Primary Productivity Measurement Using Carbon-14 and Nitrogenous Nutrient Dynamics in the Southeastern Sea of Korea

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한국 동남해역의 해양기초생산력 (C^{14}) 과
질소계영양염 동적 관계

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Abstract: The daily net primary production by phytoplankton in the southeastern sea of Korea in October 1985 ranged from 0.7 to 2.7 gC m^{-2} d^{-1} and averaged to be 1.3 gC m^{-2} d^{-1}. Surface total chlorophyll ranged from 0.97 to 3.59 mg chl m^{-3}. Primary production by nano-phytoplankton ($< 20 \mu m$) ranged from 43 to 97% in the surface layer. Optimum light intensity (I_{opt}) was around 300 to 700 μE s^{-1} m^{-2}. Surface primary production from 9:00 to 15:00 h was evidently inhibited by strong light intensity beyond the I_{opt}. Phytoplankton near the base of euphotic zone (30-40m) showed extremely low I_{opt} suggesting adaptation to a low light environment. Since I_{opt} represents the history of light experience of phytoplankton at a given depth, the extent of variation in I_{opt} of phytoplankton at different depth seems to be related to the intensity of turbulence mixing in the surface mixed layer. From the present study, ammonium excretion by macrozooplankton ($> 350 \mu m$) contributes from 3 to 19% of daily total nitrogen requirement by phytoplankton in this area. Calculation of upward flux of nitrate to the surface mixed layer from the lower layer, based on the simple diffusion model, approximates 3% of nitrogen requirement by phytoplankton. However, large portion of nitrogen requirement by phytoplankton remains unexplained in this area. In upwelling area near the coast, advective flux might be the major source for the nitrogen requirement by phytoplankton. This study suggests that the major nitrogen source for the phytoplankton growth might come from the pelagic regeneration by nano- and micro-sized heterotrophic plankton. Enhancement of primary production during the passage of the warm Tsushima Current is discussed in relation with nutrient dynamics and hydrographic processes in this area.

요약 : 1985년 10월의 한국 동남해역에서의 식물성 부유생물에 의한 기초 생산력은 0.7에서 2.7 gCm^{-2} d^{-1}의 범위를 갖으며 본 해역의 평균 기초 생산력은 1.3gCm^{-2}d^{-1}이었다. 표층 총 Chlorophyll 양은 0.97에서 3.59 mg chlm^{-3} 의 범위에 나타났다. 표층에서의 nano-phytoplankton ($< 20 \mu m$) 의 기초 생산력은 43 내지 97%에 이르렀다. 적정광도의 범위는 300에서 700 μE s^{-1}m^{-1} 이었다. 표층 기초 생산력은 1opt 를 벗어나는 오전 9시부터 오후 3시까지 광저하 현상을 보였다. 표광층 기저부의 식물성 부유생물은 매우 1opt 를 보이며 이는 이 층의 식물성 부유생물이 장시간 낮은 광도하에 머물러 낮은 광도에 적응하였음을 보여 준다. 1opt은 부유식물의 주변 광도에 대한 적응을 나타내주기 때문

에 여러 수층의 Iopt 의 변화정도는 해양에서의 수직와류혼합의 강도와 밀접한 관계를 나타낸다. 본 연구해역에서는 macrozooplankton에 의한 ammonium 분비에 의한 영양염 재생산은 식물부유생물의 일일 질소영양염 요구량의 3~19%를 공급하고 있으며 nitrate 의 수직확산에 의해 밀도약층 하부로 부터 공급되는 영양염은 식물성 부유생물의 일일 질소영양염 요구량의 약 3%를 공급하고 있음이 밝혀졌다. 국지적으로 용승류에 의한 하층으로 부터의 영양염 공급은 연안에 가까운 용승역에서 중요한 영양염 공급원이 될 가능성이 있다. 본 연구를 통하여 본 해역에서의 구조적 영양염 주요 공급과정은 20 μm이하의 미세 부유생물에 의한 수괴 자체내의 영양염 재순환에 의하고 있음을 암시한다. 본 연구를 통하여 대마난류의 기초 생산력은 한국 해역을 통과하는 과정에서 활발한 영양염 재순환 및 국지적인 용승류 및 연안수의 유입등과 식물성 부유생물의 촉진된 성장을 통하여 증가되고 있음이 밝혀졌다.

