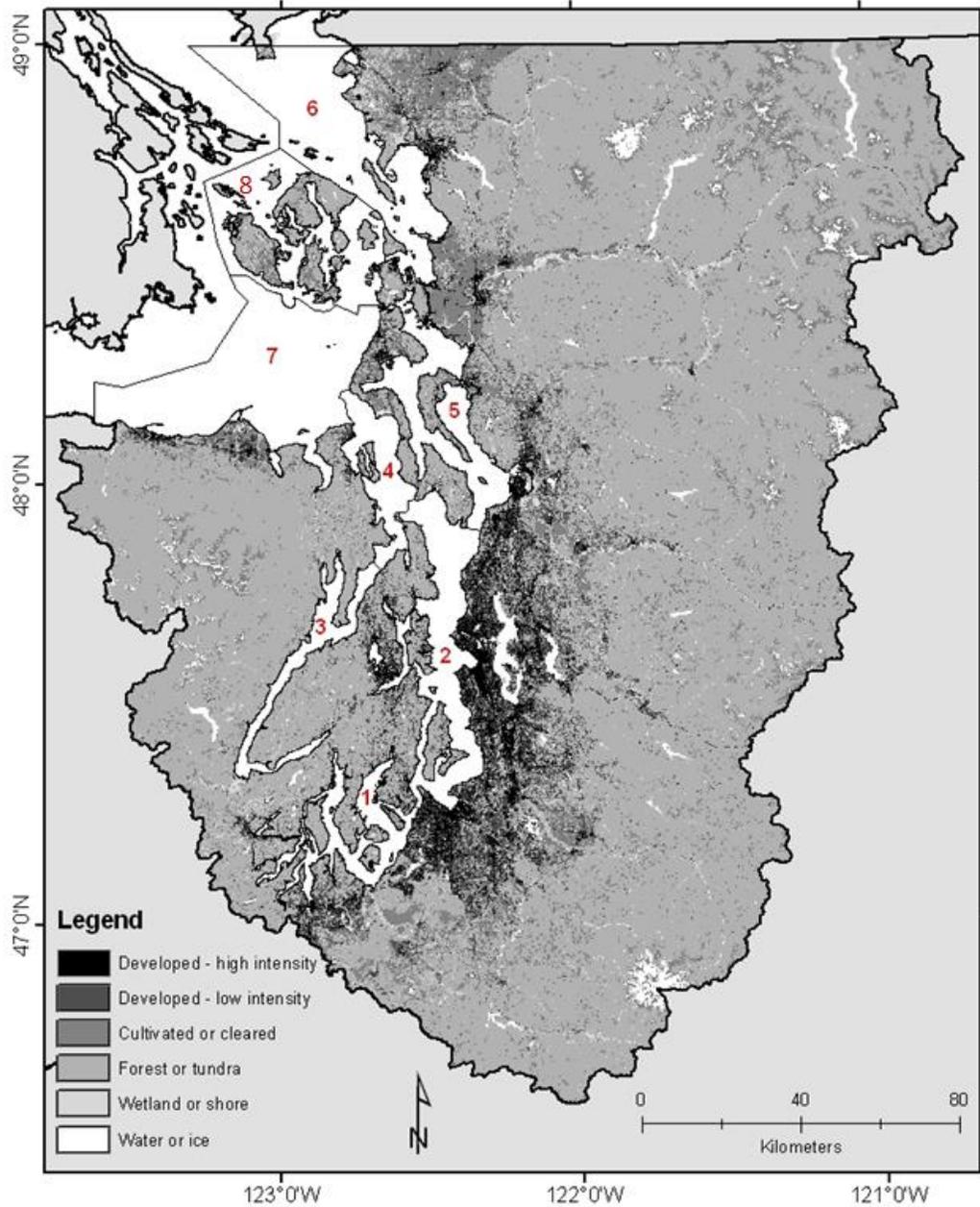
Puget Sound is an urbanized inland sea with multiple sub-basins (Ebbesmeyer et al. 1988) Sub-basins are characterized by deep (> 100 m) bathymetry, some with shallow sills separating them, and vary with respect to riverine inputs and connectivity with the Strait of Juan de Fuca. This bathymetry and geomorphology results in systematic variation in temperature, salinity, stratification, and water residence among sub-basins (Moore et al. 2008).

Within Puget Sound, Chinook salmon are listed as threatened under the Endangered Species Act, and most populations have witnessed strong declines in abundance over the last 50 years (Myers et al. 1995). Juveniles are known for their life history variation, with extended residence in freshwater (Healey 1991, Zimmerman et al. 2015, Hall et al. 2018) and in large river deltas (Healey 1980, Munsch et al. 2019) being a common theme across their range. Chinook salmon migrate as subyearlings (much growth in estuarine and marine waters) or as yearlings (much growth in freshwater). The focus of this study was on subyearling migrants, as they are the most common life history type in Puget Sound and they are most likely to be sensitivity to feeding conditions during their early residence in marine waters.

Additional life history variation occurs in marine waters. A portion of Chinook salmon in the Salish Sea are known to overwinter or further extend residence within the Salish Sea as “blackmouth” (Chamberlin et al. 2011), while a subset continues on to ocean migration. In addition, adults exhibit variation in maturation, returning to Puget Sound rivers after 2-6 years (Healey 1991). Estimates of marine survival, based primarily on coded-wire tagged hatchery groups, varies between 0.005 and 0.05 over the last 40 years, with some evidence of increasing mortality (Ruff et al. 2017) across that time period.

Potential causes for declines in abundance and survival include not only bottom-up drivers during early marine residency, but also freshwater and estuarine habitat loss (Magnuson and Hilborn 2003, Hall et al.

2018), increased toxic contaminants (Meador 2013), increasing predation from marine mammals, overharvest, and cumulative effects. While this analysis focuses solely upon potential bottom-up effects, we acknowledge the strong potential for other potential drivers that may work in concert or synergistically to create low marine survival annually.



**Figure 2.** Greater Puget Sound, divided into eight basins: 1 - South Sound, 2- Central Sound, 3 - Hood Canal, 4 - Admiralty Inlet, 5 - Whidbey Basin, 6 - South Georgia Strait, 7- Strait of Juan de Fuca, and 8 - San Juan Islands. Gray-scale denotes different types of land use.

## Data

Physical, chemical, phytoplankton and zooplankton data were synthesized to find connections between environmental conditions and salmon growth in Puget Sound. This study focused on data from three years: 2011, 2014 and 2015. These years had contemporaneous monitoring of environmental, plankton and Chinook salmon data in seven defined basins in Puget Sound (Figure 2, Table 1). All data reported below were assigned to 1 of 7 basins identified for this study (Figure 1). The 7 basins identified in this study are: Admiralty, Central Sound, Hood Canal, San Juan Islands, South Georgia Strait, South Sound and Whidbey and abbreviated in this report as A, CS, HC, SJI, SGS, SS and W respectively.

## Environmental Data

Environmental data were combined from multiple sources with differing sampling frequency and platforms (Table 1). Environmental data presented here were depth-averaged over the top 0-30 m, which corresponds to the depth range of the oblique zooplankton net tows and typical depth range for fish movement. Profile data were used to compute an index of water-column stratification defined as the difference between the average sigma-t (density) in the bottom 10 meters and the average sigma-t in the upper 10 meters (Newton et al. 2003).

**Table 1.** Environmental data collected as part of this study. Columns show the data sources, data variables, sampling frequency and websites to learn more about the data. Modeled variables are in bolded in the text.

Data Source	Data	Data Frequency	Data Website
Washington Ocean Acidification Center Salish Sea Cruises	<b>Conductivity, temperature, pressure,</b> oxygen, fluorescence, pH and PAR sensors; <b>chlorophyll</b> , oxygen, nutrients, dissolved inorganic carbon and total alkalinity laboratory samples	2014: July and September 2015: April, July and September	<a href="http://nvs.nanoos.org/CruiseSalish">http://nvs.nanoos.org/CruiseSalish</a>
University of Washington, Applied Physics Laboratory NEMO Cruises	<b>Conductivity, temperature, pressure,</b> oxygen, fluorescence, pH and PAR sensors; <b>chlorophyll</b> , oxygen, nutrients, dissolved inorganic carbon and total alkalinity laboratory samples	2011; October 2014: June and October 2015: May and November	<a href="http://nvs.nanoos.org/CruiseSalish">http://nvs.nanoos.org/CruiseSalish</a>
University of Washington, Applied Physics Laboratory ORCA Buoys	<b>Conductivity, temperature, pressure,</b> oxygen, fluorescence and turbidity sensors	Four profiles a day in summer and down to 1 profile a day in winter, due to solar radiation limits	<a href="https://nwem.apl.washington.edu/">https://nwem.apl.washington.edu/</a> , <a href="http://nvs.nanoos.org/Explorer">http://nvs.nanoos.org/Explorer</a>
Washington Department of Ecology	<b>Conductivity, temperature, pressure,</b> oxygen, fluorescence, PAR and turbidity sensors; <b>chlorophyll</b> , nutrients, dissolved inorganic carbon and total alkalinity laboratory samples	Typically 3 to 4 times a month, minimum of 2, for all years with except in December 2014 when no sampling occurred	<a href="https://ecology.wa.gov/Research-Data/Monitoring-assessment/Puget-Sound-and-marine-monitoring">https://ecology.wa.gov/Research-Data/Monitoring-assessment/Puget-Sound-and-marine-monitoring</a>
King County	<b>Conductivity, temperature, pressure,</b> oxygen, fluorescence and PAR sensors; <b>chlorophyll</b> and nutrients laboratory samples	Monthly and often semi-monthly for all years	<a href="https://green2.kingcounty.gov/marine/">https://green2.kingcounty.gov/marine/</a>

## Zooplankton Data

The Salish Sea Marine Survival Project (SSMSP) has been collecting and analyzing zooplankton in Puget Sound since 2014 as part of a marine monitoring program using both vertical and oblique net tows. Zooplankton samples were collected approximately bi-weekly by eight groups at fourteen stations throughout Puget Sound between March 2014 and December 2015 and taxonomically analyzed by J. Keister's laboratory at University of Washington following protocols described in Keister et al. (2017).

Samples were analyzed for abundance ( $\#/m^3$  of taxa and converted to biomass ( $mg\ C/m^3$ ). While the program includes collection of vertical and oblique net tows, only zooplankton biomass data from the oblique net tows (60-cm diameter, 335- $\mu m$  mesh bongo tows over the upper 30 m of the water column) were used in this analysis to align with fish position in the upper portion of the water column.

