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Net community production and dark community respiration in a *Karenia brevis* (Davis) bloom in West Florida coastal waters, USA

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Abstract

Oxygen-based productivity and respiration rates were determined in West Florida coastal waters to evaluate the proportion of community respiration demands met by autotrophic production within a harmful algal bloom dominated by *Karenia brevis*. The field program was adaptive in that sampling during the 2006 bloom occurred where surveys by the Florida Wildlife Research Institute indicated locations with high cell abundances. Net community production (NCP) rates from light-dark bottle incubations during the bloom ranged from 10 to 42 $\mu\text{mole O}_2 \text{ L}^{-1} \text{ day}^{-1}$ with highest rates in bloom waters where abundances exceeded $10^5 \text{ cells L}^{-1}$. Community dark respiration (*R*) rates in dark bottles ranged from <10 to 70 $\mu\text{mole O}_2 \text{ L}^{-1} \text{ day}^{-1}$ over 24 h. Gross primary production derived from the sum of NCP and *R* varied from ca. 20 to 120 $\mu\text{mole O}_2 \text{ L}^{-1} \text{ day}^{-1}$. The proportion of GPP attributed to NCP varied with the magnitude of *R* during day and night periods. Most surface communities exhibited net autotrophic production ($\text{NCP} > R$) over 24 h, although heterotrophy ($\text{NCP} < R$) characterized the densest sample where *K. brevis* cell densities exceed $10^6 \text{ cells L}^{-1}$.

Keywords

Florida; *Karenia brevis*; Net production; Respiration

1. Introduction

The magnitude of primary production and community respiration varies seasonally in temperate coastal waters (Duarte et al., 2004; Smith and Kemp, 1995). For example, in the productive surface waters of the Menai Strait, North Wales, autotrophic production exceeds community dark respiration during the development phase of the spring diatom bloom, while in summer respiration rates are greater than net production (Blight et al., 1995). The difference between gross primary production (GPP) and community dark respiration (*R*) determines the magnitude of net community production (NCP). Positive NCP rates occur when gross primary production rates exceed community dark respiration rates (Williams, 2000). In general, coastal pelagic ecosystems in temperate latitudes exhibit positive values of NCP in spring through early summer, while surface waters are often heterotrophic ($\text{NCP} < 0$) during much of the remainder of the year (Hashimoto et al., 2006; Serret et al., 1999). The relative magnitude of NCP and *R* determine the metabolic balance of the surface

community, with autotrophic metabolism characterized by $NCP > 0$. Heterotrophic community metabolism, in contrast, occurs where $NCP < 0$ (Duarte et al., 2004).

While production and respiration rates have been characterized in several coastal and oceanic surface communities, rates of NCP, GPP and R have been quantified in relatively few dinoflagellate-dominated communities. In the coastal embayment of Ría de Vigo, northwest Spain, NCP and GPP were evaluated over a single diel period during a 'red tide' dominated by *Ceratium furca*, *Scrippsiella trochoidea*, and *Dinophysis acuminata* (Alvarez-Salgado et al., 1998). However, the magnitude of GPP was extrapolated from ^{14}C uptake (NCP) by an algorithm, and thus did not include direct measurements of GPP or R. Rates of GPP, NCP, and dark plus light respiration were assessed in a *Peridinium*-dominated bloom in Lake Kinneret, Israel (Luz et al., 2002). Diverse rate measurements provided insight into the different physiological mechanisms (Mehler reaction, alternative oxidase pathway, 'photorespiration') that consumed oxygen in the photoautotrophic community during the day (Luz et al., 2002).

Two physiological characteristics of dinoflagellates could potentially enhance rates of R in dinoflagellate blooms relative to R in diatom blooms. First, dinoflagellates have inherently high cellular respiration rates. Dinoflagellates cultured at saturating light intensities exhibit high ratios of maximum dark respiration ($R_{\max}$) to maximum photosynthesis ($P_{\max}$) relative to other phytoplankton taxa. A review of published photosynthesis and respiration rates led Geider and Osborne (1989) to conclude that Dinophyceae have higher mean ratios of $R_{\max}:P_{\max}$ than three other microalgal taxa and cyanobacteria. Langdon (1993a) similarly found that despite considerable species-specific variation, mean $R_{\max}:P_{\max}$ ratios for bacillariophyceae (0.16 ± 0.06 , $n = 37$), chlorophyceae (0.13 ± 0.07 , $n = 15$), cyanophyceae (0.10 ± 0.07 , $n = 2$), and prymnesiophyceae (0.16 ± 0.04 , $n = 8$) are lower than dinophyceae (0.35 ± 0.17 , $n = 17$). Since dinoflagellates appear to possess inherently high respiration costs to maintain cell metabolism, dinoflagellate blooms may possess higher rates of R relative to GPP than diatom blooms. This condition would result in reduced NCP rates. While many productivity studies have been conducted on dinoflagellate blooms utilizing ^{14}C incorporation, few, to our knowledge, have included simultaneous production and respiration rates derived from changes in oxygen or dissolved inorganic carbon.

