

## Upscaling primary production estimates: Regional and global scale estimates of microphytobenthos production

### Abstract

Large-scale assessment of microphytobenthic production is a desirable goal for ecosystem modeling and prediction efforts. Several problems confound our ability to extrapolate from published measures to regional and global scale estimates, however. There are no adopted standards for measurement of microphytobenthic biomass and production. Most measurements have been obtained in relatively shallow habitats in temperate habitats, with few measurements from deeper, polar or tropical locations, and large regions of the world lack any measurements. Variability in published estimates of biomass and production, as well as estimates of photo-physiological parameters, is uncomfortably large and limits utility of mean values of any of these. Newer techniques for large scale estimation of biomass and production hold promise, but require ground-truthing with robust in situ measurements. Ultimately, the diverse nature of microphytobenthic assemblages themselves may account for much of the observed variability, and require a more synthetic understanding of the ecology of these organisms before we can generate large-scale estimates of their biomass and production with confidence.

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The importance of microphytobenthic production in shallow marine ecosystems, including estuaries and coastal waters, has been well established by many studies throughout the world (see reviews by MacIntyre *et al.* 1996; Miler *et al.* 1996; Cahoon 1999; Underwood and Kromkamp 1999). Microphytobenthic production can equal or exceed phytoplankton production, supports significant secondary production, alters the properties of shallow sediments, and plays a key role in nutrient cycling in these ecosystems. Extrapolation of microphytobenthic production estimates from point or local scales to regional or even global scales of measurement has obvious implications for ecosystem modeling and management. However, efforts to do so lag behind similar efforts to extrapolate phytoplankton production on such large scales, e.g., Longhurst *et al.* (1995).

The problem of estimating microphytobenthos production on regional and global scales encompasses several challenging issues. Two papers have generated global estimates of microphytobenthic production, one of approximately 0.34 Gt (=  $10^9$  metric

tons) C yr<sup>-1</sup>, based on an average productivity estimate of 50 g C m<sup>-2</sup> yr<sup>-1</sup> for the depth interval 0-50 m (Charpy-Robaud and Sournia 1990), the other of approximately 0.5 Gt C yr<sup>-1</sup>, based on regionally- and depth-weighted production estimates from approximately 108 studies (Cahoon 1999). Large-scale regional estimates, i.e., on the scale of the Baltic Sea, have not been attempted. There have been efforts to estimate microphytobenthic production in more restricted waters, such as individual estuaries (Thornton *et al.* 2002) or fjords (Glud *et al.* 2002), but extension of results from these studies to larger scales has not been attempted with much confidence. Virtually all individual studies of microphytobenthic biomass and production have been limited in their scope of time, space, or methodology, making extension of results to larger scales of time and space problematic.

There are some interesting parallels with the problems of estimating phytoplankton biomass and production at large scales, including the need for development of standard or at least comparable measurement techniques, generation of large sets of reliable and representative measurements, and adoption of methods for extracting predictive physiological information from remotely sensible properties. However, synoptic estimation of the biomass and productivity of the microphytobenthos at large spatial scales of space or time presents significant additional complications inherent in the organisms, their habitats, measurement techniques, and the logistic constraints these necessarily impose.

The ecological characteristics of and differences between estuarine phytoplankton and microphytobenthos have been reviewed thoroughly elsewhere (MacIntyre *et al.* 1996; Miller *et al.* 1996; Underwood and Kromkamp 1999) and do not require extensive elaboration here. A brief summary of the relevant considerations must include the effects of sediment substrates on microphytobenthos biomass and taxonomic composition (Cahoon 1999; Cahoon *et al.* 1999), attenuation of light by both the overlying water column and the sediment itself, considering also the changes in light fields during the emersion/immersion cycle in the intertidal zone (Serôdio and Catarino 1999), patchiness of microphytobenthos at various spatial scales and in response to different factors (Azovsky *et al.* 2000), and variability in physiological rates driven by temperature, light, environmental stress, and behavioral responses (Barranguet *et al.* 1998; Underwood *et al.* 1999; Serôdio and Catarino 2000). These factors complicate efforts to model microphytobenthic primary productivity, although limited attempts have been made with some success (Guarini *et al.* 2000*a, b*; Thornton *et al.* 2002).

