

PHYTOPLANKTON DYNAMICS IN OFF-CHANNEL HABITATS OF  
THE LOWER COLUMBIA RIVER ESTUARY

By

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CERTIFICATE OF APPROVAL

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This is to certify that the Master's thesis of  
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## Abstract

Shallow, off-channel sloughs in the lower Columbia River provide critical habitat to 13 stocks of threatened or endangered juvenile Pacific salmon (*Oncorhynchus* spp.). We examined water quality parameters (temperature, dissolved oxygen and nutrients) and phytoplankton dynamics in three off-channel habitats (Whites Island, Campbell Slough, and Franz Lake Slough) that differ in terms of their inherent hydrogeomorphic features in the spring and summer months between 2011 and 2015. Both abiotic and phytoplankton data were analyzed in the context of varying flow conditions at seasonal and inter-annual time scales. The years of study included two that had higher-than-average discharge (2011, 2012), two that had near-average discharge (2013, 2014), and one that had below-average river discharge (2015), thus providing an excellent spectrum of conditions for investigation.

During low-discharge periods, off-channel habitats differed from the mainstem in terms of water temperature, dissolved oxygen dynamics, and nutrient concentrations. Phytoplankton species succession varied from year to year as well as on a seasonal basis, with more dramatic shifts observed at poorly connected sites during low water years. Through Non-metric Multidimensional Scaling (NMDS), significant variations among phytoplankton assemblages were observed that depended on seasonal patterns of river discharge and relative connectivity of off-channel habitats to the mainstem.

High abundances of cyanobacteria (up to 450,000 cells mL<sup>-1</sup>) were observed during the summer months at the two sites with slower water exchange with the mainstem (Campbell Slough and Franz Lake Slough). Known toxin-producing taxa, including *Microcystis* sp., *Dolichospermum* sp. and *Merismopedia* sp., dominated the cyanobacteria assemblages. Canonical Analysis of Principal Coordinates (CAP) indicated that water temperature and dissolved inorganic phosphorus (DIP) were major factors driving the variance among phytoplankton assemblages. Moderate positive correlations between cyanobacteria and DIP and moderate negative correlations between cyanobacteria and N:P were observed during times of low flow.

The data indicate that despite the fact that the mainstem Columbia possesses low dissolved nutrient concentrations and has good water quality relative to many other big river systems, shallow water habitats appear to be vulnerable to periods of poor water quality in the summer months.

## Chapter 1: Introduction

Large rivers support complex and dynamic ecosystems as well as human industry. In rivers that flow through major metropolitan areas, there is often a trade-off between providing resources and infrastructure that benefit the human population (i.e., flood control, shipping, and hydropower) and preserving habitat quality for native organisms that rely on physical and biogeochemical aspects of the river for their survival (Sparks, 1995). Unlike lakes or the ocean, lotic habitats possess highly complex geomorphologies that influence how flow is distributed through the system. The dependence of habitat characteristics on both flow and geomorphology is reflected in the term ‘hydrogeomorphology’ (Scheidegger, 1973; Sidle and Onda, 2004). In a river-floodplain system, both the main channel and shallow, off-channel habitats possess unique hydrogeomorphic features that can influence local and regional biogeochemical cycles, creating a mosaic of habitats and adapted biological communities.

The importance of connectivity between riverine sites that differ in hydrogeomorphology has recently been stressed as an important, and often overlooked aspect of conservation biology (Pringle, 2003), although habitat connectivity has been a cornerstone of terrestrial-based conservation biology practices for some time. Alterations in flow dynamics in river-floodplain systems worldwide over the last century (including diking, channel diversion and depletion of groundwater) have effectively decoupled the relationship between natural flow patterns and predictable responses of biological communities in aquatic systems. Impoundments behind dams often store large volumes of water that would otherwise be transported downstream, effectively reducing connectivity between deep river channels and shallow floodplain habitats (Baxter, 1977; Ward and Stanford, 1995) and limiting exchange of nutrients, sediment and aquatic organisms in a lateral direction.

Connectivity between main channels of large rivers and their floodplains is crucial for sustaining aquatic food webs, both in off-channel sites and in the mainstem. Reductions in connectivity between shallow water habitats and mainstem channels can effectively reduce inputs of primary production to river habitats, since shallow water habitats tend to be sites of high biological productivity compared to the mainstem channel (Junk et al., 1989). Through a simple NPZ (nutrient-phytoplankton-zooplankton) model, Cloern (2007) showed that high primary production in shallow water habitats can fuel pelagic food webs in the mainstem channel when there is sufficient connectivity between the two habitats, thus alleviating food limitation which is often observed in higher consumers such as fish within river systems (Lopez et al., 2006). Further evidence of the importance of floodplain habitats to aquatic food webs comes from a study in the Sacramento River which showed that juvenile salmon had faster growth rates and greater prey consumption in floodplain habitats compared to the mainstem channel, even at temperatures likely to induce physiological stress (Sommer et al., 2001).

Periods of reduced connectivity in lower river reaches are associated with increased spatial heterogeneity of habitats, which increases the net influence of in-site biogeochemical processes in isolated habitats (Thomaz et al., 2007). Although periods of disconnectivity between mainstem rivers and their shallow floodplains is usually followed by an increase in biological diversity on a region-wide (gamma) scale due to variation in underlying hydrogeomorphic conditions, the lack of exchange of nutrients and propagule organisms between aquatic environments eventually leads to decreases in local (alpha) diversity over sustained periods of time as local resources are extinguished (Thomaz et al., 2007). Thus, river-floodplain systems depend on temporal variation in flooding events to invoke a variety of successional stages in riverine ecosystems and maintain diverse populations of aquatic organisms year round.

The lag time between large flood events and reductions in diversity—and between initial decreases in connectivity and reductions in biological diversity—presents a unique challenge to river managers who strive to balance human needs and ecosystem health. Phytoplankton communities respond quickly and predictably to environmental factors including water temperature, nutrient availability and flushing time (McCormick and Cairns, 1994); thus, monitoring phytoplankton in relation to abiotic parameters is one way to effectively address ecosystem responses to change in spite of the typical lag time in whole ecosystem response.

This study examines water quality and phytoplankton population dynamics in three established juvenile salmon habitats—shallow, off-channel sloughs—in the lower Columbia River that differ in terms of hydrologic and biogeochemical profiles. The Columbia River constitutes a dynamic ecosystem that has been heavily influenced by human activities that have altered its flow, including diking, dredging and channelization, as well as the construction of dams for hydropower generation (Sherwood et al., 1990). The construction of dams over the last several decades has resulted in both physical impediments to fish migration and significant losses in riparian habitats that support juvenile fish. As a result of these changes, native salmonid populations have undergone significant declines (Bottom et al., 2005), which has prompted substantial restoration efforts, and ultimately led to the classification of the lower Columbia River as a waterway of national significance by the Environmental Protection Agency under the National Estuary Program (NEP) in 1996 (Lower Columbia Estuary Partnership, 1999).

Characterization of the phytoplankton community in the context of abiotic variables has important implications for ecosystem integrity. A previous study (Maier and Simenstad, 2009) found that phytoplankton represent a significant portion of the base of the food web for juvenile salmon in the Columbia River, at least during early spring when diatom abundance is high. Other

studies have suggested that shallow water habitats support higher production than the mainstem (Lopez et al., 2006; Sommer et al., 2001), and therefore serve as critical sources of organic matter that fuel growth of higher consumers in riverine ecosystems. In addition to analyzing spatial and temporal trends in bulk chlorophyll and primary production, evaluating phytoplankton community structure on a more detailed taxonomic level can be a useful tool for managers wanting to make a quick assessment of overall water quality. Well-established patterns of phytoplankton community succession have implications for phenology of consumers and for overall ecosystem health. Shifts in community succession patterns can inform managers about physical and chemical changes to aquatic ecosystems, and particular taxa (specifically diatoms) have been meticulously classified and given values as indicators of trophic status (Kelly and Whitton, 1995; Kelly, 1998) based on their sensitivities to phosphate.

The overall aim of this thesis study is to characterize patterns in primary production in off-channel habitats the context of physical and chemical conditions that vary both spatially and temporally, in order to inform managers that have a vested interest in the recovery of salmonids in the Columbia River. Several previous studies have looked at phytoplankton community dynamics in the mainstem channel of the river (Haertel et al., 1969; Lara-Lara et al., 1990; Sullivan, 1997; Prahel et al., 1997; Maier, 2014), however this is the first study to describe phytoplankton communities in off-channel habitats. Specifically, the objectives of this study are to i) characterize abiotic conditions (dissolved nitrogen and phosphorus, dissolved oxygen, and temperature) in off-channel habitats in comparison to the mainstem, ii) compare patterns of phytoplankton species succession between sites and over varying time scales (seasonally and interannually) and iii) identify environmental conditions associated with recurring summer cyanobacteria blooms, which may pose a threat to endangered juvenile salmon. This study

encompasses five years of monitoring data (2011-2015) that vary in terms of hydrologic regimes, including higher than average discharge (2011-2012), near-average discharge (2013 and 2015) and a drought year (2015) in which discharge was far below average. Our hypothesis is that both water quality parameters and phytoplankton communities in off-channel habitats of the lower Columbia River are controlled primarily by river discharge, which affects connectivity between off-channel sites and the mainstem. We hypothesize that periods of low connectivity associated with low river discharge effectively create distinct ecosystems that differ from the mainstem to varying degrees based on inherent hydrogeomorphic attributes. In contrast, during periods of high river discharge, both water quality parameters and phytoplankton communities closely resemble the mainstem.

## **Chapter 2: Influence of hydrogeomorphology on biogeochemical characteristics of off-channel habitats in the lower Columbia River**

### **Introduction**

Shallow, floodplain areas typically differ from deep mainstem channels in terms of light availability, temperature, flow velocity and dissolved oxygen dynamics. The degree of difference between environmental parameters in shallow areas and the mainstem depends on relative hydrological connectivity (Thomaz et al., 2007). Because off-channel habitats are typically much shallower than the main channel, they tend to warm faster, particularly during summer months. Off-channel habitats that are far removed from the mainstem also tend to have slower flushing times (Sommer et al., 2004), and are thus minimally impacted by tidal fluctuations during periods of low water elevation. Channels that are highly sinuous are also less likely to experience major disturbances to aquatic organisms during flood events, compared to channels with straight paths that are in close proximity to the mainstem (Amoros and Bornette, 2002).

Temperature is one of the most important environmental parameters controlling aquatic community structure, due to temperature-driven effects on physical structure of the water column, including stratification and hypoxia, and because many aquatic organisms have temperature thresholds for optimal physiological functioning and phenological aspects of their life cycles. For example, many aquatic insects use temperature cues for timing of larval emergence, which can influence food availability for insectivorous fish (Ward and Stanford, 1982). High temperatures also affect physiological functions in vertebrates, particularly among fish (Coutant, 1977). Salmonids are highly sensitive to temperature fluctuations, since temperature influences their ability to efficiently metabolize and grow (Beechie et al., 2013). Water temperature can have a direct impact on juvenile salmon usage of shallow water habitats, as suboptimal growth and increased predation risk increases for juvenile salmon reared at

temperatures above 16 °C (Marine and Cech, 2004). If water in shallow, refuge habitats is too warm, juvenile salmonids may avoid those habitats altogether and instead risk predation and starvation in deeper, cooler areas of a river (Sommer et al., 2001; Vigg and Burley, 1991).

In productive aquatic systems in temperate environments, warm temperatures are sometimes associated with hypoxia, particularly in environments where water residence time is long. As surface temperatures warm, water column mixing is reduced, which often leads to blooms of high-temperature and high-light adapted phytoplankton such as cyanobacteria (Paerl and Huisman, 2008). Phytoplankton can produce excess oxygen via photosynthesis during the day, which is consumed by respiring bacteria at night, establishing a diel pattern of daytime increases in dissolved oxygen and nighttime decreases in dissolved oxygen (Tyler et al., 2009; D'Avanzo and Kremer, 1994). As phytoplankton blooms senesce, respiration by decomposing bacteria exceeds photosynthesis; in highly eutrophic systems, hypoxia can persist throughout the diel cycle for extended periods and have detrimental effects on benthic organisms and fish (Paerl et al., 1998). This phenomenon is more common in lentic environments where slow-flushed water stratifies easily, but it has also been observed in estuaries (Paerl et al., 1998; Stanley and Nixon, 1992) and more recently in the Klamath River, which has connections to shallow impoundments (Otten et al., 2015). Shallow, backwater sites in the highly regulated upper Mississippi River (Houser, 2005) are characterized by fine, highly organic sediments that create favorable conditions for low dissolved oxygen, implying that off-channel habitats (such as those in this study) are highly susceptible to hypoxia. Hypoxic conditions have been associated with spatial and temporal avoidance of particular habitats by juvenile fish (Craig and Crowder, 2005; Ludsin et al., 2009) including juvenile salmonids (Birtwell and Kruzynski, 1989); therefore



monitoring of dissolved oxygen levels in these study sites is a critical factor in determining overall ecosystem health.

Depending on river discharge and connectivity between off-channel sites and the mainstem, off-channel habitats can act as either sources or sinks of dissolved nutrients in a river floodplain ecosystem (Junk et al., 1989). Both nitrification (Strauss et al., 2004) and denitrification (Houser and Richardson, 2010) have been found at higher rates in shallow floodplain areas compared to the main channel, although total dissolved nutrient concentrations in backwater sites may not reflect these fluxes as uptake of  $\text{NO}_3^-$  in backwaters is usually rapid (Houser and Richardson, 2010). Warmer temperatures that are typical of off-channel habitats may exacerbate nitrification rates, as growth rate of nitrifying bacteria responds positively to warmer temperatures (Strauss et al., 2004). Dissolved, bioavailable phosphorus in estuarine rivers is controlled by environmental factors that are physical (runoff, burial and release from sediments), chemical (salinity) and biological (assimilation by plants and algae). River discharge has been identified as a factor controlling physical versus biological control of dissolved phosphorus in the agriculturally influenced Minnesota River (James and Larson, 2008), with higher biological control during periods of low discharge (inverse correlation of phosphate with chlorophyll concentration) and greater physical control of dissolved phosphorus during periods of high discharge due to equilibration with particulate phosphorus in suspended sediment. Nutrient concentrations in shallow water sites impact juvenile salmon indirectly via control of primary production, which may impact both dissolved oxygen content and prey availability.

Since population models suggest that the juvenile stage of the salmonid life cycle is particularly sensitive to environmental conditions (Kareiva et al., 2000), targeting habitats that are heavily used by juvenile salmonids is a reasonable strategy for improving long-term

population recovery. However, in order for restoration to be effective, the benefits of these habitats for salmon must be assessed and characterized in terms of spatial and seasonal variability. The following chapter will focus primarily on characterizing biogeochemical aspects of shallow water habitats of the lower Columbia River that reflect the degree of connectivity between shallow water habitats and the mainstem.

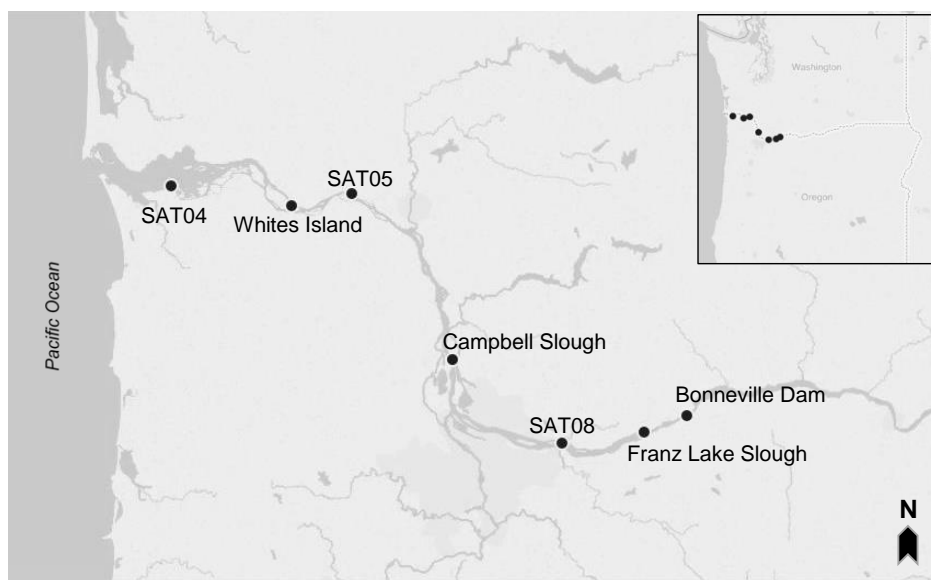
## **Methods**

### *Study Area*

The Columbia River is a large, regulated river characterized by an extensive network of hydroelectric dams. The Columbia River drainage basin covers >660,000 km<sup>2</sup> and encompasses portions of Canada and six of the United States (Sherwood et al., 1990). The Columbia River discharge peaks between April and June during the spring freshet, which is driven by snowmelt (Sherwood et al., 1990). The freshet transports large amounts of sediment and minerals from the mountainous upper watershed into the lower river. Although the Columbia has comparatively lower dissolved nitrogen and phosphorus concentrations compared to many large rivers worldwide and is not considered to be eutrophic (Meybeck, 1982), it is thought to support higher levels of phytoplankton production than it did in the past before dams were installed because of changes in light penetration that have accompanied a reduction in sediment loading (Prahl et al., 1997; Sullivan et al., 2001).

The lower Columbia River, which extends from Bonneville Dam to the mouth at the Pacific Ocean, has been classified into eight distinct level-3 hydrogeomorphic reaches, as designated in the Columbia River Estuary Ecosystem Classification scheme (Simenstad et al., 2011). Hydrogeomorphic reaches are characterized in terms of flow velocity, broad-scale physiography, influence of major tributaries, and potential impact of toxic contaminants. The

three sites included in this study—Franz Lake Slough, Campbell Slough and Whites Island—are located in different reaches of the lower river, which differ in terms of their hydrologic features. Franz Lake Slough is located within Reach H (“Western Gorge”), the narrowest of the lower river reaches. Due to its proximity to Bonneville Dam, water levels in this section of the river are primarily regulated by discharges from the dam rather than by tidal fluctuations. Campbell Slough is located within Reach F (“Middle Tidal Flood Plain Basin”), which is influenced largely by inflows from the urbanized and nutrient-rich Willamette River. Reach F has the widest valley bottom of the freshwater reaches, and has historically been dominated by wetland and swamp habitats, although it is currently influenced by many anthropogenic alterations to flow (i.e. diking, dredging, channelization) around the Portland/Vancouver metropolitan area. Whites Island is located within Reach C (“Volcanics Current Reversal”), which has less variation in water level than other reaches (Jay et al., 2014). Reach C also has the steepest valley bottom of the eight reaches, and has been described as a “transport reach” due to high fluvial energy in this section of the river.



**Figure 1.** Map showing locations of the three shallow-water study sites (Whites Island, Campbell Slough, and Franz Lake Slough) along the lower Columbia River and relative locations of mainstem continuous in situ sensors (SAT04, SAT05 and SAT08). Bonneville Dam marks the limit of tidal influence in the Columbia River estuary. Inset shows the Pacific Northwest region of the United States, which encompasses the study sites.

