The net metabolic balance of the open ocean: A test of the nutrient loading hypothesis

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1 Abstract

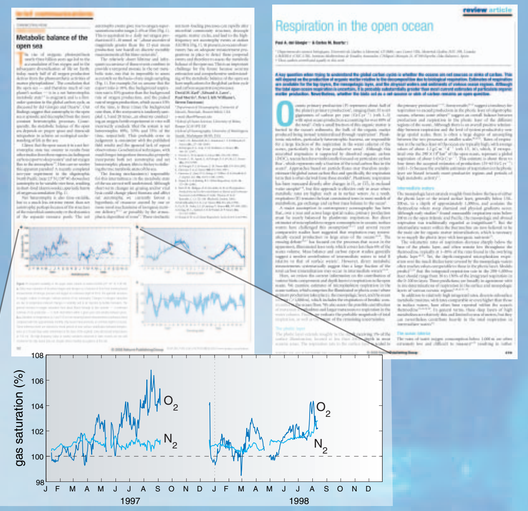
It has recently been suggested that net autotrophy in the oligotrophic North Pacific Ocean is episodic, and decoupled from the more constant rate of respiration (R). To test this hypothesis, we conducted a series of nutrient loading experiments wherein nutrient-rich deep water was mixed, in variable proportions, with surface waters collected from selected oligotrophic stations. Several results were consistent with the ecological predictions of the hypothesis including: (1) nutrient additions stimulated the growth of phytoplankton, (2) gross primary production (GPP) increased dramatically while respiration remained relatively constant, and (3) the metabolic balance shifted temporarily from net heterotrophic (GPP < R) to net autotrophic (GPP > R). These results indicate that stochastic loading of nutrients, as might occur from aperiodic mixing events, can rapidly alter microbial community structure, decouple organic matter cycles, and lead to a time- and space-dependent mosaic of microbial metabolism in the open sea. A proper accounting of both phases will be needed to achieve accurate estimation of the net metabolic balance in these ecosystems.

2 Introduction and Rationale

The need to understand the global carbon cycle has become increasingly important over recent years, but even today there are gaps in our knowledge of open ocean metabolism and the mechanisms driving the oligotrophic ocean's carbon cycle.

It has been proposed that the oligotrophic open ocean is in a state of net heterotrophy when observed by traditional methods (del Giorgio *et al.* 1997, Duarte & Agusti 1998, del Giorgio & Duarte 2002). However this is contrary to geochemical evidence which includes carbon export to the deep ocean, net oxygen flux to the atmosphere and decreasing surface DOC concentrations from the center to the edge of the North Pacific subtropical gyre (NPSG) (Smith *et al.* 2002, Emerson *et al.* 1995, Nijjar & Keeling 2000, Abel *et al.* 2000).

Emerson *et al.* (2002) have observed episodic increases in oxygen saturation in surface waters near the Hawaii Ocean Time-series (HOT) Station ALOHA using gas tension sensors, suggesting bursts of net community production (NCP). In parallel to this work a recent study (Williams *et al.* submitted) attempted to define an annual budget of oxygen flux with monthly sampling at Station ALOHA, but even this high-resolution sampling strategy was not frequent enough to capture these events. As a result of this work it was suggested (Karl *et al.* 2003) that these bursts of NCP were fueling a more stable base-line of respiration which would led to a more balanced budget of production. These results lead to an experiment to try and replicate conditions of positive NCP by loading oligotrophic surface water with nutrient-rich deep water.



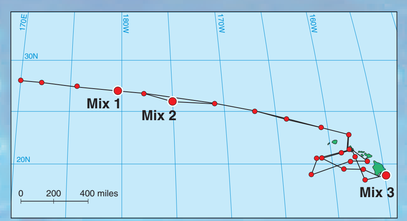
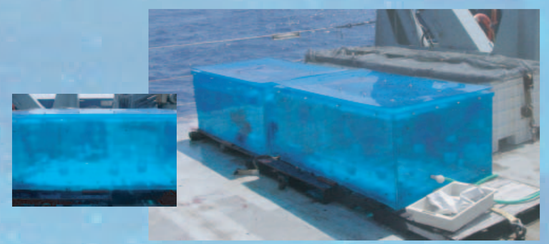


Figure1. Track of cruise MP9 and the locations where water was sampled for mixing experiments 1-3.



3 Method

Experimental work was carried out on the MANTRA component of the Biocomplexity program, cruise MP9, July-August 2003 in the NPSG (**Figure 1**). To test the nutrient loading hypothesis, varying quantities of nutrient-rich deep water were added to nutrient-poor surface water collected from within the mixed layer. The water was mixed into acid-cleaned polycarbonate carboys with a total volume of approximately 25 liters (**Figure 2**). **Table 1** details the parameters presented in this poster that we measured to track biological activity.

