

MINIREVIEWS

A Sea of Change: Biogeochemical Variability in the North Pacific Subtropical Gyre

David M. Karl

*School of Ocean and Earth Science and Technology, Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822***ABSTRACT**

The North Pacific Subtropical Gyre (NPSG) is the largest ecosystem on our planet. However, this expansive habitat is also remote, poorly sampled, and therefore not well understood. For example, the most abundant oxygenic phototroph in the NPSG, *Prochlorococcus*, was described only a decade ago. Other novel *Bacteria*, *Archaea* and *Eukarya*, recently identified by nucleic acid sequence analysis, have not been isolated. In October 1988, an ocean time-series research program was established to study ecosystem processes in the gyre, including rates and pathways of carbon and energy flow, spatial and temporal scales of variability, and coupling of ocean physics to biogeochemical processes.

After a decade of ecosystem surveillance, this sentinel observatory has produced an unprecedented data set and some new views of an old ocean. Foremost is evidence for dramatic changes in microbial community structure and in mechanisms of nutrient cycling in response to large-scale ocean-atmosphere interactions. These and other observations demand reassessment of current views of physical-biogeochemical processes in this and other open-ocean ecosystems.

Key words: oceanography; microbial ecology; nutrients; climate; biodiversity; food webs; microbiology.

INTRODUCTION

Approximately one-half of global primary production, an amount equivalent to 500×10^{15} g of carbon per annum, is supported by the photosynthetic activities of microscopic plankton in the world's oceans (Falkowski 1994). Within the marine environment, oceanic provinces far removed from land account for most of the primary production. These open-ocean regions, termed subtropical gyres, collectively occupy approximately 40% of the surface of the Earth. The most extensive of these gyres is the North Pacific Subtropical Gyre (NPSG), which at the ocean's surface extends from approximately 15°N to 35°N latitude and 135°E to 135°W

longitude (Figure 1). With a surface area of approximately 2×10^7 km², the NPSG is the largest circulation feature on our planet (Sverdrup and others 1946) and the earth's largest contiguous biome. Homologous habitats are also present in the South Pacific Ocean, the Indian Ocean, and in both hemispheres of the Atlantic Ocean (Blackburn 1981).

The NPSG ecosystem is very old; present boundaries have persisted since the Pliocene (approximately 10^7 years BP), or earlier (McGowan and Walker 1985). This great age and relative isolation were the primary factors leading to the development of an hypothesized "climax-type" community and the motivation behind the establishment of a multiyear observational program centered near 28°N, 155°W in an area dubbed the "Climax region" (Venrick 1995). A Climax community refers to a

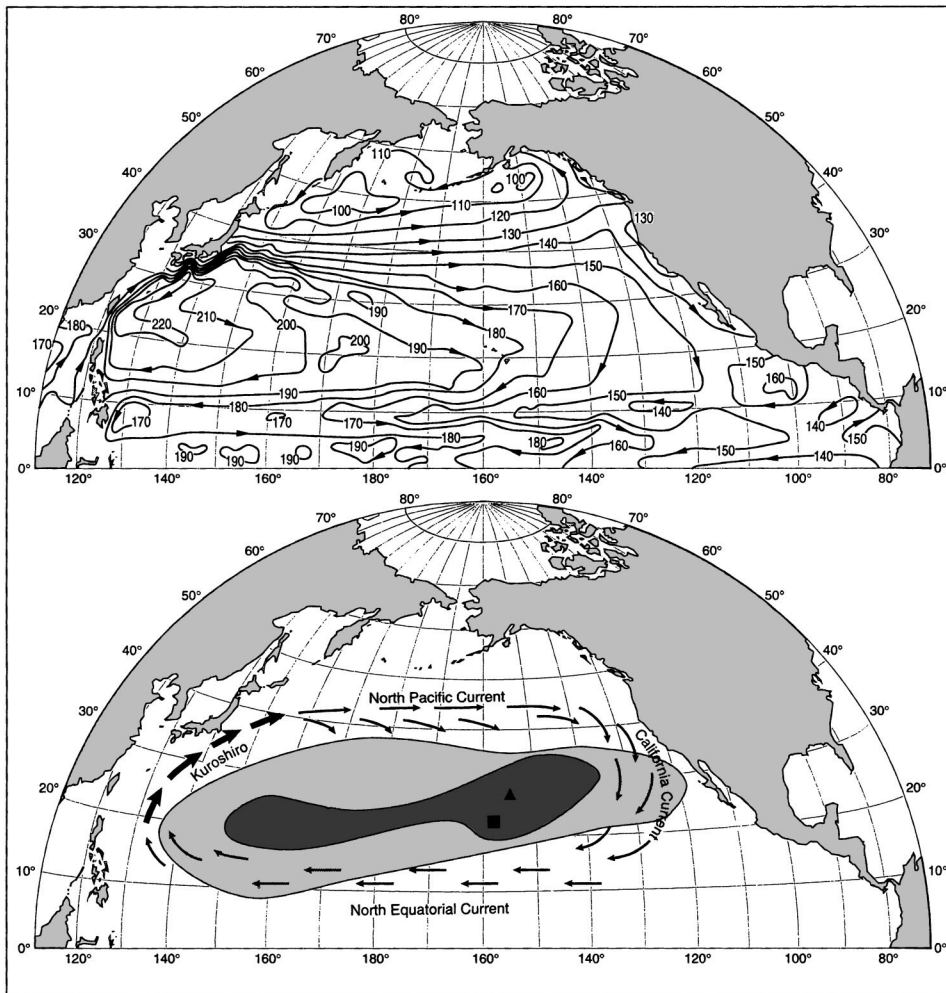


Figure 1. Map of the North Pacific Ocean showing several important features of the NPSG. **Top** Dynamic topography of the sea surface in dyn-cm relative to 1000 dbar based on historical hydrographic observations. Arrows show the direction of geostrophic flow. Redrawn from Wyrtki (1975). **Bottom** Major circulation features in the North Pacific that collectively define the approximate boundaries of the NPSG. Also shown is the estimated range of central Pacific Ocean mesozooplankton based on an analysis of the fidelity of mesozooplankton species. The dark area is the core of the Central Pacific fauna (100% fidelity) and the lighter shade defines the 60% fidelity boundary. Redrawn from McGowan (1974). Note that Stas. ALOHA (■) and CLIMAX (▲) are both located in the core region.

more or less permanent and final stage of succession that is inseparably connected with both habitat characteristics and climate (Clements 1916, 1936). Climate affects the seascape and, hence, community structure and dynamics.

Because of the role of the ocean as a potential sink for the increasing burden of atmospheric CO_2 , it is imperative that ecological processes in open-ocean ecosystems are understood. Nevertheless, few comprehensive investigations of the NPSG have ever been attempted. Once thought to be a homogeneous, static habitat, there is increasing evidence that the NPSG exhibits substantial physical, chemical, and biological variability on a variety of time and space scales. Wind-forced currents and meso-scale eddies interact to produce vigorous vertical motions (Lee and others 1994) that can deliver short-lived pulses of nutrients, without warning, to habitats that are otherwise nutrient starved. Recent field results, obtained largely during the Hawaii Ocean Time-series (HOT) research program (Karl and Lukas 1996), have raised provocative questions concerning ecosystem structure, function, and tem-

poral variability. The old adage, "nothing is constant but change," now appears to be a reasonable description of biogeochemical processes in the NPSG. The more that is learned about this interesting and remote habitat, the less appears to be understood.

This review contrasts the historical perspective of the NPSG ecosystem with the emerging views of this very old ocean. Foremost in importance are recent data indicating the numerical dominance of two separate groups of prokaryotic photoautotrophs not even known to exist before 1980, the role of microbial food webs, and the existence of a broad spectrum of mesoscale physical variability. The latter includes discrete eddies, near-inertial water motions, and internal tides, all of which can cause mixing of water masses with resultant impacts on ecosystem dynamics. Consideration is also given to the hypothesis that interdecadal changes in climate, perhaps resulting from accumulation of greenhouse gases, may result in coupled changes in plankton community structure and biogeochemi-

cal processes. A revised ecological model for the NPSG accommodates these new data sets and provides a research prospectus for the future.

CHARTING THE COURSE TOWARDS A GENERAL ECOLOGICAL UNDERSTANDING OF THE NPSG

Similar to most fields of study, present ecological understanding of the NPSG is based upon the results of many discrete scientific contributions over several decades. It is important to emphasize that the motivation for studies of open ocean ecosystems has changed dramatically with time. The earliest investigations documented the distributions and abundances of planktonic assemblages. Later, an emphasis was placed on rates and controls of photosynthesis and fish production. More modern studies focus on biodiversity and the effects of climate on ecosystem dynamics. Although many of the truly pioneering research efforts were flawed due to improper methodology or lack of scientific understanding about the habitat or populations under investigation, they successfully planted the seeds of curiosity for future generations of oceanographers.

The worldwide voyage of the *HMS Challenger* (1872–1876) is generally considered to mark the beginning of oceanography as a scientific discipline. Two explicit goals of the *Challenger* Expedition were (a) to determine the chemical composition of seawater and the organic matter in suspension and (b) to study the distribution and abundance of various communities of organisms. These well-formulated objectives are as relevant today as they were more than a century ago.

In 1875, on the leg from Yokohama to Honolulu, *Challenger* occupied several stations in the NPSG and collected plant and animal specimens as well as numerous seawater samples. Much of this research effort was, ironically, dedicated to study of the deep-sea habitats (greater than 1000 m) rather than much more accessible surface waters. This situation was due in large part to the great scientific debates of the day, including the hypothesis of an “azoic” zone at great depths (Hedgpeth 1957), and the nature of a recently described deep-sea slime, *Bathypolius haeckelii* (Huxley 1900). Both were eventually proven to be incorrect based, in large part, on results from the *Challenger* Expedition.

In 1929, the research vessel *Carnegie*, built and operated by the Department of Terrestrial Magnetism of the Carnegie Institute of Washington, conducted the first detailed plankton investigation of the NPSG. Unfortunately, this expedition was abruptly terminated when the vessel was destroyed by fire in Apia, Samoa. The biological program on

the San Francisco-to-Samoa leg included the collection of plankton samples in the upper 100 m of the NPSG water column by using nets and pumps. Discrete water samples were also collected for measurements of dissolved nutrients and oxygen. The data from this Pacific Ocean transect clearly documented coherence of discrete plankton assemblages with water types that could be identified by common chemical characteristics (Graham 1941). For example, a positive correlation was shown between plankton biomass and surface-water phosphate concentration. It was also demonstrated that regardless of latitude, the presence of “new water” (that is, upwelled waters enriched in phosphate) resulted in increased plankton production.

The “modern” era of oceanographic studies in the North Pacific did not begin until about 1950, during the postwar period of rapid growth and expansion of the Scripps Institution of Oceanography (SIO). In 1950, Roger Revelle led a two-ship expedition, “Operation Mid-Pacific,” to study many of the previously unexplored portions of the central and western North Pacific Ocean. In 1953, the “Transpac Expedition” collected water and plankton samples at 141 stations across the North Pacific. Later that decade, Joseph Reid organized one of the most ambitious oceanographic expeditions ever attempted; the “North Pacific Expedition” or NORPAC. NORPAC involved 21 research vessels from 14 institutions and provided a nearly synoptic view of conditions in the Pacific Ocean, north of approximately 20°N latitude for summer 1955 (NORPAC Committee 1955). The excitement and adventure of these and other pathfinding ocean voyages are presented in the historical accounts by Raitt and Moulton (1967) and Shor (1978).

During this same period, the worldwide Danish *Galathea* Deep-Sea Expedition (1950–52) made a major contribution to our understanding of the oceanic carbon cycle. Although the focus of this expedition was on life in the deep sea, especially ocean trenches, a secondary objective was the measurement of rates of photosynthetic production in the surface waters of the ocean. On the San Francisco-to-Honolulu leg, Steemann Nielsen (1956) made the first modern measurements of photosynthesis in the NPSG. His new ¹⁴C tracer method (Steemann Nielsen 1956) was crucial for detecting the relatively low rates of organic matter production in the gyre, a value that he reported as approximately 200 mg C m⁻² d⁻¹ for 24-h incubations. Based on measurements subsequently obtained in all major ocean basins during the *Galathea* Expedition, it was concluded that organic matter production in the sea was approximately equal to that on land. This unexpected result is now well confirmed.

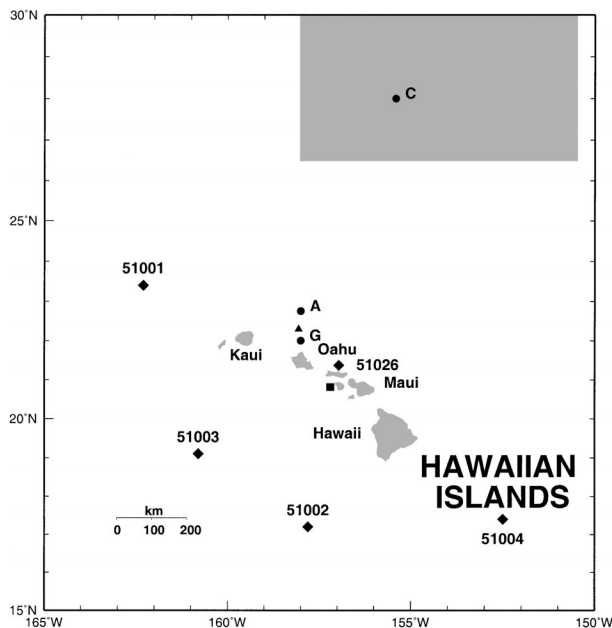


Figure 2. Map of a portion of the NPSG showing the Hawaiian Islands relative to the locations where past and present research activities have been conducted, including: Sta. ALOHA (A), the CLIMAX “region” (shaded box) and Sta. Climax (C), Sta. GOLLUM (G), the MOBY-SeaWIFS buoy (■), HALE-ALOHA buoy (▲), and the network of NOAA-NDBC meteorological buoys (◆). The PRPOOS and VERTEX-5 ocean stations were colocated with Sta. Climax at 28°N, 155°W.

Despite these heroic field efforts, there was very little observational basis for the development of a comprehensive ecological or biogeochemical understanding of the NPSG biome. Even the most accessible epipelagic habitat remained *aqua incognita* through the early 1960s when progress toward this goal was first made during the “Ursa Major” (Aug–Oct 1964) and “Zetes” (Jan 1966) expeditions organized by scientists from SIO (SIO Ref. #67–5, SIO Ref. #70–5). Data obtained on the plant and animal populations marked the beginning of what would become a two-decade long series of cruises to the NPSG (Hayward and others 1983). Observations made during this series of “Climax-region” (Figure 2) cruises provided an unprecedented view of the NPSG habitat and served as the basis for an initial conceptual model of ecosystem structure and dynamics.

By making repeat measurements of key physical, chemical, and biological parameters, invaluable information on scales of ocean variability and on the relationships of organisms to physical forcing was obtained. However, of the 18 cruises conducted between 1971 and 1985, 70% occurred in summer (June–Sept) and 35% in August. Consequently, habitat sampling was seasonally biased. Further-

more, elucidation of low frequency variability (greater than 1 year) also may have been compromised because no observations were made in 1970, 1975, 1978–79, 1981, or 1984 (Hayward 1987). Despite these and several other sampling limitations, the Climax program data sets continue to provide high-quality information on the NPSG ecosystem and serve as a crucial benchmark for comparison to contemporary data sets.

In parallel, but not in conjunction, with these mostly SIO-based investigations, extensive ecological field studies were conducted by scientists from the Institute of Oceanology, USSR Academy of Sciences. In certain respects these latter studies were more comprehensive especially in their focus on microbial assemblages, that is, bacteria, phytoplankton and protozoans, carbon and energy flux pathways and rates (Kriss 1962; Vinogradov and Shushkina 1989; Vinogradov and others 1997), and ecosystem modeling (Vinogradov and others 1973).

In addition to the Climax-region study already mentioned, several other unrelated biogeochemical time-series research programs were initiated during the past few decades; however, only one remains active. From January 1969 to June 1970, a deep-ocean hydrostation (Sta. Gollum), patterned after the successful hydrostation “S” near Bermuda, was established by scientists at the University of Hawaii at a location 47 km north of Oahu (22°10′N, 158°00′W; Figure 2). The water depth (4760 m) and location were selected to be beyond the biogeochemical influences of the Hawaiian Ridge (Doty and Oguri 1956). Approximately monthly, 13 2-d research cruises were conducted to observe and interpret variations in particulate organic matter distributions in the water column and other physical and chemical parameters (Gordon 1970).

During a series of related cruises from 1969 to 1972 conducted under the code name “Bug Safari,” K. Gundersen and colleagues from the University of Hawaii began a systematic investigation of microbial processes in the NPSG. This was the first comprehensive, biogeochemical investigation conducted in the NPSG, with separate research components on optics, dissolved gases, trace metals, inorganic and organic nutrients, and microorganisms (phytoplankton, cyanobacteria, heterotrophic and chemolithoautotrophic bacteria, protozoa, and fungi). These complementary field measurements focused on nitrogen and carbon transformations, including rates of primary production, respiration, nitrification, and dinitrogen (N₂) fixation (Gundersen and others 1976) and were, in many regards, ahead of their time.

In 1986, a biogeochemical time-series station was established near the northeastern boundary of the

NPSG (33°N, 139°W) as one component of the VERTICAL Transport and EXchange (VERTEX) research program. A major objective of VERTEX was to investigate seasonality in carbon export from the euphotic zone in relation to contemporaneous rates of primary production. During an 18-month period (October 1986 to May 1988), the station was occupied for seven 1-week periods at approximately 3-month intervals. In addition to standard hydrographic surveys, samples also were collected to measure dissolved and particulate inorganic and organic matter, trace metals, plankton populations, microbial food web processes and rates of primary production, and nitrogen assimilation (Knauer and others 1990; Harrison and others 1992). Significant temporal variability was documented for primary production and particle flux, but no clear relationships were observed between primary production and physical processes. Despite the comprehensive scope and intensity of the VERTEX project, the sampling frequency was deemed inadequate to resolve much of the natural variability in this oligotrophic oceanic ecosystem.

Based on data collected during this first century of exploration and research of the NPSG (circa 1880–1980), a basic scientific understanding of ecological processes in this habitat, sufficient to formulate meaningful hypotheses for future investigation, was developed. In response to growing awareness of the ocean's role in climate and global environmental change, and the need for additional and more comprehensive oceanic time-series measurements, the Board on Ocean Science and Policy of the National Research Council sponsored a workshop on "Global Ocean Flux Study" (GOFS), which served as an eventual blueprint for the Joint-GOFS (or JGOFS) program (National Research Council 1984). In 1986, the International Council of Scientific Unions established the International Geosphere-Biosphere Programme: A Study of Global Change (IGBP), and the following year JGOFS was designed as a Core Project of IGBP. US-JGOFS research efforts focus on the oceanic carbon cycle, its sensitivity to change, and the regulation of the atmosphere-ocean CO₂ balance (Brewer and others 1986). The broad objectives of US-JGOFS were to determine and understand on a global scale the time-varying fluxes of carbon and associated biogenic elements in the ocean, and to evaluate the related exchanges of these elements with the atmosphere, the sea floor and the continental boundaries (Scientific Committee on Ocean Research 1990). To achieve these goals, the committee defined four separate program elements: (a) process studies to capture key regular events, (b) long-term time-series observations at strategic sites, (c) a global survey of relevant oceanic

properties (for example, CO₂), and (d) a vigorous data interpretation and modeling effort to disseminate knowledge and generate testable hypotheses.

In 1988, a deep ocean station was established north of Hawaii within the NPSG to address these scientific goals and needs (Karl and Winn 1991; Karl and Lukas 1996). In 1998, the still ongoing Hawaii Ocean Time-series (HOT) program completed 100 separate research cruises to Sta. ALOHA (22°45'N, 158°W; Figure 2) with comprehensive seasonal coverage. The HOT program has already assembled the largest and most comprehensive ecological data set for the NPSG, and is scheduled to continue into the next millennium. These new measurements, with a focus on microbial rates and processes have yielded unexpected results that challenge certain past views of NPSG biogeochemical cycles.

NORTH PACIFIC SUBTROPICAL GYRE: HABITAT CHARACTERISTICS

The NPSG is characterized by warm (higher than 24°C) surface waters with low nitrate concentrations (less than 50 nM) but relatively high dissolved organic nitrogen (DON) concentrations (5–6 μM), seasonally variable surface mixed layers (40–100 m), low standing stocks of living organisms (1–2 mmol C m⁻³), and a persistent deep-water (100–125 m) chlorophyll *a* (chl *a*) maximum layer (DCML; Figure 3). The euphotic zone of the NPSG sometimes has been described as a "two-layer" system; the uppermost, light-saturated, nutrient-limited layer (0–75 m), which supports high rates of primary production, and a lower, light-limited, nutrient-saturated layer (Knauer and others 1984; Small and others 1987).

