Investigating nitrogen remineralization in the mesopelagic with molecular and geochemical approaches

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Estimates of bacterial carbon demand apparently exceed POC supply

Steinberg et al. 2008; Giering et al. 2014
What does the nitrogen budget in the upper mesopelagic tell us?

Respiration: \[ \text{CH}_2\text{O} + \text{O}_2 \rightarrow \text{CO}_2 + \text{H}_2\text{O} \]

Nitrification: \[ \text{NH}_3 + 2 \text{O}_2 \rightarrow \text{NO}_3^- + \text{H}^+ + \text{H}_2\text{O} \]

Two advantages:

Unlike carbon respiration, we can measure N remineralization directly.

Less concern about excluding particle-associated processes.
Patterns in the distribution and activity of nitrifying organisms in the Pacific

Balancing PON export and N demand, and the fuel for autotrophy in the mesopelagic

Asking the microbes about the mesopelagic
Central California Current: 2007, 2009

Equatorial Pacific: 2011
“METZYMME”

Siegel et al. 2014, GBC

Eastern Tropical South Pacific: 2009, 2010
“ETSP”
THE EXPERIMENTAL DECOMPOSITION AND REGENERATION OF NITROGENOUS ORGANIC MATTER IN SEA WATER

THEODOR VON BRAND, NORRIS W. RAKESTRAW AND CHARLES E. RENN

3. The main stages in the decomposition are: dead body—ammonia—nitrite—nitrate.

Von Brand et al. 1937
**Fig. 2.** Series IV. The decomposition of nitrogenous organic matter in mixed plankton, showing the appearance of soluble nitrogen compounds in the water in which it is suspended. Plankton previously filtered through No. 8 bolting silk.
Nitrification proceeds in two steps by two separate groups of organisms

ammonia oxidation: $\text{NH}_3 \rightarrow \text{NH}_2\text{OH} \rightarrow \text{NO}_2^-$

nitrite oxidation: $\text{NO}_2^- \rightarrow \text{NO}_3^-$

Most ammonia oxidation in the ocean carried out by ammonia-oxidizing archaea (AOA).

All cultivated marine nitrifiers (AOA and NOB) are chemolithoautotrophic . . . fussy, slow growing.

*Nitrospina gracilis*

Watson and Waterbury 1971
Nitrogen remineralization is linked to production of nitrous oxide ($N_2O$)

Nevison et al. 2003
Santoro et al. 2010; *Environ. Microbiol.*
AOA and NOB correlated throughout the Pacific

\[ \text{log}_{10} \text{Nitrospina} \text{ 16S rRNA genes (mL}^{-1}) \]

\[ \text{log}_{10} \text{AOA amoA genes (mL}^{-1}) \]

California Current (CN)
ETSP
METZYME

\[ R^2 = 0.82 \]
\[ m = 0.86 \]

Santoro, unpublished
Offset between ammonia oxidation and nitrite oxidation

Santoro, Buchwald, Casicotti; unpublished
See also Lipschultz et al. 1990; Füssel et al. 2012
Significant relationships between rates and clade-specific gene abundance

Same relationship demonstrated by Smith et al. (2014) for Monterey Bay
Two AOA ecotypes across the Western Equatorial Pacific.

METZYME PIs: Carl Lamborg and Mak Saito
Balancing PON export and N demand, and fuel for autotrophy in the mesopelagic
Relating nitrification rates and PON flux

Ward and Zafiriou 1988, redrawn in Ward 2008

Newell et al. 2011

Arabian Sea

ETNP

Ward and Zafiriou 1988, redrawn in Ward 2008
Pls: Karen Casciotti, Doug Capone, Will Berelson, Angie Knapp
Collaborators: Carly Buchwald and Rachel Foster
Foster, Santoro, and Berelson unpublished
5/6 trap samples: No detectable AOA or NOB.

Archaeal amoA abundance (x10^3 genes mL^-1)

Nitrification rate (nmol m^-2 d^-1)
Depth integrated nitrification from the base of the euphotic zone to 200 m.

PON loss over the same interval.

Trap data: Will Berelson (USC)
Trap PON loss is balanced by nitrification rate.
How much autotrophy in the mesopelagic could be fueled by nitrification?

Carbon export: 6 Pg C y\(^{-1}\)  
(Siegel et al. 2014)

Nitrogen export: 0.91 Pg N y\(^{-1}\)

C fix:N ox for AOA: 1:19  
(Könneke et al. 2014)

0.05 Pg C y\(^{-1}\) fixed by AOA  
0.01 Pg C y\(^{-1}\) fixed by NOB

Or about 7% of proposed mesopelagic C fixation.

6.5 \times 10^{13} \text{ mol C y}^{-1}  
(0.8 Pg y\(^{-1}\))

Herndl et al. 2005
What do the microbes themselves tell us about the mesopelagic?
Two clades of AOA in the open ocean

WCA
- Cal Current 68_6790_75_20_D09
- San Francisco Bay DQ148664_SF_CB20_9
- *Nitrosopumilus maritimus*
- ALOHA, 200m EF106943_HF200_15E20
- Gulf of California EU340511_GOC-C-60-1
- Sargasso Sea AACY020420743
- **CN25E_amoA**
- **CN75E_amoA**
- Gulf of California EU340467_GOC-G-60-4
- Peru upwelling FJ79199
- Sargasso Sea AACY022879949
- Cal Current cDNA 24_6760_25m_cDNA
- Cal Current cDNA 17_6790_50m
- Cal Current 53_6790_150m_cDNA_E07
- **CN150E_amoA**
- DQ148760_ETNP_17
- Sargasso Sea AACY022417858

WCB
- 59_6760_500m_cDNA_C08
- ALOHA EF106911_HF770_38H24
- ALOHA EF106944_HF500_19K23
- Cal Current 34_6760_500_10_B05
- Black Sea DQ148697_BS15_7_20
- EF106922_HF4000_28N04
- EU810229_natlanic_clone_V4
- EF106919_HF4000_22M05
- EU340552_GOC-C-450-18
- 67_6760_500m_cDNA_C09
- 35_6760_100m_cDNA
- 639_6760_50_15_G05

Depth:
- **Cenarchaeum symbiosum**
- Alpine soil clone DQ534697
- SoilFosmid54d9
- Nitrososphaera gargensis
- Nitrosocaldus yellowstonii
Depth partitioning of AOA ecotypes across the Western Equatorial Pacific.

But what do these ecotypes mean?
Only four AOA cultures from the open ocean

Growth rate $= 0.17 \text{ d}^{-1}$, doubling time $\sim 4 \text{ d}$

Santoro and Casciotti, 2011; *ISMEJ*
With Chris Dupont (JCVI) and Mak Saito (WHOI)
GOS data mapped at 90% nucleotide ID
The abundance of ammonia oxidizers (AOA) and nitrite oxidizers (NOB) are tightly coupled in the mesopelagic, and the abundance of specific clades can be correlated with rates.

PON flux and nitrogen remineralization can be balanced in the upper mesopelagic.

The distribution of microorganisms in the mesopelagic may tell us about the processes happening there, but we lack cultures of representative organisms with which to fully interpret the data.
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