

FINAL TECHNICAL REPORT TO  
THE OFFICE OF NAVAL RESEARCH

Dr. Daniel Kamykowski - NORTH CAROLINA STATE UNIVERSITY

'Small-scale Physical Processes Related to the Dynamic  
Photosynthetic Response of Phytoplankton Entrained in the  
Euphotic Zone of the Ocean".

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## RATIONALE

Phytoplankton directly influence many optical and acoustic characteristics of the oceanic water column. Under nutrient sufficient conditions (Falkowski et al., 1992), phytoplankton activity is regulated both by the varying photosynthetically active photon fluence density (PPFD) exposure and by the photosynthetic potential of the individual cells throughout the water column (Marra, 1978a; 1978b).

PPFD at the sea surface varies over a range of time scales due to clouds, and day/night and seasonal cycles (Kirk, 1983). Subsurface PPFD exhibits spectral changes with depth due to wavelength-dependent exponential attenuation (Kirk, 1983). Additional temporal variation in subsurface PPFD results from dissolved organic matter (DOM) and particulate organic matter (POM) patchiness (Parsons et al., 1984a). Near surface water motion, the net effect of turbulent mixing, surface and internal gravity waves, wind drift, Langmuir circulation and larger scale flow (Denman and Gargett, 1983), transports algal cells through the fluctuating PPFD field. Some cells act like neutral Lagrangian particles, but most possess an inherent motility due to buoyancy (Snayda, 1970; Walsby and Reynolds, 1980) or swimming (Roberts, 1981; Kamykowski et al. 1988). The physical and biological motion vectors combine to determine phytoplankton trajectories. Since the emphasis here is PPFD exposure of individual phytoplankton cells, vertical displacement is of primary concern (Kamykowski, 1990; Yamazaki and Kamykowski, 1990). One aspect of the work in his report dealt with the development of the Physical Motion Instrument (PMI) to monitor water motion over biologically significant time scales.

In a previous review, Falkowski (1984) emphasized the need for in-situ work that includes both O<sub>2</sub> and CO<sub>2</sub> fluxes to advance our understanding of the time-space relationships that influence phytoplankton photosynthesis. An in-situ approach includes the complex relationships between PPFD intensity and the light spectrum in the natural water column. The combined measurement of O<sub>2</sub> and CO<sub>2</sub> fluxes provides a useful indicator of the instantaneous state of photosynthesis in response to fluctuating light fields. Although work with diverse natural communities provides useful information, an accurate assessment of how distinct phytoplankton species respond to fluctuating light benefits from work with axenic, single-species cultures under realistic upper ocean conditions. Various aspects of a species' complex photosynthetic mechanism (Falkowski, 1984) result in both rapid responses due to minor biochemical changes accompanying fluorescence modification and lengthier responses such as sun-shade adaptation (Prezelin, 1981) and photoinhibition (Neale, 1987). When the

environmental variability exceeds the adaptability of a given species, succession to a new species with a more appropriate range of photosynthetic potential often occurs (Sakshaug et al., 1987; Caron et al., 1988). Therefore, measurements on single species from representative functional groups (Richardson et al., 1983) must be analyzed to examine the scope of interspecies responses. A second aspect of this report deals with improvements to the ONR-funded Self-contained Underwater Photosynthesis Apparatus (SUPA), a facility that originally measured the temperature, PPF<sub>D</sub> exposure, and the O<sub>2</sub> and CO<sub>2</sub> fluxes of an enclosed phytoplankton culture at sea

