Heterotrophic activity in the sea revisited

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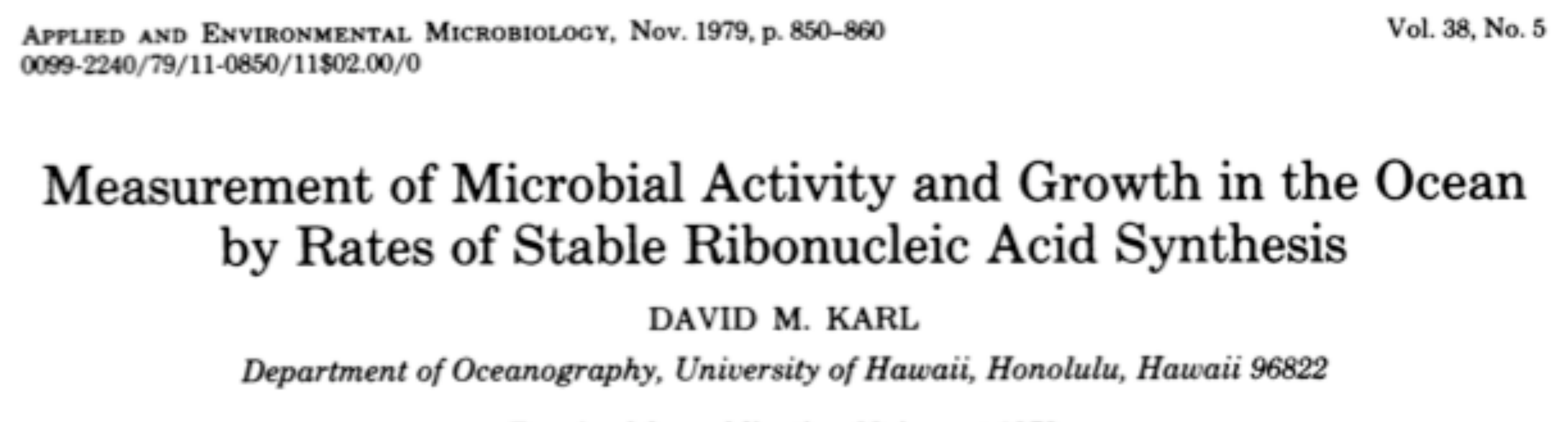
2010 C-MORE symmer course in Microbial oceanography,
Univ. of Hawaii, 15 June, 2010

Outline

- A brief history.
- Carbon flux through prokaryotes
- Metabolic balance
- Do we measure primary production properly?
- Cell mortality and the emperor new suite of clothes.
- Non-phytoplankton drivers of heterotrophic activity.
- External sources of organic matter: significance and use



APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Nov. 1979, p. 850–860 Vol. 38, No. 5
0099-2240/79/11-0850/11$02.00/0

Measurement of Microbial Activity and Growth in the Ocean by Rates of Stable Ribonucleic Acid Synthesis

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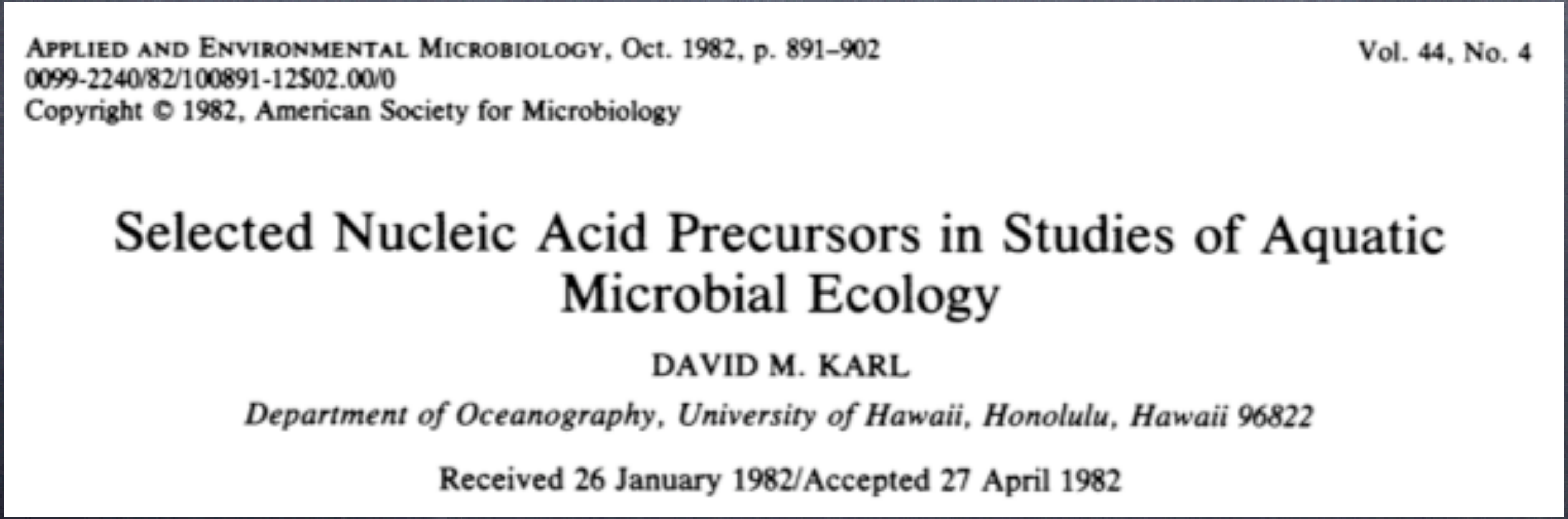
Received for publication [illegible] August 1979



APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Oct. 1982, p. 891–902 Vol. 44, No. 4
0099-2240/82/100891-12$02.00/0

Selected Nucleic Acid Precursors in Studies of Aquatic Microbial Ecology

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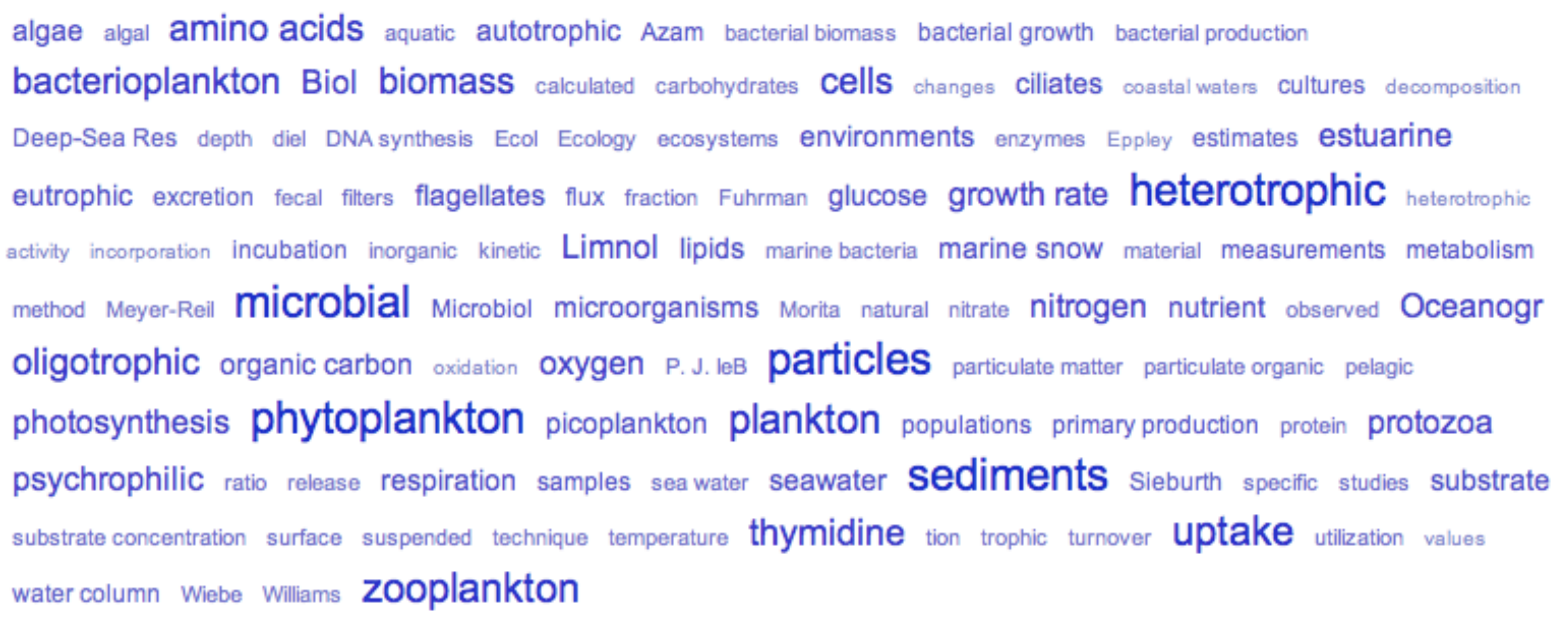
Heterotrophic activity in the sea, 1981
15 Volume NATO conference series: Marine sciences
John E. Hobbie *and Peter Le.B. J. Williams*

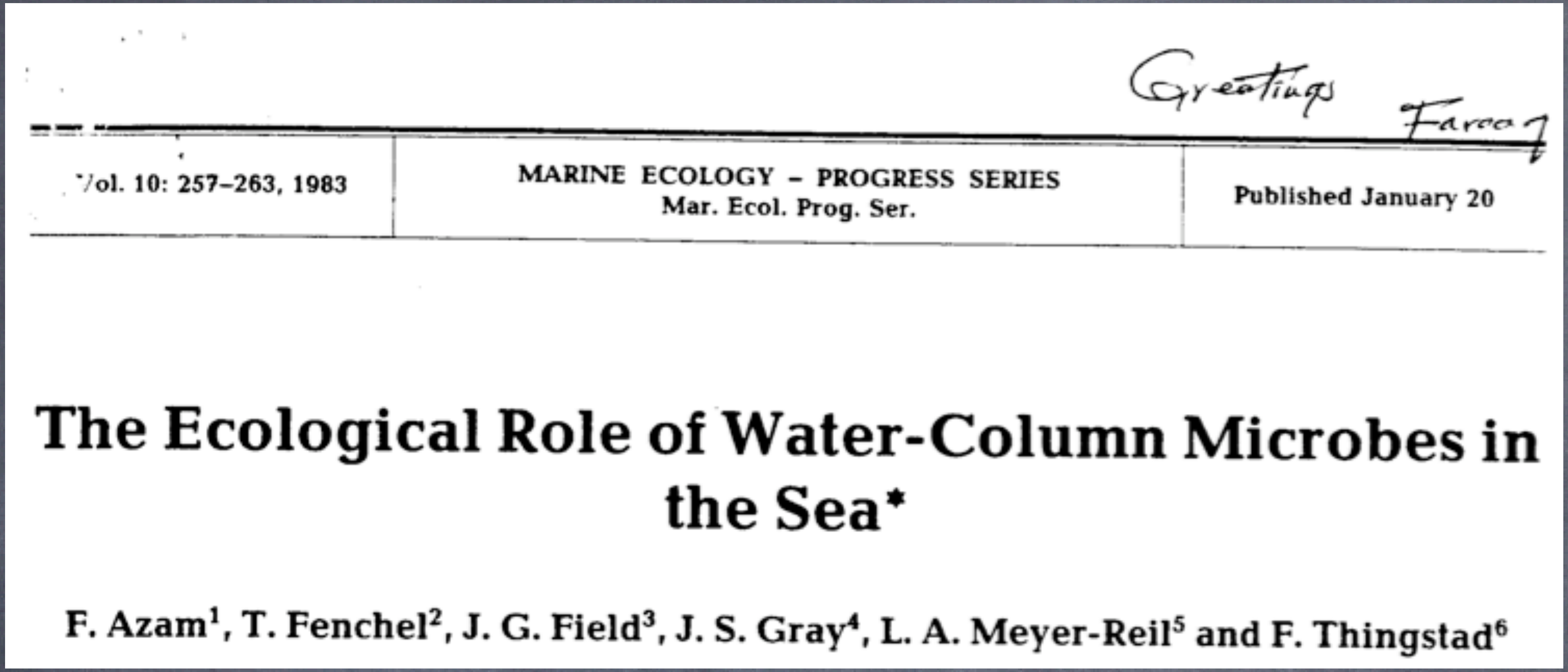


algae algal amino acids aquatic autotrophic Azam bacterial biomass bacterial growth bacterial production
bacterioplankton Biol biomass calculated carbohydrates cells changes ciliates coastal waters cultures decomposition
Deep-Sea Res depth diel DNA synthesis Ecol Ecology ecosystems environments enzymes Eppley estimates estuarine
eutrophic excretion fecal filters flagellates flux fraction Fuhrman glucose growth rate heterotrophic heterotrophic
activity incorporation incubation inorganic kinetic Limnol lipids marine bacteria marine snow material measurements metabolism
method Meyer-Reil microbial Microbiol microorganisms Morita natural nitrate nitrogen nutrient observed Oceanogr
oligotrophic organic carbon oxidation oxygen P. J. leB particles particulate matter particulate organic pelagic
photosynthesis phytoplankton picoplankton plankton populations primary production protein protozoa
psychrophilic ratio release respiration samples sea water seawater sediments Sieburth specific studies substrate
substrate concentration surface suspended technique temperature thymidine tion trophic turnover uptake utilization values
water column Wiebe Williams zooplankton

“The acceptance by non-microbiologists that bacteria plays an important role in the marine food web has been, and to some extent still is, an act of faith

Varios considerations lead to the conclusion that a substantial proportion of plankton production reaches eventually the bacteria- The exact fate of this material...is not known”

P.J.LeB Williams (1981)

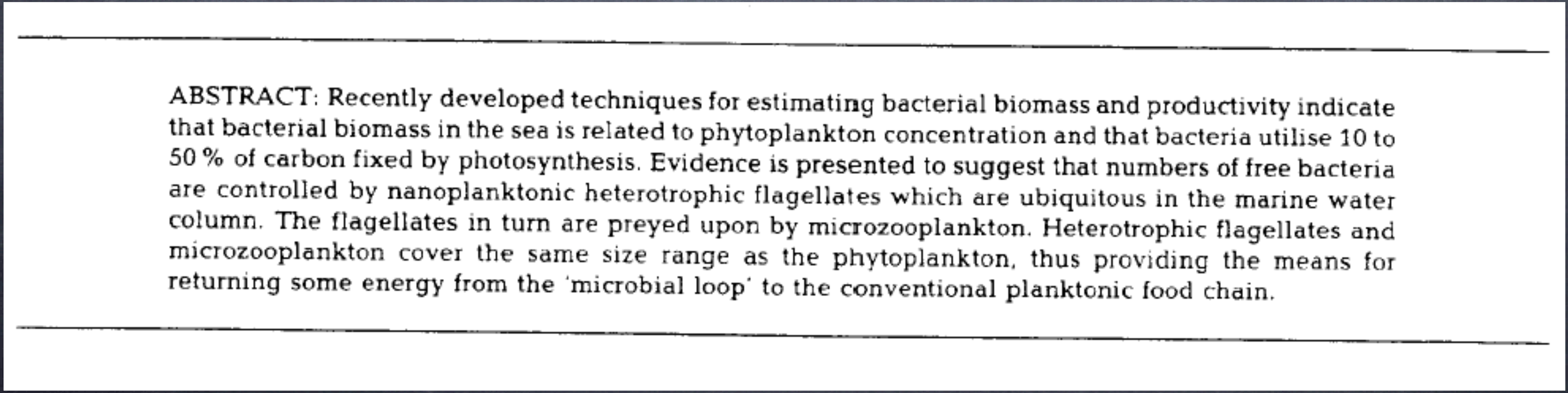


Greetings
Farooq

Vol. 10: 257–263, 1983
MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser.
Published January 20

The Ecological Role of Water-Column Microbes in the Sea*

F. Azam[1], T. Fenchel[2], J. G. Field[3], J. S. Gray[4], L. A. Meyer-Reil[5] and F. Thingstad[6]

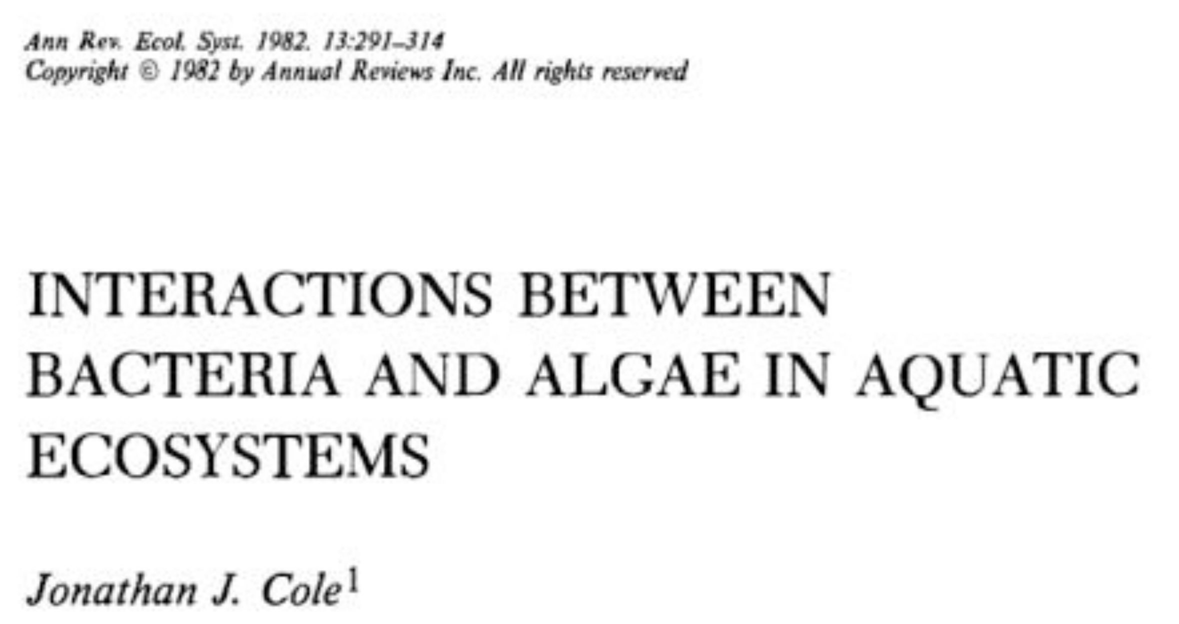


ABSTRACT: Recently developed techniques for estimating bacterial biomass and productivity indicate that bacterial biomass in the sea is related to phytoplankton concentration and that bacteria utilise 10 to 50 % of carbon fixed by photosynthesis. Evidence is presented to suggest that numbers of free bacteria are controlled by nanoplanktonic heterotrophic flagellates which are ubiquitous in the marine water column. The flagellates in turn are preyed upon by microzooplankton. Heterotrophic flagellates and microzooplankton cover the same size range as the phytoplankton, thus providing the means for returning some energy from the 'microbial loop' to the conventional planktonic food chain.

Vol. 43: 1–10, 1988 | MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published March 24

Bacterial production in fresh and saltwater ecosystems: a cross-system overview

Jonathan J. Cole, Stuart Findlay, Michael L. Pace



Ann Rev. Ecol. Syst. 1982. 13:291–314

INTERACTIONS BETWEEN BACTERIA AND ALGAE IN AQUATIC ECOSYSTEMS

Jonathan J. Cole[1]

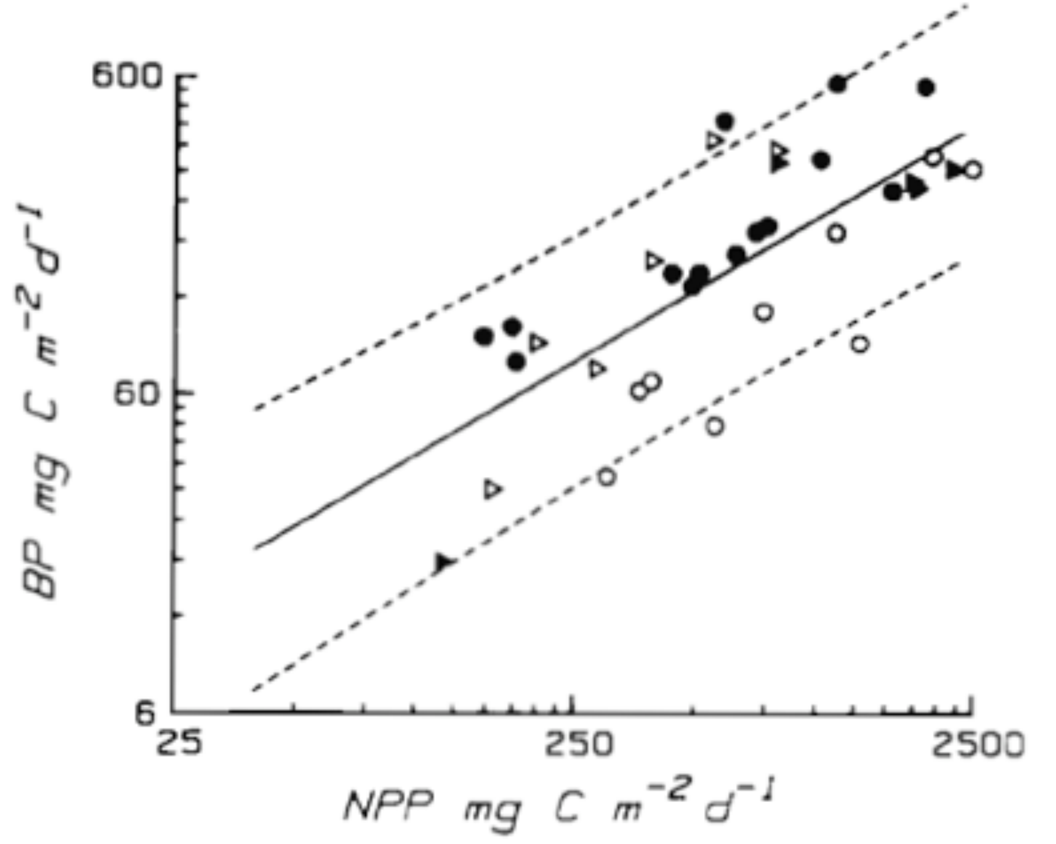
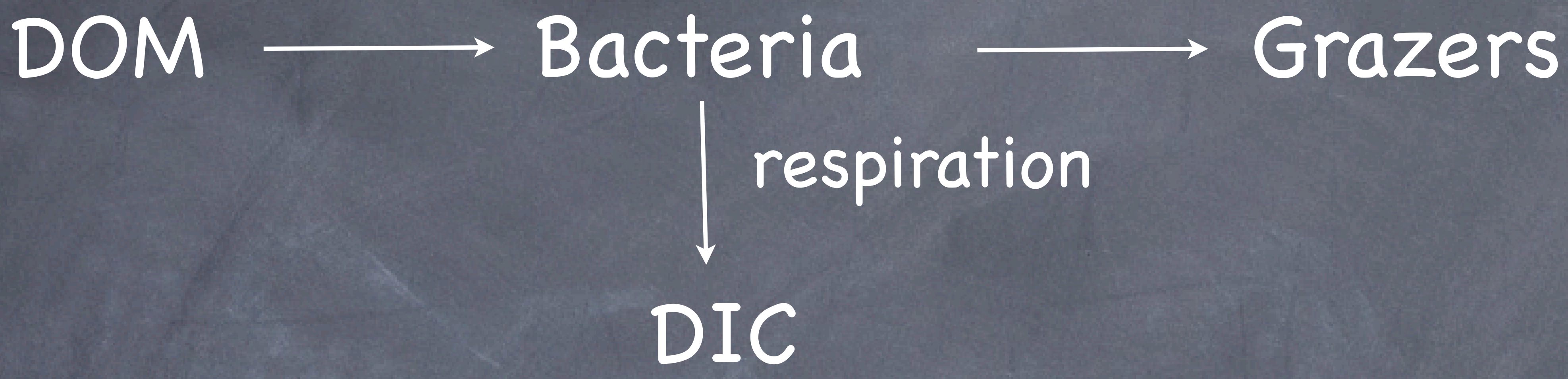


Fig. 3. Areal relation between primary production (NPP; X-axis) and bacterial production (BP; Y-axis) expressed per unit area for the entire water column. Symbols are as in Fig. 1. Regression line (Log Y = 0.75 Log X + 0.093) is shown with 90 % confidence limits for the individual predictions of BP

Bacterial production equal, on average, 20% of primary production



DOM → Bacteria → Grazers

respiration

DIC

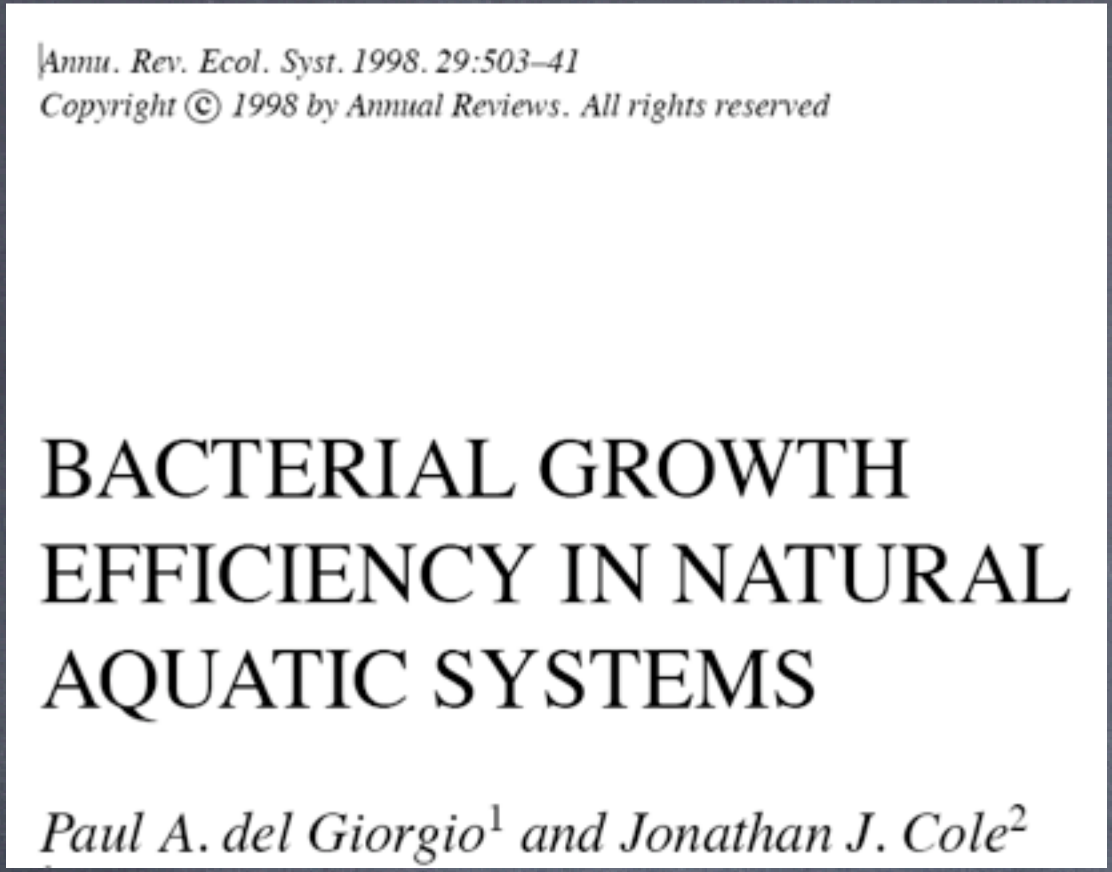
$$\text{Carbon Flux} = \text{Production} + \text{Respiration}$$

$$\text{Bacteria Growth Efficiency} = \frac{\text{Production}}{\text{C Flux}}$$

(Growth Yield)

Measurement

- C flux = $B_{production} + B_{respiration}$
- C flux = $\Delta B_{biomass} + B_{respiration}$
- C flux = ΔDOC
- BGE recalculating these expressions
- in regrowth cultures in the dark and the absence of protists grazers