Time-series observations of chl *a* and chl *a* fluorescence per autotrophic cell measured at Sta. ALOHA by using flow cytometry, have revealed two opposing seasonal cycles: (a) in the upper euphotic zone (0–50 m), chl *a* concentration increases in winter and decreases in summer, and (b) in the lower euphotic zone (100–175 m), chl *a* concentration increases in spring and decreases in fall (Letelier and others 1993; Winn and others 1995). The seasonal variations in the upper euphotic zone are a consequence of photoadaptation in response to changing mixed-layer depths and light intensities. In the lower portion of the euphotic zone, the increases in chl *a* reflect the net growth and accumulation of photoautotrophic biomass as a consequence of increased light intensities. These fundamentally different responses of cellular chl *a* content to changing irradiance complicates any straightforward extrapo-

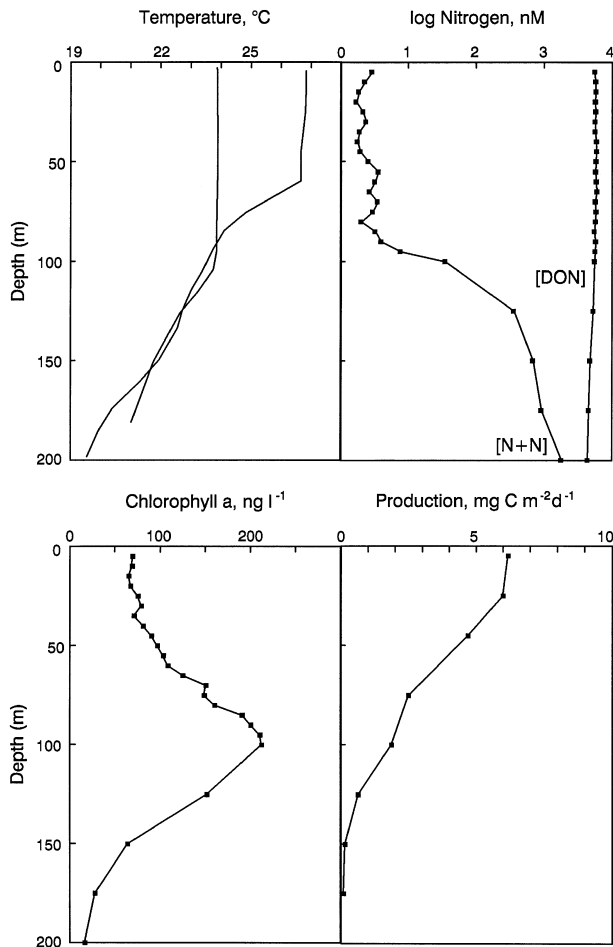


Figure 3. Typical patterns of the vertical distributions of selected physical, chemical, and biological parameters in the NPSG. The base of the euphotic zone, defined here as the depth where net ^{14}C incorporation is equal to zero, is approximately 175 m. Clockwise from upper left: temperature ($^{\circ}\text{C}$) vs depth showing a typical summer vs winter profile and corresponding changes in mixed (isothermal) layer depth; \log_{10} concentrations (nM) of nitrate (N + N) and dissolved organic nitrogen (DON) vs depth; chlorophyll *a* ($\mu\text{g L}^{-1}$) vs depth; and primary production ($\text{mg C m}^{-2} \text{d}^{-1}$) vs depth. Compiled from the HOT program data base (<http://hahana.soest.hawaii.edu>).

lation of chl *a* to biomass (Karl and Dobbs 1998), including satellite remote sensing.

Within the NPSG, the major pathways for nutrient recharge are from below, via vertical eddy diffusion, and by horizontal transport from adjacent, nutrient-rich systems (Reid and others 1978). Because the combined flux of nutrients from these processes is small, surface waters of the NPSG are chronically nutrient impoverished. Furthermore, the near-zero nutrient concentration gradient routinely observed in the upper 100 m of the water column (Figure 3) suggests that continuous vertical

nutrient flux cannot be the primary source of dissolved inorganic nutrients (for example, nitrate and phosphate) to the upper euphotic zone (Hayward 1991).

Large-scale characterization of the NPSG, based on surface dynamic height relative to 1000 m, places the center of the gyre at 20°N (Figure 1, top). The western portion of the NPSG (west of 180° longitude) has greater physical variability than the eastern portion (Kenyon 1978; Shulenberg 1978), a feature also reflected in satellite-derived, sea-surface topographic measurements (Munch 1996). These latter data provide support for the possible existence of two separate central gyral systems in the North Pacific Ocean (Sverdrup and others 1946). Because of the large dimensions of the NPSG it is likely that atmosphere–ocean climate forcing may affect subregions differently. For example, El Niño Southern Oscillation (ENSO) impacts might be expected to have a strong zonal gradient.

Surface circulation (above 50 m) is driven by wind and maintained by mass distribution. The geostrophic nature of the major clockwise (anticyclonic) circulation assures wind-driven convergence of surface waters in the NPSG (Reid and others 1978). It serves to isolate these relatively large gyre ecosystems and to restrict exchanges with adjacent current systems (Figure 1). The advective field suggests horizontal currents less than 4 cm s^{-1} and implies, by Ekman convergence, a mean vertical downwelling of $2\text{--}3 \text{ cm d}^{-1}$ through the main thermocline (Niiler and Reynolds 1984).

Zonal and meridional transects across the NPSG have documented low, or nonexistent, horizontal gradients in most physical and biological characteristics, especially compared with other marine ecosystems (Venrick 1971, 1979; McGowan and Williams 1973; Shulenberg 1978; Hayward and others 1983; Hayward and McGowan 1985; Matrai 1986; Hayward 1987). As a consequence of these circulation features, the NPSG is thought to be a semienclosed, stable and relatively homogeneous habitat. These results suggest that serial observations from a strategically located site may be extrapolated to the larger region of interest. This assumption underlies establishment of Sta. ALOHA ($22^{\circ}45'\text{N}$, 158°W) as a NPSG benchmark (Karl and Winn 1991; Karl and Lukas 1996).

Each winter, extratropical cyclones track across the North Pacific from west to east, approximately every 5–7 d. The strong winds associated with these storms impulsively force the upper ocean, resulting in a deepening of the upper mixed layer and a cooling associated with both enhanced evaporation and entrainment of cooler waters from below (Karl

and Lukas 1996). This intermittent local forcing is important in determining the annual cycle in the surface waters of the NPSG habitat.

Recent studies have documented that the NPSG contains a vigorous field of mesoscale variability, including discrete eddies, near-inertial motions, and internal tides (Venrick 1990). They can cause significant lifting of water into the euphotic zone and can modify conditions in the upper ocean. Lateral heterogeneity also has been reported for the NPSG in winter; for example, Gregg (1976) reported a mixed layer of 110 m that was separated by a few kilometers from one only 10 m deep. Furthermore, and in contrast to the large-scale view, variable horizontal currents with time scales of 1–30 d and space scales of 1–200 km are nearly tenfold greater than expected, implying vertical circulations two orders of magnitude greater than the mean for this region (Niiler and Hall 1988). These unsteady conditions have implications for resupply of nutrients and for the distribution, abundance, and metabolic activities of plankton populations in the NPSG.

Finally, there is ample evidence to suggest that major changes in the structure of the NPSG habitat can occur over interannual to decadal time periods. For example, Levitus and Antonov (1995) documented relatively large changes in the upper-ocean temperature (up to 0.5°C) over periods as short as 3 years. It also has been shown that major and sometimes abrupt “regime shifts” can result from changes in the position of atmospheric (for example, Aleutian Low) or oceanic (for example, West Wind Drift) features (McGowan and others 1998), and it is even possible for the boundaries of the NPSG to shift accordingly. These habitat changes all can have profound effects on biological and biogeochemical processes. Unfortunately, lack of systematic time series of sufficient length to observe these decadal (or longer) disturbances precludes comprehensive ecological understanding at present.

NUTRIENT DYNAMICS: ROLE OF STOCHASTIC PHYSICAL PROCESSES

Broad-scale descriptions of general ocean circulation and major biogeochemical cycles, summarized above, ignore many potentially important but more stochastic events that may affect the local resupply of nutrients to the surface ocean. The previous perception of the NPSG as a marine desert supported by steady diffusional supply of essential nutrients from beneath the thermocline is no longer tenable.

Based on systematic analysis of steady state nutrient flux versus nutrient demand, Hayward (1987,

1991) hypothesized that episodic mixing events must occur in the NPSG. Unfortunately, historical measurements were insufficient for resolving the nutrient budget discrepancies, and the theory of potential physical mechanisms to sustain these enhanced nutrient inputs was not well developed. These smaller scale, physical processes generally are lumped together into the term “turbulence” (Gargett 1997; Moum 1997). Large-scale budget equations consistently require more turbulent mixing in the main thermocline and below than is typically observed (Moum 1997), suggesting an incomplete understanding of these crucial turbulent mixing processes.

Several attempts to improve estimates of vertical diffusion rates in the open ocean (Lewis and others 1986; Ledwell and others 1993) have failed to lead to budget reconciliation. As discussed by Karl and others (1992), even the most conservative nitrate demand estimate for the NPSG cannot be supported by the steady state, cross-isopycnal nitrate diffusion rates estimated for this region. At Sta. ALOHA, the 0–100-m depth-integrated inventory of $[\text{NO}_3 + \text{NO}_2]$ varies by nearly three orders of magnitude (0.03 to 19.6 mmol N m⁻²; Figure 4), indicating that aperiodic mixing events may be important sources of nutrients. Of the six recorded “high nutrient” events, the four largest were all in late winter when the frequency of occurrence of both mesoscale eddies and wind-driven Ekman transport processes is high. Field results from the inaugural deployment of a physical–biogeochemical mooring near Sta. ALOHA clearly documented the March 1997 event (Letelier and others 1999), and we now believe that stochastic nutrient injections into the euphotic zone are normal features of the oligotrophic gyre. A characterization of the biological response at different time scales to such mesoscale physical perturbations has not been achieved.

Stochastic events of major ecological significance may be short lived and are undoubtedly under-sampled by present ship-based observation programs. Even the approximately monthly sampling schedule adopted in the HOT program is too infrequent to resolve these important, but intermittent, nutrient injections. Turbulent vertical motions of the water column may control photophysiology, gross and net primary production, and food web structure. There are at least four different physical mechanisms that could influence rate of nutrient supply to surface waters of the NPSG: (a) internal waves and tides, (b) cyclonic mesoscale eddies, (c) wind-driven Ekman pumping, and (d) atmospheric storms.

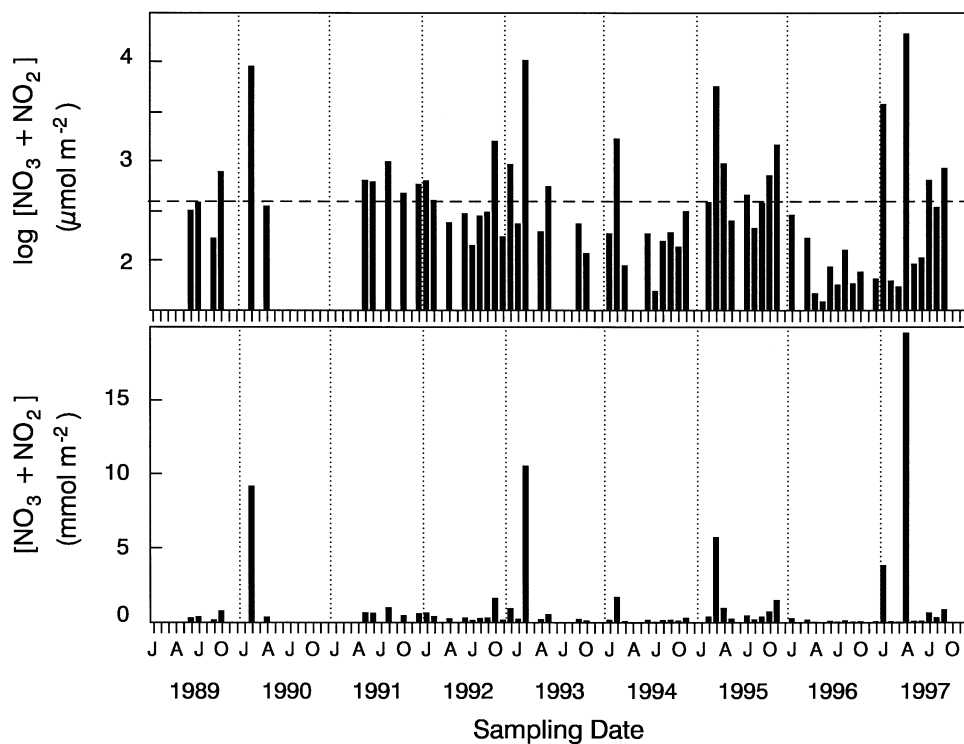


Figure 4. Temporal variability in the 0–100 m depth-integrated inventories of nitrate ($\text{NO}_3 + \text{NO}_2$) measured at Sta. ALOHA. The lower graph shows the ($\text{NO}_3 + \text{NO}_2$) concentration (mmol m^{-2}) for each cruise, and the upper graph is a representation of the \log_{10} transformed data set ($\mu\text{mol m}^{-2}$). The dashed line in the upper graph is the 9-y mean ($392 \mu\text{mol m}^{-2}$; $n = 60$). The large peaks, usually occurring in late winter, are manifestations of stochastic mixing events.

Internal waves propagating horizontally along isopycnal surfaces are ubiquitous in deep-ocean environments (Garrett and Munk 1972). McGowan and Hayward (1978) were first to document a relationship between episodic mixing and rates of plankton productivity. On a cruise to the Climax region of the NPSG during winter of 1969, they observed a deep mixing event that they attributed to enhanced internal wave activity. This physical event was sufficient to double the local rate of primary production (McGowan and Hayward 1978). More recently, during HOT-52 (February 1994), relatively rapid (less than 1 d) changes in the depth profiles of potential density consistent with the above-mentioned physical model were observed (Karl and others 1996). Measured nitrate concentrations of 53 nM at 85 m and 155 nM at 111 m, approximately an order of magnitude above “normal” concentrations, provided direct evidence of nutrient entrainment into the euphotic zone.

Mesoscale eddies, the so-called “internal weather” of the oceans (Krom and others 1993), have been observed in the NPSG for more than two decades (Bernstein and White 1974); however, until recently it had been difficult to determine their influence on biogeochemical processes. Although the

mechanism of eddy genesis is not well documented, cyclonic eddies are thought to be produced by interactions of wind stress and water circulation. Their counterclockwise rotation leads to a doming upward of isopycnals and a general shoaling of the nutricline. This physical process can result in enhanced primary production in the impact region (Falkowski and others 1991). It also has been suggested that local increases in chl *a* observed in zonal traverses of the NPSG may be manifestations of recent eddy pumping of nutrients (Venrick 1990). In addition to the effect on total production, there was enhanced nitrate-based or new production. Plankton growth rates also were enhanced (Allen and others 1996).

Sea-surface divergence from local wind forcing can cause mesoscale eddy-like upwelling as a result of Ekman pumping. During March–April 1997 a long (approximately 40 d) intense doming of the thermocline was observed near Sta. ALOHA with both moorings and ships (Letelier and others 1999). It resulted in a significant transport of new nutrients into the euphotic zone followed by accumulation of chl *a*. The NASA Scatterometer (NSCAT), a satellite sensor for surface wind vectors, was operational during this period, and a preliminary analysis of

these data by M. Freilich suggested upward vertical velocities in excess of 5 m d^{-1} .

Direct field observations during storm events also have implicated wind forcing as an important mechanism for enhanced nutrient supply to the euphotic zone. DiTullio and Laws (1991) reported increases in a variety of planktonic rate processes after an intense low pressure disturbance in the NPSG. Areal chl *a* concentration doubled relative to prestorm values, and primary production and new production both increased substantially, in the case of new production by 400% (DiTullio and Laws 1991). Coincident pigment analyses indicated that all major phytoplankton groups except cyanobacteria increased immediately after passage of the low-pressure disturbance. In response to this same stochastic event, total microbial biomass [as measured by particulate adenosine triphosphate (ATP) concentration] increased fivefold, and the rate of particulate matter export from the euphotic zone increased threefold (Taylor 1989). Interestingly, the mechanism invoked to accommodate the field observations was wet deposition (by precipitation) of NO_3^- and iron from the atmosphere, rather than vertical mixing of nutrients from below. Atmospheric dust deposition measured during this same observation period confirmed a large event coincident with the storm.

In more than 100 cruises to Sta. ALOHA over the past decade during all seasons, we have never observed surface-ocean enrichments of NO_3^- that were within even an order of magnitude of DiTullio and Laws' (1991) reported value of 600 nM. This disparity demonstrates the potential importance of rare, short events in understanding of coupled physical-biogeochemical processes in the NPSG. These field observations may help to reconcile previously reported ecosystem nutrient imbalances measured for the subtropical North Pacific (Hayward 1987; Karl and others 1992) and perhaps other geochemical anomalies elsewhere in the world ocean. If these stochastic events are characteristic of the NPSG in general, and I believe that they are, then mass balance will never be achieved unless a comprehensive time-series program is implemented, preferably with continuous measurements. This situation is not unique to the NPSG. Recent field studies in the North Atlantic subtropical gyre also have documented the role of mesoscale eddies for the supply of nutrients (McGillicuddy and others 1998).

MICROBIAL LOOP PROCESSES

Microorganisms generally are classified on the basis of size, nutritional, and physiological characteristics

or phylogeny. Regardless of the criterion used, broad diversity is revealed. The microscopic, photosynthetic organisms in the ocean traditionally have been referred to as phytoplankton ("plant" plankton), a term initially reserved for eukaryotic algae (Strickland 1965). This terminology is dated but is still used extensively in the scientific literature. Biologists now recognize three major lines of evolution or domains: *Bacteria*, *Archaea*, and *Eukarya* (Woese 1994; Pace 1997). Although the terms "bacteria" and "algae" have been used to refer to the "heterotrophic bacteria" (bacterioplankton) and the "photosynthetic eukaryotic algae" (phytoplankton), it is now well known that most of the algae in the NPSG are actually *Bacteria* (that is, cyanobacteria, formerly known as blue-green algae).

Johnson and Sieburth (1979) first described *Synechococcus* and another unknown phototroph (called type II cells) from ultrastructure. The type II cells were, nearly a decade later, shown by flow cytometric, pigment, and ultrastructure analyses to be *Prochlorococcus* (Chisholm and others 1988, 1992). In the NPSG, these two groups of *Bacteria* account for a majority of the photoautotrophic standing stock (Campbell and Vaultot 1993; Campbell and others 1994) and nearly all of the primary production (Liu and others 1997). Based on 16S rRNA gene sequence analysis, *Prochlorococcus* and *Synechococcus* belong to a single clade (96–98% identical in their 16S rRNA), with two deeply branching lineages of *Prochlorococcus* and three for *Synechococcus* (Urbach and others 1998). *Prochlorococcus* strains are further divided into high-light-adapted and low-light-adapted groups (Moore and others 1998). Within each group there appears to be a high diversity in both phylogeny and photophysiology. While the presence of pigments suggests a photoautotrophic mode of nutrition, neither photoheterotrophy (assimilation of organic substrates by using light energy) nor mixotrophy (combined autotrophic and heterotrophic metabolism) can be ruled out. Consequently, for the NPSG, the previous conceptual view of "phytoplankton-bacterial interactions" must now be replaced by "bacterial-bacterial interactions," which may include all currently known modes of metabolism. This issue is not merely semantics, it is oligotrophic ocean ecology and evolution *par excellence*.

Representatives of the domain *Archaea* are also known to be widely distributed in the marine environment and may even be a significant constituent of microbial biomass in selected habitats (DeLong and others 1994). Most previous analyses of "heterotrophic bacteria," for example, by direct microscopy, inadvertently included both *Archaea*

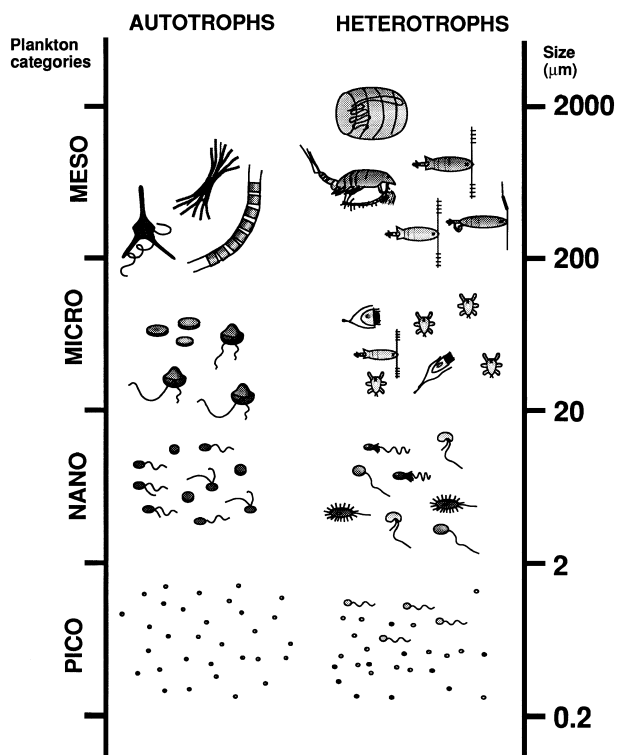


Figure 5. Representative classification of planktonic organisms by size showing the diversity of various autotrophic and heterotrophic groups based on the organization scheme of Sieburth and others (1978). Size, per se, cannot be used to separate autotrophs from heterotrophs in NPSG plankton assemblages. Courtesy of Albert Calbet.

and phototrophic *Bacteria*. This previous misrepresentation of fundamentally different phylogenetic and physiological groups underscores the diversity and complexity of natural microbial communities and demonstrates how our ecological interpretations are governed to a large extent by methodology.