To sort out the relative importance of various processes theoretically, scaling procedures typically are utilized. Lewis et al. (1984a; 1984b) place the combined effect of varying PPF<sub>D</sub> and photosynthetic potential of existing phytoplankton populations at a given time into a robust nondimensional framework based on simple assumptions concerning turbulent mixing, euphotic zone depth and photoadaptation rate. To predict future states of productivity over regions of the ocean from current phytoplankton distributions, models are required with appropriate parameterizations of important small scale physical and biological processes. Both Eulerian (Martin, 1986; Price et al., 1986) and Lagrangian (Woods and Onken, 1983; Kamykowski, 1990; Yamazaki and Kamykowski, 1990) models of particle dispersion in the upper ocean are useful in different contexts (Lande and Lewis, 1989). Continued real progress, however, requires field data to test model assumptions and provide insight into how dynamics of relevant vertical water motion (Weller and Price, 1988; Gargett, 1989) and organism behavior affect the kinetics of photoadaptation (Cullen and Lewis, 1988; Kamykowski, 1979; Denman and Marra et al., 1985; Neale and Richardson, 1987) and the photosynthetic potential of individual species (Richardson et al., 1983). Such field observations require innovative instrumentation like PMI and SUPA to determine the coherences among the photosynthetic response, vertical water motion and incident radiation. A third aspect of this report is to describe models that combine water motion, behavior and physiology using computer facilities that were expanded using the ONR-SORP funds. These models were generated with the expectation that supporting data from PMI and SUPA eventually will be available.

## GENERAL

This ONR-SORP grant was written to support collaborative work with Dr. Tom Curtin, ONR. Separate ONR and NSF funding was available to

develop and deploy the Self-contained Underwater Photosynthesis Apparatus (SUPA) discussed below and to model. The funds in this ONR-SORP grant were primarily allocated to support the development of the Physical Motion Instrument (PMI) by Dr. Curtin to provide information on how SUPA should be moved in the upper mixed layer of the ocean. Some funds also were allocated to upgrade SUPA and to expedite the modeling effort.

### PHYSICAL MOTION INSTRUMENT (PMI)

The PMI is an array of current sensors nested symmetrically along two orthogonal axes each one meter long crossing at the center. When the normal to the plane is oriented vertically, the vertical velocity component and one horizontal component are measured independently at the end of each axis. At the center, the two horizontal velocity components are measured at 0.4 cm intervals over a range of 25 cm along each axis. This arrangement permits calculation of velocity gradients and thus the vertical component of vorticity over a range of scales, and enables comparison of the small scale structure with the one meter scale flow gradients derived from the corners. Fundamental issues are the spatial and temporal coherence of the velocity/vorticity field in this scale range and the best sampling strategy for measuring ocean velocity fluctuations that affect phytoplankton productivity.

Performance criteria considered in evaluating the best flow sensing method for the objectives included: (1) low zero velocity drift, such that a mean flow can be accurately measured in both high amplitude unsteady flow and low amplitude quiescent conditions; (2) adequate temporal response to resolve high frequency surface gravity wave motion; (3) linear amplitude response over the full range of velocity, typically 0 to 2 m/s; (4) cosine or otherwise stable angular response in the plane of measurement; (5) negligible response to flow orthogonal to the plane of measurement (cross talk); (6) low sensitivity to fouling to minimize calibration compromise over long intervals of deployment; (7) mechanical ruggedness to withstand deployment shocks, storm event forces and long term wear; (8) potential for coincident temperature, conductivity, pressure and particle type/concentration measurement; (9) low power consumption to enable long term, remote deployment; (10) low cost and modular design to enable large arrays. Non-mechanical speed and direction sensing components best satisfy frequency response and ruggedness criteria. The principal types of non-mechanical speed sensors are electromagnetic, acoustic and laser. Electromagnetic sensors are based on the emf induced

by a conductor (seawater) moving through a magnetic field (earth's or locally produced). Acoustic and laser sensors are based either on backscatter doppler shift or dual pulse correlation, forward scatter dual pulse coherence or reciprocal time of flight. The electromagnetic (EM) method was chosen to minimize the sensitivity of the measurement to suspended particle and bubble concentrations and non-Lagrangian behavior.

EM sensors in various compact configurations have been fabricated previously, and many have worked acceptably. A central problem with this type of sensor has been the low induced output voltage when power is limited for magnetic field generation. The low signal-to-noise ratio necessitates high gain amplification leading to problems with zero drift. In addition, the emf sensing electrodes have inherent, transient electrochemical potential differences as well as potential differences related to local boundary layer modification. The relatively slow drifting electrochemical differences can be effectively eliminated by ac driving, either electrically or mechanically. The boundary layer related differences can be controlled by physically isolating electrodes from the flow and/or a geometry with reproducible boundary layer effects related to the flow field measurement volume (the e-folding volume of magnetic field intensity). Examples and discussion of boundary layer effects have been given by Aubrey et al. (1984). Complete calibration includes potential differences due to both flow through the measurement volume and flow altering the electrode boundary layer.

