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Using Bio-Optics to Reveal Phytoplankton Physiology from a Wirewalker Autonomous Platform

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ABSTRACT. Rapid, wave-powered profiling of bio-optical properties from an autonomous Wirewalker platform provides useful insights into phytoplankton physiology, including the patterns of diel growth, phytoplankton mortality, nonphotochemical quenching of chlorophyll *a* fluorescence, and natural (sun-induced) fluorescence of mixed communities. Methods are proposed to quantify each of these processes. Such autonomous measurements of phytoplankton physiological rates and responses open up new possibilities for studying phytoplankton in situ, over longer periods, and under a broader range of environmental conditions.

INTRODUCTION

The Wirewalker (Rainville and Pinkel, 2001; Pinkel et al., 2011) is an autonomous platform that uses wave energy to propel an instrument package vertically along a wire suspended from a buoy at the sea surface, achieving roughly 200 profiles per day to 100 m depth. Because the energy required for profiling is independent of the battery payload, the Wirewalker can add an order of magnitude to the typical profiling frequency of other autonomous profiling platforms such as floats and gliders, which must allocate 30% to 60% of their energy toward buoyancy control. The ability to profile rapidly over long periods is important for resolving submesoscale physical dynamics, as described in Lucas et al. (2017, in this issue), and diel cycles in phytoplankton physiology, as shown here.

The Wirewalker profiling mechanism is relatively simple: when a cam within the profiler is engaged, the profiler can only descend, and is propelled downward by each wave oscillation. When the profiler reaches a stopper hose at the lower weighted terminus, the cam releases and the profiler ascends smoothly, decoupled from the wave motion. The descent rate of the Wirewalker depends on the amplitude and frequency of the surface wave field (Pinkel et al., 2011), though it successfully "walks" the wire under a broad range of wave conditions.

The Wirewalker assembly consists of a GPS-tracked surface buoy (Figure 1a), the wire (of variable length from 10 m to 500 m; Figure 1b), the instrumented Wirewalker platform (Figure 1c), and a ballast weight to maintain the wire in a vertical orientation under a range of wave and current conditions (Figure 1d). Various other instrumentation can be suspended at or below the ballast weight. For example, on a series of recent deployments, author Omand and colleagues used a bungee to absorb the wave energy (Figure 1e) and suspended an array of particle-intercepting sedimentation traps with a time-lapse marine snow camera (Figure 1f) and a second ballast weight below (Figure 1g).

This article presents bio-optical measurements from two Wirewalker deployments. The first data set is from a 48-hour deployment at 27.7°N, 139.5°W on a 125 m wire during Schmidt Ocean Institute's Sea to Space Particle Investigation in January/February 2017 (Figure 2). Sea state was high during the deployment, with 4 m significant wave height. The average descent rate of the Wirewalker was about 0.4 m s^{-1} and the ascent was 0.7 m s^{-1}, quickly reaching a terminal velocity determined by a combination of buoyancy and drag (Figure 2b). The time required to make a complete round-trip profile varied from seven minutes to 10 minutes (Figure 2a). Temperature, salinity, and depth were measured with a Maestro CTD system (Richard Branker Research), and an integrated WET Labs Ecotriplet measured chlorophyll *a* fluorescence (FL), chromophoric dissolved organic matter (CDOM), and backscatter at λ = 700 nm. Downwelling solar irradiance was measured with a JFE Advantech cosine miniature photosynthetically active radiation (PAR) sensor. Beam attenuation was measured with a WET Labs C-Star (λ = 550 nm) mounted vertically with brackets that allowed a minimally interrupted flow past the sensing volume during ascent. Beam attenuation coefficient (c_p) was converted to a proxy for particulate organic carbon concentration (POC_{cp}) following Claustre et al. (1999) and Cetiníc et al. (2012).

