

- Heavy metal tolerance of marine phytoplankton. 3. Combined effect of copper and zinc ions in cultures of four common species. *J. Exp. Mar. Biol. Ecol.* **25**: 37-55.
- , D. MALNES, AND A. JENESEN. 1980. Heavy metal tolerance of marine phytoplankton. 4. Combined effect of zinc and cadmium on growth and uptake in some marine diatoms. *J. Exp. Mar. Biol. Ecol.* **42**: 39-54.
- CAIN, J. R., D. C. PASCHAL, AND C. M. HAYDEN. 1980. Toxicity and bioaccumulation of cadmium in the colonial green alga, *Scenedesmus obliquus*. *Arch. Environ. Contam. Toxicol.* **9**: 9-16.
- CANTERFORD, G. S. 1980. Formation and regeneration of abnormal cells of the marine diatom *Ditylum brightwellii* (West) Grunow. *J. Mar. Biol. Assoc. U.K.* **60**: 243-253.
- DAVEY, E. W., J. J. MORGAN, AND S. J. ERICKSON. 1973. A biological measurement of the copper complexation capacity of seawater. *Limnol. Oceanogr.* **18**: 993-997.
- GUILLARD, R. R., AND J. H. RYTHER. 1962. Studies on marine planktonic diatoms. 1. *Cyclotella nana* Hustedt and *Detonula confervacea* (Cleve) Gran. *Can. J. Microbiol.* **8**: 229-239.
- HUGHES, D. J. 1981. An interspecific comparison of trace metal toxicity to marine phytoplankton. *Mass. Inst. Technol. R. M. Parsons Lab. Tech. Note 25*.
- LEWIN, J. C. 1954. Silicon metabolism in diatoms. 1. Evidence for the role of reduced sulfur compounds in silicon utilization. *J. Gen. Physiol.* **37**: 538-599.
- MANAHAN, S. E., AND M. J. SMITH. 1973. Copper micronutrient requirement for algae. *Environ. Sci. Technol.* **7**: 829-833.
- MOREL, F. M., J. G. RUETER, D. M. ANDERSON, AND R. R. GUILLARD. 1979. Aquil: A chemically defined phytoplankton culture medium for trace metal studies. *J. Phycol.* **15**: 135-141.
- MOREL, N. M., J. G. RUETER, AND F. M. MOREL. 1978. Copper toxicity to *Skeletonema costatum* (Bacillariophyceae). *J. Phycol.* **14**: 43-48.
- PASSOW, H., A. ROTHSTEIN, AND T. W. CLARKSON. 1961. The general pharmacology of the heavy metals. *Pharmacol. Rev.* **13**: 185-224.
- RUETER, J. G., S. W. CHISHOLM, AND F. M. MOREL. 1981. The effect of copper toxicity on silicic acid uptake and growth in *Thalassiosira pseudonana* (Bacillariophyceae). *J. Phycol.* **17**: 270-278.
- , AND F. M. MOREL. 1981. The interaction between zinc deficiency and copper toxicity as it affects the silicic acid uptake mechanisms in *Thalassiosira pseudonana*. *Limnol. Oceanogr.* **26**: 67-73.
- SAKAGUCHI, T., T. TSUJI, A. NAKAJIMA, AND T. HORIKOSHI. 1979. Accumulation of cadmium by green microalgae. *Eur. J. Appl. Microbiol. Biotechnol.* **8**: 209-215.
- SAY, P. J., AND B. A. WHITTON. 1977. Influence of zinc on lotic plants. 2. Environmental effects on toxicity of zinc to *Hormidium uvulare*. *Freshwater Biol.* **7**: 379-384.
- STEEMANN NIELSEN, E., AND L. KAMP-NIELSEN. 1970. Influence of deleterious concentrations of copper on the growth of *Chlorella pyrenoidosa*. *Physiol. Plant.* **23**: 828-840.
- SUNDA, W. G., AND P. A. GILLESPIE. 1979. The response of a marine bacterium to cupric ion and its use to estimate cupric ion activity in seawater. *J. Mar. Res.* **37**: 761-777.
- , AND R. R. GUILLARD. 1976. Relationship between cupric ion activity and the toxicity of copper to phytoplankton. *J. Mar. Res.* **34**: 511-529.
- WESTALL, J. C., J. L. ZACHARY, AND F. M. MOREL. 1976. MINEQL: A computer program for the calculation of chemical equilibrium composition of aqueous systems. *Mass. Inst. Technol. R. M. Parsons Lab. Tech. Note 18*.

