From individuals to populations

Heterosigma cell. Photo: M. Black

Heterosigma Harmful Algal Bloom. Photo: K. Fredrickson

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Outline

1. Motivations: Large-scale models vs. small-scale heterogeneity

2. Observations: Statistics of movement at the individual level

3. Derivations: Spatially-explicit models of populations

4. Approximations: Large-scale effects of unresolved heterogeneity

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Societal applications of biogeochemical modeling


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Four degrees of warming 'likely'

By David Shukman
Environment correspondent, BBC News

In a dramatic acceleration of forecasts for global warming, UK scientists say the global average temperature could rise by 4C (7.2F) as early as 2060.

The Met Office study used projections of fossil fuel use that reflect the trend seen over the last 20 years.

Campaigners tried to point up the urgency of the UN climate talks

Their computer models also factored in new findings on how carbon dioxide is absorbed by the oceans and forests.

The finding was presented at an Oxford University conference exploring the implications of a 4C rise.

The results show a "best estimate" that 4C (measured from pre-industrial times) will be reached by 2070, with a possibility that it will come as early as 2060.

Richard Betts of the Met Office

"Previously we haven't looked

COPENHAGEN SUMMIT 2009

KEY STORIES
• Britons creating 'more emissions'
• $100bn a year for climate safety

Response of diatoms distribution to global warming and potential implications: A global model study

L. Bopp,[1] O. Aumont,[2] P. Cadule,[3] S. Alvain,[1] and M. Gehlen[1]

GEOPHYSICAL RESEARCH LETTERS, VOL. 32, L19606, doi:10.1029/2005GL023653, 2005

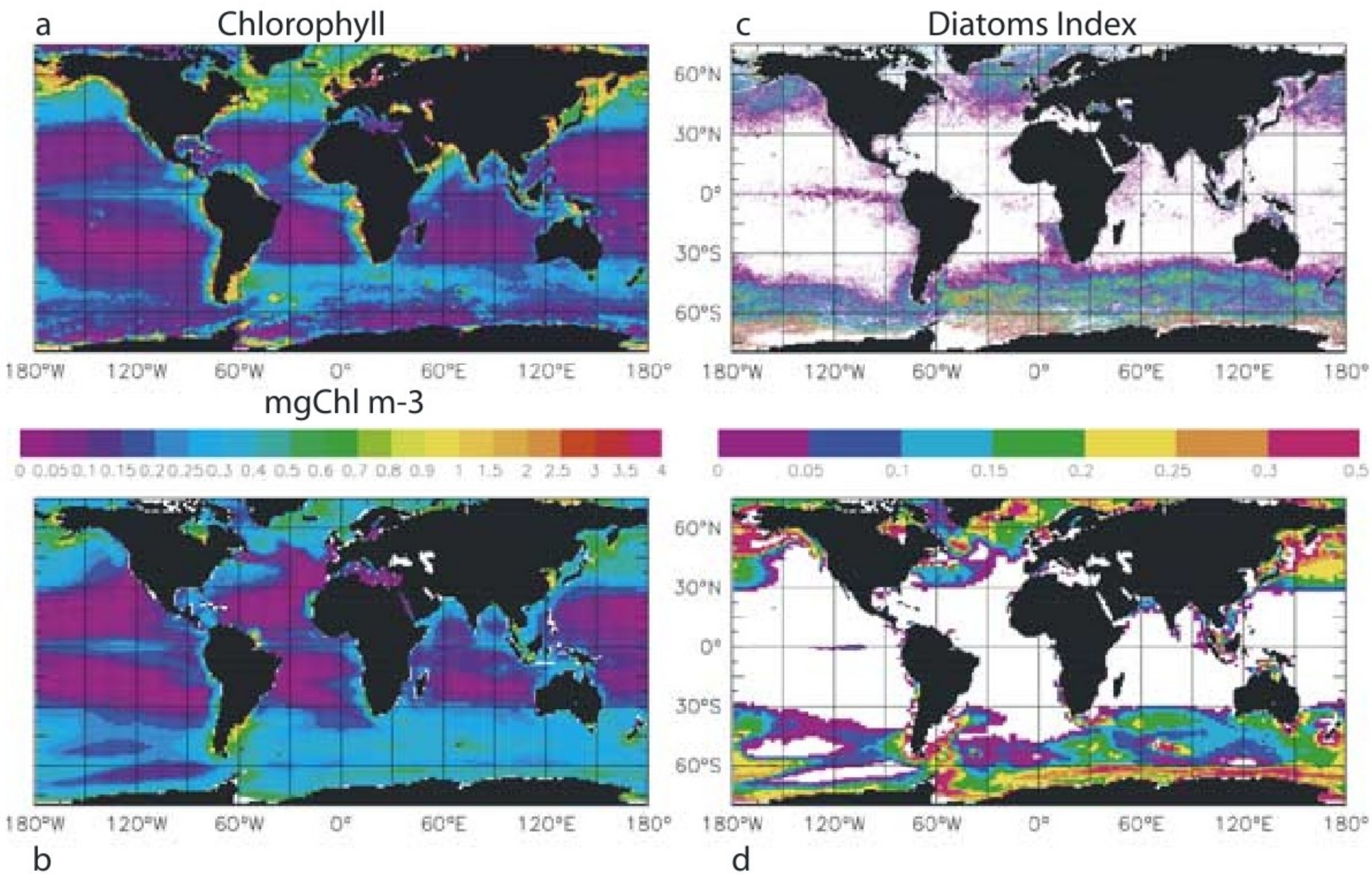
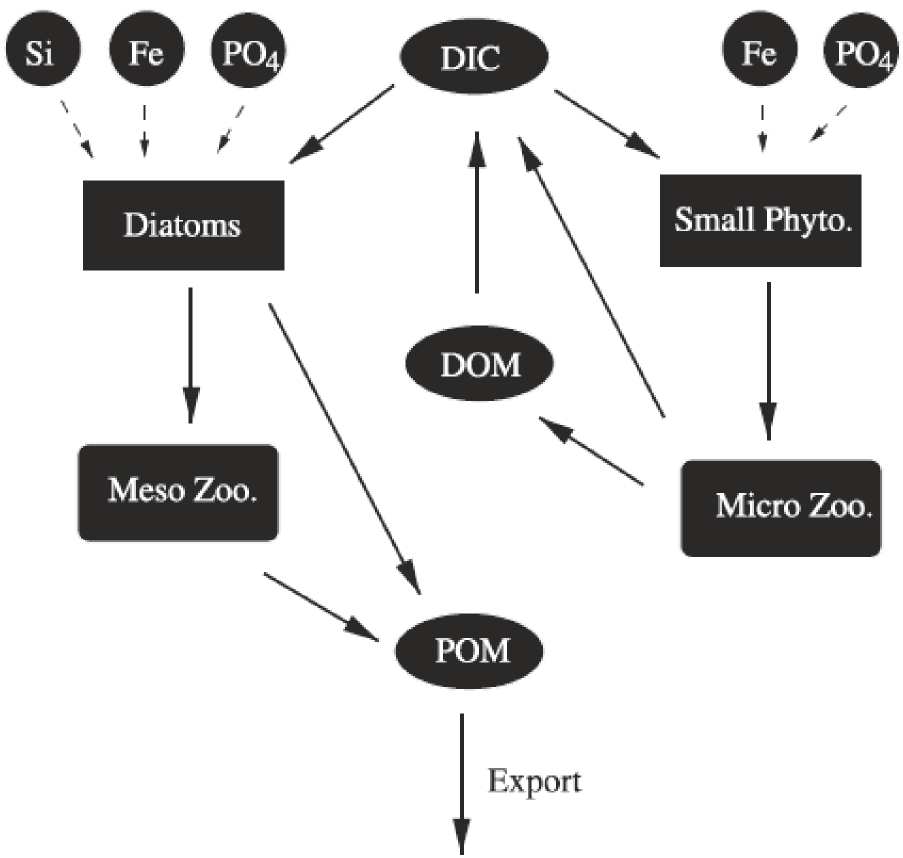


