IMPACTS OF THE ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) ON LARGE LAKES: INFLUENCE OF VERTICAL TURBULENT MIXING

DISSERTATION

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ABSTRACT

Hydrodynamics strongly influences the role of benthic filter feeders in benthic-pelagic trophic coupling in large lakes. In this dissertation I investigate the interactions of vertical turbulent mixing, light and particulate and dissolved constituents in a large lake, Lake Erie. An Acoustic Doppler Profiler was used to investigate the hydrodynamics of a near shore region of the Lake Erie western basin and then incorporated the measured parameters in a numerical simulation to estimate the amount of phytoplankton biomass consumed by zebra mussel grazing in the benthos. The modeled results were then compared with vertical profiles of algal abundance. Diel average eddy diffusivity estimates varied from 10^{-5} to 10^{-4} \text{ m}^2\text{s}^{-1} at the sample site location. The simulations indicate that eddy diffusivities of this order of magnitude can result in extremely low algal biomass near the benthos, while the upper water column remains relatively unaffected. Discounting inputs from algal reproduction, I estimate that between 8 and 67% of the algal biomass is consumed each day at the sample site, depending on the shape and magnitude of the diffusivity profile. Measured vertical biomass profiles have a zone of algal depletion near the benthos, but little evidence of depletion near the surface. I found the daily flow of algal biomass into the benthos was strongly coupled with the magnitude of turbulent mixing, suggesting the flux of algal
biomass into the benthos was small compared with previously published estimates that ignored the paucity of turbulent mixing occurring.

Vertical mixing can also cause changes in exposure to incident radiation. The depth of the wind-mixed layer and diel thermoclines often determine the light climate of individual plankters, which, due to the random nature of turbulence can be different for plankters at the same depth. Time scales associated with photoresponse are often similar to various mixing time scales, on time scales of minutes to hours. I develop a method to estimate primary productivity, considering the effects of vertical turbulent mixing. The indirect temperature gradient microstructure method was used for calculating energy dissipation, from which I obtain Lagrangian diffusivity estimates. I then apply literature values of photosynthetic parameters (the slope and shape of the photosynthesis-irradiance curve) and a random walk simulation, using the diffusivity estimates, to predict the light climate of the phytoplankton and thus the primary productivity. I find that at some points in time and space, notably in early morning convective mixing, that photosynthesis may be underestimated by as much as 45%. However, diel thermocline formation reduces this effect, trapping algae near the surface and causing near surface declines in production. Separated from the source of mixing, the surface wind-shear, the lower water column primary production is still increased by more than 15% relative to the static model.
Patterson et al. (1985) found that six factors influence the vertical oxygen budget in the central basin: 1) Vertical mixing; 2) exchange across the air-water interface; 3) photosynthesis; 4) community respiration; 5) sediment oxygen demand (benthic respiration); and 6) horizontal transport. However, since that time, the trophic status of the lake has undergone profound changes due to the changing phosphorus loading and introduction of the exotic zebra mussel into the lake. Zebra mussels may introduce a large sink for oxygen within the hypolimnion as they spread across the fine sediment (Haltuch et al. 2000). I therefore test the importance of hypolimnion thickness on oxygen depletion, a measure of the total loss of oxygen in the hypolimnion over time (expressed per unit area). I found that hypolimnion thickness is a major factor in hypolimnion oxygen depletion. Entrainment events, which reduced the thickness of the hypolimnion, can increase the oxygen depletion rather than alleviate it. I also test the role of transport processes, across variation in time and depth, in oxygen transport in the central basin using an oxygen budget at differing times of day and quantify the relative importance of four different transport processes. I found that the only significant process in oxygen depletion is bottom shear, caused by hypolimnetic current and influenced by bottom roughness (including biotic roughness caused by zebra mussels) and current speed, which prevents or allows the limitation of the delivery of oxygen to the benthos. Decreases in bottom shear, lead to decoupling of the hypolimnion thickness-oxygen depletion relationship and control by the intensity of the mixing.
I dedicate this dissertation to Dad, for showing me the fun of science, to Dave for showing me how to do it, and to Mom and Coleen for showing me it's not the only important concept in the world.
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INTRODUCTION

Vertical mixing processes and thermal structure of large lakes can impact the biological processes both through vertical transport processes and the exponential decay of light with depth (Imberger and Patterson 1990). While extensive research in Lake Erie has increased understanding of both physical and biological dynamics, a synthesis of the physics and biology is currently lacking.

Vertical transport of constituents in the water column is controlled by the generation of turbulence by surface shear at the air-water interface, bottom shear, shear at the thermocline, and convection (Figure 1; Ivey and Imberger 1991). Surface shear can vary widely in importance in Lake Erie, as a dominant process (relative to the other mixing processes) during storm events, but with little impact during periods of calm (McCune 1998, Ivey and Patterson 1984). In addition, the penetration of wind mixing is often limited not only by the seasonal thermocline, but can also be limited by more
ephemeral and weaker diel stratification (Schertzer and Sawchuk 1990, Brainerd and Gregg 1993). The degree of stratification can also impact the likelihood of transport across the thermocline by turbulent water movement (MacIntyre 1993). Bottom shear, while often sporadic and spatially variable, can be significant when bottom currents are strong, such as during seiche events, and often results in a completely mixed hypolimnion (McCune 1998, Ivey and Patterson 1984, Ivey and Boyce 1982). Due to the strong density gradient that develops between the epilimnion and the hypolimnion, the shear stress generated there does not often contain enough energy to cause mixing and entrainment across the density gradient. However, these episodic entrainment events are a primary way for delivery of oxygen-rich water to the hypolimnion (a 'reverse entrainment' event) and also may control the thickness of the hypolimnion and are thus important (Patterson et al. 1985, Ivey and Boyce 1982). The most constant mixing process in Lake Erie is convection through nightly surface cooling. McCune (1998) demonstrated that this nightly event causes mixing equivalent in magnitude to severe storm events, breaking up diel thermoclines and deepening the mixed layer.

Vertical mixing in the central basin of Lake Erie was studied extensively in the 1980s. Ivey and Boyce (1982) applied a mixing model to the hypolimnion of the central basin, investigating entrainment events, mixing of epilimnion, oxygen-rich waters down into the oxygen-poor hypolimnion. Such events were found to be instrumental in prevention or delay in the onset of anoxia in the basin. Ivey and Patterson (1984) extended this work, applying a vertical mixing model incorporating the entire water column. They demonstrated that convection, wind stirring and thermocline shear
production were all important in vertical mixing estimates. Patterson et al. (1985) combined this mixing model with a primary production model to produce a summer oxygen budget for the Lake Erie central basin. They were thus able to examine the factors causing hypolimnetic anoxia and, to some extent, offer predictive ability to lake managers. Some of these factors include those influencing vertical transport, which Bedford and Abdelrhman (1987) reviewed in comparison to equivalent parameters in coastal oceanography. Most recently, Shertzer and Sawchuck (1990) applied Lam and Shertzer's (1987) heat flux model to the central basin. Similarly, Boyce et al. (1989), investigated the thermal structure of the Great Lakes and its impact on circulation patterns.

As vertical movement of phytoplankton by turbulent motion is typically two or more orders of magnitude greater than typical algal sinking velocities (MacIntyre and Melack 1995), turbulent transport of algae within and out of the photic zone can impact both primary production and oxygen budgets, especially as the photosynthetic response of algae to light intensity is non-linear, with a gradually decreasing slope as well as photoinhibition at high light intensity (Patterson 1991). Benthic filter feeders are also limited by vertical transport of algae (Frechette and Bourget 1985a, b; Frechette et al. 1989; Peterson and Beal 1989), influencing both the availability and quality of food to the benthos (Monismith et al. 1990). Vertical mixing, especially due to bottom shear production, can also cause resuspension of phytoplankton, which would otherwise be trapped in the sediment (MacIntyre and Melack 1995). Similarly, both oxygen transport
from the surface, and benthic sediment oxygen consumption can influence the oxygen concentrations throughout the water column (Patterson et al. 1985).

In this dissertation, I investigate the interaction of biological and physical dynamics in Lake Erie, as influenced by vertical transport processes, at three levels: 1) the physical coupling between the benthos and the pelagic, 2) the transport of particulate constituents in the water column, and 3) the transport of dissolved constituents in the water column.

In the first of these areas of research, benthic-pelagic coupling, I explore the specific case of the zebra mussel’s (*Dreissena polymorpha*) consumption of pelagic algae. The mussel has often been implicated in the increased water clarity in Lake Erie (see below), without proper quantification of the role of water movements (e.g., Bunt et al. 1993, MacIsaac et al. 1992). However, the mussels are in the benthos and are linked to the algae, planktonic, through mixing processes, limiting mussel algal consumption (Figure 2). I test the null hypothesis that vertical turbulent transport processes do not alter the rate of delivery of algae to the benthic zebra mussel in western Lake Erie.

The second area of investigation is the transport of particulates within the water column. This transport is of special importance in determining the light climate experienced by the algae, whether in terms of ultraviolet radiation (Xenopoulos and Bird 1997) or photosynthetically active radiation (PAR, Franks and Marra 1994). I look at the predicted movement of algae and how this impacts the light climate of the algae throughout the water column (Figure 3). I test the null hypothesis that mixing processes
will not significantly alter the light climate or primary production of algae in the central basin of Lake Erie.

Last, transport of dissolved solutes is likewise of import, whether evolution of nutrients from the benthos and transport within the water column, the production and transport of CO$_2$, the transport of dissolved organic and inorganic carbon (DOC and DIC), and many other specific examples. Due to the historic problems with eutrophication and summer oxygen depletion in the central basin hypolimnion and phosphorus loading controls designed to reduce this depletion, I investigate the role of vertical transport processes in the hypolimnion oxygen problem and the influence of the hypolimnion thickness. To do this, I create an oxygen budget, parameterized for Lake Erie, and test the importance of different mixing parameters by varying them from measured mixing profiles in the central basin, Lake Erie (Figure 4).
Figure 1. Schematic of water column forcing functions: 1) Surface wind shear, 2) Shear at the thermocline, in some cases leading to entrainment and 'reverse entrainment' events, 3) bed shear and 4) convection from surface cooling.
Figure 2. Sources, sinks and transport of phytoplankton biomass within the western basin, Lake Erie. Phytoplankton production is a source, zebra mussels are a sink and transport provides linkages between the components.
Figure 3. Light history of two algal cells starting at the surface mixed vertically through an exponentially decaying light profile.
Figure 4. Graphic representation of the oxygen budget in the western basin, Lake Erie during the summer.
CHAPTER 1

THE IMPACT OF A BENTHIC FILTER FEEDER: LIMITATIONS IMPOSED BY PHYSICAL TRANSPORT OF ALGAE TO THE BENTHOS

The zebra mussel, *Dreissena polymorpha*, was introduced into the Great Lakes in the late 1980's. Despite the investment of substantial resources to evaluate its impact on the existing aquatic ecosystem, a number of issues remain largely unresolved. In particular, neither the zebra mussel's direct impact on Great Lakes phytoplankton and zooplankton community dynamics, nor its indirect effects on fish community stability are understood. Since their benthic habitat and lack of mobility limit their access to food, zebra mussels depend on transport mechanisms such as settling (algal sinking), turbulent vertical transport, horizontal advection and resuspension to bring food to them. Thus, any evaluation of the impact of the zebra mussels on the phytoplankton community must be based on a fundamental understanding of both phytoplankton dynamics (changes in population size due to mortality and reproduction) and physical dynamics (transport
throughout the water column due to turbulent mixing, advection, swimming or settling) within the system. In this chapter, I present a mathematical model and field measurements of turbulent mixing as a contribution to our understanding of the physical dynamics of zebra mussel-algal interactions.

Using estimates of population densities and clearance rates, researchers have speculated that zebra mussels could strip the entire Lake Erie western basin of algae in less than one day, or even upwards of 18 times per day (MacIsaac et al. 1992, Bunt et al. 1993, Makarewicz et al. 1999). However, although phytoplankton abundances are now lower and cyanobacteria blooms less frequent than they were prior to 1988, the algal seasonal succession patterns have persisted (Wu and Culver 1991; Figure 1.1). Hence, zebra mussel feeding has not completely overwhelmed phytoplankton production, in part because consumption rates are limited by the rate of delivery of algae to the bottom. Many studies of zebra mussel feeding rates to date have been based on laboratory work using well-mixed tanks rather than realistic field conditions that take into account the algal delivery rates to the lake bottom and mussels’ repeatedly filtering the same water (Yu and Culver 1999). In addition, recent research indicates a strong correlation between mussel grazing and hydrodynamic forcing (MacIsaac et al. 1999)

Modeling trophic dynamics of the Lake Erie ecosystem without including the effects of physical processes limits the models’ appropriateness both as management tools and as means to further our basic understanding of the lake ecosystem. For example, western Lake Erie is commonly described as completely mixed, and estimates
of zebra mussel grazing are based upon this assumption (e.g., MacIsaac et al. 1992). However, western basin temperatures vary as much as 1-2 °C with depth at noon (Pontius and Culver, unpublished data), a gradient of sufficient magnitude to influence the rate of turbulent mixing in the water column significantly (McCune 1998).

