1) Are gyres like chemostats?
Yes: Slow, Stable, Steady-State or
No: Fast, Unstable & Non-steady-state
2) PDO, Domain Shift, and long-term patterns in gyre productivity

Class 26, Th 4 December 2008

Slide 1 1) Are gyres like chemostats?

Yes: Slow, Stable, Steady-State or

No: Fast, Unstable & Non-steady-state

2) PDO, Domain Shift, and long-term patterns in gyre productivity

NOTES:

Remaining Lecture Schedule

- Class 26, Th 12/4/08
  - Gyre production and the solution to the great debate over gyre productivity
  - Final exam questions posted in afternoon
- Class 27, 12/9/08
  - Satellite Remote Sensing
  - No bacterial processes in 2008
- Class 28, 12/11/08
  - Final Class, Vertical migration
- Final Exam, 9 am - Noon12/15 Monday
  - 3 hour closed book
  - UMB in classroom, Amherst & Lowell: pdf will be mailed to proctors
  - Jaclyn starting at 10 am (do others want to start later too?)
- Term papers (5-10 pages double spaced) due 12/22 by email (or earlier)

Slide 2 Remaining Lecture Schedule

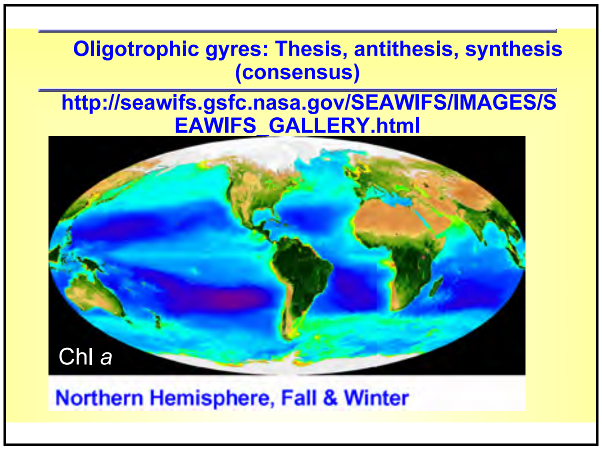
NOTES:

Readings for these classes

- Upwellling, PDO
  - Chavez, F. P., J. Ryan, S. E. Lluch-Costa & C. Miguel Ñiquen. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science *299*: 217-221.
- Gyres
  - Chapter 15
  - Platt et al. 1989. Biological production of the oceans: the case for a consensus. Mar. Ecol. Prog. Ser. *52*: 77-88.
  - Chavez et al. 2003.
- Satellite Remote Sensing
- Microbial Processes

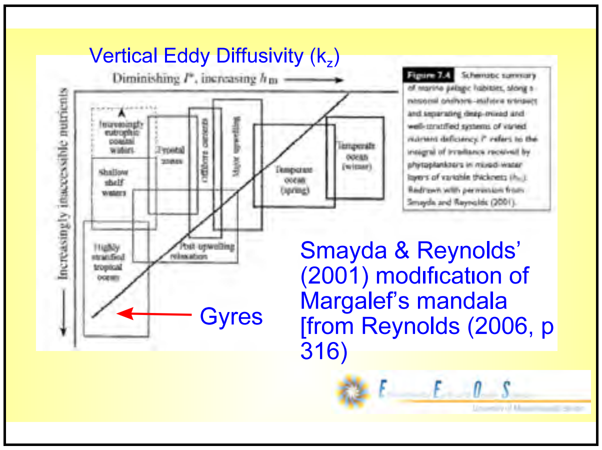
Slide 3 Readings for these classes

NOTES:



Slide 4 Oligotrophic gyres: Thesis, antithesis, synthesis (consensus)

NOTES:



Slide 5

NOTES:

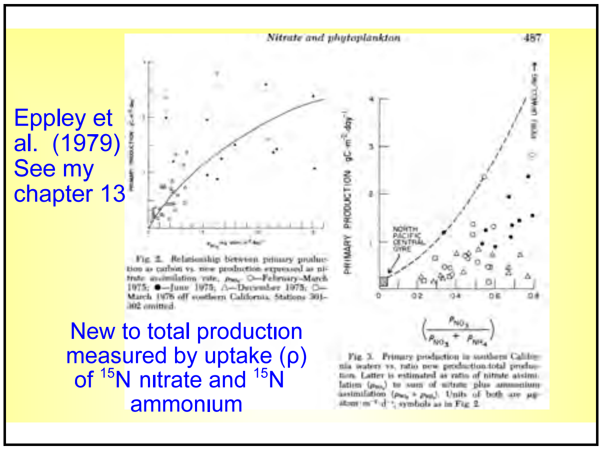
The *f* ratio

Ratio of new to total production

That fraction of production which can be coupled to nutrient inputs from outside the system of interest (Dugdale & Goering 1967). Operationally, new production is often regarded as the component of production coupled to nitrate uptake, since nitrate is the major form of nitrate below the nutracline. Occasionally, new production can include production coupled to reduced nitrogen compounds (*e.g.*, urea) from sewage and riverine input (*cf.*, *f* -ratio, Regenerated Production).

