ABSTRACT

GRABOWSKI, KATHRYN EVE. Near Bottom Dinoflagellate Populations on the Northwest Florida Shelf. (Under the direction of Dr. Daniel Kamykowski.)

The toxic dinoflagellate *Karenia brevis* is most commonly sought near the sea surface 18-74 km from shore due to the historical occurrence of bloom events. Hydrographic conditions on the west Florida shelf alternate between two seasonal conditions. From November through April, the water column generally is well-mixed to the bottom with an offshore gradient of colder, less saline inshore temperatures to warmer, more saline offshore temperatures. From May through October, vertical stratification exists across the shelf. Phytoplankton succession models suggest that diatoms may be favored near-bottom at least early in the succession sequence where the euphotic zone reaches the sediments, while dinoflagellates, using vertical migration to transit between the nutrient-rich sediments to the base of the euphotic zone, may be favored near-bottom as the sediments descend below the euphotic zone. Field and laboratory observations as well as computer models focused on *Karenia brevis* suggest that seed populations for coastal blooms under upwelling favorable conditions may exist near the sediment interface after water column stratification sets in and the sediments contain higher nutrient levels than the water column. Cruises during July 2009 and October 2008 provide a seasonal sequence of the cross-shelf expression of the summer/fall condition on the northwest Florida shelf. Transects between the 20-70m depth

contours were sampled for hydrographic character using ACROBAT and CTD surveys and for nutrients, pigments and phytoplankton composition using CTD/rosette water collections. Water samples collected from selected depths including near the sediment interface were analyzed on the FlowCAM for phytoplankton community composition. During July 2009 cross-shelf, a pycnocline existed between 10-20 m depth, the 1% light level reached to about 45 m depth, nitrate-nitrite concentrations started increasing about 10 m above the sediment interface out to 50 m depth and then increased below 40m depth across the rest of the outer shelf, and a chlorophyll *a* maximum occurred between 20-30 m depth. Near-bottom, dinoflagellates were 2-8 times more abundant than diatoms everywhere on the shelf, especially between 35-55m, except at one 20 m station. Time series samples, collected along the 50 m contour following a drogue with a holey sock extending between 28-40 m, suggest trends of a dinoflagellate distribution pattern suggestive of diel vertical migration. Dinoflagellates clearly dominated the near-bottom water over diatoms across the shelf probably due to late succession influences like selective grazing on diatoms and microphytobenthos activity inshore as well as increased hydrographic influences. Dinoflagellates found near bottom also have the migration capability to access vertically separated light and nutrient resources offshore. The October 2008 cruise results provide insight into changes in physical, chemical and biological changes and phytoplankton succession patterns associated with the transition from horizontal stratification to well-mixed water columns that form a cross-shelf hydrographic gradient. A wind event between successive transects during the October cruise showed how disturbance events can influence

near bottom phytoplankton distributions. Before the wind event the distribution of near bottom phytoplankton was highly structured and after the distribution of near bottom phytoplankton was more evenly distributed along the bottom. This wind event served as the transition between seasonal succession cycles of near bottom phytoplankton populations. Such near-bottom populations may serve as seed possible near-shore dinoflagellate blooms, responding to upwelling favorable winds and behavioral accumulation at coastal fronts. The October 2008 cruise results provide insight into changes in physical, chemical and biological changes and phytoplankton succession patterns associated with the seasonal transition from horizontal stratification in the summertime to well-mixed water columns that form a cross-shelf hydrographic gradient in the wintertime, promoting succession changes.

Near Bottom Dinoflagellate Populations on the Northwest Florida Shelf

by
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DEDICATION

I dedicate this thesis to my family. I dedicate this to my husband, with his love and support I would have never accomplished such a feat. To my parents and my sister who have supported me for all my life, no matter what. Also, thank you to my new family for their support of our future.

BIOGRAPHY

Katy was born in Howard County, Maryland in May of 1984. After nine years in Maryland, she moved to her now hometown of Huntersville, NC where she lived throughout high school. She enjoyed math and science courses in high school and they eventually led to attending North Carolina State University in 2002. During her junior year, Katy attended Duke Marine Laboratory Summer Program which motivated her to complete her bachelor's degree in Biological Oceanography in 2006. After taking a year off to work on Lake Gaston, NC and meet her husband, Katy returned to NC State to work for her master's degree under the guidance of Dr. Daniel Kamykowski studying phytoplankton in the Gulf of Mexico. During her graduate career Katy had the pleasure of participating in several amazing cruises in the Gulf of Mexico as well as completed an internship at Mote Marine Lab. At Mote Marine Lab out of Sarasota Fl., Katy worked up Dr. Gary Kirkpatrick on the innovated Brevebuster in the Gulf of Mexico. As Katy is finishing up her master's degree at North Carolina State, she heads to a position as an Oceanographer for the Naval Oceanographic Office at Stennis Space Center in Mississippi.

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CHAPTER 1: LITERATURE REVIEW

Margalef's Model

Margalef (Margalef, 1978, Margalef et al., 1979) described a seasonal phytoplankton succession as a mix between habitat dynamics and phylogenetic morphologies of phytoplankton species. The degree of turbulence as well as the amount of readily available nutrients comprises the habitat dynamics scale used for the succession model (Margalef, 1978, Margalef et al., 1979). The dynamics of the habitat based on this scale can relate to the phylogenetic life forms of phytoplankton that are most suitable to occupy a certain type of habitat (Margalef, 1978, Margalef et al., 1979). The phylogenetic life form selected by the habitat dynamics ranges from species succession of r-selected species in higher turbulence areas with high nutrients and eventually leads to K-selected species in lower turbulence and nutrient habitats. For example, for Harmful Algal Blooms, the Margalef's succession model initially predicts a succession from first diatoms in higher turbulence and nutrient habitats then leading to rounded dinoflagellates, and eventually to flattened dinoflagellates as nutrients and turbulence dissipates (Margalef et al., 1979).

Smayda and Reynolds (2001; hereafter SR) updated the succession model based on Margalef's model that includes vertical nutrient distribution correlated with changing degrees of turbulence. SR tested their succession model built on the Margalef model based on

Reynolds C-S-R model of freshwater phytoplankton (Reynolds,1987). In this CSR model, Reynolds distinguishes between three different adaptive strategies to changing habitat exhibited by freshwater phytoplankton. Colonists (C) species are generally small, fast growing r-selected cells that can be invasive and usually has a high surface to volume ratio. Stress tolerant (S) species are those K-selected cells that are large and slow growing, but tend to conserve biomass to withstand situations of nutrient stress. Ruderal (R) species are tolerant of most physical disturbances such as spring mixing and usually are found to be light harvesting species. The adaptive strategies, or life forms, of each distinct group (C, S, and R) allow each group to become the dominant group when their physical environment is best suited for survival. Using this life form dominance strategy applied in the C-S-R model, SR were able to identify nine major life form classes in which to organize dinoflagellate species that may succeed diatoms: Type I *Gymnodinioids*, Type II *Peridinians/Prorocentroids*, Type III *Ceratians*, Type IV Frontal Zone Taxa, Type V Upwelling Relaxation Taxa, Type VI Coastal Current Entrained Taxa, Type VII *Dinophysoids*, Type VIII Tropical Oceanic Flora, and Type IX Tropical Shade Flora Seasonal habitat hydrodynamics, changing nutrients and turbulence structure of the column (or the mixed layer depth) are used to select preferable life-forms which determine the succession pattern of other life form types. The SR updated life form succession model will be used here to predict the succession of dinoflagellate life-forms that will succeed benthic diatoms. Diatoms are commonly found near the sediment interface on the northwest Florida shelf to utilize near bottom nutrient concentrations in shallow water columns through the hydrodynamic seasonal cycle. If the models are correct, a

revised succession model will predict that dinoflagellates can share the sediment interface for nutrients where near bottom diatoms generally dominate in certain specific conditions that select for dinoflagellates over diatoms near bottom (Smayda and Reynolds, 2001).

The West Florida Shelf has been seasonally plagued with HABs for hundreds of years (Steidinger et al., 1998). Referring to the SR model, this system shows an onshore-offshore gradient of nutrients and turbulence mainly associated with seasonal frontal zones and upwelling. The gradient of turbulence also influences the depth of the mixing layer. Seasonally on the West Florida Shelf, phytoplankton species will have to endure fairly high winter-spring shear stress from the shelf to the coast as a major selective component of the life forms capable of surviving in this type of system (He & Weisberg, 2002). The water column is well mixed or just slightly stratified, and much of the habitat dynamics, when considered in the context of the succession model, would favor larger diatoms over dinoflagellates due to penetrating surface winds. As the column becomes more stratified as temperature increases in summer-fall and winter-spring storm forcing declines (He & Weisberg, 2002) the sediment interface habitat type changes and different phytoplankton life forms may supplement near bottom diatoms or respond to cross shelf flows (upwelling or downwelling) yielding coastal fronts (Cahoon, 1999). This changed habitat type, when applied to the model, yields results for three main life-forms of dinoflagellates to succeed near bottom diatoms: Type IV for species associated with frontal zone taxa like *Gymnodinium* and *Alexandrium*, Type V for species associated with upwelling relaxation

taxa such as *Gymnodinium* and *Lingulodinium* species, and finally Type VI for coastal current entrained taxa such as *Gymnodinium* and *Ceratium* species (Smayda and Reynolds, 2001). These life form types are all characterized by chain formation, strong phototaxic abilities, specialized toxin production associated with red tides, and controlled and flexible motility (Smayda and Reynolds, 2001). Some species such as *Gymnodinium* can span several categories due to their adaptability in many different types of environments including low light and nutrient habitats. All of these form types naturally occur on the West Florida Shelf and on the NW Florida shelf and are adapted for survival in this type of system, with low nutrient levels and variable shear stress from frontal events, as well as the ability to survive and bloom in upwelling zones (Tester & Steidinger, 1997, Smayda & Reynolds, 2001, Vargo et al., 2008). The dynamics of the system at any particular moment in time will determine the succession pattern of life forms and rate of change of these life-form types (Smayda & Reynolds, 2001). The seasonal changes in the habitat, mainly the amount of stratification of the water column and shear stress on the cells, is responsible for forcing changes in the habitat type according to the succession model, causing a succession shift in species occupying the column.

Past research

Three phytoplankton species exhibited diel vertical migration in the field for photosynthesis and near-bottom nutrients sources: *Akashiwo sanguinium, Gonyaulax*

polygramma, and *Karenia brevis.* The first documented vertical migration of a phytoplankton species was *Akashiwo sanguinium,* in the Gulf of California (Kiefer & Lasker, 1975). Using fluorescence profile and cell counts, migration was based on a measured 1 m/h swimming speed through the water column on an approximate 12 hour swimming cycle (Kiefer & Lasker, 1975). *Gonyaulax polygramma* and *Karenia brevis* were both documented as exhibiting diel vertical migration in the Gulf of Mexico off Panama City FL. The *Gonyaulax polygramma* species, tracked in the Gulf of Mexico in 1980, apparently was associated with an upwelling event that provided nitrogen as a near bottom sources (Kamykowski, 1980). The most recent documented species exhibiting near-bottom diel vertical migration is *Karenia brevis* in the Gulf of Mexico off Panama City, FL in October, 2000 (Kamykowski, personal communication). Two populations were observed at different depths within the water column. Time series fluorescence profiles and cell counts showed that the populations were exhibiting diel vertical migration within the water column on 12 hour cycles with swimming speeds of approximately 1 m/hr. The 12 hour cycles showed aggregated populations near the sediment bed around midnight and near the surface during the daylight hours. Since two published sightings of phytoplankton populations were found in the Gulf of Mexico near Panama City, FL this area was selected as the test site for the study discussed here.

DVM

All of the dinoflagellate life form types commonly found on the West Florida Shelf (Type VI, V, and VI) has the ability to undergo diel vertical migration (DVM) through the water column. The WFS is extremely oligotrophic, with low concentrations of nitrogen and phosphorus throughout the water column (Dragovich, 1961). This DVM ability allows cells to descend to nutrient sources in the underlying water column and to ascend to water column to depths with a higher photosynthetically active radiation (PAR) to support photosynthetically driven carbon fixation for growth and survival of the cell. Individual cells have a motility rate on the order of ~1-2 m/hr for DVM based on species (Eppley et al., 1968, Kamykowski, 1995), and the rate of DVM can vary based on the individual cell's internal physiological state (Kamykowski & McCollum, 1986). The rate of motility of an individual cell will be used to determine the net distance of migration capability between the sediment nutrient source and a PAR depth for photosynthesis. In laboratory experiments, *Karenia brevis* cells have shown the ability to penetrate a sediment interface for nutrient uptake when the upper portion of the mesocosm is nitrate depleted and a nutrient source is available below the sediment interface (Sinclair et al., 2006). These experiments clearly showed that with a lack of vertical water motion, a cell will clearly penetrate the top few centimeters of the sediment layer for nocturnal nutrient uptake affecting the spatio-temporal distribution of a population (Sinclair et al., 2006).

Other environmental and cellular characteristics may determine the types of dinoflagellates that occupy a given location on the shelf. Temperature plays an important role in dinoflagellate swimming speeds and may be used as a proxy to predict cell types found near the sediment interface (Kamykowski and McCollum, 1986). Dinoflagellate species can migrate at a range of speeds as determined by a range of temperatures. Each species has a unique swimming speed vs. temperature curve for a given set of environmental conditions, within which there is an optimal temperature range for optimal swimming speeds (Kamykowski and McCollum, 1986). A cell can acclimate to a temperature, but there is some degree of inhibition associated with the temperature change before normal swimming speeds can resume (Kamykowski and McCollum, 1986). Past studies have found a general relationship for dinoflagellate species in which a low range of temperatures (1-13 ºC) and a high range of temperatures (31-38 ºC) cause cells to stop migration, but a mid-range temperature scale can promote efficient migration on the scale of 96-598 um/s (Kamykowski and McCollum, 1986). Within the optimal temperature range for migration, dinoflagellate species swimming speeds are broken down amongst common body types or subclasses: armored dinokont (*Dinophysiphycidae*), unarmored dinokont (*Peridiniphycidae/Gymnodiniphycidae*), and desmokont (*Prorocentrophycidae*) (Kamykowski and McCollum, 1986). For example, laboratory experiments have suggested that cellular swimming speeds increase with body size, until a cell size of ~35 um is reached and swimming speed begins to decrease with cell size (Kamykowski and McCollum, 1986). This distinction of body type on swimming speed may be used to determine which species, or

more generally which body types, are most capable of the swimming speeds needed to migrate between a near bottom nutrient source and a PAR depth higher in the water column as well as acclimate to the temperatures differences of deeper water vs. surface water. The relationship between temperature, cell size, and swimming speeds can be as a proxy to determine the species/body type of cells migrating to the sediment interface for nutrients. Swimming speeds can have an effect of the spatial distribution of populations of different dinoflagellate species when faced with the same environmental resources and each species has the ability to migrate to an environment within it can grow most effectively under an acclimated temperature range (Kamykowski and McCollum, 1986).

WFS

The West Florida shelf has a unique hydrodynamic system in which to apply SRs model predictions. The northwest Florida shelf off of the Florida and Alabama coastline, near Panama City Fl., is narrower than the western shelf off the central coast of Florida. The northwest Florida shelf also has a greater degree of sloping that can experience dramatic changes in stratification seasonally by physical influences such as waves (surface and internal) (Tolbert & Austin, 1959), tidal currents (He and Weisberg, 2002), long-shore and cross-shore flows (Tolbert & Austin, 1959), as well as upwelling (Kamykowski, 1980) and downwelling events. The overlying water column on the shelf is generally oligotrophic and phytoplankton competition for nutrients below the thermocline can become intense. As air

temperatures rise with the onset of summer, sea surface temperatures also rise with the highest recorded May through November (He & Weisberg 2002). The increase in sea surface temperature relates to the inverse relationship to oceanic nutrient sources, making the upper warmer column more nutrient depleted than the lower column (Kamykowski et al., 2002). Changing sea surface temperatures are an indication of changing stratification patterns across the shelf.

For the half of the year, November to April, stronger winds cause the water column to be well mixed on the northwest shelf (Walsh et al, 2003). While the column is well mixed, there is a horizontal gradient of vertically uniform temperature, salinity, nutrients, and chlorophyll from the coastline to the outer shelf (Walsh et al, 2003). As the atmosphere warms, eventually the well mixed column and thermal gradient from the coastline to the shelf turns slowly to a normal vertically stratified water column. Winds create an upwelling/downwelling component of a nutrient-rich water mass near the coastline allowing vertical stratification occasionally to break the surface in fronts. The stratification pattern contributes to very low oceanic nutrient availability, especially of nitrogen which is often growth limiting for marine phytoplankton, throughout the upper water column. An alternate source of nutrients in this oligotrophic water column may be the sediment interface which is comprised mostly of coarse, sandy sediments (Cahoon, 1999). Seepage of nutrients buried in sediments as well as the sinking of organic matter to the sediment layer from other

phytoplankton blooms like *Trichodesmium* has the ability to allow sediments to provide higher nutrient levels than found in the overlying column (Walsh et al., 2001).

The sediment interface within the euphotic zone has been a known source of nutrients for the microphytobenthos, such as algae, including but not limited to diatoms and permanently benthic dinoflagellates (Cahoon, 1999). Microphytobenthos as referred to in this study includes any alga that lives predominantly in the benthos. Microphytobenthos cells, including some dinoflagellates will live in the porewater a few centimeters from the water/sediment interface and within the first few centimeters of the sediment. These cells are able to maintain net growth rates since the sediment layers they occupy are within reach of enough light penetration to sustain adequate photosynthesis. Cahoon states the compensation depth for microphytobethnic cells is at approximately 0.1% PAR (1999). Studies have shown that microphytobethnic species can utilize nutrients available within the top layer of sediments (Cahoon, 1999). Depending on the strength of seasonal upwelling currents on the shelf (~200m isobaths) changes in the standing stock of nitrogen will influence the relative amount of nitrogen in the sediments versus water column farther inshore (~30m isobaths) (Walsh et al., 2003). Vertical profiles at the 30m isobaths showed responses of increased chlorophyll concentrations at the sediment interface when the standing stock of nitrogen at the 200m isobaths was elevated (Walsh et al., 2003). Nutrient uptake rates for these organisms can become altered with different light intensities (Cahoon, 1999). Since diatom have no individual swimming capabilities, they must occupy a habitat that has sufficient PAR

for photosynthesis, typically on the inner shelf, and has sufficient nutrients to maintain growth. Their main motility mechanism is through localized currents or changes in density to follow isopycnals within the water column. Some dinoflagellates species that are not a permanent member of the microphytobenthos niche, such as *Karenia brevis*, exhibit shade adaptation and therefore can function well, though not exclusively (Schaeffer et al., 2007), at low light intensities (Walsh et al., 2003). This allows these dinoflagellate species to take advantage of nutrients at the sediment interface at depths where PAR attenuation is too low for the growth of microphytobenthic algae and near bottom upwelling plume diatoms. CDOM input from local estuaries in the region can also diminish the amount of PAR reaching the sediment interface, further increasing the selection of shade adapted dinoflagellates over that of microphytobenthic cells (Walsh et al., 2003). When applying this idea to the northwest Florida shelf, microphytobenthic species such as diatoms should generally dominate the sediment interface for nutrients at depths of approximately 20-50m depending on light reaching the sediment interface (Cahoon, 1999). Where the compensation depth of 0.1% PAR does not reach the nutrient rich sediment interface, the microphytobenthic and water column diatoms can no longer survive without swimming capabilities up into the water column. Due a microphytobenthos tendency for enhanced nutrient utilization during daylight, nutrient sources in the sediments may also be shared, or partitioned, between day and night nutrient uptake by benthic diatoms and dinoflagellates in this same depth range (Sinclair et al., 2006).

LJK Model

Liu et al., (2001) used a Eularian model to examine how nutrient availability influences dinoflagellate vertical distribution based on a realistic physiological model. The model was originally based on *Karenia brevis* cells, a common red tide dinoflagellate, on the northwest Florida shelf. The model examined how *K. brevis* cells responded to a surface coastal plume, an offshore upwelling near bottom plume, a persistent upwelling cross shelf, near bottom plume, and surface sources such as *Trichodesmium* supplied nitrogen as triggered by atmospheric dust inputs (Liu et al., 2001). Cells were programmed to migrate vertically within the water column at speeds based on internal cellular states for carbon (photosynthesis) for ascent and nitrogen (uptake rates) for descent (Liu et al., 2001a, 2001b, Sinclair et al, 2006). Generally, cells ascended as rapidly as possible toward higher PAR levels to perform photosynthesis if internal carbon pool were low and cells descended as rapidly as possible if internal nitrogen pools were low. The different nutrient supply scenarios allowed for bloom-like concentrations of dinoflagellate populations to form at the surface or bottom. Of particular interest for present purposes was the near bottom aggregations that the model simulated based mainly on persistent upwelling plume located at the sediment interface.

We propose that stratification of very low nutrient levels throughout the water column will be advantageous to dinoflagellates. As microphytobenthic organisms, like diatoms, take up nutrients from porewater and within the top layer of the sediment interface and migrate to

the sediment surface to photosynthesize, near bottom water column dinoflagellates will migrate to the sediment interface to ingest nutrients left in or diffusing out of the sediments at night and migrate up into the water column to photosynthesize during the day. Nutrient profiles will show the column to be almost depleted of nutrients except for a small source at the sediment interface. This may be a signal for dinoflagellate species to migrate to the sediment interface for nutrients instead of competing for them at the surface. Dinoflagellates generally will exist at low concentrations near the sediments due to lower light levels for photosynthesis.

Dinoflagellates will dominate the sediment interface at a depth between the microphytobenthos/water column diatom domination depth and depth at which enough light penetration is available to perform adequate photosynthesis for growth based in vertical migration. For our study we are testing the 1% PAR depth as the compensation depth for the benthic DVM niche. We are also focusing on depths that the 1% light level reaches within a distance from the sediment interface that is within the migration range of dinoflagellates over a 24 hour cycle, migrating at speeds typically seen in these dinoflagellates species. At the sediment interface, seed populations of dinoflagellate are able to survive until conditions on the shelf are ideal for bloom initiation and transport via upwelling currents in the late summer months, during normal red tide seasons. These unique shelf dynamics, especially the changes in nutrient stratification, lend to the hypothesis of the existence of near bottom dinoflagellate populations at certain depths on the shelf. While major easterly wind events

causing a downwelling component lead to the initiation of blooms from upper water column populations on the northwest Florida shelf (Tester & Steidinger, 1997) naturally occurring upwelling events from westerly wind event during the same season can sweep the sediment interface of benthic populations and transport them to the coast as an upwelling related mechanism for bloom initiation.

The concept of near bottom dinoflagellate populations with a near bottom nutrient source was originally modeled by (Liu et al., 2001), but was updated to include various physical parameters to make the model applicable to the west Florida shelf (Janowitz and Kamykowski, 2006). The model examined dinoflagellate cell and population behavior toward a nutrient front (25m depth contour) created via an offshore-flowing surface nutrient plume from the bay coupled with a nutrient flux from the sediments driven toward the coast by onshore-flowing upwelling currents (Janowitz and Kamykowski, 2006). The nutrient fluxes were estimated using a variety of possible sources and concentrations from coastal, offshore, and mid-shelf upwelling plumes, *Trichodesmium* supplied nitrogen, as well as atmospheric dust (Janowitz and Kamykowski, 2006). Approximately 1 cell/ml were added to the model initially via the lower half (~22m) of the water column inflow at the 40m isobath (Janowitz and Kamykowski, 2006). To stimulate the cells to migrate to the sediment interface for nutrient uptake, each cell's migration was regulated by its own internal biochemical composition, ex. the cell's internal carbon and nitrogen concentrations as well as variable light exposure (Janowitz and Kamykowski, 2006). The biochemical connections to

migration were based on diel vertical migration mesocosm experiments using biochemically (carbon and nitrogen concentrations) unequal daughter cells (Kamykowski, 1998). Cells low in carbon concentration will swim upward toward the surface for higher PAR values to perform photosynthesis and increase carbon concentration and lowering nitrogen concentration in the process (Janowitz and Kamykowski, 2006). Once the internal carbon concentration reaches a maximum threshold limit, or the internal nitrogen concentration reaches a minimum threshold limit, the cell will then begin to swim toward a nitrogen gradient exceeding 0.01 μM/m at swimming speed that is variable for each individual cell depending on several external (light, etc.) and internal (carbon and nitrogen pools) (Janowitz and Kamykowski, 2006). In this model, the nitrogen gradient leads the cell to the sediment interface which has higher nitrogen measurements than the overlying oligotrophic column (Janowitz and Kamykowski, 2006). Daylight simulations showed cells flowing onshore via the upwelling plume toward the nutrient front at 25m. The cells will initially swim upward toward the surface to fulfill their carbon requirements then swim down toward the nitrogen gradient near the sediment interface (Janowitz and Kamykowski, 2006). While some cells were washed offshore while near the surface performing photosynthesis, most of the cells quickly became entrained in the front (Janowitz and Kamykowski, 2006). Once entrained in the front, all cells will be transported onshore since the front reverses the nutrient gradient, and cells will swim upward to the surface for nutrients and carbon (Janowitz and Kamykowski, 2006). Onshore of the front, the model's distribution of the dinoflagellate population is determined by the current flows, the PAR field, and the nutrient field (Janowitz

and Kamykowski, 2006). The bottom boundary layer created by the effect of simple linear shear from sediment interface was also considered in the model, but laboratory experiments concluded it to be negligible and did not inhibit a cell's DVM rates and could be utilized by the populations for enhanced migration and aggregation of cells near bottom (Liu et al, 2002). The model showed that the sediment associated bottom nutrient source was not necessary (except in terms of population/cell size) for entrainment of cells in the front to occur, all that was needed for entrainment was a negligible upward nutrient gradient offshore of the nutrient plume (Janowitz and Kamykowski, 2006). In other words, as long as the nitrogen gradient increased deeper in the water column and there were strong enough upwelling conditions, cells chose to migrate toward the nutrients deeper in the column and were swept onshore by upwelling currents. Hence, cells appeared at the surface near-shore once the nutrient gradient was sufficiently reversed (upward) by the input of coastal nutrients.

Not every species of dinoflagellate on the WFS will utilize the sediment interface for nutrient uptake. Species with sufficient motility for DVM between the light and nutrient sources will be able to take advantage of that niche. For example, a cell migrating at ~1m/hr from the sediment interface will only be able to migrate 12m up in the water column for photosynthesis. As long as a depth 12m from the sediment interface has sufficient light penetration to perform adequate photosynthesis to support growth, this cell should be able to take advantage of the sediment nutrient source. Dinoflagellate species with the ability to

perform adequate photosynthesis at low light regimes are ideal for this benthic niche. Also, species with the ability to utilize both inorganic and organic nitrogen, such as *Karenia brevis*, found in the sediments will have a better chance to take up these nutrients during both light and dark regimes (Sinclair et al, 2006, Sinclair & Kamykowski, 2006).

If our hypothesis of the existence of near bottom vegetative dinoflagellate populations at the sediment interface is true, then this could be a seed population which could act as an alternate strategy to resting cysts and which would make this stratification pattern from well mixed to stratified extremely important in dinoflagellate population dynamics. This hypothesis incorporates well into SR model of the succession of diatoms to dinoflagellates. The habitat dynamics, particularly of nutrients and turbulence, of the sediment interface on the shelf compared to the upper water column where dinoflagellates usually reside are different enough to cause a change in succession. In deeper columns offshore, as the euphotic zone begins to separate from the sediment interface, the habitat structure changes physically and biologically. Physically, nutrient gradients and turbulence levels change according to the succession model to such a degree that they will warrant a change biologically from diatoms to dinoflagellates. We propose to field test this succession model incorporated with Janowitz and Kamykowski's near bottom dinoflagellate populations associated with a nutrient front to discover if these near bottom dinoflagellate populations can exist and the implications of their existence.

Major questions

- In the field, do dinoflagellates actually exist at the sediment interface and how does their distribution compare with the diatom populations near bottom?
- How are near bottom phytoplankton distributed across the shelf?
    - Distribution over Time and with Depth
    - How could the existence of near bottom dinoflagellates influence surface algal blooms?

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CHAPTER 2:

Near Bottom Dinoflagellate Populations on the Northwest Florida Shelf during July 2009.

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Abstract

Harmful Algal Bloom dinoflagellate populations of *Karenia brevis* in the Gulf of Mexico are most commonly sought near the sea surface between 18-74 km from shore. During summer conditions with vertically stratified water columns across the shelf, phytoplankton succession models suggest that diatoms may be favored near-bottom at least early in the succession sequence where the euphotic zone reaches the sediments, while dinoflagellates, using vertical migration to transit between the nutrient-rich sediments to the base of the euphotic zone, may be favored near-bottom as the sediments descend below the euphotic zone. Computer models focused on *Karenia brevis* previously suggested that seed populations for coastal blooms under upwelling favorable conditions may exist near the

sediment interface after water column stratification sets in and the sediments contain higher nutrient levels than the water column. A cruise during July 2009 sampled the cross-shelf expression of the summer condition on the northwest Florida shelf. Transects between the 20-70m depth contours were sampled for hydrographic character using ACROBAT and CTD surveys and for nutrients, pigments and phytoplankton composition using CTD/rosette water collections. Water samples collected from selected depths including near the sediment interface were analyzed on the FlowCAM for phytoplankton community composition. Across the shelf, a pycnocline existed between 10-20 m depth. The bottom of the euphotic zone or the 1% light level reached to a depth of about 45 m. Nitrate-nitrite concentrations started increasing at and 10 m above the sediment interface out to 50 m depth and then increased below 40m depth across the rest of the outer shelf, and corresponding chlorophyll *a* showed a chlorophyll *a* maximum occurred near bottom between 20-30 m depth. Near-bottom, dinoflagellates were 2-8 times more abundant than diatoms everywhere on the shelf, especially between 35-55m, except at one 20 m station. Time series samples, collected along the 50 m contour following a drogue with a holey sock extending between 28-40 m, exhibited a dinoflagellate distribution pattern suggestive of diel vertical migration. During July 2009, dinoflagellates clearly dominated the near-bottom stratified water column across the shelf probably due to late succession influences like selective grazing on diatoms and dielly varying microphytobenthos nutrient utilization activity inshore and the migration capability to access vertically separated light and nutrient resources offshore. Such diffuse, near-bottom dinoflagellate populations are staged to seed possible near-shore dinoflagellate

blooms, including *Karenia brevis*, in response to upwelling favorable winds and behavioral accumulation at coastal fronts.

Introduction

Dinoflagellate populations in the Gulf of Mexico, in particular on the west Florida shelf, are most commonly sought near surface due to constrained sampling efforts, not just because of assumed organism photosynthetic needs (Steidinger et al., 1977, Tester and Steidinger, 1997). Dinoflagellate populations exist at various depths including the sediment interface (Steidinger & Williams, 1970) 18-74 km offshore and are considered responsible for many harmful algal blooms on the Florida coastline (Steidinger et al., 1977, Tester and Steidinger, 1997). A series of models were developed based on field observations of migrating near bottom dinoflagellate populations as well as laboratory studies focusing on the nutrient uptake and migration capabilities of dinoflagellates to provide insight into the development and migration of algal blooms in the Gulf of Mexico.

