New and regenerated production at the Iberian margin.

Results of the Belgica BG 9714 cruise

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Introduction

Our investigations during the ongoing OMEX phase I project have underlined the importance of vertical transport of nitrate in sustaining primary production at the ocean margin of the North-eastern Atlantic. Overall nitrate uptake rates (new production) paralleled carbon fixation rates and *f*-ratio followed the well-known function of nitrate (Elskens et al. 1998, Joint et al., 1998). However, these studies emphasised a leading role for ammonium in regulating the removal of nitrate (Elskens et al., 1996). Ammonium started to accumulate in the water column in late spring and during this period, both remineralisation data and turn-over times of ammonium supported that the generation of ammonium and possibly other reduced nitrogen substrates meet the daily nitrogen requirement of the phytoplankton. The mechanism of supply and the kinetics of utilisation of dissolved inorganic nitrogen are believed to play a critical role in determining the productivity, size structure and species succession of phytoplankton communities of the world's ocean (Harrison et al., 1996). Therefore, the work described here is an attempt to investigate more systematically the kinetics of nitrate and ammonium uptake and the inhibitory effects of ammonium on nitrate uptake with natural plankton assemblages in waters seasonally regulated by upwelling events.

Recent estimates of carbon and nitrogen fluxes through plankton compartments at the Iberian region indicate that up to 50% of the measured primary production between upwelling pulse might be supported by recycled nitrogen (Bode and Varela, 1994). Questions remain on the contribution of each different nitrogen species (inorganic and organic) and on effects of their ratios on the nitrogen uptake regime. A second objective of this work was, therefore, to assess the relative importance of uptake of organic nitrogen sources, using urea as a target compound.

Methods

A CTD-rosette, equipped with 10 litre Niskin bottles, was used for sampling large amounts of surface water required for the incubation experiments and assaying biogeochemical parameters. Nutrient concentrations were determined aboard. Nitrate+nitrite analyses were performed with a Technicon Autoanalyser II, while ammonium and urea were manually analysed according to Koroleff (1969) and Goeyens et al. (1998), respectively. Suspended matter for particulate organic carbon (POC) and particulate nitrogen (PN) determinations was collected on precombusted (450 °C) Whatmann GF/F filters, dried at 60 °C and stored in polystyrene Petri dishes until analysed in the home lab. Measurements were carried out with a Carlo Erba NA 1500 CN Analyser, after carbonate elimination in HCl saturated vapour.

Experiments for the determination of nitrogen uptake rate were started by addition of labelled (^{15}N, 99 %) nitrate, ammonium or urea into 0.7 l polycarbonate incubation bottles. Tracer additions resulted in increases of the concentration which are similar to the analytical detection limit, i.e. approximately 0.1 µM for nitrate and 0.05 µM for ammonium and urea, respectively. All incubations were carried out during 6 hours in an incubator, thermostated with running seawater and illuminated with an incident radiation of 200 µE m^{-2} s^{-1}. PN, collected on Whatmann GF/F filters after incubation, was converted to dinitrogen by a modified Dumas combustion technique and ^{15}N abundance was assayed by emission spectrometry using Jasco NIA-1 and N-151 ^{15}N analysers (Fiedler and Proksch 1975). Rates of uptake were calculated from the equations of Dugdale and Goering (1967).

Results

Nitrate, ammonium and urea distribution patterns

Vertical profiles of nitrate, ammonium and urea concentrations along the main OMEX transects O2N, O2P and O2S are illustrated in Fig. 1. At the oceanic stations (> 2000 m), nitrate was almost totally exhausted. We observed near detection limit values (0.1 µM) in the upper 50m. In the coastal zone, especially transects O2P and O2N, residual nitrate concentrations up to 4 µM were found. Ammonium concentrations ranged from 0.08 to 0.3 µM with maxima usually located in subsurface (e.g. transect O2S). Urea concentrations ranged from 0.1 to 0.6 µM, but there is no obvious spatial trend. As for ammonium, when there was a maximum, it was located in subsurface. Except at the coastal stations (~ 100m), the availability of the N-sources for phytoplankton nutrition was urea > ammonium > nitrate.

N-uptake rates and f-ratio

Total nitrogen production exhibited spatial variability along the OMEX sections with values ranging from 8 to 28 nM h^{-1} (Fig. 2). Overall N-uptake rates were low in the oceanic waters reaching higher levels on the shelf and in the coastal zone. The relative contributions of nitrate, ammonium and urea to the total N-production were 5 to 47%, 17 to 54% and 31 to 78%, respectively. It follows that the *f*-ratio was significantly below 0.5 indicating a system running on regenerated production (Fig. 2).

