AN ABSTRACT OF THE THESIS OF

Megan J. Wolf for the degree of Honors Baccalaureate of Science in Biology presented on November 24, 2008. Title: Spatial and Temporal Variations in Respiration Rates and Hypoxia on the Oregon Shelf.

Abstract approved:

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Francis Chan

Inner shelf hypoxia has occurred along the Oregon coast between the latitudes 44ºN and 45ºN since 2002 with increasing duration and intensity, posing a threat to marine life. The objective of this research was to determine whether variation in respiration rate explains spatial and temporal variation in hypoxia. Dissolved oxygen concentrations of water samples were measured over time using a fluorescence-based oxygen meter, the Fibox. This method was found to be highly correlated to the established Winkler titration ($R^2 = 0.987$). Respiration rates were found to increase from 45ºN to 44.6ºN and to decrease from 44.6ºN to 44.2ºN. From August to September 2007, along the 44.3ºN line, respiration rates became slightly faster, while along 44.9ºN line, they became slightly slower. There is a high correlation between respiration rate and depth ($R^2 = 0.604$), temperature ($R^2 = 0.755$), and initial dissolved oxygen concentration measured by either the Conductivity-Temperature-Depth instrument ($R^2 = 0.812$) or by the Fibox ($R^2 = 0.780$). There is a low correlation between respiration rate and chlorophyll-a concentration ($R^2 = 0.239$). Direct experiments revealed that artificially adding oxygen or carbon to the system increases respiration rate, indicating that the system is not saturated with oxygen or carbon.

Key Words: respiration rate, hypoxia, Oregon coast

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Spatial and Temporal Variations in Respiration Rates and Hypoxia on the Oregon Shelf

by

Megan J. Wolf

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I understand that my project will become part of the permanent collection of Oregon State University, University Honors College. My signature below authorizes release of my project to any reader upon request.

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Megan J. Wolf, Author

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CONTRIBUTION OF AUTHORS

Dr. Francis Chan and Kristina McCann gathered the September 2007 respiration rate data reported in this thesis. Kimberly Page-Albins, M.S., gathered the data from the Conductivity-Temperature-Depth instrument reported in this thesis.

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INTRODUCTION

Hypoxia on the Oregon Shelf

Inner shelf hypoxia has occurred along the central Oregon coast since 2002 with increasing duration and intensity, posing a threat to marine life. Dissolved oxygen concentrations in the ocean are considered hypoxic when they reach <1.43 ml/l. While hypoxic waters tend to appear along the outer and middle portions of the continental shelf, hypoxia close to the shore is unusual, and thus the organisms inhabiting the inner shelf are less likely to be accustomed to a low oxygen environment. Massive die-offs of fish and invertebrates have resulted from hypoxic conditions in the California Current System, damaging both marine ecosystems and fisheries (10). Hypoxic regions with resultant massive die-offs of marine life are called dead zones. Periodic dead zones have occurred along the Oregon coast, culminating in the 2006 dead zone, characterized as larger, thicker, lower in oxygen, and longer lasting than any other previously recorded (17) (Figure 1).

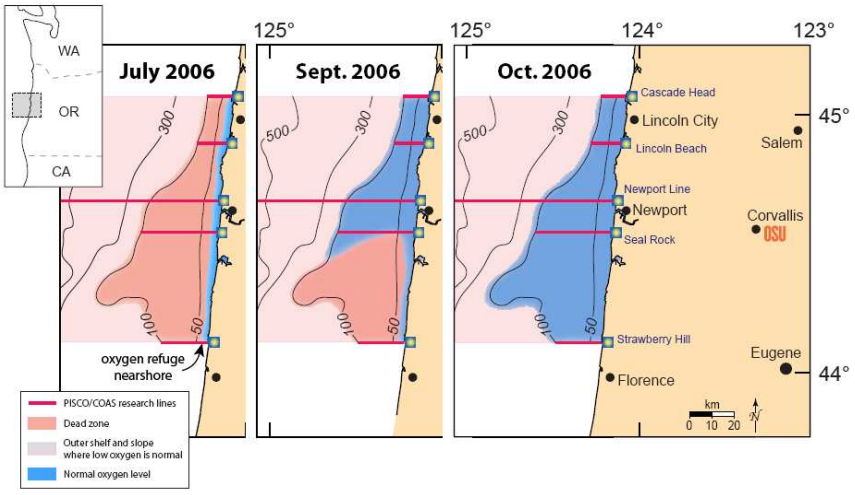


Figure 1. Spatial and temporal variations in hypoxia in 2006. (17)

The productivity of a region is coupled to local respiration, which is a mechanism by which hypoxia develops. On the Oregon shelf, the oxygen concentration of coastal waters is regulated strongly by wind-driven ocean currents. Northerly winds set up the north-to-south California Current extending from southern British Columbia to southern Baja California. While the top layer of water is pulled southward, it is deflected 45^{o} westward due to the Coriolis Effect. Each succeeding layer pulls frictionally on the layer below it with 45^{o} of deflection, so the wind's force decreases with depth as wind energy is lost to friction. The net effect, called Ekman Transport, is that these surface layers are transported 90^{o} (westward) to the southward wind direction. This causes a deficit of water near the coastal surface, which in turn results in an upwelling of deeper, oxygen-poor, but nutrient-rich water to the lighted zone (Figure 2).

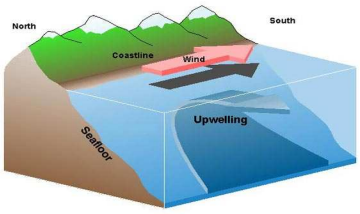


Figure 2. Upwelling on the Oregon coast. (13)