Assay	Method	References
Dissolved oxygen production and respiration	Computer controlled Winkler titration. 24 h light and dark incubations (n=6)	Carritt & Carpenter (1966) Williams & Jenkinson (1982)
Chlorophyll: pigments a, b, c and pheopigments	Filter samples, chlorophyll extracted in 100% acetone. Measured on Turner Designs TD-700 fluorometer.	Strickland & Parsons (1972) Walschmeyer (1994)
Dissolved Inorganic Phosphate [DIP]	MAGnesium-Induced Coprecipation (MAGIC)	Karl and Tien (1992)

Table 1. Measurements and methods for the data shown on this poster.

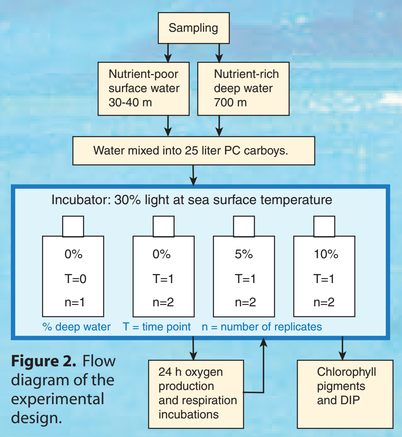
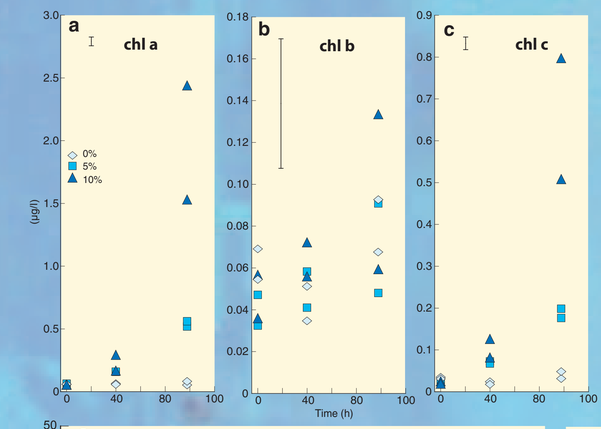


Figure 2. Flow diagram of the experimental design.

4 Results



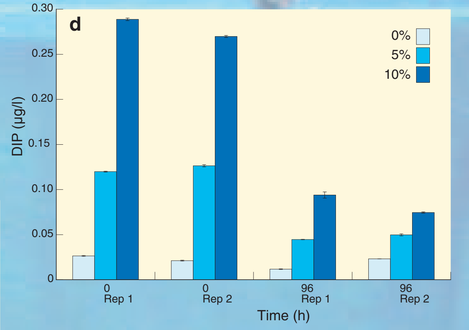


Figure 3. Mixing experiment 2, 4 days in duration. **a, b, c,** Time course measurements for both incubation replicates of chlorophyll pigments a, b and c respectively, error bars are the analytical standard error around the mean. Chlorophyll a and c show a distinct increase throughout the experiment with an increasing response with greater additions of deep water. Chlorophyll b showed no significant response over time or with differing additions of deep water. **d,** DIP (M) at the start and end of the experiment, error bars show 1 standard error. Phosphate uptake rates based on the 4 day experiment averaged standard error 1.62.1, 19.00.2 and 48.80.1 nM d^{-1} for the 0%, 5% and 10% deep water additions respectively.