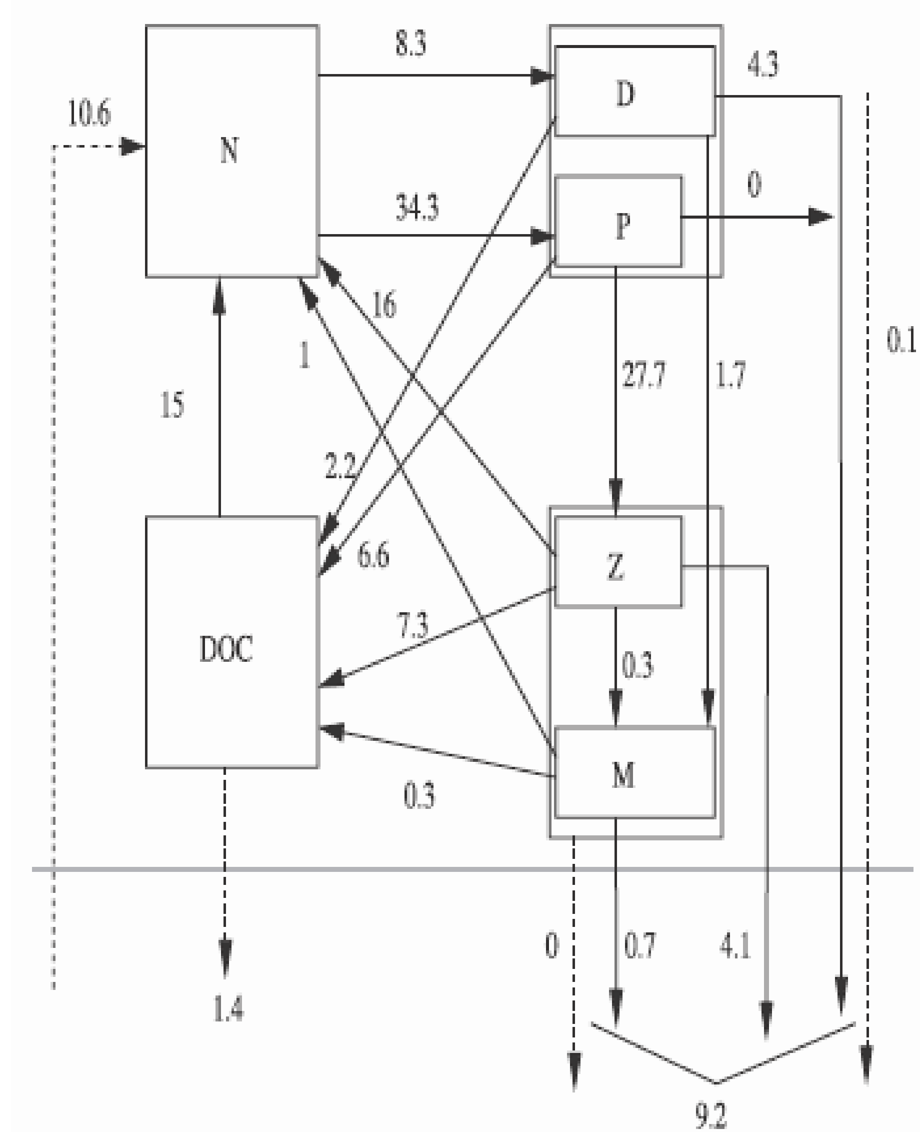
Figure 1. Satellite-derived and simulated distributions (a) and (b) of chlorophyll in mgChl m^{-3} and (c) and (d) of a diatoms index. The four panels represent climatological years, based on 1997–2003 SeaWiFs archive (Figures 1a and 1c) and on the first 10 years of our simulation (Figures 1b and 1d). The diatoms index represents the relative time in a year when diatoms are blooming, i.e., we divide the number of months when diatoms are blooming by the total number of months: PHYSAT directly diagnoses diatoms blooms [*Alvain et al.*, 2005] (Figure 1c) and diatoms blooms are diagnosed in the model when [*Chl*] > 0.5 mgChl m^{-3} and diatoms relative abundance >45% (Figure 1d).

Hamburg model of the Oceanic Carbon Cycle (HAMOCC5)

Aumount et al. (2003), Bopp et al. (2003, 2005)



Model schematic



Annual mean carbon flux (Gt C yr^{-1})

HAMOCC5: Biogeochemical model mechanics

Aumount et al. (2003)

A bunch of equations establishing key transfer mechanisms …

Table 1. Source/Sink Budget Due to Biogeochemical Processes in the Top 100 m of the Ocean Model

Sources/Sinks	
$S(P)$	$\mu^P L_m L_P P - m_P \frac{(P-P_{min})}{K_P+P} P - g_Z(P)Z - \gamma_P(P-P_{min})$
$S(D)$	$\mu^D L_m L_D D - m_D \frac{(D-D_{min})}{K_D+D} D - g_M(D)M - \gamma_D(D-D_{min})$
$S(D^\star)$	$\left(\frac{Si}{C}\right)\mu^D L_m L_D D^\star - m_D \frac{D}{K_D+D} D^\star - g_M(D)\frac{D^\star}{D} M - \gamma_D \frac{D^\star}{D}(D-D_{min})$
$S(Z)$	$\epsilon_Z \sigma_Z g_Z(P)Z - m_Z(Z-Z_{min}) - \gamma_Z(Z-Z_{min})$ - $g_M(Z)M$
$S(M)$	$\epsilon_M \sigma_M (g_M(D)+g_M(Z))M - m_M(M-M_{min}) - \gamma_M(M-M_{min})$
$S(DOC)$	$\gamma_P(P-P_{min})P + \gamma_D(D-D_{min})D + \gamma_Z(Z-Z_{min}) + \gamma_M(M-M_{min}) - r_{doc}(N)\,DOC$
$S(POC)$	$F_1 - r_{poc}POC$
$R_{C:P}S(N)$	$-\mu^P L_m L_P P - \mu^D L_m L_D D + \sigma_Z(1-\epsilon_Z)g_Z(P)Z + m_Z(Z-Z_{min}) + \sigma_M(1-\epsilon_M)(g_M(D)+g_Z(Z))M + m_M\epsilon_{can}(M-M_{min}) + r_{doc}(N)DOC$ $+ r_{poc}POC$
$S(Si)$	$-\left(\frac{Si}{C}\right)\mu^D L_m L_D D^\star + r(Si)$
$S(Fe)$	$\left(\frac{Fe}{C}\right)^P(-\mu^P L_m L_P P + \gamma_P(P-P_{min}) + \gamma_Z(Z-Z_{min}) + \gamma_M(M-M_{min}) + m_M(1-\epsilon_{can})(M-M_{min}) + \sigma_Z(1-\epsilon_Z)g_Z(P)Z$ $+ \sigma_M(1-\epsilon_M)g_M(Z)M + \left(\frac{Fe}{C}\right)^D(-\mu^D L_m L_D D + \sigma_M(1-\epsilon_M)g_M(D)M + \gamma_D(D-D_{min})D) + \left(\frac{Fe}{C}\right)^P - \left(\frac{Fe}{C}\right)^D \epsilon_M \sigma_M g_M(D)\,M$ $+ r_{poc}PFe - \lambda_{scav}\max(0, (Fe - 0.6\,nM))$
$S(PFe)$	$G(P, D, Z, M, z) - r_{poc}PFe$

HAMOCC5: Biogeochemical model mechanics

Aumount et al. (2003)

… modulated by a bunch of regulatory functions …

Table 2. Source/Sink Terms for Phytoplankton and Zooplankton

Process	Equation	Reference
	Phytoplankton	
Growth rate	$\mu = \frac{f(T)f(L)}{\sqrt{f(T)^2+f(L)^2}}$	*Jassby and Platt* [1976]
Light limitation	$f(L) = I_0 \alpha \mathrm{PAR} \frac{1}{z} \int_z e^{-kz} dz$	
Temperature dependence	$f(T) = ab^{cT}$	*Eppley* [1972]
Nutrient limitation for P	$L_P = \min\left(\frac{N}{K_N^P+N}, \frac{Fe}{K_{Fe}^P+Fe}\right)$	
Nutrient limitation for D	$L_D = \min\left(\frac{N}{K_N^D+N}, \frac{Fe}{K_{Fe}^D+Fe}, \frac{Si}{K_{Si}^D+Si}\right)$	
Chl/C in phytoplankton	$\frac{Chl^\star}{C} = \left(\frac{Chl}{C^M} - \left(\frac{Chl}{C}^M - \frac{Chl}{C}^m\right)\min\left(\frac{L}{I_{par}^{max}}, 1\right)\right)L_{P,D}$	*Doney et al.* [1996]
	Microzooplankton	
Grazed nanophytoplankton	$g_Z(P) = g_Z \frac{P}{K_Z+P}$	*Fasham et al.* [1990]
	Mesozooplankton	
Grazed diatoms	$g_M(D) = g_M \frac{p_D D}{K_M+p_D D+p_Z Z}$	*Fasham et al.* [1990]
Grazed microzooplankton	$g_M(Z) = g_M \frac{p_Z Z}{K_M+p_D D+p_Z Z}$	*Fasham et al.* [1990]
Preference for diatoms	$p_D = \frac{\pi_D D}{\pi_D D+\pi_Z Z}$	*Fasham et al.* [1990]
Preference for Z	$p_Z = \frac{\pi_Z Z}{\pi_D D+\pi_Z Z}$	*Fasham et al.* [1990]
	DOC	
Remineralization rate	$r_{doc}(N) = d_0 \frac{N}{N+k_d}$	*Six and Maier-Reimer* [1996]
	POC	
Export	$F_1 = (TPP_1 + TPP_2) \frac{\partial}{\partial z}\left(\frac{z}{100}\right)^{-0.8}$	*Suess* [1980]
Phytoplankton POC	$TPP_1 = \int_0^{100m}\left(m_P \frac{(P-P_{min})}{K_P+P} P + m_D \frac{(D-D_{min})}{K_D+D} D\right)dz$	
Zooplankton POC	$TPP_2 = \int_0^{100m}((1-\sigma_Z)g_Z(P)Z + (1-\sigma_M)(g_M(D)$ $+ g_Z(Z))M + m_M(1-\varepsilon_{can})(M-M_{min}))dz$	
	Silicate	
Export	$r(Si) = TSI \frac{\partial}{\partial z}\left(e^{-\frac{z}{6km}}\right)$	*Maier-Reimer* [1993]
Biogenic Si Production	$TSI = \int_0^{100m}\left(m_D \frac{D}{K_D+D} D^\star + g_M(D)\frac{D^\star}{D} M + \gamma_D \frac{D^\star}{D}(D-D_{min})\right)dz$	

HAMOCC5: Biogeochemical model mechanics

Aumount et al. (2003)

… specified by a bunch of parameters.

