1:6; field of view, 21 by 14 cm), Oceanic 2001 strobe, and Kodachrome 25 film. Resolution was usually sufficient to count individual zooids of bryozoans (<1 mm). Number of photographs per coral varied with coral size from one to four. Intervals between censuses were 4 days during the first year, and weekly thereafter. Most cryptic species require 1 week to heal lesions >1 to 2 mm [S. R. Palumbi and J. B. C. Jackson, *J. Exp. Mar. Biol. Ecol.* **64**, 103 (1982)]. Some sponges regenerate more rapidly [J. B. C. Jackson and S. R. Palumbi, in *Biologie des Spongaires*, C. Levi and N. Boury-Esnault, Eds. (Colloquium International, Centre National de la Recherche Scientifique, no. 291, Paris, 1979), p. 303], so that small injuries to these species would have been missed in our photographs.

11. Abundances were determined for the distinctive community found between 0 and 8 cm from coral edges [J. B. C. Jackson, *J. Exp. Mar. Biol. Ecol.* **75**, 37 (1984)]. Altogether 40,916 points were examined in seven repeated censuses of a 0.16-m^2 area.
12. Different sets of random points were followed for 6-week periods beginning in June 1983, August 1983, March 1984, August 1984, and September 1985; a minimum of 4028 points were followed per census. Only the most abundant groups were examined, including the five commonest species of cheilostomes, all pink and purple crustose algae, and all sponges; together these taxa cover almost 60% of the undersurface studied.
13. On the basis of counts within a 2-m^2 quadrat placed around each coral at 4- to 8-day intervals, densities dropped from 3.3 (SD, 0.48; $n = 45$) to 0.05 (SD, 0.02; $n = 45$) per square meter. By September 1985, densities had increased to 0.30 (SD, 0.60; $n = 45$) per square meter.
14. Principally *Diadema*, as evidenced by characteristic feeding scars [J. B. C. Jackson, in *Biotic Interactions in Recent and Fossil Benthic Communities*, M. J. S. Tevesz and P. L. McCall, Eds. (Plenum, New York, 1983), pp. 39–120, figure 21B].
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20. Young zooids are bright red and unfouled by epibionts, middle-aged zooids are reddish brown and lightly fouled, and old zooids are dark brown and heavily fouled (*16, 23*). Numbers of points overlying grazed and ungrazed zooids (G/U): young, 12/622; middle-aged, 23/474; old, 107/181; total, 1419; $\chi^2 = 298$, $P < 0.0001$, 2 df.
21. Feeding on both crustose algae (G/U: 214/1658 = 0.13) and old *Steginoporella* (G/U: 107/181 = 0.59) was higher than feeding on all other encrusting organisms combined (G/U: 53/3193 = 0.02). These differences are highly significant for each group ($\chi^2 = 231$ for crustose algae and 772 for old *Steginoporella*: $P < 0.0001$ with 1 df in both cases).
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23. Total predation before the die-off was 6.9% of cover in 6 weeks, and the average for the three following censuses (before *Diadema* started to increase) was 1.6%. This result suggests that *Diadema* had grazed 5.3% of the total cover every 6 weeks. To estimate annual rates, we assumed that the urchins grazed independently of previous grazing (that is, they could feed again at the same spot, which was observed). The amount of space remaining ungrazed by *Diadema* after 1 year (that is, 8.66 measurement periods or 52 weeks divided by 6 weeks per census) was $(1 - 0.053)^{8.66} = 0.62$. Thus the amount grazed by *Diadema* was $1 - 0.62 = 38\%$ of the total space available.
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26. This study was made possible by the field assistance of M. J. Boyle, G. Bruno, M. Gleason, and T. P. Hughes. Comments by M. Buzas, H. Caffey, N. Knowlton, H. Lessios, K. McGuinness, E. Weil, and two reviewers improved the manuscript. Supported by NSF grants OCE-82-15469 and OCE-84-15712. Contribution of the Discovery Bay Marine Laboratory, Jamaica.

