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Microbial Transformations of Organic Matter at Oceanic Interfaces: A Review and Prospectus

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The title of this article may seem a bit presumptuous or at least premature in the sense that marine microbiologists have only quite recently entered the quantitative phase of their investigations of the distribution, biomass, and in situ metabolic activities of sea microbes. Nevertheless, I believe that summarizing the results of preliminary studies will serve to define more clearly the important questions and will help to formulate a more productive research prospectus. Throughout this discussion I will attempt to identify what I consider to be important prospects for future oceanographic investigations.

The central theme that I would like to consider is that of microbially mediated transformations of carbon at oceanic interfaces. There are at least two major ideas to pursue and develop:

1. The ocean is not simply a well-mixed homogeneous fluid, not even on scales of meters or less, but in fact the oceans contain numerous inhomogeneities that result in the establishment of significant physical and chemical discontinuities especially on scales of millimeters to centimeters.

2. There is a close association between the physical and the chemical discontinuities and regions of elevated microbial biomass and activity. Furthermore, I hope to demonstrate that a majority of the biogeochemical transformations occur within these marine interfaces. The transformations most relevant to the present discussion are the production, early diagenesis, and remineralization of organic matter; however, similar scenarios may be invoked to explain the distributions of inorganic nutrients, bioreactive trace metals, and isotopic ratios of carbon, oxygen, and nitrogen.

During the late 19th century, Certes, Fischer, and Russell independently concluded that the world's oceans contained large and diverse populations of autochthonous microorganisms. However, it is only in recent years that microbiological oceanographers have begun to appreciate the complex ecological functions and metabolic interactions among individual microbial groups and between microorganisms and higher trophic levels [*Strickland*, 1971; *Pomeroy*, 1974; *Sieburth*, 1976]. Historically speaking, the terms bacteriology and microbiology have generally been used interchangeably since it was originally perceived that bacteria were the only microorganisms worth studying. Strictly speaking, however, all microscopically small (≤150 μm) organisms inhabiting the sea should be discussed collectively as 'marine microorganisms.' Therefore, recognition must be given to several distinct groups of microorganisms that differ significantly in their morphological characteristics and physiological capabilities (Table 1). The only common, unifying feature of the entire group is their small size and correspondingly high surface/volume ratios. This characteristic is extremely important from a metabolic point of view for it allows the marine microorganisms to maximize their interaction with the abiotic environment. The discussion and data that follow relate to the entire 'microbial community' without further resolution into its component parts; however, future studies in microbiological oceanography and marine biogeochemistry would undoubtedly benefit from a careful analysis of the structure of individual microbial assemblages.

One conceptual point regarding marine microorganisms in relation to discontinuities might not be obvious to nonmicrobiologists. Microorganisms live in microenvironments that are generally defined on scales of micrometers or less. Consequently, the environment sensed by the individual cells may be distinct from the chemical composition of the surrounding bulk fluid. This is important to the microbiologist and geochemist since it provides a mechanism for the occurrence of anaerobic processes in otherwise aerobic environments. The measurement of *p*H, redox level, dissolved oxygen, or dissolved organic and inorganic nutrients in bulk seawater or interstitial waters of sediments may have little bearing on the chemistry of the microbial environments and may in fact mislead the investigator with regard to the dominant metabolic processes. These microenvironments are created by the presence of particles and

TABLE 1. Representative Marine Microorganisms

Group	Approximate Size Range	General Characteristics
Procaryotes		
Eubacteria (also: bacterioplankton, picoplankton)	0.2–1.5 μm	very large and diverse group that includes photoautotrophs, chemoautotrophs, chemoorganotrophs, aerobes, and anaerobes
Cyanobacteria (also: blue-green bacteria, blue-green algae)	1–10 μm	this group can carry out oxygenic (evolve O_2) or anoxygenic photosynthesis; often exist as aggregates, filaments, or as epiphytes; some species can fix N_2
Eucaryotes		
Microalgae (also: phytoplankton)	1–50 μm	this group is a diverse assemblage of eucaryotic unicells with the common shared characteristic of oxygenic photoautotrophy
Protozoa (also: protozooplankton)	10–100 μm	heterotrophic eucaryotic unicells capable of absorbing dissolved nutrients as well as ingesting small particles such as detritus, bacteria, and some microalgae; included in this group are tintinnids, foraminifera, radiolaria, amoebae, and acantharia
Yeasts/fungi	variable	fungi are eucaryotic spore-forming organisms that generally exist as filaments (mycelia) on plant, animal, or nonliving surfaces; yeasts are unicellular and have lost their ability for mycelial growth
Micrometazoa (also: metazooplankton)	35–150 μm	this group includes all multicellular microbes (excluding fungi) some of which are only temporary members (naupliar or larval stages); may be algal grazers, carnivores, filter feeders, or osmotrophs