An additional factor that could influence community rates of GPP and R in dinoflagellate blooms is that many dinoflagellate species are mixotrophic, and utilize dissolved and particulate nutritional sources to supplement photoautotrophy (Stoecker, 1998). Mixotrophy is a common nutritional strategy in several species that form dense harmful algal blooms (HABs) (Burkholder et al., 2008). Dinoflagellates with mixotrophic capabilities can acquire nutrition from organic sources during periods when inorganic nutrients are insufficient to sustain high population densities from photoautotrophy (Nygaard and Tobiesen, 1993). Under some environmental conditions, mixotrophy could confer a competitive advantage relative to obligate autotrophy (Tittle et al., 2003), and potentially influence the magnitude of primary production relative to respiration (Stickney et al., 2000).

The eastern Gulf of Mexico experiences blooms of the harmful alga *Karenia brevis* (Davis), previously described as *Gymnodinium breve* and *Ptychodiscus brevis* (Daugbjerg et al., 2000), on an almost annual basis (Steidinger et al., 1998; Steidinger, 2009). Cell densities of *K. brevis* in West Florida coastal waters can attain bloom concentrations in any month, although blooms that exceed 10^5 cells L^{-1} occur most frequently between late summer and winter. Background concentrations of 10^3 cells L^{-1} are found throughout the year in Gulf of Mexico surface waters (Tester and Steidinger, 1997). *K. brevis* is mixotrophic, utilizing dissolved organic nitrogen and phosphorus sources (Mulholland et al., 2006; Bronk et al., 2004; Vargo et al., 2008). *K. brevis* also ingests the photosynthetic prokaryote

Synechococcus (Jeong et al., 2005; Glibert et al., 2009). The mixotrophic nature of this dinoflagellate, coupled with the characteristically high cellular respiration of dinoflagellates, could contribute to high respiration demands relative to autotrophic production in *Karenia* blooms. Furthermore, high bacterial abundances exist in *Karenia* blooms and could also enhance community respiration rates (Buck and Pierce, 1989; Heil et al., 2004).

Primary productivity rates on the order of 1 to $>5 \text{ gC m}^{-2} \text{ day}^{-1}$ are characteristic of *K. brevis* blooms when autotrophic carbon fixation is determined with ^{14}C methodology (Redalje et al., 2008; Vargo, 2009). Carbon-specific growth rates of surface populations within *K. brevis* blooms vary from <0.1 (2001 bloom), to rates $>0.5 \text{ day}^{-1}$ in a 1999 bloom (Table 3, Redalje et al., 2008). The relatively low growth rates suggest that although primary production rates are high, the net carbon fixation can sustain populations that divide once every few days. The photophysiological characteristics of *K. brevis* have been assessed in cultures and natural populations over diel periods to characterize photosynthetic capabilities (Evens et al., 2001), although any diel pattern in *R* is presently unknown. To our knowledge, no respiration rates have been determined in *K. brevis* blooms. Although production rates are fairly well-documented in *Karenia* blooms, it is the balance between photosynthesis and respiration that determines cell growth rates.

There have been relatively few observations of the diel patterns of dark respiration rates in marine surface waters. Dark bottle incubations sampled at periods of several hours suggest that respiration is linear over periods of days (Robinson and Williams, 2005), and dark respiration rates are typically assumed to be constant (Aristegui and Harrison, 2002; Marra and Barber, 2004). However, dark respiration rates determined by oxygen probes are typically enhanced for several minutes following a transition from light to dark in cultures (e.g. Falkowski et al., 1985) and natural populations (Langdon, 1993b; Pringault et al., 2007). Diel respiration rates in freshwater ponds with dense photoautotrophic biomass indicate that community dark respiration can decline throughout much of the night following peak rates at sundown (Markager and Sand-Jensen, 1989; Fukushima et al., 2000). Enhanced respiration near sundown is consistent with maximum utilization of recent photosynthate at the end of the day, with declining substrate for respiration through the night. Additionally, the photo-dependent degradation of organic matter during the day could potentially fuel enhanced bacterial respiration (Gustavson et al., 2000).

Since *K. brevis* remains at the surface throughout most of the day, one objective of our study was to determine the diel pattern of dark respiration in bloom populations by observing changes in oxygen incubations from dawn-to-dusk (12 h) and after 24 h (dawn of the next day). We hypothesized that the inherently high respiration demands in dinoflagellates could be reflected in a relatively high proportion of GPP as *R*, in contrast to the initially high NCP rates observed in diatom blooms.

2. Materials and methods

2.1. Monitoring of *K. brevis* distributions

The nearshore distribution of *K. brevis* in west Florida coastal waters is monitored on a weekly basis by the Fish and Wildlife Research Institute (FWRI) of the Florida Fish and Wildlife Conservation Commission. One liter surface samples are routinely collected between Tampa Bay and Ft Myers FL, preserved with Lugol's solution, and examined at the FWRI Laboratory in St. Petersburg, FL for HAB species identification and quantitative cell counts. When feasible, volunteers provide preserved samples from locations on the Florida east coast and northwest Florida shoreline. The weekly data are provided online as summary reports with maps of *Karenia* surface distributions at <http://research.myfwc.com/gallery/>.

The weekly reports provided bloom locations that we sampled for productivity and respiration measurements during the summer of 2006.

