THE EFFECTS OF VARYING NUTRIENT CONCENTRATION ON BIOLOGICAL PRODUCTION IN UPWELLING REGIONS

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ABSTRACT

The maximum steady state yield of a marine ecosystem is set by the input of primary nutrient, and the associated rate of production that is termed "new production." At the simplest conceptual level, new production can be related directly to, and estimated from, nitrate input or nitrate uptake. Using such a simple assumption, one can predict that, for a given vertical velocity during upwelling, the new production at 15°S, Peru, would be about twice that of the upwelling center at northwest Africa, as a consequence of the Atlantic's relative nutrient poverty. However, "regenerated" nitrogen production, based upon nitrogen recirculated through grazing pathways, also increases with increased new nitrogen production.

Additional complexities arise from the adaptive responses of phytoplankton to upwelling conditions. The maximum specific nitrate uptake rate is a function of the initial nitrate concentration, but the actual rate realized is often reduced below maximum by other environmental factors, e.g., deep mixing. This occurs in northwest Africa, where high upwelling rates induced by high wind stress do not compensate for low source-water nutrient concentrations caused by deep mixing of the phytoplankton.

There are other direct effects of nitrate concentration on phytoplankton physiology, including enhanced assimilation number. So the responses of phytoplankton to increased nitrate input and concentration should be nonlinear and will probably approximate an exponential relationship.

RESUMEN

La máxima productividad sostenida de un ecosistema marino estable está determinada por el aporte de nutrientes primarios y por el ritmo de producción correspondiente, denominado "nueva producción". Al más simple nivel conceptual, la nueva producción puede ser relacionada directamente a, y estimada directamente de la entrada o del consumo de nitrato. Usando un supuesto tan simple, se puede predecir que para una velocidad vertical de afloramiento dada, en Peru, a los 15°S, la nueva producción sería el doble que la del noroeste de Africa, como consecuencia de la pobreza relativa de nutrientes en el Atlántico. Sin embargo, la producción "regenerada" de nitrógeno, basada en el nitrógeno recirculado a través de los ciclos de pastoreo, también aumenta con el incremento en la producción de nitrógeno nuevo.

Complicaciones adicionales se generan por la respuesta adaptativa del fitoplancton a las condiciones de afloramiento. El máximo ritmo de incorporación específica de nitrato es una función de la concentración inicial de nitrato, pero el ritmo realmente alcanzado está a menudo por debajo del máximo debido a otros factores ambientales, e.g., mezcla a profundidad. Esto ocurre en el noroeste de Africa donde fuertes vientos inducen altos ritmos de afloramiento, pero no compensan el bajo contenido en nutrientes de las aguas de origen, provocado por la mezcla de fitoplancton hasta capas profundas.

Existen otros efectos directos de la concentración de nitrato sobre la fisiología del fitoplancton, incluyendo el aumento en el número de asimilación. En consecuencia, las respuestas del fitoplancton al aumento del aporte y concentración de nitratos deberían ser no-lineales y probablemente se aproximen a una relación exponencial.

INTRODUCTION

Recent investigations of major coastal upwelling systems of the world have indicated that there are consistent differences between areas in the magnitude and seasonal distribution of biological production (Codispoti et al. 1982). Although some of these differences are due to the persistence and intensity of upwelling, the depth of the mixed layer, and the presence of an undercurrent on the shelf, the primary variable is the vertical flux of inorganic nutrients (Barber and Smith 1981). In this paper I will discuss how nutrient flux and nutrient concentration, especially nitrate, affect the magnitude and patterns of biological production in coastal upwelling systems.

Source waters for upwelling, usually from depths of 200 m or less (Barber and Smith 1981), show differences in nutrient concentration as a result of oceanic circulation patterns. For example, the North Atlantic is notably poor in nutrients because there are more exports than imports across the equator (Redfield et al. 1963). These differences in source-water concentration are reflected in the reported values of the maximum surface nitrate concentration (Table 1). These

TABLE 1
High Nutrient Concentrations Observed at the Surface in Different Upwelling Regions*

Region	Reference	NO_3^- μg-at.l^{-1}	$PO_4^=$ μg-at.l^{-1}	Diss. Si μg-at.l^{-1}	
Aleutian Islands 53°N, 170°W	Hood and Kelley (1976)	30	2.5	70	
Coastal Peru	Hafferty et al.	27	2.2	22	Sta. 207
15°S	(1978)	21	2.2	31	Sta. 344
Somali coast north of 10°12′N	Smith and Codispoti (1979)	20	1.6	16	
N.W. Africa	Friebertshauser et al.	12	1.0	7	Sta. 14
22°N	(1975)	11	1.0	8	Sta. 161
Mediterranean Sea 43°N, 5°E	Minas (1968)	—	0.1	—	
Pt. Conception, Calif.	OP1, Hydro† (1981)	32	2.4	33	Sta. 123
Pt. Conception, Calif.	OP2, Hydro† (1983)	21	2.7	27	Sta. 78

