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

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October 1, 2019

#### Abstract

## 8 1 Introduction

There are many simultaneous pathways by which regional climate can drive q interannual or longer-term variation in primary production in coastal and es-10 tuarine waters. Changes in riverflow volume and timing, deep inputs from the 11 open ocean, wind patterns, surface heating, and cloud cover and hence light 12 availability—a partial list—all affect primary production by distinct mecha-13 nisms. These climate-linked environmental factors are often highly correlated 14 in historical time series, but may not maintain these correlations into the future 15 as the climate changes; as a result, statistical approaches struggle to identify 16 the specific mechanisms driving historical variability, or the possibly distinct set 17 of mechanisms that will drive future change in marine food webs. 18

The gold standards in this type of research are long multivariate time series 19 with good spatial coverage (e.g. CalCOFI in Southern California) and coupled 20 hydrodynamic-biogeochemical models driven by regional climate downscalings, 21 well-validated on a range of system levels and scales. These comprehensive 22 datasets generally do not exist, and multi-decadal regional simulations are so 23 cumbersome that even when they do exist, there are invariably system levels 24 at which the key mechanisms have never been directly verified and uncertainty 25 has not been systematically examined. An alternate use of models—which we 26 suggest deserves more articulation and recognition in global change biology—is 27 as a means of *rejecting* hypotheses rather than promoting them: that is, as a 28 means of ranking and winnowing a tangle of competing mechanisms, as a guide 29 for further empirical research. 30

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 37 experienced tenfold declines in marine survival over the past 30 years (Zimmer-38 man et al., 2015), while chinook and coho on the outer Washington and British 39 Columbia coasts have not shown any matching trend. Active hypotheses that 40 might explain this long-term decline are extremely diverse, encompassing in-41 creases in predators, declines in forage fish, changes in physical habitat, chem-42 ical pollution, and many other factors; but within this field of inquiry is the 43 fundamental question of whether bottom-up changes beginning at the base of 44 the marine food web could be responsible. Tracing changes in phytoplankton 45 production step-by-step through the long trophic chains that support salmon is 46 well beyond the scope of this study, but with existing oceanographic and earth-47 system models we are able to begin to evaluate potential past and future trends 48 in i) annual primary production and ii) the timing of the spring bloom. We 49 also analyze patterns in *iii*) spring and summer phytoplankton concentrations, 50 motivated by a non-trophic hypothesis: the possibility that dense phytoplank-51 ton blooms during critical outmigration times change the underwater light field 52 sufficiently to disrupt visual search. 53

Second, harmful blooms of the dinoflagellate Alexandrium catenella, which 54 produces powerful neurotoxins that lead to paralytic shellfish poisoning (PSP), 55 have increased in Puget Sound over the past half-century (Moore et al., 2011). 56 The seasonal/spatial window of opportunity for A. catenella harmful algal blooms 57 (HABs) has been linked to high water temperatures, and this window has ex-58 panded over recent decades and is projected to expand further (Moore et al., 59 2011, 2015). Within the window of opportunity, the occurrence of Alexandrium 60 blooms is likely tied to local oceanography via the transport and dispersion of 61 overwintering cysts (Horner et al., 2011)—dynamics that have provided signif-62 icant predictive ability elsewhere (McGillicuddy et al., 2011)—but also tied to 63 phytoplankton community dynamics and succession. For our purposes, the phe-64 nology of the spring bloom (ii), as well as iv) the occurrence or non-occurrence 65 of strong nutrient limitation in summer, serve as a bridge from Puget Sound 66 oceanography and regional climate to the ecological dimensions of Alexandrium 67 HABs, which a lack of detailed, sustained observations has to date left in the 68 realm of speculation (Moore et al., 2015). 69

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.

### 74 1.1 Initial conceptual model

<sup>75</sup> Our a-priori conceptual diagram (Fig. 1) does not include every possible route
 <sup>76</sup> 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  $(X \longrightarrow Y)$  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, 77 2002; Banas et al., 2014; Moore et al., 2015). In general, primary production 78 is regulated by light availability (pathway  $\mathbf{L}$ ) and nutrient availability ( $\mathbf{S}$ ). In 79 addition, temperature  $(\mathbf{H})$  affects both the maximum growth rate of the phy-80 toplankton community and the rate of losses to microoplankton and other 81 grazers. Light limitation is regulated by incoming photosynthetically available 82 radiation (PAR) and hence cloud cover (pathway A, D); the per-meter un-83 derwater light attenuation, which varies strongly with watershed inputs (**B**); 84 and also vertical mixing and advection  $(\mathbf{K}, \mathbf{O})$ , which control the depth range 85 over which phytoplankton cells are dispersed and hence the light level they 86 experience. Nutrient flux into the euphotic zone is also controlled by vertical 87 mixing and advection  $(\mathbf{R}, \mathbf{R})$ , and potentially by changes in the concentration 88 of nutrients in incoming ocean water  $(\mathbf{T}, \mathbf{U})$ . In other estuaries, changes in 89 river-derived nutrients would be of first-order importance as well, but nutrients 90 in Puget Sound are overwhelmingly ocean-derived (Mackas and Harrison, 1997; 91 Mohamedali et al., 2011). Watershed-derived nutrients have been found to have 92 notable effects on Puget Sound water quality (Khangaonkar et al., 2019) but 93 these effects are spatially limited (Banas et al., 2014), and the conceptual model 94 and analysis in this study are designed to describe the main stem of Main Basin, 95 away from localised areas of more intense river influence. 96

Along-channel gradients in nutrients and phytoplankton concentration are 97 relatively weak in Main Basin (*Winter et al.*, 1975, analysis below) and this 98 invites us to consider primary production in a 1-D, single-water-column frame-99 work, a modified version of a classic open-ocean scenario. Seasonally varying 100 stratification and mixing are the crucial physical controls on primary production 101 in this classic, mid-latitude framework, with mixing regulating light limitation 102 in early spring (**K**) and hence the timing of bloom initiation, and regulating 103 nutrient availability through the late spring and summer  $(\mathbf{P})$ , once the phy-104 toplankton have drawn down the initial stock of euphotic-zone nutrients left 105 over from winter. Near-surface mixing is driven in part by wind stress  $(\mathbf{E})$ , and 106 in part (in shallow areas especially) by the tides; we have assumed that the 107 tides do not respond significantly to climate change and neglected them in our 108 schematic, which is meant to represent mechanisms of variability and change 109 on annual to decadal scales. The intensity of mixing that results from a given 110 input of wind or tidal energy is strongly regulated by stratification, and con-111 versely stratification records a history of the amount of mixing that has recently 112 occurred  $(\mathbf{J})$ . Since measurements of stratification are far easier and far more 113 common than measurements of turbulent mixing, the literature often elides the 114 distinction and refers to "the effect of stratification on primary production": 115 but in a highly dynamic, advective environment like an estuary, the distinction 116 between "mixed" water and "mixing" water—that is, low stratification and high 117 turbulent mixing intensity—is potentially very important (Collins et al., 2009; 118 Franks, 2015). Riverflow affects estuarine hydrography and energetics through 119 a complex set of feedbacks, but in a first approximation, it drives changes in 120 stratification directly (I), and changes in mixing only indirectly ( $\mathbf{I} \rightarrow \mathbf{J}$ ). Surface 121 heating can also affect stratification  $(\mathbf{F})$ , although this effect is usually weaker 122

<sup>123</sup> than river/salinity effects in temperate estuaries.

