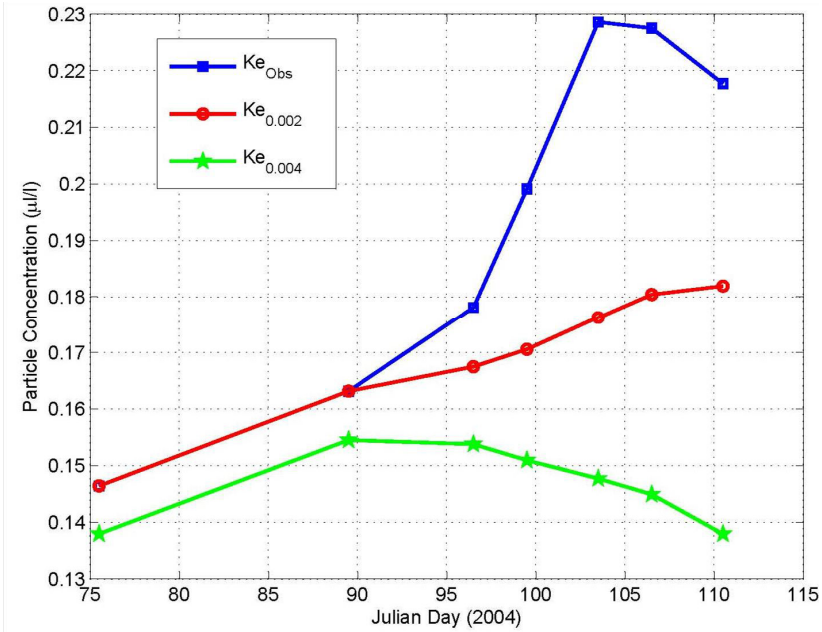

Figure 2. 30. Simulated particle concentration (phytoplankton) at MWY for three different eddy diffusion time series; the observed series (☐), a constant eddy diffusion of 0.002 m^2/s after JD 89.5 (o), and a constant eddy diffusion of 0.004 m^2/s (★). Results are the depth-averaged concentration from 0 to 10 meters.