2.2. Bloom sampling

Before the 2006 bloom began, 'pre-bloom' sampling was initiated at the Mote Marine Laboratory dock at New Pass, FL, an entrance to northern Sarasota Bay (Fig. 1; Table 1). This region of the West Florida coast experienced high and persistent concentrations of *K. brevis* throughout an extensive and prolonged bloom in 2005 that declined in January 2006 (see Hu et al., 2006). In our study, samples were collected at the Mote dock on May 10, 11, 31 and June 1, 2006 during the 'pre-bloom' period when *K. brevis*, if detected, was $<10^3$ cells L^{-1} .

We began sampling locations at which *K. brevis* was present at $>10^4$ cells L^{-1} after the FWRI monitoring program identified a bloom near Ft Myers. Samples were collected at dawn, when *K. brevis* is often concentrated at the sea surface (Heil, 1986). Sampling at dawn permitted diurnal rates of production and dark respiration based on changes in dissolved oxygen, plus nocturnal rates of respiration.

Surface samples were collected on July 27 in Pine Island Sound at two stations (Table 1). Two stations were sampled on September 13 within 5 km of New Pass, FL (Fig. 1), where cell abundances exceeded 10^5 cells L^{-1} (Table 1). Cell densities declined along the entire west Florida coast in October. Two stations were occupied on October 11 and 12 near Boca Grande Pass, where *K. brevis* abundance was $>10^4$ cells L^{-1} . The final sampling was completed on November 16, with one station located at the entrance to New Pass, and a second further offshore at the 15 misobath (Table 1). A total of 12 stations were occupied for oxygen-based measurements of NCP and *R* during the 2006 bloom.

2.3. Light–dark bottle incubations

Light and dark bottles were incubated to establish rates of NCP and *R* over diel cycles with changes in dissolved oxygen concentrations determined at approximately 12-h intervals. These intervals correspond to day (dawn-to-dusk) and night (dusk-to-dawn). As illustrated in Fig. 2, oxygen concentrations measured at dawn (initial) and in dark bottles after 24 h (dawn on the following day) provide dark respiration rates for a full day–night interval (R_{24} , Fig. 2). However, if dark bottle incubations are initiated at dawn, as is customary, the 24 h incubation effectively integrates the dark community respiration over the final 24 h of a 36 h period without illumination (night–day–night). The simultaneous light bottle incubations over 24 h, in contrast, integrate net community production during the day (NCP_{12}), and the subsequent dark respiration at night (R_{night}). This yields a net community production rate for 24 h (NCP_{24}). Dark respiration in the light bottle at night (R_{night}) corresponds to the final 12 h of a 24 h incubation, while respiration at night in the dark bottle (R_{nd}) is the dark respiration during the last 12 h of a 36 h period of darkness if the incubations are initiated at dawn. The respiration at night in the dark bottle, R_{nd} , is equivalent to $R_{24} - R_{day}$ (Fig. 2). We assessed these various contributions to community dark respiration from the light and dark bottles to determine if surface communities exhibit enhanced rates of dark respiration at night relative to that during the day. Given that *K. brevis* accumulates at the sea surface during the day, we hypothesized that the respiration could be enhanced in the light bottles at night (R_{night}) relative to that in dark bottles during the preceding day (R_{day}).

Seawater was collected within 1 h of sunrise. A 5 L horizontal Niskin bottle was lowered to collect seawater from 0.5 m depth. The bottle was fitted with silicone seals and a silicone rubber closing mechanism to minimize contamination. Initial oxygen concentrations were measured with seawater siphoned from the Niskin bottle into three 125 mL glass titration

flasks. Winkler reagents were added, and the titration flasks were stored in 1 L plastic jars filled with tap water. The submersion of the bottles prevented evaporation in the flasks before the Winkler titrations could be completed.

Seawater was siphoned from the Niskin into three, or where sufficient volume was still available, four 1 L polycarbonate bottles. Although 125 mL glass flasks are frequently used for oxygen incubations, the polycarbonate bottles were used to minimize trace metal contamination, as in ^{14}C studies (Fitzwater et al., 1982). Incubations in 3.3 mm thick polycarbonate bottles filled with 0.2 μm filtered seawater have demonstrated that oxygen concentrations are unaffected by exchange with external seawater over periods of 24 h (C. Langdon, Pers. Comm.). The polycarbonate bottles were initially soaked in dilute micro-solution and then rinsed with 18 M Ω water. The bottles were subsequently soaked for 3 days in 0.5N Baker Intranalyzed HCl and then rinsed with 18 M Ω water. Following this initial cleaning, the bottles were rinsed with dilute acid and water between samplings.

Each polycarbonate bottle was filled with seawater so that the meniscus extended above the top. The seawater was then capped with clear plastic (PVDC) film to prevent formation of air bubbles in the incubation bottles under the plastic cap. This technique is routinely used in microzooplankton grazing experiments to eliminate air bubble formation in polycarbonate bottles, since the presence of air bubbles can enhance cell lysis in protests (Gifford, 1988). In our incubations, the plastic film prevented air bubbles which could bias oxygen measurements. The dark bottles were covered with opaque foil, and suspended with the light bottles at 0.5 m depth from a floating clear plastic frame. The incubations were begun within 1 h of dawn. Light and dark bottles were retrieved at sundown, with seawater siphoned into triplicate 125 mL glass titration flasks from one each of the light bottles and dark bottles. Winkler reagents were added, and each 125 mL titration flask was stored in a 1 L plastic jar filled with water to prevent formation of air bubbles during transit (Zhang et al., 2002). Oxygen concentrations were determined within a week by amperometric titration (Culbertson and Huang, 1987) in the laboratory of C. Langdon.

