Light in shallow waters: A brief research review

Steven G. Ackleson¹

Office of Naval Research, 800 N. Quincy Street, Arlington, Virginia 22043

Abstract

Until recently, optical processes in shallow water, where a large portion of solar photons penetrate to the ocean floor, has received little attention outside of a relatively small number of modeling and remote sensing investigations. In the open ocean, scales of variability in relation to optical attenuation length often permit the treatment of the inwater light field as a one-dimensional, depth-dependent problem. In shallow waters hosting productive benthic ecosystems, such as coral reefs or seagrasses, the in-water light field is often three-dimensional in character. In the past decade, quantitative investigations of benthic optical properties and the resulting shallow-water light field have been conducted, fueled by a variety of new sensors designed specifically to address the shallow water problem. Recent publications, as well as the papers contained in this volume, illustrate the rich diversity and interdisciplinary nature of shallow-water optical problems and highlight important issues that should attract closer attention in the future.

When sunlight penetrates the ocean surface and propagates down into the water column, portions of the electromagnetic energy are absorbed and scattered at rates that are determined by, in addition to pure water, the concentrations of colored dissolved and particulate matter that make up the water mixture. The ocean radiative transfer problem and, to a lesser extent, the nature of optically important matter in ocean water is well understood in areas where the depth of the ocean floor is greater than the depth of sunlight penetration. In this situation, variability in the subsurface light field under a specified illumination condition and surface wave field (Walker 1994) is largely determined by the distribution of optically important matter dissolved and suspended in the water column, and light intensity generally decreases with depth in accordance with Beer's Law (Jerlov 1976; Kirk 1983; Mobley 1994). In shallow water, where the depth is much less than the potential for light to penetrate, a large fraction of the subsurface light reaches the ocean floor, where portions of the light energy are absorbed, reflected back into the overlying water column, or re-emitted as fluorescence. The subsurface light field in shallow water is not only a function of the properties of the water mixture, but also of the depth and properties of the ocean floor. Depending on water depth and benthic optical properties, light intensity might decrease more rapidly than expected, remain constant throughout the water column, or even increase with depth (Maritorena et al. 1994).

Although the fundamental radiative transfer processes do not change in response to water depth, the environmental context does, and this affects the assumptions and boundary conditions necessary to solve the radiative transfer problem. In the ocean volume, it is most often appropriate to treat the water column as plane-parallel and infinite in horizontal extent because the geometric scales of constituent variability are much greater than the length scales of optical propagation. This is typically the case in simulations of ocean pri-

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mary production (e.g., Brock et al. 1993; Platt et al. 1994) and surface mixed layer dynamics (e.g., Denman 1973; Dickey 1983) and in ocean color algorithm development (Gordon et al. 1988). This greatly simplifies the radiative transfer problem since one need only be concerned with variability in the vertical dimension. Within shallow water, the spectral composition and intensity of the light field can change significantly in response to the optical properties and orientation of benthic structures across horizontal distances that are short compared to light propagation distance.

Many of the techniques and approaches to investigate light in the deep ocean are relevant in the shallow ocean, but they are insufficient to address the entire problem. In order to completely understand the details of how light is distributed within the shallow ocean, new tools and approaches must be developed that take into account the complex distribution, structure, and optical properties of benthic features associated with these ecologically and economically important biomes.

Research motivation

The need to understand light fields as they pertain to primary production is well appreciated. In shallow water, knowledge of time-dependent insolation is key to benthic primary production simulation and prediction. Shallow benthic marine ecosystems, such as kelp beds, seagrass meadows, and coral reefs, are highly productive, surpassing at times even the most productive terrestrial plant assemblages (e.g., Mann 1972; McRoy and McMillan 1977), and serve as important nurseries, habitats, and places of refuge for many species of fish and shellfish (Smith 1978; Sorokin 1993; Hemminga and Duarte 2000). The combined optical properties of the various features that comprise these ecosystems have a first-order effect on the intensity and spectral composition of the adjacent light field. Hence, there exists a need to better characterize benthic optical properties in general. Likewise, a better understanding of benthic optical processes will eventually lead to better monitoring techniques and an improved understanding of how these important ecosystems respond to short-term forces, such as storms and

¹ Corresponding author (ackless@onr.navy.mil).

pollution events, as well as long-term environmental change, such as climate and sea level.

