Appendix J.
Microalgal Biomass and Primary Productivity

This appendix contains summaries, descriptions, and statistics reflective of regional microalgal biomass and primary productivity observational data sets, and comparisons with model predictions. For definitions of terms, including statistical performance metrics, refer to the glossary in the main report.

ADA Accessibility

This appendix may contain tables, graphics, and images that may not meet accessibility standards. The Department of Ecology is committed to providing people with disabilities access to information and services by meeting or exceeding the requirements of the Americans with Disabilities Act (ADA), Sections 504 and 508 of the Rehabilitation Act, and Washington State Policy #188. To request an ADA accommodation, contact the Environmental Assessment Program Publications Coordinator at EAPPubs@ecy.wa.gov or call 564-669-3028. For Washington Relay Service or TTY call 711 or 877-833-6341. Visit Ecology's website for more information.[1]

[1] https://ecology.wa.gov/about-us/accessibility-equity/accessibility

Table of Contents

Page

Biomass and Primary Production Rates **2**
Brief overview of phytoplankton characterization and bloom timing in the U.S. Salish Sea 2
Long-term chlorophyll-a data sets in the U.S. Salish Sea 4
Measurements of primary productivity in Puget Sound 16
Highlights of SSM primary production algorithms 18
Chlorophyll-a predictions 19
Comparison of Predicted and Observed Biomass in 2014 using Chlorophyll-a as a Proxy **22**
Comparison of Observed and Predicted Primary Production Rates **28**
Summary **33**
References **34**

Biomass and Primary Production Rates

Primary, microalgal production is the foundation of marine ecosystem function and nutrient cycling. Winter et al. (1975) aptly described key processes that drive large primary production variability in Puget Sound, including vertical mixing due to bathymetric features and local winds, density-driven stratification, variations in incoming solar radiation, and freshwater flows. SSM simulates each of these drivers.

Microalgal biomass, expressed in units of carbon in the water column, is often estimated via a proxy, chlorophyll-a, the dominant photopigment in pelagic phytoplankton. Chlorophyll-a can be coupled with other observations and estimates of the carbon to chlorophyll ratio to estimate total biomass in terms of carbon. In Puget Sound, we have a long history of year-round (generally monthly) chlorophyll-a measurements at specified long-term stations, whereas carbon to chlorophyll-a (C:Chl-a) ratio observations are less abundant.

Primary production rate or productivity is the rate of growth in terms of mass per area per time and has long been recognized as a parameter that is not easily measured (Jassby and Platt 1976; Cloern et al. 2014). Primary productivity data sets in Puget Sound are available for shorter spans of time than chlorophyll-a measurements.

When comparing biomass or primary productivity data with model predictions, Cerco and Noel (2004) point to the importance of fully considering the details of the measurements and their approaches so that comparisons with simulations are most meaningful. Accordingly, the following sections provide a brief overview of the most abundant phytoplankton species (which can impact the C:Chl-a ratio), timing of blooms, chlorophyll-a measurements as a proxy for phytoplankton biomass and primary production measurements in the U.S. Salish Sea. We then present SSM predictions and comparisons with observations.

Brief overview of phytoplankton characterization and bloom timing in the U.S. Salish Sea

Phifer (1933) identified diatoms at Friday Harbor, San Juan Island, finding four species of diatoms (*Chaetocerus compressus, Chaetocerus debilis, Chaetocerus radicans,* and *Skeletonema costatum*) that comprised about 65% of the total number of cells present from about 50 species he collected from May to June 1931. The predominant diatom genus present was *Chaetocerus*.

In addition to diatoms, dinoflagellates constitute the other important group of marine phytoplankton that inhabit WA waters of the Salish Sea (Thomson and Phifer 1936). About half of the species of dinoflagellates are autotrophs or mixotrophs and so have the capability to produce organic carbon via photosynthesis (Taylor et al. 2008).

Collias et al. (1974) published the *Atlas of physical and chemical properties of Puget Sound and its approaches* based on measurements from 1954 through 1966. While biological metrics were not included in that compilation, the markedly different surface dissolved oxygen levels featured in the atlas point to the timing and spatial extent of blooms. We see, for example, that dissolved oxygen became saturated or supersaturated at the surface as early as March from Admiralty Inlet, through the Main Basin to Devil's Head, in 1960. And those surface waters were generally saturated with dissolved oxygen during cruises that occurred May through September in multiple years (1953, 1954, 1955, 1957, and 1958). These data portray the seasonal period of higher density blooms.

Newton et al. 1997 reported that at most Puget Sound stations, blooms tend to occur in April and May and in September and October, but some stations within embayments/ inlets also experience blooms throughout the summer. For example, Eisner and Newton (1997) reported that blooms in Budd Inlet in 1992 – 1994 occurred from March through October, with the largest blooms occurring in July through September.

NOAA's compilation of Puget Sound research cites one to three diatom genera as numerically dominant in the spring bloom (*Chaetocerus, Skeletonema, Thalassiosira,* and *Coscinodiscus*), with a reported potential succession to dinoflagellates later in the summer (NOAA 1981). NOAA also reported that the toxic and red tide dinoflagellate, *Gonyaulaux catenella*, the agent producing saxitoxin, which causes paralytic shellfish poisoning, had never been recorded in Puget Sound before 1978. Data suggested at that time that dinoflagellates were more abundant in South Sound and in embayments.

Horner (1992) observed microflagellates less than 10 µm, followed by the size fraction 10 to 20 µm were the top fractions of dinoflagellates in cells per liter, and identified *Dinophysis acuminata* and *Peridinium spp.*, in Budd Inlet in March 1992. Horner (2003) reported that *Pseudo-nitzschia spp*. are common in Pacific Northwest marine waters and are present in every month of the year, though they are rarely the dominant genus in blooms.

More recently, reviewing over a ten-year span of data, Hannach (2022) found that *Chaetocerus* is the dominant diatom genus within the King County stations with blooms from spring to late summer and contributing close to half the annual phytoplankton biomass. Regarding flagellates, Hannach (2022) reported that their proportions vary greatly from year to year. *Ceratium*, gymnodinioid dinoflagellates, and *Akashiwo sanguinea* were the largest contributors to flagellate biomass, together making up on average 55% of the total flagellate biovolume, and small unidentified dinoflagellates and *Heterosigma* were the most abundant flagellate categories. These are all mixotroph organisms except for the gymnodinoid dinoflagellates, which are heterotrophs. Another showy, heterotrophic dinoflagellate that often attracts attention when blooming is *Noctiluca*. Pool et al. (2015) documented the spatial extent of Noctiluca blooms in Puget Sound in 2011 – 2015.

In terms of carbon to chlorophyll ratios(C:Chl-a), Jakobsen and Markager (2016), via a large study comprised of over 7500 temperate seawater samples, determined that C:Chl-a increased from spring to summer. The summer C:Chl-a ratios values ranged from 20 to 96, and these ratios were related to the annual mean of the total nitrogen concentration.

Using volumetric image analysis, Hannach (2022) reports a POC:Chl-a (w/w) median ratio on an annual basis of 75 g/g at the central basin locations, reflective of the large seasonal variability of species and environmental drivers reported, as well as non-phytoplanktonic particulate carbon. Spilling et al. (2015) conducted experiments on parameters driving the growth of a *Chaetocerus* species. They found that the C:Chl a ratio had a wider range at the lowest temperature during exponential growth, ranging from 16 to 48 (weight ratio) at 3°C compared with 17 – 33 at 11°C. Chan(1980) found that for equal cell volume, diatoms have a lower C:Chl-a ratio than dinoflagellates. He also found that as the succession of diatoms to dinoflagellates occurs from spring to summer due to differences in light, temperature, and nutrient availability, the C:Chl-a ratio increases with increasing nutrient availability. So, C:Chl-a ratios vary and depend on environmental factors, even when focusing on a single phytoplankton species.

Long-term chlorophyll-a data sets in the U.S. Salish Sea

Western Washington University recently made available a long-term set of oceanographic observations from Shannon Point Marine Center (SPMC), located in Anacortes (Van Alstyne et al. 2024). Figure J-1 shows the location of the SPMC. Chlorophyll data in this data set are available starting in November 1992 through 2023, though not continuously over that time. Every month of the year is represented for most years, often for about 9 days or more, but there are years with missing observations in some months.

SPMC data can be geographically considered representative of waters flowing in the Rosario Strait, in the northern portion of the Washington waters of the Salish Sea. The chlorophyll-a concentrations at this station are relatively low year-round (mean = 0.87 µg/L and median = 0.52 µg/L). A maximum value (75.2 µg/L) occurred only once (in March 1995) and constitutes an almost two orders of magnitude high outlier, far beyond the interquartile range. Otherwise, as seen in Figure J-2 (top), concentrations fluctuate between winter lows and summer highs, with a few high outliers that stay below 20 µg/L. The interquartile range is 0.29 – 1.01 µg/L. The lowest monthly mean occurs in January (0.23 µg/L), and the highest monthly mean is in July (1.44 µg/L).

The Northwest Association of Networked Ocean Observing Systems (NANOOS), a regional association directed by UW, posts current and historical data from seasonal UW Salish Sea cruises from 1998 to the present. Stations measured during these cruises are shown in Figure J-1. Chlorophyll measurements are available from about spring 2016 to present in that data set for cruises through the Strait of Juan de Fuca to the Main Basin, and within the Main Basin, Hood Canal, and Whidbey Basin. Figure J-2 (bottom) shows the NANOOS data plotted over time. The interquartile range is 0.12 – 0.80 µg/L, median and mean equal 0.28 and 0.87µg/L, respectively. Outliers, values above 1.5 times the interquartile range, occur more often than at SPMC, and range more widely up to the peak observation (99.47 µg/L). The lowest and highest monthly means in this data set vary by region, as shown in Table J-1.

Though high concentrations of chlorophyll produced during intense blooms are more consistently found and higher in magnitude within the Puget Sound observations in the NANOOS data set—as is clear when comparing the plots in Figure J-2 which have a higher y-axis scale for the NANOOS data set plot— the interquartile range and mean are similar to the SPMC data from the Rosario Strait. This is not too surprising since the NANOOS data set also contains a large portion of measurements within the more open northern waters of the Salish Sea, including waters from the Strait of Juan de Fuca, Haro Strait and Admiralty Inlet (which is a confusing misnomer, as it is not an inlet at all, but refers to the waters flowing between the Strait of Juan de Fuca and the Puget Sound).

Within Central Puget Sound, King County started reporting chlorophyll-a bi-monthly at eight to ten ambient marine stations in 2008 (Stark and Martin 2022). At most of these central basin stations, Stark (2022) reports that the highest chlorophyll concentrations usually occur during the spring bloom around April, indicated by surface chlorophyll-a levels increasing to around 20–35 µg/L.

The Department of Ecology's Marine Monitoring Unit (Ecology-MMU) maintains the longest running chlorophyll-a data set spanning over 25 stations throughout the WA waters of the Salish Sea, with greater station resolution inside Puget Sound. Data are collected monthly and are available upon request for the last fifty years, except for the year 2020. Aside from that, the data set has only a few other limited gaps. Data quality before 1999 varied.

The Ecology data set can be split into pre- and post-1999, when laboratory methods and field collection methods consistent with standard oceanographic procedures and quality assurance plans were implemented. Since 1999, no significant method changes have confounded data trends (Bos et al. 2015). Figure J-3 contains a map of stations that have mostly remained unchanged from those utilized between 1973 and 1998, though not all stations are monitored every year. A few new stations were added over time, as shown in Figure J-3.

The post-1999 data set includes both bottle/laboratory and in situ fluorescent profiling measurements collected by sensors. We focus in this appendix on a review of the bottle measurements for two reasons: (1) the earlier measurements consisted of only bottle measurements, (2) in situ fluorescence measurements may exhibit biases (Roesler et al. 2017). However, appendices E-H contain comparisons of all chlorophyll-a measurements with model predictions, including those conducted via in situ fluorescence, for completeness.

C. Krembs (personal communication, February 2025) noted that in a highly stratified region like Hood Canal, discrete measurements at 0, 10, and 30 m can miss the chlorophyll-a maxima most of the time and so may not be the best measurement choice. In situ fluorescent profiles are calibrated based on discrete samples at 10 and 30m to avoid surface quenching of photopigment by sunlight, and regression methodologies (Laws and Archie 1981; Ricker 1973) applied during the fluorescent instrument calibration are intended to account for natural variability.