Lack of standard methodology complicates comparisons among results from different studies of microphytobenthic biomass and production. About 50% of the reported production estimates from estuarine and coastal habitats world-wide have been derived from oxygen exchange measurements. Radiotracer techniques (<sup>14</sup>C uptake) have been used in approximately 40% of similar studies. The remainder employed various other methods, including estimates of primary production from relationships between light intensity and chlorophyll biomass (Fuji *et al.* 1991; MacIntyre and Cullen 1996), CO<sub>2</sub> exchange measured by infrared gas analysis (Wilkinson 1981; Schories and Mehlig 2000), and oxygen profiles measured by microprobes (Glud *et al.* 2002). More recently fluorescence-based measures, such

as PAM fluorometry (Kromkamp *et al.* 1998; Barranguet and Kromkamp 2000; Serôdio *et al.* 2001; Glud *et al.* 2002; Serôdio 2003) have been employed, although considerable methodological problems remain to be resolved (Perkins *et al.* 2002). Some cross-comparisons of methods have found reasonable agreement (Revsbech *et al.* 1981; Glud *et al.* 2002), but others have shown significant differences between simultaneous measurements using different methods (Perkins *et al.* 2002).

Large-scale geographical coverage of microphytobenthic production measurements is very patchy, with many potentially important areas of the world under-sampled or not sampled at all (Cahoon, 1999; Table 1). Furthermore, the total number of studies worldwide is strikingly small when one considers the numbers of measurements of phytoplankton biomass and production in contrast, e.g., Longhurst *et al.* 1995; Agawin *et al.* (2000). Most studies have been conducted in Europe and North America, for obvious reasons of funding, logistics, and local relevance. In contrast, estuarine and coastal habitats in many portions of the world, particularly polar and tropical regions, have been poorly studied. Large areas with few, if any, studies of microphytobenthic production include the Russian and Canadian Arctic, the Indian Ocean basin, most of the South and Central American coasts, and most of south and east Asia. Consequently, although estimates of microphytobenthos biomass and production in temperate zones may be relatively representative, our knowledge of these parameters in polar and tropical zones is based on an uncomfortably small number of studies in surprisingly few locations (Cahoon 1999 and more recent studies cited here), making accurate global estimates difficult.

Microphytobenthos production and biomass estimates are most confidently established in estuarine and other shallow (<20 m depth) habitats in temperate (30°-60° latitude) waters. On the order of 66 published studies of microphytobenthos production and biomass in such habitats yield average values of approximately 50-100 g C m<sup>-2</sup> yr<sup>-1</sup> and 80-130 mg chl *a* m<sup>-2</sup>, respectively, with lower values from a smaller number of measurements at greater depths. The problem of extrapolating even reasonably approximate estimates of microphytobenthic production in estuaries is illustrated by examining the data for European and North American studies. Using estimates from 26 published studies (cited in Cahoon 1999 or later references; Meyercordt *et al.* 1999; Herman *et al.* 2001) a mean value for annual estuarine production (as reported or as calculated in Cahoon 1999) integrated over all depths reported was 97 g C m<sup>-2</sup> yr<sup>-1</sup> with a standard deviation of 102 in European estuaries (including the Baltic and Mediterranean Seas). Similarly, results from 34 studies in U.S. and Canadian estuaries yielded a mean estimate of annual microphytobenthic production of 104 g C m<sup>-2</sup> yr<sup>-1</sup>, with a standard deviation of 93 (Cahoon 1999). The substantial variability in these estimates from the most well-studied regions of the world indicate important sources of variation. Fewer (~19) and more spatially clustered studies in tropical (0°-30° latitude) waters yield generally higher values, mean = 527 g C m<sup>-2</sup> yr<sup>-1</sup> with a standard deviation of 856, and biomass values of 90-350 mg chl *a* m<sup>-2</sup>, with lower values at deeper depths. Even fewer studies (~6) have been conducted in polar (60°-90° latitude) waters, yielding production estimates lower than elsewhere, mean = 24 g C m<sup>-2</sup> yr<sup>-1</sup> with standard deviation of 20, but relatively high biomass estimates (320-450 mg chl *a* m<sup>-2</sup>), if sparse and probably unrepresentative. The paucity of microphytobenthos production and biomass data from large

regions of the world, including areas where these are likely to be highly significant, makes most regional and global estimates uncertain. Although additional studies similar to those that have been published might usefully increase the confidence of these estimates, improvement would be incremental and subject to the vagaries listed above.

