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The Application of Quantum Yield of Nitrate Uptake to Estimate New Production in Well-Mixed Waters of the Yellow Sea: A Preliminary Result

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New production (NP) values in well-mixed waters of the Yellow Sea were estimated using two different methods and were compared with each other; one is from the quantum yield model of nitrate uptake and chlorophyll *a*-specific light absorption coefficient, and the other is from a traditional ^{15}N-labelled stable isotope uptake technique. The quantum yields of nitrate uptake were highly variable, ranging from 0.0001 to 0.04 mol NO_3^- Ein^{-1}, and the small values in this study might have resulted from either the partitioning into nitrate uptake of little portions of light energy absorbed by phytoplankton or that phytoplankton may predominantly utilize other N sources (e.g. ammonium and/or urea) than nitrate. The estimates (0.54–8.47 nM h^{-1}) of NP from the quantum yield model correlated well ($r^2 = 0.67$, $p<0.1$) with those (0.01–4.93 nM h^{-1}) obtained using the $^{15}NO_3$ uptake technique. To improve the ability of estimating NP values using this model in the Yellow Sea, more data need to be accumulated in the future over a variety of time and space scales.

Key words: New production, Quantum yield of nitrate uptake, The Yellow Sea

INTRODUCTION

New production (NP) is the portion of primary production supported by newly available nitrogen forms (mainly, nitrate), whereas regenerated production is supported by nutrients recycled (mainly, ammonium and urea) within the euphotic zone (Dugdale and Goering, 1967; Eppley and Peterson, 1979). The concept of NP is central for linking the relationships among nitrogenous nutrients, phytoplankton production and export production in the biogeochemical elemental cycles in the sea. A large number of methods have been suggested for estimating NP, each with its own methodological limitation and applicable time and space scales (Eppley, 1989; Platt *et al.*, 1992). Of the methods, stable isotope ^{15}N labelled nitrate-based method has been widely employed for estimating NP at a variety of oceanographic areas over the last three decades since its introduction by Dugdale and Goering (1967). Despite the most direct and relatively unambiguous measurement, however, the stable isotope method is not only time-consuming and laborious but also requires special facility, thereby limiting its extensive usefulness. Further, additional problems associated with the bottle incubation techniques have been recognized (Eppley, 1980; Dugdale and Wilkerson, 1986). In these contexts, rapid and non-intrusive, alternative approaches for the estimation of NP need to be developed. Much greater efforts have so far been made on the estimation of primary production, e.g. from the satellite images (Platt and Sathyendranath, 1988; Sathyendranath *et al.*, 1989; Morel and André, 1991; Lee *et al.* 1996; Behrenfeld and Falkowski, 1997) and from bio-optical models based on light-pigment relation (Bidigare *et al.*, 1992 and references therein) or fluorescence (Kiefer *et al.*, 1989; Kiefer and Reynolds, 1992; Falkowski and Kolber, 1993). By comparison, the rapid and non-intrusive methods for the estimation of NP are relatively limited and are mostly based on the relationship between satellite-derived sea surface temperature and nitrate concentrations in certain favorable conditions

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such as upwelling areas and tidal front region (Dugdale *et al.*, 1989; Sathyendranath *et al.*, 1991; Morin *et al.*, 1993; Kudela and Dugdale, 1996).

The assimilatory process of nitrate by phytoplankton is the most reducing-energy dependent reaction following the carbon fixation (Syrett, 1981), and is usually light-dependent process (MacIsaac and Dugdale, 1972; Fisher *et al.*, 1982), indicating that nitrate uptake can be described in terms of irradiance (e.g. by the Michaelis-Menten rectangular hyperbola, MacIsaac and Dugdale, 1972; Kanda *et al.*, 1989; Cochlan *et al.*, 1991; Kudela *et al.*, 1997), similar to photosynthesis vs. irradiance (P-I) relationship for carbon uptake. In such case, nitrate uptake-irradiance parameters (i.e. the light-saturated uptake rate of nitrate, the light-limited slope of the curve, and the half-saturation irradiance) and further quantum yield of nitrate uptake (ϕ_{NO3}; mole NO_3^- reduced per mole photons absorbed) could be derived in a similar manner to P-I parameters (Healey, 1980; Kudela *et al.*, 1997). In this study, we report the preliminary result to estimate NP in well-mixed waters of the Yellow Sea using bio-optical data such as quantum yield of nitrate uptake and chlorophyll *a*-specific light absorption coefficient.