Three phytoplankton species exhibited diel vertical migration in the field for photosynthesis and near-bottom nutrients sources: *Akashiwo sanguinium, Gonyaulax polygramma,* and *Karenia brevis.* The first documented vertical migration of a phytoplankton species was *Akashiwo sanguinium,* in the Gulf of California (Kiefer & Lasker, 1975). Using fluorescence profile and cell counts, migration was based on a measured 1 m/h swimming speed through the water column on an approximate 12 hour swimming cycle (Kiefer & Lasker, 1975). *Gonyaulax polygramma* and *Karenia brevis* were both documented as exhibiting diel vertical migration in the Gulf of Mexico off Panama City FL. The *Gonyaulax polygramma* species, tracked in the Gulf of Mexico in 1980, apparently was

associated with an upwelling event that provided nitrogen as a near bottom sources (Kamykowski, 1980). The most recent documented species exhibiting near-bottom diel vertical migration is *Karenia brevis* in the Gulf of Mexico off Panama City, FL in October, 2000 (Kamykowski, personal communication). Two populations were observed at different depths within the water column. Time series fluorescence profiles and cell counts showed that the populations were exhibiting diel vertical migration within the water column on 12 hour cycles with swimming speeds of approximately 1 m/hr. The 12 hour cycles showed aggregated populations near the sediment bed around midnight and near the surface during the daylight hours. Laboratory experiments have shown that Karenia brevis cells do have the ability to migrate into the sediments for nutrient uptake (Sinclair et al., 2006). The models presented here incorporate these observations and laboratory studies to describe populations. This study serves as a field test for the further development of models of near bottom dinoflagellate populations.

LJK Model

The first model was developed to see if dinoflagellate populations could exist at different depths within the water column, other than just at the surface, and how the cells behaved at different depths. Liu et al. (2001) applied Eulerian models to examine how nutrient availability influenced dinoflagellate vertical distribution using a laboratory-based physiological model originally constructed for *Karenia brevis*, a common red tide

dinoflagellate on the northwest Florida shelf. The biochemical connections to migration were based on diel vertical migration mesocosm experiments using biochemically (carbon and nitrogen concentrations) flexible daughter cells (Kamykowski, 1998, Sinclair et al., 2006). The model examined how *K. brevis* cells responded to nutrients available as a surface coastal plume a persistent upwelling cross shelf, near bottom plume, an offshore upwelling near bottom plume, and offshore surface sources such as *Trichodesmium* supplied nitrogen as triggered by atmospheric dust inputs (Liu et al., 2001). Cells were programmed to migrate vertically within the water column at speeds based on internal cellular carbon quotas modulated by photosynthesis/respiration for ascent and on internal cellular nitrogen quotas based on nutrient uptake/synthesis rates for descent (Liu et al., 2001a, 2001b, Sinclair et al, 2006). Generally, cells ascended as rapidly as possible toward higher PAR levels to perform photosynthesis if carbon quotas were low and descended as rapidly as possible to seek higher nutrients if nitrogen quotas were low. The different nutrient supply scenarios allowed for concentrations of dinoflagellates to form at the surface or bottom of the water column. Of particular interest for present purposes were the near bottom aggregations that formed in response to a persistent near bottom nutrient source which could also be interpreted as a sediment flux.

MPB Cartoon/ Seasonal Hydrodynamics

Once the original model showed that dinoflagellates were able to exist near bottom due to a nutrient source, the next step in the process was to discover how these near bottom

populations were able to survive in the lower water column. Also, since the mechanisms of bloom initiation is still unclear, this near bottom population is pertinent to bloom initiation that does not begin with a surface dinoflagellate population. The mechanisms by which a near bottom dinoflagellate population is maintained could provide useful information about seed populations contributing to bloom development.

Near bottom dinoflagellate populations could survive on nutrients found at the sediment interface from upwelling plumes or regenerated nutrients fluxing out of or within the sediment possibly resulting from a previous *Trichodesmium* or other phytoplankton blooms at the surface (Liu et al., 2001a, Walsh & Steidinger, 2001). In the case of sediment fluxes, laboratory mesocosm experiments have shown that *K. brevis* cells are able to penetrate the top of the sediment layer for nutrient uptake from pore water (Sinclair et al., 2008). While there are constraints to the dinoflagellate populations living near bottom, the idea of near bottom dinoflagellates may be a little studied mechanism for bloom initiation.

The sediment interface along the northwest Florida shelf is generally dominated by diatoms and other microphytobenthos (Cahoon, 1999). Since diatoms do not have the migration capabilities of dinoflagellates, they must occupy a habitat with nutrient sources and enough light penetration for photosynthesis (Fig. 1). Also sharing the nutrients seeping from the sediment interface with phytoplankton are microphytobenthos (Cahoon, 1999). There is a negative relationship between increasing amounts of fine sediment and microalgal biomass near bottom thus constraining the distribution of the microphytobenthos populations (Cahoon, 1999). Without the ability to migrate into the water column, the amount of light

penetrating to the sediment interface and the amount of turbidity reaching the sediment interface also regulates the distribution of these populations (Cahoon, 1999). These factors keep the microphytobenthos communities and pelagic diatoms communities with similar nutrient and light requirements near shore where they share nutrient sediment fluxes. Since microphytobenthos most actively utilize nutrients in daylight, sediment fluxing nutrients are more available to phytoplankton at night (Cahoon, 1999).

The Gulf of Mexico is an ideal habitat for a near bottom phytoplankton / microphytobenthos niche, as it is known for very clear waters and high light penetration. In deeper columns on the shelf, where light does not penetrate to the sediment interface, the diatom/microphytobenthos cease to dominate the near bottom nutrient sources and other phytoplankton species have the opportunity to utilize this nutrient source. If dinoflagellates are to dominate at the sediment nutrient source, then the bottom of the euphotic zone (1% PAR) ideally occurs within a 12hr. migration of the sediment interface of cells capable of swimming at 1-2 m/hr (Kamykowski, 1995, Eppley et al., 1968). This would place the primary area of the shelf which would be ideal for dinoflagellate dominance near bottom within the 20-60m isobaths.

While the 20-60m isobaths on the west Florida shelf may provide the main requirements for near bottom dinoflagellate populations, other physical parameters need to be present for net phytoplankton growth. Turbulence and stratification of the water column are important factors in the ability for cells to thrive. Stratification on the northwest Florida shelf can change in response to physical influences such as waves (surface and internal) (Tolbert &

Austin, 1959), tidal currents (He and Weisberg, 2002), long-shore and cross-shore flows (Tolbert & Austin, 1959), as well as upwelling (Kamykowski, 1980) and downwelling events. From November to April, stronger winds and lower incident solar radiation cause the water column to be well mixed on the northwest shelf (Walsh et al, 2003). While the column is well mixed, there is a horizontal gradient of vertically uniform temperature, salinity, nutrients, and chlorophyll from the coastline to the outer shelf (Walsh et al, 2003; Grabowski et al., 2010). As the atmosphere warms and winds calm, the well mixed column and horizontal thermal gradient from the coastline to the shelf turns slowly to a vertical highly stratified water column of temperature, salinity, PAR, and nutrients (Walsh et al., 2003; Grabowski et al., 2010). Near bottom nutrient sources develop that are more likely to lead to a dinoflagellate response as was proposed by the original LJK model, and be able to maintain phytoplankton populations with this nutrient front.

Janowitz/Kamykowski Model

If a near bottom dinoflagellate population develops and is maintained, how does it become a surface bloom? LJK provided for dinoflagellate aggregation based on nutrient availability near bottom, cell growth, and the subsequent transport of the aggregate to the surface. Janowitz & Kamykowski (2006) further investigated the transport of diffuse near bottom dinoflagellate populations to a coastal front where swimming behavior interacted with frontal currents. As before, in this Eulerian model, each cell's migration was regulated by its own internal biochemical composition and the sediment interface became a source for

nutrient concentrations that were scarce in the overlying oligotrophic water column. The model predicted that near bottom nutrient sources associated with offshore upwelling or sediment flux was capable of attracting and sustaining a population dinoflagellate cells (Janowitz & Kamykowski, 2006). This near bottom population was advected shoreward through common upwelling currents transporting dinoflagellate cells undertaking diel vertical migrations between the sediment interface and the bottom of the euphotic zone (Janowitz & Kamykowski, 2006). At 25m, an upwelling front maintained by the flow dynamics formed with coastal water inshore of the front (Janowitz & Kamykowski, 2006). The bottom population was transported onshore by upwelling favorable advection and the near shore nutrient sources, cell behavioral responses, and frontal circulation patterns acted as a "trapping" mechanism to aggregate a bottom population at the surface as a full bloom (Janowitz & Kamykowski, 2006). This model suggests that a bottom dinoflagellate population could act as an important seed population source to surface coastal algal blooms.

Objectives

Cumulative observations in conjunction with modeling studies have shown that dinoflagellate cells that have the ability to migrate and exist at many depths, including the sediment interface, and form aggregates in response to a nutrient source. Models have also shown that a dinoflagellate population existing at the sediment interface can be transported shoreward and become concentrated at the surface in response to a near shore front. This paper reports the results of a July 2009 cruise on the northwest Florida shelf to:

1. Characterize the seasonal hydrography of the shelf during the summer stratified regime.
2. Explore the composition of the near bottom phytoplankton community including species dominance, depth/concentration variability, and cell size distribution.

   H1: We hypothesize dinoflagellates dominate in summer stratified regimes

   1) Characterizing the hydrography

   2) Analyzing community composition.

   H2: We hypothesize dinoflagellates exhibit a seasonal succession cycle

   1) Analyzing community composition by time

   H3: We hypothesize that dinoflagellates will dominate near bottom in depths where the euphotic zone separates from the sediment interface

   1) Analyze community composition by depth

Methods

General

An 8 day cruise on the R/V Pelican took place 8-15 July 2009 in the Gulf of Mexico on the northwest Florida shelf near Panama City FL, to sample a well stratified continental shelf. Acrobat profiles and 17 CTD/Rosette stations (9 out and 8 back) were completed

along two cross shelf transects forming a ‘V’ between the 20-70m depth contour lines (Fig. 2). In addition, two sets of time series stations were occupied following a drogue with a holey sock, one with the sock extending between 23-30 m in a 38 m water column and the other between 28-40 m in a 50 m water column.

Field Methods

An initial cross shelf transect was taken with an Acrobat to determine further station sites. Acrobat profiling of the ‘V’ shaped transect occurred in two 4 hr legs, one 4hr period for each side of the ‘V’, separated by about 12 hours (Fig. 2). The Acrobat was instrumented to collect information on salinity, temperature, density, light attenuation, CDOM fluorescence, dissolved oxygen, oxygen saturation, turbidity, and chlorophyll *a* concentrations. The profiles taken by the Acrobat were focused on undulated between 1m from the surface and 1 m from the sediment interface at depth contours between 20-70 m. These profiles described the structure of the water column across the shelf.

Seventeen stations were occupied along the two V-shaped transects (A 1-17) between the 20 and 70m depth contours, separated at regular intervals cross shelf (Fig. 2). Also, two time series transects (B&C) were taken with sampling every three hours for 30hr and 24hr, respectively (Fig. 9,15). The first time series (B) followed a holey sock drogue along the 30-35 m depth contour (Fig. 9), while the second time series (C) followed the drogue along the

50-53 m depth contour (Fig. 15). CTD casts were taken at each station measuring: depth, light attenuation, temperature, salinity, density, oxygen concentration, PAR attenuation, beam transmission, and chlorophyll fluorescence. The PAR distribution with depth and PERI are based on the beam transmission measurement calibrated against Secchi depths in the day time.

At each station several types of water samples were collected. Niskin bottle samples (~5L) were taken with attention focused near the sediment interface. Niskin bottle samples were taken as close to the sediment interface as possible, then at 2m intervals as well as the thermocline and the surface. For Chlorophyll *a*, 500 ml of water were filtered through 25mm GF-F filters (Strickland & Parsons 1968), wrapped in aluminum foil, and frozen in the ship board scientific cooler (Strickland and Parsons, 1968). For nutrients, 10 ml of the seawater from the chlorophyll filtration were frozen. Approximately 125ml of seawater were preserved with 4-5% of a Formalin and Tetra-borate solution at a concentration of 9 parts preservative to 1 part plankton biomass (Parsons et al., 1984). Near bottom, 10 µm net samples were taken at each station. Several Niskin bottles of approximately 5L each were triggered near bottom (20-25L total), brought on the deck, and then poured through the net and the volume recorded. The net was completely immersed in pre-filtered seawater as the sample was poured. Net samples were also preserved with 4-5% of a Formalin and Tetra-borate solution.

Lab Methods

Water samples for nutrients were thawed and analyzed against a standard of natural seawater with low nitrate concentrations. An automated method using the Seal Analytical QuAAtro Segmented Flow Analyzer system with a 10mm flow cell was used for analysis. In this method a standard of nitrate is reduced to nitrite at an approximate pH of 8, in a copperized cadmium reduction coil. The nitrite then reacts under the acidic conditions with sulfanilamide, is further complexed with naphthylethylene-diamine dihydrochloride (NEDD), and forms an azo dye that is measured at 550nm in the 10mm flow cell (American Public Health Association).

Chlorophyll filters were allowed to soak for 24 hours in 5 mls of 90% acetone in a freezer and centrifuged for pigment extraction (Strickland and Parsons, 1968). The fluorometer was calibrated using culture samples of *Thalassiosira weissflogii* and *Prorocentrum* filtered on a 47mm GF-F filter, measured on a spectrophotometer (Strickland and Parsons, 1968). Fluorescence readings were taken at a wavelength of 664 nm with an acidification step using on a Turner Fluorometer (Strickland and Parsons, 1968).

For phytoplankton identification, the samples were fairly dilute. A 100 ml sample was settled in Utermohl settling chambers for 24 hrs, with all organisms collected in the bottom plate. To test the efficiency of the settling and FlowCAM method of analysis, several tests were performed to gain an efficiency rate. Active cultures of *Prorocentrum minimum* were used for these tests, since this species is common on the WFS. A subsample of 10 ml was

taken from each culture and mixed thoroughly to keep the cells as uniform as possible. Of the subsample, 5 ml were tested with the FlowCAM under the same set up used for cruise samples for cell counts. Another 5ml of the subsample was preserved with the Formalin and Tetra-borate solution and ~45 ml of filtered sea water were settled in a 50ml Utermohl settling chamber for 24hrs. This settled sample was then analyzed in the FlowCAM to compare cell counts to the previous unsettled subsample. This experiment was performed in triplicate. This comparison of cell counts between settled and unsettled samples yielded an approximately 70% efficiency rate in our technique.

For field samples, approximately 2 ml collected from the bottom plate of the 100 ml settling column was rinsed with 3 ml of filtered seawater to ensure all organisms were collected from the settling slide. The 5 ml sample was then size fractionated through a 100um mesh and analyzed on the FlowCAM. The FlowCAM was set up on auto image mode with the 100um flow cell and the 10x objective while pumping at an average setting of about 7 on fast mode. Size filters were applied to isolate and capture particles between 10-100 μm in diameter (ESD). To ensure no contamination between samples the flow cell was cleaned thoroughly with filtered seawater and methanol between samples. Niskin samples from the bottom two depths and near bottom net filtrations were subject to the FlowCAM analysis.

Analysis

Data collected along the transect via the CTD was processed using Seabird software and later analyzed in lab using SBE Data Processing and Ocean Data View (ODV) software. CTD profiles of temperature, salinity, sigma-t, and PAR were constructed with the ODV software for the vertical water column at all stations across the transect. The potential euphotic zone depths (PERI) for both day and night, as well as PAR measurements, were calculated from beam transmission measurements calibrated against Secchi depths in the daylight. Chlorophyll *a* and nitrate-nitrite determinations for each profile at each station along the transect was further analyzed with ODV. The vertical profiles interpolated with ODV software made it easier to compare the results from the profiles taken by the Acrobat.

Results

Cross shelf Transect

Survey Acrobat Maps

The two Acrobat tows of ~4 hours each were taken prior to station sampling to characterize the hydrography on the shelf synoptically (Fig. 2). Temperature measurements

for both sides of transect ranged between ~22 ºC at the sediment interface and ~27 ºC at the surface and formed a mid-depth thermocline ranging between 10m inshore to 25m offshore (Fig. 3a,e). Salinity ranged from 35-36 in the upper 20m of the vertical column and was over 36 in the lower part of the water column from approximately 25m to the sediment interface (Fig. 3b,f). The resulting potential density profile showed a high degree of stratification with warmer, lower salinity water in the upper half of the water column, and cooler, higher salinity water in the lower half of the water column to the sediment interface (Fig. 3c,g). Chlorophyll *a* measurements derived by fluorescence on both sides of the transect show that the upper water column to ~20m had <0.5 µg/L, while the lower water column to the sediment interface showed 0.5 and 1.5 µg/L (Fig. 3d,h). A chlorophyll *a* maximum occurred near bottom at approximately the 30m contour with ~1.5 µg/L (Fig. 3d,h).

Survey CTD Stations

The CTD survey spanned between 20-65m depth across the shelf at 17 stations in a "V" formation with 8 equally spaced stations on either side and one at the deepest point (Fig. 2). Temperature ranged from 20 ºC near bottom to 28 ºC at the surface and formed a mid-depth thermocline ranging between 10m inshore to 25m offshore (Fig. 4a). The coldest water was found at the bottom of the 65m station measuring ~17.5 ºC. Salinity below 20m depth was fairly stable, measured between 36-37 (Fig.4b), while in the upper 20m salinity ranged from 34.5 at the 65m station to ~35 at the inshore stations. Sigma-t exhibited strong

stratification of the water column, surface density profile was influenced by salinity while deeper density was influenced by temperature (Fig. 4c)

The inshore sections of both sides of the 'V' occurred in daylight, while the offshore section occurred at night (Fig. 5a). PERI, a deviation of light attenuation based on Secchi measurements or beam attenuation showed that the bottom of the euphotic zone or the 1% PAR light level separated from the sediment interface at approximately 40-45m (Fig. 5b). Thus, only water columns greater than 50m received PAR insufficient for net photosynthesis at the sediment interface. Nitrate-nitrite concentrations were concentrated near the sediment interface at all stations across the transect with a nitrocline at about 20m above the bottom. The upper 20m of the water column was always found to be depleted of nitrate-nitrite (<<1 µg/L) across both sides of the transect (Fig. 5c). NO3+NO2 concentrations near bottom were measured at approximately 2 µg/L in depths less than 40m, then measurements increased to ~4 µg/L between 40-50m near bottom, and the highest concentrations of 8-10 µg/L were found at the sediment interface at the 55-65m depth contour (Fig. 5c). Chlorophyll *a* concentrations were generally low at <0.03 µg/L at all depths across the shelf except for two distinct near bottom chlorophyll *a* maxima present at approximately the 30m contour with concentrations approaching 0.15µg/L (Fig. 5d).

Based on FlowCAM results, dinoflagellates accounted for the majority of the counted phytoplankton population at all stations between 20-70m across transect A (Fig. 6). Inside the 30 m contour, diatoms concentrations found were usually less than 2000 cells/L near the

bottom across the entire transect (Fig. 6). Dinoflagellates showed much higher concentrations near bottom ranging from 4000-13000 cells/L (Fig. 6). The mean for dinoflagellates found near bottom for transect A was 8322 +/- 2894 cells/L, a standard error of 701.9, and the 95% confidence limits range is +/- 1488 cells/L. The means for diatoms found near bottom for transect A was 784.1 +/- 378.3, cells/L, 91.75 standard error, and 95% confidence limits range +/- 194.5 cells/L. The difference in the mean values between dinoflagellate and diatom groups is greater than would be expected by chance and according to t-tests and there is a statistically significant difference between the mean values groups according ($t=10.64$, $df=17$, at $P = <0.001$ and $alpha=.05$). The dinoflagellate and diatom classes were further sub-divided (Fig. 7) with diatoms represented by pennates and centrics, and dinoflagellates by *Prorocentrophycidae*, *Peridiniphycidae/Gymnodiniphycidae*, and *Dinophysiphycidae*. For diatoms, pennate abundance (200-850 cells/L) exceeded centric abundance (0-700 cells/L) for the majority of stations along the transect, though centrics were much more abundant inshore of ~35m (800-900 centrics/L vs.200-400 pennates/L) (Fig. 7). Centrics (mean 359.4 +/- 297.5, standard error 72.16, 95% confidence Interval +/- 152.9) exceeded pennates (mean 448 +/- 211.4, standard error 51.27, 95% confidence Interval +/- 108.7) at the two shallower stations at 23m and 27.5m and were more abundant at the other inshore stations, and at one deeper station at 50m (Fig. 7). For the two dominant dinoflagellate sub-groups, *Peridiniphycidae/Gymnodiniphycidae* (mean 4657 +/-1589, standard error 385.4, 95% Confidence Interval +/- 817.1) counts of 2200-7100 cells/L exceeded *Prorocentrophycidae* (mean 3574 +/- 1450, standard error 351.8, 95% Confidence

Interval +/- 745.8) counts of 2000-6000 cells/Lat almost all stations across the transect except for two inshore stations (26m and 22m) where *Prorocentrophycidae* concentrations were greater by almost 2000 cells/L (Fig.7). *Peridiniphycidae/Gymnodiniphycidae* cells, while very abundant inshore, showed their highest concentrations (>7000 cells/L) to be at deeper stations (58m and 47m contours) near bottom (Fig. 7). The differences in the median values among the treatment groups were greater than would be expected by chance and there is a statistically significant difference between the means of each subclass according to ANOVA tests ($F= 91.84$, $F_{critical}=2.798$, $df=3$, $p = <0.001$). While comparison between two diatom subclasses or two dinoflagellate subclasses were not statistically significant, comparisons between any dinoflagellate subclass to any diatom subclass were statistically significant according to Tukey multiple pairwise comparison tests. Size class distribution analysis was also preformed on the dinoflagellate concentrations that were collected across the transect (Fig. 8). Overall, the dominant size class over the entire transect was the 11-20 µm size range by approximately 10% over any other size classes, followed by the 21-30 µm size class and the 0-10 µm size class (Fig. 8). Concentrations of larger size classes > 50µm usually only made up less than 10% of the near bottom phytoplankton population, less than 10000 cells/L (Fig. 8). Several size classes showed similar peaks at approximately the same depth contours on both legs of the cross shelf 'V'. For example, in the 11-20 µm size range, peaks occurred at 66 m and then at ~35 m and ~20 m (Fig. 8), showing a pattern of size class distribution that spans across the shelf. There is a statistically significant difference of the means between size classes according to ANOVA ($df=3$,$P = <0.001$). Tukey multiple

pairwise comparison tests show a statistically significant difference between larger size classes compared to smaller size classes but not a significant difference between similar smaller size classes.

Time Series CTD Stations at the 30-35m Contour

During the first time series transect (B), CTD/Rosette samples were taken over a 30 hour time period, following a holey sock drogue that moved along the 30-35 depth contour (Fig. 9). The coldest temperatures occurred near bottom at 22.5 ºC and warmest at the surface of ~27.5 ºC throughout the entire time series (Fig. 10a). The highest salinities were in the lower 20m of the water column to the sediment interface of 36-36.5 and lowest salinities were in the upper 20m of the vertical water column of 34-35.5 (Fig. 10b). Sigma-t profile was stable with the highest density of 24 kg/m^3 in the lower 25m of the column and lowest density of 22-24 kg/m^3 at the surface (Fig. 10c).

Secchi and beam transmission readings showed the night to day to night transition over the time series (Fig. 11a) with 9 hours of dark and 12 hours of daylight followed by another 6 hours of darkness. PERI calculations throughout the time series showed that the 10% PAR level was fairly consistent at ~20m and the bottom of the euphotic zone (1% PAR) was at the sediment interface for the majority of time series (Fig. 11b). At two samples periods, 2 hrs. and 9 hrs., the euphotic zone did not penetrate to the sediment interface (Fig.

11b). At 2hrs, around sun rise, the bottom of the euphotic zone was at 30m in a 40m vertical column, and at 9 hrs., around sun set, the bottom of the euphotic zone was at 35m in a 40m vertical column (Fig. 11b). Near bottom nitrate-nitrite concentrations were higher (1.5 µM) at the very beginning of the transect (dusk) and decreased rapidly to <0.25 µM by sun rise of the first night (Fig.11c). Throughout the daylight period nitrate-nitrite concentrations near bottom were approximately 0.5 µM, and at sunset the concentration decreased to 0.25 µM, and continued to decrease throughout the night to concentrations of less than 0.25 µM (Fig. 11c). The highest concentrations of nitrate-nitrite found near bottom were usually during the daylight hours then decreased as the night wore on and increased during the day (Fig. 11c). Near bottom chlorophyll *a* was 0.15 µg/L at the beginning of the transect at night near bottom at 40m with lower concentrations of chlorophyll *a* approaching 0 µg/ at 30m in the 40m column (Fig. 11c). At sunrise, chlorophyll *a* concentrations were consistent in the bottom 10m of the water column to the sediment interface at 0.3 µg/L (Fig. 11d). During the daylight hours the profile of chlorophyll *a* in the bottom 10m of the 40m column was stratified with concentrations <0.1 µg/L at the sediment interface and 0.3 µg/L at 30m (Fig. 11d). At sunset the bottom 10m of the 40m column was uniform with chlorophyll *a* concentrations of ~0.25 µg/L (Fig. 11d). During the last night of the time series the bottom 10m of the 40m column had a higher chlorophyll a concentration at the sediment interface of ~0.3 µg/L and concentrations of 0.1 µg/L at 10m from the bottom (Fig. 11d). The pattern of chlorophyll distribution through the time series showed higher bottom (~ 40 m depth)

concentrations at night and higher concentrations ~10 m above the bottom at 30 m depth during the day (Fig. 11d).

FlowCAM field samples for time series B were analyzed for percent abundance of dinoflagellates and diatoms that made up the phytoplankton population near bottom (Fig. 12). The analysis of samples taken 8m from the bottom in a 40m water column showed that dinoflagellates (mean 7596 +/- 2216, standard error 668.1, 95% confidence intervals +/- 1488) usually made up ~80-90% (~4000-10000 cells/L) of the counted phytoplankton population while diatoms (mean 1285.4 +/- 485.3, standard error 146.3, 95% confidence interval +/- 326) only made up 10-20% (<2000 cells/L) of that population, with very little fluctuation in concentrations over day and night periods (t-tests between dinoflagellates and diatoms measured a statistical difference of means with: t=9.226, df=11, alpha=.05) (Fig. 12). Samples taken at the sediment interface showed dinoflagellates (mean 7318.1+/- 1970, standard error 594.2, 95% confidence interval +/- 1324) continued to have the highest abundance of the counted phytoplankton population making up 60-90% of the population (3400-10300 cells/L) over diatoms (mean 2363 +/- 861.2 , standard error 259.6, 95% confidence interval +/- 578.5) which made up only 10-40% (1200-400 cells/L), but with a much more pronounced fluctuation of concentrations over day-night periods, in particular at sunrise (Fig. 12). Statistical t-tests showed a difference in means between dinoflagellates and diatoms near bottom with t= 7.639, df=14, and alpha=.05. Numerical FlowCAM results for dinoflagellates showed a similar day/night transition of the dinoflagellates concentrations

between samples at the sediment interface and from 8m off the bottom (Fig. 13). Throughout the entire time series, phytoplankton subclass distributions also showed the dominance of any dinoflagellates subclass over that of diatom subclasses (Fig. 13). The dinoflagellate subclass distribution was dominated mainly by *Peridiniphycidae/Gymnodiniphycidae* and *Prorocentrophycidae* cells, while very few *Dinophysiphycidae* cells were found for the July cruise and were not included in major analyses (Fig. 13). In the mid column samples (8m from the bottom) for the majority of the transect, the concentrations of *Peridiniphycidae/ Gymnodiniphycidae* cells were between ~2000-7500 cells/L (mean 4552 +/- 1713, standard error 516.5, 95% confidence interval of +/- 1150) were more abundant than *Prorocentrophycidae* cells at concentrations between 1000-4500 cells/L (mean 2820 +/- 874.7, standard error 263.7, 95% confidence interval of +/- 587.6), except for during the second night of the time series (at ~23hrs.) when *Prorocentrophycidae* cells showed a small dominance over *Peridiniphycidae/Gymnodiniphycidae* cells in mid samples (Fig. 13a). The concentrations of diatoms partitioned between pennates (mean 760 +/- 230.9, standard error 69.64, 95% confidence intervals of +/- 155.1) and centrics (mean 518.1 +/- 359.3, standard error 108.3, 95% confidence interval of +/- 241.4) fluctuated throughout the time series in mid column samples and were fairly consistently at <1000 cells/L for mid samples (Fig. 13a). A similar pattern of phytoplankton dominance was seen in samples taken as close to the sediment interface as possible (Fig. 13b). Again, *Peridiniphycidae/Gymnodiniphycidae* was the dominant dinoflagellate over that of *Prorocentrophycidae* for most of the time series, though there were many more instances of a more even distribution between the two

subclasses (6hrs., 12-15hrs., and 24-30hrs.) than in the mid samples. *Peridiniphycidae/Gymnodiniphycidae* cells ranged in concentrations from ~1500-4000 cells/L and *Prorocentrophycidae* ranged from ~1700-7500 cells/L over the time series (Fig. 13). Bottom samples of diatom subclasses were similar to mid column samples in that pennate (mean 727.2 +/- 443.6, standard error 133.7, 95% confidence interval +/- 298) and centric (mean 1516 +/- 940.7, standard error 283.6, 95% confidence interval +/- 631.9) dominance fluctuated over the course of the time series in concentrations between 0-2000 cells/L (Fig. 13b), with one exception of a high centric dominance (~4000 cells/L) over pennates (<3000 cells/L) at the end of the time series (22-30hrs.). *Peridiniphycidae/Gymnodiniphycidae* cells (mean 4385 +/- 1705, standard error 514.1, 95% confidence interval +/- 1145) dominated over that of *Prorocentrophycidae* cells near bottom (mean 2816 +/- 835.7, standard error 251.9, 95% confidence interval +/- 561.4). ANOVA tests did show a difference in means of each phytoplankton subclass for bottom ($F= 24.79$, $p<.001$, f crit= 2.922, df=3, alpha=.05) and mid samples ($F= 52.27$, $p<.001$, f crit= 2.92, df=3, alpha=.05). A comparison of mid (8m from the bottom) and bottom samples showed an inverse relationship of dinoflagellates between the two. During daylight periods the dinoflagellate subclasses *Prorocentrophycidae* and *Peridiniphycidae* had higher concentrations in mid samples compared to bottom samples (Fig. 13a, b). During nighttime periods, dinoflagellate subclass concentrations near bottom seemed to be greater than or equal to dinoflagellates concentrations in mid samples (Fig. 13a, b)

Size class analysis of the dinoflagellate cells of bottom and mid column samples showed similar results to similar depths in the survey transect (A) (Fig. 14). For both mid and bottom samples, the majority of the time series were dominated by the 11-20 µm size class, closely followed by the 21-30 µm sized cells (Fig. 14). One exception to the 11-20 µm cell size dominance was found in the mid samples during the first night of the transect, when there was a dominance of 20-31 µm dinoflagellates (~550 cells/L) over that of the 11-20 µm dinoflagellates (~300 cells/L) (Fig. 14a). Smaller size classes of 0-10µm cells were concentrated < 250 cells/L in mid samples (Fig. 14a). Larger size classes of 50-100µm usually showed concentrations of less than 100 cells/L in mid samples (Fig. 14a). In samples taken near bottom, the 11-20 µm size class dinoflagellate cells dominated throughout the entire time series, ranging from 150-600 cells/L, while the 21-30 µm sized dinoflagellates showed concentrations of 100-550 cells/L (Fig. 14b). Smaller sized cells, 0-10 µm were concentrated at less than 100 cells/L, and larger cells 50-100 µm were also concentrated at less 100 cells/L near bottom (Fig. 14b). Another notable observation of the size class analysis was that though the 11-20um cells dominated at the bottom for the entire transect, peak concentrations are usually much higher during the night periods of the transect compared to day periods (Fig. 14b). Likewise, peak concentrations of 21-30µm sized cells in bottom samples were higher during the day periods compared to night periods during the time series (Fig. 14b).