Marine ecologists have quantified the influences of fluid mechanics on benthic filter feeders for many years. For example, Muschenheim (1987) studied the feeding ecology of a marine polychaete and concluded that most food is transported horizontally in the low flow water near the bottom (concentration boundary layer). Vertically settling seston becomes potential food when it enters this boundary layer, but a strong concentration gradient develops with a localized depletion zone near the bed when the filter feeding organisms remove seston faster than it is replaced. Other researchers have also found a decrease in phytoplankton concentration near benthic filter feeders in the field (Buss and Jackson 1981; Frechette and Bourget 1985a, b; Peterson and Black 1987; Frechette et al. 1989; Peterson and Beal 1989) and in laboratory experiments (Wright et al. 1982, Wildish and Kristmanson 1984). Vertical feeding height (e.g. height above the bottom) attained by an organism (Jumars and Nowell 1984, Monismith et al. 1990) can thus determine the quantity and quality of its food supply and its rate of growth (Frechette and Bourget 1985b, Frechette et al. 1989). These conclusions are based on work in marine intertidal zones where long fetches and large tidal fluxes provide more constant and larger turbulent energy inputs than those available in Lake Erie. Nevertheless, MacIsaac et al. (1992, 1999) also found algal depletion in the concentration boundary layer (1.5 m thick) over zebra mussel beds in the western basin of Lake Erie.
Because mixing processes in Lake Erie are less constant and weaker than their marine counterparts, the availability of food for the benthic filter feeder, the zebra mussel, is determined by vertical mixing caused by differential flow or shear within the boundary layer.

Zebra mussels represent a large benthic biomass (150 g dry soft tissue·m⁻² at the site in 1995) and excrete large amounts of ammonia and phosphate (Arnott and Vanni 1996, James et al. 1997). At the same time, returning these nutrients to the euphotic zone also requires a mass transport mechanism. Therefore, understanding the role of nutrient and phytoplankton transport in the Lake Erie ecosystem requires identifying and quantifying the important physical, biological and chemical processes controlling that transport.

I carried out a series of field experiments in the shallow western basin (mean depth = 7 m) of Lake Erie to evaluate shear velocity and estimate eddy diffusivity. I then used these estimates of the magnitude of physical mixing in the water column in a series of simulations to determine the impact of the hydrodynamic forcing on the delivery of algae to the benthos.

Methodology:

*The models:* The abundance of algae in the concentration boundary layer depends on the algal settling rate, horizontal advection of phytoplankton, turbulent mixing above the bed, the consumption rate of the zebra mussels, and external sources and sinks due to
phytoplankton production and grazing by other organisms such as zooplankton (Cloern 1991, Lucas et al. 1999). The interaction of these physical and biological processes ultimately determines how much phytoplankton will be available to the zebra mussels at the bed. For the present analysis, I have assumed horizontal gradients and external sources and sinks can be neglected. This assumption is justified when the time scales of horizontal advection and production are large compared to the time scales of vertical mixing, settling, and zebra mussel consumption (c.f., Koseff et al. 1993). However, production time scales estimated in this chapter ranged from 0.5 day$^{-1}$ to 3.3 day$^{-1}$ (see discussion), which indicate they must be included. Horizontal advection, while important, is here disregarded for the purposes of comparison with earlier mussel consumption estimates (MacIsaac et al. 1992, MacIsaac et al. 2000, Bunt et al. 1993, Ackerman et al. 2001).

Under the above conditions, the effects of vertical mixing, settling, and zebra mussel consumption on the phytoplankton biomass without phytoplankton production can be modeled with a one dimensional advection-diffusion equation (Cloern 1991):

$$\frac{\partial F}{\partial t} + w_s \frac{\partial F}{\partial z} = \frac{\partial}{\partial z} \left( K \frac{\partial F}{\partial z} \right)$$  \hspace{1cm} (1.1)

where F is the concentration of the phytoplankton, t is time, $w_s$ is the settling velocity of the phytoplankton, z is the vertical coordinate, and K is the vertical eddy diffusion. The
boundary conditions involve the total flux, that is, vertical transport, of phytoplankton. At the water surface \((z = H)\), there is no flux, hence no loss or gain of phytoplankton:

\[
w_s F - K \frac{\partial F}{\partial z} = 0 \quad \text{at} \quad z = H
\]

(1.2)

At the bottom \((z = 0)\), the phytoplankton flux equals the consumption rate of the zebra mussels (Frechette et al. 1989):

\[
w_s F - K \frac{\partial F}{\partial z} = -\alpha F \quad \text{at} \quad z = 0
\]

(1.3)

where \(\alpha\) is the clearance rate of the mussels and \(\alpha F\) (evaluated at the bottom) is the algal consumption rate.

Before the system defined by Equations (1.1)-(1.3) can be solved, values for the parameters must be specified. I used a settling velocity, the rate of algal sinking, of 1 m·day\(^{-1}\) (Hutchinson 1967; given that vertical eddy diffusion can transport algal particles several orders of magnitude more rapidly, the smaller differences in sinking between most algal types is unimportant) and a zebra mussel clearance rate \(\alpha = 25 \text{ m}^3\text{·m}^{-2}\text{·day}^{-1}\) (see Discussion section). To estimate the eddy diffusivity, I assume rough, turbulent flow (the sample site, (Figure 1.2) dictated this flow assumption as described below;
that can be described by a logarithmic velocity profile (Hinze 1975):

\[ u = \frac{u_*}{\kappa} \ln \left( \frac{z}{z_0} \right) \]  

(1.4)

where \( u_* \) is the shear velocity (a measure of the shear stress at the bed), \( \kappa = 0.4 \) is the von Kármán constant, and \( z_0 \) is a length scale related to the bottom roughness (a measure of where the flow becomes stagnant above the bed). Estimates of the shear velocity and \( z_0 \) can be obtained by measuring the velocity at a series of points above the bed. When the horizontal component of velocity is plotted against the natural logarithm of the distance above the bottom (Equation 1.4, e.g., Figure 1.3), \( u_* \) and \( z_0 \) can be computed from the slope and the intercept, respectively. Then, I assume turbulent diffusivity of phytoplankton to be equal to that of momentum, and the eddy diffusivity can be estimated with (Fischer et al. 1979, p. 106, figure 1.4a)

\[ K = \kappa u_* z \left( 1 - \frac{z}{H} \right) \]  

(1.5)

However, as this profile of \( K \) was originally developed for use in the riverine environment, in the simulations I have also employed a constant diffusivity (Figure 1.4b), which will serve for comparison.
Including a source term, phytoplankton production, allows for a better assessment of the mussels' impact in the western basin:

$$\frac{\partial F}{\partial t} + w_0 \frac{\partial F}{\partial z} = \frac{\partial}{\partial z} \left( K \frac{\partial F}{\partial z} \right) + \mu F \quad \text{(1.6)}$$

where the last term is the addition of a phytoplankton source term, $\mu F$, with $\mu$ the phytoplankton production rate. The boundary conditions remain unchanged. If steady state is assumed, the rate of production will be equal to the rate of consumption, resulting in no net clearance of algae from the water column. This state is solved numerically via multiple iterations of the solution to Equation (1.6) until there is no 24 h change in total algal biomass, B.

After the parameters were specified, I solved the system (Equations 1.1-1.3 and Equation 1.6) numerically with a method similar to that used by Koseff et al. (1993; see appendix A). I used the Crank-Nicolson method with central differences for the diffusion terms and an upwind difference for the sinking term. Following Koseff et al. (1993), I add a small minimum eddy diffusivity to the profile in (Equations 1.5); the minimum is typically 1000 times smaller than the depth averaged diffusivity. This prevents the generation of artifacts unrelated to the mixing profiles in the simulation results caused by an artificial barrier to mixing when the diffusivity approaches zero. I adopted a fully implicit formulation for the boundary conditions since spurious oscillations develop when the Crank-Nicolson scheme is used (Douglas 1961). Typical values for the time step and grid spacing were 30 seconds and 0.035 m, respectively. A set of simulations was run to confirm that the results did not depend on these choices and that they matched analytical solutions for simple cases.
To compare with previous methods of estimating zebra mussel impact, I compared two other models of zebra mussel consumption, here called 'linear' and 'well-mixed'. The linear model corresponds to the pumping rate of mussels combined with areal estimates of zebra mussel numbers to estimate the amount of water filtered by mussels per square meter per day. It is then assumed that there is no refiltration and that algal concentrations remain constant. This translates into a linear decay of algal concentration, dB/dt, with time:

$$\frac{dB}{dt} = -\frac{\alpha}{H}B_0$$  \hspace{1cm} (1.7)

where B is the total phytoplankton biomass, \( \alpha \) is again mussel clearance rate, H is the height of the water column, and \( B_0 \) is the initial algal biomass. Solving this system, we find that the biomass, B, at any time, t, is related to a linear decay model:

$$B = B_0 \left(1 - \frac{\alpha}{H}t\right)$$  \hspace{1cm} (1.8)

In order for the assumptions this model to hold true, the lake must remain completely static and algal sinking rates must equal the zebra mussel clearance rate, \( \alpha \). Despite the unusual nature of these assumptions, this model has been used as a 'theoretical' maximum value for mussel impacts on Lake Erie (MacIsaac et al. 1992, Bunt et al. 1993). To include production, the right side of Equation (1.8) becomes

$$B_0 \left[(1 + \alpha / \mu H)e^{\mu t} - \alpha / \mu H\right]$$

which then causes the equation to deviate from linear decay except for \( \mu t \ll 1 \). However, this complicated scheme is not included, as Equation (1.8) is used for comparison with previous work and is not a realistic model.
The well-mixed model can be described as an exponential decay, with the rate of decay determined by the clearance rate of the mussels and the height of the water column:

\[
\frac{dB}{dt} = -B \frac{\alpha}{H} \quad (1.9)
\]

where the parameters are as above. Production can easily be included in this model:

\[
\frac{dB}{dt} = B \left( \mu - \frac{\alpha}{H} \right) \quad (1.10)
\]

where \( \mu \) is again phytoplankton production. The solution to both of these systems is an exponential decay function where the rate of decay is related to mussel consumption and the height of the water column (Equations 1.9 and 1.10) and phytoplankton production (Equation 1.10):

\[
B = B_0 e^{(-\alpha/H)t} \quad (1.11)
\]

\[
B = B_0 e^{(\mu-\alpha/H)t} \quad (1.12)
\]

where the parameters are as above. If steady state is assumed \((dB/dt=0)\), phytoplankton production can be estimated:

\[
\mu_0 = \frac{\alpha}{H} \quad (1.13)
\]

This rate will be compared to the steady state numerical solution to Equation (1.6).

**Field Methods:** I performed the experiments in the western basin of Lake Erie (USA) offshore of Gibraltar Island (41°40’ lat., 82°50’ long.; Figure 1.2). I sampled the bottom 3 m of the 5 m of water (ranging from 4-6 m due to seiche activities), approximately 50
m from shore, from June until September 1995. The bed consisted of 5-10 cm cobble, with clumps of zebra mussels ranging from 5-20 cm. The zebra mussel (*Dreissena polymorpha*) dominated the benthic community with between 10,000 and 20,000 mussels·m⁻² and up to 150 g mussel dry soft tissue·m⁻² (Pontius and Culver 2001).

I measured water velocity measurements using a Sontek 3 MHz acoustic Doppler profiler (ADP), which I deployed on a steel tripod facing downward, recording the data via a 60 m cable to a shore-based computer. Using the ADP, I measured water velocities in 25-cm strata (bins) from the bottom to three meters above the bottom, with the computer recording time-averaged vertical profiles of the three dimensional velocity fields every 20 min. I sampled continuously throughout the summer, interrupted only by two electronic failures resulting from lightning strikes on 24 June and 25 August. I used the horizontal components of velocity to estimate $u^*$ and $z_0$ and, in turn, the eddy diffusivity ($K_z$) using Equations (1.4) and (1.5). A power spectrum (Welch method) was generated using the horizontal velocities time series from 1 m above the bottom, in order to determine if the forcing mechanisms at this site were characteristic of the whole. Profiles with good fits ($r^2 > 0.5$) were included in a 24-h average diffusivity ($K_{\text{avg}}$, obtained from Equation 1.5 with 24 h averaged $u^*$). I obtained wind speeds corresponding to the sample dates from the Great Lakes Forecasting System (GLFS; Kelly et al. 1998), which are averaged over 6-h intervals to compare with measured mixing parameters. I measured vertical temperature and oxygen profiles daily using a YSI (Yellow Springs Instruments) dissolved oxygen probe in order to determine if there was significant stratification during the sampling periods.
I measured vertical phytoplankton abundance distribution three times per week using two shore-based 10-channel peristaltic pumps. I pumped water samples from a sampling apparatus deployed on the ADP tripod at fixed depths, 6, 12, 24, 36, 49, 61, 98, 148, 200 and 250 cm above the bed. Tubes from the sampler passed to shore inside an opaque plastic pipe. I flushed the tubes by passing twice the tube volume through the tubes prior to collecting samples at 30 mL min\(^{-1}\) in order for the samples to represent the stratum from which each was taken and so that the 3 L samples used for analysis were integrated over time (100 min). Phytoplankton samples were preserved using Lugol’s fixative and were enumerated using an inverted microscope to produce phytoplankton biomass (mg wet weight:L\(^{-1}\)) profiles versus depth for each sample date.