With regard to nutrition, one also can anticipate a broad range of characteristics. Ecological role reversals, such as algal phagotrophy, bacterial predation, and protozoan osmotrophy, as well as other metabolic adaptations for living in a fluctuating environment (for example, multiphasic transport systems and diet switching) may be commonplace in the NPSG. Furthermore, the recent discovery of novel *Archaea* genes (Bult and others 1996) suggests that additional diversity exists and may have important implications for models of global carbon-pool dynamics. As Karl and Dobbs (1998) recently lamented, "One might legitimately ask, what else don't we know?"

Characterizations of plankton on the basis of cell size have been used extensively in marine ecology (Sieburth and others 1978; Figure 5). The use of

these arbitrary size classifications (picoplankton, 0.2–2 μm ; nanoplankton, 2–20 μm ; microplankton, 20–200 μm ; mesoplankton, 0.2–2 mm) is appealing due to ease of experimental manipulation. Raven (1986) has summarized numerous physiological consequences of cell size, many of which relate to the fitness of the organism in a given habitat. Foremost among them is the competitive advantage of resource (nutrients and light) acquisition as mean cell size decreases. Even among *Eukarya*, tiny coccoid morphology confers adaptive advantage in the sea, but this reduction in size also hides the significant genetic diversity that otherwise occurs in these little "balls" of pigmented biomass (Potter and others 1997).

Before 1978, photoautotrophic plankton populations in the NPSG were thought to be dominated by eukaryotic microorganisms, especially monads, flagellates, and to a lesser extent diatoms (Beers and others 1975, 1982). The primary consumers were thought to be relatively large, mesozooplankton (less than 200 μm). This traditional view of an active eukaryotic phytoplankton–herbivore grazing food chain has changed radically during the past 2 decades (Glover 1991) and is still evolving.

Based on the abundance of class-specific photosynthetic pigments and direct electron microscopic observations of water samples collected from Sta. ALOHA, *Prochlorococcus*-like microorganisms constitute approximately 50% of total chl *a*. Another prokaryote, *Synechococcus*, and two picoeukaryotic algal groups, Prymnesiophytes and Pelagophytes, together accounted for most of the remainder of the standing stock of phototrophic cells (Andersen and others 1996). Cells larger than 8 μm (for example, diatoms and dinoflagellates) were rare. Nevertheless, under certain conditions these larger species of *Eukarya* are abundant in the NPSG, especially in surface waters during summer (Scharek and others 1999a). In the contemporary view of the NPSG, the photoautotrophic picoplankton-supported microbial food web is always present, whereas the larger eukaryote-grazer food chain is ephemeral. Time and space integration are crucial for assessing the relative roles of these independent production processes.

Several fundamental discoveries, beginning with microscopic evidence for the presence of a large population of heterotrophic bacteria (Daley and Hobbie 1975; Hobbie and others 1977), have resulted in a revolution in thinking about carbon and energy flow in open-ocean ecosystems. Pomeroy (1974) first articulated a revised trophic role for heterotrophic marine bacteria by emphasizing the potential importance of microbially based food webs.

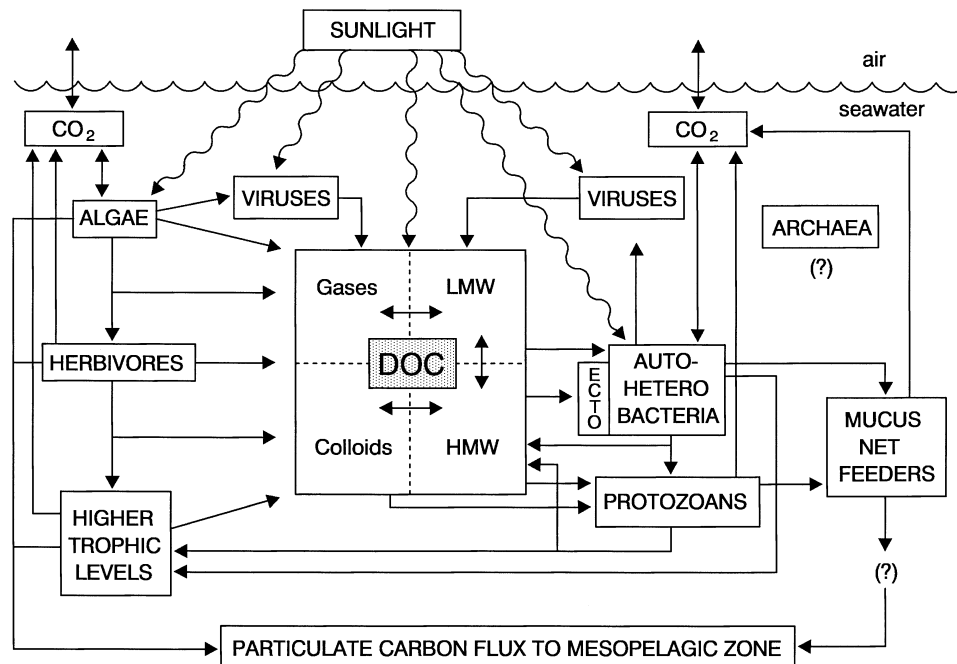


Figure 6. Schematic representation of the oceanic food web showing, on left, the classic pathway of carbon and energy flow through the photosynthetic *Eukarya* to herbivores and on to higher trophic levels. Depicted on the right is the microbial food web, which uses energy stored in the nonliving, detrital carbon pool to produce microbial biomass that can reenter the classic pathway of carbon and energy flow. Cell-associated ectoenzymes (ECTO) enable *Bacteria* to use high molecular weight (HMW) DOC in addition to the more traditional low molecular weight (LMW) and gaseous carbon substrates. Also shown in the microbial food web are viral particles and *Archaea*. At the present time, there is only rudimentary knowledge of the role of *Archaea* in the oceanic food web. Shown at the bottom of this diagram is the downward flux of particulate carbon (and energy), which is now thought to fuel most subeuphotic zone processes. The classic algae-herbivore grazer pathway is most important in this regard. Adapted and redrawn from Karl (1994).

In this new paradigm, microbial production fueled by assimilation of dissolved organic matter (DOM) sustains a supplemental pathway for carbon and energy flow to higher trophic levels (Figure 6). It was initially thought that DOM was too dilute to be used efficiently by microorganisms. However, despite low bulk concentrations of individual organic compounds (pM to nM range), bacteria readily transport and assimilate selected substrates (Fuhrman 1992).

Growth efficiency (GE) of picoheterotrophs (that is, production of biomass scaled to consumption of food, usually expressed as percentage of carbon) is of great importance in quantitative assessment of microbial secondary production. If GE of consumer communities is high (greater than or equal to 60%), then secondary production can exceed contemporaneous primary production (Winn and Karl 1984; Strayer 1988). For example, in a simple trophic-level model with three consumers each operating at 60% GE, 100 g of primary production could support a total of nearly 120 g of secondary production (that is, $[100 \times 0.6] = 60$ plus $[60 \times 0.6] = 36$ plus $[36 \times 0.6] = 21.6$), with additional carbon and energy

remaining for assimilation (Strayer 1988). Although respiration (CO_2 production) cannot exceed primary production (CO_2 fixation) at steady state, heterotrophic production (organic matter production), in theory, can. However, as Scavia (1988) has emphasized, heterotrophic bacteria do not fit easily into most conceptual models of trophodynamics because the DOM that supports them is derived from all trophic levels (Figure 6).

Although the microbial loop has received much attention during the intervening years, including detailed biological studies of bacteria, viruses, algae, protozoans, and their interactions (for example, Williams 1981; Azam and others 1983; Fenchel 1988; Fuhrman 1992; Hobbie 1994; Azam 1998), many important aspects are still unresolved. Foremost are questions pertaining to both total rate and overall efficiency of transfer of carbon and energy through the open-ocean microbial food web and controls on microheterotrophic production. Microbially based food webs initially were thought to operate with high efficiency of mass transfer (Williams 1981), but more recent and direct analyses suggest that the GE of microheterotrophs on dis-

solved organic matter in open-ocean ecosystems is in the range of 10–20% (Carlson and Ducklow 1996). Given the fact that at least two trophic transfers, and usually more, are required to channel microheterotrophic production back into the traditional food web (Figure 6), it now appears that the microbial food web acts largely as a sink for carbon and energy. The ecological significance appears to be centered on remineralization, including respiration, rather than biomass production. As Fenchel (1988) correctly observed, ecosystems are always sinks and tend to favor remineralization.

From an ecological perspective, important yet unresolved aspects of the microbial loop hypothesis concern controls on bacterial abundance, including both production and removal. Traditionally, “bacteria” were thought to be strict chemoorganoheterotrophs supported by the large and chemically diverse pool of DOM (Azam and others 1983). However, *Bacteria* in the NPSG also are known to function as photolithoautotrophs, so major revision of this paradigm is necessary (Figure 6). It is conceivable, even likely, that mixotrophic metabolism (that is, the simultaneous expression of autotrophic and heterotrophic modes) is selected for in situ. Organic nutrients can play a dual metabolic role, supplying both essential bioelements (C, N, P) and energy. The fact that organic nutrient assimilation is common among photoautotrophs is not well appreciated from an ecological perspective (Bonin and Maestrini 1981). Furthermore, without additional information on the ecological role of planktonic *Archaea* (pure cultures do not exist) and on the potential metabolic versatility of *Prochlorococcus* (pure cultures are only recently available), it may be premature to comment further on the potential flows of carbon and energy through these complex microbial food webs. Even for the more well-studied *Eukarya*, most of the laboratory culture work has been conducted using coastal, not open-ocean, isolates. Consequently, present knowledge of microbial loop processes is a flexible outline, rather than a rigid dogma.

The distribution and abundance of microorganisms is controlled by both bottom-up (that is, resource control, including both inorganic and organic nutrients) and top-down (that is, predator control, including phagotrophic protozoans, predatory bacteria, and virus infection) processes. DOM is produced by a number of distinct metabolic and ecological processes including direct (deliberate and inadvertent) release from photoautotrophs, inefficient grazing (“sloppy feeding”), excretion, defecation, and death (Figure 6). Among the other more well-established pathways, viral infection and subsequent cell lysis are now recognized as potentially

important processes of DOM production in pelagic habitats (Figure 6). Each process might be expected to produce a separate list of organic compounds with variable residence times. The more refractory compounds would accumulate and eventually dominate ambient DOM pools. Consequently, steady state DOM concentration per se may provide little if any ecological information regarding individual compound bioavailability or potential for supporting microbial growth.

For the NPSG, the mean age of the surface DOM pool, based on direct ^{14}C measurements, is approximately 1500 y (Williams and Druffel 1987; Druffel and Williams 1990). By comparison, the surface-ocean particulate carbon pool (which includes both living cells and nonliving particulate detritus) appears to be in $^{14}\text{C}:^{12}\text{C}$ isotopic equilibrium with the dissolved inorganic carbon pool and thus relatively young (Druffel and Williams 1990). These data on natural ^{14}C abundances place a major constraint on the rates and pathways of DOM production and use in the surface ocean. Inability to characterize the large and dynamic DOM reservoir and to quantify most trophic transfer efficiencies precludes serious efforts to model the open-ocean microbial food web.

Several things do seem certain with regard to microbial food web dynamics in the NPSG (Figure 6): (a) prokaryotes, and especially *Bacteria*, dominate both standing stocks (Table 1) and fluxes of carbon and energy, (b) heterotrophic microbial food webs provide only a negligible particulate matter subsidy to the “classic” food web, and (c) the phylogenetic and physiological diversities of prokaryotic assemblages are essential for sustaining the cycles of major and trace bioelements.

THE OCEANIC CARBON CYCLE: PRIMARY PRODUCTION AND RESPIRATION

The large and dynamic oceanic reservoir of carbon, approximately 4×10^{19} g distributed unequally among dissolved and particulate constituents with various redox states, plays an important role in global biogeochemical cycles (Table 1). The two largest pools are dissolved inorganic carbon (DIC) and the less oxidized pool of mostly uncharacterized, dissolved organic carbon (DOC). Chemical disequilibrium between DIC and organic matter is produced and maintained by numerous, mostly biologically mediated, conversions between dissolved and particulate carbon pools. These processes define the oceanic carbon cycle.

Primary conversion of oxidized DIC to reduced organic matter is generally restricted to the euphotic zone of the world ocean via photosynthesis. The

Table 1. Summary of Carbon Inventories and Carbon Fluxes for the NPSG Euphotic Zone Based on Data Collected at Sta. ALOHA^a**I. Carbon Inventories**

Parameter	Depth Range (m)	Average Concentration ($\mu\text{mol C m}^{-3}$)	Method	Comments
DIC	0–50	2.01×10^6	Coulometry	Surface waters are increasing at a rate of approximately $1 \mu\text{mol C m}^{-2} \text{ yr}^{-1}$
	50–200	2.05×10^6		
DOC	0–50	93,300	High-temp Combustion	Steep decreasing gradient from surface to 200 m
	50–200	78,000		
PC	0–50	2250	High-temp Combustion	Large seasonal changes (two- to threefold) in standing stock with summer maxima
	50–200	1417		
Total microbial biomass	0–50	750	ATP	Based on $C = \text{ATP} \times 250$
	50–200	500		
Phototroph biomass	0–50	380	chl <i>a</i>	Mostly (>80%) autotrophic bacteria; based on $C = \text{chl} \times 50$ (0–50 m) and $C = \text{chl} \times 15$ (50–200 m)
	50–200	155		
Hetero-bacteria biomass	0–50	417	Flow cytometry	Includes <i>Archaea</i> ; based on 10 fg C/cell extrapolation
	50–200	278		
Mesozooplankton	0–175	100	Oblique 1 m ² plankton net tows	Threefold seasonal variation with spring-summer maxima

II. Carbon Fluxes

Process	Depth Range/ Ref. Depth (m)	Rate ($\text{mol C m}^{-2} \text{ yr}^{-1}$)	Method	Comments
NPP	0–150	14.5	“Standard” in situ ¹⁴ C production (12 hr)	Mean from 74 cruises over 9 years
GPP	0–150	20–30	Particulate plus dissolved in situ ¹⁴ C (12 hr)	DOC-14 production rate has been increasing at Sta. ALOHA with time due to onset of P-limitation
HBP	0–150	4–5	³ H-leucine L/D incubation	Light stimulation of HBP presumably due to coupled production of DOC by PP
Particle export	at 150	0.8–1.0	Sediment traps	Mean of 74 cruises over 9 years

GPP, gross primary production; HBP, hetero-bacteria production; NPP, net primary production.

^aReferences: Karl and others (1996), Emerson and others (1997), Karl and Dobbs (1998), HOT program Data Reports and M. Landry (unpublished data).

supply of reduced carbon and energy required to support subeuphotic zone metabolic processes is ultimately derived from the upper ocean and is transported down by advection and diffusion of dissolved organic matter (Toggweiler 1989), gravitational settling of particulate matter (McCave 1975), and by vertical migrations of pelagic animals (Longhurst and Harrison 1989) and phytoplankton (Villareal and others 1993). Each of these processes,

collectively termed the “biological pump” (Volk and Hoffert 1985), operates under the control of both physical (light, temperature, and turbulence) and biological (species composition, growth rate, and food web structure) processes. For open-ocean ecosystems like the NPSG, relative contributions of these processes are poorly known.

Accurate and precise estimation of primary productivity in the marine environment is required for

understanding of both contemporary and past carbon cycles. The low-nutrient, open-ocean habitats of our planet are sometimes considered analogues of terrestrial deserts owing to their low standing stocks of living organisms and presumed low rates of organic carbon production. This traditional view of oligotrophic ocean biogeochemistry is now changing because of the long-term studies conducted at Sta. ALOHA in the North Pacific Ocean (Karl and others 1996) and at a sister station near Bermuda in the North Atlantic Ocean (Michaels and Knap 1996).

To understand biologically mediated carbon fluxes in the pelagic environment, it is important to differentiate between gross primary production (GPP), net primary production (NPP equals GPP minus photoautotrophic respiration), and net community production (NCP equals GPP minus both photoautotrophic and heterotrophic respiration). These are very different ecosystem properties (Williams 1993). Even in waters seemingly depleted in inorganic nutrients, both nutrient assimilation and GPP occur at substantial rates as a result of rapid nutrient cycling. This "spinning wheel" pelagic ecosystem (Goldman 1984) may be supported by the presence of aggregates of particulate organic matter that provide microenvironments that are enriched in required inorganic and organic nutrients.

Shulenberg and Reid (1981) noted that a subsurface oxygen (O_2) supersaturation maximum develops each summer in the NPSG; the magnitude of this feature can be used to constrain the rate of NPP. Based largely on data collected in the Climax region, they concluded that the implied O_2 production estimates were significantly greater (up to 5.4 times) than estimates derived from ^{14}C uptake (Shulenberg and Reid 1981). This provocative conclusion that the production of organic matter in the NPSG may have been "seriously underestimated" was challenged by Platt (1984) on both theoretical and analytical grounds. Platt (1984) concluded that it may be misleading to compare fluxes that are measured on different time and space scales.

Reid and Shulenberg (1986) countered with a defense of their initial interpretation and a rebuttal of Platt's (1984) main criticisms. They ended their letter to the editor with the statement, "Platt's numbers support our case." In their second formal correspondence on this matter, Platt and Harrison (1986) emphasized that "the would-be iconoclast must bear the burden of proof" given the potential ecological and biogeochemical implications of their conclusion.

Motivated, in part, by these conflicting estimates of primary production, R. Eppley and colleagues (Eppley 1982; Laws and others 1984) conducted

two field studies in the NPSG during August 1982. The Plankton Rate Processes in Oligotrophic Oceans (PRPOOS) program confirmed that previous field measurements may have underestimated rates of primary production by two to threefold. However, in the absence of a more comprehensive time-series study, it was impossible to derive an accurate estimate of annual production for this region or even to distinguish methodological change from ecosystem change.

Because the NPSG is a large habitat, with extensive temporal and spatial scales of variability, it is unlikely that a precise global survey of primary production will ever be achieved by direct measurement. Consequently, one must rely upon regional productivity compilations of uneven measurement density (Longhurst and others 1995). In the most commonly referenced global map of primary production (Koblentz-Mishke and others 1970), NPSG values are reported as less than $36 \text{ g C m}^{-2} \text{ yr}^{-1}$. Even the more recent data compilations of Eppley and Peterson (1979) and Berger (1989) list primary production values of 26 and 15–35 $\text{g C m}^{-2} \text{ yr}^{-1}$, respectively, for the NPSG.

Based on the nearly decade-long set of observations and measurements at Sta. ALOHA, it now appears that present rates of primary production in these low biomass regions and therefore in the ocean as a whole are much greater than had been considered in field studies conducted before the mid-1980s. Primary production rates measured at Sta. ALOHA approximately monthly during the period October 1988 to December 1997 varied from 219 to 1055 $\text{mg C m}^{-2} \text{ d}^{-1}$ based on the in situ ^{14}C technique. The 9-y mean of 473 $\text{mg C m}^{-2} \text{ d}^{-1}$ (standard deviation = 123 $\text{mg C m}^{-2} \text{ d}^{-1}$; median = 471; $n = 74$) is two to three times greater than most previous measurements in this region (Figure 7).

