Nutrient patchiness, phytoplankton surge-uptake and turbulent history: a theoretical approach and its experimental validation

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ENTANGLING NUTRIENT PATCHINESS IN THE OCEAN

Investigations of small- and micro-scale distributions of bacteria, phytoplankton and zooplankton populations revealed their patchy character. **While evidence now also exists for micro-scale nutrient patchiness[1], direct observations of micro-scale nutrient distributions are still lacking and cannot be achieved with present day techniques**. Such information is nevertheless critically needed to bridge the gap between nutrients distribution and phytoplankton uptake to improve our general understanding of structures and functions in marine systems.

Microscale nutrients patchiness was investigated during a series of 3 sampling experiments conducted adrift in the coastal waters of the eastern English Channel in summer 1996, 1997 and 1998.

HIGH FREQUENCY LAGRANGIAN SAMPLING

- **Continuous sampling (z=0.25)**
  - through a sea-water intake mounted on a suspended hose
  - 1m away from the hull of the vessel
- **Directly processed (Technicon auto-analyser II)**
  - by means of a rail wheel pump
  - connected to 1.5 mm diameter plastic tubing
- **8 to 15 time series of [NH_4^+] recorded**
  - duration = 1 hour
  - sampling frequency = 0.33 Hz

VALIDATION

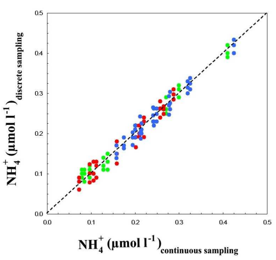

Figure 1: Mean values of [NH_4^+] times series recorded in 1996, 1997 and 1998, plotted against [NH_4^+] simultaneously estimated from sub-surface Niskin bottle samples. The different colours correspond to sampling under different flow speed *v* conditions: red (v ~1 m s^{-1}), blue (v ~ 0.5 m s^{-1}) and green (v ~ 0.2 m s^{-1}).

Highly significant linear regression (p<0.01)

↓

Validity of our high-resolution sampling procedure

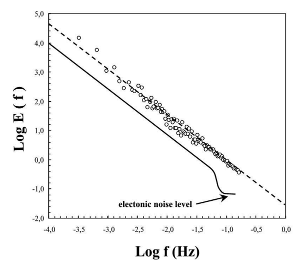

Figure 2: The power spectrum *E(f)*. *f* = frequency of a [NH_4^+] time series recorded in 1997. The strong linearity of the power spectrum indicates a scaling behaviour over the whole range of scales. The spectrum expected in case of noise contamination in the processing chain, presenting a high-frequency roll-off towards the electronic noise level, is shown for comparison

Absence of any kind of noise contamination

TIME SERIES

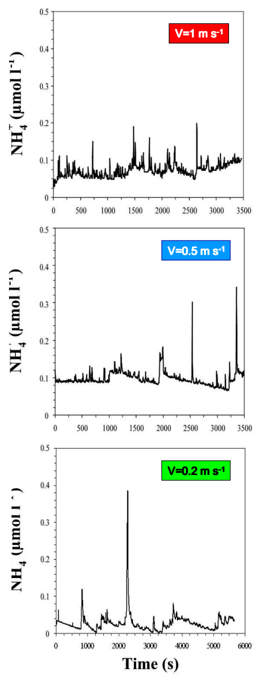

Figure 3: Samples of high-resolution (0.33 Hz) [NH_4^+] time series recorded in the Eastern English Channel in 1996, 1997 and 1998 (from top to bottom) for different values of the tidal current speed *v* (m s^{-1}).

More patchy [NH_4^+] distributions under weaker hydrodynamic conditions (i.e. the tidal current speed *v*)

INTERMITTENT DISTRIBUTION

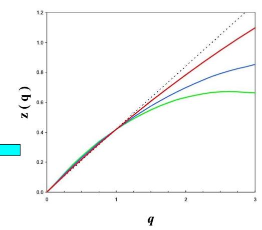

Figure 4: Illustration of the empirical function estimated for [NH_4^+] time series under different conditions of flows, 1 m s^{-1} (red), 0.5 m s^{-1} (blue) and 0.2 m s^{-1} (green). The black dotted line = theoretical non-intermittent case.

All time series significantly diverged from a non-intermittent distribution.

Their stochastic properties were related to turbulent mixing intensities with a clear increase in nonlinearity (i.e. intermittency) under conditions of decreasing turbulence

References cited:
[1]Blackburn N, Fenchel T, Mitchell JG (1998) Microscale nutrient patches in planktonic habitats shown by chemotactic bacteria. *Science* 282. [2]Currie DJ (1984) Microscale nutrient patches: Do they matter to the phytoplankton ? *Limnol. Oceanogr*. 29. [3] Baird ME, Lemsey SM (1999) Toward a mechanistic model of plankton population dynamics. J. Plankton. Res. 21. [4]MacKenzie BR, Legget WC (1993) Wind-based models for estimating the dissipation rates of turbulence energy in aquatic environments: empirical comparisons. *Mar. Ecol. Prog. Ser.* 94: 207-216

NUTRIENT PATCHINESS AND PHYTOPLANKTON UPTAKE

Nutrient uptake by phytoplankton cells is usually described by the Monod equation, which is strictly equivalent to the Michaelis-Menten equations. These classical models supposed steady state conditions, i.e. a homogenous distribution of the limiting nutrient in time. **As stressed by Currie[2] no experimentally substantiated model of nutrient uptake under fluctuating nutrient conditions exists.** Currie[2] theoretically demonstrated that patchiness will have a negative effect so long as uptake is less efficient at higher nutrient concentration than at low ones. This is true under the general assumption that the parameters of the Michaelis-Menten kinetics remain constant irrespective of ambient nutrient concentration[2]. This assumption is, however, unrealistic considering the demonstrated abilities of nutritionally limited phytoplankton cells to enhance their uptake of nutrients in the presence of ephemeral point source.

