NATIONAL UNDERSEA RESEARCH PROGRAM Research Report 88-1

Biogeochemical Cycling and Fluxes Between the Deep Euphotic Zone and Other Oceanic Realms

Catherine R. Agegian,
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PREFACE

The National Undersea Research Program (NURP) of the National Oceanic and Atmospheric Administration supports *in situ* investigations in the oceans and large lakes of the world. By placing investigators safely undersea to conduct manipulative experiments not possible within the limitations of traditional laboratory and ship-based research, the NURP researchers will develop knowledge about processes in biological, chemical, and physical systems in the oceans and large lakes and across the boundaries of their basins in order to provide a sound basis for decisions governing uses of the ocean and its resources.

Program activities are supported with a wide array of advanced undersea sampling and sensing platforms including manned submersibles, remotely operated vehicles, and saturation habitats.

Occasionally, NURP sponsors symposia and workshops to disseminate results of past investigations and to possibly guide future research activities. In December 1986, NURP sponsored a symposium to reconsider the processes which govern the uptake of carbon dioxide by marine plants and transport of carbonate and organic carbon particles to the deep sea. The symposium was conducted in association with the annual meeting of the Western Society of Naturalists and was supported through grant NA 87AA-D-UR031 with the National Undersea Research Center at the University of Hawaii. A report, prepared and submitted under the terms of that grant, which covers the symposium presentations is herein presented in its entirety, as part of the NURP Research Report series.

The Research Report series published by the NURP is intended to provide the marine community with the results of program-sponsored symposia and workshops in a timely fashion. Reports in this series do not necessarily reflect NURP policy. Comments on the report are welcome and may be addressed to:

Director
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6010 Executive Boulevard
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BIOGEOCHEMICAL CYCLING AND FLUXES BETWEEN THE DEEP EUPHOTIC ZONE AND OTHER OCEANIC REALMS

Catherine R. Agegian

Hawaii Institute of Geophysics
University of Hawaii
Honolulu, HI 97822

INTRODUCTION

The magnitude of the impact of man's activities on global biogeochemical cycles has resulted in attempts to obtain more precise quantification of elemental cycles and fluxes within and between the major global reservoirs. Within the ocean reservoir, biogeochemical processes occurring in the euphotic zone are the most studied, the least understood, and the most important component contributing to elemental cycling and fluxes in other oceanic realms. The overall goal of this symposium is to evaluate our current understanding of the euphotic zone of open ocean and neritic oligotrophic systems and to identify gaps in our knowledge and new directions for future research.

The depth of the euphotic zone in the ocean is defined as the depth in which there is ample light for net (P>R) photosynthesis, commonly less than 1% of incident irradiance. Recently, technological and methodological advances have enabled a reevaluation of current notions of marine photobiology, especially photosynthetic activity at these low light levels. Using manned submersibles, Littler et al. (1985) and Agegian and Abbot (1985) have recorded macroscopic plant life at depths with <0.0004% of surface illumination. Estimates of primary production by deep water coralline algae at 1% of incident irradiance (Littler et al., 1985) were equivalent to rates measured in shallow water environments. The photosynthetic activity of macroscopic algae at the recorded depth limits has never been measured in situ; therefore, the possibility that heterotrophic processes replace photosynthesis in marine algae at these depths cannot be excluded. The occurrence of phagotrophy in "autophototrophic" microorganisms has been documented in some marine algal nanoflagellates grown under low light conditions (Estrep and Sieburth, 1986). The degree to which marine plants may be photoautotrophic, heterotrophic or phagotrophic at low light levels may confound our current notions of trophodynamics and elemental cycling in the euphotic zone.

Conventional views of ecological energetics dictate that almost all reduced carbon in the shallow ocean is derived,

ultimately, from CO_2 fixed by unicellular and macroscopic algae living in the upper layer of the euphotic zone. Data collected by investigators working on the multidisciplinary VERTEX program (Knauer, Martin, Karl et al., 1986) indicate that the oligotrophic North Pacific euphotic zone may function as two distinct systems. Although measured rates of primary production are consistently higher (Knauer, et al., 1984; Small et al., 1986) in the upper part of the euphotic zone (approx. 0-50 m), most of this production is recycled and retained within this zone. "New" production may occur at greater depths (50-150 m) supported by an allochthonous supply of nutrients. "New" production in the ocean has been defined as the particulate organics formed by primary production from allochthonous nitrogen sources (Eppley and Peterson, 1979). The allochthonous supply of nutrients for new production in open ocean waters removed from river runoff and sewage comes from two sources: (1) atmospheric sources such as particulate fallout from remote land sources or N gas flux, and (2) horizontal and/or vertical advection and diffusion of nutrients from waters below the euphotic zone. Therefore, new production occurring at the base of the euphotic zone or at greater depths (chemolithotrophy) may be the primary source of organic particles to the deep sea.

Conceptually, the two-layer euphotic zone may apply equally well to oligotrophic neritic environments; however, this approach has not been systematically applied to benthic systems. Coral reef ecosystems (equivalent to the top-layer of the euphotic zone) are driven largely by recycling processes (Kinsey, 1985; Smith, 1984), and very little carbonate or organic carbon produced by photosynthesis is lost to adjacent open ocean waters. Deep water banks (60-200 m) formed around islands and atolls during lower stands of sea level may be sites of "new" benthic production driven by an allochthonous supply of nutrients from water below the euphotic zone. Indeed, these banks are sites of major commercial fisheries (Munroe, 1979) in tropical and subtropical waters.

Benthic carbonate and organic carbon particles produced on deep water banks may be transported horizontally to adjacent open ocean waters. Betzer et al. (1984) suggested that the flux of pelagic carbonate particles could not account for the excess alkalinity observed at intermediate depths in waters in the western North Pacific. Calculated estimates of benthic carbonate production (Agegian et al., 1988) indicate that highly reactive carbonate particles (i.e. aragonite and magnesian calcites) produced by calcareous algae on deep water banks (60-200 m) and transported to adjacent open ocean waters may contribute to the alkalinity (Fiadero, 1980) and calcium (Tsunogai and Watanabe, 1981) anomalies observed in intermediate depth waters of the western Pacific Ocean. The quantitative significance of benthic carbonate and organic carbon produced on deep water banks to the carbon cycle of the ocean reservoir is, at present, unknown.

The goals of this symposium are (1) to reassess the textbook definition of the euphotic zone with respect to the biological and ecological adaptations of marine algae at low irradiance levels (2) to evaluate the depth distribution of recycled vs. new primary production in the euphotic zone of oligotrophic ocean waters, (3) to estimate the importance of new primary production in global biogeochemical cycles of the ocean and (4) to speculate on evolutionary changes in primary production of reconstructing the physico-chemical history of the euphotic zone over a geologic time scale. Ultimately, a reconsideration of the factors influencing the uptake of carbon dioxide by marine plants and transport of carbonate and organic carbon particles to the deep sea will provide an understanding of the level at which the ocean reservoir serves as a sink for natural or anthropogenic changes in atmospheric carbon dioxide.

CARBONATE PRODUCTION AND FLUX FROM A MID-DEPTH BANK ECOSYSTEM, PENGUIN BANK, HAWAII

Catherine R. Agegian[1]
Fred T. Mackenzie[1,2,3]
Jane S. Tribble[1,3]
Chris Sabine[1,2]

Hawaii Institute of Geophysics[1]
Department of Oceanography[2]
Department of Geology and Geophysics[3]
University of Hawaii

INTRODUCTION

In the oligotrophic ocean, far from areas of riverine input or upwelling, primary production in the euphotic zone may be stratified (Small et al., 1987) into a shallow layer with high rates of recycled production and a deeper layer characterized by low levels of production which, in part, may be classified as "new" production (Eppley and Peterson, 1979). This "new" production is thought to be fueled by upward eddy diffusion of nutrients from the nutricline.

Mid-depth banks, submerged topographic features with average depths ranging from 50 to 150 m, are present throughout the tropical and subtropical Pacific. These banks may be sites of both benthic and pelagic new production driven by vertical transfer of nutrients from the nutricline, because their depth range coincides with the deeper layer of the euphotic zone, close to the upper levels of the nutricline (Figure 1).

In this paper we report results of in situ measurements of benthic carbonate production on Penguin Bank, a mid-depth bank in the Hawaiian Archipelago, indicating that mid-depth banks are environments of significant carbonate production relative to surrounding shoal-water areas in the Pacific. Furthermore, we hypothesize that these Pacific bank environments may be sites of significant new production in the oligotrophic ocean, and a source of carbon for the open ocean.

Production on mid-depth banks, in the deep euphotic zone, is contrasted with that of shoal-water environments, shallow reefs, and atolls, which takes place entirely in the shallow euphotic zone. These shallow environments are typically characterized as highly productive ecosystems in a nutrient poor environment. Although some new production takes place via fixation of atmospheric nitrogen by some reef-dwelling organisms (Wiebe, et al., 1975; Wilkinson and Sammarco, 1983), coral reef ecosystems are considered to be driven largely by recycling processes

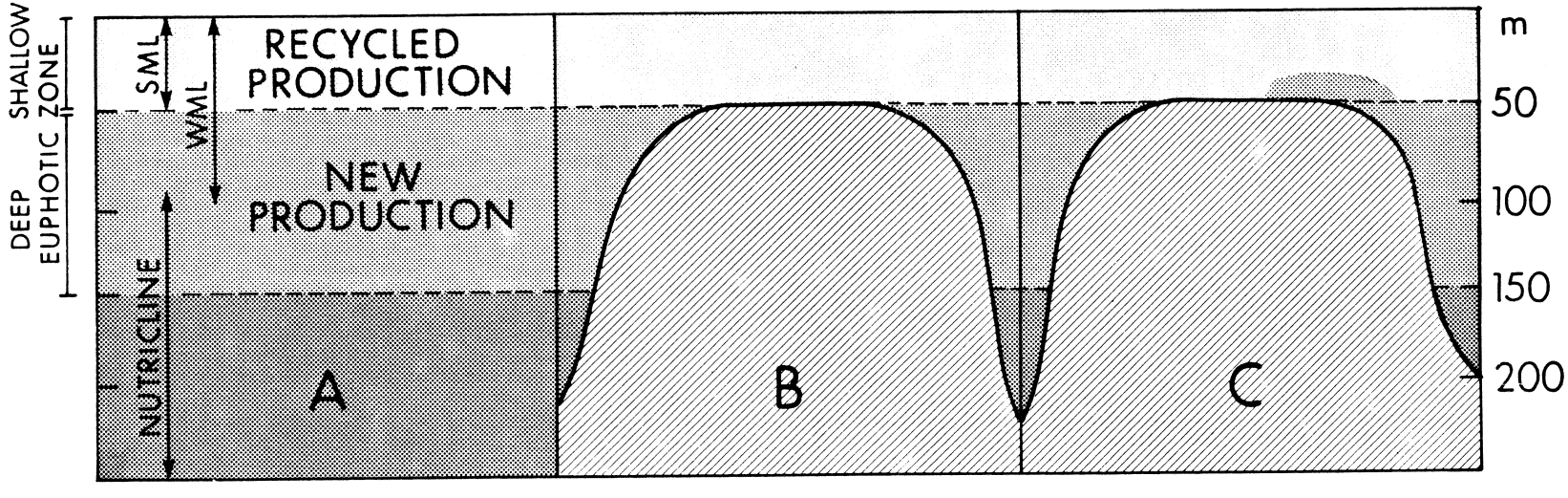

Figure 1. Schematic diagram of the two-layered euphotic zone in an oligotrophic open ocean environment and in a mid-depth bank ecosystem. (A) Hypothesized two-layer euphotic zone in the open ocean showing shallow euphotic zone dominated by recycled production and deep euphotic zone characterized by new production. Depth ranges of the mixed layer in the summer (SML), Winter (WML), and nutricline are depicted by arrows. (B) Average depth of mid-depth banks in the Hawaiian Archipelago at the interface between zones of recycled and new production, (C) Shallow mixed layer in summer months represents the most nutrient-limited scenario, and probable addition of new nutrients by tidal pumping mechanism.

(Table 1 in Gladfelter and Kinsey, 1985). Very little carbonate or organic carbon produced by photosynthesis in these shallow environments in the Pacific appears to be lost to adjacent open ocean waters.

Recent studies indicate that significant photosynthetic activity occurs at the low light levels present at the depth of mid-depth banks. Using manned-submersibles, Littler et al. (1985) and Agegian and Abbott (1985) recorded macroscopic plant life at depths with less than 0.0004% of surface illumination. Estimates of primary production by deep water coralline algae at 1% of incident irradiance were equivalent to rates measured in shallow water environments (Littler et al., 1985); however, the photosynthetic activity of macroscopic algae at the recorded depth limits has never been measured. Therefore, the possibility that heterotrophic processes replace photosynthesis in marine algae at depth cannot be excluded.

Penguin Bank (Figure 2) and other banks in the Hawaiian Archipelago (Figure 3) comprise an area six times that of adjacent shoal-water reefs (0-50m). Notable physico-chemical features of Penguin Bank are (1) the depth range (50-100m) is similar to that of banks and shelves through the Pacific basin formed during past low stands of sea level; (2) the bank top lies within the deep layer of the euphotic zone; (3) the edges of the bank (near depths of 100m) coincide with the top of the nutricline depth around the Hawaiian Archipelago; and (4) sediment accumulation on top of the bank is probably minimal because of the open morphology of the bank. Therefore, Penguin Bank, and mid-depth bank ecosystems in general, provide a physical, chemical, and biological setting for carbonate production by benthic and pelagic calcareous organisms that is distinct from both adjacent shallow water reef ecosystems and the open ocean euphotic zone.

PENGUIN BANK ECOSYSTEM

Physical Dynamics

The physical morphology of mid-depth banks may be an important factor influencing both the extent of allochthonous nutrient input to the deep euphotic zone and the transfer of bank-derived materials to the adjacent open ocean. In contrast to open ocean environments, topographic interaction between Penguin Bank and the surface tidal regime may provide additional mechanisms other than eddy diffusion for nutrient input to the deep euphotic zone environment (Figure 1). Wyrtki et al. (1969) showed that the current regime on Penguin Bank is strongly influenced by the surface tides (Figure 4). During low tides, water flows from the southeast to the northwest, counter to the direction of the tradewinds. The flow reverses for a short period of time on a rising tide, until high tide. As the tide

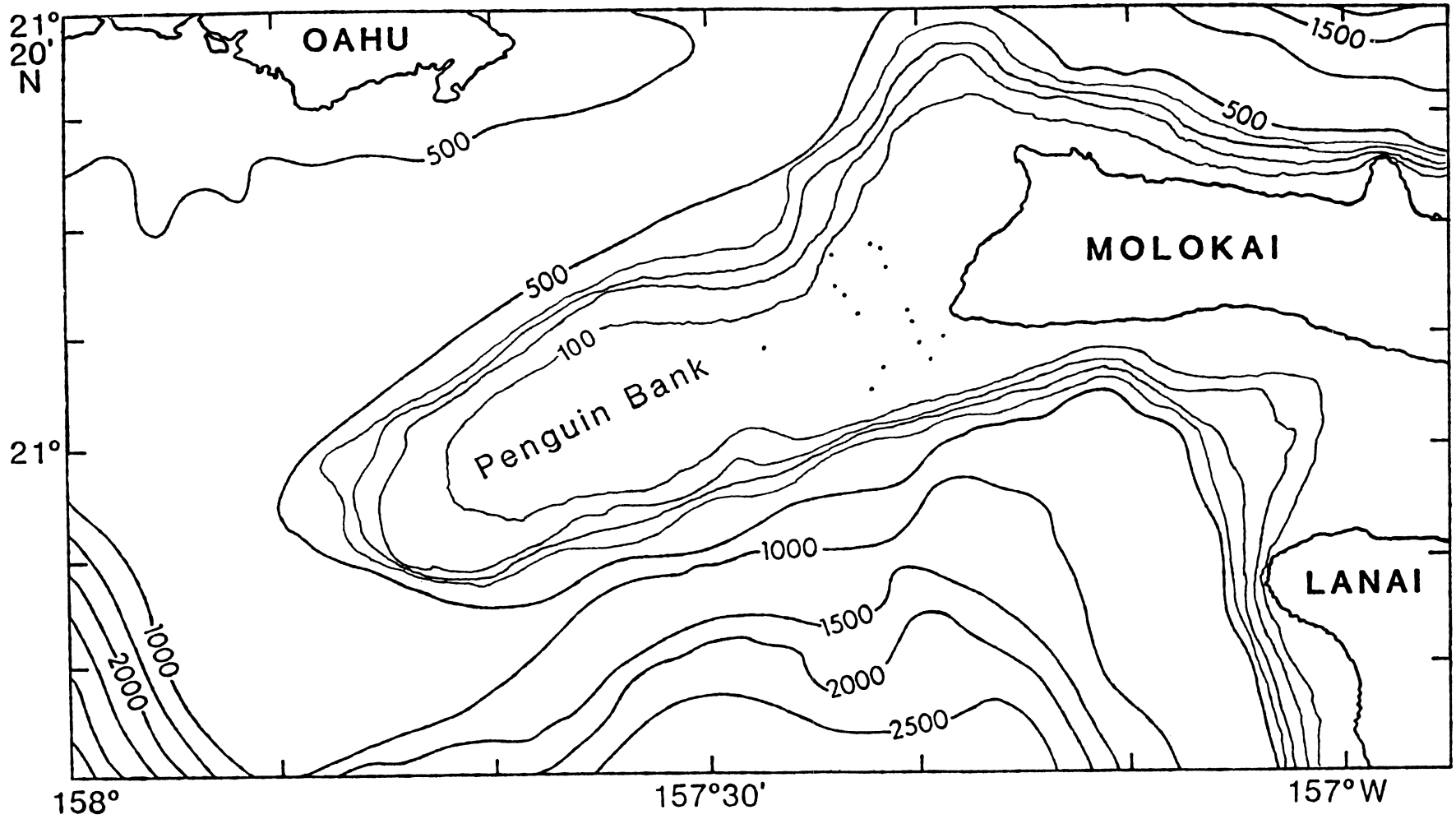

Figure 2. Bathymetric map of Penguin Bank. Bathymetric contours are in meters.

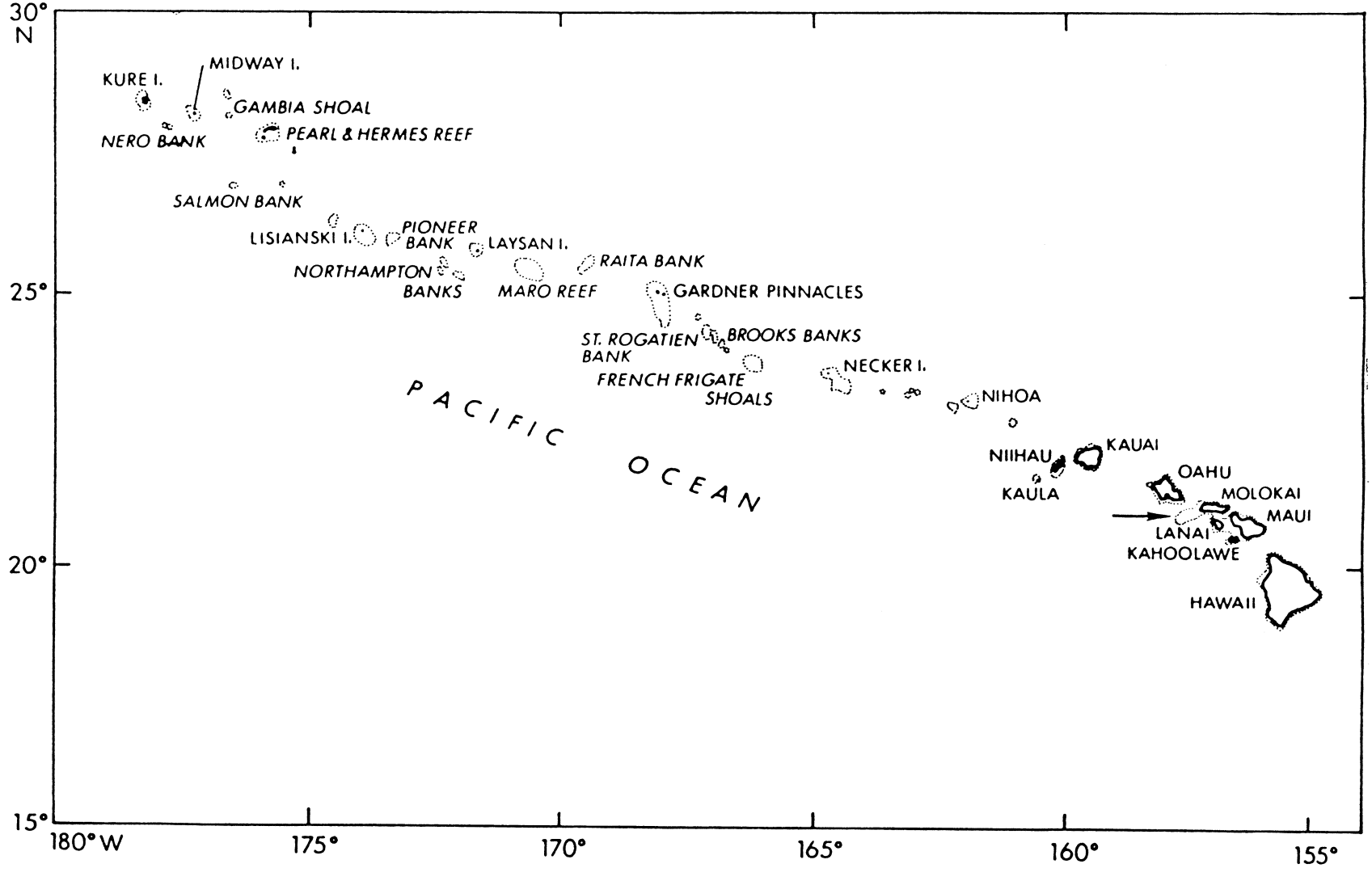

Figure 3. Map of the Hawaiian Archipelago showing the distribution of mid-depth banks (indicated by dashed contour lines at 100 m).

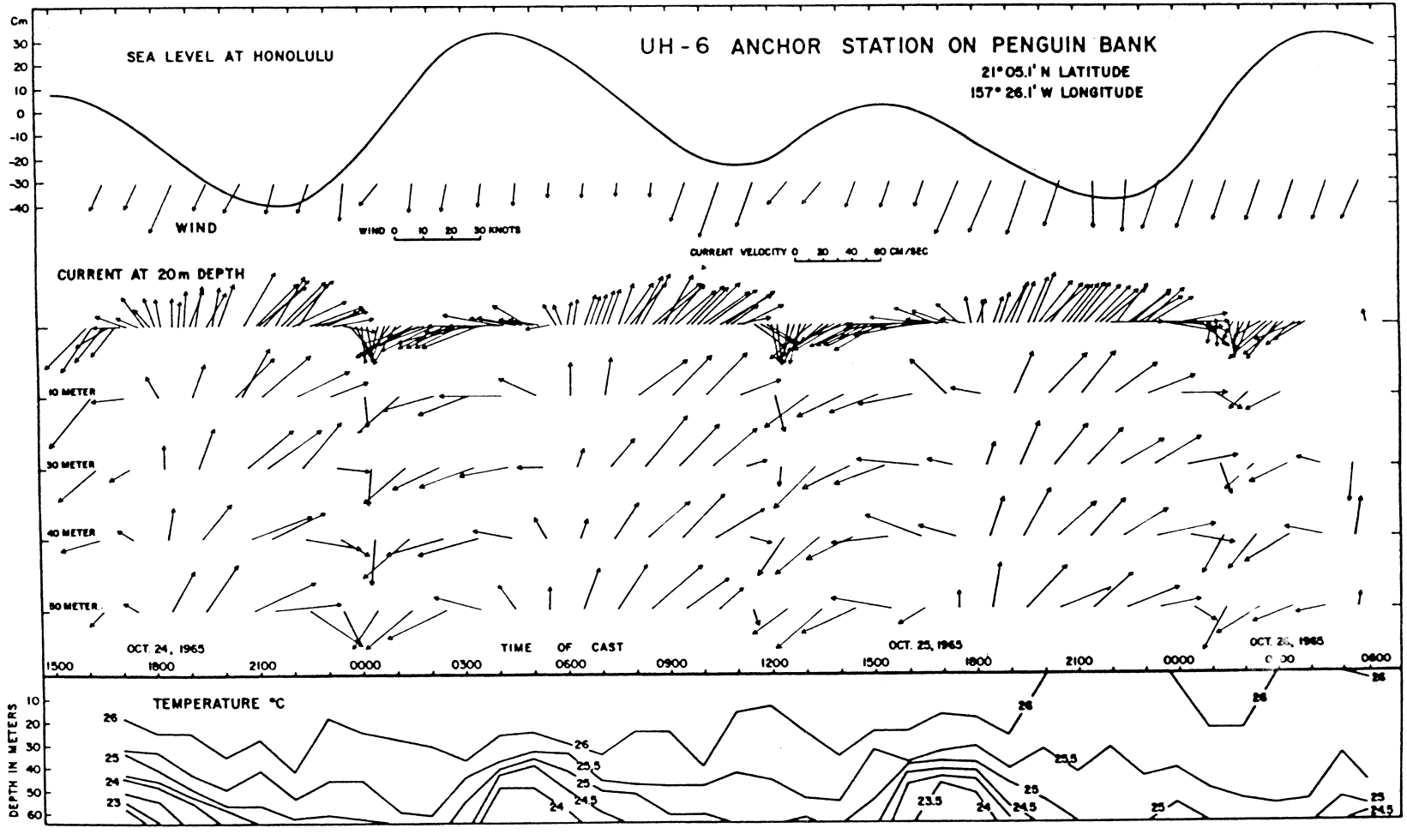

Figure 4. Results of current meter studies at one site on Penguin Bank. Tide, wind, and temperature variations are shown over a three day period. The temperature observations show that after each high water, colder water flushes over the top of Penguin Bank. Figure adapted from Wyrtki et al. (1969).

falls, a cold water mass from deeper depths along the side of the bank impinges on top of the bank (Figure 4). Preliminary evidence obtained during a recent cruise indicates that a "nutrient pump" driven by internal tidal energy may provide a significant input of dissolved inorganic nutrients (Figure 5) to the deep layer of the euphotic zone of Penguin Bank. This influx of nutrients from depth may be fueling new production on the bank, although the relative contribution of this process to total production cannot be quantified from these data. The enhancement of nutrient input to banks and shelves at similar depths resulting from tidally-induced phenomena has been described in other environments (Sandstrom and Elliott, 1984; Pingree and Mardell, 1981). However, the importance of this phenomena to benthic and pelagic carbonate production in oligotrophic environments has not been evaluated nor has the magnitude and specific areas of Penguin Bank where this phenomenon might occur been documented.

Strong tidal currents may also enhance the flux of particulate as well as dissolved matter over the bank. Penguin Bank is a relatively flat, submerged platform with depths ranging from 50 to 100m. At greater depths the bank slopes steeply to the sea floor. In contrast to shoal-water environments where carbonate sediments are effectively retained within the reef structure (Smith et al., 1971), the bank morphology is open and sediments do not appear to accumulate significantly on top of the bank (Moberly et al., 1975).

Biological Communities

It is not surprising to find that mid-depth bank communities have a biological species composition and community structure different from that found in shallow water reef areas (Agegian and Abbot, 1985; Agegian and Mackenzie, 1989). Penguin Bank and other banks throughout the tropical and subtropical Pacific are important sides of bottomfish and benthic invertebrate fisheries (Munroe and Williams, 1985). Although the distribution of individual species of bottomfish with depth is well documented (Ralston and Polovina, 1979), very little is known about the nature of the interaction of the fishery and the bank. The extent to which the fisheries utilize the bank environment for food, shelter or other functions is unknown.

Benthic community surveys and collections of the dominant calcareous benthic organisms on Penguin Bank were made with the submersible Makali'i (Agegian and Abbott, 1985). Color video recording and still photography taken continuously throughout all dives provide a permanent record of the bottom cover of the benthic community. The principal components of the calcareous benthic community on Penguin Bank consist of an unattached assemblage of coralline red algae, calcareous green algae (primarily Halimeda), bryozoans, pen shells, and benthic

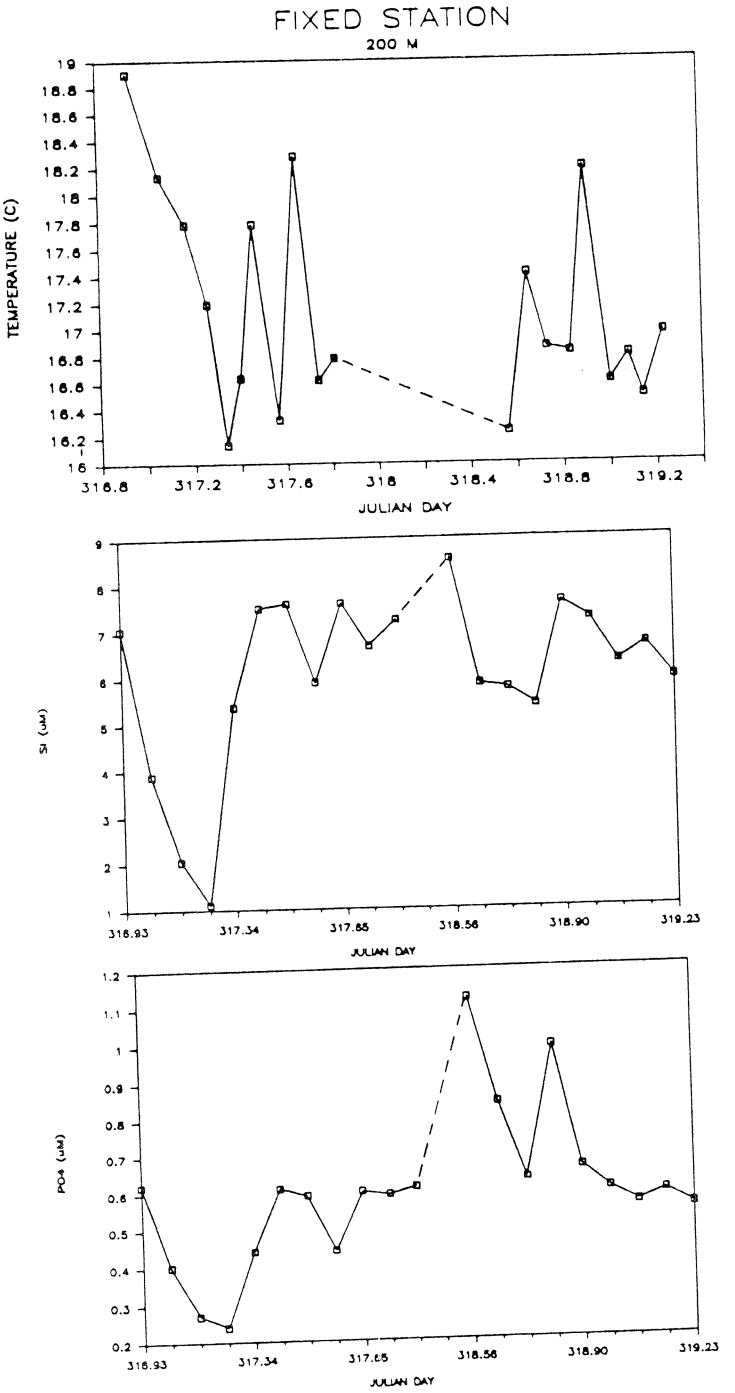

Figure 5. Variations in temperature and the concentrations of dissolved inorganic phosphate and silica with time at a fixed site along the southern edge of Penguin Bank at 200 m depth. Large variations in the physico-chemical properties of seawater at depth are possibly related to internal tidal energy impinging on the slopes of the bank resulting in vertical displacements of the water column. Dashed line --- period of no observations.

foraminifera. A similar community composition was described from dredge hauls made at comparable depths from Kure Atoll (Dana, 1970), and throughout the Northwestern Hawaiian Islands (Adey et al., 1982). The high abundance of bryozoans, typically rare on tropical and subtropical reefs, and the low abundance of hermatypic corals, are features distinguishing the mid-depth bank calcareous community from adjacent shoal-water environments. The mid-depth bank assemblage of calcareous organisms resembles the composition of shoal-water carbonate facies from more northern latitudes (Figure 6), where mean surface seawater temperature is colder.

The magnesium content of calcitic deep-water benthic organisms is, in general, lower than that of their shallow reef counterparts. The mineralogical composition of the benthic organisms is either magnesian calcite, aragonite, or a mixture of the two phases (Table 1). The average magnesium content of the magnesian calcite component of all organisms is 12.1 mole % $MgCO_3$.

Pacific mid-depth banks, in general, lie within the deep euphotic zone at the top of the nutricline, hence, deep water, benthic, calcareous organisms are influenced by physico-chemical properties of seawater that are distinctly different from those of shoal-water reefs and lagoons. Mid-depth banks are characterized by lower seawater temperature and carbonate saturation state (Figure 7), in comparison to immediate shoal-water environments. Consequently, the magnesium content of calcitic benthic organisms, which is largely influenced by temperature and the calcite saturation state of seawater (Agegian, 1985; Mackenzie and Agegian, 1988) is, in general, lower in the skeletons of deep water organisms than in their shoal-water counterparts.

Sediment Mineralogy

A comparison of the mineralogy of the organisms and sediments found on Penguin Bank suggests that the sediments are formed <u>in situ</u> rather than sedimented as the skeletons of benthic and planktonic organisms living in the shallow euphotic zone (Agegian and Mackenzie, 1989). The magnesium content of the magnesian calcite in these sediments ranges between 11-18 mole % $MgCO_3$ (Figure 8); the majority of samples (93%) have magnesium contents within the range of composition of the benthic organisms (12-16 mole % $MgCO_3$) on the bank.

Magnesium calcite biogenic particles are the dominant component of the sediments at depths between 50-110m (Figure 9) comprising on the average 50-80% of each size fraction. The average percentage of aragonite is low and constant over most of the size fractions but increases in the two largest fractions. The composition of the sediments is dominated by high magnesian

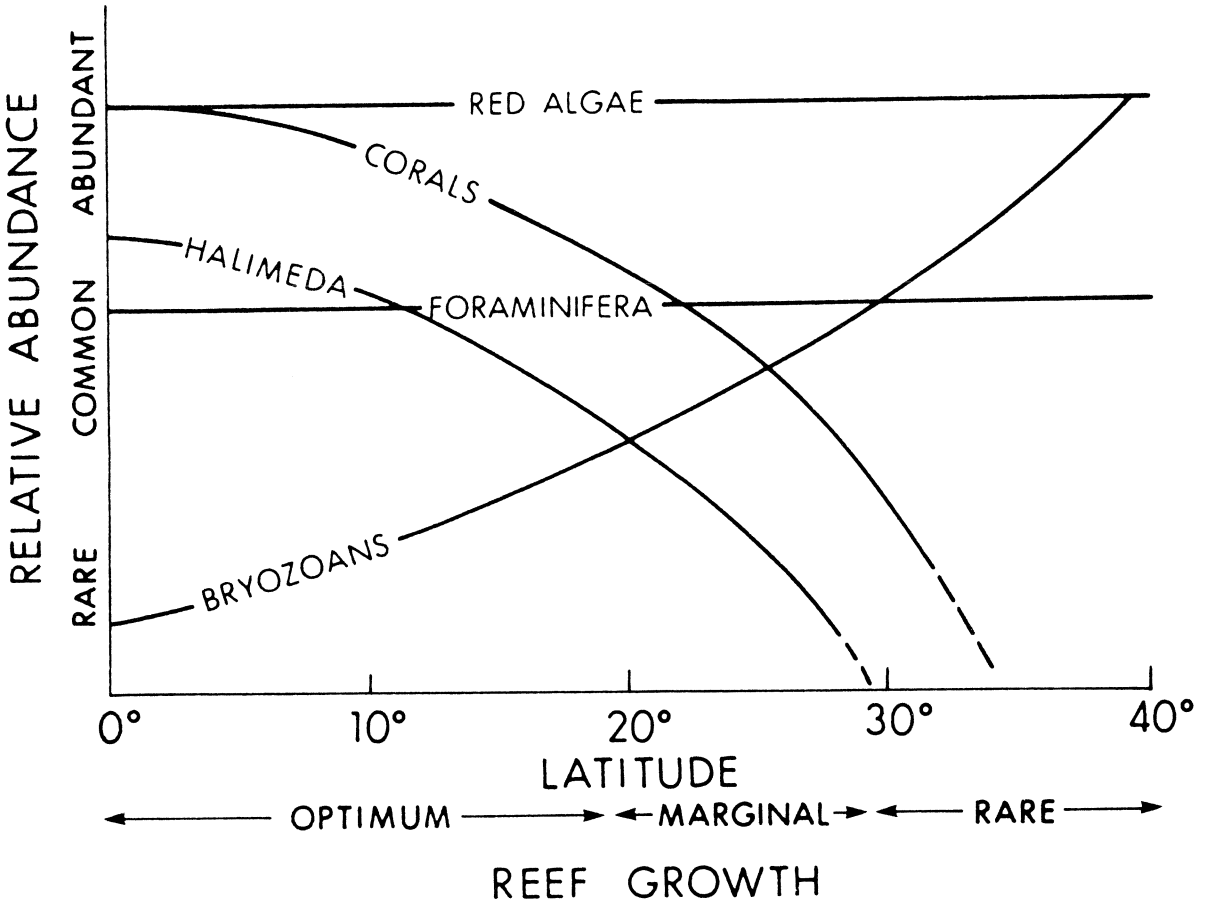

Figure 6. Relative abundance of calcareous organisms in carbonate facies with altitude (from Schlanger and Konishi, 1975).

Table 1. Mineralogy and magnesium content of dominant organisms on Penguin Bank determined by x-ray diffraction (HMC-Magnesian calcite; ARG-aragonite)

Organism	%HMC	%ARG	Magnesium Content (mole $\%MgCO_3$)
Coralline Algae			
Lithothamnium	100.0	--	16.3
Mesophyllum	100.0	--	14.6
Foraminifera	100.0	--	14.3
Brissid Urchins	88.2	11.8	12.3
Bryozoan #1	83.2	16.8	6.8
Bryozoan #2	100.0	--	9.9
Bryozoan #3	100.0	--	10.2
Mean (S.D.,n)			12.1 (3.3, 7)
Halimeda	--	100.0	--
Peysonellia	--	100.0	--

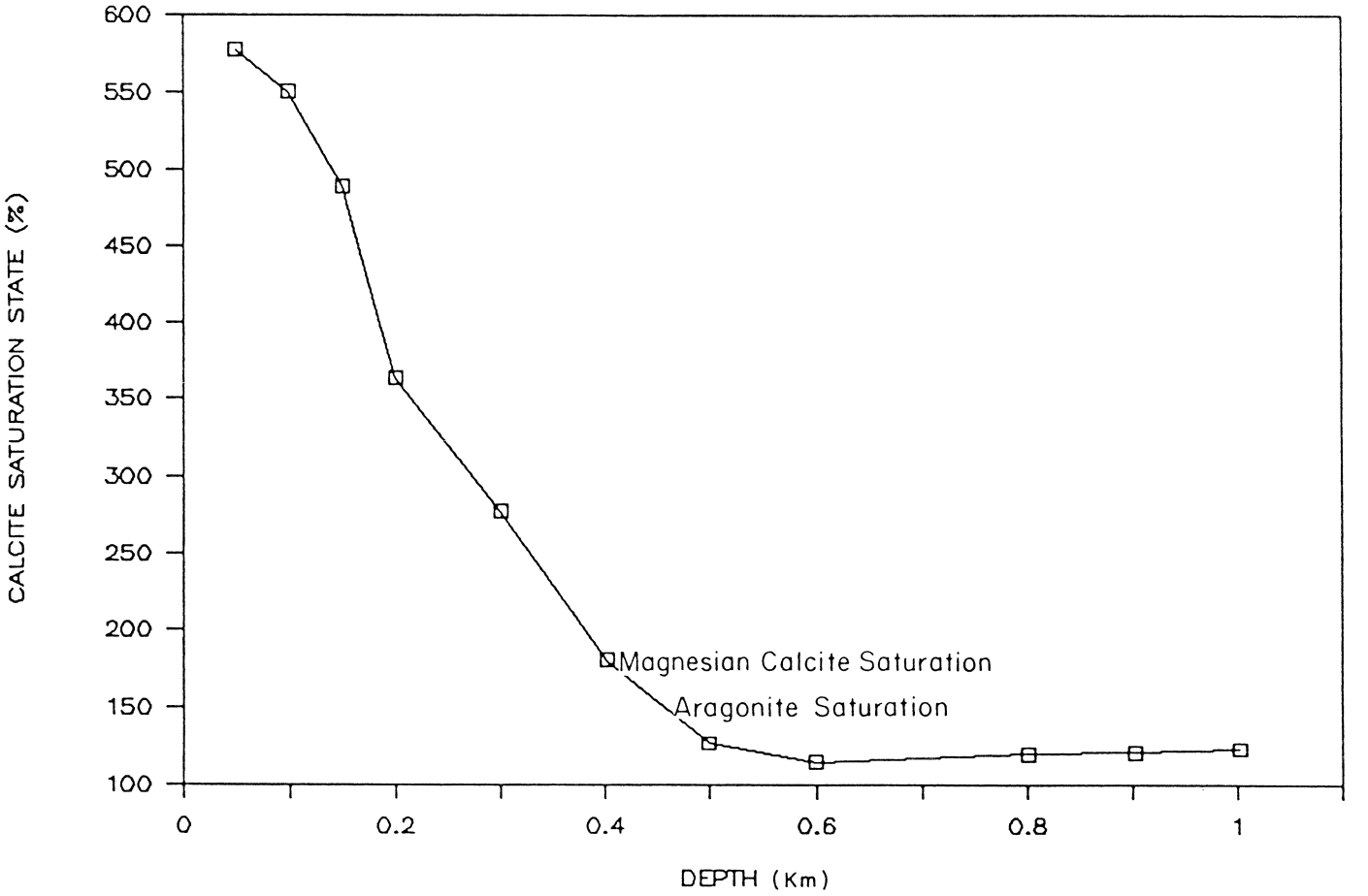

Figure. 7. Calcite saturation state of seawater at one site south of Penguin Bank determined from comparison of ion concentration product (ICP) with apparent equalibrium constant (K'_c). Carbonate species distribution calculated from alkalilnity and pressure- and temperature-corrected pH of water samples. The depth of seawater saturation with respect to argonite and magnesian calcite (12 mole % $McCo_3$, Bischoff et al., 1987) is also shown.

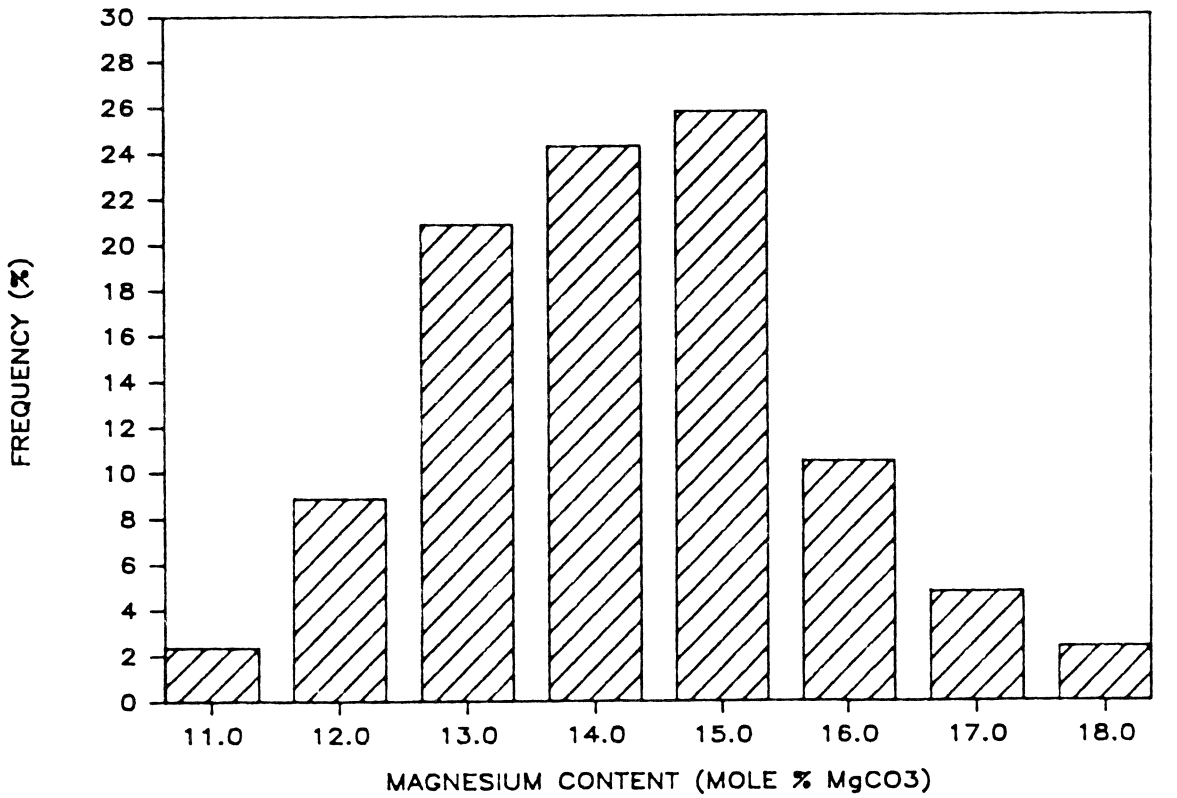

Figure 8. Histogram showing the frequency of sediment samples as a function of the magnesium content of the calcite component of sediments on Penguin Bank, Hawaii.

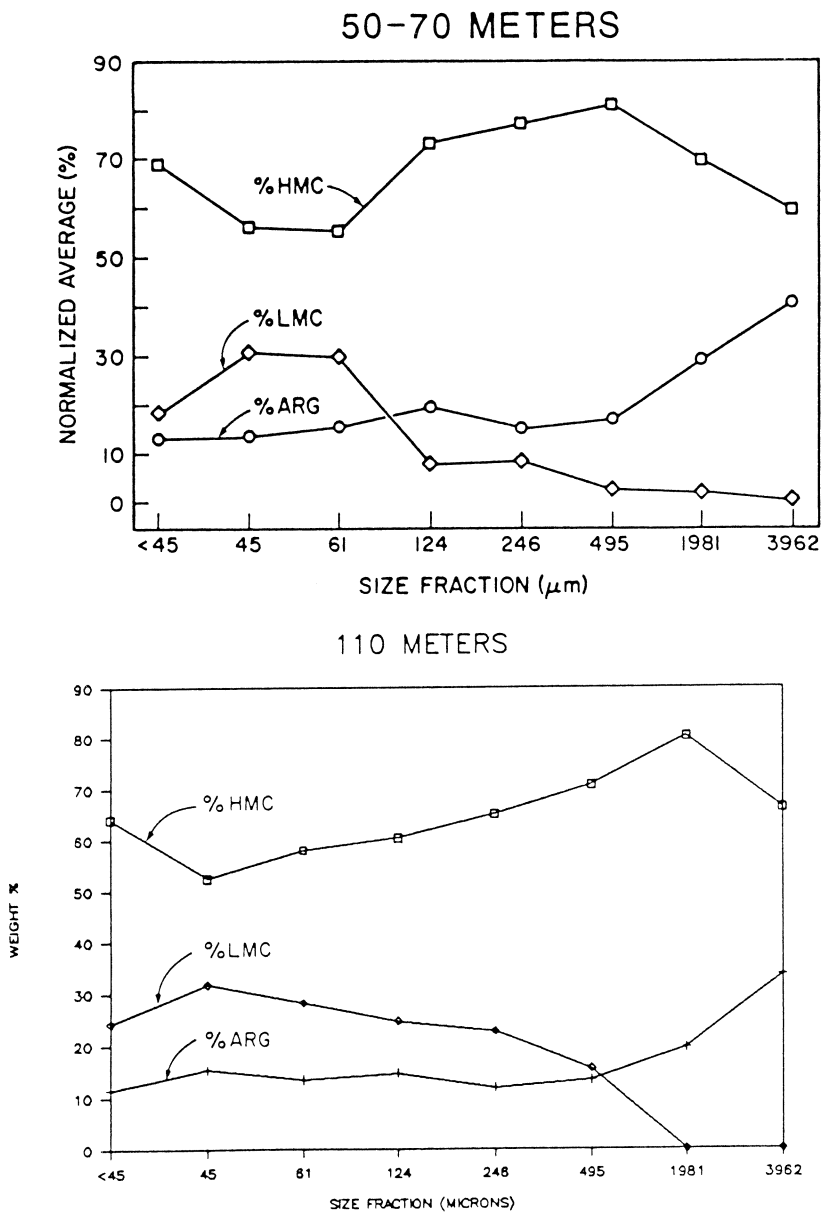

Figure 9. (A) Average normalized percentage of high magnesian calcite, low magnesian calcite (few mole % $MgCO_3$), and aragonite by size fraction of sediment samples taken on Penguin Bank between 50-70 m; (B) weight percent of high magnesian calcite, low magnesian calcite, and aragonite by size fraction of a sediment sample taken at a depth of 110 m on the north slope of Penguin Bank.

calcite (>7 mole % $MgCO_3$) and aragonite in the large size fractions, and by high magnesian calcite and low magnesian calcite (<1-2 mole % $MgCO_3$) in the small size fractions. This low magnesian calcite probably represents principally the input of pelagically derived sediments to the top and slopes of the bank.

Benthic Carbonate Production

The importance of benthic carbonate production on Penguin Bank was estimated using three in situ methods (Table 2). Settling blocks were deployed at a depth of 70m for periods up to one year to obtain estimates of carbonate production from the settlement of coralline algal crusts. Calcareous crusts were scraped off the surfaces of the blocks, cleaned of organic matter with hydrogen peroxide, then dried and weighed. Carbonate production was determined from the weight, divided by the total surface area of the block and length of time the block had remained in the field. Carbonate production estimated by this method was low, 190 g $m^{-2}y^{-1}$ (Table 2), compared to shallow water coralline algal counterparts.

Short-term (four hour) in situ incubations were conducted on Penguin Bank by placing a portion of the benthic community inside a plexiglas box and measuring the changes in alkalinity inside the sealed incubation chamber. Carbonate production was calculated from changes in the total alkalinity of the seawater enclosed inside the chamber and stoichiometric relationships. Community carbonate production using this method was higher, 380 g $m^{-2}y^{-1}$ (Table 2), as might be expected because the incubation included a larger percentage of the total benthic calcareous community.

An ecosystem level estimate of carbonate production on Penguin Bank was made by taking alkalinity samples at a depth of 10 meters above the top of the bank (approximately 60m depth) alongside a current drogue as it drifted over the bank for a period of approximately 26 hours. Carbonate production was calculated from the change in total alkalinity during the daytime segment of the drift, the current speed, and drift transect length, and from the approximation that the water mass affected by the alkalinity change was 10m thick. Carbonate production estimated by this method, which includes both pelagic and benthic components of the calcareous communities, is comparable to estimates obtained using similar methods in shallow water reef environments (Table 2). Further verification of the significance of carbonate production on the bank is indicated by the overall depression of the total alkalinity of seawater in contact with the bank at 50m relative to offshore measurements at the same depth. Similar observations have been made by Cloud (1962) and Droxler et al. (1988) in areas of high carbonate production.

Table 2. Comparison of *in situ* rates of carbonate production by shallow and deep water coralline algae and a deep water benthic calcareous community.

	($g\ CaCO_3 m^{-2} y^{-1}$) SD;N)
[Shallow water coralline algae] (0-10m) (from Agegian, 1985)	
branched	200×10^2 (1,200;120)
crusts	21×10^2 (400;20)
[Deep water coralline algae] (70 m)	
crusts	1.9×10^2 (30;20)
[Shallow water reef environments] (from Gladfelter and Kinsey, 1985)	$3 \times 10^2 - 180 \times 10^2$
[Deep water calcareous community] (70 m)	
coralline algae, *Halimeda*, bryozoans	3.8×10^2
[Mid-depth bank ecosystem] (60 m)	
planktonic and benthic calcareous community integrated over 10 m	43×10^2

These preliminary assessments of carbonate production on Penguin Bank suggest that, given the widespread distribution and abundance of this benthic community and extensive surface area of the banks throughout the Hawaiian Archipelago, mid-depth banks may be potentially significant sources of reactive carbonate particles composed of magnesian calcite and aragonite mineralogy to the open ocean.

Flux of Carbonate Particles

The flux of carbonate particles to depths of 450m was quantified using a bottom-moored MULTITRAP sediment trap array (described in Knauer et al., 1979) with twelve traps deployed at each of seven depths along a single string. The trap array was moored on the north side of Penguin Bank at a bottom depth of 550m for ten days. Granulometric and SEM analysis of the inorganic material revealed that the shells of gastropod larva (protoconchs) and bivalves of benthic origin (Figure 10) were abundant in the larger size fraction along with planktonic foraminifera and pteropods. The inorganic flux (predominantly calcium carbonate with very minor amounts of amorphous silica and aluminosilicates) was highest at 50m and 450m (Figure 11) with a minimum at 200m. The largest inorganic flux at all depths occurred in the fine fraction (<45um) (Figure 12). Fine-grained magnesian calcite particles were found in trap samples at all depths analyzed. In the <45um size fraction, high magnesian calcites contributed 50-70% of the total carbonate mass (Figure 13). These particles may be potential sources of alkalinity via dissolution at depths shallower than those for pelagic aragonite and calcite dissolution.

POTENTIAL IMPORTANCE OF THE FLUX OF MID-DEPTH BANK PARTICLES

From these preliminary investigations and observations on Penguin Bank, we conclude that banks of this type can be important sites of carbonate production, and act as sources of carbonate particles for the open ocean and deep sea. To gain some idea of the magnitude of the potential global flux of carbonate particles of benthic origin to intermediate depth waters, including benthic production from mid-depth banks, we offer the following calculations and preliminary conclusions.

The percent area covered by calcareous benthic communities on Penguin Bank, about 25%, applied to the total mid-depth bank area in the Hawaiian Archipelago (1.6×10^{10} m^2) with an in situ community carbonate production of 400 gram $CaCO_3$ m^{-2} y^{-1} would result in an annual production of 1.6×10^{12} grams $CaCO_3$, an amount equivalent to estimated shallow water production in the Hawaiian Archipelago (Agegian, 1985). Estimated total benthic carbonate production between 0-100m in the Hawaiian Archipelago (1.8×10^{10} m^2) is approximately 3.9×10^{12} grams $CaCO_3$ y^{-1}. As a crude comparison, the average global carbonate production for

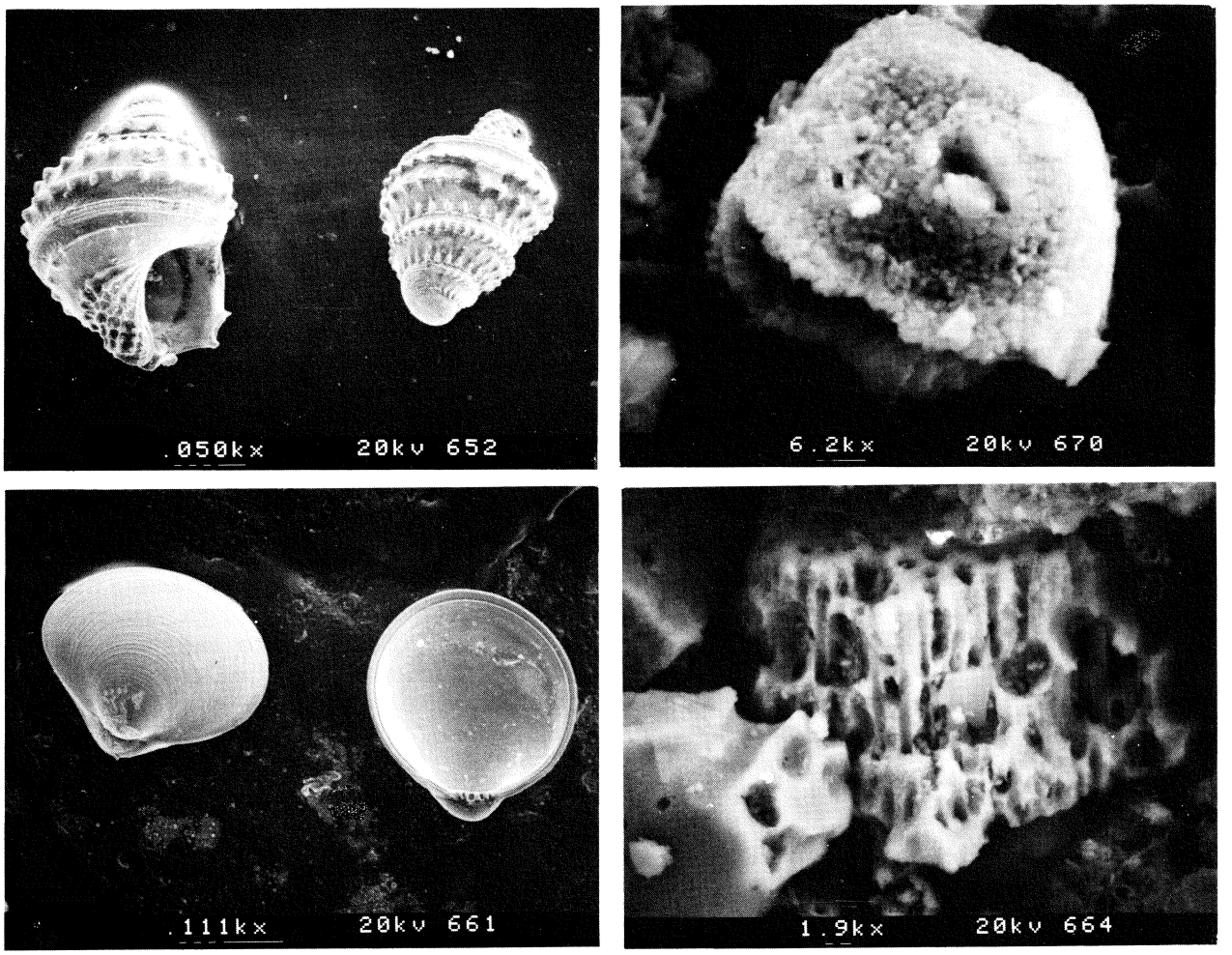

Figure 10. SEM photomicrograph showing particles of benthic origin collected in sediment traps on the north side of Penguin Bank. Protoconch (upper left, Muricacea) and bivalves (lower left, Nuculidae, Fellinidae) are larval shells of benthic organisms. Benthic-derived carbonate particles (upper and lower right) are composed of magnesian calcite.