The difference in oxygen concentration between the mean of triplicates values from the Niskin bottle (initial O_2) and that from the light bottle sampled at dusk (12 h) is designated NCP_{12} (see Fig. 2). The change in oxygen concentration between the initial oxygen concentration and that in the dark bottle sampled at dusk (12 h) is the dark respiration rate during the day, R_{day} (Fig. 2). The difference in oxygen concentration between the light bottle sampled at dusk (12 h), and that at the following dawn (24 h), is designated the dark respiration rate at night, R_{night} (Fig. 2). Note that the 'end point' of a 24 h light bottle incubation would be equal to NCP_{24} , the difference between NCP_{12} and R_{night} . The difference in oxygen concentrations between the initial O_2 concentration and that in a dark bottle incubated for 24 h is designated as R_{24} , which is equivalent to the sum of R_{day} and R_{nd} (Fig. 2).

We evaluated the total daily community respiration from two estimates. The first estimate is designated as R_T and equals the sum of the R_{day} and R_{night} . This mirrors respiration in a natural community that is exposed to surface conditions throughout a light-dark cycle. The second estimate is derived from the 24 h dark bottle (R_{24}). To our knowledge, there have been no comparisons of the day or night contributions to total respiration within natural dinoflagellate populations.

Hourly rates of net oxygen production and dark respiration were calculated from hours elapsed during the dawn-to-dusk and dusk-to-dawn intervals, respectively. The times for sampling at local sunrise and sunset were calculated with the U.S. Naval Observatory algorithm available at http://aa.usno.navy.mil/data/docs/RS_OneYear.php. Hourly

production and respiration rates were normalized to the corresponding chlorophyll *a* concentration to yield rates as $\mu\text{mol O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$. The chlorophyll-specific respiration rates are compared to published rates from phytoplankton cultures to assess the potential contribution of photoautotrophs and heterotrophs to community respiration.

2.4. Cell abundances, chlorophyll *a* concentrations

Duplicate aliquots of one hundred ml were collected from the Niskin bottle and filtered onto Whatman GF/F filters for fluorometric chlorophyll *a* analysis by the method of Holm-Hansen and Reimann (1978). Filters were stored in plastic test tubes in a freezer with desiccant and analyzed within 1 month of sampling. Pigments were extracted with absolute methanol and the fluorescence read before and after acidification in a Turner designs TD-700 fluorometer. A 10–15 mL aliquot from the Niskin was preserved with Lugol's preservative for *K. brevis* cell counts. The preserved samples were analyzed at the Mote Marine Laboratory within a week of collection.

3. Results

3.1. *K. brevis* distributions in summer, 2006

K. brevis was absent in samples collected at New Pass during May and June (Table 1; Fig. 3). The FWRI monitoring program also reported *K. brevis* at undetectable to low concentrations throughout the spring of 2006. Surface chlorophyll *a* concentrations at New Pass were generally $<3 \mu\text{g L}^{-1}$ throughout this 'pre-bloom' period (Fig. 3). In late June 2006, the FWRI monitoring program reported that *K. brevis* was present at concentrations $<5 \times 10^5 \text{ cells L}^{-1}$ offshore of Ft. Myers (see Fig. 1). By mid-July it had attained concentrations of 10^5 to $10^6 \text{ cells L}^{-1}$ within Pine Island Sound (Fig. 1). In August and September the bloom progressed to the north along the coast. This seasonal pattern parallels the northwesterly flow on the west Florida shelf in response to summer winds (Yang and Weisberg, 1999). *K. brevis* was present at concentrations of 10^5 to $10^6 \text{ cells L}^{-1}$ between Pine Island Sound and Sarasota Bay in late summer. By the final week of August, the FWRI sampling program revealed a patchy distribution between Ft. Myers and Tampa Bay with concentrations ranging from $<10^5$ to $>10^6 \text{ cells L}^{-1}$. In early October, *Karenia* abundance was maximal in nearshore waters adjacent to Boca Grande Pass where cell densities exceeded $10^5 \text{ cells L}^{-1}$. By November, abundances had decreased to $<10^5 \text{ cells L}^{-1}$. In early December *K. brevis* was undetectable in surface waters along the west Florida coast.

