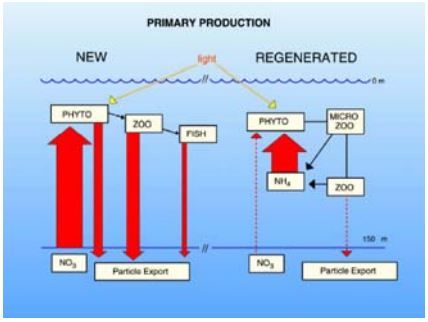
Plankton production is supported by 2 types of nitrogen:

1) new production supported by external sources of N (e.g. NO_3^- and N_2),
2) *recycled or regenerated* production, sustained by recycling of N.



-Why does this generalization apply to the open sea but not near shore environments?

The f-ratio

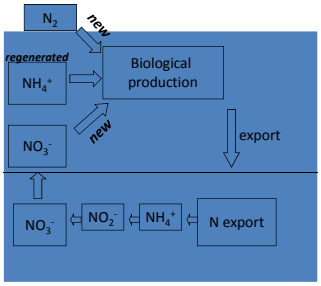
Assumptions:
1) N_2 fixation is low
2) Steady state system
3) Euphotic zone nitrification is low

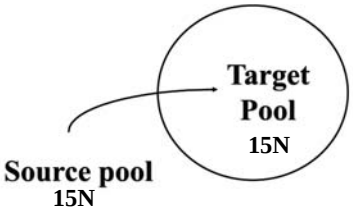
$$f = (VNO_3^-)/ (VNO_3^- + \sum VN_R)$$

Note N_R includes regenerated forms of N uptake (historically thought to include urea and NH_4^+)

Mathematical description linking new production and organic matter export. At steady state, nitrogen input is balanced by nitrogen export.

Under steady state (i.e. nitrate input balanced by export/grazing loss), if export is less than input, biomass accumulates. This biomass must eventually be exported to keep the system in steady state.





$$\text{Net Uptake Rate} = \frac{\frac{^{15}N}{\text{atom \% of target}}}{\text{atom \%} \times \text{Time}} \times [\text{target}]$$

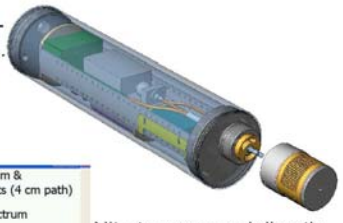
^{15}N of source

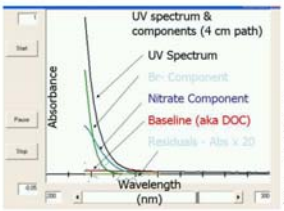
Determining the f-ratio

- Incubate seawater in the presence of trace $^{15}NO_3^-$, $^{15}NH_4^+$, and sometimes ^{15}N-urea
- Calculate NO3-, NH4+, and "DON" uptake
- What makes this difficult for the oligotrophic ocean?

Autonomous sensing of nitrate

MBARI In Situ Ultraviolet Spectro-photometer (ISUS). Now commercially available from Satlantic.

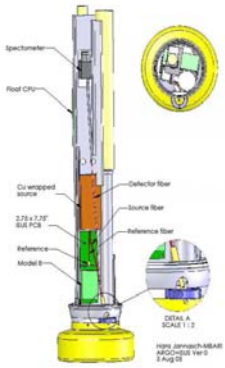


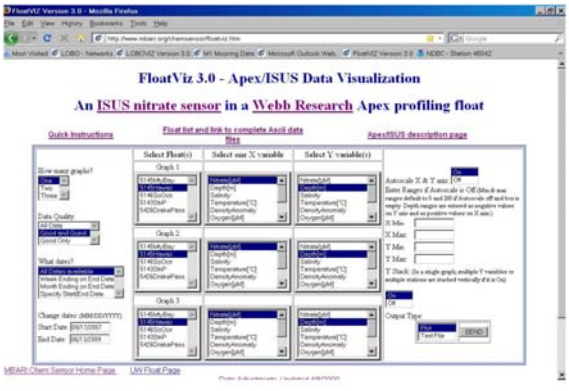


Nitrate measured directly using UV absorption spectrum from 217 to 240 nm (Johnson & Coletti, Deep-Sea Res. I, 49, 1291 2002).