I simulated algal biomass dynamics with depth and time using Equation (1.1), as in Cloern (1991), based on initial conditions of a uniform algal distribution with depth for both typical and maximal values of \(K_x\), and using both constant (\(K_x\) does not change with depth) and parabolic (\(K_x\) is distributed as in Equation (1.5)) distributions of \(K_x\) with depth. I compared these simulations with results from a completely mixed model (i.e., very large \(K_x\)). I also compared the results with those predicted by a model that assumes zebra mussels have complete access to all algae in the water column without refiltration of water previously cleared of algae. I call this model “the linear model” because it results in a linear reduction of algal biomass with time. I also compare these results with other work using the non-dimensional diffusivity \(K^*=K_x/\alpha H\).
Results

Temperature vertical profiles at the site varied less than 0.1°C during the sampling period. Time averaged mean horizontal currents ranged from 0.93 to 4.63 cm•s⁻¹, with wind velocities from the same periods ranging from 1-15 m•s⁻¹ (Table 1.1). Though water velocity did not appear to correspond with wind speed, the stronger currents tended to coincide with winds from the north. I fit time averaged vertical profiles of horizontal velocity versus ln z for each date. This line, which has a slope u•• • κ⁻¹ and intercepts the z-axis at z = z₀, the roughness length (2.5 cm for this profile, on 12 September, Figure 1.3). I estimated diffusivity using Equation (1.5), which causes the diffusivity to be distributed parabolically in the water column (Figure 1.4a). For example, evaluating the average K for 12 September 1995, I obtain $K_{avg} = 1.2 \times 10^{-5}$ m²•s⁻¹. I used this procedure to evaluate $K_{avg}$ for each date (Table 1.1), dropping those dates having more than 50% of the profiles with regression fits ($r^2 < 0.5$). The power spectrum was calculated from 10 June 1995 until the first lightning strike on 23 June (Figure 1.5). There were large peaks at 92.5 h and 14.9 h, with smaller peaks at 8.4 h, 6.2 h, and 4.2 h. The roughness length, z₀, varied from 7 cm to as great as 20 cm. There was no diel signal. I found shear velocities and the corresponding diffusivities to vary (Table 1.1), depending primarily on wind direction. The lack of data in the two periods between 22 June and 24 August and again between 24 August and 11 September reflects the periods required for repairs after direct lightning strikes caused electronic failures in the ADP.

Algal biomass varied widely with depth in June and July (Figures 1.6, solid line), with values from samples near the benthos (i.e. zebra mussels) being very low, while
further away, biomass increased exponentially. During August and September, a
different trend was apparent (Figures 1.6, dashed line). Examination of the algae samples
indicates increases in phytoplankton biomass near the bottom were composed of the
Cyanobacterium, Microcystis, a vertically migrating (buoyant) species often rejected by
zebra mussels (Lisa Babcock-Jackson, Ohio State University, personal communication).

Discussion:

Comparison to previous field measurements: These Lake Erie results are consistent with
previous physical studies. I found that the power spectrum of vertical horizontal
velocities (at 1 m above bed) for period of 10 June 1995 to 23 June 1995, corresponded to
the Lake Erie weather cycle (96 h), the first mode seiches (14 h), the second mode
seiches (9 h), the third mode seiches (6 h) and the cross-basin seiche (3 h) (Figure 1.5;
Hamblin 1987). The second mode seiches are comparatively weak as the sample site was
very close to the second mode node. A diel signal was absent; the sampling captured
only the influence of bed shear and did not have the capability to detect convective events
or diel thermocline formation because these do not influence horizontal currents. Thus,
the results are characteristic of both the western basin and shallow regions of the lake as a
whole. Royer et al. (1987) found currents varying from 1-10 cm s\(^{-1}\), while Bedford and
Abdelrhman (1987) predicted velocities of 1-5 cm s\(^{-1}\) during calm weather and 10-20
cm s\(^{-1}\) during storm events, comparing favorably with the results (Table 1.1). Shear
velocities (\(u_*\), a shear stress measure) were slightly less than expected for the exposed
site, varying from 0.13 to 1.66 cm s\(^{-1}\), almost one order of magnitude less than those
predicted by Bedford and Abdelrhman (1987). However, the estimates of \(z_0\) were higher
23
than expected, due to the zebra mussel covered cobbles (though the cobbles were on the order of 8-10 cm, the mussel druses, large clumps of zebra mussels increased the size of the roughness elements to 20-30 cm.)

The magnitude of eddy diffusivities varied from $10^{-5}$ to $10^{-4}$ m$^2$·s$^{-1}$, corresponding roughly to wind direction (Table 1.1), due to the location of the sample site on the north side of an island (Figure 1.2). Storm events in Lake Erie's much deeper, central basin have been found to support diffusivities as high as $10^{-2}$ m$^2$·s$^{-1}$ (McCune 1998). I did not obtain values this high in western Lake Erie at least in part due to daily averaging of current speeds which, while more representative of conditions on the lake, could not capture short term, high intensity events. These events are likely ecologically less important than less intense mixing events, since they overwhelm the mussel filtering capacity (Ackerman 1999). That is, the sediment load causes the mussels to stop filtering.

*Mussel impacts on algae:* I found a strong depletion of algal biomass in samples near the benthos in early and mid summer (Figure 1.6, solid line). The mussels were able to consume much of the algae in the near bed region, a zone of depletion similar to that found by MacIsaac et al. (1999). However, the algal abundance and composition of the upper water column remains similar to that found prior to the introduction of the zebra mussel (Wu and Culver 1991, Figure 1.1). In late August and into September, I found an increase in algal biomass (dominated by the cyanobacterium *Microcystis*) near the benthos, as opposed to a zone of depletion (Figure 1.6).
While I observed little evidence of algal depletion away from the benthos, others have estimated much greater algae consumption from the whole water column by zebra mussels, based upon clearance estimates (Hogan and Mills 1997; Bunt et al. 1993; MacIsaac et al. 1992, 1999) and bioenergetics models (Madenjian 1995). Their estimates of clearance rates (m³•m⁻²•day⁻¹) indicate that a volume equivalent to that of the entire water column can theoretically be filtered completely once per day by small-bodied individuals (Bunt et al. 1993) to between 3.5 and 18.8 times per day by the whole community (MacIsaac et al. 1992). However, it has been unclear how close to the theoretical maximum filtering (pumping) rate the mussel community actually achieves, and what fraction of the algae in the water column is consumed per day. Yu and Culver (1999) also found refiltration of water previously cleared of algae can decrease the mussels' impact on the algal population, while Hogan and Mills (1997) observed decreased clearance rates as algal concentrations decreased.

*Field parameterized simulations of algal consumption:* Using the field results, I can compare the algal dynamics with space and time predicted by the “linear model” of MacIsaac et al. (1992) and others, the totally mixed reactor model, and the field parameterization of Equation (1.1). I have used a clearance rate (a) of 25 m³•m⁻²•day⁻¹ (resulting in filtering a volume equivalent to the entire 7m water column 3.5 times per day) as a compromise value between various sources for the clearance calculations for a community of 10,000 – 20,000 zebra mussels•m⁻², which is typical for western Lake Erie hard substrate areas. Without production, and beginning with an algal concentration of
400 mg·m⁻³ (2800 mg·m⁻²), the time course of algae remaining for the "linear model" and the fully mixed reactor model (exponential decay) are initially (i.e., for the first 3 h) similar (Figure 1.7). However, for a completely mixed water column, the algae are never completely filtered from the lake, whereas the linear model predicts that to occur after 6.8 h, at which time only 63 % of the algae have been removed from a completely mixed basin and, at 24 h, 97 %.

However, the western basin of Lake Erie is not a completely mixed system, though this is a common assumption for aquatic systems that do not form a strong seasonal thermal stratification. The completely mixed assumption is useful for calculating filtering impacts of mobile grazers distributed throughout the phytoplankton, such as zooplankton, but because zebra mussel adults are bound to the benthos within the benthic boundary layer, they do not have access to algae in the entire water column. Instead, they have access to the flux of particles entering the benthic boundary layer, as expressed by Equation (1.3).

For the same 7 m water column used in the calculations above, I estimated an upper bound for consumption (K=10⁻³ m²·s⁻¹), using an atypically high value for the diffusivity and a parabolic diffusivity distribution. I found that the estimated amount of algae removed by the mussels is much less than that predicted by the either the linear or completely mixed (exponential decay) models (Figure 1.7). After 6.8 h (when 100 % and 63% of the algae have been removed in the previous models, respectively), Equation (1.1) estimates that only 5 % of the algae has been removed as they are mixed into the
boundary layer. At 24 h, only 15% has been mixed into the boundary layer to be consumed by the mussels. This value is comparable to the values predicted by Madenjian’s (1995) bioenergetic approach that predicted that up to 26% (± 10%) of the algal production of the western basin could be removed by the mussels daily.

Diffusivities of $10^{-3}$ m$^2$ s$^{-1}$ value are not typical of the sample site, however. Though maximal measured diffusivity values approached $10^{-4}$ m$^2$ s$^{-1}$, those on the order of $10^{-5}$ m$^2$ s$^{-1}$, were more typical (Table 1.1). Using the first value, only 8% of the biomass would be cleared in a 24 h period. In fact, larger diffusivities, while bringing more algae to the benthic boundary layer, may negatively impact the mussels' ability to clear the algae by overloading the mussels with suspended sediment (Ackerman 1999).

Lower diffusivity near the water surface and in the boundary layer at the bottom reduce algal transport to the benthos with the parabolic profile. The importance of these regions can be noted if, instead of this parabolic distribution, I assume a constant value of diffusivity with depth. With $K_z = 10^{-3}$ m$^2$ s$^{-1}$, up to 89% of the water column’s biomass will be cleared in 24 h (Figure 1.8a), while a value of $K_z = 10^{-4}$ m$^2$ s$^{-1}$ allows the mussels to consume 49% of the algae (Figure 1.8b). The more typical values, $K_z = 10^{-5}$ m$^2$ s$^{-1}$, and lower magnitude mixing, $K_z = 10^{-6}$ m$^2$ s$^{-1}$, consume 27% and 18% of the algae respectively (Figure 1.8c,d). Below these lower values, the profiles become dominated by the sinking rate of algae, resulting in reduced mussel consumption ($K^ \star < 10^{-4}$, Figure 1.8.)
Changing the shape of the diffusivity profile with depth strongly affects the changes in the vertical distribution of algae over 24 h (Figure 1.9a-d) and hence the estimates of grazing rates by zebra mussels. Assuming a parabolic (Equation 1.6) distribution of diffusivity, consumption drops compared with the constant diffusivity (Figure 1.8). Low diffusivities generate very thin layers of algal depletion, and there is not enough mixing to counteract sinking in the surface waters (Figure 1.10d). More typical values of $10^{-5}$ m$^2$s$^{-1}$ were still dominated by algal sinking and had less impact on productivity (Figure 1.9c). Higher average diffusivities caused a evening of the algal biomass with depth, with zones of depletion near the benthos (Figure 1.9 a,b). However, even with high diffusivity, there was little impact on the algal biomass (Figure 1.9a).

Comparing these results with other similar work, we find that our estimates of algal consumption (with constant diffusivity) are higher (Figure 1.10). Here, $K^*$ is a non-dimensional number which can be used to compare between locations and systems and is presented on a log scale. Low values of $K^*$ indicate reduced mixing, increased water height, H, or increased filtering capacity, $\alpha$. At our site, two of these, H and $\alpha$, are constant, therefore, $K^*$ varies with K. At low $K^*$, the consumption is bounded by the sinking rate of the algae, $w_s$. At the higher $K^* = 1$, the consumption approaches the fully mixed model. Cloern (1991) first used a similar model in a marine tidal system with parabolic diffusivity profiles, $K=5 \times 10^{-5}$ m$^2$s$^{-1}$, $K^* = 0.625$, found algal clearance rates of 6.3 % over 24 h. Increasing mixing by 1 order of magnitude increase consumption to 33 % over 24 hours. The results from Cloen (1991) include a source term, resulting in decreased clearing at low $K^*$. Ackerman et al. (2001) investigated the impacts of zebra mussels across a single dressenid mussel bed in western Lake Erie, working over a single
mussel bed, and estimated clearance from beginning to end, in addition to physical parameters. At $K^* = 1.25$, they found 40% algal clearance across the bed (per day).

A strong correlation between hydrodynamic processes and benthic feeding has been consistently observed in the marine literature (Koseff et al., 1993; Fréchette and Bourget 1985a, b; Wildish and Kristmanson, 1979). Over the zebra mussel beds (i.e. the western basin) in Lake Erie, these forces are proven to be equally if not more important, because Lake Erie’s average diffusivities (Table 1.1) are consistently two orders of magnitude below the high diffusivities generated by tidal flows in shallow marine systems (on the order of $10^{-2} \text{m}^2\text{s}^{-1}$). It is therefore important for us to obtain a better understanding of the hydrodynamic forces that dominate the feeding of the benthic zebra mussel.

Studies of central Lake Erie have indicated that both penetrative convection and wind-induced surface shear can be important factors in driving the mixing of the water column (McCune 1998). Similarly, these forces may play a role both in the prevention of the western basin from mixing and in delivering algae to the benthos. In addition, the delivery rate of algae to the mussels at the site may be an upper bound; many western basin sites may have significantly lower diffusivities. The large areas of fine silt and sand in the western basin are evidence of lower-energy inputs in these locations, as fine sediment is suspended from high energy sites and deposited in low energy sites. While further study is needed to more completely understand the variability in space and time of the hydrodynamic forces both in other inshore areas and in the lower energy offshore
environment, the results are consistent with other recent work linking dreissenid feeding to mixing processes (Ackerman 1999).

Estimates of zebra mussel impact on phytoplankton abundance, both in this chapter and in others, have been based on consumption of a standing crop of algae (MacIsaac 1992, 1999, Bunt et al. 1993, Makarewicz et al. 1999) ignoring photosynthesis and algal reproduction. It is clear, however, that production has been sufficient to allow algal succession patterns to persist (Wu and Culver 1991), and that algal growth must to some degree lessen the impact of the zebra mussels on the algal community. We lack comprehensive estimates of phytoplankton production in large lakes in general, and in Lake Erie’s western basin in particular, to model its impact.