Photosynthesis in the NPSG can vary significantly on time scales ranging from daily to interdecadal. Karl and others (1996) have reported a greater than threefold range in daily irradiance (from 17.9 to 58.2 $\text{mol quanta m}^{-2} \text{ d}^{-1}$) at Sta. ALOHA due to a combination of seasonal and local meteorological (that is, clouds) effects. Even under conditions of constant surface irradiance, vertical oscillations of isopycnals as a result of inertial-period internal waves can have a major effect on photosynthesis. These vertical displacements can cause transient changes in the chl *a* per unit irradiance in the euphotic zone and changes in the nutrient concentrations at the base of the euphotic zone. Given the 31-h inertial period at Sta. ALOHA and assuming a conservative internal wave amplitude of 18 m, populations at the DCML (approximately 100 m)

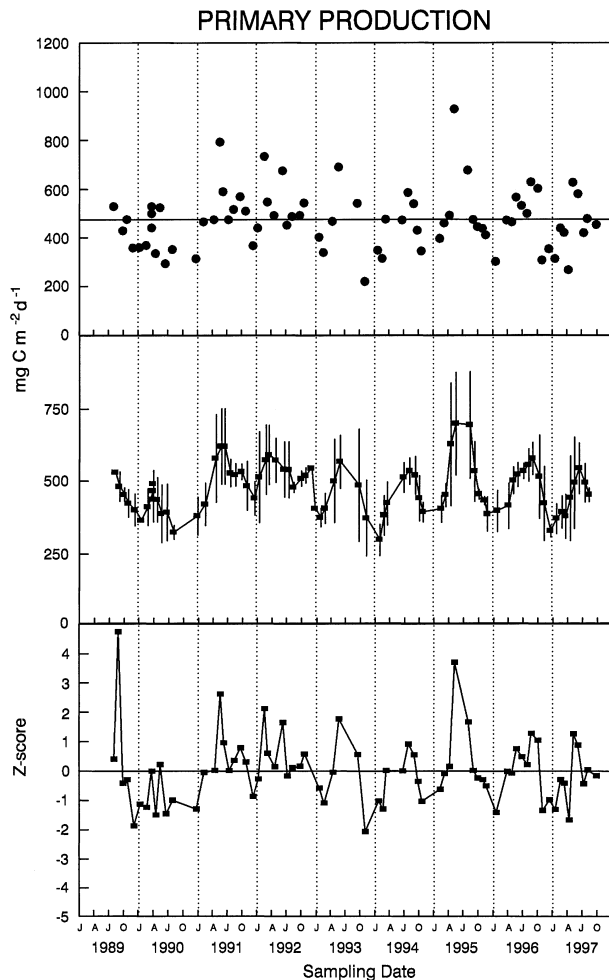


Figure 7. Temporal variability in depth-integrated (0–200 m) primary production measured at Sta. ALOHA over the first 9 y of the HOT program. **Top** Total euphotic-zone primary production ($\text{mg C m}^{-2} \text{d}^{-1}$) measured during in situ ^{14}C incubation experiments approximately monthly. The solid line is the mean value ($473 \text{ mg C m}^{-2} \text{d}^{-1}$) for the full data set ($n = 74$). **Center** Three-point running mean (± 1 SD) for the data presented in the top panel. **Bottom** Standard deviate (Z-scores; $Z = [\text{value} - \text{mean}] / \text{SD}$) for the primary production data set showing evidence for both seasonal and interannual variability.

can experience day-to-day irradiance variations of more than threefold (Letelier 1994; Letelier and others 1996). Variable cloud cover could make these differences even larger. Symmetrically vertically oscillating communities always receive more light than fixed-depth communities; the increase is related to amplitude of the internal waves and the magnitude of the extinction coefficient (Fahnenstiel and others 1988). Static incubations at fixed reference depths may underestimate the in situ productivity of phytoplankton assemblages exposed to vertical mixing (Marra 1978).

Seasonal variations of primary production rates in the NPSG are also well documented, with predictable summer maxima (Figure 7). Ironically, summer conditions are the most stratified, and nutrient fluxes from beneath the euphotic zone would be expected to be minimal. Both interannual (Figure 7) and interdecadal variations are also evident.

del Giorgio and others (1997) recently reported that respiration (R) exceeds NPP in unproductive systems, such as open-ocean regions like the NPSG (that is, where NPP is less than $70\text{--}120 \mu\text{g C l}^{-1} \text{d}^{-1}$). Based on similar, comprehensive analysis of GPP and R data sets from a variety of open-ocean habitats, Duarte and Agusti (1998) reported that, on average, P:R for open ocean ecosystems was 1.71 (range 0.05–45.7) but that approximately 25% of the 280 total analyses suggested net heterotrophy. Furthermore, it appeared that the slope of the power relationship between R and P was less than 1.0, implying that community respiration declined more slowly toward unproductive systems than did production (Duarte and Agusti 1998). The minimum value of P for an open ocean ecosystem to be net autotrophic (that is, P greater than R) was $0.035 \text{ g O}_2 \text{ m}^{-3} \text{d}^{-1}$, or approximately $1 \text{ mmol C m}^{-3} \text{d}^{-1}$, assuming a photosynthetic quotient of 1.0. Typical rates of P for the NPSG, based on short-term ^{14}C uptake measurements from the HOT program data, range from 0.1 to $0.5 \text{ mmol C m}^{-3} \text{d}^{-1}$ for the upper water column (Karl and others 1998). Even if GPP exceeds ^{14}C -based estimates in the NPSG by a factor of 2, an assumption that is partially supported by field data (Grande and others 1989; Karl and others 1998), then much of the NPSG would still be net heterotrophic based on the independent analyses of del Giorgio and others (1997) and Duarte and Agusti (1998).

There are at least two important implications of these conclusions. First, net heterotrophy can only be sustained if there are allochthonous inputs of reduced inorganic or organic carbon to provide the required energy subsidy. Second, net heterotrophic ecosystems would act as CO_2 sources rather than CO_2 sinks. Neither of these descriptions seems appropriate for the NPSG in current conceptual ecological framework. A reconciliation of this enigma is a high-priority research objective.

Geider (1997) challenged the conclusions of del Giorgio and others (1997) faulting the methodology used to estimate “heterotrophic” respiration. Geider (1997) also points out that the seasonal accumulation of O_2 in near surface waters and the measured loss of fixed carbon in sinking particulate matter both indicate net photosynthesis (that is, P greater than R) in the oligotrophic ocean.

Williams (1998) was also incredulous that open-ocean regions, such as the NPSG, could be sustained as net heterotrophic systems and used an independent analysis to suggest that the del Giorgio and others (1997) conclusions may be flawed. The major difference in the treatment of these experimental data is that Williams (1998) used 0–100-m depth-integrated estimates whereas del Giorgio and others (1997) used separate volumetric determinations. Although there were systematic depth-dependent trends in the P:R ratio for the NPSG data sets, the mean 0–100-m depth-integrated net community production (NCP) was $-0.9 \pm 43 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, a value that was indistinguishable from metabolic balance (Williams 1998). In the absence of time-series data, instantaneous photosynthesis and respiration measurements may mask a succession or alternation of periods of net autotrophy vs net heterotrophy on seasonal to decadal time scales (for example, Sherr and Sherr 1996) and therefore may be subject to misinterpretations. Furthermore, the very small net fluxes of oxygen, despite high rates of photosynthesis and respiration, present an unique analytical challenge.

THE OCEANIC CARBON CYCLE: NEW AND EXPORT PRODUCTION

There are at least two major sources of nutrients used to support plankton rate processes in the euphotic zone: (a) the local regeneration of simple forms of elements (for example, NH_4^+) resulting from the combined metabolic activities of metazoan and microbial processes, and (b) the influx of distantly produced “new” nutrients (generally NO_3^-) imported to the euphotic zone from greater ocean depths by upward advection and diffusion, by horizontal transport (Falkowski and Raven 1997), or by atmospheric deposition. In 1967, Dugdale and Goering formalized their now unifying concept of new and regenerated nutrients and therefore new and regenerated primary production of organic matter in the sea.

In their original presentation, Dugdale and Goering (1967) were very explicit on several key issues: (a) new nutrients can be derived from multiple sources (atmosphere, land, and deep water) that are all dependent upon fundamentally different renewal mechanisms, (b) any one of several elements could be used as the common currency, and (c) with regard to N-based considerations, if bacterial N_2 fixation ($\text{N}_2 \rightarrow \text{NH}_4^+ \rightarrow \text{organic N}$) or bacterial nitrification ($\text{NH}_4^+ \rightarrow \text{NO}_2^-/\text{NO}_3^-$) were found to be quantitatively important N flux pathways, there would need to be a reconsideration of new and

regenerated controls. Platt and others (1992) have recently presented a thoughtful review of the new production formalism complete with ecological implications ranging from paleo to modern habitats.

If it is assumed that phytoplankton production in the NPSG is N limited, and that rates of bacterial N_2 fixation and nitrification and horizontal transport of nutrients are all negligible relative to rates of gross organic N production, then total N assimilation can be treated as the sum of $[\text{NH}_4^+]$ plus $[\text{NO}_3^-]$ uptake and can be measured using appropriate ^{15}N -labeled isotopic tracers. This simplification also assumes that organically bound dissolved N (for example, urea and amino acids) is not readily assimilated by primary producers and that heterotrophic bacteria do not assimilate inorganic nitrogen compounds; neither assumption is true for the NPSG (Laws and others 1985; Sahlsten 1987).

The fraction of the total N assimilation that is supported by new nutrients, in this example, the rate of NO_3^- uptake [that is, $f = (\text{NO}_3^- - \text{N}) / (\text{NO}_3^- - \text{N} + \text{NH}_4^+ - \text{N})$], also is referred to as the “*f*-ratio” (Eppley and Peterson 1979). The *f*-ratio is one measure of the efficiency of ecosystem function (Quiñones and Platt 1991). In the NPSG, regenerated primary production is typically 10–20 times greater than new primary production ($f = 0.05\text{--}0.10$), indicative of a very inefficient system with regard to new production.

The new production paradigm has provided a conceptual framework for studies linking primary production and particle export. If biological steady state is assumed, or if primary and new production measurements are compared over sufficiently long periods (months to years), then new production in a given ecosystem is equivalent to the amount of primary production that is available for export, a value that is quantitatively balanced by resupply of production rate-limiting nutrients (Eppley and Peterson 1979; Eppley and others 1982; Eppley 1989; Knauer and others 1990).

In theory, export production would include losses of both dissolved and particulate matter. However, as Margalef (1978) has so eloquently stated, “any atom is more likely to travel downwards when in a particle than in solution;” and this predicts a more significant role for processes that favor export of particulate matter. Aggregation and mass sedimentation of living phytoplankton must be considered the epitome of export production. This mechanism is responsible for the rapid delivery of “fresh,” biodegradable organic matter to the deep-sea benthos (Billett and others 1983; Smith and others 1996). Most models of the biological pump assume that short grazing food chains lead to high new

production ($f > 0.5$) and high export, whereas complex microbial food webs lead to high recycling ($f < 0.1$) and low export.

For the NPSG, Michaels and Silver (1988) have shown that the size distribution of pelagic primary producers and the trophic structure of the consumer populations determine both the composition and magnitude of the exported particulate materials. Community structure controls all. As H. B. Bigelow so aptly noted, "all fish is diatoms" (cited by Dugdale and Wilkerson 1992). A modern assessment might state that new production, that is, that portion of gross primary production supported by allochthonous nutrients and that at steady state is available for export to higher trophic levels including fishes, is dependent largely on the growth of diatoms and other large, eukaryotic phytoplankton. A major conceptual problem, however, is that diatom biomass is a relatively minor component of the standing stock of phytoplankton in the NPSG (Ondrusek and others 1991; Letelier and others 1993). These two opposing viewpoints can be reconciled if one invokes stochastic processes as major factors in control of new and export production.

Existence of both external and internal pulses is the general rule in natural ecosystems (Odum and others 1995), and in this regard the NPSG does not appear exceptional. Both seasonal and stochastic forces may be important for stimulating otherwise inefficient or dormant components of the ecosystem. These, in turn, could lead to periods of enhanced ecosystem production, biomass accumulation, or predator-prey oscillations.

The classic marine grazing food chain—algae, zooplankton, and fish—can now be considered as a variable phenomenon in a sea of microbes. Although the flow of carbon and energy through this traditional pathway is relatively small compared with the more dominant and complex microbial food web, the aperiodic stimulation of the classic grazing food chain may be important for control of export production and for biological sequestration of atmospheric CO₂. Results from the HOT program have documented a complex temporal pattern of particle export that suggests two major events per annum; one in late winter and a second in late summer (Karl and others 1996). Based on the nitrogen isotopic abundance of sinking particles collected in a bottom-moored sediment trap deployed at Sta. ALOHA, Karl and others (1997) have suggested that the two events are derived from fundamentally different ecological processes. The winter pulse (with a mean $\delta^{15}\text{N} = 4.83$) is hypothesized to be largely supported by nitrate ($\delta^{15}\text{N} = 6.5$) supplied by stochastic upwelling events. By con-

trast, the late summer pulse (with a mean $\delta^{15}\text{N} = 1.53$) is largely supported by nitrogen supplied by bacterial N₂ fixation ($\delta^{15}\text{N} = 0$).

The sudden pulses of inorganic nutrients from aperiodic intrusions of nutricline water into the euphotic zone select for the diatom-copepod-fish food chain and result in a coupled export of particulate matter. Although the microbial food web continues to be active, it is "overprinted" by the growth of eukaryotic algae that respond quickly to the allochthonous supply of nutrients. It is essential to study the signal, as well as the background. Each summer, as stratification intensifies, there is selection for N₂-fixing organisms and a pulse of N₂-supported new production. Near the end of the summer, a second pulse of nutrients that appears to be derived from death and autolysis of near-surface plankton fuels another rapid bloom of eukaryotic algae and subsequent export pulse of particulate matter (Karl and others 1996). It should be emphasized that both strong and weak mixing can enhance new and export production, the former by import of NO₃⁻ and the latter by providing a habitat conducive for N₂-fixing organisms in surface waters (Karl and others 1992, 1995).

Wiegert and Penas-Lado (1995) compared the effects of upwelled pulses of nutrients with a constant supply of an equivalent annual flux. In their simulation model of an open-ocean pelagic community, nutrient pulsing produced a rich dynamical behavior and complex trophic structure that was obliterated under constant nutrient supply. These ecosystem pulses are inherently transient and stochastic and therefore difficult to observe and study. From investigations conducted elsewhere in the world ocean, diatoms are known to be important in mediating particle export directly as aggregated, senescent cells or indirectly as a result of macrozooplankton grazing (Peinert and others 1989), even if they rarely dominate the standing stocks of phytoplankton cells.

The role of the ocean as a net sink in the global carbon cycle is dependent largely upon the balance between the export flux of planktonic primary production (Eppley and Peterson 1979; Williams and von Bodungen 1989) and the rate of dissolved nutrient resupply by upward eddy diffusion. When particulate export is expressed as a percentage of contemporaneous primary production, this value is termed the export ratio (Baines and others 1994). Results from broad-scale, cross-ecosystem analyses suggest that the export ratio in oceanic habitats is a positive, nonlinear function of total integrated primary production (Suess 1980; Martin and others 1987; Pace and others 1987; Wassman 1990), with values ranging from less than 10% in oligotrophic

waters to less than 50% in productive coastal regions. It should be emphasized, however, that the field data from which the existing export production models were derived are extremely limited and that open-ocean habitats like the NPSG are underrepresented (Baines and others 1994). Because a majority of global ocean primary and export production occurs in subtropical gyre habitats (Martin and others 1987), it is important to understand the mechanisms that control the biological pump to make accurate and meaningful predictions of the response of the oceanic carbon cycle to global environmental change.

When the new production concept was developed by Dugdale and Goering (1967), accurate measurements of marine nitrification rates were not available. Nevertheless, they stated, "If nitrification rates are eventually shown to be sufficiently higher than has been assumed, the assumption that nitrate is a nonregenerated nutrient form in the euphotic zone would have to be modified" (Dugdale and Goering 1967, p. 205). Recent improvements in techniques for measurement of nitrification rates in the sea indicate a significant role for this process (Olson 1981; Ward and others 1982); the validity of the new production concept as it is commonly applied has come into question (Ward and others 1989; Dore and Karl 1996). Furthermore, if the NPSG was actually N limited, one might expect that N_2 -fixing bacteria would be selected for, forcing the ecosystem to limitation by the next least abundant required nutrient, relative to plankton population requirements (von Liebig's Law; in the case of the NPSG, most likely P or one of several trace metals).

Recent results have indicated that N_2 fixation in the NPSG may presently supply up to 50% of new N (Karl and others 1997). Both conceptually and ecologically, N_2 -supported new production is fundamentally different from NO_3^- -supported new production even though the two were considered together in the original new vs regenerated model of Dugdale and Goering (1967). When NO_3^- enters the euphotic zone from below by vertical advection and diffusion, it is delivered with a suite of other required major (for example, C, P, and Si) and trace (for example, Fe) elements in the proper stoichiometry to sustain biological activity. However the process of N_2 fixation serves to decouple export from new nutrient import, which can lead to changes in the elemental stoichiometry of surface-ocean particulate and dissolved organic matter and selection for or against certain groups of microorganisms (Karl and others 1997). Significant rates of N_2 -based new production eventually would result in severe P and perhaps Si limitation because, in the NPSG,

these vital nutrients are supplied from below. Furthermore, selective separation of the otherwise coupled N-P-Si cycles by vertically migrating microbial assemblages (Karl and others 1992; Villareal and others 1993) or positively buoyant particulate matter may further complicate these mass-balance considerations. These observations suggest that it may be inappropriate to assume that biogeochemical processes in the NPSG conform to the current new vs regenerated dichotomy; a revised paradigm may be required.

The critical role of large, eukaryotic phytoplankton in the production of exportable particulate matter cannot be overstated, and in this context the importance of aperiodic, pulsed events is paramount. However, Legendre and Le Fèvre (1989) have shown that there is no a priori direct equivalence between the new production and export production concepts. The former concerns particulate matter production by photoautotrophs and the latter is controlled by numerous trophic levels. In their bifurcation model (Figure 8), they emphasize the importance of primary production—export processes for large vs small photoautotrophic cells and the critical role of gravitational sinking, which may partially be controlled by hydrodynamics. For example, export production is maximized if large phototrophs grow, aggregate, and then sink. At the opposite end of the continuum, export is minimized when phototrophic picoplankton fuel a complex microbial food web. At Sta. ALOHA, there appears to be an episodic diatom aggregation-sinking event in late summer (Scharek and others 1999a, 1999b) that could be the manifestation of a N_2 -supported "echo" bloom after disappearance, by autolysis, of the seasonally accumulated, N_2 -fixing *Trichodesmium* population, as suggested by the ^{15}N isotopic signatures of sinking organic matter (Karl and others 1997). A large proportion of the exported diatom cells are full of cytoplasm, contain chl *a* and otherwise appear to be healthy. The aggregates sink relatively rapidly (greater than 200 m d^{-1}) and reach the 5000-m seabed as "bioavailable" organic matter. This and other evidence not summarized here clearly documents the importance of episodic export in the NPSG, and the complexities of modeling an ecosystem where high-export cell aggregation and low-export microbial loop processes can occur simultaneously.

SPATIAL AND TEMPORAL PATTERNS IN PLANKTON COMMUNITY STRUCTURE

In 1961 G. E. Hutchinson published his now classic paper, the "Paradox of the Plankton" (Hutchinson

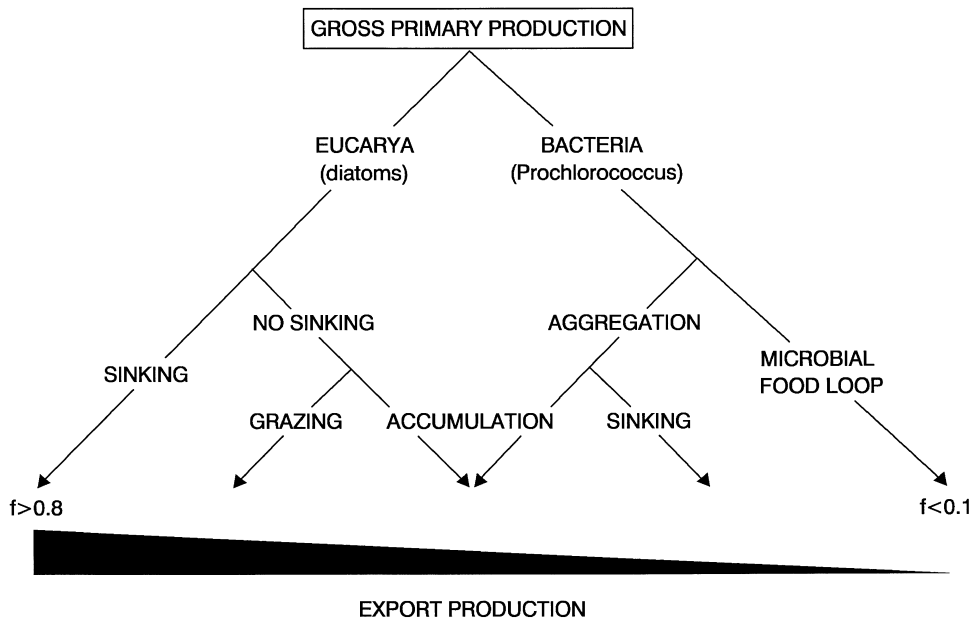


Figure 8. Conceptual view of major controls on re-cycled vs export production in the sea. This model suggests the existence of several major bifurcations that may occur simultaneously in oligotrophic regions, such as the NPSG. Redrawn from Legendre and LeFèvre (1989).

1961), on the coexistence of related species, particularly phytoplankton, in the relatively isotropic and unstructured marine environment. Consequently, an initial goal of NPSG ecosystem research was to study the biogeography of the region including measurements of species composition and diversity.

Fager (1963) and Johnson and Brinton (1963) independently hypothesized that there were recurrent, organized groups of planktonic organisms that conformed to the broad distributions of identifiable water-mass characteristics. These multiple species associations of oceanic phytoplankton and zooplankton had predictable concordance in their rank-order abundances, providing strong evidence for grouping (Fager and McGowan 1963). By these analyses, the NPSG was shown to be a distinct faunal province with unique planktonic assemblages (Figure 1).