Table 3. Biological Parameter Values and Definitions[a]

Symbol	Unit	Value	Definition
		Phytoplankton Size-Classes	
a	day^{-1}	0.851	growth rate at 0°C
b		1.066	temperature sensitivity of growth
c	$°C^{-1}$	1	temperature dependence of growth
α	$day^{-1} m^2 W^{-1}$	0.03	initial slope of P-I curve
k	$m^2 (W\ day)^{-1}$	0.025	light extinction coefficient
I_0	$W\ m^{-2}$		irradiance at the surface
PAR		0.40	photosynthetically active radiation
K_N	$\mu mol\ P\ L^{-1}$	0.03/0.1	half-saturation constant for phosphate uptake
K_{Fe}	$nmol\ Fe\ L^{-1}$	0.02/0.12	half-saturation constant for iron uptake
K_{Si}^D	$\mu mol\ Si\ L^{-1}$	0.8–8	half-saturation constant for silicate uptake
P_{min}, D_{min}	$\mu mol\ C\ L^{-1}$	0.01	minimum phytoplankton concentration
K_P, K_D	$\mu mol\ C\ L^{-1}$	0.05	half-saturation constant for phytoplankton mortality
γ	day^{-1}	0.05/0.03	exudation rate of DOC
m_P	day^{-1}	0.008	specific mortality rate of nanophytoplankton
m_{min}	day^{-1}	0.01	minimum mortality rate of diatoms
m_{max}	day^{-1}	0.2	maximum mortality rate of diatoms
$\frac{Chl}{C^M}$	mg Chl $(mg\ C)^{-1}$	$\frac{1}{37}$	maximum \raise 1pt\frac{{Chl}\over{C}} ratio
$\frac{Chl}{C^M}$	mg Chl $(mg\ C)^{-1}$	$\frac{1}{90}$	minimum \frac{{Chl}\over{C}} ratio
I_{par}^{max}	$W\ m^{-2}$	90	critical irradiance for photoadaptation
$\left(\frac{Si}{C}\right)^{av}$	$\mu mol\ Si\ (\mu mol\ C)^{-1}$	0.13	average $\frac{Si}{C}$ for diatoms
		Zooplankton Size-Classes	
ϵ		0.4	grazing efficiency
σ		0.15/0.25	egestion as faecal pellets
g	day^{-1}	14/3	maximum grazing rate
K_Z, K_M	$\mu mol\ C\ L^{-1}$	18	half-saturation constant for grazing
π_D, π_Z		0.5, 0.5	mesozooplankton feeding preferences
m	day^{-1}	0.01/0.05	specific mortality rate
γ	day^{-1}	0.25/0.05	excretion rate of DOC
ϵ_{can}		0.7	POC loss from higher trophic levels
Z_{min}, M_{min}	$\mu mol\ C\ L^{-1}$	0.01	minimum zooplankton concentration
		Organic Matter	
λ_{DOC}	day^{-1}	0.01	DOC remineralization rate
k_d	$\mu mol\ P\ L^{-1}$	0.3	half-saturation constant for DOC remineralization
r_{poc}	yr^{-1}	0.24	detrital breakdown rate
$R_{C:P}$		122:1	Redfield ratio of carbon to phosphate
		Iron	
$\frac{Fe}{C}^P$		4×10^{-6}	ratio of iron to carbon in zooplankton and nanophytoplankton
$\frac{Fe}{C}^{min}$		3×10^{-6}	minimum ratio of iron to carbon in diatoms
$\frac{Fe}{C}^{\star}$		17×10^{-6}	slope of the ratio of iron to carbon for diatoms
λ_{scav}^0	yr^{-1}	0.005	minimum scavenging rate of iron
$\lambda_{scav}^{\star}$	$yr^{-1}\ (\mu mol\ C\ L)^{-1}$	5×10^3	slope for the scavenging rate of iron

[a]When two values are given (separated by a /), the first value refers to the smallest size-class (nanophytoplankton or microzooplankton) and the second value refers to the largest size-class (diatoms or mesozooplankton).

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$S(D^\star)$	$\left(\frac{Si}{C}\right)\mu^D L_m L_D D^\star - m_D \frac{D}{K_D+D} D^\star - g_M(D)\frac{D^\star}{D} M - \gamma_D \frac{D^\star}{D}(D-D_{min})$
$S(Z)$	$\epsilon_Z \sigma_Z g_Z(P)Z - m_Z(Z-Z_{min}) - \gamma_Z(Z-Z_{min})$ - $g_M(Z)M$
$S(M)$	$\epsilon_M \sigma_M (g_M(D) + g_M(Z))M - m_M(M-M_{min}) - \gamma_M(M-M_{min})$
$S(DOC)$	$\gamma_P(P-P_{min})P + \gamma_D(D-D_{min})D + \gamma_Z(Z-Z_{min}) + \gamma_M(M-M_{min}) - r_{doc}(N)\,DOC$
$S(POC)$	$F_1 - r_{poc}POC$
$R_{C:P}S(N)$	$-\mu^P L_m L_P P - \mu^D L_m L_D D + \sigma_Z(1-\epsilon_Z)g_Z(P)Z + m_Z(Z-Z_{min}) + \sigma_M(1-\epsilon_M)(g_M(D)+g_Z(Z))M + m_M\,\epsilon_{can}(M-M_{min}) + r_{doc}(N)DOC$ $+ r_{poc}POC$
$S(Si)$	$-\left(\frac{Si}{C}\right)\mu^D L_m L_D D^\star + r(Si)$
$S(Fe)$	$\left(\frac{Fe}{C}\right)^P(-\mu^P L_m L_P P + \gamma_P(P-P_{min}) + \gamma_Z(Z-Z_{min}) + \gamma_M(M-M_{min}) + m_M(1-\epsilon_{can})(M-M_{min}) + \sigma_Z(1-\epsilon_Z)g_Z(P)Z$ $+ \sigma_M(1-\epsilon_M)g_M(Z)M + \left(\frac{Fe}{C}\right)^D(-\mu^D L_m L_D D + \sigma_M(1-\epsilon_M)g_M(D)M + \gamma_D(D-D_{min})D) + \left(\frac{Fe}{C}\right)^P - \left(\frac{Fe}{C}\right)^D \epsilon_M\,\sigma_M g_M(D)\,M$ $+ r_{poc}PFe - \lambda_{scav}\max(0, (Fe - 0.6\,nM))$
$S(PFe)$	$G(P, D, Z, M, z) - r_{poc}PFe$

HAMOCC5: Dynamics of “small phytoplankton”, *P*

Change in local density of small phytoplankton = Spatial transport by physical processes + Sources and sinks due to biological processes

$$S(P) = \mu^P L_m L_P P - m_P \frac{(P-P_{min})}{K_P+P} P - g_Z(P)Z - \gamma_P(P - P_{min})$$

Source/sink rate

Production of new cells ∝ *P*, limited by nutrients, light, temperature

Mortality ∝ *P* (except at low density)

Consumption by microzooplankton ∝ *Z*, regulated by $g_z(P)$

Exudation of *DOC* ∝ *P* (except at low density)

HAMOCC5: Biogeochemical model mechanics

Aumount et al. (2003)

Phytoplankton

Growth rate	$\mu = \frac{f(T)f(L)}{\sqrt{f(T)^2+f(L)^2}}$
Light limitation	$f(L) = I_0 \alpha \mathrm{PAR} \frac{1}{z} \int_z e^{-kz} dz$
Temperature dependence	$f(T) = ab^{cT}$
Nutrient limitation for P	$L_P = \min\left(\frac{N}{K_N^P+N}, \frac{Fe}{K_{Fe}^P+Fe}\right)$
Nutrient limitation for D	$L_D = \min\left(\frac{N}{K_N^D+N}, \frac{Fe}{K_{Fe}^D+Fe}, \frac{Si}{K_{Si}^D+Si}\right)$
Chl/C in phytoplankton	$\frac{Chl^\star}{C} = \left(\frac{Chl}{C^M} - \left(\frac{Chl^M}{C} - \frac{Chl^m}{C}\right)\min\left(\frac{L}{I_{par}^{max}}, 1\right)\right)L_{P,D}$

Microzooplankton

Grazed nanophytoplankton	$\boxed{g_Z(P) = g_Z \frac{P}{K_Z+P}}$

$$\boxed{g_Z(P) = g_Z \frac{P}{K_Z+P}}$$

Mesozooplankton

Grazed diatoms	$g_M(D) = g_M \frac{p_D D}{K_M+p_D D+p_Z Z}$
Grazed microzooplankton	$g_M(Z) = g_M \frac{p_Z Z}{K_M+p_D D+p_Z Z}$
Preference for diatoms	$p_D = \frac{\pi_D D}{\pi_D D+\pi_Z Z}$
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g = 14 day^{-1}

K_Z = 18 $\mu mol\ C\ L^{-1}$

Trophic Interaction Rates (Functional Responses)

Assumptions:

1) The amount of food found and eaten is proportional to time spent searching (T_{search})

2) It takes time to chew, swallow and digest food (a.k.a. food handling time, $T_{handling}$)

3) Foragers must spend part of the time searching and part of the time handling food

Question:

How much food does an animal obtain e.g., when food is abundant (T_{search} is short) or when food is scarce (T_{search} is long)?