In Main Basin as in other estuaries, the density contrast between river and 124 ocean inputs drives an "in-up-out" overturning or estuarine circulation (M, N, 125  $\mathbf{Q}$ ), which regulates the system's overall residence time. The "up" branch of 126 this circulation is the mechanism of mean vertical advection mentioned above, a 127 potentially important contributor to near-surface nutrients  $(\mathbf{R})$ . The inclusion 128 of upward advection reflecting the system-scale circulation and residence time 129 is the crucial addition that turns a generic water-column model into a estuar-130 ine water column (Winter et al., 1975; Collins et al., 2009). The along-channel 131 component of the estuarine circulation also needs to be included in tracer bud-132 gets if along-channel tracer gradients are large, although we find that for Main 133 Basin chlorophyll and nitrate they are not (Sec. 2.3.1), and care must be taken 134 to preserve mass conservation in tracer budgets in any case. 135

The aim of this study is to compare the strength of the many interwoven 136 pathways in this conceptual model, in a general, scaling sense rather than a de-137 tailed, scenario-specific sense, and produce a simplified conceptual model that 138 eliminates the second-order factors that are overwhelmed by other mechanisms 139 on interannual and longer timescales. This requires associating a scale of vari-140 ation with each atmospheric, watershed, and oceanic driver (Fig. 1, blue), and 141 a sensitivity with each mechanistic link (arrows). Estimates of these quantities 142 were assembled from a family of recent model studies that, together, more or 143 less span the timescales and levels of physical and biological process detail re-144 quired. The results suggest specific research agendas for future oceanographic, 145 atmospheric, and hydrological modelling in Puget Sound and its watershed. 146

## $_{147}$ 2 Methods

#### 148 2.1 Observations

In situ time series Nutrients and biomass Monthly sampling at Washington 149 Department of Ecology (DOE) long-term monitoring station PSB003 provided 150 core time series of temperature, salinity, chlorophyll, nitrate and ammonium 151 at our study site, at approximately monthly resolution. Chlorophyll estimates 152 are from calibrated fluorometer profiles at 0.5 m resolution, while, nitrate and 153 ammonium concentrations are from bottle samples, generally at 1, 10 and 30 154 meter depth (Fig. 3). In our analysis, near-surface temperature  $T_{20}$  is defined 155 as 0–20 m average of approximately monthly observations from PSB003, 1999– 156 2017 (Fig. 4). Density stratification  $\delta \rho$  is defined as the difference between 5–20 157 m average density and 0–5 m average density. 158

**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.

homish, Stillaguanish and Skagit, which supply a much larger freshwater flux 164 that enters Main Basin not far down-estuary (see Banas et al. (2014) for map-165 ping of the influence of individual river inputs across seasons in the MoSSea 166 model). Including discharge from all eight of these rivers, instead of only the 167 four up-estuary rivers, slightly increases the Pearson coefficient of the regression 168 analysis below (Sec. 3.1). Most of these observational records run from 1964-169 present, except for the Deschutes (1991–) and Nisqually (1978–). These rivers 170 with shorter records represent only 1% and 3.8% of total riverflow, respectively. 171

#### 172 2.2 Models

<sup>173</sup> Past and new analysis of six models were synthesized in this study (Table 1).

174 **LiveOcean** is a coupled physical-biogeochemical forecast model for the Salish 175 Sea and Pacific Northwest outer coast (Fig. 6, built using the Regional Ocean

<sup>176</sup> 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: in

Model	Domain	Type	Time period	References
NNRP/WRF	Atmosphere	3D	1950-2010	Dulière et al.
				(2011)
ROMS	Coastal ocean	3D	2003 - 2009	Stone et al.
Cascadia				(2018)
LiveOcean	Coastal ocean	3D	2017 - 2019	
	+ Salish Sea			
PS-1D	Salish Sea	1D	representative	this study
			seasonal cycle	
SOG	Salish Sea	1D	1968 - 2010	Collins et al.
				(2009), Allen
				and Wolfe
				(2013)
CCSM3/WRF/	Atmosphere $+$	3D	2040s projection	Moore et al.
ROMS	Coastal ocean			(2015)
	+ Salish Sea			

Table 1: Ocean and atmospheric models used in this study.

this study we use the archived forecasts from 2017–2018 as a de facto hindcast. 178 179 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 180 atmospheric forcing from a WRF (Weather Research and Forecasting) model 181 run by the UW Mesoscale Analysis and Forecasting Group. Davis et al. (2014) 182 describes the model's plankton dynamics in detail, including parameterization 183 and validation using a variety of observations from the outer coast. Siedlecki 184 et al. (2015) describes the dissolved-oxygen component. 185

Two years of hourly physical variables were extracted from LiveOcean along 186 an east-west section line close to PSB003 (Fig. 2). All data were tidally av-187 eraged using a Godin filter and subsampled into daily values, and horizontally 188 averaged. Vertical diffusivity  $\kappa_n$  was averaged over the top 20 m, and stratifica-189 190 tion  $\delta \rho$  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. 191 Coordinated time series of three driving variables were also defined: wind stress 192  $\tau$  at the same section line, rms tidal velocity  $u_T$ , and riverflow  $Q_r$  from the 193 USGS observations described above. 194

LiveOcean, and the MoSSea model of Puget Sound which preceded it 195 (Sutherland et al., 2011), have both been used to quantify the estuarine ex-196 change flow in Puget Sound, although never on the interannual timescale of 197 greatest interest here. Results to date from an unpublished analysis of daily 198 variation in exchange volume flux over 2017 (MacCready et al., in prep.) in-199 dicate that the classic theories of estuarine circulation, which would suggest 200 useful scaling relationships between riverflow and the exchange flow, simply do 201 not apply: tidally averaged volume flux through Admirality Inlet does not in-202 crease during periods of increased riverflow, but in fact decreases slightly. This 203



Figure 6: Domain of the LiveOcean model, showing the river inputs included *(left)* atop bathymetry, and horizontal resolution *(right)*.

volume flux does show a significant correlation with the along-channel density 204 gradient  $d\rho/dx$ , its proximate driver (not shown). However, we speculate that 205  $d\rho/dx$  is fundamentally controlled not by total riverflow in Puget Sound (where 206 the largest sources of freshwater are distributed spatially and the largest of all, 207 the Fraser River, in fact enters from the "ocean" end), but rather by gradients 208 in river influence, which are likely modulated by wind as well as by the rivers 209 themselves. Untangling these effects is beyond the scope of this report, and so 210 we treat the exchange flow as an independent environmental driver in its own 211 right, presumably linked strongly to hydrological and atmospheric drivers, but 212 by patterns we cannot presently resolve. LiveOcean results from 2017 are used 213 to set an upper limit on the interannual variability of the seasonally-averaged 214 exchange flow, for comparison with other drivers. 215

**ROMS Cascadia** is an antecedent to LiveOcean, a hindcast model that re-216 solves outer-coast physics and biogeochemistry at 1.5 km resolution over the 217 continental shelf and more coarsely offshore, and includes Salish Sea physics-218 not biogeochemistry—also at 1.5 km resolution, significantly coarser than the 219 2017- version of LiveOcean used here. Giddings et al. (2014) described and 220 validated the model physics for 2004–2007 and Stone et al. (2018) subsequently 221 described interannual variation in shelf and slope waters using a 2003–2009 222 hindcast. 223

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)



Figure 7: Comparison betwenn NNRP/WRF shortwave radiation and SeaTac observations of cloud cover for summer and spring. Left plot shows both daily time series. Right plot shows the negative correlation between the two time series.

