Harmful Algae 38 (2014) 95–100

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

Comparative diel oxygen cycles preceding and during a *Karenia* bloom in Sarasota Bay, Florida, USA

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ARTICLE INFO

Article history:
Available online 14 June 2014

Keywords:
Net community production
Respiration
Karenia brevis

ABSTRACT

The diel change in dissolved oxygen concentrations were recorded with an automated incubator containing a pulsed oxygen sensor in Sarasota Bay, Florida. The deployments occurred during a 'pre-bloom' period in May to June 2006, and during a harmful algal bloom dominated by *Karenia brevis* in September 2006. The diurnal (daylight) increase in dissolved oxygen concentrations varied from 16 to 104 μmol O_2 l^{-1} with the corresponding nocturnal decrease in oxygen varying from 16 to 77 μmol O_2 l^{-1}. Nocturnal respiration consumed 42–113% of the diurnal net oxygen production with the minimum and maximum during the pre-bloom period. Hourly production rates closely followed fluctuations in irradiance with maximum rates in the late morning. Hourly oxygen utilization rates (community respiration) at night were highest during the first few hours after sunset.

1. Introduction

Harmful algal blooms occur on the west Florida shelf almost every year (Heil and Steidinger, 2009). The dominant bloom species is *Karenia brevis* Davis (Daugbjerg et al., 2000), a dinoflagellate that produces brevetoxins responsible for neurotoxin shellfish poisoning (NSP) and respiratory distress from the inhalation of brevetoxins in aerosols (Kirkpatrick et al., 2004). The costs of treating NSP and respiratory distress, as well as lost revenue from tourism, in the affected coastal communities can amount to millions of dollars (Larkin and Adams, 2007; Hoagland et al., 2009). Consequently, studies of *K. brevis* blooms have concentrated on factors that regulate their temporal and spatial distributions, as well as cell physiology and toxicity, to better understand the factors that regulate bloom formation, persistence and termination (Vargo, 2009). Natural populations of *K. brevis* undergo a diel vertical migration during which cells aggregate at the surface during the day (Schaeffer et al., 2009; Heil et al., 2014). *K. brevis* is positively phototactic and negatively geotactic (Kamykowski et al., 1998), and at dusk cells disperse by swimming from the surface.

The cellular physiology of *Karenia brevis* includes photoprotective processes that allow this species to maintain relatively high photosynthesis rates while exposed to high irradiance at the surface. Evens et al. (2001) examined cultures exposed to natural irradiance, both including and excluding ultraviolet (UV) radiation, to document diurnal patterns in cellular composition, photosynthetic and photoprotective pigments, photosystem II quantum yield, as well as net oxygen production. The diurnal pattern of pigments and PSII maximum quantum yield was analogous to that in other pelagic photoautotrophs, although *K. brevis* exhibits resistance to the deleterious effects of UV radiation. Dissolved oxygen concentrations in cultures exposed to natural irradiance rapidly increased during the morning, remained constant or increased slightly throughout the afternoon, irrespective of exposure to UV radiation. The diurnal pattern in dissolved oxygen suggests the photoprotective mechanisms present in *K. brevis* permits this species to maintain high productivity rates throughout the day when cells are aggregated at the surface.

Maximum respiration rates (R_{max}) in dinoflagellates typically consume a relatively higher proportion of light-saturated primary production (P_{max}) than other phytoplankton taxa. Geider and Osborne (1989) concluded that the R_{max}:P_{max} ratios in Dinophyceae cultures (0.35 ± 0.15) were higher than in Bacillariophyceae (0.14 ± 0.10), Chlorophycea (0.11 ± 0.05), Prymnesiophyceae (0.10 ± 0.04), and Cyanobacteria (0.07 ± 0.05). A similar comparison was reported by Langdon (1993a) and indicates that at saturating irradiance dinoflagellates characteristically possess relatively higher cellular respiration demands than other taxonomic groups. Although photosynthesis and respiration rates have been examined in dinoflagellate cultures, few respiration rates have been measured in natural dinoflagellate blooms. Ragotskie and Pomeroy (1957)

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http://dx.doi.org/10.1016/j.hal.2014.05.010
1568-9883/

measured primary production and respiration rates in a *Gymnodinium* spp. bloom in Georgia coastal waters where net community production rates were several-fold higher than daily respiration rates. Tyler et al. (2009) also assessed community production and respiration rates in a summer dinoflagellate bloom within the Delaware Costal Bays. Community respiration rates from dissolved oxygen probes were sufficiently high such that bottom waters were hypoxic by late afternoon. Odum et al. (1955) measured dark respiration in two experiments during a Florida *Gymnodinium* (*Karenia brevis*) 'red tide' in 1954, but no daily rates were compared with primary production. Net community production (NCP) and dark respiration rates were assessed from oxygen light-dark bottle incubations during a *K. brevis* bloom in 2006 (Hitchcock et al., 2010), where production frequently exceeded respiration in 24 h incubations. In summary there are few in situ respiration measurements from dinoflagellate blooms to assess the respiration demands relative to primary production. If maximum respiration rates consume a relatively high proportion of primary production in dinoflagellate populations, then the net primary production over a diel period may be relatively lower in blooms than in 'non-bloom' communities.