MATERIALS AND METHODS

Study area and sample collection

This study was performed on June and November 1997 at coastal (station A) and offshore (station B) stations in the Yellow Sea, respectively (Fig. 1). For measurements of phytoplankton variables and nitrate uptake rates, seawater samples were collected with 5 or 10 l Niskin bottles for depths corresponding to 100, 15, and 1% surface light penetration depths within the euphotic zone. The euphotic depth was determined by multiplying the Secchi disc depth by 2.7.

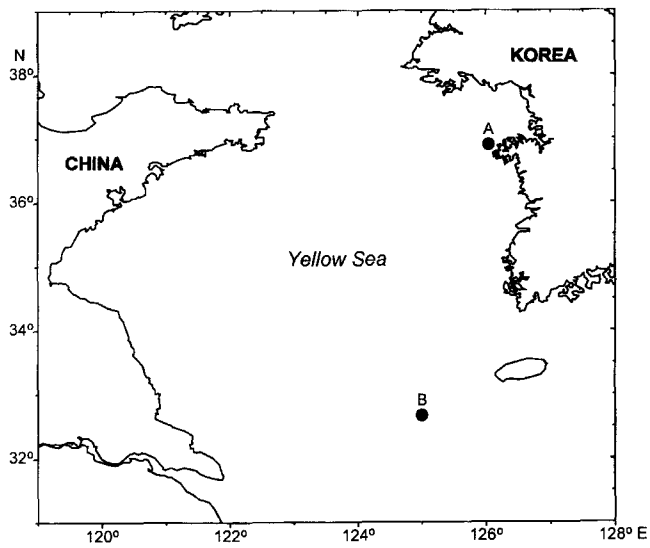

Fig. 1. Map of the study area showing the sampling stations during this study. The quantum yields of nitrate uptake were determined on June and November 1997 at stations A and B, respectively.

Measurements of environmental and phytoplankton variables

Water temperature and salinity were measured with a CTD system (SBE-911) mounted on a rosette sampler. Chlorophyll *a* (Chl *a*) concentrations were measured by a spectrophotometric method (Parsons *et al.*, 1984) after filtration (<100 mm Hg) onto Whatman GF/F filters. Chl *a*-specific light absorption coefficients of phytoplankton (a_{ph}^*, m^2 mg Chl a^{-1}) were estimated from Chl *a* concentration using the empirical equation suggested by Bricaud *et al.* (1995). Samples for analysis of nitrate concentration were filtered through Whatman GF/F filters and the filtrates were stored frozen (−20°C) and analyzed later with a Bran+Luebbe Autoanalyzer (Model TRAACS 2000) by the method of Parsons *et al.* (1984). Surface solar irradiance was measured over 10 min intervals using an LI-190SA quantum sensor and recorded with an LI-1000 DataLogger (LI-COR, Inc.). Downward scalar irradiance was measured using an INF-300 (Biospherical Instruments Inc.).

