AN ABSTRACT OF THE THESIS OF

LeAnn Conlon for the degree of Master of Science in Marine and Environmental Science presented on April 19th, 2013

Title: Effects of climate change on coral reef benthic-pelagic coupling in a tropical coastal ecosystem: A theoretical study

Abstract approved:

Nasseer Idrisi/Tyler B. Smith

Coral reefs are important ecosystems with a rich biodiversity. However, these ecosystems have become vulnerable to accelerated climate change and are deteriorating worldwide due to environmental stress. Zooplankton play an important role in heterotrophic feeding for some species of coral and may help offset the effects of stressors on corals such as increased ocean heating. The zooplankton associated with the deep chlorophyll maximum zone (DCMZ), may provide a concentrated source of heterotrophic nutrition for mesophotic corals south of St. Thomas, USVI. We studied the dynamics of plankton south of St. Thomas at Hind Bank using the Regional Ocean Modeling System (ROMS) as well as characterizing the shelf edge ocean structure. Changes in heat flux due to global climate change may alter the depth of the DCMZ and impact the important planktonic food source for corals. It was hypothesized that changes in heat flux due to global climate change will reduce plankton concentrations at Hind Bank, USVI. These predictions were tested empirically by ACP and CTD data and with simulations through the use of an ocean model. Passive tracers representing plankton were released in ROMS and dispersal was simulated under historic climatological conditions and increased heat flux conditions. Vertical chlorophyll and density profiles showed a well-defined DCMZ and upper mixed layer in the warm months, which began to deteriorate as the cool season approached. There was diel vertical migration occurring year round, with a larger ACP backscatter signal in the warmer months when compared with cooler months. This indicates greater abundances of zooplankton present on the shelf edge in the warmer months, possibly due to the DCMZ being located below the shelf edge in the winter. Simulations showed a decrease in depth of the upper mixed layer in the increased heat flux model of 15.4 meters. While particles were present at the reef in both control and increased heat flux scenarios, the reef in the increased heat flux scenario experienced an overall decrease in particle concentration of approximately 22.2%.

Effects of climate change on coral reef benthic-pelagic coupling in a tropical coastal ecosystem: A theoretical study

by

LeAnn Conlon

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I understand that my thesis will become part of the permanent collection of the University of the Virgin Islands Library. My signature below authorizes release of my thesis to any reader upon request.

LeAnn Conlon

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Table of Contents

List of Figures

Introduction

Coral reefs are important coastal ecosystems within the tropical regions of the world and maintain a rich biodiversity rivaling tropical rainforests (Bellwood et al. 2004, Bellwood et al. 2005). The myriad of species from which humans have been able to use as a food resources and marine natural products for medicines and other industrial uses are testaments to the importance of coral reefs (Moberg and Folke 1999). However, the most important aspect of the biodiversity associated with coral reef ecosystems is the stability these systems bring to adjoining ecosystems through benthic-pelagic coupling and the integration of land-sea ecosystems. In spite of the wide recognition of the importance of coral reefs, along with other key ecosystems, these ecosystems have become vulnerable to accelerated climate change and are deteriorating worldwide. There have been quite a few studies covering various topics, such as increasing diseases in corals (Hoegh-Guldberg 1999), ocean acidification (Orr et al. 2005), and thermal stress (Hughes et al. 2003). Other studies have shown that mesophotic reefs may be an important source of new coral to shallower reef corals that are exposed to greater environmental stressors than their deeper counterparts (Lesser et al. 2009, Kahng et al. 2010). However, very little research has been done on the potential impact of climate change on mesophotic reefs (Bongaerts et al. 2010).

The deep chlorophyll maximum zone (DCMZ) occurs at the depth of the pycnocline, between the upper mixed layer (UML) and the layer beneath that is typically rich in nutrients. The irradiance level and nutrient concentration at the interface between the two density layers may stimulate bloom conditions that manifests into the DCMZ. Nutrient input is the limiting factor in formation of the DCMZ in tropical latitudes (Cullen 1982).

The location of the DCMZ may be of importance to mesophotic coral reefs, affecting the availability of heterotrophic food sources. Zooplankton play an important role in heterotrophic feeding by some species of coral (Porter 1974, Sebens et al. 1996). Depending on the depth of the DCMZ, the zooplankton feeding in the DCMZ may be available as a concentrated source of nutrition for coral, as numerous studies have shown high zooplankton densities in areas of high primary production (Fiedler 1982, Herman 1983). There have been numerous studies that have confirmed the ability of zooxanthellate corals to feed heterotrophically when light is a limiting factor (Wellington 1982, Sebens et al. 1996, and Holbreque et al. 2004a.). Some species of coral can switch between heterotrophy and autotrophy depending on light availability, with deeper corals relying more heavily on heterotrophy (Anthony and Fabricius 2000).

In addition to helping to meet the metabolic needs of the coral, heterotrophic feeding can offset the effects of bleaching (Grottoli et al. 2006) and has been shown to have a positive effect on growth rates of the common scleractinian coral *Madracis mirabilis* (Leichter and Genovese 2006). Therefore, changes in the location of the DCMZ may impact heterotrophic feeding opportunities and growth of corals.

Climate change may have important environmental and economic impacts. In the tropics, seasonal changes tend to be relatively small compared with temperate latitudes, so any shift from normal parameters may cause relatively large ecosystem changes. For example, climate change in the tropics increases tropical cyclone formation and intensity (Knutson et al. 1998, Mann and Emanuel 2006). Increased cyclone formation and intensity may result may result in coral damage (Lirman and Fong 1997), resuspension of sediments (Dickey et al. 1998), and economic consequences (Costanza and Farley 2007).

Climate change has the potential to change the location of the DCMZ and impact the availability of zooplankton for heterotrophic feeding by coral. Decreased vertical mixing due to climate change has the potential to cause chaos in phytoplankton biomass (Huisman et al. 2006), potentially affecting DCMZ location and formation. Additionally, the vertical position of the DCMZ is directly correlated with the thickness of the UML and pycnocline location (Hobson and Lorenzen 1972), which in turn is determined by the net heat flux at the ocean-atmosphere interface and amount of mixing due to wind (Mellor and Durbin 1975, Marchuk et al. 1977). Globally, the depth of the DCMZ changes seasonally as the pycnocline depth changes, becoming shallower in the summer due to surface heating and deeper in the winter due to surface cooling (Hobson and Lorenzen 1972). Therefore, it is probable that increased heat flux due to climate change will also cause the pycnocline and DCMZ to become shallower, though this has not been studied extensively in the tropics. A rise in ocean temperatures may cause more stable density stratification that results in a decrease in penetration of wind driven mixing (Mellor and Durbin 1975, Marchuk et al. 1977). This increased stratification would result in less mixing and a thinner UML (Mellor and Durbin 1975, Marchuk et al. 1977, Balaguru et al. 2012). Therefore, warmer ocean temperatures may result in the shoaling of the DCMZ and could affect the availability of zooplankton for heterotrophic feeding by coral. These changes in heat flux may positively or negatively affect zooplankton delivery to coral depending on plankton location.

A mesophotic reef containing the *Montastraea annularis* species complex (MACX), an important group of reef building coral in the U.S. Virgin Islands, is found south of St. Thomas, U.S. Virgin Islands. This reef is located near the shelf edge at a depth of approximately 40 meters. This area is the location of the Hind Bank Marine Conservation District, a regionally important area that is approximately two thirds coral reef (Smith et al. 2010). This area has high coral cover compared with nearshore reefs, indicating that this area may be better protected from stressors that affect other reefs (Smith et al. 2008, Smith et al. 2010).

It is possible that decreased light levels at mesophotic depths may lead to an increased dependence on heterotrophic feeding by MACX at Hind Bank. There is a decrease in autotrophy in *M. Cavernosa* with increases in depth; there is a strong shift towards heterotrophy between 45 and 61 meters (Lesser at al. 2010). It is also possible that lettuce coral reefs (*Agaricia spp*.) present at the shelf edge at depths of 60 to 80 meters (Smith et al. 2012) would benefit from increased levels of plankton as well. Therefore, the elevated levels of zooplankton found within the DCMZ may provide an important source of nutrients for corals feeding in this area. The DCMZ at Hind Bank is typically located at the depth of the reef in the summer, around 40 meters in depth. It is deeper in the winter, around 110 meters in depth. While the DCMZ is typically deeper than the majority of the mesophotic reef in the winter, it is possible that upwelling or other mechanisms of transport onto the shelf would make the zooplankton associated with the DCMZ available to corals.

This project assesses the impacts of changes in heat flux on the vertical locations of the DCMZ at Hind Bank. It is important to understand that climate change has the ability to affect the depth of the UML due to changes in heat flux at the ocean-atmosphere interface. Changes in the location of the DCMZ may affect the availability of zooplankton for heterotrophic feeding by mesophotic coral reefs. This may have negative consequences for these reefs if they rely more heavily on heterotrophic feeding due to reduced light levels at depth. Additionally, strength of the DCMZ and therefore concentrations of zooplankton depends heavily on light and nutrient concentrations. Currently there is a lack of understanding of the impacts climate change has on the vertical position of the DCMZ in the tropics.

It is hypothesized that an increase in heat flux will cause a reduction in the concentrations of plankton available to the mesophotic reef at Hind Bank, USVI due to a decrease in depth of the DCMZ. This hypothesis was tested using field data and modeling. Field data was collected using a Nortek Aquadopp current profiler (ACP) and CTD casts to determine acoustic backscatter from zooplankton and the depth of the DCMZ, respectively. These data were used to determine the depth of the UML and DCMZ as well as relative changes in plankton concentrations throughout the year. Modeling was done using the Regional Oceanic Modeling System (ROMS) for control and increased heat flux to the ocean surface scenarios to determine the effects of increased heat flux on possible plankton location and UML depth.

Methods

Site Description

Hind Bank is located approximately 12 kilometers south of St. Thomas, USVI (18.20234 N, 65.00171 W) (Fig. 1). Hind Bank is the location of a mesophotic coral reef at approximately 40 meters depth, located within one kilometer of the shelf edge. In the warm season (May through November), the DCMZ is located at the shelf edge; in the cool season (December through April) it is below the shelf edge (Smith et al 2010).