The second data set is from a six-day deployment in the Bay of Bengal in June 2014 as part of the Air-Sea Interaction Regional Initiative. FL was measured with a Turner Cyclops 7 fluorometer and physical variables with a Sea-Bird SBE 49. A TriOS Ramses hyperspectral cosine radiometer measured downwelling irradiance in ~3–4 nm width bands spanning from 300 nm to 950 nm. In the following sections, we describe three phytoplankton physiological responses implied from these Wirewalker deployments:

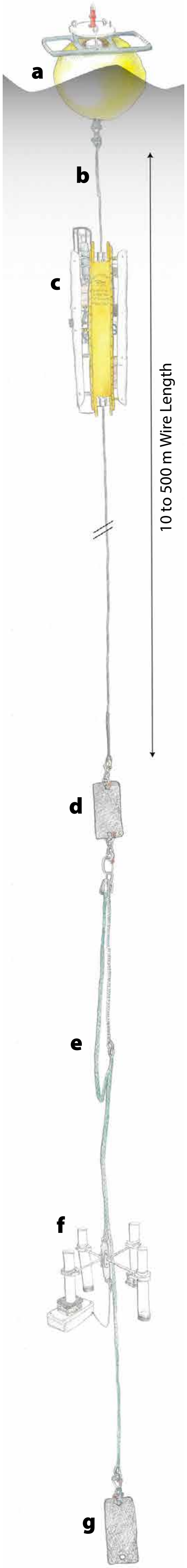

FIGURE 1. Components of the bio-optical Wirewalker platform. *Watercolor painting by M.M. Omand and K. Carlson*

(1) diel cycles in phytoplankton growth and losses, (2) nonphotochemical quenching of chlorophyll *a* fluorescence, and (3) natural (sun-induced) chlorophyll *a* fluorescence during daylight hours.

PHYTOPLANKTON GROWTH AND LOSS

During the 2017 deployment from R/V *Falkor* during the Sea to Space Particle Investigation, the Wirewalker approximately followed the ship-based current measurements integrated over the upper 60 m of the water column. The mixed layer (defined by $\Delta\rho$ = 0.05 kg m^{-3}) varied between 100 m and 125 m depth, with relatively homogeneous temperature and salinity characteristics throughout this layer and over the two-day deployment. In contrast, POC_{cp} (Figure 2c) and FL (Figure 2e) showed a marked diel cycle. We assume that at this oligotrophic open ocean site, variability in POC_{cp} is primarily due to changes in phytoplankton biomass. The depth-resolved time series of POC_{cp} reveals a minimum at dawn and a maximum at dusk, reflecting losses at night, and growth + losses (A in Figure 2d) during the day. This finding is consistent with other studies that have observed diel cycles in c_p or dissolved oxygen concentration within the euphotic zone from moorings (Stramska and Dickey, 1992) and floats (Claustre et al., 1999; Dall'Olmo et al., 2011).

Following these prior studies, a linear fit between POC_{cp} and time (red dashed line, Figure 2d) is applied to the nighttime declines in POC_{cp}. These declines in POC_{cp} may be due to grazing, remineralization, vertical mixing, or sinking of particles. Assuming that the losses are constant between night and day, the fits are extrapolated to local noon, and the difference ΔPOC_{cp} calculated (B in Figure 2d). This reflects the total amount of phytoplankton growth through photosynthesis that occurred over the course of the day. An equation reflecting this balance can be written as

$$\frac{\Delta POC_{cp}}{\Delta t} = \mu \overline{POC_{cp}}, \tag{1}$$

where ΔPOC_{cp} is the difference between the two extrapolated curves (B in Figure 2d), Δt is the day length (here 11 hours), $\overline{POC_{cp}}$ is the average POC concentration over the 24-hour cycle, and μ is the growth rate. The losses can be calculated as the difference between the total change (A) minus the daytime change (B). This method requires a number of assumptions: that losses are constant between night and day, that there is little vertical or horizontal flux into or out of our system, and that c_p changes are primarily due to biomass changes (and not cell divisions/size, community, or advection of gradients). However, with appropriate measurements, many of these assumptions can be tested, and this method offers a way to autonomously measure two phytoplankton rates that are central to most coupled physical-biological models.