Uptake and inhibition kinetics

Nitrogen uptake kinetic experiment were designed to investigate the concentration-dependent uptake of nitrate and ammonium and the inhibition of nitrate uptake by additions of ammonium with natural phytoplankton assemblages (Fig. 3). The data for the concentration-dependent uptake were fitted by non-linear least square procedures to a Michaelis-Menten equation:

$$r_N = \frac{r_{max}.N}{K_N + N} \qquad (1)$$

where N is the nutrient concentration, ρ_N is the uptake rate, ρ_{max} is the maximum uptake rate and K_N is the half-saturation constant for uptake.

The inhibition of nitrate uptake by ammonium additions was fitted by means of a variation of the Michaelis-Menten equation in which nitrate uptake is first normalised to the observed rate at zero ammonium addition:

$$r_{NO3}(rel) = 1 - \left(\frac{I_{max}.\Delta NH_4}{K_i + \Delta NH_4} \right) \qquad (2)$$

where NH_4 is the added ammonium, I_{max} is the maximum realised inhibition (value from 0 to 1) and K_i is the half-saturation constant for inhibition.

Overall the precision of parameter estimates averages 10-30%. Maximum uptake rates of nitrate and ammonium covaried, but ρ_{max} (NH_4) almost always exceeded ρ_{max} (NO_3) especially in oceanic water. The variability was less than an order of magnitude, i.e. 7 ρ_{max} (NH_4) 27 nM h^{-1} and 4 ρ_{max} (NO_3) 25 nM h^{-1} (Fig. 3). The half-saturation constant for NH_4 uptake ranged between 0.04 to 0.44 µM covarying with ambient ammonium concentrations. NO_3 half-saturation constant could only be approximated in oceanic waters (i.e. K_N + NO_3) because of the detection limits for nitrate determination, but observations (Fig. 3) suggest that on an average basis K_N (NH_4) was K_N (NO_3). The variability in ρ_{max} and K_N-values reflects most likely variations in phytoplankton biomass and community structure. The inhibition half-saturation constant (K_i) was similar to K_N-values (Fig. 3), but K_i concentrations in oceanic waters (~ 0.13-0.4 µM) always exceeded K_N (0.06-0.09 µM). Inhibition was rarely complete even at 2µM ammonium, with I_{max} ranging from 0.6 to 1. With respect to the ecological significance of these results, it should be borne in mind that inhibition is a highly variable

process. It largely depends on interspecies differences and changing environmental conditions and it includes both short-term as well as long-term regulations (Dortch, 1990). Therefore, the approach used here has to be considered at best as a compromise between data acquisition and resulting predictive power. With ambient ammonium varying from 0.08 to 0.3 µM, K_i from 0.06 to 0.9 µM and I_{max} from 0.6 to 1, it can be stated that the degree of nitrate uptake inhibition might range between 5 to 76%.

Preliminary Conclusions

There is an agreement between the measured N-flux rates and the availability of the corresponding N-sources. This study underlines the role of urea which can represents up to 78% of the total N-production. Accordingly, the *f*-ratio is low (0.05 - 0.47) indicating the predominance of regenerated production.

On an average basis, K_N values for both nitrate and ammonium were close to the ambient nutrient concentrations suggesting that measured flux rates were equivalent to $\rho_{max}/2$. It follows that if N-pulse occurs (upwelling event), N-uptake rates will probably increase.

Maximum uptake rates of nitrate and ammonium covaried, but ρ_{max} (NH_4) almost always exceeded ρ_{max} (NO_3) suggesting a better efficiency for ammonium utilisation by phytoplankton.

K_i-values covaried with K_N, but inhibition was rarely complete (I_{max} 1). The potential reduction of nitrate uptake rates was then calculated to range between 5 to 76%. For the oceanic stations, however, $K_i > K_N$, these are characteristics of N limited-environment; the phytoplankton taking the available N-source.

