Vertical structure of the open ocean: biology of the mixed layer

Factors affecting primary productivity

Light intensity
Nutrients: N, P, S_i & Fe
Temperature
Grazing (zooplankton)

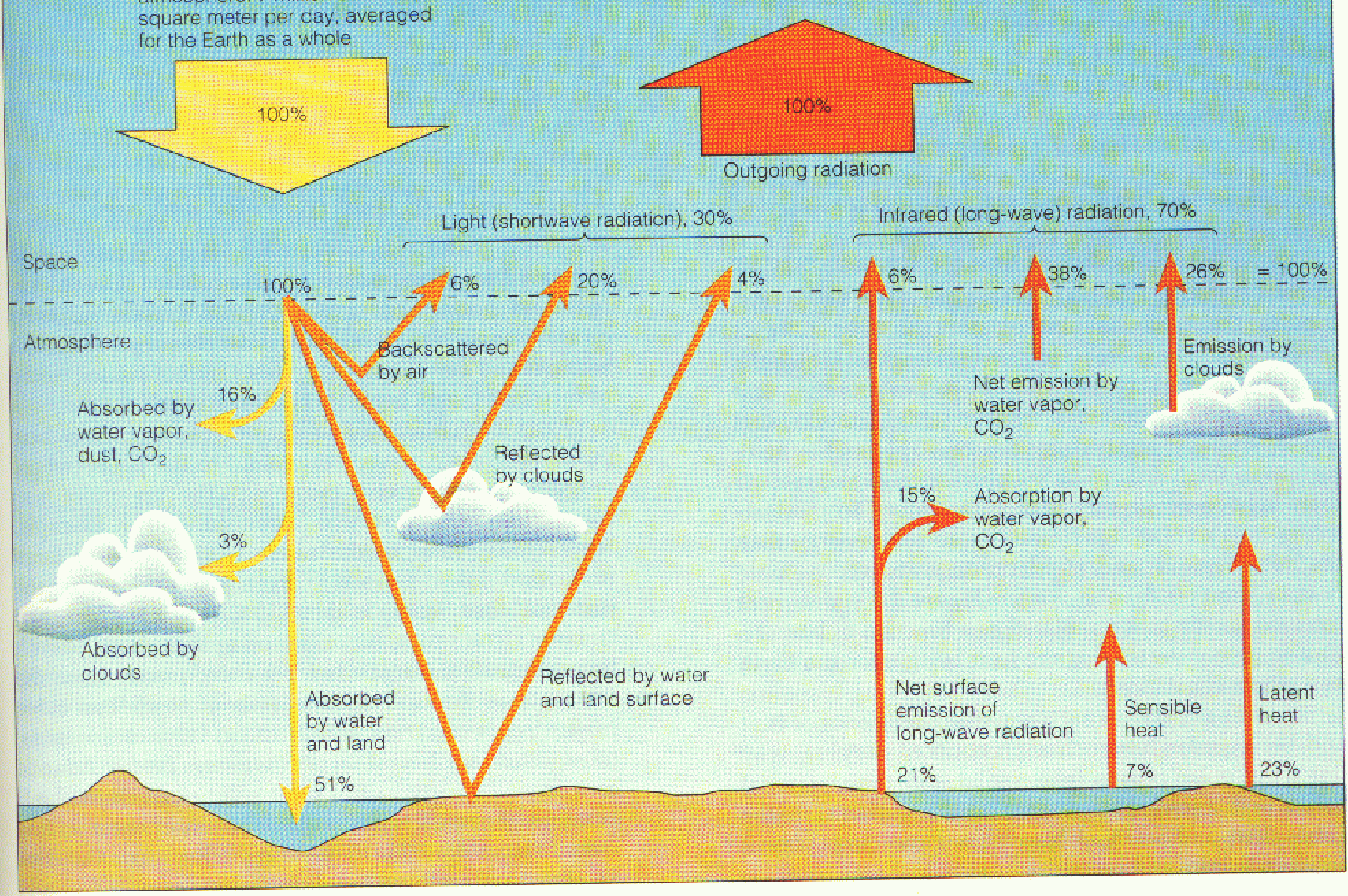
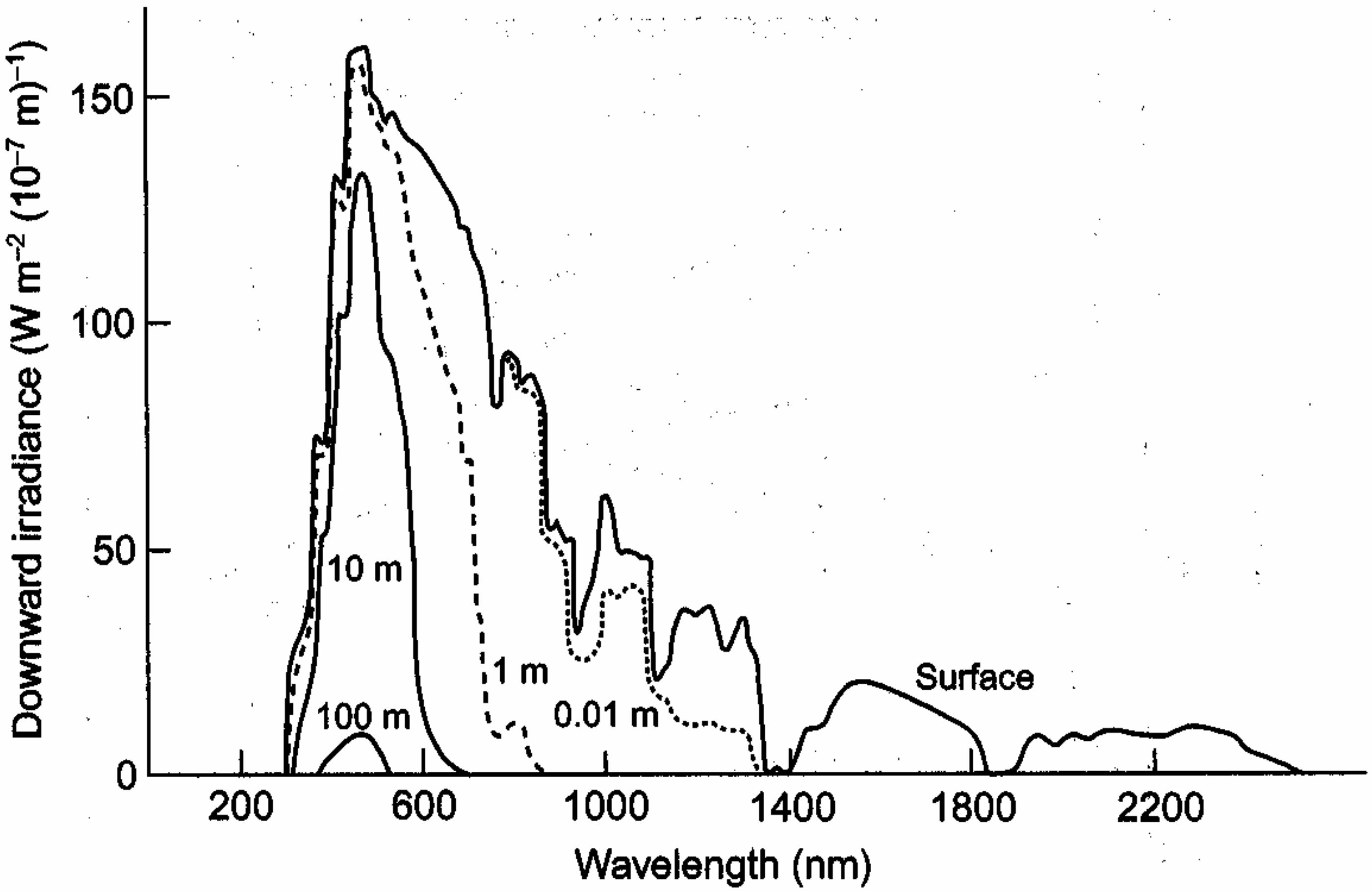
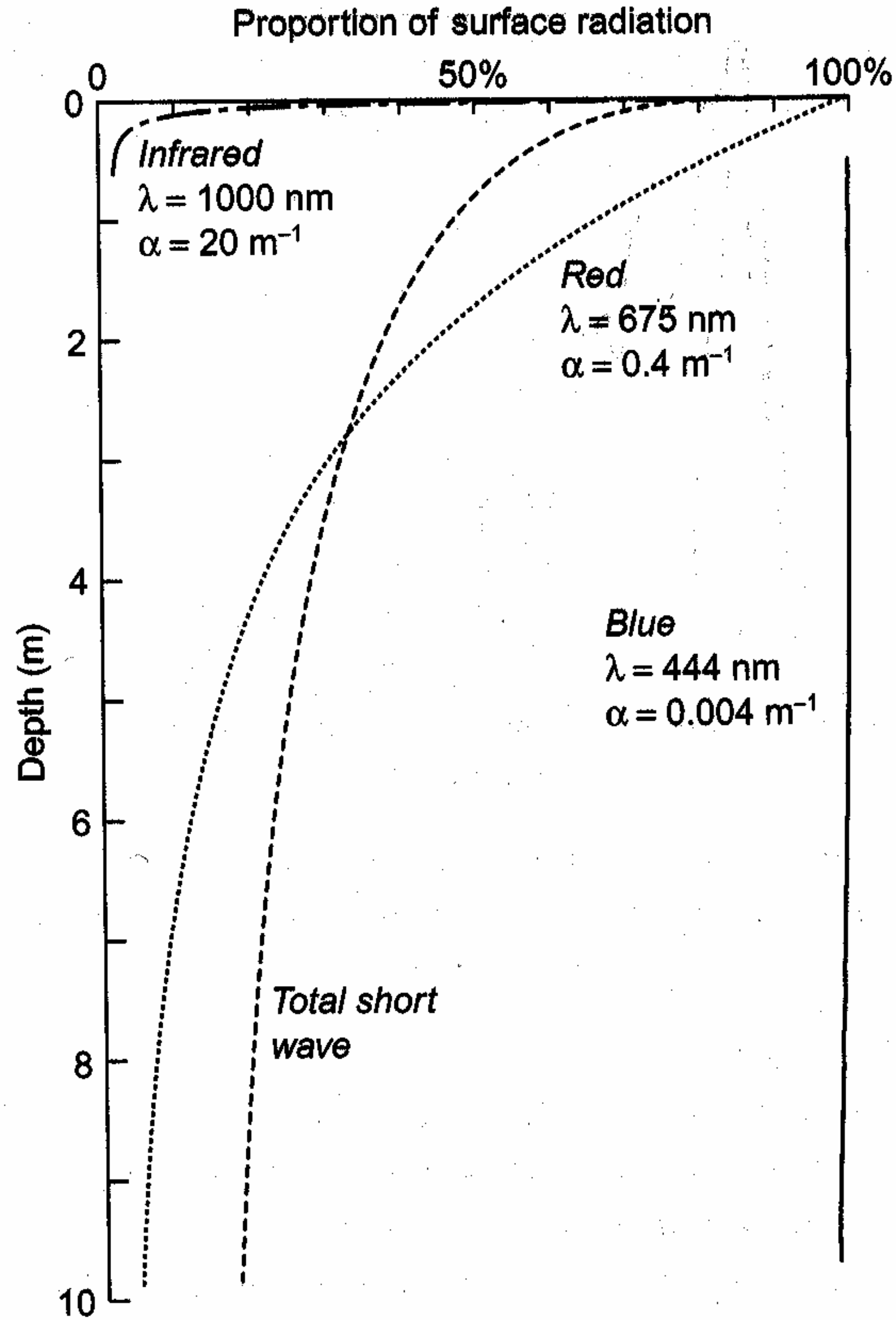


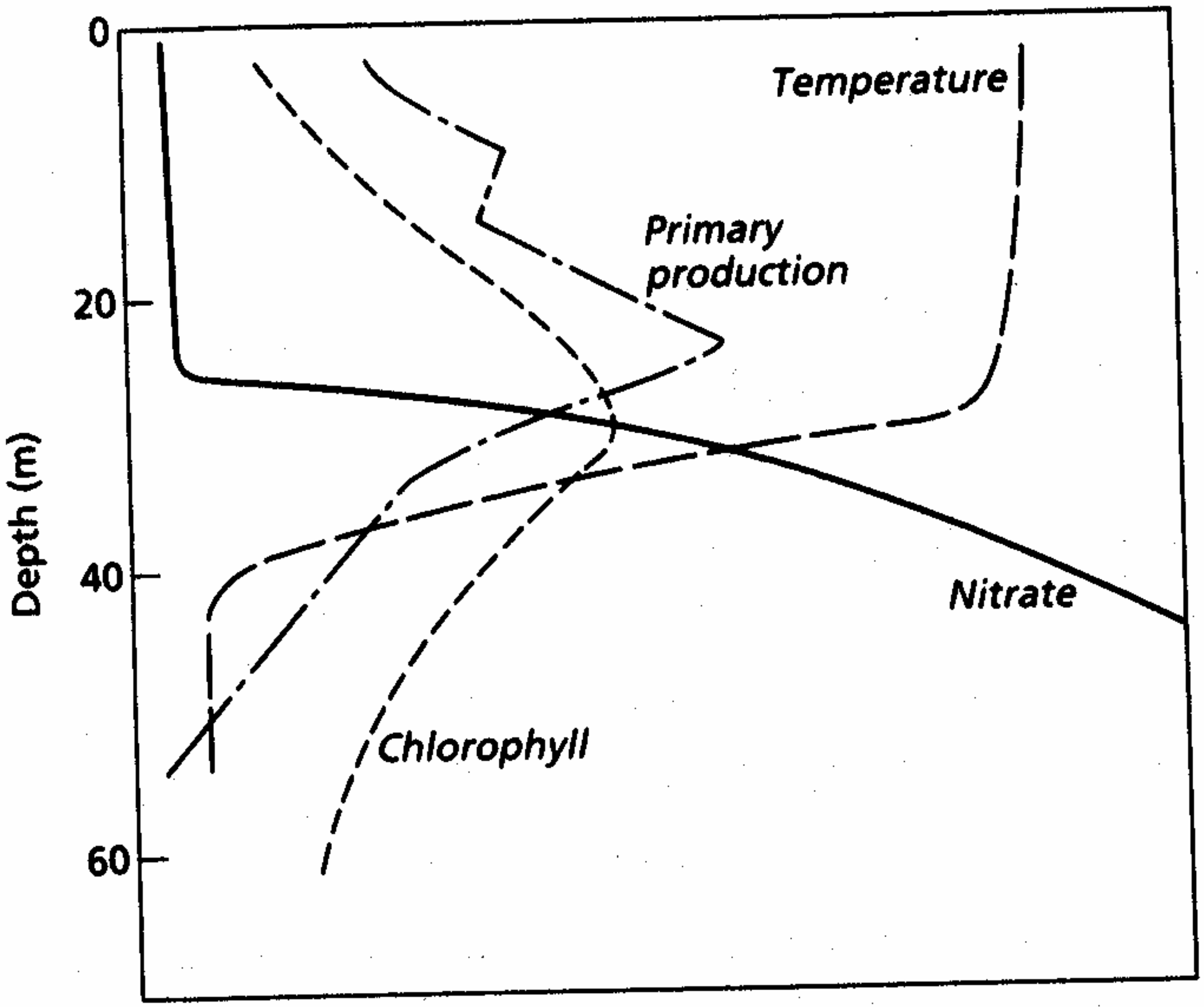
Figure 7.6 The heat budget for the Earth. On an average day, about half of the solar energy arriving at the upper atmosphere is absorbed at the Earth's surface. Light (short-wave) energy absorbed at the surface is converted into heat. Heat leaves the Earth as infrared (long-wave) radiation. Since input equals output over long periods of time, the heat budget is balanced.



3.02 Spectrum of short-wave radiation reaching the sea surface and four depths. …te the progressive elimination of longer wavelengths as depth increases. From …lov (1976).



Proportion of surface radiation
0
50%
100%
0
2
4
6
8
10
Depth (m)
Infrared
λ = 1000 nm
α = 20 m⁻¹
Red
λ = 675 nm
α = 0.4 m⁻¹
Blue
λ = 444 nm
α = 0.004 m⁻¹
Total short wave


0
20
40
60
Depth (m)
Temperature
Primary
production
Nitrate
Chlorophyll

- Absorption of radiation resulting to heat gain through the top few meters of the ocean. On the other hand, heat loss is almost entirely from the top centimeter.
- Losses occur mainly through evaporation, infrared (long-wave) radiation, and conduction
- As the upper layer of the ocean is usually stirred up by wind waves or by convection that is generated by the loss of heat at the surface, the temperature in the stirred layer remains constant with depth. This is called (surface) mixed layer

