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Pelagic community respiration on the continental shelf off Georgia, USA

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Abstract The South Atlantic Bight (SAB) has been a focus for the study of continental shelf ecosystem respiration during the past two decades. However, two questions concerning respiration in this area have yet to be answered. First, why do previous estimates of respiration in the SAB exceed measured carbon fixation rates by almost an order of magnitude? Second, considering that bacteria are responsible for most of the pelagic community respiration in the SAB, why is respiration almost uniform from the coastline to the shelf break, while bacterial production estimates decrease offshore? This study addresses these critical questions by presenting new pelagic community respiration data that were collected across the entire width of the continental shelf off Georgia, USA from June 2003 to May 2006. The respiration was calculated as in vitro changes of dissolved oxygen and dissolved inorganic carbon concentrations during deck incubations. The measured respiration rates ranged from 0.3($\pm$0.1) to 21.2($\pm$1.4) mmol m^{-3} day^{-1}. They followed a clear seasonal pattern, being lowest over the entire shelf in winter and reaching maxima in summer. Summertime respiration rates were highest on the inner shelf and decreased with distance offshore. Consistent with this trend, bacterial abundance measurements taken during the sampling month of July 2005 followed a pattern of seaward decline. The SAB organic carbon fluxes calculated from the respiration data are close to the estimates for primary production, which resolves a long-standing mystery regarding perceived carbon imbalance in the SAB.

Keywords Respiration · Continental shelf · Southeastern United States · South Atlantic Bight · Bacteria · Organic carbon flux

Abbreviations

BOD	Biochemical oxygen demand
CFZ	Coastal frontal zone
DIC	Dissolved inorganic carbon
DO	Dissolved oxygen
pCO_2	Partial pressure of carbon dioxide
RQ	Respiratory quotient
SAB	South Atlantic Bight
SSS	Sea surface salinity
SST	Sea surface temperature

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Introduction

Most organic carbon flux studies on continental shelves have focused solely on carbon fixation processes due to the relative ease of the ^{14}C technique (Steemann-Nielsen 1952) for measuring primary production (Jahnke and Craven 1995; del Giorgio and Williams 2005). However, estimates of primary production on continental shelves are often subject to large uncertainties and errors. These uncertainties arise from the fact that continental shelf ecosystem production is strongly dependent on nutrient intrusions that are highly variable in magnitude and patchy in distribution (Yoder et al. 1985). Several assumptions related to the frequency and extent of such intrusions have to be made in order to estimate annual primary production (Lee et al. 1991; Menzel 1993).

Recent studies have shown that although metabolic systems are charged up by intermittent photosynthesis, they are most likely discharged by steady respiration (Aŕistegui and Harrison 2002; Karl et al. 2003; Williams and del Giorgio 2005). Because respiration integrates all organic carbon sources to the ecosystem both spatially and temporally, it is likely a better index for the flow of organic carbon through the biota (Jahnke and Craven 1995; Williams and del Giorgio 2005). More importantly, understanding decomposition processes (in addition to fixation processes) is an essential component in the efforts to understand coastal carbon cycling.

Richly studied relative to the meager global database of continental shelf respiration rates (Williams and del Giorgio 2005), the South Atlantic Bight (SAB) has been the location for three shelf-wide respiration studies (Griffith et al. 1990; Griffith and Pomeroy 1995; Pomeroy et al. 2000). Despite intensive study, unanswered questions remain for this region (Menzel 1993). First, considering that bacteria are responsible for most of the respiration (Hopkinson et al. 1989; Griffith et al. 1990), the uniformly high rates of respiration from onshore to offshore (Pomeroy et al. 2000) in summer are hard to reconcile with a seaward decrease of bacterial production (Griffith et al. 1990). Second, estimates of water column respiration in the SAB are so much (6–20 times) higher than primary production estimates that it is impossible to find adequate allochthonous organic carbon supply to account for the difference (Yoder 1985; Menzel 1993; Pomeroy et al. 2000).

This study set out to try to resolve the carbon budget discrepancies by measuring respiration across the region with greater spatial and temporal resolution and using what we argue are improved methods. Specifically, we measured respiration in larger, submerged bottles following changes in dissolved oxygen (verified with measurements of changes in dissolved inorganic carbon) over 24 h. Further, we measured respiration along three transects on nine cruises spanning all four seasons to assess spatial and temporal variability. Following these efforts, the carbon budget of the SAB may not be as imbalanced as previously thought. This study is also an important part of an overall effort to understand controls on sea surface pCO_2 and the associated air-sea CO_2 fluxes in the SAB shelf (Jiang et al. 2008a; Jiang et al. 2009; Cai, unpublished data).

Study site and methods

Site description

The climate of the continental shelf off Georgia, USA is subtropical with a surface water temperature range of 10–30°C. The shallow shelf extends 130 km out to the shelf break where the water depth is about 60 m. The continental shelf has traditionally been divided into three regimes: the inner shelf, from the coastline to the 20-m isobath (roughly 45 km offshore); the middle shelf, from the 20-m to the 40-m isobath (roughly 90 km offshore); and the outer shelf, from the 40-m to the 100-m isobath (roughly 130 km offshore) (Fig. 1). The north-flowing Gulf Stream runs along the shelf break.