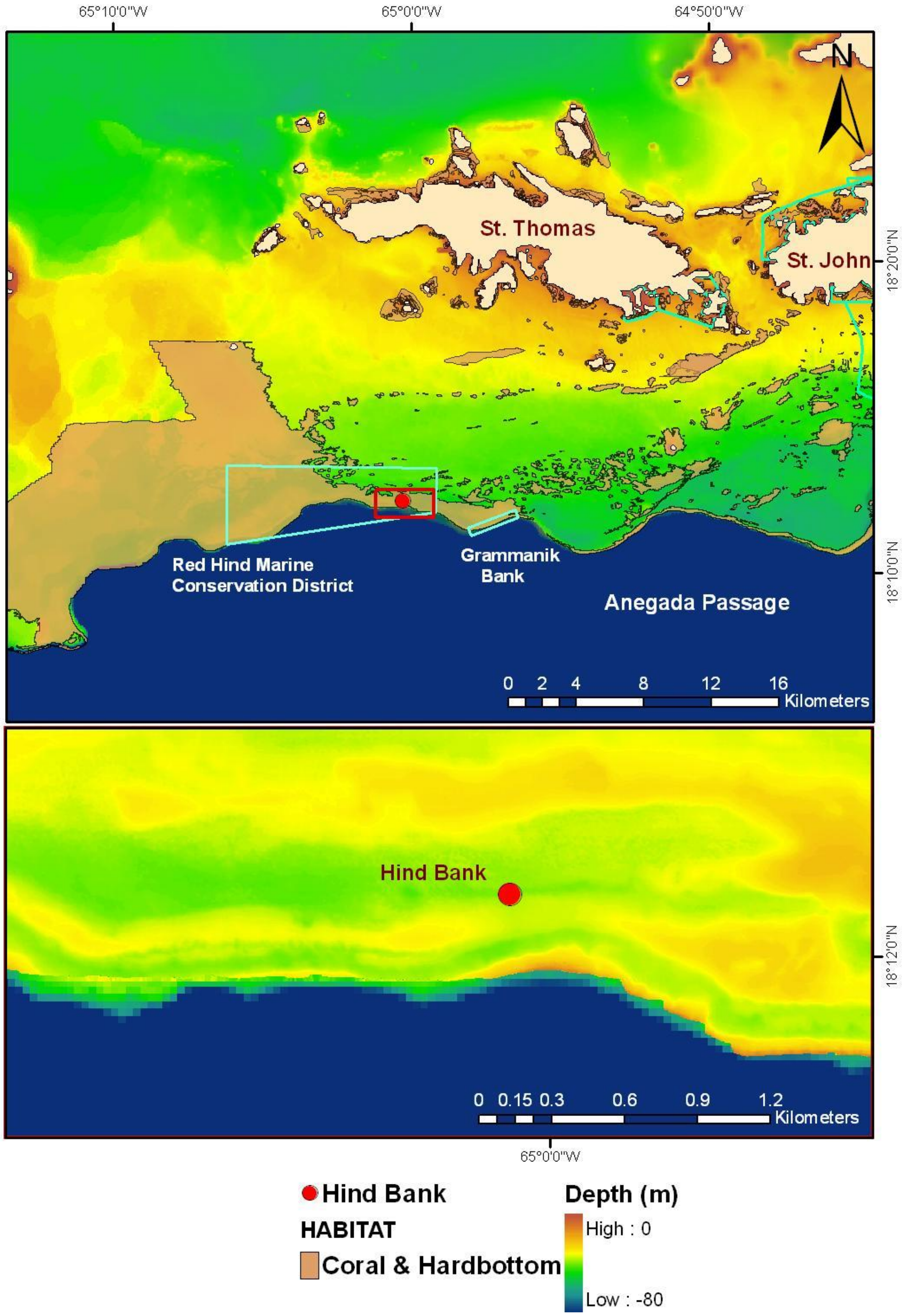

Figure 1. Site map showing the shelf edge south of St. Thomas, USVI. Red circle shows ACP location. Close-up shows Hind Bank bathymetry and ACP location relative to the shelf edge.

Field Data Collection

The field data collection regime for this study consisted of three sampling days and took place from aboard a UVI research vessel, the R/V Garuppa, during September, October, and November 2012 near Hind Bank, USVI. Each sampling day consisted of two sampling periods, one during the day and one at night. During each sampling period, real-time casts using a CTD sensor were done to determine the depth of the DCMZ and UML using the fluorometer output (Sea Bird Electronics 25 CTD 2543993-0407, SBE 3F Temperature 034654, SBE 4C Conductivity 043237, SBE 18-I pH Sensor 180580, SBE 29 Pressure Sensor 290554, SBE 43 Dissolved Oxygen Sensor 431106, WETLabs Fluorometer FLNTURT-618, Li-Cor PAR Sensor SPQA 3806). Depth of the UML was defined to be the depth of the start of the thermocline. The DCMZ was defined followed the procedure outline in Cullen et al. (1981), briefly, chlorophyll fluorescence was averaged over the entire depth of the CTD cast, and areas of the cast above mean chlorophyll fluorescence were considered the DCMZ. (Cullen 1981). Additionally, wind speed data was taken from the CariCOOS data buoy located south of St. John, USVI (18.2488 N, 64.7626W) (http://gyre.umeoce.maine.edu/data/gomoos/buoy/html/VI1.html).

Aquadopp Current Profiler (ACP) Backscatter Data

An upward-looking 600 kHz Aquadopp Current Profiler (ACP) was used for this project and was deployed at Hind Bank for the three month duration of the study. It was programmed to collect data for one minute every five minutes in order to provide high resolution data. The ACP instrument primarily attenuates backscatter from particles similar in size to zooplankton (Flagg and Smith 1989, Heywood et al. 1990); a 600kHz ACP can provide fine enough resolution to detect particles as small as 0.1mm in diameter (Holliday and Pieper 1980). As a result, changes in ACP backscatter can indicate relative changes in concentration of zooplankton in the water column based on changes in backscatter signal strength and assuming the backscatter signals originate from zooplankton. The instrument divided the water column into 40 vertical bins, each one meter in thickness. Historical ACP data from 2007 to 2012 at Hind Bank were also used. All ACP data were then processed and analyzed using Nortek Storm software. For these data, daytime backscatter was taken at 12:00 PM while nighttime backscatter was taken at 12:00 AM.

Regional Oceanic Modeling System

ROMS is a terrain following primitive equations ocean model and was used to simulate the movement of plankton at Hind Bank. A control simulation of the Virgin Islands basin (17° to 19° N, 63° to 66° W) was configured and run for a calendar year. These simulations incorporated tides, 32 vertical levels and had a horizontal resolution of 1.93 km^2 for each gridpoint. To simulate movement of plankton, neutrally buoyant passive tracers were added below the UML at depths between 80 and 110 meters to show the movement and location of the particles throughout the year. This will show an approximation of plankton location, though it is important to remember that these simulations do not take into account behaviors such as diel vertical migration. Tracers were defined to continuously replenish themselves in this location to avoid dissipation of particles. To show how changes in heat flux affect the DCMZ location, an additional simulation was used. This simulation used the same parameters as the control simulation but with a 10% increase in heat flux impinging on the ocean surface, which corresponds roughly with year 2040 of the IPCC global warming scenarios (IPCC 2007).

Analysis of particle concentration from the ROMS simulations at Hind Bank was done at the coordinates of the ACP (18.20234 N, 65.00171 W). Particle concentrations were analyzed at the ROMS vertical level in contact with the benthos in order to simulate concentrations of zooplankton that may be available to corals at those coordinates.

Statistical Analyses

A linear regression was used to test the relationship between wind speed and UML depth. ACP backscatter at two meters above the instrument by month and upwelling by month were analyzed using a one way analysis of variance (ANOVA) to determine changes in backscatter throughout the year. Backscatter at the shelf edge between seasons and between models was analyzed between day and night using Student's t-tests. Tukey HSD tests were done on the ACP backscatter data and the ROMS particle concentration data by month following the ANOVAs to determine which months were significantly different. A Kruskal-Wallis test was used on UML depth data from CTD casts by month to determine if there was a significant difference in depth among months.

Results

Physical data at shelf edge

There was a well-defined pycnocline and DCMZ during the warm months, but this deteriorated as the transition to the cool season began (see below). Wind speed for 2012 was generally between 1 and 14 m/s (Fig 2).

September

Wind speeds were between 4 and 6 m/s for the September 10th and 11th sampling day (Fig. 3). CTD casts were similar for both day and night. The depth of the UML was around 60 meters, with the DCMZ around 50 meters (Fig. 4). Salinity and density followed each other closely with an abrupt increase around 20 meters.

October

There were relatively low wind speeds a few days before the October sampling day, with wind speeds around 1 m/s the morning of October 18th (Fig 5). The thermocline and DCMZ were located at approximately 35 to 40 meters during the day of October 18th (Fig. 6). There were sharp increases in salinity and density at that depth as well.

The DCMZ moved slightly deeper, approximately 40 to 50 meters that evening (Fig. 7). The thermocline was shallower than it was that morning, around 25 meters. There were increases in salinity and density around 25 to 30 meters as well. In both casts on the 18th there appears to be a layer of lower salinity in the upper five meters of the water column, possibly indicating a freshwater or brackish water lens.

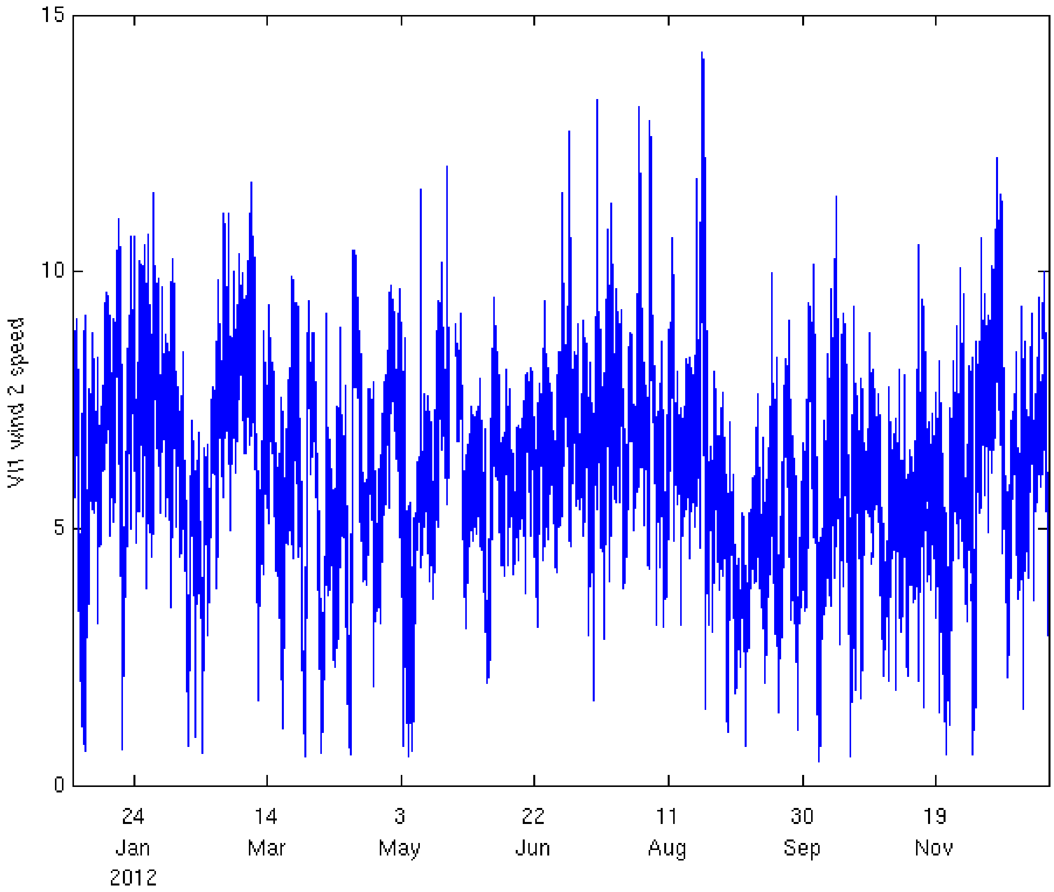

Figure 2. Wind speed for 2012 (m/s). Data was taken from the CariCOOS data buoy located south of St. John, USVI, and calculated as hourly averages.

