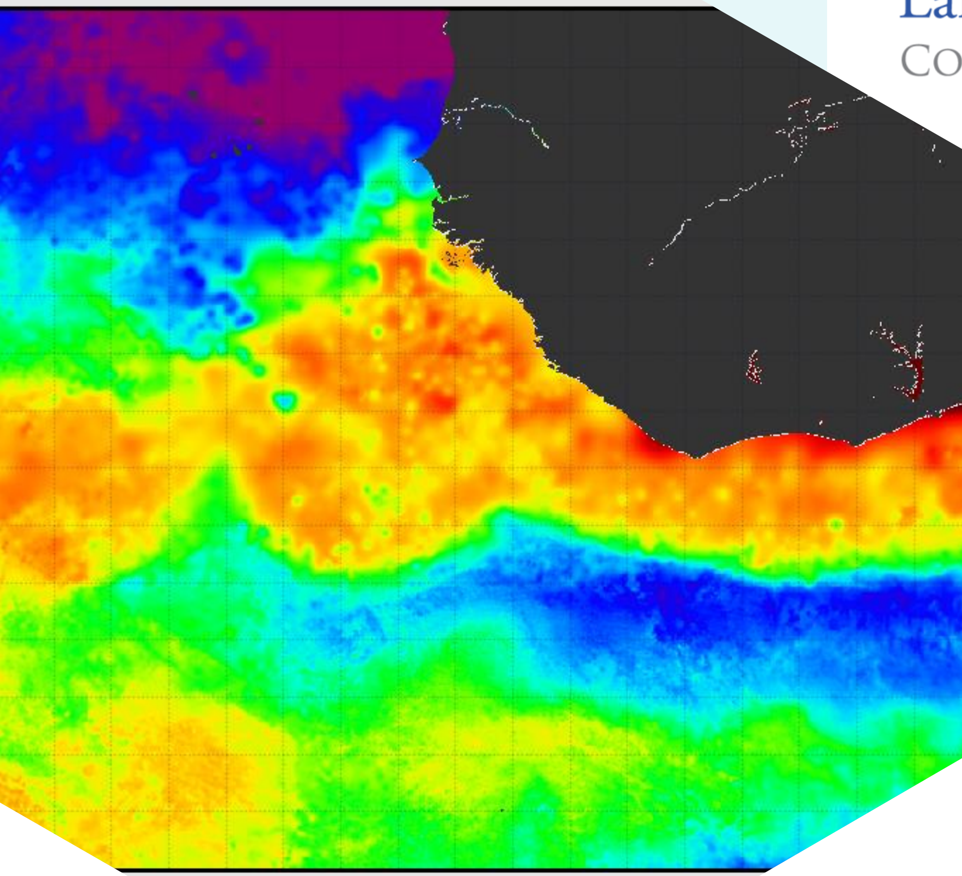


Lamont-Doherty Earth Observatory
COLUMBIA UNIVERSITY | EARTH INSTITUTE

Triatlas Summer School

Phytoplankton Biomass and Primary Production in the Equatorial Atlantic – Who, How much, and why?

Ajit Subramaniam & Ana Fernandez-Carrera

Phytoplankton – why do we care?

- **Base of the marine food web – photosynthesis uses sunlight to convert water and CO_2 to organic carbon and producing O_2 (oceans provide over 20% of the protein consumed by humans)**

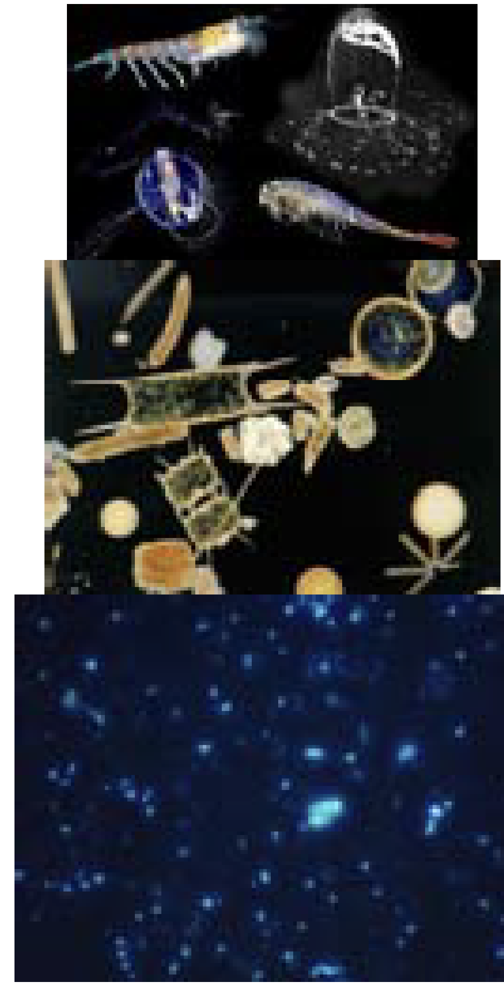
- **Provides 50% of the oxygen we breath (every second breath you take!)**

- **Controls climate and makes this planet habitable (takes up CO_2, a greenhouse gas, from the atmosphere and converts it to organic carbon, some fraction of which sinks to the sea floor)**

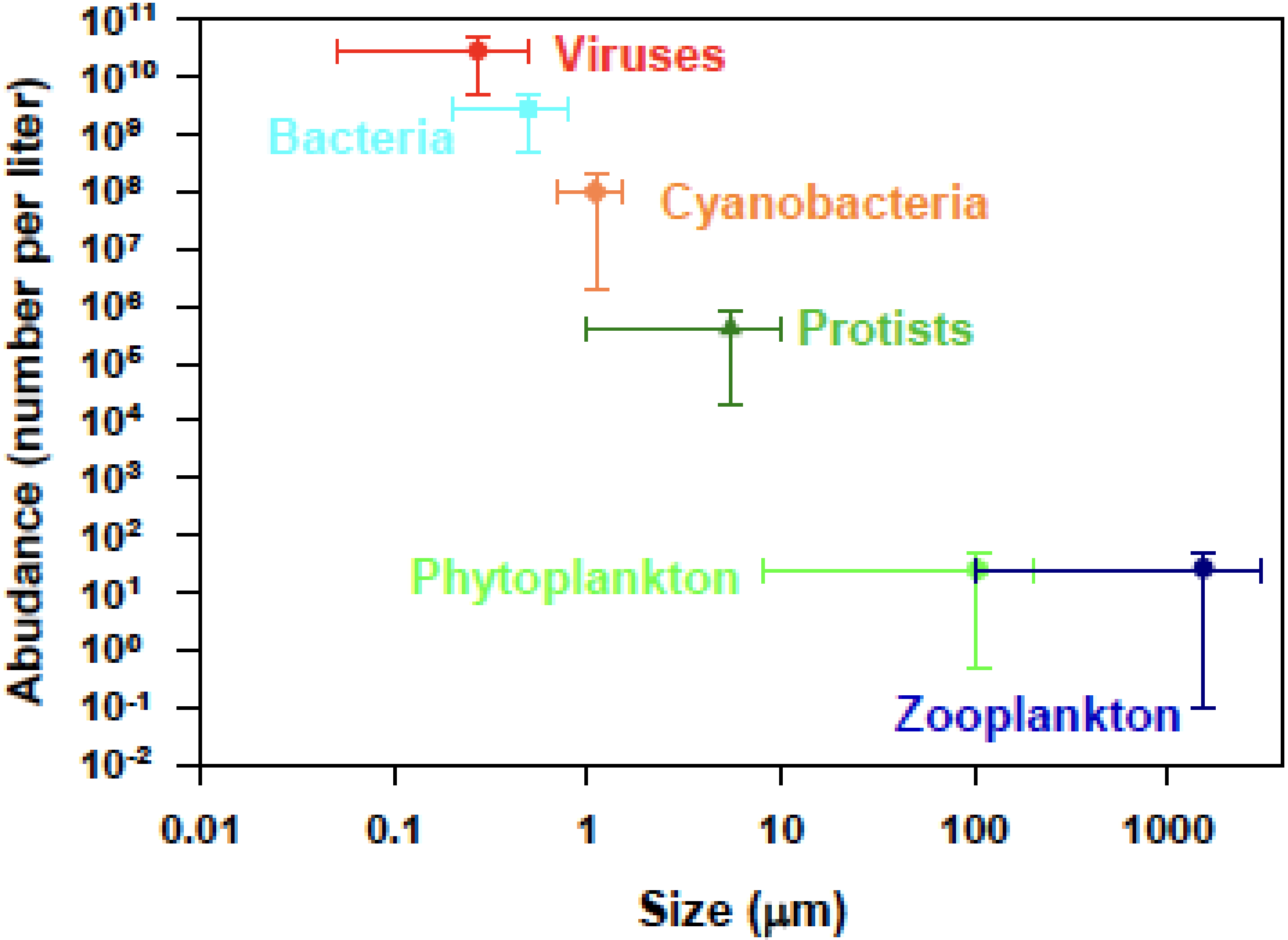
- ***Prochlorococcus*, a marine cyanobacteria, is probably the most abundant plant (photosynthetic organism) on the planet**

In a “typical” liter of seawater…

• Fish	None
• Zooplankton	10
• Diatoms	1,000
• Dinoflagellates	10,000
• Nanoflagellates	1,000,000
• Cyanobacteria	100,000,000
• Prokaryotes	1,000,000,000
• Viruses	10,000,000,000



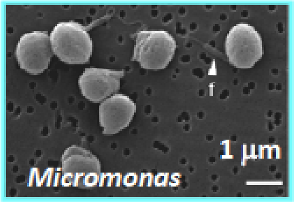
High abundance does not necessarily equate to high biomass. Size is important.



Major divisions and classes of photosynthetic plankton in the ocean

- Prokaryotes
  - Cyanobacteria

- Eukaryotes:
  - Chlorophyta (green algae); include the following classes:
    - Chlorophyceae
    - Prasinophceae
    - Euglenophyceae



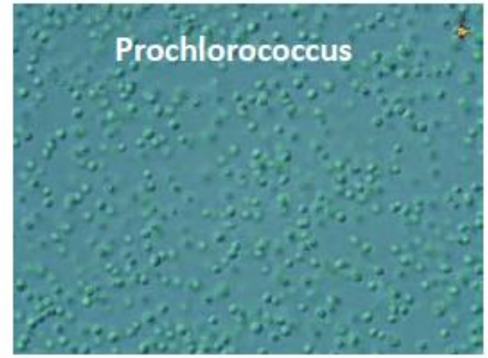
  - Chromophyta (brown algae); include the following classes:
    - Chrysophyceae
    - Pelagophyceae
    - Prymnesiophyceae
    - Bacillariophyceae (diatoms)
    - Dinophyceae (dinoflagellates)
    - Cryptophyceae (crytophytes)
    - Phaeophyceae (phaeophytes)

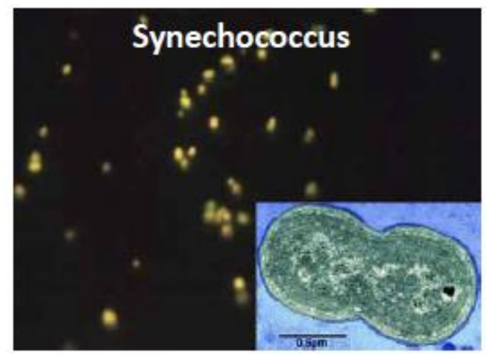
  - Rhodophyta (red algae)-mostly macrophytes

Marine cyanobacteria

- **Cyanobacteria: major groups of cyanobacteria in the oceans include: *Prochlorococcus, Synechococcus, Trichodesmium, Crocosphaera, Richelia***
  - **Wide range of morphologies: unicellular, filamentous, colonial**
  - **Some species fix N_2**
  - **Hugely abundant in the open sea – often dominate photosynthetic biomass and production**

- Contain zeaxanthin



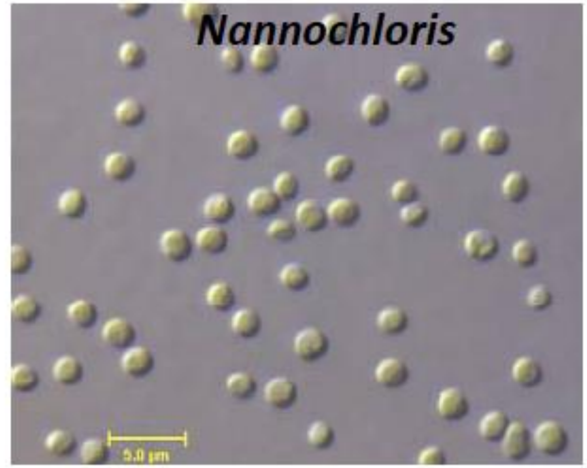


Many images from: http://www.sb-roscoff.fr/Phyto/gallery/main.php?g2_itemId=19

Chlorophyta (green algae)

- Chlorophytes
  - Contain Chl *b*
  - Uncommon in open ocean; mostly freshwater.
  - Very diverse (more than 7000 species described)
  - Can be single cells or colonies, coccoid or flagellated
  - *Chlorella, Chlamydomonas, Dunaliella*

- Prasinophytes
  - Contain Chl *b*
  - Predominately unicellular
  - Relatively common, but not abundant in ocean
  - Can be single cells or colonies, coccoid, biflagellated, or quadri-flagellated

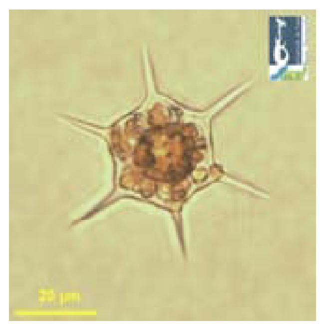


Chromophyta (brown algae)

- **Pelagophytes**
  - Contain Chl *c*
  - Very common in open ocean.
  - Coccoid or monoflagellated

Pelagomonas

- **Chrysophytes**
  - Contain Chl *c*
  - Relatively rare in open ocean
  - Mostly bi-flagellated (flagella of unequal length)



Dictyocha

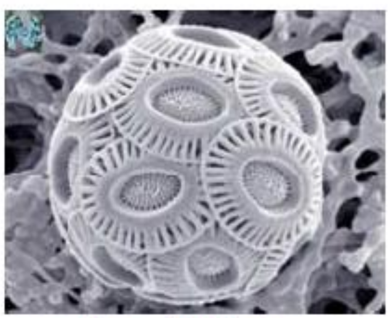
- **Cryptophytes**
  - Contain Chl *c*
  - Contain carotenoid alloxanthin
  - Contain phycoerythrin or phycocyanin
  - Flagellated unicells

Rhodomonas salina

Images from: http://planktonnet.sb-roscoff.fr/index.php#search

Chromophyta (brown algae)-Cont.

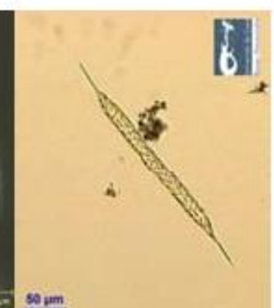
- **Prymnesiophytes**
  - Mainly biflagellates
  - Very common in open ocean
  - 2-5 µm
  - Some species form $CaCO_3$ plates (coccoliths)



Emiliana huxleyi

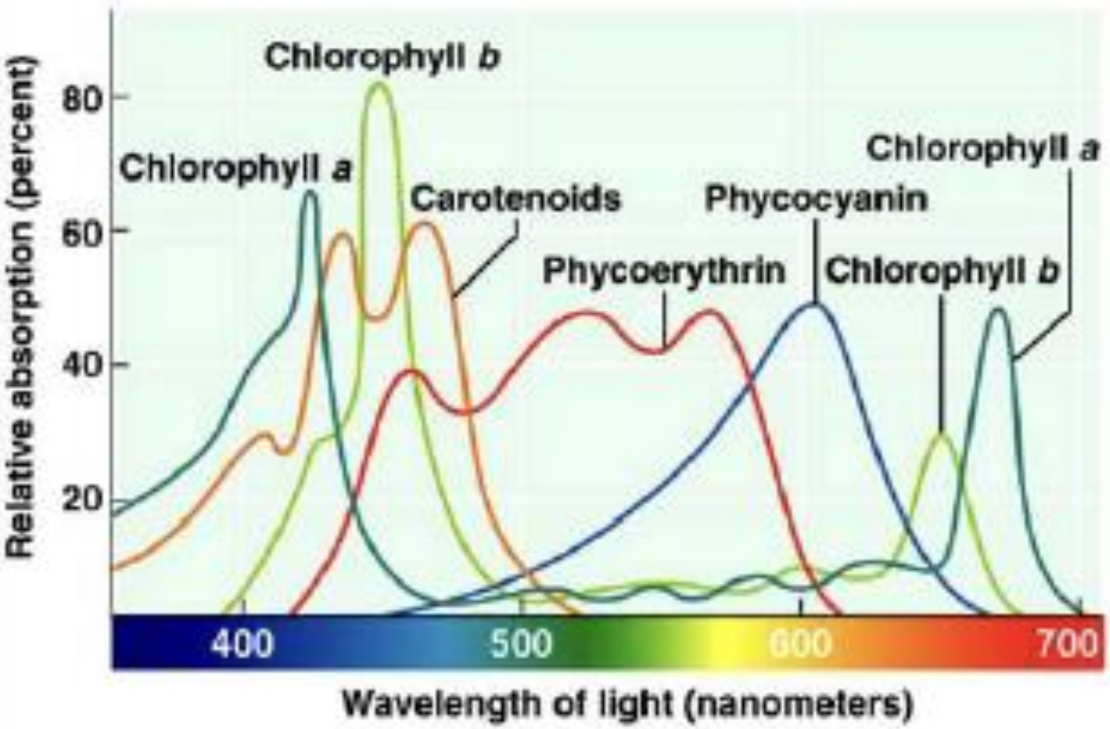
- **Bacillariophytes**
  - Ubiquitous
  - All contain Chl *c* and carotenoid fucoxanthin
  - Rigid silica-impregnated cell wall
  - Many form colonies
  - 2 prominent cell morphologies: centric and pennate

Coscinodiscus



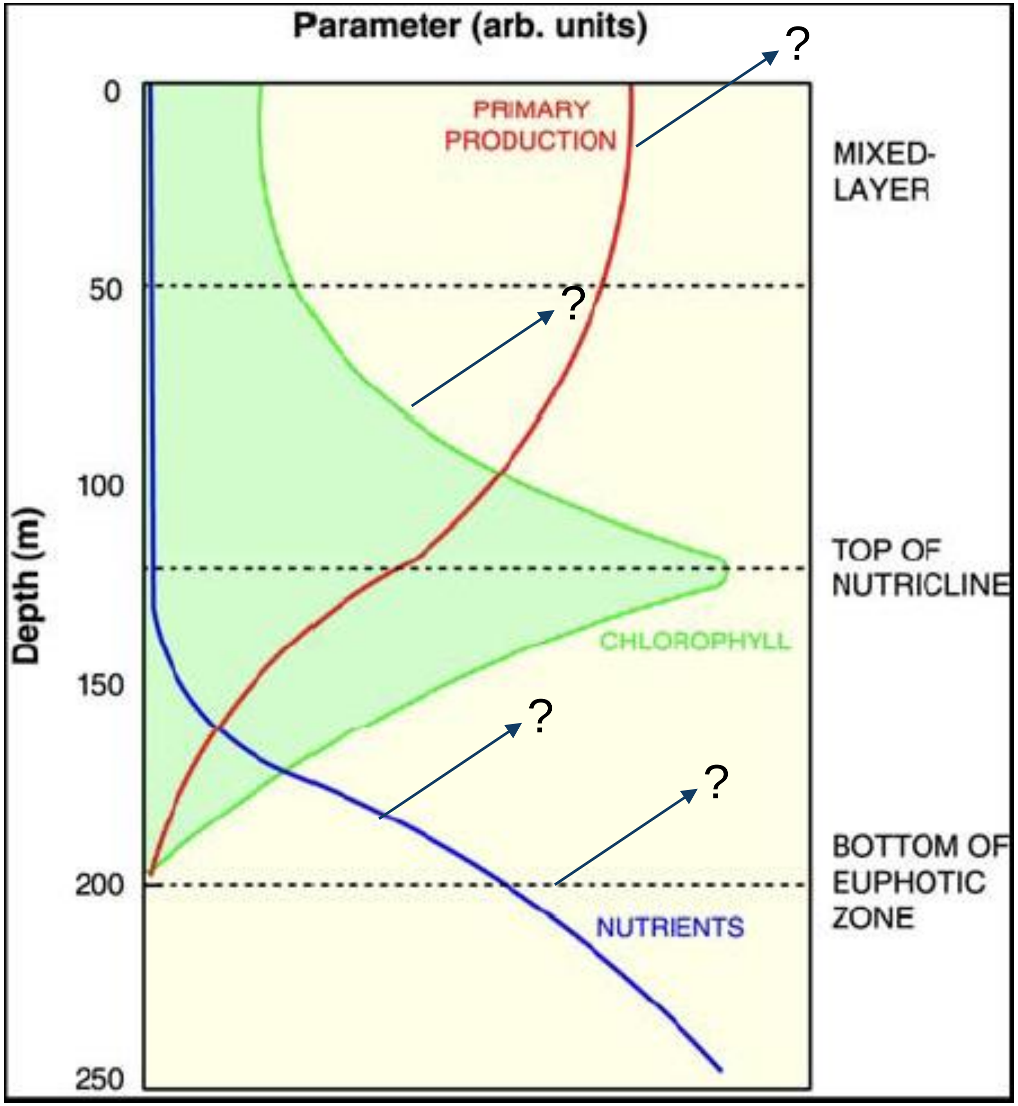
Rhizosolenia

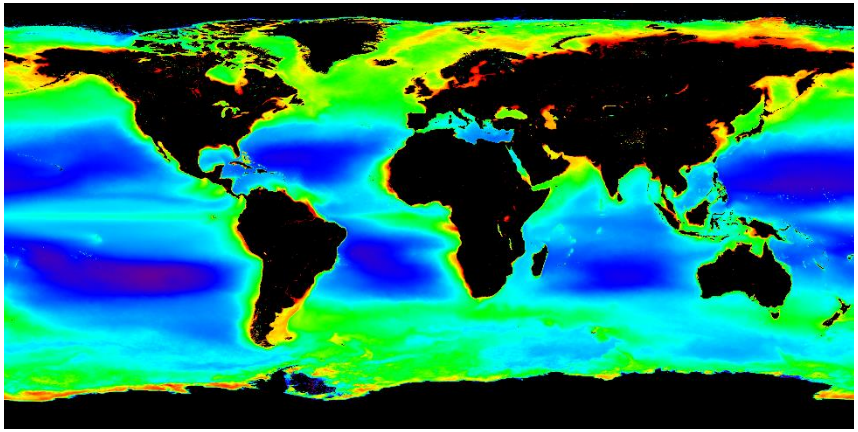
- **Dinophytes**
  - Possess the carotenoid peridinin
  - Widely distributed (estuaries, open ocean)
  - Mostly unicellular and autotrophic, but colorless heterotrophs can also be abundant
  - 2 flagella
  - Many are bioluminescent and some case toxic red tides blooms



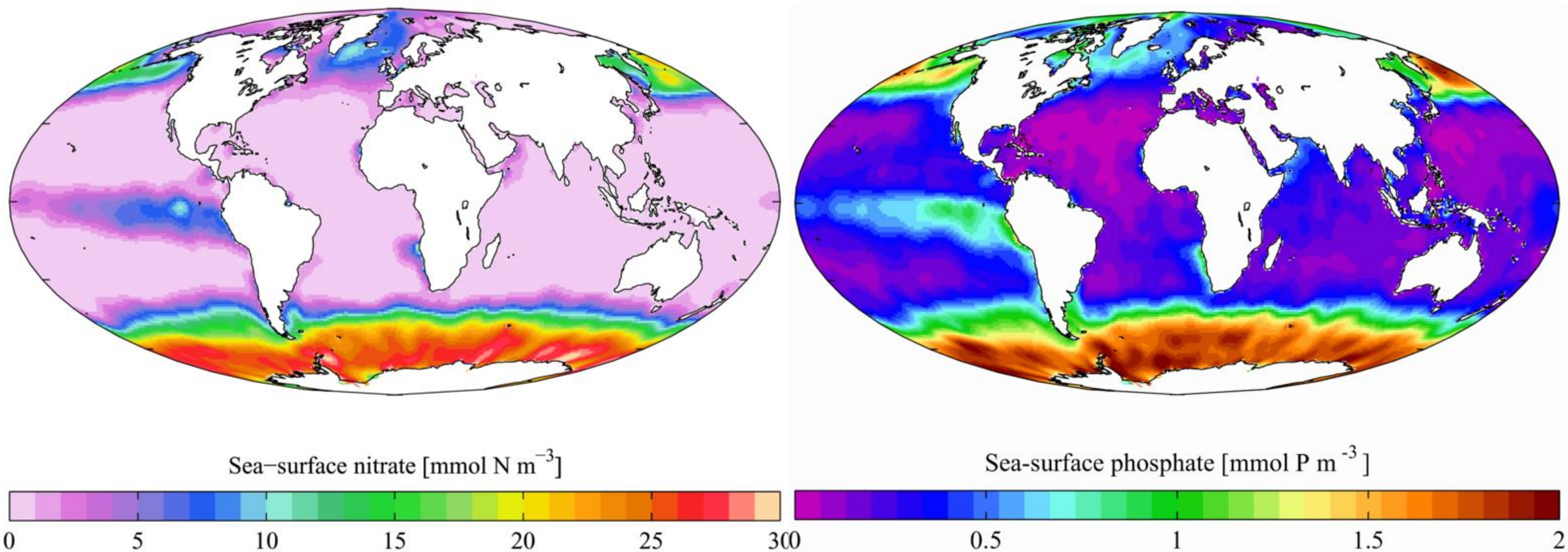
Carotenoids and biliproteins extend the spectral region able to support plankton growth; thus light forms an important environmental control on phytoplankton evolution.

How are they distributed in the world oceans and what controls this distribution?