The trend in algal vertical distribution observed in August and September, an increase of algal biomass above the mussels (Figure 1.6 dashed line), may be explained by the resurgence of the toxic cyanobacterium Microcystis. A large bloom of Microcystis first appeared in August 1995 (Culver et al. 1999). Various researchers (Arnott and Vanni 1996, Heath et al. 1995, Holland et al. 1995, James et al. 1997) have attributed such blooms, including a subsequent bloom in 1998, to the excretion of nitrogen and phosphorus by zebra mussels. However, while Microcystis is therefore an integral part of the zebra mussel problem, it has two qualities which cause it to interfere with estimates of the impacts of the zebra mussels on the phytoplankton community: first, it migrates vertically in order to obtain the best light and nutrient regimens, and second, large colonies are rejected by zebra mussels and may reenter the water column (Vanderploeg et
al. 2001). Thus the phytoplankton maximum observed in Figures (1.6) is a product both of the alga's migration and the zebra mussels' preference not to consume it.

In addition, production is strongly influenced by and interacts with the intensity of mixing (Figure 1.11). Solving equation 1.13, the steady state production, $\mu_0 = 3.33 \text{ day}^{-1}$, for the well-mixed case. Numerically solving Equation 1.6 for the steady state, not completely mixed, $\mu$ is significantly less when mixing is low (Figure 1.11 a-c). As $K^*$ approaches 1, $\mu$ also approaches the steady state solution (Figure 1.11 d). However, typical phytoplankton replacement rates in Lake Erie range from 1-2 day$^{-1}$ (Graham et al. 1996). This makes the extreme diffusivities less likely to be representative of mussel impacts on the lake.

The link between increased cyanobacterial production and zebra mussel excretion, despite the importance of zebra mussel consumption, is becoming more evident (Arnott and Vanni 1996, Heath et al. 1995, Holland et al. 1995, James et al. 1997). The delivery of nitrogen and phosphorus excreted by the zebra mussels out of the boundary layer is limited by turbulent mixing, just as phytoplankton consumption in the benthos is limited by the algal delivery rate into the boundary layer. Thus, a measurement of nutrient gradients above the benthos, simultaneous with measurements of eddy diffusivities, is needed in order to get accurate estimates of the impacts of nutrient regeneration by the zebra mussels.
Conclusions

In summary, the series of field experiments in a near shore region of Lake Erie, produced diffusivity estimates that did not exceed $10^{-4}$ m$^2$s$^{-1}$ (averaged over 24 h periods) despite small storm events. Modeled algal depletion was strongly linked to the shape of the diffusivity profile, varying from 8 to 67% in a 24 h period, indicating both that the linear model for estimating algal consumption grossly overestimates zebra mussel consumption, and that there is a strong need for research into the shape of the diffusivity profiles in large lakes. I begin to investigate this problem in Chapters 2 and 3 using temperature gradient microstructure data. Vertical algal profiles taken during the sampling verify that algal depletion is strongly influenced by hydrodynamic forcing. I recommend that future efforts to estimate the impact of the benthos on the planktonic algal community be linked to estimates of algal productivity and hydrodynamic forcing.
<table>
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<th>Date</th>
<th>Water velocity (cm·s⁻¹)</th>
<th>Wind Velocity (m·s⁻¹)</th>
<th>z₀ (cm)</th>
<th>u* (cm·s⁻¹)</th>
<th>K_avg (x10⁻⁴ m²·s⁻¹)</th>
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Table 1.1. Physical parameters variation at our sample site. Mean (24 h) horizontal water velocity at 1 m was measured using the acoustic Doppler profiler, whereas mean wind velocity and direction were obtained from the Great Lakes Forecasting System (Kelly et al. 1998). The shear velocity, u*, and the roughness length, z₀, were calculated by regression using Eq.4 with 20 minute time intervals and averaging of the resultant shear velocities over 24 h for each date. Only profiles with r² > 0.5 were used to develop the average, and those dates with more than 50% of the profile regressions r² > 0.5 are included below. The mean diffusivity, K_avg was calculated from the shear velocity using Eq. 1.5 in the 5 m water column. The distribution of the shear velocities was examined with histograms and found to be normally distributed; confidence intervals were generated with normally distributed standard error in u*, below.
Figure 1.1. Seasonal algal patterns before (1988) and after (1989) zebra mussels became abundant in Lake Erie. After Wu and Culver (1991).
Figure 1.2. Location of the sampling site, between Gibraltar Island and Middle Bass Island in the western basin of Lake Erie.
Figure 1.3: Regression fit of time averaged horizontal velocities versus \( \ln z \), used in estimation of \( u_* \) and \( z_0 \) for 12 Sept 1995. This fit is for one 20 minute period \( (r^2 = .75) \).
Figure 1.4. Distribution of $K_z$ in the water column, given by Equation (1.5a-c) for a depth averaged diffusivity of $10^{-3} \text{ m}^2\text{s}^{-1}$ with a constant (a) and parabolic (b) diffusivity distribution with respect to depth.
Figure 1.5. Power spectrum of horizontal velocities, summer 1995. From left to right, peaks correspond to the storm cycle, 1\textsuperscript{st} mode seiche, second mode seiche, third mode seiche, and a combination of the fourth mode and cross basin seiche.
Figure 1.6. Algal distributions for early and late summer. The solid line indicates profiles before 1 August 1995 and the dashed line is after 21 August 1995.
Figure 1.7. Comparison of the time course of algal abundance according to equation (1), the totally mixed reactor model, and the "linear model." Zebra mussels are at the bottom of a 7 m water column, and are sufficiently abundant to process a volume of 25 m³·m⁻²·day⁻¹, beginning with an initial algal concentration of 2,800 mg·m⁻² wet weight. For Equation (1.1), I used a depth averaged $K_z = 10^3$ m²·s⁻¹ and a parabolic diffusivity distribution (see text).
Figure 1.8. Algal simulations without production with constant diffusivity with depth and changing diffusivity intensity (a) $10^{-3}$, (b) $10^{-4}$, (c) $10^{-5}$, and (d) $10^{-6} \text{m}^2\text{s}^{-1}$. The vertical lines are 2 h contours of time, with $B_0=400 \mu\text{g/L}$. 
Figure 1.9 Algal simulations with parabolic diffusivity profiles, with diffusivity intensity (a) $10^3$, (b) $10^4$, (c) $10^5$, and (d) $10^6$ m$^2$/s$^{-1}$. The vertical lines are 2 h contours of time, with $B_0=400$ μg/L.
Figure 1.10. Non-dimensional diffusivity, $K^*$, plotted versus the percent algae predicted cleared by the advection-diffusion simulations. The hollow points represent measured diffusivity $K$ at our site with corresponding predicted algal consumption. The dashed line at the top of the figure represents the completely mixed model, which equation 1.1 approaches at large $K$ or low $H$, when $K^*=1$. The results from Cloern (1991) include a source term, resulting in decreased clearing at low $K^*$. Ackerman et al. (2001) worked over a single mussel bed and estimated clearance from beginning to end, in addition to physical parameters.
Figure 1.11 Algal simulations with production source term and constant diffusivity profiles, with diffusivity intensity (a) $10^{-3}$, (b) $10^{-4}$, (c) $10^{-5}$, and (d) $10^{-6}$ m$^2$s$^{-1}$. The vertical lines are 2 h time contours, with $B_0=400$ μg/L. Here, μ is the numerical steady state algal reproduction solution (0% cleared in 24 h).
CHAPTER 2

PRIMARY PRODUCTION AND THE VERTICAL STRUCTURE AND TRANSPORT OF ALGAE

Phytoplankton are subjected to various stresses due to water motion. For example, vertical mixing can cause changes in exposure to incident radiation. The depth of the wind-mixed layer and diel thermoclines often determine the light climate of individual plankters, which can be different for plankters at the same depth due to the random nature of turbulence (Franks and Marra 1994). Time scales associated with photoresponse (the physiological adaptation of algae to varying light conditions) are often similar to various mixing time scales, on time scales of minutes to hours (MacIntyre et al. 2000). Therefore, mixing processes can often introduce a lag in photoresponses in an alga, which are adapted to light based on the light history of the alga, rather than the current light level to which they are exposed.
$^{14}\text{C}$ and dissolved oxygen bottle methods for estimating primary production will often be inaccurate when turbulent time scales are short. Bottles are often incubated over the course of the daylight period or, to obtain gross production, over a 24 h period. These time scales are long compared to time scales of photoadaptation. Shorter incubation times of two to four hours, while comparable to photoresponse time scales, require extensive extrapolation, to obtain a daily rate of photosynthesis and introduce larger error. Furthermore, fixed strings of bottles separate phytoplankton from physical water movements, whereas no such impediment exists in the water column.

Thus, models of primary production incorporating wind-mixing models and the consequent variation in light for the phytoplankton are now being used to estimate primary production. For example, several wind-mixing models predict mixing parameters from the ‘law of the wall’ dissipation estimates (Kamykowski et al. 1994, Franks and Marra 1994, Yamazaki and Kamykowski 1991). These models assume that the total shear stress applied due to the wall (the air-water interface in this case) exponentially decreases (relative to the free stream velocity) of horizontal water velocity away from the wall and until it approaches the free stream velocity, allowing estimations of the energy dissipation and mixing intensities. From these, time-dependent displacement of phytoplankters from an initial distribution can be estimated. So, phytoplankton production can be more accurately estimated from the more realistic light histories obtained for individual plankters.

While these wind-mixed production models can be used to obtain estimates of production in the ocean, they are of more limited utility in lakes. Conventional

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definitions of the wind-mixed layer (a layer defined by the temperature profile) often do not coincide with the actively turbulent mixing layer, defined by the layer receiving wind-induced energy dissipation (Yamazaki and Kamykowski 1991). For example, in a situation with low wind stress and a deep mixed layer, the wind shear stress may not penetrate to the base of the 'wind-mixed layer' and thus the Eckman layer may be thinner than the 'wind-mixed layer' or epilimnion (Denman and Gargett 1983).

In addition, diel thermoclines often prevent the mixing of algae throughout the photic zone, creating shallow wind-mixed layers. Thus, wind-mixed models cannot be applied throughout much of the photic zone, limiting the applicability of the models. Neither do these models take into account convective mixing (mixing induced by surface cooling), which can often dominate mixing in large lakes for much of the morning (McCune 1998). Therefore, we require a better method of measuring the vertical displacement of algae throughout the day by turbulent mixing than that produced by wind-stress based models.

In this chapter, I use the indirect thermal microstructure method for calculating energy dissipation, from which I obtain Lagrangian diffusivity estimates. I use measured photosynthetic parameters, including maximum photosynthetic rate, initial slope of the production-light curve, and photoinhibition, and apply random walk simulations of 20 minute duration using the diffusivity estimates to predict the light climate of the phytoplankton. I then use this model to estimate primary productivity in the central basin.
of Lake Erie from field measurements of thermal microstructure and light intensity with depth, comparing it to a standard in situ or static model.

Random Walk Model

The vertical movement of a plankter over time can be estimated using a random walk model, where the random jump follows a normal distribution with a mean of zero and a standard deviation \((2K_D \Delta n)^{\frac{1}{2}}\), where \(K_D\) is the Lagrangian diffusion coefficient, and \(\Delta n\) is a discrete time step (adapted from Yamazaki and Kamykowski 1991, physical portion). The mean square displacement of the plankter can be represented as

\[
< Z(t) >^2 = 2q\lambda t \tag{2.1}
\]

where \(q\) is the r.m.s (root mean square) turbulent velocity and \(\lambda\) is the integral scale of the turbulent velocity autocorrelation (Taylor 1921). Assuming turbulence is isotropic, that is, spherically symmetric, \(q\) can be related to the dissipation rate \(\varepsilon\) and the size of the large, energy containing eddies, \(l_e\) by

\[
\varepsilon = \frac{q^3}{l_e} \tag{2.2}
\]

Tennekes and Lumley (1972) express the Taylor microscale, \(l_T\), as

\[
l_T = \left(\frac{15\nu}{2\varepsilon}\right)^{\frac{1}{2}} q \tag{2.3}
\]

where \(\nu\) is the kinematic viscosity. Thus, provided the turbulence is isotropic, the integral time scale can be related to the Taylor microscale,
\[ \lambda = \frac{l_T}{q} = \left( \frac{7.5 \nu}{\varepsilon} \right)^{\frac{1}{2}} \]  

(2.4)

The Lagrangian diffusion coefficient can then be equated (Taylor 1921) to

\[ K_D = \left( \frac{1}{2} \right) \frac{d \langle Z(t) \rangle^2}{dt} = ql_T \]  

(2.5)

Assuming the energy containing eddy length is equivalent to the Osmidov length \( l_o \), a measure of eddy size, and

\[ l_s = l_o = \left( \frac{g}{\varepsilon N^2} \right)^{\frac{1}{3}} \]  

(2.6)

where \( N \) is the buoyancy frequency, defined by

\[ N^2 = g \frac{d \rho}{\rho \, dz} \]  

(2.7)

where \( g \) is gravity, \( \rho \) is the density of water, and \( d \rho / dz \) is the gradient of density with respect to depth. Substituting into the diffusivity equation (2.5)

\[ K_D = \left( 7.5 \right)^{\frac{1}{2}} \left( \frac{d \rho}{\rho \, dz} \right)^{\frac{1}{2}} \]  