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other diffusion barriers and by the metabolic activities of the microorganisms themselves.

Physical and chemical discontinuities are widespread in the marine environment (see list) and comprise potentially unique and complex habitats for the growth of marine microorganisms. How important are these various oceanic discontinuities in controlling microbial activities and growth?

Predominantly Physical Discontinuities
- Bubbles
- Thermoclines, haloclines and pycnoclines
- Man-made/introduced surfaces
- Water mass boundaries

Predominantly Chemical Discontinuities
- Nutriclines
- Oxic-anoxic interfaces
- Animal digestive tracts

Physical/Chemical Discontinuities
- Air-sea interface
- Ocean-sediment interface
- Animal/plant surfaces
- Suspended particles
- Aerosols
- Coastal and estuarine fronts
- Sea ice–seawater boundaries
- Animal tubes and burrows

Before discussing some of the data on microbial transformations of carbon at oceanic discontinuities, two major obstacles that have contributed to the dearth of knowledge on this subject are worth mentioning:

1. The most critical concern at the present time is the lack of reliable unequivocal methods for assessing the biomass, metabolic activities, and growth rates of microorganisms in nature. This overwhelming need for new methods is not yet fully realized or understood by the entire marine scientific community. The following list presents a summary of available methods for evaluating the standing stocks, metabolic activities, and growth rates of microorganisms in the ocean. In this regard it should be emphasized that each individual method is designed to evaluate a different property of the system, and it is up to the investigator to determine which variable (biomass, metabolism, or growth) should be measured. For example, cell numbers or biomass measurements by themselves may be misleading in terms of determining the potential for biogeochemical transformations. Marine chemists and geologists are well aware of the distinction between concentration and activity as it relates to reaction kinetics and chemical equilibria. The same analogy should be used to study microbial assemblages in the marine environment. Further distinctions can be made between metabolic activity (or total energy transformation) and growth (that portion of the energy transformation that is ultimately coupled to biosynthesis). Metabolically active but nongrowing cells may have a greater chemical impact on the environment than efficient, rapidly growing cells. Biologists are generally interested in growth, while geochemists are interested in total metabolic activity. Future studies in marine biogeochemistry should give careful consideration to the microbiological methods selected, and, if necessary, new methods should be devised and evaluated for use in specialized investigations [*Karl*, 1980].

Biomass

Direct microscopy (examples: light, phase contrast, epifluorescence, immunofluorescence, electron beam instruments)

Cultural (example: enrichment cultures for isolating specific physiological/metabolic groups)

Biochemical indices (example: chl *a*, ATP, lipopolysaccharide, muramic acid)

Physiological Potential

Adenylate energy charge

Specific enzyme activities (examples: dehydrogenase, alkaline phosphatase, nitrogenase, glutamine synthetase)

Metabolic Activity

Rate of production of end products/metabolites (examples: small molecular weight organics, O_2, CO_2, CH_4)

Monitor fate of isotopically labeled electron donors or acceptors

Use of specific redox dyes or tetrazolium salts to assess in vivo processes

Oxygen respirometry

Microautoradiography

Microcalorimetry

Growth Rate

Rate of biomass-related production during timed incubations (examples: chl *a*, ATP, POC, protein, RNA)

Rates of incorporation of labeled precursors into 'stable' macromolecules (examples: lipids, protein, cell walls, RNA)

Use of elemental composition ratio data (example: C : N : P)

GTP/ATP ratios

Cell Division Rate

Rate of incorporation of labeled precursors into DNA

Microscopic observations of cell division (i.e., frequency of dividing cells)

Measure increase in cell number during timed incubations

2. The organization and research objectives of most major microbiological oceanographic investigations conducted to date have precluded detailed sampling of oceanic discontinuities and only rarely include integrated microbiological investigations. The few data that do exist have been in part serendipitous and consequently not very extensive or complete. Furthermore, the resolution of our data is limited by the temporal and spatial frequencies of our sampling schedules. Most biological oceanographic research has been conducted in an expeditionary manner with limited opportunities to evaluate diel or seasonal cycles.