The PMI incorporates two types of EM sensor: macroscale velocity sensors (MVS) at the ends of each axis and small-scale velocity sensors (SVS) along the axes. For the MVS, a new low cost amplifier circuit was designed for low signal-to-noise ratio and high common mode rejection, providing very low zero drift, and a new geometry was developed to control boundary layer and fouling problems and improve ruggedness and deployment flexibility. The magnetic field is generated by a Helmholtz coil arrangement as suggested by Olson (1972), however the electrodes and coils are constructed differently. The coil units are solid, rather than open, providing a ducted flow measurement volume within a highly uniform field. Identical sets of electrodes are flush mounted on opposing faces of the sensor (co-plane with the coils) and connected in parallel. The complete configuration is mechanically robust and hydrodynamically symmetric, providing reliable, precise measurements (Sorrell, et.al., 1990).

The MVS has been designed to incorporate measurement of tilt, temperature, conductivity, pressure and optical beam attenuation without

external modification to its geometry. For variables such as conductivity and beam attenuation the configuration is ideal. Another design feature is the sensor's function as an integral, load bearing element within a semi-rigid spar. A modular system may be configured as a series of discrete sensor units interconnected mechanically by variable length spar elements and electrically by an interface bus to a central compass/controller/data logger/power supply. The result is a compact, integrated sensor array that can be networked for cost-effective, long term measurement of gradients.

The SVS consists of two orthogonal linear arrays, each with 64 electrodes (0.4 cm uniform spacing), flush mounted on an open face inside and co-planer with a single coil creating a dipole magnetic field. The flow induced electrical potential difference between any two pairs of electrodes may be calculated from the measured emf across the arrays, enabling the coherence over a range of scales to be determined from time series data. Data obtained during field trials of the PMI at Duck, NC, have proven the ability of the SVS to detect signals in the ocean even under benign, low energy conditions. Further laboratory work is necessary, however, to precisely define the transfer function between measured voltage gradients and the structure of the inducing flow field.

## SUPA

A Self-contained Underwater Photosynthesis Apparatus (SUPA) has been designed to measure photosynthetic response of a single species phytoplankton culture to PPFd variations in-situ (Kirkpatrick, 1990). The PMI has been designed to measure velocity field temporal fluctuations over a range of spatial scales simultaneously from 1 m to 0.4 cm to examine the coherence of velocity and velocity gradient (e.g., vorticity) in a local volume. Coupled together with SUPA, PMI can also be used as a vertical motion sensor for interactive control of SUPA operating in a quasi-Lagrangian mode. The prototype instruments have been successfully demonstrated in field trials (Kirkpatrick, et al., 1990) and currently are being refined.

SUPA resolves photosynthetic and physiological responses to in situ PPFd and temperature variations by simultaneous measurement of both carbon uptake and oxygen evolution at one minute intervals. Carbon assimilation is determined through the measurement of pH (Stumm and Morgan, 1981; Axelsson, 1988), alkalinity corrections due to uptake of nitrate (Goldman and Brewer, 1980). Measurements include: the minutes to hours response of a culture to light fluctuations, the PPFd-dependent,

light-saturated photosynthetic rates and inhibition parameter, the variation of dark respiration rate, and the PPFD-dependent variation in PQ, an indicator of physiological state (Bell, 1985; Langdon, 1987). Features of this instrument include: 1) a quartz culture chamber extending the response spectrum into the ultraviolet; 2) a system to control the pH (total CO<sub>2</sub>) and dissolved oxygen that allows unattended deployments in situ up to 48 hours; 3) a microprocessor based control and data acquisition system providing flexibility in sampling through software modification.

An Ocean Optics spectrometer, purchased with funds from this ONR-SORP grant, was added to SUPA. The present configuration uses a dual fiber optic unit with two SUPA housings. One fiber is incorporated into the SUPA housing that contains a culture of the phytoplankton species of interest; the second fiber is incorporated into an identical SUPA housing that contains DI water. The readings from the two fibers simulate a dual beam spectrophotometer and provide information on the spectral absorbance of the phytoplankton culture in real time as the SUPA units are moved through the upper mixed layer. This capability used with the other SUPA probes potentially provides the ability to monitor the short time scale changes in quantum efficiency exhibited by the enclosed phytoplankton cells that have a known PPFD history in a natural water column.