Our field program sampled *K. brevis* populations for productivity and respiration measurements based on the observations of the FWRI monitoring program. The initial sampling of surface *K. brevis* populations occurred on July 27 and 28 in Pine Island Sound where cell densities ranged from 1.5 to $1.6 \times 10^6 \text{ cells L}^{-1}$ with corresponding chlorophyll *a* concentrations of 8.0 – $9.9 \mu\text{g L}^{-1}$ (Fig. 3). Cell concentrations varied from 8.8×10^5 to $2.8 \times 10^6 \text{ cells L}^{-1}$ in September at New Pass when surface chlorophyll *a* concentrations were 11.1 and $17.2 \mu\text{g L}^{-1}$, respectively (Fig. 3). Cell abundances had declined in the third sampling on October 11 and 12 near Boca Grande Pass with *K. brevis* present at 1.25×10^5 and $9.3 \times 10^4 \text{ cells L}^{-1}$, and chlorophyll concentrations of ca. $3 \mu\text{g L}^{-1}$. In November, cell concentrations had declined along the entire West Florida coast with our final sampling was at New Pass where *Karenia* cell densities were ca. $1.3 \times 10^5 \text{ cells L}^{-1}$ and chlorophyll *a* concentrations were 1.1 – $1.5 \mu\text{g L}^{-1}$ (Table 1).

3.2. Rates of NCP and R

Prior to the initiation of the *Karenia* bloom, rates of NCP at New Pass ranged from 8 to $32 \mu\text{mole O}_2 \text{ L}^{-1} \text{ 12 h}^{-1}$ ($n = 4$) with corresponding dark respiration rates of 2 – $14 \mu\text{mole O}_2 \text{ L}^{-1} \text{ 12 h}^{-1}$ (Fig. 3). Net community production normalized to chlorophyll and daylength

yield values of 1.0–1.5 $\mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$. The chlorophyll-specific respiration rates during the day varied from 0.1 to 0.9 $\mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$. Respiration rates were less than NCP in the mid-May samples, and exceeded NCP in the May 31 to June 1 samples (Fig. 3). Values of R_T for the full 24 h incubation exceeded NCP on May 31 and June 1 (Fig. 3). This pattern suggests that the surface plankton community underwent a physiological change at New Pass from an autotrophic ($\text{NCP} > R_T$) to heterotrophic metabolism ($\text{NCP} < R_T$) in early summer.

The highest productivity and respiration rates in west Florida coastal waters occurred where *K. brevis* cell concentrations exceeded $10^5 \text{ cells L}^{-1}$, and surface chlorophyll *a* concentrations were $>5 \mu\text{g L}^{-1}$. Rates of NCP ranged from 20 to 40 $\mu\text{mole O}_2 \text{ L}^{-1} 12 \text{ h}^{-1}$ in Pine Island Sound in July and at New Pass in September. At these locations *K. brevis* densities ranged from 10^5 to $10^6 \text{ cells L}^{-1}$ with chlorophyll *a* concentrations of 5–15 $\mu\text{g L}^{-1}$. NCP rates normalized to chlorophyll *a* and daylength produced lower values during the peak bloom period than during October and November. The rates of NCP in July and August ranged from 0.15 to 0.40 $\mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$, with corresponding hourly respiration rates of 0.03–0.15 $\mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$. During October and November, in contrast, the chlorophyll-specific production increased to 0.4–0.9 $\mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$, while respiration rates were similar to those in July and August, at 0.04–0.10 $\mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$.

Total daily respiration rates (R_T) in surface waters with high *K. brevis* concentrations were often higher than rates observed in May and June, before the initiation of the bloom. Rates of dark respiration during the day (R_{day}) and night (R_{night}) in bloom waters also frequently exceeded those in surface waters prior to the initiation of the bloom (Fig. 3). Total respiration (R_T) was generally less than, or equal to, NCP in surface populations where *K. brevis* was present at $<10^6 \text{ cells L}^{-1}$ (Fig. 3). This condition corresponds to an autotrophic ($\text{NCP} > R_T$) or balanced ($\text{NCP} = R_T$) community metabolism. An exception occurred on September 2 where *K. brevis* exceeded $10^6 \text{ cells L}^{-1}$. At that station, the R_{night} rate (53.5 $\mu\text{mole O}_2 \text{ L}^{-1} 12 \text{ h}^{-1}$) exceeded NCP (42.4 $\mu\text{mole O}_2 \text{ L}^{-1} 12 \text{ h}^{-1}$) with a R_T value (71.1 $\mu\text{mole O}_2 \text{ L}^{-1} 24 \text{ h}^{-1}$) that was 1.6-fold greater than NCP. In this sample the metabolic balance of the community was heterotrophic.

Rates of 24-h dark respiration were assessed in five incubations to compare the change in dark bottle oxygen concentrations during the daytime (R_{day}) with those in dark bottles at night (R_{nd}). Respiration in the dark bottle at night was linearly related to respiration in the dark bottle during the preceding day (R_{day}) by the relationship:

$$(R_{\text{nd}}) = 1.20(R_{\text{day}}) - 1.41 \quad (1)$$

with $r^2 = 0.95$. This relationship suggests the decline in oxygen concentrations in dark bottles was essentially linear over time scales of 12–24 h, as previously reported for other surface waters (Robinson and Williams, 2005).