Table J-2 contains percentile values for both pre- and post-1999 Ecology data sets. Table J-3 shows the means, which are in a similar range (around 4 µg/L), but four times higher than the WWU and NANOOS data sets. The Ecology data set means are reflective of the fact that these data sets represent observations mainly within the greater Puget Sound and include waters with restricted flushing, such as within multiple embayments. The median value is 1.90 and

1.52 µg/L, respectively, for the pre- and post-1999 periods. The interquartile range for these data sets is 0.70 – 5.33 and 0.51 – 5.17, respectively, for the pre- and post-1999 periods.

Figure J-4 shows the Ecology-MMU pre- and post-1999 discretely sampled chlorophyll-a data at 0, 10, and 30 m plotted over time. The pre-1999 data set has a maximum value of 466 µg/L (in Hood Canal station HCB004 on August 2, 1995), which was removed so that the scale of the plot would be commensurate with the rest of the data. It is the highest value ever recorded. Post-1999, the peak value recorded was 249.15 µg/L, coincidentally also measured at station HCB004 on September 14, 2000.

Given that the data are split roughly in half (25 years for each half) and comprised of mostly the same stations, it is interesting to note that there are 3.6 times more data points above 30 µg/L in the post 1999 data (166 data points above 30 µg/L) than in the pre-1999 period (46 data points above 30 µg/L).). Chl-a samples were not kept frozen during transport in coolers before 1999, which may have resulted in serious bias to the pre-1999 data (personal communication with C. Krembs in February 2024).

Even though there are dozens of measurements above 30 µg/L, Table J-2 shows that 30 µg/L falls within the 99^{th} and 99.5^{th} percentiles of the distributions in both the pre- and post-1999 data sets. This indicates that values above 30 µg/L do exist but constitute the tail end of the distributions at percentiles greater than the 99.5^{th} percentile.

Figures J-5 and J-6 contain boxplots of the chlorophyll-a data grouped by station and ordered from lowest to highest median value. The station with the lowest concentrations measured pre-1999 was the NRR001 (Tacoma Narrows) station, located in an area of high vertical mixing. The two next lowest stations pre-1999 are HCB003 and HCB007 in Hood Canal, showing only one event higher than 20 µg/L. The station with the highest chlorophyll measurements in the pre-1999 data set is QMH002 (Quartermaster Harbor). Conversely, in the post-1999 data set, new stations in the Strait of Juan de Fuca were added (SJF00, SJF002, and SJF001), which constitute the stations with the lowest concentrations in that data set. HCB003 and HCB007 moved up in order of higher concentrations, both with at least one excursion above 50 µg/L in the post-1999 data set. The station with the highest concentrations measured in that data set was ELD002 (Eld Inlet in South Sound).

In addition to that long-term data set, Ecology conducted various special studies over the years. A notable one is the South Puget Sound Study, which was focused on all south sound inlets and the area of the main basin south of Edmonds. The study consisted of Phases 1 and 2. During this study, Roberts et al. (2008) observed that blooms typically occurred one month earlier and at higher levels in South Sound than in Central Sound.

Albertson et al. (2002) reported marine water quality conditions for Phase 1 of the South Sound study. Their observations on seasonality and spatial distribution of chlorophyll-a are summarized as follows: "During both April and September cruises, high concentrations (chlorophyll a > 40 µg/L) were observed in surface waters, but these blooms are a highly localized phenomenon. Transects of Carr and Case Inlet show that these blooms have restricted horizontal and vertical distributions even within an inlet."

For the second phase of that study, Roberts et al. (2008) reported: "The highest chlorophyll-a concentrations (>30 µg/L) were observed during spring and summer 2007 in Budd, Totten, Eld, Henderson, Carr (central and north) and Case Inlets, as well as north Pickering Passage and Oakland Bay. The lowest levels relative to other stations were found at the Nisqually Reach and Tacoma Narrows stations and generally during the winter at all stations."

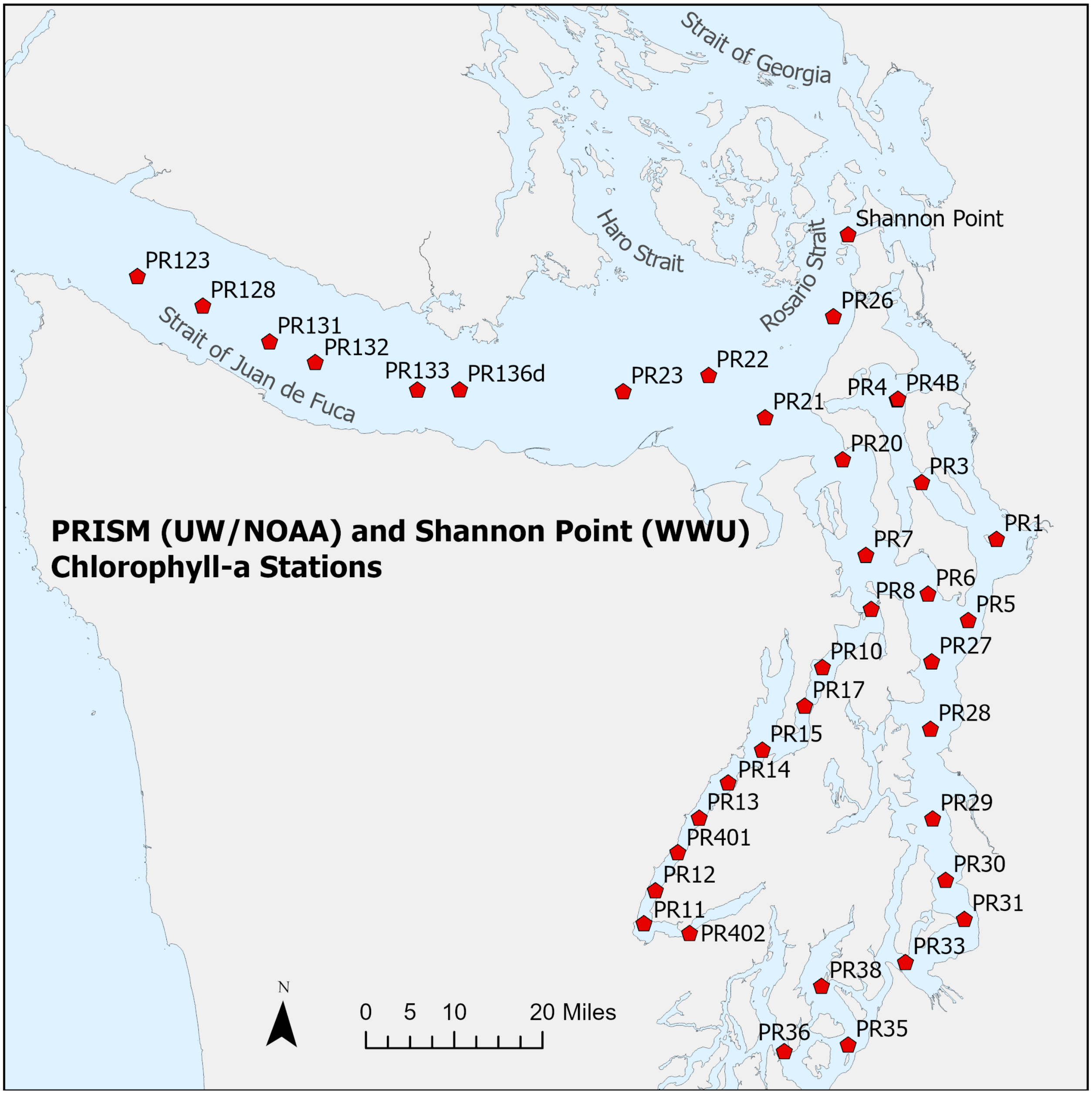

Figure J-1. Map of PRISM(NANOOS) UW and WWU (Shannon Point) chlorophyll-a stations.

Table J-1. Observed Chlorophyll-a (Chl-a) Statistics for NANOOS Data (2016 – 2024).

Region	Average Chl-a (µg/L)	Min Chl-a (µg/L)	Max Chl-a (µg/L)	Station and Date of Max
Admiralty	1.23	0.00	30.64	PR7 (05/06/2023)
March	0.50	0.45	0.81	
April	1.22	0.00	9.93	
May	1.04	0.01	30.64	
June	2.51	1.23	11.27	
July	1.39	0.10	15.53	
September	0.94	0.00	6.03	
October	1.46	0.03	5.72	
Hood Canal	1.20	0.00	100.39	PR12 (07/25/2018)
April	1.43	0.00	56.42	
June	2.43	0.00	19.19	
July	1.26	0.00	100.39	
September	0.80	0.00	27.09	
Main Basin	0.62	0.00	70.58	PR28 (05/06/2023)
March	0.35	0.14	2.18	
April	0.71	0.00	27.29	
May	0.78	0.04	70.58	
June	0.86	0.00	25.36	
July	0.74	0.00	50.60	
September	0.41	0.00	57.04	
October	0.62	0.03	9.83	
SJF	0.69	0.00	47.06	PR22 (07/12/2017)
March	0.25	0.06	0.72	
April	0.56	0.02	3.96	
May	0.47	0.05	18.03	
June	0.82	0.12	5.03	
July	0.84	0.00	47.06	
September	0.98	0.00	14.54	
October	0.29	0.00	10.18	
South Sound	1.40	0.00	54.16	PR38 (07/11/2023)
April	1.52	0.00	27.32	
July	1.33	0.00	54.16	
September	1.35	0.00	23.72	
Whidbey Basin	1.39	0.00	73.60	PR4 (06/27/2022)
April	1.34	0.00	45.58	
June	3.62	0.00	73.60	
July	1.15	0.00	60.68	
September	1.28	0.00	46.21	
Overall	0.95	0.00	100.39	PR12

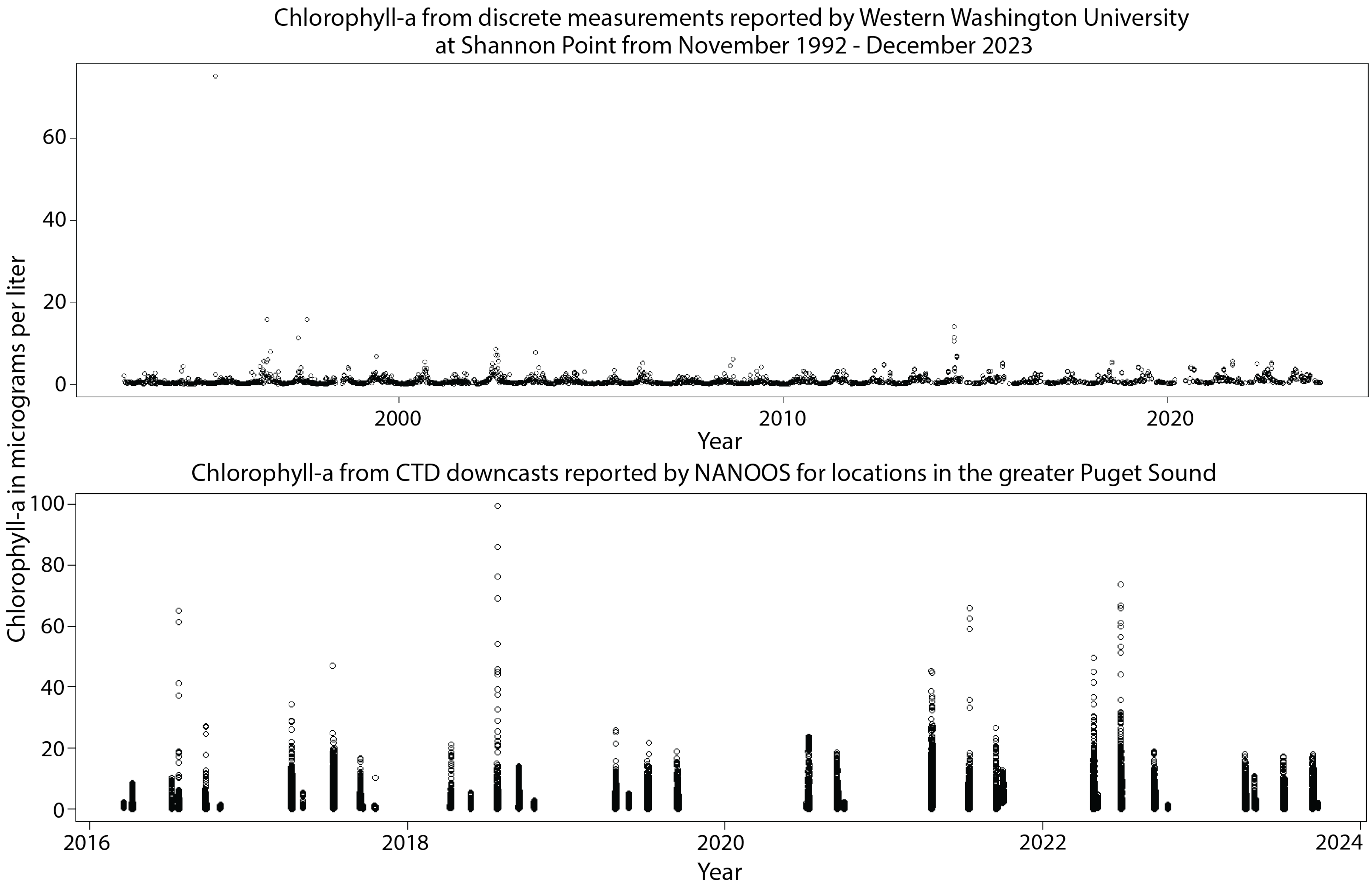

Figure J-2. Time series plots of chlorophyll-a from WWU Shannon Point Station (top) and NANOOS data set (bottom)

