Climate impacts on patterns of phytoplankton production in Puget Sound, USA: A model synthesis and narrowing of hypotheses


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Abstract

1 Introduction

There are many simultaneous pathways by which regional climate can drive interannual or longer-term variation in primary production in coastal and estuarine waters. Changes in riverflow volume and timing, deep inputs from the open ocean, wind patterns, surface heating, and cloud cover and hence light availability—a partial list—all affect primary production by distinct mechanisms. These climate-linked environmental factors are often highly correlated in historical time series, but may not maintain these correlations into the future as the climate changes; as a result, statistical approaches struggle to identify the specific mechanisms driving historical variability, or the possibly distinct set of mechanisms that will drive future change in marine food webs.

The gold standards in this type of research are long multivariate time series with good spatial coverage (e.g. CalCOFI in Southern California) and coupled hydrodynamic-biogeochemical models driven by regional climate downscalings, well-validated on a range of system levels and scales. These comprehensive datasets generally do not exist, and multi-decadal regional simulations are so cumbersome that even when they do exist, there are invariably system levels at which the key mechanisms have never been directly verified and uncertainty has not been systematically examined. An alternate use of models—which we suggest deserves more articulation and recognition in global change biology—is as a means of rejecting hypotheses rather than promoting them: that is, as a means of ranking and winnowing a tangle of competing mechanisms, as a guide for further empirical research.

This study consists of a synthesis of results from hydrodynamically simple (1D) and detailed (3D) models of Puget Sound, USA and the greater Salish
Sea, organized around an effort to reduce a conceptual diagram of possible climate-impact pathways from spaghetti (Fig. 1) to a focused research agenda. Primary production affects countless aspects of the marine ecosystem but we have organized our analysis around two larger concerns.

First, chinook, steelhead, and coho salmon runs in the Salish Sea have all experienced tenfold declines in marine survival over the past 30 years (Zimmerman et al., 2015), while chinook and coho on the outer Washington and British Columbia coasts have not shown any matching trend. Active hypotheses that might explain this long-term decline are extremely diverse, encompassing increases in predators, declines in forage fish, changes in physical habitat, chemical pollution, and many other factors; but within this field of inquiry is the fundamental question of whether bottom-up changes beginning at the base of the marine food web could be responsible. Tracing changes in phytoplankton production step-by-step through the long trophic chains that support salmon is well beyond the scope of this study, but with existing oceanographic and earth-system models we are able to begin to evaluate potential past and future trends in i) annual primary production and ii) the timing of the spring bloom. We also analyze patterns in iii) spring and summer phytoplankton concentrations, motivated by a non-trophic hypothesis: the possibility that dense phytoplankton blooms during critical outmigration times change the underwater light field sufficiently to disrupt visual search.

Second, harmful blooms of the dinoflagellate *Alexandrium catenella*, which produces powerful neurotoxins that lead to paralytic shellfish poisoning (PSP), have increased in Puget Sound over the past half-century (Moore et al., 2011). The seasonal/spatial window of opportunity for *A. catenella* harmful algal blooms (HABs) has been linked to high water temperatures, and this window has expanded over recent decades and is projected to expand further (Moore et al., 2011, 2015). Within the window of opportunity, the occurrence of *Alexandrium* blooms is likely tied to local oceanography via the transport and dispersion of overwintering cysts (Horner et al., 2011)—dynamics that have provided significant predictive ability elsewhere (McGillicuddy et al., 2011)—but also tied to phytoplankton community dynamics and succession. For our purposes, the phenomenology of the spring bloom (ii), as well as iv) the occurrence or non-occurrence of strong nutrient limitation in summer, serve as a bridge from Puget Sound oceanography and regional climate to the ecological dimensions of *Alexandrium* HABs, which a lack of detailed, sustained observations has to date left in the realm of speculation (Moore et al., 2015).

Ultimately we would want to evaluate spatial variation in metrics –iv) in detail, but for this study we confine ourselves to a typical location in central Main Basin (Fig. 2), insofar as there is any typical location in this complex inland sea.

### 1.1 Initial conceptual model

Our a-priori conceptual diagram (Fig. 1) does not include every possible route from regional climate to primary production, but rather a pre-selection based
Figure 1: Potential mechanistic pathways from regional climate variability to primary production in the main stem of Puget Sound, away from areas of localized, strong terrestrial influence. Each arrow \((X \rightarrow Y)\) can be read as “Interannual and longer-term variability in \(X\) causes interannual variability and longer-term in \(Y\)”: shorter timescales of variation are not included. Patterns of primary production are represented by four metrics (green shaded box) which have been hypothesized to drive two types of further ecological effects (right). Other pathways of influence on salmon marine survival and *Alexandrium* HABs, e.g. direct temperature effects on *Alexandrium* growth (Moore et al., 2015), are omitted. Compare Fig. 20.
Figure 2: Map of study area. —Washington Department of Ecology (DOE) long-term monitoring station PSB003 (black square), near West Point, is the focus of the analysis.
on past research in this system (Winter et al., 1975; Newton and Van Voorhis, 2002; Banas et al., 2014; Moore et al., 2015). In general, primary production is regulated by light availability (pathway L) and nutrient availability (S). In addition, temperature (H) affects both the maximum growth rate of the phytoplankton community and the rate of losses to microzooplankton and other grazers. Light limitation is regulated by incoming photosynthetically available radiation (PAR) and hence cloud cover (pathway A, D); the per-meter underwater light attenuation, which varies strongly with watershed inputs (B); and also vertical mixing and advection (K, O), which control the depth range over which phytoplankton cells are dispersed and hence the light level they experience. Nutrient flux into the euphotic zone is also controlled by vertical mixing and advection (R, R), and potentially by changes in the concentration of nutrients in incoming ocean water (T, U). In other estuaries, changes in river-derived nutrients would be of first-order importance as well, but nutrients in Puget Sound are overwhelmingly ocean-derived (Mackas and Harrison, 1997; Mohamedali et al., 2011). Watershed-derived nutrients have been found to have notable effects on Puget Sound water quality (Khangaonkar et al., 2019) but these effects are spatially limited (Banas et al., 2014), and the conceptual model and analysis in this study are designed to describe the main stem of Main Basin, away from localised areas of more intense river influence.

Along-channel gradients in nutrients and phytoplankton concentration are relatively weak in Main Basin (Winter et al., 1975, analysis below) and this invites us to consider primary production in a 1-D, single-water-column framework, a modified version of a classic open-ocean scenario. Seasonally varying stratification and mixing are the crucial physical controls on primary production in this classic, mid-latitude framework, with mixing regulating light limitation in early spring (K) and hence the timing of bloom initiation, and regulating nutrient availability through the late spring and summer (P), once the phytoplankton have drawn down the initial stock of euphotic-zone nutrients left over from winter. Near-surface mixing is driven in part by wind stress (E), and in part (in shallow areas especially) by the tides; we have assumed that the tides do not respond significantly to climate change and neglected them in our schematic, which is meant to represent mechanisms of variability and change on annual to decadal scales. The intensity of mixing that results from a given input of wind or tidal energy is strongly regulated by stratification, and conversely stratification records a history of the amount of mixing that has recently occurred (J). Since measurements of stratification are far easier and far more common than measurements of turbulent mixing, the literature often elides the distinction and refers to “the effect of stratification on primary production”; but in a highly dynamic, advective environment like an estuary, the distinction between “mixed” water and “mixing” water—that is, low stratification and high turbulent mixing intensity—is potentially very important (Collins et al., 2009; Franks, 2015). Riverflow affects estuarine hydrography and energetics through a complex set of feedbacks, but in a first approximation, it drives changes in stratification directly (I), and changes in mixing only indirectly (I \rightarrow J). Surface heating can also affect stratification (F), although this effect is usually weaker.
than river/salinity effects in temperate estuaries.