Time Series CTD Stations at the 50m Contour

The second time series transect (C) was similar to the first time series (B), but this transect followed a holey sock drogue along the 50m depth contour for a period of 24 hours (Fig. 15). Temperature ranged from ~30 ºC at the surface and ~22 ºC near the sediment interface and salinity ranged from ~33 at the surface and ~36.5 near the sediment interface (Fig. 16a,b). Sigma-t was ~21 g/cm³ at the surface due to warmer, lower salinity water and ~26 g/cm³ near bottom due to colder, higher salinity water with a pycnocline at ~10m (Fig. 16c).

Secchi and beam transmission readings showed the transition from daytime light attenuation in the water column to negligible light attenuation at night over the time series 6 hours of daylight, then darkness for 12 hours, then back to daylight for 6 hours (Fig. 17a). PERI measurements made from the beam transmissometer on the CTD through the water column and calibrated with Secchi measurements during the day showed that throughout the time series the bottom of the euphotic zone (1% PAR) to be at 45m depth (Fig. 17b). These readings also showed that the euphotic zone never penetrated to the sediment interface in the ~50 contour (Fig. 17b). Nitrate-nitrite concentrations near bottom ranged from 2-4 µg/L over the course of the time series in the 50m column (Fig. 17c). During the night period of the time series there was more nitrate-nitrite at the sediment interface (4µg/L) compared to daytime concentrations of approximately 2-3µg/L (Fig. 17c). The highest concentrations of

chlorophyll a found near bottom were during the nighttime period with concentrations of 0.1µ g/L compared to daytime near bottom concentrations of less than 0.05 µg/L (Fig. 17d).

Over the entire period of the time series (C), both day and night periods, dinoflagellates dominated over diatoms at all sampled depths between 20-60m, though in mid samples (8m from the bottom) concentrations between the two were much more similar than in bottom samples and top (16m from the bottom) samples (Fig. 18). In samples taken 16m from the sediment interface (top samples) dinoflagellates made up between 60-90% (~2500-7000 cells/L) of the phytoplankton population, while diatoms made up only 10-40% (at most ~2000 cells/L) of the population (Fig. 18a). At sunset in top samples (9 hours) the dinoflagellate and diatom populations were at their closest concentrations (40% diatoms, 60% dinoflagellates), but as the nighttime continued, the concentrations changed to ~10% diatoms and ~90% dinoflagellates at sunrise (21 hours) (Fig. 18a). In mid column samples (8m from the bottom), concentrations of diatoms ranged between 10-50% (~300-2500 cells/L) of the population and dinoflagellates comprised between 50-90% (1000-18000 cells/L) of the counted phytoplankton population over the course of the time series (Fig. 18b). At sunset (6 hours), diatoms and dinoflagellates showed similar concentrations in mid column samples (50% diatoms, 50% dinoflagellates) compared to sunset (18 hours) when dinoflagellates comprised 90% of the population and diatoms only comprised 10% of the population 8m from the bottom (Fig. 18b). Samples taken at the sediment interface also show a greater abundance of dinoflagellates (~2500-15000 cells/L) making up 60-90% of the

phytoplankton population compared to diatoms (~900-2900 cells/L) making up only 10-40% of the population (Fig. 18c). Again, the concentrations of dinoflagellates and diatoms were closest at sunset (40% diatoms, 60% dinoflagellates) and continued to separate during the night when at approximately midnight (12 hours) dinoflagellates comprised 90% of the population and diatoms comprised only 10%, this appeared earlier in the night compared to mid and top samples where the largest difference in percent dominance was found at sunrise (~18-21 hours) (Fig. 18c). There seems to have been an inverse relationship between the concentrations of dinoflagellates between the bottom samples and mid/top samples (8m/16m from the bottom) over the course of the time series (Fig. 19). During daylight hours top and mid samples had higher concentrations of both dinoflagellate subclasses for the majority of the day compared to bottom samples (Fig. 19). During nighttime periods, bottom samples had the highest concentrations of dinoflagellate subclasses compared to mid and top samples (Fig. 19). Diatoms tend to remain at the highest concentrations in bottom samples rather than mid or top samples during the entire time series, regardless of the day/night transition (Fig. 19). In top samples, dinoflagellate cells had a mean of 4808 +/- 1967, standard error 743.6, 95% confidence interval +/- 1819 and for diatoms the mean is 1305 +/- 478, standard error 180.6, 95% confidence interval +/- 442. There is a statistically significant difference in the means of dinoflagellates and diatoms in top samples according to ANOVA (F=4.5769, df=7, alpha=.05). In mid samples, dinoflagellates had a mean of 7131 +/- 5802, standard error 1934, 95% confidence interval +/- 4459 and diatoms has a mean of 1611 +/- 620.6, standard error 206.8, 95% confidence interval +/- 477. There is also a statistically significant different

in the means of dinoflagellates and diatoms in mid samples according to ANOVA (F=2.83, df= 8, alpha=.05) In bottom samples, dinoflagellates had a mean of 8195 +/- 4405, standard error 1468, 95% confidence interval +/- 3386 and diatoms have a mean of 2035 +/- 895.7, standard error 298.5, 95% confidence interval +/- 688.5. There is a statistically significant difference between mean dinoflagellates and diatoms in bottom samples according to ANOVA (F=4.1110, df=9, alpha=.05).

All depths show that the most abundant phytoplankton subclass found is the *Peridiniphycidae/Gymnodiniphycidae* cells followed closely by the *Prorocentrophycidae* cells at all depths sample throughout the time series, though the difference between the two subclasses is not statistically significant at any depth according to t-tests, which is similar to the results from Transect A. Pennate and centric diatoms at all depths were found to have similar concentrations that were always much lower than that of all other dinoflagellate subclasses found near bottom at any depth sampled. The difference between pennate and centric concentrations is not statistically significant according to t-tests. ANOVA comparisons tests between all subclasses of phytoplankton show a statistically significant difference between the means of dinoflagellates subclasses and diatoms subclasses at top (F=15, f crit=3.159 df=3, alpha=.05, p<.001), mid (F=8.412, f critical=3.008, p<.001, alpha=.05), and bottom samples (F=18.91, f critical= 3.00, p<.001, alpha=.05).

From a size class perspective (Fig. 20a, b), top and mid samples showed a close relationship among the concentrations of cells of each size class. The 11-20 µm size class

dominated throughout making up 10-30% population in top samples and 5-70% of the population in mid samples, followed by the smallest size class of 0-10 µm making up 5-20% of the population in top samples and 5-45% of the population in mid samples, while larger size classes 21-100 µm made up less than 10% of the population in top and mid samples (Fig. 20a, b). Top and mid samples were fairly cohesive in their size class distribution and it should also be noted that concentrations in top and mid samples were much lower than bottom samples and there was not as much of a difference in concentrations between day and night compared to bottom samples (Fig. 20a,b). There is a larger mixture of size classes of phytoplankton cells in the bottom samples. Tukey multiple pairwise comparison tests showed a statistically significant difference between the means of larger size classes compared to smaller size classes but not a significant difference between similar size classes. During both daylight periods (0-6 hrs and 18-24hrs), bottom samples were clearly dominated by the 11-20 µm size class comprising 15-30% the first day and 25-65% the second day, followed by 0-10 µm size class comprising 15-25% of the population the second day (Fig. 20c). Nighttime periods (6-18hrs) showed a higher concentration of 11-20 µm size classes near sunset (6hrs) of 35% of the population and sunrise (15-18hrs) of ~70% of the population, with a distinct peak of 21-30 µm sized cells at midnight (~12hrs) that made up almost 100% of the dinoflagellate population near bottom (Fig. 20c).

Discussion

The hydrography across the shelf during the July 2009 cruise represented the typical summertime regime normally found on the northwest Florida shelf. As characterized for the west Florida shelf (Walsh et al., 2003), the water column was vertically stratified according to Acrobat and CTD data. Offshore temperatures in the deepest columns (~60m) sampled normally ranged from approximately 20ºC near bottom to ~28ºC at the surface, while the inshore temperature range was smaller range between the bottom (~22.5ºC) and the surface (~25ºC) (Fig. 4a). Salinity pattern across the shelf was similar to temperature with a larger range in the deepest columns (~60m) between 36.5 at the bottom and 34.5 at the surface and a smaller range in shallower columns (~30m) of 36 at the bottom and ~34.5 at the surface (Fig. 4b). Sigma-t derived from temperature and salinities showed stable stratification of the water column across the shelf with colder, saltier water near bottom and warmer, fresher water at the surface (Fig. 4c). The bottom of the euphotic zone (1% PAR) was consistently between 40-45m across the shelf (Fig. 5b, 11b, 19b), so that in columns shallower than 45m the euphotic zone penetrated to the sediment interface. Nitrate-nitrite concentrations were consistently found to higher at the sediment interface compared to the overlying water column (Fig. 5c, 11c, 19c). This was especially true in the deeper water column (>50m) where the highest concentrations of nitrate-nitrite (~8 µg/L) at the sediment interface was found compared to the overlying water column which showed concentrations of less than 1ug/L nitrate-nitrite (Fig. 5c). In response to the high nutrient concentrations at the sediment

interface, patches of higher chlorophyll a also occurred near bottom (Fig. 5c, 17c). Inshore in columns where the euphotic zone still penetrates the sediment interface chlorophyll a maximum of ~0.1µg/L were often found at the sediment interface in water columns less than 40m (Fig. 5d, 11d). Given the stability provided by stratification and clarity of the water column across the shelf along with the near bottom sources of nitrate-nitrite and the corresponding chlorophyll a concentrations at the sediment interface, phytoplankton, including dinoflagellates, is able to sustain a population at the sediment interface.

From the FlowCAM results of the survey Transect A , dinoflagellates exist near bottom and dominate over diatom cells at all depths contours to share in the utilization of sediment nutrient concentrations, not just at depths beyond where the euphotic zone separates from the sediment interface (Fig. 6). Inshore of the 45 m contour, these pelagic populations must compete with the microphytobenthos for sediment nutrients. If benthic algae require light for nutrient uptake, then the pelagic dinoflagellates that aggregate at the sediments at night can utilize the sediment resources based on dark uptake (Sinclair et al. 2006). This dark adapted uptake of nutrients at the sediment interface would explain why higher concentrations of the subclasses of both dinoflagellates found were higher at the sediment interface at night rather than during the daytime. During the daytime, concentrations of dinoflagellates would be expected to be higher in water column seeking adequate light for photosynthesis. The distance which cells can migrate between the nutrient rich sediment interface and the bottom of the euphotic zone is based on migration speed (Kamykowski &

McCollum 1986). Since the euphotic zone extends to the sediment in shallow water, there is no specific selection for dinoflagellate cell size based on swimming speed.

In deeper water columns outside of the depth where the euphotic zone separates from the sediment interface (>45m), the difference in concentrations of dinoflagellates relative to diatoms increased (Fig. 6). Dinoflagellates are capable of migrating between the sediment and the euphotic zone whereas diatoms cannot. The dominate size class is 11-20μm with significant contributions from 21-30 μm. (Fig. 8). These size classes are typical for *Prorocentrophycidae, Peridiniphycidae,* and *Gymnodiniphycidae* cells (Fig. 7) and span probable swimming speeds from 100-500 μm/s (Kamykowski & McCollum 1986). These speeds allow cells to range between the sediment interface and 4-22m above the sediment interface in 12 hours. Swimming speed comparisons for different dinoflagellate species suggest that cells ~35μm in diameter exhibit the fastest swimming speeds of ~600 μm/s (Kamykowski & McCollum 1986). The size and shape of the cell can affect the swimming speed of a cell as well as its distribution near bottom. Larger cells are not always found near bottom, despite their enhanced swimming speed, because the cell may not easily penetrate into the sediments to uptake nutrients. A mid range cell size of 11-20μM was found to be the most abundant cell size associated with the near bottom niche. Elevated nutrient concentrations at the sediment interface are adequate to provide a nutrient source for these cells compared to the rest of the oligotrophic overlying water column (He & Weisberg, 2003). Based on swimming speed dependence on cell size, smaller, slower swimming cells

(11-20μm) should be limited to near the 45 m contour under the sampled July 2009 conditions, while the larger size, faster swimming cells class (21-30 mm) should be capable of surviving farther offshore.

Differential peaks in chlorophyll a that show a tendency toward higher concentrations at night near the sediment interface suggest that dinoflagellate populations may be accumulating near the sediment interface as a result of diel vertical migration. However, the FlowCAM dinoflagellate concentration data are not sufficiently statistically robust to describe temporal trends. At best, the 30-35 m contour concentrations tend to oscillate without a clear relationship to the day/night cycle, the 50 m contour concentrations tend to increase through the time series. The near bottom size class data suggest, however, that the 21-30 μm size class is more abundant at the 50 m contour than at the 30-35m contour. These data support the hypothesis that larger, faster swimming dinoflagellates may thrive on the outer shelf under the sampled July conditions. (Fig. 13, 19).

Several aspects of the July 2009 data set provide support for the Janowitz & Kamykowski (2006) model. Nutrients were available near the sediment interface and the euphotic zone penetrated to the 45m depth. A near bottom chlorophyll maximum occurred at the ~30m contour. Dinoflagellates dominated over diatoms near the bottom across the shelf to the 65 m contour. While the biological aspects of the Janowitz & Kamykowski model were based of *Karenia brevis* (swimming speed, nitrogen uptake, photoinhibition, etc.), only a few *K. brevis* cells were identified against a background of primarily *Prorocentrophycidae*.

The data suggest that a general dinoflagellate niche on the west Florida shelf. The July 2009 conditions did not include upwelling favorable winds, but the near-sediment dinoflagellate populations were staged for onshore transport under upwelling favorable conditions.

Further studies on near bottom dinoflagellate populations on the northwest Florida shelf would provide more insight into the accuracy of the previously published models. In situ measurements of nutrient uptake, especially nocturnal uptake, and diel vertical migration rates by dinoflagellate cells near bottom would increase the accuracy of existing models. Near bottom dinoflagellate populations could have major implications in the initiation, formation, and transportation of algal blooms on the coastlines. Insights on the near bottom dinoflagellate populations could easily be added to current algal bloom models in the Gulf of Mexico to more accurately describe, predict, and monitor algal blooms on the northwest Florida shelf.

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FIGURES

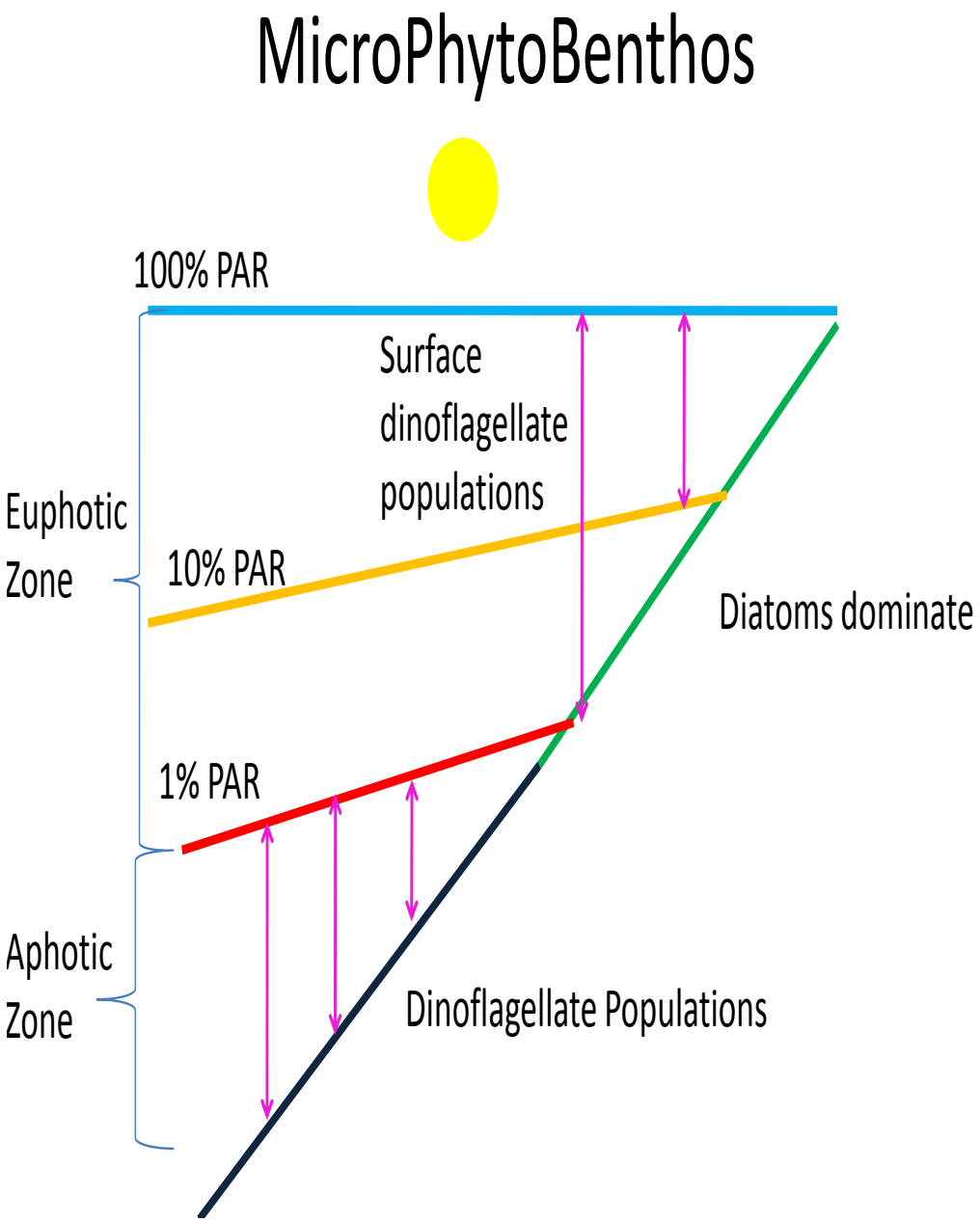

Figure 1. Proposed microphytobenthos separation of sediment bound nutrients.

Transect A

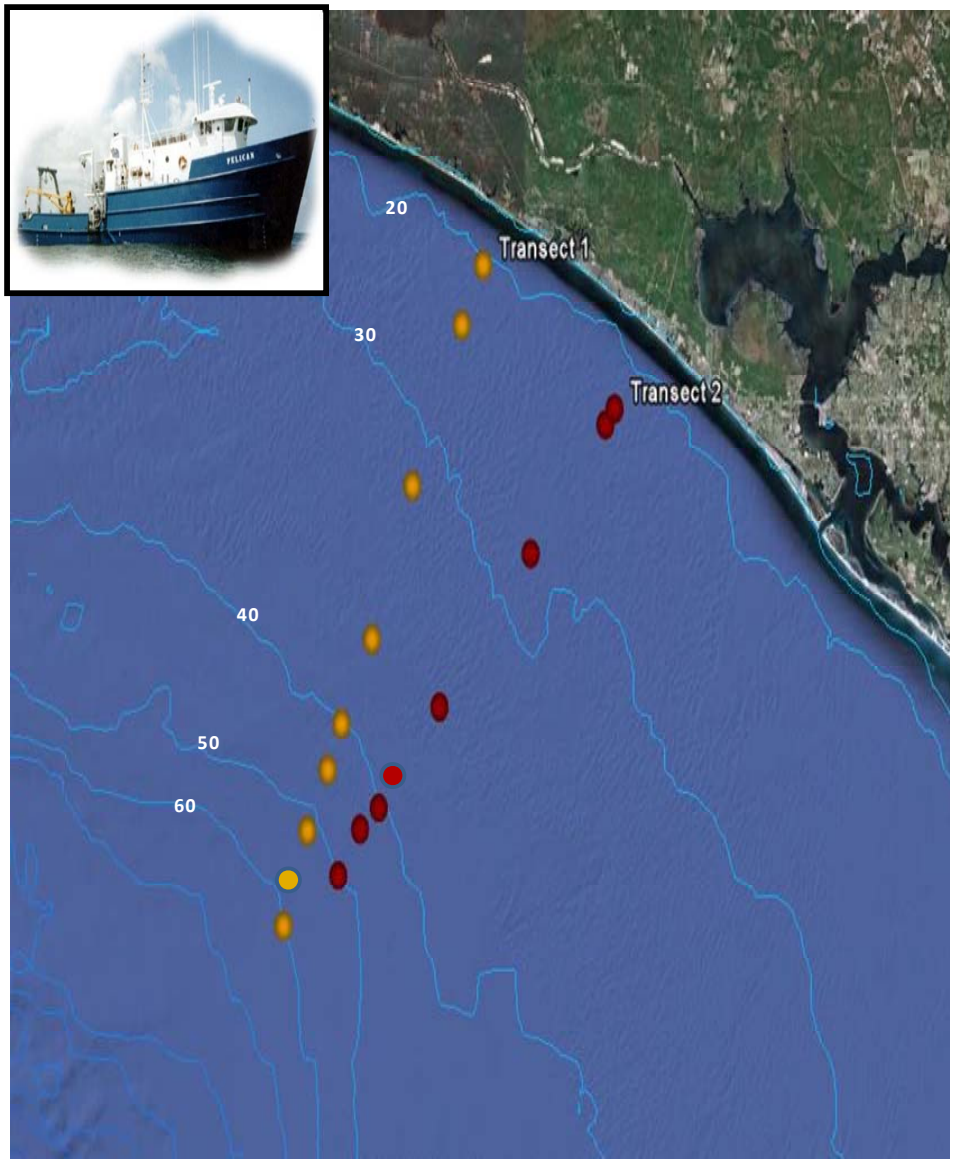

Figure 2.17 stations between 20-60m for Transect A on the northwest Florida shelf in July 2009

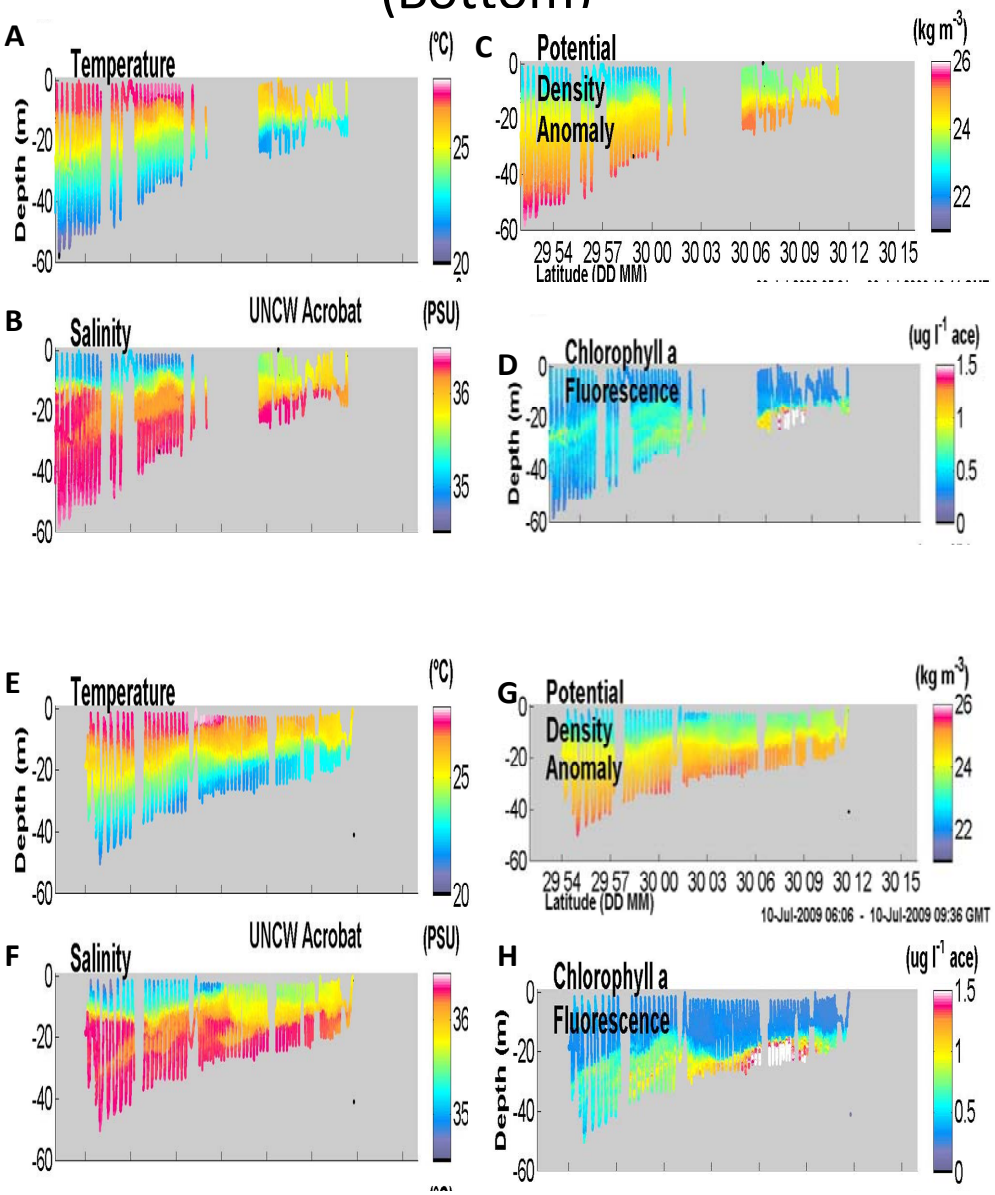

Figure 3. Acrobat transect surveys, 4 hour tows. Stations A9-A1 (60m-20m) recorded A) Temperature, B) Salinity, C) Potential density , and D) Chlorophyll a Fluorescence, stations A9-A17 (60m-20m) recorded E) Temperature, F) Salinity, G) Potential density, H) Chlorophyll a Fluorescence

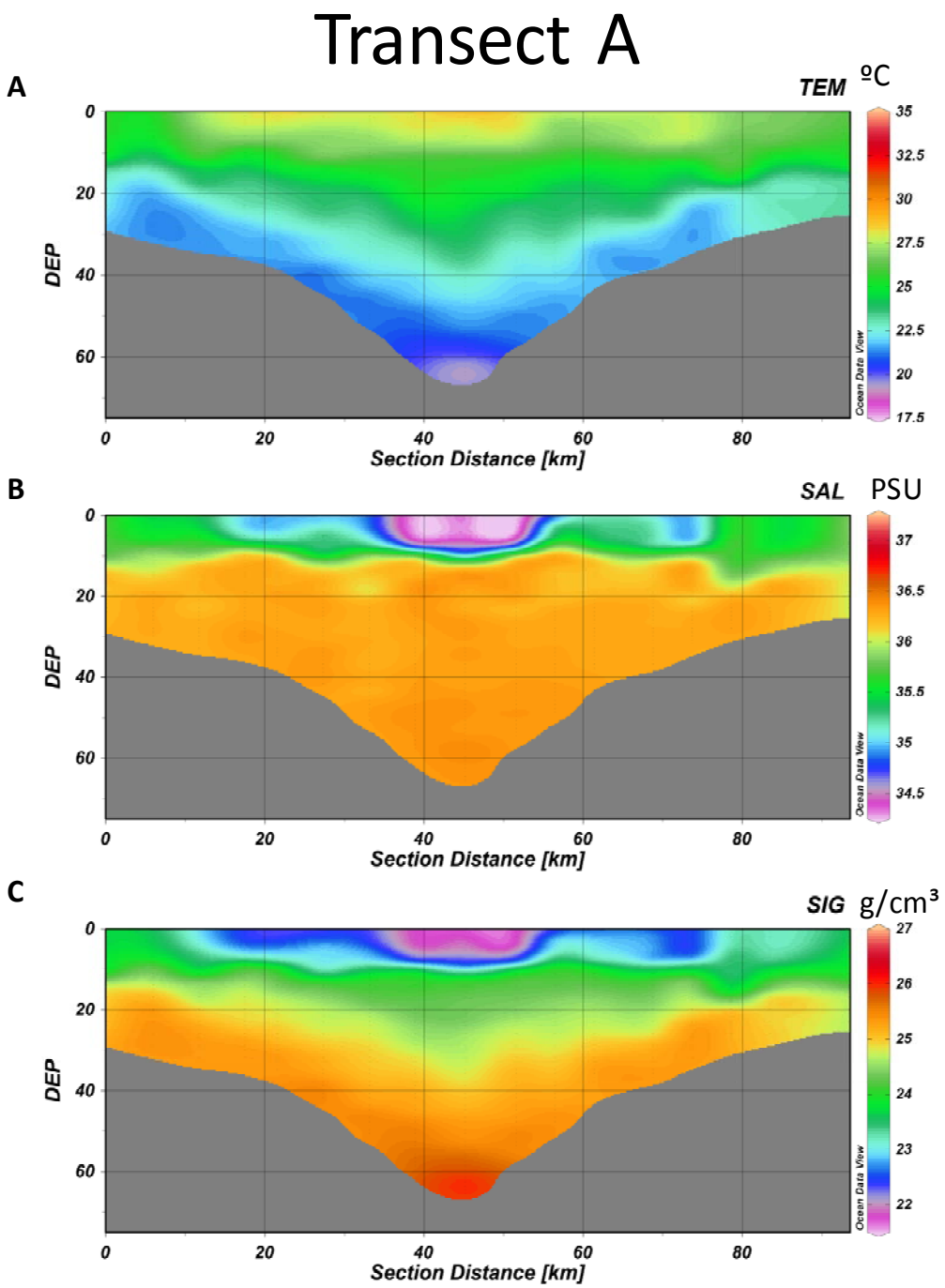

Figure 4. ODV displays of A) Temperature, B) Salinity, and C) Sigma T across Transect A.