The range of habitats in which microphytobenthic biomass and production have been studied is also very biased. Approximately half of all studies have been conducted in the intertidal zone (Table 1), all but a very few of these in relatively sheltered estuarine ecosystems. The substrates most frequently described in these studies were muddy, and characterized by epipellic forms, in contrast to the microphytobenthic assemblages found on sandier substrates, e.g., Guarini *et al.* (2000a, b). Very few studies have examined microphytobenthos biomass and production in truly exposed habitats (Steele and Baird 1968; Souza and David 1996). As noted above, the intertidal zone imposes significantly different physical constraints on microphytobenthos than subtidal habitats, including enhanced risk of displacement, stronger variation in exposure to light, temperature, and salinity extremes during immersion/emersion cycles, and enhanced exposure to ultraviolet radiation. Therefore it is important to consider the differences in the species composition and physiological responses that may characterize the intertidal and subtidal microphytobenthos in deriving broader scale estimates of biomass and production, e.g., Thornton *et al.* (2002).

Most studies of microphytobenthic production have spanned relatively small depth ranges. Only 18 studies have measured production at depth ranges exceeding 5 m, and of these only 9 have spanned a range >5 m including the intertidal zone (References in Cahoon 1999; Kühl *et al.* 2001; Glud *et al.* 2002). Some of these show interesting and potentially useful relationships between depth and production, e.g., Plante-Cuny (1978), Sundbäck (1986), Charpy-Robaud (1988), but they are scattered across global regions and habitat types. Failure to establish sufficiently robust depth relationships for microphytobenthic production limits the reliability of depth-integrated and, therefore, spatially integrated production estimates. However, depth may not be an appropriate proxy for light flux, complicating extrapolation of P-E relationships in shallow waters into deeper waters. Inherent variability in microphytobenthos and their controlling factors, including patchiness, light fields, substrates, community types, and physiological responses, further complicate extrapolation of production measurements and derived models.

Knowledge of the basic photosynthetic physiology of microphytobenthos can provide powerful tools for estimating production with knowledge of basic parameters, i.e., light intensity, biomass (chlorophyll a), and temperature, although microphytobenthos present a more complicated situation than phytoplankton. Some empirical relationships have been described in the literature, e.g., Santos *et al.* (1997), Thornton *et al.* (2002). However, review of published studies ranging from empirical field studies to modeling studies reveals large variations in estimates of basic photosynthetic parameters of microphytobenthos (Table 2). Mean values from individual published studies of the saturating light intensity,  $E_k$ , range over 3 orders of magnitude, with the lowest values derived from studies of microphytobenthos in polar regions (Palmisano *et al.* 1985; Rivkin and Putt 1987; Kühl *et al.* 2001). Estimates of the maximum, biomass-normalized photosynthetic rate,  $P_{max}^b$ , also span approximately

Table 1. Spatial distribution of intertidal and subtidal studies measuring microphytobenthic production by all methods as of 2003. Data are numbers of published studies, from Cahoon (1999) and more recent References cited here.

Basin		Subtidal	Intertidal
	Sub-basin		
Atlantic Ocean		14	31
	Gulf of Mexico/Caribbean	8	2
	Mediterranean	4	–
	Black Sea	–	–
	Baltic Sea	3	–
Antarctic Ocean		2	–
Arctic Ocean		4	–
	Russian Arctic	–	–
	Canadian Arctic	–	–
Indian Ocean		2	1
	Persian Gulf	–	–
Pacific Ocean		7	7
	Bering Sea	–	–
	East Asia	–	2
	Gulf of California	3	–
	SE Asia-Australia	1	1
	New Zealand		