Annu. Rev. Ecol. Syst. 1998. 29:503–41
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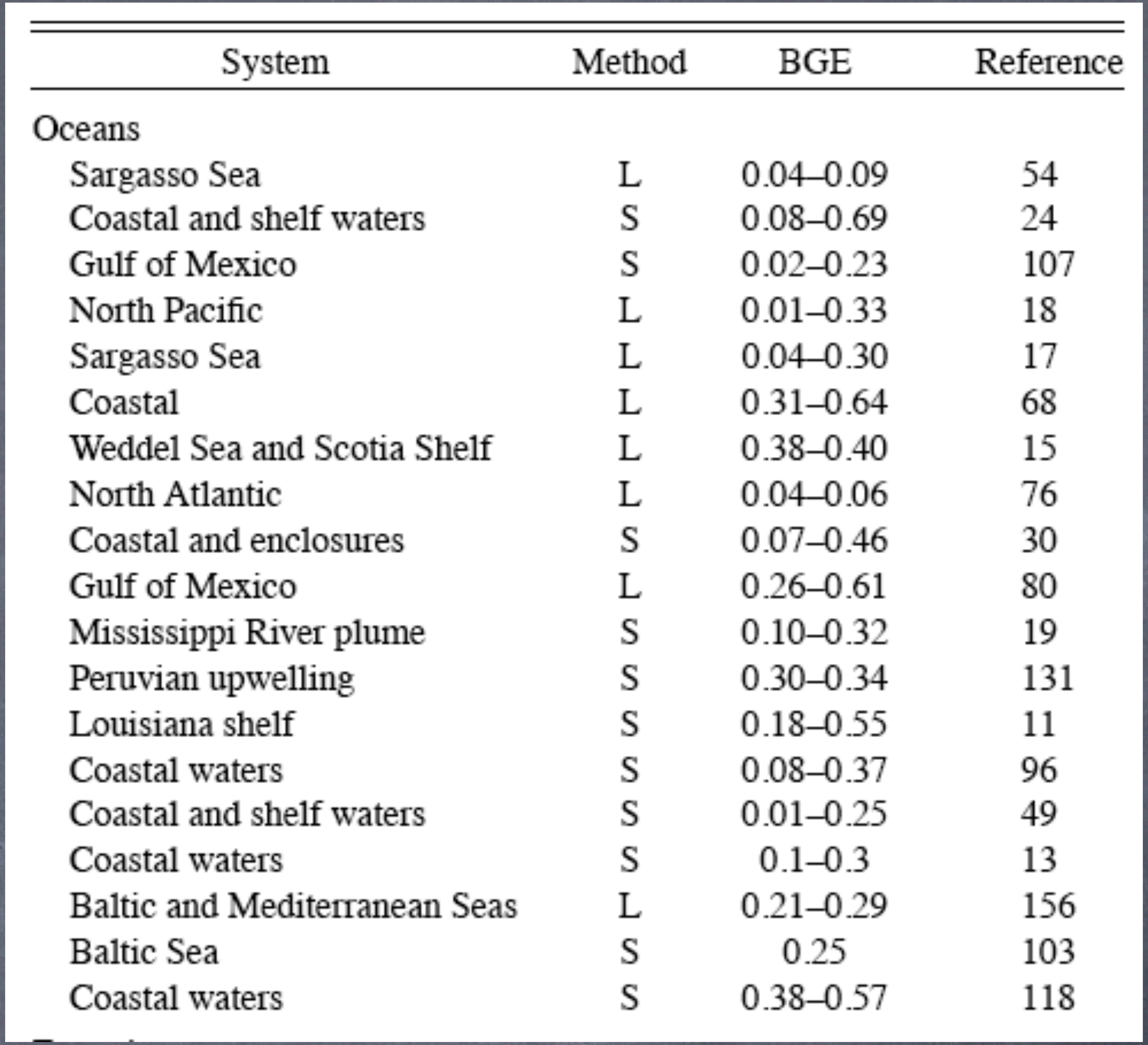
BACTERIAL GROWTH EFFICIENCY IN NATURAL AQUATIC SYSTEMS

Paul A. del Giorgio[1] *and Jonathan J. Cole*[2]

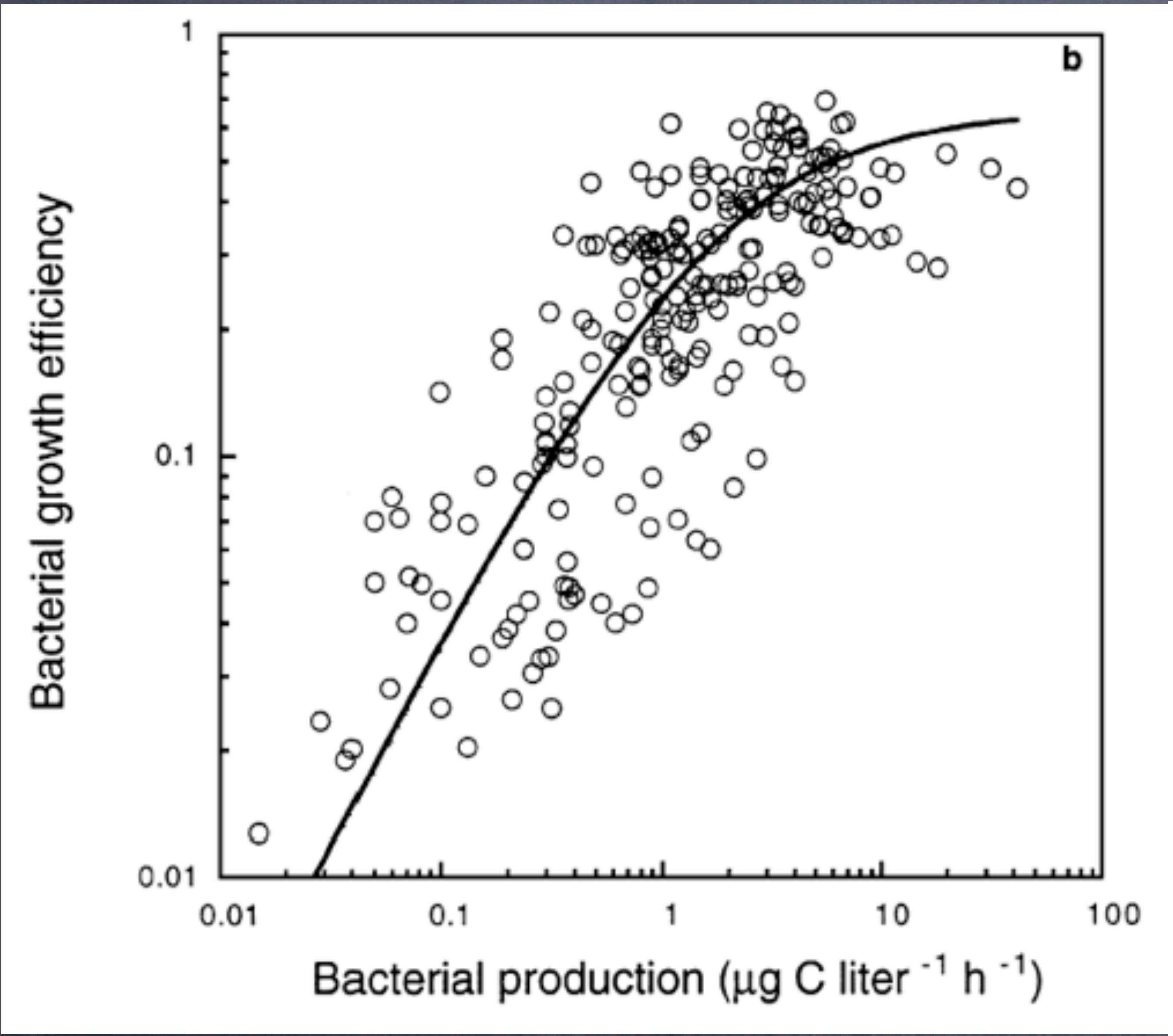


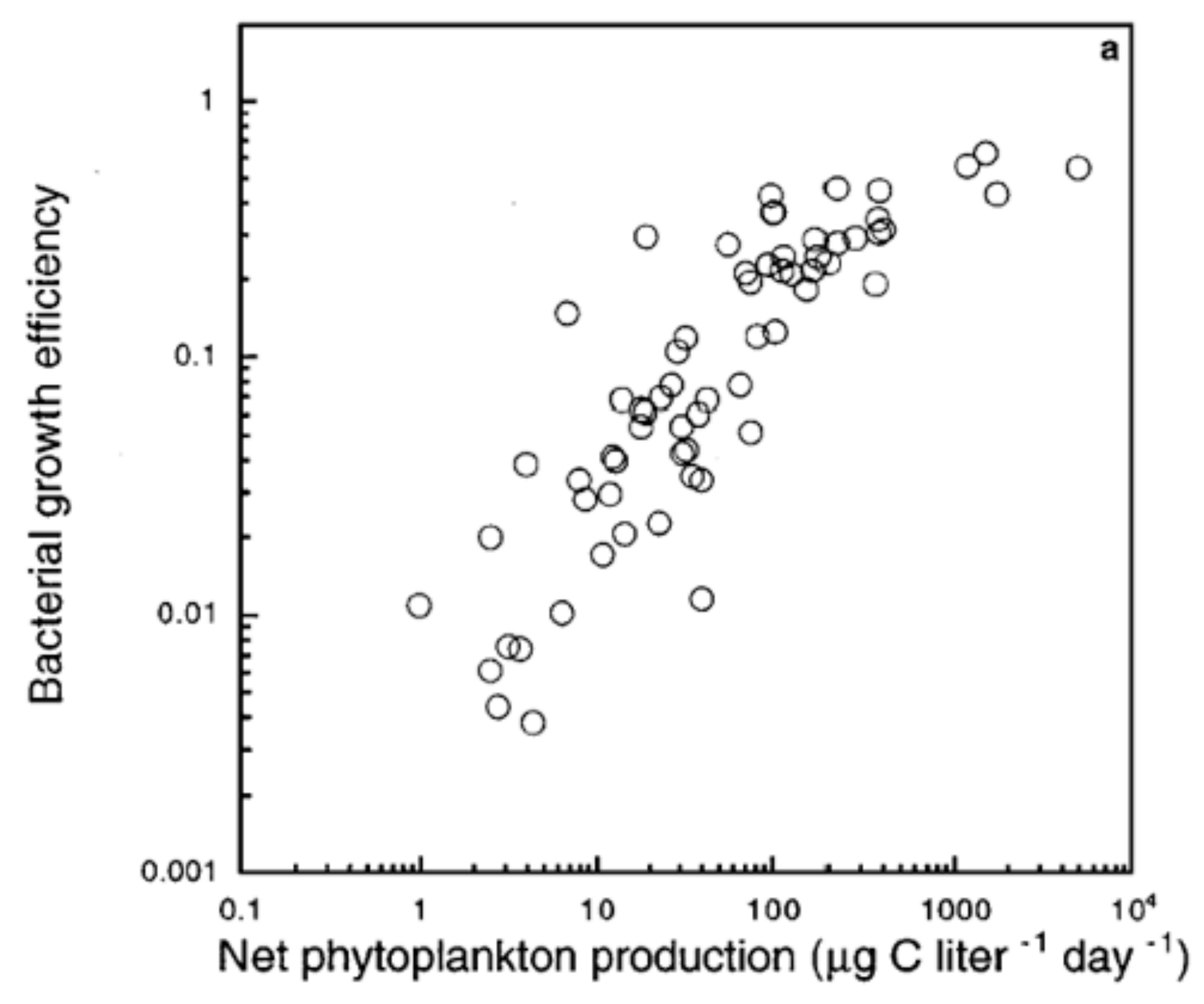
System	Method	BGE	Reference
Oceans			
Sargasso Sea	L	0.04–0.09	54
Coastal and shelf waters	S	0.08–0.69	24
Gulf of Mexico	S	0.02–0.23	107
North Pacific	L	0.01–0.33	18
Sargasso Sea	L	0.04–0.30	17
Coastal	L	0.31–0.64	68
Weddel Sea and Scotia Shelf	L	0.38–0.40	15
North Atlantic	L	0.04–0.06	76
Coastal and enclosures	S	0.07–0.46	30
Gulf of Mexico	L	0.26–0.61	80
Mississippi River plume	S	0.10–0.32	19
Peruvian upwelling	S	0.30–0.34	131
Louisiana shelf	S	0.18–0.55	11
Coastal waters	S	0.08–0.37	96
Coastal and shelf waters	S	0.01–0.25	49
Coastal waters	S	0.1–0.3	13
Baltic and Mediterranean Seas	L	0.21–0.29	156
Baltic Sea	S	0.25	103
Coastal waters	S	0.38–0.57	118

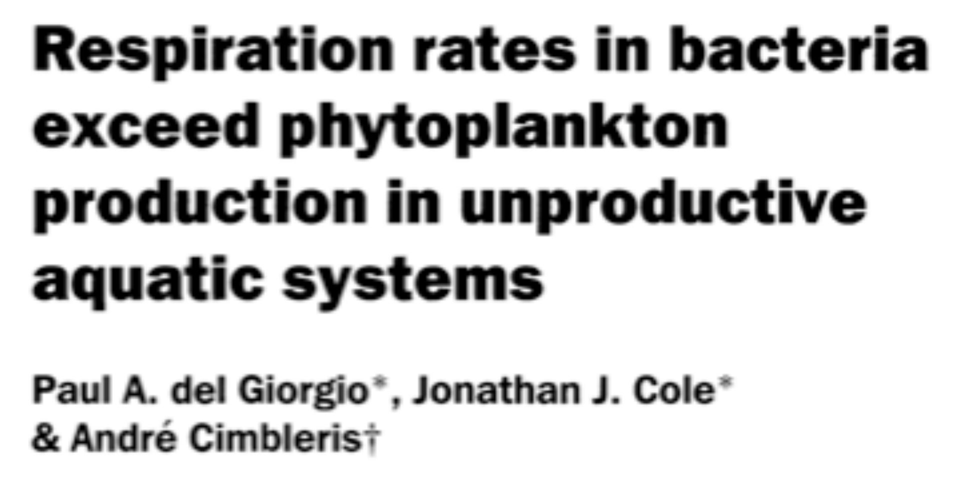
“Estimates of BGE for natural planktonic bacteria range from <0.05 to as high as 0.6... In the most dilute, oligotrophic systems, BGE is as low as 0.01; in the most eutrophic systems, it plateaus near 0.5. Planktonic bacteria appear to maximize carbon utilization rather than BGE. A consequence of this strategy is that maintenance energy costs (and therefore maintenance respiration) seems to be highest in oligotrophic systems.”

$$\mathrm{BR} = 3.70 \times \mathrm{BP}^{0.41},\ r^2 = 0.46\,(\text{model I})$$

$$\mathrm{BR} = 3.42 \times \mathrm{BP}^{0.61},\ r^2 = 0.46\,(\text{model II})$$

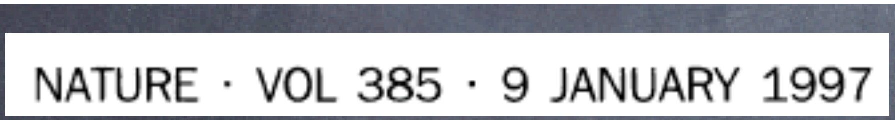




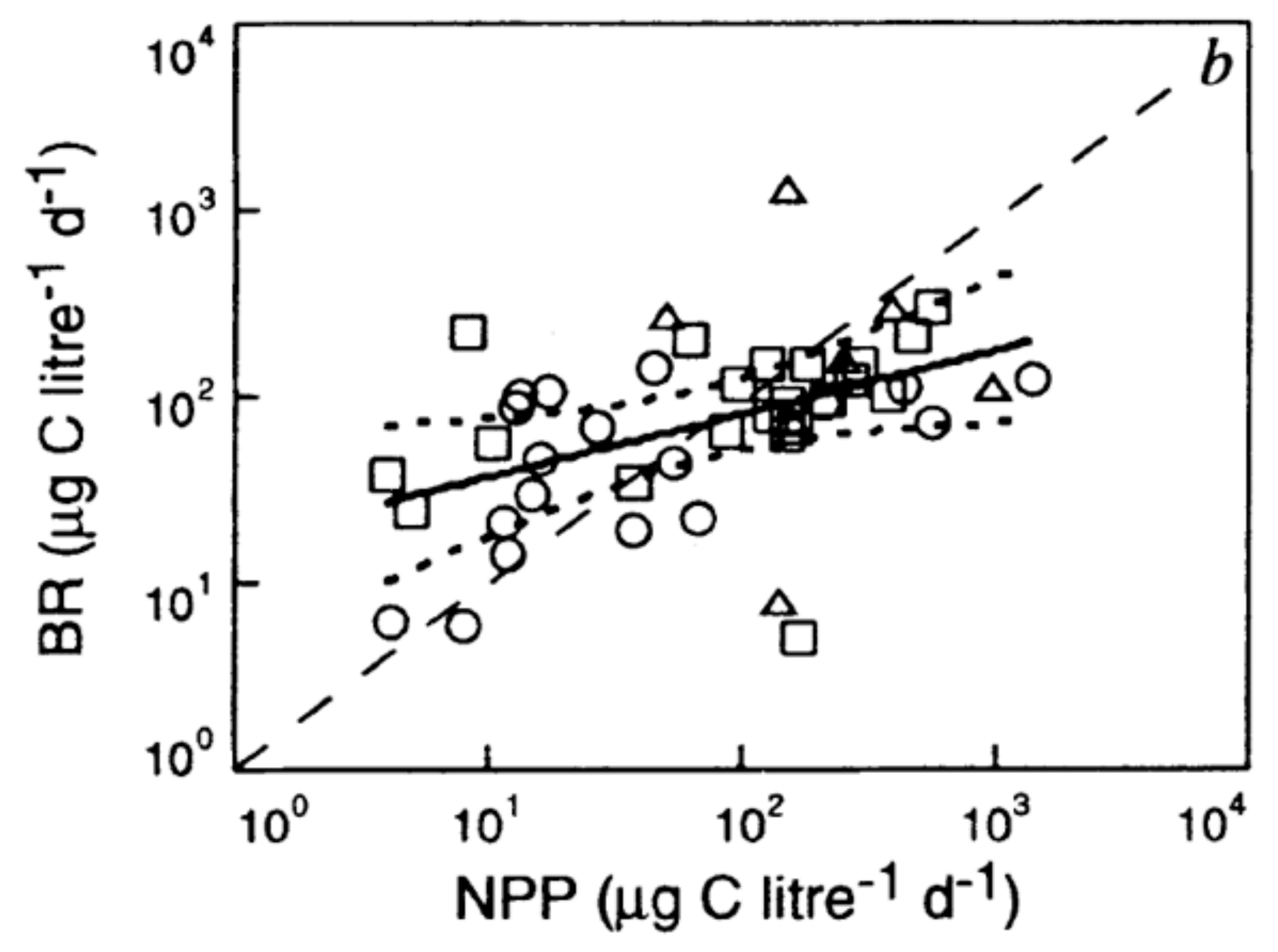


Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems

Paul A. del Giorgio*, Jonathan J. Cole* & André Cimbleris†



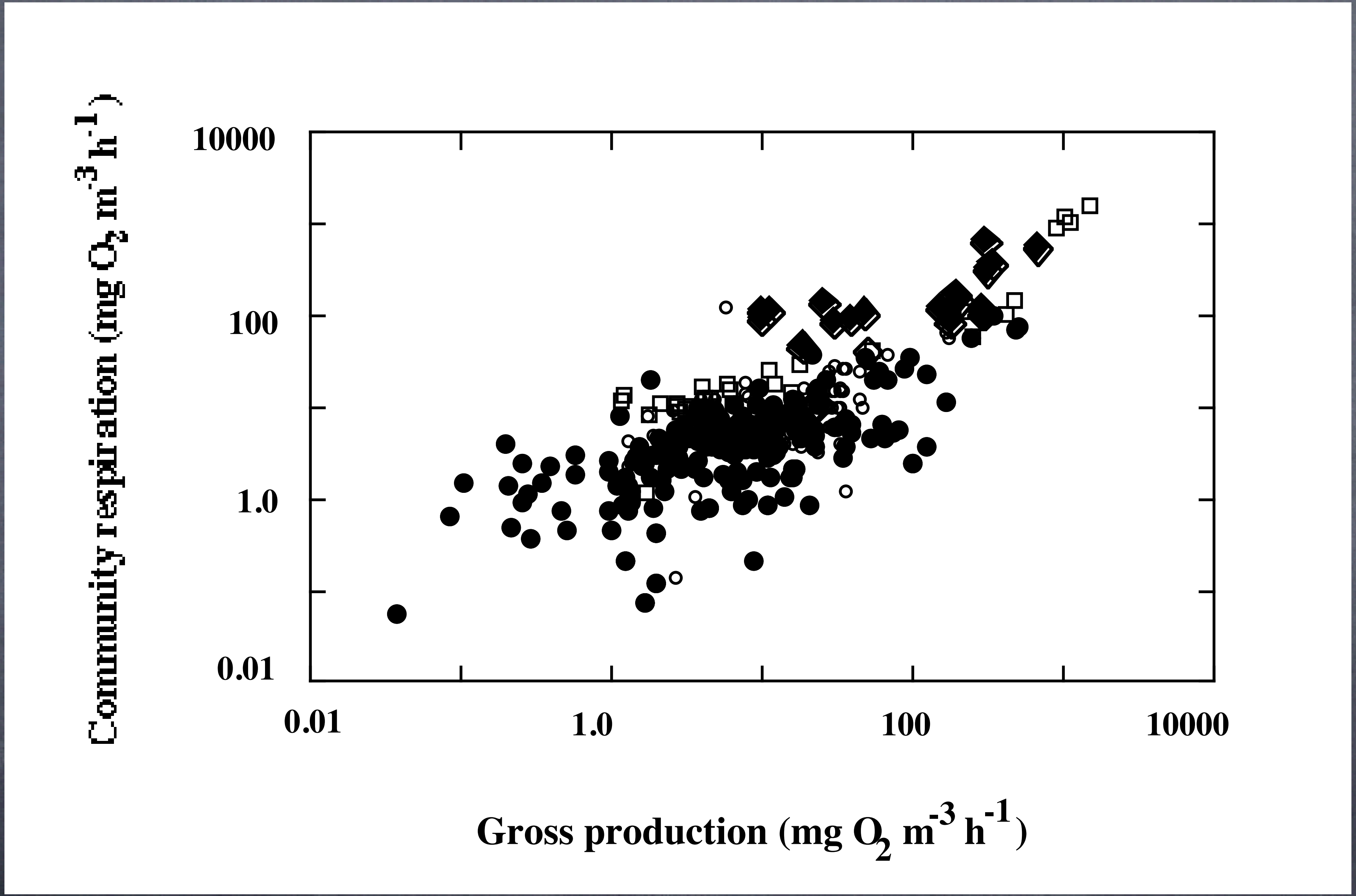
NATURE · VOL 385 · 9 JANUARY 1997



"We report here that bacterial respiration is generally high and tends to exceed phytoplankton net primary production in oligotrophic systems"

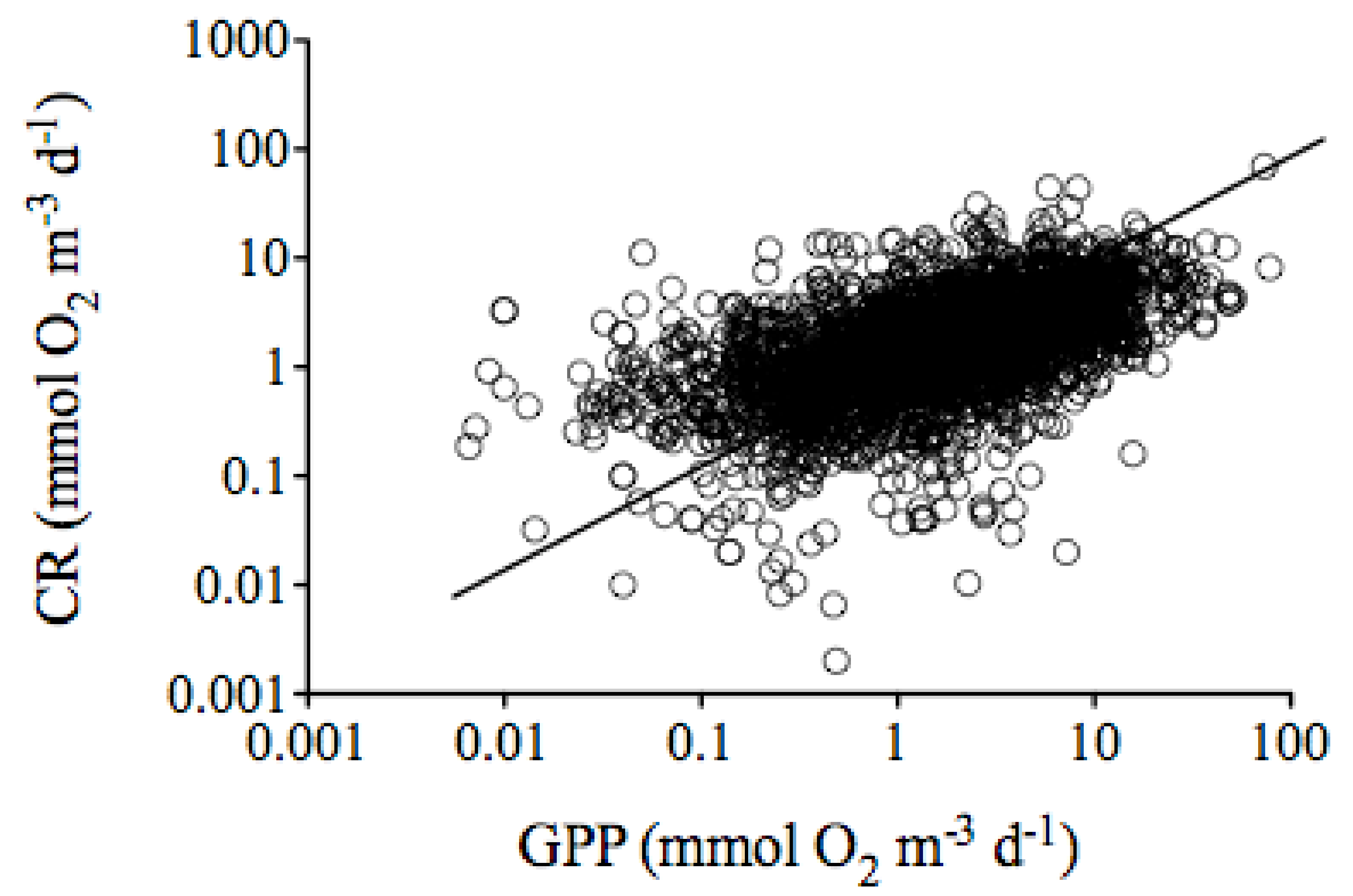
A general (non-linear) relationship between R and P in aquatic ecosystems

($R \sim P^{0.4\text{-}0.8}$)



Duarte & Agustí, Science (1998)