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Can Microscale Chemical Patches Persist in the Sea? Microelectrode Study of Marine Snow, Fecal Pellets

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Microelectrode studies demonstrate the existence of persistent oxygen and *p*H gradients around flocculent, macroscopic marine particles known as marine snow. Oxygen is partially, but continuously, depleted within and around marine snow in the dark and can be completely depleted within large fecal pellets. Boundary layers hundreds of micrometers thick are maintained despite advection of fluid past the particles. The existence of chemical microhabitats on the scale of millimeters around macroscopic particles in the pelagic zone may significantly influence the distribution and activity of marine microorganisms and permit processes requiring low oxygen, including denitrification.

THE EXISTENCE OF PELAGIC MICROzones enriched in nutrients, oxygen, or dissolved organic matter has been hypothesized to explain high growth rates of phytoplankton and bacteria in seemingly impoverished oceanic waters (*1–4*). Microzones of nutrient enrichment would attract microorganisms and support high metabolic activity, whereas microzones of oxygen-depleted water might support denitrification or even permit sulfate reduction or methanogenesis. Although microscale nutrient patches lasting a few tens of seconds are produced by zooplankton excretion and potentially affect the course of competition and coexistence among phytoplankton (*5*), it has been argued that chemical gradients on the scale of millimeters cannot persist in the planktonic environment because they could not be maintained against processes of molecular or turbulent diffusion (*6, 7*).

However, the pelagic zone contains abundant macroscopic particles, both flocculent aggregates known as marine snow and the fecal pellets of zooplankton, whose large size and high microbial activity (*8, 9*) could produce and maintain microscale chemical gradients. Using microelectrodes to measure oxygen and *p*H, we have demonstrated that oxygen is partially depleted within marine snow particles in the dark and may become fully depleted in large fecal pellets. The boundary layer surrounding the particles further increases the volume of the microzone. We present experimental evidence (i) that microscale chemical gradients can persist in the ocean against processes of advection and diffusion on a scale significant to microorganisms and (ii) that these patches may have important implications for nutrient recycling in the sea.

Particles of marine snow (flocculent, macroscopic particles consisting of phytoplankton, detritus, bacteria, and fecal pellets embedded in a mucous matrix) ranging from 1 to 4 mm in diameter were collected by hand in small cylinders by scuba divers in surface waters of the Santa Barbara Channel, California (*10*). All particles were maintained at 18°C and tested within 1 to 24 hours after being collected. Freshly defecated fecal pellets were also obtained from planktonic macrocrustaceans collected by net and aged for up to 3 days in sterile seawater in the laboratory at 25°C. Each individual particle was placed in a small cone, 7 mm high and 3.5 mm in radius, made from 120-μm mesh-size plankton net, which sat in a 30-ml vessel filled with filtered seawater maintained at 18° to 20°C. A stream of fine bubbles emitted from a pipette tip placed near the bottom of the vessel outside the cone was used to mix water throughout the vessel. This bubble stream produced a suction effect, advecting water toward it from the cone and the rest of the vessel. Measurements of the time required for a fine suspension of carmine particles placed within 500 μm of the marine snow to leave the cone indicated that current velocities around the particles were on the order of 0.04 cm sec^{-1}.

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Calibrated oxygen (*11*) and *p*H (*12*) microelectrodes with sensing tips of 2.5 μm and 38 μm, respectively, were introduced into the experimental vessel by two micromanipulators under a stereoscopic microscope (*13*). Oxygen and *p*H gradients in and around the individual particles were measured in the light and dark after steady state had been established (generally requiring 2 to 3 minutes after light conditions were altered) and were monitored for 1 to 12 hours under each light condition. Oxygenic photosynthesis rates in the particles were measured as the initial slope of oxygen depletion rate after the light was turned off (*14*).

Oxygen concentrations at the surface of the particles of marine snow were elevated above ambient seawater concentrations at both low and high light intensities (Fig. 1, A and B), indicating photosynthetic activity. Microscopic examination indicated that healthy-looking phytoplankton were abundant throughout the particles of marine snow (Table 1). However, within large particles, oxygenic photosynthesis took place primarily at the particle surface and decreased considerably inside the particles. The rate at which the oxygen flows away from or into the particle is proportional to the oxygen gradient. The steeper oxygen gradient outside the particle in the light suggested that more oxygen might be flowing out than was being used internally. Oxygen concentration dropped below ambient seawater concentrations at the center of the particle, even at high light intensity (Fig. 1A). This result indicates that microbial respiration inside the large particle reported in Fig. 1A exceeded rates of photosynthetic oxygen production, which suggests degradation of organic matter within the particle center. Mineralization of organic matter by active microbes may supply nutrients that support the enhanced photosynthetic activity at the particle surface. A similar, although less pronounced, phenomenon was observed in a smaller particle (Fig. 1B).