An equally compelling motivation for investigating light in the shallow ocean is the need to better understand the role that coastal ecosystems play in the global ocean carbon cycle and the resulting influence on climate (Sundquist and Broecher 1985 and articles therein). Estimations of global primary production associated with marine phytoplankton are generally on the order of 1.8×10^{16} g C yr⁻¹ (Ryther 1969; Falkowski and Woodhead 1992). In comparison, global production by benthic macrophytes is estimated to be 5.4 \times 10¹⁴ g C yr⁻¹ (Duarte and Cebrian 1996), or 3% of the production attributable to marine phytoplankton. Reports of carbon fixation by corals range between 5 and 20 g C m^{-2} d⁻¹ (Sorokin 1993), which, when combined with their global aerial coverage estimated to be 6×10^5 km², results in a production rate of between 1 and 4 \times 10¹⁵ g C yr⁻¹, or between 5 and 20% of global marine phytoplankton production. The microphytobenthos is another potentially important shallow-ocean carbon pool, estimated to constitute another 5×10^{14} g C annually (Cahoon 1999). Although these values are admittedly based on relatively few observations and should, therefore, be viewed as rough orders of magnitude, they nonetheless highlight the production potential of shallow benthic ecosystems and the need to better understand the role that they play in the larger ocean carbon budget.

The potential effects of climate warming and sea level rise on the shallow-water marine environment have not been explored in any great detail. Although it is difficult to envision sea level changing to such an extent as to significantly affect present-day benthic environments based solely on light availability, on regional scales, changes in precipitation patterns could affect water transparency as well as the seaward flux of terrestrial nutrients. In addition, long-term changes in environmental factors, such as ocean temperature and exposure to ultraviolet radiation, can potentially affect sensitive benthic ecosystems, such as coral reefs (Coles and Jokiel 1978; Jokiel and York 1984; Lesser et al. 1990; Hayes and Goreau 1991; Hoegh-Guldberg 1999). On the other hand, a significant rise in sea level would surely create new areas of benthic habitat as low-lying areas become inundated. It would seem, therefore, that long-term monitoring requirements in the form of in situ sensors and remote sensing techniques go hand-in-hand with the need to build the fundamental knowledge base necessary to predict shallow-water habitat change.

In any field of scientific inquiry, understanding is built on the ability to make key observations. Many of the sensors and techniques developed to measure the optical properties of ocean water and subsurface light fields in optically deep areas of the ocean can be applied directly to shallow water. In fact, with readily available sensors for measuring smallscale distributions in water column absorption and light scatter, it could be argued that our ability to characterize the optical properties of the water column has outpaced our ability to assess the significance of the resulting observations. With so much observational work yet to be conducted using available instruments, there is scant reason to invest heavily in new instrumentation to investigate the ocean water column. The shallow ocean floor, on the other hand, offers a completely different situation in which advancement of knowledge is limited by our inability to make key observations. Although new ideas for diver-operated sensors and underwater imaging systems have been developed specifically for investigating aspects of the shallow ocean floor (Mazel 2001), instruments are limited in number, are often difficult-to-operate prototypes that tend to be application- or user-specific, and as yet are not readily available through commercial vendors.

The color of the ocean contains information regarding the shallow ocean floor as well as the intervening water column. Remote sensing of ocean color has shown great promise in applications to coastal ecosystem surveying and monitoring (Colwell 1983; Mumby et al. 1997, 1998). However, as in problems of ecosystem modeling, the development of future systems and associated data analysis techniques depends on how well the details of the radiative transfer process within these shallow ocean environments are understood. Algorithms for determining bathymetry and bottom type, for example, assume that seafloor reflectance is not a function of viewing geometry and that inelastic scattering processes such as fluorescence are negligible. Although these assumptions may be valid, they have not been subjected to rigorous testing and their adoption has been based on computational convenience and a lack of observational capability rather than a complete understanding of the optical processes involved.

Historical investigations

As with any new field of inquiry, the best place to start is with a definition of terms (Table 1). The issue in shallow water is not the water column, since the properties, quantities, and associated units developed from investigations in the optically deep ocean are equally applicable to the shallow-ocean water column. Rather, the issue is the ocean floor and the variety of ways to describe how light is reflected back into the water column.