<sup>227</sup> model, as described by *Dulière et al.* (2011).

Daily values of wind stress over Main Basin, 1950–2010, were calculated from 228 wind speed at 13 grid points in NNRP/WRF, converted to wind stress following 229 Large and Pond (1981) (Fig. 9). To validate these model results, we compared 230 the wind speed time series with data from the SeaTac Airport station (Fig. 8). 231 A step change in the SeaTac observations is visible at the end of the 1990s, likely 232 the result of a change in the anemometer position (Wan et al. (2010)). After 233 the step change, NNRP/WRF and SeaTac observations show similar variations. 234 Daily value of PAR values over Main Basin, 1950–2010, were calculated as 235 43% of downward shortwave flux at the same 13 grid points in NNRP/WRF. The 236 time series of PAR is well-correlated with sunrise-to-sunset average cloudiness 237 from the SeaTac Airport station, 1965–1996 (Fig. 7). 238

**CCSM3/WRF/ROMS** is a regional climate–ocean projection, constructed 239 by downscaling the global CCSM3-A1B model through WRF, and then using 240 this, along with hydrological projections for Puget Sound rivers and the Fraser 241 River, to drive a variant of the ROMS Cascadia model. Moore et al. (2015) de-242 scribe a projection for the 2040s made using this coupled system, in comparison 243 with a "present-day" (1988) reference case, in the context of potential climate 244 impacts on *Alexandrium* HABs. The major forcing changes in this scenario can 245 be summarized as increased air temperatures, a shift toward earlier riverflow, 246 and intensified summer upwelling, all close to the mean of the CMIP3 (IPCC 247 AR4) ensemble, with offshore oceanic boundary conditions held constant. The 248 responses of the marine system to this scenario (Moore et al., 2015) are sum-249 marized in Table 2. 250

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 betwenn 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	$\pm$ 0.7 m s <sup>-1</sup>	spring-summer
Stratification	+ 20%	spring
Stratification	$\sim 0$	summer
Noar surface temperature	+ 2  °C	spring
Near-surface temperature	+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 256 hindcasts; the sensitivity of spring bloom date to temperature, as calculated by 257 Allen and Wolfe (2013) from a 1968–2010 hindcast; sensitivity of bloom date 258 to light, from Dec-Mar average cloud cover (Allen and Wolfe, 2013) and the 259 approximation that as cloud cover varies between 0 and 100%, daily-average 260 PAR varies by  $\sim 60 \text{ W m}^{-2}$ ; and the sensitivity of bloom date to mixing, from 261 the sensitivity of bloom date to Dec-Mar average wind stress combined with 262 the mixing-wind relationship already mentioned. 263

**PS-1D** is a 1D model designed as a quick-running "sandbox" in which to ex-264 plore the parameter space of the LiveOcean biogeochemical model (Davis et al., 265 2014); determine how its parameterization needs to be changed to correctly rep-266 resent Main Basin as opposed to the offshore waters for which it was originally 267 developed; and perform the numerical experiments which allow us to define 268 scales of sensitivity of each primary-production metric to each environmental 269 driver (Fig. 1). This model has not been previously described in the literature 270 and so we explain it at a medium level of detail below. The full description is 271 expected to appear in Nguyen (2020). 272

### 273 2.3 The PS-1D model

#### 274 2.3.1 Physical setup

The physical "sandbox" of the PS-1D model is designed to reproduce a repre-275 sentative seasonal cycle at one location in central Main Basin, as a base case 276 around which we can perform experiments addressing the sensitivity of phyto-277 plankton dynamics to environmental conditions and to the assumed biological 278 parameters. These analyses have more the flavor of laboratory or mesocosm 279 experiments than historical analysis—doubling the turbulent mixing, halving 280 the incoming light, etc.—and do not attempt to resolve event-scale fluctuations, 281 for which a 1D model would likely be fundamentally inappropriate. 282

In this 1D model, a water column of  $\sim 200$  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 287 flow depends, because of mass conservation, on the along-channel gradient in the 288 lower-layer incoming volume flux (Fig. 10). The mid-water-column maximum 289 in  $w_{adv}$  (Fig. 11) was estimated from the MoSSea model (Sutherland et al., 290 2011) as  $\Delta Q L^{-1} B^{-1}$ , where  $\Delta Q = 3500 \text{ m}^3 \text{ s}^{-1}$  is the difference in lower-layer 291 volume fluxes between MB\_M and MB\_S, L = 26 km is the distance between 292 the two sections, and B = 5 km is the channel width. In tuning and sensitivity 293 experiments below, the shape of the vertical profile of  $w_{adv}$  was kept constant 294 and multiplied by a factor representing increases and decreases in the exchange 295 flow. 296

<sup>297</sup> Observations of chlorophyll, nitrate and ammonium of PRISM stations along <sup>298</sup> Puget Sound (black solid points in Fig. 2) in June and December showed negli-<sup>299</sup> gible gradients in Main Basin (around  $10^{-3}$  at PSB003: not shown). The small <sup>300</sup> gradients are consistent with the conclusion of *Winter et al.* (1975) that hor-<sup>301</sup> izontal advection is not an important term in the budgets of these tracers in <sup>302</sup> Main Basin.