Analysis: Time budget $T_{search} = c\, d^{-1}$, d = food concentration

Fraction of time searching $$F = \frac{T_{search}}{T_{search} + T_{handling}}$$

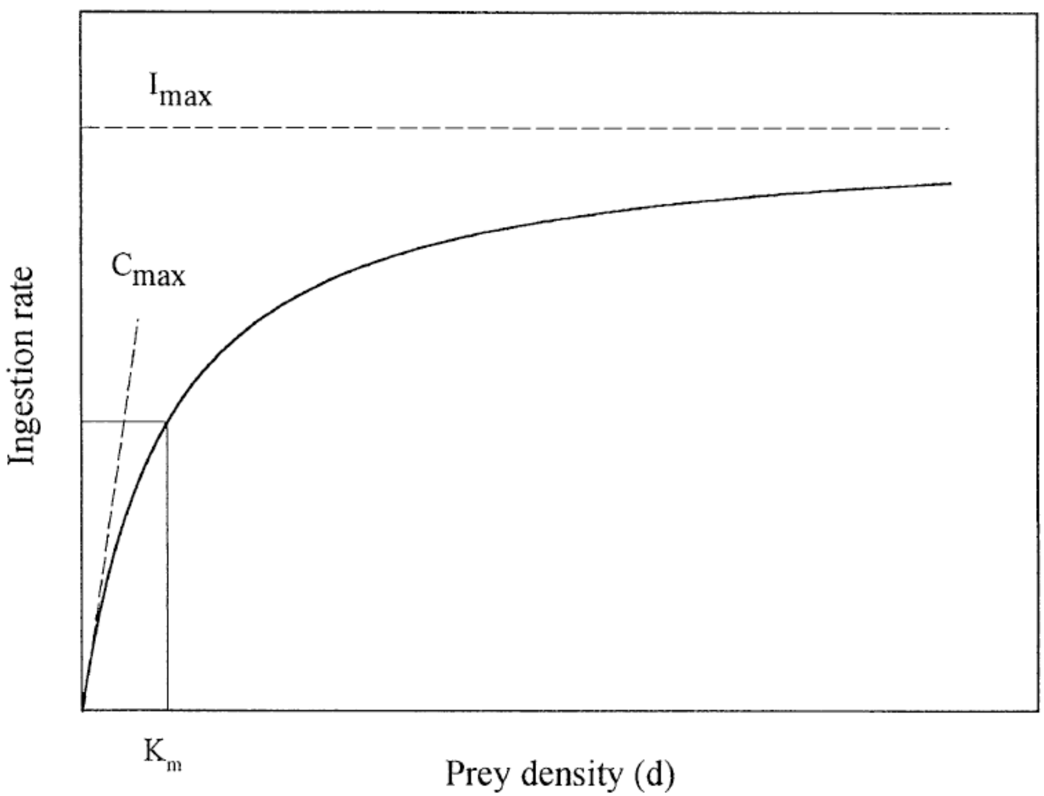
Average feeding rate $$= \frac{F}{T_{search}} = \frac{d}{c + d\, T_{handling}}$$

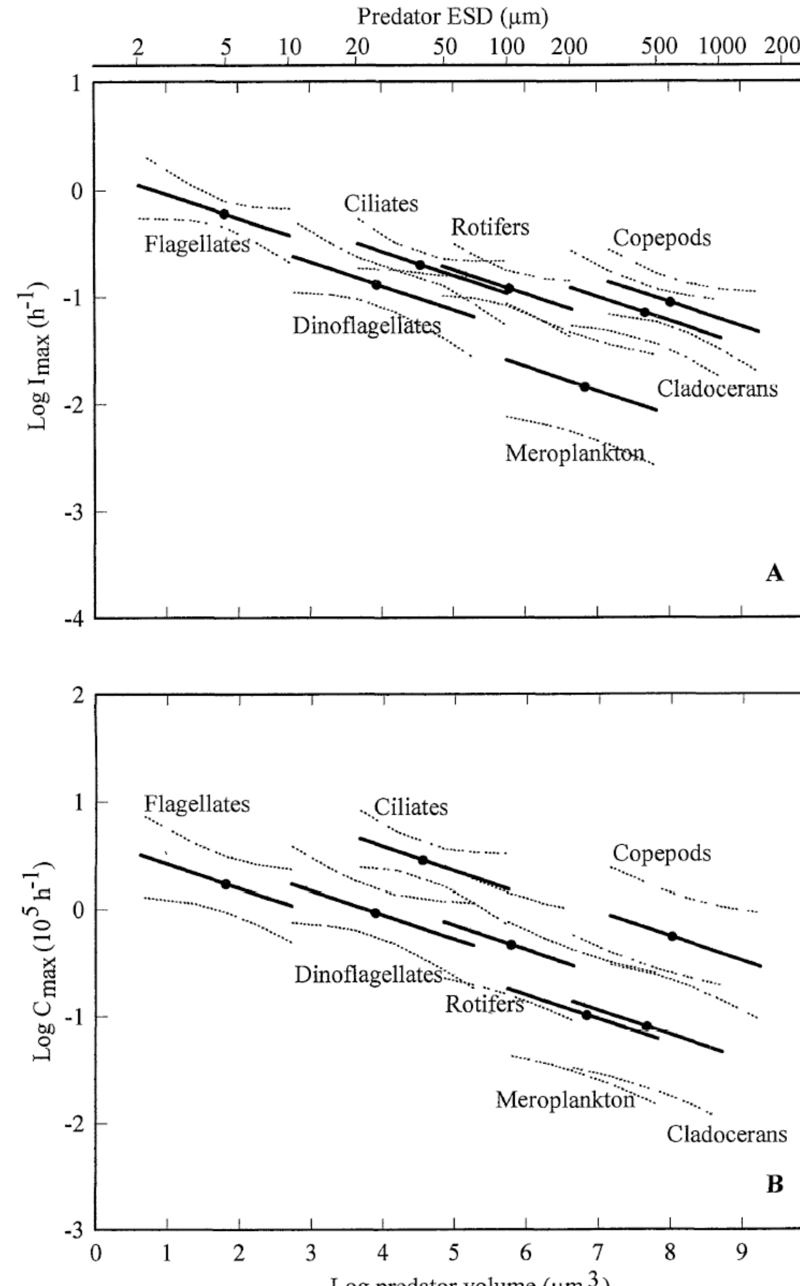
Functional Response: Concentration and Consumption

e.g. Hansen *et al.* 1997

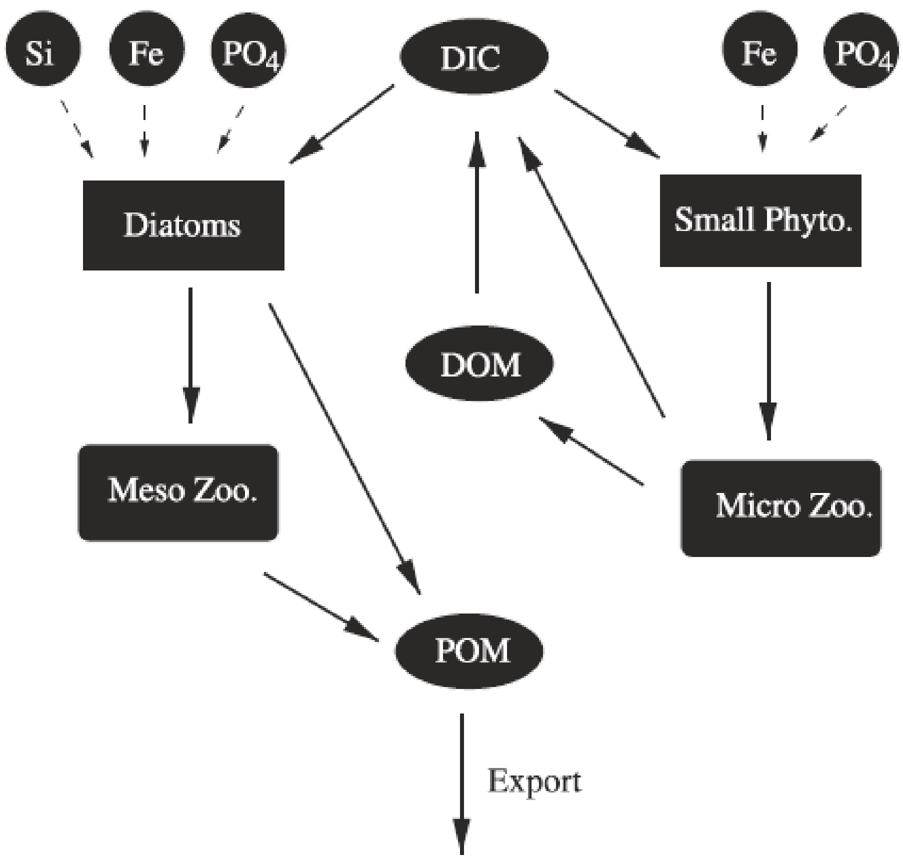
Consumption of resources is a non-linear function of resource concentration.