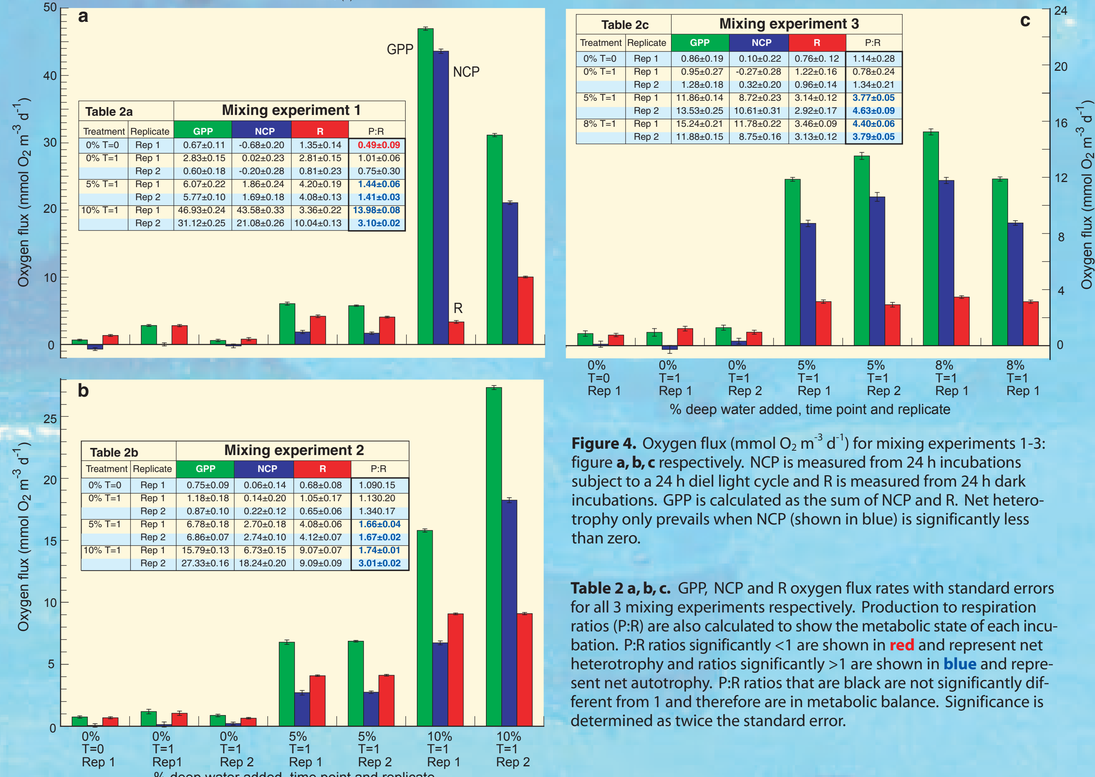


Table 2a

Treatment	Replicate	Mixing experiment 1 GPP	NCP	R	P:R
0% T=0	Rep 1	0.67±0.11	-0.68±0.20	1.35±0.14	**0.49±0.09**
0% T=1	Rep 1	2.83±0.15	0.02±0.23	2.81±0.15	1.01±0.06
	Rep 2	0.60±0.18	-0.20±0.28	0.81±0.23	0.75±0.30
5% T=1	Rep 1	6.07±0.22	1.86±0.24	4.20±0.19	**1.44±0.06**
	Rep 2	5.77±0.10	1.69±0.18	4.08±0.13	**1.41±0.03**
10% T=1	Rep 1	46.93±0.24	43.58±0.33	3.36±0.22	**13.98±0.08**
	Rep 2	31.12±0.25	21.08±0.26	10.04±0.13	**3.10±0.02**

Table 2b

Treatment	Replicate	Mixing experiment 2 GPP	NCP	R	P:R
0% T=0	Rep 1	0.75±0.09	0.06±0.14	0.68±0.08	1.090.15
0% T=1	Rep 1	1.18±0.18	0.14±0.20	1.05±0.17	1.130.20
	Rep 2	0.87±0.10	0.22±0.12	0.65±0.06	1.340.17
5% T=1	Rep 1	6.78±0.18	2.70±0.18	4.08±0.06	**1.66±0.04**
	Rep 2	6.86±0.07	2.74±0.10	4.12±0.07	**1.67±0.02**
10% T=1	Rep 1	15.79±0.13	6.73±0.15	9.07±0.07	**1.74±0.01**
	Rep 2	27.33±0.16	18.24±0.20	9.09±0.09	**3.01±0.02**

Table 2c

Treatment	Replicate	Mixing experiment 3 GPP	NCP	R	P:R
0% T=0	Rep 1	0.86±0.19	0.10±0.22	0.76±0. 12	1.14±0.28
0% T=1	Rep 1	0.95±0.27	-0.27±0.28	1.22±0.16	0.78±0.24
	Rep 2	1.28±0.18	0.32±0.20	0.96±0.14	1.34±0.21
5% T=1	Rep 1	11.86±0.14	8.72±0.23	3.14±0.12	**3.77±0.05**
	Rep 2	13.53±0.25	10.61±0.31	2.92±0.17	**4.63±0.09**
8% T=1	Rep 1	15.24±0.21	11.78±0.22	3.46±0.09	**4.40±0.06**
	Rep 2	11.88±0.15	8.75±0.16	3.13±0.12	**3.79±0.05**

Figure 4. Oxygen flux (mmol O_2 m^{-3} d^{-1}) for mixing experiments 1-3: figure **a, b, c** respectively. NCP is measured from 24 h incubations subject to a 24 h diel light cycle and R is measured from 24 h dark incubations. GPP is calculated as the sum of NCP and R. Net heterotrophy only prevails when NCP (shown in blue) is significantly less than zero.

Table 2 a, b, c. GPP, NCP and R oxygen flux rates with standard errors for all 3 mixing experiments respectively. Production to respiration ratios (P:R) are also calculated to show the metabolic state of each incubation. P:R ratios significantly <1 are shown in **red** and represent net heterotrophy and ratios significantly >1 are shown in **blue** and represent net autotrophy. P:R ratios that are black are not significantly different from 1 and therefore are in metabolic balance. Significance is determined as twice the standard error.

5 Conclusions

- It is possible to quickly alter the metabolic balance of the oligotrophic surface waters of the NPSG with the addition of nutrient-rich deep water.
- Large increases in P:R ratios show a decoupling of GPP from R.
- Differing responses in chlorophyll a, b and c suggest a change of inital phytoplankton community structure following the nutrient additions.
- The rate of phosphate drawdown was observed to be dependent on the size of the nutrient perturbation.

As the other samples and data become available it will help us to understand and resolve the way in which oligotrophic planktonic communities respond to nutrient injections. The additional parameters measured include nutrients (phosphate, nitrate + nitrite and silicate), flow cytometry, ^{14}C production and bacterial ^{3}H leucine production.

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