**Vertical mixing** The vertical diffusivity for tracers  $\kappa_v$  was likewise taken 303 from the 2006 hindcast of the MoSSea model. A climatological vertical profile 304 was constructed by taking the cross-sectional average diffusivity as a function of 305 depth (Fig. 12, black dots) and then averaging in time (blue line). As analysed 306 further below using LiveOcean output, monthly or seasonal variation in mixing 307 appears to be secondary to shorter-timescale variation, and so we have held 308 mixing constant in our representative seasonal cycle. As for vertical advection, 309 experiments in which the intensity of mixing is varied multiply this mean profile 310 by a constant. 311

**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

$$E(z) = E_0 \exp\left[-(att_{bg} \ z + att_{fw} \int_z^0 (32 - S(z'))dz' + att_P \int_z^0 P(z')dz'\right] \ (1)$$

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

These are crucial model parameters, and among the most likely to vary be-317 tween estuarine and coastal environments. Prior to running the model, historical 318 Puget Sound observations were used to estimate these coefficients and deter-319 mine if they substantially different from the values found by Davis et al. (2014) 320 for the Washington–Oregon shelf. Euphotic-zone depths from three years of 321 monthly transmissometer profiles (Newton and Van Voorhis, 2002) agreed well 322 with Secchi Disk depths, which makes euphotic-zone depths a good source to es-323 timate light fields. A linear regression of light attenuation (back-calculated from 324 euphotic depth) and chlorophyll, omitting winter samples, showed high correla-325 tion  $(R^2 = 0.7)$  in the Newton and Van Voorhis (2002) dataset. However, light 326 attenuation is commonly expected to depend on constituents of freshwater as 327 well, and so we used the full record of 19 years (1999 - 2017) DOE sampling at 328 PSB003, which provides coordinated observations of beam attenuation, chloro-329 phyll, salinity, and turbidity. An empirical relationship from Shannon (1975) 330 was used to convert beam attenuation to light attenuation. Turbidity and salin-331 ity are highly correlated in the PSB003 dataset, and a linear regression for light 332 attenuation as a function of chlorophyll and salinity (as in Eq. (1)) showed high 333 correlation  $(R^2 = 0.64)$  and tight bounds on coefficients. 334

The estimate of light attenuation by chlorophyll from this linear model 335 (0.023) was consistent with that derived from the Newton and Van Voorhis 336 337 (2002) three-year dataset described previously (0.026). However, a regression to the PSB003 data omitting salinity explained almost as much variance as the 338 model with salinity. This suggests that salinity or freshwater fraction is not an 339 effective proxy for light attenuation by river-derived material in Puget Sound, 340 possibly because freshwater in Puget Sound originates in such a diversity of 341 watersheds (Cuo et al., 2009; Banas et al., 2014). Thus in PS-1D,  $att_{fw}$  is 342 set to 0, not to imply that river inputs do not cause light attenuation, but to 343 indicate that we lack a useful predictor of this effect. Instead, the mean ef-344 fect of watershed-derived turbidity and dissolved organic matter is captured in 345 the background light attenuation  $att_{bq}$ , which is far higher than attenuation by 346 undiluted seawater in the Davis et al. (2014) model currently used in LiveOcean 347 (Table 3). 348

#### 349 2.3.2 Phytoplankton dynamics

The biogeochemical model in PS-1D is a six-compartment nitrogen budget, nitrate (NO<sub>3</sub>), ammonium (NH<sub>4</sub>), phytoplankton biomass (P), microzooplankton

biomass (Z), and small and large detritus (SD, LD). All six stocks are measured 352 in mmol nitrogen  $m^{-3} = \mu M N$ ; we assume a chlorophyll:nitrogen ratio of 2.5 353  $(mg chl) (mmol N)^{-1}$  to compare the model with observations. Apart from 354 dividing the dissolved inorganic nutrient pool into NO<sub>3</sub> and NH<sub>4</sub> fractions (to 355 match available observations), the model structure and functional forms closely 356 follow Davis et al. (2014), who provide a thorough description, rationale, and 357 validation against nutrient, biomass, and growth- and grazing-rate data from 358 the outer coast. Only the phytoplankton component is described below. 359

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

$$\mu(E, NO_3, NH_4) = \mu_0 \left(\frac{N_{tot}}{k_{min} + 2\sqrt{k_{min}N_{tot}} + N_{tot}}\right) \left(\frac{\alpha E}{\sqrt{\alpha^2 E^2 + \mu_0^2}}\right) \quad (2)$$

where the effective total nutrient concentration  $N_{tot}$  is given by

$$N_{tot} = NO_3 + \varphi_{\rm NH4} NH_4 \tag{3}$$

The uptake preference  $\varphi_{\text{NH4}} = 2$  to take into account that NH<sub>4</sub> is taken up faster than NO<sub>3</sub>. 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 367 on temperature;  $\mu_0$  and other vital rates in the model are defined at typical 368 ambient temperatures, and we assume the temperature-driven change in these 369 rates during one simulation is small compared with other modes of variation and 370 uncertainty (e.g. changes in species composition, or error in the nutrient or light-371 limitation formulations). However, in the sensitivity analysis below, we quantify 372 the likely effect of temperature by adjusting  $\mu_0$ , along with maximum grazing rate and remineralization rate, by a factor  $Q_{10}^{\Delta T/10^{\circ}C}$  for a mean temperature 373 374 shift of  $\Delta T$ . We assume  $Q_{10} = 2$ , a common rule of thumb for temperature 375 response in phytoplankton (Eppley, 1972; Bissinger et al., 2008). 376

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 timeaverage and depth-average of December observations, when the water column is close to homogeneous: initial NO<sub>3</sub> concentration is 27.85  $\mu$ M 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.

#### 384 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 optimisa-391 tion" (PSO, Poli et al. (2007)). In PSO a number of imagined entities—the 392 "particles"—are placed in a search space that consists of a summary measure of 393 goodness-of-fit, the "cost," as a function of the parameters being tuned. Each 394 particle then determines its movement through the search space by combin-395 ing aspects of the history of its own search (its current position and the best 396 fit/lowest cost previously found) with the best fit found across the other mem-397 bers of the swarm, as well as random perturbations. Eventually the swarm as 398 a whole, like a flock of birds collectively foraging for food, is likely to converge 399 on the global optimum of the fitness function. 400

The cost function was defined using the Willmot skill score

$$WSS_{MAE} = 1 - \frac{\frac{1}{N} \sum_{i=1}^{i=N} |m_i - o_i|}{\frac{1}{N} \sum_{i=1}^{i=N} (|m_i - \bar{o}| + |o_i - \bar{o}|)}$$
(4)

where  $m_i$  and  $o_i$  are N matched pairs of model estimates and observations of chlorophyll (Chla), nitrate (NO<sub>3</sub>) and ammonium (NH<sub>4</sub>).

The PSO was run for 300 iterations until each of the 11 parameters con-403 verged, after which we ran a set of 11 experiments varying one parameter at a 404 time, in order to determine whether model behaviour was sensitive to the differ-405 ence between the PSO-derived value and the original Davis et al. (2014) value 406 (Fig. 13). Results allowed us to rank the PSO-derived parameters from greatest 407 effect on model behaviour (initial growth-light slope ( $\alpha$ ), phytoplankton mortal-408 ity  $(m_P)$  to least (sinking rate of detritus, aggregation rate of phytoplankton). 409 This indicates that there are indeed some, but fewer than 11, parameters in the 410 LiveOcean biogeochemical model that need to be changed in order to correctly 411 describe Main Basin. To make a final, practical decision regarding which pa-412 rameters to change, the PSO-derived parameter set was replaced by the original 413 values one at a time, and the series of changes in WSS assessed: at the end, 414 initial growth-light slope  $\alpha$ , phytoplankton mortality  $m_P$ , zooplankton grazing 415 half-saturation  $K_0$ , maximum phytoplankton growth rate  $\mu_0$ , nitrification rate 416  $r_{nitr}$ , and remineralization rate  $r_{remin}$  were changed (Table 3). 417

Model outputs using the final tuned parameters showed good agreement with the observed seasonal cycle of euphotic-zone-integrated NO<sub>3</sub> (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.