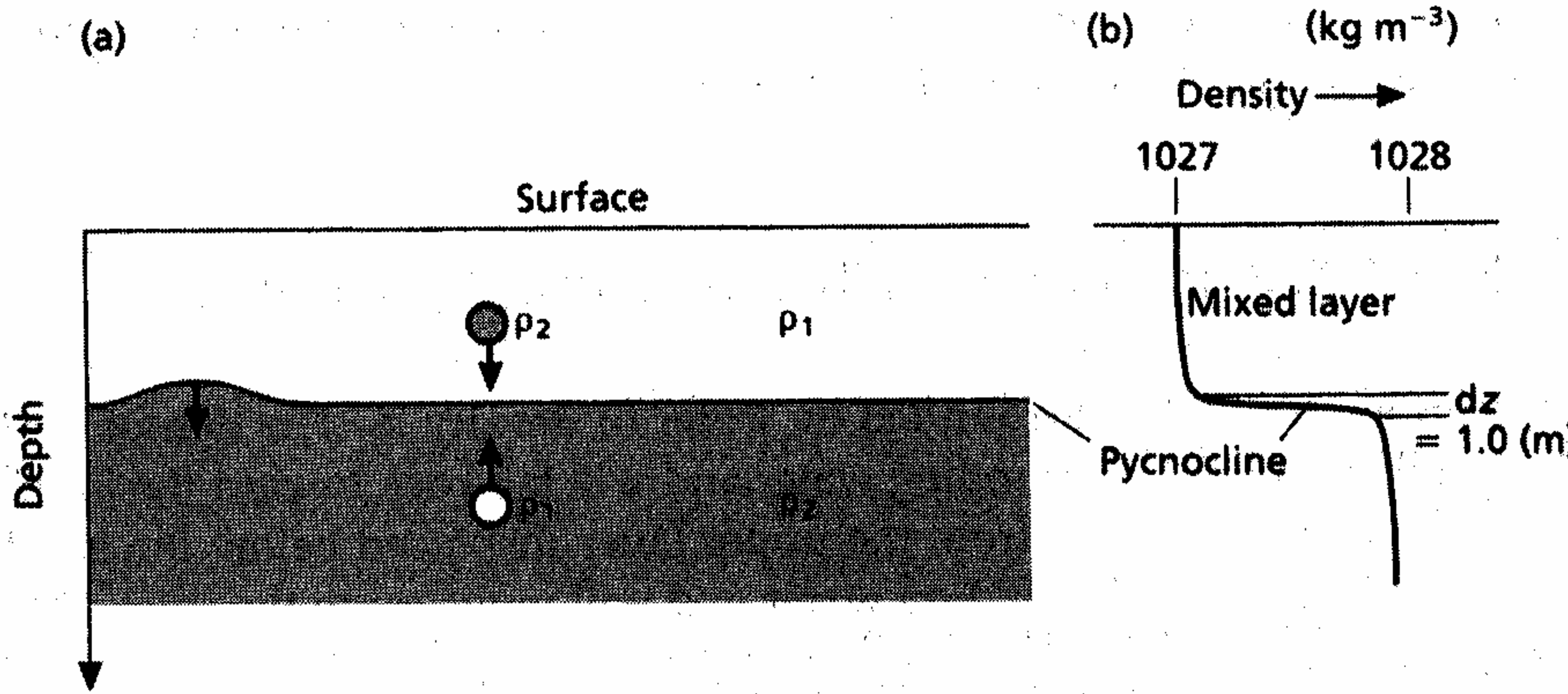
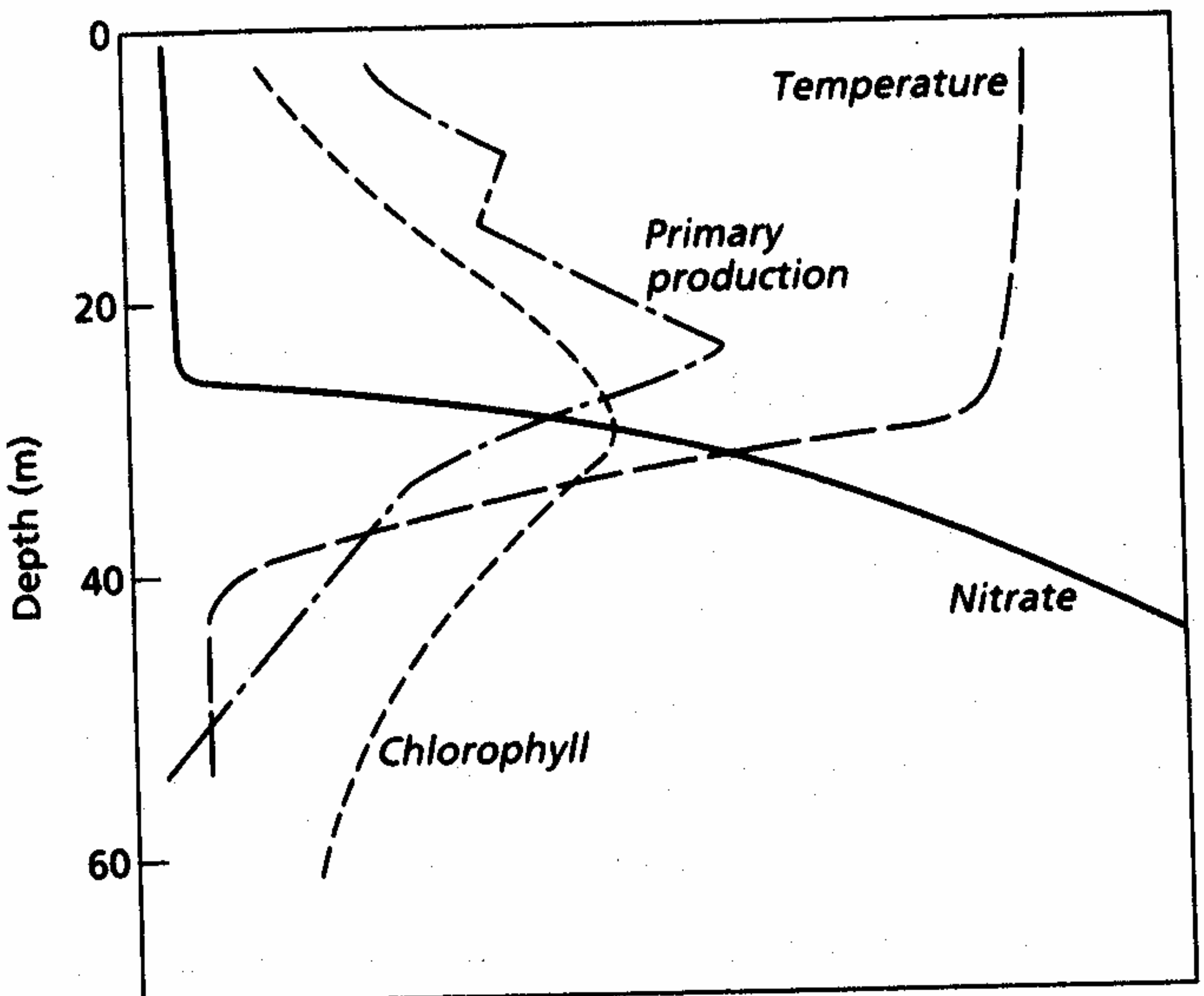
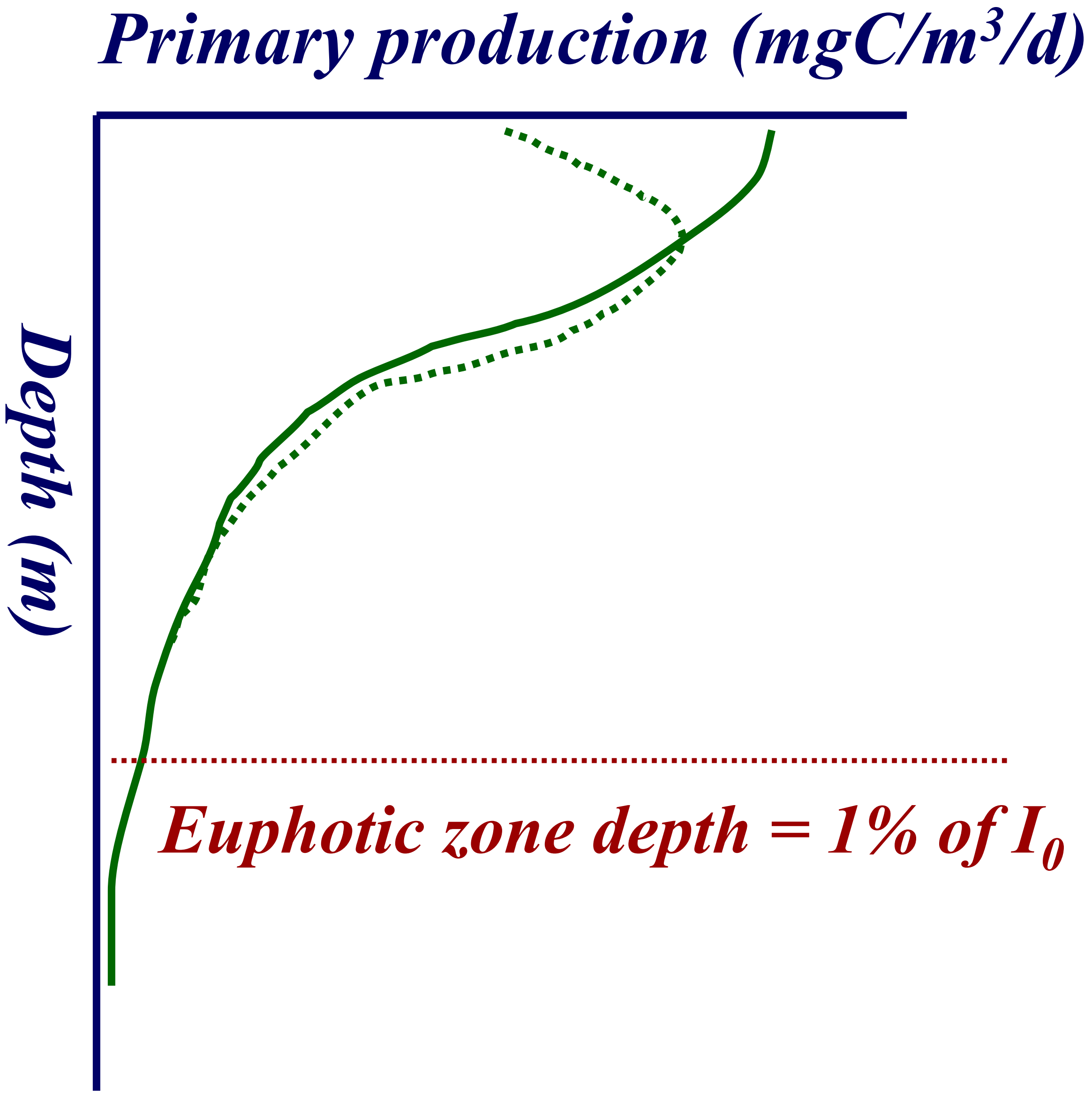


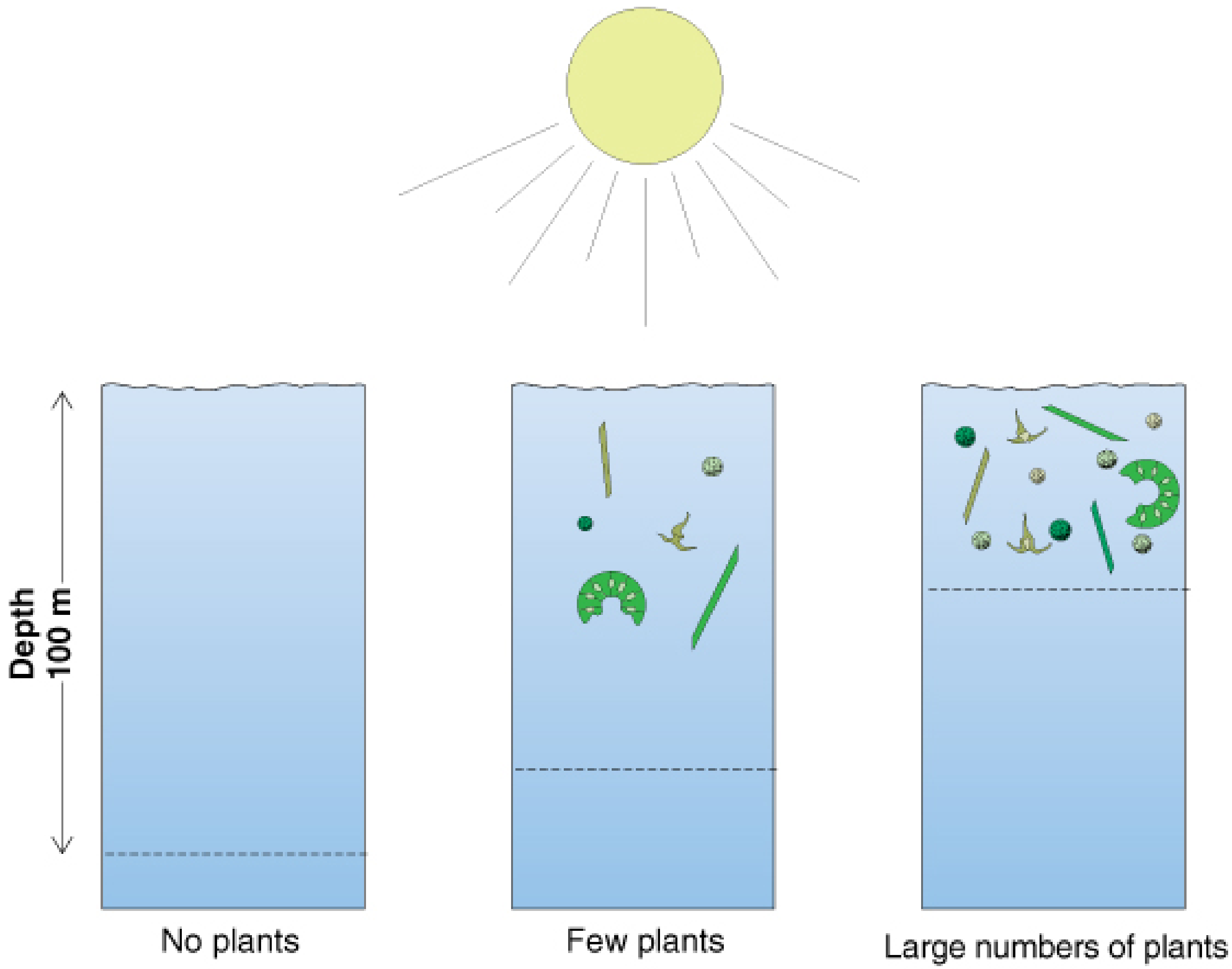
Fig. 3.04 (a) A cross-section through two layers of homogeneous water having unequal density separated by a thin pycnocline. Displacements above or below the pycnocline give rise to the buoyancy forces indicated by the arrows. (b) A vertical profile of the density through the two layers.

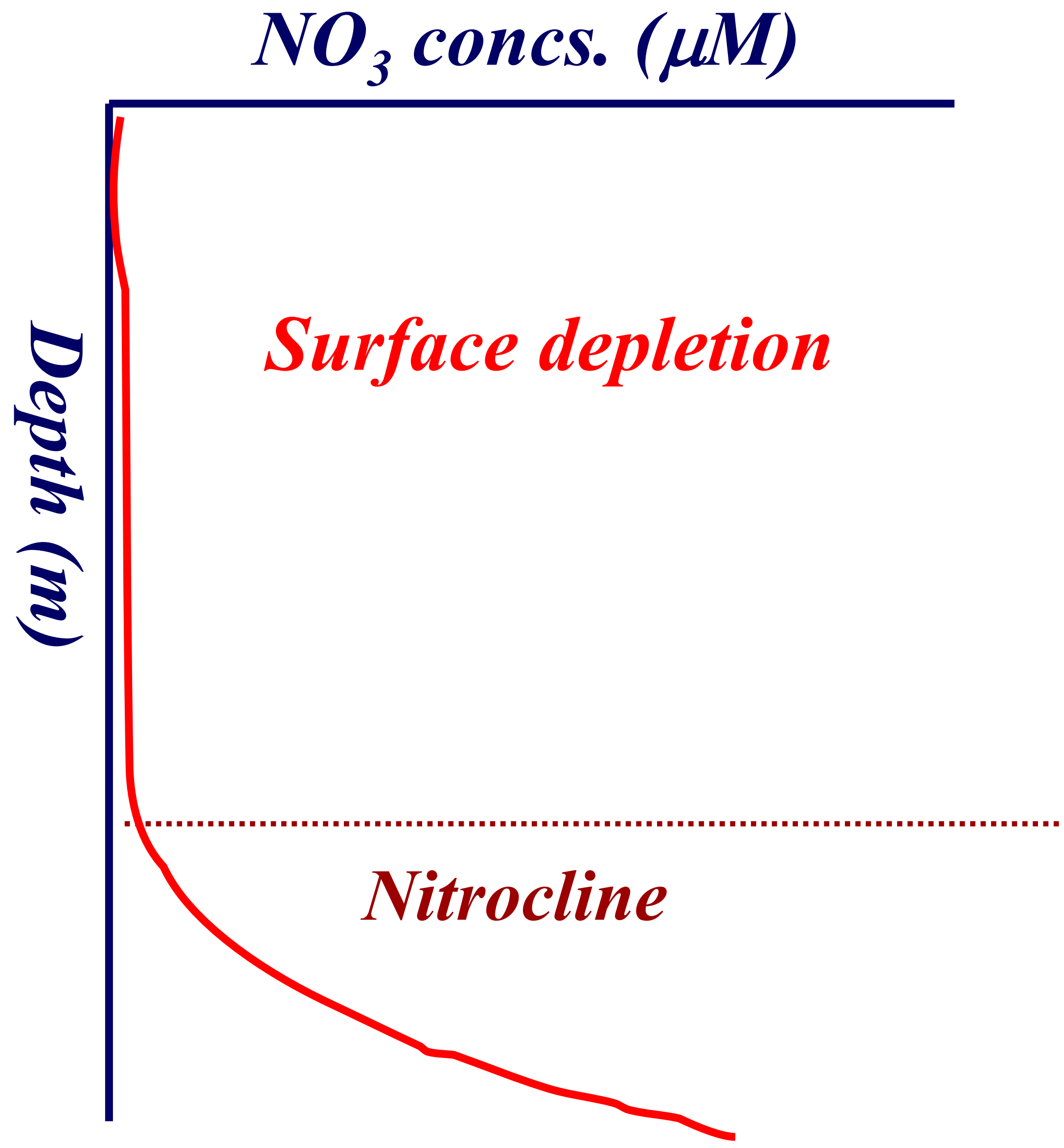
- The fact that energy must be supplied by the turbulent motions for vertical mixing to occur in the pycnocline presents a barrier to vertical transport
- This barrier has important biological consequences: the phytoplankton grow mostly in the upper layer but the supply of nutrients from the lower layer into the upper layer is, to some degree, blocked by the pycnocline

Phytoplankton production in tropical and subtropical oceans

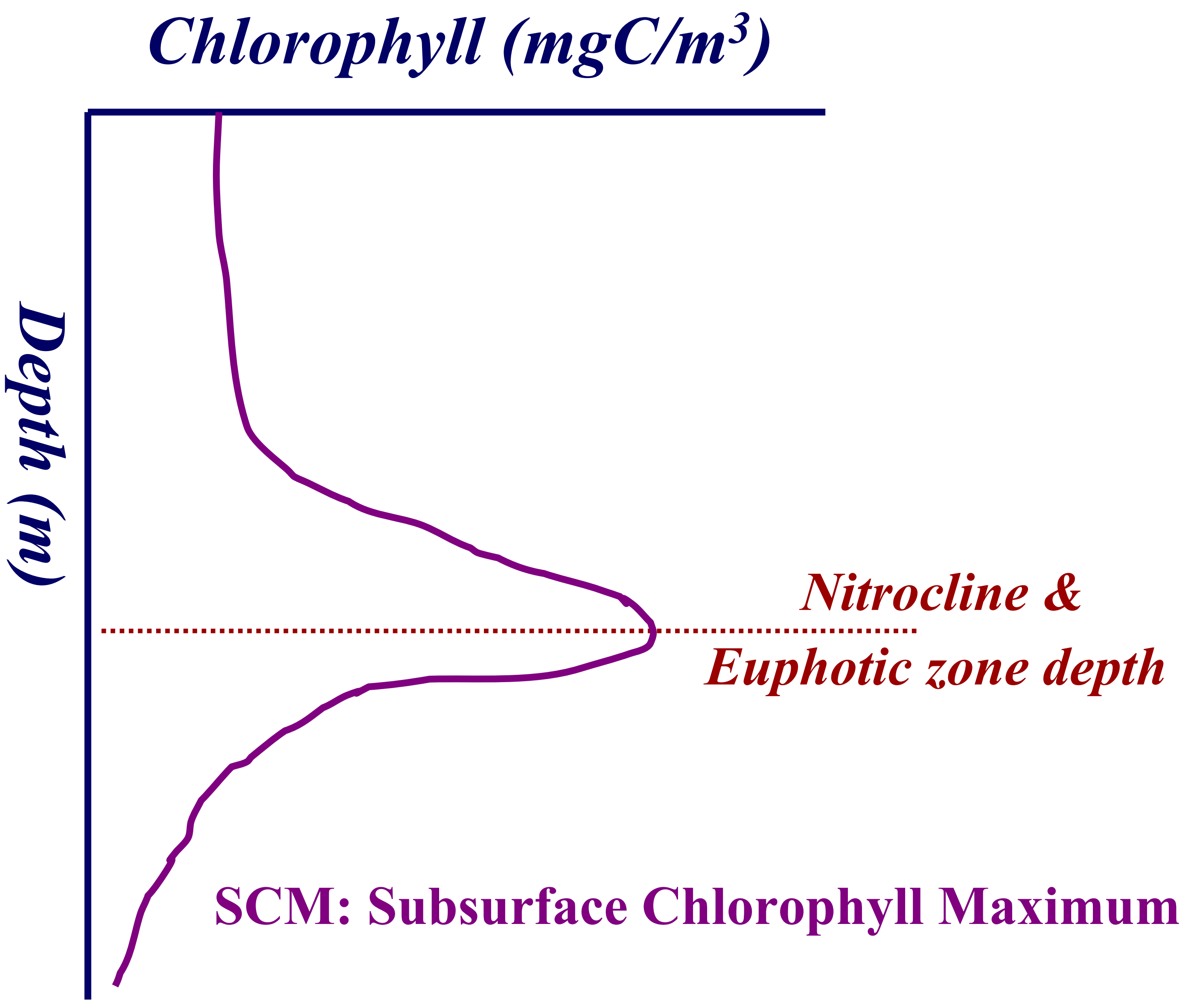



Primary production (mgC/m3/d)
Depth (m)
Euphotic zone depth = 1% of I0


Depth
100 m
No plants
Few plants
Large numbers of plants



NO_3 concs. (μM)
Depth (m)
Surface depletion
Nitrocline


Chlorophyll (mgC/m3)
Depth (m)
Nitrocline &
Euphotic zone depth
SCM: Subsurface Chlorophyll Maximum

The subsurface chlorophyll maximum and peak of primary production in tropical waters are a response to the slow turbulent diffusion of nitrate upwards through the thermocline.