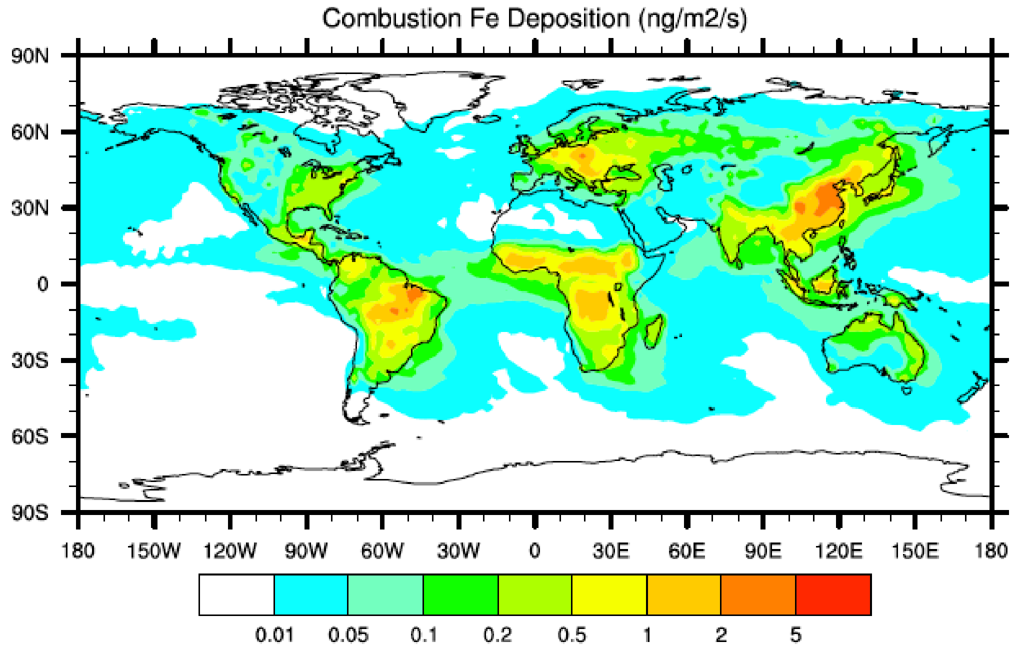


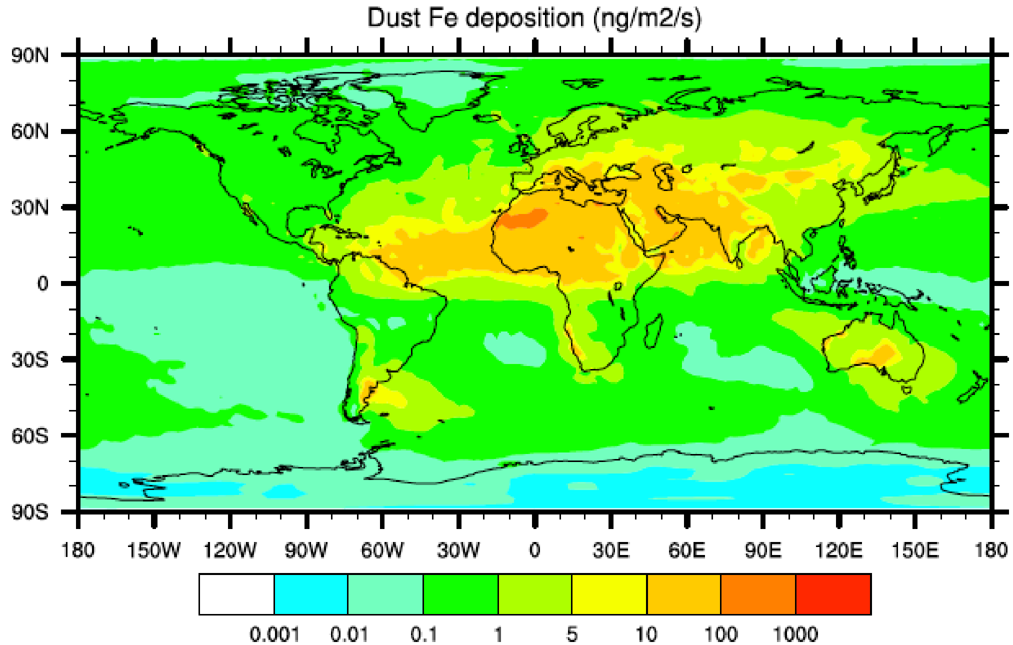


https://oceancolor.gsfc.nasa.gov/l3/

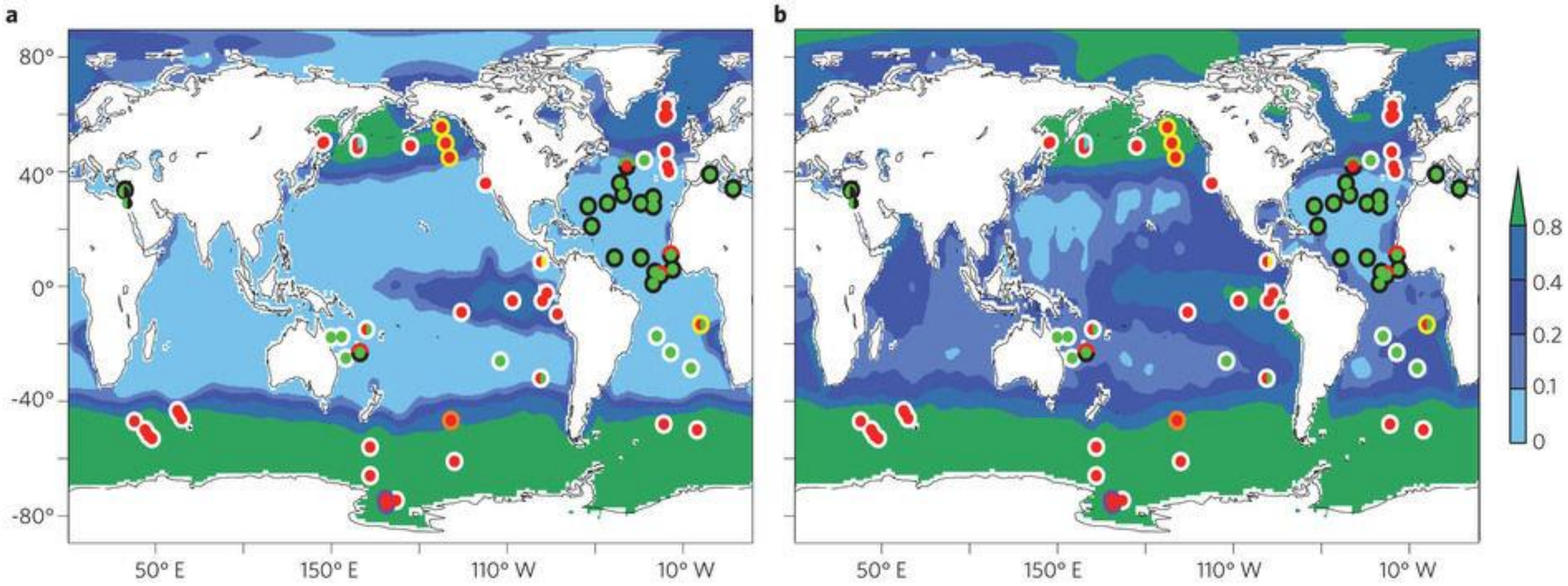


Sea−surface nitrate [mmol N m−3]
0
5
10
15
20
25
30
Sea-surface phosphate [mmol P m -3]
0
0.5
1
1.5
2


Combustion Fe Deposition (ng/m2/s)
90N
60N
30N
0
30S
60S
90S
180
150W
120W
90W
60W
30W
0
30E
60E
90E
120E
150E
180
0.01
0.05
0.1
0.2
0.5
1
2
5


Dust Fe deposition (ng/m2/s)
90N
60N
30N
0
30S
60S
90S
180
150W
120W
90W
60W
30W
0
30E
60E
90E
120E
150E
180
0.001
0.01
0.1
1
5
10
100
1000

Global Patterns of Phytoplankton Nutrient Limitation



Background = mean surface nitrate Background = mean surface phosphate

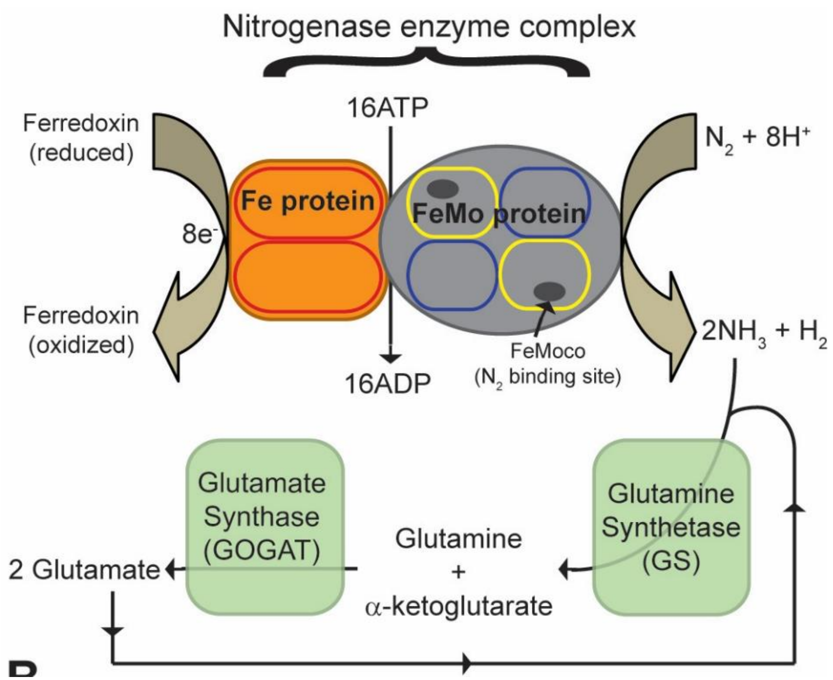
Green dots = N-limitation in experiment, Red = Fe limited in experiment

Moore et al. 2013

N_2 fixation

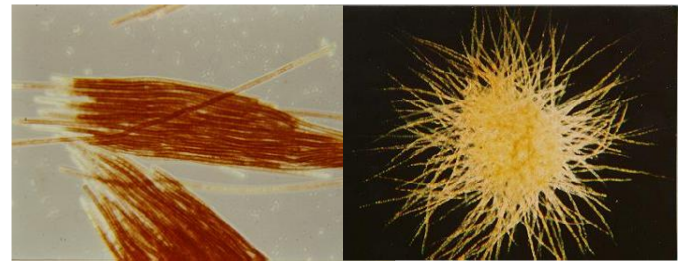
$N_2 + 8e^- + 8H^+ + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP$

- High energy
- Requires Fe,
  Mo, and P
- O_2 sensitive
- Warm waters,
- High light



Trichodesmium spp.

Trichodesmium **is a marine, filamentous, colony forming cyanobacteria that fixes N_2**



Photos: John Waterbury

Actually several species

Occurs widely in the oligotrophic tropical and subtropical oceans

Visible to naked eye

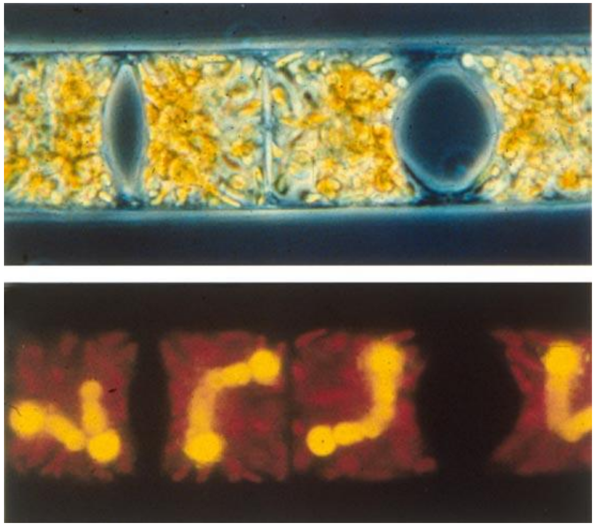
Diatom-diazotroph assemblages

Symbiont: *Richelia* – heterocystous

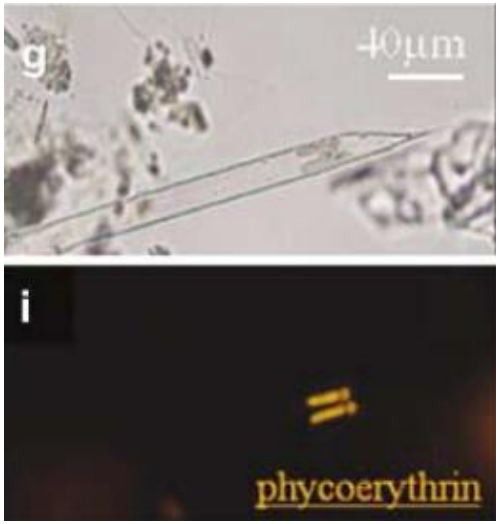
Host: *Hemiaulis*, *Rhizosolenia*

Tropical and subtropical

- Need Silica!



Dave Caron

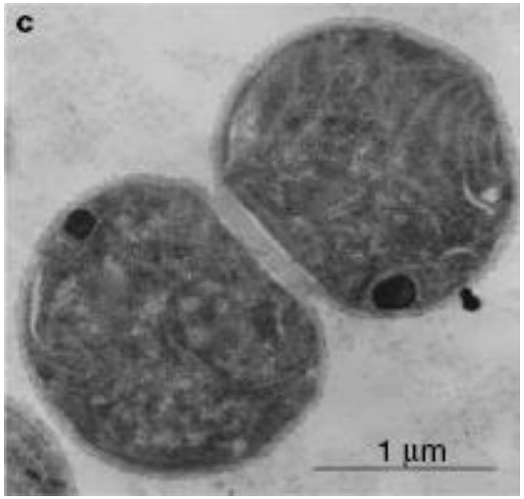


Bar Zeev et al., *ISME J.*, 2008

Small, diazotrophic cyanobacteria

Recognized recently as abundant, widespread, and important to global N_2 fixation

- Group A – uncultured
- Group B – *Crocosphaera*
- Group C – uncultured



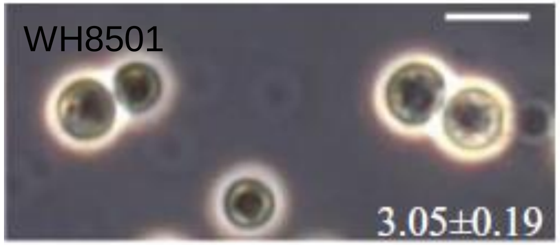
Zehr et al., Nature, 2001

Crocosphaera

3-6 μm spherical cells

Fix carbon during day, nitrogen at night

Can be abundant and widespread throughout subtropics and tropics



Webb et al., *EM*, 2009

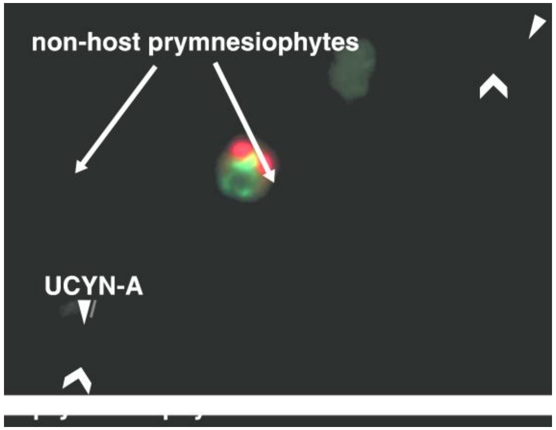
UCYN-A

Genome suggested it lives in close association or symbiosis with other organisms (Tripp et al., *Nature*, 2010)

- Lacks photosystem II, TCA cycle, biosynthetic pathways for some amino acids and purines

Subsequent research found 3 types of UCYN-A

- One lives inside a coastal prymnesiophyte alga (coccolithophore)
- One lives with an uncultured, unidentified prymnesiophyte alga
- Third one remains unknown
  (probably similar lifestyle)



Heterotrophic bacteria N-fixers

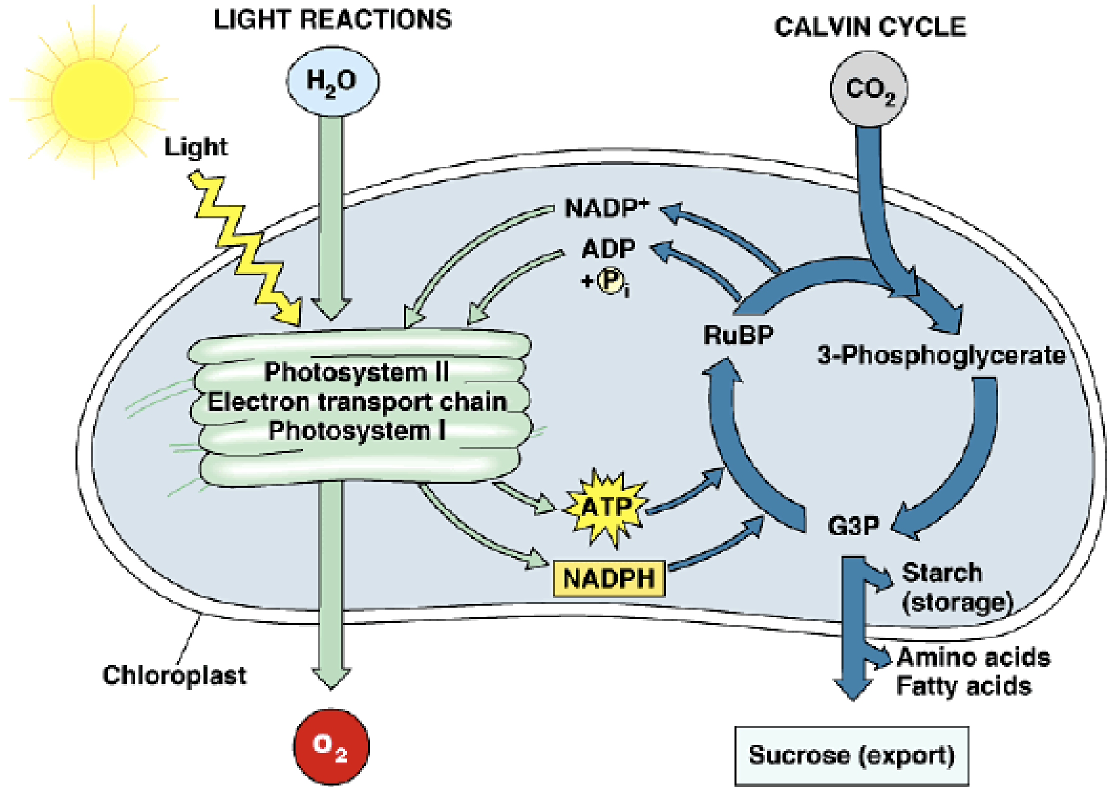
Only known from recovered DNA

Found in many locations

Little understanding of how they look, live, level of activity

- **Two main forms of biomass production:**
  - **Primary production: is the rate of biomass synthesis via reduction of CO_2; in the ocean this is mostly controlled by the growth and biomass of photosynthetic organisms.**
  - **Secondary production: formation of biomass via assimilation of organic matter; controlled by growth and biomass of chemoheterotrophs (heterotrophic bacteria, zooplankton, etc.)**

- Absorption of light energy by pigments or photoproteins (light antenna) excites e^- in these molecules; these molecules then pass e^- to protein complexes (reaction centers) via an electron transport chain.
- The transfer of electrons through the transport chain creates reducing power (NADPH) and chemical energy (ATP).
- Energy and reducing power gained from light harvesting are used to reduce CO_2 to organic matter (dark reactions).



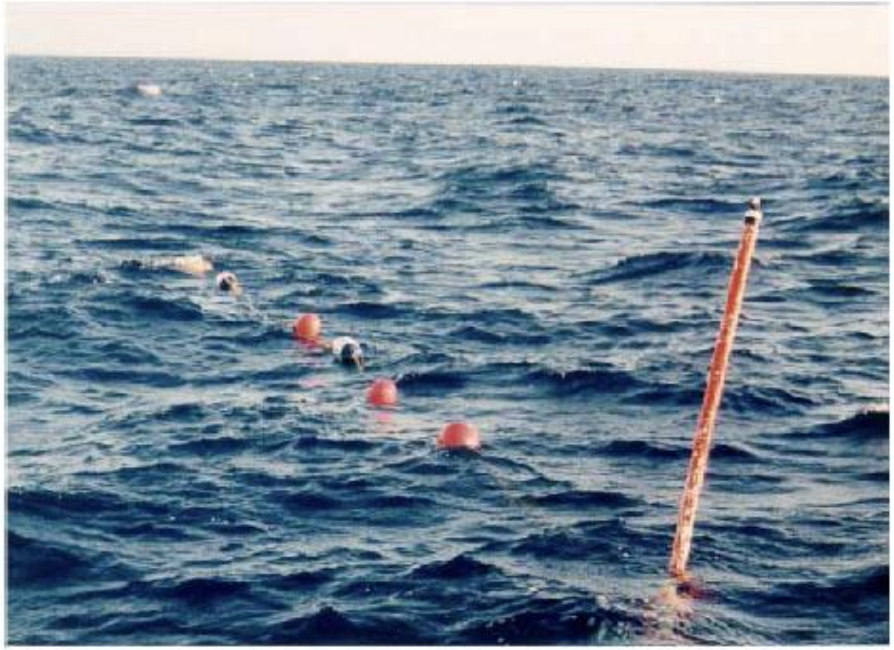
Photosynthesis:

$$6CO_2 + 12H_2O \xrightarrow{\text{Sunlight}} C_6H_{12}O_6 + O_2 + 6H_2O + \text{heat}$$

Commonly used methods for measuring aquatic photosynthesis

- Changes in O_2 concentrations – incubations (Gaarder and Gran 1927) and *in situ* dynamics.
- CO_2 assimilation: stable or radioisotopes of carbon (^{13}C or ^{14}C) – technique first applied by Steeman-Nielsen 1951.
- Oxygen isotope disequilibria (^{18}O, ^{17}O, ^{16}O)
- Satellite remote sensing

Primary production approach 1: ^{14}C-bicarbonate assimilation



- Examine assimilation of ^{14}C (as bicarbonate) by plankton.
- Add ^{14}C labeled HCO_3^- to bottles containing seawater; incubate in the light.
- Harvest plankton by filtration, acidify the filter, and count radioactivity (using liquid scintillation counter) assimilated into plankton biomass during incubation period.
- Rate of primary production is determined by the amount of ^{14}C-label assimilated into particles relative to the total DIC pool

Typically PAR (400-700 nm) transparent polycarbonate bottles are used for these experiments...but UV is excluded.

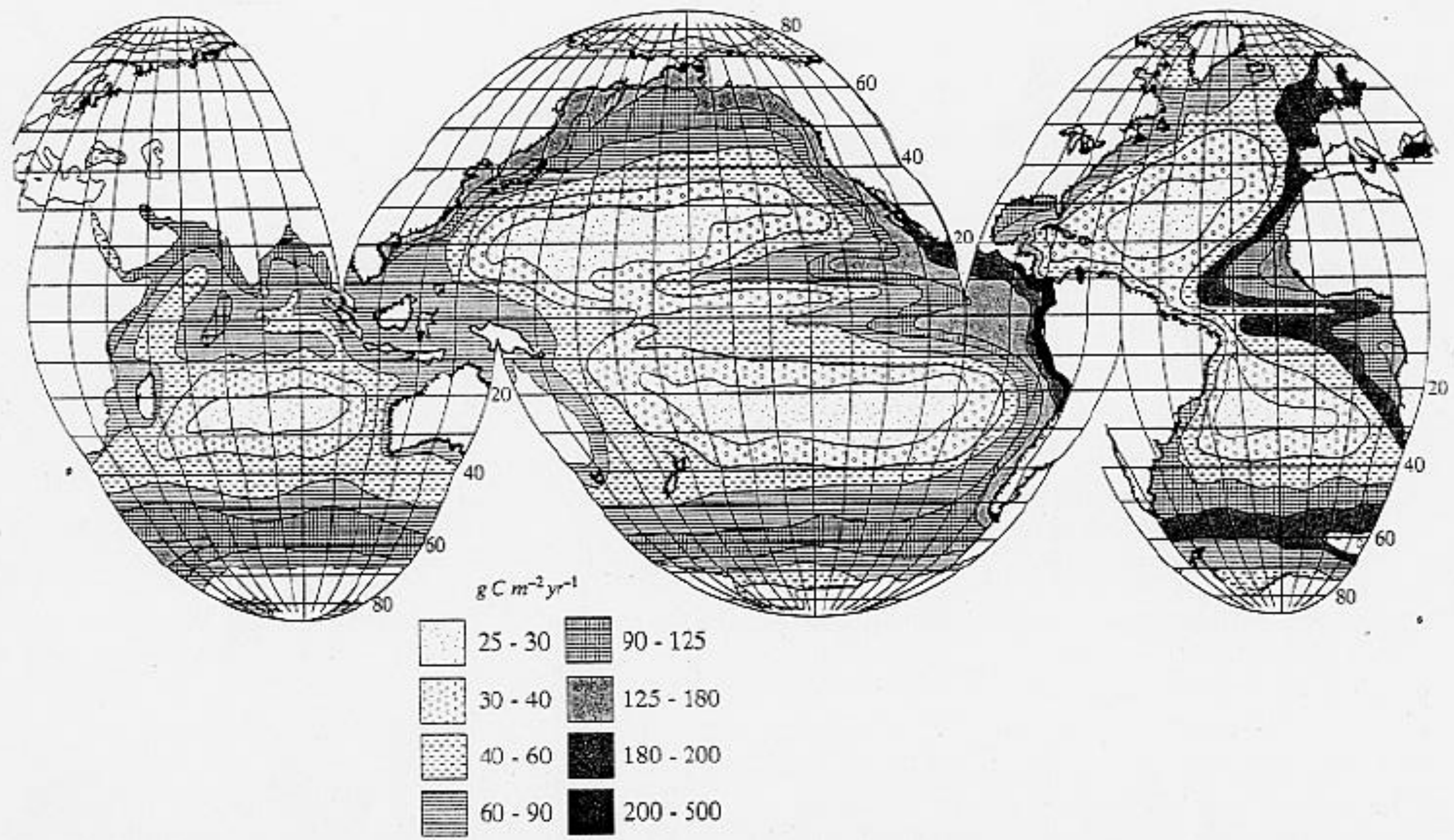
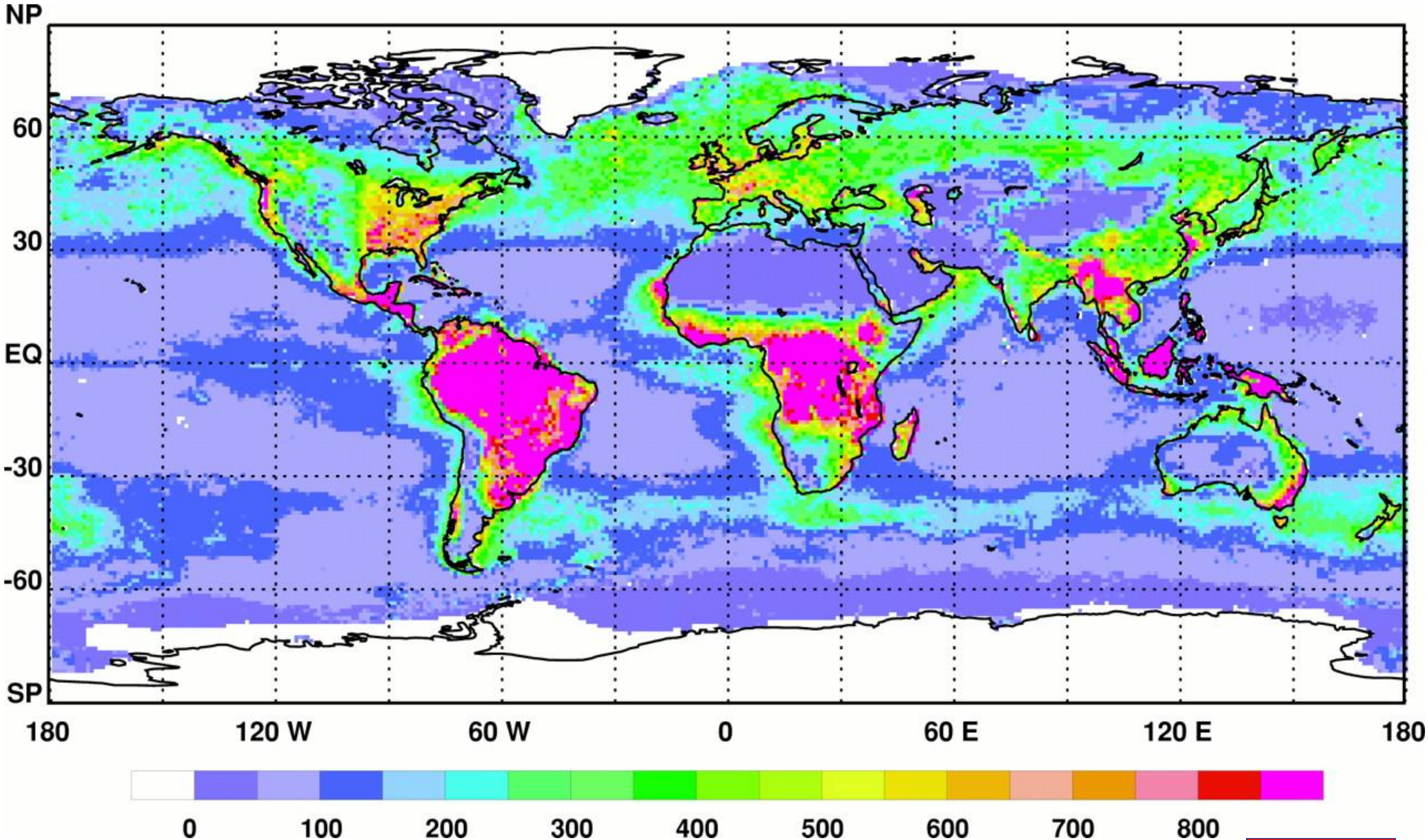


Figure 11.1 *Map of the distribution of net primary production in the world ocean, combining about 9000 measurements, mostly by the ^{14}C method, with estimates based on the phosphate concentration in regions without productivity data. From these data Berger et al. (1988, 1989) estimated the world total to be 27 Gt per year, expressed as carbon.* (Berger et al. 1989, with the coding key from Berger et al. 1988.)

Laborious! Does not account for temporal (seasonal) change - not synoptic

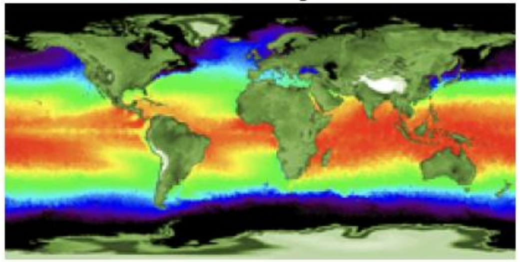
OR you can do it from a satellite

Global annual NPP (in grams of C per square meter per year) for the biosphere, calculated from the integrated CASA-VGPM model.