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Particulate matter resuspension via metabolically produced gas bubbles from benthic estuarine microalgae communities

Abstract—Gas bubbles originating from interstitial and epibenthic organisms in *Thalassia testudinum* culture and field systems were observed to rise and resuspend adsorbed particulate matter. In culture, 307.9 ml of gas were evolved and 0.97 g dry wt of particulate matter was resuspended·m⁻²·24 h⁻¹. In situ studies in Tampa Bay, Florida, yielded similar values for gas production, but higher particu-

late loads. Chromatographic analyses of the bubbles indicated that the major component was photosynthetically produced oxygen. The resuspended particulate matter was 70-96% inorganic; the organic fraction consisted of living organisms and detrital material. This phenomenon may be important in the sediment kinetics and nutrient cycles of estuarine systems.

Estuarine productivity is ultimately controlled by the availability of nutrients to the flora; it is important to understand the mechanisms by which these nutrients are recycled to the water, lost to the ocean or atmosphere, or buried in the sediments. The kinetics of particulate matter in estuarine systems are extremely complex (Oviatt and Nixon 1975). Sedimented particulate material is resuspended by tides and winds. Benthic communities can convert it into dissolved nutrients, while bioturbation increases the transport of these nutrients back to the overlying waters. The cycle may then be repeated as particulate organic matter can form by the adsorption of dissolved and colloidal carbon onto gas bubbles (Johnson and Cooke 1980). The high densities of microorganisms and detritus within organic particles and aggregates make them loci of metabolic activity and nutrient regeneration in the water (Lenz 1977). The bubbles associated with this particulate matter have been thought to result mainly from turbulence of the water, although gas bubbles are produced as a result of benthic metabolic activity (Whelan 1974; Oremland and Taylor 1977).

During studies of *Thalassia testudinum* in laboratory culture, we observed particulate matter being carried to the water surface attached to gas bubbles originating from the sediments. These assemblages would stay at the air-water interface for periods up to several minutes before the bubbles burst, releasing the particles. The bubbles were associated with microalgae, primarily the unarmored dinoflagellate *Amphidinium carterae*, a species known to have a benthic and interstitial habitat. We report here on studies that indicate that this activity resuspends a significant portion of particulate matter. We collected both the evolved gas bubbles and the associated particles using simple traps which minimized benthic community disturbance while permitting unrestricted exchange between collection areas and the surrounding water (Fig. 1). This avoided the effects of a closed system over long sam-

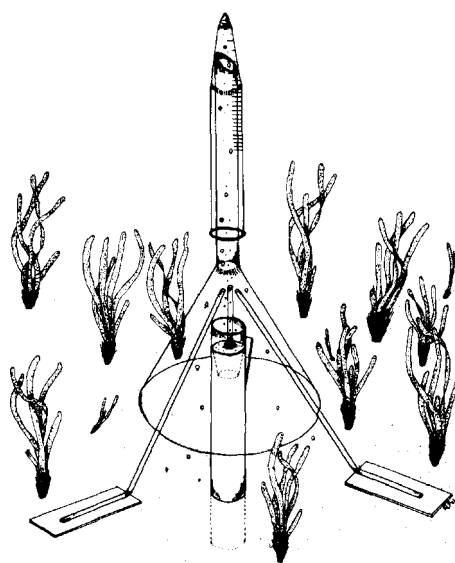


Fig. 1. Illustration of gas/sediment trap in *Thalassia testudinum* meadow. Trap consists of a glass funnel (mouth 14.2-cm i.d., stem 1.0-cm i.d.) supported 5 cm above the sediment surface by three glass legs. Gas bubbles were collected in an inverted 25-ml graduated centrifuge tube. Particulate matter was collected in a microfernbach flask cap (2.2-cm i.d.) ballasted by a Neoprene stopper inserted into a PVC tube (2.7-cm o.d.). Area sampled is 150 cm². All components were acid-washed (10% HNO₃) which prevented bubbles from attaching to surfaces.

pling periods (4–12 h), since alteration of chemical equilibria and nutrient transfer across the sediment-water interface can affect benthic metabolism.

