Uptake Kinetics of Phytoplankton in presence of Nutrient Interaction: Lessons from JGOFS Experiments in the Indian Ocean

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Summary: Analysis of experiments of McCarthy et al (1999) on the inhibitory effect of ammonium on nitrate uptake by phytoplankton suggests that the uptake kinetics has the properties of *similarity* and *hyperbolicity*. A formulation based on these two properties leads to a recently proposed kinetic relation for the interaction of nitrate and ammonium. It represents the observations of McCarthy et al (1999) more accurately than several earlier relations. The consequences of using three uptake relations with kinetic parameters determined on the basis of these experiments are examined by 3D simulations of a biological-physical model in the North Indian Ocean using climatological forcing. The spatial variations of the annual average primary productivity for the three uptake relations are compared with SeaWiFS data, and the distribution for the relation based on similarity and hyperbolicity is found to compare most favourably.

Similarity in Multi-nutrient Kinetics:

We write the 2-nutrient kinetic relation as:

$$r_i = Pf(I)v_i(N_1, N_2) \qquad (1)$$

Notation is given in Table 2. If v_i can be expressed as a product of a function of N_1 and a function of N_2, we say that the kinetic relation for i th nutrient has the property of **similarity**. Then we may write

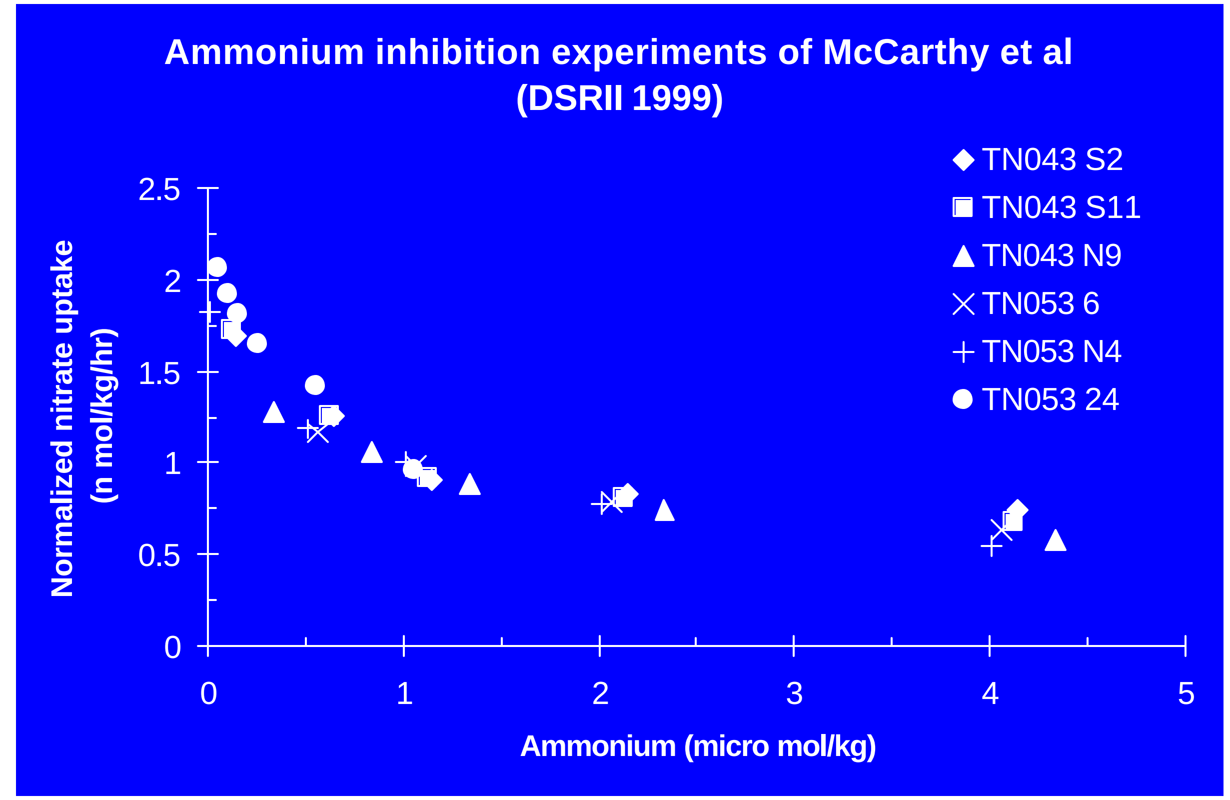
$$v_i = g_i(N_1)h_i(N_2) \qquad (2)$$

In that case, in an experiment in which *only* nitrate N_1 is varied, the uptake normalized with respect to a reference value $r_i^{\,r}$ for $N_1^{\,r}$ is given by

$$\frac{r_i}{r_i^{\,r}} = \frac{g_i(N_1)}{g_i(N_1^{\,r})} \qquad (3)$$

The above conclusion implies that as *the normalized uptake depends only on* N_1*,* the results of several such experiments on the same phytoplankton population would collapse on to a single curve. A similar conclusion can also be drawn for an experiment in which ammonium concentration N_2 is varied.