### *Site Characteristics*

Three sites within the lower Columbia River (Franz Lake Slough, Campbell Slough and Whites Island; Fig. 1) were surveyed during the spring and summer months. All three sites are located within the range of tidal influence in the lower Columbia River, which extends from the river mouth to Bonneville Dam (rkm 234). Tidal influence is strongest at the mouth of the river and relatively weak at Bonneville Dam.

Franz Lake Slough (rkm 221) connects Franz Lake, located in Pierce National Wildlife Refuge, to the mainstem Columbia River. Campbell Slough (rkm 179) connects Campbell Lake, located within Ridgefield National Wildlife Refuge, with the mainstem Columbia River. Whites Island (rkm 72) is a small channel located within a dredge-material island (Puget Island) in the mainstem of the Columbia River off of Cathlamet Channel. Campbell Slough and Whites Island are located downstream of the Columbia River's confluence with the urbanized Willamette River, while Franz Lake Slough is upstream of the confluence. In situ sensors in the mainstem river at SAT08 (upstream of Willamette confluence) and SAT05 (downstream of the confluence of the Willamette and Columbia Rivers) are used in this study to estimate the influence of Willamette River flows on downstream sites (i.e., Campbell Slough and Whites Island).

The three sites differ in terms of habitat structure and vegetation type. Beaver dams along the channel to Franz Lake created an area of shallow-water wetlands around the slough, which contains mostly willow (*Salix* sp.) saplings and small stands of willow, ash (*Fraxinus* sp.) and cottonwood (*Populus* sp.). Invasive Reed Canary Grass (*Phalaris arundinaceae*) was prevalent in Franz Lake Slough prior to 2011, but high inundation levels during the spring of 2011 destroyed a large fraction of the *P. arundinaceae* population, which was replaced primarily with *Polygonum amphibium* in the subsequent years. Campbell Slough is surrounded by a large expanse of emergent marsh containing primarily Wapato (*Sagittaria latifolia*) and Reed Canary Grass (*Phalaris arundinaceae*). The land surrounding Campbell Slough consists of former pasture land that was actively grazed by cattle until 2007. Whites Island is characterized by high marsh with few willow trees.

Whites Island has the shallowest channel bed of the three sites, with an average width:depth ratio (W:D) of 47.1, and the sampling location is located approximately 0.20 km from the connection with the mainstem channel (the closest of all three sites). Campbell Slough is also relatively shallow with average W:D of 37.7, and is located furthest from the mainstem at approximately 1.5 km inland. Sampling in Franz Lake Slough occurred approximately 0.35 km inland from the mainstem, where W:D is about 28.6. Additional information about each site is included in Table 1.

**Table 1.** Physical parameters corresponding to three study sites (data from Sagar et al., 2013)  
W:D=Width to Depth; CRD = Columbia River Datum.

Site	rkm	Distance from mainstem (km)	Channel depth (m)	W:D ratio	Thalweg elevation (m, CRD)
Franz Lake Slough	221	0.35	0.6	28.6	0.99
Campbell Slough	179	1.5	0.56	37.7	0.77
Whites Island	72	0.2	0.78	47.1	0.37

*Sample collection and data sources*

Temperature ( $^{\circ}\text{C}$ ) and dissolved oxygen ( $\text{mg L}^{-1}$ ) were recorded continuously every 30-60 min by in situ sensors (Yellow Springs Instruments, models 6600EDS and 6920V2) deployed at Franz Lake Slough, Campbell Slough, and Whites Island during all five years of the study between April and July, with varying dates and lengths of deployment (see Table 2). The instruments were cleaned and calibrated approximately every three weeks. Mainstem temperature ( $^{\circ}\text{C}$ ) and dissolved oxygen ( $\text{mg L}^{-1}$ ) were recorded continuously (every 2 s) by in situ sensors at 0.3 m depth at SAT04. Dissolved oxygen (DO) concentrations recorded in  $\text{mg L}^{-1}$  both in the study sites and in the mainstem were converted to % saturation using equations from Garcia and Gordon (1992). Water elevation (ft.) was determined from USGS gage 14144700 in the mainstem Columbia River near Vancouver, WA.

Whole-water grab samples were collected from near the surface of the water (<1 m) every 2-4 weeks between April and July at Franz Lake Slough, Campbell Slough and Whites Island from 2011–2014 and between April and August in 2015. Campbell Slough was not sampled in April 2011 when high water levels made the site inaccessible. All three sites were

sampled three times throughout the month of May in 2013, and mean cell abundances were calculated for each month of sampling.

Water was collected in 1 L dark plastic bottles, then stored on ice in plastic coolers for <12 h prior to subsampling for phytoplankton abundance and species composition and dissolved nutrient analysis. Phytoplankton subsamples were preserved in duplicate with 1% Lugol's iodine solution and stored at room temperature in the dark until analysis. Samples for the determination of dissolved nutrients were filtered in duplicate through 25 mm GF/F filters (Whatman) and stored at -20° C pending analysis.

#### *Chlorophyll a*

Chlorophyll a was determined either spectrophotometrically (2011-2013) using Thermo Electron spectrophotometer or fluorometrically (2014-2015) using a Trilogy<sup>®</sup> fluorometer (Turner Designs) following cold acetone extraction using the non-acidification method (Welschmeyer, 1994). Aliquots (100-300 mL) of whole water grab samples (described above) were vacuum-filtered in triplicate onto 25 mm GF/F filters under low light conditions and stored at -80 °C prior to extraction in 90% acetone at -20 °C for 24 h.

#### *Dissolved nutrients*

Samples for dissolved nutrients were filtered through combusted (450°C, 4.5 h) GF/F filters and stored in 30 mL acid-washed, high density polyethylene bottles (HDPE; Nalgene). Dissolved nutrients (nitrate, nitrite, ortho-phosphate, and ammonium) were determined colorimetrically using a Rapid-Flow Analyzer (Astoria Pacific) according to the methods of Antweiler et al. (1996). Samples were calibrated against NIST standards for nitrate and phosphate to ensure that measured values were accurate.

### *ΔT and ΔO<sub>2sat</sub>*

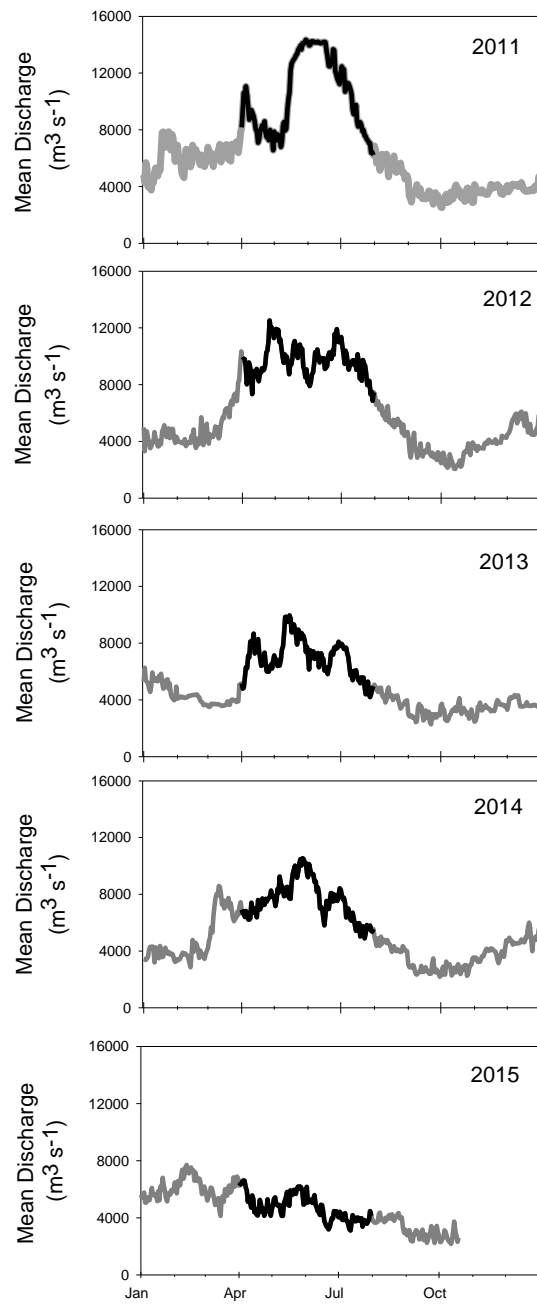
ΔT is defined in this study as the date-matched difference between daily mean water temperature (°C) measured at a given site by YSI sondes and daily mean water temperature (°C) in the mainstem (0.3 m depth) at SAT04. Similarly, ΔO<sub>2sat</sub> is defined in this study as the date-matched difference between dissolved oxygen (%saturation) measured at a given site by YSI sondes and dissolved oxygen (%saturation) in the mainstem (0.3 m depth) at SAT04. Although both SAT05 and SAT08 are closer in proximity to the study sites, SAT04 was chosen because the data stream from this station was more complete than the other two; data gaps at the other sites prevented a consistent comparisons between either of those mainstem sites and temperature and DO values at the three shallow water habitats over the entire time series. For example, SAT08 was not deployed prior to 2013 and was non-functional for a large portion of 2014. SAT05 was non-functional during April and May 2013, April-July 2014, and April-June 2015. SAT04 was deployed and functional throughout the course of this study, with the exception of relatively short periods (<10 d) in May 2012 and April 2015. Although SAT04 is located further downstream than the three study sites, temperatures were not statistically different from SAT05 and SAT08 (one-way ANOVA,  $F(2,336) = 0.12$ ,  $p = 0.89$ ). The mean temperature difference between SAT04 and SAT05 was 0.56 °C (n=354), and the mean temperature difference between SAT04 and SAT08 was 0.21 °C (n=279). Therefore, data from SAT04 was deemed suitable for conducting comparisons with the mainstem for the three study sites. See Appendix A for plots comparing mean daily temperatures between SAT04, SAT05 and SAT08.

## **Results**

### *Hydrologic conditions*



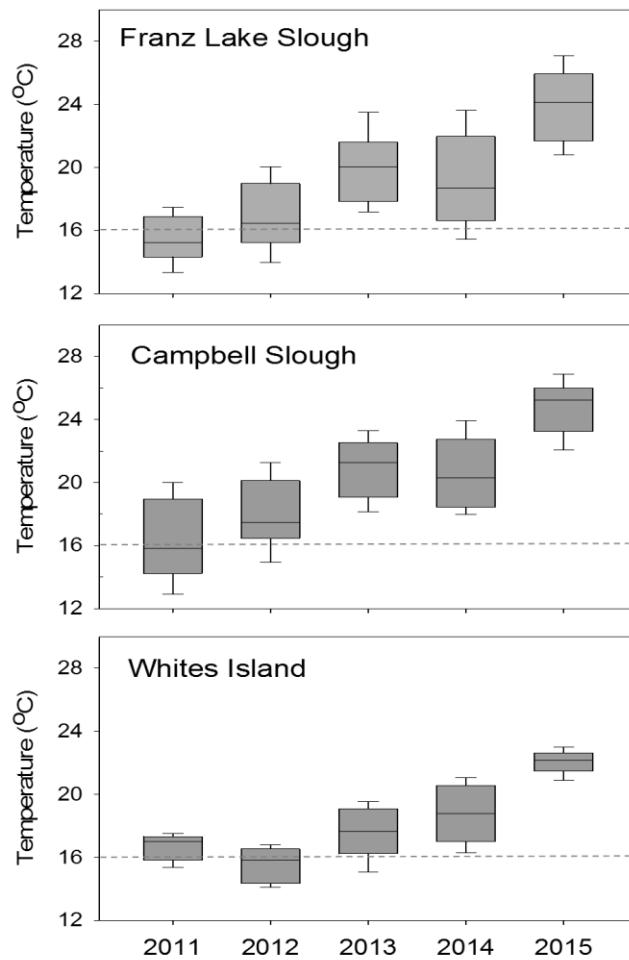
A typical seasonal discharge pattern was observed in each of the first four years of the study (2011-2014), where a distinct freshet occurred in late May-early June (Fig. 2). In contrast, 2015 was characterized by the distinct lack of a late-spring freshet, resulting from anomalously low precipitation and reduced snowpack throughout the fall and winter. Discharge peaks in 2011 ( $14,343 \text{ m}^3 \text{ s}^{-1}$ ) and 2012 ( $12,519 \text{ m}^3 \text{ s}^{-1}$ ) were higher than the 10-year average ( $10,592 \text{ m}^3 \text{ s}^{-1}$ ), while those in 2013 and 2014 were close to the 10-year average ( $9,964 \text{ m}^3 \text{ s}^{-1}$  and  $10,540 \text{ m}^3 \text{ s}^{-1}$  for 2013 and 2014, respectively). Discharge in 2015 was far below average, with a peak of only  $7,702 \text{ m}^3 \text{ s}^{-1}$  in early April and no distinct freshet in May/June.



**Figure 2.** Hydrographs showing mean daily discharge ( $\text{m}^3 \text{s}^{-1}$ ) from Bonneville Dam during the years 2011–2015. Data in black correspond to the study period (April 1–July 31), which constitutes the typical time period of juvenile salmonid residence in shallow water habitats in the lower Columbia River.

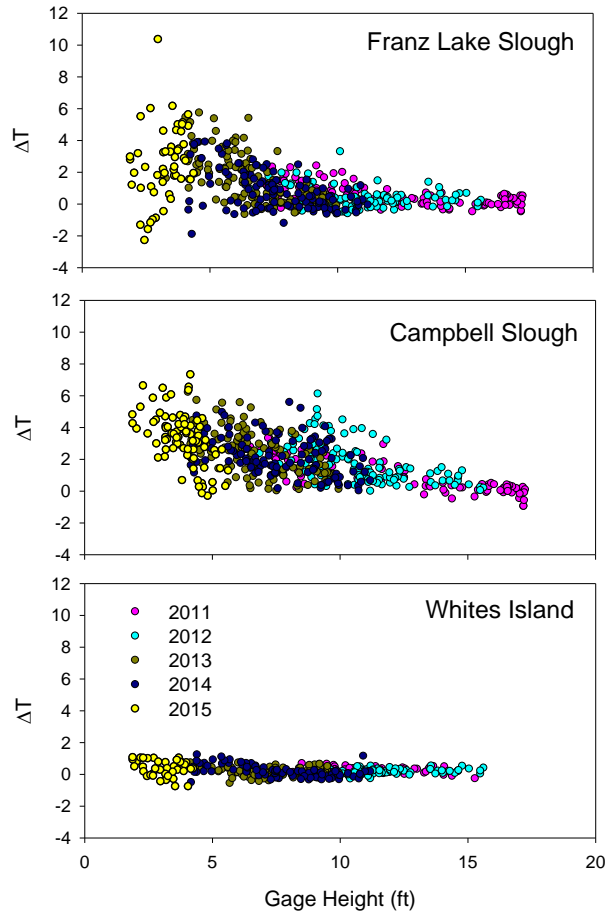
## Temperature and Dissolved Oxygen

All sites had cooler-than-average summer water temperatures during years with high discharge (2011, 2012) and warmer-than-average summer water temperatures during years with lower discharge (2013, 2014; Fig. 3). At all three sites, summer water temperatures in 2015 were the warmest of the five-year period. Higher water temperatures in 2015 were associated with low water elevation in the sloughs, low river discharge, and the absence of a spring freshet.



**Figure 3.** Box and whisker plots showing range of water temperatures (°C) between June 1–July 31 at the three study sites from 2011-2015. Line inside of boxes represents median temperature while error bars represent upper and lower quartiles. Dashed line represents 16 °C threshold for optimal growth conditions for juvenile salmonids.

Average monthly temperatures were consistently lower at Whites Island than at Campbell Slough or Franz Lake Slough during all five years of the study. The highest daily average temperature of the five-year period was observed at Franz Lake Slough (32.57 °C, 7/29/15; Fig. 3). Whites Island consistently exhibited a smaller range in mean daily temperatures compared to either Campbell Slough or Franz Lake Slough (Fig. 3). Variations in dissolved oxygen and temperature among the off-channel sites and between each off-channel sites and the mainstem ( $\Delta T$  and  $\Delta O_{2sat}$ ) were greatest when river flows and water elevation were low, reflecting the reduced connectivity to the mainstem under these conditions. These differences were modulated by individual site characteristics, such as width:depth ratio and distance from the mainstem (Table 1). The relationship between water elevation and temperature offset ( $\Delta T$ ) between each site and the mainstem river at SAT04 differed between the three sites (Fig. 4). During low-water years (2013, 2014 and 2015),  $\Delta T$  for Franz Lake Slough–SAT04 and for Campbell Slough–SAT04 were much greater than in high-water years (2011 and 2012), although within each year there was a large range in  $\Delta T$  values (up to 12 °C) at both Campbell Slough and Franz Lake Slough.  $\Delta T$  values were higher at Franz Lake Slough compared to Campbell Slough during low-water years (Fig. 4), but lower during high-water years. At Whites Island,  $\Delta T$  was always small (<1 °C), even during low-water years. At both Franz Lake Slough and Whites Island, the greatest number of days during which  $\Delta T$  fell below zero – meaning that mean daily temperatures were lower in off-channel sites than in the mainstem – were observed 2015.