Acknowledgements

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TRANSECT 02S

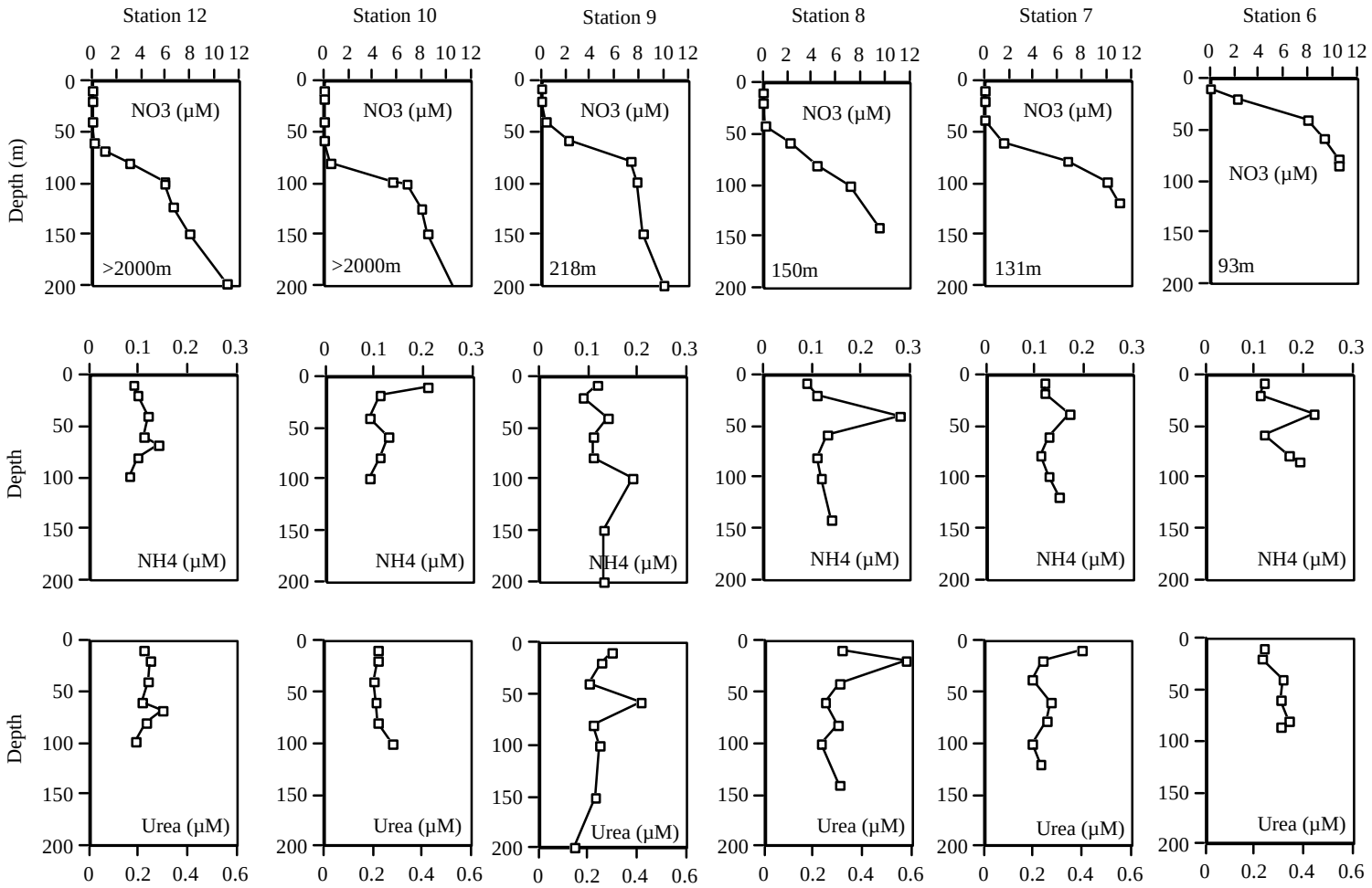
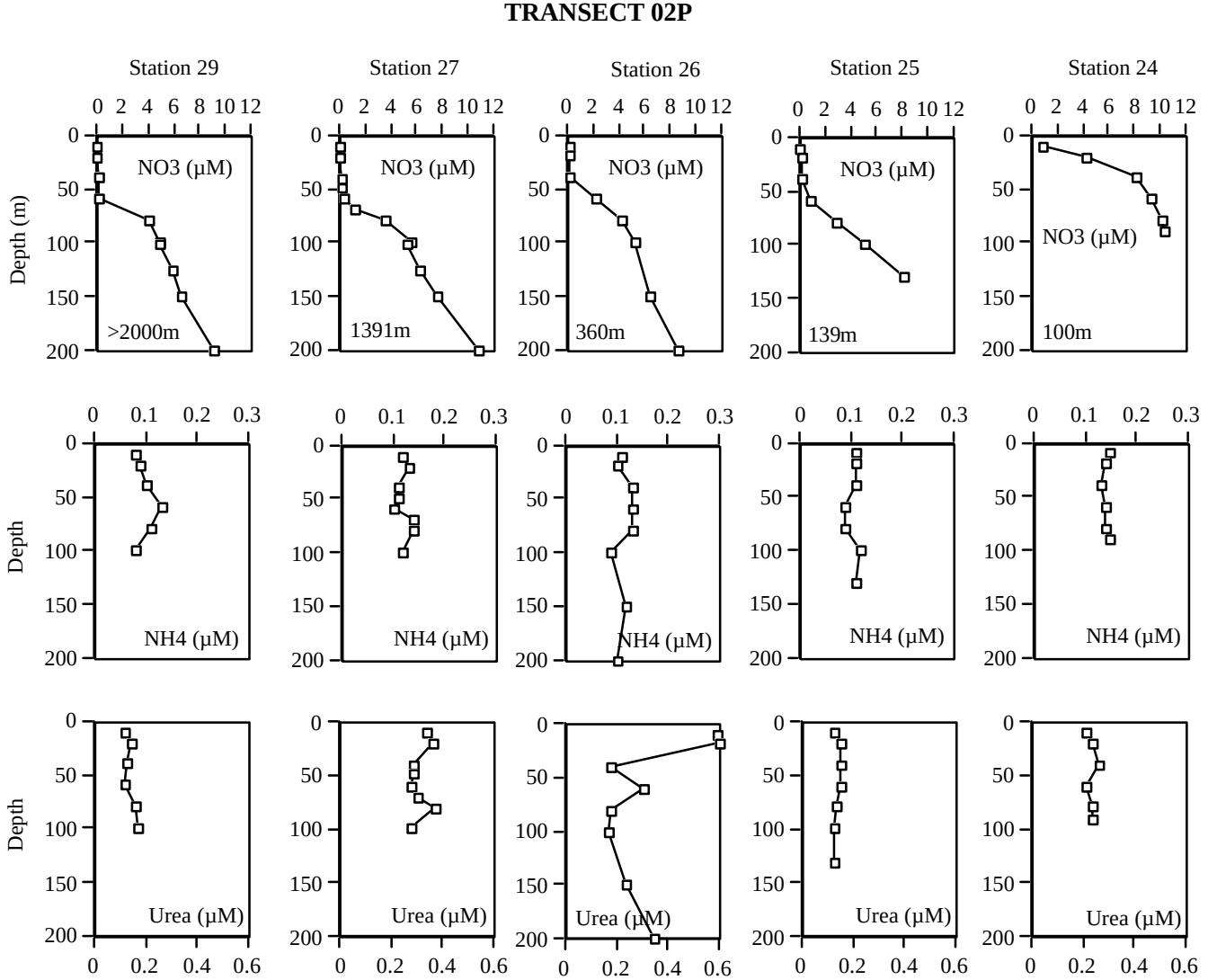