### <sup>424</sup> 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<sub>3</sub>, red triangles), and ammonium (NH<sub>4</sub>, 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.

Parameter	Description	$\mathbf{Unit}$	Davis et al.	PS-1D
$\operatorname{att}_{\operatorname{bg}}$	Light attenuation by water column	$m^{-1}$	0.05	0.15
$\operatorname{att}_{\operatorname{fw}}$	Light attenuation by fresh water	$\mathrm{m}^{-1}$	-0.0065	0
$\operatorname{att}_{\operatorname{P}}$	Light attenuation by phytoplankton	$\mathrm{m}^{-1}~\mu\mathrm{M}~\mathrm{N}^{-1}$	0.03	0.026
$\mu_0$	Maximum phytoplankton growth rate	$d^{-1}$	1.7	4
${ m k_{min}}$	Minimum half-saturation for $NO_3$	$\mu { m M}~{ m N}$	0.1	0.1
$\alpha$	Initial growth-light slope	$(W m^{-2})^{-1} d^{-1}$	0.07	0.027
$\varphi_{NH_4}$	Preference for $NH_4$		2	2
$\mathrm{m}_{\mathrm{P}}$	Phytoplankton mortality	$d^{-1}$	0.1	0.163
$m_{agg}$	Phytoplankton loss via aggregation	$(\mu M N)^{-1} d^{-1}$	0.05	0.05
$I_0$	Zooplankton maximum ingestion rate		4.8	4.8
$\mathrm{K}_{0}$	Zooplankton grazing half-saturation	$\mu { m M}~{ m N}$	3	5.3
$\epsilon$	Microzooplankton growth efficiency		0.3	0.3
$m_{MZ}$	Microzooplankton mortality	$d^{-1}$	2	2
$f_{ex}$	Fraction of grazing excreted to $NH_4$		0.5	0.5
$r_{\rm remin}$	Detrital remineralisation rate	$d^{-1}$	0.1	0.25
$w_{s_{SD}}$	small detritus sinking rate	${\rm m}~{\rm d}^{-1}$	8	8
$w_{s_{LD}}$	large detritus sinking rate	${\rm m~d^{-1}}$	80	80
$r_{nitr}$	Nitrification rate		0.1	0.035

Table 3: Final PS-1D tuned parameters for Main Basin, compared with *Davis* et al. (2014) values for the outer coast.  $\mu$ MN = mmol nitrogen m<sup>-3</sup>.



Figure 14: Final PS-1D model outputs (blue line) against observations (gray solid points) of chlorophyll (Chla), nitrate (NO<sub>3</sub>), and ammonium (NH<sub>4</sub>). Chla, NO<sub>3</sub>, and NH<sub>4</sub> were calculated as average integratal over euphotic depth

<sup>427</sup> including turbulent mixing, while the SOG model provides a point of compar-<sup>428</sup> ison for several of these estimates. We use five phytoplankton metrics (i-iv in<sup>429</sup> Sec. 1, with *iii*) subdivided):

- <sup>430</sup> 1. Total annual primary production  $PP_{tot}$ , converted to units of g C m<sup>-2</sup> <sup>431</sup> yr<sup>-1</sup> assuming a C:N ratio of 106:16 mol:mol;
- <sup>432</sup> 2. Date of the spring bloom  $t_{bloom}$ , defined as the day of year when cu-<sup>433</sup> mulative, vertically-integrated phytoplankton biomass reached 15% of its <sup>434</sup> annual total;
- 435
   3. Phytoplankton concentration during the seasonal period and depth layer
   436 associated with steelhead outmigration (*P*<sup>steelhead</sup><sub>outmigr</sub>), mid April-first week
   437 of June (yeardays 109–159), and 0–2 m depth;
- 4. Phytoplankton concentration during chinook outmigration in summer P<sup>chinook</sup><sub>outmigr</sub>
   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<sup>-3</sup>.

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 are related by  $R = aD^b$ , then a and b can be estimated by a linear regression between log D and log R, and the sensitivity of R to D is given by

$$\frac{\partial(\log R)}{\partial(\log D)} \equiv b \tag{5}$$

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  $t_{bloom}$  associated with interannual variability in spring wind stress  $\tau$ , via the effect of wind stress on turbulent mixing ( $\mathbf{E} \to \mathbf{K} \to \mathbf{L}$ , Fig. 1), is given by

$$\Delta t_{bloom} = \Delta(\log_{10}\tau) \cdot \frac{\partial(\log_{10}\kappa_v)}{\partial(\log_{10}\tau)} \cdot \frac{\partial t_{bloom}}{\partial(\log_{10}\kappa_v)}$$
(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 aver-448 ages, i.e. the variance of Apr–Jun (spring) or Jul–Sep (summer) averages across 449 a number of years. (Scales of variation denoted by  $\Delta$  are defined through-450 out as 2 standard deviations.) In some cases, we have no means of calculat-451 ing interannual variation in this way: for example, variation in the exchange 452 flow (and hence vertical advection, under our assumptions) has been calcu-453 lated across one annual cycle in LiveOcean (MacCready et al., in prep) but 454 never across a useful ensemble of years. In these cases, we interpret the known 455 event-scale (10 d) variation as a high upper bound on the unknown interan-456 nual variation. In other cases, it is not clear whether seasonal averages are 457 indeed the timescale on which the environment drives variation in phytoplank-458 ton dynamics. For example, across three years of data from a high-time-459 resolution profiling buoy in Carr Inlet in South Puget Sound (ORCA, 2011-460 2013, https://nwem.apl.washington.edu/about\_proj\_ORCA.shtml), it is possible 461 462 to identify three events in which a transient peak in stratification is followed by a transient phytoplankton bloom (arrows, Fig. 15); whereas correlations be-463 tween stratification and chlorophyll on the monthly scale and longer are weak 464 to nonexistent. Thus we calculated and report event-scale (10 d) variation for 465 select quantities as an aid to interpretation and source of follow-on hypotheses. 466



Figure 15: Bottom–surface density difference ("drho,", in  $sigma_t$  units) and chlorophyll (vertically integrated, mg m<sup>2</sup>) 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.



Figure 16: Histograms of stratification, mixing and environmental forcing at a section across central Main Basin, from the LiveOcean model, 2017–2018.



Figure 17: Scatter plots of stratification  $\log_{10} \delta \rho$  versus drivers.

# 467 **3** Results

### 468 3.1 Dynamics of stratification and mixing

In the time series derived from LiveOcean, stratification  $\delta \rho$  is significantly cor-469 related with and mixing  $\kappa_v$  and riverflow  $Q_r$  with maximum lagged correlation 470 471 occuring 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 472 of estuarine circulation in which stratification primarily reflects the competition 473 between the homogenizing effect of mixing and the stratifying effect of river 474 discharge. Near-surface mixing  $\kappa_v$  is significantly correlated with wind stress  $\tau$ 475 and stratification  $\delta \rho$ , but not tidal velocity  $u_T$  or river discharge  $Q_r$  (Fig. 18). 476 Variation in near-bottom mixing is, in contrast, primarily explained by the tides 477 (not shown). 478

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).