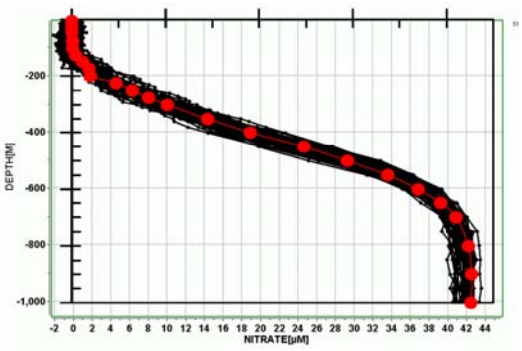
ISUS integrated into APEX float.

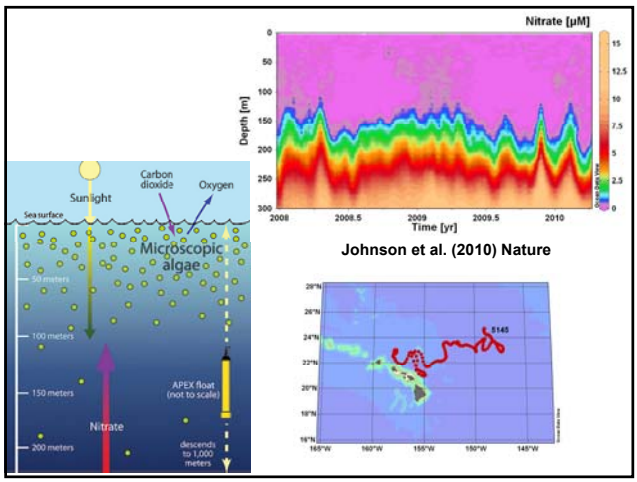
- 44 joule/NO_3^- measurement
- 60 NO_3^- meas./profile to 1000 m
- Detection limit ~0.5 µM
- Float endurance 260 profiles to 1000 m. ~4 year life at 5 day cycle time.
- Requires Iridium comms. & Li batteries





Red dots are HOT mean NO_3^- profile.





Not all "new" nutrients are introduced to the euphotic zone from below…

- Atmospheric deposition (both dry and wet) can form an important source of nutrients.
- Advection: lateral input of nutrients
- N_2 fixation

Assimilation of N by N_2 fixation

- N_2 fixation is the primary mode of nitrogen introduction to marine and terrestrial ecosystems.
- N_2 fixation converts N_2 to NH_3; exclusively prokaryotic process
- Requires significant energy expensive

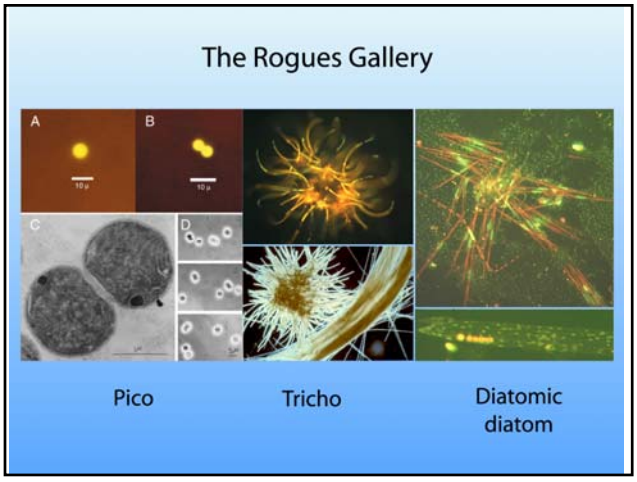
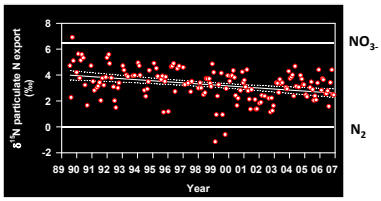


Table 1. Annual particulate nitrogen export fluxes at Station ALOHA.

Year	Total PN flux (mmol N m^{-2} yr^{-1})	δ^{15}N-F_{PN}* (‰ vs. air N_2)	N_2-supported fraction (%)	Contributions to flux (mmol N m^{-2} yr^{-1}) N_2	NO_3^-
1990	145	3.85	41	59	86
1991	111	3.21	51	56	55
1992	80	3.58	45	36	44
1993	86	4.15	36	31	55
1994	80	3.81	41	33	47
1995	81	3.76	42	34	47
1996	87	4.04	38	33	54
1997	113	3.29	49	56	57
1998	116	3.21	51	59	57
1999	122	2.03	69	84	38
2000	113	3.05	53	60	53

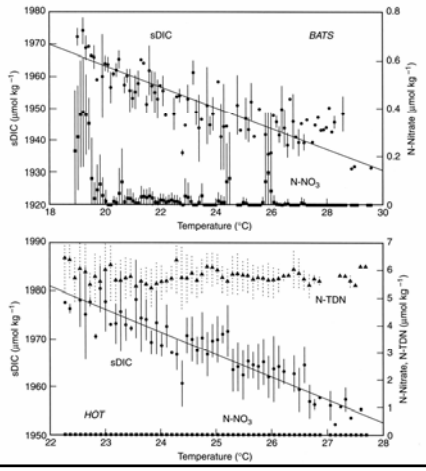
* Flux-weighted annual average.