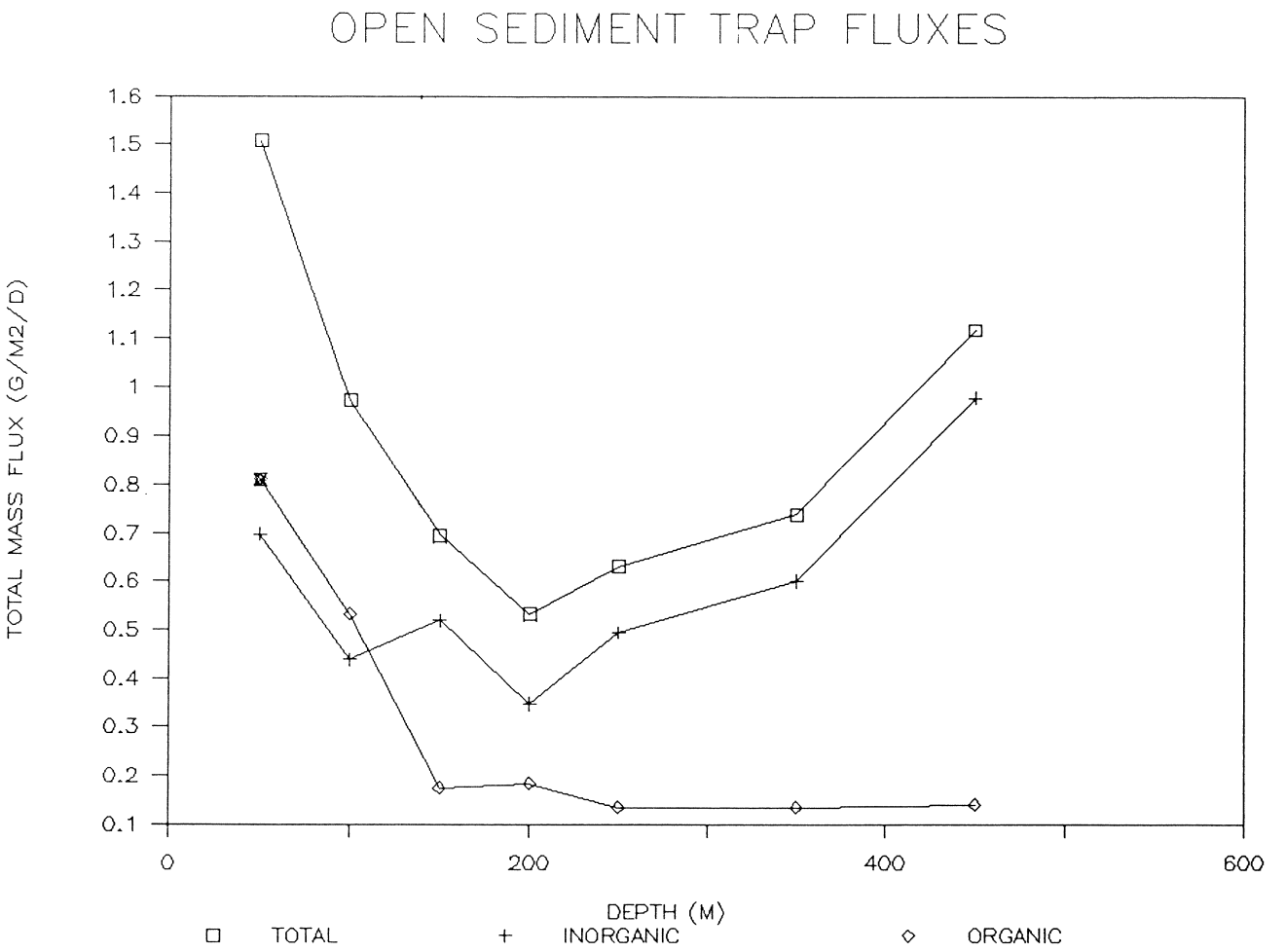

Figure 11. Total, inorganic (principally calcium carbonate), and organic material mass fluxes as a function of depth determined from samples collected from a 10 day sediment trap deployment on the north side (bottom depth 550 m) of Penguin Bank.

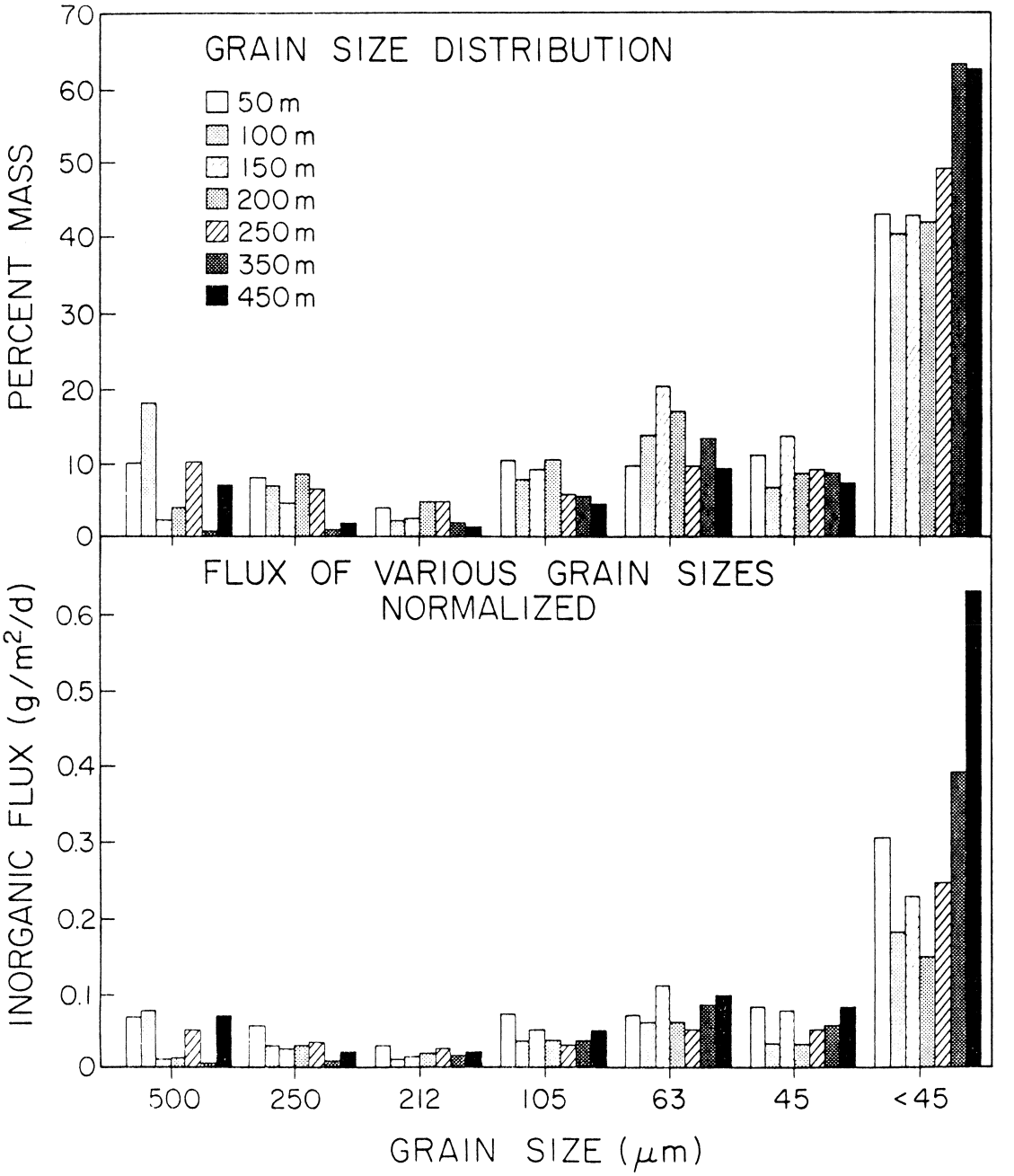

Figure 12. Histograms showing (A) percent of total inorganic mass at each depth by size fraction; (B) inorganic flux at each depth by size fraction. Fine-grained particles (<45 um) represent the greatest percentage of inorganic mass flux at all depths.

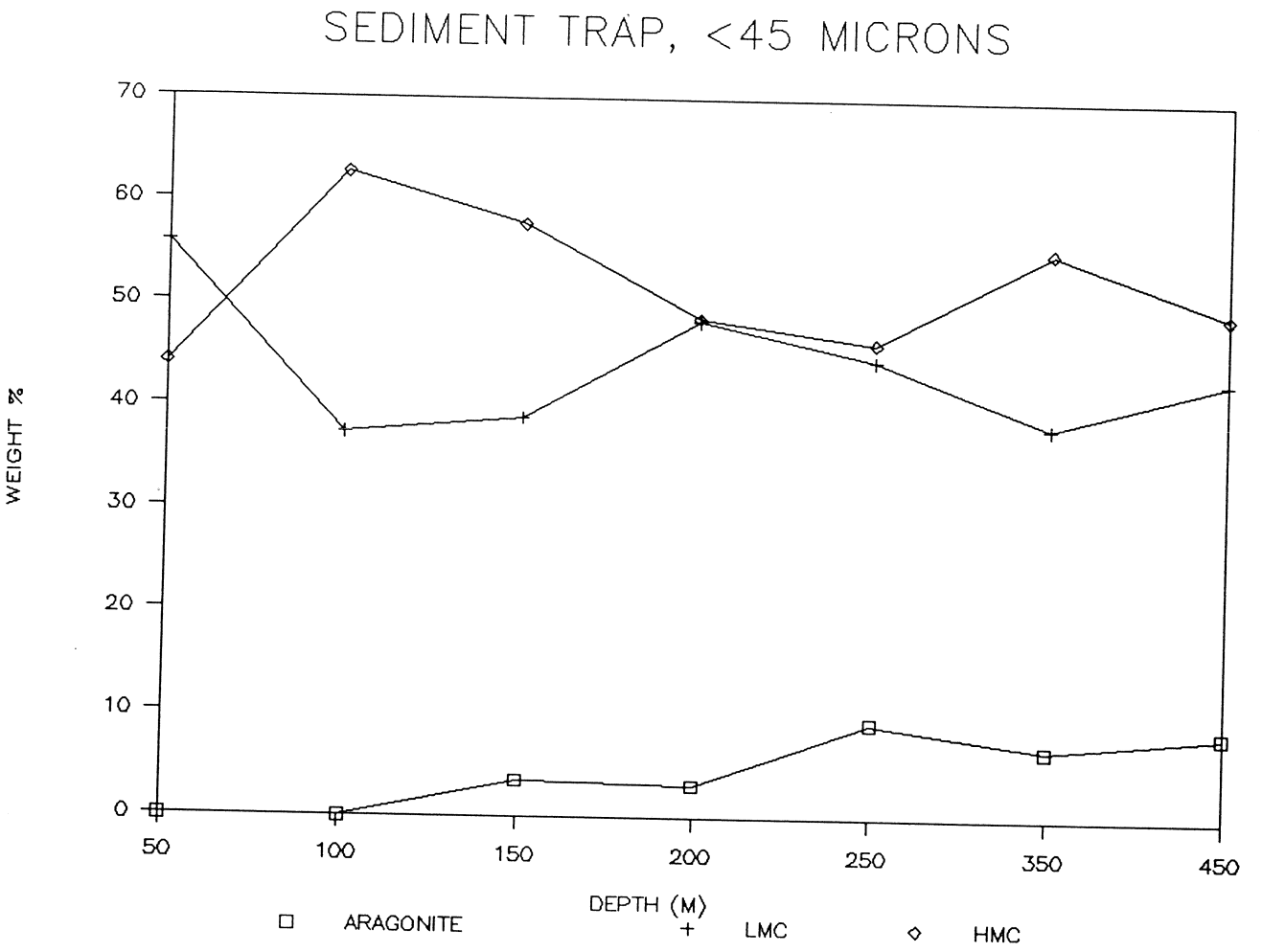

Figure 13. Depth distribution of the weight percent of high magnesian calcite, aragonite, and low magnesian calcite in the fine-grained size fraction (<45 um) of seven sediment trap samples.

the pelagic ocean, 27 grams $CaCO_3$ m^{-2} y^{-1} (Broecker, 1974), applied to the total deep and shallow water Hawaiian Archipelago area would result in an annual open ocean carbonate production of 4.9×10^{11} grams $CaCO_3$ y^{-1}.

This benthic production estimate leads us to conclude that magnesian calcite and aragonite production by benthic organisms from shoal-water reefs and mid-depth banks throughout the Pacific may be of importance to the regional carbonate budget of the open ocean waters forming a portion of the Central North Pacific Gyre. In the Pacific, saturation or slight undersaturation with respect to calcite occur at depths much shallower than saturation depths in the Atlantic. Undersaturation with respect to the more soluble phases, aragonite and magnesian calcite, is found at even shallower depths (Figure 7). Indeed, structural disorder, high trace element content, and complex microarchitecture of the skeletal particles produced on banks enhance their reactivity and potential for dissolution at relatively shallow depths (Bischoff et al., 1987; Mackenzie et al., 1983; Walter, 1983).

Dissolution of benthically produced carbonates may account for a percentage of the alkalinity maximum (Fiadeiro, 1980; Betzer et al., 1984) observed at intermediate depths in western North Pacific waters. The distribution of the alkalinity excess at intermediate depths in the Pacific (Figure 14) was determined from GEOSECS data (Broecker et al., 1979) as the difference in total alkalinity (normalized to a salinity of 35 ppt) at two potential temperatures, at the alkalinity maximum at a depth of approximately 2.5 km and at a depth of approximately 4 km. The contours shown in Figure 14 in part reflect hydrographic conditions (Craig, et al., 1972), and indicate the presence of (1) a significant pelagic input of carbonate material, (2) a significant benthic input of carbonate materials from reefs and mid-depth banks in the tropical and subtropical western Pacific or (3) both pelagic and benthic input of carbonate material, the magnitude of which has yet to be documented. This alkalinity maximum cannot be accounted for on a mass basis simply by settling and dissolution of pelagic calcite (Betzer et al., 1984). Approximately 0.35 grams $CaCO_3$ m^{-2} d^{-1} from another source must be dissolved at intermediate depths to account for the excess alkalinity.

The potential importance of benthic derived carbonate particles to this phenomenon can be assessed by a calculation comparing the magnitude of benthic carbonate production to the carbonate flux in the Pacific Ocean needed to account for excess alkalinity. The value of benthic carbonate production between 0-100m determined in this study of 2.2×10^2 g m^{-2} y^{-1} applied to the tropical-subtropical reef area of the Pacific Ocean between 0-100m (approximately 2.7×10^{12} m^2; Smith, 1978; 1972) yields a total production of magnesian calcite and aragonite of 5.9×10^{14} g y^{-1} in tropical and subtropical waters. The average temperate

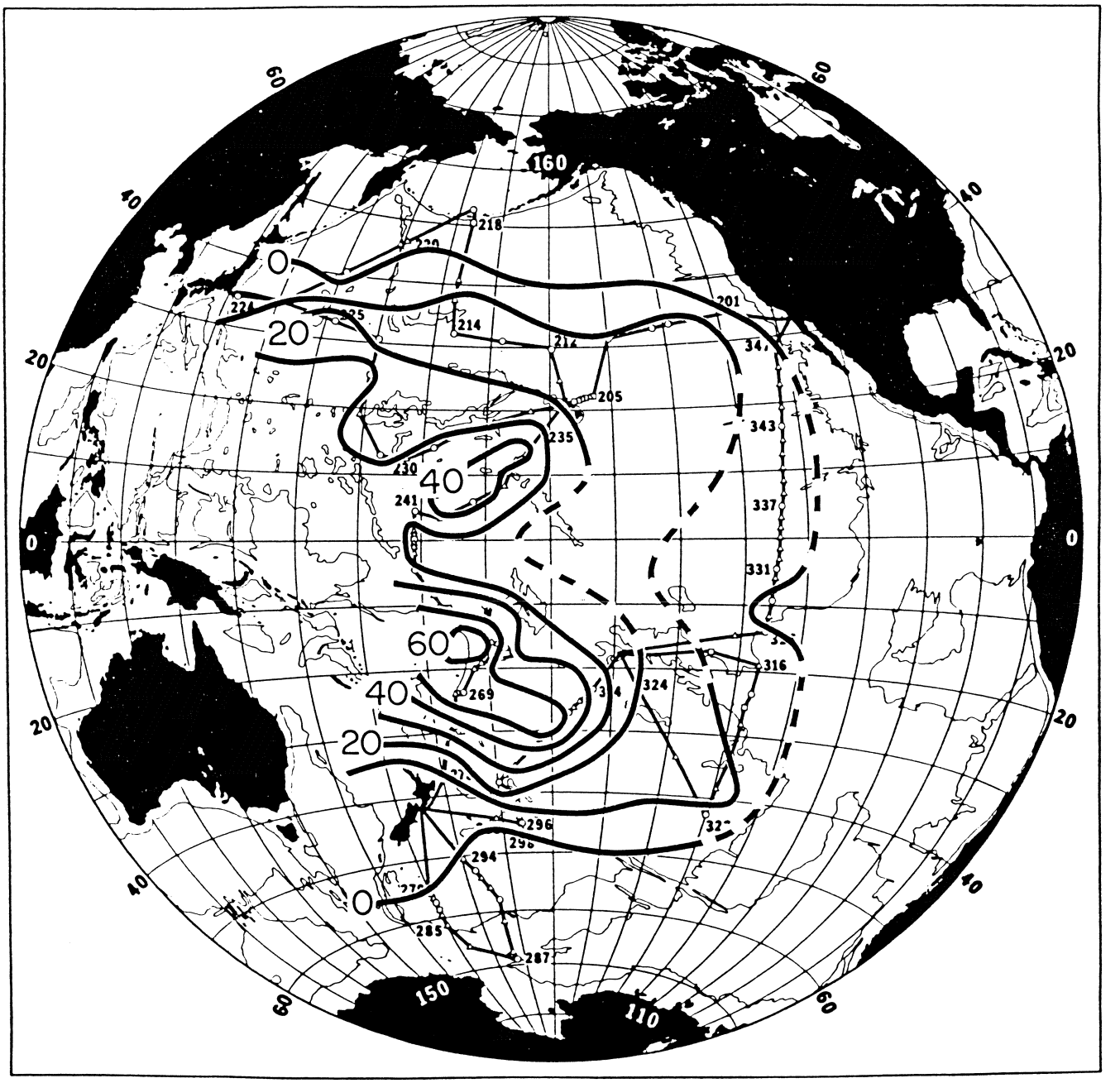

Figure 14. Isopleths of excess total alkalinity (ueq/kg and normalized to a salinity of 35 ppt) at intermediate depths (=2,500 m) in the Pacific. Excess alkalinity determined as the difference between the alkalinity at a potential temperature of 1.5°C and the alkalinity at a potential temperature of 0.8°C. All data are from Takahashi et al., 1980.

shallow water carbonate production of 4.0 x 10^2 g m^{-2} y^{-1} (Smith, 1972) applied to the temperate shallow water area between 0-30m (8.0 x 10^{11} m^{-2}; Smith, 1978; Menard and Smith, 1966) results in an annual temperate production of 3.2 x 10^{14} g y^{-1}. Therefore, the estimated total benthic carbonate production in the Pacific Ocean is 9.1 x 10^{14} g y^{-1}, and if dispersed throughout the entire Pacific Ocean area (180 x 10^{12} m^2) could result in a potential carbonate flux of 0.014 g m^{-2} d^{-1}.

Obviously, only a portion of the total amount of benthic carbonate production may be transported and encounter waters where it dissolves. Smith (1972) attributed the lack of carbonate sediment accumulation on the temperate mainland shelf of southern California to sediment dispersal and subsequent dissolution. Land (1979) calculated that approximately 79% of modern reef productivity measured on the North Jamaican Island slope dissolved in adjacent deep water. We do not know what percentage of benthic-derived carbonate particles dissolves during transport or after redeposition and exposure at the sediment-water interface. If a value of 50% were applicable to the Pacific environment then about 25% of the observed alkalinity excess of 0.035 grams m-2 d-1 could be attributed to dissolution of aragonite and magnesian calcite of benthic origin. Whatever the case, the production, transport and magnitude of the subsequent dissolution of benthic carbonate production needs to be considered in the alkalinity balance of open ocean water.

CONCLUSIONS

Based on preliminary observations and calculations, we hypothesize that production and flux of carbonate material from mid-depth banks to the open ocean may be significant, and as yet unaccounted for, components in the global biogeochemical cycles of carbon and calcium. Future research efforts should focus on biogeochemical cycling processes occurring within coastal ocean boundaries as well as the open ocean.

Mid-depth banks may be sites of enhanced new production which serve to support important commercial fisheries in tropical and subtropical ocean environments. The potential yield of a fishery fueled by new production will be different than one driven principally by recycled production. An understanding of the biogeochemical dynamics of these ecosystems will provide the framework from which to properly manage and possibly enhance these fisheries. We recommend that future fisheries investigations take an ecosystem approach in addition to studies which emphasize organisms in the upper levels of the food web.

ACKNOWLEDGMENTS

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REFERENCES

Adey, W.H., Townsend, R.A., and Boykins, W.T. 1982. The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. Smithsonian Contrib. to Marine Sci. #15. 75 pp.

Agegian, C.R. 1985. Biogeochemical ecology of Porolithon gardineri (Foslie). Ph.D. dissertation, University of Hawaii, 178 pp.

Agegian, C.R. and Abbott, I.A. 1985. Deep water macroalgal communities: a comparison between Penguin Bank, Hawaii and Johnston Island. Proc. 5th Int. Coral Reef Congress. Tahiti, 5:46-50.

Agegian, C.R. and Mackenzie, F.T. 1989. Calcareous organisms and sediment mineralogy on the mid-depth bank in the Hawaiian Archipelago. Accepted Pac. Sci.

Betzer, P.R., Byrne, R.H., Acker, J.G., Lewis, C.S., Jolley, R.R., and Feeley, R.A. 1984. The Oceanic Carbonate System: A Reassessment of Biogenic Controls. Science 226: 1074-1077.

Bischoff, W.D., Mackenzie, F.T., and Bishop, F.C. 1987. Stabilities of synthetic magnesian calcites in aqueous solution: Comparison with biogenic materials. Geochim. Cosmochim. Acta. 51:1413-1423.

Broecker, W.S. 1974. Chemical Oceanography. Harcourt Brace Jovanovich, Inc., N.Y. 214 pp.

Broecker, W.S., Takahashi, T., Simpson, H.J., and Peng, T.-H. 1979. Fate of fossil fuel carbon dioxide and the global carbon budget. Science 206:409-418.

Cloud, P.E. 1962. Environment of calcium carbonate deposition west of Andros Island, Bahamas. U.S. Geol. Survey Prof. Paper 350, 138 pp.

Craig, H., Chung, Y., and Fiadeiro, M. 1972. A Benthic Front in the South Pacific. Earth Planet. Sci. Lett. 16:50-65.

Dana, T.F. 1970. On reef corals of the worlds most northern atoll (Kure: Hawaiian Archipelago). Pac. Sci. 25:80-87.

Droxler, A.W., Morse, J.W., and Kornicker, W.A. 1988. Controls on carbonate mineral accumulation in Bahamian basins and adjacent Atlantic Ocean sediments. Jour. Sed. Petr. 58:120-130.

Eppley, R.W. and Peterson, B.J. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282:677-680.

Fiadiero, M. 1980. The alkalinity of the deep Pacific. Earth and Planet. Sci. Letters. 49:499-505.

Gladfelter, E.H. and Kinsey, D.W. 1985. Metabolism, calcification, and carbon production. II. Organism Level Studies. Proceedings of the Fifth International Coral Reef Congress. 4:527-539.

Kinsey, D.W. 1985. Metabolism, calcification, and carbon production. I. Systems Level Studies. Proceedings of the Fifth International Coral Reef Congress. 4:505-526.

Knauer, G.A., Martin, J.H., and Bruland, K.W. 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the Northeast Pacific. Deep Sea Res. 26A:97-108.

Land, L.S. 1979. The fate of reef-derived sediment on the North Jamaican island slope. Mar. Geol. 29:55-71.

Lewis, J.D. 1985. Metabolism, calcification and carbon production. III. Seminar Discussion. Proceedings of the Fifth International Coral Reef Congress. 4:540-542.

Littler, M.M., Littler, D., Blair, S., and Norris, J.N. 1985. Deepest known plant life discovered on an uncharted seamount. Science 227:57-59.

Mackenzie, F.T. and Agegian, C.R. 1988. Biomineralization and tentative links to plate tectonics. In: Proc. 5th Internatl. Conf. Biomineral., Plenum Press (in press).

Mackenzie, F.T., Bishcoff, W.D., Bishop, F.C., Liojens, M., Schoonmaker, J., and Wollast, R. 1983. Magnesian calcites: Low temperature occurrence, solubility, and solid solution behavior. In: Carbonates: Mineralogy and Chemistry, ed. R.J. Reeder, Mineral. Soc. America, Reve. Mineral. 11:97-144.

Menard, H.W. and Smith, S.M. 1966. Hypsometry of ocean basin provinces. J. Geophys. Res. 71:4305-4325.

Moberly, R., Campbell, J.F., and Coulbourn, W.T. 1975. Offshore and other sand resources for Oahu, Hawaii. UHIHI-SEAGRANT-TR-75-03. 36pp.

Munroe, J.L. and Williams, D.Mcb., 1985. Assessment and management of coral reef fisheries: Biological, environmental, and socio-economic aspects. Fifth Int. Coral Reef Congress. Tahiti, 4:5454-581.

Pingree, R.D., and Mardell, G.T. 1981. Slope turbulence, internal waves and phytoplankton growth at the Celtin Sea shelf break. Phil. Trans. R. Soc. Long., A302: 663-682.

Ralston, S. and Polovina, J. 1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. Bull. 80-435-448.

Sandstrom, H. and J.A. Elliott. 1984. Internal tide and solitons on the Scotian shelf: A nutrient pump at work. J. Geophys. Res. 89:6415-6426.

Schlanger, S. and Konishi, K. 1975. The geographic boundary between coral-algal and the bryozoan-algal limestone facies: a paleolatitude indicator. IX Int. Cong. Sed., Nice.

Small, L.F., Knauer, G.A., and Tuel, M.D., 1987. The role of sinking fecal pellets in stratified euphotic zones. Deep-Sea Res. 34:1705-1712.

Smith, S.V. 1972. Production of Calcium carbonate on the mainland shelf of Southern California. Limnol. Oceanogr. 17:28-41.

Smith, S.V. 1978. Coral reef area and contributions of reefs to processes and resources of the world's oceans. Nature 273:225-226.

Smith, S.V., Roy, K.J., Schiesser, H.G., Sheperd, G.L., and Chave, K.E. 1971. Flux of suspended calcium carbonate ($CaCO_3$), Fanning Island Lagoon. Pacific Sci. 25:206-220.

Takashi, T., Broecker, W.S., Bainbridge, A.E., and R. F. Weiss. 1980. Carbonate chemistry of the Atlantic, Pacific, and Indian Oceans: the results of the Geosecs expeditions. 1972-1978. Lamont-Doherty Geological Observatory, Technical Report No. 1, CV-1-80, Palisades, N.Y., 211 pp.

Walter, L.M. 1983. The dissolution kinetics of shallow-water carbonate grain types: Effects of mineralogy, microstructure, and solution chemistry. Ph.D. Thesis, University of Miami, Miami, Fl. 318 pp.

Wiebe, W.J., Hohannes, R.E., and Webb, K.L. 1975. Nitrogen fixation in a coral reef community. Science 188:257-259.

Wilkinson, C., and Sammarco, P. 1983. Effects of fish grazing and damselfish territoriality on coral reef algae. II. Nitrogen fixation. Mar. Ecol. Prog. Ser. 3:15-19.

Wyrtki, K., Burks, J.B., Latham, R.C., and Patzert, W. 1969. Oceanographic observations during 1965-1967 in the Hawaiian Archipelago. Hawaii Inst. of Geophysics., Univ. of Hawaii. HIG-67-15.

IMPORTANCE OF THE EUPHOTIC ZONE IN THE GLOBAL LAND AND OCEAN CARBON AND PHOSPHORUS CYCLES AND FLUXES

Fred T. Mackenzie
Department of Oceanography and Hawaii Institute of Geophysics
University of Hawaii
Honolulu, HI 96822

Abraham Lerman
Department of Geological Sciences
Northwestern University
Evanston, IL 60201

INTRODUCTION

Within the past few years a number of research initiatives have been proposed to study global systems. Three immediately come to mind: the International Geosphere-Biosphere Program, the Global Ocean Fluxes Program, and the Global Sedimentary Geology Program. Although the specific goals of these programs differ somewhat, the intention is to investigate the global Earth system and its response to perturbations.

One approach to an understanding of global scale processes and perturbations is the modeling exercise. Of particular interest to us during the past two decades has been the construction of global biogeochemical cycling models. In this paper two such models of the carbon and phosphorus cycles are presented, and two scenarios for perturbations of these cycles developed. Emphasis is placed on the interactions between the land and oceanic euphotic zone. It will be shown that changes in continental weathering rates and terrestrial productivity can influence on a time scale of decades the chemistry of the euphotic zone. Also, the importance of the coastal marine environment to considerations of global ocean fluxes is demonstrated based on the results of the modeling exercises.

Biogeochemical Cycling Models

Many natural chemical substances circulate through the environment and are important to the chemistry and biology of the earth. The circulation of a particular substance -- as defined by its reservoirs, processes affecting it, and fluxes, is termed its biogeochemical cycle. Biogeochemical cycles vary in time and spatial scales. The long-term circulation of earth materials, the exogenic cycle, represents one extreme in which materials are transported through the atmosphere to the land, and through the

soils to streams that carry materials to the oceans. In the oceans, stream-borne solids, and some originally dissolved substance now part of solids, sink and become sea-floor sediments, and some substances are returned to the atmosphere. Oceanic residence times of dissolved substances vary from less than the mixing time of the ocean (~1600 years) to 10^8 years. Reservoir sizes in the exogenic system can be huge; that of carbonate in sediments is 600×10^{20} grams.

On the other extreme are the biogeochemical cycles of substances in systems smaller than the global exogenic. In soils, rivers, and estuaries, for example, the circulation of a substance may be described in terms of reservoir sizes of less than tons and turnover times measured in days.

The concepts and principals related to modeling of biogeochemical cycles have been developed extensively (e.g., Garrels and Mackenzie, 1971; Mackenzie and Wollast, 1977; Lerman, Garrels and Mackenzie, 1975; Lerman, 1979; Holland, 1978; Lasaga, 1981; Wollast, 1986). The mathematical treatment used is briefly discussed below with reference to Figure 1.

Figure 1 represents a system of four reservoirs with two-way fluxes between the reservoirs for substance i. For a closed system at steady state, the mass of substance i in each reservoir (M_i), and each flux of i (F_{ij}) between reservoirs are constant, and no material enters or departs the system; therefore,

$$(1) \qquad \underset{J}{EF_{ij}} = \underset{J}{EF_{ji}} \quad (i \neq j)$$

The fluxes are measured in units of mass $time^{-1}$, usually in terms of mols or grams $year^{-1}$, and commonly are taken as proportional to the reservoir mass from which the flux is emanating; that is,

$$(2) \qquad F_{ij} = k^i{}_j M_i,$$

where k_{ij} is a rate constant with dimensions $time^{-1}$ (usually $year^{-1}$). If a flux were second order, its magnitude is a function of both the mass of the source and receiving reservoirs,

$$(3) \qquad F_{ij} = k_{ij} M_i M_j \; O$$

The reciprocal of the rate constant k has been defined as the residence time lambda, and for J fluxes of a substance i for a single reservoir with mass M_i,

$$(4) \qquad lambda_i = 1/ k_{ij} \; O$$

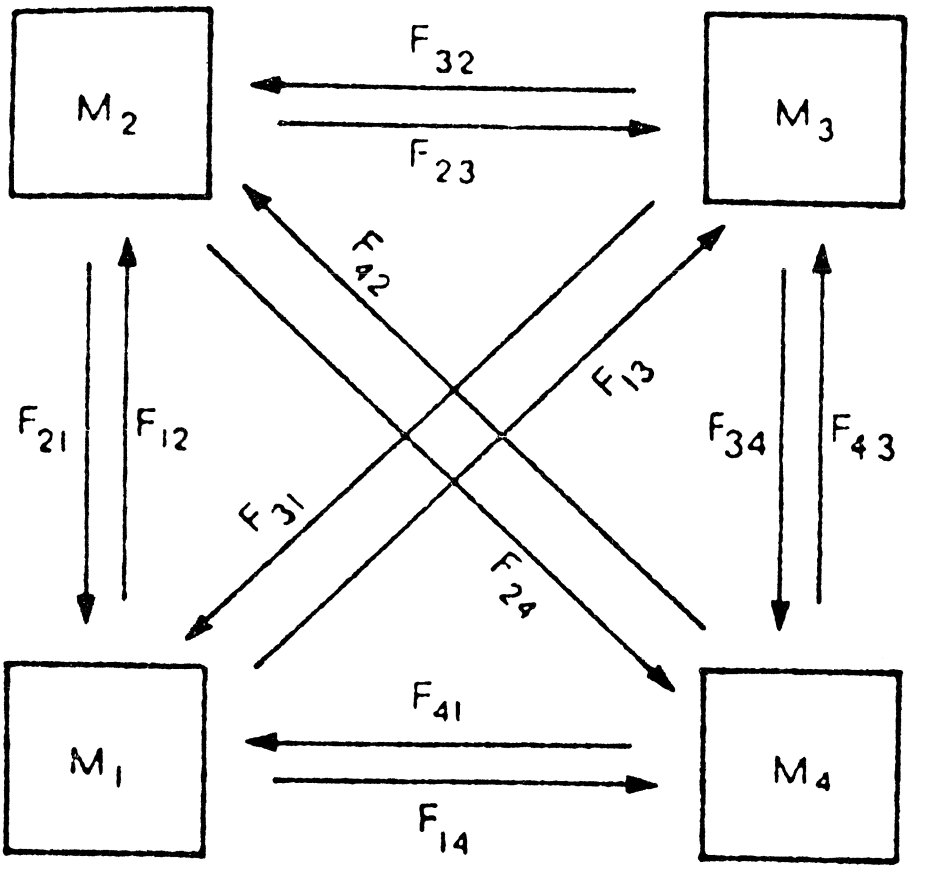

Figure 1. Simplified box model of a closed biogeochemical cycle of a substance. Reservoir content of the ith substance (M_i, in units of mass) and fluxes between reservoirs (F_{ij}, in units of mass time $^{-1}$) are shown.

From substitution of equation (2) into equation (1), we obtain

$$(5)\quad \sum_J Ek_{ij}M_j = M_i \sum_J Ek_{ij}, \qquad (i \neq j)$$

and at steady state

$$(6)\quad \sum_J Ek_{ji}M_j - M_i \sum_J Ek_{ij} = 0$$

For a system in a transient state (one disturbed by a perturbation for example), the fluctuation of the mass of i in a reservoir with time becomes

$$(7)\quad dM_i/dt = \sum_J Ek_{ji}M_j - M_i \sum_J Ek_{ij},$$

where $i \neq j$, $i, j = 1 \ldots n$. This equation represents a series of n differential equations for a system with n number of reservoirs.

For the carbon and phosphorus biogeochemical cycles, the first step in the modeling exercise is to derive steady state cycles for these elements. These are shown in Figures 2 and 3. Details of the methods used to obtain reservoir masses and fluxes are given in Lerman, Mackenzie, and Geiger (1987). Suffice it to say that derivation of such cycles requires synthesis and evaluation of a broad base of data from a variety of disciplines. The cycles shown were derived omitting any man-made effects, like fossil fuel burning. Furthermore, not all authors agree on the magnitude of reservoirs and fluxes shown in these figures. It is important to note, however, that these figures represent coupled land and ocean cycles, with distinct reservoirs for coastal materials. After the steady state cycle has been obtained, rate constants for the fluxes shown are calculated from equations (2) and (3). Details of the calculations are given in Lerman, Mackenzie, and Geiger (1987). We are now in a position to perturb the carbon and phosphorus biogeochemical cycles and evaluate responses to perturbations using equation (7).

Perturbations and their Meaning for the Euphotic Zone

Two general processes in perturbing the global land-ocean C and P biogeochemical cyclings will be considered, those of weathering and bioproductivity. The coastal waters-biota and surface ocean-ocean biota reservoirs (Figs. 3, 4) include the deep and shallow euphotic zones, and thus are important to considerations of the effects of perturbations on the euphotic zone. Residence times of C and P in the reservoirs including the euphotic zone are:

CARBON: LAND AND OCEAN CYCLE

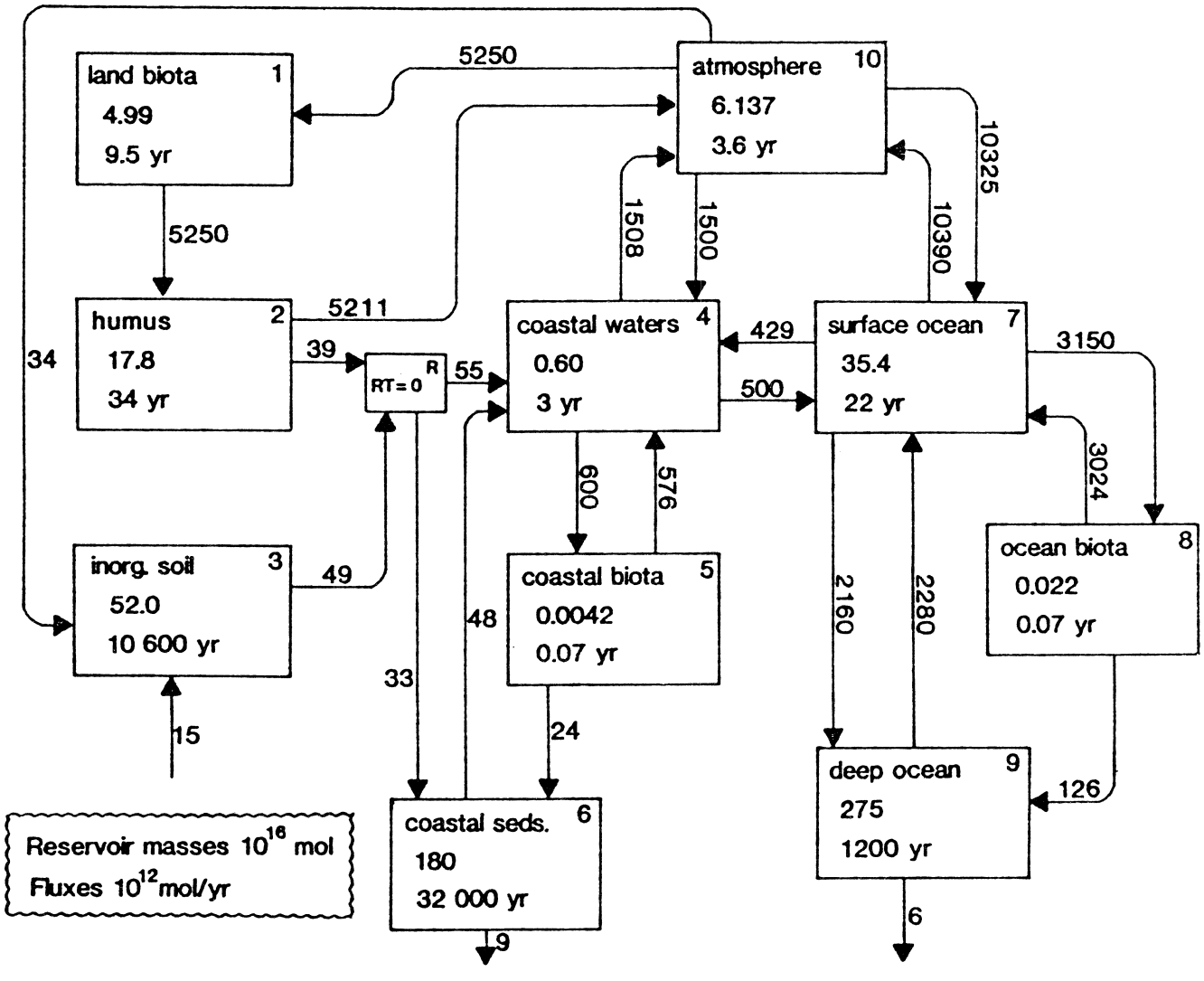

Figure 2. Global coupled land-ocean biogeochemical cycle of carbon. The euphotic zone is represented by the coastal waters-biota and surface ocean-ocean biota reservoirs in this diagram. Reservoir masses are in units of 10^{16} mol C, and fluxes in units of 10^{12} mol C y^{-1}. Residence time in years shown at bottom of boxes.

PHOSPHORUS: LAND AND OCEAN CYCLE

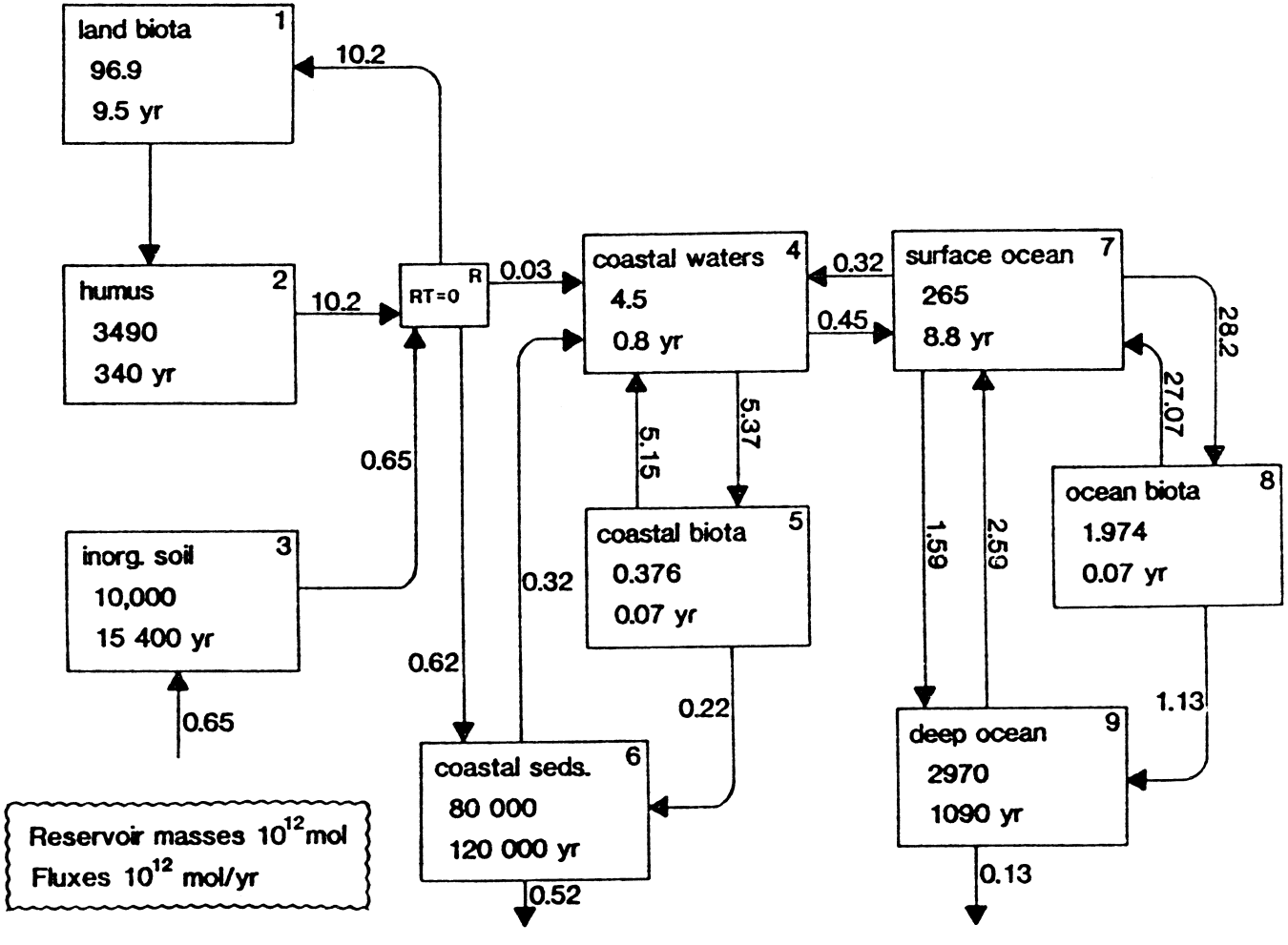

Figure 3. Global coupled land-ocean biogeochemical cycle of phosphorus. The euphotic zone is represented by the coastal waters-biota and surface ocean-ocean biota reservoirs in this diagram. Reservoir masses are in units of 10^{12} mol P, and fluxes in units of 10^{12} mol P y^{-1}. Residence time in years shown at bottom of boxes.

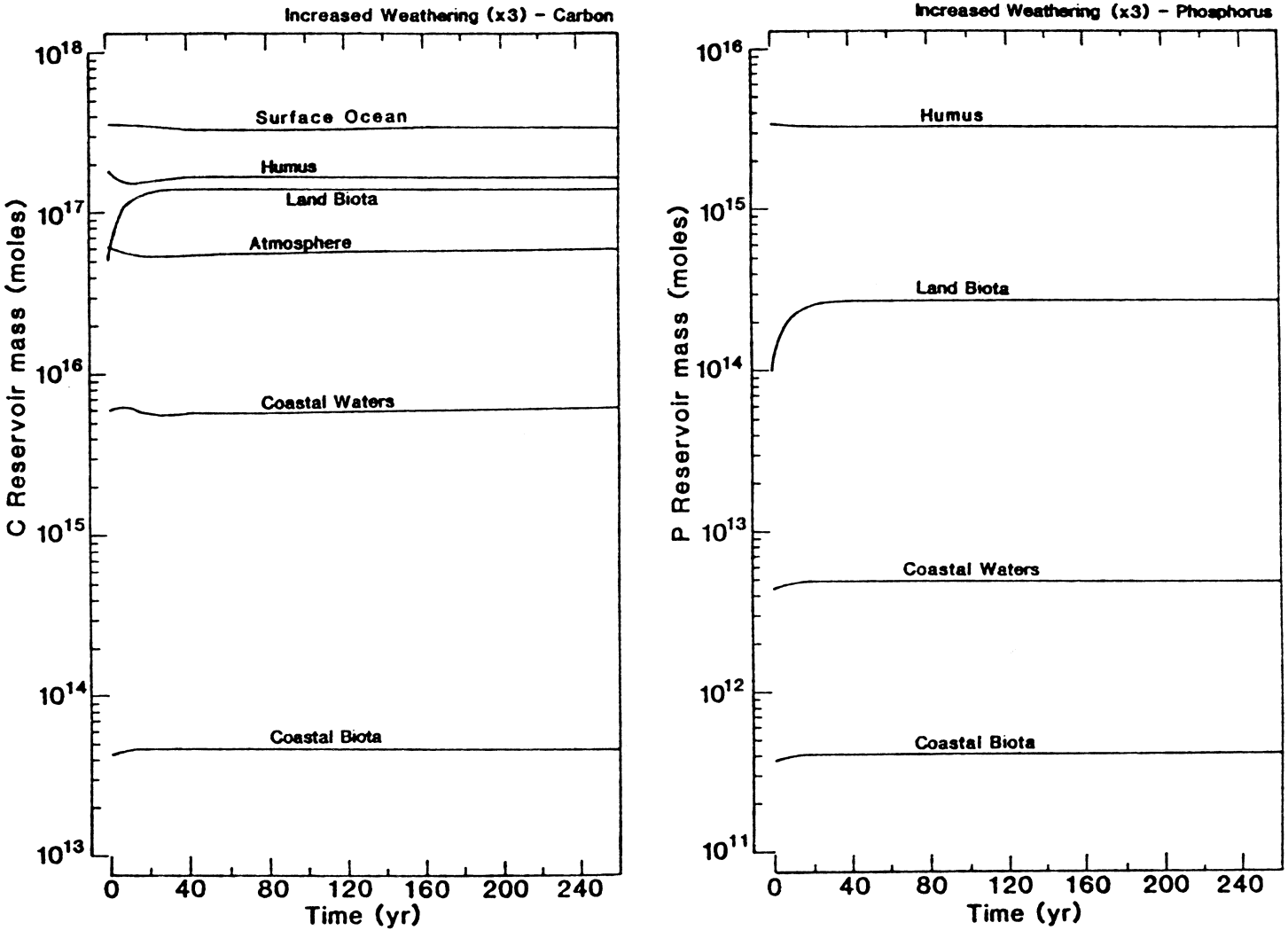

Figure 4. Results of 3x increased continental weathering rate on major affected C and P reservoirs in Figures 2 and 3. Reservoir masses are in units of moles.

	C	P
	(years)	
Coastal Waters	3	0.08
Coastal Biota	0.07	0.07
Surface Ocean	22	8.8
Ocean Biota	0.07	0.07

Note that in both the carbon and phosphorus models there is a net flux of these elements from the coastal to open ocean environment. Also, the coastal and ocean biotic reservoirs representing the masses of these elements in both the shallow and deep euphotic zone should aim at separation of the shallow-water reservoirs of Figures 3 and 4 into deep and shallow euphotic zones, and fluxes between these environments.

Scenario 1, Increased weathering rates

In this scenario, the global continental weathering rate is instantaneously increased three times. This scenario has some application to changes in weathering rates that have been proposed for short and long periods of geologic time. The average weathering rate of the continents during the past 600 million years of Earth history (the Phanerozoic) was about 60 x 10^{14} g y^{-1} (Garrels and Mackenzie,1971), whereas the preindustrial society rate was 100 x 10^{14} g y^{-1} (Judson, 1964), and today's rate is 240 x 10^{14} g y^{-1} (Gregor, 1968; Garrels and Mackenzie, 1971; Holland, 1978). Changes in weathering rates can be a result of human or natural events. Some authors contend that the high weathering rates of today are due to society's activities of deforestation, cultivation, and construction. Others argue that the high rate is a result of weathering and erosion of pre-existing, easily erodible, Pleistocene glacial deposits. Whatever the cause this scenario illustrates the responses of the oceanic cycles of carbon and phosphorus to such a perturbation on a decadal to centuries-long time scale.

The responses of the major reservoirs affected in the carbon and phosphorus cycles are shown in Figure 4. In the case of the instantaneous 3x weathering perturbation the reservoirs shown respond on a time scale of decades. The major effect of increasing continuously over time the weathering rate up to 3x today's rate would be to spread out the response times of the reservoirs shown in Figure 4.

Obviously the phosphorus and carbon cycles are linked through the process of photosynthesis. In these models production in the ocean is assumed to be limited by phosphorus, and the C:P ratio of the oceanic biota is taken as 106:1 (Redfield, 1934).

What major events take place as a result of this weathering perturbation, particularly to the coastal and open-ocean euphotic zones? Because of the increased weathering rate, the flux of P from the inorganic soil and humus reservoirs to streams is increased, whereas the flux of carbon from the humus to the atmosphere is increased. These increased fluxes result in a decline in the C and P humus reservoir masses with time, and a rapid increase in the C and P masses of the land biota. For an instantaneous perturbation, the C and P land biotic reservoirs grow by 200% in about 30 years. For the atmosphere, CO_2 initially decreases because of bioproductivity on land and in the ocean.

The ocean's response is initial increases of carbon and phosphorus in coastal waters and biota. These initial increases are followed by a slow decline of C and P in these reservoirs (on the order of 100 to 200 years) owing to exchange of these elements between the coastal reservoirs of C and P and the surface open ocean, and eventually the deep ocean. The important point here is that the coastal euphotic zone responds rapidly to an instantaneous perturbation, in this case weathering on land, and that relaxation of the perturbation is affected by exchange between the coastal zone and open ocean. This result is probably not unexpected, but it does emphasize the links between the land and ocean cycles of C and P, and the role of the coastal ocean in the biogeochemical cycling and fluxes of these elements.

With flooded shelves like we have today, increased riverine fluxes of P to the ocean affect first the near-shore environment by stimulation of production. If sea level were lower, erosion of organic-rich shelf areas could lead to increased nutrient fluxes to and increased production in the open ocean. The results of a lowered sea level on the C and P cycles would be like those of increased erosion rates, except that an extensive coastal zone would be lacking. Thus, an extension of the model leads to the conclusion that lowered sea levels during Pleistocene glacial stages would result in enhanced sizes of both the land and oceanic C biotic reservoirs, and a drawdown of CO_2 in the atmosphere. As suggested previously (Broecker and Peng, 1982), these are two of the causes suggested for the observed low CO_2 contents of ice cores, and hence the atmosphere, during the last glacial (Berner, Stauffer and Oeschger, 1979).

Scenario 2, High weathering rate, low bioproduction

In this scenario the weathering rate is increased by 1.5 times, and bioproductivity on land is decreased by 0.25. Both changes are instantaneous. This scenario may have some application to present-day global environmental problems. It has been argued that weathering rates may be increasing because of increased deforestation and cultivation practices, and increased rates of delivery of acid S and N components, originally from

fossil fuel burning, to the soil via rain or dry deposition. Increased atmospheric fluxes of S and N to the land, along with ozone, hydrocarbons, and trace metals, plus man's physical disturbance of habitats, have been suggested as global causes for decreased bioproductivity on land (see e.g., The Global 2000 Report to the President, 1980, for discussion of the above). The reservoir changes owing to these perturbations are shown in Figure 5.

Because of decreased terrestrial productivity and increased erosion rates, the C and P humus and land biotic reservoir masses decrease rapidly. Atmospheric CO_2 increases initially because of decreased organic production and organic humus decay by about 60% in 30 years, then declines to a new steady state as the ocean slowly equilibrates with the increased levels of atmospheric CO_2. The coastal reservoirs initially rise in their C and P contents, and then decline slowly with time as these elements are transferred to the open ocean. The result of the P transfer, in particular, is a steady increase in the mass of the open ocean biota with increasing time. Once more we see the rapid response of the euphotic zone, in this case both the coastal and open ocean zones, to an instantaneous perturbation on land. This conclusion, along with the results of scenario 1, emphasizes the link between events on land, and the coastal zone as an interactive reservoir between the land and open ocean. The global oceanic fluxes of C and P are strongly influenced by changes in fluxes of these elements between the land and other reservoirs on a relatively short time scale. The global euphotic zone may respond on a time scale of decades to changes of C and P cycling rates occurring on land. These conclusions are not new, but the modeling exercise aids in quantifying the time scales involved and the magnitudes of the reservoir changes.