<sup>484</sup> The sensitivity of stratification to temperature is derived directly from the



Figure 18: Scatter plots of mixing  $\log_{10} \kappa_v$  versus drivers.

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 489 row describes a family of model runs in which one driving variable at a time 490 was varied around its base-case value. Sensitivities are not normalised and are 491 expressed in disparate units, and thus are difficult to evaluate in themselves; 492 they constitute an intermediate step in the overall scaling analysis. Independent 493 estimates of the sensitivity of spring bloom date to mixing, temperature, and 494 light (in the southern Strait of Georgia, not Main Basin) were also calculated 495 from the SOG model (Table 5), as described in Sec. 2.2. 496

<sup>497</sup> Means and scales of variation for all other quantities required for the final <sup>498</sup> scaling analysis are given in Table 6. Scales of variation in turbulent mixing <sup>499</sup>  $(\log_{10} \kappa_v)$  are derived from the sensitivities reported in Table 4. Other quantities <sup>500</sup> are derived directly from observational and model time series as described in <sup>501</sup> 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  $\pm$  0.2 in log<sub>10</sub> units, or 60%), while on the interannual scale, wind stress variations largely average out and drive much less variance in mixing ( $\pm$  0.05 vs. 0.12–0.14 in log<sub>10</sub> 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 s	stratification an	$d \ wind \ stress$				
Regression	$\log_{10} \kappa_v = a + b \cdot \log_{10} \rho_z + c \cdot \log_{10} \tau$						
equation							
Intercept	a	$-2.56 \pm 0.57$	LiveOcean,				
			2017 - 2018				
Sensitivity of	$b \equiv \frac{\partial (\log_{10} \kappa_v)}{\partial (\log_{10} \kappa_v)}$	$-0.89 \pm 0.37$	LiveOcean,				
mixing to	$O(\log_{10} \delta p)$		2017-2018				
stratification							
Sensitivity of	$\partial(\log_{10}\kappa_v)$	$0.67\pm0.29$	LiveOcean,				
mixing to wind	$C \equiv \frac{1}{\partial (\log_{10} \tau)}$		2017 - 2018				
stress		0.83	SOG				
Other sensitivities							
Sensitivity of	$\partial(\delta  ho)$	1.87	DOE obs., spring				
stratification to	$\overline{\partial Q_r}$	1.14	summer				
riverflow							
Sensitivity of	$\frac{\partial(\delta\rho)}{\partial T_{22}}$	0.18	Equation of state				
stratification to	0120		at 30 psu, $12^{\circ}$ C;				
surface			assumes no change				
temperature			below 20 m				

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

spring values from Table 6 for  $t_{bloom}$  and  $P_{outmigr}^{steelhead}$ , summer values for  $P_{outmigr}^{chinook}$ and  $\delta t_{nut}$ , and whichever is larger in each case for  $PP_{tot}$ . Estimates are also 513 514 given for long-term change over 50 y, under the single climate projection used 515 in CCSM3/WRF/ROMS (Table 2). Estimates of spring-bloom-date variation 516 based on event-scale variability in the drivers, as opposed to seasonal averages, 517 are also shown; the analogous calculations for the other phytoplankton metrics, 518 which describe seasonal patterns rather than events, would not be interpretable. 519 However, the expected variability driven by the exchange flow (via  $w_{adv}$ ) and 520 via changes in light attenuation are expressed as "much less than the variability 521 one would calculate based on event-scale changes in  $w_{adv}$  and  $att_{bq}$ ," since we 522 lack a basis for quantifying the interannual variation in seasonal averages of 523 these drivers. 524

Results are given in the same units as the base-case values of the five metrics, 525 which are also shown in Table 7 for comparison. For each metric, the scale-526 setting, largest effects are marked with a \*\*, and other effects within half an 527 order of magnitude, or a factor of 3, are marked with a \*. These categories 528 together are considered "major effects" and the others are considered "minor." 529 Either variation in surface PAR or the effect of riverflow on turbulent mixing 530 (via stratification) is the scale-setting driver for each of the five metrics, and 531 the effect of light attenuation is consistently in the class of potential major 532 effects. Interannual variation in  $N_{deep}$  does not have a major effect on any 533 of the phytoplankton metrics. Other drivers (wind stress, the exchange flow, 534

8	n spring bloon $\begin{array}{c} \begin{array}{c} & t_{bloom} \\ \hline & \\ \end{array} \end{array} \left( \begin{array}{c} \\ \end{array} \right) \\ \begin{array}{c} t_{bloom} \\ \hline \end{array} \right) \\ \begin{array}{c} \end{array} \left( \begin{array}{c} \\ \end{array} \right) \\ \begin{array}{c} \end{array} \right) \\ \begin{array}{c} \end{array} \\ \begin{array}{c} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \right) \\ \begin{array}{c} \end{array} \\ \begin{array}{c} \\ \end{array} \end{array} \right) \\ \begin{array}{c} \\ \end{array} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \\ \end{array} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \\ \end{array} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \\ \end{array} \\ \end{array} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \\ \begin{array}{c} \\ \end{array} \\ $
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All values are derived from	
Response of phytoplankton metrics (columns) to variability in physical drivers (rows).	v experiments in PS-1D except for three values estimated from SOG for comparsion.
Table 5:	senstivit



Figure 19: Relationship between  $\log_{10}$  stratification (5–20 m density minus 0–5 m density) and  $\log_{10}$  riverflow (summed for the eight rivers discussed in Sec. 2.1) in historical observations. Separate regressions are shown for spring (light green) and summer (dark green), although the slopes of these regressions are not significantly different ( $p \downarrow 0.05$ ). A larger marker is used to highlight the drought year 2001 discussed by Newton et al. (2003).

near-surface temperature) are found to have potentially major effects on some
 metrics but not others.