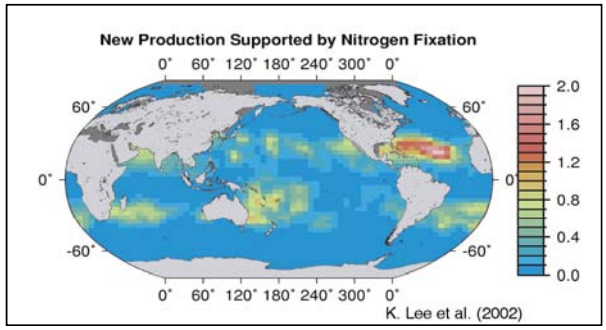
At Station ALOHA, N_2 fixation appears to contribute ~30-84% of new production



Each annual cycle at HOT and BATS has significant Dissolved Inorganic Carbon (DIC) drawdown, but not enough nitrate is present in surface water to support growth.

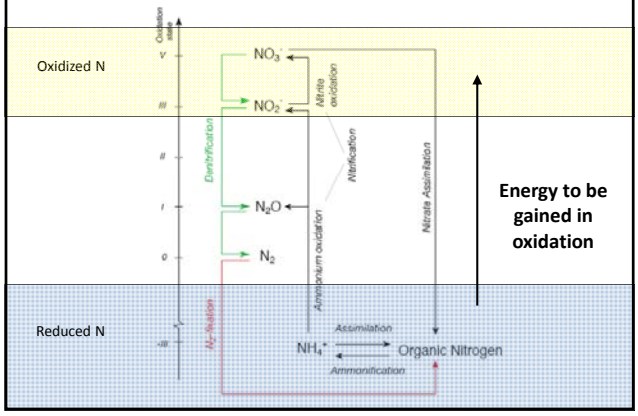
from Karl et al. in Fasham, Ocean Biogeochemistry





Global estimate of N_2 fixation based on N-DIC drawdown in NO_3^- depleted warm waters is equivalent to 0.8 ±0.3 Pg C yr^{-1}

Let's look at dissimilatory nitrogen transformations



Energy to be gained in oxidation

Dissimilatory nitrogen transformations

$NH_2OH \rightarrow NO \rightarrow N_2O$

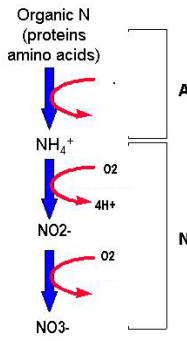
Nitrification: $NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$

Denitrification: $NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$

Anammox: $NO_2 + NH_4^+ \rightarrow N_2 + 2H_2O$

Nitrification

- Biological oxidation of NH_3 to NO_3^- using oxygen as terminal electron acceptor.
- Two step process; ammonia oxidation followed by nitrite oxidation; both reactions yield energy.
- NO_2^- serves as an important intermediate; incomplete nitrification also yields N_2O.



Ammonification

Degradation of organic N to ammonium occurs during heterotrophic metabolism.

Nitrification

Nitrification is a 2 step process that is mediated by different groups of microbes. The first step (termed ammonium oxidation) oxidizes NH_4^+ to NO_2^-, and the second step converts NO_2^- to NO_3^-.

Aerobic regeneration of nitrogen

Complete decomposition of organic matter

$(CH_2O)_{106}(NH_3)16H_3PO_4 + 138O_2 \Rightarrow 106CO_2 + 122H_2O + 16HNO_3 + H_3PO_4$

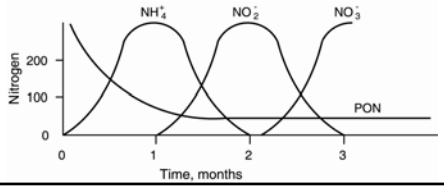
Multi-step process. First step is the breakdown of amino acids to NH_4^+; this process is mediated by heterotrophic microorganisms

$2NH_4^+ + 3O_2 \Rightarrow 2NO_2^- + 4H^+ + 2H_2O$

$2NO_2^- + O_2 \Rightarrow 2NO_3^-$

These reactions yield energy (but not much…)

