Water column oxygen dynamics within the coastal gradient in the
northeastern Gulf of Mexico inner shelf

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Abstract

This study quantified the coastal gradients of salinity, temperature, nutrients, chlorophyll and oxygen along a transect from 5 to 18 m depth in the northeastern Gulf of Mexico (NEGOM) through measurements of water column profiles over 4.5-years and recordings of probes mounted at 0.5 m above the seafloor over 2-years. The main goal was to determine the influences of the coastal gradients on water column oxygen concentration distributions. Apalachicola River discharge affected the study region as reflected in low-salinity surface layers. Decreasing rates of oxygen production and consumption from the shallowest station to the deepest station were attributed to measured coastal gradients of nutrients and the decreasing influence of seafloor processes with increasing distance from shore. Water column photosynthetic oxygen production at a realistic irradiance of $200 \mu\text{E m}^{-2} \text{s}^{-1}$ ranged from 0.5 to $4.5 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$, and dark consumption rates from 0.2 to $2.6 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$. Based on July irradiance profiles and associated production and consumption rates, the water column in July 2009 produced 0.9 ($1 \text{ SD} = 0.2$) $\text{g C m}^{-2} \text{ d}^{-1}$ with rates remaining relatively constant over the length of this coastal transect. Benthic boundary layer production reaching 26% to 43% of the surface layer production underlines the role of the benthic boundary layer for production in the inner shelf. Oxygen in the benthic boundary layer never decreased below 73% air saturation, and hypoxic zones, as reported from shelf areas west of the study region, did not occur. Oxygen production exceeded consumption suggesting an autotrophic system.

Keywords

Oxygen, coastal gradient, primary production, benthic respiration, West Florida Shelf, Northeastern Gulf.

Abbreviations

NEGOM = Northeastern Gulf of Mexico

dw/dw= Dry weight to dry weight ratio

PAR = Photosynthetically active radiation

Chl= Chlorophyll *a*

NTU = Nephelometric turbidity units

SD = 1 Standard deviation

1. Introduction

Understanding the oxygen dynamics and controls of production and consumption processes in the coastal zone is central for assessing the functioning of the shelf in the cycles of matter and for identifying trends that may indicate fundamental changes in the ecosystem (Canfield et al., 1993; Glud, 2008). Oxygen is an indicator of the fate of carbon and carbon flux, of system metabolism in a changing climate, and a respondent to external forcing functions. Oxygen thus is also an important indicator of ecosystem health, e.g. coastal eutrophication fueled by riverine runoff of fertilizers and the burning of fossil fuels caused an exponential spread of coastal hypoxic zones since the 1960s (Diaz and Rosenberg, 2008). Oxygen concentrations determine the ability of an ecosystem to sustain fisheries or whether harmful sulfides may be produced. Bottom waters are of particular interest in terms of oxygen because the settlement of decaying plankton can cause high oxygen consumption rates at the seafloor, a process that is most pronounced in upwelling areas and coastal waters prone to planktonic blooms resulting from eutrophication (Lohrenz et al. 1997, Rabalais et al. 1996). Understanding the current drivers of oxygen dynamics therefore can enable us to identify and quantify other anthropogenic influences in the future as those that may result from ocean warming, increases in carbon dioxide, changes in nutrient discharge to the ocean or catastrophic events (McQuatters-Gollop et al., 2009). A key requirement for the evaluation of change in oxygen and its magnitude is the availability of baseline data that can be used as reference (Duarte et al., 2009). In light of the recent major crude oil spill in the northern Gulf in 2010, it has become apparent that a record of baseline oxygen dynamics in this coastal region did not exist. Here we present results of a long-term study that focused on

water column and boundary layer oxygen dynamics in the coastal gradient of the northeastern Gulf of Mexico (NEGOM) inner shelf.

The NEGOM, which includes the northern section of the West Florida Shelf (Fig. 1), is a shallow, broad continental margin and about 300 km wide at Florida's Big Bend coast (Weisberg et al., 2005). Little information is available on the processes that affect oxygen in the shelf waters of the NEGOM, in contrast to the well-studied northwestern Gulf of Mexico, where the Mississippi outflow causes large oxygen fluctuations and coastal hypoxic zones (Rabalais et al., 2007; Rabalais et al., 2002; Turner et al., 2006). The NEGOM is influenced by the Apalachicola River, the largest river in Florida, which drains a watershed of approximately 50000 km², including the Atlanta metropolitan area, and discharges 140 to >5000 m³ s⁻¹ into the Gulf of Mexico (Livingston, 2000). Occasionally Mississippi River water moves eastward and can affect the NEGOM and West Florida Shelf (He and Weisberg, 2002b). Currents in the NEGOM shelf are driven mainly by tidal forces and wind (Marmorino, 1983a, b), and during fall and winter, southeasterly winds produce downwelling, while in spring and summer, the wind regime is predominantly northwesterly favoring upwelling (He and Weisberg, 2002a). River discharge and upwelling supply nutrients to the NEGOM shelf, and the ensuing algal bloom can periodically extend from the Big Bend region far into the eastern Gulf of Mexico (Gilbes et al., 2002; Morey et al., 2009). Nonetheless, the reported water column primary productivity rates south of this study region on the West Florida Shelf are relatively low, as reflected in oxygen production rates ranging from 0.02 to 0.21 mmol O₂ ml⁻³ h⁻¹ (Vargo et al., 1987; Wanninkhof et al., 1997).

This study was initiated to address the lack of oxygen concentration data and information on oxygen dynamics in the inner shelf of the NEGOM. The main goal of this work was to determine the influences of the coastal gradients (in salinity, temperature, nutrients, chlorophyll) on water column oxygen concentration distributions, because so far, the dynamics of oxygen in the NEGOM and the factors influencing these dynamics were poorly quantified. Oxygen measurements in the water column were conducted over 4.5-years, and over 2-years at 0.5 m above the seafloor to determine magnitudes and the spatial and temporal changes of dissolved oxygen along a transect from the nearshore (3.7 km off shore, 5 m water depth) to 29 km offshore (18 m depth). Our results provide baseline data for future studies in the NEGOM, a region anticipating rapid coastal development.

2. Methods

2.1 Study transect

Our measurements were conducted along a transect in the NEGOM extending 29 km in a southeastern direction from the coast off St. Teresa, FL, to K-Tower, a retired US Air Force tower that now is used as a hydrographic and meteorological measurement station (Fig. 1; White et al., 2011). The transect was located approximately 50 km east of the mouth of Apalachicola River that discharges into Apalachicola Bay, an estuary enclosed by barrier islands. Due to this proximity, the Apalachicola River and Bay waters influenced the water composition at the transect. During the study period (2007-2011), the average nutrient concentrations in the bay were 11.8 (1 SD = 12.1) $\mu\text{mol l}^{-1}$ inorganic

nitrogen, 0.15 (1 SD = 0.10) $\mu\text{mol l}^{-1}$ orthophosphate, and 21.5 (1 SD = 12.5) $\mu\text{mol l}^{-1}$ silicic acid (Apalachicola National Estuarine Research Reserve, <http://cdmo.baruch.sc.edu/get/landing.cfm>).

Insert Figure 1 here

The sediment in this region is composed of mostly quartz sands with some shell hash, and sediment organic carbon content is $< 0.1\%$ (dw/dw). Five stations, named Station A (5 m water depth), Station ab (7 m), B (10 m), Station bc (15 m), and Station C (18 m) were established on the transect line, along which the water depth increased almost linearly (Fig. 1). Station A, the station closest to the shore, was protected from the open Gulf by a barrier island on the southwest side (Dog Island), and a shallow sand reef on the southeast side (Dog Island Reef).

The water column profiles of salinity, temperature, turbidity, chlorophyll *a* (via fluorometry), and dissolved oxygen (via fluorometry) were measured nearly monthly with a YSI 6600 multi-parameter probe at all stations (weather permitting) from 4 April 2007 to 21 September 2011 for 31 sampling trips (White et al., 2011). The probe was mounted in a cage, lowered to the bottom and raised to the surface, while collecting data at 1-second intervals. The data were binned within 1 m depth intervals.

Discrete water samples were taken, weather permitting, almost every month from 22 July 2008 to 15 September 2010 (14 samples from Station A, 12 from Station B, and

11 from Station C). Water samples for profiles after July 2008 were collected along with the data collection from the multi-parameter probes. Water for oxygen production and consumption measurements was collected using Niskin bottles or buckets (near-surface only) from 0.5 and 4.5 m water depth for Station A; 0.5, 5, and 9.5 m for Station B; and 0.5, 9, and 17.5 m depth for Station C. For one study year (August 2007 to August 2008), surface water (0 - 1 m) was collected for nutrient analysis (dissolved inorganic nitrogen (DIN), nitrate+nitrite (NO_x), ammonium (NH_4^+), phosphate (PO_4^{3-}), silicic acid (Si(OH)_4)) via colorimetric methods described in Grasshoff et al. (1999). On 11 January 2008, nutrient samples were also collected from the boundary layer (0.5 m above seafloor) at Station C.