In Main Basin as in other estuaries, the density contrast between river and ocean inputs drives an “in–up–out” overturning or estuarine circulation (M, N, Q), which regulates the system’s overall residence time. The “up” branch of this circulation is the mechanism of mean vertical advection mentioned above, a potentially important contributor to near-surface nutrients (R). The inclusion of upward advection reflecting the system-scale circulation and residence time is the crucial addition that turns a generic water-column model into a estuarine water column (Winter et al., 1975; Collins et al., 2009). The along-channel component of the estuarine circulation also needs to be included in tracer budgets if along-channel tracer gradients are large, although we find that for Main Basin chlorophyll and nitrate they are not (Sec. 2.3.1), and care must be taken to preserve mass conservation in tracer budgets in any case.

The aim of this study is to compare the strength of the many interwoven pathways in this conceptual model, in a general, scaling sense rather than a detailed, scenario-specific sense, and produce a simplified conceptual model that eliminates the second-order factors that are overwhelmed by other mechanisms on interannual and longer timescales. This requires associating a scale of variation with each atmospheric, watershed, and oceanic driver (Fig. 1, blue), and a sensitivity with each mechanistic link (arrows). Estimates of these quantities were assembled from a family of recent model studies that, together, more or less span the timescales and levels of physical and biological process detail required. The results suggest specific research agendas for future oceanographic, atmospheric, and hydrological modelling in Puget Sound and its watershed.

2 Methods

2.1 Observations

**In situ time series** Nutrients and biomass Monthly sampling at Washington Department of Ecology (DOE) long-term monitoring station PSB003 provided core time series of temperature, salinity, chlorophyll, nitrate and ammonium at our study site, at approximately monthly resolution. Chlorophyll estimates are from calibrated fluorometer profiles at 0.5 m resolution, while, nitrate and ammonium concentrations are from bottle samples, generally at 1, 10 and 30 meter depth (Fig. 3). In our analysis, near-surface temperature $T_{20}$ is defined as 0–20 m average of approximately monthly observations from PSB003, 1999–2017 (Fig. 4). Density stratification $\delta \rho$ is defined as the difference between 5–20 m average density and 0–5 m average density.

**Riverflow** Time series of riverflow $Q_r$ (Fig. 5) were derived from USGS gauge data combined with corrections for gauged/ungauged watershed area, as in the setup of the LiveOcean model described below. $Q_r$ is defined as the sum of flows from four rivers that enter Puget Sound up-estuary from the study location (Deschutes, Nisqually, Puyallup and Green), as well as the Cedar, Sno-
Figure 3: Chlorophyll, nitrate, and ammonium data from Washington Department of Ecology station PSB003 in central Main Basin. Approximately 160 profiles over 17 years for Chlorophyll and 130 profiles over 12 years for nitrate and ammonium are shown.

Figure 4: Annual surface temperature from monthly observations 1999–2018 showed averaged for the spring and the summer season.
Figure 5: Total riverflow from the eight Puget Sound rivers included in the analysis (see text), shown as (top) 10-day averages April–September of individual years, and (bottom) annual averages 1964–present.

### 2.2 Models

Past and new analysis of six models were synthesized in this study (Table 1).

**LiveOcean** is a coupled physical-biogeochemical forecast model for the Salish Sea and Pacific Northwest outer coast (Fig. 6, built using the Regional Ocean Modeling System (ROMS). It has produced continuous 3 d forecasts since 2013, with a switch to much higher resolution (500 m) in the Salish Sea in 2017.
Table 1: Ocean and atmospheric models used in this study.

<table>
<thead>
<tr>
<th>Model</th>
<th>Domain</th>
<th>Type</th>
<th>Time period</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>LiveOcean</td>
<td>Coastal ocean + Salish Sea</td>
<td>3D</td>
<td>2017–2019</td>
<td></td>
</tr>
<tr>
<td>PS-1D</td>
<td>Salish Sea</td>
<td>1D</td>
<td>representative seasonal cycle</td>
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In this study we use the archived forecasts from 2017–2018 as a de facto hindcast. LiveOcean is forced by the global ocean model HYCOM on its outer boundary, daily flow estimates for 45 rivers based on USGS gauge data, and high-resolution atmospheric forcing from a WRF (Weather Research and Forecasting) model run by the UW Mesoscale Analysis and Forecasting Group. *Davis et al.* (2014) describes the model’s plankton dynamics in detail, including parameterization and validation using a variety of observations from the outer coast. *Siedlecki et al.* (2015) describes the dissolved-oxygen component.

Two years of hourly physical variables were extracted from LiveOcean along an east–west section line close to PSB003 (Fig. 2). All data were tidally averaged using a Godin filter and subsampled into daily values, and horizontally averaged. Vertical diffusivity $\kappa_v$ was averaged over the top 20 m, and stratification $\delta \rho$ was defined over the top 20 m as for DOE observations (Fig. 16). This depth range was chosen to isolate processes relevant to phytoplankton growth. Coordinated time series of three driving variables were also defined: wind stress $\tau$ at the same section line, rms tidal velocity $u_T$, and riverflow $Q_r$ from the USGS observations described above.

LiveOcean, and the MoSSea model of Puget Sound which preceeded it (*Sutherland et al.*, 2011), have both been used to quantify the estuarine exchange flow in Puget Sound, although never on the interannual timescale of greatest interest here. Results to date from an unpublished analysis of daily variation in exchange volume flux over 2017 (MacCready et al., in prep.) indicate that the classic theories of estuarine circulation, which would suggest useful scaling relationships between riverflow and the exchange flow, simply do not apply: tidally averaged volume flux through Admirality Inlet does not increase during periods of increased riverflow, but in fact decreases slightly. This
volume flux does show a significant correlation with the along-channel density gradient \( d\rho/dx \), its proximate driver (not shown). However, we speculate that \( d\rho/dx \) is fundamentally controlled not by total riverflow in Puget Sound (where the largest sources of freshwater are distributed spatially and the largest of all, the Fraser River, in fact enters from the “ocean” end), but rather by gradients in river influence, which are likely modulated by wind as well as by the rivers themselves. Untangling these effects is beyond the scope of this report, and so we treat the exchange flow as an independent environmental driver in its own right, presumably linked strongly to hydrological and atmospheric drivers, but by patterns we cannot presently resolve. LiveOcean results from 2017 are used to set an upper limit on the interannual variability of the seasonally-averaged exchange flow, for comparison with other drivers.

**ROMS Cascadia** is an antecedent to LiveOcean, a hindcast model that resolves outer-coast physics and biogeochemistry at 1.5 km resolution over the continental shelf and more coarsely offshore, and includes Salish Sea physics—not biogeochemistry—also at 1.5 km resolution, significantly coarser than the 2017–version of LiveOcean used here. *Giddings et al.* (2014) described and validated the model physics for 2004–2007 and *Stone et al.* (2018) subsequently described interannual variation in shelf and slope waters using a 2003–2009 hindcast.

**NNRP/WRF** is a regional hindcast of weather and climate, 1950–2010. It was constructed by downscaling the global, course-scale atmospheric NCAR/NCEP Reanalysis (NNRP) with the Weather Research and Forecasting (WRF)
model, as described by Dutièere et al. (2011).

Daily values of wind stress over Main Basin, 1950–2010, were calculated from wind speed at 13 grid points in NNRP/WRF, converted to wind stress following Large and Pond (1981) (Fig. 9). To validate these model results, we compared the wind speed time series with data from the SeaTac Airport station (Fig. 8). A step change in the SeaTac observations is visible at the end of the 1990s, likely the result of a change in the anemometer position (Wan et al. (2010)). After the step change, NNRP/WRF and SeaTac observations show similar variations.

Daily value of PAR values over Main Basin, 1950–2010, were calculated as 43% of downward shortwave flux at the same 13 grid points in NNRP/WRF. The time series of PAR is well-correlated with sunrise-to-sunset average cloudiness from the SeaTac Airport station, 1965–1996 (Fig. 7).

CCSM3/WRF/ROMS is a regional climate–ocean projection, constructed by downscaling the global CCSM3-A1B model through WRF, and then using this, along with hydrological projections for Puget Sound rivers and the Fraser River, to drive a variant of the ROMS Cascadia model. Moore et al. (2015) describe a projection for the 2040s made using this coupled system, in comparison with a “present-day” (1988) reference case, in the context of potential climate impacts on Alexandrium HABs. The major forcing changes in this scenario can be summarized as increased air temperatures, a shift toward earlier riverflow, and intensified summer upwelling, all close to the mean of the CMIP3 (IPCC AR4) ensemble, with offshore oceanic boundary conditions held constant. The responses of the marine system to this scenario (Moore et al., 2015) are summarized in Table 2.