INTRODUCTION

Present study area is located in the southeastern sea of Korea where the warm Tsushima Current enters the Japan Sea. This area has been known as a narrow bottle neck entrace into the Japan Sea with an average depth of about 150m. Several investigators found upwelling near the coast induced by prevalent surface wind or by change of relative vorticity (An, 1974; Seung, 1974; Lee and Na, 1985). Since the warm Tsushima Current enters the Japan Sea as the major branch of the Kuroshio with low nutrients and biomass, it is of interest to determine the primary productivity and rates of nutrient supply through various biochemical and physical processes. To understand the overall processes controlling primary production, quantification of the dynamic rates of nutrient transformation and light adaptation is imperative. Among the nutrients, nitrogen is the most important in the marine environment. However, there has been no effort to identify the major nitrogenous nutrient sources and quantify their contributions to primary production in this study area.

Most of the measurements of oceanic net primary productivity have been achieved by C-14 method since Steemann Nielsen (1952). Despite the high sensitivity of the C-14 method, earlier data showed underestimation of primary production due to numerous artifacts and bias which have been extensively discussed elsewhere (Gieskes et al., 1979; Carpenter and Lively, 1980; Peterson, 1980). Recently, many of those artifacts and bias have been corrected by marine ecologists using C-14 method. Oxygen method compared with C-14 method has been suffered from the poor sensitivity, time consuming incubation, and artifacts from the aerobic bacterial growth during long time incubation, which is not fit for the measurement of low primary productivity in the ocean. Megard et al. (1985) demonstrated that oxygen method have potential problem since assimilation quotients (CO_2 assimilated/O_2 produced) are variable depending on light and nutrients. In this study, we used simulated *in situ* C-14 incubation method to measure primary production. Tophographic characteristics of this area lead us to speculate whether the primary production can be enhanced after passage of the warm Tsushima Current over this narrow bottle neck area.

It is well known that marine phytoplankton has the ability of light-shade adaptation in various ways (Falkowski, 1979). Such adaptations seem to be closely related with stability of the water column. Photosynthesis-irradiance curves at various light levels can give proper estimation of vertically integrated primary production and provide better parameters to develope the prediction model for the aquatic primary production. The purposes of this paper are (1) to determined the primary production in this area, (2) to evaluate the relationship between light-shade adaptation and water column stability and (3) to identi-

fy the major nitrogenous nutrient sources and (4) to quantify their relative contributions to phytoplankton nitrogen demand to understand the dynamic relationship between the nitrogenous nutrients and primary productivity in this area.

MATERIALS AND METHODS

Primary production

Net primary productivity was determined at 5 stations in the southeastern sea of Korea in early October 1985 (Fig 1.). Water samples were collected with Van Dorn and Niskin water sampler at three vertical depths (0, 15-20 and 30-40m) above the euphotic depth. Each depth interval sample was treated with carbon-14 and incubated *in situ* on deck at different light intensities (100, 66, 35, 21 and 2% of incident light). The recommendations of Carpenter and Lively (1980) were followed for the uptake measurement and incubation methods. C-14 bicarbonate stocks were purchased from Amersham International plc (U.K.) and working solution was freshly prepared before cruise by diluting the stocks to approximately 2 μCi ml^{-1}. B.O.D.

Fig. 1. Map showing sampling stations.

bottles (300ml) were used as the incubation vessels. During incubations, proper light attenuation was obtained by screening with black nylon mesh. Dark bottles were sprayed with flat black enamel and wrapped with black electrician's tape. For the nanoplankton primary productivity, nanoplankton were fractionated by passage of the surface sample through 20 μm Nytex mesh before incubation. All the glasswares used were acid washed and rinsed again with ambient filtered seawater before incubations. Incubations were usually performed for less than 2 hours on deck under natural illumination, since long term incubation has been known to underestimate the primary productivity by twofold in the extreme case (Gieskes et al., 1979).

Incubations were terminated by filtration of samples on Whatman GF/C glass fiber filters. Samples were filtered again with 10 ml of prefiltered ambient seawater to wash inorganic C-14 retained in wet filters. Filtered samples were then kept frozen in a dry ice box until counting their fixed C-14 activities by liquid scintillation technique. Before counting, filtered samples were acid-fumed in a desiccator with HCl for 10 minutes to strip off the inorganic C-14 absorbed in the filter. Instagel (Packard) was used as scintillation cocktail which showed high counting efficiency (more than 90%) with wet filter samples. C-14 activity of working solution and quenching of samples were determined with external standardization and corrected by automatic efficiency control of liquid scintillation counter (Packard Tricarb C).