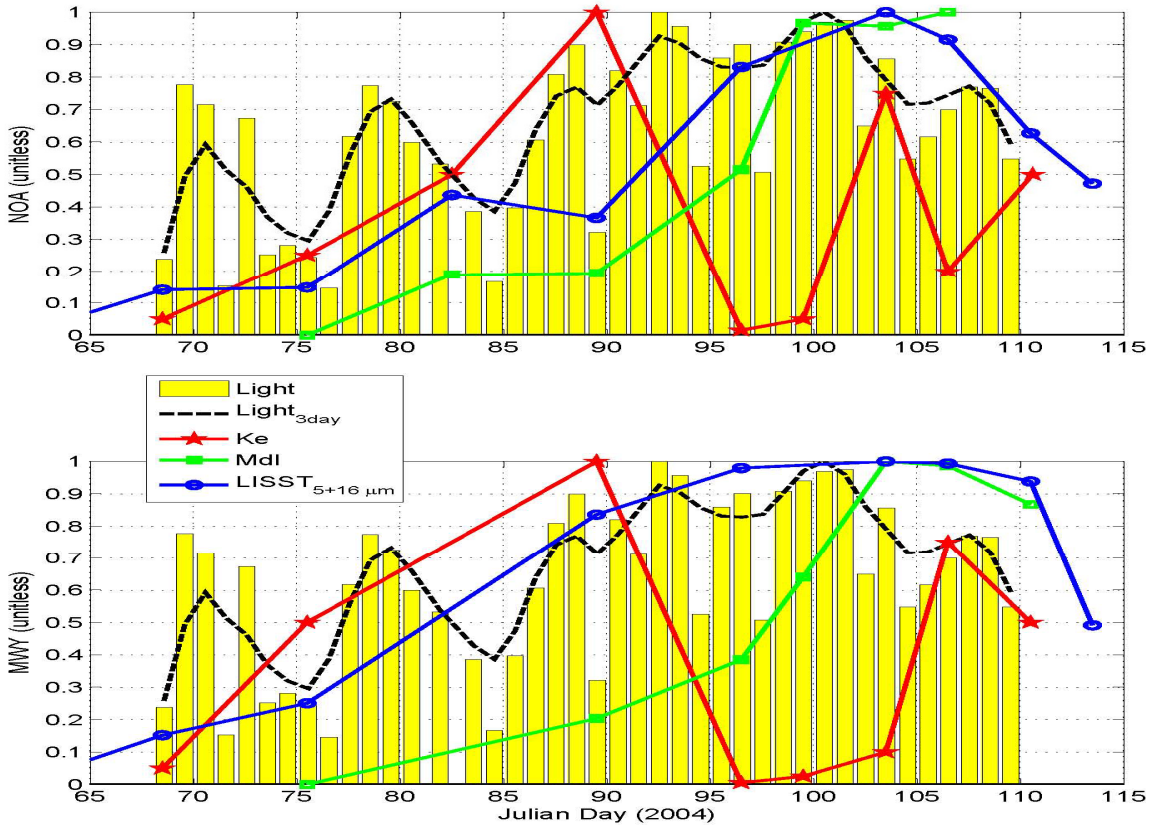

Figure 2. 31. Normalized observations for daily-averaged light (yellow bars), three-day running-average light (dashed) , LISST 5+16 µm particle concentrations (o), Ke (★), and simulated particle concentrations (☐). All data has been normalized for better presentation.

2.4.2.3 Effect of Isotherm Tilt

In Section One, it was shown that a persistent isotherm tilt existed prior to and during the early-spring diatom bloom. This tilt created a longitudinally varying STL, which was deepest at the north end of the lake and became shallower to the south end of the lake. The hydrodynamics that create the tilt upwell bottom water at SWA and transport bottom and surface water downwind, which creates a downwind flux of phytoplankton from SWA to MWY to NOA. The tilt affects the depth-averaged photosynthesis rate (2.22), while the downwind transport affects the horizontal flux that was assumed negligible in the Advective/Reactive Diffusion model. In this section, effects of the longitudinally varying STL are presented and the potential effects of a horizontal flux from MWY to NOA are investigated.

Prior to the diatom bloom, the STL depth was much deeper at NOA compared to SWA and the depth-integrated photosynthesis rate would be less at NOA compared to SWA. Up to JD 89.5, the isotherms tilted upward from north to south and the STL depth at NOA ranged from 25 to 42 meters, while the STL depth at SWA ranged from 10 to 20 meters (Table 2. 10). During this time, model results and the vertically uniform LISST profiles suggest eddy diffusion was sufficient to uniformly mix phytoplankton across the depth. Because phytoplankton concentrations were increasing over time in the STL, the STL depth was less than the critical depth. As a result, the photosynthesis equation (2.22) can be integrated over the STL depth to assess effects of the isotherm tilt.

The greater STL depth at NOA produced a smaller depth-integrated photosynthesis rate (compared to SWA) such that the multiple growth factor (m_F) was smaller at NOA than at SWA; mF was determined by photosynthesis limitations rather than phosphate limits (Table 2. 18). The multiple growth factor at NOA does not exceed SWA until the tilt is at a neutral position near JD 99.5 (Table 2. 18). These results suggest that SWA should be more productive than NOA and MWY because of the shallower STL depth at SWA, but observations do not support this conclusion. Phytoplankton concentrations at SWA were less than those at MWY and near those at NOA (Figure 2. 7). Previous modeling showed growth at SWA would exceed observations unless upwelling and advection losses were included. The tilt affects

the phytoplankton growth through the depth-integrated photosynthesis rate, which has a more significant north-south effect than north-to-south differences in phosphate concentration.

Table 2. 18. Phytoplankton growth limitations based on the observed hydrodynamic and environmental conditions at NOA, MWY, and SWA for days noted. Light and temperature limits are the depth-integrated photosynthesis effect on growth, and Z_{STL} is the depth of the STL (Table 2. 10).