Initial collections from the cultures yielded about 1 g dry wt of particulate material resuspended and 307.09 ml of gas evolved · m⁻² · 24 h⁻¹ (Table 1). These values indicated a significant phenomenon, but may have represented an artifact of the culture conditions. We did in situ experiments in a natural seagrass meadow and in a shallow mangrove-lined lagoon without seagrasses. We carefully placed the traps along transects while floating over the study areas (max depth 1.5 m), since gas bubbles are liberated from the upper sediment layers of *Thalassia* beds when disturbed (Oremland and Taylor 1977).

Gas evolution values from the labora-

Table 1. Dry weight of resuspended particulate material and volume of gas collected in gas/sediment traps.

Site	Gas production		Particulate resuspension	
	(ml·150 cm ⁻² ·h ⁻¹)*	(ml·m ⁻² ·12 h ⁻¹)†	(mg·150 cm ⁻¹ ·h ⁻¹)*	(g·m ⁻² ·12 h ⁻¹)†
Culture system				
Daylight‡	0.301±0.078	242.0	0.82±0.05	0.66
Night§	0.082±0.017	65.9	0.38±0.39	0.31
Seagrass meadow				
Daylight	0.351±0.111	282.2	5.16±3.05	4.15
Night	0.018±0.011	14.4	1.29±0.53	1.04
Mangrove lagoon#				
Daylight	0.861±0.457	688.8	10.28±1.23	8.26
Night	0.239±0.247	192.2	8.41	6.77

* ±1 SD.

† Values were calculated from means of hourly rates.

‡ From 0800–2000 hours.

§ From 2000–0800 hours.

^{||} Study site located at Lassing Park (St. Petersburg).# Lagoon surrounded by a vegetated shoreline containing three mangrove species (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*) and is 1.6 km north of Port Manatee, Florida.

tory and natural seagrass systems in daylight were remarkably similar (Table 1). The higher rates of particulate resuspension in situ were due to finer sediments and to the presence of detrital particles which were more effectively resuspended by the bubbles. Culture system sediments consisted of a coarse shell hash (aragonite) with little detritus, and from which a larger proportion of bubbles was released without particulate material attached. Values for gas production and particulate resuspension were highest in the lagoon site. Detritus derived from seagrass and mangrove leaf litter provides a substantial nutrient input to coastal estuaries and supports a very productive interstitial microflora (Snedaker and Lugo unpubl.; Klug 1980). Sediment samples collected from both field sites contained high densities (>10⁶ cells·liter⁻¹) of two dinoflagellates, *Gyrodinium fissum* and *Peridinium foliaceum*, common in Tampa Bay. Other microalgae and blue-greens were prevalent in the samples, but at much lower densities. The distribution of these organisms in all three systems was patchy, evident in the sediment coloration, and indicated by the high standard deviations of the data. Several factors seem to be responsible for the lower rates of gas production (and associated particulate resus-

pension) in the seagrass systems. *Thalassia* reduces the area of the sediment–water interface, and the leaf blades form a canopy reducing the amount of light reaching the sediments; both factors may decrease the amount of photosynthetically produced O₂ per unit area. *Thalassia* also contains internal lacunae which may reduce gas bubble evolution since gases produced in the sediments can diffuse and be stored in the rhizomes (Oremland and Taylor 1977).

Gas production and particulate resuspension in all three systems were reduced by 75% at night; the lagoon again had the highest values (Table 1). The production of gas at night suggested that it was not totally composed of photosynthetically produced oxygen, although the gradual escape of oxygen trapped in the sediment might have accounted for the night production. Diffusion of photosynthetically generated gases stored in the lacunar spaces of *Thalassia* may also result in bubble production after photosynthesis has ceased (Hartman and Brown 1967). The night gas bubbles might also result from CH₄ and CO₂ constantly produced in the sediments migrating toward the sediment–water interface (Whelan 1974).