Experiments by McCarthy et al (1999) support this hypothesis (See Fig. on the left.).



Hyperbolicity in Multi-nutrient Kinetics:

If v_i has the following form

$$v_i = \frac{\mathrm{A} + \mathrm{B}N_j}{\mathrm{C} + N_j} \qquad (4)$$

for some coefficients A, B and C, which do not depend on N_j, the relation is said to be **hyperbolic with respect to N_j**. Then the curve of uptake or normalized uptake of i th nutrient an experiment, in which N_j alone is varied, is a rectangular hyperbola with N_j = -C and v_i = B as asymptotes. The main justification for this property comes from enzyme kinetics. The relation of Yajnik and Sharada (2002) is based on both these properties (Table 1).

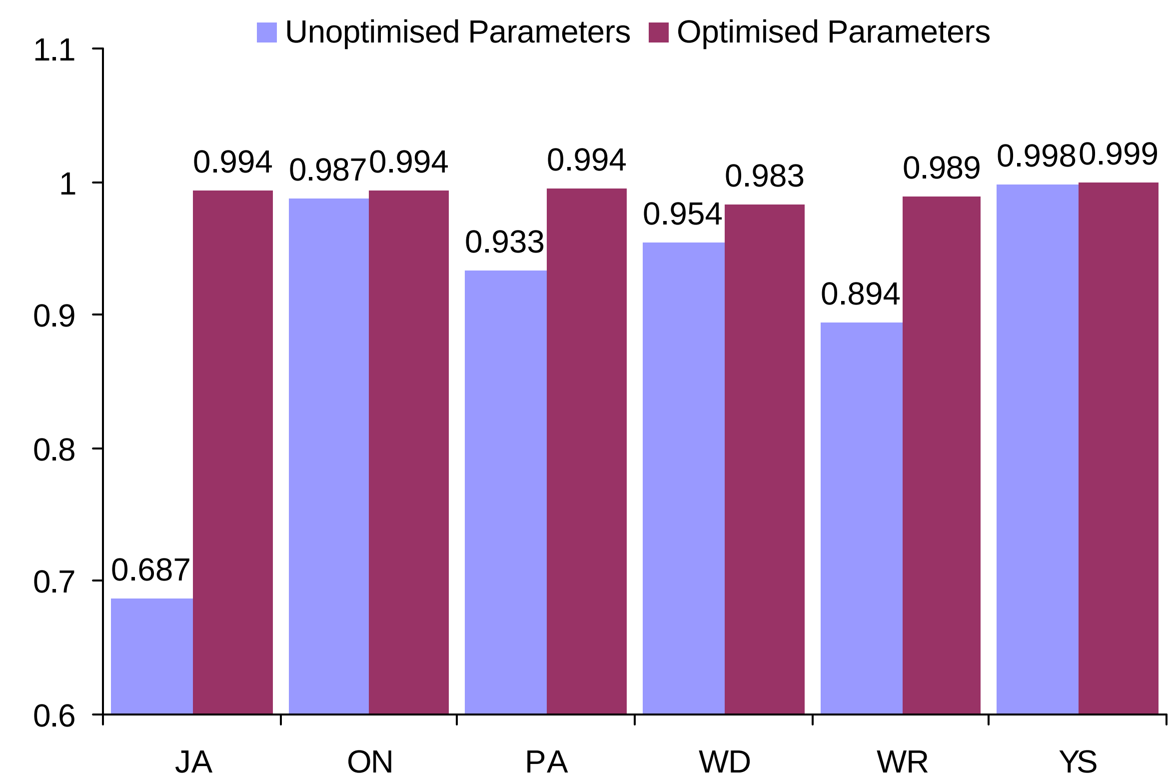
Table 1 Kinetic relations proposed by various authors