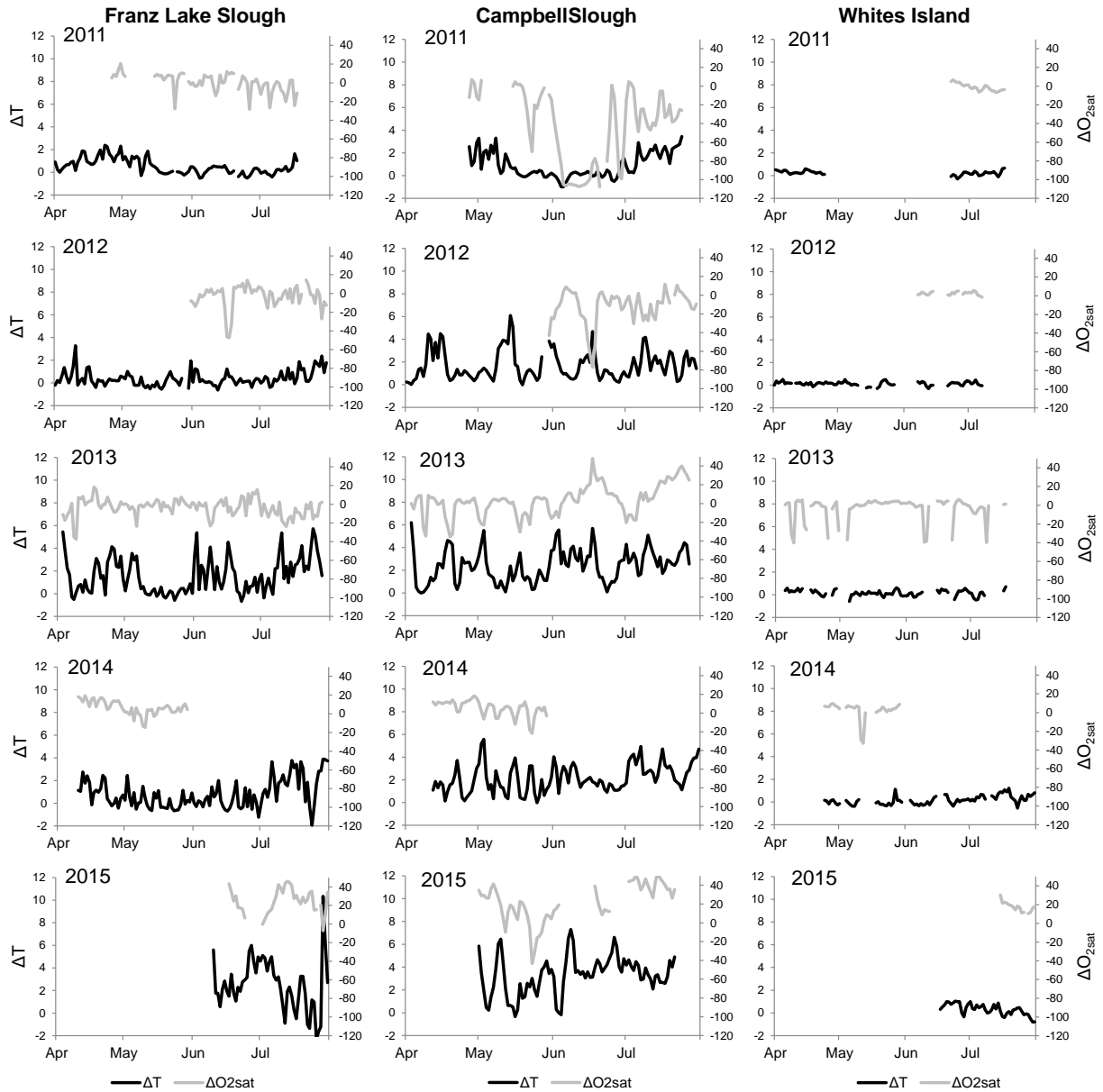


**Figure 4.** Scatter plots showing mean daily gage height (ft) measured at USGS gage 14144700 on the x-axis and mean daily difference in water temperatures ( $\Delta T$ ,  $^{\circ}\text{C}$ ) between study sites and mainstem conditions measured at 0.3 m depth at SAT04. Plots are colored by year with 2011 (pink), 2012 (light blue), 2013 (olive green), 2014 (dark blue) and 2015 (yellow).

Figure 5 shows differences in temperature ( $\Delta T$ ) and percent saturation of dissolved oxygen relative to equilibrium with the atmosphere ( $\Delta O_{2\text{sat}}$ ) between each study site and the mainstem Columbia River at SAT04.  $\Delta T$  and  $\Delta O_{2\text{sat}}$  were greater at Franz Lake Slough and Campbell Slough than at Whites Island. However,  $\Delta T$  was smallest at Campbell Slough during periods of high flow, notably during the freshet of 2011. At that time, water elevation at Campbell Slough was likely high, indicating a greater degree of connectivity to the mainstem.

Interestingly,  $\Delta\%O_{2sat}$  at Campbell Slough was low during this period, reaching nearly  $-120\%$  relative to the mainstem. Low DO concentrations tend to occur when aerobic respiration exceeds photosynthesis. It is possible that low in-water light levels that are typically observed during the spring freshet shift the balance between primary production and respiration during these time periods. Overall, there was a lack of seasonality in  $\Delta T$  between off-channel sites and the mainstem (Fig. 5). Instead, variations in  $\Delta T$  followed episodic events such as precipitation or pulsed releases of water from Bonneville Dam.

Dissolved oxygen (DO) concentrations were rarely significantly higher in shallow water areas than in the mainstem, with a few exceptions that included late summer 2013 (Campbell Slough) and between late June and early August in 2015 (all three sites). There was a co-occurrence of lower DO saturation and higher temperatures in the off-channel sites relative to the mainstem during several short ( $\sim 5$  d) periods throughout the data set. These short periods of low DO relative to the mainstem likely reflected higher rates of respiration of organic matter.



**Figure 5.** Differences in water temperature ( $\Delta T$ ,  $^{\circ}\text{C}$ ) and dissolved oxygen ( $\Delta\text{O}_{2\text{sat}}$ , % saturation relative to equilibrium with the atmosphere) measurements by YSI sondes at the study sites (Franz Lake Slough, Campbell Slough, and Whites Island) and in the mainstem at 0.3 m depth at SAT04. Black lines represent temperature differences ( $\Delta T$ ) and gray lines represent differences in percent saturation of dissolved oxygen ( $\Delta\text{O}_{2\text{sat}}$ ). Gaps in data represent periods during which sondes and/or sensors were either not deployed or were non-functional.

### *Dissolved Nutrients*

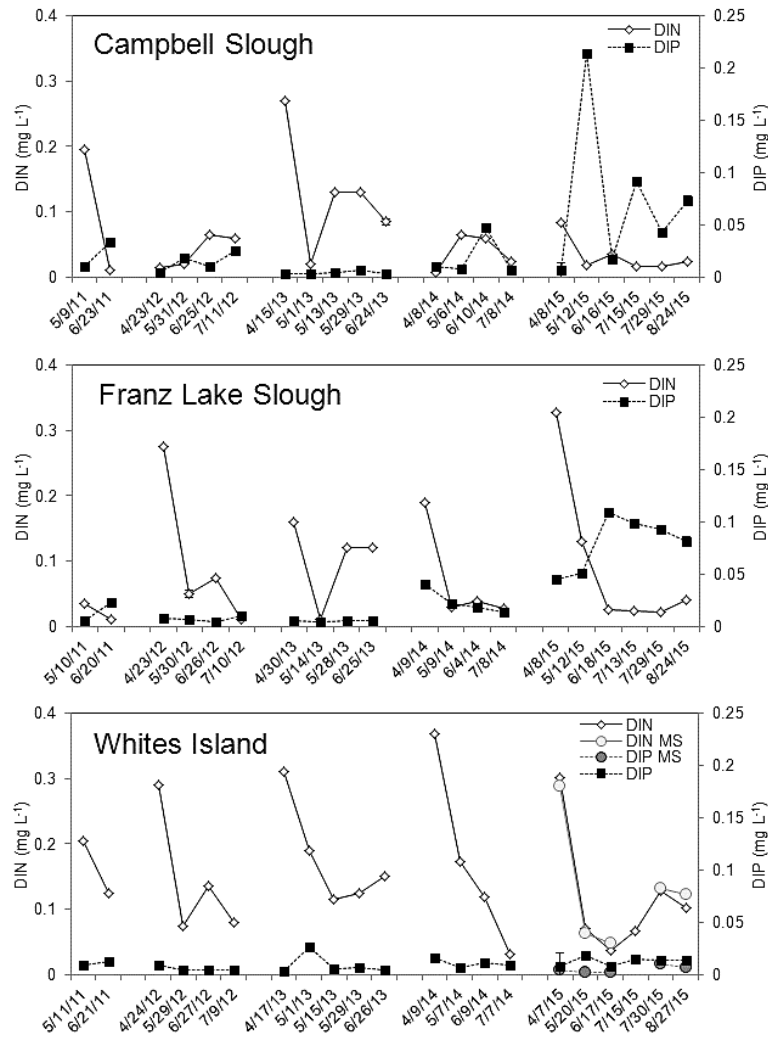
$\Sigma$ DIN concentrations at Whites Island were similar to mainstem concentrations in Cathlamet Channel near Elochoman Marina (rm 38, downstream of Whites Island) during each year of the study, with values peaking in April each year ( $>0.20 \text{ mg L}^{-1}$ ) and declining between April and June (Fig. 6; note that there were not enough data collected in 2011 to confirm this pattern, since nutrients were only measured in May and June that year). A similar trend was observed at Franz Lake Slough, with the exception of 2013, when elevated  $\Sigma$ DIN ( $0.12 \text{ mg L}^{-1}$ ) was observed in late May and early June (Fig. 6).  $\Sigma$ DIN concentrations were far lower at Campbell Slough during the early spring compared to the two other sites and to the mainstem at SAT05 (Appendix B), except in 2013 when  $\Sigma$ DIN in April at Campbell Slough was  $0.27 \text{ mg L}^{-1}$  ( $0.26 \text{ mg L}^{-1} \text{ NO}_3^-$ ,  $0.01 \text{ mg L}^{-1} \text{ NH}_4^+$ ) compared to  $0.16$  and  $0.31 \text{ mg L}^{-1}$  at Franz Lake Slough and Whites Island, respectively.

DIP was always relatively low at Whites Island ( $<0.05 \text{ mg L}^{-1}$ ; Fig. 6). Franz Lake Slough and Campbell Slough both had higher concentrations of DIP in 2014 and 2015 compared to 2011, 2012, or 2013. The highest DIP concentration was  $0.21 \text{ mg L}^{-1}$ , observed at Campbell Slough in May 2015.

As with dissolved nutrient concentrations, there was no consistent seasonal pattern in  $\Sigma$ DIN:DIP (N:P) molar ratio at any of the three sites during any of the five years (Fig. 7), except for generally higher ratios in early spring, likely due to high  $\Sigma$ DIN inputs. Both Campbell Slough and Whites Island had very high N:P ratios ( $>200$ ) in April of 2013, likely caused by a large influx of  $\Sigma$ DIN from the Willamette River during that time period. Franz Lake Slough and Campbell Slough frequently had N:P ratios  $<16$ , which is indicative of potential nitrogen limitation at those sites (Redfield, 1934). In contrast, N:P at Whites Island rarely fell below 16.

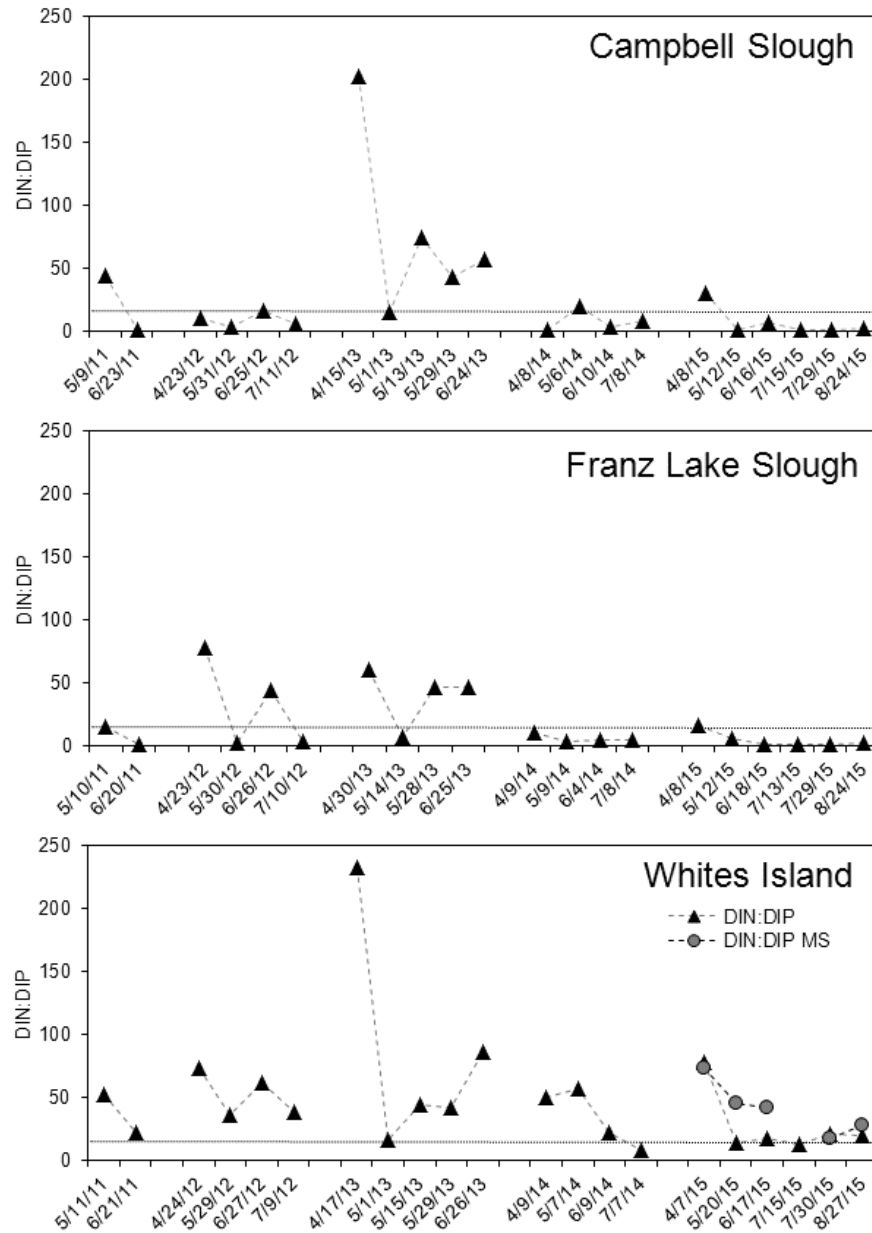


Similar to concentrations of  $\Sigma$ DIN and DIP, N:P in the mainstem river was similar to Whites Island (but not Campbell Slough or Franz Lake Slough) during the 2015 season, although with slightly higher N:P ratios in the mainstem compared to the sample site in May and June 2015.



**Figure 6.** Time series of dissolved nutrient data at three study sites (Franz Lake Slough, Campbell Slough and Whites Island) between 2011 and 2014 and comparison of mainstem dissolved nutrients to Whites Island in 2015. Dissolved Inorganic Nitrogen (DIN) is the composed of  $\text{NO}_2^-$ ,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  and Dissolved Inorganic Phosphorus (DIP) is composed of  $\text{PO}_4^{3-}$ . DIN in study sites is represented by filled black squares with dashed black lines between distinct points of measurement, while DIP in study sites is represented by unfilled white diamonds with solid black lines between distinct points of measurement. DIN and DIP in the mainstem Columbia River in 2015 were collected at the surface in Cathlamet Channel approximately 1,000 m downstream of the entrance to Whites Island.  $\Sigma$ DIN in the mainstem is

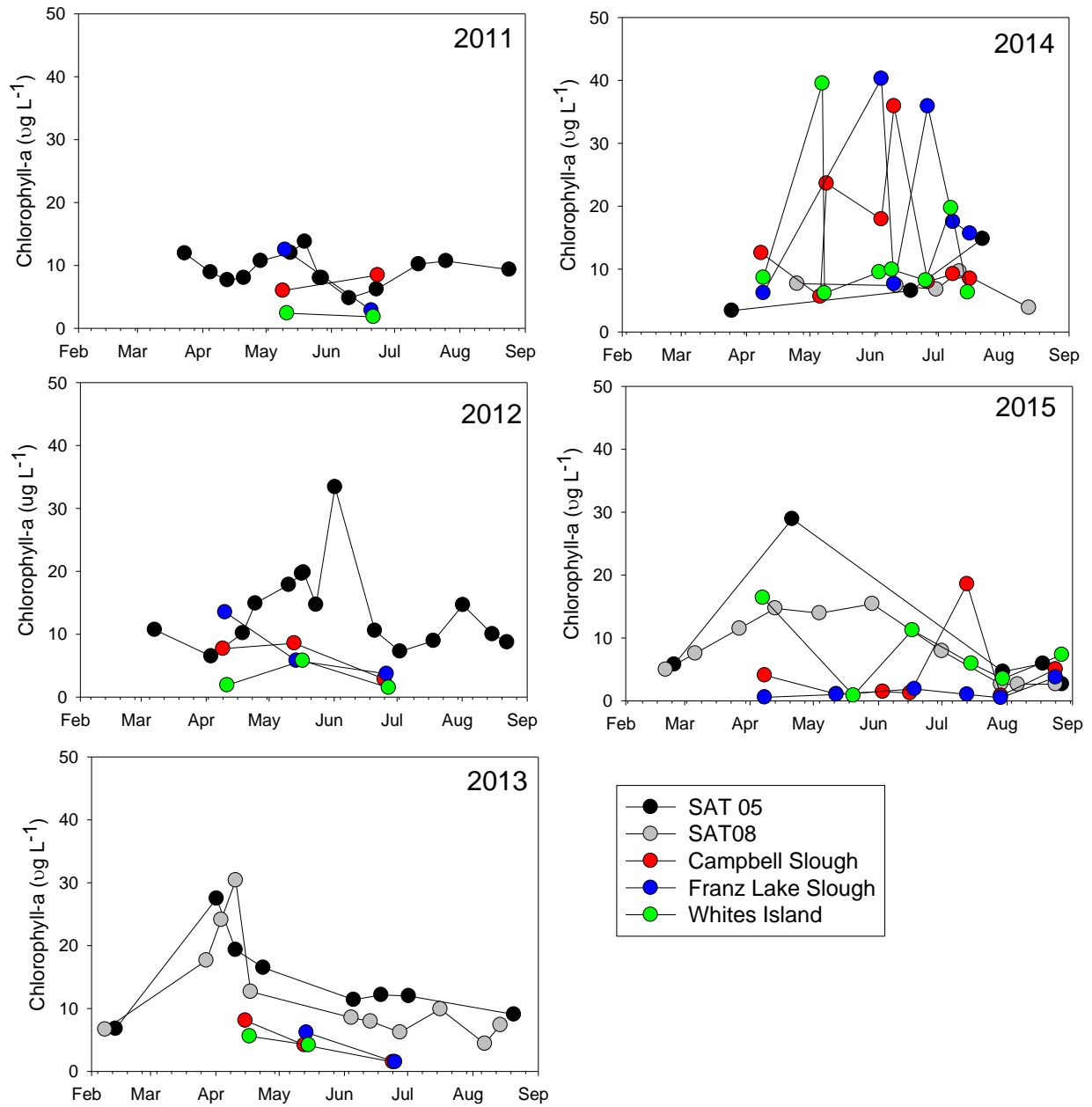
represented by unfilled circles with solid gray lines between distinct points of measurement, while DIP in the mainstem is represented by gray-filled circles with dashed gray lines between distinct points of measurement. Error bars represent standard error for duplicate samples.



**Figure 7.** Molar ratio of N:P during the study (2011-2015). Filled black triangles represent molar N:P ratio at sampling sites. Filled gray circles represent molar N:P ratio in the mainstem, collected at the surface in Cathlamet Channel approximately 1,000 m downstream of the entrance to Whites Island. Horizontal line indicates a N:P ratio of 16 (Redfield ratio).

### *Chlorophyll a*

Bulk concentrations of chlorophyll a can be used a rough measure of production in aquatic habitats. Chlorophyll a concentrations were usually higher in mainstem sites (SAT05 and SAT08) earlier in the season (April), and often continued to be elevated in the mainstem relative to off-channel sites throughout the season (Fig. 8). Campbell Slough saw increasing chlorophyll a concentrations later in the season, surpassing production in the mainstem during summer months in 2011, 2014 and 2015. Primary production in the mainstem at both SAT05 and SAT08 was much lower in 2014 than in other years, while primary production in all three study sites were higher than average in 2014 (Fig. 8). Productivity at Whites Island was lower on average in high water years (2011 and 2012) than in years where discharge was closer to the 10-year average (2013 and 2014). Unlike the mainstem sites which showed a consistent seasonal peak in primary production in the spring (with the exception of 2014), chlorophyll a in study sites followed more variable seasonal patterns, often with large peaks followed by dramatic declines at the next sampling event. It is important to note that chlorophyll a data in this study should be interpreted with a degree of caution, as a change in methods occurred between 2013 and 2014. Chlorophyll a in study sites in 2014 and 2015 was determined fluorometrically, which is significantly more sensitive than the spectrophotometric method used from 2011-2013. Many samples taken in 2011-2013 were below the limit of spectrophotometric detection ( $1 \text{ mg chl L}^{-1}$ ), and were not included in Figure 8.



