Light fluctuations are key in modulating plankton trophic dynamics and their impact on primary production

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Light fluctuations are key in modulating plankton trophic dynamics and their impact on primary production

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Scientific Significance Statement

In the North Atlantic ocean, the deepest depth to which surface waters mix has been considered a key factor controlling initiation of the spring phytoplankton bloom, because mixing affects light availability for phytoplankton growth of vertically entrained cells. However, the effect of mixing-related light availability on the relative rates of phytoplankton growth vs. losses due to herbivorous grazers is not well known. Based on at-sea incubation and light-manipulation experiments, this study provides evidence that phytoplankton’s instantaneous and herbivores delayed responses to light fluctuations are key modulators of the balance between phytoplankton growth and grazing rates, suggesting light as a potential, easily retrievable predictor of when and where in the ocean grazing may represent a noteworthy loss factor of phytoplankton production.

Abstract

Surface-ocean mixing creates dynamic light environments with predictable effects on phytoplankton growth but unknown consequences for predation. We investigated how variations in average mixed-layer (ML) irradiance shaped plankton trophic dynamics by incubating a Northwest-Atlantic plankton community for 4 days at high (H) and low (L) light, followed by exposure to either sustained or reversed light intensities. In deep-ML (sustained L), phytoplankton biomass declined ($\mu = -0.2 \pm 0.08 \text{ d}^{-1}$) and grazing was absent. In shallow-ML (sustained H), growth exceeded grazing ($\mu = 0.46 \pm 0.07 \text{ d}^{-1}; g = 0.32 \pm 0.04 \text{ d}^{-1}$). In rapidly changing ML-conditions simulated by switching light-availability, growth and grazing responded on different timescales. During rapid ML-shoaling (L to H), $\mu$ immediately increased (0.23 ± 0.01 d$^{-1}$) with no change in grazing. During rapid ML-deepening (H to L), $\mu$ immediately decreased (0.02 ± 0.09 d$^{-1}$), whereas grazing remained high ($g = 0.38 \pm 0.05 \text{ d}^{-1}$). Predictable rate responses of phytoplankton growth (rapid) vs. grazing (delayed) to measurable light variability can provide insights into predator-prey processes and their effects on spatio-temporal dynamics of phytoplankton biomass.

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Author Contribution Statement: F.M. conceived the study. F.M., G.F., and E.H. collected the data. All authors analyzed the data and contributed to writing the manuscript.

Data Availability Statement: The data sets generated for this study are available at the SeaWiFS Bio-optical Archive and Storage System (SeaBASS) maintained by the NASA Ocean Biology Processing Group. Data can be accessed at https://seabass.gsfc.nasa.gov/archive/URI/menden-deuer/NAAMES/naames_3/archive/NAAMES3_AT38_PlanktonLightExperiment_Sta6.txt.

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The North Atlantic spring phytoplankton bloom has traditionally been explained as resulting from changes in the ocean physical environment promoting phytoplankton growth. A large research focus has been placed on light as a primary factor limiting phytoplankton growth, and on unraveling mechanisms that alleviate phytoplankton light limitation. Among the factors that have been considered, the depth of active mixing, often described using the mixed layer depth (MLD) as a proxy, has received sustained attention (Sverdrup 1953; Huisman et al. 1999; Siegel et al. 2002; Waniek 2003; Mahadevan et al. 2012; Ferrari et al. 2015) because MLD directly affects the light available for phytoplankton growth as cells are vertically mixed.

Over the past 10 yr, a hypothesis has been developed that links MLD to predator-prey processes (Behrenfeld 2010; Behrenfeld and Boss 2014). This hypothesis, known as the Disturbance-Recovery Hypothesis (DRH), focuses on the balance between phytoplankton growth and grazing losses, the latter largely due to herbivorous protists (Steinberg and Landry 2017). The DRH proposes that MLD-driven seasonal alterations in predator-prey coupling act as a key mechanism governing phytoplankton biomass accumulation rates and how they vary over the yearly cycle, including when the spring bloom initiates (Behrenfeld and Boss 2014). Changes in MLD can affect plankton concentrations, thereby influencing encounter rates between planktonic predators and prey (Prairie et al. 2012). Importantly, fluctuations in MLD are also associated with fluctuations in irradiance, both of which can be large and rapid (Morison et al. 2019). While the predictable effect of light on phytoplankton growth is incorporated into many models, the effect of light changes on grazing is poorly known and generally not considered.