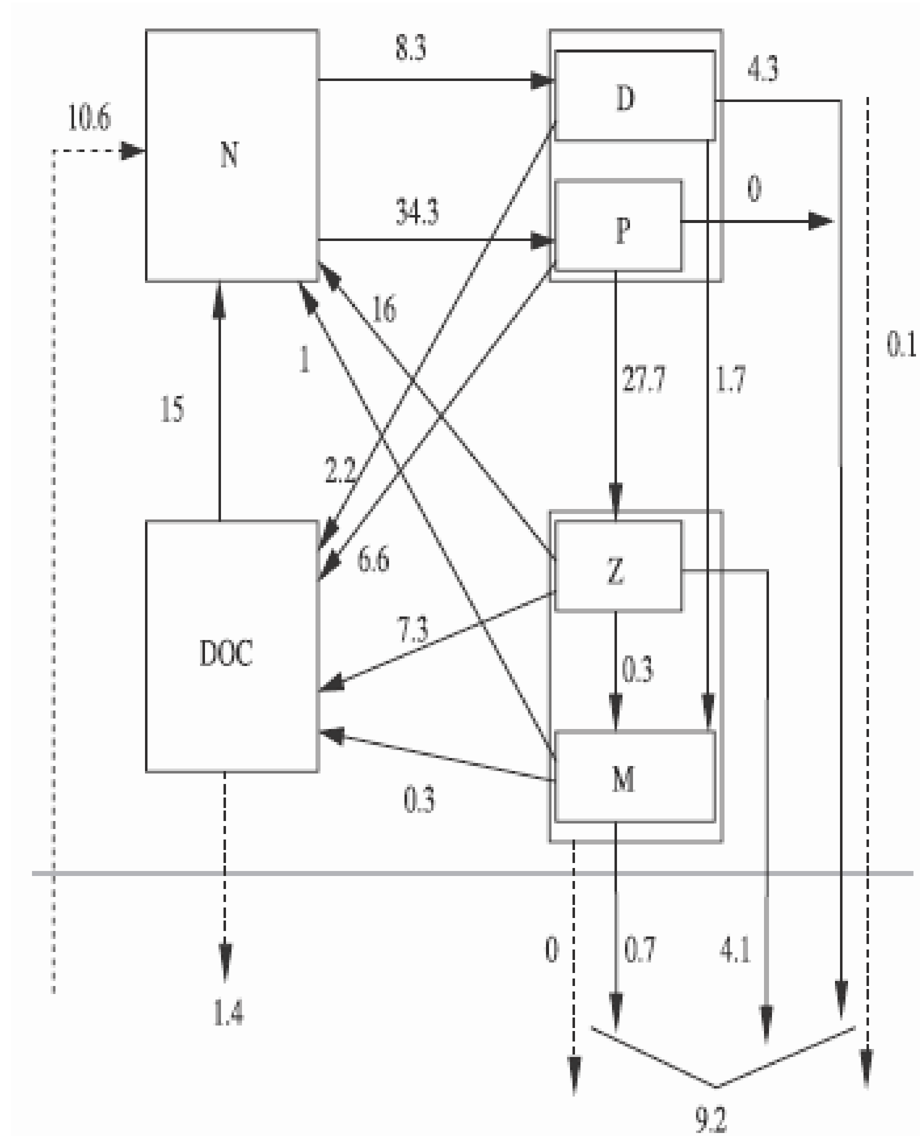
$$I(r) = \frac{c_0 r}{c_1 + r}$$





Hamburg model of the Oceanic Carbon Cycle (HAMOCC5)





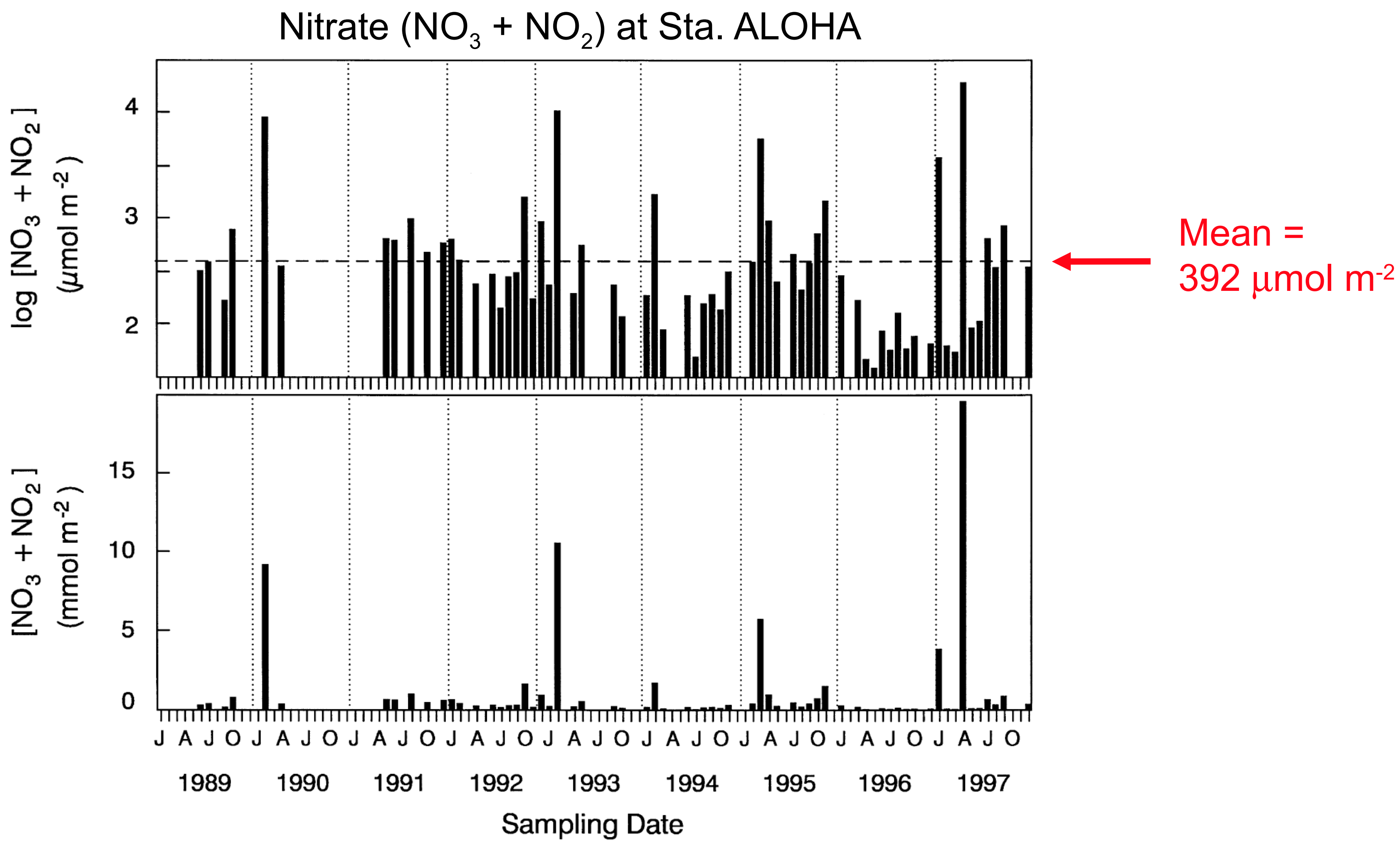
What's needed to increase resolution...?

Marine ecosystems are highly diverse.

Marine environments are spatially and temporally heterogeneous across a wide spectrum of scales.