*Modified from Codispoti (1984)
†Unpublished data reports

range from 32 μg-at.l^{-1} at Point Conception down to 11 at 22°N in northwest Africa (or even to 0 in the Mediterranean Sea). The range of dissolved silicon concentration maxima is even greater, from 70 μg-at.l^{-1} in the Aleutian upwelling to 7 in northwest Africa. The depth of upwelling source water varies with wind stress and other factors such as the depth of the pycnocline near the coast. The upper pycnocline is deficient in dissolved silicon relative to nitrate as a result of the slower regeneration of silicon (Dugdale 1972). During weak upwelling, when the source water comes from the upper part of the pycnocline (Dugdale 1983), dissolved silicon tends to be low relative to nitrate. Dissolved silicon is likely to play a major role in species concentration and diatom production in upwelling systems. However, the remainder of this paper will deal with the effects of nitrate.

EQUIVALENCE OF NITRATE FLUX AND NEW PRODUCTION

Although nitrogen may not always be the limiting primary nutrient for productivity of marine phytoplankton, ^{15}N can be used as a tracer to follow the partitioning of nitrogen during biological use and regeneration, and to evaluate the components of the phytoplankton production cycle.

Nitrate uptake is considered as a measure of "new production" (Dugdale and Goering 1967) or potential yield—the amount of production that can be removed from the system without causing its collapse—whereas uptake of ammonium and certain other organic-N compounds such as urea represent the "regenerated" or circulating nitrogen. Together these make up the "total" or primary production. Carbon fixation, the more common measure of primary production, is therefore based upon both new and regenerated nitrogen.

In an eastern boundary upwelling system, the vertical motion of the water near the coast feeds nitrate into the euphotic zone (Wooster and Reid 1963). The resulting rate of new production can be calculated with suitable assumptions from estimates of the vertical velocities and the nitrate concentration of the source water, as Andrews and Hutchings (1980) have done for the Cape Upwelling region of South Africa. In a similar way, it can be predicted, for a given vertical velocity during upwelling, that the new production at 15°S, Peru, would be about twice that of the upwelling center at northwest Africa, as a consequence of the low levels of nutrients of the North Atlantic (Table 1).

The resultant potential yield or new production enters the ecosystem, and a portion is regenerated through grazing and excretion of ammonium and organic nitrogen compounds (mainly urea; McCarthy 1972) by zooplankton and other heterotrophic members of the food web. This serves to support a higher rate of primary production than would nitrate alone. The regenerated production that occurs when these nitrogen compounds are taken up may constitute up to 50% of the total nitrogen production in upwelling regions (Table 2). Under these conditions, for each unit of nitrate upwelled, one unit of ammonium (plus some organic nitrogen) is maintained in the regeneration cycle between phytoplankton and grazers. This

TABLE 2
Mean Values of Nitrate and Ammonium Uptake Parameters for a Series of Cruises to Upwelling Regions

Region	Cruise	Nitrate product. (mgat/m^2/d)	Ammonium product. (mgat/m^2/d)	Total N product. (mgat/m^2/d)	Nitrate product. (%)	$V_{max}NO_3^-$ (/h)	$V_{max}NH_4^+$ (/h)	Z_m mixed layer depth[a] (m)
Peru	Anton Bruun-15	—	—	—	—	0.0367	0.0167	12
	Pisco	30	10	40	75	0.0358	0.0172	13
Africa	JOINT-I	15.2	6.6	21.8	70	0.0192	0.0139	38
	CINECA-Charcot II	10.6	9.7	20.3	52	0.0221	0.0139	—

[a] Examples of the mixed-layer depths encountrered when the nitrogen uptake data were taken. They may differ from the depths that would be obtained from an examination of all the stations taken during each cruise.

Modified from Codispoti et al. (1982)

regenerated nitrogen thus amplifies the effect of nutrient concentration and results in a twofold increase in total nitrogen production and accompanying carbon production, but not overall yield.

