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Light-mediated release of dissolved organic carbon by phytoplankton

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ABSTRACT

Laboratory and field studies were carried out to examine the effects of irradiance variability on dissolved organic carbon (DOC) extracellular release by phytoplankton (ER) and the response of natural bacteria assemblages. In axenic laboratory cultures, ER was 3× greater in cultures shifted to 330 μmol photons m^{-2} s^{-1} compared to cultures kept at their cultured irradiance, 110 μmol photons m^{-2} s^{-1}. Natural bacterial assemblages incubated in the dark for 24 h in algal-free culture filtrate generated from both light treatments consumed the DOC from the high-light treatment at a faster rate than that for the low-light treatment. Field measurements in the coastal waters of the northeastern Gulf of Mexico (GOM) and the Eastern North Pacific (ENP) mirrored the laboratory findings, with short-term increases in DOC concentrations occurring concurrently with short-term increases in irradiance, followed by rapid consumption by bacteria. Where no diurnal irradiance increase was observed (overcast skies), no increase in DOC concentration was observed. An experiment using ^{14}C as a tracer for plankton interactions (GOM) was consistent with data on bulk DOC concentrations. For all the field measurements, the rate of irradiance change was correlated with the quantity of DOC released. Collectively these results indicated that release of DOC by phytoplankton populations as a function of incident irradiance can be significant and may have important implications for estimates of ocean carbon flux.

1. Introduction

DOC in the ocean is one of the largest reservoirs of carbon on the planet (Hansell and Carlson, 1998). Small changes in this inventory, therefore, can profoundly affect fluxes of carbon across the ocean surface and the export flux of carbon to depth (Carlson, 2002). Although sources and sinks for DOC have been identified (Hansell and Carlson, 2001), limited data exist regarding changes to the inventory. Marine DOC concentrations are generally found in a narrow range (40–80 μM C; see Carlson, 2002) within larger variations in net primary production (Behrenfeld and Falkowski, 1997). These relative variations may indicate tight coupling between production and consumption processes (Carlson and Ducklow, 1996). For example Lancelot and Billen (1984) demonstrate tightly coupled short-term oscillations between primary and bacterial production in the North Sea and the English Channel. Experiments conducted by Carlson and Ducklow (1996) in the northwestern Sargasso Sea show increased bacterial production when the ambient labile DOC concentration is higher than the average mixed layer concentration. Similarly rapid turnover of labile plankton-derived DOC has been demonstrated in northeastern Pacific surface waters (Cherrier and Bauer, 2004; Cherrier et al., 1996). On the other hand, Fouilland and Mostajir (2010) in their analysis of an extensive database going back to Cole et al. (1988), conclude that bacteria are independent of phytoplankton activities, a controversial conclusion (see Fouilland and Mostajir, 2011; Morán and Alonso-Sáez, 2011).

Current satellite based estimates put oceanic primary production at 41–77 Gt yr^{-1} (del Giorgio and Duarte, 2002). As satellite sensors cannot 'see' dissolved primary production, estimates from satellite ocean color probably miss the effects of dissolved organic carbon (DOC) release on net community production. In fact, much of the organic carbon contributed by phytoplankton to the upper ocean (possibly more than 50%) is in the dissolved form (del Giorgio and Cole, 1998; Williams, 2000, 2004). For this reason, the oceanic flux of carbon may be underestimated (Marañón et al., 2004).

After decades of research, the consensus (Carlson, 2002) is that extracellular release (ER) is a normal function of phytoplankton cells. It averages about 13% of primary production, while varying between 0 and 80%, and appears to be related to the level of productivity (Baines and Pace, 1991; Lancelot, 1983; Lancelot and Billen, 1984; Morán and Estrada, 2001; Zlotnik and Dubinsky, 1989). Beyond this, Carlson (2002) notes little agreement on the environmental conditions influencing ER, that is, how it might be affected by high or low irradiance, or nutrients. Literature reports going back to the 1970s suggest that phytoplankton release DOC under changing irradiance conditions (Hu and Smith, 1998; Mague et al., 1980; Panzenbock, 2007; Thomas, 1971; Wood et al., 1992).