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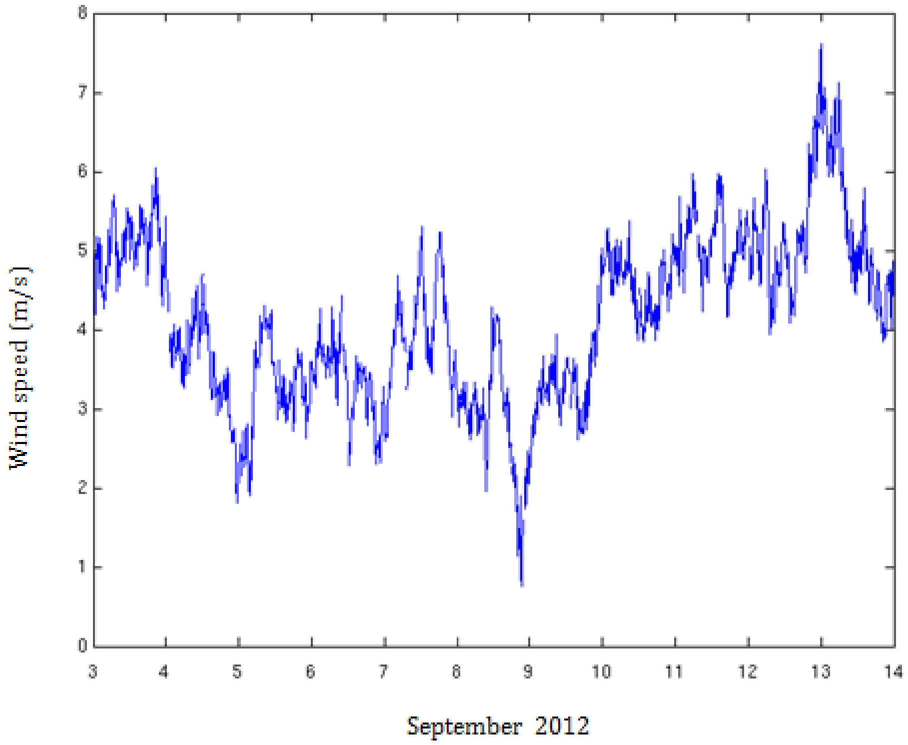


Figure 3. Wind speeds (m/s) for September 3rd through 13th, 2012. Data was taken from the CariCOOS data buoy located south of St. John, USVI, and calculated as hourly averages.

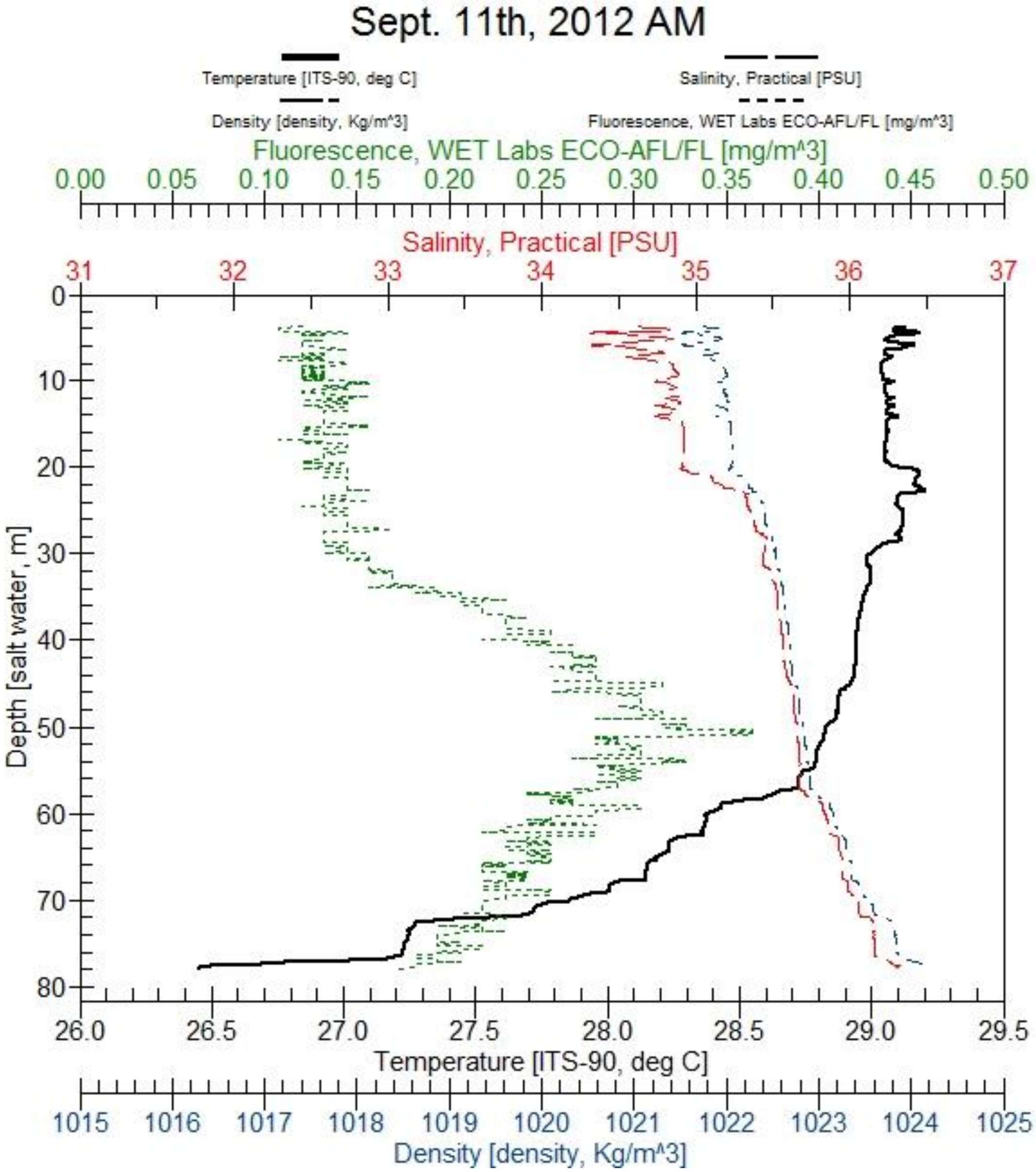


Figure 4. CTD cast from the morning of September 11th, 2012. Figure shows changes in temperature, density, chlorophyll fluorescence, and salinity by depth.

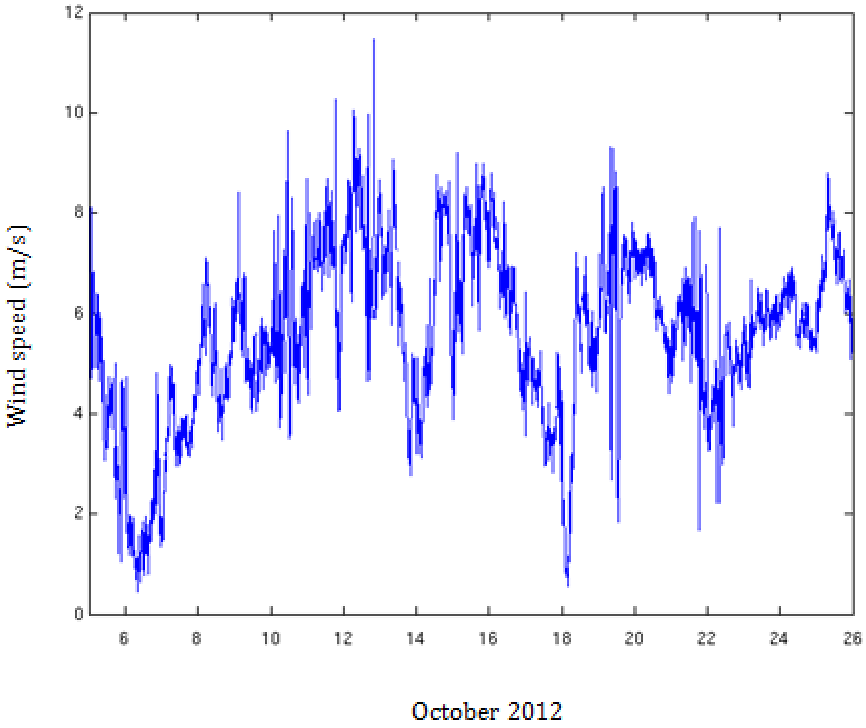


Figure 5. Wind speeds (m/s) for October 6th through 25th, 2012. Data was taken from the CariCOOS data buoy located south of St. John, USVI, and calculated as hourly averages.