Day	Site	k_d (1/m)	Z_{STL} (m)	I_o (W/m^2)	$f(I(Z_{mix}))$	$l(N_{PO4})$	$h(T)$	$f(I(Z_{mix}))\bullet l(N_{PO4})\bullet h(T)$ (m_F)
68.5	NOA	0.538	42	96	0.075	0.318	0.530	0.013
	MWY		35		0.090	0.294	0.524	0.014
	SWA		10		0.314	0.273	0.539	0.046
75.5	NOA	0.548	25	98	0.125	0.310	0.547	0.021
	MWY		25		0.125	0.264	0.555	0.018
	SWA		12		0.261	0.268	0.542	0.038
89.5	NOA	0.514	25	129	0.155	0.290	0.606	0.027
	MWY		22		0.176	0.195	0.588	0.020
	SWA		20		0.194	0.259	0.670	0.034
99.5	NOA	0.549	13	379	0.376	0.268	0.688	0.069
	MWY		13		0.376	0.161	0.683	0.041
	SWA		14		0.350	0.250	0.658	0.058

When the duration of the tilt is less than the horizontal travel time (t_U=L/U) from MWY to NOA or from SWA to MWY, the three areas are effectively isolated and phytoplankton biomass will be a function of the net growth rate, except SWA will be subject to upwelling and downwind transport (§2.4.2.1 and §2.4.2.2). When the duration of the tilt is longer than the horizontal travel time, phytoplankton from SWA are advected to MWY and phytoplankton from MWY are advected to NOA. As phytoplankton are advected from south to north, they experience deeper mixing and different nutrient concentrations but growth is still positive; the biomass continues to grow but at a slower rate. Under this scenario, the phytoplankton biomass should be larger at NOA compared to MWY and SWA, yet phytoplankton biovolume is greater at MWY than NOA; however at NOA, *D. (L.) ashlandi* species counts were much higher much earlier than at MWY or SWA and they appeared to be synchronized with the phytoplankton biomass (Figure 2. 6 and Figure 2. 7). The zooplankton growth rate (proportional to the phytoplankton grazing rate (2.25)) could be supported by the flux of phytoplankton upwind of NOA (2.34).

$$F_Z Zc = u\frac{\partial c}{\partial x} \tag{2.34}$$

Where Z is zooplankton concentration, F_Z is the grazing rate per animal, Z is the animal concentration, c is the phytoplankton concentration, and u is horizontal velocity. Scaling equation (2.34) provides an estimate of the horizontal velocity required to meet a given zooplankton concentration and filtering rate (2.35).

$$u = F_Z Z \Delta x \tag{2.35}$$

Where Δx is the distance between MWY and NOA ($\Delta x \approx 9500$ m).

On JD 90 of 2004, the adult *D. (L.) ashlandi* concentration was about 8.2 org/l and the calibrated filtering rate was 0.001 l/org/day, which requires a horizontal velocity of 0.0009 m/s (0.09 cm/s); a filtering rate of 0.002 l/org/d gives a velocity of 0.18 cm/s. In 2003 the zero to 20 meter depth-averaged horizontal velocity was 0.47 cm/s (Table 2. 13). The measured and scaled velocities agree very well and suggest the synchronized relation between zooplankton and phytoplankton could result from advective flux of phytoplankton rather than localized phytoplankton growth. Phytoplankton growth provides a classic predator-prey relationship where the maximum prey densities occur before the maximum predator densities (Kot, 2001), which is observed at MWY (Figure 2. 7).

2.5 Discussion

In the previous section, I showed that during the bloom period the phytoplankton biomass was dependent on the relative magnitude of eddy diffusion and its vertical distribution. Also shown was the effect of the isotherm tilt on depth-averaged photosynthesis; deeper mixing at NOA produced a smaller depth-averaged photosynthesis rate than the shallower mixing depth at SWA. In this section, I tie these findings together to present a model of the diatom bloom during 2004; the model describes the physical process that defined the bloom.

The bloom is segmented into three phases A, B, and C (Figure 2. 32). During phase A, the wind conditions maintained the isotherm tilt for about 19 days and eddy diffusion was relatively high. These conditions produced a persistent northward horizontal velocity that may or may not have a transport time (between locations) less than the 19-day duration, but NOA, MWY, and SWA can be effectively isolated from each other.

During this time, diatom biomass was increasing at NOA and MWY with the increasing incident light. The persistent northward winds maintained the isotherm tilt and produced a net northward flow. As the diatoms were advected northward, they continued to grow but were also mixing over a deeper STL depth, which decreased the depth-averaged photosynthesis rate; however, biomass continued to increase because the net growth was positive. In addition to the diatoms, zooplankton are advected northward and collect at the north end of the lake. Here the zooplankton biomass increased faster (than elsewhere in the lake) because the diatom food supply is both growing and being advected into NOA from upwind. At NOA, the observed zooplankton was maintained mostly by the advective flux of diatoms, because scaling analysis showed the zooplankton biomass could be maintained with a reasonable horizontal velocity and modeling results showed diatom growth is reasonably simulated without horizontal advection.