We compared the composition of bubbles collected during the day and those

collected at night. Gases were analyzed by gas chromatography (Hewlett Packard 5840A) using a thermal conductivity detector and Poropak Q columns (Bailey and Beauchamp 1973). This technique gives composite peaks for N_2 and O_2 , but CO_2 , H_2S , H_2 , and CH_4 are separated. Most of the day collections consisted of 98–99% (by volume) O_2 and N_2 , with 0.06% CO_2 . Similar values reported for sediment bubbles collected during the day in *Thalassia* beds of the Florida Keys indicate the presence of photosynthetically generated O_2 (Oremland and Taylor 1977). Trace amounts ($\leq 0.02\%$) of H_2 were also detected in some of our day samples. Hydrogen production reflected the presence of unicellular algae and reducing sediments (Greenbaum et al. 1978). Gas bubbles collected at night had slightly lower O_2 and N_2 levels and higher CO_2 concentrations (0.2–0.6%) denoting greater contributions from respiration. One night sample from the seagrass bed had a peak of H_2S . Sulfide was unexpected in the released gas bubbles as it is usually oxidized in the water (Fenchel and Riedl 1970). However, the composition of sediment gas bubbles from *Thalassia* beds can fluctuate, with low O_2 levels in the evening and early morning (Oremland and Taylor 1977). Low levels of CH_4 (0.1%) were detected in day and night samples from the lagoon, but not from either seagrass system; sulfur may be limiting at this site as CH_4 is produced after SO_4^{2-} is reduced (Whelan 1974). The internal cycling of compounds across the redox-potential discontinuity layer complicates interpretation of these patterns since gases that are released from the sediments may only reflect the biota of the upper few centimeters (Fenchel and Riedl 1970). The dominance and composition of gas production in the daytime suggests that photosynthetic activity is the major metabolic process responsible for the gas bubbles in the systems we studied.

Particulate matter resuspended by these metabolically produced gas bubbles (Table 2) could account for up to 50% of that attributed to resuspension by

Table 2. Composition of resuspended particulate matter in Tampa Bay.

Site	Dry wt	Organic matter	
		(g·m ⁻² ·yr ⁻¹)	
Lassing Park			
11 Dec 79	3,029.5	545.3	242.4
27 Feb 80	2,405.4	240.5	106.9
Port Manatee			
10 Jan 80	6,033.4	362.0	160.9

* Carbon = organic matter/2.25 (Iturriaga 1979).

tidal movement in shallow bay systems (Oviatt and Nixon 1975). Since the composition of the two fractions is similar (3–5% carbon, as determined by ashing), it is understandable why this process may have been overlooked in conventional sediment traps. Examining data from the seagrass community, we calculated that the equivalent of 10–24% of the total carbon fixed annually by a *T. testudinum* community (1,000 g C·m⁻²·yr⁻¹; Odum et al. 1959) could be resuspended by gas bubbles. This is about equal to the amount of carbon fixed by algae epiphytic on *Thalassia* (Jones 1968). Resuspension in the lagoon is equivalent to 25% of the carbon fixed annually by a mangrove forest (638 g C·m⁻²·yr⁻¹; Snedaker and Lugo unpubl.). Present analyses of the resuspended particulate matter from the seagrass systems showed the presence of photosynthetic organisms (Table 3). This was not surprising since benthic microalgae can attach themselves to sediment particles (Hartwig 1978). Chlorophyll *a* and pheophytin *a* levels for resuspended particles were similar to those reported for sedimenting particles from other coastal locations (Iturriaga 1979). The higher Chl *a* : Pheo *a* ratios of the culture particulate materials indicated more living material and less detritus, reflecting the “youth” of this system. Carotenoid levels of the particulate material were 1.5–1.7 times that of the chlorophyll *a*, once again indicating the presence of microalgae as carotenoids are often the dominant pigments in dinoflagellates and diatoms (Goodwin 1974).

Table 3. Pigment concentrations (1: mg·ml⁻¹ gas evolved; 2: mg·mg⁻¹ part.) and ratios of resuspended particulate matter collected in gas/sediment traps.