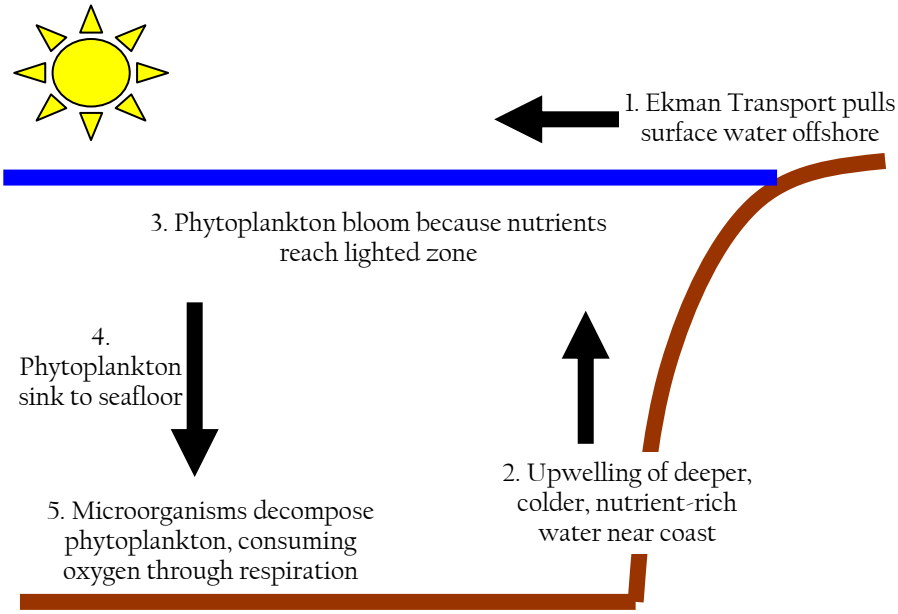


Figure 3. Successive upwelling cycles produce lower oxygen concentrations at the sea floor.

Nutrient inputs fuel phytoplankton blooms that subsequently sink to the sea floor, where they are decomposed by microorganisms which consume oxygen through respiration, thereby further lowering the oxygen concentration at the sea floor. In this way, successive upwelling cycles can result in hypoxic conditions (Figure 3).

The area of interest extends out to sea to the 100 meter depth contour of the continental shelf between 44ºN and 45ºN. The severity of hypoxia in this region exhibits a strong north-south gradient: hypoxic conditions are more severe south of Newport (44.6ºN) than north of Newport. A strong coastal upwelling jet travels from north to south along the edge of this continental shelf, creating a north-south gradient in the speed of flushing along the coast (Figure 4). In the relatively wide shelf south of Newport, slower currents lead to reduced rates of flushing for the system. Conversely, the relatively narrow shelf north of Newport lies in closer proximity to the coastal upwelling jet, and thus it is subjected to faster currents and more frequent flushing. This interaction between the region's strong coastal upwelling jet and topography give rise to distinct patterns in water residence times and surface productivity (Figure 5).

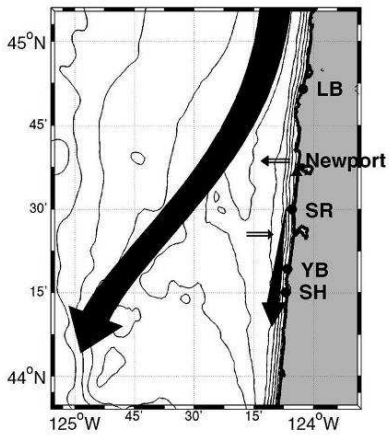


Figure 4. Strong coastal upwelling jet. (Kircinich, Barth, OSU)

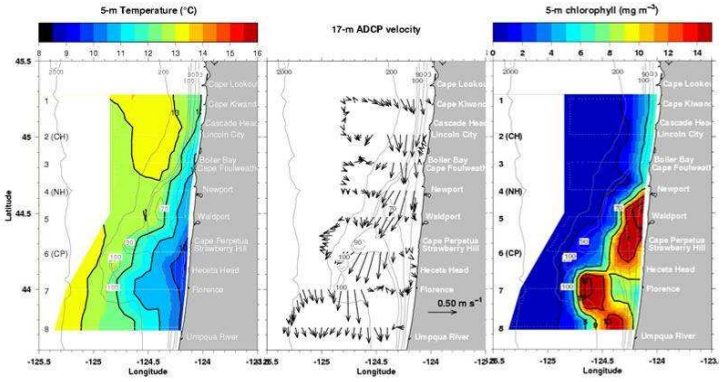


Figure 5. Variation in temperature, current velocity, and chlorophyll concentration. (Barth, COAS)

Given the variation in hypoxia severity and the proposed mechanism by which hypoxia develops, it is important to investigate the planktonic respiration rates in this area. While respiration rates have been studied in other hypoxic systems, such as the Louisiana shelf (7), little work has been done along the Oregon coast. Determining respiration rates on the Oregon shelf may assist in determining whether the north-south gradient in hypoxia severity is driven by differences in surface productivity or differences in water residence times.

If differences in surface productivity are driving variation in hypoxia, then we would expect to see variation in respiration rates, thus causing variation in local dissolved oxygen concentrations. If this hypothesis is true, then our results should indicate higher respiration rates in the south than the north, in order to be consistent with the spatial gradient we observe in hypoxia severity.

An alternative hypothesis is that even if respiration drives oxygen concentrations down in a particular region, hypoxic conditions might not develop if the region is being continually flushed by better oxygenated water. In that case, any effect of respiration rate variation would be overshadowed by variation in the amount of time that a given parcel of water sat on the continental shelf. The slower currents observed in the south would allow more time for hypoxia to develop, while the faster currents observed in the north would continually flush that region with better oxygenated water. If differences in water residence times are driving hypoxia variation, then our results should indicate respiration rates consistent in both the north and south.

The first objective of this research is to determine if respiration rates vary in space and time. If respiration rates do vary spatially and temporally, the second objective is to

compare respiration rates to other characteristics of the sampling sites. Identifying the factors which control respiration rate can allow us to predict how respiration rates are likely to change as those characteristics of the system change.

Respiration in Marine Ecosystems

Quantifying respiration in the ocean is essential to understanding the ocean's role in the global carbon cycle and its implications for atmospheric carbon dioxide levels (3, 5, 14). Regarding spatial variability in ocean respiration, the photic layer is the primary respiratory contributor, followed by the mesopelagic layer, although respiration in the latter occurs over a greater volume of water. In the ocean interior, respiration occurs at a relatively low rate, making it difficult to measure. Temporal variation in respiration may also occur, such as during periods of upwelling, when areas may exhibit higher productivity and, as a result, higher levels of respiration (6).

Variation in respiration, however, does not necessarily reflect corresponding variation in productivity. For instance, in terms of spatial variation, while respiration and productivity may be coupled over a large area, they may be uncoupled over a small area. Similarly, in terms of temporal variation, the two processes may be coupled over millennia, but remain uncoupled over a shorter time scale, since ancient reservoirs of dissolved organic carbon may be harnessed for respiration (6). For these reasons, it may be difficult to predict respiration at any given site based on local productivity.