**Figure 8.** Chlorophyll a concentrations ( $\mu\text{g L}^{-1}$ ) at the three study sites (Campbell Slough, red; Franz Lake Slough, blue; and Whites Island, green) and at the two mainstem sites (SAT05, black; SAT08, gray).

## Discussion

Differences in biogeochemical characteristics among the study sites can be viewed as a function of connectivity to the mainstem. Connectivity, defined by Pringle (2001) as the water mediated transfer of matter, energy and organisms between elements of the hydrological cycle, is influenced by hydrogeomorphology, and therefore the degree to which habitats are connected varies with the magnitude of river flow and with geomorphic features, including channel width and depth as well as distance from the mainstem. For example, water temperatures and dissolved oxygen saturation at Whites Island were nearly always the same as in the mainstem channel, due to a high degree of connectivity between the two habitats during all seasons. The high degree of connectivity between the Whites Island site and the mainstem is driven by tidal fluctuations as well as the proximity of the sampling site to the mainstem. In contrast, connectivity between both Franz Lake Slough and Campbell Slough and the mainstem can be considered to be low, especially during periods of low water elevation when there were large fluctuations in  $\Delta T$  at both sites, which included warming up to 10 °C relative to the mainstem. Thus, connectivity varies seasonally with the river hydrograph at sites that are less influenced by tidal fluctuations or that are located further away from the mainstem.

The data indicated that connectivity between mainstem and off-channel habitats is strongly driven by the seasonal river hydrograph, as well as tidal flows. Connectivity to mainstem habitats is important for several reasons. Some of the primary determinants of ideal habitat for salmonids and other fish include suitable water quality and availability of sufficient prey resources. Campbell Slough and Franz Lake Slough each showed lower connectivity to the mainstem (as defined by greater differences in biogeochemical properties relative to a common site, SAT04), which was manifest as warmer average daily temperatures and greater fluctuations

in dissolved oxygen saturation. These characteristics likely make both Campbell Slough and Franz Lake Slough suboptimal for salmonid use during low-flow periods. However, primary production was frequently higher at these sites compared to the mainstem or to Whites Island, which could indicate greater availability of prey resources relative to Whites Island or to the mainstem.

Nutrient concentrations at the shallow water sites were generally slightly lower than in the mainstem, which is consistent with higher primary production (which would draw down nutrients) at those sites. It is notable that during low-flow conditions (especially in 2015), DIP concentrations at Campbell Slough and Franz Lake Slough were frequently higher than the mainstem. Elevated nutrient levels could indicate local sources of DIP, such as from runoff from adjacent agricultural fields, which are not diluted by high flows during periods of elevated discharge, as has been seen in the River Rhine and its floodplains (Venterink et al., 2003). Nutrient concentrations at Campbell Slough were generally more variable both inter- and intra-annually compared to the other two sites, which is consistent with localized sources and sinks that act independently of nutrient transformations in the mainstem.

The sites included in this study were selected for long-term monitoring by the Lower Columbia Estuary Partnership because they support endangered salmon stocks during critical juvenile life stages (Sagar et al., 2013). Based on the data, Whites Island is likely a more suitable habitat for juvenile salmon in terms of temperature and lower potential for development of hypoxia during periods of low flow. Furthermore, although primary production is higher at Campbell Slough and Franz Lake Slough later in the season, Whites Island supports higher primary production than the other two sites earlier in the season, possibly due to higher inputs of phytoplankton populations from the mainstem during the spring bloom. Because Whites Island

supports high primary production in the early spring when temperatures are best suited for juvenile salmon, it is likely to provide high-quality juvenile habitat for early-run species (e.g., spring Chinook, *Oncorhynchus tshawytscha*). However, late-run salmon stocks (i.e. Coho, *Oncorhynchus kisutch*) could benefit from higher production at sites like Campbell Slough and Franz Lake Slough, despite the potential for poor water quality in those sites later in the season.

Given the sensitivity of salmonids to water temperature, it is likely that high summer temperatures at Campbell Slough and Franz Lake Slough may negatively impact salmonid use of these habitats. In 2015, mean daily temperature values exceeded thresholds of 16 °C (threshold for optimal juvenile salmonid growth; Beechie et al., 2013) at Campbell Slough after April 29 and 24 °C (threshold above which juvenile Chinook salmon mortality has been observed; Beechie et al. 2013 and references therein) at Campbell Slough after June 20 and Franz Lake Slough after June 26. At all three sites there were more days with mean daily temperatures exceeding the 16 °C in 2013, 2014, and especially 2015 compared to 2011 and 2012 (Table 2). Notably, there were more frequent observations of mean daily temperatures above the 16 °C threshold at Campbell Slough than at the other two sites (Table 2). It is interesting to note, however, that there were several days when mean daily temperature was a degree or more lower than the mainstem at both Campbell Slough, and to a greater extent at Franz Lake Slough (Table 3). This implies there may be sources of cool groundwater at these sites that could serve as thermal refugia when temperatures in the mainstem exceed optimal thresholds.

**Table 2.** Number of occurrences of mean daily temperatures >16 °C at the three study sites over the five-year period. To compensate for missing sonde data, it was assumed that daily mean temperatures after the last day of available data continued to increase. In 2015, sondes at Franz Lake Slough and Whites Island were not deployed until the date listed as the earliest instance of 16 °C, when temperatures already exceeded 16 °C. It is likely that there were several more days with mean daily temperatures >16 °C.

Site		2011	2012	2013	2014	2015
Franz Lake Slough	<i># days &gt;16 °C</i>	30	36	63	51	52+
	<i>earliest instance 16 °C</i>	7/2	6/16	5/6	6/6	6/10*
Campbell Slough	<i># days &gt;16 °C</i>	33	59	67	71	85
	<i>earliest instance 16 °C</i>	6/29	5/14	5/2	5/2	4/29
Whites Island	<i># days &gt;16 °C</i>	31	35	42	51	45+
	<i>earliest instance 16 °C</i>	7/1	6/27	6/7	6/8	6/17*

\*Date of deployment of sondes.

**Table 3.** Proportion of days at Franz Lake Slough when mean daily temperature was lower than the mainstem Columbia River at SAT 08, and maximum negative temperature difference between Franz Lake Slough and SAT 08.

	n	% days in which $\Delta T < 0$	max $-\Delta T$ (°C)
April '13	28	18%	-0.30
May '13	31	32%	-0.84
June '13	31	10%	-0.13
July '13	28	0%	<i>n/a</i>
April '14	0	<i>n/a</i>	<i>n/a</i>
May '14	0	<i>n/a</i>	<i>n/a</i>
June '14	4	100%	-6.95
July '14	31	10%	-2.15
April '15	0	<i>n/a</i>	<i>n/a</i>
May '15	0	<i>n/a</i>	<i>n/a</i>
June '15	21	0%	<i>n/a</i>
July '15	31	23%	-2.20



## **Chapter 3: Phytoplankton dynamics in off-channel habitats of the lower Columbia River**

### **Introduction**

As primary producers, phytoplankton play a major role in both the response of river ecosystems to alterations in flow and in subsequent effects on trophic web structure (Wehr and Descy, 1998). Because of their fast growth rates (compared for instance, to macroinvertebrates) and sensitivity to chemical components of aquatic systems, phytoplankton respond quickly and predictably to environmental changes (McCormick and Cairns, 1994), and can be used as bioindicators of eutrophication and pollution in lakes and rivers (Kelly and Whitton, 1995). Thus, examination of phytoplankton communities can be used as a cost-effective tool to inform managers about the effects of physical and chemical alterations to a large river system on overall ecosystem health.

In addition to light availability, phytoplankton production in rivers is controlled by two factors: river discharge and nutrient loading (Cloern, 1991; Paerl et. al 1998), depending on the structure of the river system and land use patterns of the drainage basin. Unlike small rivers and streams where discharge stirs up nutrients and meroplankton from sediments and effectively increases pelagic production, phytoplankton production in large river systems is usually inversely correlated with discharge (Wehr and Descy, 1998). This is mainly due to short residence times that occur when discharge is elevated, which limit phytoplankton population growth. True nutrient limitation in large rivers is unlikely (Reynolds and Descy, 1996); however, high inputs of macronutrients in river systems from non-point sources can play a role in controlling phytoplankton abundance and community composition (Basu and Pick, 1996). Eutrophication—the process whereby biomass in a system increases due to excess inputs of nutrients—is a problem in many industrialized river systems around the world, and has caused

major shifts in phytoplankton communities (Turner and Rabalais, 1994; Kelly and Whitton, 1995; Paerl et al., 2007).

Arguably the most severe threat associated with phytoplankton comes from cyanobacteria blooms that tend to occur in eutrophic waters during summer months when temperatures are relatively warm and mixing is incomplete (Paerl, 2008). Many species of freshwater cyanobacteria are capable of producing toxins (known as cyanotoxins), including hepatotoxic microcystins. Exposure to microcystins has been shown to reduce growth rate compared to unexposed juveniles in several clades of fish, producing dose-dependent decreases in survival rate and causing morphological abnormalities of both exterior body parts and internal organ systems (Malbrouck and Kestemont, 2006). Microcystins can also bioaccumulate during transfer through the aquatic food web (Kozlowsky-Suzuki et al., 2012). Non-toxic threats posed by cyanobacteria blooms include respiration-induced hypoxia associated with bloom die-off, decreased CO<sub>2</sub>, increased pH, and reduced light penetration (Paerl et al., 2001; Havens, 2008). Hypoxia following degradation of large cyanobacteria blooms is often responsible for large fish kills (Paerl et al., 1998; McIness and Quigg, 2010) and reduced diversity of benthic invertebrates (Josefson and Widbom, 1988). Shading of the water column by surface blooms of cyanobacteria can lead to loss of submerged aquatic vegetation in shallow water habitats (Havens, 2008) as well as decreased visual clarity for benthic-feeding fish (Engström-Ost et al., 2006).

Annual high abundances of cyanobacteria have been documented in large river systems worldwide. The Murray-Darling River system in Australia experiences annual blooms of the toxic cyanobacteria *Anabaena circinalis*, which have been largely attributable to stratification stemming from low flow conditions in warm summer months (Maier et al., 2001). The lower Nakdong River in South Korea has a recurring bloom of *Microcystis* and other common

cyanobacterial taxa in the late summer (Ha et al., 2002). In Europe, the Meuse River (Hungary) and the Rhine River (Germany) both experience short bloom periods where cyanobacteria dominate over diatoms during summer months (Ibelings et al., 1998). In the United States, recurrent blooms of toxin-producing cyanobacteria have been found in several regulated temperate river systems including the Ohio River (Wehr and Thorp, 1997), Hudson River (prior to invasion by *Dreissena polymorpha*) (Smith et al., 1998), and upper Mississippi River (Manier, 2014). Cyanobacteria are more likely to be found in systems that experience low flow periods in the summer, due to their inherent morphological and functional traits such as colony formation and buoyancy regulation (Fraisse et al., 2013). On the other hand, river systems with higher flows such as the Loire River (France) tend to support higher diversity of diatoms and chlorophytes throughout the season (Descy et al., 2012). In rivers that experience annual recurrences of cyanobacteria blooms and other nuisance phytoplankton blooms, mitigation and dispersal of blooms has been accomplished either via flow regulation and prescribed release events (Mitrovic et al., 2011, Jeong et al., 2006), or via nutrient reduction (Paerl et al., 2004).

High abundances of cyanobacteria may influence juvenile salmonid health both directly and indirectly. Surface blooms of cyanobacteria can curb light penetration into benthic zones leading to loss of submerged vegetation that provides refuge from predators to juvenile fish (Werner et al., 1983, Rozas and Odum, 1988). As blooms die off and sink, decomposition of cyanobacterial biomass reduces oxygen in the benthic zone, which can be acutely toxic to benthic invertebrates and to several fish species, including salmonids (Colby et al., 1972, Mustafa et al., 2011). In the event of microcystin production, toxins in the water column may be directly ingested by juvenile salmon, or their prey. Historically, high concentrations of microcystins have been associated with low density and low diversity of larval chironomidae

(Kaczorowska and Kornijow, 2012), the preferred food source of juvenile salmonids in the lower Columbia River (Sagar et al., 2013). Various isomers of microcystin have also been shown to be acutely toxic to some zooplankton, including the cladoceran *Daphnia* spp. (Rorhlak et al., 2001), a widely available (although not preferred) food source for juvenile salmonids in the Columbia River during summer months (Sagar et al., 2013).

From a management standpoint, it is important to identify major controllers of primary production, especially when phytoplankton blooms threaten native and endangered species. Multivariate, ordination-based techniques are often employed to elucidate patterns in variation amongst coupled biotic and abiotic samples in order to identify significant factors that affect variance in biological communities. In an attempt to characterize patterns of variation and identify underlying causes, this chapter analyzes phytoplankton abundance and species composition in the context of water quality variables using both traditional analytical methods (i.e. time series and regression analyses) and multivariate statistics (Nonmetric Multi-dimensional Scaling, NMDS, and Canonical Analysis of Principal Coordinates, CAP).

## **Methods**

### *Environmental data*

Environmental data used in the analysis of phytoplankton population dynamics includes temperature, dissolved oxygen, and dissolved nutrients (nitrate+nitrite, ortho-phosphate, and ammonium). These data are presented in Chapter 2, where the methods associated with their measurements can be found.

### *Phytoplankton identification and enumeration*

Phytoplankton samples were settled in cylindrical counting chambers as aliquots of either 27 mL or 12 mL and settled for a minimum of 24 h (Utermöhl, 1958). In each sample, at least 400 cells were counted at both 400X and 200X magnification using a minimum of five fields of view on an inverted light microscope (Leica DMIL). A half-chamber scan for large and rare taxa was performed at 100X magnification. Phytoplankton taxa were identified to the lowest possible taxonomic rank (most often genus). Cell abundances of the same taxon observed at both 400X and 200X were averaged in the calculation of total cell abundance in a sample. For filamentous cyanobacteria (excluding *Dolichospermum* sp.), cell numbers of ten filaments in each sample were counted, and the mean of those cell counts was applied to all filaments counted in that particular sample.

#### *Multivariate Statistical Analyses*

Nonmetric Multi-dimensional Scaling (NMDS) and Canonical Analysis of Principal Coordinates (CAP) routines were performed using PRIMER-E v.7 with PERMANOVA+. NMDS is a multivariate technique that identifies the degree of similarity between biological communities among a group of samples in a data set. In NMDS, samples are typically represented in 2-dimensional ordination space using distance between sample points as a measure of similarity of biological communities; short distances represent relatively high similarity between samples, while longer distances represent relatively low similarity between samples.

Major phytoplankton taxa were selected for multivariate analyses if their abundance constituted at least 10% of total phytoplankton abundance in any sample. Taxa that did not meet these criteria were excluded from analysis. Two NMDS analyses were run for this study that included i) all major phytoplankton taxa (NMDS<sub>total</sub>) and ii) only major diatom taxa

(NMDS<sub>diatom</sub>). Abundances for 25 major phytoplankton taxa (NMDS<sub>total</sub>) and 10 major diatom taxa (NMDS<sub>diatom</sub>) were standardized by sample and the data were square-root transformed in order to achieve a normal distribution of the data prior to analysis.

Canonical Analysis of Principal Coordinates (CAP) is an analytical technique that uses canonical correlation to determine the degree to which environmental factors explain variability among biological communities. A Bray-Curtis resemblance matrix was assembled using the standardized, square-root transformed phytoplankton abundance data and six environmental variables including  $\text{NO}_2^- + \text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ , mean daily water temperature, mean daily dissolved oxygen saturation, and mean daily discharge (at Bonneville Dam). Environmental data were normalized prior to analysis to compare variables at the same scale. Samples with missing environmental data were excluded from multivariate analyses. A total of 70 samples were analyzed in both NMDS analyses, and a total of 38 samples were included for CAP.

## Results

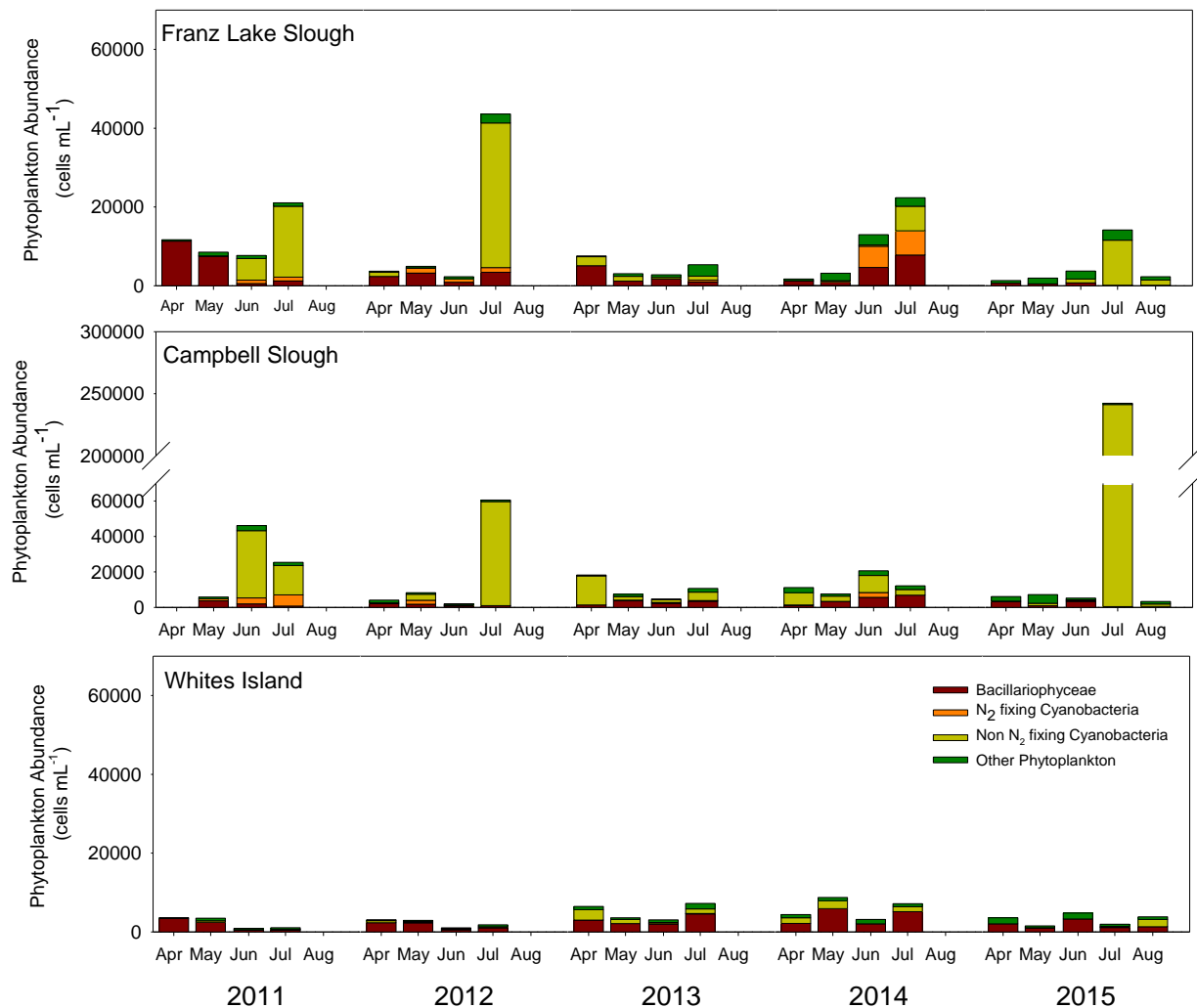
### *Major taxa*

25 major taxa, including 10 diatoms (Bacillariophyceae), 2 cryptophytes, 8 chlorophytes, 4 cyanobacteria and 1 other (grouped dinoflagellates) were identified based on relative contribution to total phytoplankton abundance. Common chlorophyte taxa included *Scenedesmus* spp., *Micratinium* sp., *Ankistrodesmus* sp., and several clades of colonial forms including *Eudorina* sp., *Dictyosphaerium* sp., *Gloeocystis* sp., and *Sphaerocystis* sp. For multivariate analyses, colonial chlorophytes (excluding *Micratinium* sp. and cf. *Spondylosium* sp.) were grouped into one taxonomic category due to uncertainty in identification. Several small, unicellular flagellated chlorophytes were also common but were difficult to identify, and were therefore also summed into one taxonomic variable. Small, unicellular unflagellated

chlorophytes were grouped into a separate taxonomic variable. Four major cyanobacteria taxa (*Microcystis* sp., *Dolichospermum* sp., *Merismopedia* sp., and unidentified filamentous cyanobacteria) were determined to be major phytoplankton taxa. Major diatom taxa are discussed later in this chapter. A complete list of major phytoplankton taxa can be found in Appendix D.