At SWA the diatom biomass is low because upwelled bottom water is mixed with surface waters, which dilutes the biomass and the surface water mass is then advected downwind. The combined effect occurred at a rate faster than the population can grow. The lower biomass would not support the same zooplankton population observed at NOA and upwelling and horizontal velocities at SWA could exceed zooplankton swimming speeds. MWY appears to be the optimal region for growth because upwelling and zooplankton grazing are absent and horizontal advection is less than at SWA because of the deeper STL. Compared to NOA, the shallower STL at MWY allows a larger depth-averaged photosynthesis rate.

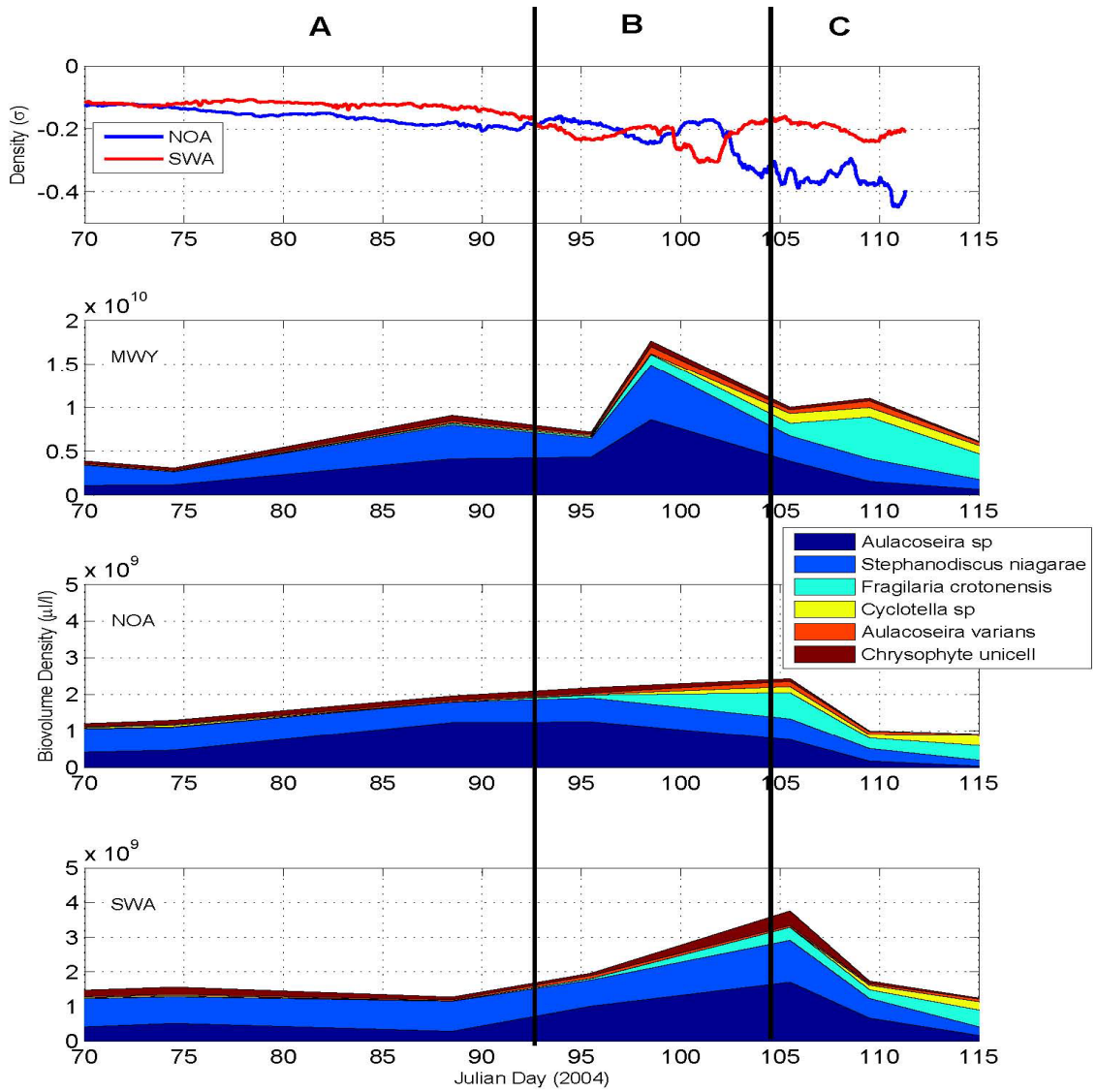

Figure 2. 32. Three phases A, B, and C of the diatom bloom in 2004. The phases are characterized by changes in the hydrodynamic regime shown by the average density at NOA and SWA. Isotherms tilt upward from north to south in Phase A; the isotherm tilt seesaws during phase B; and the isotherms resume an upward tilt from north to south in phase C.

During phase B the tilt seesawed and eddy diffusion was relatively low. The seesaw action affected the relative STL depths and upwelling conditions at SWA and the smaller vertical diffusive flux produced a correspondingly higher effective growth rate (net growth rate less diffusive flux). During this time, the relaxation of eddy diffusion allowed a higher effective growth rate across the lake and biomass increased at the three locations. The shifting wind directions and resultant seesawing of the isotherm causes the horizontal velocities to oscillate north and south, and thus the persistent northward diatom food flux decreased and zooplankton densities dropped at NOA.

However, zooplankton grazing was probably sufficient ($F_Z Z = (0.001)(8.2) = 0.008 \quad 1/\text{day}$) to suppress growth at NOA compared to MWY and SWA, which had much smaller zooplankton densities. Because phytoplankton at SWA were diluted by upwelling conditions, the initial biomass would be smaller compared to NOA or MWY and biomass would always be proportionally smaller for comparable growth rates at the three locations.