SOG is a 1D physical–biogeochemical model for the southern Strait of Georgia designed for hindcasting and prediction of the timing of the spring phytoplankton bloom, as described in detail by Collins et al. (2009) and Allen and Wolfe (2013). Here it provides independent estimates of four sensitivities calculated from LiveOcean and PS-1D (albeit in the Strait of Georgia, not Main Basin):
Figure 8: Comparison between NNRP/WRF model output and SeaTac observations of wind stress. Left plot shows both daily time series. Right plot shows SeaTac observation versus WRF/NNRP model output.

Figure 9: $\log_{10}$ wind stress daily output from WRF/NNRP model. (top) 10 d averages, 1950–2010, superimposed as a function of yearday. (bottom) Spring (Apr–Jun) and summer (Jul–Sep) averages.
Variable | Change | Season
---|---|---
Wind speed | ± 0.7 m s\(^{-1}\) | spring–summer
Stratification | + 20% | spring
| ~ 0 | summer
Near-surface temperature | + 2 °C | spring
| + 3 °C | summer

Table 2: Estimates of future trends in environmental drivers, from a downscaled climate projection (CCSM3/WRF) coupled to ROMS Cascadia as described in Moore et al. (2015). Trends are reported as the absolute change between 2040s projections and a baseline circa 1990.

the sensitivity of mixing to wind stress, from daily values in 2005 and 2007 hindcasts; the sensitivity of spring bloom date to temperature, as calculated by Allen and Wolfe (2013) from a 1968–2010 hindcast; sensitivity of bloom date to light, from Dec–Mar average cloud cover (Allen and Wolfe, 2013) and the approximation that as cloud cover varies between 0 and 100%, daily-average PAR varies by ~ 60 W m\(^{-2}\); and the sensitivity of bloom date to mixing, from the sensitivity of bloom date to Dec–Mar average wind stress combined with the mixing–wind relationship already mentioned.

PS-1D is a 1D model designed as a quick-running “sandbox” in which to explore the parameter space of the LiveOcean biogeochemical model (Davis et al., 2014); determine how its parameterization needs to be changed to correctly represent Main Basin as opposed to the offshore waters for which it was originally developed; and perform the numerical experiments which allow us to define scales of sensitivity of each primary-production metric to each environmental driver (Fig. 1). This model has not been previously described in the literature and so we explain it at a medium level of detail below. The full description is expected to appear in Nguyen (2020).

2.3 The PS-1D model

2.3.1 Physical setup

The physical “sandbox” of the PS-1D model is designed to reproduce a representative seasonal cycle at one location in central Main Basin, as a base case around which we can perform experiments addressing the sensitivity of phytoplankton dynamics to environmental conditions and to the assumed biological parameters. These analyses have more the flavor of laboratory or mesocosm experiments than historical analysis—doubling the turbulent mixing, halving the incoming light, etc.—and do not attempt to resolve event-scale fluctuations, for which a 1D model would likely be fundamentally inappropriate.

In this 1D model, a water column of ~ 200 meter depth was divided into thirty layers, with thinner layers near the surface and thicker layers at the bottom. Within this grid, the model consists of a set of coupled ordinary differential
Figure 10: Schematic of physical processes in Main Basin. The study site lies midway between MB_M and MB_S, which define the span used to estimate along-channel gradients.

equations, each one a budget for one biogeochemical tracer (see Sec. 2.3.2).

**Advection** The upward velocity $w_{adv}$ representing the estuarine exchange flow depends, because of mass conservation, on the along-channel gradient in the lower-layer incoming volume flux (Fig. 10). The mid-water-column maximum in $w_{adv}$ (Fig. 11) was estimated from the MoSSea model (Sutherland et al., 2011) as $\Delta Q \ L^{-1} \ B^{-1}$, where $\Delta Q = 3500 \ m^3 \ s^{-1}$ is the difference in lower-layer volume fluxes between MB_M and MB_S, $L = 26$ km is the distance between the two sections, and $B = 5$ km is the channel width. In tuning and sensitivity experiments below, the shape of the vertical profile of $w_{adv}$ was kept constant and multiplied by a factor representing increases and decreases in the exchange flow.

Observations of chlorophyll, nitrate and ammonium of PRISM stations along Puget Sound (black solid points in Fig. 2) in June and December showed negligible gradients in Main Basin (around $10^{-3}$ at PSB003: not shown). The small gradients are consistent with the conclusion of Winter et al. (1975) that horizontal advection is not an important term in the budgets of these tracers in Main Basin.

**Vertical mixing** The vertical diffusivity for tracers $\kappa_v$ was likewise taken from the 2006 hindcast of the MoSSea model. A climatological vertical profile was constructed by taking the cross-sectional average diffusivity as a function of depth (Fig. 12, black dots) and then averaging in time (blue line). As analysed further below using LiveOcean output, monthly or seasonal variation in mixing appears to be secondary to shorter-timescale variation, and so we have held mixing constant in our representative seasonal cycle. As for vertical advection, experiments in which the intensity of mixing is varied multiply this mean profile by a constant.

**Light** Surface light in PS-1D is taken directly from the regional weather model used to drive MoSSea. Photosynthetically active radiation (PAR) is assumed to be 43% of downward shortwave radiation. PAR at a given depth, $E(z)$, is
Figure 11: Vertical velocity profile in the base case of PS-1D.

Figure 12: Vertical profiles of the vertical diffusivity for tracers, cross-sectionally averaged in one year of 3D model output (MoSSea, 2006: Sutherland et al. (2011)). Black dots show daily values, grouped by month, and the blue line (repeated across panels) is the climatological profile used in the PS-1D base case.
modelled using three light-attenuation coefficients as

$$E(z) = E_0 \exp \left[ - (\text{att}_{bg} z + \text{att}_{fw} \int_z^0 (32 - S(z'))dz' + \text{att}_P \int_z^0 P(z')dz') \right]$$  \hspace{1cm} (1)

where $E_0$ is PAR at the surface ($z = 0$). The coefficient $\text{att}_{bg}$ is the per-meter attenuation by pure seawater; $\text{att}_{fw}$ represents attenuation by particles and dissolved organic matter associated with freshwater (mathematically speaking, attenuation that is correlated with salinity deficits); and $\text{att}_P$ represents light attenuation by the modelled phytoplankton themselves, i.e., self-shading.

These are crucial model parameters, and among the most likely to vary between estuarine and coastal environments. Prior to running the model, historical Puget Sound observations were used to estimate these coefficients and determine if they substantially different from the values found by Davis et al. (2014) for the Washington–Oregon shelf. Euphotic-zone depths from three years of monthly transmissometer profiles (Newton and Van Voorhis, 2002) agreed well with Secchi Disk depths, which makes euphotic-zone depths a good source to estimate light fields. A linear regression of light attenuation (back-calculated from euphotic depth) and chlorophyll, omitting winter samples, showed high correlation ($R^2 = 0.7$) in the Newton and Van Voorhis (2002) dataset. However, light attenuation is commonly expected to depend on constituents of freshwater as well, and so we used the full record of 19 years (1999 - 2017) DOE sampling at PSB003, which provides coordinated observations of beam attenuation, chlorophyll, salinity, and turbidity. An empirical relationship from Shannon (1975) was used to convert beam attenuation to light attenuation. Turbidity and salinity are highly correlated in the PSB003 dataset, and a linear regression for light attenuation as a function of chlorophyll and salinity (as in Eq. (1)) showed high correlation ($R^2 = 0.64$) and tight bounds on coefficients.

The estimate of light attenuation by chlorophyll from this linear model (0.023) was consistent with that derived from the Newton and Van Voorhis (2002) three-year dataset described previously (0.026). However, a regression to the PSB003 data omitting salinity explained almost as much variance as the model with salinity. This suggests that salinity or freshwater fraction is not an effective proxy for light attenuation by river-derived material in Puget Sound, possibly because freshwater in Puget Sound originates in such a diversity of watersheds (Cuo et al., 2009; Banas et al., 2014). Thus in PS-1D, $\text{att}_{fw}$ is set to 0, not to imply that river inputs do not cause light attenuation, but to indicate that we lack a useful predictor of this effect. Instead, the mean effect of watershed-derived turbidity and dissolved organic matter is captured in the background light attenuation $\text{att}_{bg}$, which is far higher than attenuation by undiluted seawater in the Davis et al. (2014) model currently used in LiveOcean (Table 3).