CONCLUSIONS

A major purpose of this paper was to present, briefly, new steady-state models of the global carbon and phosphorus biogeochemical cycles. These models are developed without fluxes from the activities of society. In these models, the open ocean receives materials from the land via the atmosphere (in the case of C), and via the coastal zone (in the case of C and P). This division of the ocean into coastal and open ocean reservoirs is a more realistic model of the ocean, particularly when the influence of perturbations on land on the oceanic environment are being investigated.

The euphotic zone of the global ocean reacts on a time scale of decades to perturbations of the land reservoirs for the scenarios of increased continental weathering rate and increased weathering rate plus decreased terrestrial productivity. Consideration of global ocean fluxes of elements must take into account the linkage between the land, the coastal marine

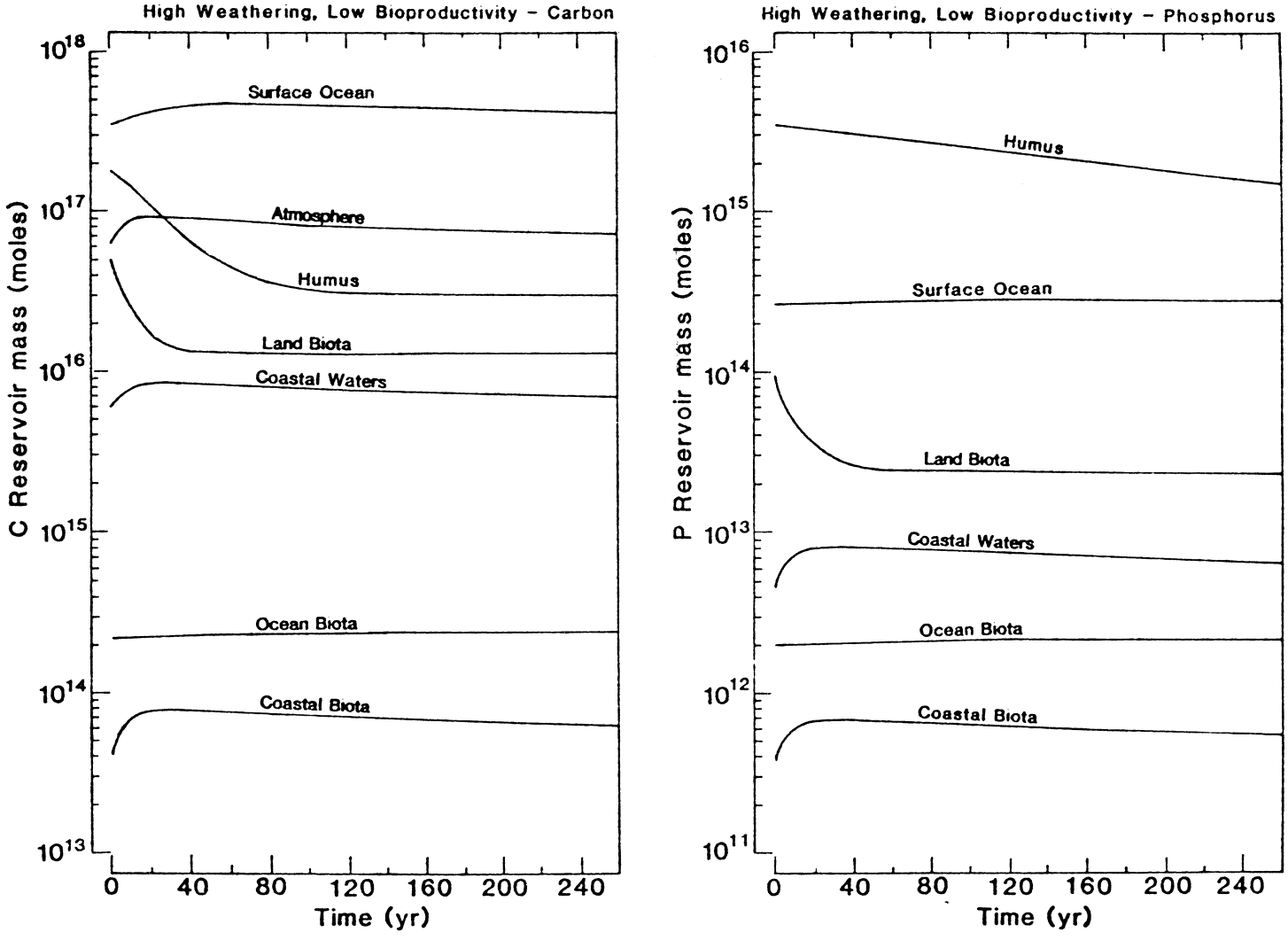

Figure 5. Results of 1.5x increased continental weathering rate and decreased (0.25x present-day) terrestrial production rate on major affected C and P reservoirs. Reservoir masses in units of moles.

environment, and the open ocean. To understand the global ocean system even on a time scale of decades requires knowledge of material transport between the coastal and open ocean.

ACKNOWLEDGMENTS

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REFERENCES

Berner, W., B. Stauffer and H. Oeschger. 1979. Past atmospheric composition and climate, gas parameters measured in ice cores. Nature 275:53-55.

Broecker, W. S. and T. -H. Peng. 1982. Tracers in the sea, Eldigio Press, Palisades, NY, 690 pp.

Garrels, R. M. and F. T. Mackenzie. 1971. Evolution of sedimentary rocks, W. W. Norton, NY, 397 pp.

Garrels, R. M. and F. T. Mackenzie. 1972. A quantitative model for the sedimentary rock cycle. Marine Chemistry 1:27-41.

Gregor, B. 1970. Denudation of continents. Nature 228:273.

Holland, H. D. 1978. The chemistry of the atmosphere and oceans. J. Wiley and Sons, NY, 351 pp.

Judson, S. 1968. Erosion of the land. Am. Sci. 56:356-374.

Lasaga, A. C. 1981. Dynamic treatment of geochemical cycles. In: A. C. Lasaga and R. J. Kirkpatrick (Eds.), Kinetics of geochemical processes. Mineral. Soc. Am., Rev. in Mineral. 8:69-110.

Lerman, A. 1979. Geochemical processes in water and sediment environments. J. Wiley and Sons, NY, 481 pp.

Lerman, A., F. T. Mackenzie and R. M. Garrels. 1975. Modeling of geochemical cycles: Phosophorus as an example. In: E. H. T. Whitten (Ed.), Quantitative studies in the geological sciences. Geol. Soc. Am. Memoir 142:205-218.

Lerman, A., F. T. Mackenzie and R. G. Geiger. 1987. Environmental chemical stress effects in carbon and phosphorus cycles. In: S. A. Levin (Ed.), Ecotoxicology In press.

Mackenzie, F. T. and R. Wollast. 1977. Thermodynamic and kinetic controls of global chemical cycles of the elements. In: W. Stumm (Ed.), Global chemical cycles and their alteration. Dahlem Konferenzem, Berlin, pp. 45-59.

Redfield, A. C. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of the plankton. James Johnstone Memorial Volume, Liverpool, pp. 177-192.

The Global 2000 Report to the President, v.2. 1980. U.S. Government Printing Office, Washington, 766 pp.

Wollast, R. 1986. Basic concepts in geochemical modelling. In: P. Buat-Menard (Ed.), The role of air-sea exchange in geochemical cycling. D. Reidel Pub. Co., NY, pp. 1-34.

THEORETICAL CALCULATION OF THE DEPTH OF THE EUPHOTIC ZONE IN THE SEA

Paul G. Falkowski

Oceanographic Sciences Division
Department of Applied Science
Brookhaven National Laboratory
Upton, New York 11973

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INTRODUCTION

Photosynthesis is, by far, the major source of organic carbon in the sea (Falkowski, 1980). The photosynthetic process, carried out in aquatic ecosystems by phytoplankton and macroalgae, is a coupled oxidation-reduction reaction, where the energy of light is converted to chemical bond energy. With the exception of some obligate anaerobic photosynthetic bacteria, all photosynthetic organisms are oxygenic, that is, light is used to photo-oxidize water, producing oxygen, electrons, and protons. Oxygen, which is the waste product in the photosynthetic reaction, diffuses out of the cell, while the electrons and protons are used to reduce the substrate CO_2 to organic carbon compounds.

By themselves, photosynthetic pathways do not meet all of the metabolic demands of a cell. For example, to make proteins the cell must synthesize nucleic and amino acids. Almost all of the intermediate metabolites needed to synthesize macromolecules arise from oxidizing reduced carbon compounds, such as sugars, in another coupled oxidation-reduction pathway called respiration. The effect of respiration is to produce CO_2 and consume O_2. When the rate of photosynthetic oxygen evolution (or CO_2 consumption) equals the rate of respiratory oxygen consumption (or CO_2 evolution), there is no net gain of organic carbon by the organism. The balance between these two processes on a diel basis occurs at some finite irradiance level, the compensation light intensity. The euphotic zone is defined as that portion of the water column where net photosynthesis occurs, i.e., from the surface to the depth corresponding compensation light intensity.

Commonly the compensation light intensity is taken to be the 1% light depth, although numerous measurements have indicated that the compensation point is often lower but also highly variable (Parsons et al., 1984). While almost all of the integrated net photosynthesis may occur between the surface and

the 1% light depth, if only 3% of the carbon fixed in the ocean occurs below the 1% light depth it would amount to approximately one gigaton of carbon fixed yearly. This is approximately 20% of the annual input of CO_2 into the atmosphere by the combustion of fossil fuels, and could be a significant sink for CO_2 which is not accounted for in current carbon budgets. Thus, from the standpoint of global geochemical cycles of carbon, establishing the lower limit of the euphotic zone is important, especially if one is concerned with budgeting carbon. Unfortunately, with present methods, it is difficult to determine the compensation light intensity in the field; however, it is possible to mathematically model (i.e., calculate) a lower limit. To this end, I will attempt to describe one approach to modeling the lowest light intensity which can support gross photosynthesis and then estimate (i.e., guess) what the euphotic zone might be.

Factors in the Model

There are five basic factors which determine the compensation light level: (1) the maximum quantum yield of photosynthesis; (2) the photosynthetic quotient; (3) the absorption cross-section of the photosynthetic apparatus; (4) the maximal lifetime of the electron transport components in the photosynthetic apparatus; and (5) respiration rate. For simplicity, we shall assume that the maximum quantum yield of photosynthesis is constant at 0.125 O_2/quanta and that the photosynthetic quotient is 1.0. Let us now examine the other factors individually.

The absorption cross-section. A water column behaves like a monochrometer; in the clearest ocean waters light penetrates best in a waveband centered around 475 nm (Fig. 1). In order to sustain photosynthetic electron flow, light must be absorbed and the excitation energy transferred to the photosynthetic reaction centers, where primary charge separation actually occurs. All photosynthetic organisms therefore have evolved light harvesting systems which contain a variety of chlorophylls and accessory pigments bound to specific proteins. These pigment-protein complexes serve as the "antennae" for the photosynthetic electron transport machinery (see Prezelin, 1981 for a review). There is a tremendous diversity in pigmentation within photosynthetic organisms, and almost all organisms are capable of changing the "size" or "number" of the antennae in response to growth irradiance conditions (Falkowski and Owens, 1980).

Let us first consider the effective optical absorption cross section of the photosynthetic apparatus. This cross section is represented by the overlap of the absorption spectra of the photosynthetic pigments and the spectral irradiance field (Dubinsky et al., 1986). At the surface of the ocean, where visible light is almost equally available at all wavelengths (i.e., the light is "white"), and therefore the optical

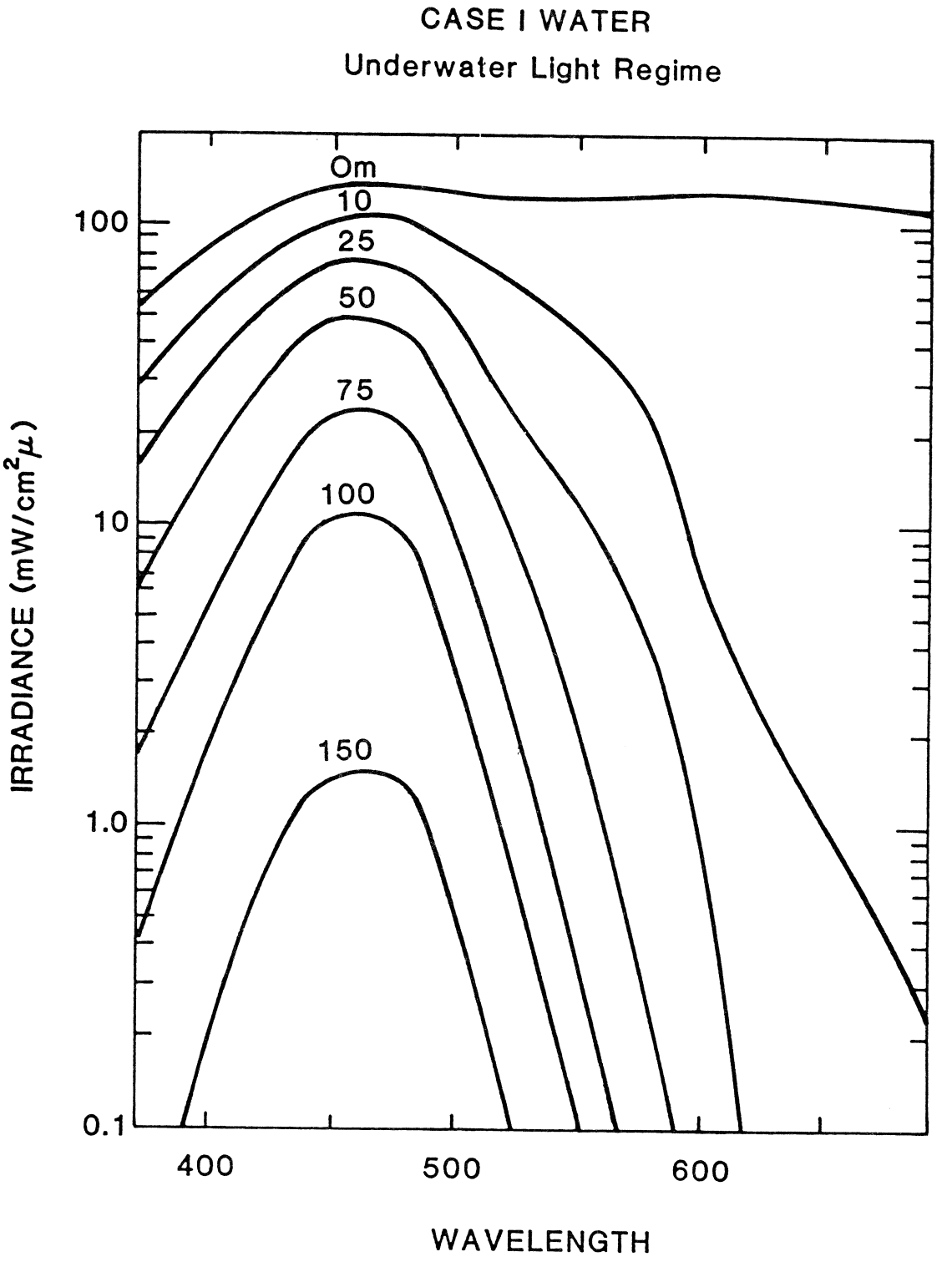

Figure 1. Spectral irradiance profiles from specified depths in the open ocean (after Jerlov, 1968).

absorption cross section may be simply approximated by the in vivo absorption spectra of the cells. Deep in the water column, however, as the light field narrows to a band in the blue-green region of the spectrum, the overlap between the absorption spectra of the photosynthetic pigments and the spectral distribution of the light becomes a critical factor which determines the light harvesting potential of a cell. Different phyla have markedly different potentials for absorbing the available light. For example, blue-green algae (cyanobacteria) have light harvesting antennae called phycobilisomes which are macromolecular structures arranged on photosynthetic membranes (Gantt, 1980). The absorption spectra of phycoerythrium and phycocyanin, two pigments which are found in phycobilisomes, have very little overlap with the submarine light field found deep in clear open ocean waters (Fig. 2a). The lack of overlap between the absorption spectra and the spectral irradiance suggests that deep chlorophyll maxima are unlikely to contain many photosynthetically active cyanobacteria; they do not "see" much of the light.

In contrast, the absorption spectra of the chl a/b protein complexes found in chlorophytes and other green algae has a high absorption cross section in the blue-green region (Fig. 2b). Similarly, both the peridinin-chl a-complex found in dinoflagellates, and the fucoxanthin chl a/c-complex in diatoms and chlorophytes virtually completely overlap the deep oceanic spectral irradiance fields (Fig. 2c). Thus, these algal groups are, at least, capable of absorbing light deep in the water column of the open ocean.

Let us now consider another absorption cross section, the absorption cross section of Photosystem II (PSII) (Ley Mauzerall, 1982). The "Z" schema of photosynthesis requires that for each O_2 molecule evolved, a minimum of eight photons must be absorbed, four by PSII, where water is oxidized, and four by Photosystem I, where a strong reductant (NADPH) is formed (Clayton, 1980). The absorption cross-section of PSI is generally larger than that of PSII, hence the rate of photon absorption by PSII generally limits photosynthetic electron flow at low photon flux densities (Dubinsky et al., 1986). The absorption cross section of PSII (o_{PSII}) can be determined at a given wavelength by measuring the oxygen evolved in a series of flashes and varying the flash intensity (Ley and Mauzerall, 1982). The relationship between flash energy (E) and the oxygen flash yield Y can be described by a cumulative one-bit Poisson function:

$$(1)\quad Y = 1 - e^{-oE}$$

where o is the effective absorption cross section of PSII. In Chlorella vulgaris, the absolute values of o range from 38 to 110 A^2/PSII, at 596 nm, depending on the growth irradiance (Ley and Mauzerall, 1982). We can estimate (from the in vivo absorption

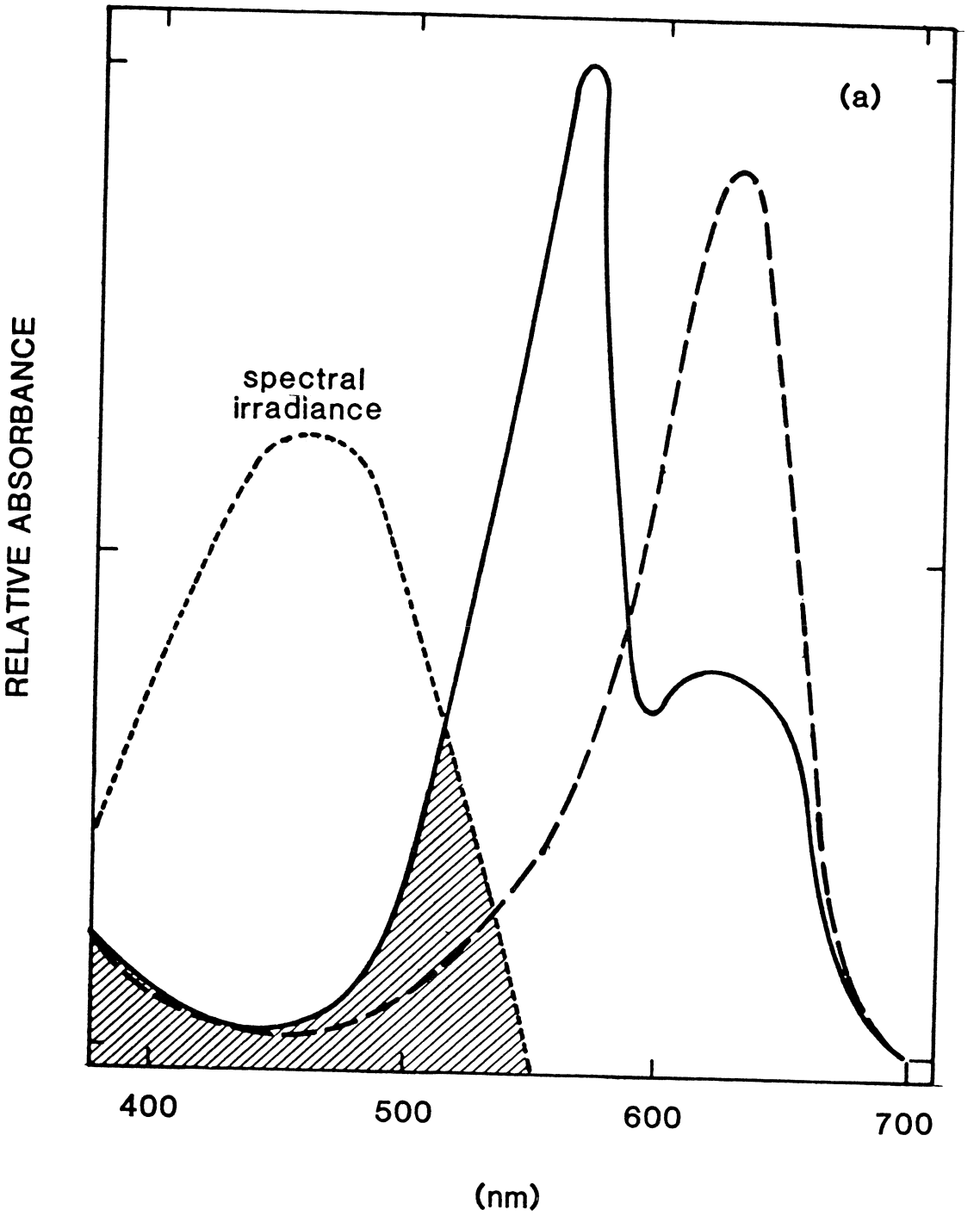

Figure 2(a). Intersection of absorption spectra with the submain light field at 100 m for (a) blue-green algae with phycoerythtium (solid line) and phycocyanin (dashed line).

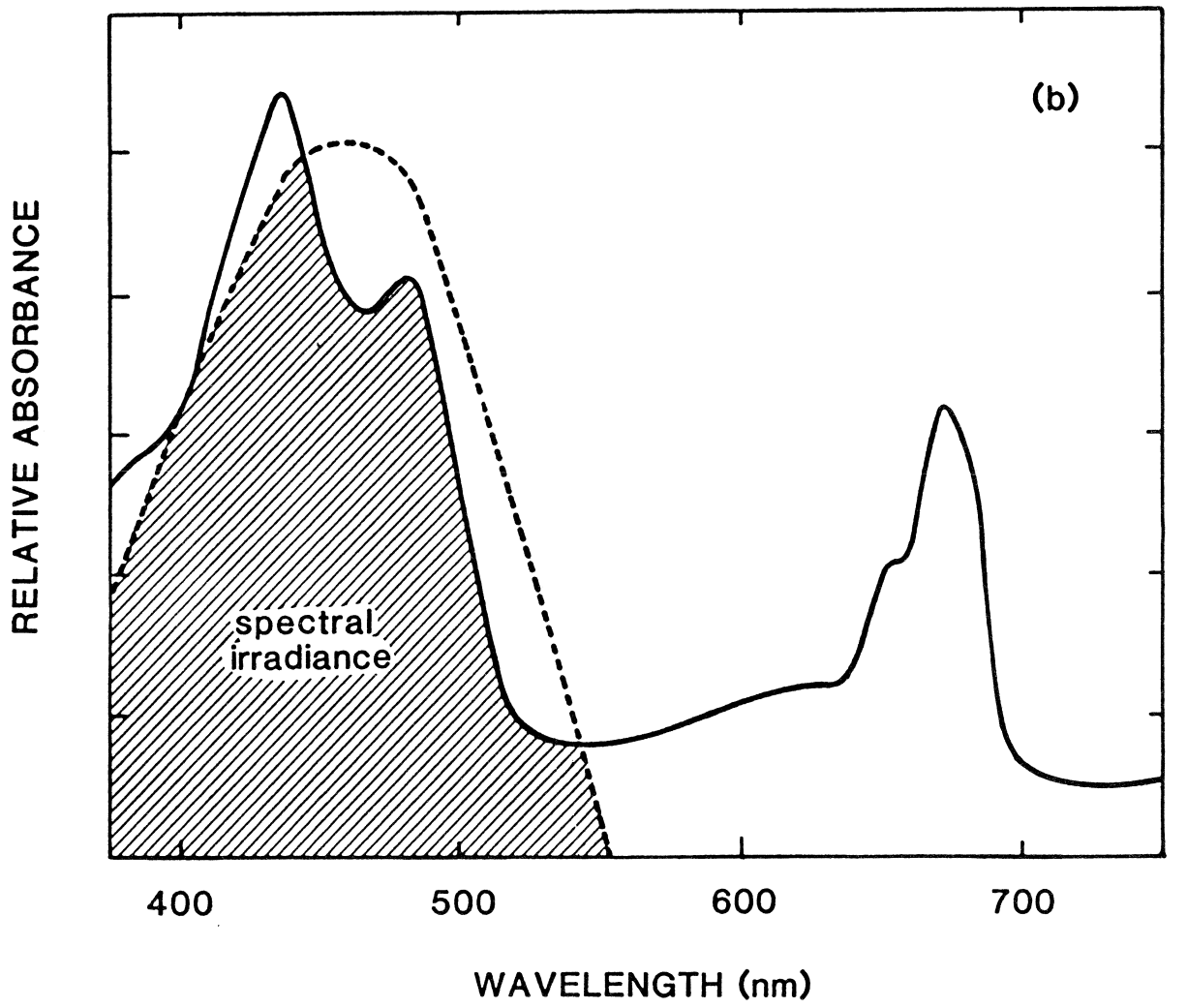

Figure 2(b). Intersection of absorption spectra with the submain light field at 100 m for (b) green algae with chl a and b.

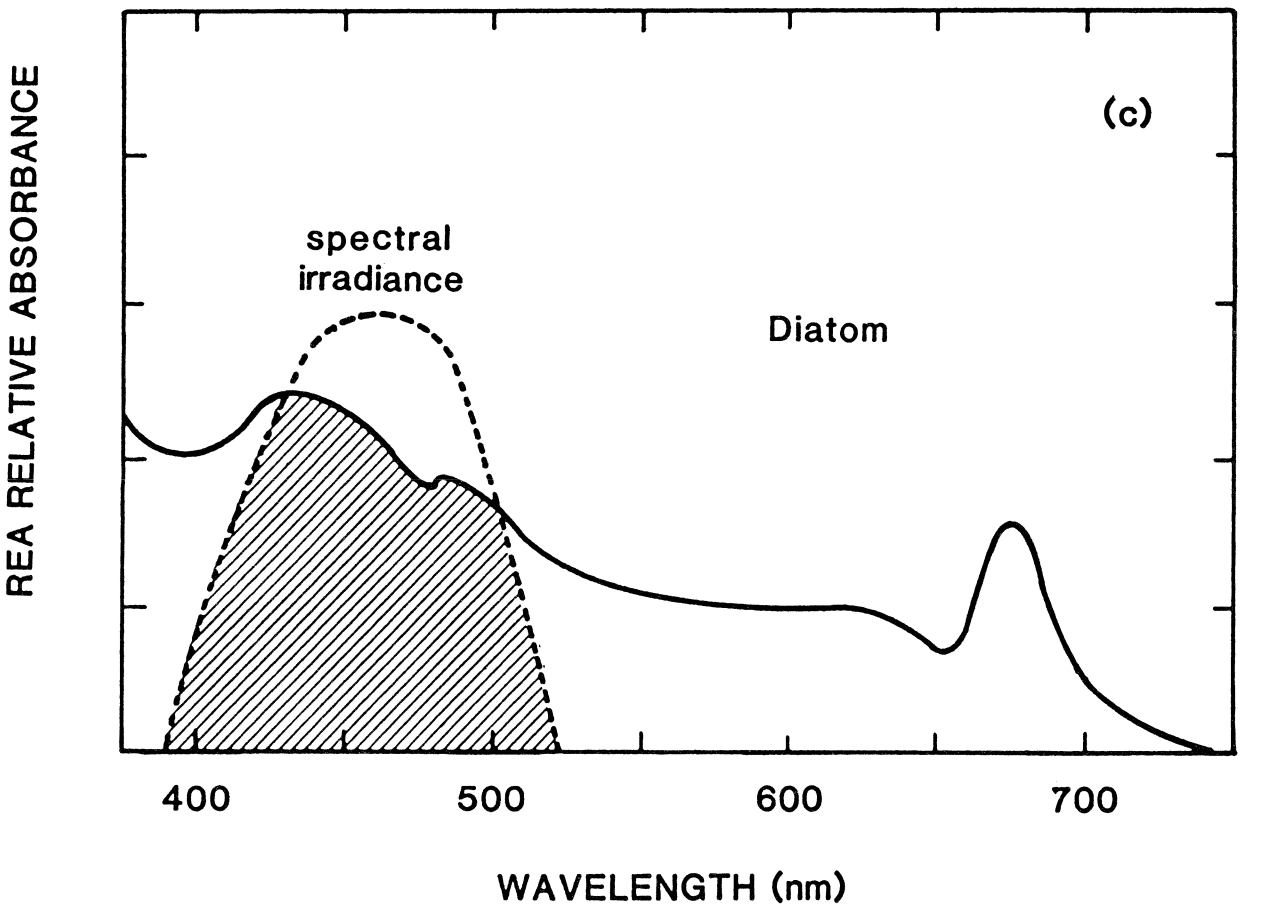

Figure 2(c). Intersection of absorption spectra with the submain light field at 100 m for (c) a diatom with fucoxanthin.

spectra of this organism) that the effective cross section is about fivefold higher at 495 nm than at 596 nm; thus the largest effective absorption cross section of PSII at 475 nm is approximately 500 A^2.

Lifetimes of S_3. All photosynthetic organisms have evolved with very similar molecular machinery for oxidizing water. The evolution of oxygen is thought to occur in a protein complex, the oxygen evolving complex (OEC), which contains four Mn^{++} atoms. Charge accumulation occurs in series, with the absorption of one photon leading to the accumulation of one electron. This may be represented by a series of reactions within each OEC, where oxygen is evolved only after a PSII reaction center absorbs four successive photons:

$$\begin{array}{cc} & \overset{hv}{\longrightarrow}S_1\overset{hv}{\longrightarrow}S_2\overset{hv}{\longrightarrow}S_3\overset{hv}{\longrightarrow}S_4 \\ S_o & \\ 2H_2O & 1e^-\ \ 1e^-\ \ 1e^-\ \ 1e^- \\ \multicolumn{2}{c}{\underbrace{\qquad\qquad\qquad\qquad\qquad\qquad}_{O_2 + 4H^+}} \end{array} \tag{2}$$

The series is biophysically characterized by an oscillation in O_2 evolution when light is provided in discrete, short flashes. Kok and coworkers (1970) proposed that charge accumulates in each photosystem, independent of all other photosystems, and the charge accumulation led to the generation of higher "S" state. In the terminology used by Kok, O_2 is evolved only by reaction centers which are in S_3.

In the dark adapted cells most (~75%) of the reaction centers are in S_1, and the remainder are in S_0 (Diner and Joliot, 1977). Thus, in a train of flashes, O_2 will be evolved on the third flash and on every fourth flash thereafter. Eventually this oscillation is changed by "misses" or "double hits" and the S states become random.

The lifetime of S_3 is about 1 sec in Chlorella (Falkowski, in press; Diner and Joliot, 1977) (Fig. 3).

Calculating the lower limit of gross photosynthesis. From knowledge of the apparent absorption cross section of PSII and the lifetime of S_3, we can calculate the lower limit of gross photosynthesis. Assume incident solar irradiation at the surface (I_o) is 2000 umole quanta $m^{-2}s^{-1}$ ($\doteq$ 2 x 10^{20} quanta $m^{-2}s^{-1}$) and 1 m^2 = $10^{20}A^2$. Therefore,

$$I_o = 2 \text{ quanta } A^2\ s^{-1}. \tag{3}$$

If o is 500 A^2 at 475 nm, then each PSII reaction center receives 1000 quanta/s at the surface.

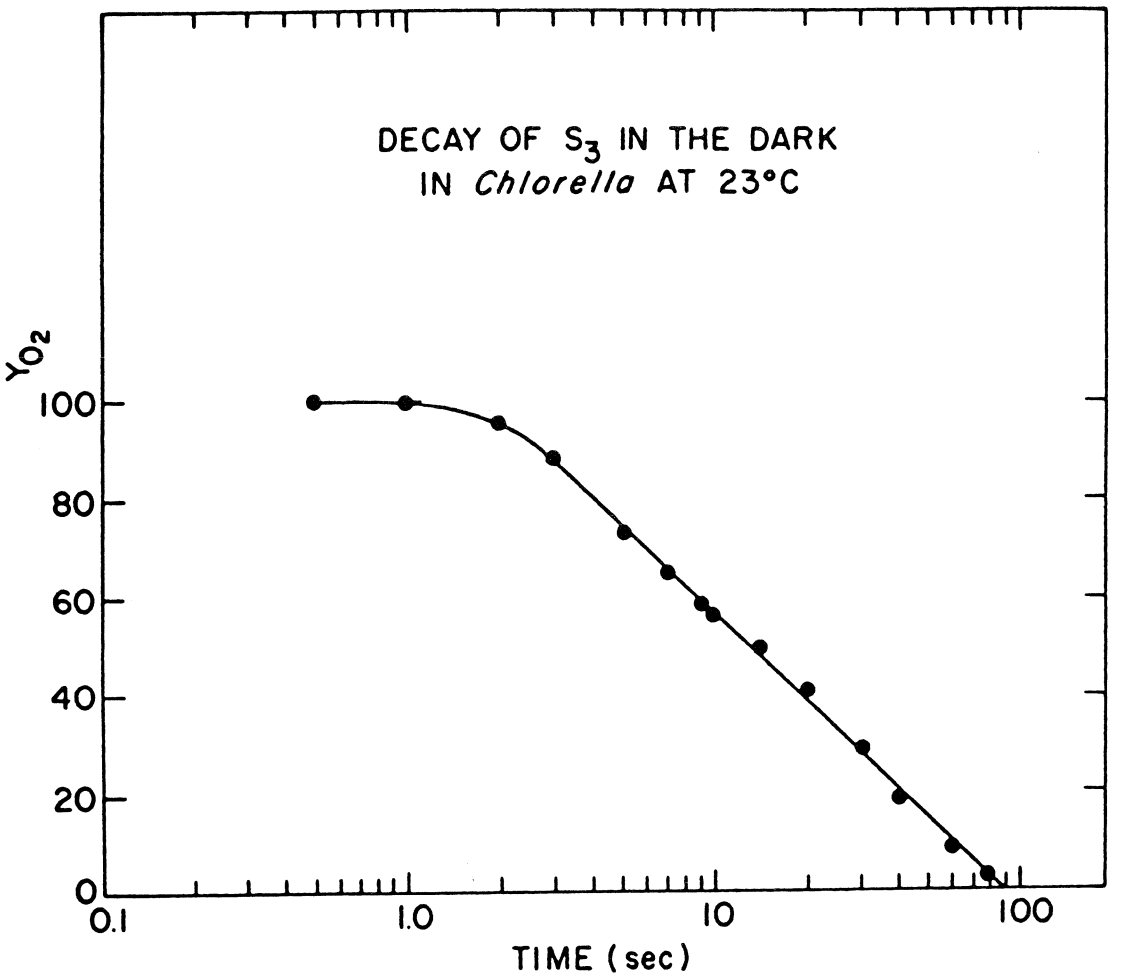

Figure 3. The decay of S_3 in Chlorella pyrenoidosa.

To maintain O_2 evolution (S_3), each PSII requires a minimum of 1 quanta s^{-1}. Thus, the maximum depth at which O_2 can be evolved is about 0.1% of the surface irradiance, which corresponds to approximately 400 m in the clearest oceanic waters.

Respiration. The major obstacle to determining compensation light intensities is the inability to measure respiration of phytoplankton in the sea. From a number of laboratory studies it is clear that respiration generally decreases with decreasing growth irradiance levels, e.g., (Falkowski et al., 1985). In the steady state respiration is related linearly to growth rates.

The relationship between growth and respiration for heterotrophic organisms is given by:

$$(4)\quad u_r = c \times u_g + u_o$$

where u_r is the specific respiration rate ($time^{-1}$), and c is the ratio of carbon lost as CO_2 in respiratory processes associated with growth relative to the carbon assimilated into new cells (Raven and Beardall, 1981). In photosynthetic organisms, numerical solutions to Eq. (4) are complicated by the fact that in the light it is difficult to measure "dark" respiration (Falkowski and Owens, 1978). Numerical analysis of laboratory data suggests that P/R ratios approach 1.0 only when gross photosynthesis approaches zero (e.g., Falkowski et al., 1985). This obviously is impossible, as it suggests that a cell in the dark does not respire; the inconsistency of this conclusion with reality points out the signal/noise problem of measuring P/R ratios even under "ideal" laboratory conditions.

Growth irradiance relationships show a wide range of compensation irradiance levels for steady-state growth. Data for the main diatom Skeletonema costatum suggest that the compensation light intensity for growth in white light is ca. 2.5 x 10^{16} quanta $m^{-2}s^{-1}$ (Falkowski and Owens, 1980), which is about an order of magnitude lower than the theoretically calculated lowest level of light required to sustain photosynthetic electron transport. Clearly this species is capable of making a very large antenna. In contrast, other species, such as the green alga Dunaliella tertiolecta, the diatom Thalassiosira weisflogii, and the dinoflagellate Prorocentrum micans have compensation irradiance levels for growth around 5 to 10 x 10^{18} quanta $m^{-2}s^{-1}$ (Falkowski et al., 1985), which corresponds roughly to between 0.5 and the 1% light depths in the sea (Parsons et al., 1984).

Calculation of Carbon Fixed Near the Base of the Euphotic Zone

Let us assume that at the 0.1% light depth the P/R ratio is 1.0; what might be the maximum photosynthetic carbon fixed immediately above the compensation light depth?

Assume that the photosynthetic reaction centers receive sufficient light to drive 1 e^-/s, and that chl *a* at this depth is 0.05 ug/l (a generous number), 0.05 ug chl *a* = 5.5×10^{11} moles chl *a*. If each photosynthetic unit contains 3000 chl *a* / O_2, contains 4 PSII reaction centers, and receives 4 quanta s^{-1} (i.e., 1 quanta PSII/s^{-1}), then the rate of O_2 evolution is given by:

$$\frac{5.5 \times 10^{11} \text{ moles chl } a}{3000 \text{ moles chl } a/\text{mole } O_2^{-1} s^{-1}} = 1.83 \times 10^{-14} \text{ moles } O_2 \text{ } s^{-1}$$

$$= 66 \text{ pmoles } O_2 \text{ } l^{-1} \text{ } hr^{-1}$$

Assume a photosynthetic quotient of 1.0

$$= 791 \text{ pgC } l^{-1} \text{ } hr^{-1}$$

Assume a 12-hr day:

$$= 95 \text{ ng C } l^{-1} \text{ } d^{-1}$$

$$\sim 0.2 \text{ ug C ug Chl}^{-1} \text{ } d^{-1}$$

Assume cells are very shade adapted and have a c/chl ratio of 25 (w/w).

$$u = \frac{0.2 \text{ ug C ug chl}^{-1} \text{ } d^{-1}}{25 \text{ ug Chl ug C}^{-1}} = 8 \times 10^{-3} \text{ } d^{-1}$$

SUMMARY

The calculations presented here are highly simplified and based on a theoretical understanding of photosynthesis and respiration. From these calculations a number of important points emerge.

1. Defining the euphotic zone in the ocean is much easier than measuring it. It is possible, with present technology, to measure the absorption cross section of Photosystem II and the number of reaction centers in an S_3 state at ambient irradiance levels by using a "pump and probe" fluorescence technique (Falkowski et al., 1986). While measurements of these parameters in natural waters may provide data on photosynthetic processes under ambient conditions, they will not necessarily lead to definitive measurements of the lowest limit of net photosynthesis.

2. Respiration rate measurements of phytoplankton in the sea are almost completely nonexistent. The problem of quantifying respiration relative to calculating the depth of the euphotic zone is well recognized (Yentsch, 1975). It may be possible to measure respiration in the light and photosynthesis simultaneously using ^{180}C and/or ^{13}C in isotope dilution experiments (e.g., Brown and Weiss, 1959); however, it is unclear if this technique will be sensitive enough for oligotrophic waters. Furthermore, deep in the euphotic zone microbial respiration is probably more significant than phytoplankton respiration (e.g., Karl and Knauer, 1984), and almost any direct measure of respiration will tend to overestimate the contribution of phytoplankton to the total. These vexing problems have no solutions in the near term.

3. While the rate of carbon fixation by phytoplankton deep in the euphotic zone is vanishingly low, when even the infinitesimally small rates are integrated over the water column from, for example, the 0.1% to 1% light depths, it amounts to a significant input of fixed carbon to the oceans. Clearly, integrating the contribution of this carbon to the oceanic or global carbon budgets is desirable, but direct verification is almost impossible. To some extent, sediment trap data (e.g., Knauer, et al., 1984) may help to quantify low rates of primary production deep in the euphotic zone.

REFERENCES

Brown, A. H. and D. Weiss. 1959. Relation between respiration and photosynthesis in the green alga Ankistrodesmus braunii. Plant. Physiol. 34:224-234.

Clayton, R. K. 1980. Photosynthesis: Physical mechanisms and chemical patterns. Cambridge University Press, New York, 281 pp.

Diner, B. A. and P. Joliot. 1977. Oxygen evolution and manganese. In: A. Trebst and M. Avron (Eds.), Photosynthetic electron transport and photophosphorylation. Encyclopedia of Plant Physiology, New Series, Vol. 5, pp. 187-205.

Dubinsky, Z., P. G. Falkowski, and K. D. Wyman. 1986. Light harvesting and utilization by phytoplankton. Plant Cell Physiol. 27:1335-1349.

Falkowski, P. G. In press. The photosynthetic light reactions. In: R. A. Alberte and R. Barber (Eds.), Marine photosynthesis. Oxford University Press, New York.

Falkowski, P. G., K. D. Wyman, A. C. Ley and D. Mauzerall. 1986. Relationship of steady-state photosynthesis to fluorescence in eucaryotic algae. Biochem. Biophys. Acta. 849:183-192.

Falkowski, P. G., A. Dubinsky and K. Wyman. 1985. Growth-irradiance relationships in phytoplankton. Limnol. Oceanogr. 30:311-321.

Gantt, E. 1980. Structure and function of phycobilisomes: Light harvesting pigment complexes in red and blue-green algae. Int. Rev. Cytol. 66:45-80.

Jerlov, N. G. 1968. Optical Oceanography. Elsevier, NY, 194 pp.

Karl, D. M. and G. A. Knauer. 1984. Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: Evidence for multiple zones of biological activity. Deep-Sea Res. 31:221-243.

Knauer, G. A. J. H. Martin and d. M. Karl. 1984. The flux of particulate organic matter out of the euphotic zone. Global Ocean Flux Study. Workshop Proc. Natl. Acad. Sci., pp. 136-150.

Kok, B., B. Forbush and M. McGloin. 1970. Cooperation of charges in photosynthetic oxygen evolution - I. A linear four step mechanism. Photochem. Photobiol. 11:457-475.

Ley, A. C. and D. Mauzerall. 1982. Absolute absorption cross-sections for photosystem II and the minimum quantum requirement for photosynthesis in Chlorella vulgaris. Biochem. Biophys. Acta. 680:95-106.

Parsons, T. R., M. Takahaski and B. Hargrave. 1984. Biological Oceanographic Processes, 3rd ed. Perganon Press, New York, 330 pp.

Prezelin, B. B. 1981. Light reactions in photosynthesis. In: T. Platt (Ed.), Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210, Ottawa, pp. 1-43.

Raven, J. A. and J. Beardall. 1981. Respiration and photorespiration, T. Platt (Ed.). Can. Bull. Fish. Aquat. Sci. 210, Ottawa, pp. 55-82.

Yentsch, C. S. 1975. Critical mixing depth -- a problem in the measurement of respiration. In: J. J. Cech, Jr., D. W. Bridges and D. B. Horton (Eds.), Proc. of TRIGOM Symp. on Marine Respiration. Res. Inst. Gulf of Maine, pp. 1-10.

DEEP-WATER BENTHIC MACROALGAL COMMUNITIES WITH EMPHASIS ON FLORIDA AND THE BAHAMAS

M. Dennis Hanisak
Stephen M. Blair

Marine Botany Department
Harbor Branch Oceanographic Institution
5600 Old Dixie Highway
Fort Pierce, FL 34946

ABSTRACT

The development of research submersibles has allowed scientists of various disciplines to ask new questions and re-address old ones about the world's oceans. The Johnson Sea-Link submersibles are being used to discover and study deep-water benthic macroalgal communities in Florida and the Bahamas. While their full extent is not yet known, communities of richly diverse and abundant algae have been found in areas of suitable substrate and favorable water quality. Zonation patterns are evident in these communities. In all cases, the deepest (to ca. 270 m) plants are crustose red algae. Fleshy algae, in particular certain green algae, can be found in depths as great as ca. 200 m. The few measurements of productivity that have been made on these plants are higher than previously expected and indicate that the contribution of deep-water benthic macroalgae should be included in global estimates of primary production. The degree to which these plants are grazed by herbivores is unknown. Physiological studies on these algae may elucidate new mechanisms for adaptation to their deep-water environment. Although research on these organisms is in its infancy, it is clear that a study of the biology of deep-water macroalgae will be richly rewarding.

INTRODUCTION

Marine macroalgae account for approximately 10% of total marine primary production, with most of the remainder attributed to phytoplankton (Ryther, 1963). However, in benthic habitats in estuarine and coastal waters where there is adequate substrate and light levels, the primary productivity of macroalgae on an areal basis can exceed that of the phytoplankton by one or two orders of magnitude (Blinks, 1955; Ryther, 1963; Mann, 1973). Recent studies (e.g., Littler et al., 1985, 1986) have indicated that benthic macroalgae are capable of growing at much greater depths than previously believed and that the contribution to primary productivity by macroalgae growing on deep reefs in certain parts of the world could be significant.

A major breakthrough in the study of deep-water macroalgae has been the development of research submersibles (Earle, 1985). Phycologists have begun to document the existence of a deep-water flora that is rich in both abundance and diversity. This unique flora is composed of many species that had been previously considered rare or had not been described at all (Eiseman, 1979; Eiseman and Moe, 1981; Eiseman and Norris, 1981; Eiseman and Blair, 1982; Eiseman and Earle, 1983). This paper briefly reviews what is known about deep-water benthic macroalgae, with an emphasis on Florida and Bahamian waters.

What are deep-water macroalgae?

The expression "deep-water algae" is a somewhat imprecise one as the depths for the lower limit of plant growth reported by different investigators vary by an order of magnitude (Table 1). Most of the available information on the role of macroalgal communities is from studies conducted on macroalgal communities in shallow temperate habitats where turbidity levels are frequently high due to runoff from continental land masses and, thus, the light penetration in the water column is relatively low (Fig. 1A). Consequently, the depth of the euphotic zone is shallow and the lower limit of macroalgal growth may be only 15 m or less. However, in the clear, oligotrophic waters of the tropics and subtropics, light penetration is much greater than elsewhere (Fig. 1B). In such areas, benthic macroalgal communities have been found (Littler et al., 1985, 1986) at depths greater than those previously believed possible. Thus, the term "deep-water algae" is a relative one and actually relates more directly to light levels than depth per se.

The study of deep-water macroalgal communities has been limited by the ability of phycologists to make direct, in situ observations in the sea. Until recently, knowledge of these plants has been quite limited and has been restricted to information obtained from dredging records or from collections of rare and unusual algae that have been occasionally cast ashore following severe storms. Various dredging techniques have been important in early attempts at assessing the composition of deep-water macroalgal communities (e.g., David et al., 1904; Taylor, 1928; Humm, 1956; Adey and MacIntyre, 1973; Dewreede and Jones, 1973; Doty et al., 1974). However, such limited methods provide only a fragmented, and poorly quantified, glimpse of deep-water communities.

With the introduction of SCUBA in the 1950s, marine botanists were able to extend their direct observations of macroalgal communities from the intertidal zone to the shallow subtidal (i.e., to depths of ca. 30 m) and maximally to a depth of ca. 65 m (e.g., Gilmartin, 1960). While these depths encompass the full depth distribution of macroalgae in many

Table 1. Depth records of benthic macroalgae selected from different locations around the world.

Depth (m)	Location	Algal Type	Reference
15	Helgoland	red coralline algae	Luning and Dring 1979
45	Gulf of Maine	encrusting coralline algae ("Lithothamnion glaciale association")	Sears and Cooper 1978
100	Newfoundland	"encrusting algae"	Hooper 1985
150-200	Belize	rhodoliths	J.C. Lang 1971 (cited as a personal communication in Adey and MacIntyre 1973)
174	Discovery Bay, Jamaica	crustose red algae and green filamentous algae	Lang 1974
200	Tongue of the Ocean, Bahamas	rhodoliths	J.W. Porter 1972 (cited as a personal communication in Adey and MacIntyre 1973)
228	Enewetak Atoll	crustose coralline algae	Hillis-Colinvaux 1985, 1986b
250	Glover's Reef, Belize	crustose coralline	James and Ginsburg 1979
250	Johnson Atoll, Line Island	crustose coralline algae	Agegian and Abbott 1985
268	San Salvador "Sea Mount," Bahamas	crustose coralline	Littler et al. 1985, 1986

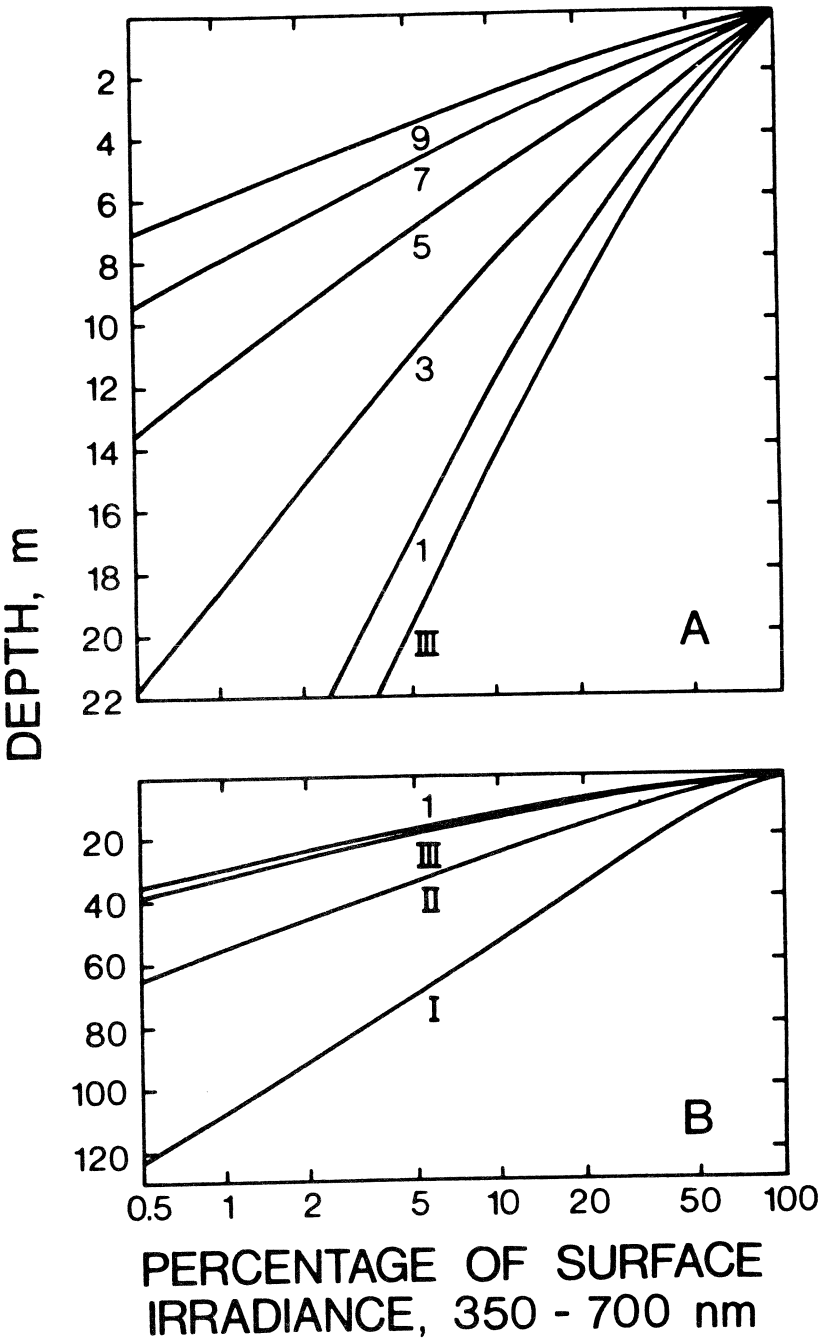

Figure 1. Depth profiles for downward irradiance (350-700 nm) for different coastal (A) and oceanic (B) Jerlov water types. Redrawn from Jerlov (1968).

temperate areas, it was clear that macroalgae in the tropics and subtropics could grow at depths significantly greater than those that could be observed with the use of SCUBA.

The development of research submersibles (Earle, 1985) has extended the observations on marine plants to depths greater than those possible with SCUBA. Although the few observations made on deep-water macroalgal communities have been scattered among locations all around the world (Table 1), several conclusions about these communities can be made. First, the deepest benthic macroalgae are crustose coralline red algae belonging to the subfamily Melobesiodeae of the Corallinaceae. Unfortunately, taxonomic difficulties in this group have resulted in very little taxonomic discrimination of these algae. A great deal of work will be needed before the basic systematics of these algae are resolved and such questions as to whether or not these specific deep-water crusts also occur in shallow water can be answered. Second, it is possible that some attached blue-green algae or boring green algae (e.g., Ostreobium) may occur at depths as great or greater than those reported for the red algal crusts. The uncertainty of this statement is due to the high degree of difficulty in collecting these types of organisms which might be responsible for the observed tinting of substrates often seen from submersibles at the bottom of the euphotic zone. Third, variations in the observed depth range of macroalgal growth are due primarily to differences in the level of photon flux densities reaching the substrate. However, in this regard, it is surprising how few measurements of photon flux density have been made in deep-water macroalgal communities. Sustained, continuous measurements of underwater irradiance such as those made by Luning and Dring (1979) would be highly desirable.

The remainder of this paper will focus on deep-water macroalgal communities that have been studied off the coast of Florida and in the Bahamas. Given the imprecise nature of the expression "deep-water macroalgae", this term will be used henceforth in this paper to refer to macroalgae growing below SCUBA depth (i.e., 40 m). These communities under present investigation by the authors and others are located in an excellent area for such studies because of the diverse macroalgal flora, the high water clarity, and the proximity of a major research submersible program located at the Harbor Branch Oceanographic Institution in Fort Pierce, Florida.

Deep-water macroalgal communities off the coast of Florida

There is little known about the deep-water algae of the tropical and subtropical western Atlantic. Early collections by naturalists such as Louis Agassiz and Archibald Menzies and the more recent work of Taylor (1930, 1942) and Howe and Taylor (1931) recorded many new species, some of which are known only from their original collections. In the Gulf of Mexico, Taylor

(1928) collected benthic macroalgae via dredging to depths greater than 100 m. More recent work (Dawes and van Breedveld, 1969; Cheney and Dyer, 1974; Eiseman and Blair, 1982) has added to the available knowledge on the deep-water macroalgae in the Gulf. In particular, Cheney and Dyer (1974), using SCUBA, described a macroalgal community with a distinct tropical affinity and a seasonal pattern of abundance and diversity, both of which were maximal in the summer. This pattern of seasonality contrasts with what previous investigators using dredging (e.g., Dawes and van Breedveld, 1969) had reported for the Gulf. However, this difference could be due to the preferential harvesting of larger plants, which are more likely to be considered perennials, when dredging techniques are employed. Humm and Taylor (1961) postulated a floral diversity gradient with depth; this hypothesis was supported by the submersible observations of Eiseman and Blair (1982) who found a much greater tropical affinity to the deep-water flora of the northwest Gulf of Mexico as compared to shallow-water habitats in this region.

The most extensive study of deep-water macroalgae in the western Atlantic has been made along the continental shelf of North Carolina (Schneider, 1974, 1975a, b, 1976; Schneider and Searles, 1973, 1975, 1976; Searles, 1972; Searles and Schneider, 1978, 1980) and South Carolina (Wiseman and Schneider, 1977). Yet despite the tremendous activity on the study of the Carolina flora, relatively scant attention has been paid in recent years to macroalgae off the extensive eastern coast of Florida, with investigations having been limited to relatively shallow-water communities (Phillips, 1961; Juett et al., 1976; Benz et al., 1979; Hall and Eiseman, 1981).