During phase C, winds were consistently northward and the isotherms again tilted upward from north to south and eddy diffusion increased to moderately high values. The increase in eddy diffusion reduced the effective growth rate, phosphate limitations became more significant ($\ell(N_{PO4})$=0.161), and increasing zooplankton grazing at MWY and SWA further reduced the net growth rate. The isotherms tilted upward from north to south, which decreased the depth-averaged photosynthesis at NOA and effects from upwelling diluted the phytoplankton biomass at SWA.

In §2.4 phytoplankton response at NOA, MWY, and SWA were determined to be isolated because growth scales were smaller than horizontal transport scales; however, one might speculate the observed phytoplankton/zooplankton population at NOA represent Lagrangian transport of a phytoplankton/zooplankton patch upwind of NOA. Typical predator/prey relations show prey population peaks before the predator population (Figure 2. 33); such a response was observed at MWY and SWA, but not at NOA (Figure 2. 7 for the diatoms and *D. (L.) ashlandi* M+F). If a phytoplankton/zooplankton patch was advected into NOA, typical predator/prey relations suggest the peak diatom bloom would have occurred before the patch reached NOA (Figure 2. 33). This patch would have started upwind of NOA, for arguments sake let the patch start near MWY (scenario 1) or SWA (scenario 2) and let it advected northward at velocities given in Table 2. 13.

For the first scenario, then one could expect another patch to start near SWA and advect to MWY in the same amount of time and produce a similar phytoplankton/zooplankton response observed at NOA. Expected results for scenario one results were not observed. For the second scenario, one might observe the typical predator/prey response at MWY; however, this scenario would require a persistent isotherm tilt lasting at least 46 days for a 0.47 cm/s horizontal

velocity (Table 2. 13). The expected time scales for scenario two is much greater than the observed persistence of the isotherm tilt. In addition, Lagrangian transport would produce a time lag in the initiation of the phytoplankton bloom at three locations, but observations showed the bloom occurred nearly simultaneously at NOA, MWY, and SWA (Figure 2. 7). Given these results, the observed phytoplankton/zooplankton responses were unlikely a result of Lagrangian transport of a phytoplankton/zooplankton patch(s).