The remainder of this article will focus on the microbiology of four important and widely distributed oceanic discontinuities: (1) the dissolved O_2 minimum layer and its associated pycnocline, (2) the chemical discontinuity at the interface between oxic and anoxic marine environments, (3) coastal oceanic fronts, and (4) suspended particles.

Dissolved O_2 Minimum Zone

Most heterotrophic processes in the sea proceed with the use of dissolved molecular oxygen, which is energetically the most favorable terminal acceptor for electrons during cellular metabolism. The vertical distribution of O_2 in the sea is characterized by an intermediate depth minimum, usually located between 300 and 1000 m and nearly always at the σ_t = 27.2 density surface regardless of depth or latitude [*Richards*, 1957]. However, the exact mechanisms responsible for the formation and maintenance of this permanent feature have not been unequivocally elucidated. Both the dynamic conditions of oceanic circulation

and in situ decomposition of organic matter have been suggested as important processes.

Most of the hypotheses are based upon indirect observations and models rather than on direct microbiological investigations. Nevertheless, *Sorokin* [1971] has reported a large subsurface maximum in bacterial numbers and productivity in the O_2 minimum layer of the tropical Pacific. A similar increase in biomass has been reported by *Karl et al.* [1976] for the North Atlantic Ocean (Figure 1). Biomass estimates based on ATP concentrations revealed an extremely large subsurface maximum centered at a depth of 800–1000 m, corresponding to the O_2 minimum and to the 27.2 σ_t surface. Although no particulate organic carbon data were available from this hydrostation, the authors suggested that sinking organic detritus (also with a mean density of 1.0272 g/cm^3) achieved neutral buoyancy and was accumulating within the discontinuity layers of the permanent pycnocline and that this hypothetical accumulation represented the input of reduced carbon and energy required to sustain these in situ heterotrophic processes. Thermoclines and haloclines are known to accumulate particulate organic materials [*Biggs and Wetzel*, 1968; *Parsons and Seki*, 1970].

Recently, I have obtained additional data from stations located off Monterey, California, and in the Columbian Basin of the Caribbean Sea that provide direct evidence of elevated microbial growth rates (as measured by rates of