Relation	Uptake of nitrate for for optimal radiance, ν_1	Uptake of ammonium for optimal radiance, ν_2
Wroblewski (WR)	$\frac{V_1 N_1}{k_1 + N_1} e^{-\gamma N_2}$	$\frac{V_2 N_2}{k_2 + N_2}$
O'Neill et al (ON)	$\frac{k_2 V_1 N_1}{k_1 k_2 + k_2 N_1 + k_1 N_2}$	$\frac{k_1 V_2 N_2}{k_1 k_2 + k_2 N_1 + k_1 N_2}$
Walsh & Dugdale (WD)	$\frac{V_1 N_1}{k_1 + N_1}(1 - aN_2)$, if $N_2 \le 1/a$; 0, if $N_2 > 1/a$.	$\frac{V_2 N_2}{k_2 + N_2}$
Jamart et al (JA)	$\frac{s_1 V_1 N}{k(0.2 + 0.16N) + N}$, if $N \le 5$; $\frac{s_1 V_1 N}{k + N}$, if $N > 5$.	$\frac{s_2 V_2 N}{k(0.2 + 0.16N) + N}$, if $N \le 5$; $\frac{s_2 V_2 N}{k + N}$, if $N > 5$.
Parker (PA)	$\frac{V_1 N_1}{k_1 + N_1} \frac{k_2}{k_2 + N_2}$	$\frac{V_2 N_2}{k_2 + N_2}$
Yajnik & Sharada (YS)	$\frac{V_1 N_1}{k_1 + N_1} \frac{1 + aN_2}{1 + bN_2}$	$\frac{V_2 N_2}{k_2 + N_2}$

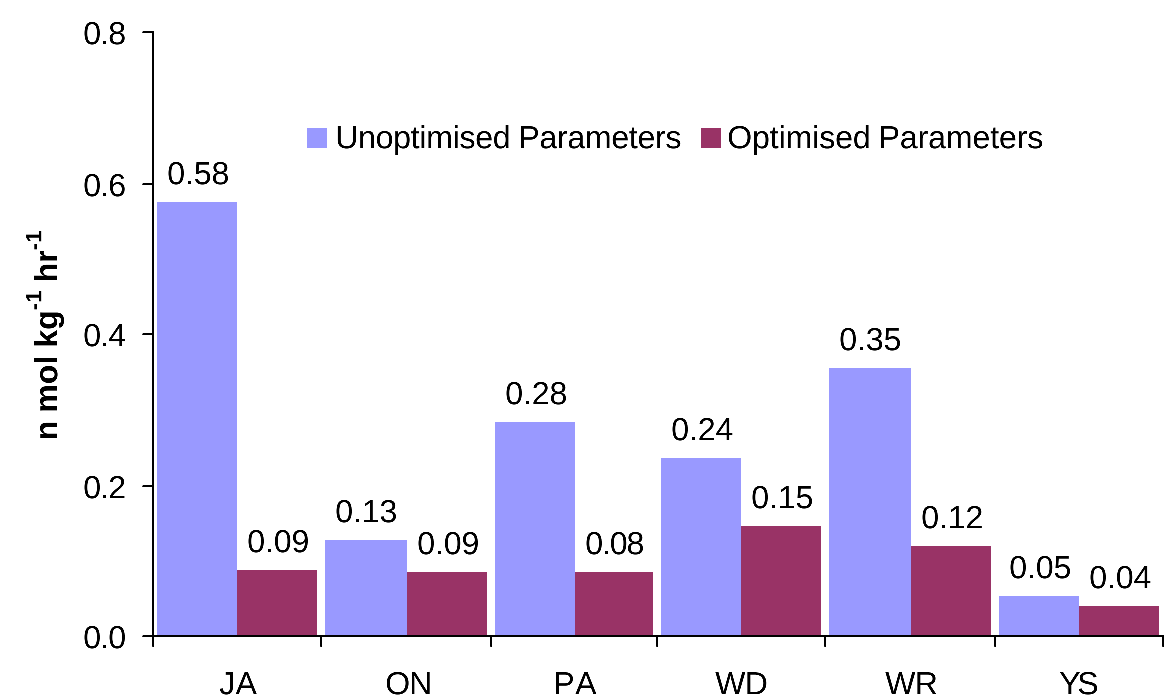
Table 2 Notation for the kinetic relations