The details of how light is reflected from a surface are contained in the bidirectional reflectance distribution function, BRDF (Nicodemus et al. 1977).

BRDF(
$$\theta_i, \phi_i, \theta_r, \phi_r$$
)
= $dL_r(\theta_r, \phi_r)[L_i(\theta_i, \phi_i)\cos \theta_i d\Omega_i(\theta_i, \phi_i)]^{-1}$

L is radiance, θ is the nadir angle relative to the sediment surface, ϕ is the azimuthal angle around the local normal, and the subscripts i and r refer to incident and reflected directions, respectively. All other expressions of surface reflectance can be expressed as a function of the BRDF and the illumination conditions (*see* Mobley et al. [2003] for a more complete discussion of the relationships between different reflectance formulations).

Much of the earliest work in shallow-water radiative transfer involved statistical approaches to modeling the details of light propagation, in which the bottom boundary consisted of a flat, homogeneous seafloor having a Lambertian reflectance property (Plass and Kattawar 1972; Gordon and Brown 1974); that is, the BRDF was constant and the brightness of the ocean floor did not change, regardless of view angle.

Table 1. Ocean optical quantities, symbols, and units.

| Quantity | Symbol | Units |
|--|-----------------|----------------------------|
| Radiometric quantities | | |
| Radiance | L | $W m^{-2} sr^{-1} nm^{-1}$ |
| Irradiance | Ε | $W m^{-2} nm^{-1}$ |
| Inherent optical properties (independent of radiance distribution) | | |
| Absorption coefficient | а | m^{-1} |
| Volume scattering fucntion | β | $m^{-1} sr^{-1}$ |
| Scattering coefficient | b | m^{-1} |
| Backscattering coefficient | b _b | m^{-1} |
| Beam attenuation coefficient | с | m^{-1} |
| Single scattering albedo | $\omega_{ m o}$ | |
| Bidirectional reflectance distribution function | BRDF | sr^{-1} |
| Apparent optical properties (function of radiance distribution) | | |
| Attenuation coefficient | Κ | m^{-1} |
| Q factor | Q | sr |
| Irrandiance reflectance $(E_{\text{reflected}}/E_{\text{incident}})$ | \tilde{R} | |
| Remote sensing reflectance $(L_{reflected}/E_{incident})$ | $R_{ m rs}$ | sr^{-1} |

These simulations were limited in scope because of the computational resources available at the time and did not include inelastic light scatter. No attempt was made to validate the model simulations with field measurements, primarily because the instrumentation was not available. An approach to replacing the constant reflectance factor with a morphologybased parameterization of a seagrass canopy was reported by Ackleson and Klemas (1986) using a one-dimensional analytical approach to solving the irradiance-based transfer problem; however, as in the previous work, the means to validate the model in the field were not available. Mobley et al. (1993) reported an intermodel comparison representing a comprehensive set of environmental scenarios that included the effects of an optically shallow water column. Although the simulations included the usual assumption of Lambertian ocean floor reflectance and comparisons with field measurements were not considered, the work indicated that the resulting simulations were at least consistent between models using a variety of numerical approaches to solve the radiance-based problem. A comprehensive text on the general subject of oceanic radiative transfer was published the following year (Mobley 1994). In that same year, the first instance of an ocean radiative transfer model validation effort was reported-a simple one-dimensional irradiance model was compared with field measurements (Maritorena et al. 1994). The model accurately predicted in-water measurements of spectral irradiance, and the most significant result was the verification of light intensification adjacent to a highly reflective ocean floor.

Throughout this same period, measurements of the spectral characteristics of the in-water light field became commonplace as inexpensive, robust, submersible radiometers became commercially available (Smith et al. 1984; Mueller and Austin 1992; Hooker and Maritorena 2000) and as the research community learned how to construct and use them optimally (Gordon and Ding 1992; Leathers et al. 2001). The vast majority of the reported in-water light field observations represent deep areas of the ocean where the subsurface light field is unaffected by the ocean floor. However, a small number of scientists experimented with radiometers deployed on or immediately above the ocean floor (e.g., to monitor the irradiance available for photosynthesis in seagrass and coral ecosystems, Wetzel and Penhale 1983; Dennison 1987; Lesser et al. 2000).