NON-PHOTOCHEMICAL QUENCHING

When a phytoplankton cell is exposed to light that exceeds the amount that can be used for photosynthesis, fluoresced, or efficiently quenched at the photosystem reaction centers, the cell sustains oxidative damage to the photosynthetic thylakoid membrane (Barber, 1994). As a result, phytoplankton have evolved various protective responses, collectively called non-photochemical quenching (NPQ). NPQ occurs

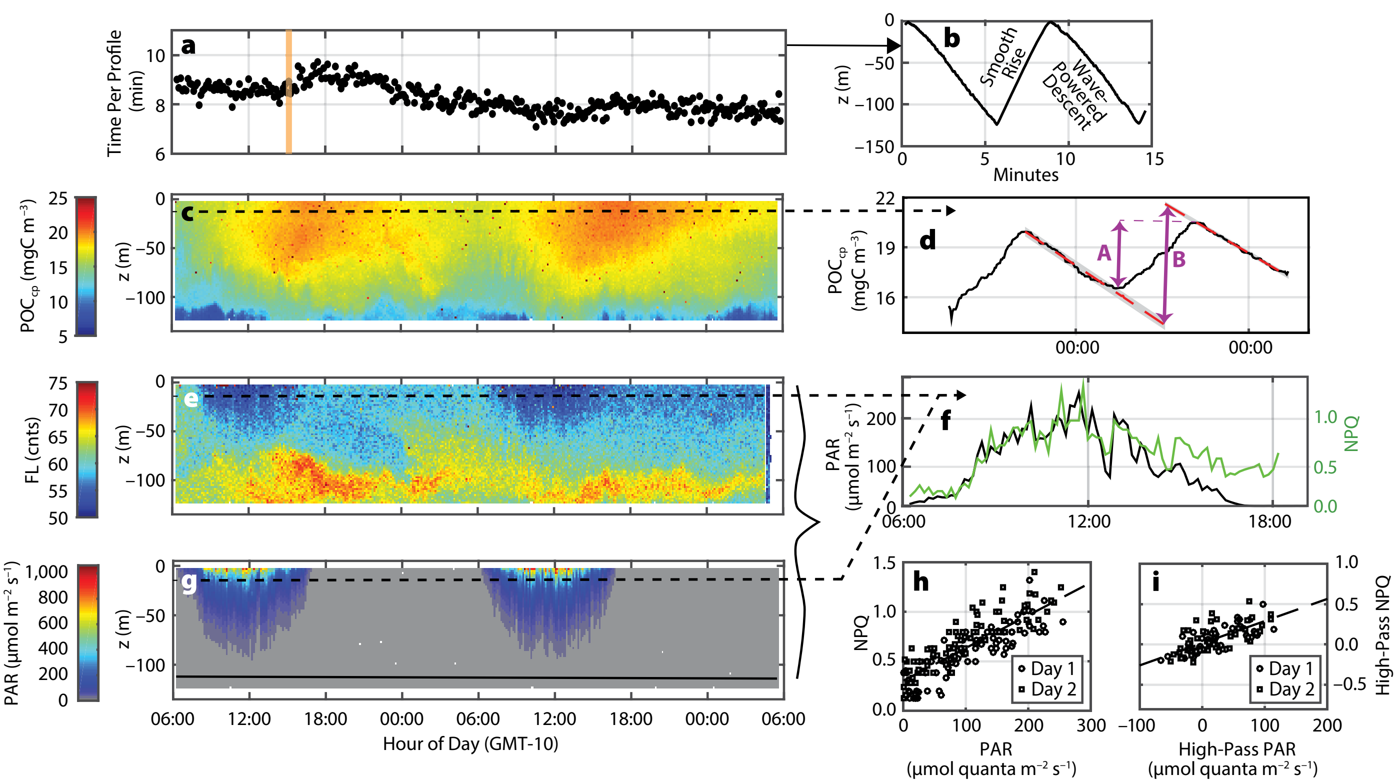

FIGURE 2. Data from a 48-hour Wirewalker deployment in the North Pacific subtropical gyre in February 2017. (a) Time series of the minutes between successive Wirewalker profiles, and (b) an example of two profiles (collected at 15:00). (c) Depth-resolved time series of particulate organic carbon concentration (POC_{cp}), and (d) the mean POC_{cp} over the upper 15 m of the water column, with linear nighttime fits (90% confidence intervals appear in gray) showing the net daytime growth (A) and extrapolated to reflect the total daytime growth (B). (e) Depth-resolved time series of chlorophyll *a* fluorescence (FL), and (g) photosynthetically active radiation (PAR). (f) The nonphotochemical quenching (NPQ, green) and PAR (black) over the upper 15 m of the water column show strong correlations (h) over the full diel cycle, and (i) after high-pass filtering. These patterns were consistent on both day 1 (circles) and day 2 (squares).

on various time scales, including rapid responses due to switching pigment from light harvesting to quenching, and slower ones that involve the manufacture of additional photo-protective pigments (Demmig-Adams and Winter, 1988) and results in suppression of FL (Figure 2d) under high light conditions (Figure 2f), as observed in the upper 50 m of the water column in the subtropical gyre. NPQ is defined as

$$NPQ = \frac{FL(t)_{dawn} - FL(t)_{day}}{FL(t)_{day}}, \tag{2}$$

reflecting the changes in FL over the course of the day relative to the dark-adapted FL just before sunrise. Wirewalker's rapid profiles allow a very highly resolved view (in depth and time) of this process. The NPQ (here averaged over the upper 15 m, green line, Figure 2f) increases over the course of the day, peaking at noon when PAR is also highest (black line, Figure 