Symbol	Comment
i	Index i = 1 for nitrate, = 2 for ammonium
r_i	Uptake of i th nutrient (mM-N day^{-1})
N_i	Concentration of i th nutrient (μM-N lt^{-1})
n_i	Uptake rate of i th nutrient for optimal irradiance (day^{-1})
V_i	Asymptotic uptake rate of nitrate/ammonium (day^{-1})
P	Phytoplankton biomass (μM-N lt^{-1})
I	Photosynthetically active irradiance (μE m^{-2} s^{-1})
N	$= N_1 + N_2$
s_1, s_2	Switching factors in JA defined by the following. If $N_2 > N_{cr}$, $s_1 = 0$ & $s_2 = 1$; if $N_2 < N_{cr}$, and $N_1 = N_{cr}$, $s_1 = 1$ & $s_2 = 0$; otherwise, $s_1 = N_1/N$ & $s_2 = N_2/N$

Correlation coefficient for calculated and experimental values of McCarthy et al (1999) (n=30)



Standard deviation for calculated values and experimental values of McCarthy et al (1999) (n=30)



Observations of McCarthy et al (1999) at stn S11 and values given by kinetic relations

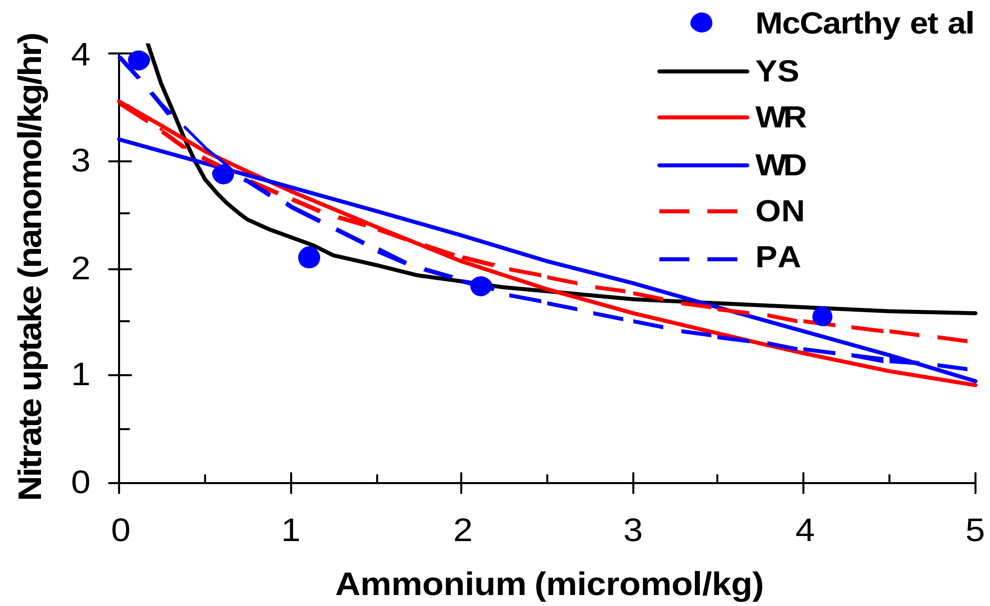
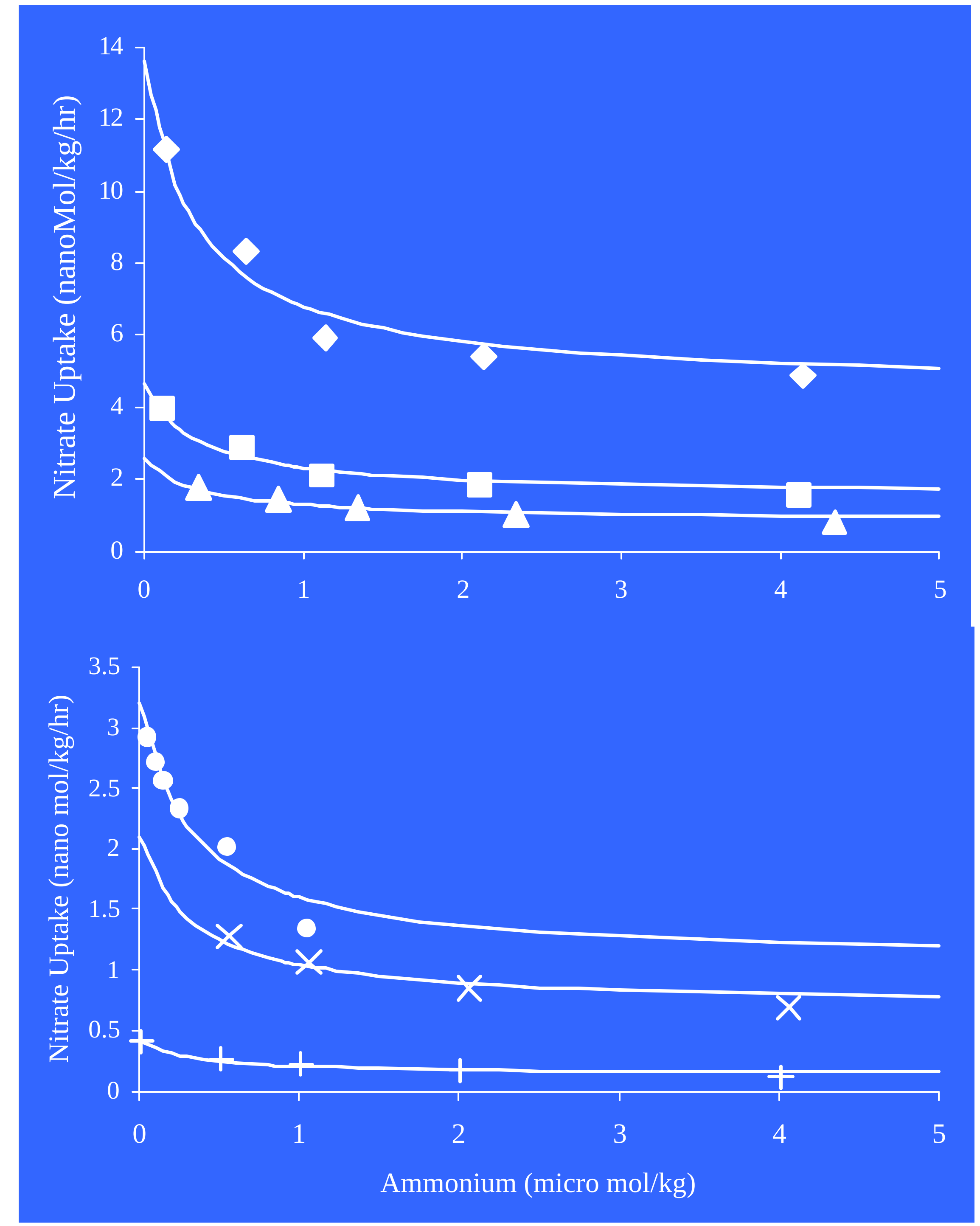