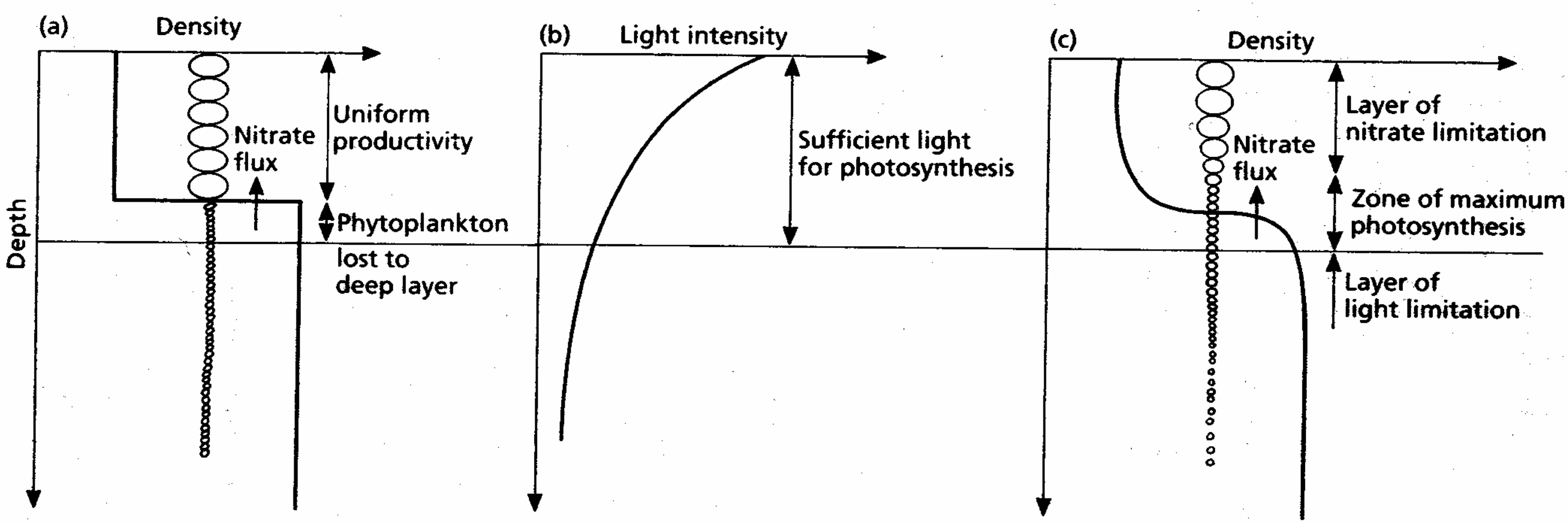
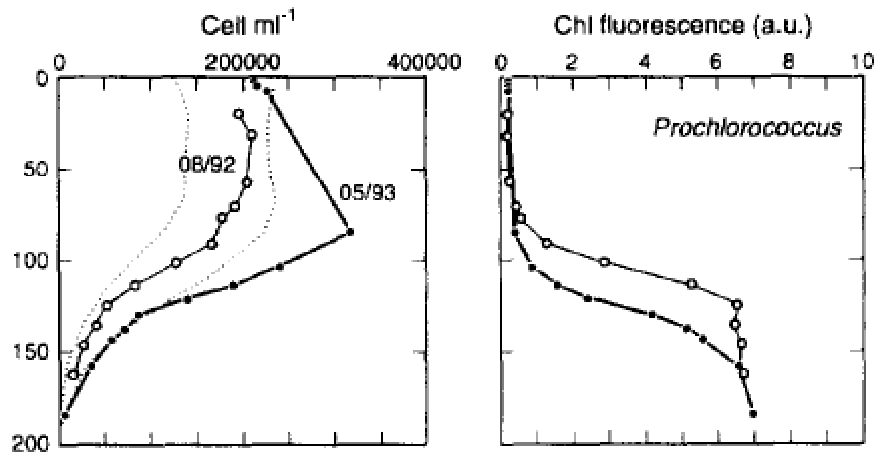


Fig. 3.06 (a) A vertical density profile through a thin pycnocline separating two homogeneous layers. The rate of vertical mixing, symbolized by the circles, changes abruptly through the pycnocline, and is high above and low below the pycnocline. (b) A vertical profile of the average light intensity with an indication of the depth where phytoplankton growth is light-limited. (c) A vertical density profile similar to (a) except that the density increases and the vertical mixing decreases gradually through the pycnocline.

L. Campbell *et al.*



SCM is caused by photoadaptation!
So the carbon to chl ratio for the surface and deep phytoplankton populations are different.
Therefore chl is not a good estimate of biomass!

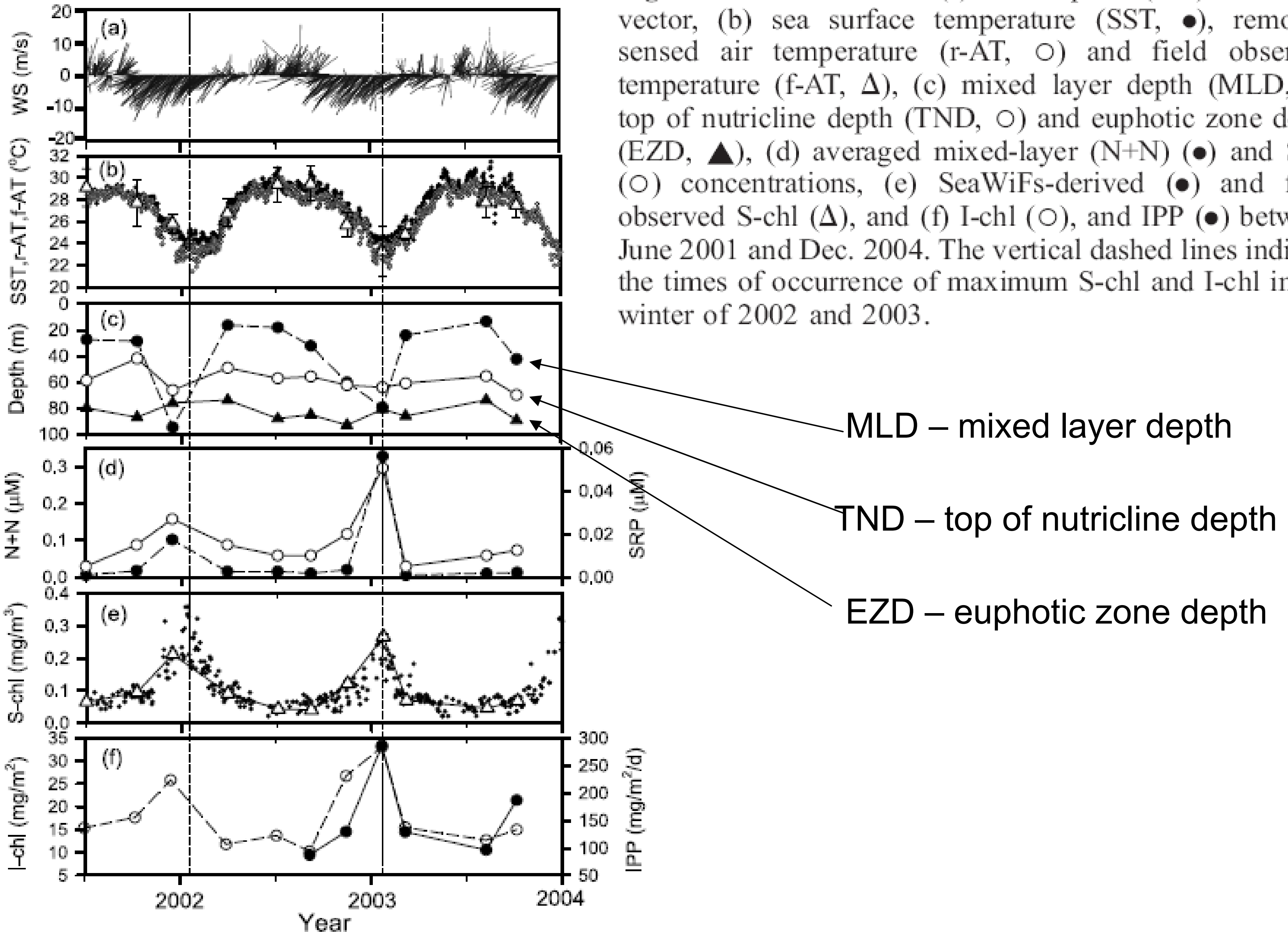


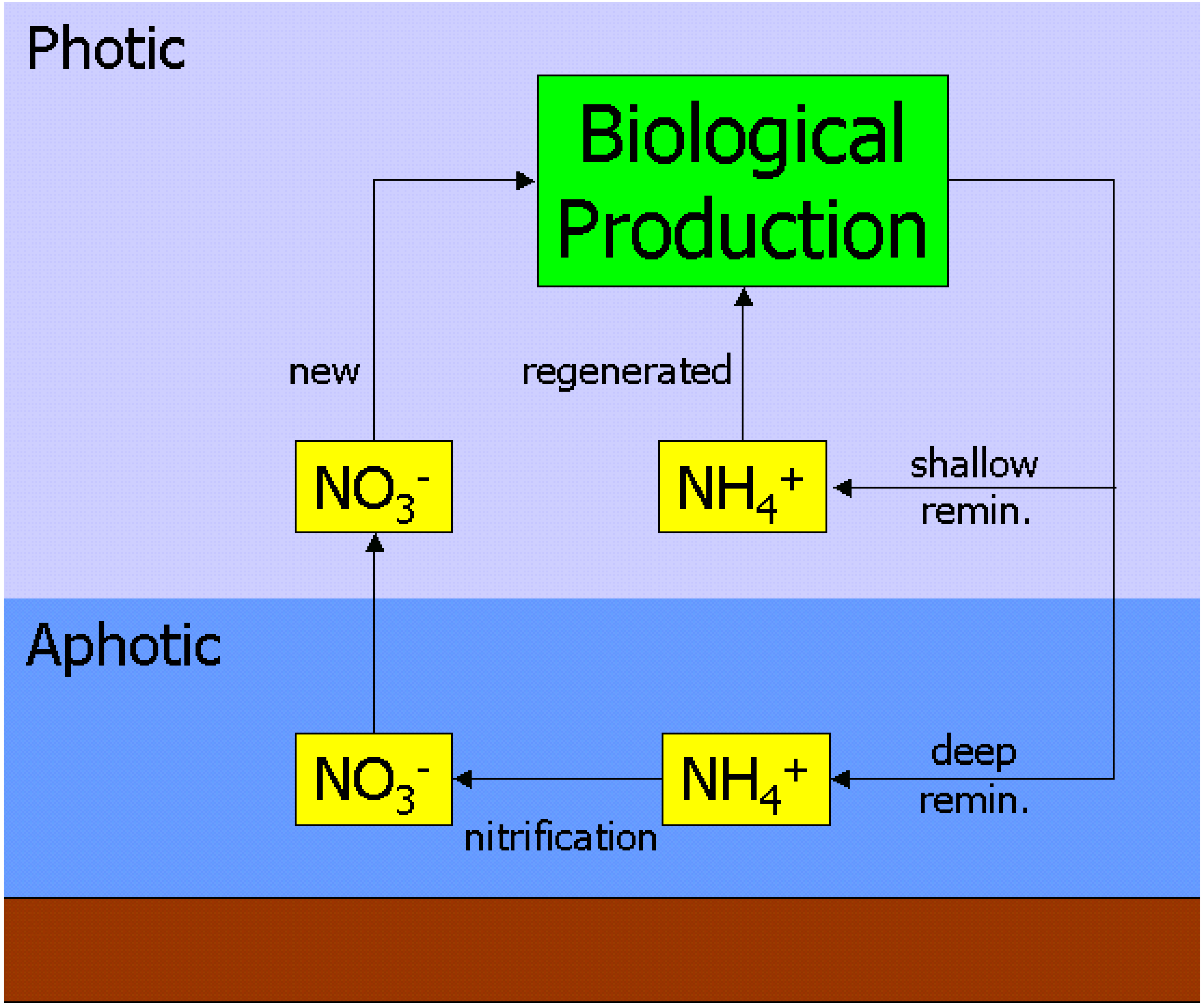
Figure 2. Variations in (a) wind speed (WS) and wind vector, (b) sea surface temperature (SST, ●), remotely sensed air temperature (r-AT, ○) and field observed temperature (f-AT, Δ), (c) mixed layer depth (MLD, ●), top of nutricline depth (TND, ○) and euphotic zone depth (EZD, ▲), (d) averaged mixed-layer (N+N) (●) and SRP (○) concentrations, (e) SeaWiFs-derived (●) and field observed S-chl (Δ), and (f) I-chl (○), and IPP (●) between June 2001 and Dec. 2004. The vertical dashed lines indicate the times of occurrence of maximum S-chl and I-chl in the winter of 2002 and 2003.

- “new” and “regenerated” production (Dugdale and Goering 1967)
- the *f* ratio – the ratio of new production to total production (Eppley and Peterson 1979)

New production – use “new” nitrogen, e.g., NO_3^- and N_2 (also = export production)

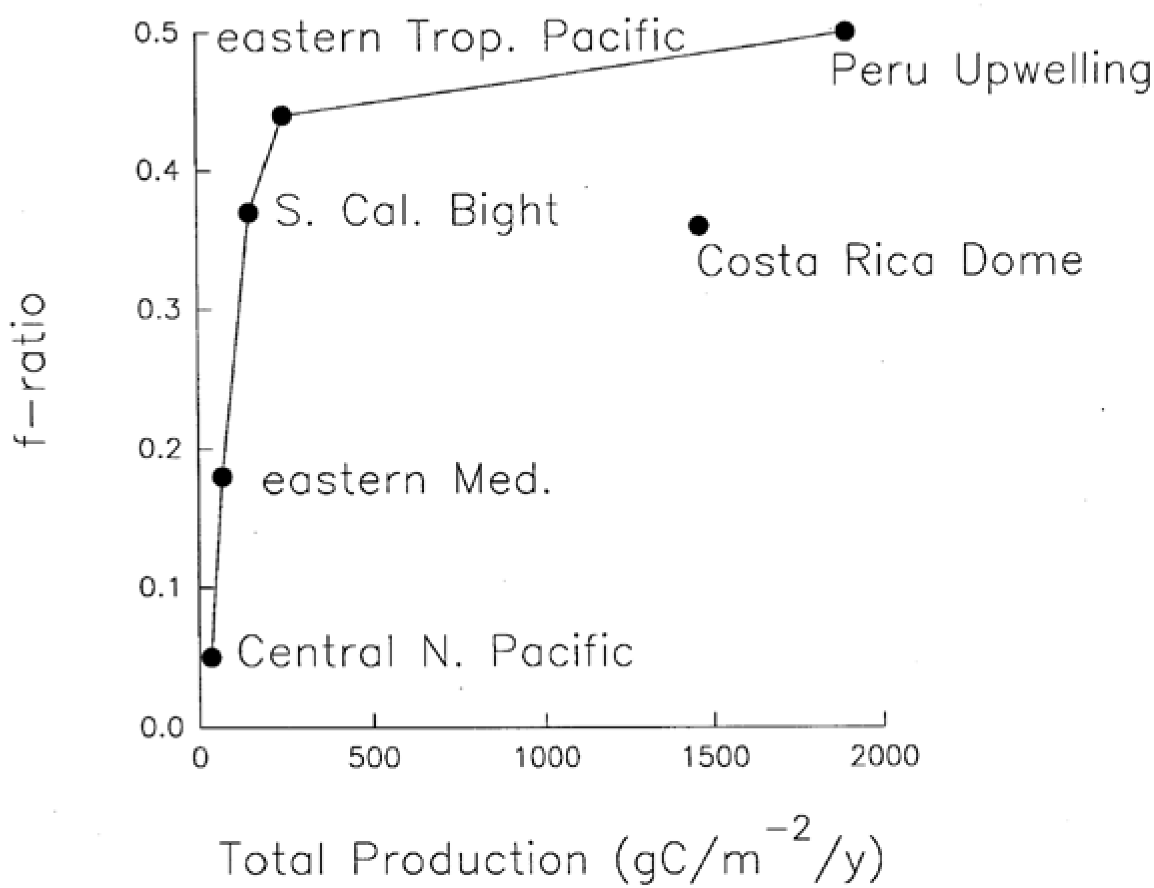
Regenerated production – use regenerated nitrogen, e.g., NH_4^+ and urea.

In steady-state conditions the nitrogen removed from the mixed layer by sinking, or by predators that leave the area, must be balanced by the vertical transport of new nitrogen


Photic
Biological Production
new
regenerated
NO_3^-
NH_4^+
shallow remin.
Aphotic
NO_3^-
NH_4^+
deep remin.
nitrification

- If *Prochlorococcus* can not use nitrate, a major component of the oceanic phytoplankton is not directly related to the supply of nitrate from deep water. It is incapable of new production. Instead it is unusually efficient at harvesting light at low intensities near the base of the mixed layer, and utilizes recycled nitrogen in the form of ammonium excreted by other organisms.

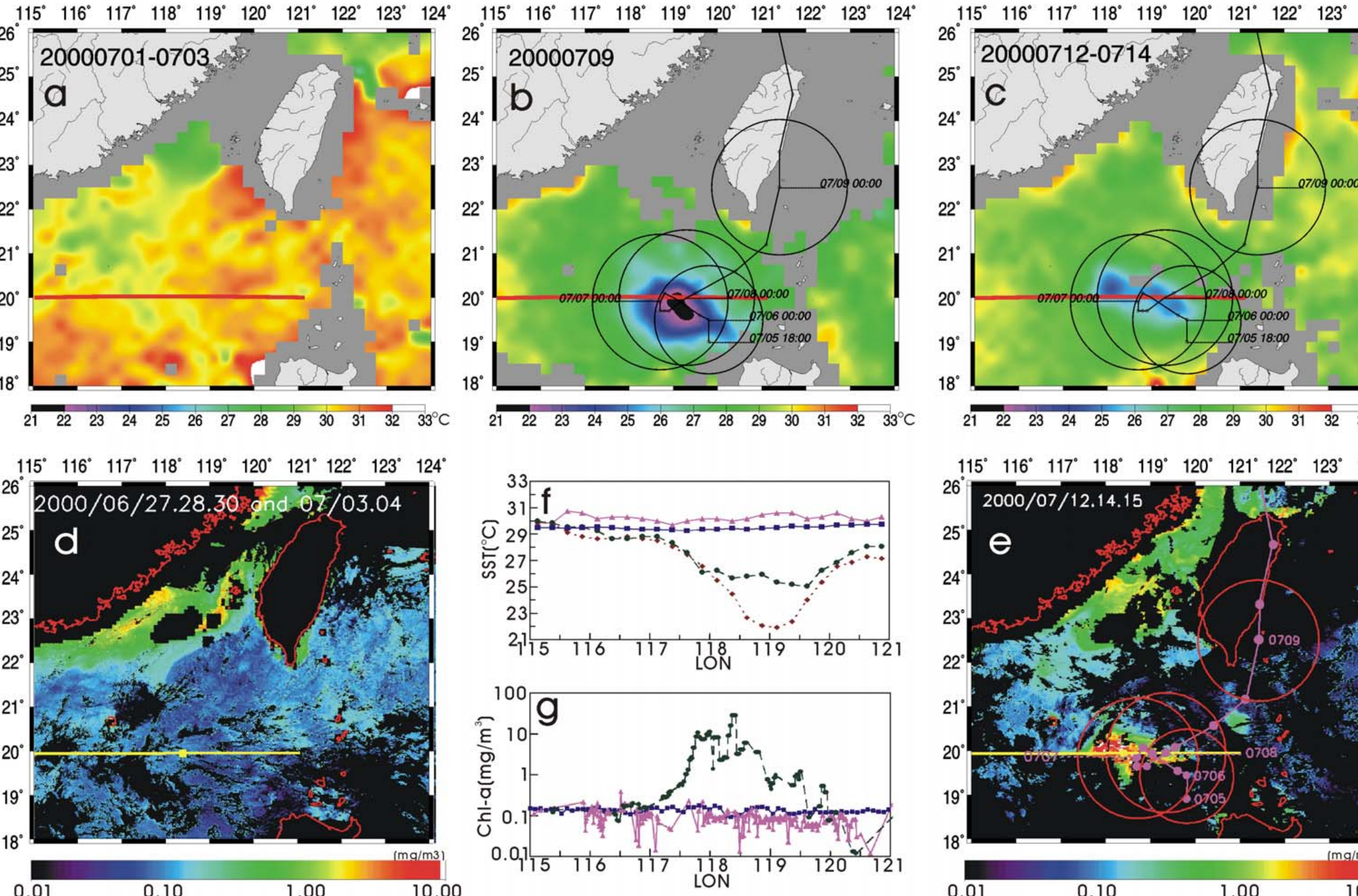
New Production as a f(Total Production)