Measurement of nitrate uptake rate

Nitrate uptake rates (new production, NP) were measured using the stable isotope ^{15}N as a tracer (Dugdale and Wilkerson, 1986). Seawater samples were transferred into 250 ml polycarbonate bottles covered with perforated nickel screens (Stork Veco, Bedford, Massachusetts) to simulate *in situ* light conditions. Samples were inoculated with $K^{15}NO_3$ (99.3 atom% ^{15}N) at the final tracer addition of 1 μM and incubated for 4 h in an on-deck incubator cooled with continuously flowing surface seawater. After incubation, the samples were filtered (<100 mm Hg) onto pre-combusted (4 h at 450°C) Whatman GF/F filters (diameter 25 mm) and stored dry at 60°C until analysis of $^{15}N/^{14}N$ ratio with an Europa Roboprep-Tracermass GC-MS (Owens, 1988). Particulate nitrogen-specific (V) and absolute (ρ) uptake rates were calculated according to Dugdale and Wilkerson (1986). Chl *a*-specific nitrate uptake rate was calculated by

dividing ρ by the Chl *a* concentration and designated as V^{Chl}. The effects on calculated uptake rates of adding excess ^{15}N-tracers to some samples were further considered and corrected according to Eppley *et al.* (1977).

Parameters of nitrate uptake-irradiance curve and the estimation of quantum yield of nitrate uptake

The uptake rate vs. irradiance relationship for nitrate was obtained by short-term (4 h) shipboard ^{15}N-labelled nitrate incubations of surface water samples following the protocol described above. The 7 different light levels were produced by using the perforated nickel screens, with a dark bottle covered with black tape. Nitrate uptake vs. irradiance data were fitted into the modified Michaelis-Menten type model including dark N uptake (Cochlan *et al.*, 1991b) using a computerized, iterative, non-linear least-squares technique (SigmaPlot for windows, ver 6.0, SPSS Inc.). Curve fitting procedures provided estimates of V_{max}^{Chl} (the light-saturated rate of nitrate uptake) and K_{LT} (an estimate of the minimum irradiance required to light-saturate rate of nitrate uptake). The α values (the light-limited slope of nitrate uptake) were derived from V_{max}^{Chl} / K_{LT}.

Maximum quantum yield ($\phi_{NO3\text{-}max}$) for nitrate uptake was estimated by dividing the a by the a_{ph}^{*}. The operational quantum yield at depth (z) was estimated as follows;

$$\phi_{NO3}(z) = \phi_{NO3\text{-}max} \cdot \left(\frac{K_{LT}}{Q_{PAR}(z)}\right) \cdot \tanh\left(\frac{Q_{PAR}(z)}{K_{LT}}\right) \quad (1)$$

where $Q_{PAR}(z)$ is downward scalar irradiance at depth, z. This equation is originally an absorption-based production model for estimating the quantum yield of photosynthesis (ϕ_c) at depth (Bidigare *et al.*, 1992), but in this study the ϕ_c was substituted for ϕ_{NO3}. Assuming that the maximum quantum yield was constant within the euphotic zone during this study, we used the surface values at each station to estimate the operational quantum yield at depth. New production values (ρNO_3) were then estimated as the product of ϕ_{NO3} and total quanta absorbed by phytoplankton (AQ_{ph});

$$\rho NO_3 = \phi_{NO3} \times AQ_{ph} \quad (2)$$

RESULTS AND DISCUSSION

Physico-chemical and bio-optical values at two stations (Stns) are presented in Table 1. Water temperature and salinity were homogeneous throughout the water column at both stations during this study (data not shown), and water temperature within the euphotic zone ranged from 14.8°C at Stn A in June 1997 to 20.2°C at Stn B in November 1997. Nitrate concentrations within the euphotic zone were as high as 3.4 to 7.5 μM. Chl *a* concentrations within the euphotic zone varied by 2 orders of magnitude, with maximum and minimum values of 1.48 mg m^{-3} at the base of the euphotic zone at Stn A and 0.07 mg m^{-3} at the surface at Stn B. The a_{ph}^{*} values ranged from 0.016 to 0.037 m^2 mg Chl a^{-1} and were ca. 2-fold greater at Stn B than at Stn A. The ρ_{NO3} values (determined with $^{15}NO_3$ uptake) ranged from 0.01 (at the bases of the euphotic zone of both stations) to 4.93 nM h^{-1} (at the surface of Stn A) and tended to decrease with depth, strongly indicating the light-dependence of nitrate uptake in the study area.