Given the lack of knowledge of the deep-water macroalgal community of the continental shelf off the coast of Florida, a survey of this community was undertaken with the research submersibles Johnson Sea-Link I and Johnson Sea-Link II in an area from St. Lucie Inlet to the Lake Worth Inlet near Palm Beach, Florida. The substrate in this area includes large areas of rubble and reefs suitable for the growth of benthic macroalgae (Eiseman, 1979). Approximately 200 species belonging to 109 genera have been identified from this survey (Hanisak and Blair, in press), over 70% of which are red algae. A distinct zonation is apparent in this community, with two apparent associations of species: one in depths less than 40 m and a second at depths greater than 60 m. The area between 40 and 60 m appears to be a transition between the two major zones (Eiseman, 1978).

There appears to be a significant seasonal variability in the species diversity of the deep-water macroalgal community on the continental shelf, with the greatest number of species collected between May and July (Hanisak and Blair, in press). Although not yet quantified, macroalgal abundance seems to be highly correlated with macroalgal diversity and has the same

seasonal pattern. This agrees with the SCUBA observations made by Cheney and Dyer (1974) for the macroalgal community from 25-60 m in the Gulf of Mexico. Many species of the eastern continental shelf were found to be reproductive throughout the year, with the number of reproductive species highest from June to August which approximated the period of maximal species diversity (Hanisak and Blair, in press). However, when reproductive frequency was expressed as a percentage of reproductive species to the number of species present in each month, two peaks (January and August) are apparent.

An example of how little is known about the actual extent of deep-water macroalgal communities is the case of the green alga Anadyomene menziesii. This large, spectacular alga was first collected by Archibald Menzies in 1802 from dredge samples taken at ca. 40 m at an unknown location in the Gulf of Mexico. This taxon was only briefly described from Menzies' samples by W. H. Harvey in 1858 and was not collected again until 1952 when the U. S. Fish and Wildlife vessel Oregon collected some samples in dredgings from a depth of ca. 80 m at a station off the Yucatan peninsula (Humm, 1956). Additional samples were obtained by the Oregon two years later off of the Dry Tortugas at depths of ca. 400 m, although it is improbable that these latter specimens were attached and growing at that depth (Humm, 1956). Thus, a period of 150 years elapsed between the first two collections of this species. Yet recently, Hanisak (1986) reported that this rare plant forms extensive underwater meadows off the Dry Tortugas. Such a population could have a major influence on other trophic levels in the community and merits additional study. The full distributional range and abundance of this species will not be known until a more detailed survey of the Gulf of Mexico can be made. Given the extensive areas that are below SCUBA range but still within the euphotic zone, it is expected that other interesting deep-water macroalgal communities will be discovered with submersibles in the future.

Deep-water macroalgal communities of the Bahamas

It is in the clear, oligotrophic waters of the Bahamas that benthic macroalgae penetrate deeper than anywhere else in the world. Previous, limited observations on the depth of these algae in the depth range of 175-250 m (Table 1) have been supplanted by the recent discovery off San Salvador Island of a crustose red alga living at depths to 268 m (Littler et. al., 1985, 1986). Perhaps even more interesting than this depth record itself is the complexity and diversity of the deep-water macroalgal community in this area. Cluster analysis demonstrated the existence of four algal zones in this community: a Lobophora zone down to ca. 90 m, a Halimeda zone from ca. 90-130 m, a Peysonnelia zone from ca. 130-189 m, and a crustose red algal zone from 189-268 m (Littler et al., 1985, 1986). The top of the San Salvador "Seamount" (ca. 70 m) was found to be covered by

a rich, multi-layered macroalgal community growing on a bed of rhodoliths composed of various coralline algae. Lobophora variegata was the dominant organism in this area with ca. 60% coverage; other important species in the canopy of this community included Dictyota divaricata, Halimeda copiosa, H. discoidea, Caulerpa racemosa var. peltata and Kallymenia westii. Because of the multiple layers of algal growth, the total coverage was estimated to be at least 160% across the top of the "Seamount."

The same basic zonation pattern observed off San Salvador Island has been noted at several other sites in the Bahamas (Hanisak, unpublished) although never at a diversity as high or depths as great as at the "Seamount." In general, the deep-water algal community of the Bahamas, at depths greater than 60 m, is dominated by green algae, particularly species of Halimeda (Blair and Norris, 1988), Johnson-sea-linkia profunda, and an undescribed gelatinous green alga. Johnson-sea-linkia profunda is the deepest known fleshy alga, with a depth record of ca. 200 m off of San Salvador Island.

There appear to be few brown algae in the deep-water flora. Most notable are Lobophora variegata which can form lush, multitiered populations throughout the Bahamas at ca. 60-90 m, and Sargassum hystrix, which appears to be the deepest dwelling brown alga to be directly observed in situ, with a maximally recorded depth of 115 m off San Salvador Island (Hanisak et al., unpublished).

Fleshy red algae are not abundant in these deep-water communities although localized areas may have significant populations of Cryptonemia luxurians. The paucity of fleshy red algae at depth has been attributed (Eiseman and Earle, 1983) to grazing by fish, but this claim has not been substantiated. The deepest living macroalgae of all, however, are certain crustose red algae which have been found growing down to depths of 268 m (Littler et al., 1985, 1986). As previously mentioned, these algae have presented some taxonomic difficulties that have not yet been resolved. This same area is also rich in rhodoliths or algal nodules which are composed of several crustose red algae (Littler et al., unpublished). Concentrations of such rhodoliths have been commonly found in depths of ca. 50-150 m on continental shelves and oceanic offshore banks (Adey and MacIntyre, 1973).

To date, collections around San Salvador Island have been restricted to the fall months (October and November). Even with this relatively small sampling, a total of 60 genera, with 88 species, excluding the subfamily Melobesiodeae of the Corallinaceae, have been identified to date (Table 2). These values are similar to those identified for the Florida collections made during the spring months. However, the lower limit of macroalgal growth is much deeper in the Bahamas than in

Table 2. List of genera and observed depth ranges for macroalgae collected by submersible off San Salvador Island, Bahamas (1981-1985). Note: all collections have been restricted to October and November of 1981, 1983, and 1985.

Division	Genera	Depth Range (m)
Chlorophyta	Anadyomene	60-90
	Avrainvillea	60-70
	Caulerpa	60-75
	Cladophora	37
	Codium	70-90
	Cystodictyon	60
	Halimeda	60-150
	Johnson-sea-linkia	60-200
	Microdictyon	60-90
	Ostreobium	60-150
	Pseudocodium	60
	Struvea	60
	Udotea	37-70
	Valonia	60-90
Phaeophyta	Dictyopteris	60
	Dictyota	37-75
	Lobophora	60-90
	Sargassum	60-90
	Sphacelaria	60
	Stypopodium	67-75
	Turbinaria	90
Rhodophyta	Antithamnion	60-90
	Anothrichium	60
	Botryocladia	60-90
	Callithamnion	60-90
	Centroceras	37-60
	Ceramium	37-75
	Champia	60-70
	Chondria	60
	Chrysymenia	60
	Coelarthrum	60
	Corallina	60
	Crouania	60
	Cryptomenia	70
	Dasya	60-75
	Digenia	60
	Fosliella	60-150
	Galaxaura	60-70
	Gloioderma	60

Table 2 (cont'd.)

Gracilaria	60
Griffithsia	37
Halodictyon	90
Hypnea	60
Jania	60
Kallymenia	60-90
Laurencia	60-70
Lomentaria	60
Martensia	60
Melobesiodeae-1	60-268
Melobesiodeae-2	60-150
Melobesiodeae-3	60-150
Peyssonnelia	60-150
Polysiphonia	37-90
Seirospora	60
Titanophora	67-70
Undescribed Delisseriaceae-1	67-70
Undescribed Delisseriaceae-2	60
Wrangelia	60-75
Wrightiella	60
Wurdemannia	60

Florida (Fig. 2); the presence of benthic macroalgae at such depths is due to the high water clarity that exists around the Bahamian archipelago. At present it is not clear how representative these deep-water macroalgal communities are of those in adjacent areas such as the Caribbean and South America. Continued study of deep-water macroalgal communities will be needed to obtain a better understanding of their biogeography.

Ecology of deep-water macroalgae

Previous scientific investigations of deep-water macroalgae have concentrated primarily on their systematics and floristics; little is known about the ecology of these algae, and experimental work on these organisms has been essentially nil. It is now appropriate to put this flora into broader perspective and to begin to focus on the ecology and physiology of these interesting algae.

Given the high potential primary productivity rates of shallow, coastal-water macroalgal communities (e.g., Blinks, 1955; Mann, 1973), the recent discoveries of extensive deep-water macroalgal communities could have a significant impact on the understanding of carbon flux in the sea. This may be particularly important in the oligotrophic waters of the tropics where phytoplankton productivity is relatively low. Any significant increase in the depth of what is considered to be the euphotic zone would result in a significant increase in the contribution of macroalgae in calculations of global marine primary productivity. In this regard the data presented by Littler et al. (1985, 1986) should stimulate interest in the production ecology of deep-water algae. Perhaps most surprisingly, these plants were shown to be capable of photosynthetic rates comparable to their shallow-water counterparts, even though plants at the top of the San Salvador "Seamount" were found to be growing at photon flux densities approximating those traditionally believed to designate the bottom of the euphotic zone (ca. 1-2% of surface levels). More startling was the existence of the red algal crust growing from 210-268 m, where light levels were estimated to be only 0.0015-0.027 uE $m^{-2}s^{-1}$ (Littler et al., 1986). This value is well below what has previously been considered (Luning, 1981) as the minimal light requirement for macroalgal growth. These observations and a previous one (Larkum et al., 1967) suggest that the photosynthetic efficiency of deep-water algae is quite high; however, it would be desirable to measure this efficiency more carefully, perhaps with techniques such as those used by Falkowski and co-workers (see Falkowski, this volume) for phytoplankton. Falkowski (this volume) has calculated that the lowest levels of photon flux density at which plants could be photosynthetic is ca. 0.02% of the maximal surface radiance. This value contrasts with the *in situ* observance of Littler et al. (1986) of the red algal crusts growing at 0.00005-0.0009% of

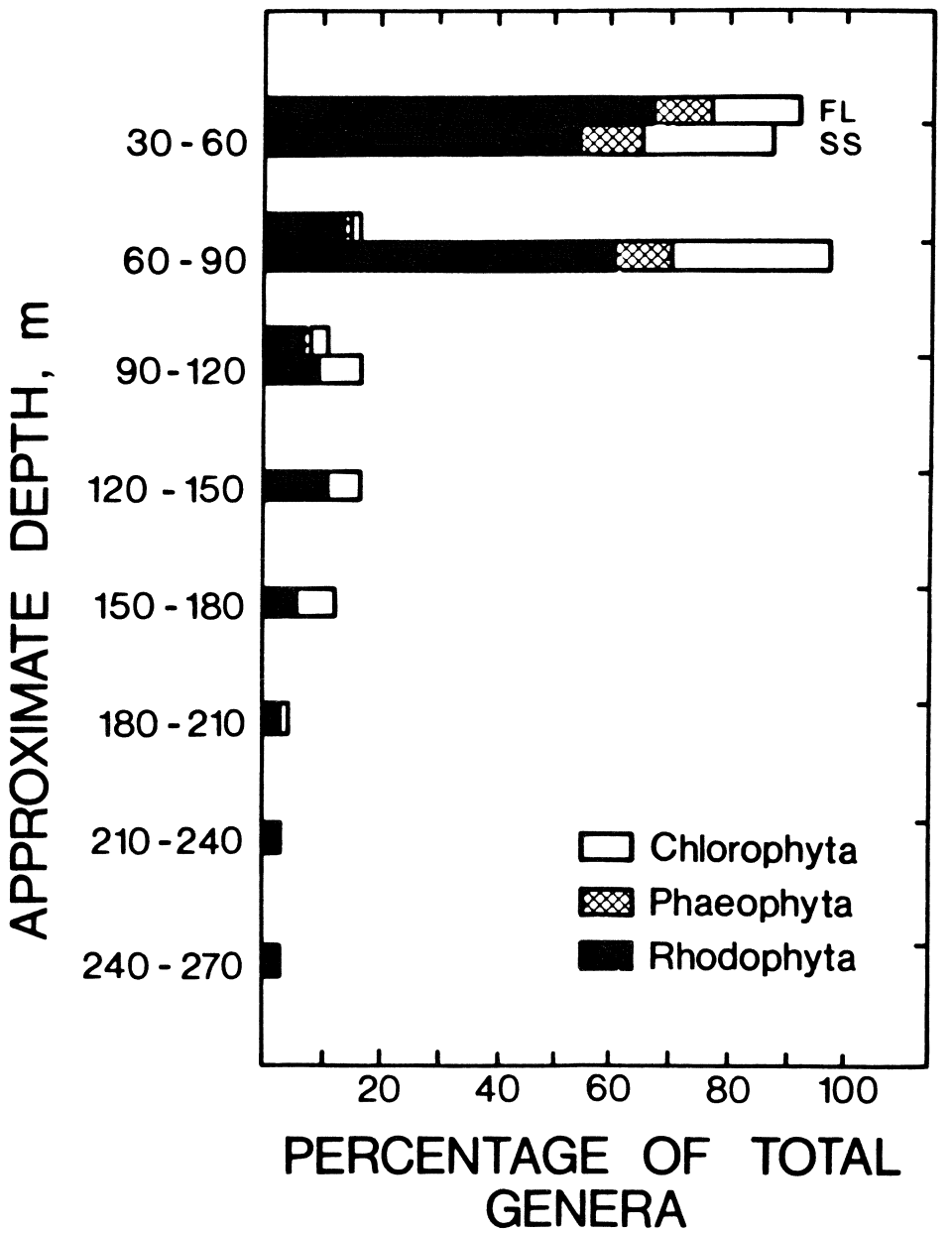

Figure 2. Depth distribution for the genera in the three major macroalgal divisions from collections made off the east coast of Florida (FL) and San Salvador Island (SS; see also Table 2). No macroalgae were observed in the Florida study at depths greater than 120 m.

the surface irradiance. This difference in observed versus theoretical values might be explained in two ways. First, the theoretical calculations derived primarily from experiences with phytoplankton and all of the assumptions made might not apply to benthic algae growing at extremely low light levels. For example, Halldal (1968) reported a photosynthetic response for an endozoic Ostreobium at an irradiance equivalent to ca. 0.007 uE $m^{-2}s^{-1}$, a value in the range reported by Littler et al. (1986) for the deep-water coralline crusts. Second, if the theoretical calculations do apply for these algae, photoheterotrophic fixation of carbon may be involved. While photoheterotrophy cannot be ruled out for this organism, it was shown (Littler et al., 1985, 1986) that samples of this crust collected from the "Seamount" were autotrophic at photon flux densities of ca. 20 uE $m^{-2}s^{-1}$. Additional research is needed to determine which of these scenarios is correct.

In addition to being important sources of photosynthetically fixed carbon, certain deep-water macroalgae are important to the geology of reefs. Crustose coralline algae are important to the development of reef structure (Littler and Littler, 1984) and certain erect calcareous algae, particularly Halimeda, are important to sedimentation and the overall carbonate budgets of reefs (Hillis-Colinvaux, 1980, 1986a). The importance of deep-water macroalgae as producers of carbonate has only been examined by Jensen et al. (1985) who measured the photosyntheses and calcification rates of four species of Halimeda at in situ levels of photon flux density. Given the high biomass of deep-water populations of Halimeda and their measured calcification rates, the contribution of this genus to carbonate production in deep-water reefs must be major. This has been substantiated by Hoskin et al. (1986) who recently reported that Halimeda fragments constituted 32-63% (by volume) of the sediments in the fore-reef and deep-reef communities off the Little Bahama Bank. In Hawaii, Agegian (this volume) has found that both the organic carbon and carbonate productivity are lower for deep-water algae than for their shallow-water counterparts. Moreover, this production depends on a tidally-driven allochthonous source of nutrients and, therefore, constitutes "new" production on the reef. Thus, there is increasing evidence that documents the role of deep-water algae in the biogeochemical cycling of reefs.

Deep-water macroalgae appear to have a number of morphological and physiological adaptations for life in their low-light habitats. In terms of functional form groupings (sensu Littler and Littler, 1980), crustose algae extend throughout the depth range of macroalgal growth and include the deepest known taxa. Deep-water fleshy algae tend to be foliose or flat forms; these forms, such as Johnson-sea-linkia profunda have relatively thin, spreading thalli (Eiseman and Earle, 1983) that presumably would maximize the absorption of photons. Similarly, the increase in utricle size with depth in Halimeda copiosa is

believed (Blair and Norris, in press) to increase the surface area available for the capture of photons.

Our observations of individual species via submersible indicate that their depth distribution is usually sharply delineated. While several factors could contribute to the observed patterns, it seems that irradiance, which has long been considered to be the major factor in determining the depth distribution of macroalgae, is the most likely candidate. Macroalgae have been shown (e.g., Ramus, 1981, 1982) to have several mechanisms for increasing thallus absorptance when irradiance limits photosynthesis. Most commonly, as depth increases, the amount of chlorophyll in the photosynthetic tissue and the ratio of accessory pigments to chlorophyll a increases (e.g., Ramus et al., 1976; Yokohama and Misonou, 1980; Perez-Bermudez et al., 1981). Also, the accessory pigment siphonaxanthin and its precursor loroxanthin have been hypothesized to enable green algae to live at great depths (Kagegama et al., 1977; Yokohama and Kagegama, 1973; Yokohama, 1981, 1983). Ultimately, photon absorption is limited by the organization of pigment protein complexes (see Falkowski, this volume).

The zonation patterns of macroalgal divisions observed for communities in both Florida and the Bahamas (Fig. 2) are consistent to what the model of Dring (1981) predicted for clear oceanic water. This pattern, with red algae growing deeper than green algae, which, in turn, grow deeper than brown algae, appears to occur throughout the world (e.g., Gilmartin, 1960; Larkum et al., 1967; Drew, 1969; Agegian and Abbott, 1985; Hillis-Colinvaux, 1985). It is tempting to relate the observed zonation of the major algal groupings to their different pigment contents and to revive the century-old debate (Engelmann, 1883; Berthold, 1882; Oltmanns, 1892; Gaidukov, 1903) on complementary chromatic adaptation. In essence, this theory suggests that red algae are best adapted to grow at great depths because they possess the photosynthetic pigment phycoerythrin, which complements the spectral quality of light available at that depth which is essentially monochromatic blue light (Fig. 3). However, recent research (Ramus, 1983), albeit on shallow-water species, suggests that this theory is not valid. Rather, the apparent chromatic adaptation of red seaweeds appears to be coincidental with their adaptations for photosynthesis at low light levels (Dring, 1981). Moreover, it is not likely that the zonation patterns of deep-water algae are due to their spectral response as there is actually very little change in the spectral composition of irradiance below 40 m (Drew, 1983). Macroalgae, regardless of their phylogeny, appear to be "intensity adapters" whose "ecological imperative" is to become "optically black" when necessary (Ramus, 1983).

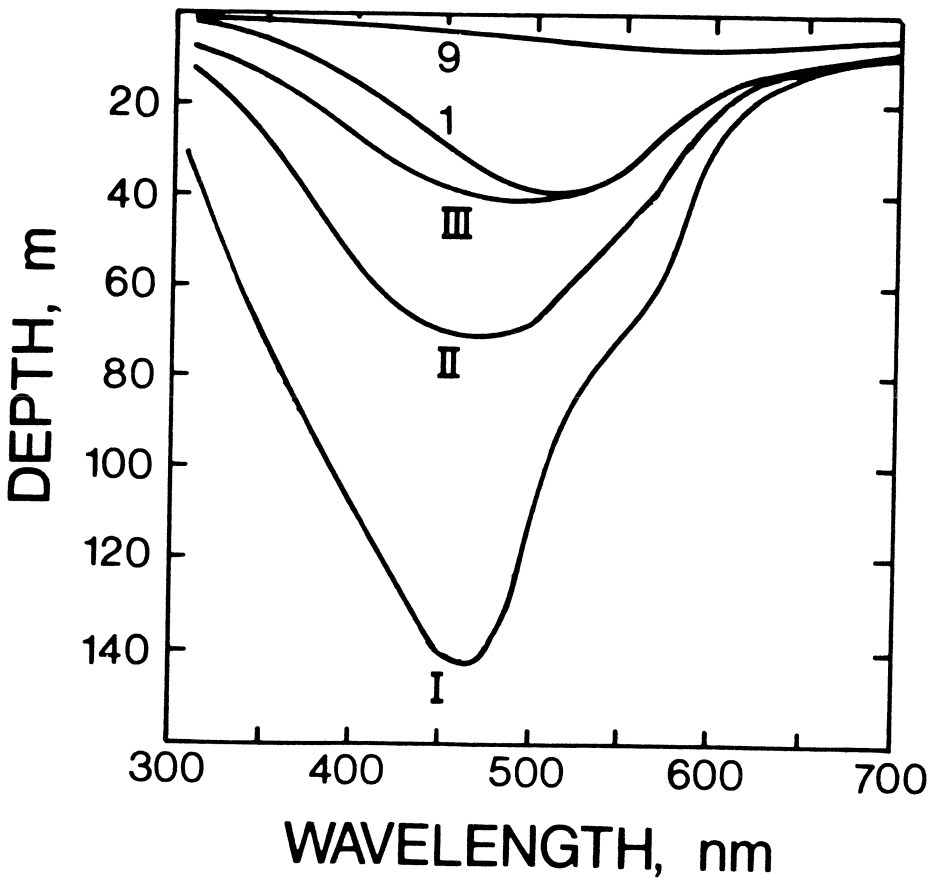

Figure 3. The spectral distribution of irradiance at depth is a function of the water type (see Fig. 1). Depicted here is the 1% irradiance level. Redrawn from Jerlov (1968).

The most likely explanation of the ecological success of crustose red algae at depth relates to their functional form (sensu Littler and Littler, 1980). Algal crusts tend to be relatively long-lived, slow-growing plants with low rates of metabolism (e.g., photosynthesis and respiration). In this regard, low respiration rates (see Falkowski, this volume) may be most important for survival at such great depths. It would be desirable to measure the in situ rates of metabolism for these crusts as well as their photosynthetic efficiencies under carefully controlled conditions.

The matter of seasonality of deep-water communities is unresolved. As indicated earlier, there is conflicting evidence (e.g., Dawes and van Breedveld, 1969; Cheney and Dyer, 1974) as to the seasonality of deep-water macroalgae in the Gulf of Mexico. Sears and Cooper (1978) and Sears and Wilce (1970) suggested that such communities in the northwest Atlantic have a high degree of seasonal stability. As described earlier, there is clear evidence for seasonality in diversity and reproduction of deep-water macroalgae on the east continental shelf of Florida. At present, there is no available information on seasonality for deep-water macroalgae in the Bahamas. Obtaining this basic information has been hindered by the lack, to date, of year-round submersible operations in the Bahamas.

CONCLUSION

Clearly, deep-water macroalgae offer both challenges and rewards to those who study them. The major restraint to their study is the high operating costs involved with using submersibles (Earle 1985 cites a range of $7,000 to $25,000 per day, including the cost of the support vessel). Perhaps the development of simpler, less expensive one-person submersibles (Earle, 1985) or unmanned, remotely operated vehicles (ROV's) will accelerate the exploration of deep-water benthic communities by marine botanists.

As access to deep-water macroalgae increases, knowledge on all aspects of the biology of these organisms will be enhanced. Continued systematic studies will lead to the description of new species and be important to an understanding of marine biogeography. Measurements on the primary productivity and the fate of this production in grazing and detrital food chains will document the trophic interactions of deep-water macroalgae with other members of their community. The possible existence of photoheterotrophy by deep-water macroalgae will be examined to determine if such a mechanism exists that extends their depth distribution. Research on calcification rates and nutrient dynamics will elucidate further the role of these algae in biogeochemical cycling and fluxes in the marine environment. Lastly, because of their unique environment, members of this flora will become extremely useful tools in fundamental studies

on the ecology and physiology of algae. By integrating floristic, ecological and physiological information, a comprehensive picture of the nature of these communities will emerge and their role in marine environments better understood.

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REFERENCES

Adey, W. H. and I. G. MacIntyre. 1973. Crustose coralline algae: A re-evaluation in the geological sciences. Bull. Geo. Soc. Am. 84:883-904.

Agegian, C. R. and I. A. Abbott. 1985. Deep water macroalgal communities: A comparison between Penguin Bank (Hawaii) and Johnston Atoll. Proceedings of the Fifth International Coral Reef Congress 5:47-50.

Benz, M. C., N. J. Eiseman and E. E. Gallaher. 1978. Seasonal occurrence and variation in standing crop of a drift algal community in the Indian River, Florida. Bot. Mar. 22:413-420.

Berthold, G. 1882. Uber die verteilung der algen in Golf von Neapel nebst einem verzeichnis derbishes daselbst beobachten arten. Mitt. Zool. Sta., Neapel 3:393-536.

Blair, S. M. and J. N. Norris. 1988. The deep-water species of the genus Halimeda Lamouroux (Halimedaceae, Chlorophyta) from San Salvador Island, Bahamas: Species composition, distribution and depth records. Coral Reefs 6:227-236.

Blinks, L. R. 1955. Photosynthesis and productivity of littoral marine algae. J. Mar. Res. 14:363-373.

Cheney, D. P. and J. P. Dyer. 1974. Deep water benthic algae of the Florida Middle Ground. Mar. Biol. 27:185-190.

David, T. W. E., G. H. Halligan and A. E. Finckh. 1904. Report on dredging at Funafuti, Section VII. In: The atoll of Funafuti, Report of the Coral Reef Committee, Royal Society, pp. 151-158.

David, C. J. and J. F. van Breedveld. 1969. Benthic marine algae. Memoirs Hourglass Cruises, Vol. I, Pt. II. Marine Research Laboratories, Department of Natural Resources, St. Petersburg, Florida, 47 pp.

DeWreede, R. and E. C. Jones. 1973. New records of Sargassum hawaiiensis (Sargassaceae, Phaeophyta). A deep water species. Phycologia 12:59-62.

Doty, M. S., W. J. Gilbert and I. A. Abbott. 1974. Hawaiian marine algae from seaward of the algal ridge. Phycologia 13:345-357.

Drew, E. A. 1969. Photosynthesis and growth of attached marine algae down to 130 meters in the Mediterranean. Proc. Int. Seaweed Symp. 6:151-159.

_____. 1983. Light. In: R. Earll and D. G. Erwin (eds.), Sublittoral ecology. Clarendon Press, Oxford.

Dring, M. J. 1981. Chromatic adaptation of photosynthesis in benthic marine algae: An examination of its ecological significance using a theoretical model. Limnol. Oceanogr. 26:271-284.

Earle, S. A. 1985. Equipment for conducting research in deep waters. In: M. M. Littler and D. S. Littler (eds.), Handbook of Phycological Methods; Ecological Field Methods: Macroalgae. Cambridge University Press, New York, pp. 233-249.

Eiseman, N. J. 1978. Observations on the marine algae occurring from 30-100 meter depths on the east coast of Florida. J. Phycol. 14(S):25.

_____. 1979. Marine algae of the east Florida continental shelf I. Some new record of Rhodophyta, including Scinaia incrassata sp. nov. (Nemaliales: Chaetangiaceae). Phycologia 18:355-361.

Eiseman, N. J. and S. M. Blair. 1982. New records and range extensions of deep-water algae from East Flower Garden Bank, Northwestern Gulf of Mexico. Contrib. Mar. Sci. 25:21-26.

Eiseman, N. J. and S. A. Earle. 1983. Johnson sea-linkia profunda, a new genus and species of deep-water Chlorophyta from the Bahama Islands. Phycologia 22:1-6.

Eiseman, N. J. and R. L. Moe. 1981. Maripelta atlantica sp. nov. (Rhodophyta, Rhodymeniales), a new deep-water alga from Florida. J. Phycol. 17:299-308.

Eiseman, N. J. and J. Norris. 1981. Dudresnaya patula sp. nov., an unusual deep-water alga from Florida. J. Phycol. 17:186-191.

Engelmann, T. W. 1883. Farbe und assimilation. Bot. Ztg. 41: 1-29.

Gaidukov, N. 1903. Weitere untersuchungen uber den einfluss farbegen lichtes auf die farbung der oscillarien. Ber Dtsch. Bot. Ges. 2:484-493.

Gilmartin, M. 1960. The ecological distribution of the deep water algae of Enewetok Atoll. Ecology 41:210-221.

Hall, M. O. and N. J. Eiseman. 1981. The seagrass epiphytes of the Indian River, Florida. I. Species list with descriptions and seasonal occurrence. Bot. Mar. 24:139-146.

Halldal, P. 1968. Photosynthetic capacities and photosynthetic action spectra of endozoic algae of the massive coral Favia. Biol. Bull. 134:411-424.

Hanisak, M. D. 1986. Discovery of a community dominated by the "rare", deep-water green alga, Anadyomene menziesii. Abstract of a paper presented at the joint meeting of the American Society of Limnology and Oceanography and the Phycological Society of America. Kingston, RI, June 23-26, 1986.

Hanisak, M. D. and S. M. Blair (in press). The deep-water macroalgal community of the East Florida continental shelf. Helgolander Meersunters.

Harvey, W. H. 1858. Nereis boreali americana. Pt. 3, Chlorospermae. Smithsonian Contributions to Knowledge 10:1-140.

Hillis-Colinvaux, L. 1980. Ecology and taxonomy of Halimeda: Primary producer of coral reefs. Adv. Mar. Biol. 17:1-327.

_____. 1985. Halimeda and other deep fore-reef algae at Enewetak Atoll. Proceedings of the Fifth International Coral Reef Congress 5:9-14.

_____. 1986a. Deep water populations of Halimeda in the economy of an atoll. Bull. Mar. Sci. 38:155-169.

_____. 1986b. Halimeda growth and diversity of the deep fore-reef of Enewetak Atoll. Coral Reefs 5:19-21.

Hooper, R. G. 1985. Depth limits of the benthic algae of Newfoundland and the Grand Banks. Br. Phyc. J. 20:186.

Hoskin, C. M., J. K. Reed and D. H. Mook. 1986. Production and off-bank transport of carbonate sediment, Black Rock, southwest Little Bahama Bank. Mar. Geol. 73:125-144.

Howe, M. A. and W. R. Taylor. 1931. Notes on new or little known marine algae from Brazil. Brittonia 1:7-33.

Humm, H. J. 1956. Rediscovery of Anadyomene menziesii, a deep-water green alga from the Gulf of Mexico. Bull. Mar. Sci. 6:346-8.

Humm, H. J. and S. E. Taylor. 1961. Marine Chlorophyta of the upper west coast of Florida. Bull. Mar. Sci. Gulf Carib. 11:321-380.

James, N. P. and R. N. Ginsburg. 1979. The seaward margin of Belize Barrier and Atoll Reefs. Blackwell Scientific, London, 201 pp.

Jensen, P. R., R. A. Gibson, M. M. Littler and D. S. Littler. 1985. Photosynthesis and calcification in four deep-water Halimeda species (Chlorophyceae, Caulerpales). Deep-Sea Res. 32:451-464.

Jerlov, N. G. 1968. Optical oceanography. Elsevier Publishing Company, New York. 194 pp.

Juett, L., C. J. Miller, S. J. Moore and E. S. Ford. 1976. Summer marine algae at Vero Beach, Florida. Fla. Sci. 39:76-80.

Kageyama, A., Y. Yokohama, S. Shimura and T. Ikawa. 1977. An efficient excitation energy transfer from a carotenoid, siphonaxanthin to chlorophyll a observed in a deep-water species of chlorophycean seaweed. Plant & Cell Physiol. 18:477-480.

Lang, J. C. 1974. Biological zonation at the base of a reef. Am. Sci. 62:272-281.

Larkum, A. W. D., E. A. Drew and R. N. Crosett. 1967. The vertical distribution of attached marine algae in Malta. J. Ecol. 55:361-371.

Littler, M. M. and D. S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: Field and laboratory tests of a functional form model. Am. Nat. 116:25-44.

Littler, M. M. and D. S. Littler. 1984. Models of tropical reef biogenesis: the contribution of algae. Progress in Phycological Research 3:323-364.

Littler, M. M., D. S. Littler, S. Blair and J. N. Norris. 1985. Deepest known plant life discovered on an uncharted seamount. Science 227:57-59.

_____. 1986. Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: Distribution, abundance and primary productivity. Deep-Sea Res. 33:881-892.

Luning, K. 1981. Photobiology of seaweeds: Ecophysiological aspects. Proc. Int. seaweed symp. 10:35-55.

Luning, K. and M. J. Dring. 1979. Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. Helgolander wiss. Meeresunters 32:403-424.

Mann, K. H. 1973. Seaweeds: Their productivity and strategy for growth. Science 182:975-981.

Oltmanns, F. 1892. Uber die kultur und lebensbedingungen dere meeresalgen. Jb. Wiss. Bot. 23:349-440.

Perez-Bermudez, P. M. Garcia-Caracosa, M. J. Cornejo and J. Segura. 1981. Water-depth effects on photosynthetic pigment content of the benthic algae Dictyota dichotoma and Udotea petiolat. Aquat. Bot. 11:373-377.

Phillips, R. C. 1961. Seasonal aspect of the marine algal flora of St. Lucie Inlet and adjacent Indian River, Florida. Quart. J. Fla. Acad. Sci. 24:135-147.

Ramus, J. 1981. The capture and transduction of light energy. In: C. S. Lobban and M. J. Wynne (eds.), The biology of seaweeds. Blackwell Scientific, Oxford, pp. 458-492.

_____. 1982. Englemann's theory: The compelling logic. In: L. Srivastava (ed.), Degradative processes in marine macrophytes. Walter de Gruyther, Berlin, pp. 29-46.

_____. 1983. A physiological test of the theory of complementary chromatic adaptation. II. Brown, green and red seaweeds. J. Phycol. 19:173-178.

Ramus, J., S. I. Beale, D. Mauzerall and K. L. Howard. 1976. Changes in photosynthetic pigment concentration in seaweeds as a function of water depth. Mar. Biol. 37:231-238.

Ryther, J. H. 1963. Geopgraphic variations in productivity. In: M. N. Hill (ed.), The sea. Wiley, New York, 2:347-380.

Schneider, C. W. 1974. North Carolina marine algae. III. A community of Ceramiales on a glass sponge from 60 meters. Bull. Mar. Sci. 24:1093-1101.

_____. 1975a. North Carolina marine algae. V. Additions to the flora of Onslow Bay, including the reassignment of Fauchea peltata Taylor to Weberella Schmitz. Br. Phycol. J. 10:129-138.

_____. 1975b. North Carolina marine algae. VI. Some Ceramiales (Rhodophyta), including a new species of Dipterosiphonia. J. Phycol. 11:391-39.

_____. 1976. Spatial and temporal distributions of benthic marine algae on the continental shelf of the Carolina. Bull. Mar. Sci. 26:133-151.

Schneider, C. W. and R. B. Searles. 1973. North Carolina marine algae. II. New records and observations of the benthic offshore flora. Phycologia 12:201-211.

_____. 1975. North Carolina marine algae. IV. Further contributions from the continental shelf, including two news species of Rhodophyta. Nova Hedwig. 26:83-96.

_____. 1976. North Carolina marine algae. VII. New species of Hypnea and Petroglassum (Rhodophyta, Gigartinales) and additional records of other Rhodophyta. Phycologia 15:51-60.

Searles, R. B. 1972. North Carolina marine algae. I. Three new species from the continental shelf. Phycologia 11:19-24.

Searles, R. B. and C. W. Schneider. 1978. A checklist and bibliography of North Carolina seaweeds. Bot. Mar. 21:99-108.

_____. 1980. Biogeographic affinities of the shallow and deep-water benthic marine algae of North Carolina. Bull. Mar. Sci. 30:732-736.

Sears, J. R. and R. A. Cooper. 1978. Descriptive ecology of offshore, deep-water, benthic algae in the temperate western North Atlantic Ocean. Mar. Biol. 44:309-314.

Sears, J. R. and R. T. Wilce. 1970. Reproduction and systematics of the marine alga Derbesia (Chlorophyceae) in New England. J. Phycol. 6:381-392.

Taylor, W. R. 1928. The marine algae of Florida with special reference to the Dry Tortugas. Publ. 379, Carnegie Institution, Washington, D.C., 219 pp.

Taylor, W. R. 1930. Algae collected by the Hassler, Albatross and Schmitt expeditions. I. Marine algae from Brazil. Am. J. Bot. 17:627-634.

_____. 1942. Caribbean marine algae of the Allan Hancock Expedition, 1939. Allan Hancock Atl. Exped. 2:1-193.

Wiseman, D. R. and C. W. Schneider. 1977. Investigations of the marine algae of South Carolina. I. New records of Rhodophyta. Rhodora 78:516-524.

Yokohama, Y. 1981. Distribution of the green light-absorbing pigments siphonoxanthin and siphonein in marine green algae. Bot. Mar. 24:637-640.

_____. 1983. A xanthophyll characteristic of deep-water green algae lacking siphonaxanthin. Bot. Mar. 26:45-48.

Yokohama, Y. and A. Kageyama. 1977. A carotenoid characteristic of chlorphycean seaweeds living in deep coastal waters. Bot. Mar. 20:433-436.

Yokohama, Y. and T. Misonou. 1980. Chlorophyll a:b ratios in marine benthic green algae. Jap. J. Phycol. 28:219-223.

NEW PRODUCTION AND VERTICAL FLUX OF PARTICULATE ORGANIC MATTER FROM EUPHOTIC ZONE WATERS OF THE NORTHEAST PACIFIC OCEAN

George A. Knauer
Center for Marine Science
University of Southern Mississippi
National Space Technology Laboratories
NSTL, MS 39529

ABSTRACT

It has been almost 100 years since Alexander Agassiz first proposed that meso- and bathy-pelagic organisms are nourished by a "rain" of organic detritus from overlying surface waters. However, only recently have we begun to understand this important transport process. This new understanding has been developed from data collected during the last decade, which indicate that it is the relatively rare large particles (> 100 um) that are primarily responsible for the majority of the downward vertical mass flux in the sea.

This paper presents selected results from the NSF funded Vertical Transport and Exchange Experiment (VERTEX) which uses free-floating sediment traps to study the role that large particles play in material transport. Specifically, we will examine relationships between primary production and sediment trap collected organic material sinking out of the euphotic zone in order to estimate the important oceanographic variable, new production.

In the classic sense, "new" production is defined by Dugdale and Goering (1967) as that fraction of the total primary production nitrogen requirement derived from newly available forms of nitrogen such as NO_3-N or N_2-N. In oceanic environments, the principal source of this new nitrogen is derived from upwelling and diffusion of nutrients from deeper waters below the euphotic zone. The balance and usually larger fraction of the total primary production nitrogen requirement is derived from nitrogen compounds that are recycled through euphotic zone food webs and is termed "regenerated" production. Here, ammonia and perhaps urea are generally considered to be the most important forms of regenerated nitrogen while other organic nitrogen compounds such as amino acids are less so (Eppley and Peterson, 1979).

Note that although new production results from inputs of new nitrogen from allochthonous sources such as upwelling, it can also be considered as equivalent to the downward vertical flux of

particulate organic nitrogen (PON) out of the euphotic zone. This construct has important implications for oceanographers since the sinking of organic matter links meso- and bathy-pelagic food webs to surface primary production and also represents an important pathway for the downward transport of many elements and compounds (Broecker and Peng, 1982; Angel, 1984; Fowler and Knauer, 1986). However, there has recently been a tendency by some oceanographers to consider new production in a more generic sense; that is, not only within the context of nitrogen flux but also, as it may relate to particulate flux in general (e.g., carbon). This is primarily the result of developing perspectives in the global geosciences (Waldrop, 1986) which continue to deal with such thorny problems as global carbon cycles and their relationship to long term changes in atmospheric CO_2 (e.g. Sarmiento and Toggweiler, 1984; Dymond and Lyle, 1985). The relationship between primary particle production and disposition (i.e., What is the ultimate fate of these particles?) is clearly relevant to these and other related problems (e.g., see Global Ocean Flux Study, proceedings of a workshop, 1984) and has become an area of active study; understandably, new production has also been incorporated into the current lexicon of important oceanographic parameters to be determined. Indeed, a primary goal of the important Global Ocean Flux Study (GOFS) is "To understand, in terms of mechanisms and rates, the relation between surface primary productivity and the flux of particles from the euphotic zone and its dependence upon factors such as upper mixed layer physics, trophic structure, and chemical transformations." (Brewer et al., 1986). Thus, the question becomes, does a fundamental relationship exist between oceanic primary production and the vertical export of various forms of organic matter? At this point, the answer to the question must be a qualified "maybe". For example, there have been a number of sediment trap studies which have demonstrated what appear to be obvious relationships between primary production and euphotic zone particle flux (e.g. Deuser and Ross, 1980; Knauer and Martin, 1981; Honjo, 1982; Lorenzen et al., 1983) and some of these include models. Suess (1980) and Betzer et al. (1984) have attempted to model the downward flux of trap-collected carbon while Lee and Cronin (1982) have modelled the downward flux of trap-collected nitrogen as a function of primary production. Martin et al. (1987) have simply modelled carbon flux as a function of depth without reference to primary production. Note that although these models provide a food beginning they do not provide information on the specific mechanisms involved which are needed to understand the vertical transport system. For example, Suess' model does not differentiate between new and regenerated primary production, whose ratio is known to vary between different marine ecosystems (Eppley and Peterson, 1979 and see Table 1). More importantly, none of these models account for depth-dependent changes in the rate of new large particle production which has been observed by a number of investigators (e.g., see Knauer and Martin, 1981;

Table 1.--Ocean primary production by water type and estimates of new production

	Area ($x10^6 km^2$)	Primary Production ($gCm^{-2}yr^{-1}$)	New Production (% total)
Oligotrophic waters of central parts of subtropical halistatic areas	148	25.6	6
Transitional waters between subtropical and subpolar zones; extremity of the area of equatorial divergences	83	51	13
Water of equatorial divergence and oceanic regions of subpolar zones	86	73	18
Inshore waters	39	124	30
Neritic waters	11	365	46
Totals	356		

Modified from Eppley and Peterson (1979).

Urrere and Knauer, 1981; Karl et. al., 1984; Knauer and Knauer, 1984 and refs. therein). That depth-dependent changes occur is illustrated by the VERTEX data shown in Figure 1. For example, in Figure 1a there are obvious increases in the downward flux of carbon indicated by the capital letters B and C. Note that while areas of increased carbon flux (capital letters B, C, E, F, H, I and K) often correspond to maxima, they were not chosen because at this depth there were increases in trap-collected AL, carbon, larvacean houses and fecal pellet fluxes. A specific example of depth-dependent particle flux increases is given for fecal pellets in Table 2. From the table, it is clear that the flux of pellets was high in surface waters (0-200 m) decreased through the 200-700 m range (depending on pellet size class) and then displayed a number of distinct subsurface maxima between 600-1100 m. Clearly, much work remains to be done before we can understand the relationship between surface produced particles and their subsequent fate in aphotic zone waters. For example, it should be noted that depending on station location (i.e., off shore vs. coastal) some of these subsurface increases may be the result of a combination of both in situ and lateral transport processes, although considerably more field work will be required before we can accurately determine the qualitative and quantitative impact of organic particles with reference to lateral transport.

Returning to the central topic, what do we know about the relationship between primary production and new production? Using N-15 techniques, Eppley and Peterson (1979) found that new production varied directly with total primary carbon production and ranged from 6% in oligotrophic waters to 46% in neritic waters (Table 1). However, the use of N-15 to determine new production is a particularly difficult procedure and accurate interpretation of results require the utmost experience. For this reason, other techniques have been sought. One of these procedures involves the placement of sediment traps directly below the euphotic zone to measure the downward vertical flux of nitrogen and to compare this value with total primary producer fixed nitrogen (i.e., N flux out/total N fixed = new production). It should be emphasized here, that with the N-15 technique the use of sediment traps for this purpose is not without difficulty (e.g., see Knauer et al., 1984a) and close attention to appropriate time scales is mandatory (Platt and Harrison, 1985).

While only a few studies have directly measured the ratio of particulate carbon or nitrogen flux to primary carbon and nitrogen production, fewer still have attempted to compare N-15 estimates coincidentally with sediment trap measurements. Knauer and Martin (1981) obtained a new production value of 31% studying primary production and nitrogen fluxes at a coastal California station, while Eppley, using N-15 procedures at the same station obtained a value of 50%. Welschmeyer (1986) attempted to compare new production as measured by NO_3 uptake vs. "near-surface"

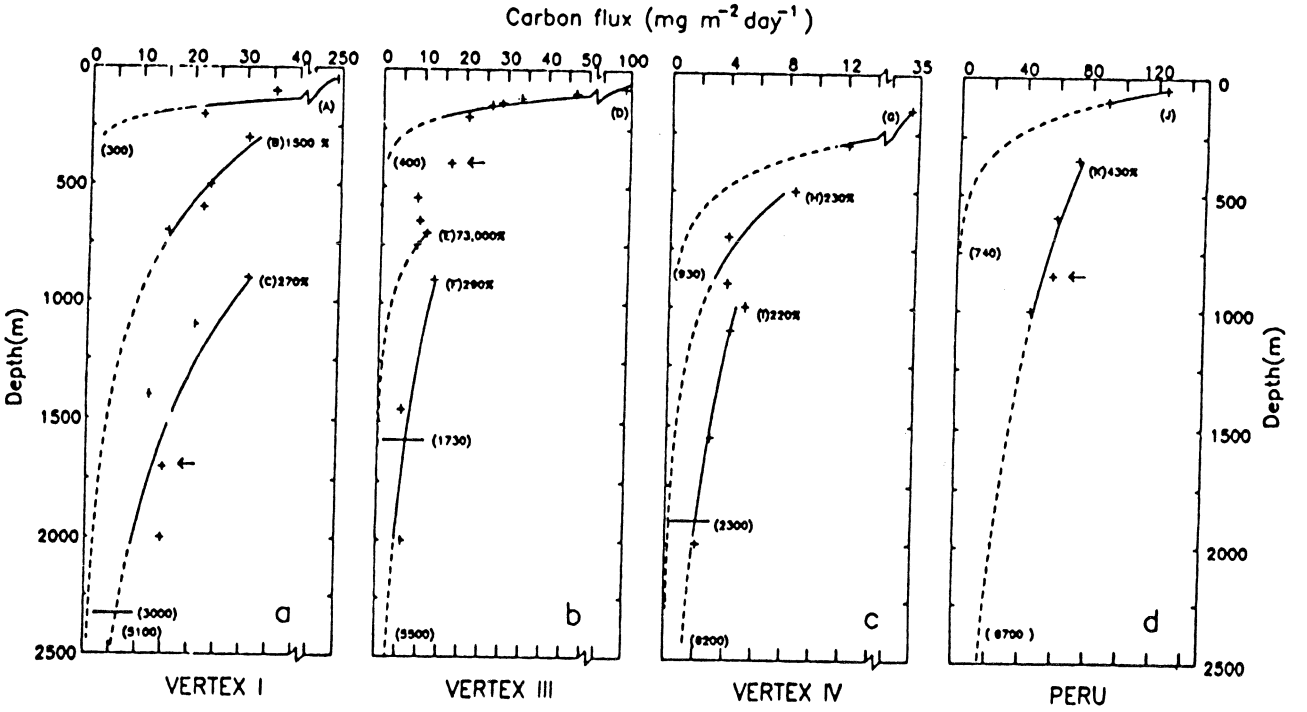

Figure 1. Organic carbon flux at four Pacific Ocean trap deployment sites. Solid lines represent a best fit using equation of the form $C - C_o e^{-dz}$ where C is the rate of particulate organic carbon loss, C_o is the carbon flux at zero model depth (designated by capital letters in the figure), z is depth and $d(m^{-1})$ is the "decay" or loss constant. Capital letters B, C, E, F, H, I, and K refer to aphotic areas of relative increases in organic carbon flux. Modified from Knauer et al. (1984b).

Table 2.--Fecal pellet fluxes (total and by size and morphological classes) measured during VERTEX I. All data are expressed as numbers of pellets $m^{-2}d^{-1}$.

Depth (m)	Elliptical pellets (mm) 0.05	0.10	0.15	Cylindrical pellets (mm) 0.05	0.10	0.15	Round pellets	Coiled pellets	Total pellet flux
50	406	348	0	4257	3135	348	1625	348	10469
100	23261	1567	58	2109	1567	813	3677	290	33343
200	46096	23241	116	1258	1974	697	7373	0	80755
300	26705	6192	619	1780	3057	406	3154	0	42883
500	21384	6289	813	1761	1761	252	2206	0	34465
600	31988	11088	658	2652	1819	135	948	0	49289
700	33653	24132	2283	2361	2574	677	2845	0	68757
900	48341	31543	2322	2109	1529	135	2632	0	88611
1100	42632	28679	812	1297	735	310	3213	0	77678
1400	19913	20281	464	774	813	542	948	0	43735
1700	14359	12907	987	406	735	232	697	0	30324
1950	6579	8399	522	464	851	232	213	0	17262

From Karl and Knauer, 1984.

nitrogen flux using sediment traps at a station in the Western Caribbean and concluded that at least in this case, NO_3 uptake was balanced by downward nitrogen flux (Fig. 2).

Perhaps the most extensive sediment trap derived estimates of new production have been compiled by the VERTEX group. Using the MULTITRAP system described in Knauer et al. (1979 and see Fig. 3) together with clean techniques (Fitzwater et al., 1982) and in situ incubations to measure primary production, nine separate estimates of N flux (new production) have been obtained from both coastal and oligotrophic North Pacific waters (Table 3). It is readily apparent, that as has been found by other investigators (e.g., see Table 1), low values of new production (5-16%) were found for oligotrophic waters while significantly higher values (17-43%) were found for coastal waters. Thus, assuming both N-15 and sediment trap derived estimates are reasonably accurate, we can conclude not unexpectedly, that nutrient recycling is considerably more efficient in oligotrophic surface waters. The specific mechanisms for this are not as yet completely understood but are most probably related to differences in trophic structure between neritic and oceanic planktonic communities.

Although there appears to be an obvious difference in new production between coastal and oceanic systems, can we say that a significant relationship between the downward vertical flux of particulate organic nitrogen and primary productivity exists? The plot of these two variables taken from the nine VERTEX stations is shown in Figure 4 and the relationship is significant ($P<0.01$). Using the linear regression model given in the Figure 4 legend and assuming a C:N ratio of 6.6, new production increases from 13-25% over the primary productivity range of 245-1140 mg C m^{-2} d^{-1}. Note however, that confidence (dashed lines, Fig. 4) in predicting new production using our model is quite poor. In reality it must be stressed that statistical significance does not always imply an actual relationship. This can be illustrated for our oligotrophic sites with depths >100 m (Fig. 4, solid squares). Here, new production as measured by PON flux was essentially constant ($X = 7.23 + 1.59$ mg N m^{-2} d^{-1}). While such observations are bothersome in the sense that we had, a priori, expected to find more strength in the relationship, it is now apparent that a greater sampling effort will be needed to resolve the issue.

Thus, in terms of new production, we must conclude at this point in time that relative to nitrogen, our data are still too limited to provide an accurate statistical estimator of new production using sediment trap methodology. This is especially true given our lack of understanding with respect to both spatial and temporal variability, although Martin et al. (1987) would argue that at least for open ocean areas, spatial and temporal variations with respect to carbon flux are minimal. This is

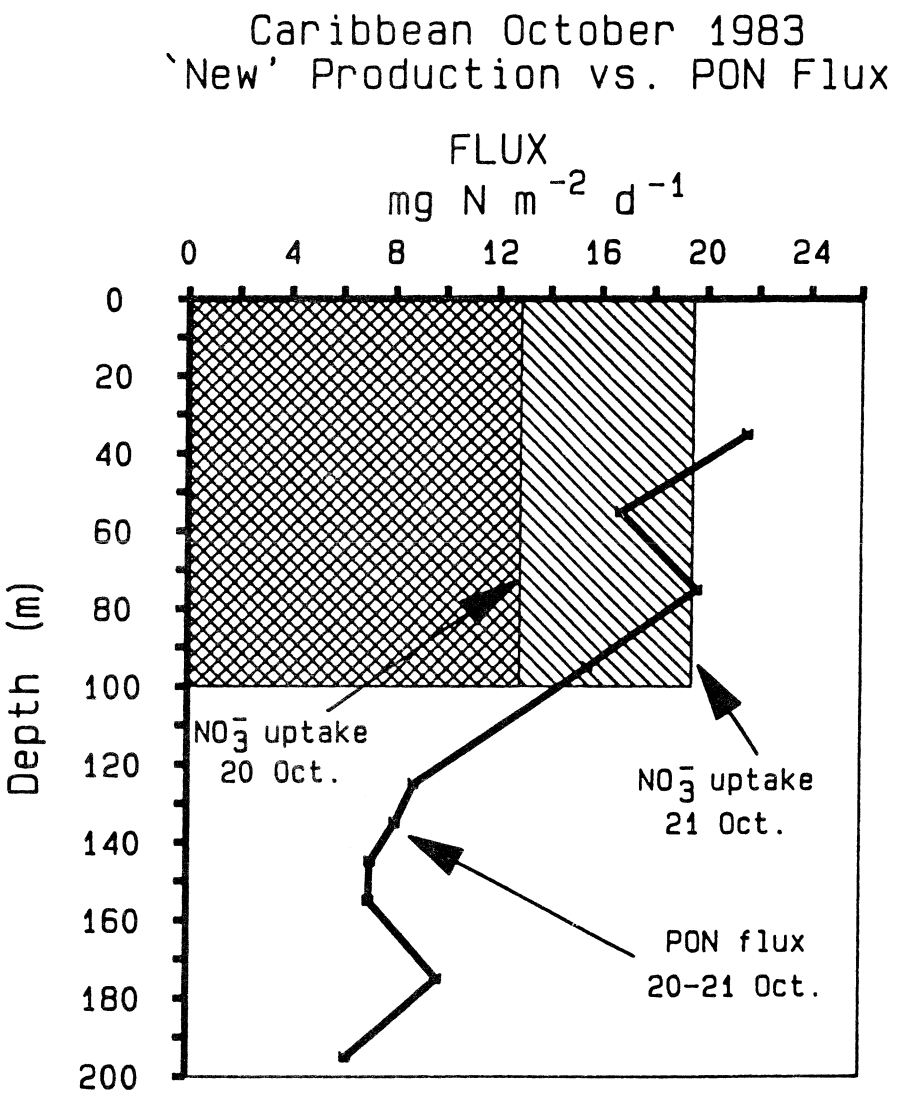

Figure 2. Comparison of new production (NO_3^- uptake) and downward PON flux in the Western Caribbean. N-15 determinations of nitrate uptake were made by J.J. McCarthy. Data represent the integrated nitrate uptake down to 100 m. Areal rates were 12.5 mg N m^{-2} d^{-1} on 20 Oct. and 19.3 mg n m^{-2} d^{-1} on 21 Oct. Sediment trap fluxes were based on a 2-day deployment from 20-21 Oct. New production and PON flux were approximately balanced at the base of the 100 m layer. From Welschmeyer (1986).

