# RELATIVE ASSIMILATION NUMBERS OF PHYTOPLANKTON ACROSS A SEASONALLY RECURRING FRONT IN THE CALIFORNIA CURRENT OFF ENSENADA

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## ABSTRACT

Higher surface chlorophyll *a* concentrations (Chl *a*) and integrated primary productivity (PP) have been reported for the cold side of a seasonally recurring front in the California Current. To test the hypothesis that greater PP at the cold side may partially be due to higher assimilation numbers (mgC·mgChl $a^{-1}\cdot h^{-1}$) of phytoplankton than those on the warm side, we generated photosynthesis-irradiance (P-I) curves for whole communities sampled across the front. Our data do not support the hypothesis. No differences were evident between our relative assimilation number values from both sides of the front. Higher PP values at the cold side seem to be due to the shallower subsurface Chl *a* maximum, which causes less limitation of light for the phytoplankton.

## RESUMEN

Se han reportado valores más altos de concentración superficial de clorofila (Clf *a*) y productividad primaria integrada (PP) para el lado frío de un frente estacionalmente recurrente en la Corriente de California. En julio de 1985 generamos curvas fotosíntesis-irradiancia de comunidades de fitoplancton muestreadas a través del frente para probar la hipótesis de que la mayor PP en el lado frío se debe parcialmente a que los números de asimilación (mgC·mgClf $a^{-1}\cdot h^{-1}$) son mayores que los del lado caliente. Nuestros datos no apoyan la hipótesis. Los valores de números de asimilación relativos de ambos lados no muestran una diferencia evidente. Los valores más altos de PP del lado frio parecen deberse a una posición más somera del máximo subsuperficial de Clf *a*, lo cual causa una menor limitación de luz para el fitoplancton.

## INTRODUCTION

Studying satellite images of phytoplankton pigments off California, Peláez and McGowan (1986) described a latitudinally oriented, sharp front just south of San Diego. This front starts about 160 km off the coast and extends some 500 km offshore. It is a persistent feature of the region. According to these authors, its phytoplankton pigment content changes approximately threefold over a distance of some 50 kilometers. The front retains its identity throughout the year, though it may wobble, tilt, or change position. In addition, the pigment gradient across the boundary changes markedly with time. During summer, the boundary shifts slowly to the south, reaching its southernmost position by mid- or late summer (off Ensenada, Baja California). The boundary is sharp and distinct in spring and early summer. By late summer, however, it is distinctly less intense (the pigment gradient is not as steep), and its outer edge erodes and ruptures. Peláez and McGowan (1986) also indicated that the large-scale phytoplankton pigment patterns for a given season tended to reappear from one year to another in the three years analyzed. Thomas and Strub (1990) reported similar dynamics at a zonally oriented frontal region within the California Current north of 33°N.

In order to describe the vertical structure and dynamics of the physical, chemical, and biological properties associated with the persistent, seasonally recurring feature studied by Peláez and McGowan (1986), the FRONTS cruise aboard RV *New Horizon* of the Scripps Institution of Oceanography (SIO) was carried on in July 1985 (Haury et al. 1986). As part of this project, we studied the photosynthesis-irradiance relationship of phytoplankton communities sampled across the front.

Simultaneous to our cruise, an independent study was being made by Prézelin et al. (1987) and Smith et al. (1987) across a coastal front in the Southern California Bight. Prézelin et al. (1987) reported on the diurnal patterns of size-fractionated photosynthetic parameters and on the algal groups dominating the phytoplankton communities across the front. Their data showed that either nannoplankton or netplankton can dominate natural phytoplankton assemblages in coastal frontal regions. Their study documents the range of variability possible in diurnal patterns of size-fractionated photosynthesis and illustrates that a general view of the size-dependency in assimilation numbers and diurnal patterns of photosynthesis cannot be supported.

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The purpose of our work was to report on the changes of assimilation numbers ($P_m^B$), or maximum photosynthetic rates in per unit chlorophyll *a* at optimum irradiance, of whole phytoplankton communities sampled across the Ensenada front described by Peláez and McGowan (1986). To generate the P-I curves, incubation experiments were performed only at noon; thus we describe only spatial changes of assimilation numbers. The hypothesis to be tested is that greater primary productivity at the cold side of the front may partially be due to higher assimilation numbers of phytoplankton. This will help to explain the strong changes of pigment concentrations and primary productivity across the front.