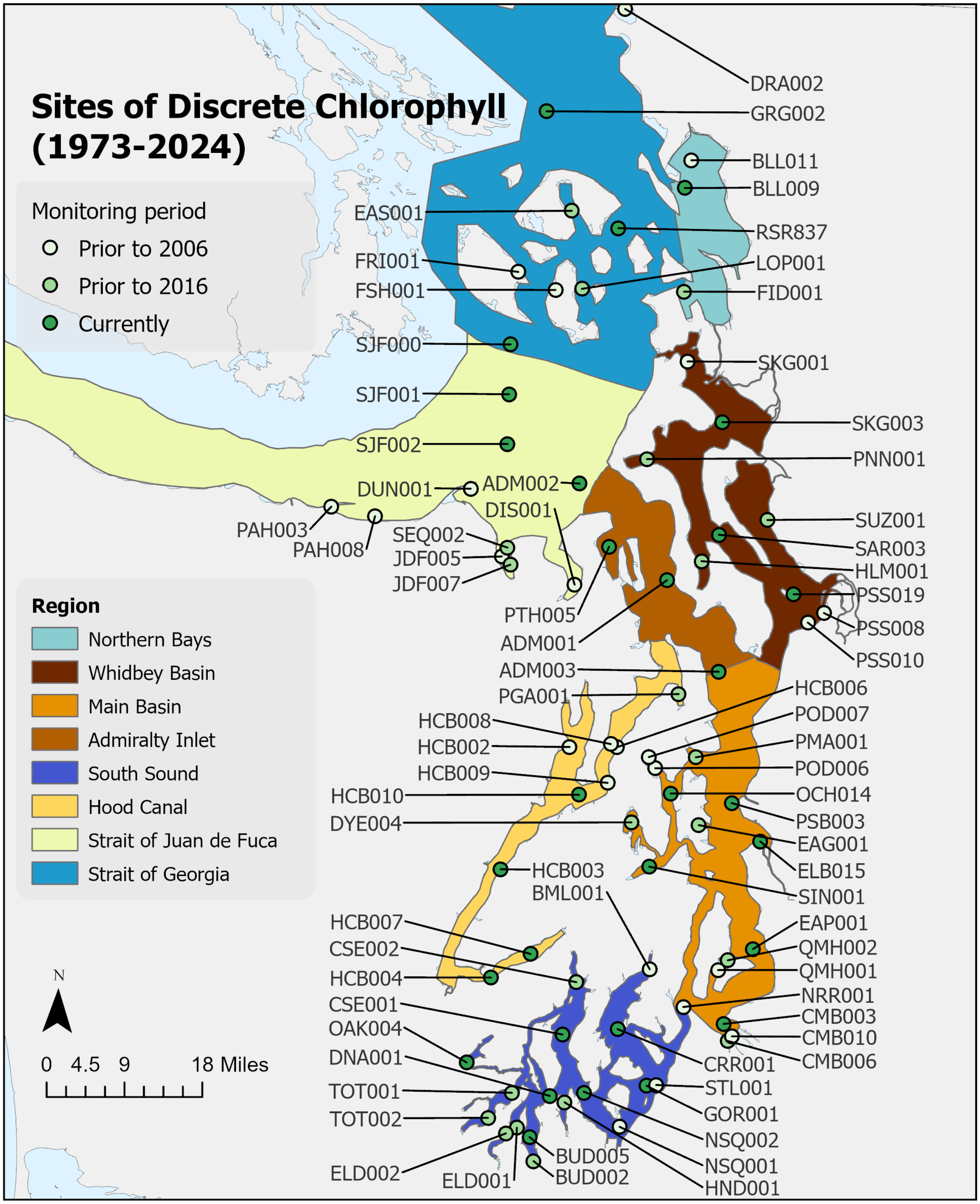

Figure J-3. Ecology Marine Monitoring Unit (MMU) chlorophyll-a stations

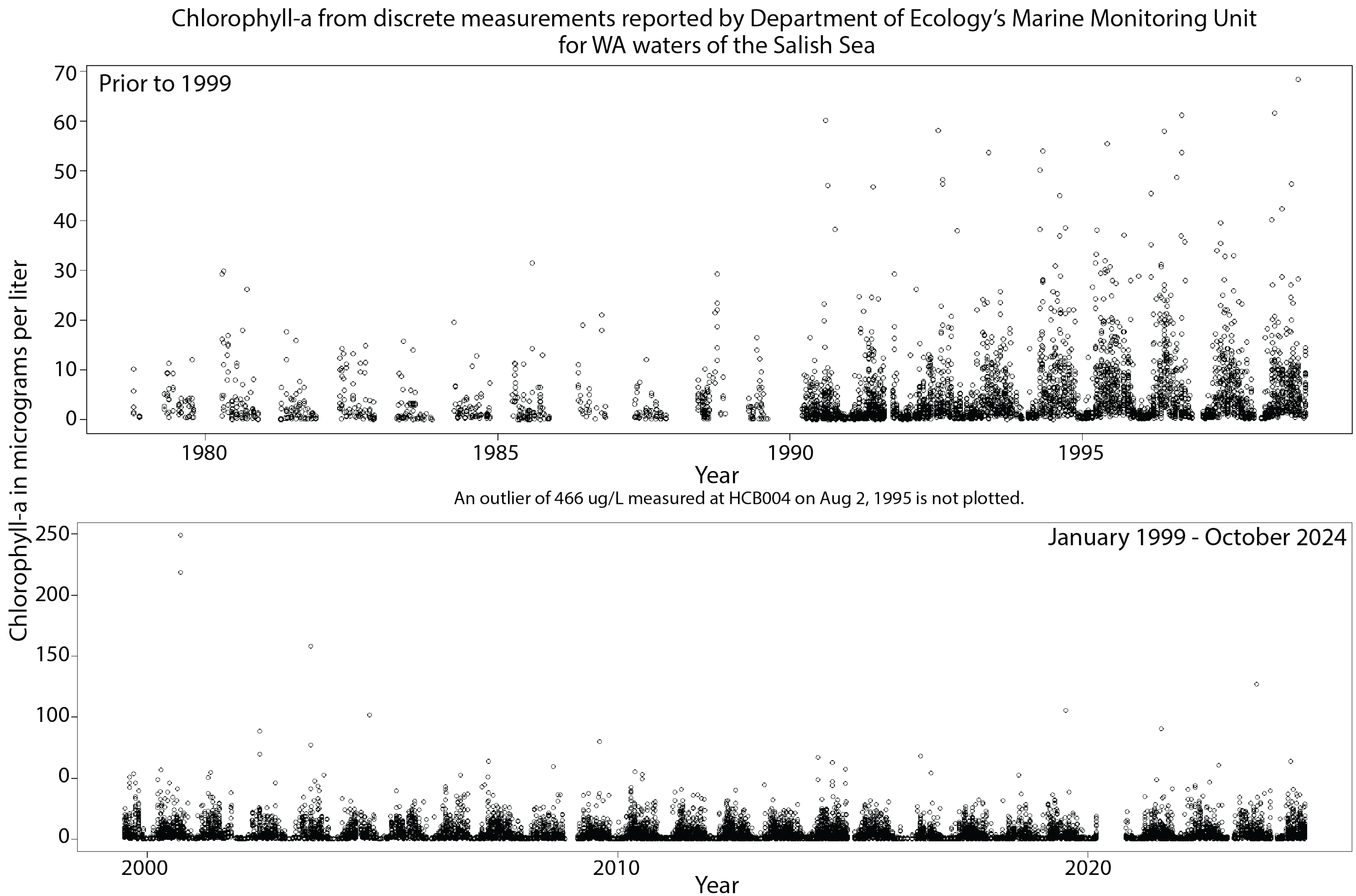

Figure J-4. Time series plots of chlorophyll-a from the WA Department of Ecology's Marine Monitoring Unit. Data from 1973 to 1998 (top) and from 1999 to 2024(bottom).

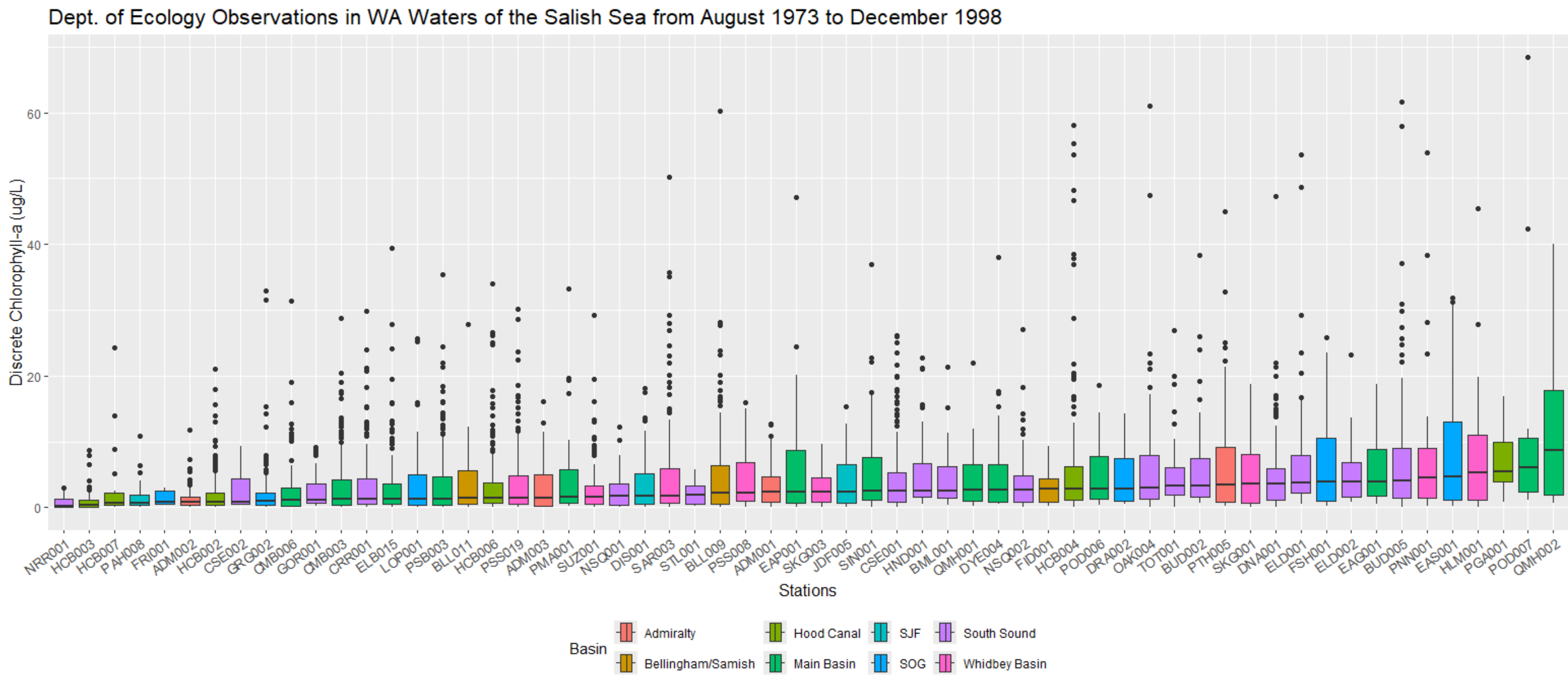

Figure J-5. Boxplots by station of chlorophyll-a from WA Department of Ecology's Marine Monitoring Unit. Data prior to 1999.