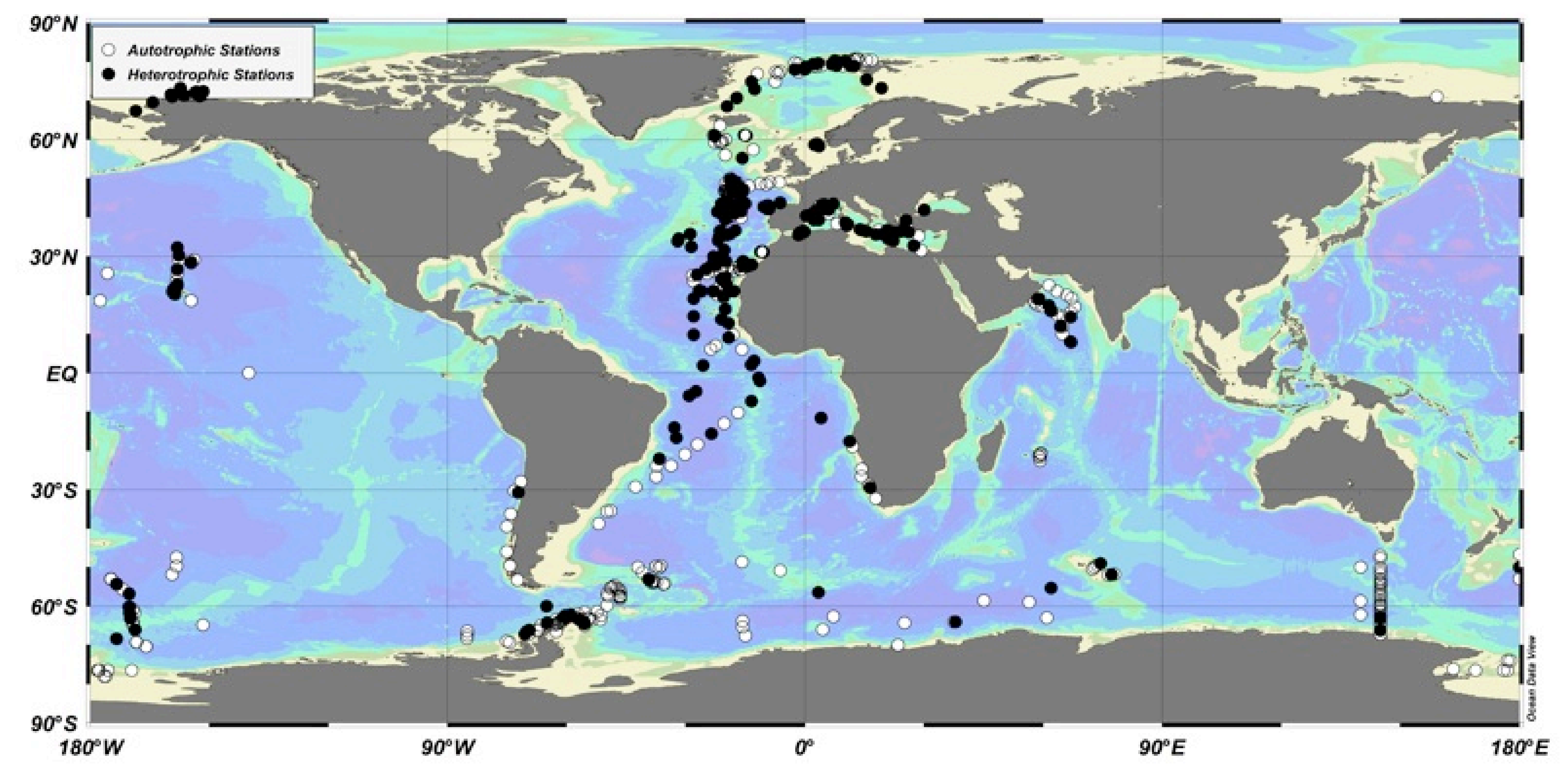
Confirmed with a larger (N = 3,000) data set



Threshold GPP for metabolic balance = 1.50 mmol O_2 m^{-3} d^{-1}

Regaudie-de-Gieux and Duarte (in prep)

Heterotrophic communities abound in the N Atlantic, Arctic and Mediterranean



Regaudie-de-Gieux and Duarte (in prep)

Global Scaling of Plankton Metabolism in the Upper Ocean

$GPP = 144.78$ Gt C y^{-1}

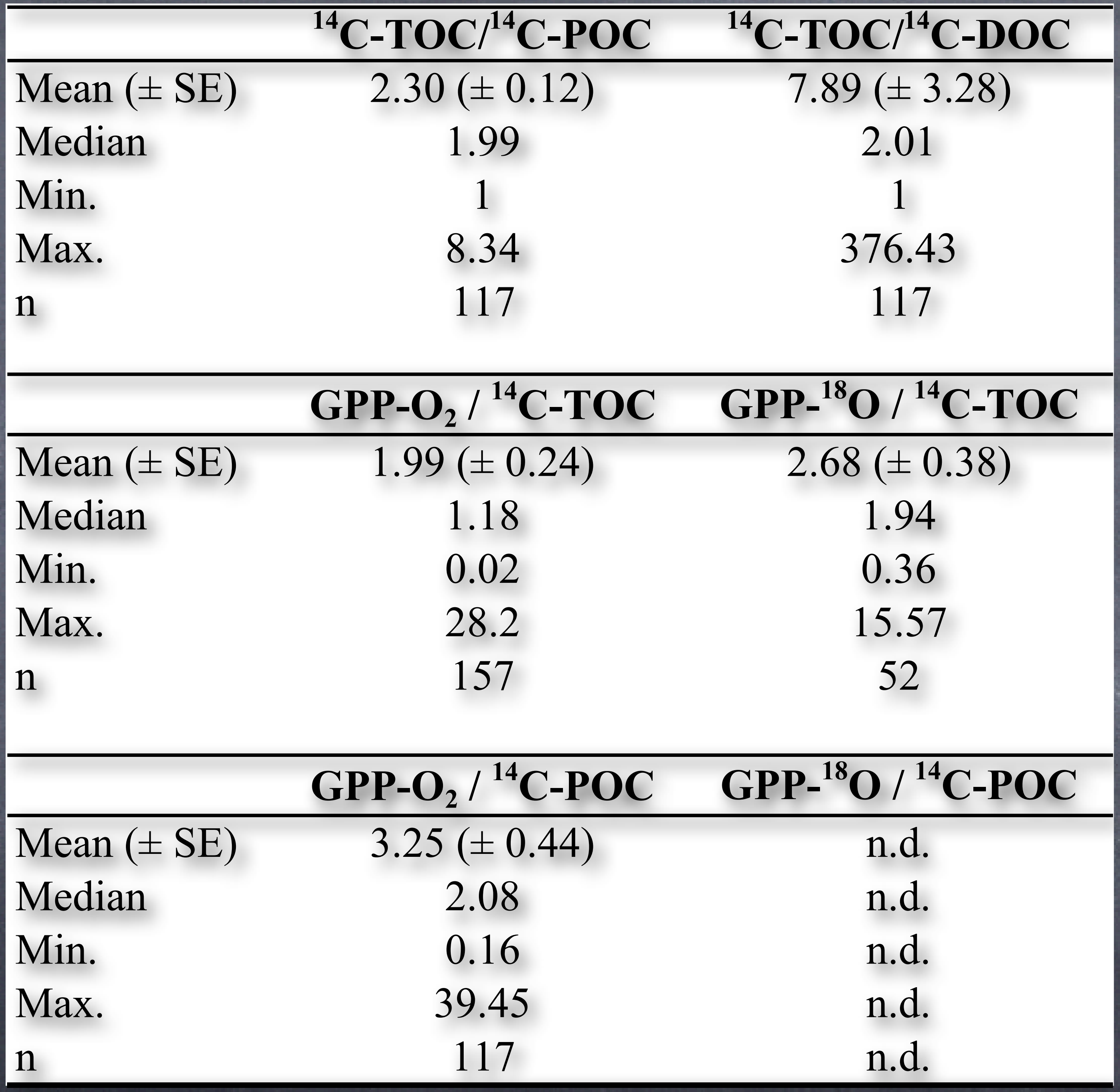
$CR = 169.60$ Gt C y^{-1}

$NCP = -19.22$ Gt C y^{-1}

GPP > 3 times estimated from remote sensing

1. GPP underestimated?
2. External sources of C

What does primary production measure?

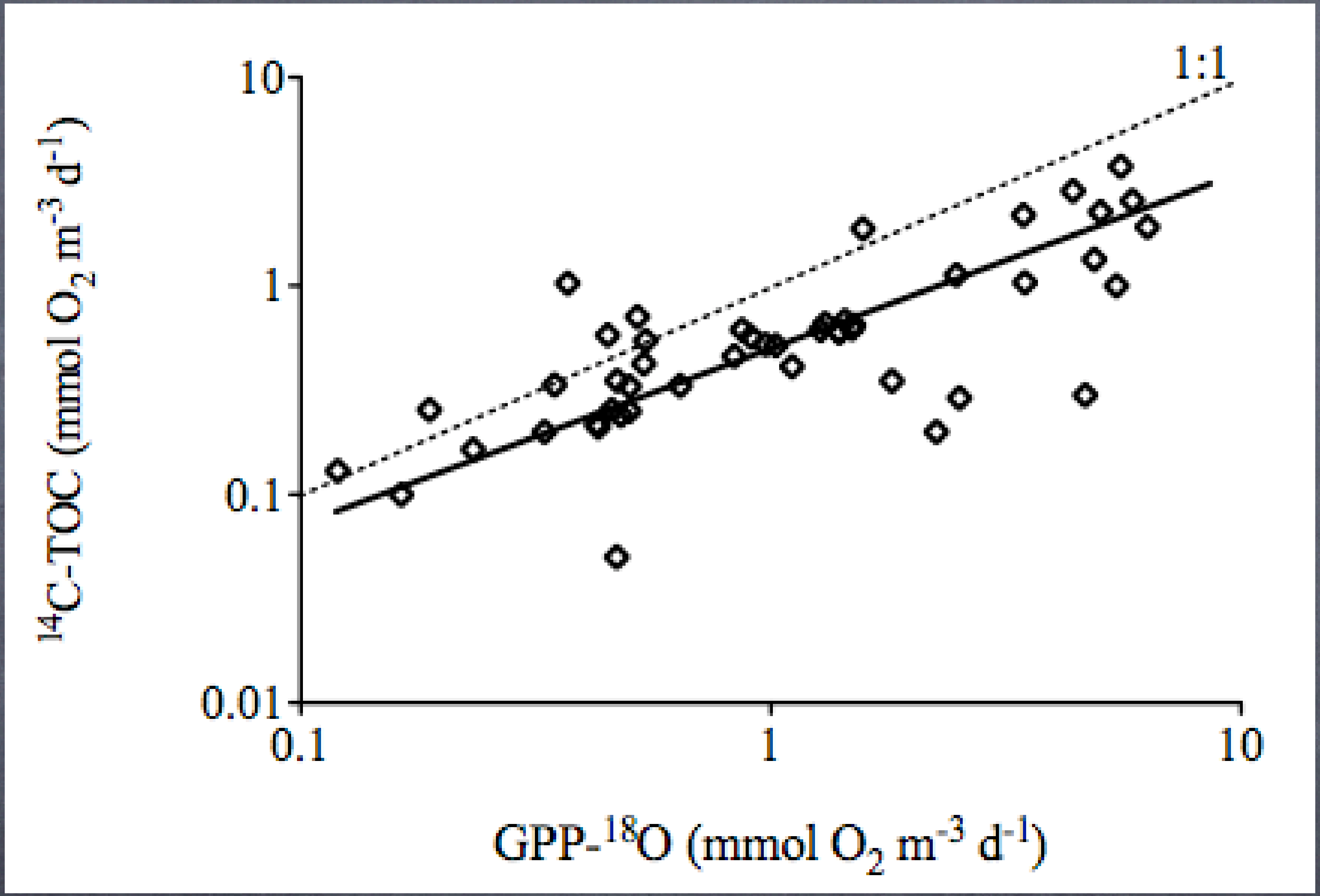


	^{14}C-TOC/^{14}C-POC	^{14}C-TOC/^{14}C-DOC
Mean (± SE)	2.30 (± 0.12)	7.89 (± 3.28)
Median	1.99	2.01
Min.	1	1
Max.	8.34	376.43
n	117	117

	GPP-O_2 / ^{14}C-TOC	GPP-^{18}O / ^{14}C-TOC
Mean (± SE)	1.99 (± 0.24)	2.68 (± 0.38)
Median	1.18	1.94
Min.	0.02	0.36
Max.	28.2	15.57
n	157	52

	GPP-O_2 / ^{14}C-POC	GPP-^{18}O / ^{14}C-POC
Mean (± SE)	3.25 (± 0.44)	n.d.
Median	2.08	n.d.
Min.	0.16	n.d.
Max.	39.45	n.d.
n	117	n.d.

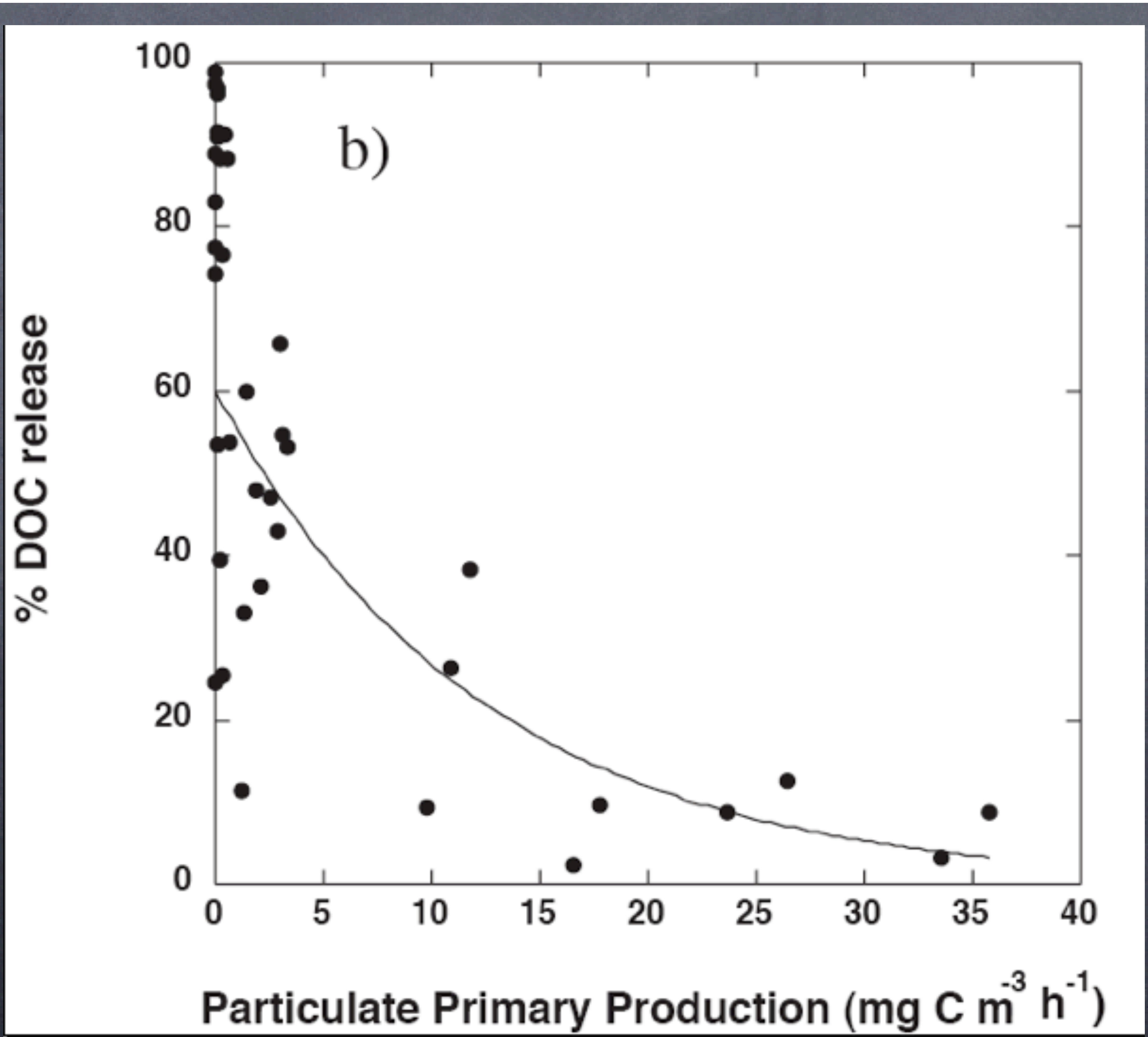
Regaudie-de-Gioux et al. (in prep)



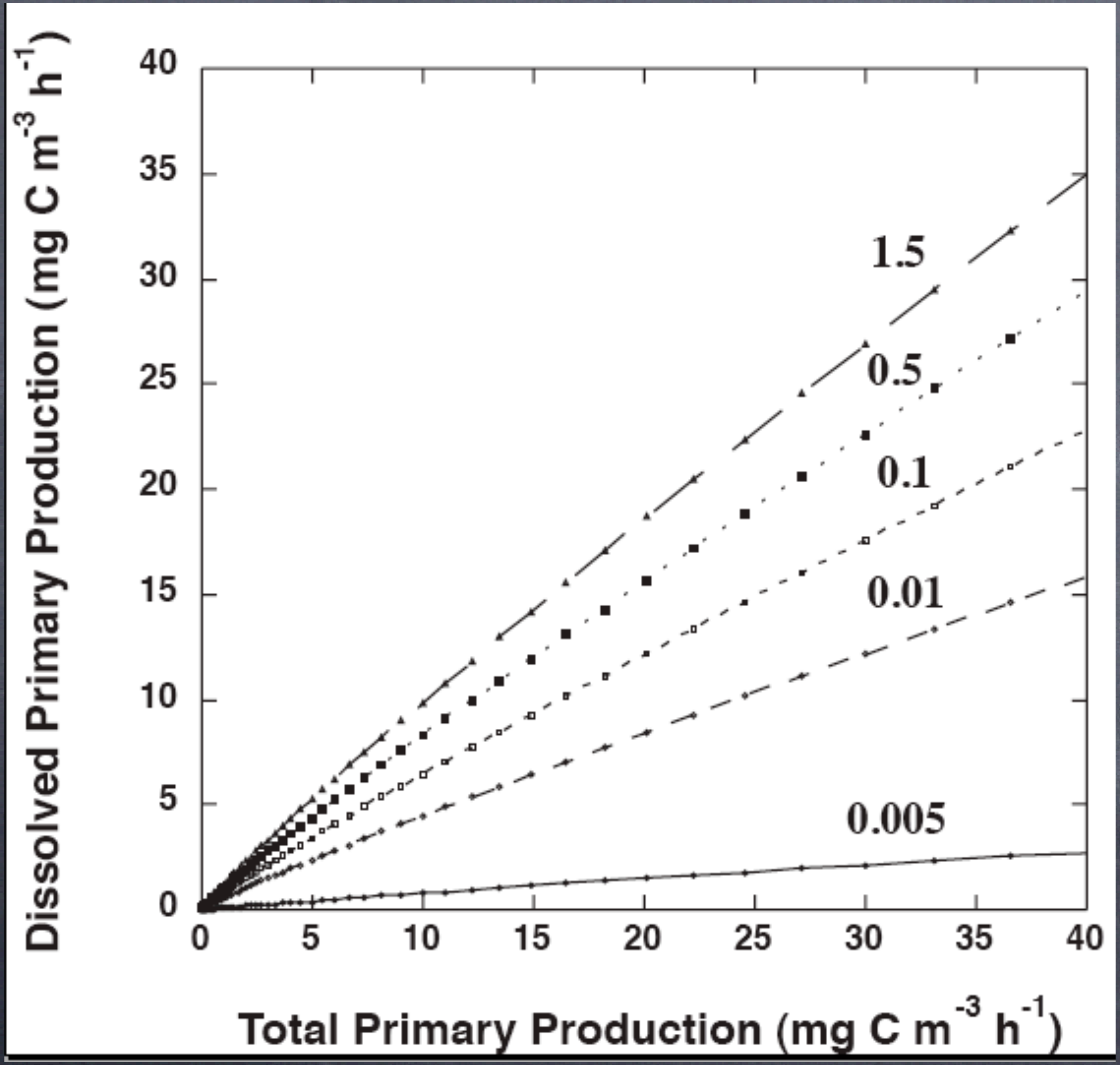
Regaudie-de-Gioux et al. (in prep)

Phytoplankton cell death explains high organic carbon release in the subtropical ocean

Patricia Alonso-Laita & Susana Agustí

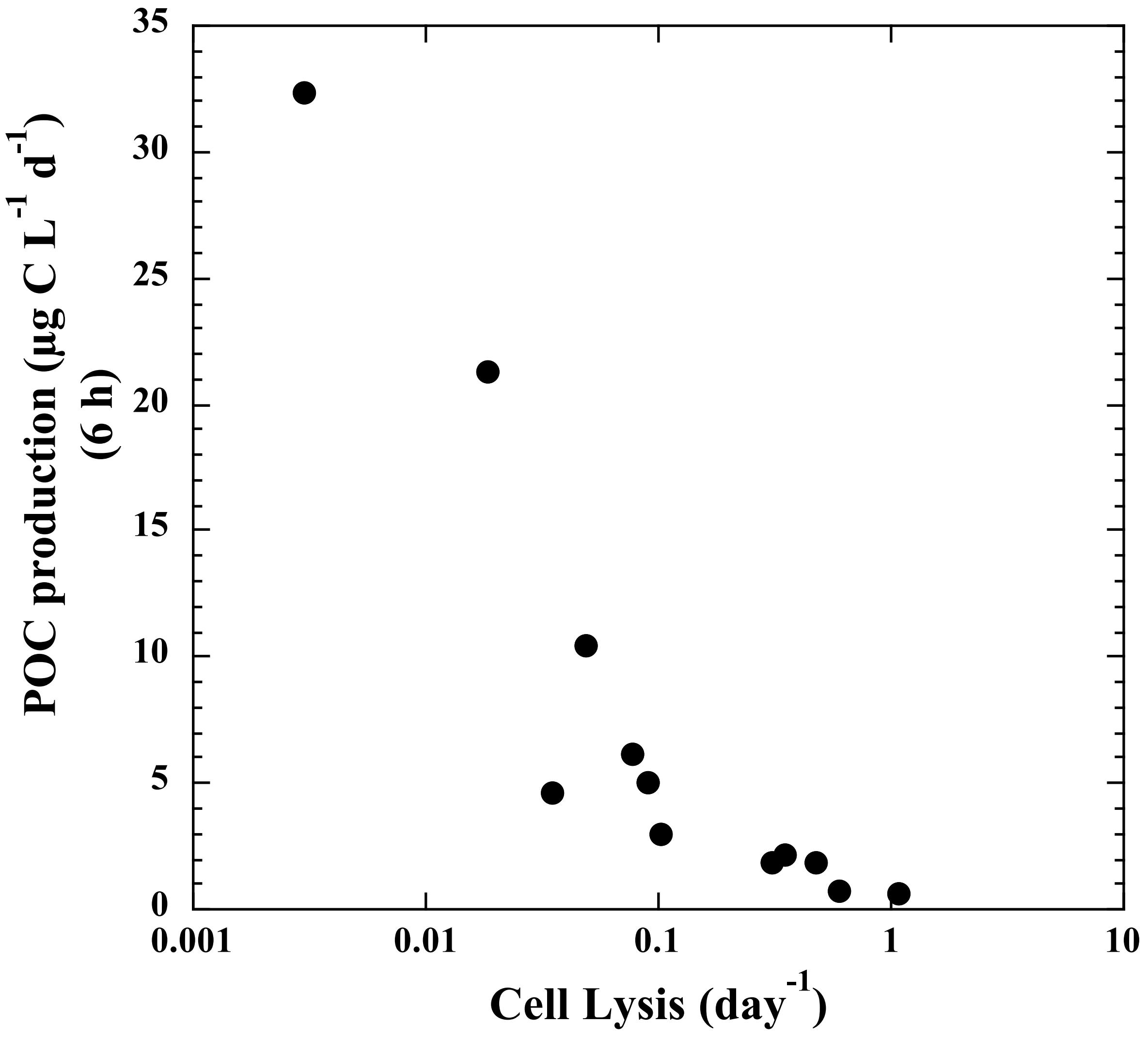


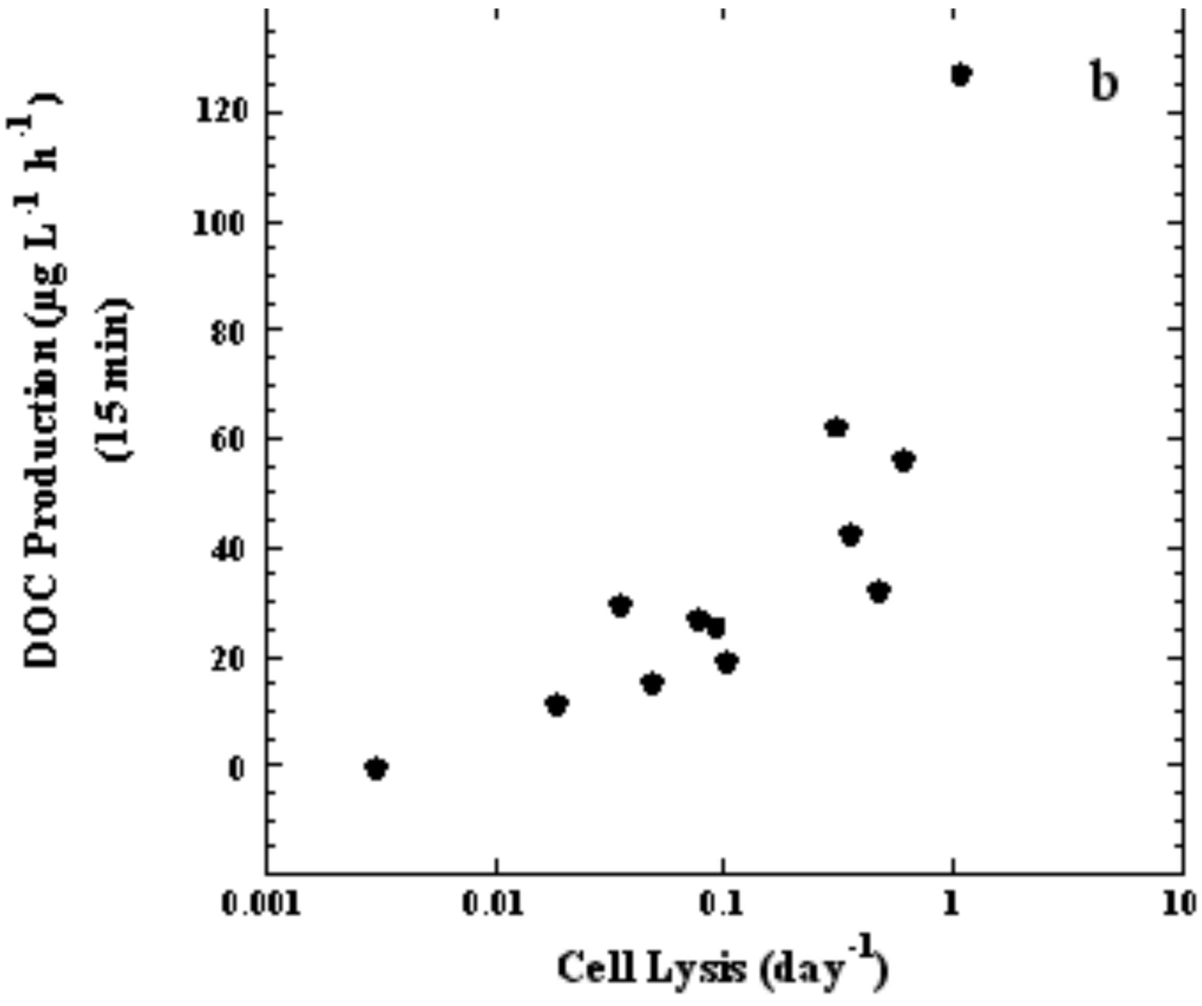
DOC release for any given Total PP depends on the cell lysis rates



Alonso-Laita and Agustí (in prep)