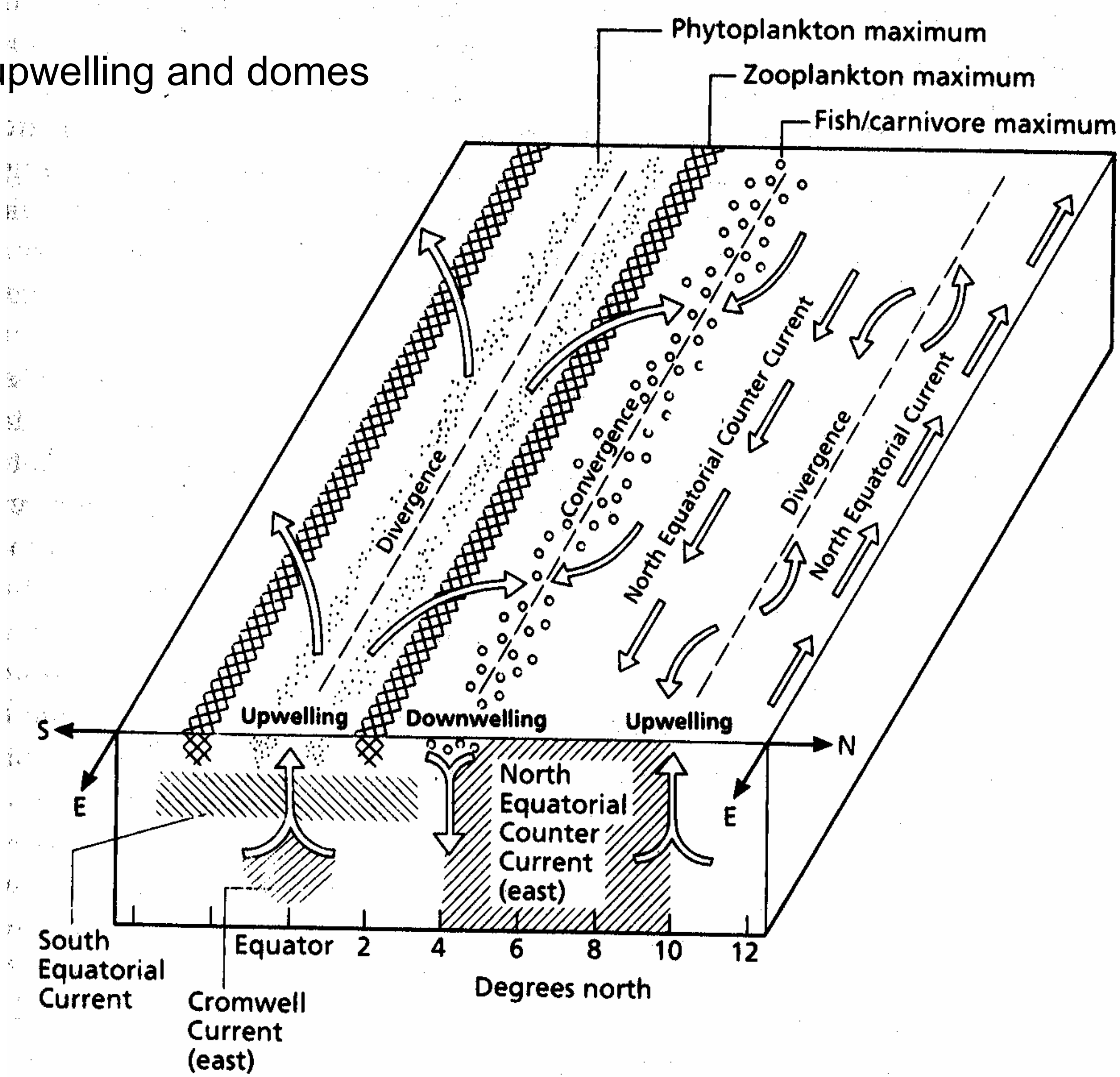
Eppley & Peterson, 1979

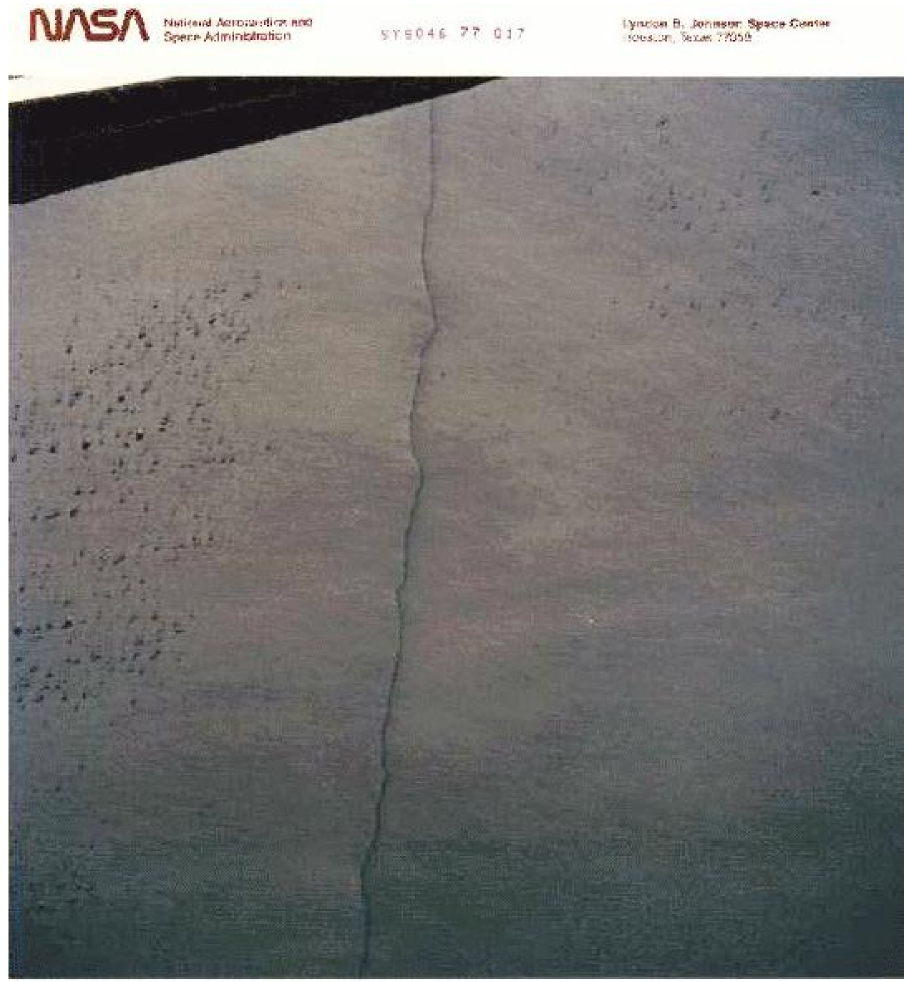
- The turbulent diffusion coefficient, K_v, is very difficult to measure directly. Calculated vertical eddy diffusivity in stratified tropical and subtropical waters, using various methods, was rather low, of the order of 0.01-0.05 x 10^{-4} m^2 s^{-1}.
- Using the equation $F = K_v\, dN/dz$, it is calculated that the vertical fluxes of nitrate averaged 0.1-0.2 mmol N m^{-2} d^{-1}, which is stoichometrically equivalent to a carbon fixation rate around 0.1 mmol C m^{-2} d^{-1}
- This very low figure indicates that in the absence of special upwelling situation, the new production in oceanic waters is extremely low and is limited by the stable vertical structure with its pycnocline barrier and low level of vertical transport of nitrate and other nutrients.
- However, ….special mixing events
- Also nitrogen fixation!

New Evidence for Enhanced Ocean Primary Production Triggered by Tropical Cyclone (Lin et al., 2003c; *GRL)*

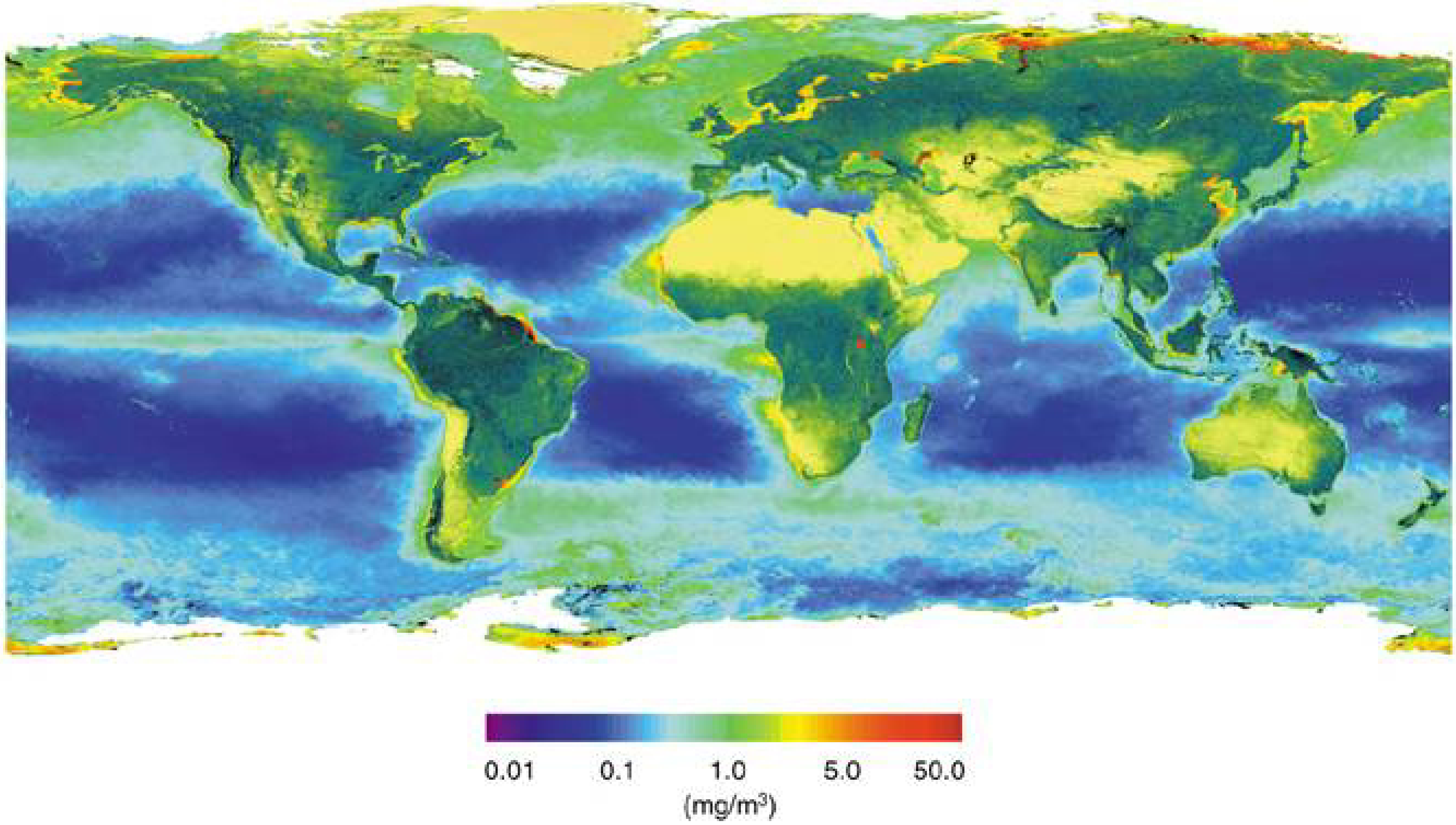


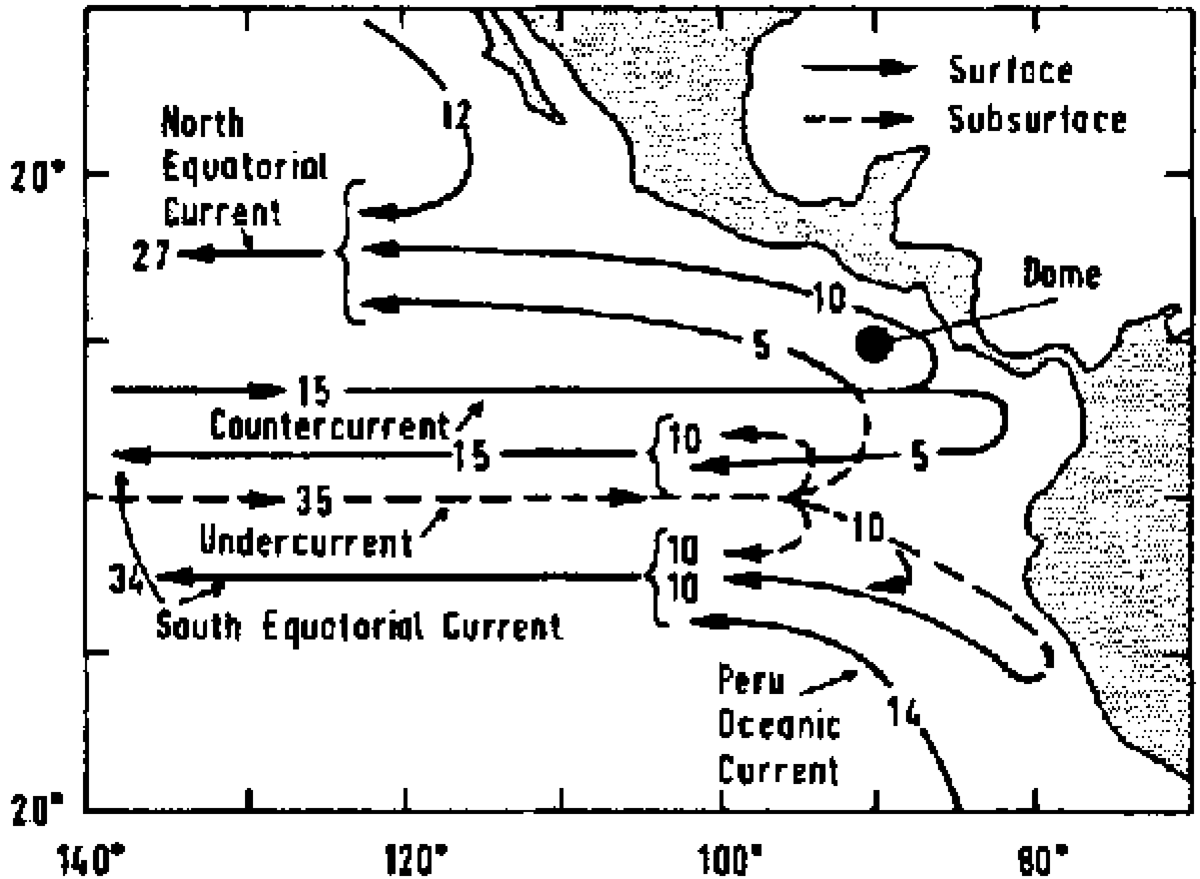
Equatorial upwelling and domes



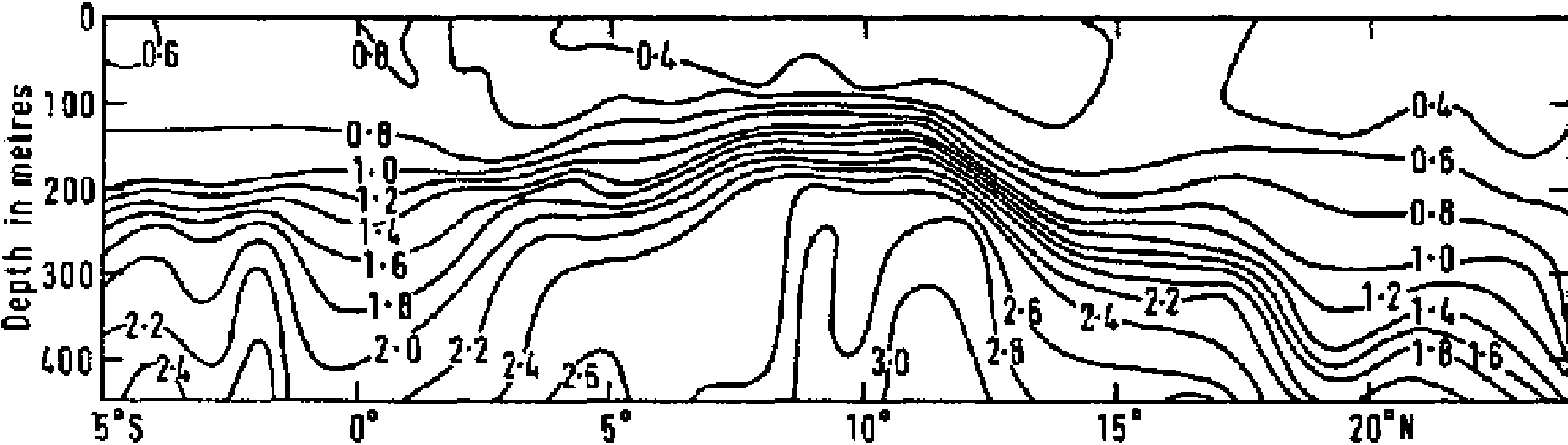


A Line in the Sea
(Yoder et al., 1994. Nature 371: 689-692)


0.01
0.1
1.0
5.0
50.0
(mg/m3)



Currents in the Eastern Tropical Pacific during the period June to December (Wyrtki, 1966); the figures represent transports in cm³ 10^{12}/sec



a section of the Costa Rica dome, in phosphorus (μM) (Cromwell, 1958)

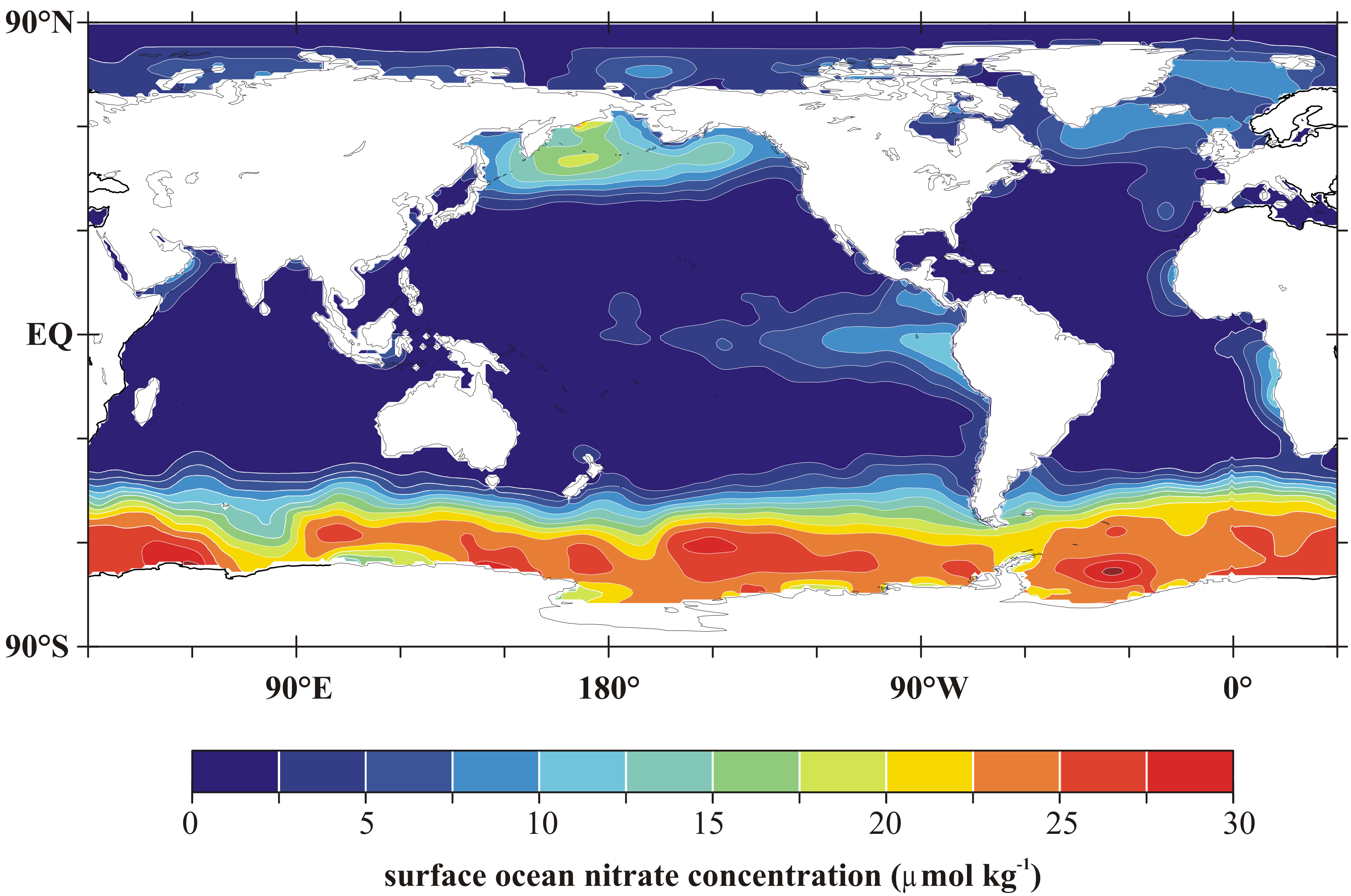
- Average pp in equatorial Pacific Ocean: 325 g C m^{-2} y^{-1}, which is 4 time higher than old estimates
- Method improvement or a systematic increase?