Between April and October 2011, zooplankton were collected using surface tows (0.75 m diameter, 500  $\mu m$  mesh, set within 6 m of the surface) at multiple stations throughout Puget Sound as part of an EPA-funded study (Greene et al. 2012). Samples were analyzed for abundance ( $\#/m^3$ ) of taxa in J. Cordell and J. Keister’s laboratories at UW and converted to biomass ( $mg\ C/m^3$ ) for these analyses. The zooplankton biomass data for each taxa were summed for each station for each sampling event. The EPA and SSMSP studies sampled different water depths and sites and used different methods. The data sets were used together in this study and methodological differences were accounted for by using year as a random effect in statistical models (see below). Table 2 summarizes sample counts for both zooplankton and fish.

**Table 2.** Zooplankton and fish samples for each year by basin.

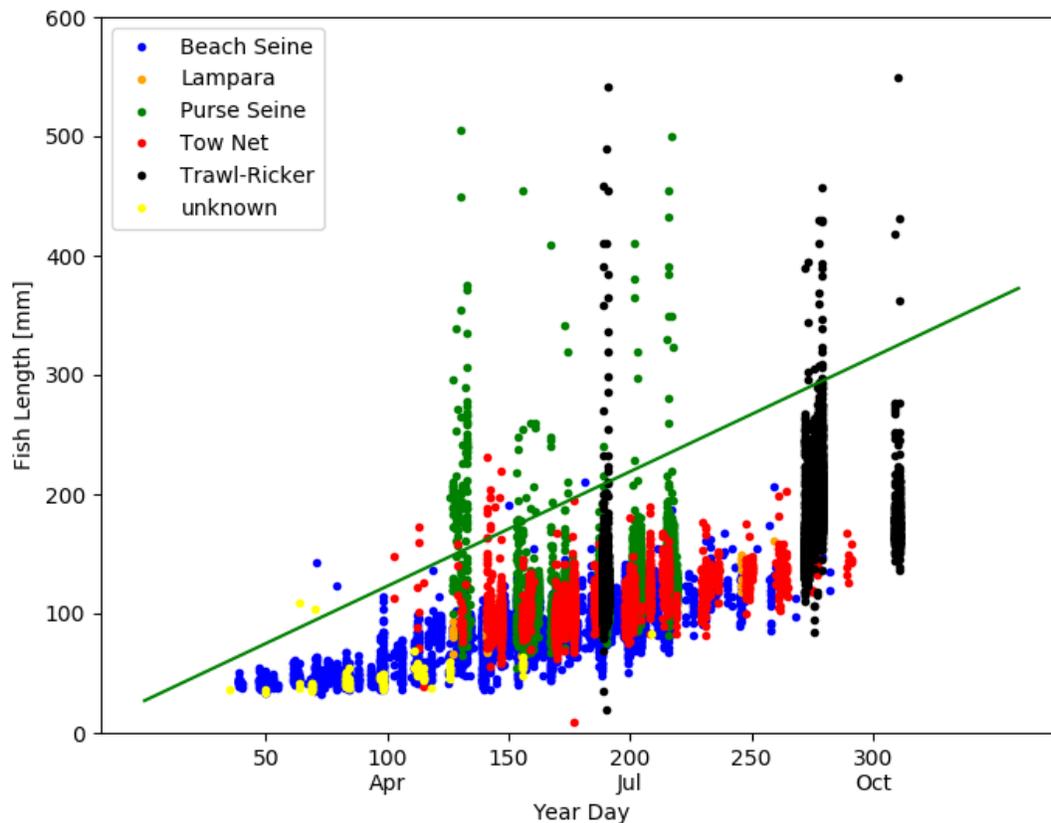
Year	Basin	Fish Length Samples	Fish Weight Samples	IGF Samples	Zooplankton Samples
2011	Admiralty	214	214	57	27
2011	Central Sound	627	627	155	48
2011	Hood Canal	139	139	137	48
2011	San Juan Islands	9	9	9	0
2011	South Georgia Strait	173	173	173	53
2011	South Sound	804	804	210	52
2011	Whidbey	412	412	144	62
2014	Admiralty	72	72	0	0
2014	Central Sound	301	301	0	27
2014	Hood Canal	43	43	0	0
2014	San Juan Islands	221	221	146	30
2014	South Georgia Strait	407	407	131	0
2014	South Sound	1690	1690	0	72
2014	Whidbey	1757	1757	310	43
2015	Admiralty	302	302	6	24
2015	Central Sound	282	282	0	34
2015	Hood Canal	0	0	0	21
2015	San Juan Islands	93	93	77	31
2015	South Georgia Strait	740	740	225	31
2015	South Sound	1243	1243	0	60
2015	Whidbey	1903	1903	307	89

## Fish Data

We synthesized data on fish size and growth from multiple survey efforts in Puget Sound in 2011, 2014, and 2015. Juvenile salmon were collected using various gear types as they transitioned from shoreline environments to deep water: 1) beach seines and lampara nets along subtidal shorelines, 2) Kodiak trawls

(also referred to as tow-net) in subtidal neritic environments, and 3) purse seines and midwater trawls in deeper epipelagic environments. The frequency of these sampling efforts varied in different years and portion of the season (Fig. 3).

Because the current study is focused on size, growth, and marine survival of sub-yearling migrant Chinook salmon (those individuals we hypothesize to be most sensitive to bottom-up effects within Puget Sound), we filtered data by eliminating fish that were older than 1 year. There are two life history types of Chinook salmon that we targeted for exclusion: yearling migrants and Puget Sound blackmouth. Yearlings migrate to marine waters in the spring at 90-150 mm length, while blackmouth are generally captured in deeper waters later in the season at sizes > 200 mm. However, all fish including subyearlings grow over time, so identification of subyearlings is more challenging later in the year based on just size alone. By examining annuli in scales of a subset of fish and size frequencies over time in different sampling gears (Figure 3), we created an upper limit that removed fish > 100 mm early in the season, large individuals from sampling in deeper waters later in the season, and less than 1.5% of the distribution across the entire season (Figure 3). Fish with a condition factor greater than 20 were also removed as outliers. This filtering resulted in a coherent dataset of primarily subyearling fish collected in multiple sampling efforts across the time period of interest. All subsequent analyses of size and growth focused on this putative subyearling subset of fish collections.



**Figure 3.** Fish length by year day color-coded by gear type: beach seine (blue), lampara (orange), purse seine (green), tow net (red), trawl (black) and unknown (yellow). The line shown in green,  $y = 0.96x + 27$  was used as the cutoff for fish of unknown age.

Individual fish size included measurement of length (fork length in mm), biomass (g wet weight), and condition factor ( $\text{biomass}/(0.01 \cdot \text{length})^3$ , Bolger and Connolly 1989). After examining the data, we restricted analyses of individual size to condition factor because it showed much lower autocorrelation with day of capture than length and biomass.

Scales and otoliths were collected from a subset of fish to obtain measurements of individual growth. Metrics of growth focused on insulin-like growth factor (IGF) and the outer two increment widths from scales. Methods for the former measurement can be found in Chamberlin et al. (2016), while methods for the latter can be found in Gamble et al. (2019). After initial data analysis, we focused on IGF as our metric of growth due to the sparseness of data on growth increment measurements. IGF tends to increase allometrically (Journey 2019): after accounting for basin, year, and gear type effects, we detected positive correlations between IGF and length ( $r=0.36$ ), biomass ( $r=0.37$ ), and condition factor ( $r=0.23$ ). Hence, for statistical analysis of IGF, we removed the effect of size by using the residuals of the regression of IGF with individual condition.

### ***Statistical Modeling***

Before the fish data could be modeled with the covariates, the environmental and plankton covariate data had to be paired with the fish data, as not all samples were collected on the same dates. Data were paired by averaging the data collected between 30 days before and up to 1 week after the fish collection date.

We used linear mixed effects models to test for linkages between independent and dependent variables (Table 3) A linear mixed effects model (LMM) is a statistical model that accounts for both fixed and random effects, where in addition to predictor variables, the variance in the responses due to hierarchy or non-independence in the data (random effects) can be accounted for. Random effects give structure to the error term and are useful to better statistically control factors that were not systematically tested within the analysis (e.g., year-specific effects, gear type differences). Because of known variation among years and sub-basins, we used year (2011, 2014, 2015) and sub-basin (each of the seven sub-basins) as the random effects in our models.

To assess our hypothesized linkages within the ecosystem, we tested multiple models with chlorophyll, zooplankton, IGF-residuals, and fish condition factor as dependent variables (Table 3) using the lmer function in the lme4 package for R (R Core Team 2019) and fit by the restricted (residual) maximum likelihood (REML) estimation method (Bates et al. 2015). The data distribution of fish condition and IGF-residuals approximated a Gaussian distribution to use linear models. Temperature, salinity, and stratification index, and in some cases chlorophyll concentrations and zooplankton biomass were modeled as independent variables (fixed effects) and gear type, year and basin were modeled as random effects. A wide range of model configurations were tested to find the best model. Configurations varied by using different combinations of predictors, adding predictor term interactions, and by varying the random effects.

We used standard model selection procedures (Burnham and Anderson 2006) to identify the best model(s), by comparing the model Akaike's Information Criterion (AIC) scores (Akaike 1974) and conditional coefficient of determination,  $R^2$ , as a measure of goodness of fit for generalized mixed-effect models (Nakagawa and Schielzeth 2013), and diagnostic plots to determine whether residual variation was randomly distributed. The model with the lowest AIC score has the best ability to fit the data, and additional parameters are penalized in an effort to prevent over-fitting;  $R^2$  gives the variance explained by the entire model including both fixed and random effects. Akaike's Information Criterion scores can only be compared between models if the number of observations (dependent variables) used in the models are the same.

**Table 3.** Variables used in statistical analyses to demonstrate bottom-up linkages with marine survival. DV = dependent variable, IV = independent variable.