The relationship between surface chlorophyll *a* concentrations and R_T indicates that community respiration demands increased with increased pigment biomass (Fig. 4a). This relationship was evident if R_T was summed from $R_{\text{day}} + R_{\text{night}}$, or derived from a 24 h dark bottle (R_{24}). Although there was considerable scatter in R_T at low chlorophyll *a* concentrations, the respiration values from the R_T and R_{24} estimates were similar, except at high pigment concentrations. The sum of R_{day} and R_{night} was greater at high chlorophyll concentrations than R_{24} due to the fact that respiration at night was greater in the light bottles than in the dark bottles (Fig. 4b). In contrast to the comparable respiration rates in dark bottles during the day and night, the respiration rates in light bottles at night (R_{night})

were often higher than those in dark bottles (R_{day}) during the preceding day (Fig. 4b). The R_{day} rates ranged from <5 to $20 \mu\text{mole O}_2 \text{ L}^{-1} 12 \text{ h}^{-1}$, while those for R_{night} ranged from 5 to $>50 \mu\text{mole O}_2 \text{ L}^{-1} 12 \text{ h}^{-1}$ (Fig. 4b). In the dense *K. brevis* community sampled on September 2, R_{night} was nearly 3-fold higher than R_{day} .

Two estimates of daily GPP were derived from NCP_{12} and NCP_{24} with respiration rates measured at 12 and 24 h. One estimate of GPP was derived from the sum of NCP_{12} and R_{T} . Under these conditions, surface communities are mainly autotrophic with net community production (NCP_{12}) typically exceeding R_{T} . Rates of NCP_{12} increased from 5 to $60 \mu\text{mole O}_2 \text{ L}^{-1} 12 \text{ h}^{-1}$, as the GPP increased from 20 to $80 \mu\text{mole O}_2 \text{ L}^{-1} \text{ day}^{-1}$ (Fig. 4c). At higher GPP values, the NCP_{12} remained near maximum rates of $40 \mu\text{mole O}_2 \text{ L}^{-1} \text{ day}^{-1}$. The second estimate of GPP was derived from the sum of NCP_{24} (the 24 h light bottle) and R_{24} (from the 24 h dark bottle). In this estimate (filled symbols in Fig. 4c), the GPP values are higher than corresponding rates derived from NCP_{12} and R_{T} . This difference can be attributed to the inclusion of R_{nd} in GPP. The NCP_{24} rates are lower than NCP_{12} at any given level of GPP due to the inclusion of nighttime respiration in the light bottle, R_{night} (Fig. 4c). Under these conditions, dark respiration contributes to GPP such that a higher proportion of communities correspond to heterotrophic metabolism with community $R_{24} > \text{NCP}_{24}$.

4. Discussion

4.1. Productivity and respiration rates of *K. brevis*

Previous measurements of primary production rates in *K. brevis* blooms have primarily relied on ^{14}C methodology. To our knowledge, the only previous oxygen-based measurements of net community productivity were completed in 1954 (Odum et al., 1955). Assuming a 12-h day, a daily NCP of $16.8 \mu\text{mole O}_2 \text{ L}^{-1} \text{ day}^{-1}$ was measured during March 1954 in surface waters collected south of Sanibel Island and incubated under fluorescent lights. Cell concentrations in that bloom were about $3 \times 10^5 \text{ cells L}^{-1}$. A second incubation with surface waters from coastal Englewood, FL in April 1954 yield an NCP of $<2 \mu\text{mole O}_2 \text{ L}^{-2} \text{ day}^{-1}$. The rate from the March incubation is comparable to NCP_{12} values during October and November 2006, when *K. brevis* concentrations were decreasing along the west Florida coast (Table 2).

In general, the NCP_{12} values in 2006 are comparable to the productivity studies in *K. brevis* blooms based on H^{14}CO_3 uptake (Table 2). Vargo et al. (1987) summarized ^{14}C -based productivity rates from *K. brevis* blooms in 1980. Volumetric rates for ^{14}C productions calculated from that report varied from 10.4 to a maximum of $15 \mu\text{mole C L}^{-1} \text{ day}^{-1}$. Assuming a photosynthetic quotient of approximately 1.25, these rates are similar to those measured with oxygen incubations in 2006. During a 2001–2002 bloom, maximum productivity rates ranged from ca. 20 to $>120 \mu\text{g C L}^{-1} \text{ h}^{-1}$ (Heil et al., 2004). Utilizing a photosynthetic quotient of 1.25 and 8 h incubation period, the carbon fixation rates convert to 12.8 to $84.8 \mu\text{mole O}_2 \text{ L}^{-1} 8 \text{ h}^{-1}$, within the range of NCP_{12} measured from the oxygen incubations (Fig. 3). Bendis et al. (2004) determined light-saturated production (P_{max}) from photosynthesis-light intensity curves during the 2001–2002 bloom. When *K. brevis* concentrations exceeded $10^5 \text{ cells L}^{-1}$, the equivalent carbon fixation rates for an 8 h photoperiod at saturating intensities ranged from 6.7 to $64.4 \mu\text{mole C L}^{-1} \text{ h}^{-1}$ with a median value of $17.8 \mu\text{mole C L}^{-1} \text{ h}^{-1}$ (average rate of $25.2 \mu\text{mole C L}^{-1} \text{ h}^{-1}$). These values are within the range of our oxygen incubations, although maximum rates from the 2001–2002 bloom exceeded those in 2006. This could be attributed to higher cell abundances sampled in the 2001–2002 bloom. Cell densities in 2001–2002 were 4×10^6 to $1.8 \times 10^7 \text{ cells L}^{-1}$, and therefore several-fold higher than the maximum cell abundances in 2006.

