

# Allometric scaling of community metabolism in estuaries and large oceanic provinces



OCB Summer Workshop 2019

**Nick Nidzieko**  
**UC Santa Barbara**

**Willie Haskell**  
**MBARI**

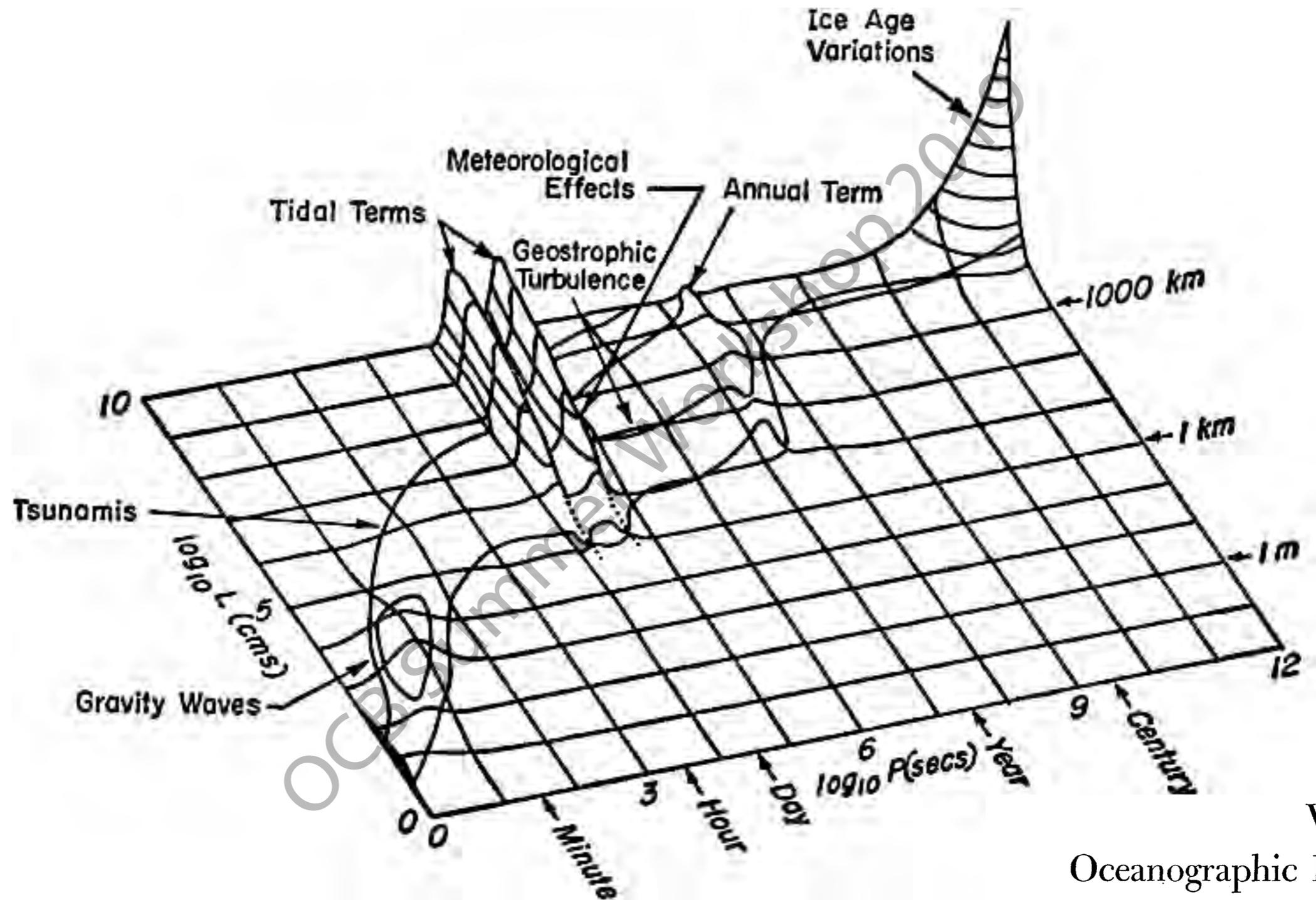
**[ucsbcoastlab.org](http://ucsbcoastlab.org)**

**OCB Summer Workshop June 27, 2019**

Each day as the sun rises and retires  
the beautiful green bays like great creatures  
breathe in and out.

*Odum & Hoskins, 1958*

As oceanographers, we are interested in processes that span many orders of magnitude in space and time

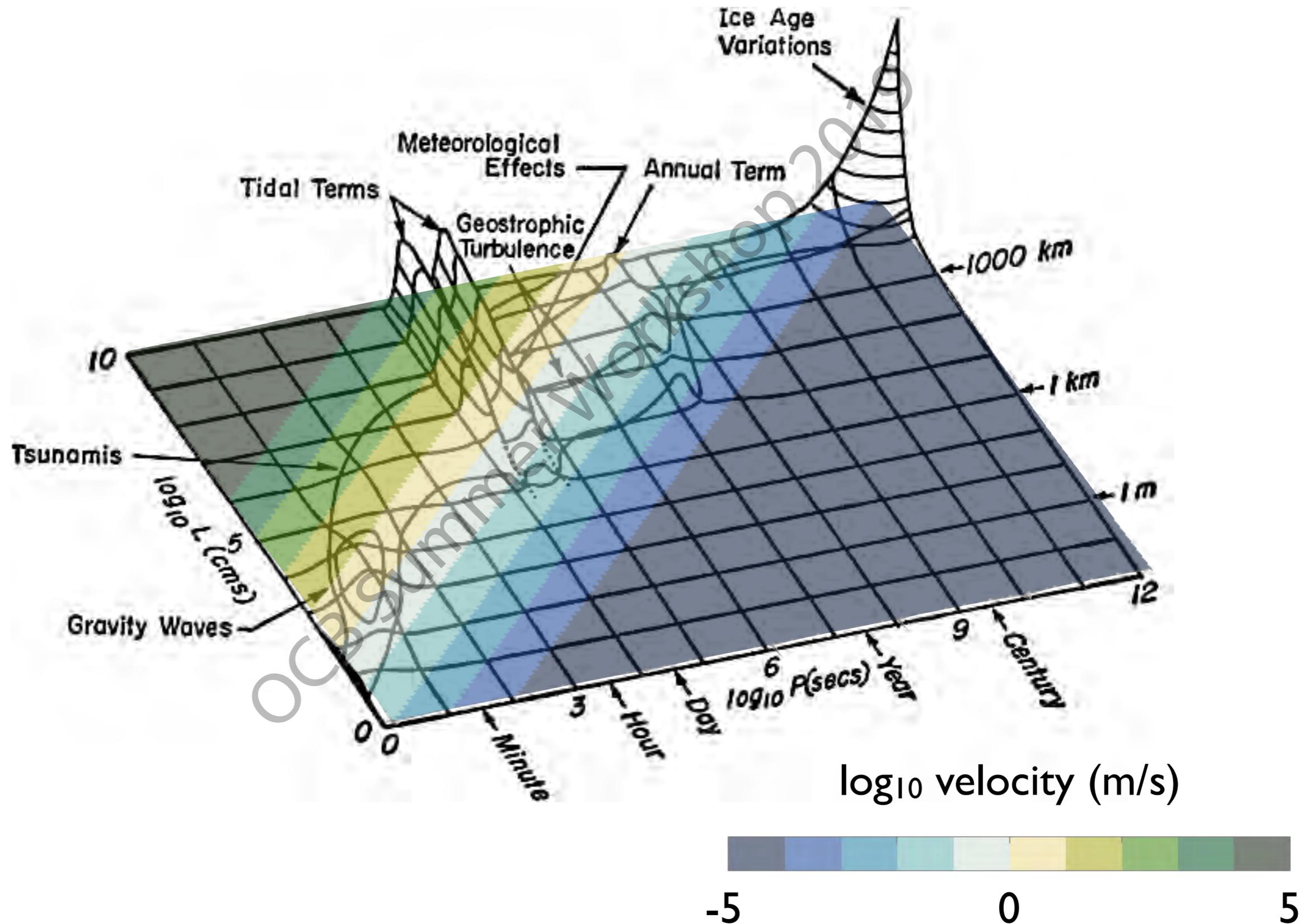


## Varieties of Oceanographic Experience

The ocean can be investigated as a hydrodynamical phenomenon as well as explored geographically.

Henry Stommel

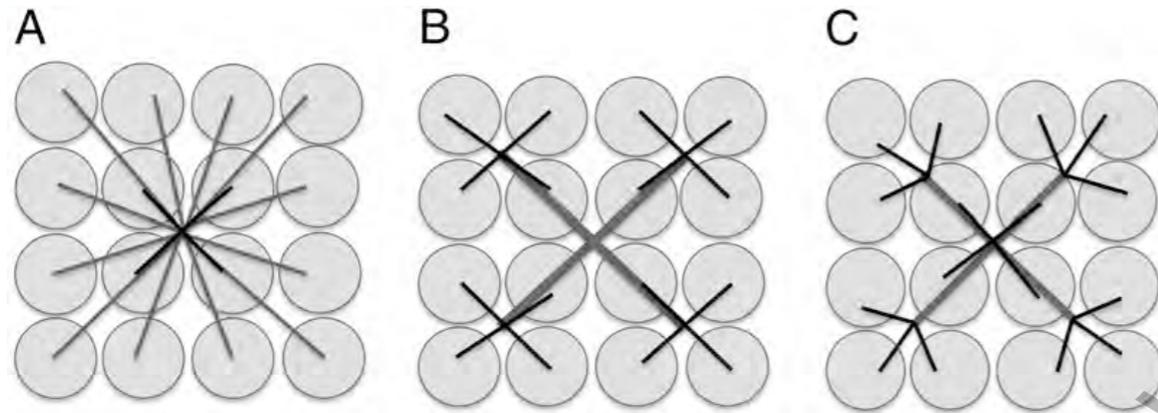
But velocities of interest only span a few orders of magnitude



# How velocity scales with size is a fundamental aspect of organismal biology

## A general basis for quarter-power scaling in animals

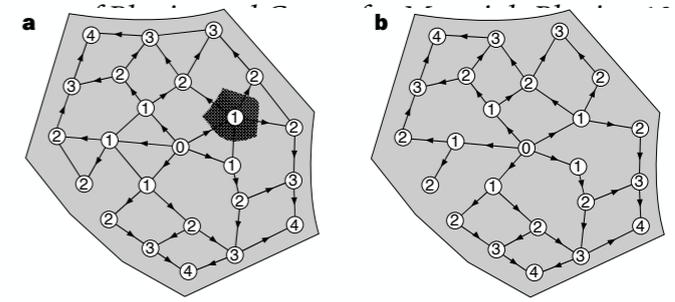
Jayanth R. Banavar<sup>a</sup>, Melanie E. Moses<sup>b,c,1</sup>, James H. Brown<sup>c,d,1</sup>, John Damuth<sup>e</sup>, Andrea Rinaldo<sup>f</sup>, Richard M. Sibly<sup>g</sup>, and Amos Maritan<sup>h</sup>



letters to nature

## Size and form in efficient transportation networks

Jayanth R. Banavar<sup>\*</sup>, Amos Maritan<sup>†</sup> & Andrea Rinaldo<sup>‡</sup>



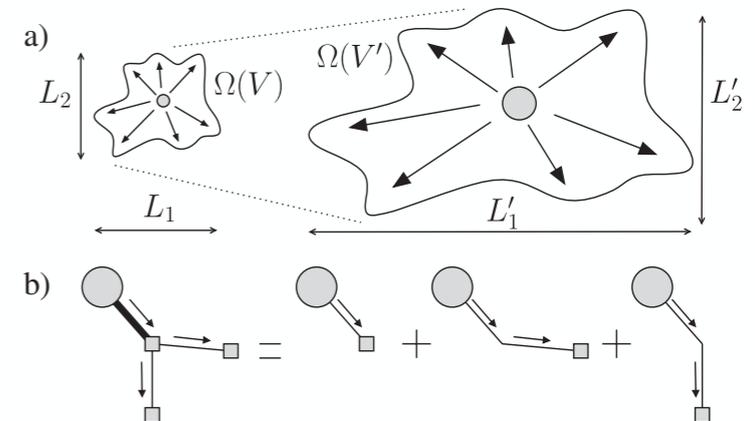
PRL 104, 048702 (2010)

PHYSICAL REVIEW LETTERS

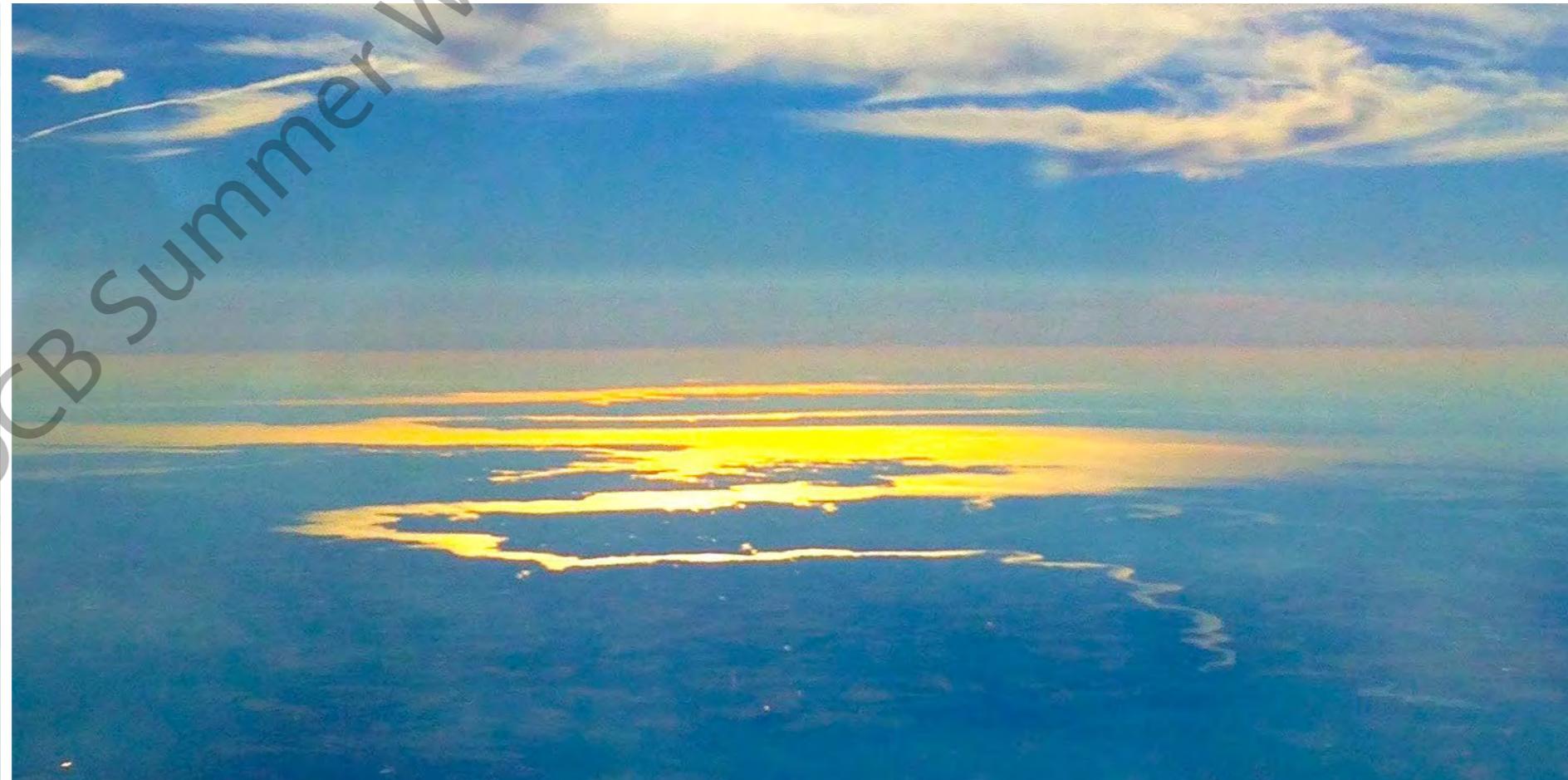
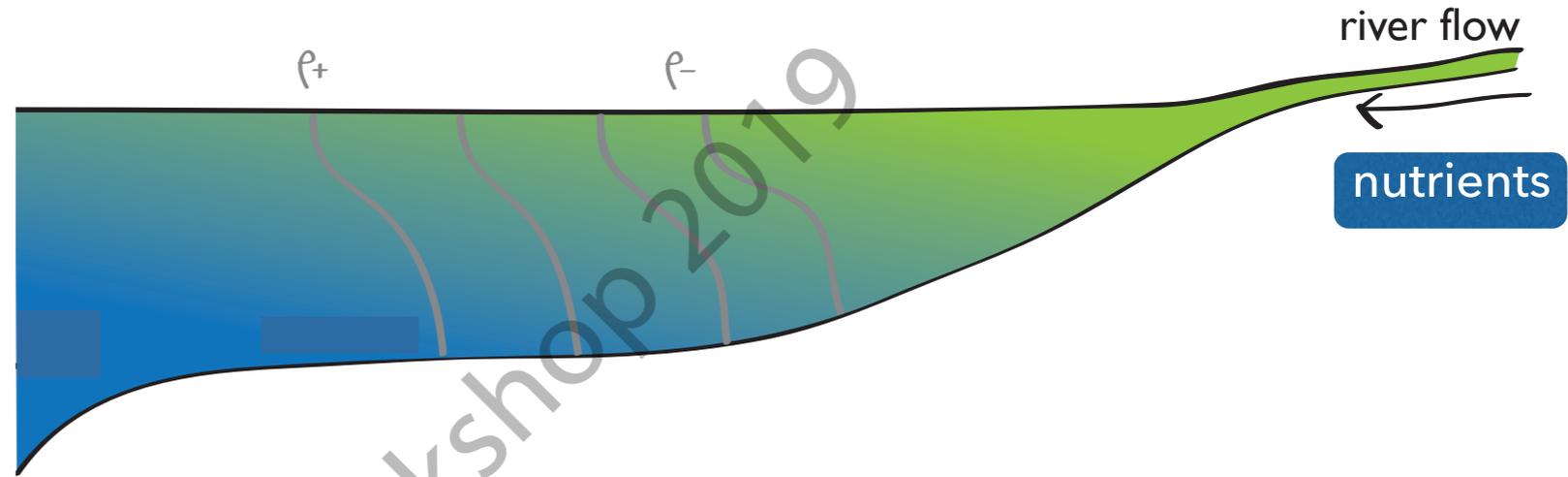
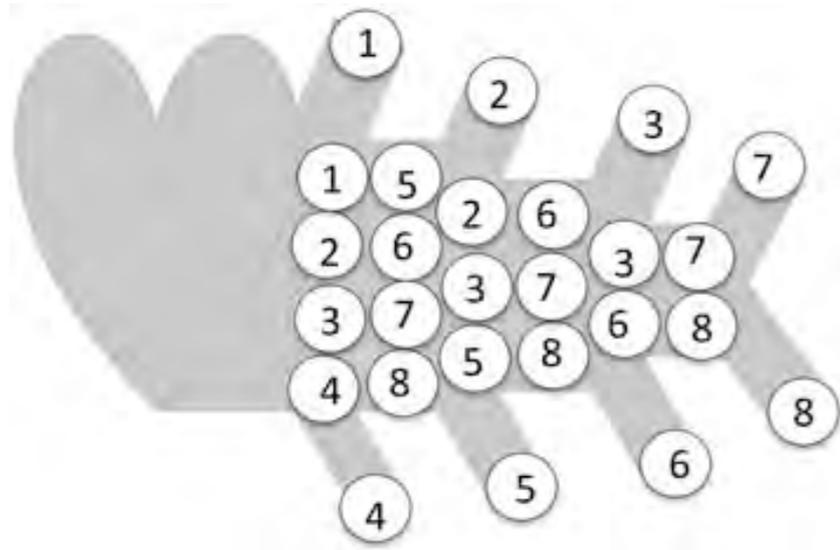
week ending  
29 JANUARY 2010