The coastline features a series of barrier islands, with extensive salt marshes between the barrier islands and the coastline (Menzel 1993). Tides flood and drain the salt marsh estuaries twice daily and transport sediments and organic materials back and forth between the continental shelf and the estuaries (Hopkinson 1985). From north to south, the Savannah, Ogeechee, and Altamaha Rivers supply freshwater to this region (Fig. 1). For most of the year, a coastal frontal zone (CFZ) located 10–30 km offshore separates a low salinity coastal current from

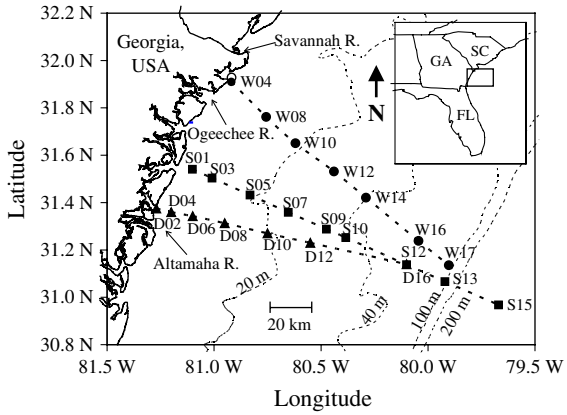

Fig. 1 Study area is the continental shelf off Georgia, USA. Respiration was measured on three transects: *filled circles* are the stations on W-transect (starting from Wassaw Sound), *filled squares* are the stations on S-transect (starting from Sapelo Sound), and *filled triangles* are the stations on D-transect (starting from Doboy Sound)

waters further offshore (Blanton 1981). The CFZ presents a dynamic barrier to the seaward transport of dissolved and particulate materials introduced from the rivers and estuaries.

Shelf water shoreward of the CFZ is turbid, containing accumulated discharge of the river and water exchanged with intertidal salt marshes (Jiang et al. 2008b). Production here is mainly driven by nutrients that are recycled (Hanson et al. 1990) and resuspended from the sediments (Jahnke et al. 2005). The middle and outer shelves are strongly influenced by the Gulf Stream. Intrusions can be induced by Gulf Stream meanders and eddies (Atkinson et al. 1984). During fall, winter, and spring, cross-shelf density gradients restrict the intruded water to the outer shelf (Atkinson et al. 1984). In summer, when aided by upwelling-favorable winds, the offshore water may penetrate to the middle or even inner shelf as subsurface intrusions and stay on the shelf for weeks (Atkinson et al. 1984).

Materials and methods

A total of nine cruises were conducted along three transects (Fig. 1) to measure pelagic community respiration on the continental shelf off Georgia. The surveys were carried out on W-transect in June 2003, June 2004, and October 2004; on D-transect in August 2003; and on S-transect in January 2005, March 2005, July 2005, October 2005, and May 2006 (Fig. 1). These three nearby transects are viewed to be similar (except for the very nearshore areas) in their biogeochemical properties according to a study that covered a more extensive area between North Carolina and Florida (Jiang et al. 2008a). They showed much smaller alongshore variations compared to those in the cross-shelf direction (Jiang et al. 2008a). Not all stations were sampled for respiration during all cruises due to personnel constraints. Surface water temperature and salinity were recorded continuously with an onboard flow-through system on the research vessel. Vertical temperature and salinity profiles were measured at each sampling station with a Sea-Bird Electronics SBE-25 CTD. In August 2003, sea surface pCO_2 (partial pressure of carbon dioxide) was also measured on D-transect. A detailed description of how pCO_2 was determined can be found in Jiang et al. (2008a).

Respiration measurements were performed onboard. Water samples were taken using 30-l Niskin bottles from the surface. The water was then transferred into six 300-ml black rubber-covered BOD bottles (for DO measurement) and six 250-ml glass bottles (for DIC measurement). Three of the 300-ml BOD and three of the 250-ml glass bottles were killed immediately with 150 and 125 µl of saturated mercuric chloride ($HgCl_2$) solution, respectively. Stoppers with pointed ends were used to avoid bubbles in all bottles. The 250-ml glass bottles were wrapped with aluminum foil. Then all the bottles were incubated dark for 24 h in coolers through which in situ seawater continuously flowed. The duration of the incubation was chosen based on time course measurements showing linear decreases in DO over 24 h (Fig. 2). In order to avoid contamination, the killed and live samples were incubated in separate coolers.

At the end of incubation, 125 µl of saturated mercuric chloride reagent was added to the three non-preserved 250-ml glass bottles. Then, all six 250-ml glass bottles were stored in a refrigerator on the ship and analyzed for DIC concentration in the lab within 2 days after each cruise using an automated DIC analyzer with a precision of 0.1% (Cai and Wang 1998). The changes of DO concentration during incubation in the 300-ml BOD bottles were measured onboard using a spectrophotometric Winkler method (Pai et al. 1993). At the end of incubation, all BOD

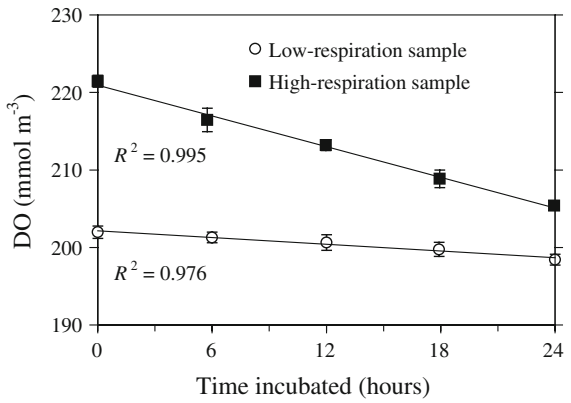

Fig. 2 Time courses of dissolved oxygen concentration during incubation (examples). *Filled squares* show the dissolved oxygen change for a high-respiration water sample and *open circles* show a low-respiration water sample. The high-respiration sample was collected from Station W04 on 20 June 2005 (Fig. 1); and the low-respiration sample was collected from a station off Cape Canaveral, FL (Latitude: 28.52N, Longitude: 80.48W) on 3 August 2005

bottles (i.e., live and killed samples) were immediately fixed by adding 2.5 ml of manganese chloride and 2.5 ml of alkaline iodide reagents. After being vigorously shaken for about 1 min, the BOD bottles were stored in the dark. When most of the flocculation had settled, the bottles were reopened and 2.5 ml of sulfuric acid solution was added. The mixture was then gently stirred with a magnetic stirrer until all the precipitate had dissolved. Absorbance was measured onboard within 3 min using a Shimadzu UV-1700 spectrophotometer. The spectrophotometric Winkler method has a precision of 0.1% and a detection limit of 0.25 mmol m^{-3} for the onboard measurement.