Studies on the direct effect of light on grazing are scarce. Evidence that grazing can be enhanced under increased irradiance largely relies on species-specific responses measured in laboratory settings that may not be representative of in situ community response (Strom 2001 and see references in Moeller et al. 2019). Light may affect grazing indirectly if grazers feed at higher rates on faster growing prey cells (Strom 2002 and references therein), or via the influence of light on phytoplankton size-structure (Finkel et al. 2004). Few studies have investigated the effect of irradiance on the coupling between phytoplankton growth and grazing mortality rates in natural open-ocean plankton communities. Using dilution experiments conducted at multiple depths, Landry et al. (2011) observed a decoupling of growth and loss processes at depth due to larger vertical decrease in growth than in grazing. Other studies using light manipulations (Calbet et al. 2012) or vertical transplants of natural communities (Gutiérrez-Rodríguez et al. 2016) have yielded conflicting results that indicated either tightening or loosening of the level of coupling with decreased irradiance.

Our objective was to identify how shifts in MLD influence the balance between phytoplankton growth and mortality due to microzooplankton grazing. During a North Atlantic cruise, we incubated an in situ plankton community using light manipulations as proxies for hypothetical, yet realistic scenarios of large shifts in MLD, which are frequently observed in the North Atlantic during the springtime “transition” (Waniek 2003; Lacour et al. 2017; Morison et al. 2019). Our results suggest that based on the temporal and directional variability of the average irradiance in the mixed layer, it may be possible to predict the relative dynamics of phytoplankton growth and grazing losses.

**Methods**

The experiment was conducted during the third campaign of the North Atlantic Aerosols and Marine Ecosystem Study (NAAMES) aboard the R/V Atlantis (Behrenfeld et al. 2019). The sampling station, located at 53°18′N and 39°30′W, was occupied from 13 September 2017 to 18 September 2017.

**Experimental setup**

On September 14 (T0), surface seawater (8 m) was collected predawn using the CTD rosette sampler. Seawater was gently transferred from the Niskin bottles into six 4-liter polycarbonate bottles via a silicone tube, with a 200 μm mesh to remove mesozooplankton. Bottles were amended with 10 μmol L\(^{-1}\) nitrate and silicate and 1 μmol L\(^{-1}\) phosphate. Sets of replicate 4-liter bottles were placed in two separate deck-board incubators covered with screening mesh that reduced incoming irradiance to approximately 1% and 65%. Incubators were maintained at ambient sea-surface temperature by ship-supplied flow-through seawater. A data-logger (Onset Hobo) in each incubator recorded light intensity (lux) and temperature at 5 min intervals. Incident photosynthetically active radiation (PAR) data were obtained from ship measurements (see Graff and Behrenfeld 2018). Incubations lasted 4 days (T0–T96), a duration representative of the timescale of the intermittent nature of the mixing layer in the North Atlantic (Lacour et al. 2017; Morison et al. 2019).

After 4 days (T96), water from all bottles in each light treatment was pooled, and used to determine rates of phytoplankton growth and grazer-induced mortality under four simulated mixing scenarios: (1) Sustained deep-mixing: water originating from the low light treatment was incubated maintaining the same low light intensity; (2) Rapid mixed-layer shoaling: water from the low light treatment was incubated under the opposite high light treatment; (3) Sustained shallow-mixing: water originated from the high light treatment was incubated maintaining the original high light intensity; and (4) Rapid mixed-layer deepening: water from the high light treatment was incubated under the opposite low light treatment.

Rates were quantified using the two-point dilution method (Chen 2015; Morison and Menden-Deuer 2017). The experiments followed our standard protocol (Morison et al. 2019).
and included duplicate bottles of both whole seawater (100% WSW) and 20% WSW dilution treatment. Due to limited water volume, to obtain the filtered seawater needed for the dilution, we used GF/F filtrate (0.7 μm) obtained from chlorophyll a (Chl a) analyses done at the same station, and filtered it further through a 0.45 μm cartridge filter (Pall). Bottles were amended with macronutrients as described above. To serve as a nutrient control, an additional 100% WSW bottle was prepared without adding nutrients. Bottles were placed in the treatment-relevant deck-board incubators for 24 h. To provide gentle agitation, the bottles were suspended from lines running across the top of the incubators.