## Optimal Form of Branching Supply and Collection Networks

Peter Sheridan Dodds<sup>\*</sup>



# In this talk, we'll apply ideas from the metabolic theory of ecology to marine ecosystems



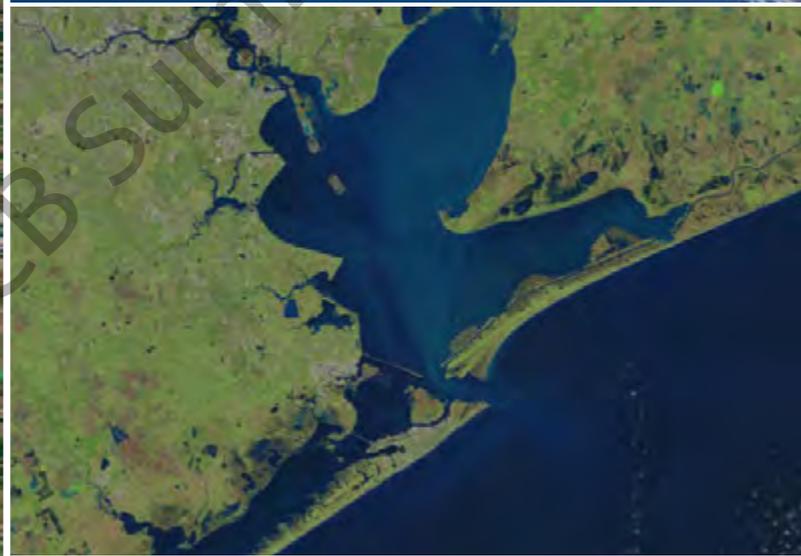
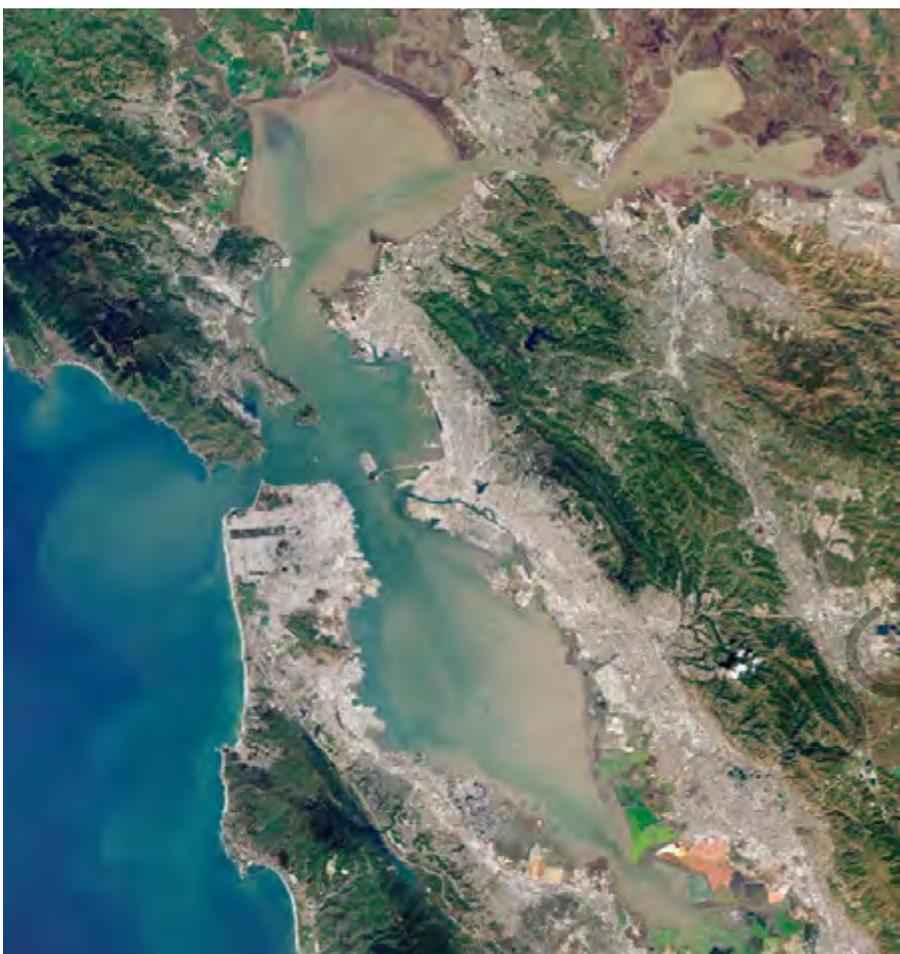
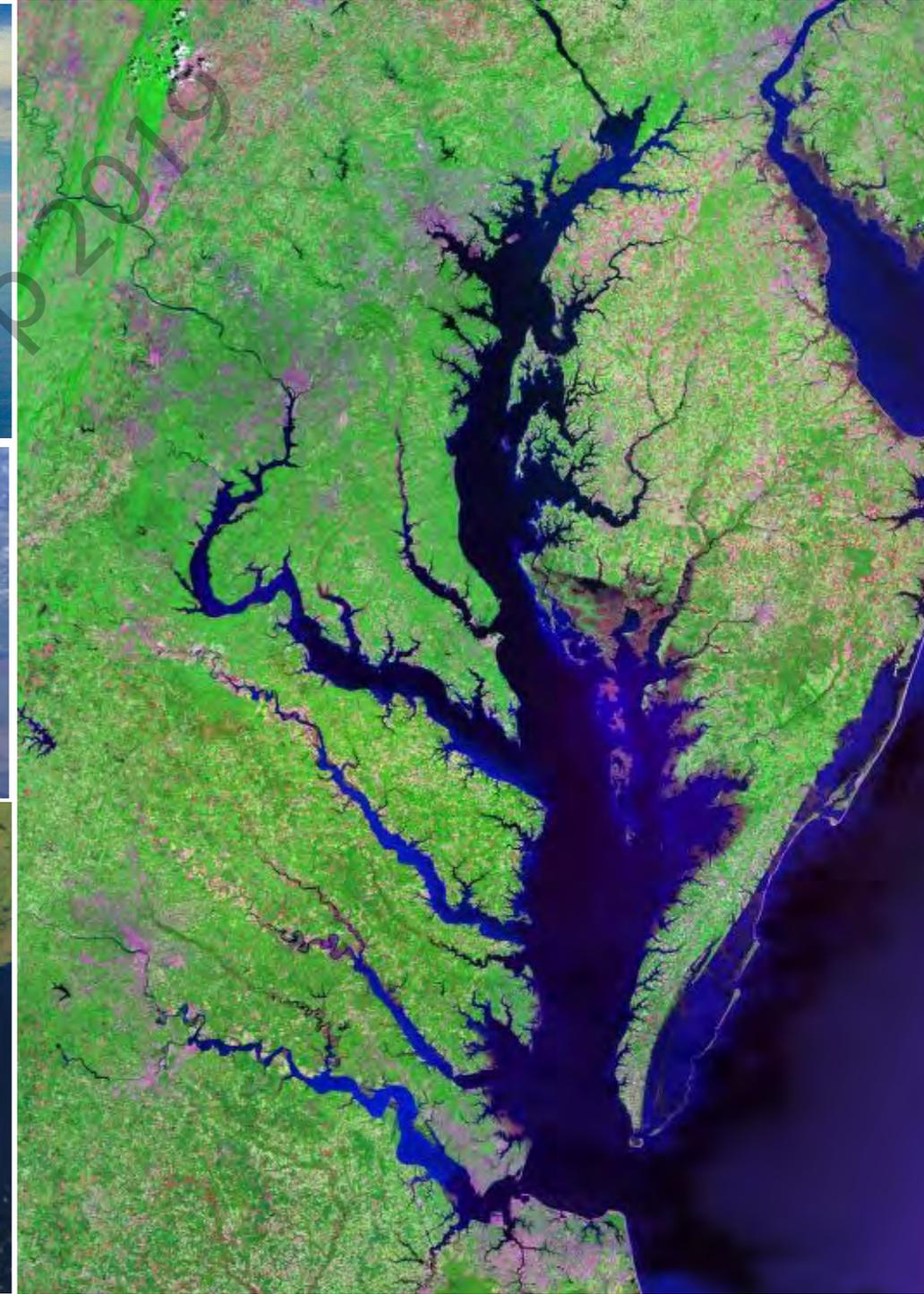
# Basic Idea

Use biology to measure physical processes

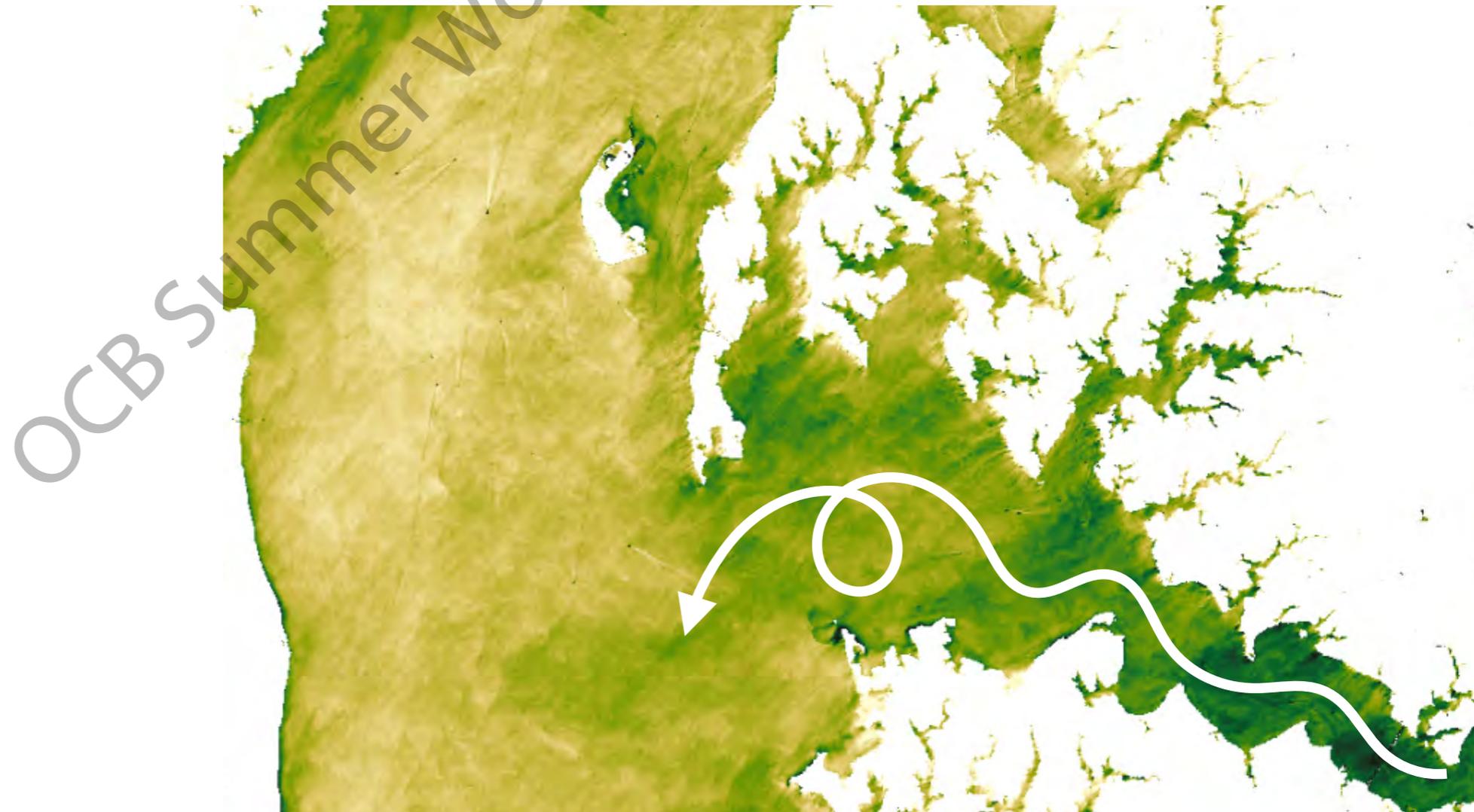
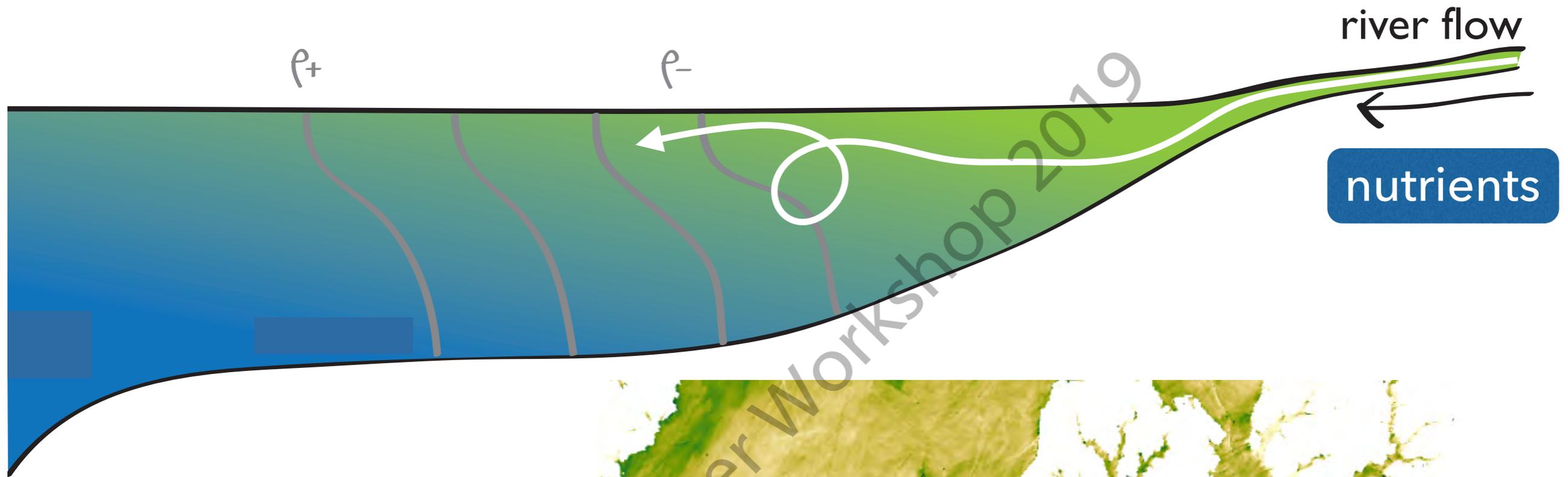


# Goal/motivation

To understand mixing across seemingly diverse systems

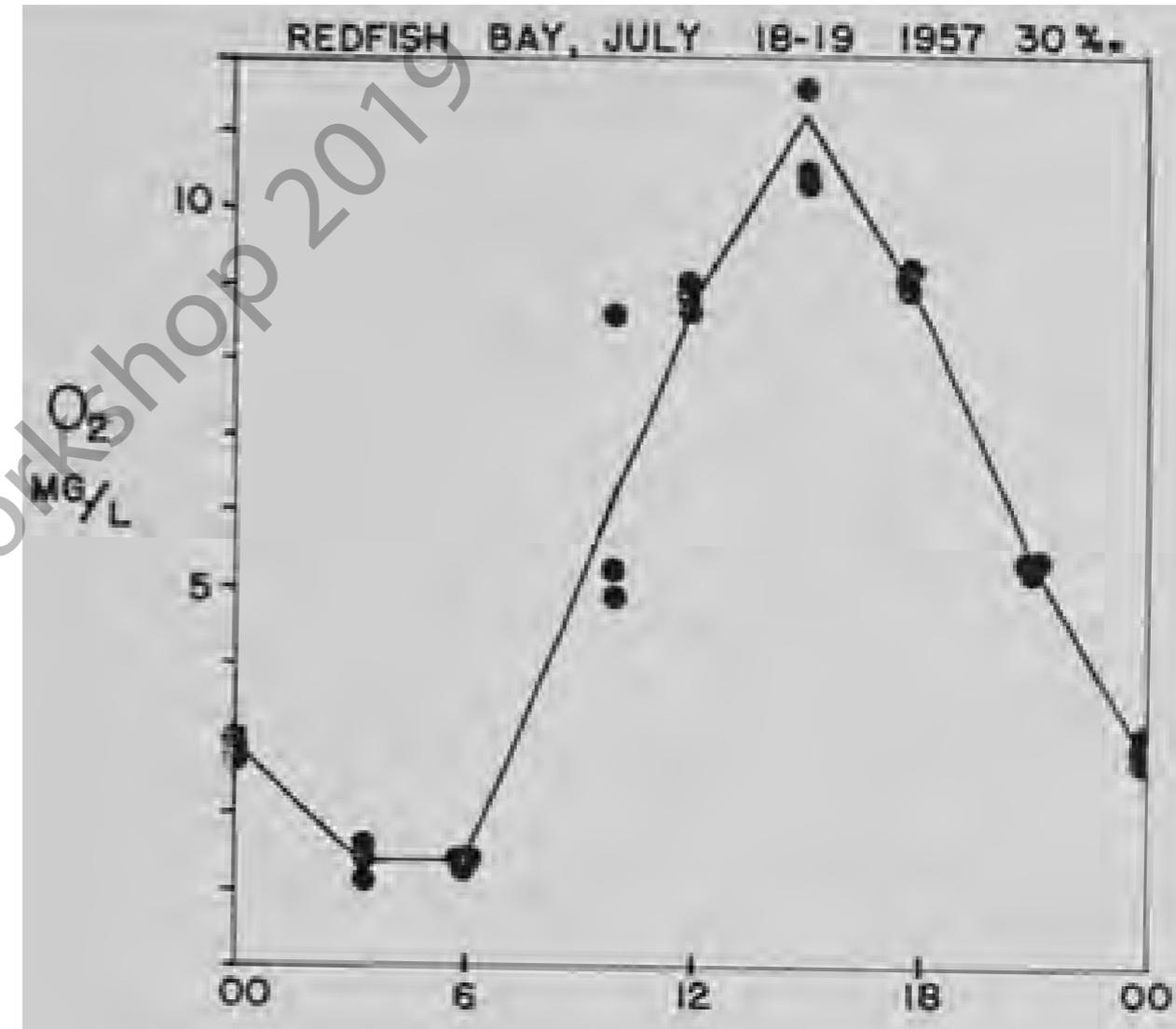
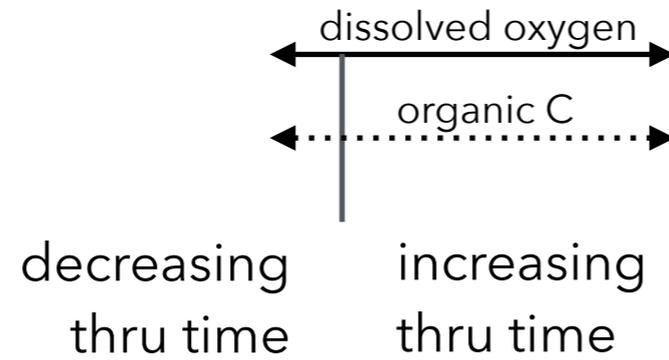


**Rationale** Primary producers reflect the integrated result of nutrient mixing & transport



# Approach Measure ecosystem metabolism – the sum of metabolic processes of resident organisms

Measurements



Comparative Studies on the Metabolism of Marine Waters<sup>1</sup>

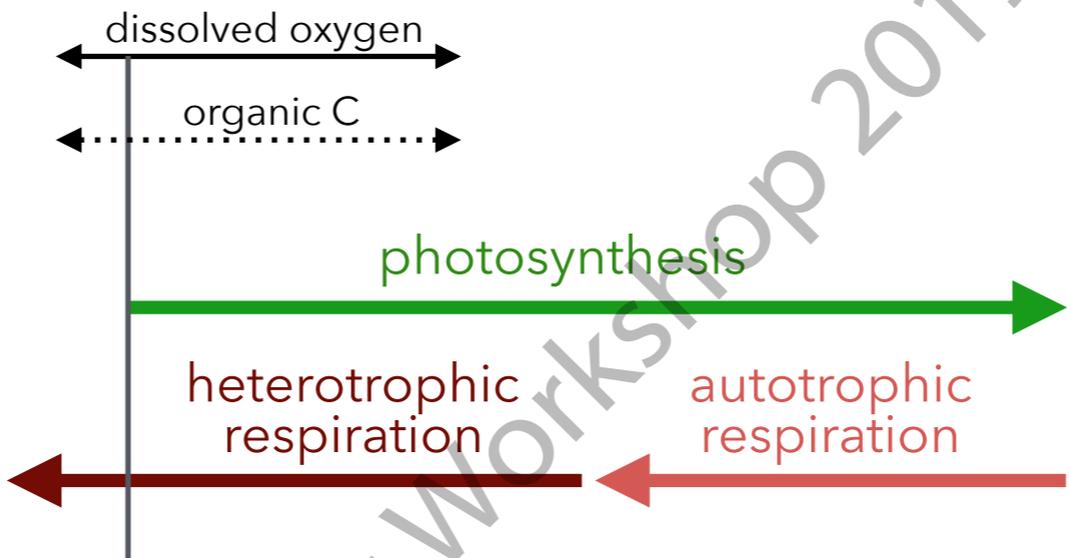
HOWARD T. ODUM AND CHARLES M. HOSKIN

*Institute of Marine Science  
The University of Texas  
Port Aransas, Texas*

# Approach Measure ecosystem metabolism – the sum of metabolic processes of resident organisms

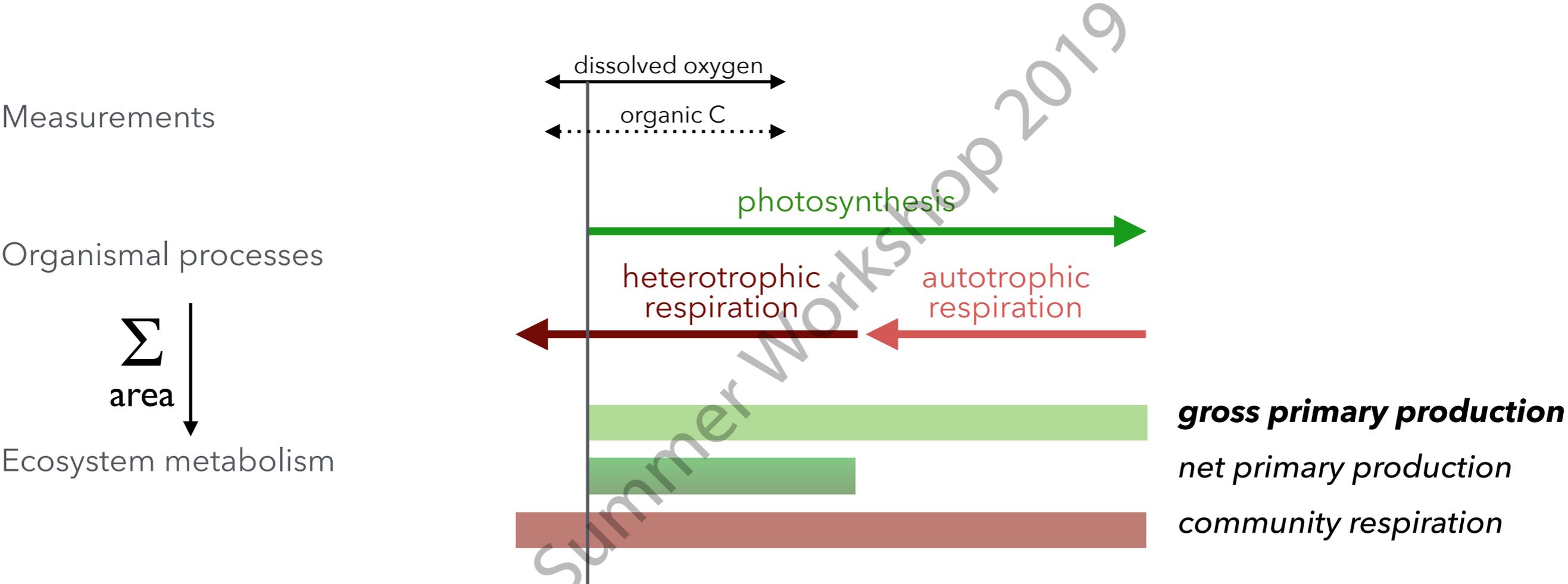
Measurements

Organismal processes

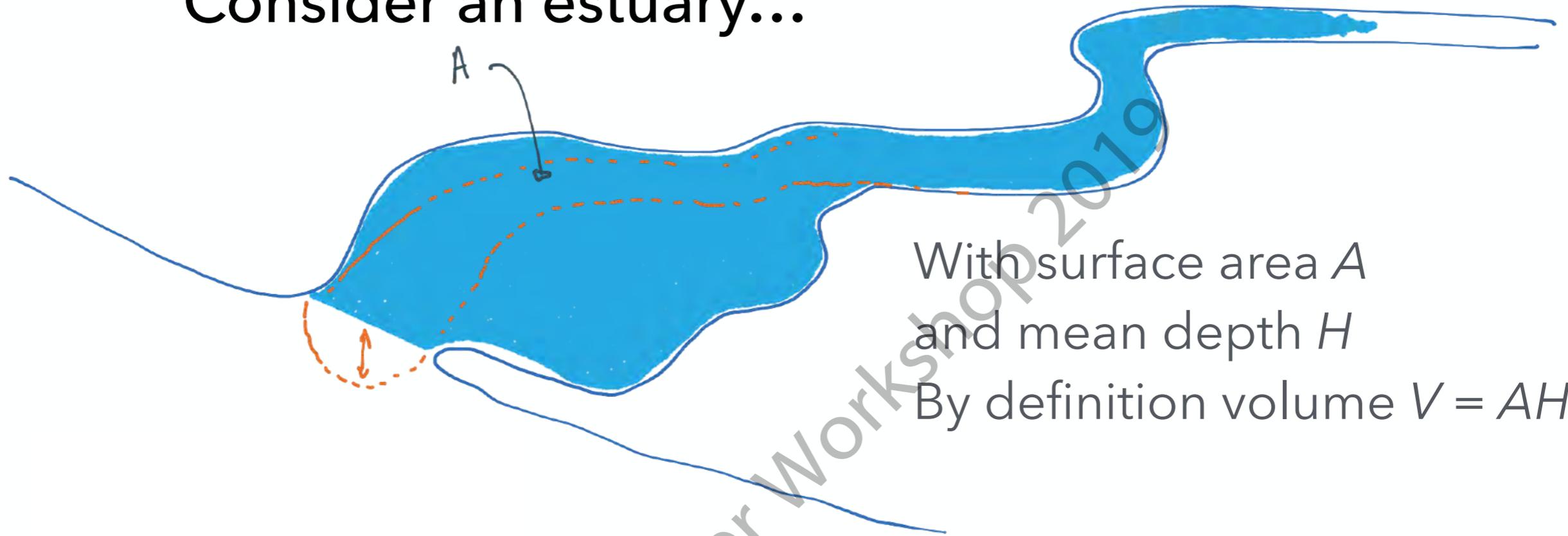


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# Approach Measure ecosystem metabolism – the sum of metabolic processes of resident organisms