Lysis rates control the partition between POC and DOC production



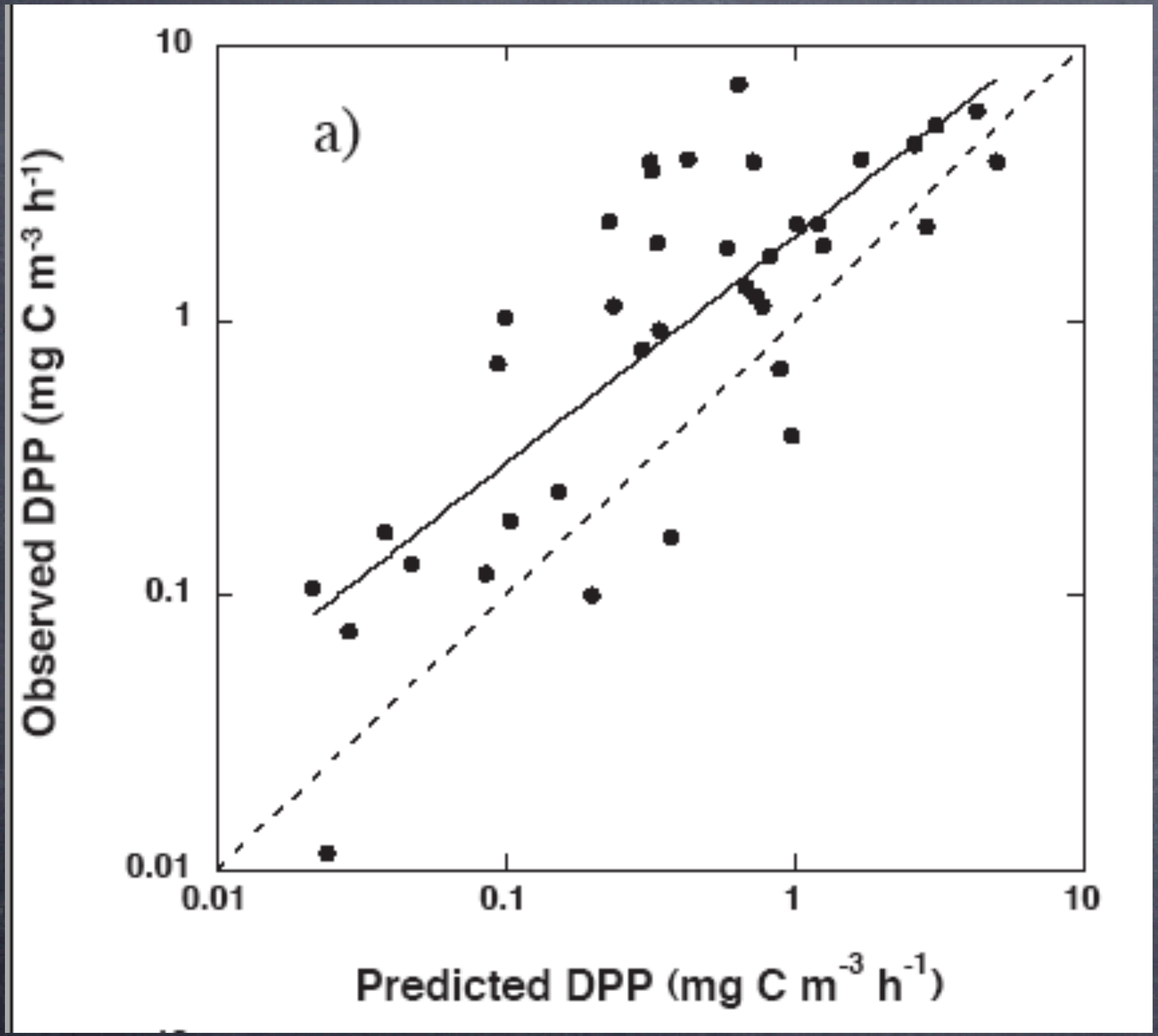


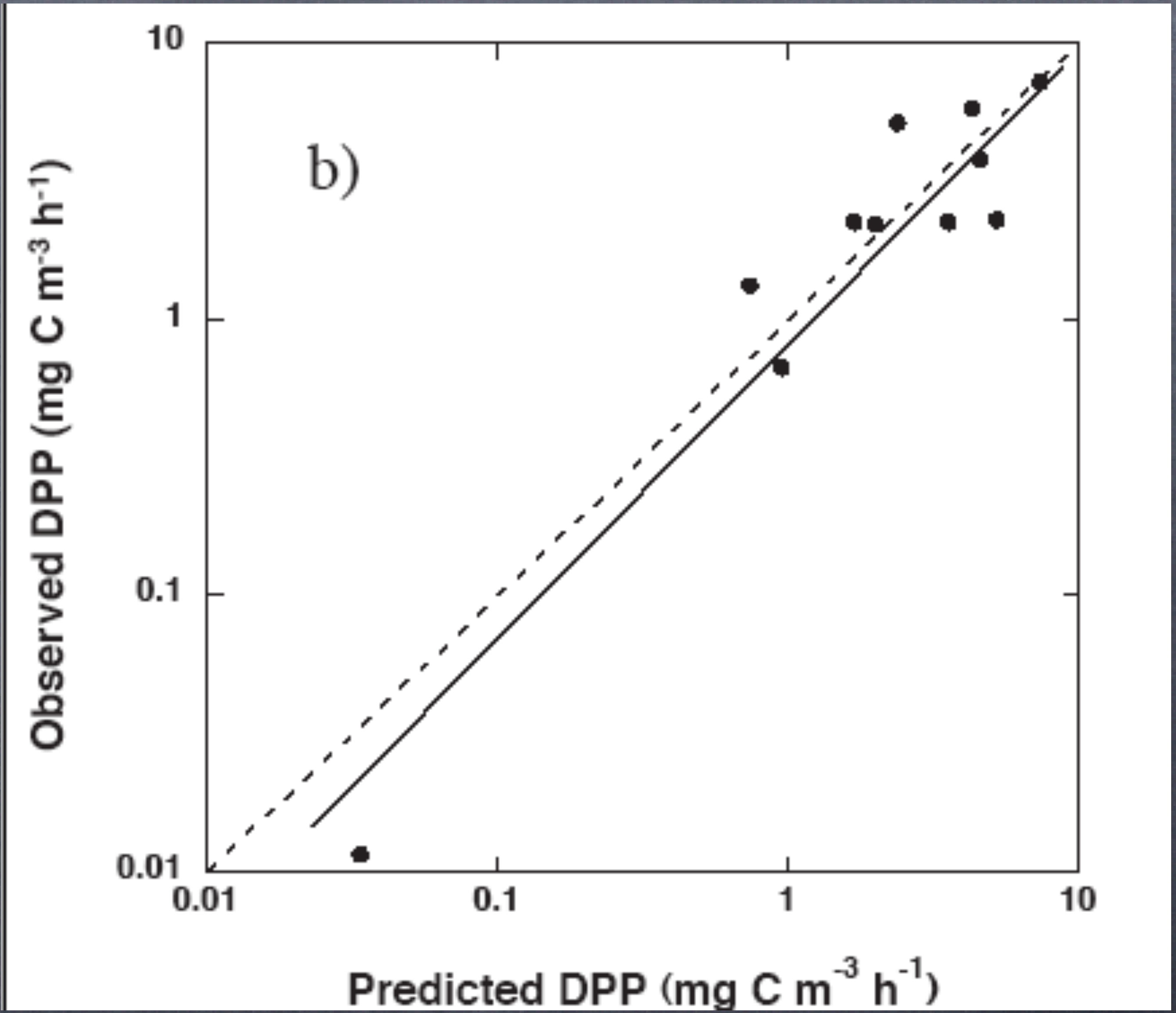
Duarte et al. (in prep)

Predicting DOC release from lysis rates and the % death cells

$$TPP - (TPP \cdot e^{-lysis})$$

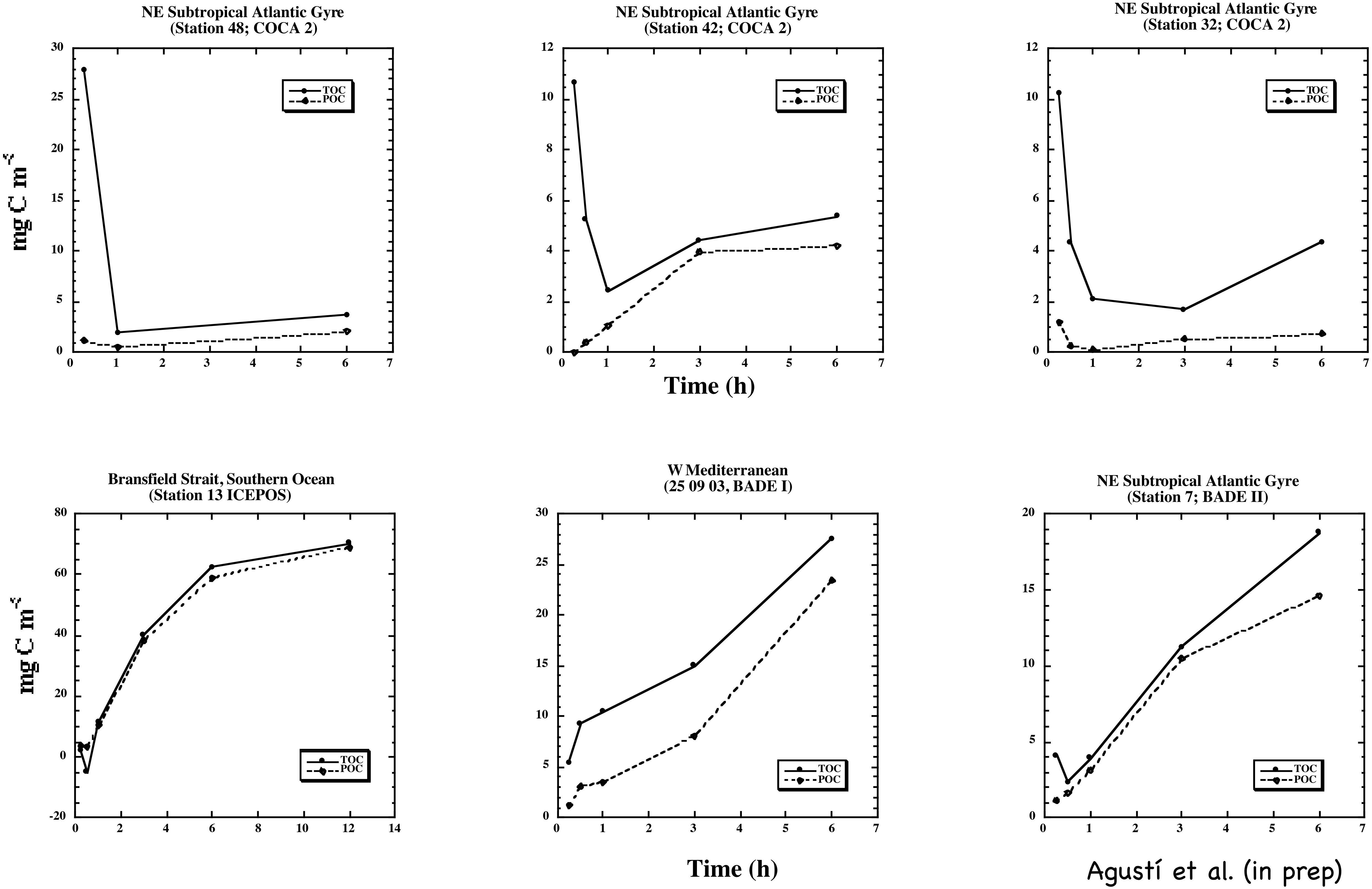
$$TPP \frac{\%DC}{100}$$





Alonso-Laita and Agustí (in prep)

Time series DI^{14}C addition experiments reveal intense dynamics at short time scales



NE Subtropical Atlantic Gyre
(Station 48; COCA 2)

NE Subtropical Atlantic Gyre
(Station 42; COCA 2)

NE Subtropical Atlantic Gyre
(Station 32; COCA 2)

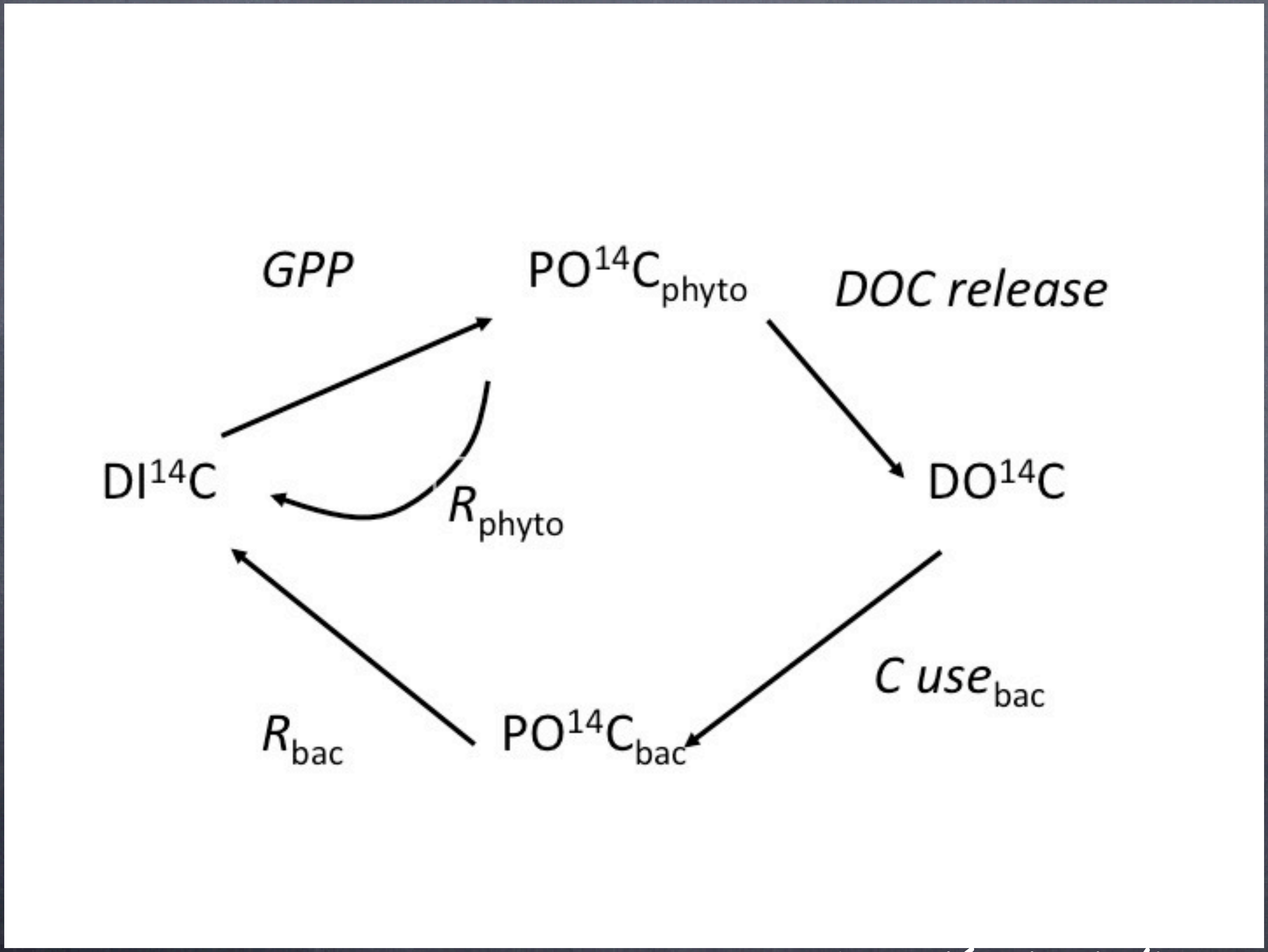
Bransfield Strait, Southern Ocean
(Station 13 ICEPOS)

W Mediterranean
(25 09 03, BADE I)

NE Subtropical Atlantic Gyre
(Station 7; BADE II)

Agustí et al. (in prep)

The flux from DIC into POC, then DOM and uptake and subsequent respiration by bacteria can be extremelly fast (a few minutes)



Agustí et al. (in prep)

Consequences:

1. ^{14}C incorporation into particulate material grossly underestimates gross primary production in oligotrophic waters since much of the organic carbon is incorporated by bacteria and respired within the incubation interval.

2. Phytoplankton mortality and subsequent lysis allows for the rapid [minutes; see Stocker et al. (2008)] use of primary production by bacteria, so that much of primary production goes unnoticed by conventional measurements ("The Emperor New Suite of Clothes").

Thoughts

- Difficulties to reconcile autotrophic and heterotrophic activity may be partially due to flaws in the basis for the comparison, which should be a total C budget. ^{14}C-PP grossly (by a factor of 3, underestimates GPP in oligotrophic water)
- Is phytoplankton the sole source of DOC to support heterotrophic activity?

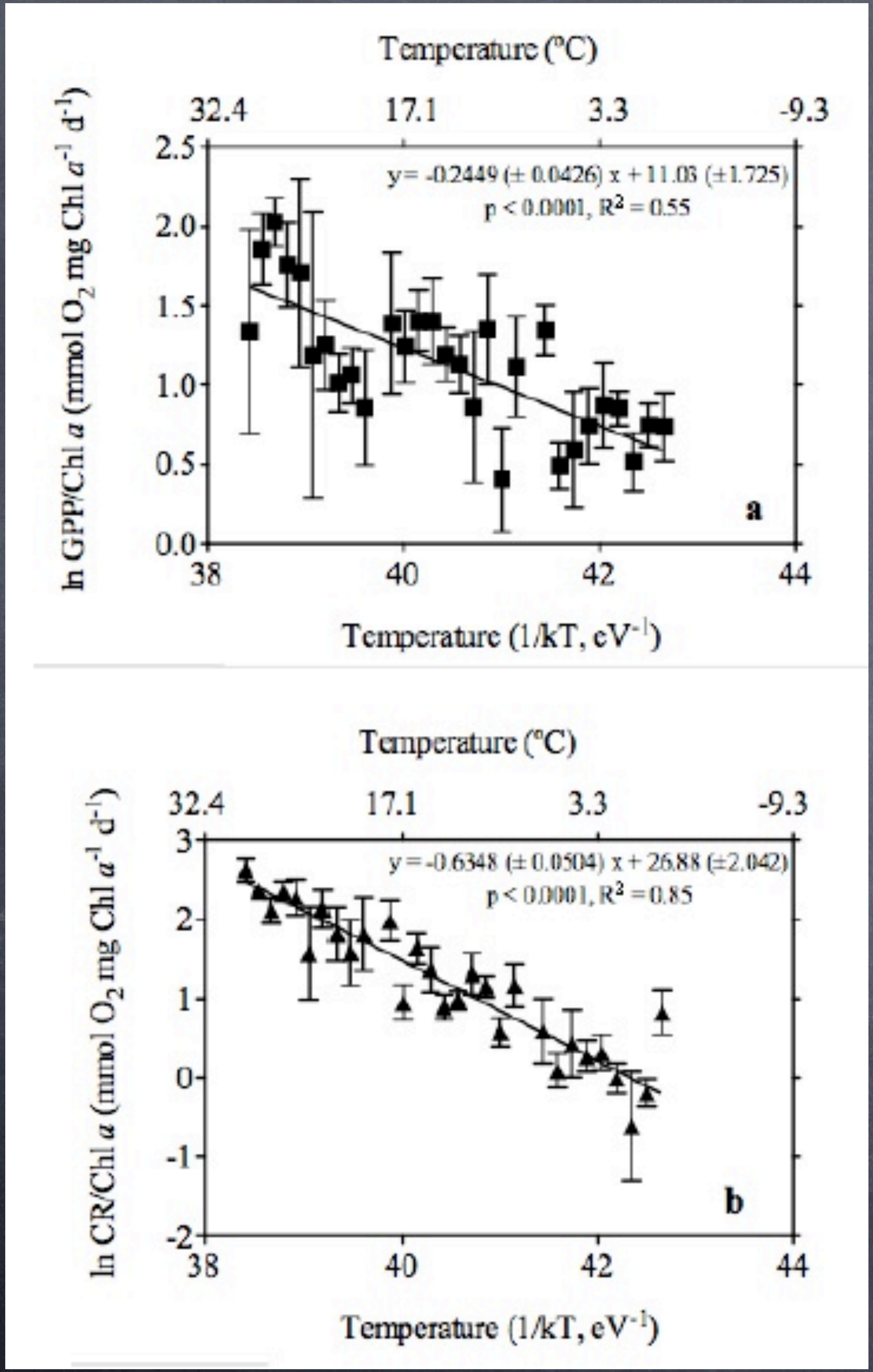
One more caveat

Does it incorporate all relevant fluxes?

ANOXIGENIC photosynthesis ~ 5 % of photosynthesis (claims up to 15%)

ANAMOX ?

Ammonium oxidation by Archaea (claims of 2 - 5

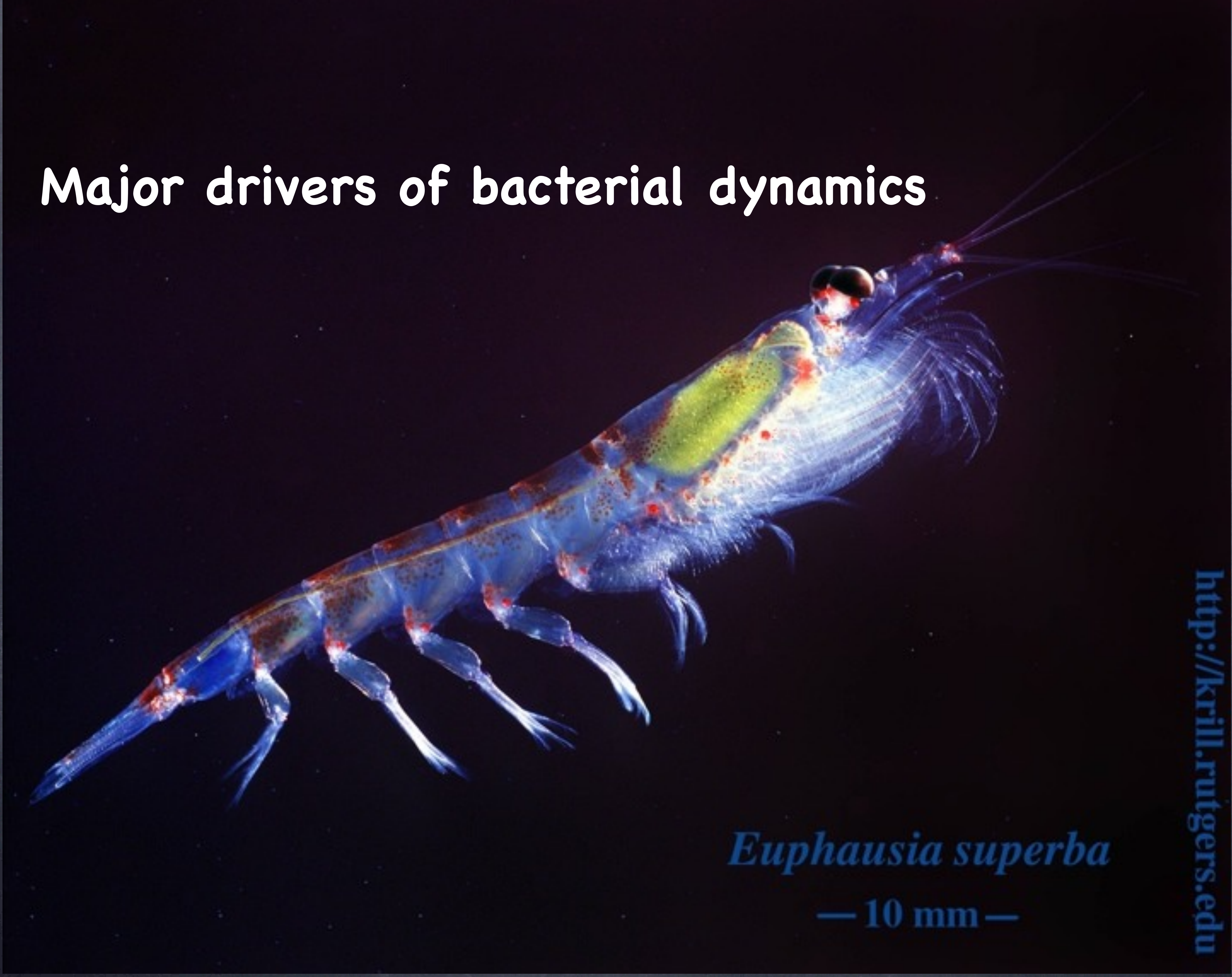


Respiration increases faster than primary production with increasing temperature

Consequences under global warming?