Table 3 Parameters used in calculating nitrogen uptake with kinetic relations for comparison with McCarthy et al's experiments

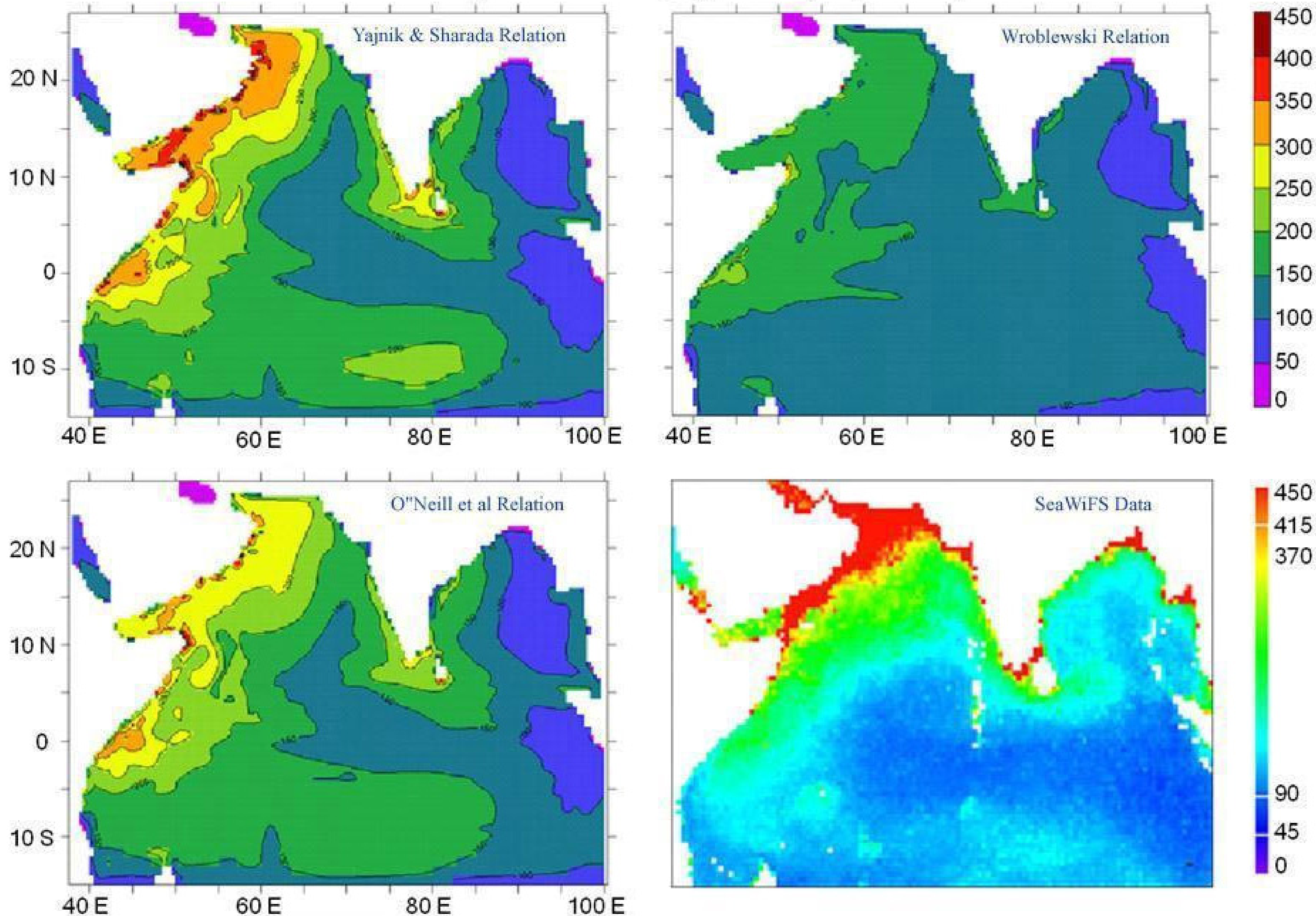
Parameter	Relation	Value	
		Unoptimised	Optimised
k_1 (mMol N m^{-3})	WR	1	1
	ON	0.2	0.27
	YS	0.5	1
	PA	3.69	1
	WD	1.5	1
k_2 (mMol N m^{-3})	WR	1	1
	ON	0.1	0.26
	YS	0.5	1
	PA	0.25	1.82
	WD	1.5	1
V_1/V_2	PA	0.575	1
	All others	1	1