Table 1. Physico-chemical and bio-optical values at two stations where quantum yield of nitrate uptake was measured during this study in the Yellow Sea.

Date/Stn	Depth (m)	Temp. (°C)	$[NO_3^-]$ (μM)	Chl *a* (mg m^{-3})	$Q_{PAR}(z)^{\dagger}$ (μEin m^{-2} s^{-1})	a_{ph}^{*} ‡ (m^2 mg Chl a^{-1})	AQ_{ph} ¶ (μEin m^{-3} s^{-1})	$\phi_{NO3}(z)$ ζ (mol NO_3^- mol Ein^{-1})
Jun. 1997/A	0	14.8	4.76	0.89	363.66	0.0182	5.891	0.0001
	10	14.8	7.46	1.24	88.60	0.0167	1.835	0.0005
	20	14.8	4.45	1.48	14.85	0.0159	0.349	0.0008
Nov. 1997/B	0	20.2	3.44	0.07	42.61	0.0370	0.110	0.0213
	8	20.2	3.74	0.17	0.76	0.0287	0.004	0.0404

†Downward scalar irradiance between 400 and 700 nm at depth.
‡Chl *a*-specific absorption coefficient of phytoplankton, calculated from Chl *a* concentration according to Bricaud *et al.* (1995).
¶ Total quanta absorbed by phytoplankton at depth.
ζQuantum yields of nitrate uptake at depth were estimated using an absorption-based production model developed by Bidigare *et al.* (1992), assuming that both maximum quantum yield of nitrate uptake and K_{LT} (an estimate of the minimum irradiance required to light-saturated rate of nitrate uptake) were constant with depth.