During the July 2005 cruise, bacterial abundance samples were collected on S-transect at the same stations where respiration was measured (except for the two farthermost stations). Duplicate samples from each Niskin bottle were immediately fixed with formalin (2% formaldehyde, final concentration) and kept refrigerated. Using gentle vacuum pressure, cells were collected onto polycarbonate membrane filters (0.2 μm pore size). Duplicate filters for each sample were stained for several minutes with DAPI (4′,6′-diamidino-2-phenylindole), and bacterial counts on 20 random fields (about 20 cells per field) were performed using an epifluorescence microscope (Yager et al. 2001). Duplicate filters usually agreed to within 10%. Reported abundances are the average of duplicate samples.

To calculate the organic carbon flux in the SAB, the respiration data of each survey were linearly interpolated from the coast to the shelf break with a resolution of 0.1 km. The mean respiration rate per unit of area (R_{mean}, unit: mmol m^{-2} day^{-1}) in the sampling month was calculated as:

$$R_{\text{mean}} = \frac{\sum_{i=1}^{n} R_i d_i}{n} \quad (1)$$

where R_i is the respiration value at point i, which is derived from linear interpolation (unit: mmol m^{-3} day^{-1}), d_i is the corresponding water depth (unit: m). Then the calculated R_{mean} was multiplied by the total area of the SAB (90,600 km^2, Menzel 1993) to get the organic carbon flux in the SAB. R_{mean} in months when repeated surveys were conducted was calculated as the average of all the surveys in that month. R_{mean} in months when no surveys were available were approximated from measurements in adjacent months based on linear inter-seasonal interpolation. Finally, the annual respiration rate was calculated as the average of all 12 months.

Results

Hydrographic data

Sea surface temperature (SST) on the continental shelf off Georgia showed large cross-shelf gradients in winter and was relatively uniform over the whole shelf in summer (Fig. 3). In winter months (January and March 2005), temperature was lowest on the inner shelf (13–14°C) and increased towards the outer shelf (20–25°C). In summer months (June 2003, August 2003, June 2004, and July 2005), SST across the whole continental shelf was between 27 and 31°C, without much spatial variation. In October 2004 and October 2005, the SST dropped slightly to 25–27°C. Sea surface salinity (SSS) measurements (Fig. 3) confirm the existence of the CFZ near shore (10–30 km offshore). In all sampling months, SSS was lowest close to shore (25–33) and increased sharply towards the open ocean value (36.5) at the CFZ. SSS on the inner shelf showed the greatest seasonal variation.

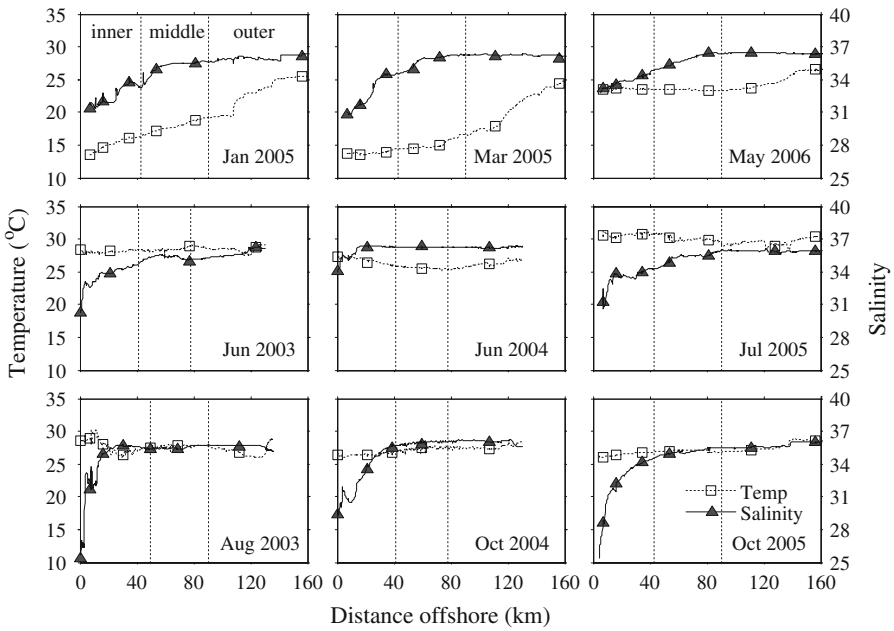

Fig. 3 Spatial distributions of sea surface salinity and temperature on the continental shelf off Georgia. *Filled triangles* are the sea surface salinity on the sampling stations, and *solid lines* are the underway sea surface salinity. *Open squares* are the sea surface temperature on the sampling stations, and *dotted lines* are the underway sea surface temperature. The *x*-axis is the seaward distance from the coastline. *Vertical dotted lines* separate the inner, middle, and outer shelf

Vertical distributions of temperature and salinity show that the shelf was stratified from June to August, and well-mixed in other months (Fig. 4). During June 2003, August 2003, June 2004, and, July 2005, stratifications can be clearly seen from the temperature data, with warm surface water staying above cold bottom water. Stratification was particularly evident in August 2003 when one of the strongest bottom water penetrations in years was observed in the SAB. During October 2004, January 2005, March 2005, October 2005, and May 2006, the shelf was well-mixed (Fig. 4).

Respiratory quotient

Respiration rates calculated from DIC and DO generally agreed. The respiratory quotient (RQ), which is the ratio of CO_2 evolution to O_2 consumption, showed no clear seasonal or spatial pattern. Respiration rates measured from DIC were plotted against those from DO, and the regressed RQ value was 1.09 ± 0.17 (Fig. 5), not significantly different from 1 and close to the range (0.9–1.1) as reported by Hopkinson (1985) for a nearshore station in the same area. Since the DO and DIC based respiration rates were not significantly different, we averaged them for all analyses, unless pointed out otherwise.