Light intensities at depth intervals of each station were measured by LICOR underwater quantum sensor. For the calculation of depth integrated primary production, the observed extinction coefficient was used to find the depths corresponding to the light intensities of simulated *in situ* incubations. Intermittently, incident light intensities just below the surface were measured and daily insolation was measured for the
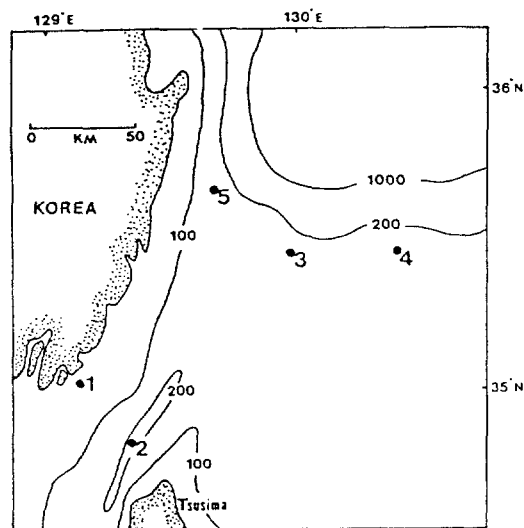
estimation of daily primary production.

Nutrients and chlorophyll

Dissolved inorganic nutrients such as ammonium, nitrate, nitrite, phosphate and silicate were spectrophotometrically measured (Perkin-Elmer 552S) following to Solorzano (1969) and

Strickland and Parsons (1972). The samples were stored in a freezer during cruise and kept frozen ($-20°C$) in the laboratory until analysis. Standards were prepared with deionized distilled water, especially for ammonium, and run before analysis of the duplicated sample Total chlorophyll concentrations were measured with an *in vivo* fluorometer (Turner Field Fluorometer)
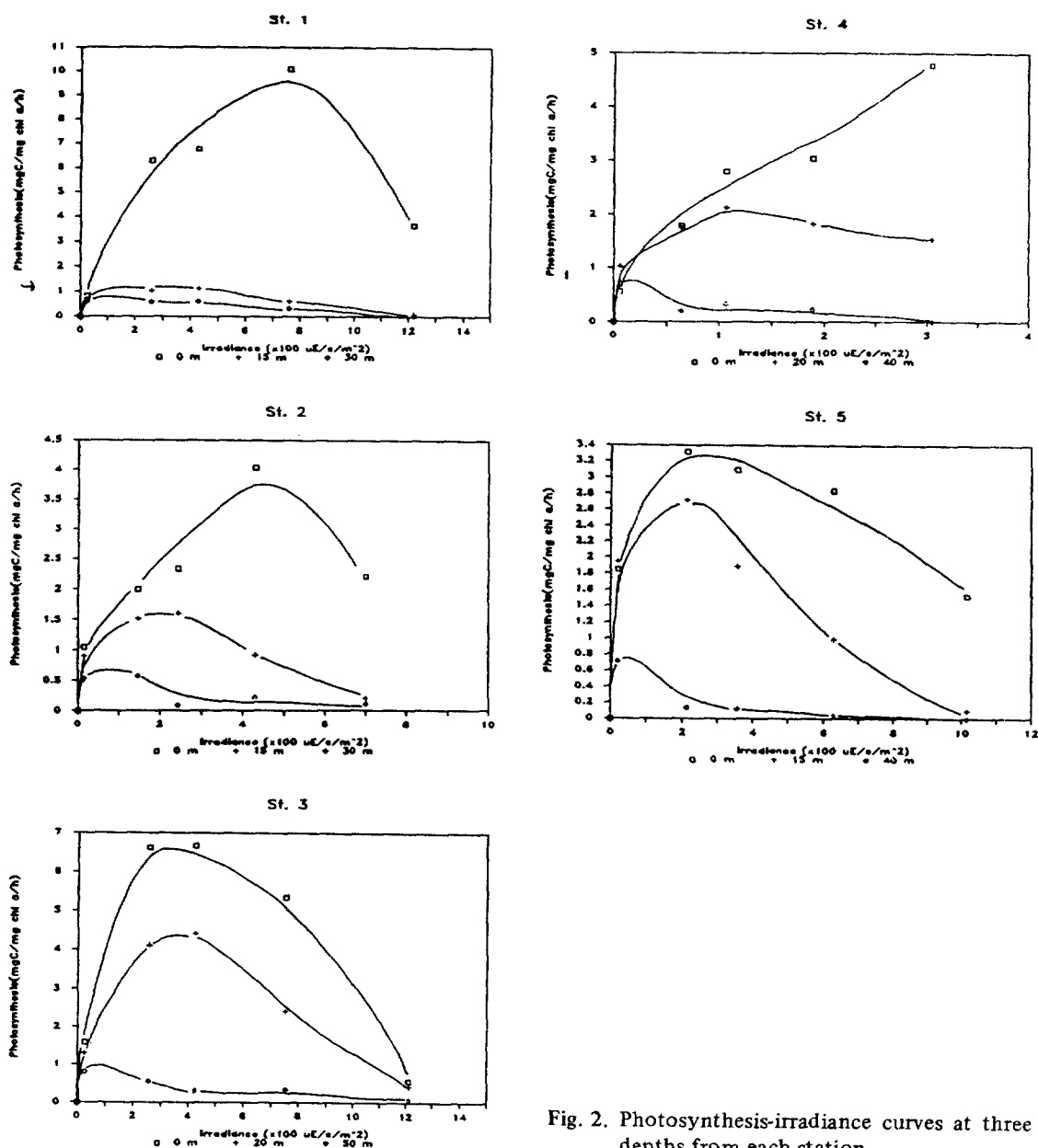
Fig. 2. Photosynthesis-irradiance curves at three depths from each station.