Aperiodic nutrient supply in the North Pacific Subtropical Gyre

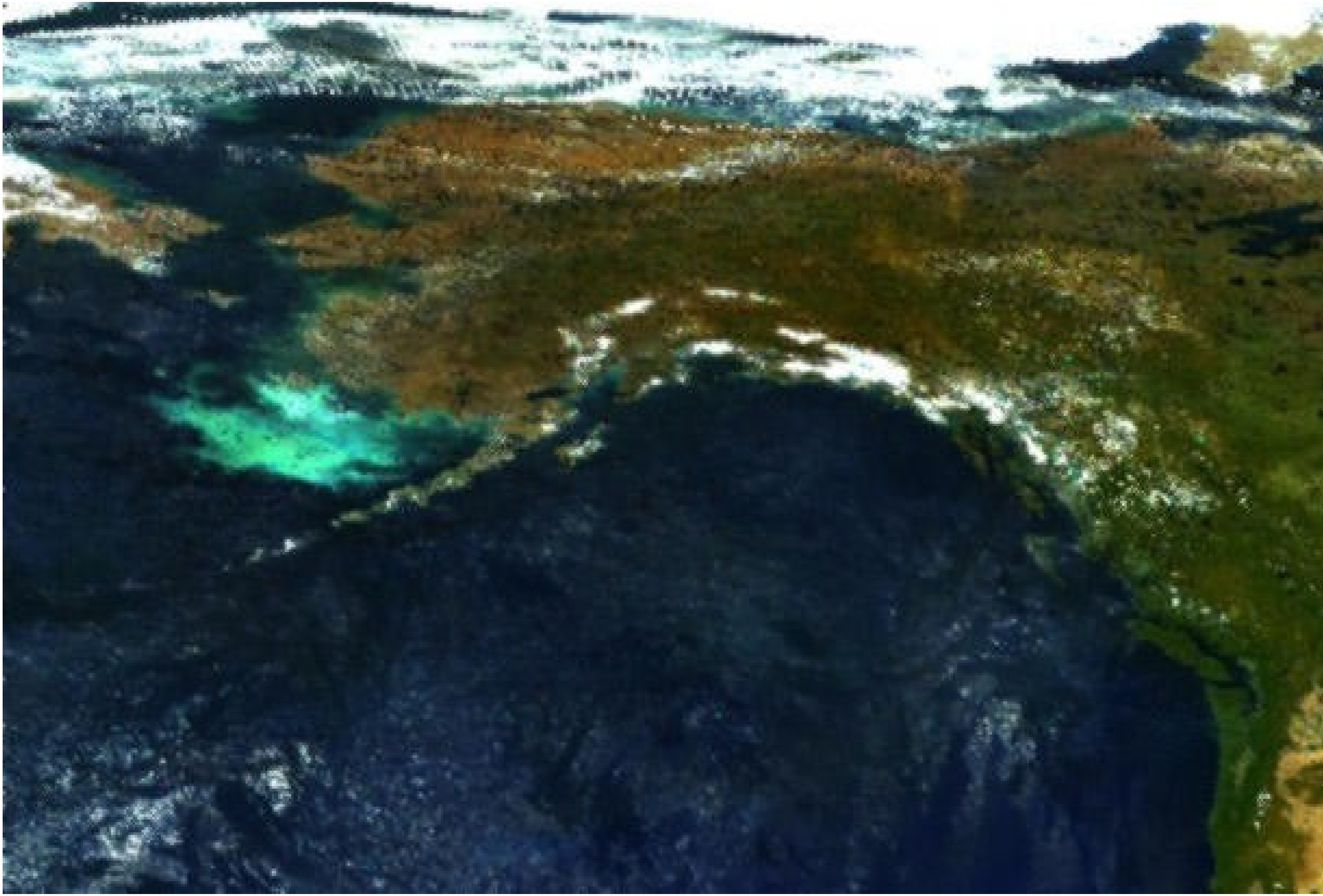
"Broad-scale descriptions of general ocean circulation and major biogeochemical cycles … ignore many potentially important but more stochastic events that may affect the local resupply of nutrients to the surface ocean." Karl (1999)



Nutrient supply mechanisms:

internal waves & tides, mesoscale eddies, Ekman pumping, atmospheric storms

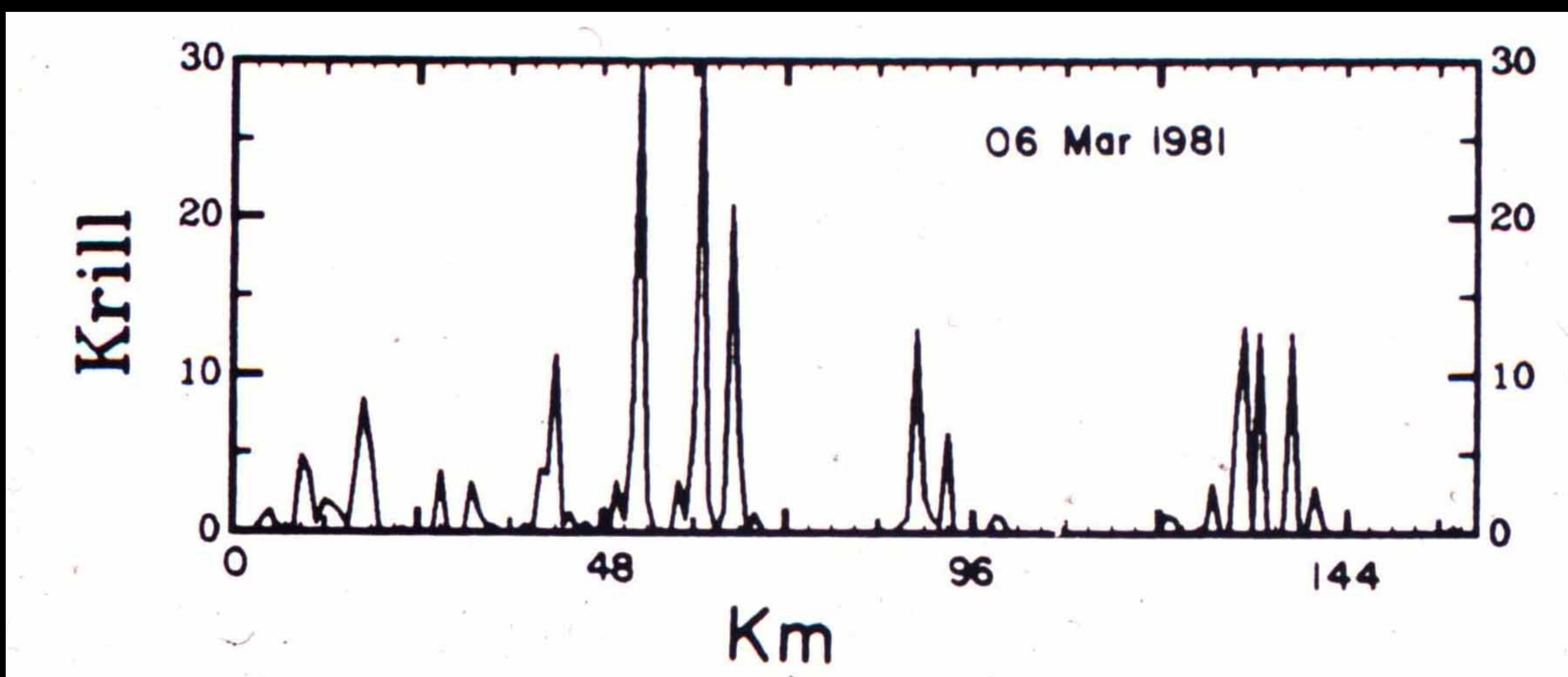
Coccolithophorid (*Emiliania huxleyi*) bloom in the Bering Sea