Nitrification: predominately mediated by chemoautotrophic microbes (best studied are *Nitrosomonas* and *Nitrobacter*)



Recent isolation and cultivation of an abundant archaeal ammonium oxidizer

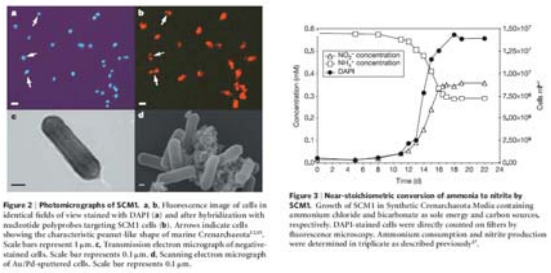
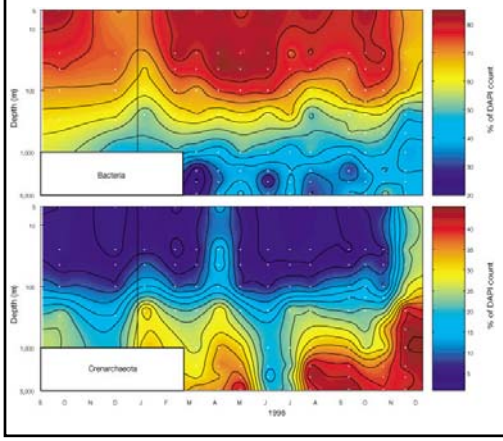
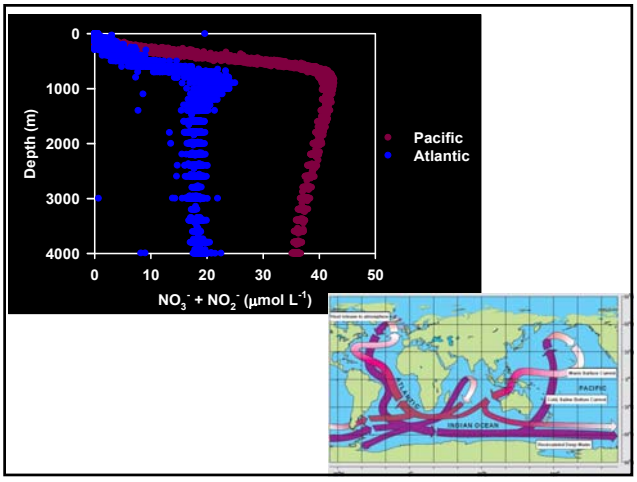


Figure 2 | **Photomicrographs of SCM1. a, b.** Fluorescence image of cells in identical fields of view stained with DAPI (**a**) and after hybridization with nucleotide polyprobes targeting SCM1 cells (**b**). Arrows indicate cells showing the characteristic peanut-like shape of marine Crenarchaeota[3,5,19]. Scale bars represent 1 μm. **c.** Transmission electron micrograph of negative-stained cells. Scale bar represents 0.1 μm. **d.** Scanning electron micrograph of Au/Pd-sputtered cells. Scale bar represents 0.1 μm.

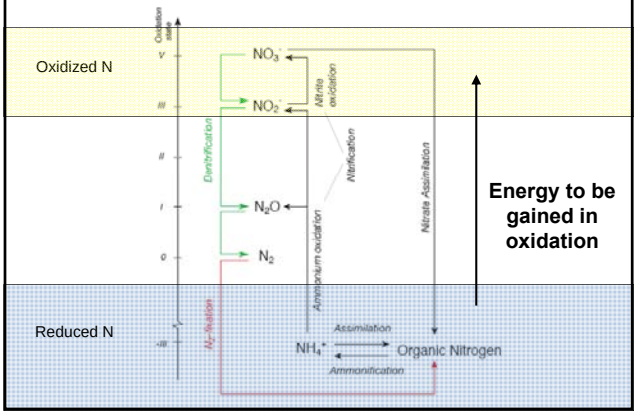
Figure 3 | **Near-stoichiometric conversion of ammonia to nitrite by SCM1.** Growth of SCM1 in Synthetic Crenarchaeota Media containing ammonium chloride and bicarbonate as sole energy and carbon sources, respectively. DAPI-stained cells were directly counted on filters by fluorescence microscopy. Ammonium consumption and nitrite production were determined in triplicate as described previously[17].