(2.8)

which can be further simplified to

\[ K_D = 2.7 \varepsilon^{\frac{1}{3}} \nu^{\frac{1}{3}} N^{-1} \]  

(2.9)

where, again, \( \varepsilon \) is the energy dissipation, \( \nu \) is the kinematic viscosity, and \( N \) is the buoyancy frequency. However, this method creates an artificially large assemblage of particles in areas of low diffusivity. In addition to the random component, therefore, I have added an advective component to the random walk (Visser 1997, See Appendix B).
In order to estimate energy dissipation using the indirect method, I first compare the temperature gradient spectrum to the Batchelor spectrum of temperature gradient fluctuations (Gibson and Schwartz 1963)

\[ S(k) = \left( \frac{a}{2} \right)^{1/2} \frac{\chi_\theta f(\alpha)}{k_B D} \]  

(2.10)

where \( k \) is wave number, \( a \) is a universal constant, \( \chi_\theta \) is the temperature dissipation variance given by,

\[ \chi_\theta = 6D \int_0^\infty S(k)dk = 6D \left( \frac{\partial T'}{\partial z} \right)^2 \]  

(2.11)

where \( D \) is molecular diffusivity, \( T' \) is temperature fluctuation, \( z \) is depth, \( k_B \) is the Batchelor wave number, \( \epsilon \) is the kinetic energy dissipation rate, \( v \) is the kinematic viscosity, and \( \alpha = k k_B^{-1} (2a)^{1/2} \) is a non-dimensional wave number. \( f(\alpha) \) is defined by:

\[ f(\alpha) = \alpha \left( e^{-\frac{\alpha^2}{2}} - \alpha \int_0^\infty e^{-\frac{x^2}{2}} dx \right) \]  

(2.12)

Assuming the cutoff wave number, \( k_c = k_B \) then:

\[ \epsilon_B = \frac{k_c^4}{\nu D} \]  

(2.13)

the energy dissipation rate derived from the Batchelor spectrum. I then use this in equation (2.9) to calculate the diffusivity rate within the water column.
Light Distribution

Sunlight variation with time may be modeled using a cubic sinusoidal expression (Franks and Marra 1994)

\[ I_t = I_m \sin^3 \left( \frac{\pi t}{d} \right) \]  

(2.14)

where \( I_t \) is the light intensity at time \( t \), \( I_m \) is the maximum light intensity (at solar noon, e.g., 1000 \( \mu \text{mol} \cdot \text{photons} \cdot \text{s}^{-1} \cdot \text{m}^2 \), figure 2.1a), \( t \) is the time of day, measured from dawn, and \( d \) is the day length (e.g. 12 h). Light at any depth is then be modeled as a simple exponential decay equation, given that although PAR is a wide range of wavelengths, it still follows approximately to an exponential decay:

\[ I_n = I_t e^{-kz} \]  

(2.15)

where \( I_n \) is the light at depth \( z \) at time \( t \), \( k \) is an extinction coefficient (\( k=0.1 \) for example, figure 2.1b), which is calculated from PAR profiles where available and obtained from Secchi disk readings where not available, and \( I_t \) will be obtained from meteorological data (NOAA weather data).

The photosynthesis-irradiance curve for an algal assemblage can be described with two factors: the initial slope of the curve, \( \alpha \), and the light saturated maximum photosynthetic rate \( P_m \). Production is thus a function of the photosynthesis-irradiance curve and the light intensity:

\[ P(I) = f(\phi, P_m, I) \]  

(2.16)

where \( P \) and \( P_m \) are in terms of production per gram chlorophyll a (Figure 2.1a,b; Figure 2.2; Platt et al. 1980 ).
Combining the irradiance-specific production curve and the light extinction curve, I calculate the specific production of the cells from the random walk simulation. I then normalize the simulation results by dividing the results by predicted static light-photosynthesis curves.

I collected data at two times during 1997 for one week periods in May and August approximately 5 km offshore Fairport Harbor, OH, in the central basin of Lake Erie (Figure 2.3). Microprofiler data were collected using a free-falling instrument designed by Precision Measurements Engineering called a Self-Contained Autonomous Microprofiler (SCAMP). We used the SCAMP to sample temperature and temperature gradients, in order to estimate energy dissipation and $K_D$ (above, figure 2.4), as well as dissolved oxygen and fluorescence. The temperature, temperature gradients, and dissolved oxygen were sampled at 100 Hz, resulting in one-millimeter resolution, while the fluorescence was sampled at a ten-millimeter resolution. Profiles were divided into equal one-meter segments. Batchelor fits were performed using maximum likelihood estimates as in Ruddick et al. (2000). Secchi depths were measure in order to calibrate the light extinction model (equation 2.15).

Results

I found both a diel and seasonal component to the intensity of mixing in the central basin. Morning profiles, both in May and August were dominated by convection, as a continuation of the nighttime cooling (Figure 2.4a,c). Here, the vertical axis is depth.
from the surface for each panel. The first panel is the temperature profile, measured at 1mm intervals. The second panel is the energy dissipation, a measure of the input of energy into the system in each segment, with the x axis plotted on a logarithmic scale. The third panel is the buoyancy frequency (squared), a measure of stratification. In the May panels, without seasonal stratification, the axis ranges from 0 to 0.2, while in August, the seasonal thermocline needs an increase in the axis, from 0 to 0.5. May cooling overnight caused mixing from the surface to penetrate to near the depth of the developing seasonal thermocline at 10 m with dissipation estimates ranging from $10^5$ m$^2$s$^{-3}$ at the surface to $10^9$ m$^2$s$^{-3}$ one meter above the thermocline. In August, the mixing caused by the convection did not reach the thermocline, which had lowered to 14 m with dissipation ranging from $10^7$ to $10^8$ m$^2$s$^{-3}$. In both these cases, there was also a wind-mixing component that had a greater impact near the surface and less extension into the water column. I found that the input of solar heating caused secondary stratification to develop by noon in both May and August (Figure 2.4b,d). This stratification limited the penetration of energy to the top several meters, as seen is Figure 2.4b,d. The only input of energy affecting this region of the photic zone was due to the wind. However, there was a small input of turbulent energy due to the shear caused at the base of the seasonal epilimnion at 14-15 m (Figure 2.4d).

This mixing translates into varying trajectories of algal cells (Figure 2.5). Increases in mixing ($K_D$) result in larger average 'walks' through the water column. Each simulation of the released cells (500 cells) is then exposed to light, resulting in a variation in specific primary production that can then be compared to a static or immobile cell's
specific production (Figure 2.6a,b). In order to more easily interpret this, I have plotted the median (-o-) and quartiles (---+) for each depth over all of the simulations.

Normalizing the results by the results predicted by a non-mixing model, I will show the relative impact of the mixing at each specific depth (Figure 2.7a-d). In these figures, the solid line again represents the static case, results to the left of the line representing decreases in production and to the right increases, relative to the static case. In May, there was an increase in relative production, increasing from 0.5 m, where the production was equal to the static case, to a 40% increase by three meters through the rest of the photic zone (Figure 2.7a). By afternoon, increased light levels and the near-surface diel thermocline caused photoinhibition beyond that predicted by the static case (Figure 2.7b). This region extended to two meters with a 15-20% increase in the median production below four meters. August morning normalized production showed a similar pattern to the May morning profiles (Figure 2.8a). This is expected due to the similarity in energy dissipation profiles, discussed above. However, due to increased light penetration in the clear-water phase (a seasonal reduction in algal biomass, Wu and Culver 1991), there was an increased region of photo inhibition at the surface. The day simulations were similarly exaggerated at the surface by the increased light penetration, and there was greater impact in the lower water column (Figure 2.8b). However, total production was strongly influenced by the penetration of light into the water column and its interaction with the abundance of chlorophyll (Figures 2.9 a,b and 2.10 a,b). Total areal production was therefore similar in the mixing and static models in both May and August.

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Discussion

Convective events characterized the morning profiles in both May and August. Despite the increasing sun intensity, air temperatures were cool enough to sustain convection through the morning, until the sun increased the thermal stratification (Figures 2.4 a-d). The dissipation produced by convection was one to several orders of magnitude greater than the wind mixing evident during the day profiles (Figure 2.4a,c). In addition, the dissipation extended much deeper into the water column (to 9-10 m in May and 12-13 m in August).

Mixing processes in large lakes are often dominated by these events. Imberger and Ivey (1991) investigated convection using temperature gradient microstructure. They found that, unlike mechanically driven mixing (for example, wind mixing), the intensity of the convection is related to the distance from the source of cooling (negative buoyancy). Thus, despite the linear decline in energy input by the convection they predict as the mixed layer is penetrated (to 90% of the mixed layer depth where a convective plume is predicted to have lost all its energy) convection can still allow deeper penetration than mechanical forcing mechanisms. They found that convection is one of four forcing mechanisms controlling mixing in lakes. Ivey and Patterson (1984) also investigated the role of convection in lakes, particularly in Lake Erie. Using season-long simulations, they determined that convection is a dominant influence on the distribution of temperature (and thus mixing) within the upper mixed layer (i.e. the epilimnion). Other constituents both dissolved, such as oxygen (Patterson et al. 1985), and particulate, as in the algae in this study, must also be transported with temperature in the water.
column (Batchelor 1959). McCune (1998) found that Lake Erie convection caused mixing of intensities (eddy diffusivities of order $10^{-2}$ m$^2$s$^{-1}$) similar to storm events and occurred nightly, rather than on the episodic basis characteristic of storms.

Warming of surface waters can greatly impact the penetration of turbulent energy into the water column. I found near surface thermoclines in all profiles collected, excepting those collected in storm events. The resulting increase in near surface stratification, as evidenced by the buoyancy frequency separates the near surface waters from the deeper water (Figure 2.4b,d). MacIntyre (1993) investigated this phenomenon, also using a SCAMP, in shallow (~3m), lakes and found that near surface thermoclines (1-2m) could energetically divide the water column into actively mixing regions and regions controlled by buoyancy (stratification). Lorke (1998), studied a combination of temperature gradient and shear microstructure in Lake Muggelsee, a large, shallow lake, found that diel changes in temperature structure cause large changes in forcing mechanisms. These mechanisms actually cause increases in near surface mixing, by introducing new sources of shear and differential flow. However, as MacIntyre (1993) as well as this study (Figure 2.5d) found, this structure can separate this upper region and its sources of mixing from deeper waters. Xenopoulos et al. (1998) found that near-surface thermoclines can have direct impact on algal populations through controlling the light climate the algae experience. They found that the onset of a near surface thermocline (~2.5 m) coincided with a negative correlation between UVB radiation and phytoplankton biomass in Lac Cromwell, Quebec. This correlation was absent before the
thermocline formation and indicated that thermal stratification and turbulence are key components in UVB impacts on phytoplankton.

While convective cooling is an important, if not the most important, contributor to mixing in temperate lakes and Lake Erie in particular, the development of near-surface thermoclines stops this process early in the day, typically by 10 am at the sample site. Development of near-surface thermoclines each day leaves most of the photic period to be dominated by other forcing factors, notably wind mixing. The peak light intensity period, from 10 am to 2 pm was dominated by near surface wind mixing with little penetration of mixing events into the water column (Figure 2.4b,d). Xenopoulos and Schindler (2001) investigated the role of wind in near surface thermoclines in the 39 boreal lakes in the Experimental Lake Area. They found that wind velocities were an important factor in controlling the formation of near surface thermocline. High wind velocities prevented the formation of these transient thermoclines and thus allowed deeper mixing. The ultimate examples of wind mixing in Lake Erie occurred during two storm events, one each in May and August. Though sampling was unsafe during the peak of these storms, sampling during the early and later portions of the storms indicate the importance of these mixing events. As these types of events correspond to decreased light levels (i.e. clouds) the immediate importance to photosynthesis is minimal. Long-term impacts such as redistribution of nutrients and oxygen, however, are important. I will examine the impacts of these events in detail in Chapter 3.
The normalized primary production profiles (figures 2.7 and 2.8) also had seasonal and diel components that corresponded to changes in the mixing mechanisms. I found a large increase in relative production in morning profiles, characterized by deep and strong convective mixing, and lower light levels (Figure 2.7a, Figure 2.8a). In May, the increase was approximately 40% for much of the photic zone. However, there is a near surface decline related to surface algal cells mixing away from the light without an opportunity for increased light since the surface is reflective. In August, morning profiles also showed a 40-50% increase for much of the water column. The near surface decrease was more pronounced due to the increase in water clarity and decreased buoyancy frequency. May day production profiles were characterized by strong surface photoinhibition, a decrease in relative production of approximately 5-8% compared to the static case (Figure 2.7b). Much lower increases in relative production were apparent lower in the water column, with a peak increase of ~18%. I found a large increase in production in August noon profiles below the surface thermal stratifications (Figure 2.8b). The decrease in mixed layer stratification combined with shear at the base of the mixed layer serves to resuspend the algal particles toward the photic zone. However, despite the 250-300% increases in these lower waters, this type of mixing would have much less of an impact than the surface mixing on the total production due to the reduced light levels (an increase of 250% over a very small value is still small). This is evident in the total production in both May and August, comparing the static to mixing models (Figures 2.9 a,b and 2.10 a,b).
In smaller lakes, the difference between static experiments and the photosynthesis estimates incorporating the light climate of actual phytoplankton should be less. Smaller lakes experience less mixing and often have less light penetration, both factors which decrease the depth of the mixed layer (Fee et al. 1996). In larger lakes, the importance of light penetration lessens as wind mixing, with an increased fetch, becomes a dominant factor and the mixed layer depth increases (Mazumder and Taylor 1994). Reduced mixed layer depth in turn reduces the vertical trajectories of the phytoplankton and the impact of mixing. While mixing in these cases is less important to photosynthesis, it can still impact phytoplankton in other ways. Near surface thermoclines can trap phytoplankton in high light waters, that may increase the ability of the algae to photosynthesize, but increased UV radiation may rapidly destroy or inhibit these phytoplankton (Xenopoulos et al. 1998, Xenopoulos et al. in prep). In addition, the decreased mixing in these smaller lakes, relative to large lakes, is comparatively more important in the delivery of nutrients within the photic zone. However, this mixing can be too weak for cross thermocline mixing, thus limiting the supplying of nutrients in the photic zone to precipitation and runoff (Fee et al. 1994)