Microbes are responsible for the majority of respiration that occurs in the ocean, while contributions by metazooplankton and vertebrates are less significant. Among microbes, however, the relative contributions of various size classes may differ,

depending upon the local abiotic and biotic environmental factors. Identifying the primary respiratory contributors in a particular system may aid in predicting the effect of changing organism populations on total respiration rates for that system (8, 9). Additionally, microbe respiration rates have been shown to decline exponentially with increasing depth (1).

The area of interest is part of the California Current System, which as a whole has displayed unusual characteristics in recent years. Atypically high chlorophyll concentrations (19, 20) and particularly strong upwelling (15) have been observed in the California Current System recently. Studies have been conducted to investigate whether these anomalies are due to climate change acting on this system. Climate warming in certain portions of the California Current System has resulted in a shallower source of upwelling, and therefore fewer nutrients at the surface, leading to a reduced zooplankton population (18). Climate warming has also been linked to intensifying wind currents along the ocean surface, thereby accelerating upwelling (2).

The Oregon coastal shelf is of particular interest in the discussion of carbon cycles because during the upwelling season it acts as a net carbon sink. Several characteristics of Oregon's coastal upwelling system—its large preformed nutrient concentration, its nitrate-limited primary production, and its modest warming—allow it to behave differently from other open ocean systems (12).

MATERIALS AND METHODS

Field Sample Collection

During research cruises on board the R/V Elakha during July - September 2007, water samples were collected at locations between latitudes 44ºN and 45ºN extending to the 100 meter depth contour of Oregon's continental shelf. Names and locations of the sample collection sites are given below (Figure 6). Water was captured in a Niskin bottle at the sea floor, then brought up to the surface and transferred to an inverted 300 ml glass-stoppered biochemical oxygen demand (BOD) bottle containing a stir bar using rubber tubing. Air bubbles were flushed out to prevent contamination by atmospheric oxygen.

	Decimal Latitude ºN	Decimal Longitude ºW		Decimal Latitude ºN	Decimal Longitude ºW
Southern Lines			Northern Lines		
Strawberry Hill			Newport		
SH-15	44.25	124.12	NH1	44.65	124.08
SH-30	44.25	124.13	NH5	44.65	124.17
SH-50	44.25	124.17	NH3	44.65	124.13
SH-70	44.25	124.25	NH10	44.65	124.28
SH-100	44.25	124.45			
Wakonda			Lincoln Beach		
WK-15	44.39	124.10	LB-15	44.86	124.05
WK-30	44.39	124.12	LB-30	44.86	124.07
WK-50	44.39	124.17	LB-50	44.86	124.08
WK-70	44.39	124.28	LB-70	44.86	124.15
WK-80	44.39	124.42	LB-100	44.86	124.20
Seal Rock			Cascade Head		
SR-15	44.50	124.10	CH-15	45.00	124.02
SR-30	44.50	124.10	CH-30	45.00	124.03
SR-50	44.50	124.17	CH-50	45.00	124.07
SR-70	44.50	124.25	CH-70	45.00	124.10
			CH-100	45.00	124.15

Figure 6. Names and locations of sample collection sites. Approximate depths in meters are given after the hyphen in the location name.

Winkler Titration for Dissolved Oxygen

Upon collection, one set of samples was immediately fixed with a solution of manganese chloride and a mixture of sodium hydroxide with sodium iodide, according to the established Winkler titration method (16) for measuring dissolved oxygen (DO) concentrations in water (Figure 7). A white precipitate of $Mn(OH)_2$ formed, which was oxidized by the DO in the water sample. Next, sulfuric acid was added, and then the iodine was titrated with sodium thiosulfate and a starch indicator. The sodium thiosulfate was standardized with potassium iodate. The amount of DO at the time of fixation is directly proportional to the amount of iodine present.

$$Mn^{2+} + 2OH^- \rightarrow Mn(OH)_2$$
$$2Mn(OH)_2 + O_2 \rightarrow 2MnO(OH)_2$$

$$Mn(OH)_2 + 2H^+ \rightarrow Mn^{2+} + 2H_2O$$
$$MnO(OH)_2 + 4H^+ + 2I^- \rightarrow Mn^{2+} + I_2 + 3H_2O$$

$$I_2 + 2S_2O_3^{2-} \rightarrow 2I^- + S_4O_6^{2-}$$

Figure 7. Winkler reaction.

The Winkler titration method can only be used once to measure the DO concentration of a given sample. After fixation, the sample is no longer viable. This chemical approach can be used to identify the current DO concentration at a given location, but cannot be used to perform the continuous measurements of samples with dynamic DO concentrations necessary to determine respiration rate.

Fluorescence-based Measure of Dissolved Oxygen

A second set of samples collected at each site was not fixed with Winkler reagents, but instead sealed and incubated in a temperature-controlled environment. The samples were also shielded from light to prevent planktonic photosynthesis which would increase

the DO concentration. Using a fluorescence-based oxygen meter, the Fibox (manufactured by PreSens), DO concentrations of these samples were measured at various time points for up to 200 hours.

Unlike the Winkler titration method, the Fibox can make multiple measurements of the same sample. Furthermore, this fluorescence-based probe can continuously monitor a closed sample non-invasively, so the sample is not contaminated by atmospheric oxygen during measurements. After gluing sensor spots inside the glass BOD bottles, measurements can be taken by attaching the probe to the exterior of the bottle. The probe emits light pulses through the glass bottle onto the sensor spot containing an oxygen-sensitive fluorophore, or more specifically, a transition metal complex (11) (Figure 8). Dissolved oxygen present in the sample alters the fluorophore's fluorescence properties to a degree proportional to the dissolved oxygen concentration.

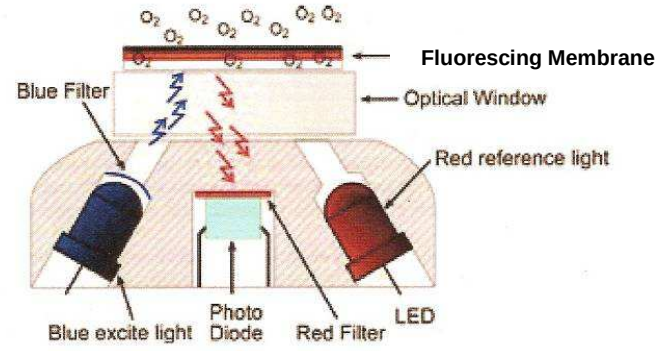


Figure 8. Mechanism of fluorescence-based oxygen meter. (11)

In terms of measuring dynamic oxygen concentrations, one limitation is that the oxygen bound to the fluorophore may be in disequilibrium with dissolved oxygen pools in instances where respiration or production rates are high (11). For our purposes, however, changes in dissolved oxygen during our measurements will be exceedingly small compared to the rate of equilibration between the dissolved oxygen bound in the fluorophore and the dissolved oxygen concentration of the sample.