which has been calibrated with spectrophotometric measurement of chlorophyll before cruise. Total dissolved inorganic carbon was calculated by a single point titration of seawater (the pH method) following to Almgren et al. (1983) and Strickland and Parsons (1972). Other parameters such as pH, temperature, salinity and transparency were measured simultaneously.

RESULTS

Assimilation numbers (photosynthesis per unit chlorophyll) were usually higher at the surface than at the intermediate depth and bottom of the euphotic layer. In this area, photosynthesis-irradiance curves (Fig. 2.) obtained from three depth intervals were not identical suggesting adaptation of phytoplankton community to different light regimes. Photosynthesis of surface samples were clearly inhibited above 800 μE s^{-1} m^{-2} which corresponded around 9:00 a.m. to 3:00 p.m. Photosynthesis of intermediate depth samples showed lower optimum irradiance point (I_{opt}) than that of the surface samples ranging from 100 to 350 μE s^{-1} m^{-2} Especially photosynthesis at the bottom of the euphotic layer showed extremely
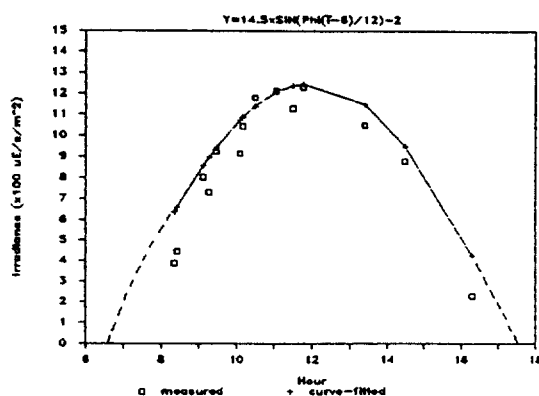

Fig. 3. Record of instantenous insolation and predicted time dependent light levels which were used for the estimation of daily integrated primary production.

low assimilation numbers and I_{opt} (around 2% of the surface light level). In most of the intermediate depth and bottom samples, I_{opt} were closely matched to the light levels of their sampling depths.

Light intensity over daytime showed a typical sinusoidal curve (Fig. 3.). Time variant surface light intensity was curve-fitted as following:

Irradiance (x 100 μE s^{-1} m^{-2})=14.5 x

sin (phi x (t − 6)/12) − 2.   (1)

Depth integrated daily primary productivity from the above calculation ranged from 0.70 at st. 1 to 2.74 gC m^{-2} h^{-1} at st. 4 averaging 1.31 gC m^{-2} h^{-1} in October in the southeastern coastal waters of Korea. Primary productivity of nanoplankton was averaged to be 66% of total primary productivity in this area.