Chl a and grazer community composition analyses

Subsamples were taken at T0 from the source seawater, and again at T48 and T96 from each replicate bottle. These subsamples were used for analyses of Chl a (80 mL) and for Lugol’s preserved samples to quantify microzooplankton species composition and abundance (T0 = 500 mL, T48 and T96 = 100 mL from each replicate bottle). Chl a extraction and determination followed Morison and Menden-Deuer (2017). Microzooplankton were enumerated using the Utermöhl (1958) method. Settled volumes of 10–25 mL were used and the entire surface area of the chamber was counted at ×200 magnification. All ciliates and > 15 μm dinoflagellates were enumerated. Taxa known to be mixotrophic were distinguished from heterotrophic taxa (Stoecker et al. 2009; Jeong et al. 2010; Flynn et al. 2013 and references therein). Microzooplankton biomass was estimated based on approximated geometric shapes and published volume to carbon conversion factors (Putt and Stoecker 1989; Menden-Deuer and Lessard 2000). Although heterotrophic nanoflagellates contribute to the grazing rates measured, they were not enumerated as the Utermöhl method underestimates their abundance (Davis and Sieburth 1984).

Rate estimation

Phytoplankton growth and herbivorous grazing rates were estimated from changes in total extracted Chl a. The Chl a measurements made at the final time-point of the 4-day incubation (T96) were used for the initial 100% WSW treatment, and Chl a concentration was further determined in triplicates from the initial 20% WSW dilution, and from each replicate bottle at the end of each experiment. The phenotypic responses of phytoplankton cells to changes in ambient light conditions known as photoacclimation (Gutiérrez-Rodriguez et al. 2010 and references therein) can introduce artifacts in estimating phytoplankton growth rates. Therefore Chl a was adjusted following Morison et al. (2019), using flow-cytometry (FC) data obtained from 200 μL aliquots of < 40 μm screened WSW analyzed live on a Guava® easyCyte Flow Cytometer. Samples were run at 14.4 μL min⁻¹ for 3 min. Three phytoplankton groups (Synechococcus spp., pico- and nanoeukaryotes) were distinguished based on their forward scatter and red (695/50) emission parameters with 488 nm excitation, and orange (620/52) emission parameters with 532 nm excitation. For each sample, we calculated a photoacclimation index (Phi) from initial and final FC measurements of red fluorescence to forward scatter ratio (FLR : FSC), the latter being used as a proxy for Chl a : carbon. These ratios were obtained for each phytoplankton group, weighted according to each group’s contribution to total FLR, and summed to obtain a phytoplankton community ratio. The 4-day incubation bottles had initially been amended with nutrients, which may have influenced their Phi estimates (Cloern et al. 1995); however, no difference in_phi was found between nutrient-amended and non-amended dilution-experiment bottles. Phi values < 1 indicate a decrease in the FLR : FSC ratio (i.e., less Chl a per unit of biomass), values > 1 indicate an increase in the ratio (more Chl a per unit of biomass), and values = 1 indicate no change. The apparent phytoplankton growth rate (k, d⁻¹) in each bottle was then estimated taking Phi into account by using the equation

\[ k = \left(1 + \Phi \right) \left(\frac{P_D}{P_O} - 1\right) \]

where \( P_D \) represents the achieved dilution factor in the diluted treatment determined from initial Chl a concentration. Phytoplankton in situ instantaneous growth rates (μ, d⁻¹) were determined as the sum of the grazing rate and the apparent growth rate in the WSW treatment without added nutrients, using the equation

\[ \mu = P_D \left( k - \left(1 - \Phi \right) \right) \]

where \( P_D \) and \( P_O \) are Chl a concentration at the beginning and the end of the experiment.

Grazing rates (g, d⁻¹) were calculated based on k values from nutrient-amended replicates using the equation

\[ g = \left(k_{\text{dil}} - k_{\text{1}}} \right) / \left(1 - D\right) \]

where the subscripts dil and 1 correspond to the nutrient-amended diluted and undiluted treatments, respectively, and D represents the achieved dilution factor in the diluted treatment determined from initial Chl a concentration. Phytoplankton in situ instantaneous growth rates (μ, d⁻¹) were determined as the sum of the grazing rate and the apparent growth rate in the WSW treatment without added nutrients, using the equation

\[ \mu = m + k_{\text{100N}} \]

Accumulation rates (r) were estimated as \( r = \mu - g \), and primary production consumed (%PP) was determined as the \( g : \mu \) ratio.