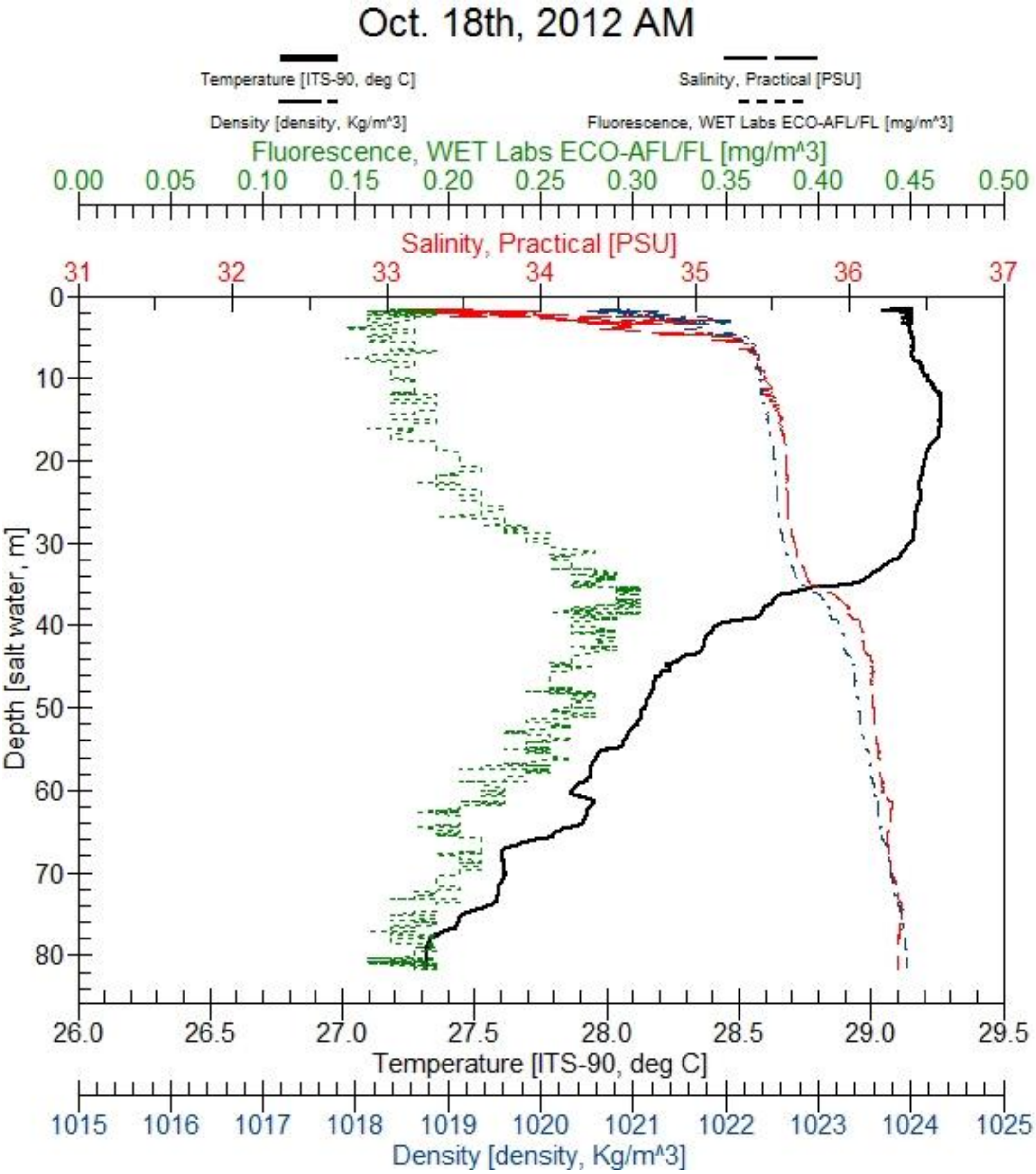


Figure 6. CTD cast from the morning of October 18th, 2012. Figure shows changes in temperature, density, chlorophyll fluorescence, and salinity by depth.

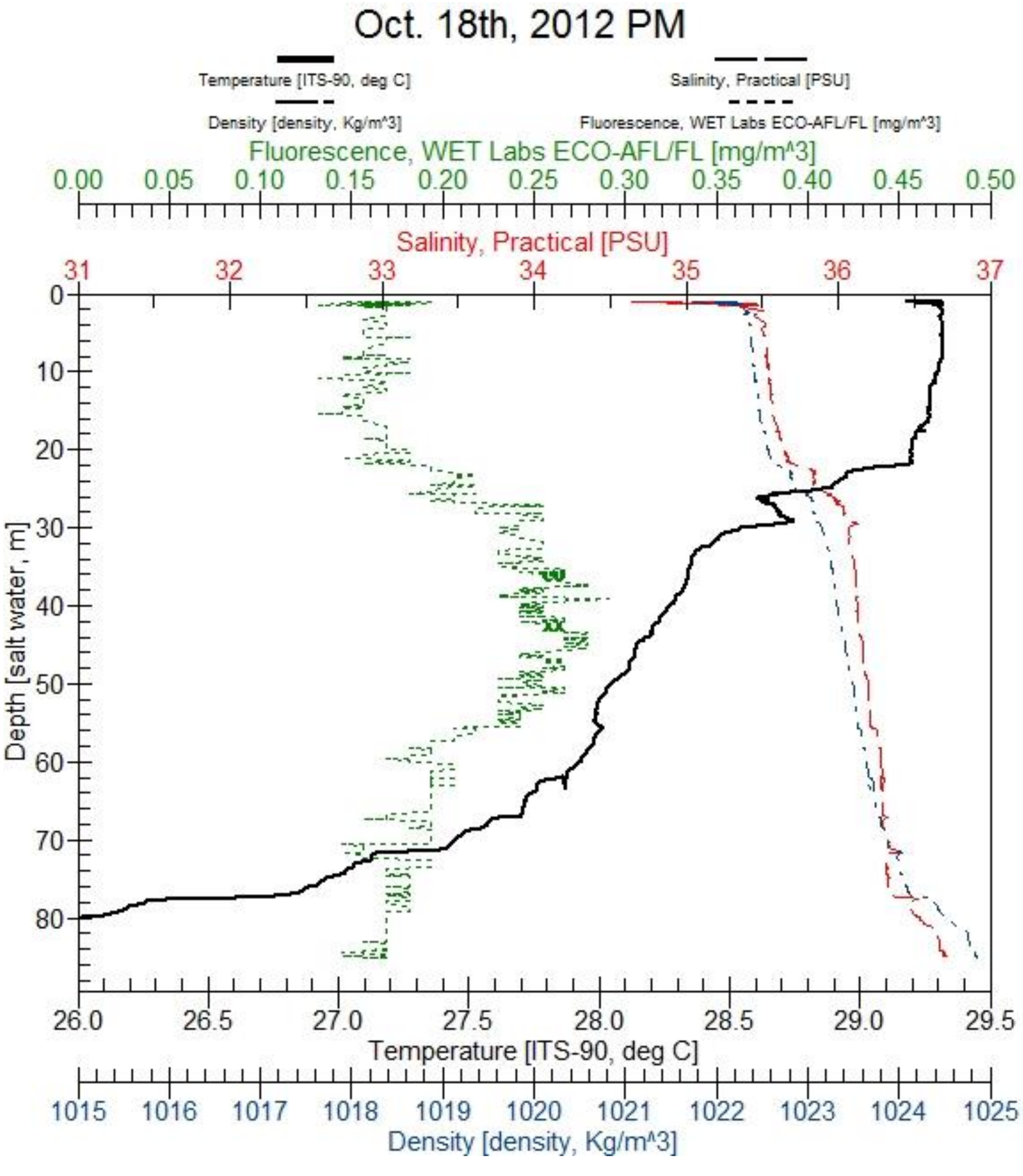


Figure 7. CTD cast from the evening of October 18th, 2012. Figure shows changes in temperature, density, chlorophyll fluorescence, and salinity by depth.

November

Wind speeds for the sample day in November were between 2 and 8 m/s (Fig. 8). The stratification in the November CTD casts was less well defined (Fig. 9). During the evening of November 20th, there appears to be a thermocline and DCMZ at around 80 meters. Density and salinity were not as well defined, with several small increases in the profile. The next morning, there was a possible DCMZ around 85 meters, though it may have been deeper (Fig. 10). The thermocline appeared to be around 40 meters. There was a layer of low salinity in the upper five meters of the water column. There were breaks in density and salinity around 20 meters.

Average depth of the UML during the sample period (September through November) was 45.0 meters ± 3.9 SEM for all 6 CTD casts. The depth of the UML was relatively constant from night to day; it varied highly from month to month.

There was a significant, positive, linear relationship between wind speed 24 hours before the sampling period and UML depth ($R^2=0.76$, $p=0.022$) (Fig. 11).

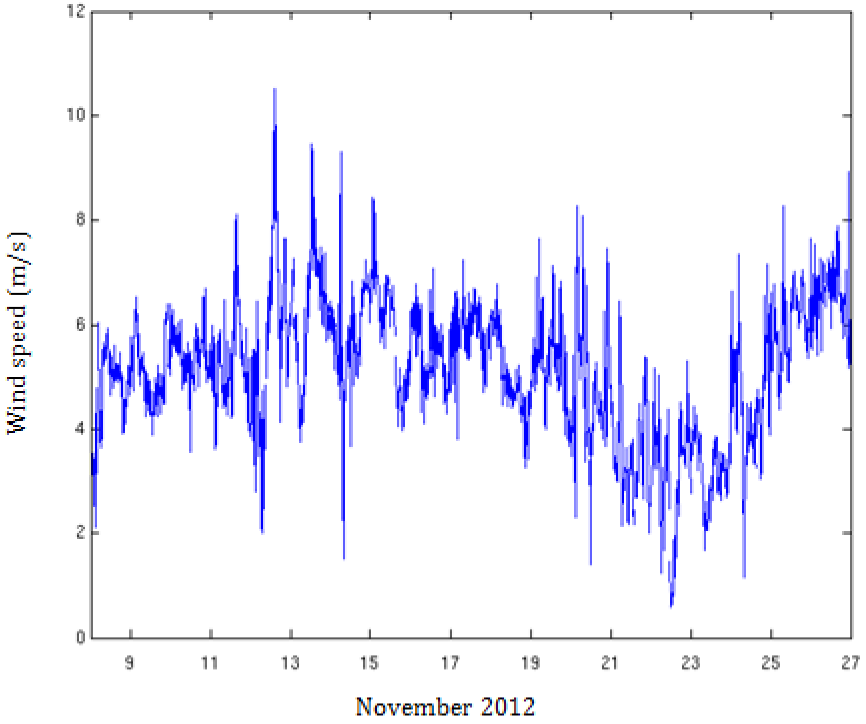


Figure 8. Wind speeds (m/s) for November 9th through 26th, 2012. Data was taken from the CariCOOS data buoy located south of St. John, USVI, and calculated as hourly averages.