At most of the stations, water columns were well stratified and strongly developed pycnoclines and matching nutriclines could be found near the 40-50m (Fig. 4.) Nutrients were depleted through the surface mixed layer. Nitrate and silicate increased below 50m. However, ammonium showed very low concentration throughout the water column. Nitrite showed maximum concentration near the pycnocline at most of the stations. Subsurface chlorophyll maximum layers were found near the pycnocline at sts. 2, 3 and 4 (Fig. 4.). At st. 5 near Ulgi, surface nitrate and silicate concentrations were higher than any other stations. This area has been known as upwelling region by others (An, 1974; Seung, 1974; Lee and Na, 1985). Surface chlorophyll maximum was pronounced at this station and this observation is consistent to that of Shim and Park (1984) who found surface chlorophyll maximum and matching upwelling in the southwestern sea of Korea.

Nutrient flux can be expressed as sum of advection and diffusion term as below:

$$F = K_z (dC/dz) + wC,   (2)$$

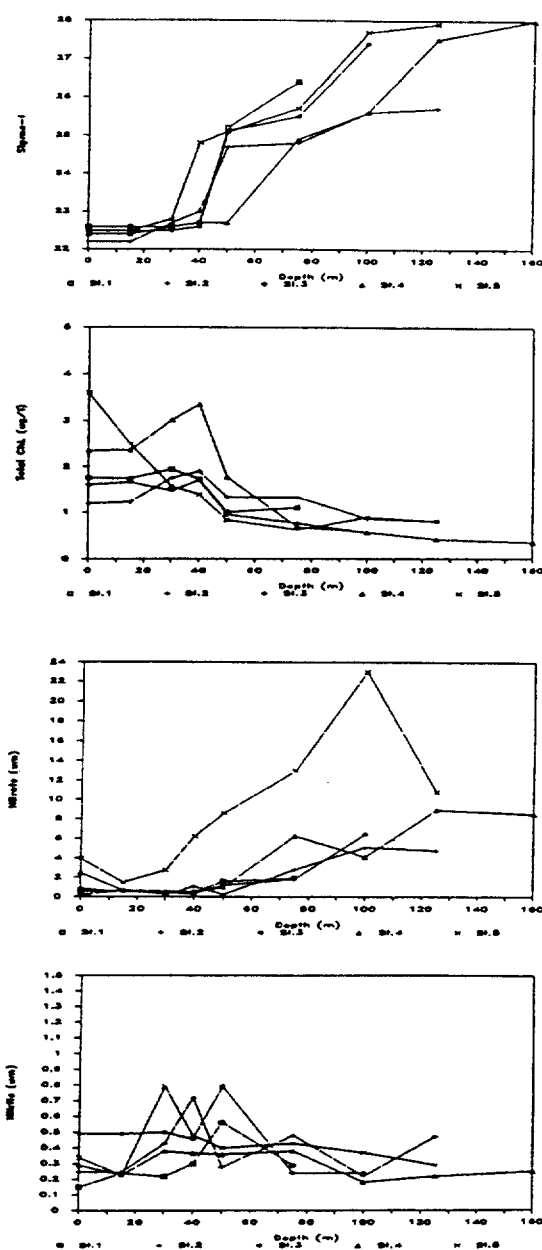where K_z is the vertical eddy diffusivities, dC/dz
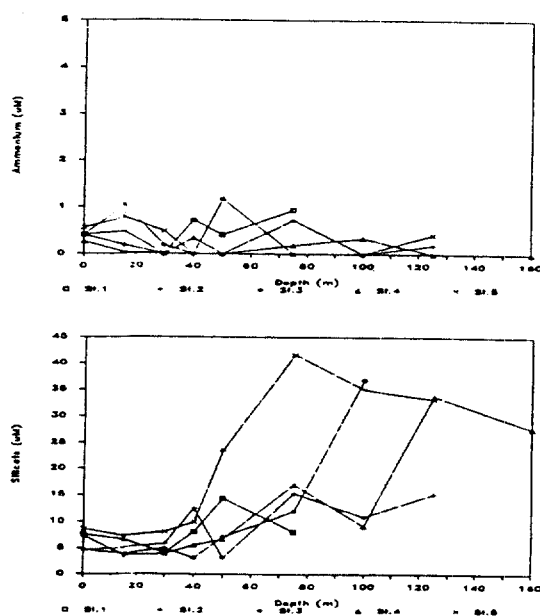
Fig. 4. Vertical distribution of density, chlorophyll and nutrients (in μM) at each station.

between the K_z and the stability ($d\delta t/dz$) in eastern tropical Pacific water as a following equation:

$$K_z \ (cm^2 \ s^{-1}) = 643.0 \ x \ E^{-1.61}, \tag{3}$$

where E is the stability of the water column.