Respiration rates

The measured respiration rates in all sampling months ranged from 0.3(±0.1) to 21.2(±1.4) mmol m^{-3} day^{-1} (Fig. 6). Wintertime (January and March 2005) respiration rates were very low [0.3(±0.1)–3.3(±0.8) mmol m^{-3} day^{-1}] and showed no systematic variation from the inner shelf to the Gulf Stream (Fig. 6). However, large cross-shelf gradients of respiration rates were seen from May to October. At this time of the year, respiration rates on the inner shelf were much greater than those on the middle and outer shelves (Fig. 6). During August 2003, a middle shelf respiration maximum were seen at about 40–60 km offshore (Fig. 6).

Respiration rates in this area showed large seasonal variation, with the magnitude of seasonal variation decreasing with distance offshore. On the inner shelf, respiration rates in the summer months of June through August [15.4(±2.5)–21.2(±1.4) mmol m^{-3} day^{-1}] were nearly an order of magnitude higher than those in winter [2.6(±1.1)–3.2(±0.5) mmol m^{-3} day^{-1}] (Fig. 6). In contrast, the respiration rates on the outer shelf did not show much seasonal variation (Fig. 6).

Summertime respiration rates were inversely correlated with sea surface salinity (Fig. 7a), showing

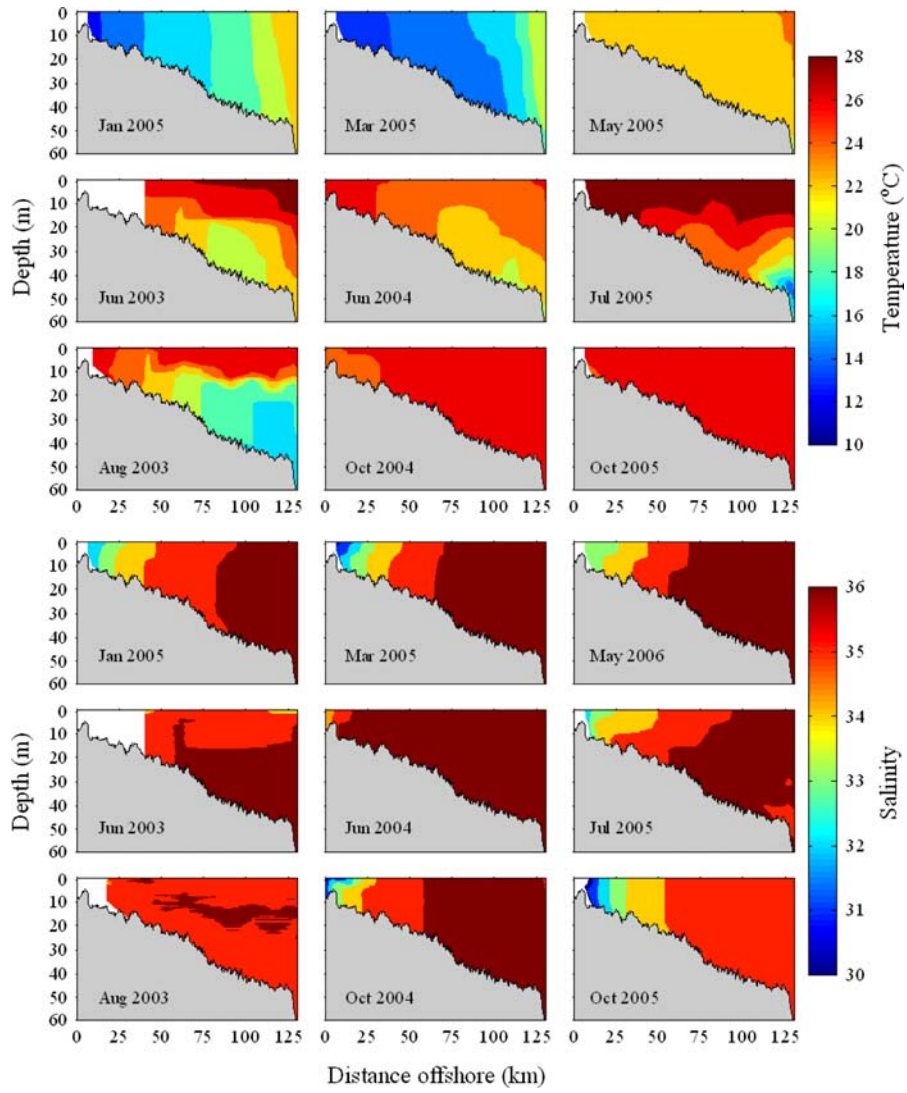

Fig. 4 Vertical distributions of temperature and salinity on the continental shelf off Georgia during all sampling months. The *upper nine panels* show temperature, and the *lower nine panels* show salinity

that freshwater supply, likely rich in terrestrial matter, strongly influences the respiration on the inner shelf. In contrast, wintertime respiration rate (January and March 2005) did not show a clear relationship with salinity (Fig. 7b).

The inner shelf respiration rate exhibited a good logarithmic relationship with sea surface temperature (Q_{10}, the factor by which the rate increases for every 10-degree temperature rise, was 3.0 ± 1.4), suggesting that temperature played an important role in controlling the seasonal variation of respiration (Fig. 8a). On the outer shelf, however, the respiration rates were much less dependent on the relatively stable SST (24–31°C) (Fig. 8b).

Bacteria

Bacterial abundance ranged from 0.36(±0.01) to 4.95(±0.23) × 10^6 cells ml^{-1}. It was highest nearshore and decreased with distance from the coastline (Fig. 9a). Where samples were collected in tandem, the offshore decrease in bacterial abundance accounted for much of the cross-shelf variability in pelagic community respiration ($R^2 = 0.992$; Fig. 9b).