The technical area that historically has received most of the attention regarding light propagation in shallow water is remote sensing. Starting in the late 1960s, reports appearing in conference proceedings and journals addressed applications of aerial and space photography and some early multispectral photographic systems to the detection of submerged features associated with bathymetry and seafloor composition (e.g., Ross 1969). With the launch of the first LANDSAT series of satellites, many researchers acknowledged the potential for developing automated analysis techniques and reported on work related to bathymetric mapping and surveys of benthic plant communities (Colwell 1983 and references therein; Ackleson and Klemas 1987). Methods for inverting expressions of water-leaving radiance for water depth and bottom reflectance require a priori knowledge of the spectral response of the dominant water column constituents and, for lack of more accurate information, assumptions of a Lambertian BRDF for the ocean floor (Lyzenga 1981; Lee et al. 1999). Despite considerable advances in remote sensor design, robust bathymetric and bottom type remote sensing algorithms based on radiometrically corrected ocean color data have remained elusive due in part to our limited knowledge of shallow-water optical characteristics and the details of how light interacts with the ocean floor.

Recent accomplishments

Over the course of the past decade, ocean optical investigations have increased in number and scope because of an appreciation for global variability in ocean color as measured from space (Mitchell 1994 and references therein), the development of affordable in situ instruments to measure subsurface light fields and ocean optical properties (Maffione 2001 and references therein), and the development of highly accurate radiance-based radiative transfer models capable of running on standard desk- or laptop computers (Mobley 1994 and references therein). However, with respect to optically shallow environments, the primary advances that have enabled scientists to make quantitative optical observations of the ocean floor (e.g., diver-operated sensors) were only realized in the past 5 yr (Mazel 2001 and references therein). The assumption of a constant BRDF was investigated, and although appropriate under certain circumstances, field observations indicated that, in most illumination geometries, seafloor reflectance is significantly different from a Lambertian surface (Voss et al. 2000). Deviation of the BRDF from a Lambertian surface is related to the structural complexity of benthic communities in ways that are not completely understood. Preliminary model studies suggest that such differences can have a significant effect on the shallow-water light field (Mobley et al. 2003). Furthermore, the details of how light is reflected appear to be controlled, at least in part, by factors such as sediment characteristics, the presence of polymers and other biogenous matter, and surface morphology, such as the presence of sand ripples and larger sand waves, although the details of these relationships are presently unknown. Radiance-based radiative transfer models are under development that include the effects of seafloor geometry (Mobley and Sundman 2003; Zaneveld and Boss 2003) and three-dimensional sessile structures extending into the overlying water column, as in the case of a seagrass canopy (Zimmerman 2003). It is also worth pointing out that significant advances are being made in simulating the structural details of complex benthic ecosystem components (Kaandrop and Kubler 2001) that could, in the future, be used to model the three-dimensional light field in complex benthic environments. Benthic sources of fluorescence, for example from coral, have also been shown to measurably affect the shallow-water light field (Fuchs 2001).

At the same time, driven primarily by issues of national defense, novel approaches to imaging the seafloor were developed and made available for civilian applications (see Jaffe et al. 2001 and references therein). Perhaps the most intriguing development in the area of underwater imaging is the ability to map benthic spectral fluorescence over areas approaching several square kilometers at spatial scales of <1cm², approaching, for example, the size of a single coral polyp (Mazel et al. 2003). However, as in the case of ocean color remote sensing, technology has outpaced the collection of in situ observations, and automatic signal analysis techniques designed to aid imagery interpretation are still in the early stages of development. In addition, the technology was developed for national defense in support of applications to mine warfare operations; applications to ecological problems will likely have to wait for investments from funding agencies and user groups outside of the military research establishment.