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Despite the recognition of the relationship between light and DOC release, this phenomenon has not been formally quantified with respect to its potential contribution to the global carbon budget nor has it been analyzed with respect to its impact on the microbial food web. Here we report experiments that examine the effects of short-term changes in irradiance on dissolved organic carbon release by phytoplankton and the response of heterotrophic bacteria. We first present results from laboratory experiments demonstrating ER in a diatom in response to a transition to high irradiance, and utilization of the released DOC by natural assemblages of bacteria. In a second set of experiments, we show that the quantity of DOC in surface waters can vary with natural irradiance variability, and use ^{14}C to trace the flow of carbon into the phytoplankton, to released DOC, and into bacteria over the course of a photoperiod.

2. Methods

2.1. Culture experiments

Time series culture experiments were carried out first to assess DOC release by the centric marine diatom, *Thalassiosira weissflogii*, as a function of increased irradiance, and second, to evaluate the utilization of the light-mediated DOM exudate by indigenous bacterial populations. Axenic cultures of *T. weissflogii* were obtained from the Provasoli-Guillard National Center for Culture of Marine Phytoplankton (CCMP). Cultures were grown and maintained with sterile f/10 media (Guillard, 1975) in a temperature-controlled circulating water tank kept at 20 °C. The cultures were grown at 110 μmol photons m^{-2} s^{-1} (saturating for this species) supplied by Phillips 40 W cool-white fluorescents on a 12:12-h light:dark cycle. Cultures were periodically tested for the presence of marine bacteria (i.e. General Marine Test Medium, CCMP), and were monitored daily for growth via *in vivo* fluorescence (Turner Designs 10-AU). Cultures were considered acclimated when there was no significant difference between the slopes of four or more growth curves (*F*-test, Zar, 1996). Single-day experiments were performed when cultures were in early-exponential growth and timed so that they occurred while all flasks exhibited similar fluorescence readings.

For the first culture-based experiment, inocula from the axenic *T. weissfloggii* cultures in early-exponential growth were placed in 4 L flasks with 3 L of sterile f/10 media, and returned to the tank. At the beginning of the photoperiod 4 d later (T0), flasks were either exposed to higher irradiance (330 μmol photons m^{-2} s^{-1}) or maintained at the same irradiance levels (110 μmol photons m^{-2} s^{-1}). Due to a limitation of temperature-controlled circulating water tanks for this experiment, incubations with light-shifted cultures and those maintained at lower light were carried out sequentially. The average chlorophyll-a (Chla) per cell at the beginning of the incubations was 1.3 pg Chla $cell^{-1}$. Both the low- and high-light cultures were sampled at intervals over the course of the 12 h incubation, for enumeration and bulk DOC concentration measurements. Phytoplankton samples (10 mL) were preserved with 2% acid Lugol's solution (Throndsen, 1978). The remaining 100 mL was gently vacuum-filtered through precombusted GF/F filters (effective pore size, 0.7 μm) and the filtrate was distributed into precombusted (525 °C for 4 h) EPA VOA vials with HCl-washed Teflon-lined caps, and frozen for subsequent analysis of DOC. Incubations were run in triplicate.

There was not enough culture filtrate after the above experiment for subsequent time series incubations to evaluate bacterial utilization of the light-mediated DOC exudate. Thus, a separate experiment was conducted using the same protocol for both growing the *T. weissflogii* and exposing the cultures to varying irradiances, but no subsamples were removed over the 12-h incubation period. Instead, after 12 h, the diatoms were removed via gentle vacuum filtration through precombusted GF/F filters and the filtrate saved to serve as the inoculum media for the bacterial utilization experiment. The average DOC concentration of the filtrate produced by light-shifted cultures was 151 μM and that for cultures maintained at lower light was 68 μM (Fig. 1b).