In the dark, photosynthetic oxygen production ceased and respiratory activity caused partial oxygen depletion of as much as 45.8% inside the particle compared with that in ambient seawater (Fig. 1, A and B, and Table 1). Oxygen depletion persisted at a stable low level as long as the particles were kept in the dark (up to 12 hours). Oxygen depletion was greatest within larger particles (Table 1), and a boundary layer depleted of oxygen extended out to 800 μm from the particle surface (Fig. 1A). The large change in slope of the oxygen gradient at the particle surface and a more gradual slope in the interior of the particle indicates that dark respiration was maximum at the particle surface. High respiration is attributed to the abundance of bacteria (up to 9.4×10^7 per particle) together with the respiration of protozoans and phytoplankton (Table 1).

The lower *p*H values inside the particles in the dark indicate respiratory activity. The ΔpH would be primarily a function of increased CO_2 concentration within the particle. The ΔpH observed for the 4-mm particle in Fig. 1A was merely up to 0.22 (ΔCO_2 = 110 μm), indicating relatively fast diffusion rates between particles and the surrounding seawater.

Anaerobic conditions were never observed within the marine snow tested. The gelatinous matrix and amorphous nature of these particles coupled with the advection of water past the particles apparently allowed relatively rapid flux of oxygen into the particle, which counterbalanced the rate of oxygen consumption and produced a stable level of oxygen depletion within the particle.

Anaerobic conditions were observed within a large crustacean fecal pellet (6.2 mm long) found attached to a particle of marine snow (Fig. 1C). Oxygen was depleted within 100 μm of the surface of the pellet in areas where the peritrophic membrane remained intact.