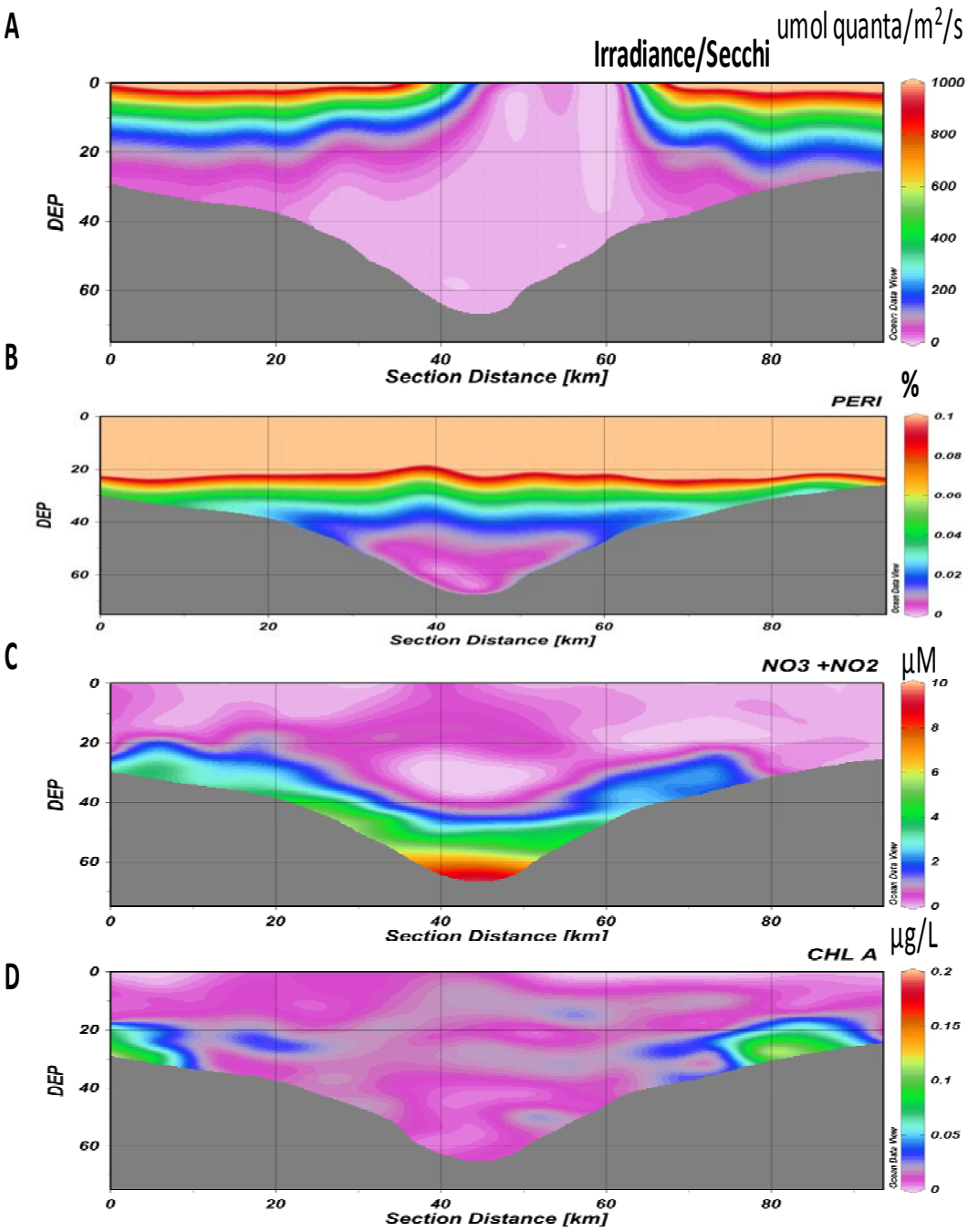

Figure 5. ODV displays of A) Secchi-based PAR distributions, B) Peri data with light stratification showing the bottom of the euphotic zone (10-1% PAR), C) NO3+NO2, and D) Chlorophyll a measurements taken at stations along Transect A by the CTD

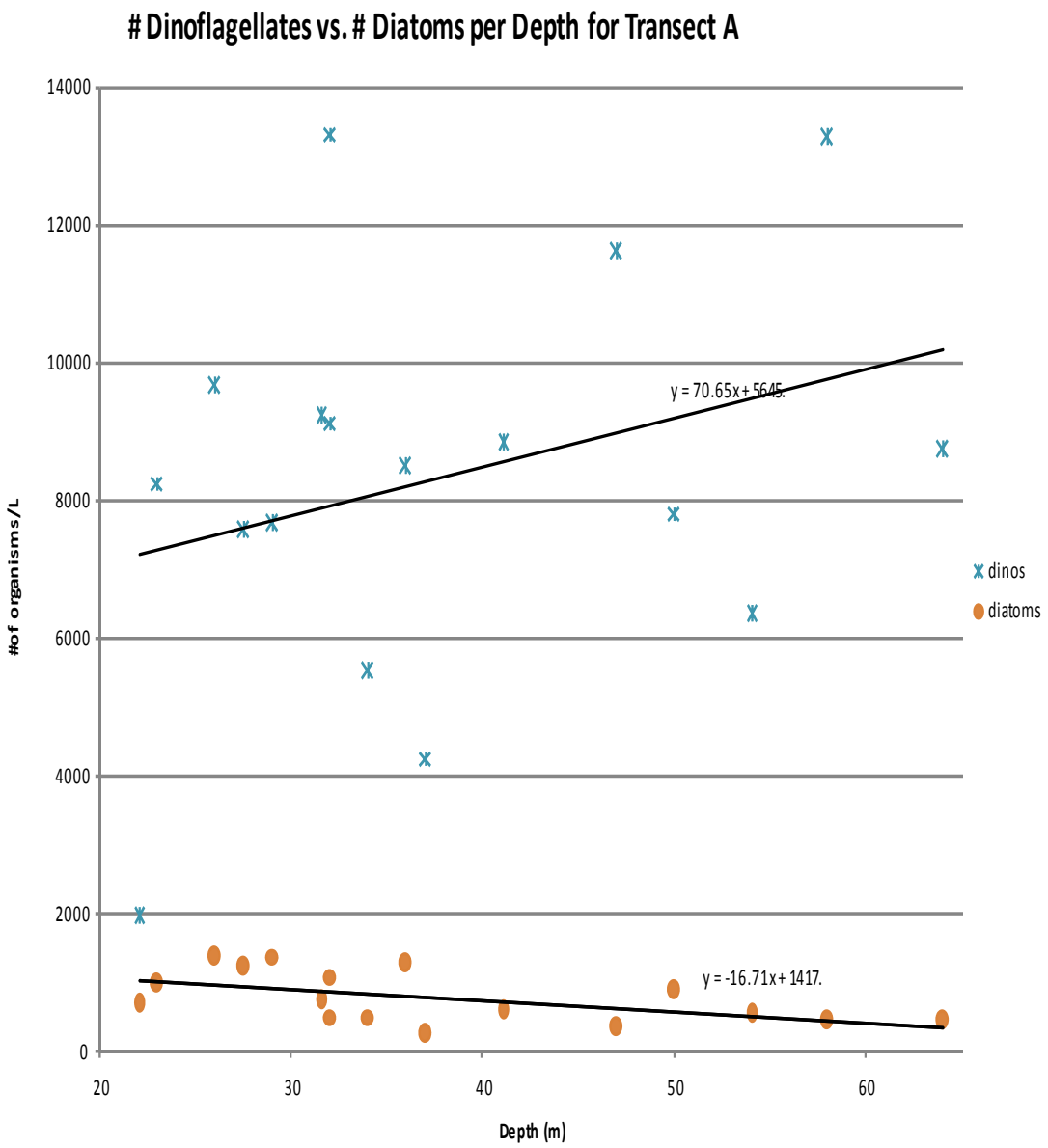

Figure 6. Percentages of dinoflagellates vs. percentage of diatoms across Transect A, depths between 20-60m across the shelf.

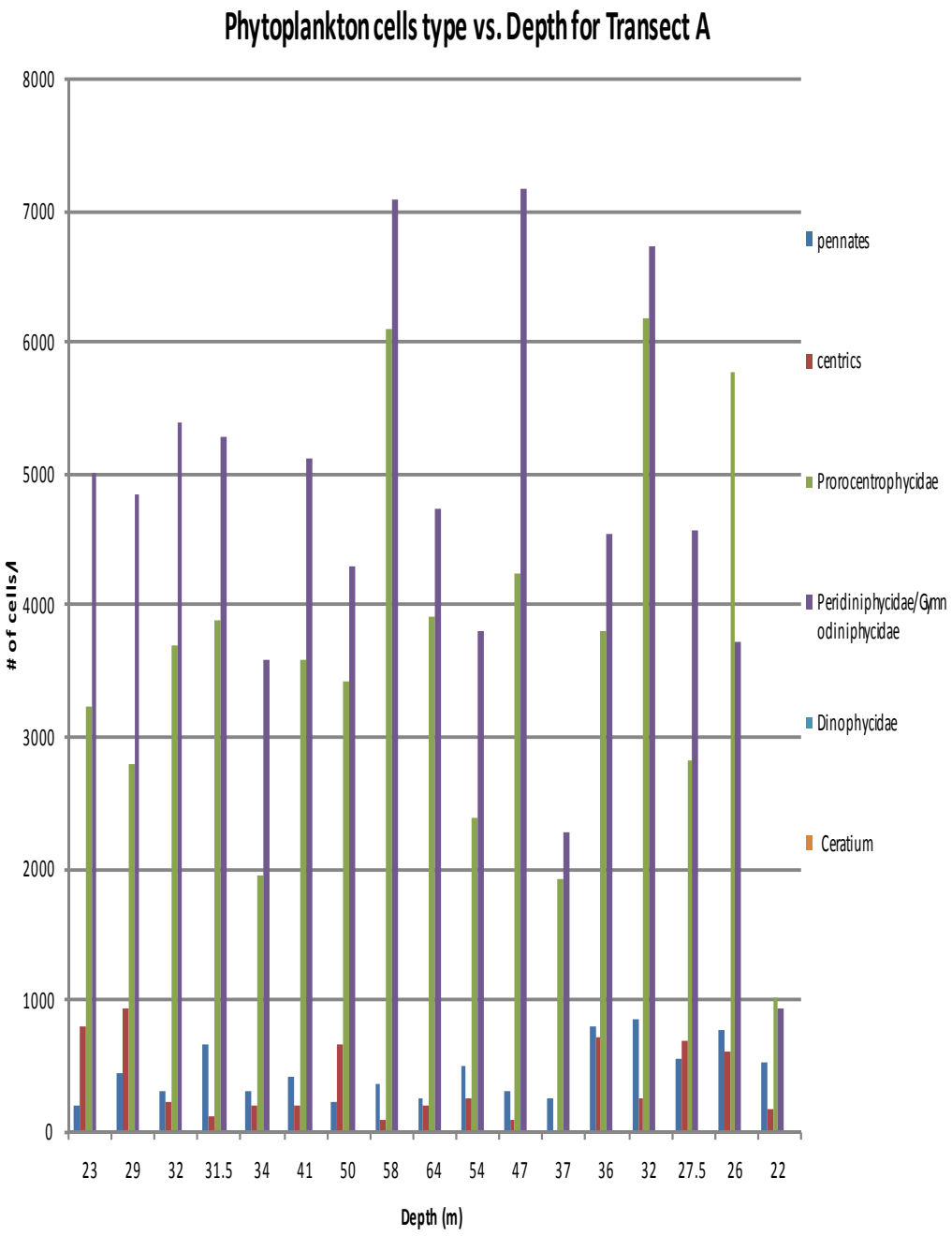

Figure 7. Phytoplankton subclass concentrations per 2mls across Transect A, depths 20-60m

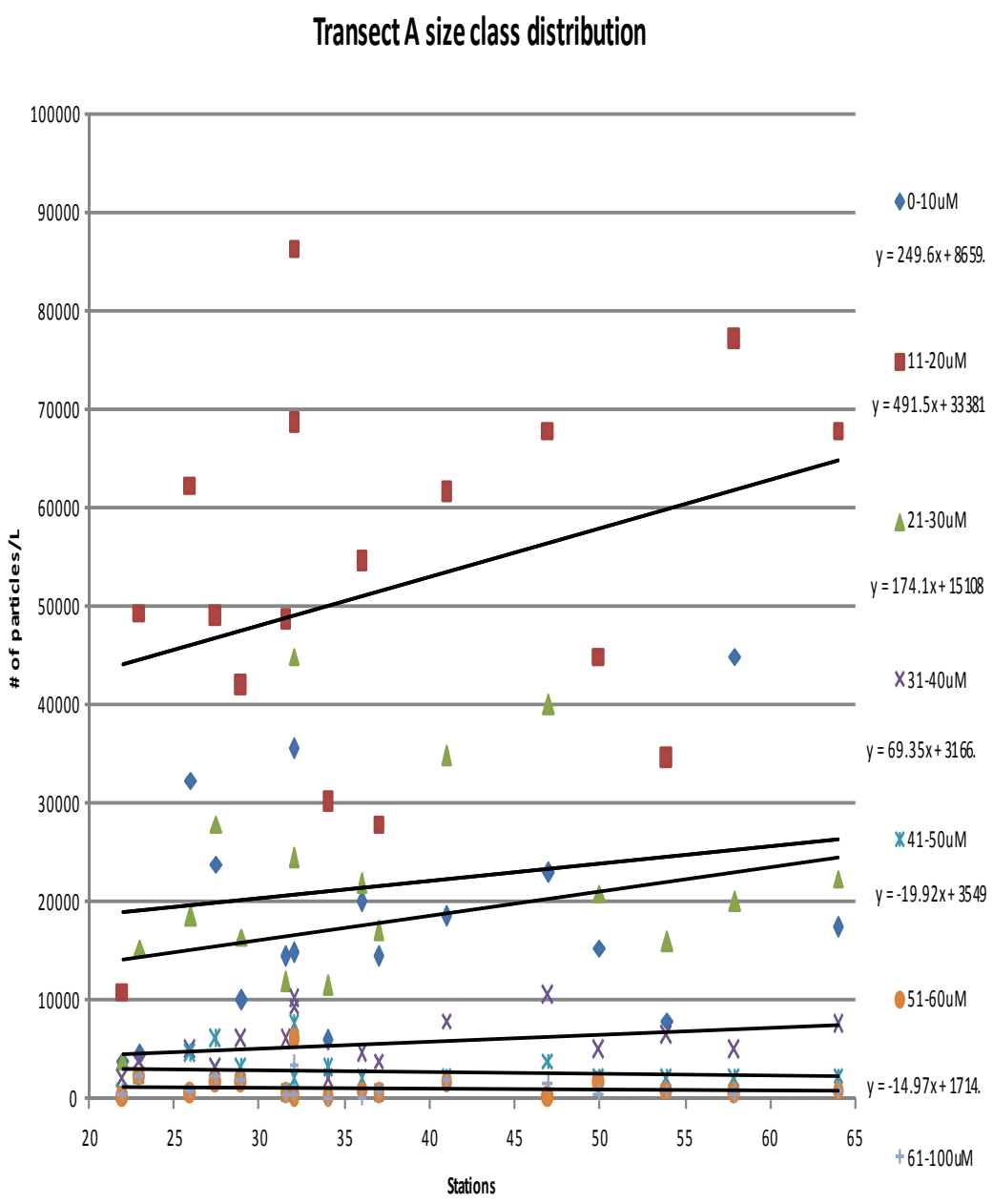

Figure 8. Dinoflagellate size class distribution near bottom across Transect A (20-60m)

Time Series B

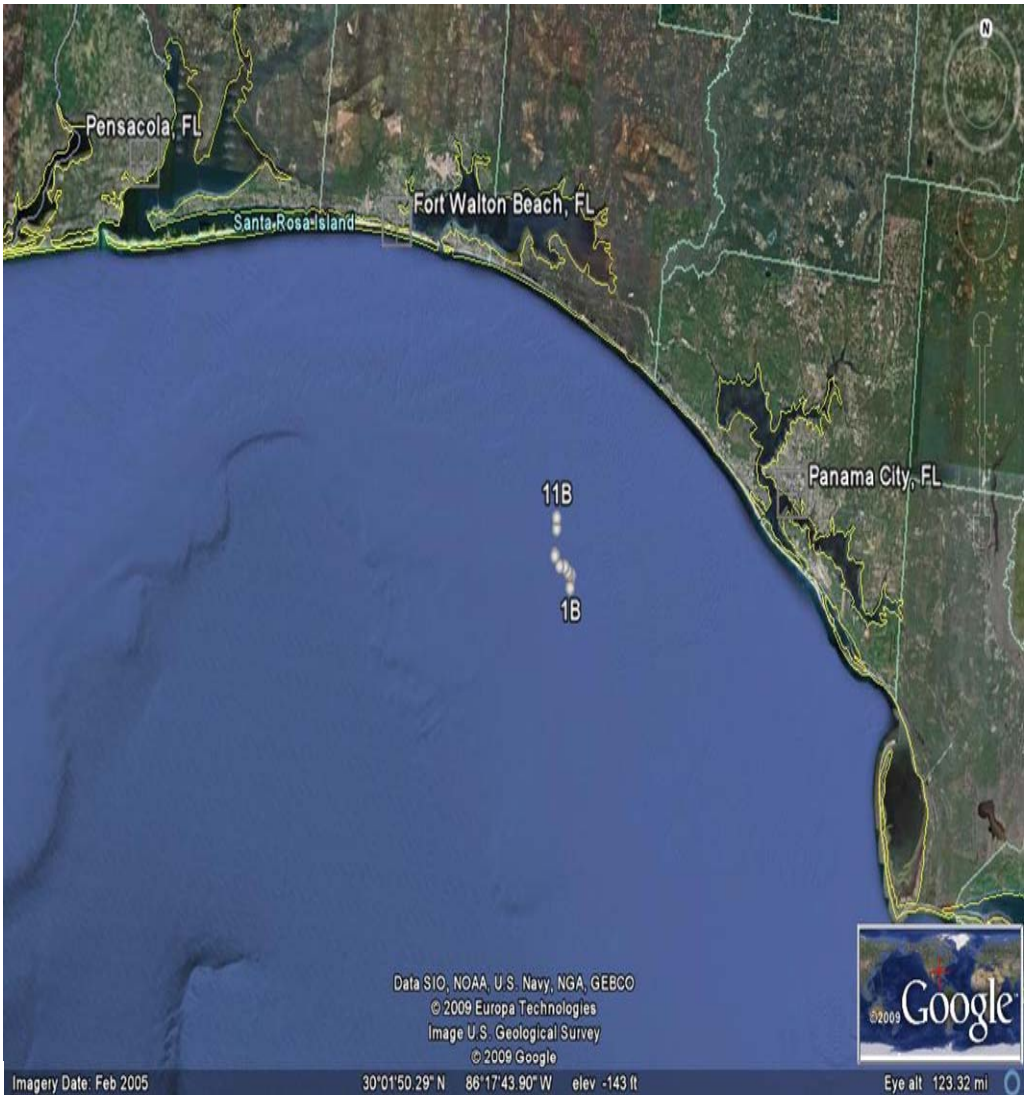

Figure 9. Stations 1-11 for Time Series B on the northwest Florida shelf along the 35m depth contour.

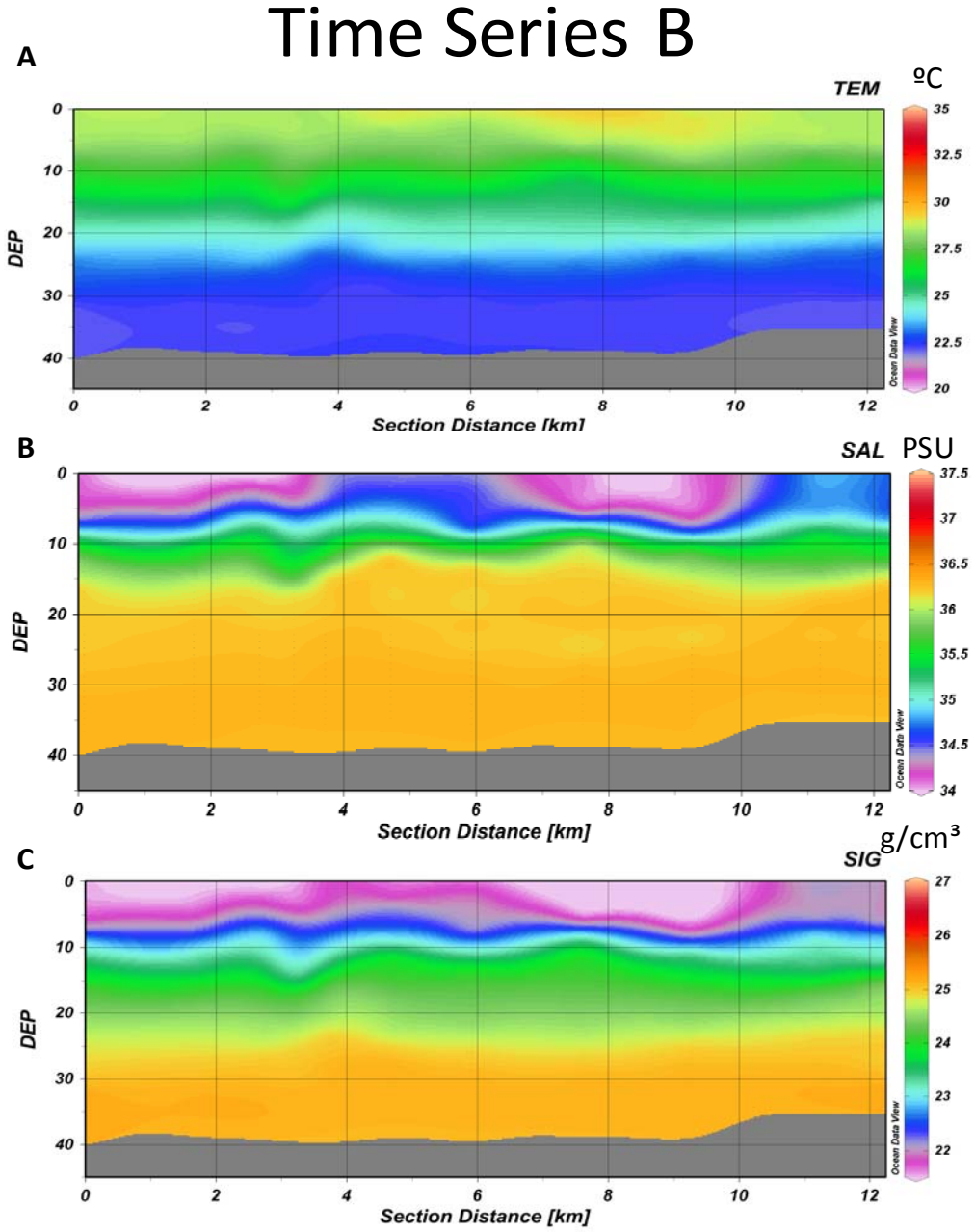

Figure 10. ODV data from CTD profiles showing water column stratification of A) Temperature, B) Salinity, and C) Sigma T along Time Series B at the 30-35m depth contour.

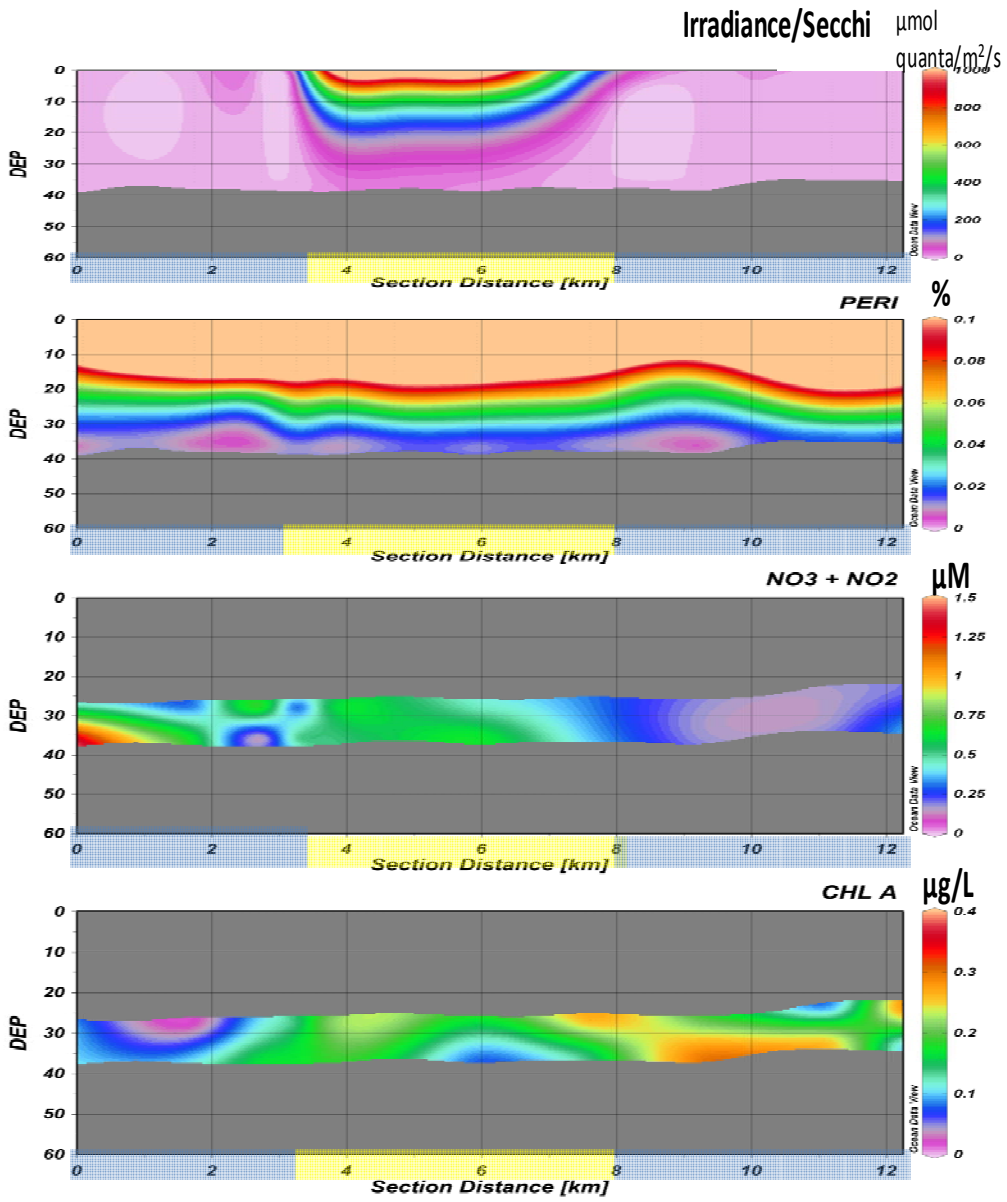

Figure 11. ODV data showing day/night periods based on A) Secchi-based PAR distributions, B) Peri data with light stratification showing the bottom of the euphotic zone (10-1% PAR), C) Nitrate-nitrite distributions, and D) Chlorophyll a concentrations near bottom along Time Series

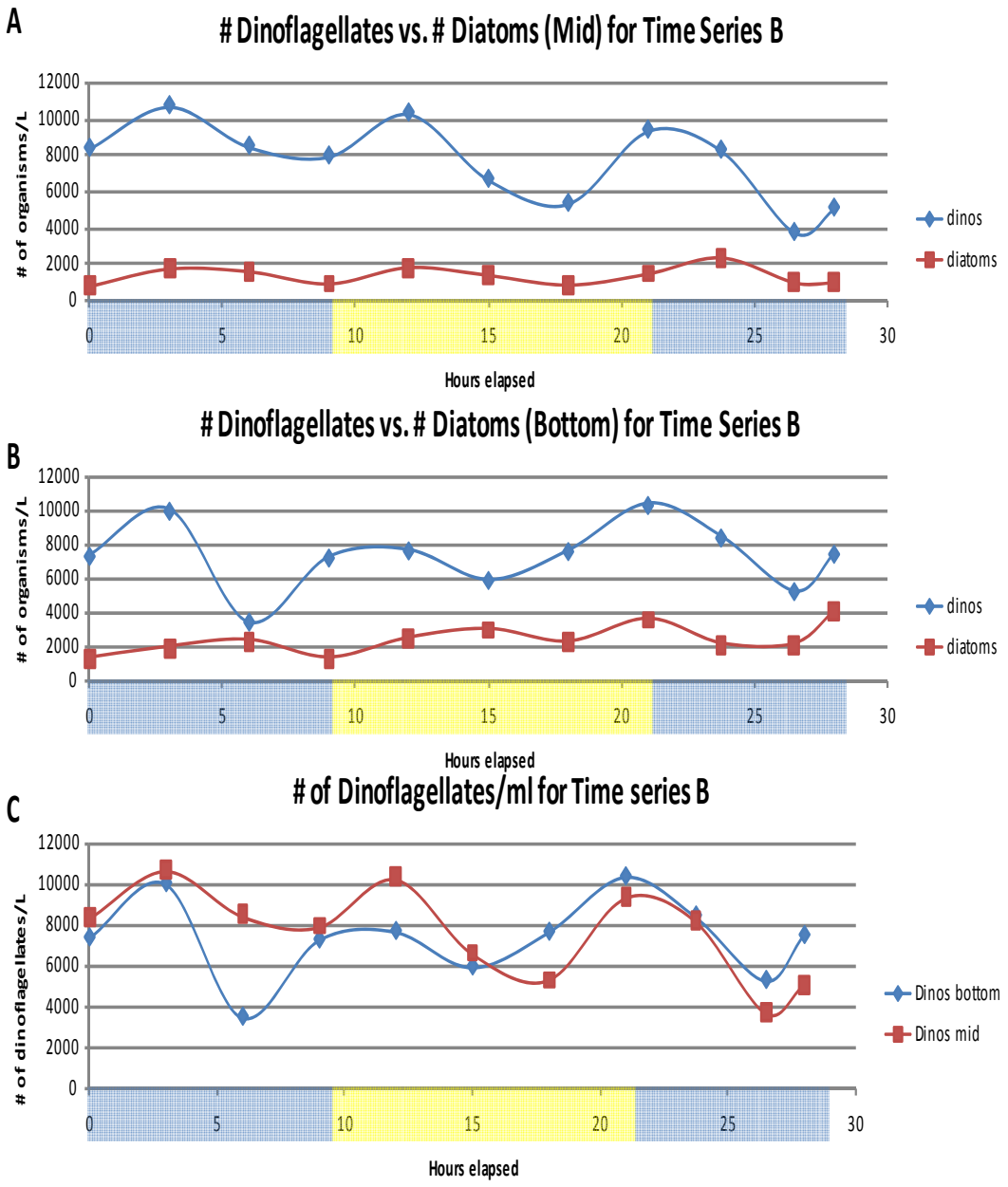

Figure 12. Counts of dinoflagellate and diatoms A) 8m from the sediment interface and B) near bottom across Time Series B at the 30-35m depth contour. Counts of dinoflagellates in bottom vs. mid samples.