Ψ (mMol N $m^{-3})^{-1}$	WR	1.462	0.27
a (mMol N $m^{-3})^{-1}$	YS	1	0.72
b (mMol N $m^{-3})^{-1}$	YS	3	2.6
α (mMol N $m^{-3})^{-1}$	WD	0.25	0.14
N_c	JA	0.5	4.35
k	JA	1	0.24

Experiments of McCarthy et al and kinetic relation (YS) with optimized parameters



3D Simulation Results and Observations

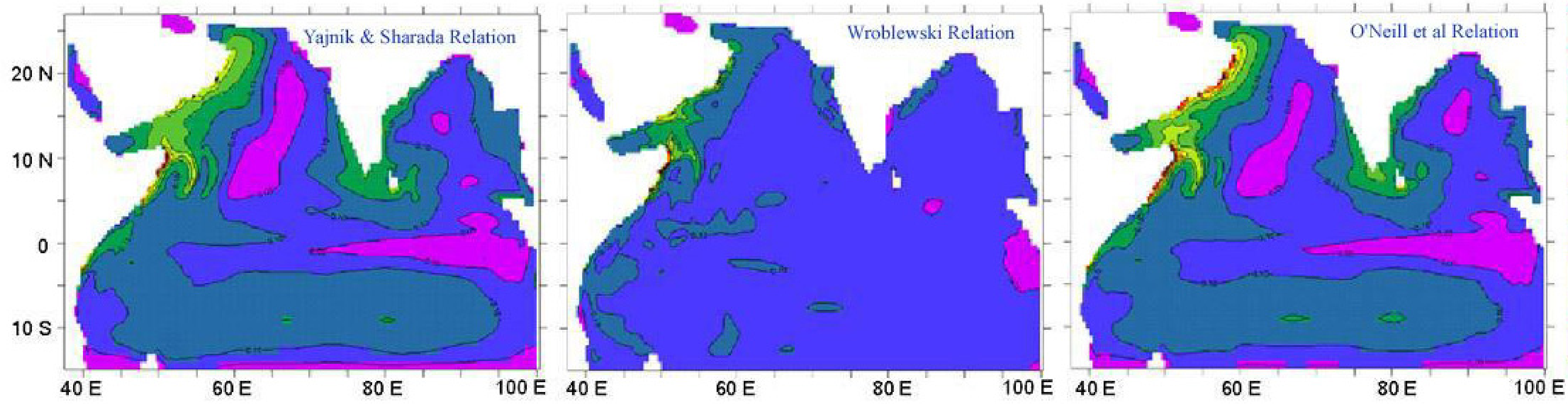
Annual Primary Productivity (gC m^{-2} yr^{-1}) in Euphotic Zone