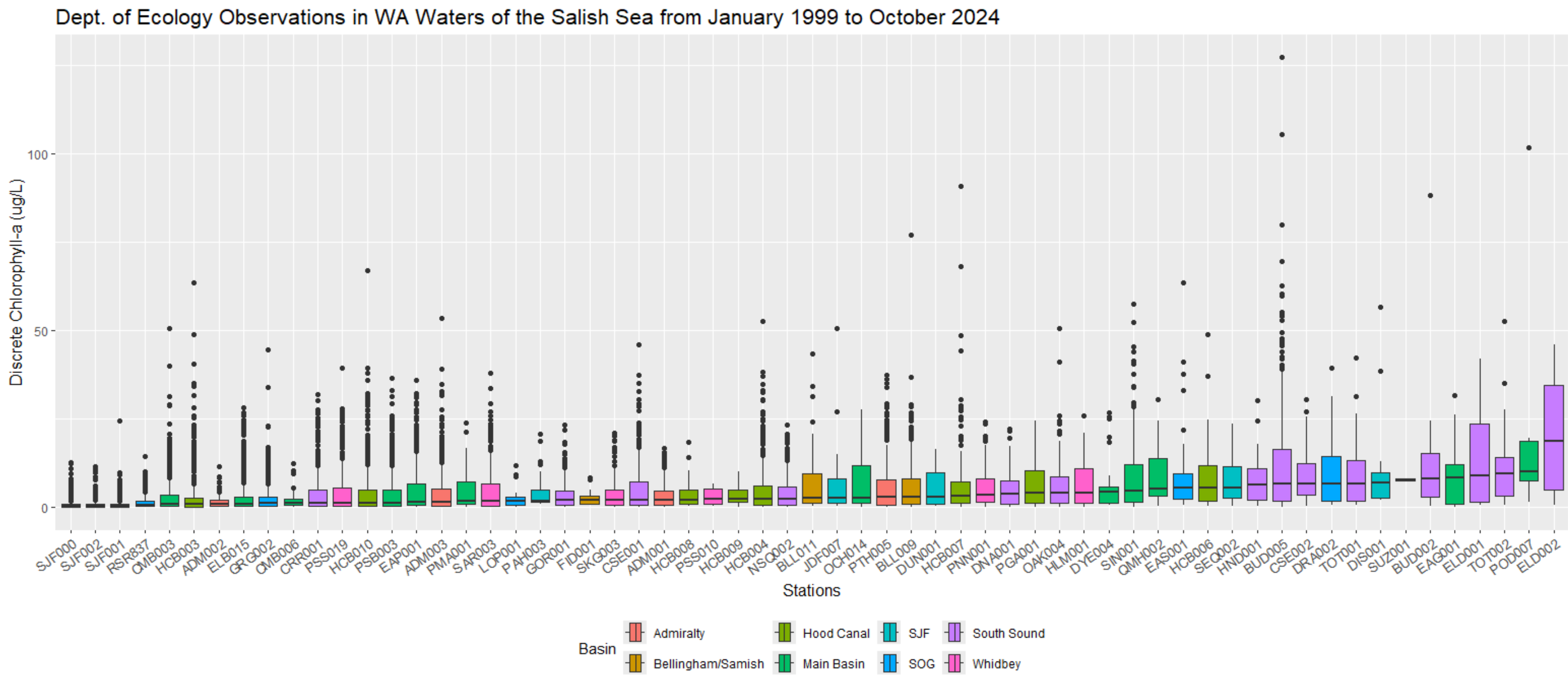

Figure J-6. Boxplots by station of chlorophyll-a from WA Department of Ecology's Marine Monitoring Unit. Data from 1999 to 2024.

Table J-2. Observed chlorophyll-a percentiles in µg/L for Ecology's Marine Monitoring Unit's data sets (pre and post 1999).

Percentile	25%	50%	75%	80%	90%	95%	97%	98%	99%	99.50%	99.75%	99.76%	99.99%	99.999%
Observations from 8/1973 to 12/1998	0.70	1.90	5.33	6.70	10.90	15.40	19.62	23.25	29.24	38.04	47.68	48.08	64.96	68.06
Observations from 1/1999 to 10/2024	0.51	1.52	5.17	6.65	11.56	16.99	20.89	24.00	29.34	36.67	45.85	46.09	172.48	243.72

Table J-3. Observed chlorophyll-a mean in µg/L for Ecology's Marine Monitoring Unit's (MMU) data sets (pre and post 1999).

MMU's Chlorophyll-a Data Sets	Mean
August 1973 to December 1998	4.36
January 1999 to October 2024	4.23

Measurements of primary productivity in Puget Sound

Although various researchers have measured productivities in Puget Sound (e.g., Winter et al. 1975; Campbell et al. 1977), reporting varies both in time-averaged values and incubation times, which can impact the outcome of the measurement. Welch (1968) reported 4 to 5 g C/m^2 /day during the peak annual bloom in 1965 near the mouth of the Duwamish. Newton et al. (1998) reported almost 6 g C/m^2 /day peak GPP in Budd Inlet. Campbell et al. (1977) reports spring peaks equivalent to 5.8, 4.8 g and 5.6 C/m^2 /day during 1966, 1967, and 1975 respectively, at a main basin station off West Point. The highest peak value reported at that station occurred at the end of August in 1975 and was close to 10 g C/m^2 /day.

We are aware of two systematic efforts to measure primary productivity in Puget Sound using similar methodologies and averaging times. Ebbesmeyer and Helseth (1977) reported primary productivities for the central Puget Sound observed between the years 1964 and 1967 using ^{14}C tracer methods. The highest peak value reported is 6.5 g C/m^2/day, and the highest annual mean value reported is 2.3 g C/m^2/day. The peak values measured in the 1960s and 1970s for the Main Basin are lower than peak values measured decades later in the Main Basin, as discussed below.

Between 1997 and 2007, Ecology either conducted or partnered with others to conduct primary productivity measurements in Puget Sound. Primary production rates within Ecology's Marine Monitoring program were obtained using modifications to methods originally published by Strickland and Parsons in 1968 and are referenced in Newton et al. (1998).

The primary production measurement method Ecology used consists of adding ^{14}C-labeled bicarbonate to seawater samples collected from six depths at specified light levels within the euphotic zone (near 100%, 50%, 25%, 12%, 6%, and 1% surface irradiance), as determined from Secchi disk calculations. The mass of carbon uptake into algal cells due to photosynthesis was calculated from the count of liquid scintillation activity measured in the filtered solids post-24-hour incubation after exposure to light levels that mimic in situ conditions (Newton et. al. 1998; Newton and Reynolds 2002; Newton and Van Voorhis 2002). Ecology's database includes measurements at each depth, and reported values are depth-integrated.

Primary production measurement methodologies can be prone to biases (Vandermuelen et al. 2022). Observations based on ^{14}C uptake can present difficulties in interpretation due to various confounding effects from light and dark algal respiration, refixation of respired ^{14}C, and differences in incubation protocols (Cloern et al. 2014 and references contained therein). Notably, these measurements are published as "primary productivity," but do not distinguish whether they are "net" or "gross." This reflects a challenge in specifying whether the observations represent GPP, which is defined as purely the photosynthetic rate (Bender et al. 1987), or net productivity, which includes a measure of algal respiration. Bender et al. (1987) suggests that ^{14}C productivity measurements may fall between CO_2 net production, representative of NPP, and GPP.

Only a subset of the primary production data in the Ecology database has been published to date. Projects using ^{14}C-derived primary productivity data included UW-led projects such as the Coastal Intensive Site Network (CISNET) and Puget Sound Regional Synthesis Model (PRISM). Data through 2003 were compiled into the Ecology database and were quality-assured and analyzed. However, based on available documentation, it is unclear whether data after 2003 went through a quality assurance process.

Even though the general method approach employed for the historic primary productivity measurements in Ecology's database was the same when using on-deck ambient light incubations, they cannot be directly compared to measurements in the laboratory at UW because incubation procedures varied. On-deck incubations allow for variable light regimes to simulate the solar radiation diel cycle while adjusting for lower light levels at depth using shading screens (personal communication with J. Newton, August 19, 2024).

On the other hand, light levels in laboratory incubations were kept constant during the time of incubation. A researcher who worked with Professor Mary Jane Perry's laboratory, one of the UW principal investigators, stated that the incubations took place under constant light conditions corresponding to each simulation of in situ depth (B. Sackmann, personal communication, July 22, 2024). In the compiled data set, we believe most samples were on-deck measurements performed under variable light, but this is not entirely clear based on available documentation. Whether light levels were kept constant or not is important for interpretation.

Descriptions of productivity within both South Sound and locations in Main Basin are illustrative. Researchers point out higher productivity in South Sound locations as well as within the Main Basin in two separate studies highlighted below.

Newton and Reynolds (2002), referring to primary productivity in South Sound, found that:

"April had the highest [productivity] values (around 6000 mg-C/m^2 d), reflecting the spring bloom, while July and September had moderate values (around 3000 mg-C/ m^2 d) and December had very low values (~30 mg-C/ m^2 d), reflecting light limitation and cold temperatures. These values are similar to those reported in Budd Inlet (Newton et al. 1998) and are relatively high when compared to other estuaries, suggesting that South Puget Sound is very productive. Spring (April) integrated productivity values at all South Puget Sound stations were quite similar, ranging from 5,100 to 6,400 mg-C /m^2/d. Spatial variation increased during the summer months (July and September) with ranges from 2,300 to 4,300 and 2,100 to 5,200 mg-C/ m^2 d, respectively."

Newton and Van Voorhis (2001) studied four sites over three years in the central main basin and north of it: West Point, Point Wells, Admiralty Inlet, and Possession Sound. West Point reached the highest mean daily productivity averaged over all three years, 3190 mg C/m^2/day. However, individual peak daily measurements were much higher:

"Seasonal variation in production is well-defined for all four stations, with values integrated over the euphotic zone during summertime (May – September) as high as 13,000 mg/m^2/d which drop to less than 100 mg C m^2/d during wintertime. During the middle of the growing season (April – June), a reduction in production was measured at all stations. Similar variation in biomass, as measured by chlorophyll a, was also seen."

Highlights of SSM primary production algorithms

SSM is a carbon-based model. To simulate primary production, SSM computes at each time step and spatial node the mass of carbon that phytoplankton photosynthesize. Jassby and Platt (1976) developed a mathematical formulation for the relationship between photosynthesis and light, which Cerco et al. (2004) incorporated into the biogeochemical ICM algorithms employed in SSM. Their formulation is coded in SSM as shown in the equations below, calculated at each time step.

GPP1= P1 (I,K) * B1 (I,K)

GPP2=P2 (I,K) * B2 (I,K)

GPP (I,K)= (GPP1+GPP2) * D(I) *DZ2D(I,K)

NETP1= (P1 (I,K) * (1- PRSP1)-BM1 (I,K))*B1 (I,K)

NETP2= (P2 (I,K) * (1- PRSP2)-BM2 (I,K))*B2 (I,K)

NPP(I,K)=(NETP1+NETP2)* D(I) *DZ2D(I,K)

Where:

I: Horizontal index

K: Vertical index

P1(I,K) and P2 (I,K): Production rate of algal groups 1 and 2 at I, K (d^{-1})

GPP1 (2): Gross primary production of algal groups 1 or 2 (g C/m^3/day)

NETP1 (2): Net primary production of algal groups 1 or 2 (g C/m^3/day)

D(I): Current depth at I (m)

DZ2D(I,K): Delta-sigma value at I, K (dimensionless)

PRSP1 (2): Fraction of production consumed in photorespiration for algal groups 1 and 2

(0 < PRSP < 1)

BM1(2): Basal metabolism of algal groups 1 and 2 (d^{-1})

B1(2): Algal biomass for groups 1 and 2 (g C/m^3)

GPP(I,K): Gross primary productivity (g C/m^2/day)

NPP(I,K): Net primary productivity (g C/m^2/day)

Two values of the carbon-to-chlorophyll ratio are employed in SSM. For algal group 1, the ratio is 37, and for algal group 2, the ratio is 50 g C/g Chl-a. These ratios are within the wide range of measured ratios in Puget Sound. Algal group 1 can be thought of as corresponding to the diatom group in the spring bloom. The carbon to chlorophyll ratio (C:Chl-a) for algal group 1 in the SSM is within the range that Spilling (2015) reported for a species of *Chaetocerus*, a key dominant genus in our domain. The ratio for algal group 2, which corresponds to the latter mix of diatoms and dinoflagellates in the summer and fall, is about 35 % higher than the spring ratio, which agrees with Chan's (1980) findings that for equal cell volume, diatoms have a lower C:Chl-a ratio than dinoflagellates.

Chlorophyll-a predictions

Figures J-7 and J-8 show planview maps of the predicted chlorophyll-a depth-averaged annual maxima, minima, and mean for each of the four years that we have conducted model runs. SSM predicts that the highest chlorophyll levels occur in terminal inlets and embayments. This spatial pattern remains similar across all years.