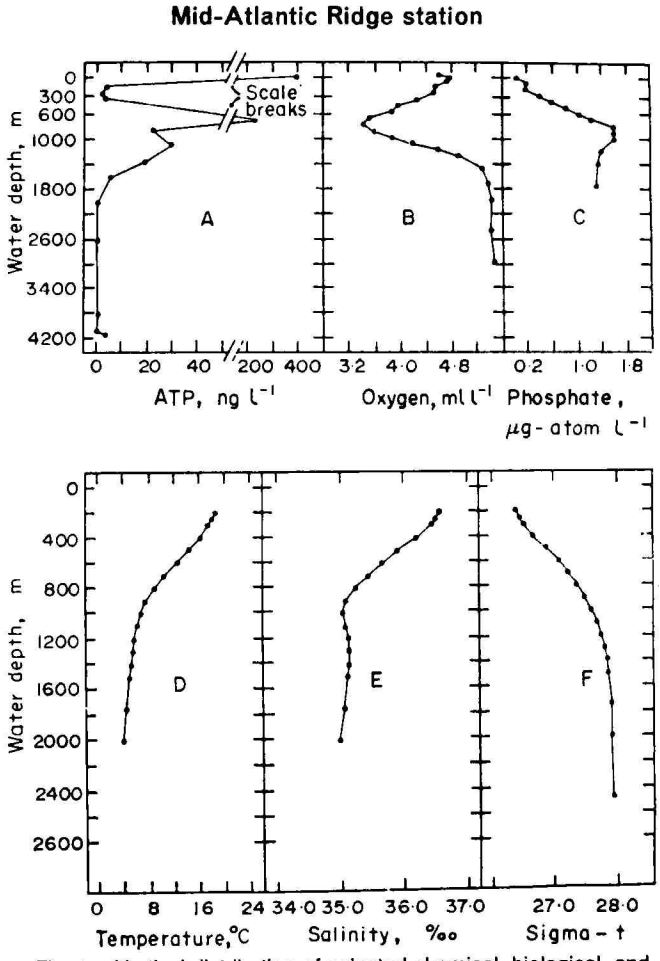


Fig. 1. Vertical distribution of selected chemical, biological, and physical variables at a station located over the Mid-Atlantic Ridge. (*a*) ATP, (*b*) oxygen, (*c*) phosphate, (*d*) temperature, (*e*) salinity, and (*f*) density. [From *Karl et al.*, 1976]

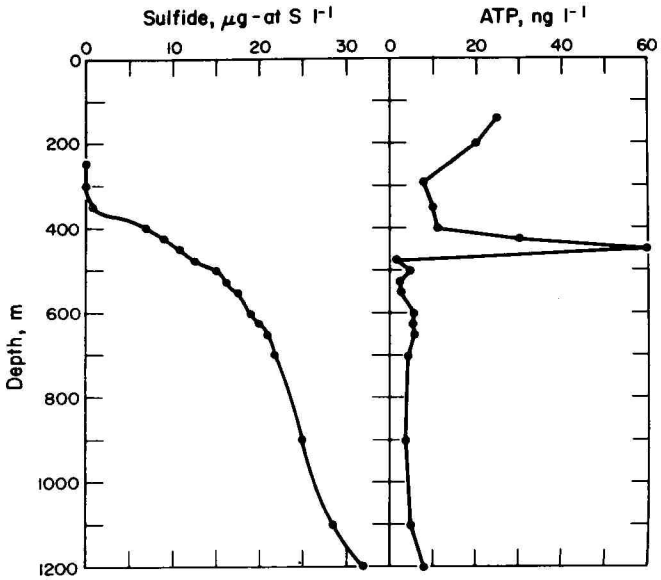


Fig. 2. The vertical distribution of sulfide and ATP at a station in the eastern basin of the Cariaco Trench. [From *Karl et al.*, 1977]

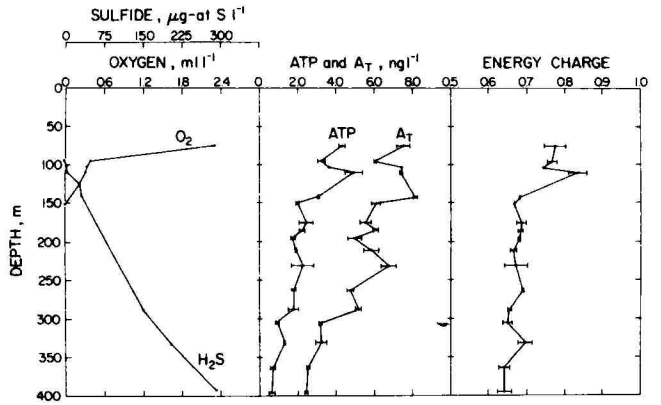


Fig. 3. Vertical distribution of HS^-, O_2, ATP, A_T (total adenylates), and (adenylate) energy charge for the upper 400 m of the water column in the western basin of the Black Sea. [From *Karl*, 1978]

RNA synthesis) within the O_2 minimum zone [*Karl*, 1979; *Fellows et al.*, 1981]. Although it had been suggested previously that the entire biogeochemical cycle of organic carbon was restricted to the top 200 m of the water column [*Menzel and Ryther*, 1968], it is now apparent that these ideas must be modified to accommodate the recent microbiological biomass and rate data. An intermediate depth zone of active microbial growth may serve as an important site for nutrient regeneration and the early diagenesis of organic matter and may also represent an important source of reduced carbon (secondary production) for mesopelagic and deep-sea communities.