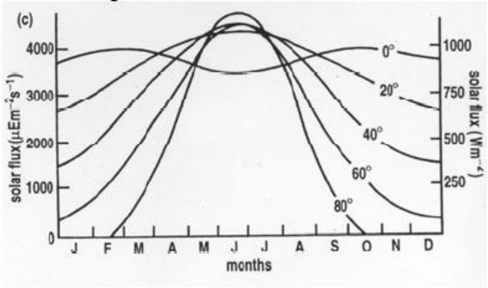


Published by AAAS

C B Field et al. Science 1998;281:237-240



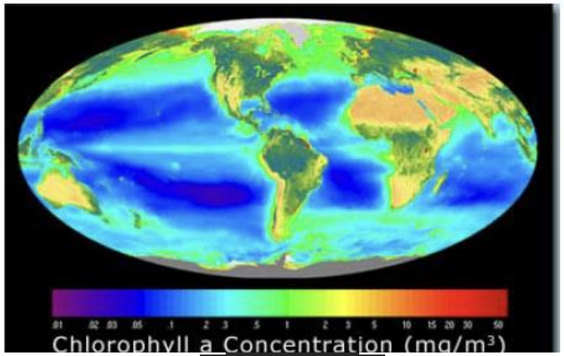
Temperature



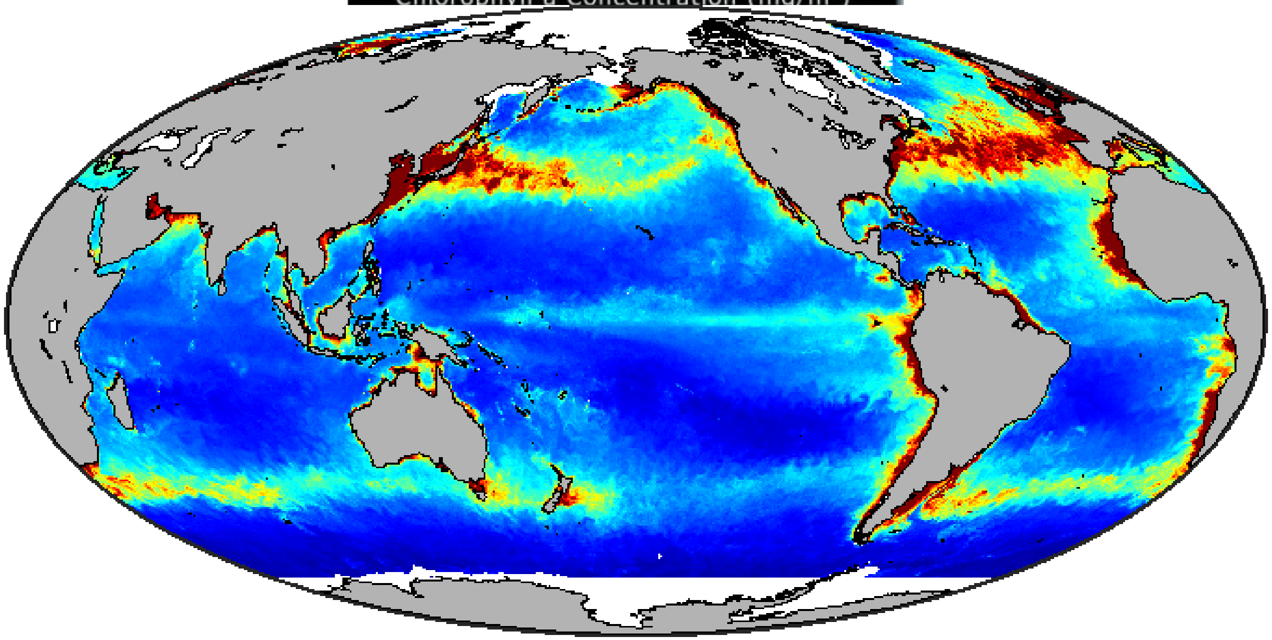
PAR

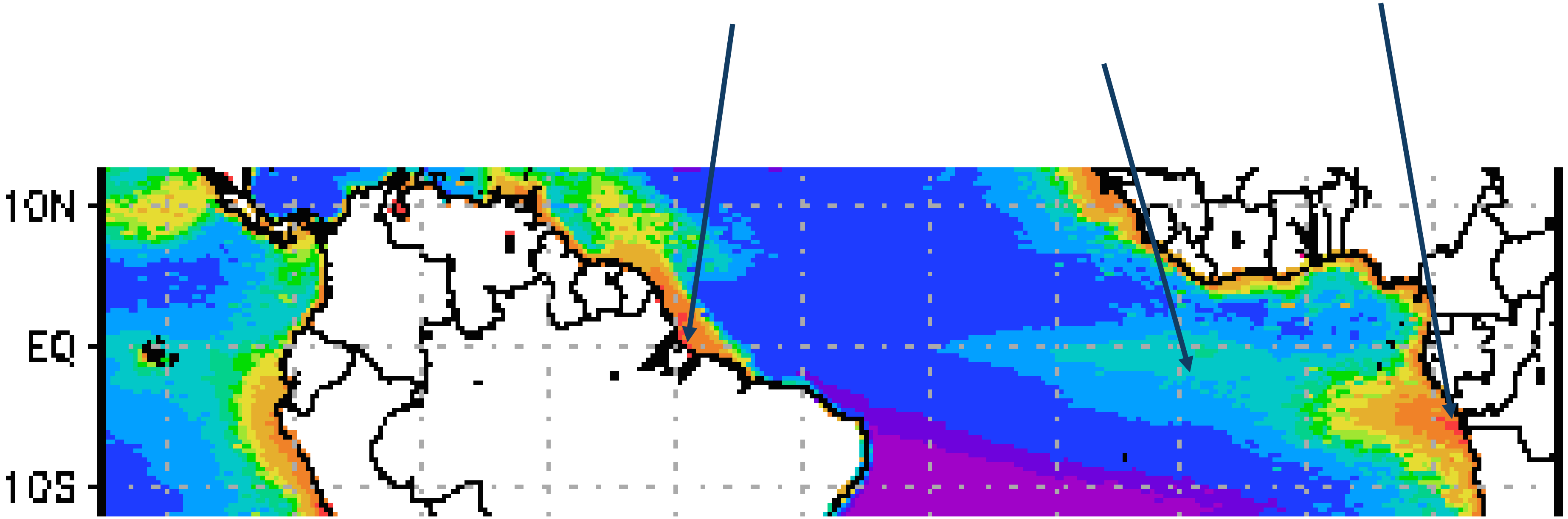
Satellites can provide measurements of temperature, sea surface irradiance, and chlorophyll.
Need models that relate these to primary production.

http://sites.science.oregonstate.edu/ocean.productivity/index.php



Chlorophyll



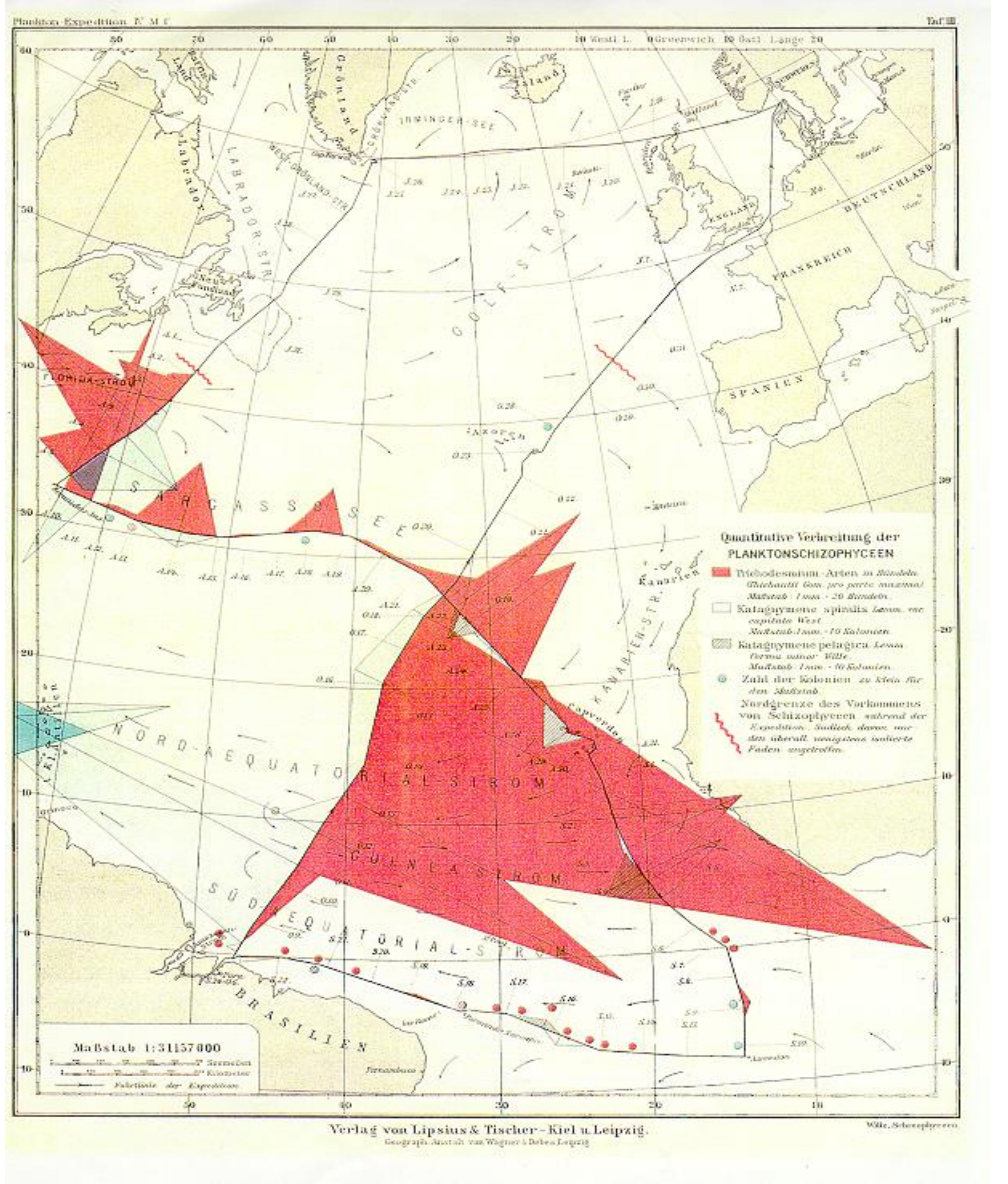


And now the Tropical Atlantic Ocean

Considered best studied of the global oceans

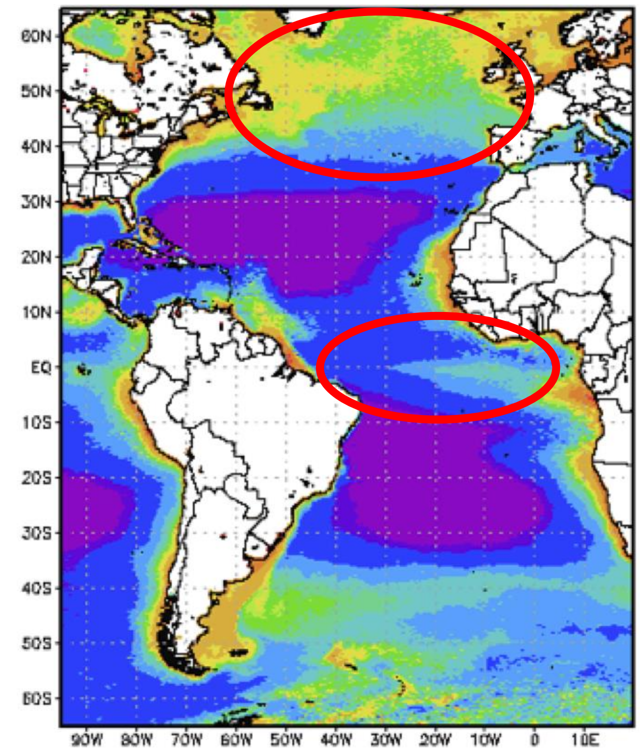
- Bermuda Atlantic Time Series Station
- JGOFS North Atlantic Bloom Experiment
- GLOBEC
- More North Atlantic Bloom Experiment
- NAAMES – yet more North Atlantic Bloom Experiment
- Countless European studies (RIDGEMIX etc)
- Atlantic Meridional Transect
- And more Meridional Transect studies from Spain and Germany

Historical Studies of Tropical Atlantic
Willie, Humboldt Expedition 1899



	Subarctic (51°N–70°N)	Temperate (36°N–50°N)	Subtropics (11°N–35°N)	Tropics (10°N–10°S)
Area (10^6 km^2)	3.1	5.4	23.0	11.0
Production (GtC y^{-1})	1.0	1.0	3.2	2.5

Longhurst (1993) calculated that the Tropical Atlantic domain (10ºN–10ºS) including the Equatorial Atlantic made a bigger contribution to carbon fixation than the entire open ocean North Atlantic spring bloom region that includes the subarctic and temperate oceans (70º–35ºN)



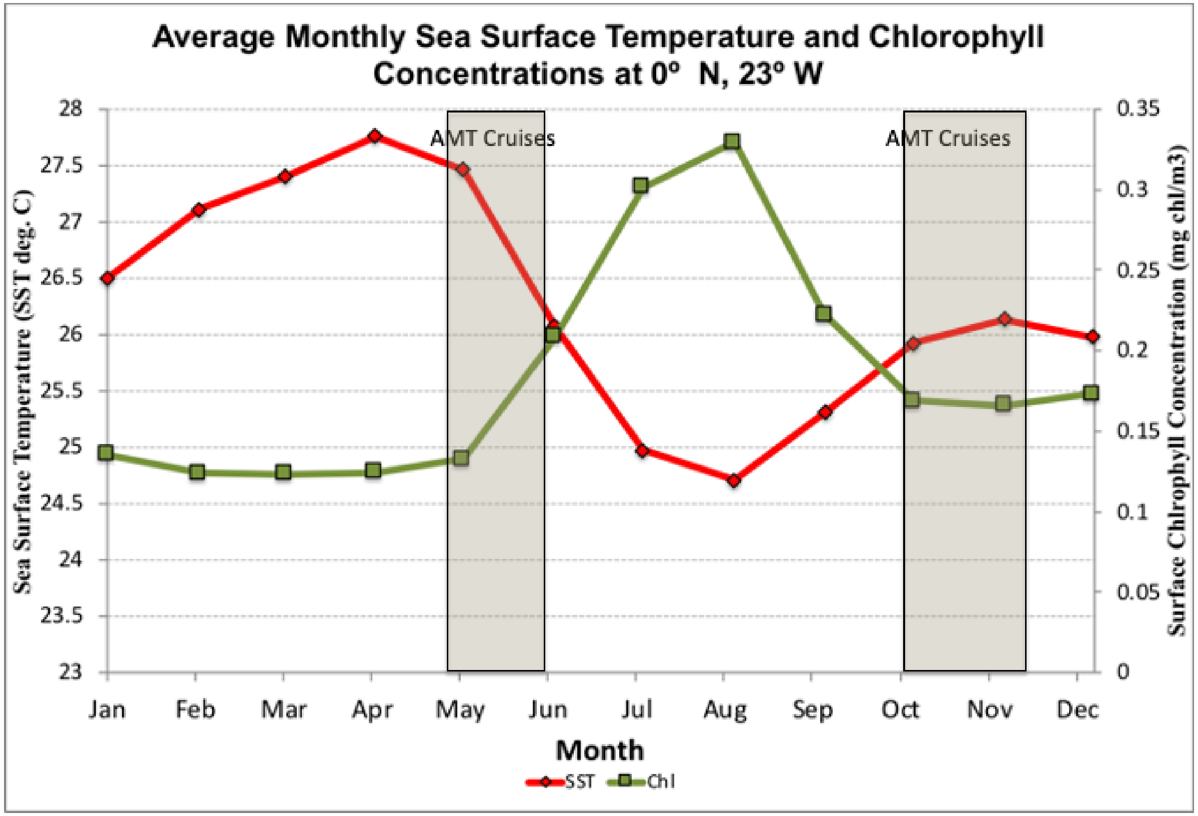
Mercator Projection Imperialism!

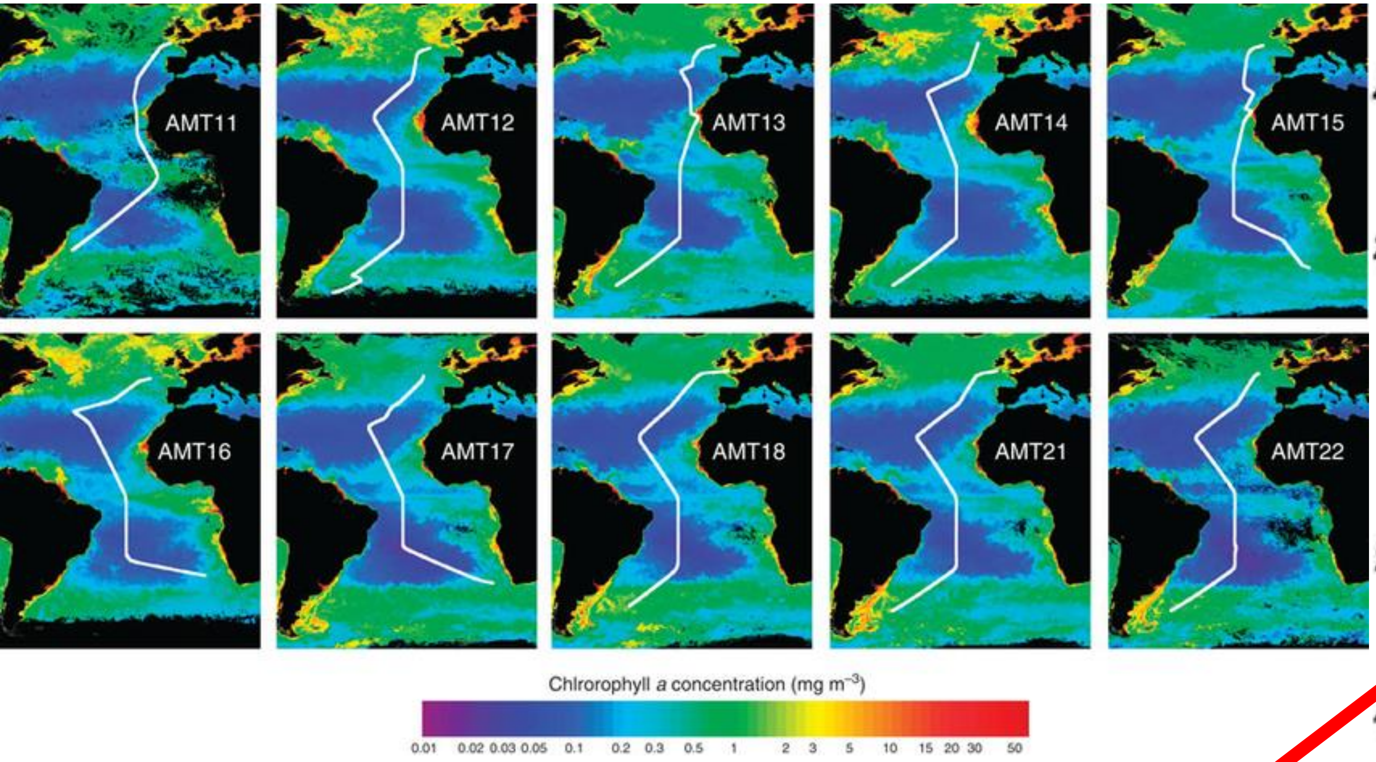
Much of what we know about phytoplankton in the Tropical Atlantic has come from the AMT Program

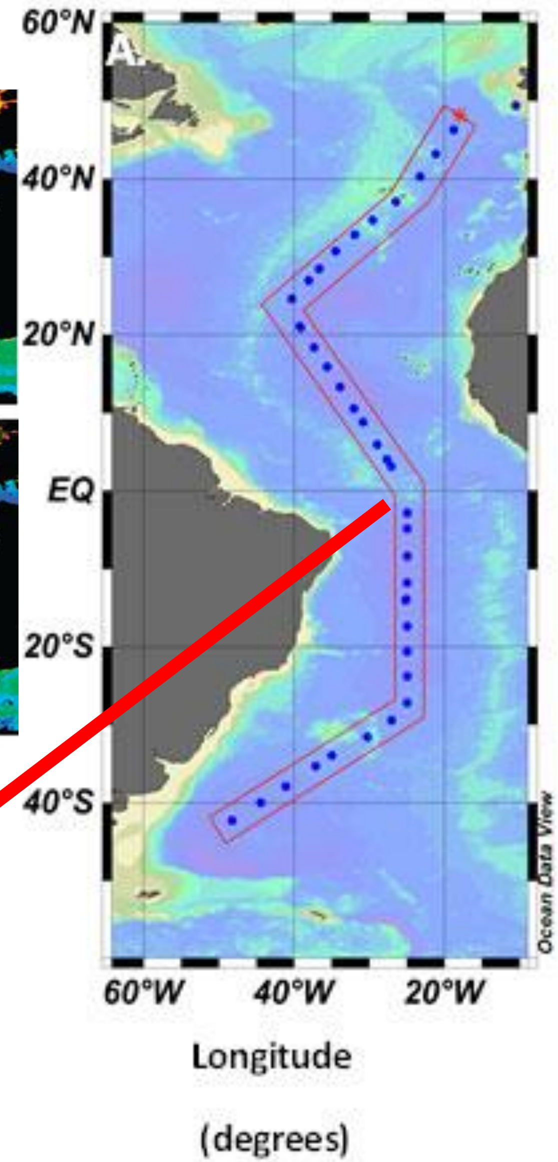
In 2015 the AMT programme had produced over 200 refereed journal articles, including three special issues of journals and AMT data has contributed to over 70 PhD theses.

Timing is everything

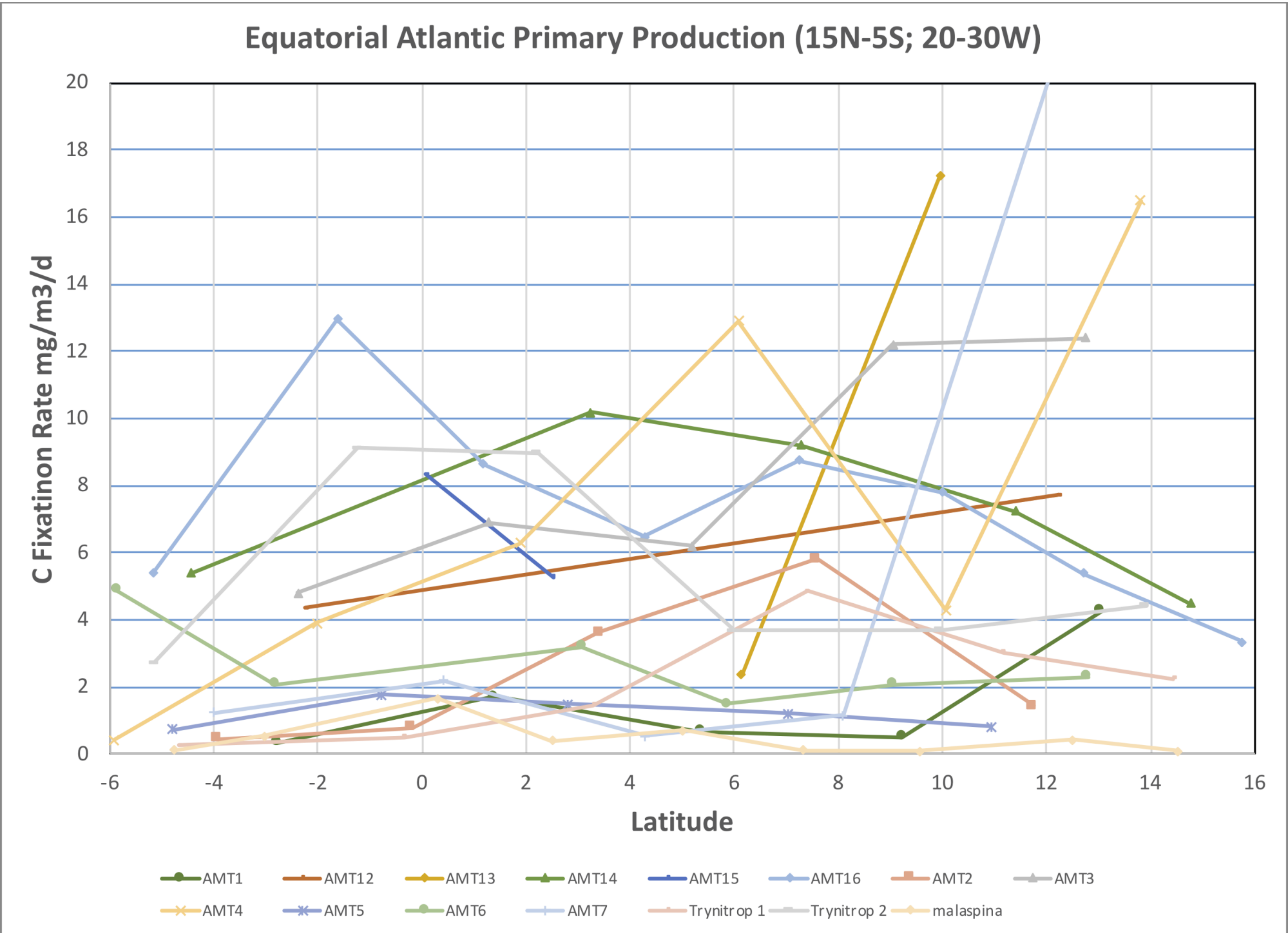
Cruise	Departure	Date
AMT 1	UK	Sep-95
AMT 2	Port Stanley	Apr-96
AMT 3	UK	Sep-96
AMT 4	Port Stanley	Apr-97
AMT 5	UK	Sep-97
AMT 6	Cape Town	May-98
AMT 6B	Port Stanley	Apr-98
AMT 7	UK	Sep-98
AMT 8	Port Stanley	Apr-99
AMT 9	UK	Sep-99
AMT 10	Montevideo	Apr-00
AMT 11	UK	Sep-00
AMT 12	Port Stanley	May-03
AMT 13	UK	Sep-03
AMT 14	Port Stanley	Apr-04
AMT 15	UK	Sep-04
AMT 16	Cape Town	May-05
AMT 17	UK	Oct-05
AMT 18	UK	Oct-08
AMT 19	UK	Oct-09
AMT 20	UK	Oct-10
AMT 21	UK	Sep-11
AMT 22	UK	Oct-12
AMT 23	UK	Oct-13
AMT24	UK	Sep-14





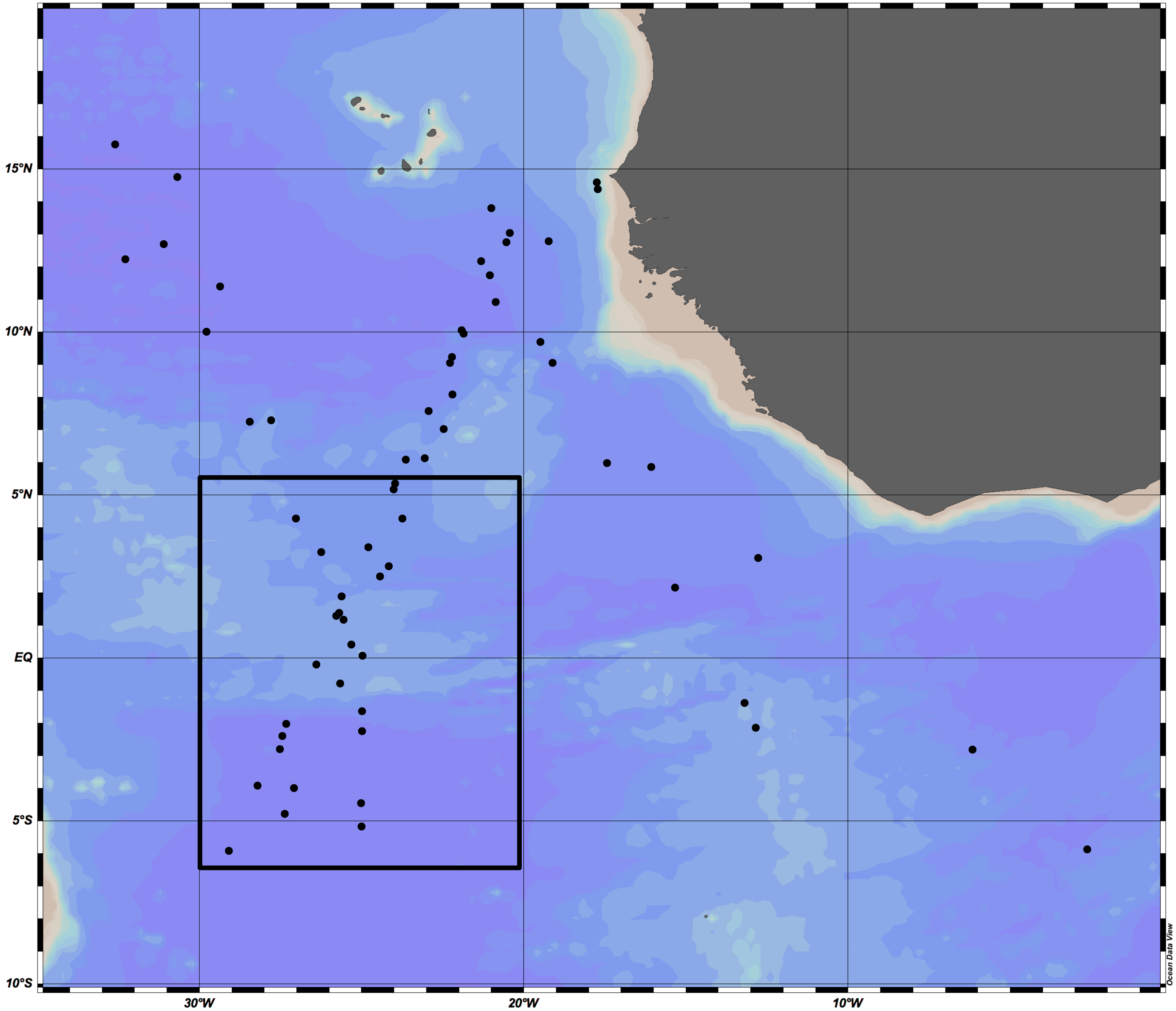


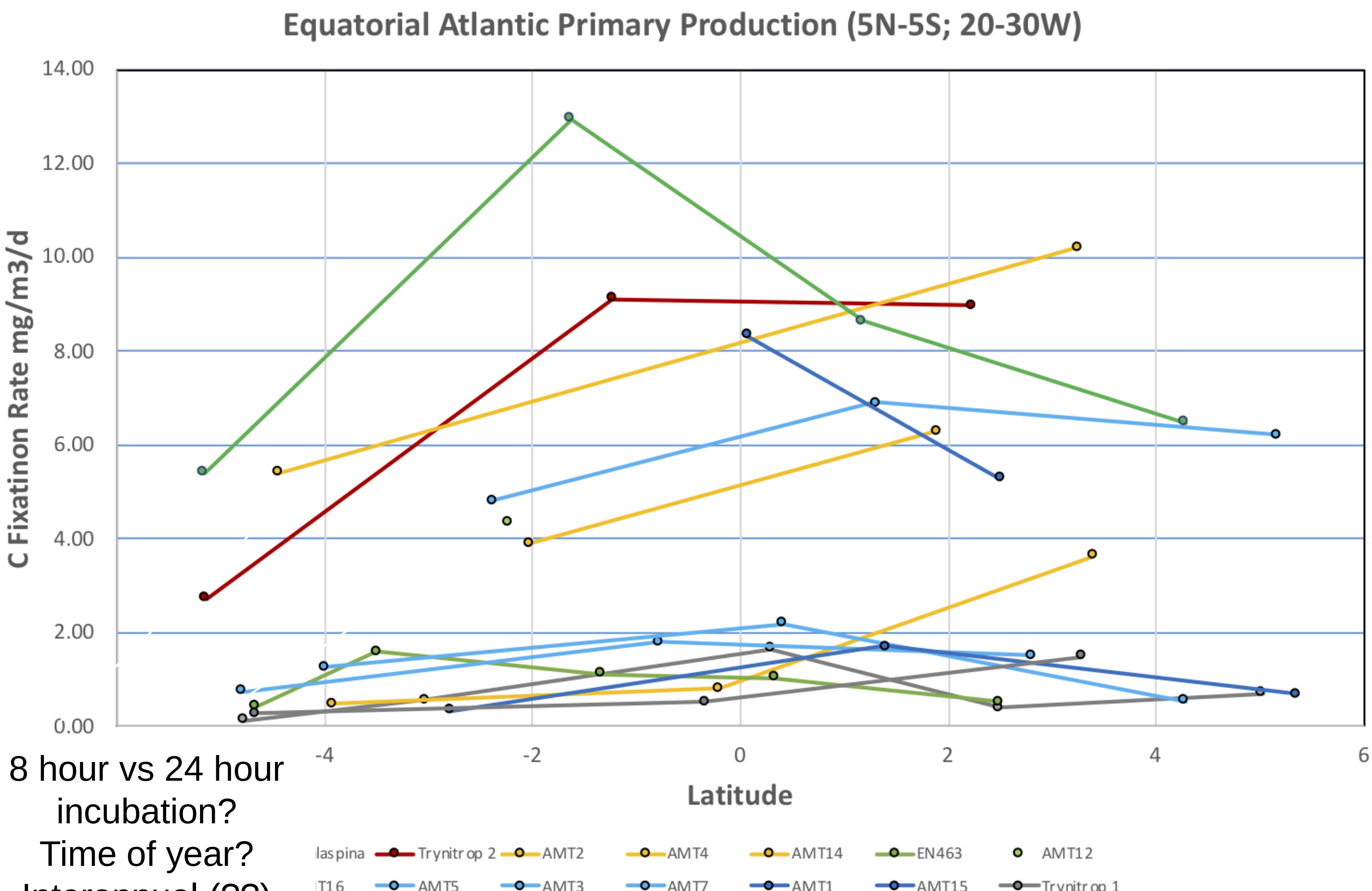
Few rate measurements from
the Equatorial Upwelling