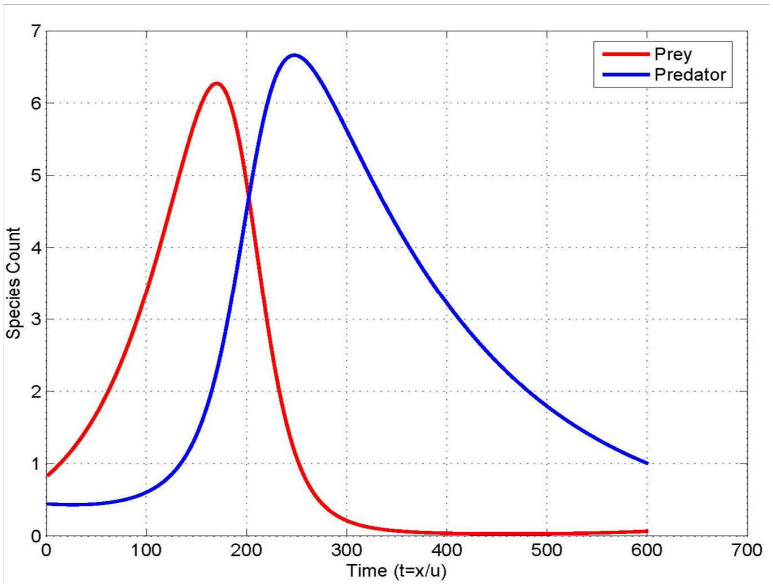

Figure 2. 33. Theoretical predator/prey response for a predator that has no incubation period. The time scale can be represented as Lagrangian transport t=x/u, where x is distance and u is horizontal velocity.

Conditions at NOA may not reflect conditions further north in the lake because the lake bottom gets shallower towards the northern shore. NOA is about 5 km from the end of the lake and the location is in about 42 meters of water. At times the density interface (thermocline) intersected the lake bottom at NOA and at times it was above the lake bottom. Somewhere between NOA and the shore, the depth-averaged photosynthesis will become a function of bottom depth alone, because the isotherms will intersect the lake bottom at this point. At this point or farther north, the depth-averaged photosynthesis rate will be less significant than phosphate limitations and their multiplicative effect will be greater than the effect at SWA. This depth appears to be between 15 and 20 meters based on modeling results from Table 2. 18. North of this depth range, diatom dynamics would be independent of the water depth and

effects of the isotherm tilt, phytoplankton kinetics would be governed by nutrients and temperature kinetics, and the growth rate would increase with decreasing depth. A larger growth rate could produce a larger phytoplankton biomass which would support a larger zooplankton biomass.

2.5.1 Relevance of this Study to Other Studies

This study provides additional insight about hydrodynamic conditions and effects prior to and during the early-spring diatom bloom in Lake Washington. The first Lake Washington studies were concerned with its initial eutrophic state and its subsequent recovery to a mesotrophic state. The transfer of untreated sewage from the lake allowed a unique opportunity for a whole-lake experiment that could assess the importance of phosphorous loading to a lake's trophic state (Edmondson, 1994). During this period of time, 1970 into the 1980's, the body of environmental science was concerned with whole-lake response to pollution and moderately concerned about lake hydrodynamics, which was typically quantified as well mixed or thermally stratified; Lake Wahington topics discussed conditions that limited phytoplankton growth during summer stratification (Edmondson, 1972; Richey, Devol, and Perkins, 1975; Lehman, 1978; Devol and Packard, 1978; Richey, 1979; Edmondson and Lehman, 1981). The spring blooms were also dominated by undesirable phytoplankton (cyanobacteria) and the drive was to understand the fundamental conditions that determined the phytoplankton community. This study had a more specific goal; the interest was how hydrodynamics affected the current diatom population (desirable phytoplankton) prior to and during the bloom and how these conditions contributed to the observed spatial variability in diatom biomass in Lake Washington.

Others recognized the under-studied seasonal succession of Lake Washington's phytoplankton population; these studies investigated the conditions that contributed to or defined phytoplankton succession over the year generally segmented by season (Arhonditsis, Brett, and Frodge, 2003; and Arhonditsis, Winder, Brett, and Schindler, 2004). Specific studies about the spring bloom or hydrodynamic influences were not possible because the available data was too sparse in space and time. This study recognized the relations between hydrodynamic and growth time scales and that hydrodynamic conditions could only affect the diatoms if