## METHODS AND MATERIALS

The FRONTS cruise was divided into two legs. During the first leg, from 1 to 11 July 1985, an intensive series of CTD casts was made to find the boundary. A strong cold frontal area was also detected in satellite AVHRR images sent to the ship (Haury et al. 1986). During this leg we performed $^{14}$C incubations to describe the vertical distribution of $P_m^B$ for three hydrographic stations (A, B, and C; figure 1). Vertical profiles of photosynthetically active radiation (PAR) were obtained with a Biospherical Instruments quantum scalar irradiance meter, model QSP 170BR. We monitored PAR from the sun and sky with a solar hemispherical sensor (BIQSIM, model QSR-240).

Samples were collected, in special casts, from depths corresponding to 100%, 50%, 25%, 10%, and 1% of irradiance incident just below the surface ($E_0$). Samples were obtained with 7-l Niskin bottles with clear neoprene rubber closures. Sixteen subsamples were drawn from each depth into 125-ml incubation glass bottles, which were inoculated with $^{14}$C as $NaHCO_3$. Two replicate samples from each depth were incubated on board, in sunlight, at each of eight irradiances: 88%, 60%, 45%, 22%, 5.5%, 4%, 3%, and 1% of solar irradiance measured on deck. The incubator consisted of acrylic tubes with black plastic filter screens to control irradiance. Incubation irradiances were measured inside empty bottles and tubes. Incubations were done between 1100 and 1400 hrs. After about 2 hours of incubation, samples were filtered onto 0.45-μm-pore membrane filters and placed in scintillation vials. One-half ml of 10% HCl was added to each sample, which was then allowed to sit uncovered at room temperature for 12 hours (after Lean and Burnison 1979). Then 10 ml of scintillation fluor were added to each sample, and the samples were taken to SIO where the radioactivity was determined with a scintillation Beckman LS 100 counter.

During the second leg, 12 to 23 July, we ran eight $^{14}$C incubation experiments to determine $P_m^B$ for samples from depths corresponding to 100% and 50% $E_0$ (stations D through K, figure 1). Incubations were done at noon, as in the first leg, but instead of two replicate samples from each depth we used five at each incubation irradiance. Two incubation experiments of the first leg and four of the second were done for stations at the warm side of the front, the other five experiments were done for stations at the cold side (figure 1).

Two transects across the front were sampled during the second leg. The southwest-to-northeast transect was covered three consecutive times, while the northwest-to-southeast transect was covered only once, with a total of 37 hydrographic stations for both transects (Haury et al. 1986). Besides these 37 stations, we occupied 8 more for our incubation experiments, so that our sampling was done around 1000 hrs. For each sampled depth, we also measured dissolved oxygen concentration ($O_2$), nutrients ($PO_4$, $NO_3$, $NO_2$, and $SiO_2$), chlorophyll *a* (Chl *a*), phaeopigments, and phytoplankton abundance.

We determined $O_2$ by the Winkler method as modified by Carpenter (1965), using the equipment

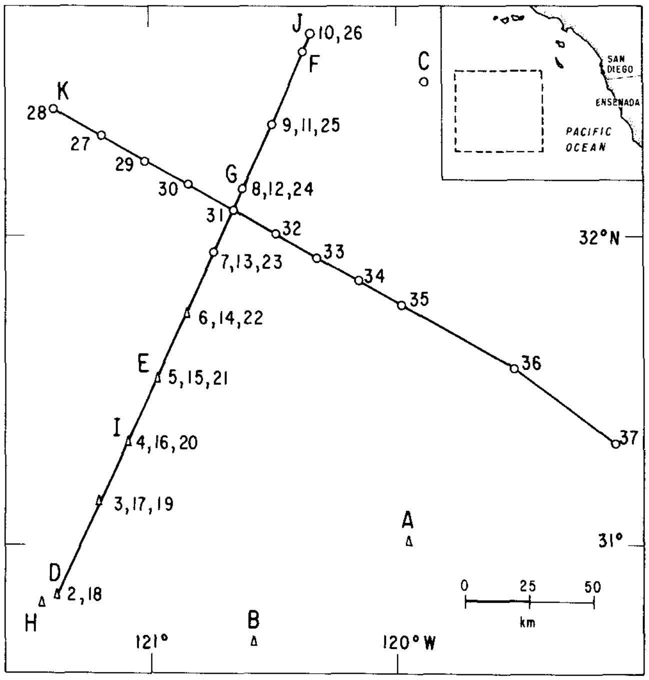

Figure 1. Station locations for second leg of FRONTS cruise. Letters indicate the positions of our incubation experiment stations. Data reported by Haury et al. (1986) are from stations represented by numbers. *Triangles* represent stations from the warm side of the front; *circles* represent those from the cold side.