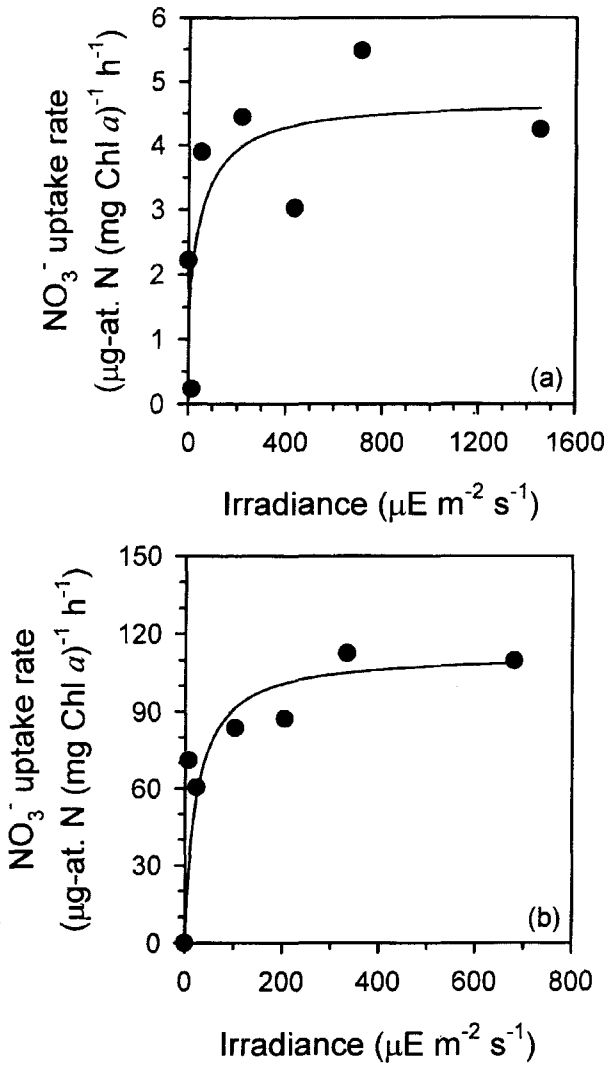

Fig. 2. Nitrate uptake as a function of irradiance at the surface samples in (a) June and (b) November 1997 in the Yellow Sea. The curved plots were fitted directly to the Michaelis-Menten equation modified for dark uptake, and kinetic parameters of V_{max}, K_{LT}, and α were derived (see text). (a) For data in June, V_{max}, K_{LT}, and α values were 3.4 μg-at. N (mg Chl *a*)$^{-1}$ h^{-1}, 61.6 μEin m^{-2} s^{-1}, and 0.54×10^{-4} mg-at. N (mg Chl *a*)$^{-1}$ h^{-1} (μEin m^{-2} s^{-1})$^{-1}$, respectively. (b) For data in November, V_{max}, K_{LT}, and α values were 112.5 μg-at. N (mg Chl *a*)$^{-1}$ h^{-1}, 23.8 μEin m^{-2} s^{-1}, and 4.73×10^{-3} mg-at. N (mg Chl *a*)$^{-1}$ h^{-1} (μEin m^{-2} s^{-1})$^{-1}$, respectively.

Nitrate uptake vs. irradiance data measured with surface samples at two stations are plotted in Fig. 2. The kinetic parameters of nitrate uptake showed the large variations between two stations; the V_{max}^{Chl} value (112.5 μg-at. N mg Chl *a*$^{-1}$ h^{-1}) at Stn B was 34-fold greater than that (3.4 μg-at. N mg Chl *a*$^{-1}$ h^{-1}) at Stn A. The α value (0.47×10^{-2} mg-at. N mg Chl *a*$^{-1}$ h^{-1} (μEin m^{-2} s^{-1})$^{-1}$) at Stn B was two orders of magnitude greater than that (0.54×10^{-4} mg-at. N mg Chl *a*$^{-1}$ h^{-1} (μEin m^{-2} s^{-1})$^{-1}$) at Stn A, indicating that nitrate uptake by phytoplankton at Stn B was more sensitive to low light intensity than at Stn A. The $\phi_{NO3\text{-}max}$ values were also highly variable and were 0.0008 and 0.04 mol NO_3^- Ein^{-1} at Stns A and B, respectively. The ϕ_{NO3} values ranged from 0.0001 (at the surface at Stn A) to 0.04 mol NO_3^- Ein^{-1} (near the base of the euphotic zone at Stn B) and were two orders of magnitude greater at Stn B than at Stn A (Table 1). There are at least two possible explanations for this large difference of ϕ_{NO3} values between two stations: (1) the partitioning into nitrate uptake of light energy absorbed by phytoplankton might be much smaller at Stn A than at Stn B, (2) phytoplankton may predominantly utilize other N sources (e.g. ammonium and/or urea) than nitrate at Stn A than at Stn B.

There are a few data in the marine environments to which the ϕ_{NO3} or $\phi_{NO3\text{-}max}$ values from this study can be compared. Only Kudela and Chavez (1997), within an upwelling plume in the Monterey Bay, California, reported the similar ϕ_{NO3} values (0.002–0.073 mol NO_3^- Ein^{-1}) to those from this study. Compared to the theoretical upper limit of quantum yield of photosynthesis (0.08 mol C Ein^{-1}; Sakshaug, 1993; Falkowski and Raven, 1997), our ϕ_{NO3} values are smaller, suggesting that the estimated values during this study are reasonable. Using the obtained ϕ_{NO3} values, we further estimated the ρ_{NO3} values ranging from 0.54 to 8.47 nM h^{-1} (Fig. 3). Despite the fact that surface kinetic parameters ($\phi_{NO3\text{-}max}$ and K_{LT}) were used for estimating ϕ_{NO3} values at depths during this study, the estimated ρ_{NO3} values correlated well ($r^2 = 0.67$, $p<0.1$) with those obtained using the $^{15}NO_3$ uptake techniques (Fig. 3, inset). Further, when data from this study were plotted and analyzed together with those obtained by Kudela and Chavez (1997), the estimated ρ_{NO3} values were also significantly correlated ($r^2 = 0.73$) to those measured with the $^{15}NO_3$ uptake techniques.