Regional fluxes for SAB

Our calculated organic carbon flux through respiration in the SAB is 28(±5) × 10^{12} gC $year^{-1}$, which

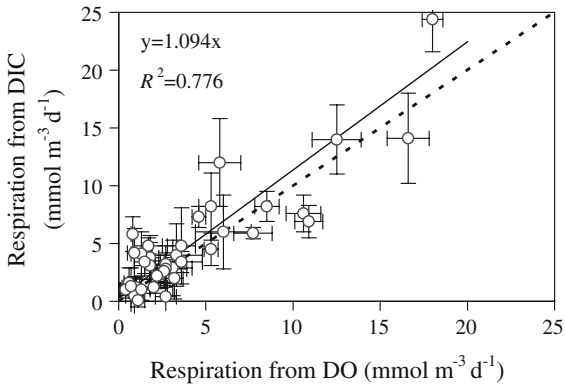

Fig. 5 Respiration rates measured from dissolved inorganic carbon plotted against those measured from dissolved oxygen. The *solid line* is from Model II regression of the data, and the *dotted line* represents unity of the two variables

is smaller than the estimate based on primary production (35×10^{12} gC year^{-1}, Yoder 1985) (Table 1). When benthic respiration (Jahnke et al. 2000) is added, the total organic carbon flux through respiration (both water column and benthic) in the SAB is $45(\pm 10) \times 10^{12}$ gC year^{-1}. This is not significantly different from the total organic carbon production (water column + benthic primary production) of 44×10^{12} gC year^{-1}, given the uncertainties involved (Table 1).

However, one needs to keep in mind that the flux calculation was based on dark incubation only, and respiration in the light could be higher than that in the dark (Michelou et al. 2007). The calculation also assumed uniform respiration rate from the surface to the bottom, which may not be the case in the field (especially during summer when stratification occurs on the shelf). The simple average of respiration in each month without consideration of the frequency of subsurface intrusions may also cause uncertainties.

Discussion

Comparison with earlier studies

The results of this study differ from those of previous studies (Table 2). First, our summertime respiration rates decrease quickly offshore, with the inner shelf respiration rates being close to those in the nearby estuaries (Pomeroy et al. 2000; Cai, unpublished data) and the outer shelf respiration rates approaching to the same level as those in the open ocean (Robinson et al. 2002; Maixandeau et al. 2005; Morán et al. 2007). This spatial trend is similar to those recently observed in other continental shelves (e.g., northern Mediterranean continental shelf, La

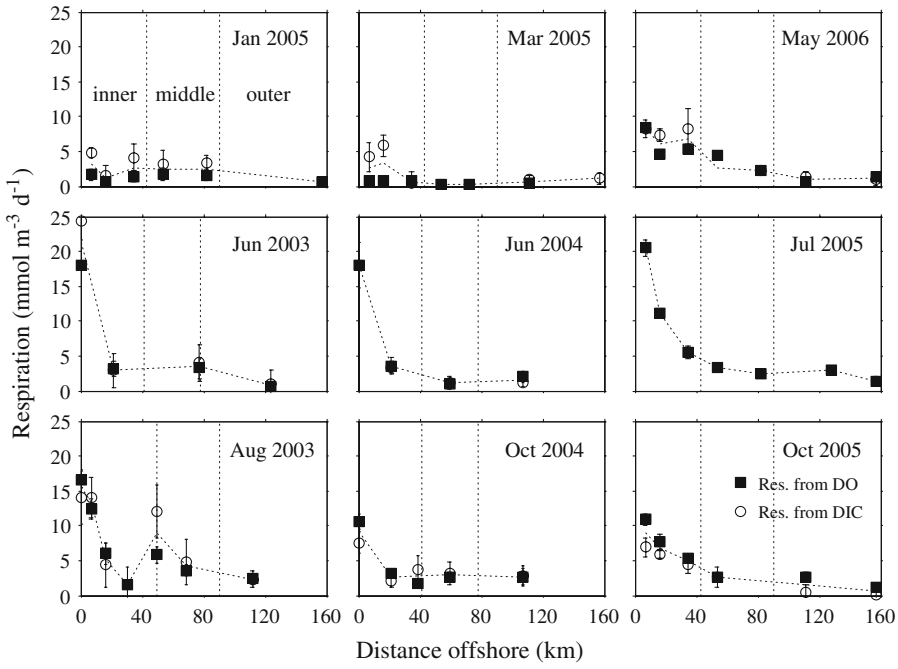

Fig. 6 Spatial distributions of surface water pelagic community respiration on the continental shelf off Georgia. *Filled squares* are respiration rates from dissolved oxygen measurements, and *open circles* are respiration rates from dissolved inorganic carbon measurements. The *dotted lines* connect the averages of the dissolved oxygen and dissolved inorganic carbon respiration rates. The *x*-axis is the seaward distance from the coastline. *Vertical dotted lines* separate the inner, middle, and outer shelf

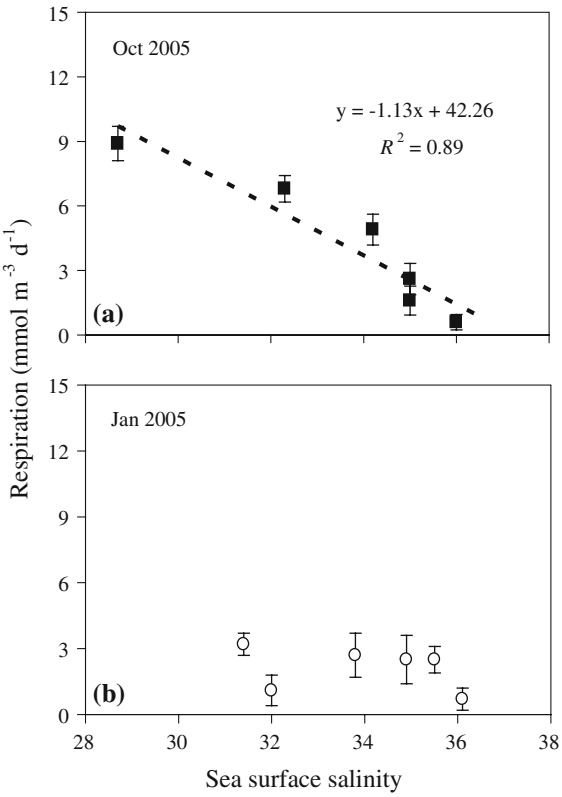

Fig. 7 Relationships between respiration rate and sea surface salinity in **a** October 2005 (warm month) and **b** January 2005 (cold month). The *dashed line* in **a** is from linear regression