three orders of magnitude, with some evidence of variation between radiotracer-derived estimates and those derived from dissolved oxygen exchange (DOE) methods (Wolfstein and Hartig 1998). Estimates of the slope of the production-irradiance relationship,  $\alpha$ , vary by much less, just somewhat more than one order of magnitude. Finally, estimates of biomass-normalized production,  $P^b$ , essentially all field measurements, vary by perhaps as much as two orders of magnitude. Much of the variation among the values of these several parameters must inevitably result from the different methodologies and artifacts involved in the respective studies, including different techniques for measuring production, chlorophyll *a*, and light intensity. Some of the variation obviously arises from the differing times and locations at which studies were conducted; some of the ranges of values in Table 2 reflect these differences within individual studies. However, substantive differences among the basic photosynthetic physiological characteristics of microphytobenthos themselves cannot be ruled out. Thus, there is no firm basis for using arbitrarily chosen values of these physiological parameters to upscale estimates of microphytobenthic production from one habitat or season to larger scales of space and time. Such efforts must still rely on empirical measurements to offer much confidence.

Table 2. Values of microphytobenthic photosynthetic parameters reported in published literature:  $E_k$  (saturating light intensity,  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ),  $P_{\text{max}}^{\beta}$  (maximum, biomass-normalized photosynthetic rate,  $\text{mg C mg chla}^{-1} \text{h}^{-1}$ ),  $\alpha$  (slope of P-E relationship,  $\text{mg C mg chla}^{-1} \text{h}^{-1} (\mu\text{mol photons m}^{-2} \text{s}^{-1})^{-1}$ ),  $P^{\beta}$  (biomass-normalized photosynthetic rate,  $\text{mg C mg chla}^{-1} \text{h}^{-1}$ ).

Reference	$E_k$	$P_{\text{max}}^{\beta}$	$\alpha$	P
Steele & Baird 1968	–	–	–	0.14-1.78
Admiraal & Peletier 1980	–	0.1-13	–	–
Hargrave <i>et al.</i> 1983	–	0.1-7	–	–
Rasmussen <i>et al.</i> 1983	160-360	–	0.013-0.028	0.16-0.57
Colijn and de Jonge 1984	–	0.43-0.49	–	–
Palmisano <i>et al.</i> 1985	11	0.21	0.022	–
Mills & Wilkinson 1986	300->750	3.74	–	–
Rivkin & Putt 1987	6	–	0.08-0.10	0.53-0.60
Blanchard & Montagna 1992	108-215	2.98-20.0	0.01-0.16	–
Brotas & Catarino 1995	–	–	0.0021	–
MacIntyre & Cullen 1995	–	–	0.035-0.08	~1-12
Barranguet <i>et al.</i> 1998	150-450	3-12.7	0.008-0.042	–
Kromkamp <i>et al.</i> 1998	450-1200	–	–	–
Wolfstein & Hartig 1998	56-297	0.66-1.59 <sup>14C</sup> 1.70-4.10 <sup>DOE</sup>	0.011-0.057	–
Uthicke & Klumpp 1998	482-975	–	–	–
Meyercordt & Meyer-Reil 1999	27-367	4.04-54.2	0.017-0.339	–
Meyercordt <i>et al.</i> 1999	26-240	4.8-17.0	0.026-0.188	0.5-8.80
Barranguet & Kromkamp 2000	200-400	2-18	0.015-0.035	–
Goto <i>et al.</i> 2000	110	0.95	0.008540.4-0.8	–
Guarini <i>et al.</i> 2000b	460	11.2	0.024	–
Miles & Sundbäck 2000	–	–	–	0.26-0.52
Kühl <i>et al.</i> 2001	4.6-6.9	–	–	–
Perkins <i>et al.</i> 2001	750	0.20	–	–
Glud <i>et al.</i> 2002	33	–	–	–
Guarini <i>et al.</i> 2002	16-30	2.3-4.7	0.033-0.165	–
Perkins <i>et al.</i> 2002	160-420	–	0.021-0.028	–