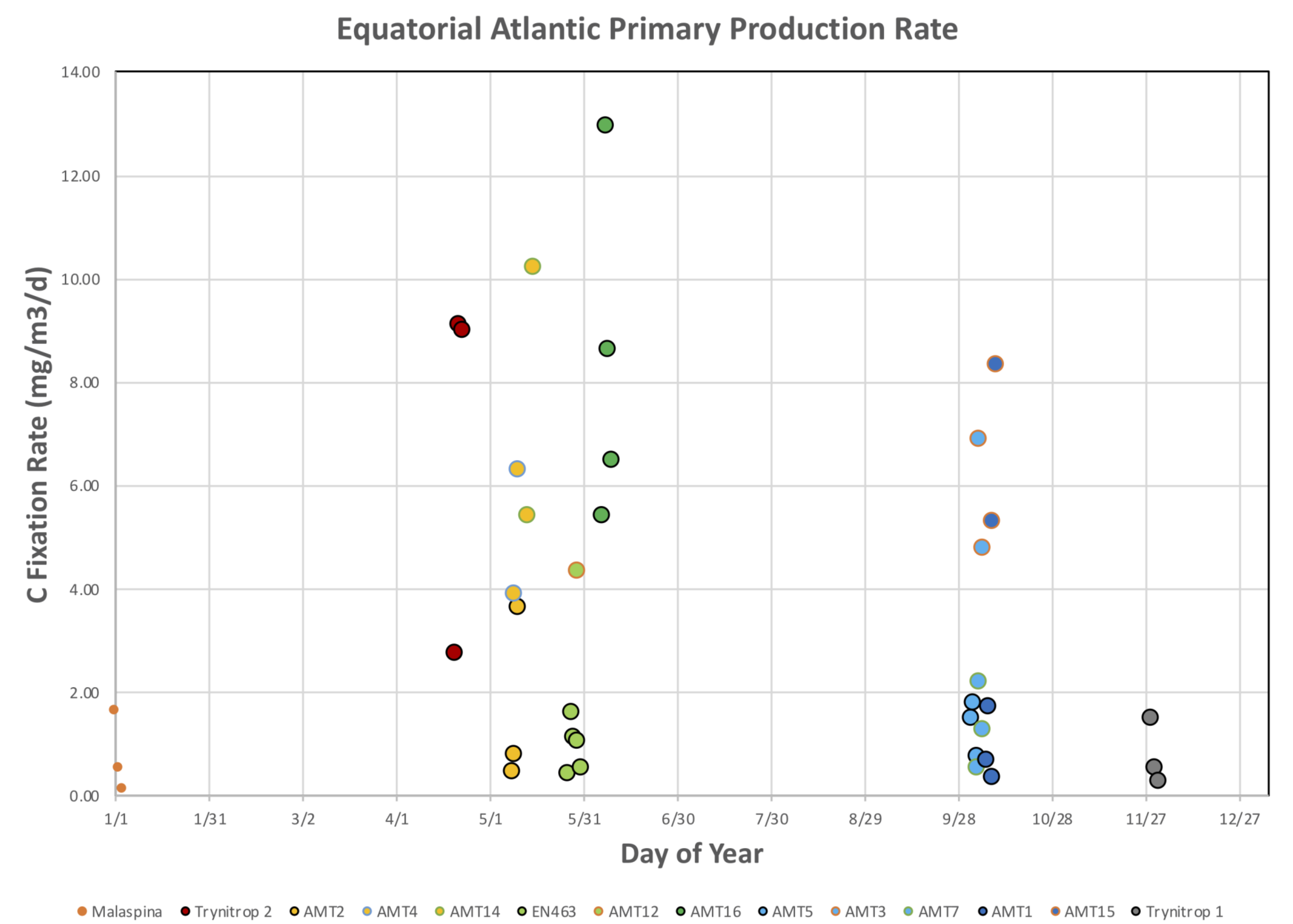
Equatorial Atlantic Primary Production (15N-5S; 20-30W)
C Fixatinon Rate mg/m3/d
Latitude
20
18
16
14
12
10
8
6
4
2
0
-6
-4
-2
0
2
4
6
8
10
12
14
16
AMT1
AMT12
AMT13
AMT14
AMT15
AMT16
AMT2
AMT3
AMT4
AMT5
AMT6
AMT7
Trynitrop 1
Trynitrop 2
malaspina

Station Locations

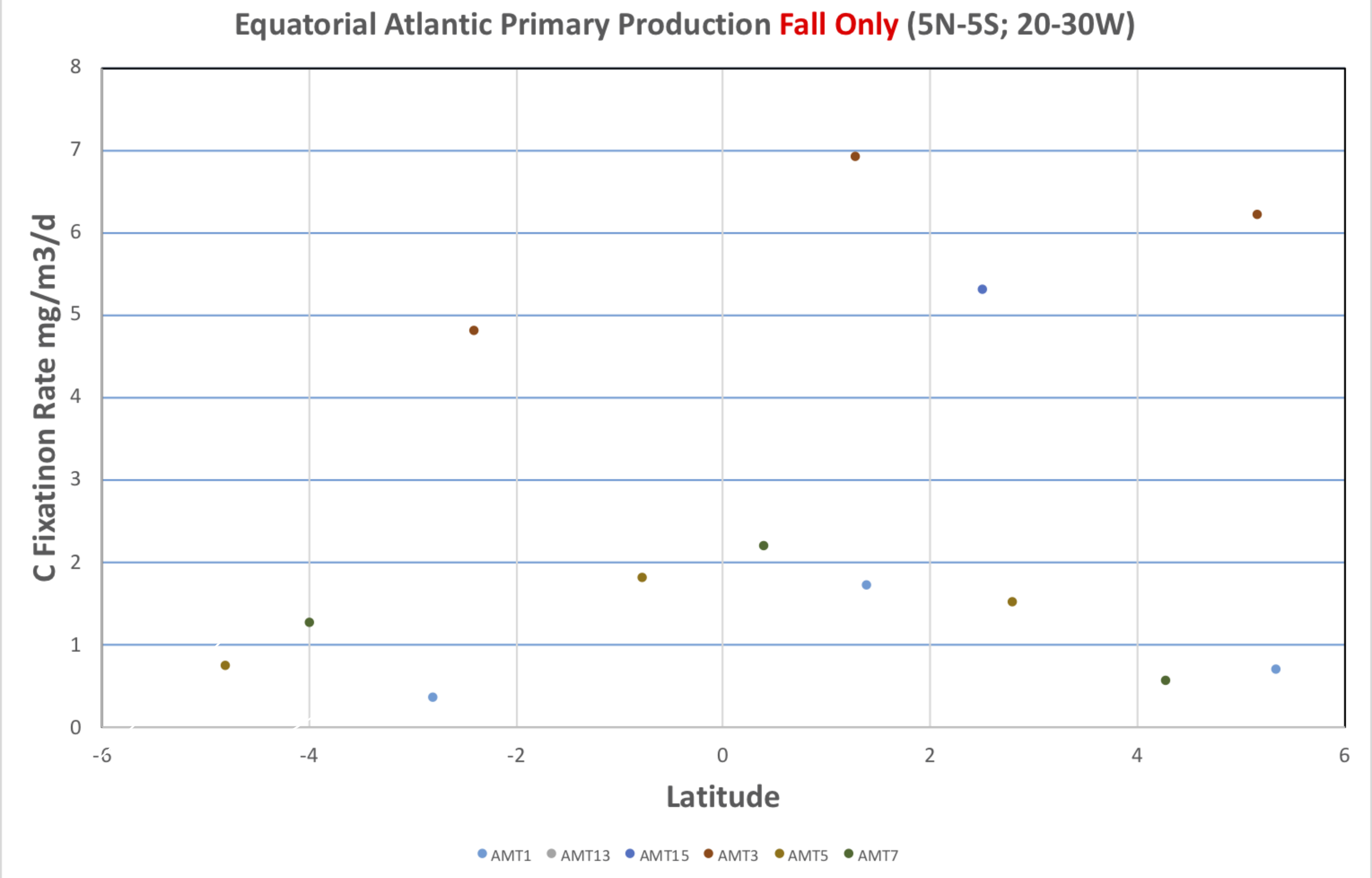




8 hour vs 24 hour incubation?
Time of year?
Interannual (??) differences



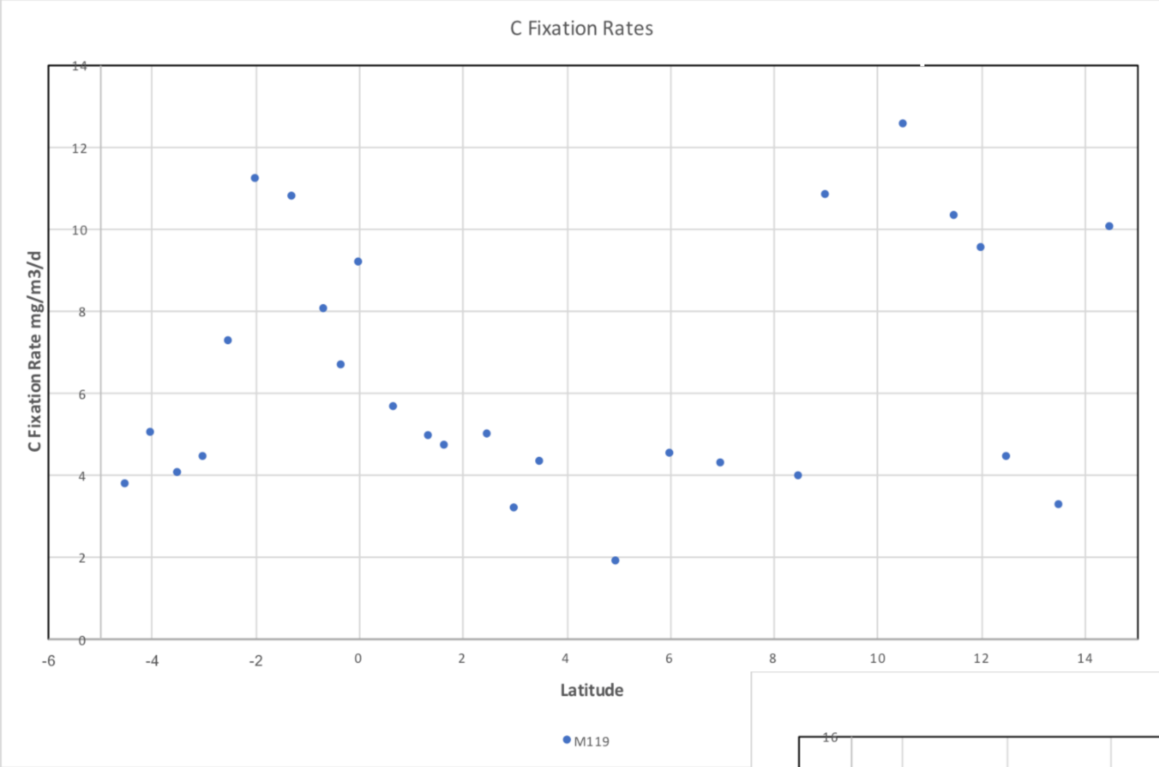
Equatorial Atlantic Primary Production Rate
C Fixation Rate (mg/m3/d)
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
1/1
1/31
3/2
4/1
5/1
5/31
6/30
7/30
8/29
9/28
10/28
11/27
12/27
Day of Year
Malaspina
Trynitrop 2
AMT2
AMT4
AMT14
EN463
AMT12
AMT16
AMT5
AMT3
AMT7
AMT1
AMT15
Trynitrop 1


Equatorial Atlantic Primary Production Fall Only (5N-5S; 20-30W)
C Fixatinon Rate mg/m3/d
Latitude
8
7
6
5
4
3
2
1
0
-6
-4
-2
0
2
4
6
AMT1
AMT13
AMT15
AMT3
AMT5
AMT7

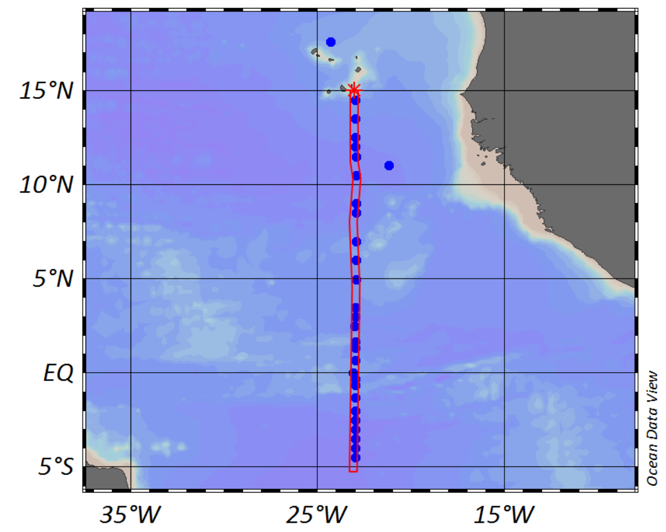
All the data shown in the slides below is original unpublished data.

Manuscripts are currently under preparation.

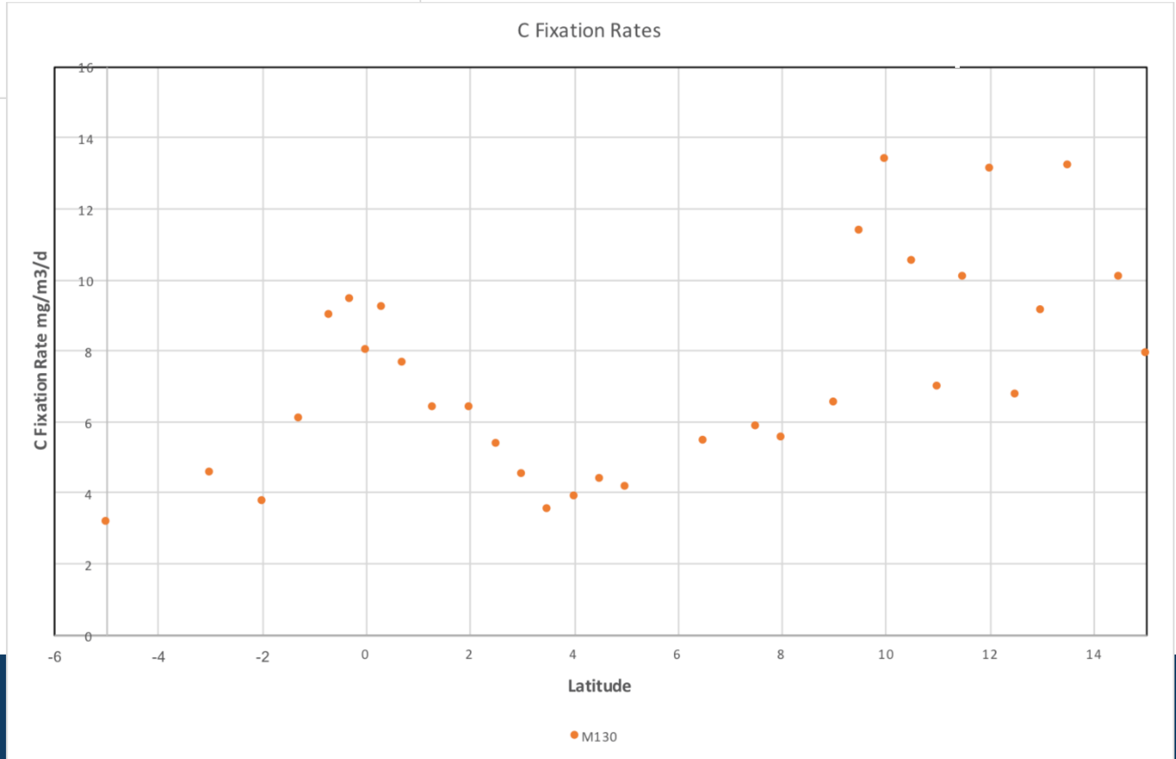
Data are not open yet, and cannot be used without the authors consent.



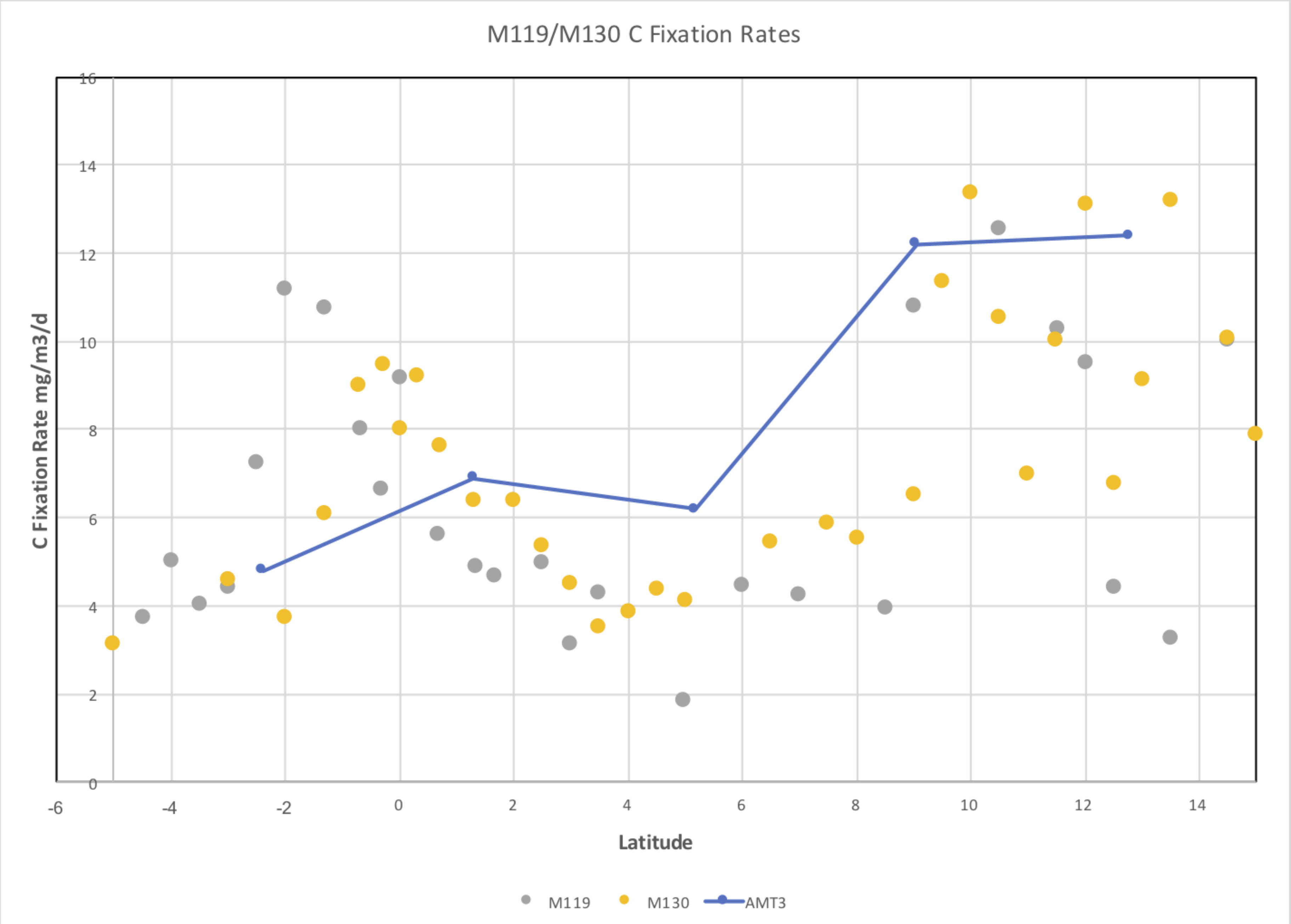
C Fixation Rates
C Fixation Rate mg/m3/d
0
2
4
6
8
10
12
14
-6
-4
-2
0
2
4
6
8
10
12
14
Latitude
M119



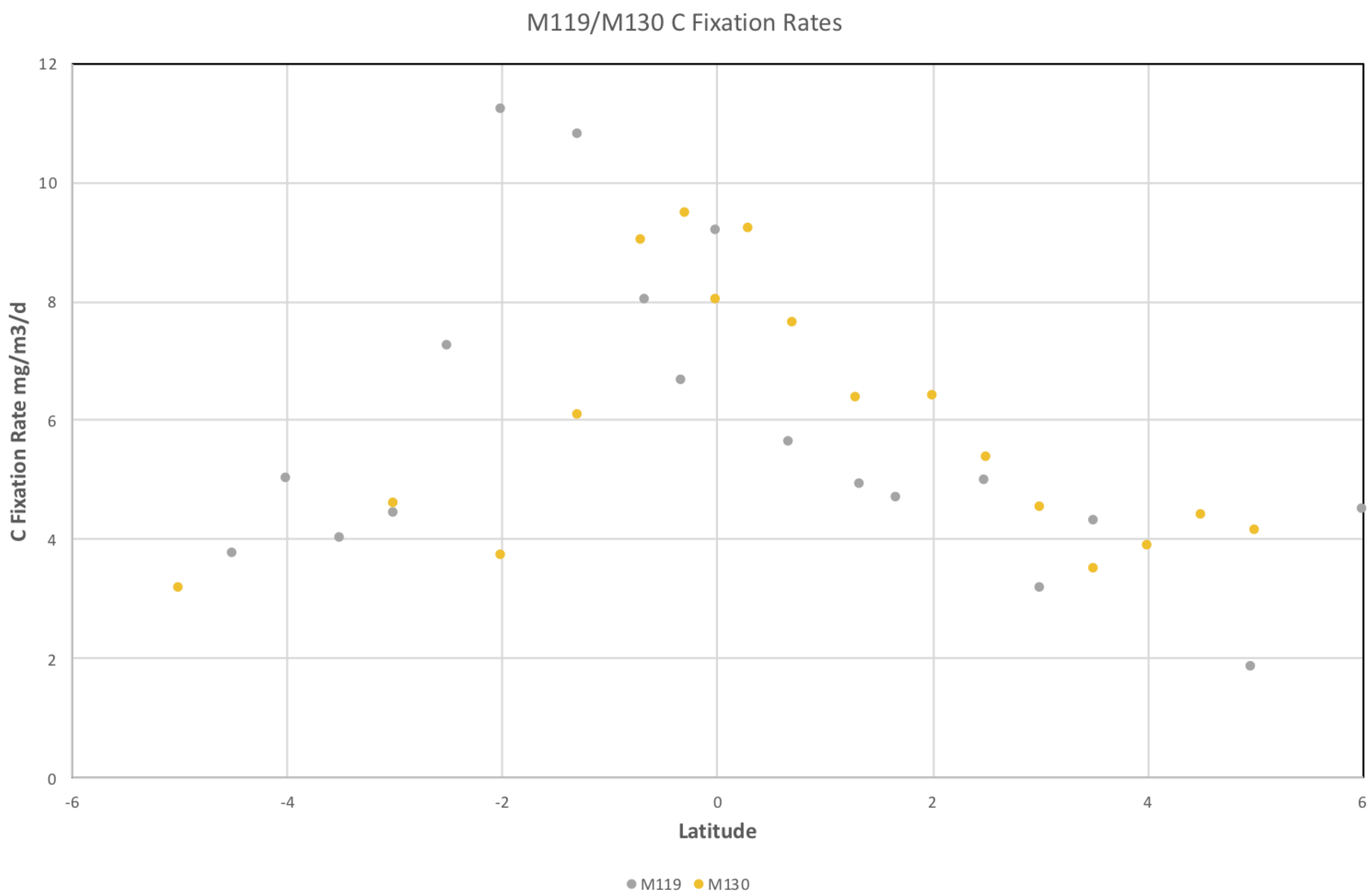
15°N
10°N
5°N
EQ
5°S
35°W
25°W
15°W
Ocean Data View



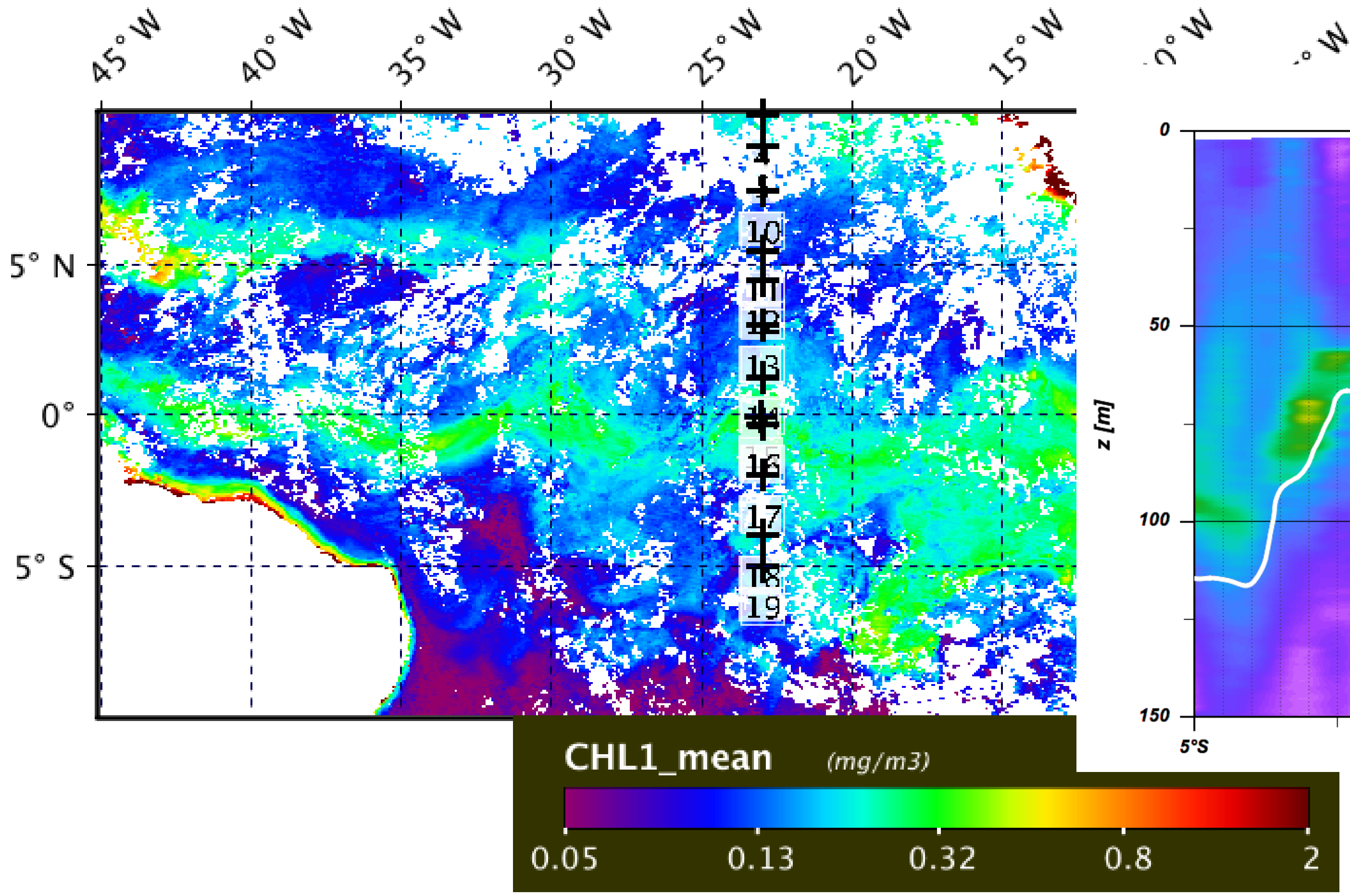
C Fixation Rates
C Fixation Rate mg/m3/d
0
2
4
6
8
10
12
14
16
-6
-4
-2
0
2
4
6
8
10
12
14
Latitude
M130