## MODELING

Kamykowski (1990), using a random walk simulation, investigated how physical and biological vectors combine in a three-stratum mixed layer to influence phytoplankton distributions. The average vertical eddy diffusivity coefficient scaled after Sundby (1983) decreased by one order of magnitude in each successive stratum. Following the discussion in Denman and Gargett (1983), the upper layer included Langmuir circulation as a large turbulent eddy. Two different motility patterns based on buoyancy (sinking, neutral and floating cells) and swimming (dinoflagellate, slow ciliate and fast ciliate) were compared under various physical forcings (Yamazaki and Kamykowski; 1990). They also examined population distributions of variously motile phytoplankton but in a continuous, unstratified, wind-driven mixed layer characterized by an exponentially decreasing dissipation profile with a lower boundary defined by the Ekman depth. The PPFD exposure of each cell was recorded. Distributions of a dinoflagellate at three different wind speeds and the profiles of the PPFD exposure for each cell differed markedly from that of

a cell in the absence of turbulence and to a threshold value below which photo-stress is assumed to occur.

The modeling effort during the term of the ONR-SORP grant emphasized incorporation of a photoadaptation submodel into the previously described random walk Lagrangian models (Kamykowski, et al., 1994) and into a version of the Price et al. (1986) Eulerian model of the upper mixed layer (Janowitz and Kamykowski, 1991). A model by Denman and Marra (1986) provides a time-dependent response to the PPFD history experienced by a phytoplankton cell. The completed Lagrangian turbulence-behavior-photoadaptation model provides the depth and instantaneous photosynthetic rate of an individual algal cell with an assigned sinking rate that is randomly mixed based on an assigned wind speed in an independently random PPFD field. Successive runs of the model provide a population ensemble of the species under consideration that reflects the range of photosynthetic history of a group of cells at a given time and place in the water column. Alternate computation routines are under investigation (Yamazaki, personal communication). The Eulerian turbulence-convection-photoadaptation model calculates the changes in the temperature and the photosynthetic rate profiles over the diel cycle. The photosynthetic rate at a given depth is influenced by the redistribution of the phytoplankton cells due to vertical mixing and to the average effect of ensemble photoadaptation of the mixed population. Comparisons with published field data are reported (Kamykowski et al., 1996). These working models and their ongoing refinements provide a framework and motivation for the specific field experiments planned in the future. Comprehensive data sets are required to fully test model parameterizations and performance.

Additional modeling has examined dinoflagellate orientation in a Lagrangian context (Kamykowski, and Yamazaki, 1996; Kamykowski et al., 1997). The background for these models is summarized in Jones (1993) and Kamykowski (1995). In general, the individual cells adjust their orientation based on their environmental experiences (ex. PPFD, nutrients, temperature) in the upper ocean and on their internal physiological state (ex. storage pool size, cell cycle stage). These models provide a different and possibly more realistic result compared to cells that simply swim toward the light during the daytime and away from the surface at night. Supporting laboratory experiments are underway

## DISCUSSION

Although additional funds were not requested through the ONR-SORP program after 1994 due to the shifting research interests of Dr. Tom Curtin, the work described above, to which the ONR-SORP funds contributed, is continuing. SUPA deployments in support of modeling efforts are planned for September, 1996. Eventual coupling with the PMI still is desirable.

## REFERENCES

- Aubrey, D.G., Spenser, W.G. and J.H. Trowbridge. 1984. Dynamic response of electromagnetic current meters. WHOI Technical Report, WHOI-84-20.
- Axelsson, L. 1988. Changes in pH as a measure of photosynthesis by marine macroalgae. *Marine Biology* 97: 287-294.
- Bell, L. N. 1985. Energetics of the photosynthesizing cell. *Soviet Scientific Reviews Supplement Series, Vol 5*. Harwood Academic Publishers, New York. pp 159-163.
- Brand, L. E. 1982. Genetic variability and spatial patterns of genetic differentiation in the reproduction rates of the marine coccolithophores *Emeliana huxleyi* and *Gelphycapsa oceanica*. *Limnology and Oceanography* 27: 236-245.
- Caron, L., A. Mortan-Bertrand and H. Jupin. 1988. Effect of photoperiod on photosynthetic characteristics of two marine diatoms. *Jour. Exp. Mar. Biol. Ecol.* 123: 211-226.
- Cullen, J. J. and M. R. Lewis. 1988. The kinetics of photoadaptation in the context of vertical mixing. *Jour. of Plankton Research* 10: 1039-1063.
- Denman, K. L. and A. E. Gargett. 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnology and Oceanography* 28: 801-815.
- Denman, K. L. and J. Marra. 1986. Modelling the time dependent photoadaptation of phytoplankton to fluctuating light. In J. C. J. Nihoul (ed) *Marine Interfaces Ecohydrodynamics*. Elsevier