#### *Seasonal patterns in phytoplankton species composition and abundance*

There were consistent seasonal and inter-site differences among phytoplankton assemblages in the study. Diatoms (Class Bacillariophyceae) accounted for a large proportion of total phytoplankton abundance during the spring (April-May) at Whites Island and Franz Lake Slough every year (Fig. 9). In contrast, Campbell Slough had high diatom abundances in the spring (April-May) of 2011, 2012, and 2015, but not 2013 and 2014. At Whites Island, the dominance of diatoms continued through the summer months during every year of the study, while Franz Lake Slough and Campbell Slough had high abundances of cyanobacteria (at least 10,000 cells mL<sup>-1</sup>) during the summer months (June and July) almost every year. Other phytoplankton taxa, consisting mostly of cryptophytes (Class Cryptophyceae) and green algae (Class Chlorophyceae) were abundant (up to about 3,000 cells mL<sup>-1</sup>) at various points throughout this study, but rarely constituted a majority in phytoplankton assemblages. Plots of seasonal and interannual variation in abundances of non-diatom and non-cyanobacteria taxonomic groups can be found in Appendix F.



**Figure 9.** Time series of phytoplankton community at all three study sites (cells mL<sup>-1</sup>, left). Dark red bars represent Bacillariophyceae (diatoms), orange bars represent nitrogen-fixing cyanobacteria, light-green bars represent non nitrogen-fixing cyanobacteria and dark green bars represent all other phytoplankton.

Total cyanobacteria abundances at Campbell Slough and Franz Lake slough followed similar seasonal patterns (Fig. 9), with high abundances typically occurring in June and July. A notable exception to this pattern is April, 2012 when about 20,000 cells mL<sup>-1</sup> of non-nitrogen fixing cyanobacteria were observed in Campbell Slough. The timing of elevated abundances of cyanobacteria was similar at both sites—for example, high abundances were observed in July,

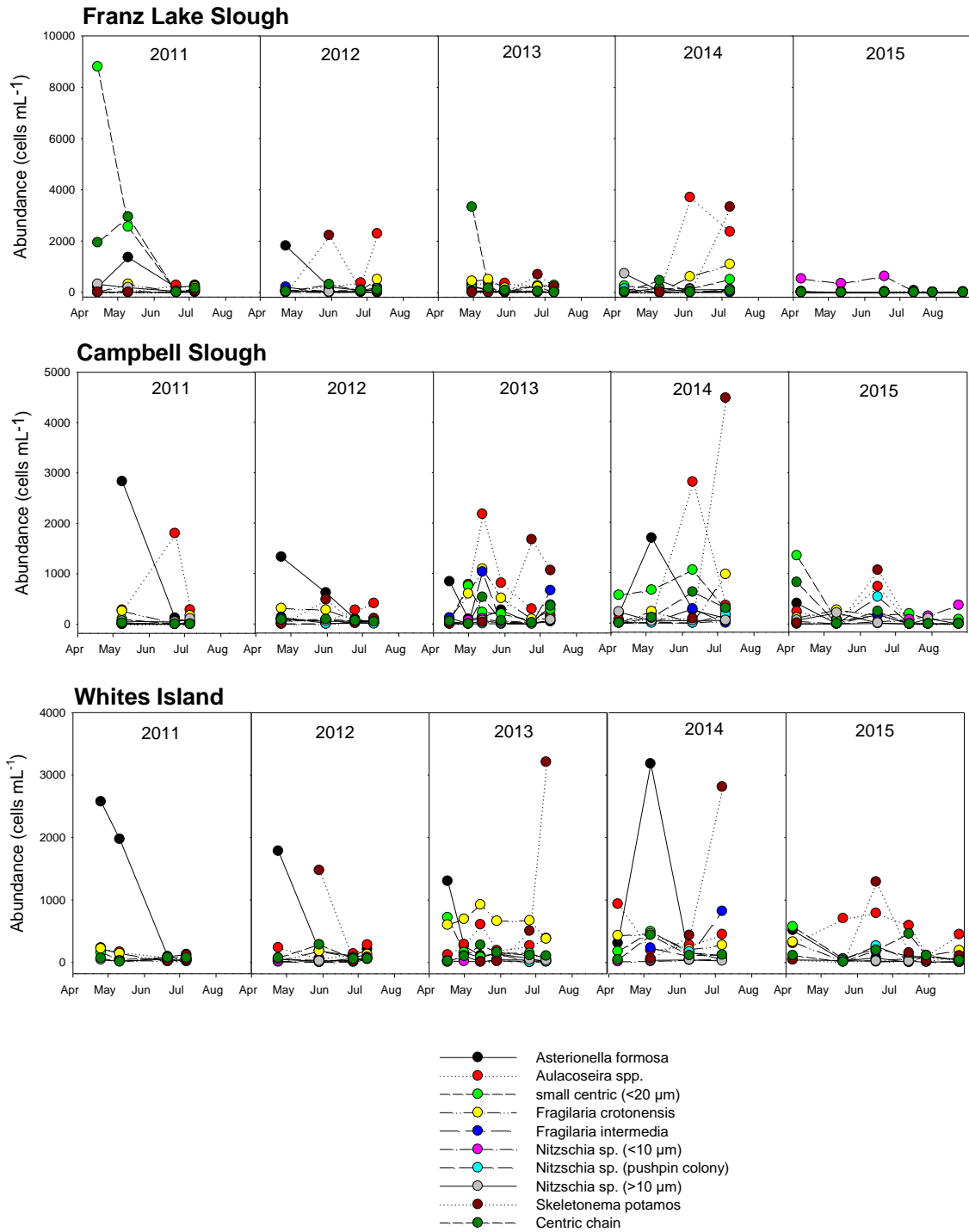


2012 following low abundances in June, 2012 (Fig. 9) – although the scales of abundance and the taxonomic composition varied somewhat.

Diatom community composition varied within sites and between seasons at all three sites. In the two high water years (2011 and 2012), *Asterionella formosa* accounted for a large proportion of the diatom assemblage during the spring months leading up to the freshet (April-May; Fig. 10). *Aulacoseira* spp. were present at high abundances, but tended to occur slightly later in the season than *A. formosa*, usually in May and June and occasionally into July at Franz Lake Slough (2012 and 2014). Small (<20 µm) centric diatoms, both solitary and colonial, were sporadically abundant and tended to be present at high abundances during early spring periods (notably in April 2011 at Franz Lake Slough). *Skeletonema potamos* was abundant each year at all three sites, although to a lesser extent at Franz Lake Slough compared to Campbell Slough or Whites Island. This species tended to dominate the diatom community later in the summer, between June and July.

*A. formosa* was consistently most abundant (>1,000 cells mL<sup>-1</sup>) during early spring at Whites Island from 2011-2014, but present at low abundance during the spring of the drought year (2015). Interestingly, *Aulacoseira* spp. were present at high abundances throughout 2015 at Whites Island. Diatom abundance and diversity at Franz Lake Slough was very low in 2015, and was comprised almost entirely of small (<10 µm) *Nitzschia* sp.

At all three sites, diatom assemblages were dominated by a small number of species (1-2 species) at a time during 2011 and 2012 compared to 2013 and 2014 in which several diatom species tended to co-dominate in the same sample, particularly at Campbell Slough and Whites Island (Fig. 10).



**Figure 10.** Succession of major diatom taxa at Franz Lake Slough, Campbell Slough and Whites Island between April 1 and August 31, 2011-2015.

### *Inter-annual variability in phytoplankton species composition and abundance*

Mean total abundance of phytoplankton (mean of total abundance during all sampling dates in one season) at Whites Island was lower during high water years (2011 and 2012) than in years where discharge was closer to the 10-year average (2013 and 2014). In Campbell Slough and Franz Lake Slough, the opposite pattern was observed, although high abundances during 2011 and 2012 were primarily the result of increased cyanobacteria in summer months. Mean total diatom abundance in Campbell Slough was higher in 2013 and 2014 than 2011 and 2012, while mean total diatom abundance varied between years at Franz Lake Slough (highest in 2011). Total cyanobacteria abundance at both Franz Lake Slough and Campbell Slough was higher during the summers of 2011 and 2012, with relatively lower abundances during summer months in 2013 and 2014.

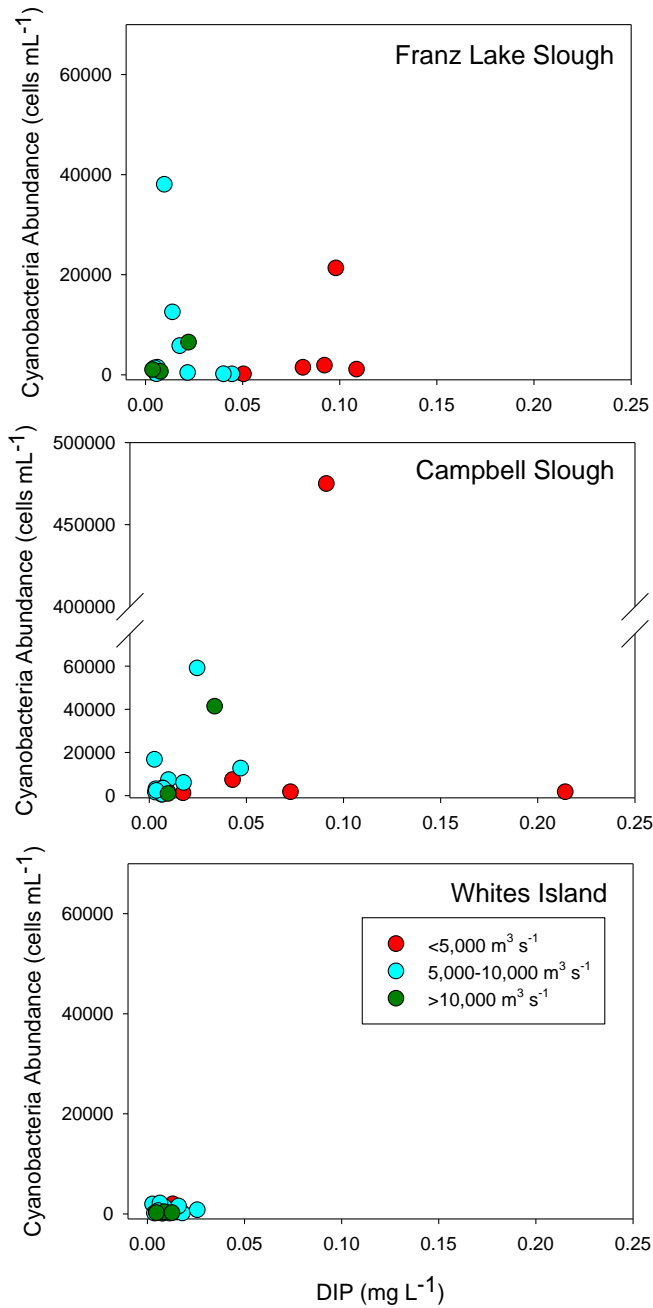
High abundances of cyanobacteria were observed primarily in the late summer after the annual freshet subsided. Although total cyanobacteria abundances at Campbell Slough and Franz Lake slough followed similar seasonal patterns (Fig. 9), population dynamics of particular species differed between the two sites and among the years examined. For example, in June and July 2014, higher abundances of *Dolichospermum* sp. were observed at Franz Lake Slough compared to Campbell Slough. Perhaps the most notable difference among the two sites was the very high abundance (monthly average of about 237,000 cells mL<sup>-1</sup>) of *Merismopedia* sp. observed at Campbell Slough in July 2015, which was reduced to 1,130 cells mL<sup>-1</sup> by August 2015. *Merismopedia* sp. was absent in Whites Island during that time period and present in Franz Lake Slough only at very low abundance (<50 cells mL<sup>-1</sup>).

At both Franz Lake Slough and Campbell Slough, cyanobacteria populations tended to be dominated by non-nitrogen-fixing cyanobacteria (primarily *Microcystis* sp.), although nitrogen-

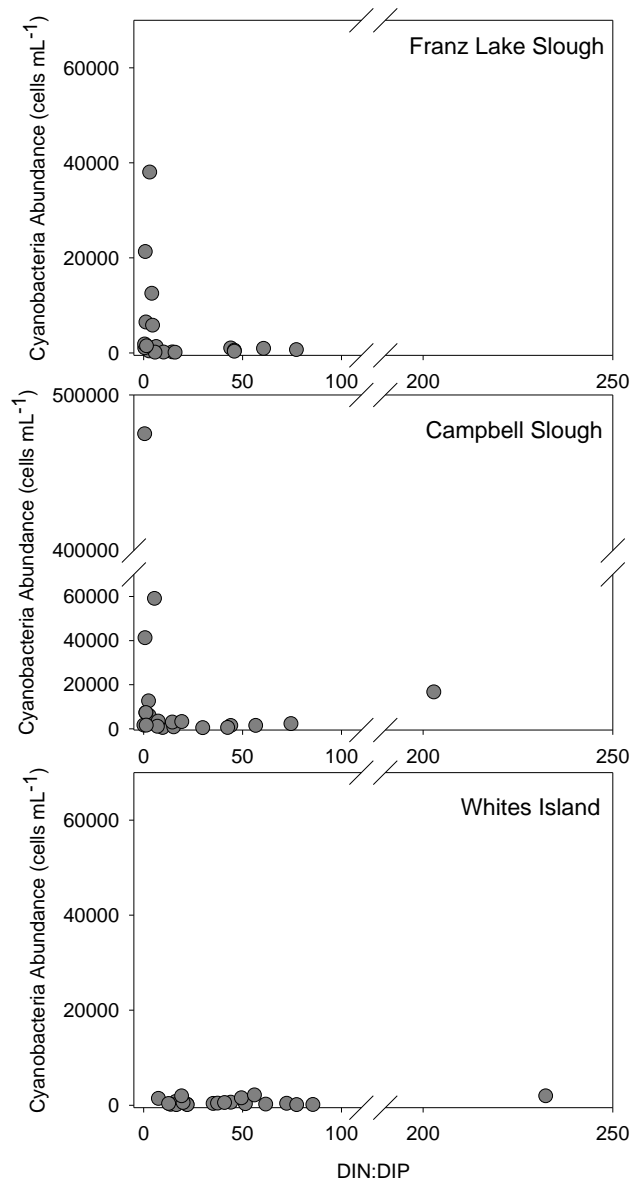
fixing cyanobacteria (primarily *Dolichospermum* sp.) were present during most years and were seen in greater numbers ( $>10,000$  cells  $\text{mL}^{-1}$ ) in June and July of 2014 in Franz Lake Slough. *Dolichospermum* sp. was more prevalent in both Campbell Slough and Franz Lake Slough during 2011 and 2012 than the latter three years of this study.

#### *Cyanobacteria abundances and abiotic variables*

No statistically significant relationships were observed between cyanobacteria abundances and  $\Sigma\text{DIN}$  at any of the three sample sites (data not shown). At Campbell Slough and Franz Lake Slough, high abundances of cyanobacteria ( $>20,000$  cells  $\text{mL}^{-1}$ ) were observed when DIP was moderately high (between 0.01 and 0.10  $\text{mg L}^{-1}$ ), but not when DIP was above 0.10  $\text{mg L}^{-1}$  (low flow periods, Fig. 11). High abundances of cyanobacteria ( $>20,000$  cells  $\text{mL}^{-1}$ ) were observed only when  $\Sigma\text{DIN:DIP}$  was low ( $<10$ ) (Fig. 12), with the exception of Campbell Slough during May, 2013 when high  $\Sigma\text{DIN}$  was observed and  $\Sigma\text{DIN:DIP}$  was  $>200$ .



**Figure 11.** Scatter plots showing cyanobacteria abundance (cells mL<sup>-1</sup>) in relation to DIP concentrations (mg L<sup>-1</sup>) at the three study sites. Samples were grouped according to mean daily discharge at Bonneville Dam (indicated by color coding). Red circles indicate mean daily discharge <5,000 m<sup>3</sup> s<sup>-1</sup>; blue circles indicate mean daily discharge between 5,000-10,000 m<sup>3</sup> s<sup>-1</sup>; green circles indicate mean daily discharge >10,000 m<sup>3</sup> s<sup>-1</sup>.