The Fibox probe was calibrated in an oxygen-free environment and an air-saturated environment before each set of measurements. At each time point, DO concentration measurements were taken in μmol/l every second for up to 1.5 minutes. The average of the last 10 values was used. For most samples, measurements were taken at 6 time points spaced approximately every 20 hours. During measurements, BOD bottles were placed on a stir plate. A stir bar had been placed in the bottle at the time of collection. Stirring during measurements prevented oxygen stratification within the sample. Measurements were taken with temperature compensation, so the Fibox temperature probe was placed in the same 10ºC water bath containing the incubated BOD bottles. Measurements were converted to ml/l. Differences in DO concentration between time points (abbreviated T) 1 through 6 were calculated as follows: T6-T5, T5-T4, T4-T3, T3-T2, T2-T1, then T6-T4, T5-T3, T4-T2, T3-T1, then T6-T3, T5-T2, T4-T1, then T6-T2, T5-T1, then T6-T1. These differences were divided by the exact number of hours elapsed between two particular time points. All 15 rates were averaged to produce the respiration rate of a particular sample.

RESULTS

Comparison of Fibox and Winkler Methods

Since measuring dissolved oxygen concentration via the Fibox is not as well established as the Winkler titration, it was necessary to verify that the Fibox method produced accurate and precise results under our prospective experimental conditions. Measuring the dissolved oxygen (DO) concentration of a sample with the Fibox, then

performing the Winkler titration on that same sample, allowed for the comparison of these two methods (Figure 9).

We found that DO measurements taken by the Fibox and the Winkler titration methods were highly correlated with an R^2 value of 0.987 (Figure 9). This gives us confidence in the precision and reproducibility of the Fibox for measuring DO concentrations.

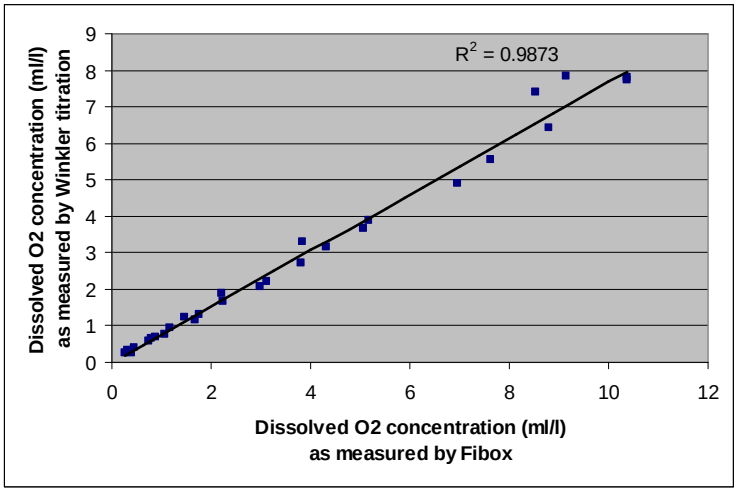
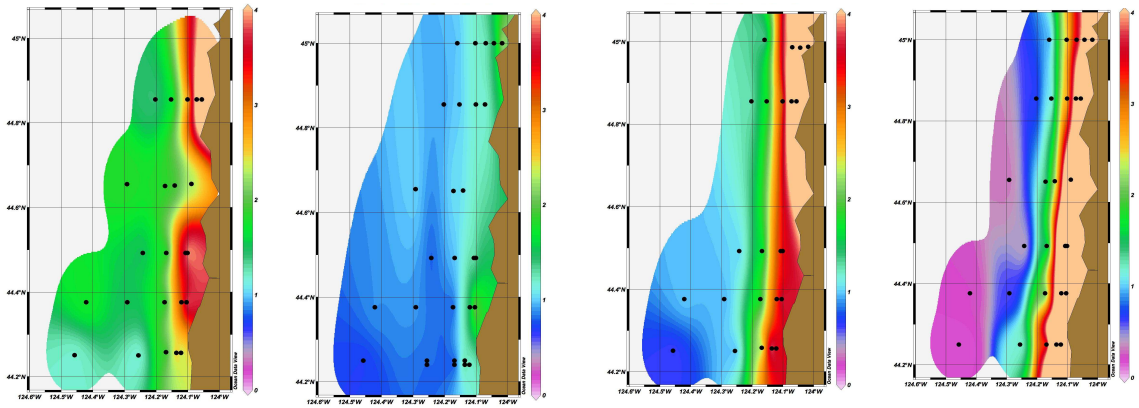


Figure 9. Comparison of Winkler titration and Fibox methods. Data collected 08/16/07 from SH, SR, WK and 08/17/07 from NH, CH, LB.

Spatial and Temporal Variations in Dissolved Oxygen Concentrations

During May through August 2007, dissolved oxygen concentration measurements were taken by the Seabird-43 dissolved oxygen sensor on the Conductivity-Temperature-Depth (CTD) instrument and verified by the Winkler method (Figure 10). In each of the four plots, the coastline is shown on the right. The right axis displays increasing DO values from bottom (0 ml DO/l) to top (4 ml DO/l). The bottom axis depicts increasing longitude from right (124ºW) to left (124.6ºW). The left axis shows increasing latitudes from bottom (44.2ºN) to top (45ºN). Dots represent sampling sites. Results indicate lower DO concentrations in the south as well as further offshore.



May 2007 June 2007 July 2007 August 2007

Figure 10. Dissolved oxygen concentrations May – August 2007. (Figure source: F. Chan, OSU)

Spatial Variation in Respiration Rates

In order to determine if respiration rates vary spatially, respiration rates were measured along 6 latitudinal lines: SH (44.3ºN), WK (44.4ºN), SR (44.5ºN), NH (44.7ºN), LB (44.9ºN), and CH (45.0ºN) over two consecutive days, 08/16/07 and 08/17/07. Respiration rates were plotted against latitude controlling for depth (Figure 11). As a consequence, the right axis from bottom to top can be considered a rough approximation of increasing depth and increasing longitude. Respiration rates appear to increase moving southward from 45ºN to 44.6ºN and to decrease moving southward from 44.6ºN to 44.2ºN.