Oceanography Serie; 42 (Amsterdam) p. 341-360.

Falkowski, P. G. 1984. Physiological response of phytoplankton to natural light regime. Jour. of Plankton Research 6: 295-307.

Falkowski, P. G., R. M. Greene and R. J. Geider. 1992. Physiological limitations on phytoplankton productivity in the ocean. Oceanography 5:84-91.

Gargett, A. E. 1989. Ocean turbulence. Annual Review Fluid Mechanics 21: 419-457.

Goldman, J.C. and F.G. Brewer. 1980. Effect of nitrogen source and growth rate on phytoplankton-mediated changes in alkalinity. Limnology and Oceanography 25: 352-357.

Janowitz, G. S. and D. Kamykowski. 1991. An Eulerian model of phytoplankton photosynthetic response in the upper mixed layer. Journal of Plankton Research 13: 983-1002.

Jones, R. I. 1993. Phytoplankton migrations: patterns, processes and profits. *Ergebn. Limnol.* 39 67-77.

Kamykowski, D. 1979. The growth response of a model *Gymnodinium splendens* in stationary and wavy water columns. *Marine Biology* 50: 289-303.

Kamykowski, D., S. A. McCollum and G. J. Kirkpatrick. 1988. Observations and a model concerning the translational velocity of a photosynthetic marine dinoflagellate under variable environmental conditions. *Limnology and Oceanography* 33: 66-78.

Kamykowski, D. 1990. A random walk model examining how phytoplankton distribute in the upper mixed layer. In e. Graneli, B. Sandstrom, L. Edler, and D. M. Anderson (eds). *Toxic Marine Phytoplankton*. Elsevier (New York). p. 183-188.

Kamykowski, D., H. Yamazaki and G. S. Janowitz. 1994. A Lagrangian model of phytoplankton photosynthetic response in the upper mixed layer. *Journal of Plankton Research* 16:1059-1069.

Kamykowski, D. 1995. Trajectories of autotrophic marine dinoflagellates. *J. Phycol.* 31:200-208

- Kamykowski, D. G. B. Janowitz, G. J. Kirkpatrick and R. E. Reed. 1996. A study of time-dependent primary productivity in a natural upper ocean mixed layer using a biophysical model. *Journal of Plankton Research* (In Press).
- Kamykowski, D. and H. Yamazaki. 1996. A study of metabolism-influenced orientation in marine dinoflagellate diel vertical migration. *Limnology and Oceanography* (In Press).
- Kamykowski, D., H. Yamazaki, A. K. Yamazaki and G. J. Kirkpatrick. 1997. A comparison how different orientation behaviors influence dinoflagellate trajectories and photoresponses in turbulent water columns. *NATO ASI on Harmful Algal Blooms*. (In Review).
- Kirk, J. T. D. 1983. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge Univ. Press (Cambridge, U. K.). 401 p.
- Kirkpatrick, G. J., T. B. Curtin, D. Kamykowski, M. D. Feezor, M. D. Sartin and R. E. Reed. 1990. Measurement of photosynthetic response to euphotic zone physical forcing. *Oceanography Magazine* 3: 18-22.
- Lande, R and M. R. Lewis. 1989. Models of photoadaptation and photosynthesis by a gal cells in a turbulent mixed layer. *Deep-sea Research* 36: 1161-1175.
- Langdon, C. 1988. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. II. A general review. *Journal of Plankton Research* 10: 1291-1312.
- Lewis, M. R., J. J. Cullen and T. Platt. 1984a. Relationships between vertical mixing and photoadaptation of phytoplankton: Similarity criteria. *Marine Ecology Progress Series* 15: 141-149.
- Lewis, M. R., E. P. W. Horne, J. J. Cullen, N. S. Oakey and T. Platt. 1984b. turbulent motions may control phytoplankton photosynthesis in the upper ocean. *Nature* 311: 49-50.
- Marra, J. 1978a. Effect of short-term variation in light intensity on photosynthesis of a marine phytoplankton: A laboratory simulation study. *Marine Biology* 46: 191-202.

