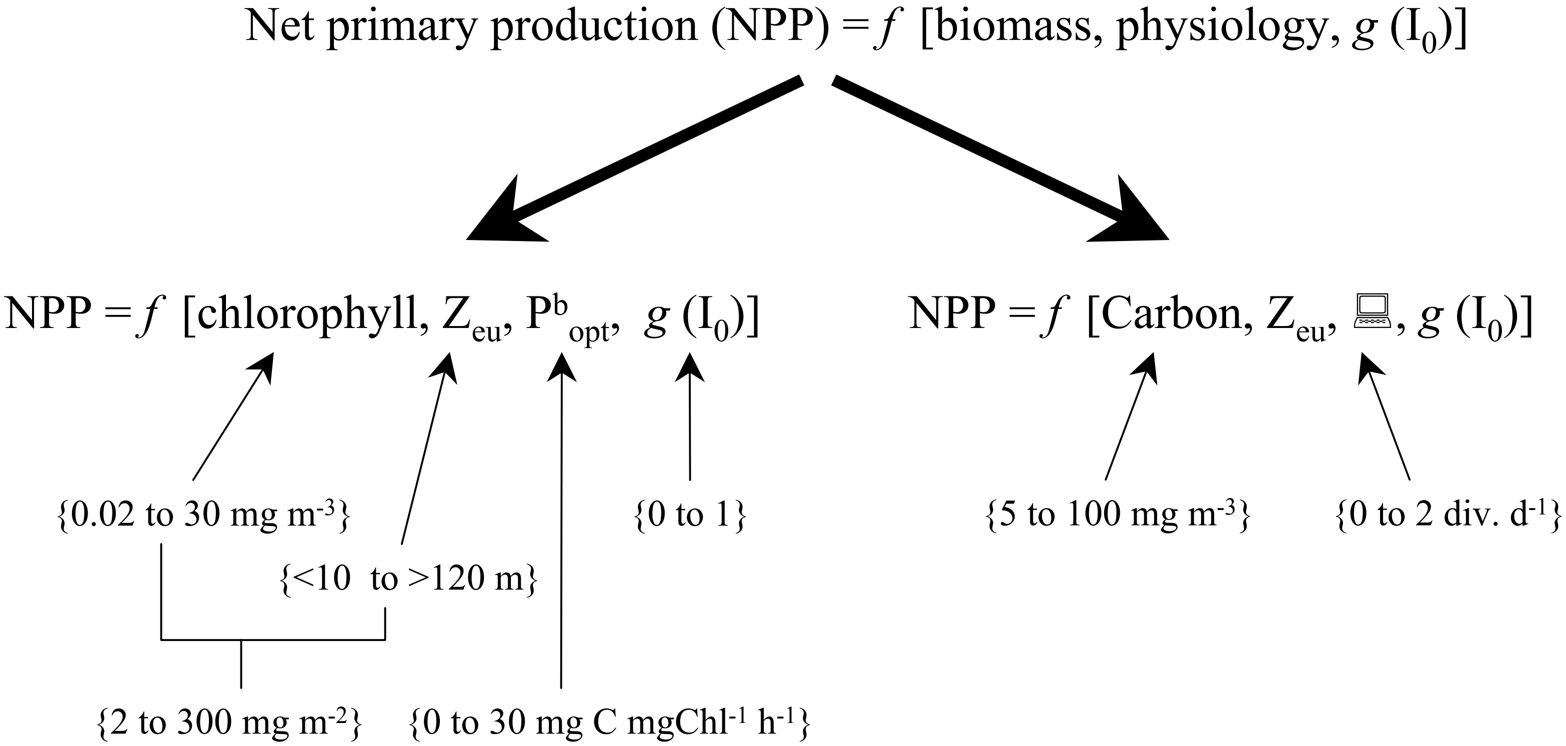


Net primary production (NPP) = f [biomass, physiology, $g\,(I_0)$]

NPP = f [chlorophyll, Z_{eu}, P^b_{opt}, $g\,(I_0)$]

NPP = f [Carbon, Z_{eu}, 💻, $g\,(I_0)$]

{0.02 to 30 mg m^{-3}}

{<10 to >120 m}

{0 to 1}

{2 to 300 mg m^{-2}}

{0 to 30 mg C $mgChl^{-1}$ h^{-1}}

{5 to 100 mg m^{-3}}

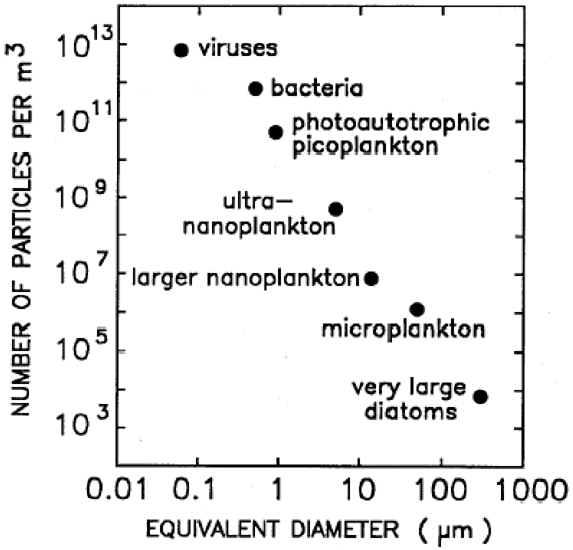
{0 to 2 div. d^{-1}}

14 Steps

(1) Light scattering 🔔 # particles

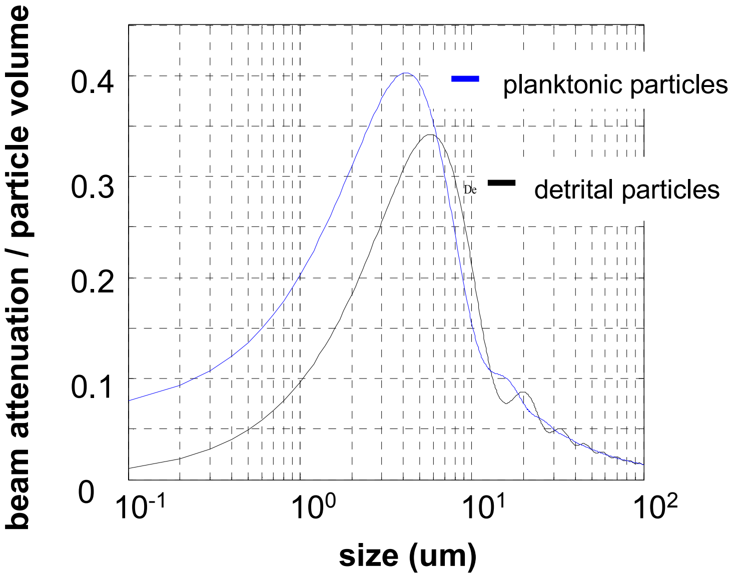
(2) Common measures of scatter:
particulate beam attenuation (c_p)
particulate backscatter coeff. (b_{bp})

(3) Open—ocean particle size spectra relatively conserved

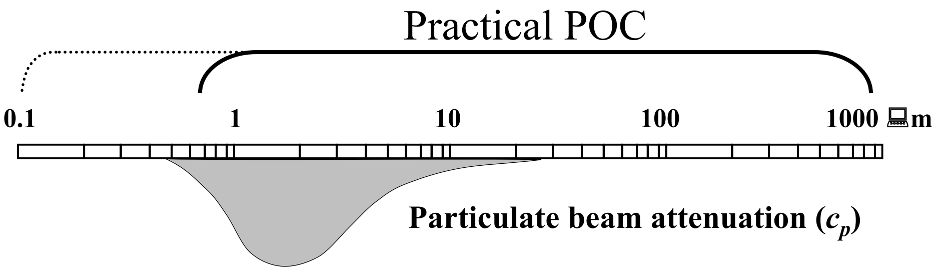


(4) c_p is:

- dominated by particles in the phytoplankton size domain
- sensitive to inorganic particles in the 0.5 to 20 💻m size range
- insensitive to submicron bacteria,
  'pure water' values are measured when 10^6 bacteria are present