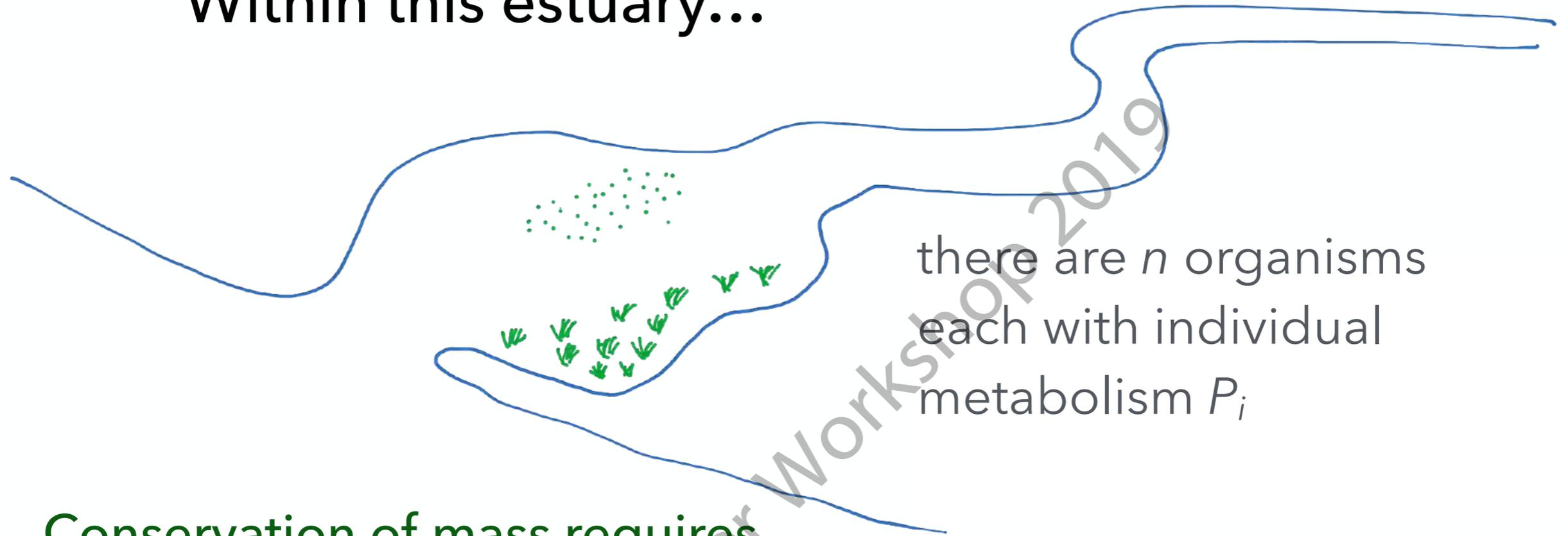
Consider an estuary...



With surface area  $A$   
and mean depth  $H$

By definition volume  $V = AH$

Within this estuary...



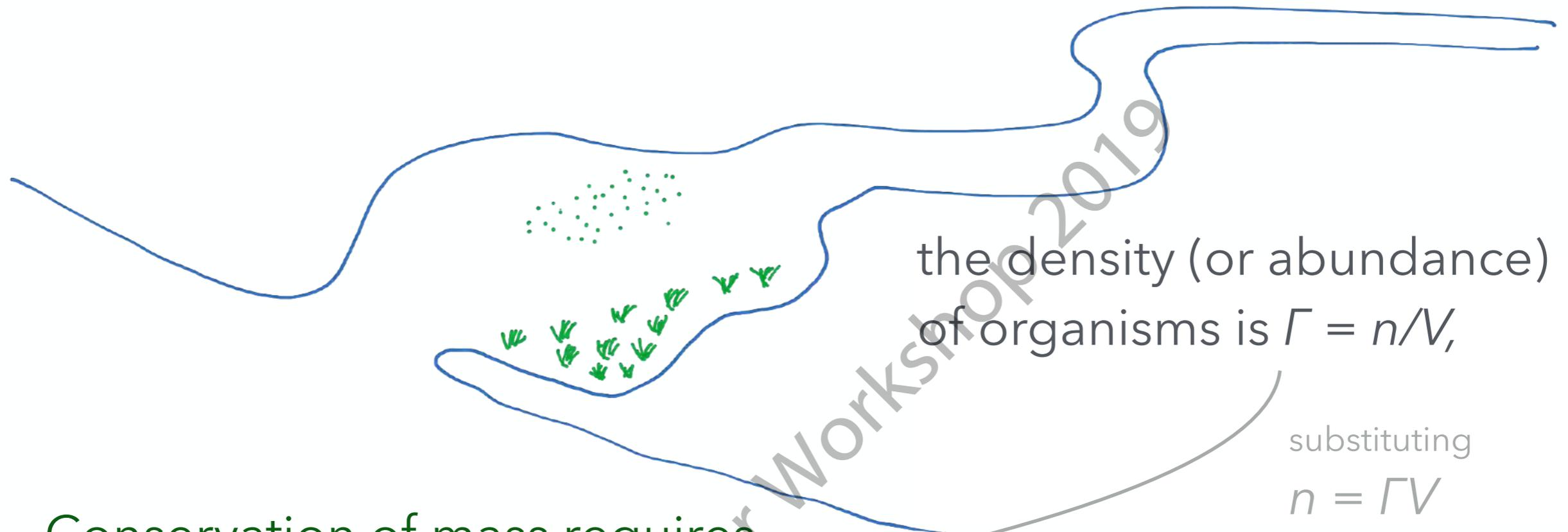
there are  $n$  organisms  
each with individual  
metabolism  $P_i$

Conservation of mass requires

$$P = \sum_n P_i = n \langle P_i \rangle$$

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Total productivity is the specific productivity times size



the density (or abundance)  
of organisms is  $\Gamma = n/V$ ,

substituting  
 $n = \Gamma V$

Conservation of mass requires

$$P = \sum_n P_i = n \langle P_i \rangle$$

and defining  
 $E = \Gamma \langle P_i \rangle$   
specific metabolism

**Total Productivity:  $P = EV$**

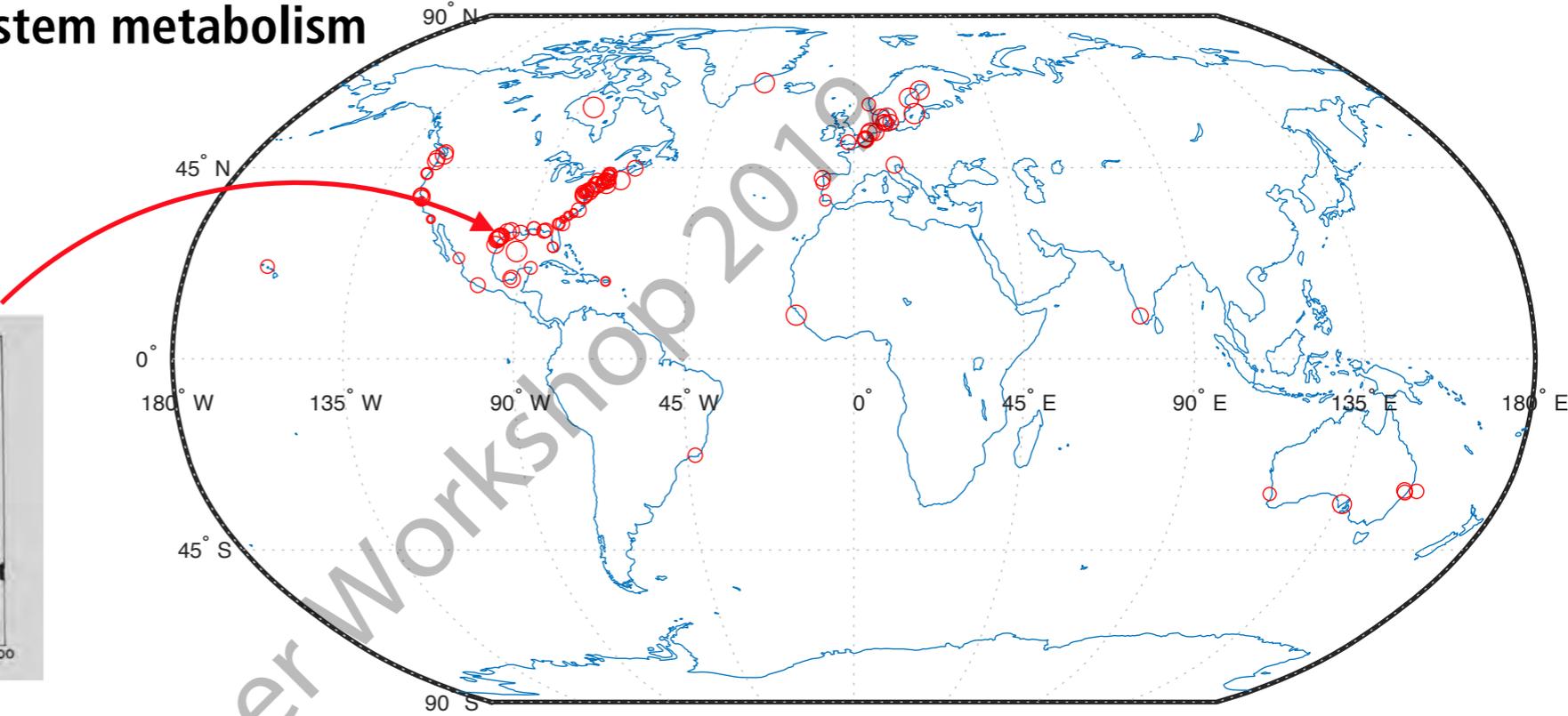
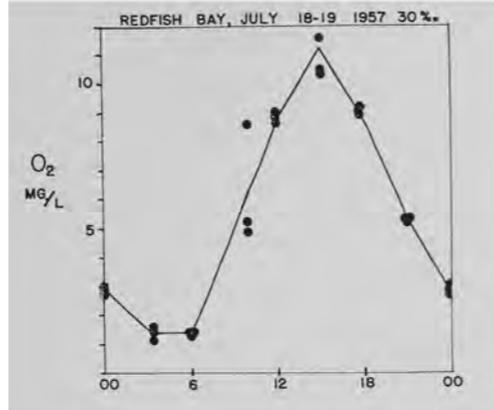
# To investigate metabolism/size scaling, we compiled 134 published estimates of ecosystem metabolism

## Allometric scaling of estuarine ecosystem metabolism

Nicholas J. Nidzieski<sup>a,1</sup>

<sup>a</sup>Department of Geography, University of California, Santa Barbara, CA 93106

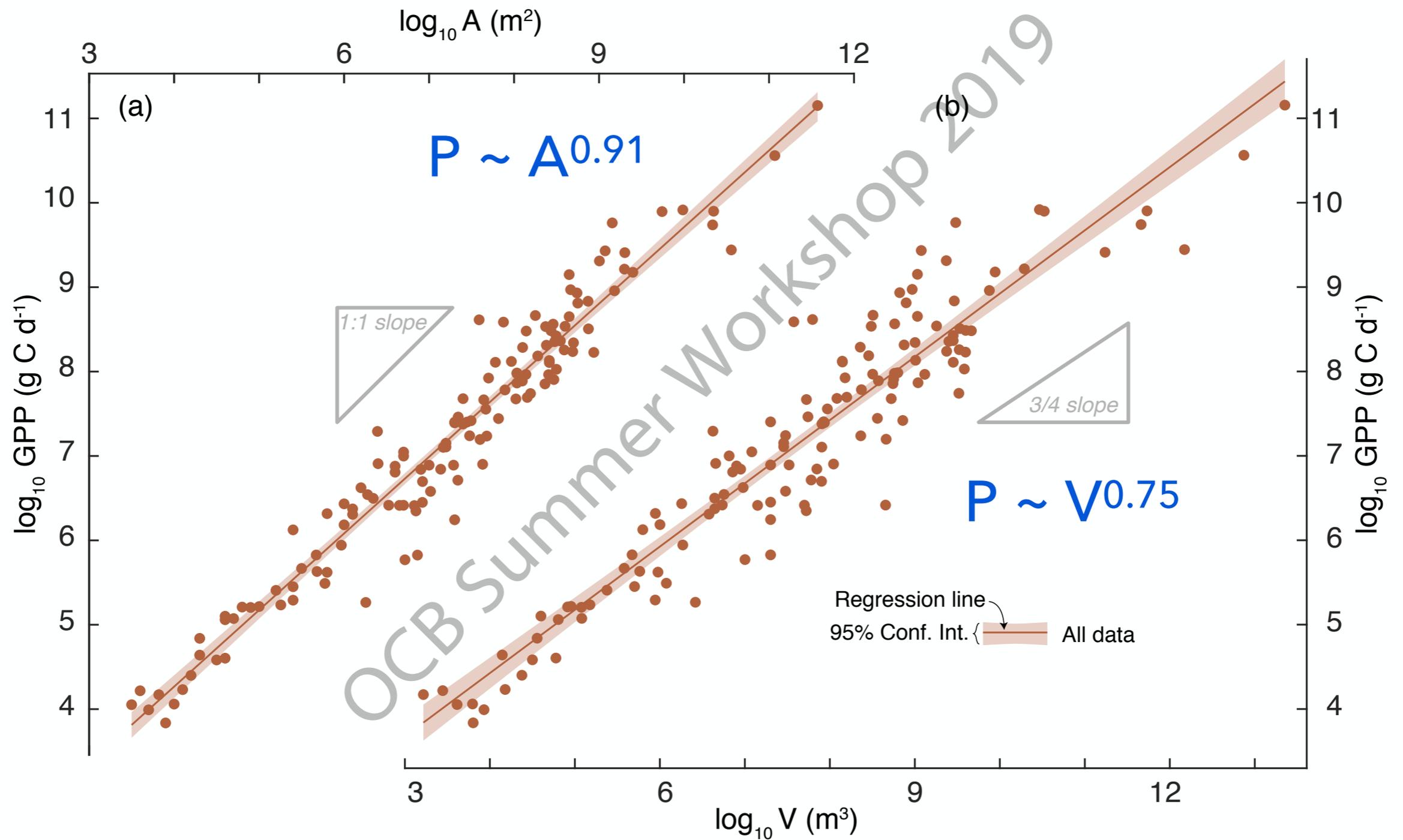
PNAS | June 26, 2018 | vol. 115 | no. 26 | 6733–6738



H A V P

Location	Geometry					Gross Primary Production			
	Lat. °N	Lon. °E	Depth m	Area log <sub>10</sub> m <sup>2</sup>	Volume log <sub>10</sub> m <sup>3</sup>	Benthic	Pelagic g C m <sup>-2</sup> d <sup>-1</sup>	Specific	Total log <sub>10</sub> g C d <sup>-1</sup>
Århus Bugt	56.093	10.191	12 c	8.50 [1]	9.58 [1]			0.34 [2]	8.03 c
Aabenraa Fjord	55.024	9.504	23 [3]	7.49 [4]	8.86 c			0.84 [2]	7.42 c
ACE Basin (Big Bay Creek)	32.494	-80.324	1.3 [5]	3.50 [5]	3.61 c			3.57 [5]	4.05 c
ACE Basin (St. Pierre)	32.523	-80.357	1.8 [5]	4.30 [5]	4.56 c			3.46 [5]	4.84 c
Alewite Cove	41.312	-72.100	0.8 [6]	5.26 [6]	5.18 c	0.51 [7]	0.44 [7]	0.95 [7]	5.23 c
Apalachicola Bay (Bottom)	29.786	-84.875	1.8 [5]	7.20 [5]	7.46 c			0.89 [5]	7.15 c
Apalachicola Bay (Surface)	29.786	-84.875	1.8 [5]	7.20 [5]	7.46 c			0.81 [5]	7.11 c
Augustenborg Fjord	54.945	9.831	5.1 c	7.14 [1]	7.85 [1]			0.51 [2]	6.84 c
Baltic Sea	58.000	20.000	60 [8]	11.57 [8, 9]	13.35 c	0.01 [7]	0.44 [7]	0.38 [8, 9]	11.15 c
Bissel Cove	41.548	-71.432	0.2 [6]	3.82 [6]	3.22 c	2.09 [7]	0.15 [7]	2.25 [7]	4.17 c
Bojorquez Lagoon	21.126	-86.758	1.7 [10]	6.39 [10]	6.62 c			7.91 [10, 11]	7.29 c
Boston Harbor	42.338	-70.985	5.8 [12]	8.03 [12]	8.80 c			0.89 [13, 14]	7.98 c
Bothnian Bay	64.000	23.000	41 [15]	10.56 [15]	12.17 c	0.01 [7]	0.07 [7]	0.08 [7]	9.44 c
Bothnian Sea	63.000	19.000	63 [15]	11.07 [15]	12.87 c	0.01 [7]	0.20 [7]	0.21 [7]	10.56 c

# Result Ecosystem metabolism scales nonlinearly with ecosystem size

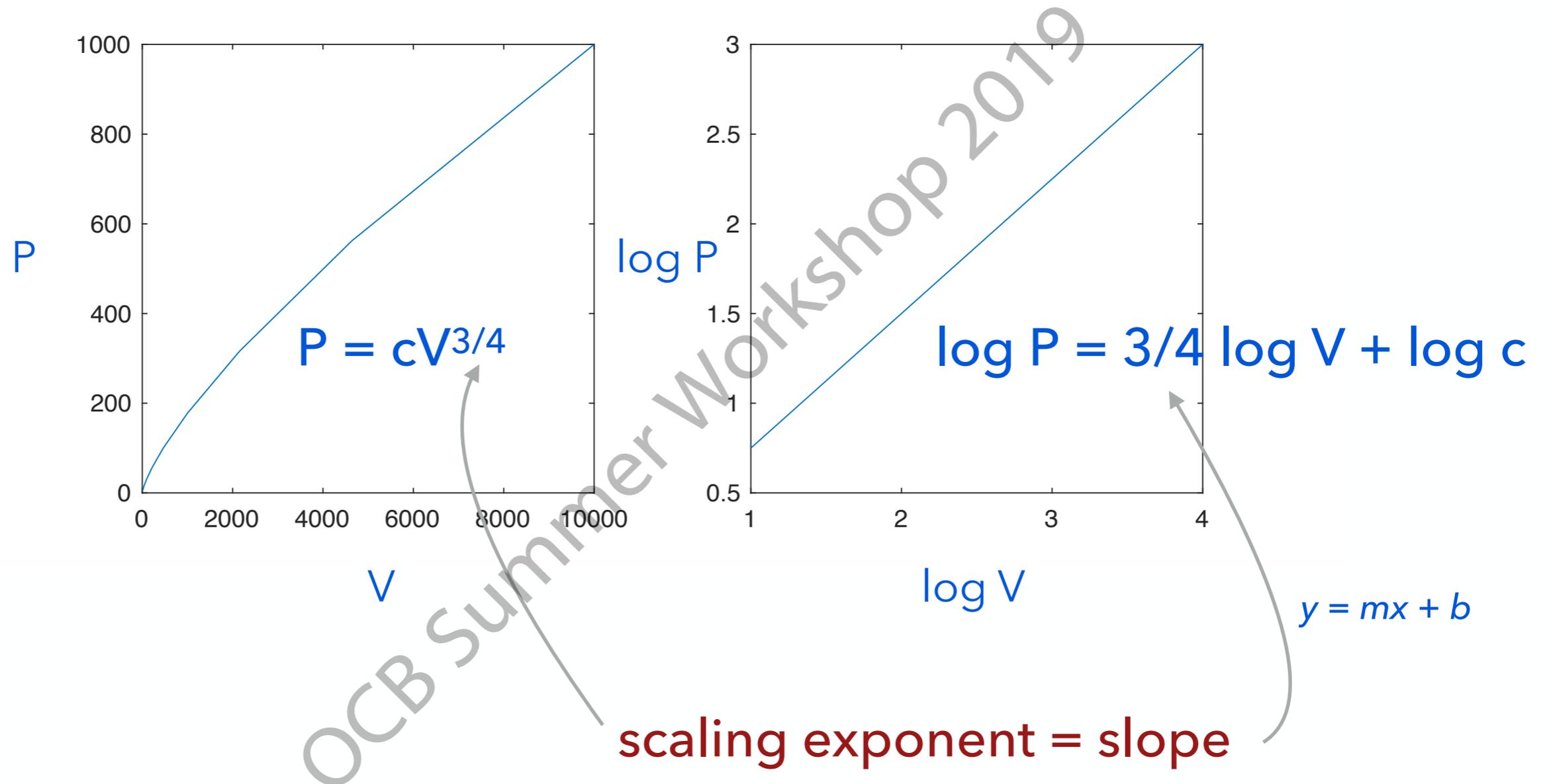


## Allometric scaling of estuarine ecosystem metabolism

Nicholas J. Nidziko<sup>1</sup>

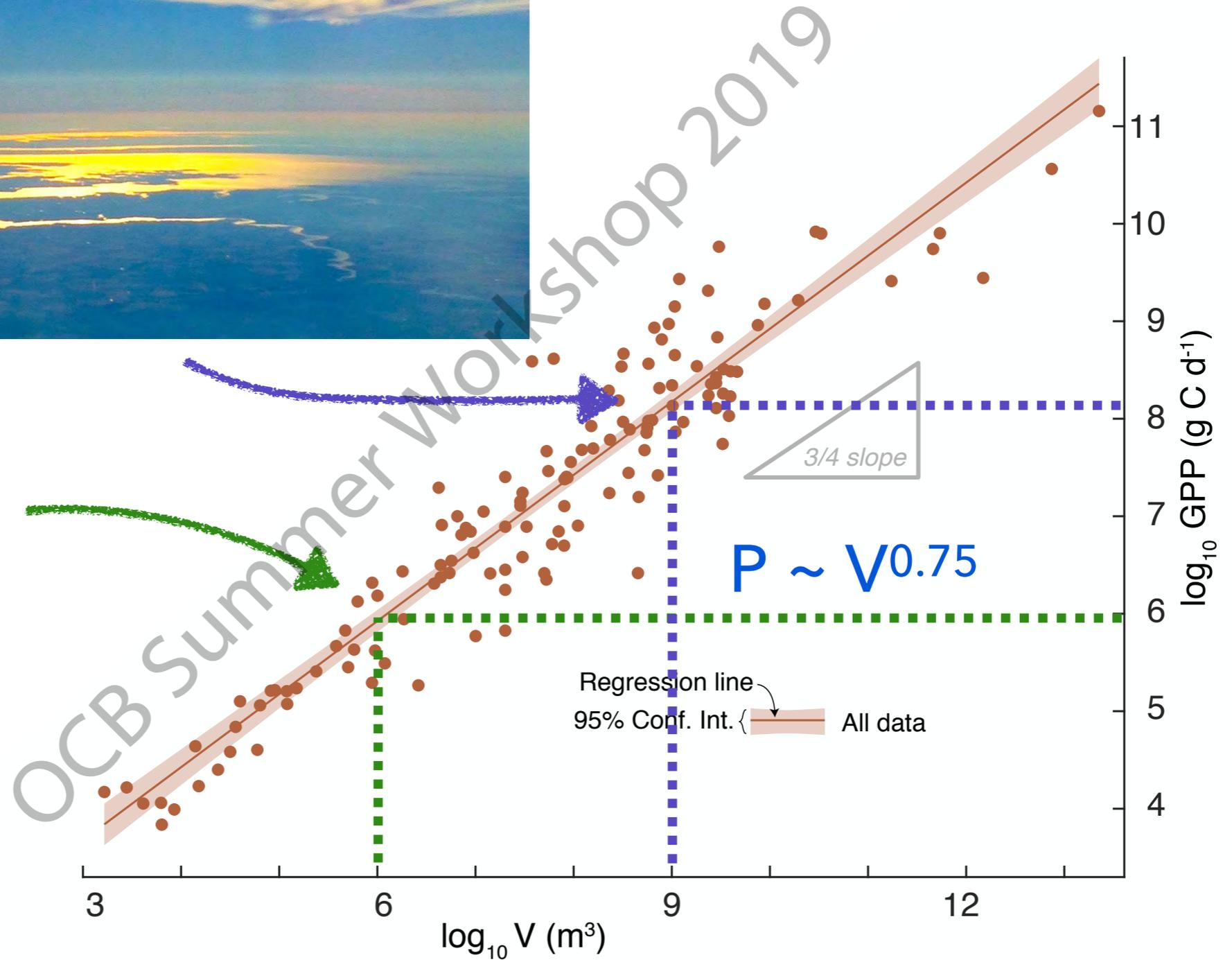
<sup>1</sup>Department of Geography, University of California, Santa Barbara, CA 93106