Results

Incubation conditions

During the 4-day incubation, daily-integrated incident PAR averaged 16.8 ± 4.8 mol m⁻² d⁻¹, ranging from 11.3 mol m⁻² d⁻¹ on the first day to 21.4 mol m⁻² d⁻¹ on the third day. Light intensity in the incubators reflected the daily variations in PAR. A constant difference in light intensities between the high and low light treatments was maintained, the light intensity in the low light treatment representing an average of 8% ± 2% of that in the high light treatment, excluding the first day when it was only 1.5%. Water temperature in the high light incubator averaged 12.3°C compared to 12°C in the low light incubator.

Plankton community

At T0, small cells dominated the phytoplankton community. The < 10 μm fractions represented 81% of total Chl a concentration (0.9 ± 0.06 μg L⁻¹; Fig. 1a). Over the 4 days at low light, Chl a increased by approximately 40%, most of it during the first 48 h, and at high light Chl a continuously increased by a total of 180% (Fig. 1b). In order to quantify
how much of the increases in Chl $a$ were due to cells’ photo-physiological response to changes in light-exposure, we quantified changes in FLR : FSC ratios from the FC data (Fig. 1c). This approach was validated by the significant good agreement between total FLR and corresponding Chl $a$ concentration for all samples analyzed over the entire duration of the experiment (model II regression, $p < 0.0001$, $R^2 = 0.95$), suggesting that the FC analyses captured the bulk of the phytoplankton community (Fig. 1d). At low light, the initial 48 h increase in Chl $a$ was largely due to cellular adjustment in pigment content, with no further adjustment after 48 h (Fig. 1c). When photoacclimation was taken into account to provide biomass-based estimates of phytoplankton accumulation rates (Table 1), at low light there was no significant difference between the first and last 48 h in phytoplankton accumulation rates ($t$-test, $n = 3$, $p = 0.12$). High light accumulation rates were ~ 40 times greater than accumulation rates at low light (overall averages: $0.38 \pm 0.02 \text{ d}^{-1}$ vs. $0.01 \pm 0.03 \text{ d}^{-1}$, respectively; Fig. 1e).

The grazer community was composed of ciliates and dinoflagellates in similar proportions. At T0, total abundance was 16,000 cells L$^{-1}$, 56% of which were dinoflagellates and the remaining 44% were ciliates, yet ciliates contributed the larger fraction of total biomass (54% of 16.8 $\mu$g C L$^{-1}$). The majority of dinoflagellates (59%) were < 20 $\mu$m, but cells > 20 $\mu$m contributed the larger fraction of the biomass (57%). The same was true for ciliates, whose abundance was dominated by < 20 $\mu$m organisms (56%), but whose biomass was dominated by > 20 $\mu$m cells (84%), mainly due to the presence of 25–40 $\mu$m Strombidium spp. Species known to be mixotrophic dominated both abundance (70%) and biomass (78%). On T96, microzooplankton biomass had increased by ~ 25% at high light (20 $\mu$g C L$^{-1}$) whereas a slight decrease was observed at low light (15.7 $\mu$g C L$^{-1}$). There was no major

![Figure 1](image.png)

**Fig. 1.** Characterization of the phytoplankton community incubated for 4 d under low and high light intensities: (a) chlorophyll size distribution in the source water used in the incubation (T0). (b) Total Chl $a$ concentration ($\mu$g L$^{-1}$) over time (hours) under the two light regimes. (c) Photoacclimation index calculated using flow cytometry data of red fluorescence (FLR) and forward scatter (FSC). Values < 1 indicate a decrease in fluorescence per unit of biomass, values > 1 indicate an increase in fluorescence per unit of biomass, and values = 1 indicate no change (see the text for details). (d) Ordinary least squares linear regression (model II) of flow cytometry measurements of total red fluorescence vs. extracted Chl $a$ ($\mu$g L$^{-1}$). Regression line is shown (red) with 95% confidence intervals (gray lines). (e) Phytoplankton biomass accumulation rates ($\text{d}^{-1}$) based on Chl $a$ shown in (b) adjusted for photoacclimation using indices shown in (c). For both (c) and (e), dark and clear symbols represent low and high light treatments, respectively. Error bars in (a), (b), and (e) represent one standard deviation of the mean of triplicate measurements.
change in the relative contribution of mixotrophic and heterotrophic taxa at either light intensity.