2.3.2 Phytoplankton dynamics

The biogeochemical model in PS-1D is a six-compartment nitrogen budget, nitrate ($\text{NO}_3$), ammonium ($\text{NH}_4$), phytoplankton biomass ($P$), microzooplankton
biomass (Z), and small and large detritus (SD, LD). All six stocks are measured in mmol nitrogen m\(^{-3}\) = µM N; we assume a chlorophyll:nitrogen ratio of 2.5 (mg chl) (mmol N)\(^{-1}\) to compare the model with observations. Apart from dividing the dissolved inorganic nutrient pool into NO\(_3\) and NH\(_4\) fractions (to match available observations), the model structure and functional forms closely follow Davis et al. (2014), who provide a thorough description, rationale, and validation against nutrient, biomass, and growth- and grazing-rate data from the outer coast. Only the phytoplankton component is described below.

Phytoplankton growth rate \(\mu\) at a given depth and time, as function of PAR \(E\) and nutrients, is given by

\[
\mu(E, \text{NO}_3, \text{NH}_4) = \mu_0 \left( \frac{N_{\text{tot}}}{k_{\text{min}} + 2 \sqrt{k_{\text{min}} N_{\text{tot}} + N_{\text{tot}}}} \right) \left( \frac{\alpha E}{\sqrt{\alpha^2 E^2 + \mu_0^2}} \right)
\]

where the effective total nutrient concentration \(N_{\text{tot}}\) is given by

\[
N_{\text{tot}} = \text{NO}_3 + \varphi_{\text{NH}_4} \text{NH}_4
\]

The uptake preference \(\varphi_{\text{NH}_4} = 2\) to take into account that NH\(_4\) is taken up faster than NO\(_3\). The first bracketed quantity is a nutrient-limitation factor, similar to a Michaelis-Menten (Holling type II) saturating response, but incorporating the “optimal uptake” model of Smith et al. (2009). The second bracketed quantity is a light-limitation factor, written in terms of the initial slope of the photosynthesis-irradiance curve \(\alpha\). \(E\) depends on depth and phytoplankton concentration \(P\) according to Eq. (1).

As in the original Davis et al. (2014) model, there is no explicit dependence on temperature; \(\mu_0\) and other vital rates in the model are defined at typical ambient temperatures, and we assume the temperature-driven change in these rates during one simulation is small compared with other modes of variation and uncertainty (e.g. changes in species composition, or error in the nutrient or light-limitation formulations). However, in the sensitivity analysis below, we quantify the likely effect of temperature by adjusting \(\mu_0\), along with maximum grazing rate and remineralization rate, by a factor \(Q_{10}^{\Delta T/10\degree C}\) for a mean temperature shift of \(\Delta T\). We assume \(Q_{10} = 2\), a common rule of thumb for temperature response in phytoplankton (Eppley, 1972; Bissinger et al., 2008).

Each model simulation is two years, with the annual cycle repeated exactly, and the first year discarded as spinup. The model is initialised based on the time-average and depth-average of December observations, when the water column is close to homogeneous: initial NO\(_3\) concentration is 27.85 µM N, and the same value is imposed as a bottom boundary condition (at 200 m depth) over the course of the simulation, as a simple means of representing the continual resupply of nutrients via the estuarine circulation.

### 2.3.3 Parameter optimisation

Apart from the light attenuation parameters, which were defined from historical data as described above, and parameters that are essentially structural choices
or assumed to be universal, there are 11 parameters in the biogeochemical model that might plausibly differ between the Puget Sound and outer-coast ecosystems, and thus require a systematic investigation before settling on an adaptation of the Davis et al. (2014) model for use in PS-1D.

The 11 unknown parameters were tuned using “particle swarm optimisation” (PSO, Poli et al. (2007)). In PSO a number of imagined entities—the “particles”—are placed in a search space that consists of a summary measure of goodness-of-fit, the “cost,” as a function of the parameters being tuned. Each particle then determines its movement through the search space by combining aspects of the history of its own search (its current position and the best fit/lowest cost previously found) with the best fit found across the other members of the swarm, as well as random perturbations. Eventually the swarm as a whole, like a flock of birds collectively foraging for food, is likely to converge on the global optimum of the fitness function.

The cost function was defined using the Willmot skill score
\[
WSS_{\text{MAE}} = 1 - \frac{1}{N} \sum_{i=1}^{N} |m_i - o_i| \over \sum_{i=1}^{N} (|m_i - \bar{o}| + |o_i - \bar{o}|) \tag{4}
\]

where \(m_i\) and \(o_i\) are \(N\) matched pairs of model estimates and observations of chlorophyll (Chla), nitrate (NO\(_3\)) and ammonium (NH\(_4\))

The PSO was run for 300 iterations until each of the 11 parameters converged, after which we ran a set of 11 experiments varying one parameter at a time, in order to determine whether model behaviour was sensitive to the difference between the PSO-derived value and the original Davis et al. (2014) value (Fig. 13). Results allowed us to rank the PSO-derived parameters from greatest effect on model behaviour (initial growth-light slope (\(\alpha\)), phytoplankton mortality (\(m_P\)) to least (sinking rate of detritus, aggregation rate of phytoplankton). This indicates that there are indeed some, but fewer than 11, parameters in the LiveOcean biogeochemical model that need to be changed in order to correctly describe Main Basin. To make a final, practical decision regarding which parameters to change, the PSO-derived parameter set was replaced by the original values one at a time, and the series of changes in WSS assessed: at the end, initial growth-light slope \(\alpha\), phytoplankton mortality \(m_P\), zooplankton grazing half-saturation \(K_0\), maximum phytoplankton growth rate \(\mu_0\), nitrification rate \(r_{nitr}\), and remineralization rate \(r_{remin}\) were changed (Table 3).

Model outputs using the final tuned parameters showed good agreement with the observed seasonal cycle of euphotic-zone-integrated NO\(_3\) (Fig. 14). The model captures phytoplankton bloom timing accurately, as well as mean spring-summer concentrations, but does not show transient peaks as high as some seen intermittently in spring and summer data. The model’s winter and summer ammonium concentrations are consistent with observations.