We thus introduce hereafter a modelling procedure that might account for the observed surge-uptake of nutrient based (i) on the detailed stochastic properties of intermittent nutrient distributions, and (ii) on a simple adaptive representation of phytoplankton surge-uptake for nutrients.

SIMPLIFIED MODEL OF NUTRIENT SURGE UPTAKE UNDER INTERMITTENT CONDITIONS

Assuming statistical independence between nutrients, phytoplankton and turbulent fields, the uptake of nutrients can be thought as a two step process:

- the encounter between a phytoplankton cell and nutrient
- the actual nutrient uptake

β = encounter kernel due to turbulence
C_λ = ambient intermittent concentration

With the encounter rates, *E* expressed as:

$$E = \beta C_\lambda \qquad (1)$$

Ability of phytoplankton to enhance their nutrient uptake in the presence of ephemeral point source[3]

J = instantaneous nutrient uptake rate (µmol cell^{-1} s^{-1})

$$J \sim E \times C_\lambda \qquad (2)$$

Eq. (2) simply rewrites as:

$$J \sim C_\lambda^2 \qquad (3)$$

The average *J* of phytoplankton cell exposed to an INTERMITTENT nutrient distribution:

$C_0 = \langle C_\lambda \rangle$ is the average nutrient concentration experienced by cells

$$\langle J \rangle_{inter} \sim C_0^2\, \lambda^{K(2)} \qquad (4)$$

The average *J* of phytoplankton cell exposed to a HOMOGENOUS nutrient distribution:

$$\langle J \rangle_{homo} \sim C_0^2 \qquad (5)$$

From the comparisons of Eqs. (4) and (5):

$$\langle J \rangle_{inter} > \langle J \rangle_{homo} \qquad (6)$$

EXPERIMENTAL VALIDATION

Surge uptake rates were estimated on **natural phytoplankton communities** during **drift cruises** in the eastern English Channel under **different turbulent conditions**.

- **2 [NH_4^+] tested: 0.5µM & 2 µM.** Concentrations were measured before addition and 5 minutes after the pulse.
- **Surge uptake rates, ρ (µmol µgC^{-1} min^{-1}):** estimated from consumption and weighted by the phytoplankton biomass
- **The dissipation rate of turbulent energy induced by the tidal flow (ε, m^2 s^{-3}):** estimated from the drift speed and the water column depth[4].
- **Low *in situ* [NH_4^+] (< 1 µM)**

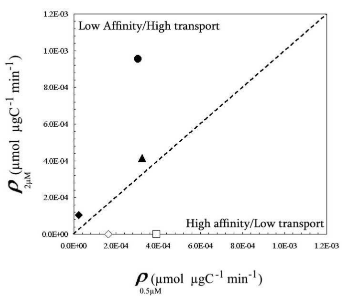

Figure 5: Surge uptake rates after a pulse of 2 µM versus surge uptake rates after a pulse of 0.5 µM (µmol µgC^{-1} min^{-1}). Closed symbol, values recorded on stations characterized by high turbulence levels (i.e. $\varepsilon > 10^{-5}$ m^2 s^{-3}). Open symbols, values recorded on stations characterized by low turbulence levels (i.e. $\varepsilon < 10^{-5}$ m^2 s^{-3}).

High ε	Low ε
+++ Uptake rates	+++ Uptake rates
High [NH_4^+] pulses (2 µM)	Low [NH_4^+] pulses (0.5 µM)
↓	↓
INCREASE IN Transport rate	INCREASE IN Affinity for NH_4^+

THEORETICAL APPROACH

Potential **effect of intermittent nutrient distributions on phytoplankton uptake** estimated from Eqs. (4) and (5) as:

$$\frac{\langle J \rangle_{inter}}{\langle J \rangle_{homo}} \propto \lambda^{K(2)}$$

Using the values of the intermittency parameter *K(2)* & λ estimated for [NH_4^+] distributions under varying conditions of flow velocities: **Increases in *J* by:**

- 4.20-fold → velocity = 0.20 m s^{-1}
- 2.65-fold → velocity = 0.50 m s^{-1}
- 1.48-fold → velocity = 1.00 m s^{-1}

Under nutrient limitation + no significant differences in the average [NH_4^+] ($C_0 = \langle C_\lambda \rangle$)

High ε	Low ε
Low density [NH_4^+] patches	**High** density [NH_4^+] patches
+++ Depleted	+ Depleted
Low uptake rates; Low affinity for [NH_4^+]	Transport limitation
OPTIMAL UPTAKE STRATEGY	OPTIMAL UPTAKE STRATEGY
INCREASE IN Transport rate	INCREASE IN Affinity for NH_4^+

CONCLUSION

The results of our observations and theoretical model suggest that:

1) For same [NH_4^+], the distribution of NH_4^+ is controlled by turbulence, switching from a more homogeneous to a more heterogeneous distribution respectively under high and low turbulence intensities.

2) The turbulent regime experienced by phytoplankton cells, here referred to as their 'turbulent history' will condition their affinity to NH_4^+ and its transport rate.

As a consequence, any uptake experiments conducted on natural phytoplankton communities would be intrinsically influenced, by their turbulent history.

Acknowledgements: We acknowledge the captain and the crew of the NO 'Côtes de la Manche', Dr. V. Gentilhomme & Prof. J.C. Dauvin.
This work was supported by the PNEC 'Manche Orientale-sud Mer du Nord', the Australian Research Council and Flinders University (South Australia).