**Phytoplankton growth and grazing mortality rates under contrasting mixing scenarios**

Rates are summarized in Table 1. Sustained deep-mixing (Fig. 2a) induced a decline of phytoplankton biomass ($\mu = -0.2 \pm 0.08 \text{ d}^{-1}$) that was not explained by losses due to grazing ($g = 0$), which could have resulted from sustained exposure to low light affecting phytoplankton growth or from other potential sources of mortality, such as viral lysis or programmed cell-death (Bidle 2016), neither of which were quantified here. In contrast, under sustained shallow mixing (Fig. 2c), growth exceeded grazing ($\mu = 0.46 \pm 0.07 \text{ d}^{-1}$ vs. $g = 0.32 \pm 0.04 \text{ d}^{-1}$, respectively), resulting in 62% PP consumed. Under conditions that simulated rapid mixed-layer

### Table 1. Rates (± SD) of apparent phytoplankton growth (4-d incubation: $k$, d$^{-1}$) and instantaneous growth (mixing scenarios: $\mu$, d$^{-1}$) as well as grazer-induced mortality ($g$, d$^{-1}$) measured under experimental light manipulations (H = high light intensity, L = low light intensity). Growth rates ($k$ and $\mu$) are shown before and after adjustment for photoacclimation (see “Methods” section for details). There was no difference in photoacclimation between diluted and nondiluted treatments, and thus whether an adjustment was applied or not, grazing rates remained unchanged.

| Treatment                      | Light   | Nonadjusted rates | Adjusted rates | $g$ (d$^{-1}$) |
|-------------------------------|---------|-------------------|----------------|---------------|
| 4-day incubation              |         |                   | $k$            | $g$           |
| Phytoplankton net growth rates |         |                   | $k$            | $g$           |
| T0–T48                        | L       | 0.20 (0.02)       | 0.05 (0.02)    | —             |
| T48–T96                       | L       | −0.03 (0.06)      | −0.03 (0.06)   | —             |
| T0–48                         | H       | 0.31 (0.00)       | 0.44 (0.00)    | —             |
| T48–T96                       | H       | 0.22 (0.03)       | 0.30 (0.03)    | —             |
| Mixing scenarios              |         |                   | $\mu$          | $g$           |
| Phytoplankton instantaneous growth rates | | | | |
| Sustained deep-mixing         | L to L  | −0.13 (0.08)      | −0.23 (0.08)   | 0.00          |
| Rapid shoaling                | L to H  | −0.04 (0.08)      | 0.23 (0.08)    | 0.00          |
| Sustained shallow-mixing      | H to H  | 0.56 (0.07)       | 0.46 (0.07)    | 0.32 (0.04)   |
| Rapid deep-mixing             | H to L  | 0.45 (0.09)       | 0.02 (0.09)    | 0.38 (0.05)   |

**Fig. 2.** Rates (d$^{-1}$) of phytoplankton growth ($\mu$), grazing mortality ($g$), and biomass accumulation ($r$) under four mixed layer scenarios simulated using light as a proxy of (a) sustained deep mixing, (b) rapid shoaling, (c) sustained shallow mixing, and (d) rapid mixed layer deepening. Error bars represent one standard deviation of the mean of duplicate experiments. Grazing was measured but not detected in the sustained deep mixing and rapid shoaling conditions, denoted with x.
shoaling (Fig. 2b), growth was immediately enhanced relative to sustained low light exposure \( (\mu = 0.23 \pm 0.01 \text{ d}^{-1}) \), whereas no immediate light-enhancing effect on grazing was observed, with grazing rates not significantly different from zero. Under rapid mixed-layer deepening (Fig. 2d), growth was immediately negatively affected by light reduction \( (\mu = 0.02 \pm 0.09 \text{ d}^{-1}) \), whereas grazing \( (\gamma = 0.38 \pm 0.05 \text{ d}^{-1}) \) remained indistinguishable from the rate measured in the sustained high light treatment. The switch from high to low light was the only condition under which grazing exceeded growth and all PP was removed by grazing. Thus, changes in light intensity instantaneously altered phytoplankton growth rates, whereas grazing rates responded in a lagged fashion.

**Discussion**

The results presented here indicate that MLD-induced shifts in the average mixed-layer irradiance are key modulators of the balance between phytoplankton growth and grazing rates. These observations support an intriguing hypothesis that shifts in light availability could provide useful insights into the qualitative balance between growth and loss processes. Grazing pressure remains a challenging measurement with low data resolution across space, time, and environmental and biological conditions. Since irradiance is an easily and remotely measurable variable, it may be a useful predictor of when and where in the ocean grazing may represent a noteworthy loss factor of primary production.