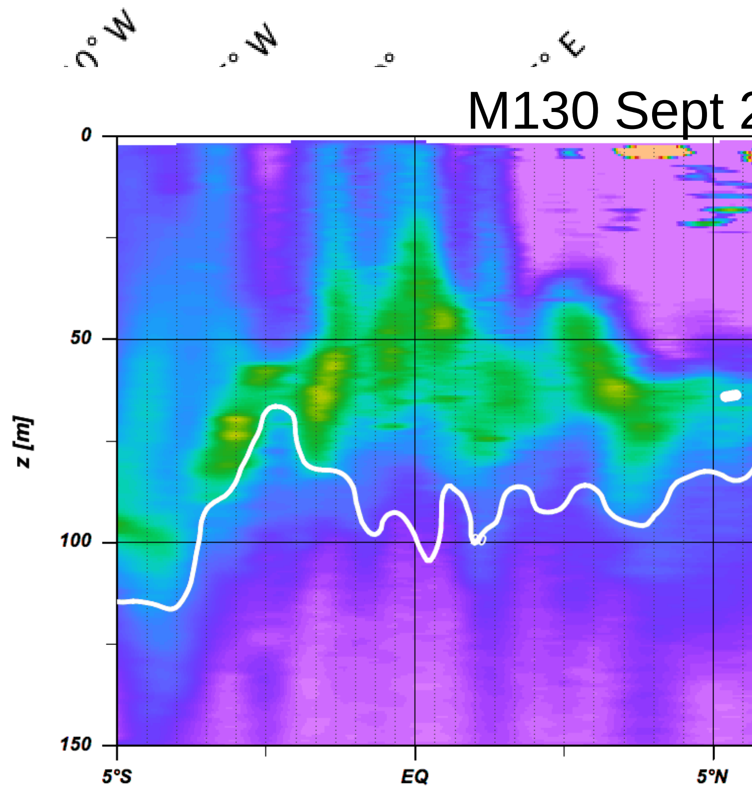


M119/M130 C Fixation Rates
C Fixation Rate mg/m3/d
Latitude
16
14
12
10
8
6
4
2
0
-6
-4
-2
0
2
4
6
8
10
12
14
M119
M130
AMT3


M119/M130 C Fixation Rates
C Fixation Rate mg/m3/d
12
10
8
6
4
2
0
-6
-4
-2
0
2
4
6
Latitude
M119
M130

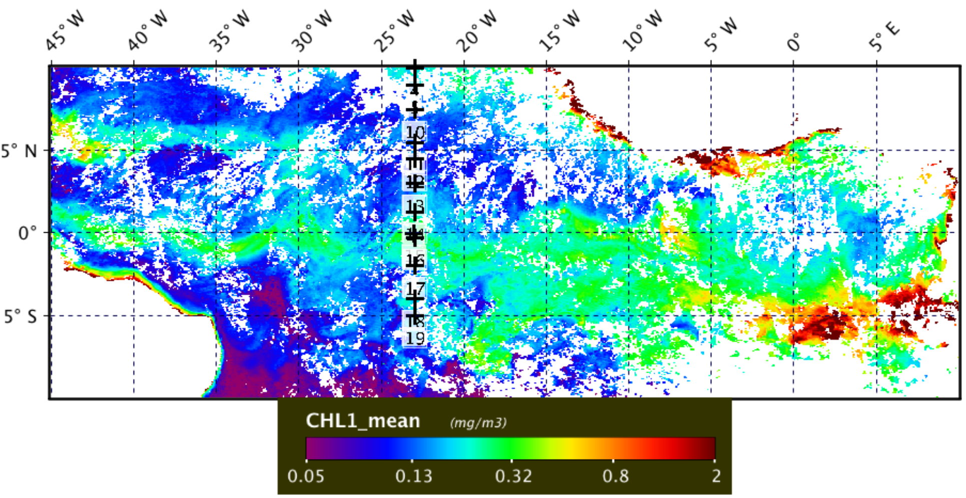
13-20 2016 Sept Composite

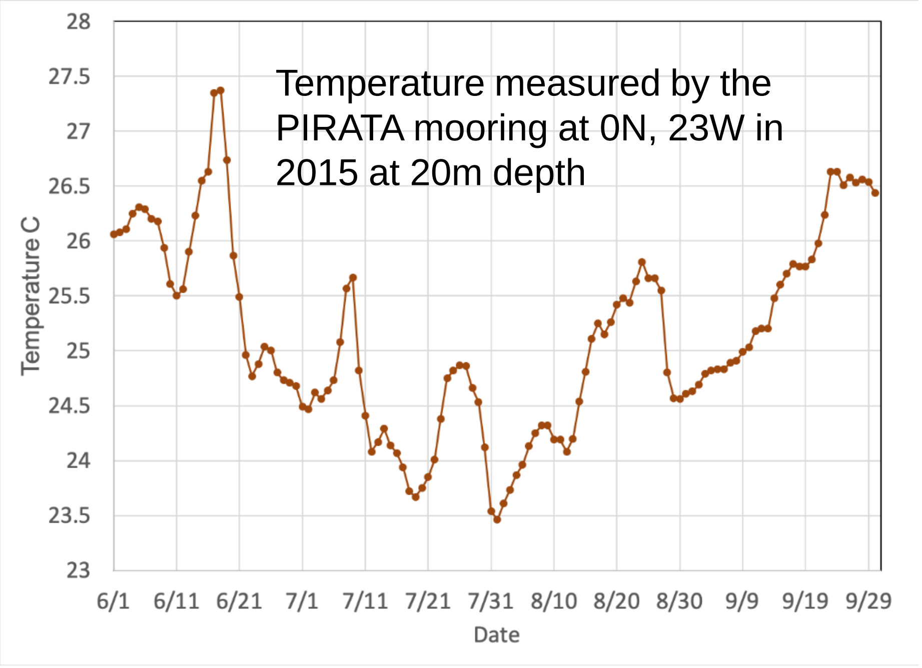




Hypothesis

Tropical Instability Waves are important drivers for nutrient supply at the Equator





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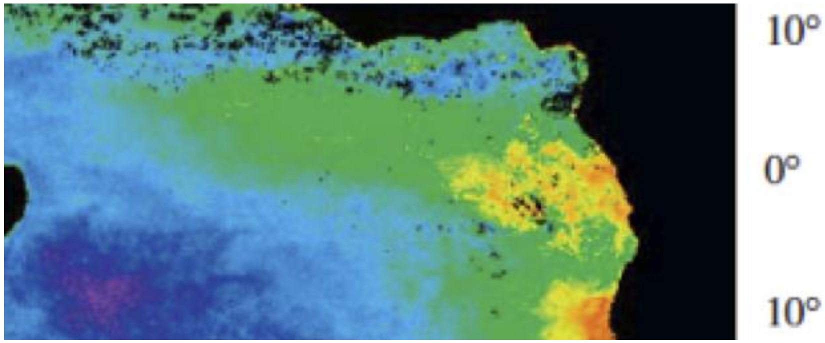
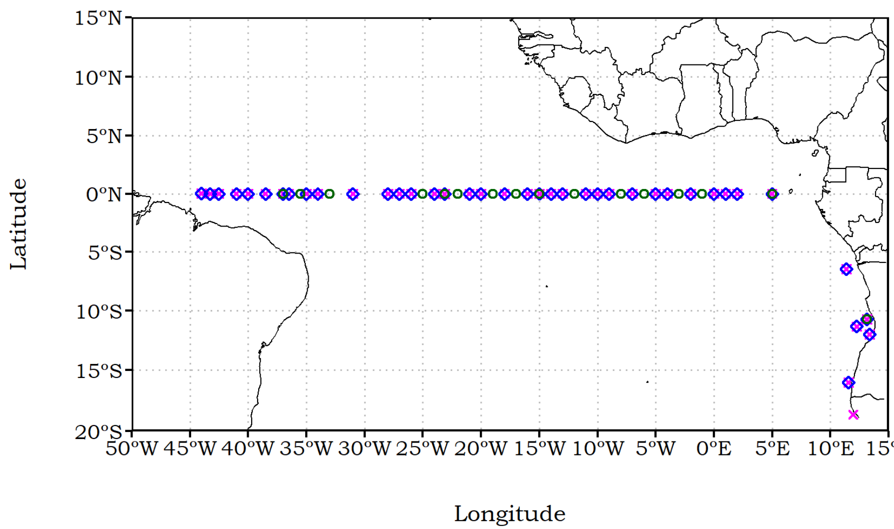
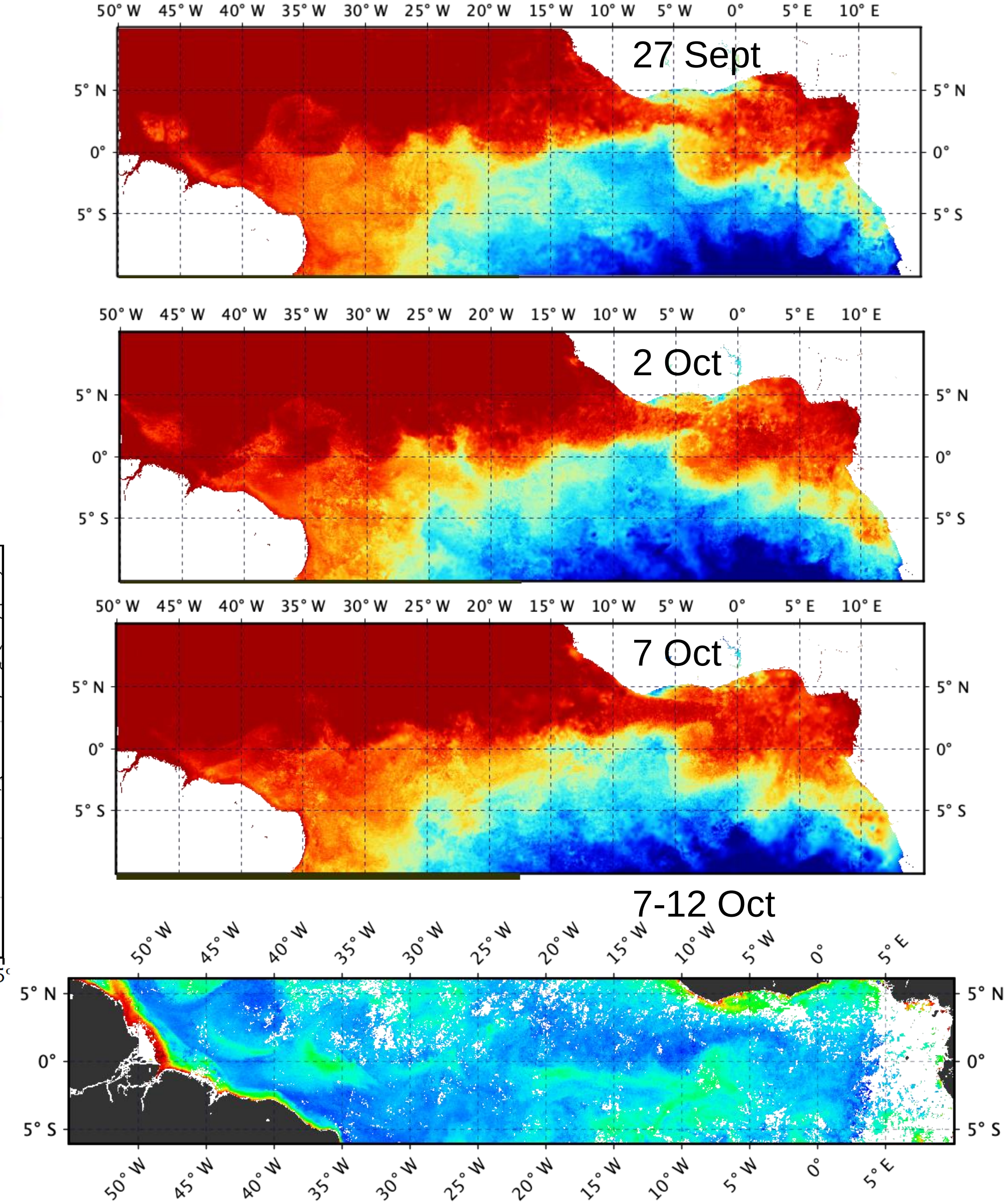
Seasonal Composite of Equatorial Upwelling





M158 cruise (Sep 28-Oct 22, 2019)

2019



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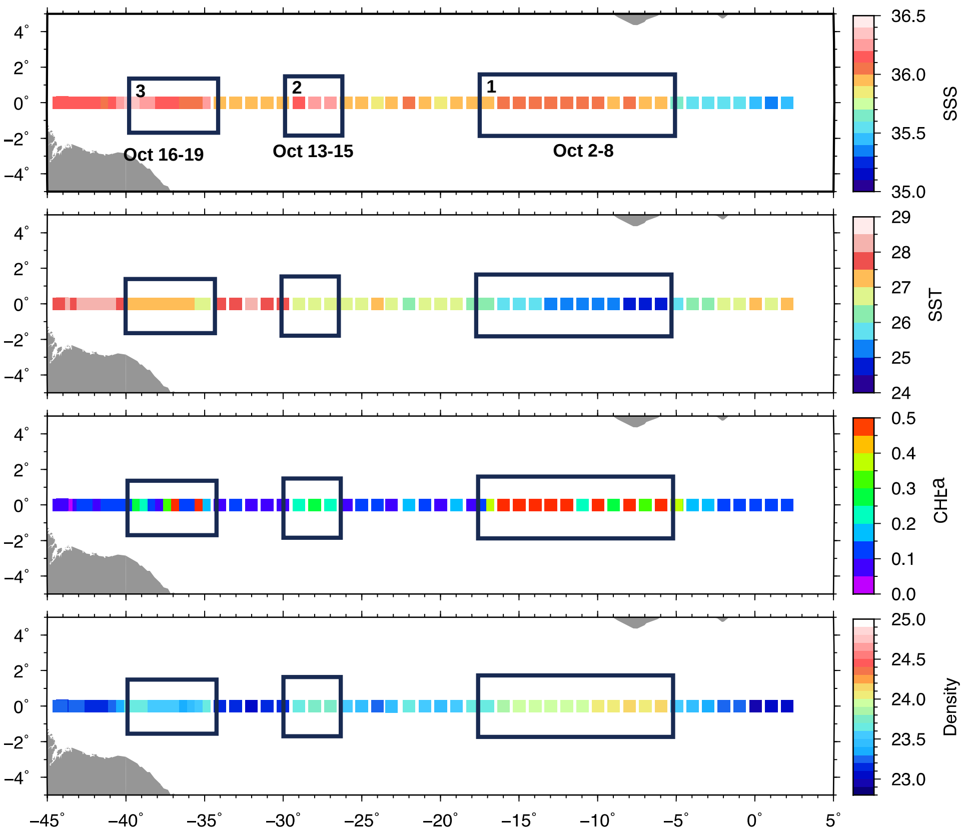
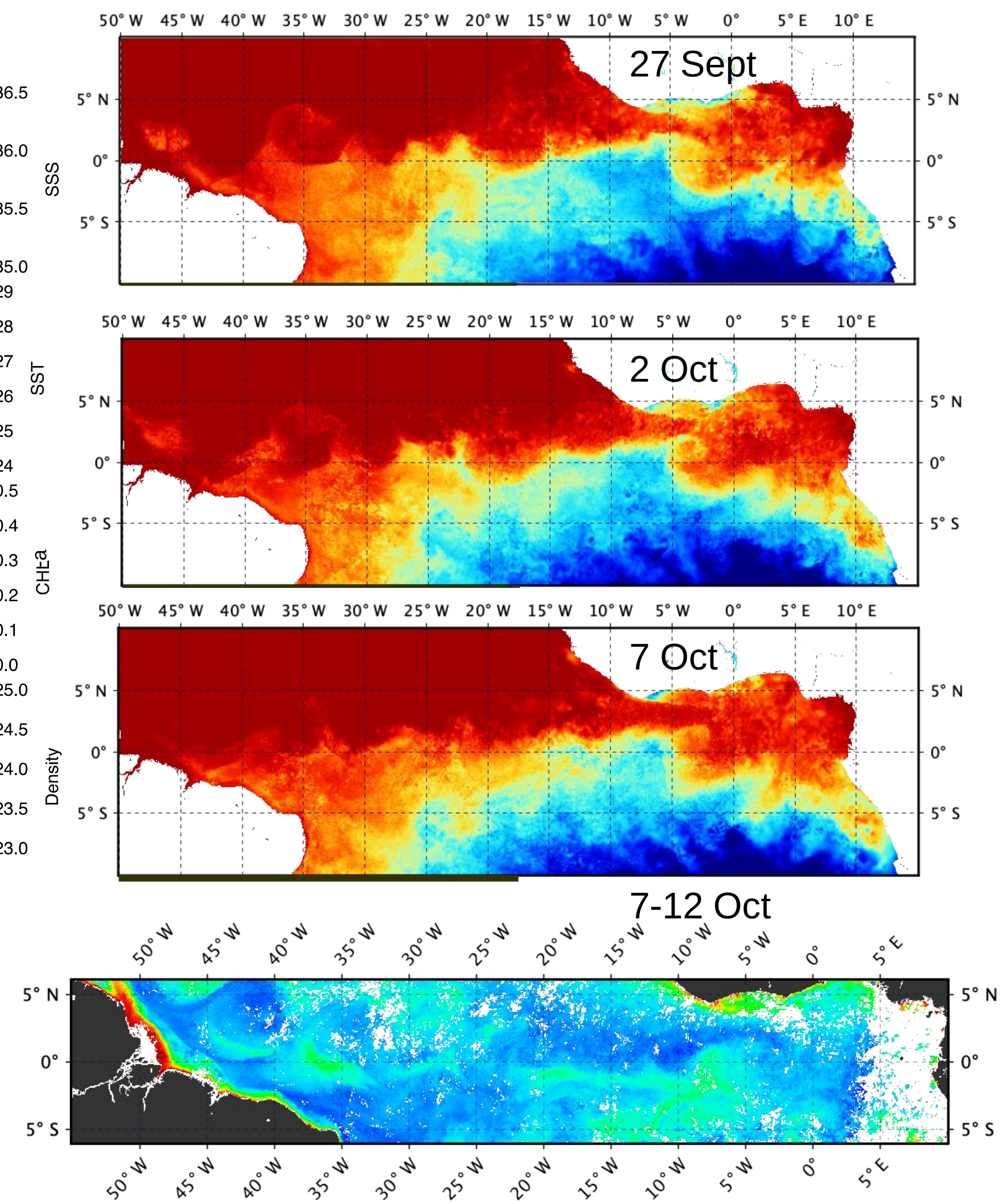
M158 cruise (Sep 28-Oct 22, 2019)

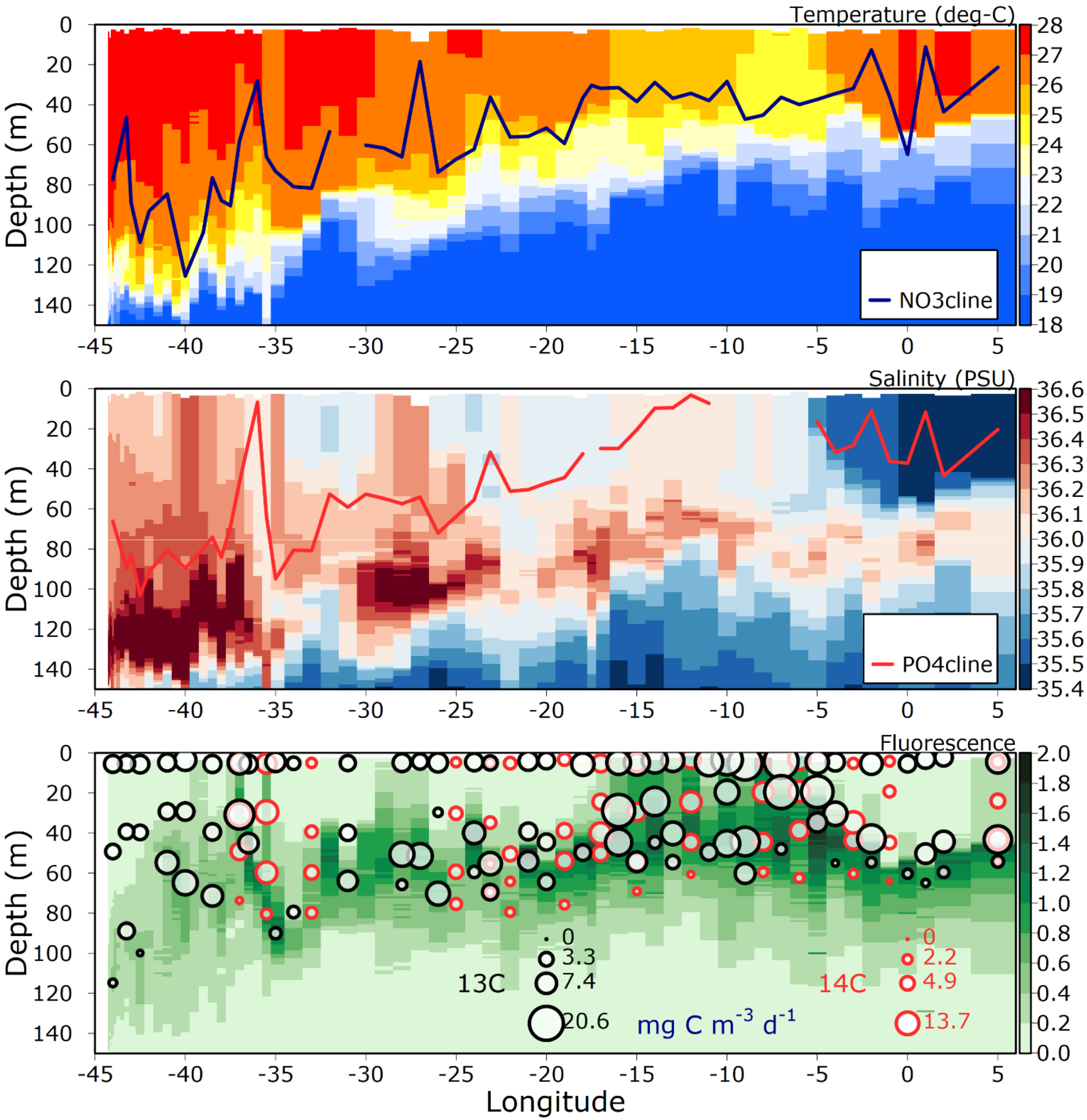
In-situ



Satellite

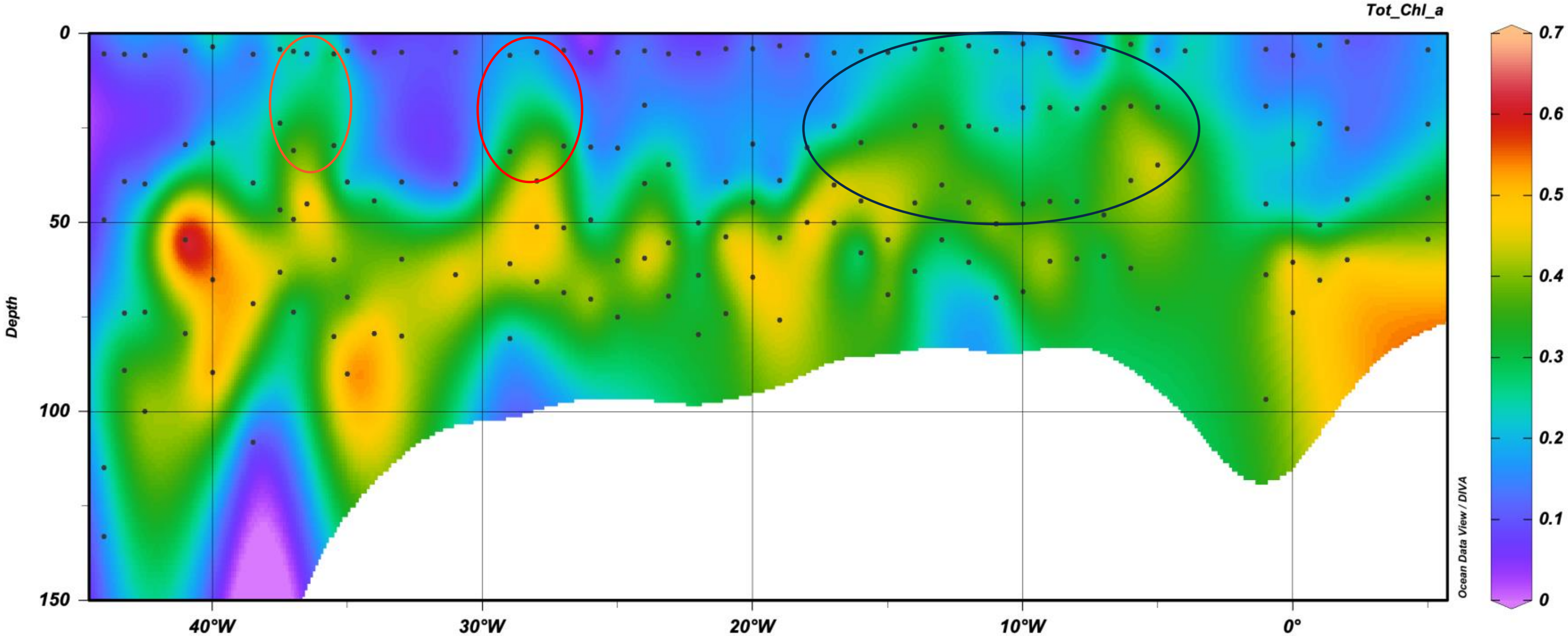


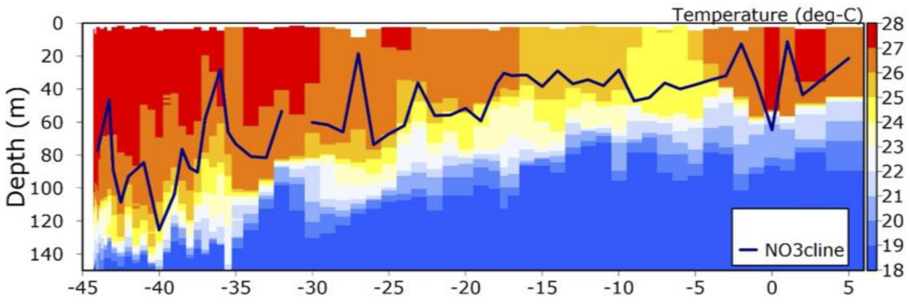
Mean surface (0-10 dbar average) salinity, temperature, chlorophyll-a and density from CTDs taken during Meteor 158-1, 2019 hydrographic section. Boxes (1, 2 and 3) indicate surface property anomalies during the chlorophyll-a increase events on Oct. 2-8, 13-15 and 16-19.

