Oceanic Carbon Cycle and Global Environmental Change: A Microbiological Perspective

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Summary

The oceanic carbon reservoir plays a vital role in global biogeochemical cycles. Transformations of carbon are determined by the distributions and metabolic activities of marine microorganisms. These reversible, reduction-oxidation reactions collectively define the oceanic carbon cycle. Longterm records of microbiological variables in the marine environment are rare, so it is presently impossible to differentiate natural variability from that induced by anthropogenic activities. Since 1988, we have conducted time-series measurements of bioelement (C, N, P, Si) cycle processes at a site characteristic of the N. Pacific gyre. Natural variability is large and appears to be controlled by global scale atmosphere-ocean forcing. Time-series studies will ultimately contribute the data sets that are necessary to validate existing ecological models and have already provided a source of novel hypotheses.

1. Introduction

Contemporary scientific issues related to the atmospheric accumulation of greenhouse gases and their effects on global environmental change demand a comprehensive understanding of both the carbon cycle and global ecology. Consequently, detailed *in situ* investigations of terrestrial and marine microbial populations are necessary prerequisites for developing a predictive capability for global environmental change. To be useful, these investigations need to address broad questions regarding the distributions, abundances, diversity and controls of microbial populations, their effects on the chemical composition of the surrounding habitats and their response to physical perturbations. Ideally, these field studies should be conducted at strategic sites that are representative of larger regions. Furthermore, these ecological studies should be conducted for at least a decade, and preferably longer, in order to distinguish natural variability from that induced by human activities. This is, indeed, a significant challenge and a departure from the equally important, detailed laboratory and field studies that comprise much of our discipline. Microbiologists, by definition, have traditionally focused on the microscopic features of our planet. It is, therefore, a major departure for some of us to ignore the microscope in favor of the tele-

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scope. Nevertheless, microbial ecologists have an obligation to improve our understanding of the global carbon cycle and to help monitor global environmental change because many of the first order scientific concerns involve activities attributable to microorganisms.

2. Global and oceanic carbon cycles

The global inventory of carbon is approximately 4-5 x 10^{19} g (40-50 x 10^3 Gt), distributed unequally among four active reservoirs (20): atmosphere (1.7%), terrestrial (4.5%), geological (8.9%) and oceanic (85%). The small size of the atmospheric reservoir and the large size of the oceanic reservoir are both of great importance in issues related to global climate and environmental variability. Since the beginning of the industrial revolution, humankind has been returning to the atmosphere carbon that accumulated over millions of years in fossil fuels and carbonate minerals, and is conducting an uncontrolled, global scale biogeochemical experiment (17). Since 1800, the atmospheric inventory of CO_2 has increased by about 30% (24), and will continue to rise as world population increases. This perturbation in the global carbon cycle is likely to result in a redistribution of mass among the active reservoirs and attendant alterations in exchange rates and, perhaps, exchange processes. However at the present time we have only a rudimentary understanding of the rates of transfer and the mechanisms that comprise the global carbon cycle.

Since 1958, C.D. Keeling and colleagues have made high precision measurements of the atmospheric concentrations of CO_2 at Manua Loa, Hawaii and have documented both the total amount and the rates of increase of CO_2 (Figure 1). Their Hawaii CO_2 data set is unique and one of the most important of any that currently exist in the earth sciences literature. Today a network of CO_2 monitoring stations around the world are making similar measurements, so we are fairly confident of the global atmospheric inventory despite the variable seasonal fluctuations and large interhemispherical differences that exist (Figure 1). Because CO_2 is a known greenhouse gas (i.e., it can absorb long wavelength infrared radiation emitted from the earth's surface causing a warming of the lower atmosphere), an increased atmospheric CO_2 inventory should result in increased temperature on the earth with numerous physical and ecological consequences.