Clearly, our experimental design did not reproduce the water-column variability in instantaneous light associated with turbulent mixing through a vertical light gradient (Franks 2015). “Static” incubations performed at a constant light may introduce artifacts in the estimation of in situ rates of phytoplankton growth (Ross et al. 2011). Our goal, however, was to identify the consequences for plankton population dynamics of shifts in average mixed-layer irradiance that accompany large and rapid changes in MLD. The included controls, which maintained constant light levels, allowed contrasting plankton responses to changing vs. constant light levels, and provide insights about the effect of the directionality of the light change (i.e., increase or decrease).

Our measurements show that growth and grazing responded to changes in light intensity on different timescales, providing insight into the mechanisms that contribute to fluctuations in phytoplankton biomass accumulation. Importantly, the response of grazing rates to rapid light switches was always delayed compared to phytoplankton growth rates, irrespective of the directionality. Ultimately, we propose that the offset in timescales of resource utilization, instantaneous for phytoplankton, delayed for herbivores, is a foundational process governing phytoplankton biomass accumulation.

Under the mixed-layer shoaling scenario, the decoupling between growth and grazing rates in response to a rapid increase in light opened a window of opportunity for phytoplankton biomass to accumulate. A similar delayed response of grazing vs. the immediate growth of phytoplankton during a rapid springtime ML shoaling following a deep mixing event has been observed in the North Atlantic and the resulting decoupling of growth from loss processes was identified as a contributing mechanism to the formation, patchiness, and magnitude of the spring bloom (Morison et al. 2019).

When a deep-mixing event was simulated by reduced light exposure following a period of sustained high light, phytoplankton growth rates immediately decreased in comparison with the sustained high light treatment, whereas grazing rates remained similar in magnitude in both light treatments. Obviously, these results do not take into account factors other than light affecting predator-prey processes when the mixed layer deepens, which were not reproduced in our experiments. Importantly, deep-mixing entrainment of plankton-free deep water is expected to reduce grazing rates by diluting plankton density, thus decreasing encounter rates (Landry and Hassett 1982; Visser and Kjørboe 2006; Behrenfeld 2010). Deep mixing would also dilute viruses, and thus limit viral infection (Mojica et al. 2016), although already infected cells may still be subject to lysis. There are cases, however, when surface plankton may be mixed down with limited dilution and change in predator-prey encounter rates. Dilution may be minimized if the depth of mixing remains within the euphotic zone, or if mixing entrains plankton by eroding a subsurface biomass maximum layer. Furthermore, plankton in surface waters can be subjected to rapid light fluctuations such as those simulated in our experiment due to daily changes in cloud cover, which according to our present findings could differentially affect growth and grazing rates.

Knowledge of grazing impact in the global ocean is based on invaluable but relatively sparse field measurements (Schmoker et al. 2013), which limits the crucial understanding of processes regulating primary production and export. Here we provide evidence that shifts in average irradiance, such as those induced by shoaling or deepening of the mixed layer, exert—within 24 h from when a shift occurred—a predictable effect on the balance between phytoplankton growth and grazing mortality. Thus knowledge of when and over what timescale these shifts in light availability occur could potentially serve as a predictive tool to develop a comprehensive understanding of the impact of grazing on ocean primary production. By retrieving daily records of PAR, such as can be obtained from satellite data at high spatial resolution (Frouin et al. 2012), it is possible to derive estimates of the daily average irradiance in the mixed layer using additional remote sensing products, such as PAR attenuation coefficient and MLD (Brewin et al. 2015). Similar estimates could also be derived using data from the myriad of free-drifting profilers crisscrossing the global ocean (Roemmich et al. 2009). A compiled time-series of average mixed-layer irradiance would reveal when, how often, and in what direction average

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irradiance changes, and application of our findings may be tested against actual data of primary production and accumulation rates, also retrievable from autonomous remote platforms. High temporal and spatial resolution of biological measurements, including rate estimates of plankton population dynamics, that can be obtained from remote platforms has remained challenging, thus an easily retrievable predictive variable such as light would be an invaluable tool to understanding ocean carbon cycling and ecosystem function.

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Conflict of Interest
None declared.