hydrodynamic time scales were similar or larger than the diatom growth scales. The persistence of the hydrodynamic conditions (isotherm tilt) was found to be comparable to or greater than diatom growth scales. It was found the persistent hydrodynamic conditions arise when the internal wave period is greater than the periodicity of the applied wind stress. Previous Lake Washington studies suggested wind had an indeterminate effect on hydrodynamic conditions. Analyses found the hydrodynamic conditions created an isotherm tilt, which produced a longitudinally varying mixed layer depth that affected the depth-integrated photosynthesis rate. The depth-integrated photosynthesis controlled north/south growth rates more than nutrient limitation from north/south nutrient gradients; whereas, previous studies hypothesized nutrient loads from the Cedar and Sammamsih Rivers determined longitudinal differences in chlorophyll *a* (Arhonditsis, Brett, and Frodge, 2003). Analyses also determined the Cedar River had negligible affect on hydrodynamic conditions at the south end of the lake. Upwelling conditions at SWA were never considered previously but modeling and literature provides substantial evidence that upwelling has a significant effect on the diatom population near SWA. This study provided evidence that the longitudinal difference in the diatom and zooplankton biomass was determined by hydrodynamic conditions rather than hydrologic nutrient loads.

Previous Lake Washington modeling efforts suggested the timing of the spring diatom bloom was controlled by the relaxation of vertical eddy diffusion, and analyses of observed chlorophyll a time series suggested the diatom bloom occurred before significant thermal stratification developed (Walters, 1980 and Arhonditsis, Winder, Brett, and Schindler, 2004). This is the first study in Lake Washington that quantified the vertical distribution and magnitude of eddy diffusion and assessed it affect on the diatom bloom; the timing and size of the 2004 bloom was found to depend on both the vertical distribution and magnitude of vertical eddy diffusion. For Lake Washington, this study is the first effort that quantified cause and effect relations between observed hydrodynamic, nutrient, and temperature conditions and the observed diatom distributions, concentrations, and growth.

To the general body of literature on Lake Limnology, this study adds information about the cause and effect relations between lake hydrodynamics and the diatom

population, and how these relations affect the spatial variability of the phytoplankton. Light, nutrients, and temperature are environmental variables that affect phytoplankton growth and species succession (Foy and Gibson, 1993; Sebastian, Interlandi, and Kilham, 2001; Arhonditsis, Winder, Brett, and Schindler, 2004; Sommer, 1994), but their spatial and temporal variability and specific affect are often inferred by statistical analyses based on the average water temperature, wind, or incident light (Arhonditsis, Winder, Brett, and Schindler, 2004; Felip and Catalin, 2000; Barbiero et al., 2000). Vertical mixing is often assumed uniform in the horizontal direction (Wall, Briand, and Ottawa, 1980; Viner and Kemp, 1983). In this study spatial and temporal differences were specifically described by hydrodynamic conditions, such as isotherm tilting that resulted in a longitudinally variable mixing depth. The cause and duration of the tilt was functionally determined by the surface wind stress, vertical stratification, and temporal response of the first mode internal wave.

Cause and effect relations between the hydrodynamics and phytoplankton response have been studied before, but they have not specifically investigated the bloom period nor conditions as weakly stratified as Lake Washington. Relations between hydrodynamic conditions and subsequent biological response were limited to higher levels of stratification (summer time or saline lake) and the period of observation ranged from several hours to about 14 days (Eckert, Imberger, and Saggio, 2002; Saggio and Imberger, 2001; MacIntyre et al., 1999; MacIntyre and Jellison, 2001; Sharples et al., 2001). These studies primarily investigated hydrodynamic conditions that enhance vertical mixing across the thermocline or pycnocline and fluxing of nutrients from depths replete in nutrient into depths depleted of nutrients. This study found vertical eddy diffusion directly affected phytoplankton by mixing it out of the euphotic zone into the aphotic zone; the phytoplankton bloom occurred when vertical diffusion balanced sinking velocities, but the diffusive flux rate was less than the phytoplankton growth rate. Modeling showed diatom growth or bloom response depended on the strength of vertical mixing rather than nutrient limitations.

In Lake Washington, persistent northward winds created a persistent upwelling condition at the south end of the lake which diluted and transported phytoplankton out of the region faster than it could grow. Robarts et al. (1998) observed similar

conditions in Lake Biwa, Japan but the imposed wind stress was from a passing typhoon. This study showed upwelling and the associated isotherm tilt can occur for significant lengths of time under moderate wind speeds and weak vertical stratification. These conditions have been observed before in Kootenay Lake, British Columbia, but their effects on the phytoplankton population had not been studied (Stevens et al., 1996; Wiegand and Carmack, 1986). This study integrated the works of others who have studied specific aspects of phytoplankton response to light, nutrients, and temperature with those who studied hydrodynamic responses in stratified lakes subject to surface wind stress. This integrated study showed how persistent winds created the hydrodynamic conditions that determined phytoplankton distributions along the length of the lake. How the resultant isotherm tilt created a variable mixed layer depth, which affected the depth-integrated photosynthesis that was the controlling term in multiplicative growth response function. Modeling results and previous works (Farrow and Stevens, 2003; Verhagen, 1994; Monismith 1986) were integrated to show how upwelling conditions dilute the phytoplankton biomass and advect it out of region near SWA.