YSI multi-probes of the same type as used for the water column were deployed in bottom mounts from 12 March 2008 to 6 January 2011 at Station A, 19 June 2008 to 10 October 2010 at Station B (with a gap between 19 January 2009 and 4 July 2010 because of electrical problems), and 12 March 2008 to 9 November 2010 at Station C to assess potential influences of the sediment on water column oxygen dynamics. The sensors of the multi-parameter probe took measurements at 0.5 m above the sea floor at 15 min intervals. Irradiance intensity was measured at the same height above the sediment as photosynthetically active radiation (PAR) with a LICOR[®] planar PAR sensor pointing straight up. Wiper mechanisms kept the sensing surfaces of the oxygen, chlorophyll and PAR sensors clean of settling sediment. The multi-parameter probes were retrieved monthly for cleaning and data downloading. Bad weather delaying service, damage to instruments, and biofouling interfered with data collection, leading to gaps in the time series. Data were flagged as compromised or missing when 1) the probe's supply voltage

dropped below recommended values, 2) the calibration data were outside acceptable bounds, or 3) when data showed unrealistic temporal changes or negative values.

2.2 Production and Consumption

Oxygen production and consumption measurements of the water samples were started within a few hours after sample collection in an environmental chamber set to in-situ temperature and a full spectrum irradiance intensity of $200 \mu\text{E m}^{-2} \text{s}^{-1}$ (PAR). This intensity was chosen to represent realistic irradiance intensity reaching the boundary layer at all three stations on a sunny summer day and was determined with irradiance profiles and moored PAR sensors (Table 2). A Hach[®] Rugged LDO1001 oxygen optode was mounted in the neck of each of the glass bottles containing the water samples for the production and consumption measurements. The probe was programmed to record the oxygen concentration at 5 min intervals. The water was kept well-mixed with a stirring magnet during the entire incubation. Three bottles were incubated for each station and water depth (bottom, mid, or surface). Net primary production values were derived from oxygen change over time. Oxygen consumption rates were measured in the same setup under dark conditions.

Production rates were measured over a range of different irradiance intensities to assess the potential range of photosynthetic oxygen production for the irradiance intensities occurring during the day. Because we did not isolate the primary producers, but measured whole community metabolism, our laboratory tests produced community irradiance response curves that differ from standard PI-curves because they are affected by heterotrophic organisms. For these measurements, water samples from bottom, mid,

and surface water were collected in triplicate from each of the 3 main stations once in July 2011. The water samples were incubated in 1 L glass bottles as described above and maintained at in situ temperature inside a water bath placed in a sunlit area outside. Eight different irradiance intensities were adjusted and maintained for 60-minute time periods by a stack of black window screens mounted above the bottle setup. Irradiance intensity at the bottles was constantly logged with a LICOR[®] spherical PAR sensor attached to a LICOR[®] LI-1400 data logger. Periods of 10 minutes of irradiance exposure were followed by 10 minutes of complete darkness by covering the entire system by a thick opaque tarpaulin. Three periods for each irradiance intensity were averaged to produce values for mean oxygen production. The same was done for the dark periods to calculate average consumption rates. This dark respiration measured during daytime was not equal to dark respiration during nighttime due to differences in, e.g., photorespiration, cytochrome pathway respiration or the Mehler reaction (Ogren, 1984). The differences caused by these reactions, however, are relatively small (Burris, 1977; Lewitus and Kana, 1995; Lloyd et al., 1977), and we chose the alternating production-respiration measurements during daytime irradiance hours in order to avoid introducing artifacts that would arise from changes in the plankton community over time.

2.3 Environmental data

Irradiance intensities at the water surface were taken from the nearby Apalachicola National Estuarine Research meteorological station at East Point, FL, at 29 47.45' N, -84 53.00' W (NOAA, 2012); these data are accessible through the National Estuarine Research System (<http://cdmo.baruch.sc.edu>). Irradiance penetration through the water column was measured at all stations on 28 July 2009 through a PAR sensor (LICOR[®])

mounted to the CTD lowered from the research vessel from the surface to approximately 1 m above the seafloor. Wind, cloud cover, and precipitation data collected by NOAA weather data buoy NDBC #SGOF1 at 29° 24.42' N, 84° 39.78' W (NOAA, 2011) were used to determine meteorological influences on water column conditions. To assess the potential influence of riverine input on production at the study transect, we related our primary productivity data to Apalachicola River discharge recorded by the US Geological Survey Station 02359170 near Sumatra, FL (29° 56.95' N, 85° 0.93' W) (USGS, 2011).

2.4 Statistical treatment and definition of seasons

Standard deviations listed reflect one standard deviation and are presented as (1 SD = value of standard deviation). The significance of the relationship between the variables in linear regressions was tested using F-statistics, and the differences between two regression slopes were tested using t-statistics according to Sachs and Reynarowych (1984). The Kolmogorov–Smirnov test was used to determine whether data sets follow a normal distribution. To test whether two sets of data were significantly different from each other, the t-test was used after testing for normal distribution of the data sets. Where the Kolmogorov–Smirnov test did not indicate normal distribution, we applied the Mann-Whitney U-test or the Wilcoxon signed-rank test where two related samples were compared (Sachs and Reynarowych, 1984). The *p*-value listed in the statistic test results is the probability of observing an effect, and “df” indicates the degrees of freedom. The significance or alpha (α) level is the probability level for rejection of the null hypothesis, and all tests used an alpha of 0.05 (5%) unless indicated otherwise. We used the winter solstice (Dec. 21/22), vernal equinox (Mar. 20), summer solstice (Jun. 20/21), and

autumnal equinox (Sep. 22/23) as separators between seasons where seasonal results are reported.

3. Results

The main characteristics of the water column and sediment are presented in Table 1. The text addresses vertical profiles first, then the changes observed along the transect (lateral gradient), and reports the average trends observed during the 4-year period (spring 2007-spring 2011) unless indicated otherwise.

The water column in the inner shelf in the NEGOM was characterized by non-hypoxic conditions at all times, warm temperatures, and a low salinity surface layer (0-2 m) with increased chlorophyll concentrations compared to subsurface water (> 2 m) (Wilcoxon test: $p = 0.0117$, $p < 0.05$, Fig. 2). Results from statistical testing assessing the significance of the vertical gradients are presented in Table 2A and differences of the gradients between seasons in Table 2B.

Insert Table 1 here

Insert Figure 2 here

Insert Table 2A here

Insert Table 2B here

The seasonal averages calculated for each station's surface, mid water and bottom layers revealed coastal spatial gradients, reflected in steady changes in major environmental parameters with increasing distance from the shore (Fig. 3, Table 3).

Insert Figure 3 here

Insert Table 3 here

3.1 Salinity, Temperature and Density

The salinity profiles typically showed a thin, pronounced surface layer (approximately 2 m thick) with reduced salinity and then a gradual increase in salinity with depth, except at the most offshore Stations bc and C during winter (Fig. 2). The average water column salinity was lowest in spring (32.8 (1 SD = 2.96)) and steadily increased throughout the year to reach maximum values in winter (34.4 (1 SD = 2.0)). This trend was most pronounced in the surface layer (0-1 m), where in spring had an average salinity of 29.6 (1 SD = 1.2) and then gradually became saltier to reach almost full marine salinity (33.2 (1 SD = 2.5)) in winter (Fig. 3). A subsurface salinity minimum (decrease by ~ 1 ppt) could be observed between 5 and 8 m water depth at all stations seaward of station ab in summer and fall. Salinity increased with distance from the coast, with the steepest lateral gradient in winter (0.12-0.25 ppt km⁻¹), and the weakest in summer (0.05-0.06 ppt km⁻¹) (Fig. 3). These salinity gradients led to lateral density gradients that were significantly steeper in spring compared to fall (Table 3).

Water temperatures in fall, winter, and early summer were relatively homogenous over the entire water column depth (Fig. 2). The average winter temperature was 14.4(1 SD = 0.7)°C. Seasonal warming in spring produced vertical gradients with increasing temperatures toward the surface, which disappeared in early summer when homogenous warm temperatures (28.8 (1 SD = 0.1)°C) were recorded at all stations and water depths. The wintertime lateral gradient of increasing temperatures towards the ocean reversed during spring, when the shallower waters warmed more rapidly, and became flat during the beginning of summer. Shallow waters cooled more rapidly than deeper water in fall, reinstating a gradient with increasing temperatures toward offshore (Fig. 3).

The water column density profiles were governed by salinity and followed similar trends as the salinity profiles (Fig. 2). The average water column density decreased from 1025.7(1 SD = 1.5) kg m⁻³ in winter to 1020.5(1 SD = 2.1) kg m⁻³ in summer, when the development of steeper lateral density gradients in deeper layers was occasionally observed (e.g., 8 Aug. 2007, 7-9 m: Station B: 4.0 kg m⁻³ m⁻¹, bc: 2.8 kg m⁻³ m⁻¹, Station C: 2.3 kg m⁻³ m⁻¹, 28 Jul 09: 9-11 m, bc: 9.2 kg m⁻³ m⁻¹, Station C: 2.3 kg m⁻³ m⁻¹). The lateral water column density gradient weakened between spring (0.10-0.19 kg m⁻³ km⁻¹) and fall (0.02-0.05 kg m⁻³ km⁻¹).

3.2 Oxygen

Oxygen concentrations were typically highest at the surface reaching up to 118% air saturation (Station A, 8 Aug. 2007, 228.8 mmol m⁻³) and generally showed a relatively steady decline with water depth (Fig. 2, Table 2). The highest average water column oxygen concentrations (102.0(1 SD = 1.4)% saturation) and most homogenous oxygen

distributions were recorded during winter, while the summer measurements were characterized by the lowest average concentrations (97.5(1 SD = 3.8)%) and a more rapid decline of oxygen with increasing water depth (Table 2). The lowest oxygen concentrations were recorded at the deeper water Stations bc and C during summer (Fig. 2, minima e.g.: Station bc: 8 Aug. 2007, 79.2%, 154.6 mmol m⁻³, Station C: 8 Jun 08, 73.6%, 147.3mmol m⁻³).

The average surface to bottom oxygen gradient became less steep toward offshore, first rapidly from -2.3 mmol m⁻³m⁻¹ at Station A to -1.1 mmol m⁻³m⁻¹ at Station B, and then more gently toward Station bc, reaching -0.9 mmol m⁻³m⁻¹ at Station C (Fig. 4). The differences in this gradient decline between shallower and deeper stations were statistically not significant due to the relatively large variability in the gradient at Station A.

Insert Figure 4 here

The average water column oxygen concentration decreased with distance from shore (Fig. 3, Station A: 100.2 (1 SD = 9.9) %, Station C: 98.2 (1 SD = 6.1) %). This trend was significant in all seasons (Table 3). The average lateral gradients in oxygen saturation steepened significantly between winter and summer, and spring and summer, and became significantly less between summer and fall (Table 3). While the lateral oxygen gradient in the surface layer (0-1 m) changed by less than ± 0.05 %km⁻¹ throughout the year, the gradient in the benthic boundary layer (0.5 m above seabed) between winter and summer steepened by one order of magnitude (winter: -0.12 %km⁻¹, spring: -0.20 %km⁻¹, summer

-0.41 %km⁻¹) and in fall rapidly reversed to less than the winter value (-0.04 %km⁻¹, Fig. 3).

3.3 Chlorophyll

The chlorophyll concentrations in the water column along the transect were lowest in spring (0.90(1 SD = 0.81) mgm⁻³) and highest in summer (2.10(1 SD = 1.15)mgm⁻³) and during the study period reached 5 mgm⁻³. At Station A, Chl_a concentrations increased from the surface to the bottom, and this trend was significant in winter and fall (Fig. 2, Table 2A). At all other stations, Chl_a concentrations typically showed high concentrations in the surface layer, coinciding with the layer of reduced salinity. Below this layer, Chl_a concentrations decreased to a minimum and then increased again towards the bottom. The highest water column Chl_a concentrations were always recorded at the nearshore Station A (3.1(1 SD = 3.8)mgm⁻³), intermediate at Station B (1.7(1 SD = 5.9)mgm⁻³) and the lowest offshore at Station C (0.6(1 SD = 2.0)mgm⁻³). This lateral gradient was most pronounced in the subsurface layers (significant in the boundary layer 0-1 m above seafloor in winter and summer, Table 3), while the surface layer concentrations showed large variations with no clear lateral trend. The average water column Chl_a along the transect over time revealed a seasonal pattern with three main concentration peaks over the course of the year, recorded in February/March/April, July, and October/November (Fig. 5).

Insert Figure 5 here

3.4 Nutrients

The nutrient concentrations in the surface water layer (0-1 m) along the transect were low throughout the study period (Fig. 6, $\text{DIN} < 1.5 \text{ mmol m}^{-3}$, $\text{PO}_4^{3-} < 0.25 \text{ mmol m}^{-3}$ and $\text{Si(OH)}_4 < 8 \text{ mmol m}^{-3}$).

Insert Figure 6 here

Insert Table 4 here

NH_4^+ dominated DIN (contributing 80-91% of the DIN) and reached 2.4 mmol m^{-3} during summer. The nutrient concentrations from samples collected in January 2008 from the benthic boundary layer were low ($\text{DIN}: 0.90 \text{ mmol m}^{-3}$, $\text{NO}_x: 0.01 \text{ mmol m}^{-3}$, $\text{NH}_4^+: 0.89 \text{ mmol m}^{-3}$, $\text{PO}_4^{3-}: 0.08 \text{ mmol m}^{-3}$ and $\text{Si(OH)}_4: 0.27 \text{ mmol m}^{-3}$). The seasonal surface water sampling revealed gradients of decreasing DIN, PO_4^{3-} and Si(OH)_4 concentrations from the shore toward offshore during winter, and for NH_4^+ , this gradient was statistically significant (Table 4). Except for Si(OH)_4 , these trends of decreasing concentration with distance from shore disappeared during spring, when DIN and PO_4^{3-} concentrations were lowest at Station A, and DIN and Si(OH)_4 reached their lowest values during the year. In summer, DIN increased with distance from shore similar to spring, but with a steeper gradient. In contrast, PO_4^{3-} and Si(OH)_4 in summer declined toward offshore. The summer trends of DIN, PO_4^{3-} and Si(OH)_4 were statistically significant (Table 4). These PO_4^{3-} and Si(OH)_4 gradients persisted with similar magnitudes in fall, while the lateral DIN gradient

disappeared during this season. N/P ratios along the transect ranged from 4 to 20. The data suggest a decrease in N/P from winter (16.8 (1 SD = 3.5)) to fall (8.1 (1 SD = 3.2)) and an increase of N/P with distance from shore, but these trends were statistically not significant (Table 4)

3.5 Production and consumption rate measurements

The irradiance profiles recorded at the stations in July 2009 showed exponential light intensity decay with water depth at all stations with attenuation coefficients ranging from 0.68 (1 SD = 0.28) m^{-1} at Station B to 0.43 (1 SD = 0.33) m^{-1} at Station C (Fig. 7).

Insert Figure 7 here

On the sunny day in July 2009, when the light intensity profiles were measured, the average PAR levels ranged from 250 to 850 $\mu\text{E m}^{-2} \text{s}^{-1}$ in the surface layer (0-1 m) and 64 $\mu\text{E m}^{-2} \text{s}^{-1}$ to 355 $\mu\text{E m}^{-2} \text{s}^{-1}$ in the boundary layer (0.5 m above sediment) at Stations A and C, respectively. The oxygen gross production rates measured at a realistic in-situ irradiance of 200 $\mu\text{E m}^{-2} \text{s}^{-1}$ in the water sampled along the transect ranged from 0.5 to 4.5 $\text{mmol O}_2 \text{m}^{-3} \text{h}^{-1}$, and the dark consumption rates from 0.2 to 2.6 $\text{mmol O}_2 \text{m}^{-3} \text{h}^{-1}$. For the same irradiance of 200 $\mu\text{E m}^{-2} \text{s}^{-1}$, both production and consumption were higher in the bottom boundary layer compared to those in the surface layer (Fig. 8, Wilcoxon test: production $n = 12$, $p = 0.0047$, $p < 0.05$, consumption $n = 12$, $p = 0.0029$, $p < 0.05$). Figure 8 suggests trends of oxygen production and consumption increase with depth and

decrease with distance from shore, but these trends are not statistically significant because of the variability of the data.

Annual production averaged over the water column exceeded annual consumption by a factor of 2.0 (1 SD = 0.4), with higher values in winter and summer and the lowest ratio in fall (1.5) (Fig. 9). The production to consumption ratios (Production/Respiration ratios, P/R) between the seasons were not statistically different and the annual P/R ratios did not differ significantly between surface layer (1.8 (1 SD = 0.3)) and boundary layer (1.7 (1 SD = 0.1)).

Insert Figure 8 here

Insert Figure 9 here

The measurements of potential rates of water column oxygen production through incubation of water samples at different irradiance intensities revealed an increase of the average water column oxygen production by $1.43(1 \text{ SD} = 0.01) \mu\text{mol m}^{-3} \text{ s}^{-1}$ per $1000 \mu\text{E m}^{-2} \text{ s}^{-1}$ irradiance increase with no significant differences between stations (Fig. 10).

Insert Figure 10 here

4. Discussion

4.1 Water column characteristics

The water column along the transect in the NEGOM showed typical characteristics of a subtropical inner shelf environment in a humid climate, with coastal freshwater input producing a thin (< 2 m) surface water layer with lower salinity and density overlying an otherwise relatively well mixed water column throughout the year (Fig. 2) (Sharples, 1997). Mixing of the freshwater into deeper layers along the transect resulted in a lateral gradient with a less saline water column near the coast and higher salinity offshore (Fig. 3). The Apalachicola River discharge typically reaches its highest rates during February and March and lowest rates in August (Fig. 1), also typical of a subtropical coastal environment (Piola et al., 2000). As a result, the lateral salinity gradient was steepest in winter and spring, and least developed in summer (Fig. 3). The subsurface salinity minimum observed at Stations B, bc and C between spring and fall is attributed to either sinking of less saline and at times slightly colder surface water, currents bringing in another water mass, or a mixing event. The data do not reveal where this low salinity water mass originated.

The water column average temperature response to seasonal irradiation changes decreased with water depth. Vertical mixing caused fairly homogenous temperatures throughout the water column except during spring, when temperature in the deeper water layers trailed behind the rapid temperature increase in the surface layer, resulting in the steepest vertical temperature gradients recorded during all seasons (Fig. 2). Similarly, cooling in fall and winter was more rapid at the shallower stations, in contrast to spring,

where no pronounced vertical gradients were observed. Cooling from the surface and increased wave action during fall resulted in stronger water column mixing than in the spring (NOAA, 2011 wave heights:

http://www.ndbc.noaa.gov/view_climplot.php?station=42036&meas=wh).

4.2 Oxygen

Oxygen profiles showed little influence of density stratification, but rather direct and indirect effects of temperature, mixing by waves and currents, and biological activity. The relatively steady oxygen decrease between surface and bottom layer (Fig. 2) suggest that mid-water column processes had less influence on oxygen distribution, and that exchange with the atmosphere and photosynthetic production in the surface layer, and respiration processes in the bottom boundary layer and seafloor governed the vertical concentration gradient. Manickchand-Heileman et al. (1998) concluded from a mass-balance trophic model for the continental shelf of the southwestern Gulf of Mexico that only about 10% of primary production is consumed in the water column, which supports this hypothesis. The scaling of primary production and benthic respiration with irradiation and temperature produced the most pronounced surface to bottom oxygen gradients during summer (-0.82 (1 SD = 0.18) % m^{-1}) and the most uniform water column oxygen distribution during winter (-0.23 (1 SD = 0.12) % m^{-1}). This quadrupling of the vertical gradients between winter and summer rapidly reversed in fall due to dropping water column temperatures (Fig. 2).

High biological activity throughout the water column combined with decreasing water depth caused a steepening of the vertical oxygen profiles toward the coast. The

mixing by waves and currents was not strong enough to eliminate these gradients.

Increasing bottom water currents nearing the shore, mainly caused by waves, enhanced exchange between seabed and water column and thereby also benthic production and consumption. The average depth of the wave base at the stations (Fig. 1), determined from ADCP data (Maksimova and Clarke, 2013), suggest that waves had negligible influence on the seafloor at Station C (depth of wave base $\approx$ station depth), moderate influence at Station B (wave base depth $\approx 1.6 \times$ station depth) and strong influence at Station A (wave base $\approx 2 \times$ station depth) (Fig. 1). Where wave orbital motion reaches the seafloor, it causes pore water exchange in the permeable sands that dominate this study region (Precht and Huettel, 2003, 2004; Wiberg and Harris, 1994), enhancing oxygen production and consumption through advective transport of organic matter and oxygen into the sediment and the release of anoxic pore waters and photosynthetic oxygen from the bed (Huettel et al., 2014; Huettel et al., 2003). This is supported by measurements of oxygen fluxes in a sandy sublittoral area at the mouth of West Falmouth Harbor (Massachusetts) with the non-invasive eddy correlation technique (i.e. a technique that does not affect the flow and light conditions at the sediment surface) that revealed a strong correlation between bottom currents and oxygen flux (Berg et al., 2013).

Photosynthesis of marine benthic autotrophs is correlated to water flow through the enhancement of transport of oxygen, carbon dioxide and nutrients at the algal cells (Berninger and Huettel, 1997; Cook and Roy, 2006; Koch, 1994; Mass et al., 2010). On the other hand, the flow-induced pore water exchange can substantially boost benthic respiration as shown in flume experiments by Forster et al. (1996), who reported a 91% increase in total oxygen uptake in permeable sediments with a 11 cm s^{-1} increase of

flow under dark conditions. The declining oxygen concentrations approaching the sediment surface we recorded during daylight conditions indicate that benthic respiration occurred at a higher rate than benthic production along the transect.

Our data suggest that surface to bottom oxygen gradients steepened by one order of magnitude when water depth became shallower than 8 m (Fig. 4, gradient change rate Stations A→B: $0.12 \text{ mmol m}^{-3} \text{ m}^{-1} \text{ km}^{-1}$ vs. Stations B→C: $0.01 \text{ mmol m}^{-3} \text{ m}^{-1} \text{ km}^{-1}$), however, because of the limited number of stations, this change is not statistically supported. Such an increase can be caused by frequent sediment resuspension produced by surface waves at the shallow Stations A and ab. At these stations, the average wave orbital motion at the seafloor exceeded 20 cm s^{-1} , the threshold for sediment erosion and resuspension. The latter was shown to cause substantial increases in respiration rates (Almroth et al., 2009; Almroth-Rosell et al., 2012).

Mortenson (2013) suggests that under calm conditions, oxygen concentrations along the transect could also be influenced by tidal water exchange (using Fourier analysis), but we could not detect relationships between tide and any of the other parameters measured at the stations.

The generally higher oxygen concentrations near the shore (up to 118 % saturation at Station A, in Aug. 2007) are attributed to the higher photosynthetic oxygen production in this zone boosted by terrestrial nutrient input and stronger mixing. Dissolved inorganic nitrogen (DIN) concentrations in the Apalachicola Bay outflow were about one order of magnitude higher than the DIN concentrations measured along the transect in the surface water, which contained most of the freshwater input throughout the year (Fig. 6).

Nevertheless, the low salinity surface layer usually was associated with high chlorophyll concentrations (Fig. 2), suggesting that nutrients in the freshwater component supported phytoplankton growth. This hypothesis is backed by observations by Gilbes et al. (1996) and Morey et al. (2009), who reported that satellite images show a plume of enhanced surface layer chlorophyll along the West Florida Shelf during phases of high Apalachicola River discharge. Current models show that this plume can be pushed into this study area (Morey et al., 2003; Weisberg et al., 2005).

Bay water and coastal runoff produced a lateral concentration gradient of inorganic nitrogen and phosphorus that became apparent during winter, when primary productivity was lowest (Fig. 6). The winter N/P ratios averaged 17 and, thus, were close to the Redfield ratio. Despite maximum nutrient-rich freshwater input in February/March (Fig. 1), the coastal nutrient gradients largely disappeared during spring and concentrations reached their annual minima suggesting high usage and possibly nutrient limitation. This hypothesis is supported by spring N/P ratios of 13 despite phosphate concentrations $< 0.1 \text{ mmol m}^{-3}$ and Apalachicola Bay N/P of 62. During summer, there was a steep lateral gradient of N/P from 5 at Station A to 17 at Station C (0.5 km^{-1}) underlining high N usage and possibly N limitation at the shallowest stations despite the coastal N-input. The lateral gradient of N increasing offshore with PO_4^{3-} and Si(OH)_4 decreasing offshore supports that N was a heavily consumed nutrient in nearshore stations and possibly a limiting factor.

The relatively high correlation ($r^2 = 0.6$ to 0.9) between oxygen and chlorophyll content suggests that local phytoplankton dominated the generation of oxygen and was at least indirectly responsible for oxygen consumption in the water column (Fig. 11).

Insert Figure 11 here.

Oxygen and chlorophyll concentrations were positively correlated in the upper water layer (0-3 m), except at Station A. Below the upper water layer, this trend reversed and oxygen concentrations decreased with increasing chlorophyll concentrations (Fig. 11). Oxygen concentration at Station A was negatively correlated to chlorophyll concentration throughout the water column likely because of the strong mixing at Station A and the relatively stronger oxygen consumption in the lower layers compared to the production in the upper water layers. Besides this exception, the increase of oxygen concentration with increasing chlorophyll concentration in the upper water column appeared strongest near the coast and less pronounced offshore, while oxygen concentration decrease with increasing chlorophyll concentration in the lower layers grew with increasing distance from the shore (difference of slope test between bc and C in winter: $t = -2.3865$, $df = 19$, $p = 0.0276$, $p < 0.05$, in summer: $t = -13.8541$, $df = 19$, $p = 2.2E-11$, $p < 0.05$). The decreasing availability of light and nutrients averaged over the water column promoted respiration relative to oxygen production with increasing distance from shore. These lateral trends were most pronounced during summer, when higher irradiation and associated temperature increase enhanced production as well as oxygen consumption processes.

The water column thus goes through seasonal oxygen concentration oscillations that have the largest amplitude in the benthic boundary layer, where the lateral

oxygen concentration gradient steepened by one order of magnitude between winter and summer (winter: $-0.04 \text{ \% m}^{-3} \text{ km}^{-1}$, summer: $-0.41 \text{ \% m}^{-3} \text{ km}^{-1}$). In this layer, the lowest oxygen concentrations observed during the study were measured and coincided with Chla concentration maxima near the bottom (August 8, 2007: 79.2%, $154.6 \text{ mmol m}^{-3}$, August 6, 2008: 73.6%, $147.3 \text{ mmol m}^{-3}$, July 28, 2009: 79.1%, $160.2 \text{ mmol m}^{-3}$, July 13, 2011: 74.96%, $147.28 \text{ mmol m}^{-3}$). The oxygen concentrations thus never became a limiting factor for aerobic life (Claireaux et al., 2000; Craig and Crowder, 2005).

4.3 Primary productivity

Our measured production/respiration ratios (P/R, average = 2) suggest that the water column in this area is net autotrophic, i.e., more oxygen and organic matter is produced than consumed. Sporadically high rates of oxygen consumption in the fall, regardless of oxygen production rates, led to a low correlation ($R^2 = 0.48$) for that season. (Fig. 9). At an irradiance of $600 \text{ } \mu\text{E m}^{-2} \text{ s}^{-1}$, water column gross production along the transect at all stations and depths was on average 2.8 (1 SD = 1.3) $\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$. Our photosynthesis rates, at both a relatively low irradiance intensity (0 to $1.7 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ at $100 \text{ } \mu\text{E m}^{-2} \text{ s}^{-1}$) and saturating irradiance intensity (0.7 to $7.5 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ at $1000 \text{ } \mu\text{E m}^{-2} \text{ s}^{-1}$), were statistically not different from rates reported from estuarine and coastal Gulf of Mexico environments (Murrell et al., 2009, Yates et al. 2007, Del Castillo et al. 2000, Mortazavi et al. 2000, Table 5), but significantly higher (U-test, $p < 0.05$) than reported for outer shelf regions in the Gulf (Chen et al. 2000, Wanninkhof et al. 1997, Vargo et al. 1987, Hitchcock et al. 2000, Table 5) or subtropical regions of similar distance from shore from the Pacific Ocean (Aguirre-Hernández et al., 2004).

Insert Table 5 here

Our values were very similar to those measured by Del Castillo et al. (2000) ($0.33\text{--}1.63\text{ mmol O}_2\text{ m}^{-3}\text{ h}^{-1}$), which were measured relatively close to the transect (at 29.6°N , 85.1°W ~60 km west), and larger than those reported by Hitchcock et al. (2000) ($0.28\text{--}0.38\text{ mmol O}_2\text{ m}^{-3}\text{ h}^{-1}$), observed about 50 km south of this study region. Walsh et al. (2003) reported a phytoplankton primary production of $1.8\text{ g C m}^{-2}\text{ d}^{-1}$ along the 40-m isobath farther south in this region and increasing oxygen production and consumption rates with decreasing water depth. Using the light profiles we measured along the transect in July and the production and respiration rates determined for July water exposed to different irradiation rates, we obtain water column primary production rates of $0.6\text{ to }1.2\text{ g C m}^{-2}\text{ d}^{-1}$ (Fig. 12). Plotting production rates for surface, mid water and boundary water layers indicated that production in each layer increased toward the coast, with the boundary layer reaching approximately 26% (offshore Station C) to 43% (nearshore Station A) of the surface layer production. This increase toward the shore partly compensated the effect of decreasing water depth on total water column production, so that the latter remained relatively constant ($0.9\text{ (1 SD = 0.2) g C m}^{-2}\text{ d}^{-1}$) over the length of the coastal transect.

Insert Figure 12 here

The Louisiana coastal shelf, influenced by the Mississippi and Atchafalaya Rivers, may have experienced primary production rates (3.5 ($1 \text{ SD} = 2.1$) $\text{g C m}^{-2} \text{ d}^{-1}$; Quigg et al., 2011) three times greater than those we found in the summer. The inner shelf area we investigated, which was influenced by the Apalachicola River discharge and coastal runoff, had rates that were more than double those reported from oligotrophic subtropical and tropical environments (Burford et al., 2012; Jiang et al., 2011; Webster et al., 2002). We identify this area as upper meso- to eutrophic, following Nixon's (1995) classification, who defined coastal areas with production rates $> 300 \text{ g C m}^{-2} \text{ y}^{-1}$ ($0.8 \text{ g C m}^{-2} \text{ d}^{-1}$) as eutrophic.

Manmade activities that cause high nutrient concentrations in rivers threaten coastal waters and shelf ecosystems (Bianchi et al., 2013; Galloway et al., 1995; Seitzinger et al., 2005). As a consequence, coastal hypoxic zones are increasing worldwide, and are now considered one of the most severe threats to marine ecosystems (Diaz and Rosenberg, 2008). One of the largest river-induced hypoxic zones occurs annually in the northwestern Gulf of Mexico, where the Mississippi River releases nutrients into the shelf. The oxygen dynamics of this region have been the subject of numerous studies (Bianchi et al. 2010, Rabalais et al., 2007, Rabalais et al., 2004; Rabalais et al., 2002; Turner and Rabalais, 1994). In contrast, very little information is available for the coast east of the Mississippi Delta, and the NEGOM that is affected by the Apalachicola River discharge. We did not find any indications of hypoxia at our site but the rapid coastal development and population growth in the Apalachicola River watershed and on the Florida Panhandle coast may lead to an increase in nutrient

discharge and organic matter to the coast. Monitoring the oxygen dynamics in the NEGOM can provide warning signs for a deterioration of the system.

4.4 Conclusions

This study provides a long-term data set characterizing the coastal gradient of key environmental variables in the inner shelf 400 km east of the Mississippi Delta, with emphasis on the spatial and temporal dynamics of water column oxygen. The transect data reflect the influence of the energy maximum in the coastal zone (Huettel et al. 2014), with enhanced production at the shallow sites characterized by increased terrestrial nutrient input, irradiation reaching the sediment, and wave mixing. The vertical and horizontal gradients measured along the transect emphasized the role of the seafloor as a major factor influencing oxygen dynamics in the coastal water column. The time series indicated that the inner NEGOM shelf is an autotrophic environment with relatively high oxygen concentrations that never dropped to levels that could affect aerobic lifeforms. With the consistent patterns in the vertical and horizontal gradients this study quantified, it provides baseline data that can be used to quantify long-term trends in the NEGOM.

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Tables

Table 1. Characteristics of the sediments and water column along the study transect.

Station	Depth (m)	Latitude	Longitude	Median grain size (μm)	Salinity (ppt)	Temp. ($^{\circ}\text{C}$)	Density (kg m^{-3})	O_2 ($\mu\text{mol l}^{-1}$)	Chl a (mg m^{-3})	Turbidity (NTU)	Daily max. light at 0.5 m above seafloor (PAR $\mu\text{E m}^{-2} \text{s}^{-1}$)
A	5	29° 51.50' N	84° 31.50' W	269	0.5 - 37	11 - 31	997 - 1028	177 - 265	0.1 - 12.3	0.3 - 3.5	0.4 - 448
ab	7	29° 48.00' N	84° 31.00' W		5 - 37	11 - 30	1001 - 1027	200 - 249	0.1 - 20.5	0.3 - 3.0	
B	10	29° 47.67' N	84° 28.33' W	313	5 - 37	11 - 30	1001 - 1026	213 - 242	0.1 - 115	0.3 - 2.8	1.4 - 317
bc	15	29° 43.80' N	84° 25.15' W		0.8 - 36	11 - 31	997 - 1027	193 - 240	0.1 - 3.2	0.3 - 2.7	
C	18	29° 39.90' N	84° 22.29' W	428	1 - 36	17 - 30	997 - 1027	168 - 235	0.1 - 29	0.3 - 2.9	1 - 267

Table 2 A. Slopes of the vertical gradients of salinity, temperature, density, oxygen and chlorophyll for the four seasons. Grey text identifies slopes that are statistically not significant ($p > 0.05$). Chl.S lists values for the subsurface chlorophyll profiles (> 2 m depth), i.e. the profiles below the chlorophyll subsurface minimum.

Parameter	Winter			Spring			Summer			Fall		
	Slope	r^2	p	Slope	r^2	p	Slope	r^2	p	Slope	r^2	p
Station A												
Sal. (ppt)	0.759	0.921	9.6E-03	0.511	0.207	4.4E-01	1.454	0.887	1.7E-02	0.754	0.654	9.8E-02
Temp. (°C)	-0.110	0.822	3.4E-02	-0.104	0.605	1.2E-01	0.087	0.514	1.7E-01	-0.065	0.860	2.3E-02
Dens. (kg m ⁻³)	0.616	0.921	9.6E-03	0.414	0.250	3.9E-01	1.072	0.895	1.5E-02	0.611	0.659	9.5E-02
O ₂ (μmol l ⁻¹)	-1.615	0.908	1.2E-02	-0.956	0.117	5.7E-01	-4.049	0.965	2.8E-03	-1.883	0.759	5.4E-02
O ₂ (% air sat.)	-0.361	0.723	6.8E-02	-0.318	0.245	4.0E-01	-1.051	0.900	1.4E-02	-0.474	0.767	5.1E-02
Chl. (mg m ⁻³)	0.304	0.892	1.6E-02	0.287	0.745	5.9E-02	0.491	0.878	1.9E-02	0.250	0.973	1.9E-03
Chl.S (mg m ⁻³)	0.457	0.998	2.1E-04	0.176	0.197	6.5E-01	0.563	0.823	1.2E-01	0.275	0.944	2.6E-02
Station ab												
Sal. (ppt)	0.558	0.756	2.9E-02	0.762	0.793	2.2E-02	0.618	0.541	9.3E-02	0.234	0.966	1.3E-03
Temp. (°C)	0.016	0.159	4.0E-01	-0.072	0.546	9.2E-02	-0.003	0.005	8.9E-01	0.019	0.130	4.5E-01
Dens. (kg m ⁻³)	0.429	0.752	3.0E-02	0.589	0.823	1.7E-02	0.491	0.570	8.2E-02	0.284	0.779	2.5E-02
O ₂ (μmol l ⁻¹)	-1.935	0.907	6.1E-03	-1.083	0.680	4.7E-02	-2.095	0.912	5.5E-03	-0.739	0.819	1.8E-02
O ₂ (% air sat.)	-0.340	0.926	4.2E-03	-0.170	0.869	1.0E-02	-0.711	0.987	2.9E-04	-0.144	0.687	4.5E-02
Chl. (mg m ⁻³)	0.101	0.450	1.4E-01	-0.154	0.816	1.8E-02	-0.087	0.366	1.9E-01	-0.007	0.002	9.3E-01
Chl.S (mg m ⁻³)	0.204	0.926	8.8E-03	-0.092	0.508	1.8E-01	0.018	0.036	7.6E-01	0.126	0.737	6.3E-02
Station B												
Sal. (ppt)	0.234	0.895	3.7E-03	0.385	0.400	1.0E-01	0.262	0.298	1.6E-01	0.296	0.524	5.9E-02
Temp. (°C)	-0.008	0.337	1.4E-01	-0.163	0.693	2.4E-02	-0.025	0.506	6.4E-02	0.052	0.934	1.8E-03
Dens. (kg m ⁻³)	0.195	0.902	3.3E-03	0.375	0.431	9.1E-02	0.222	0.364	1.2E-01	0.226	0.525	5.9E-02
O ₂ (μmol l ⁻¹)	-1.315	0.954	1.0E-03	-0.525	0.918	2.5E-03	-1.294	0.909	2.9E-03	-1.382	0.909	2.9E-03
O ₂ (% air sat.)	-0.378	0.947	1.3E-03	-0.302	0.985	1.8E-04	-0.545	0.984	2.0E-04	-0.341	0.963	7.2E-04
Chl. (mg m ⁻³)	0.026	0.075	4.8E-01	-0.029	0.050	5.6E-01	0.113	0.543	5.4E-02	-0.078	0.448	8.4E-02
Chl.S (mg m ⁻³)	0.102	0.861	1.1E-02	0.074	0.813	1.9E-02	0.178	0.944	2.7E-03	-0.034	0.630	6.2E-02
Station bc												
Sal. (ppt)	0.103	0.976	1.8E-04	0.234	0.535	3.1E-02	0.322	0.846	3.5E-03	0.115	0.288	1.1E-01
Temp. (°C)	0.002	0.095	3.3E-01	-0.084	0.948	6.0E-04	-0.013	0.690	1.3E-02	0.008	0.382	6.6E-02
Dens. (kg m ⁻³)	0.091	0.980	1.3E-04	0.210	0.633	1.8E-02	0.261	0.866	2.7E-03	0.098	0.340	8.1E-02
O ₂ (μmol l ⁻¹)	-0.741	0.976	1.8E-04	-0.757	0.894	1.9E-03	-1.923	0.971	2.4E-04	-0.539	0.827	4.3E-03
O ₂ (% air sat.)	-0.222	0.979	1.5E-04	-0.356	0.972	2.2E-04	-0.813	0.964	3.4E-04	-0.158	0.973	2.1E-04
Chl. (mg m ⁻³)	0.026	0.335	8.3E-02	-0.019	0.048	4.8E-01	0.137	0.956	4.6E-04	0.032	0.671	1.4E-02
Chl.S (mg m ⁻³)	0.042	0.833	5.1E-03	0.027	0.802	6.9E-03	0.152	0.973	2.7E-04	0.032	0.722	1.3E-02
Station C												
Sal. (ppt)	0.047	0.898	1.3E-03	0.163	0.498	2.8E-02	0.141	0.221	1.2E-01	0.092	0.228	1.2E-01
Temp. (°C)	0.009	0.803	4.0E-03	-0.097	0.962	2.7E-04	-0.024	0.702	8.7E-03	-0.003	0.202	1.4E-01
Dens. (kg m ⁻³)	0.046	0.925	7.8E-04	0.161	0.630	1.4E-02	0.135	0.304	7.7E-02	0.083	0.299	7.9E-02
O ₂ (μmol l ⁻¹)	-0.647	0.990	3.3E-05	-0.678	0.946	4.6E-04	-1.727	0.943	5.0E-04	-0.590	0.795	4.3E-03
O ₂ (% air sat.)	-0.211	0.991	3.1E-05	-0.383	0.963	2.6E-04	-0.829	0.960	2.9E-04	-0.219	0.975	1.4E-04
Chl. (mg m ⁻³)	-0.013	0.015	6.5E-01	-0.016	0.077	3.3E-01	-0.025	0.045	4.5E-01	-0.014	0.056	4.0E-01
Chl.S (mg m ⁻³)	0.045	0.934	7.8E-04	0.015	0.813	4.4E-03	0.027	0.195	1.6E-01	0.012	0.491	3.5E-02

Table 2 B. Statistical comparisons of the vertical gradients (slopes) for the measured water column parameters between seasons using t-statistics. Black numbers indicate significant differences in the slope between the two seasons listed in the respective column label ($p < 0.05$). Ch. S indicates p -values for the subsurface chlorophyll gradient changes between seasons.

Parameter	Winter Spring	Winter Summer	Winter Fall	Spring Summer	Spring Fall	Summer Fall
	p	p	p	p	p	p
Station A						
Sal. (ppt)	6.9E-01	7.7E-02	9.9E-01	2.0E-01	7.2E-01	1.6E-01
Temp. (°C)	9.1E-01	1.3E-02	2.2E-01	3.2E-02	4.7E-01	2.5E-02
Dens. (kg m ⁻³)	6.5E-01	1.0E-01	9.9E-01	2.1E-01	7.0E-01	2.1E-01
O ₂ (μmol l ⁻¹)	9.1E-01	2.8E-02	5.9E-01	1.0E-01	6.7E-01	6.3E-02
O ₂ (% air sat.)	1.7E-01	3.9E-03	7.1E-01	8.6E-04	2.4E-01	2.9E-02
Chl. (mg m ⁻³)	8.9E-01	1.8E-01	4.4E-01	2.0E-01	7.2E-01	6.8E-02
Chl.S (mg m ⁻³)	5.1E-01	7.2E-01	1.2E-01	4.7E-01	8.1E-01	4.0E-01
Station ab						
Sal. (ppt)	3.8E-01	8.4E-01	5.9E-01	6.5E-01	9.8E-01	7.5E-01
Temp. (°C)	2.6E-02	4.7E-01	6.9E-03	7.8E-02	8.3E-01	3.6E-02
Dens. (kg m ⁻³)	3.5E-01	7.8E-01	5.3E-01	6.8E-01	9.4E-01	7.2E-01
O ₂ (μmol l ⁻¹)	8.5E-03	6.1E-05	4.2E-01	4.2E-07	8.3E-02	1.7E-01
O ₂ (% air sat.)	1.4E-03	7.0E-01	9.4E-01	8.1E-04	9.2E-02	7.6E-01
Chl. (mg m ⁻³)	1.6E-03	2.5E-02	2.8E-02	3.0E-01	8.9E-06	3.4E-04
Chl.S (mg m ⁻³)	3.1E-03	2.6E-02	3.9E-01	1.9E-01	1.2E-02	4.0E-02
Station B						
Sal. (ppt)	3.9E-01	8.5E-01	1.3E-01	5.8E-01	3.2E-01	1.8E-01
Temp. (°C)	1.0E-03	9.8E-02	4.0E-03	3.0E-03	3.6E-02	4.6E-02
Dens. (kg m ⁻³)	2.6E-01	8.0E-01	1.3E-01	4.2E-01	4.4E-01	1.8E-01
O ₂ (μmol l ⁻¹)	4.0E-02	7.4E-04	5.5E-01	1.7E-07	2.8E-01	6.5E-01
O ₂ (% air sat.)	1.7E-06	9.1E-01	3.8E-01	1.0E-04	5.1E-02	3.7E-01
Chl. (mg m ⁻³)	3.3E-01	9.7E-02	1.8E-04	2.7E-02	2.1E-04	9.5E-03
Chl.S (mg m ⁻³)	6.4E-02	2.1E-03	3.9E-02	7.6E-05	1.7E-02	2.1E-01
Station bc						
Sal. (ppt)	4.1E-02	5.3E-06	5.7E-02	2.3E-01	1.3E-01	2.0E-01
Temp. (°C)	3.1E-14	3.6E-05	4.4E-04	6.6E-12	2.4E-01	4.0E-03
Dens. (kg m ⁻³)	1.2E-02	2.9E-06	5.7E-02	3.5E-01	1.4E-01	1.9E-01
O ₂ (μmol l ⁻¹)	1.6E-07	4.9E-13	1.1E-01	3.6E-10	4.5E-01	4.7E-02
O ₂ (% air sat.)	2.0E-01	3.6E-12	8.1E-02	3.7E-11	1.0E-01	9.5E-01
Chl. (mg m ⁻³)	4.9E-03	6.9E-09	2.6E-07	4.2E-08	1.2E-07	4.4E-04
Chl.S (mg m ⁻³)	2.2E-02	7.7E-11	4.7E-03	9.5E-13	2.8E-03	9.4E-02
Station C						
Sal. (ppt)	8.4E-03	1.7E-01	4.0E-02	7.9E-01	8.3E-02	7.8E-02
Temp. (°C)	3.3E-19	5.8E-09	1.6E-04	5.8E-12	6.0E-02	1.9E-02
Dens. (kg m ⁻³)	8.6E-04	9.1E-02	4.1E-02	6.8E-01	9.8E-02	8.6E-02
O ₂ (μmol l ⁻¹)	1.1E-09	9.2E-15	1.0E-01	2.4E-10	5.6E-01	3.9E-02
O ₂ (% air sat.)	4.4E-04	5.5E-11	6.1E-02	1.5E-08	1.1E-01	8.1E-01
Chl. (mg m ⁻³)	3.3E-01	7.8E-01	3.7E-06	5.3E-01	1.2E-08	3.8E-06
Chl.S (mg m ⁻³)	1.2E-05	2.3E-01	5.0E-03	8.3E-01	2.8E-03	3.6E-03

Table 3. A: Slopes of the water column horizontal gradients of salinity, temperature, density, oxygen and chlorophyll for the four seasons. Grey text identifies slopes that are statistically not significant ($p > 0.05$). Chl. (B) lists values for the chlorophyll concentration in the boundary layer (0-1 m above seafloor). B: Statistical evaluation of the changes in horizontal gradients between seasons.

A	Winter			Spring			Summer			Fall		
	Slope	r^2	p	Slope	r^2	p	Slope	r^2	p	Slope	r^2	p
Salinity	0.24	0.41	5.9E-02	0.46	0.68	1.4E-02	0.39	0.58	2.4E-02	0.28	0.64	1.7E-02
Temp.	0.05	0.19	1.8E-01	-0.09	0.71	1.1E-02	0.00	0.01	7.8E-01	0.10	0.25	1.3E-01
Density	0.18	0.42	5.4E-02	0.39	0.70	1.1E-02	0.32	0.62	2.0E-02	0.22	0.69	1.2E-02
O ₂ Sat	-0.25	0.87	2.6E-03	-0.30	0.83	4.0E-03	-0.70	0.95	6.5E-04	-0.19	0.55	2.8E-02
Chl	-0.10	0.28	1.1E-01	-0.10	0.41	5.7E-02	-0.07	0.11	3.0E-01	-0.42	0.13	2.5E-01
Chl (B)	-0.21	0.85	2.5E-02	-0.12	0.52	1.7E-01	-0.19	0.81	3.7E-02	-0.27	0.70	7.9E-02
B												
	Winter	Winter	Winter	Spring	Spring	Summer						
	Spring	Summer	Fall	Summer	Fall	Fall						
	p	p	p	p	p	p						
Salinity	7.6E-02	2.1E-01	6.8E-01	6.2E-01	1.0E-01	3.1E-01						
Temp.	3.6E-04	9.3E-02	4.7E-01	3.6E-05	8.1E-04	4.8E-02						
Density	3.3E-02	1.6E-01	6.2E-01	4.5E-01	4.5E-02	2.4E-01						
O ₂ Sat	3.2E-01	9.2E-09	2.7E-01	4.2E-07	8.6E-02	4.6E-08						
Chl	9.7E-01	7.3E-01	2.9E-01	6.8E-01	2.9E-01	2.6E-01						
Chl (B)	6.2E-01	8.0E-01	4.7E-01	8.3E-01	2.5E-01	3.7E-01						

Table 4. A: Slopes of the horizontal gradients of NO_x, NH₃, PO₄, Si(OH)₄, TN, N/P in the surface water layer (0-1 m) for the four seasons. Grey text identifies slopes that are statistically not significant ($p > 0.05$).

Parameter	Winter			Spring			Summer			Fall		
	Slope	r ₂	p	Slope	r ₂	p	Slope	r ₂	p	Slope	r ₂	p
NO _x	0.004	0.202	4.5E-01	0.007	0.708	7.4E-02	-0.001	0.042	7.4E-01	0.004	0.154	5.1E-01
NH ₃	-0.027	0.788	4.4E-02	-0.001	0.012	8.6E-01	0.023	0.806	3.9E-02	-0.003	0.189	4.7E-01
DIN	-0.024	0.553	1.5E-01	0.006	0.341	3.0E-01	0.022	0.804	3.9E-02	0.001	0.006	9.0E-01
PO ₄	-0.003	0.685	8.4E-02	0.000	0.050	7.2E-01	-0.003	0.877	1.9E-02	-0.004	0.662	9.4E-02
Si(OH) ₄	-0.085	0.274	3.6E-01	-0.116	0.691	8.1E-02	-0.213	0.892	1.6E-02	-0.199	0.882	1.8E-02
N/P	0.220	0.395	2.6E-01	0.055	0.022	8.1E-01	0.475	0.898	1.4E-02	0.217	0.466	2.0E-01

	Winter	Winter	Winter	Spring	Spring	Summer
	Spring	Summer	Fall	Summer	Fall	Fall
	p	p	p	p	p	p
NO _x	5.6E-01	3.9E-01	9.9E-01	7.7E-02	6.2E-01	4.4E-01
NH ₃	2.4E-02	3.0E-03	3.1E-02	1.9E-02	6.8E-01	1.2E-02
DIN	6.5E-02	1.6E-02	1.4E-01	8.9E-02	6.1E-01	8.1E-02
PO ₄	8.7E-02	9.2E-01	4.4E-01	4.2E-02	6.3E-02	4.3E-01
Si(OH) ₄	7.5E-01	2.1E-01	2.6E-01	1.7E-01	2.2E-01	8.3E-01
N/P	5.6E-01	2.1E-01	9.9E-01	1.2E-01	5.4E-01	1.6E-01

Table 5. Comparisons of gross primary production rates and respiration rates in terms of oxygen production and consumption from previous studies. “SD” columns denote 1 standard deviation for the preceding column’s parameter.

Source	Date	Location	Depth (m)	n	GP P	SD	Resp mmol O ₂ m ⁻³ h ⁻¹	SD	Chla mgm ⁻³	O ₂ mmolm ⁻³
Jiang et al., 2011	31-Jun to 5-Aug-2008	Aodi, Taiwan	4.5	6 and 9 †	0.69	0.42	0.24	0.11	0.5	207
	4-Jun to 12-Jun 2008	NanwanBay, Taiwan	3	14 and 25 †	0.71	0.30	0.28	0.16		212
Williams 1998**	May 1989 and Jun 1991	NE Atlantic Ocean	10	29	0.44	0.08	0.28	0.25		
	Sep-1994	Arabian Sea	10	7	0.42	0.17	0.40	0.08		
	1990-1993	Mediterranean Sea	10	18	0.33	0.17	0.17	0.08		
	Sep-1984	N central Pacific	10	5	0.06	0.02	0.05	0.08		
Gubelit et al. 2010** ‡	2002-2006	Shore of Neva Bay estuary, Baltic Sea	0.5	3	79					30.2(Aug)-371(Jun)
Webster et al. 2002*	17-Dec-1997	Lake Illawarra, Australia, 34 30'S (brackish lagoon)	5		0.34				1.6	203
Gutierrez-Rodriguez et al. 2011 ***	2004-2005	Blanes Bay, Mediterranean, Spain	20	31	0.30	0.10	0.16	0.10	0.54	
Krause-Jensen et al. 2012 ** ‡	1980-2008	Limfjorden, Denmark, nutrient-replete basins	4.6		1.05				5	
	1980-2008	Limfjorden, Denmark, nutrient-rich basins	4.6		1.52				13	
Sallonet al. 2011 * ** ‡	Jun and Jul 2008	Amundsen Gulf, Beaufort Sea, Canada	100		0.05	0.03			0.89	
Daneriet al. 2012 *	Jan-07	Bay of Collumo, Chile, no bloom	10		3.04	0.82	0.72	0.20	2	
	Feb-07	Bay of Collumo, Chile, bloom	10		19.2 7	9.07	1.86	1.07	6.3	
Hargrave et al. 1983 *	summer 1979	Peck's Cove, Bay of Fundy, Canada	0.5	4	1.24	0.68	0.29 **		2.75	
	summer 1979	Minas Basin, Bay of Fundy, Canada	0.5	3	0.77	0.26			1.13	
Burford et al. 2012 ** ‡	Dec-08	Buffalo Creek, Darwin, Australia	1.6	3	4.75	3.65			90	90.6
	Oct 07 and Mar 08	Myrmidon Creek, Darwin Australia	4.6	6	0.18	0.11			2.68	163

	Oct 07 and Mar 08	Reference Creek, Darwin Australia	4.6	6	0.21	0.03		2.83	163
Chen et al. 2000* ** ‡	1993-1994	Offshore Louisiana, beyond continental shelf	0-200		0.03				
	1993-1994	Surface layer depth <25m Louisiana Coast	0-25	764	0.14	0.13		0.1-5.0	
Wanninkh of et al. 1997 **	Apr-96	W FL Shelf		27	0.14	0.4	0.06	0.3	
Yates et al. 2007**	Oct-2003	Tampa Bay	0.5	4	15.5		7.75	5	190
	Mar-2000	Florida Bay	0.5	3	8.84		4.42	<5	220
Vargo et al. 1987 *		West FL Shelf,							
** ‡	1980	nearshore	<20		0.27				
	1980	West FL Shelf, offshore	20-100		0.08			<0.3	
		West FL Shelf, nearshore during bloom event	6.4		1.83			2.5	
Murrell et al. 2009	summers 2003, 2004	Shoals Pensacola Bay upper water column	0.7	7	0.66	0.27	0.48	0.16	6.9
	summers 2003, 2004	Channel: Pensacola Bay upper water column	1.125	9	1.04	0.47	0.74	0.30	9.0
	summers 2003, 2005	Channel: Pensacola Bay lower water column	3.375	8	0.35	0.37	0.44	0.33	4.6
Del Castillo et al. 2000 *	Mar-95	Apalachicola River transect, 22 km offshore			1.63			1	
	Mar-95	Apalachicola River transect, 56 km offshore			0.33			0.5	
Mortazavi et al. 2000 *** ‡	1993-1996	Apalachicola Bay, Florida	8		1.13			1.63	
Hitchcock et al. 2000	Apr-96	W FL shelf, a little SE of K- tower: 29 N, 84 W	25		0.33	0.75	0.21	0.5	1.8
This study	2008-2010	Site A	5	15	1.87	1.02	0.99	0.38	8.88
	2008-2010	Site B	10	11	1.72	0.53	0.96	0.62	5.67
	2008-2010	Site C	18	13	1.33	0.57	0.77	0.28	1.99

* calculated from carbon, assumes a PQ of 1.3

** calculated from rate per day, assumes photosynthesis over 12 hours a day

† first n is for GPP, second n is for respiration

‡ calculated from depth-integrated data, average of 100 m if >100 m

Figure legends

Figure 1. A: Locations of the stations along the study transect. Bottom mounted instruments were placed at Stations A, B and C (black circles). Additional vertical water column profiling was done at Stations ab and bc (grey circles). B: Station mean water depth (open circles) and mean depth of the wave base (solid circles) with distance from shore. The wave base is defined as the depth at which the wave orbital water movement decreased to $e^{-\pi} \approx 0.04$ or 4% of the surface value (Dean and Dalrymple, 1991) and is estimated as wavelength/2. Whiskers denote 1 SD. C: Apalachicola river discharge 2007-2011: Maximum March $800 \text{ m}^3 \text{ s}^{-1}$, minimum August $180 \text{ m}^3 \text{ s}^{-1}$, data from USGS <http://waterdata.usgs.gov/nwis/>; black line indicates best fit 4th-order polynomial function.

Figure 2. Seasonal means of water column profiles measured at the 5 stations along the transect during the study period (winter n = 6, spring n = 10, summer n = 10, and fall n = 5). All data from each season over the study period were averaged within each meter-depth bin. The official end dates of the respective seasons (solstice or equinox) were used to assign data to seasons.

Figure 3. A: Average horizontal gradients measured at the 5 stations along the transect (winter n = 6, spring n = 10, summer n = 10, and fall n = 5). Seasonal trends are shown for the surface layer (grey triangles, 0-1 m), mid water layer (white circles) and boundary layer (black squares, 0-1 m above seafloor). B: gradient change graphs depict the slope of

least squares linear regressions in the measured parameters over distance from shore in km between seasons for surface, mid, and bottom water. The error bars depict 1 standard deviation.

Figure 4. Slopes of the average annual vertical oxygen profiles along the transect. The grey area depicts the depth range (< 8 m) where the wave orbital motion was strong enough to resuspend the sediment. White circles represent shallower stations. Black circles represent deeper stations (difference between slopes: standard error:0.057, $t = 1.3967$, $df = 27$: $p = 0.1738$)

Figure 5. Spatial and temporal distribution of average Chl a concentrations integrated over the entire water column along the transect. Each horizontal layer presents measurements made in the year indicated on the y-axis. The dotted vertical helper lines indicate an offshore bloom in the late winter (February, first dotted reference line on the left), a spring bloom in March/April with a maximum near the coast, an early summer maximum more offshore and a fall bloom in October/November.

Figure 6. Seasonal nutrient distributions in the surface water layer (0-1 m) along the transect. Black circles: DIN, grey circles NH_4^+ , white circles: NO_x , black triangles: PO_4^{3-} , white diamonds: Si(OH)_4 . The large symbols at the left side of each figure (at km = 1) represent the respective nutrient concentrations in Apalachicola Bay, and for DIN and

silicic acid scaled according to the right axes of the respective graphs (Apalachicola Bay data are from the Apalachicola Estuarine Research Reserve, available at <http://cdmo.baruch.sc.edu>).

Figure 7. Irradiation profiles measured on 28 July 2009 along the transect and associated average attenuation coefficients. Some measurements in the lower section of the profile at station C failed due to sensor contamination. Surface irradiation data from the Apalachicola Estuarine Research Reserve are available at <http://cdmo.baruch.sc.edu>.

Figure 8. Calculated average vertical and horizontal profiles of oxygen production and oxygen consumption during the study for a realistic irradiation of $200 \mu\text{E m}^{-2} \text{s}^{-1}$. The productivity rates shown are gross productivity. Top figure: Open circles: Station A, grey circles: Station B, black circles: Station C. Error bars are standard deviation. Station A n = 15 (bottom n = 8 and surface n = 7), Station B n = 12 (bottom mid and surface n = 4), and Station C n = 15 (bottom mid and surface n = 5) Bottom figure: open circles: surface water, grey circles: mid water, black circles: bottom water.

Figure 9. Water column production/respiration ratios plotted for the four seasons. P/R ratios did not differ significantly between surface, mid water and bottom layers and seasons. The slopes of the regression lines were statistically significant except for fall

(Winter: $df = 18$, $p = 0.0002$, $p < 0.05$, Spring: $df = 12$, $p = 0.0231$, $p < 0.05$, Summer: $df = 15$, $p = 0.0060$, $p < 0.05$, Fall: $df = 10$, $p = 0.7718$, $p > 0.05$).

Figure 10. Oxygen production in water samples collected in July 2011 at Stations A (white triangles), B (grey circles) and C (black squares) exposed to different irradiance intensities. Production rates were binned for irradiance intensities $< 500 \mu\text{E m}^{-2} \text{ s}^{-1}$, $500\text{--}1,000 \mu\text{E m}^{-2} \text{ s}^{-1}$, and $> 1,000 \mu\text{E m}^{-2} \text{ s}^{-1}$. For all stations, $n = 15$ of low irradiance, $n = 6$ for mid-irradiance (except for surface water from Stations B and C, where $n = 3$), and $n = 3$ for high irradiance.

Figure 11 A and B: Relationships between oxygen and chlorophyll content of the water for A: the surface layers ($< 3 \text{ m}$, no surface layer trend at Station A) and B: subsurface layers ($\geq 3 \text{ m}$). C and D: Relationships between oxygen and chlorophyll content in the subsurface layers ($\geq 3 \text{ m}$) at Stations A (white triangles), ab (black triangles), B (grey squares), bc (grey circles), and C (black circles) for C: Winter and D: Summer. Note different Y-axes in all graphs.

Figure 12. Primary production estimates for the entire water column (black squares, right axis), and surface (white circles), mid-water (grey circles) and boundary layers (black circles) along the transect for a sunny day in July. The estimates are based on a 12 h light period, the irradiance profiles shown in Fig. 7 and the irradiance/production relationships shown in Fig. 10. Error bars depict standard deviation of estimates based on minimum, average and maximum irradiance/production ratios.

Figures

Figure 1, Santema et al.

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