Oxic-Anoxic Interfaces

It is generally believed that anaerobic marine waters are geographically restricted to a few permanently anoxic basins such as the Black Sea, the Cariaco Trench, Lake Nitinat, and several Norwegian fjords. However, the waters of numerous coastal environments (e.g., Santa Barbara Basin, Skan Bay, Long Island Sound, etc.) become periodically anoxic especially during conditions of high organic carbon productivity or restricted vertical circulation. Moreover,

TABLE 2. Nucleotide Fingerprints of Microbial Communities at the Galapagos Rift

Sample Location	Type	ATP*	A_T*	GTP : ATP*
Surface seawater, 50 m	filtered	130 ± 32 ng l^{-1}	340 ± 112 ng l^{-1}	0.16 ± 0.08
Deep seawater, 2400 m	filtered	1.7 ± 0.3 ng l^{-1}	3.4 ± 0.3 ng l^{-1}	< 0.075
Garden-of-Eden vent	filtered	491 ± 151 ng l^{-1}	1494 ± 553 ng l^{-1}	0.86 ± 0.17
Garden-of-Eden vent	settled particles	1943 ± 1143 ng g^{-1}	4248 ± 2031 ng g^{-1}	0.89 ± 0.35

*All values are given as the mean ±1 standard deviation.

anoxic conditions are frequently encountered in marine sediments and might also be expected to occur in diffusion-limited microenvironments such as within suspended detrital particles. Therefore, the importance of microbial processes occurring at oxic-anoxic interfaces is undoubtedly of much greater global significance with regard to organic carbon transformations than one may suspect upon cursory examination of an 'oxidized' ocean.

If one examines the vertical distribution of microbial biomass within a permanently anoxic marine basin, such as the Cariaco Basin off Venezuela (Figure 2), a peak in biomass associated with the oxic-anoxic interface is evident. These data suggest the presence of a thin, dense layer of viable micoorganisms, which presumably exists as a consequence of this specialized habitat.

ATP (biomass) data by themselves are insufficient to distinguish between a passive accumulation of viable cells at a density interface and active in situ bacterial growth. During a subsequent investigation of the Black Sea a bacterial plate at the O_2-H_2S interface (~125 m) was again observed. Furthermore, a corresponding peak in adenylate energy charge (EC_A) provided evidence that this vertically restricted zone of elevated biomass was also a zone of potential metabolism and growth (Figure 3) [*Karl*, 1978]. The increase in ATP and EC_A ratio occurred within a portion of the water column where both O_2 and HS^- coexist, rather than distinctly above or below the anoxic zone.

Before leaving the topic of oxic-anoxic interfaces, I would like to mention briefly one final unique oceanic region, the Galapagos Rift hydrothermal vents. At a depth of approximately 2400 m on the Galapagos Rift (and elsewhere on the East Pacific Rise), several areas of active hydrothermal fluid discharge have recently been discovered and investigated [*Corliss et al.*, 1979]. Each specific vent field was found to have associated with it an extremely dense community of macroinvertebrates which in certain cases approached 100% cover. If the turbid, oxygen-poor, sulfide-rich vent waters are filtered and their particulate contents examined microscopically, numerous bacterial aggregates (some associated with elemental sulfur deposits) are observed. Biomass estimates (based on ATP measurements) revealed that the vent exit waters contained 300–400 times as much microbial carbon as the 'control' deep water collected at 2400 m (Table 2). Settled particles had ATP levels comparable to intertidal and coastal subtidal marine sediments. Given these biomass estimates and the presumed rates of vent water discharge, the total mass flux of microbial cells must be substantial. The GTP : ATP ratios (relative index of growth rates) were an order of magnitude higher than the control deep waters and exceeded those measured for the surface microbial populations (Table 2). Subsequent measurements of the rates of RNA synthesis (C. Winn and D. Karl, unpublished data, 1980) have confirmed the hypothesis of accelerated in situ growth at the hydrothermal vent chemocline.

Typically, life in the deep sea is extremely sparse primarily because the abyssal environment is so far removed from the surface euphotic zone where the primary fixation of CO_2 occurs. The abundance of life in the deep-sea Galapagos Rift environment is totally uncoupled from energy derived from the sun. Instead, it has been proposed that the vent ecosystem is fueled by bacterial chemosynthesis [*Karl et al.*, 1980]. Unlike chemosynthetic organic productivity at previously investigated oxic-anoxic interfaces, the hydrothermal vent production is truly primary in the sense that the reduced inorganic compounds (especially HS^-) arise from geothermal pyrolysis reactions and are, therefore, independent of preformed organic matter.