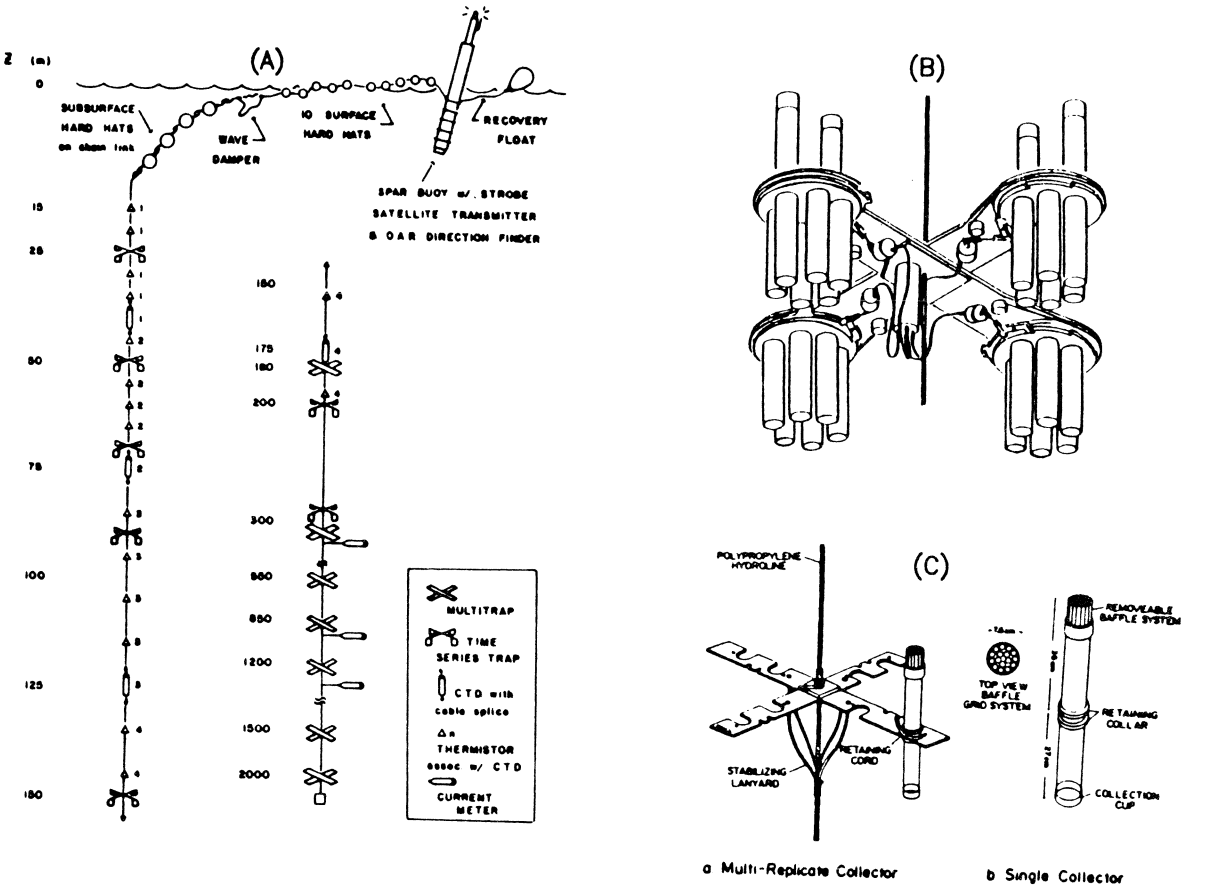

Figure 3.--Free-floating sediment tap array (MULTITRAPS) used in the upper water column during VERTEX (A). Array includes OAR transmitter/stobe, ARGOS satellite system for location/recovery, in situ CTD's, and thermistor chains (see box inset). Array contains both timeseries MULTITRAPS containing 8 individual collectors (B), as well as standard MULTITRAPS containing up to 14 individual collectors (C).

Table 3.--Estimates of new production (=Nitrogen flux out of the euphotic zone) determined from integrated primary production and sediment trap data collected from coastal, mesotrophic, and oligotrophic stations in the Pacific Ocean. From Knauer et al., 1984b.

Location	Depth(m) of euphotic zone	Primary production (mg C $m^{-2}d^{-1}$)	Reference trap depth(m)	Flux(mg C $m^{-2}d^{-1}$)		New production N flux / N fixed * 100
				Carbon	Nitrogen	
			— Coastal —			
Central California December 1978	50	690	65	152	26	22
Central California VERTEX 1 Sept.'80	50	520	50	212	40	43
Central California VERTEX 5c June'84	50	1140	50	335	52	26
Peru El Niño May'83	50	730	50	125	22	17
			— Mesotrophic —			
Mexico VERTEX 2 Nov.'81	100	760	120	38	7	5
Mexico VERTEX 3 Nov.'82	100	470	100	47	8.5	10
			— Oligotrophic —			
Hawaii VERTEX 4 Aug.'83	150	400	150	29	5	7
N.E. Pacific VERTEX 5a June'84	125	245	150	41	6.2	14
N.E. Pacific VERTEX 5b June'84	125	325	130	70	9	16

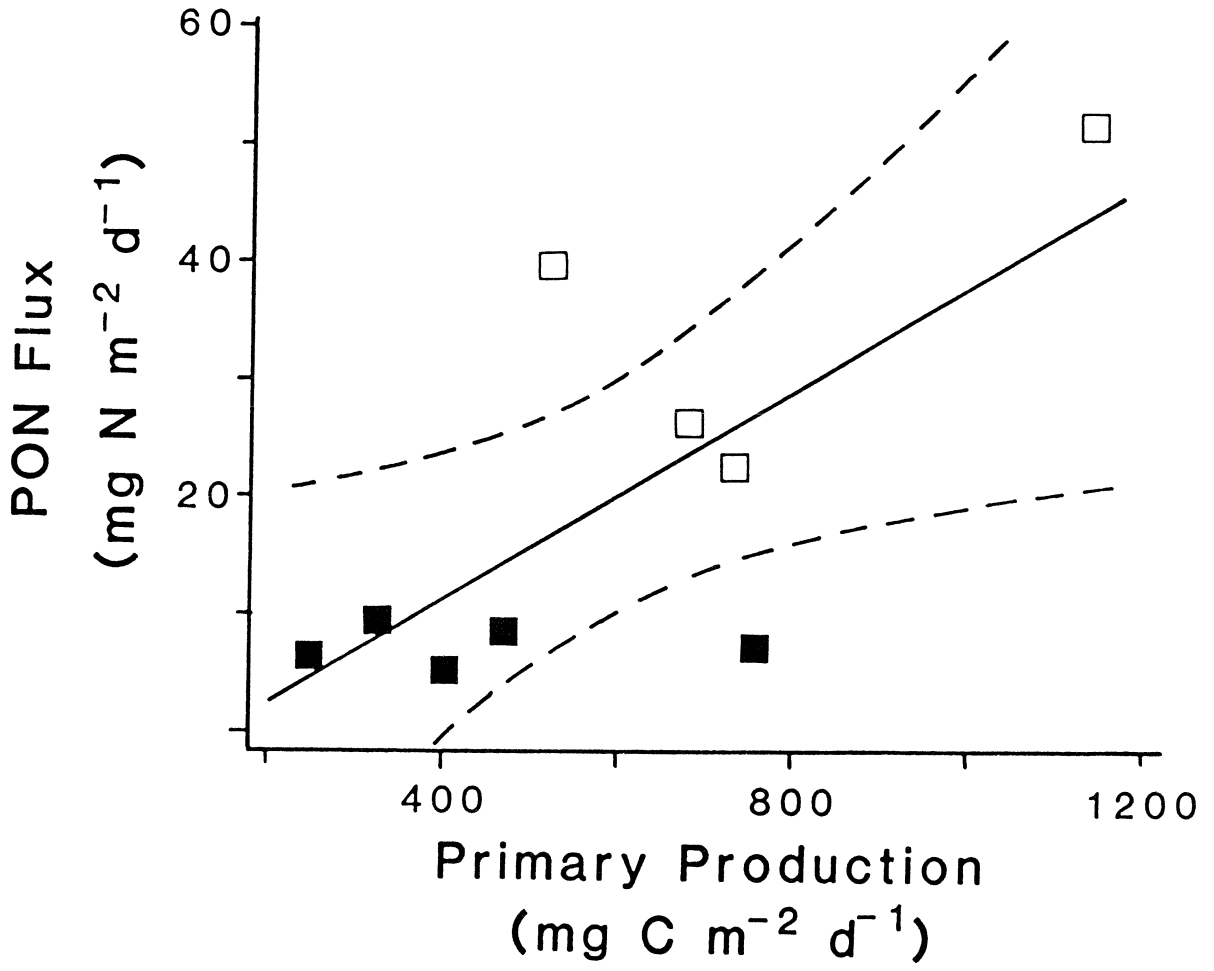

Figure 4.--Relationship between primary production and vertical flux of particulate organic nitrogen (PON) measured in traps located at the base of the euphotic zone for nine VERTEX stations. Regression model: PON = 0.0439 PP - 6.17, r^2 = 0.52, F = 7.57, P < 0.01. Solid squares represent stations with deep euphotic zones ($\geq$ 100 m, Table 2) and open squares represent stations with euphotic zones of 50 m. Broken lines are the 95% confidence intervals for the regression. From Pace et al., 1987.

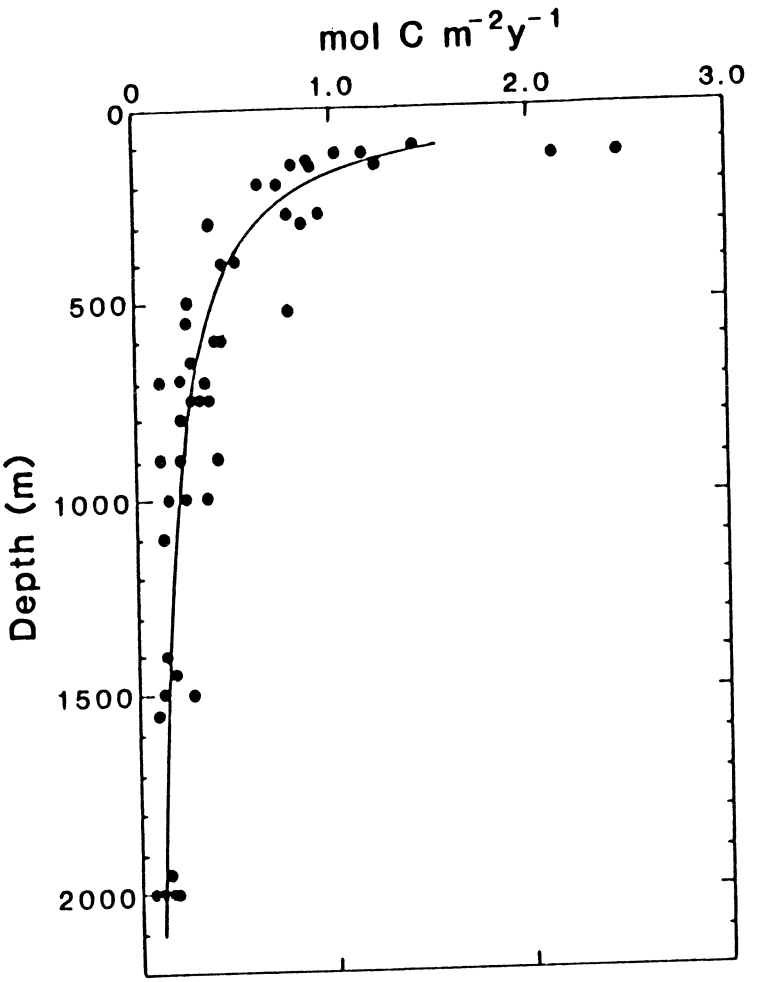

Figure 5.--Open Ocean Composite (OOC) fluxes for C using the means of replicates at various depths from 6 VERTEX stations in the Pacific Ocean; $F = 1.53(z/100)^{-0.858}$; $r^2 = 0.81$; $n = 48$. From Martin et al., 1987.

illustrated in Figure 5. Here, the mean carbon flux vs. depth from six separate VERTEX stations have been combined to produce an Open Ocean Composite (OOC). The data were fitted with a power function (see legend, Fig. 5) and depending on the required resolution (i.e., the discontinuities shown in Fig. 1 are obscured/ignored by this treatment) spatial and temporal variations do indeed appear minimal. Nonetheless, with specific reference to sediment trap-derived new production estimates, more data are needed; the VERTEX group is now attempting to rectify this problem through a new seasonal study at an oceanic station in the N.E. Pacific Ocean, designed to measure the variability of primary productivity and PON flux over an annual cycle.

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REFERENCES

Angel, M. V. 1984. Detrital organic fluxes through pelagic ecosystems. In: M. J. R. Fasham (Ed.), Flows of energy and materials in marine ecosystems. Plenum Press, New York, pp. 475-516.

Betzer, P. R., W. J. Showers, E. A. Laws, C. D. Winn, G. R. Ditullio and P. M. Kroopnick. 1984. Primary productivity and particle fluxes on a transect of the equator at 153°W in the Pacific Ocean. Deep Sea Res. 31:1-11.

Brewer, P. G., K. W. Bruland, R. W. Eppley and J. J. McCarthy. 1986. The global ocean flux study (GOFS): Studies of the U. S. GOFS program. Eos 67:827-832.

Broecker, W. S. and T. -H. Peng. 1982. Tracers in the sea. Lamont-Doherty Geological Observatory, Palisades, NY, pp. 690.

Deuser, W. G. and E. H. Ross. 1980. Seasonal changes in the flux of organic carbon to the deep Sargasso Sea. Nature 283:364-365.

Dugdale, R. C. and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. and Oceanog. 12:196-206.

Dymond, J. and K. Lyle. 1985. Flux comparisons between sediments and sediment traps in the eastern tropical Pacific: Implications of atmospheric CO_2 variations during the pleistocene. Limnol. and Oceanog. 30:699-712.

Eppley, R. W. and B. J. Perterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282:667-680.

Fitzwater, S. E., G. A. Knauer and J. H. Martin. 1982. Metal contamination and its effects on primary production measurement. Limnol. Oceanog. 27:544-551.

Fowler, S. W. and G. A. Knauer. 1986. Role of large particles in the transport of elements and organic compounds through the oceanic water column. Prog. Oceanogr. 16:147-194.

Global Ocean flux study: Proceedings of a workshop. 1984. National Academy Press, Washington, D.C.

Honjo, S. 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. Science 218:883-884.

Karl, D. M. and G. A. Knauer. 1984. Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: Evidence for multiple zones of biological activity. Deep-Sea Res. 31:221-243.

Karl, D. M., G. A. Knauer, J. H. Martin and B. B. Ward. 1984. Bacterial chemolithotrophy in association with sinking particles. Nature 309:54-56.

Knauer, G. A., J. H. Martin and K. W. Bruland. 1979. Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the Northeast Pacific. Deep-Sea Res. 26: 97-108.

Knauer, G. A. and J. H. Martin. 1981. Primary production and carbon-nitrogen fluxes in the upper 1,500 m of the Northwest Pacific. Limnol. Oceanog. 26:181-186.

Knauer, G. A., D. M. Karl, J. H. Martin and C. N. Hunter. 1984a. In situ effects of selected preservatives on total carbon nitrogen and metals collected in sediment traps. Mar. Res. 42:445-462.

Knauer, G. A., J. H. Martin and D. M. Karl. 1984b. The flux of particulate organic matter out of the euphotic zone. Global ocean flux study: Proceedings of a workshop. National Academy Press, Washington, D.C.

Lee, C. and C. Cronin. 1982. The Vertical flux of particulate organic nitrogen in the sea: Decomposition of amino acids in the Peru upwelling area and the equatorial Atlantic. Mar. Res. 40:227-251.

Lorenzen, C. J., N. A. Welschmeyer and A. E. Copping. 1983. Particulate organic carbon flux in the subartic Pacific. Deep-Sea Res. 30:639-643.

Martin, J. H. and G. A. Knauer, D. M. Karl and W. W. Broenkow. 1987. Carbon cycling in the Northeast Pacific. Deep-Sea Res. In press.

Pace, M. L., G. A. Knauer, D. M. Karl and J. H. Martin. 1987. Vertical flux of particulate organic matter in the Northeast Pacific: Relationship with depth, primary production, and new production. Nature, In press.

Platt, T. and W. G. Harrison. 1985. Biogenic fluxes of carbon and oxygen in the ocean. Nature 318:55-58.

Sarmiento, J. R. and J. R. Toggweiler. 1984. A new model for the role of the oceanic in determining atmospheric pCO_2. Nature 308:621.

Suess, E. 1980. Particulate organic carbon flux in the oceans--surface productivity and oxygen utilization. Nature 288:260-263.

Urrere, M. A. and G. A. Knauer. 1981. Zooplankton fecal pellet fluxes and vertical transport of particulate organic material in the pelagic environment. Plank. Res. 3:369-387.

Waldrop, M. M. 1986. Washington embraces global earth sciences. Science 233:1040-1042.

Welschmeyer, N. D. 1986. Near-surface particulate flux: An in situ tracer of trophic interaction in the upper ocean processes. Global ocean flux workshop #3, March 1986. Horn Point Laboratories, MD.

THE NANOALGAL PEAK IN THE DIM OCEANIC PYCNOCLINE: IS PHOTOSYNTHESIS AUGMENTED BY MICROPARTICULATES AND THEIR BACTERIAL CONSORTIA?

John McN. Sieburth
Graduate School of Oceanography
University of Rhode Island
Bay Campus, South Ferry Road
Narragansett, RI, USA 02882-1197

ABSTRACT

Studies of the last decade have shown the nature, numbers and importance of the phototrophic picoplankton and nanoplankton, revised our thoughts about low oceanic primary productivity and have indicated that the growth of phytoplankters in natural populations may not be limited by environmental concentrations of nutrients. Natural populations of oceanic nanoalgae are dominated by members of the Prymnesiophyceae, Prasinophyceae, and Chrysophyceae. Many of these species like those in the genus Chrysochromulina can be both thigmotactic [seeking out and attaching to surfaces] and bacterivorous [obtaining part of their nutrition from the ingestion and digestion of bacteria]. Although often less numerous than the cyanobacteria, nanoalgae have a larger biomass.

The nanoalgal peak occurs in the lower boundary of the upper ocean, which is the dimly lit depths of the seasonal pycnocline that is impenetrable for microparticulates 40-80 um in size that aggregate, accumulate, and apparently ferment to produce the well known peak of methane in this "false benthos." Consortia of both aerobic and anaerobic bacteria in these redox active microparticulates may provide nutrients via newly recognized aspects of the methane, sulfur, phosphorous, and nitrogen cycles. Much of the microparticulate material appears to be fermenting fecal debris. Limiting photosynthetically active radiation (PAR) may be supplemented by photosynthetically active bacterial luminescence (PABLum) provided by the luminescent enteric bacteria, whose emission spectra overlaps much of the absorption spectrum of natural assemblages of phytoplankton. The thigmotactic behavior of the nanoalgae, in common with that of flagellated bacteria, chloroplast-lacking nanoflagellates, and the ciliates, would allow them to attach directly to particulates and allow them to be utilized by the metazooplankton grazers directly via a "thigmotactic shunt," thereby avoiding the energetically less efficient sequence of grazing steps hypothesized to occur in the "microbial loop." The apparent synergism and syntrophy between nanoalgae and bacteria, in their microhabitat of microparticulates, may explain in part the unexpected productivity of nanoalgae in the deep chlorophyll maximum of the seasonal pycnocline where solar radiation is apparently below the compensation point.

INTRODUCTION

In the preceding paper, Paul Falkowski discussed the biophysical and molecular basis for the adaptation of algae to low light. The bottom line was a theoretical calculation of just how long an alga could survive at depth. To me, as a marine microbial ecologist, a more pertinent question is why do oceanic nanoalgae that peak in the dim waters of the oceanic summer pycnocline at depths of 80 to 125 meters (Davis et. al., 1985; Murphy and Haugen, 1985) to form the deep chlorophyll maximum (Shulenberger and Reid, 1981) accumulate, persist, and function there? These small eucaryotes peak well below the larger microplankton and the smaller chroococcoid cyanobacteria. The ability of the nanoalgae to better utilize the dim blue-violet light occurring at the bottom of the euphotic zone has been reported by Glover et al. (1986, 1987). But are there other factors that are important for their prevalence in the pycnocline? The properties of thigmotaxis (stereotaxis) and bacterivory (mixotrophy) in many of the dominant nanoalgae, as well as the presence of bacterial consorts that provide nutrients and possibly photons, may also be factors in the sustenance of nanoalgae at the oceanic pycnocline where light and nutrients are potentially limiting.

In order to acquaint the audience with this habitat and its microorganisms during my paper at Hilo, I first illustrated the types of cells in the microbial plankton with a color micrograph of an image observed with epifluorescence microscopy. I then illustrated the vertical distribution of cyanobacteria and nanoalgae through the mixing layer and into the pycnocline. The taxonomic affinities of the "picoalgae" and the nanoalgae that slip through 3 um Nuclepore filters in unpreserved samples were then illustrated with black and white transmission electron micrographs that showed their diagnostic ultrastructure and one of the thigmotactic organelles, the haptonema. The effect of the absence of bacteria on the loss of motility and abnormal aggregation of nanoalgae in axenic culture was then shown in a series of color slides. The important processes of thigmotaxis and bacterivory in an important genus of nanoalgae, the Chrysochromulina, was then shown in a drawing from Parke et al. (1955). The attenuation of light with depth as illustrated by Goldman (1986) indicates to me that the nanoalgae peak below the threshold of usable light. How can this be?

The pycnocline apparently offers a habitat enhanced by aggregated particles and bacteria similar to that envisioned by Goldman (1984). In contrast to large particle transport through the water column (Fowler and Knauer, 1986; Knauer this symposium), the decay of suspended microparticles by fermentative and oxidative bacteria in situ may be providing much of the nutrients required by the associated nanoalgae. Oxygen-depleted particles are potential sites for nitrogen-fixation by

heterotrophic bacteria in nitrogen-depleted oxygenated seawaters (Paerl and Prufert, 1987; Paerl and Carlton, 1988). Similarly, some 30-45% of bound phosphorous is released by bacterial reduction as the highly volatile and insoluble gas phosphine (Devai et al., 1988), which might be available to phosphorous-depleted micro-organisms. Methane cycle bacteria are present in successful xenic cultures that are refractory to axenic culture. These bacterial consortia are presumably from fermenting fecal fragments that not only provide bacterial prey for bacterivorous species of nanoalgae but may glow from the bacterial luminescence of their enteric bacteria. The emission spectra of luminescent bacteria, which overlaps the action spectra of the algal chlorophylls, was then illustrated. This information was synthesized into an hypothesis, in which the thigmotactic and bacterivorous behavior of the nanoalgae, coupled with the degradative, nutrient-enhancing and luminescent properties of their associated bacteria could be crucial factors in the sustenance of nanoalgae in the dim waters of the seasonal pycnocline/deep chlorophyll maximum.

Populations and Distribution of the Smaller Plankton

The plankton that dominates oceanic waters and coastal waters between diatom blooms are the cells smaller than 20 um in diameter. These cells pass through even the finest mesh plankton nets. Hans Lohmann, who called these small cells the nannoplankton (sic), obtained them by centrifuging water samples (Lohmann, 1911). The smallest plankton includes bacteria, protozoa, and algae. Since then, every few years someone rediscovers that biomass and activity in the water column are associated with the smaller particles, but its significance is only now being recognized by the phytoplankton community (Herbland and Bouteleiller, 1981; Stockner and Antia, 1986; Platt and Li, 1986). One reason is that the rapid enumeration of the autofluorescing photobacteria and the protists in the smaller size fractions [picoplankton, 0.2-2.0 um; nanoplankton, 2.0-20 um in diameter, Sieburth et al., 1978] awaited the development of Nuclepore filters with exact porosities and epifluorescene microscopes. The nuclear stain DAPI, non-specific cell wall stains, and the autofluorescence of thylakoids and chloroplasts (see references in Davis et al., 1985) permits one to differentiate between photosynthetic and non-photosynthetic cells. The occurrence of photosynthetic cyanobacteria and nanoalgae together with non-photosynthetic bacteria that are both free and aggregated into flocs was shown in my talk with a deleted figure. This color micrograph was to portray the cells that are central to my talk. It represents the microbiota that exist in several microliters of seawater. The concept of the microlitersphere where all the trophic modes essential for the microbial fabric of life in the sea are contained in just a few microliters of seawater is discussed by Sieburth and Davis (1982)

and Sieburth (1986). The deleted micrograph illustrated the nanoalgae which, in addition to being phototrophic, can be mixotrophic and eat bacteria for nutrients (Parke et al., 1955; Estep et al., 1986). Also shown were the cyanobacteria that the nanoalgae can outcompete at depth, as well as aggregated non-photosynthetic bacteria that can be active redox centers containing both fermentative and oxidative species.

The vertical distribution of cyanobacteria belonging to the picoplankton (0.2-2.0 um) and the eucaryotes that are usually larger occurring mainly in the nanoplankton (2-20 um) is shown in Figure 1. There is usually a 20 meter or larger gap between their peaks, with the nanoalgae occurring at greater depth. Since some investigators feel that fixation with formaldehyde or glutaraldehyde destroys some of these forms (Murphy and Haugen, 1985; Glover et al., 1986), they work with unpreserved samples. The disadvantages of this are that the living preparations can be affected by predation from the time of sampling until the completion of analysis, the thigmotactic forms can attach to the walls of the container, and that living cells can squeeze through filter pores that would otherwise exclude them in preserved samples. By not having preserved cells, these investigators can not examine their ultrastructure by transmission electron microscopy in thin section and in whole mounts. Such microscopy is necessary to determine the taxonomy of both picoalgae (Johnson and Sieburth, 1982) and nanoalgae (Estep et al., 1984). Without knowing the important species in the Prymnesiophyceae, Prasinophyceae, and Chrysophyceae in natural populations in the open ocean, the potential importance of their thigmotaxis and bacterivory central to this conceptual paper would not have been recognized.

Dominant Taxa of Picoalgae and Nanoalgae

The picoplankton size fraction present in preserved seawater is filtered through 3 um Nuclepore filters, concentrated by ultracentrifugation, embedded in agar, epoxy resin, thin sectioned, and put on TEM grids in order to observe the ultrastructure of the cells by transmission electron microscopy (Johnson and Sieburth, 1982). Most of the cells in such preparations are non-photosynthetic bacteria, but the thylakoids and chloroplasts of the phototrophs are easily discernable. The nature and diversity of the oxygenic photobacteria (Johnson and Sieburth, 1979) and eucaryotes (Johnson and Sieburth, 1982) in this smaller size fraction are shown in Figure 2. The three oxygenic photobacteria so far encountered in the open sea are the small and numerous cells of Synechococcus (the Type I cell of Johnson and Sieburth, 1979), and the larger but fewer cells of Synechocystis that require warm waters (Watson et al., in press) and our Type II cell that has recently been identified as a new prochloron-like species (Chisholm et al., 1988). The

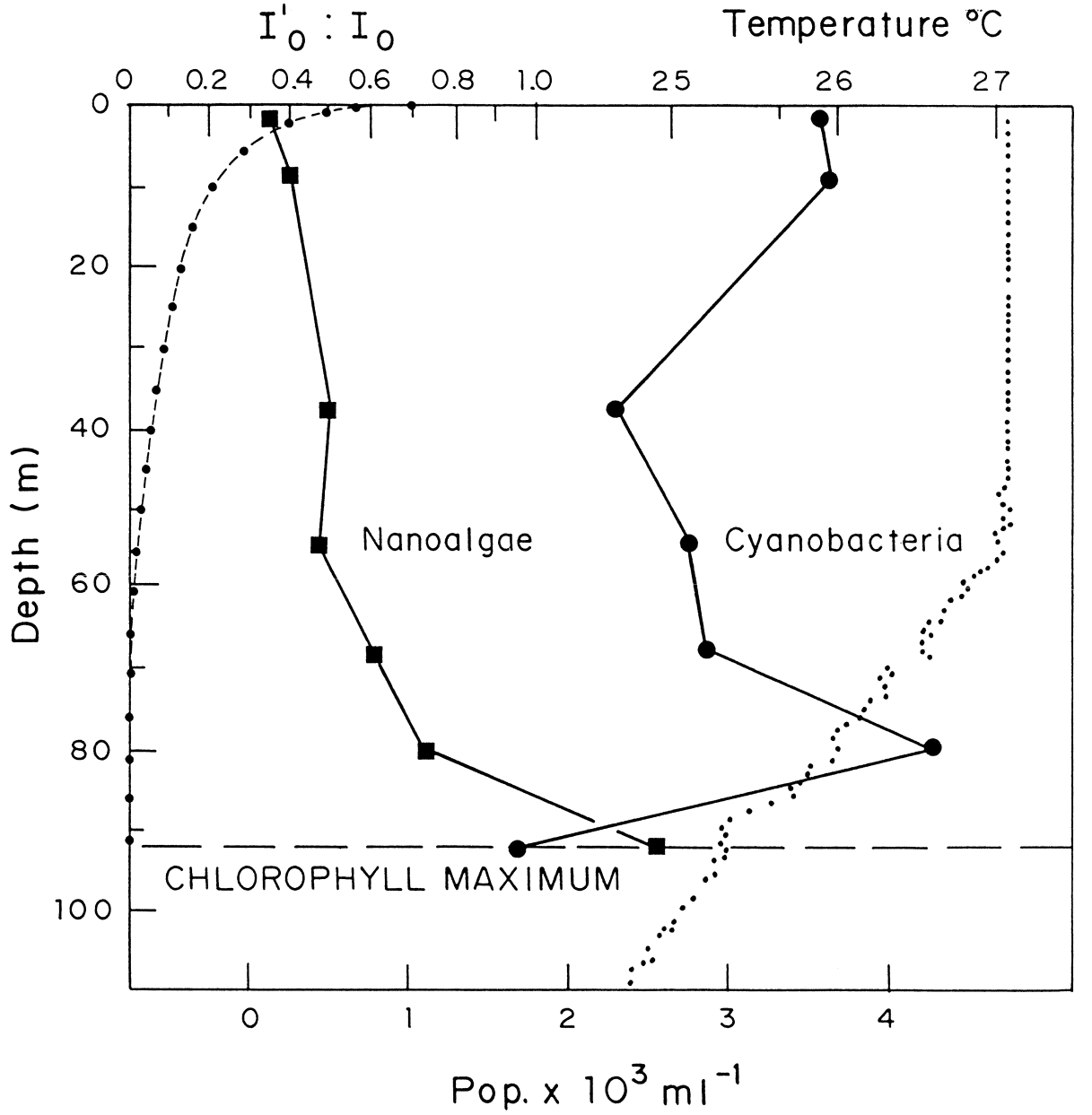

Figure 1. The vertical distribution of picoalgae and nanoalgae in oceanic waters of the Sargasso Sea illustrating how the larger nanoalgae dominate in the dim waters of the summer pycnocline (adapted from Glover et al., 1987) compared to light attenuation in the Sargasso Sea (from Goldman, 1986).

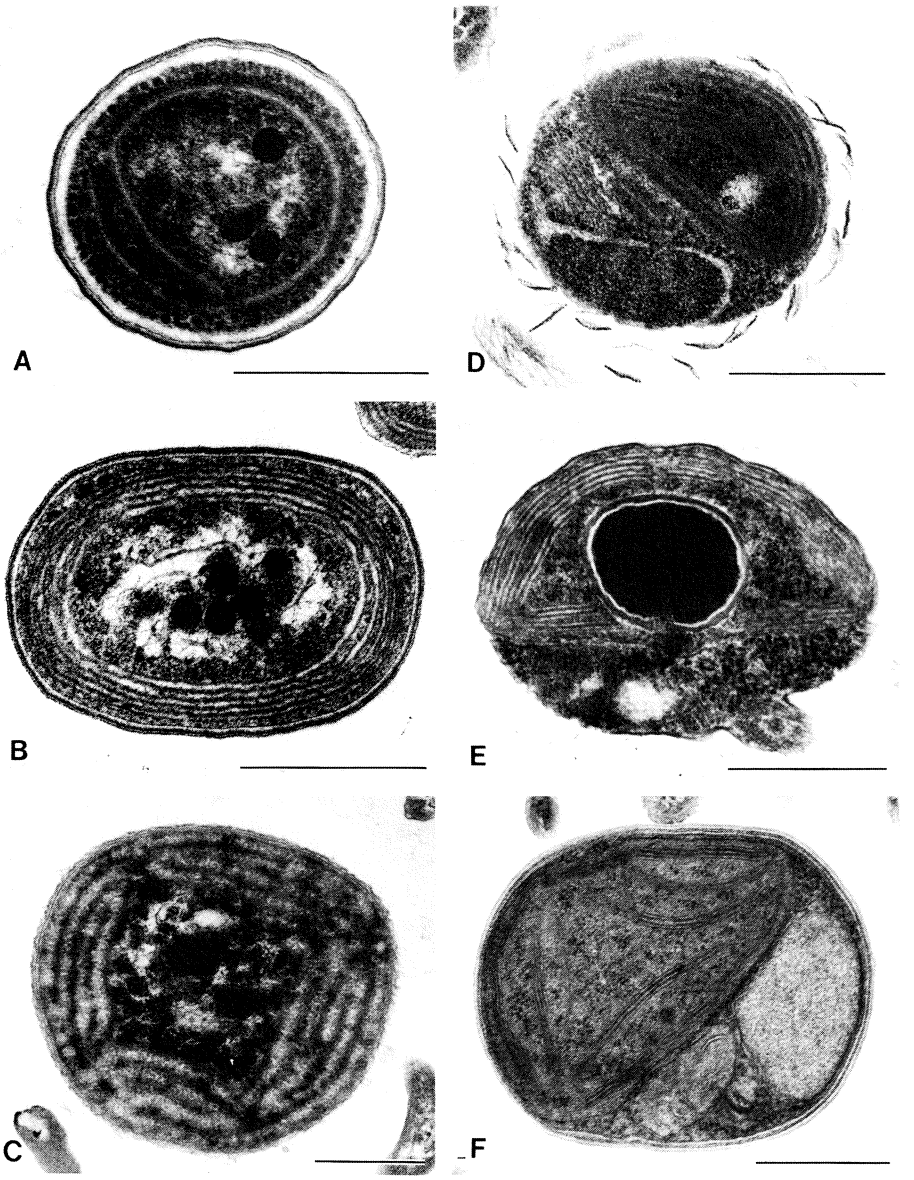

Figure 2. Dominant forms of oxygenic photobacteria and eucaryotes present in natural assemblages of oceanic picoplankton. The oxygenic photobacteria include: A) the dominant form of cyanobacterium in the genus Synechococcus; B) a deeper occurring photobacterium recently identified as a new prochlorophyte; and C) a Synechocystis-like cell which is larger but rarer than Synococcus. The oceanic picoalgae include: D) a minute species of Mamiella, an aflagellated prasinophyte; E) the non-scaled prasinophyte Micromonas pusilla; and F) a variety of Chlorella-like forms. All marker bars = 0.5 um.

eucaryotic algae in the picoplankton observed by Johnson and Sieburth (1982), include the aflagellated but non-scaled prasinophyte, Micromonas pusilla, another atypical prasinophyte lacking a flagellum but containing scales typical of the genus Mamiella, which is probably the smallest known eucaryotic cell having a diameter of just 0.5 um, and the ubiquitous species of Chlorella found in both coastal and open ocean waters. Not illustrated is the inshore chrysophyte recently described as Aureococcus anophagefferens that caused a brown tide in Narragansett Bay during 1985 in which the cessation of feeding resulted in catastrophic shellfish losses (Sieburth, et al., 1988).

The nanoalgae on the other hand include Chrysophytes like Chrysamoeba that have pseudopods and are thigmotactic and Prymnesiophytes (Haptophytes) like Chrysochromulina that have an organelle, the haptonema inserted between their pair of flagella, that is used for attachment (Parke et al., 1955, 1956). These larger cells often have characteristic scales, spines, and other structures that are very helpful in taxonomy. In samples of natural populations, these cells are usually examined in whole mounts. The nanoprotists in natural populations occur in approximately equal numbers of cells possessing and lacking chloroplasts (Davis et al., 1985). Their examination by just transmission electron microscopy (Thomsen, 1986) or scanning electron microscopy (Booth, 1982) fails to distinguish between cells containing and lacking chloroplasts. In order to differentiate nanoprotists in whole mounts that either possess or lack chloroplasts, Davis and Sieburth (1984) developed a sequential epifluorescence and electron microscopic (SEEM) procedure that plots the location of chloroplast containing cells on formvar coated TEM grids with epifluorescence microscopy aboard ship and then examines the grids with transmission electron microscopy later ashore. Species in the Prymnesiophyceae, Prasinophyceae, and Chrysophyceae accounted for some 75% of the cells observed at ten oceanic stations in a low latitude transect of the North Atlantic Ocean (Estep et al., 1984). The dominant forms encountered were Chrysocromulinids in the dominant Prymnesiophyceae, distinguished by their distinctive scales and coiled haptonema. Chloroplast-lacking nanoflagellates from the same samples were preliminarily characterized by Davis (1982).

Bacterial Requirement by the Nanoalgae: Raison d'etre for Thigmotaxis and Bacterivory?

There are very few isolates of the nanoalgae obtained from oceanic waters. In response to a discussion about the paucity of information but potential importance of the nanoplankton in Sea Microbes (Sieburth, 1979), Luigi Provasoli and Robert Guillard submitted and obtained an NSF grant to culture and study the

nanoalgae which resulted in a number of isolates that are maintained by the Provasoli-Guillard Culture Collection of Marine Phytoplankton at Bigelow Laboratory, West Boothbay Harbor, ME. A feature of these xenic unialgal cultures is that they resist attempts to be made axenic. When made axenic, the cultures often die out or do poorly. This was illustrated in the talk with color slides that were to be used to make another color plate. Two pairs of xenic and axenic nanoalgae from an oceanic station just south of Bermuda were compared. The cells in the axenic cultures were aflagellated and aggregated, while those in the xenic culture were flagellated and dispersed. A micrograph of a Chrysamoeba in a xenic culture showed a healthy cell with filopodia used in both motility and bacterivory, while the cells in an axenic culture were aflagellated and aggregated. This means that axenic strains are both taxonomically and functionally different algae than their xenic counterparts. The nanoalgae growing with their bacterial consorts are self replicating ecosystems representing microbial life in just microliters of seawater.

Active bacterivory in the Chrysochromulinids was well documented by the papers of Parke et al. (1955, 1956). An example of the wonderfully informative sketches in these papers that illustrated attachment to a substrate with the haptonema (required for thigmotaxis) and the ingestion of bacteria and graphite particles necessary for bacterivory has been reproduced in Figure 3. The importance of these species and their processes described over three decades ago is only now being recognized. While studying the taxonomy of the Provasoli-Guillard oceanic isolates, the presence of ingested cells were observed in species of both Ochromonas and Chrysamoeba (Estep et al., 1986). Work in this lab with Lars Tranvik and that of Karen Porter at the University of Georgia shows a definite trend of freshwater flagellates to increase their ingestion rate with increasing lake depth and decreasing light, respectively. In situ grazing rates at different light intensities and spectral qualities with depth in the open sea should be determined.

The Habitat of the Pycnocline

The problem of growth at low light and limiting nutrients has been addressed by Goldman (1986) who determined C:N:P ratios in the chrysophycean nanoalga Pavlova lutheri under various conditions as shown in Figure 4. The Redfield ratio was obtained at low light but not limiting nutrients. The chemical composition of both laboratory and natural phytoplankton populations can be used as an index of nutrient deficiencies that occur at all light intensities. His results support the hypothesis that oceanic phytoplankton are growing at rates close to infinity that was proposed by Goldman et al. (1979). This simple diagnostic approach could be used to compare the condition

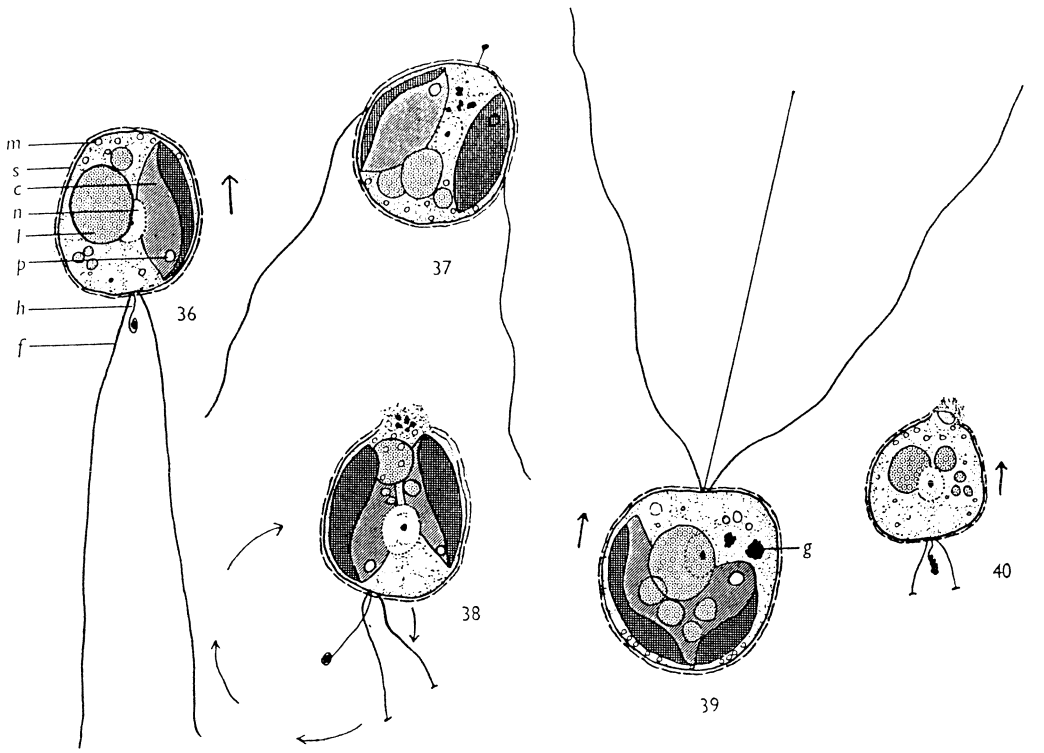

Figure 3. An example of a typical nanoalga in the dominant class Prymnesiophyceae, Chrysochromulina minor, showing its swimming, phagotrophic, and thigmotactic activity. [36] A rapidly swimming individual with the flagella (f) and haptonema (h) behind the body. [39] An individual swimming with flagella and fully extended haptonema in front of the body with ingested graphite (g) towards the flagellar pole. [40] Swimming individual lacking a chromatophore, with trailing flagella and coiled haptonema and ingested bacterium at the non-flagellar pole. Thigmotactic individuals are anchored to a surface with the haptonema; [37] small mass of ingested graphite near flagellar pole, [38] individual swinging in clockwise circles from anchoring point with minute ingested particles at the non-flagellar pole (from Parke et al., 1955).

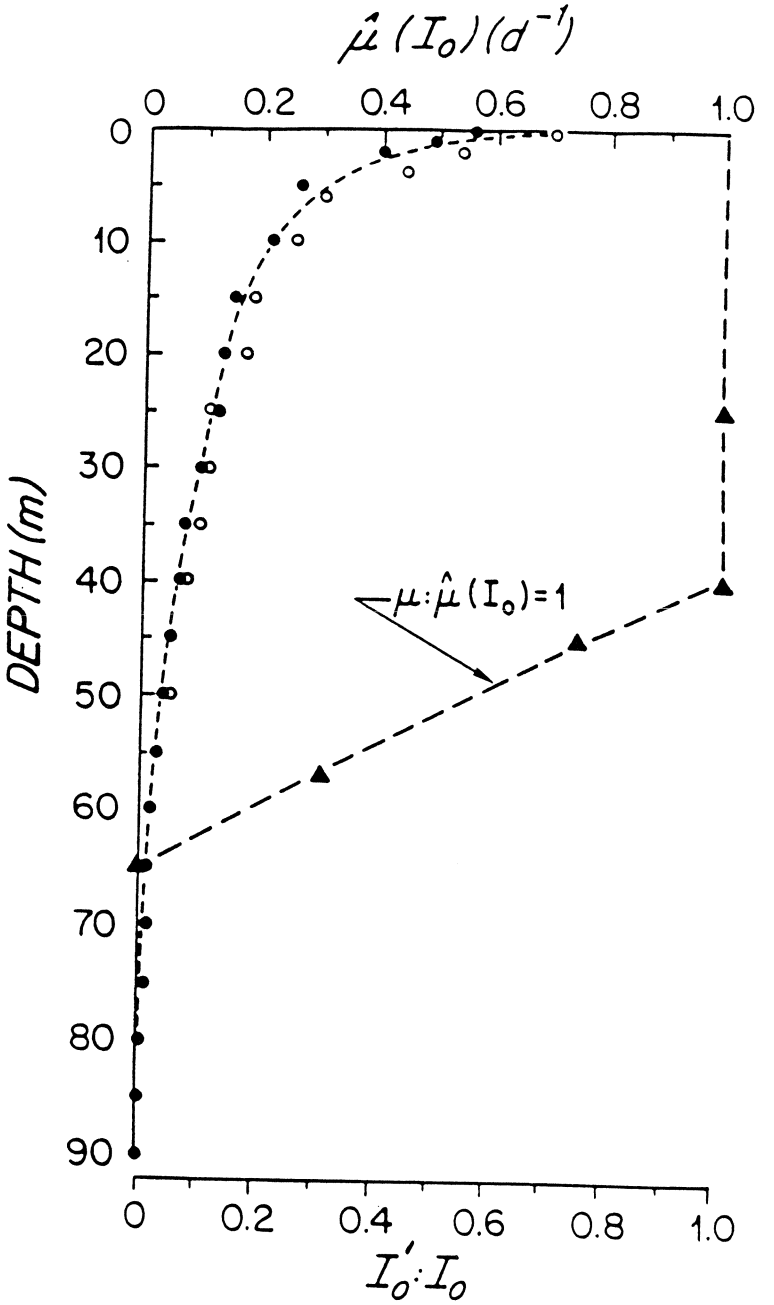

Figure 4. Comparison of the attenuation of surface irradiance (circles) in the Sargasso Sea with nutrient unlimited maximum growth rate of the nanoalga Pavlova lutheri (triangles) as a function of depth (From Goldman, 1986).

of nanoalgae grown with and without their bacterial consorts and with and without prey bacteria. Such studies are indicated for a greater understanding of nanoalgal growth under hypophotic conditions such as occur deep in the pycnocline of oceanic waters. Herbland and Voituriez (1979) have characterized the typical tropical structure of the nutracline which coincided with the chlorophyll maximum and primary productivity maximum. The upper layer was oxygen saturated and the lower layer was undersaturated. In the Weddell Sea, phytoplankton assemblages from the pycnocline generally sank slower than those from the surface (Johnson and Smith, 1986).

The cells responsible for the deep chlorophyll maximum (Shulenberger and Reid, 1981) and productivity at the bottom of the euphotic layer (Bienfang et al., 1984) are of interest. In addition to the low intensity of light penetrating to the pycnocline, the spectral quality of that light appears to be very important. Glover et al. (1986) presented evidence that a nanoalgal prasinophyte had greater photosynthetic and growth efficiencies than a cyanobacterium in dim blue-violet light that would occur in the pycnocline. This approach was expanded by Glover et al. (1987). In general, smaller algal species were more efficient photosynthetically than larger algae from the same pigment group when light color was not a factor. Nanoalgae photosynthesized and grew most efficiently in low intensity blue-violet and blue light while the cyanobacteria were most efficient in dim green light. Glover et al. (1986) state that light quality may only be part of the success of the nanoalgae at depth. They state that since they sink at negligible rates, they can attribute biomass peaks below the surface mixed layer to in situ growth. But the concentration of these cells in the pycnocline could also be due in part to their attachment to the 40-80 um microparticulates which carry them to the denser waters of the pycnocline where they accumulate.

The importance of microparticulates (Sieburth, 1983; Goldman, 1984) in creating the habitat of the pycnocline, which may act like a "false benthos," has been discussed previously (Sieburth, 1983, 1986). The main basis for this speculation is a good one--the presence of a small but very persistent peak of methane in the oceanic summer pycnocline. The literature is cited in the references in Sieburth (1987). A typical vertical profile for observed methane concentrations is given in Figure 5. Elevated concentrations occur throughout the pycnocline, but a peak exists mid-way. Scranton and Brewer (1977) speculated that this peak was due to either algal metabolism or to anoxic micro-environments. An ambitious study that attempted to more accurately pinpoint the source and site of methanogenesis in the upper ocean concluded that methane maxima are based on in situ biological production, controlled by physical processes, and that methanogenesis occurs within reducing microenvironments (Burke et al., 1983). Reducing environments in marine snow and

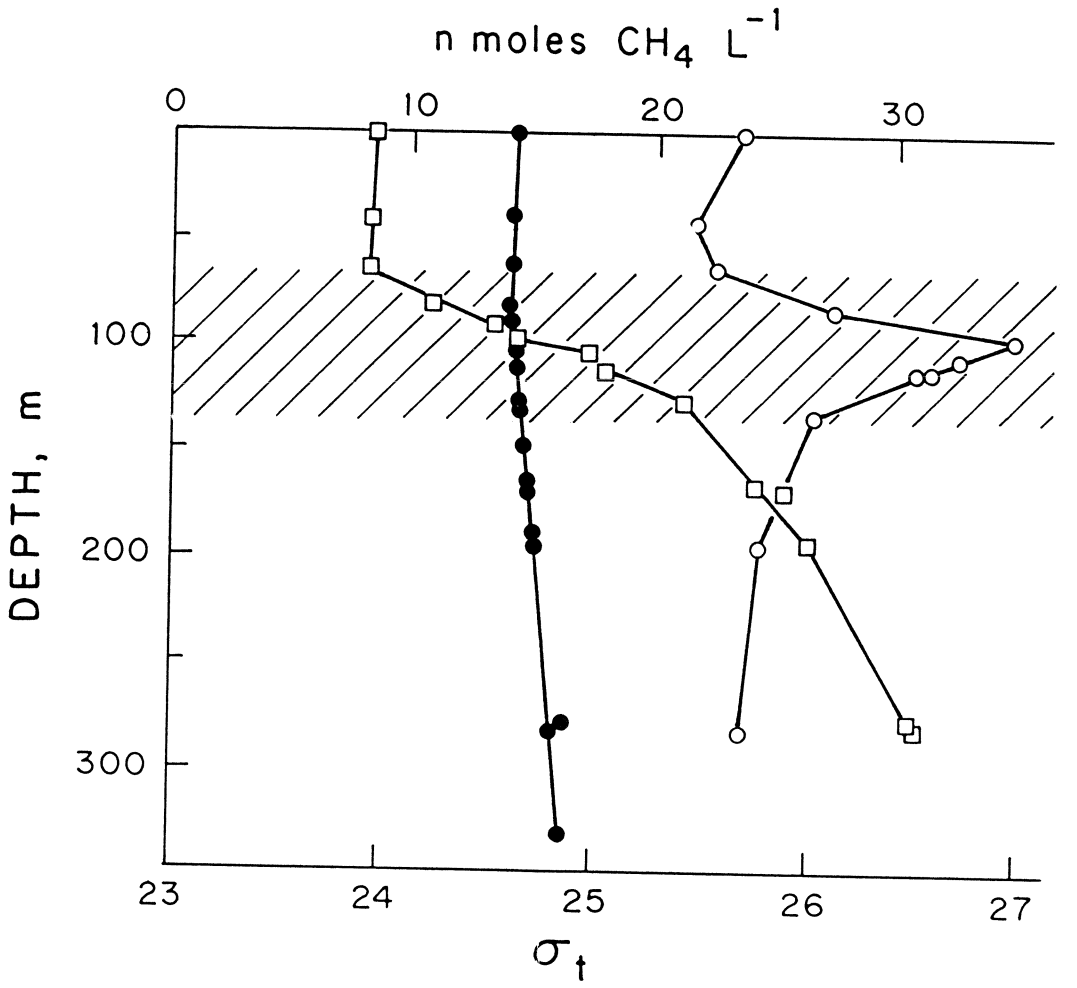

Figure 5. The expected (filled circle) and observed (empty circle) values for methane compared to the pycnocline (striped area) as indicated by density (empty squares). (Adapted from Scranton and Brewer, 1977).

fecal pellets have been reported recently by Alldredge and Cohen (1987). There appears to be sufficient observations to conclude that in the pycnocline and the upper ocean at least, if not throughout the water column, that methanogenesis occurs in particles of fecal origin derived from algae. The void until recently has been that no one had cultured or isolated methane-producing and methane-oxidizing bacteria from the oxygenated waters of the open ocean.

The Presence of Fermentative and Oxidative Bacteria of the Methane Cycle in Decaying Microparticulates

The depolymerization of biopolymers and their fermentation and oxidation to yield the substrates that can be utilized for methanogenesis are shown in Figure 6. The basic precursors for methanogenesis are the end products of fermentation, carbon dioxide, and hydrogen that are used by hydrogenophilic methanogens. Hydrogen, if allowed to accumulate, would inhibit fermentation. Formate and acetate are also key methanogenic substrates. Non-methanogenic substrates like ethanol and lactate can be oxidized to acetate that is used by acetophilic methanogens. Substrates that can be used for methanogenesis by methylophilic methanogens are methanol and the primary amines methylamine, dimethylamine, and trimethylamine that arise from the degradation of the widely occurring osmoticum, glycine betaine (King, 1984). The conversion of fermentable substrate to methane by bacterial consortia is about 40% (Jones et al., 1984). It is interesting to note that at low light levels algal cells produce high levels of polysaccharide (Hitchcock et al., 1986).

With the exception of the methanogenic enrichments of Oremland (1979) inoculated with zooplankton and fish guts, methanogens cultured from oxygenated ocean water have not been reported. The evidence for an upper ocean methane cycle may be more easily obtained by culturing aerobic methane-oxidizers than by culturing the strictly anaerobic methanogens. Although Hutton and ZoBell (1949) readily cultured methane-oxidizing bacteria from marine muds, the enrichment of 100 ml samples of seawater failed to yield methanotrophs. Our first attempts to isolate methanotrophs from 100 ml portions of oceanic seawater resulted in 23 positive enrichments from which the first oceanic methane-oxidizing bacterium, Methylomonas pelagica, was isolated and described (Sieburth et al., 1987). This cell has the ultrastructure of Type I methanotrophs with a stack of cytomembranes similar to that of the type species, Methylomonas methanica. What we were attempting to culture was not a particle associated form like the Type I methanotrophs, but a planktonic cell with a unique cytomembrane suggestive of either a methane oxidizer or an ammonium oxidizer (the Type III cell of Johnson and Sieburth, 1979). After repeated failures with both substrates, we used methylamine that contains both ammonia and

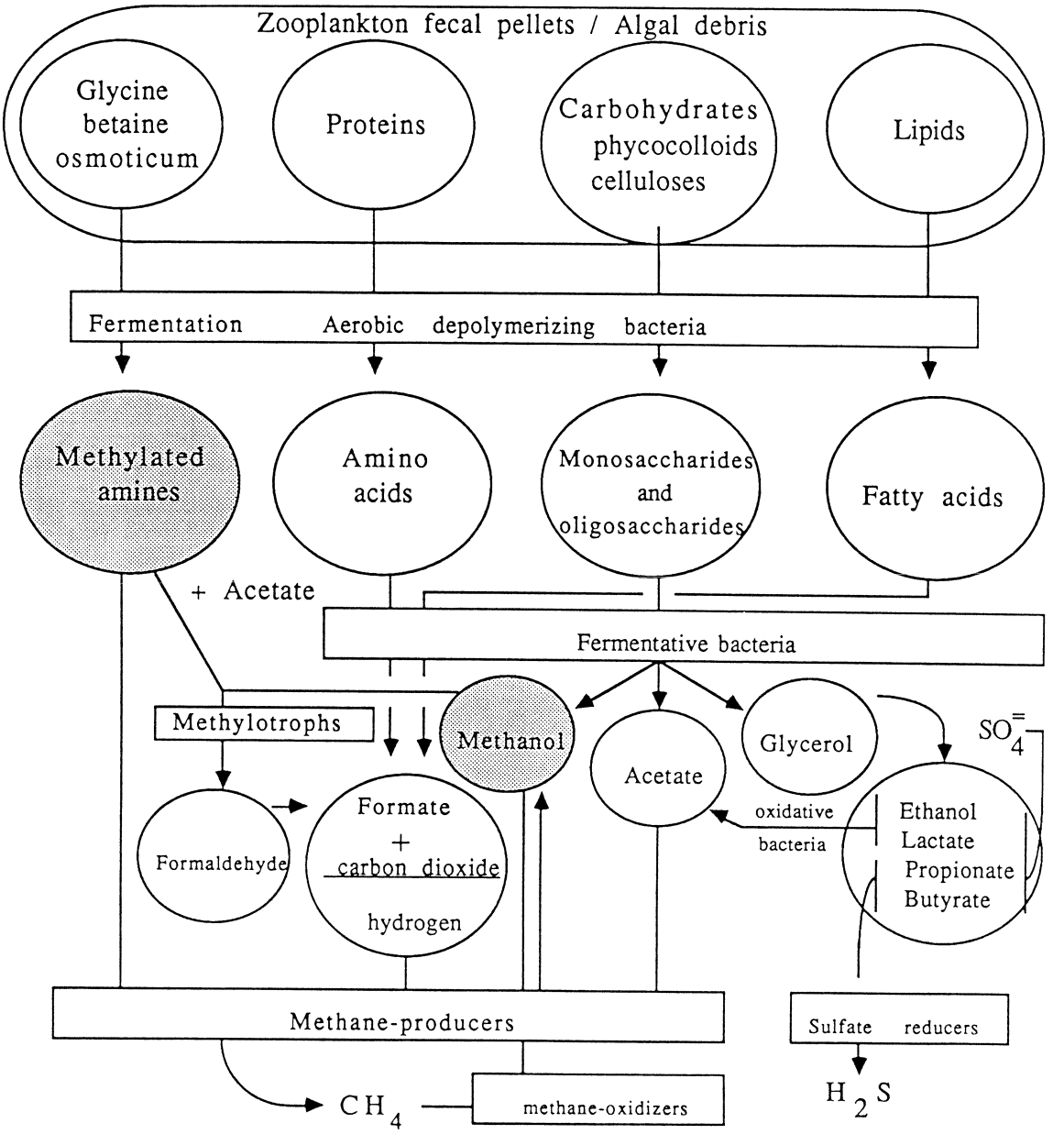

Figure 6. The mandatory dissimilatory processes for the decomposition of organic matter in algal debris through depolymerization, fermentation, and oxidation that much occur in the upper ocean to ensure continued productivity. Methylotrophic substrates are shaded. (From Sieburth, in press).

methane. With this substrate, all water samples from all depths and locations sampled in both nearshore and open ocean waters yielded turbid growth (Fig. 7A,A). Isolates growing on methylamine, however, were just methylamine oxidizers similar to those in the genus Methylophaga (Janvier et al. 1985) which lack a distinctive ultrastructure.