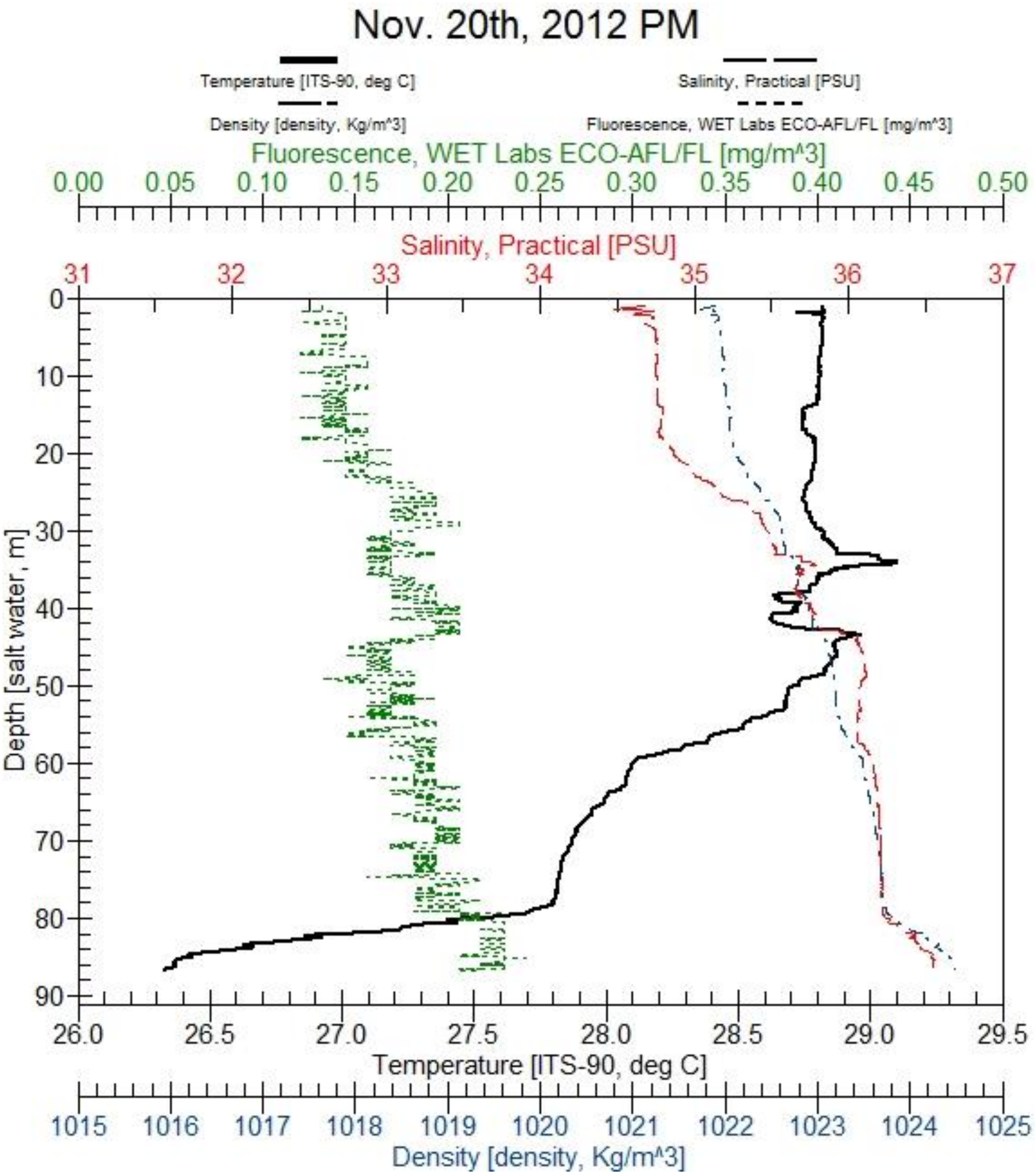


Figure 9. CTD cast from the evening of November 20th, 2012. Figure shows changes in temperature, density, chlorophyll fluorescence, and salinity by depth. Strong stratifications present in earlier casts are beginning to break down.

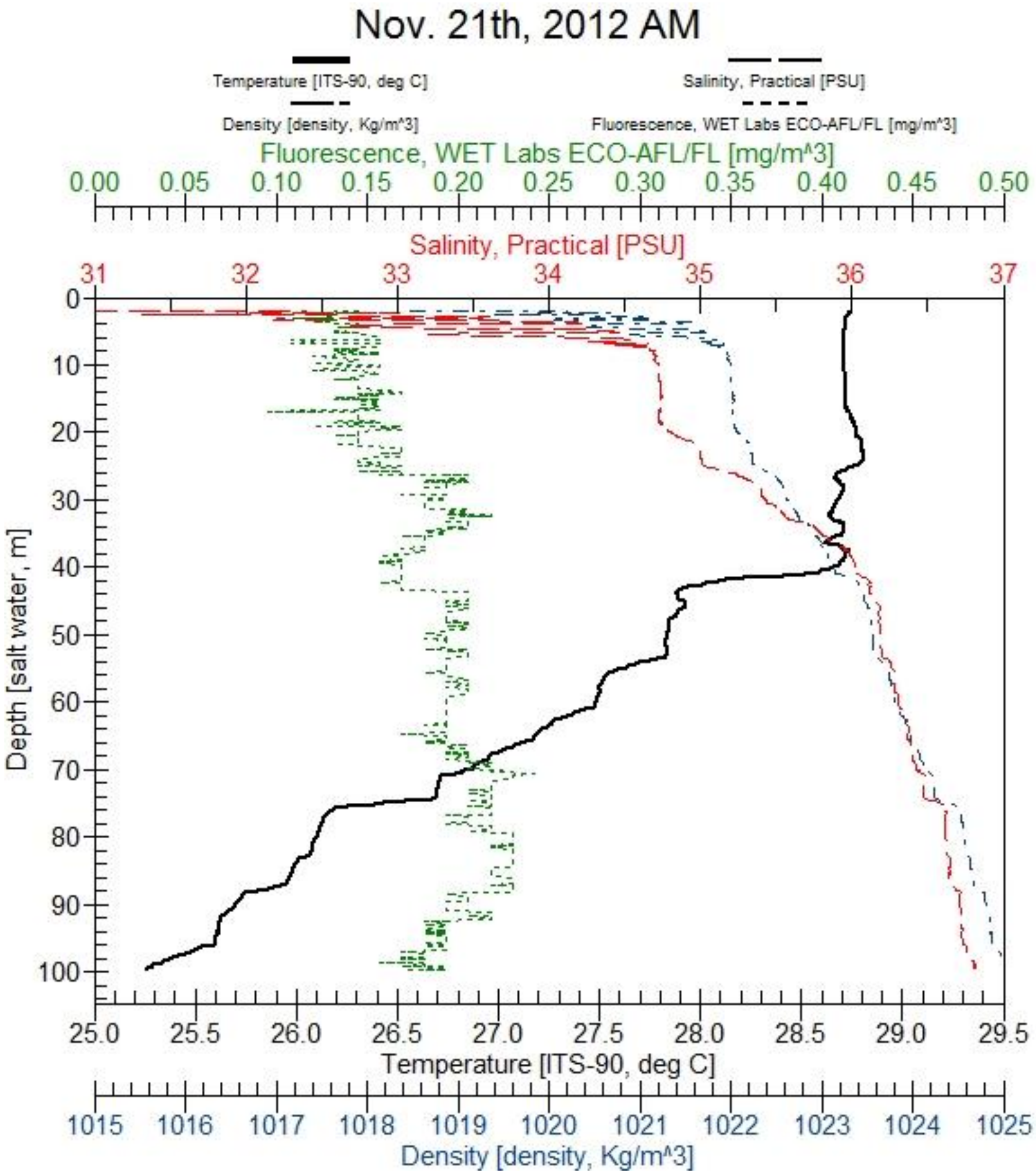


Figure 10. CTD cast from the morning of November 21th, 2012. Figure shows changes in temperature, density, chlorophyll fluorescence, and salinity by depth. Strong stratifications present in earlier casts began to break down.

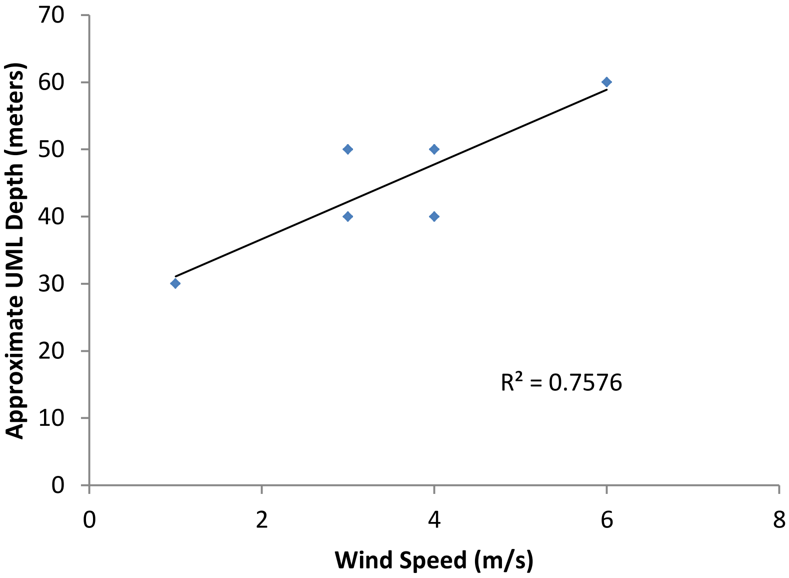


Figure 11. Approximate UML depth (meters) versus wind speed (m/s) for the September through November sampling period. There was a positive, linear, significant relationship between the two variables (R^2=0.76, p=0.022).

ACP Data

ACP data two meters above the instrument showed increases in backscatter occurring from between around midnight to a few hours after dawn, indicative of diel vertical migration (Fig. 12 and 13). Tidal data from the ACP pressure sensor were asynchronous with backscatter peaks, indicating that the backscatter is likely not due to bottom sediment being resuspended by tidal flow.

Historical ACP data from the benthos (two meters above the ACP) at Hind Bank show an increase in backscatter intensity during the night in the warm season (May through November) (Fig. 14). A one way ANOVA showed significant differences in nighttime backscatter intensity by month two meters above the ACP ($p<0.0001$, $n=5$) (Fig. 15). A Tukey HSD test revealed differences among months. There was no difference in cool season months, with January, February, March, April, November, and December being grouped together. The greatest amount of backscatter occurred in July and August.

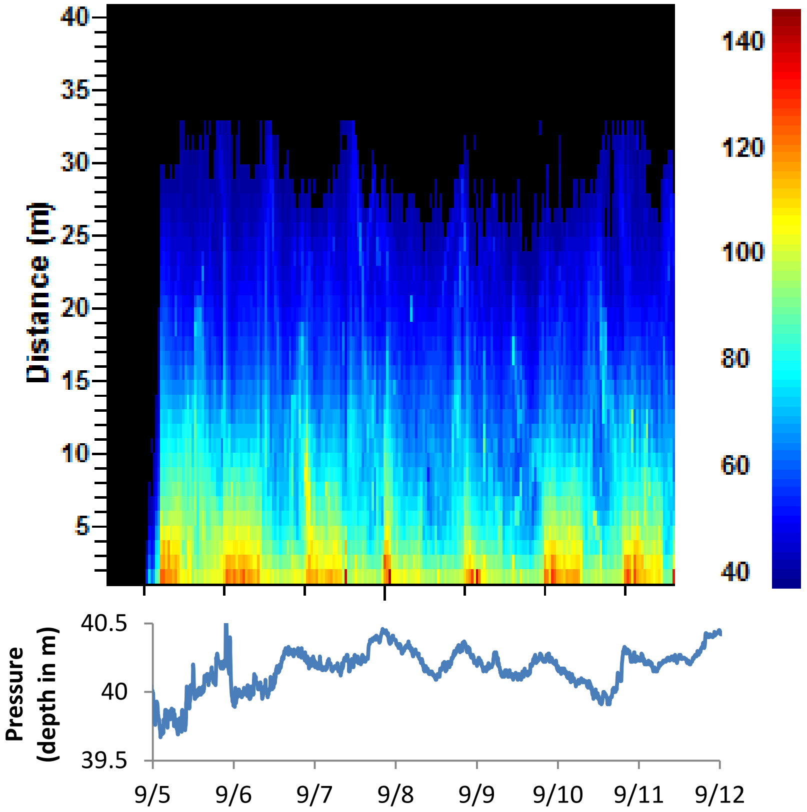


Figure 12. Example of high resolution ACP backscatter data at Hind Bank during the warm season with pressure sensor data to show tides. Data was processed by Nortek Storm software. Figure shows average signal strength (counts) by distance from ocean floor (meters) from September 5th through 11th, 2012. Peaks in backscatter data signify an increase in particles in the water column and are indicative of diel vertical migration.