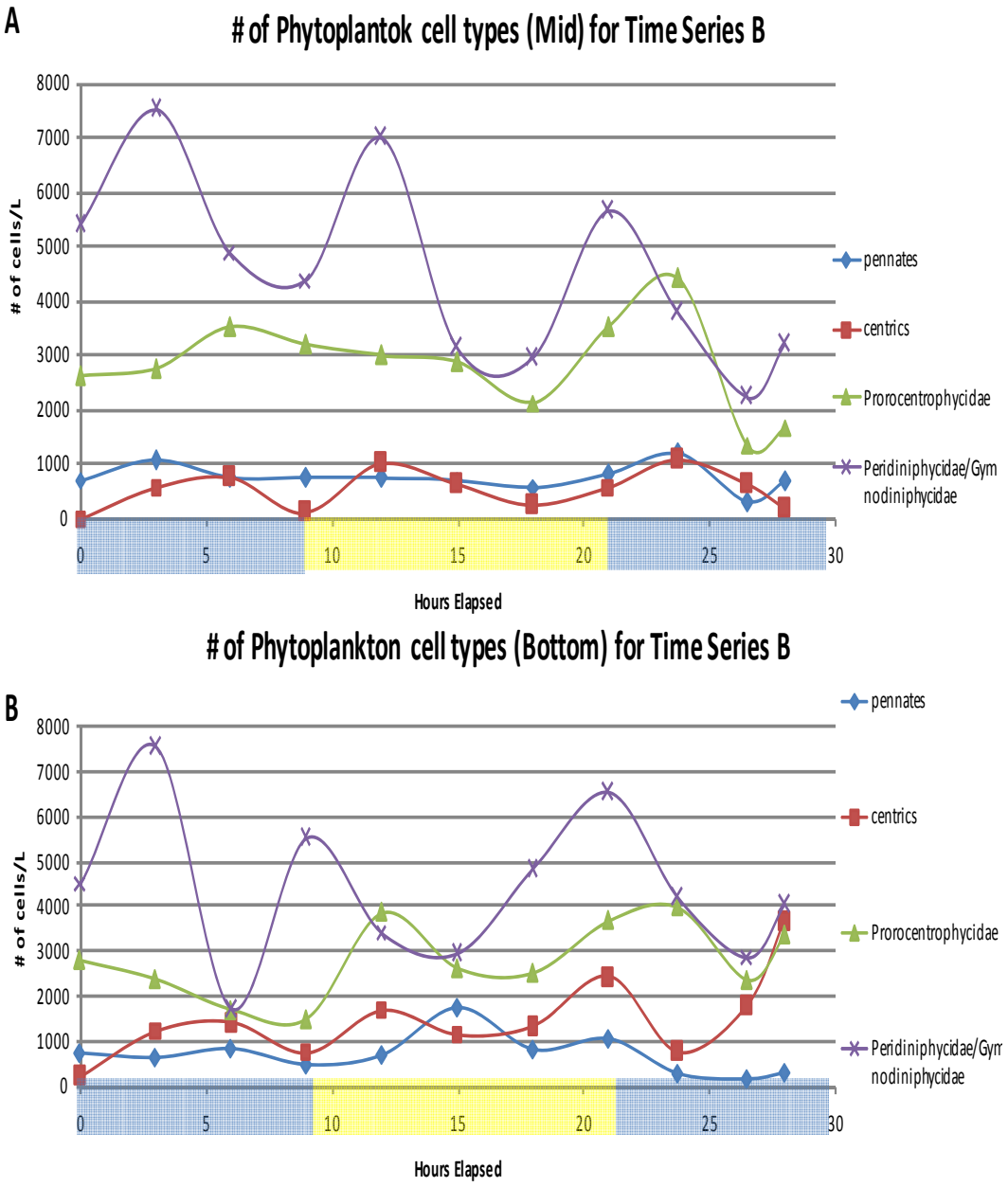

Figure 13. Counts per ml of phytoplankton subclasses at A) 8m above the sediments and at B) the sediment interface over day and night periods for Time Series B at the 30-35m depth contour.

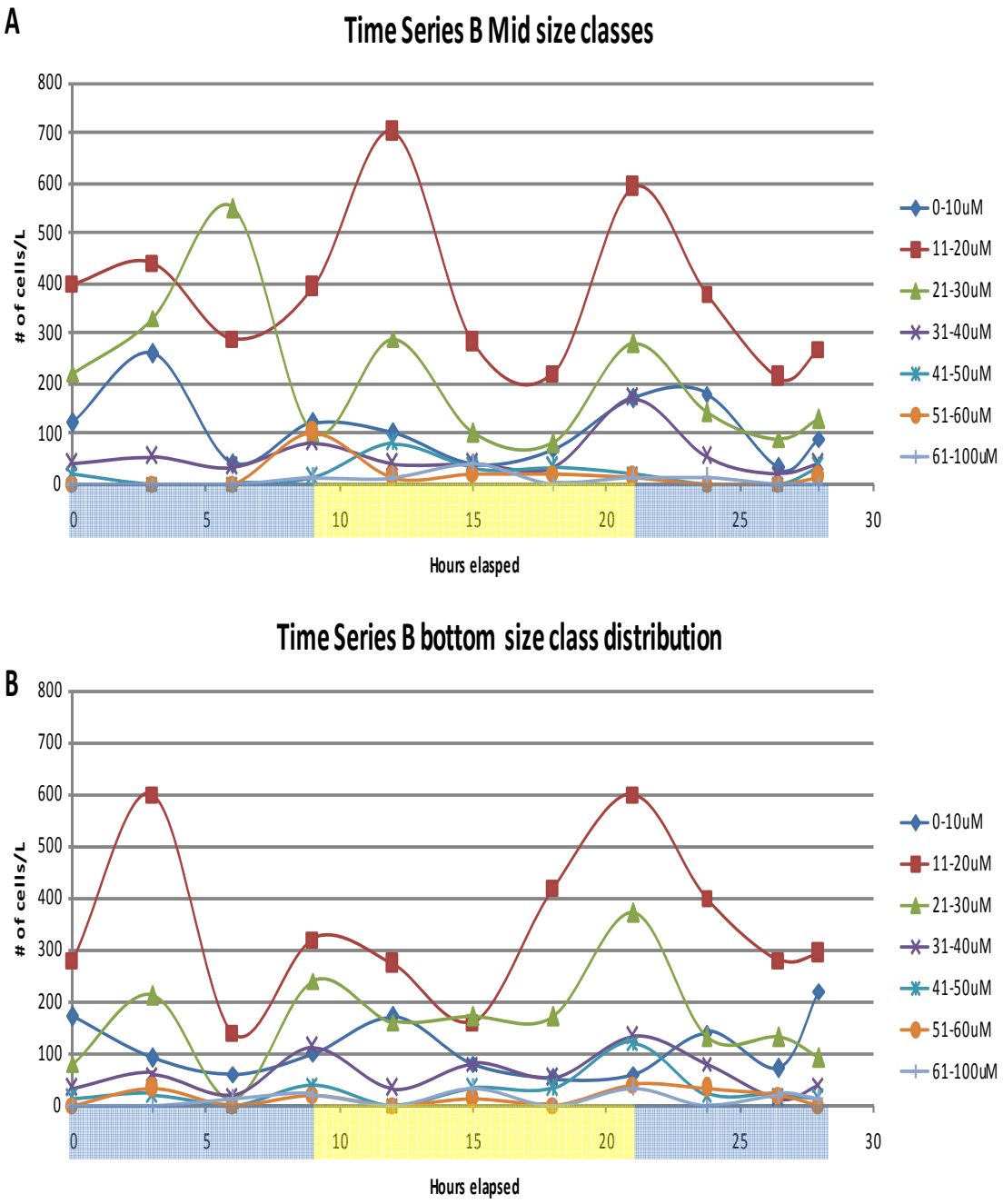

Figure 14. : Dinoflagellate size class distribution at A) 8m off the bottom and B) at the sediment interface for Time Series B at the 30-35m depth contour.

Time Series C

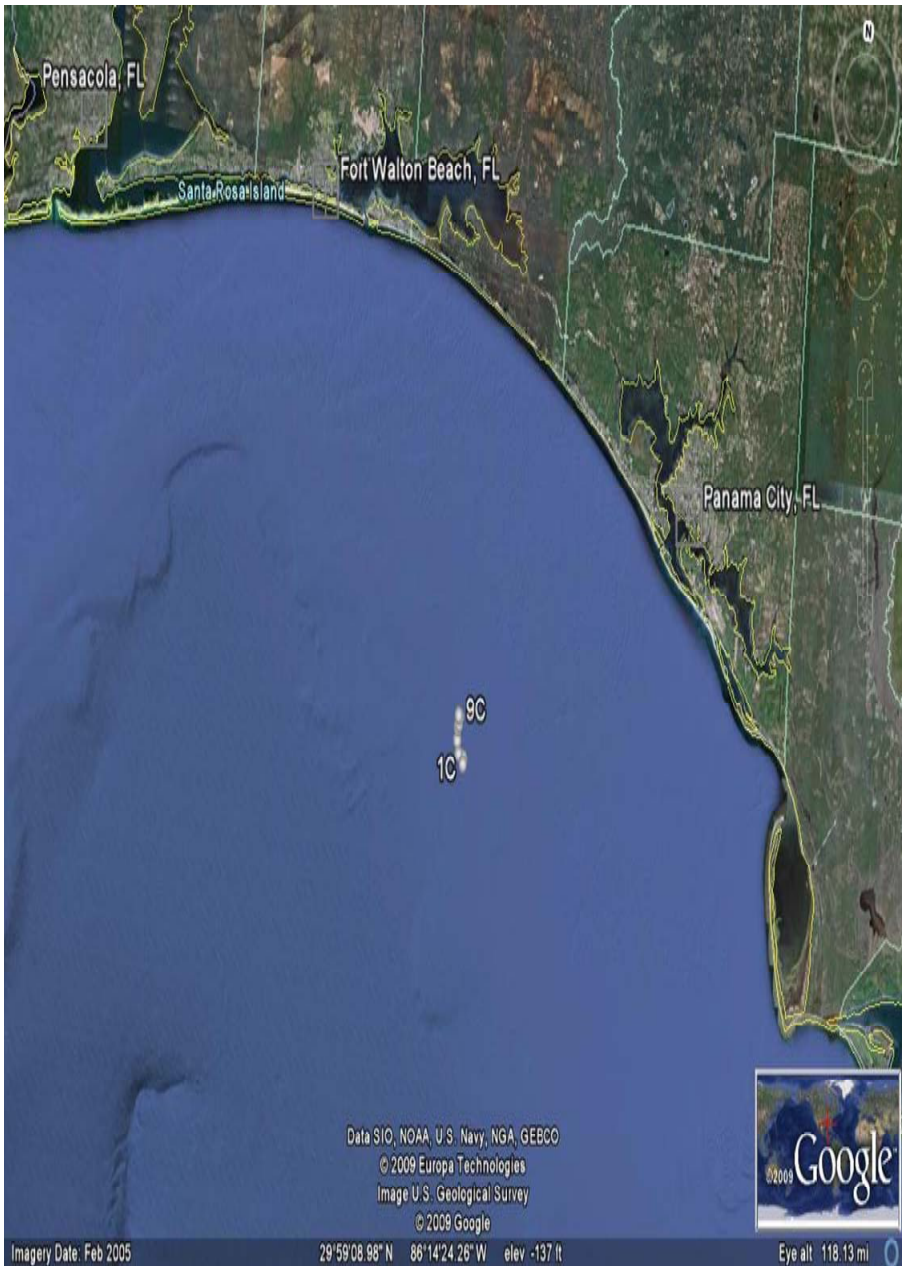

Figure 15. Stations 1-9 for Time Series C at the 40-45m depth contour.

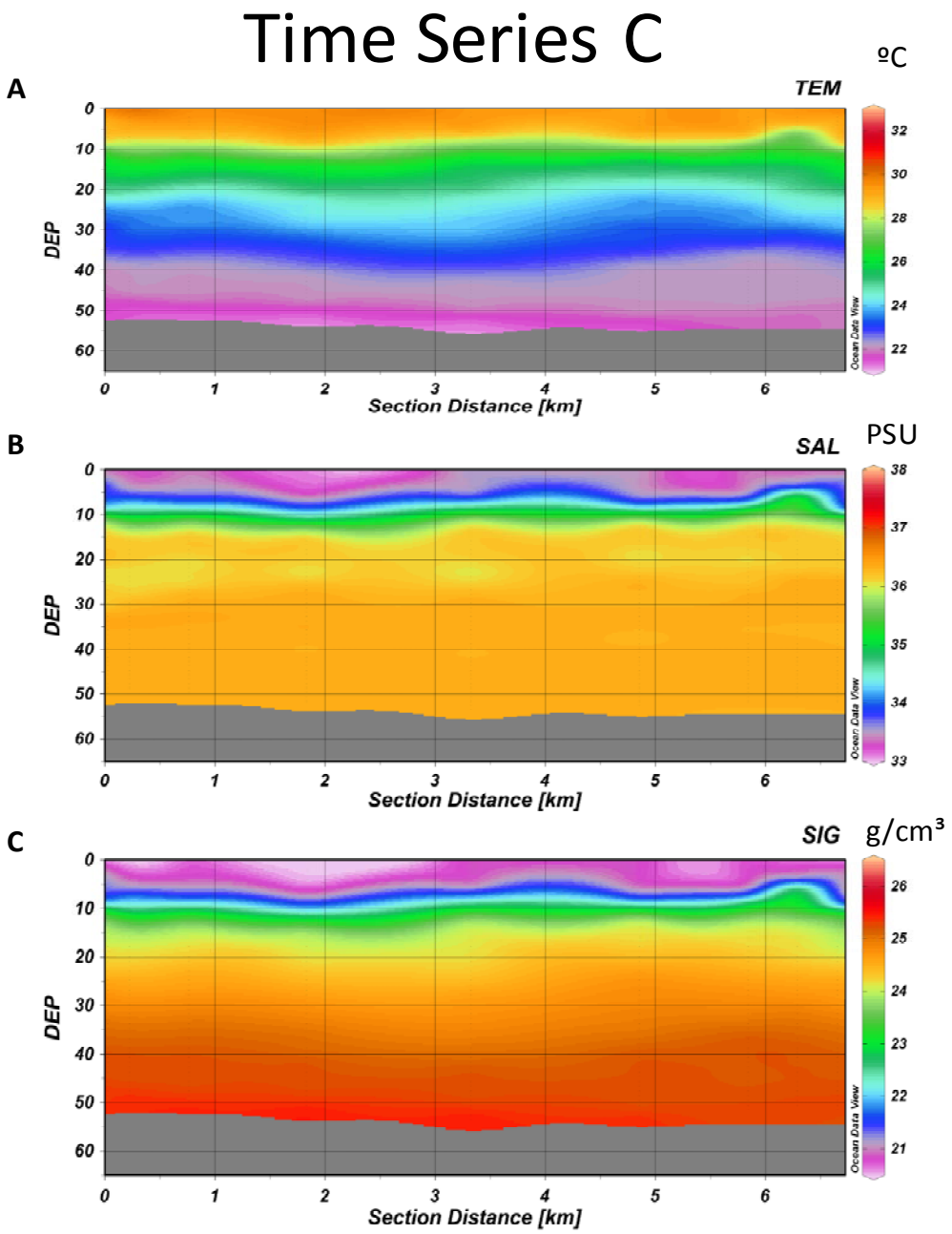

Figure 16. ODV data from CTD profiles showing the vertical water column stratification of A) Temperature, B) Salinity, and C) Sigma T across Time series C at the 40-45m depth contour.

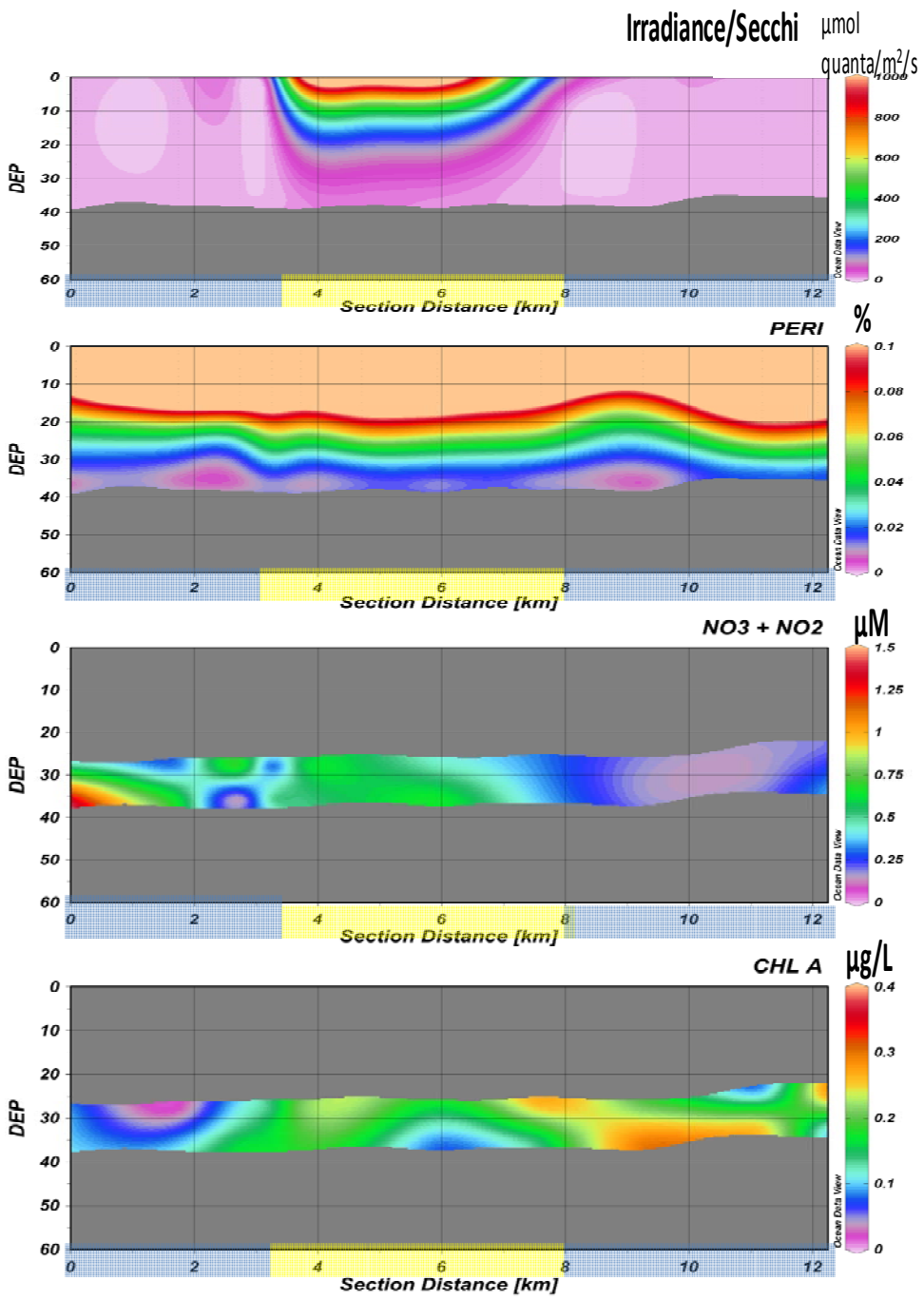

Figure 17. ODV data from CTD profiles showing A) Secchi-based PAR distributions, B) Peri data with light stratification showing the bottom of the euphotic zone (10-1% PAR), C) near bottom nitrate-nitrite sources and D) chlorophyll a

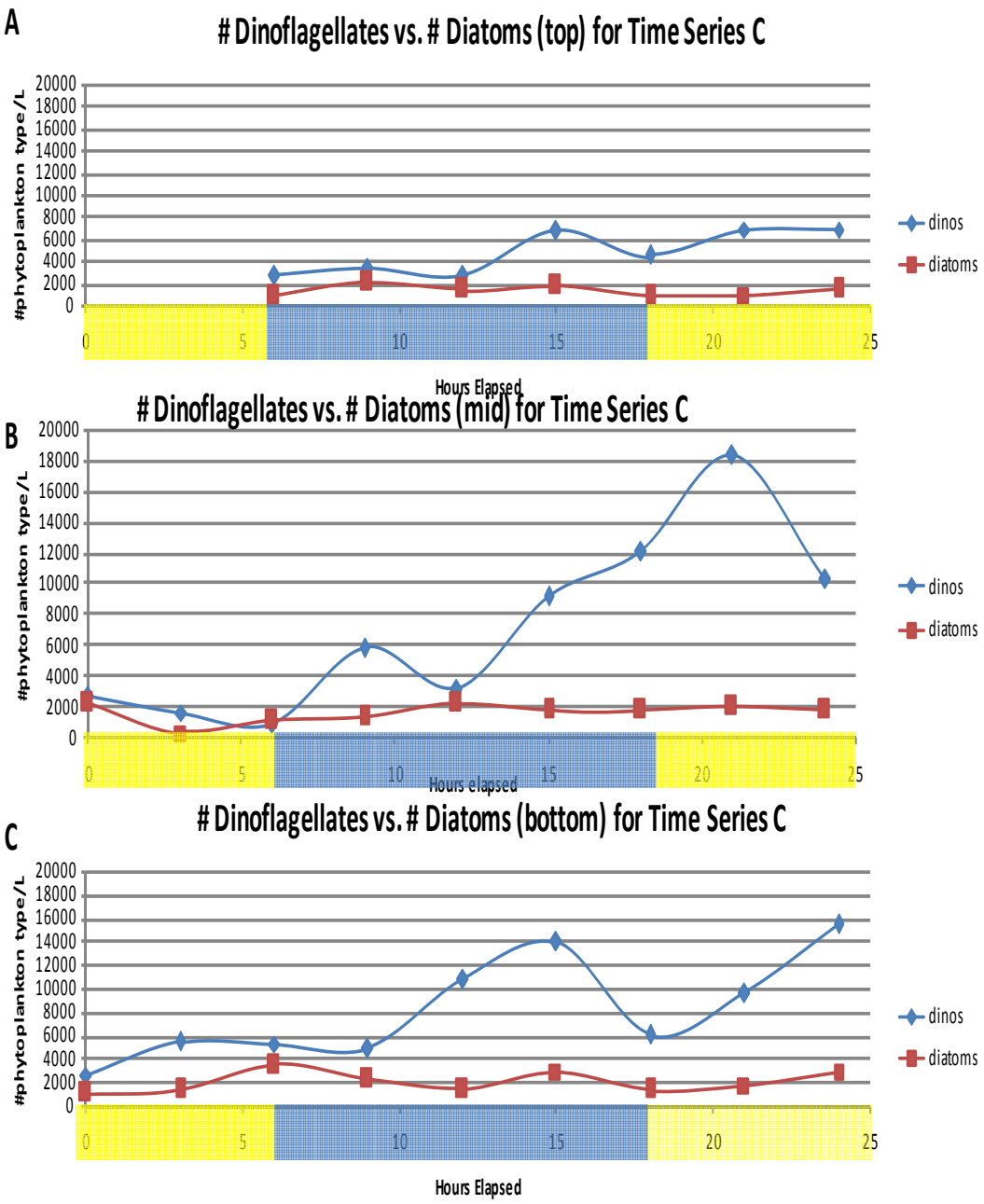

Figure 18. Percentage of dinoflagellates vs. diatoms per ml at the A) 16m from the bottom, B) 8m from the bottom and C) at the sediment interface over day/night periods for Transect C at the 40-45m depth contour

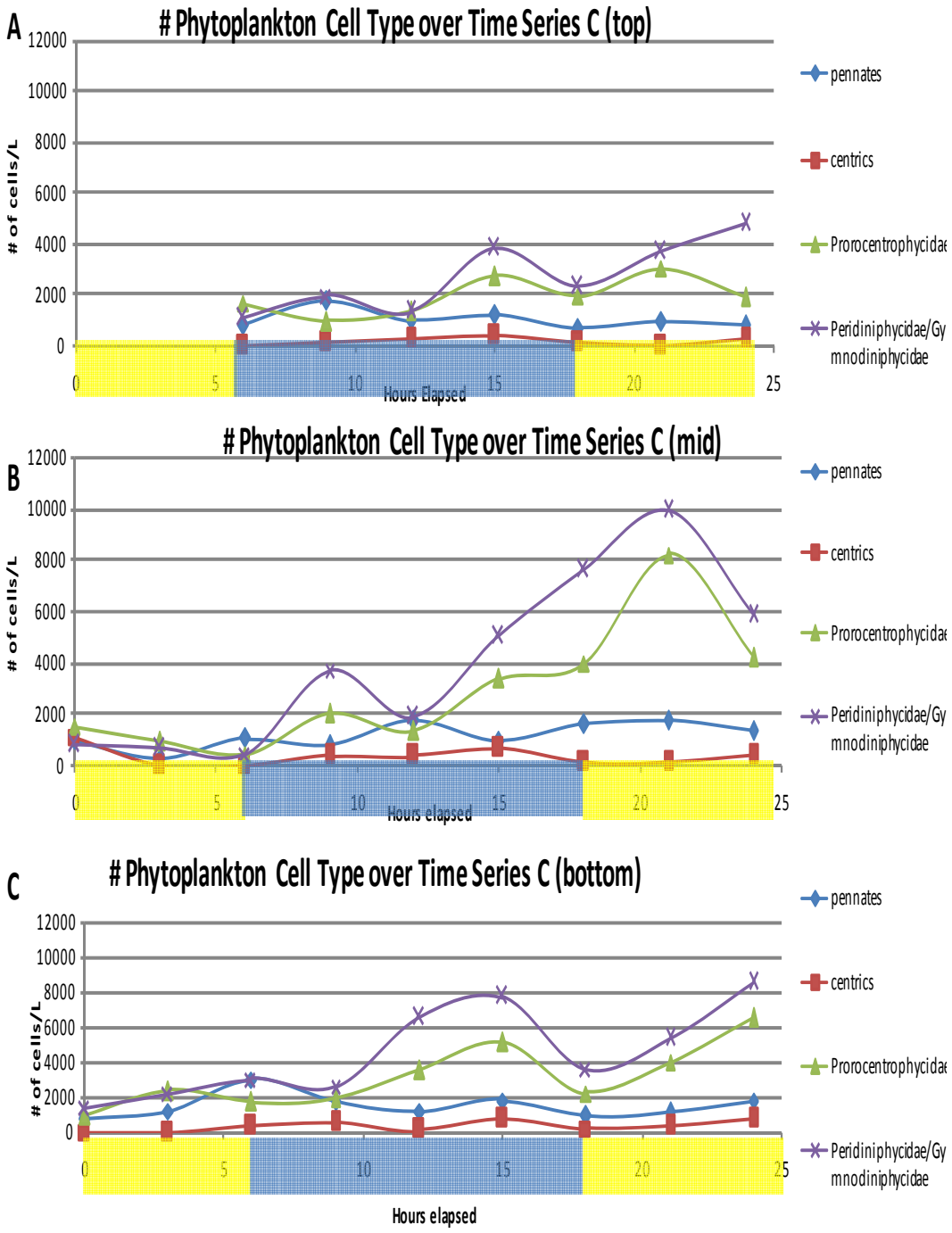

Figure 19. A) top (16m), B) mid (8m), and C) bottom distributions of phytoplankton subclasses per ml along Time Series C at the 40-45m depth contour.

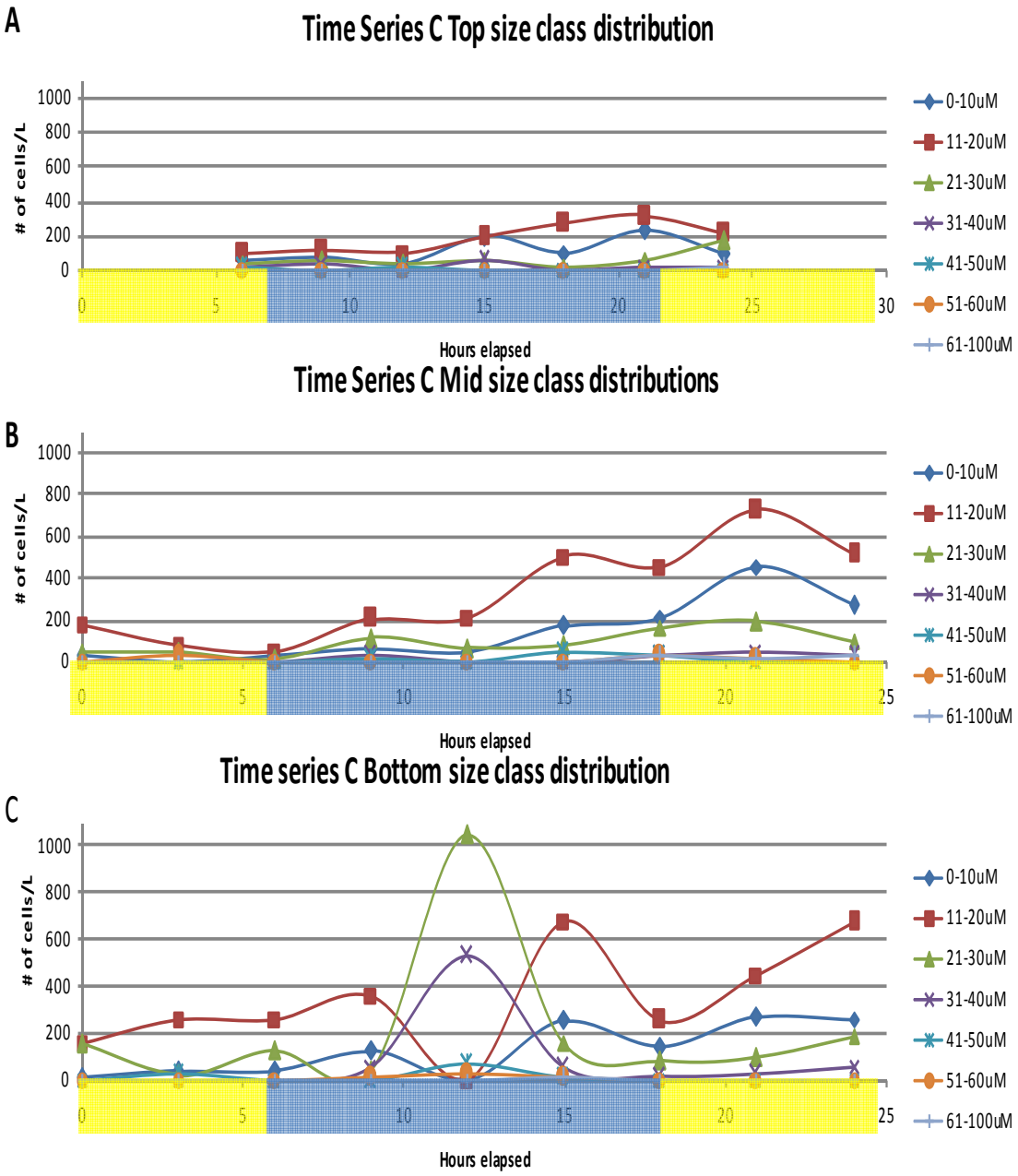

Figure 20. Dinoflagellate size class distribution at A) top or 16 from the sediment interface, B) mid or 8m from the sediment interface, and C) bottom or at the sediment interface over Time Series C at the 40-45m depth contour

CHAPTER 3:

Near Bottom Dinoflagellate Populations on the Northwest Florida Shelf during October 2008.

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North Carolina State University[1], University of North Carolina Wilmington[2], Louisiana Universities Marine Consortium[3]

Abstract

Historical measurements show that hydrographic conditions on the west Florida shelf alternate between two seasonal conditions. From November through April, the water column generally is well-mixed to the bottom with an offshore gradient of colder, less saline inshore water to warmer, more saline offshore water. From May through October, vertical water column stratification exists. A transition between these conditions was sampled during an October 2008 cruise to the northwest Florida shelf. A cross-shelf transect was sampled before and after a front passed through the area. ACROBAT and CTD surveys characterized water column hydrography and CTD/rosette water collections characterized nutrients, pigments and phytoplankton composition. Water samples collected from selected depths including near the

sediment interface were analyzed on the FlowCAM and with HPLC-CHEMTAX for phytoplankton community composition. Before front passage, the cross-shelf water column exhibited variable stratification due both to complex temperature and salinity influences. The bottom of the euphotic zone or the 1% light level was at about 20 m depth. Nitrate-nitrite concentrations ranged from ~2 µM at 40 m and increased below that depth, and in response, chlorophyll a concentrations were <1 µg/L inshore of 30 m and between 0.15 and 0.25 µg/L offshore of 30 m. Both diatoms and dinoflagellates were present at the sediment interface. After front passage, the cross-shelf water column exhibited weak stratification with temperature (24.5 to 26.5 ºC) and salinity (34.8 to 35.6) increasing offshore. The bottom of the euphotic zone or the 1% light level was at about 15 m depth throughout the transect. Nitrate-nitrite concentrations were measured at ~2 µM in the 60 m water column , and in response, mid-depth chlorophyll a concentration maxima between 0.03 and 0.06 µg/L occurred between 10-40 m depth. General trends showed that before the wind event diatoms contributed much more to the phytoplankton community in water columns shallower than 35 m, than after the wind event. Dinoflagellates tended to have a higher percent abundance than diatoms at the sediment interface between 35-60 m before and after the wind event. The wind event caused the near-bottom population to be redistributed, with dinoflagellates dominating diatoms from 20-60 m. The cruise results provided insight into changes in physical, chemical and biological changes and phytoplankton succession patterns associated with the transition from horizontal stratification to well-mixed water columns that formed a cross-shelf hydrographic gradient.

Introduction

The west Florida in the Gulf of Mexico is one of the broadest continental shelves in North America (He & Weisberg, 2002). For the majority of the shelf, isobath contours are smooth and run parallel to the coastline (He & Weisberg, 2002). Waters flow along the shoreline to the southeast in the spring and to the northwest in the late summertime to create two distinct hydrographic regimes (He & Weisberg, 2002). The entire west Florida shelf is oligotrophic with nitrate concentrations often <0.1 µM (He & Weisberg, 2002). The present study focuses on the northwest corner of the West Florida shelf along the panhandle, near Pensacola FL, with narrower isobath contours but similar hydrography ending at DeSoto Canyon where upwelling is prominent (He & Weisberg, 2002).

The hydrographic regime on the west Florida shelf of the Gulf of Mexico is well-studied largely due to the annual occurrence of *Karenia brevis* blooms (He & Weisberg, 2002, Walsh et al., 2003). The cross-shelf hydroghraphic structure exhibits significant seasonal changes typical of temperate zone continental shelves (He & Weisberg, 2002). From November to April, the vertical water column on the shelf is usually well-mixed (Walsh et al, 2003) resulting from winter storms acting on a poorly stratified water column exposed to relatively low incident solar radiation. This type of winter hydrographic regime takes place when surface temperatures are cooling and convective mixing of the water column produces the horizontal cross shelf gradient with a well mixed vertical water column (He & Weisberg,

2002). Colder, lower salinity water is found near the coastline associated with riverine output and warmer, higher salinity water is found on the outer edge characteristic of the central Gulf of Mexico causing a cyclonic baroclinc type of circulation (He & Weisberg, 2002). As incident solar radiation and sea surface temperatures increase, a shift in the seasonal hydrodynamic regime occurs (Walsh et al, 2003, He & Weisberg 2002). As sea surface temperatures increase starting in April and increasing into late summer, vertical stratification takes over with warmer waters near the surface and cooler waters near-bottom influenced by upwelling from the outer shelf (He & Weisberg, 2002). This seasonal hydrodynamic shift is accompanied by increases in lower water column nitrate and chlorophyll concentrations (Walsh et al, 2003). During the summer/fall hydrodynamic regime, the changes in stratification can allow for the development of harmful algal blooms on the shelf (Walsh et al, 2003). At the end of the summer season, decreasing incident solar radiation and increasing storms (tropical hurricanes and subtropical cyclones) mark the end of the summer hydrodynamic regime, destroying the vertical stratification of the column and mixing the water column back to the winter condition (Walsh et al, 2003).

Seasonally on the West Florida Shelf, phytoplankton species will have to deal with fairly high winter-spring vertical mixing from the coast to the outer shelf as a major selective component of the life forms capable of surviving in this type of system (Smayda and Reynolds, 2001). Many of the habitat dynamics, when considered in the context of a phytoplankton succession model (Smayda and Reynolds, 2001), would favor larger diatoms

over dinoflagellates due to penetrating surface winds. The water column becomes more stably stratified with the continued warming and as summer continues to increase sea surface temperatures and winter-spring storm forcing declines, the sediment interface becomes a suitable habitat and motile phytoplankton may supplement microphytobenthic diatoms near bottom.

Phytoplankton populations that reside near bottom on the west Florida shelf seasonally throughout the year include cyanobacteria, microflagellates, diatoms, and dinoflagellates Walsh et al., 2003). The near bottom microfloral biomass is generally two to four time greater than the phytoplankton population in the overlying oligotrophic water column, when CDOM limitation is not a factor (Walsh et al., 2003). During the winter hydrographic regime, when there is minimal CDOM restricting light penetration in the water column, microflagellates and diatoms dominate near bottom phytoplankton populations, utilizing water column nutrients and light exposure based on frequent mixing events to move through the euphotic zone (Walsh et al., 2003). As the summertime seasonal stratification sets in nitrogen pools in the sediments are restricted to the lower layer. Upwelling events that may penetrate to localized convergence fronts nearshore during late summer months can bring nutrients from deeper water columns onto the shelf. CDOM from local estuaries that enter shallower coastal waters (<10m) and from *Trichodesmium* blooms between 10-60m (Walsh et al., 2003) can limit light penetration to promote the growth of shade adapted vertically migrating phytoplankton, (Walsh et al., 2006).

In this paper, we report on the shift in seasonal hydrodynamic regimes on the northwest Florida shelf. The phytoplankton community structure is examined in the context of the hydrographic regime to which it is adapted, the hydrographic regime by which it is redistributed, and the new regime to which it must adapt. The Smayda and Reynolds (2001; hereafter SR) succession model provides a preliminary structure on which to organize the seasonal succession of near bottom phytoplankton. This succession model focuses on the life forms of phytoplankton able to adapt to a habitat based on the nutrient availability and degree of turbulence in a habitat. SR tested their succession model built on the Margalef model and Reynolds C-S-R model of freshwater phytoplankton (Reynolds, 1987). In this CSR model, Reynolds distinguishes between three different adaptive strategies to changing habitat exhibited by freshwater phytoplankton. Colonists (C) species are generally small, fast growing r-selected cells that can be invasive and usually has a high surface to volume ratio. Stress tolerant (S) species are those K-selected cells that are large and slow growing, but tend to conserve biomass to withstand situations of nutrient stress. Ruderal (R) species are tolerant of most physical disturbances such as spring mixing and usually are found to be light harvesting species. The adaptive strategies, or life forms, of each distinct group (C, S, and R) allow each group to become the dominant group when their physical environment is best suited for survival. Using this life form dominance strategy applied in the C-S-R model, SR were able to identify nine major life form classes in which to organize dinoflagellate species that may succeed diatoms: Type I *Gymnodinioids*, Type II *Peridinians/Prorocentroids*, Type III *Ceratians*, Type IV Frontal Zone Taxa, Type V Upwelling Relaxation Taxa, Type VI

Coastal Current Entrained Taxa, Type VII *Dinophysoids*, Type VIII Tropical Oceanic Flora, and Type IX Tropical Shade Flora Seasonal habitat hydrodynamics, changing nutrients and turbulence structure of the column (or the mixed layer depth) are used to select preferable life-forms which determine the succession pattern of other life form types. The SR updated life form succession model will be used to predict the succession of dinoflagellate life-forms that will succeed benthic diatoms. Diatoms are commonly found near the sediment interface on the northwest Florida shelf to utilize near bottom nutrient concentrations in shallow water columns through the hydrodynamic seasonal cycle. Dinoflagellate life forms can share the sediment interface and utilize the nutrient concentrations in certain conditions with diatoms if conditions are suitable for the dinoflagellate life form to succeed (Smayda and Reynolds, 2001).

Methods

A cruise in the Gulf of Mexico took place between 15-21 October 2008 and was planned to represent the end of the stratified season on the northwest Florida Shelf. The study area (Fig. 1) was selected because the narrower shelf allows shorter cruises to cover the depth interval of interest. The cruise was approximately 7 days in length and a cold front passed through the study area midway through the cruise dividing it into pre-front and post-front

segments (Fig. 2). Both a pre-front transect composed of 8 stations and a post-front transect composed of 9 stations were occupied (Fig. 1). The stations were distributed between the 20-60m depth contour lines, at ~5m increments. The 20m starting depth placed the sediment interface within the estimated euphotic zone. The offshore extent of the transect was selected to include the situation in which the base of the euphotic zone was accessible in 12 hours by dinoflagellate cells starting at the sediment interface and swimming at approximately1-2 m/hr (Eppley et al., 1968; Kamykowski, 1995) .

Field Methods

Each transect included MIDAS ship monitoring for meteorological (incident PAR, wind speed and direction) and near-surface oceanographic variables (temperature, salinity, chlorophyll a fluorescence, beam attenuation & transmission). Acrobat profiling included surface PAR, subsurface PAR, temperature, salinity, dissolved oxygen, chlorophyll a fluorescence, CDOM fluorescence, beam attenuation/transmission. Derived variables included percent irradiance at depth, density and oxygen saturation. The Acrobat undulated approximately between 1m below the surface and 1m above the sediment interface along a cross shelf transect between the 20-60m depth contours. These profiles were used to determine the structure of the water column across the study area to identify transect structure suitable for further sampling by the CTD/rosette. Transect BA (Fig. 1) is the focus of the present paper. CTD cast results included surface PAR, subsurface PAR, pressure,

temperature, salinity, oxygen concentration, Peri, chlorophyll a fluorescence, and beam attenuation/transmission. Derived variables included percent PAR attenuation with depth and Peri measurements based on the beam transmission measurement calibrated against Secchi depths in the day time, depth, sigma-t, and oxygen saturation. Niskin bottle samples (5L) were generally triggered near the sediment interface and then at 2m intervals (~9 bottles) as well as mid-depth in the remaining water column to the surface and at the surface. Water was processed for nutrients (nitrate-nitrite concentrations), chlorophyll *a*, HPLC pigment analysis, and phytoplankton species composition from selected depths. Chlorophyll a samples were taken by filtering 500ml of water from each depth sampled with the Niskin bottle using 25mm GF-F filters and then ~10mls of the resulting filtered seawater was frozen for nutrient analyses. The filters were wrapped in aluminum foil and frozen in the ship board scientific cooler then transported to the laboratory (Strickland and Parsons, 1968). Approximately 1000mls of water at each depth were filtered through a 2.5 cm diameter GF-F filters, under a low pressure vacuum (< 200 mmHg) and frozen with liquid nitrogen and stored for 6-9 months for later HPLC/ChemTAX analysis in the laboratory. Approximately 125ml were preserved with 4-5% Formalin and Tetra-borate solution at a concentration of 9 parts preservative to 1 part plankton biomass (Parsons et al., 1984) and were later be analyzed on the FlowCAM.

Net samples were taken at each station to gain a broader view of the population at the sediment interface. Net samples consisted of 15-20L samples taken from Niskin bottles at a

depth as close to the sediment interface as possible at each station and poured through the 10µm net on the ship deck and concentrated in the cod end. Samples were washed in glass jars and preserved with 4-5% Formalin and tetra-borate solution.

Lab Methods

Nutrient samples were thawed and analyzed against a standard of natural seawater with low nitrate concentrations. An automated method using the Seal Analytical QuAAtro Segmented Flow Analyzer system with a 10mm flow cell was used for analysis.

Chlorophyll filters were allowed to soak for 24 hours in 5 mls of 90% acetone in a freezer and centrifuged for pigment extraction (Strickland and Parsons, 1968). The fluorometer was calibrated using culture samples of *Thalassiosira weissfloggi* and *Prorocentrum* filtered on a 47mm GF-F filter, measured on a spectrophotometer (Strickland and Parsons, 1968). Fluorescence readings were taken at a wavelength of 664 nm with an acidification step using on a Turner Fluorometer (Strickland and Parsons, 1968).

HPLC-ChemTAX analysis was performed on water samples filtered from the same stations/depths as the FlowCAM samples. Excess water was removed and the filters were analyzed in the dark on a Shimadzu dual LC10-AT vp and Controller SCL-10A vp binary gradient pump. Pigments on the filters were extracted after they were allowed to incubate for 18-24 hours in an acetone solution. The supernatant separated from the filter was extracted

and inserted into smaller amber vials. The HPLC analysis was run with solvent A of 80% methanol and 20% ammonium acetate and a solvent B of 80% methanol and 20% acetone. Spectra measurements between 380-700nm were taken every 2 seconds and peaks were identified based on retention time (Pickney).

Samples for phytoplankton identification collected at depth from Niskin bottles and nets were transported to the laboratory and analyzed. Since the samples were fairly dilute, 100mls of the sample were settled in Utermohl settling chambers for 24 hrs, with all organisms collected in the bottom plate. This amount, approximately 2mls, was collected from the bottom plate, rinsed with 3mls of filtered seawater to ensure all organisms were collected from the settling slide. A test using cultures of similar dinoflagellates was used to show the recovery efficiency of the Utermohl settling method and FlowCAM. Results showed that over 70% of each sample was recovered by the FlowCAM after settling. The sample, approximately 5mls, was then size fractionated through a 100µm mesh and analyzed on the FlowCAM. The FlowCAM was set up on auto image mode with the 100µm flow cell and the 10x objective and pumping at an average setting of about 7 on fast mode. Electronic size filters were applied to isolate and capture particles between 10-100um in diameter (ESD). To ensure no contamination between samples the flow cell was cleaned thoroughly with filtered seawater and methanol between samples. Samples from the bottom two sample depths were the focus of the FlowCAM samples analyzed as well as net filtrations between 30 and 50 m depth and select depths on each transect for comparisons. Phytoplankton

initially was divided into diatoms, dinoflagellates and other. Subsequently, diatoms were divided by symmetry into pennates and centrics, while dinoflagellates, based on the desmokont vs. dinokont body type divisions, were divided into *Prorocentrophycidae*, *Dinophysiphycidae*, and *Peridiniphycidae/ Gymnodiniphycidae* (Tomas, 1997).

Analysis

Data collected along the transect via the Seabird CTD were later analyzed in the laboratory using SBE Data Processing (Sea-Bird Electronics, Inc.) and Ocean Data View (ODV) software. CTD profiles of temperature, salinity, sigma-t, and PAR were constructed with the ODV software for the vertical water column at all stations across the transect. Chlorophyll *a* filters taken at depths at each station as well as nitrate-nitrite samples; each profile at each station along the transect was further analyzed with ODV. The vertical profiles interpolated along transect using ODV software made it easier to compare the results from the profiles taken by the Acrobat.

Results

The wind event from ~day 2 to ~day 4 of the cruise split the cruise into 'pre-front' passage and 'post-front' passage legs (Fig. 1&2). Runs along Transect BA (Fig.1) before and after the wind event (transect timing highlighted in red; Fig. 2) captured a seasonal shift in cross-shelf hydrographic structure and the phytoplankton community response to that shift.

Pre-Front

Acrobat profiles (Fig. 3a,b,and c) and CTD stations (Fig 3d,e,f) revealed a complex cross shelf hydrographic structure. Based on temperature, the water column appeared to be weakly stratified to the 40m contour, inverted to the 50m contour, and weakly stratified beyond 50m (Fig. 3a,d). Salinity profiles from the Acrobat and CTD showed a similar type of stratification. Inshore to the 40m contour there was a weak stratification of salinity, that could almost be classified as well mixed, and an inverted stratification found past the 50m contour, with higher salinities found near bottom compared to the surface (Fig. 3b,e). Sigma-t profiles derived from CTD data and potential density profiles from the Acrobat show stratification across the shelf from inshore to the 50m contour (Fig. 3c, f). Density measurements derived from temperature and salinity profiles of the water column from the CTD showed stable stratification in deeper water columns (>50m), with the highest values found near the sediments offshore of 50m (Fig. 3c,f). The bottom of the euphotic zone

separated from the sediment interface at approximately 20m (Fig. 4a). Nitrate-nitrite concentrations were generally lower mid column than at the surface (4-5 µM) and near bottom (4 µM) in inshore columns out to the 40m contour (Fig. 4b). At the sediment interface, nitrate-nitrite concentrations were low (~2µM) in water columns less than 40m but increased to ~6µM at approximately 45-50m depth (Fig. 4b). Four chlorophyll *a* maxima were found with measurements of 0.8 µg/L at the sediment interface located between 25-30m depth and measurements of 0.4 ug/L at 15m, 30m, and near bottom between 35-45m depth (Fig. 4c). Chlorophyll concentrations at other locations along the transect generally were less than 0.2 ug/L (Fig. 4c).

Based on HPLC/CHEMTAX, the highest concentration of diatoms at the sediment interface were found inshore of the 30-35m depth contour (0.4-0.5 µg/L chlorophyll *a*) except for a patch just past the 40m depth contour where diatoms comprised approximately 0.3 µg/L chlorophyll *a* near bottom (Fig. 5a). Across the transect, the upper water column was comprised of very low concentrations (<0.2 µg/L chlorophyll *a*) of diatoms (Fig. 5). Outside of the 20m depth contour, a patch of dinoflagellates occured at the 30-35m depth contour that was made up of 0.6-0.7 µg/L *Gyro/Gymnodinoid* dinoflagellate chlorophyll *a* near bottom at a similar location as the near bottom inshore diatom patch (Fig. 5b). *Peridinoid* dinoflagellates also showed a maximum between the 30-35m contours, but appeared to have the highest concentrations (0.025 µg/L chlorophyll *a*) mid column at approximately 18-20m and not near bottom where their concentrations in the 35m column

were less than 0.005 µg/L chlorophyll *a* (Fig. 5c). Concentrations of dinoflagellates were generally higher than concentrations of diatoms across the shelf.

FlowCAM samples (Fig. 6) paralleled the HPLC results and showed low concentrations of both diatoms and dinoflagellates at the sediment interface at all stations sampled across the shelf between 20-60m. At all stations between 30m and 55m, dinoflagellates (1500-9500 cells/L) dominated the near bottom phytoplankton populations over diatoms (800-2800 cells/L) except at one 40m depth station where diatoms dominated over dinoflagellates by almost 300 cells/L (Fig. 6). For dinoflagellates the mean was 3495 +/- 2667, standard error 943.03, 95% confidence interval +/- 2229 and the mean for diatoms was 2273 +/- 2302, standard error 814, 95% confidence interval 1924. At most depths, including the 30m near bottom chlorophyll a maximum, there is a statistically significant difference between the means of dinoflagellates and diatoms according to ANOVA at T=0.9803, df= 14, alpha=.05. Of the diatoms populations found near bottom, pennates were 80% more abundant than centrics at depths <35m with counts of ~2300 pennates/L vs. ~180 centrics/L (pennates comprised ~80% of diatom population at the 35m contour maxima), while centrics were 55% more abundant at depths >35m, comprising approximately 55% of the diatom population (550 centric/L vs. ~300 pennates/L) at the 55m depth contour near bottom (Fig. 7a). According to ANOVA tests between the means of pennates and centrics there is not a statistical difference (F=.0867, p=.7726, f crit.= 4.600, alpha=.05). Near bottom dinoflagellate populations were mainly comprised of *Prorocentrophycidae,* and

Peridiniphycidae/ Gymnodiniphycidae cells with a few *Dinophysiphycidae* and *Ceratium* cells interspersed (Fig. 7b). *Ceratium* dinoflagellate cells, a subclass of *Gymnodinium* cells, were found inshore of the 25m depth contour, but negligible concentrations in deeper columns, the highest concentrations found at the 25m contour of over 50% (~2300 cells/L) (Fig. 7b). *Peridiniphycidae/Gymnodiniphycidae* cells dominated in deeper water columns outside of the 50m contour comprising approximately 70% of the near bottom phytoplankton populations (~1300-1900 cells/L) (Fig. 7b). *Prorocentrophycidae* and *Dinophysiphycidae* cells dominated over *Peridiniphycidae/ Gymnodiniphycidae* cells at mid shelf columns of approximately 30-45m (Fig. 7b). These findings are just trends and are not statistically significant according to ANOVA tests at F= 1.019.

Post-front

After the wind event, temperature and salinity were vertically well mixed to the sediment interface with a narrow gradient of cooler, fresher water (24.5 ºC, 34.8 PSU) inshore and warmer, higher salinity water (26.5 ºC, 35.6 PSU) offshore (Fig.8a,b,d,e). Sigma-t values from the CTD, as well as potential density values from the Acrobat, agreed with the temperature and salinity profiles and showed the water column to be well mixed to the bottom over a limited range (23.2-23.6 g/cm³) throughout the entire water across the shelf (Fig. 8c,e). The bottom of the euphotic zone (1% PAR) separated from the sediment interface at the ~20m depth contour as it had before the wind event, but with areas of

perturbations in the euphotic zone reflecting turbulence caused by the wind event (Fig. 9a). Nitrate-nitrite concentrations across the shelf were redistributed all the way to the 60m depth contour with concentrations < 0.03µM throughout the entire vertical water column across the shelf (Fig. 9b). Three chlorophyll *a* maxima were present with ~0.6µg/L near bottom at approximately 30-35m (Fig. 9c) and with ~0.4µg/L at various depths between the 45-60m depth contours. Chlorophyll *a* concentrations were also redistributed due to the wind event with concentrations < 0.5µg/L over most of the transect, but usually slightly higher concentrations were found near bottom and at mid column (~0.3 µg/L) rather than at the surface (0-0.2 µg/L) even after the wind event (Fig. 9c).

HPLC/CHEMTAX analysis of field sample (Fig. 10a) also showed uniform distributions of both diatoms and dinoflagellates across the transect after the wind event. There was no clear definition of the change in species dominance with depth as we saw before the wind event. Diatom concentrations made up approximately 0.1 µg/L chlorophyll *a* near bottom at the ~25m and ~35m depth contours (Fig. 10a). At all other depth contours across the shelf, as well as at mid column and surface depths, diatom populations made up less than 0.01 µg/L chlorophyll *a* (Fig. 10a). *Gyro/Gymnodinoid* dinoflagellate populations across the shelf near bottom also declined due to the wind event (Fig. 10b). A few small concentrations of *Gyro/Gymnodinoid* cells were found near bottom to make up less than 0.2 µg/L chlorophyll *a* at 25m, 35, and 55m, while at the mid column depths and the surface across the shelf, *Gyro/Gymnodinoid* cells made up less than 0.1 µg/L chlorophyll *a* (Fig.

10b). *Peridinoid* dinoflagellate cells were found to be in the lowest concentrations of all phytoplankton cell types analyzed. The most notable concentration of *Peridinoid* cells after the wind event was found at approximately 20m depth within the 30m contour column (Fig. 10c).

FlowCAM analysis showed a redistribution of near bottom diatom and dinoflagellate populations. Dinoflagellates uniformly dominated (600-4000 cells/L) diatoms (400-2500 cells/L) post-front from 20-60m depth across the transect (Fig. 11). The highest concentrations of diatoms were found at the 25-30m contour and the 50m contour, but diatoms never exceeded 35% of the counted phytoplankton populations near bottom (Fig. 11). Dinoflagellates concentrations generally made up 55-75% of the counted phytoplankton population near bottom at all depths across the shelf (Fig. 11). The mean for dinoflagellates was 2292 +/- 1003, standard error 354.7, 95% confidence interval +/- 838.7 and the mean for diatoms was 912.5 +/- 680.7, standard error 240.6, 95% confidence interval +/- 569.1. There is a statistically significant difference between the dinoflagellates and diatoms means according to ANOVA at the F=3.219, df=12, alpha=.05. Diatom and dinoflagellate subgroups also reflected the same type of population distribution. At all station between 20-60m, except for the 55m station, the near bottom diatom populations were dominated by pennates (400-2000 cells/L) over centrics (0-400 cells/L), with a pennate maximum at the 50m depth contour (Fig. 12a). At the 55m depth, centrics made up ~55% (~430 cells/L) of the diatom population and pennates only made up ~45% (~320 cells/L) of the near bottom

diatom population (Fig. 12a). At all other depths, pennates were more abundant, especially at the 25m contour where they made up 100% of the diatom population near bottom and at the 45-50m contours where they made up 80-90% of the diatom population (Fig. 12a). FlowCAM samples showed that there is a statistically significant difference in the means of pennates and centric according ANOVA at F=4.241, p=.0585, f crit.=4.600, alpha=.05 across for the entire transect at all depths, not just in shallower areas where the euphotic zone penetrates to the sediment interface as was seen before the wind event. Near bottom dinoflagellate populations were dominated by *Prorocentrophycidae* cells (500-2600 cells/L) at all stations between 20-60m over *Peridiniphycidae/ Gymnodiniphycidae* cells (200-1500 cells/L) which together generally comprised ~50% of the dinoflagellate population(Fig. 12b) . One exception to this was at the 25m depth contour where *Peridiniphycidae/ Gymnodiniphycidae* cells and *Prorocentrophycidae* cells were made up of almost equal concentrations of the near bottom dinoflagellate populations (Fig. 12b). *Dinophycidae* cells and *Ceratium* cells were found at negligible concentrations near bottom across the shelf at all depths (Fig. 12b). The difference in means of each dinoflagellate subclass were also statistically significant according ANOVA F=36.85, p<.001, df=3, f crit. = 3.072 across the entire transect.

HPLC vs. FlowCAM

We compared the field results taken before and after the wind event by both HPLC/ChemTAX and FlowCAM and analyzed the concentrations of phytoplankton groups with both. HPLC/ChemTAX results reflected dinoflagellate species identified by their characteristic pigments, where as FlowCAM results reflected the dinoflagellate species that were able to be identified by morphology. By using both methods we could get a better, more widespread, description of the diatom and dinoflagellate classes that made up the chlorophyll maxima we were seeing.

Chlorophyll *a* concentrations (µg/L) from both instruments showed a chlorophyll *a* maximum near bottom at the 30m contour of approximately 0.8 µg/L before the wind event (Fig. 4c). HPLC/ChemTAX results suggested that the chlorophyll *a* maximum near bottom was comprised of at least 0.4 µg/L contributed by diatoms (Fig. 5a). The FlowCAM reported that the chlorophyll *a* maximum was made up of 30% diatoms or approximately 0.24 µg/L of chlorophyll a is contributed by diatoms of the total 0.8ug/L of chlorophyll *a* (Fig. 6). As far as dinoflagellate species contributing to the chlorophyll *a* maximum near bottom, FlowCAM and HPLC/ChemTAX divided the dinoflagellate community into different subclasses, making the results hard to compare. HPLC/ChemTAX results identified the major dinoflagellate species found were *Gyrodinium* and *Peridinium* cells (Fig. 5a, b). FlowCAM results showed that the pre-front near bottom chlorophyll *a* maximum was comprised of dinoflagellate subclasses such as of *Prorocentrophycidae, Peridiniphycidae/*

Gymnodiniphycidae, *Dinophysiphycidae* and *Ceratium* (Fig7b). Both methods did identify that *Peridiniphycidae/ Gymnodiniphycidae* cells were present at relatively low concentrations compared to the other dinoflagellate cells. After the wind event, the chlorophyll *a* maximum was still at the sediment interface at 30m and both methods showed a lowered concentration of chlorophyll *a* (~0.4 µg/L) compared to before the wind event (Fig. 9c). HPLC/ChemTAX results showed that diatoms made up ~0.1 µg/L of the total 0.4 µg/L chlorophyll *a* in the patch (Fig. 10a), approximately 20% of the total. FlowCAM results showed that diatom cells made up ~30% of the phytoplankton cells in this patch (Fig. 11). According to HPLC/ChemTAX results for dinoflagellate subclasses, *Gyrodinium* cells contributed approximately 0.2 µg/L to the total chlorophyll *a* found in the near bottom patch (Fig. 10b), while *Peridiniphycidae/ Gymnodiniphycidae* cells only contributed ~0.03 µg/L chlorophyll *a* (Fig. 10c). FlowCAM results showed a similar lowered concentration of *Peridiniphycidae/ Gymnodiniphycidae* cells (~35%) compared to *Prorocentrophycidae* cells (over 60%) (Fig. 12b).

The wind event affected both the hydrography of the water column and the shelf as well as the phytoplankton populations near bottom (Fig. 13). CTD casts showed that the water column was stratified before the wind event, but after the wind event CTD casts showed that the water column had become well mixed vertically (Fig. 13). Before the wind event diatoms and dinoflagellates were found at similar concentrations near bottom and they tentatively shared in the uptake of nutrients at the sediment interface at all depths nearshore

and offshore (Fig. 13). At the 30m depth contour, before the wind event, there was a chlorophyll maximum near bottom, and FlowCAM samples showed the highest counts of both dinoflagellates and diatoms near bottom here (Fig. 13). The wind event redistributed this population near bottom and after the wind event dinoflagellates to appear to have a higher abundance than diatoms the near bottom (Fig. 13). The wind event also destroyed the chlorophyll maximum initial found at the 30m depth contour. After the wind event a near bottom chlorophyll maximum was found at the 50m depth contour (Fig. 13). This may or may not be the same population that was at the 30m depth contour before the wind event being pushed into deeper water from the wind event.

Discussion

1) Transition Implications Based on Observations

Before the wind event the water column was stratified, but not as strongly as one would have seen earlier in the summer (Fig. 13a). These conditions indicated that the summertime seasonal regime of strong stratification (Grabowski et al., 2010) was waning and transitioning into the winter regime. Briefly summarizing the conditions before the wind event, temperature and salinity profiles indicated patchy pockets across the shelf that

combined to provide stable stratification across the shelf (Fig. 3). Sigma-t profiles showed the denser water was found off shore of the 50m depth contour and near bottom (Fig. 3). The euphotic zone, separated from the sediment interface at ~20m, defining the near bottom light condition (Fig. 4) while nitrate-nitrite profiles with elevated near bottom concentrations defined the nutrient condition influencing existing cross shelf phytoplankton community structure (Fig. 4). The chlorophyll *a* maximum found near bottom at the 25 contour (Fig. 4) was mostly comprised of at 68% dinoflagellates at the 25m contour and 58% at the 35m contour). Concentrations of diatoms at the 30m contour of 40%, but lower diatom concentrations were found at the 25m contour of <10% and ~30% at the 35m contour (Fig. 6). Outside of the 50m contour, dinoflagellates clearly dominated near bottom comprising over 50% of the phytoplankton population compared to 35% diatoms (Fig. 6).

After the wind event, the water column was well mixed (Fig. 13b) and most profiles showed an even distribution of physical, chemical and biological characteristics throughout the entire column (Fig. 13). Briefly summarizing the conditions after the wind event, temperature and salinity profiles showed uniform water column conditions from surface to sediment, but a warming trend with increasing salinity offshore as coastal water transitioned to Gulf of Mexico water (Fig. 8). This type of temperature and salinity gradient would induce a baroclinc type of circulation on the entire water column (He & Weisberg, 2002) Sigma-t profiles showed uniformly dense water columns with only a weak increase across the shelf (Fig. 8). The euphotic zone had shoaled somewhat and nitrate-nitrite concentrations

were depleted throughout the entire column, even at the sediment interface, earning the label "oligotrophic" that is normally associated with the Gulf of Mexico (Vargo et al., 2008), especially in the winter regime (Fig. 9). Small patches of higher chlorophyll *a* concentrations still existed, especially near the sediment interface where the wind event may have resuspended sediments in susceptible areas. This inshore resuspension increased pennate dominance over centric diatoms, as the pennate diatoms previously buried in the sediments likely were resuspended with the sediment in response to the wind event. The same resuspension of previously buried *Prorocentrophycidae* cells may be the cause of their dominance over that of *Peridiniphycidae/ Gymnodiniphycidae* cells after the wind event. Wind mixing may not have reached to the bottom offshore, therefore sediment was not resuspended there (Fig. 9 & 12). Eventually, after successive wind events associated with the late fall season, the chlorophyll maxima would be destroyed resulting in more evenly distributed chlorophyll *a* throughout the water column.

2) Predictions Based on Margalef's Model

The changes in the degree of stratification, light penetration and nutrient availability in the water column associated with the seasonal transition were likely to elicit a succession change in phytoplankton species dominance (Fig. 14). To a first approximation, the phytoplankton community composition after the wind event was a mixed version of the more stratified phytoplankton community structure in the water column prior to the wind event

with additional contributions from the previously sediment-bound phytoplankton community mixed into the water column. Part of the reason is that the change in hydrodynamics of the shelf was instantaneous and there is a lag in the change in phytoplankton because phytoplankton growth rates exceed the time required for physical restructuring of the water column. The Margalef succession model can be applied to help predict the species succession to be expected in the near bottom phytoplankton population in response to the seasonal transition. A transition between dinoflagellate species and diatom species is predicted in Margalef's model based on the seasonal hydrodynamic state of the shelf.

2a) Comparison between the Model and the Phytoplankton Community due to the Wind Event

Before the wind event in the shallower inshore water column, light reached the sediment interface since the base of the euphotic zone (1% PAR) was near the sediment layer at approximately 25-30m (Fig. 4). At depths >30m, light no longer reached the sediment interface since it was well below the euphotic zone, so there is a distinct euphotic and aphotic zone in deeper water column. Our results have shown that in water columns less than 30m where the euphotic zone reaches the sediments, diatoms tend to dominate the sediment interface to utilize nitrate-nitrite pools of greater than 4uM (Fig. 6). Diatoms, like dinoflagellates, need both adequate nutrients and light for photosynthesis to maintain their cell growth, but unlike dinoflagellates, individual diatom cells do not have similar migration

and swimming capabilities of dinoflagellates. Therefore, diatoms must occupy a habitat that has both adequate light and nutrients to maintain growth. The dominance of diatoms in shallow water columns is consistent with Margalef's succession model in which invasive, r-selected species of fast growing phytoplankton species will dominate where nutrients are highly available as they are in these shallower water columns inshore due to terrestrial inputs of nutrients.

Beyond the 30m contour, light is limiting at the sediment interface. Margalef's model suggests a change in species dominanace to dinoflagellates that can access the required nutrient and light resources, in particular dinoflagellate species that tolerate intermittent mixing due to limited vertical penetration of wind-induced turbulence (Fig. 6). Nutrient sources are provided by sediment based regeneration and deep water source at the outer shelf. Dinoflagellate cells can migrate between the sediment interface for nutrient uptake and the bottom of the euphotic zone (the 1% PAR depth). Each individual dinoflagellate cell will migrate at its own pace depending on the species swimming capabilities (Kamykowski et al. 1992) and the internal need for either photosynthate or dissolved nutrients to maintain growth**.** Field samples showed a dominance of dinoflagellates over diatoms in deeper water column outside of 30m supporting Margalef model suggested. Dinoflagellate samples indicated a strong presence of *Prorocentrophycidae* and *Peridiniphycidae/ Gymnodiniphycidae* cells dominating the dinoflagellate population at the sediment interface before the wind event (Fig. 7). According to Margalef's model the dinoflagellate population

should have been at first a mix between colonist dinoflagellate species such as *Prorocentrophycidae, Peridiniphycidae/ Gymnodiniphycidae* cells which are small, r-selected speceis that can grow faster to counterbalance destruction of their fragile populations from wind and other disturbance events. Smaller dinoflagellate cells also have smaller internal pools to fill from nutrient uptake and photosynthesis to be able to maintain individual growth, which works to their benefit in in a low nutrient environment. Since these *Prorocentrophycidae* cells are much smaller, they can also easily be resuspended from within the sediments during periods of turbulence, along with smaller diatoms like pennates. In this way these dinoflagellates can more quickly achieve greater abundances than other dinoflagellate counterparts (Smayda & Reynolds, 2001). *Prorocentrophycidae* cells are usually found along with diatoms during early spring time blooms as the water column begins to be weakly stratified (Smaya & Reynolds, 2001), which is the reason why they were found with pennates shortly after the wind event when conditions were similar throughout the water column. Smayda suggested that habitat types that favor *Prorocentrophycidae* cells and smaller *Gymnodiniphycidae* cells high resources and high energy habitats, are often associated with red tide events (2001).

As nutrient concentrations at the sediment inteface became depleted from use and stratification of the column increased, models predict that the population trend moves toward higher concentrations of *Gymnodiniphycidae* and *Dinophycidae* cells (Smayda & Reynolds, 2001). From field samples at all depths after the wind event, *Prorocentrophycidae* cells

dominated over that of other dinoflagellate subclasses and pennates comprised the majority of diatoms over that of centrics at most depths, especially inshore where the wind event reached the sediment interface and resuspended sediment and smaller cells (Fig. 12). With the resuspension of sediments, while smaller pennates and *Prorocentrophycidae* cells were resuspended, larger, heavier centrics and *Gymnodiniphycidae* and *Dinophycidae* cells were not. Part of this may be due to our sampling method as larger centric diatoms and *Gymnodiniphycidae* and *Dinophycidae* cells may have been resuspended but in the time that passed after the wind event until the samples were taken, the larger cells may have already settled out of the water column near the sediment interface.

At the end of the summer and into early fall, stronger frontal events across the shelf continue to change the succession of near bottom phytoplankton species. Species that are more tolerant of stresses and disturbance such as the wind event will be the most abundant near bottom. Once the water column becomes well mixed, representing the wintertime seasonal hydrodynamic cycle, phytoplankton species that have the ability to survive on low levels of nutrients will become the most abundant at the sediment interface.

2b) Model Predictions of how the Phytoplankton Community Should Evolve Seasonally

During the transition between seasonal hydrodynamic cycles, the northwest Florida shelf experiences increase wind and storm activity. Phytoplankton species that are tolerant of these stresses and disturbances, that are strong enough to affect the ocean bottom, will become the most abundant species near bottom. Succession of dinoflagellate cells near bottom turn toward ruderal species, such as larger *Gymnodinoid, Alexandrium,* and *Ceratium* cells, which are often associated with frontal zones and upwelling dominated. (2001). These species are larger and slow growing but generally conserve biomass and can tolerate nutrient stress and shear stress near bottom as well as low light conditions (Smayda & Reynolds, 2001) .

Once the hydrodynamics of the shelf offically change over to the wintertime regime, characterized by a mixed water column and an onshore to offshore gradient with low near bottom nutrients present, the succession of phytoplankton near bottom will eventually return to diatom dominated. Since a well mixed water column will diffuse the summertime near bottom nutrient concentrations throughout the water column, dinoflagellates will also diffuse throughout the water column and some very low concentrations will still exist at the sediment interface. Due to the lack of migration capabilities, diatoms will dominate over dinoflagellates at the sediment interface in a well mixed column up to a critical depth of mixing and light penetration. The succession models by Smayda and Reynolds (2001) can

be used to predict which species of phytoplankton will tend to have a higher percent abundance near bottom as the shelf shifts into its winter seasonal hydrodynamic regime. During stratification, the compensation depth as the bottom of the euphotic zone determined where on the shelf dinoflagellates, capable of migrating between sediment and euphotic zone, were likely to dominate over water column diatoms. As the shelf shifts into its winter regime, the water column becomes well mixed and unstratified to the sediment interface. Critical depth or the ratio between phyotosynthesis and respiration (Sverdrup, 1953) is then important for defining the growth environment for phytoplankton community character and abundance.

For phytoplankton populations to increase in a well mixed water column, the critical depth must be deeper than the depth of the mixed layer (Sverdrup, 1953). The critical depth can usually be assumed to be 5-10 time the depth of the compensation depth (Sverdrup, 1953). If the depth of the mixed layer is greater than the critical depth, then the phytoplankton population will remain small, but if the depth of the mixed layer is shallower than the critical depth, then the phytoplankton population can increase, but grazers present can impede this progress (Sverdrup, 1953). Post-front, the critical depth (Z_c) was ~50 m across shelf calculated as $Z_c = 0.8 \times 11.57 \times I_o / I_c \times k_{PAR}$ according to Nelson & Smith (1991) with the irradiance at the ocean surface is I_o = 40 mole photons / m^2 /day derived from SeaWiFS, the irradiance at the photocompensation depth is I_c = 35 umole photons / m^2 / s , and k_{PAR} = 0.24 based on Fig. 8). In the winter condition represented by the shelf after the wind event, the sediment interface defines the mixed layer depth across the inner shelf when

the wind forcing penetrates to bottom of the water column. Diatoms can grow in continuously mixing water columns across the shelf where the sediment interface is above the critical depth, but the potential for net growth decreases as the sediment depth and the critical depth converge. Further offshore, the phytoplankton response depends on the actual depth of the mixing layer relative to the critical depth. If water column mixing is intermittent, then dinoflagellate motility may provide a selective advantage to utilize relatively meager light and nutrient resources in the winter water column. Mixing intermittency can provide temporal complexity to winter phytoplankton species composition to replace the spatial complexity more characteristic of the summer condition. Intermittent mixing of the water column may provide an ideal habitat for fast growing and stress tolerant dinoflagellates to dominate. The temporal characteristics between a mixing and intermittent mixing column can allow for a smaller scale succession pattern in terms of near bottom phytoplankton populations across the shelf to take place.

The gradient of photosynthesis vs. respiration (eg. critical depth) will determine the gradient by which either diatoms or dinoflagellates dominate the sediment nutrient flux. The succession begins near bottom with a shift in dinoflagellates from r-selected species that are small colonist species that are invasive, fast growing and do well in stratified energy replete habitats to K selected species which are slow growing adapatable species and are tolerant to low nutrient conditions. Based on sigma t profiles from the CTD, the mixed layer across the shelf between 20-70m, always penetrated to the sediment interface, even when the sediment

interface was deeper than the critical depth (~50m). Phytoplankton populations in mixing water columns that are mixing to the sediments and are deeper than the critical depth will be very low in cell concentration. Since there is a greater net respiration rate vs. photosynthesis rate in these deeper water columns, the phytoplankton populations, if it is able to survive, should not grow in population size and should be made up of dinoflagellates that are more adaptable to low nutrient and light environments, such as *Gymnodinoids*. Highest concentrations of phytoplankton, especially diatoms, will be found throughout water columns that are shallower than the critical depth, decreasing in concentrations as net photosynthesis is approximately the same net respiration as the water column reaches the point of the critcal depth, and lowest concentrations of phytoplankton throughout the water column will be found in the deepest water columns that are mixing to the sediments but are deeper than the critcal depth.

3) Conclusions

I do predict that the sediment interface will supply of enough nutrients to maintain a low concentration of dinoflagellate cells year around, even during the wintertime hydrographic regime on the shelf. During the winter seasonal cycle, the water is well mixed and nutrient concentrations diffuse throughout, but enough nutrients are still present at the sediment interface to maintain a small concentration of phytoplankton cells. Dinoflagellate cells may choose to stay at the sediment interface in the wintertime since there is no other

distinct higher concentration of nutrient to migrate towards. Diatoms will also be present year around at the sediment interface, but in areas of the shelf that are shallower than the critical depth during the wintertime when the column is well mixed and shallower than the bottom of the euphotic zone in the summertime since the column is stratified. The maintainence of this near bottom population may serve as a seed population that can be used in bloom initiation. This population can be concentrated at nutrient fronts then upwelling to the surface and transported to the coastline to become a typical surface algal bloom (Lui et al., 2001). Depending on the species of dinoflagellates occupying the near bottom seed population, the resulting surface bloom has the ability to be a harmful algal bloom, with the same characteristics of an originally surface oriented bloom.

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FIGURES

October Cruise Transects and Stations

Figure 1. October 2008 cruise transect outline.

Wind events

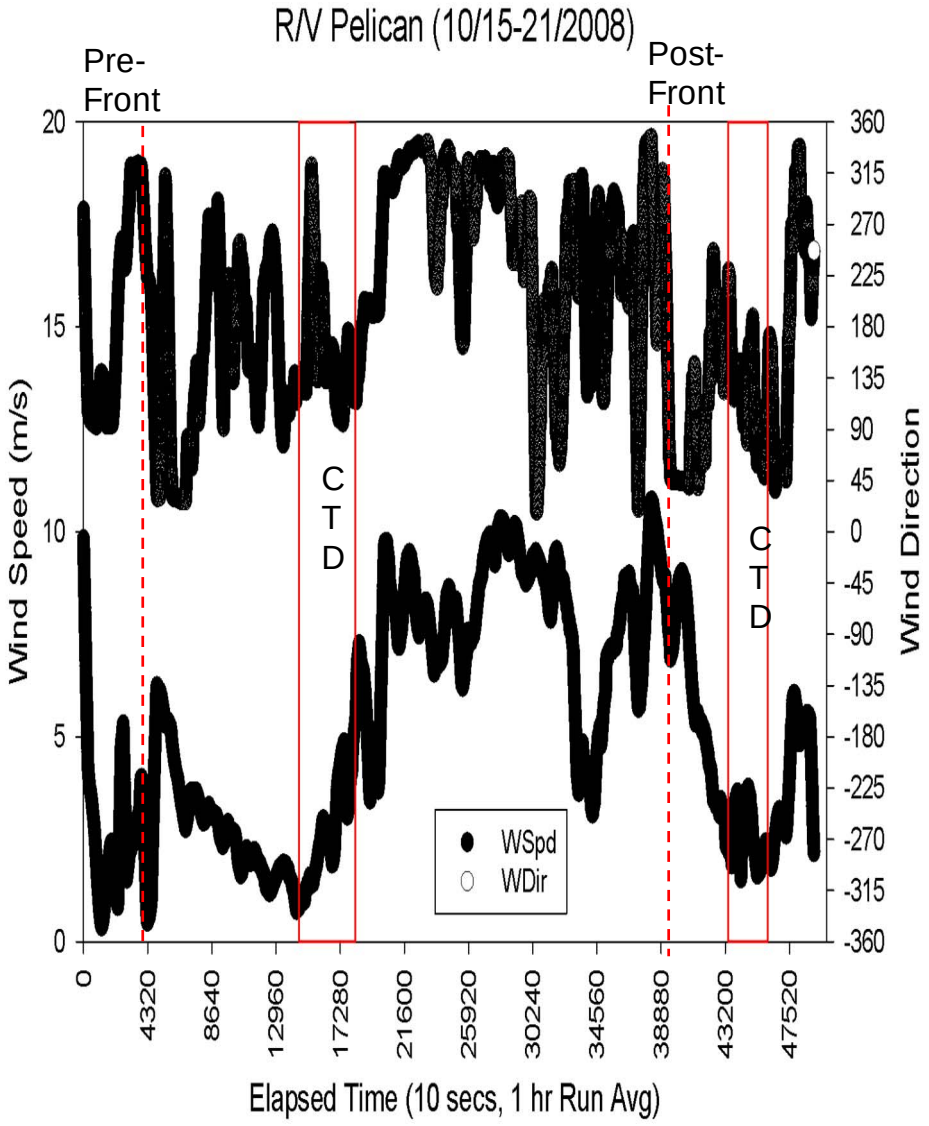

Figure 2. Wind speeds showing the wind event experience during the October 2008 cruise and the timing of the transects before and after the event.

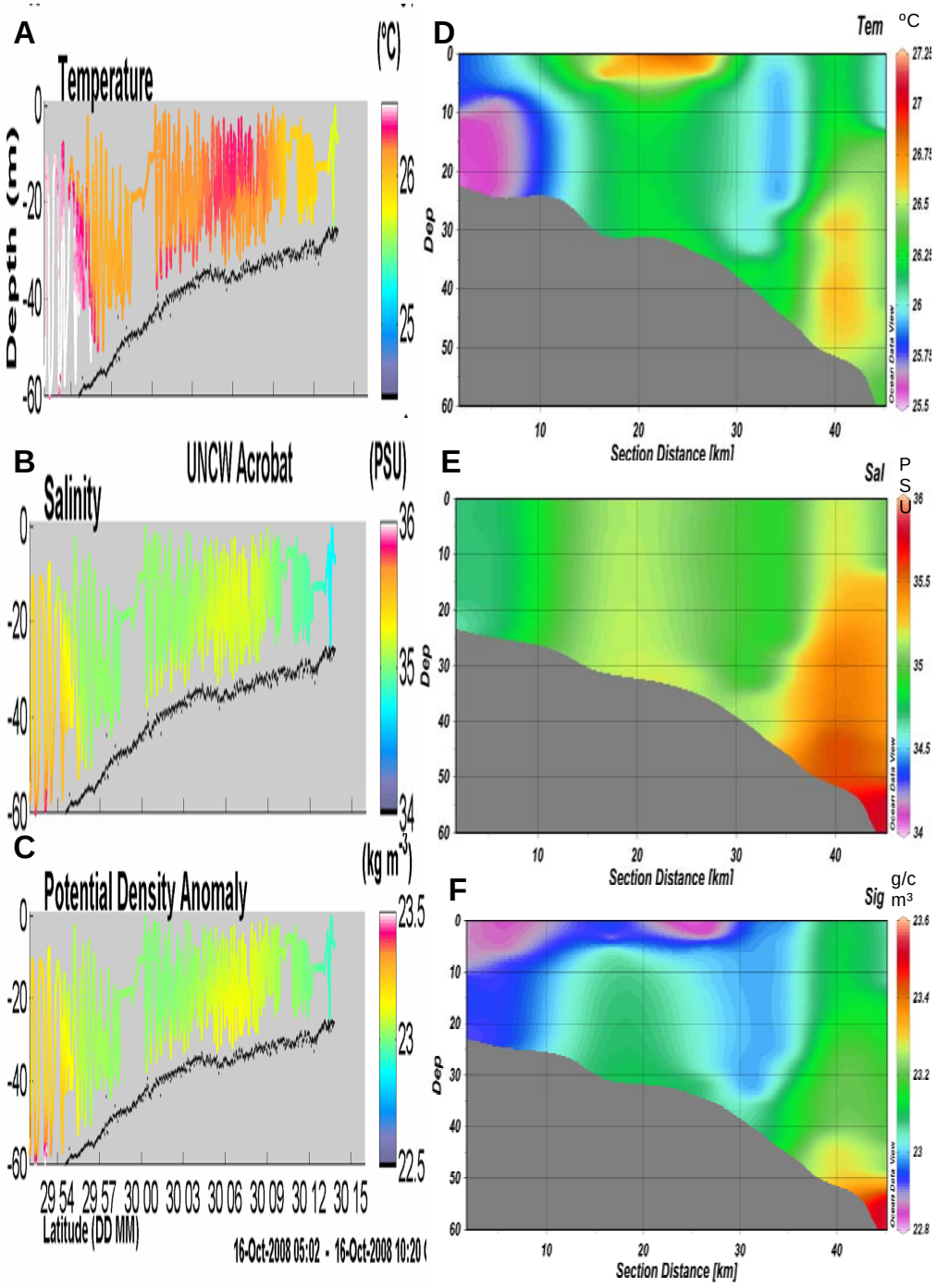

Figure 3. Acrobat profiles of A)Temperature B) Salinity C) Potential Density and CTD profiles of D) Temperature, E) Salinity, and F) Density before the wind event.

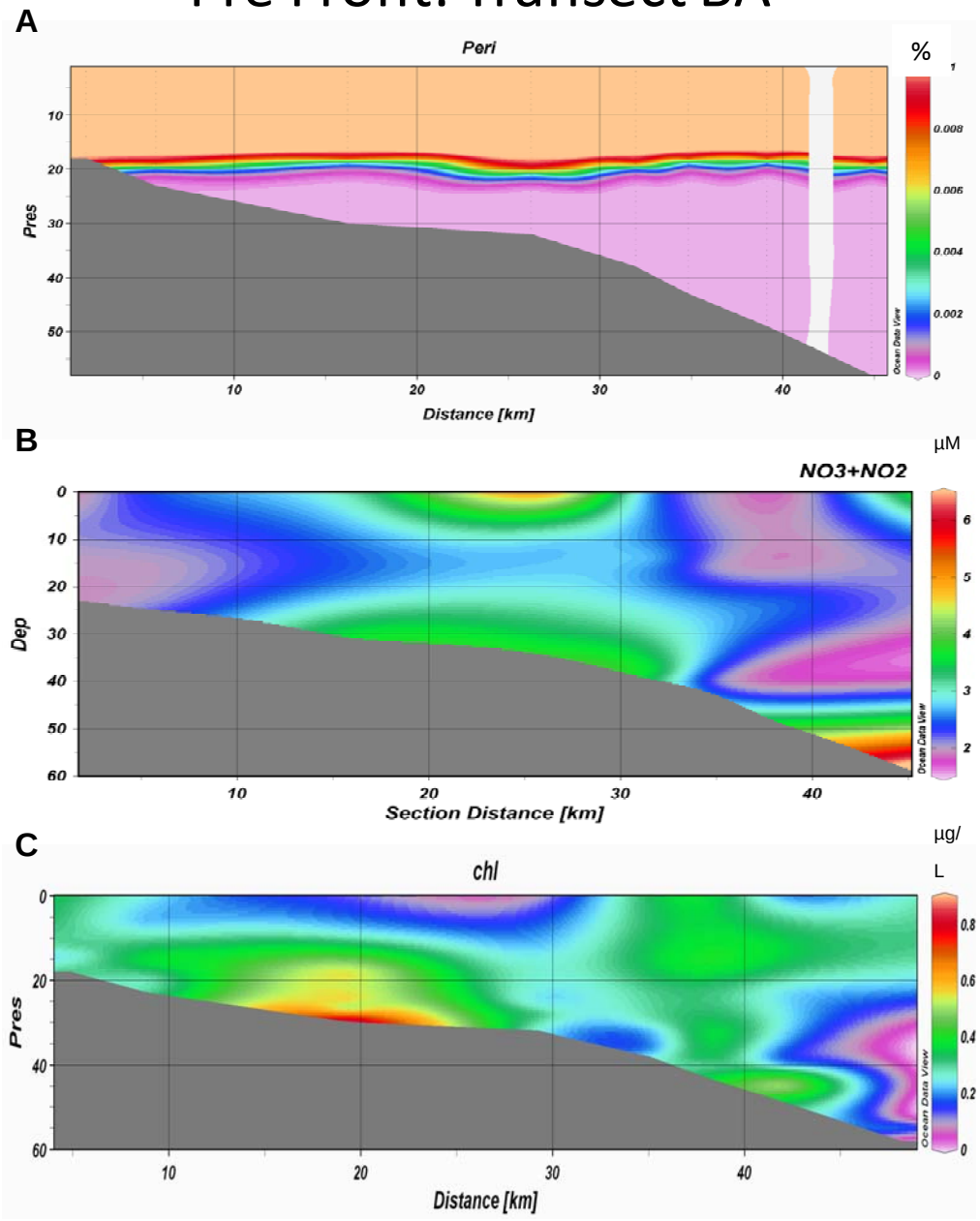

Figure 4. ODV data from CTD profiles shows the water column is stratified in terms of A) Peri, B) Nitrate-Nitrite concentrations, and C) Chlorophyll a before the wind event from HPLC results.

Pre Front: Transect BA

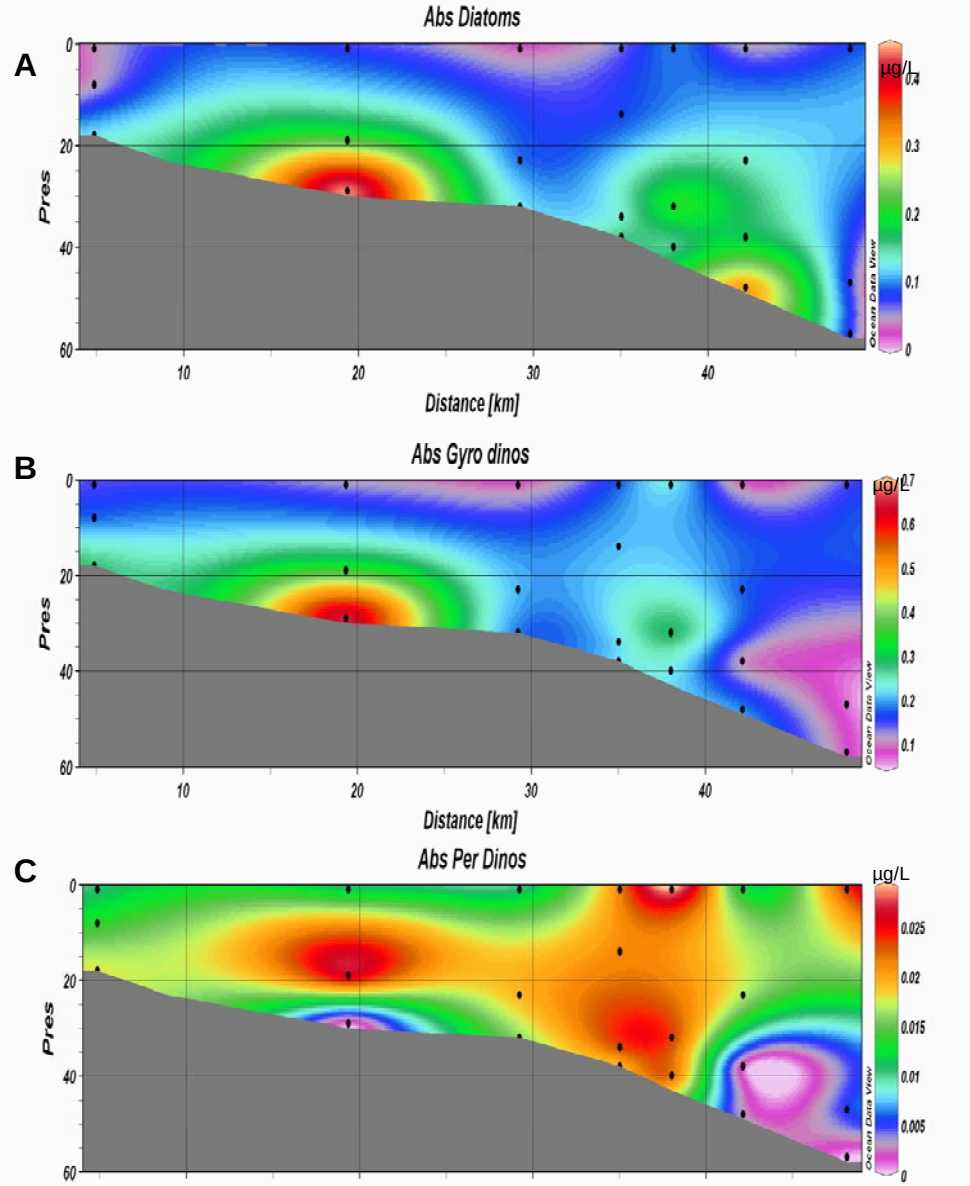

Figure 5. HPLC and ChemTAX results of A) diatoms and two dinoflagellate subclasses: B) *Gyrodinium* dinoflagellates and C) *Peridinium* dinoflagellates, found in field samples before the wind event.

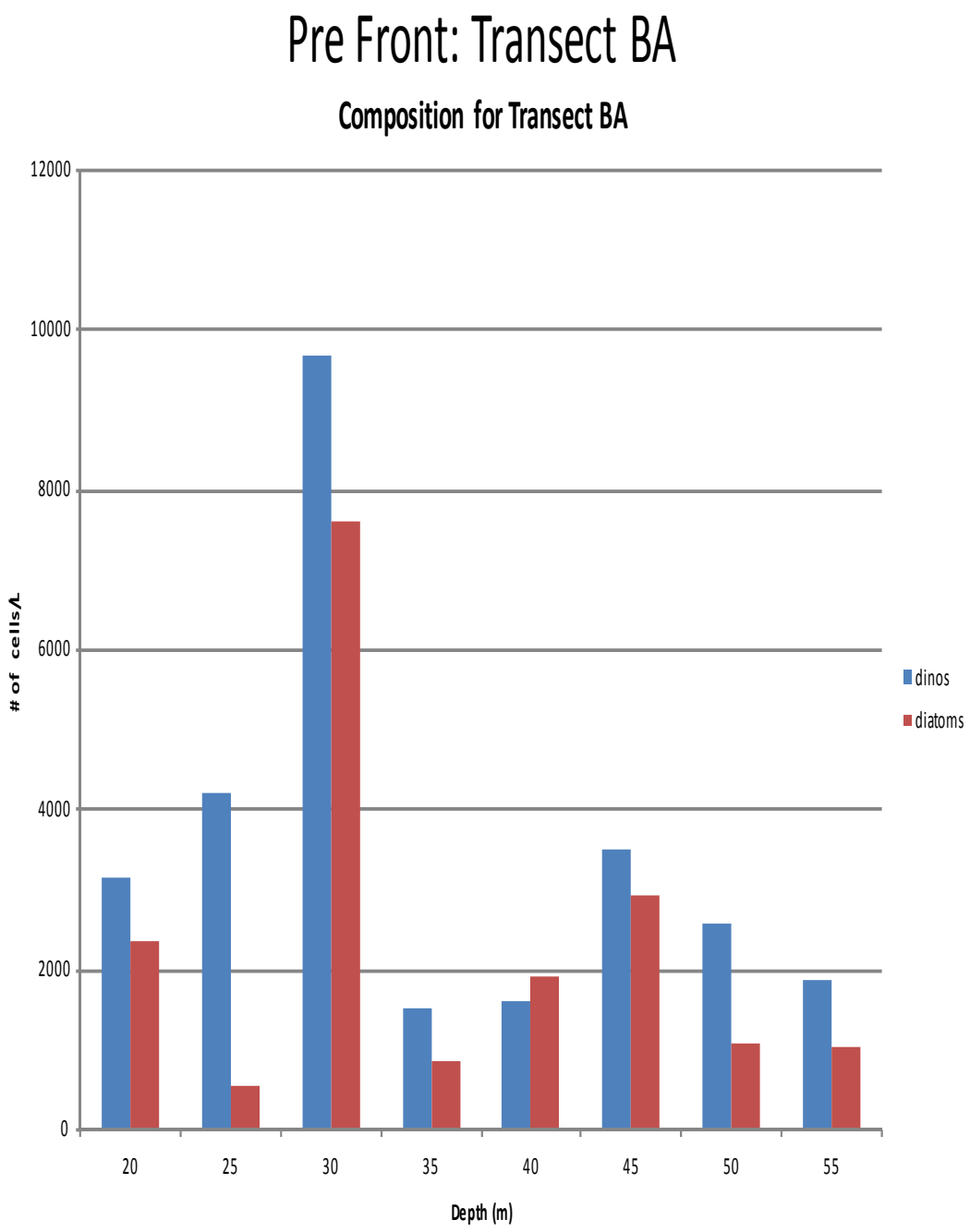

Figure 6. FlowCAM field samples taken near bottom show that the same population as found by the Acrobat is found at primarily between 20-30m depth before the wind event and there is evidence of dinoflagellates and diatoms.

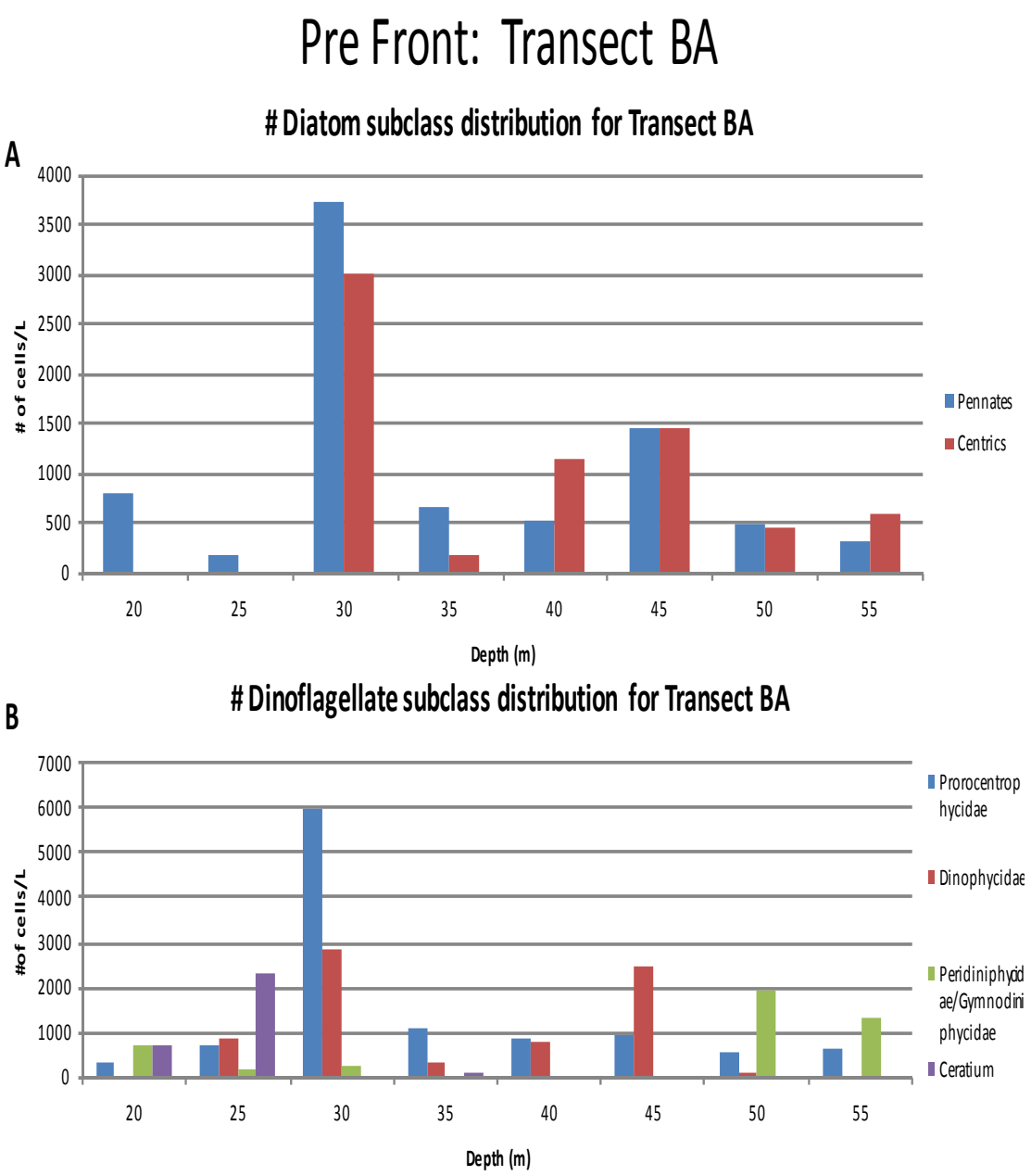

Figure 7. Percentage of A) Diatoms and B) Dinoflagellate subclass distribution along Transect BA and BC before the wind event.

Post Front: Transect 2BA

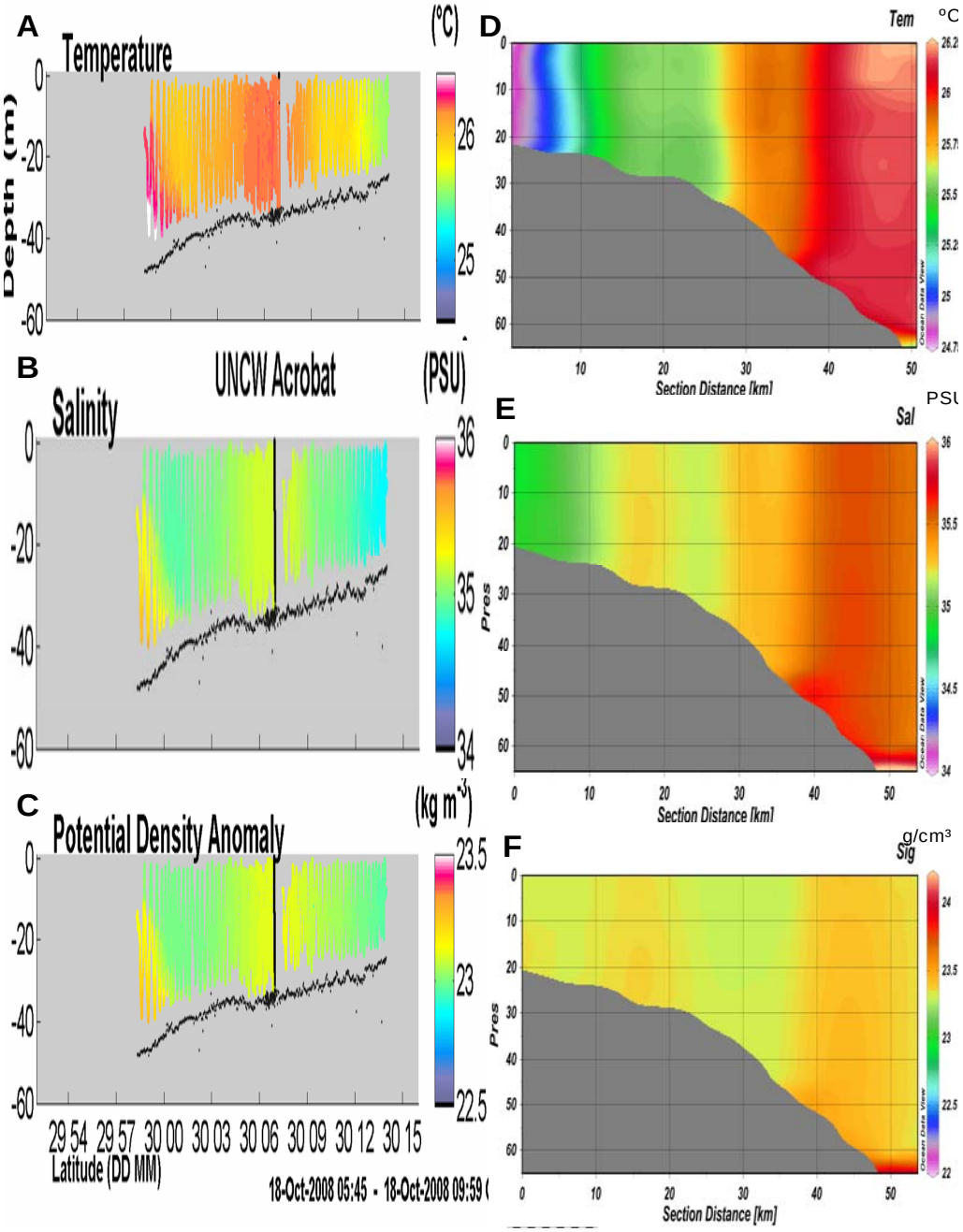

Figure 8. Acrobat profiles of A) Temperature, B) Salinity, and C) Potential density and CTD profiles of D) Temperature E) Salinity, and F) Sigma t after the wind event.

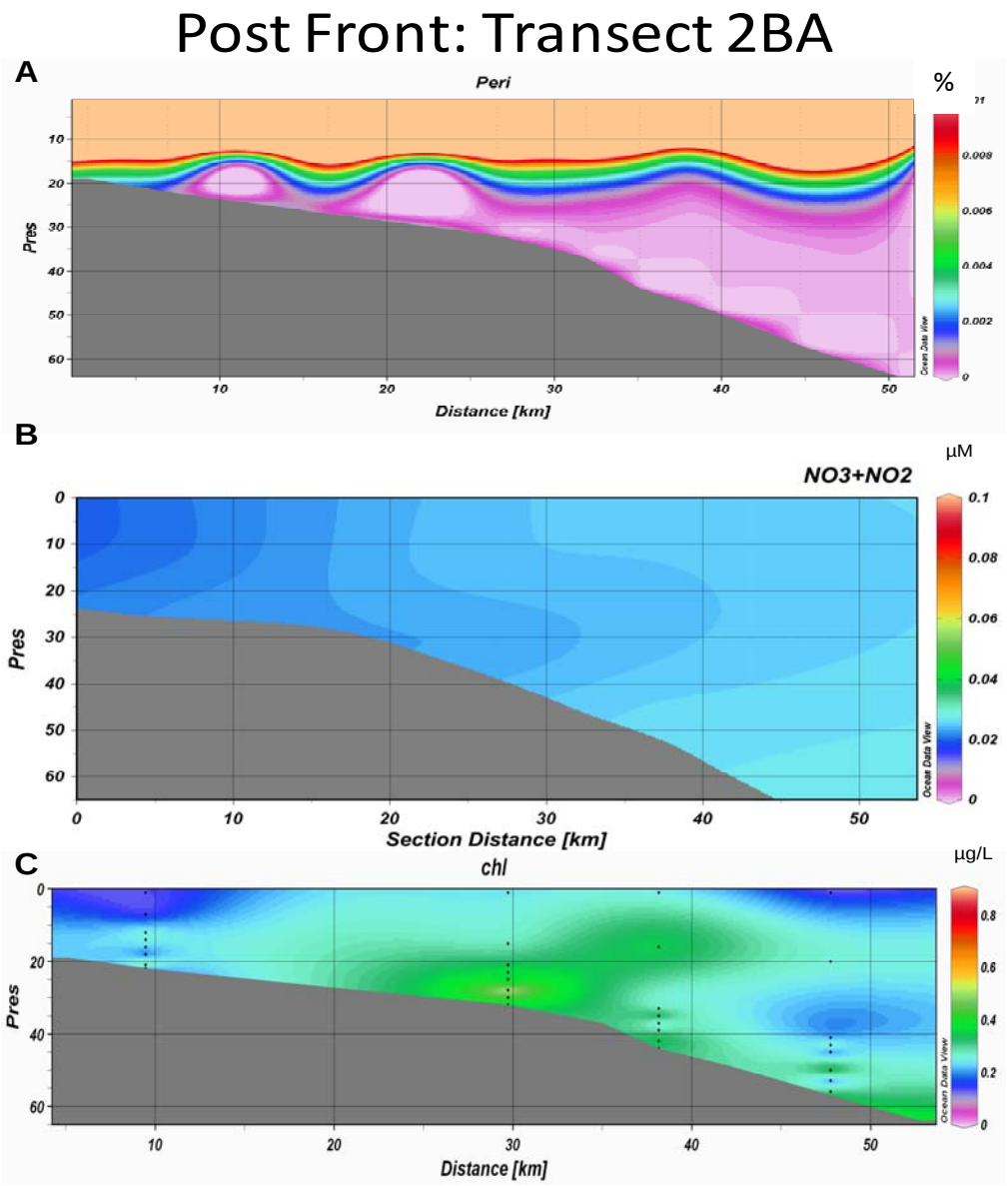

Figure 9. ODV data taken from the CTD shows a well mixed vertical water column after the wind event via A) Peri data, B) Nitrate-Nitrite concentrations throughout the water column C) a small Chlorophyll a concentration near bottom at approximately 30m from HPLC results.

Post Front: Transect BA

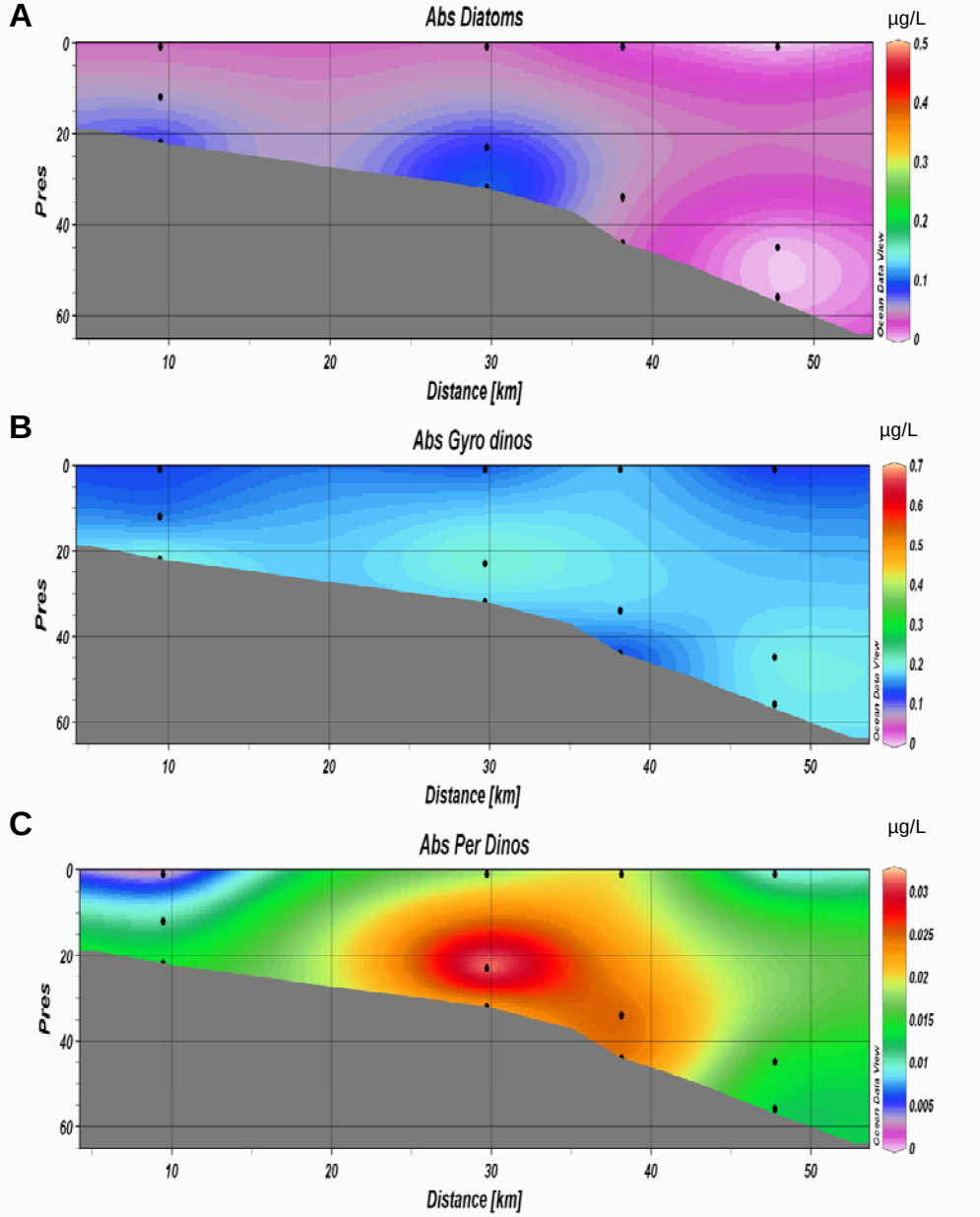

Figure 10. HPLC and Chemtax samples for Transect 2BA after the wind event for A) diatoms, B) Gyrodinium dinoflagellates, and C) Peridinium dinoflagellates.

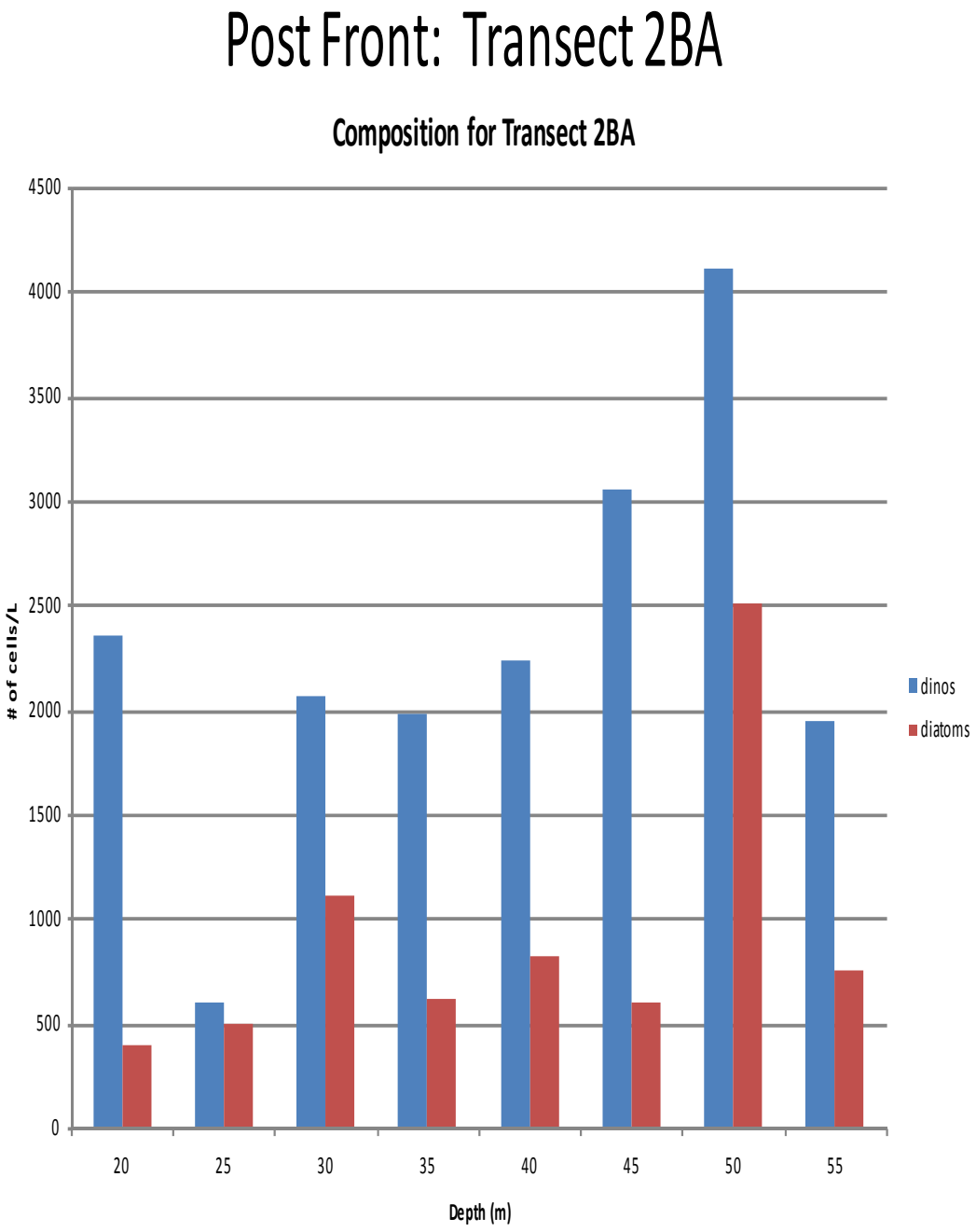

Figure 11. After the wind event, along transect 2BA, field samples taken near bottom show that the populations of dinoflagellates dominate over diatoms at all depths.

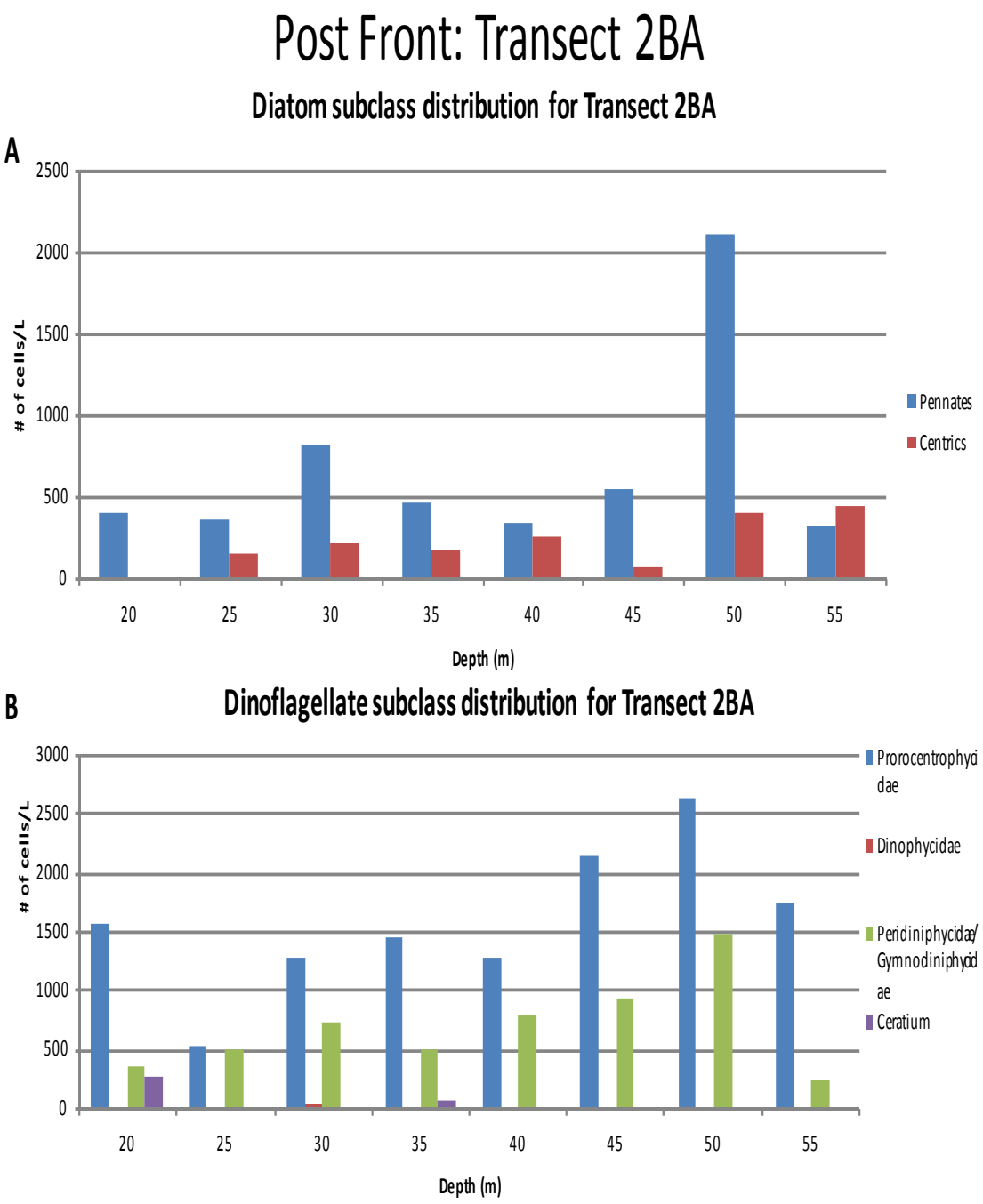

Figure 12. Percentages of A) Diatoms and B) Dinoflagellate subclasses distributed along both legs of the transect after the wind event.

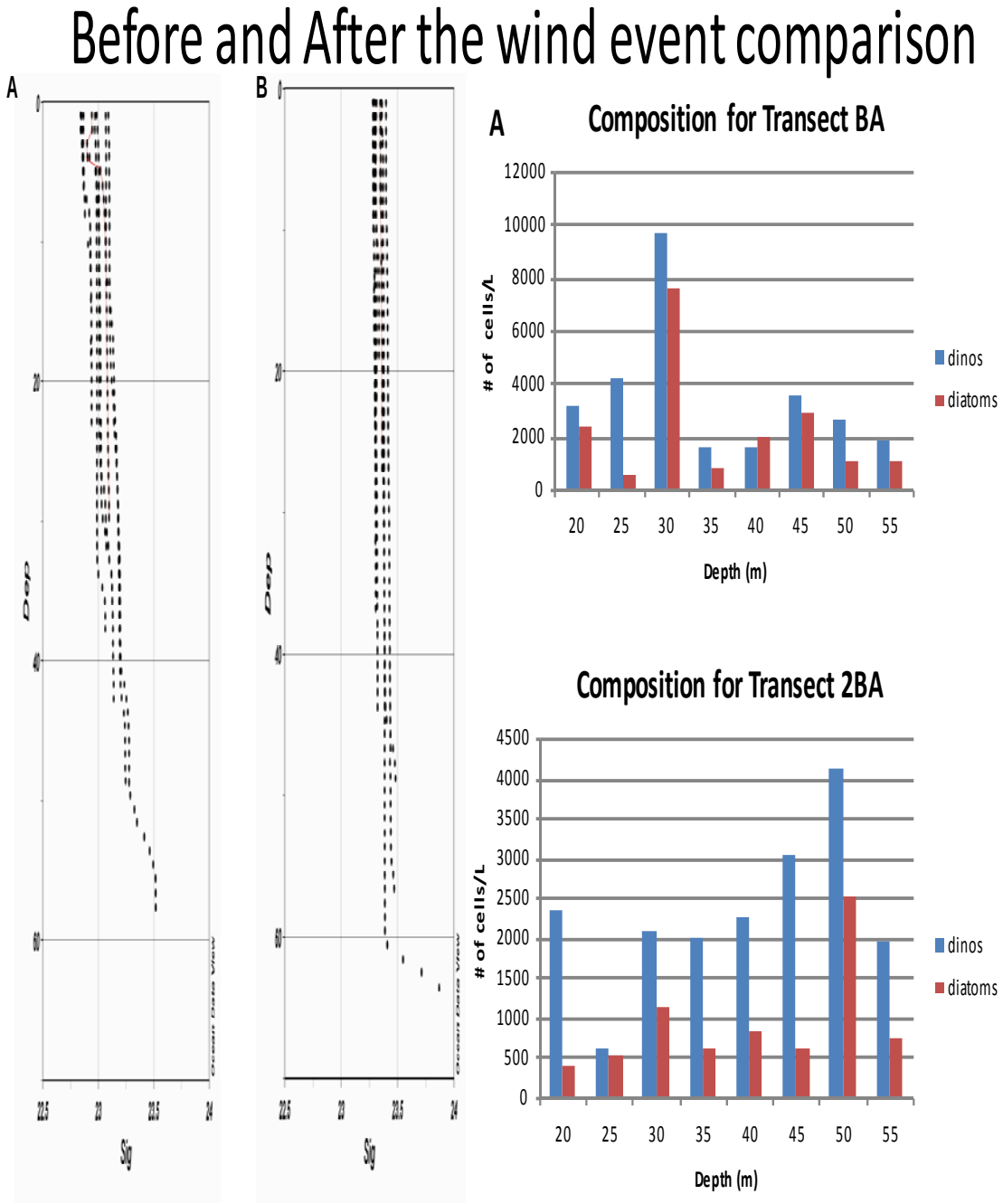

Figure 13. Water column stratification and dinoflagellate vs. diatom counts for A) before and B) after wind event via CTD casts and FlowCAM samples. Wind event made the column well mixed and redistributed any chlorophyll concentrations.

CHAPTER 4:

These BENDiM cruises sought to provide *in situ* field evidence to test hypotheses concerning near bottom phytoplankton populations on the northwest Florida shelf in the Gulf of Mexico during the stratified condition that exist between May and October. The initial hypotheses were:

1) Different dinoflagellates species dominate the BenDiM niche in different months and at different depth contours as species' size and motility provide a selective advantage to span the distance between adequate nutrients and light.

2) At water depths shallower than the MPB compensation depth, near-bottom water column nutrients are partitioned between pelagic diatoms (day) and dinoflagellates (night) and sediment: sea interface nutrients are partitioned between MPB algae (day) and BenDiM dinoflagellates (night).

3) At water depths deeper than the MPB compensation depth, the BenDiM niche occurs when water clarity supports a dinoflagellate DVM between adequate nutrients and light for net population growth.

Based on FlowCAM analysis of the net size fraction, dinoflagellate populations dominated near bottom in July with continued dominance into October. The October 2008 cruise data provided a characterization of the transitional fall/winter hydrographic regime on

the northwest Florida shelf. Due to the wind event mid-cruise, comparisons were made of changing phytoplankton growth conditions with respect to light and nutrients and the redistribution of the phytoplankton community. Succession models were applied to infer likely changes in future phytoplankton community structure. The July 2009 cruise data provided a characterization of the stratified summer hydrographic regime on the northwest Florida shelf, described the phytoplankton growth conditions with respect to light and nutrients, established dinoflagellates as a dominant component of the phytoplankton community especially near the sediment interface, and provided insight into the spatial cross shelf patterns and temporal sequences at selected depth contours. Based on the results we were able to make progress on all of the initial hypotheses. The following are the suggestions I would make to continue this research.

Future Implications

The October cruise gave further insight into the seasonal transition of the physical regime across the water column and a first look in the effects of the seasonal transition on the near bottom phytoplankton community. The phytoplankton community near bottom did not have the chance to fully react and adapt to the changing physical conditions across the shelf caused by the wind event we experienced during the cruise. Continued sampling of near bottom communities during the winter regime would help to determine the characteristics of

the phytoplankton community near bottom during the winter time seasonal regime across the shelf. This would also allow more information to be gathered to compare the dominance transition between dinoflagellates and diatoms near bottom between the two regimes, and compare the stratification vs. critical depth hypothesis. More sampling during the summertime regime would also allow more details to be gathered about the species dominance near bottom and how well the near bottom phytoplankton population can be fit into succession models that have already been proposed as well as succession models that still need to be developed to apply to this population in the Gulf of Mexico.

The data collected from the July cruise was able to verify certain aspects of the series of models developed to investigate phytoplankton populations near bottom across the northwest Florida shelf. These models were developed using *Karenia brevis* as the test species for determining rates of motility and nutrient uptake. Our field samples from the July cruise show that there are many more *Prorocentroid* cells compared to *Karenia brevis* cells, though *Gymnodinoid* cells which include *Karenia brevis* were present. Subsequent models would better represent the near bottom dinoflagellate populations if *Prorocentroid* cells were included as an alternate test species for determining motility and nutrient uptake rates in these and future models.

The mechanics of the models could also benefit from a comparison of laboratory vs. field measurements of nutrient uptake ability of near bottom phytoplankton populations. Laboratory experiments were use to determine the rates of nutrient uptake by an individual

dinoflagellate cell in light vs. dark at the sediment interface (Sinclair, 2006). Based on the internal nutrient and carbon pools the rate of nutrient uptake and DVM within the water column was determined in these laboratory studies. A good comparison would be to measure these same rates of individual cells in the field as to laboratory experiments and adjust the model to reflect real time DVM and nutrient uptake rates. These rates may also need to be adjusted to reflect the DVM and nutrient uptake rates of different dinoflagellate species, such as *Prorocentroid* cells instead of just *Karenia brevis* cells, which are also found in near bottom dinoflagellate populations.

More accurate detailed information could be gathered about near bottom dinoflagellate populations if there was a continuous monitoring effort in the field. I would suggest monitoring near bottom population levels with moored or glider-equipped Brevebusters that would take in situ samples to cue in on increases in concentrations of near bottom dinoflagellate populations. Using an instrument such as the Brevebuster to investigate these populations would be beneficial since it has the capability to distinguish between concentrations of a limited number of dinoflagellate species in situ, instead of having to take live or fixed samples back to the lab for analysis. The Brevebuster also has the capability of negating the effects of CDOM in the absorbance measurements used to determine dinoflagellate concentrations, which is a conflicting factor in many other instruments in giving accurate dinoflagellate concentrations. Also, the monitoring of near bottom nutrient sources due to upwelling and sediment flux of nitrogen may help to give

clues on where near bottom populations may begin to accumulate. By trying to identify any near bottom currents in conjunction with the near bottom nutrient sources, we could begin to identify areas on the shelf that would drive the near bottom populations toward concentrating and trapping populations in fronts to bring the population to the surface and transport them to the coastline, as described as “trapping” from J&K model (Janowitz & Kamykowski, 2006).

By using all of this data collected to describe near bottom populations, newer models can be constructed to refine HAB initiation, concentration, and transportation on the northwest Florida shelf in the Gulf of Mexico. If these new models of the near bottom phytoplankton population were added to current HAB models, they may begin to better predict the occurrence of a bloom.

These are a few of the directions that I believe future research in this area should be leading to. There are many more to be explored. Any future and continuing research would continue to shed more light on this system and may lead to future progress in the field of harmful algal blooms.