Based on analysis of the zooplankton community structure, the Central North Pacific "biotic province" had high species diversity (that is, number of species), high equitability (that is, evenness of the rank order abundance), and a low degree of seasonal and interannual variability in total zooplankton standing stock (McGowan 1974). With respect to copepods, the most numerous group of mesozooplankton, there were approximately 125 species (McGowan and Walker 1979). The copepod community was highly structured, and the structure appeared to be well regulated and resilient. Furthermore, no differences in the order of copepod species dominance were observed for NPSG plankton samples separated in time (30 min to 16 yr) or horizontally in space (100 m to 1000 km), despite small scale, mesoscale, and seasonal and interannual variability

in the physical structure of the habitat (McGowan and Walker 1985). Consequently, it was concluded that maintenance of the high diversity and numerical dominance of zooplankton in this old, large, self-contained ecosystem was not the result of physical disturbance but rather was probably a result of biological interactions (McGowan and Walker 1985).

Venrick (1971) used a similar recurrent group analysis to examine the distribution and abundance of selected eukaryotic phytoplankton species in water samples collected from NPSG (Venrick 1971, 1982, 1990). Her analyses revealed the stable presence of two distinct floral assemblages, segregated by depth with a transition near 100 m (Venrick 1982, 1992). There were 245 and 231 individual species observed in the shallow and deep zones, respectively; however, approximately 20 species accounted for 90% of the individuals in each depth stratum (Venrick 1990). The shallow zone (0–75 m) was primarily nutrient limited, and the deep zone (deeper than 75 m) was primarily light limited (Venrick 1982, 1990, 1993). Similar to the results for copepods, the apparently competing phytoplankton species were found in stable coexistence, suggesting niche diversification, disequilibrium from spatial-temporal habitat heterogeneity or, perhaps, herbivory (Venrick 1982). Based on data collected in the NPSG over a 12-y period (1973–85), Venrick (1990) documented a slow and nondirectional change in the relative abundances of 194 of the species, particularly diatom species in the deep-water assemblage. Nevertheless, the magnitude of the change in rank-order abundance during this

12-y period was small relative to differences observed between the two depth strata on any given cruise. Her observations supported the previous conclusions of high stability in population structure (Venrick 1990).

It is important to emphasize that the zooplankton and phytoplankton species analyzed in these studies collectively represent less than 10% of the total standing stock of living organisms (Table 1 and Figure 5). It is now well documented that the NPSG is a "microbial ecosystem," and no comprehensive phylogenetic study of the dominant NPSG assemblages has been conducted. In the absence of these critical phylogenetic data sets, Li (1997) has suggested that autotrophic marine picoplankton could be categorized, instead, by their cellular bio-optical properties by using flow cytometry. The resultant "cytometric" diversity, based largely on cell size and pigment composition, may be as relevant to ecological studies as conventional taxonomic classification.

Despite present inability to map picoplankton (including *Bacteria*, *Archaea*, and small *Eukarya*) species assemblages in the NPSG over large space and time scales, it seems reasonable to assume that coherent patterns corresponding to the water mass-dependent distributions of mesozooplankton and of larger eukaryotic photoautotrophs eventually might be revealed. It is certain that the most abundant photoautotrophic and chemoheterotrophic species in the NPSG have eluded pure culture, which is a sobering commentary on the level of understanding of the largest biome on Earth!

THE "GREENING" OF THE NPSG

The influence of climate variability on oceanic biogeochemical cycles, especially that which occurs on decade-to-century time scales, is not well understood. Because of their large thermal inertia, the oceans are expected to play a major role in climate variations on time scales of decades to centuries (Deser and others 1996). If community stabilization is a universal tendency under ruling climate (that is, the Climax community theory), then community change can be expected during variations in climate. Although there are several case studies documenting impacts of climatic variability on structure and function of selected marine ecosystems, especially fisheries (Mysak 1986; Polovina and others 1994; Mantua and others 1997; McGowan and others 1998), few data exist on changes in new or export production pathways or rates that could be incorporated into global carbon sequestration models. One major obstacle is the potential lag between physical perturbation and ecological response and the general resiliency of natural communities to external

physical forcing. One might predict an abrupt, threshold response that may be time lagged rather than slow, gradual ecological change.

When trade winds persist for several years, they accumulate surface water in the western Pacific, and upper-layer heat storage, or upper-ocean volume, is increased in a hydrographic region called the "warm pool" (Barber 1992). To track the total heat storage, Wyrski (1985) developed an upper-layer volume index (Figure 9, top) that may provide diagnostic information on the El Niño and La Niña states of these low-latitude regions. The HOT program began when this index was at a decade-long minimum and has made most of its field observations during a period of unprecedented and more-or-less continuous change (Figure 9).

The coupled interactions between tropical and midlatitude climate in the North Pacific, that is, teleconnections, have been known since the classic work of Sir Gilbert Walker nearly 75 years ago (Bjerknes 1969). The El Niño Southern Oscillation (ENSO), with alternating episodes of warm and cold water in the equatorial Pacific, is one of the better known phenomena (Figure 9). Dramatic changes in this and other ENSO-related indices (for example, Cold Tongue Index, Southern Oscillation Index; Zhang and others 1997) document the importance of decadal habitat variability. Furthermore, both frequency and duration of El Niño-favorable conditions have increased over the past several decades (Trenberth and Hoar 1997), especially during the period of the HOT program (Figure 9). It remains to be seen if these variations in coupled ocean-atmosphere processes in the equatorial Pacific propagate to and impact NPSG ecosystems and whether the increasing burden of atmospheric carbon dioxide will interact with these complex global ocean processes. These are but a few exciting challenges for the future.

A major and abrupt shift in the North Pacific climate system occurred during 1976–77, manifesting itself as an intensification and eastward shift of the Aleutian low-pressure system during winter (Trenberth 1990; see Figure 10). Both changes meant that the counterclockwise circulation around the low-pressure system was pumping more warm air northwards to Alaska while sending anomalously cold air to the south (Kerr 1992). This pattern resulted in a decade-long cooling phase in the sea surface of the NPSG. Over the midlatitudes of the North Pacific, the regime shift also was marked by more vigorous winter circulation and southwest extension of the prevailing westerlies for the period following 1975–76 (Graham 1994). Coincident with these sea-surface anomalies, subsurface (100–125

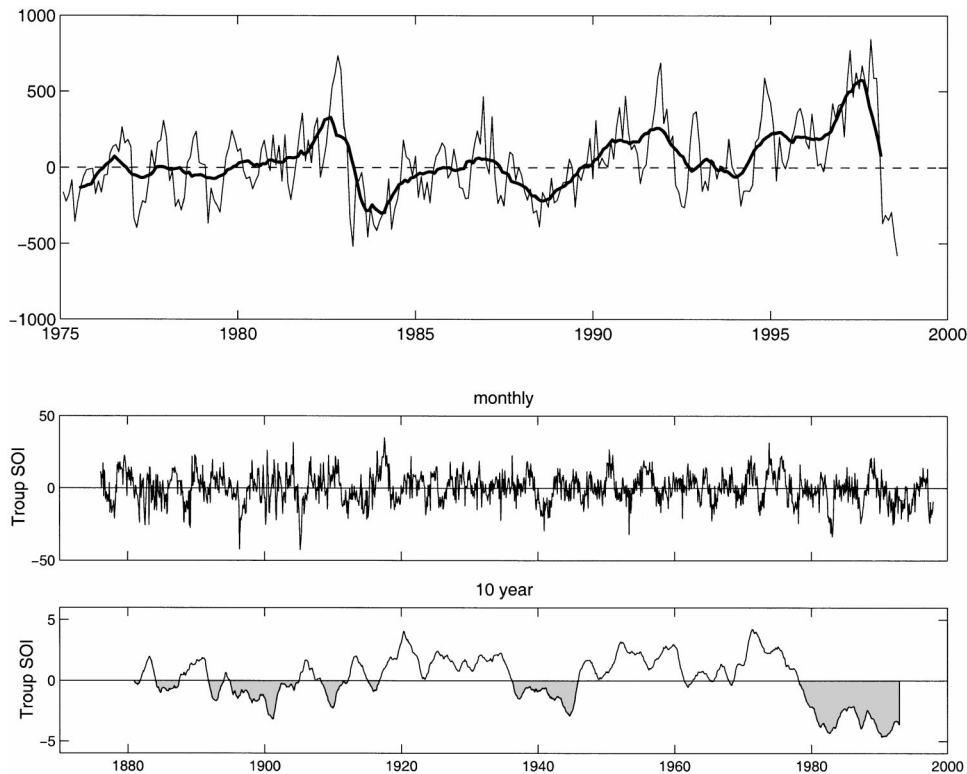


Figure 9. The “pulse” of climate variability in the Pacific Ocean as revealed by two independent indicators of the El Niño–La Niña oscillation. **Top** Upper layer volume in the tropical Pacific between 15°N and 15°S in 10^{14} m³ relative to its mean value of 70×10^{14} m³ (Wyrski 1985). Data and data analysis from University of Hawaii’s Sea Level Center (UHSLC) data product “Upper Ocean Volume” (<http://uhslc.soest.hawaii.edu>). **Bottom** The Troup Southern Oscillation Index (SOI) defined as: $[10] \times [dP_T - dP_D]/SD$, where dP_T and dP_D are the monthly sea level pressure anomalies (monthly mean pressure minus the 1882–1998 mean) at Tahiti (T) and Darwin (D), respectively, and SD is the standard deviation of the difference for the month in question (Troup 1965). 10-y running mean of the monthly Troup SOI values, as above, showing the unprecedented frequency and duration of negative SOI since the late 1970s. Negative SOI values are El Niño favorable. Extended periods of negative SOI result in increased stratification of the subtropical North Pacific gyre that favors the growth of the *Trichodesmium*, a nitrogen-fixing cyanobacterium (see text). The two major time-series programs conducted in the NPSG to date, Climax (1965–1985) and HOT (1988–present) were conducted during potentially different large-scale environment conditions.

m) warming was observed in the NPSG (Zhang and others 1998). This combination of colder surface water and warmer subsurface water may have enhanced winter mixing in the region of the thermocline and hence increased the flux of new nutrients into the euphotic zone. These anomalous winter conditions persisted until 1988 when there was a return to the “normal” state.

In 1987, Venrick and others (1987) reported that the average euphotic zone (0–200 m) chl *a* concentration in the oligotrophic North Pacific Ocean during summer (May–Oct) had nearly doubled from 1968 to 1985 (Figure 11). Their data set, collected in the Climax region, included at least one depth profile from each of the 12 years during this observation period. The sampling frequency was insufficient to determine whether the chl *a* increase had been continuous over time or whether there

had been a “step-function” increase between 1973 and 1980 (Venrick and others 1987). The authors attributed their field observations to the North Pacific regime shift that caused an enhanced nutrient flux and resulted in a significant long-term change in the carrying capacity of the NPSG ecosystem. However, no direct measurements of nutrient loading were presented.

Subsequent ecosystem analyses supported the interpretation of a climate-driven enhancement of productivity of various trophic levels of the marine ecosystem. Ebbesmeyer and others (1991) compiled normalized changes in 40 different environmental variables ranging from the salmon catch in Alaska to intensity of the winter North Pacific westerlies to solar radiation in Puget Sound that displayed similar temporal coherence with the 1976–77 regime shift (Figure 10). As mentioned previously, low-fre-

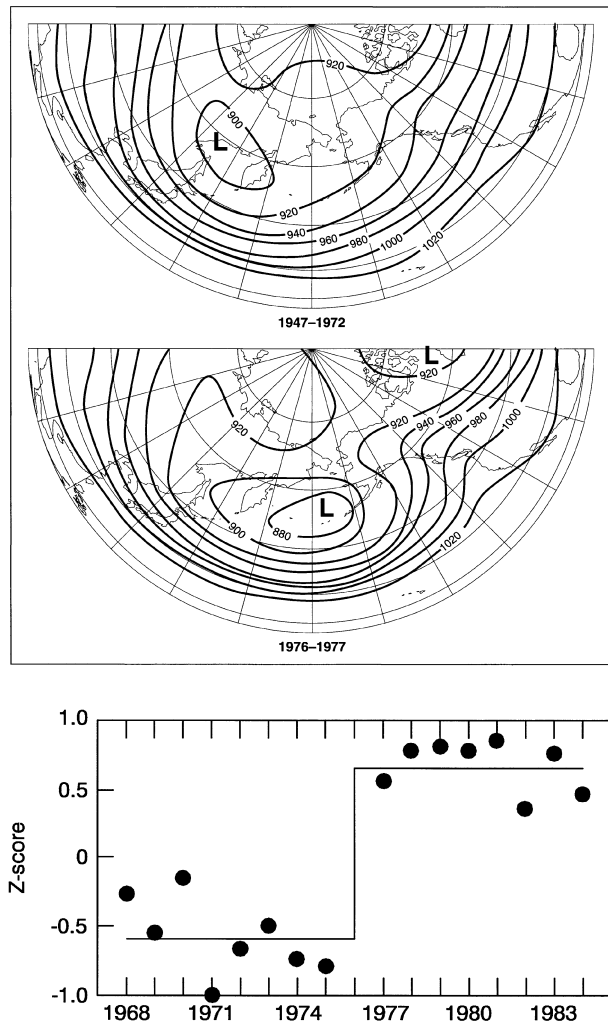


Figure 10. Potential cause and effect of the 1976-77 regime shift in North Pacific climate. **Top** and **Center** Mean 700 mb contours (tens of feet) for the 1976-77 winter period (Dec-Feb) compared with the long-term mean (1947-72) winter conditions. These data show the intensification and eastward shift in the Aleutian low-pressure system, redrawn from Namias (1978). **Bottom** Seventeen-year time series of the standard deviate (Z-scores; $Z = [\text{value} - \text{mean}] / \text{SD}$) averaged by year, for a diverse group of 40 environmental variables showing the coherent step function or regime shift. Redrawn from Ebbesmeyer and others (1991).

quency climate events are undoubtedly important in maintaining the diversity and structure of the oligotrophic marine ecosystem, and they would not have been detected without time-series data sets.

This abrupt shift in climate beginning in the mid-1970s is not unique and appears to be one example of a recurring pattern of interdecadal climate variability referred to as the Pacific (inter) Decadal Oscillation, or PDO (Mantua and others 1997). There has been an impressive amount of research conducted over the past decade seeking an

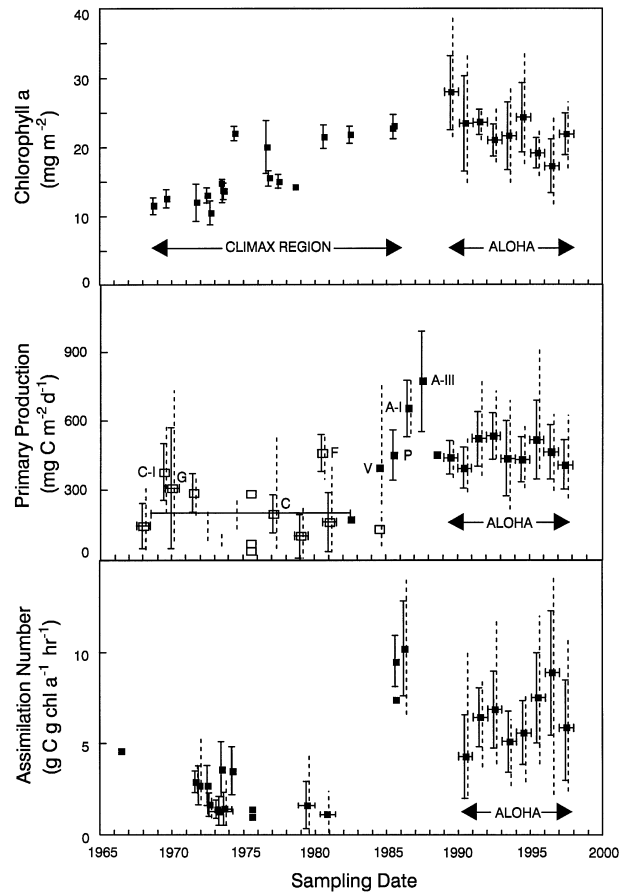


Figure 11. Composite time-series analysis of phytoplankton community parameters for samples collected in the subtropical North Pacific Ocean. Measurements include: **top** euphotic zone depth-integrated chlorophyll *a* concentrations, **center** euphotic zone depth-integrated rates of primary production, and **bottom** light-saturated assimilation number. These data were obtained from numerous sources and locations but derive largely from oceanographic investigations at or near the CLIMAX region and Sta. ALOHA. Where shown, dashed vertical lines represent the range of multiple observations for a given cruise, season, or study, and solid, vertical bars indicate ± 1 SD of the mean value. Where shown, horizontal bars indicate the duration of multicruise data sets. Selected data sets from important expeditions are noted by the following: AI and AIII, Asian Dust in Oligotrophic Seas (ADIOS) I and III cruises, C, CLIMAX time series; C-I, CLIMAX-I; F, FIONA (one cruise in the CLIMAX time series); G, GOLLUM; P, Plankton Rate Processes in Oligotrophic Oceans (PRPOOS) cruise; V, Vertical Transport and Exchange (VERTEX) cruise. Redrawn from Karl and others (1999).

understanding of the cause(s) of this climatic variability. It has included both retrospective analyses of ocean observation programs and coupled ocean-atmosphere and ocean general circulation modeling efforts (Graham 1994; Miller and others 1994).

Table 2. A Comparison of Several Autotrophic Plankton Parameters for Samples Collected in the NPSG before and after the Hypothesized Domain Shift^a

Parameter	Pre-1976	Post-1985	Change (%)
Chl <i>a</i> (mg m ⁻²)			
0–25 m	1.5 ± 0.7	2.0 ± 0.7	+33
75–200 m	7.4 ± 1.5	14.8 ± 3.1	+100
0–200 m	12.5 ± 2.8	22.6 ± 4.8	+80
Pheo (mg m ⁻²)			
0–25 m	0.5 ± 0.3	1.4 ± 0.7	+140
75–200 m	7.8 ± 2.1	24.6 ± 7.2	+215
0–200 m	9.7 ± 2.0	30.0 ± 8.4	+209
Chl <i>b</i>	Low	High	Moderate
Chl <i>c</i>	High	Low	Large
Primary production (mg C m ⁻² d ⁻¹)	200–250	450	+200
Dominant species (domain)	Monads, flagellates, and nonthecate dinoflagellates (Eukarya)	<i>Prochlorococcus</i> , <i>Synechococcus</i> (Bacteria)	—
Soluble reactive P (mmol m ⁻²) 0–100 m	10–35	5–10	greater than –50
Dissolved silica (mmol m ⁻²) 0–100 m	200–700	100–150	greater than –50

^aData collected from numerous sources, primarily Beers and others (1982), Hayward (1987), Venrick et al. (1987), Campbell and others (1994), Scripps Institution of Oceanography (SIO) Data Reports #74-20, 75-6, 90-3, 90-4, 91-28, 93-17, and HOT program data sets (<http://hahana.soest.hawaii.edu>). Nutrient data for region 20–30°N, 140–170°W as reported in the National Oceanic Data Center, U.S. Department of Commerce World Ocean Database 1998 and the HOT program data base (<http://hahana.soest.hawaii.edu>). Adapted from Karl et al. (1999).

There are at least two separate but not mutually exclusive models to explain these climate variations. According to Trenberth (1990), the regime shift appears to be the result of the presence of persistently warm waters in tropical Pacific caused by high frequency and long duration of El Niño (that is, warm) conditions and lack of La Niña (that is, cold) periods during 1976–88. The on–off seesaw of El Niño Southern Oscillation (ENSO) got stuck “on” for a period of approximately 10 yr, altering the general climatic conditions, especially in winter, over the NPSG. The climate shift also might represent a change in the background state of the coupled ocean–atmosphere system of the tropical Pacific, rather than being a direct manifestation of increased frequency and duration of ENSO events (Graham 1994). Furthermore, it has been suggested that planetary-scale oceanic waves generated by ENSO events may account for ocean circulation anomalies a decade later in the midlatitudes of the North Pacific (Jacobs and others 1994; Chelton and Schlax 1996). Recently Zhang and others (1998) have documented subsurface ocean teleconnections between the tropics and subtropics in the North Pacific Ocean that may be another key to understanding these decadal climate variations. These data sets and models are both complex, but suffice to say that a physical understanding and future prediction of

these important decadal climatic variations has nearly arrived. Regardless of the cause, the documentation of these large-scale, atmosphere–ocean interactions emphasizes the role of external forcing of plankton communities in the NPSG.