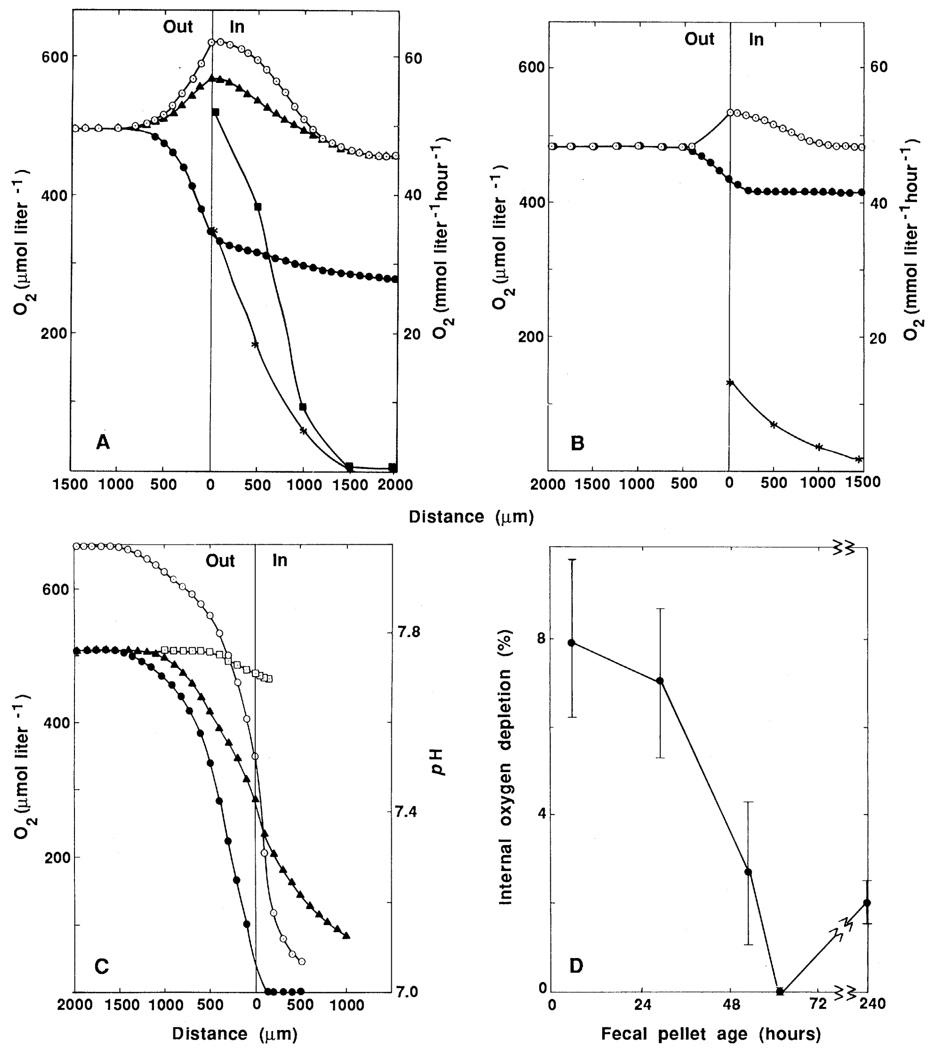

Fig. 1. Profiles of oxygen, *p*H, and oxygenic photosynthesis across individual particles of marine snow and fecal pellets, determined with microelectrodes. Three to four replicate profiles obtained for each particle showed negligible variability and were highly repeatable. Light was provided by a 150-W halogen lamp through a 4-mm-wide fiber optic that allowed quantum flux of up to 1500 μE m^{-2} sec^{-1} at the particle surface. (**A**) Microgradients across a single marine snow particle of 3.8 mm^3 volume (4.1 mm in diameter): (○) oxygen profile and (■) oxygenic photosynthesis at light intensity of 1400 μE m^{-2} sec^{-1}; (▲) oxygen profile and (*) oxygenic photosynthesis at 250 μE m^{-2} sec^{-1}; (●) oxygen profile in the dark. (**B**) Microgradients across a single marine snow particle of 11.0 mm^3 (2.8 mm in diameter): (○) oxygen profile and (*) oxygenic photosynthesis at 250 μE m^{-2} sec^{-1}; (●) oxygen distribution in the dark. (**C**) Microgradients of oxygen and *p*H across a large, 3.4-mm^3 (6.21 mm long, 0.41 mm wide) crustacean fecal pellet of unknown origin found attached to a particle of marine snow: (●) oxygen distribution in the dark through the intact membrane; (▲) oxygen distribution through a ruptured portion of the membrane; (○) *p*H profile; (□) oxygen profile across a freshly defecated, 0.02-mm^3 pellet (0.06 mm wide) of the kelp mysid *A. sculpta*. (**D**) Mean percentage of oxygen depletion (±1 SD) within fecal pellets of the euphausiid *E. pacifica* as a function of pellet age in the laboratory at 25°C. Pellet sizes and composition are given in Table 1.

Table 1. Size, composition, degree of oxygen depletion, and ΔpH across particles of marine snow and fecal pellets. Diatoms, especially *Chaetoceros* spp., *Skeletonema costatum, Rhizosolenia acta*, and *R. denticulata, Nitzchia pacifica*, and *Coscinodiscus* spp., made up more than 80% of the phytoplankton by number. Dinoflagellates, including *Peridinium* spp., *Prorocentrum* sp., and *Ceratium lineatum* and some coccolithophorids, were also present. Abundances of bacteria were determined with epifluorescence microscopy after mild sonication and staining with acridine orange (*8*). Values of ΔpH in the light were obtained at a light intensity of 250 $\mu E\ m^{-2}\ sec^{-1}$, corresponding to light intensity 10 m deep in the Santa Barbara Channel. Numbers in parentheses are replicate pellets.

Particle	Diameter (mm)	Volume (mm^3)	Phytoplankton (no. per particle)	Bacteria ($\times 10^6$ per particle)	O_2 depletion (% in dark)	ΔpH	
						Dark	Light
Marine snow							
1	1.0	1.0	105	4.8			
2	1.5	1.6	464	4.1	12.8		
3	2.1	5.0	1612	34.0	21.1	0.16	0.10
4	2.8	11.2	646	23.0	14.0		
5	2.8	11.0	683	4.3	15.4	0.12	
6	4.1	32.8	4037	94.0	45.8	0.22	0.15
Fecal pellets							
Unknown	0.41	3.4	0	37.0	100	0.91	0.9
Acanthomysis sculpta	0.06	0.02	19	5.4	6.0		
Euphausia pacifica							
4-hour (6)	0.12	0.02	0	0.6	8.0		
28-hour (5)	0.09	0.02	0	0.6	6.0		
52-hour (5)	0.13	0.02	0	0.4	2.7		
240-hour (2)	0.10	0.03	0	0.4	2.1		