2.4 Integration of models and observations

The PS-1D model just described is our principal means of quantifying the sensitivity of various measures of phytoplankton production to environmental factors,
Figure 13: Results from varying one parameter at a time around the set of optimised parameters. The original Davis et al. (2014) parameter values (blue lines) and PSO-derived values (red lines) are indicated. Left y–axis shows model behaviour of chlorophyll (Chla, green squares), nitrate (NO$_3$, red triangles), and ammonium (NH$_4$, orange circles), and right y–axis is for model as a whole (black circles). X–axes are ranges of parameters in which they are varied.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Unit</th>
<th>Davis et al.</th>
<th>PS-1D</th>
</tr>
</thead>
<tbody>
<tr>
<td>att$_bg$</td>
<td>Light attenuation by water column</td>
<td>m$^{-1}$</td>
<td>0.05</td>
<td>0.15</td>
</tr>
<tr>
<td>att$_fw$</td>
<td>Light attenuation by fresh water</td>
<td>m$^{-1}$</td>
<td>-0.0065</td>
<td>0</td>
</tr>
<tr>
<td>att$_p$</td>
<td>Light attenuation by phytoplankton</td>
<td>m$^{-1}$ µM N$^{-1}$</td>
<td>0.03</td>
<td>0.026</td>
</tr>
<tr>
<td>$\mu_0$</td>
<td>Maximum phytoplankton growth rate</td>
<td>d$^{-1}$</td>
<td>1.7</td>
<td>4</td>
</tr>
<tr>
<td>$k_{min}$</td>
<td>Minimum half-saturation for NO$_3$</td>
<td>µM N</td>
<td>0.1</td>
<td>0.1</td>
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<tr>
<td>$\alpha$</td>
<td>Initial growth-light slope</td>
<td>(W m$^{-2}$)$^{-1}$ d$^{-1}$</td>
<td>0.07</td>
<td>0.027</td>
</tr>
<tr>
<td>$\varphi_{NH_4}$</td>
<td>Preference for NH$_4$</td>
<td>d$^{-1}$</td>
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<td>2</td>
</tr>
<tr>
<td>$m_P$</td>
<td>Phytoplankton mortality</td>
<td>(µM N)$^{-1}$ d$^{-1}$</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>$m_{agg}$</td>
<td>Phytoplankton loss via aggregation</td>
<td>µM N</td>
<td>4.8</td>
<td>4.8</td>
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<tr>
<td>$l_0$</td>
<td>Zooplankton maximum ingestion rate</td>
<td>µM N</td>
<td>3</td>
<td>5.3</td>
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<tr>
<td>$\epsilon$</td>
<td>Microzooplankton growth efficiency</td>
<td>(W m$^{-2}$)$^{-1}$ d$^{-1}$</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>$m_{MZ}$</td>
<td>Microzooplankton mortality</td>
<td>d$^{-1}$</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>$f_{ex}$</td>
<td>Fraction of grazing excreted to NH$_4$</td>
<td>d$^{-1}$</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>$r_{rem}$</td>
<td>Detrital remineralisation rate</td>
<td>d$^{-1}$</td>
<td>0.1</td>
<td>0.25</td>
</tr>
<tr>
<td>$w_{PED}$</td>
<td>small detritus sinking rate</td>
<td>m d$^{-1}$</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>$w_{PLD}$</td>
<td>large detritus sinking rate</td>
<td>m d$^{-1}$</td>
<td>80</td>
<td>80</td>
</tr>
<tr>
<td>$r_{nitr}$</td>
<td>Nitrification rate</td>
<td>d$^{-1}$</td>
<td>0.1</td>
<td>0.035</td>
</tr>
</tbody>
</table>

Table 3: Final PS-1D tuned parameters for Main Basin, compared with Davis et al. (2014) values for the outer coast. µMN = mmol nitrogen m$^{-3}$. 

19
including turbulent mixing, while the SOG model provides a point of comparison for several of these estimates. We use five phytoplankton metrics (i–iv in Sec. 1, with iii subdivided):

1. Total annual primary production $PP_{tot}$, converted to units of g C m$^{-2}$ yr$^{-1}$ assuming a C:N ratio of 106:16 mol:mol;

2. Date of the spring bloom $t_{bloom}$, defined as the day of year when cumulative, vertically-integrated phytoplankton biomass reached 15% of its annual total;

3. Phytoplankton concentration during the seasonal period and depth layer associated with steelhead outmigration ($P_{steelhead}$), mid April–first week of June (yeardays 109–159), and 0–2 m depth;

4. Phytoplankton concentration during chinook outmigration in summer $P^{chinook}_{outmigr}$, first week of June–mid September (yeardays 159–258), 0–15 m depth;

5. Incidence of strong nutrient stress in summer $\Delta t_{nut}$, defined as the count of days on which surface nutrient concentration is less than 3 mmol m$^{-3}$.

The LiveOcean model, along with historical observations, provides the means of determining the relationships between turbulent mixing and riverflow, wind stress, stratification. Mixing intensity, riverflow, stratification, and wind stress magnitude were all log-transformed, so that power-law relationships among them can be described by constant sensitivities: if a driver $D$ and response
\[ R \text{ are related by } R = aD^b, \text{ then } a \text{ and } b \text{ can be estimated by a linear regression between } \log D \text{ and } \log R, \text{ and the sensitivity of } R \text{ to } D \text{ is given by} \]
\[
\frac{\partial (\log R)}{\partial (\log D)} = b \tag{5}
\]

As described above, a combination of observations and model hindcasts/projections allows us to quantify variability in the atmospheric, oceanic, and watershed drivers themselves. Relating these scales of variability in drivers to the associated variability in phytoplankton metrics is a matter of multiplication and the chain rule: for example, the variability in spring bloom date \( t_{\text{bloom}} \) associated with interannual variability in spring wind stress \( \tau \), via the effect of wind stress on turbulent mixing (\( E \rightarrow K \rightarrow L \), Fig. 1), is given by
\[
\Delta t_{\text{bloom}} = \Delta (\log_{10} \tau) \cdot \frac{\partial (\log_{10} \kappa_v)}{\partial (\log_{10} \tau)} \cdot \frac{\partial t_{\text{bloom}}}{\partial (\log_{10} \kappa_v)} \tag{6}
\]

In general, each arrow in Fig. 1 represents one sensitivity, or partial derivative like the two that appear in 6, although the distinction in Fig. 1 between mechanisms that affect light limitation and mechanisms that affect nutrient limitation is a matter of interpretation rather than an explicit calculation. This analysis is a scaling exercise, and we endeavour not to overinterpret differences that are smaller than a factor of three.

The primary timescale of analysis is interannual variation in seasonal averages, i.e. the variance of Apr–Jun (spring) or Jul–Sep (summer) averages across a number of years. (Scales of variation denoted by \( \Delta \) are defined throughout as 2 standard deviations.) In some cases, we have no means of calculating interannual variation in this way: for example, variation in the exchange flow (and hence vertical advection, under our assumptions) has been calculated across one annual cycle in LiveOcean (MacCready et al., in prep) but never across a useful ensemble of years. In these cases, we interpret the known event-scale (10 d) variation as a high upper bound on the unknown interannual variation. In other cases, it is not clear whether seasonal averages are indeed the timescale on which the environment drives variation in phytoplankton dynamics. For example, across three years of data from a high-time-resolution profiling buoy in Carr Inlet in South Puget Sound (ORCA, 2011–2013, \( \text{https://nwem.apl.washington.edu/about\_proj\_ORCA.shtml} \)), it is possible to identify three events in which a transient peak in stratification is followed by a transient phytoplankton bloom (arrows, Fig. 15); whereas correlations between stratification and chlorophyll on the monthly scale and longer are weak to nonexistent. Thus we calculated and report event-scale (10 d) variation for select quantities as an aid to interpretation and source of follow-on hypotheses.
Figure 15: Bottom–surface density difference ("drho," in \( \sigma_t \) units) and chlorophyll (vertically integrated, mg m\(^2\)) at the Carr Inlet ORCA buoy, for 2011 (blue), 2012 (green), and 2013 (red). Each point represents one day. The shaded time period in the left panels is expanded in the right panels. Three event-scale phytoplankton blooms associated with event-scale peaks in stratification are marked with arrows.
3 Results

3.1 Dynamics of stratification and mixing

In the time series derived from LiveOcean, stratification $\delta \rho$ is significantly correlated with and mixing $\kappa_v$ and riverflow $Q_r$ with maximum lagged correlation occurring for 8 days of lag (Fig. 17). It is not significantly correlated with wind stress $\tau$ and tidal velocity $u_T$. These results are consistent with a classical view of estuarine circulation in which stratification primarily reflects the competition between the homogenizing effect of mixing and the stratifying effect of river discharge. Near-surface mixing $\kappa_v$ is significantly correlated with wind stress $\tau$ and stratification $\delta \rho$, but not tidal velocity $u_T$ or river discharge $Q_r$ (Fig. 18). Variation in near-bottom mixing is, in contrast, primarily explained by the tides (not shown).

These results suggest a two-step approach in which we first predict mixing as a function of wind stress and stratification via a multiple regression on LiveOcean time series, yielding a pair of useful sensitivities (Table 4); and second find the sensitivity of stratification to riverflow directly from DOE observations (Fig. 19).

The sensitivity of stratification to temperature is derived directly from the
linearised equation of state of seawater (Table 4). The simplifying assumption that surface warming has no effect below 20 m makes this value—which indicates a very small effect in any case—an upper bound.