- Marra, J. 1978b. Phytoplankton photosynthetic response to vertical movement in a mixed layer. *Marine biology* 46: 203-208.
- Marra, J., K. Heinenmann and G. Landriau, Jr. 1985. Observed and predicted measurements of photosynthesis in a phytoplankton culture exposed to natural irradiance. *Marine Ecology Progress Series* 24: 43-50.
- Martin, P. J. 1986. Testing and comparison of several mixed-layer models. Tech. Rep. 23 p. Nav. Ocean Res. and Develop. Natl. Space Tech. Lab., Miss.
- Neale, P. J. 1987. Algal photoinhibition and photosynthesis in the aquatic environment. In D. J. Kyle, C. D. Osmond and C. J. Arntzen (eds). *Photoinhibition*. Elsevier Science Publishers B. V. (Amsterdam). P. 39-65.
- Neale, P. J. and P. J. Richerson. 1987. Photoinhibition and the diurnal variation of phytoplankton photosynthesis - I. Development of a photosynthesis -irradiance model from studies of in situ responses. *Jour. of Plankton Research* 9: 167-193.
- Olsen, J.R. 1972. Two-component electromagnetic flowmeter. *J.Mar.Tech.Soc.*, 6(1): 19-26.
- Parsons, T. R., M. Takahashi and B. Hargrave. 1984a. *Biological Oceanographic Processes*. 3rd ed. Pergamon Press (Oxford). 330 p.
- Prezelin, B. B. 1981. Light reactions in photosynthesis. *Can. Bull. Fish. and Aqua. Sci.* 210: 1-43.
- Price, J. F., R. A. Weller and R. Pinkel. 1986. Diurnal cycling: Observations and models of the upper ocean response to diurnal heating, cooling and wind mixing. *Jour. Geophys. Res.* 91: 8411-8427.
- Richardson, K., J. Beardall and J. A. Raven. 1983. Adaptation of unicellular algae to irradiance. An analysis of strategies. *New Phyto.* 93: 157-191.
- Roberts, A. M. 1981 Hydrodynamics of protozoan swimming. In M. Lewandowsky and S. H. Hutner (eds). *Biochemistry and Physiology of Protozoa*. Vol. 4. Academic Press (New York) p. 5-66.

Sakshaug, E., S. Demers and C. M. Yentsch. 1987. *Thalassiosira oceanica* and *T. pseudonana*. Two different adaptational responses. *Marine Ecology Progress Series* 41: 275-282.

Smayda, T. J. 1970. The suspension and sinking of phytoplankton in the sea. *Ocean. Mar. Bio., Ann. Rev.* 8: 353-414.

Sorrell, F.Y., Curtin, T.B. and M.D. Feezor. 1990. An electromagnetic current meter-based system for application in unsteady flows. *IEEE J. Ocean. Engr.* 15:373-379.

Stumm, W. and J.J. Morgan. 1981. *Aquatic Chemistry*. John Wiley & Sons, New York. pp 780.

Walsby, A. E. and C. S. Reynolds. 1980. Sinking and Floating. In I. Morris (ed). *The Physiology and Ecology of Phytoplankton*. Univ of Calif. Press (Berkeley). p. 371-412.

Weller, R. A. and J. F. Price. 1988. Langmuir circulation within the oceanic mixed layer. *Deep-sea Res.* 35: 711-747.

Woods, J. D. and F. Onken. 1982. Diurnal variation and primary production in the ocean - preliminary results of a Lagrangian ensemble model. *Jour. of Plank. Res.* 4: 735-756.

Yamazaki, H. and D. Kamykowski. 1990. The vertical trajectories of motile phytoplankton in a wind-mixed water column. *Deep-Sea Res.* 38: 219-241.