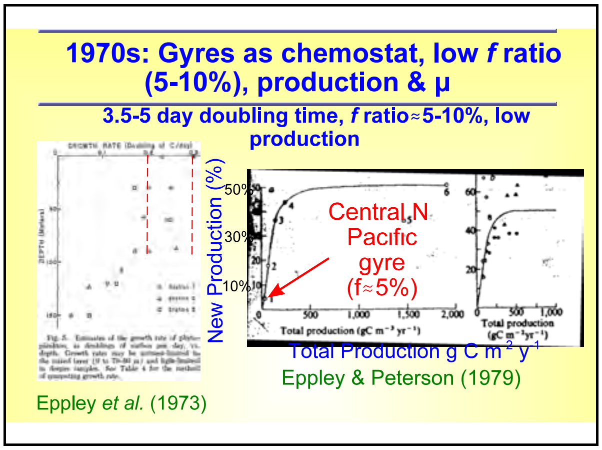
Slide 6 The f ratio

NOTES:



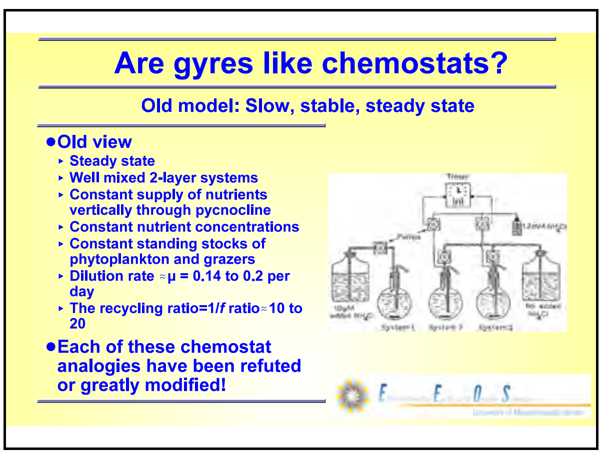
Slide 7

NOTES:



Slide 8 1970s: Gyres as chemostat, low f ratio (5-10%), production & μ

NOTES:



Slide 9 Are gyres like chemostats?

NOTES:

Steady State & Equilibrium

See Gallagher's Appendix of terms for full version

A system with properties that do not change with time is in **steady state**, which is not synonymous with **equilibrium.** In systems governed by chemical reactions or other rate equations, the equilibrium concentrations of substrates and products are governed by rate equations such as:

$$A + B \underset{k_2}{\overset{k_1}{\rightleftharpoons}} AB$$

The chemical reaction described by the equation is in equilibrium if the concentrations of A, B, and AB are in the ratios governed by the reaction coefficients k_1 and k_2. That is, the rate of the forward reaction equals the rate of the reverse reaction. A set of reversible processes that have reached equilibrium is often called a dynamic equilibrium. See Gallagher's Appendix on Vista4/Blackboard

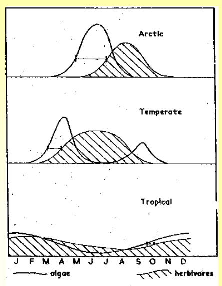
Slide 10 Steady State & Equilibrium

NOTES:

Production in oligotrophic gyres

Figure from Cushing (1957)

- **Old view of gyres**
  - **Like a chemostat**
    - Slow, steady, stable
    - Low *f* ratios
    - Low production
  - **5-day doubling times**
    - Low relative growth rates
- **New view**
  - **Not like a chemostat**
    - Vertical structure
    - Episodic production
    - Long-term changes in production
    - Relatively high effective *f* ratios
  - **Fast and closely coupled primary and secondary production**
    - Production relatively high
    - High relative growth rates



Slide 11 Production in oligotrophic gyres

NOTES:

The great productivity debate

Thesis, antithesis, synthesis

- See Peterson 1980 for review
  - Riley's O_2-based Global production **126** x 10^9 tons
  - Steeman-Nielsen's: **15** x 10^9 tons
- Are gyres like slow chemostats?
  - Old view (Thesis): yes
    - Primary production: 100-200 mg C m^{-2} d^{-1}
    - New:regenerated production, *f* ratio, < 0.1
    - 3- to 5-day doubling times for phytoplankton
  - Antithesis: Steady-state but with high productivity
    - Shulenberger & Reid, Gieskes & Kraay (1984)
  - Synthesis (Platt et al. 1989): Non steady-state systems

Slide 12 The great productivity debate

NOTES:

Eppley (1980): low gyre μ [.15 d^{-1}]

But, primary production as high as 550 mg C m^{-2} d^{-1}

- **Estimated μ using**
  - **^{14}C production: μ ≈0.15d^{-1} or 4.6 day doubling time**
  - **Grazing rates in bottles μ ≈0.09 d^{-1} or 7.7-day doubling time**
  - **Cell death (including grazing) μ ≈0.19 d^{-1} or 3.7 day doubling time**

Table 1. Estimates of photosynthetic production as carbon in the central North Pacific gyre. Rate units are day^{-1}, normalized to the phytoplankton standing stock as carbon (∿10 mg C m^{-3}). The depth of the euphotic zone is about 100 m.

	Range	Mean	Reference
Net increase in POC by ^{14}C method	0.02–0.34	0.15	Sharp et al. (18)
Grazing in bottles		0.09	Jackson (9)
Cell death		0.19†	Venrick, Beers & Heinbokel (10)
Extracellular release or organic ^{14}C		0.04*	
Dark loss of ^{14}C from particles	0.01–0.17	0.08	Eppley & Sharp (44)
	Total	0.55	
		~5.5 mg C m^{-3} d^{-1}	
		~550 mg C m^{-2} d^{-1}	

†May include grazing loss as well as spontaneous cell death.
*Assumed to be 25% of net ^{14}C incorporation into particles. This rate may be larger if non-radioactive organic carbon is also released.