Archaea 20-40% of total picoplankton in meso- and bathypelagic waters



Let's look at dissimilatory nitrogen transformations

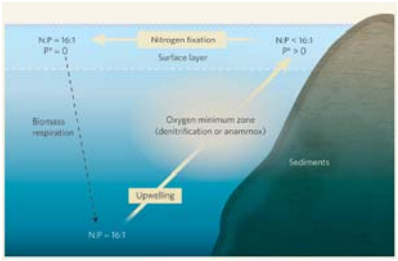


Energy to be gained in oxidation

Denitrification

The reduction of NO_3^- and NO_2^- to N_2 during heterotrophic respiration of organic matter. Occurs predominately in anaerobic or suboxic environments.

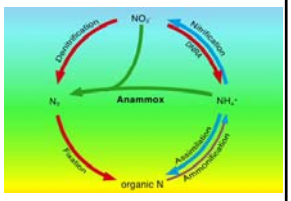
$C_{106}H_{175}O_{42}N_{16}P + 104\ NO_3^- \Rightarrow 106CO_2 + 60N_2 + H_3PO_4 + 138\ H_2O$



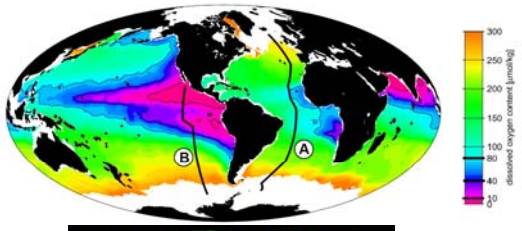
NO_3^- and NO_2^- are used as terminal electron acceptors during heterotrophic respiration.

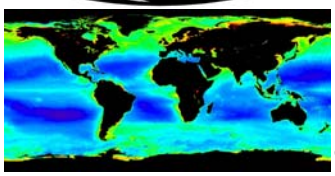
Anaerobic ammonium oxidation (anammox)

- $NH_4^+ + NO_2^- \Rightarrow 2N_2 + 2H_2O$
- Anaerobic ammonium oxidation
- Major source of N_2 gas (along with denitrification)
- Anoxic sediments, marine water column, and sewage wastewater
- Mediated by *Planctomyces*

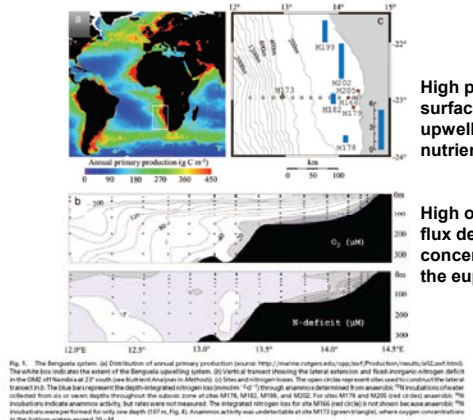


Oxygen concentrations along the 26.9 kg m^{-3} isopycnal surface (~500 m in the N. Pacific)



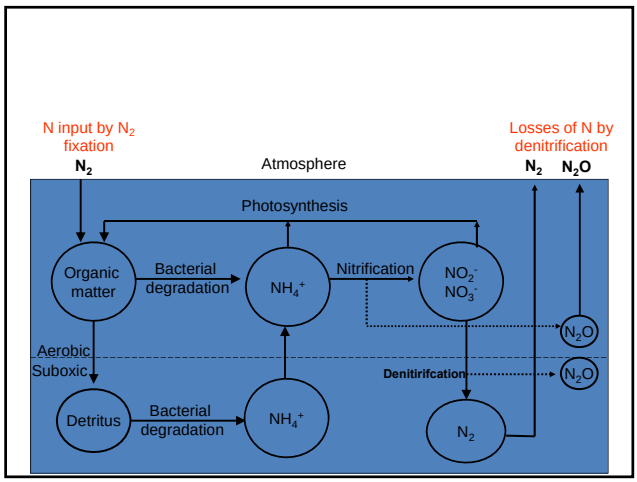


Chlorophyll distributions



High productivity in surface water due to upwelling of nutrients.

High organic matter flux depletes O_2 concentrations below the euphotic zone.



Global Nitrogen Budget

Process	*Nitrogen Flux ($TgN\ yr^{-1}$)*
Sources	
Pelagic N_2 fixation	120 ± 50
Benthic N_2 fixation	15 ± 10
River input (DON)	35 ± 10
River input (PON)	45 ± 10
Atmospheric deposition	50 ± 20
Total Sources	**265 ± 55**
Sinks	
Organic N export	1
Benthic denitrification	180 ± 50
Water column denitrification	65 ± 20
Sediment burial	25 ± 10
N_2O loss to atmosphere	4 ± 2
Total Sinks	**275 ± 55**

1 Tg = 10^{12} g