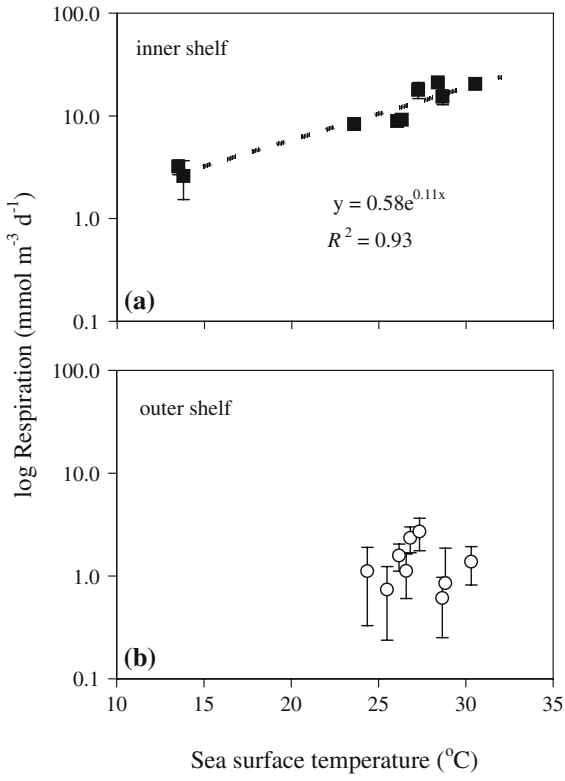

Fig. 8 Relationships between respiration rate and sea surface temperature on **a** the inner shelf and **b** the outer shelf. The inner shelf data is from the most close-to-shore station, and the outer shelf data is from the most offshore station. *Y*-axis is in logarithm scale. The *dashed line* in **a** is from exponential regression

Ferla et al. 2006; East China Sea, Chen et al. 2006), but contrasts sharply with the largely uniform onshore-offshore summertime respiration rates measured by Pomeroy et al. (2000) (Table 2). Second, our inner shelf respiration rates show a seasonal variation (the inner shelf respiration rates in summer were almost an order of magnitude higher than in winter) as large as that in the nearby estuaries (Pomeroy et al. 2000; Cai, unpublished data). In contrast, the inner shelf respiration rates of Pomeroy et al. (2000) are almost invariant throughout the year (Table 2).

Finally, our overall respiration rates are considerably lower than those of Griffith et al. (1990) (Table 2). In the following, we will discuss the methodological differences that might contribute to the discrepancies between our respiration results and those of earlier studies.

The three prior shelf-wide respiration studies in the SAB were all based on in vitro incubations of seawater and the ensuing changes in DO concentration. However, a variety of different methods were used. Griffith et al. (1990) and Griffith and Pomeroy (1995) incubated their samples in 45-ml chambers for $<$2 h and monitored the DO change using a Nester electrode, while Pomeroy et al. (2000) incubated their samples in 125-ml glass bottles within a incubator for 12 h and measured the DO changes using Winkler titration. Studies have shown that electrodes could consume oxygen and thus overestimate respiration (McKinnon et al. 2007), perhaps explaining the higher rates measured by Griffith et al. (1990) and Griffith and Pomeroy (1995). The method of Pomeroy et al. (2000), however, could suffer from nonlinear DO decrease during incubation (Pomeroy et al. 1994). Since the reported average values in Pomeroy et al. (2000) are a combination of electrode-based data that were previously reported in Griffith and

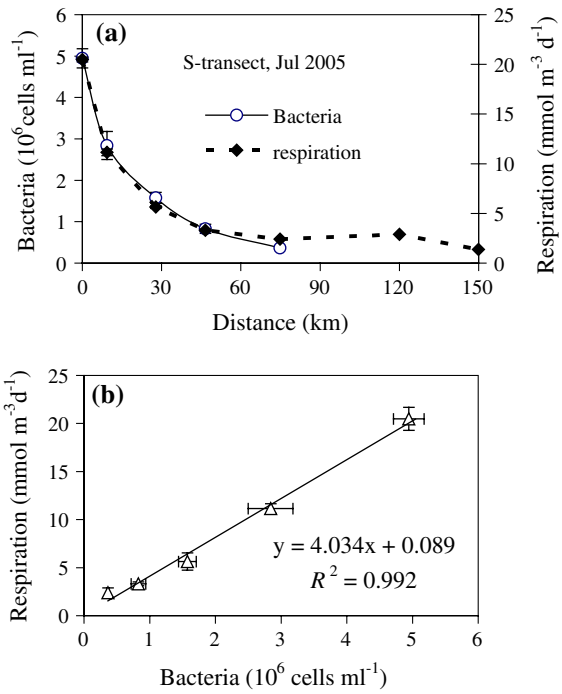

Fig. 9 Respiration rate and concentration of bacteria on S-transect in July 2005. **a** Shows the spatial distributions of respiration rate and concentration of bacteria. The *x*-axis is the seaward distance from the coastline. **b** Shows the relationship between respiration rate and concentration of bacteria. The *solid line* in **b** is from Model II regression

Pomeroy (1995) and newer data based on the Winkler method, the higher average values could again be due to the methods. Supporting this idea is the fact that the Winkler-based estuarine respiration rates reported by Pomeroy et al. (2000) are comparable with and have similar seasonal patterns as our inner shelf rates.