Figure 1: Vertical profiles of nitrate, ammonium and urea during BG 9714



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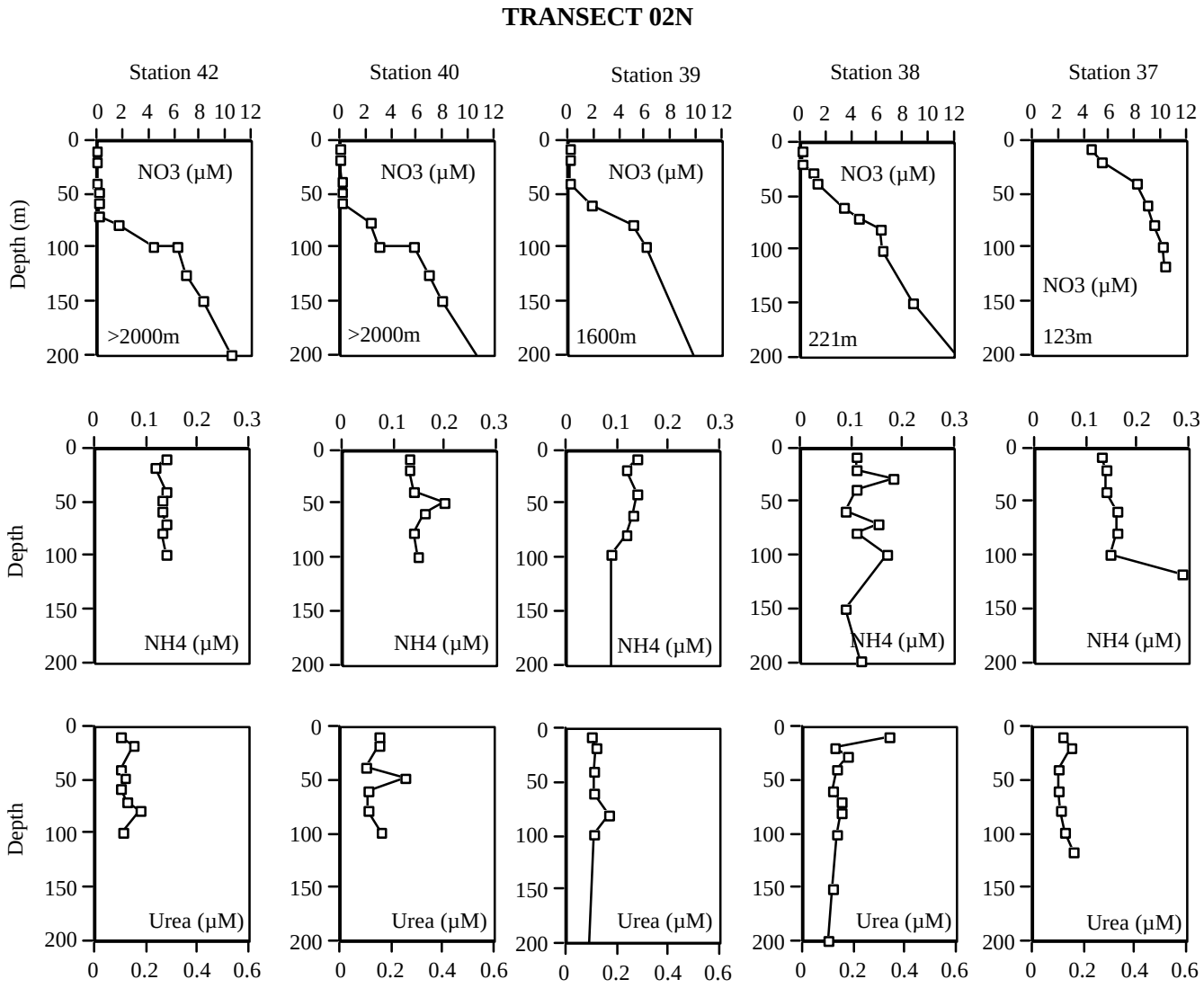