A more careful examination of the methylamine enrichments, however, indicated that a pellicle (surface skin) was present in some enrichments that could be due to methane-oxidizing bacteria (Fig. 7A,C). Some of these enrichments apparently accumulated methane in the headspace of these aerobic enrichments made in gas permeable polycarbonate flasks (Fig. 7,B2). This was apparently due to methanogens whose methane coenzyme F_{420} made some of the cells autofluoresce (Fig. 7, B1). An explanation of this paradoxical methanogenesis is given in Figure 7B. The aerobic methylamine oxidizers apparently cause aggregations of bacteria including oxygen tolerant methanogens to go anoxic. Anaerobic methylotrophy then produces methane, thereby providing further reduced substrate for oxidation and the maintenance of anoxic microsites for the oxygen tolerant, but strictly anaerobic methanogens to grow.

Methanogenic enrichment cultures have been made using natural, oxygenated seawater samples from both Narragansett and Chesapeake Bays. Most probable number estimations made with whole water, filters with a 2.7um porosity, and their filtrates indicated that the methanogens are indeed associated with particles and that culturable methane-producing particulates number in the hundreds per liter. Copepod fecal pellets obtained in sediment traps are an excellent inoculum for enriching both methane-producing and methane-oxidizing bacteria. The algal debris in the fecal pellets of these algavores must be providing the raw materials for fermentation and methanogenesis by the processes illustrated in Figure 6. But are the algae themselves providing fermentable debris and methylated substances that can enrich for the bacteria in the methane cycle? A few selected phototrophs were used to inoculate flasks of sterile seawater from the Sargasso Sea enriched with trace nutrients and supplemented with all three primary amines. The results are summarized in Table 1. Many of these enrichments soon became turbid with oxidative forms. Some of these also accumulated methane in the headspace. Some 8 ml of these xenic cultures were also analyzed for the presence of methylated substances by gas chromatography (King et al., 1983), and some of these substances could be detected. These results are very preliminary, but they do indicate that xenic algae in general may enrich for bacterial consorts that are not only aerobic methylotrophs but are also anaerobic methylotrophs producing methane. Some of these xenic algae with methylotrophic bacterial consorts have been maintained in the lab for decades. The Provasoli isolates and similar nanoalgae at the P-G CCMP should be studied in detail to learn

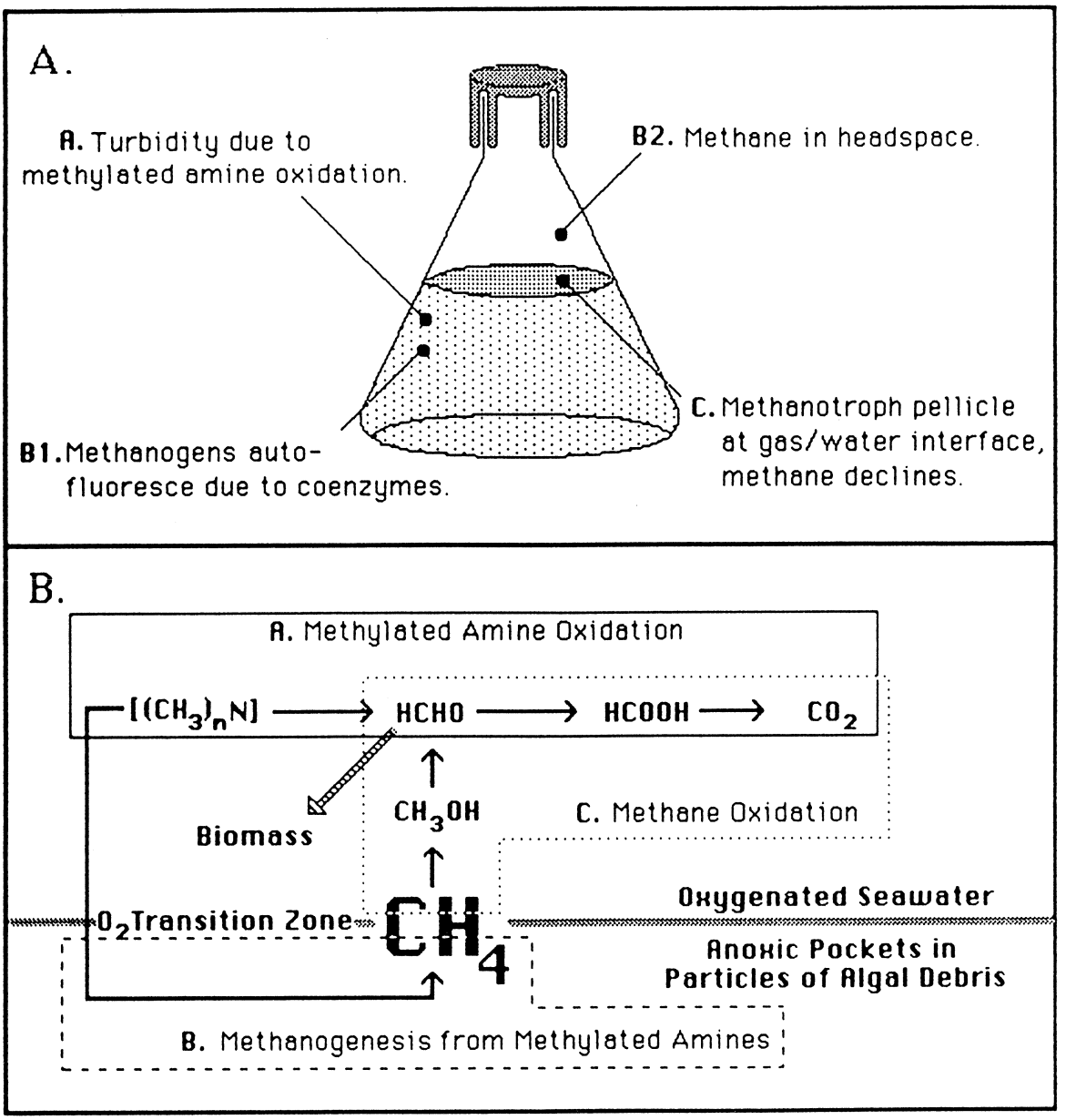

Figure 7. Changes that occur in a sample of oxygen-saturated seawater after enrichment with 0.1% methylamine. A. Apparent changes occurring in the seawater in which the azurin indicator goes from the oxidized pink form to the colorless reduced form while the culture becomes turbid [A], and shows evidence of methanogenesis [B1, B2] and methanotrophy [C]. B. The chemical reactions that presumably occur and explain the above changes in the incubated seawater samples.

Table 1. The occurrence of methylated amines and dimethyl sulfide in xenic cultures of phototrophs, and the methylotrophic and methanogenic activity of their bacterial consorts upon enrichment.

Phototroph	Methylated Substances (Peak area, arbitrary units)				Bacterial Activity[1]					
					Oxidation			Methanogenesis		
	MMA	DMA	TMA	DMS	MMA	DMA	TMA	MMA	DMA	TMA
Diatoms										
Bacteriastrum	ND	ND	ND	ND	+	+	+	+	+	+
Cyclotella	0	0	0	4.3	+	-	-	+	-	-
Dinoflagellates										
Gymnodinium	0	1.1	47	3466	+	-	+	+	-	+
Chrysophytes										
Chrysamoeba	0	0.3	18	136	+	+	+	+	-	-
Ochromonas	34	0	4	428	-	-	+	-	-	-
Cyanobacteria										
*211	0	0	0	0	+	ND	ND	-	ND	ND
*220	25	0	0	0	+	ND	ND	-	ND	ND
Prymnesiophyte										
Phaeocystis	0	0	3	60	+	+	-	-	-	-

[1] Oxidation indicated by turbidity, Methanogenesis indicated by methane accumulation in the headspace.

ND = not done

more about their bacterial consorts and the hypotheses developed in this paper.

Do Fermenting Fecal Fragments Provide Photosynthetically Active Bacterial Luminescence (PABLum) for the Nanoalgae?

The smaller phototrophs in the picoplankton such as the cyanobacteria and species of Chlorella that are ingested by copepods are not digested and pass into their fecal pellets intact (Johnson et al., 1982). When such fecal pellets are obtained at aphotic depths in sediment traps, the undigested phototrophs are often in a state of division (Silver and Alldredge, 1981). Do these algae have sufficient metabolites to complete cell division in the dark? Is the cell cycle arrested by darkness (Chisholm et al., 1980)? Or are these cells receiving sufficient photons within the fecal pellets to carry on limited cell division? There are reports of glowing marine snow observed by deep divers and those in submersibles when making dark adapted descents through depths of water stratification (Baguet, et al., 1983; Orzech and Nealson, 1986). We know from the literature that luminescent bacteria are fermentative enteric forms (Hastings and Nealson, 1977). We also know that when they are at a sufficient density, about 5×10^7 cells ml^{-1}, they release an activator for the luciferin-luciferase system that make the whole bacterial biomass glow (Nealson et al., 1970). The raison d'etre for this process has not been determined. But, it is conceivable that the nondigested picophototrophs and the enteric bacteria have evolved a synergism whereby the phototrophs obtain crucial photons to maintain photosynthesis while the enteric bacteria obtain crucial organic exudates to sustain each other at least in the pycnocline or DCM and maybe even during the relatively long journey through abyssal depths to the benthos. But fecal pellets can be too small or too fragmented to sink through the pycnocline, and these microparticulates about 40-80 um in diameter which accumulate and ferment to yield methane as previously discussed must also accumulate to yield luminous clouds of marine snow in the pycnocline where nanoalgae also accumulate.

When I look at the emission spectra of different luminescent bacteria (Ruby and Nealson, 1977) compared to the relative absorption spectrum of a natural phytoplankton assemblage from the Caribbean Sea (Lewis et al., 1986) as shown in Figure 8, I am impressed that there is a considerable overlap between the two. I can imagine that thigmotactic nanoalgae might seek out these decaying particulates through chemosensory transduction, and attach to them, where the mixotrophic species (Estep et al., 1986) are provided with concentrated bacterial prey. On this microscale, these nanoalgae would be sitting on a glowing source of photons that could supplement low levels of PAR. One can make a simple calculation to see if a photosynthetic cell coated

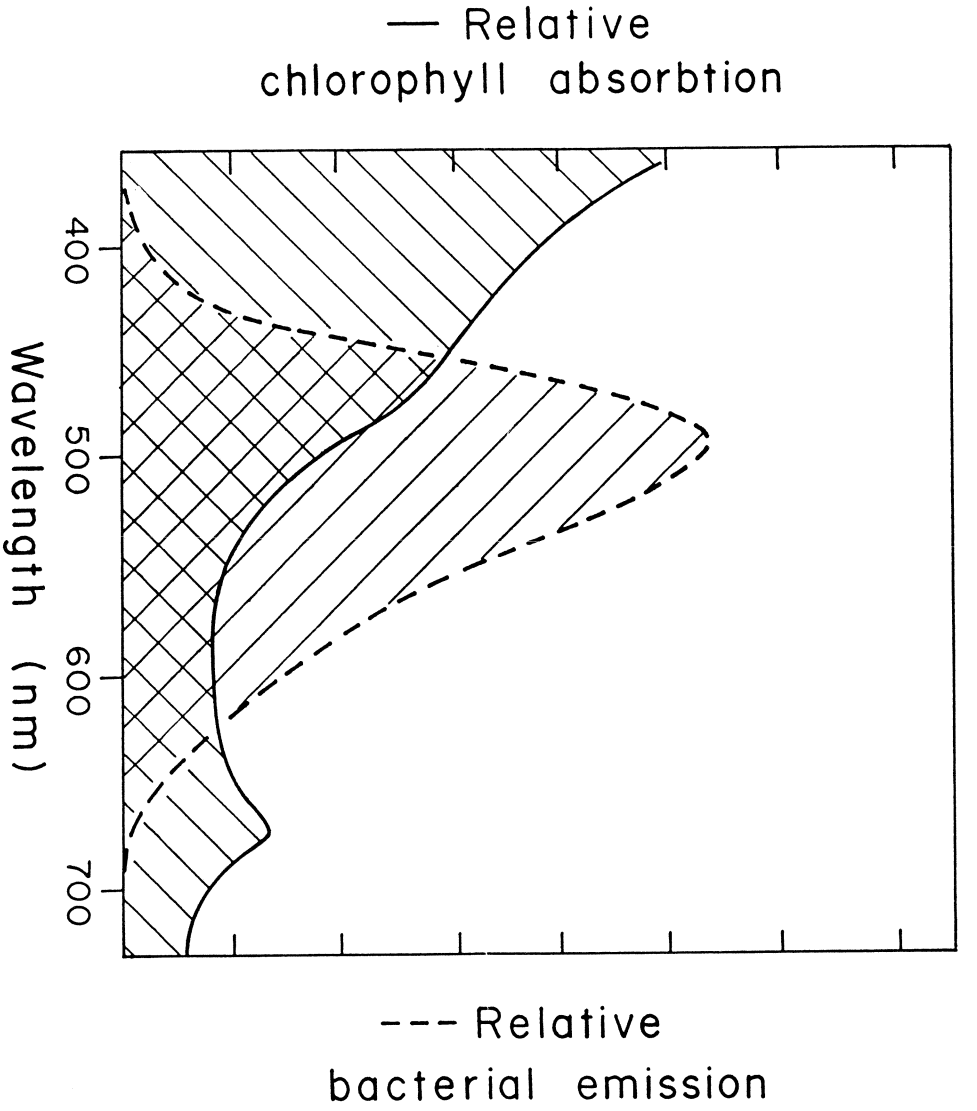

Figure 8. The overlap in the in vivo emission spectrum of luminescent bacteria (from Ruby and Nealson, 1977) with the in vivo absorption spectrum of a natural phytoplankton assemblage from the Caribbean Sea (from Lewis et al., 1986).

with luminescing enteric bacteria in a fermenting fecal pellet could receive sufficient photons (quanta) to maintain itself.

Assume that a typical luminescent bacterium measures 0.5 x 2.0 um and covers 1 um^2 and that its light emission is the ideal 10^4 quanta/cell/sec (Nealson and Hastings, 1979). Converting this to m^2, then a lawn of luminescent bacteria could account for 10^{16} quanta/m^2/sec. The light intensity permitting the maintenance of Skeletonema costatum at its compensation point reported by Falkowski (1980), when converted from $uE.m^{-2}.sec^{-1}$, yields 2 X 10^{16} $quanta.m^{-2}.sec^{-1}$. This is quite impressive as it is in the ball park. The blue-green peak of the luminescent bacteria would presumably be ideal for cyanobacteria and perhaps Chlorella. If it is theoretically possible to maintain an algal cell by bacterial luminescence alone, then it could also be a supplement to PAR for the nanoalgae associated with fermenting fecal fragments in the dim pycnocline and deep chlorophyll maximum in the open sea.

The possibility that cyanobacteria and Chlorella can grow in the dark in a culture of a luminescent bacterium such as Photobacterium fischeri and that nanoalgal growth at low light can be augmented with bacterial luminescence should be tested. These experiments should compare the relative contribution of heterotrophy (mixotrophy) and photosynthetically active bacterial luminescence. If the latter actually happens, it could explain in part phenomena such as the persistence and reproduction of Prorocentrum marie-lebouriae for months during its transport in the dim pycnocline up Chesapeake Bay (Tyler and Seliger, 1978). This mechanism may not be necessary as this species adapts rapidly to low light intensities (Harding, 1988).

Summary: A Hypothetical Model for Bacterial Sustenance of Nanoalgae in the Pycnocline

My start in marine microbiology was an investigation into the nature of the "bacteriological sterility" of Antarctic birds that was well documented by seven expeditions at the turn of this century (Sieburth, 1965). It showed that the prymnesiophyte, Phaeocystis pouchetii, released acrylic acid by hydrolysis of a methylated compound that was inhibitory at the acidic pH of the bird gut (Sieburth, 1960, 1965). Luigi Provasoli even then was a factor in my life, as he obtained a culture of Phaeocyctis pouchetii from Mary Parke and grew sufficient cells so that I could determine the content of acrylic acid. Since then I have periodically studied how bacteria and algae work together to sustain each other. This essay has tried to summarize how this could happen to a specific but very important group of algae, the nanoalgae, which appear to be largely mixotrophic and thigmotactic and to be concentrated along with particulates in the dim pycnocline. I have attempted to illustrate the main

ideas of this syntrophy in Figure 9. The classic food chain that ignores most of the microbiology is shown on the right side. The hypothetical "microbial loop" proposed by Azam et al. (1983) is shown on the left side. If microbial predation was limited to such a sequential process as it is in the macrobiological world, then the contribution of the more numerous but smaller cells would be quite small. The microbiologists who armchaired the hypothetical microbial loop in a bar may be unaware of the ability of cells from the bacteria up through nanoflagellates, microflagellates, and the ciliates to be attracted to and to associate with particulate surfaces, and the significance of this to feeding efficiencies. Since metazooplankton filter-feed on particulates colonized by a spectrum of all sizes of microbial life, then these forms will be ingested and used with an equal efficiency. The contribution will be proportionate to the product of their volumes and their populations and at an efficiency of some 60% (Calow, 1977).

This hypothetical shunting of all sizes of the microbiota directly to the metazooplankton via particulates has been termed the "thigmotactic shunt," and it is shown in the central part of Figure 9. Also shown is the stippled area of the pycnocline where aggregating microparticulates concentrate with the nanoalgae. If technically feasible, the luminescence of enteric bacteria may supplement low levels of photosynthetically active radiation with photosynthetically active bacterial luminescence (PABLum). Another feature of the hypothesis and figure is the in situ release of organic and inorganic nutrients (Goldman, 1984) by the bacterial consorts of the nanoalgae on the microparticulates and bacterial aggregations. The nutrients supplied in this manner (Gilbert, 1982) could make those required by the hypothesis of "new production" (Dugdale and Goering, 1967; Jenkins and Goldman, 1985; Pace et al., 1987) of lesser importance. These processes include nitrogen fixation in hypoxic microsites (Paerl and Prufert, 1987; Paerl and Carlton, 1988) and the release of phosphorous from anoxic habitats as the volatile and insoluble gas phosphine (Devai et al., 1988). There is much new information accumulating about processes in anoxic microsites. When it is all assembled, it outlines a larger picture whereby the synergism or syntrophy of multitrophic processes centered on microparticulates and dominated by nanoalgae and their bacterial consorts could explain in large measure the significantly large productivity in the open sea predicted from the microbiological studies conducted aboard the R/V Trident by this lab (Sieburth, 1977; Burney et al., 1979) and expanded on during the R/V Endeavor cruises (Burney et al., 1981, 1982; Johnson et al., 1981, 1983) and now being confirmed by the studies of the multi-investigator PRPOOS program, among others (Marra and Heinemann, 1987).

It is ironic but fitting that the Chrysochromulinids and other nanoalgae in the Prymnesiophyceae that produce glycine

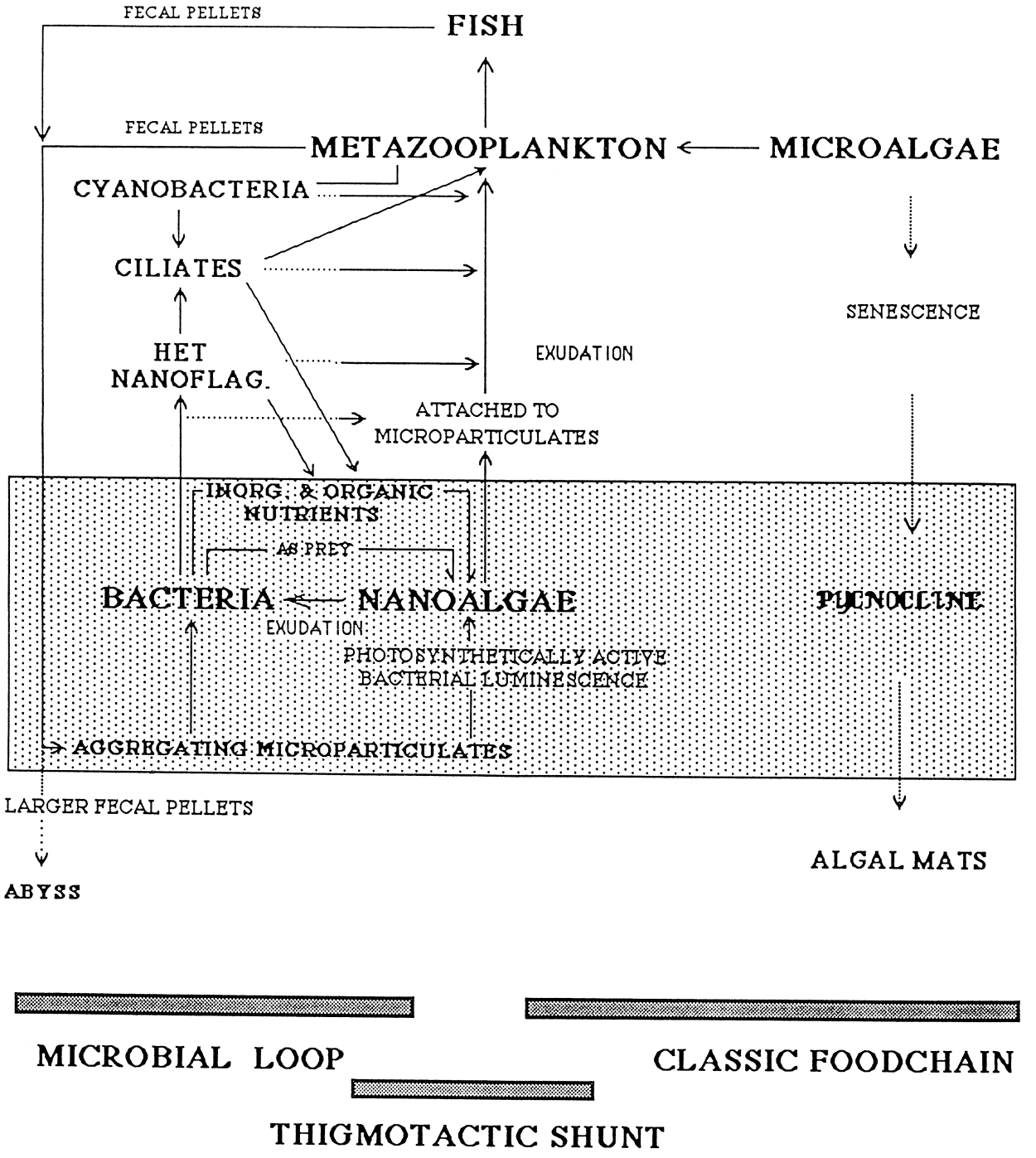

Figure 9. A hypothetical scheme that explains how nanoalgae may be sustained by their bacterial consorts and the processes of thigmotaxis, bacterivory, and perhaps photosynthetically active bacterial luminescence. The classic food chain that largely overlooks the microbiota is on the right, while the energetically inefficient microbial loop is on the left side, while a much more energetically efficient thigmotactic shunt is hypothesized in the center.

betaine (GBT), a major osmoticum and source of methylated amines that can initiate the upper ocean methane cycle that I am currently working on, is the same algal group involved in my initial marine studies three decades ago. The compound, dimethylsuluphonioproprionate (DMSP), that hydrolysed to release acrylic acid that caused antibiosis in penguins, is another major methylated osmoticum. It shows that almost everything one does is interconnected if he or she will step back far enough to take in the panorama. I undoubtedly have some of the details wrong, but the overall image I have tried to create might have merit.

ACKNOWLEDGMENTS

The author thanks the convener, the Western Society of Naturalists, and NOAA for the opportunity to prepare and present the ideas in this conceptual paper. It was written as a celebration of the end of an era, as Luigi Provasoli was closing his laboratory and packing for his retirement home at Lago di Varese near his beloved Milano. "Vai con Dio, mio mico." The nanoalgae we are working with in conjunction with the Provasoli-Guillard Culture Collection of Marine Phytoplankton at the Bigelow Marine Laboratory, West Boothbay Harbor, Maine, were isolated by Luigi in the Sargasso Sea, and he and his long-time associate Irma J. Pintner were fascinated by their bacterial requirement, the subject of this paper. This paper is based on algal work with Kenneth W. Estep, who worked closely with Luigi, Bob and Maureen Keller, and on C_1 bacterial studies conducted with Nicholas J. P. Owens from IMER, Plymouth, while a guest investigator on a John Murray studentship. I thank Ron Kiene for obtaining the gas chromatographic data on the algal cultures while he was in the laboratory of Doug Capone at Stony Brook, Long Island, New York, Mary Scranton for the initial methane analyses, Hilary Glover and Joel Goldman for a critical reading of a rough draft, and Paul Falkowski for discussions and calculations on compensation point light levels. The microbiology and chemistry of methane cycle bacteria is being conducted with my research associates Paul W. Johnson and Kenneth M. Johnson. This work has been supported by the Biological Oceanography Program of the National Science Foundation through recent Grants OCE-8121881, -8316614, -8511365, and -8710085.

REFERENCES

Alldredge, A. L. and Y. Cohen. 1987. Can microscale chemical patches persist in the sea? Microelectrode study of marine snow, fecal pellets. Science 235:689-691.

Azam, F. T., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil, and F. Thingstad. 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. 10:257-263.

Baguet, F., J. Piccard, B. Christophe, and G. Marechal. 1983. Bioluminescence and luminescent fish in the Straits of Messina from the mesoscaphe "Forel." Mar. Biol. 74:221-229.

Bienfang, P. K., J. P. Szyper, M. Y. Okamoto, and E. K. Noda. 1984. Temporal and spatial variability of phytoplankton in a subtropical ecosystem. Limnol. Oceanogr. 29:527-539.

Booth, B. C., J. Lewin, and R. E. Norris. 1982. Nanoplankton species predominant in the subarctic Pacific in May and June 1978. Deep-Sea Res. 29:185-200.

Burke, R. A. Jr., D. F. Reid, J. M. Brooks, and D. M. Lavoie. 1983. Upper water column methane geochemistry in the eastern tropical Pacific Ocean. Limnol. Oceanogr. 28:19-32.

Burney, C. M., K. M. Johnson, D. M. Lavoie, and J. McN. Sieburth. 1979. Dissolved carbohydrate and microbial ATP in the North Atlantic: Concentrations and interactions. Deep-Sea Res. 26A:1267-1290.

Burney, C. M., P. G. Davis, K. M. Johnson, and J. McN. Sieburth. 1981. Dependence of dissolved carbohydrate concentrations upon small scale Sargasso Sea. Mar. Biol. 65:289-296.

Burney, C. M., P. G. Davis, K. M. Johnson, and J. McN. Sieburth. 1982. Diel relationships of microbial trophic groups and in-situ dissolved carbohydrate dynamics in the Caribbean Sea. Mar. Biol. 67:311-322.

Calow, P. 1977. Conversion efficiencies in heterotrophic organisms. Biol. Rev. 52:385-409.

Chisholm, S. W., F. M. M. Morel, and W. S. Slocum. 1980. The phasing and distribution of cell division cycles in marine diatoms. In: Primary Productivity in the Sea. P. G. Falkowski, ed., Plenum Press, New York, pp. 281-300.

Chisholm, S. W., R. J. Olson, E. R. Zetter, J. Waterbury, R. Goericke, and N. Welschmeyer. 1988. A novel free-living prochlorophyte occurs at high cell concentrations in the oceanic euphotic zone. Nature, 334:340-343.

Davis, P. G. 1982. Bacterivorous flagellates in marine waters. Ph.D. thesis. University of Rhode Island. 255 pp.

Davis, P. G. and J. McN. Sieburth. 1984. Differentiation and characterization of individual phototrophic and heterotrophic microflagellates by sequential epifluorescence and electron microscopy. Trans. Am. Micros. Soc. 103: 221-227.

Davis, P. G., D. A. Caron, P. W. Johnson and J. McN. Sieburth. 1985. Phototrophic and apochlorotic components of the picoplankton and nanoplankton in the North Atlantic: Geographic, vertical, seasonal and diel distributions. Mar. Ecol. Prog. Ser. 21:15-26.

Devai, I., L. Felfoldy, I. Wittner, and S. Plosz. 1988. Detection of phosphine: new aspects of the phosphorous cycle in the hydrosphere. Nature 333:343-345.

Dugdale, R. C. and J. J. Goering. 1967. Uptake of new and generated forms of nitrogen in primary productivity. Limnol. Oceanogr. 12:196-206.

Estep, K. W., P. G. Davis, P. E. Hargraves, and J. McN. Sieburth. 1984. Chloroplast containing microflagellates in natural populations of North Atlantic nanoplankton, their identification and distribution; including a description of five new species of Chrysochromulina (Prymnesiophyceae). Protistologica 20:613-634.

Estep, K. W., P. G. Davis, M. D. Keller and J. McN. Sieburth. 1986. How important are oceanic algal nanoflagellates in bacterivory? Limnol. Oceanogr. 31:646-650.

Falkowski, P. G. 1980. Light-shade adaptation in marine phytoplankton. In: Primary Productivity in the Sea, P. G. Falkowski, ed., Plenum Press, New York, pp. 99-119.

Fowler, S. W. and G. A. Knauer. 1986. Role of large particles in the transport of elements and organic compounds through the oceanic water column. Prog. Oceanogr. 16:147-194.

Gilbert, P. M. 1982. Regional studies of daily, seasonal and size fraction variability in ammonium remineralization. Mar. Biol. 70:209-222.

Glover, H. E., M. D. Keller and R. R. L. Guillard. 1986. Light quality and oceanic ultraphytoplankters. Nature. 319: 142-143.

Glover, H. E., M. D. Keller and R. W. Spinrad. 1987. The effects of light quality and intensity on photosynthesis and growth of marine eukaryotic and prokaryotic phytoplankton clones. J. Exp. Mar. Biol. Ecol. 105:137-159.

Goldman, J. C. 1984. Conceptual role for microaggregates in pelagic waters. Bull. Mar. Sci. 35:462-476.

Goldman, J. C. 1986. On phytoplankton growth rates and particulate C:N:P ratios at low light. Limnol. Oceanogr. 31:1358-1363.

Goldman, J. C., J. J. McCarthy, and D. G. Peavey. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature 279:210-215.

Harding, L. W., Jr. 1988. The time-course of photoadaptation to low-light in Prorocentrum mariae-lebouriae (Dinophyceae). J. Phycol. 24:274-281.

Hastings, J. W. and K. H. Nealson. 1977. Bacterial bioluminescence. Ann. Rev. Microbiol. 31:549-595.

Herbland, A. and A. Le Bouteiller. 1981. The size distribution of phytoplankton and particulate organic matter in the equatorial Atlantic Ocean: Importance of ultraseston and consequences. J. Plankton Research 3:659-673.

Herbland, A. and B. Voituriez. 1979. Hydrological structure and analysis for estimating the primary production in the tropical Atlantic Ocean. J. Mar. Res. 37:87-101.

Hitchcock, G. L., J. C. Goldman and M. R. Dennett. 1986. Photosynthate partitioning in cultured marine phytoplankton: Metabolic patterns in a marine diatom under constant and variable light intensities. Mar. Ecol. Prog. Ser. 30:77-84.

Hutton, W. E. and C. E. ZoBell. 1949. The occurrence and characteristics of methane-oxidizing bacteria in marine sediments. J. Bacteriol. 58:463-473.

Janvier, M. C., C. Frehl, F. Grimont, and F. Gasser. 1985. Methylophaga marina gen. sp. nov. and Methylophaga thalassica sp. nov., Marine Methylotrophs. Internat. J. Syst. Bacteriol. 35:131-139.

Jenkins, W. J. and J. C. Goldman. 1985. Seasonal oxygen cycling and primary production in the Sargasso Sea. J. Mar. Res. 43:465-491.

Johnson, P. J. and J. McN. Sieburth. 1979. Chroococcoid cyanobacteria in the sea: A ubiquitous and diverse phototrophic biomass. Limnol. Oceanogr. 24:928-935.

Johnson, P. J. and J. McN. Sieburth. 1982. In-situ morphology and occurrence of eucaryotic phototrophs of bacterial size in the picoplankton of estuarine and oceanic waters. J. Phycol. 18:318-327.

Johnson, P. J., H.-S. Xu, and J. McN. Sieburth. 1982. The utilization of chroococcoid cyanobacteria by marine protozooplankters but not by calanoid copepods. Ann. Inst. Oceanogr., Paris, 58(S):297-308.

Johnson, K. J., C. M. Burney, and J. McN. Sieburth. 1981. Enigmatic marine ecosystem metabolism measured by direct TCO_2 and O_2 flux in conjunction with DOC release and uptake. Mar. Biol. 65:49-60.

Johnson, K. J., P. G. Davis, and J. McN. Sieburth. 1983. Diel variation of TCO_2 in the upper layer of oceanic waters reflects microbial composition, variation and possibly methane cycling. Mar. Biol. 77:1-10.

Johnson, T. O. and W. O. Smith. 1986. Sinking rates of phytoplankton assemblages in the Weddell Sea marginal ice zone. Mar. Biol. Prog. Ser. 33:131-137.

Jones, W. J., J.-P. Guyot, and R. S. Wolfe. 1984. Methanogenesis from sucrose by defined immobilized consortia. Appl. Environ. Microbiol. 47:1-6.

King, G. M. 1984. Metabolism of trimethylamine, choline, and glycine betaine by sulfate-reducing and methanogenic bacteria in marine sediments. Appl. Environ. Microbiol. 48:719-725.

King, G. M., M. J. Klug, and D. R. Lovely. 1983. Metabolism of acetate, methane and methylated amines in intertidal sediments of Lowes Cove, Maine. Appl. Environ. Microbiol. 45:1848-1853.

Lewis, M. R., R. E. Warnock, and T. Platt. 1986. Photosynthetic response of marine picoplankton at low photon flux. In Photosynthetic Picoplankton, T. Platt and W. K. W. Li, eds., Canadian Bulletin of Fisheries and Aquatic Sciences 214:235-250.

Lohmann, H. 1911. Uber das Nannoplankton und die Zentrifugiering kleinster Wasserproben zur Gewinnung desselben in Lebendem Zustand. Int. Rev. ges Hydrobiol. Hydrogr. 4:1-38.

Marra, J. and K. R. Heinemann. 1987. Primary production in the North Pacific Central Gyre: some new measurements based on ^{14}C. Deep-Sea Res. 34:1821-1829.

Murphy, L. S. and E. M. Haugen. 1985. The distribution and abundance of phototrophic ultraplankton in the North Atlantic. Limnol. Oceanogr. 30:47-58.

Nealson, K. H., T. Platt and J. W. Hastings. 1970. Cellular control of the synthesis and activity of the bacterial luminescent system. J. Bacteriol. 104:313-322.

Nealson, K. H. and J. W. Hastings. 1979. Bacterial bioluminescence: Its control and ecological significance. Microbiol. Rev. 43:496-518.

Oremland, R. S. 1979. Methanogenic activity in plankton samples and fish intestines: A mechanism for in situ methanogenesis in oceanic surface waters. Limnol. Oceanogr. 24:1136-1141.

Orzech, J. K. and K. H. Nealson. 1986. Bioluminescence of marine snow. In: Aggregate Dynamics in the Sea, A. Alldredge, ed. ONR Workshop Report AIBS, p. 194.

Pace, M. L., G. A. Knauer, D. M. Karl and J. H. Martin. 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature 325:803-804.

Paerl, H. W. and L. E. Prufert. 1987. Oxygen poor microzones as potential sites of microbial N_2 fixation in nitrogen-depleted aerobic marine waters. Appl. Environ. Microbiol. 53:1078-1087.

Paerl, H. W. and R. G. Carlton. 1988. Control of nitrogen fixation by oxygen depletion in surface-associated microzones. Nature 332:260-262.

Parke, M., I. Manton and B. Clarke. 1955. Studies on marine flagellates. II. Three new species of Chrysochromulina. J. Mar. Biol. Ass. U.K. 34:579-609.

_____. 1956. Studies on marine flagellates. III. Three further species of Chrysochromulina. J. Mar. Biol. Ass. U.K. 35:387-414.

Platt, T. and K. W. Li. 1986. Photosynthetic picoplankton. Can. Bull. Fish. Aquat. Sci. 214:1-583.

Ruby, E. C. and K. H. Nealson. 1977. A luminous bacterium that emits yellow light. Science 196:432-434.

Scranton, M. I. and P. G. Brewer. 1977. Occurrence of methane in the near-surface waters of the western subtropical North Atlantic. Deep-Sea Res. 24:127-138.

Shulenberger, E. and J. L. Reid. 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum and primary productivity reconsidered. Deep-Sea Res. 28A:901-919.

Sieburth, J. McN. 1960. Acrylic acid, an "antibiotic" principle in Phaeocystis blooms in Antarctic waters. Science 132: 676-677.

_____. 1965. Microbiology of antarctica. In: Biogeography and Ecology in Antarctica. P. Van Oye and J. Van Mieghem, eds., Monographie Biologicae, Vol. XV. Dr. W. Junk Publ., The Hague, pp. 267-295.

_____. 1976. Bacterial substrates and productivity in marine ecosystems. Ann. Rev. Ecol. Syst. 7:259-285.

_____. 1977. International Helgoland Symposium: Convener's report on the informal session on biomass and productivity of microorganisms in planktonic ecosystems. Helgoander wiss. Meeresunters. 30:697-704.

_____. 1979. Sea microbes. Oxford University Press, New York and London, 491 pp.

_____. 1983. Microbiological and organic-chemical processes in the surface and mixed layers. In: Air sea exchange of gases and particles. P. S. Liss and W. G. N. Slinn, eds., NATO Advanced Study Institute, D. Reidel Publ. Col, Dordrecht, Holland, pp. 121-172.

_____. 1984. Protozoan bacterivory in pelagic marine waters. In: Heterotrophic activity in the sea. J. E. Hobbie and P. J. LeB. Williams, eds., Plenum Press, NY, pp. 405-444.

_____. 1986. Dominant microorganisms of the upper ocean: Form and function, spatial distribution and photoregulation of biochemical processes. In: Dynamic processes in the chemistry of the upper ocean. D. Burton, P. G. Brewer and R. Chesslet, eds., Plenum Press, NY, pp. 173-195.

_____. 1987. Contrary habitats for redox-specific processes: Methanogenesis in oxic waters and oxidation in anoxic waters. In: Microbes in the sea, M. A. Sleigh, ed., Ellis Horwood Limited, Chinchester and John Wiley & Sons, NY, pp. 11-38.

Sieburth, J. McN. In press. The trophic roles of bacteria in marine ecosystems are complicated by synergistic-consortia and mixotrophic-cometabolism. In: Themes in Marine Microbiology. E. B. G. Jones and D. Miller, eds., Pergamon Press.

Sieburth, J. McN. and P. G. Davis. 1982. The role of heterotrophic nanoplankton in the grazing and nurturing of planktonic bacteria in the Sargasso and Caribbean Seas. Ann. Inst. Oceanogr., Paris 58(S):285-89.

Sieburth, J. McN., P. W. Johnson, M. A. Eberhardt, M. E. Sieracki, M. Lidstrom and D. Laux. 1987. The first methane-oxidizing bacterium from the upper-mixing layer of the deep ocean: Methylomonas pelagica sp. nov. Current Microbiol. 14:285-293.

Sieburth, J. McN., P. W. Johnson, and P. E. Hargraves. 1988. Ultrastructure and ecology of Aurecoccus anophagefferens gen. et sp. nov. (Chrysophyceae); the dominant picoplankter during a bloom in Narragansett Bay, Rhode Island, summer 1985. J. Phycol. 24:416-425.

Sieburth, J. McN., V. Smetacek and J. Lenz. 1978. Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol. Oceanogr. 23:1256-1263.

Silver, M. W. and A. L. Alldredge. 1981. Bathypelagic marine snow: Deep-sea algal and detrital community. J. Mar. Res. 39:501-530.

Stockner, J. G. and N. J. Antia. 1986. Algal picoplankton from marine and freshwater ecosystems: a multidisciplinary perspective. Can. J. Fish. Aquatic. Sci. 43:2472-2503.

Thomsen, H. A. 1986. A survey of the smallest eucaryotic organisms of the marine plankton. In: Photosynthetic Picoplankton. T. Platt and W. K. W. Li, eds., Canadian Bulletin of Fisheries and Aquatic Sciences 214:121-158.

Tyler, M. A. and H. H. Seliger. 1978. Annual subsurface transport of a red tide dinoflagellate to its bloom area: Water circulation patterns and organism distributions in the Chesapeake Bay. Limnol. Oceanogr. 23:227-248.

Watson, S. W., F. W. Valois, D. Franks, and J. B. Waterbury. In press. The novel nitrogen-fixing unicellular cyanobacterium cultured from the tropical Atlantic Ocean. Arch. Mikrobiol.

OCEAN CARBON FLUX: GLOBAL MAPS OF PRIMARY PRODUCTION AND EXPORT PRODUCTION

W. H. Berger, K. Fischer, C. Lai, G. Wu

Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

ABSTRACT

We present two global maps of primary production, the first based on a new compilation of about 8000 published productivity measurements (>90% by radiocarbon methods) and the second on an algorithm for conversion of phosphate concentrations to productivity. Global ocean productivity is 26.9 GtC $m^{-2}y^{-1}$, of which 44% are delivered in the Pacific, 22% in the Atlantic, 17% in the Indian Ocean, and 13% in the Antarctic (south of 50S).

Based on published trapping data, we propose equations converting primary production to export production. The simplest of these, modelled after Suess (1980), is

$$J(z) = 0.2\ PP\ /\ z$$

where z is given in units of 100m, and PP is the primary production. Thus, 20% of the primary production is exported across the 100m level, and 10% across 200m depth. The formula is valid for the upper 1000m. Accordingly, the export at 100m (comparable to "new" production) is 5.4 GtC $m^{-2}y^{-1}$. A "best-fit" equation yields 4.3 GtC $m^{-2}y^{-1}$. These estimates overlap with previous ones (3.5 and 4.7 GtC $m^{-2}y^{-1}$; Eppley and Peterson, 1979).

For fluxes at greater depth a term representing more slowly decomposing organic matter is added, so that

$$J(z) = 0.17\ PP\ /\ z\ +\ r\ *\ PP$$

where r is near 1%. Other algorithms for calculating the flux of organic carbon to the seafloor, given primary production, yield fits to the data which are of comparable goodness.

Results emphasize the well-known dichotomy between coastal green ocean and open blue ocean, with respect to organic carbon production, export, and deposition. The rim of the ocean (coastal ocean and subpolar regions) accounts for one half the total productivity and for more than 80% of the flux to the seafloor.

One corollary of this dichotomy, for the interpretation of Pleistocene continental slope deposits, is that during glacial

time organic carbon burial should increase on the upper slope because the drop in sealevel brings this region closer to shore, and thus within the realm of coastal conditions. An increased glacial burial rate for organic carbon would decrease the glacial atmospheric CO_2 content.

INTRODUCTION

There is a new sense of urgency in studying the deep-sea carbon cycle. The reason is the inexorable increase of carbon dioxide in the atmosphere, which is due to the burning of fossil fuel (see Sundquist and Broecker, 1985), and which is expected to result in substantial warming of the earth's surface (Hansen et al., 1984). Actually, the rate of CO_2 increase is less than the rate of release to it: only about one half of the CO_2 released stays in the atmosphere. The rest, presumably, mostly ends up in the ocean.

The future behavior of the ocean as a carbon sink depends both on physical and biological reaction of the system to warming. For example, if deep mixing should decrease due to an overall increase in density contrast from surface to deep waters, the rate of removal of excess CO_2 will decrease as well, since the deep reservoirs will become less accessible to the atmosphere. Likewise, if a decrease in mixing increases the ratio of carbonate to organic carbon in the particles precipitated in the photic zone, then less CO_2 will be transferred from the surface waters to the deep-water pool.

An especially interesting aspect of the carbon budget, in this context, is the possibility that the present pattern of organic carbon export from the photic zone will change as a result of warming. If mixing and upwelling in coastal regions were decreased, for example, oxygen minima would weaken, and the storage of carbon in slope sediments would diminish. The end effect, presumably, would be a decrease in the efficiency with which the ocean extracts excess CO_2 from the atmosphere.

The exploration of such scenarios presupposes a better understanding of the carbon cycle than we now have. In particular, one would like to know exactly how primary productivity translates into carbon flux to deeper waters and into supply of carbon to the seafloor around the continental margins.

In the following discussion we describe an algorithm approach to the task of mapping the organic carbon flux, beginning with primary production (using the traditional definition based on radiocarbon fixation) and proceeding from there to estimates of transfer to deep waters and to the seafloor.

THE TASK

The task, in essence, is to gain a thorough understanding of the workings of the productivity pump, which keeps the carbon dioxide in the atmosphere low with respect to the equilibrium value for the ocean-atmosphere system (Fig. 1).

The pump depends on photosynthesis for carbon fixation and on the export of organic particles from the photic zone. This export reduces the CO_2-content of the water layer in contact with the atmosphere, hence the atmospheric concentration is less than it would be without the pump. The efficiency of the biological pump depends on the global distribution, in space and time, of primary production and on the fraction of this production escaping recycling within the mixed layer. Also, pump efficiency depends on the carbonate/carbon rain ratio: carbon fixation removes CO_2 but carbonate fixation adds free CO_2 to the system because of a decrease in alkalinity. Thus, it is necessary to make quantitative geographic maps of productivity, of export production, and of the rain ratio carbonate/organic carbon in the export.

Our chief interest here is to obtain a map of the downward transfer of organic matter, the "J-flux," which depends on the export production as well as on the rates of sinking and remineralization during settling. The various stages of the carbon path, and the nomenclature here used, are shown in Figure 2.

At the top of the flow path is PP_T, the traditional primary production as measured by the Steemann Nielsen method. We start with 100 units (e.g., 100gC $m^{-2}yr^{-1}$), aware that not all photosynthesis is included in the value and that, in fact, zooplankton growth may be involved also in the traditional primary production measurement. Of these 100 units, about 10 sink out of the fertile zone, which may be taken as the upper 200 meters of the water column. This is the export production.

For low productivity water, most of the export production is from the lower portion of the euphotic zone (e.g., Jenkins and Goldman, 1985; Coale and Bruland, 1987), presumably deriving substance from the "deep chlorophyll maximum" (Venrick, 1982; Gieskes and Kraay, 1986). For high productivity waters it comes predominantly from the uppermost layers, because light does not penetrate as deeply. The export is quickly reduced by scavenging and decay, so that only 1 unit reaches the seafloor as gross deposition. Of this amount, typically less than 10% is buried as net deposition.

The schematic applies to the open ocean situation. Fluxes are considerably higher in a coastal ocean setting, where primary production is much greater, and more of the export reaches the shallow seafloor (Rowe and Deming, 1985). The proportion buried

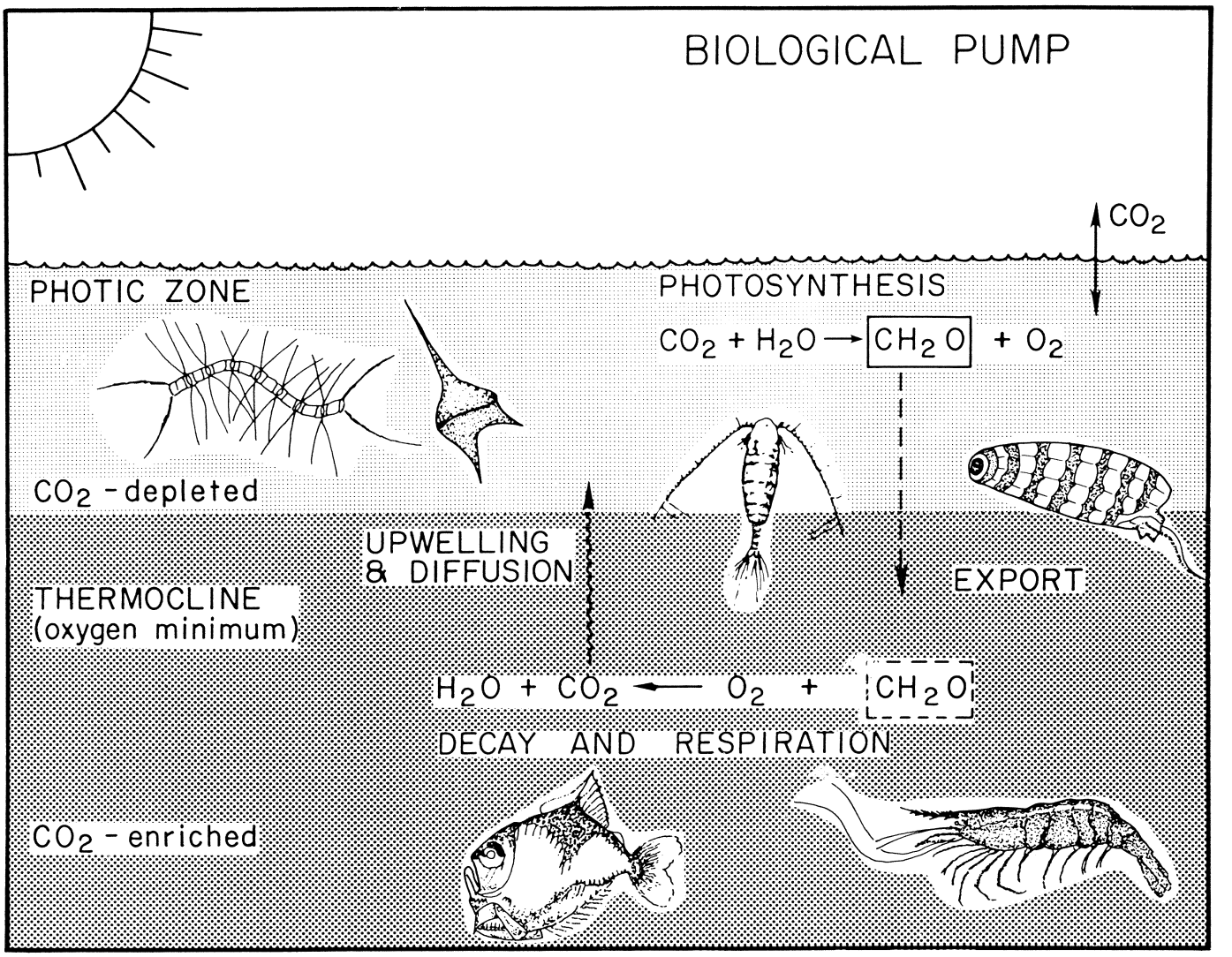

Figure 1. The biological pump in the ocean removes carbon from the surface layer and transfers it to deeper layers through export production.

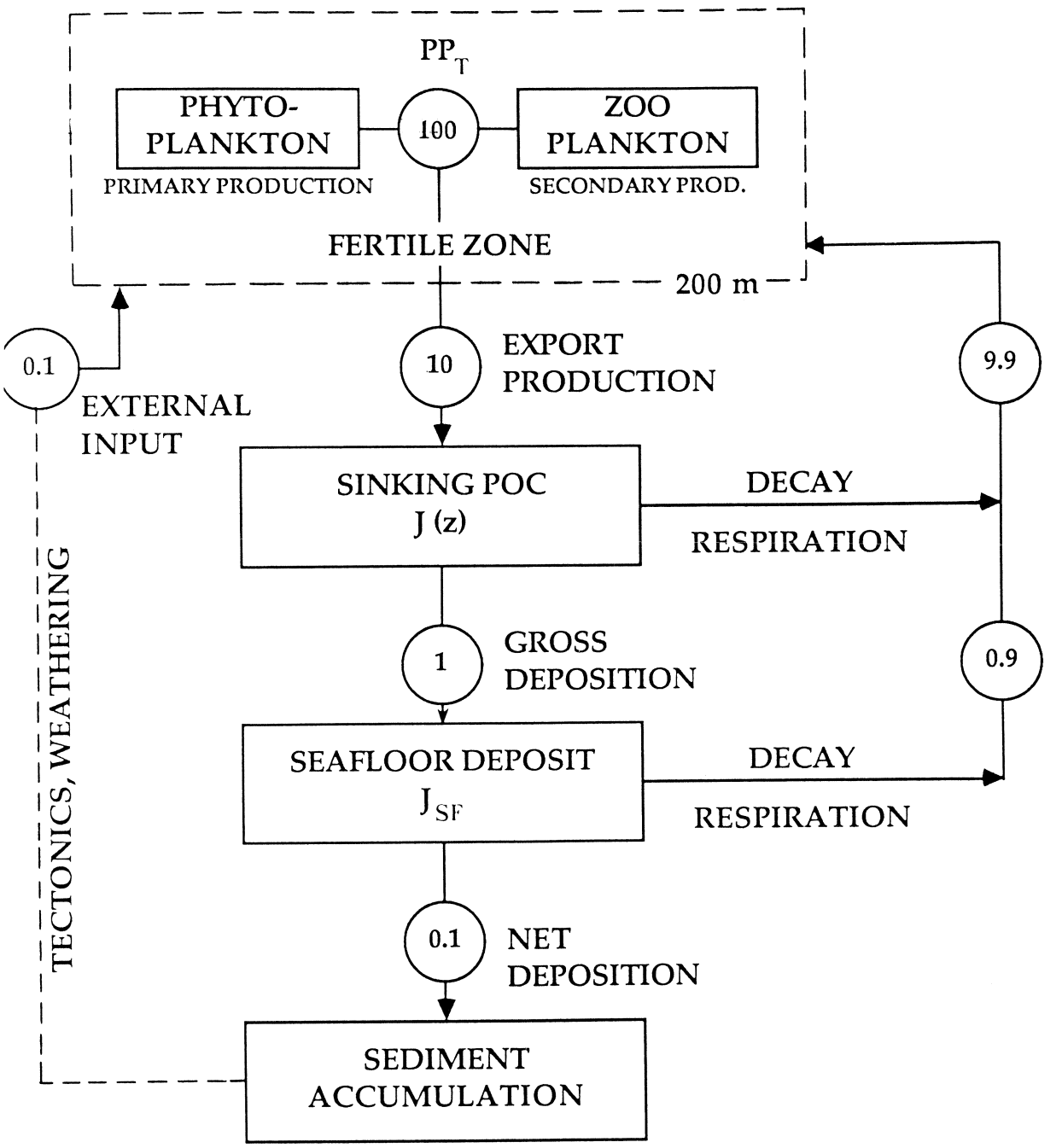

Figure 2. Marine carbon cycle, schematic. Flux in percent of primary production (which contains elements of zooplankton activity in its traditional ^{14}C-index form: hence PP_T).

also is considerably greater here than in the open sea (Mueller and Suess, 1979).

The patterns of deposition of organic carbon are as yet known only in outline: important questions such as the effect of oxygen concentration on burial rates are being hotly debated. In general, however, it is safe to assume that by far the larger portion of the organic carbon arriving on the seafloor is consumed near the interface, except in certain areas close to the coast which have high rates of mixing and sedimentation.

In what follows, we use the marine carbon cycle as shown in Figure 2 as a guide, touching on each of the elements depicted, from top to bottom, and summarizing various attempts at quantification, including our own.