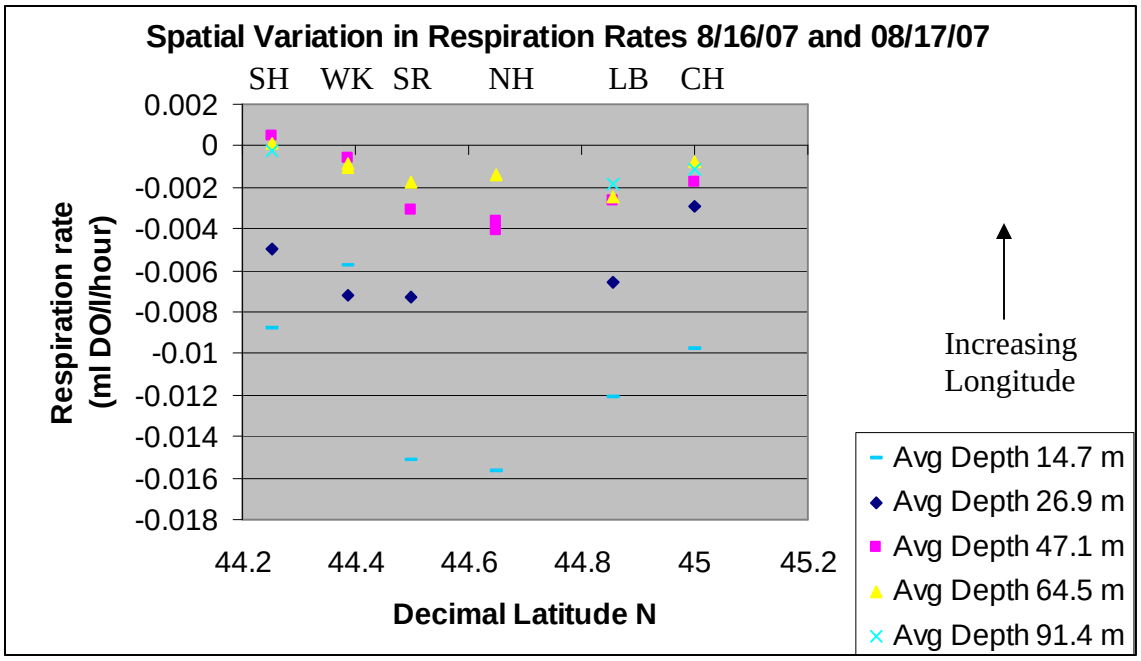


Figure 11. Spatial variation in respiration rates.

Temporal Variation in Respiration Rates

In order to determine if respiration rates vary over time, the respiration rate at a particular location was measured in both August and September. Results from four longitudes along the Strawberry Hill (44.3ºN) latitude line on 08/16/07 and 09/17/07 indicate that respiration rates remain stable or become slightly faster from August to September (Figure 12). Results from four longitudes along the Lincoln Beach (44.9ºN) latitude line on 08/17/07 and 09/19/07 indicate that respiration rates become slightly slower from August to September. (Figure 13).

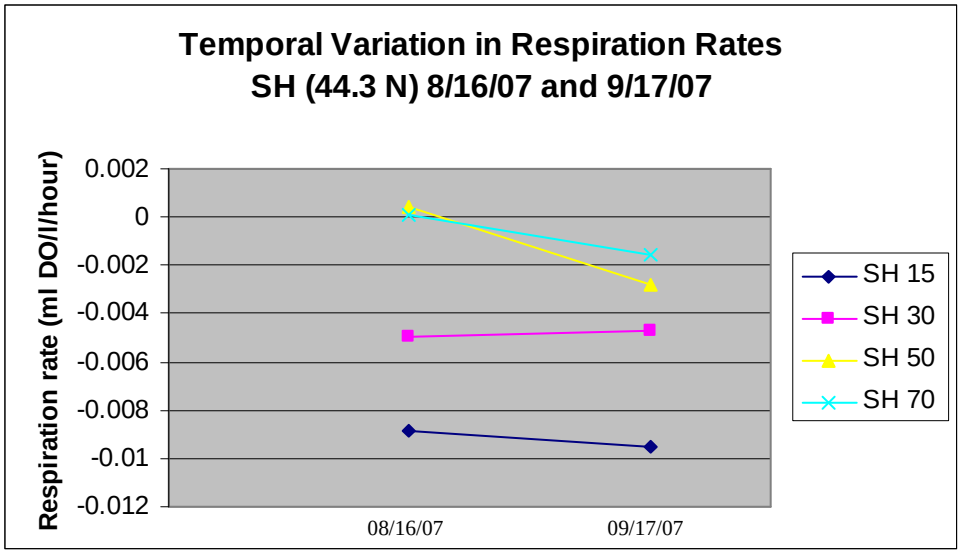


Figure 12. Temporal variation in respiration rates at Strawberry Hill.

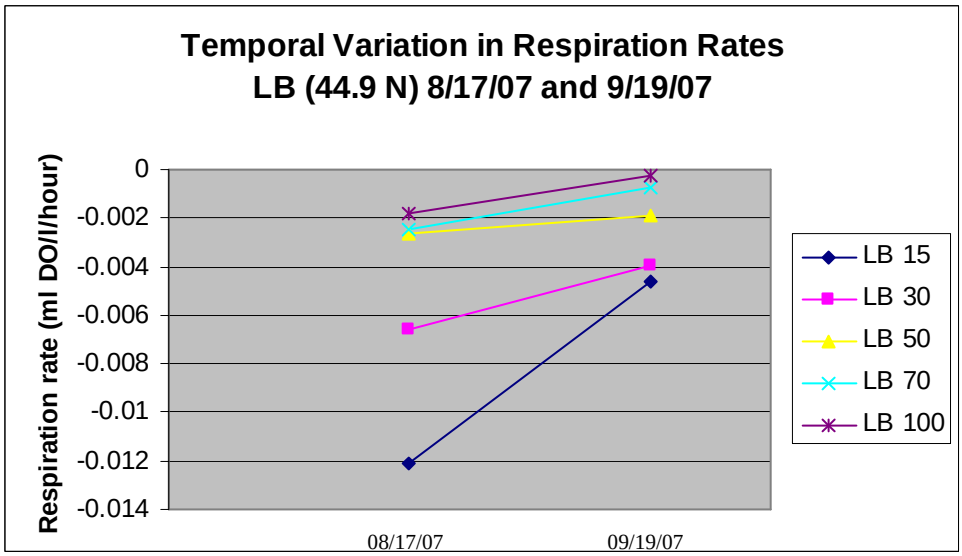


Figure 13. Temporal variation in respiration rates at Lincoln Beach.