Data from the ongoing HOT program at Sta. ALOHA, which also includes occasional sampling in the Climax region, extend the previous analysis of euphotic zone chl *a* concentrations for nearly another decade and now provide a 30-year chronology for the NPSG ecosystem (Figure 11). The combined Climax–ALOHA data sets document that the mean euphotic zone chl *a* concentration from the period Oct 1988 to Dec 1997 (HOT program results) is also significantly greater than the pre-1976 mean Climax program chl *a* concentration (Table 2). These changes, if caused by climate variations, could have important implications for biogeochemical and fisheries modeling, especially if they reflect differences in plankton community structure or food web interactions. Variations in chl *a* also may affect carbon production and export and deep-sea benthic processes, thereby altering local rates and pathways of carbon sequestration. Biogeochemical models based on historical or even contemporary observations may not be accurate predictors of future trends.

In addition to chl *a* variability, there is also a 30-y chronology of primary production and mixed-layer (0–25 m) assimilation numbers (that is, the light-saturated, chl *a*-normalized rate of autotrophic carbon fixation). Compared with the 17-y Climax program mean of approximately 200 mg C m⁻² d⁻¹, the average rate of primary production measured during the HOT program is more than twice as high (Figure 11). Likewise, the assimilation number in surface waters increased at least threefold since the early 1980s. While it is impossible to estimate the consequences of methodological improvements over this 30-y observation period, I believe that these planktonic rate processes, along with the pigment data discussed previously, result from fundamental changes in phytoplankton community structure that ultimately derive from climate-related habitat variations.

Wind stress, heat, and water exchange, in addition to variations in gyre circulation are all biogeochemically relevant physical determinants. The characteristics of the rate of supply of major nutrients and trace elements, as well as light quality and quantity, ultimately establish ecosystem structure, including carrying capacity and productivity. Slight or even subtle alterations of the habitat can result in large changes in, for example, vertical eddy-diffusivity rates and hence nutrient recharge and productivity (Falkowski and others 1991; McGillicuddy and Robinson 1997). Both Venrick and others (1987) and Polovina and others (1994) suggested that changes in the subtropical North Pacific after the 1976 climate step were a result of increased mixed-layer depths and a higher frequency of deep mixing events due especially to an intensification of the Aleutian low-pressure system in late winter. This vigorous mixing might be expected to enhance nutrient input to the euphotic zone and stimulate ecosystem productivity. However, it is important to emphasize that the Aleutian low-pressure system returned to its normal, pre-1976, condition in 1988 just at the start of the HOT program. The chl *a*, on the other hand, has remained at the elevated “regime-shift” concentrations (Figure 11 and Table 2). Given the rapid growth rates of microorganisms in the NPSG (1–2 d⁻¹) and relatively rapid turnover of particulate organic matter pools (10–20 d) it is unlikely that the oceanic biogeochemical response to climate forcing or relaxation would have a decadal lag.

The PDO phenomenon covaries with the Southern Oscillation Index (SOI) and the Cold Tongue Index (CTI), two independent climate features that correlate with El Niño–La Niña cycles (Mantua and others 1997). Because increased nutrient flux is

predicted to occur during the positive PDO phase of the North Pacific climate cycle, the marine ecological response might be expected to be a classic “bottom-up” response, increased inorganic resource supply, leading to increased photoautotrophic biomass, followed by increases in the production of higher trophic levels. In their comprehensive review of this topic, Mantua and colleagues (1997) suggest that recurrent ocean–atmosphere variations centered over the midlatitude North Pacific basin may act to constrain interannual ENSO variability, rather than vice versa. Both mechanisms would lead to correlations between the indices but with potentially fundamentally different predictions for biogeochemical processes.

Based on an analysis of available instrumental data combined with air temperature reconstructed from North American tree rings, Minobe (1997) has recently documented a 50–70 y North Pacific climate oscillation that has existed for at least 300 yr. It is conceivable that this oscillation and the interdecadal PDO, with an approximately 20–30 y frequency, are superimposed onto higher frequency interannual and seasonal habitat variations resulting in a complex, time-varying mosaic. Some biological changes (for example, enhanced nutrient uptake) are rapid, while others require growth and reproduction or even natural selection over many generations. Depending on the phase of these independently timed cycles, these interactions could create a spectrum of dynamical behavior that might border on chaos; hence, an understanding of cause and effect may be difficult to achieve. As Sir Gilbert Walker stated more than half a century ago, “I think the relationships of world weather are so complex that our only chance of explaining them is to accumulate the facts empirically” (cited in Horel and Wallace 1981). I believe this is also an accurate assessment of complex ecological and biogeochemical processes in the NPSG.

NEW VIEWS OF AN OLD OCEAN: THE EMERGING HOT PROGRAM LEGACY

Long-term ecological studies are predicated on the straightforward assertion that certain processes, such as succession, climate change, and other habitat disturbances, are long-term processes and must be studied as such (Strayer and others 1986). Indeed there are many examples in the scientific literature where interpretations from short-term ecological studies are at odds with similar data sets collected over much longer time scales. Because it is difficult to observe slow or abrupt environmental changes directly, much less to understand the fundamental

cause and effect relations of these changes, Magnuson (1990) has coined the term “the invisible present” to refer to these complex ecological interactions. As data accumulate in a long-term ecological study, new phenomena become apparent and new understanding is derived.

Since October 1988, a comprehensive suite of ocean measurements and results of in situ experiments have been obtained at the oligotrophic Sta. ALOHA in the NPSG. Core measurements were selected to provide a data set to evaluate existing C-N-P biogeochemical models and, if necessary, to improve them. Foremost in importance among the various ecosystem processes under investigation are (a) the flux of carbon at the air–sea interface, and (b) the rates and control mechanisms of the biological pump. Equally important are the observed time-dependent changes in microbial biomass and biodiversity, and the relationships of these observed ecosystem changes to the broader extratropical climate forcing, such as El Niño Southern Oscillation (ENSO) and other large-scale, ocean–atmosphere interactions. The emergent data set from the HOT program is unique, robust, and rich with previously undocumented phenomena. The scientific results of the HOT research program are providing an unprecedented view of biogeochemical cycles in a previously undersampled region of the world ocean.

At the beginning of the HOT program in 1988, biogeochemical processes in the NPSG were thought to be well understood. New and export production were limited by the supply of nitrate from below the euphotic zone, and rates of primary production were thought to be largely supported by locally regenerated nitrogen (Hayward 1987, 1991). Photosynthetic rates were low (less than 200–250 mg C m⁻² d⁻¹; Berger 1989) and eukaryotic micro- and nanophytoplankton assemblages dominated the photoautotrophic biomass (Beers and others 1975, 1982). Neither *Prochlorococcus* (now recognized as the most abundant oxygenic photoautotroph in terms of numbers and biomass) nor planktonic *Archaea* had been discovered. Potentially important biogeochemical fluxes, such as photosynthetic production of dissolved organic matter (sometimes referred to as excreted or exuded organic matter) and N₂ fixation, were thought to be negligible.

The contemporary view recognizes the NPSG as a very different ecosystem (Table 2). Based on the decade-long Hawaii Ocean Time-series (HOT) program data sets, we hypothesize that there has been a fundamental shift from N limitation to P limitation (Karl and others 1995; Karl and Tien 1997). Nutrient availability, both absolute concentrations and concentration ratios, are important for establishing

community structure and, hence, new and export production pathways and rates. For example, N₂-fixing *Bacteria* would be selected under conditions of a low N:P supply ratio and diatoms and other Si-containing microbes would be selected against under low Si supply. It has been hypothesized that the observed alternation from N to P limitation was initiated by selection for N₂-fixing bacteria (including *Trichodesmium*, some species of *Synechococcus* and a variety of potential endosymbiotic associations between N₂-fixing bacteria and eukaryotic organisms) that occurred in response to changes in the NPSG habitat, especially increased stratification (Karl and others 1995). Furthermore, the prerequisite habitat changes may be direct consequences of the recently increased frequency and duration of ENSO-favorable climate conditions and the previously discussed atmosphere–ocean teleconnections. These posited changes in biodiversity and nutrient dynamics also may help explain the apparent decade-scale changes in rates of primary production in the NPSG that spawned a generation of field experiments and renewed interest in oceanic gyre processes.

Several lines of evidence from Sta. ALOHA suggest that N₂ fixation is an important contemporary source of new nitrogen for the pelagic ecosystem of the subtropical North Pacific Ocean. These independent measurements and data syntheses include: (a) *Trichodesmium* population abundances and estimates of their potential rates of biological N₂ fixation, (b) assessment of the molar N:P stoichiometries of surface-ocean dissolved and particulate matter pools and development of a one-dimensional model to calculate N and P mass balances, (c) seasonal variations in the natural ¹⁵N isotopic abundances of particulate matter exported to the deep sea and collected in bottom-moored sediment traps, and (d) observations on secular changes in soluble reactive P (SRP), soluble nonreactive P (SNP), and dissolved organic N (DON) pools during the period of increased rates of N₂ fixation (Karl and others 1997). Furthermore, Zehr and others (1998) have recently discovered the presence of potentially novel N₂-fixing microorganisms in the NPSG by amplification of previously unknown nitrogenase genes. It is conceivable, even likely, that at least part of N₂-supported new production at Sta. ALOHA may be attributed to heterotrophic as well as photoautotrophic *Bacteria*.

Although N budget estimates suggest that N₂ fixation may presently supply up to half of the N required to sustain particulate matter export from the euphotic zone, the observations from Sta. ALOHA also suggest that this relatively high percentage of N₂-supported production may represent a

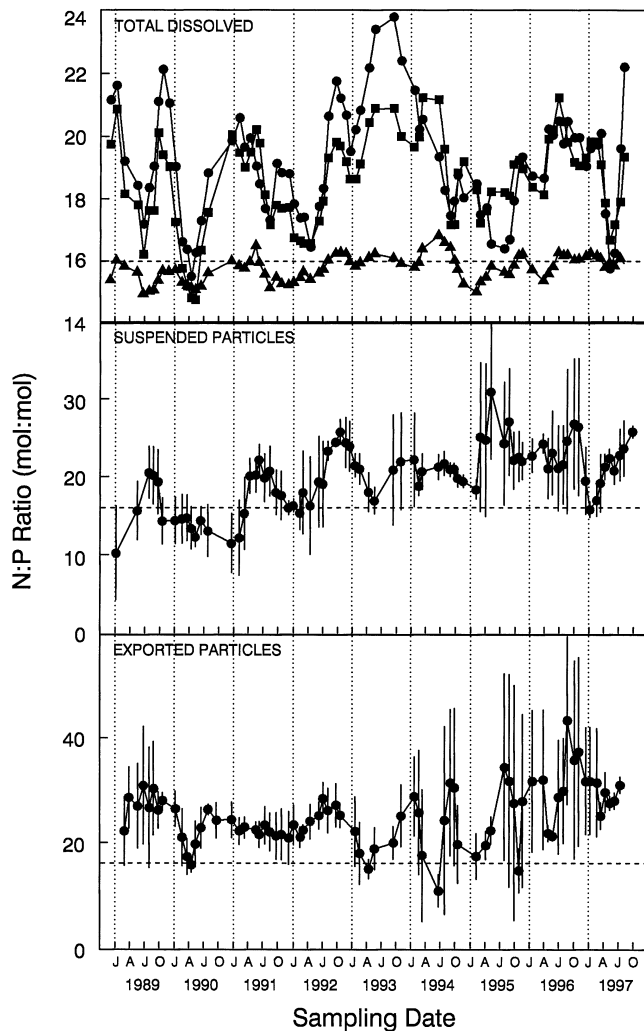


Figure 12. Time series of N and P analyses of dissolved and particulate matter, presented as N:P (mol:mol) ratios, for top dissolved matter, center suspended particulate matter, and bottom exported particulate matter. The top panel shows the 3-point running mean N:P ratios for 0–100 m (●), 100–200 m (■), and 200–500 m (▲) portions of the water column. The center panel shows the 3-point running mean (± 1 SD) for the average suspended particulate N:P ratio measured in the upper portion (0–100 m) of the water column on each cruise (depth-integrated particulate N \div depth-integrated particulate P). The bottom panel shows the 3-point running mean (± 1 SD) for the average N:P ratio of the sediment trap–collected particulate matter at the 150-m reference depth. The Redfield ratio (N:P = 16) is represented by a dashed line in all three panels. From Karl and others (1997).

transient ecosystem state reflecting either oceanic variability or, perhaps, an unusual state established in response to the well-documented decade-long shift in North Pacific climate (Karl and others 1997, 1999). This altered view of biogeochemical dynamics in the NPSG may have profound influence on how one models ecosystem processes, including the potential impacts of natural or human-induced environmental change.

Redfield and his colleagues (Redfield 1958; Redfield and others 1963) were first to point out that inorganic N and P beneath the euphotic zone, presumably derived from the remineralization of exported organic matter, are in approximate stoichiometric balance with the N:P content of newly produced organic matter. Under these balanced ecosystem conditions, there can be no net sequestration of carbon unless the characteristic remineralization length scale for C exceeds that measured for N and P, as appears to be the case for the NPSG (Christian and others 1997).

At Sta. ALOHA, we have observed both seasonal and interannual variations in N:P ratios of dissolved and particulate matter pools that correspond with the hypothesized alternations in NO_3 -supported and N_2 -supported phases of new production (Figure 12). The large positive deviations from Redfield N:P stoichiometry are, in part, manifestations of the growth of N_2 -fixing *Bacteria*. *Trichodesmium* is well known for characteristically high N:P ratios (Karl and others 1992), a feature that is most likely a physiological response to P limitation. These observations are consistent with P limitation of organic matter production. Furthermore, the TDN:TDP molar ratio in surface waters greatly exceeds the expected 16:1 Redfield ratio (Ryther and Dunstan 1971; Fanning 1992), again suggesting an excess of N relative to P (Figure 12).

During episodes of enhanced nutrient flux, surface-water N:P returns to the canonical Redfield stoichiometry after injection of waters from more than 200 m into the euphotic zone (Figure 11; Karl

and others 1997). This shift could have important consequences for nutrient control of ecosystem processes and implications for modeling carbon sequestration in the subtropical North Pacific gyre. If the C:P ratio of exported matter exceeds the C:P ratio of imported nutrients, as it does in the NPSG during episodes of P limitation, then there will be net sequestration of carbon to the interior of the ocean. Furthermore, these pulsed inputs and exports also may play a key role in the maintenance of community diversity (Hutchinson 1941, 1961; Margalef 1978; Harris 1986).

An increased turnover rate of P, relative to N, is probably insufficient to satisfy P demands during the periods of enhanced N_2 fixation. There must be some specific mechanism responsible for spatially uncoupling P from N in the water column and for concentrating P near the sea surface. Processes such as upwelling, eddy diffusion, and deep vertical mixing do not selectively transport P into the surface ocean and therefore would not be expected to stimulate N_2 fixation. Furthermore, N_2 -fixing *Trichodesmium* blooms are generally observed during periods of extreme calm (Carpenter and Price 1976; Karl and others 1992, 1995) when turbulent mixing processes would be at a minimum. Atmospheric deposition would likewise appear to be ineffective for stimulating N_2 fixation because the N:P ratio of both wet and dry deposition appears to be enriched in N (by one to two orders of magnitude) relative to cellular requirements (Duce 1986). The challenge, then, is to devise a model for formation of N_2 -fixing plankton blooms that is consistent with both physiological and field data and that might serve as the basis for one or more testable hypotheses. Specifically, selection for N_2 -supported new production during anomalously calm periods needs to be explained.

Today the NPSG ecosystem supports a high rate of gross primary production ($750\text{--}1000\text{ mg C m}^{-2}\text{ d}^{-1}$) much of which is rapidly cycled through microbial food webs (up to 50% of the daily gross primary production appears as DOM), in part due to the observed shift from a N-limited to a P-limited ecosystem (Karl and others 1998). This coupled intensification of both N (via N_2 fixation) and P cycles in the NPSG has caused major shifts in plankton community structure and in rates and mechanisms of organic matter production and remineralization (Figure 13; Karl and others 1999). For example, there appears to have been a selection for *Bacteria* and a dramatic shift from a eukaryote-dominated to a prokaryote-dominated photoautotrophic species assemblage with numerous attendant biogeochemical and ecological consequences.

EPILOGUE

It is always fashionable to criticize existing views, especially if the standing outlook can be termed dogma (Eppley 1981). Until recently the NPSG was considered to be part of a vast global marine desert that had very little influence on the oceanic cycles of C and associated bioelements. This view has been challenged by recent field estimates of planktonic rate processes and, in particular, from the comprehensive HOT program data sets.

Science is a world of ideas and progress in science is limited ultimately by the emergence of new hypotheses and by the ability to test them (Pomeroy 1981). Therefore, it is difficult and, perhaps, dangerous to predict future trends in science. However, one thing that seems almost certain is that repeated hydrographic sections and biogeochemical time-series measurements at selected open ocean sites will continue to be used in the study of the NPSG. No existing biogeochemical model captures the complexity and heterogeneity of the NPSG. Marine biogeochemical modeling is inherently data driven and significant progress will only be achieved with close collaboration between observationalists and modelers (Doney 1998). Long-term biological data sets are of demonstrable value in research and may be the only hope for documenting and, eventually, predicting ecosystem change.

During the past two decades development of novel observational platforms, including ocean buoys and earth-orbiting satellites, has provided new opportunities for continuous and synoptic observations of the world ocean. Measurements from moored and free-drifting buoys have yielded an invaluable data base for investigations of air-sea interactions, ocean circulation, and biological productivity. Autonomous deep-sea moorings are "windows" into the water column that provide opportunities to view both high- and medium-frequency (minutes to years) habitat variability. Although focus to date has been on surface meteorology and physical oceanographic processes, such as heat and mass flux, ocean currents, wave phenomena, and water-mass variability, the recent and continuing development of novel optical and chemical sensors affords opportunity to expand mooring missions to include relevant problems in ocean biogeochemistry (Dickey 1991; Hayes and others 1991; Chavez and others 1994; Dickey and others 1997). In particular, ocean color satellites, such as Sea-viewing Wide Field-of-view Sensor (SeaWiFS), will be invaluable for the detection of local and mesoscale, short-lived "bloom" phenomena that could never be adequately sampled by surface ships,

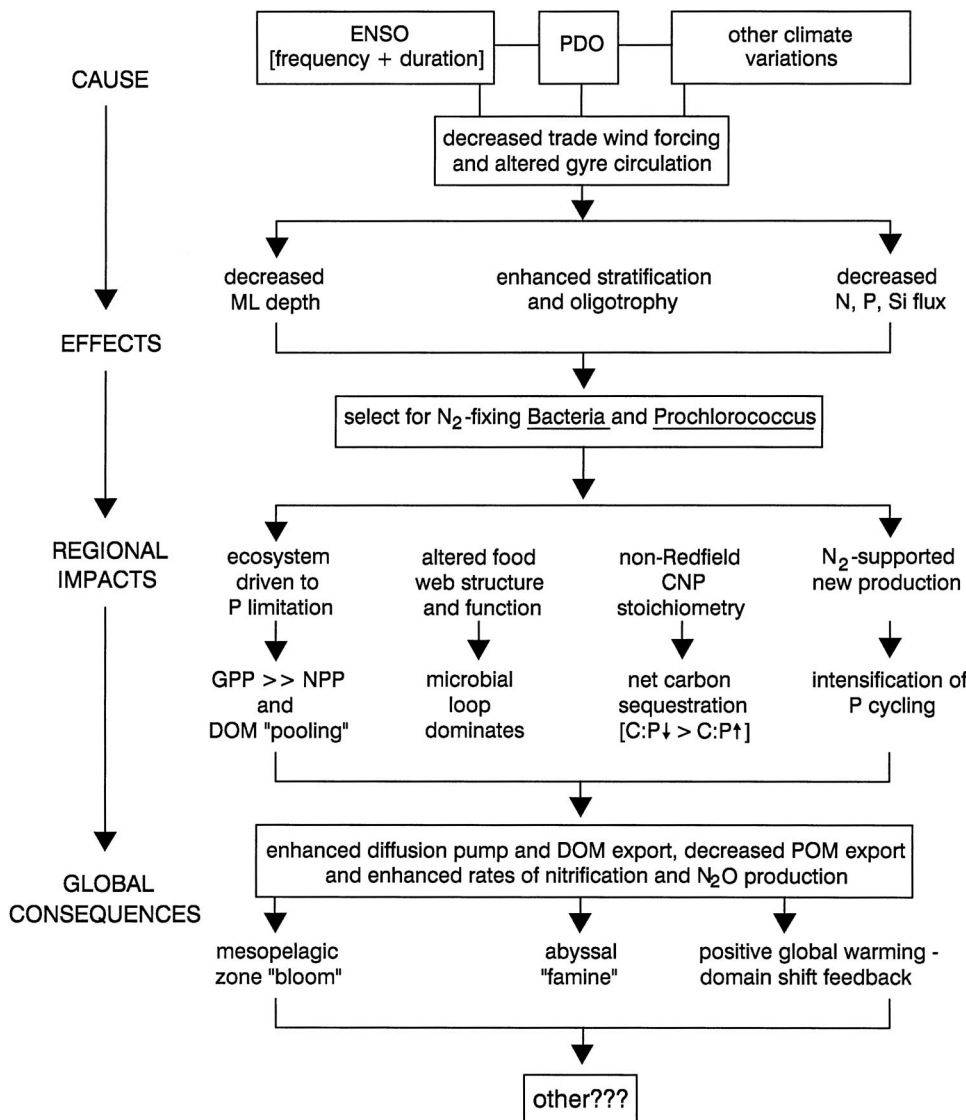


Figure 13. Hypothetical view of the effects of climate variability on ecosystem structure and function in the NPSG based, in part, on results obtained during the decade-long HOT research program. Changes in the stratification of the surface ocean have affected nutrient and trace element budgets and have selected for N₂-fixing bacteria and *Prochlorococcus* resulting in a domain shift from predominantly *Eukarya* to predominantly *Bacteria*. Numerous biological consequences have been observed and others are expected.

moored instruments, autonomous vehicles, or drifting buoys. Also, a more efficient and coordinated use of the existing merchant vessel network could provide the much-needed sea-truth calibration data as well as opportunities for sample collection and return. Greater use of mesocosm enclosures or natural-ocean enrichment experiments, such as the recent iron fertilization experiment (Coale and others 1996), could also provide much-needed information on nutrient dynamics, species succession, and food-web interactions (Carpenter and others 1995).