2f). NPQ is highly correlated with PAR over both days (r^2 = 0.73, Figure 2h). A high-pass filter applied to the time series (with a cutoff frequency of 0.3 cph) is also well correlated—demonstrating that much of the variability in FL is due to NPQ changes on time scales less than the 10-minute time scale of successive profiles (r^2 = 0.40, Figure 2i). In future studies, the Wirewalker may offer ways to unravel these various physiological responses, their rates, and their responses to variation in sunlight.

NATURAL FLUORESCENCE

During a cruise in the Bay of Bengal in June 2013, an upward-facing hyperspectral radiometer mounted on the Wirewalker (Lotliker et al., 2016) provided a proxy for "natural" (sun-induced) FL (e.g., Kitchen and Pak, 1987). In order to isolate the red light produced by FL from the downwelling solar irradiance, the measured light intensity between 680 nm and 685 nm was integrated, divided by the PAR, and plotted during daylight hours only (Figure 3a). This method yielded better results for isolating the natural FL signal than other methods, such as the line-height approach used to derive normalized fluorescence line height from ocean color (Behrenfeld et al., 2009). The natural fluorescence proxy is clearly related to the stimulated fluorescence, with both signals showing a subsurface maximum that is sandwiched between the 22 kg m^{-3} and 23 kg m^{-3} isopycnals (white lines, Figure 3). The relative difference between these two time series may reflect physiological changes over the day (because they reflect two different types of FL), or they may be due to methodological issues. The Wirewalker buoy has a small surface expression (~1.5 m^2), and a dark-colored underside helps to minimize shadowing and reflection. Analysis of data from an onboard tilt sensor and upward-facing GoPro camera is presently underway to determine the sensor angle relative to nadir and to quantify the effect of shadowing—all important factors in the pursuit of high-quality apparent optical properties (Kirk, 1994). Pending these analyses, the preliminary results shown here suggest that bio-optical sensors on the Wirewalker may one day allow us to autonomously determine the fluorescence quantum yield of mixed phytoplankton communities.