### 537 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.

#### 541 4.1 Primary production

Annual primary production, perhaps by integrating over so many transient as-542 pects of the plankton dynamics, shows the clearest results, the strongest sepa-543 ration between major and minor effects. Variation in light limitation outweighs 544 variation in nutrient limitation, in the sese that an increase in vertical mixing 545 (which decreaes light exposure but increases nutrient supply) has an overall neg-546 ative effect on  $PP_{tot}$  seasonally-averaged incoming PAR appears to be sufficient 547 to drive  $\sim 15\%$  variation in annual primary production (Table 7). Sample-to-548 sample variation in background light attenuation—i.e. all effects of water-mass 549 variation and freshwater influence, excluding self-shading by phytoplankton—is 550 on the same scale ( $att_{bg} = 0.15 \pm 0.03 \text{ m}^{-1}$ : Table 3) and varying  $att_{bg}$  on 551 this scale in the PS-1D model also leads to ~ 15% changes in  $PP_{tot}$ , but we 552 expect that much of this variability in  $att_{bq}$  averages out on seasonal timescales. 553

Source	USGS obs., 1964–2018	NNRP/WRF, $1950-2010$	LiveOcean, 2017–2018	DOE obs.		see Table 4	NNRP/WRF, 1950–2010	continental slope,	ROMS Cascadia,	2002 - 2009		DOE obs.,	December LiveOcean, 2017				
Comments	spring summer	spring	spring summer	0–20 m, spring summer	spring, via $ au$ spring, via $\delta a$ . $\Omega_{-}$	summer, via $\delta\rho$ , $Q_r$	spring summer								derived from $Q_{ex}$	confidence limits on regression	
Event-scale variation (2 s.d.) $\Delta x  \Delta(\log_{10} x)$	0.28 0.38	0.24	0.440.44		0.16	0.15 0.24	34 43						1500		0.99	0.03	ıg analysis.
Interannual variation (2 s.d.) $\Delta x  \Delta(\log_{10} x)$	0.19 0.22	0.082 0.078	)	$1.2 \\ 0.8$	0.05	0.05 0.14	8.6 8.6	0.02		1.4		2.8					ty used in the scalin
$Log mean \ (\overline{\log_{10} x})$	3.1 2.8	-1.9 -2	- 0.04 -0.3		-3.8	-3.8											ntal variabili
$Mean$ $(\overline{x})$	$1300 \\ 680$	0.015 0.012	1.25 0.57	10.2 $12.9$	$2.5\times10^{-4}$	$2.0  imes 10^{-4}$	119 112					27.6	3500		2.34	0.15	of environme
Symbol	$Q_r$	μ	$\delta  ho$	$T_{20}$		$\kappa_v$	$E_0$	$\Delta  ho_{oc}$				$N_{deep}$	$Q_{ex}$		$w_{adv}$	$att_{bg}$	: Estimates
Units	${ m m}^3~{ m s}^{-1}$	$\mathbf{Pa}$	${\rm kg}~{\rm m}^{-3}$	D°	- -	$m^2 s^{-1}$	${ m W~m^{-2}}$	${\rm kg}~{\rm m}^{-3}$				mmol $m^{-3}$	${ m m}^3~{ m s}^{-1}$		$m  day^{-1}$	$\mathrm{m}^{-1}$	Table 6
Quantity	Riverflow	Wind stress	Stratification	Temperature		Mixing	Surface PAR	Ocean	sourcewater	density Ocean	sourcewater	Main Basin	deep nutrients Exchange flow	transport	Vertical advection	Background light	avvenuarion

	ual primary roduction	Date	e ot spring c	loom	Phyto steelhead	conc. during d outmigration	Phyto - chinook	conc. during outmigration	Duratic nutri	on of strong ent stress
	$PP_{tot}$		$t_{bloom}$		$(\operatorname{spri}_{P})$	$\mathop{\mathrm{ing}} olimits, \left( 0-2\ \mathrm{m} ight)$	$P_{e}$	$\operatorname{ner}, \operatorname{0-15} \operatorname{m})$	5	$\delta t_{nut}$
Base-case value	1140		127			27		36		8
gC	$0~{\rm m}^{-2}~{\rm yr}^{-1}$		yearday		Ĩ	${ m g~C}~m^{-3}$	mg	$_5 ~{ m C} ~m^{-3}$		d
$\begin{array}{c} Scale \ of \ variability  50 \ \overline{y} \\ in \ \rightarrow \ via \ \bot \end{array}$	Interann.	50 y	Interann.	Event	50 y	Interann.	50 y	Interann.	50 y	Interann.
Wind stress $\tau$ (via 5	2	0	1.1	3.3	0	0.52	0.57	0.19	土 11	4
mixing)										
Riverflow $Q_r$ (via 5.1 stratification and mixing)	10	-3.7	7.5**	$13^{*}$	1.8	3.5** 3.5	0	0.79	0	$16^{**}$
Errohon and Anni A	102		1 1 1	и 1		Ø €1		0.00		*00 1
via vertical $\sqrt{ex}$	CI ≯⁄			0.1		10'N ≫		70.0		07 3
advection)										
Deep nutrient	25		0			0.64		0.87		2.8
concentration										
$N_{deep}$										
Near-surface 30	18	<u>ب</u>	1.8		0.42	0.25	-0.09	0.024	11	2.8
temperature $T_{20}$										
Surface PAR $E_0$	$170^{**}$		$7.6^{**}$	$38^{**}$		$3.3^{**}$		3** 0		$8.6^{*}$
Background light attenuation $att_{bg}$	$\ll 170^*$		$\ll 4.5^*$	4.5		$\ll 1.4^*$		$\ll 2.3^*$		$\ll 18^*$

Fable 7: Scales of variation in five metrics of phytoplankton production ( $PP_{tot}$ , etc.) associated with seven climate-linked lrivers ( $\tau$ , etc.). Interan. and Event indicate interannual variation in seasonal averages, and variation among 10 d averages vithin one season, respectively, and are given as an absolute value corresponding to 2 s.d. of variation in the driver. 50 $\prime$ indicates total change between $\sim$ 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 otentially of the same order of magnitude (i.e. within a factor of 3).	
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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 559  $PP_{tot}$  on interannual and longer timescales. This may be because changes in 560 mixing have opposite effects in spring (via light) and summer (via nutrient sup-561 ply), or because while turbulent mixing shows intense variation on short time 562 and spatial scales, it is relatively steady in seasonal averages (2 s.d. < 40%563 variation, compared with around threefold variation over a typical tidal cycle). 564 The other metrics in our analysis suggest the increased process complexity be-565 hind phytoplankton dynamics on event to seasonal scales, as opposed to annual 566 averages. 567

#### 568 4.2 Spring bloom timing

Variation in surface PAR (via variation in cloud cover) again emerges as a crucial 569 influence on variation in spring bloom timing in central Main Basin (Table 7, 570 Fig. 20). Historical variation in seasonally-averaged  $E_0$  is sufficient to explain 571 perhaps a 15 d range of spring bloom dates ( $\pm$  2 s.d.: Table 7), while event-572 (10 d) scale variation in  $E_0$  is several times larger (Table 6) and leads to more 573 than 2-month variation in  $t_{bloom}$  in PS-1D ( $\pm$  2 s.d.). The actual historical 574 variation in  $t_{bloom}$  in Main Basin is unclear, since monthly DOE sampling could 575 easily miss the bloom entirely and high-time-resolution ORCA chlorophyll time 576 series are only available for a handful of years. However, the longer model-577 based estimate is close to the assessment by Newton and Van Voorhis (2002) 578 (spring bloom March–May, 1999–2001) and also close to observed spring-bloom 579 variability over 60 years in the southern Strait of Georgia. 580