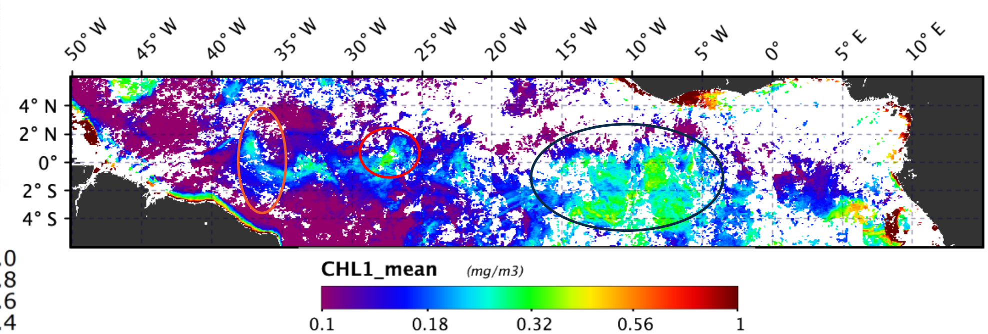


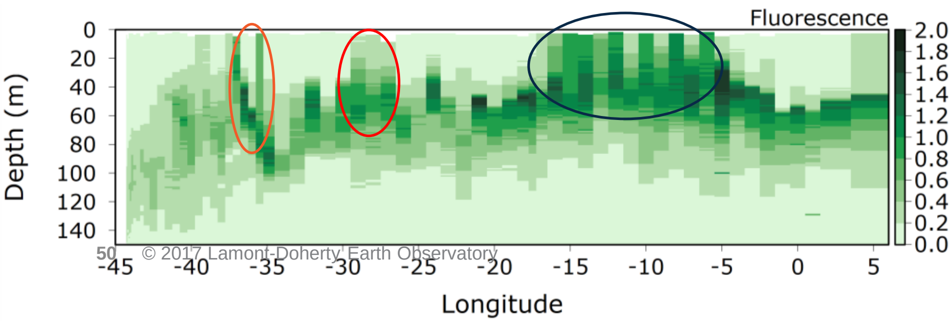
Temperature (deg-C)
Depth (m)
NO3cline
Salinity (PSU)
PO4cline
Fluorescence
13C
14C
mg C m-3 d-1
Longitude

HPLC Total Chl a

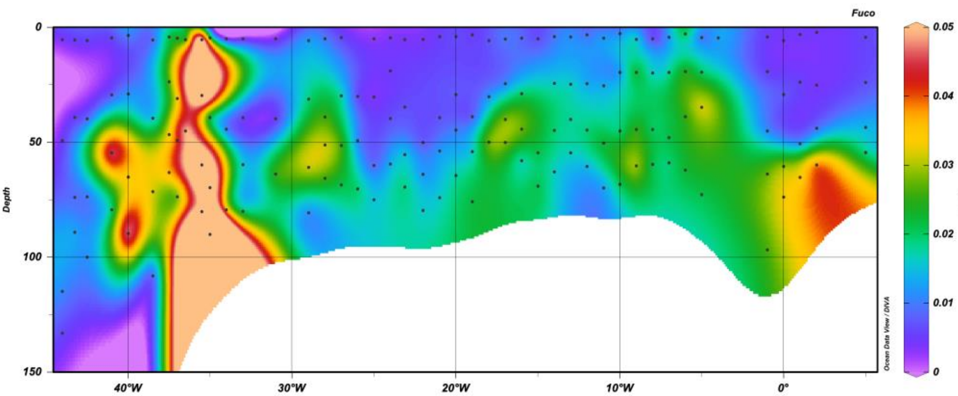




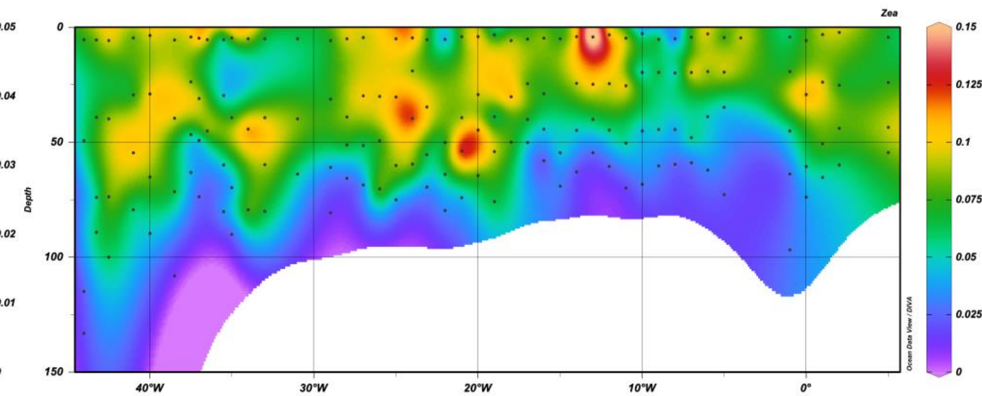


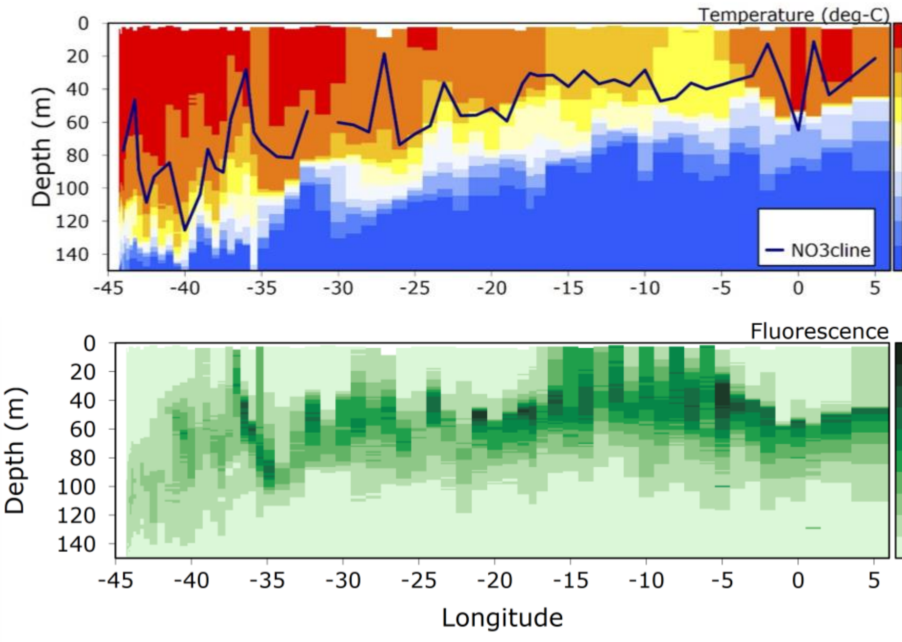


Fucoxanthin mg/m^3

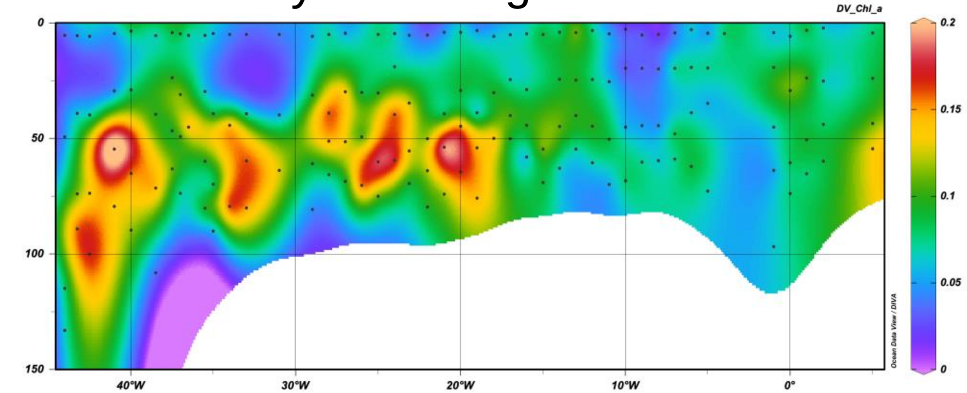


Zeaxanthin mg/m^3

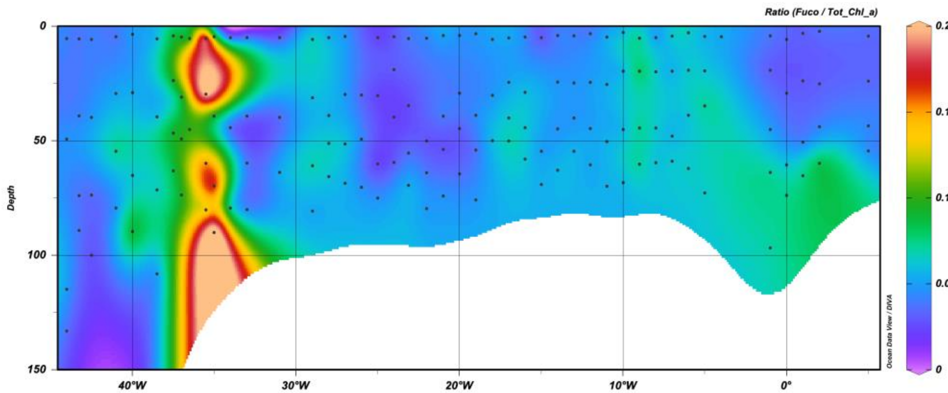




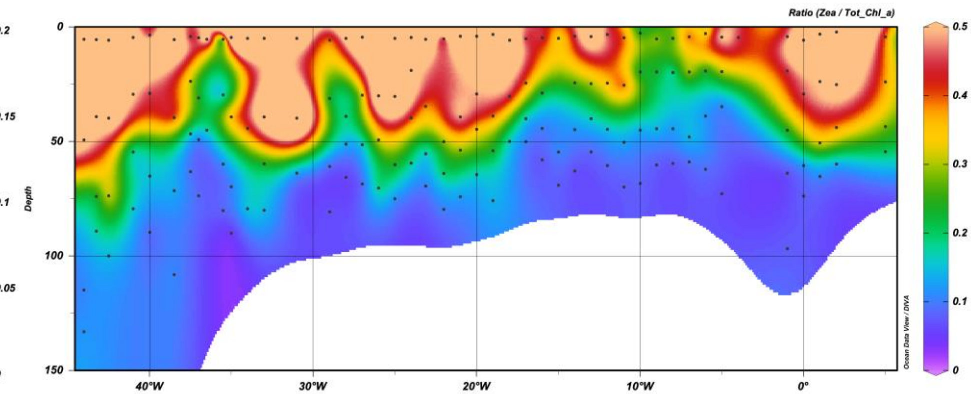
Divinyl Chl *a* mg/m^3

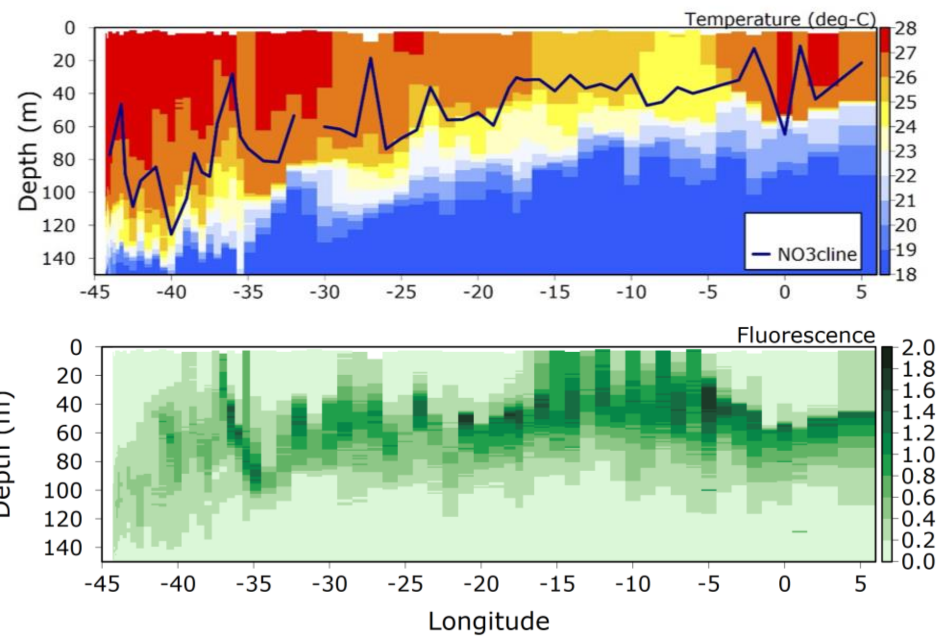


Fucoxanthin/T Chl *a*

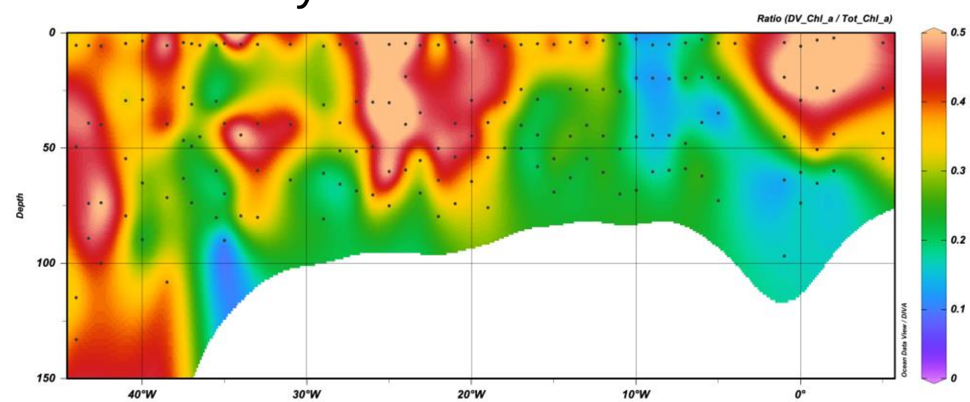


Zeaxanthin/T Chl *a*

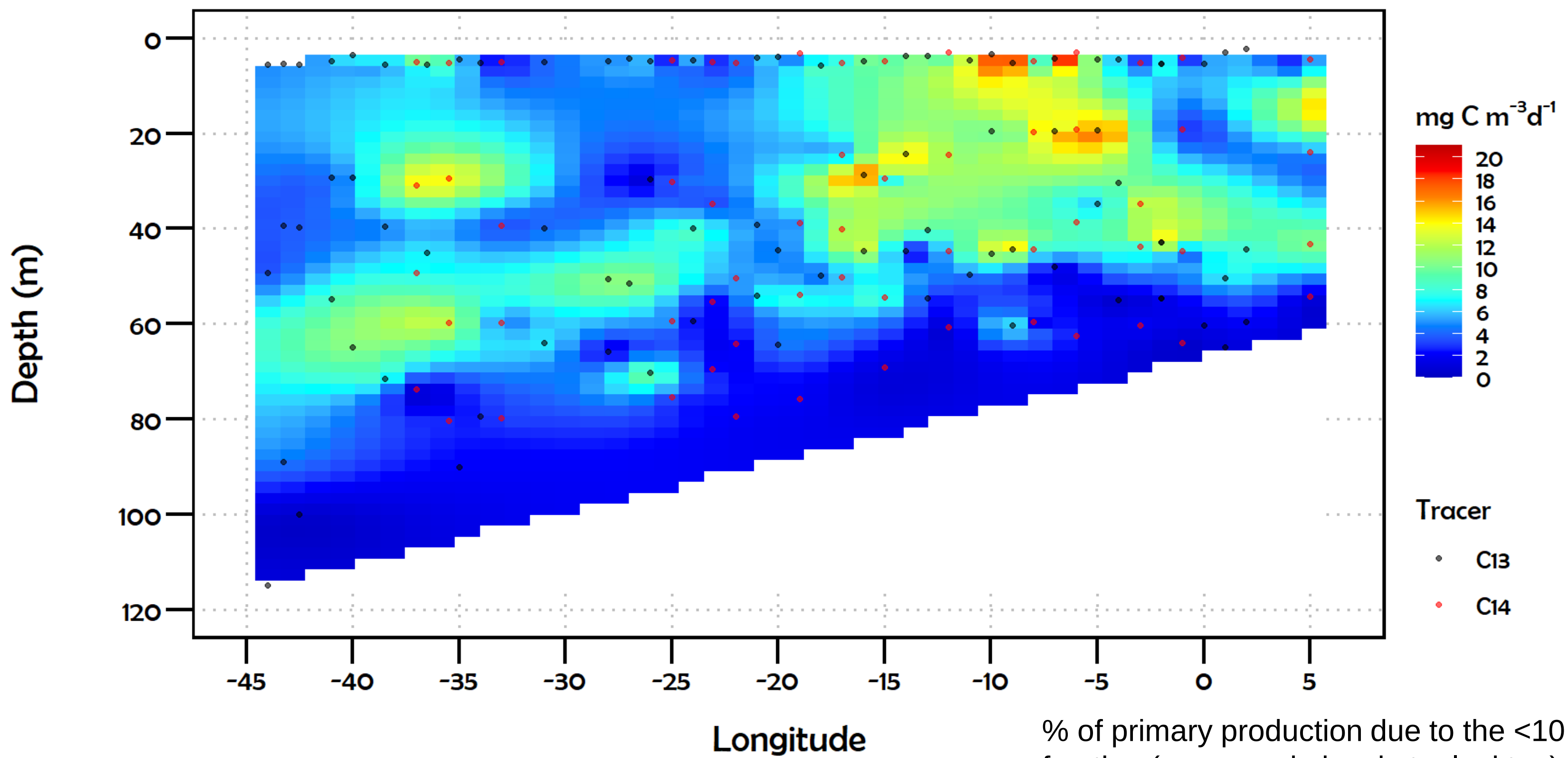


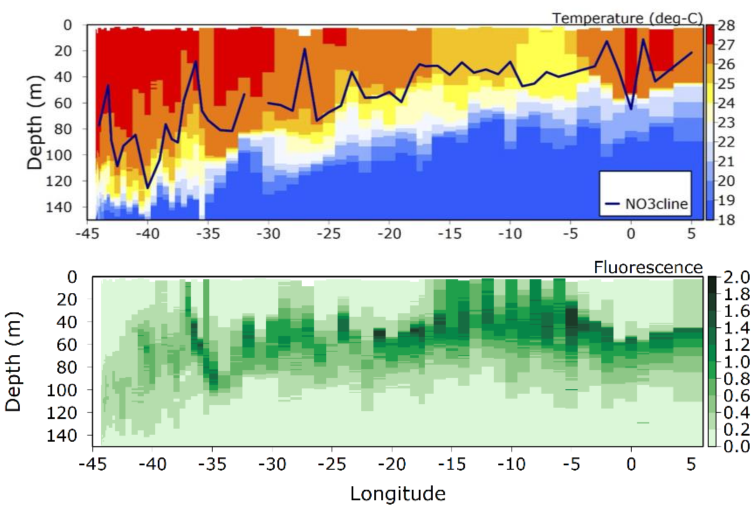


Divinyl Chl *a*//T Chl *a*

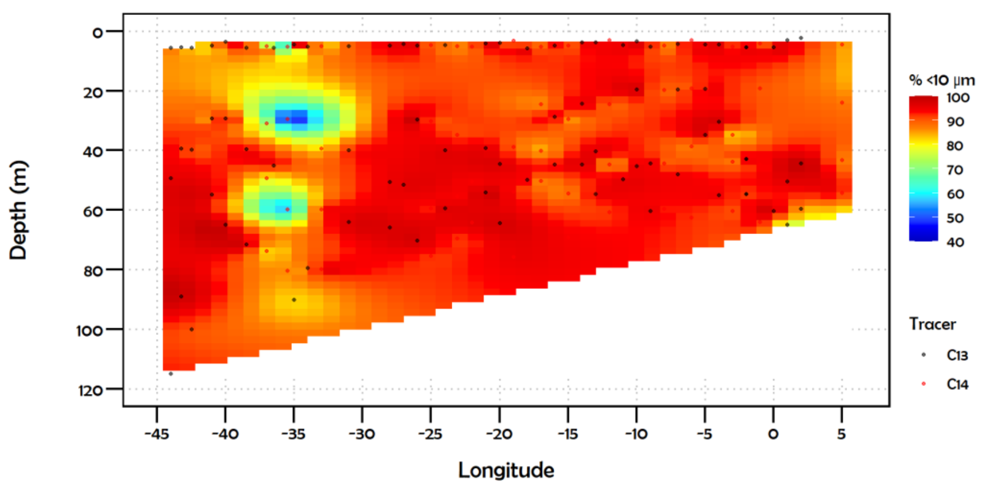


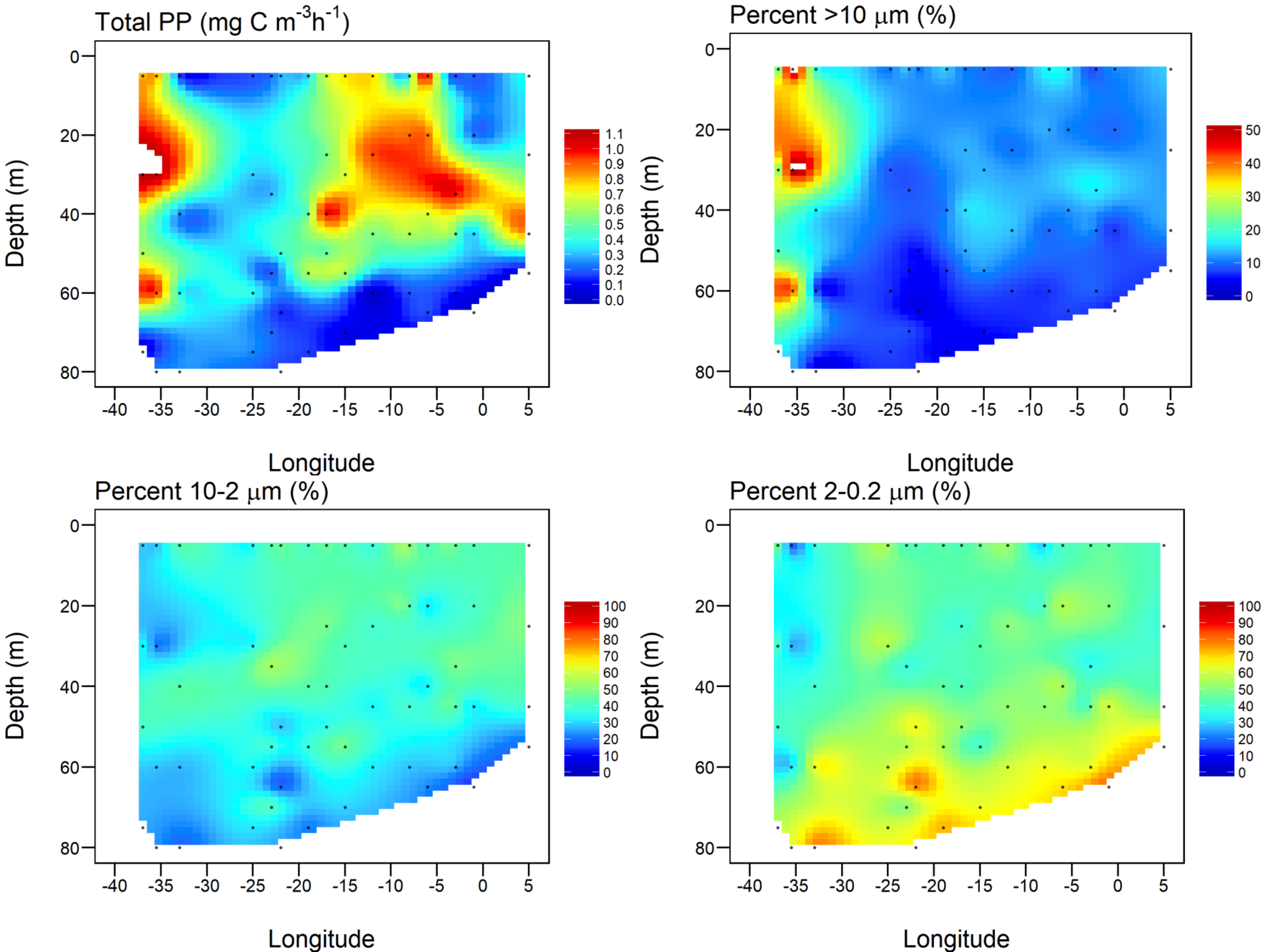
13C and 14C total primary production

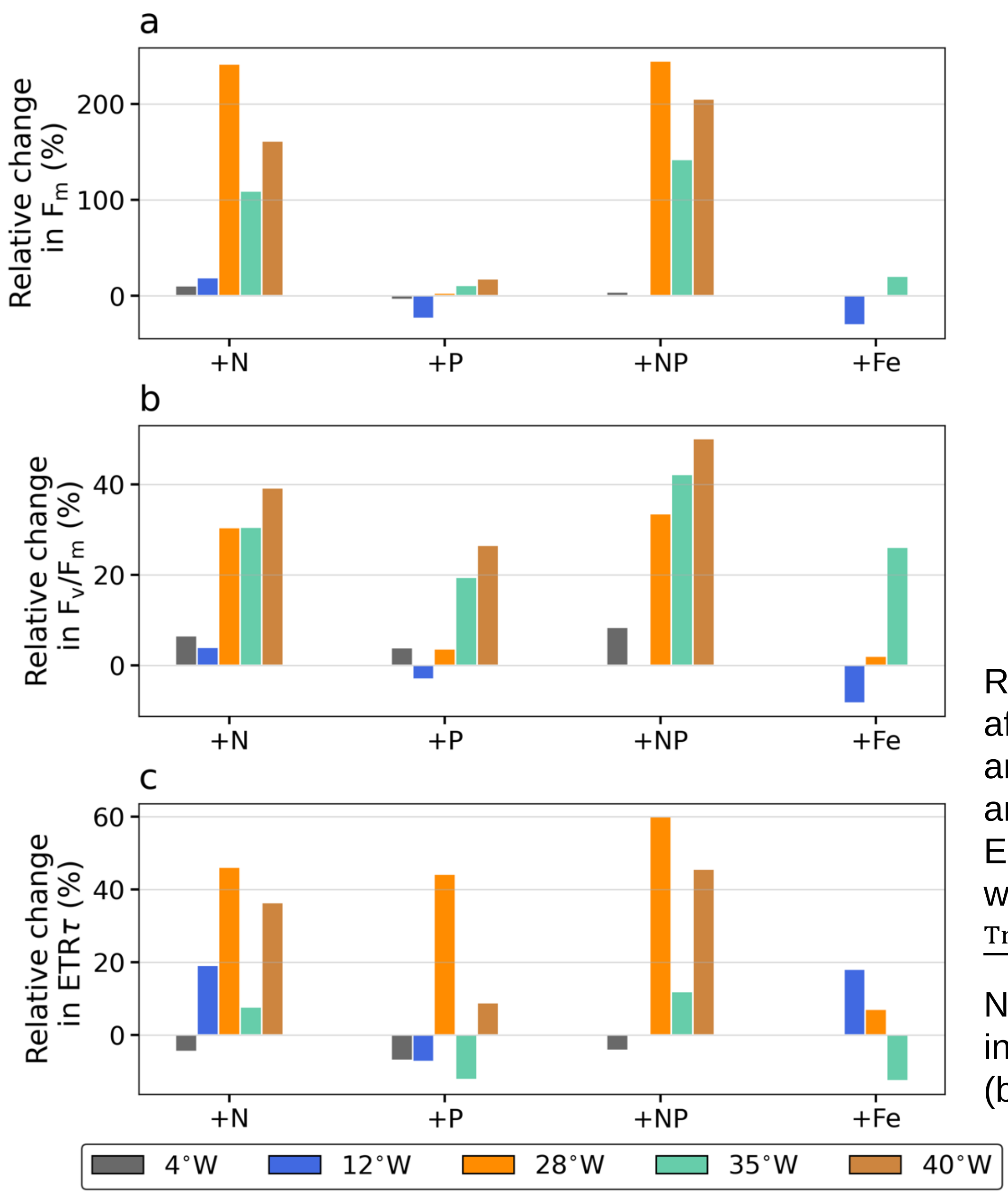




% of primary production due to the <10 µm size fraction (nano- and picophytoplankton)



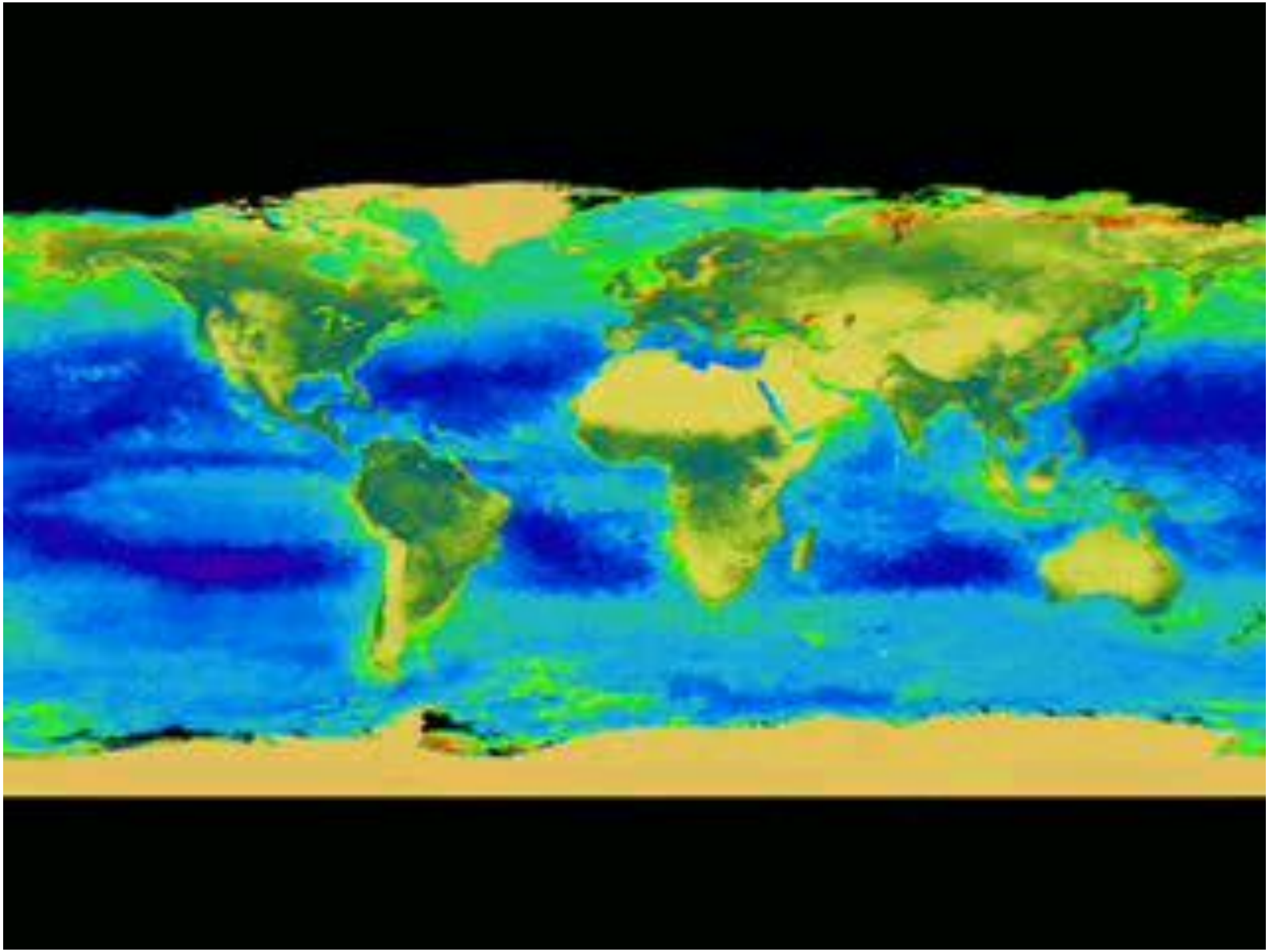

Total PP (mg C m-3h-1)
Percent >10 μm (%)
Percent 10-2 μm (%)
Percent 2-0.2 μm (%)
Depth (m)
Longitude

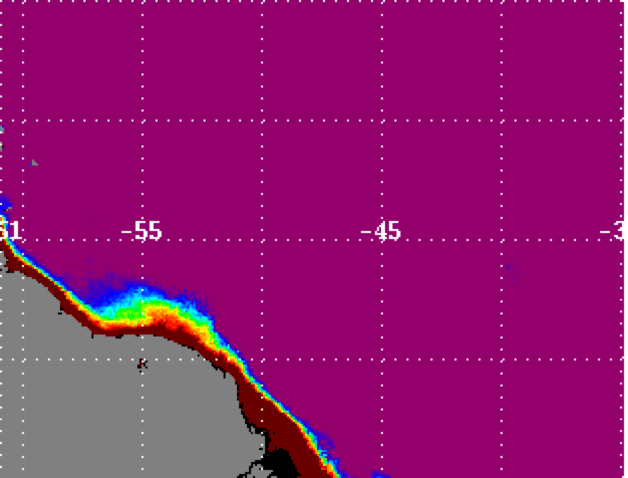


Relative changes in photophysiology 24h after nutrient amendment. **a)** F_m, **b)** F_v/F_m, and **c)** ETRτ. Treatments included amendment with, +N, +P, +NP and +Fe. Each bar color indicates location where NAE was initiated. Change was calculated as $\frac{\text{Tretment}^{24h} - \text{Control}^{24h}}{\text{Control}^{24h}}$ for each parameter. Note the NAE at 4°W (gray bars) didn't include a +Fe treatment, and the NAE 12°W (blue bars) didn't include a +NP treatment.