Recall from log laws that a slope not equal to 1 in log space indicates a nonlinear (allometric) relationship



*Here, we might say "P scales with V to the 3/4<sup>ths</sup>"*

# Result An estuary that is 1000 times bigger is not necessarily 1000 times as productive



## Allometric scaling of estuarine ecosystem metabolism

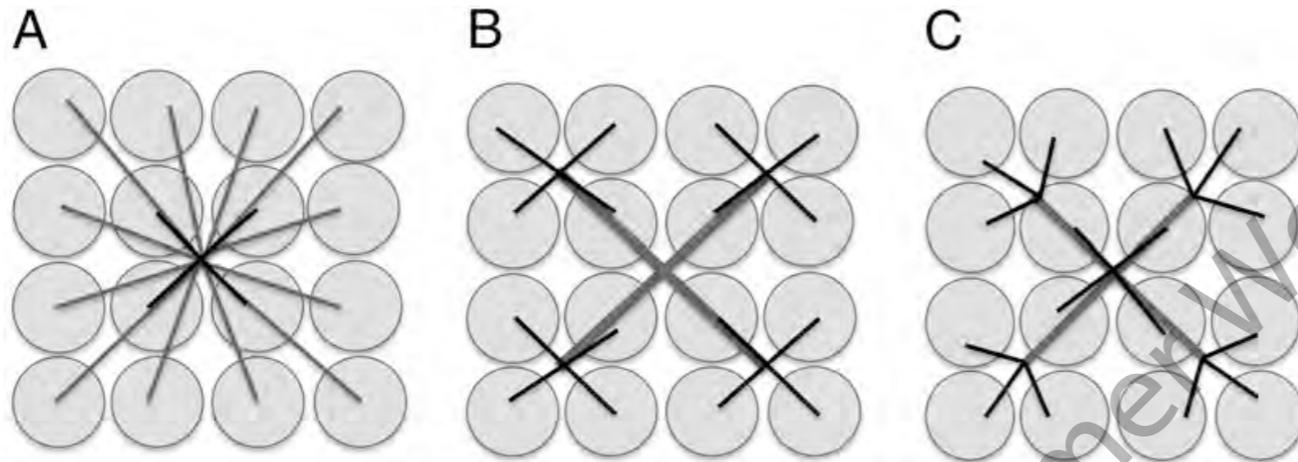
Nicholas J. Nidziko<sup>1</sup>

<sup>1</sup>Department of Geography, University of California, Santa Barbara, CA 93106

# Quarter-power scaling is explained by theoretical arguments for organismal metabolism

## A general basis for quarter-power scaling in animals

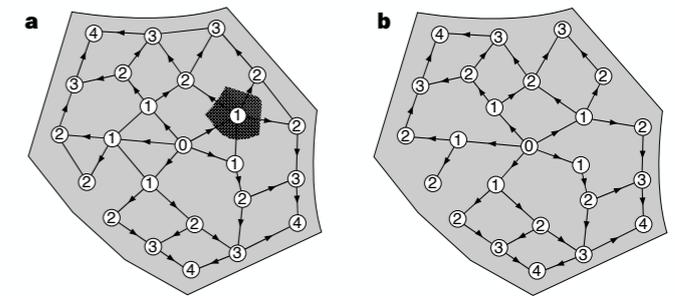
Jayanth R. Banavar<sup>a</sup>, Melanie E. Moses<sup>b,c,1</sup>, James H. Brown<sup>c,d,1</sup>, John Damuth<sup>e</sup>, Andrea Rinaldo<sup>f</sup>, Richard M. Sibly<sup>g</sup>, and Amos Maritan<sup>h</sup>



letters to nature

## Size and form in efficient transportation networks

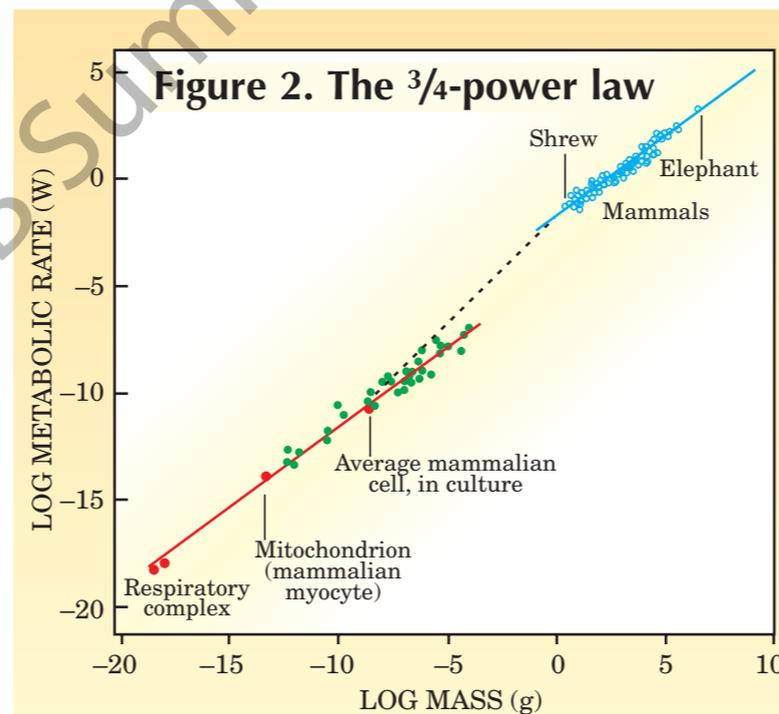
Jayanth R. Banavar<sup>\*</sup>, Amos Maritan<sup>†</sup> & Andrea Rinaldo<sup>‡</sup>



## Life's Universal Scaling Laws

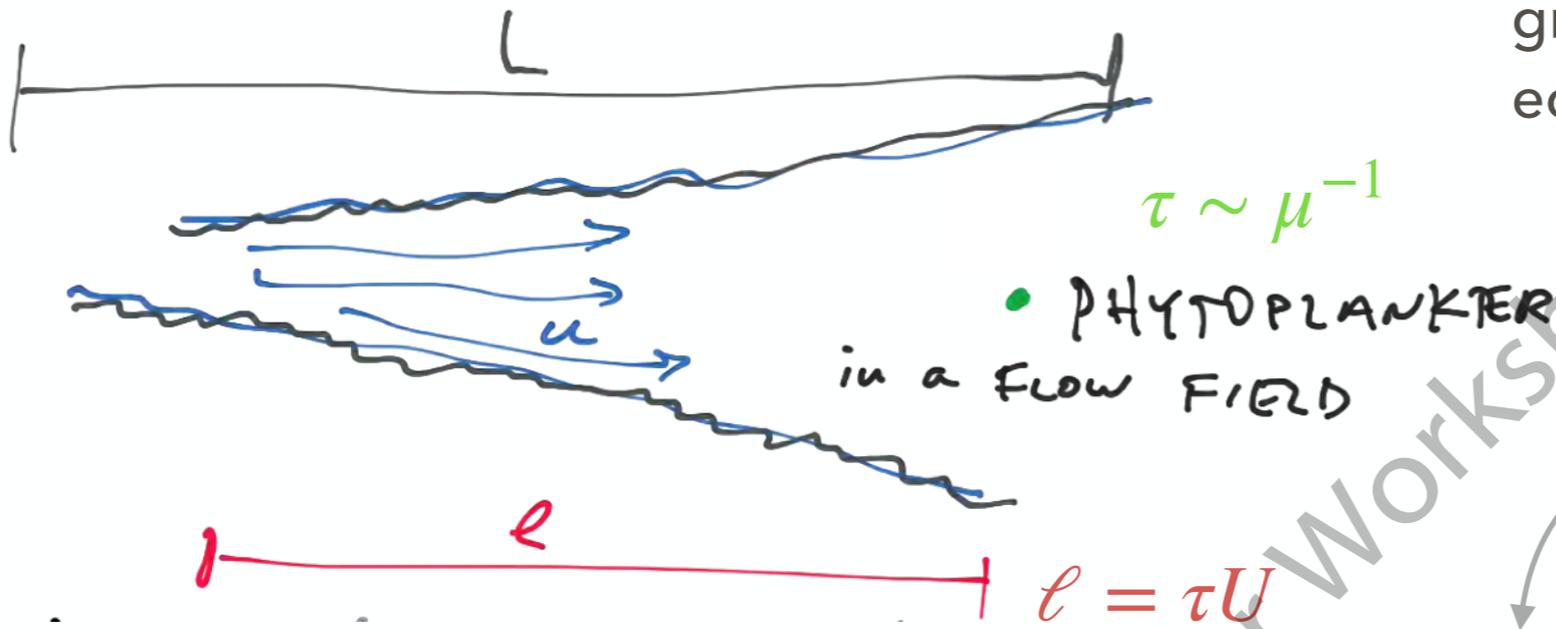
Geoffrey B. West and James H. Brown

September 2004 Physics Today



# One insight from MTE theory: Ecosystem metabolism scales as a ratio of biological to physical rates

$\ell$  is a length scale proportional to the growth rate  $\mu$  and independent of ecosystem size



$$E \ell^D \sim V^0$$

equivalently

$$E \sim \ell^{-D}$$

$$P = EV$$

$$P \sim \left(\frac{L}{\ell}\right)^D \sim \left(\frac{L\mu}{U}\right)^D \sim \left(\frac{T_R}{\tau}\right)^D$$

where

$$T_R = L/U$$

D is the dimensionality of the system

## A general basis for quarter-power scaling in animals

Jayanth R. Banavar<sup>a</sup>, Melanie E. Moses<sup>b,c,1</sup>, James H. Brown<sup>c,d,1</sup>, John Damuth<sup>e</sup>, Andrea Rinaldo<sup>f</sup>, Richard M. Sibly<sup>g</sup>, and Amos Maritan<sup>h</sup>

<sup>a</sup>Department of Physics, Pennsylvania State University, University Park, PA 16802; <sup>b</sup>Department of Computer Science, University of New Mexico, Albuquerque, NM 87131; <sup>c</sup>Department of Biology, University of New Mexico, Albuquerque, NM 87131; <sup>d</sup>Santa Fe Institute, Santa Fe, NM 87501; <sup>e</sup>Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106; <sup>f</sup>Laboratory of Ecohydrology, Ecole Polytechnique Fédérale de Lausanne, CH-1015 Lausanne, Switzerland; <sup>g</sup>School of Biological Sciences, University of Reading, Whiteknights, Reading RG6 6AS, United Kingdom; and <sup>h</sup>Dipartimento di Fisica, Università di Padova, Istituto Nazionale di Fisica Nucleare, sez. Padova, I-35131 Padua, Italy

Contributed by James H. Brown, July 9, 2010 (sent for review June 7, 2010)

# Another insight: transport time scales differently for deep and shallow systems

Q is the size of the transport network (i.e., the estuary)

Equating

$$P \sim Q^{D/D+1} \quad (\text{network scaling})$$

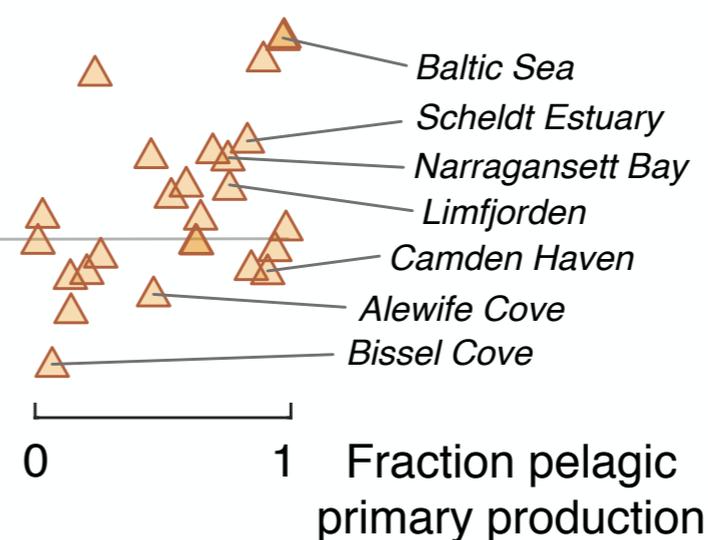
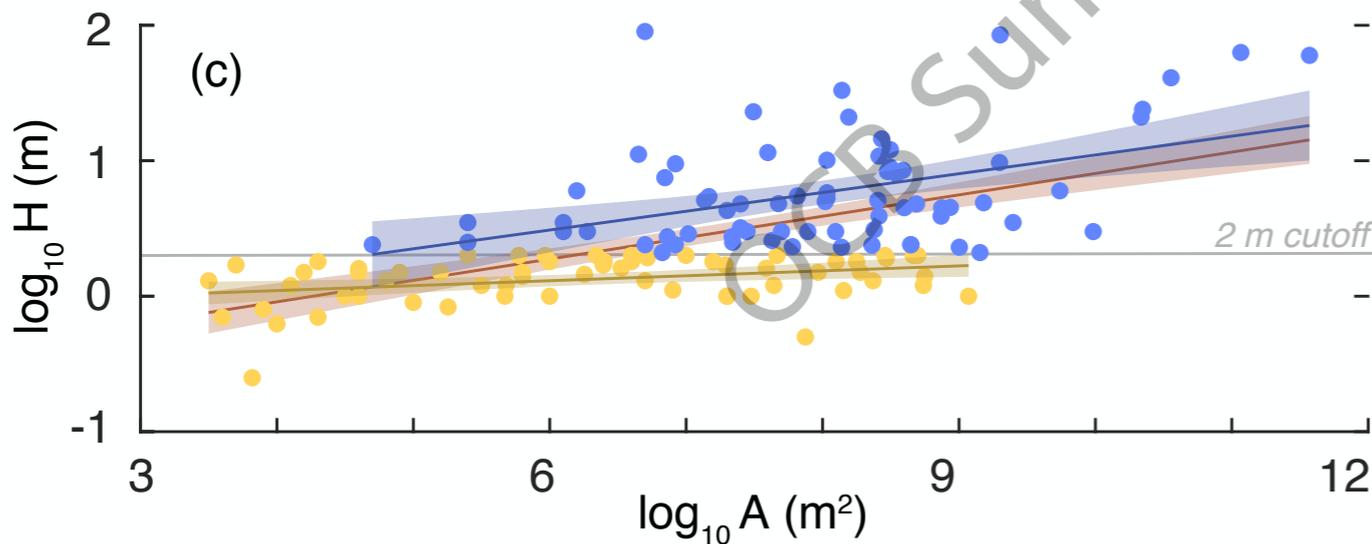
$$P \sim \left(\frac{T_R}{\tau}\right)^D \quad (\text{transport/growth})$$

Transport time:  $T_R \sim Q^{1/(D+1)}$

Noting that  $Q \sim V \sim L^3$

shallow  $T_R \sim L$   $U \sim L^0$

deep  $T_R \sim L^{3/4}$   $U \sim L^{1/12}$

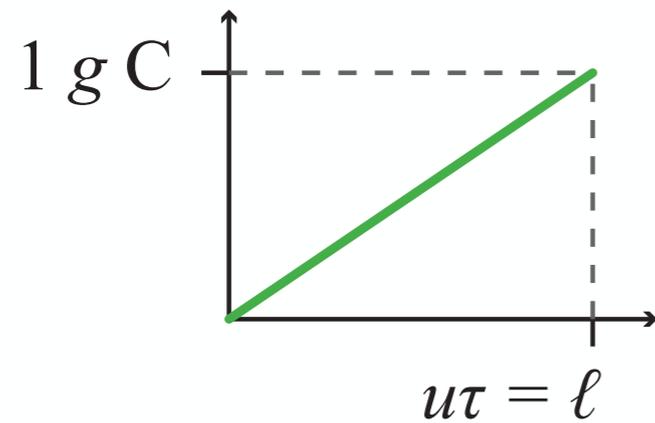
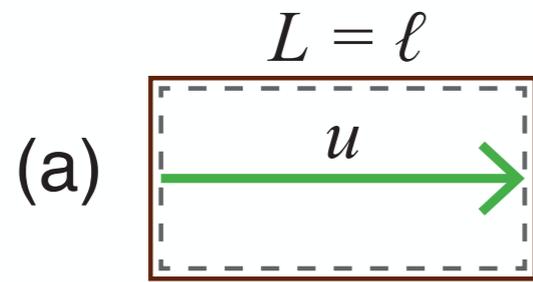


## Allometric scaling of estuarine ecosystem metabolism

Nicholas J. Nidzieski<sup>1</sup>

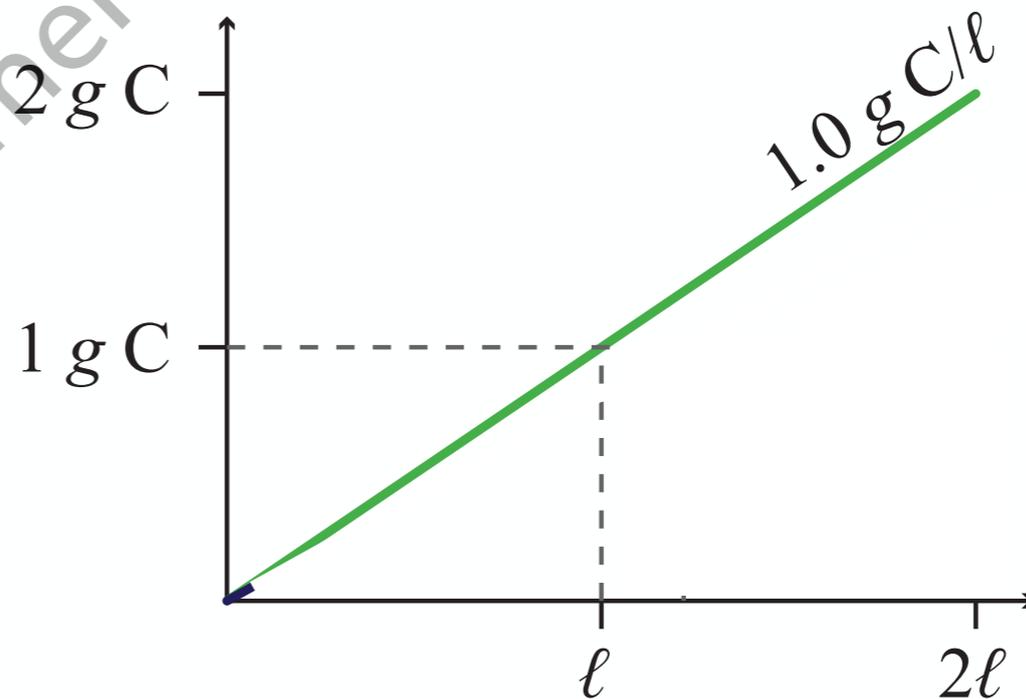
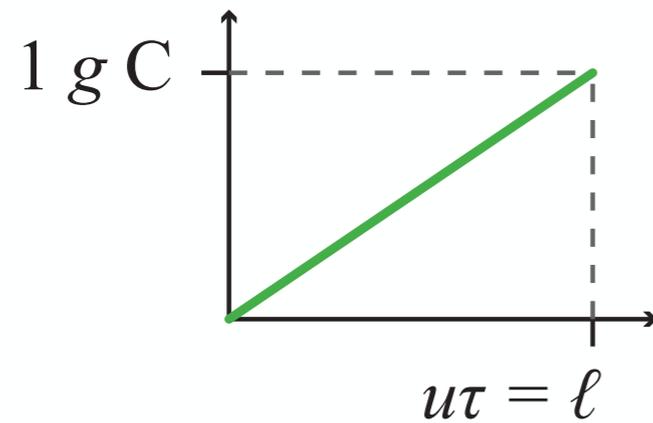
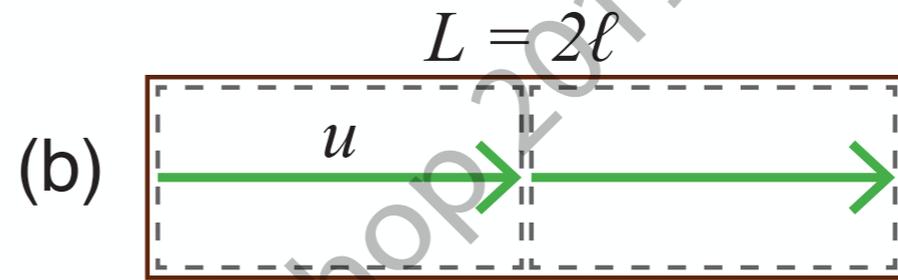
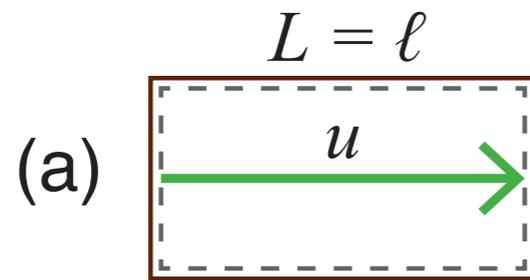
<sup>1</sup>Department of Geography, University of California, Santa Barbara, CA 93106