Current state of research

Most quantitative observations in shallow water have been reported in the past 5 yr, and it is fair to say that the variety of papers contained in this issue constitutes a milestone in our understanding of the subject. But how far has our knowledge advanced in this research area? Any topic of scientific inquiry progresses more or less along a common path from infancy to maturity. The path can be divided into four general phases-discovery, characterization, simulation, and application, although the phases are not completely distinct and one could argue about the degree of overlap. Initially, a feature or phenomenon is discovered based on observations collected without any underlying hypothesis by a relatively small number of curious individuals who then report on the potential significance. An integral part of this phase is the development of the instrumentation required to make basic observations. The new sensors or combinations of existing sensors developed to make such observations tend to be researcher-specific prototypes. In the characterization phase, the limited number of reported observations are intriguing enough to attract the attention of a more diverse group of researchers. Although the overall problem is understood to be interdisciplinary in scope, much of the new knowledge is the result of scientists operating independently within the confines of a single discipline. With time, enough new observations are collected that relationships between observations become apparent, and the research moves from purely descriptive work toward hypothesis testing. Instrumentation developed in the previous phase becomes more standardized, and with time, the more useful sensors might be offered commercially. In the simulation phase, the growing set of observations and established relationships form a foundation of knowledge that serves as the basis on which to develop and test descriptive models. Observations are turned into mathematical formulae and the formulae into algorithms for the purpose of expanding knowledge through numerical simulations and, to the extent possible, making predictions. The observational work is increasingly interdisciplinary and concerned with model validation and filling gaps in the existing set of observations. Quantitative remote sensing development could be included in this phase since much of the associated algorithm development is based on physical models and the validation methods are similar to those necessary for testing physical models. The final phase, application, is the payoff to society as observational techniques, predictive models, and the accumulated knowledge base are used to address problems of general concern.

When applied to a totally new area of research, one can see how various activities would flow from one phase to another with a certain amount of feedback as new knowledge results in the realization that new observational capabilities are required. However, the broader topic of radiative transfer is not new. Researchers have been modeling the propagation of radiant energy through scattering and absorbing media for nearly a century (Schuster 1905), and the ocean represents a medium to which the existing theories apply. Advances in atmospheric radiative transfer, for example, could easily be applied to the ocean with due consideration of boundary conditions and optical properties. This is why highly sophisticated models could be developed in the 1970s, a quarter of a century before the oceanographic community was capable of validating the results with in-water observations.

The papers presented in this volume primarily address aspects of the characterization and simulation phases, although potential applications are evident. Likewise, it could be argued that there is a small portion of discovery in many of the papers, even though this does not appear to be the primary focus of any. One would expect elements of discovery to abound in such a relatively new area of research, and perhaps the apparent under-representation in this volume is more the result of journal focus than an accurate characterization of community activity. Although the sample size is small, this analysis suggests that the pace of research has been such that, in less than a decade, the research community focused on benthic optical processes has successfully developed key instrumentation and collected enough observations to begin testing numerical simulations. In a few cases, the knowledge gained is sufficient to start addressing issues of societal concern. Although many difficult problems remain, one thing is certain: the relatively small research community that has developed during the past few decades is diverse, well coordinated, and well poised to address the challenges that lie ahead.

References

ACKLESON, S. G., AND V. KLEMAS. 1986. Two-flow simulation of the natural light field within a canopy of submerged aquatic plants. Appl. Opt. 25: 1129–1136.

_____, AND _____. 1987. Remote sensing of submerged aquatic vegetation in lower Chesapeake Bay: A comparison of LAND-SAT MSS and TM imagery. Remote Sens. Environ. 22: 235– 248.

- BROCK, J., S. SATHYENDRANATH, AND T. PLATT. 1993. Modeling the seasonality of subsurface light and primary production in the Arabian Sea. Mar. Ecol. Prog. Ser. **101**: 209–221.
- CAHOON, L. B. 1999. The role of benthic microalgae in neritic ecosystems, Oceanogr. Mar. Biol. 37: 47–86.
- COLES, S. L., AND P. L. JOKIEL. 1978. Effects of temperature on photosynthesis and respiration in hermatypic corals. Mar. Biol. 43: 209–216.
- COLWELL, R. N. 1983. Manual of remote sensing. American Society of Photogrammetry.
- DENMAN, K. L. 1973. A time-dependent model of the upper ocean. J. Phys. Oceanogr. **3:** 173–184.
- DENNISON, W. C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquat. Bot. **27:** 15–26.
- DICKEY, T. D. 1983. The influence of optical water type on the diurnal response of the upper ocean. Tellus **35B**: 142–154.
- DUARTE, C. M., AND J. CEBRIAN. 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41: 1758–1766.
- FALKOWSKI, P. G., AND A. D. WOODHEAD. 1992. Primary productivity and biochemical cycles in the sea. Plenum Press.
- FUCHS, E. 2001. Separating the fluorescence and reflectance components of coral spectra. Appl. Opt. **40**: 3614–3621.
- GORDON, H. R., AND O. B. BROWN. 1974. Influence of bottom depth and albedo on the diffuse reflectance of a flat homogeneous ocean. Appl. Opt. **13**: 2153–2159.
 - —, AND K. DING. 1992. Self-shading of in-water optical instruments. Limnol. Oceanogr. 37: 491–500.
 - , O. B. BROWN, R. H. EVANS, J. W. BROWN, R. C. SMITH,