Spatial variability in krill biomass in the Southern Ocean

K. Daly

R. R. Veit



Antarctic krill (*Euphausia superba*) near Elephant Island

Video taken at *ca*. 2 meters depth by R. R. Veit

Thin layers in East Sound, Orcas Island, WA

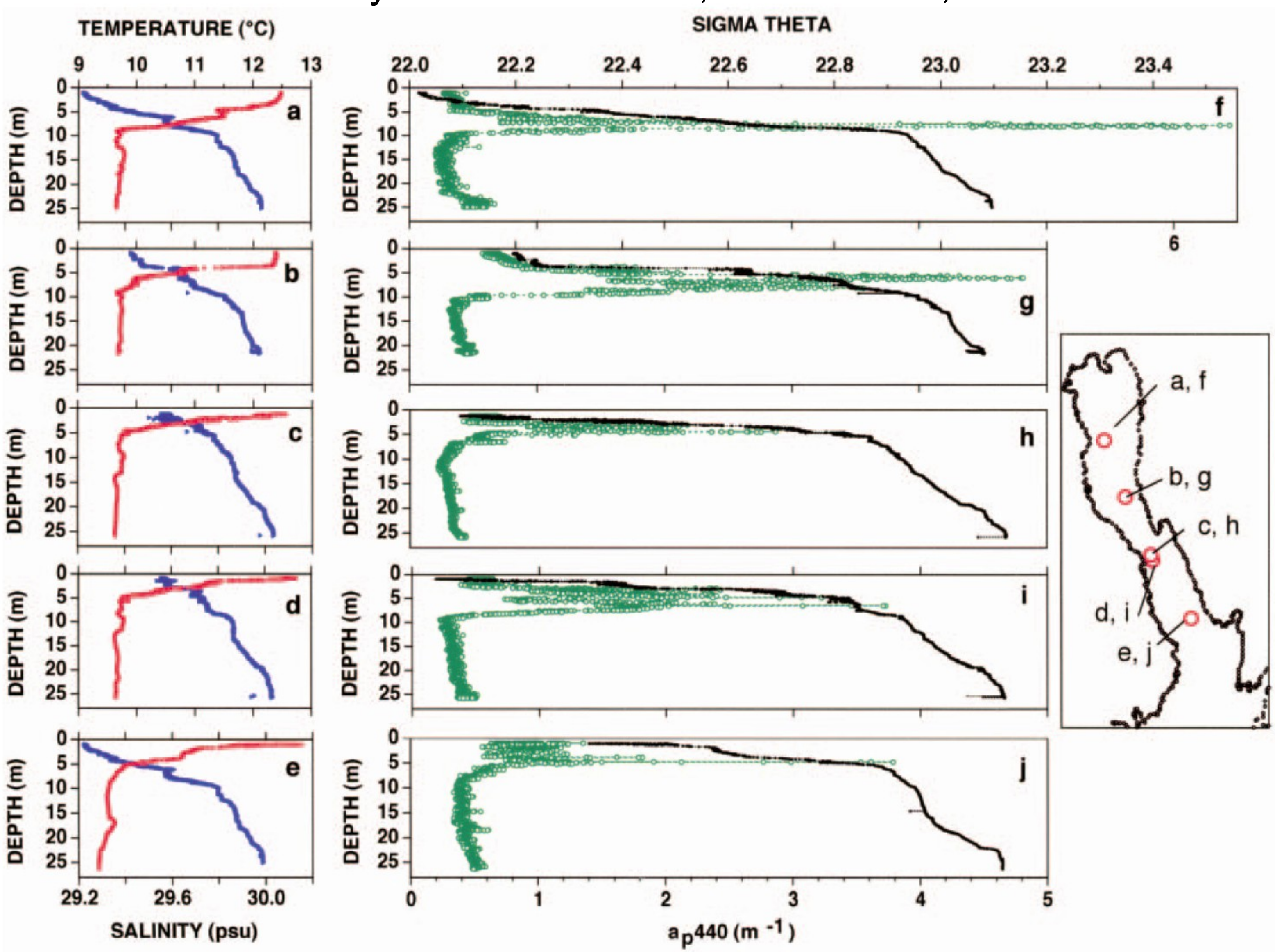


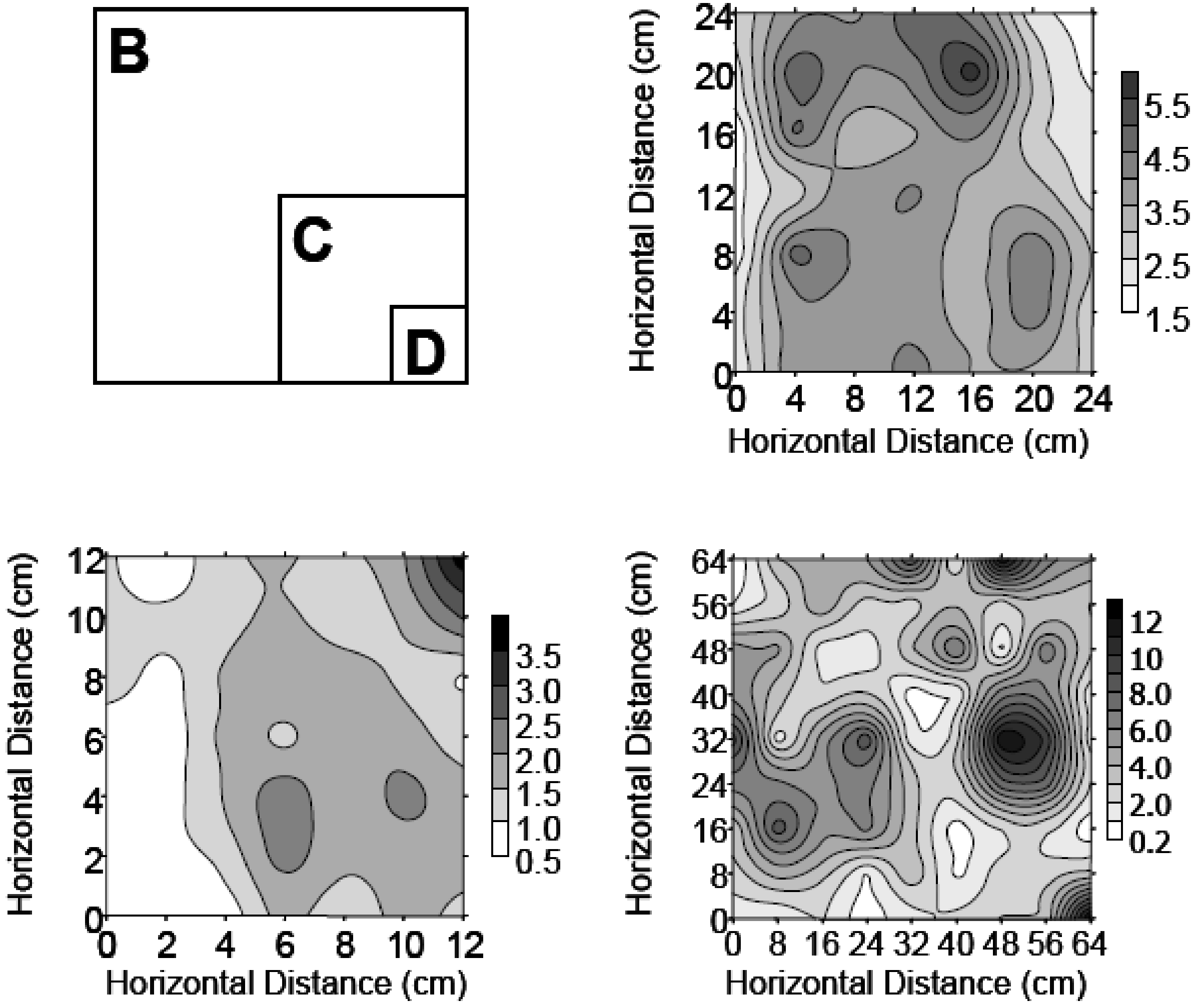
Fig. 5. Initial physical and optical structure in East Sound on May 23, 1996. (a–e) Temperature (red) and salinity (blue) profiles; (f–j) particulate absorption, a_p440 (green) and sigma theta (black) profiles. Inset map shows stations where samples were collected

SIGMA THETA
PARTICULATE ABSORPTION
TEMPERATURE
SALINITY

Rines et al. (2002) Mar. Ecol. Prog. Ser. 225:123-137

Fine-scale variability in cell abundance

Waters (2003)



[eukaryotic cell abundance (x 10^3 cells ml^{-1})]

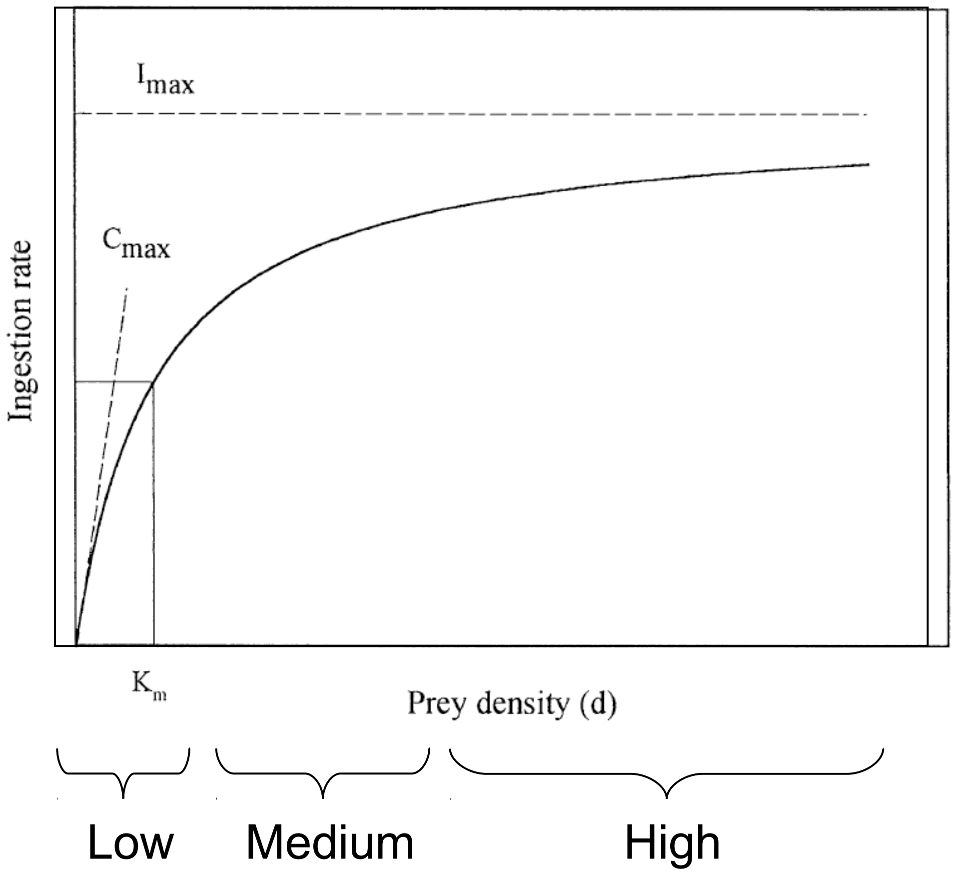
2-dimensional syringe sampler array data:
consumers and resources vary by >10x over a few cms.