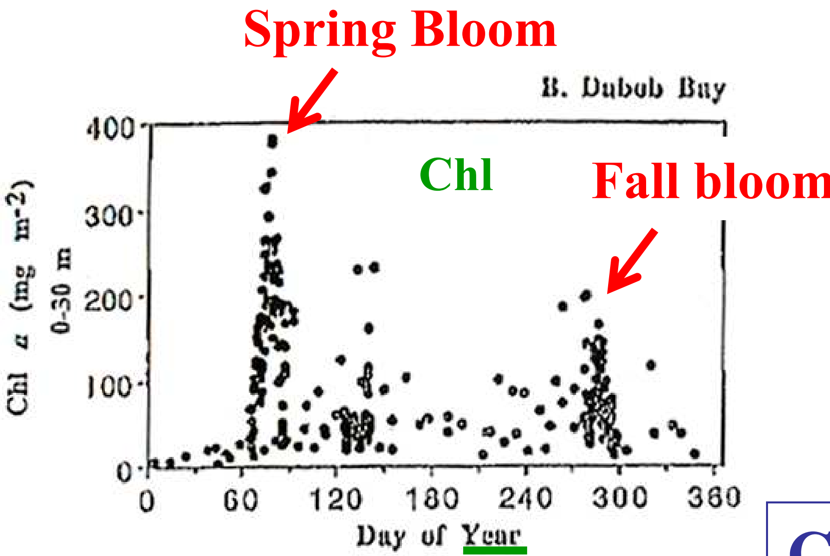
Typical primary production rates

Regions	Rates (mgC m^{-2} d^{-1})
Oligotrophic ocean	50-200
Shelves	500-2000
Coastal upwelling	2000-5000
Estuaries, Polar blooms	2000-10,000

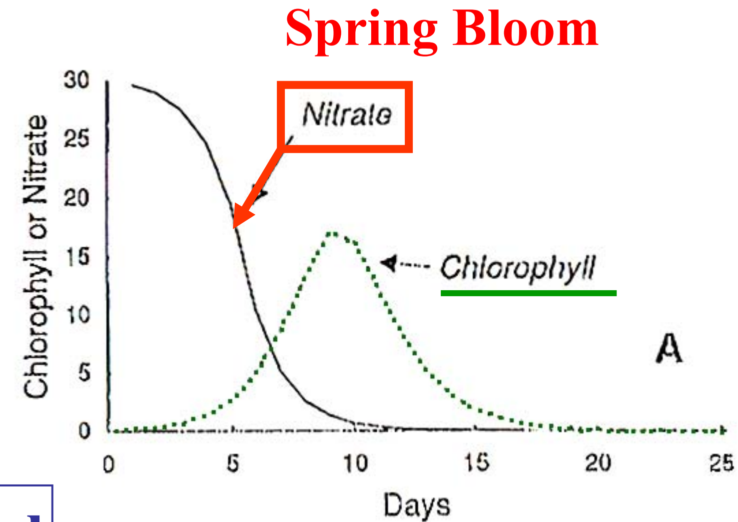
The paradox of high nitrate and low chlorophyll scheme

Nitrate concentrations in surface water – the "HNLC" regions

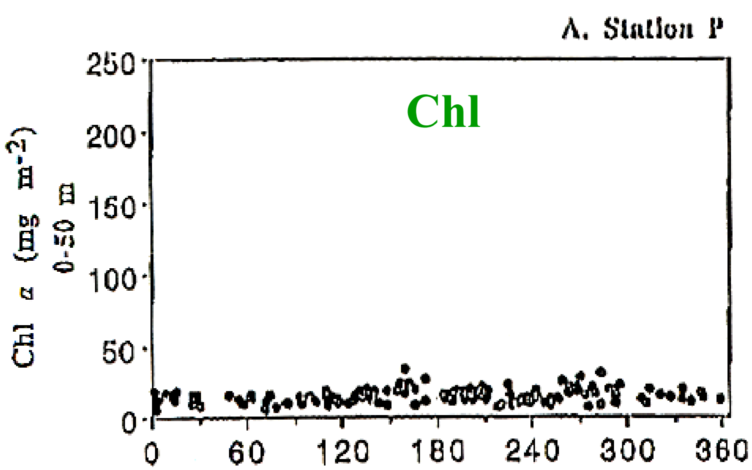


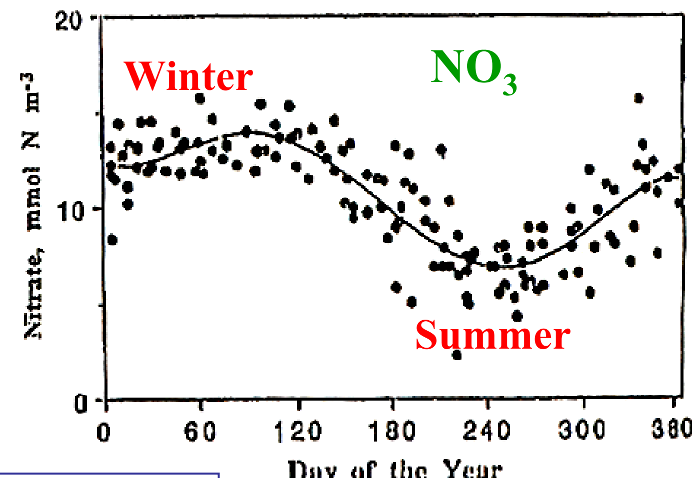


A. Phytoplankton standing stock (as Chl a)



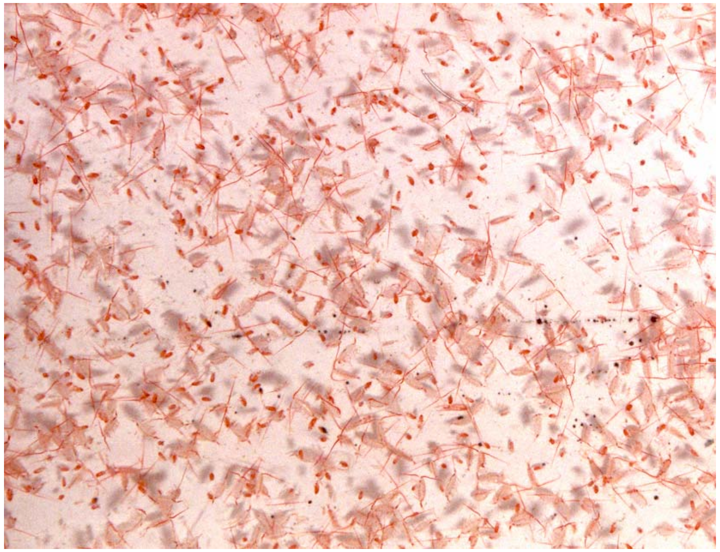
Coastal



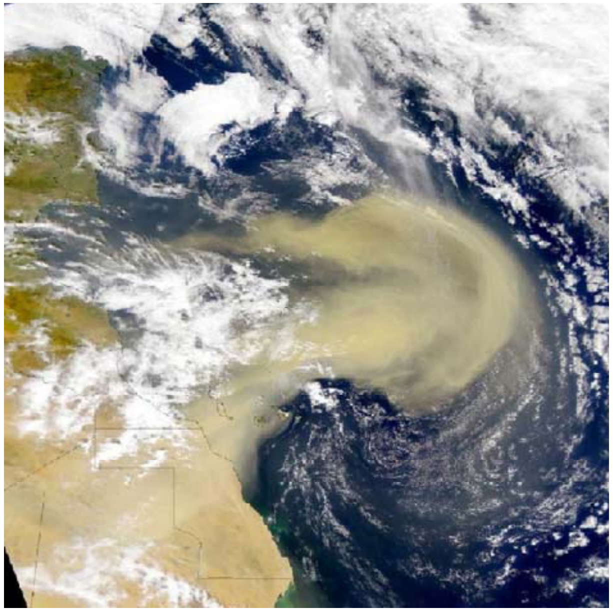


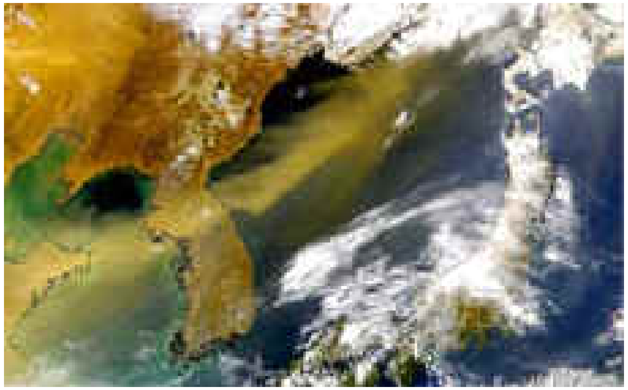
(from Frost, 1993)

Stn P – Open Ocean



The traditional explanation for the lack of a spring phytoplankton blooms in the northeastern subarctic Pacific is that the grazing of larger Neocalanus species may control phytoplankton stocks and prevent blooms





Martin (1990) proposed an alternative explanation, that the very low levels of available Fe limit phytoplankton production and result in the persistence of substantial concentrations of major nutrients in HNLC regions (Martin and Fitzwater, 1988; Martin et al., 1989).

"Give me a half tanker of iron, and I will give you an ice age."

John Martin

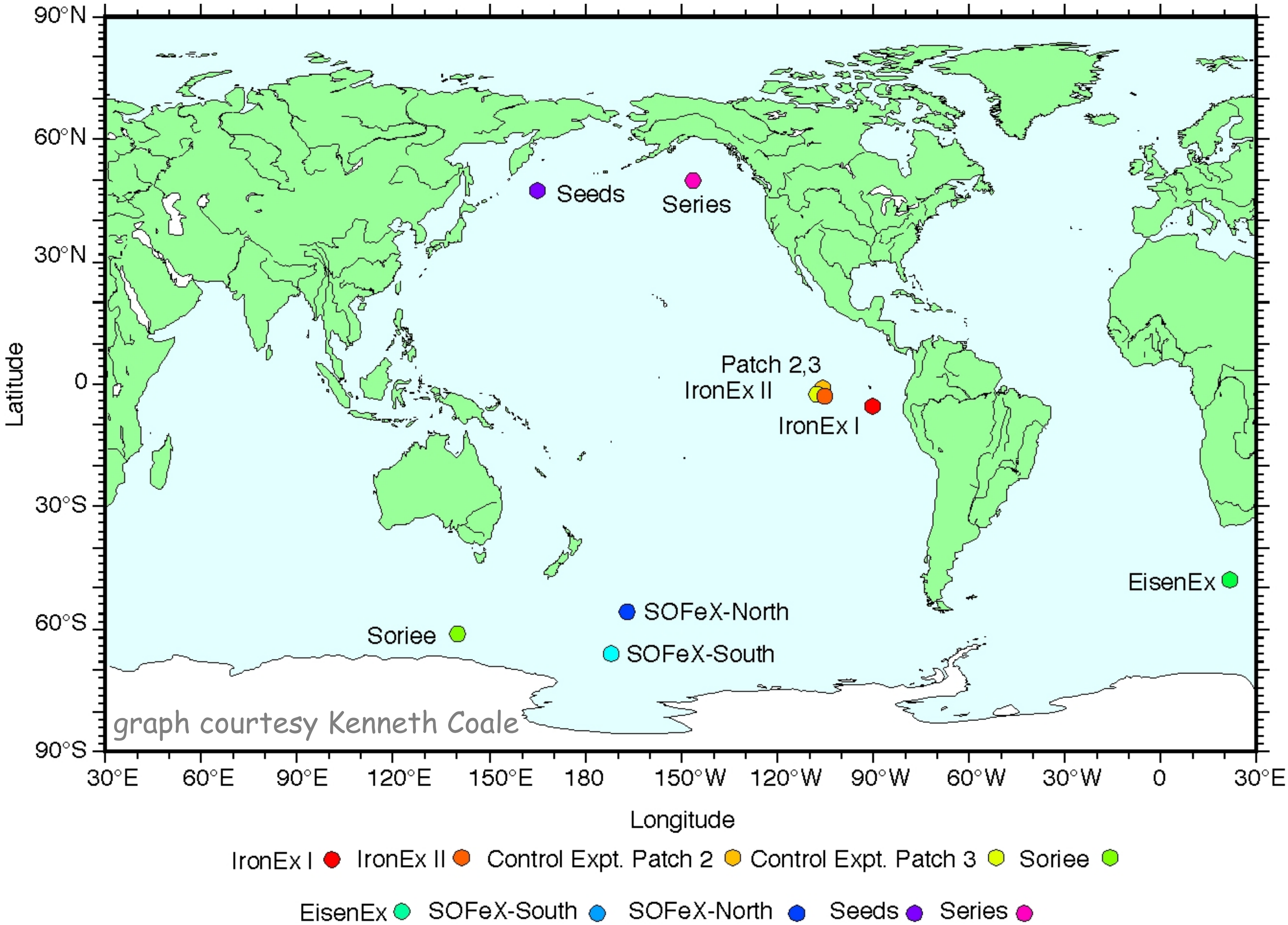
Role of Iron in Cellular Processes

1) **Photosynthesis – PSI & PSII**
2) **Respiration – Electron transport system**
3) **Chlorophyll Synthesis**
4) **NO_3 Reduction**

$$\boxed{NO_3^-} \xrightarrow[\text{Reductase}]{\text{Nitrate}} \boxed{NO_2^-} \xrightarrow[\text{Reductase}]{\text{Nitrite}} \boxed{NH_4^+}$$

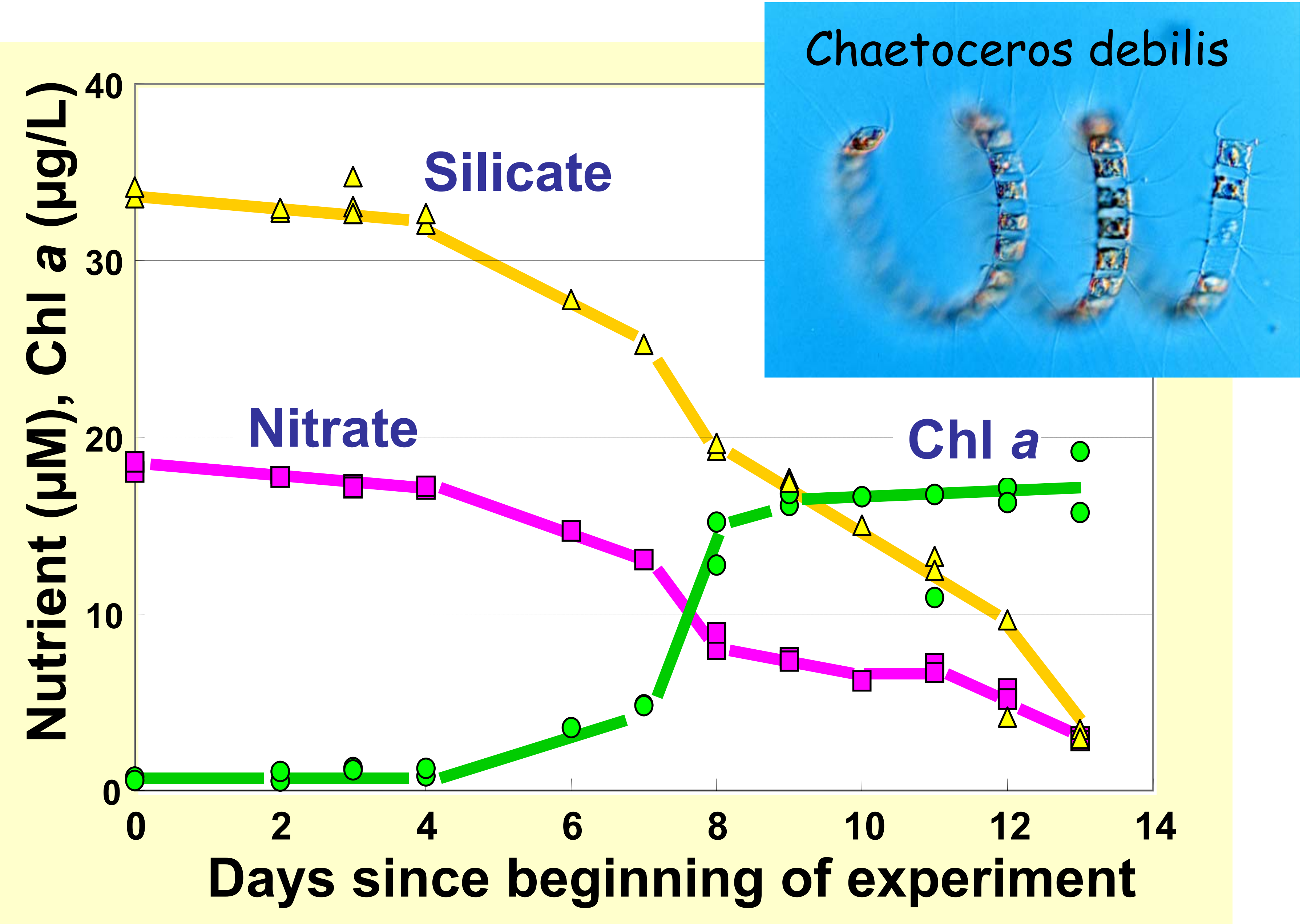
1 Fe (Nitrate Reductase)

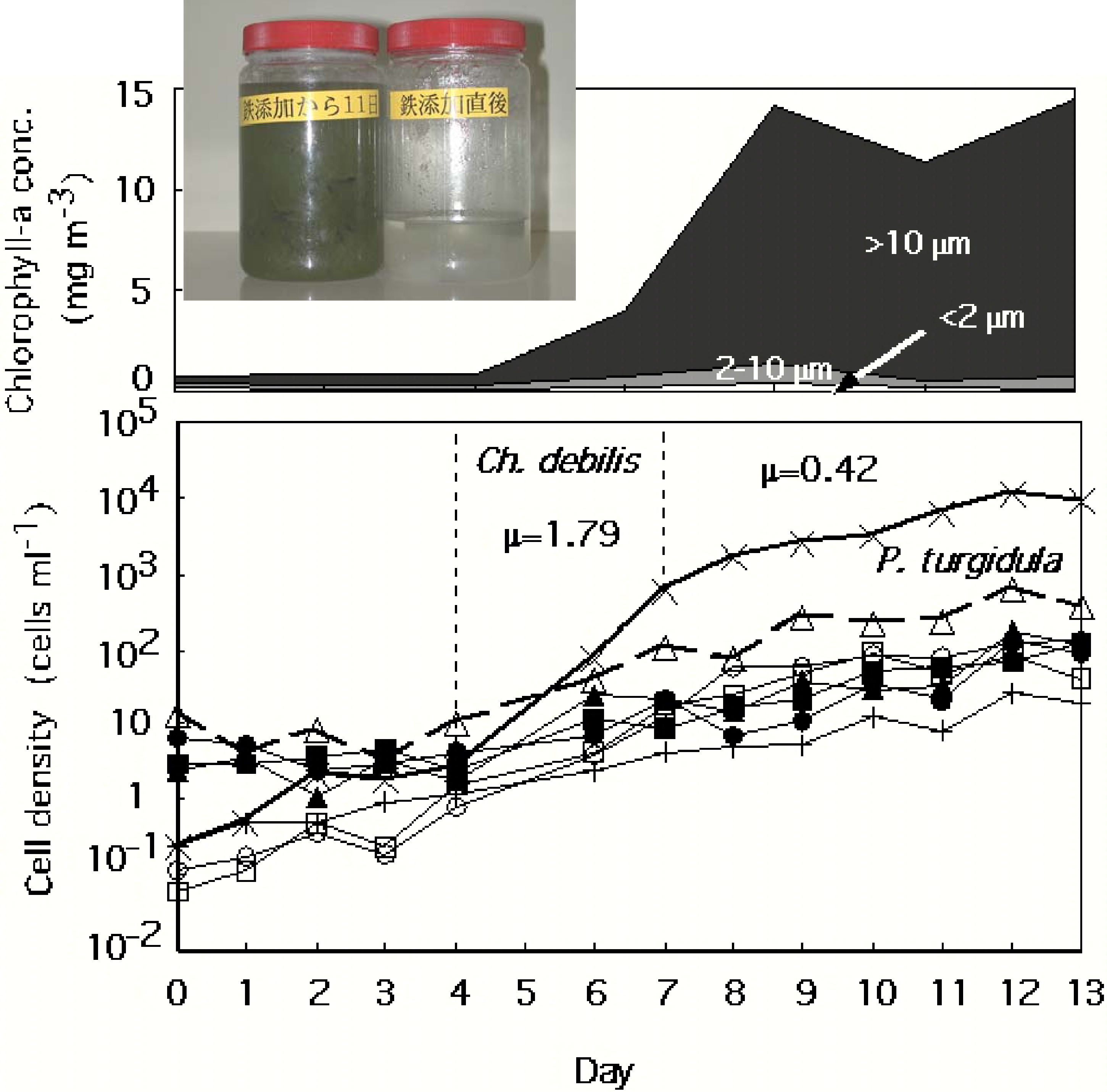
5 Fe (Nitrite Reductase)



not yet shown: Eifex 2004 (Polarstern) and Seeds II 2004

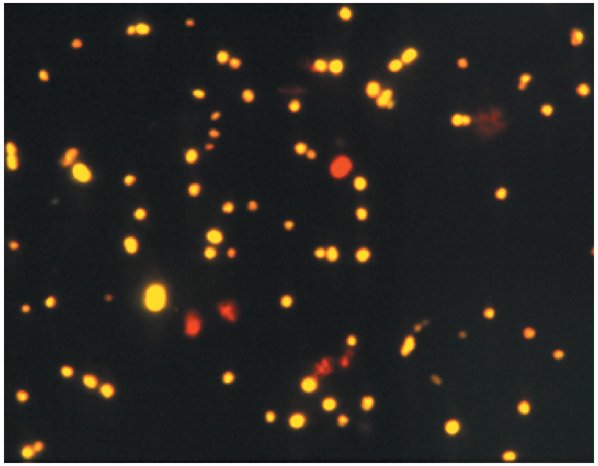
Time-series data of nutrients and Chl *a*

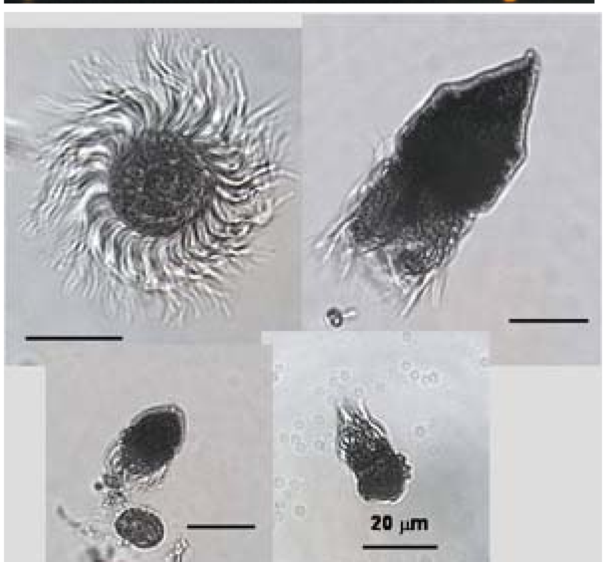




鉄添加から11日
鉄添加直後
Chlorophyll-a conc. (mg m-3)
15
10
5
0
>10 µm
<2 µm
2-10 µm
Cell density (cells ml-1)
10^5
10^4
10^3
10^2
10
1
10^-1
10^-2
Ch. debilis
µ=1.79
µ=0.42
P. turgidula
0 1 2 3 4 5 6 7 8 9 10 11 12 13
Day

Present view





- Low iron concentration prevent diatoms bloom, shifting phytoplankton community to picoplankton dominant

- Microzooplankton grazing controls picoplankton dominated phytoplankton stocks

- Silicate?
- Light?
- Temperature?