and procedure outlined by Anderson (1971). We used an automated analyzer at sea to determine nutrients, with procedures similar to those described in Atlas et al. (1971). Chlorophyll was measured with a fluorometric technique (Yentsch and Menzel 1963; Holm-Hansen et al. 1965). Chl *a* samples were obtained with 0.45-μm-membrane filters. We extracted pigment following Venrick and Hayward (1984): we placed the filters in scintillation vials containing 10 ml of 90% acetone, and refrigerated them for 24 hours. The samples were then brought to room temperature; their fluorescence was determined, before and after acidification, with a Turner Designs fluorometer. Phytoplankton abundance was determined by the Utermöhl (1958) inverted microscope technique, and cells greater than 8 μm were counted apart from the smaller ones.

Photosynthesis data (per $m^3$) were normalized per unit Chl *a* to obtain assimilation ratios ($P^B$). Photosynthesis-irradiance curves were drawn, and assimilation numbers ($P^B_m$) were estimated by eye-fitting, in each case, with the mean of $P^B$'s for the replicates at the optimum irradiance. Then, all $P^B_m$'s were divided by the largest one of our data set (2.88 $\mathrm{mgC \cdot mgChl}\ a^{-1} \cdot h^{-1}$) to obtain relative assimilation numbers ($RP^B_m = \frac{P^B_m}{P^B_m(\mathrm{max})}$). The $^{14}C$ activity added to the incubating samples was constant, but unfortunately its absolute value is uncertain, which is why we use relative assimilation numbers instead of absolute values.

## RESULTS

The temperature front was detected at station 6, 31°44.8′N, where the 18°C isotherm was almost vertical from the surface to 35-m depth (figure 2a). Across the front, measured sea-surface temperatures ranged from more than 19°C at the south, to less than 16.5°C at the north, in a distance of about 160 km. Surface Chl *a* values ranged from less than 0.08 $mg \cdot m^{-3}$ at the warm side of the front to more than 0.25 $mg \cdot m^{-3}$ at the cold side (figure 2b).

The isopleths showing the vertical distribution of Chl *a*, $O_2$, $NO_3$, $PO_4$, and $SiO_2$ sloped upward from the warm to the cold side, mainly at the front itself (figure 2b–f). The subsurface Chl *a* maximum changed depth from about 90 m at the south to near 10 m at the north, and its concentration changed slightly from about 0.30 $mg \cdot m^{-3}$ at the south to about 0.25 $mg \cdot m^{-3}$ at the north. The two northernmost stations had a homogeneous vertical distribution of Chl *a* from the surface to 70 m, with values between 0.20 and 0.30 $mg \cdot m^{-3}$. The subsurface $O_2$ maximum did not coincide with the Chl *a* maximum: the $O_2$ maximum was between 50 and 60 m at the south of the front and between 30 and 40 m at the north.