Chronic undersampling is a fact of life in oceanography (Platt and others 1989) and still constrains the interpretation of available field data. Neither spatial heterogeneity nor temporal intermittency are well resolved by expeditionary field work, and the dimensions and dynamics of the NPSG preclude comprehensive sampling. Even decade-long ocean observa-

tion programs, such as HOT, are inadequate to answer some of the first-order questions regarding biogeochemical response to climate variability and environmental change. However, every successful time series must have a beginning, and in the case of the NPSG, the HOT program scientists now have their analytical finger firmly on the ecological pulse of this important biome.

ACKNOWLEDGMENTS

I thank the Editors, S. Carpenter and M. Turner, for this opportunity to contribute a review article on Earth's largest biome and L. Lum and L. Fujieki for their help in its preparation. K. Björkman, C. Benitez-Nelson, R. Letelier, P. Jumars, S.W. Chisholm, and an anonymous referee provided constructive criticism and suggestions for improvement. I also thank A. Calbet for his permission to use Figure 5.

Numerous individuals published the original ideas that are summarized herein, and I especially acknowledge L. Pomeroy, F. Azam, E. Venrick, T. Hayward, J. McGowan, M. Huntley, S. Chisholm, R. Eppley, R. Dugdale, T. Platt, J. Reid, E. Laws, R. Lukas, and the HOT program scientists and ancillary investigators for their original, pathfinding contributions on the NPSG. The HOT program is currently supported by National Science Foundation grants (OCE96-17409; D.M.K., P.I. and OCE98-11921; Roger Lukas, P.I.) and by the State of Hawaii. SOEST Contribution #4808 and U.S. JGOFS Contribution #511.

REFERENCES

- Allen CB, Kanda J, Laws EA. 1996. New production and photosynthetic rates within and outside a cyclonic mesoscale eddy in the North Pacific subtropical gyre. *Deep-Sea Res* 43:917-36.
- Andersen RA, Bidigare RR, Keller MD, Latasa M. 1996. A comparison of HPLC pigment signatures and electron microscopic observations for oligotrophic waters of the North Atlantic and Pacific Oceans. *Deep-Sea Res II* 43:517-37.
- Azam F. 1998. Microbial control of oceanic carbon flux: the plot thickens. *Science* 280:694-6.
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F. 1983. The ecological role of water-column microbes in the sea. *Mar Ecol Prog Ser* 10:257-63.
- Baines SB, Pace ML, Karl DM. 1994. Why does the relationship between sinking flux and planktonic primary production differ between lakes and oceans? *Limnol Oceanogr* 39:213-26.
- Barber RT. 1992. Geologic and climatic time scales of nutrient variability. In: Falkowski PG, Woodhead AD, editors. *Primary productivity and biogeochemical cycles in the sea*. New York: Plenum Press. p 89-106.
- Beers JR, Reid FMH, Stewart GL. 1975. Microplankton of the North Pacific Central Gyre. Population structure and abundance, June 1973. *Int Rev Ges Hydrobiol* 60:607-38.
- Beers JR, Reid FMH, Stewart GL. 1982. Seasonal abundance of the microplankton population in the North Pacific central gyre. *Deep-Sea Res* 29:227-45.
- Berger WH. 1989. Global maps of ocean productivity. In: Berger WH, Smetacek VS, Wefer G, editors. *Productivity of the ocean: present and past*. New York: John Wiley and Sons. p 429-55.
- Bernstein RL, White WB. 1974. Time and length scales of baroclinic eddies in the central North Pacific Ocean. *J Phys Oceanogr* 4:613-24.
- Billett DSM, Lampitt RS, Rice AL, Mantoura RFC. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302:520-2.
- Bjerknes J. 1969. Atmospheric teleconnections from the equatorial Pacific. *Monthly Weather Rev* 97:163-72.
- Blackburn M. 1981. Low latitude gyral regions. In: Longhurst AR, editor. *Analysis of marine ecosystems*. New York: Academic Press. p 3-29.
- Bonin DJ, Maestrini SY. 1981. Importance of organic nutrients for phytoplankton growth in natural environments: implications for algal species succession. In: Platt T, editor. *Physiological bases of phytoplankton ecology*. Ottawa: Department of Fisheries and Oceans. p 279-91.
- Brewer PG, Bruland KW, Eppley RW, McCarthy JJ. 1986. The global ocean flux study (GOFS): status of the U.S.GOFS program. *EOS Trans Am Geophys Un* 67:827-32.
- Bult CJ, White O, Olsen GJ, and others 1996. Complete genome sequence of the methanogenic archaeon, *Methanococcus jannaschii*. *Science* 273:1058-73.
- Campbell L, Vault D. 1993. Photosynthetic picoplankton community structure in the subtropical North Pacific Ocean near Hawaii (station ALOHA). *Deep-Sea Res* 40: 2043-2060.
- Campbell L, Nolla HA, Vault D. 1994. The importance of *Prochlorococcus* to community structure in the central North Pacific Ocean. *Limnol Oceanogr* 39:954-61.
- Carlson CA, Ducklow HW. 1996. Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea. *Aquat Microb Ecol* 10:69-85.
- Carpenter EJ, Price CC (IV). 1976. Marine *Oscillatoria* (*Trichodesmium*): Explanation for aerobic nitrogen fixation without heterocysts. *Science* 191:1278-80.
- Carpenter SR, Chisholm SW, Krebs CJ, Schindler DW, Wright RF. 1995. Ecosystem experiments. *Science* 269:324-7.
- Chavez FP, Herliem R, Thurmond G. 1994. OASIS - Acquisition system for moorings/drifters. *Sea Tech* 35:51-9.
- Chelton DB, Schlax MG. 1996. Global observations of oceanic Rossby waves. *Science* 272:234-8.
- Chisholm SW, Olson RJ, Zettler ER, and others 1988. A novel free-living prochlorophyte abundant in the oceanic euphotic zone. *Nature* 334:340-3.
- Chisholm SW, Frankel SL, Goericke R, Olson RJ, Palenik B, Waterbury JB, West-Johnsrud L, Zettler ER. 1992. *Prochlorococcus marinus* nov. gen. Nov. sp.: an oxyphototrophic marine prokaryote containing divinyl chlorophyll *a* and *b*. *Arch Microbiol* 157:297-300.
- Christian JR, Lewis MR, Karl DM. 1997. Vertical fluxes of carbon, nitrogen, and phosphorus in the North Pacific Subtropical Gyre near Hawaii. *J Geophys Res* 102:15667-77.
- Clements FE. 1916. Plant succession. An analysis of the development of vegetation. Carnegie Inst., Washington D.C. 242:1-512.
- Clements FE. 1936. Nature and structure of the climax. *J Ecol* 24:253-84.
- Coale KH, Johnson KS, Fitzwater SE, Gordon RM, Tanner S, Chavez FP, Ferioli L, Sakamoto C, Rogers P, Millero F, Steinberg P, Nightingale P, Cooper D, Cochlan WP, Landry MR, Constantinou J, Rollwagen G, Trasvina A, Kudela R. 1996. A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* 383:495-501.
- Daley RJ, Hobbie JE. 1975. Direct counts of aquatic bacteria by a modified epi-fluorescent technique. *Limnol Oceanogr* 20: 875-82.
- del Giorgio PA, Cole JJ, Cimleris A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* 385:148-51.
- DeLong EF, Wu KY, Prezelin BB, Jovine RVM. 1994. High abundance of Archaea in antarctic marine picoplankton. *Nature* 371:695-7.
- Deser C, Alexander MA, Timlin MS. 1996. Upper-ocean thermal variations in the North Pacific during 1970-1991. *J Climate* 9:1840-55.
- Dickey TD. 1991. The emergence of concurrent high-resolution physical and bio-optical measurements in the upper ocean and their applications. *Rev Geophys* 29:383-413.

- Dickey TD, Frye D, Jannasch HW, Boyle E, Knap AH. 1997. Bermuda sensor system testbed. *Sea Tech* 38:81-6.
- DiTullio GR, Laws EA. 1991. Impact of an atmospheric-oceanic disturbance on phytoplankton community dynamics in the North Pacific Central Gyre. *Deep-Sea Res* 38: 1305-29.
- Doney SC. 1999. Major challenges confronting marine biogeochemical modeling. *Global Biogeochem Cycles*. (in press).
- Dore JE, Karl DM. 1996. Nitrification in the euphotic zone as a source for nitrite, nitrate, and nitrous oxide at Station ALOHA. *Limnol Oceanogr* 41:1619-28.
- Doty MS, Oguri M. 1956. The island mass effect. *J Cons Perm Int Explor Mer* 22:33-7.
- Druffel ERM, Williams PM. 1990. Identification of a deep marine source of particulate organic carbon using bomb ^{14}C . *Nature* 347:172-4.
- Duarte CM, Agusti S. 1998. The CO_2 balance of unproductive aquatic ecosystems. *Science* 281:234-6.
- Duce RA. 1986. The impact of atmospheric nitrogen, phosphorus, and iron species on marine biological productivity. In: Buat-Menard P, editor. *The role of air-sea exchange in geochemical cycling*. Dordrecht, The Netherlands: D. Reidel Publishing Company. p 497-529
- Dugdale RC, Goering JJ. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol Oceanogr* 12:196-206.
- Dugdale R, Wilkerson F. 1992. Nutrient limitation of new production in the sea. In: Falkowski PG, Woodhead AD, editors. *Primary productivity and biogeochemical cycles in the sea*. New York: Plenum Press. p 107-122.
- Ebbesmeyer CC, Cayan DR, McLain DR, Nichols FH, Peterson DH, Redmond KT. 1991. 1976 step in the Pacific climate: forty environmental changes between 1968-1975 and 1977-1984. In: Betancourt JL, Tharp VL, editors. *Proceedings of the 7th Annual Pacific Climate (PACCLIM) Workshop*. California Department of Water Resources. Interagency Ecological Studies Program Technical Report 26.
- Emerson S, Quay P, Karl D, Winn C, Tupas L, Landry M. 1997. Experimental determination of the organic carbon flux from open-ocean surface waters. *Nature* 389:951-4.
- Eppley RW. 1981. Relations between nutrient assimilation and growth in phytoplankton with a brief review of estimates of growth rate in the ocean. In: Platt T, editor. *Physiological bases of phytoplankton ecology*. Ottawa: Department of Fisheries and Oceans. p 251-63.
- Eppley RW. 1982. The PRPOOS program: a study of plankton rate processes in oligotrophic oceans. *EOS Trans Am Geophys Un* 163:522.
- Eppley RW. 1989. New production: history, methods, problems. In: Berger WH, Smetacek VS, Wefer G, editors. *Productivity of the ocean: present and past*. New York: John Wiley & Sons. p 85-97.
- Eppley RW, Peterson BJ. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282:677-80.
- Eppley RW, Renger EH, Betzer PR. 1982. The residence time of particulate organic carbon in the surface layer of the oceans. *Deep-Sea Res* 29:311-23.
- Fager EW. 1963. Communities of organisms. In: Hill MN, editor. *The sea: ideas and observations on progress in the study of the seas, volume 2*. New York: Interscience Publishers. p 415-37.
- Fager EW, McGowan JA. 1963. Zooplankton species groups in the North Pacific. *Science* 140:453-60.
- Fahnenstiel GL, Scavia D, Lang GA, Saylor JH, Miller GS, Schwab DJ. 1988. Impact of inertial period internal waves on fixed-depth primary production estimates. *J Plankton Res* 10:77-87.
- Falkowski PG. 1994. The role of phytoplankton photosynthesis in global biogeochemical cycles. *Photosyn Res* 39:235-58.
- Falkowski PG, Raven JA. 1997. *Aquatic photosynthesis*. Malden, MA: Blackwell Science.
- Falkowski PG, Ziemann D, Kolber Z, Bienfang PK. 1991. Role of eddy pumping in enhancing primary production in the ocean. *Nature* 352:55-8.
- Fanning KA. 1992. Nutrient provinces in the sea: concentration ratios, reaction rate ratios, and ideal covariation. *J Geophys Res* 97:5693-712.
- Fenchel T. 1988. Marine plankton food chains. *Ann Rev Ecol Syst* 19:19-38.
- Fuhrman J. 1992. Bacterioplankton roles in cycling of organic matter: the microbial food web. In: Falkowski PG, Woodhead AD, editors. *Primary productivity and biogeochemical cycles in the sea*. New York: Plenum Press. p 361-83.
- Gargett AE. 1997. Physics to fish: interactions between physics and biology on a variety of scales. *Oceanography* 10:128-31.
- Garrett C, Munk W. 1972. Oceanic mixing by breaking internal waves. *Deep-Sea Res*. 19:823-32.
- Geider RJ. 1997. Photosynthesis or planktonic respiration? *Nature* 388:132.
- Glover HE. 1991. Oceanic phytoplankton communities: our changing perception. *Rev Aquat Sci* 5: 307-31.
- Goldman JC. 1984. Oceanic nutrient cycles. In: Fasham MJR, editor. *Flows of energy and materials in marine ecosystems*. New York: Plenum Press. p 137-70.
- Gordon DC, Jr. 1970. Chemical and biological observations at station Gollum, an oceanic station near Hawaii, January 1969 to June 1970. Hawaii Institute of Geophysics Report, HIG-70-22.
- Graham HW. 1941. Plankton production in relation to character of water in the open Pacific. *J Mar Res* 4:189-97.
- Graham NE. 1994. Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s: observations and model results. *Climate Dyn* 10: 135-62.
- Grande KD, Williams PJLeB, Marra J, Purdie DA, Heinemann K, Eppley RW, Bender ML. 1989. Primary production in the North Pacific gyre: a comparison of rates determined by the ^{14}C , O_2 concentration and ^{18}O methods. *Deep-Sea Res* 36:1621-34.
- Gregg MC. 1976. Finestructure and microstructure observations during the passage of a mild storm. *J Phys Oceanogr* 6:528-55.
- Gundersen KR, Corbin JS, Hanson CL, Hanson ML, Hanson RB, Russell DJ, Stollar A, Yamada O. 1976. Structure and biological dynamics of the oligotrophic ocean photic zone off the Hawaiian Islands. *Pac Sci* 30:45-68.
- Harris GP. 1986. *Phytoplankton ecology: structure, function, and fluctuation*. New York: Chapman and Hall.
- Harrison WG, Harris LR, Karl DM, Knauer GA, Redalje DG. 1992. Nitrogen dynamics at the VERTEX time-series site. *Deep-Sea Res* 39:1535-52.
- Hayes SP, Mangum LJ, Picaut J, Sumi A, Takeuchi K. 1991. TOGA-TAO: a moored array for real-time measurements in the tropical Pacific Ocean. *Bull Am Meteor Soc* 72:339-47.
- Hayward TL. 1987. The nutrient distribution and primary production in the central North Pacific. *Deep-Sea Res* 34:1593-1627.
- Hayward TL. 1991. Primary production in the North Pacific Central Gyre: a controversy with important implications. *Trends Ecol Evol* 6:281-4.

- Hayward TL, McGowan JA. 1985. Spatial patterns of chlorophyll, primary production, macrozooplankton biomass, and physical structure in the central North Pacific Ocean. *J Plankton Res* 7:147–67.
- Hayward TL, Venrick EL, McGowan JA. 1983. Environmental heterogeneity and plankton community structure in the central North Pacific. *J Mar Res* 41:711–29.
- Hedgpeth J.W. 1957. Introduction. In: Hedgpeth JW, editor. *Treatise on marine ecology and paleoecology*. Colorado: Geological Society of America. p 1–16.
- Hobbie JE. 1994. The state of the microbes: a summary of a symposium honoring Lawrence Pomeroy. *Microb Ecol* 28: 113–6.
- Hobbie JE, Daley RJ, Jasper S. 1977. Use of Nuclepore filters for counting bacteria by fluorescence microscopy. *Appl Environ Microbiol* 33:1225–8.
- Horel JD, Wallace JM. 1981. Planetary-scale atmospheric phenomena associated with the Southern Oscillation. *Monthly Weather Rev* 109:813–29.
- Hutchinson GE. 1941. Ecological aspects of succession in natural populations. *Am Naturalist* 75:406–18.
- Hutchinson GE. 1961. The paradox of the plankton. *Am Naturalist* 95:137–45.
- Huxley L. 1900. *Life and letters of Thomas Henry Huxley*. New York: D. Appleton and Company.
- Jacobs GA, Hurlburt HE, Kindle JC, Metzger EJ, Mitchell JL, Teague WJ, Wallcraft AJ. 1994. Decade-scale trans-Pacific propagation and warming effects of an El Niño anomaly. *Nature* 370:360–3.
- Johnson MW, Brinton E. 1963. Biological species, water-masses and currents. In: Hill MN, editor. *The sea: ideas and observations on progress in the study of the seas. Volume 2*. New York: Interscience Publishers. p 381–414.
- Johnson PW, Sieburth J McN. 1979. Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. *Limnol Oceanogr* 24:928–35.
- Karl DM. 1994. Accurate estimation of microbial loop processes and rates. *Microb Ecol* 28:147–50.
- Karl DM, Dobbs FC. 1998. Molecular approaches to microbial biomass estimation in the sea. In: Cooksey KE, editor. *Molecular approaches to the study of the ocean*. London: Chapman & Hall. p 29–89.
- Karl DM, Lukas R. 1996. The Hawaii Ocean Time-series (HOT) program: background, rationale and field implementation. *Deep-Sea Res II* 43:129–56.
- Karl DM, Tien G. 1997. Temporal variability in dissolved phosphorus concentrations in the subtropical North Pacific Ocean. *Mar Chem* 56:77–96.
- Karl DM, Winn CD. 1991. A sea of change: monitoring the oceans' carbon cycle. *Environ Sci Tech* 25:1976–81.
- Karl DM, Letelier R, Hebel DV, Bird DF, Winn CD. 1992. *Trichodesmium* blooms and new nitrogen in the North Pacific gyre. In: Carpenter EJ, Capone DG, Rueter JG, editors. *Marine pelagic cyanobacteria: Trichodesmium and other diazotrophs*. Netherlands: Kluwer Academic Publishers. p 219–37.
- Karl DM, Letelier R, Hebel D, Tupas L, Dore J, Christian J, Winn C. 1995. Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991–92 El Niño. *Nature* 373:230–4.
- Karl DM, Christian JR, Dore JE, Hebel DV, Letelier RM, Tupas LM, Winn CD. 1996. Seasonal and interannual variability in primary production and particle flux at Station ALOHA. *Deep-Sea Res II* 43:539–68.
- Karl D, Letelier R, Tupas L, Dore J, Christian J, Hebel D. 1997. The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* 388:533–8.
- Karl DM, Hebel DV, Björkman K, Letelier RM. 1998. The role of dissolved organic matter releases in the productivity of the oligotrophic North Pacific Ocean. *Limnol Oceanogr*, 43:12–15.
- Karl DM, Bidigare RR, Letelier RM. 1999. Climate-related, long-term changes in plankton community structure and productivity in the subtropical North Pacific Ocean. *Nature*, in revision.
- Kenyon KE. 1978. The shallow salinity minimum of the eastern North Pacific in winter. *J Phys Oceanogr* 8:1061–9.
- Kerr RA. 1992. Unmasking a shifty climate system. *Science* 255:1508–10.
- Knauer GA, Redalje DG, Harrison WG, Karl DM. 1990. New production at the VERTEX time-series site. *Deep-Sea Res* 37:1121–34.
- Knauer GA, Martin JH, Karl DM. 1984. The flux of particulate organic matter out of the euphotic zone. In: *Global Ocean Flux Study. Proceedings of a Workshop; 1982 Sept 10–14; Washington, DC: National Academic Press.* p 136–50.
- Koblentz-Mishke OJ, Volkovinsky VV, Kabanova JG. 1970. Plankton primary production of the world ocean. In: Wooster, WS, editor. *Scientific exploration of the South Pacific*. Washington, DC: National Academy of Science. p 183–93.
- Kriss AE. 1962. *Marine microbiology*. Great Britain: Oliver & Boyd.
- Krom MD, Brenner S, Kress N, Neori A, Gordon LI. 1993. Nutrient distributions during an annual cycle across a warm-core eddy from the E. Mediterranean Sea. *Deep-Sea Res* 40:805–25.
- Laws EA, Haas LW, Bienfang PK, Eppley RW, Harrison WG, Karl DM, Marra J. 1984. High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. *Limnol Oceanogr* 29:1161–9.
- Laws EA, Harrison WG, DiTullio GR. 1985. A comparison of nitrogen assimilation rates based on ¹⁵N uptake and autotrophic protein synthesis. *Deep-Sea Res* 32:85–95.
- Ledwell JR, Watson AJ, Law CS. 1993. Evidence for slow mixing across the pycnocline from an open-ocean tracer-release experiment. *Nature* 364:701–3.
- Lee D-K, Niiler PP, Warn-Varnas A. 1994. Wind-driven secondary circulation in ocean mesoscale. *J Mar Res* 52:1–25.
- Legendre L, Le Fèvre J. 1989. Hydrodynamical singularities as controls of recycled versus export production in oceans. In Berger WH, Smetacek VS, Wefer G, editors. *Productivity of the ocean: present and past*. New York: John Wiley & Sons. p 49–63.
- Letelier RM. 1994. *Studies on the ecology of Trichodesmium spp. (Cyanophyceae) in the central North Pacific gyre*. Ph.D. dissertation, University of Hawaii.
- Letelier RM, Bidigare RR, Hebel DV, Ondrusek M, Winn CD, Karl DM. 1993. Temporal variability of phytoplankton community structure based on pigment analysis. *Limnol Oceanogr* 38: 1420–37.
- Letelier RM, Dore JE, Winn CD, Karl DM. 1996. Seasonal and interannual variations in photosynthetic carbon assimilation at Station ALOHA. *Deep-Sea Res* 43:467–90.
- Letelier RM, Karl DM, Abbott MR. 1999. Integration of research vessel, autonomous mooring and satellite time-series data to resolve biogeochemical variability in the North Pacific subtropical gyre. Submitted to *J Geophys Res*