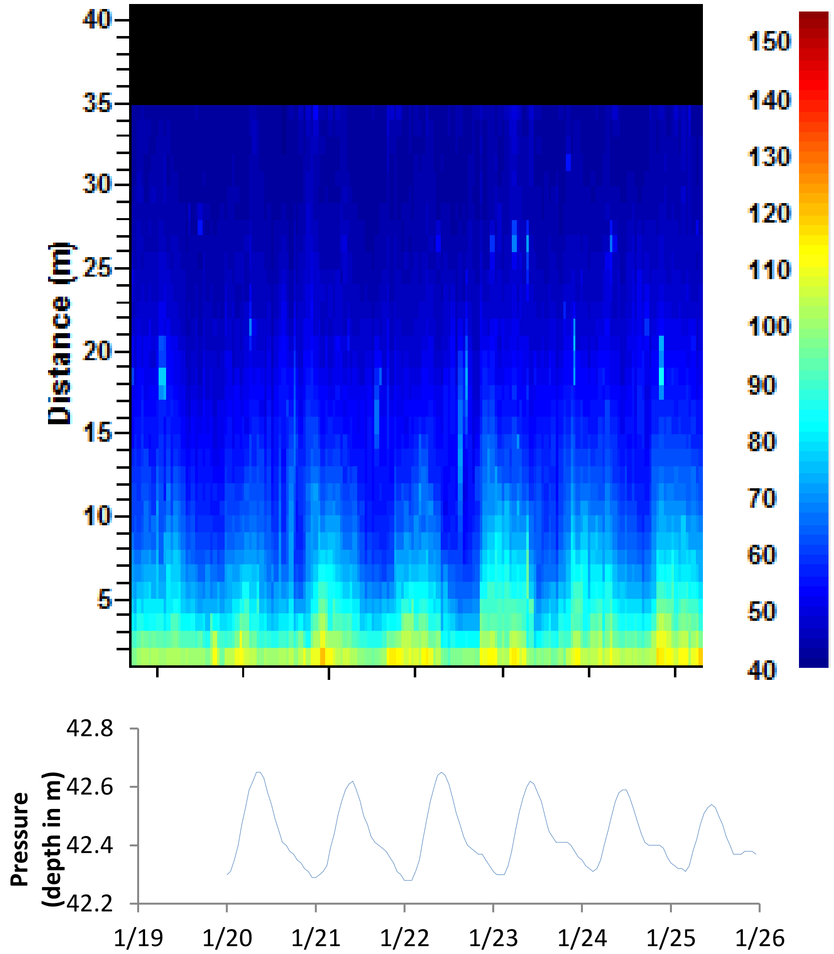


Figure 13. Example of ACP backscatter data at Hind Bank during the cool season with pressure sensor data to show tides. Data was processed by Nortek Storm software. Figure shows average signal strength (counts) by distance from ocean floor (meters) during January 20th through 26th, 2012.

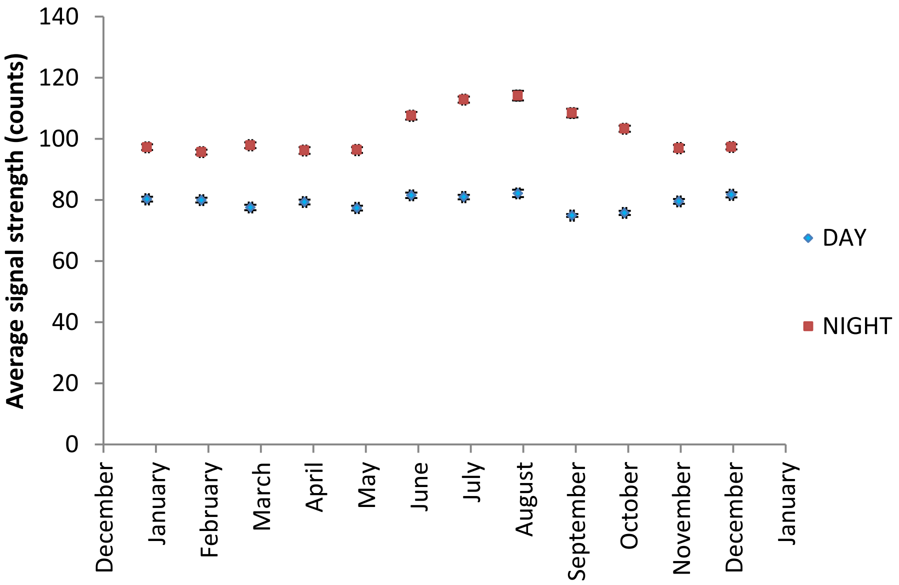


Figure 14. Average monthly ACP backscatter (average signal strength in counts) ± SEM from years 2007 to 2012. Backscatter data is from two meters above ACP and is broken into daily and nightly backscatter.

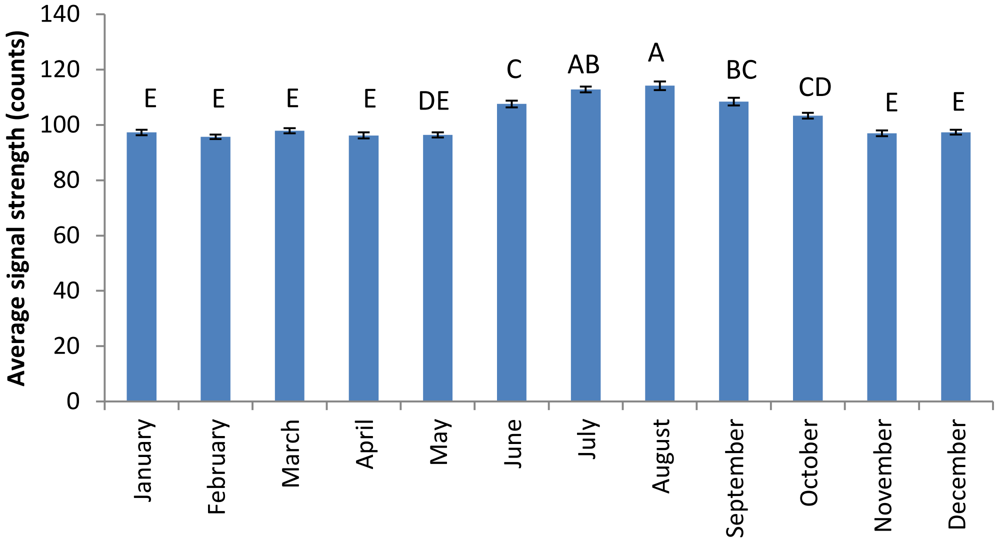


Figure 15. Average nighttime monthly ACP backscatter (average signal strength in counts) ± SEM from years 2007 to 2012 showing significant differences among months. Backscatter data is from two meters above ACP. A one way ANOVA found a significant difference in backscatter between months ($p<0.0001$, $n=5$). A Tukey HSD test revealed that overall, warm season months were significantly different from cool season months. Letters show differences between months as determined by the Tukey HSD test.

ROMS

The greatest overall seasonal change in sea surface temperature from the control simulation to the increased heat flux simulation occurred during the warm season (May through November); cooler months (December through April) did not experience as great of a change. The increase in temperatures in sea surface temperature for the increased heat flux model was approximately 1° C above than the control model simulation.

Depth of the bottom of the UML in the control simulation for the sampling dates (September through November) deepened gradually. Depth of the UML was approximately 45 meters during the September sampling day, and gradually moved deeper to approximately 70 meters during the November sampling day. Difference in depth of the UML on the first of every month over a year was on average 15.4 meters ± 4.6 SEM shallower in the increased heat flux simulation compared to the control model simulation.

Tracer particles that were released beneath the thermocline at approximately 100 meters were present on the shelf edge in both control and increased heat flux scenarios. Average concentration of particles at the ACP location ranged from 0.22 ± 0.01 SEM in February to 0.12 ± 0.004 SEM in July for the control simulation and 0.17 ± 0.05 SEM in February to 0.09 ± 0.04 SEM in December for the increased heat flux simulation. The highest monthly average in particle concentration occurred in September of the control simulation with 0.23

± 0.01 (Fig. 16). Concentrations of particles present at Hind Bank at any given day varied for both simulation (Fig. 17).

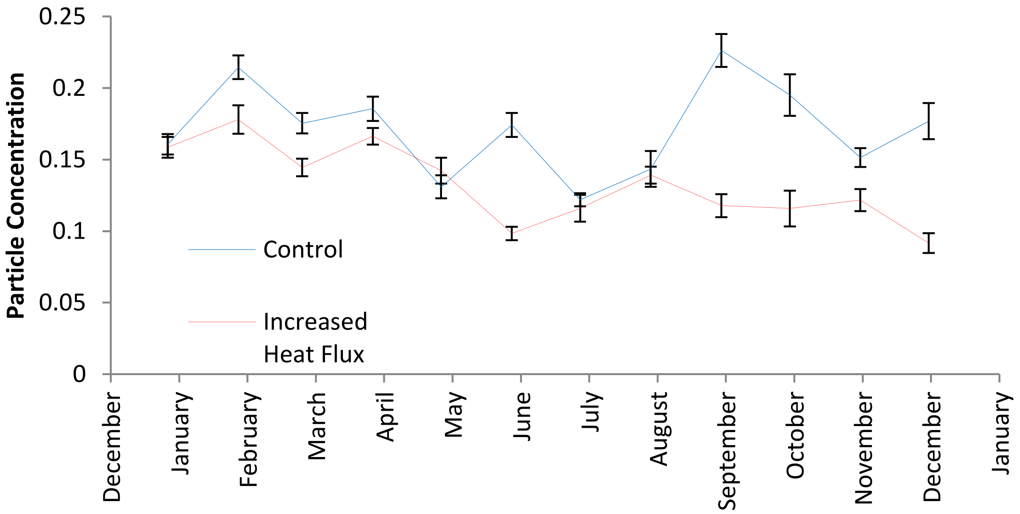


Figure 16. Average concentration of particles at the shelf edge by month for control and increased heat flux scenarios. Particle concentration is unitless and represents proportion of particles released.