<b>Data</b>	<b>Definition</b>	<b>DV or IV</b>	<b>Reference</b>
Temperature	Average of water temperature 0-30 m depth	IV	Newton et al. 2003
Salinity	Average of salinity (ppt) 0-30 m depth	IV	Newton et al. 2003
Stratification	Density at max depth – density 0-30 m depth	IV	Newton et al. 2003
Standing stock biomass	Average chlorophyll concentration (mg/l) 0-10 m depth	Both, depending upon linkage	Moore et al. 2008
Zooplankton	Total biomass of zooplankton (mg C/m <sup>3</sup> ) collected from 0-30 m	Both, depending upon linkage	Keister et al. 2017
Fish growth	Residual of IGF - condition factor regression	DV	Chamberlin et al. 2016
Fish condition factor	(biomass/(0.01*length) <sup>3</sup> )	DV	Bolger and Connolly 1989

## Results

### *Temporal and spatial patterns of water density components*

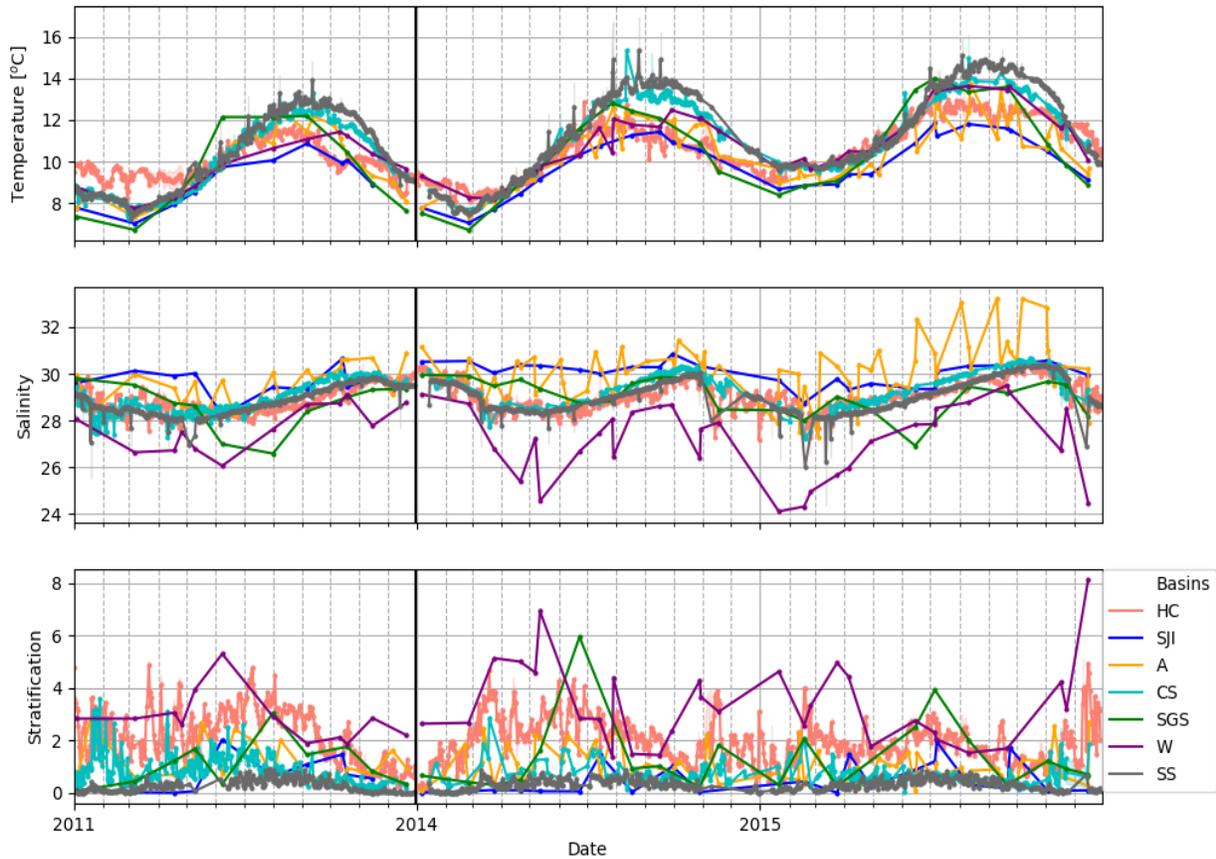
Salinity in the top 30 m varied throughout Puget Sound (Figure 4): basins connected directly to the Strait of Juan de Fuca had the highest salinity (A, SJI), while basins with large freshwater inputs had the lowest salinity (W, SGS, SS). As density in Puget Sound is largely driven by variation in salinity with more minor effects from temperature, water-column density stratification patterns followed this regional salinity pattern. Periods of low salinity in Whidbey and South Georgia Strait basins correspond to peaks in stratification. Winds and/or tides are able to break down stratification such as is observed in Admiralty Basin. The high salinity peaks that are periodically observed there likely correspond to oceanic water intrusions or strong mixing events that bring deep waters to the surface. In contrast, lack of mixing and long and narrow geometry supports a stratified water column, such as is observed in Hood Canal (Figure 4).

Interannual differences in the top 30-m salinity average were evident as well, but these were not consistent between the basins. In Admiralty Basin, there were periods of higher salinity in 2015 compared to 2014, with 2011 showing the lowest salinity. In Whidbey Basin, salinity was much lower in 2014 and 2015 as compared to 2011. Periods of low salinity typically correspond to higher stratification in most basins (W, SGS, HC, CS).

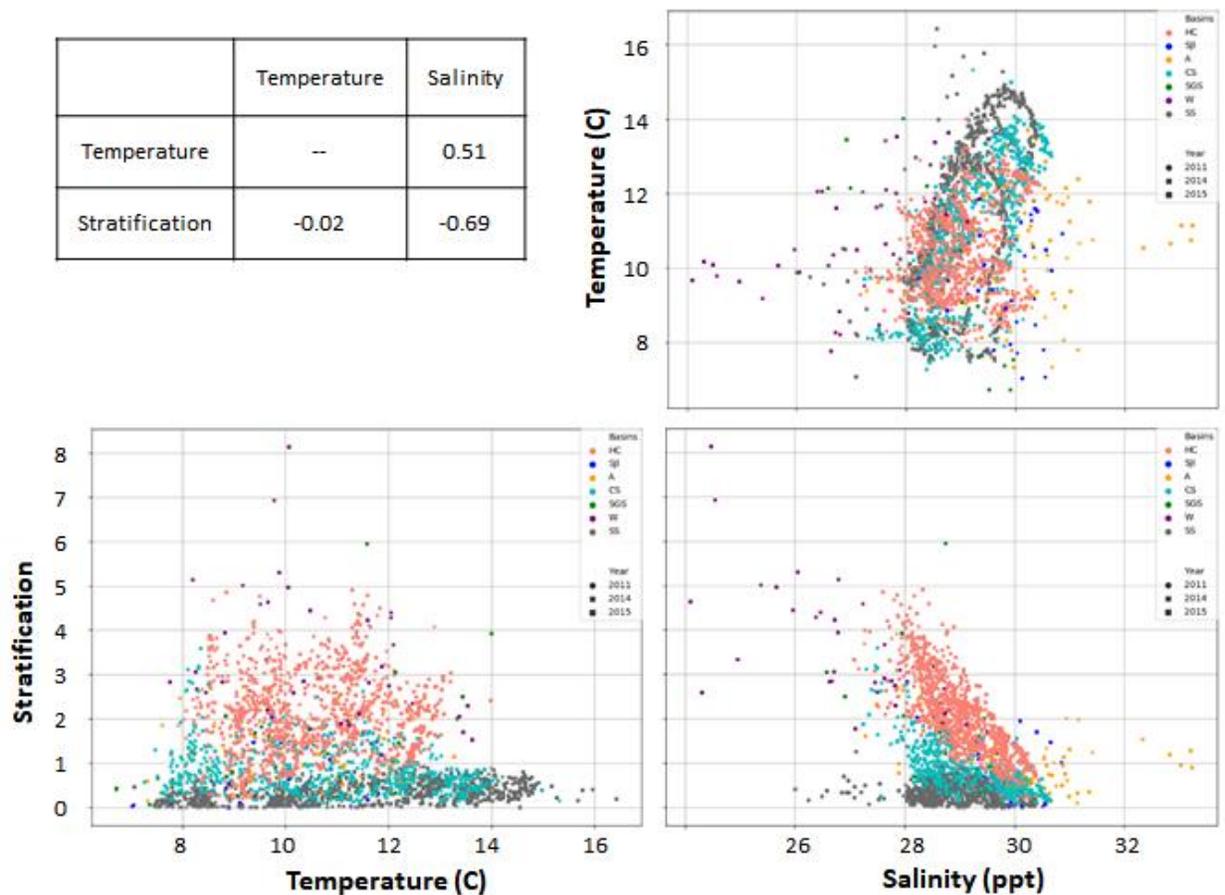
The annual average water temperature (top 30 m) varied over the three years (Figure 4), and reflected the influence of the 2014-2016 marine heat wave (Bond et al. 2015, PSEMP 2015 and 2016). Average annual temperatures over the top 30 m were 9.79°C in 2011, 10.51°C in 2014, and 11.28°C in 2015. The annual averages for each basin followed that pattern over the three years for all but Central Sound where the average in 2014 was higher than 2015. Northern basins (SJI, W, A, SGS) and Hood Canal tended to have lower water temperatures compared to southern basins (CS, SS). Seasonally, all basins had their lowest

upper 30-m water temperatures in winter and their highest temperatures in late summer to early autumn with a gradual change connecting the highs and lows. Central Sound and South Sound had the highest summer to early autumn water temperatures of the seven basins for all years. Water temperatures in Hood Canal were higher between January and May compared to other basins in 2011. In 2015, upper 30-m water temperatures in all basins started out warmer than in 2011 and 2014 and remained higher throughout the year, again, likely reflecting the influence of the marine heat wave.

These spatial and temporal patterns were evaluated via statistical analysis to assess the correlations of environmental metrics relevant to bottom-up processes in Puget Sound. The strongest of these patterns was between salinity and stratification, followed by temperature and salinity (Figure 5). These metrics exhibited strong annual and geographic variation, although the same general correspondence applied within years or basins.



**Figure 4.** Time series for 2011 and 2014-2015 by basin for 0-30 m average temperature (top panel), 0 – 30 m average salinity (middle panel), and water-column stratification (bottom 10 m  $\sigma_t$  - upper 10 m  $\sigma_t$ , bottom panel). Black vertical line indicates a disjoint time interval and separates 2011 from 2014-2015. Basin abbreviations used in the legend are: HC = Hood Canal, SJI = San Juan Islands, A = Admiralty, CS = Central Sound, SGS = South Georgia Strait, W = Whidbey, and SS = South Sound.



**Figure 5.** Scatter plots of 0-30 m average temperature, 0-30 m average salinity, and water-column stratification (bottom 10 m  $\sigma_t$  - upper 10 m  $\sigma_t$ ), color-coded by basin and symbol coded by year. Basin abbreviations used in the legend are: HC = Hood Canal, SJI = San Juan Islands, A = Admiralty, CS = Central Sound, SGS = South Georgia Strait, W = Whidbey, and SS = South Sound. Year abbreviations used in the legend are: circle = 2011, X = 2014, and square = 2015. Table in upper left corner reports standardized correlations estimated from linear mixed effects models incorporating basin and year as random effects.