Another difference between our method and those of the prior studies is that the early respiration studies in this area all measured DO concentrations at the beginning and the end of the incubation (Griffith et al. 1990; Griffith and Pomeroy 1995; Pomeroy et al. 2000), while we used killed control and measured the live samples as well as the control together at the end of the incubation. The advantage of our method is that any possible problems associated with non-respiratory uptake of O_2 (Pamatmat 1997) or instrument drift were effectively avoided. Although our preliminary experiments did not show significant differences between the initial DO concentrations and those of $HgCl_2$-killed samples (data not shown), more systematic comparisons are needed to investigate this issue.

There are other differences between our method and those of the earlier studies. First, we used larger incubation bottles (~300 ml), as studies suggest that the linearity of oxygen uptake increases with increasing container size (Hopkinson 1985). Second, we kept the BOD bottles under water inside in situ seawater flowed-through coolers instead of keeping them inside dry incubators, as neck-drying of BOD bottles during incubation could be a serious problem for DO measurement (Labasque et al. 2004). Third, we incubated the samples longer (24 h) to minimize the error due to small DO changes in short incubations. Finally, our DO based results are verified by DIC based measurements from independent bottle incubations, and the spatial and seasonal variations of the respiration results are more consistent with other biogeochemical processes, as will be discussed below.

Table 1 Organic carbon fluxes estimated from primary production and respiration in the SAB (surface area = 90,600 km^2, Menzel 1993) (units: 10^{12} gC year^{-1})

Processes	Organic carbon fluxes	References
Water column primary production	35 ± ?	Menzel (1993)
Benthic primary production[a,b]	9 ± 6[a,b]	Jahnke et al. (2005)
Total primary production	44 ± *E* (*E* > 6)	–
Water column respiration	28 ± 5	This study
Benthic respiration[a]	17 ± 9[a]	Jahnke et al. (2005)
Total respiration	45 ± 10	–

[a] Base on study of the middle shelf

[b] Because light does not penetrate to the bottom on the inner shelf; when benthic primary production over the SAB was estimated, the surface area used (61,700 km^2) did not include the inner shelf

Table 2 Pelagic community respiration on the continental shelf off Georgia: comparison between previous investigations and the current study

Respiration rates (mmol m^{-3} day^{-1})						References
Inner shelf		Middle shelf		Outer shelf		
Summer	Winter	Summer	Winter	Summer	Winter	
43.1	8.3	ND	ND	ND	ND	Hopkinson (1985)
30.0	7.6	ND	ND	ND	ND	Hopkinson et al. (1989)
148–190	ND	48–115	ND	30–96	ND	Griffith et al. (1990)
74.4	11.5	67.2	2.0	62.4	2.5	Griffith and Pomeroy (1995)
22.8 ± 1.9	26.4 ± 3.4	31.2 ± 6.7	16.8 ± 2.6	24.0 ± 7.2	7.2 ± 2.4	Pomeroy et al. (2000)
15.5 ± 5.4	2.9 ± 0.5	2.5 ± 0.9/8.9 ± 2.7[a]	1.3 ± 1.4	1.8 ± 0.8	0.8 ± 0.5	This study

ND no data

[a] The middle shelf respiration rates in summer differed greatly depending on whether subsurface intrusions were present or not, here we list the respiration results for the two scenarios

Respiration versus temperature and supply of organic matter

The respiration patterns observed in this study are similar to those usually observed, with the seasonal temperature cycle and supply of organic matter probably being the most important controlling factors (Hopkinson and Smith 2005). This study shows that respiration rates on the inner shelf changed with season at a much greater magnitude than those on the outer shelf. This is partly due to the larger seasonal temperature range on the inner shelf. Inner shelf SST during winter (as low as 10°C) was substantially lower than during summer (~30°C); while the SST on the outer shelf was more stable throughout the year (from ~20°C in winter to ~30°C in summer) (Fig. 3). The offshore weakening of seasonal dependence of respiration was also reported in the same region by Hopkinson (1985), Hopkinson et al. (1989) and Griffith et al. (1990).

In summer, when SST was almost uniform from the coastline to the shelf break (Fig. 3), respiration was most likely controlled by organic matter supply. The summertime offshore decrease in respiration rate is consistent with previous observations showing that allochthonous organic carbon inputs (Hopkinson et al. 1989; Moran et al. 1991; DeAlteris 2007) and primary production (Yoder et al. 1993; Verity et al. 1993) are highest nearshore where rivers and salt marshes are a strong influence. This is also consistent with the fact that interactions between water column and sediments help resuspension of more organic detritus shoreward of the CFZ (Pomeroy et al. 1983; Pomeroy 1985), and the CFZ significantly diminishes cross-shelf exchange of both dissolved and particulate constituents (Blanton 1981).

Respiration and bacteria

Size-fractionated experiments have shown that bacteria and microprotozoa are responsible for 65 and 85% of the pelagic community respiration in the nearshore and offshore SAB, respectively (Griffith et al. 1990). It is therefore expected that respiration rates should follow bacterial activity. In this study, we found a remarkably good correlation between respiration and bacterial abundance along a single transect in July 2005 when both respiration and bacterial abundance were measured (Fig. 9). This correlation is expected when turnover (due to mortality from bacterivory or bacteriophage) is high and bacterial abundance well reflects bacterial activity. Other regions have also exhibited good correlations between bacterial abundance and respiration (Robinson et al. 2002), although the relationship breaks down when data sets from many regions are combined (Robinson and Williams 2005).

However, one needs to be aware that we are comparing respiration rates with bacterial abundance, while in fact bacterial abundance is not necessarily equivalent to bacterial activity. In addition, other planktonic communities might contribute significantly

to the respiration (e.g., about 35 and 19% in nearshore and offshore area of Georgia shelf water, respectively, Griffith et al. 1990).