3.2 Environmental variation and phytoplankton dynamics

Results from sensitivity experiments in PS-1D are summarised in Table 5. Each row describes a family of model runs in which one driving variable at a time was varied around its base-case value. Sensitivities are not normalised and are expressed in disparate units, and thus are difficult to evaluate in themselves; they constitute an intermediate step in the overall scaling analysis. Independent estimates of the sensitivity of spring bloom date to mixing, temperature, and light (in the southern Strait of Georgia, not Main Basin) were also calculated from the SOG model (Table 5), as described in Sec. 2.2.

Means and scales of variation for all other quantities required for the final scaling analysis are given in Table 6. Scales of variation in turbulent mixing \( \log_{10}(\kappa_v) \) are derived from the sensitivities reported in Table 4. Other quantities are derived directly from observational and model time series as described in Sec. 2.

As expected, variation in riverflow, wind stress, and PAR is markedly larger on the 10 d scale than in seasonal averages. This result is true for both spring (Apr–Jun) and summer (Jul–Sep) records. On the event scale, wind and riverflow/stratification drive strong variability in turbulent mixing of similar magnitude (approximately ± 0.2 in \( \log_{10} \) units, or 60%), while on the interannual scale, wind stress variations largely average out and drive much less variance in mixing (± 0.05 vs. 0.12–0.14 in \( \log_{10} \) units, or 10% vs. 32–38% variation).

The final quantification of the various mechanistic pathways leading to phytoplankton dynamics (Fig. 1) is summarised in Table 7, which combines estimates of variability in drivers (Table 6) with estimates of sensitivities (Tables 4 and 5), as in Eq. (6). Results are given for the interannual timescale, using
Near-surface mixing as a function of stratification and wind stress

Regression equation

\[ \log_{10} \kappa_v = a + b \cdot \log_{10} \rho_z + c \cdot \log_{10} \tau \]

| Intercept | a | -2.56 ± 0.57 | LiveOcean, 2017–2018 |
| Sensitivity of mixing to stratification | b | -0.89 ± 0.37 | LiveOcean, 2017–2018 |
| Sensitivity of mixing to wind stress | c | 0.67 ± 0.29 | LiveOcean, 2017–2018 |

| Other sensitivities |
| Sensitivity of stratification to riverflow | \( \partial (\delta \rho) \over \partial Q_r \) | 1.87 | DOE obs., spring |
| Sensitivity of stratification to surface temperature | \( \partial (\delta \rho) \over \partial T_{20} \) | 0.18 | Equation of state at 30 psu, 12°C; assumes no change below 20 m |

Table 4: Relationships among vertical diffusivity, stratification, riverflow, wind stress, and temperature.

Spring values from Table 6 for \( t_{\text{bloom}} \) and \( P_{\text{steelhead}}^{\text{outmigr}} \), summer values for \( P_{\text{chinook}}^{\text{outmigr}} \) and \( \delta t_{\text{nut}} \), and whichever is larger in each case for \( P_{\text{tot}} \). Estimates are also given for long-term change over 50 y, under the single climate projection used in CCSM3/WRF/ROMS (Table 2). Estimates of spring-bloom-date variation based on event-scale variability in the drivers, as opposed to seasonal averages, are also shown; the analogous calculations for the other phytoplankton metrics, which describe seasonal patterns rather than events, would not be interpretable.

However, the expected variability driven by the exchange flow (via \( w_{\text{adv}} \)) and via changes in light attenuation are expressed as “much less than the variability one would calculate based on event-scale changes in \( w_{\text{adv}} \) and \( \text{att}_{\text{bg}} \),” since we lack a basis for quantifying the interannual variation in seasonal averages of these drivers.

Results are given in the same units as the base-case values of the five metrics, which are also shown in Table 7 for comparison. For each metric, the scale-setting, largest effects are marked with a **, and other effects within half an order of magnitude, or a factor of 3, are marked with a *. These categories together are considered “major effects” and the others are considered “minor.”

Either variation in surface PAR or the effect of riverflow on turbulent mixing (via stratification) is the scale-setting driver for each of the five metrics, and the effect of light attenuation is consistently in the class of potential major effects. Interannual variation in \( N_{\text{deep}} \) does not have a major effect on any of the phytoplankton metrics. Other drivers (wind stress, the exchange flow,
<table>
<thead>
<tr>
<th>$Sensitivity$ of $\rightarrow$ to $\downarrow$</th>
<th>Annual primary production</th>
<th>Date of spring bloom</th>
<th>Phyto. conc. during steelhead outmigration (spring, 0–2 m)</th>
<th>Phyto. conc. during chinook outmigration (summer, 0–15 m)</th>
<th>Duration of strong nutrient stress (summer)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$PP_{tot}$ (gC m$^{-2}$ yr$^{-1}$)</td>
<td>$t_{bloom}$ (yearday)</td>
<td>$P_{steelhead}$ (mg C m$^{-3}$)</td>
<td>$P_{chinook}$ (mg C m$^{-3}$)</td>
<td>$\delta t_{nut}$ (d)</td>
<td></td>
</tr>
<tr>
<td>$\log_{10} \kappa_v$ (log$_{10}$ m$^2$ s$^{-1}$)</td>
<td>$-32$</td>
<td>$20$</td>
<td>$-9.4$</td>
<td>$3.5$</td>
<td>$-72$</td>
</tr>
<tr>
<td>$w_{adv}$ (m d$^{-1}$)</td>
<td>$-78$</td>
<td>$7.6$</td>
<td>$0.52$</td>
<td>$0.32$</td>
<td>$-23$</td>
</tr>
<tr>
<td>$N_{deep}$ ($\mu$M N)</td>
<td>$8.9$</td>
<td>$0$</td>
<td>$0.23$</td>
<td>$0.31$</td>
<td>$-2$</td>
</tr>
<tr>
<td>$T_{20}$ ($^{\circ}$C)</td>
<td>$15$</td>
<td>$-1.5$</td>
<td>$0.21$</td>
<td>$-0.03$</td>
<td>$3.5$</td>
</tr>
<tr>
<td>$E_0$ (W m$^{-2}$)</td>
<td>$20$</td>
<td>$-0.88$</td>
<td>$0.38$</td>
<td>$0.35$</td>
<td>$1$</td>
</tr>
<tr>
<td>$att_{bg}$ (m$^{-1}$)</td>
<td>$-5700$</td>
<td>$150$</td>
<td>$-48$</td>
<td>$-78$</td>
<td>$-600$</td>
</tr>
</tbody>
</table>

Table 5: Response of phytoplankton metrics (columns) to variability in physical drivers (rows). All values are derived from sensitivity experiments in PS-1D except for three values estimated from SOG for comparison.
near-surface temperature) are found to have potentially major effects on some metrics but not others.

4 Discussion

The results in Table 7 suggest useful simplifications to the tangle of mechanistic pathways in our initial conceptual model. Refined conceptual models for each phytoplankton metric are shown in Fig. 20.