### ***Temporal and spatial patterns of oxygen, nutrients, phytoplankton, and zooplankton***

Two variables we considered in exploratory analysis -- dissolved oxygen and dissolved inorganic nitrogen (DIN) -- were not included in our hypothesized linkages and subsequent models, but are nonetheless relevant from the perspective of bottom-up drivers. Dissolved oxygen is critical for survival of heterotrophs, such as zooplankton and fish, but negative effects from hypoxia occur only at very low values (<5 mg/l, Farrell and Richards 2009). This is particularly true for salmon in Puget Sound -- hypoxia in the region most commonly occurs at depth and juvenile salmon are surface oriented. Upper 30-m dissolved oxygen levels for all basins followed a similar seasonal pattern over the three years with increased oxygen in the spring and lower values in autumn and winter, consistent with spring blooms as indicated by surface chlorophyll values (Figure 6). All basins, except Hood Canal, had similar dissolved oxygen values over the three years. Hood Canal had the lowest oxygen levels of all the basins, largely influenced by hypoxic conditions that typically persist through fall below 10 m at Twanoh in the relatively shallow (~40 m) and strongly stratified Southern Hood Canal (PSEMP 2015 and 2016). Hood

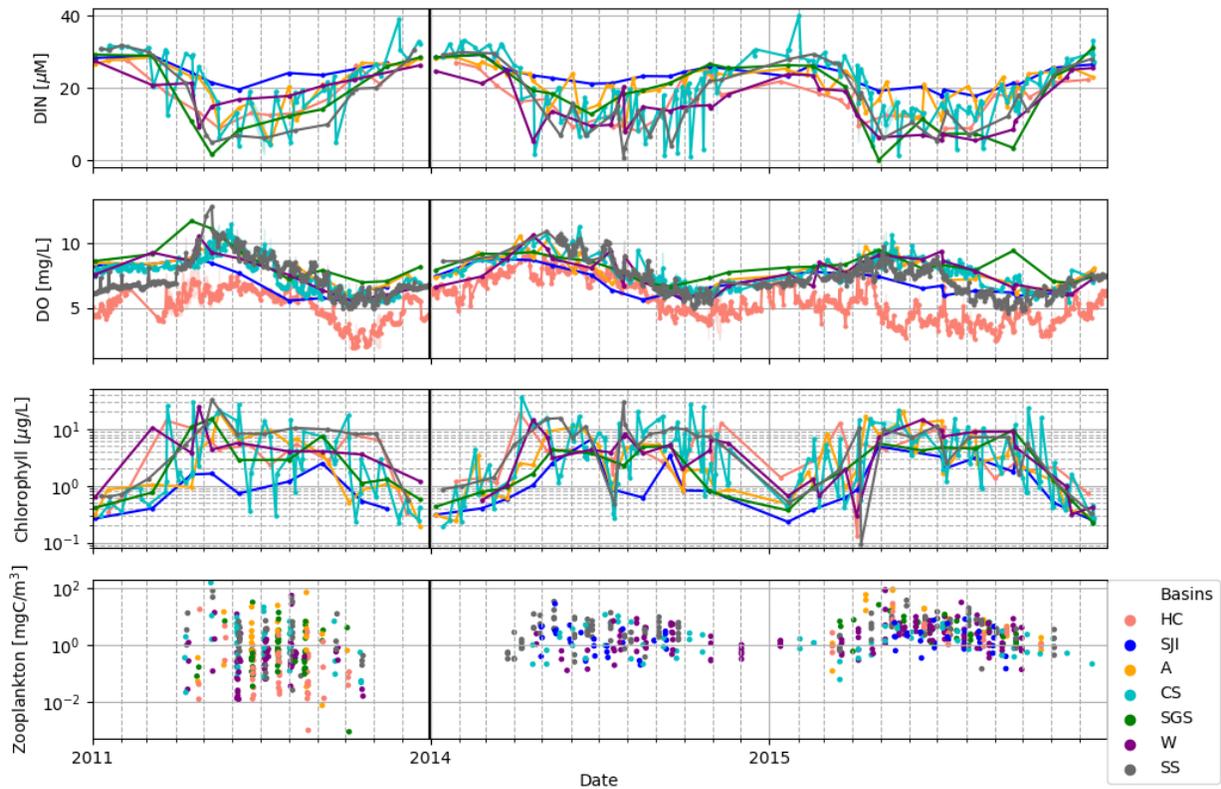
Canal hypoxic conditions occurred in the fall in 2011 and 2014, although they occurred earlier in 2015. In other basins with strong water-column stratification, W and SGS, lower oxygen values are typically at depths deeper than 30 m. In the basins with weak water-column stratification (A, SJI, CS,SS), oxygen values stay above or at 5 mg/L (a value considered above biological stress conditions for fish) due to mixing. Upper 30-m oxygen concentrations were generally highest in 2011, followed by 2014, with 2015 having the lowest values. With the exception of Hood Canal, upper 30 m oxygen concentrations were above levels that incur biological stress (<5 mg/L) or hypoxia (<2 mg/L). There were distinct spikes in the upper 30-m dissolved oxygen that correspond to high concentration spikes in chlorophyll and low concentrations of DIN, consistent with oxygen production as a byproduct of photosynthesis from phytoplankton blooms (Figure 6).

Chlorophyll is an indicator of the biomass or standing stock of phytoplankton, the base of Puget Sound's foodweb (Strickland 1983). Concentrations of upper 30-m DIN and chlorophyll tend to vary inversely; DIN was lower between May and October when chlorophyll was higher, as would be expected from phytoplankton uptake of DIN. There were no clear differences between the years except that DIN values in Whidbey Basin stayed consistently lower between May and October in 2014 and 2015 as compared to 2011. The lower values in Whidbey Basin did not coincide with corresponding changes in increased dissolved oxygen or increased chlorophyll concentration. Upper 30-m chlorophyll values ranged from 0.06 to 44.3  $\mu\text{g/L}$  and were similar among the basins, indicating food available at the base of the marine food web. South Sound, Central Sound, Hood Canal and Whidbey basins all had large decreases in chlorophyll concentration in April 2015, but a similar decline in dissolved oxygen was not observed here. Chlorophyll concentrations tended to be higher between April and October with much variability between the years. There were no clear differences between the years except that values in the San Juan Islands basin stayed consistently lower between April and October in 2011 compared to the other years.

Zooplankton biomass in 2011 varied over a larger range with lower monthly averages compared to 2014 and 2015 (Figure 6). However, because methodologies differed, comparisons should be made with caution. The 2011 data came from surface (0-5 m range) tows, whereas the 2014 and 2015 came from oblique tows that sampled down to 30 m. For the two years with the same sampling methodology, zooplankton biomass was higher in 2015 than in 2014.

Using linear mixed effects models, we examined how chlorophyll concentrations and zooplankton biomass tracked multiple environmental parameters. We hypothesized that chlorophyll concentrations would vary as a function of temperature, salinity, or stratification. We found strong evidence for a single best model (Table 4) that included both linear and quadratic temperature and salinity terms, and a negative linear effect of stratification (Figure 7). These fixed effects explained approximately 36% of the variation in chlorophyll concentrations across Puget Sound in the three different years. The predicted quadratic relationships exhibited a monotonically increasing relationship of chlorophyll with temperature and a unimodal function with salinity (Figure 8), although the "descending" side of the unimodal relationship at salinities <27 ppt is based on relatively few observations (Figure 7). A second model that assumed linear relationships of all three variables explained about the same amount of variation and captured most of the same pattern as the best model (Table 4).

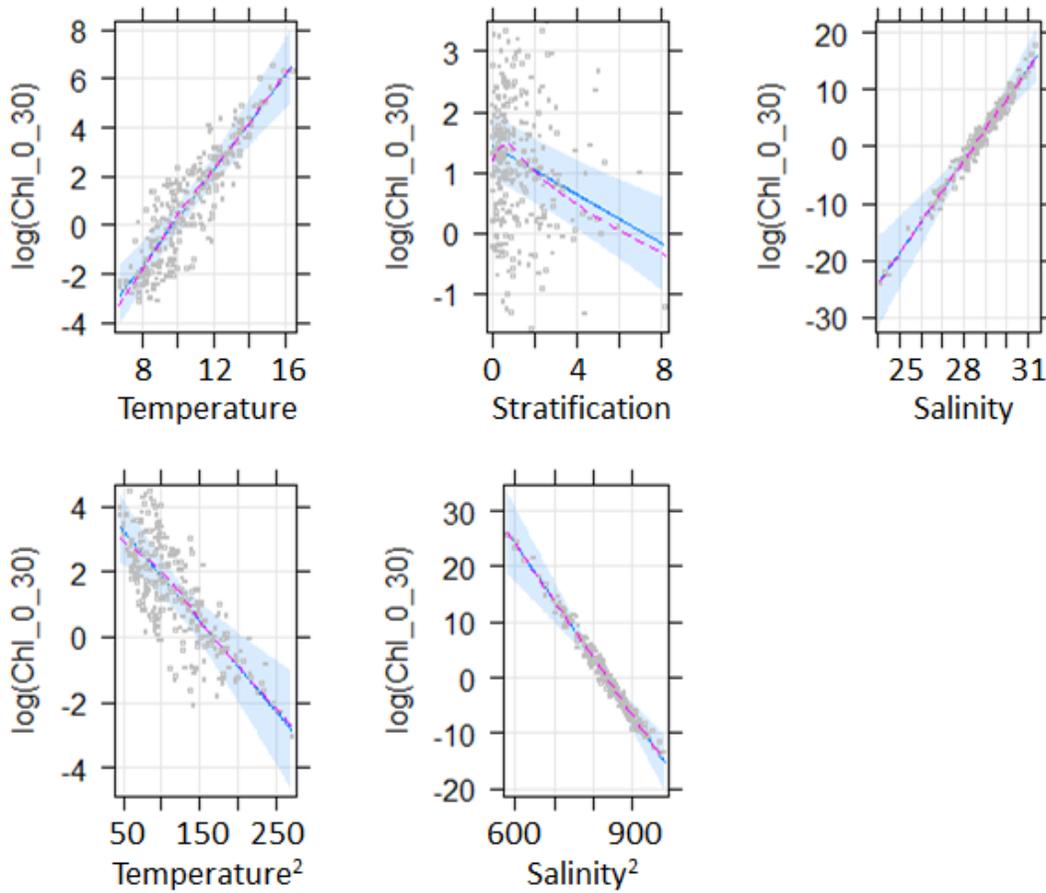
We hypothesized that zooplankton biomass would vary as a function of temperature, salinity, stratification, or chlorophyll concentrations. The best model (Table 5) included a positive effect of chlorophyll and a negative effect of stratification (Fig. 9), although a competing model with similar AIC and slightly better  $R^2$  predicted an additional positive effect of salinity (Table 5).