PRIMARY PRODUCTION

The most commonly used global map of primary production of the ocean is the one by Koblentz-Mishke and co-workers (1970), which was made in the 1960's. It has been reproduced widely, usually with minor modifications (e.g., Cushing, 1975; Steemann Nielsen, 1975; Berger, 1976; Broecker and Peng, 1982; Eppley, 1984; Parsons et al., 1984; Romankevich, 1984).

In general, the values of productivity given in the Koblentz-Mishke map (Fig. 3) are those derived from the type of radiocarbon measurement introduced during the Galathea Expedition (Steemann Nielsen, 1956), complemented by other methods giving comparable results (see e.g. Fogg, 1975). In addition, Koblentz-Mishke and co-workers used indirect indicators (e.g. phytoplankton abundance) to fill in large regions where measurements were absent or sparse.

Since the construction of this map, much controversy has developed about the meaning of Steemann Nielsen productivity values (Eppley and Sharp, 1975; Venrick et al., 1977; Gieskes et al., 1979; Carpenter and Lively, 1980, Eppley, 1981; Gieskes and Kraay, 1984). It is now commonly assumed that this method distinctly underestimates "actual" productivity, that is the gross rate of carbon fixation. Factors between 1.5 and 2 have been suggested for this discrepancy (refs. in Sundquist, 1985) and even higher ones (2.5 to 4) for polar areas (Rivkin and Putt, 1987).

Evidently, measurements are influenced by grazing and mortality during incubation. Also, a strong case has been made that nano- and pico-plankton are responsible for a large portion of total photosynthesis (Malone, 1980; Vinogradov, 1981; Smith et al., 1984; also see Platt and Li, 1986). Although such small organisms would be retained on the membrane filters used in

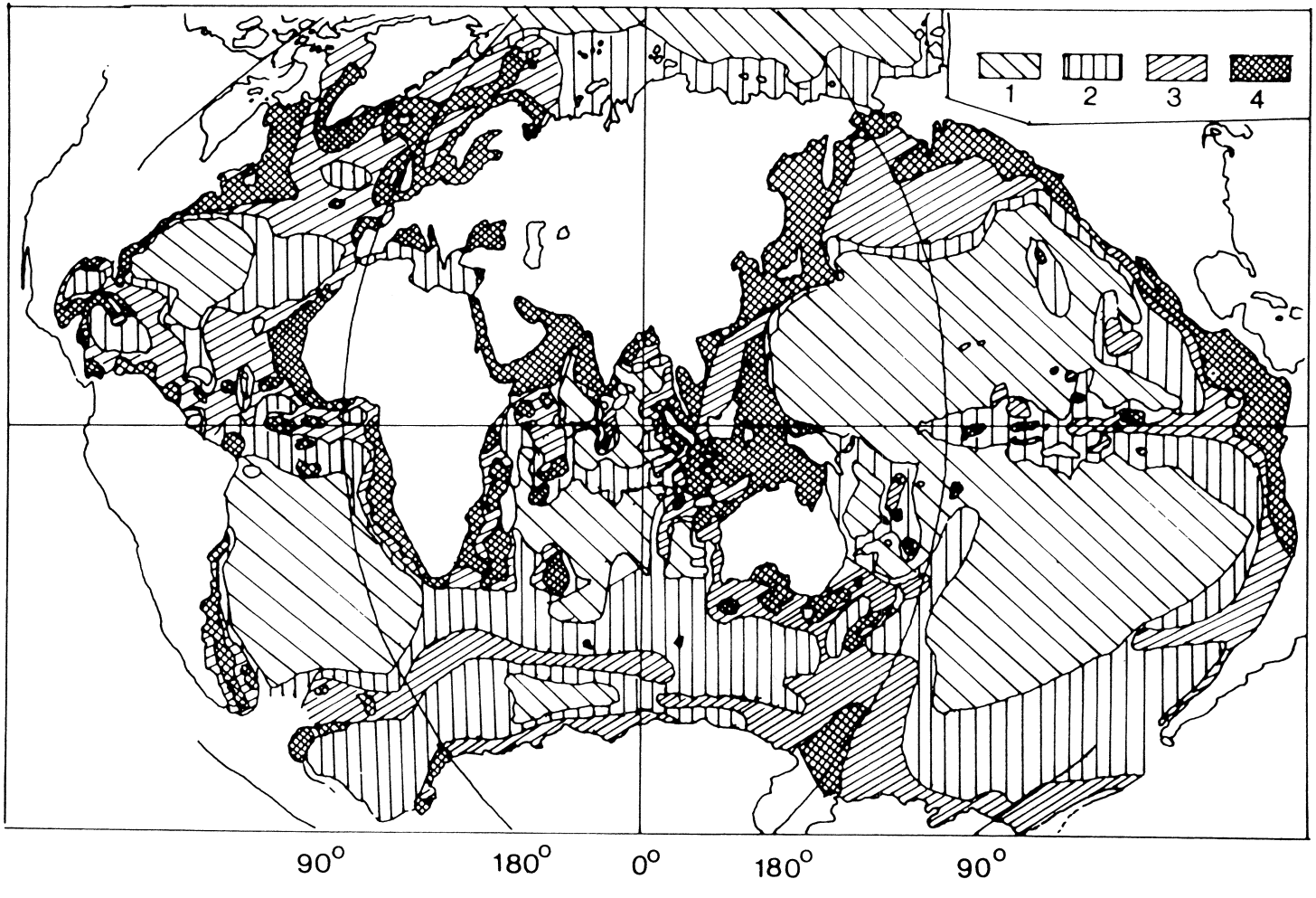

Figure 3. Primary productivity of the world ocean according to Koblentz-Mishke et al. (1970), as redrawn by Steemann-Nielsen (1975). In gC $m^{-2}yr^{-1}$: 1, less than 36; 2, 36 to 54; 3, 54 to 90; 4, greater than 90. The original has an additional category in many coastal areas: greater than 180 (but not off South America!). An up-to-date version is in Romankevich (1984).

^{14}C studies, the amount caught would be small relative to their productivity, because they are rapidly consumed by microheterotrophic organisms. Such microheterotrophs may be more abundant than hitherto assumed (Smith et al., 1984). In addition, considerable carbon fixation may be taking place at rather low light intensities, below the traditional euphotic zone boundary (Li et al., 1983; Platt et al., 1983).

Based on the phenomenon of a shallow oxygen maximum in the northern Pacific, Shulenberger and Reid (1981) suggested independently that "the overall productivity of the open ocean may have been seriously underestimated," a proposition which engendered much discussion (Platt, 1984; Reid and Shulenberger, 1986; Craig and Hayward, 1987). According to Platt and Harrison (1986, p.273) the issue is serious:

"If, after due consideration, we finally concluded that primary productivity was not measured accurately by the ^{14}C method, we should be obliged to reject data in which very large resources have been invested over a long period, together with the conventional wisdom based upon them. Among the issues that would have to be rethought are the major geochemical cycles of the ocean; the role of the ocean biota as a possible buffer in the global CO_2 crisis, and its effect on the future climate of the earth, and the upper limit to global productivity and food from the sea."

We do not wish to address these complex issues here. For our purposes, that is, the mapping of flux toward the seafloor, any reasonable definition of productivity will serve, as long as it can be calibrated to the downward flux of organic carbon. Thus, when using the terms "primary production" or "productivity" we mean the rate of carbon fixation as measured by traditional methods, that is, the Steemann Nielsen method or an equivalent measure. This measure may be considered a productivity-index, which is given in terms of flux, for convenience. Mapping of such a productivity-index is mainly hindered by the lack of standardization of measurement, and by the sparsity of data and their variability and inhomogeneity in coverage. If there are interannual long-term trends in productivity in the open ocean (Venrick et al., 1987), this would pose a major problem for the type of study here attempted.

Considering that two decades have passed since the compilation of the Koblentz-Mishke map, it seemed worthwhile to attempt a new global compilation. Our survey includes measurements made from 1944 through 1985, using radiocarbon (more than 90% of the data) and oxygen determinations, integrated over the photic zone. Most of the data were taken from reports in English. Also, we used articles in Spanish and French (mainly for the Mediterranean), and we obtained unpublished data from a number of correspondents. Approximately 8000 measurements are represented in the compilation.

Problems arose in averaging data because of the great variability of primary production in mid- and high-latitudes (Cushing, 1981) and because of patchiness and seasonality in general (e.g., Raymont, 1963; Zeitzschel, 1973; Cushing, 1975; Parsons et al., 1984). Also, interannual variability (Barber and Chavez, 1986) made the task difficult. Annual estimates were made for locations where a sufficient number of seasonal values were available. In other cases, map values were estimated from the spot data alone, considering the season(s) of measurement. Results are shown as (subjectively drawn) contours of "average primary production" (Fig. 4). The data coverage is given also, to provide a sense of data density and confidence (Fig. 5). In areas of low data density, phosphate concentration at 100m depth was used to guide interpolation.

Our map, on the whole, is quite similar to that of Koblentz-Mishke et al., even in some details. Both maps show the large oligotrophic areas of the central gyres, the equatorial high productivity zones in the Pacific and Atlantic, the high coastal ocean fertility, and the major upwelling regions. In addition, the numerical ranges of productivities given show much overlap.

However, the maps differ in some important respects, too. For example, large areas of the ocean in the Koblentz-Mishke (K.-M.) map are shown having productivities of less than 100 mgC $m^{-2}d^{-1}$, corresponding to < 35 gC $m^{-2}yr^{-1}$. In our map, the area with such low values is considerably smaller, especially in the Pacific realm. Also, in the K.-M. map typical values for the eastern tropical Pacific range from 50 to 100 gC $m^{-2}yr^{-1}$; in ours the range is typically 60 to 150 gC $m^{-2}yr^{-1}$. In contrast, in the Atlantic their values for the tropics tend to be somewhat higher than ours (50 to 85 versus 35 to 60, typically). According to W. Gieskes (pers. comm., Apr. 1987), this higher value more nearly agrees with his measurement series in the region.

The station coverage map (Fig. 5) shows that there is a great inhomogeneity in coverage, from more than 150 determinations per 10 degree square to zero. The most densely sampled areas are predominantly in the northern Indian Ocean, the northeast Pacific, off the U.S. east coast, in the northern North Atlantic, and off Northwest Africa. The unsampled regions are in the southern portions of the major oceans, mainly between 30 and 60 degrees South. In fact, some measurements do exist in these regions (e.g., El-Sayed, 1970), but they were only used here if the production was given as integrated over the euphotic zone. Coverage in the Antarctic region is sparse, perhaps enough for educated guesses but probably inadequate considering the importance of the region for the carbon cycle.

It is evident from the coverage map that extensive gaps exist and that guesswork is unavoidable. It is reasonable to fill in the blanks using the distribution of nutrients and of light: a substantial body of literature exists on the topic of modelling primary production from these parameters (Platt et al., 1977). Indeed, interpolation and extrapolation of productivity values

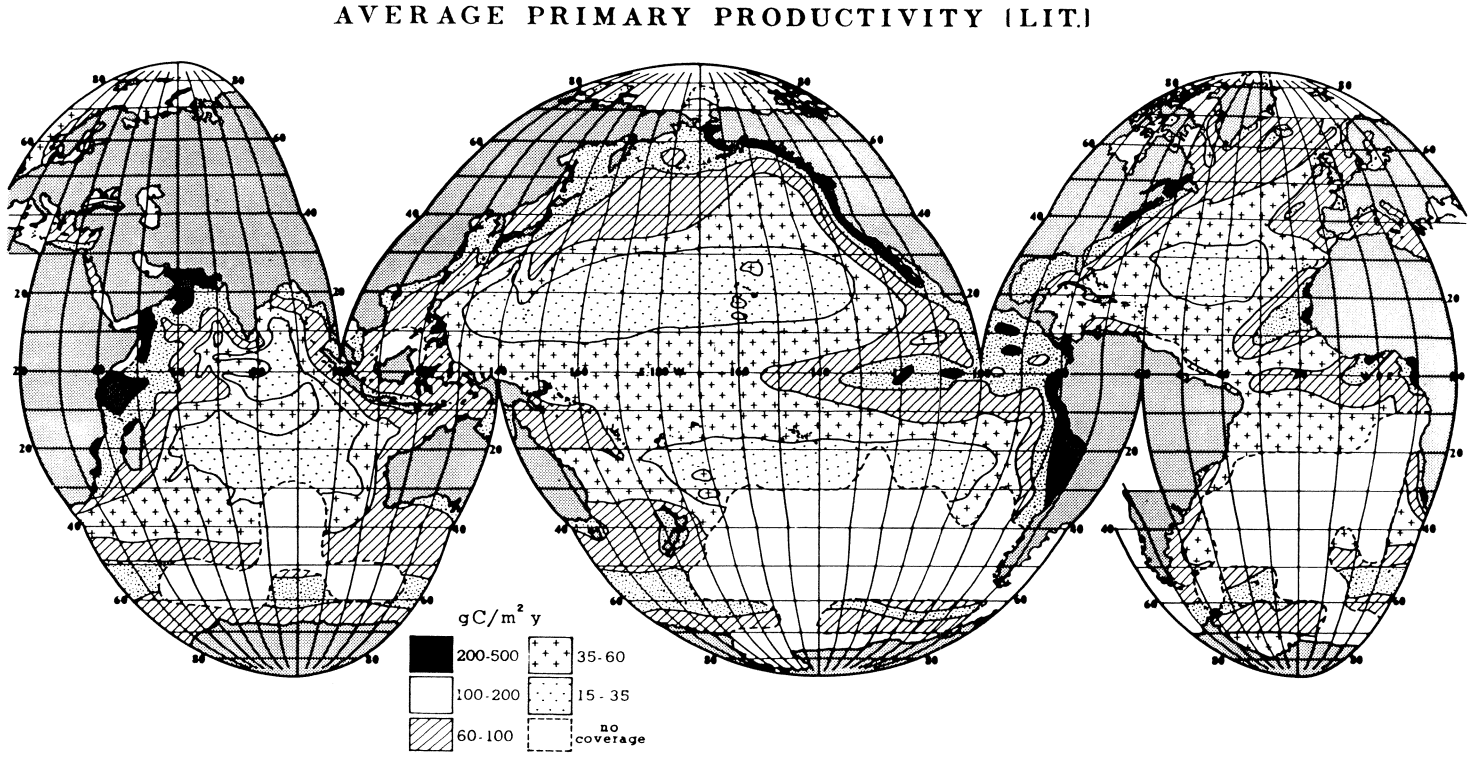

Figure 4. Average annual primary production of the global ocean based on selected data compiled from the literature (almost entirely radiocarbon determinations). Only vertically integrated productivity measurements were used. In areas with good data coverage syntheses were consulted; in those with spotty coverage (most of the ocean) averages were made considering the season(s) of measurement.

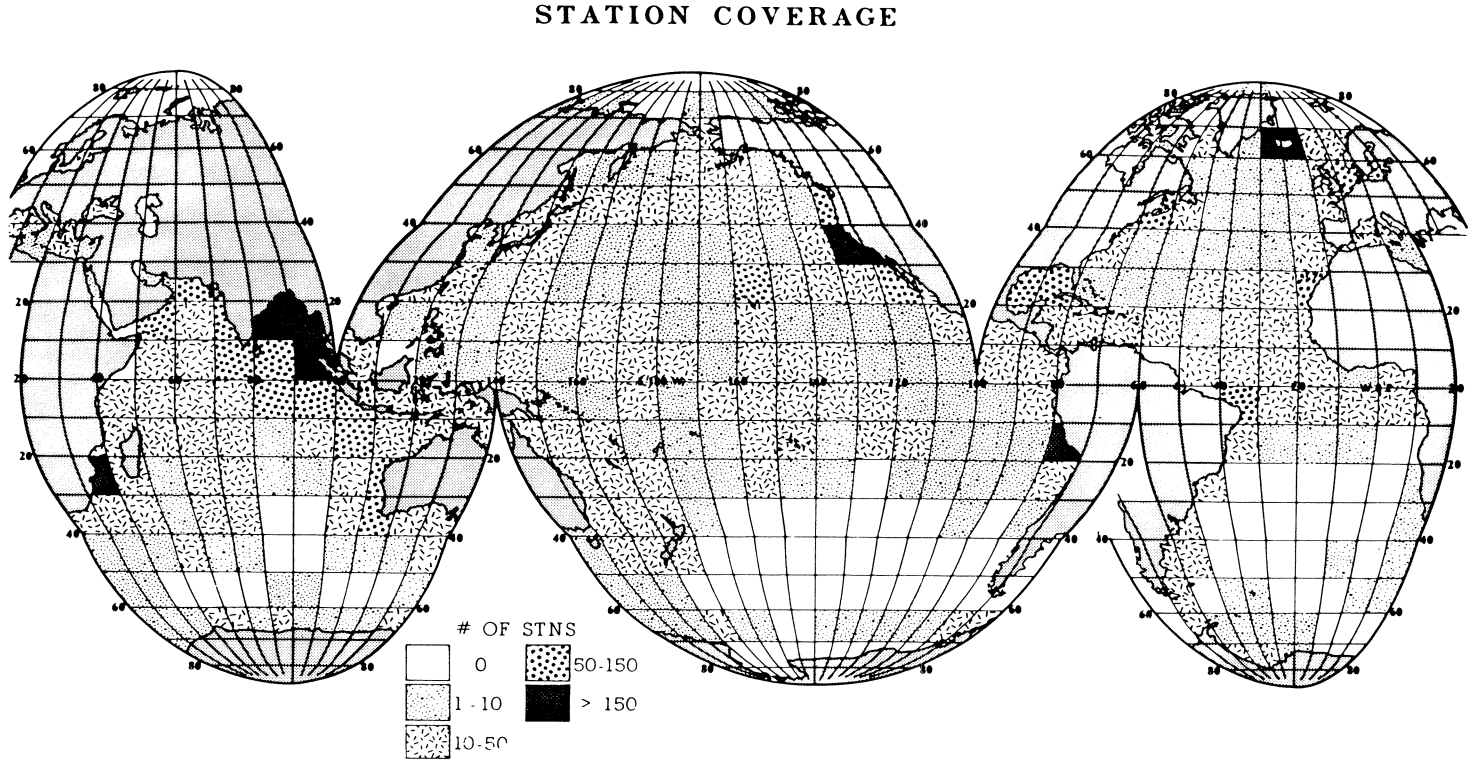

Figure 5.--Number of measurements available for producing Figure 4, per 10 degree square.

based on nutrient distributions has a long tradition, going back to Sverdrup (1955) and Fleming (1957) (see Fig. 6). Considering the amount of information available to these pioneers their maps are most remarkable, in particular the bold quantitative extrapolations of Fleming, based on the limited data from the Galathea Expedition.

The rather high values of productivity in Antarctic regions suggested in these early maps reflect the impressive evidence, from many expeditions and from fisheries, for enormous fertility of the Southern Ocean during the summer months. However, as an annual average, the estimates seem high compared with later studies (e.g., El-Sayed, 1970, Fig. 5; see, however, Rivkin and Putt, 1987), and perhaps indicate a tendency to overvalue the importance of availability of nutrients as compared with that of light.

To avoid similar bias, we used trial-and-error calculations to find algorithms for the conversion of phosphate concentration at 100m depth (P_{100}) and latitude into primary production values. Phosphate concentration was taken as a measure of availability of nutrients and latitude as an index for irradiance. For target productivity values we used various data sets from well-studied regions, spanning a wide range of latitudes and fertility. For the nutrient effect we assumed a relationship of the form

$$PP = \exp (P_{100} * (1 - P_{100}/a) + b) \qquad <1>$$

which combines an exponential growth response to nutrient supply with a negative feedback ($1 - P_{100}/a$) reflecting saturation as well as decrease in the thickness of the photic zone due to turbidity. The terms a and b are adjusted for best fit; b provides a lower limit for PP at very low nutrient concentrations, when recycling within the photic zone dominates the system entirely. From our data sets, we found that a=10 and b=3.1. With P_{100} measured in mmol per m^3, PP is in $gCm^{-2}yr^{-1}$, integrated over the photic zone. For phosphate distribution we used the map (see Fig. 7) of Reid et al., 1978.

Nutrient supply is only effective when light is supplied simultaneously. We define, therefore, an "effective phosphate concentration" as a function of latitude, as follows:

$$P_{eff} = P_{100} * \cos(L^3 / 79^3 * pi/2) . \qquad <2>$$

The cosine function expresses the assumption that irradiation is maximal at the equator and negligible at the poles. L is the latitude. The third power on L heavily weights the high latitudes, and the denominator sets the latitude (50 deg.) beyond which a decrease in irradiation first becomes significant. P_{eff} is entered into Equation 1 to obtain the estimate for primary production PP.

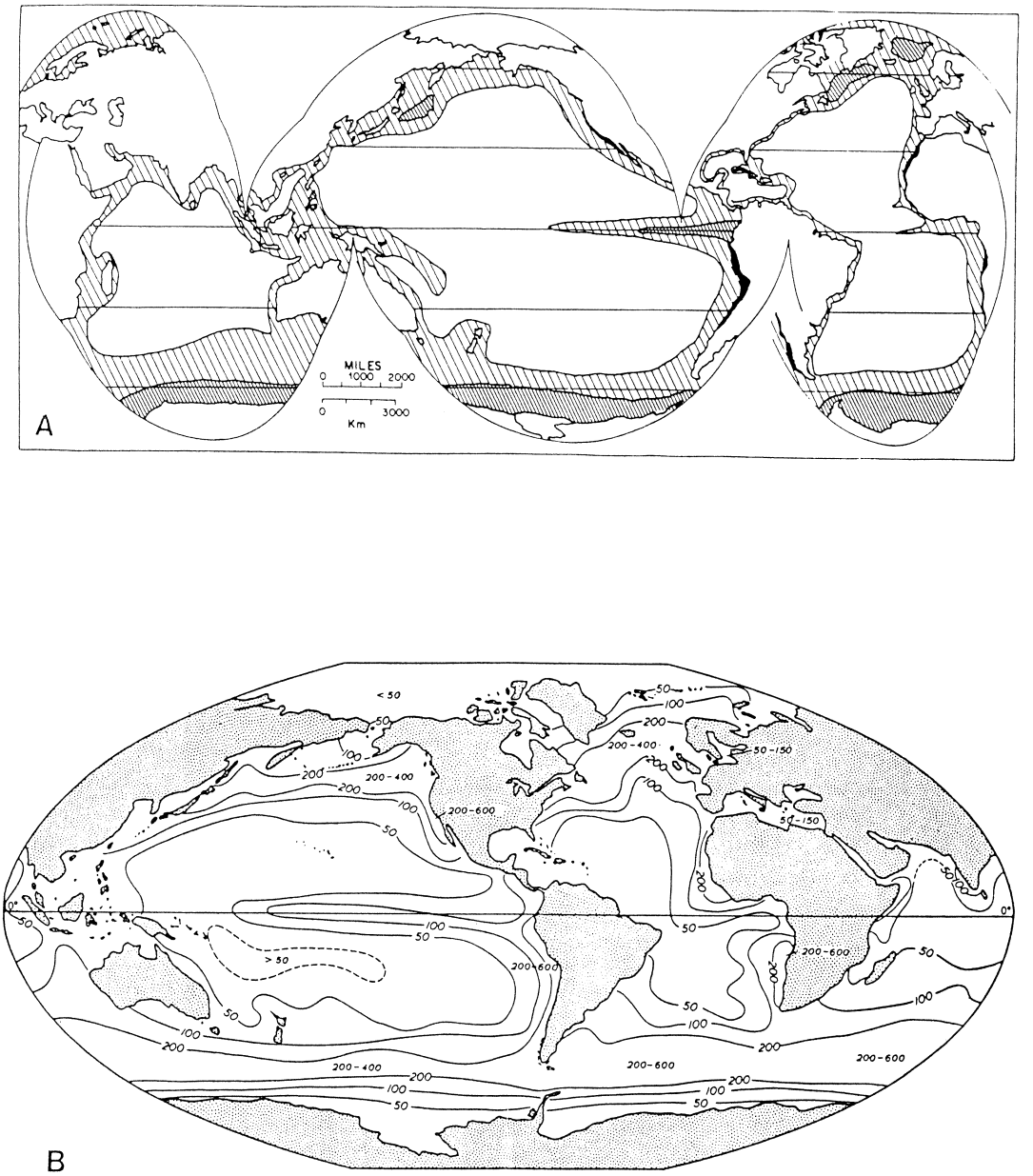

Figure 6. Early maps of primary production, based on a few measurements and the distribution of nutrients. a, Sverdrup (1955) "Schematic representation of the probable relative productivity of ocean areas. Heavy shading indicates very productive areas, light shading moderately productive regions"; b, Fleming (1957), contours in gC $m^{-2}y^{-1}$.

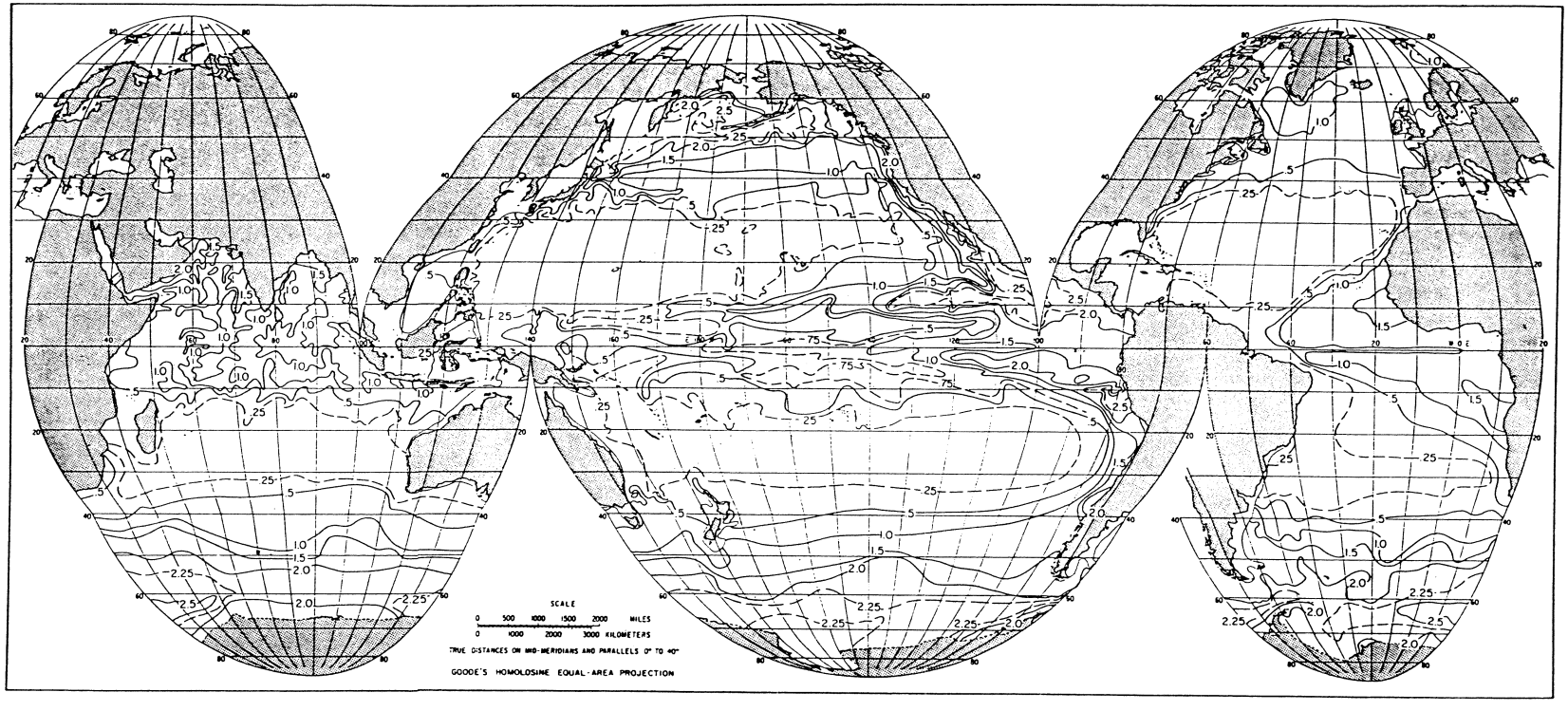

Figure 7. Distribution of phosphate at one hundred meters depth in the global ocean, in mmol per cubic meter. From Reid et al. (1978). Courtesy of J. Reid.

The use of these two functions provided very encouraging results for the open ocean, but failed for the coastal ocean. The reason is that mixing and upwelling are stimulated along the continents through onshore and offshore winds, eddy formation in boundary currents, and tidal dissipation. Thus, the rate of supply of nutrients from deeper waters is greatly enhanced along the coast.

We found that this effect is largely independent of the actual phosphate concentrations (although more detailed studies may show that a dependency does exist). We formulated a "distance-from-land effect" which simulates the presence of additional phosphate, as follows:

$$P_{apparent} = P_{100} + 10 / \{D \ . \qquad <3>$$

The distance from land, D, must be greater than 100km. The correction becomes insignificant for distances greater than 1000km.

The sequence of synthesizing a primary production map from phosphate at 100m, then, is Equation 3 to Equation 2 to Equation 1. The result of the transform exercise is shown in Figure 8. An overall similarity of the map based on the literature compilation (Fig. 4) and the map derived from the phosphate transform-equations (Fig. 8) is apparent. This similarity, of course, is not surprising because representative values in the first map (Fig. 4) formed the targets for the development of transform equations to generate the second (Fig. 8).

To obtain a sense of the goodness-of-fit between the compilation-based and transform-based maps, we averaged the primary production values for 10 degree squares for both, and calculated the percent difference (Fig. 9).

The difference map shows that the fit is quite good: for about one half of the area the transform is within 20% of the target, and over another one third, within 35%. The transform yields higher values (>35%) in about 10% of the squares, and lower ones in 5% (<35%). In effect, for 85% of the ocean, the transform values are within the range of uncertainty of the original compilation.

In some distinct regions notable discrepancies exist, and the transform may not adequately predict productivity here: (1) along the U.S. east coast and within the Gulf Stream, (2) in the trade-wind belt of the north-eastern Pacific, and (3) in the monsoon-dominated regions of the Indian Ocean. This indicates that the three factors we used are insufficient to parameterize the physical processes governing primary production.

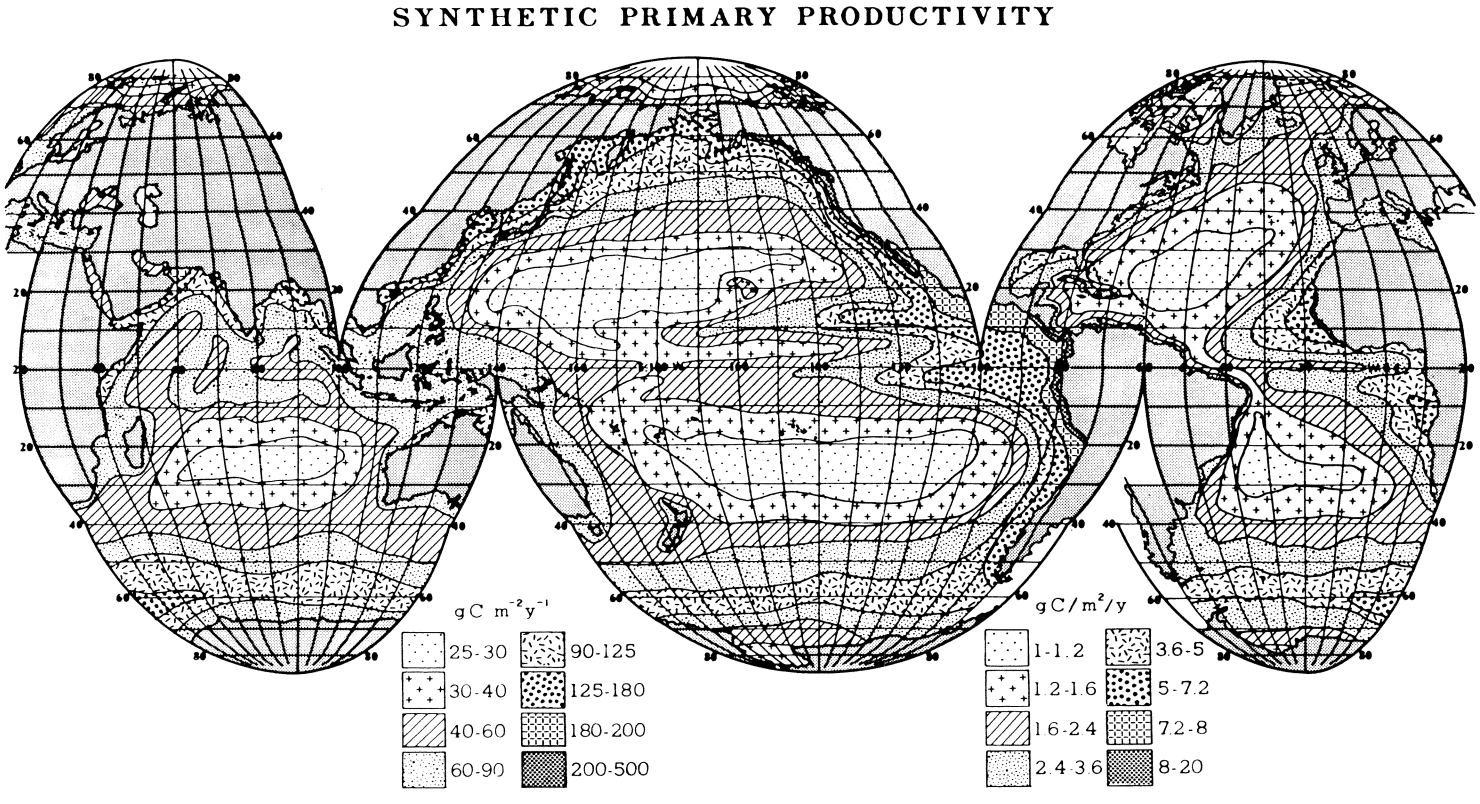

Figure 8. Map of calculated primary production of the world ocean (scale on left) and of J-flux from the photic zone at 400 to 500 m depth (scale on right). For export production at 200 m use 10 percent of scale on left. Calculations are based on (1) phosphate distributions (Fig. 7), (2) latitude, and (3) distance from shore (see text).

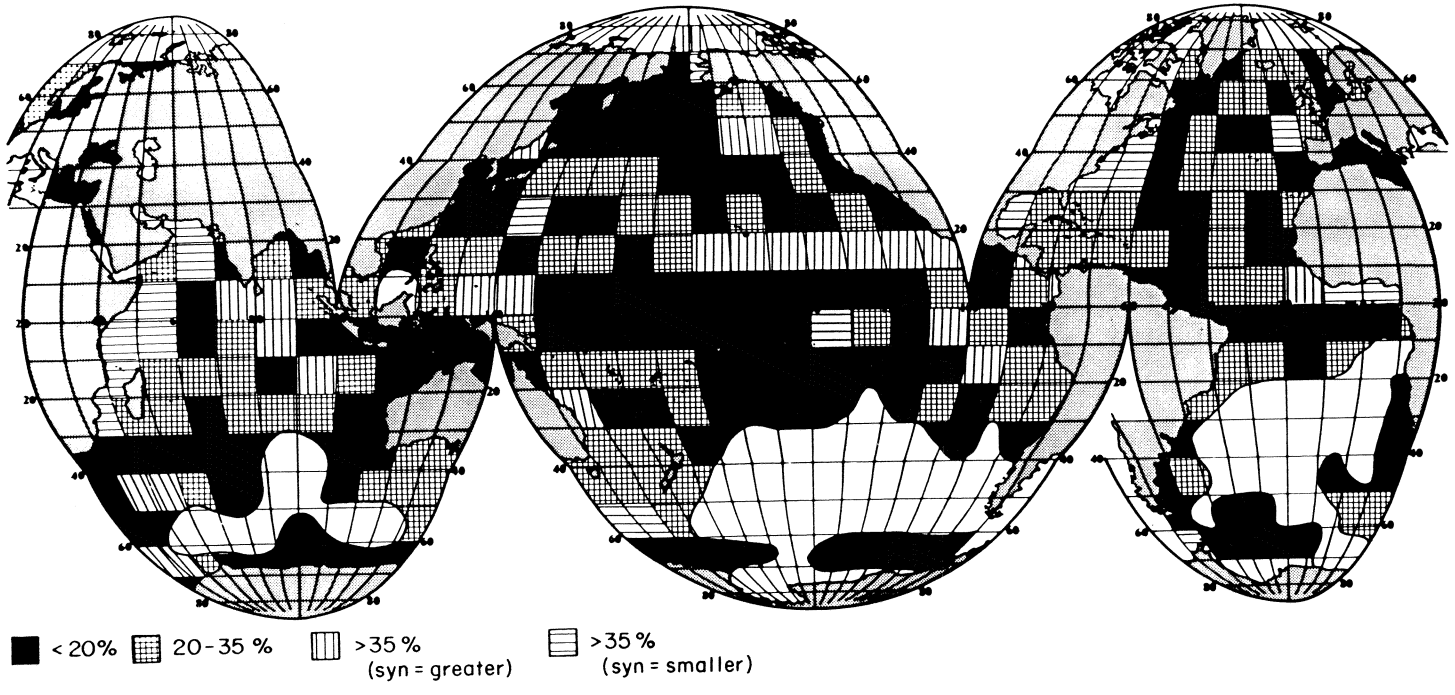

Figure 9. Difference between the calculated primary production (Fig. 8) and the PP-compilation (Fig. 4). Over most of the ocean the difference is less than a factor of 1.35. Systematic deviations appear in the monsoon regions (calculated values low off Africa, high south of India), in the North Equatorial Current in the Pacific (calculated values much too high), and in the Gulf Stream region (calculated values too low). Reasons presumably have to do with diverging and converging waters and depth of mixing.

Relationship to the shelf and distance from the shelf edge might be a better predictor than distance from the shore, for example. Simply redefining D in Equation 2 appropriately (in terms of distance to shelf edge, and with a minimum value tied to shelf water depth) would remove the low values along the eastern seaboard. It would also increase the PP values for the North Sea, and for the Indonesian shelf areas, where our values seem low compared with published and unpublished information of Dutch workers, by a factor of about two (Winfried Gieskes, pers. comm., April 1987). In addition, the strength of boundary currents, the intensity of upwelling, and the seasonality of mixed layer thickness, among others, will have to be investigated as possible factors for refinement of our simple algorithm. Again, we emphasize that the algorithm is not designed for inshore waters within less than 100km of the coast.

This same point also emerges from a matrix comparison of values by geographic region and productivity categories (Table 1). The extent of areas with similar productivity is much the same (this is especially clear when comparing Sections A and C), excepting the innermost part of the coastal ocean, that is, the category 200-500 gC $m^{-2}yr^{-1}$. This latter category is distinctly underrepresented by our algorithm. The reason is that the primary production associated with upwelling is dependent on a number of poorly constrained factors and is difficult to model (Harrison et al., 1980).

In Table 1 we also summarize the absolute values for annual productivity for the major ocean basins, based on Figure 4, and interpolating using nutrient distributions. Our value of 27 Gt C for the global ocean primary production compares well with published values. Sundquist (1985) lists 21 global marine primary productivity values obtained in the 1960's and 1970's. Our value of 27 is the median of these estimates. Eppley and Peterson (1979) give 19.1 and 23.7 as two separate estimates, while Romankevich (1984) suggests 25 Gt C for net primary production. A recent estimate by Martin et al. (1987), based on work in the northeast Pacific and comparisons with elsewhere, puts global open ocean productivity at 42 Gt C per year.

In this connection, the distribution of differences between the phosphate transform map and the Koblentz-Mishke map is of interest. Differences are minor over some large regions (Fig. 10, black and cross-ruled squares), but are substantial in others. Our calculated values are generally higher in the Pacific and the Southern Ocean and lower in the North Atlantic and in large portions of the Indian Ocean.

We hesiate to urge any one of the three maps at hand (Figs. 3, 4, 8) as clearly superior to the other two. Instead, we suggest that the differences give a good sense of the uncertainties involved in this type of compilation, at this particular level of effort. We prefer the phosphate transform map because it appears

Table 1. Estimates of Global Ocean Primary Production, Based on Information From Figures 4 and 8.

gC/m2.yr	a pacif	b cst	c ind	d cst	e atl	f cst	g seas	h arct	i anta	sum
A										
200-500	1	12	2	9	0	5	0	0	0	29
100-200	21	37	6	10	4	11	4	0	68	161
60-100	93	29	38	13	47	18	10	0	60	308
35-60	134	8	53	1	95	8	0	6	5	310
15-35	102	0	35	0	26	0	0	28	0	191
sum	351	86	134	33	172	42	14	34	133	999
B										
200-500	0	2	0	0	0	0	0	0	0	2
180-200	1	11	0	0	1	0	0	0	0	13
125-180	18	27	0	2	2	3	0	0	5	57
90-125	28	9	1	11	9	12	0	0	62	132
60-90	55	33	37	18	37	16	11	0	54	261
40-60	100	3	62	3	49	10	0	9	9	245
30-40	87	0	22	0	50	1	0	7	2	169
25-30	66	0	11	0	24	0	3	18	0	122
sum	355	85	133	34	172	42	14	34	132	1001
C										
200-500	0	2	0	0	0	0	0	0	0	2
100-200	36	43	1	9	8	10	0	0	42	149
60-100	66	37	37	22	41	21	11	0	79	314
35-60	152	3	75	3	79	11	0	13	10	346
15-35	101	0	20	0	44	0	3	21	1	190
sum	355	85	133	34	172	42	14	34	132	1001
D										
200-500	.1	1.3	.2	1.0	.0	.5	.0	.0	.0	3.1
100-200	1.1	1.9	.3	.5	.2	.6	.2	.0	3.4	8.1
60-100	2.5	.8	1.0	.4	1.3	.5	.3	.0	1.6	8.3
35-60	2.4	.1	1.0	.0	1.7	.1	.0	.1	.1	5.6
15-35	.9	.0	.3	.0	.2	.0	.0	.3	.0	1.7
sum	7.0	4.1	2.8	1.9	3.4	1.7	.5	.4	5.2	26.9

A: share (per mil) of ocean areas in the various production categories, for Figure 4. B: similar to A, for Figure 8. C: same as in B, but categories changed to make comparable with A. D: primary production in 10 GtC y^{-1} (gigatons per year). Categories: a open Pacific; b coastal Pacific; c and d Indian Ocean; e and f Atlantic; g adjacent seas, Atlantic; h Arctic; i Antarctic S of 50 S.

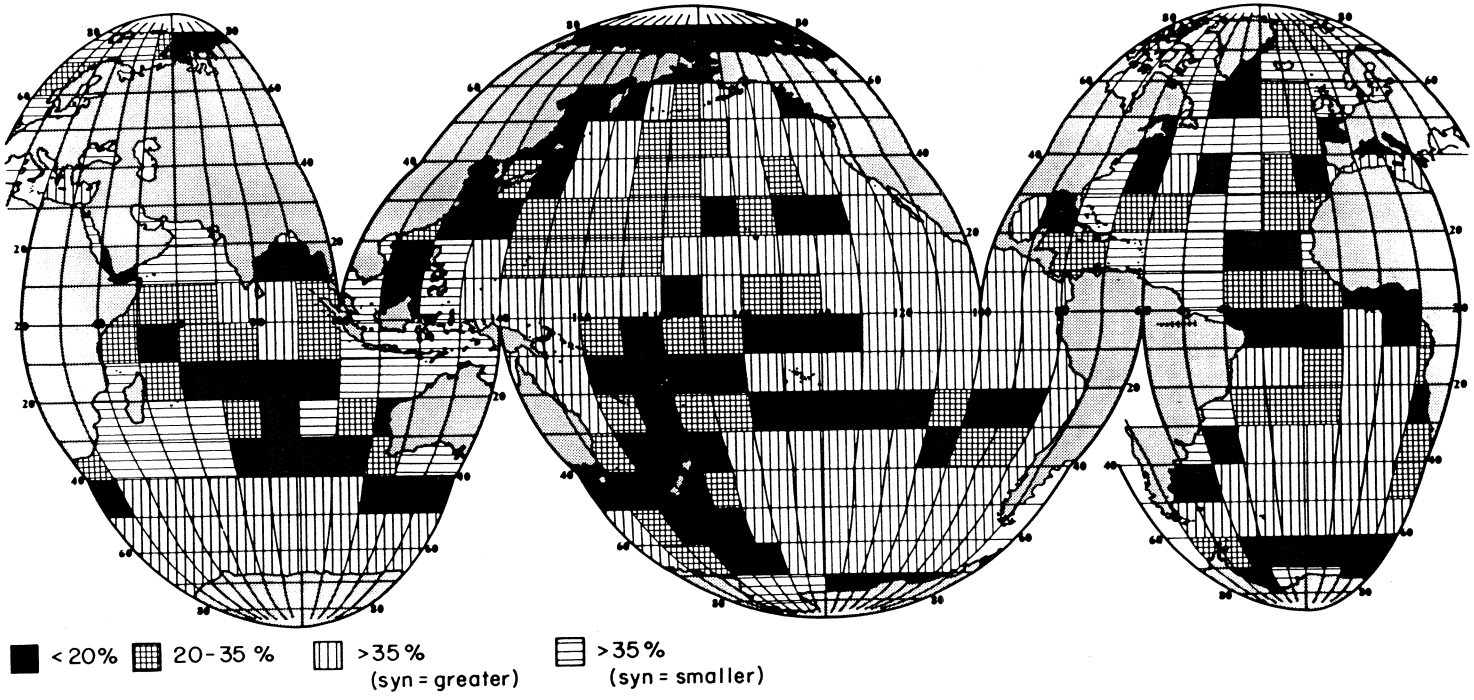

Figure 10. Difference between the calculated primary production (Fig. 8) and the original map of Koblentz-Mishke et al. (1970). Calculated values generally exceed those of K.-M. in the Pacific and in the southern oceans. Calculated values are low with respect to K.-M. in the western North Atlantic.

it is less subject to many of the errors mentioned, including inhomogeneous coverage. However, we do defer to measurement where these are available in sufficient density and quality. At this point, the synthetic map is a useful basis for discussion, and we employ it next to estimate the distribution of export flux from the fertile zone.

EXPORT PRODUCTION AND J-FLUX: PREVIOUS RESULTS

The most direct way to measure the downward export of particulate matter from the photic zone is to deploy traps to catch the falling material (Berger and Soutar, 1967). Systematic trapping surveys in the ocean began only about a decade ago (Wiebe et al., 1976; Honjo, 1978, 1980; Hinga et al., 1979; Knauer et al., 1979; Rowe and Gardner, 1979). Thus, data are still very sparse.

A first summary of ocean trapping data was published by E. Suess in 1980. Suess plotted the ratio carbon flux / mean annual primary production at each trapping site against depth of deployment, to obtain a sense of the export production and its fate in passage to the seafloor (Fig. 11).

Suess (1980) suggested the following equation to describe the relationship between flux at depth z and productivity PP:

$$J_z = PP / (0.0238 * z + 0.212); (z > 49m) . \qquad <4>$$

For 100m depth, which may be taken as the bottom of the photic zone, this equation yields $J_{100} = 0.386PP$, that is, it predicts that 38.6% of primary production leaves the upper water layer. The flux derived from this export decreases as 1/z with depth in the water column. The data (Fig. 11) indicate that this estimate is at the high end of the range. Thus, this equation tends to overestimate the flux just below the photic zone.

For depths below several hundred meters, the Suess equation reduces to

$$J_z = 40 * PP / z \qquad <5>$$

which seems to fit the mid-water data quite well. At abyssal depths, this equation underestimates the flux. The probable reason is that at greater depth the rate of decomposition slows greatly because the most easily oxidized matter disappears quickly in the (warmer) upper layers.

A reevaluation of Suess' analysis was offered by Betzer et al. (1984). They show two regression curves of J-flux on depth using Suess' compilation, one for high and one for low productivity. The one intersects 100m near 30%, the other near 15%. From their

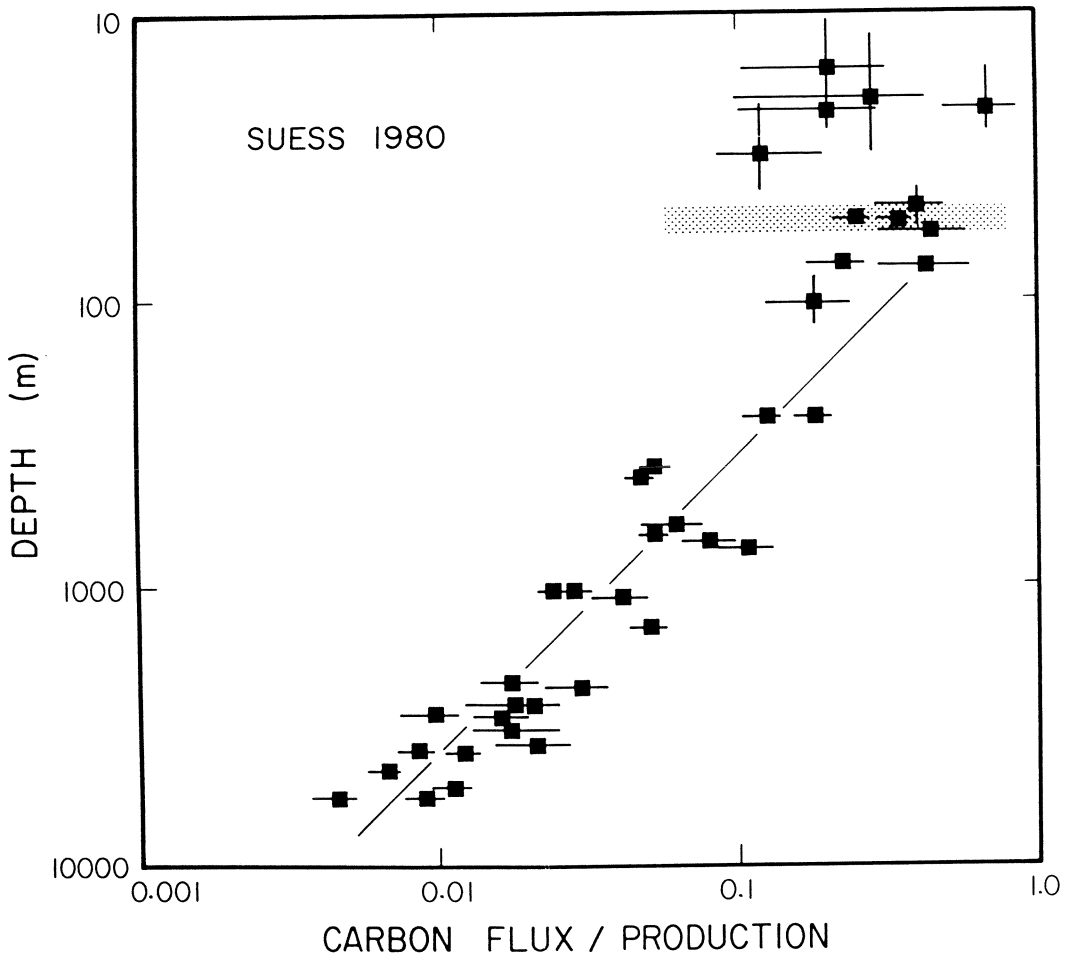

Figure 11. Compilation of trap data and fit of same by Suess (1980).

graph it is also evident that shallow traps were preferentially set in more productive waters, and deep ones in blue waters, which tends to confuse the issue concerning the relative importance of effects of productivity and of depth.

The equation Betzer et al. propose is:

$$J_z = 0.409 * PP^{1.41} / z^{0.628} . \qquad <6>$$

This formulation assumes that the portion of primary production exported grows as primary production increases. For a typical blue-water PP-value of 40gC $m^{-2}yr^{-1}$, for example, the equation predicts a carbon flux at 100m which is 10% of PP. For a typical green-water value of 160gC $m^{-2}yr^{-1}$, carbon flux at 100m is 18% of PP. This means that the flux expected from green-water production would exceed that from the blue-water by a factor of eight, rather than by a factor of four. The exponent on z expresses a decay which is slower than the 1/z rule of Suess.

There is no doubt that the Betzer et al. equation fits the data to which it was targeted very well indeed (Fig. 12). The question remains, of course, whether the findings from this fit can be generalized to the global ocean.

It is reasonable to look for a non-linear effect of productivity on the export flux. High productivity is invariably associated with a vigorous external supply of nutrients to the photic zone, consistent with transform Equations 1 and 3, discussed earlier. For steady state, this supply must be balanced by export of nutrients, that is, by downward flux of organic matter.

The downward flux is a constant portion of primary production only if internal nutrient recycling increases at the same rate as the production based on the external supply of nutrients, the "import-stimulated" production. This is unlikely because the efficiency of grazing (and hence of recycling) is decreased under bloom-type conditions. Under such conditions, grazing cannot keep pace with algal growth, and recycling decreases relative to import-stimulated production.

The relationship between primary production and export flux can be estimated from the measurements and generalizations on "new production" introduced by Dugdale and Goering (1967) and expanded by Eppley and Peterson (1979). The latter estimate a "new production" of 6% of primary production in oligotrophic waters, and one of 30% in coastal oceans (Table 2).

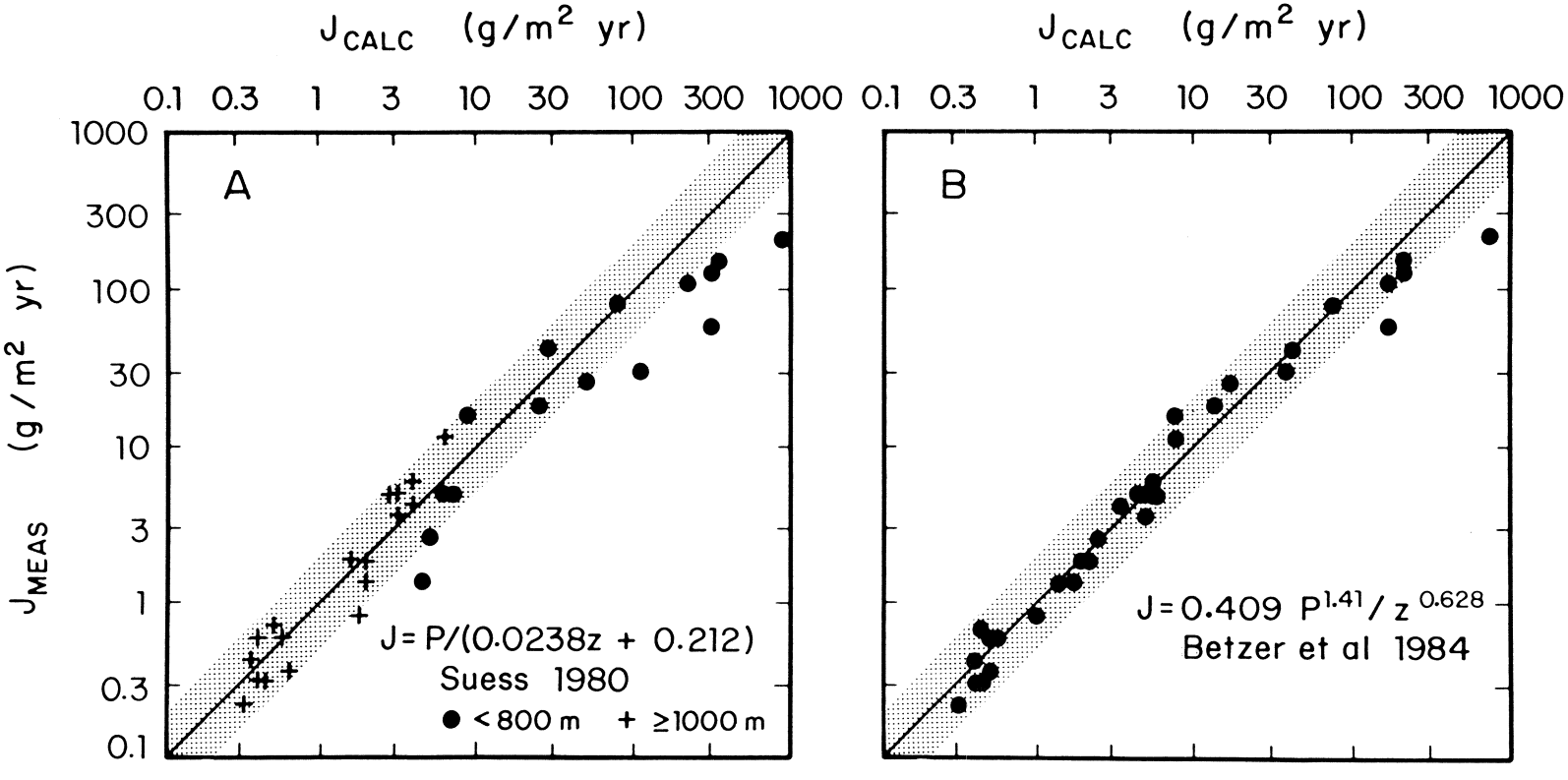

Figure 12. Data in Suess (1980), fitted by Suess equation (left) and by the equation of Betzer et al. (1984) (right).