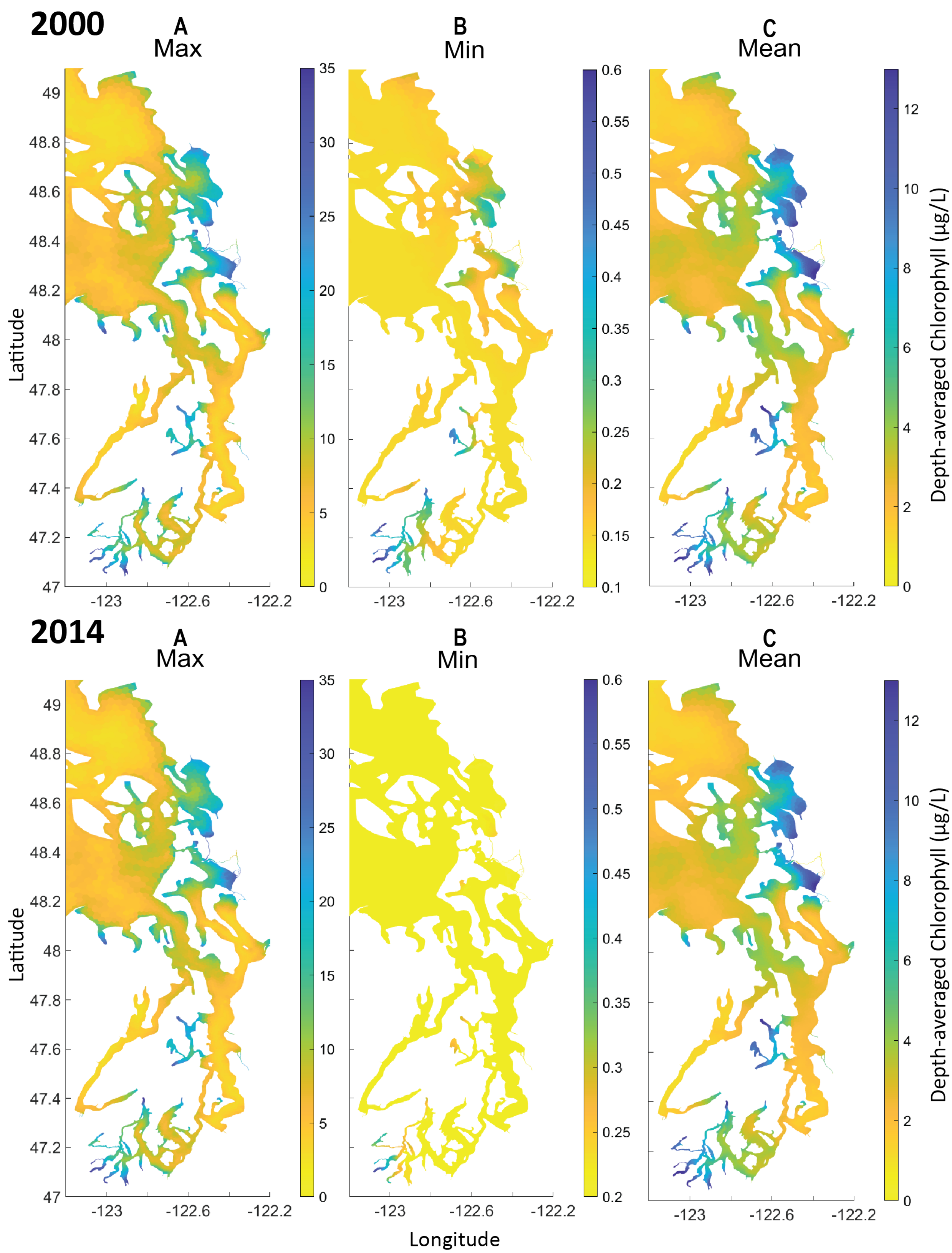

Figure J-7. Planview maps of maximum, minimum, and mean depth-averaged chlorophyll-a SSM predictions for the years 2000 (top) and 2014 (bottom).

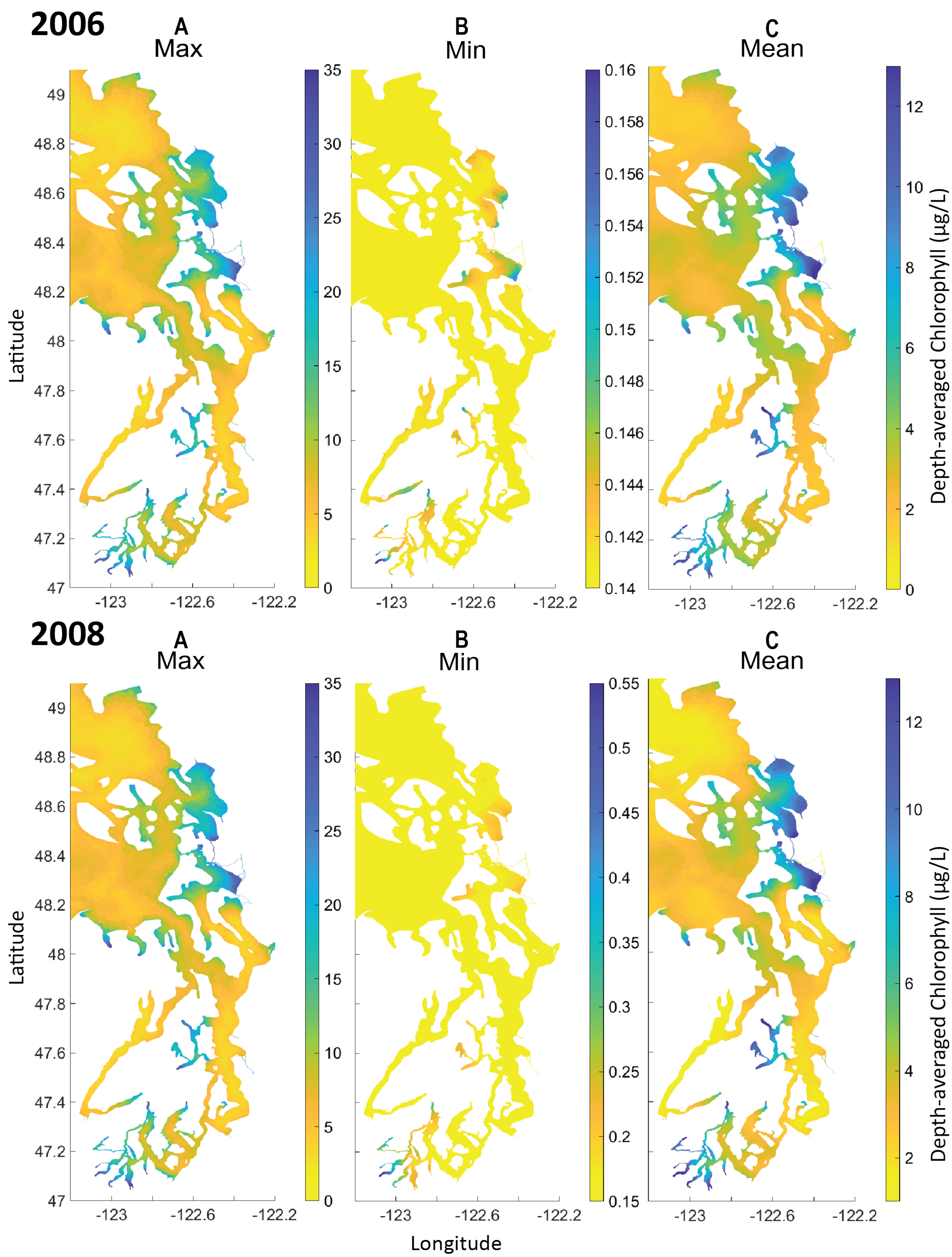

Figure J-8. Planview maps of maximum, minimum, and mean depth-averaged chlorophyll-a SSM predictions for the years 2006 (top) and 2008 (bottom).

Comparison of Predicted and Observed Biomass in 2014 using Chlorophyll-a as a Proxy

Predicting biomass in terms of chlorophyll-a within a daily or sub-daily timestep presents challenges to both mechanistic and empirically based models (Stow et al. 2003). The reason for this is the stochasticity inherent in the system dynamics and the complexity of systemic drivers. Particularly vexing phenomena to simulate are subsurface chlorophyll maxima layers, which result from intricate biogeochemical interactions and can occur on vertical scales of 1 m down to very thin layers and are often the result of stratification, shear, and nutrient gradients, among other drivers (Cullen 2015).

Mechanistic models are designed to predict averages at temporal and spatial scales, which cannot resolve relatively short-term peaks and subscale patchy algal blooms. We paired predictions with observations in both space and time in the strictest sense for comparative purposes. Predictions are paired with the closest coincident observations in time (within 0.5 hours) at the corresponding vertical layer and geographical measurement location. Appendices E-H contain a full set of model skill plots and statistics (scatterplots, time series, time-depth plots, and depth profiles) comparing chlorophyll-a predictions to observations at every site individually. Overall performance varies slightly by year, with a correlation coefficient for chlorophyll-a falling around 0.5, and the RMSE ranging from around 3-5 micrograms per liter.

An established target for model performance specific to chlorophyll predictions does not exist, but it is relevant to consider the predictive error relative to the observational range. Scott Wells (S. Wells, personal communication, 2020) suggested the use of the mean absolute error (MAE) divided by the range of the observations, referred to here as MAE fraction or MAE_f.

Table J-4 shows that the overall MAE_f for all years falls within 1 and 1.7 percent. Overall, prediction errors for all years are well within the lower quartile of the range of observations. Upon segregating the prediction/observations pairs by measurement location, model skill among locations varied, and most stations in 2014 (37 out of 41 or about 90%) had MAE_f below 25% of the observational range. Figure J-9 shows the MAE_f statistic for all locations where measurements are available for 2014.

As shown in Figure J-10, while the shape of the predicted and observed cumulative distribution functions is similar, both exponential functions approach an asymptote around 5 µg/L; the observations have a longer tail, which is truncated in the figure so that the scale between the two of them is comparable. The model underpredicted peak algal bloom events, thus underpredicting chlorophyll-a maxima at the tail end of the observed distribution. Table J-5 shows that the 99.975th percentile of the observed distribution is around 30 µg/L, but a few much larger values, above 100 µg/L, were measured and represent values above the 99. 99th percentile of the distribution. On the other hand, in terms of the medians, Table J-5 shows that the model underpredicted the median by 0.25 µg/L in 2000, and overpredicted it by 0.6 µg/L, 0.43 µg/L, and 0.3 µg/L in 2006, 2008, and 2014, respectively.

To further visualize the seasonal biomass predictions in relation to observations, Figure J-11 contains boxplots ordered by month of the paired observed and predicted values at three locations in 2014 within inlets (SIN001 is in Sinclair Inlet and HCB007 in Lynch Cove, Hood Canal) and an embayment (ELB015 is in Elliott Bay).

In some cases, the median predictions are higher than the observed and vice versa, yet modeled and observed ranges overlap in most cases and months. The model reproduces the low concentrations in January and February. In March, it predicted the spring bloom in 2014 in SIN001 and HCB007, but not in ELB015. The model generally predicted the magnitude and timing of the biomass at SIN001 for the rest of the year, whereas at HCB007 it underpredicted the magnitude of the biomass in July, August, October, and November. In ELB015, the model overpredicted the magnitude of the observed biomass in April but underpredicted it in June. Nonetheless, given the naturally high variability in phytoplankton biomass, the model reasonably reproduced biomass within the observed ranges.