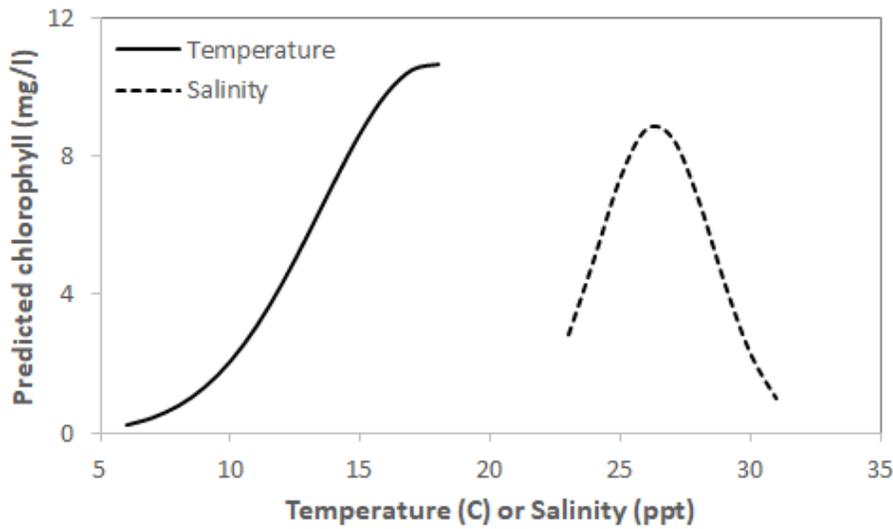
**Figure 6.** Time series for 2011 and 2014-2015 by basin for 0-30 m average dissolved inorganic nitrogen (DIN, top panel), 0-30 m average dissolved oxygen (DO, 2nd panel), 0-30 m average chlorophyll concentration (3rd panel) and zooplankton biomass (bottom panel). Black vertical line indicates a disjoint time interval and separates 2011 from 2014-2015. Basin abbreviations used in the legend are: HC = Hood Canal, SJI = San Juan Islands, A = Admiralty, CS = Central Sound, SGS = South Georgia Strait, W = Whidbey, and SS = South Sound.

**Table 4.** Model comparison of chlorophyll concentrations. The best model is highlighted in orange (dAIC = 0). R<sup>2</sup> marginal reports effects of independent variables, while R<sup>2</sup> conditional includes influence of random effects.

Model#	Model	Randoms	AIC	dAIC	REML	R2 marginal	R2 conditional
1	Temp	Year/Basin	3298.19	128.00	3288.20	0.22	0.35
2	Strat	Year/Basin	3593.38	423.20	3583.40	0.00	0.18
3	Sal	Year/Basin	3591.41	421.22	3581.40	0.00	0.20
4	Temp + Strat	Year/Basin	3304.68	134.50	3292.70	0.22	0.35
5	Temp + Sal	Year/Basin	3237.87	67.69	3225.90	0.30	0.42
6	Strat + Sal	Year/Basin	3597.06	426.87	3585.10	0.00	0.19
7	Sal + Temp + Strat	Year/Basin	3214.56	44.38	3200.60	0.34	0.52
8	Sal + Temp + Temp2 + Strat	Year/Basin	3205.01	34.82	3189.00	0.34	0.50
9	Sal + Temp + Strat + strat2	Year/Basin	3217.89	47.71	3201.90	0.33	0.49
10	Sal + Sal2 + Temp + Strat	Year/Basin	3179.65	9.46	3163.60	0.37	0.53
11	Sal + Sal2 + Temp + Temp2 + Strat	Year/Basin	3170.18	0.00	3152.20	0.36	0.51
12	Sal+ Sal2 + Temp + Temp2	Year/Basin	3183.48	13.30	3167.50	0.33	0.44
13	Sal + Sal2 + Temp +Temp2 + Strat +Strat2	Year/Basin	3177.11	6.93	3157.10	0.37	0.53



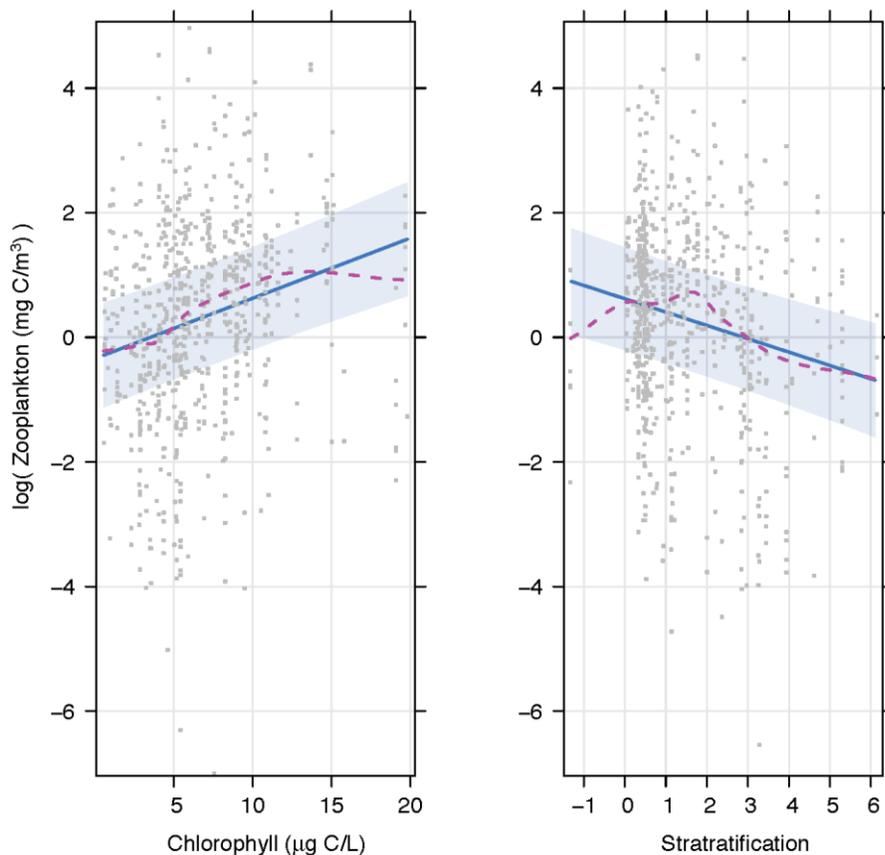
**Figure 7.** Partial regressions for the best linear mixed effects model of chlorophyll. Panels summarize the role of each model predictor when holding the other predictors fixed. The blue line is the partial regression line of the predictor and shaded blue area is a pointwise 95% confidence band for the fitted values. The dashed pink line is the loess nonparametric-regression of the residuals (gray dots) to indicate departures of the prediction from observed central tendencies.



**Figure 8.** Predicted chlorophyll concentrations as a function of the observed range of temperature (solid line) or salinity (dashed lines) when other model variables were held constant at average values.

**Table 5.** Model comparison of zooplankton biomass. The best model is highlighted in orange (dAIC = 0). R<sup>2</sup> marginal reports effects of independent variables, while R<sup>2</sup> conditional includes influence of random effects.

Model #	Model	Random	AIC	dAIC	R2 marginal	R2 conditional
1.00	Temp	Year	2553.29	61.36	0.00	0.21
2.00	Sal	Year	2550.58	58.65	0.00	0.20
3.00	Strat	Year	2519.56	27.63	0.04	0.21
4.00	Chl	Year	2507.76	15.83	0.05	0.26
5.00	Temp + Sal	Year	2556.88	64.95	0.00	0.21
6.00	Temp + Strat	Year	2525.36	33.43	0.04	0.22
7.00	Temp + Chl	Year	2514.11	22.18	0.05	0.27
8.00	Sal + Strat	Year	2516.48	24.55	0.05	0.23
9.00	Sal + Chl	Year	2512.08	20.15	0.06	0.25
10.00	Strat + Chl	Year	2491.93	0.00	0.08	0.25
11.00	Temp + Sal + Strat	Year	2523.06	31.13	0.05	0.23
12.00	Temp + Sal + Chl	Year	2517.67	25.74	0.06	0.26
13.00	Temp + Strat + Chl	Year	2497.10	5.17	0.08	0.27
14.00	Sal + Strat + Chl	Year	2492.41	0.48	0.09	0.27
15.00	Temp + Sal + Strat + Chl	Year	2498.61	6.68	0.09	0.27
16.00	Temp + Sal + Strat + Chl	Year	2498.61	6.68	0.09	0.27
17.00	Strat + Strat2 + Chl + Chl2	Year	2502.79	10.86	0.09	0.26
18.00	Strat + Chl + Chl2	Year	2497.42	5.49	0.09	0.26

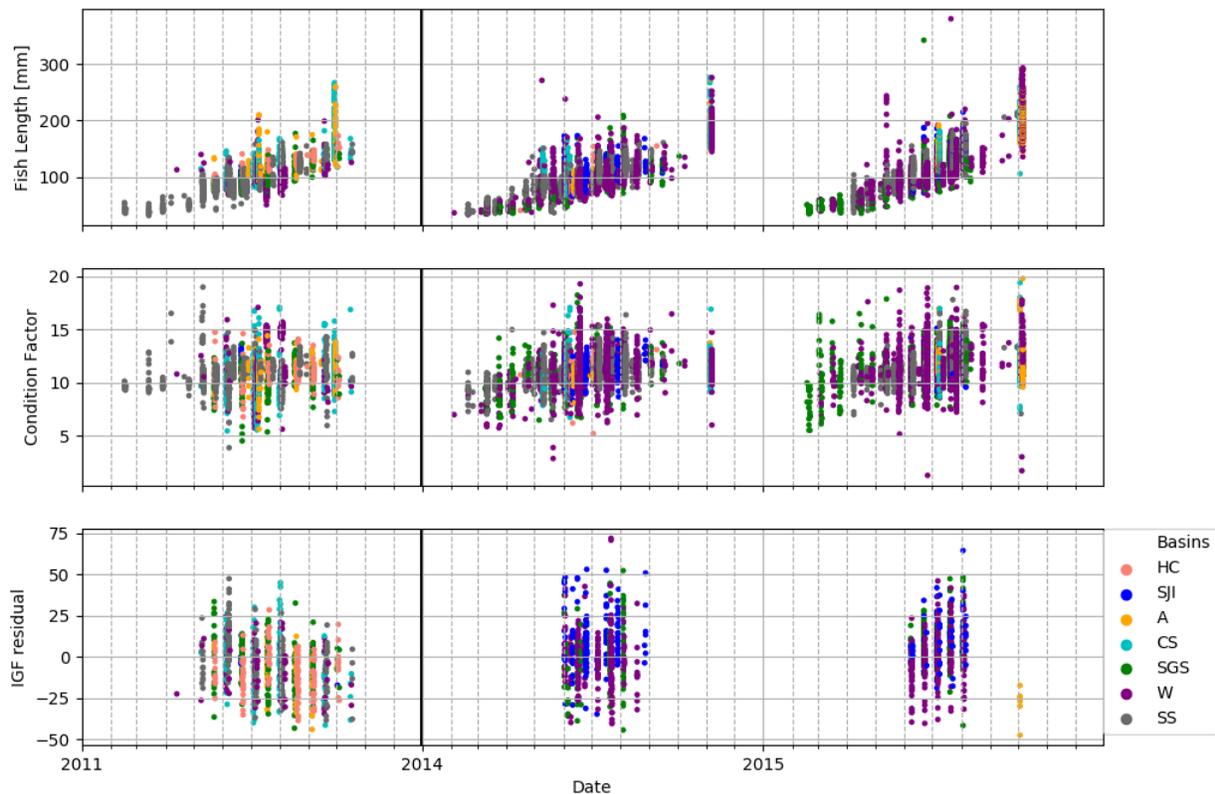


**Figure 9.** Zooplankton partial regressions for chlorophyll biomass and stratification. Panels summarize the role of each model predictor when holding the other predictors fixed. The blue line is the partial regression line of the predictor and shaded blue area is a pointwise 95% confidence band for the fitted values. The dashed pink line is the loess nonparametric-regression of the residuals (gray dots) to indicate departures of the prediction from observed central tendencies.