Conclusions

The use of measured energy dissipation with a phytoplankton random walk model is an important step in finding tools to accurately measure photosynthesis in lakes, and in parallel, the upper ocean. Using this method, I have found that phytoplankton production may be underestimated by traditional methods from 15% to 50% in some regions of the water column. This may be compounded by underestimation of production in the $^{14}$C
methods used in most primary production experiments (Smith et al. 2000, Riegman and Coljin 1991). In addition, there is more surface inhibition of production, especially when near surface algae are trapped during strong diel stratification events. This increase in production may explain the resistance to algal sinks such as the invasive zebra mussel and the persistence of traditional seasonal algal cycles (Wu and Culver 1991). In addition, I have incorporated an advective component into the model in order to avoid artificial conclusions that have plagued earlier work in this field (Visser 1997, Yamazaki and Kamykowski 1994, Kamykowski et al. 1994, Franks and Marra 1994). However, while application of these types of models, accounting for the impacts of mixing, to aquatic systems is appropriate for accurate estimates of primary production, in this system I found that while there is strong evidence for mixing caused changes production with depth, they do not strongly influence total water column productivity.
Figure 2.1 a and b. Diel light profile with surface noon value of 1000 \( \text{\mu mol} \text{ photons s}^{-1} \text{ m}^{-2} \) and an extinction coefficient \( k=0.1 \).
Figure 2.2. Variation of specific production as a function of light intensity. Data used to calculate this relationship were taken from Patterson et al. 1985.
Figure 2.3. Sample site near Fairport Harbor, OH in the central basin of Lake Erie.
Figure 2.4 a-d. Energy dissipation measurements for (a) morning and (b) day May (1997) and (c) morning and (d) day August (1997). The plot is a series of boxes with the ends of each box the quartiles, a vertical line at the median and outliers (results outside the quartiles) given by ' +'s.
Figure 2.5. Temperature profile taken using the SCAMP at 1330, 23 May 1997.
Figure 2.6. Random walk for one cell released at the surface (0 cm) with a May, morning mixing regime. N=500 simulated cells were released every 10 cm.
Figure 2.7. Specific production simulations with quartiles (---+) and median (—o—) estimates plotted versus depth for morning and day profiles with static case line (solid dark line), May 1997.
Figure 2.8 a and b. Specific production estimates normalized by static line (solid vertical line at 1) for May morning and day profiles. The light lines (—–) are the quartiles and solid (—o—) the median estimates.
Figure 2.9 a and b. Specific production estimates normalized by static line (solid vertical line at 1) for August morning and day profiles. The light lines (—+-) are the quartiles and solid (–o–) the median estimates.
Figure 2.10 a and b. Total production predicted by static (dashed) and mixing (solid) models along with total areal production for 21-23 May 1997.
Figure 2.11 a and b. Total production predicted by static (dashed) and mixing (solid) models along with total areal production for 6-9 August 1997.
CHAPTER 3

OXYGEN DYNAMICS IN THE CENTRAL BASIN OF LAKE ERIE

Extensive anthropogenic eutrophication caused the Lake Erie of the 1970s to be referred to as the ‘lake that died’. One of the main causes of this was the loading of phosphorus into the lake, estimated to exceed 25 thousand metric tons (Janus and Vollenweider 1981). While periodic anoxia has always existed in Lake Erie (Delorme 1982), as early as 1960, eutrophication was recognized as a problem leading to increased occurrences of anoxia in the central basin (Carr 1962). Eutrophication, and the water quality issues associated with it including central basin hypoxia, led to the implementation of the Great Lakes Water Quality Agreement (IJC 1978). Bertram (1993) investigated the link between the eutrophication and hypolimnion hypoxia from 1970-1991. He found that the reduction in phosphorus inputs coincided with reductions of total phosphorus (TP) in the water column. He also concluded this led to a slight downward trend in oxygen depletion (amount of oxygen lost in the hypolimnion per time) across the same period.
However, while eutrophication may be a large factor in hypolimnion hypoxia, physical forcing and oxygen transport may be more important. Rosa and Burns (1987) found that while there has been an increase in oxygen depletion related to eutrophication from 1929 to 1980, the physics and shape of the lake might be more important. Charlton (1980) first looked at this relationship, and the relationship between hypolimnion thickness and oxygen depletion. As might be expected, he found that decreased hypolimnion thickness increased the oxygen depletion. Further, this relationship held after the frequency of anoxia had decreased following the reductions in TP in the 1980s (Charlton 1987, Charlton et al. 1993).

Patterson et al. (1985) developed the most recent comprehensive summer oxygen budget for the Lake Erie central basin in the summer. They found that six factors influence the vertical oxygen budget in the central basin: 1) Vertical mixing; 2) exchange across the air-water interface; 3) photosynthesis; 4) community respiration; 5) sediment oxygen demand (benthic respiration); and 6) horizontal transport.

Parameterizing these influences on the oxygen budget, Patterson et al. were able to predict changes in oxygen profiles, estimate the relative importance of these factors under various environmental conditions, and determine that mixing caused by shear at the base of the hypolimnion was the most important parameter in delaying the onset of anoxia in the hypolimnion. However, since this budget was tested in 1980, the trophic status of the lake has undergone profound changes, primarily due to the reduction in
phosphorus loading into the lake and the introduction of zebra mussels, both of which may have a strong influence on sediment oxygen demand. There has been continued reduction in loading of phosphorus into the lake (Dolan 1993). However, anoxic conditions periodically occur and internal nutrient loading due to the exotic dreissenids may be increasing (James et al. 1997). Arnott and Vanni (1996) demonstrated that the abundant mussels excreted nitrogen and phosphorus at high rates and low N:P levels, which may shift the trophic status of the lake toward the conditions present in the 1960s and 1970s. Thus, the question of the relationship of the physics of the oxygen budget to the lake oxygen dynamics again becomes important.

Therefore, I first test the importance of hypolimnion thickness on a critical measure of dissolved oxygen, hypolimnion oxygen depletion. Oxygen depletion, a measure of the total loss of oxygen in the hypolimnion over time (expressed per unit area) gives an understanding of the biological oxygen demand of the hypolimnion, relative to the amount of oxygen available. This demand is often dominated by the decomposition of algae from the epilimnion at the sediment water interface. Thus there is a flux of oxygen into the bed. If the hypolimnion were thoroughly mixed, we would expect the oxygen depletion to be independent of hypolimnion depth. However, if it is not well mixed, a strong oxygen gradient can develop, limiting the supply of oxygen to the bed. If this were true, the differing mixing condition brought about by differing hypolimnion thickness would cause dependence between the thickness and oxygen depletion. I then examine the processes that influence the hypolimnion thickness.

Second, I test the role of transport processes, across time and the variation with depth, in

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oxygen transport in the central basin using a short-term oxygen budget at differing times of day and I quantify the relative importance of different transport processes.

Field Sampling

The USEPA has collected data in the Lake Erie central basin since 1968 during two cruises, spring and summer, with less regular sampling dating into the 1940s. The sampling is conducted over ten sites within the basin (Figure 3.1). The sampling consists of oxygen, chlorophyll a, and temperature profiles throughout the water column. In addition, Winkler oxygen titration and total and soluble reactive phosphorus are analyzed at the top and bottom of both the hypolimnion and epilimnion with water samples collected via a rosette of Niskin bottles.

In addition, my own sampling with the SCAMP during the spring and summer of 1997 (described in detail in chapter two) will also be used. However, due to instrument failure (a close encounter with hard substrate!), oxygen data are not available during the May cruise. In 1999, SCAMP data (again, described above) were collected aboard the USEPA Lake Guardian, during the summer USEPA cruise to the USEPA’s standard central basin oxygen monitoring stations (Figure 3.1). This SCAMP sampling occurred at the same time as the EPA’s annual summer oxygen survey (described above).

The Oxygen Budget

As mentioned above, the six factors in the vertical oxygen budget in the central basin are: 1) Vertical mixing; 2) exchange across the air-water interface; 3)
photosynthesis; 4) community respiration; 5) sediment oxygen demand (benthic respiration); and 6) horizontal transport. I model the diel oxygen budget in the summer and compare current and historical USEPA oxygen depletion data in order to obtain a historical perspective on the problem and to investigate the importance of vertical transport in the hypolimnion oxygen problem.

In order to solve this system, I first describe it with the differential equation:

\[
\frac{\partial O}{\partial t} - \frac{\partial}{\partial z} \left( K \frac{\partial O}{\partial z} \right) + \mu_z - r_w = 0
\]  

(3.1)

where \( O \) is the dissolved oxygen concentration, \( t \) is time, \( z \) is depth, \( K \) is the vertical mixing coefficient, \( \mu_z \) is the production of oxygen through photosynthesis, and \( r_w \) is water column respiration. The surface and bottom of the water column are described by the boundary conditions:

\[
K \frac{\partial O}{\partial z} = -r_s
\]  

(3.2a)

\[
K \frac{\partial O}{\partial z} = F
\]  

(3.2b)

where \( r_s \) is sediment oxygen demand and \( F \) is the flux of oxygen at the surface (see Equation 3.11).

**Vertical Mixing:** In order to model the vertical transport of a dissolved constituent, such as oxygen, we must first obtain the kinetic energy equations from the total energy equation (as derived from the Navier-Stokes equations, after Osborn 1980):
\[
\frac{\partial u_i}{\partial t} + u_j \frac{\partial u_i}{\partial x_j} = -\alpha \frac{\partial p}{\partial x_i} + 2\epsilon_{ijk} \Omega_j u_k - g \delta_{i3} - \nu \frac{\partial^2 u_i}{\partial x_j \partial x_j}
\]  

(3.3)

where \( u_i \) is the velocity vector, \( t \) is time, \( p \) is pressure, \( \alpha \) is the specific volume, \( x_i \) is the distance vector (with \( x_3 \) upwards vertically), \( \epsilon_{ijk} \) is the three dimensional permutation tensor, \( \Omega_j \) is the rotation vector, \( g \) is gravity with the Kronecker \( \delta_{i3} \) (meaning gravity applies only in the vertical), and \( \nu \) is the kinematic viscosity of water. If the velocity, specific volume and pressure are written as a sum of a mean plus a fluctuation, such as 

\[ u_i = \bar{u}_i + u_i^' \],

and multiplying times the mean flow, \( \bar{u}_i \), we can write the mean kinetic energy equation as (Kundu 1990)

\[
\frac{\partial}{\partial t} \frac{1}{2} \bar{u}_i \bar{u}_i + \bar{u}_j \frac{\partial}{\partial x_j} \frac{1}{2} \bar{u}_i^2 = -\bar{u}_i \frac{\partial p}{\partial x_i} - \bar{u}_i g + \nu \frac{\partial^2 u_i}{\partial x_j \partial x_j} - \bar{u}_i u_j \frac{\partial u_i}{\partial x_j}
\]  

(3.4)

If the viscous effects on the mean motion are ignored, the velocities considered nondivergent and the specific volume term written as a product of the means, we can simplify Equation (3.4) to

\[
\frac{\partial}{\partial t} \frac{1}{2} \bar{u}_i \bar{u}_i + \bar{u}_j \frac{\partial}{\partial x_j} \frac{1}{2} \bar{u}_i^2 = -\bar{u}_i \frac{\partial p}{\partial x_i} - \bar{u}_i g - \frac{\partial}{\partial x_j} \left( \frac{u_i u_j u_i^'}{A} + \frac{(u_i^' u_i^)}{B} \right) + \frac{\partial \bar{u}}{\partial x_j}
\]  

(3.5)

The left side represents the rate of change of the mean kinetic energy (MKE). The right represents: (A), the work done by the pressure gradient minus the hydrostatic gravitational pressure gradient; (B), the divergence of the mean advection of the turbulent correlation; and (C), the loss of mean flow to turbulence, consisting of the mean shear times the Reynolds stress.
Repeating the above procedure on equation (3.1), instead multiplying by the fluctuation around the mean flow, $u'$, we can obtain the turbulent kinetic energy equation:

$$
\frac{\partial}{\partial t} \frac{1}{2} \overline{u' \bar{u}'} + \bar{u} \frac{\partial}{\partial x_j} \frac{1}{2} \overline{u' \bar{u}'} = u' \alpha \frac{\partial \rho}{\partial x_j} - \overline{(\alpha + \alpha')} \frac{\partial \rho}{\partial x_j} + \nu \frac{\partial}{\partial x_j} \overline{(u' \bar{u}')} - \frac{1}{2} \nu e' e' - \overline{(u' \bar{u}')} \frac{\partial \bar{u}'}{\partial x_j}
$$

(3.6)

where $e' = \left( \frac{\partial u'_j}{\partial x_i} + \frac{\partial u'_i}{\partial x_j} \right)$. The left side is, analogous to above, the rate of change of the turbulent kinetic energy (TKE). The right side represents (a), buoyancy production; (b), the correlation of the turbulent velocity times the turbulent pressure gradient; (c), the divergence of the viscous diffusion of the TKE; (d), the viscous dissipation, hereafter given by $\varepsilon = \frac{\nu}{2} e' e' ;$ and (e), the Reynolds stress times the mean shear (this is a production term, gained from the loss in the MKE equation, hence the (-)).