Using this equation, K_z calculated in this area ranged from 0.13 to 0.72 which are favorably comparable with others (Table. 1.). Calculated nutrient flux by simple diffusion ranged from 5.5 to 36.2 μg at-N m^{-2} h^{-1}. Upward diffusion flux at sts. 2 and 4 where the major warm Tsushima Current flow (Lee and Na, 1985) were greater than at sts. 1 and 5 located near the coast (Table. 2.).

DISCUSSIONS

The photosynthesis-irradiance curves at various depths showed variable light adaptation of phytoplankton according to their optimum light

is the slope of nitrate concentration at the pycnocline, w is upward velocity, and C is nitrate concentration below the pycnocline.

Diffusive nutrient flux across the pycnocline can be estimated from the vertical profiles of nitrite and K_z near the pycnocline. King and Devol (1979) demonstrated a close correlation

Southeastern sea St. 2
Stratified

Chunsu Bay
Well mixed
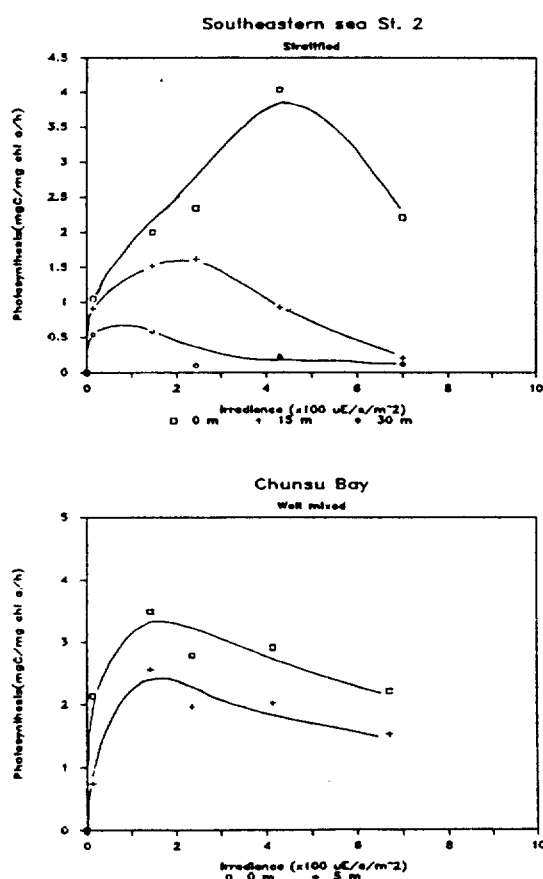
levels in the present study. Phytoplankton population in the surface layer is more light adapted than those of the lower depths. Such a variability of light adaptation might be related with the intensity of water column mixing as phytoplankters are subject to the vertical movement of water parcel. To compare the photosynthetic responses at different mixing regimes, curves were determined from the turbulent estuarine water (Chunsu Bay) of the Yellow Sea where the water column is vertically well mixed (Park and Cho, unpublished data). As shown in Fig. 5, two environments can be clearly identified into a well stratified and a vertically well mixed regime in terms of the phytoplankton adaptation to the optimum light intensity. In the turbulent

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Fig. 5. Comparison of P-I curves between stratified water column in this study area (depth 135m) and well mixed estuarine waters in the Chunsu Bay (depth 10m) in October 1985. In st. 1, 15 and 30m were equivalent to 10% and 1% of surface light level, respectively. Euphotic depth was 2.5m in the Chunsu Bay.

Table 1. Comparison of vertical eddy diffusivity (K_z) with other areas.

K_z (cm^2 s^{-1})	Areas	Sources
0.05-1.10	eastern tropical Pacific	King and Devol (1979)
0.20-0.80	north Pacific & Atlantic	Rooth & Ostlund (1972)
		Roether et al. (1970)
0.13-0.72	southeastern sea of Korea	Present study

Table 2. Calculated diffusivities and magnitudes of diffusive upward flux of nitrate at each station.

Station	K_z (cm^2 s^{-1})	Upward flux (ug at-N m^{-2} h^{-1})
1	0.27	5.5
2	0.72	26.4
3	0.67	10.2
4	0.48	36.2
5	0.13	15.7

estuarine water, it is evident that phytoplankton population below the euphotic depth ($<$ 1% of surface light) are photosynthetically active showing similar assimilation numbers, I_{opt} (near the 21% of the surface light) and a photosynthesis-irradiance curve compared with that of the surface population. It suggests that both the phytoplankters of the surface and the bottom have experienced almost the same quality and amount of light during the vigorous vertical mixing in the shallow estuarine water.