## Temporal and spatial patterns in fish data

Similar to the pattern observed for temperature, the annual average fish condition was lowest in 2011, intermediate in 2014, and highest in 2015 (Figure 10). However, annual average fish lengths were longest for 2015 (138.7 mm) and shortest for 2014 (108.6 mm); however, this difference may be due to differences in sampling dates within the years. Annual average IGF-residuals were highest in 2014 and lowest in 2011. Monthly averages of both condition factor and fish length were highest in 2015 except for February when 2011 had the highest value. However, comparisons among years and among basins is complicated by data synthesis of multiple sampling efforts: not all basins were sampled in all three years and the number of samples per basin varied each year.

Basin differences in fish length and condition were not consistent over the years but IGF-residuals were lowest in Whidbey Basin and highest in San Juan Islands Basin for all three years (Figure 10). IGF data was only available June-August for Whidbey Basin, San Juan Islands Basin and South Georgia Strait Basin for all three years. Fish length and condition data was available from all basins for all 3 years except in 2015 for Hood Canal Basin. Admiralty Basin had the longest average fish length for all three years and South Sound Basin had the shortest length in 2011 and South Georgia Strait Basin had the shortest length in 2014 and 2015. Average condition was highest in San Juan Islands Basin in 2011 and 2014 but Admiralty Basin had the highest condition in 2015. The basin with the lowest condition varied for each year; in 2011 it was South Georgia Strait, in 2014 Hood Canal, and in 2015 South Sound.



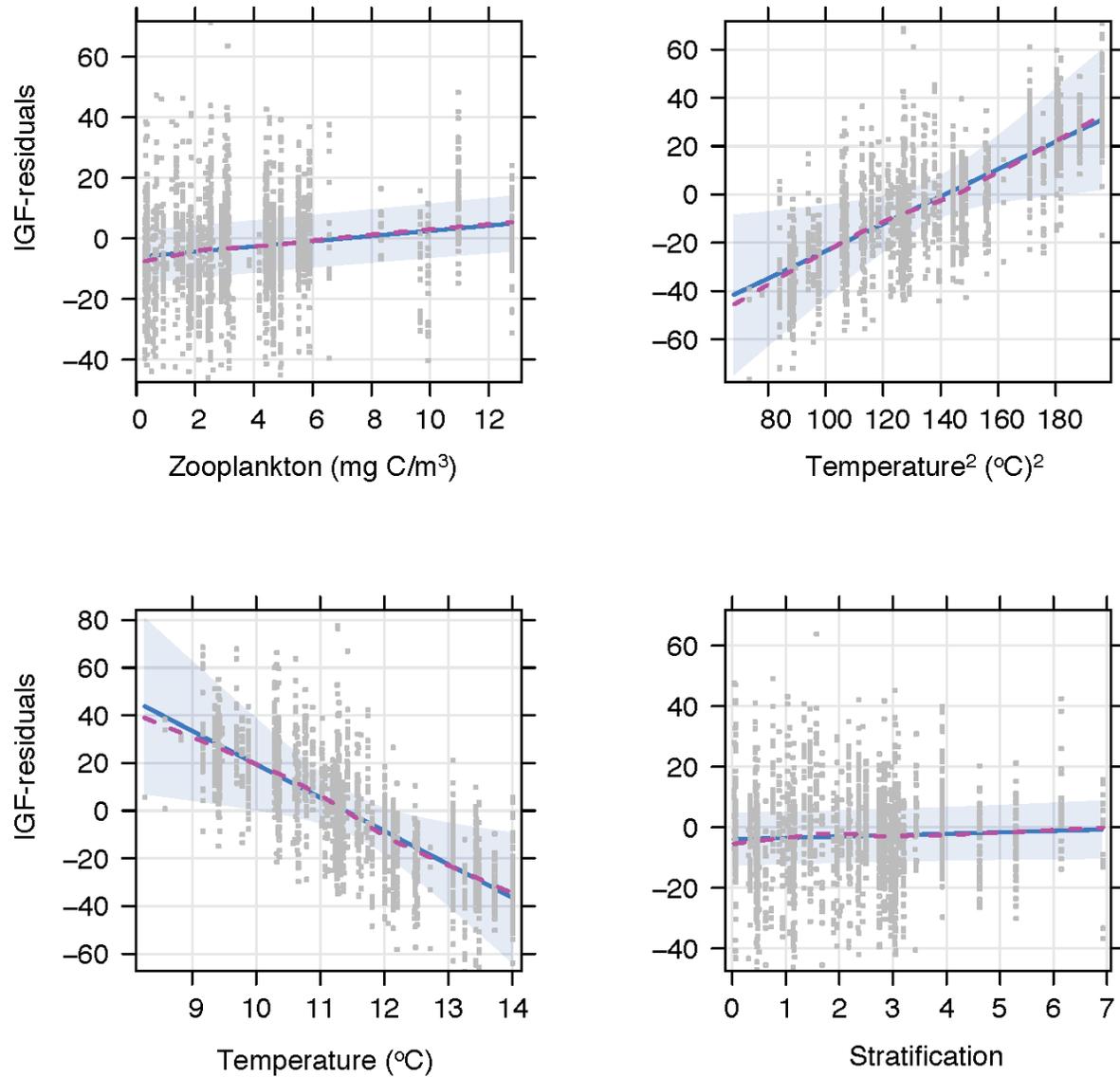
**Figure 10.** Time series for 2011 and 2014-2015 by basin for fish length (top panel), condition factor (middle panel), and IGF hormone residual (bottom panel). Black vertical line indicates a disjoint time interval and separates 2011 from 2014-2015. Basin abbreviations used in the legend are: HC = Hood Canal, SJI = San Juan Islands, A = Admiralty, CS = Central Sound, SGS = South Georgia Strait, W = Whidbey, and SS = South Sound.

## Juvenile Salmon Growth

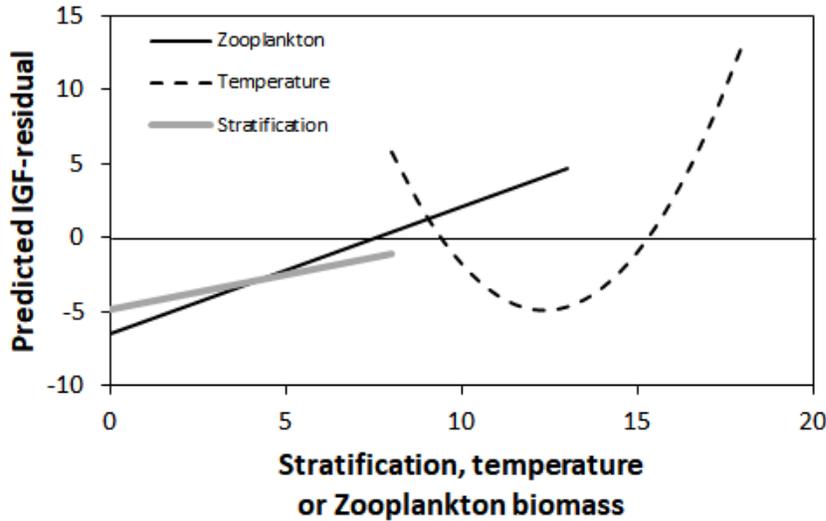
The best model for fish growth based upon IGF-residual was determined by modeling IGF-residuals as a function of water temperature, stratification and zooplankton biomass with basin and gear type as random variables. Year was excluded as a random variable because there wasn't enough data in each basin for all three years. The random variables were modeled with varying intercepts so that the mean and standard deviation of the intercepts were estimated by the model and not assumed to be the same for all basins and/or gear types. The most supported models had basin and gear type as random variables and included at least one quadratic term. A quadratic model is a linear model where the square of a predictor is added as a fixed variable. The addition of squared terms accounts for curvature in the response that can't be resolved with a linear model. The model with temperature, temperature<sup>2</sup>, stratification, and zooplankton biomass performed the best (Table 6). Growth increased linearly as a function of zooplankton biomass and stratification, but quadratic terms produced a concave function of temperature (Fig. 11, 12). Changes in temperature had a much large effect upon IGF-residuals compared to the other two variables. This is illustrated in the partial regression plots in Figure 11, which show the independent relationships of temperature, temperature<sup>2</sup>, zooplankton biomass, (zooplankton biomass)<sup>2</sup>, and stratification on IGF-residuals.

**Table 6.** LMER model selection summary for fish IGF-residuals.

Fixed Variables	Random Variables	AIC	DAIC	R <sup>2</sup>	Sample Size
Zooplankton Temperature Stratification	Gear, Basin	15357.42	2.5	0.33	1875
Temperature Stratification	Gear, Basin	15399.27	44.4	0.40	1875
Temperature Zooplankton	Gear, Basin	15360.74	5.9	0.33	1875
Stratification Zooplankton	Gear, Basin	15361.26	6.4	0.33	1875
Zooplankton + Zooplankton <sup>2</sup> Temperature Stratification	Gear, Basin	15362.58	7.7	0.33	1875
Zooplankton Temperature + Temperature <sup>2</sup> Stratification	Gear, Basin	15354.89	0.0	0.32	1875
Zooplankton Temperature Stratification + Stratification <sup>2</sup>	Gear, Basin	15361.24	6.4	0.33	1875
Zooplankton + Zooplankton <sup>2</sup> Temperature + Temperature <sup>2</sup> Stratification + Stratification <sup>2</sup>	Gear, Basin	15362.53	7.6	0.33	1875
Zooplankton + Zooplankton <sup>2</sup> Temperature + Temperature <sup>2</sup> Stratification	Gear, Basin	15359.03	4.1	0.33	1875
Zooplankton + Zooplankton <sup>2</sup> Temperature Stratification + Stratification <sup>2</sup>	Gear, Basin	15366.40	11.5	0.33	1875
Zooplankton Temperature + Temperature <sup>2</sup> Stratification + Stratification <sup>2</sup>	Gear, Basin	15358.53	3.6	0.32	1875



**Figure 11.** Fish IGF-residuals partial regressions for temperature, stratification and zooplankton biomass. Panels summarize the role of each model predictor when holding the other predictors fixed. The blue line is the partial regression line of the predictor and shaded blue area is a pointwise 95% confidence band for the fitted values. The dashed pink line is the loess nonparametric-regression of the residuals (gray dots) to indicate departures of the prediction from observed central tendencies.