Slide 13 Eppley (1980): low gyre μ [.15 d-1]

NOTES:

Antithesis: The gyres have high production

- Methodological problems with measuring production
  - Differences between O_2 and ^{14}C method
  - Fitzwater *et al.* (1982): Metal contamination may have resulted in low gyre production estimates using both the O_2 and ^{14}C technique. Later work showed that the ^{14}C spike was particularly toxic
  - Filters:
    - Too big: Very small phytoplankton cells (< 2 μm) dominate gyre production and standing stock
    - Filtration pressure too strong for delicate picoplankton
  - Incubation bottles too small
    - Gieskes et al. (1979)
  - Incubation length too long or too short (Redalje's result)
  - Failure to account for microzooplankton grazing
  - Dark uptake of DIC in C-14 method: C-4 like metabolism
  - Light quality effects, see Laws et al.

Slide 14 Antithesis: The gyres have high production

NOTES:

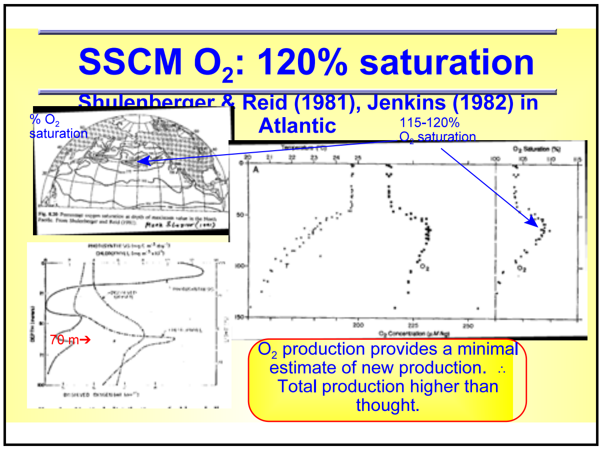
The great productivity debate

Thesis, antithesis, synthesis

- Thesis: Gyres are slow chemostats
- Revolutionary view (antithesis)
  - 1-3 g C m^{-2} d^{-1}
  - New:regenerated production, f ratio, < 0.1
  - Relative growth, μ/μ_{max} close to 1
- Late 1990s Consensus view, summarized in Platt et al. 1989
  - Primary production: up to 500 mg C m^{-2} d^{-1}
  - Metal contamination was a problem
  - Effective *f* ratio <annual> 0.3 to 0.4
  - Relative growth, μ/μ_{max} close to 0.8 to ≈1
- Emerging view in 2001-2008: Pacific decadal oscillation & regime shift
  - Venrick & Hayward: interdecadal shifts in Chl *a*
  - Karl et al. (2001), Chavez et al. (2003) Pacific interdecadal oscillation & the regime-shift hypothesis: N to P limitation in the central North Pacific gyre

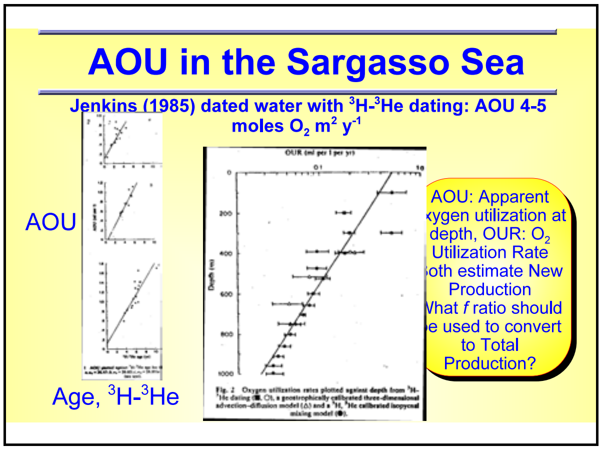
Slide 15 The great productivity debate

NOTES:



Slide 16 SSCM O2: 120% saturation

NOTES:



Slide 17 AOU in the Sargasso Sea

NOTES:

Indirect estimates of high gyre production

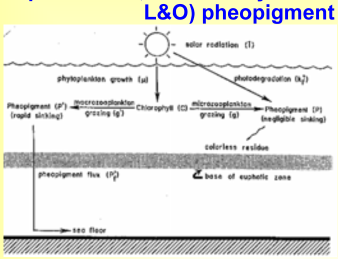
- Apparent oxygen utilization
  - Jenkins (1982): Estimated rate of consumption of organic matter at depth while following parcels of water in the North Atlantic
    - Used Helium-3 to date water masses to calibrate O_2 consumption rates
    - 4-5 mol O_2 $m^{-2}y^{-1}$ new production based on oxygen utilization *vs.* age of deep water.
    - Or 36 g C m^{-2} y^{-1} NEW PRODUCTION
    - If *f* is 10%, then Total water column primary production would be 360 g C m^{-2} y^{-1}, or roughly equivalent to coastal ecosystems
    - Jenkins confirmed estimates of **NEW PRODUCTION** by estimating NO_3^- flux to the euphotic zone and oxygen production in the surface ocean.