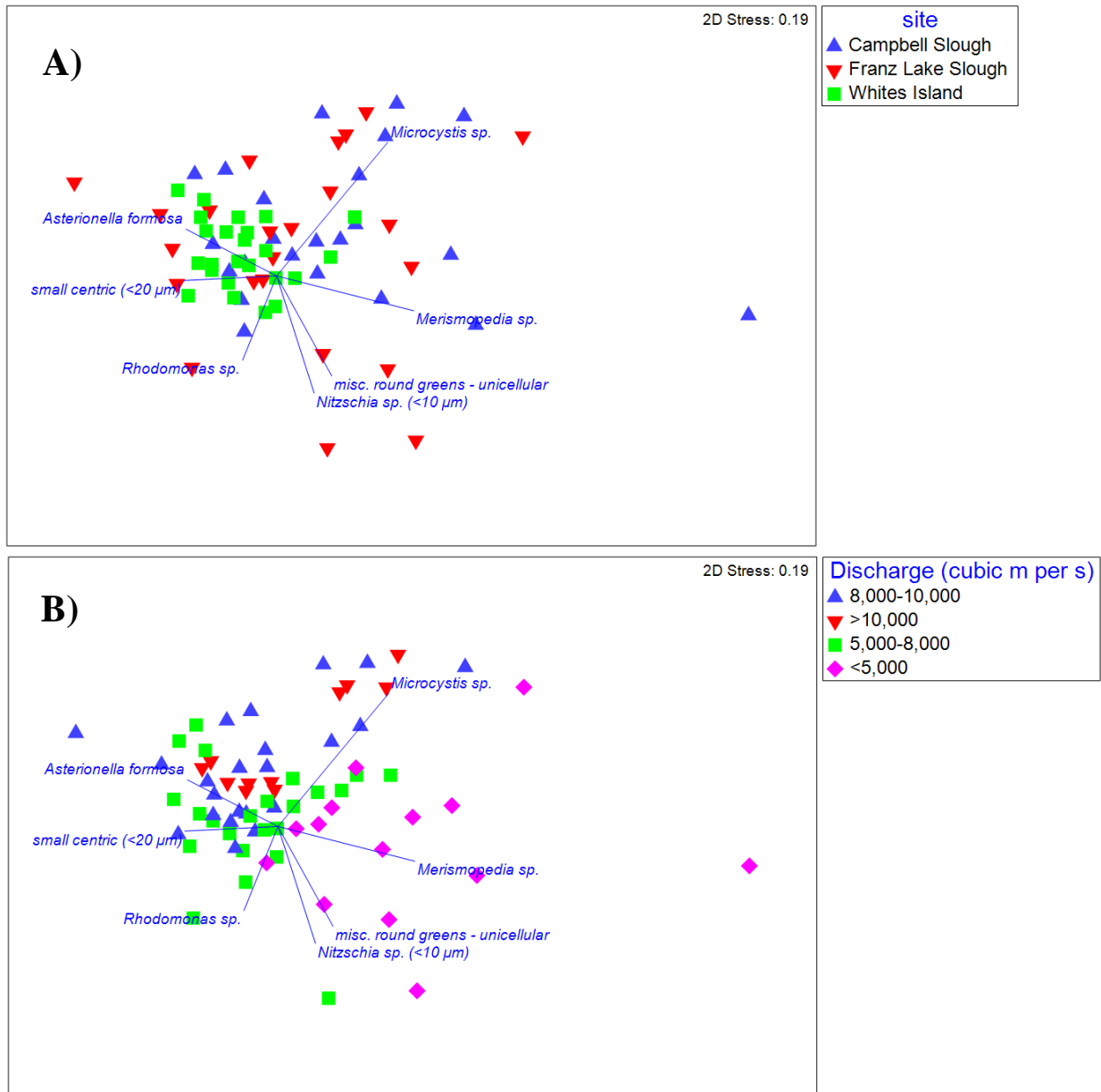
**Figure 12.** Scatter plots showing cyanobacteria abundance (cells mL<sup>-1</sup>) in relation to molar ratio of DIN:DIP at the three study sites.

### *Multivariate analyses*

In the first Non-metric Multidimensional Scaling analysis (NMDS<sub>total</sub>, all major phytoplankton taxa, Fig. 13), ordination plots were assembled with a 2D stress level of 0.19 and a 3D stress of 0.13. Distribution of samples in 2D ordination space showed that samples from Whites Island were located relatively close to each other, while samples at both Campbell

Slough and Franz Lake Slough tended to be more distantly distributed (Fig. 13A). This distribution pattern can be interpreted as higher intra-site similarity between phytoplankton assemblages at Whites Island and greater variability in phytoplankton assemblages at the other two sites. Sample distribution also revealed a horizontal gradient of samples in terms of river discharge, with different major taxa associated with varying river discharge periods.

*Merismopedia* sp., small *Nitzschia* sp. (<10  $\mu\text{m}$ ), and unicellular non-flagellated chlorophytes were higher in abundance at low discharge (<5,000  $\text{m}^3 \text{s}^{-1}$ ), while the colonial diatom *Asterionella formosa* and non-colonial small centric diatoms (<20  $\mu\text{m}$ ) were dominant at periods of higher discharge. Both *Rhodomonas* sp. and *Microcystis* sp. showed strong correlations with sample distributions (Spearman  $r > 0.4$ ). *Microcystis* sp. were higher in abundance during summer (June, July, data not shown), while *Rhodomonas* sp. did not show any clear patterns in terms of seasonality or river discharge.

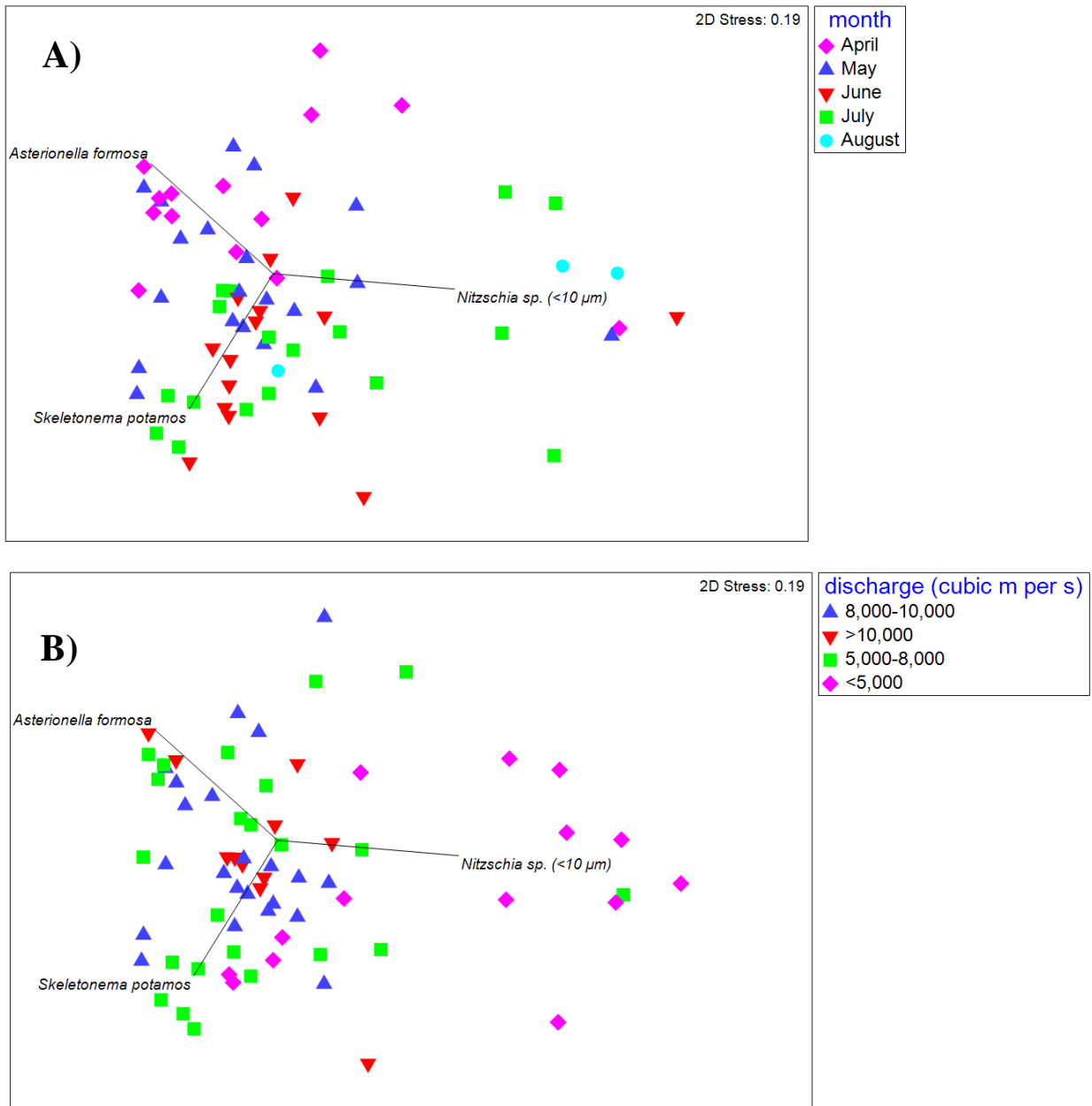


**Figure 13.** NMDS<sub>total</sub> ordination diagram showing overlays of taxonomic vectors with Spearman correlations of  $r > 0.4$ . Samples are colored by A) site and B) discharge thresholds ( $\text{m}^3 \text{s}^{-1}$ ).

Given that diatoms are also valuable indicators of water quality, we chose to perform NMDS on major diatom taxa separately from all other taxa (Fig. 14). Three major taxa – *Asterionella formosa*, *Skeletonema potamos*, and small (<10 µm) *Nitzschia sp.* – were identified

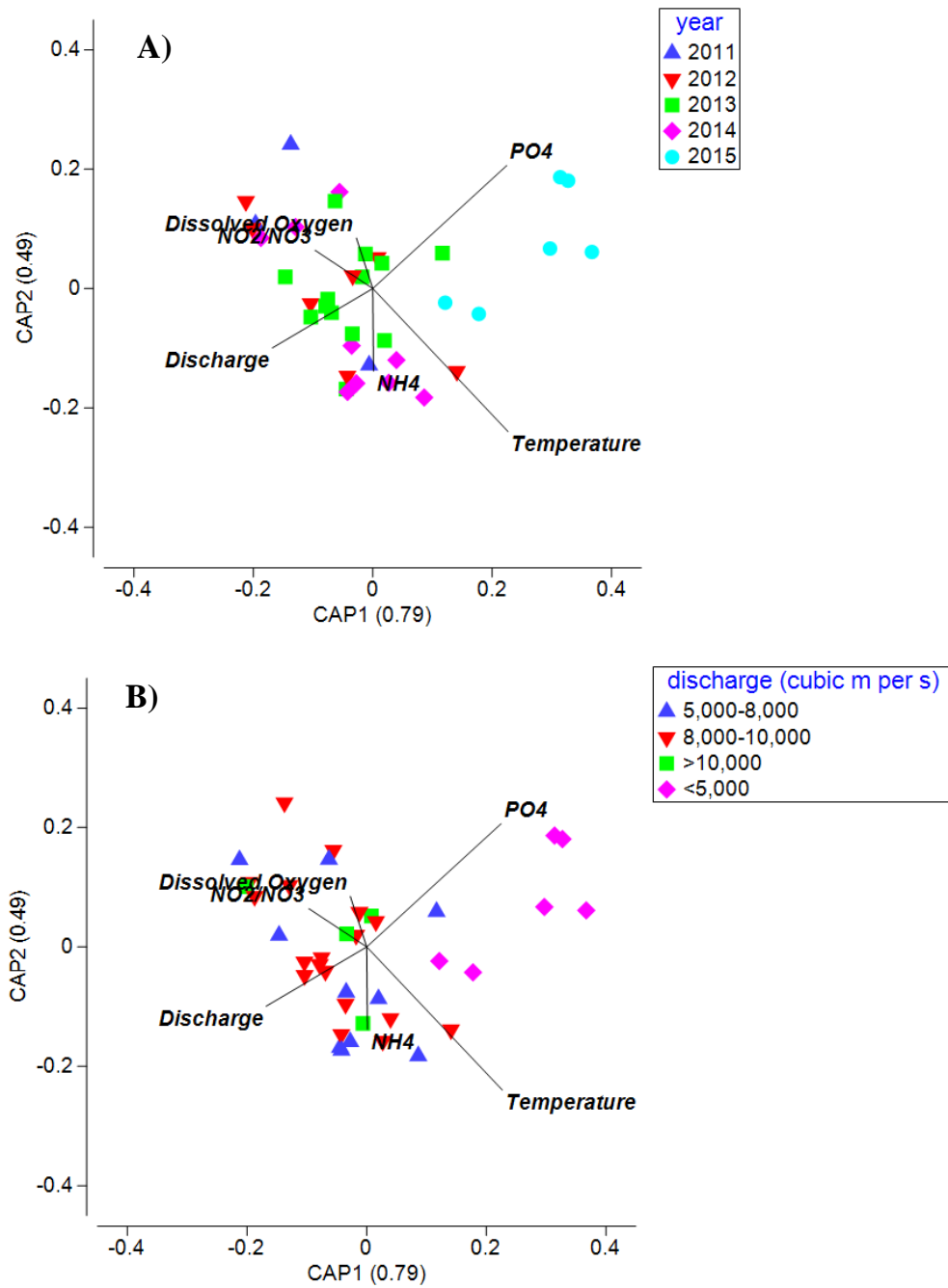


with Spearman correlations of  $r > 0.6$ . Sample distribution showed a gradient from high discharge to low discharge in a horizontal direction (Fig. 14B); samples were also distributed in a vertical gradient by month with distinct separation between spring samples (April and May) and summer samples (June, July and August) (Fig. 14A). Overlaying taxonomic vector regressions revealed an inverse relationship between *Asterionella formosa* and *Skeletonema potamos* in terms of seasonal abundances, with *A. formosa* dominant during spring and *S. potamos* dominant in summer. Among diatom taxa, patterns in distribution were also found in terms of mean daily discharge. Small ( $< 10 \mu\text{m}$ ) *Nitzschia* sp. were positively associated with periods of low discharge ( $< 5,000 \text{ m}^3 \text{ s}^{-1}$ ), while *A. formosa* and *S. potamos* were both associated with moderate to high discharge ( $> 5,000 \text{ m}^3 \text{ s}^{-1}$ ).

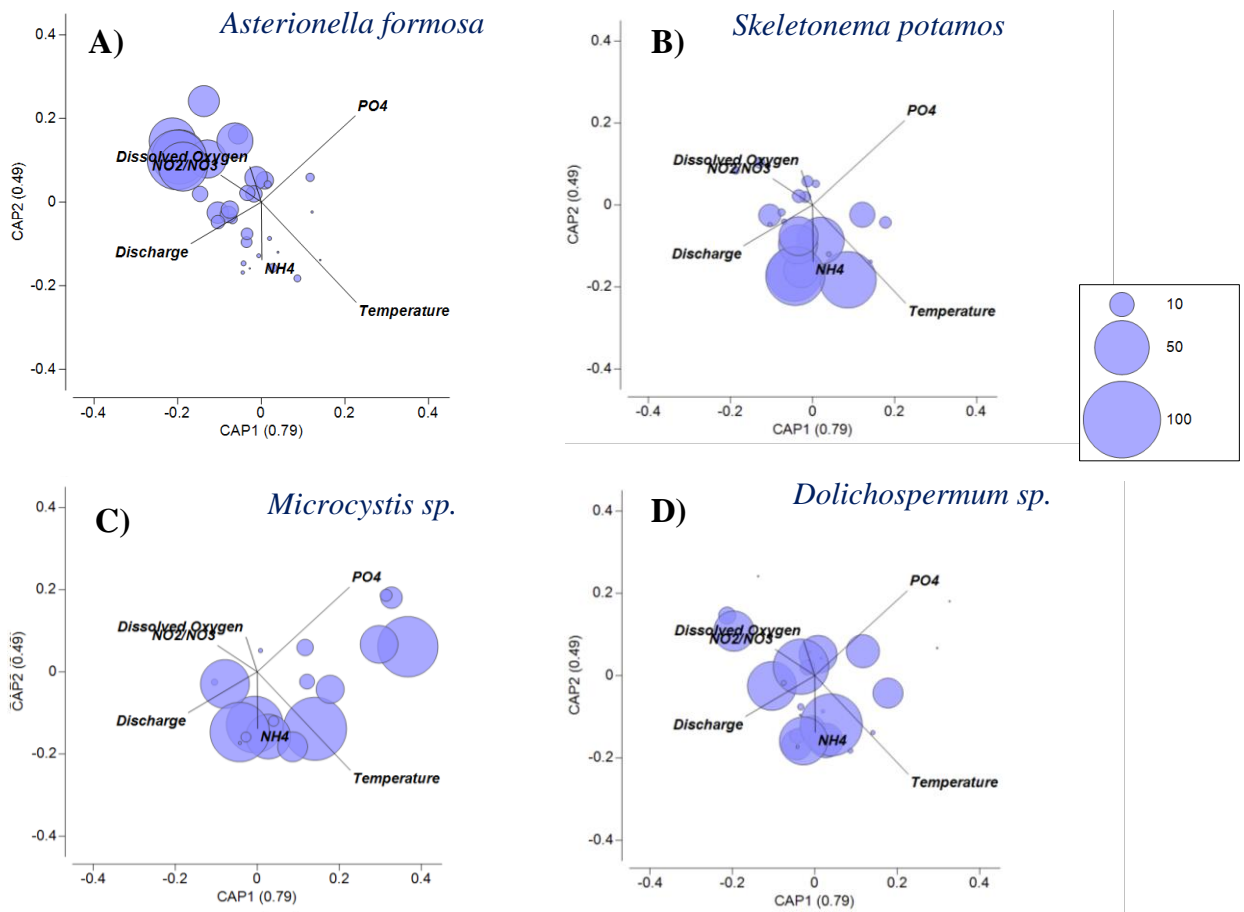


**Figure 14.** NMDS<sub>diatom</sub> ordination diagram showing overalys of taxonomic vectors with Spearman correlations of  $r > 0.6$ . Samples are colored by A) month and B) discharge thresholds ( $\text{m}^3 \text{s}^{-1}$ ).

The CAP comparing 25 phytoplankton taxa with six environmental variables produced two pairs of canonical axes, which explained 79% (CAP1) and 50% (CAP2) of the variance in correlations between phytoplankton abundance and abiotic variables (Fig. 15). Water temperature and  $\text{PO}_4^{3-}$  were positively correlated to the first CAP axis ( $r=0.600$  and  $r=0.605$ , respectively), while mean daily discharge was negatively correlated with the first CAP axis ( $r= -0.449$ ).  $\text{PO}_4^{3-}$  was positively correlated with the second CAP axis ( $r=0.551$ ), while water temperature was negatively correlated with the second CAP axis ( $r= -0.640$ ). All other environmental variables were not strongly correlated with either CAP axis. Along the first CAP axis (CAP1), there was an overall pattern of higher discharge samples on the negative side of the axis and lower discharge samples on the positive side of the axis. Samples in the lowest discharge threshold category ( $<5,000 \text{ m}^3 \text{ sec}^{-1}$ ) were taken primarily in 2015.



**Figure 15.** CAP ordination diagram showing all six environmental variables with samples colored coded by either A) year or B) discharge thresholds (m<sup>3</sup> s<sup>-1</sup>).



**Figure 16.** Bubble plots showing relative abundance of A) *Asterionella formosa*, B) *Skeletonema potamos*, C) *Microcystis sp.*, and D) *Dolichospermum sp.* overlaid onto the CAP ordination diagram. Bubble sizes correlate to relative abundance (0-100%) of taxa in a sample.