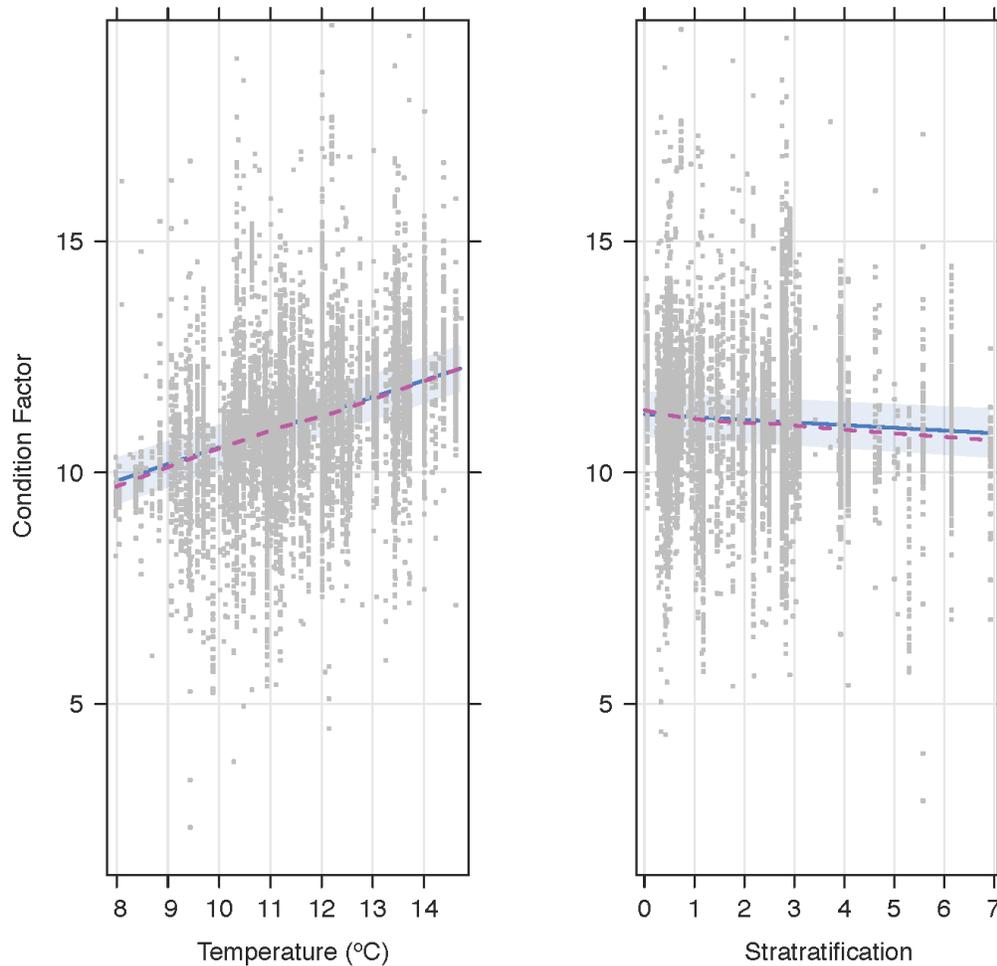
**Figure 12.** Predicted quadratic relationships between IGF-residuals and temperature (solid black line), stratification (solid gray line), or zooplankton biomass (dashed line) predicted by the linear mixed effects model, holding other parameters constant at average levels and varying each independent variable across the range of observed data.

### Juvenile Salmon Condition Factor

The best linear model for condition factor was where condition was a function of water temperature, stratification and zooplankton biomass with basin, year and gear type being used as random variables. The random variables were modeled with varying intercepts so that the mean and standard deviation of the intercepts were estimated by the model and not assumed to be the same for all basins, years and/or gear types. Data from Hood Canal Basin was omitted due to the lack of data in 2015. The strongest models (lowest AIC score and highest  $R^2$ ) had basin nested within year in addition to gear type as random variables. The model with temperature and stratification performed no better (similar  $R^2$ ) when zooplankton biomass was included (Table 7). Fish condition increased as a function of temperature but had an inverse relationship with stratification. Changes in temperature had a larger effect than changes in stratification. This is illustrated in the partial regression plots in Figure 13. Partial regressions show the independent relationships of temperature and stratification on fish condition.

Table 7. LMER model selection summary for fish condition.

Fixed Variables	Random Variables	AIC	DAIC	$R^2$	Sample Size
Zooplankton Temperature Stratification	Gear Type Year/Basin	32660.23	10.5	0.31	9549
Temperature Stratification	Gear Type Basin	32930.31	280.6	0.25	9549
Temperature Stratification	Gear Type Year/Basin	32649.7	0.0	0.31	9549

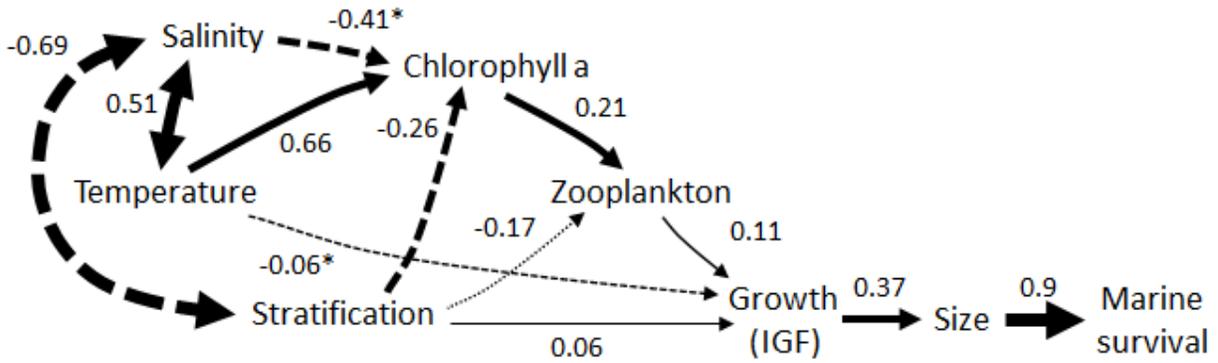


**Figure 13.** Fish condition factor partial regressions for temperature and stratification. Panels summarize the role of each model predictor when holding the other predictors fixed. The blue line is the partial regression line of the predictor and shaded blue area is a pointwise 95% confidence band for the fitted values. The dashed pink line is the loess nonparametric-regression of the residuals (gray dots) to indicate departures of the prediction from observed central tendencies.

### Links to marine survival

While it is premature to relate growth and size to marine survival for the datasets we analyzed due to lack of adult return data for recent years, a longer time series demonstrates a strong positive relationship ( $r = 0.9$ ) between biomass and marine survival of hatchery-origin Chinook salmon (Duffy and Beachamp 2011). This relationship completes the conceptual bottom-up linkages of abiotic and lower trophic metrics to marine survival (Fig. 14).

Here, abiotic processes are linked to marine survival using standardized regression outputs of each set of models of chlorophyll concentration from phytoplankton, zooplankton biomass, and growth. Note that values came from multiple independently derived models and thus have yet to be examined within a unified prediction framework (e.g., structural equation model). Nevertheless, showing relative effect sizes in the context of the conceptual framework elucidates the direction of relationships and the relative magnitude of the effects from one variable to another.



**Figure 14.** Summary of modeling results, using standardized regression coefficients to generate path weightings. Arrows point to assumed causal direction, solid lines represent positive relationships and dashed lines represent negative relationships, and line thickness is proportional to path weightings (thinnest line =  $< 0.2$ , medium line =  $0.2 - 0.5$ , thickest line =  $0.5 - 1$ ). Bidirectional arrows indicate assumed correlations and not causal inferences. Coefficients denoted with \* indicate parameters that are best represented as a nonlinear function, but modeled in this figure using a linear model. The path between size and marine survival is based on model outputs of biomass and marine survival published in Duffy and Beauchamp (2011).

## Discussion

In this document, we have provided evidence for how bottom-up processes can influence marine survival of juvenile Chinook salmon. Over three contrasting years, chlorophyll concentrations systematically varied with environmental metrics (temperature, salinity, and stratification), zooplankton biomass varied with chlorophyll concentration and environmental metrics, growth in turn increased with higher zooplankton biomass, temperature, and stratification, and individual size increased as a function of growth. Combined with previous analyses of size-dependent survival (Duffy and Beauchamp 2011), our results provide strong support that bottom-up forcing can shape marine survival in Chinook salmon. Whether this means that bottom-up mechanisms are responsible for long-term declines in survival over the last 40 years remains to be determined (see below).

We examined two metrics of individual growth processes: 1) individual growth rate as reflected by IGF concentrations and 2) condition factor, which integrates both length and biomass. The relationship between growth and size is complex, as increases in size open up additional feeding opportunities (Brodeur 1991, Keeley and Grant 2001, Chamberlin et al. 2016). Indeed, IGF and condition factor were strongly correlated, requiring us to use the residuals of IGF after accounting for variation in condition. Model comparison of IGF residuals and condition factor suggest we captured the correct causal order: IGF was more sensitive than condition factor to lower trophic patterns such as zooplankton biomass.

### *Growth conditions in recent years*

Our analysis relied on natural variation within multiple years with contrasting environmental conditions. The contrasts are most apparent in 2011 compared to 2015. In 2011, marine conditions were much cooler for a longer period of time (Fig. 4, Appendix) and the spring transition in coastal upwelling was delayed compared to more recent years. This difference translated into lower chlorophyll concentrations as well as delayed zooplankton biomass peaks by at least a month in 2011 compared to 2015. These patterns, combined with warmer temperatures, provided much better conditions for growth and increased body size (as measured by length, biomass or condition factor) in 2015 compared to 2011. The ability to achieve larger sizes allowed juvenile Chinook salmon to become piscivorous earlier in the season (Gamble et al. 2018), and consequently growth began faster (Chamberlin et al. 2016). While it is premature to

infer higher marine survival in 2015 because of poor ocean conditions on the Pacific Coast once salmon emigrated from Puget Sound (Morgan et al. 2019), abiotic and biotic processes in 2015 likely facilitated growth and survival during residence within Puget Sound compared to earlier years.