A significant and growing number of recent studies have examined new approaches to estimation of microphytobenthos distribution, biomass, and production. Optical sensor technologies offer potentially powerful methods to make rapid or even synoptic, large-scale observations of microphytobenthos through reflectance and fluorescence methods. Paterson *et al.* (1998) reported on the use of newer airborne and satellite mounted sensors to quantify microphytobenthic parameters in intertidal habitats. Roelfsema *et al.* (2002) have described use of Landsat imagery to map benthic



microalgae in the shallow subtidal zone of a tropical reef ecosystem. Radiation sensors also offer the ability to determine depth, incident PAR, and temperature, other key parameters likely to control production. New approaches, such as use of second-derivative analysis of hyperspectral reflectance data (Stephens *et al.* 2003) and new algorithms for estimating bottom depth from reflectance data (Stumpf *et al.* 2003) may help resolve several obvious limitations of remote sensing methods. However, several significant sources of variation and resolution problems remain to be resolved, including effects of the microtopography of the bottom (Carder *et al.* 2003), confounding of reflectance signals by fluorescence (Mazel and Fuchs 2003) and extracellular polymeric secretions (Decho *et al.* 2003), and the inherent optical properties of the overlying water column (Boss and Zaneveld 2003). Finally, the inherent variability of microphytobenthos must be constrained and, perhaps most important, appropriate ground-truthing techniques must be developed and applied before useful and confident estimates of regional and global scale microphytobenthos production can be derived.

One final perspective must be offered about the philosophy of our approach to the study of microphytobenthos in estuaries and other habitats. Although we tacitly recognize the ecological, physiological, and taxonomic diversity implied in our use of the concept of microphytobenthos as communities of organisms, our methods frequently do not scale appropriately. Those studies that have focused on organism-scale factors and processes have often revealed patterns of variability that confound attempts to generalize to larger scales without incurring broad confidence limits. It is useful to consider the analogy of attempting to quantify the basic properties of the great diversity of terrestrial plant communities. Given the likelihood that microphytobenthos communities are similarly diverse at regional and global scales, the uncertainties in characterizing their biomass and productivity based on limited numbers of measurements in a relatively small number of arguably unrepresentative locations using different techniques that generate highly variable estimates of basic physiological parameters in response to inherently variable environmental factors are not surprising at all.

## References

- ADMIRAAL, W., PELETIER, H. 1980. Influence of seasonal variations of temperature and light on the growth rate of cultures and natural populations of intertidal diatoms. *Mar. Ecol. Prog. Ser.* **2**: 35-43.
- AGAWIN, N.S.R., C.M. DUARTE, and S. AGUSTI. 2000. Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. *Limnol. Oceanogr.* **45**: 591-600.
- AZOVSKY, A.I., CHERTOPROOD, M.V., KUCHERUK, N.V., RYBNIKOV, P.V., and SAPOZHNIKOV, F.V. 2000. Fractal properties of spatial distribution of intertidal benthic communities. *Mar. Biol.* **136**: 581-590.
- BARRANGUET, C., and KROMKAMP, J. 2000. Estimating primary production rates from photosynthetic electron transport in estuarine microphytobenthos. *Mar. Ecol. Prog. Ser.* **204**: 39-52.
- BARRANGUET, C., KROMKAMP, J., and PEENE, J. 1998. Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. *Mar. Ecol. Prog. Ser.* **173**: 117-126.
- BLANCHARD, G.F., and MONTAGNA, P.A. 1992. Photosynthetic response of natural assemblages of marine benthic microalgae to short- and long-term variations of incident irradiance in Baffin Bay, Texas. *J. Phycol.* **28**: 7-14.
- BOSS, E., and ZANEVELD, J.R.V. 2003. The effect of bottom substrate on inherent optical properties: Evidence of biogeochemical processes. *Limnol. Oceanogr.* **48**: 346-354.