Assuming that the dissipation here described is due to random turbulence (causing mixing) rather than oscillations such as waves, and neglecting the pressure velocity correlation and the turbulent diffusion terms, applying Osborn (1980)'s assumption that the turbulence is homogeneous, meaning that the turbulence statistics do not vary in space. Under this assumption, divergences of averaged quantities are zero), we can assume that there is a steady state situation balancing the TKE production, dissipation and buoyancy production (and that $\overline{u' \alpha \partial \bar{u} / \partial x_j} \equiv (g / \rho) \bar{u}' \rho'$, Osborn 1980):
\[-(u_i'u_j') \frac{\partial u_j}{\partial x_j} = -\epsilon - \frac{u_3' \rho' g}{\bar{\rho}}\] (3.7)

where \(\rho\) is the density. The flux Richardson number, \(R_f\), is the ratio of the buoyancy flux to TKE production. For the steady state approximation to hold true, \(R_f\) must be less than a critical value of \(R_f = 0.15\) (theoretically predicted by Ellison 1957 and confirmed experimentally by Britter (1974)).

Analogous to Fickian diffusion, Boussinesq suggested that turbulent stress may be represented after Kundu (1990):

\[-u_i'u_j' = \nu_e \frac{du_i}{dx_j}\] (3.8)

where \(\nu_e\) is an eddy viscosity, a measure of the intensity of the turbulent transport of momentum. This transport of momentum is related to the transport of a conserved quantity, such as density, by \(K_e = \nu_e \text{Pr}^{-1}\), where \(\text{Pr}\) is the turbulent Prandtl number (Boegman et al. 2000). This eddy diffusivity, \(K_e\) (this is often called \(K_e\) elsewhere, but is here called \(K_e\) to represent the ‘eddy’ of eddy diffusivity and to be consistent) may be further defined as (Osborn 1980):

\[K_e = \frac{g u_3' \rho' \bar{\rho}}{N^2}\] (3.9)
where N is the buoyancy frequency (defined in chapter 2). Given the above definitions of $R_f$ and $\epsilon$, we can simplify (3.7) to:

$$K_\epsilon = \frac{R_f \epsilon}{(1 - R_f)N^2} \tag{3.10}$$

Using the upper value for $R_f = 0.15$, we find that an upper limit is $K_\epsilon = 0.2 \epsilon / N^2$, where 0.2 is referred to as the ‘mixing efficiency’. As the dissolved oxygen makes no significant contribution to the density of the water, this density transport model thus, also describes the oxygen transport (Batchelor 1959).

**Surface flux:** The surface of the water column may be both a source and a sink of dissolved oxygen. Togersen et al. (1982) suggest this flux may be modeled as dependent on a gas transfer velocity, $W_g$, and the difference between the surface water concentration, $C_s$, and the saturated concentration for the water temperature, $C^*$:

$$F = W_g (C^* - C_s) \tag{3.11}$$

where $F$ is the flux of oxygen across the air-water boundary. The gas transfer velocity is in turn dependent on the friction velocity, a measure of shear, at the water surface:

$$W_g = \frac{1}{\beta} \left( \frac{D}{\nu} \right)^{2/3} u_* \tag{3.12}$$

where $D$ is the molecular diffusivity of oxygen in water, $\nu$ is the molecular viscosity of water, $u_*$ is the shear velocity of the water (derived from microstructure measurements), and $\beta = 8.75$ is a constant (Connor 1983). $C^*$ is solely a function of temperature and altitude and may be determined as in Mortimer (1981).
Photosynthesis: Photosynthesis was determined using a photosynthetic model parameterized to photosynthetron data (Patterson et al. 1985). The model will include parameters for photoinhibition, maximum photosynthesis and quantum efficiency (as described in Equation 2.16) in a manner described by Platt et al. (1980):

\[ P = P_s \left( 1 - \exp\left(-\frac{\alpha I}{P_s}\right) \right) \exp\left(-\frac{\beta I}{P_s}\right) \]  (3.13)

where \( P_s \), \( \alpha \), and \( \beta \) are the maximum photosynthetic value, quantum efficiency, and photoinhibition parameters, and \( I \) is the intensity of light as a function of depth. I will use the light history of plankters at each depth based on microstructure as in chapter 2. The variation of light across time and depth is described in chapter 2 (above), and a depth specific chlorophyll a value is used obtained from the fluorometer.

Community respiration: Patterson et al (1985) describe community respiration, after Ganf (1980) as a function of maximum photosynthesis (above) in the epilimnion and metalimnion or thermocline region. This relationship assumes that the significant fraction of the community respiration is in fact due to phytoplankton, rather than heterotrophs. They also estimate the hypolimnion respiration is approximately 1/5 the epilimnion specific respiration in this lower light region. We will obtain actual Lake Erie values for these estimates when available and use these estimates otherwise.

Sediment oxygen demand: Sediment respiration, often indicated as responsible for central basin anoxia, is modeled as a fixed flux of oxygen at the bottom boundary of the hypolimnion related to historic estimates of central basin sediment oxygen demand obtained from the literature (Snodgrass and Fay, 1987; Snodgrass 1987).
*Horizontal transport:* Although in some cases horizontal advection may be a significant factor, I will assume for our purposes that the central basin is homogeneous horizontally. To include these spatial effects, the effects of depletion were averaged over the ten EPA sampling stations (Figure 3.1).

These five described parameters are incorporated into simulations modeling the dynamics of oxygen in the central basin. The transport model, Equations (3.1)-(3.3) is solved numerically with the surface and benthic fluxes of oxygen as boundary conditions and using diffusivities obtained from the SCAMP measurements using Osborn’s method (described above in detail). I then make a historical comparison with the EPA oxygen depletion data (from Bertram et al. 1993, and Charlton 1980) data and attempt to determine the current status of the restoration of Lake Erie, and particularly, which process is most important for central basin hypoxia.
Results

Oxygen concentrations decreased across our sampling period (figure 3.1). Here, areal oxygen concentration (g/m²) is the integration of the volumetric concentration (g·m⁻³) over depth. Each block of samples represents a series of samples from one day, with a bar indicating the extent of the block. Between days, oxygen concentrations declined, with the period from 6 August, across a storm event on 7 August, resulting in a 35% decrease. A smaller decrease was recorded overnight from 8 to 9 August.

Eddy diffusivities from the morning profiles closely followed a convective pattern, characterized by a linear decrease (on this logarithmic axis) in diffusivity from the source of the buoyancy (i.e. the surface, Figure 3.2a). Here the solid line within the boxes gives the median diffusivity, while the boxes give the quartiles and the whiskers the greatest and least values. The values at the surface ranged from $10^{-5}$ to $10^{-2}$ m²·s⁻¹ with a median of $10^{-3}$ m²·s⁻¹. The values at the thermocline (14.5m) were very low due to the strong seasonal stratification, indicating little cross thermocline transport. However, in the hypolimnion, there was significant mixing, which I attribute to bottom currents initiated by seiche activity.

By midday, the profiles resemble more closely the profile expected of a wind-dominated system, with a logarithmic decrease in diffusivity (Figure 3.2b). Values at the surface ranged from $10^{-5}$ to $10^{-6}$ m²·s⁻¹ decreasing to below $10^{-6}$ m²·s⁻¹ by 6 m. Diffusivities at the thermocline approach $10^{-7}$ m²·s⁻¹, while the diffusivities caused by hypolimnion currents are still strong, but limited to the base of the hypolimnion.

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The morning oxygen budget control (that is, with no modifications of the
diffusivity profile) was characterized by strong depletion in the hypolimnion, especially
near the bed (figure 3.3a). In this figure, each vertical line is four hours from the initial
volumetric DO concentration. Due to the strong convective mixing (figure 3.2), the
epilimnetic oxygen concentration is evenly distributed with depth, with a slight decline
near the metalimnion. With the addition of increase convection (doubling the surface
buoyancy production by the addition of energy dissipation of the form
\[ \epsilon = b_s \left( 1 - \frac{1}{H} \right) \]
where \( l \) is the distance from the surface, \( H \) is the thickness of the
mixed layer and \( b_s \) is the surface buoyancy production) this decline is eliminated, with no
effect in the hypolimnion (figure 3.3b). Increased wind-shear (doubling the surface
friction velocity, adding a dissipation profile \( \epsilon = \frac{u^2}{l} \), with \( l \) again the distance from the
surface and \( u^* \) the surface friction velocity) at the surface caused no change in the oxygen
profile, as the wind energy did not penetrate deep into the epilimnion (figure 3.3c). The
addition of increased bottom shear (again, doubling the friction velocity, this time at the
bottom) did not change the hypolimnetic oxygen profile, indicating that there was already
significant mixing keeping the hypolimnion well mixed.

Afternoon control profiles were characterized by uniformly distributed oxygen in
the epilimnion, decreasing oxygen across the thermocline, and a decreasing profile within
the hypolimnion (figure 3.3a). Increasing the convective mixing and wind shear had no
effect, as the surface waters were already well mixed (figure 3.4 b and c). Neither of
these processes had enough energy to increased cross-thermocline transport or affect the
hypolimnion. However, increasing the bottom shear, though afternoon diffusivity profiles indicated there was near bottom mixing (figure 3.2b), had the effect of removing a limit on the oxygen consumption of the sediment (figure 3.4d).

A storm occurred on 7 August, consisting of 2-3 m waves and 10-knot winds along the fetch of the lake out of the northeast. This resulted in a significant lowering of the thermocline, from 14.8 m to 15.9 m (figure 3.5). We were unable to sample during this event due to safety concerns. However, we sampled during the beginning of a similar event on 21 May 1997, with 5-7’ waves and 23-knot winds resulting in strong mixing (figure 3.6). In this figure, strong energy dissipation (a measure of energy available for mixing; see chapter 2) approaching $10^{-5} \text{ m}^2\text{s}^{-1}$ was evident from the surface to the bottom, erasing the developing seasonal thermocline. There was virtually no stratification ($N^2 < 0.05\text{s}^{-2}$) and the temperature profile varied less than 0.1 °C across the water column.
Discussion

The link between diffusivity and hypolimnion thickness was first suggested by Charlton (1980). He linked apparent changes in oxygen depletion, formerly linked only to eutrophication, with changes in the thickness of the hypolimnion. A thinner hypolimnion results in greater oxygen depletion (as a change in concentration), as there is less total oxygen available. Bertram (1993) and Charlton et al. (1993) extended this work to include more recent data, after the introduction of the Clean Water Act. Combining these data, it is apparent that not only is Charlton’s theory holding into the 1990s, but it is even more strongly supported by the recent data (figure 3.7). This may indicate that the occurrence of anoxia in the central basin may now be more strongly linked to physical forcing than to eutrophication. These data also are indicative that there are other processes at work, due to the weak correlation (Figure 3.7)

Diel changes in oxygen concentration are highly variable (figure 3.1). This is in part due to internal seiching, which can alter the thickness of the hypolimnion, and changes in the light climate and primary production. However, the largest decrease in areal oxygen concentration corresponded with a large storm event during the period of 6 to 8 August. A 35% reduction in oxygen corresponded not only to a day with little light penetration due to the storm, but to the reduction in the thermocline from 14.8 to 15.9 m, an 18% reduction in hypolimnion volume. While this relationship may seem obvious, it has powerful implications for the mixing environment in the hypolimnion. Because the primary source of oxygen depletion is the sediment, weaker hypolimnetic mixing would couple the oxygen demand, and thus the oxygen depletion, to the transport of oxygen and
the intensity of the mixing. Therefore, Charlton (1980)'s theory implies that there is significant hypolimnetic mixing. The oxygen budget confirms this relationship (figure 3.4 a and d). Weaker bottom mixing (figure 3.4a, control) results in a oxygen gradient developing across the thickness of the hypolimnion, limiting the oxygen supply to the sediment. Increasing the bottom mixing can eliminate it, as indicated by the sharpening of the gradient near the bed (figure 3.4d).

The oxygen budget was also affected by variations in the other parameters, including wind and convective cooling. Convective mixing (figure 3.2b, 3.3b) caused the epilimnetic oxygen concentration to be evenly distributed with depth, while wind-shear had little effect on the oxygen profile, as the wind energy did not penetrate deep into the epilimnion (figure 3.2c, 3.3c). As noted above, when bottom shear was large, additional bottom shear had little impact on the hypolimnetic oxygen profile (figure 3.2 a and c). However, during periods of decreased or limited bottom shear, increases in bottom shear removed developing oxygen gradients (figure 3.2 and 3.3 a and d).

Patterson et al. (1985) found that these three physical parameters dominated the transport of oxygen in the central basin, with the addition of cross thermocline transport. We found no evidence of these events. Instead, we found hypolimnion water entrained into the epilimnion through storm events, rather than the reverse (epilimnetic water entraining into the hypolimnion; figure 3.5 and 3.6). This indicates that large mixing events will decrease the volume, and hence the oxygen, in the hypolimnion (figure 3.1). While rare 'reverse entrainment' events do occur (Boyce et al. 1982) and can greatly
increase the available hypolimnetic oxygen by mixing metalimnetic and epilimnetic waters into the hypolimnion (Lam et al. 1987), these events are rare.