Functional Response: Concentration and Consumption

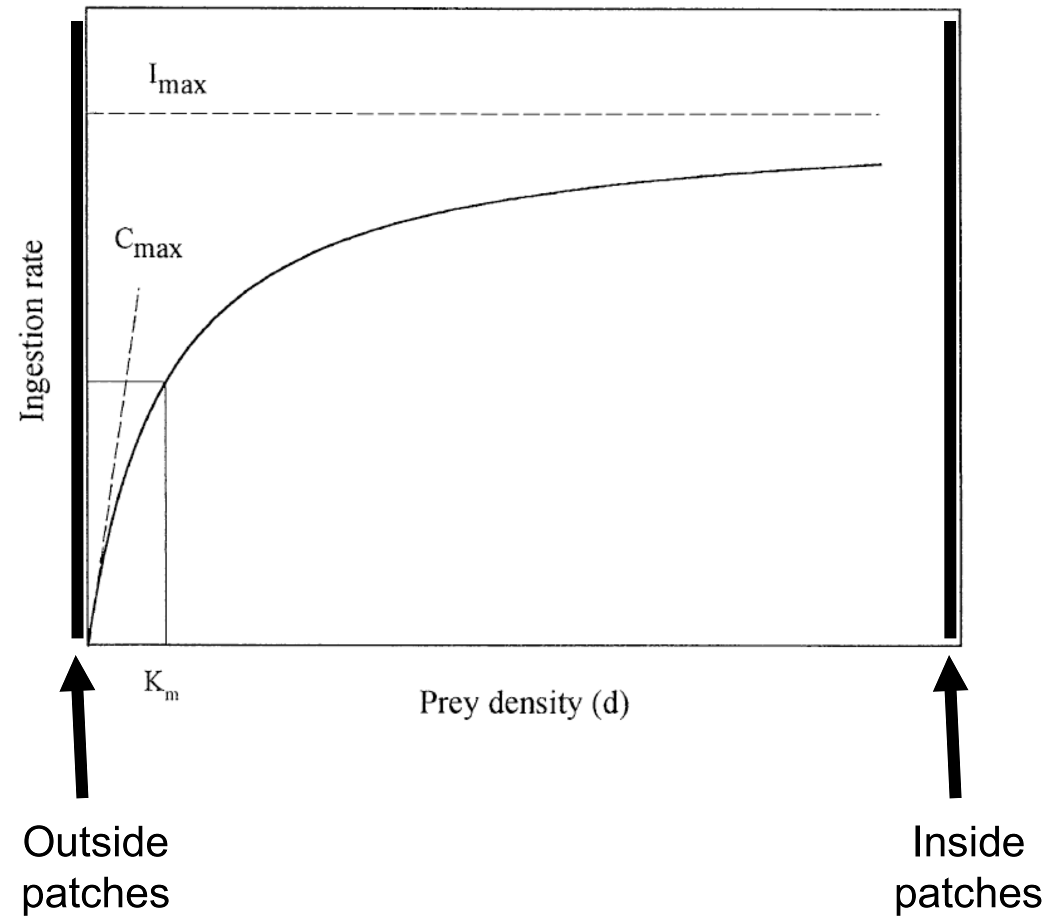
Consumption of resources is a non-linear function of mean resource density.

Consumption of resources is a function of time spent in patches.

"Mean field" resource perspective

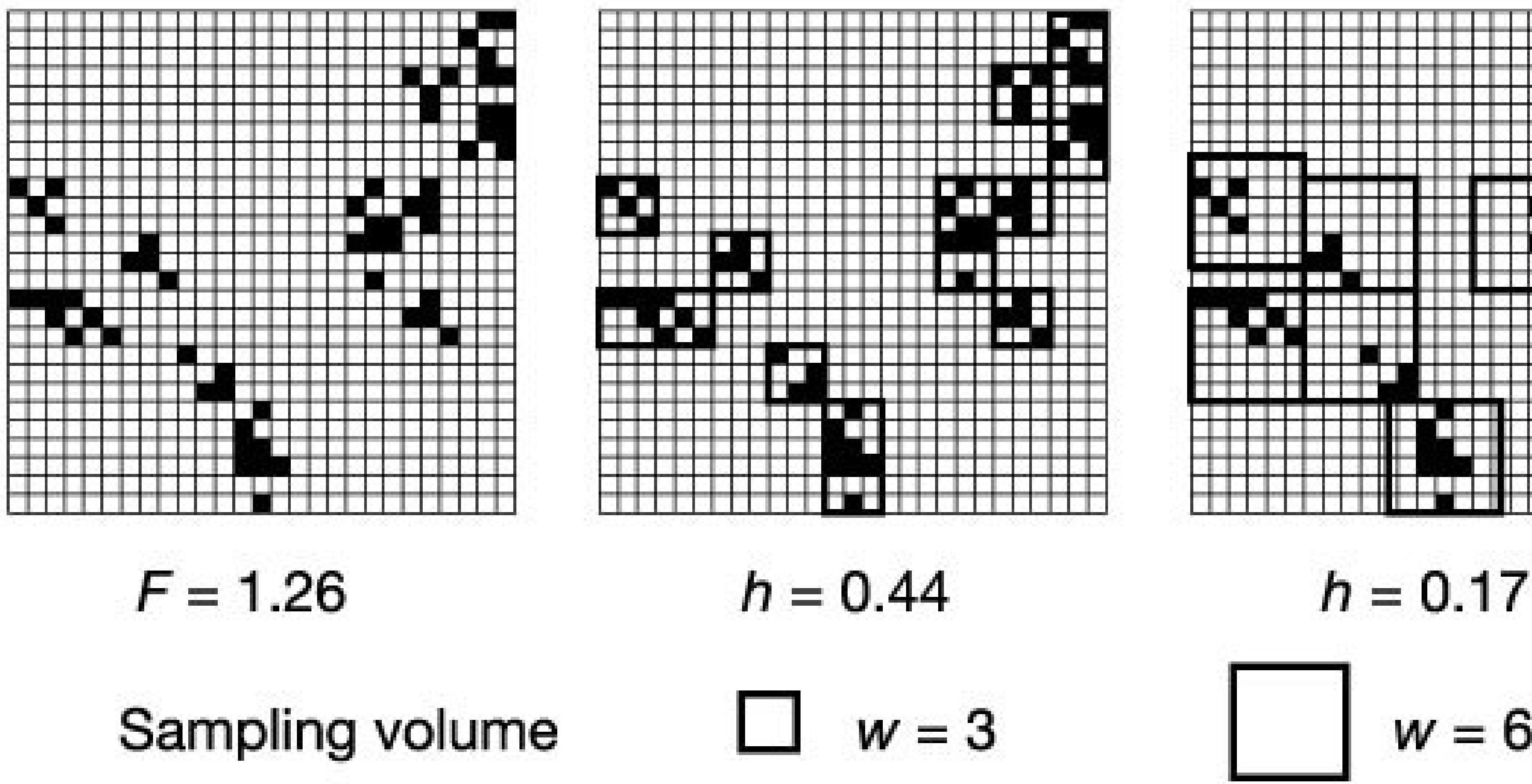


"Patchy" resource perspective



Fractal Landscapes
Haskell et al. 2002

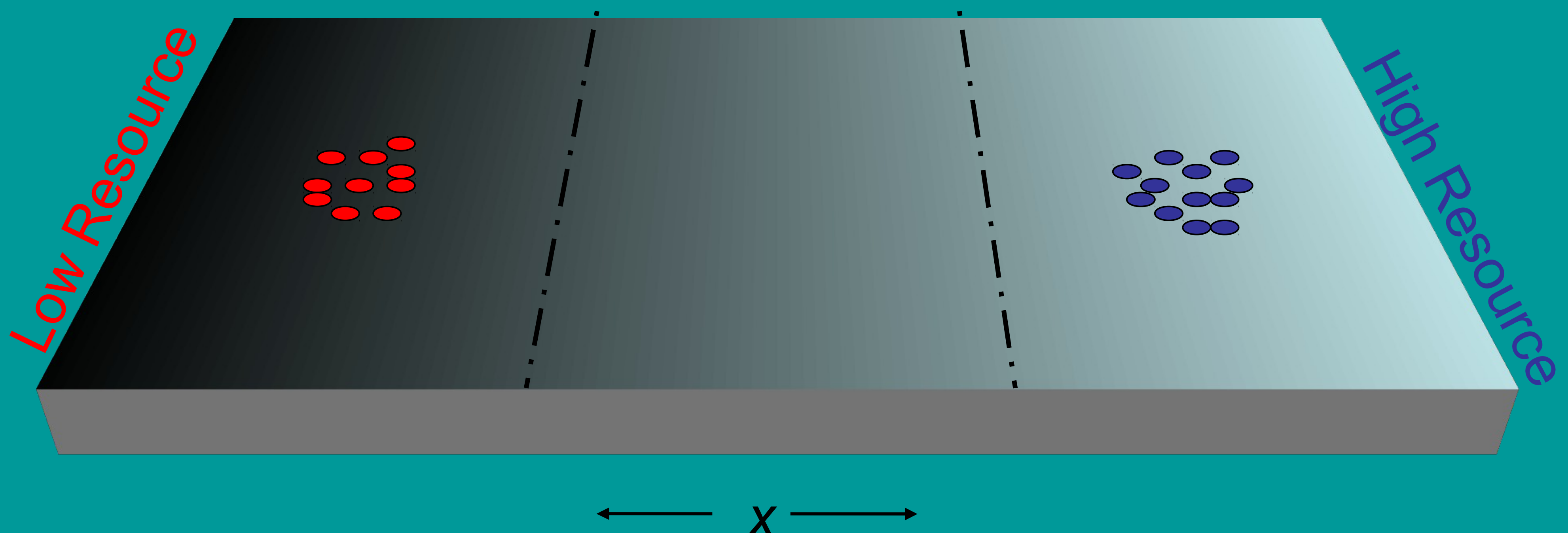
“Heterogeneity is largely missing from models of consumer-resource and other species interactions in ecology” Ritchie 2010



“The resource distribution was generated using random "Sierpinski gaskets"25. Note that the species with the larger sampling volume encounters a lower average density of resources per sampling volume but requires fewer sampling volumes to incorporate all resources.”

Foraging with sensory constraints

Biased Random Walks Mediated by Internal States



Foraging with sensory constraints

Biased Random Walks Mediated by Internal States