4.1 Primary production

Annual primary production, perhaps by integrating over so many transient aspects of the plankton dynamics, shows the clearest results, the strongest separation between major and minor effects. Variation in light limitation outweighs variation in nutrient limitation, in the sense that an increase in vertical mixing (which decreases light exposure but increases nutrient supply) has an overall negative effect on $PP_{tot}$ seasonally-averaged incoming PAR appears to be sufficient to drive $\sim 15\%$ variation in annual primary production (Table 7). Sample-to-sample variation in background light attenuation—i.e. all effects of water-mass variation and freshwater influence, excluding self-shading by phytoplankton—is on the same scale ($att_{bg} = 0.15 \pm 0.03 \text{ m}^{-1}$; Table 3) and varying $att_{bg}$ on this scale in the PS-1D model also leads to $\sim 15\%$ changes in $PP_{tot}$, but we expect that much of this variability in $att_{bg}$ averages out on seasonal timescales.
<table>
<thead>
<tr>
<th>Quantity</th>
<th>Units</th>
<th>Symbol</th>
<th>Mean</th>
<th>Log mean</th>
<th>Interannual variation (2 s.d.)</th>
<th>Event-scale variation (2 s.d.)</th>
<th>Comments</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riverflow</td>
<td>m³ s⁻¹</td>
<td>$Q_r$</td>
<td>1300</td>
<td>3.1</td>
<td>0.19</td>
<td>0.28</td>
<td>spring</td>
<td>USGS obs., 1964–2018</td>
</tr>
<tr>
<td>Wind stress</td>
<td>Pa</td>
<td>$\tau$</td>
<td>0.015</td>
<td>-1.9</td>
<td>0.082</td>
<td>0.24</td>
<td>spring</td>
<td>NNRP/WRF, 1950–2010</td>
</tr>
<tr>
<td>Stratification</td>
<td>kg m⁻³</td>
<td>$\delta \rho$</td>
<td>1.25</td>
<td>0.04</td>
<td>0.078</td>
<td>0.44</td>
<td>spring</td>
<td>LiveOcean, 2017–2018</td>
</tr>
<tr>
<td>Temperature</td>
<td>°C</td>
<td>$T_{20}$</td>
<td>10.2</td>
<td>1.2</td>
<td></td>
<td></td>
<td>0–20 m, spring</td>
<td>DOE obs.</td>
</tr>
<tr>
<td>Mixing</td>
<td>m² s⁻¹</td>
<td>$\kappa_v$</td>
<td>2.5 × 10⁻⁴</td>
<td>-3.8</td>
<td>0.05</td>
<td>0.16</td>
<td>spring, via $\tau$</td>
<td>see Table 4</td>
</tr>
<tr>
<td>Surface PAR</td>
<td>W m⁻²</td>
<td>$E_0$</td>
<td>119</td>
<td>8.6</td>
<td>34</td>
<td></td>
<td>spring</td>
<td>NNRP/WRF, 1950–2010</td>
</tr>
<tr>
<td>Ocean sourcewater density</td>
<td>kg m⁻³</td>
<td>$\Delta \rho_{oc}$</td>
<td>1.4</td>
<td>0.02</td>
<td></td>
<td></td>
<td>continental slope, ROMS Cascadia, 2002–2009</td>
<td></td>
</tr>
<tr>
<td>Ocean sourcewater nutrients</td>
<td>mmol m⁻³</td>
<td>$N_{deep}$</td>
<td>27.6</td>
<td>2.8</td>
<td></td>
<td></td>
<td>DOE obs., December</td>
<td>LiveOcean, 2017</td>
</tr>
<tr>
<td>Main Basin deep nutrients</td>
<td>m³ s⁻¹</td>
<td>$Q_{ex}$</td>
<td>3500</td>
<td>1500</td>
<td></td>
<td></td>
<td>derived from $Q_{ex}$</td>
<td></td>
</tr>
<tr>
<td>Exchange flow volume transport</td>
<td>m day⁻¹</td>
<td>$w_{adv}$</td>
<td>2.34</td>
<td>0.99</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertical advection</td>
<td>m⁻¹</td>
<td>$att_{bg}$</td>
<td>0.15</td>
<td>0.03</td>
<td></td>
<td></td>
<td>confidence limits on regression</td>
<td></td>
</tr>
</tbody>
</table>

Table 6: Estimates of environmental variability used in the scaling analysis.
### Table 7: Scales of variation in five metrics of phytoplankton production ($PP_{tot}$, etc.) associated with seven climate-linked drivers ($\tau$, etc.). *Interann.* and *Event* indicate interannual variation in seasonal averages, and variation among 10 d averages within one season, respectively, and are given as an absolute value corresponding to 2 s.d. of variation in the driver. *50 y* indicates total change between ~ 1990 and the 2040s in the CCSM3/WRF/ROMS regional climate projection, a signed quantity. ** indicates the largest or scale-setting process for each metric, and * denotes other mechanisms whose effects are potentially of the same order of magnitude (i.e. within a factor of 3).

<table>
<thead>
<tr>
<th>Metric</th>
<th>Base-case value</th>
<th>Scale of variability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual primary production</td>
<td>$PP_{tot}$</td>
<td></td>
</tr>
<tr>
<td>Date of spring bloom</td>
<td>$t_{bloom}$</td>
<td></td>
</tr>
<tr>
<td>Phyto conc. during steelhead outmigration (spring, 0–2 m)</td>
<td>$p_{steelhead outmigr}$</td>
<td></td>
</tr>
<tr>
<td>Phyto conc. during chinook outmigration (summer, 0–15 m)</td>
<td>$p_{chinook outmigr}$</td>
<td></td>
</tr>
<tr>
<td>Duration of strong nutrient stress</td>
<td>$\delta t_{nut}$</td>
<td></td>
</tr>
<tr>
<td><strong>$gC\ m^{-2}\ yr^{-1}$</strong></td>
<td><strong>1140</strong></td>
<td><strong>50</strong> Interann.</td>
</tr>
<tr>
<td><strong>yearday</strong></td>
<td><strong>127</strong></td>
<td><strong>50</strong> Interann.</td>
</tr>
<tr>
<td><strong>mg \ C m^{-3}</strong></td>
<td><strong>27</strong></td>
<td><strong>50</strong> Interann.</td>
</tr>
<tr>
<td><strong>mg \ C m^{-3}</strong></td>
<td><strong>36</strong></td>
<td><strong>50</strong> Interann.</td>
</tr>
<tr>
<td><strong>d</strong></td>
<td><strong>8</strong></td>
<td><strong>50</strong> Interann.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Driver</th>
<th>Interann. 50 y</th>
<th>Event 50 y</th>
<th>Interann. 50 y</th>
<th>Interann. 50 y</th>
<th>Interann. 50 y</th>
<th>Interann. 50 y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wind stress $\tau$ (via mixing)</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>1.1</td>
<td>3.3</td>
<td>0</td>
</tr>
<tr>
<td>Riverflow $Q_r$ (via stratification and mixing)</td>
<td>5.1</td>
<td>10</td>
<td>-3.7</td>
<td>7.5**</td>
<td>13*</td>
<td>1.8</td>
</tr>
<tr>
<td>Exchange flow $Q_{ex}$ (via vertical advection)</td>
<td>≪ 73</td>
<td>≪ 7.5*</td>
<td>7.5</td>
<td>≪ 0.51</td>
<td>≪ 0.32</td>
<td>≪ 23*</td>
</tr>
<tr>
<td>Deep nutrient concentration $N_{deep}$</td>
<td>25</td>
<td>0</td>
<td>0</td>
<td>0.64</td>
<td>0.87</td>
<td>2.8</td>
</tr>
<tr>
<td>Near-surface temperature $T_{20}$</td>
<td>30</td>
<td>18</td>
<td>-3</td>
<td>1.8</td>
<td>0.42</td>
<td>0.25</td>
</tr>
<tr>
<td>Surface PAR $E_0$</td>
<td>170**</td>
<td>7.6**</td>
<td>38**</td>
<td>3.3**</td>
<td>3**</td>
<td>8.6*</td>
</tr>
<tr>
<td>Background light attenuation $att_{bg}$</td>
<td>≪ 170*</td>
<td>≪ 4.5*</td>
<td>4.5</td>
<td>≪ 1.4*</td>
<td>≪ 2.3*</td>
<td>≪ 18*</td>
</tr>
</tbody>
</table>
Figure 20: Final ranking of pathways of climate influence on four measures of phytoplankton dynamics.
Note that the PS-1D model does not include photoacclimation by individual cells, or succession of phytoplankton populations as environmental conditions change, and either mechanism would be expected to flatten out the response to variations in light conditions. Thus the sensitivity of $PP_{tot}$ in our analysis is likely a high estimate.

Strikingly, variations in mixing and circulation have very small effects on $PP_{tot}$ on interannual and longer timescales. This may be because changes in mixing have opposite effects in spring (via light) and summer (via nutrient supply), or because while turbulent mixing shows intense variation on short time and spatial scales, it is relatively steady in seasonal averages (2 s.d. < 40% variation, compared with around threefold variation over a typical tidal cycle). The other metrics in our analysis suggest the increased process complexity behind phytoplankton dynamics on event to seasonal scales, as opposed to annual averages.