Slide from Jonathan Sherman

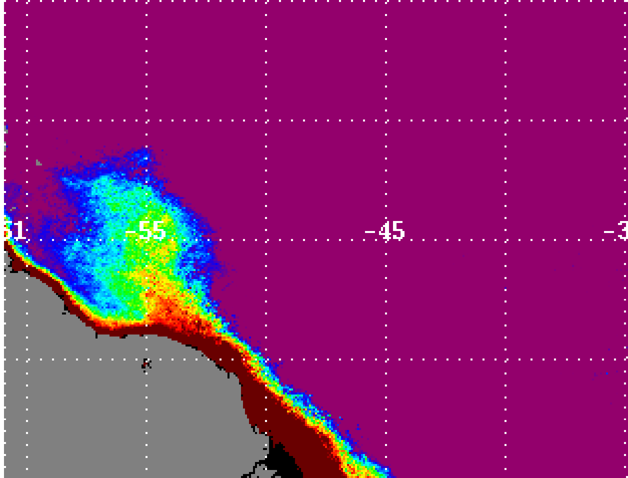
Amazon River

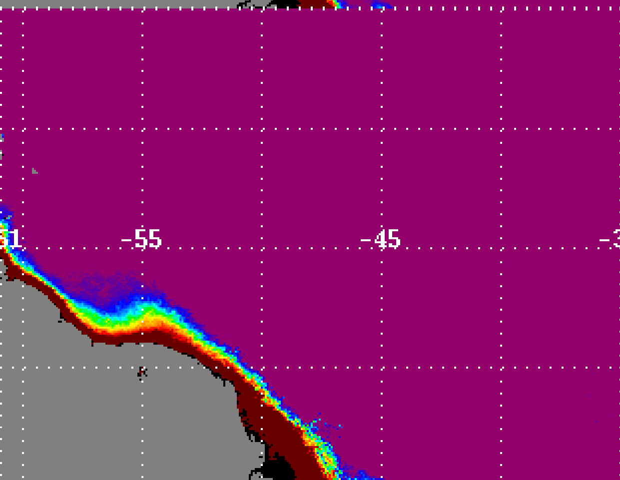




Jan
0.3 x 10^{12}

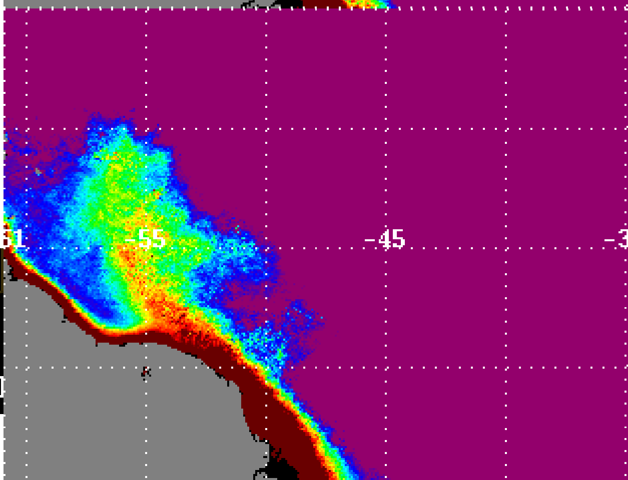
April
0.6 x 10^{12}

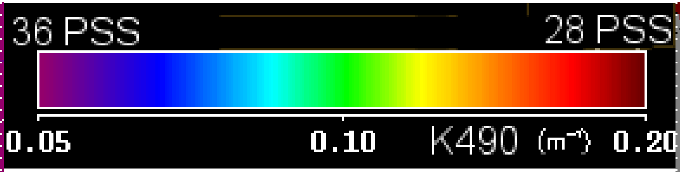


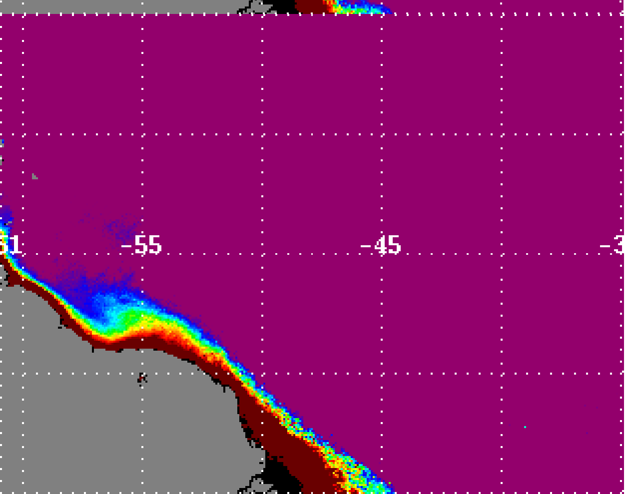


Feb
0.3 x 10^{12}

May
1.0 x 10^{12}

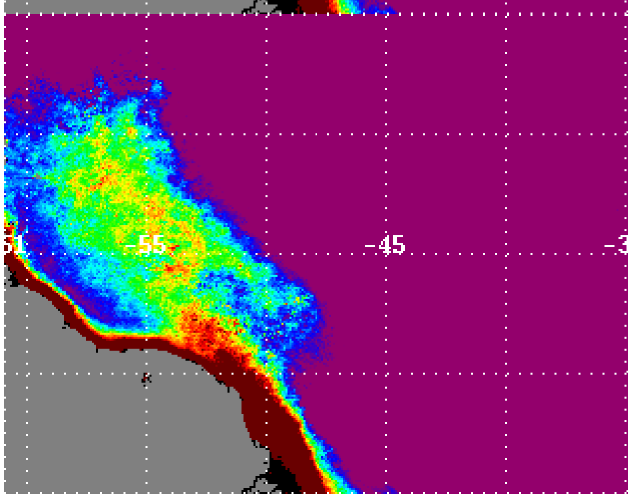


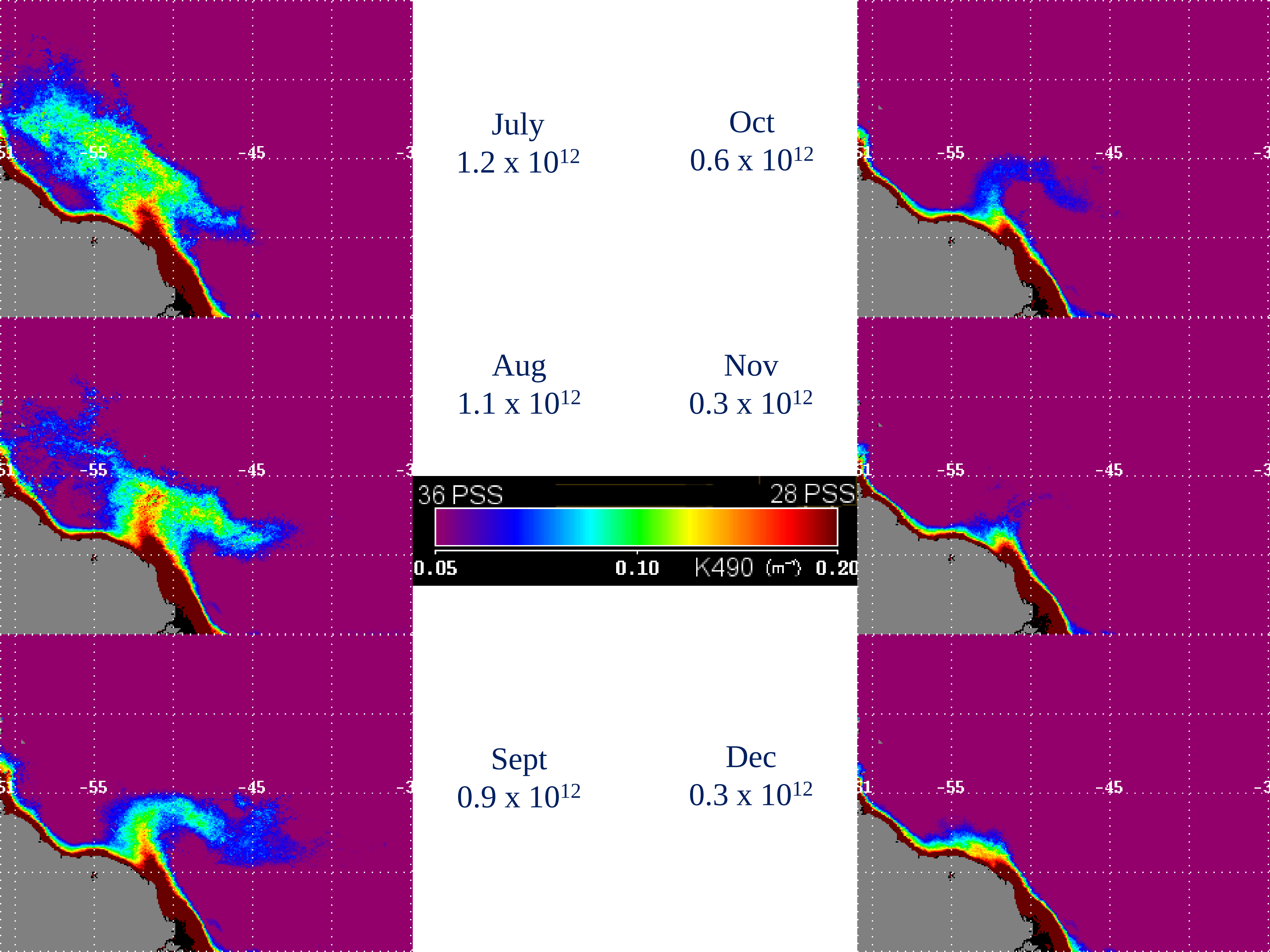


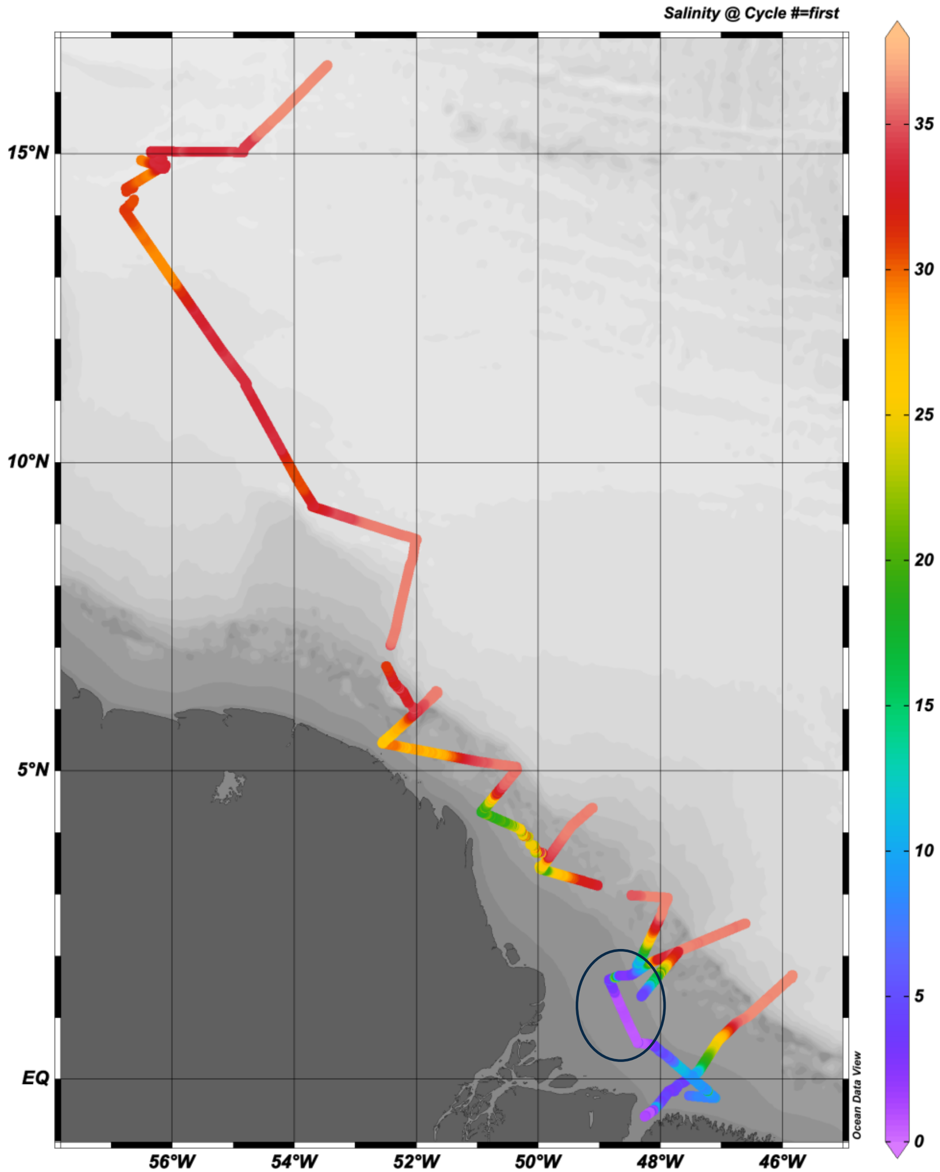


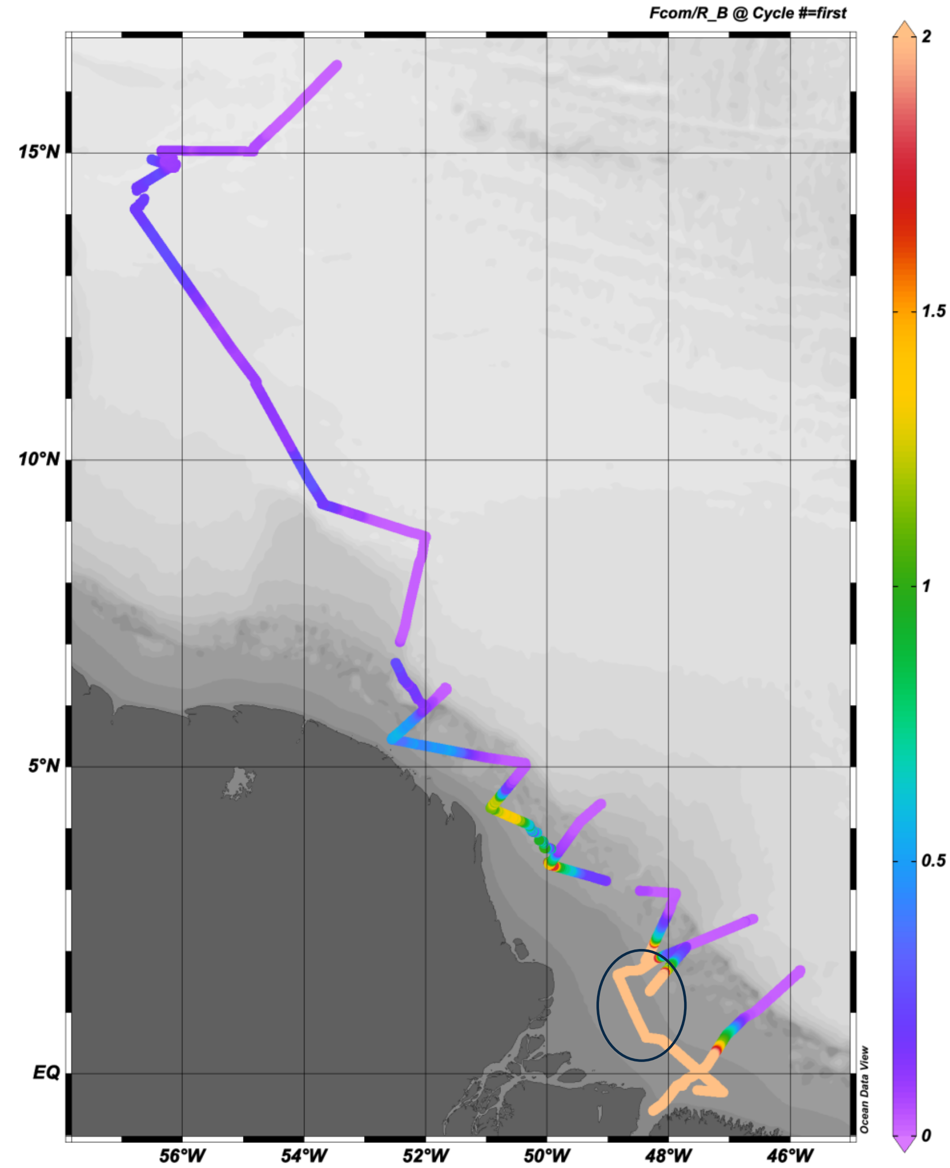
March
0.4 x 10^{12}

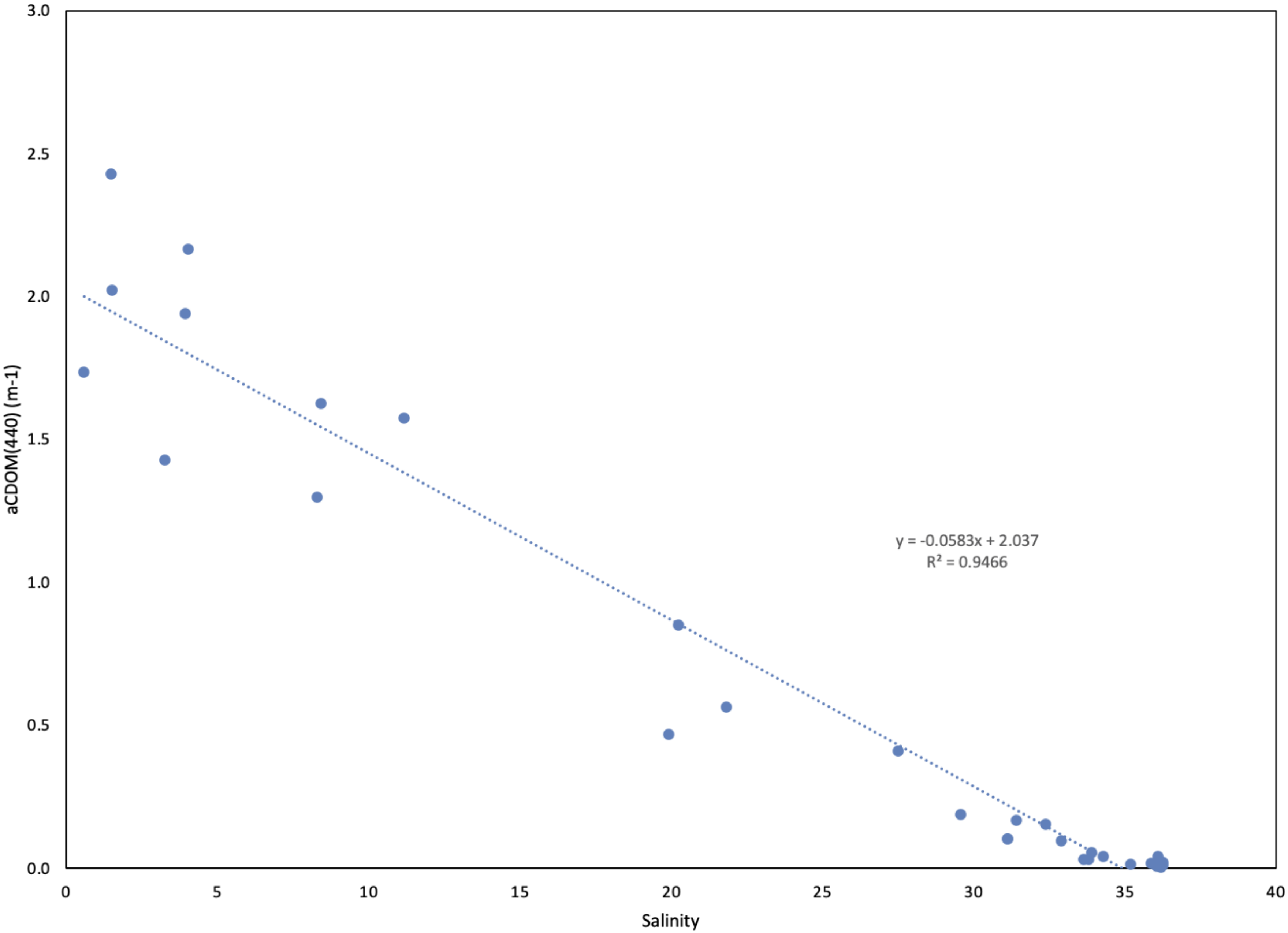
June
1.2 x 10^{12}

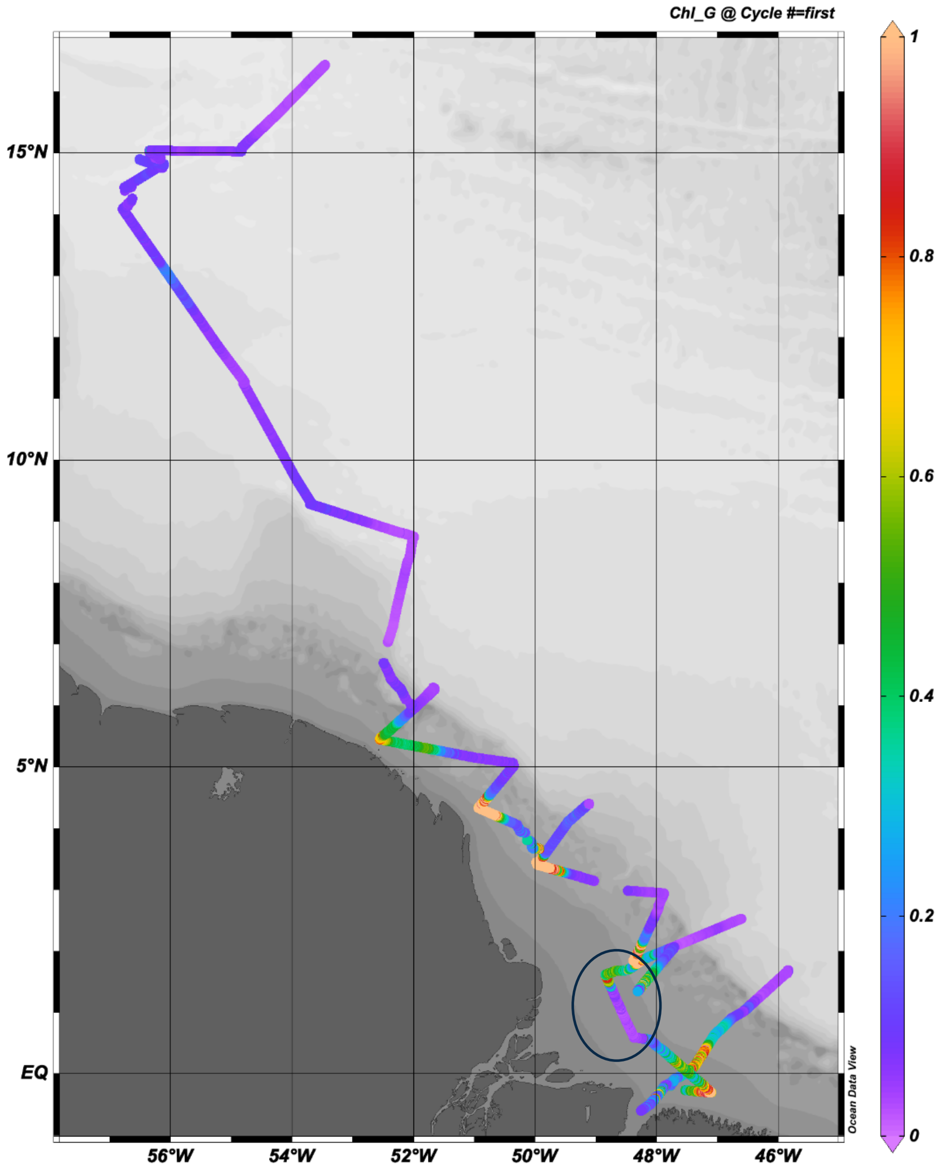


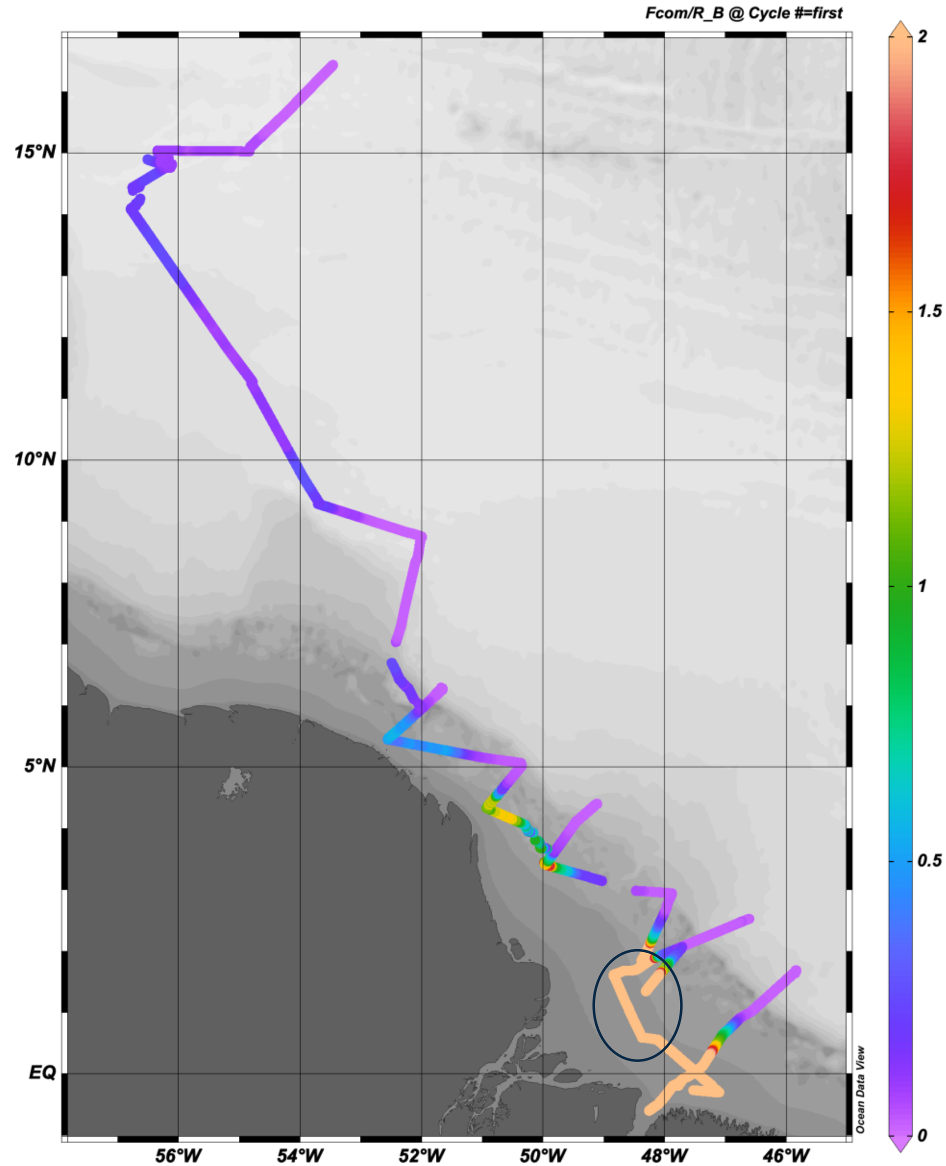

July
1.2 x 10^12
Aug
1.1 x 10^12
Sept
0.9 x 10^12
Oct
0.6 x 10^12
Nov
0.3 x 10^12
Dec
0.3 x 10^12
36 PSS
28 PSS
0.05
0.10
K490 (m⁻¹)
0.20
-55
-45

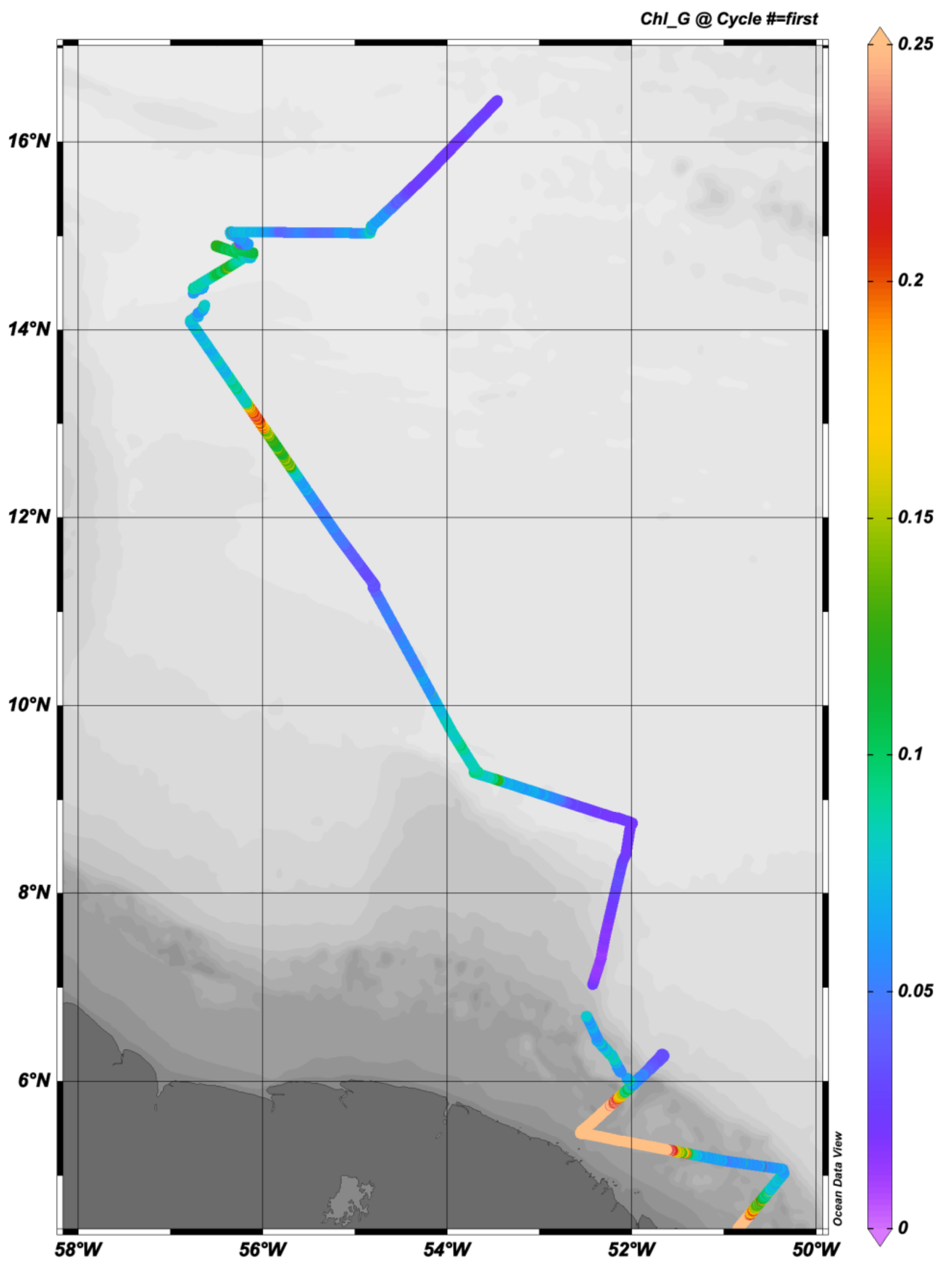

Salinity @ Cycle #=first
15°N
10°N
5°N
EQ
56°W
54°W
52°W
50°W
48°W
46°W
35
30
25
20
15
10
5
0
Ocean Data View