This study examined the diel pattern in net oxygen production and respiration in the surface plankton communities of Sarasota Bay, Florida. A series of diel records of oxygen were completed both before, and during, a *Karenia brevis* bloom. Diel oxygen cycles were recorded with an automated productivity sampler (Langdon, 1993b) that contained an oxygen probe within a 2 l clear polycarbonate chamber. The instrument was deployed in New Pass FL adjacent to the dock of the Mote Marine Laboratory. Dissolved oxygen concentrations were recorded at 10 min intervals from dawn-to-dusk to estimate diurnal net production (P_d), while nocturnal respiration (R_n) was calculated from the decrease in oxygen between dusk and dawn. Diel oxygen cycles have been frequently recorded in estuarine surface waters with oxygen sensors to estimate primary production and respiration, as well as net community metabolism (Caffrey, 2004). Oxygen sensors have typically been deployed in the 'open water' mode as described by Odum (1956). However, in an open water deployment the oxygen concentrations must be evaluated for advection (Kemp and Boynton, 1980; Caffrey, 2003) and air-sea exchange (Kremer et al., 2003). The main objectives of this study were to compare estimates of P_d and R_n in a *K. brevis* bloom, and examine variations in respiration over diel cycles. The productivity sampler enclosed a surface water sample at dawn, when *K. brevis* was concentrated near the surface (Heil et al., 2014). If R_{max}:P_{max} ratios are generally higher in dinoflagellate-dominated communities, then we hypothesized that relative to R_n, P_d may be less during a *K. brevis* bloom than during 'non-bloom' periods.

2. Materials and methods

2.1. Study location

Sarasota Bay is a shallow subtropical estuary on the west coast of Florida with an average depth of 2 m. The productivity sampler was deployed near the dock of the Mote Marine Laboratory (27.33396° N, 82.57913° W) in New Pass, an entrance to the northern basin of Sarasota Bay (Fig. 1). Environmental conditions recorded by a weather station on the dock include air and water temperature, and photosynthetic active radiation (PAR) as μmol (photons) m^{-2} s^{-1}. The environmental data is available at http://isurus.mote.org/newpass/newpass_get_weather.phtml.

A bloom of *Karenia brevis* began in July 2006 near Ft Myers Florida, approximately 120 km south of Sarasota Bay. Throughout August the bloom expanded north along the coast, and was first detected in Sarasota Bay in September. Maximum cell densities in Sarasota Bay in September exceeded 10^6 cells l^{-1} (Hitchcock et al., 2010). In October *K. brevis* cell densities deceased along the entire west Florida coast, with cell abundances in Sarasota Bay < 5000 cells l^{-1}. No *Karenia* cells were reported from any west coast samples in December.

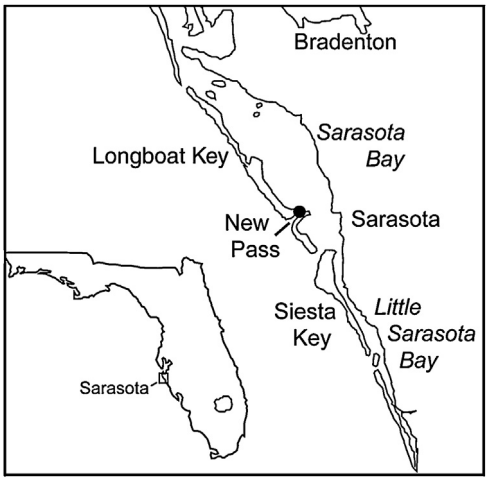

Fig. 1. Location of the productivity autosampler deployed in New Pass, Florida.

2.2. Productivity sampler

The productivity sampler provides automated sampling and measurements of dissolved oxygen concentrations at prescribed times within an incubated sample (Langdon, 1993b). The samplers have been deployed in the North Atlantic to record surface productivity on surface drifters (Langdon et al., 1995) and configured as respirometers with darkened chambers in Narragansett Bay (Langdon, 1993b). The Sarasota Bay deployments configured a sampler with a 2 l clear polycarbonate incubation chamber (Supplemental Fig. 1). Dissolved oxygen concentrations within the chamber were recorded by a pulsed oxygen electrode with an accuracy of ±3 μmol O_2 l^{-1} and a precision of 0.1 μmol O_2 l^{-1} (Langdon, 1984). The pulsed sensor has a drift of ≤0.5 μmol O_2 l^{-1} over periods of several weeks (Langdon, 1993b). Metal parts are encased in PVC, and silicone o-rings seal the chamber to reduce potential contamination.

The sampler was suspended vertically from a clear PVC frame with the top of the chamber 30 cm below the surface. The chamber opened for an hour at 06:00 local time. After the chamber closed at 07:00, dissolved oxygen concentrations were recorded at 10-min intervals throughout the next 23 h. *Karenia brevis* populations sampled at a mean depth of 50 cm below the surface at 06:00–07:00 local time likely sampled maximum *K. brevis* cell concentrations, as it is unlikely that surface aggregation behavior (Heil et al., 2014) was occurring at this hour. Hourly rates of diurnal production and nocturnal respiration were computed by a moving average (Legendre and Legendre, 1983) from seven consecutive dissolved oxygen measurements. The data are plotted from the mid-point of the seven measurements, with one value every 30 min (e.g., 00:00, 00:30, 01:00, etc.). Moving point averages of shorter time intervals (e.g. a three point moving average) produced erratic time series, which was attributed to variability in dissolved oxygen at the accuracy of the oxygen probe.

2.3. Deployments

During the 'pre-bloom' phase a total of three deployments of 2 days each were conducted on May 10–11, May 22–23, and June 2–3. A six-day deployment was conducted on September 14–19 that