Community respiration rates in *K. brevis* blooms fall within the range of estuarine community respiration compiled from 21 estuaries by Hopkinson and Smith (2005). Approximately 90% of all daily respiration rates in estuarine surface waters were $<50 \mu\text{mole O}_2 \text{ L}^{-1} 24 \text{ h}^{-1}$, with maximum values up to $250 \mu\text{mole O}_2 \text{ L}^{-1} 24 \text{ h}^{-1}$ (Hopkinson and Smith, 2005). Maximum daily rates of R_T on September 2, where *K. brevis* was $>10^6$ cells L^{-1} , was within the upper 5% of daily respiration rates reported from the survey of Hopkinson and Smith (2005). However, with the exception of that sample, the respiration rates from West Florida coastal waters are generally within the 50th percentile of pelagic respiration rates from estuarine surface waters. Thus, the respiration rates in *Karenia*-dominated surface waters were, in general, not exceptionally higher than most estuarine waters.

Chlorophyll-specific respiration rates suggest that heterotrophs contributed a major fraction of community respiration demands prior to the initiation of the 2006 *Karenia* bloom. Langdon (1993a) summarized respiration rates normalized to chlorophyll *a* from the literature for unialgal cultures. Although the numbers of studies are limited, chlorophyll-specific respiration rates vary from 0.05 to $0.10 \mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$ in diatoms, 0.05 to $0.6 \mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$ in chlorophytes, and 0.10 – $0.29 \mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$ in dinophyceae. Prior to bloom initiation, chlorophyll-specific rates were higher than those in unialgal cultures, at 0.1 – $0.9 \mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$. During the bloom, in contrast, rates were $<0.15 \mu\text{mole O}_2 (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$. This suggests that heterotrophs could account for a higher proportion of community respiration before, rather than during, the bloom.

Since dinoflagellates have enhanced cellular respiration rates relative to other phytoplankton (Geider and Osborne, 1989; Langdon, 1993a), an initial hypothesis was posed that respiration losses in *Karenia* blooms could potentially account for a large proportion of GPP. Shanley and Vargo (1993) provide cellular respiration rates from the Wilson clone of *K. brevis* at 24°C and light intensities of 24, 90, and $160 \mu\text{Einst m}^{-2} \text{ s}^{-1}$. Cellular dark respiration rates, corrected for respiration in the $<5 \mu\text{m}$ size fraction, varied from 2.4 to $6.0 \text{ pg C cell}^{-1} \text{ h}^{-1}$ at intensities of 24, 90, and $160 \mu\text{Einst m}^{-2} \text{ s}^{-1}$. There was no relationship evident between cellular respiration rates and light intensity. Net carbon fixation ranged from 10.6 to $25.6 \text{ pg C cell}^{-1} \text{ h}^{-1}$ between 24 and $160 \mu\text{Einst m}^{-2} \text{ s}^{-1}$, such that *R:Pratios* decreased from 0.32 at the lowest light level to 0.15 at $160 \mu\text{Einst m}^{-2} \text{ s}^{-1}$. These data suggest that *K. brevis* may possess lower cellular dark respiration demands, relative to maximum photosynthesis rates, than other dinoflagellates. If valid, this characteristic could explain, in part, the observation that NCP often exceeded R_T throughout the course of the 2006 bloom. Culture studies with additional clones are necessary to better characterize NCP and *R* in *K. brevis*, and improve an understanding of dinoflagellate carbon metabolism.

4.2. The metabolic balance of *K. brevis* blooms

In both estuarine (Caffrey, 2003; Hopkinson and Smith, 2005) and coastal environments (Smith and Hollibaugh, 1993), the metabolic balance of surface waters is frequently heterotrophic with community *R* exceeding NCP. Terrestrial organic sources delivered via riverine organic matter can significantly contribute to respiration rates in many nearshore ecosystems. Additionally, benthic communities also make significant contributions to the water column respiration rates in shallow waters. At temperate latitudes, pelagic blooms often exhibit autotrophic and heterotrophic phases, particularly during the temporal progression of spring diatom blooms. Temporal patterns of autotrophic and heterotrophic phasing are evident at time scales of weeks to a month in surface waters of the Bay of Palma, NW Mediterranean (Navarro et al., 2004), Sagami Bay, Japan (Hashimoto et al., 2006) and Bay of Biscay, Spain (Serret et al., 1999). The sequence of net autotrophy to heterotrophy can be fairly rapid, progressing in less than a week in mesocosms within a Norwegian Fjord (Robinson and Williams, 2005). The metabolic balance of *K. brevis*-

dominated surface waters along the west Florida coast was predominantly autotrophic, or balanced, with NCP equal to, or exceeding, R_T . The *Karenia* bloom did not exhibit a systematic progression from autotrophic to heterotrophic conditions as has been observed in temperate diatom blooms.