Coastal Oceanic Fronts

Oceanic fronts occur on horizontal scales of meters to thousands of kilometers and at all water depths. Important physical driving forces are air-sea transfers of heat and water, riverine inputs, upwelling, tidal and internal wave shear, and localized turbulent mixing [*Bowman and Esaias*, 1978]. Coastal fronts are ubiquitous and often ephemeral phenomena that can be detected by aircraft and infrared satellite remote sensing. Fronts are regions of intense convergence and are characterized by accumulations of buoyant and suspended particles, including living microorganisms. Do these physical and chemical conditions influence microbial activities and growth?

At certain seasons and under certain weather conditions, tidal fronts in the English Channel comprise recently stabilized mixed waters that are favorable for rapid and sustained growth of phytoplankton [*Pingree et al.*, 1975; *Simpson and Pingree*, 1978]. Similarly, *Traganza et al.* [1980] reported high ATP biomass and high GTP : ATP ratios for plankton assemblages entrained in the strong thermal-chemical gradients associated with newly upwelled waters off Point Sur, California. *Floodgate et al.* [1981] have recently demonstrated that the combined metabolic activities of algae, bacteria, and zooplankton entrained in a shallow sea front in Liverpool Bay were mutually beneficial, further suggesting that certain oceanic fronts may represent closed microecosystems where the rates of production, consumption, and remineralization of carbon are all enhanced.

Role of Particles

At the present time there is a major difference of opinion and data concerning the relationships between particles in the ocean and microbial activities. Although it is generally agreed that particles, especially organic detritus, represent potential microenvironments of elevated organic carbon in the sea, the experimental data on the quantitative importance of particles to microbial metabolism are equivocal.

There are two significant sampling problems that are inherent with a systematic study of particles in the ocean, which have led me to conclude that we have not yet obtained accurate or representative samples of in situ oceanic particles. The first problem regards the extremely fragile nature of the organic aggregates sometimes referred to as

marine snow [*Silver et al.*, 1978]. These frequently encountered aggregates represent unique chemical and biological entities that are distinct from the characteristics of the surrounding waters [*Trent et al.*, 1978]. The second, and perhaps more significant criticism, concerns the occurrence of relatively rare, rapidly sinking oceanic particles. *McCave* [1975] and *Fellows et al.* [1981] have emphasized the inability of conventional water bottles in obtaining representative samples of particulate organic material from seawater. Only with the aid of particle interceptor traps (i.e., 'sediment traps') can we fully assess the relationships between oceanic particles and microbial activity.

Recently, it has been reported that living microorganisms associated with sedimenting particles (sediment trap collections) may represent 100 times more biomass carbon than had previously been thought to be associated with 'organic particulate matter' [*Fellows et al.*, 1981]. Furthermore, the particle-associated microorganisms are actively growing under in situ conditions (D. Karl, unpublished data, 1981). The significance of this downward vertical flux of rapidly metabolizing microorganisms associated with oceanic particles may require that we alter our present concepts of the cycling of carbon in the sea.

In conclusion, discontinuities exist in the marine environment on scales of micrometers to tens of meters or more. The physical and chemical processes that produce and maintain these discontinuities also contribute to the formation of unique habitats for accelerated microbial metabolism and growth. Future investigations in the area of marine biogeochemistry should benefit from detailed studies of microbial assemblages at oceanic discontinuities.

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References

Biggs, R. G., and C. D. Wetzel. Concentration of particulate carbohydrate at the halocline of Chesapeake Bay, *Limnol. Oceanogr., 13*, 169–171, 1968.

Bowman, M. J., and W. E. Esaias (Eds.), *Oceanic Fronts in Coastal Processes*, Springer-Verlag, New York, 1978.