Where the membrane had ruptured, the oxygen gradient was more gradual, indicating the efficient diffusion barrier of the membrane. The number of bacteria per volume found in the large fecal pellet was considerably larger than those of the marine snow particles (Table 1). The large size of the pellet, the abundance of the bacteria community and the effective diffusion barrier of the peritrophic membrane led to total oxygen depletion within the fecal pellet. The *p*H inside the pellet dropped to *p*H 7.09, corresponding to a ΔpH of 0.91. This value corresponds in turn to an increase in CO_2 of 326 μm, slightly less than the 500-μm decrease observed for oxygen.

This fecal pellet was atypically large relative to the smaller pellets produced by common planktonic crustaceans such as euphausiids, sergestids, or mysids. Oxygen gradients were also measured across smaller, freshly defecated pellets of the kelp mysid *Acanthomysis sculpta* (Fig. 1C) and the euphausiid *Euphausia pacifica* (Fig. 1D). Only minor oxygen depletion of 14% or less (Fig. 1D) was observed inside freshly defecated pellets of these macrocrustaceans, decreasing to 3% oxygen depletion in 52-hour-old pellets. Little or no oxygen depletion was observed in pellets 2.5 days or older. Thus, it is unlikely that significant oxygen gradients would exist in microscopic fecal pellets, such as those produced by copepods and other small zooplankton.

Our laboratory study strongly supports the conclusion that microgradients exist in nature as well. Conceptually, particles in the ocean sink through a stationary fluid, whereas we moved a fluid past a stationary particle in the laboratory. However, it is the relative motion of the fluid to the particle that is important for the transfer of mass between the particle and fluid (*15*). A 4-mm particle of marine snow sinks with a velocity of approximately 0.06 cm sec^{-1} (*16*), which resembles the 0.04-cm sec^{-1} velocity of fluid advecting around the particles in the laboratory. A 4-mm sinking particle of marine snow would have a Reynolds number of 3 and a Peclet number (Pe) of 3×10^3 (*15*). The Peclet number is a measure of the relative importance of advection and diffusion as mechanisms affecting the flux of mass away from the particle. The high Pe for marine snow indicates that advection dominates and that most of the oxygen depletion would be contained in a narrow wake behind the settling particle rather than be evenly distributed around it (*15*). Our results demonstrate that even at the high Pe expected for marine snow in nature, biological activity within the particles is sufficient to maintain chemical microzones around them against advective processes.

Although we measured only oxygen and *p*H, the observed gradients are expected to be followed by gradients of nutrients, such as phosphate, ammonium, and nitrate, which are enriched to levels up to 400 times ambient levels within particles of marine snow (*17*). These patches may be unique microhabitats attracting various assemblages of pelagic microorganisms and resulting in nonrandom distributions of bacteria (*2, 3*) and in the evolution of special adaptations for nutrient uptake by phytoplankton (*1, 5*). Since marine snow occurs at an abundance of about one to ten particles per liter even in the deep sea (*18*), such microzones would be readily accessible to most motile microbes (*2, 4*), which, once within the boundary layer, would tend to remain near the particle.

Our data demonstrate that chemical gradients on the scale of millimeters can persist in the pelagic zone within and around macroscopic particles. The large particle size, the relatively high specific activity, and the diffusion barrier around these particles maintain these chemical patches. Dissimilatory nitrate reducers may be active in and around oxygen-depleted marine snow either at night or when these particles sink below the euphotic zone. The high respiration of macroscopic particles settling through the water column may contribute to the depletion of oxygen in the oxygen-minimum layer and produce unnaturally low oxygen conditions within unpoisoned sediment traps. Settling particles may also deplete oxygen from the sea floor, although this would be most significant in shallow seas or over continental slopes, where particles sinking at 50 to 100 m day^{-1} (*16*) reach the sea floor while still metabolically active.

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