If the transport time increases nonlinearly with ecosystem size, then metabolism will vary nonlinearly across ecosystems, as we observe



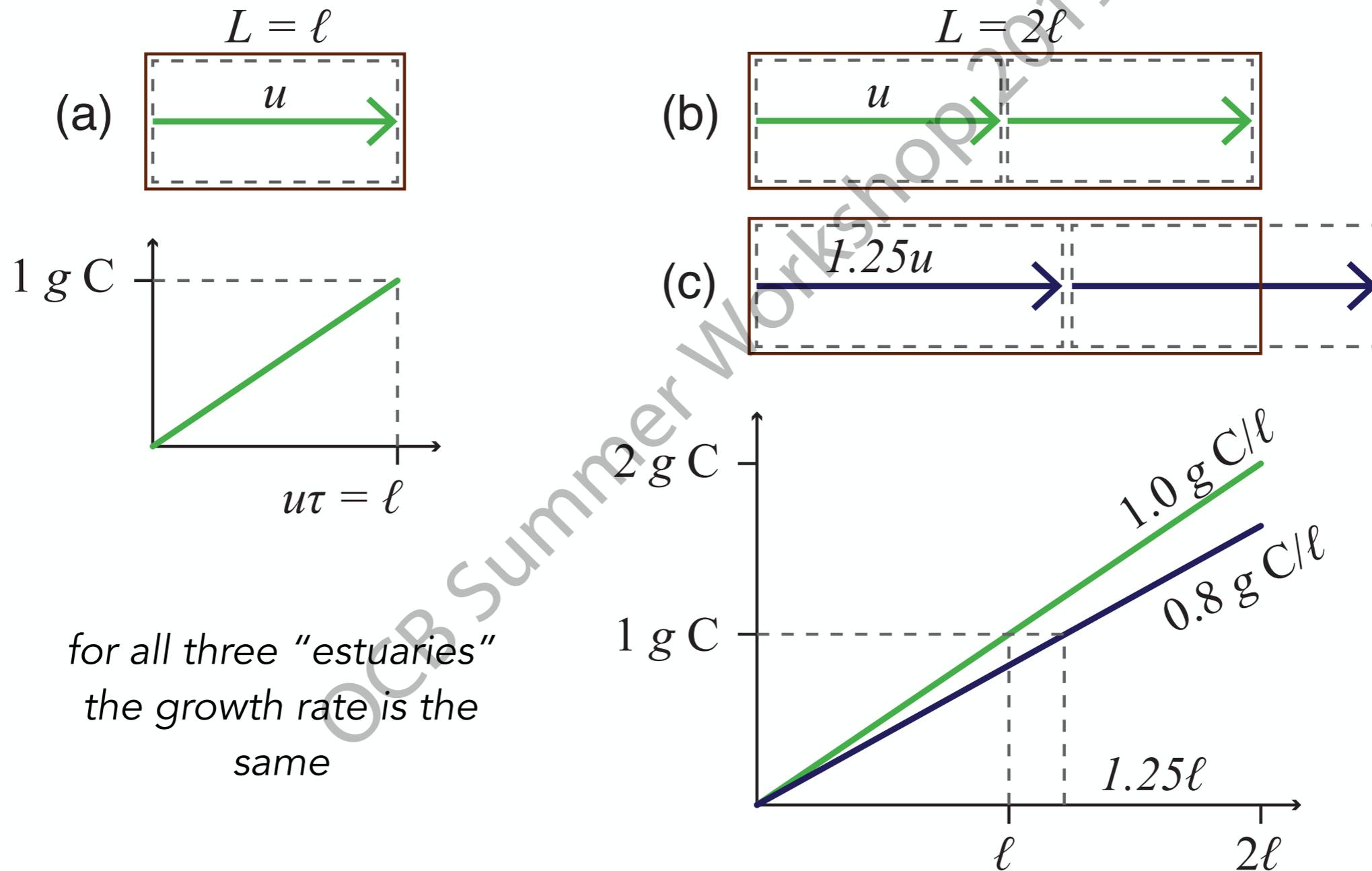
*Imagine organic C is produced as a water parcel travels through the estuary*

If the transport time increases nonlinearly with ecosystem size, then metabolism will vary nonlinearly across ecosystems, as we observe



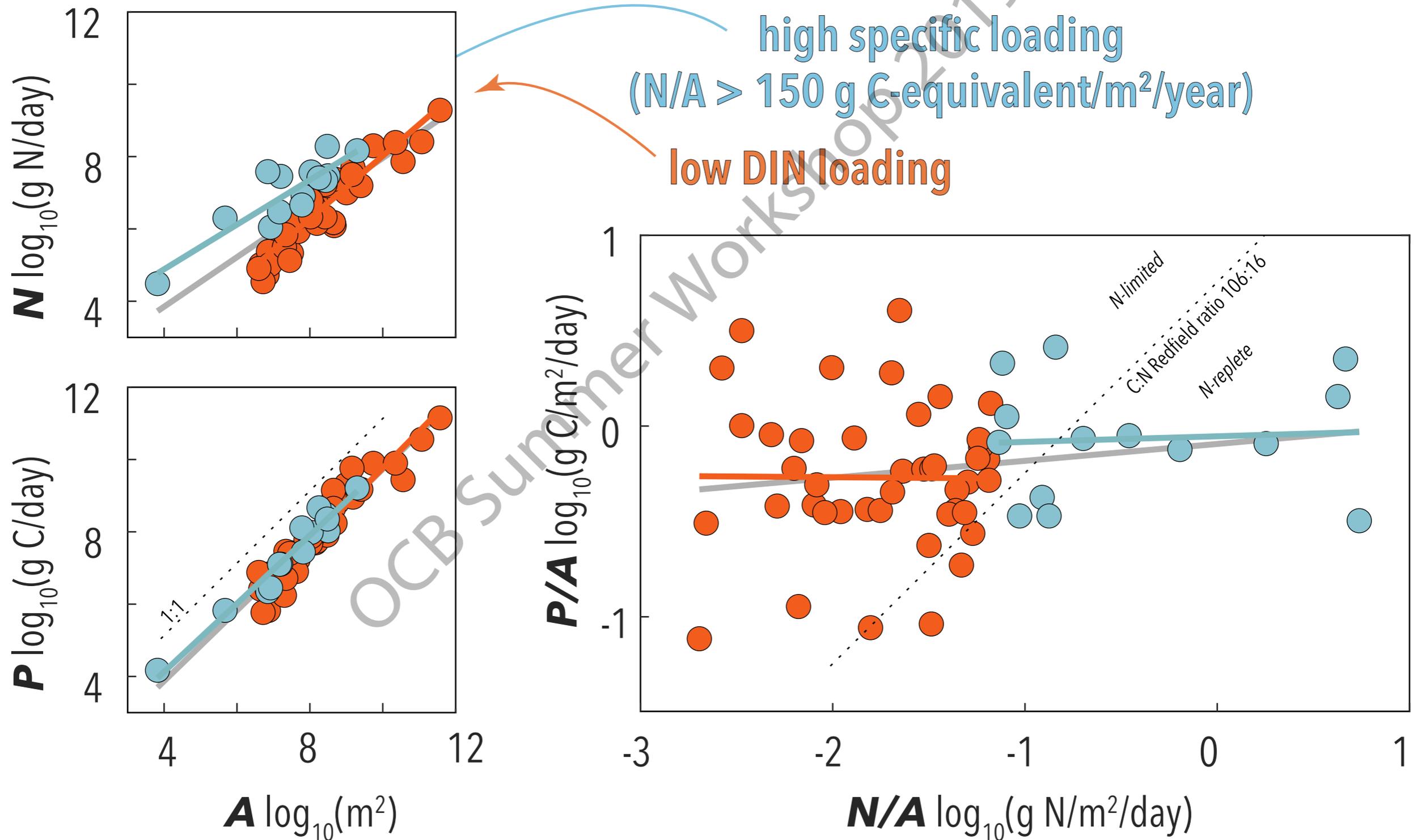
Twice as much org C is produced in a system twice as big, if  $U$  doesn't change

If the transport time increases nonlinearly with ecosystem size, then metabolism will vary nonlinearly across ecosystems, as we observe



for all three "estuaries"  
the growth rate is the  
same

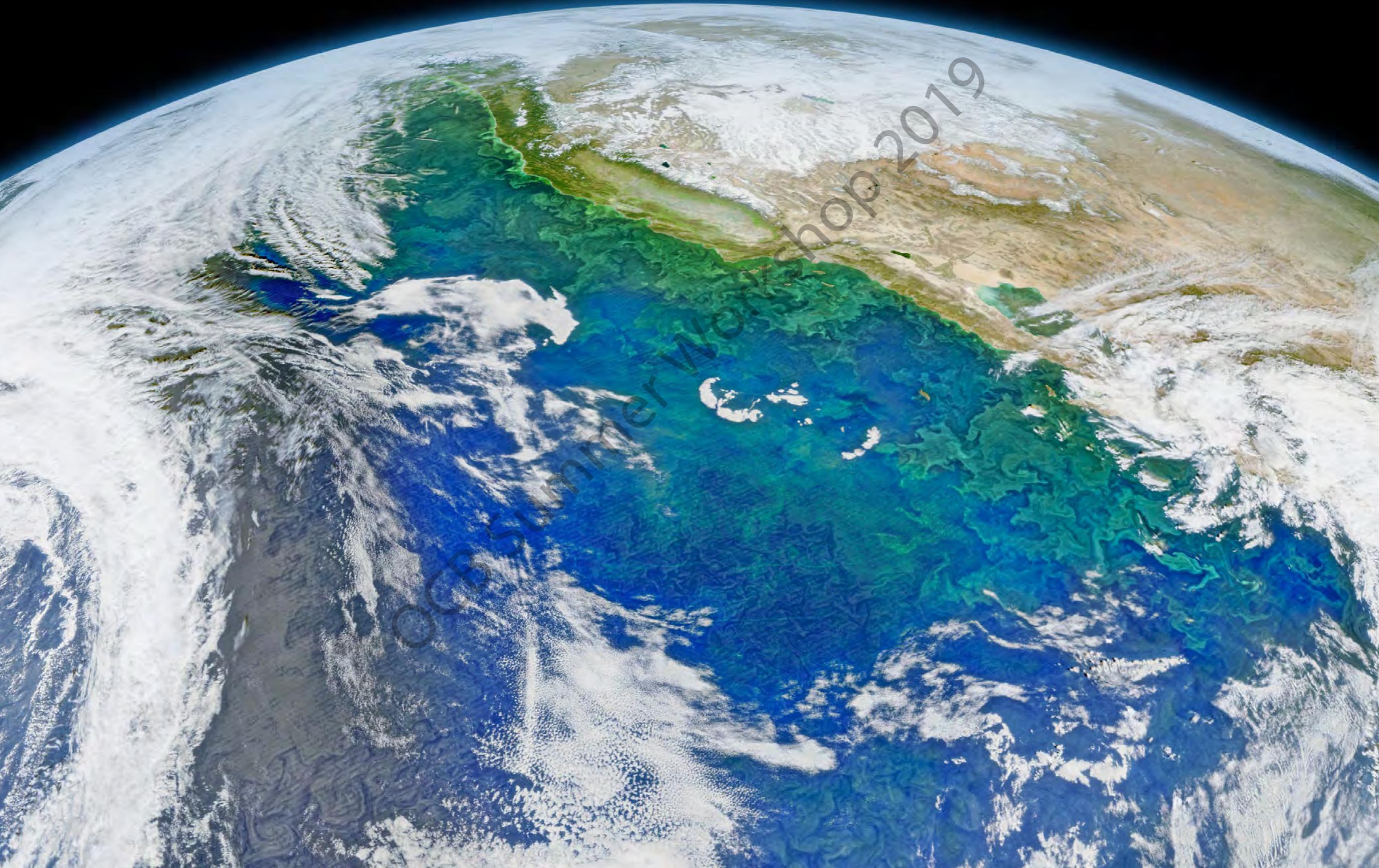
Larger estuaries have greater nitrogen loads, but higher specific loading doesn't increase specific productivity



# One explanation may be the rate at which nutrient pulses move through an estuary



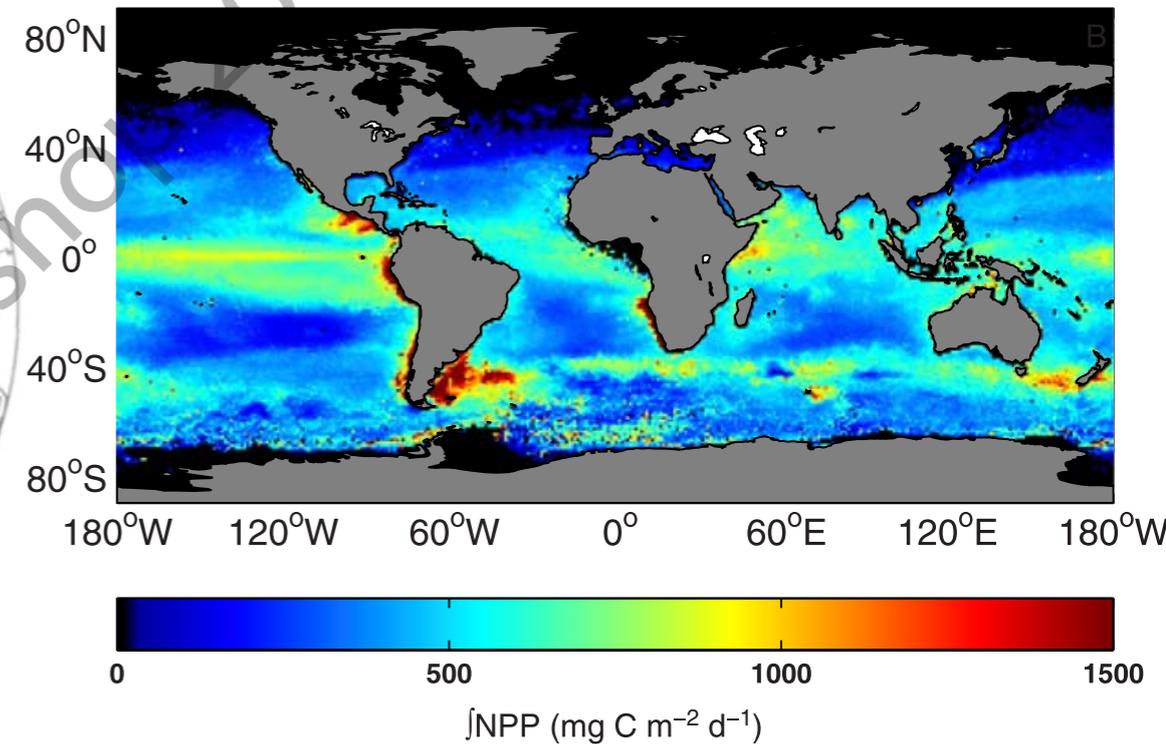
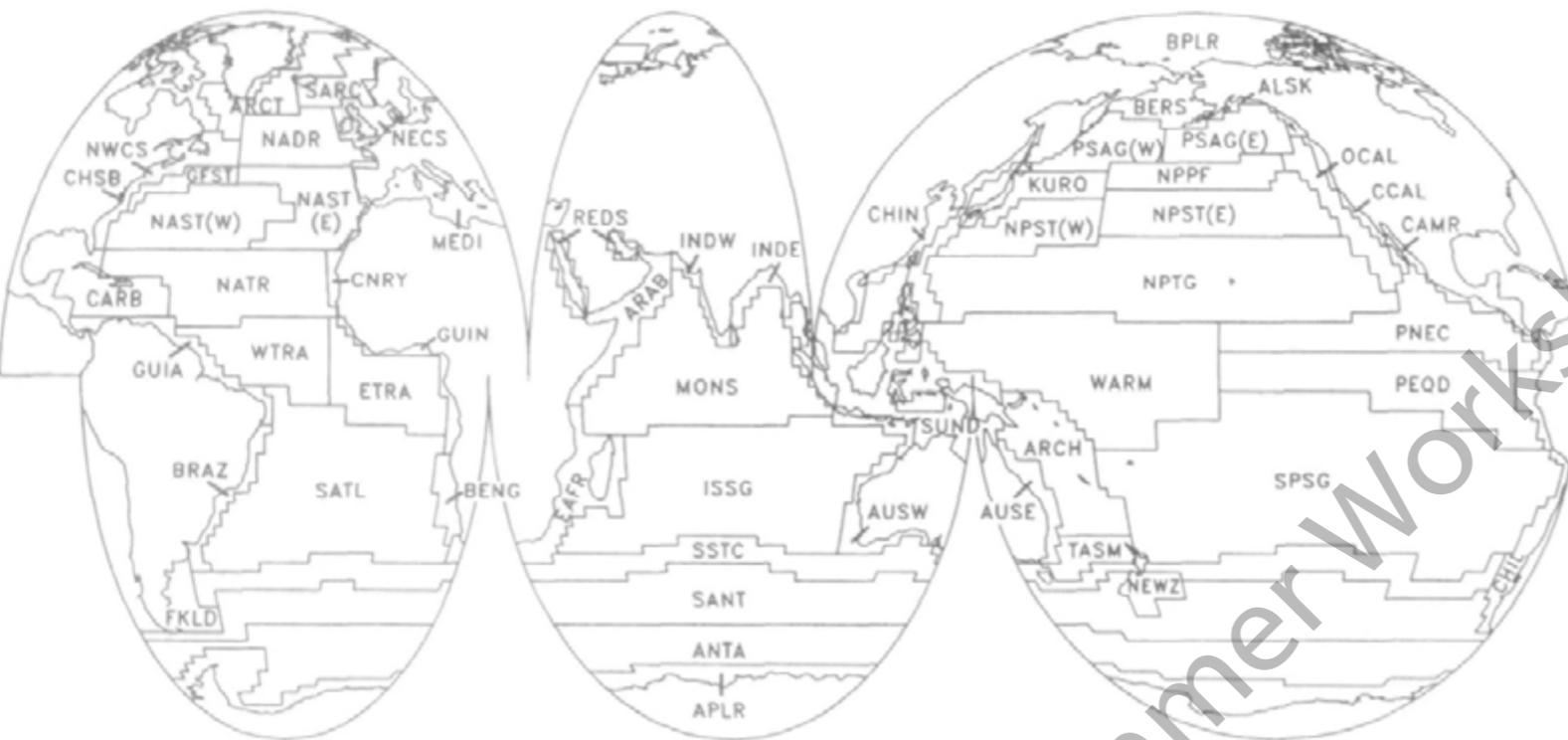
# Does size scaling apply across the oceans?



# Willie Haskell (MBARI) aggregated net primary production into a variety of biogeographic provinces

Carbon-based primary productivity modeling with vertically resolved photoacclimation

T. Westberry,<sup>1</sup> M. J. Behrenfeld,<sup>1</sup> D. A. Siegel,<sup>2</sup> and E. Boss<sup>3</sup>



Journal of Plankton Research Vol.17 no.6 pp.1245–1271, 1995

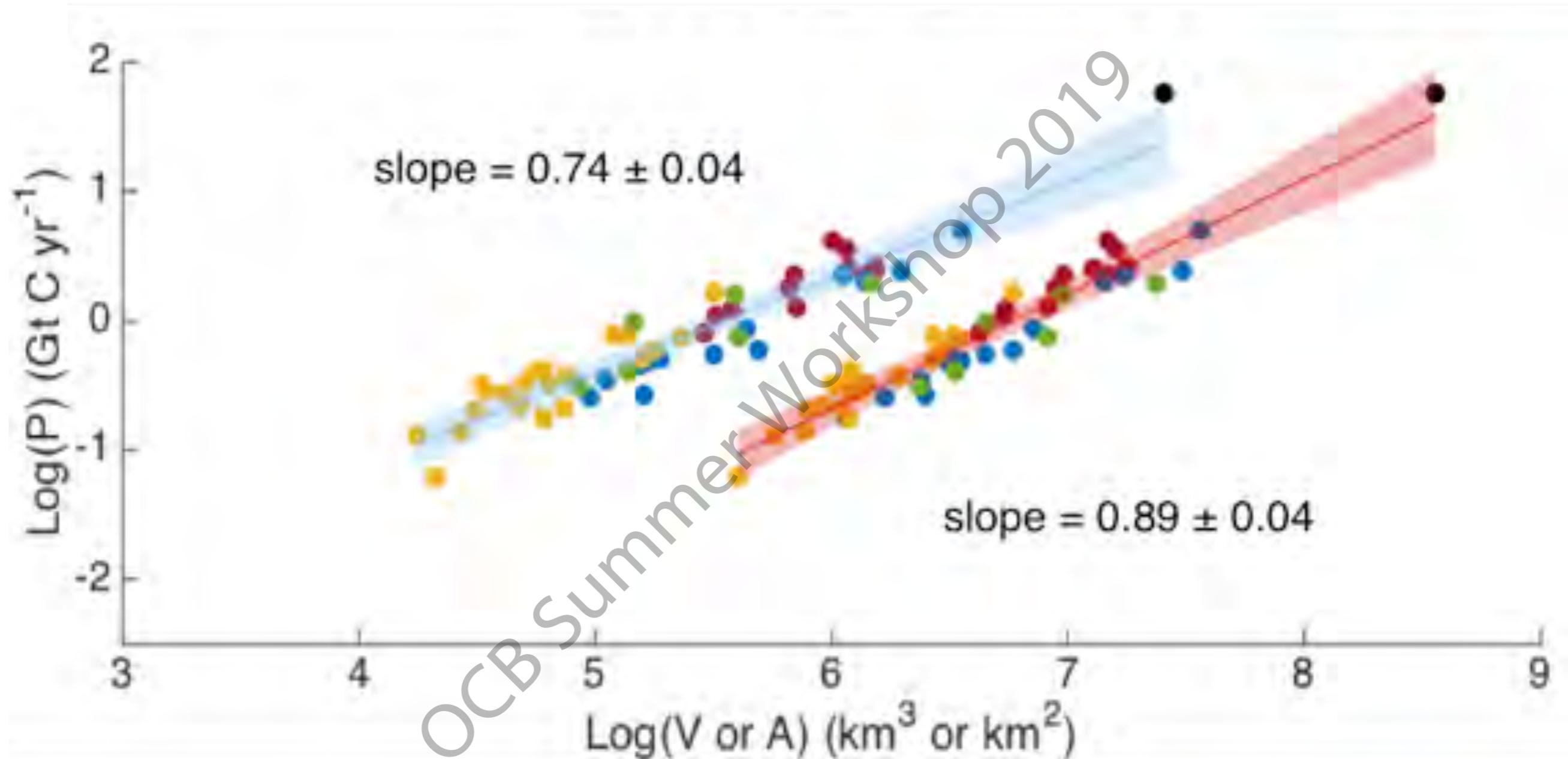
## An estimate of global primary production in the ocean from satellite radiometer data