Regaudie-de-Gioux and Duarte (in prep)

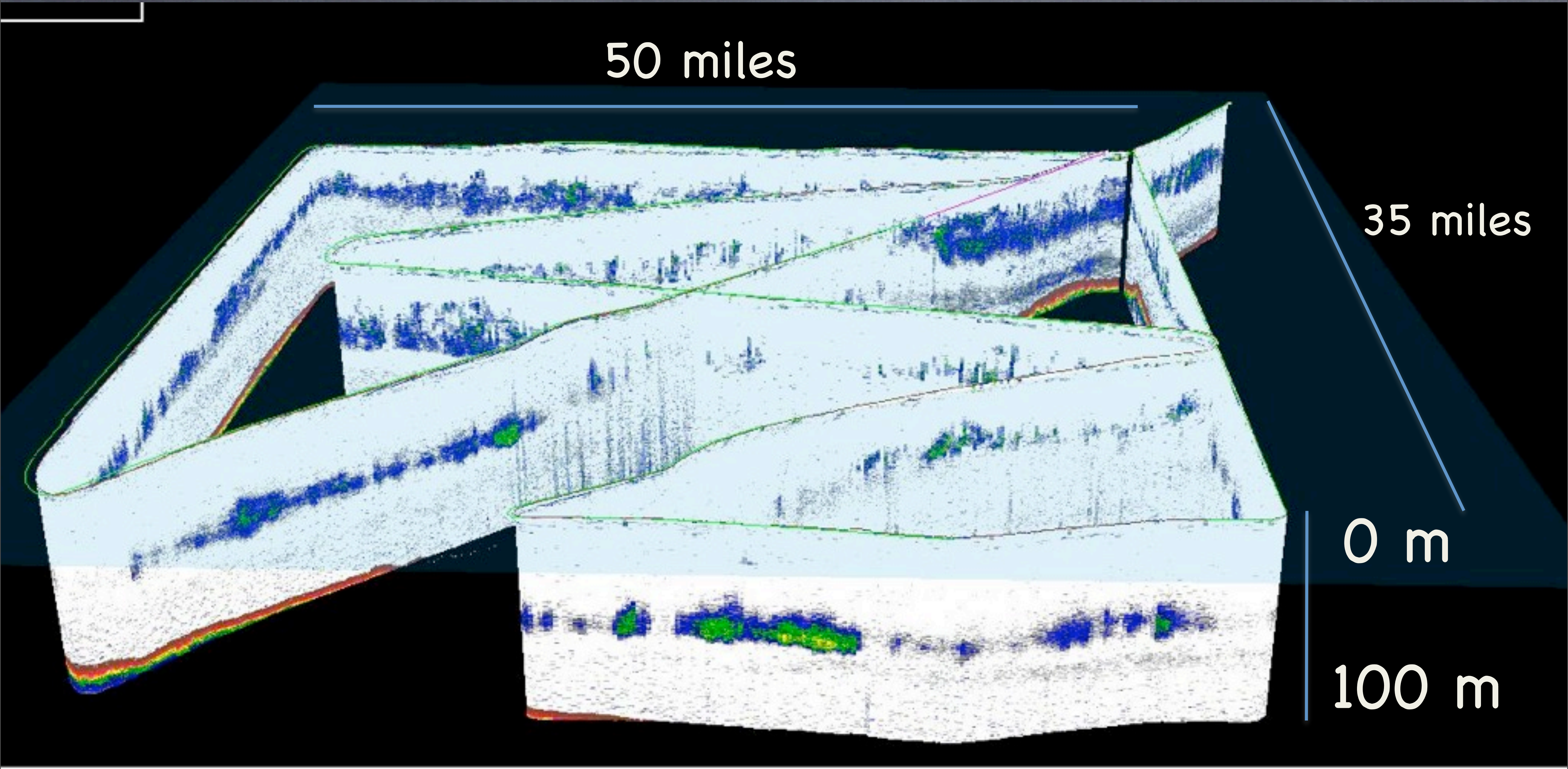
Major drivers of bacterial dynamics



Euphausia superba

— 10 mm —

Krill is highly patchy



Krill releases large amounts of DOC

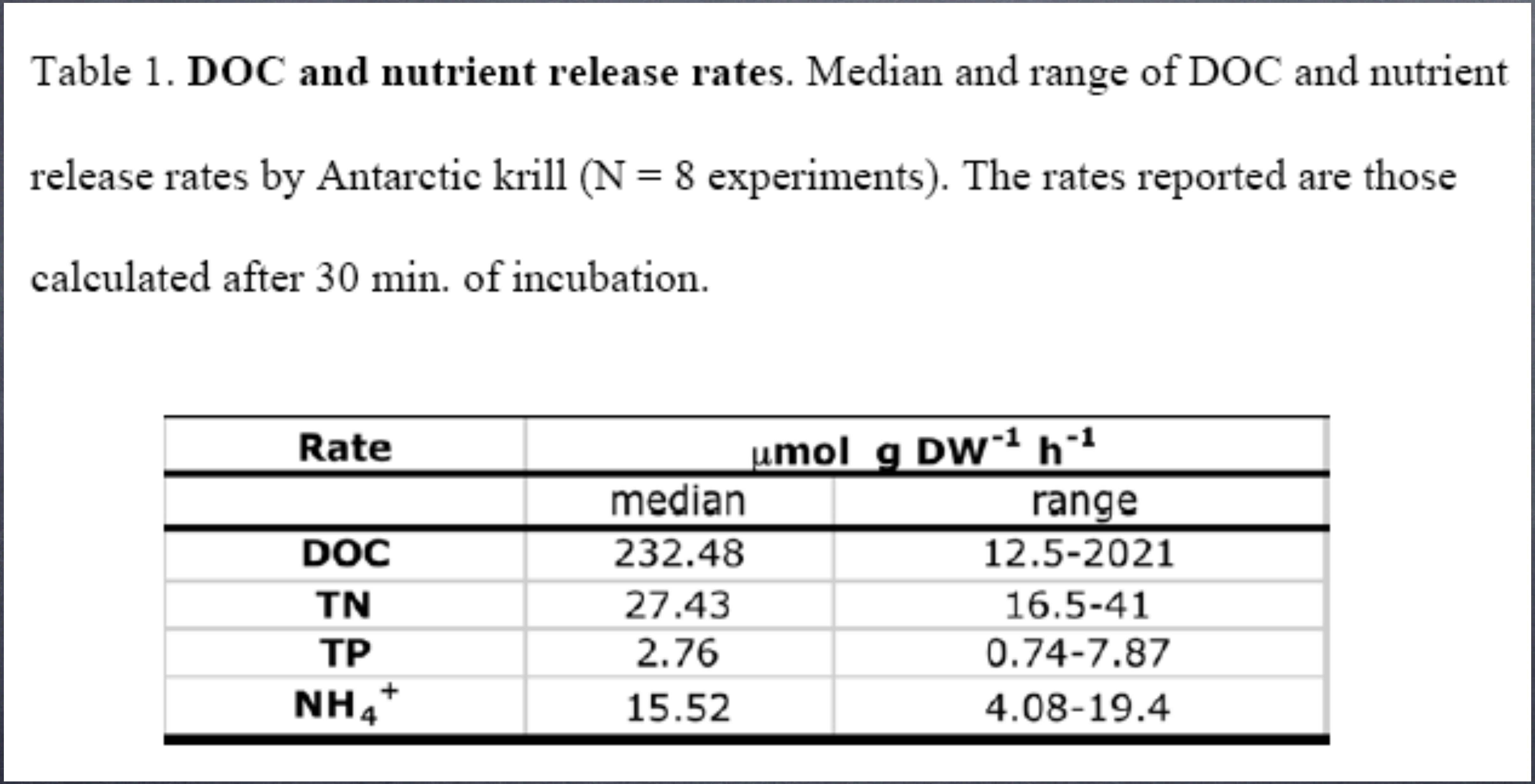
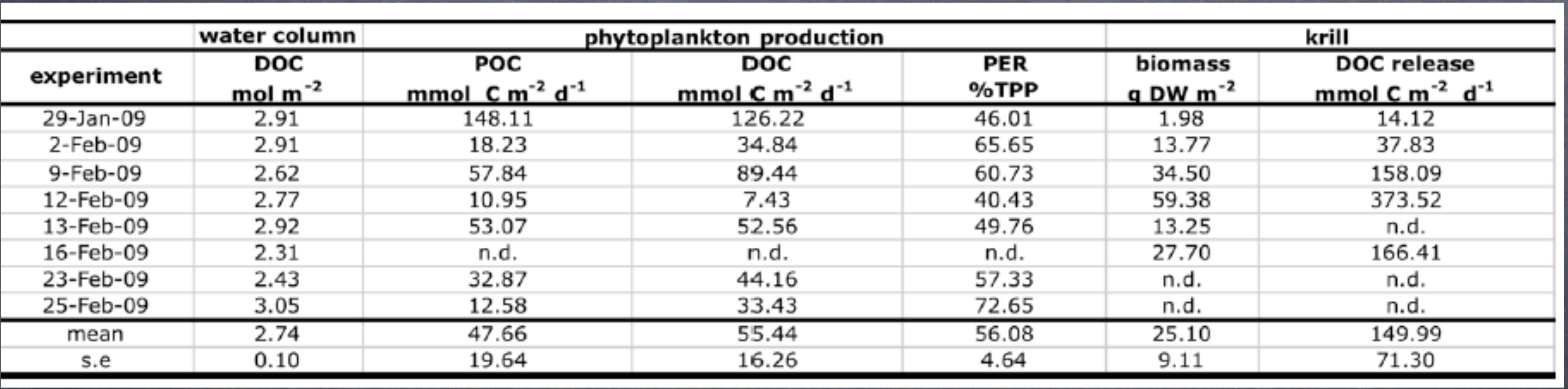


Table 1. **DOC and nutrient release rates**. Median and range of DOC and nutrient release rates by Antarctic krill (N = 8 experiments). The rates reported are those calculated after 30 min. of incubation.

Rate	μ**mol g DW^{-1} h^{-1}**	
	median	range
DOC	232.48	12.5-2021
TN	27.43	16.5-41
TP	2.76	0.74-7.87
NH_4^+	15.52	4.08-19.4

Ruiz-Halpern et al. (submitted)

Krill releases 78% of the total (phytoplankton + krill) release of DOC to the environment



	water column	phytoplankton production			krill	
experiment	DOC mol m^{-2}	POC mmol C m^{-2} d^{-1}	DOC mmol C m^{-2} d^{-1}	PER %TPP	biomass g DW m^{-2}	DOC release mmol C m^{-2} d^{-1}
29-Jan-09	2.91	148.11	126.22	46.01	1.98	14.12
2-Feb-09	2.91	18.23	34.84	65.65	13.77	37.83
9-Feb-09	2.62	57.84	89.44	60.73	34.50	158.09
12-Feb-09	2.77	10.95	7.43	40.43	59.38	373.52
13-Feb-09	2.92	53.07	52.56	49.76	13.25	n.d.
16-Feb-09	2.31	n.d.	n.d.	n.d.	27.70	166.41
23-Feb-09	2.43	32.87	44.16	57.33	n.d.	n.d.
25-Feb-09	3.05	12.58	33.43	72.65	n.d.	n.d.
mean	2.74	47.66	55.44	56.08	25.10	149.99
s.e	0.10	19.64	16.26	4.64	9.11	71.30

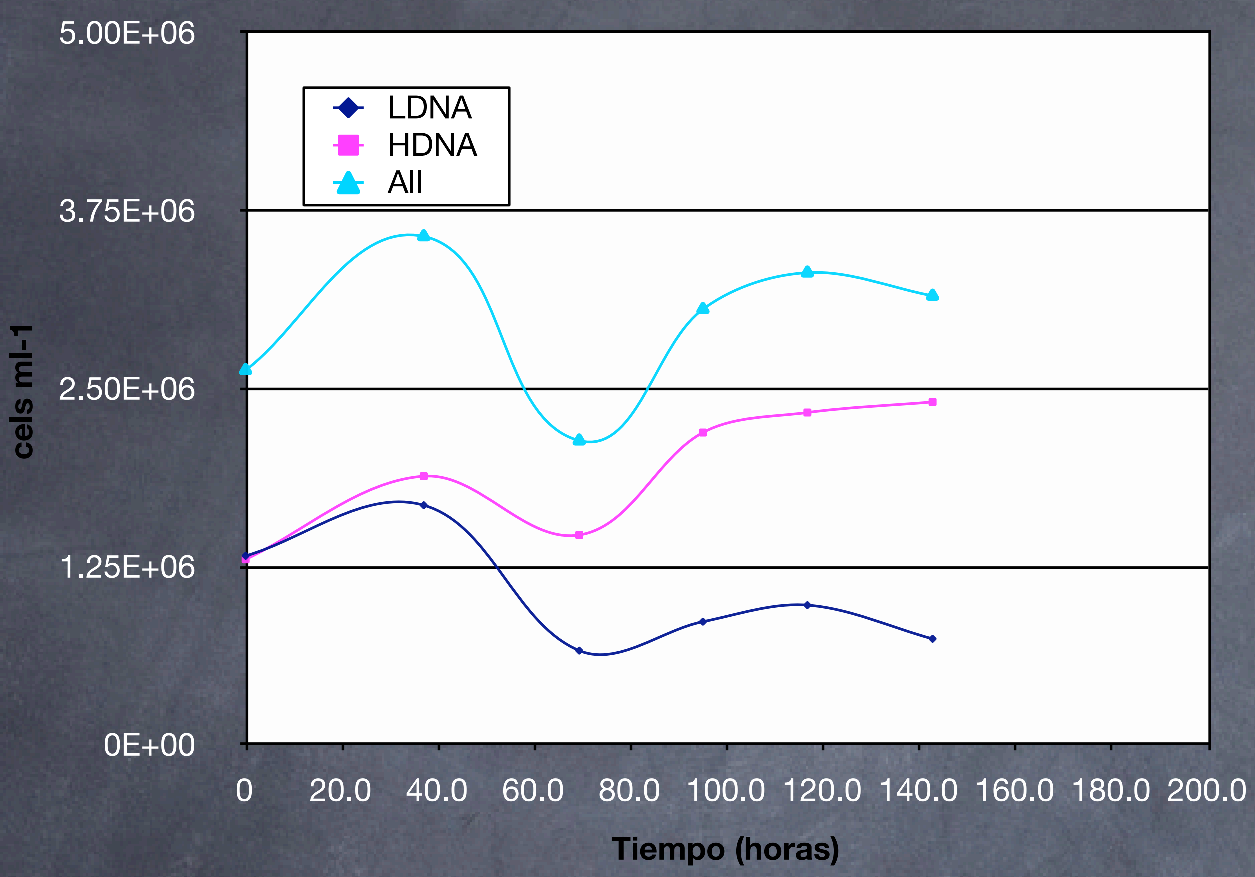
Helps explain why bacterial C demand is greater in the Southern Ocean than phytoplankton DOC production

Ruiz-Halpern et al. (submitted)

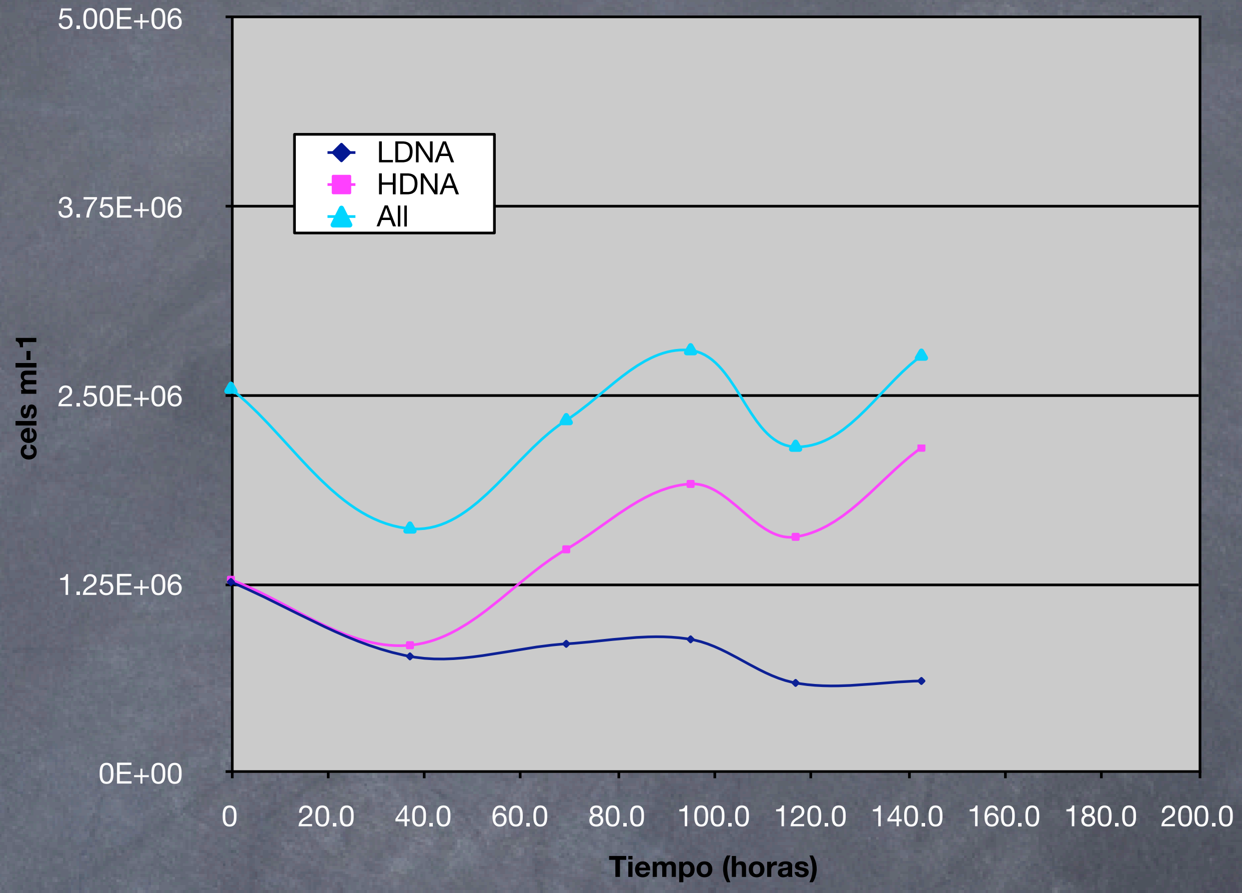
Exp 3 (Bransfield)

Huge Increase in bacterial abundance and metabolism

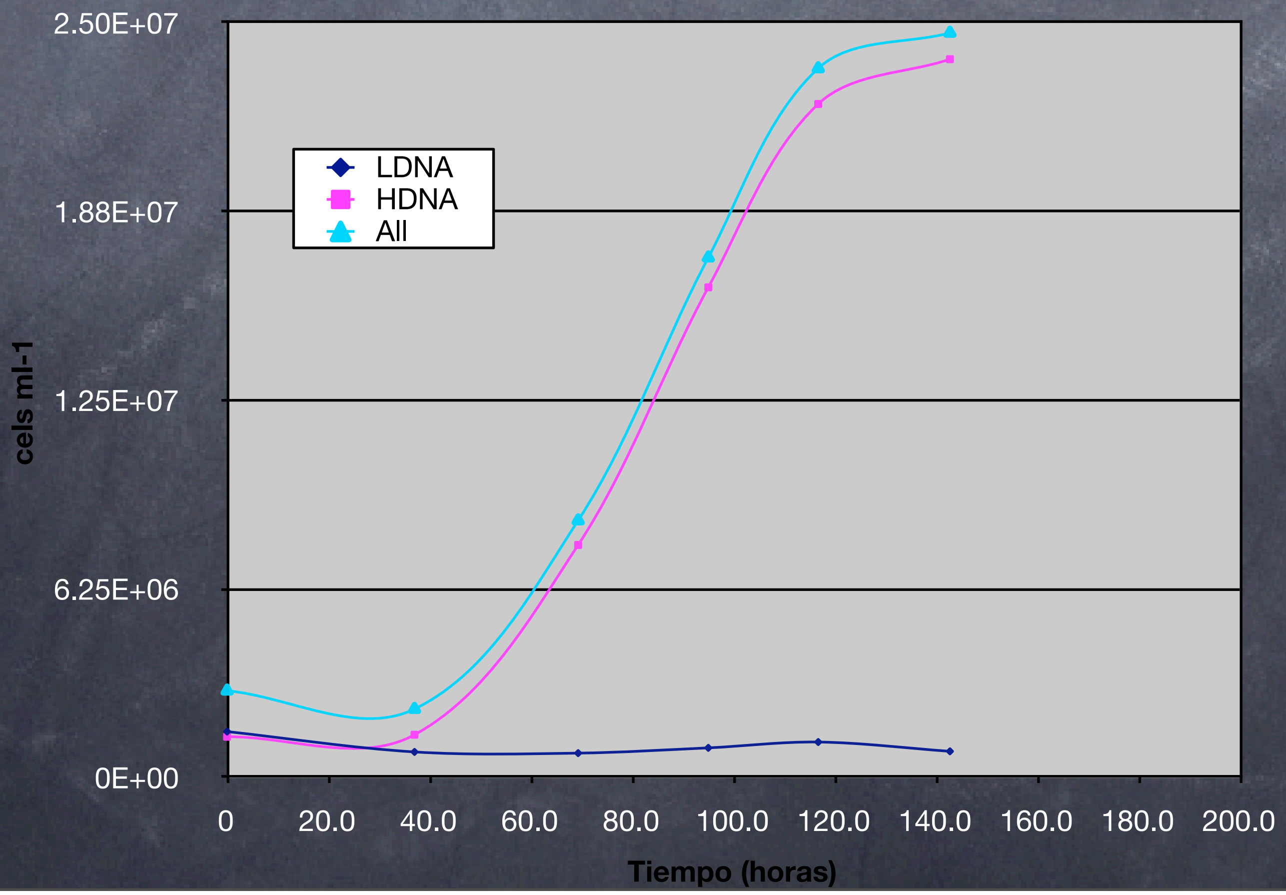
Control

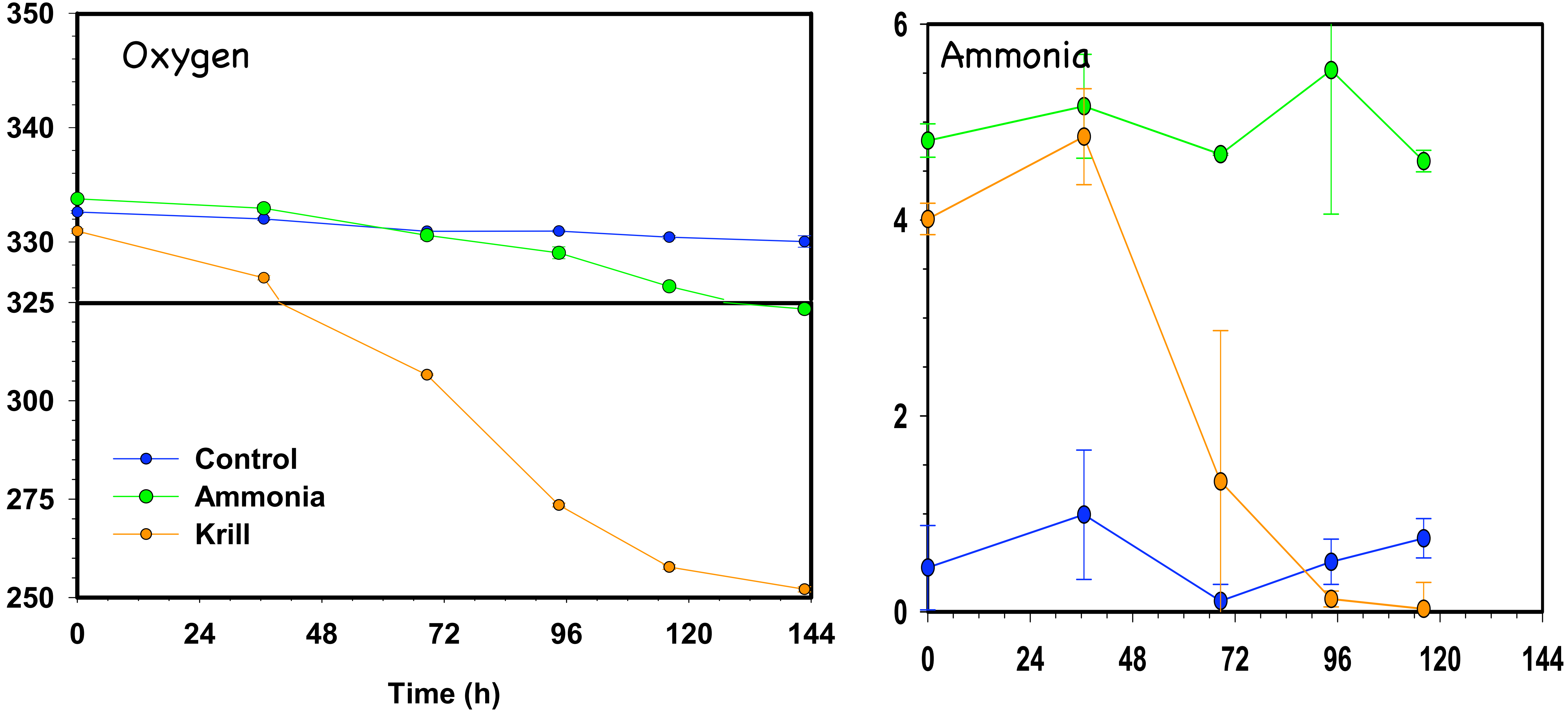


+ NH4



Krill

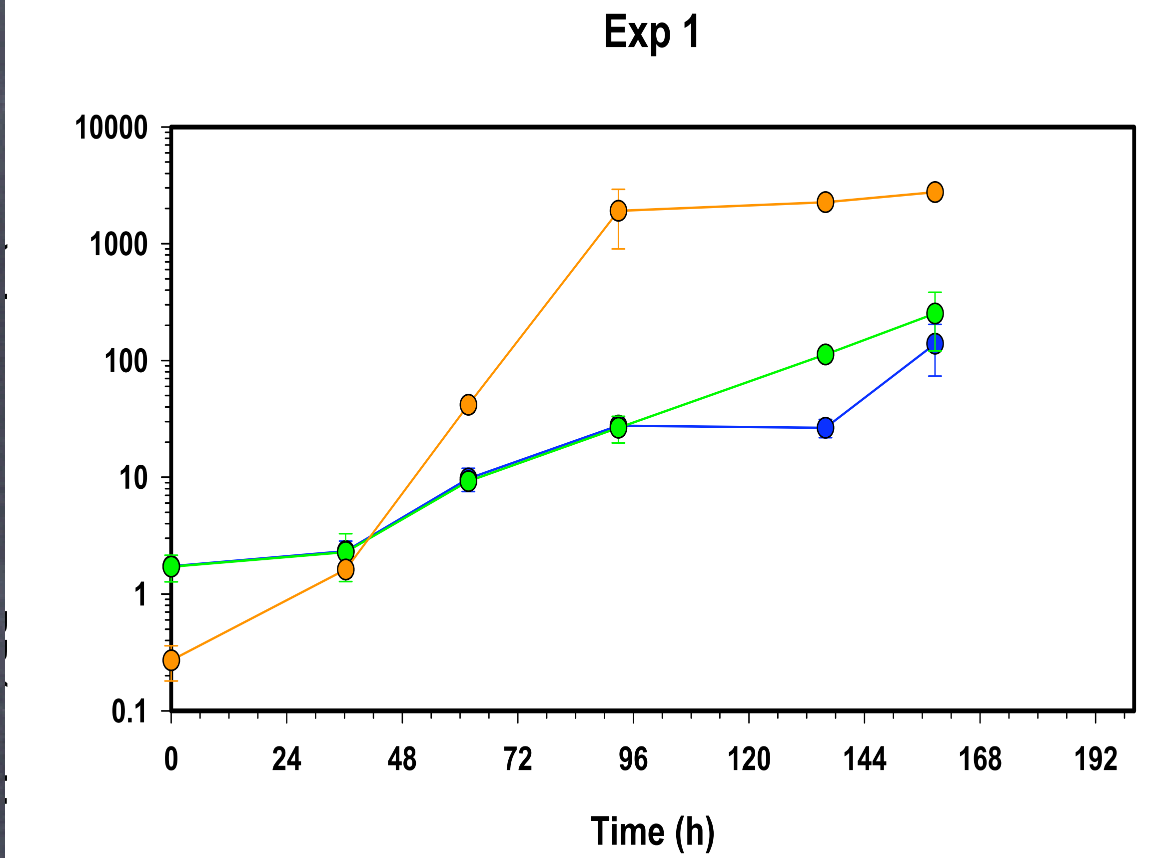


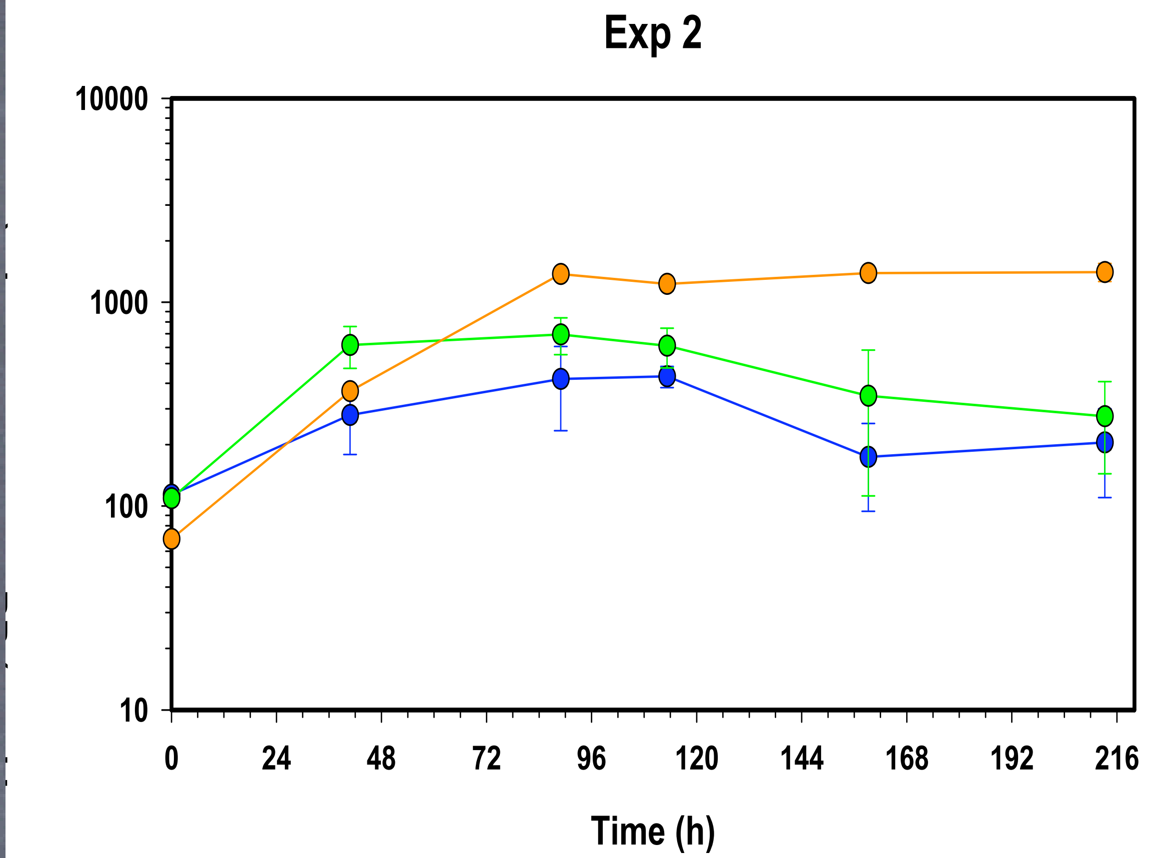


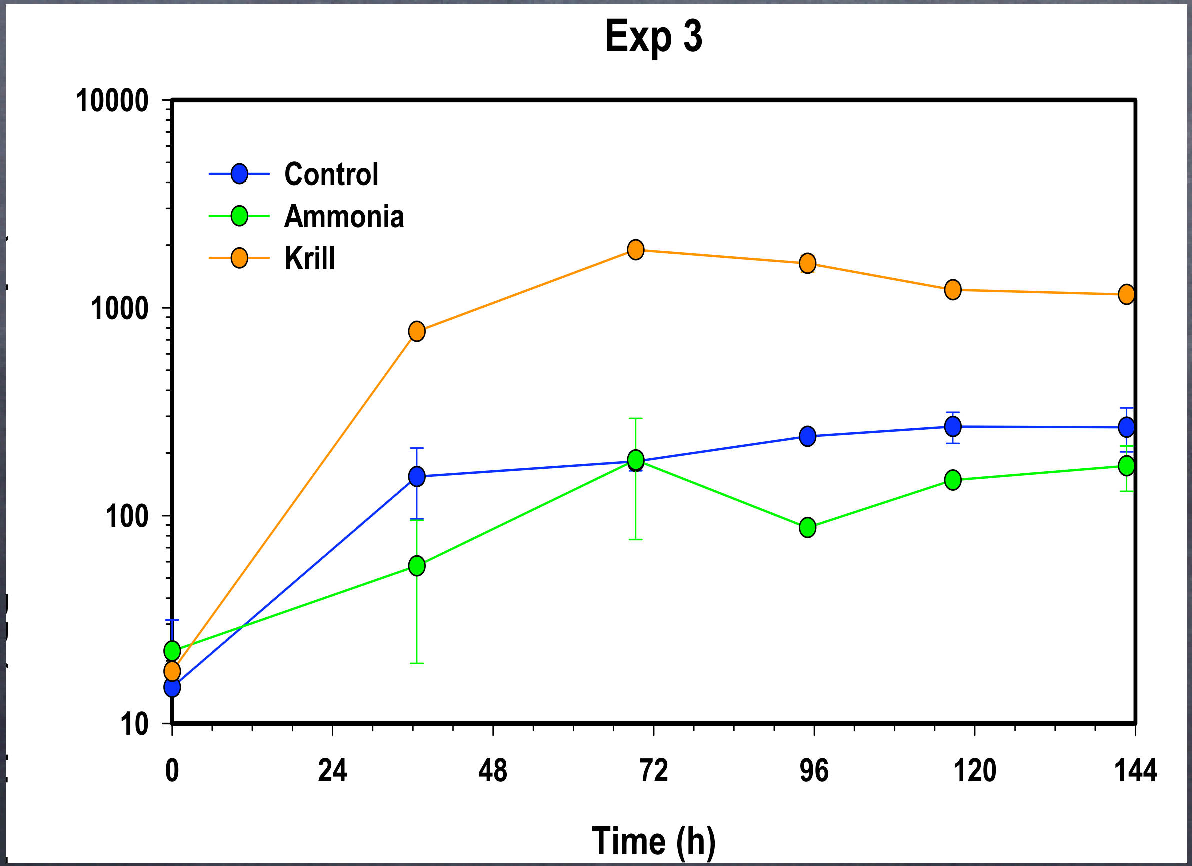
Respiration rates $\mu mol\ O_2\ L^{-1}\ h^{-1}$