The large oceanic carbon pool is comprised of dissolved and particulate constituents with variable redox states. The most ubiquitous components are the oxidized pool of dissolved inorganic carbon (DIC) and the reduced pool of mostly uncharacterized dissolved organic carbon (DOC). A chemical disequilibrium between DIC and organic matter is produced and maintained by biological processes. The reversible, largely microbially-mediated interconversions between dissolved and particulate carbon pools in the sea collectively define the oceanic carbon cycle (8). Primary con-

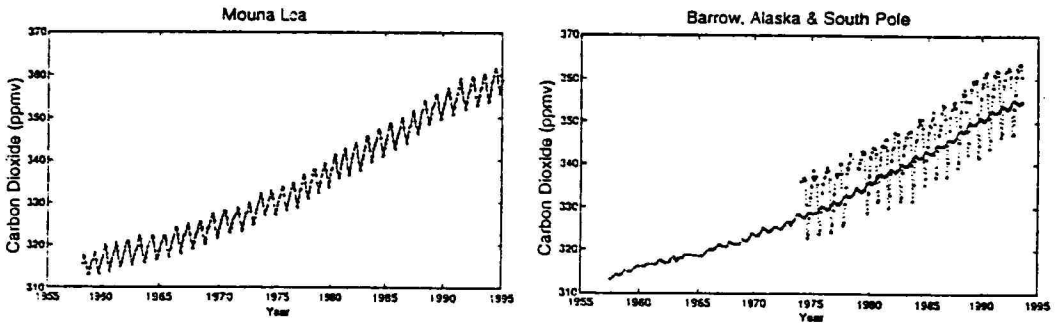


Figure 1 - Temporal changes in the concentration of CO_2 in the atmosphere at several sampling sites. [Left] Mauna Loa, Hawaii; [Right] dashed line, Pt. Barrow, Alaska; solid line, South Pole. (Data as presented in Boden *et al.* (2), from data collected by C. D. Keeling and T. P. Whorf).

version of oxidized DIC to reduced organic matter (dissolved and particulate pools) is restricted to the euphotic zone of the world ocean during the process of photosynthesis. The 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, gravitational settling of particulate matter and by the vertical migrations of pelagic organisms. Each of these individual processes, collectively termed the "biological pump" (32) is controlled by a distinct set of environmental factors and, therefore, the relative contribution of each process may be expected to vary with changes in habitat or with water depth for a given habitat.

Although much of the CO_2 that is currently accumulating in the atmosphere will eventually end up in the oceanic reservoir, the long turnover time precludes rapid readjustment. The oceans are known to play a central role in regulating the global concentration of CO_2 in the atmosphere (25), although the precise partitioning between the ocean and terrestrial spheres is not known (14, 21, 29). The contemporary role of the ocean for absorbing excess atmospheric CO_2 is dependent largely upon the export flux of planktonic primary production (4). Each year, the biological pump removes an estimated 5-7 x 10^{15} g C (5-7 Gt) from the surface waters of the world ocean. This value is equivalent to 10-20% of the annual global ocean primary production, and approximately equal to the annual input of CO_2 to the atmosphere by fossil fuel consumption (3). Euphotic zone or mesopelagic processes that give rise to increased C:N or C:P ratios with depth can potentially drive a net atmosphere-ocean flux of CO_2.

The most reliable current budget estimates of the sources and sinks of CO_2 imply a significant "missing sink" of nearly 1.8 x 10^{15} g C yr^{-1} (1.8 Gt), or approximately 25% of the annual production rate (Table 1). The existence of this large missing sink has understandably stimulated a great deal of research in this area over the past decade. Compared to the extensive global network of atmospheric CO_2 monitoring sites, the surface ocean is undersampled. It is, therefore, logical to assume that the ocean may be responsible for at least part of this large deficit. Unfortunately because of the magnitude of the oceanic reservoir of DIC and the very large annual air-sea fluxes of CO_2 that occur due to seasonal changes in temperature it is difficult to quantify adequately the net oceanic sink.

Table 1 - Intergovernmental Panel on Climate Change (IPCC) assessment of the global carbon dioxide budget for the period 1980-1989 (From: Watson *et al.* (33)).

Process	Value (Gt C yr^{-1})[1]
Sources to the Atmosphere	
fossil fuel combustion	5.4 ± 0.5
changes in land use	1.6 ± 1.0
Total Source	7.0 ± 1.2
Known Sinks	
atmospheric accumulation	3.4 ± 0.2
ocean	2.0 ± 0.8
Total SNK	5.4 ± 0.8
"Missing" sink(s)???	*1.6 ± 1.4*

[1] Gt = 10^{15} g

3. JGOFS Oceanic Time-series Stations

Systematic, long-term time-series studies of selected aquatic and terrestrial habitats have yielded significant contributions to earth and ocean sciences through the characterization of

climate trends. However, time-series investigations of the distribution and metabolic activites of marine microorganisms are rare. Examination of physical and biological data derived from the few long-term oceanic time-series that do exist provides ample incentive and scientific justification to establish additional study sites (34).