Correlations Between Respiration Rate and Site Characteristics

In order to investigate why respiration rates vary in time and space, respiration rates were plotted against other characteristics of the sampling site, such as depth, temperature, chlorophyll-a concentration, and initial DO (Figures 14-18). As an additional check for the accuracy of the Fibox method, respiration rates were plotted against DO values obtained by the CTD and DO values obtained by the Fibox. In figures 14 – 18, data was collected on 08/16/07 from WK 15, WK 30, WK 50, WK 70, WK 80, SR 15, SR 30, SR 50, SR 70, SH 15, SH 30, SH 50, SH 70, SH 100; on 08/17/07 from LB 15, LB 30, LB 50, LB 70, LB 100, NH 1, NH 3, NH 5, NH 10, CH 15, CH 30, CH 50, CH 70, CH 100; on 09/17/07 from SH 15, SH 30, SH 50, SH 70; on 09/19/07 from LB 15, LB 30, LB 50, LB 70, LB 100.

Results indicate a high correlation between respiration rate and depth (nonlinear, $R^2 = 0.604$), temperature (linear, $R^2 = 0.755$), and initial dissolved oxygen concentration measured by either the Conductivity-Temperature-Depth instrument (linear, $R^2 = 0.812$) or by the Fibox (linear, $R^2 = 0.780$). There is a low correlation between respiration rate and chlorophyll-a concentration (nonlinear, $R^2 = 0.239$).

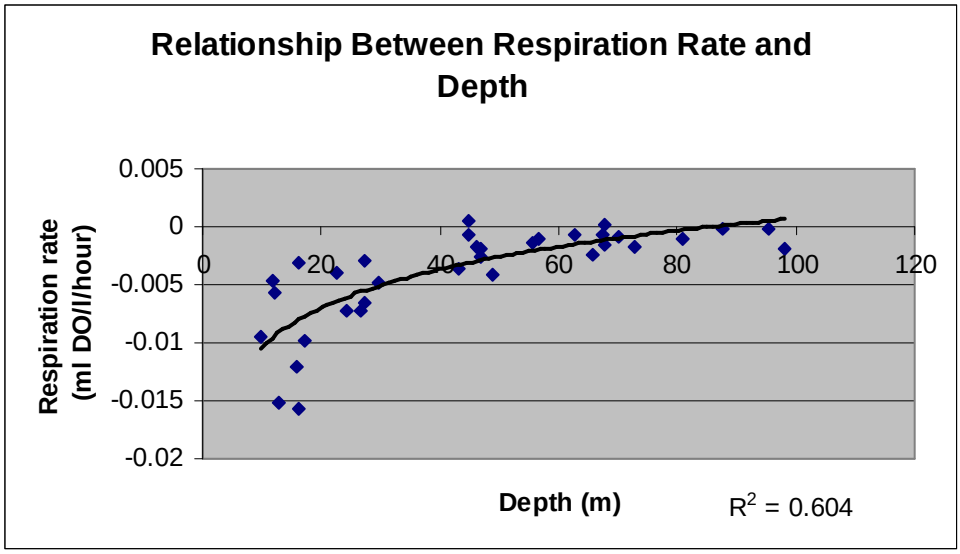


Figure 14. Relationship between respiration rate and depth.

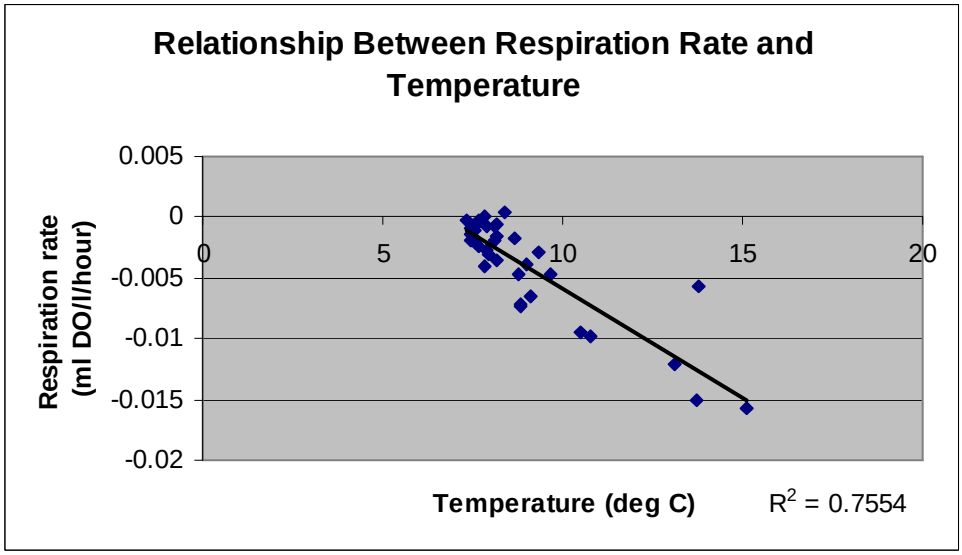


Figure 15. Relationship between respiration rate and temperature.

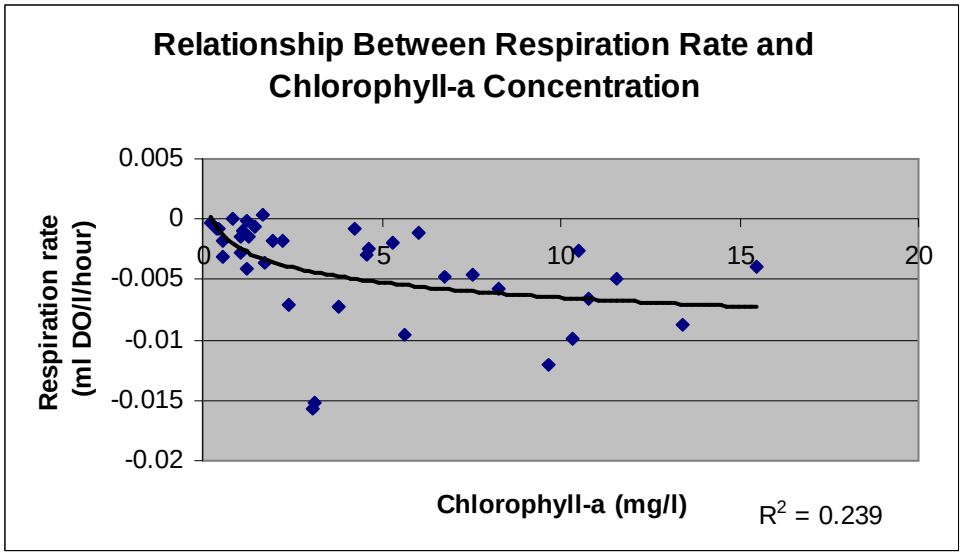


Figure 16. Relationship between respiration rate and chlorophyll-a concentration.