In the present study, assimilation numbers of the lower depths especially near the pycnocline where the phytoplankton cells are usually accumulated with chlorophyll maximum were much lower than those of the surface. Falkowski (1979) also found that photosynthetic capacity of the light adapted surface phytoplankton was higher than that of the shade adapted population in the chlorophyll maximum in a highly stratified water column in the New York Bight. From these facts, photosynthetic responses to the light-shade adaptation at various mixing intensity in the euphotic zone should be incorporated into the existing mathematical models for the better estimation of primary production. Probably approximated mixing rates can be calculated from knowledge of the time scale of light adaptation (Falkowski, 1979). Several investigators tried to find the relationship between the relative mixing rates and fluoroscene (Harris, 1980; Lewis et al., 1984) and others investigated the history of light adaptation of phytoplankton with *in vivo* fluoroscence yield using 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU) (Uehlinger, 1985; de Roos and Flik, 1985). However, parameterization of the photosynthetic responses to various hydrological mixing processes might still require more collaboration between biological oceanographers and physical oceanographers as suggested by Marra (1979).

Primary productivity measurements in the coastal waters of southeastern sea of Korea in October revealed a two layered system in the euphotic zone as proposed and shown by Dugdale (1967) and Eppley et al. (1973) in the North Pacific Ocean. Such a two layered system composed of a upper nutrient limited layer and a lower light limited but nutrient abundant layer near the pycnocline could be found where strong stratification is developed by a permanent thermocline or where a layer of a warm current overlies a cold bottom water as in this area. Primary production in the surface layer largely depend on ammonium which is rapidly recycled by zooplankton and heterotrophic microorganisms. In the bottom layer of the euphotic zone which coincides with the nutricline in this area, primary production is mostly based on the nitrate from the nutrient rich bottom water. Low assimilation numbers measured at the bottom of euphotic depth in this area can be resulted from nitrate based photosynthesis and shade adaptation at a low light intensity. It is generally known that nitrate based phytoplankton cultures show low assimilation quotients (CO_2 assimilated/O_2 produced) especially at low light meanwhile ammonium riched phytoplankton cultures show high and constant assimilation quotients at various light levels (Megard et al, 1985). As nitrate based phytoplankton should use some fraction of photochemically reduced energy for the *in vivo* reduction of nitrate during photosynthesis, phytoplankton population near the pycnocline and/or nutricline might show low assimilation numbers. By the same reason, assimilation number in the upwelling region where the phytoplankton growth is largely based on nitrate might be generally lower than that in the surface mixed layer of stratified water column (see st. 5 in Fig. 3.). Nitrite maximum found in this area near the pycnocline and/or nutricline can be partly resulted by the extracellular release of reduced nitrite during photosynthetic nitrate reduction and by bacterial nitrification (Megard et al., 1985).

It is evident that primary production is en-

hanced after passing the Korea Strait from 0.96 (average of sts. 1 and 2) to 1.55 gC m^{-2} d^{-1} (average of sts. 3, 4 and 5). It suggests that changes of nutrient dynamics occurred during the warm Tsushima Current passing through this bottle neck area. Despite of high primary production in the surface mixed layer, ambient inorganic nitrogenous nutrient concentration might not be enough to supply the nitrogen demand by phytoplankton. Daily nitrogen requirement by phytoplankton in this area amounts about 15.6 mg at-N m^{-2} d^{-1} assuming C/N ratio to be about 7. Turnover times of inorganic nitrogen which were calculated by dividing ambient nitrogen concentrations by the rates of nitrogen requiremeht by phytoplankton ranged from 1.8 (st. 4) to 6.9 (st. 5 near Ulgi) days and averaged to be 3.7 days in this area. Without continuous nitrogen supplies from various sources, nutrients in the surface mixed layer would be depleted within a few days by the phytoplankton assimilation resulting in a large decrease of primary production. Major nitrogenous nutrient sources in this area (mean depth of about 150m) might be biochemical regeneration, flux through advection and diffusion processes, terrestrial inputs and pelagic nitrogen fixation etc. Ammonium excretion by zooplankton has been known to be