Alan Longhurst, Shubha Sathyendranath<sup>1</sup>, Trevor Platt and Carla Caverhill



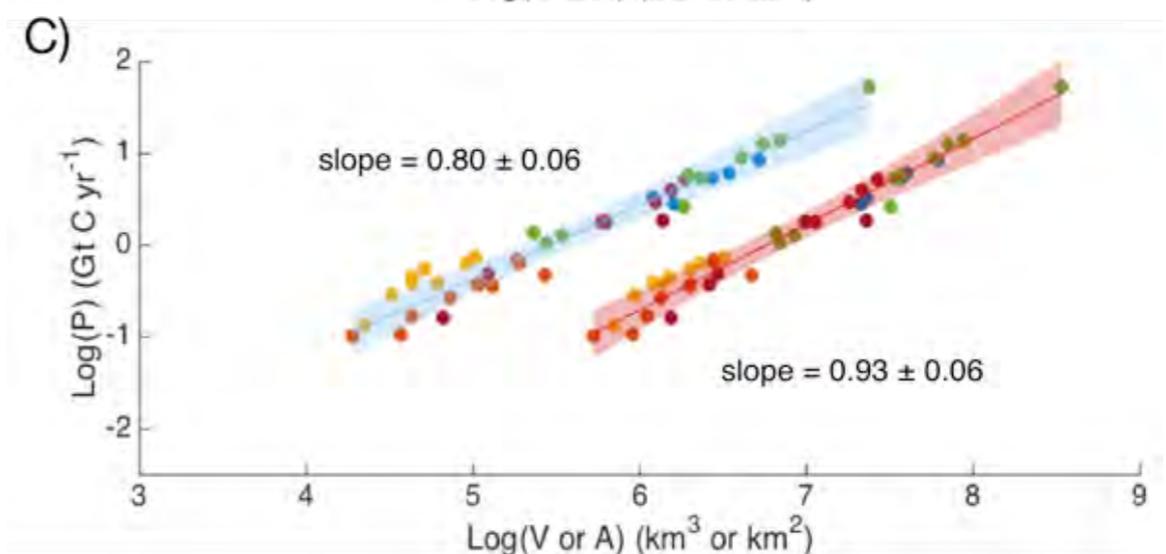
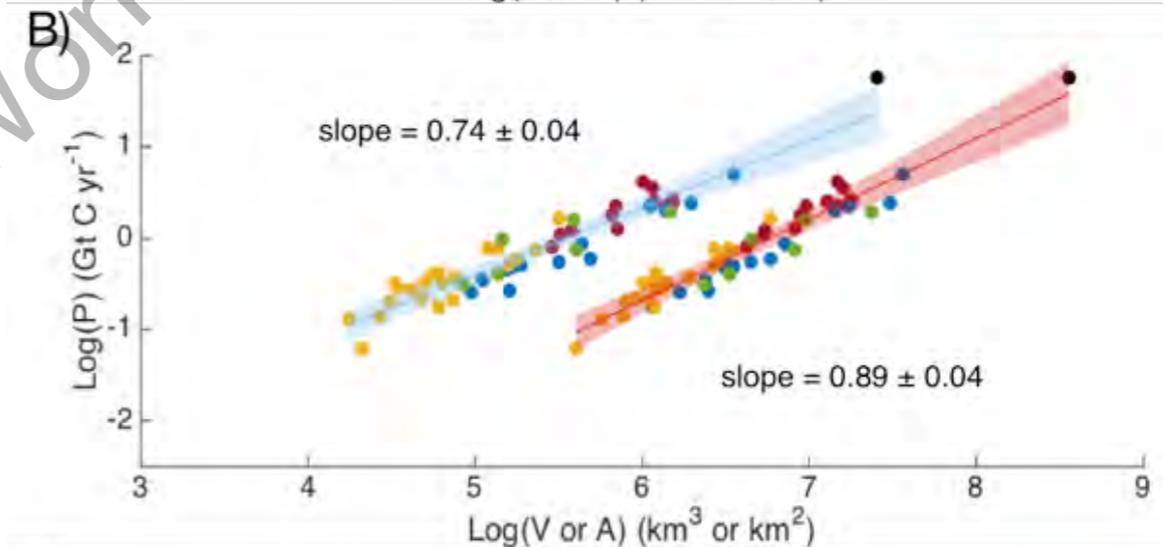
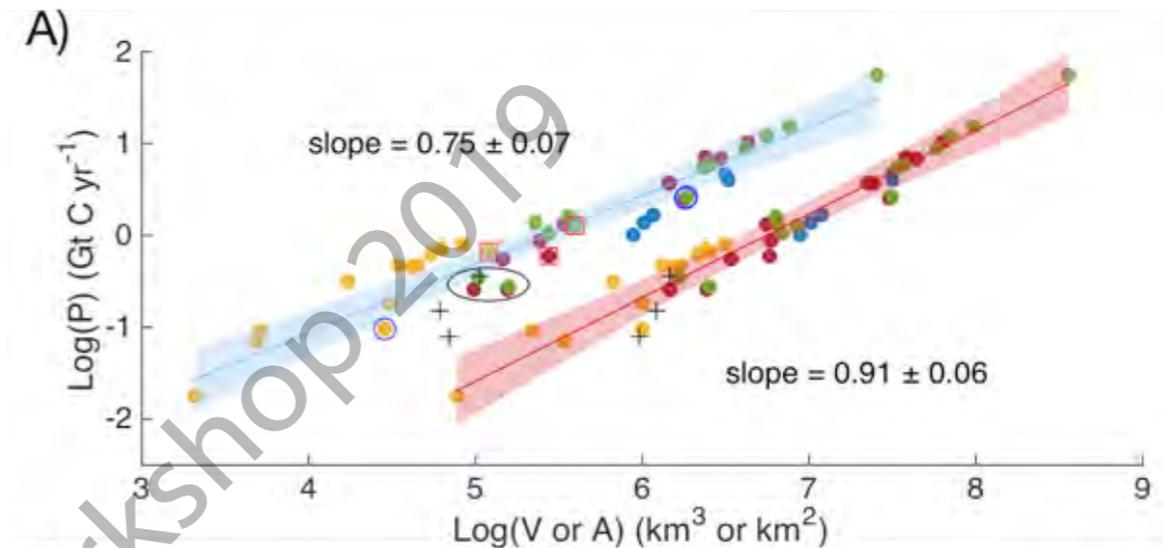
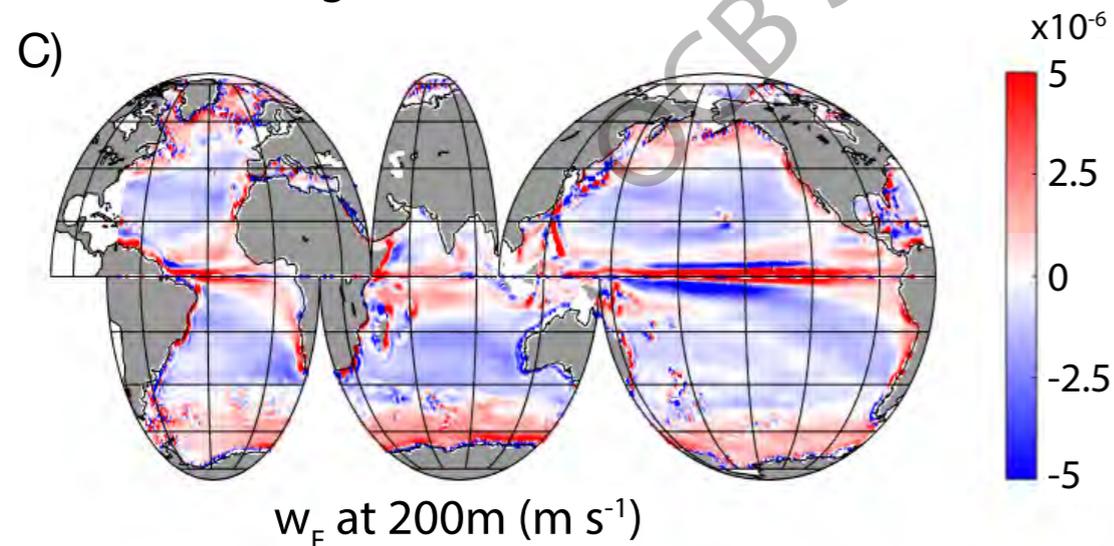
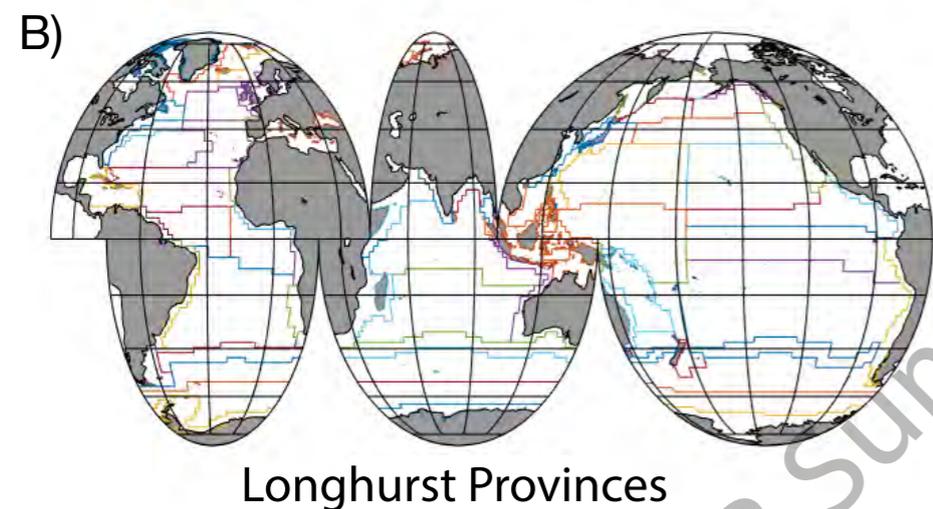
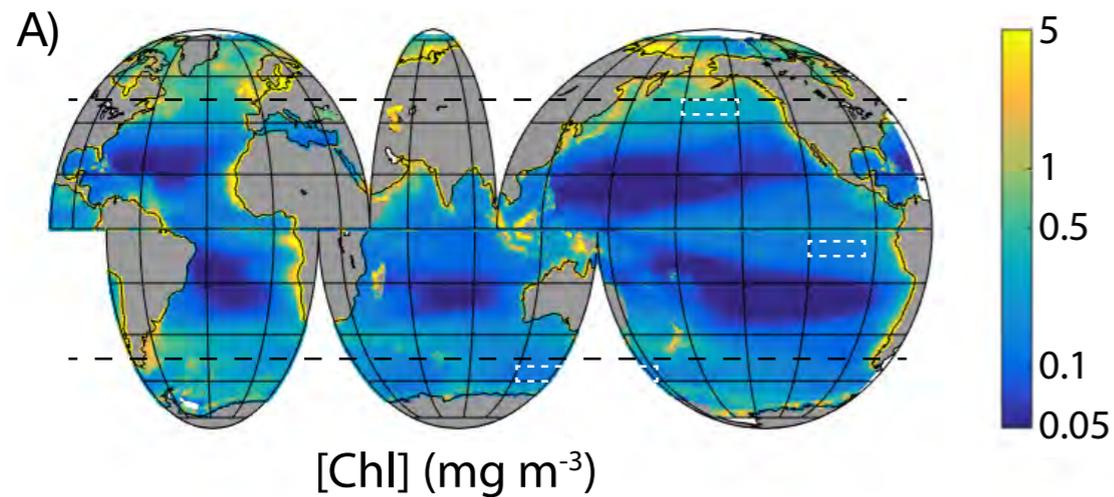
Willie Haskell, *in prep*

As with estuaries, community metabolism scales nonlinearly with ecosystem size

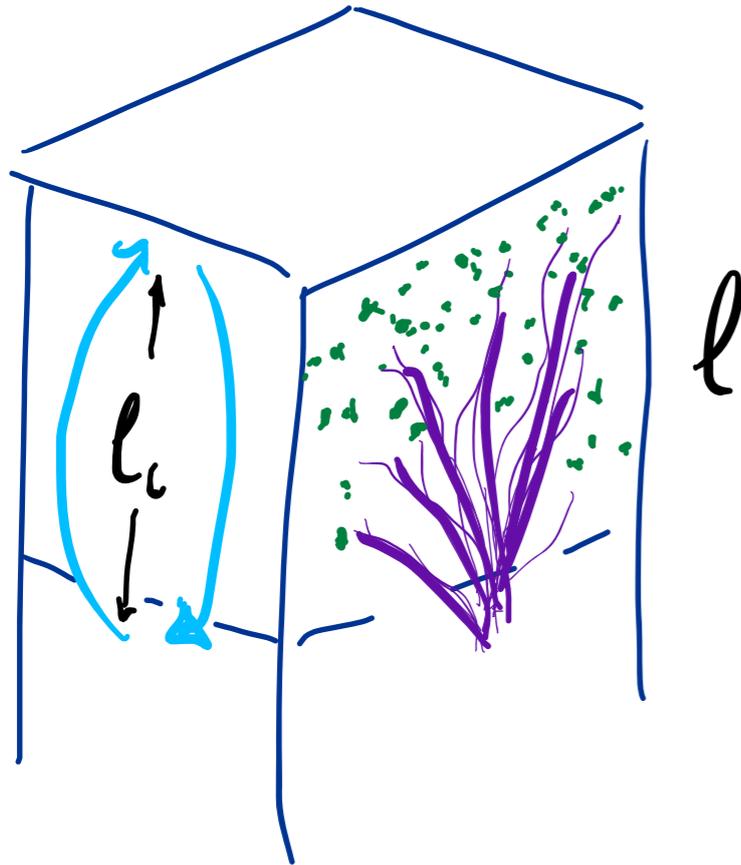


Oligotrophic (blue)  
Mesotrophic (red)  
Eutrophic (yellow)  
Total basins/Global (green).

# Similar scaling exponents emerge, regardless of how ocean basins are divided up



To understand this result, consider an isolated water column...



physical length scale

$$V_i \sim l^3$$
$$P_i \sim V_i^\alpha$$

volume of water column

productivity scaling

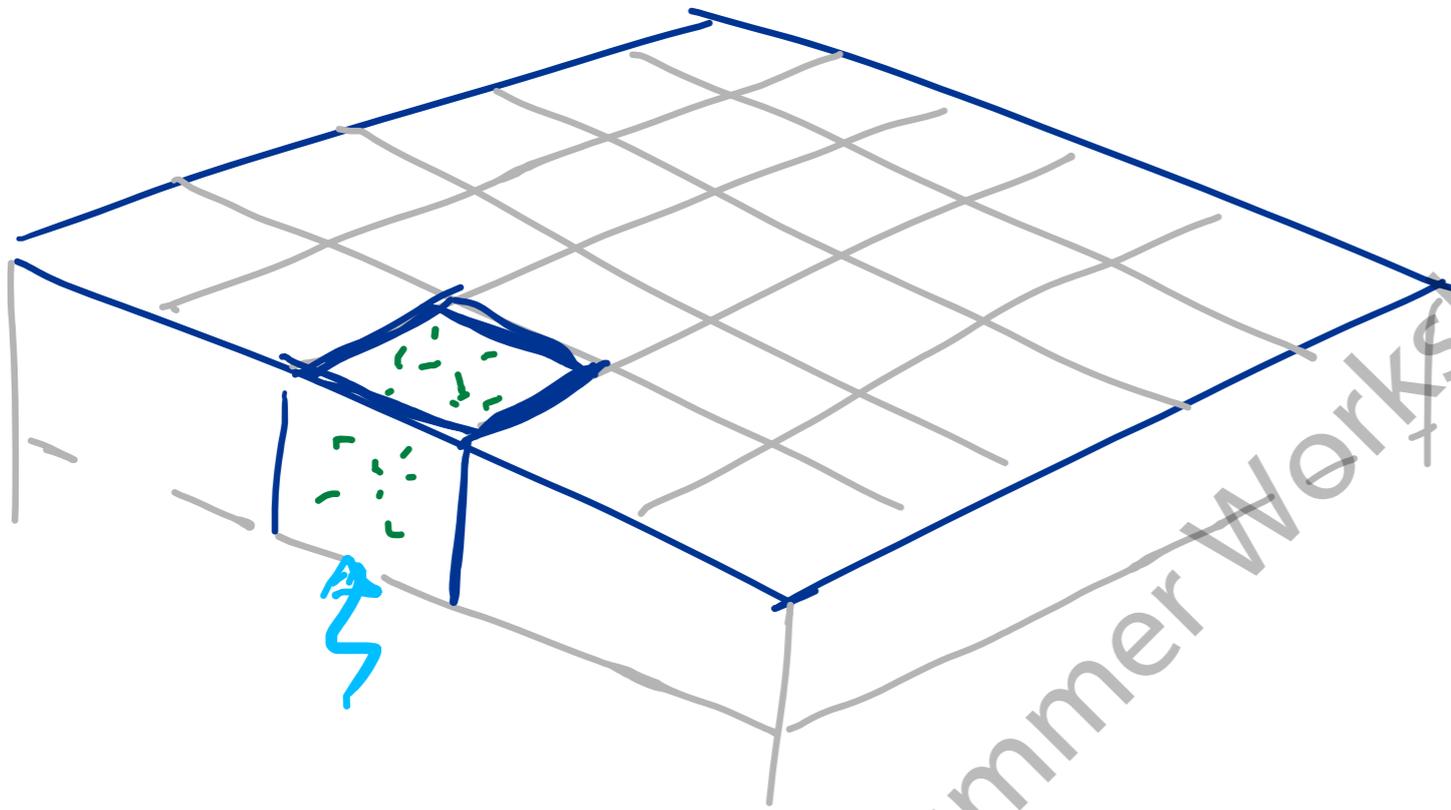
$$l_c \sim \left( \frac{\epsilon}{\mu^3} \right)^{1/2}$$

critical length scale matching growth rate to available energy ( $\epsilon$  = dissipation)

$$\mu = \tau^{-1}$$

growth rate = 1/growth timescale

Next, imagine that this water column is the only source of upwelling in a region of the ocean that is otherwise unproductive

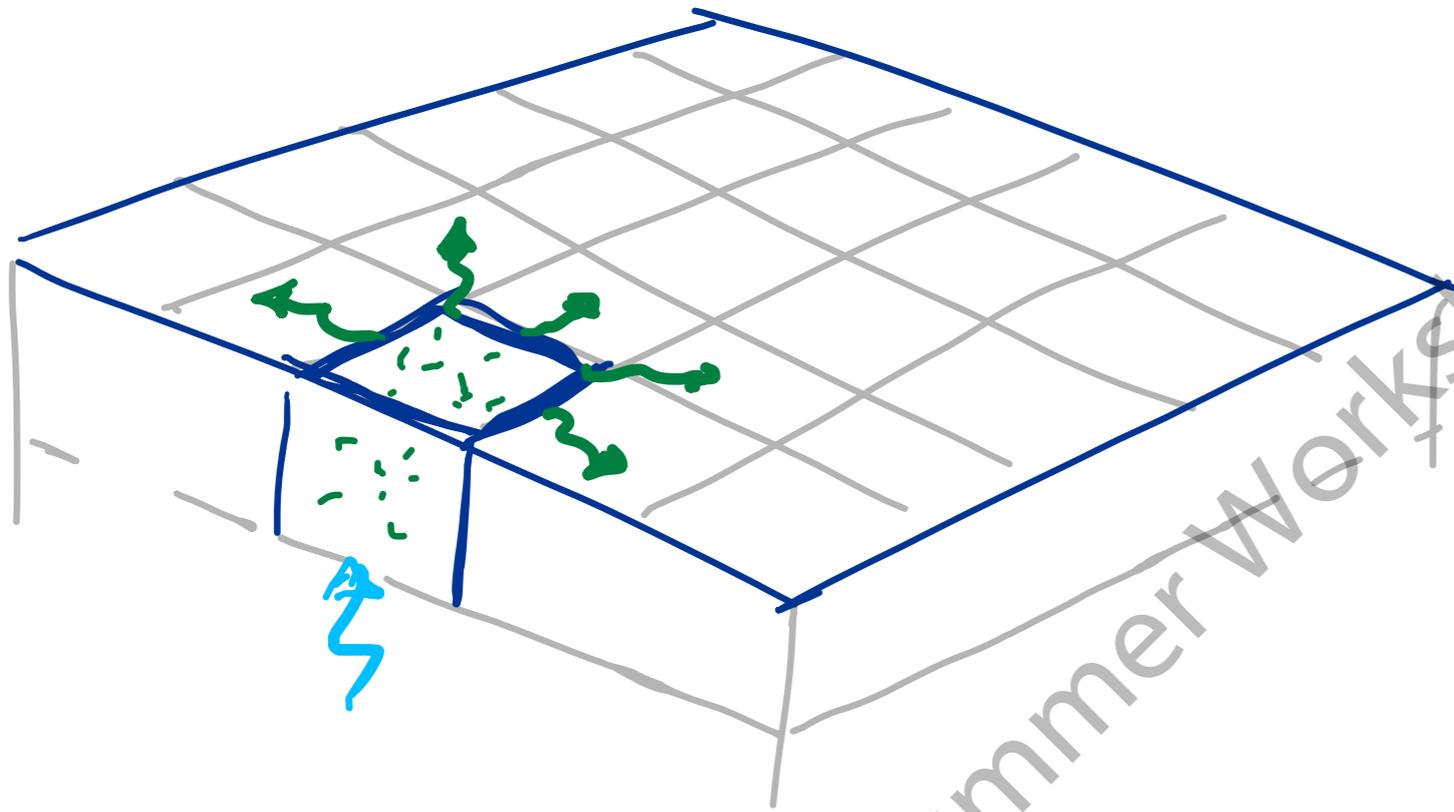


The productivity of the region is the sum of the individual water columns

$$P_{TOT} = \sum_n P_i = n \bar{P}_i$$

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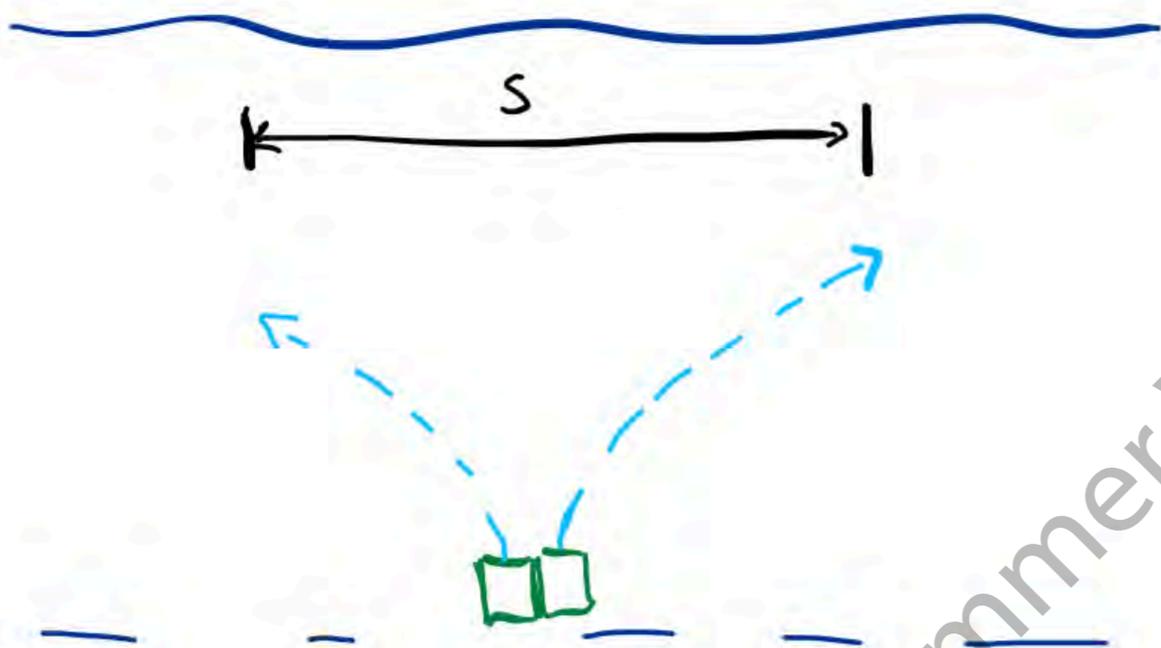
This theoretical ocean can only have increased productivity with lateral spreading coupled to continued upwelling