- BROTAS, V., and CATARINO, F. 1995. Microphytobenthos primary production of the Tagus estuary (Portugal). *Neth. J. Aquat. Res.* **29**: 333-339.
- CAHOON, L.B. 1999. The role of benthic microalgae in neritic ecosystems. *Oceanogr. Mar. Biol. Ann. Rev.* **37**: 47-86.
- CAHOON, L.B., NEARHOOF, J.E., and TILTON, C.L. 1999. Sediment grain size effect on benthic microalgal biomass in shallow aquatic ecosystems. *Estuaries* **22**: 735-741.
- CARDER, K.L., LIU, C.-C., LEE, Z., ENGLISH, D.C., PATTEN, J., CHEN, F.R., IVEY, J.E., and DAVIS, C.O. 2003. Illumination and turbidity effects on observing faceted bottom elements with uniform Lambertian albedos. *Limnol. Oceanogr.* **48**: 355-363.
- CHARPY-ROBAUD, C.J. 1988. Production primaire des fonds meubles du lagon de Tikahau (atoll des Tuamotu, Polynésie française). *Océan. Acta* **11**: 241-248.
- CHARPY-ROBAUD, C.J., and SOURNIA, A. 1990. The comparative estimation of phytoplanktonic, microphytobenthic, and macrophytobenthic primary production in the oceans. *Mar. Microb. Food Webs* **4**: 31-57.
- COLIN, F., and DE JONGE, V.N. 1984. Primary production of microphytobenthos in the Ems-Dollard Estuary. *Mar. Ecol. Prog. Ser.* **14**: 185-196.
- DECHO, A.W., KAWAGUCHI, T., ALLISON, M.A., LOUCHARD, E.M., REID, R.P., STEPHENS, F.C., VOSS, K.J., WHEATCROFT, R.A., and TAYLOR, B.B. 2003. Sediment properties influencing upwelling spectral reflectance signatures: The biofilm gel effect. *Limnol. Oceanogr.* **48**: 431-443.
- FUJII, A., WATANABE, H., OGURA, K., NODA, T., and GOSHIMA, S. 1991. Abundance and productivity of microphytobenthos on a rocky shore in southern Hokkaido. *Bull. Fac. Fish. Hokkaido Univ.* **42**: 136-146.
- GLUD, R.N., KÜHL, M., WENZHÖFER, F., and RYSGAARD, S. 2002. Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production. *Mar. Ecol. Prog. Ser.* **238**: 15-29.
- GOTO, N., MITAMURA, O., and TERAI, H. 2000. Seasonal variation in primary production of microphytobenthos at the Isshiki intertidal flat in Mikawa Bay. *Limnol.* **1**: 133-138.
- GUARINI, J.-M., BLANCHARD, G.F., and GROS, P.H. 2000a. Quantification of the microphytobenthic primary production in European intertidal mudflats – a modeling approach. *Cont. Shelf Res.* **20**: 1771-1788.
- GUARINI, J.-M., BLANCHARD, G.F., GROS, P.H., GOULEAU, D., and BACHER, C. 2000b. Dynamic model of the short-term variability of microphytobenthic biomass on temperate intertidal mudflats. *Mar. Ecol. Prog. Ser.* **195**: 291-303.
- GUARINI, J.-M., CLOERN, J.E., EDMUND, J., and GROS, P. 2002. Microphytobenthic potential productivity estimated in three tidal embayments of the San Francisco Bay: A comparative study. *Estuaries* **25**: 409-417.
- HARGRAVE, B.T., PROUSE, N.J., PHILLIPS, G.A., and NEAME, P.A. 1983. Primary production and respiration in pelagic and benthic communities at two intertidal sites in the upper Bay of Fundy. *Can. J. Fish. Aquat. Sci.* **40 (Suppl. 1)**: 229-243.
- HERMAN, P.M.J., MIDDELBURG, J.J., and HEIP, C.H.R. 2001. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. *Cont. Shelf Res.* **21**: 2055-2071.
- KROMKAMP, J., BARRANGUET, C., and PEENE, J. 1998. Determination of microphytobenthos PSII quantum efficiency and photosynthetic activity by means of variable chlorophyll fluorescence. *Mar. Ecol. Prog. Ser.* **162**: 45-55.
- KÜHL, M., GLUD, R.N., BORUM, J., ROBERTS, R., and RYSGAARD, S. 2001. Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse-amplitude-modulated (PAM) fluorometer and O<sub>2</sub> microsensors. *Mar. Ecol. Prog. Ser.* **223**: 1-14.
- LONGHURST, A., SATHYENDRENATH, S., PLATT, T., and CAVERHILL, C. 1995. An estimate of global production in the ocean from satellite radiometer data. *J. Plank. Res.* **17**: 1245-1271.
- MACINTYRE, H.L., and CULLEN, J.J. 1995. Fine-scale vertical resolution of chlorophyll and photosynthetic parameters in shallow-water benthos. *Mar. Ecol. Prog. Ser.* **122**: 227-237.
- MACINTYRE, H.L., and CULLEN, J.J. 1996. Primary production by suspended and benthic microalgae in a turbid estuary: time-scales of variability in San Antonio Bay, Texas. *Mar. Ecol. Prog. Ser.* **145**: 245-268.
- MACINTYRE, H.L., GEIDER, R.J., and MILLER, D.C. 1996. Microphytobenthos: The ecological role of the 'secret garden' of unvegetated, shallow-water marine habitats. I. Distribution, abundance, and primary production. *Estuaries* **19**: 186-201.
- MAZEL, C.H., and FUCHS, E. 2003. Contribution of fluorescence to the spectral signature and perceived color of corals. *Limnol. Oceanogr.* **48**: 401.