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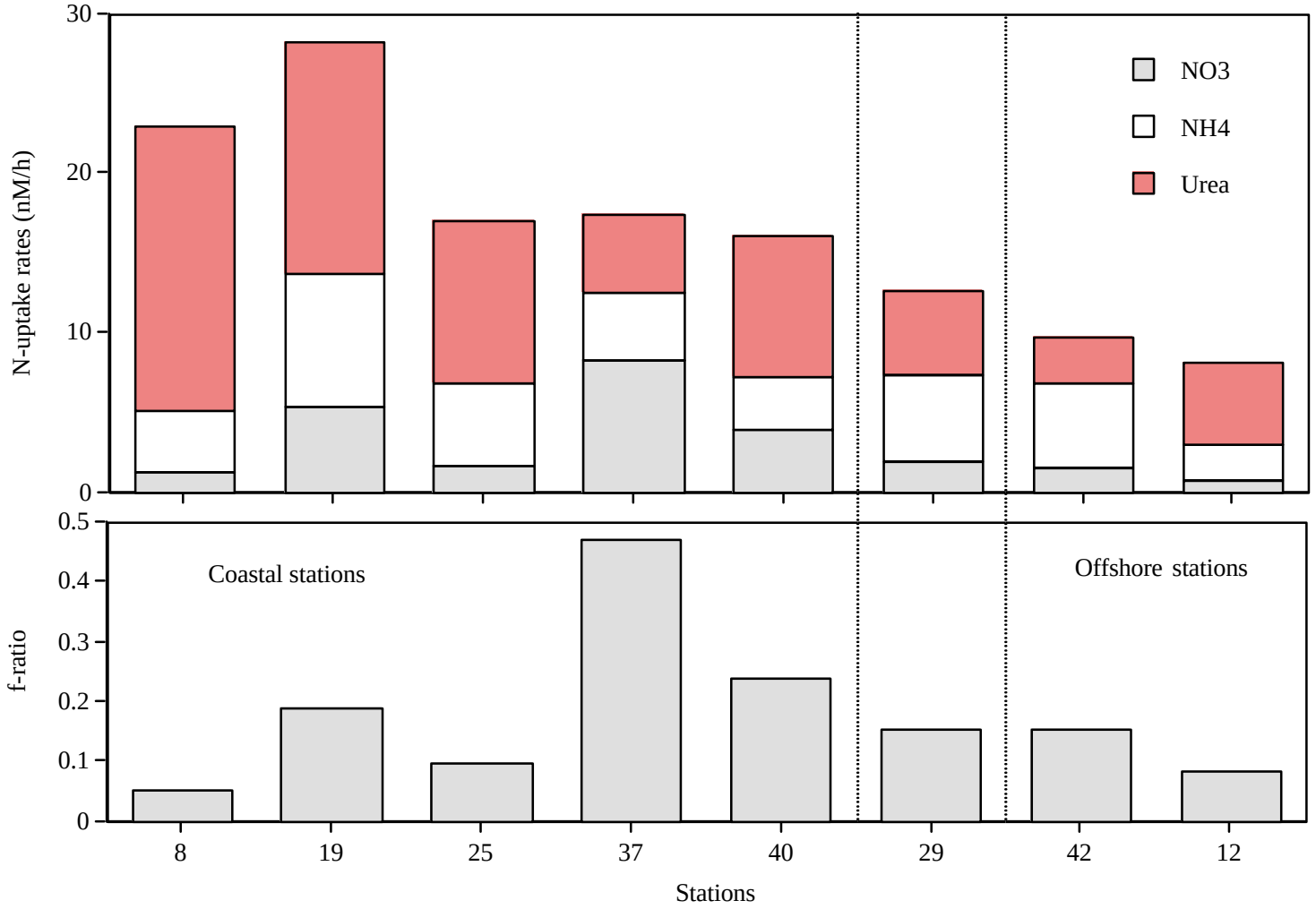

Figure 2: N-uptake rates and *f*-ratio during BG 9714 Belgica cruise.

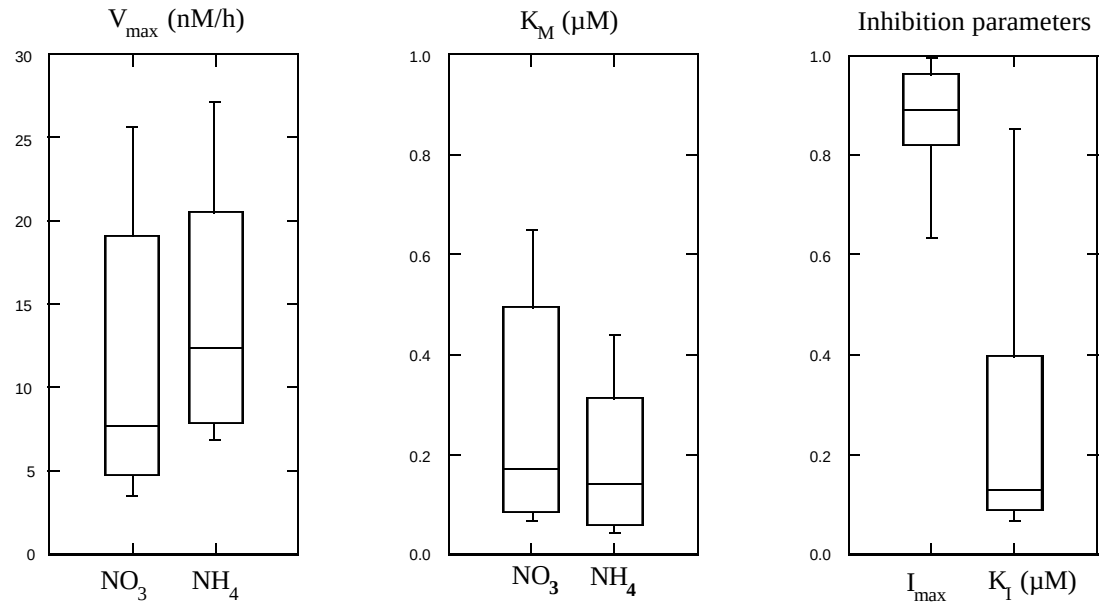

Figure 3: Box plot of kinetic parameters for nitrate and ammonium uptake rates. The box contains 50% of the data and the wiskers (bar) 95% of the data. The line in the box is the median value.