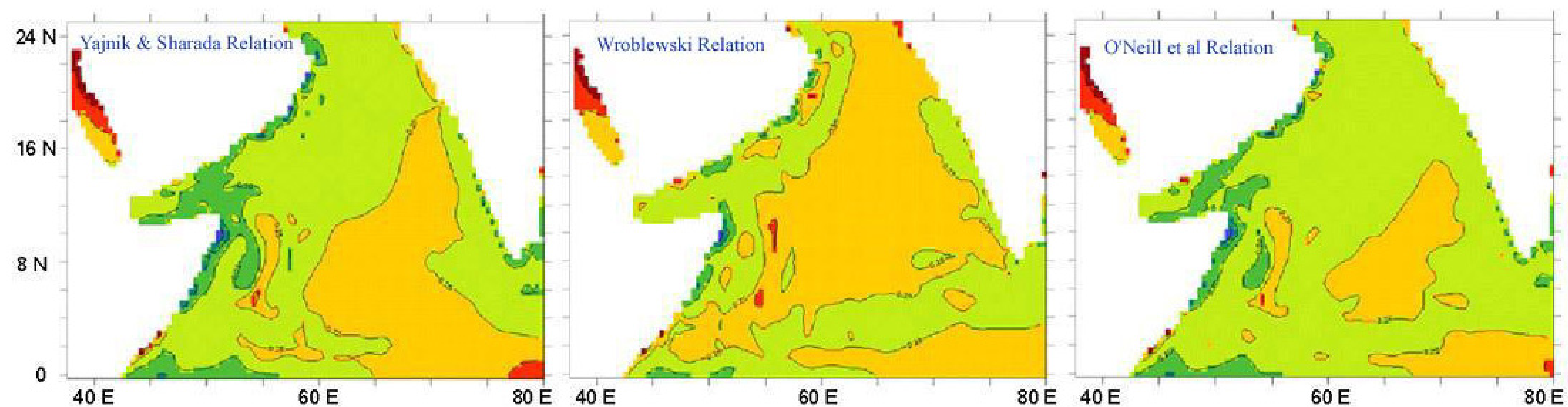
Physical model : MOM   Ecosystem : FDM

Kinetic Parameters : $k_1 = 1.7$ mMolNm^{-3}, $k_2 = 0.47$ mMolNm^{-3}, $\Psi = 1.462$ (mMolNm^{-3})$^{-1}$, $a = 0.72$ (mMolNm^{-3})$^{-1}$ $b = 2.6$ (mMolNm^{-3})$^{-1}$