2.6 Conclusions

The observed isotherm tilt resulted from persistent wind conditions that have a periodicity smaller than the fundamental period of the internal wave; these conditions produce a persistent upward tilt from north to south. The hydrodynamics that create this condition produce vigorous mixing in the STL and at the upwind end bottom waters upwell to the surface and are transported downwind. The vigorous mixing combined with the isotherm tilt created longitudinally variable mixed layer depth that resulted in a longitudinally variable depth-integrated photosynthesis rate. This effect produced a smaller depth-integrated photosynthesis rate at NOA compared to SWA, and the effect was more significant than phosphate limitations. Because of hydrodynamic conditions that created the isotherm tilt, the phytoplankton at SWA are diluted and transported through the region faster than they can grow; these conditions are also more significant than phosphate limitations. Between these two ends at MWY, growth is less affected by hydrodynamic conditions and the biomass can exceed the biomass at the two ends. The hydrodynamic conditions that maintain the tilt also produce a vertical eddy diffusion structure that reduces the effective growth rate; vertical diffusive fluxes transport phytoplankton out of the

euphotic zone but also balance or compensate for sinking losses. When hydrodynamic conditions relax, eddy diffusion relaxes and growth is independent of water depth; vertical diffusive fluxes are small relative to net growth rate and the growth in the euphotic zone (about the upper eight to ten meters of the water column for Lake Washington). The relative magnitude of vertical eddy diffusion can affect the relative size of the bloom. The physical aspects of the isotherm tilt sets conditions that determine longitudinal differences in diatom biomass and the magnitude and vertical distribution of eddy diffusion determines the size of the diatom bloom.

2.7 Future Studies

This study is the first effort for Lake Washington to quantify cause and effect relations between observed hydrodynamic, nutrient, and temperature conditions and the observed diatom distributions, concentrations, and growth. The study focused its efforts on hydrodynamics and the diatom population, but the observed hydrodynamics could significantly affect or influence spatial distributions if the zooplankton population. An interesting study would be to investigate cause and effect relations between the hydrodynamics, diatoms, and zooplankton. Does *D. (L.) ashlandi* actually congregate at the north end of the lake because the diatom population is advected there or is it also advected to the north end? At the south end of the lake, is upwelling and advection so strong that zooplankton are unable to maintain their position there? Previous studies found *Cyclops bicuspidatus* densities were greater at the north end of the lake than at the south end (Beauchamp et al., 2004). Is the north/south distribution of *Cyclops bicuspidatus* indirectly driven by hydrodynamic conditions, which advects the diatom and *D. (L.) ashlandi* populations to the north end? Such hydrodynamic conditions would affect zooplankton densities at the south end of the lake at the same time sockeye fry immigrate into Lake Washington (Beauchamp et al., 2004). Such a study would integrate disciplinary studies on hydrodynamics, phytoplankton, zooplankton, and fish. Concurrent to this study, more definitive eddy diffusion profile studies could be conducted. The studies would define the temporal and spatial variation of eddy diffusion during the early-spring period of the diatom bloom. Results could be used to assess if phytoplankton are mixed by rapid pulsed turbulent events or less frequent episodic turbulent events.

To assess the current hydrodynamic conditions (now-casting) in the lake, equation 1.7 could be used to develop a dynamic model of the isotherm tilt; this model would allow one to assess the current condition of the isotherm tilt. The model would be driven by real-time observations from a station near MWY; required data would be temperature measures over the water depth and wind speed and direction. From the temperature profiles, one can estimate vertical eddy diffusion from the change in heat content using the Advective/Diffusion equation (Ravens et al., 2000). Knowing the current isotherm tilt and eddy diffusion, one could monitor the expected timing of the diatom bloom; this would be a useful tool for the limnologist.