(5) Particle # ☟ c_p per particle ➔



(6) c_p covaries with POC

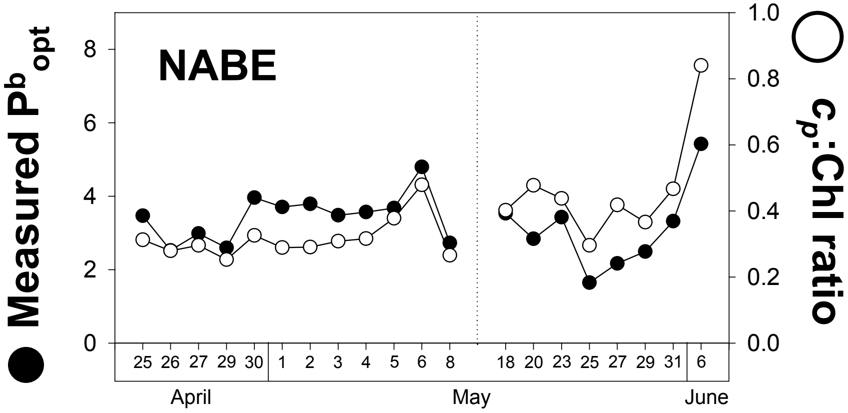
Bishop, J.K.B. 1999. *Deep-Sea Res. I*. 46:353-369.
Bishop, J. K. B., S. E. Calvert and M. Y. S. Soon (1999) *Deep-Sea Res. II* 46:2699-2733.
Claustre, H., A. Morel, M. Babin, C. Cailliau, D. Marie, J-C Marty, D. Tailliez and D. Vaulot (1999) *J. Geophys. Res*. 104:3401-3422.
Gardner, W. D., I. D. Walsh and M. J. Richardson (1993) *Deep-Sea Res. II*. 40:171-195.
Gardner, W. D., S. P. Chung, M. J. Richardson and I. D. Walsh (1995) *Deep-Sea Res. II*. 42:757-775.
Loisel, H. and A. Morel (1998) *Limnol. Oceanogr*. 43: 847-858.
Walsh, I. D., S. P. Chung, M. J. Richardson and W. D. Gardner (1995) *Deep-Sea Res. II* 42:465-477.

(7) *Therefore* – c_p should be a better estimate of phytoplankton carbon than POC

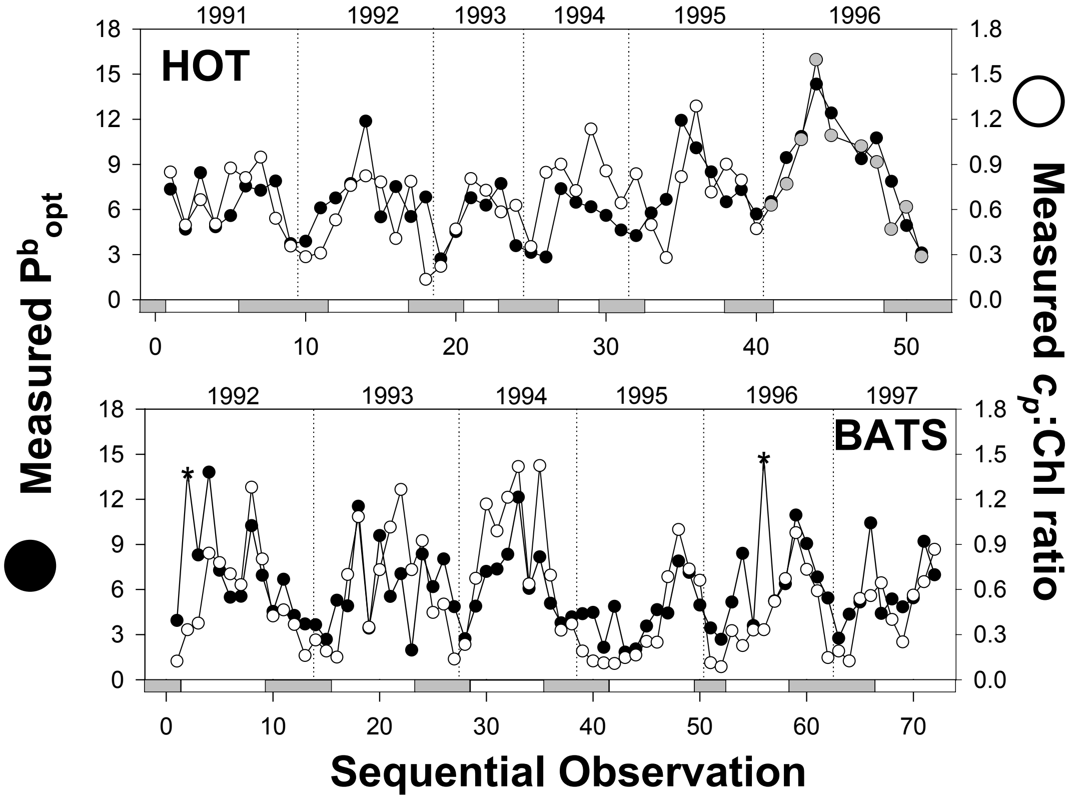
(8) *If true* – then the ratio of c_p:chlorophyll should track phytoplankton C:Chl, which is a common index of physiological variability that shares environmental dependencies with P^b_{opt} and E_k

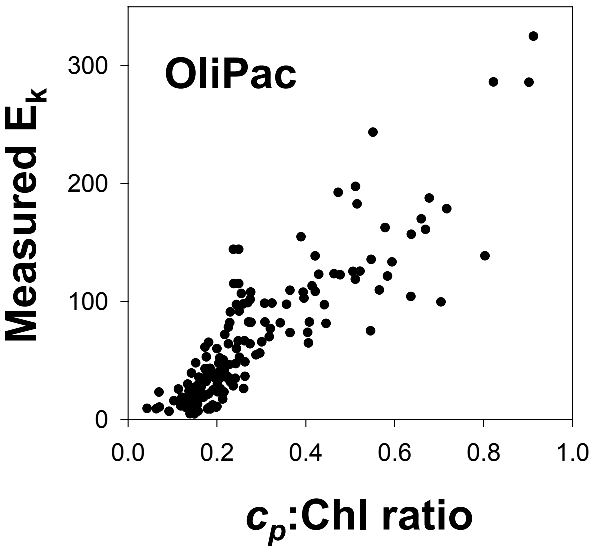
(9) c_p:chl tracks changes in P^b_{opt} and E_k

Behrenfeld & Boss (2004) *Deep-Sea Res.* 50:1537-1549



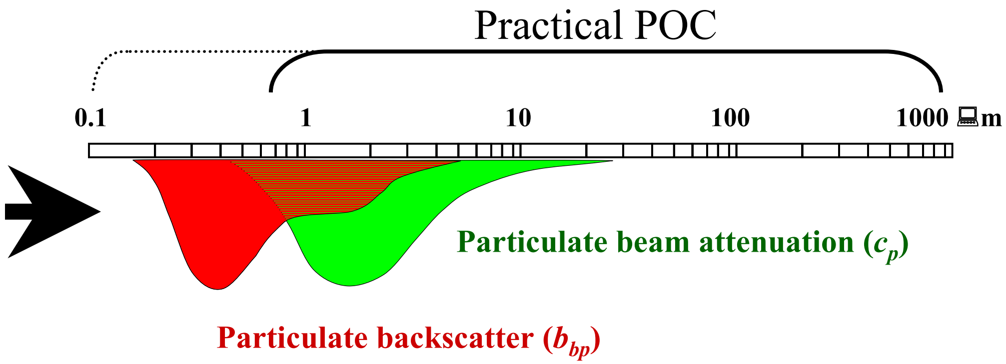
NABE Time Series





(10) Ocean color inversion algorithms give us b_{bp} , not c_p

(11) Mie calculations indicate that b_{bp} is dominated by submicron particles, but in field populations b_{bp} likely has a significant tail in the phytoplankton size domain.



(12) Satellite b_{bp} covaries with POC

Loisel, H., E. Bosc, D. Stramski, K. Oubelkheir, and P.-Y. Deschamps (2001)
Geophys. Res. Lett., 28:4203-4206.
Stramski, D., R. A. Reynolds, M. Kahru, and B. G. Mitchell (1999)
Science, 285:239-242.

(13) *Therefore* – b_{bp} should be a better estimate of phytoplankton carbon than POC

(14) *If true* – then the ratio of chlorophyll:b_{bp} should track phytoplankton Chl:C

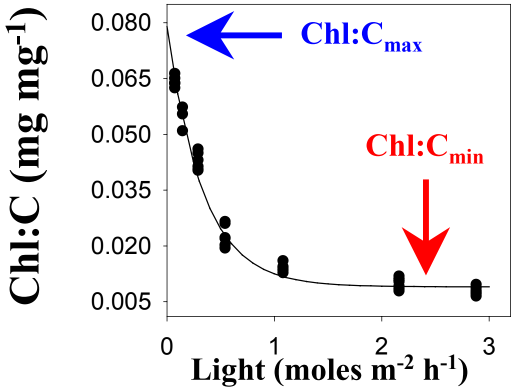
and thus phytoplankton growth rates (💻)

{once a correction of the background bacterial population is accounted for}

Chl:C physiology

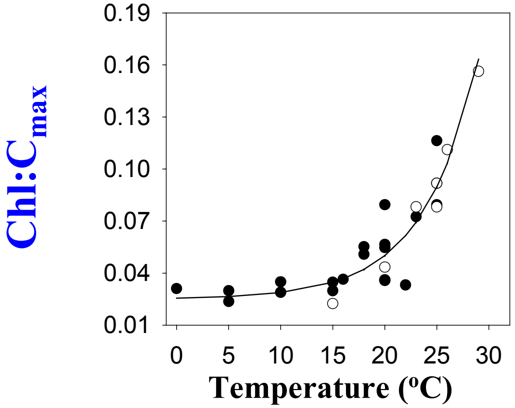
Laboratory

3 primary factors



Light

Dunaliella tertiolecta
20 °C
Replete nutrients
Exponential growth phase

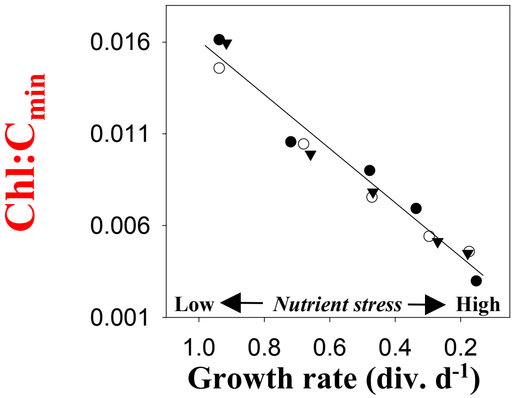


Temperature

Geider (1987) *New Phytol*. **106**: 1-34

16 species
● = Diatoms

○ = all other species



Nutrients

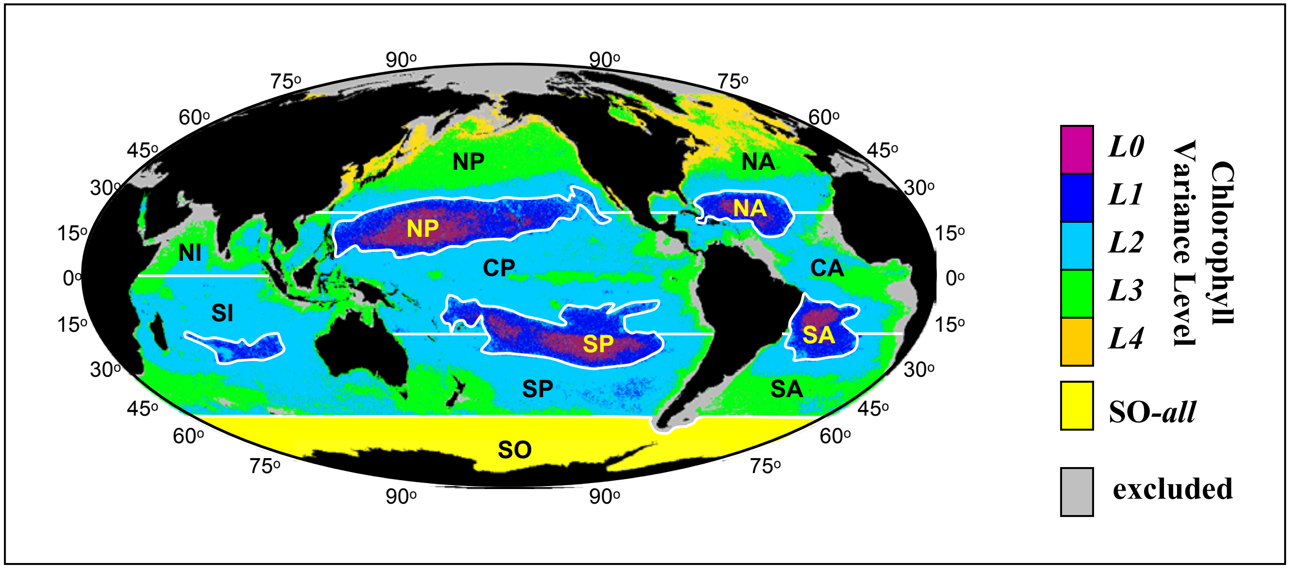
Laws & Bannister (1980)
Limnol. Oceanogr. **25**: 457-473

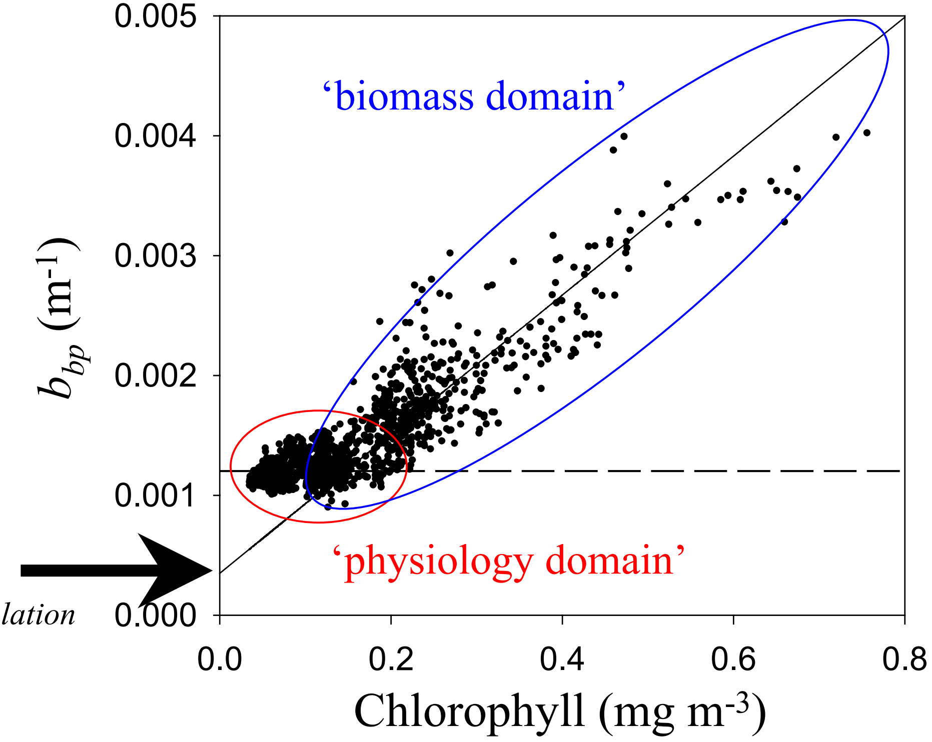
Thalassiosira fluviatilis
● = NO_3 limited cultures

○ = NH_4 limited cultures

▼ = PO_4 limited cultures

28 Regional Bins





Intercept = b_{bp} *from stable component of the bacterial population*

C = scalar ☞ (b_{bp} – intercept)

= 13,000 ☞ (b_{bp} – 0.00035)

Intercept = **0.00017 m^{-1}**

Stramski & Kiefer (1991) *Prog. Oceanogr.* 28, 343-383

Cho & Azam (1990) *Mar. Ecol. Prog. Ser.*, 63, 253-259

Phytoplankton Carbon = **25 – 35% POC**

Eppley et al. (1992) *J. Geophys. Res.*, 97, 655-661

DuRand et al. (2001) *Deep-Sea Res. II*, 48, 1983-2003

Gundersen et al. (2001) *Deep-Sea Res. II* 48, 1697-1718

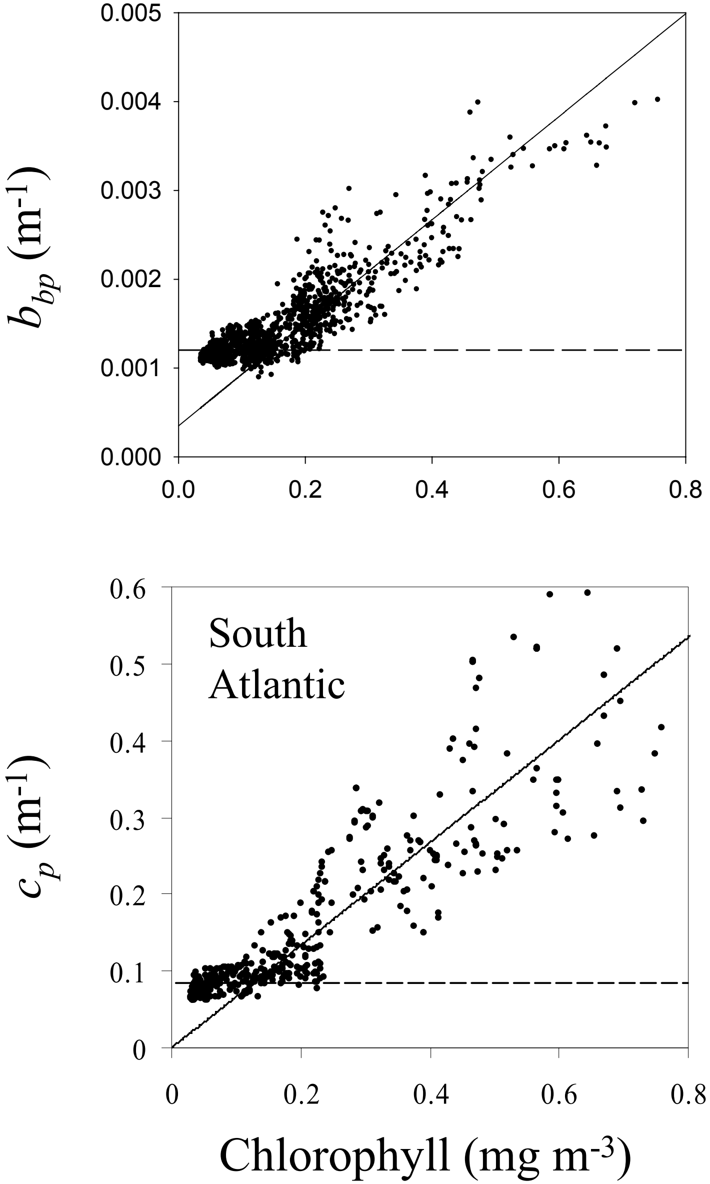
Satellite b_{bp} vs field c_p

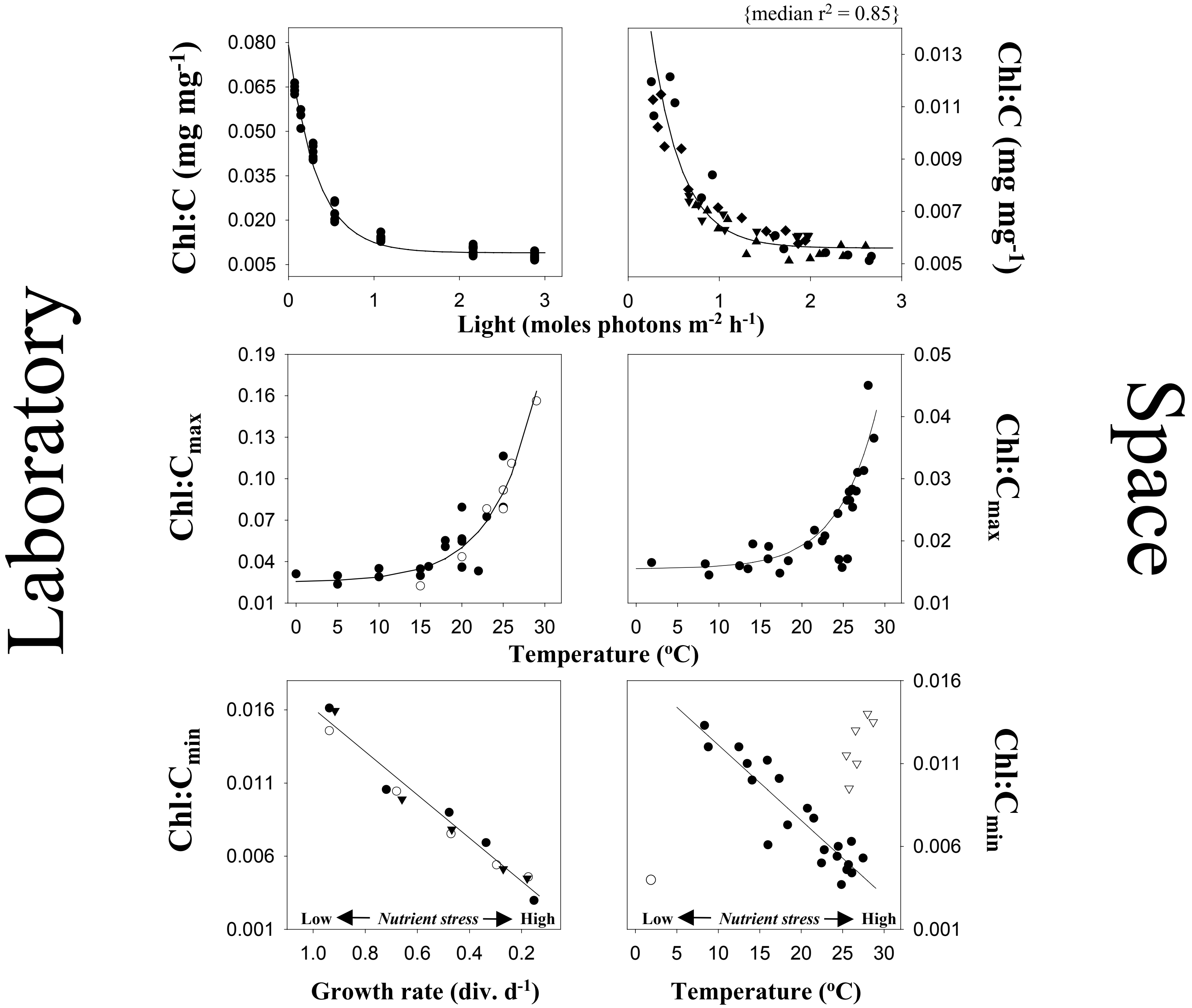
- Same bilinear pattern
- Anticipated intercept

  $b_{bp} > 0$

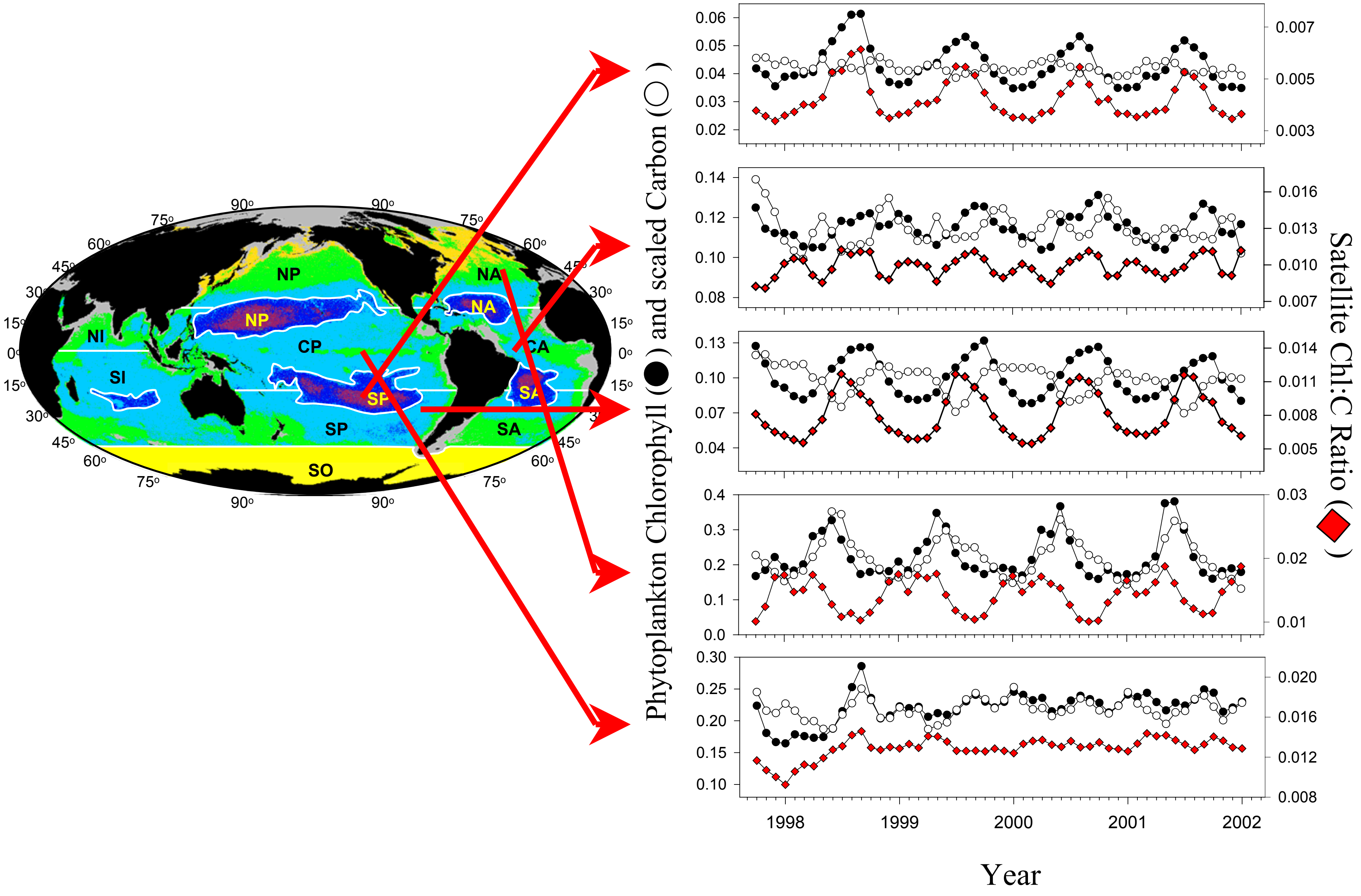
  $c_p = 0$
- Ratio of slopes = 0.0008

{phytoplankton = 0.0005 – 0.0009}




Laboratory
Space
{median r² = 0.85}
Chl:C (mg mg⁻¹)
0.080
0.065
0.050
0.035
0.020
0.005
0.013
0.011
0.009
0.007
0.005
0
1
2
3
Light (moles photons m⁻² h⁻¹)
Chl:Cmax
0.19
0.16
0.13
0.10
0.07
0.04
0.01
0.05
0.04
0.03
0.02
0.01
0
5
10
15
20
25
30
Temperature (ºC)
Chl:Cmin
0.016
0.011
0.006
0.001
Low
Nutrient stress
High
1.0
0.8
0.6
0.4
0.2
Growth rate (div. d⁻¹)
Temperature (ºC)

The 5 basic patterns



Growth rate (💻) = 💻$_{max}$ ☟ *f* (nuts, temp) ☟ *g* (light)

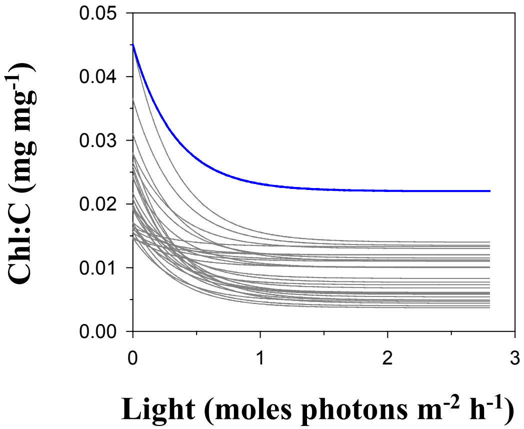
2 divisions d^{-1}

Banse (1991)

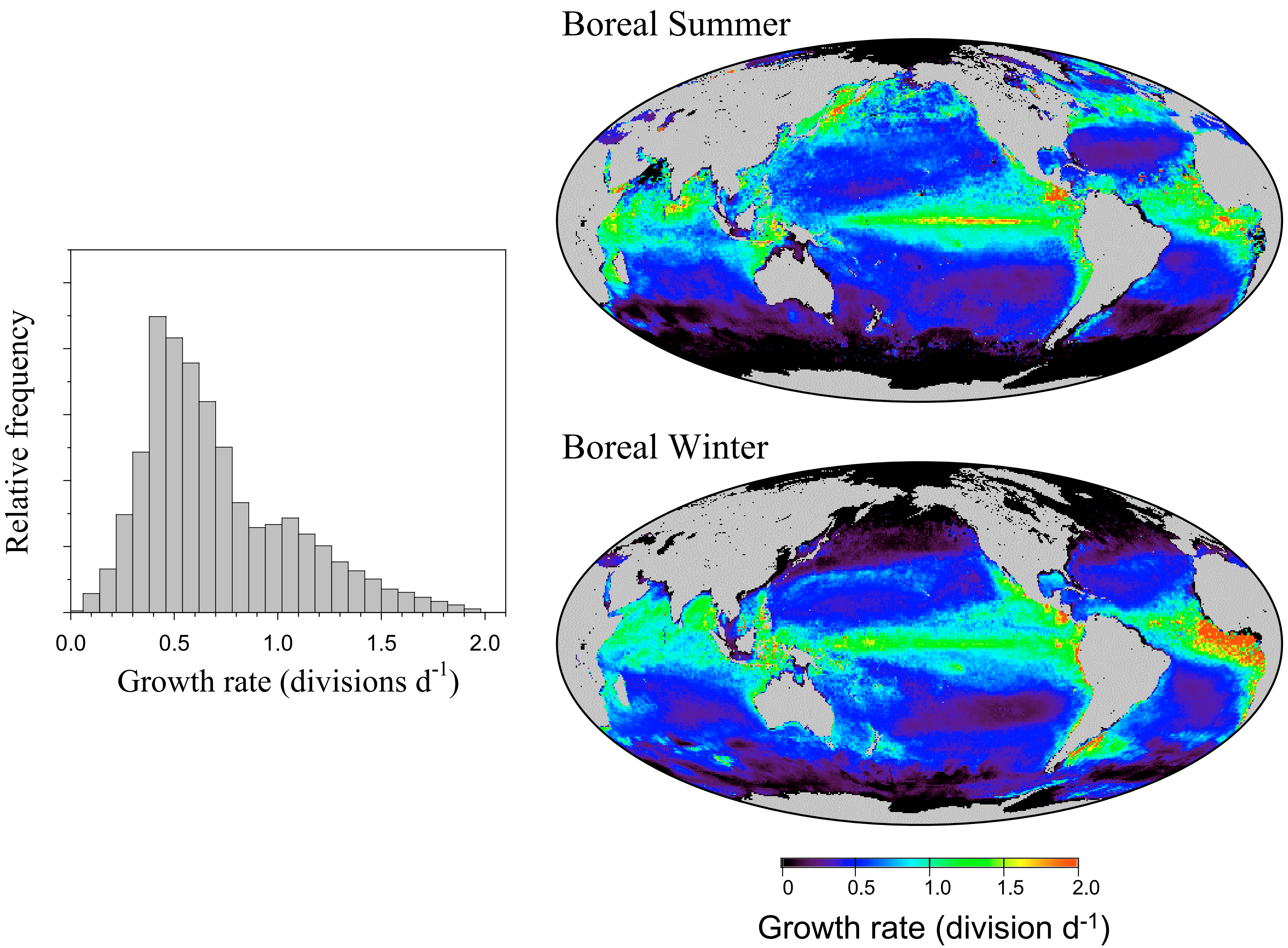
range = 0 to 1

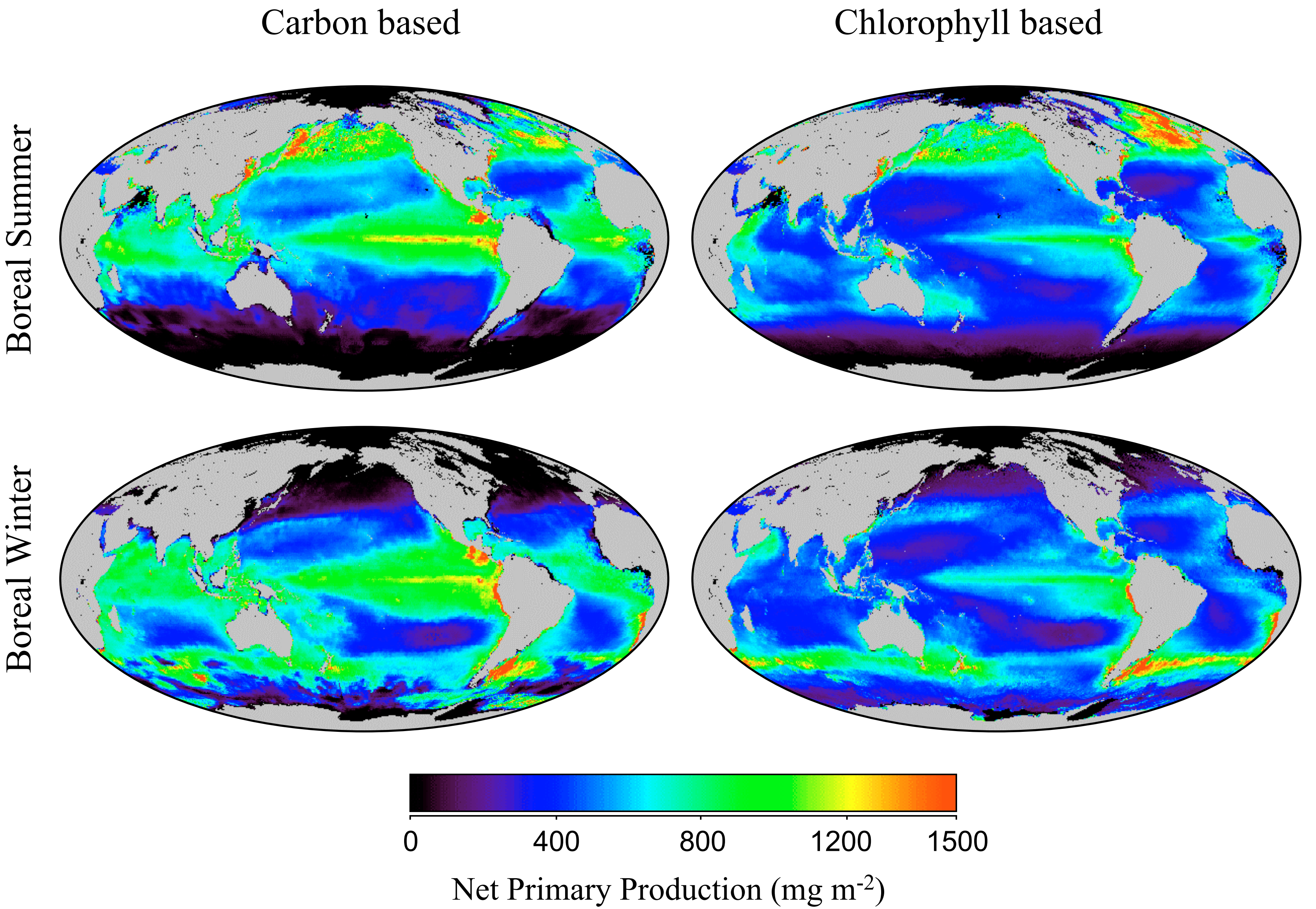
range = 0 to 1

$1 - \exp^{-3light}$

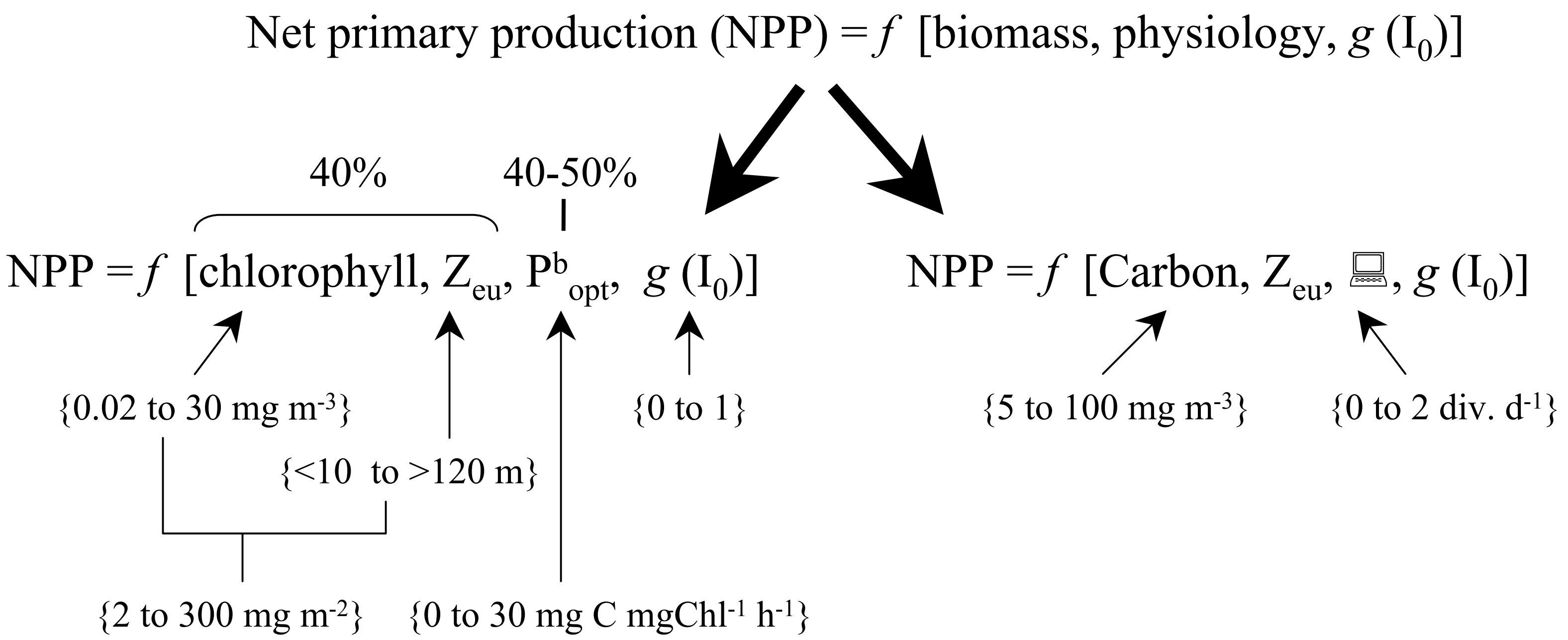


$$\frac{\text{Chl:Csat}}{(\text{Chl:C}_{N,T\text{-max}})_{\text{Light}}}$$


Relative frequency
0.0
0.5
1.0
1.5
2.0
Growth rate (divisions d-1)
Boreal Summer
Boreal Winter
0
0.5
1.0
1.5
2.0
Growth rate (division d-1)


Carbon based
Chlorophyll based
Boreal Summer
Boreal Winter
0
400
800
1200
1500
Net Primary Production (mg m^{-2})

Backup Slides



Net primary production (NPP) = f [biomass, physiology, g (I_0)]

40%

40-50%

NPP = f [chlorophyll, Z_{eu}, P^b_{opt}, g (I_0)]

{0.02 to 30 mg m^{-3}}

{<10 to >120 m}

{2 to 300 mg m^{-2}}

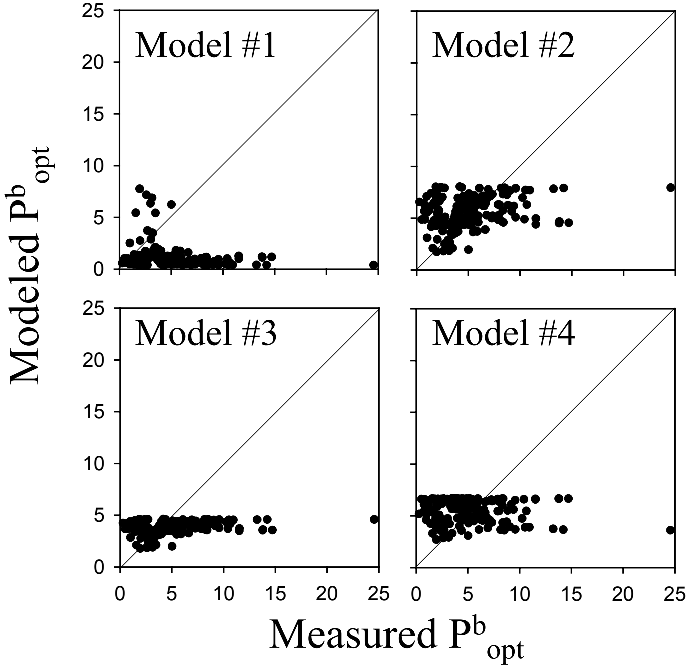
{0 to 30 mg C $mgChl^{-1}$ h^{-1}}

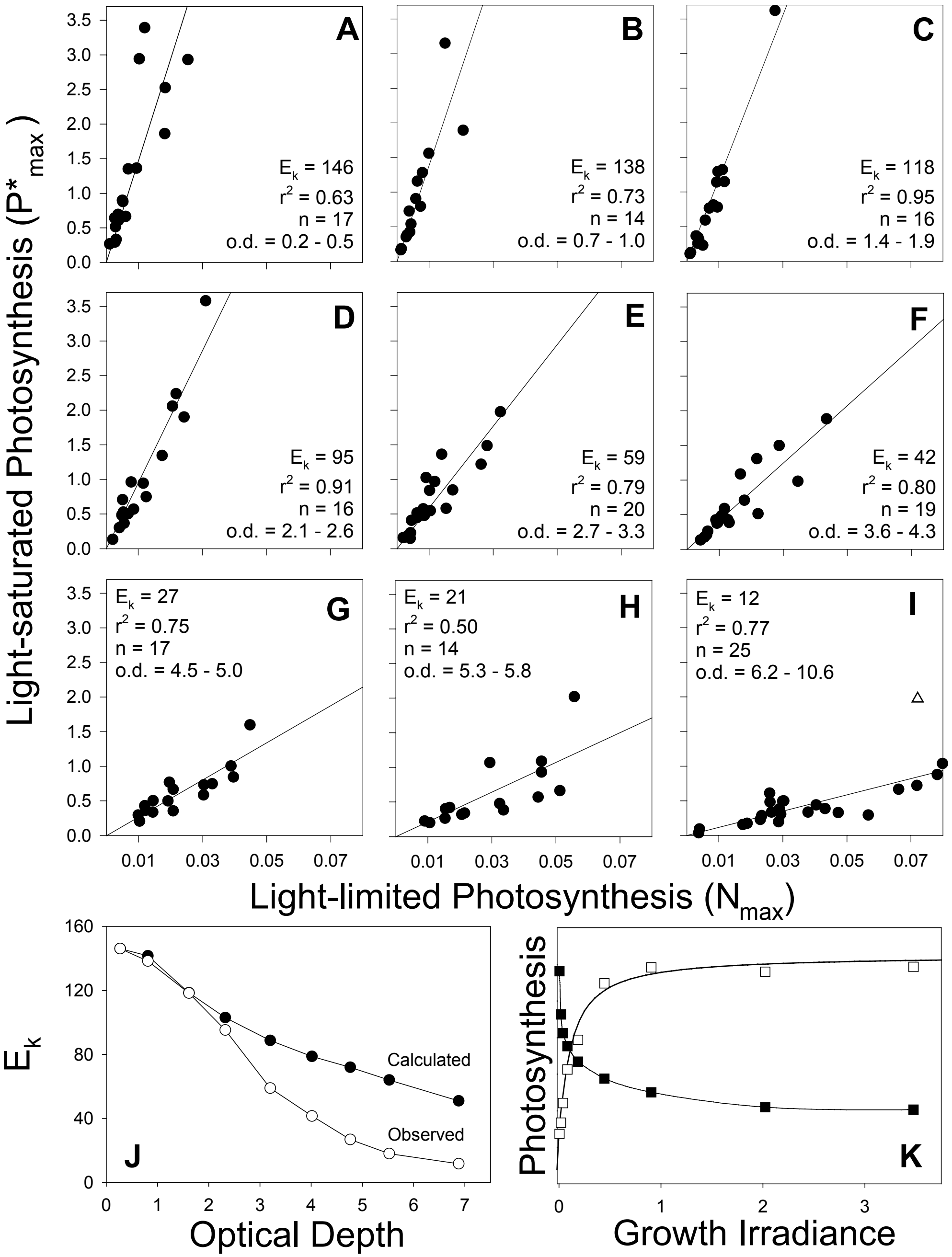
{0 to 1}

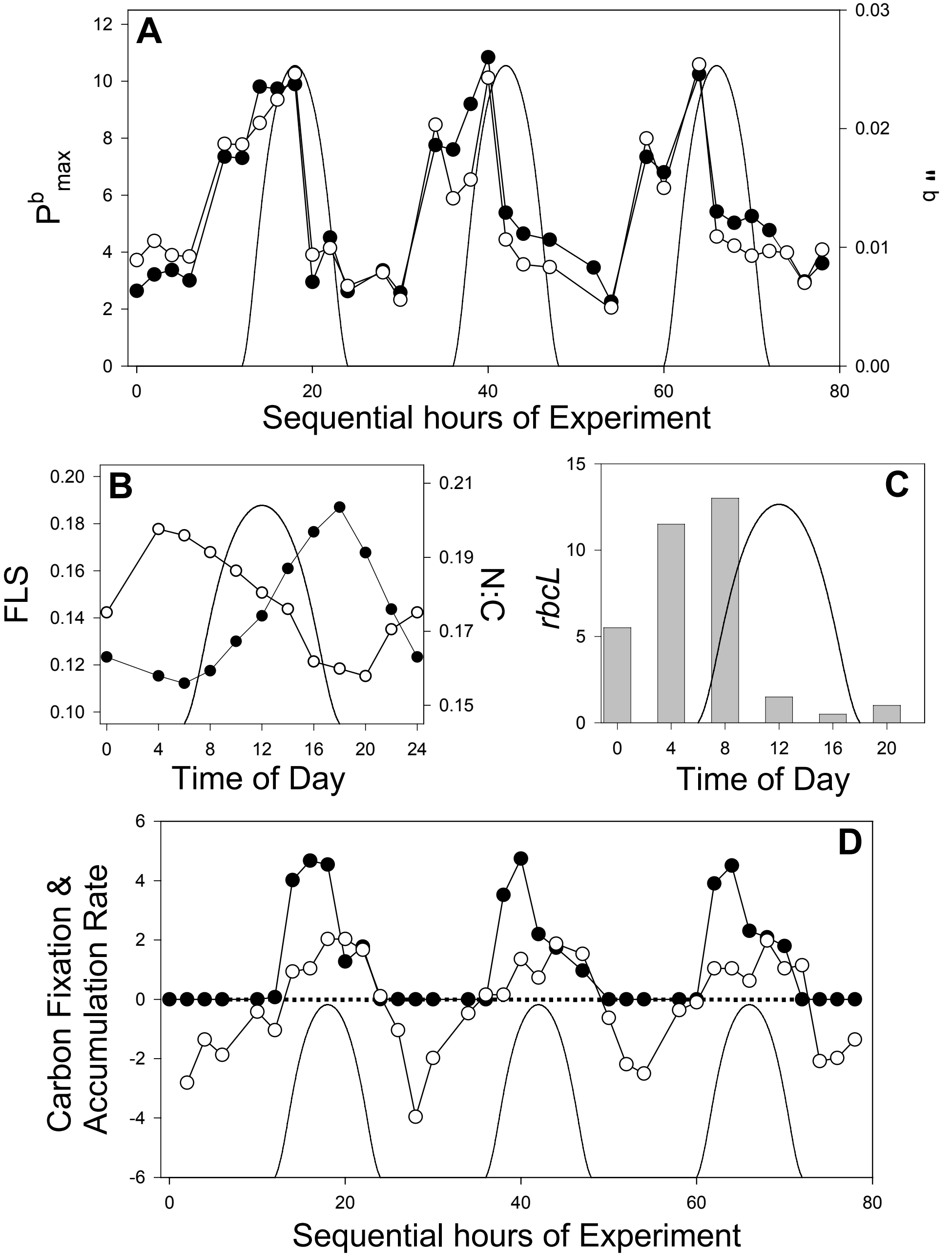
NPP = f [Carbon, Z_{eu}, 💻, g (I_0)]

{5 to 100 mg m^{-3}}

{0 to 2 div. d^{-1}}




Light-saturated Photosynthesis (P^*_{max})
Light-limited Photosynthesis (N_{max})
A
E_k = 146
r^2 = 0.63
n = 17
o.d. = 0.2 - 0.5
B
E_k = 138
r^2 = 0.73
n = 14
o.d. = 0.7 - 1.0
C
E_k = 118
r^2 = 0.95
n = 16
o.d. = 1.4 - 1.9
D
E_k = 95
r^2 = 0.91
n = 16
o.d. = 2.1 - 2.6
E
E_k = 59
r^2 = 0.79
n = 20
o.d. = 2.7 - 3.3
F
E_k = 42
r^2 = 0.80
n = 19
o.d. = 3.6 - 4.3
G
E_k = 27
r^2 = 0.75
n = 17
o.d. = 4.5 - 5.0
H
E_k = 21
r^2 = 0.50
n = 14
o.d. = 5.3 - 5.8
I
E_k = 12
r^2 = 0.77
n = 25
o.d. = 6.2 - 10.6
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0.01
0.03
0.05
0.07
J
E_k
Optical Depth
Calculated
Observed
0
40
80
120
160
0
1
2
3
4
5
6
7
K
Photosynthesis
Growth Irradiance
0
1
2
3


A
P^b_{max}
b
Sequential hours of Experiment
B
FLS
N:C
Time of Day
C
rbcL
Time of Day
D
Carbon Fixation &
Accumulation Rate
Sequential hours of Experiment

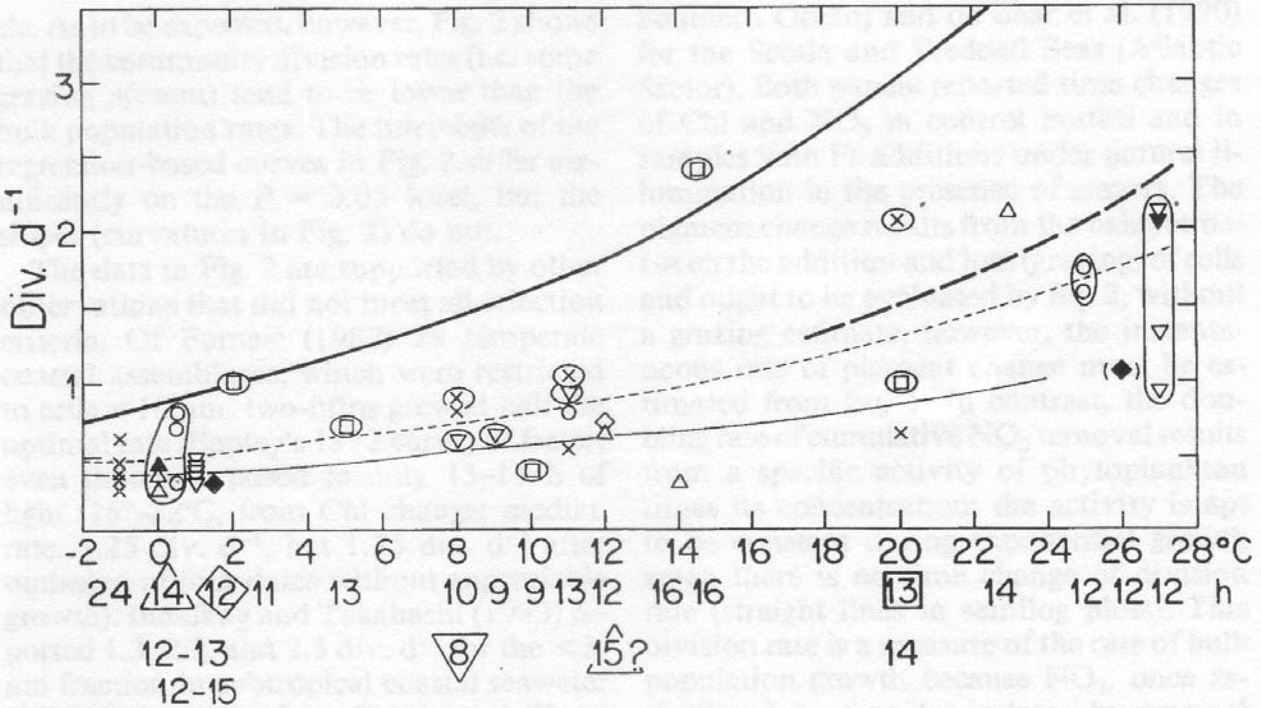


Fig. 2. Division rates for natural marine plankton in enclosures as dependent on temperature, with the "standard curve" for optimal growth (Eppley 1972) and half of this maximum (broken curve) added. Estimated daylength (h) shown below temperature scale. Filled symbols—two stations. Dashed line (from regression, *see text*) and circled or enclosed symbols—bulk population division rates [results without grazing, from dilution method, or Chl labeling (the latter for Welschmeyer and Lorenzen 1984; Downs and Lorenzen 1985; Laws et al. 1984)]; thin line and other symbols—community division rates (from Chl increases). From left: ×—Spies 1987; ▲, △—Paranjape 1987 (samples with excess NO_3); ○—Taylor and Haberstroh 1988; ▽—Sakshaug and Holm-Hansen 1986 (highest values at intermediate irradiances); ◆—Kuiper et al. 1983 (examples of high rates, No. 24, 25; temperature from Jahnke et al. 1983); □—Gifford 1988; ×—Welschmeyer and Lorenzen 1984 [table 3; ⊗—highest values except for March (second highest); ×—means of two highest values for each date; temperatures from original log books]; ▽—Downs and Lorenzen 1985 [table 3; means of two highest values for November, January and April, when NO_3 and incident irradiance were high (from original log books)]; ○—Wilkerson and Dugdale 1987 (No. 58B 2); ◇—Riemann et al. 1988 (enclosure C, 12–19 September); △—McAllister et al. 1961 (days 4–14), Antia et al. 1963 (days 8–15), both at low irradiance; △—Eppley et al. 1971 (from figure 2, 11–13 July average of NO_3 and NH_4 additions; "20°–25°C"); ○—Landry et al. 1984 (temperature estimated); ◆—Cullen et al. 1992 [mean of several stations, under low irradiance (moved from Fig. 3, not used in regression)]; ▼, ▽—Laws et al. 1984 (without offshore station F).