Periodos tiempo	Control	Amonio	Krill
1 (0-36.6)	0.017	0.023	0.112
2 (36.6-68.6)	0.033	0.072	0.619
3 (68.6-94.5)	-0.001	0.060	1.288
4 (94.5-116.16)	0.024	0.135	0.726
5 (116.16-142.7)	0.014	0.108	0.218
Final	*0.018*	*0.073*	*0.553*

Bacterial Production (pmol Leu L^{-1} h^{-1})


Exp 1


Exp 2


Exp 3

Are there lateral and atmospheric organic C inputs to the ocean?

Lateral (coastal) inputs

Shelf Region	DOC export (G mol C yr^{-1})	Shelf length (km)	DOC export per km shelf break length (Gmol C km^{-1} yr^{-1})	Source
East China Sea	414.00	250.02	1.66	Hung et al. 2000 (55)
Mid-Atlantic Bight	1595.83	777.84	2.05	Vlahos et al. 2002 (638)
East China Sea	2975.00	666.72	4.46	Hung et al. 2003 (936)
Cape Ghir (NW Africa)	258.33	111.12	2.32	Garcia-Muñoz (1234)
Mid-Atlantic Bight	500.00	950.00	0.53	Bauer (1243)
North Brazilian Shelf	2200.00	212.50	10.35	Dittmar
Ría de Vigo (Spain)			0.22	Álvarez Salgado (433)
Global	500000.00	300000.00	1.67	This work

open ocean because of the existence of a DOC differencial between coastal and open ocean waters

Barrón et al. (in prep)

Are there atmospheric organic C inputs to the ocean?

Atmospheric inputs

Oceanic Rain water DOC: 59 ± 14 µmol C/L

Aerosol have high organic C contents: 1.2 % to 37% OC

The ocean is the major sink of Persistent Organic Pollutans (~proxy for atm. TOC) Jurado et al. (2004, 2005)

If (aqueous equlibrium) [VOC]atm - [VOC]sea = 1 µmol C/L (concs. ~35 µmol C/L) then flux 5.5 Gt C/yr (Jurado et al. 2008)

Atmospheric inputs

Particulated

Gaseous organic carbon

Aerosol Organic C
$0.058\ \mathrm{Gt\ C\ yr^{-1}}$

Few rate estimates

Dachs et al. (2005), Jurado et al. (2008), Ruiz-Halpern et al. (2010),
Arrieta et al. (submitted)

Atmospheric inputs

Subtropical NE Atlantic

- Organic C inputs 15 fold > CO_2 flux
- Dominated by gaseous inputs (gaseous organic carbon 90 % of flux)
- Atmospheric inputs to the Subtropical NE Atlantic 0.7 ± 0.2 Gt C/y vs. estimated organic C deficit (net heterotrophy) of 0.5 Gt C/y (Duarte et al. 2001)

Dachs et al. (2005)

Figure 1.

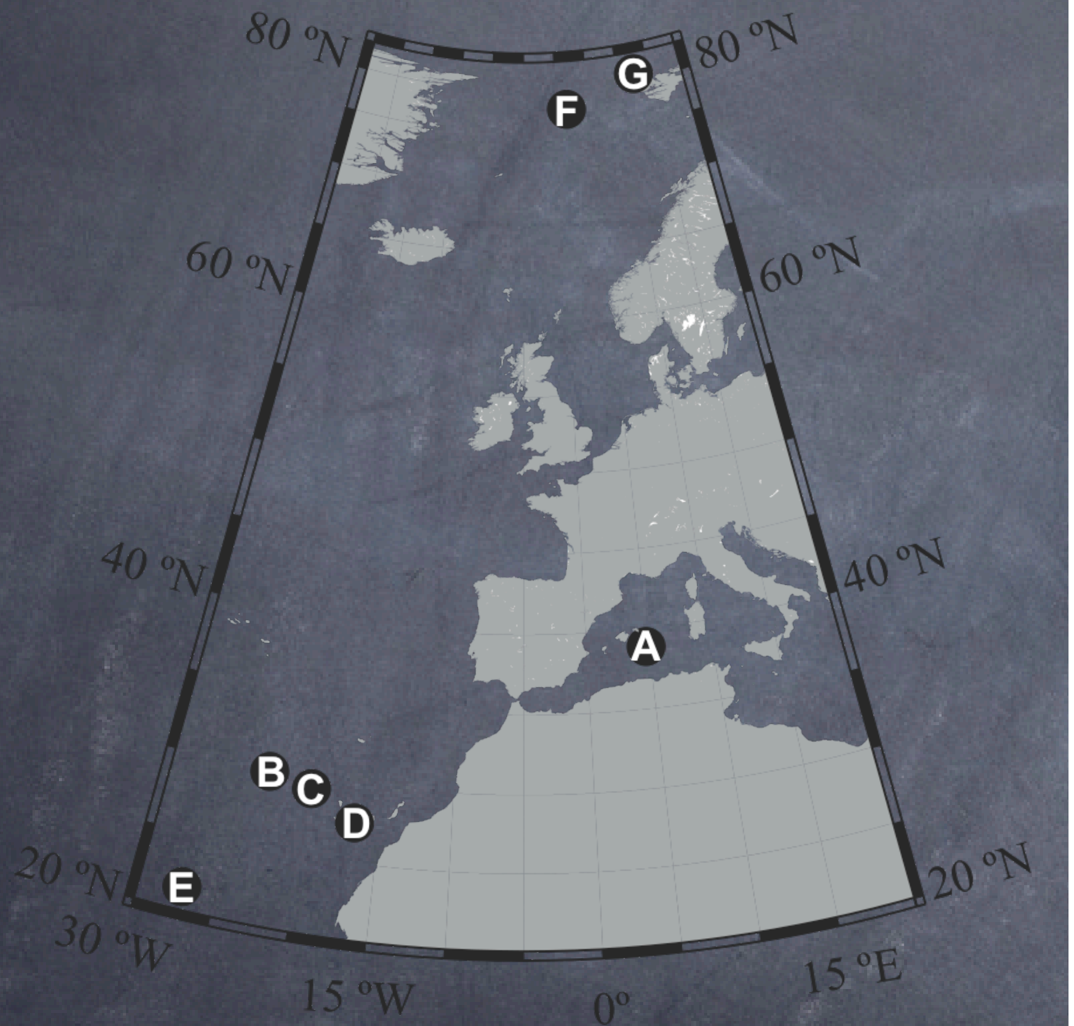
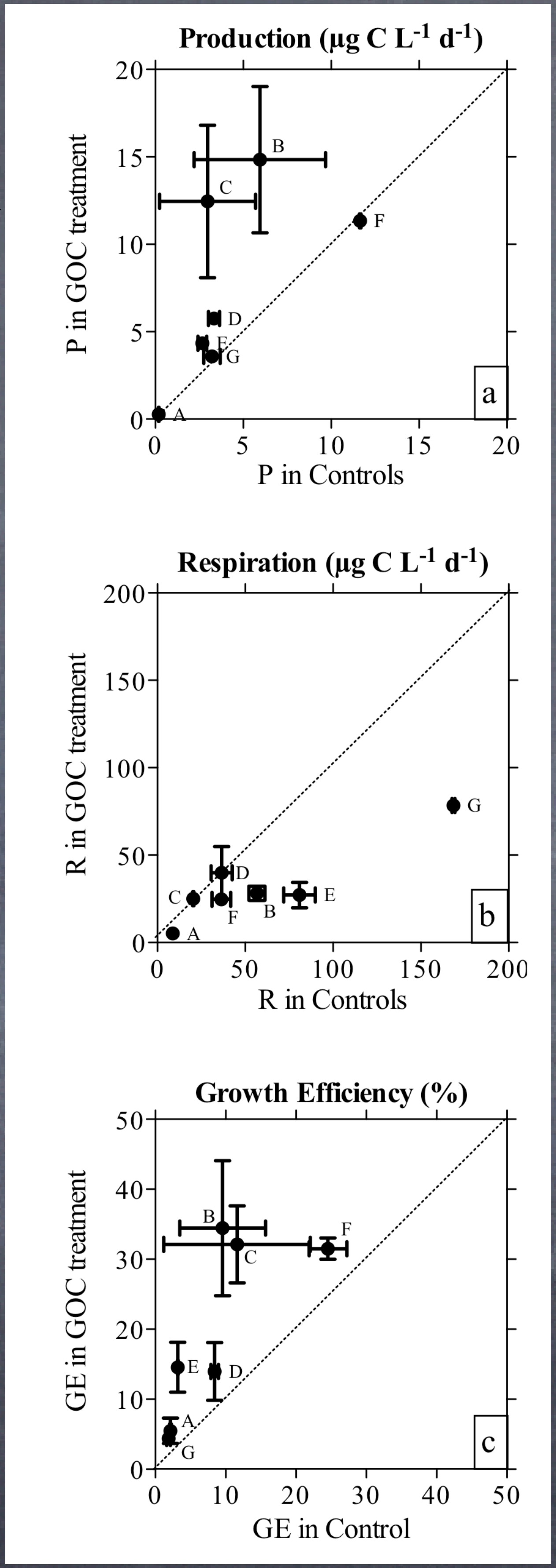
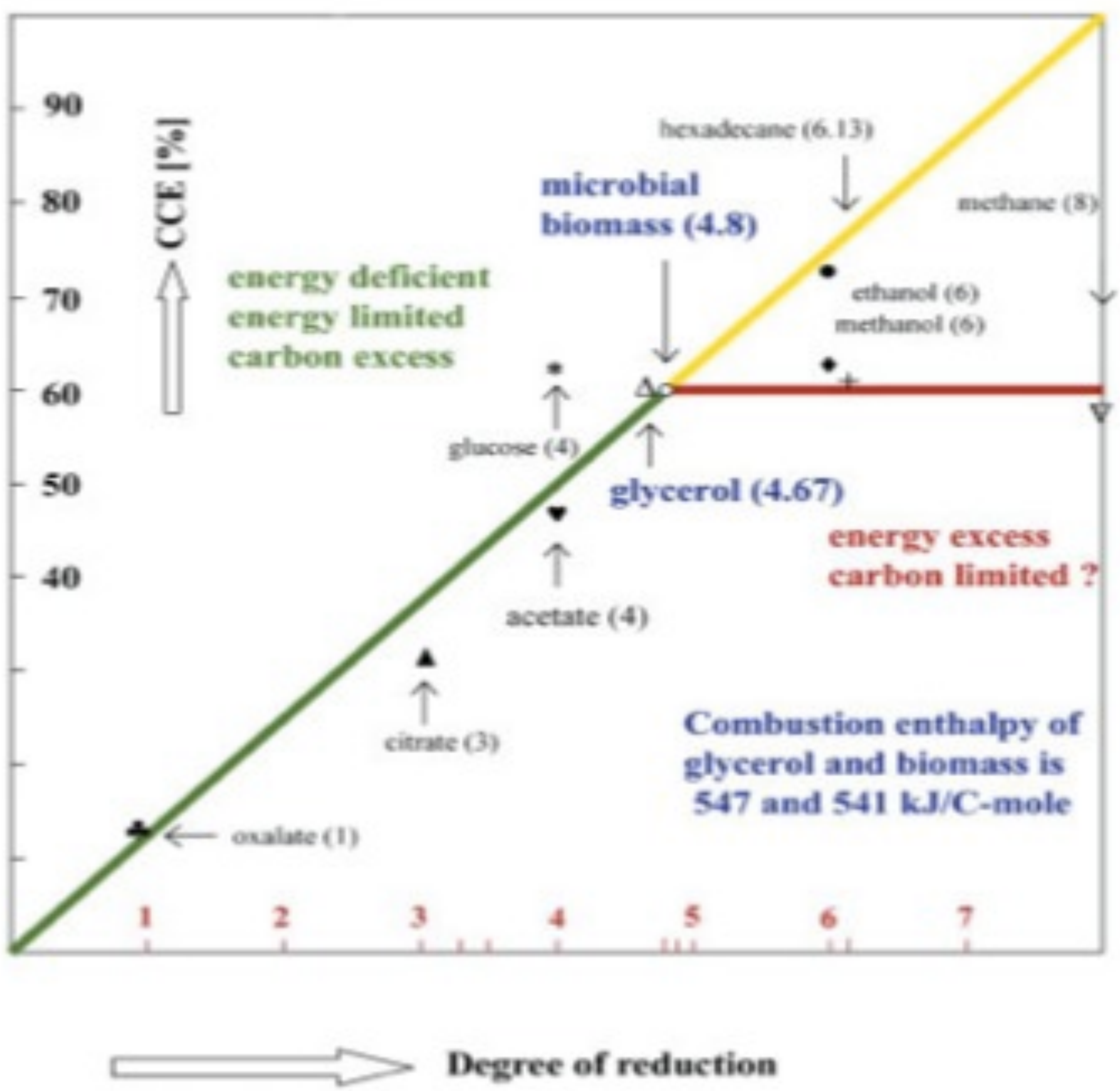


Figure 2.

Arrieta





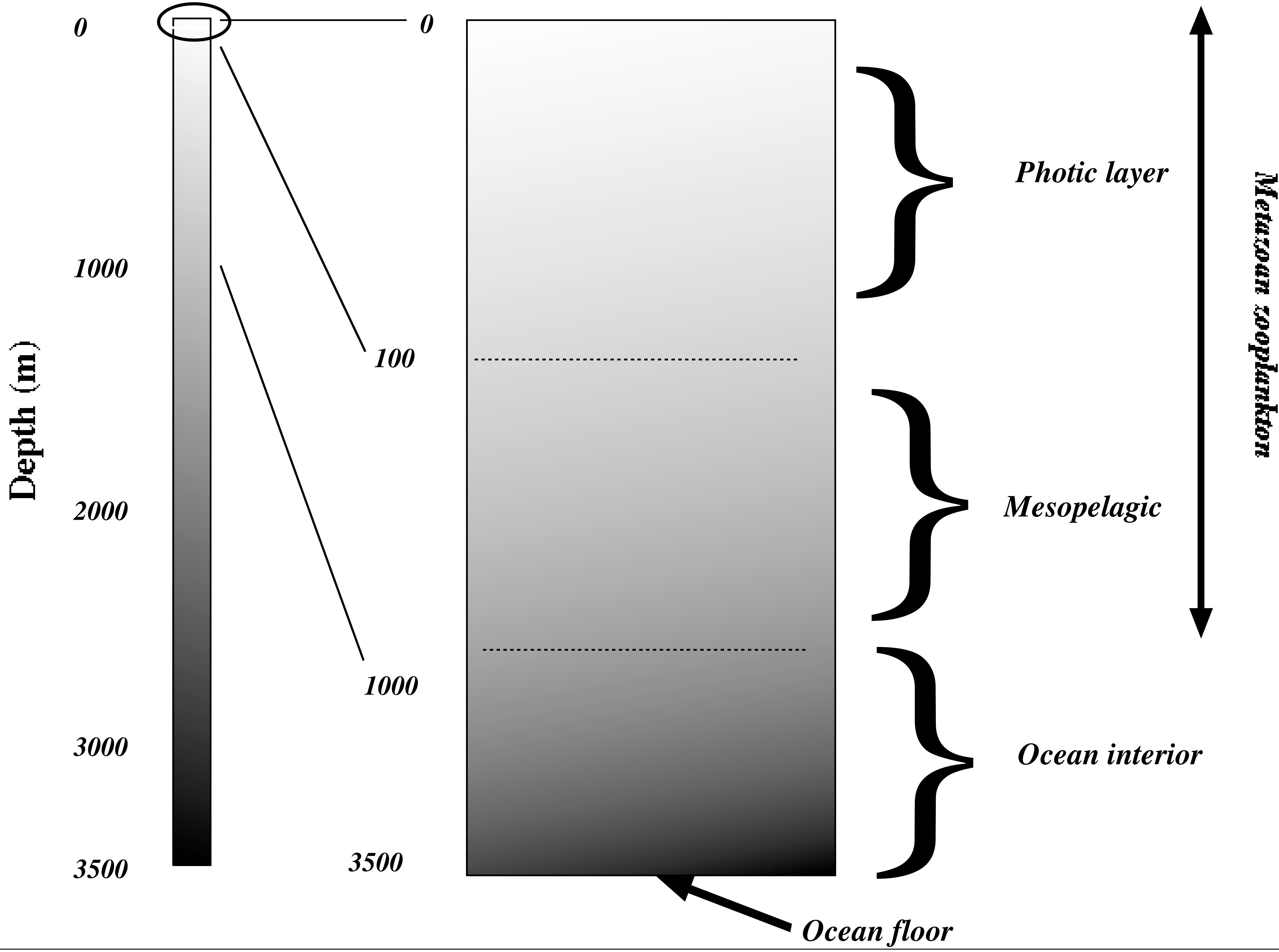
Babel (2009)

Figure 1. Relationship between the degree of reduction of heterotrophic substrates and the carbon conversion efficiency (CCE) of aerobic growth. Microbial biomass as a yardstick for the classification of heterotrophic substrates. Values in brackets denote the respective degrees of reduction.

The major known gaseous organic components of the troposphere are methane, methanol, acetone and acetaldehyde, all are more reduced than the average bacterial biomass

The degree of reduction of the substrate has been found to determine largely the carbon use efficiency. Maximum “carbon conservation” was observed when the degree of oxidation of the substrate was higher than 5 (microbial biomass having a degree of reduction of ~4.8). Bringing more reduced substrates to the level of oxidation of biomass preserves C since there is no need to burn additional material to generate reducing power.

Estimates for the photic layer only



Depth (m)

0

1000

2000

3000

3500

0

100

1000

3500

Photic layer

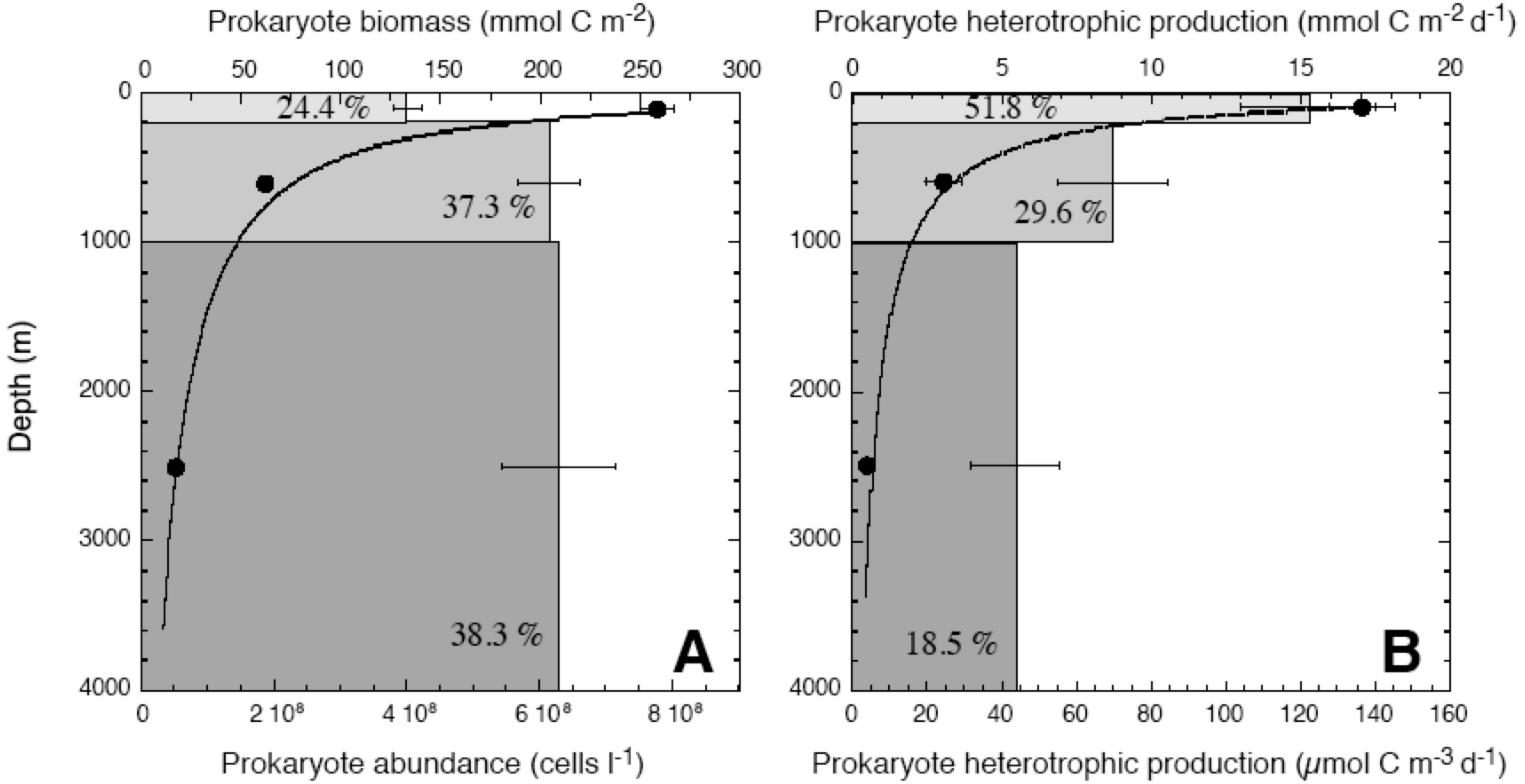
Mesopelagic

Ocean interior

Metazoan zooplankton

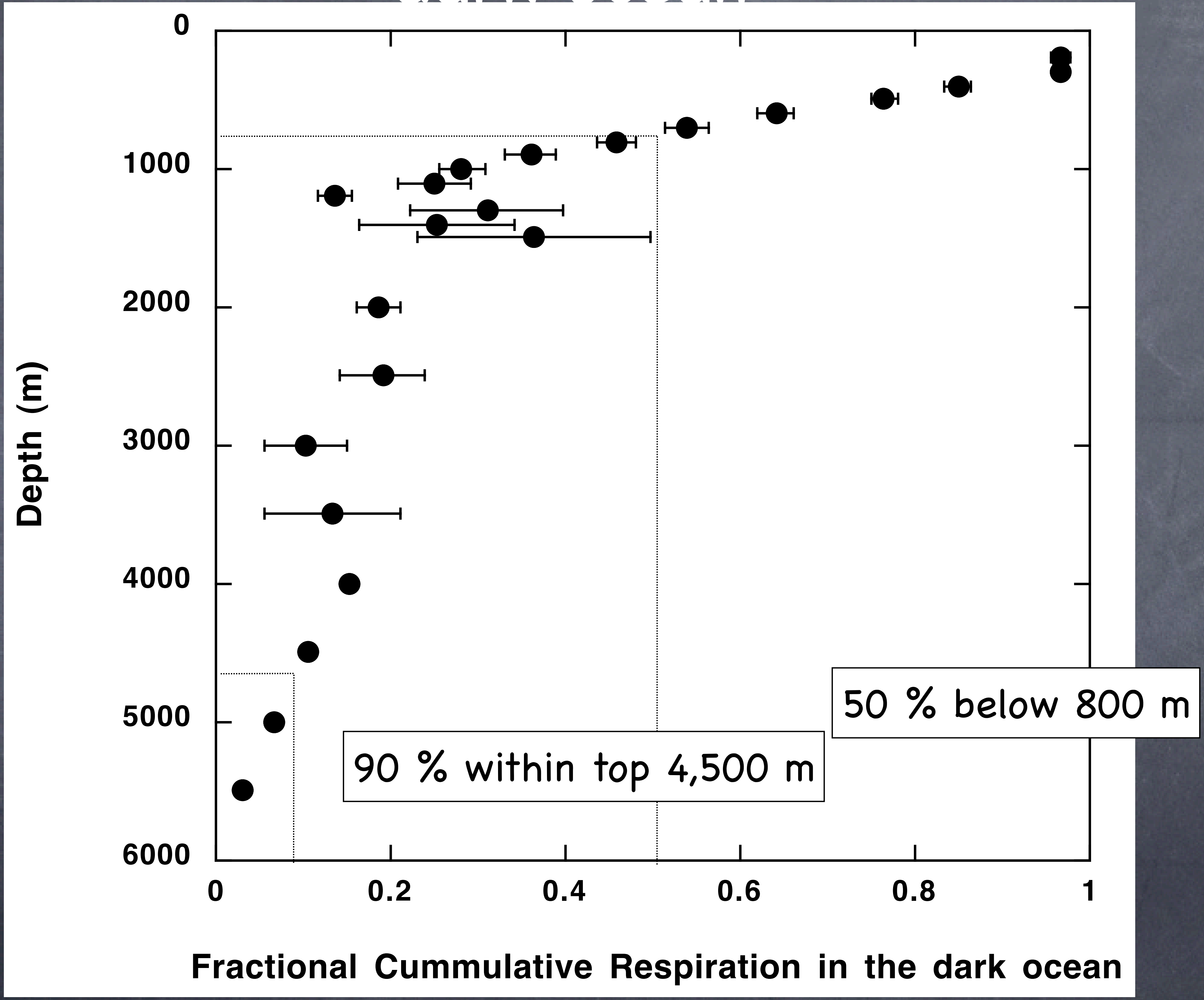
Ocean floor

Biomass and activity of deep-water (>1000 m) bacteria is very significant



Arístegui, Gasol Hendl & Duarte (en revision)