SUMMARY

Three types of phytoplankton physiological rates and responses are estimated from bio-optical measurements made using an autonomous Wirewalker platform: rate of growth and mortality over diel cycles, NPQ response to oxidation of phytoplankton cells, and a radiometric proxy estimated for natural chlorophyll *a* fluorescence. These methods offer the opportunity to broaden the coverage, durations, and range of environmental conditions in which we can evaluate phytoplankton physiological rates, but should be applied with caution. Vertical shear and horizontal advection of bio-optical gradients can confound our ability to extract the diel signal. The ideal setting for collecting observations discussed here is a deep mixed layer, where there would be little shear over the length of the wire so that the Wirewalker can move in a largely Lagrangian manner.

Wirewalker's rapid, wave-powered profiling enables a fine-scale view of the upper ocean that is challenging to achieve with other autonomous profiling platforms. Under typical operating conditions, long-endurance gliders and biogeochemical floats (e.g., BGC-Argo) each provide on the order of 1,000 profiles during deployments that last six months to four years, respectively. A similar sensor suite on a Wirewalker can profile the euphotic zone roughly 10,000 times over a month. This capability helps to clearly extract the diel signal from other competing sources of variability and is sure to provide novel insights into phytoplankton physiological processes that vary over time scales ranging from hours to days.

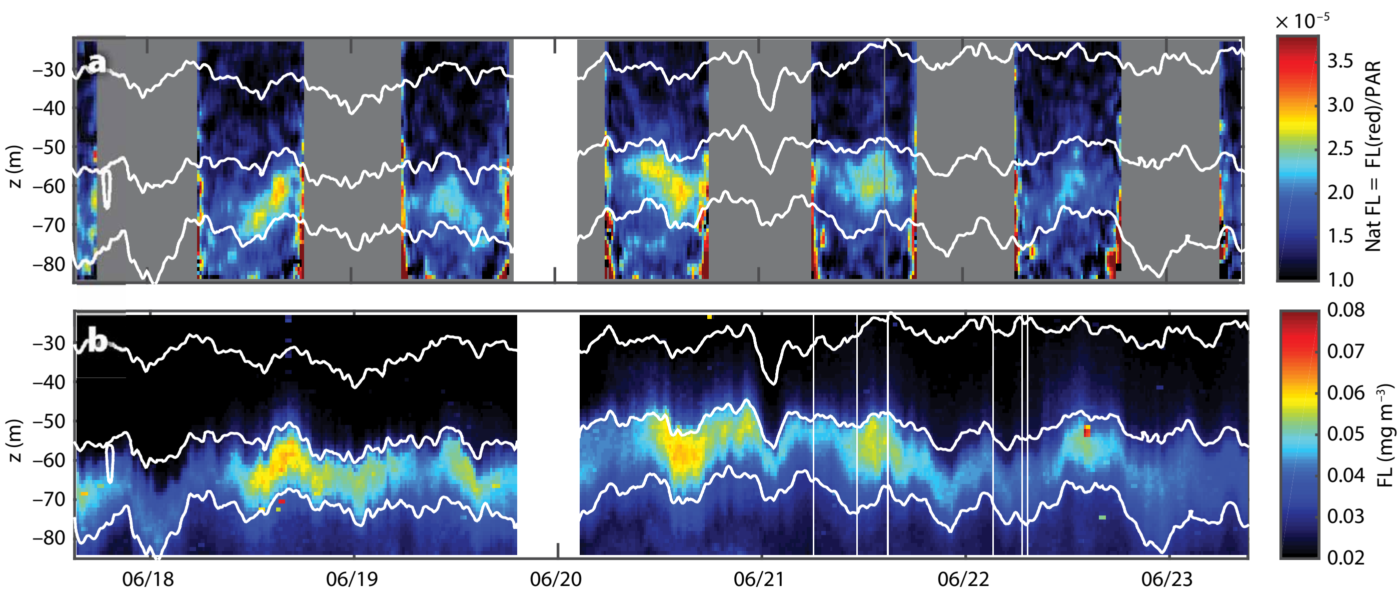

FIGURE 3. Depth-resolved time series of (a) natural fluorescence proxy derived from $I_{d,red}$/PAR measured by an upward facing hyperspectral radiometer, and (b) FL measured by a standard fluorometer. The white lines show the 21, 22, and 23 kg m^{-3} isopycnals.

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