4.2 Spring bloom timing

Variation in surface PAR (via variation in cloud cover) again emerges as a crucial influence on variation in spring bloom timing in central Main Basin (Table 7, Fig. 20). Historical variation in seasonally-averaged $E_0$ is sufficient to explain perhaps a 15 d range of spring bloom dates ($\pm$ 2 s.d.: Table 7), while event-(10 d) scale variation in $E_0$ is several times larger (Table 6) and leads to more than 2-month variation in $t_{bloom}$ in PS-1D ($\pm$ 2 s.d.). The actual historical variation in $t_{bloom}$ in Main Basin is unclear, since monthly DOE sampling could easily miss the bloom entirely and high-time-resolution ORCA chlorophyll time series are only available for a handful of years. However, the longer model-based estimate is close to the assessment by Newton and Van Voorhis (2002) (spring bloom March–May, 1999–2001) and also close to observed spring-bloom variability over 60 years in the southern Strait of Georgia.

The experiment in PS-1D that generated this estimate, in which we took event-scale variability in $E_0$, applied it over an entire annual cycle, and measured the change in spring bloom date, is mechanistically sensible enough if the spring bloom is a process with a short memory, a response to an event-scale confluence of suitable conditions. The SOG model predicts the southern Strait of Georgia spring bloom on the basis of Dec–Mar average conditions (Collins et al., 2009; Allen and Wolfe, 2013); but there is no observational evidence that the Main Basin spring bloom is a response to seasonal-average conditions in this sense, and anecdotal evidence to the contrary (Fig. 15).

Allen and Wolfe (2013) found that variations in wind stress were as important a driver of spring bloom timing variability as variations in cloud cover and light, with temperature effects playing a secondary role. PS-1D shows a lower sensitivity of $t_{bloom}$ to $E_0$ compared with SOG ($-0.88$ vs $\sim 2$ d (W m$^{-2}$)$^{-1}$), but also a lower sensitivity to temperature (1.5 vs. 4.7 d ($^\circ$C)$^{-1}$) and wind stress (20 vs. 70 d Pa$^{-1}$, Table 5). Accordingly, we find that wind mixing may have measurable effects on bloom date but appears to play a minor role compared with $E_0$, whereas riverflow-driven variation in stratification and mixing
has the same scale of effect as $E_0$ in seasonal averages. This ranking is consistent
with the finding that in Main Basin, riverflow variability has stronger effects on
mixing in spring than does wind stress (Table 6). Other than this, the minor
differences in the ranking of controls on the spring bloom between our analysis
and Allen and Wolfe (2013) appear to be driven mainly by differences in the
phytoplankton models used (PS-1D vs. SOG), rather than differences between
Main Basin and the southern Strait of Georgia as environments.

4.3 Conditions during salmon outmigration

We calculated variability in phytoplankton standing stock itself during the pre-
sumed period of juvenile steelhead and chinook outmigration and chinook out-
migration, as an indication of possible changes in the light environment during
a critical life stage for these fish. We speculate that the effect of a dense phyto-
plankton bloom on visual refuge and predation during this period would come
through light scattering, not through light attenuation, and so we cannot di-
rectly compare the changes in the underwater light field that would result from
the phytoplankton changes we model from the changes in light that drive the
phytoplankton dynamics; however, this comparison would have to be made by
studies that attempted to follow on from the results here. Overall, we find pre-
dicted changes in phytoplankton concentration, $P_{\text{steelhead}}^{\text{outmigr}}$ and $P_{\text{chinook}}^{\text{outmigr}}$, to be
quite modest, on the order of 10% (Table 7). This might reflect the structural
simplicity of PS-1D, or it might be an indication that if phytoplankton blooms
have an effect on visual predation by and on juvenile salmoni, it is primar-
ily through intense, transient, localised blooms, not through seasonal-average
conditions. Surface PAR, underwater light, and (in the case of steelhead out-
migration) riverflow effects on mixing drive the largest of these generally small
effects.

4.4 Nutrient stress in summer

Although PS-1D does not resolve phytoplankton succession, the incidence of
days in which nutrients become severely limiting can provide a clue to likely
compositional changes during summer. Nutrient limitation under warm, high-
light conditions has long been taken to encourage dinoflagellate blooms over
diatoms, including toxin-producing taxa like *Alexandrium*; however, there is no
detailed historical record in Puget Sound that supports a local link between
nutrient limitation and *Alexandrium* HABs more directly. The metric $\Delta t_{\text{nut}}$
counts the days in which surface NO3 + NH4 is less than 3 mmol m$^{-3}$ in
PS-1d, a threshold that identifies an extreme but regularly occurring level of
nutrient stress: its base-case value is 8 d per year.

Historical variation in seasonally-averaged surface PAR and in riverflow ef-
effects on stratification and mixing are both sufficient to drive variation in $\Delta t_{\text{nut}}$
between approximately 0 and 2–3 times its base-case value (Table 7). Near-
surface temperature and wind mixing do not appear likely to explain year-to-
year variability but may well drive dramatic long-term trends (toward more
frequent or sustained nutrient stress in the case of temperature, and also to-
ward higher nutrient stress if the prevailing northerly summer winds increase in
strength: Table 7, Moore et al. (2015)). Changes in the exchange flow and back-
ground light attenuation could potentially also drive nutrient-stress changes of
the same magnitude as the other mechanisms mentioned, but without a better
quantification of seasonal-average patterns in these processes we cannot be sure.

For $\Delta t_{nut}$ and to a lesser extent $t_{bloom}$, new temperature effects beyond the
range of historical variability seem likely to emerge over the next few decades,
if they have not already. Note that the effect of warming on nutrient stress
in general, as discussed here, is likely accompanied by an independent effect
of warming on Alexandrium growth rate and seasonal window of opportunity
(Moore et al., 2015).

5 Conclusion

The results of our multi-model synthesis and scaling analysis yield relatively sim-
ples pictures for interannual variation in primary production and phytoplankton
standing stock in Main Basin (Fig. 20), in which a large number of potential
pathways of climate influence can be classed as minor effects compared with
others. Results paint more complex pictures for changes in the spring bloom
date $t_{bloom}$ and the count of days of strong nutrient stress in summer $\Delta t_{nut}$,
both processes that involve event-scale changes atop seasonal changes. For these
metrics, a large number of mechanistic pathways all seem capable of producing
variations in phytoplankton dynamics on the same scale. This process com-
plexity, and not just the incompleteness of available observations, may explain
why simple correlative approaches to the Puget Sound spring bloom have never
yielded a clear picture.

Overall, this study points to variation in incoming light, i.e. variation in
cloud cover, as a leading climate influence on phytoplankton dynamics in Puget
Sound. Collins et al. (2009) and Allen and Wolfe (2013) found the same for the
timing of the spring bloom in the southern Strait of Georgia, although in that
system (and the SOG model) wind mixing plays a comparable role, whereas in
Puget Sound, riverflow effects on stratification and mixing exceed wind effects
in spring (the two mechanisms are comparable in summer). (Moore et al., 2015)
previously suggested that long-term trends in Puget Sound hydrology, toward
increased riverflow in spring and decreased flow in summer (Cuo et al., 2009,
2011), might affect phytoplankton dynamics by modulating stratification and
thus turbulent mixing. Our analysis of the relationship between riverflow and
stratification (in historical observations) and stratification and mixing (in mod-
elses) suggests that this pathway of influence likely drives significant interannual
variation in phytoplankton dynamics as well, not just long-term trends, and in
summer as well as spring.

Variations in light attenuation, beyond those explicable as phytoplankton
self-shading, also appear to be intense enough to potentially drive important
variability in primary production timing, magnitude, and nutrient limitation.
A simple approach to explaining this light-attenuation variability in terms of salinity proved to be statistically weak; a more detailed investigation of what watershed characteristics link hydrology to the marine underwater light environment, and from there to effects on primary production, is clearly called for.

To some extent, this is exactly the kind of problem that regional earth system models have the potential to address, and a problem that might usefully serve as a nucleus for the next generation of coupled atmospheric-hydrologic-marine modelling in the Puget Sound basin. At the same time, the problem highlights gaps in our process understanding that can only be addressed through high-resolution observations and process studies, such as the role of plasticity and photoacclimation in modulating the response of the Puget Sound phytoplankton community to the light environment, and in setting the timing of the spring bloom. This need for broad and coordinated collaboration among modellers and observationalists of many stripes is likely a general characteristic of the long mechanistic chains that link climate variability and change to the dynamics of marine food webs.

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References