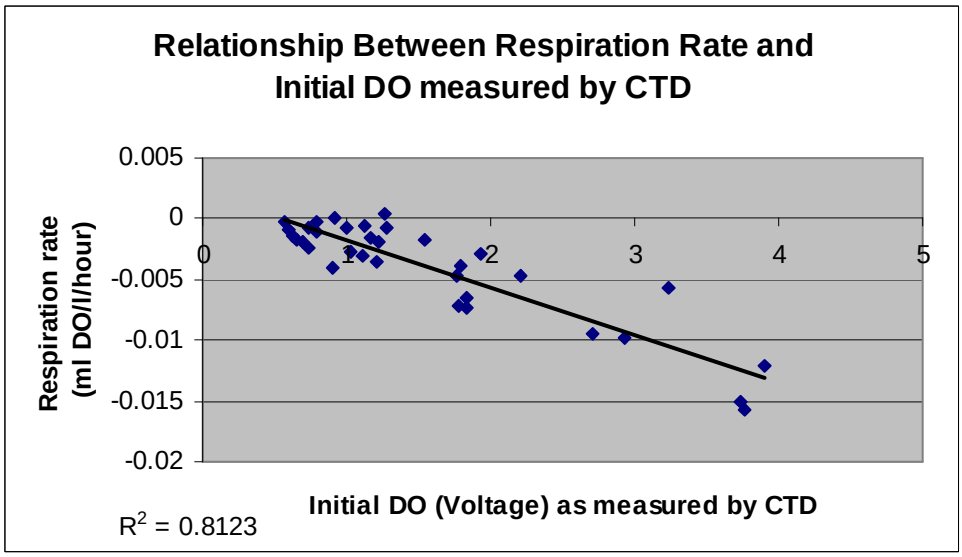


Figure 17. Relationship between respiration rate and initial DO as measured by CTD.

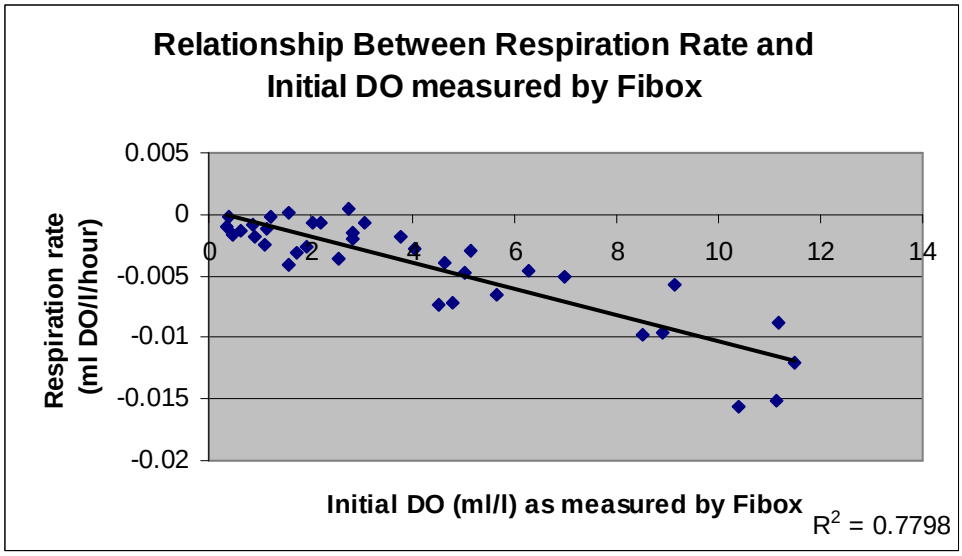


Figure 18. Relationship between respiration rate and initial DO as measured by Fibox.

Effect of Dissolved Oxygen Addition on Respiration Rate

A direct experiment was conducted to determine whether the addition of dissolved oxygen to the initial system would affect respiration rate. At each site, two BOD bottles were collected, one which was shaken vigorously to force atmospheric oxygen into the bottle and the other which was treated as a control. Results from three longitudes along the Strawberry Hill (44.3ºN) plotted against initial DO indicate that adding oxygen increases respiration rate (Figure 19).

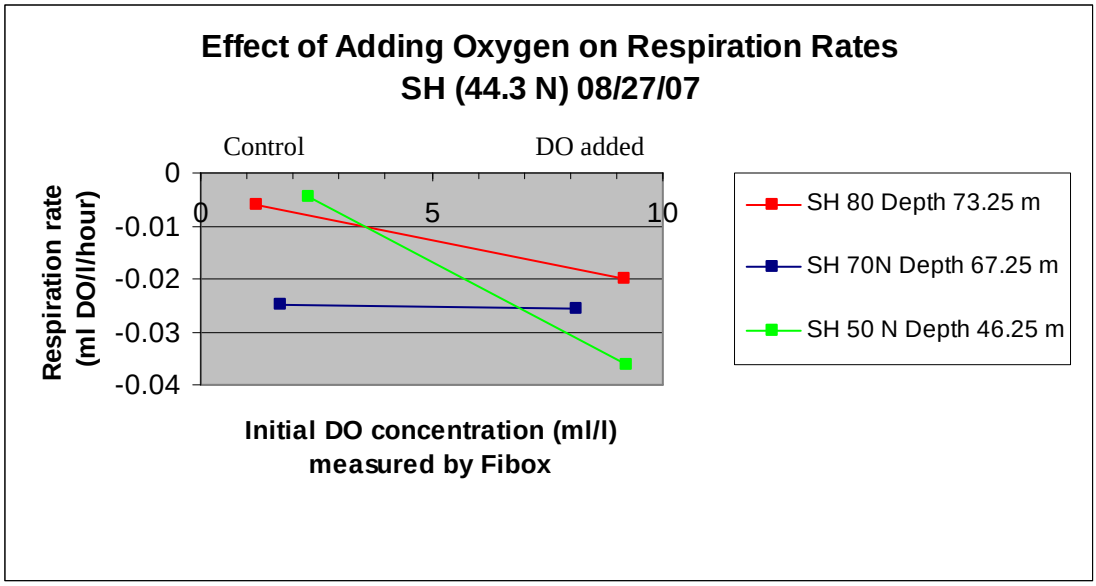


Figure 19. Effect of adding oxygen on respiration rates.