K. S. BAKER, AND D. K. CLARK. 1988. A semianalytic radiance model of ocean color. J. Geophys. Res. **93**(D9): 10,909–10,924.

- HAYES, R. L., AND T. J. GOREAU. 1991. The tropical coral reef ecosystem as a harbinger of global warming. World Rersour. Rev. 3: 306–322.
- HEMMINGA, M. A., AND C. M. DUARTE. 2000. Seagrass ecology. Cambridge Univ. Press.
- HOEGH-GULDBERG, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshw. Res. **50**: 839–866.
- HOOKER, S. B., AND S. MARITORENA. 2000. An evaluation of oceanographic radiometers and deployment methodologies. Am. Meteorol. Soc. 17: 811–830.
- JAFFE, J. S., J. MCLEAN, K. D. MOORE, AND M. P. STRAND. 2001. Underwater optical imaging: Status and prospectus. Oceanogr. 14: 64–75.
- JERLOV, N. G. 1976. Marine optics. Elsevier.
- JOKIEL, P. L., AND R. H. YORK. 1984. Solar ultraviolet photobiology of the reef coral *Pocillopora damicornis* and symbiotic zooxanthellae. Bull. Mar. Sci. **32:** 301–315.
- KAANDROP, J. A., AND J. E. KUBLER. 2001. The algorithmic beauty of seeweeds, sponges, and corals. Springer-Verlag.
- KIRK, J. T. O. 1983. Light and photosynthesis in aquatic ecosystems. Cambridge Univ. Press.
- LEATHERS, R. A., T. V. DOWNES, AND C. D. MOBLEY. 2001. Selfshading correction for upwelling sea-surface radiance measurements made with buoyed instruments. Opt. Exp. 8: 561– 570.
- LEE, Z. P., K. L. CARDER, C. D. MOBLEY, R. G. STEWARD, AND J. S. PATCH. 1999. Hyperspectral remote sensing for shallow waters: 2. Deriving bottom depths and water properties by optimization, Appl. Opt. 38: 3831–3843.
- LESSER, M. P., W. R. STOCHAJ, D. W. TAPLEY, AND J. M. SHICK. 1990. Bleaching in coral reef anthozoans: Effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs 8: 225– 232.
- , C. MAZEL, D. PHINNEY, AND C. S, YENTSCH. 2000. Light absorption and utilization by colonies of the congeneric hermatypic corals *Montastraea faveolata* and *Montastraea cavernosa*. Limnol. Oceanogr. **45**: 76–86.
- LYZENGA, D. R. 1981. Remote sensing of bottom reflectance and water attenuation parameters in shallow water using aircraft and Landsat data. Int. J. Remote Sens. 2: 71–82.
- MAFFIONE, R. A. 2001. Evolution and revolution in measuring ocean optical properties. Oceanography **14:** 9–14.
- MANN, K. H. 1972. Ecological energetics of the sea-weed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of seaweeds. Mar. Biol. **14:** 199–209.
- MARITORENA, S., A. MOREL, AND B. GENTILI. 1994. Diffuse reflectance of oceanic shallow waters: Influence of water depth and bottom albedo. Limnol. Oceanogr. **39:** 1689–1703.
- MAZEL, C. H. 2001. Optics of the sea floor. Oceanogr. 14: 54–63.
 , M. P. STRAND, M. P. LESSER, M. P. CROSBY, B. COLES, AND A. J. NEVIS. 2003. High resolution determination of coral reef bottom cover from multispectral fluorescence laser line scan imagery. Limnol. Oceanogr. 48: 522–534.
- MCROY, C. P., AND C. MCMILLAN. 1977. Production ecology and physiology of seagrass, p. 53–87. *In* C. P. McRoy and C. Helfferich [eds.], Handbook of seagrass biology. Marcel Dekker.
- MITCHELL, B. G. 1994. Coastal zone color scanner retrospective. J. Geophys. Res. **99**(C4): 7291–7292.
- MOBLEY, C. D. 1994. Light in water. Academic Press.
 - , AND L. K. SUNDMAN. 2003. Effects of optically shallow

bottoms on upwelling radiances: Inhomogeneous and sloping bottoms. Limnol. Oceanogr. 48: 329–336.

- —, AND OTHERS. 1993. Comparison of numerical models for computing underwater light fields. Appl. Opt. 32: 7484–7504.
- , H. ZHANG, AND K. J. VOSS. 2003. Effects of optically shallow bottoms on upwelling radiances: Bidirectional reflectance distribution function effects. Limnol. Oceanogr. 48: 337–345.
- MUELLER, J. L., AND R. W. AUSTIN. 1992. Ocean optics protocols for SeaWiFS validation. S. B. Hooker [ed.], NASA Technical Memorandum 104566.
- MUMBY, J. P., E. P. GREEN, A. J. EDWARDS, AND C. D. CLARK. 1997. Measurement of seagrass standing crop using satellite and digital airborne remoter sensing. Mar. Ecol. Prog. Ser. 159: 51–60.
- , ____, C. D. CLARK, AND A. J. EDWARDS. 1998. Digital analysis of multispectral airborne imagery of coral reefs. Coral Reefs 17: 59–69.
- NICODEMUS, F. E., J. C. RICHMOND, J. J. HSIA, I. W. GINSBURG, AND T. LIMPERIS. 1977. Geometrical considerations and nomenclature for reflectance. NBS Monograph 160, National Bureau of Standards.
- PLASS, G. N., AND G. W. KATTAWAR. 1972. Monte Carlo calculations of radiative transfer in the Earth's atmosphere–ocean system: I. Flux in the atmosphere and ocean. J. Phys. Oceanogr. 2: 139–145.
- PLATT, T., S. SATHYENDRANATH, G. N. WHITE III, AND P. RAVIN-DRAN. 1994. Attenuation of visible light by phytoplankton in a vertically structured ocean: Solutions and applications. J. Plankton Res. **16**: 1461–1487.
- Ross, D. S. 1969. Color enhancement of ocean cartography, p. 50-

63. *In* P. C. Badgley, L. Miloy, and L. Childs [eds.], The oceans from space. Gulf Publishing.

- RYTHER, J. H. 1969. Photosynthesis and fish production in the sea. Science **166**: 72–76.
- SCHUSTER, A. 1905. Radiation through a foggy atmosphere. Astrophys. J. 21: 1–22.
- SMITH, R. C., C. R. BOOTH, AND J. L. STAR. 1984. Oceanographic biooptical profiling system. Appl. Opt. 23: 2791–2797.
- SMITH, S. V. 1978. Coral-reef area and the conditions of reefs to processes and resources in the world's ocean. Nature 273: 225– 226.
- SOROKIN, Y. I. 1993. Coral reef ecology. Springer-Verlag.
- SUNDQUIST, E. T., AND W. S. BROECHER. 1985. The carbon cycle and atmospheric CO₂: Natural variations Archean to Present. American Geophysical Union Geographical monograph 32.
- Voss, K. J., A. CHAPIN, M. MONTI, AND H. ZHANG. 2000. An instrument to measure the bi-directional reflectance distribution function (BRDF) of surfaces. Appl. Opt. **39:** 6197–6206.
- WALKER, R. E. 1994. Marine light field statistics. Wiley.
- WETZEL, R. L., AND P. A. PENHALE. 1983. Production ecology of seagrass communities in the lower Chesapeake Bay. Mar. Tech. Soc. J. 17(2): 22–31.
- ZANEVELD, J. R. V., AND E. Boss. 2003. The influence of bottom morphology on reflectance: Theory and two-dimensional geometry model. Limnol. Oceanogr. 48: 374–379.
- ZIMMERMAN, R. C. 2003. A biooptical model of irradiance distribution and photosynthesis in seagrass canopies. Limnol. Oceanogr. 48: 568–585.

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