The experiment in PS-1D that generated this estimate, in which we took 581 event-scale variability in  $E_0$ , applied it over an entire annual cycle, and measured 582 the change in spring bloom date, is mechanistically sensible enough if the spring 583 bloom is a process with a short memory, a response to an event-scale confluence 584 of suitable conditions. The SOG model predicts the southern Strait of Georgia 585 spring bloom on the basis of Dec–Mar average conditions (Collins et al., 2009; 586 Allen and Wolfe, 2013); but there is no observational evidence that the Main 587 Basin spring bloom is a response to seasonal-average conditions in this sense, 588 and anecdotal evidence to the contrary (Fig. 15). 589

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 ~ 2 d (W m<sup>-2</sup>)<sup>-1</sup>), but also a lower sensitivity to temperature (1.5 vs. 4.7 d (°C)<sup>-1</sup>) and wind stress (20 vs. 70 d Pa<sup>-1</sup>, 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 <sup>599</sup> has the same scale of effect as  $E_0$  in seasonal averages. This ranking is consistent <sup>599</sup> with the finding that in Main Basin, riverflow variability has stronger effects on <sup>600</sup> mixing in spring than does wind stress (Table 6). Other than this, the minor <sup>601</sup> differences in the ranking of controls on the spring bloom between our analysis <sup>602</sup> and *Allen and Wolfe* (2013) appear to be driven mainly by differences in the <sup>603</sup> phytoplankton models used (PS-1D vs. SOG), rather than differences between <sup>604</sup> 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-606 sumed period of juvenile steelhead and chinook outmigration and chinook out-607 migration, as an indication of possible changes in the light environment during 608 a critical life stage for these fish. We speculate that the effect of a dense phyto-609 plankton bloom on visual refuge and predation during this period would come 610 through light scattering, not through light attenuation, and so we cannot di-611 rectly compare the changes in the underwater light field that would result from 612 the phytoplankton changes we model from the changes in light that drive the 613 phytoplankton dynamics; however, this comparison would have to be made by 614 studies that attempted to follow on from the results here. Overall, we find pre-615 dicted changes in phytoplankton concentration,  $P_{outmigr}^{steelhead}$  and  $P_{outmigr}^{chinook}$ , to be 616 quite modest, on the order of 10% (Table 7). This might reflect the structural 617 simplicity of PS-1D, or it might be an indication that if phytoplankton blooms 618 have an effect on visual predation by and on juvenile salmoni, it is primar-619 ily through intense, transient, localised blooms, not through seasonal-average 620 conditions. Surface PAR, underwater light, and (in the case of steelhead out-621 migration) riverflow effects on mixing drive the largest of these generally small 622 effects. 623

#### <sup>624</sup> 4.4 Nutrient stress in summer

Although PS-1D does not resolve phytoplankton succession, the incidence of 625 days in which nutrients become severely limiting can provide a clue to likely 626 compositional changes during summer. Nutrient limitation under warm, high-627 light conditions has long been taken to encourage dinoflagellate blooms over 628 diatoms, including toxin-producing taxa like *Alexandrium*; however, there is no 629 detailed historical record in Puget Sound that supports a local link between 630 nutrient limitation and Alexandrium HABs more directly. The metric  $\Delta t_{nut}$ 631 counts the days in which surface NO3 + NH4 is less than 3 mmol  $m^{-3}$  in 632 PS-1d, a threshold that identifies an extreme but regularly occurring level of 633 nutrient stress: its base-case value is 8 d per year. 634

Historical variation in seasonally-averaged surface PAR and in riverflow effects on stratification and mixing are both sufficient to drive variation in  $\Delta t_{nut}$ between approximately 0 and 2–3 times its base-case value (Table 7). Nearsurface temperature and wind mixing do not appear likely to explain year-toyear variability but may well drive dramatic long-term trends (toward more

frequent or sustained nutrient stress in the case of temperature, and also to-640 ward higher nutrient stress if the prevailing northerly summer winds increase in 641 strength: Table 7, Moore et al. (2015)). Changes in the exchange flow and back-642 ground light attenuation could potentially also drive nutrient-stress changes of 643 the same magnitude as the other mechanisms mentioned, but without a better 644 quantification of seasonal-average patterns in these processes we cannot be sure. 645 For  $\Delta t_{nut}$  and to a lesser extent  $t_{bloom}$ , new temperature effects beyond the 646 range of historical variability seem likely to emerge over the next few decades, 647 if they have not already. Note that the effect of warming on nutrient stress 648 in general, as discussed here, is likely accompanied by an independent effect 649 of warming on *Alexandrium* growth rate and seasonal window of opportunity 650 (Moore et al., 2015). 651

## **552** 5 Conclusion

The results of our multi-model synthesis and scaling analysis yield relatively sim-653 ple pictures for interannual variation in primary production and phytoplankton 654 standing stock in Main Basin (Fig. 20), in which a large number of potential 655 pathways of climate influence can be classed as minor effects compared with 656 657 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  $\Delta t_{nut}$ , 658 both processes that involve event-scale changes atop seasonal changes. For these 659 metrics, a large number of mechanistic pathways all seem capable of producing 660 variations in phytoplankton dynamics on the same scale. This process com-661 plexity, and not just the incompleteness of available observations, may explain 662 why simple correlative approaches to the Puget Sound spring bloom have never 663 vielded a clear picture. 664

Overall, this study points to variation in incoming light, i.e. variation in 665 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 667 timing of the spring bloom in the southern Strait of Georgia, although in that 668 system (and the SOG model) wind mixing plays a comparable role, whereas in 669 Puget Sound, riverflow effects on stratification and mixing exceed wind effects 670 in spring (the two mechanisms are comparable in summer). (Moore et al., 2015) 671 previously suggested that long-term trends in Puget Sound hydrology, toward 672 increased riverflow in spring and decreased flow in summer (*Cuo et al.*, 2009, 673 2011), might affect phytoplankton dynamics by modulating stratification and 674 thus turbulent mixing. Our analysis of the relationship between riverflow and 675 stratification (in historical observations) and stratification and mixing (in mod-676 els) suggests that this pathway of influence likely drives significant interannual 677 variation in phytoplankton dynamics as well, not just long-term trends, and in 678 summer as well as spring. 679

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 variablity 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 687 models have the potential to address, and a problem that might usefully serve 688 as a nucleus for the next generation of coupled atmospheric-hydrologic-marine 689 modelling in the Puget Sound basin. At the same time, the problem highlights 690 gaps in our process understanding that can only be addressed through high-691 resolution observations and process studies, such as the role of plasticity and 692 photoacclimation in modulating the response of the Puget Sound phytoplankton 693 community to the light environment, and in setting the timing of the spring 694 bloom. This need for broad and coordinated collaboration among modellers 695 and observationalists of many stripes is likely a general characteristic of the long 696 mechanistic chains that link climate variability and change to the dynamics of 697 marine food webs. 698

# **Acknowledgements**

This work was funded by Long Live the Kings, as part of the Salish Sea Marine Survival Project; the NOAA Monitoring and Event Response for Harmful
Algal Blooms (MERHAB) program; Marine Alliance for Science and Technology Scotland (MASTS); and University of Strathclyde. Many thanks to Eric
Salathé, Correigh Greene and Dave Beauchamp for their insights.

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