Natural planktonic bacterial assemblages were concentrated from seawater collected before dawn at Shell Point, FL, a pristine estuary approximately 50 km south of Tallahassee, FL. Seawater samples were collected from just below the surface into HCL-leached polycarbonate carboys and stored in the dark for transport back to the lab for processing (transport and processing completed within 2 h). In the laboratory, the seawater was first filtered through precombusted GF/F filters (as previously described) to remove larger organisms and detritus, and the bacteria were concentrated into 0.2 μm micro-culture capsules (Pall Corp.). This protocol ensured that no extraneous particulate carbon substrates were introduced into the incubation, but also possibly resulted in an underestimate of bacterial utilization of the light mediated DOM exudates because we were removing all bacteria >0.7 μm as well as any attached to particles.

The concentrated planktonic bacteria were then resuspended into the appropriate light treatment filtrate within 1 h of the removal of the diatoms. Bacterial concentration at the initiation of the experiment was 10^8 cells L^{-1}. Each of the bacterial incubations was run in 3 L flasks,

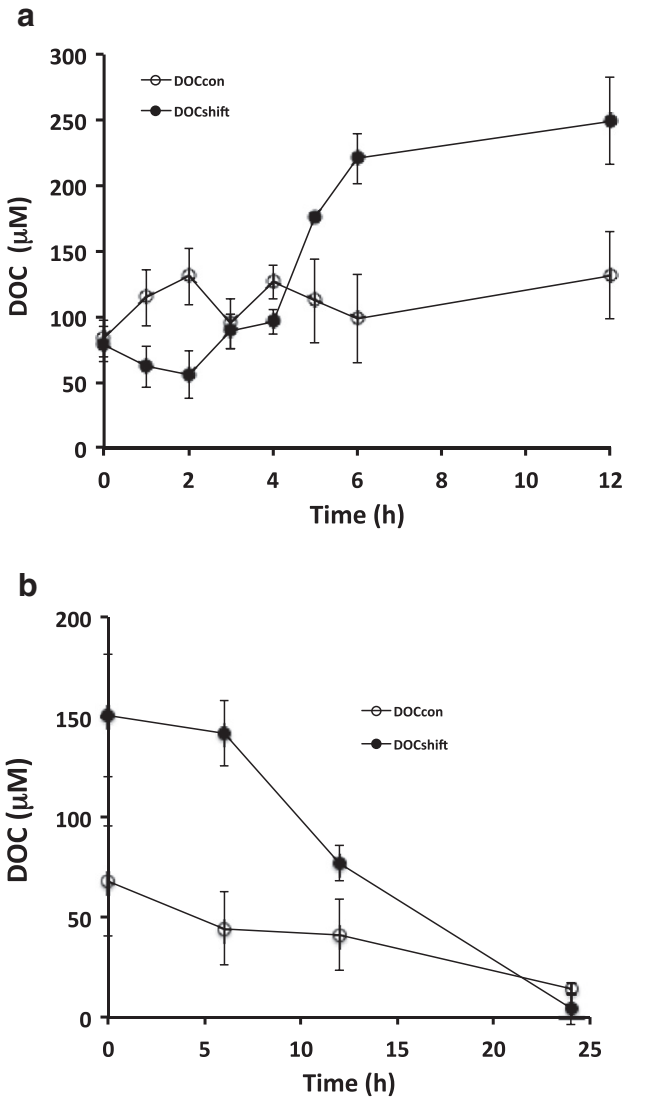

Fig. 1. a. Change in DOC concentration for axenic *Thalassiosira weissflogii* cultures shifted to 330 μmol photons m^{-2} s^{-1} (●) and those kept at their growth irradiance (110 μmol photons m^{-2} s^{-1}) (○) over the course of a 12 h photoperiod. Error bars represent ±1 standard deviation of triplicate samples. Experimental incubations were carried out sequentially. b. Change in DOC concentration over a 24 h period for bacteria incubated in filtrate derived from the light shifted culture (●) and those kept at their growth irradiance (○). Error bars represent ±1 standard deviation of triplicate samples.

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