Effect of Carbon Addition on Respiration Rate

Another direct experiment was conducted to determine whether the respiration rate of the system is carbon limited. At each site, two BOD bottles were collected, one to which glucose was added and the other which was treated as a control. Results from various longitudes along the Strawberry Hill (44.3ºN) and Lincoln Beach (44.9ºN) latitude lines plotted for the control bottle and the bottle to which glucose was added indicate that adding carbon increases respiration rate (Figure 20).

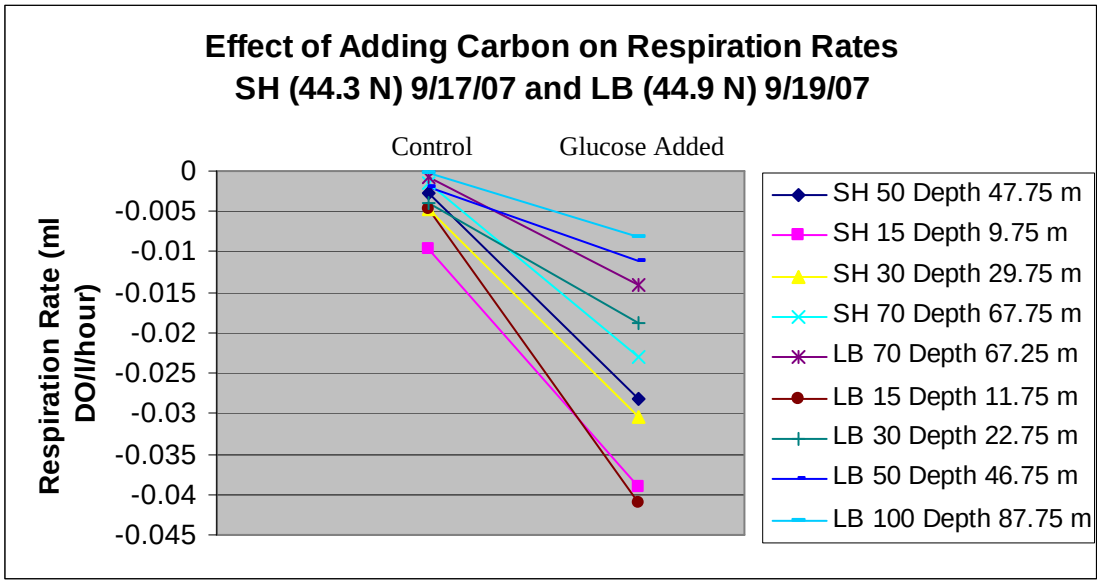


Figure 20. Effect of adding carbon on respiration rates.

DISCUSSION

Hypoxia has been shown to vary both spatially and temporally along the Oregon shelf. This variation may be explained by differences in surface productivity or differences in water residence times. Our first objective was to determine if respiration rates vary in space and time. Our second objective was to compare respiration rates to other characteristics of the sampling sites in order to identify the factors which control respiration rate.

We found that respiration rates do vary spatially (Figure 11). Respiration rates appear to increase from 45ºN to 44.6ºN and to decrease from 44.6ºN to 44.2ºN. While respiration rates did vary spatially, they were not higher as a whole in the south than in the north. In contrast, DO concentrations did differ along the north-south gradient, suggesting that respiration rates did not drive the north-south patterns in hypoxia severity.

We found that respiration rates do vary over time. Data from four longitudes along the Strawberry Hill (44.3ºN) latitude line reveal that respiration rates remain stable or become slightly faster from August to September (Figure 12). Data from four longitudes along the Lincoln Beach (44.9ºN) latitude line reveal that respiration rates become slightly slower from August to September (Figure 13).

We investigated how respiration rate correlates with other characteristics of the sampling sites. We found a high correlation between respiration rate and depth, with an R^2 value of 0.604 (Figure 14). There is also a high correlation between respiration rate and temperature, with an R^2 value of 0.755 (Figure 15).

We found a low correlation between respiration rate and chlorophyll-a concentration, with an R^2 value of 0.239 (Figure 16). This suggests that respiration in this system is not directly proportional to the productivity of this system. As stated in the introduction, while respiration and productivity are coupled over a large area and over a vast time scale, they may remain uncoupled over a small area or over a short time scale. In addition, while chlorophyll-a concentration may be a measure of phytoplankton biomass, it loses its accuracy as cells die and start to degrade. Thus, chlorophyll-a concentration may not necessarily be an accurate index of carbon that is available to microbes. Further study on the relationship between productivity and respiration in this system is necessary to produce more conclusive results.

There is a high correlation between respiration rate and initial DO measured by the CTD, with an R^2 value of 0.812 (Figure 17). We also found a high correlation between respiration rate and initial DO measured by the Fibox, with an R^2 value of 0.780 (Figure 18). This suggests that higher initial DO concentrations lead to faster respiration.

Since the CTD is a more established method for measuring DO, the fact that these two R^2 values are close to one another supports the accuracy of the Fibox as a method for measuring DO concentrations.

In a direct experiment, we found that adding oxygen to the system by shaking the BOD bottle also tended to lead to slightly faster respiration. Results from three longitudes along the Strawberry Hill (44.3ºN) latitude line reveal that respiration rates remain stable or become slightly faster when the initial DO is increased (Figure 19). This indicates that the system is not saturated with oxygen. Additional replications of this experiment are necessary to produce more conclusive results.

In another direct experiment, we found that adding carbon to the BOD bottles led to faster respiration. Results from various longitudes along the Strawberry Hill (44.3ºN) and Lincoln Beach (44.9ºN) latitude lines reveal that respiration rates become faster when carbon is increased (Figure 20). This suggests that respiration in this system is strongly carbon-limited.

In conclusion, this research suggests that respiration rates along the central Oregon coast do vary over both space and time. This variation may provide insight into the spatial and temporal variation observed in hypoxia in this area. This research also finds strong correlations between respiration rate and other characteristics of the sampling sites, which should be further investigated through additional direct experimentation. These conclusions, however, are based on a limited data set. Further research will allow us to develop a more comprehensive understanding of the factors determining respiration rates and their impact on hypoxia severity along the Oregon coast.

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