Middle shelf respiration maxima

During the sampling months of June and August of 2003, middle shelf maxima were observed on the cross-shelf distributions of respiration rates (Fig. 6). They can be better seen from the data of August 2003 when water samples were taken at a higher spatial resolution (Fig. 10a). Similar to respiration, sea surface pCO_2 measurements in August 2003 showed a middle shelf maximum (Fig. 10b), which was not seen during the other sea surface pCO_2 surveys in this area (Jiang et al. 2008a). One possibility is that the water is a body of inner shelf water that was deflected offshore. However, the salinity distribution does not support this explanation (Fig. 3).

Compared to other sampling months, August 2003 showed a strong subsurface intrusion (Fig. 4). Subsurface intrusions have been shown to impact the distribution of microbial concentrations on the SAB shelf. At the peak of subsurface intrusions, much higher than usual microbial concentrations were repeatedly found in the water above the intrusion (Pomeroy et al. 1983; Pomeroy 1985). The hydrographic data in August 2003 show that the targeted area of the intrusion coincided with the respiration maximum in the surface water (Fig. 10). Considering that microbial organisms contribute predominantly to respiration in this area (Hopkinson et al. 1989; Griffith et al. 1990), we suggest that during subsurface intrusions, the increased microbial activity in the surface water overlaying the intruded water was responsible for the middle shelf respiration maxima. Since microbial abundance or biomass was not measured for the intrusion events observed during this study, further research is needed to verify this explanation.

Organic carbon fluxes through respiration

The organic carbon fluxes through water column respiration in the SAB would be 780, 285, and 230×10^{12} gC year^{-1} based on prior respiration studies of Griffith et al. (1990), Griffith and Pomeroy (1995), and Pomeroy et al. (2000), respectively. They are 6–22 times higher than the SAB water column primary production estimate of 35×10^{12} gC year^{-1} (Yoder 1985; Menzel 1993). Thus, the SAB organic carbon budget has been considered for many years to

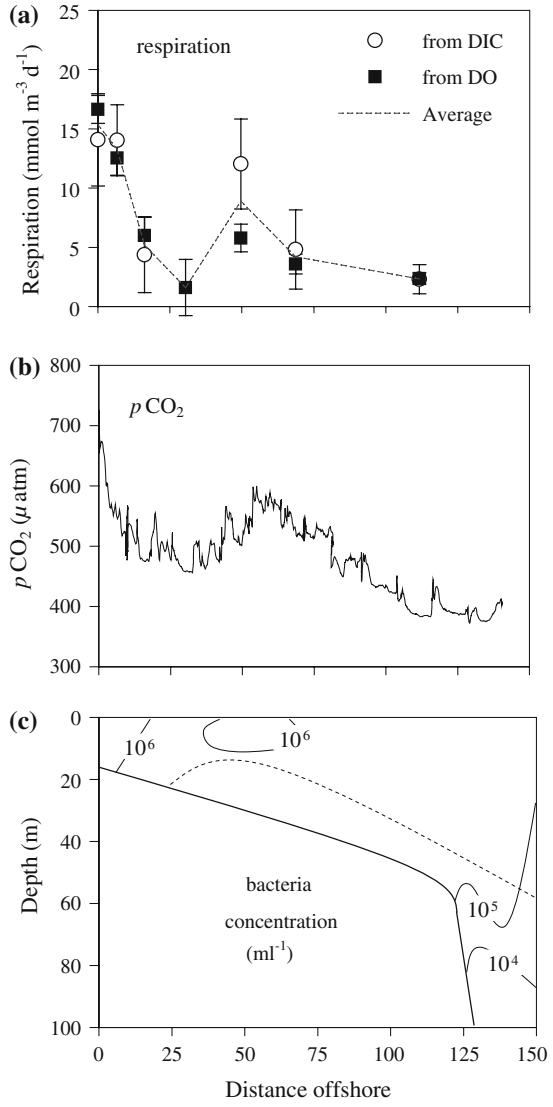

Fig. 10 **a** Shows the spatial distribution of surface water respiration rates on the continental shelf off Georgia in August 2003. *Open circles* are respiration from DIC measurement, *filled squares* are from DO measurement, and the *dotted line* connects the averages of the two methods. **b** Shows the in situ measurement of partial pressure of carbon dioxide in the surface water in August 2003. **c** Shows the typical vertical distribution of total bacteria concentration during subsurface intrusions on the continental shelf of the southeastern United States. The *solid lines* (above the bottom of the continental shelf) are concentrations of bacteria and the *dashed line* shows the intrusion (**c** is modified from Pomeroy 1985). The *x*-axis is the seaward distance from the coastline

be greatly out of balance. Studies examining particulate and dissolved organic matter flux from rivers and estuaries have been unable to find an allochthonous source of organic carbon capable of supporting this excess respiration (Menzel 1993; Pomeroy et al. 2000). Similarly, benthic primary production can not explain the large gap between respiration and primary production. Even though benthic production contributes significantly to the organic carbon production in the SAB (Nelson et al. 1999), it is usually exceeded by benthic respiration (Jahnke et al. 2000, 2005). The SAB organic carbon fluxes calculated from the respiration results of this study seem to be able to resolve the mystery of the perceived carbon imbalance. Our rates, when combined with those of Menzel (1993) and Jahnke et al. (2005) reveal an ecosystem in greater balance (Table 1). This conclusion supports the SAB ecosystem characteristic as a microbial food web with a production/respiration ratio close to 1 as prescribed by Pomeroy et al. (2000).

Comparison with global respiration on continental shelves

The average area-based pelagic community respiration in the SAB is about 300 gC m^{-2} $year^{-1}$. Wollast (1998) estimated this value to be 70 gC m^{-2} $year^{-1}$ (or 2×10^{15} gC $year^{-1}$) for global continental shelves, assuming pelagic respiration accounting for on average 30% of the continental shelf primary production. Unless the result of Wollast (1998) is an underestimation, the respiration of the SAB is at the higher end of the global database (even though the SAB is fairly shallow compared to most continental shelves). On the other hand, the large differences between these two estimates may suggest that more work is needed to constrain global estimate of respiration on continental shelves.

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