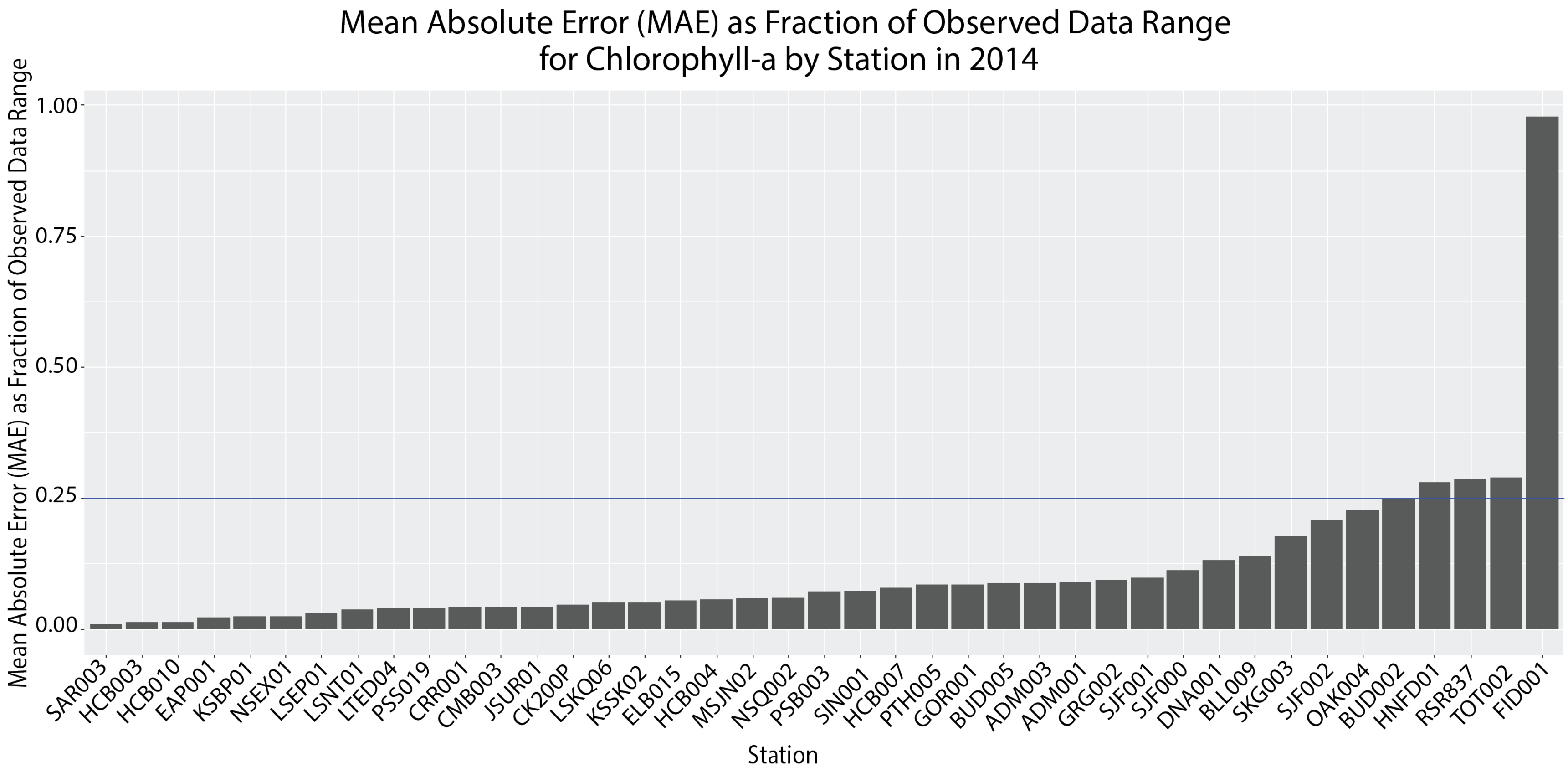

Figure J-9. Mean absolute error for chlorophyll-a as a fraction of the data range for the year 2014.

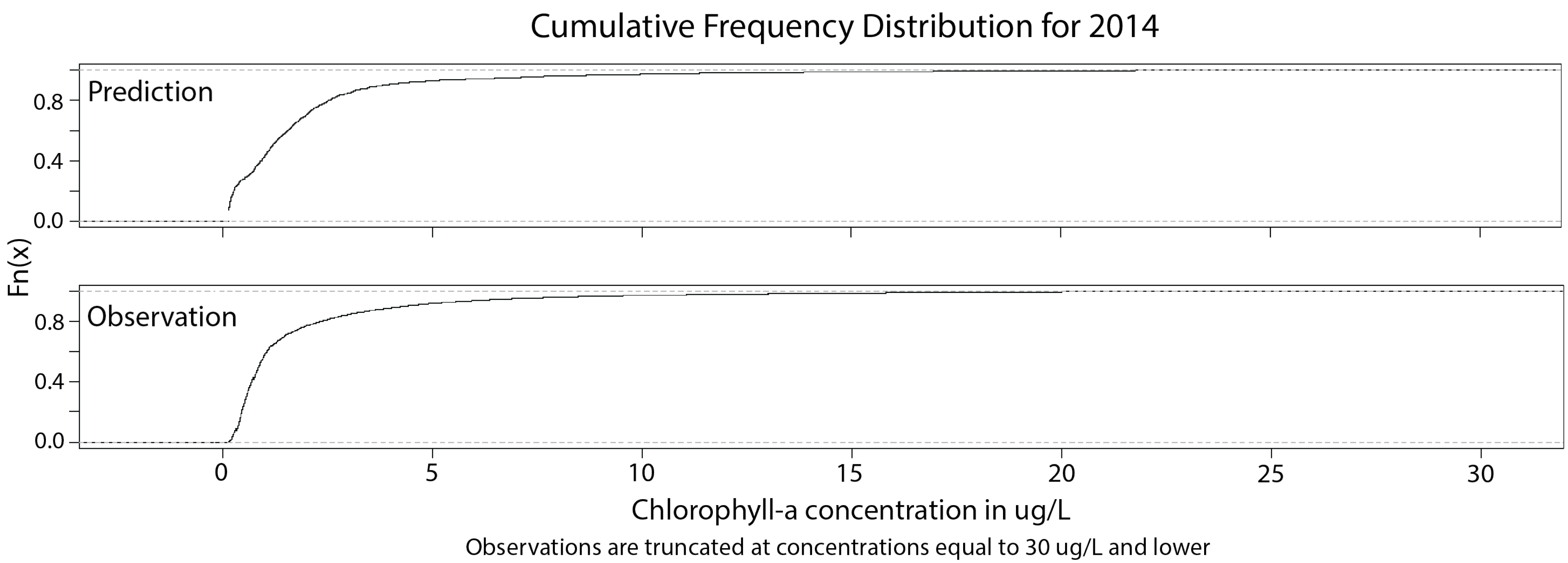

Figure J-10. Cumulative frequency distribution for chlorophyll predicted (top) and observed (bottom) for 2014. The observed cdf is truncated at 30 µg/L, which represents about the 99.8th percentile.

Table J-4. Predicted and Observed Chlorophyll-a Means and Mean Absolute Error for each Modeled Year

Year	Predicted Mean	Observed Mean	Range Observed	Mean Absolute Error (MAE)	MAE as Percent of Observed Range	MAE as Percent of 30 µg Chla/L
2014	1.93	1.94	136.35	1.37	1.0%	4.6%
2008	2.16	1.61	124.51	1.50	1.2%	5.0%
2006	2.37	2.37	166.03	1.69	1.0%	5.6%
2000	1.56	1.48	56.98	0.96	1.7%	3.2%

Table J-5. Predicted and Observed Chlorophyll-a Percentiles for 2014.

Percentile (%)	25	50	75	80	90	95	97	98	99	99.50	99.75	99.76	99.99	99.999
Predicted 2014	0.37	1.18	2.20	2.52	3.82	6.91	9.66	11.8	16.0	18.2	20.8	21	26.0	28.4
Observed 2014	0.53	0.88	1.75	2.19	4.19	6.91	9.80	12.6	17.5	21.7	28.8	29.5	114	136
Predicted 2008	0.61	1.29	2.25	2.66	4.80	7.95	10.6	12.9	16.7	19.0	20.9	21.0	26.3	26.5
Observed 2008	0.48	0.86	1.56	1.80	3.14	5.48	7.7	9.9	14.8	20.2	25.6	25.8	57.6	101
Predicted 2006	0.70	1.55	2.55	2.97	5.29	8.76	11.7	13.7	16.1	18.2	19.7	19.9	27.6	28.2
Observed 2006	0.45	0.95	2.44	2.94	5.16	8.54	11.5	14.7	22.0	32.5	45.6	46.1	149	165
Predicted 2000	0.28	0.42	1.98	2.36	3.49	6.00	8.20	10.6	14.8	17.6	19.5	19.7	27.6	27.8
Observed 2000	0.54	0.67	1.15	1.44	2.91	4.66	7.04	10.2	17.0	23.2	26.8	27.0	42.7	54.4

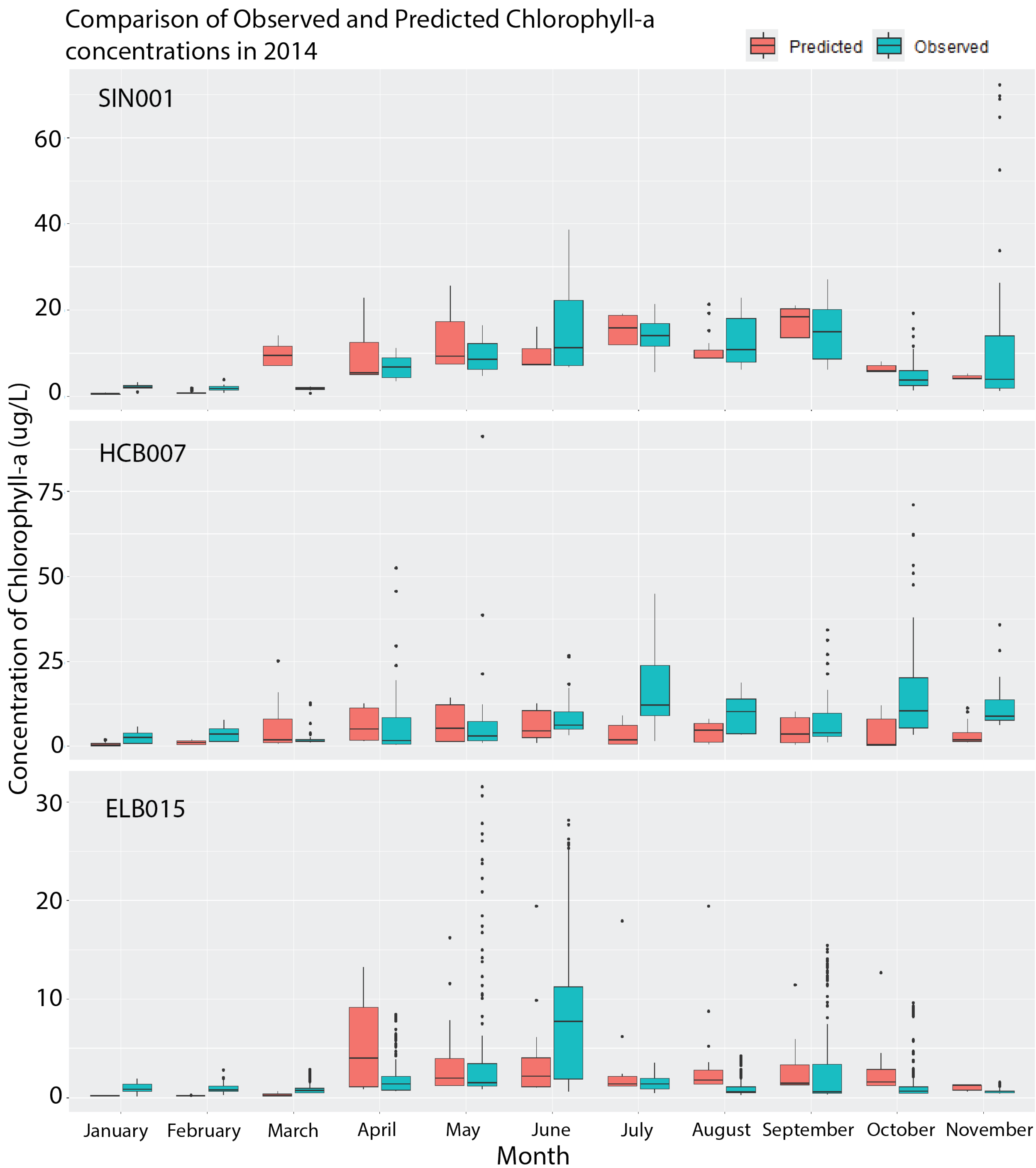

Figure J-11. Comparison of chlorophyll-a predicted and observed concentrations at 3 stations within embayments in 2014.

Sinclair Inlet (SIN001), Lynch Cove (HCB007), and Elliot Bay (ELB015).

Comparison of Observed and Predicted Primary Production Rates

Ahmed et al. (2019) compared published primary productivity data from central Puget Sound collected from October 1998 to October 2001 (Newton and VanVoorhis 2002) with predictions from a model year run for 2008, while pointing out the limitations of that analysis since inter-annual primary productivity is highly variable. We conducted a model run for year 2000 so that we can directly compare observed integrated primary productivity at Puget Sound stations with predicted values. Figure J-12 shows the locations where observational data for primary productivity are available for the year 2000.

Given the inherent difficulties in interpretation of primary productivity data based on ^{14}C uptake, and the additional differences in light incubation practices during primary productivity measurements, we are including both predicted gross primary productivity and net primary productivity in our analysis to allow for appropriate context.