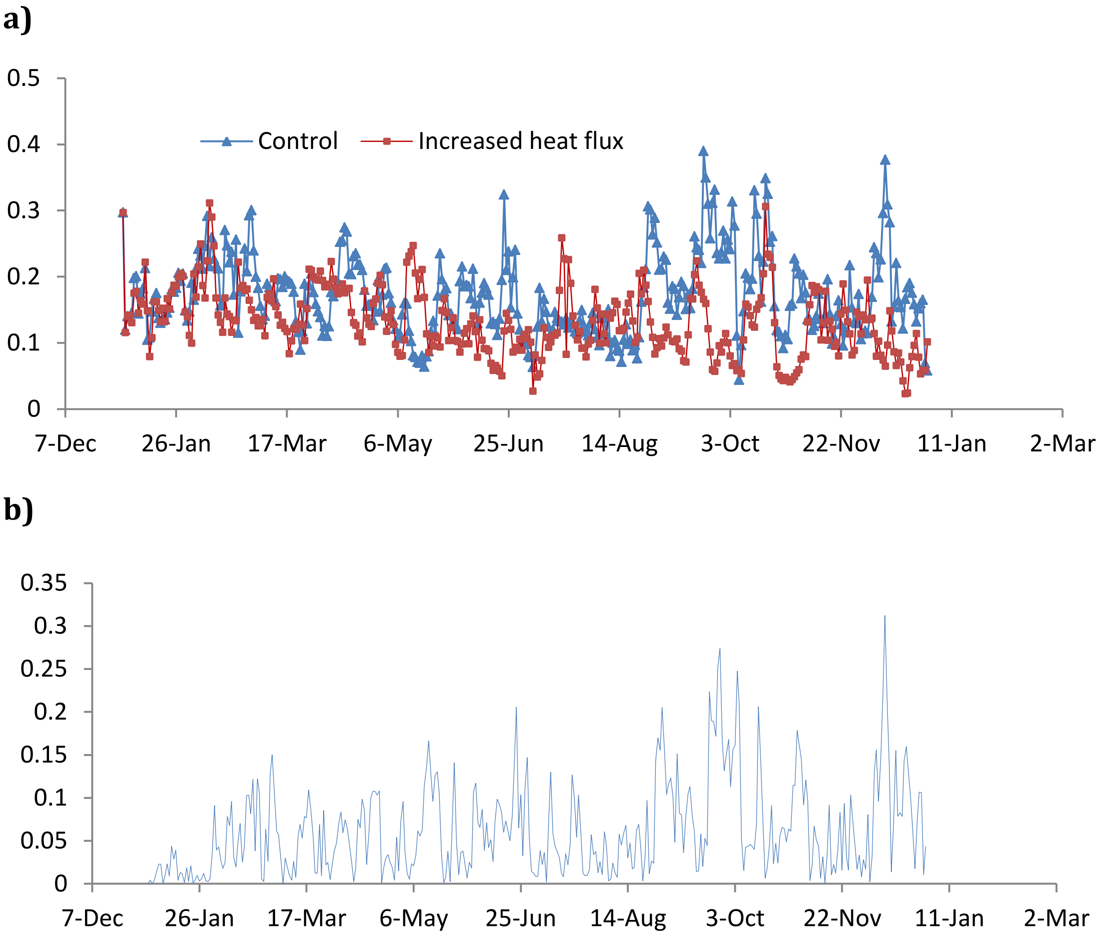


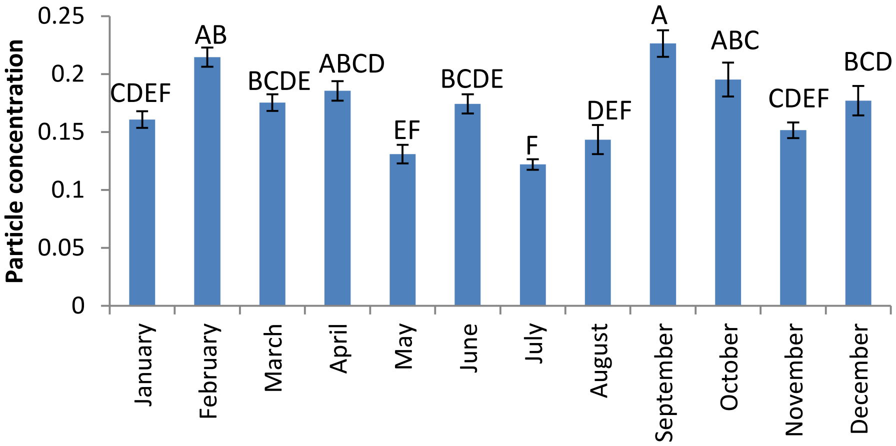
Figure 17. Daily particle concentrations at Hind Bank for (a) control and increased heat flux models and (b) absolute value of the difference between control and increased heat flux models. Particle concentration is a proportion of the total particle concentration at release and is unitless.

There was a significant difference in particle concentration between months for both the control scenario ($p<0.0001$) and increased heat flux scenario ($p<0.0001$) (Fig. 18).

There was no clear pattern when broken down by month, however when the simulated particle output are broken down by season, the cool season (December through April) had significantly higher particle concentrations for both the control model ($p=0.0245$) and the increased heat flux model ($p<0.0001$) (Fig. 19).

Overall, the average of the increased heat flux simulation over one year had significantly fewer particles than the average of the control simulation ($p<0.001$). The control simulation had an average concentration of 0.171 ± 0.003 SEM while the increased heat flux simulation had an average concentration of 0.133 ± 0.003 SEM, a decrease of 22.2%.

a)



b)

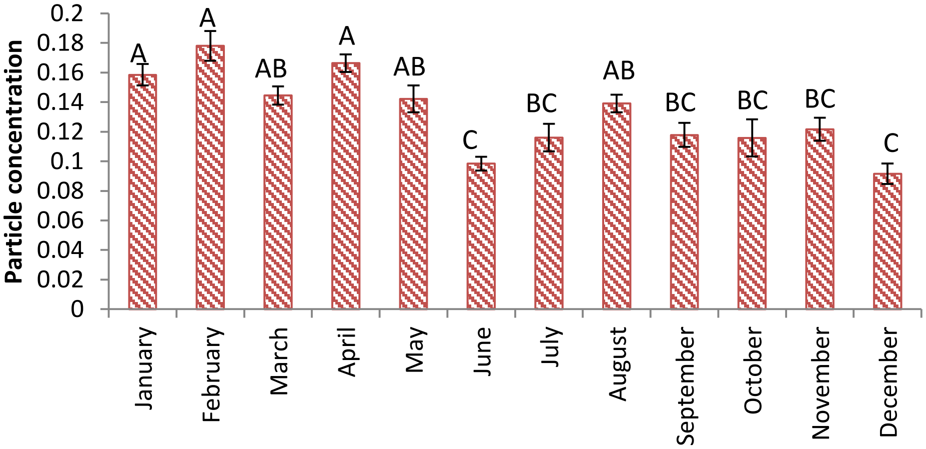


Figure 18. Average particle concentration at the ACP coordinates at Hind Bank for the control model (a) and the increased heat flux model ± SEM (b) showing significant differences among months. Particle concentration is a proportion of the total particle concentration at release and is unitless. An ANOVA showed a significant difference between months for both the control model and increased heat flux model ($p<0.0001$). Letters show differences between months as determined by a Tukey HSD test.

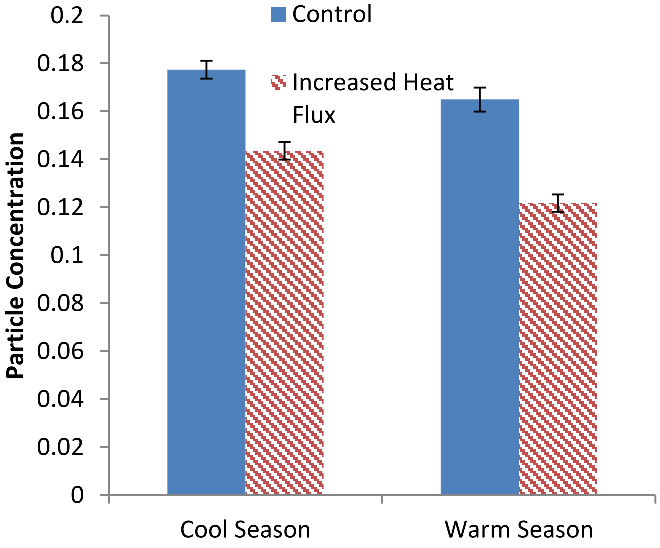


Figure 19. Average particle concentration at Hind Bank broken into warm (May through November) and cool seasons (December through April) for the control model and the increased heat flux model ± SEM. Particle concentration is a proportion of the total particle concentration at release and is unitless. Particle concentraion was significantly different for both the cool season ($p=0.0245$) and the warm season ($p<0.0001$).

Discussion

Vertical ocean structure at Hind Bank

The well-defined pycnocline and DCMZ in the warm season deteriorated as the cool season approached. The overall trend showed a gradual decrease in depth of the DCMZ as ocean temperatures cooled approaching the cool season. These data support previous findings of the seasonal changes of the DCMZ at Hind Bank (Smith et al. 2010).

The CTD casts from September are somewhat difficult to interpret. It was expected that September would have the strong stratifications and shallower UML depth found in the October casts, but this was not the case. It is possible that there is some variability in the vertical profiles that monthly sampling was not able to detect. It is likely that more frequent sampling would provide better information on processes impacting UML depth and stratification of the water column.

Changes in wind speed seem to have affected UML depth as well. Higher wind speeds 24 hours before sampling usually resulted in a deeper pycnocline and DCMZ, which supports previous findings on the impact of wind speed on mixed layer depth (Tabata at al. 1965, Adamec and Elsberry 1984). It is possible that changes in wind forcing from climate change will impact DCMZ location along with increased heat flux, especially because climate change has the potential to increase tropical storm activity (Knutson et al. 1998, Mann and Emanuel 2006).

ACP data

The major change in ACP backscatter throughout the calendar year was an increase in backscatter during the night in the warm summer months from midnight to dawn; daytime backscatter remained relatively constant throughout the year. This increase in nightly backscatter is consistent with previous studies that found an increase in nightly backscatter (Yahel et al. 2005). Previous studies have similarly detected diel vertical migration using Doppler sonar profilers (Plueddemann and Pinkel 1989).

This change in nightly summer backscatter may be due to seasonal changes in depth of the DCMZ. Zooplankton feed on the DCMZ at the shelf edge in the summer when it shoals around the reef within the detection range of the ACP upward looking field of view; in the winter the DCMZ is deeper and zooplankton would not be within the ACP field of view. The strength of vertical migrations can also be affected by the composition of the zooplankton community or environmental factors, such as light or weather (Ashijan et al. 2002).