The previous studies for rapid and non-intrusive estimation of NP are basically based on the close relationships among the satellite-derived sea-surface temperature, nitrate concentration, *f*-ratio (the fraction of NP to total primary production), and primary production (Harrison *et al.*, 1987; Dugdale *et al.*, 1989; Horne *et al.*, 1989; Sathyendranath *et al.*, 1991; Morin *et al.*, 1993; Kudela and Dugdale, 1996). However, the poor relationships among them have often been reported in various oceanographic areas, including the Yellow Sea (Park, 1999), and in these areas the alternative methods need to be considered.

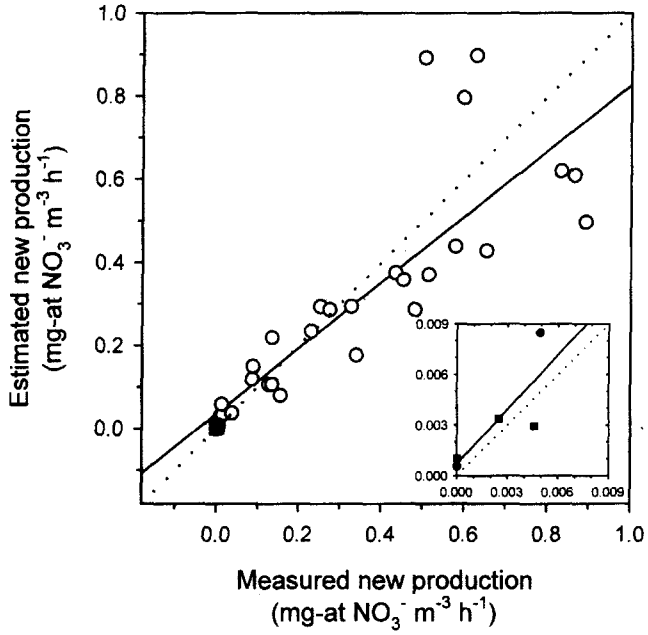

Fig. 3. Relationship between the measured and estimated new production values in the Yellow Sea during this study. The measured values were obtained using $K^{15}NO_3$ with discrete water samples within the euphotic zone; the estimated values were calculated using a quantum yield model (see text). Data are plotted together with those (open circles) from Kudela and Chavez (1997). The solid line represents a least-squares linear regression line for the pooled data. The regression line is; $y = 0.035+0.79x$ ($r^2=0.73$). The inset shows data only from the Yellow Sea during this study; closed squares and circles indicate data in June and November 1997, respectively. For only data from the Yellow Sea, the regression line is; $y=6.75\times10^{-4}+1.08x$ ($r^2=0.67$). All dotted lines represent the 1:1 correspondence.

One of the advantages for the quantum yield model is to take into account depth-dependent variations in phytoplankton properties (e.g. biomass), which particularly in the stratified waters could be poorly resolved from the satellite ocean color data limited by upper few meters of water column (Bidigare *et al.* 1992). But, the application of the quantum yield model to the field could be limited by a variety of factors, e.g. the enhanced dark NO_3^- uptake (Cochlan *et al.*, 1991; Park *et al.*, 1997) and the inhibition of nitrate uptake by ammonium (Dortch, 1990). On the other hand, to be more useful as an alternate method for estimating NP, the variability in ϕ_{NO3} value in the model should be predicted empirically by major physical, optical, and environmental parameters (e.g. temperature, light, nitrate concentration) routinely measured at sea. To improve the ability to estimate NP values using this model in the Yellow Sea, more data need to be accumulated in the future over various time and space scales.

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