- MEYERCORDT, J., and MEYER-REIL, L.-A. 1999. Primary production of benthic microalgae in 2 shallow coastal lagoons of different trophic status in the southern Baltic Sea. *Mar. Ecol. Prog. Ser.* **178**: 179-191.
- MEYERCORDT, J., GERBERSDORF, S., and MEYER-REIL, L.-A. 1999. Significance of pelagic and benthic primary production in two shallow coastal lagoons of different degrees of eutrophication in the southern Baltic Sea. *Aq. Microb. Ecol.* **20**: 273-284.
- MILES, A., and SUNDBÄCK, K. 2000. Diel variation in microphytobenthic productivity in areas of different tidal amplitude. *Mar. Ecol. Prog. Ser.* **205**: 11-22.
- MILLER, D.C., GEIDER, R.J., and MACINTYRE, H.L. 1996. Microphytobenthos: The ecological role of the 'secret garden' of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. *Estuaries* **19**: 202-212.
- MILLS, D.K., and WILKINSON, M. 1986. Photosynthesis and light in estuarine benthic microalgae. *Bot. Mar.* **29**: 125-129.
- PALMISANO, A.C., SOOHOO, J.B., WHITE, D.C., SMITH, G.A., STANTON, G.R., and BURCKLE, L.H. 1985. Shade adapted diatoms beneath Antarctic sea ice. *J. Phycol.* **21**: 664-667.
- PATERSON, D.M., DOERFFER, R., KROMKAMP, J., MORGAN, G., and GIESKE, W. 1998. Assessing the biological and physical dynamics of intertidal sediment ecosystems: A remote sensing approach. Pp. 377-390 in Barthel, *et al.* (eds.) Third European marine science and technology conference (MAST conference), Lisbon, 23-27 May 1998: Project synopses Vol. I.
- PERKINS, R.G., OXBOROUGH, K., HANLON, A.R.M., UNDERWOOD, G.J.C., and BAKER, N.R. 2002. Can chlorophyll fluorescence be used to estimate the rate of photosynthetic electron transport within microphytobenthic biofilms? *Mar. Ecol. Prog. Ser.* **228**: 47-56.
- PERKINS, R.G., UNDERWOOD, G.J.C., BROTA, V., SNOW, G.C., JESUS, B., and RIBEIRO, L. 2001. Responses of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. *Mar. Ecol. Prog. Ser.* **223**: 101-112.
- PLANTE-CUNY, M.R. 1978. Pigments photosynthétiques et production primaire des fonds meubles néritiques d'une région tropicale (Nosy-Bé, Madagascar). *Trav. Doc. L'ORSTOM* **96**, Paris.
- RASMUSSEN, M.B., HENRIKSEN, K., and JENSEN, A. 1983. Possible causes of temporal fluctuations in primary production of the Danish Wadden Sea. *Mar. Biol.* **73**: 109-114.
- REVSBECH, N.P., JØRGENSEN, B.B., and BRIN, O. 1981. Primary production of microalgae in sediments measured by oxygen microprofile,  $H^{14}CO_3$  fixation, and oxygen exchange methods. *Limnol. Oceanogr.* **26**: 717-730.
- RIVKIN, R.B., and PUTT, M. 1987. Photosynthesis and cell division by Antarctic microalgae: Comparison of benthic, planktonic, and ice algae. *J. Phycol.* **23**: 223-229.
- ROELFSEMA, C.M., PHINN, S.R., and DENNISON, W.C. 2002. Spatial distribution of benthic microalgae on coral reefs determined by remote sensing. *Coral Reefs* **21**: 264-274.
- SANTOS, P.J.P., CASTEL, J., and SOUZA-SANTOS, L.P. 1997. spatial distribution and dynamics of microphytobenthos biomass in the Gironde estuary (France). *Oceanol. Acta* **20**: 549-556.
- SCHORIES, D., and U. MEHLIG. 2000.  $CO_2$  gas exchange of benthic microalgae during exposure to air: a technique for rapid assessment of primary production. *Wetlands Ecol. Manage.* **8**: 273-280.
- SERÓDIO, J. 2003. A chlorophyll fluorescence index to estimate short-term rates of photosynthesis by intertidal microphytobenthos. *J. Phycol.* **39**: 33-46.
- SERÓDIO, J., and CATARINO, F. 1999. Fortnightly light and temperature variability in estuarine intertidal sediments and implications for microphytobenthos primary productivity. *Aquat. Ecol.* **33**: 235-241.
- SERÓDIO, J., and CATARINO, F. 2000. Modelling the primary productivity of intertidal microphytobenthos: time scales of variability and effects of migratory rhythms. *Mar. Ecol. Prog. Ser.* **192**: 13-30.
- SERÓDIO, J., MARQUES DA SILVA, J., and CATARINO, F. 2001. Use of *in vivo* chlorophyll *a* fluorescence to quantify short-term variations in the productive biomass of intertidal microphytobenthos. *Mar. Ecol. Prog. Ser.* **218**: 45-61.
- SOUSA, E.C.P.M., and DAVID, C.J. 1996. Daily variation of microphytobenthos photosynthetic pigments in Aparecida Beach – Santos (23°58'48" S, 46°19'00" W), Sao Paulo, Brazil. *Rev. Brazil. Biol.* **56**: 147-154.
- STEELE, J.H., and I.E. BAIRD. I.E. 1968. Production ecology of a sandy beach. *Limnol. Oceanogr.* **13**: 14-25.
- STEPHENS, F.C., LOUCHARD, E.M., REID, R.P., and MAFFIONE, R.A. 2003. Effects of microalgal communities on reflectance spectra of carbonate sediments in subtidal optically shallow marine environments. *Limnol. Oceanogr.* **48**: 535-546.
- STUMPF, R.P., HOLDERIED, K., SINCLAIR, M. 2003. Determination of water depth with high-resolution satellite imagery over variable bottom types. *Limnol. Oceanogr.* **48**: 547-556.