Average composite cummulative respiration in the dark ocean

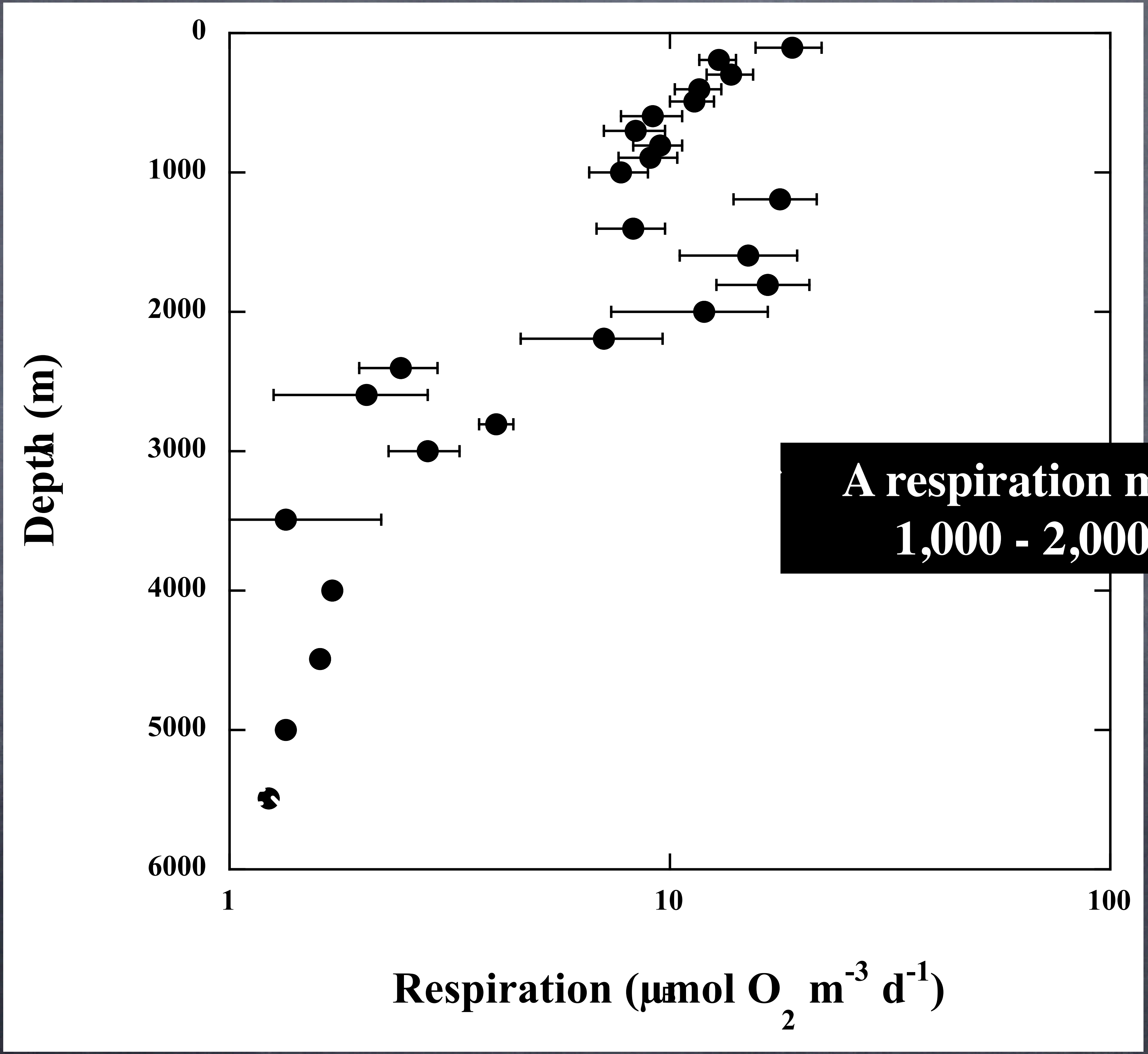


50 % below 800 m

90 % within top 4,500 m

Arístegui, Duarte & Agustí, Geophys. Res. Letters (2003)

Total R in the dark ocean = 38.1 Gt C yr^{-1}



A respiration maximum at 1,000 - 2,000 m depth

Arístegui, Duarte & Agustí, Geophys. Res. Letters (2003)

Summary

- Estimates of heterotrophic activity in the ocean have increased over the past decades.
- The large magnitude of heterotrophic activity questions our understanding of autotrophic processes as well (even if ignoring the deep ocean)
- A high carbon flux through heterotrophs compared to autotrophs in the oligotrophic ocean depends on a very fast turnover of carbon mediated by high mortality rates of phototrophs.
- Atmospheric inputs of organic carbon are significant and fuel prokaryote production in surface waters.
- Improved assessments of heterotrophic activity are essential to better understand the C budget of the ocean

Respiration in the open ocean:

Total Respiration in the Open Ocean	*Gt C year^{-1}*
• *Photic ocean (0 - 200 m)*	*37 - 42*[1]
• *Dark ocean (200 - 1000 m)*	*18 - 38*
• *Mesozooplankton*	*3*[2]
• *Vertebrates*	*0.01*[2]
• *Benthic R*	*0.65*[2]
TOTAL	*- 83*

Requires New production (+ lateral inputs) to be ~ 20 - 40 Gt C/year

del Giorgio & Duarte, Nature (2002)

Benthic respiration in the coastal ocean

Ecosystem	Surface area (10^6 km^2)	Respiration (mmol m^{-2} d^{-1})	Global respiration (Gt C yr-1)
Coral reefs	0.6	359	0.92 (13%)
Mangroves[1]	0.2	426	0.32 (5%)
Salt-marshes[1]	0.4	459	0.74 (11%)
Seagrasses	0.6	158	0.38 (6%)
Macroalgae	1.4	188	2.80 (41%)
Sediment	23.9	R = f(depth)	1.68 (24%)
Sum	27		6.84

Middelburg, Gattuso and Duarte (2004)

Constraints on respiration

Organic Carbon Budget

Production + Import = Export + Burial + Respiration

Authocthonous Inputs:

Phytoplankton 4.5 Gt C yr^{-1}

Benthic producers 5.5 Gt C yr^{-1}

Total 9.9 Gt C yr^{-1}

Imports[1] (river delivery): 0.4 Gt C yr^{-1}

Export[1] 2.0 Gt C yr^{-1}

Burial[1] 0.15 Gt C yr^{-1}

Respiration[2] 8.15 Gt C yr^{-1}

1 Low estimates 2 Includes planktonic respiration

Organic Carbon Budget

Net Production Coastal Ocean = 9.9 - 8.15 = 1.75 Gt C yr $^{-1}$

P/R ratio = 1.21

The Coastal Ocean is Net Autotrophic, Removing CO_2 and Exporting Organic C to the Open Ocean[1]

---

1. *A fraction is exported to land ecosystems as well.*

Respiration in the open ocean:

Total Respiration in the Global Ocean Gt C year^{-1}

Estuaries		1.32
Coastal Ocean	Benthic	7.44
	Pelagic	13.44
Open Ocean	Upper	120
	Mesopelagic	16.32
	Bathypelagic	2.04
	Sediment	2.04
Total Ocean R		162.6

del Giorgio & Williams (2004)

Metabolic balance of the open ocean

Production 35 - 60 Gt C year $^{-1}$

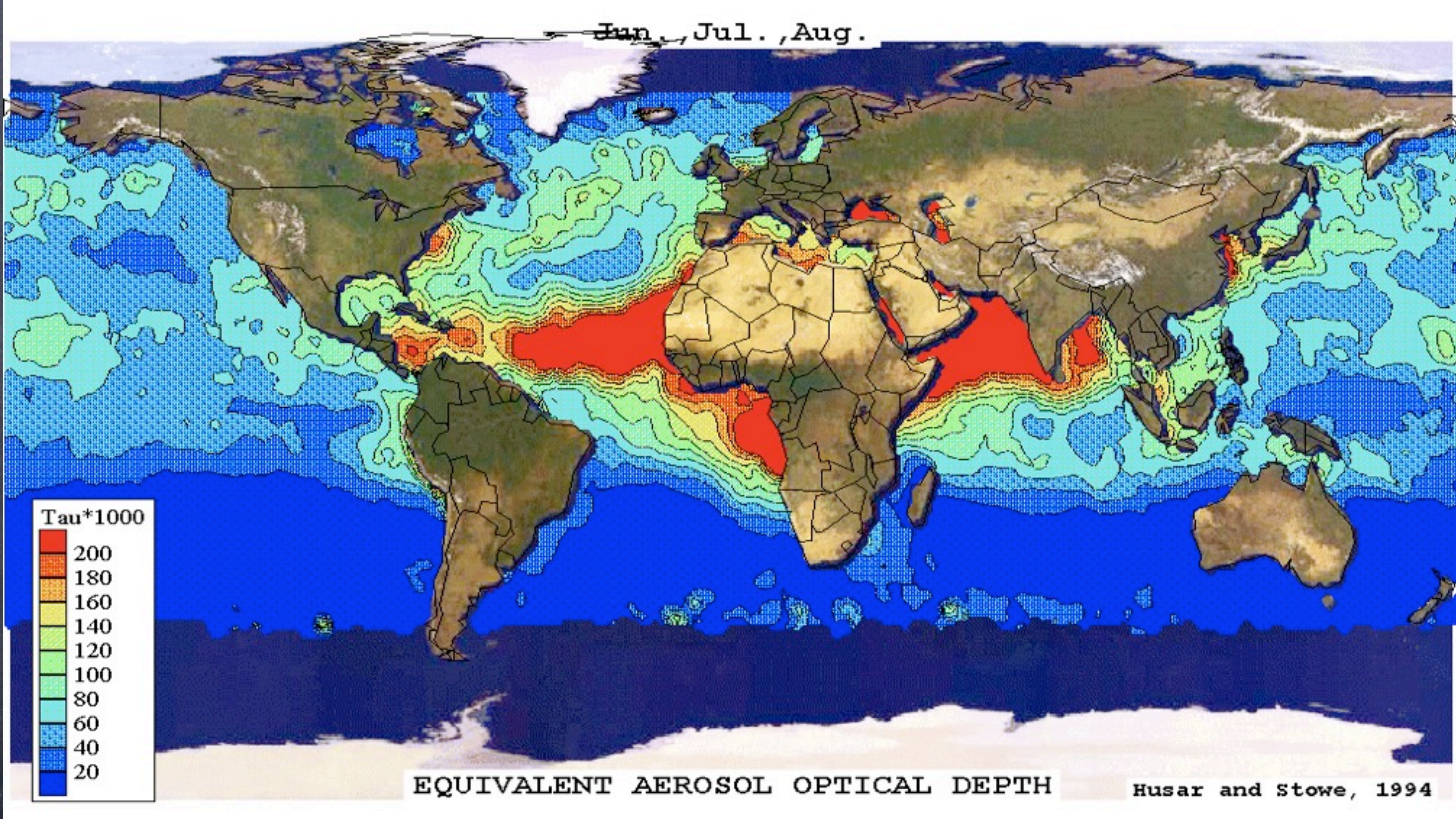
~~Respiration 160 Gt C year $^{-1}$~~

Deficit > 100 Gt C year $^{-1}$

Where does the necessary carbon come from?

External C inputs	*Gt C year $^{-1}$*
• *Rivers*	*0.45*
• *Excess coastal production*	*5 - 5.5*
• *Atmospheric inputs*	*2 - 3?*
TOTAL	***7.5 - 9***

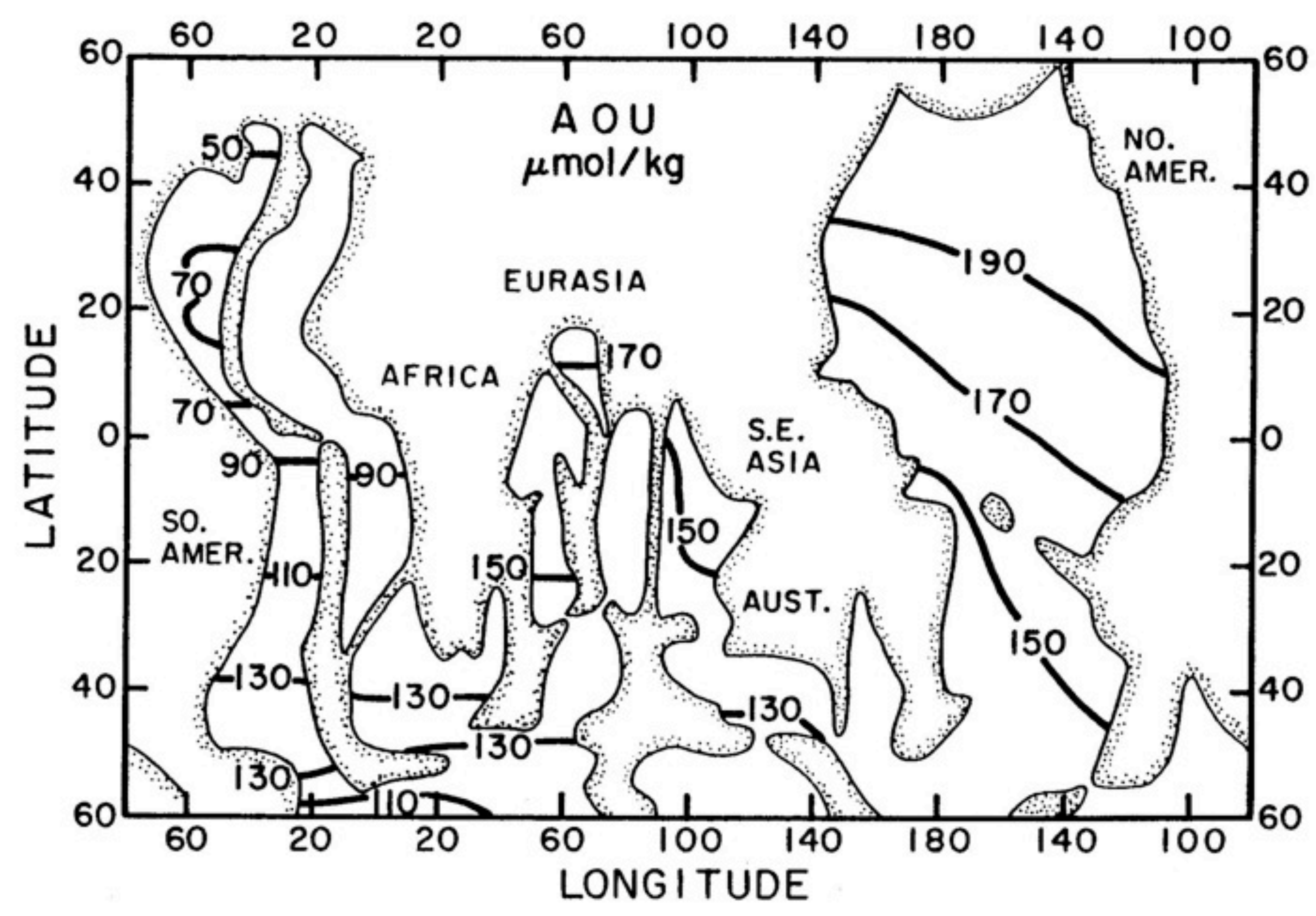
del Giorgio & Duarte, Nature (2002), del Giorgio & Williams (2004)



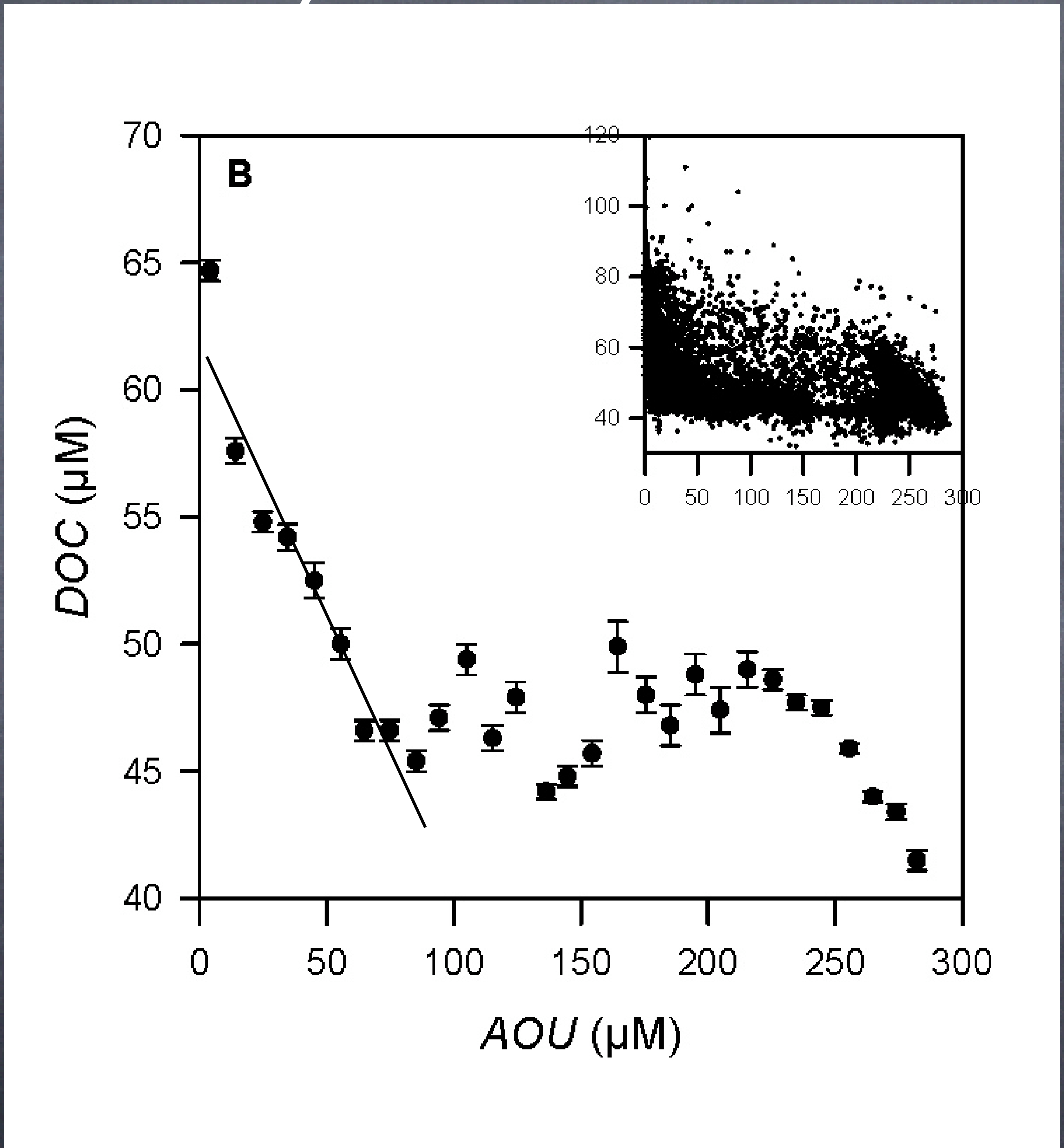
The E Subtropical Atlantic is an area with very high aerosol load

Composite satellite image of aerosols over the oceans

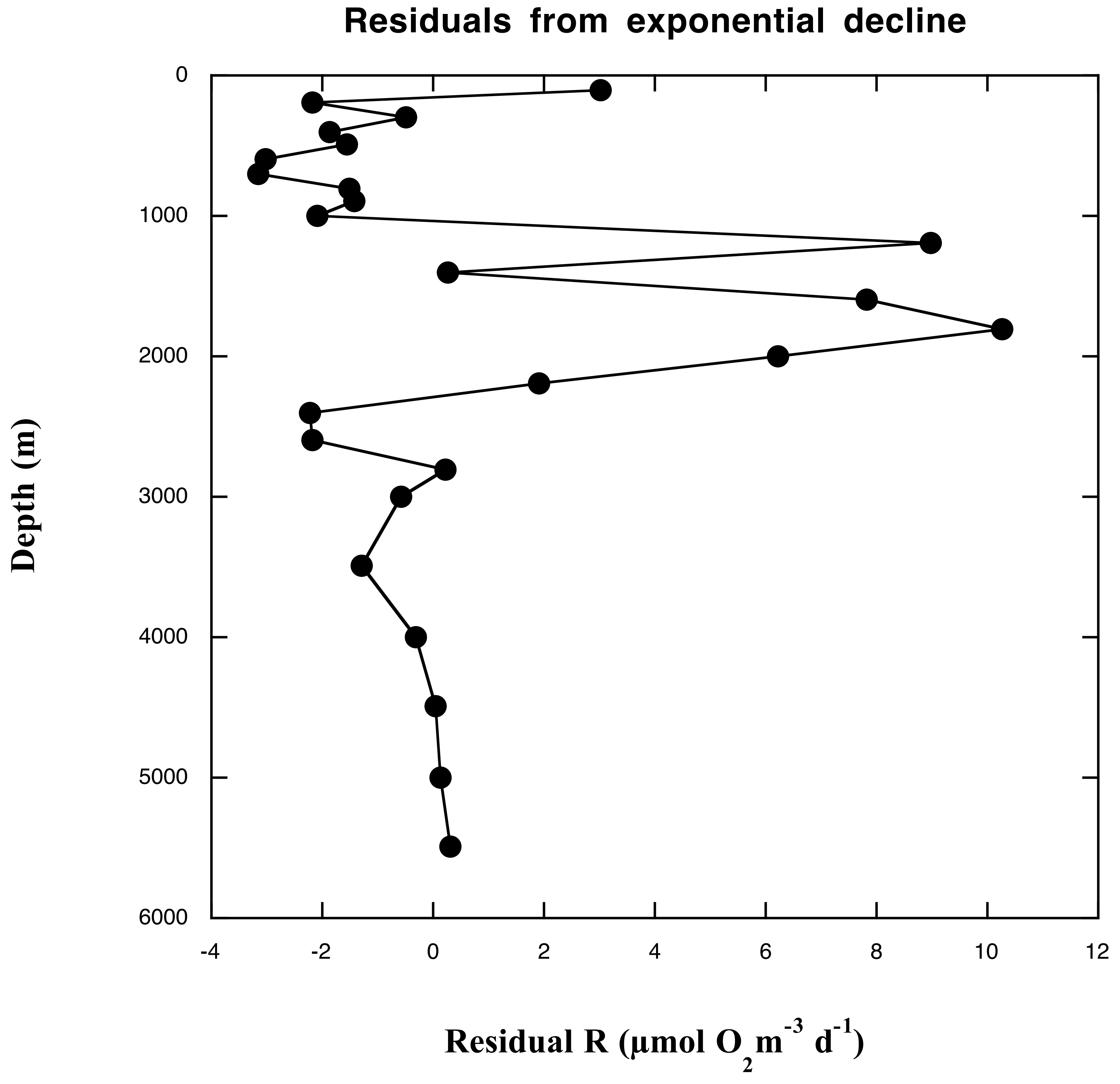
Evidence of important respiratory activity in the deep ocean from oxygen fields



This respiratory activity is only partially supported by use of semirefractory DOC



Arístegui, Duarte, Agustí et al., Science (2002)

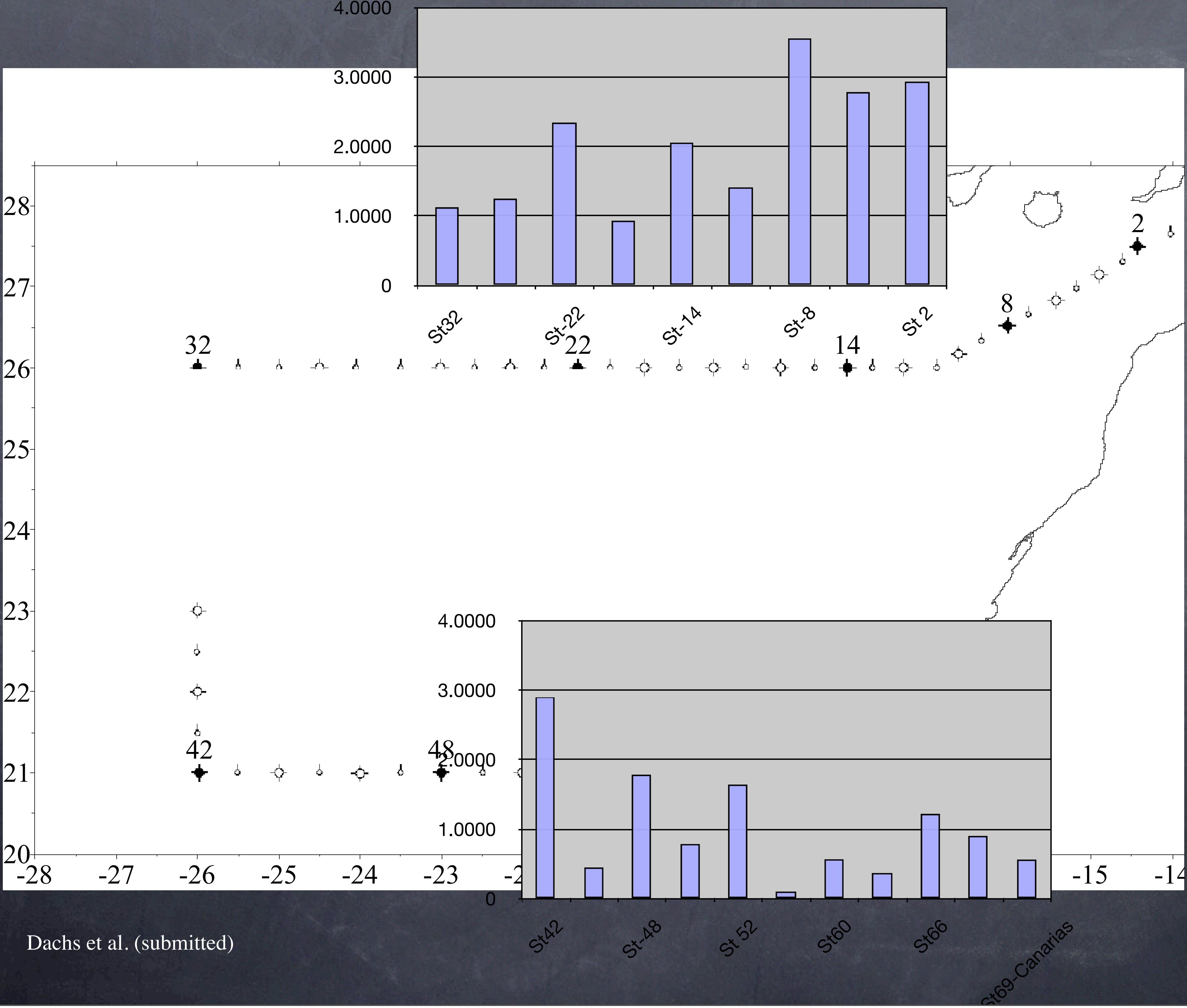


Enhanced respiration at 000 - 2000 layer

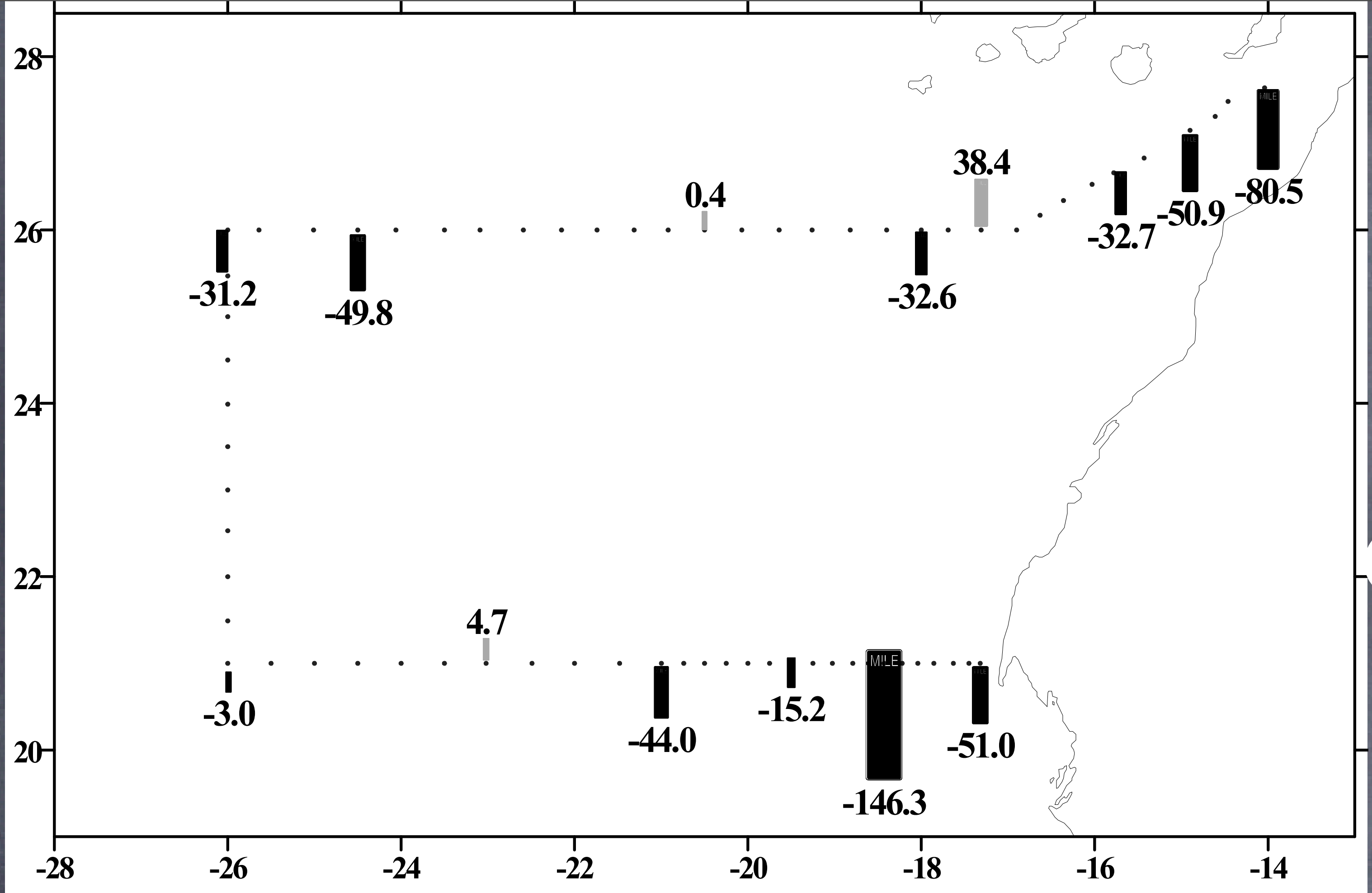
A recurrent feature in all oceans investigated

Increased activity at the base of the permanent thermocline?