The effect of increasing nutrient concentration of upwelled water on different components of the production cycle can be evaluated and then used to compare different areas. In northwest Africa, for each unit of nitrate upwelled and entering the euphotic zone there will be one unit supplying new production and one unit entering regenerated production, resulting in two units of total production. However, in Peru the nitrate concentration is doubled, and hence four units of total production result. Therefore, upwelling in the Pacific eastern boundary regions should show a total primary production two times greater than the same upwelling rate would give in North Atlantic eastern boundary situations, only because of the source water's larger nutrient concentrations. In the North Atlantic, the effect of low source-water concentration could be offset by a twofold relative increase in upwelling velocity. However, high wind stress that creates high upwelling rates also results in strong mixing. Consequently, the phytoplankton encounter decreased mean irradiance (Huntsman and Barber 1977), and productivity remains relatively low. Wind stress in northwest Africa during the JOINT I study was about three times higher than in Peru during JOINT II, 1977 (Smith 1981). The mean specific nitrate uptake rates (uptake per unit phytoplankton biomass) were lower in northwest Africa than in Peru (Table 2); a similar effect was observed by Huntsman and Barber (1977). Consequently, the integrated nitrate production for northwest Africa was half that of Peru (Table 2), despite the higher African upwelling rate, because of a combination of mixing and nitrate concentration of the source water.

EFFECT OF NITRATE CONCENTRATION ON PHYTOPLANKTON PHYSIOLOGY

Nitrate input and concentrations in the euphotic zone may also influence carbon processes more directly. When newly upwelled phytoplankton appear at the surface in an upwelling center, nitrate uptake per cell is initially low, but increases over a period of several days as adaptation to the high-irradiance, high-nutrient conditions takes place (MacIsaac et al. 1985). Carbon-related processes increase at a much slower rate during this initial period. The maximum rate of nitrate uptake achieved occurs just before nutrient limitation sets in. High nutrient concentrations postpone the onset of nutrient limitation. So high concentrations of nitrate in source water tend to lead to high maximal specific nitrate uptake rates. In Table 3, the maximum specific nitrate uptake rates for Peru can be seen to be about two times those for northwest Africa. Nutrient concentration, perhaps dissolved silicon (as in the 1977 JOINT II cruise), may affect the rate at which nitrate uptake increases, as well as the final rate achieved (MacIsaac et al. 1985). The effect of high nitrate concentrations on the maximum rate of uptake will certainly influence the length of the production cycle and consequently the spatial distribution of the phytoplankton produced from upwelled nitrate.

Nitrate concentration affects photosynthetic processes too, although the carbon-related changes from upwelling tend to occur later than the nitrogen processes (MacIsaac et al. 1985). Assimilation number, i.e., carbon fixed per unit chlorophyll at optimum irradiance, increases sharply when nitrate concentrations rise to about 10 μg-at.l^{-1} in eastern boundary upwelling (Minas et al. 1982); the data include measurements in northwest Africa and show that high assimilation numbers do not generally occur there, perhaps because of the generally low nutrient concentrations at

TABLE 3
Maximum and Minimum Values of V_{max} for Nutrient-Saturated Uptake of Nitrate and Ammonium in the Upper Euphotic Zone[a] from a Series of Cruises to Upwelling Regions

		V_{max} NO_3^- (/h)		V_{max} NH_4^+ (/h)	
Region	Cruise	min	max	min	max
Peru	Anton-Bruun	0.0170	0.0547	0.0129	0.0222
	Pisco	0.0089	0.0595	0.0268	0.0358
Northwest Africa	JOINT-1	0.0028	0.0329	0.0046	0.0261

[a] Defined here as the 100% to 30% light-penetration zone. Most values are from the 50% light depth.
Modified from Codispoti et al. (1982)

the surface during upwelling. Yet in South African coastal upwelling with higher nutrient concentrations characteristic of the south Atlantic subsurface waters, high assimilation numbers also occur (Andrews and Hutchings 1980). Results from the OPUS 1983 studies at Point Conception (unpublished) show a similar trend.

SUMMARY

A series of nonlinear positive relationships between nutrient (and especially nitrate) concentration and input and processes leading to phytoplankton production occur in upwelling regions. These relationships will lead to a more or less exponential rise in productivity as nitrate input and concentration rise. Eppley et al. (1979) found such a relationship between primary production and the proportion of nitrate uptake in southern California waters, and constructed a curve connecting Peru upwelling and the North Pacific Gyre that successfully spanned their data. Presumably, the factors discussed here are at least partially responsible for the nature of this relationship. Additional analysis of existing and future data sets from eastern boundary upwelling regions should help to refine these patterns and explain the key role of nutrients in limiting production processes in upwelling regions.

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