Corliss, J. B., J. Dymond, L. I. Gordon, J. M. Edmond, R. P. von Herzen, R. D. Ballard, K. Green, D. Williams, A. Bainbridge, K. Crane, and T. H. van Andel, Submarine thermal springs on the Galapagos Rift, *Science, 203*, 1073–1083, 1979.

Fellows, D. A., D. M. Karl, and G. A. Knauer, Large particle fluxes and the vertical transport of living carbon in the upper 1500 m of the northeast Pacific Ocean, *Deep Sea Res., 28*, 921–936, 1981.

Floodgate, G. D., G. E. Fogg, D. A. Jones. K. Lochte, and C. M. Turley, Microbiological and zooplankton activity at a front in Liverpool Bay, *Nature, 290*, 133–136, 1981.

Karl, D. M. Distribution, abundance and metabolic states of microorganisms in the water column and sediments of the Black Sea, *Limnol. Oceanogr., 23*, 936–949, 1978.

Karl, D. M. Measurement of microbial activity and growth in the ocean by rates of stable ribonucleic acid synthesis, *Appl. Environ. Microbiol., 38*, 850–860, 1979.

Karl, D. M. Cellular nucleotide measurements and applications in microbial ecology, *Microbiol. Rev. 44*, 739–796, 1980.

Karl, D. M., P. A. LaRock, J. W. Morse, and W. Sturges, Adenosine triphosphate in the North Atlantic Ocean and its relationship to the oxygen minimum, *Deep Sea Res., 23*, 81–88, 1976.

Karl, D. M., P. A. LaRock, and D. J. Shultz, Adenosine triphosphate and organic carbon in the Cariaco Trench, *Deep Sea Res., 24*, 105–113, 1977.

Karl, D. M., C. O. Wirsen, and H. W. Jannasch, Deep-sea primary production at the Galapagos hydrothermal vents, *Science, 207*, 1345–1347, 1980.

McCave, I. N., Vertical flux of particles in the ocean, *Deep-Sea Res., 22*, 491–502, 1975.

Menzel, D. W. and J. H. Ryther, Organic carbon and the oxygen minimum in the South Atlantic Ocean, *Deep Sea Res., 15*, 327–337, 1968.

Parsons, T. R., and H. Seki. Importance and general implications of organic matter in aquatic environments, in *Organic Matter in Natural Waters*, edited by D. W. Hood, pp. 1–27, University of Alaska Press, College, 1970.

Pingree, R. D., P. R. Pugh, P. M. Holligan, and G. R. Forster, Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel, *Nature, 258*, 672–677, 1975.

Pomeroy, L. R., The ocean's food web, A changing paradigm, *BioScience, 24*, 499–504, 1974.

Richards, F. A., Oxygen in the ocean, in *Treatise on Marine Ecology and Paleoecology*, edited by J. Hedgepeth, *Mem. Geol. Soc. Am., 67*, pp. 185–238, Geological Society of America, Boulder, Colo., 1957.

Sieburth, J., Bacterial substrates and productivity in marine ecosystems, *Ann Rev. Ecol. Syst., 7*, 259–285, 1976.

Silver, M. W., A. L. Shanks, and J. D. Trent, Marine snow: Microplankton habitat and source of small-scale patchiness in pelagic populations, *Science, 201*, 371–373, 1978.

Simpson, J. H., and R. D. Pingree, Shallow sea fronts produced by tidal stirring, in *Oceanic Fronts in Coastal Processes*, pp. 29–42, edited by M. J. Bowman and W. E. Esias, Springer-Verlag, New York, 1978.

Sorokin, Y. I., Abundance and production of bacteria in the open water of the central Pacific, *Oceanology, 11*, 85–94, 1971.

Strickland, J. D. H., Microbial activity in aquatic environments, *Symp. Soc. Gen. Microbiol., 21*, 231–253, 1971.

Traganza, E. D., W. Hanson, S. Bronsink, and D. Austin, Satellite inferences, GTP-microplankton productivity and chemodynamic effects of upwelling systems off Pt. Sur, CA, *Eos Trans, AGU, 61*, 1013, 1980.

Trent, J. D., A. L. Shanks, and M. W. Silver, In situ and laboratory measurements on macroscopic aggregates in Monterey Bay, *Limnol. Oceanogr., 23*, 625–635, 1978.

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