Without lateral spreading, vertical motions simply mix down existing organic N with the upward movement of inorganic N

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The relative horizontal diffusivity of upwelled nitrogen scales with dissipation and the horizontal distance,  $s$



$$\frac{1}{2} \frac{ds^2}{dt} \propto \epsilon^{1/3} s^{4/3}$$

$$\epsilon \approx \frac{L^2}{T^3}$$

Progress in Oceanography 70 (2006) 113–125  
Turbulent dispersion in the ocean

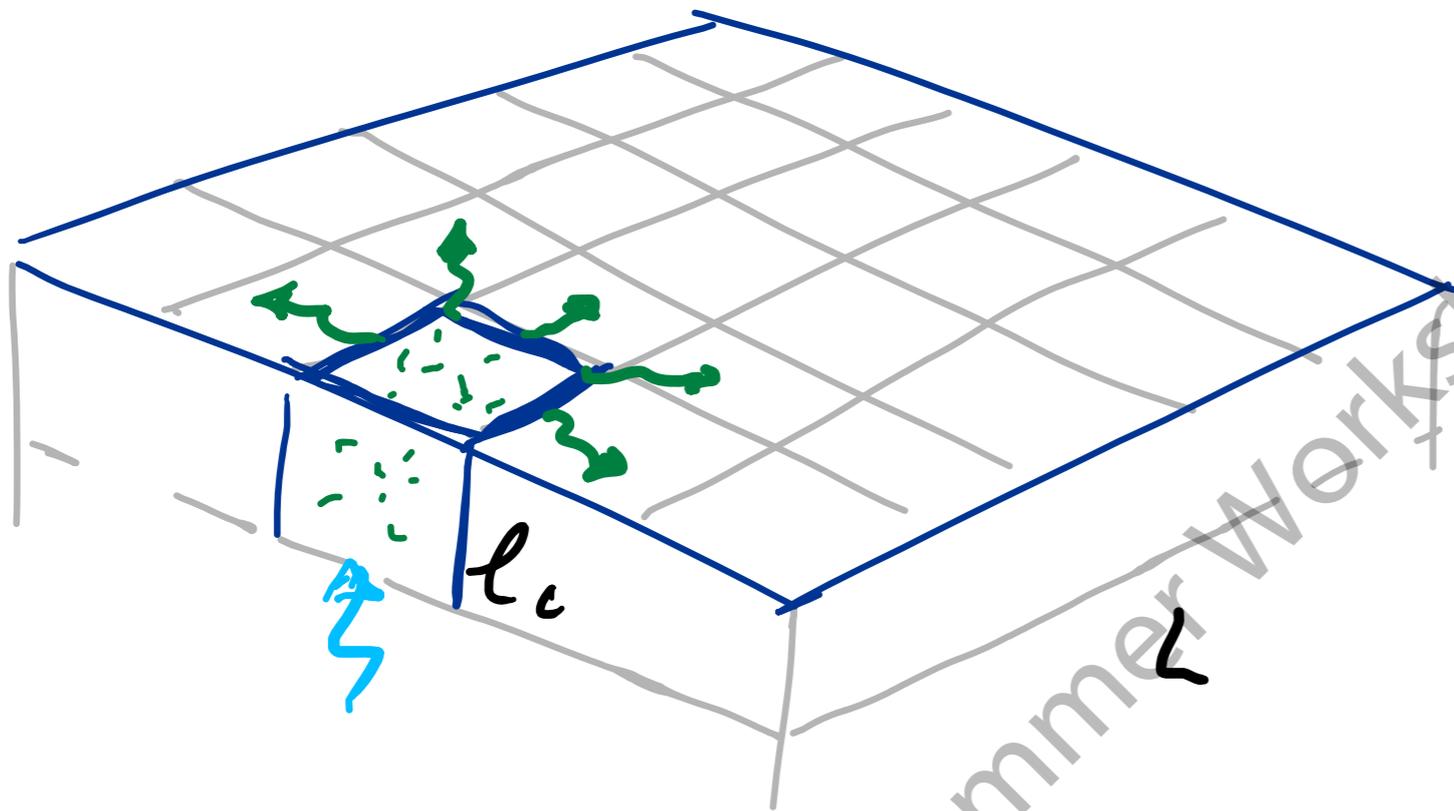
Chris Garrett \*

*Atmospheric Diffusion shown on a Distance-Neighbour Graph.*

By LEWIS F. RICHARDSON.

(Communicated by Sir Gilbert Walker, F.R.S.—Received November 7, 1925.)

Thus, for the appropriate physical regimes, we can expect both vertical mixing and lateral transport to scale with dissipation



$$\varepsilon \approx \frac{l_c^2}{\tau^3} \approx \frac{L^2}{T^3}$$

JOURNAL OF PHYSICAL OCEANOGRAPHY

**Interpreting Energy and Tracer Spectra of Upper-Ocean Turbulence  
in the Submesoscale Range (1–200 km)**

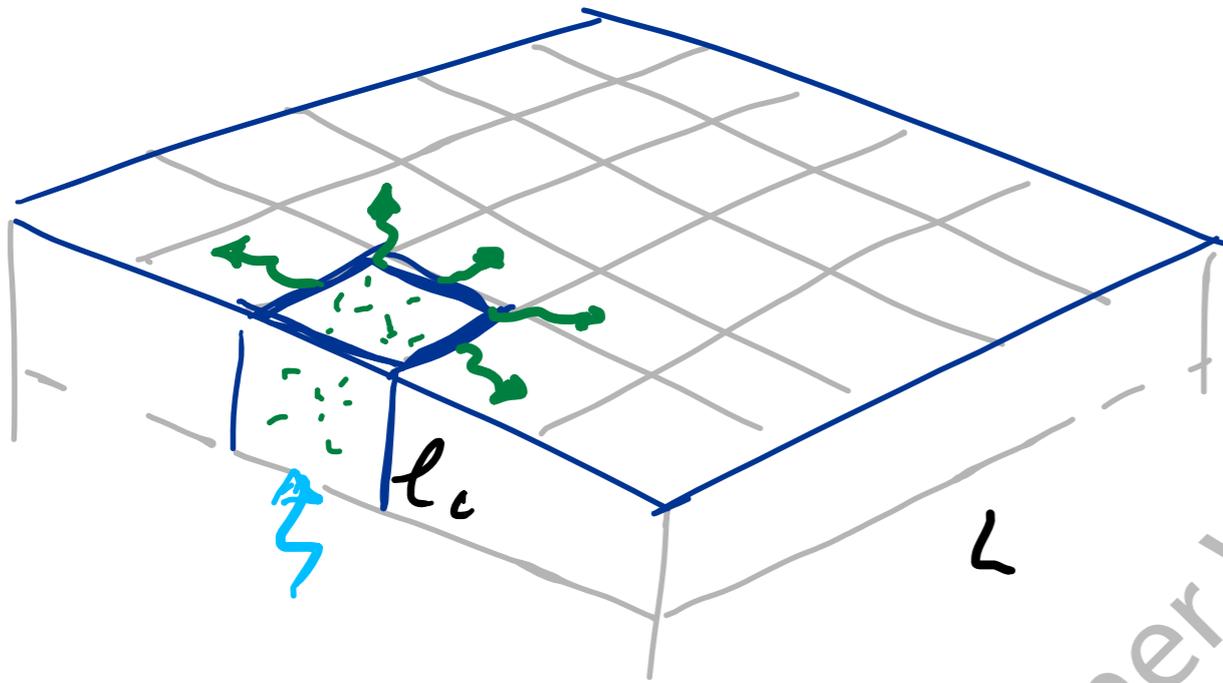
JÖRN CALLIES

*MIT/WHOI Joint Program in Oceanography, Cambridge/Woods Hole, Massachusetts*

RAFFAELE FERRARI

*Massachusetts Institute of Technology, Cambridge, Massachusetts*

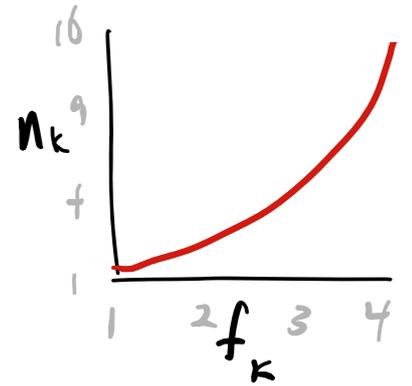
# ICBST total community metabolism scales with the same ratio of timescales found in MTE theory



$$l_c^{-2} \approx \frac{T^3}{\tau^3} \frac{1}{L^2}$$

$$n \approx \frac{L^2}{l_c^2}$$

$$n_k \approx f_k^2 = \frac{l_c^2}{l_c^2}$$

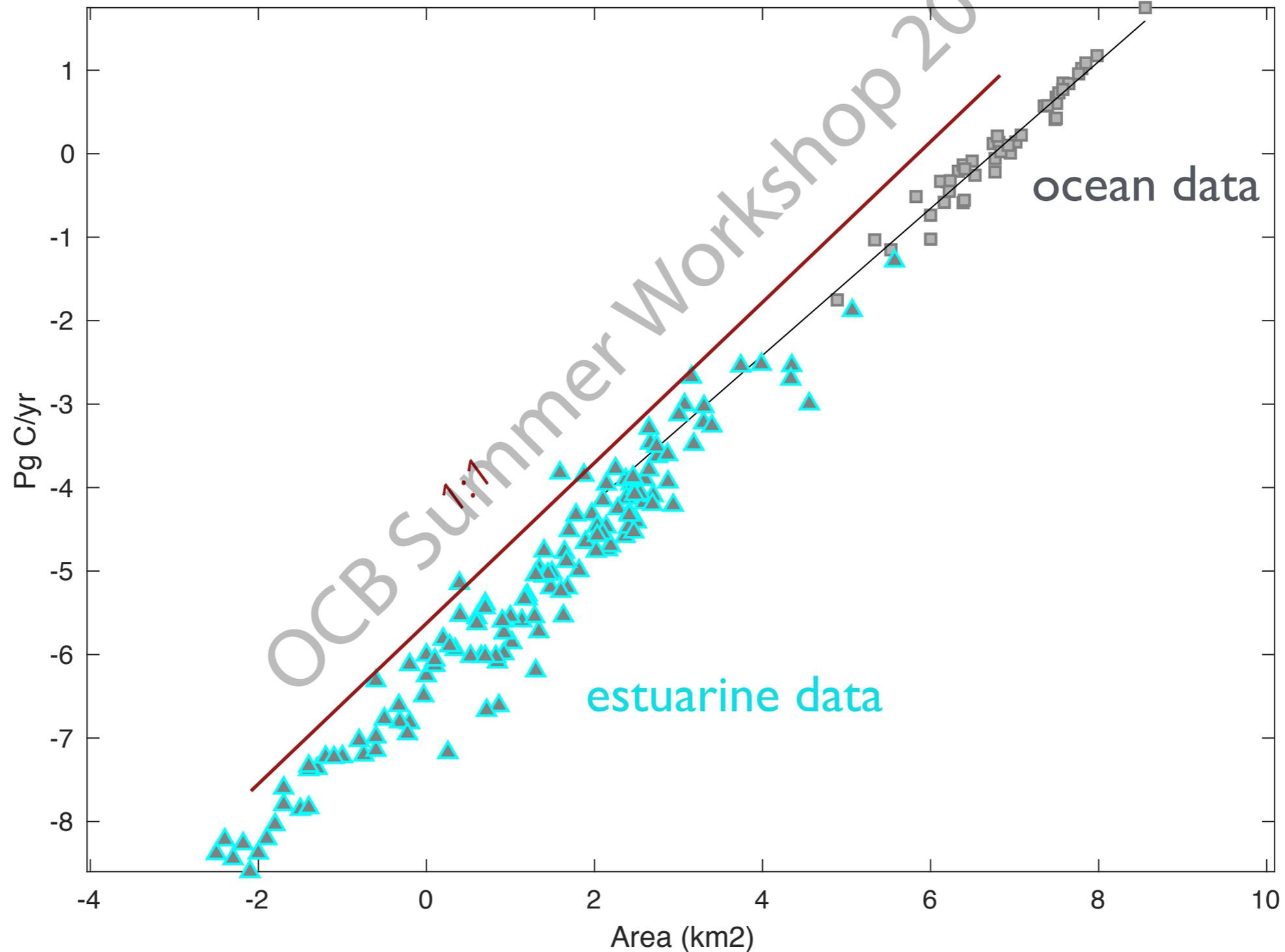


$$P_{TOT} = \sum_k \left( \sum_{n_k} P_{i,k} \right) = \sum_k n_k \bar{P}_{i,k}$$

$$P_{TOT} \approx \sum_k \frac{l_c^2}{l_{c,k}^2} \bar{P}_{i,k} \approx \sum_k \frac{l_c^2}{L^2} \frac{T^3}{\tau^3} \bar{P}_{i,k}$$

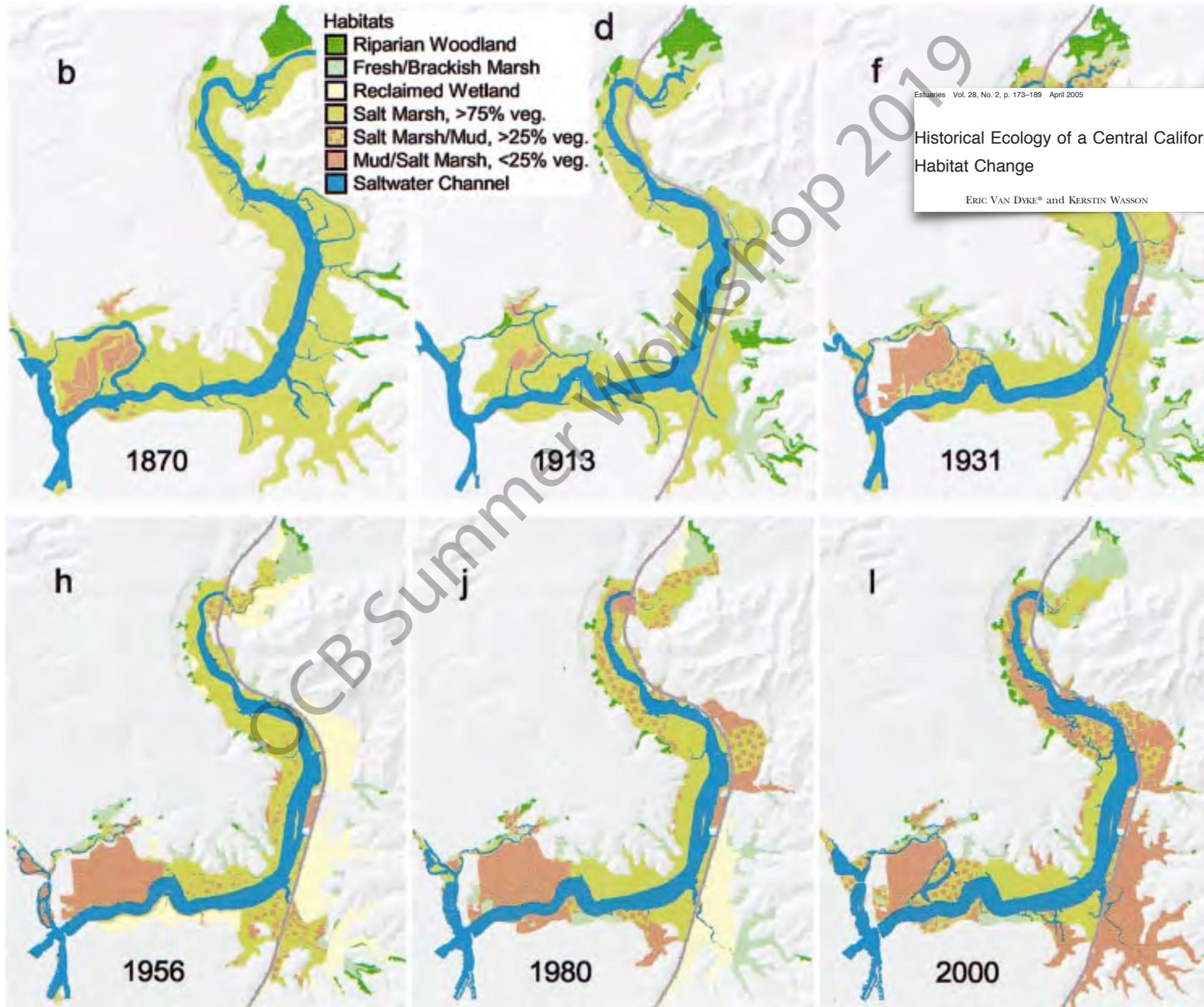
$$P_{TOT} \approx \frac{T^3}{\tau^3} \sum_k \frac{1}{n} \frac{f_k^2}{f_k^{3\alpha}} v_i^\alpha \approx \frac{T^3}{\tau^3} \sum_k \frac{n_k}{n} \frac{V_i^\alpha}{f_k^{3\alpha}}$$

What can we do with the observation that estuaries and ocean basins scale similarly with regard to primary production?



# What are some possible applications of these ideas?

(1) estimating role of lost habitats



# What are some possible applications of these ideas?

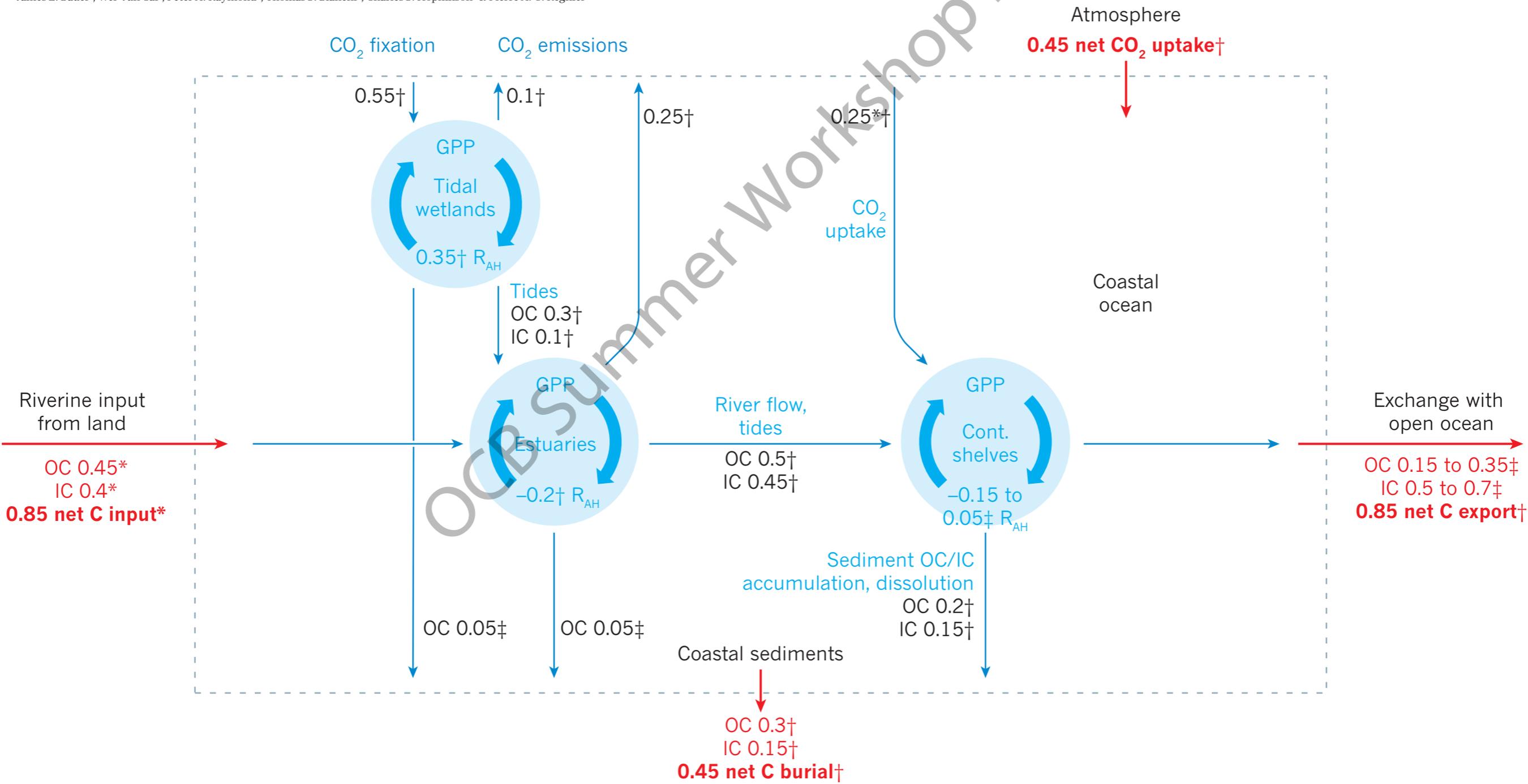
## (2) constraining current budgets

### REVIEW

doi:10.1038/nature12857

## The changing carbon cycle of the coastal ocean

James E. Bauer<sup>1</sup>, Wei-Jun Cai<sup>2</sup>, Peter A. Raymond<sup>3</sup>, Thomas S. Bianchi<sup>4</sup>, Charles S. Hopkins<sup>5</sup> & Pierre A. G. Regnier<sup>6</sup>