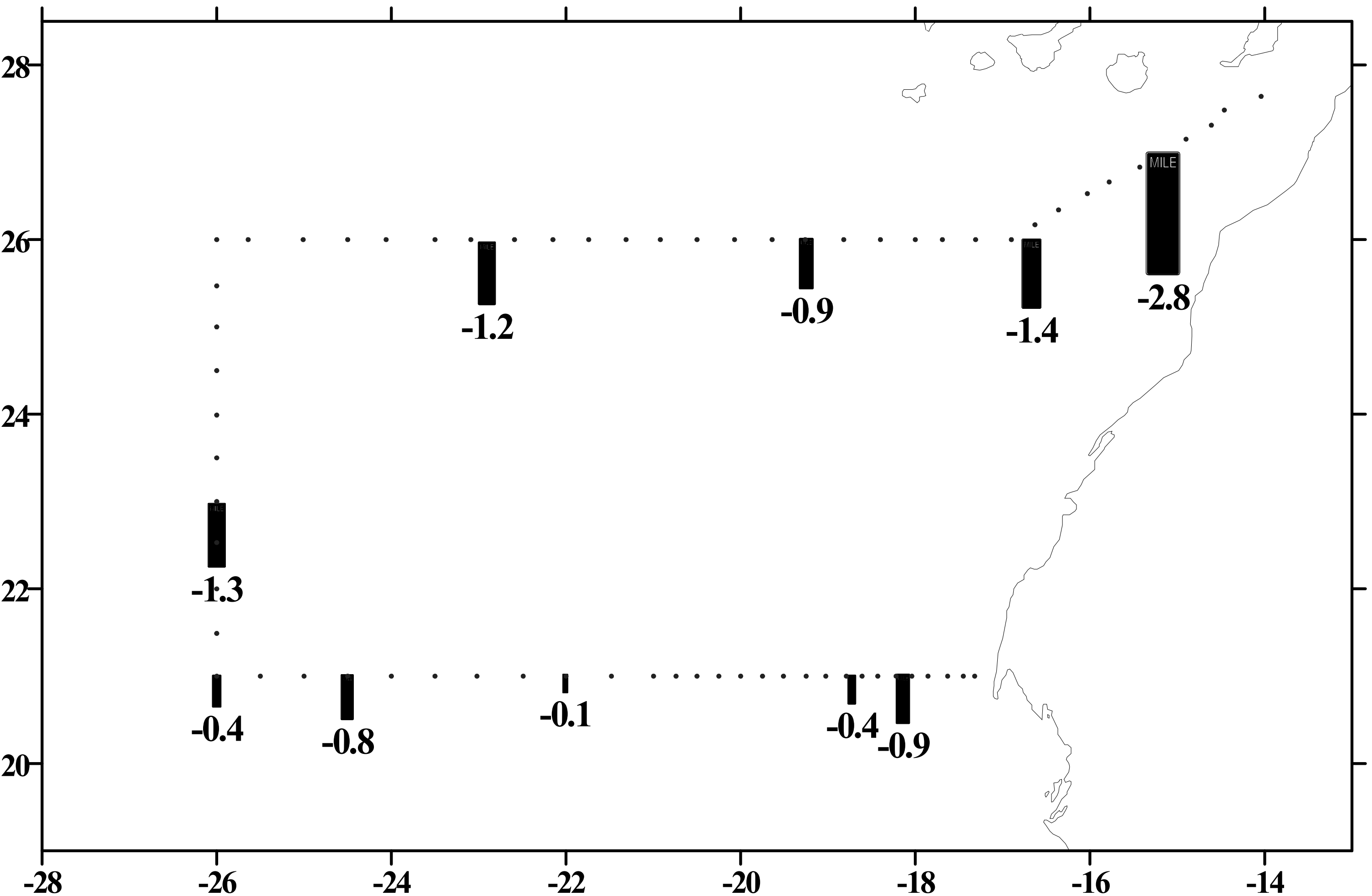
Arístegui, Duarte & Agustí, Geophys. Res. Letters (2003)



Dachs et al. (submitted)



Gaseous Organic C flux
($mmol\ C\ m^{-2}\ d^{-1}$)



Aerosol Org. C flux
($mmol\ C\ m^{-2}\ d^{-1}$)

Dachs et al. (submitted)

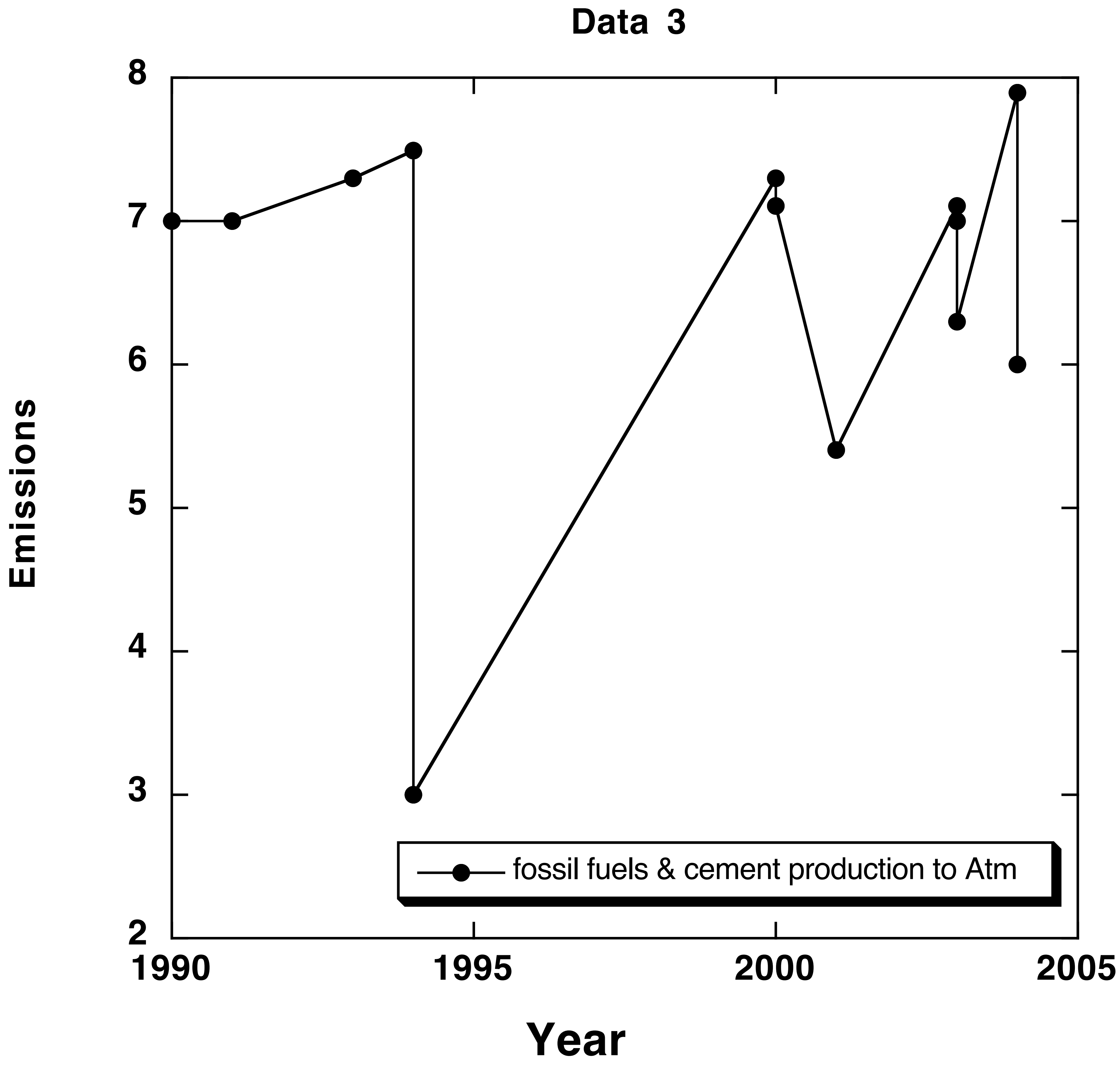
Atmospheric inputs

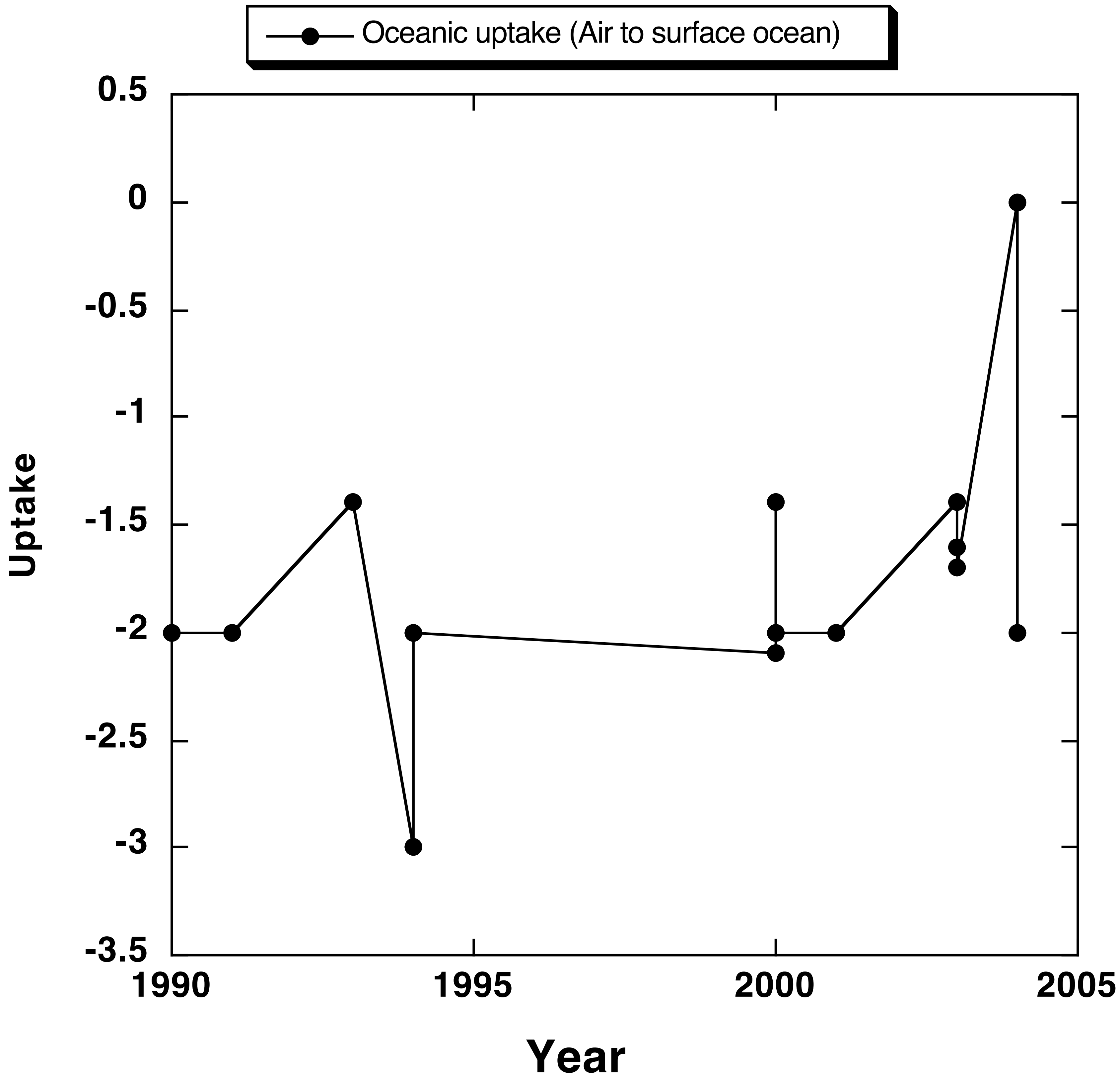
- 5 to 10 Gt C year^{-1}
- 2 to 5 fold greater than CO_2 uptake
- A neglected flux

Dachs et al. (submitted)

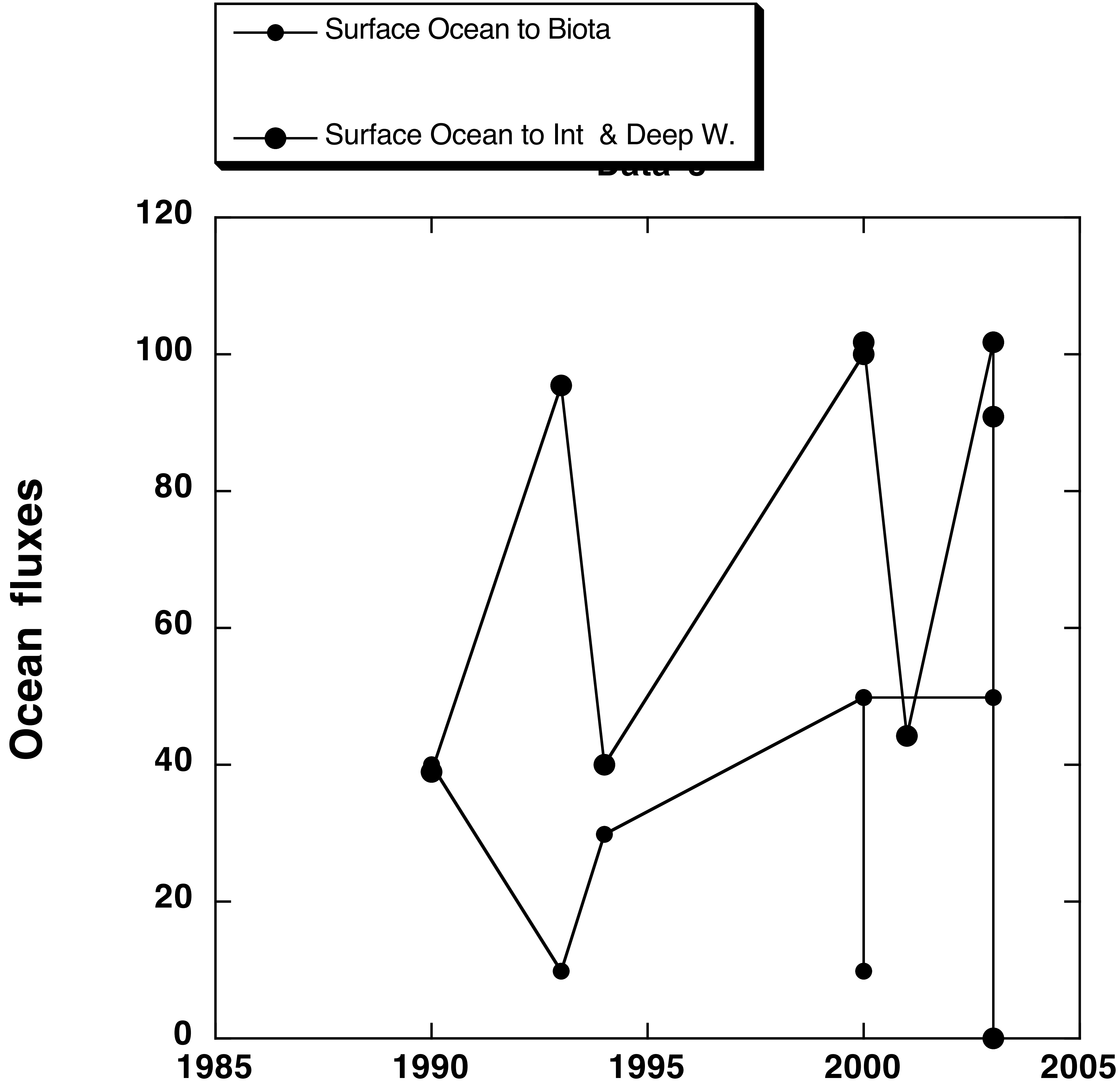
One more detail

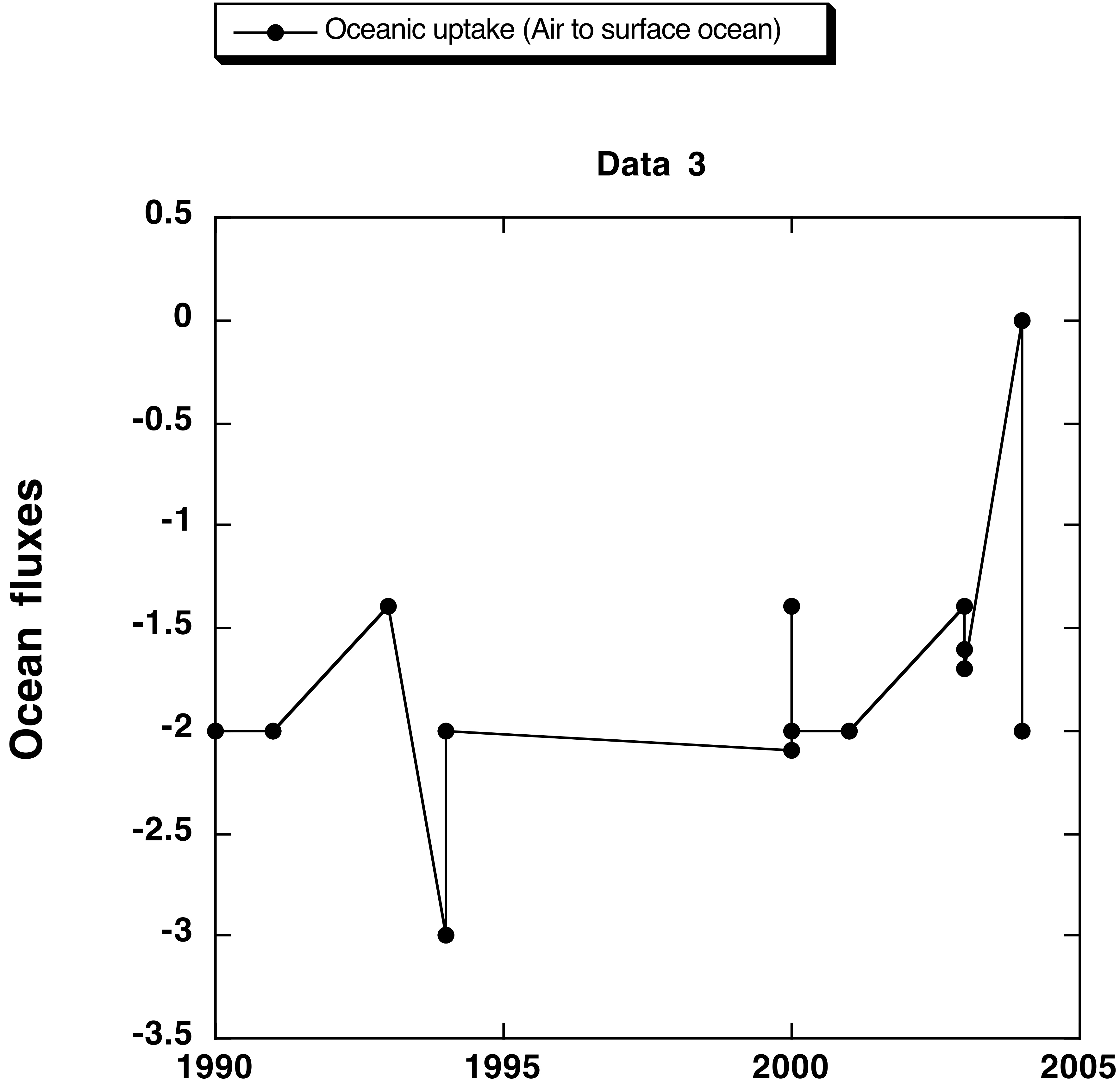
Are the estimates free of error or uncertaintiy?

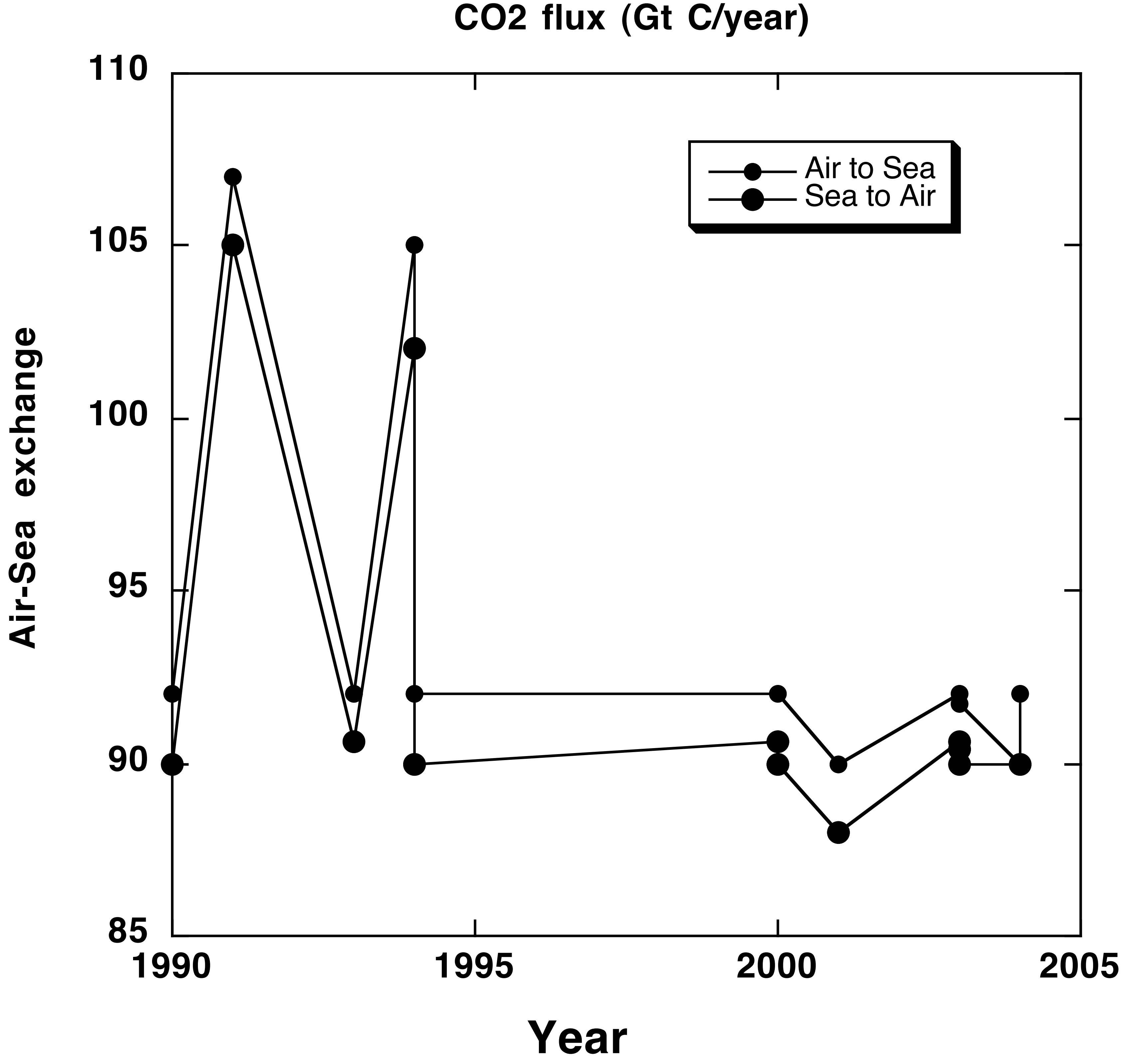

Data 3
8
7
6
5
4
3
2
Emissions
1990
1995
2000
2005
Year
fossil fuels & cement production to Atm



Oceanic uptake (Air to surface ocean)
Uptake
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1990
1995
2000
2005
Year


Surface Ocean to Biota
Surface Ocean to Int & Deep W.
Ocean fluxes
120
100
80
60
40
20
0
1985
1990
1995
2000
2005


Oceanic uptake (Air to surface ocean)
Data 3
Ocean fluxes
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1990
1995
2000
2005


CO2 flux (Gt C/year)
Air-Sea exchange
Year
110
105
100
95
90
85
1990
1995
2000
2005
Air to Sea
Sea to Air