Although *K. brevis* blooms develop in oligotrophic surface waters (Steidinger et al., 1998; Vargo et al., 2008), particulate nutrient ratios suggest that blooms develop under nutrient sufficient conditions, or alternatively exhibit P-limitation near termination (Heil et al., 2001). The capability of *K. brevis* to efficiently utilize low ambient concentrations of nitrogen and phosphorus (Steidinger et al. 1998; Vargo and Howard-Shamblott, 1990), as well as dissolved organic nitrogen and phosphorus sources (Bronk et al., 2004; Havens et al., 2004; Mulholland et al., 2006), contributes to the ability of *Karenia*-dominated communities to maintain net autotrophy in excess of community respiration demands in the oligotrophic surface waters of the west Florida shelf.

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Fig. 1. Surface chlorophyll *a* distributions on the west Florida shelf from MODIS imagery on June 11, 2006. Red corresponds to high chlorophyll concentrations and blue corresponds to low surface concentrations. The locations of Pine Island Sound (PI), Charlotte Harbor (Ch), New Pass (NP) at the entrance to Sarasota Bay (SB), and Tampa Bay (TB) are indicated. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Fig. 2.

Schematic illustration of potential change in oxygen concentration within light (open symbol) and dark (solid symbol) bottles over a day–night incubation. Night corresponds to the 12–24 h interval as indicated by the hatched bar. The net community production during the day (NCP_{12}) and that following a 24 h incubation (NCP_{24}) are changes in oxygen concentrations at open symbols. The dark respiration in the light bottle during the night is designated as R_{night} , while dark community respiration in dark bottles during the day (R_{day}) and that following the 24 h incubation (R_{24}) are solid symbols. The arrows indicate the magnitude of oxygen change in light and dark bottles over various time intervals.

Fig. 3.

Top: Chlorophyll *a* concentrations and *Karenia brevis* cell abundance in surface waters sampled from May to November in West Florida coastal waters. Locations for the individual sampling dates are in Table 1. Bottom: Net community production (NCP_{12}), diurnal dark respiration (R_{day}), and nocturnal respiration (R_{night}) in the surface waters sampled during the pre-bloom and bloom conditions.

Fig. 4.

(a) The relationship between total respiration (R_T) and chlorophyll *a* concentration in west Florida coastal surface waters, summer 2006. Open symbols are R_T as the sum of $R_{day} + R_{night}$ with crosses corresponding to R_{24} . (b) The relationship of dark respiration at night (R_{night}) to that in the day (R_{day}). The night respiration rates are derived from changes in oxygen at night in light bottles, and the day respiration rates are from changes in oxygen concentrations in dark bottles during the day. The dashed line corresponds to a 1:1 relationship. (c) The relationship between NCP and gross primary production (GPP). The NCP rates are illustrated for the 12 h day, and that measured after 24 h by subtracting R_{night} . Values of NCP above the zero intercept correspond to net autotrophic community

metabolism while negative values, below the zero intercept, correspond to a net heterotrophic community metabolism.

Table 1

The date, location, station number, latitude, longitude, and *Karenia brevis* concentration (cells L⁻¹) of surface water samples collected for production and respiration measurements in 2006. ND= not detected.

Date	Location	Station	Latitude	Longitude	<i>K. brevis</i> (cells L ⁻¹)
May 10	New Pass	1	27.3338°N	82.5793°W	ND
May 11	New Pass	2	27.3338°N	82.5793°W	ND
May 31	New Pass	3	27.3338°N	82.5793°W	ND
June 1	New Pass	4	27.3338°N	82.5793°W	ND
July 27	Pine Island Sound	5	26.6730°N	82.2212°W	1.56 × 10 ⁶
	Pine Island Sound	6	26.5602°N	82.1740°W	1.69 × 10 ⁶
September 13	Longboat Key	7	27.3454°N	82.6148°N	8.8 × 10 ⁵
	New Pass	8	27.3189°N	82.6081°W	2.88 × 10 ⁶
October 11	Boca Grande Pass	9	26.6682°N	82.3388°W	1.25 × 10 ⁵
October 12	Boca Grande Pass	10	26.6915°N	82.3248°W	9.3 × 10 ⁴
November 16	Longboat Key, 15m	11	27.2922°N	82.6380°W	1.11 × 10 ⁵
	New Pass	12	27.3257°N	82.5765°W	1.52 × 10 ⁵

Table 2

Summary of primary production rates from the west Florida shelf. Rates are based on oxygen light–dark bottle incubations (Odum et al., 1955 and this study) and ^{14}C incubations (Vargo et al., 1987; Heil et al., 2004; Bendis et al., 2004).

Study	Year	P ($\mu\text{mole L}^{-1}\text{ day}^{-1}$)	Conditions
Odum et al. (1955)	1950	16.8 ^a	Fluorescent lights,
This study	2006		NCP ₁₂ , pre-bloom, NCP ₁₂ , bloom
Vargo et al. (1987)	1980	10.4–15 ^b	
Heil et al. (2004)	2001–2002	12.8–84.8 ^c	8 h incubation
Bendis et al. (2004)	2001–2002	6.7–64.4 ^d	

^aNet oxygen production (light–dark bottle) during an 8 h laboratory incubation under florescent lights.

^bExtrapolated from depth-integrated rates of daily primary production in Table 1, Vargo et al. (1987).

^cSurface samples incubated on-deck for 8 h under natural illumination.

^dSurface samples incubated on-deck for 8 h with *K. brevis* densities exceeding 105 cells L^{-1} .