one of the major nitrogen sources for the primary production (Harris, 1959; Smith, 1978; Vargo, 1979). Nitrogen regeneration by macrozooplankton ($>$ 350 um) measured in this area was averaged to be 2.05 mg at-N m^{-2} d^{-1} (Park, 1986). It accounts about 13% of nitrogen requirement by phytoplankton in this area. Diffusive nutrient flux calculated in this study was averaged to be 0.45 mg at-N m^{-1} d^{-1}. This supports only 2.9% of nitrogen requirement by phytoplankton. As shown in Table 3, nitrogen requirement by phytoplankton is largely unbalanced by the sum of diffusive flux and nitrogen regeneration by macrozooplankton. Quantified data on the precipitation and the terrestrial inputs in this area are not available at present. Probably, river discharge of nitrogenous nutrient from the Nakdong estuary might be important near the st. 1. However, these might not be the major sources in this overall system since these inputs amounted less than 10% even in a shallow estuarine waters (Nixon and Pilson, 1983; Carpenter et al., 1985). According to the estimation made by Carpenter (1983), nitrogen fixation by *Trichodesmium* contributes less than 1% of nitrogen demand for primary production.

Several investigators reported appearance of cold water at the surface and discussed upwelling

Table 3. Primary production and contributions by macrozoplankton excretion and upward diffusion to nitrogen requirement by phytoplankton (NRP) at each station. PP represents primary productivity and NRP is calculated assuming C/N ratio to be 7.

Station	PP (gC/m^{-2} d^{-1})	(% nano PP)	NRP (C/N=7)	Macrozoopl. excretion (mg at N/m^{-2}/d^{-1})	Upward Diffusion
1	0.70	43	8.3	1.23 (14.8%)	0.13 (1.6%)
2	1.22	97	14.5	NM	0.63 (4.3%)
3	0.73	47	8.7	NM	0.24 (2.8%)
4	2.74	61	32.6	4.47 (13.7%)	0.87 (2.7%)
5	1.17	71	13.9	0.44 (3.2%)	0.38 (2.7%)
Average	1.31	66	15.6	2.05 (13.1%)	0.45 (2.9%)

process near the coast in the present study area (An, 1974; Seung, 1974; Lee and Na, 1985; Shim et al., 1985). New nitrogen input by localized upwelling process near the coast (sts. 1 and 5) can be approximated from the equation (2) considering only the last term; $F_{upwelling} = w \cdot C$. However, there is no available data on the magnitude of upwelling velocity (w) in the study area. Codispoti (1983) summarized magnitudes of the vertical velocities in the coastal upwelling region to be on the order of 10^{-3} cm s^{-1} and in the open ocean induced by the wind stress to be on the oder of $10^{-3} - 10^{-4}$ cm s^{-1}. Using these numbers (10^{-2} and 10^{-4} cm s^{-1}), lower and upper limits of contribution by the advective flux ($F_{upwelling}$) to the nitrogen requirement by phytoplankton can be approximated 2-17% at st. 1 near Pusan and 6-50% at st. 5 near Ulgi. Advective flux is presumably the major nutrient source in this localized upwelling area along the coastline especially near Ulgi. However, large fraction of nitrogen requirement for the primary production is still remaining unexplained. The most responsible nutrient source must exist ubiquitous in the water column as phytoplankton should continuousely assimilate this large fraction of nutrients from the sorrounding seawater to sustain primary production for more than a time scale of several days,. Recently, smaller zooplankton, mostly composed of protozoa and heterotrophic flagellates, are known to contribute 3 times greater than macrozooplankton (Glibert, 1982; Park et al., 1986). Taking into consideration of the above, nitrogen regeneration by nanoplankton and microzooplankton is presumably the most important nitrogen source contributing more than 40% in this area.

In conclusion, nitrogen requirement by phytoplankton in this area can be virtually met by the sum of macrozooplankton regeneration (13%), diffusive upward flux (3%), regeneration by smaller heterotrophic plankton (> 40%), advective upward flux (c.a. 30%) and remaining other sources such as advective transport from neighbouring waters where the last three terms are tentatively approximated. Present studies on primary production and nutrient dynamics in this area are of special interests for the future researches to quantify the magnitude of transportation of nutrients and particulated organic matter produced in the southeatern sea of Korea into the Japan Sea through the bottle neck entrance. In addition to upwelling, tophographically induced meandering current and piched-off cyclonic cold eddies caused by the changes of relative vorticity presumably facilitate the redistribution of nutrients and transportation of newly produced particulated organic matter into the surface of the Japan Sea through the warm Tsushima Current. Overall primary production in this area seems to be enhanced by rapid nutrient recycling and partly by the advective input of nutrients which has been transported by the cold undercurrent from the Japan Sea along the southeastern coast of Korea.

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