Slide 18 Indirect estimates of high gyre production

NOTES:

Sediment traps & gyre production

Macrozooplankton produce fast sinking fecal pellets: 100 mg C m^{-2} d^{-1}, corresponds to new production; Welschmeyer & Lorenzen's (1985, L&O) pheopigment flux



Welschmeyer, N. A. and C. J. Lorenzen. 1985. Chlorophyll budgets: zooplankton grazing and phytoplankton growth in a temperate fjord and the Central Pacific gyres. Limnol. Oceanogr. *30*: 1-21.

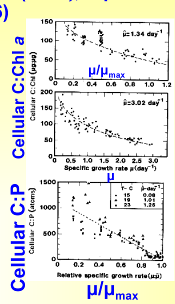
Slide 19 Sediment traps & gyre production

NOTES:

Relative growth rate μ/μ_{max}

Goldman *et al.* (1979), Goldman (1980), replotted by Harris (1986)

- Redfield ratios of phytoplankton C:N:P only attained at $\mu/\mu'_{max} \approx 1$
- Gyre phytoplankton have Redfield ratios indicate growth near μ_{max}
- Microscale nutrient patch hypothesis proposed by Goldman et al. (1979)
  - Phytoplankton taking up short-lived patches of macronutrients excreted by zooplankton
  - Possible but probably not the major mechanism



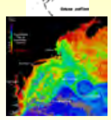
Slide 20 Relative growth rate μ/μmax

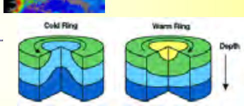
NOTES:

Excursis: Patches, Rings & Gyres

Cold core rings & storms can provide a major nutrient source to gyr

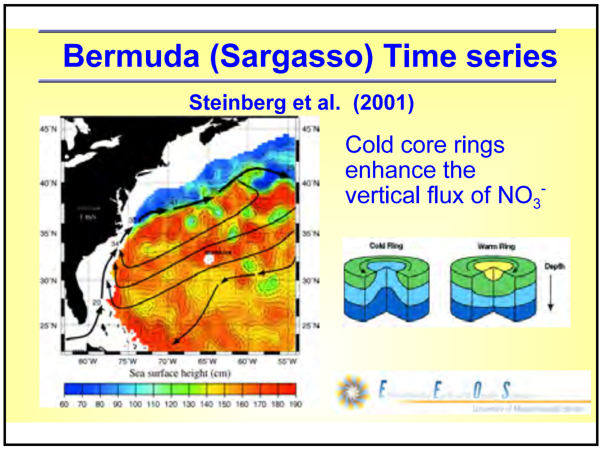
- Goldman *et al.* (1979) proposed that microscale nutrient patches (< 1 mm) fueled high gyre productivity
  - Lehman & Scavia (1982a&b, 1984) demonstrated with ^{32}P that phytoplankton could use patches
  - Sloppy feeding the likely source of patchy nutrients to phytoplankton
- Mesoscale eddies (500-1000 km scale) can provide a source of new nutrients to the gyres; Jenkins, McGillicuddy [WHOI]
- Hurricanes (cyclones) can provide nutrient input





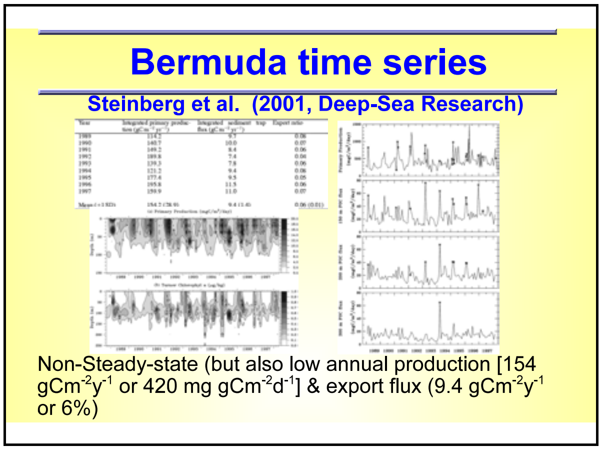
Slide 21 Excursis: Patches, Rings & Gyres

NOTES:



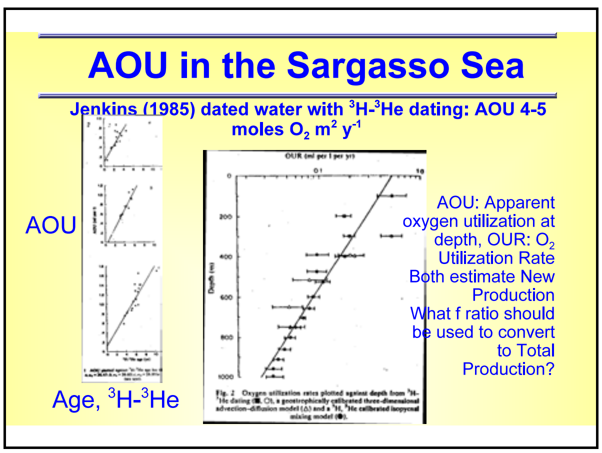
Slide 22 Bermuda (Sargasso) Time series

NOTES:



Slide 23 Bermuda time series

NOTES:



Slide 24 AOU in the Sargasso Sea

NOTES:

Are Steinberg's organic C fluxes consistent with Jenkins AOU of 4-5 mol O_2 $m^{-2}y^{-1}$? NO

=Steinberg's Export flux 9.4 $gCm^{-2}y^{-1}$ (export ratio about 6%)