Site	Chlorophyll <i>a</i> *		Pheophytin <i>a</i> †		Chl <i>a</i> : Pheo <i>a</i>	Carotenoids‡	
	1	2	1	2		1	2
Culture system	0.025	0.068	0.0017	0.0046	14.7	0.038	0.103
Seagrass meadow	0.0007	0.0134	0.0005	0.0095	1.4	0.0012	0.0229

* Chl *a* (mg·ml⁻¹ gas) = 26.7 (665₀ - 665_a) × v/V_g × L, where v is volume of acetone used in extraction (ml), V_g is volume of gas collected (ml), L is path length of cell (cm), 665₀ is absorbance before acidification, and 665_a is absorbance after acidification.

† Pheo *a* (mg·ml⁻¹ gas) = 26.7 (1.7[655₀] - 665_a) × v/V_g × L.

‡ Carotenoids (mSPU) = 10.0 (480) × v/V_g × L, where (480) is absorbance at 480 nm.

Our results show that metabolically produced gas bubbles can serve as a transport mechanism for benthic matter, including live organisms. This previously undescribed process, caused predominantly by high densities of interstitial dinoflagellates, demonstrates one more ecologically important function of this group of algae. Since estuaries provide suitable conditions for the growth of benthic and interstitial algae, this process may operate in many areas.

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References

- BAILEY, I. D., AND E. G. BEAUCHAMP. 1973. Gas chromatography of gases emanating from a saturated soil system. *Can. J. Soil Sci.* **53**: 122-124.
- FENCHEL, T. M., AND R. J. RIEDL. 1970. The sulfide system: A new biotic community underneath the oxidized layer of marine sand bottoms. *Mar. Biol.* **7**: 255-268.
- GOODWIN, T. W. 1974. Carotenoids and biliproteins, p. 176-205. *In* W. D. Stewart [ed.], *Algal physiology and biochemistry*. Univ. Calif.
- GREENBAUM, E., D. MAUZERALL, AND R. R. GUIL-LARD. 1978. Hydrogen formation by marine algae. *Biol. Bull.* **155**: 441.
- HARTMAN, R. T., AND D. L. BROWN. 1967. Changes in the composition of the internal atmosphere of submerged vascular hydrophytes in relation to photosynthesis. *Ecology* **48**: 252-258.
- HARTWIG, E. O. 1978. Factors affecting respiration and photosynthesis by the benthic community of a subtidal siliceous sediment. *Mar. Biol.* **46**: 283-293.
- ITURRIAGA, R. 1979. Bacterial activity related to sedimenting particulate matter. *Mar. Biol.* **55**: 157-169.
- JOHNSON, B. D., AND R. C. COOKE. 1980. Organic particle and aggregate formation resulting from the dissolution of bubbles in seawater. *Limnol. Oceanogr.* **25**: 653-661.
- JONES, J. A. 1968. Primary productivity of the tropical marine turtle grass *Thalassia testudinum* König, and its epiphytes. Ph.D. thesis, Univ. Miami, Florida. 196 p.
- KLUG, M. J. 1980. Detritus-decomposition relationships, p. 225-245. *In* R. C. Phillips and C. P. McRoy [eds.], *Handbook of seagrass biology: An ecosystem perspective*. Garland.
- LENZ, J. 1977. On detritus as food source for pelagic filter feeders. *Mar. Biol.* **41**: 39-48.
- ODUM, H. T., P. R. BURKHOLDER, AND J. RIVERO. 1959. Measurements of productivity of turtlegrass flats reefs, and the Bahia Fosforescente of southern Puerto Rico. *Publ. Inst. Mar. Sci. Univ. Texas* **6**: 159-170.
- OREMLAND, R. S., AND B. F. TAYLOR. 1977. Diurnal fluctuations of O₂, N₂, and CH₄ in the rhizosphere of *Thalassia testudinum*. *Limnol. Oceanogr.* **22**: 566-569.
- OVIATT, C. A., AND S. W. NIXON. 1975. Sediment resuspension and deposition in Narragansett Bay. *Estuarine Coastal Mar. Sci.* **3**: 201-217.
- WHELAN, T. 1974. Methane, carbon dioxide and dissolved sulfate from interstitial water of coastal marsh sediments. *Estuarine Coastal Mar. Sci.* **2**: 407-415.

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