Table 2. Estimates of New Production

Setting	PP ($gC\ m^{-2}y^{-1}$)	NP/PP (%)	% of total (weighted)
Oligotrophic waters	26	6	7
Transitional waters (gyre margins)	51	13	16
Equat. divergence and subpolar zones	73	18	34
Inshore waters	124	30	43
			100

(From Eppley and Peterson, 1979)

If we assume that the flux at 100m balances the "new production" (that is, the portion of productivity which is due to nutrients other than recycled ones), we obtain the following equation by fitting the values in Table 2:

$$J_{100} = 0.4 * PP^{1.9} / 100 . \quad <7>$$

This estimate assigns even greater importance to the magnitude of PP in determining J/PP than does the relationship proposed by Betzer et al. (1984) in Equation 6. Note, however, that for PP>500, which is a value occasionally found in upwelling situations, J_{100} exceeds 100% according to this equation. A negative feedback is called for so that J_z increases more slowly at high PP values. Based on a target of 50% for 500gC $m^{-2}yr^{-1}$ we suggest (1-PP/(1.5*PP+750)) for this term, so that Equation <7> becomes

$$J_{100} = 0.4 * (PP*(1-PP/(1.5*PP+750)))^{1.9} / 100 . \quad <8>$$

For PP >500 gC $m^{-2}yr^{-1}$, J/PP rises very slowly according to this equation. Eppley and Peterson (1979) suggest a ceiling on this rise by plotting a maximum of 50% for the proportion of "new production" at high productivity values. However, it appears to us that the proportion of externally supplied growth should be allowed to go well beyond 50%, and even approach 100 percent. Export production may not rise similarly because of lateral loss from a highly productive system which is no longer closed.

As concerns the decay of organic matter during settling, the 1/z rule of Suess (1980) would indeed seem to overestimate its rate, both in the open ocean and in coastal settings. In the latter, pulsing productivity tends to overwhelm the decompositional processes, and the production of heavy fecal pellets rich in clay and silt accelerates settling, so that little decay is expected to take place in transit to the seafloor for a large portion of the export production (Dunbar and Berger, 1981).

EXPORT PRODUCTION AND J-FLUX: REASSESSMENT

We next turn to the task of mapping the export production on a global scale, based on the primary productivity map, and appropriate J-flux algorithms. From the equations discussed it is apparent that the general form of the algorithm is

$$J_z = d(k_i * PP_i^{a(i)} / z^{b(i)}) \quad <9>$$

where k_i denotes the proportion of primary production of type i (e.g., dinoflagellates, diatoms, coccolithophores, etc.) which is available for export, a(i)>1 reflects the non-linear increase of export as productivity increases, and b(i)<1 describes the decreasing intensity of decay with depth, within each fraction of organic matter.

From the success of the Suess Equation (Fig. 11) we have seen that an approximation of the form

$$J_z = k * PP / z \qquad <10>$$

applies at least over limited depth intervals (say, 100m to 1000m) and for average values of productivity. Results based on a select data set (Fig. 13) suggest k=20. This means that 20% of the primary production leaves the photic zone at 100m, and 10% of the primary production remains as downward flux at 200m.

The data we have plotted in Figure 13, which include values published up to 1985, meet these two criteria: (1) trap depth was less than 1000m, and (2) primary production was measured concurrently with trap deployment. Of the 96 organic carbon flux measurements available (recorded at various depths in the water column), only 19 meet these criteria in Table 3(A).

A somewhat better fit than that provided by Equation 10 with k=20 is given by the expression

$$J(z) = 6.3 * PP / z^{0.8} . \qquad <11>$$

According to this equation, the decay is slower than that in the 1/z rule, and the input at 100m is 16% rather than 20%. For 200m the exported carbon is 9 percent of primary production. There is no indication in these data that the relationship of J to PP is non-linear, that is, the exponent on PP may be taken as 1. Of course, such a non-linear relationship may well exist and may become evident as more data are gathered. Equation 11 agrees well with results recently obtained by Martin et al. (1987), whose exponent on z of 0.858 is close to the 0.8 proposed here, and with those of Pace et al. (1987).

The conclusion from these observations is (as mentioned) that the primary production maps (Figs. 3, 4, 8) can be read directly as maps of estimated organic carbon flux, taking 16 percent at 100m, 9% at 200m, 7% at 300m, 5% at 400m, and 4% at 500m. Alternatively, following the arguments of Eppley and Peterson (1979) and of Betzer et al. (1984), we can use a non-linear transform of the type given in Equation 7. Non-linearity is expected especially for the pulsed productivity in high latitudes for which high J/PP ratios seem likely (cf. Nemoto and Harrison, 1981; Wefer et al., 1982).

For depths greater than 800m, the simple 1/z relationship is inadequate, leading to underestimation of the flux at deeper levels in the water column. Compared with the 1/z rule, fluxes at mid-water depths (1000-1500m) are much too high. Furthermore, increases of flux over that at shallower depths have been reported for mid-water levels (see Tables 3 and 4; Hinga et al., 1979; Knauer and Martin, 1981; Lorenzen, 1983; Fischer, 1984;

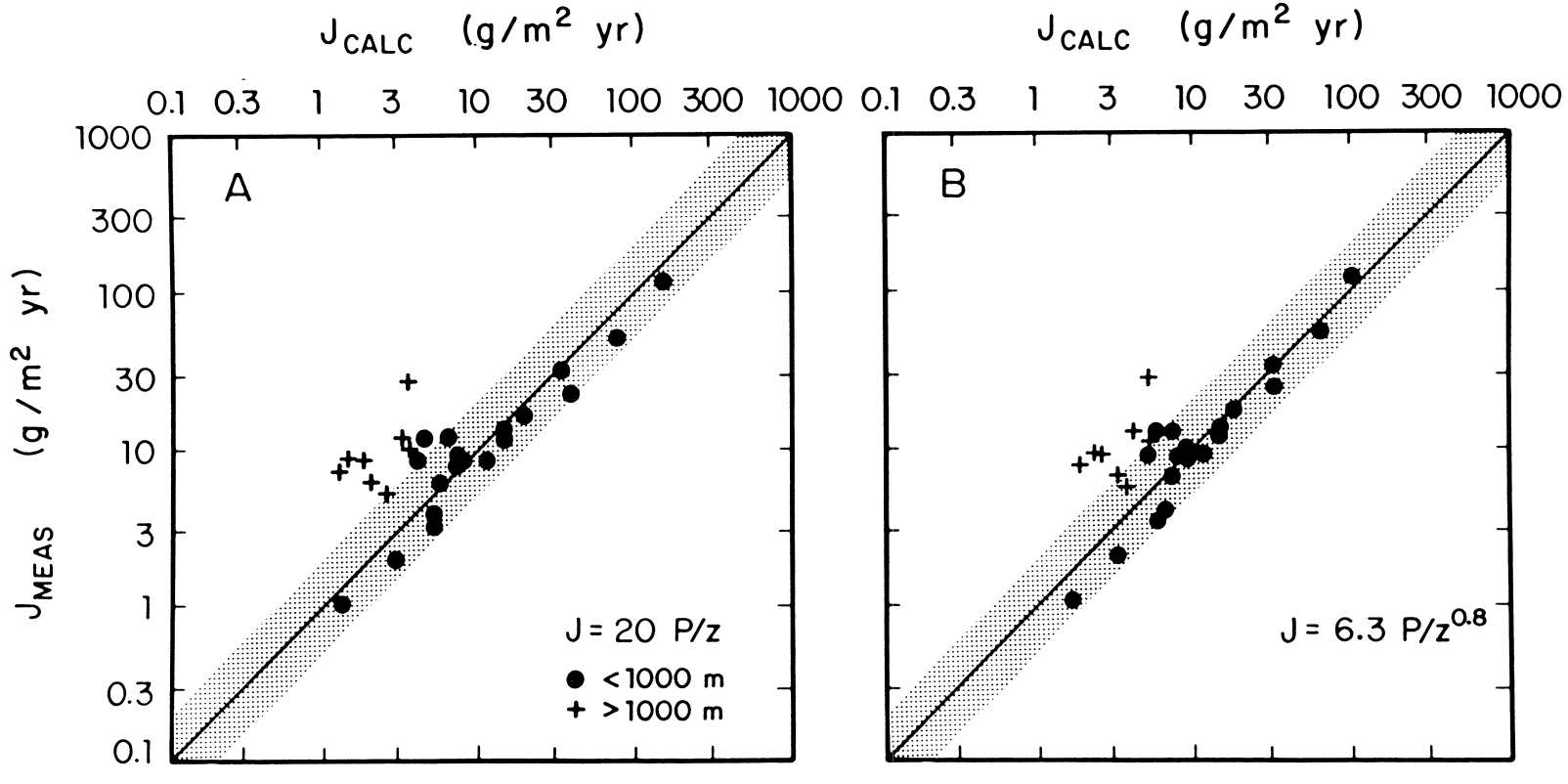

Figure 13. Selected post-Suess 1980 data (Table 3A) fitted by two equations, where z is in meters. Left: at 100 m the J-flux is 20% of primary production, and the 1/z rule applies to down to 1000 m. Right: best fit by regression.

Table 3. Published J-Flux Values, Pre-1986, Selected Data

A J-FLUX DATA FOR DEPTHS <1000m AND WITH PP MEASUREMENTS

REGION	J-FLUX	PP	J/PP(%)	DEPTH	SOURCE
CENTRAL	3.3	211	1.6	900	BETZER
PACIFIC	3.5	225	1.5	900	ET AL 1984
	1.9	119	1.6	900	
	1.0	55	1.8	900	
COASTAL	23.4	203	11.5	100	KARL,
(100KM OFF	15.1	203	7.4	200	KNAUER,1984
PT.SUR)	10.8	203	5.3	300	
	9.0	203	4.4	500	
	9.0	203	4.4	600	
	5.8	203	2.8	700	
	10.8	203	5.3	900	
COASTAL	112.7	264	42.8	35	KNAUER,
(100KM OFF	54.7	264	20.8	65	MARTIN,1981
PT.SUR)	28.8	264	10.9	150	
	9.0	264	3.4	500	
	8.3	264	3.1	750	
SUBARCTIC	12.2	178	6.9	250	LORENZEN
N.PACIFIC	11.2	178	6.3	600	ET AL 1983
	8.6	178	4.9	900	

B J-FLUX DATA FOR DEPTHS <1000m , FROM SUESS 1980

TROP.ATL.	2.5	50	5.0	389	HONJO,1978,1980
TROP.PAC.	1.3	40	3.2	378	
CNTR.N.ATL.	5.3	100	5.3	660	HINGA ET AL. 79
COASTAL	158.0	500	31.6	50	KNAUER ET AL. 79
(OFF CALIF)	92.0	500	18.4	250	
	42.0	500	8.4	700	
	33.0	150	22.0	50	
	19.0	150	12.7	250	
	17.0	150	11.3	700	
CNTR.N.PAC.	2.5	100	2.5	75	
	5.3	100	5.3	575	
COASTAL	65.0	460	14.1	55	SMETACEK ++ 78
OFF PERU	240.0	1200	20.0	50	v.BROECKEL 80
	130.0	600	21.7	70	ROWE,1979
	110.0	600	18.3	100	

C J-FLUX DATA FOR DEPTHS >900m AND WITH PP MEASUREMENTS

CENTRAL	10.1	203	5.0	1100	KARL,KNAUER
PACIFIC	5.4	203	2.7	1700	1984
	5.8	203	2.8	1950	
SUBARCTIC	10.8	178	6.1	1200	LORENZEN
N.PACIFIC	8.3	178	4.7	2000	ET AL 1983
	7.9	178	4.5	2500	
	6.8	178	3.8	3000	
COASTAL	25.9	264	9.8	1500	KNAUER,
					MARTIN, 1981

Table 4. Published J-Additional J-Flux Data, Pre-1986, PP Estimated from Maps.

REGION	J-FLUX	PP	J/PP(%)	DEPTH	SOURCE
E.TROP.	16.9	184	9.2	100	KARL ET
N.PACIFIC	9.4	184	5.1	150	AL 1984
	3.1	184	1.7	550	
	3.3	184	1.8	650	
	4.0	184	2.2	750	
SANTA BAR-	9.4	270	3.5	341	DYMOND
BARA BSN	8.6	270	3.2	381	ET AL 1981
	9.7	270	3.6	213	
	6.1	270	2.3	328	
	6.1	270	2.3	162	
PANAMA BSN	4.5	173	2.6	667	HONJO ET
	3.2	173	1.9	1268	AL 1982
	3.2	173	1.9	2265	
	3.9	173	2.3	2869	
	4.1	173	2.4	3769	
	3.8	173	2.2	3791	
	3.5	173	2.0	890	HONJO 1982
	3.9	173	2.3	2590	
	4.9	173	2.9	3560	
E.TROP.	1.3	155	.9	505	FISCHER 1984
N.PACIFIC	1.9	155	1.2	1465	
	1.1	155	.7	3075	
	1.4	155	.9	3225	
	1.5	155	1.0	3415	
	1.4	155	.9	3545	
	.9	101	.9	635	
	1.3	101	1.3	1565	
	1.3	101	1.3	2700	
	1.8	101	1.7	2883	
	1.4	101	1.4	3050	
OFF BERMUDA	.7	72	1.0	3200	DEUSER 1984
SUBARCTIC	5.4	99	5.5	1000	HONJO 1984
N.PACIFIC	3.5	99	3.5	3800	
SOHM ABYS.	.9	30	2.9	976	HONJO 1978
PLAIN	.3	30	1.1	3694	
	.4	30	1.5	5367	
DEMERARA	2.4	40	6.1	389	HONJO 1980
ABS.PLAIN	1.4	40	3.5	988	
	.6	40	1.5	3755	
	.6	40	1.5	5068	
E.HAWAII	1.3	50	2.6	378	
ABS.PLAIN	.4	50	.8	2778	
	.3	50	.6	4280	
	.2	50	.5	5582	
OFF ECUADOR	2.0	151	1.3	2570	COBLER,DYM.80
OFF BAHAMAS	5.2	61	8.5	660	HINGA ET
GULF STREAM	10.8	58	18.8	1350	AL 1979
	5.4	144	3.8	3520	
OFF BAHAMAS	2.0	58	3.4	2100	WIEBE ET AL 76
OFF CALIF.	155.9	432	36.1	50	KNAUER ET
	90.7	432	21.0	250	AL 1979
	41.4	432	9.6	700	
	32.4	432	7.5	50	
	18.7	432	4.3	250	
	16.9	432	3.9	700	
CENTRAL	24.5	40	61.8	75	
N.PACIFIC	5.4	40	13.6	575	
	4.3	40	10.9	1050	
GULF STREAM	6.5	180	3.6	2160	ROWE AND
	3.5	180	1.9	2800	GARDNER 79
	5.4	108	5.0	3500	
ROCKALL PL.	67.7	59	114.6	55	SMETACEK+ 1978
OFF PERU	236.5	345	68.6	50	v.BROECKEL 80
	128.2	345	37.2	70	ROWE 1979
	108.4	345	31.4	100	
ANTARCTIC	5.3	90	5.9	965	WEFER ET AL
	4.7	90	5.2	2540	1982

Karl and Knauer, 1984; Karl et al., 1984; also see Urrere and Knauer, 1981). Several possible reasons have been put forward for these observations: lateral influx of organic matter at depth, repackaging of slowly settling particles by deep-living zooplankton, shallow-water foraging and mid-water excretion by vertically migrating animals (bypassing), as well as other mechanisms.

The simplest hypothesis is that deviation from the 1/z rule occurs because the concentration of the less readily decomposing material within the settling organic matter increases with time and hence with depth (cf. Westrich and Berner, 1984). To take account of both the rapid decay in shallower depths and the slow decay at deeper ones, we must add at least one more term. For example:

$$J(z) = 9*PP/z + 0.7*PP/z^{0.5} \qquad <12>$$

where the flux at 100m is made up of a portion (56%) which decays rapidly, as before, and another (44%) which decays increasingly more slowly, corresponding to a square-root function of depth. A very similar decay structure can be achieved by adding together these two terms

$$J(z) = 20*PP/z + PP/200 \; . \qquad <13>$$

In this equation a slowly decaying fraction (0.5% of primary production) is added to the fast-decaying one. The difference between Equations 12 and 13 only becomes important below 4000m depth. Both fit the available data quite well (Fig. 14; data in Tables 3 and 4).

The J-flux patterns created by the various equations under discussion are shown in Table 5. It is apparent that it is information on fluxes which is lacking, rather than equations to fit the data. If we use the "best-fit" for the upper 1000m (Eq. 11, J1 in Table 5), we obtain the following export production values (GtC $m^{-2}y^{-1}$): 4.3 at 100m, 2.4 at 200m, and 1.8 at 300m. For comparison (with the 100m value), Eppley and Peterson (1979) suggest 3.5 and 4.7 GtC $m^{-2}y^{-1}$ for new production, in two separate estimates. Martin et al. (1987) propose 7.4 GtC $m^{-2}y^{-1}$ for J_{100}.

SUPPLY TO THE SEAFLOOR, BENTHIC RESPIRATION, AND GEOLOGICAL IMPLICATIONS

The various J-flux equations predict that a certain amount of the organic matter leaving the fertile zone should reach the seafloor, to be oxidized or to be buried. Depending on the depth of the seafloor, anywhere between 1 and 10% (or more in certain coastal regions) of the primary production might be expected to

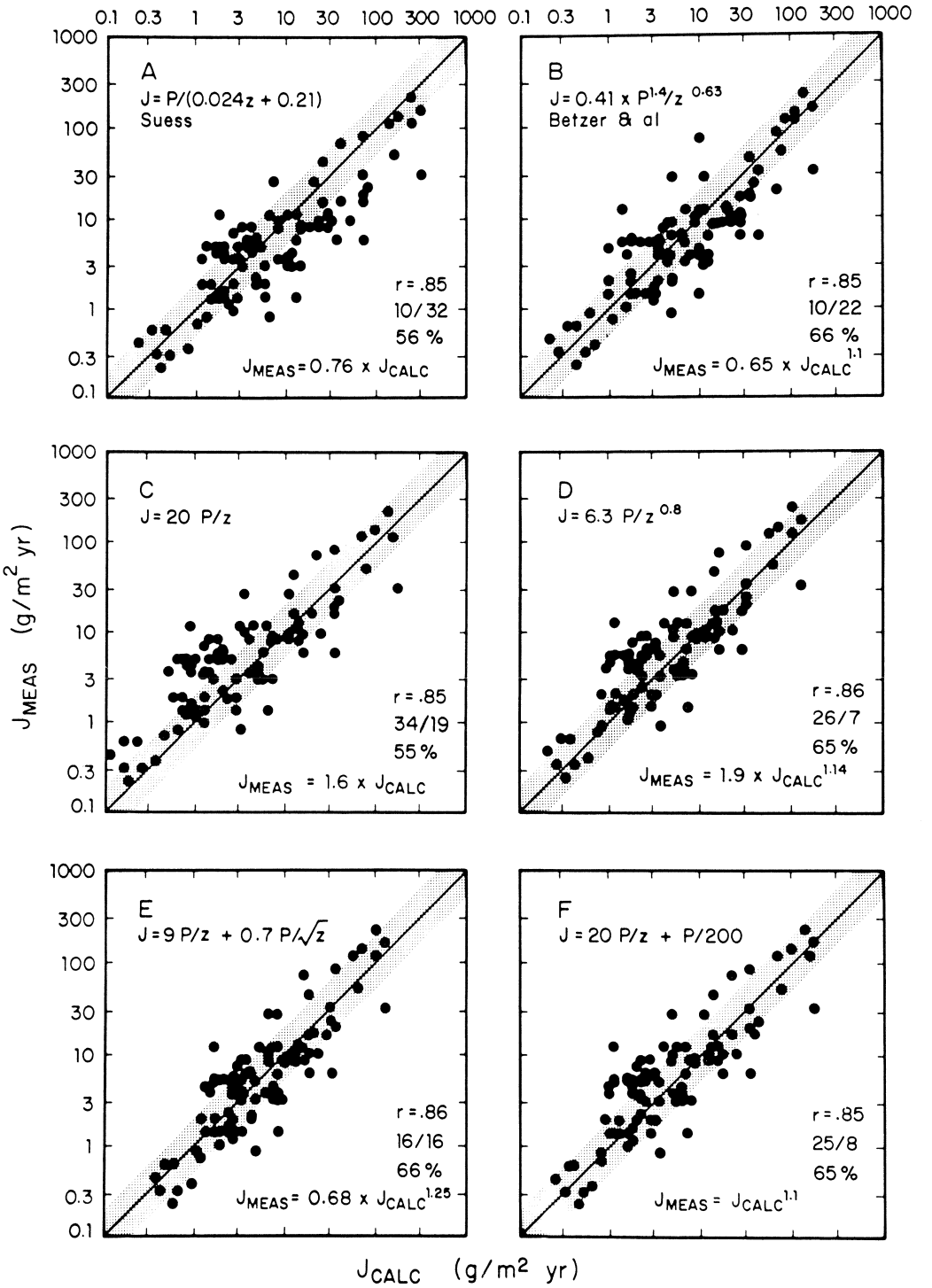

Figure 14. Fits to all available trapping data (pre-1986) using a number of equations, including those proposed by Suess (1980) (upper left) and by Betzer et al. (1984) (upper right). Each panel shows the correlation coefficient r, the number of points to the left and right of one standard deviation (e.g., 10/32), the percentage of points within one standard deviation, and the regression of the estimated on the measured J-flux.

Table 5. J-Flux Patterns Created by Various Equations Relating Organic Carbon Flux to Primary Production and Depth of Arrival (Values in Percent of PP).

EQUATIONS J(z)=f(PP,z)

J1=6.3*PP/z^0.8 (BEST FIT, SEL. DATA <1000M)
J2=20*PP/z (SIMPLEST FIT, SAME DATA)
J3=9*PP/z+0.7*PP/z^0.5 (GOOD FIT, ALL DATA)
J4=17*PP/z+PP/100 (GOOD FIT, REFRACTORY CARBON)
J5=PP/(0.0238*z+0.212) (SUESS, 1980)
J6=0.41*PP^1.41/z^0.628; PP=40 (BETZER ET AL 1984)
J7=0.41*PP^1.41/z^0.628; PP=160 (BETZER ET AL 1984)
J8=0.41*PP^1.41/z^0.628; PP=480 (BETZER ET AL 1984)

DEPTH	J1	J2	J3	J4	J5	J6	J7	J8
100	15.82	20.00	16.00	18.00	38.58	10.30	18.20	28.53
200	9.09	10.00	9.45	9.50	20.11	6.67	11.78	18.46
300	6.57	6.67	7.04	6.67	13.60	5.17	9.13	14.31
400	5.22	5.00	5.75	5.25	10.28	4.31	7.62	11.95
500	4.37	4.00	4.93	4.40	8.26	3.75	6.62	10.38
600	3.77	3.33	4.36	3.83	6.90	3.34	5.91	9.26
700	3.34	2.86	3.93	3.43	5.93	3.04	5.36	8.41
800	3.00	2.50	3.60	3.13	5.19	2.79	4.93	7.73
900	2.73	2.22	3.33	2.89	4.62	2.59	4.58	7.18
1000	2.51	2.00	3.11	2.70	4.16	2.43	4.29	6.72
1250	2.10	1.60	2.70	2.36	3.34	2.11	3.73	5.84
1500	1.81	1.33	2.41	2.13	2.78	1.88	3.32	5.21
1750	1.60	1.14	2.19	1.97	2.39	1.71	3.02	4.73
2000	1.44	1.00	2.02	1.85	2.09	1.57	2.77	4.35
2250	1.31	.89	1.88	1.76	1.86	1.46	2.58	4.04
2500	1.21	.80	1.76	1.68	1.67	1.36	2.41	3.78
2750	1.12	.73	1.66	1.62	1.52	1.29	2.27	3.56
3000	1.04	.67	1.58	1.57	1.40	1.22	2.15	3.37
3250	.98	.62	1.50	1.52	1.29	1.16	2.04	3.21
3500	.92	.57	1.44	1.49	1.20	1.10	1.95	3.06
3750	.87	.53	1.38	1.45	1.12	1.06	1.87	2.93
4000	.83	.50	1.33	1.42	1.05	1.02	1.79	2.81
4250	.79	.47	1.29	1.40	.99	.98	1.73	2.71
4500	.75	.44	1.24	1.38	.93	.94	1.67	2.61
4750	.72	.42	1.21	1.36	.88	.91	1.61	2.53
5000	.69	.40	1.17	1.34	.84	.88	1.56	2.45
6000	.60	.33	1.05	1.28	.70	.79	1.39	2.18
7000	.53	.29	.97	1.24	.60	.71	1.26	1.98
8000	.48	.25	.90	1.21	.52	.66	1.16	1.82

fuel benthic life. From the results presented (Tables 1 and 5), the coastal ocean area (18% of total), with typical production values near 150 gC $m^{-2}yr^{-1}$, generates 9 of the ocean total of 27 gigatons of carbon, that is, one third. Together with subpolar regions the rims of the ocean produce one half the total. Because of pulsing productivity and shallowness of seafloor, a substantial portion of this would be available to the benthos (say, between 1.5 and 2.5 gigatons). For the deep ocean, with an average depth of 4000m, only about 0.4 gigatons would arrive each year: a rate of supply per area which is lower by more than a factor of ten. Romankevich (1984, Fig. 39) suggests that between 1.2 and 3.3 GtC reach the bottom, on the whole.

Whatever reaches the seafloor is used rather efficiently, at least in the deep sea: there is a marked decrease, within the uppermost centimeter or so, in the concentration of organic matter in deep sea sediments (Fig. 15).

Also, there is evidence from oxygen profiles that the bulk of the oxidation process takes place in the uppermost few millimeters of the sediment (Reimers et al., 1984). It appears, then, that organic matter arriving at the seafloor is quickly used, and little remains for burial. To a first approximation, in the deep ocean, the utilization of organic matter equals the input to the seafloor, that is, the gross deposition (Bender and Heggie, 1984).

One quantitative measure of the rate of oxidation of organic materials on the seafloor is the rate of oxygen uptake, that is, benthic community respiration (Pamatmat and Banse, 1969). Measurements vary over several orders of magnitude, partly because of the use of inappropriate techniques (Smith and Hinga, 1983). The in situ techniques pioneered by K. Smith yield respiration rates which are more or less in accord with the postulate that 90% of the gross deposition is oxidized (Fig. 16).

The values of predicted respiration in Figure 16 were calculated according to the J-flux Equation 13 as follows:

$$J_{sf} = 20\ PP\ /\ Dp + PP/200 \qquad \langle 14 \rangle$$

where sf stands for seafloor, and Dp is its depth. For the calculations, depth was taken as 200, 1000, 2000, 3000, 4000, 5000, and 6000 meters, in succession. Calculations were made separately for the Atlantic and Pacific continental margins. The typical distance-from-shore to depth-of-water relationship was taken to be

$$Dist = a\ Dp^{b} + Dp^{3}\ /\ c \qquad \langle 15 \rangle$$

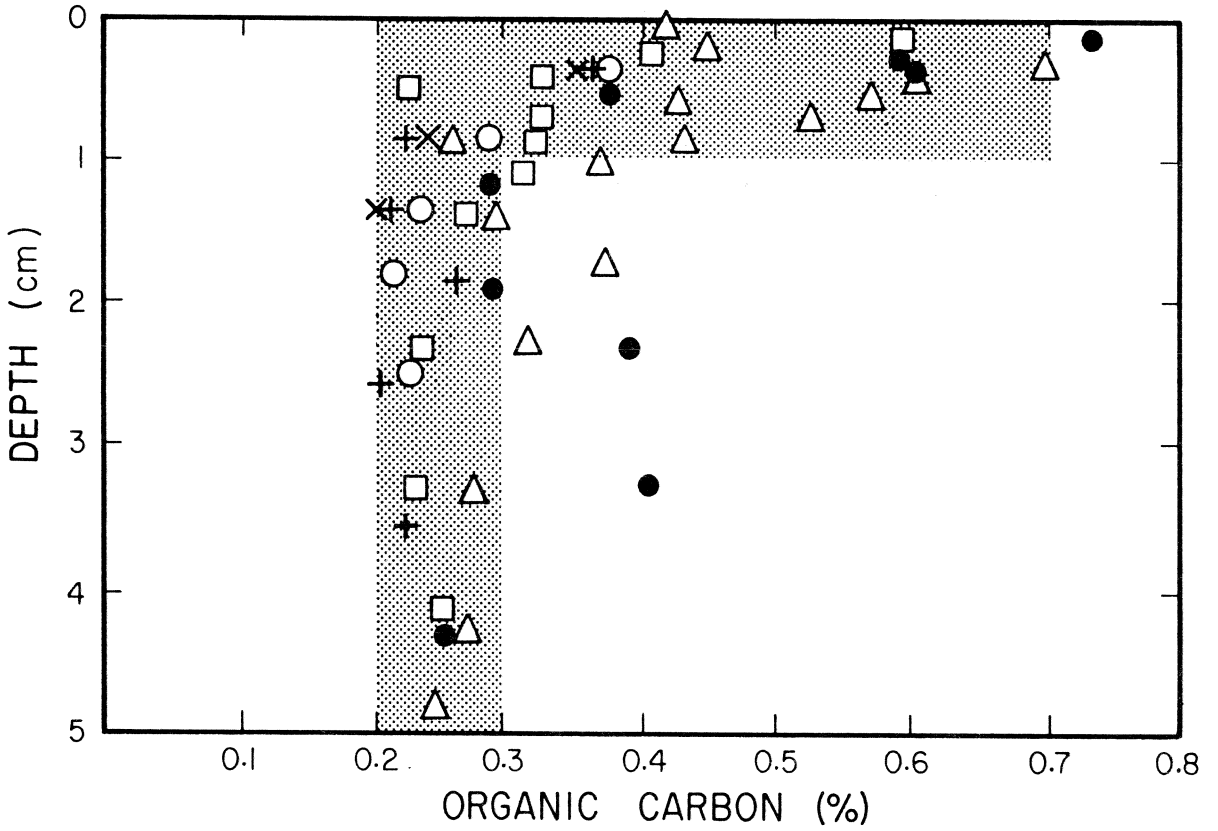

Figure 15. Particulate carbon concentration in box cores from MANOP Site C, equatorial Pacific (140 degr. W), showing rapid disappearance in the uppermost centimeter. Adapted from Emerson et al. (1985).

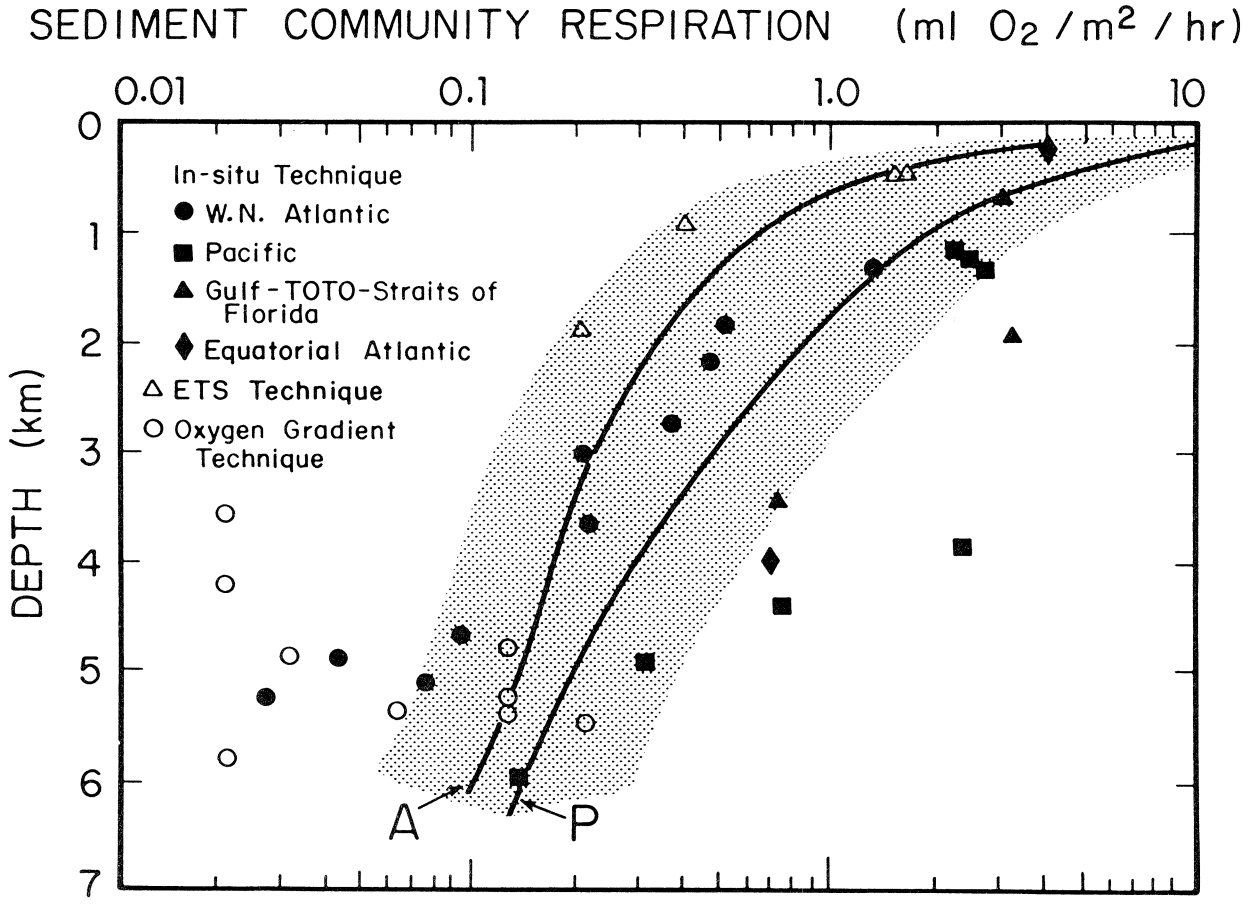

Figure 16. Calculated oxygen uptake on the seafloor as a function of depth, off the East Coast (line marked A) and off the Pacific Coast (line marked P), based on (1) regular decrease of primary production away from the coast, (2) typical depth-to-distance relationship for the Atlantic and the Pacific margins, and (3) J-flux equation. Shaded zone denotes factor of two about the estimates. Measurements shown for comparison are given in Smith and Hinga (1983).

based on inspection of the continental margins off the east and west coasts of the U.S.A. For the Atlantic side, parameters were set as follows: a=25; b=1/3; $c=5*10^8$. For the Pacific, they were set at a=1.5 and b=1/2, c remaining the same. The difference in settings describes the fact that the shelf edge is very close to shore in the Pacific compared to the Atlantic and that the continental slope is much steeper in the Pacific.

From the productivity maps, an estimate was made that primary production off the west and east coasts depends on distance in km from the shore, such that

$$PP = 10^4 / (Dist^{0.85} + 200 / Dist) + 20 . \qquad <16>$$

This set of equations, then, produces the J-flux to the seafloor from depth to the seafloor. Results show a very good fit of predicted values with measured respiration in the Atlantic. Also, the observed differences in respiration for the Atlantic and the Pacific are duplicated by this simple algorithm. It appears, then, that the differences in hypsography of eastern and western margins are sufficient to explain the coarse features of the benthic respiration patterns plotted by Smith and Hinga (1983).

To some degree, the result that bathymetry alone predicts bottom respiration may be fortuitous. The effect on productivity of low nutrient values in the North Atlantic, ultimately a consequence of anti-estuarine circulation (Redfield et al., 1963), may just be compensated by the increased pumping and mixing of deep waters along the shelf edge, from vigorous eddy-formation by the Gulf Stream.

It is interesting that at great depth the Atlantic shows unexpectedly low values of respiration, and the Pacific unexpectedly high ones throughout. Mechanisms which could be responsible for these patterns are differences in winnowing and shelf-bypassing (e.g., Walsh, 1981; Walsh et al., 1981, 1985; see, however, Rowe et al., 1986), as well as differences in the efficiency of downslope transport, which depends on intensity of bioturbation and steepness of the slope.

In conclusion, in interpreting the difference in the respiration patterns on the Atlantic and the Pacific slopes several factors have to be taken into account: (1) the blue-versus-green dichotomy which permeates the ocean's productivity patterns, together with the fact that the Atlantic seaboard is a trailing edge (wide shelf, gentle slope), and the Pacific one a leading edge (narrow shelf, steep slope), in the context of plate tectonics, (2) the Pacific-Atlantic deep water asymmetry (Redfield et al., 1963; Berger, 1970), and (3) the eastern boundary versus western boundary current asymmetry, with its different types and abundances of eddies and mixing processes.

The difference in respiration on the seafloor in offshore transects in the North Pacific and the North Atlantic has also been interpreted as indicating a generally higher productivity in the Pacific than in the Atlantic (Hinga, 1985). Our map (Fig. 4) does not support this suggestion, and Table 1 suggests that the overall values of productivity of Pacific and Atlantic (total production divided by area) are much the same.

The blue-green contrast which permeates all arguments about ocean carbon flux (or should) may be gauged by the observation that coastal productivity exceeds open ocean productivity by a factor of five to ten. The large shelf-width of slowly sinking margins, such as that of the Atlantic, tends to remove the trailing-edge slope from the highly productive coastal strip. This should lead to relatively low respiration values and, presumably, to low rates of carbon burial relative to tectonically active margins with narrow shelves and steep slopes, as on the Pacific side.

As concerns Pleistocene productivity variations, the disappearance of shelves during maximum glaciation would, according to the present analysis, result in pronounced increases in benthic productivity and carbon burial rates on continental slopes. Such changes have been documented (Mueller and Suess, 1979; Mueller et al., 1983; Lutze et al., 1986; Gardner and Hemphill-Haley, 1986; Sarnthein et al., 1987), but they may in fact be larger than expected from the shelf-effect alone.

During glacial buildup and sealevel fall, the increased burial of organic matter due to narrowing shelves should have led to a drawdown of atmospheric CO_2. This effect would constitute a positive feedback on climatic cooling and ice buildup which may be partly responsible for translating Milankovitch forcing (Imbrie and Imbrie, 1980) into Quaternary climate fluctuations.

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REFERENCES

Barber, R.T., and Chavez, F.P., 1986. Ocean variability in relation to living resources during the 1982-1983 El Nino. Nature 319:279-285.

Bender, M.L., and Heggie, D.T., 1984. Fate of organic carbon reaching the deep sea floor: a status report. Geochim. Cosmochim. Acta 48:977-986.

Berger, W.H., 1970. Biogenous deep-sea sediments: fractionation by deep-sea circulation. Bull. Geol. Soc. Am. 81:183-204.

Berger, W.H., 1976. Biogenous deep-sea sediments: production, preservation and interpretation. In: Chemical Oceanography, J.P. Riley and R. Chester (eds.), Academic Press, London, 5:265-388.

Berger, W.H., and Soutar, A., 1967. Planktonic foraminifera: field experiment on production rate. Science 156:1495-1497.

Betzer, P.R., Showers, W.J., Laws, E.A., Winn, C.D., DiTullio, G.R., and Kroopnick, P.M., 1984. Primary productivity and particle fluxes on a transect of the equator at 153^{o}W in the Pacific Ocean. Deep-Sea Res. 31:1-11.

Broecker, W.S., and Peng, T.-H., 1982. Tracers in the Sea. Eldigio Press, Palisades, 690 pp.

Carpenter, E.J., and Lively, J.S., 1980. Review of estimates of algal growth using 14C tracer techniques. In: Primary Production in the Sea, P.G. Falkowski (ed.), New York, pp. 161-178.

Cobler, R., and Dymond, J., 1980. Sediment trap experiment on the Galapagos spreading center, equatorial Pacific. Science 209:801-802.

Coale, K.H., and Bruland, K.W., 1987. Oceanic stratified euphotic zone as elucidated by ^{234}Th:^{238}U disequilibria. Limnol. Oceanogr. 32:189-200.

Craig, H., and Hayward, T., 1987. Oxygen supersaturation in the ocean: biological versus physical contributions. Science 235:199-202.

Cushing, D.H., 1975. Marine Ecology and Fisheries. Cambridge University Press, Cambridge, 278 pp.

Cushing, D.H., 1981. Temporal variability in production systems. In: Analysis of Marine Ecosystems, A.R. Longhurst (ed.). Academic Press, London, pp. 443-471.

Deuser, W.G., 1984. Seasonality of particle fluxes in the ocean's interior. In: Global Ocean Flux Study - Proceedings of a Workshop, K.W. Bruland et. al. (eds.). National Academy Press, Washington, D.C., pp. 221-236.

Dugdale, R.C., and Goering, J.J., 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. and Oceanog. 12:196-206.

Dunbar, R.B., and Berger, W.H., 1981. Fecal pellet flux to modern bottom sediment of Santa Barbara Basin (California) based on sediment trapping. Geol. Soc. Amer. Bull. 92:212-218.

Dymond, J., Fischer, K., Clauson, M., Cobler, R., Gardner, W., Richardson, M.J., Berger, W., Soutar, A., and Dunbar, R., 1981. A sediment trap intercomparison study in the Santa Barbara Basin. Earth Planet. Science Letters 53:409-418.

El-Sayed, S.Z., 1970. Phytoplankton production of the South Pacific and the Pacific Sector of the Antarctic. In: Scientific Exploration of the South Pacific, W.S. Wooster (ed.) National Academy of Sciences, Washington D.C., pp. 194-210.

Emerson, S., Fischer, K., Reimers, C., and Heggie, D., 1985. Organic carbon dynamics and preservation in deep-sea sediments. Deep-Sea Res. 32:1-21.

Eppley, R.W., 1981. Autotrophic production of particulate matter. In: Analysis of Marine Ecosystems, A.R. Longhurst (ed.) Academic Press, London, pp. 343-361.

Eppley, R.W., 1984. Relations between primary production and ocean chlorophyll determined by satellites. In: Global Ocean Flux Study - Proceedings of a Workshop, K.W. Bruland (ed.) 1984. National Academy Press, Washington, D.C., pp. 85-102.

Eppley, R.W., and Peterson, B.J., 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282:677-680.

Eppley, R.W., and Sharp, J.H., 1975. Photosynthetic measurements in the central North Pacific: the dark loss of carbon in 24 h incubations. Limnol. and Oceanog. 20:981-987.

Eppley, R.W., Renger, E.H., and Betzer, P.R., 1983. The residence time of particulate organic carbon in the surface layer of the ocean. Deep-Sea Res. 30:311-323.

Fischer, K., 1984. Particle fluxes in the eastern tropical Pacific Ocean - sources and processes. Ph.D. thesis, Oregon State University, Corvallis, 225 pp.

Fleming, R.H., 1957. General features of the ocean. In: J.W. Hedgpeth (ed.) Treatise on Marine Ecology and Paleoecology. Geological Society of America Memoir 67:87-107.

Fogg, G.E., 1975. Primary Productivity. In: Chemical Oceanography, 2nd ed., J.P. Riley and G. Skirrow (eds.), Academic Press, New York, 2:385-453.

Gardner, J.V., and Hemphill-Haley, E., 1986. Evidence for a stronger oxygen-minimum zone off central California during late Pleistocene to early Holocene. Geology 14:691-694.

Gieskes, W.W.C., and Kraay, W., 1984. State-of-the-art in the measurement of primary production. In: Flows of Energy and Materials in Marine Ecosystems, Theory and Practice, M.J.R. Fasham (ed.). Plenum, New York, pp. 171-190.

Gieskes, W.W.C., and Kraay, W., 1986. Floristic and physiological differences between the shallow and the deep nanophytoplankton community in the euphotic zone of the open tropical Atlantic revealed by HPLC analysis of pigments. Mar. Biol. 91:567-576.

Gieskes, W.W.C., Kraay, G.W., and Baars, M.A., 1979. Current C-14 methods for measuring primary production: gross underestimates in oceanic waters. Neth. J. Sea Res. 13:58-78.

Harrison, W.G., Platt, T., Calienes, R., and Ochoa, N., 1980. Photosynthetic parameters and primary production of phytoplankton populations off the northern coast of Peru. In: Coastal Upwelling, F.A. Richards (ed.). American Geophysical Union, Washington, D.C., Coastal and Estuarine Sciences 1:303-311.

Hinga, K.R., 1985. Evidence for a higher average primary productivity in the Pacific than in the Atlantic Ocean. Deep-Sea Res. 32:117-126.

Hinga, K.R., Sieburth, J.M., and Heath, G.R., 1979. The supply and use of organic material at the deep-sea floor. J. Mar. Res. 37:557-579.

Honjo, S., 1978. Sedimentation of materials in the Sargasso Sea at a 5367 m deep station. J. Mar. Res. 36:469-492.

Honjo, S., 1980. Material fluxes and modes of sedimentation in the mesopelagic and bathypelagic zones. J. Marine Res. 38:53-97.

Honjo, S., 1982. Seasonality and interaction of biogenic and lithogenic particulate flux at the Panama Basin. Science 218:883-884.

Honjo, S., 1984. Study of ocean fluxes in time and space by bottom-tethered sediment trap arrays: a recommendation. In: Global Ocean Flux Study - Proceedings of a Workshop, K.W. Bruland et al. (eds.). National Academy Press, Washington, D.C., pp. 305-324.

Honjo, S., Manganini, S.J., and Cole, J.J., 1982. Sedimentation of biogenic matter in the deep ocean. Deep-Sea Res. 31:609-625.

Imbrie, J., and Imbrie, J.Z., 1980. Modeling the climatic response to orbital variations. Science 202:943-953.

Jenkins, W.J., and Goldman, J.C., 1985. Seasonal oxygencycling and primary production in the Sargasso Sea. J. Mar. Res. 5:465-491.

Karl, D.M., and Knauer, G.A., 1984. Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: evidence of multiple zones of biological activity. Deep-Sea Res. 31:221-243.

Karl, D.M., Knauer, G.A., Martin, J.H., and Ward, B.B., 1984. Chemolithotrophic bacterial production in association with rapidly sinking particles: implications to oceanic carbon cycles and mesopelagic food webs. Nature 309:54-56.

Knauer, G.A., and Martin, J.H., 1981. Primary production and carbon-nitrogen fluxes in the upper 1500 m of the northeast Pacific. Limnol. and Oceanogr. 26:181-186.

Knauer, G.A., Martin, H.J., and Bruland, K., 1979. Fluxes of particulate carbon, nitrogen and phosphorous in the upper water column of the northeast Pacific. Deep-Sea Res. 26:97-108.

Koblentz-Mishke, O.I., Volkovinsky, V.V., and Kabanova, J.G., 1970. Plankton primary production of the world ocean. In: Scientific Exploration of the South Pacific, W. Wooster (ed.). National Academy of Sciences, Washington, D.C., pp. 183-193.

Li, W.K.W., Subba Rao, D.V., Harrison, W.G., Smith, J.C., Cullen, J.J., Irwin, B., and Platt, T., 1983. Autotrophic picoplankton in the tropical ocean. Science 219:292-295.

Lorenzen, C.J., Welschmeyer, N.A., and Copping, A.E., 1983. Particulate organic carbon flux in the subarctic Pacific. Deep-Sea Res. 30:639-643.

Lutze, G.F., Pflaumann, U., and Weinholz, P., 1986. Jungquartre Fluktuationen der benthischen Foraminiferenfaunen in Tiefsee-Sedimenten vor NW-Afrika - eine Reaktion auf Produktivitts-nderungen im Oberflchenwasser. Meteor Forschungs-Ergebnisse, Reihe C. 40:163-180.

Malone, T.C., 1980. Size-fractionated primary productivity of marine phytoplankton. In: Primary Production in the Sea, P.G. Falkowski (ed.). Plenum Press, New York, pp. 301-319.

Mueller, P.J., and Suess, E., 1979. Productivity, sedimentation rate, and sedimentary organic matter in the oceans - I. Organic carbon preservation. Deep-Sea Res. 26A:1347-1362.

Mueller, P.J., Erlenkeuser, H. and von Grafenstein, R., 1983. Glacial-interglacial cycles in oceanic productivity inferred from organic carbon contents in eastern North Atlantic sediment cores. In: Coastal Upwelling, Part B, Jorn Thiede and Erwin Suess (eds.). Plenum Press, New York, pp. 365-398.

Nemoto, T., and Harrison, G., 1981. High latitude ecosystems. In: A.R. Longhurst (ed.) Analysis of Marine Ecosystems. Academic Press, London, pp. 95-126.

Pace, M.L., Knauer, G.A., Karl, D.M., and Martin, J.H., 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. Nature 325:803-804.

Pamatmat, M.M, and Banse, K., 1969. Oxygen consumption by the seabed. II. In situ measurements to a depth of 180 m. Limnol. and Oceanogr. 14:250-259.

Parsons, T.R., Takahashi, M., and Hargrave, B., 1984. Biological Oceanographic Processes. 3rd ed. Pergamon Press, Oxford, 330 pp.

Platt, T., 1984. Primary productivity in the central North Pacific: comparison of oxygen and carbon fluxes. Deep-Sea Res. 31:1311-1319.

Platt, T., and Harrison, W.G., Reconciliation of carbon and oxygen fluxes in the upper ocean. Deep-Sea Res. 33:273-276.

Platt, T., and Li, W.K.W. (eds.), 1986. Photosynthetic Picoplankton. Can. Bull. of Fish. and Aquat. Sci., 214:583 pp.

Platt, T., Denman, K.L., and Jassby, A.D., 1977. Modeling the productivity of phytoplankton. In: The Sea, vol. 6, E.D. Goldberg (ed.). Interscience, New York, pp. 807-856.

Platt, T., Subba Rao, D.V., and Irwin, B., 1983. Photosynthesis of picoplankton in the oligotrophic ocean. Nature 300:702-704.

Raymont, J.E.G., 1963. Plankton and Productivity in the Oceans. Pergamon Press, Oxford, 660 pp.

Redfield, A.C., Ketchum, B.H., and Richards, F.A., 1963. The influence of organisms on the composition of sea-water. In: The Sea, vol. 2, M.N. Hill (ed.). Interscience, New York, pp. 26-77.

Reid, J.L., and Shulenberger, E., 1986. Oxygen saturation and carbon uptake near 28^{o}N, 155^{o}W. Deep-Sea Res. 33:267-271.

Reid, J.L., Brinton, E., Fleminger, A., Venrick, E.L., and McGowan, J.A., 1978. Ocean circulation and marine life. In: Advances in Oceanography, H. Charnock and G. Deacon (eds.). Plenum Press, New York, pp. 65-130.

Reimers, C.E., Kalhorn, S., Emerson, S.R., and Nealson, K.H., 1984. Oxygen consumption rates in pelagic sediments from the central Pacific: first estimates from microelectrode profiles. Geochim. Cosmochim. Acta 48:903-910.

Rivkin, R.B., and Putt, M., 1987. Diel periodicity of photosynthesis in polar phytoplankton: influence on primary production. Science 238:1285-1288.

Romankevich, E.A., 1984. Geochemistry of Organic Matter in the Ocean. Springer, Heidelberg, 334 pp.

Rowe, G.T., 1979. Symposium on Bio-productivity of Upwelling Ecosystems. Moscow (cit. in Suess, 1980, ref. 17).

Rowe, G.T., and Deming, J.W., 1985. The role of bacteria in the turnover of organic carbon in deep-sea sediments. J. Mar. Res. 43:925-950.

Rowe, G.T., and Gardner, W.D., 1979. Sedimentation rates in the slope water of the northwest Atlantic Ocean measured directly with sediment traps. J. Mar. Res. 37:581-600.

Rowe, G.T., Smith, S., Falkowski, P., Whitledge, T., Theroux, R., Phoel, W., and Ducklow, H., 1986. Do continental shelves export organic matter? Nature 324:559-561.

Sarnthein, M., Winn, K., and Zahn, R., 1987. Paleoproductivity of oceanic upwelling and the effect on atmospheric CO_2 and climatic change during deglaciation times. In: Abrupt Climatic Change - Evidence and Implications, W.H. Berger and L.D. Labeyrie (eds.). Reidel, Dordrecht, pp. 311-337.

Shulenberger, E., and Reid, J.L., 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered. Deep-Sea Res. 28A:901-919.

Smetacek, V., von Brockel, K., Zeitzschel, B., and Zenk, W., 1978. Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. Mar. Biol. 47:211-226.

Smith, K.L., and Hinga, K.R., 1983. Sediment community respiration in the deep sea. In: Deep-Sea Biology. The Sea, vol. 8, G.T. Rowe (ed.). Wiley-Interscience, New York, pp. 331-371.

Smith, R.E.H., Geider, R.J., and Platt, T., 1984. Microplankton productivity in the oligotrophic ocean. Nature 311:252-254.

Steemann Nielsen, E., 1956. Measuring the productivity of the sea. In: The Galathea Deep Sea Expedition 1950-1952, A.F. Bruun et al., (eds). Allen and Unwin, London, pp. 53-64.

Steemann Nielsen, E., 1975. Marine Photosynthesis with special emphasis on the ecological aspects. Elsevier, Amsterdam, 141 pp.

Suess, E., 1980. Particulate organic carbon flux in the oceans - surface productivity and oxygen utilization. Nature 288:260-263.

Sundquist, E.T., 1985. Geological perspectives on carbon dioxide and the carbon cycle. In: The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present, E.T. Sundquist and W.S. Broecker (eds.). American Geophysical Union, Washington, D.C., Geophysical Monograph 32:5-59.

Sundquist, E.T., and Broecker, W.S. (eds.), 1985. The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present. American Geophysical Union, Washington, D.C. 627 pp.

Sverdrup, H.U., 1955. The place of physical oceanography in oceanographic research. J. Mar. Res. 14:287-294.

Venrick, E.L., 1982. Phytoplankton in an oligotrophic ocean: observations and questions. Ecol. Monogr. 52:129-154.

Venrick, E., Beers, J.R., Heinbokel, J.F., 1977. Possible consequences of containing microplankton for physiological rate measurements. J. Exp. Mar. Biol. Ecol. 26:55-76.

Venrick, E.L., McGowan, J.A., Cayan, D.R., and Hayward, T. 1987. Climate and chlorophyll a: long-term trends in the central North Pacific. Science 238:70-72.

Vinogradov, M.E., 1981. Ecosystems of equatorial upwellings. In: Analysis of Marine Ecosystems, A.R. Longhurst (ed.). Academic Press, London, pp. 69-93.

von Bröckel, K., 1980. Abstract IDOE International Symposium on Coastal Upwelling, Los Angeles. (Cit. in Suess, 1980, ref. 16).

Walsh, J.J., 1981. Shelf-sea ecosystems. In: Analysis of Marine Ecosystems, A.R. Longhurst (ed.). Academic Press, London, pp. 159-196.

Walsh, J., Rowe, G.T., Iverson, R.L., and McRoy, C.P., 1981. Biological export of shelf carbon: a neglected sink of the global CO_2 cycle. Nature 291:196-201.

Walsh, J.J., Premuzic, E.T., Gaffney, J.S., Rowe, G.T., Harbottle, G., Stoenner, R.W., Balsam, W.L., Betzer, P.R., and Macko, S.A., 1985. Organic storage of CO_2 on the continental slope off the mid-Atlantic bight, the southeastern Bering Sea, and the Peru coast. Deep-Sea Res. 32:853-883.

Wefer, G., Suess, E., Balzer, G., Liebezeit, G., Muller, P.J., Ungerer, C.A., and Zenk, W., 1982. Flux of biogenic components from sediment trap deployment in circumpolar waters of the Drake Passage. Nature 299:145-147.

Westrich, J.T., and Berner, R.A., 1984. The role of sedimentary organic matter in bacterial sulfate reduction: the G model tested. Limnol. and Oceanogr. 29:236-249.

Wiebe, P.H., Boyd, S.H., and Winget, C., 1976. Particulate matter sinking to the deep-sea floor at 2000 m in The Tongue of the Ocean, Bahamas, with a description of a new sedimentation trap. J. Mar. Res. 34:341-354.

Zeitzschel, B. (ed.), 1973. The Biology of the Indian Ocean. Springer, New York, 549 pp.

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