Carbon export Flux is about 0.8 mol C m^{-2} y^{-1} year [9.4/12=.8]

Moles O_2 export flux = moles C * Photosynthetic quotient (from Redfield ratio)

=0.8 *{107 moles O_2 / 106 moles C) ≈ 0.8 moles O_2

= Using Williams et al.'s (1983) estimate of the photosynthetic quotient (see Gallagher's appendix) for phytoplankton growth on NH_4^+, 1.2, the O_2 export flux would be 0.96 mol O_2 $m^{-2}y^{-1}$

This estimate is far below the Sargasso Sea seasonal average of 4-5 mol O_2 $m^{-2}y^{-1}$ estimate by Jenkins

The BATS Sediment traps may be undersampling organic matter flux; See Butman et al. 1986 on problems with sediment traps

$$106CO_2 + 16NO_3^- + HPO_4^{2-} + 122H_2O + 18H^+ \rightarrow C_{106}H_{263}O_{110}N_{16}P_1 + 138O_2$$

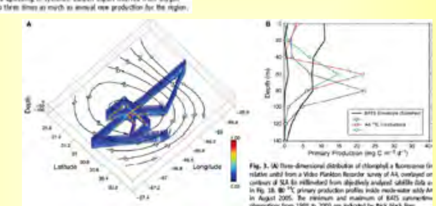
$$106CO_2 + 16NH_4^+ + HPO_4^{2-} + 108H_2O \rightarrow C_{106}H_{263}O_{110}N_{16}P_1 + 107O_2 + 14H^+$$

Slide 25 Are Steinberg's organic C fluxes consistent with Jenkins AOU of 4-5 mol O2 m-2y-1? NO

NOTES:

Eddy/Wind Interactions Stimulate Extraordinary Mid-Ocean Plankton Blooms

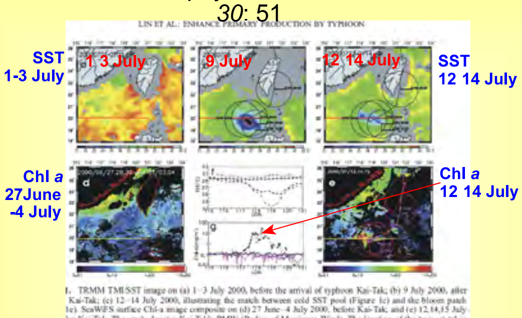
Sargasso Sea blooms caused by storms. Missed by routine BATS sampling



Slide 26

NOTES:

Pacific typhoons create blooms: Lin et al. 2003 Geophysical Research Letters *30*: 51



Slide 27

NOTES:

Vertically migrating organisms

Can increase or decrease vertical DIN flux

- Vertically migrating organisms
- Villareal *et al.* (1993)
  - Very large diatoms (*Rhizoselenia*: several mm long)
  - take up nitrate beneath nutricline and vertically migrate to the surface
    - 2-27% of flux estimated by vertical diffusivity
  - Vertically migrate to high NO_3^- zone when nutrients are depleted
- Vertically migrating zooplankton can affect flux estimates for DIN [Longhurst *et al.* 1989]

Slide 28 Vertically migrating organisms

NOTES:

Synthesis: Higher productivity & the PDO

- Better estimates of productivity
  - New estimates of primary productivity with the ^{18}O method, measuring production of ^{18}O-O_2
  - Routine use of trace-metal free incubations
    - Importance first noted by Fitzwater *et al.* (1982)
  - Better control of light quality (blue light dominates gyre illumination)
    - Laws *et al.* (1984): Primary production in the deep-blue sea
- New methods of estimating production
  - Using changes in bulk properties of seawater
  - fast repitition rate fluorescence

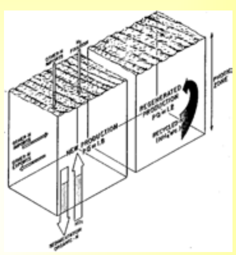
Slide 29 Synthesis: Higher productivity & the PDO

NOTES:

The effective *annual f*-ratio may be 0.3 to 0.4, not 0.05 to 0.1!

Platt *et al.* 1989 Figure 1

- **In a steady-state system**
  - Sinking rate of nitrogen is balanced by the vertical (and horizontal flux of nitrogen)
  - Oxygen utilization beneath the euphotic zone represents the horizontal sinking of primary production and should be equivalent to new production
  - New production could be measured by the vertical flux of NO_3^-
  - Total production = New production * 1/*f*
- **Problems with this 'chemostat' view**
  - Gyres may not be 'steady-state,' with mini-blooms with high f ratios
  - There can be pronounced vertical structure



Slide 30 The effective annual f-ratio may be 0.3 to 0.4, not 0.05 to 0.1!