- Levitus S, Antonov J. 1995. Observational evidence of interannual to decadal-scale variability of the subsurface temperature-salinity structure of the world ocean. *Climatic Change* 31:495-514.
- Lewis MR, Harrison WG, Oakey NS, Hebert D, Platt T. 1986. Vertical nitrate fluxes in the oligotrophic ocean. *Science* 234: 870-3.
- Li WKW. 1997. Cytometric diversity in marine ultraphytoplankton. *Limnol Oceanogr* 42:874-80.
- Liu H, Nolla HA, Campbell L. 1997. *Prochlorococcus* growth rate and contribution to primary production in the equatorial and subtropical North Pacific Ocean. *Aquat Microb Ecol* 12:39-47.
- Longhurst AR, Harrison WG. 1989. The biological pump: profiles of plankton production and consumption in the upper ocean. *Prog Oceanogr* 22:47-123.
- Longhurst A, Sathyendranath S, Platt T, Caverhill C. 1995. An estimate of global primary production in the ocean from satellite radiometer data. *J Plankton Res* 17:1245-71.
- Magnuson JJ. 1990. Long-term ecological research and the invisible present. *Bioscience* 40:495-501.
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Am Meteor Soc* 78:1069-79.
- Margalef R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1:493-509.
- Marra J. 1978. Phytoplankton photosynthetic response to vertical movement in a mixed-layer. *Mar Biol.* 46:203-8.
- Martin JH, Knauer GA, Karl DM, Broenkow WW. 1987. VERTEX: carbon cycling in the northeast Pacific. *Deep-Sea Res* 34:267-85.
- Matrai PA. 1986. The distribution of the dinoflagellate *Ceratium* in relation to environmental factors along 28°N in the eastern North Pacific. *J Plankton Res* 8:105-18.
- McCave IN. 1975. Vertical flux of particles in the ocean. *Deep-Sea Res* 22:491-502.
- McGillicuddy DJ, Jr, Robinson AR. 1997. Eddy-induced nutrient supply and new production in the Sargasso Sea. *Deep-Sea Res* 44:1427-50.
- McGillicuddy DJ, Jr., Robinson AR, Siegel DA, Jannasch HW, Johnson R, Dickey TD, McNeil J, Michaels AF, Knap AH. 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394:263-6.
- McGowan JA. 1974. The nature of oceanic ecosystems. In: Miller CB, editor. *The biology of the oceanic Pacific*. Corvallis: Oregon State University Press. p 9-28.
- McGowan JA, Hayward TL. 1978. Mixing and oceanic productivity. *Deep-Sea Res* 25:771-93.
- McGowan JA, Walker PW. 1979. Structure in the copepod community of the North Pacific central gyre. *Ecol Monogr* 49:195-226.
- McGowan JA, Walker PW. 1985. Dominance and diversity maintenance in an oceanic ecosystem. *Ecol Monogr* 55: 103-18.
- McGowan JA, Williams PM. 1973. Oceanic habitat differences in the North Pacific. *J Exp Mar Biol Ecol* 12:187-217.
- McGowan JA, Cayan DR, Dorman, LM. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281:210-7.
- Michaels AF, Knap AH. 1996. Overview of the U.S. JGOFS Bermuda Atlantic Time-series Study and the Hydrostation S program. *Deep-Sea Res* 43:157-98.
- Michaels AF, Silver MW. 1988. Primary production, sinking fluxes and the microbial food web. *Deep-Sea Res* 35:473-90.
- Miller AJ, Cayan DR, Barnett TP, Graham NE, Oberhuber JM. 1994. Interdecadal variability of the Pacific Ocean: model response to observed heat flux and wind stress anomalies. *Climate Dyn* 9:287-302.
- Minobe S. 1997. A 50-70 year climatic oscillation over the North Pacific and North America. *Geophys Res Lett* 24: 683-6.
- Moore LR, Rocap G, Chisholm SW. 1998. Physiology and molecular phylogeny of coexisting *Prochlorococcus* ecotypes. *Nature* 393:464-7.
- Moum JN. 1997. Quantifying vertical fluxes from turbulence in the ocean. *Oceanography* 10:111-5.
- Munch CL. 1996. The effect of the Hawaiian Ridge on mesoscale variability: results from TOPEX/POSEIDON. M.S. Thesis, University of Hawaii.
- Mysak LA. 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. *Can J Fish Aquat Sci* 43:464-97.
- Namias J. 1978. Multiple causes of the North American abnormal winter 1976-77. *Monthly Weather Rev* 106:279-95.
- National Research Council. 1984. *Global ocean flux study: proceedings of a workshop*, Washington, DC: National Academy Press.
- Niiler PP, Hall ML. 1988. Low-frequency eddy variability at 28°N, 152°W in the eastern North Pacific subtropical gyre. *J Phys Oceanogr* 18:1670-85.
- Niiler PP, Reynolds RW. 1984. The three-dimensional circulation near the eastern North Pacific subtropical front. *J Phys Oceanogr* 14:217-30.
- NORPAC Committee. 1955. *Oceanic observations of the Pacific: 1955, the NORPAC data*. Berkeley: University of California Press.
- Odum, WE, Odum EP, Odum HT. 1995. Nature's pulsing paradigm. *Estuaries* 18:547-55.
- Olson RJ. 1981. ¹⁵N tracer studies of the primary nitrite maximum. *J Mar Res* 39: 203-26.
- Ondrusek ME, Bidigare RR, Sweet ST, Defreitas DA, Brooks JM. 1991. Distribution of phytoplankton pigments in the North Pacific Ocean in relation to physical and optical variability. *Deep-Sea Res* 38:243-66.
- Pace NR. 1997. A molecular view of microbial diversity and the biosphere. *Science* 276:734-40.
- Pace ML, Knauer GA, Karl DM, Martin JH. 1987. Primary production, new production and vertical flux in the eastern Pacific Ocean. *Nature* 325:803-4.
- Peinert R, von Bodungen B, Smetacek VS. 1989. Food web structure and loss rate. In: Berger WH, Smetacek VS, Wefer, G, editors. *Productivity of the ocean: present and Past*. New York: John Wiley and Sons Ltd. p 35-48.
- Platt T. 1984. Primary productivity in the central North Pacific: comparison of oxygen and carbon fluxes. *Deep-Sea Res* 31: 1311-9.
- Platt T, Harrison WG. 1986. Reconciliation of carbon and oxygen fluxes in the upper ocean. *Deep-Sea Res* 33:273-6.
- Platt T, Harrison WG, Lewis MR, Li WKW, Sathyendranath S, Smith RE, Vezina AE. 1989. Biological production of the oceans: the case for a consensus. *Mar Ecol Prog Ser* 52:77-88.
- Platt T, Jauhari P, Sathyendranath S. 1992. The importance and measurement of new production. In: Falkowski PG, Woodhead AD, editors. *Primary productivity and biogeochemical cycles in the sea*. New York: Plenum Press. p 273-84.

- Polovina JJ, Mitchum GT, Graham NE, Craig MP, DeMartini EE, Flint EN. 1994. Physical and biological consequences of a climate event in the central North Pacific. *Fish Oceanogr* 3:15–21.
- Pomeroy LR. 1974. The ocean's food web, a changing paradigm. *BioScience* 24:499–504.
- Pomeroy LR. 1981. Microbial processes in the sea: diversity in nature and science. In: Hobbie JE, Williams PJ leB, editors. *Heterotrophic activity in the sea*. New York: Plenum Press. p 1–23.
- Potter D, Lajeunesse TC, Saunders GW, Andersen, RA. 1997. Convergent evolution masks extensive biodiversity among marine coccoid picoplankton. *Biodiversity Conserv* 6:99–107.
- Quiñones RA, Platt T. 1991. The relationship between the f -ratio and the $P:R$ ratio in the pelagic ecosystem. *Limnol Oceanogr* 36:211–3.
- Raitt H, Moulton B. 1967. *Scripps Institution of Oceanography: first fifty years*. Pasadena, CA: The Ward Ritchie Press.
- Raven JA. 1986. Physiological consequences of extremely small size for autotrophic organisms in the sea. In: Platt T, Li, WKW, editors. *Photosynthetic picoplankton*. *Can Bull Fish Aquat Sci* 214:1–70.
- Redfield AC. 1958. The biological control of chemical factors in the environment. *Am Sci* 46:205–22.
- Redfield AC, Ketchum BH, Richards FA. 1963. The influence of organisms on the composition of seawater. In: Hill MN, editor. *The sea: ideas and observations on progress in the study of the seas*. New York: Interscience. p 26–77.
- Reid JL, Shulenberg E. 1986. Oxygen saturation and carbon uptake near 28°N, 155°W. *Deep-Sea Res* 33:267–71.
- Reid JL, Brinton E, Fleminger A, Venrick EL, McGowan JA. 1978. Ocean circulation and marine life. In: Charnock H, Deacon G, editors. *Advances in oceanography*. New York: Plenum Press. p 65–130.
- Ryther JH, Dunstan WM. 1971. Nitrogen, phosphorus and eutrophication in the coastal marine environment. *Science* 171:1008–13.
- Sahlsten E. 1987. Nitrogenous nutrition in the euphotic zone of the Central North Pacific Gyre. *Mar Biol* 96:433–9.
- Scavia D. 1988. On the role of bacteria in secondary production. *Limnol Oceanogr* 33:1220–4.
- Scharek R, Latasa M, Karl DM, Bidigare RR. 1999a. Temporal variations in diatom abundance and downward vertical flux in the oligotrophic North Pacific gyre. *Deep-Sea Res* 46:1051–75.
- Scharek R, Tupas LM, Karl DM. 1999b. Diatom fluxes to the deep sea in the oligotrophic North Pacific gyre at Station 'ALOHA'. *Mar Ecol Prog Ser*. (in press).
- Scientific Committee on Oceanic Research. 1990. The Joint Global Ocean Flux Study (JGOFS) science plan. JGOFS Report No. 5. Paris: International Council of Scientific Unions.
- Sherr EB, Sherr BF. 1996. Temporal offset in oceanic production and respiration processes implied by seasonal changes in atmospheric oxygen: the role of heterotrophic microbes. *Aquat Microb Ecol* 11:91–100.
- Shor EN. 1978. *Scripps Institution of Oceanography: probing the oceans 1936 to 1976*. San Diego, CA: Tofua Press.
- Shulenberg E. 1978. Vertical distributions, diurnal migrations, and sampling problems of hyperiid amphipods in the North Pacific central gyre. *Deep-Sea Res* 25:605–23.
- Shulenberg E, Reid JL. 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered. *Deep-Sea Res* 28A:901–19.
- Sieburth J McN, Smetacek V, Lenz J. 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnol Oceanogr* 23:1256–63.
- Small LF, Knauer GA, Tuel MD. 1987. The role of sinking fecal pellets in stratified euphotic zones. *Deep-Sea Res* 34:1705–12.
- Smith CR, Hoover DJ, Doan SE, Pope RH, DeMaster DJ, Dobbs FC, Altabet MA. 1996. Phytodetritus at the abyssal seafloor across 10° of latitude in the central equatorial Pacific. *Deep-Sea Res* 43:1309–38.
- Stemann Nielsen E. 1956. Measuring the productivity of the sea. In: Bruun AF, and others, editors. *The Galathea Deep Sea Expedition 1950–1952*. London: George Allen and Unwin Ltd. p 53–64.
- Strayer D. 1988. On the limits to secondary production. *Limnol Oceanogr* 33:1217–20.
- Strayer D, Glitzenstein JS, Jones CG, Kolasoi J, Likens GE, McDonnell MJ, Parker GG, Pickett STA. 1986. Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. Millbrook, NY: Occasional Publication of the Institute of Ecosystem Studies, No. 2.
- Strickland JDH. 1965. Production of organic matter in the primary stages of the marine food chain. In: Riley JP, Skirrow G, editors. *Chemical oceanography*. New York: Academic Press. p 477–610.
- Suess E. 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. *Nature* 288:260–3.
- Sverdrup HU, Johnson MW, Fleming RH. 1946. *The oceans, their physics, chemistry and general biology*. New York: Prentice-Hall.
- Taylor GT. 1989. Variability in the vertical flux of microorganisms and biogenic material in the epipelagic zone of a North Pacific central gyre station. *Deep-Sea Res* 36: 1287–1308.
- Thomas WH. 1969. Phytoplankton nutrient enrichment experiments off Baja California and in the eastern equatorial Pacific Ocean. *J Fish Res Bd Can* 26:1133–45.
- Thomas WH. 1970. Effect of ammonium and nitrate concentration on chlorophyll increases in natural tropical Pacific phytoplankton populations. *Limnol Oceanogr* 15:386–94.
- Toggweiler JR. 1989. Is the downward dissolved organic matter (DOM) flux important in carbon transport? In: Berger WH, Smetacek VS, Wefer G, editors. *Productivity of the Ocean: Present and Past*. New York: John Wiley & Sons Ltd. p 65–83.
- Trenberth KE. 1990. Recent observed interdecadal climate changes in the northern hemisphere. *Bull Am Meteor Soc* 71:988–93.
- Trenberth KE, Hoar, TJ. 1997. El Niño and climate change. *Geophys Res Lett* 24: 3057–3060.
- Troup AJ. 1965. The southern oscillation. *Q J Roy Meteor Soc* 91:490–506.
- Urbach E, Scanlan DJ, Distel DL, Waterbury JB, Chisholm SW. 1998. Rapid diversification of marine picophytoplankton with dissimilar light-harvesting structures inferred from sequences of *Prochlorococcus* and *Synechococcus* (Cyanobacteria). *J Mol Evol* 46:188–201.
- Venrick EL. 1971. Recurrent groups of diatom species in the North Pacific. *Ecology* 52:614–25.
- Venrick EL. 1979. The lateral extent and characteristics of the North Pacific central environment at 35°N. *Deep Sea Res* 26:1153–78.
- Venrick EL. 1982. Phytoplankton in an oligotrophic ocean: observations and questions. *Ecol Monogr* 52:129–54.

- Venrick EL. 1990. Phytoplankton in an oligotrophic ocean: species structure and interannual variability. *Ecology* 71:1547–63.
- Venrick EL. 1992. Phytoplankton species structure in the central North Pacific: is the edge like the center? *J Plankton Res* 14:665–80.
- Venrick EL. 1993. Phytoplankton seasonality in the central North Pacific: the endless summer reconsidered. *Limnol Oceanogr* 38:1135–49.
- Venrick EL. 1995. Scales of variability in a stable environment: phytoplankton in the central North Pacific. In: Powell TM, Steele JH, editors. *Ecological time-series*. New York: Chapman & Hall. p 150–80.
- Venrick EL, McGowan JA, Cayan DR, Hayward TL. 1987. Climate and chlorophyll *a*: long-term trends in the central North Pacific Ocean. *Science* 238:70–2.
- Villareal TA, Altabet MA, Culver-Rymsza K. 1993. Nitrogen transport by migrating diatom mats in the North Pacific Ocean. *Nature* 363:709–12.
- Vinogradov MYe, Shushkina EA. 1989. Macro-scale distribution of the quantitative characteristics of plankton in the Pacific Ocean. *Oceanology* 29:87–91.
- Vinogradov MYe, Krapivin VF, Menshutkin VV, Fleyshman BS, Shushkina EA. 1973. Mathematical model of the functions of the pelagial ecosystem in tropical regions (from the 50th voyage of the R/V *Vityaz*). *Oceanology* 13:704–17.
- Vinogradov ME, Shushkina EA, Vedernikov VI, Nezlin NP, Gagarin VI. 1997. Primary production and plankton stocks in the Pacific Ocean and their seasonal variation according to remote sensing and field observations. *Deep-Sea Res* 44:1979–2001.
- Volk T, Hoffert MI. 1985. Ocean carbon pumps: analysis of relative strengths and efficiencies in ocean-driven atmospheric CO₂ changes. In: Sundquist ET, Broecker WS, editors. *The carbon cycle and atmospheric CO₂: natural variations archean to present*. Washington, DC: American Geophysical Union. p 99–110.
- Ward BB, Olson RJ, Perry MJ. 1982. Microbial nitrification rates in the primary nitrite maximum off southern California. *Deep-Sea Res* 29:247–55.
- Ward BB, Kilpatrick KA, Renger EH, Eppley RW. 1989. Biological nitrogen cycling in the nitracline. *Limnol Oceanogr* 34:493–513.
- Wassman P. 1990. Relationship between primary and export production in the boreal coastal zone of the North Atlantic. *Limnol Oceanogr* 35:464–71.
- Wiegert RG, Penas-Lado E. 1995. Nitrogen-pulsed systems on the coast of northwest Spain. *Estuaries* 18:622–35.
- Williams PJ leB. 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kieler Meeresforsch Sonderh* 5:1–28.
- Williams PJ leB. 1993. On the definition of plankton production terms. In: Li WKW, Maestrini SY, editors. *Measurement of primary production from the molecular to the global scale*. ICES marine science symposia. Volume 197. Denmark: International Council for the Exploration of the Sea. p 9–19.
- Williams PJ leB. 1998. The balance of plankton respiration and photosynthesis in the open oceans. *Nature* 394:55–7.
- Williams PJLeB, von Bodungen B. 1989. Group report: export productivity from the photic zone. In: Berger WH, Smetacek VS, Wefer G, editors. *Productivity of the ocean: present and past*. New York: John Wiley & Sons Ltd. p 99–115.
- Williams PM, Druffel ERM. 1987. Radiocarbon in dissolved organic matter in the central North Pacific Ocean. *Nature* 330:246–8.
- Winn CD, Karl DM. 1984. Microbial productivity and community growth rate estimates in the tropical North Pacific Ocean. *Biol Oceanogr* 3:123–45.
- Winn CD, Campbell L, Christian JR, Letelier RM, Hebel DV, Dore JE, Fujieki L, Karl DM. 1995. Seasonal variability in the phytoplankton community of the North Pacific Subtropical Gyre. *Global Biogeochem Cycles* 9:605–20.
- Woese CR. 1994. There must be a prokaryote somewhere: microbiology's search for itself. *Microbiol Rev* 58:1–9.
- Wyrтки K. 1975. Fluctuation of the dynamic topography in the Pacific Ocean. *J Phys Oceanogr* 5:450–9.
- Wyrтки K. 1985. Water displacements in the Pacific and the genesis of El Niño cycles. *J Geophys Res* 90:7129–32.
- Zehr JP, Mellon MT, Zani S. 1998. New nitrogen-fixing microorganisms detected in oligotrophic oceans by amplification of nitrogenase (*nifH*) genes. *Appl Environ Microbiol* 64:3444–50.
- Zhang R-H, Rothstein LM, Busalacchi AJ. 1998. Origin of upper-ocean warming and El Niño change on decadal scales in the tropical Pacific Ocean. *Nature* 391:879–83.
- Zhang Y, Wallace JM, Battisti DS. 1997. ENSO-like interdecadal variability: 1990–93. *J Climate* 10:1004–20.