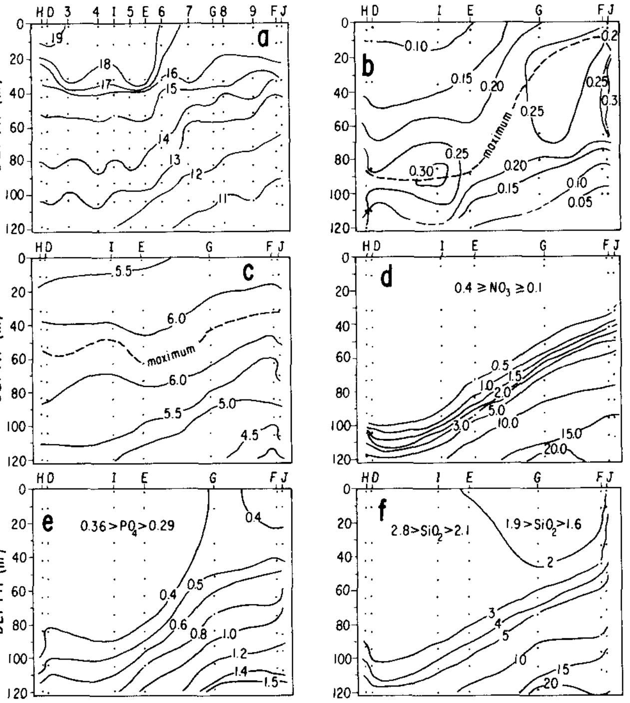

Figure 2. Vertical distributions of *a*, temperature; *b*, chlorophyll *a* ($mg \cdot m^{-3}$); *c*, oxygen ($ml \cdot l^{-1}$); *d*, nitrate (μM); *e*, phosphate (μM); and *f*, silicate (μM).

Surface values of $NO_3$ were relatively low along the whole transect, but greater than 0.1 μM. The 0.5-μM $NO_3$ isogram was deeper than 90 m at the southernmost station, and only 30 m deep at the northernmost station; below this isogram, there was a steep $NO_3$ vertical gradient, with the 5-μM isogram only 20 m deeper (figure 2d). $PO_4$ surface values were slightly greater at the cold side of the front, with concentrations of 0.4 μM, compared to values between 0.30 and 0.35 μM at the south. Conversely, $SiO_2$ surface values were slightly greater at the warm side of the front, with concentrations as high as 2.8 μM, compared to values as low as 1.6 μM at the north (figure 2). $PO_4$ and $SiO_2$ presented steep vertical gradients like $NO_3$, starting at the same depth (figure 2d–f). $NO_2$ surface values varied from undetected to 0.03 μM; its values at the nutricline were between 0.05 and 0.20 μM, with maximum values at depths changing from 105 m at the southernmost station to 60 m at the northernmost one (data not presented).

The depth corresponding to 1% $E_0$ was greater at the warm side of the front than at the cold side: 82–88 m at the warm side, and 59–65 m at the north

TABLE 1
$RP_m^B$ Values for Communities of Phytoplankton Sampled from the Indicated Light Levels, Total Phytoplankton Abundance (cells•ml$^{-1}$), and Abundance of the <8-µm Size Fraction

| STA. | | | | PHYTOPLANKTON | |
|---|---|---|---|---|---|
| | z (m) | % $E_0$ | $RP_m^B$ | TOTAL | <8µm |
| A<br>83<br>4 | 0 | 100 | 0.25 | | |
| | 8 | 50 | 0.29 | 111 | 97 |
| | 16 | 25 | 0.26 | 85 | 72 |
| | 36 | 10 | 0.39 | 74 | 62 |
| | 83 | 1 | 0.07 | 89 | 77 |
| B<br>82<br>6 | 0 | 100 | 1.00 | 114 | 68 |
| | 2 | 50 | 0.75 | 184 | 173 |
| | 14 | 25 | 0.65 | 142 | 117 |
| | 32 | 10 | 0.66 | 112 | 98 |
| | 82 | 1 | 0.24 | 116 | 106 |
| C<br>59<br>9 | 0 | 100 | 0.39 | 136 | 126 |
| | 4 | 50 | 0.28 | 104 | 91 |
| | 10 | 25 | 0.46 | 77 | 55 |
| | 24 | 10 | 0.39 | 114 | 101 |
| | 59 | 1 | 0.18 | 142 | 124 |
| D<br>85<br>14 | 0 | 100 | 0.74 | 173 | 131 |
| | 2 | 50 | 0.90 | 138 | 120 |
| E<br>88<br>15 | 0 | 100 | 0.53 | 216 | 175 |
| | 3 | 50 | 0.61 | 242 | 209 |
| F<br>65<br>16 | 0 | 100 | 0.36 | 117 | 94 |
| | 2 | 50 | 0.20 | 98 | 75 |
| G<br>64<br>17 | 0 | 100 | 0.33 | 147 | 128 |
| | 2 | 50 | 0.28 | 26 | 22 |
| H<br>86<br>18 | 0 | 100 | 0.43 | 156 | 136 |
| | 3 | 50 | 0.35 | 43 | 32 |
| I<br>85<br>19 | 0 | 100 | 0.58 | 113 | 97 |
| | 3 | 50 | 0.51 | 72 | 54 |
| J<br>61<br>20 | 0 | 100 | 0.49 | 115 | 91 |
| | 3 | 50 | 0.37 | 46 | 23 |
| K<br>61<br>21 | 0 | 100 | 0.34 | 125 | 108 |
| | 2 | 50 | 0.28 | 64 | 32 |