### ***Linkages between environmental conditions and growth and survival***

Our findings bear strong similarity to the findings of Sobocinski et al. (2018), which examined potential cumulative effects using qualitative network analysis of a complex conceptual model integrating bottom-up processes, trophic cascades, and anthropogenic impacts. Following from a number of findings in the Pacific Northwest (Mantua et al. 1997, Beckman et al. 1999, Scheurell and Williams 2005, Hooff and Peterson 2006, Moore et al. 2008, Rupp et al. 2012, Araujo et al. 2013, Burke et al. 2013), the qualitative network analysis assumed that temperature and stratification increased primary production, phytoplankton increased zooplankton biomass, zooplankton increased growth, and growth and size increased marine survival. Sobocinski et al. (2018) found strong support for bottom-up and anthropogenic effects upon marine survival. With the exception of some of the effects of temperature and stratification, these assumptions were echoed in the results of our quantitative analysis, which detected the same patterns in recent years. Whereas the qualitative network analysis directly integrated biological feedbacks, the quantitative statistical analyses reported here could test predictions based only upon correlations, and hence were sensitive to counterintuitive outcomes resulting from feedbacks (e.g., a negative relationship between zooplankton and chlorophyll concentration arising from grazing). We attempted to reduce the possibility for this error by testing putative causal relationships (e.g., higher growth when zooplankton biomass was higher) using lagged data. That our results largely matched the relationships incorporated into the qualitative network analysis suggests that the constraints we put on the statistical analysis were generally successful in uncovering causal patterns.

The standardized coefficients reported in Figure 14 are useful because they can be multiplied together along particular pathways connecting metric to metric, and multiple pathways added together, to determine the net predicted effects of one metric on another. For example, effects of chlorophyll concentration and zooplankton biomass follow a single direct pathway leading to positive effects on growth, size, and marine survival.

Abiotic metrics are more complicated because of additional possible pathways. The net effect of temperature on marine survival is the sum of the products of the coefficients along six pathways: the effect of temperature directly on growth, zooplankton, and chlorophyll, as well as the pathways through the correlated effects of salinity and stratification. These six paths combine to produce an overall negative effect of temperature upon marine survival. Note however, that the standardized coefficients utilize linear models, and the effect of temperature upon growth was one of the few strongly quadratic relationships uncovered by linear mixed effects models. At higher levels of temperature, the effect of temperature upon growth was positive, so the direct effect of temperature upon growth appears dynamic. Indeed, switching the sign of this one path results in a net benefit of increased temperature on marine survival. Hence, Fig. 14 predicts a negative overall effect of temperature upon marine survival during cooler periods and a positive effect of temperature during warmer periods. These results contrast with findings of growth and survival of Pacific Salmon from Pacific Coastal watersheds – here, cooler marine conditions facilitate better growth and survival (Beckman et al. 1999, Burke et al. 2013) by facilitating the presence of fatty acid-rich boreal copepods (Hooff and Peterson 2006). These conditions do not apply within the Sound in that cooler periods do not result in an influx of boreal copepods (Keister et al. 2017), and may help 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).

We also found linkages between marine survival and salinity and stratification. Salinity also has six paths to marine survival, two of which pass through correlated effects of temperature. These correlations also

influenced the sign of the overall effect of salinity upon marine survival. Like temperature, the overall effect of salinity upon marine survival was negative during cooler time periods and positive during warmer periods. As shown in Fig. 8, the best model predicting chlorophyll concentration revealed a non-linear pattern as a function of salinity. The overall effect of salinity upon marine survival was sensitive to the direction of the effect of salinity upon chlorophyll concentrations at relatively low salinities, but low salinity did not change the correlated effects of temperature upon marine survival.

In contrast, predicted responses to stratification were least sensitive to variation in temperature or salinity. The overall effect of stratification upon marine survival was positive, regardless of variation in the other two metrics. These results depend in part upon a positive effect of stratification on residual IGF, a finding not directly predictable from trophic relationships since the observed effects of stratification upon chlorophyll concentration and zooplankton biomass were negative (Fig. 14). Two explanations for this positive effect are that stratification facilitates osmotic transition or migration orientation. As an anadromous species, Chinook salmon must switch their osmoregulation to cope with changes in salinity of their aquatic environment. While salmon are capable of switching osmoregulation relatively quickly (within 24 hours, Hasegawa et al. 1987), they incur an energetic cost in this transition (Morgan and Iwama 1991). It is possible that stratified conditions facilitate osmotic transition and reduce its energetic burdens (Iwata and Komatsu 1984), although the levels of salinity observed in Puget Sound were much higher than reported in Iwata Komatsu (1984). It has also been suggested that juvenile salmon attend to salinity gradients to improve orientation to the ocean and that surface waters may help salmon sample these gradients (McInerney 1964).

Three nonlinear linkages also deserve special attention since these findings have the potential to mediate bottom-up processes in complex ways. The first relationship is a unimodal relationship between chlorophyll concentrations and temperature. The prediction from this relationship is that chlorophyll concentrations will decline as a function of temperature when temperature surpasses about 20 degrees, a value that has not been observed in marine waters of Puget Sound. Hence, the overall relationship for observed data is a positive effect of temperature. The second nonlinearity is a unimodal relationship between chlorophyll concentrations and salinity. These findings make sense in light of hypothesized optimal windows of productivity in the Salish Sea (Gargett 1990), although the lowest observed levels of salinity were rarely observed except near large river deltas. The third finding was higher IGF levels at both the lowest and highest levels of temperature. These findings are counterintuitive with bioenergetic models (e.g., Gamble 2018) in that growth as a function of temperature is normally a unimodal relationship with lower growth at the lowest and highest levels of temperature (Beauchamp 2009). As the patterns we observed between IGF and temperature were quite strong (Fig. 11), we suspect the inverted pattern may be the consequence of additional unexamined factors influencing growth. Most notably, temperature may have modulated presence of forage fish prey, possibly resulting in times and places where forage fish served as prey at both lower and higher temperatures. For example, 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.

### ***Trophic linkages and long-term changes in marine survival***

A variety of hypotheses have been raised regarding how bottom-up trophic dynamics may drive long-term declines in marine survival. All of them posit that conditions favoring growth have changed since the 1980s. Chief among these hypotheses are that 1) abiotic processes have shifted in unfavorable directions, 2) food supply has declined independent of abiotic conditions or 3) the timing of salmon residence or prey production have become temporally mismatched, or 4) environmental conditions are now favoring production of harmful algal blooms that are detrimental to salmon. Our study does not touch on either

temporal variation or harmful algal blooms, so the latter two of these hypotheses cannot directly be tested.

While our study lacks retrospective data to directly test the first two hypotheses, the pathways illustrated in Fig. 14 provide a basis for comparative predictions. Much in the same way Sobocinski et al. (2018) used perturbations in a qualitative network analysis framework to test for causes of declines in marine survival, theoretical perturbations using the path diagram in Figure 14 can provide a means to determine whether some potential causes are more or less likely. Of the metrics incorporated into Fig. 14, long-term metrics spanning the time period of strong declines in marine survival (Zimmerman et al. 2015, Ruff et al. 2017) and adult returns of Chinook salmon (Ford et al. 2011) are limited to abiotic variables. Long-term observations of these variables indicate gradual increases in temperature and freshening of coastal marine waters (Cummins and Masson 2014), neither of which strongly changed during the time period of the collapse in marine survival. In addition, declines in marine survival have been linked to changes in winds (Beamish et al. 2010), although re-analysis has called this into question (Wan et al. 2010, Banas et al. in prep.). Banas et al. (in prep) proposed that a more likely pathway for long-term changes in productivity may be through changes in cloud cover. All these factors are predicted to influence primary production, and hindcasts of chlorophyll concentrations suggest that standing stock biomass of phytoplankton increased during the period of 1980-2005, the same time period during which marine survival declined (Greene et al. submitted).

Of these factors, the pathways in Figure 14 indicate that minor increases in temperature might be expected to decrease growth and consequently marine survival if the temperature-growth relationship followed Figure 12 and temperature increases were minor. However, temperature increases above 12 degrees should result in an increase in marine survival. While Figure 14 also predicts marine survival declines are associated with decreased chlorophyll concentrations, hindcasts predicted increased chlorophyll concentrations during the time period of declines (Greene et al. submitted). This pattern possibly indicates a long-term decline in zooplankton biomass, the trophic intermediary between phytoplankton and marine survival. An additional unexamined trophic relationship is that between forage fish and growth, and long-term monitoring suggest declines in both adult (Siple and Francis 2016) and juvenile forage fish (Greene et al. 2015) in much of Puget Sound.

### ***Conclusions and next steps***

While our study documents strong bottom-up trophic relationships in recent years, how these have interacted to potentially produce declines in marine survival remains a complex question with multiple uncertainties. Additional effort to integrate additional factors related to primary and secondary production such as nutrients may improve certainty of abiotic influences on bottom-up dynamics. Likewise, integrating additional metrics such as forage fish abundance may improve understanding of growth and marine survival in current years. Further utilization of additional years of marine survival in ecosystem indicators contexts will improve our understanding of how marine survival tracks metrics related to bottom-up processes. In addition, integration of these results with mechanistic ecosystem models (Fulton et al. 2011) can help verify whether statistical patterns accurately reflect more complex deterministic ecosystem interactions than currently modeled in the simplified ecosystem framework represented in Figure 14. However, understanding putative bottom-up driven causes of long-term declines will likely require additional analysis of historical datasets such as body size and zooplankton biomass where available.

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## Appendix

### Summary of large-scale climate drivers, based on PSEMP reports for 2011, 2014 and 2015.

	2011	2014	2015
<b>El Niño/Southern Oscillation</b>	Strong La Niña for most of season	Neutral	Strong El Niño
<b>Pacific Decadal Oscillation</b>	Negative	Positive, strengthening over the year	Strongly positive throughout the year
<b>North Pacific Gyre Oscillation</b>	Positive	Negative starting in 2013	Strongly negative
<b>Upwelling</b>	Below average upwelling conditions	Average upwelling conditions, shift to stronger than average downwelling started in Sept	May and June stronger than average upwelling, average conditions rest of summer
<b>Spring transition</b>	May	May	May
<b>Fall transition</b>	September	September	October
<b>Precipitation and river flow</b>	Much higher than average precipitation in spring (March, April, May); below average in Aug-Oct  Higher than average river flows in Puget Sound and Fraser River	Above average precipitation with high variability  Above average river flows in spring and fall	Below average precipitation April through July  Snowpack deficit, resulting in earlier freshet and extremely below average river flows throughout summer
<b>Marine heat wave</b>	Absent	MHW emerged in winter of 2013-2014; evident throughout 2014. Upwelling kept sea temperatures near normal, then warmer by fall	Peak conditions throughout the year with strong sea temperature warm anomalies