## Discussion

### *Phytoplankton species successions*

Previous studies on the mainstem channel of the lower Columbia River (Haertel et al., 1969; Lara-Lara et al., 1990; Sullivan 1997; Maier, 2014) found that the lower river is dominated primarily by diatoms, and that diatom abundance is highest in early spring prior to the annual freshet. All previous studies saw a regular, seasonal succession from high abundances of diatoms in the spring to moderate abundances of Chlorophyceae (green algae) and low abundances of cyanobacteria (along with moderate abundances of diatoms) in the summer. The most recent study on mainstem phytoplankton dynamics in the lower Columbia River at Beaver Army Terminal (rm 53, Maier, 2014) found an annual dominance by *Asterionella formosa* prior to the spring freshet, with annually high springtime abundances of *Aulacoseira* spp. and periodically high summer abundances of *Skeletonema potamos*. Haertel et al. (1969) and Sullivan (1997) both observed high abundances of *Asterionella* and *Aulacoseira*, but did not mention *Skeletonema*, which may have increased in frequency and abundance in the lower Columbia River since those studies were performed. It is important to note that both Haertel et al. (1969) and Sullivan (1997) examined phytoplankton dynamics in the estuarine portion of the lower Columbia River (downstream of rm 53). It is possible that *Skeletonema* is more abundant upstream of their sampling locations, although it seems highly unlikely that it would not be efficiently advected downstream. Both Haertel et al. (1969) and Lara-Lara et al. (1990) concluded that phytoplankton growth in the mainstem channel of the lower Columbia River was limited primarily by light. Unfortunately, this study did not measure any index of turbidity or light availability (see Chapter 4), but we do speculate that light availability probably increased over the course of the season as flow velocity slowed down and stratification presumably took effect.

The phytoplankton succession patterns observed here were similar to what has been described in the mainstem, with early spring dominance by diatoms followed by an increase in chlorophytes and cyanobacteria later in the season (Haertel et al., 1969; Sullivan, 1997). Similarities in phytoplankton successional patterns in off-channel habitats and in the mainstem suggest that phytoplankton in off-channel sites probably originate in the mainstem, at least during periods of high flow and high connectivity. This is supported by the findings of Lara-Lara et al. (1990), who reported that there were no significant difference in rates of primary production between the mainstem channel and shallow water sites (downstream of rm 53), despite the fact that shallow water sites are thought to have longer residence times and greater light availability compared to the mainstem.

Species successions among diatoms and among all phytoplankton in an assemblage can be driven by several interrelated factors, including interspecific competition for changing nutrient resources, selective loss rates for certain species over others (e.g., via parasitism, grazing, or sinking) and by specific trophic interactions within an ecosystem (Tilman et al., 1982). Successional relationships are further complicated by high degrees of spatial and temporal heterogeneity in lotic systems. Maier and Peterson (2014) found widespread, annual parasitism of common spring diatom species (*Asterionella formosa*, *Aulacoseira* spp., *Fragilaria crotonensis*) by chytrid fungi. Variation in abundance and efficiency of chytrid parasites may contribute to interspatial and interannual variation of succession patterns in off-channel sites in terms of both timing of succession (specifically switch between spring diatoms and summer cyanobacteria) and taxonomic composition of diatom communities. Slower moving water in summer months also likely contributed to diatom sinking rates and dominance of buoyant cyanobacteria in summer months.

Competition among species for nutrient resources has also been widely cited as a driver of community succession patterns. In general, cyanobacteria have a higher minimum phosphate requirement than diatoms, while diatoms have a higher silicic acid requirement than cyanobacteria and green algae (Tilman et al, 1982 and references therein). At high Si:P, diatoms can easily outcompete green algae and cyanobacteria, while at low Si:P, cyanobacteria and green algae may be able to outcompete diatoms. Concentrations of silicic acid are high enough in the Columbia River ( $>180 \mu\text{M}$ ; J. Needoba, personal communication) that they are not likely to be limiting at any time of the year. However, temporal variability in the availability of phosphorus may have some effect on species succession in off-channel sites, and may have a stronger effect during low flow periods when low connectivity between off-channel sites and the mainstem reduces annual nutrient load to shallow areas. This could help to explain the low diatom abundance and dominance by small, *Nitzschia* sp. in Campbell Slough and Franz Lake Slough during the summer of 2015. A comparison of dominant diatom taxa based on their sensitivity to phosphorus (Trophic Diatom Index; Kelly and Whitton, 1995) found that most species of *Nitzschia* tend to occur at higher abundances when phosphate is high ( $0.035\text{--}0.3 \text{ mg L}^{-1}$ ) while *Asterionella* and *Aulacoseira* tend to be seen at higher abundances when phosphate is lower ( $0.01\text{--}0.035 \text{ mg L}^{-1}$ ). High abundances of phosphate in Franz Lake Slough throughout the 2015 season were concurrent with dominance of small *Nitzschia* sp.

Both time series of phytoplankton groups (Fig. 9) and NMDS of all major phytoplankton taxa (NMDS<sub>total</sub>, Fig. 13) revealed that high abundances of cyanobacteria taxa including *Microcystis* sp. and *Merismopedia* sp. were strongly associated with summer months and periods of low discharge. Cyanobacteria are often indicators of eutrophic conditions, and are generally thought of as nuisance species due to their unpalatability for zooplankton consumers and



association with toxicity and hypoxia (Paerl et al., 2001; Havens, 2008). The implications of this finding are significant, and are expanded upon below. Although cyanobacteria often constituted the majority of relative abundance, particularly in summer samples, it is likely that diatoms constitute the majority of phytoplanktonic carbon entering the food web, because of their relative size compared to cyanobacteria and chlorophytes (Wehr and Sheath, 2003) and their palatability and high energetic value to insect consumers (Brett et al., 2006).

NMDS<sub>diatom</sub> revealed an inverse relationship between abundances of *Asterionella formosa* and *Skeletonema potamos*, which varied on a seasonal basis. Both taxa were annually present at all three sites (although both were more abundant in Whites Island than Campbell Slough and Franz Lake Slough). Coloring the NMDS<sub>diatom</sub> ordination diagram by month of sampling shows a seasonal pattern of dominance by *Asterionella formosa* in April and May versus dominance of *Skeletonema potamos* in June and July. The nutrient data suggest that larger *Asterionella formosa* populations are associated with high  $\Sigma$ DIN, while *Skeletonema potamos* are associated with lower  $\Sigma$ DIN concentrations. High relative proportions of *A. formosa* were associated with high  $\Sigma$ DIN and low water temperatures (Fig. 16A). The data also revealed that high abundances of *Skeletonema potamos* were associated with warmer temperatures and increasing concentrations of  $\text{NH}_4^+$  (Fig. 16B). This suggests that late-succession phytoplankton species may be more likely to use  $\text{NH}_4^+$  as their nitrogen source as  $\Sigma$ DIN are probably depleted by early-succession species.

When samples from NMDS<sub>diatom</sub> were colored by flow threshold (discharge from Bonneville Dam,  $\text{m}^3 \text{s}^{-1}$ ), small *Nitzschia* sp. were found to be strongly associated with periods of low discharge ( $<5,000 \text{ m}^3 \text{ s}^{-1}$ ). This pattern is also easily observed in our time series of major diatom taxa, in which small *Nitzschia* sp. are dominant throughout the 2015 season at Franz Lake

Slough and during the summer of 2015 at Campbell Slough. Interestingly, larger *Nitzschia* sp. and pushpin-colony *Nitzschia* sp. did not follow this pattern, implying that the small *Nitzschia* sp. seen in this study are indeed a unique species.

#### *Observations of high abundances of cyanobacteria in shallow habitats*

Cyanobacteria were observed each year at all three sites, however there was a great deal of variation in relative abundance between sites and among seasons. High abundances ( $>10,000$  cells mL<sup>-1</sup>) were only observed in Campbell Slough and Franz Lake Slough during the summer months (June/July). Numerous previous studies have found that temperature and stratification are major factors influencing cyanobacteria abundance (Paerl and Huisman, 2008; Wagner and Adrian, 2009; Maier et al., 2001; Webster et al., 2000). Given that cyanobacteria abundances were generally highest during summer months and the CAP that identified temperature as a significant factor affecting phytoplankton assemblages, we can assume that cyanobacteria abundances at these study sites are strongly influenced by temperature and stratification. However, no significant, linear relationships between cyanobacteria and temperature were observed, suggesting that other environmental factors are also influencing cyanobacteria abundances.

Stratification and mixing in these sites were not quantified for this study, but we can make some theoretical predictions based on established hydrogeomorphic features. The sampling location at Whites Island is close in proximity to the mainstem (0.2 km) in the furthest downstream freshwater reach, and therefore undergoes strong daily tidal fluctuations in which the channel goes almost completely dry during low tides (personal observation). The tidal cycle is strong throughout the sampling season, even after the annual freshet subsides; therefore, it is safe to assume that residence time within the channel at Whites Island is relatively short ( $<1$  d).

Campbell Slough and Franz Lake Slough likely have longer residence times compared to Whites Island. Significant mean daily temperature differences ( $\Delta T$ ) between the mainstem and Campbell Slough and Franz Lake Slough, respectively—but not between Whites Island and the mainstem—suggest that water residence time at these two sites is long enough for water to warm more than a few degrees (i.e., at least 24 h).

Although Franz Lake Slough, like Whites Island, was sampled in close proximity to the mainstem (0.35 km), daily fluctuations in inundation at Franz Lake Slough are much less extreme than at Whites Island due to its location upstream near the far reach of tidal influence. Instead, inundation levels at Franz Lake Slough are controlled primarily by discharges from Bonneville Dam (Jay et al., 2014), which are low during the summer. Additionally, a large beaver dam near the mouth of the channel minimizes exchange of water between the Franz Lake Slough and the mainstem at times when water elevation in the mainstem is low. At Campbell Slough, the distance between the sampling site and the mainstem is long (~1.5 km) and highly sinuous, such that tidal fluctuations are small, particularly during summer months where low flow conditions could lead to some degree of stratification in the tidal channel.

In addition to temperature, cyanobacteria growth is strongly influenced by nutrient availability. In particular, previous studies have found that high abundances of cyanobacteria are associated with high concentrations of phosphorus (Schindler, 1977). However, dual control of nitrogen and phosphorus on cyanobacterial blooms has also been reported (Xu et al., 2010). No significant or predictive relationships were seen between  $\Sigma\text{DIN}$  and cyanobacteria in this study. High cyanobacteria abundances observed here showed a moderate positive correlation with DIP concentrations, although the relationship was non-linear. At the highest concentrations of DIP seen in this study, cyanobacteria abundance was low. A possible explanation for the non-linear

relationship is that the highest DIP concentrations ( $>0.10 \text{ mg L}^{-1}$ ) were observed mostly during the freshet period (May/June), when discharge was high and residence time in the slough sites was likely too short for cyanobacteria to establish dominance over diatoms, and when temperatures may not have been ideal for cyanobacterial growth. The finding of high cyanobacteria abundances at intermediate levels of DIP in this study matches patterns seen in a similar regulated river system (Upper Mississippi River, Manier, 2014), underscoring the fact that in highly regulated lotic environments it is difficult to establish linear connections between nutrient inputs and cyanobacteria growth.

Molar N:P has also been shown to affect cyanobacterial assemblages, often with low N:P associated with high cyanobacterial abundance (Smith, 1983; Smith and Bennett, 1999). In this study, high abundances of cyanobacteria ( $>20,000 \text{ cells mL}^{-1}$ ) were observed only when N:P was low ( $<10$ ). This pattern suggests that nitrogen may be a limiting nutrient at these sites, based on classical theory of phytoplankton growth and nutrient requirements (Redfield, 1934). However, cyanobacteria assemblages in this study were dominated primarily by non-nitrogen fixing taxa, which suggests that nutrient limitation was not a major factor contributing to cyanobacteria growth at these sites.

Relationships between cyanobacteria and environmental variables can be difficult to interpret in riverine environments where variations in flow affect both physical and chemical composition of the water. At any point, it is likely that several abiotic factors influenced phytoplankton growth and species composition. Through CAP, water temperature and DIP emerged as major drivers of variation in phytoplankton communities. In general, high abundances of cyanobacteria were associated with warmer temperatures and higher DIP. Among cyanobacterial taxa, some differences were observed: *Microcystis* sp. was more frequently

dominant when DIP was high, while *Dolichospermum* sp. tended to occur at greater proportions when DIP was low and discharge was high (Fig. 16C and 16D). *Merismopedia* sp. was associated with high concentrations of  $\text{NH}_4^+$  and DIP. Unidentified cyanobacterial filaments (cf. *Oscillatoria* sp.) were associated with low temperatures and higher  $\text{NO}_3^- + \text{NO}_2^-$  concentrations.

The differences among taxonomic trends have important implications for management of nuisance blooms. *Microcystis* sp., *Merismopedia* sp. and *Dolichospermum* sp. are all capable of producing microcystin; however only *Dolichospermum* sp. is capable of producing additional toxins including the potent neurotoxins anatoxin-a and saxitoxin (Chorus and Bartram, 1999). Thus, blooms of *Dolichospermum* sp. may warrant a more urgent management response than blooms of *Microcystis* sp. and *Merismopedia* sp.

## Chapter 4: Conclusions and Future Directions

### Significant Findings

This is the first report of high abundances of potentially toxic cyanobacteria in the lower Columbia River system. Cell abundances of a similar scale have warranted recreational advisories elsewhere in the Pacific Northwest (Oregon Health Authority, [www.public.health.oregon.gov](http://www.public.health.oregon.gov)), suggesting that cyanobacteria abundances observed in this study represent a serious threat to ecosystem health and should not be overlooked by managers. Analyses of abiotic factors in relation to cyanobacteria abundances revealed that ambient DIP levels must be sufficiently high to support elevated cyanobacterial growth, but N:P must also be sufficiently low (i.e. proportionally high  $\Sigma$ DIN level along with elevated DIP) to allow dominance of cyanobacteria over diatoms. Seasonality (i.e., water temperature and the subsequent effects of thermal stratification) probably also plays a significant role in regulating cyanobacterial growth, as high abundances were observed primarily during late summer months when temperatures were above 20 °C.

Phytoplankton species succession patterns described in this study can also be used by managers to make assessments of underlying conditions that may warrant restorative actions. Successional patterns that differ from the mainstem imply that unique biogeochemical processes occur in off-channel sites. High abundances of diatom taxa that differ from common mainstem species (for example small *Nitzschia* sp. in Franz Lake Slough in 2015) can be used as an indication of differing biogeochemical processes in off-channel sites and potentially poor habitat quality for ecologically important species.

Differences in both water quality parameters and phytoplankton population dynamics among study sites confirmed our hypothesis that hydrogeomorphology of off-channel habitats in the lower Columbia River affects biogeochemical cycling and ecosystem components on a local scale. We found that river discharge in the mainstem influences relative habitat connectivity at both seasonal and interannual time scales. This is evidenced by similarities between phytoplankton assemblages at all three study sites in spring (high flow) but differences between sites in summer (low flow), and by a greater degree of difference in water temperatures between study sites and the mainstem during low discharge years, regardless of season.

Relatively high connectivity between off-channel sites and the mainstem tends to promote positive water quality conditions in shallower areas, including lower temperatures, higher dissolved oxygen concentrations, lower DIP, and dominance of phytoplankton assemblages by diatoms, which are generally more nutritious compared to other phytoplankton groups (cyanobacteria and chlorophytes). In contrast, poor connectivity between habitats consistently leads to warmer temperatures, lower dissolved oxygen concentrations, higher DIP, and dominance of nuisance phytoplankton species (cyanobacteria); all of which are conditions that threaten juvenile salmonid health.

Among the three sites in this study, Whites Island consistently exhibited features of good habitat quality, even during an anomalously low discharge period (2015). On the other hand, both Campbell Slough and Franz Lake Slough were more susceptible to poor water quality conditions, which were exacerbated when connectivity was low (i.e. during low flow years and in summer months, post-freshet). Nutrient dynamics in Campbell Slough were less closely aligned to fluxes in the mainstem compared to the other two sites, which suggests that Campbell Slough is more likely to experience the negative effects of poor connectivity to the mainstem

during variable flow regimes, while Franz Lake Slough experiences those effects only during periods of low river discharge. Unlike the other two sites, conditions at Whites Island (temperature, dissolved oxygen, nutrients, and phytoplankton) nearly always mirrored the mainstem.

## **Limitations and Challenges**

This thesis encompasses a wide range of biological and environmental data from many sources; however, certain elements would greatly improve the integrity of our conclusions. Quantifications of light availability (such as PAR, Secchi depth or total suspended solids) in shallow water sites were not performed, and no formal attempts were made to calculate water residence time or degree of stratification. All three of these parameters can significantly influence the establishment and growth of phytoplankton, and may play a role in the proliferation of cyanobacteria.

This study is also missing quantitative data on zooplankton abundance and biomass both in study sites and in the mainstem. Grazing of phytoplankton by zooplankton and other consumers (i.e. larval insects) can exert strong control on total phytoplankton biomass in a system. Without this data, it is impossible to draw conclusions on the value of habitats in terms of overall production and strength of the food web. For example, higher abundances of zooplankton consumers (as described in Sagar et al., 2013) in Campbell Slough may reduce total phytoplankton standing biomass so that it appears lower than the mainstem in early spring; thus we might come to the conclusion that Campbell Slough is an inhospitable habitat for juvenile salmon in terms of food availability when in fact it could be significantly more productive than bulk chlorophyll a values imply.



A major challenge in this study, and a challenge to managers of aquatic systems worldwide, was consistent and detailed taxonomic identification of phytoplankton (Benfield et al., 2007). Phytoplankton were identified to the lowest taxonomic level possible. However, in order to meet monitoring requirements and deadlines, phytoplankton taxa were often reported as functional groups (e.g. “colonial chlorophytes”) rather than specific species, even though taxonomic diversity was probably variable. Very small species, particularly chlorophytes, were difficult to identify even at 400X magnification. Small centric and pennate diatoms (<10  $\mu\text{m}$ ) also presented a challenge. Because our phytoplankton data consisted of a mix of both specific species (e.g. *Asterionella formosa*) and functional groups (e.g. colonial chlorophytes), we could not perform explicit measurements of species diversity (such as the Shannon-Weiner index,  $H'$ ), which are commonly used to characterize aquatic habitats. An additional limitation to our phytoplankton data is characterization of communities using relative abundance instead of biovolume. Individual diatom cells are typically much larger than individual cyanobacteria cells, which can occur in large colonies of hundreds of cells (e.g., *Microcystis* sp.) This skews abundance estimates in favor of cyanobacteria, even though total biovolume of one diatom cell is often comparable to a large (100+ cells) colony of cyanobacteria.

Gaps in data also made our results difficult to interpret. Missing environmental data from YSI sondes and mainstem sensors due to non-deployment and non-functionality significantly limited our ability to make confident generalizations about differences in conditions between sites and the mainstem across seasons and years. In our multivariate analyses, missing environmental data forced a reduction in sample size (70 samples in NMDS and only 38 in CAP), and potentially valuable data was excluded from analysis.