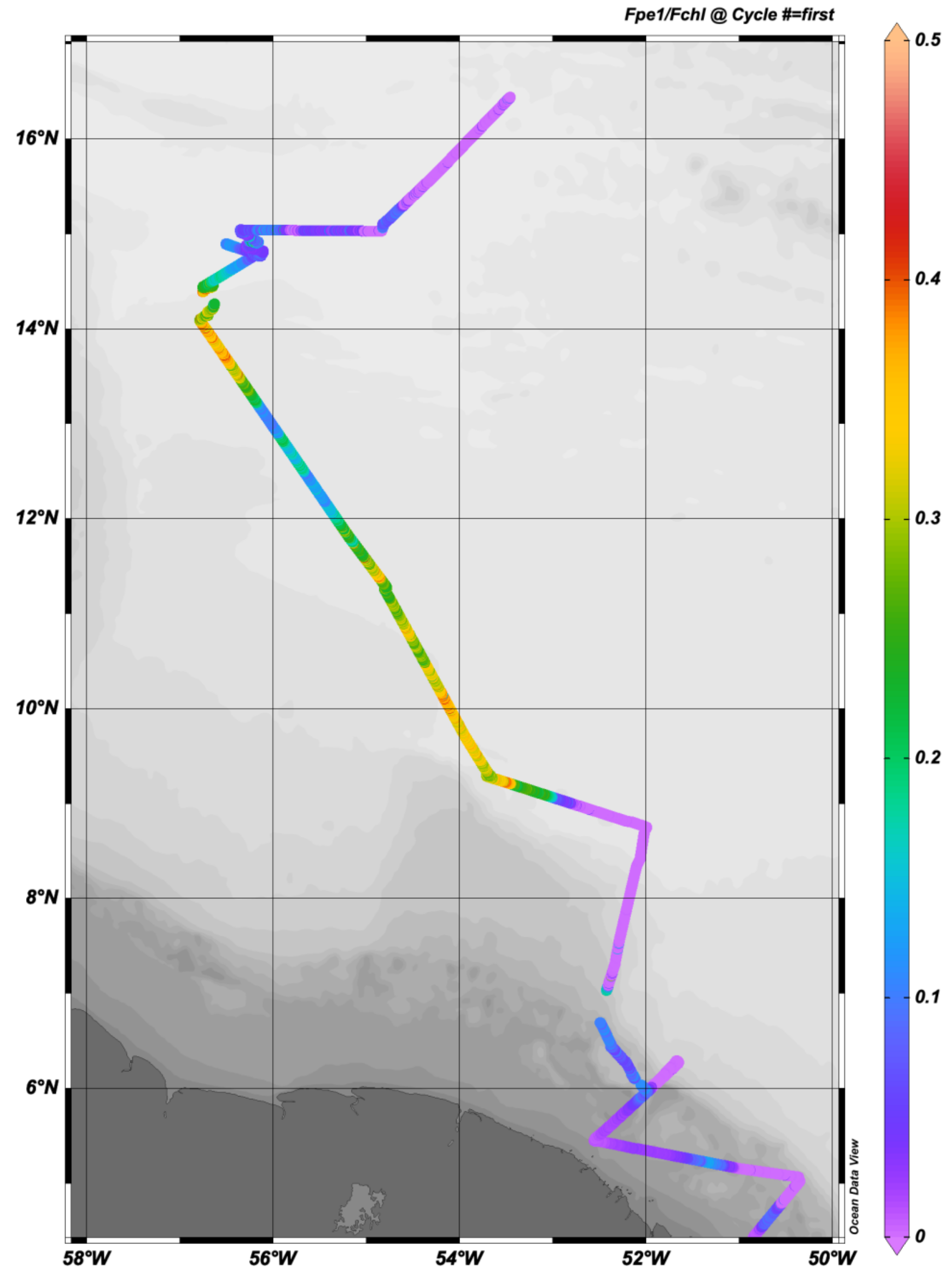

Fcom/R_B @ Cycle #=first
15°N
10°N
5°N
EQ
56°W
54°W
52°W
50°W
48°W
46°W
2
1.5
1
0.5
0
Ocean Data View

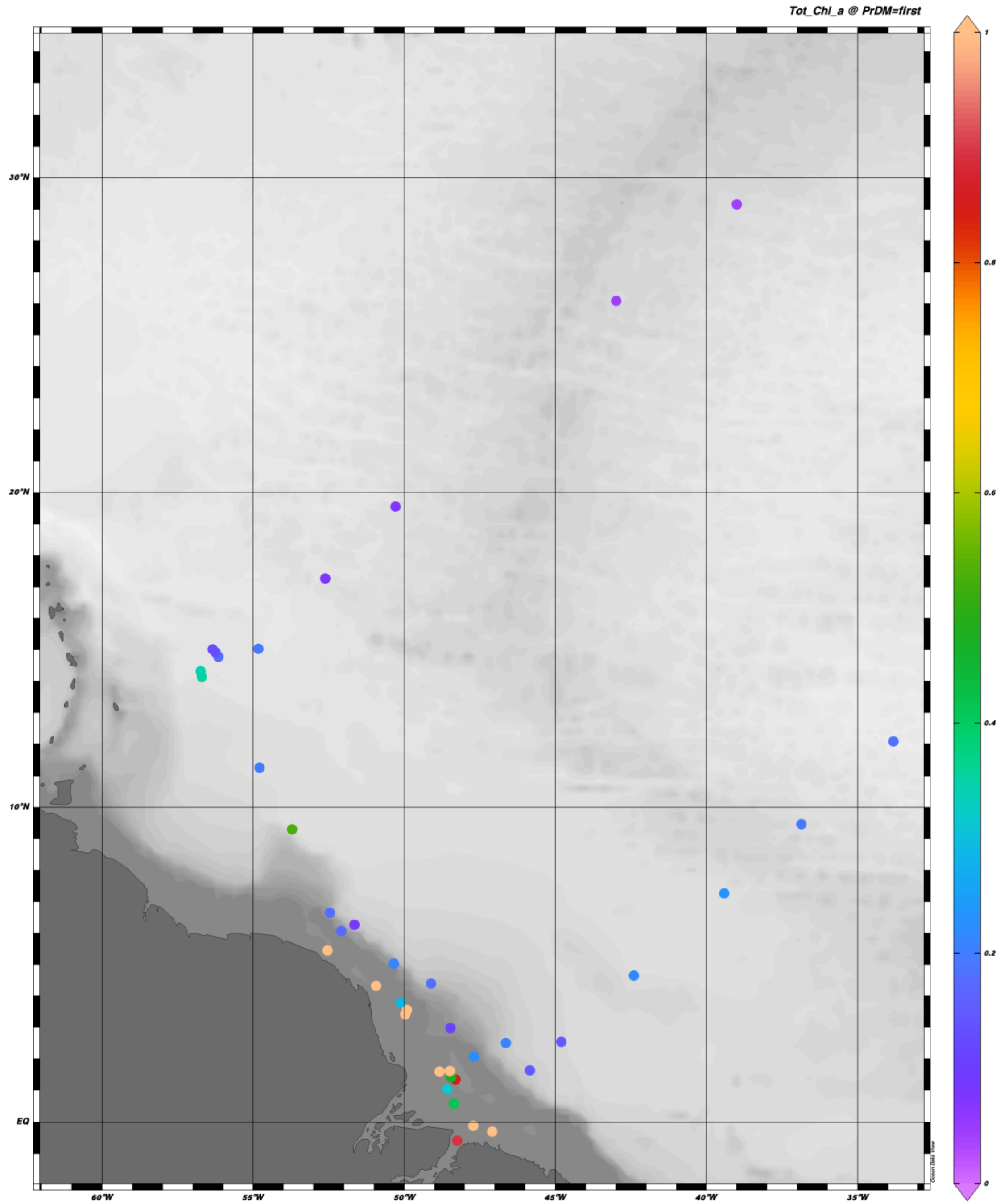

3.0
2.5
2.0
1.5
1.0
0.5
0.0
aCDOM(440) (m-1)
y = -0.0583x + 2.037
R² = 0.9466
0
5
10
15
20
25
30
35
40
Salinity


Chl_G @ Cycle #=first
15°N
10°N
5°N
EQ
56°W
54°W
52°W
50°W
48°W
46°W
1
0.8
0.6
0.4
0.2
0
Ocean Data View

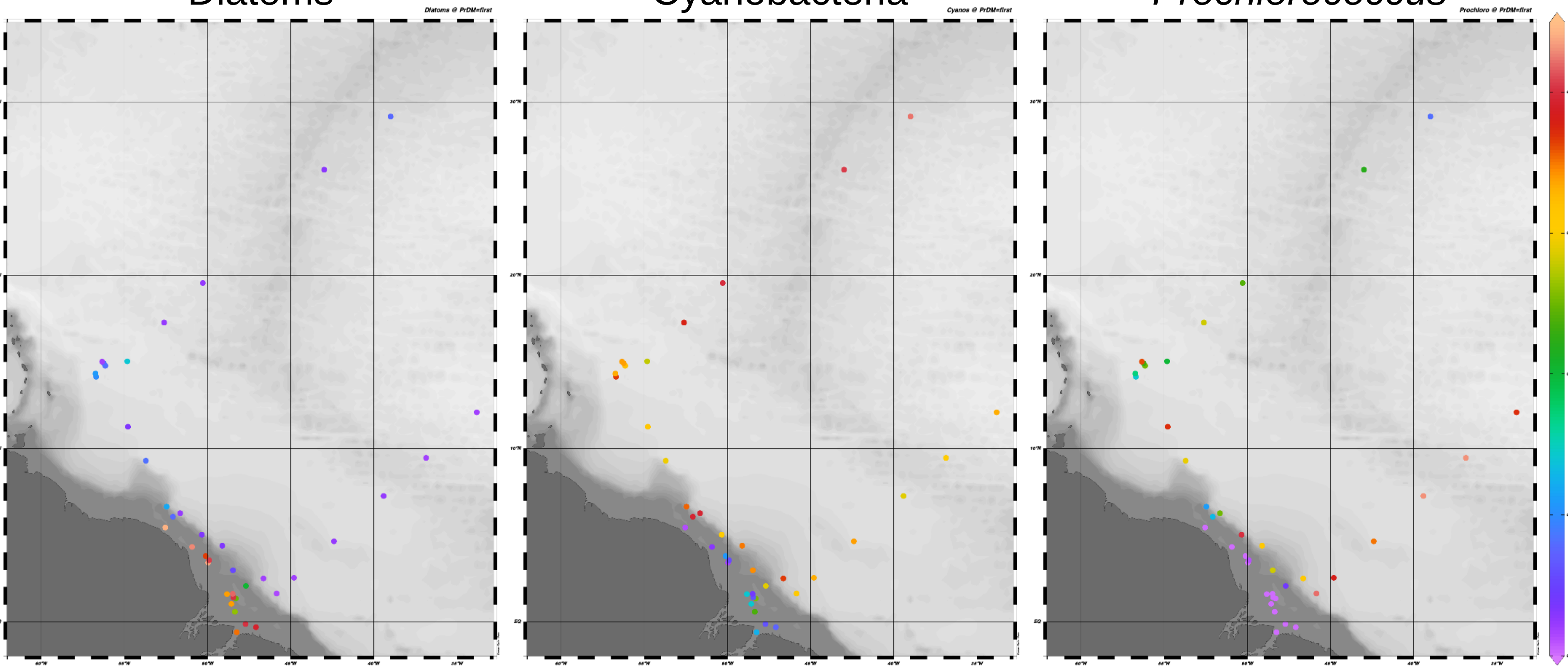

Fcom/R_B @ Cycle #=first
15°N
10°N
5°N
EQ
56°W
54°W
52°W
50°W
48°W
46°W
2
1.5
1
0.5
0
Ocean Data View


Chl_G @ Cycle #=first
16°N
14°N
12°N
10°N
8°N
6°N
58°W
56°W
54°W
52°W
50°W
0.25
0.2
0.15
0.1
0.05
0
Ocean Data View


Fpe1/Fchl @ Cycle #=first
16°N
14°N
12°N
10°N
8°N
6°N
58°W
56°W
54°W
52°W
50°W
0.5
0.4
0.3
0.2
0.1
0
Ocean Data View


Tot_Chl_a @ PrDM=first
30°N
20°N
10°N
EQ
60°W
55°W
50°W
45°W
40°W
35°W
1
0.8
0.6
0.4
0.2
0

Diatoms Cyanobacteria *Prochlorococcus*



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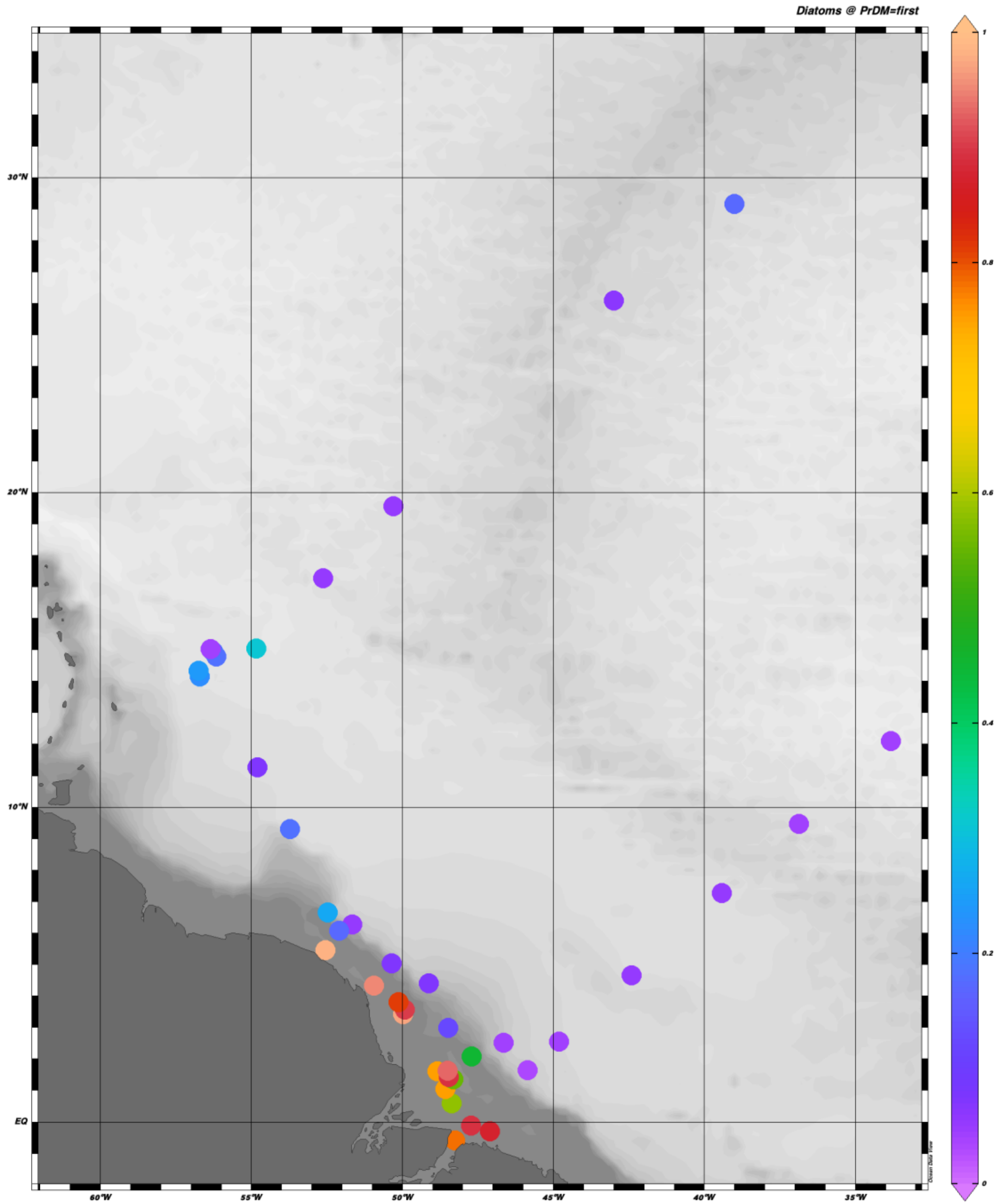
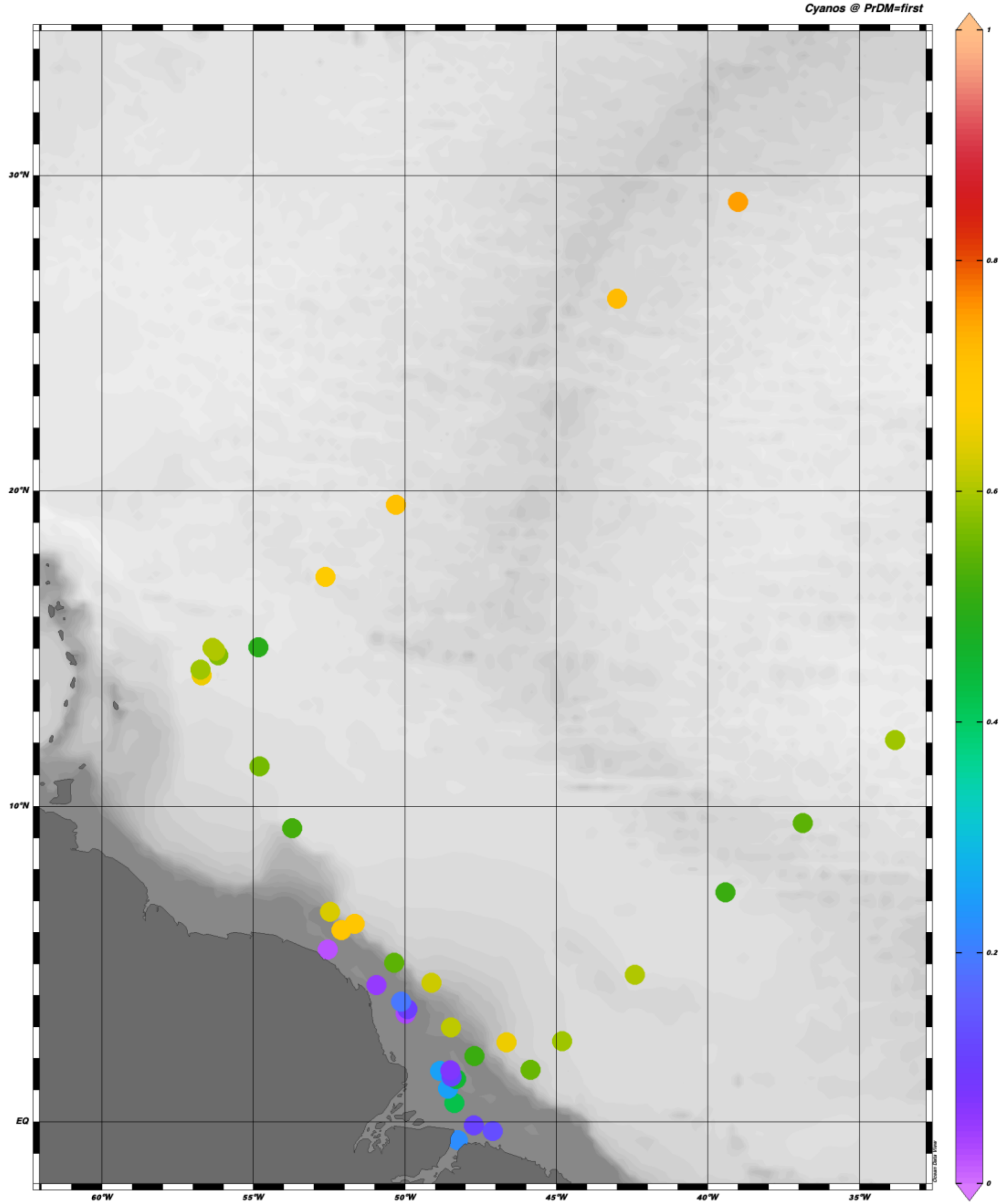
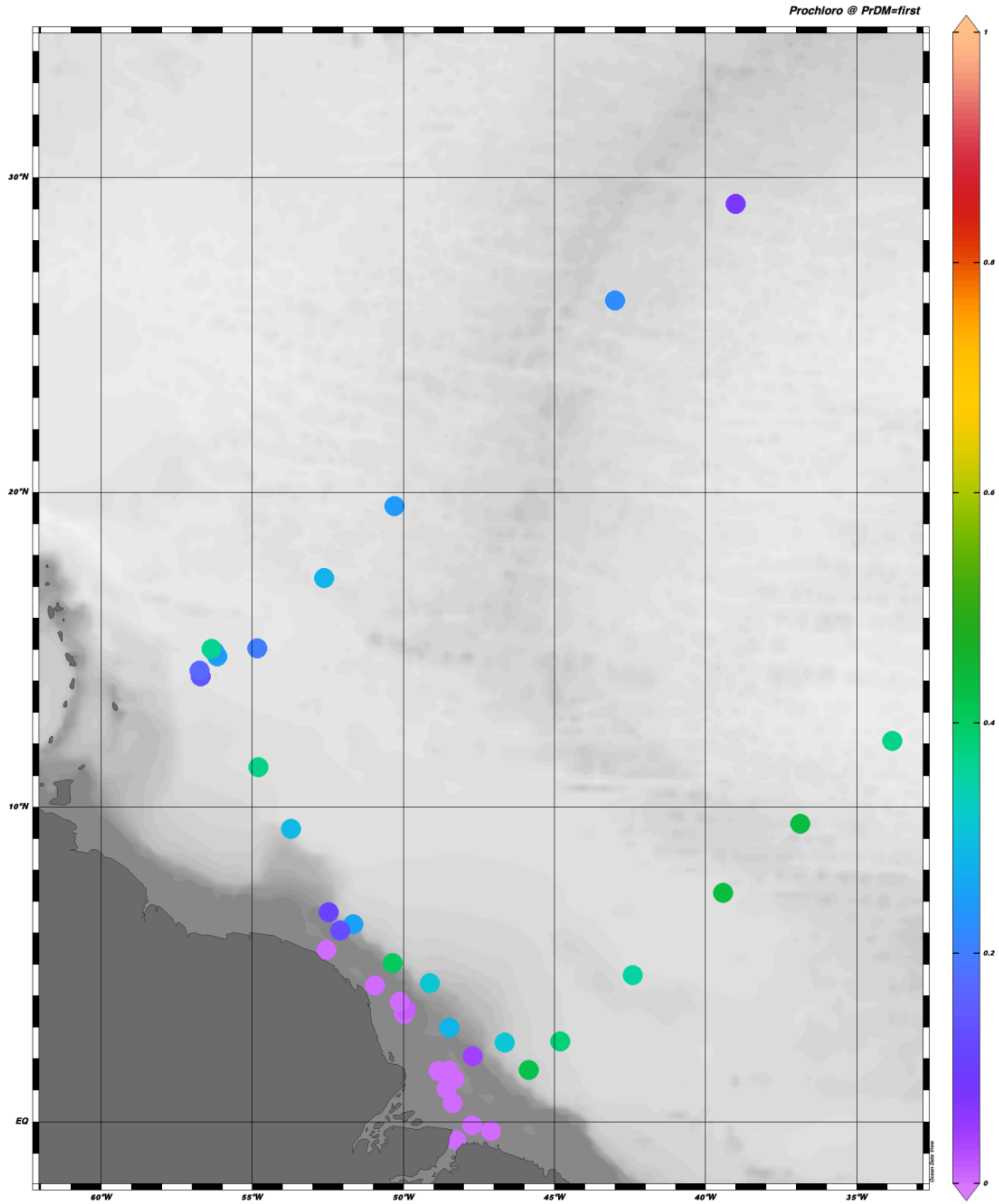


Diatoms @ PrDM=first
30°N
20°N
10°N
EQ
60°W
55°W
50°W
45°W
40°W
35°W
1
0.8
0.6
0.4
0.2
0

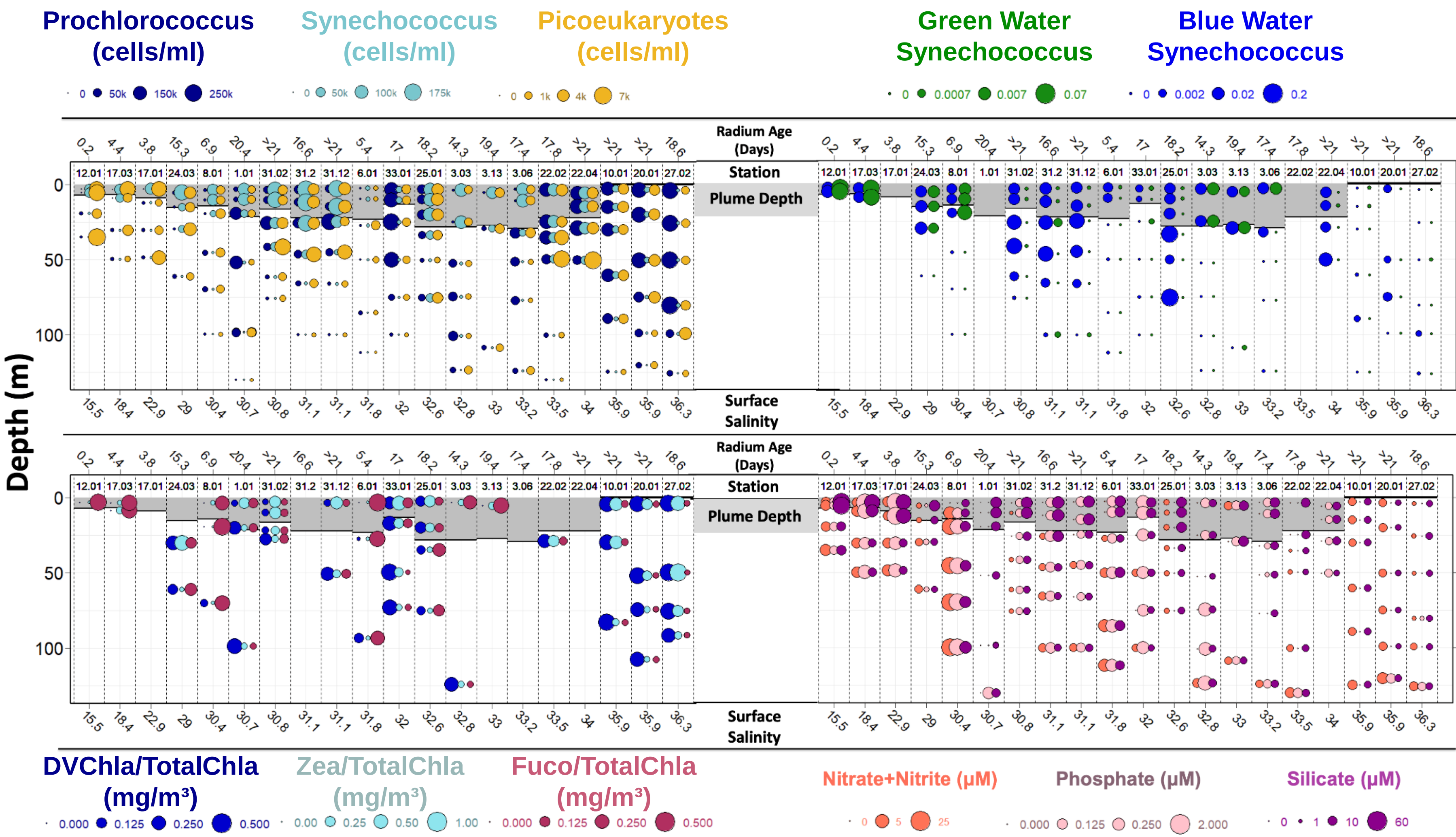
Diatoms



Cyanobacteria



Prochlorococcus



Prochlorococcus (cells/ml)
0 50k 150k 250k
Synechococcus (cells/ml)
0 50k 100k 175k
Picoeukaryotes (cells/ml)
0 1k 4k 7k
Green Water Synechococcus
0 0.0007 0.007 0.07
Blue Water Synechococcus
0 0.002 0.02 0.2
Radium Age (Days)
0.2 4.4 3.8 15.3 6.9 20.4 >21 16.6 >21 5.4 17 18.2 14.3 19.4 17.4 17.8 >21 >21 >21 18.6
Station
12.01 17.03 17.01 24.03 8.01 1.01 31.02 31.2 31.12 6.01 33.01 25.01 3.03 3.13 3.06 22.02 22.04 10.01 20.01 27.02
Plume Depth
Surface Salinity
15.5 18.4 22.9 29 30.4 30.7 30.8 31.1 31.1 31.8 32 32.6 32.8 33 33.2 33.5 34 35.9 35.9 36.3
Depth (m)
0 50 100
DVChla/TotalChla (mg/m³)
0.000 0.125 0.250 0.500
Zea/TotalChla (mg/m³)
0.00 0.25 0.50 1.00
Fuco/TotalChla (mg/m³)
0.000 0.125 0.250 0.500
Nitrate+Nitrite (µM)
0 5 25
Phosphate (µM)
0.000 0.125 0.250 2.000
Silicate (µM)
0 1 10 60