Numbers under station letters are the 1% $E_0$ depth in meters (e.g., 83), and the sampling date in July (e.g., 4).

(table 1). This is a less steep gradient than the one shown by the nutrient isograms across the front, so that the 1% $E_0$ depth is much farther into the nutricline at the cold side of the front than at the south. The 50% $E_0$ depth varied from 2 to 8 m, usually falling at 2–3 m.

Although only cells larger than about 2.5 µm are counted with our inverted microscope, nannoplankton was always the most abundant fraction (table 1). Counted cells smaller than 8 µm were between 50% and 95% of total counts, mostly falling between 75% and 85%. There was no difference in either total abundance or percent abundance of nannoplankton between the warm and the cold side of the front. Microflagellates were the dominant counted group in all cases.

All of our samples showed photoinhibition at high irradiances. Because we only had four discrete high irradiances in our incubation experiments, it was not possible to precisely determine the values of optimum or saturating light. But our data show that in most cases light saturation was reached at about 250 micro-Einsteins·m$^{-2}$·s$^{-1}$ (figure 3). Although there were some higher values of $RP_m^B$ at the warm side of the front with respect to those on the cold side, there was no clear spatial pattern. No difference was evident for $RP_m^B$ values from one side to the other of the front, or between the 100% and 50% $E_0$ depths (table 1). One standard deviation of $RP_m^B$ values for the 100% $E_0$ depth of cold stations was 0.06; that of warm stations was 0.26. For the 50% $E_0$ depth it was 0.06 for the cold stations and 0.23 for the warm stations. For stations A, B, and C, $RP_m^B$ was relatively constant from the sea surface to the 10% $E_0$ depth, but its values were lower at the 1% $E_0$ depth.

## DISCUSSION

The front has a clear effect on the spatial distribution of seawater properties down to more than 100 m. At 120 m, temperature (°C), Chl *a*, and $O_2$ were clearly lower, and nutrients were higher at the north than at the south of the front (figure 2). The