Vertical structure and phytoplankton production in temperature and polar waters

- The most important feature is the spring bloom – mainly resulted from seasonal variation of surface mixed layer depth and solar radiation

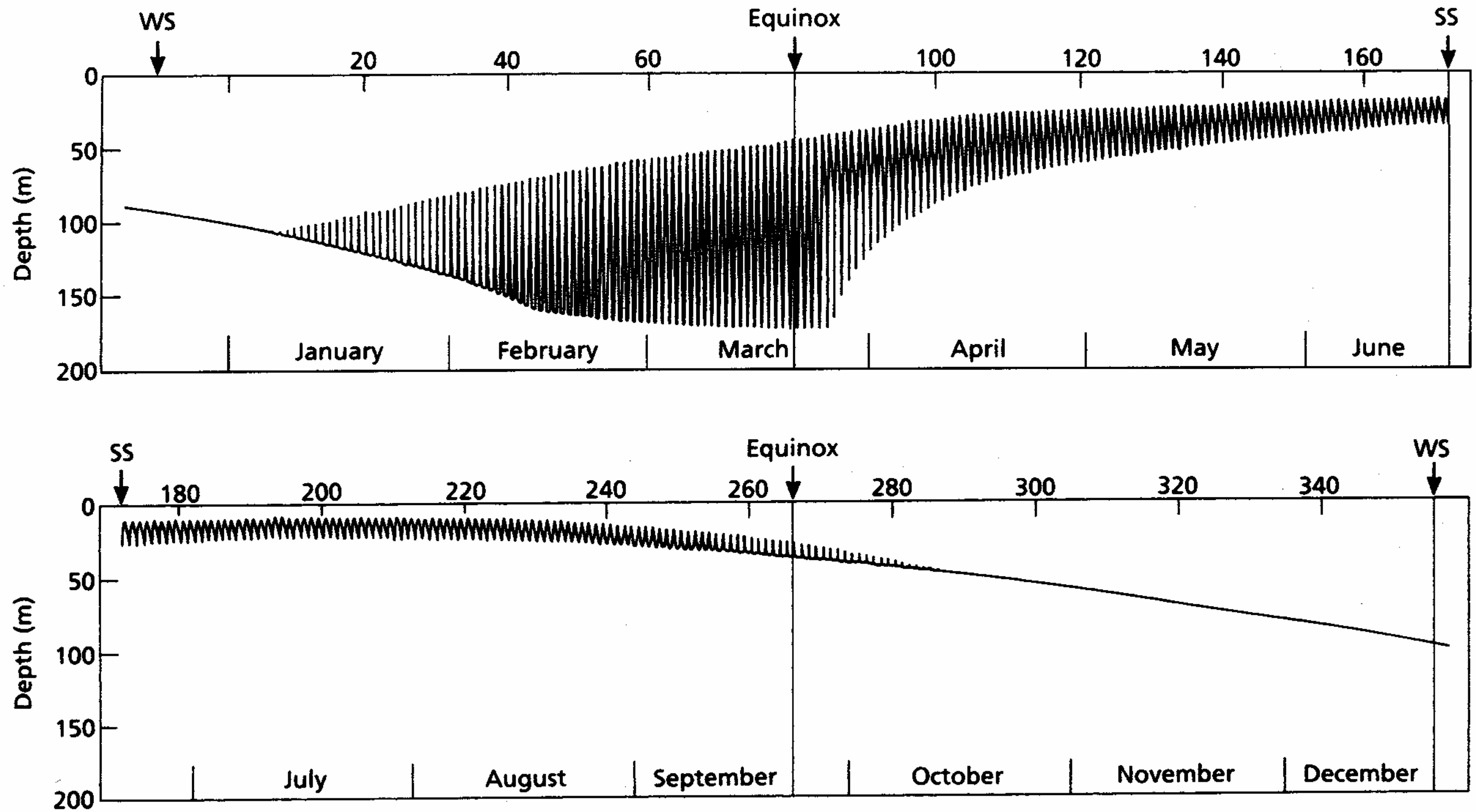
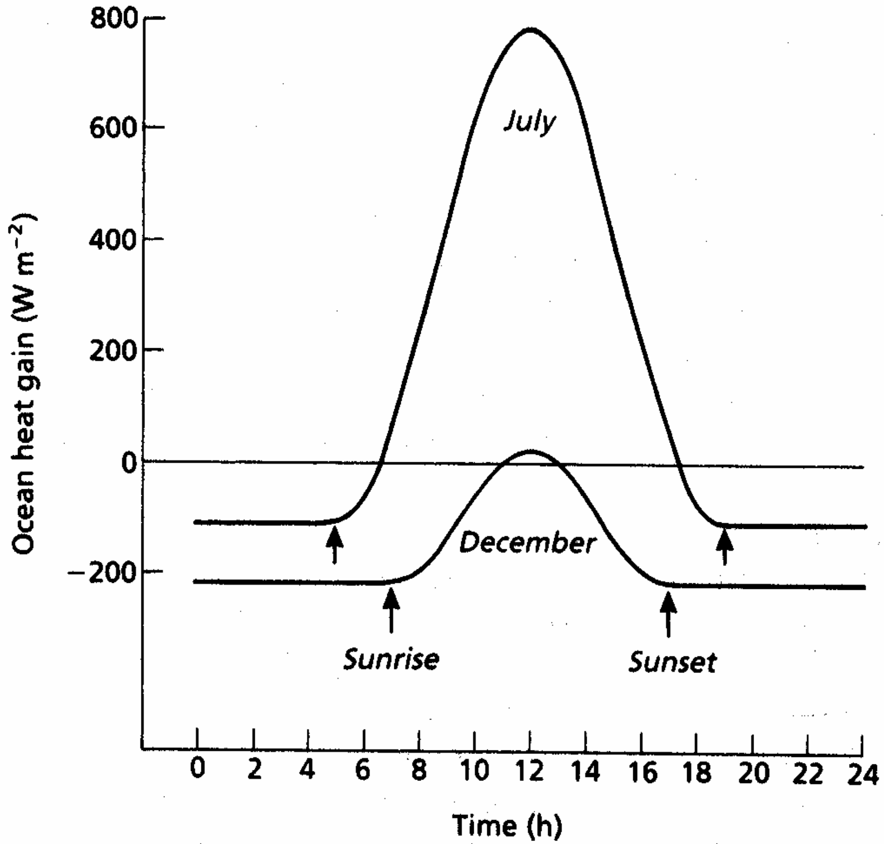
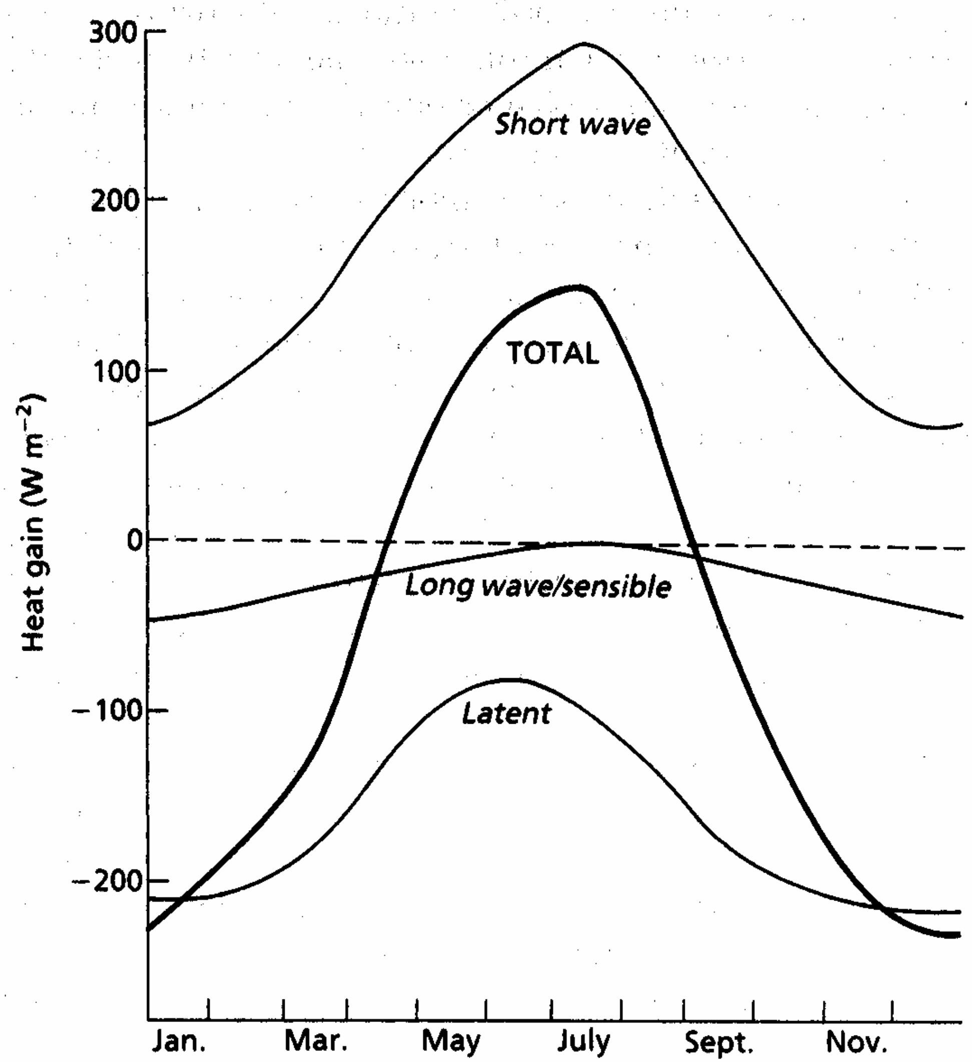


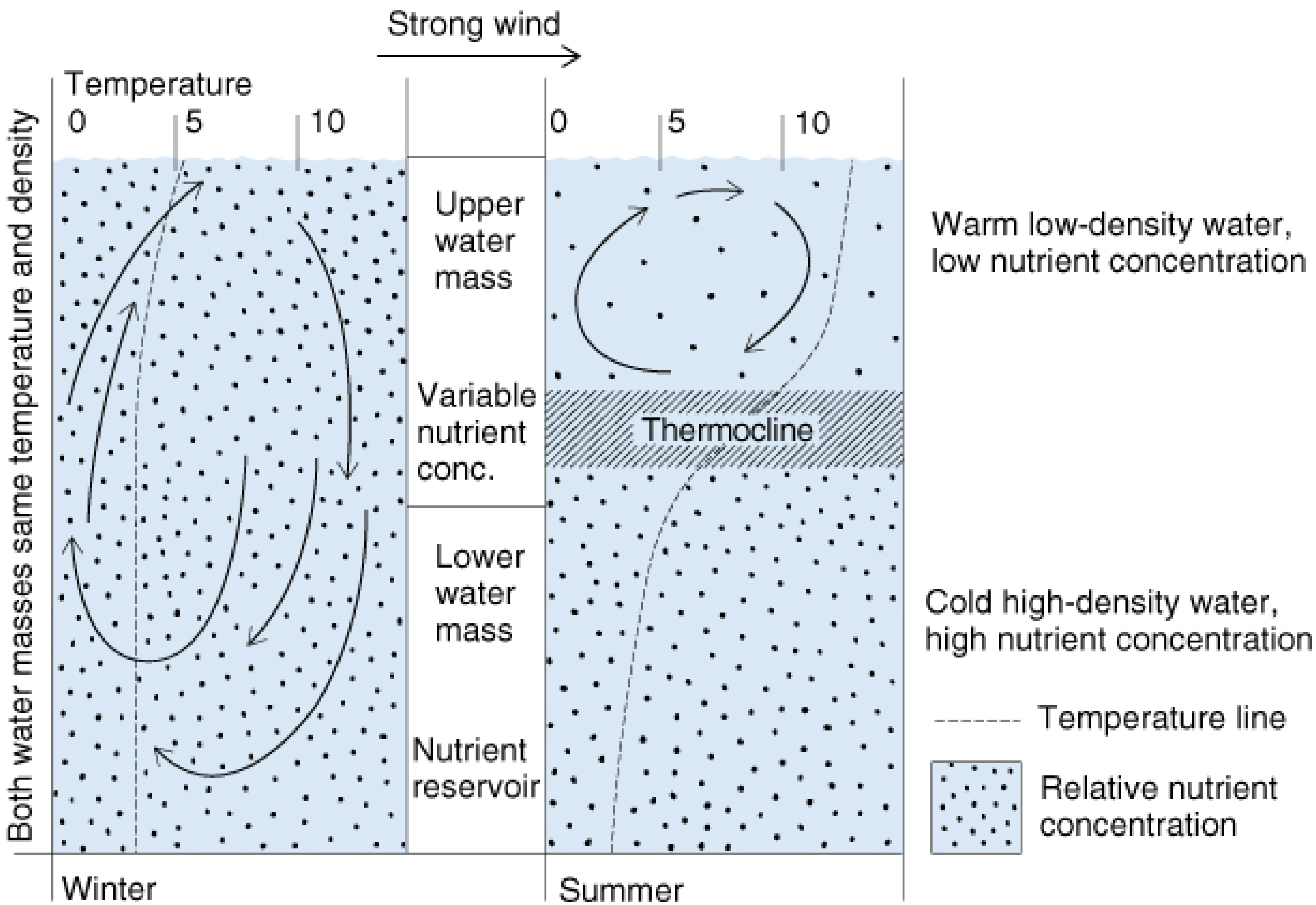
Fig. 3.09 Model simulation of the diurnal variation of the mixed layer depth over the year at latitude 41° N. Note the diurnal movement of the thermocline from January to October. WS, winter solstice; SS, summer solstice. From Woods and Barkmann (1986).

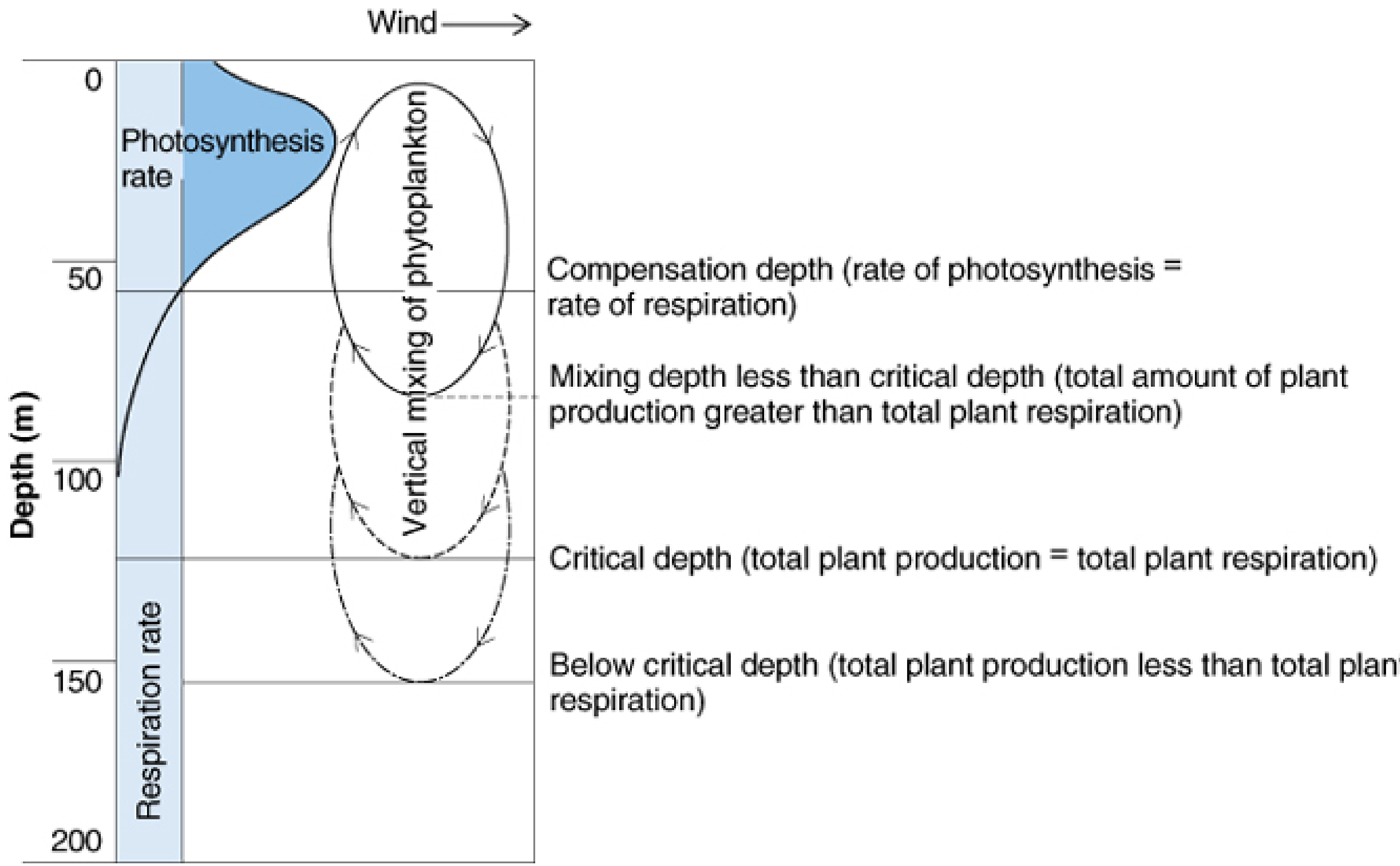


Diurnal changes in the net heat gain during an average day in July and December at 40ºN, 40ºW



Seasonal changes in net short-wave radiation, net long-wave radiation/sensible heat exchange, and latent heat exchange, and the total at 35ºN 48ºW


Strong wind
Temperature
0
5
10
Both water masses same temperature and density
Upper water mass
Variable nutrient conc.
Lower water mass
Nutrient reservoir
0
5
10
Thermocline
Winter
Summer
Warm low-density water, low nutrient concentration
Cold high-density water, high nutrient concentration
Temperature line
Relative nutrient concentration