## Future Directions

Ecosystem monitoring in these study sites will continue into the near future, with plans to conduct food web sampling into 2017. Additional years of data will only enhance our ability to assess the influence of river discharge and hydrogeomorphology on habitat conditions and phytoplankton. Zooplankton samples that are date-matched to phytoplankton samples in this study have been collected and are currently being analyzed. Adding this crucial element to our overall assessment will allow us to draw more confident conclusions on factors controlling phytoplankton growth in these sites. Additional water quality parameters, including silicic acid, pH, and specific conductivity were also measured by YSI sondes, and the addition of these factors into future analyses will broaden the scope of this work. Other types of biological data, including benthic invertebrates, invertebrates in neuston and emergent vegetation, terrestrial and submerged aquatic vegetation surveys, and juvenile salmonids in these study sites have been collected and analyzed by partners at other institutions (Pacific Northwest National Labs, NOAA Northwest Fisheries Science Center, University of Washington); incorporating some of this data in future analyses will help to further elucidate the role of phytoplankton in juvenile salmon food webs in these study sites.

We hope that challenges shared in this study will promote amendments to current monitoring protocols. For example, the use of Secchi depth as a crude measure of light availability is a simple and relatively cost-effective technique that would provide useful information on light limitation of phytoplankton growth in these habitats. Measurement of cyanobacterial toxins (e.g., microcystin) will allow us to better quantify the threat imposed by cyanobacteria on juvenile salmon and other aquatic organisms in this system. Concurrent biological sampling (phytoplankton and zooplankton) in the mainstem Columbia River will

improve our understanding of how off-channel habitats serve juvenile salmon and other aquatic organisms.

Lastly, a more in-depth look at phytoplankton and their impacts on the food web is a natural next step for the work presented here. Direct (date-matched) comparisons between phytoplankton communities in off-channel sites and in the mainstem (planned for 2016 sampling season) will allow us to directly compare phytoplankton species between habitats, instead of relying on data collected in previous studies that may be outdated. More direct measures of phytoplankton in the juvenile salmonid food web are also warranted, based on the differences between sites observed in this study. Collection of both benthic and pelagic diatoms (instead of only pelagic, as presented here) would allow us to characterize the proportion of both groups of species that are available to juvenile salmonid prey. A study is currently underway (Tausz and Peterson, ongoing research) comparing diatoms in the water column to diatoms inside the guts of preferred juvenile salmon prey (larval chironomids) in these sites. Additionally, stable isotope models of carbon and nitrogen transfer through the food web are being constructed, which will allow us to reassess the importance of phytoplankton and other sources of primary production (i.e. macrodetritus) to the juvenile salmon food web. A synthesis of those future studies and this thesis will yield a robust and detailed picture of interactions between hydrogeomorphology, water quality parameters, phytoplankton, and higher consumers in critical habitats of the lower Columbia River.

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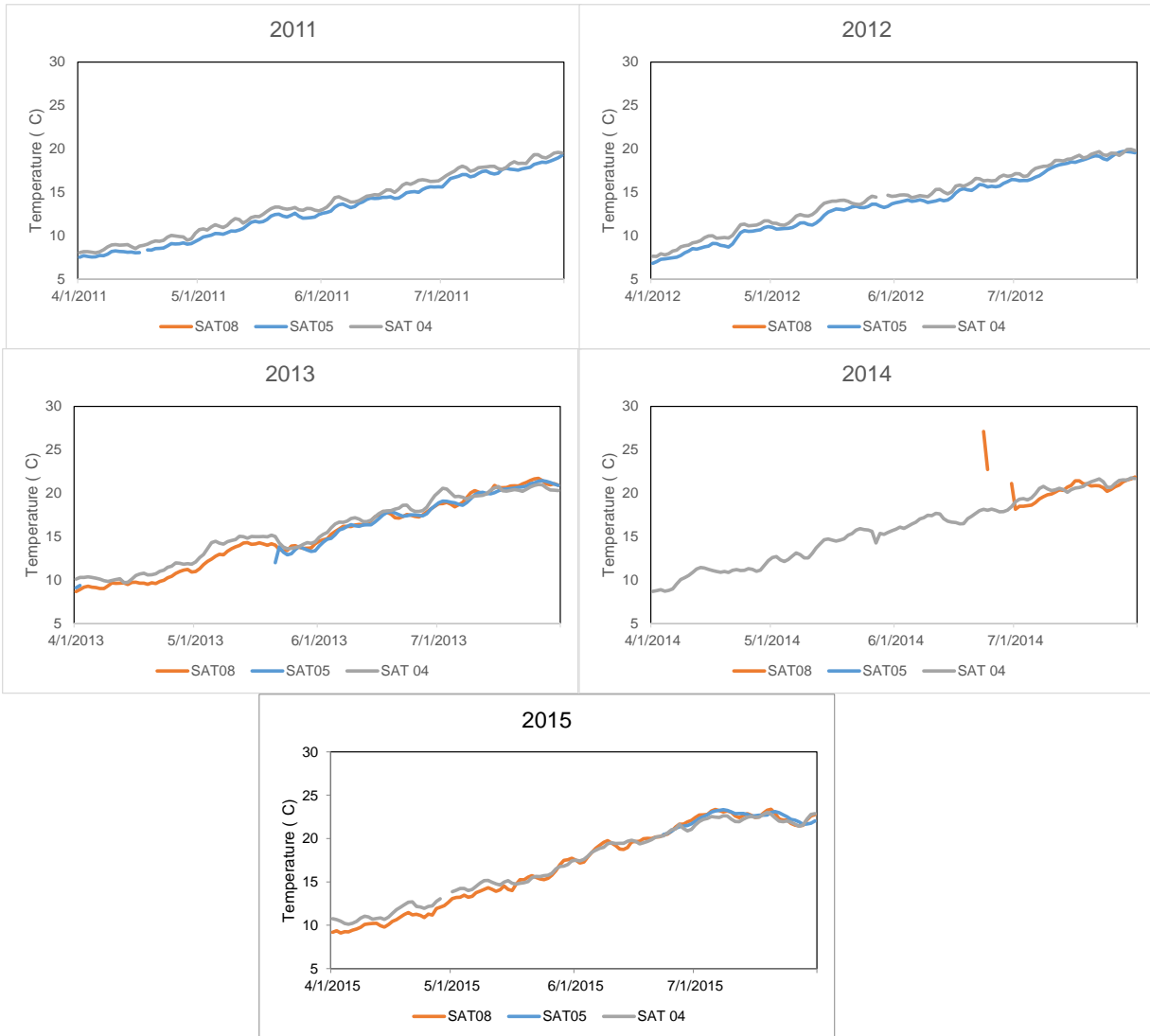
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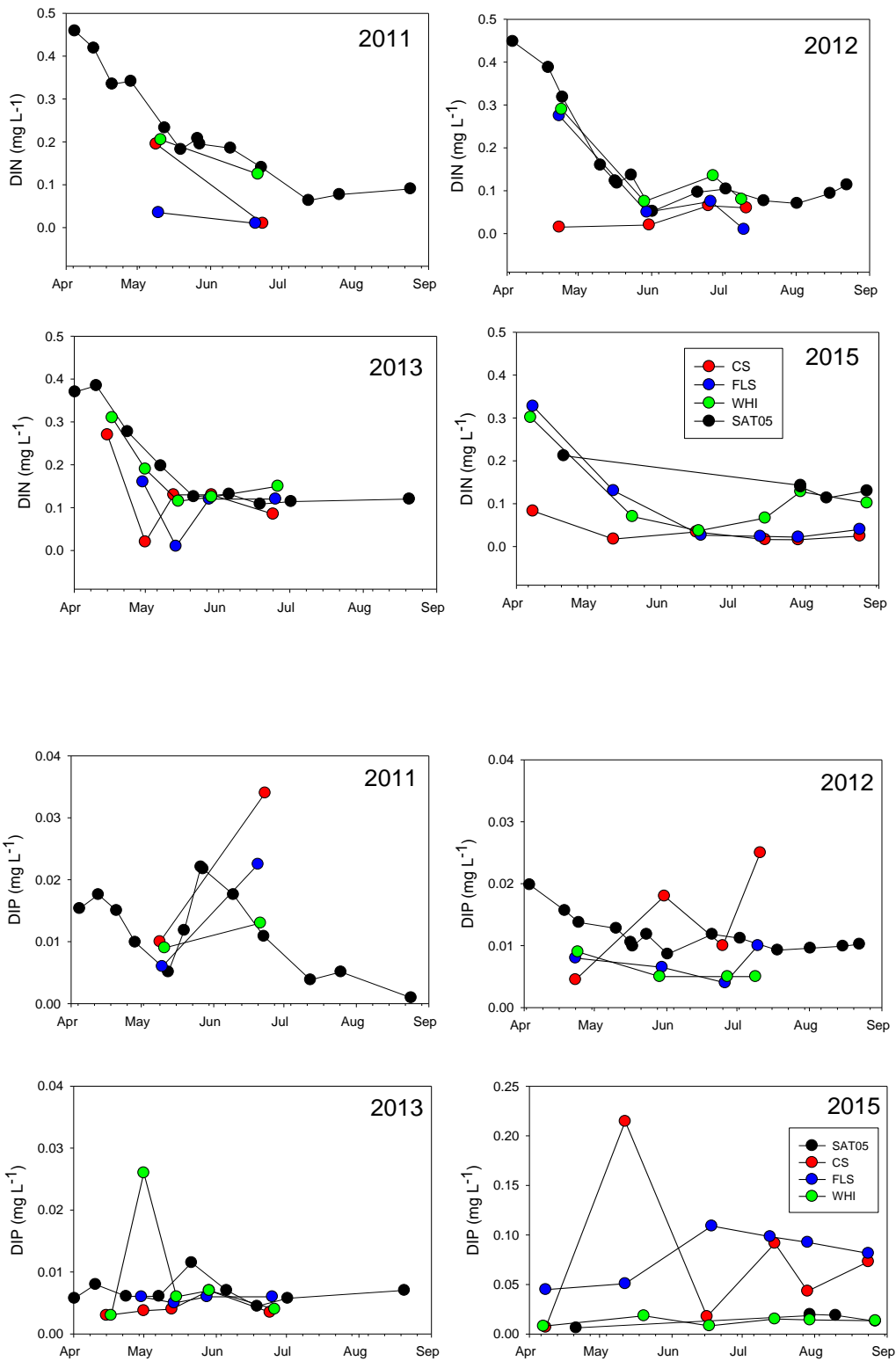
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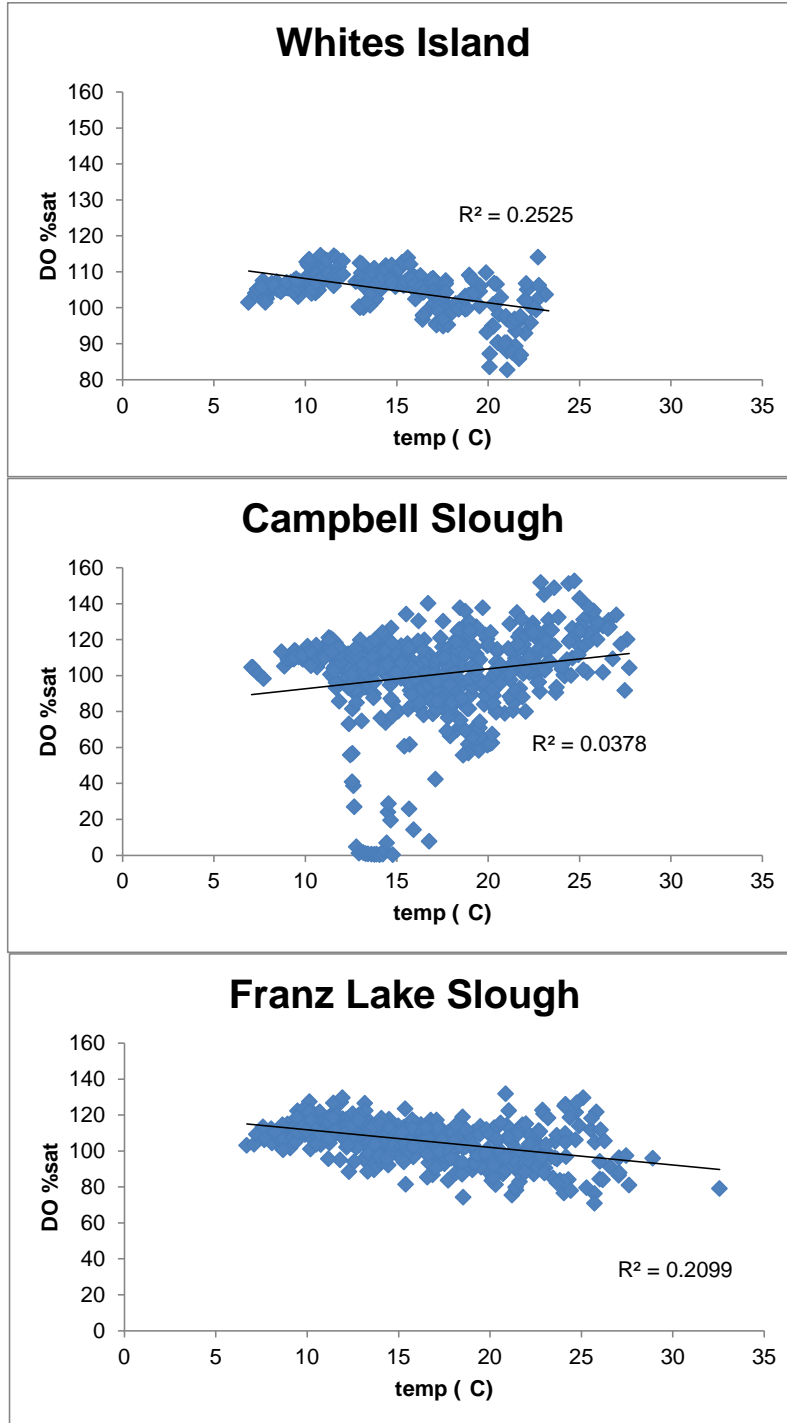
## APPENDIX A – Mean daily temperatures at mainstem sites



## APPENDIX B – Comparison of DIN and DIN between SAT05 and study sites



# APPENDIX C – Temperature (°C) vs. Dissolved Oxygen (%sat) in study sites



## APPENDIX D – List of major phytoplankton taxa

### **Diatoms (Bacillariophyceae):**

*Asterionella Formosa*

*Aulacoseira spp.*

small centric (<20 µm)

*Fragilaria crotonensis*

*Fragilaria intermedia*

*Nitzschia sp.* (<10 µm)

*Nitzschia sp.* (pushpin colony)

*Nitzschia sp.* (>10 µm)

*Skeletonema potamos*

Centric chain

### **Cryptophyceae:**

*Rhodomonas sp.*

*Cryptomonas spp.*

### **Green Algae (Chlorophyceae):**

*Ankistrodesmus sp.*

*Pyramimonas sp.*

green flagellates

misc. round greens – colonial

misc. round greens – unicellular

*Scenedesmus spp.*

*Micratinium sp.*



*cf. Spondylosium sp.*

**Blue-green Algae (Cyanobacteria):**

*Dolichospermum sp.*

*Microcystis sp.*

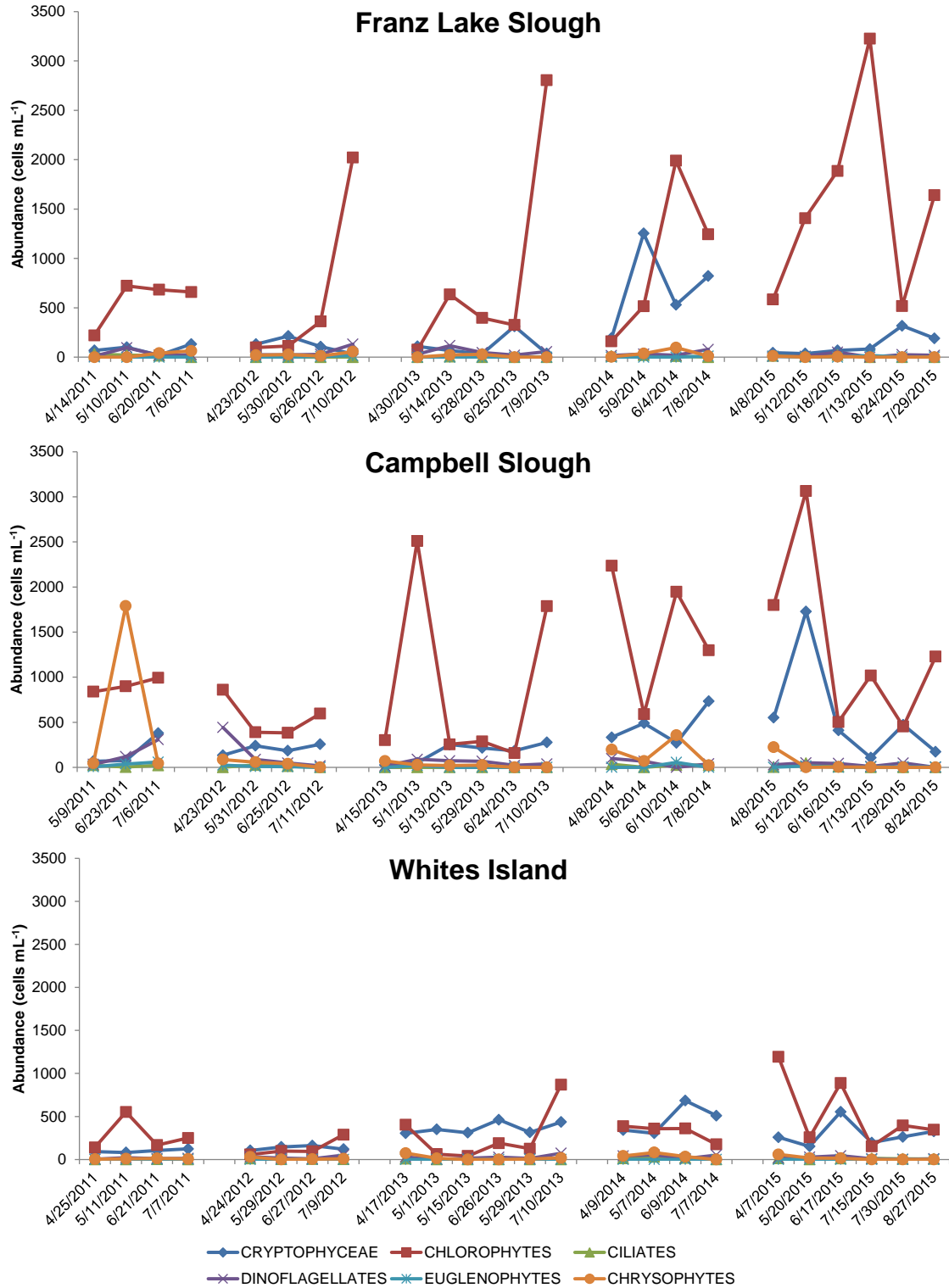
*Merismopedia sp.*

unidentified filamentous cyanobacteria (*cf. Oscillatoria sp.*)

**Other:**

misc. Dinoflagellates

## APPENDIX E – Time series of taxonomic groups excluding diatoms and cyanobacteria



## APPENDIX F – Selected Photographs



Franz Lake Slough, April 2015



Franz Lake Slough, July 2015



Beaver Dam at channel entrance to Franz Lake Slough, August 2015



Campbell Slough, July 2015