Model output for GPP and NPP was depth-integrated. GPP is zero when photosynthesis does not occur due to insufficient solar radiation. NPP is negative at hours or depths where algal cells are present, and respiring, but not photosynthesizing. To compute the predicted average GPP per day, we averaged GPP only when photosynthesis was actually occurring (non-zero). Figure J-13 shows a time series plot of all the C-14 primary productivity observations available for the year 2000 (black dots) along with the predicted net (grey dots) and gross (green dots) primary productivity for that same year. The observations fall within the range of the predictions except for a few outliers.

Figure J-14 shows the same data as Figure J-13, but grouped by station. Productivities fall within comparable ranges at most, though not all, locations for all three productivity values—observed (pink), gross predicted (green), and net predicted (blue). At Nisqually, observed and predicted NPP are close, whereas predicted GPP is higher. At Hammersely, both predictions are lower than observed. At Case-52, the predicted GPP is close to the observed, whereas the predicted NPP is lower than both. At Carr ORCA, observations are lower but closer to predicted NPP than GPP. PR25 and PR11 have very low observed productivity.

Data from Newton and Van Voorhis over 1999 – 2001 represent the highest productivity estimates in our compilation of productivity data. Ahmed et al. 2019 reported that the model was not reproducing the range of peak productivities measured when comparing observations at the three stations (West Point, Possession Sound, and Admiralty Inlet) for years 1999, 2000, and 2001 with predictions from the year 2008. At those stations, observed peak productivity values for 1999 – 2001 (11.3 g C/m^2/day) were about two times higher than predicted values for 2008 (6.8 g C/m^2/day). However, among other differences, Ahmed et al. (2019) used a different approach for computing average daily GPP. Instead of our present approach of computing daily GPP only during the hours when photosynthetic activity is occurring, Ahmed et al. (2019) averaged over all the hours of the day. This latter computation resembles NPP rather than GPP.

Additionally, to assess whether the model produces higher peak average daily GPP values corresponding to years in which observations are available, and to refine the Ahmed et al. (2019) approach, we conducted a model run for the year 2000. We also noted that productivity samples were taken at alternate locations rather than at the long-term ECY monitoring stations, from which Ahmed et al. (2019) extracted predictions for comparative purposes with observations.

At all three stations, West Point, Possession Sound, and Admiralty Inlet, observational ranges overlap predicted net and gross productivities in 2000, while observational medians are closer to NPP medians than GPP medians. Observed and predicted peak productivities for 2000 are within a similar range (see Figure J-14, Admiralty Inlet, Possession Sound, and West Point).

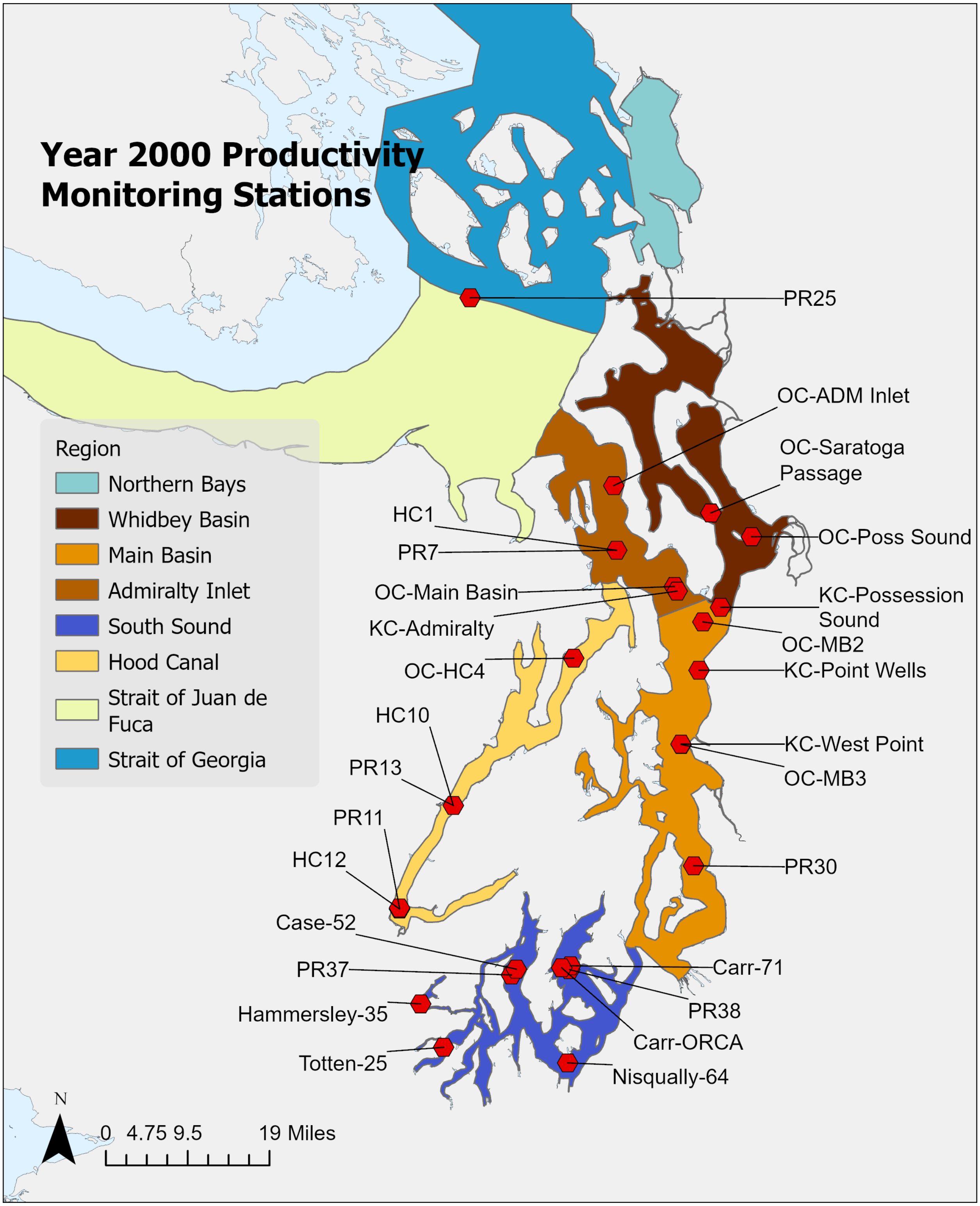

Figure J-12. Locations of observed productivity measurements compared with predictions.

Both predictions and observations correspond to the year 2000.

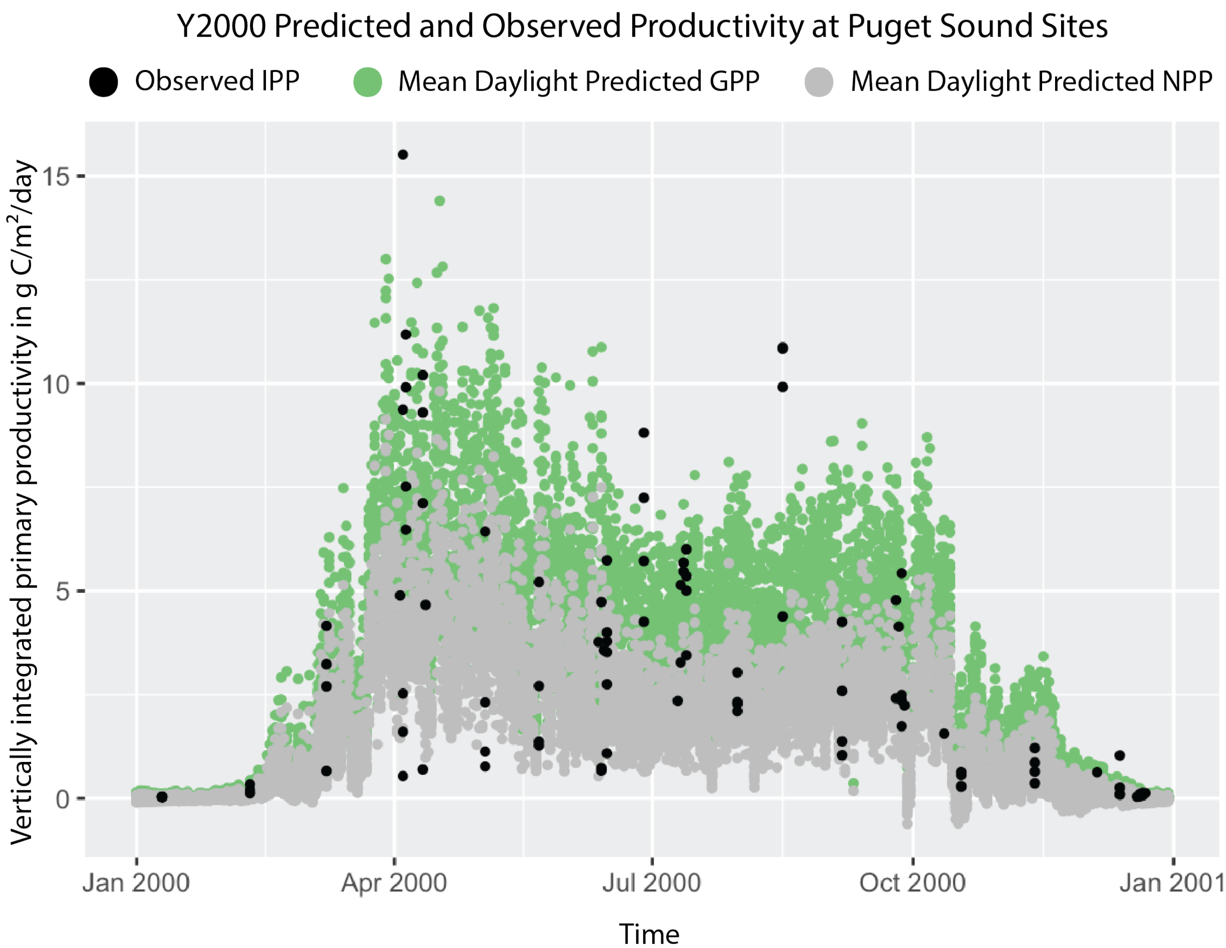

Figure J-13. Time series plot of observed productivity measurements compared with predictions for locations measured in 2000.

Both predictions and observations correspond to the year 2000.

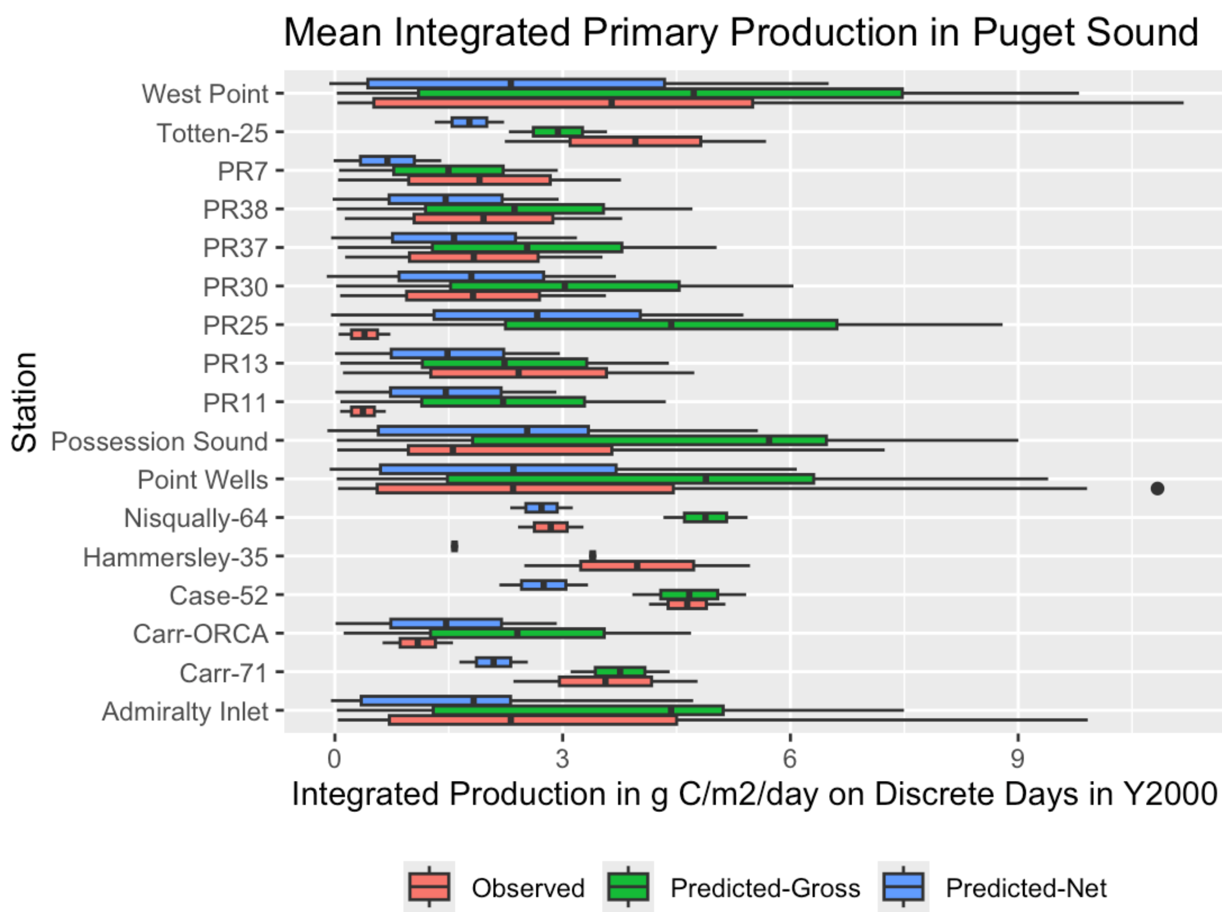

Figure J-14. Boxplots of observed productivity measurements compared with predictions for measurements in the year 2000.