Lake Erie has undergone profound changes since the 1980s when oxygen transport was first addressed. Ludsin et al. (2001), in a study of fish community dynamics, found that the recent reduction in eutrophy has encouraged the rehabilitation of the Lake Erie fish community. They also found increases and restoration of ‘intolerant’ species, those species strongly affected by chronic anoxia. The introduction of the zebra mussel also has been important in recent lake dynamics. While Wu and Culver (1991) found that the invasive mussel did not affect algal seasonal dynamics, recent *Microcystis* blooms in the western basin may ultimately be connected to them (Babcock-Jackson et al. 2002). Effler et al. (1998) reviewed the relationship between zebra mussels and oxygen in the Seneca River, NY. The introduction of the mussel caused decreases from the pre-mussel, oxygen saturated, waters to below NY State oxygen minimums.

While the stratified central basin is a vastly different system, these differences may cause even greater impacts as the mussels spread onto the central basin soft substrate (Haltuch et al. 2000). Unlike a riverine system, the August central basin is separated by a strong seasonal thermocline into the epilimnion and hypolimnion. Thus, the effects of the benthic mussels will be confined to the hypolimnion. This both limits the access of the mussel to the planktonic algae and also confines their oxygen consumption to the already limited hypolimnion.
Conclusions

Central basin oxygen depletion is becoming more strongly tied to hypolimnion thickness as the effects of eutrophication recede. Factors controlling the thickness include storm events, which decrease its thickness and rare ‘reverse entrainment’ events, which not only increase the thickness of the hypolimnion, but also introduce oxygen rich epilimnetic waters into the oxygen poor hypolimnion. Entrainment events caused by severe storms mixed hypolimnetic waters into the epilimnion are linked to the decreases in hypolimnion thickness. Bottom shear was found to be the controlling factor in limiting sediment oxygen demand. As bottom shear decreases, the link between hypolimnion thickness and sediment oxygen demand becomes weaker and the link between the magnitude of the hypolimnetic mixing and the oxygen profile becomes more important. Thus, we need to study the seasonal and diel variations in bottom shear, which will not only allow predictions of oxygen depletion, but may allow predictions of reverse entrainment events.
Figure 3.1. Areal oxygen concentration on 6-9 August 1997.
Figure 3.2 a and b. Averaged eddy diffusivity profiles for morning (a) and day (b) for August 1997.
Figure 3.3 a-d. Oxygen budget simulations for morning, 6-9 August 1997
Figure 3.4 a-d. Oxygen budget simulations for day profiles, 6-9 August 1997.
Figure 3.5. Change in temperature profile from 1553, 6 August 1997 to 1428, 8 August 1997.
Figure 3.6. Temperature, energy dissipation and buoyancy frequency during the beginning of a storm event, 21 May 1997.
Figure 3.7. Oxygen depletion rates in the central basin. (from Bertram et al. (1993) with additional USEPA data.)
Figure 3.8. Relationship between oxygen depletion and hypolimnion thickness with data from the 1970s (Charlton 1980) and 1980s and 1990s (Bertram 1993) and the regression given by Charlton 1980.
APPENDIX A: Numerical solution to Equation (1.1)

The one dimensional vertical transport equation used in chapter 1 (and similarly in Chapter 3):

\[
\frac{\partial F}{\partial t} + w_z \frac{\partial F}{\partial z} = \frac{\partial}{\partial z} \left( K \frac{\partial F}{\partial z} \right)
\]

A1.1

with boundary conditions

\[
w_z \frac{\partial F}{\partial z} - K \frac{\partial F}{\partial z} = 0 \quad \text{at } z = H
\]

\[
w_z \frac{\partial F}{\partial z} - K \frac{\partial F}{\partial z} = \alpha F \quad \text{at } z = 0
\]

is solved numerically in the following manner. First, a grid is set up with vertical axis representing depth from \( z=0 \) to \( z=H \) and \( n=400 \) vertical grid points:

\[n\]
\[n-1\]
\[
\ldots
\]
\[j+1\]
\[j\]
\[j-1\]
\[
\ldots
\]
\[2\]
\[1\]

and time in the horizontal grid axis. Then equation A1.2 can be solved at each grid point by using the definition of a definite integral across a small space, in this case the space
between the grid points:

$$\frac{\partial}{\partial z} \left( K \frac{\partial F}{\partial z} \right) - \frac{w_s}{L} \frac{\partial F}{\partial t} = \frac{\partial F}{\partial t}$$  \hspace{1cm} A1.2

First, \( A \), in equation A1.2 can be made discrete across the grid interval:

$$\frac{F_j^{n+1} - F_j^n}{\Delta t} = \frac{\partial}{\partial z} \left( K \frac{\partial F}{\partial z} \right)_{j}^{n+1} - \frac{\partial}{\partial z} \left( K \frac{\partial F}{\partial z} \right)_{j}^{n} \hspace{1cm} A1.3$$

$$\frac{\partial}{\partial z} \left( K \frac{\partial F}{\partial z} \right)_{j} = \frac{1}{\Delta z} \left[ K_{j+1} \frac{F_{j+1}^{n+1} - F_j^n}{\Delta z} - K_j \frac{F_j - F_{j-1}^n}{\Delta z} \right] \hspace{1cm} A1.4$$

where \( \Delta z \) is the distance between grid points and \( K_j = 1/2(K_j + K_{j+1}) \). Defining \( s_j = K_j \Delta t / (\Delta z)^2 \),

$$F_j^{n+1} - F_j^n = \frac{1}{2} \left[ s_{j+1} (F_{j+1}^{n+1} - F_j^{n+1}) - s_{j} (F_{j+1}^{n+1} - F_{j-1}^{n+1}) \right]$$

$$\ldots s_j (F_{j+1}^{n} - F_j^{n}) - s_{j} (F_{j}^{n} - F_{j-1}^{n}) \right]$$ A1.4

Setting up a tridiagonal system,

$$s_{j+1} F_{j+1}^{n+1} + (2 + s_j + s_{j+1}) B_{j}^{n+1} - s_j B_{j-1}^{n+1} =$$

$$= s_{j+1} B_{j+1}^{n} + (2 - s_j - s_{j+1}) B_{j}^{n} + s_j B_{j-1}^{n} \hspace{1cm} A1.5$$

the boundary can be included:

$$- K \frac{\partial F}{\partial z} = 0, z = 0$$

$$\Rightarrow \frac{1}{2\Delta z} \left[ F_{n}^{n+1} - F_{n+1}^{n+1} + F_{n}^{n} - F_{n-1}^{n} \right] = 0$$ A1.5

$$\Rightarrow F_{n}^{n+1} - F_{n+1}^{n+1} = -F_{n}^{n} + F_{n-1}^{n}$$

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and at the bottom
\[-K \frac{\partial F}{\partial z} = \alpha F, z = -H\]
\[\Rightarrow -\frac{K_z}{2\Delta z} [F^{n+1}_2 - F^{n+1}_1 + F^n_2 - F^n_1] = \alpha (F^{n+1}_1 + F^{n+1}_2 + F^n_1 + F^n_2)\]

A1.7

collecting terms from A1.8 and defining \(p_2 = \alpha \Delta z / 2K_z\):
\[-F^{n+1}_2 + F^{n+1}_1 - F^n_2 + F^n_1 = p_2 (F^{n+1}_1 + F^{n+1}_2 + F^n_1 + F^n_2)\]
\[\Rightarrow -(1 - p_2)B^{n+1}_2 = (1 + p_2)B^n_2 + (p_2 - 1)B^n_1\]

A1.8

collecting terms and defining \(p_2 = \alpha \Delta z / 2K_z\):
\[-F^{n+1}_2 + F^{n+1}_1 - F^n_2 + F^n_1 = p_2 (F^{n+1}_1 + F^{n+1}_2 + F^n_1 + F^n_2)\]
\[\Rightarrow -(1 - p_2)B^{n+1}_2 = (1 + p_2)B^n_2 + (p_2 - 1)B^n_1\]

A1.6

Thus, the system to solve is \(AB^{n+1} = CB^n\) where \(A=\)

\[
\begin{bmatrix}
1 - p_2 & -(1 - p_2) & 0 & 0 & \ldots & 0 & 0 & 0 \\
-s_2 & 2 + s_2 + s_3 & -s_3 & 0 & \ldots & 0 & 0 & 0 \\
0 & -s_3 & 2 + s_3 + s_4 & -s_4 & \ldots & 0 & 0 & 0 \\
0 & 0 & \ldots & \ddots & \ddots & \vdots & \vdots & \vdots \\
0 & 0 & 2 + s_j + s_{j+1} & s_{j+2} & 0 & \ldots & 0 & 0 \\
0 & 0 & 0 & -s_{m-1} & 2 + s_{m-1} + s_m & -s_m & \ldots & \vdots \\
0 & 0 & 0 & 0 & \ldots & 0 & 0 & 1 \\
\end{bmatrix}
\]

and \(C=\)

\[
\begin{bmatrix}
0 & 0 & 0 & 0 & \ldots & 0 & 0 & 0 \\
2 - s_j - s_3 & s_j & 0 & 0 & \ldots & 0 & 0 & 0 \\
0 & s_j & 2 - s_j - s_4 & s_4 & \ldots & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \ddots & \vdots & \vdots & \vdots \\
0 & 0 & 2 - s_j - s_{j+1} & s_{j+2} & 0 & \ldots & 0 & 0 \\
0 & 0 & 0 & -s_{m-1} & 2 - s_{m-1} - s_m & s_m & \ldots & \vdots \\
0 & 0 & 0 & 0 & \ldots & 0 & 0 & 0 \\
\end{bmatrix}
\]
Now, part 'B' (Equation A1.2) can be included using a one sided difference with Crank-Nicolson

\[ w_j \frac{\partial F}{\partial z} \bigg|_j = \frac{w_j}{2\Delta z} \left( F_{j+1}^{n+1} - F_j^{n+1} + F_j^n - F_{j-1}^n \right) \text{ at } j=n \]  

A1.8

and defining \( c = w_s \Delta t / \Delta z \). The system then is

\[
(c - s_{j+1})F_{j+1}^{n+1} + (2 - c + s_j + s_{j+1})F_j^{n+1} - s_j F_{j-1}^{n+1} = \]

\[
= (-c + s_{j+1})F_{j+1}^n + (2 + c - s_j - s_{j+1})F_j^n + s_j F_{j-1}^n \]  

A1.9

The boundary conditions are similarly modified:

\[
\frac{w_s}{2} \left( F_{nz}^{n+1} + F_{nz-1}^{n+1} \right) - K \frac{F_{nz}^{n+1} - F_{nz-1}^{n+1}}{\Delta z} = 0 \Rightarrow \]

\[
(1 - p_{w,nz})F_{nz}^{n+1} - (1 + p_{w,nz})F_{nz-1}^{n+1} = 0 \]  

A1.10

where \( p_{w,nz} = w_s \Delta z / 2K_{nz} \) and the bottom boundary condition is

\[
-(1 + p_{a,2} - p_{w,2})F_2^{n+1} + (1 - p_{a,2} + p_{w,2})F_1^{n+1} = 0 \]

where \( p_{a,2} = \alpha \Delta z / 2K_2 \) and \( p_{w,2} = w_s \Delta z / 2K_2 \). These can then be included into the tridiagonal system.
APPENDIX B: Description of a diffusive random walk model

The random walk of a particle in chapter 2 can be simulated in 1 dimension over a series of times steps, $\delta t$, by

$$z_{n+1} = z_n + \frac{K'(z_n)\delta t}{a} + R\left[2\frac{r^{-1}K\left(z_n + \frac{1}{2}K'(z_n)\delta t\right)}{b}\right]^\frac{1}{2}$$  \hspace{1cm} (A2.1)

where $R$ is a normally distributed random process with mean 0 and standard deviation $r$ (Visser 1997). In this equation, ‘$a$’ is a non-random advective component from high diffusivity to low diffusivity. This prevents particles from artificially collecting in areas of low diffusivity. In addition, the diffusivity used in calculating the walk is displaced in ‘$b$’ by $\frac{1}{2}K'(z_n)\delta t$ which more reasonably represents the mixing intensity experienced by the particle. This equation, when solved for many particles, can be equated to the advection-diffusion differential equation

$$\frac{dC}{dt} - \frac{d}{dz}\left(K\frac{dC}{dz}\right) = 0$$  \hspace{1cm} (A2.2)

where $C$ is the concentration of particles,
with boundary conditions
\[ K \frac{dC}{dz} = 0 \] at \( z=0 \)
and \( z=H \)
resulting in reflecting surface and bottom of the mixed layer.

This is in contrast to the traditional random walk model:
\[ z_{n+1} = z_n + R \left( 2r^{-1} K(z_n) \delta t \right)^{\frac{1}{2}} \] A2.3

In this case, the distance of the walk is determined at the initial location and there is no advective component. This equation corresponds to the advection diffusion equation
\[ \frac{dC}{dt} - \frac{d^2}{dz^2}(KC) = 0 \] A2.4

Equation A2.4 is equivalent to equation A2.2 only when there is a constant diffusivity with respect to depth. Similarly, if the diffusivity is not constant, equation A2.3 will cause artificial congregations of particles in areas of low diffusivity, leading to erroneous explanations of particles found in these areas in situ (e.g. Yamazaki and Kamykowski 1994).
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