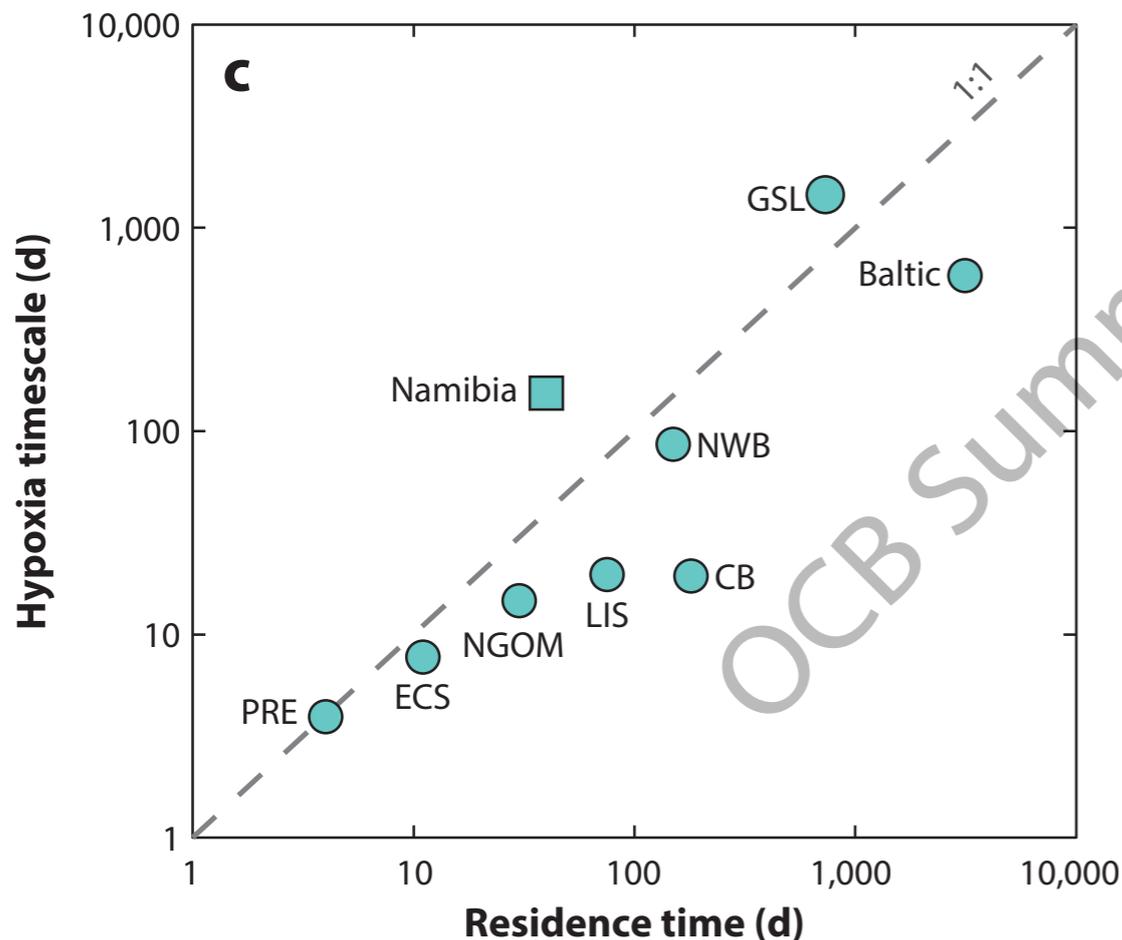
# What are some possible applications of these ideas?

## (3) interpreting other spatial patterns

*Annual Review of Marine Science*

### Biogeochemical Controls on Coastal Hypoxia

Katja Fennel<sup>1</sup> and Jeremy M. Testa<sup>2</sup>

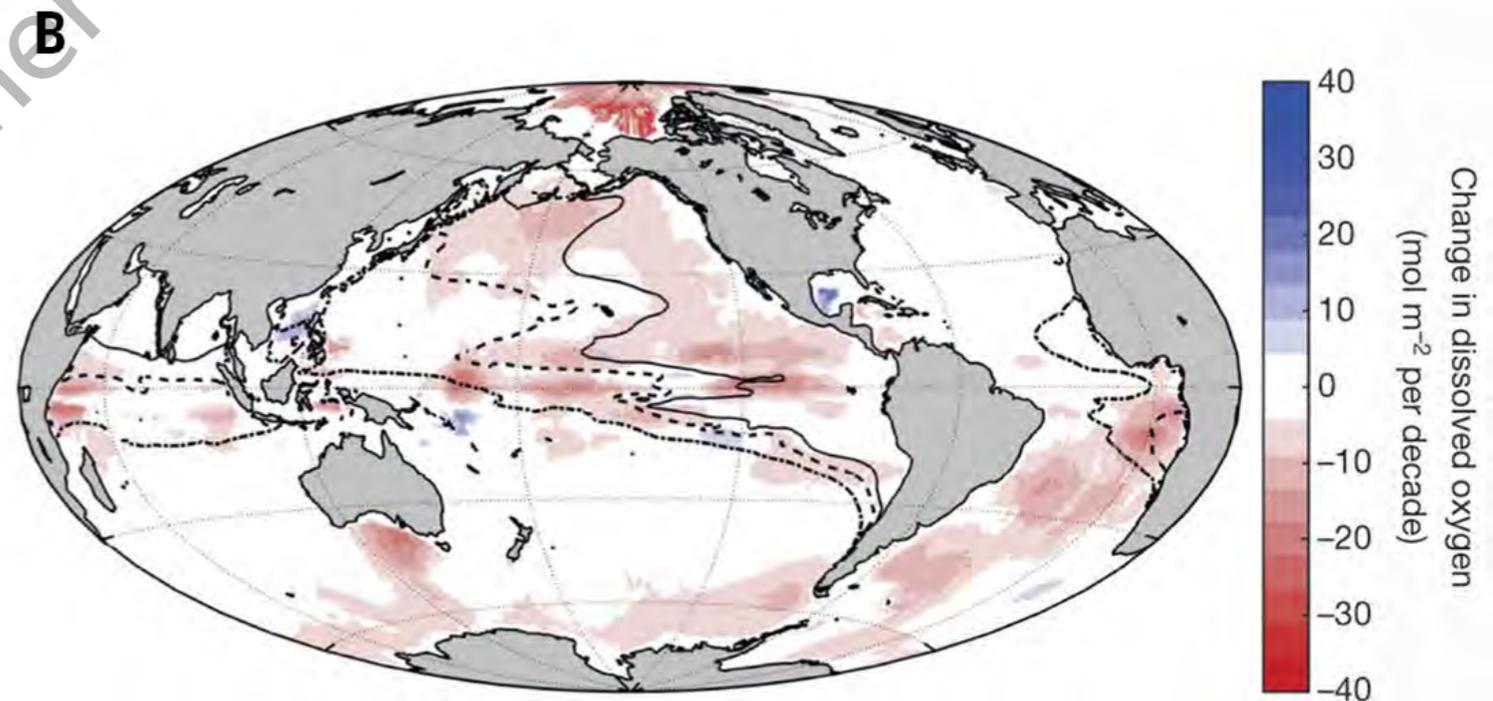


### REVIEW

OCEANS

## Declining oxygen in the global ocean and coastal waters

Denise Breitburg,<sup>1\*</sup> Lisa A. Levin,<sup>2</sup> Andreas Oschlies,<sup>3</sup> Marilaure Grégoire,<sup>4</sup> Francisco P. Chavez,<sup>5</sup> Daniel J. Conley,<sup>6</sup> Véronique Garçon,<sup>7</sup> Denis Gilbert,<sup>8</sup> Dimitri Gutiérrez,<sup>9,10</sup> Kirsten Isensee,<sup>11</sup> Gil S. Jacinto,<sup>12</sup> Karin E. Limburg,<sup>13</sup> Ivonne Montes,<sup>14</sup> S. W. A. Naqvi,<sup>15†</sup> Grant C. Pitcher,<sup>16,17</sup> Nancy N. Rabalais,<sup>18</sup> Michael R. Roman,<sup>19</sup> Kenneth A. Rose,<sup>19</sup> Brad A. Seibel,<sup>20</sup> Maciej Telszewski,<sup>21</sup> Moriaki Yasuhara,<sup>22</sup> Jing Zhang<sup>23</sup>



# What are some possible applications of these ideas?

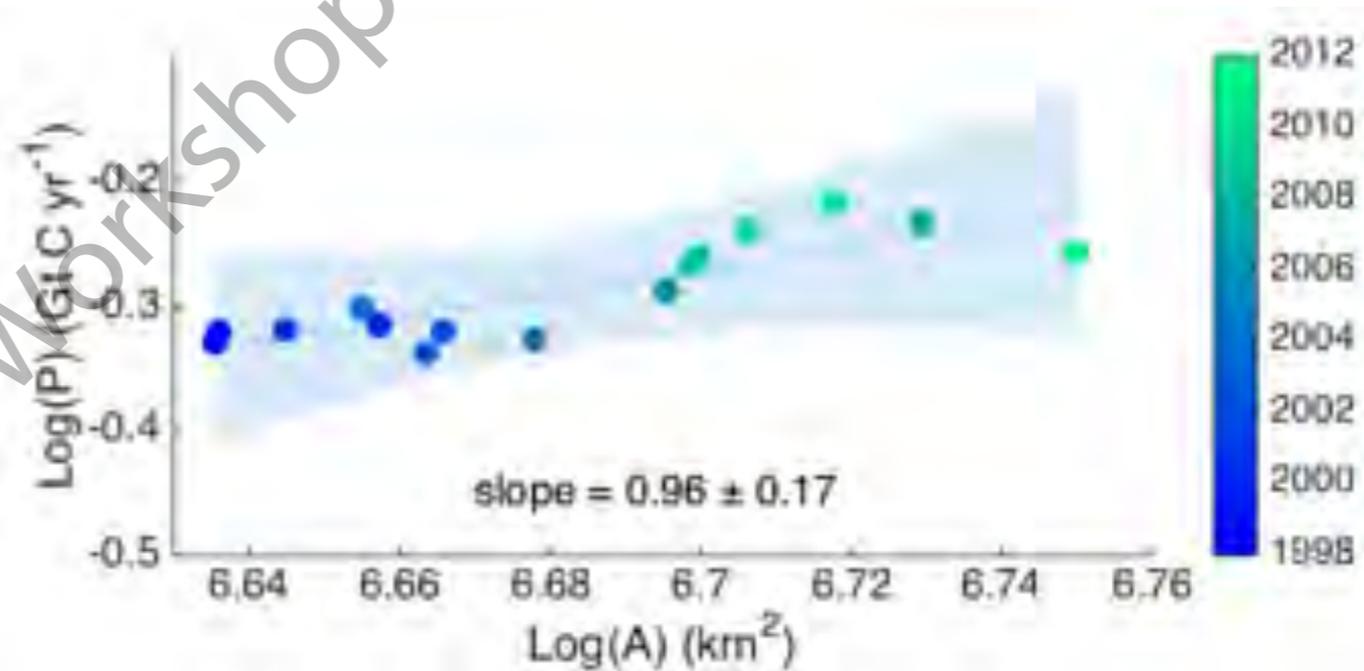
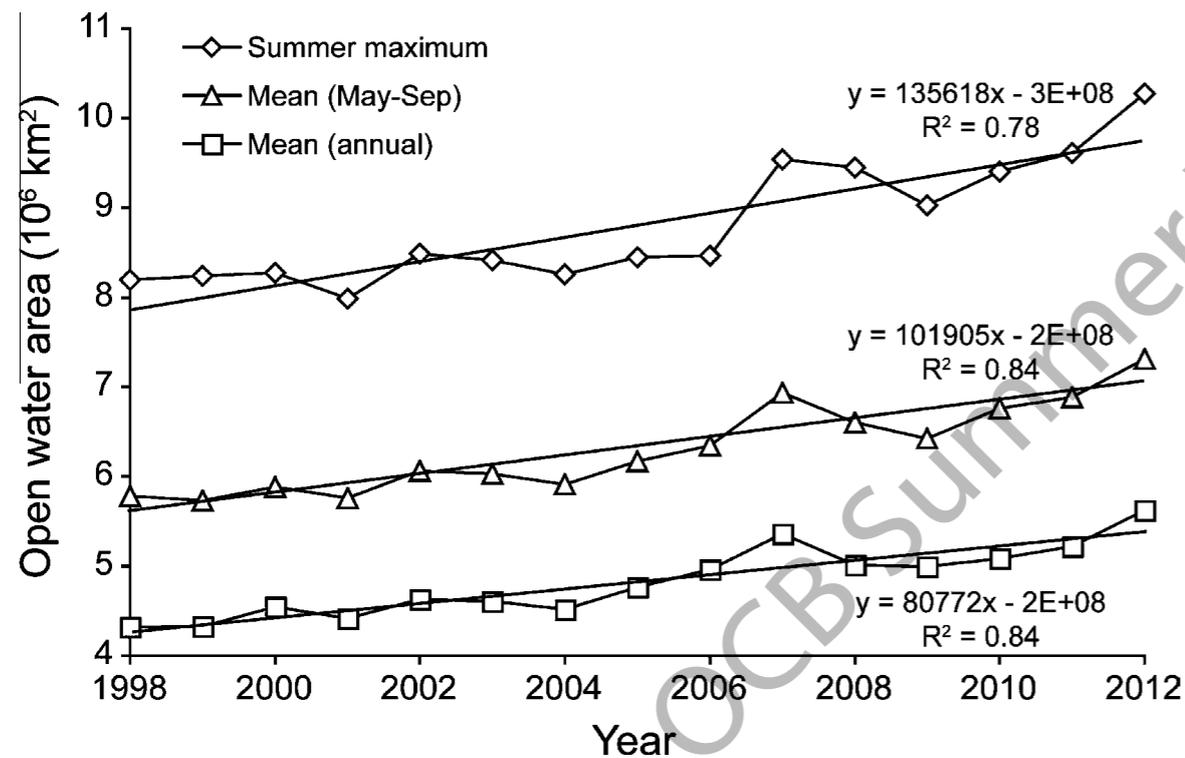
## (4) predicting future states

Progress in Oceanography 136 (2015) 60–70

### Continued increases in Arctic Ocean primary production

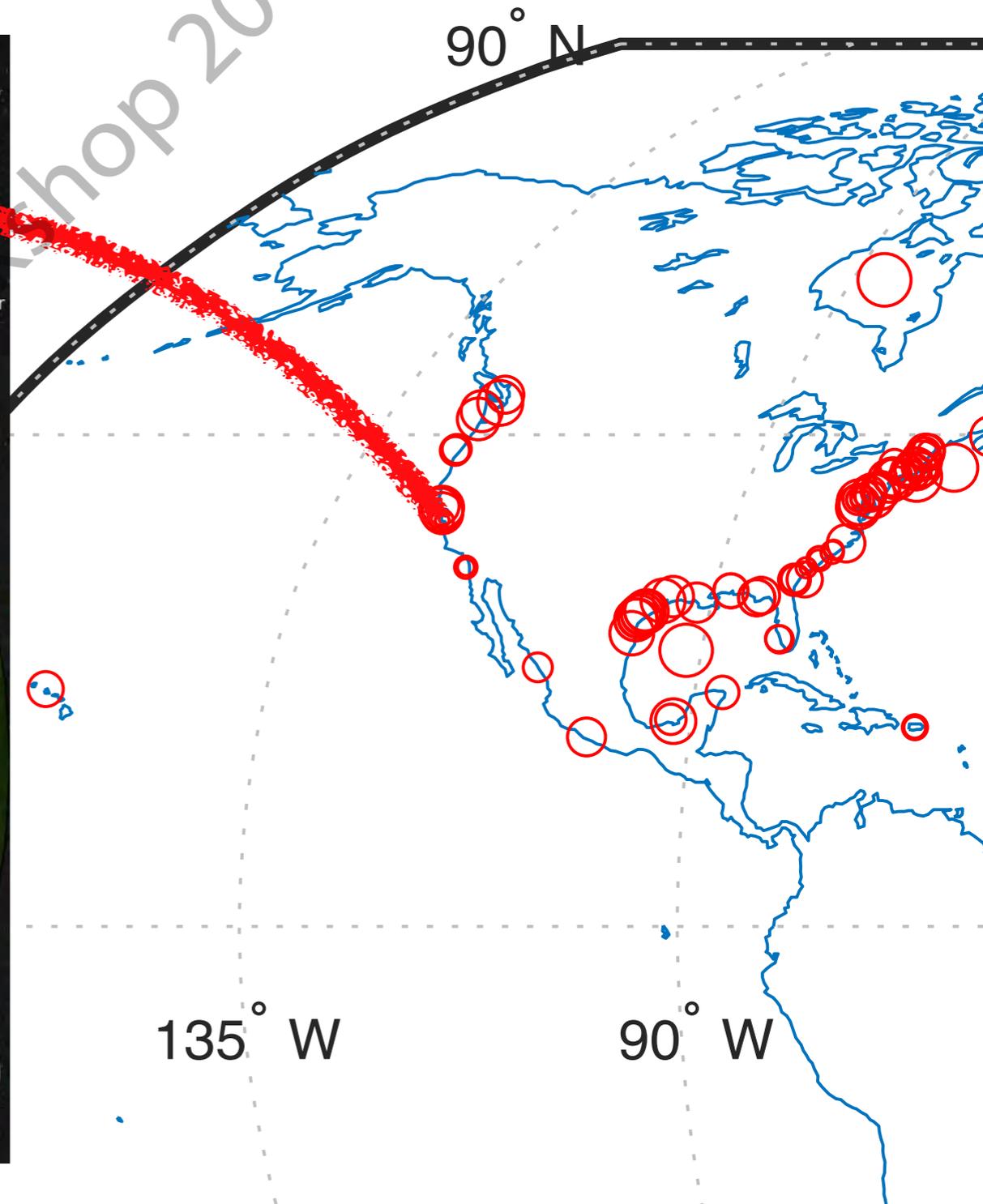
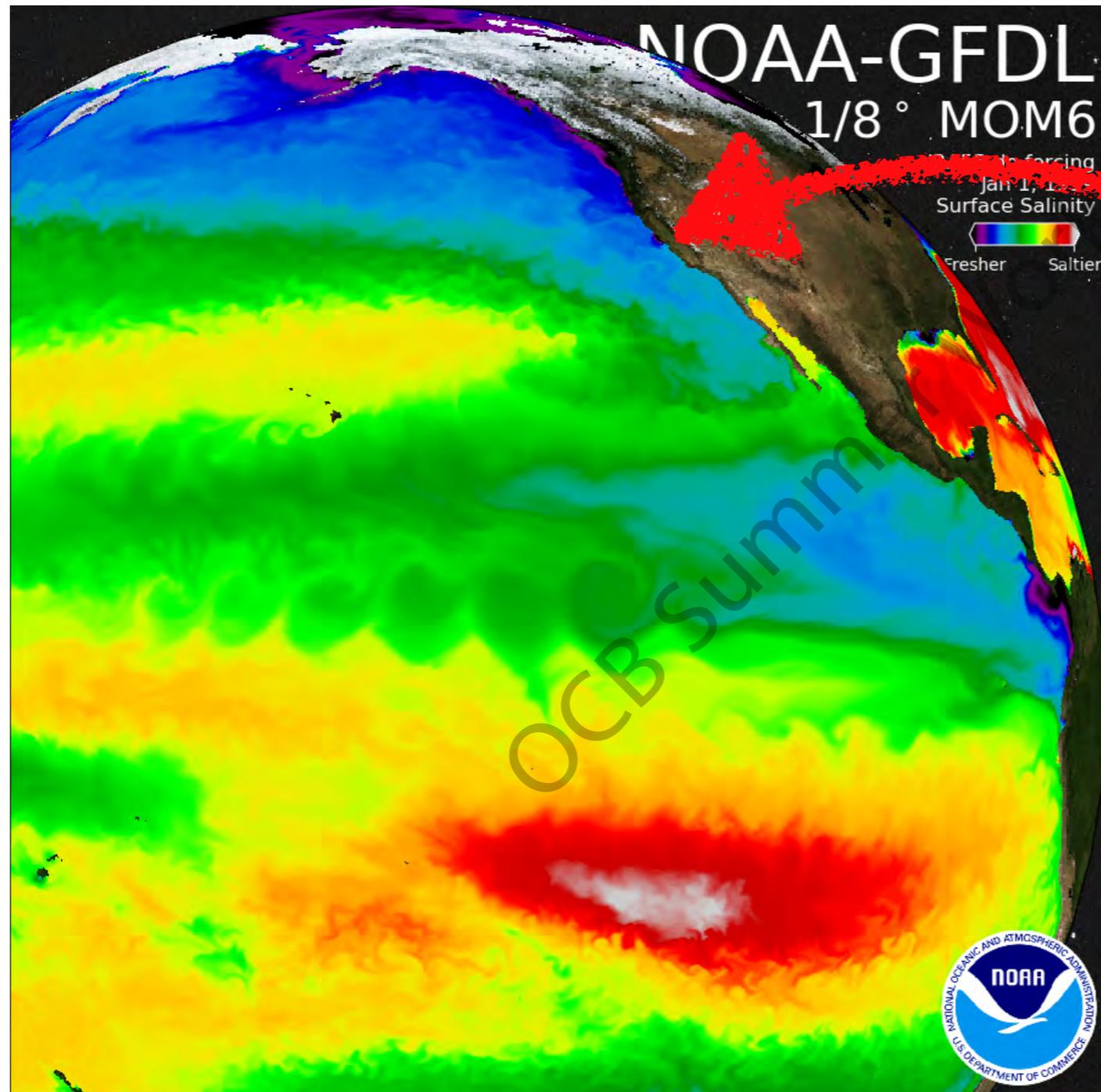
Kevin R. Arrigo\*, Gert L. van Dijken

Department of Earth System Science, Stanford University, Stanford, CA 94305, USA



**Fig. 2.** Changes in the amount of open water area in the Arctic Ocean between 1998 and 2012 based on three different metrics (summer maximum open water area, mean open water area between 1 May and 31 September, and annual mean open water area).

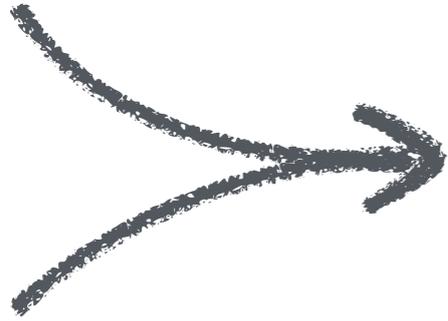
What are some possible applications of these ideas?  
(5) parameterizing sub-grid scale processes in GOMs



# In summary

Estuaries

Ecosystem metabolism scales nonlinearly with size  
*(related to changes in transport time driven primarily by depth)*



area-productivity relationships

*metabolic scaling theory  
may provide insights into  
estuarine and ocean physics*

Ocean

Community metabolism scales nonlinearly with size  
*(related to changes in transport time that scale with dissipation?)*