Summary

Microalgal growth dynamics are difficult to measure, particularly in a highly variable environment such as the Washington waters of the Salish Sea. Thus, to reduce the uncertainty in the comparison of observational data with predictions, the alignment in time and location is critical, and predictions must be evaluated within the full context of what the observations represent. While this approach was not followed in earlier analysis (Ahmed et al. 2019), in this analysis, we have incorporated these considerations.

Predicted and observed chlorophyll-a, as a proxy for biomass, compare satisfactorily, and the model adequately reproduces seasonal and spatial variations of biomass. The model produces an exponential cumulative frequency distribution for chlorophyll-a that is like the observed one. However, SSM underpredicted peak algal bloom events, thus underpredicting chlorophyll-a maxima at the far tail end of the observed distribution (beyond the 99.75th percentile).

Mechanistic models predict values at temporal and spatial scales that do not resolve short-term peaks and subscale patchy algal blooms, which might contribute substantially to the ecosystem's available organic carbon production. Overall, prediction errors for all years fell well within the lower quartile of the range of observations, and the mean absolute error was between 1% and 1.7% of the observational range. Locally, agreement between predictions and observations is not as strong at all locations. Upon segregating the prediction/observations pairs by measurement location, model skill among locations varied, and most stations in 2014 (37 out of 41 or about 90%) for 2014 have a mean absolute error fraction below 25% of the observational range.

A re-analysis of a previous comparison (Ahmed et al. 2019) between observed and predicted productivities that match the observations in time and space showed that observational ranges overlap both predicted net and gross year 2000 productivities, while observational medians are closer to NPP medians than GPP medians. Productivity observations are reasonably represented by the model. The model generally matches the productivity median and peak magnitudes for observed and predicted values in the year 2000.

References

Ahmed A., C. Figueroa-Kaminsky, J. Gala, T. Mohamedali, G. Pelletier, and S. McCarthy. 2019. Puget Sound Nutrient Source Reduction Project, Volume 1: Model Updates and Bounding Scenarios. Publication 19-03-001. Washington State Department of Ecology, Olympia. https://apps.ecology.wa.gov/publications/SummaryPages/1903001.html

Albertson, S., Erickson, K., Newton, J., Pelletier, G., Reynolds, R., Roberts, M. 2002. South Puget Sound Water Quality Study Phase 1, Washington Department of Ecology Publication, https://apps.ecology.wa.gov/publications/SummaryPages/0203021.html

Bender M., Grande K., Johnson Kenneth, M.J., Williams P. J. Le B., Sieburth J., Pilson M., Langdon C., Hitchcock G., Orchardo J., Hunt C., Donaghay P., Heine mann K. 1987. A comparison of four methods for determining planktonic community production, *Limnology and Oceanography*, 32, doi: 10.4319/lo.1987.32.5.1085

Bos, J., M. Keyzers, L. Hermanson, C. Krembs, and S. Albertson, 2015. Quality Assurance Monitoring Plan: Long-Term Marine Waters Monitoring, Water Column Program, Washington Department of Ecology Publication, https://apps.ecology.wa.gov/publications/SummaryPages/1503101.html

Campbell, Serena, Peterson, W., Postel, J. 1977.Phytoplankton Production and Standing Stock in the Main Basin of Puget Sound, Final Report, University of Washington, Department of Oceanography

Cerco, C., M. Noel and S. Kim. 2004. Three-dimensional eutrophication model of Lake Washington. EL-TR-04-12. U.S. Army Engineer Research and Development Center, Vicksburg, MS. Unpublished Appendix

Cerco, C. and Noel, M. 2004. Process-based primary production modeling in Chesapeake Bay, Marine Ecology Progress Series, 252:45 – 58

Chan, A.T. 1980. Comparative physiological study of marine diatoms and dinoflagellates in relation to irradiance and cell size II Relationship between photosynthesis, growth and carbon/chlorophyll-a ratio, Journal of Phycology, 16: 428 – 432. https://doi.org/10.1111/j.1529-8817.1980.tb03056.x

Cloern, J., Foster, S., Kleckner A. 2014. Phytoplankton primary production in the world's estuarine-coastal ecosystems. Biogeosciences, 11, 2477 – 2501

Collias, E.E., N. McGary, and C.A. Barnes. 1974. Atlas of physical and chemical properties of Puget Sound and approaches. Washington Sea Grant 74-1. Seattle, WA.

Cullen, J. 2015. Subsurface Chlorophyll Maximum Layers: Enduring Enigma or Mystery Solved? Annu. Rev.. Mar. Sci. 7:207–39

Ebbesmeyer, C. and Helseth, J. 1977. An Analysis of Primary Production Observed during 1966 – 1975 in Central Puget Sound, Washington, Report by Evans-Hamilton, Inc. for the Municipality of Metropolitan Seattle.

Eisner, L. and Newton, J. 1997. Budd Inlet Focused Monitoring Report for 1992, 1993 and 1994, WA Department of Ecology publication 97-327 https://apps.ecology.wa.gov/publications/documents/97327.pdf

Hannach, G. 2022. King County Marine Conditions 2008–2019 Report Series: Phytoplankton. Water and Land Resources Division, Seattle, Washington.

Horner, R. 1992 observations recorded in spreadsheet (PHYT_REW) during contract with WA ECY, obtained from S. Pool, Marine Monitoring Unit, 2024

Horner, R. 2003. Identification of Some Pseudo-nitzschia Species from Western Washington Waters in Proceedings of the Eighth Canadian Workshop on Harmful Marine Algae Stephen S. Bates (Editor) Canadian Technical Report of Fisheries and Aquatic Sciences 2498

Jakobsen H. and Markager, S. 2016.Carbon-to-chlorophyll ratio for phytoplankton in temperate coastal waters: Seasonal patterns and relationship to nutrients, Limnol. Oceanogr. 61, 1853–doi: 10.1002/lno.10338

Jassby, A. and Platt, T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton, Limnol. Oceanogr. 21, 540

Laws, E. A. and Archie, J. W., 1981. Appropriate use of regression analysis in Marine Biology, Marine Biology 65, 13 – 16.

Newton, J.A., S.L. Albertson, and A.L. Thomson. 1997. Washington State Marine Water Quality in 1994 and 1995, Department of Ecology publication 97-316, https://apps.ecology.wa.gov/publications/SummaryPages/97316.html

Newton, J.A., M. Edie, and J. Summers. 1998. Primary productivity in Budd Inlet: Seasonal patterns of variation and controlling factors. Pp. 132–151 in Puget Sound Research '98 Proceedings.Puget Sound Action Team, Olympia, Washington.

Newton, J., and R.A. Reynolds. 2002. Oceanographic Field Studies in South Puget Sound, Chapter 2 of South Puget Sound Water Quality Study, Phase 1. Publication 02-03-021. Washington State Department of Ecology, Olympia. https://apps.ecology.wa.gov/publications/SummaryPages/0203021.html

Newton, J., and K. Van Voorhis. 2002. Seasonal Patterns and Controlling Factors of Primary Production in Puget Sound's Central Basin and Possession Sound. Publication 02-03-059. Publication 19-03-001 page 91 January 2019 Washington State Department of Ecology, Olympia. https://apps.ecology.wa.gov/publications/SummaryPages/0203059.html

NOAA. 1981. A Summary of Knowledge of Puget Sound Related to Chemical Contaminants, Technical Memorandum OMPA-13, Boulder, CO.

Phifer, L.D. 1933. Seasonal distribution and occurrence of planktonic diatoms at Friday Harbor. University of Washington Publications in Oceanography 1(2): 39–81.

Pool, S., Krembs C., Bos, J. and Sackmann, B. 2015. Physical, Chemical, and Biological Conditions during Noctiluca Blooms in an Urban Fjord, Puget Sound. Washington State Department of

Ecology poster, Publication No. 15-03-040, https://apps.ecology.wa.gov/publications/documents/1503040.pdf

Ricker, W.E. 1973. Linear Regressions in Fishery Research. Journal of the Fisheries Board of Canada. 30: 409 – 434.

Roberts, M., J. Bos, and S. Albertson. 2008. South Puget Sound Dissolved Oxygen Study: Interim Data Report. Washington State Department of Ecology, Olympia, WA. Publication No. 08-03-037. https://apps.ecology.wa.gov/publications/summarypages/0803037.html

Roesler C., Uitz J., Claustre H., Boss E., Xing X., Organelli E., et al. 2017. Recommendations for obtaining unbiased chlorophyll estimates from in situ chlorophyll fluorometers: A global analysis of WET labs ECO sensors: Unbiased chlorophyll from in situ fluorometers. Limnol. Oceanog.: Methods 15, 572–585. doi: 10.1002/lom3.10185

Spilling K, Ylöstalo P, Simis S, Seppälä J. 2015. Interaction Effects of Light, Temperature and Nutrient Limitations (N, P and Si) on Growth, Stoichiometry and Photosynthetic Parameters of the Cold-Water Diatom Chaetoceros wighamii. PLoS ONE 10(5): e0126308. doi:10.1371/journal. pone.0126308

Stark, K. 2022. King County Marine Conditions 2008–2019 Report Series: Chlorophyll and Pheophyton Results. Water and Land Resources Division, Seattle, Washington.

Stark, K. and Martin, T. 2022. King County Marine Conditions Report Series 2008 – 2019: Marine Monitoring Program Overview. Water and Land Resources Division. Seattle, Washington

Stow, C., Roessler, C., Borsuk, M., Bowen, J., and Reckhow, K. 2003. Comparison of Estuarine Water Quality Models for Total Maximum Daily Load Development in Neuse River Estuary, Journal of Water Resources Planning and Management, Vol. 129, No. 4, ASCE, ISSN 0733-9496/2003/4-307–314

Strickland, J.D.H. and Parsons, T.R. 1968. A Practical Handbook of Seawater Analysis. Bulletin of Fisheries Research Board of Canada, 167, 1 – 311.

Taylor, F.J.R., Hoppenrath, M. & Saldarriaga, J.F. 2008. Dinoflagellate diversity and distribution. *Biodivers Conserv* **17**, 407–418. https://doi.org/10.1007/s10531-007-9258-3

Thompson T.G. and Phifer. 1936. The plankton and the properties of surface waters of the Puget Sound region, University of Washington Publications in Oceanography, Volume 1, No. 5, pp. 111 – 134

UW [University of Washington]. 2024. Website accessed on 8/6/2024, https://www.ocean.washington.edu/story/SoO_Introduction_and_a_Brief_History

Van Alstyne, K. Haug, C., Lee, H-Y, McKeen, G., T. Schwarck, N., Strom, M. 2024. Water Quality Data Collected at Western Washington University's Shannon Point Marine Center in Anacortes, Washington, USA: 1974 – 2023. figshare. Dataset. https://doi.org/10.6084/m9.figshare.25206959.v3

Vandermuelen, R., Chaves, J., Mannino, A. Reconciling Estimates of Oceanic Primary Productivity from Cells to Satellites 2022. In: IOCCG Protocol Series 2022. IOCCG, Dartmouth, NS, Canada. doi:http://dx.doi.org/10.25607/OBP-1835

Welch, E. 1968. Phytoplankton and related water-quality conditions in an enriched estuary. Journal Water Pollution Control Federation 40(10): 1711–1727.

Winter, D.F., K. Banse, and G.C. Anderson. 1975. The dynamics of phytoplankton blooms in Puget Sound, a fjord in the Northwestern United States. Marine Biology 29: 139–176.