NOTES:

Platt *et al.*'s concensus

Reconciling high short-term rates with bulk properties

- Fallacy of the average and mismatched time scales
  - The *f* ratios in the gyre are much higher than 0.1; 30% to 40% would be more reasonable
  - **2 g C m^{-2} d^{-1} production with the low Chl *a* standing stocks in the gyres would violate the quantum requirements of photosynthesis**
- Two-layered vertical structure
  - Low *f* ratios in surface
  - High *f* ratios at nutracline
  - Vertical nitrate flux trapped at the subsurface chlorophyll maximum
- Non-steady-state
  - Blooms due to rainfall events & mesoscale eddies, hurricanes, cyclones, typhoons
  - Pacific: Long-term increases in Chl *a*, species composition, and nutrient input due to PDO
  - Temporal decoupling of autotrophy & heterotrophy

Slide 31 Platt et al.'s concensus

NOTES:

The fallacy of averages

Estimating total production from indirect estimates

$$\overline{XY} \neq \overline{X}\,\overline{Y} \quad \text{(unless } X, Y \text{ independent).}$$
$$\overline{XY} = \overline{X}\,\overline{Y} + Covariance_{X,Y}$$
$$\overline{XY} = \overline{X}\,\overline{Y} + r_{X,Y}\sqrt{s^2_X\, s^2_Y}\,.$$
where, $r_{X,Y}$ = correlation between X and Y

s^2_X = Variance of X.

$\overline{X}$ = Mean of X

$$P_T = P_{new}\,\frac{1}{f\text{-ratio}}$$
$$\overline{P_T} = \overline{P_{new}} \times \overline{\frac{1}{f\text{-ratio}}} + Covariance(P_{new}, \tfrac{1}{f}).$$
$$= \overline{P_{new}} \times \overline{\frac{1}{f\text{-ratio}}} + r_{(P_{new}, \frac{1}{f})}\sqrt{s^2_{P_{new}} \times s^2_{\frac{1}{f}}}.$$

Welsh et al. 1988. The fallacy of averages. Amer. Natur. 132: 277-288.

Slide 32 The fallacy of averages

NOTES:

Thermodynamic constraints

Effective *f* ratio can't be much lower than 0.4

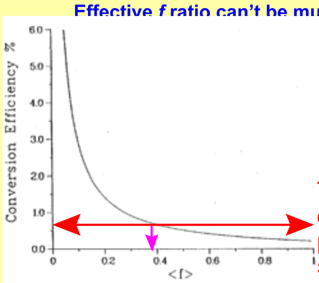


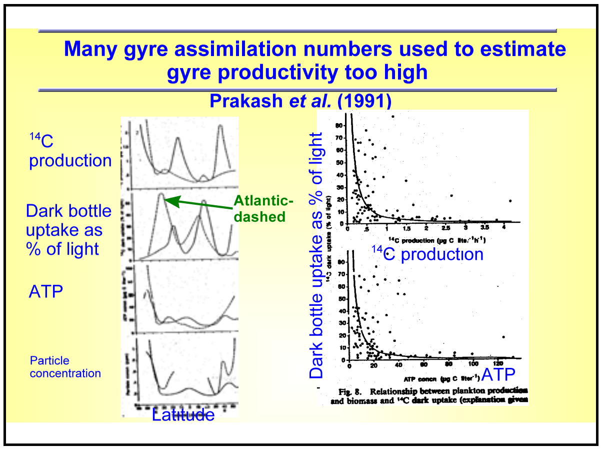
Fig. 2. Implied photosynthetic conversion efficiency as a function of annually averaged *f*-ratio at Station S in the Sargasso Sea, assuming that new production is 5 mol O_2 m^{-2} yr^{-1}

...mes 5 mole O_2 ...production ...Goldman 1985)

Thermodynamic efficiency of photosynthesis: 5-10%

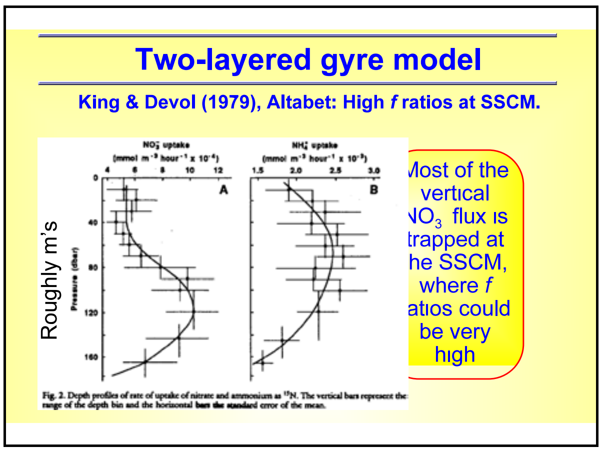
Slide 33 Thermodynamic constraints

NOTES:



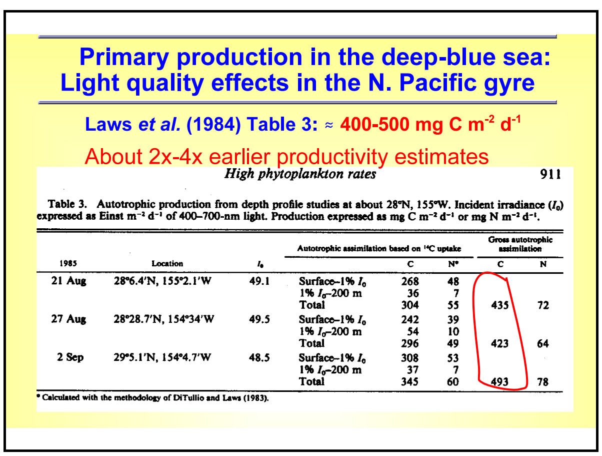
Slide 34 Many gyre assimilation numbers used to estimate gyre productivity too high

NOTES:



Slide 35 Two-layered gyre model

NOTES:



High phytoplankton rates 911

Table 3. Autotrophic production from depth profile studies at about 28°N, 155°W. Incident irradiance (I_0) expressed as Einst $m^{-2}\ d^{-1}$ of 400–700-nm light. Production expressed as mg C $m^{-2}\ d^{-1}$ or mg N $m^{-2}\ d^{-1}$.