- SUNDBÄCK, K. 1986. What are the benthic microalgae doing on the bottom of Laholm Bay? *Ophel. Suppl.* **4**: 273-286.
- THORNTON, D.C.O., DONG, L.F., UNDERWOOD, G.J.C., and NEDWELL, D.B. 2002. Factors affecting microphytobenthic biomass, species composition and production in the Colne Estuary (UK). *Aq. Microb. Ecol.* **27**: 285-300.
- UNDERWOOD, G.J.C., and J.C. KROMKAMP. 1999. Primary production by phytoplankton and microphytobenthos in estuaries. *Adv. Ecol. Res.* **29**: 93-153.
- UNDERWOOD, G.J.C., NILSSON, C., SUNDBÄCK, C., WULFF, A. 1999. Short-term effects of UVB radiation on chlorophyll fluorescence, biomass, pigments, and carbohydrate fractions in a benthic diatom mat. *J. Phycol.* **35**: 656-666.
- UTHICKE, S., and D.W. KLUMPP. 1998. Microphytobenthos community production at a near-shore coral reef: seasonal variation and response to ammonium recycled by holothurians. *Mar. Ecol. Prog. Ser.* **169**: 1-11.
- WILKINSON, V. 1981. Production ecology of microphytobenthos populations in Manukau Harbour. M.S. thesis, Univ. Auckland, New Zealand.
- WOLFSTEIN, K., and HARTIG, P. 1998. The Photosynthetic Light Dispensation System: application to microphytobenthic primary production measurements. *Mar. Ecol. Prog. Ser.* **166**: 63-71.