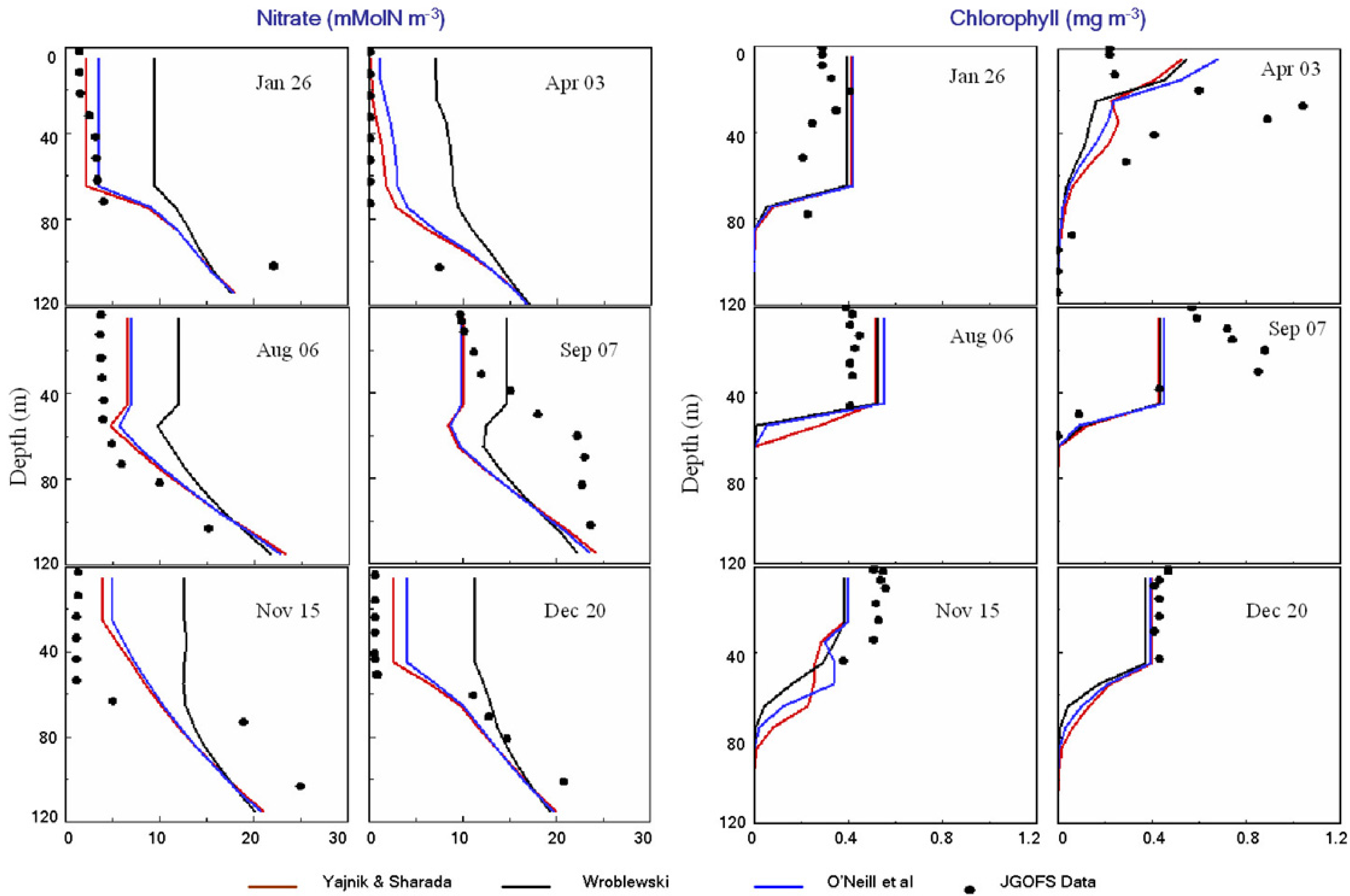
Annual f-ratio in Euphotic zone



Annual Particle Export Ratio at 120 m



Profiles of Nitrate and Chlorophyll at JGOFS Station S4 (19 N, 59 E)



Conclusions

- Similarity and hyperbolicity are believed to be fundamental properties of multi-nutrient kinetics.
- A kinetic relation based on these properties for ammonium-nitrate system represents the experimental results of McCarthy et al (1999) more accurately than other kinetic relations.
- Results of 3 D simulations for three kinetic relations (ON, WR, YS) for the North Indian Ocean with climatological forcing are compared with Satellite and cruise data (SeaWiFS and JGOFS). Annual primary productivity for two relations (ON, YS) compares more favourably with SeaWiFS data than WR relation. Profiles of nitrate and chlorophyll for these two also agree better with JGOFS data at station S4. However, none of the relations capture subsurface chlorophyll maximum due to the treatment of large scale convection in the physical oceanographic model.
- Accurate representation of multi-nutrient kinetics is necessary for reliable simulation of marine ecosystem.

Details are given in the following references:

Sharada, M. K., Yajnik K. S. and Swathi, P. S. Evaluation of six relations of kinetics uptake by phytoplankton in multi-nutrient environment using JGOFS experimental results. Communicated to *DSR II.*

Swathi, P. S., Sharada, M. K. and Yajnik, K. S., 2000. A coupled physical-biological-chemical model for the Indian Ocean. *Proceedings of Indian Academy of Sciences (Earth and Planetary Sciences)*, 109: 503-537.

Yajnik, K.S. and Sharada, M.K., 2002. Ammonium inhibition of nitrate uptake by phytoplankton: Implications of recent experiments on modelling. C-MMACS Research Report CM 0201.

Yajnik, K.S. and Sharada, M.K., 2003. Hyperbolic least square method of estimation of nutrient kinetics parameters in marine biology. C-MMACS Research Report CM 0301.

Yajnik, K. S. and Sharada, M. K. Ammonium inhibition of nitrate uptake by phytoplankton: A new relation based on similarity and hyperbolicity. Communicated to *Current Science*.