The ACP tidal data appear to follow the tidal pattern experienced in St. Thomas. The ACP backscatter is asynchronous with the diurnal tidal data, indicating that the backscatter peaks are probably not caused by tidal resuspension of sea floor sediments.

Increases in ACP back scatter at the shelf edge during the summer could indicate that the mesophotic corals located there may have increased opportunities for heterotrophic feeding. The fact that this occurs in the summer may be especially beneficial to coral (Grottoli et al. 2006). Increased heterotrophic feeding by corals may protect coral if their symbiotic algae die off in a bleaching event due to elevated summer ocean temperatures (Grottoli et al. 2006).

ROMS

In the increased heat flux simulation, the increased heat flux decreases the capacity to form the DCMZ at the shelf edge. Higher heat flux may inhibit particle convergence in this area, possibly similar to the chaos described by the simulations of Huisman et al. (2006). Increased heat flux scenario model output indicate that the Hind Bank coral reef may have opportunities for heterotrophic feeding year round, but may be exposed to higher zooplankton concentrations in the winter. This may be beneficial to the coral reef at Hind Bank if it depends on heterotrophic feeding due to reduced light levels at depth as proposed by Anthony and Fabricius (2000). While average particle concentrations are higher in the winter, the highest monthly peak in particle abundance occurs in September, one of the months with the highest ocean temperatures in the Virgin Islands. This peak in plankton may help to offset the effects of bleaching caused by warm ocean temperatures in summer months (Grottoli et al. 2006).

The ROMS simulations verified the occurrence of upwelling onto the shelf edge at Hind Bank. The high variability of particle concentrations at the shelf edge indicates that tides or internal waves may play a role in determining how much plankton reaches the shelf edge; plankton has been shown to be transported onto reefs by currents and internal waves (Roman et al. 1990, Leichter et al. 1998). Although, the ACP data indicate the bulk of nighttime zooplankton appearing on the shelf edge is likely due to diel vertical migration and not by any physical mechanism.

This is the first modeling study of its kind to determine the effects of climate change on UML depth in the tropics. The decrease in particles in contact with the shelf edge may be to be due to a decrease in depth of the UML in the climate change scenario.

ACP Backscatter and ROMS comparison

Higher ACP backscatter during the summer is consistent with increased particle concentrations in ROMS during September and October as reflected by the average climatology scenario (control model run), showing an agreement in particle convergence at Hind Bank. There are discrepancies, however; overall particle concentrations were higher in the cool season when compared with the warm season in the ROMS simulations but not the ACP backscatter. It is possible that this discrepancy is due to the lack of particle behavior in the simulations.

This may also be due to differences in actual and model bathymetry, or possibly due to simulation resolution.

Simulation limitations

These simulations have several limitations that should be considered. The ACP that was used at Hind Bank for data collection is one point on the bank, whereas the grid point in the simulation that contains that point is much larger. Each grid point is relatively large, at 1.96 km^2. While this size grid still provides a good approximation of particle concentrations and ocean parameters at Hind Bank, it is important to remember that data from the ACP and from the simulations do not come from the same sized area. This difference in size may be responsible for discrepancies between ACP and simulation output. The large size of each grid point may cause inaccuracies in data; for example average temperature in the grid point containing the study site was on average lower than what would be expected from CTD data due to the fact that the grid point contains some of the area off the shelf where cooler water is located. Additionally, the bathymetric data used by ROMS is also an approximation of actual bathymetry, so it may vary slightly from the actual bathymetry. However, it should still provide a close approximation of heat flux and particle concentrations.

Additionally, the particles used in these simulations are passive. Actual zooplankton will have behaviors such as vertical movement in the water column, which is not represented by these simulations. The simulations also do not take into account effects of light and nutrients on particle location.

Possible effects of light and nutrients on phytoplankton location

Decreases in depth of the upper mixed layer shown by the ROMS simulations may affect growth rates of phytoplankton and therefore how much food would be available to zooplankton. The depth at which phytoplankton respiration is equal to production is known as the critical depth, and at this depth there is no net gain in primary productivity (Sverdrup 1953, Nelson and Smith 1991, Chiswell 2011). Historical CTD casts from the area have shown this depth to be approximately 80 meters. Therefore, a DCMZ that is close to but not below this depth will be larger due to the increased nutrients found at that depth but still be located in a depth of adequate light penetration.

It is possible that a shoaling of the thermocline as seen in the increased heat flux simulation may contribute to a decrease in primary production and result in less food for zooplankton due to reduced nutrients located at the UML-isopycnal layer interface. While there would initially be more nutrients available from the layer below the UML, they may be used more quickly due to increased light penetration at the shallower DCMZ depth. As a result, it is possible that the decrease in depth of the DCMZ will result in a smaller phytoplankton bloom due to fewer nutrients located there. However, it is not known to what extent the 15.4 meter difference between the control and increased heat flux scenarios shown by the model would affect light and nutrient levels and therefore primary production. It is possible that over time it would result in the DCMZ location moving to a deeper pycnocline, which would be beneficial for the plankton due to higher nutrient levels at depth. However, this plankton production may not be available to the mesophotic corals.

The effect of climate change on the global oceans and primary productivity

By 2050, it is predicted that there will be global increases in UML temperature. In some parts of the world, an increase of as much as four degrees Celsius is predicted (Blanchard et al. 2012). Near sea floor temperatures may increase by one to two degrees (Blanchard et al. 2012).

Climate change is also predicted to negatively impact primary production throughout the global oceans. These decreases in primary production are predicted to be as great as 60% for the year 2050, though it varies by location (Blanchard et al. 2012). As a result, there is likely to be less zooplankton available for heterotrophic feeding as well. Reduction in primary production due to climate change, along with the decreased ability for the DCMZ to form at the shelf edge in the increased heat flux scenario, could drastically reduce the amount of zooplankton available to corals.

The effects of climate change on corals

Increased heat flux may have an impact on the corals themselves; high water temperatures have been shown to cause coral bleaching (Glynn 1992, Hoegh-Guldberg 1999). It is possible that the tolerance for increased heating will be exceeded in the next few decades (Hoegh-Guldberg 1999). Climate change is likely to continue in the future, and as a result it is predicted that in the next 50 years there will be a shift away from domination of reef building corals on the reefs (Hoegh-Guldberg 1999). Mesophotic reefs such as the one located at Hind Bank can act as refugia for the corals located at the reefs (Smith et al. 2008, Smith et al. 2010), but how climate change will affect these refugia has not been studied. In the event of increased heat flux, mesophotic corals may be exposed to cooler water than their shallow water counterparts if the thermocline is above the reef. However, overall the water will be warmer so mesophotic corals may still be affected, though they may be better protected than shallower corals. As a result, a decrease in plankton in the event of climate change may be particularly harmful as corals may need to feed heterotrophically to compensate for their loss of zooxanthelle (Grottoli et al. 2006). Increased ocean acidification from climate change may further harm corals by compromising carbonate accretion and skeletal growth (Hoegh-Guldberg et al. 2007). Therefore, global warming may impact coral reefs in multiple ways: a decrease in primary productivity, an increase in coral bleaching, a decrease in their skeletal formation abilities, and a decreased ability for the DCMZ to form.

Heterotrophic feeding of coral on different zooplankton groups

The presence of zooplankton at the reef does not necessarily indicate that corals will be able to use them for heterotrophic feeding. Many types of zooplankton, such as copepods, are able to avoid capture by corals (Sebens et al. 1996). However, copepods tend to dominate zooplankton samples in the Caribbean, with 89% of zooplankton samples being composed of copepods in Discovery Bay, Jamaica (Heidelberg et al. 2004). Local zooplankton samples at Hind Bank consist of 74% copepods (appendix). While corals will consume copepods if they catch them, corals tend to feed more heavily on less abundant, slower organisms such as isopods, amphipods, and crab larvae (Sebens et al. 1996).

Future Research

There are a number of avenues that could be explored to expand upon this project. It would be beneficial to do additional field research in the winter months and perform more frequent CTD casts to gain a better understanding of changes occurring in the water profile throughout the year.

There is also more that can be done to determine the effects of changes in UML depth on the strength of DCMZ blooms as it relates to light penetration and nutrient levels, as this has the possibility to affect levels of phytoplankton and therefore zooplankton. This research only takes into account water movement and not light availability on possible plankton location, something that should be incorporated into future models.

It would also be beneficial to determine to what extent the mesophotic reef at Hind Bank relies on heterotrophic feeding at different times throughout the year. If the energetic needs from plankton were known for coral at different depths and heating conditions, it would be possible to gain a better understanding of how much the movement of the DCMZ would affect the energetic balance of corals.

Lastly, there are more opportunities to expand the modeling aspect of this project. ROMS simulations could be done that incorporate changes in wind forcing and it would also be useful to give the passive particles behaviors that resemble the diel vertical migration observed by the ACP backscatter data. If possible, it would be useful to reduce the size of the model grid points used in order to increase accuracy of the simulations.

Conclusion

The UML and DCMZ south of St. Thomas varies in depth by season and is typically located on the shelf during the warm months and below the shelf during the cool months. The stability of the UML is broken down in the cool season by environmental changes; the well-defined pycnocline and DCMZ deteriorated as the cool season approached.

There appears to be diel vertical migration occurring with an increase in migration in the summer months, which may help counteract coral bleaching at this time (Grottoli et al. 2006). This is probably due to the DMCZ being located deeper in the winter months, where it will not be detected as backscatter by the upward looking ACP.

The concentration of particles at Hind Bank varies daily, possibly due to changes in tides or breaking internal waves at the study location, both of which have been shown to transport zooplankton onto and off of reefs (Roman et al. 1990, Leichter et al. 1998). Particle concentrations were in agreement between ACP backscatter and the ROMS control simulation during the summer but not in the winter, possibly due to the lack of particle behavior in the ROMS simulations.

During the increased ocean heating scenario there was a decrease in concentrations of particles in contact with the shelf edge and a decrease in depth of the UML. If the mesophotic reefs at Hind Bank rely on heterotrophic feeding throughout the year, increased heat flux may negatively affect the heterotrophic feeding ability of the reefs due to a decrease in plankton available at the shelf edge. A decrease in heterotrophic feeding ability of reefs in the event of climate change would cause added stress at a time when reefs are already experiencing global decreases in plankton and bleaching from warmer water temperatures.

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APPENDIX

Appendix - List of zooplankton found at Hind Bank

Zooplankton Group	Total Percentage
Copepod	73.75
Chaetognath	6.29
Hydrozoan	4.94
Amphipod	4.23
Shrimp larvae	3.29
Crab larvae	1.72
Mysid shrimp	1.66
Fish egg	1.66
Gastropod	0.75
Fish larvae	0.63
Stomatopod	0.33
Bivalve	0.26
Megalops	0.16
Cephalopod	0.16
Polychaete	0.14
Lobster larvae	0.03
Isopod	0.01