Wind
0
50
100
150
200
Depth (m)
Photosynthesis rate
Respiration rate
Vertical mixing of phytoplankton
Compensation depth (rate of photosynthesis = rate of respiration)
Mixing depth less than critical depth (total amount of plant production greater than total plant respiration)
Critical depth (total plant production = total plant respiration)
Below critical depth (total plant production less than total plant respiration)

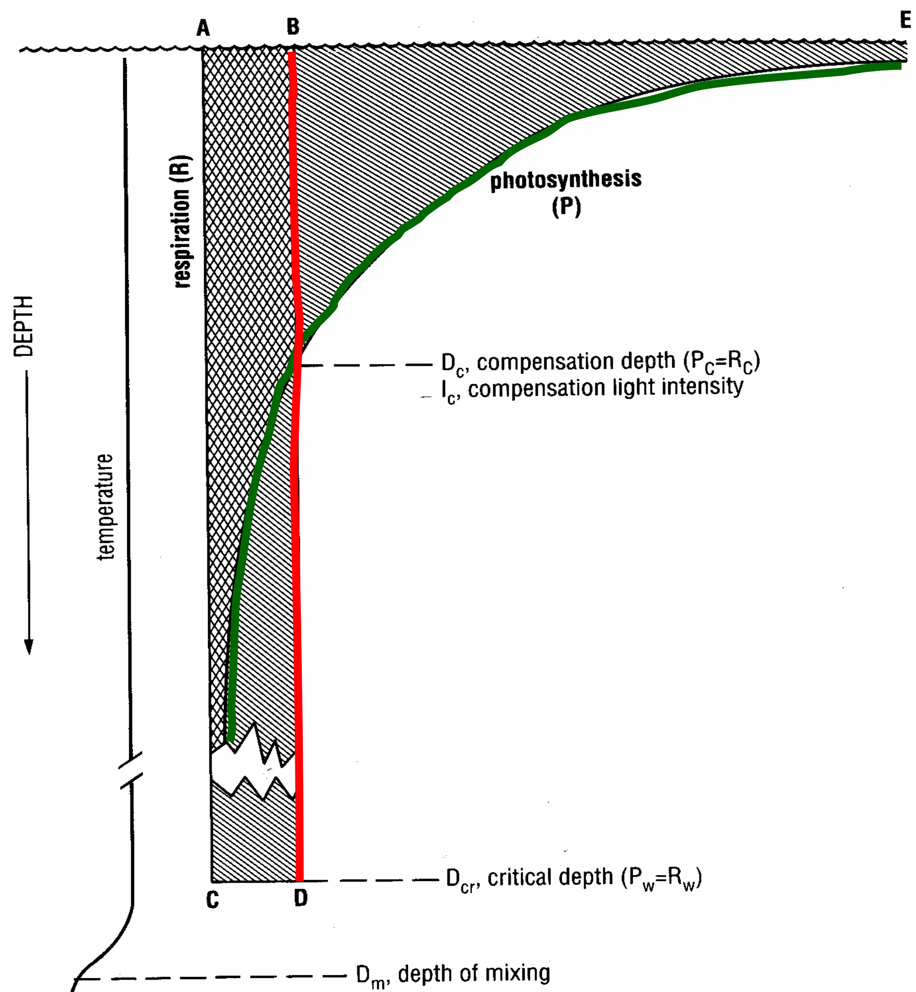


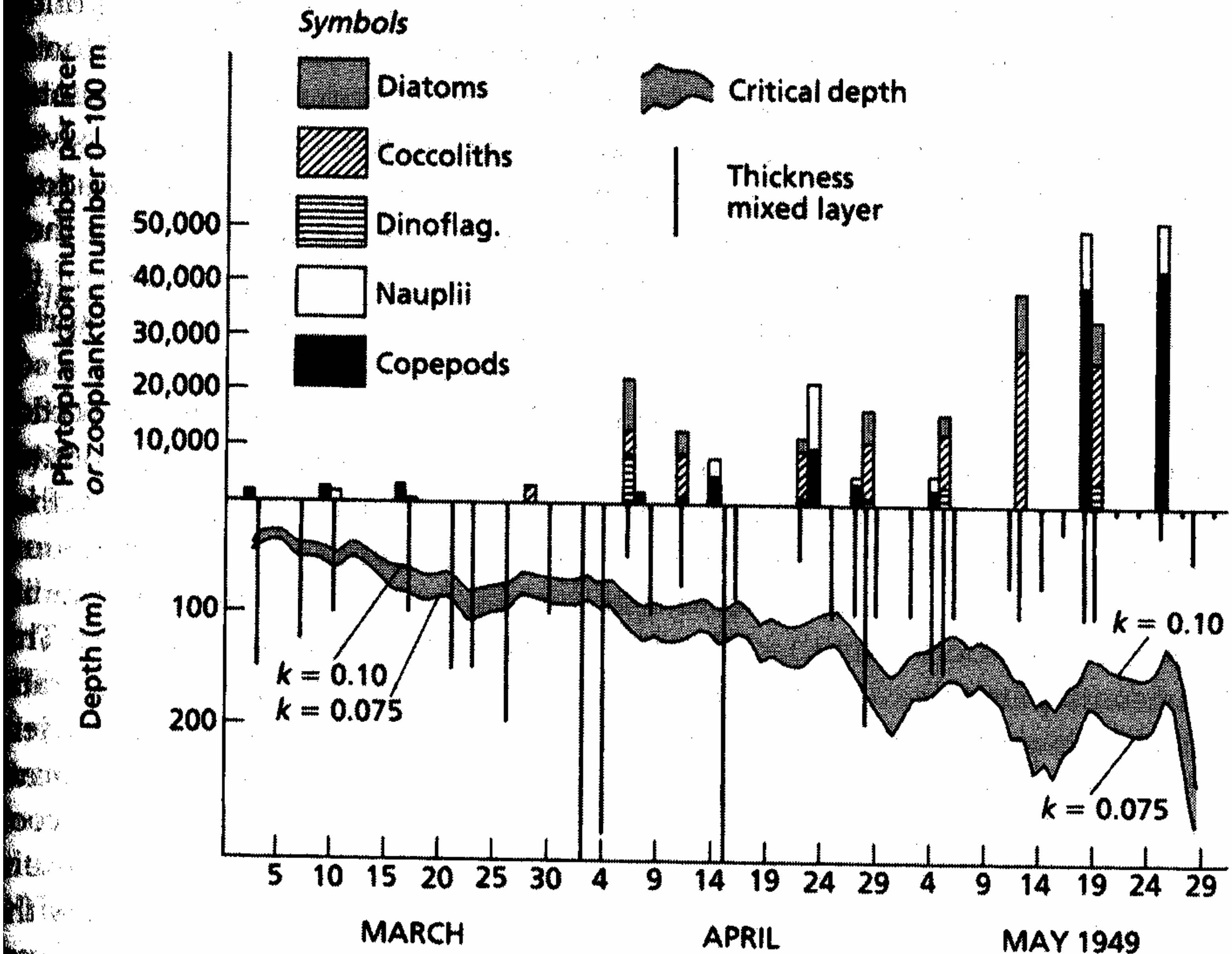
Figure 3.6 An illustration of the relationships among the compensation light depth, the critical depth, and the depth of mixing. At the compensation depth (D_c), the light intensity (I_c) is such that the photosynthesis of a single cell (P_c) is equal to its respiration (R_c); above this depth there is a net gain from photosynthesis ($P_c > R_c$) and below it there is a net loss ($P_c < R_c$). As phytoplankton cells are mixed above and below the compensation depth, they experience an average light intensity (I_D) in the water column. The depth at which I_D equals I_c is the critical depth (D_{cr}) where photosynthesis throughout the water column (P_w) equals phytoplankton respiration throughout the water column (R_w). The area bounded by points A, B, C and D represents phytoplankton respiration, and the area bounded by points A, C and E represents photosynthesis; these two areas are equal at the critical depth. When the critical depth is less than the depth of mixing (D_m) (as illustrated in this figure), no net production takes place because $P_w < R_w$. Net production of the phytoplankton ($P_w > R_w$) only occurs when the critical depth lies below the depth of mixing.

D_C : $P = R$ (mgC m^{-3} d^{-1})

D_{CR} : $\int P = \int R$ (mgC m^{-2} d^{-1})

$D_m < D_{CR}$ → $\int P > \int R$
→ Bloom

$D_m > D_{CR}$ → $\int P < \int R$
→ No bloom


Symbols
Diatoms
Coccoliths
Dinoflag.
Nauplii
Copepods
Critical depth
Thickness mixed layer
Phytoplankton number per liter or zooplankton number 0–100 m
50,000
40,000
30,000
20,000
10,000
Depth (m)
100
200
k = 0.10
k = 0.075
k = 0.10
k = 0.075
5
10
15
20
25
30
4
9
14
19
24
29
4
9
14
19
24
29
MARCH
APRIL
MAY 1949

Large scale turbulence and phytoplankton performance

- Phytoplankton cells are at times carried from the surface to great depth on a time scale of 1-10 hours, and are thus exposed to a fluctuating light regime.
- Whether phytoplankton cells in a fluctuating light regime are more productive than they would be if exposed to light of a constant average value?
- Experimental evidence are contradictory, but the difference may have been caused by the fact that some biochemical processes in the cells acclimate rapidly to the changing light, while others change too slowly for there to be any noticeable response.
- In any case, the metabolic response of cells exposed to fluctuating light is not very different from the response of those exposed to the same amount of light delivered at a constant rate

The poleward migration of the spring bloom

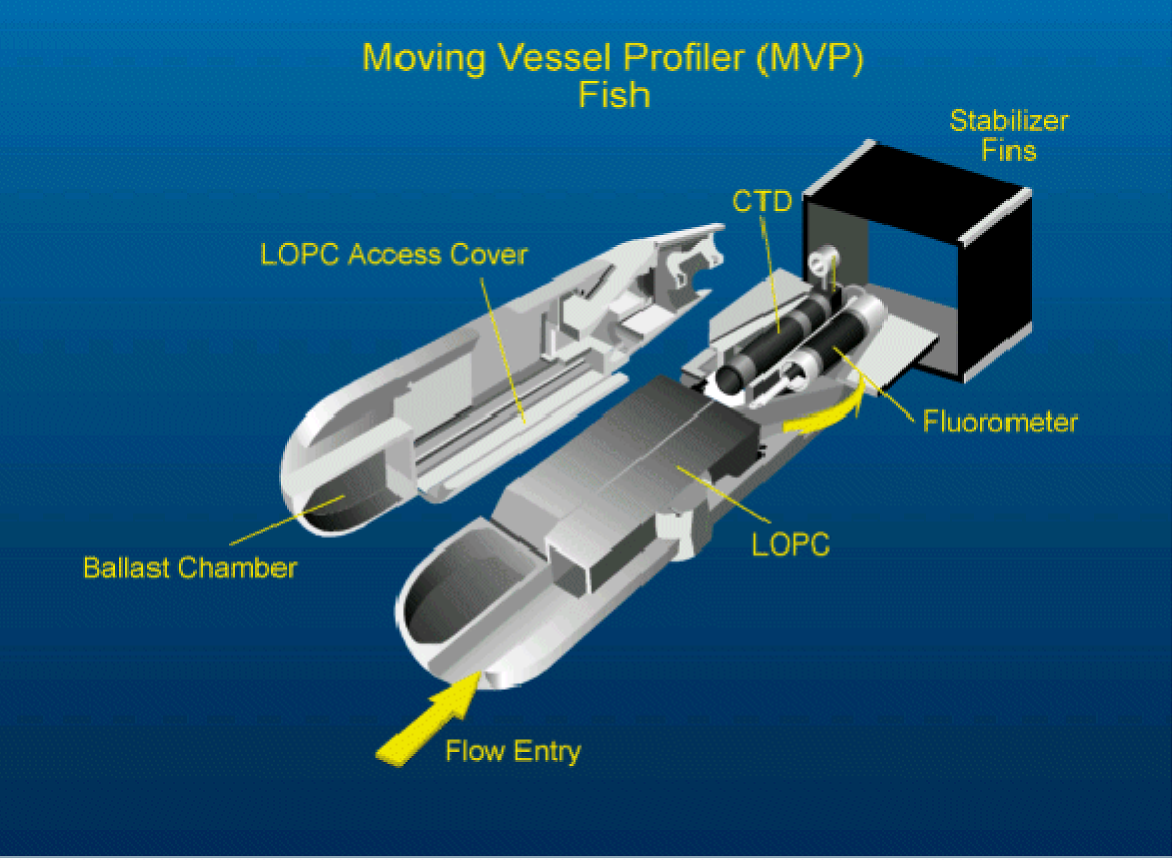
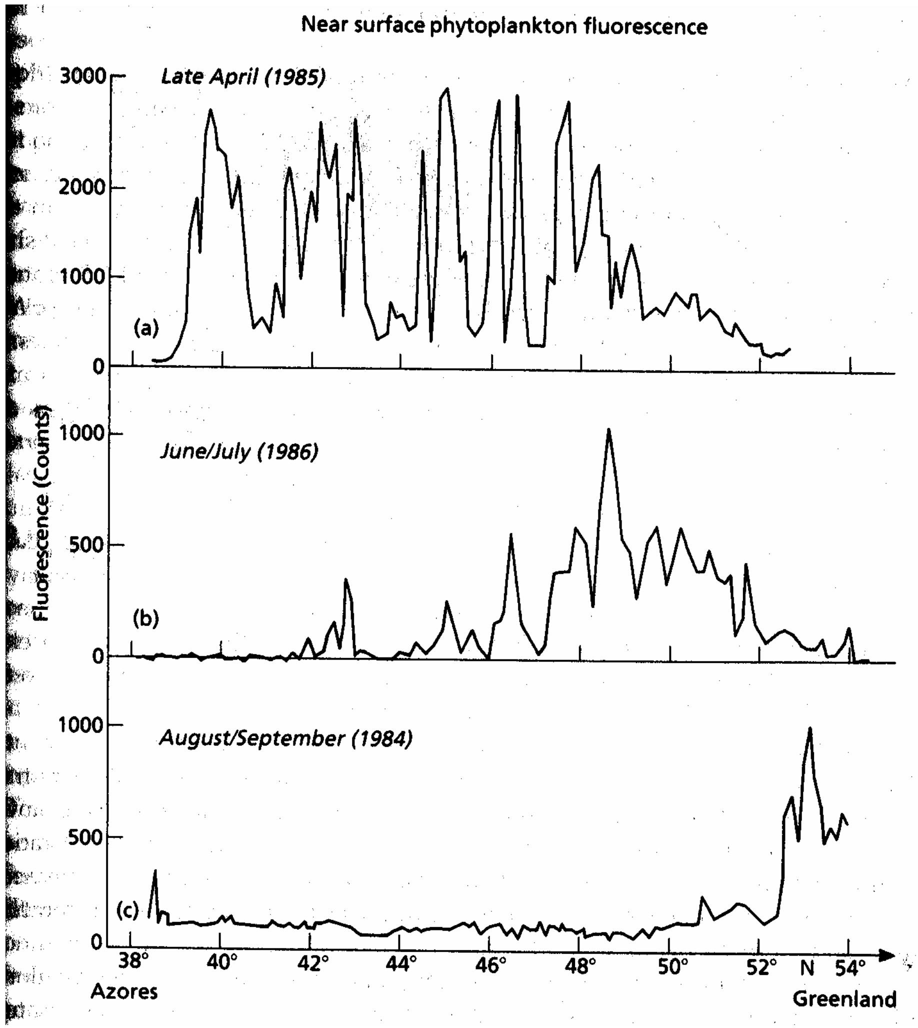


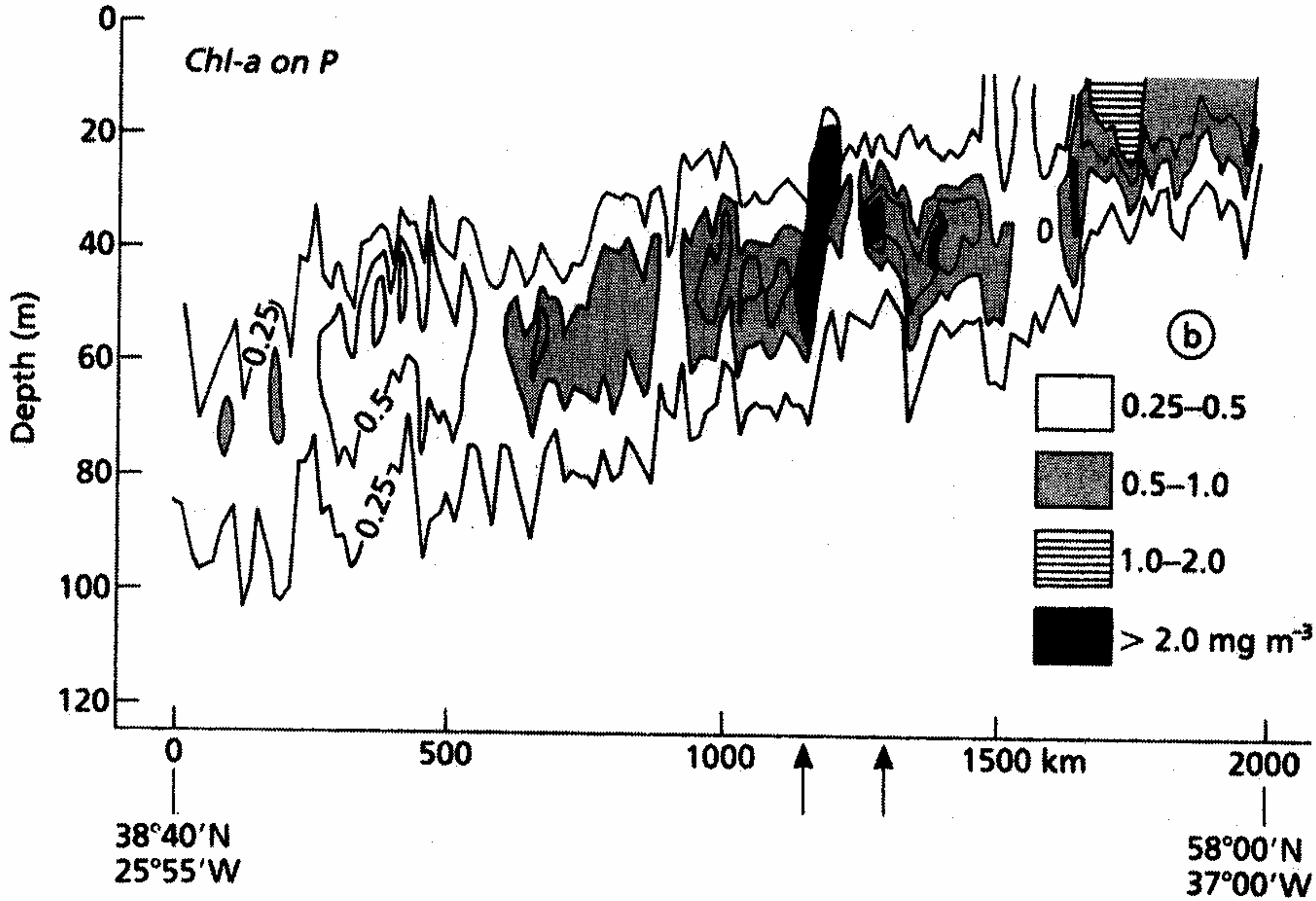
Fig. 13. The multi-sensor free-fall fish used with the Moving Vessel Profiler enabling continuous profiling to 250 m at full vessel speeds of 12-14 kts. The fish contains the LOPC, CTD, and fluorometer.

- SeaSoar is the world's leading open ocean towed undulating data acquisition vehicle. It is capable of undulating from the surface to 500 metres at tow speeds of up to 12 knots.



Near-surface chl fluorescence at 3 times of the year on a transect lying between the Azores and Greenland, showing poleward migration of chl maximum. Wolf and Woods (1988)

Horizontal migration of the near-surface chlorophyll maximum did not keep pace with the northward movement of the region of mixed-layer shallowing, but followed the slow propagation of the 12ºC isotherm outcrop – there may be a temperature limitation of bloom process



Vertical distribution of chlorophyll on a transect between the Azores and Greenland in late summer. Note that the zone of maximum chl gets progressively more shallow as one moves north (Wolf and Woods, 1988).