1985	Location	I_0		Autotrophic assimilation based on 14C uptake: C	N*	Gross autotrophic assimilation: C	N
21 Aug	28°6.4′N, 155°2.1′W	49.1	Surface–1% I_0	268	48		
			1% I_0–200 m	36	7		
			Total	304	55	435	72
27 Aug	28°28.7′N, 154°34′W	49.5	Surface–1% I_0	242	39		
			1% I_0–200 m	54	10		
			Total	296	49	423	64
2 Sep	29°5.1′N, 154°4.7′W	48.5	Surface–1% I_0	308	53		
			1% I_0–200 m	37	7		
			Total	345	60	493	78

* Calculated with the methodology of DiTullio and Laws (1983).

Slide 36 Primary production in the deep-blue sea: Light quality effects in the N. Pacific gyre

NOTES:

Post Platt et al. (1989) Developments

- Karl's domain shift hypothesis
  - The Pacific gyre can switch from N to P limitation
  - The Pacific is more iron limited than the Atlantic and N fixation can be limited by Fe availability
- Pacific Decadal oscillation accounts for the nearly 2x increase in Chl *a* and production

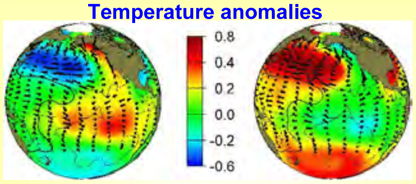
Slide 37 Post Platt et al. (1989) Developments

NOTES:

Pacific Decadal Oscillation (PDO)

PDO strongly related to long-term ENSO patterns

Temperature anomalies



Warm phase on CA coast; cool in gyre

Cold phase on CA coast; warm in gyre

http://tao.atmos.washington.edu/pdo/

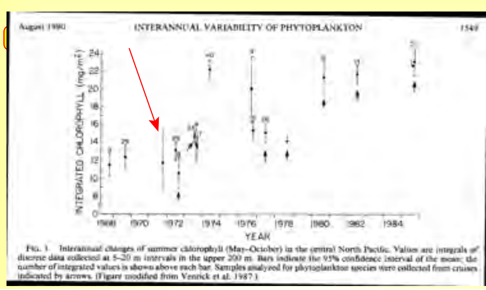
EEOS630

Slide 38 Pacific Decadal Oscillation (PDO)

NOTES:

Pacific decadal oscillation: 2x Chl *a* increase from '68 to '84, esp at SSCM

Venrick *et al.* (1987), Venrick(1990)

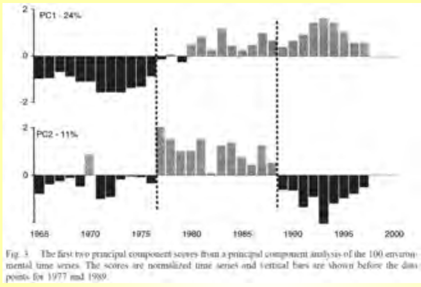


Slide 39 Pacific decadal oscillation: 2x Chl a increase from '68 to '84, esp at SSCM

NOTES:

Pacific Regime shifts (1977, 1989)

Hare & Mantua (2000, Prog. Oceanogr.)



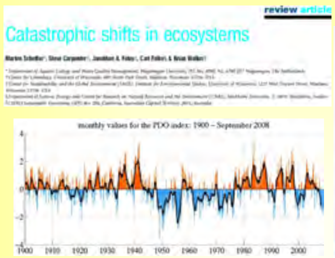
Slide 40 Pacific Regime shifts (1977, 1989)

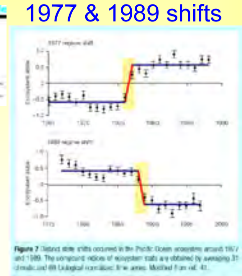
NOTES:

PDO Regime Change/Domain Shift

Scheffer et al. 2001 Nature *413*: 591-596

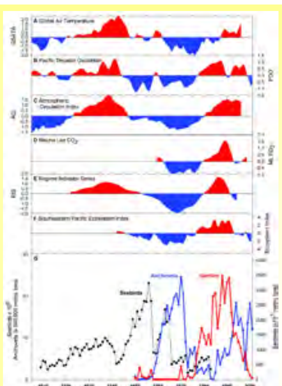
1977 & 1989 shifts





Slide 41 PDO Regime Change/Domain Shift

NOTES:

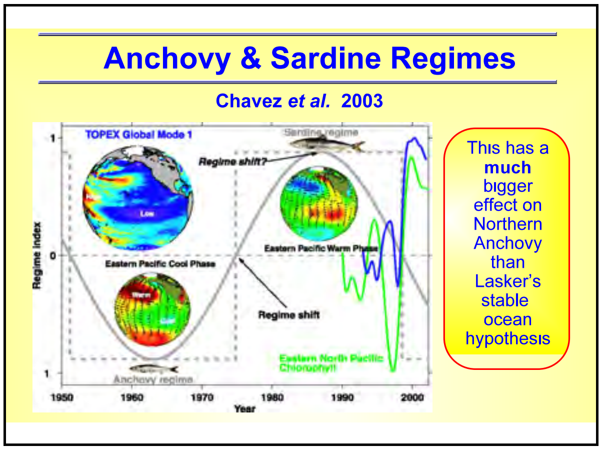


PDO Regime Changes Sardines off Peru with warm phases, Anchoveta with cold phases