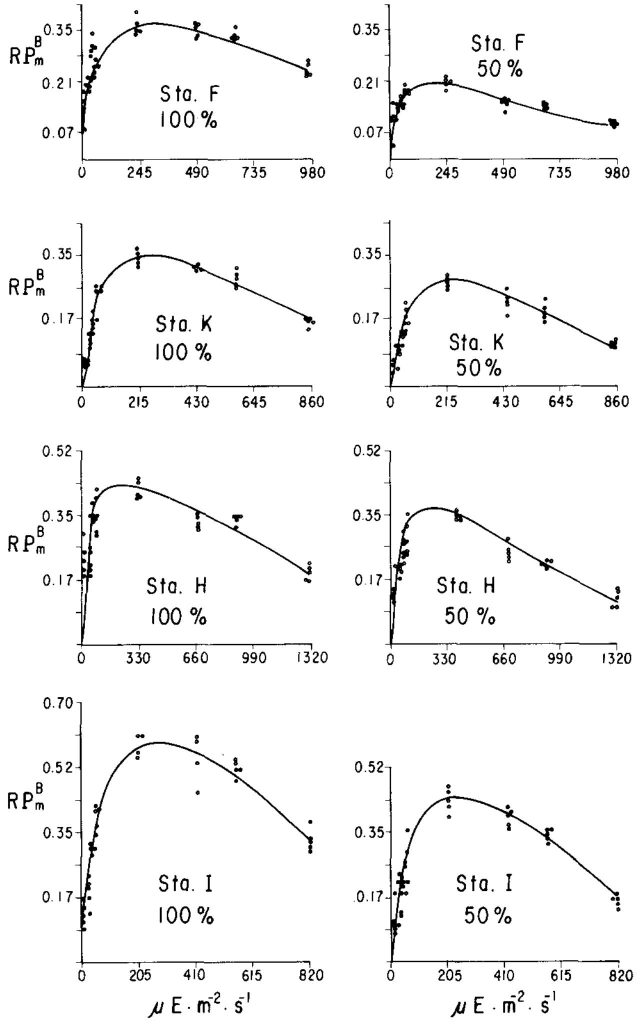

Figure 3. Examples of photosynthesis-irradiance curves for two stations at the cold side of the front (F and K), and two at the warm side (H and I). Sampled light levels (percentages) are beneath the station letters. μE means micro-Einsteins (micromoles of photons).

subsurface Chl *a* maximum is a widespread feature mainly present in summertime, but often also found during winter (Shulenberger and Reid 1981; Alvarez-Borrego and Gaxiola-Castro 1988; J. J. Cullen, Bigelow Laboratory, pers. comm.). It does not seem to occur so deep in the coastal waters of the California Current (Venrick et al. 1973). South of the front, salinity presented a subsurface minimum (Haury et al. 1986), closely coinciding with the Chl *a* maximum. South of the front, surface salinity was 33.6‰, and it was 33.3‰ at the minimum. North of the front, S‰ values were very uniform, around 33.3‰, from the sea surface to 60 m. This uniformity, a weaker thermocline, and the homogeneous vertical Chl *a* distribution at stations G, F, and J, and also from the sea surface to around 70 m all indicate relatively stronger mixing processes at the north of the front than at the south.

Integrated primary productivity for the water column was between two and three times greater to the north of the front than to the south, although integrated Chl *a* was only slightly higher at the north (data from Haury et al. 1986). The highest Chl *a* values were distributed from the sea surface to 70-m depth at the north, whereas at the south they were distributed between 70 and 120 m (figure 2b). Thus, greater integrated primary productivity at the north resulted from more light being available to phytoplankton there. Surface Chl *a* values at the north side of the front were an order of magnitude lower than those considered to be characteristic of coastal conditions. Conditions at the south of the front were similar to those reported for the central North Pacific by Hayward (1987). The subsurface $O_2$ maximum had values up to 0.3 $ml \cdot l^{-1}$ higher at the north of the front than at the south, and this also indicates higher primary productivity at the north. This $O_2$ maximum is a summer feature arising from the photosynthetic production of oxygen, which accumulates because the overlying density cap retards its equilibration with the atmosphere (Shulenberger and Reid 1981).

Our data do not support the hypothesis that higher primary productivity at the north was due to a higher photosynthetic potential per unit of chlorophyll. Relative assimilation numbers were practically the same at both sides of the front. Thus differences in primary productivity across the front are not due to differences in light adaptation of the phytoplankton communities. At the north, the 1% $E_0$ depth was well into the nutricline. However, this greater nutrient availability did not cause higher $RP_m^B$'s.

Light saturation, or optimum light, for samples from 50% and 100% light levels was reached in most cases at 22%–28% $E_0$ (figure 3). This indicates phytoplankton's adaptation to relatively low light levels, and, in turn, its relatively long residence times at depths higher than those from which it was sampled. The phytoplankton sampled from 0–8-m depth may have moved up and down the water column to depths at least greater than 20 m. Falkowski (1983) examined the hypothesis that the recent light history of phytoplankton contains information about vertical mixing processes in the euphotic zone. He used a model to estimate vertical displacement rates of phytoplankton in the New York Bight. Lewis et al. (1984) concluded that the vertical mixing induced by turbulence largely controls the photosynthetic performance of algae in nature. $RP_m^B$

values of the 1% $E_0$ depth at stations A, B, and C (table 1) were lower than those of shallower depths. This was due to phytoplankton's greater residence time at depth in the first case. When phytoplankton become conditioned to lower irradiances, assimilation numbers decrease (Prézelin and Matlick 1980; Falkowski 1981).

Prézelin et al. (1987) studied the diurnal changes of assimilation numbers for phytoplankton communities sampled from the 80%, 10%, and 1% $E_0$ depths, across a coastal front in the Southern California Bight. Our results agree with those of Prézelin et al. in that, contrary to previous reports of netplankton flagellates dominating frontal boundaries, the nannoplankton was the most abundant size fraction.

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