- North Pacific vs. North Atlantic
  - Shallower mld mainly due to lower salinity
  - Continued biological production throughout the winter
  - Mostly based on observation from Alaskan Gyre, and it is a HNLC region. There is a distinctive difference between the eastern and western subarctic Pacific (see Harrison et al. 1999, 2004, Liu et al. 2004, Suzuki et al. 2002)

The Antarctic divergence

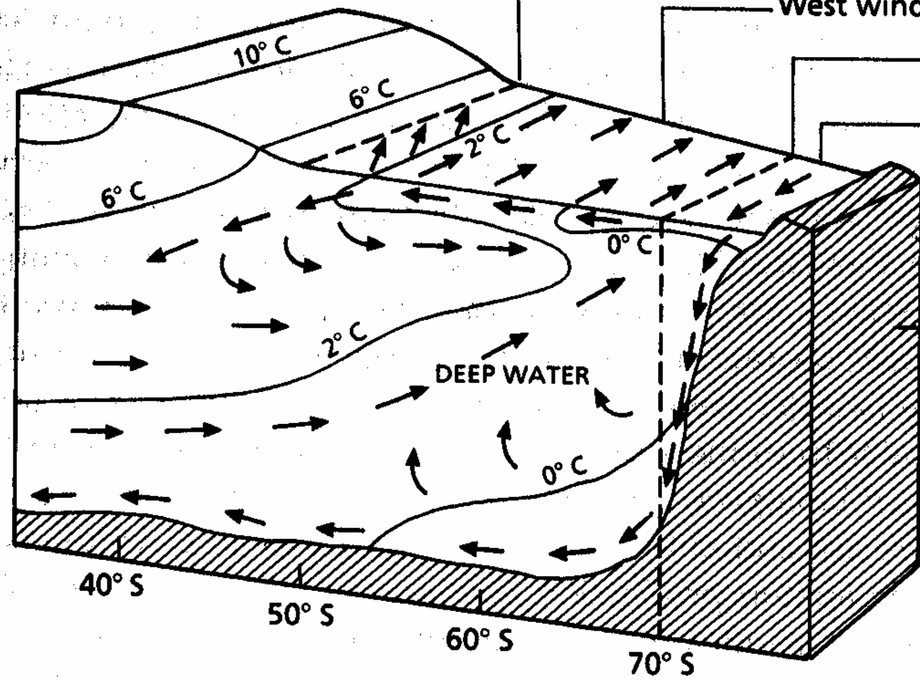
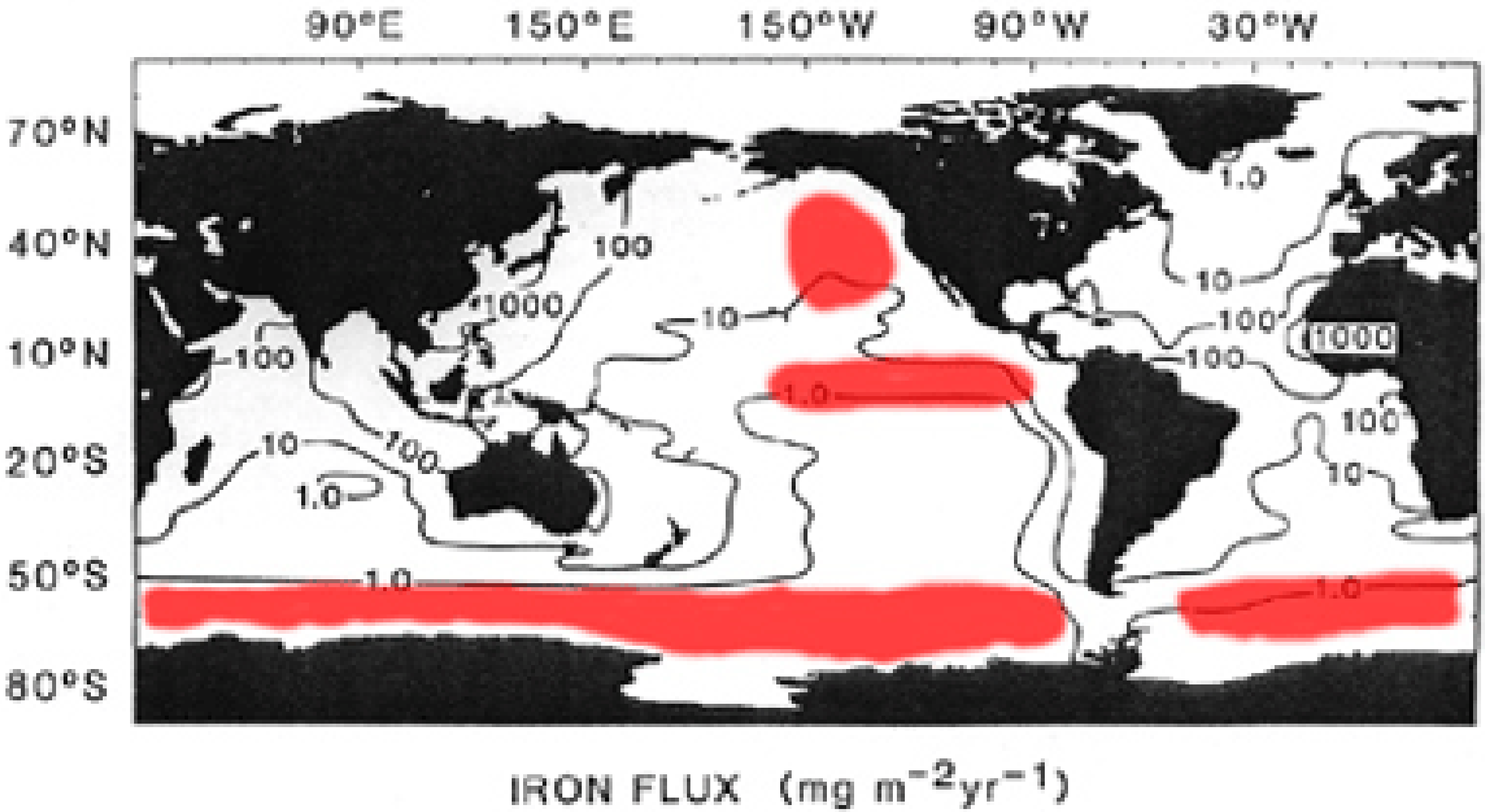


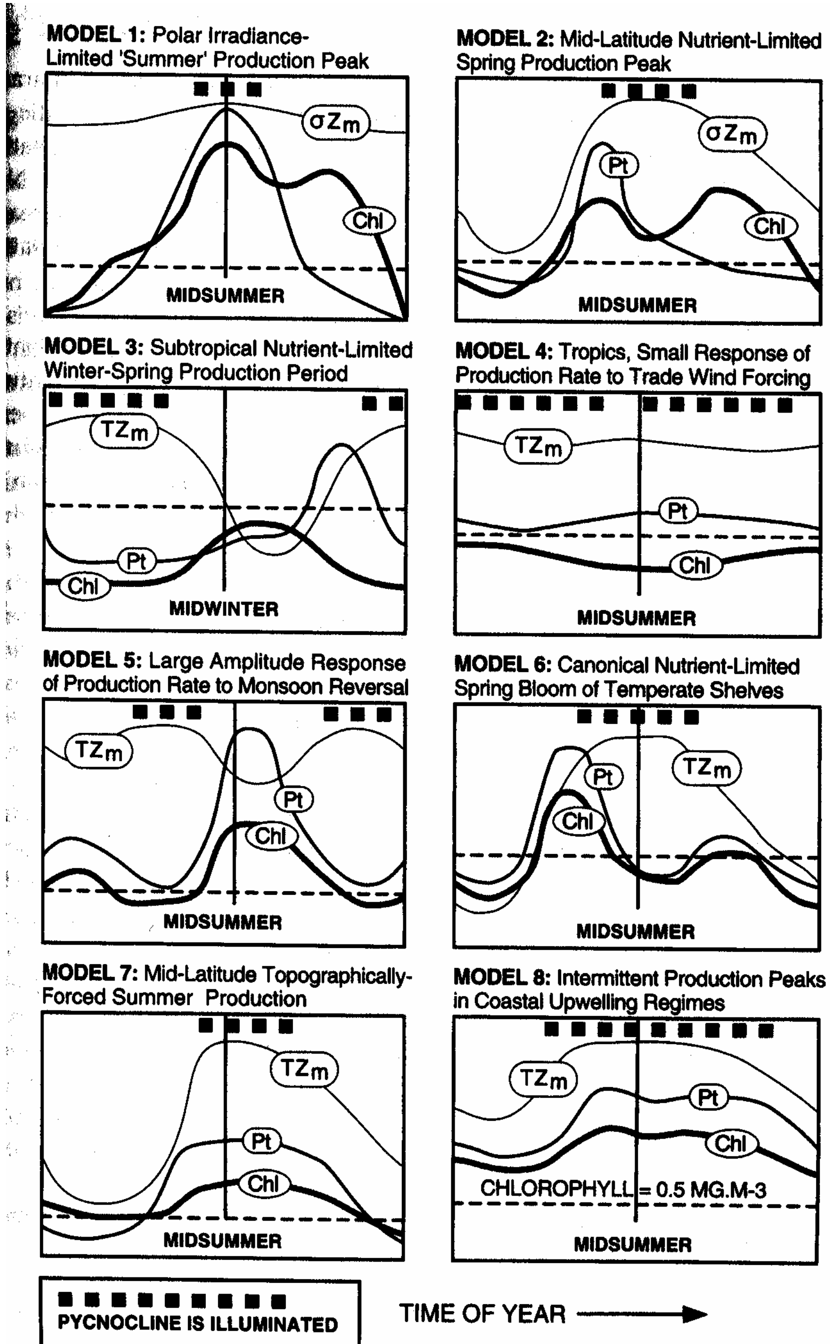
Fig. 3.16 Diagram of the Southern Ocean to show the Antarctic divergence and the Antarctic convergence. Antarctica is on the right, and north is to the left.

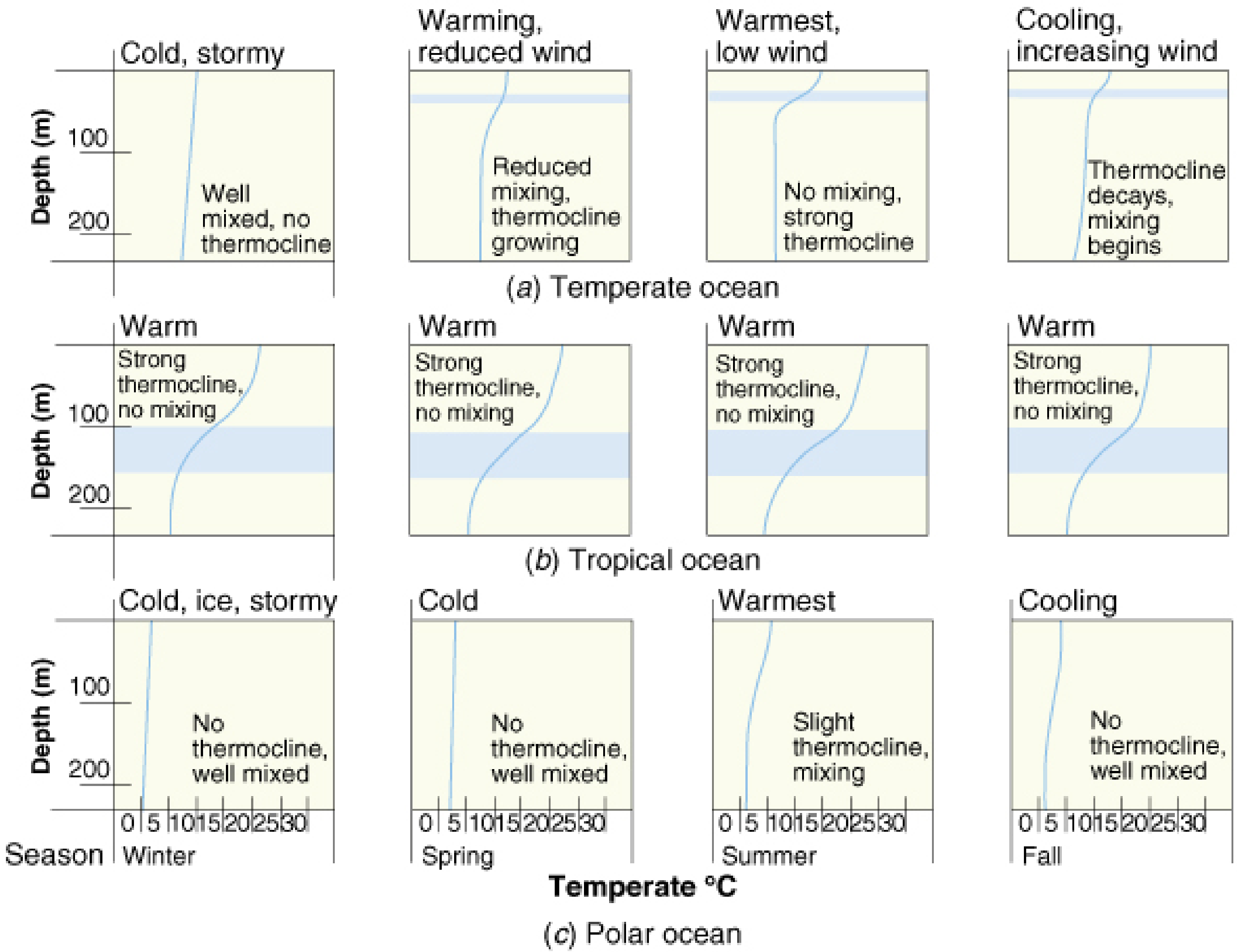


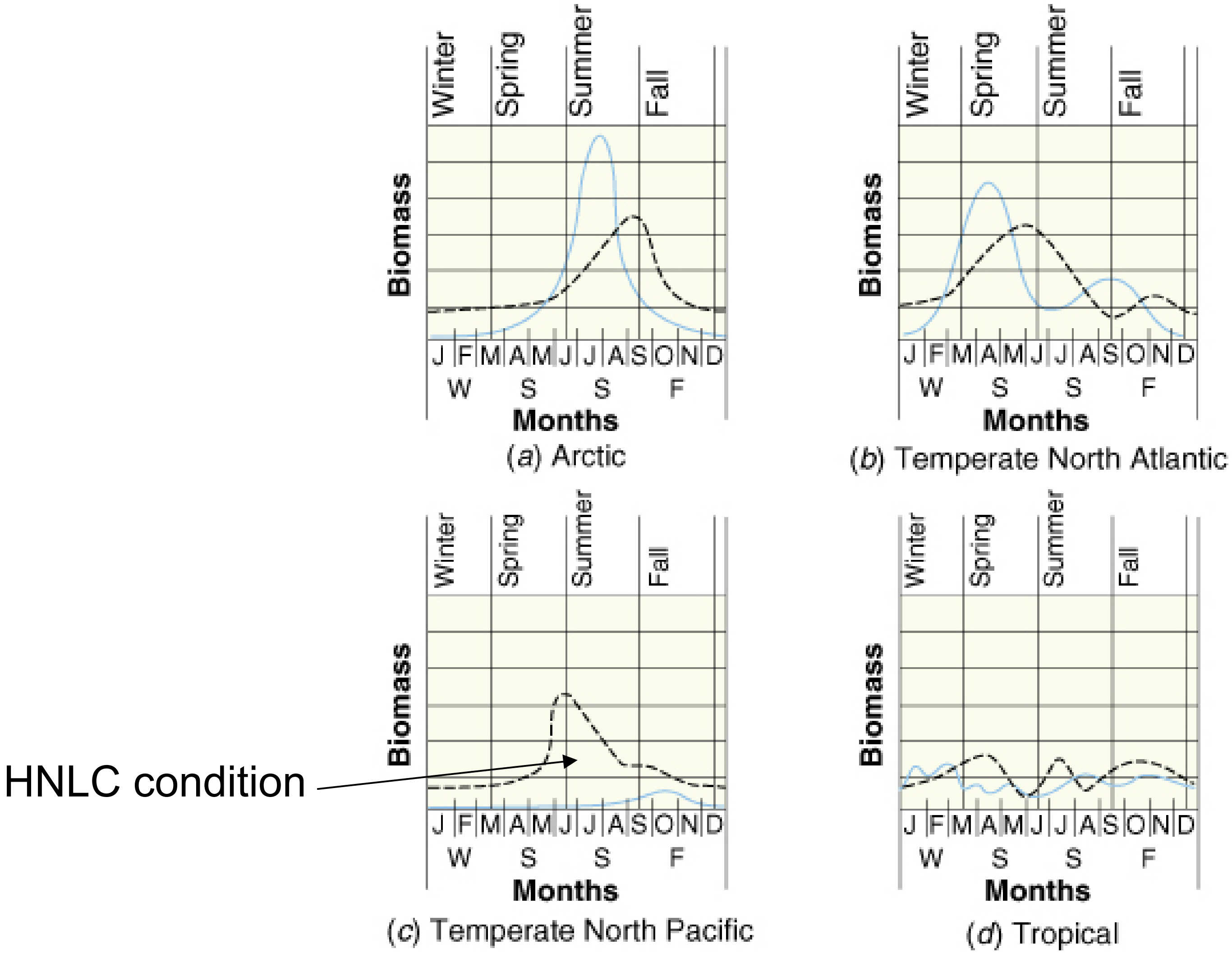
A HNLC region!

An integrated world view of pp

- 4 biomes
  - westerlies
  - polar
  - trades
  - coastal boundary zone
  - exceptional regions
- 56 biogeochemical provinces based on the seasonal patterns of pp and chl accumulation
- 8 distinct groups of seasonal cycles


MODEL 1: Polar Irradiance-Limited 'Summer' Production Peak
σZm
Chl
MIDSUMMER
MODEL 2: Mid-Latitude Nutrient-Limited Spring Production Peak
σZm
Pt
Chl
MIDSUMMER
MODEL 3: Subtropical Nutrient-Limited Winter-Spring Production Period
TZm
Pt
Chl
MIDWINTER
MODEL 4: Tropics, Small Response of Production Rate to Trade Wind Forcing
TZm
Pt
Chl
MIDSUMMER
MODEL 5: Large Amplitude Response of Production Rate to Monsoon Reversal
TZm
Pt
Chl
MIDSUMMER
MODEL 6: Canonical Nutrient-Limited Spring Bloom of Temperate Shelves
Pt
TZm
Chl
MIDSUMMER
MODEL 7: Mid-Latitude Topographically-Forced Summer Production
TZm
Pt
Chl
MIDSUMMER
MODEL 8: Intermittent Production Peaks in Coastal Upwelling Regimes
TZm
Pt
Chl
CHLOROPHYLL = 0.5 MG.M-3
MIDSUMMER
PYCNOCLINE IS ILLUMINATED
TIME OF YEAR


Cold, stormy
Warming, reduced wind
Warmest, low wind
Cooling, increasing wind
Depth (m)
100
200
Well mixed, no thermocline
Reduced mixing, thermocline growing
No mixing, strong thermocline
Thermocline decays, mixing begins
(a) Temperate ocean
Warm
Strong thermocline, no mixing
(b) Tropical ocean
Cold, ice, stormy
Cold
Warmest
Cooling
No thermocline, well mixed
Slight thermocline, mixing
0 5 10 15 20 25 30
Season
Winter
Spring
Summer
Fall
Temperate °C
(c) Polar ocean


Winter
Spring
Summer
Fall
Biomass
J F M A M J J A S O N D
W S S F
Months
(a) Arctic
(b) Temperate North Atlantic
(c) Temperate North Pacific
(d) Tropical
HNLC condition

Estimating global pp

- Using satellite data and bio-optical modeling
- Relatively accurate for chl estimate, but not pp
- Simplicity vs complexity

Photosynthetic rates derived from satellite-based chlorophyll concentration

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Abstract

We assembled a dataset of ^{14}C-based productivity measurements to understand the critical variables required for accurate assessment of daily depth-integrated phytoplankton carbon fixation (PP_{eu}) from measurements of sea surface pigment concentrations (C_{sat}). From this dataset, we developed a light-dependent, depth-resolved model for carbon fixation (VGPM) that partitions environmental factors affecting primary production into those that influence the relative vertical distribution of primary production (P_z) and those that control the optimal assimilation efficiency of the productivity profile (P^B_{opt}). The VGPM accounted for 79% of the observed variability in P_z and 86% of the variability in PP_{eu} by using measured values of P^B_{opt}. Our results indicate that the accuracy of productivity algorithms in estimating PP_{eu} is dependent primarily upon the ability to accurately represent variability in P^B_{opt}. We developed a temperature-dependent P^B_{opt} model that was used in conjunction with monthly climatological images of C_{sat}, sea surface temperature, and cloud-corrected estimates of surface irradiance to calculate a global annual phytoplankton carbon fixation (PP_{annu}) rate of 43.5 Pg C yr^{-1}. The geographical distribution of PP_{annu} was distinctly different than results from previous models. Our results illustrate the importance of focusing P^B_{opt} model development on temporal and spatial, rather than the vertical, variability.

zooplankton

- Lack of data
- Usually abundant in the mixed layer, and most abundant just above the thermocline
- Complicated by vertical migration