In response to the 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 International Geosphere-Biosphere Programme: A Study of Global Change (IGBP) was established in 1986. One of the essential core components of this program, the Joint Global Ocean Flux Study (JGOFS), was established in 1987 to focus on the ocean's carbon cycle and on the associated air-to-sea fluxes of CO_2 (5).

The broad objectives of U.S.-JGOFS are: (1) to determine and understand on a global scale the time-varying fluxes of carbon and associated biogenic elements in the ocean and (2) to evaluate the related exchanges of these elements with the atmosphere, the sea floor and the continental boundaries (26). To achieve these goals, four separate program elements were defined: (1) process studies to capture key regular events, (2) long- term time-series observations at strategic sites, (3) a global survey of relevant oceanic properties (e.g., CO_2) and (4) a vigorous data assimilation effort to interpret results, disseminate knowledge and generate testable hypotheses.

In 1988, two open ocean time-series hydrostations were established with support from the U.S. National Science Foundation (NSF): one in the western North Atlantic Ocean near the historical Panulirus Station (Bermuda Atlantic Time-Series; BATS) and the other in the subtropical North Pacific Ocean near Hawaii (Hawaii Ocean Time-series; HOT). These programs were established and have been operated by scientists at Bermuda Biological Station for Research and the University of Hawaii, respectively, on behalf of the ocean sciences community. The primary HOT program site, Station ALOHA, is located in deep water (>4,500 m) approximately 100 km north of Oahu (Figure 2). The main research objective of the initial 10-

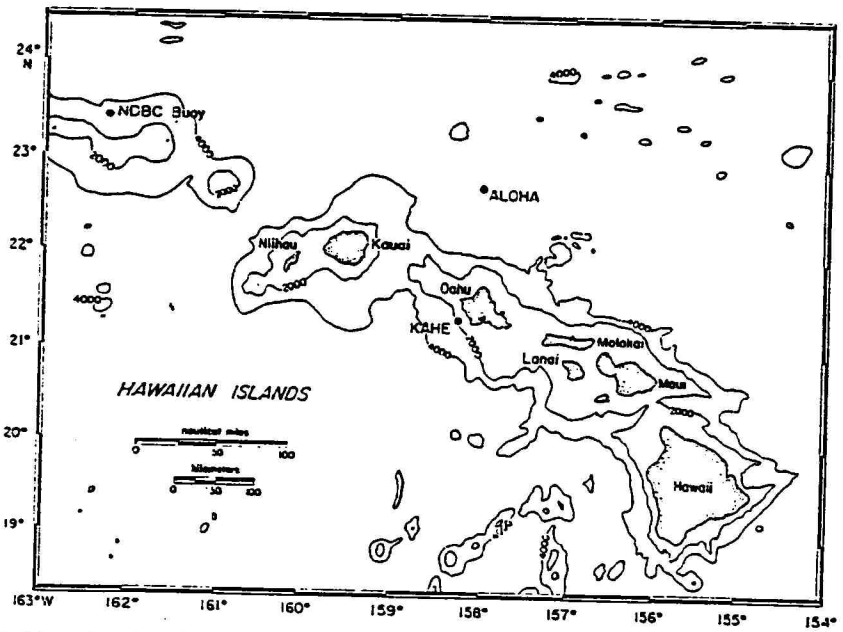


Figure 2 - Map showing the location of the HOT deep water station ALOHA (A Long-term Oligotrophic Habitat Assessment), the HOT coastal station Kahe and the NOAA-National Data Buoy Center (NDBC) meteorclogical buoy.

year phase of HOT (1988-1997) is to maintain this hydrostation as a North Pacific oligotrophic ocean benchmark for observing and interpreting physical and biogeochemical variability, including carbon pool dynamics. The sampling design includes repeated measurements of a suite of core parameters (13) at approximately monthly intervals, compilation of the data and rapid distribution to the scientific community. Eventually the data set will be used to improve existing models and to generate meaningful hypotheses for future study.

4. Microbial processes in the oligotrophic North Pacific

The subtropical gyre of the North Pacific Ocean is characterized by permanent density stratification, and even during winter season the long-term climatology indicates fairly shallow mixed-layer depths. Consequently, the surface waters in these mid-latitude regions are chronically nutrient-impoverished. Furthermore, the near-zero nutrient concentration gradient routinely observed in the upper 100 m of the water column suggests that vertical nutrient flux cannot be the primary source of dissolved inorganic nutrients (e.g., nitrate and phosphate) to the upper euphotic zone (7).

The observed separation of light in the surface waters from inorganic nutrients beneath the euphotic zone predicts that the surface ocean ecosystem is not only oligotrophic (low standing stocks of nutrients and biomass), but that it also supports a low production rate of organic matter. Ironically, most of the water column primary production occurs in the upper 75 m (e.g., ~80% of total; 15) where inorganic nutrient concentrations are generally below the detection limits of standard seawater analysis techniques. Consequently, total ecosystem productivity must be largely supported by local nutrient regeneration processes or by non-conventional, allochthonous inputs of nutrients.

Because subtropical ocean gyres are dominant habitats of the world ocean (Pacific Ocean = 90 x 10^6 km^2 and Atlantic Ocean = 31 x 10^6 km^2 together accounting for approximately 40% of the world ocean), accurate estimation of global ocean production relies upon adequate and reliable measurement of gyre productivity. While most historical (pre-1980) estimates of North Pacific subtropical gyre productivity support the prediction of a virtual biological desert with annual production ~50 g C m^{-2} (1) most recent measurements suggest that the production can be higher by at least a factor of two (9).

Based on a systematic analysis of steady-state nutrient flux versus nutrient demand, Hayward (6) hypothesized that stochastic habitat variability must occur in the North Pacific gyre. Unfortunately, historical measurements are insufficient for resolving the nutrient budget discrepancies. Several attempts to improve estimates of vertical diffusion rates in the open ocean (16) have failed to lead to budget reconciliation. As discussed by Karl *et al.* (10), even the lowest measured rates of primary production for the oligotrophic North Pacific (~0.1 mol N m^{-2} yr^{-1}, assuming a molar C:N ratio of 6.6 and a mean euphotic zone *f*- ratio of 0.1) cannot be supported by the steady-state cross isopycnal nitrate diffusion rates estimated for this region.

It was recently suggested that biological communities of the subtropical North Pacific gyre also exhibit change on decadal time scales in response to ocean-atmosphere interactions. Venrick *et al.* (31) reported a long-term increasing trend in the chl *a* concentration at the CLIMAX site in the central North Pacific Ocean (approximately 28°N, 155°W). Although their time-series record has large data gaps (up to 3 yr in duration), they suggest that summertime concentrations of chl *a* (May-October) have nearly doubled during the period 1968-1985. Concomitant increases in winter winds and a decrease in sea surface temperature at this site have apparently altered both the habitat and the carrying capacity of the

epipelagic ecosystem (31). Such low frequency climate events are undoubtedly important in maintaining the diversity and structure of the oligotrophic marine ecosystem and would not be detected without time-series data sets.

Our ongoing oceanic time-series study at Station ALOHA has provided an unprecedented view of the complexity of the coupled physical and biological processes that occur in this subtropical habitat. Of greatest importance to our quantitative assessment of the global carbon cycle are: (1) the discovery of relatively high annual rates of primary and export production (~14 moles C m^{-2} yr^{-1} and 1 mole C m^{-2} yr^{-1}, respectively; 9) compared to historical estimations that are 2-3 fold lower (1), (2) the conclusion that the subtropical ocean is a sink for approximately 0.7-0.8 moles of CO_2 m^{-2} yr^{-1} (35), compared to previous estimations that were approximately one-half that value (29), (3) the importance of N_2 fixation as a source of "new" nitrogen and (4) the temporal decoupling of organic matter production, export and decomposition. The latter two processes, in particular, may be responsible for the observed shift from a N-limited to a P-limited ecosystem (11) and for the sequestration of atmospheric CO_2 into dissolved organic matter (12).

These major ecosystem changes and subsequent perturbation to the oceanic carbon cycle are, at least in part, the result of a large scale ocean-atmosphere phenomenon referred to as the El Niño-Southern Oscillation (ENSO; 18). ENSO affects global weather patterns, polar ice dynamics and the rates and mechanisms of numerous components of the global carbon cycle. At Station ALOHA, for example, the 1991-93 ENSO conditions favored the growth and accumulation of the N_2 fixing bacterium, *Trichodesmium*, with large changes in rates of primary production and formation of organic matter with a non-Redfield (23) bioelemental composition (Table 2; 11). A large accumulation of dissolved organic matter was also observed during this period of observation (11). This latter potential sink of CO_2 (i.e., DOM) has not been considered in global carbon budgets.

Table 2 - Effects of ENSO on biogeochemical processes in the subtropical North Pacific gyre.

"Normal" conditions	ENSO conditions
1. Variable mixed-layer depth (40-100 m)	1. Near-surface stratification, shallow mixed-layers
2. Vigorous near-surface currents	2. Currents variable and slack
3. *Trichodesmium* present, but low rates of N_2-fixation	3. *Trichodesmium* abundant, high rates of N_2-fixation
4. Moderate primary production and export	4. High primary production and low export
5. NO_3-based new production	5. N_2-based new production
6. N-limited	6. P-limited

ENSO conditions (i.e., negative Southern Oscillation Index [SOI]; 30) have dominated the period 1983-1993, a condition that is unprecedented in this century (22). Furthermore, one of the most intense (1982-83) and one of the longest (1991-93) ENSO periods on record occurred during that decade. I hypothesize that these high intensity and long duration ENSO events may have led to fundamental changes in the North Pacific gyre ecosystem that are only now being resolved by HOT program scientists (Figure 3).

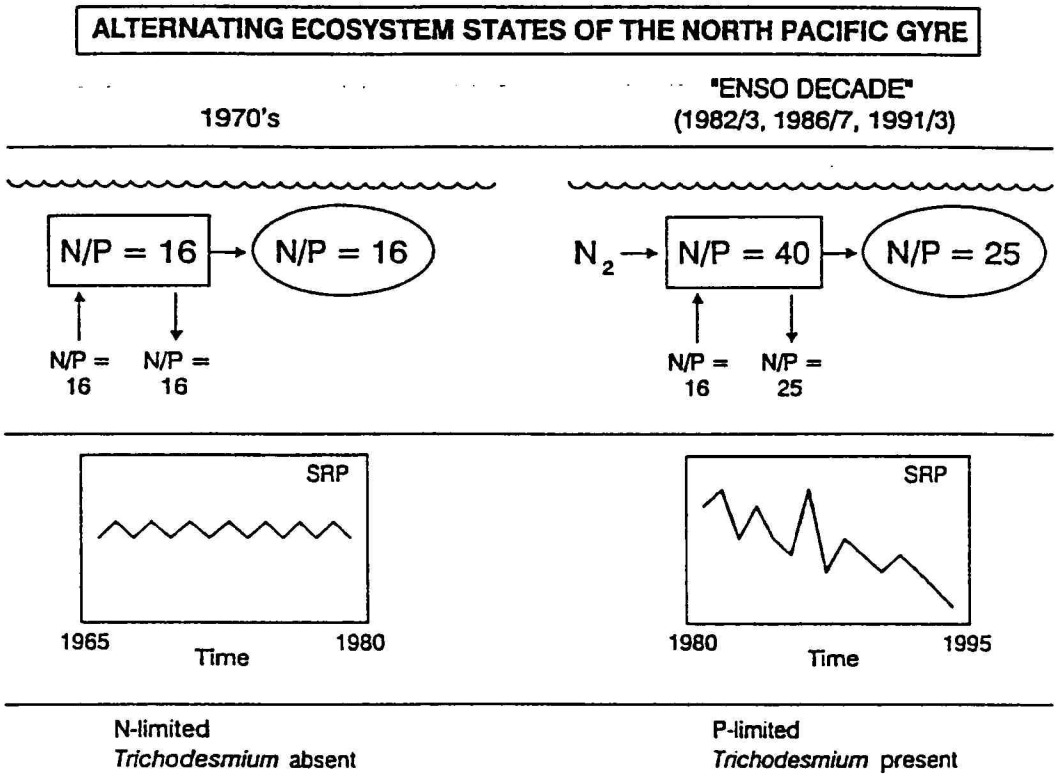


Figure 3 - Schematic presentation of the ENSO-controlled alternating ecosystem states hypothesis for microbial assemblages in the subtropical North Pacific Ocean. During extended periods of weak or brief ENSO events (1970's) new production in the upper water column is fueled by upward eddy diffusion of nutrients from beneath the euphotic zone. The production and export of both particulate organic matter (POM; shown as boxes) and dissolved organic matter (DOM; shown as ovals) is in approximate Redfield N:P balance (i.e., 16:1). N_2 fixation by *Trichodesmium* and other cyanobacteria is negligible and the concentrations of soluble reactive phosphorus (SRP) is approximately constant with time. During periods when either very large or prolonged ENSO events occur (or both; e.g., 1982-1993) the supply of nutrients from below is reduced, N_2 fixation by *Trichodesmium* and other competent microorganisms provide a local supply of new nitrogen and the system is driven to P- limitation. A characteristic feature of *Trichodesmium* is their non-Redfield N:P coupling and this process affects the chemical composition of suspended and sinking POM and of surface ocean DOM. As a direct result of N_2 assimilation, there is a net removal of SRP from the surface ocean. This "alternating ecosystem states" hypothesis was developed to explain several long-term ecosystem trends observed at Station ALOHA. A field evaluation of selected ecological predictions is currently underway.

A preliminary upper water column carbon budget for Station ALOHA for the period of the HOT program suggests that up to 50% of the apparent net flux of CO_2 may be sequestered as DOC (Table 3). At the present time it is impossible to know whether this observed trend is ENSO controlled. However, regardless of the cause it is evident that non steady-state, decadal scale processes appear to control the dynamics of microbial populations in the subtropical North Pacific gyre and ultimately influence the global ocean cycles of carbon and associated bioelements.

Table 3 - Upper water column carbon budget at Sta. ALOHA (1989-1994).

Process	Value (mol C m^{-2} yr^{-1})
Inputs	
atm-ocean CO_2 exchange[1]	+0.8
eddy diffusivity[2]	+0.5
upwelling[3]	+0.05
Exchanges	
gross primary production4	14.1
H-bacterial production4	2.7
Exports	
particle flux[4]	-0.9
Euphotic Zone Accumulations	
DOC[5]	+0.4

[1] average annual input determined by direct measurements (35)
[2] estimated from measured DIC gradient and estimated eddy diffusivity coefficient (Kv) of 3.7 x 10^{-4} m2 sec^{-1} (16)
[3] calculated from upward vertical velocity (w) of 0.012 m d^{-1} (19)
[4] measured in HOT program
[5] estimated from measured rate of accumulation of dissolved organic matter in the upper 100 m at Station ALOHA (12)

5. Prospectus

Long-term time series programs present special problems for research scientists in general (27) and for oceanographers in particular (28, 36). The emergent physical and biogeochemical HOT program data set (Table 4) suggests that other oceanic time-series programs should be developed. As the HOT program matures we anticipate a greater level of data synthesis and the

Table 4 - Internet access to the HOT time-series data base and other information on program implementation and scientific progress.

Address or file	Data or information available
INTERNET (ftp)	
mana.soest.hawaii.edu (or 128.171.154.9)	work station's address
cd/pub/hot	to access HOT data and information base once connected to *mana*
Readme.first	provides general information about the data base
/pub/hot/protocols	HOT Program Field and Laboratory Protocols Manual, updated periodically
/pub/hot/publication-list	HOT program publication list, updated quarterly
WORLD WIDE WEB	
http://hahana.soest.hawaii.edu/	work station's address

publication of many novel observations on physical, chemical and microbiological variability in the subtropical North Pacific gyre. Only through comprehensive, transdisciplinary research programs like JGOFS can we expect to improve our understanding of the oceanic carbon cycle and of the microbial communities that largely control the flow of carbon in the biosphere.

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