Chavez et al. (2003) Fig. 1; Peruvian fish landings

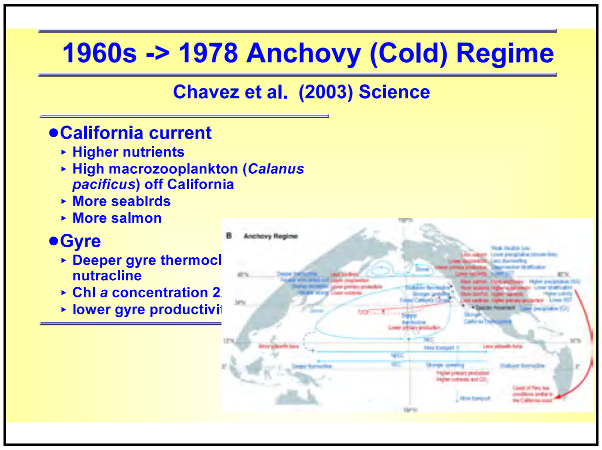
Slide 42

NOTES:



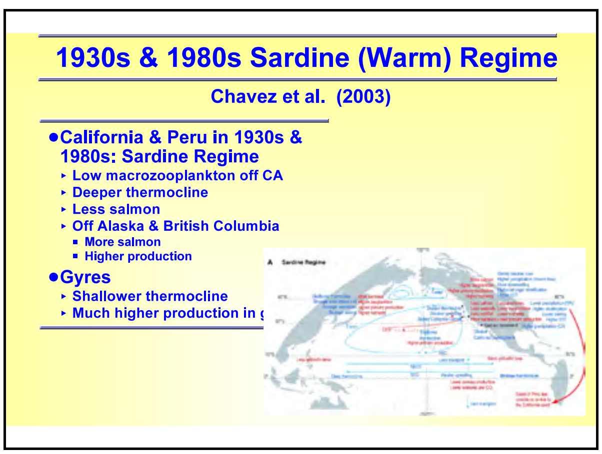
Slide 43 Anchovy & Sardine Regimes

NOTES:



Slide 44 1960s -> 1978 Anchovy (Cold) Regime

NOTES:

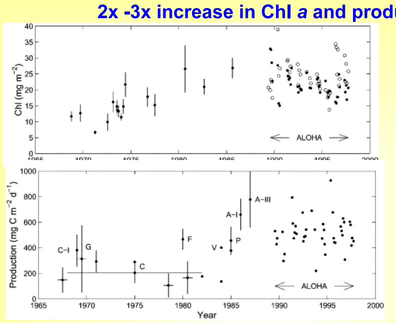


Slide 45 1930s & 1980s Sardine (Warm) Regime

NOTES:

The domain-shift hypothesis

2x -3x increase in Chl *a* and production



Karl et al. (2001): No strong evidence for trace metal effects on production

Slide 46 The domain-shift hypothesis

NOTES:

Trichodesmium & gyre N_2 fixation

Mat-forming N_2-fixing cyanobacterium, Capone et al. (1997)

Karl: regime change with more Fe in Pacific in the 1990s

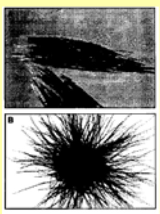
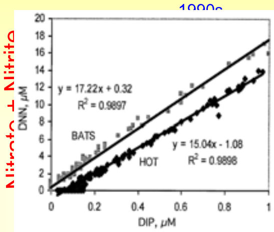


Fig. 1. Examples of *Trichodesmium* colonies. (A) Fusiform or tuft of *Trichodesmium* culture IMS 101; (B) radial or puff colony of *T. thiebautii*. Colonies are typically ~2 to 5 mm in length (fusiform) or diameter (radial) and are composed of tens to hundreds of aggregated filaments (trichomes). Each trichome consists of tens to hundreds of cells (typically ~100); cells are generally 5 to 15 µm in diameter but can range up to 50 µm in length (75) (photos by H. Paerl).



More Fe-rich dust & N fixation in Atlantic (Wu et al. 2000)

Slide 47 Trichodesmium & gyre N2 fixation

NOTES:

Conclusions on gyres

From stable deserts to non-steady-state systems

- Thesis
  - Gyres as chemostat: slow (desert-like, 5-d doubling time), slow production (slow) stable, steady-state
- Antithesis: high µ, high productivity (>> 1 g C m^{-2} d^{-1})
- Synthesis: high µ, moderate production, non steady-state on short & long time scales
  - Mesoscale eddies, storms that produce short-term blooms important in controlling DIN flux: episodic
  - Effective *f* ratios, over the monthly time scale, are high, roughly 30-40%
- Long-term decadal scale changes in nutrient input to the gyres, due to the Pacific decadal oscillation (PDO)
  - Doubling of Chl *a* from the 1960s to the 1980s
  - Regime change due to
    - change in depth to the nutracline
    - enhanced Fe input: Increased frequency of N_2 fixing *Trichodesmium* in the Pacific in the 1990s

Slide 48 Conclusions on gyres

NOTES: