PRIMARY PRODUCTION IN OCEANIC GYRES: IS THE GREAT PRODUCTIVITY DEBATE OVER?

TABLE OF CONTENTS

Assignment

TOPIC

Is the phrase 'oligotrophic gyre' an oxymoron?

REQUIRED READING

Platt, T., W. G. Harrison, M. R. Lewis, W. K W. Li, S. Sathyendranath, R. E. Smith, and A. F. Vezina. 1989. Biological production of the oceans: the case for a consensus. Mar. Ecol. Prog. Ser. *52*: 77-88.

SUPPLEMENTAL

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.

Eppley, R. W. 1980. Estimating phytoplankton growth rates in the central oligotrophic oceans. Pp. 231-242 *in* P. G. Falkowsky, ed., Primary productivity in the sea. Plenum Press, New York. *[Contains the classic compilation of the old view of gyre production, including estimates that the gyres act like a chemostat with a dilution rate ≈ 0.2 d^{-1}]*

Gieskes, W. W. & G. W. Kraay. 1984. State-of-the-art in the measurement of primary production. Pp. 171-190 *in* M. J. R. Fasham, ed., Flows of Energy and Materials in Marine Ecosystems, Plenum.

Glover, H. E., B. B. Prezelin, L. Campbell, M. Wyman, and C. Garside. 1988. A nitrate dependent *Synechococcus* bloom in surface Sargasso sea water. Nature *331*: 161-163. *[They document a very short-lived (3 d) Synechococcus bloom after a rainfall. As discussed by **Platt et al. (1989)**, intermittent NO_3^- pulses and blooms may reconcile short-term incubation results with bulk measurements of primary production.]* {**2**, **6**, **15**}

Grande, K. D., P. J. LeB. Williams, J. Marra, D. J. Purdie, K Heinemann, R. W. Eppley and M. L. Bender. 1989. Primary production in the North Pacific gyre: a comparison of rates determined by the ^{14}C, O_2 concentration and ^{18}O methods. Deep-Sea Res. *36*: 1621-1634.

Karl, D. M., R. R. Bidigare and R. M. Letelier. 2001. Long-term changes in plankton community structure and productivity in the North Pacific subtropical gyre: the domain shift hypothesis. Deep-Sea Res. *48*: 1449-1470. *[Over 30 years, Chl <u>a</u> and primary production in the North Pacific subtropical gyre doubled while silicate and phosphorus decreased. This domain shift towards prokaryotes has altered geochemistry & food webs]* {**10**}

Laws, E. A., G. D. DiTullio, K. L. Carder, P. R. Betzer, and S. Hawes. 1990. Primary productivity in the deep blue sea. Deep-Sea Res. *37*: 715-730. *[Light quality is important in estimating production. Simulated in situ incubations may underestimate production]*

Comments on Gyre Production and the Great Debate

Are the rates of primary production in the oligotrophic gyres being underestimated by a factor of 10 by measurements made with the ^{14}C technique (*i.e.*, 1 to 2 g C m^{-2} d^{-1} instead of 100-200 mg C m^{-2} d^{-1})? Many biological oceanographers argue that primary production in the gyres may exceed 1 g C m^{-2} d^{-1}, with specific growth rates of 1 to 2 doublings per day. If true, the phrase 'oligotrophic gyre' is an oxymoron and many of our most firmly held notions of global production must be abandoned. The great debate on this issue continues, but **Platt *et al.* (1989)** describe a consensus view of levels of gyre production intermediate between those proposed by Eppley and those described by **Shulenberger & Reid (1981)**, **Gieskes & Kraay (1984)**, and others.

In 1983-1985 many investigators set out to test the hypothesis that the old ^{14}C methods were wrong. This program was called PRPOOS for Plankton rate processes in the oligotrophic seas. The two major cruises of this program are described by Laws *et al.* (**1984**, **1987**). The 1984 study describes primary production near Hawaii and the 1987 study describes primary production rates, measured with the latest trace-metal clean methods, in the heart of the Central North Pacific gyre.

METHODOLOGICAL PROBLEMS WITH THE ^{14}C METHOD

There appears to be a consensus emerging, described by **Platt *et al.* (1989)**, that old estimates of primary production may be low by factors of 2 to 3, not 10. The debate hinges first on the following methodological problems with the ^{14}C technique:

▶   **Metal contamination** (full references in Chapter 2). Until recently, biological oceanographers did not use 'metal-clean' techniques. **Fitzwater *et al.* (1982)** showed using trace-metal clean incubations that biological oceanographers were probably killing the phytoplankton with metal contamination, especially cupric ion, during incubations. The ^{14}C-bicarbonate spike or metal Niskin samplers may have been a major source of contamination. Metal contamination is not believed to be a serious problem in neritic waters. Oceanic phytoplankton may be no more sensitive to copper contamination than neritic phytoplankton, but the relatively lower concentration of organic ligands in oceanic waters may result in higher free-ion activity, and hence toxicity, if oceanic samples are contaminated.

   Kerr (1986) wrote a popular press report, "The ocean's deserts are blooming," based on the first oral presentation from the PRPOOS Π's at a national meeting. He concluded from the talks that metal contamination had inhibited primary production, producing the earlier low ^{14}C estimates. The PRPOOS papers don't support this contention. The PRPOOS investigators found ^{14}C production rates twice those measured earlier, but metal contamination was not the major cause of the change. **Marra & Heineman (1984)** and **Cullen *et al.* (1986)** also tested for toxic metal contamination in their work and found little evidence for it. **Cullen *et al.* (1986)** analyzed the fluorescence

yield of phytoplankton cells before and after incubations, and found little difference. Had the phytoplankton been exposed to toxic heavy metals, the fluorescence yield would have greatly increased. Most recent studies in the gyres have adopted trace-metal clean procedures for estimating primary production.

It is somewhat ironic that metals, such as iron, might be limiting phytoplankton productivity in many of the same oceanic areas for which metal contamination is a key problem in primary production estimates. The late John Martin proposed that primary productivity in large parts of the world's oceans are iron limited. These areas include the Southern Ocean, the subarctic Pacific and the equatorial divergence.

▶ **Filters too big**. The filters used in early estimates of primary production may not have captured the picoplankton (<1μm), especially small procaryotic prochlorophytes and cyanobacteria, now known to be the dominant phytoplankton in gyres in terms of numbers, biomass and production **(Li *et al.* 1983)**.

▶ **The incubation bottles might have been too small**. **Gieskes *et al.* (1979)** argued that small containers were a major cause of low productivity numbers in earlier expeditions to the gyres. Open-ocean phytoplankton may be especially vulnerable to enclosure or the enhanced metal contamination from the glass or plastic surfaces of enclosure vessels. During an incubation, the relative and total abundances of phytoplankton might change greatly. Incubations are now routinely carried out in large bottles. **Laws *et al.* (1987)** tested for a bottle-size effect in their cruise to the Central North Pacific gyre but found no clear effect.

▶ The incubations length may be inappropriate (either too long or too short). **Peterson (1980)** argued that short incubations are best, but strangely, often the production from one long incubation exceeds the integrated production from shorter incubations (**Gieskes & Kraay 1984**). Short incubations do not allow an estimate of the relatively large night-time respiration rates, so Eppley's standard procedure of 24-h incubations produces results that are the easiest to interpret.

▶ Failure to adequately account for microzooplankton grazing in bottles.

▶ Many studies of ^{14}C-carbon uptake in oceanic areas did not subtract DIC uptake in dark controls or DCMU controls. Banse (ASLO meeting 1988) pointed out this problem. **Harris *et al.* (1989)** have shown that dark uptake of DIC can be comparable to that in the light. Failure to subtract the dark bottle or DCMU blank can produce gross overestimates of production. **Prakash *et al.* (1991)** resurrected a 20-year old data set to show that dark uptake of ^{14}C was comparable to light uptake in oligotrophic waters.

Platt *et al.* (1989) reviewed data indicating that assimilation numbers and photosynthetic quantum efficiencies from gyre incubations often exceed theoretical maxima. **Laws *et al.* (1990)** also present reasons for high initial slopes in P *vs.* I curves. Some of the problem may lie in the tight coupling between photosynthetic absorption efficiency and submarine light fields (see next item).

▶ The simulated *in situ* method, using white light and neutral density filters, did not adequately control for changes in light quality. This may have led to underestimates (*e.g.*,

Laws *et al.*, 1990) or overestimates (**Grande *et al.* [1989]**) of production in the deep blue sea. It has long been known that many photosynthetic processes are affected by light quality as well as quantity (*e.g.*, Wallen & Geen, see light handout for more references). Simulated *in situ* techniques often use full-spectrum white light, attenuated by neutral-density filters. Phytoplankton grow with light dominated by the blue and green wavelengths (red light is selectively absorbed), and have photosynthetic pigments which can selectively absorb light in these wavelengths. Calculation of Chl *a* absorption coefficients based on surface light spectra may lead to quantum efficiencies exceeding theoretical maxima (**Laws *et al.*, 1990**).

▸ Open-ocean populations may exhibit some features of C_4-like metabolism (as defined by **Morris 1980**), a decoupling of carbon assimilation and N assimilation (**Collos 1989**), and may have high rates of photorespiration. These processes would lead to low bottle estimates of production, particularly using short-term ^{14}C spikes. This problem is now being assessed with ^{18}O incubations (**Grande *et al.*, 1989**)

RECONCILING CONTRADICTORY GYRE PRODUCTION ESTIMATES

The problems with the ^{14}C technique arose largely over difficulties with reconciling the low primary production estimates and specific growth rates calculated using this technique with the higher rates observed using other methods (both direct and indirect). **Kerr (1986)**, in a Science article, regards metal contamination as the 'smoking gun', which accounts for the low primary production rates in the gyres. In an important paper, **Cullen *et al.* (1986)** found little evidence for phytoplankton cell loss or metal contamination using DCMU-induced fluorescence yield. **Cullen *et al.* (1986)** found low rates of specific growth, consistent with the traditional view of open-ocean production. Earlier, **Marra & Heinemann (1984)** had found little evidence for metal contamination.

The O_2 method is not sensitive enough for most oceanic areas. Grande introduced the sensitive ^{18}O-labeled H_2O method to estimate primary production and photorespiration rates in gyres. A variety of alternatives to standard ^{14}C-incubations have been described for estimating primary production, specific growth rates, and relative specific growth rates (μ/μ_{max}). These include

Direct higher estimates of primary production

Gieskes *et al.* (**1979**, **1984**) estimated high primary production rates in large, metal-free enclosures. Recent measurements from the PRPOOS program indicate that primary production estimates can be increased by using trace-metal clean techniques (*e.g.*, **Laws *et al.* 1987**), but metal contamination alone may not account for differences between the older and new productivity estimates.

It is important to note that many of the studies providing direct estimates of high production require photosynthetic efficiencies exceeding the maximum possible (**Platt *et al.* 1984**, **1989**). The major reason for this appears to be the relatively large dark uptake of DIC.

Indirect estimates of high gyre production

▶ **Turnover times** In the 1970s, George Jackson calculated the grazing rate of zooplankton and, assuming steady state, predicted approximately 5-day turnover times for phytoplankton standing stock. Turnover times of the NH_4^+ pool were also long, corresponding to 4-5 day doubling times [See **Eppley (1980, p. 236)** for review].

▶ **The linear biomass hypothesis and allometric arguments** **Sheldon (1984)** had concluded that the rates of total primary production needed to fuel the secondary production of ciliates and nanoflagellates in the open ocean was much higher than that estimated by the ^{14}C technique. Banse countered by arguing that the P:B ratio of ciliates is quite low (for their body size), and therefore a relatively high ciliate biomass could be supported with relatively low primary production. The recent high rates of heterotrophic bacterial production in the gyres require relatively high rates of total production to provide the DOM supply used by bacteria (either through direct leakage (*e.g.*, Fogg) or as an indirect effect of grazing (Jumars *et al.*, 1989)
Sheldon (1984) analyzed the size spectrum of organisms in the gyres. He had earlier proposed the "linear biomass hypothesis," arguing that the biomass in each base-2 size class was virtually the same from bacteria to whales. Based on allometric scaling arguments, he predicted that the smallest organisms must have higher growth rates than were being estimated at the time to support this very non-pointy ecological pyramid.

▶ **Apparent oxygen utilization** **Jenkins (1982)** estimated the apparent oxygen utilization below the pycnocline in oceanic areas. He estimated the O_2 consumption at depth at 4-5 M $O_2 m^{-2} y^{-1}$. Given a photosynthetic quotient of about 1.3-1.6, this is equivalent to 3 M C $m^{-2} y^{-1}$, or 36 g C $m^{-2} y^{-1}$. The flux of organic material needed to fuel these respiratory costs is equivalent to new production. If **Eppley & Peterson's (1979)** *f*-ratio estimate is correct (<10%), then total phytoplankton production must exceed 360 g C$m^{-2} y^{-1}$. If this rate of primary productivity is correct, total primary production had been grossly underestimated by a factor of about 10.

Jenkins confirmed his 4-5 mole $O_2 m^{-2} y^{-1}$ estimate using two other techniques. He estimated "new production" by estimating the increase in O_2 in the euphotic zone during the growing season. He has also estimated the flux of NO_3^- from deep water using the NO_3^-:^{3}He ratio. Both techniques again produce estimates of new production of 3 M C$m^{-2} y^{-1}$.

Jenkins (9/20/91 UMASS/Boston seminar), stated in response to a question, that he suspects that the problems in the ^{14}C technique could have underestimated production by a factor of about 2. The real culprit was the extrapolation of an *f* ratio, observed at short time scales, to an annual *f*-ratio. The annual *f*-ratio is probably much higher than **Eppley & Peterson (1979)** predicted, perhaps higher than 40-50%.

▶ **Subsurface oxygen accumulation** **Shulenberger & Reid (1981)** and **Jenkins & Goldman (1985)** estimated high primary production rates from the accumulated oxygen concentrations in the oceanic euphotic zone at the subsurface chlorophyll maximum (SSCM). There the oxygen concentration is often 120% of the saturation level expected if seawater at that temperature had equilibrated with the atmosphere. Supersaturation is

possible because the pycnocline is located above the nutracline in the Pacific, allowing significant concentrations of photosynthetically produced O_2 to accumulate. This accumulated oxygen corresponds to new production, and as **Platt et al. (1989)** discuss, **Shulenberger & Reid's (1981)** new production rates were higher than the total production rates being estimated by the ^{14}C method.

Platt (1984), **Platt & Harrison (1986)**, and **Platt et al. (1989)** reviewed and criticized the assumptions behind the **Shulenberger & Reid's (1981)** estimated oxygen production. They argued that some of the increase could have been due to physical introduction of oxygen by bubbles, a conclusion confirmed by **Craig & Hayward (1987)**. They also argued that **Shulenberger & Reid (1981)** didn't know how long the oxygen had been accumulating within the pycnocline. However, **Craig & Hayward (1987)** found that most of the oxygen supersaturation was due to net primary production. **Platt et al. (1989)** further argue that the variance associated with these new production rates are large enough that the "old view" of new production can't be refuted.

▶ **Sediment traps** High rates of primary production have been estimated from POC and PON fluxes to sediment traps (**Pace et al. 1987**, **Welschmeyer & Lorenzen 1985**). In a steady-state ocean, these fluxes correspond to new production. In order to compute total production from these fluxes, these vertical fluxes must be combined with an estimate of new to total production, the *f*-ratio. **Eppley & Peterson (1979)** estimated the *f* ratio to be 5-10% in oligotrophic waters.

Lewis et al. (1986) measured the vertical eddy diffusion coefficient using shear probes and calculated the "new production" in the Atlantic. They concluded that the rates of nitrate input to the euphotic zone were inadequate to support the high rates of production implied by the sediment trap work. Some studies point to the importance of horizontal nitrate flux, mesoscale eddies, and episodic pulses of nitrate into the euphotic zone. Other studies, such as work by Butman (**1986**, **Butman et al. 1986**), have found sediment traps to be poor sampling devices.

▶ **High relative μ_{max}** **Goldman et al. (1979)** noted that oceanic phytoplankton have elemental ratios in accord with the Redfield-Ketchum-Richards ratio, and that in chemostats such ratios are attained only when phytoplankton growth approaches μ_{max}.

Goldman et al. (1979) introduced the **microscale nutrient patch hypothesis** to explain their findings (Chapter 4: Nutrients), but current thought is tending toward large intermittent mesoscale pulses of NO_3^- as providing the necessary nutrients. Goldman, Glibert and McCarthy and others have shown that oceanic phytoplankton appear to be adapted to take up pulses of nutrients. Although George Jackson and Williams & Muir discounted the importance of micro-scale patches, Lehman & Scavia confirmed their importance in the laboratory. Currie pointed out that the densities of zooplankton and phytoplankton used by Lehman and Scavia never occur in nature, and Lehman seemed to agree in his rebuttal paper.

It is important to note that phytoplankton can have μ/μ_{max} ratios approaching 1.0, and yet having low μ values (*e.g.*, 0.2 d^{-1}). **DiTullio & Laws (1986)** have developed a protein-specific ^{14}C labeling method for estimating the C:N ratio of phytoplankton. Since Goldman (**1980**, **1986**) convincingly demonstrated that the C:N ratio is directly related to

the relative growth rate, they can estimate μ/μ_{max}. They find that this ratio is high in the gyres.

▶ **Vertically migrating organisms   Longhurst *et al.* (1989)** documented a significant flux of reduced nitrogen compounds by vertically migrating nekton. Zooplankton ingest phytoplankton near the surface and digest and excrete some of this material at depth. This downward flux would have to be balanced by enhanced vertical or horizontal NO_3^- fluxes. Either the rate of total production or the *f*-ratio needs to be increased greatly.

Vertically migrating zooplankton can produce a net loss of nitrogen from the gyre euphotic zone by feeding on N-rich phytoplankton in the surface and respiring NH_4^+ at depth. However, vertically migrating phytoplankton can produce a positive entry on the Nitrogen balance sheet. Villareal *et al.* (**1993**, 1996) document the important role of vertically migrating diatoms, which can take up nutrients at the nutracline, store it at very high concentrations (5 mM) in an intracellular vacuole, and migrate to the euphotic zone for later photosynthesis. These organisms, which transport NO_3^- through the pycnocline, can account for up to one quarter of the NO_3^- flux estimated from vertical eddy diffusion calculations.

A CONSENSUS

Platt *et al.* (1989) review many of the different methods used to estimate open-ocean production and attempt to produce a consensus view. It is interesting to note that the author list for this paper doesn't include the major proponents of the view that gyre production rates have been underestimated. In 1994, I asked Eric Shulenberger whether he had joined the **Platt *et al.* (1989)** consensus view. He hadn't.

The *in situ* [14]C method and the bulk O_2 methods do not necessarily conflict if the time-scales of production differ or if the assumptions made by **Shulenberger & Reid (1981)** were wrong (**Platt 1984**, **Platt et al. 1989**). The O_2 methods based on changes in bulk seawater properties -- either oxygen utilization or oxygen production at the pycnocline -- integrate over weeks to months of production, while the ^{14}C method integrates over hourly time-scales. New production in the gyres may be episodic and would be missed by oceanographic cruises but reflected in the O_2 production and deficit below the euphotic zone.

The fallacy of the average and mismatched timescales

Platt *et al.* (1989) base their consensus view on the argument that new production rates, not total production rates, have been underestimated in the past. The key to the argument is based on the fallacy of the average[11] (*i.e.*, the mean of a product does not equal the product of means unless the variables are independently distributed):

---

[1]Welsh, A. N., A. T. Peterson and S. A. Altmann. 1988. The fallacy of averages. Amer. Natur. 132: 277-288.

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

(1)

Using a sediment trap, one obtains an estimate of P_{new}, the new production rate, with a characteristic time scale of days to months. In order to estimate P_T, the total production, one needs to estimate the f-ratio, usually measured with an ^{15}N incubation with a time scale less than an hour.

$$P_T = P_{new}\ \frac{1}{f\text{-}ratio}.$$

(2)

P_{new} and f are believed to have a strong positive correlation, therefore there should be a strong negative correlation between P_{new} and $[f\text{-ratio}]^{-1}$. One can still have a high P_{new} and low mean f-ratio (*i.e.*, high $[f\text{-ratio}]^{-1}$) and yet have a low mean P_T (*e.g.*, annual or monthly production). In order for this to occur, there must be temporal variability in P_{new} and f-ratio (*i.e.*, the variances, s^2, must be large) and there must be a negative correlation between P_{new} and $[f\text{-ratio}]^{-1}$.

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

(3)

This analysis is a bit simplistic. **Platt *et al.* (1989)** propose a double integral (integrating over time and depth) to evaluate $<f>$ and argue that the effective f-ratio is probably 0.3 or more over monthly time scales. There can be temporal variability in the f-ratio and P_{new} and vertical variance in the f-ratio and P_{new}. Both the temporal and vertical cross-correlation between f-ratio and P_n must be assessed to calculate P_T from sediment-trap data or data on O_2 respiration rates at depth. The temporal variance in the f-ratio and P_{new} may be introduced by mesoscale oceanographic phenomena (*e.g.*, decaying cold-core rings), storms, or perhaps horizontal advection.

Glover *et al.* (1988) document a 3-d NO_3^--dependent bloom of *Synechococcus* in the Sargasso Sea. They arrived on station in the Sargasso Sea, took samples, and then sat through a rainstorm. The storm was quickly followed by a bloom of *Synechococcus*, which persisted for just a few days. It may have been grazed by heterotrophic nanoflagellates. **Glover *et al.* (1988)** couldn't determine what caused the bloom. It might have been vertical mixing of nutrients from the storm, or the rain may have added an essential trace metal (*e.g.,* Zn or Fe). This paper does provide clear documentation of the episodic nature of production in the gyres. During most periods, it might appear that there is little production, but this apparent calm may be interspersed by rapid periods

of production that are quickly grazed away. The gyres are not in steady-state over time scales of weeks. It is this temporal variability that is the key to Platt et al.'s reconciliation between low production and low f ratios observed in most cruises to the gyres and the apparent higher production measured by changes in the bulk properties of seawater (e.g., organic matter flux and oxidation rates in deeper waters). These changes in bulk properties are measuring these episodic episodes of higher production associated with much higher f ratios.

The vertical variance could be due to a two-layered vertical structure, with the lower layer at the subsurface Chl *a* maximum having a higher *f*-ratio and P_n. **Jenkins & Goldman (1985)** proposed such a structure to reconcile O_2 and carbon production estimates. They argued that the oligotrophic ocean can be likened to a "spinning wheel" at the surface where most of the production in based on regenerated nutrients and is respired in the surface. At the base of the euphotic zone, production is based on new nitrate and much of this production settles out of the euphotic zone.

LONG-TERM CHANGES IN GYRES

Venrick *et al.* (1987) have proposed another explanation to reconcile the old rates of primary production and the newer higher rates. They have documented an increase in Chl *a* concentration in the N. Pacific gyre on the multidecadal time scale. **Venrick (1990)** shows that the rank order of phytoplankton species groups has shown a long-term decade long-trend in the N. Pacific gyre. This change is more pronounced in the phytoplankton groups in the deeper parts of the

FIG. 1. Interannual changes of summer chlorophyll (May–October) in the central North Pacific. Values are integrals of discrete data collected at 5–20 m intervals in the upper 200 m. Bars indicate the 95% confidence interval of the mean; the number of integrated values is shown above each bar. Samples analyzed for phytoplankton species were collected from cruises indicated by arrows. (Figure modified from Venrick et al. 1987.)

Figure 1. Water column Chl *a* concentrations at the Central North Pacific gyre. From **Venrick (1990)**

water column. Diatom species composition has changed more than other groups. **Venrick (1990)** also documented an approximate doubling of Chl *a* concentrations between the late 1960s and the mid 1980s (see Fig. 1). This decadal change in Chl *a* concentrations corresponds to increased nutrient flux and production in the 1980s. This pattern is one part of the phenomenon now known as the Pacific decadal oscillation (reviewed by **Chavez et al. 2003**).

Karl *et al.* (2001), based on the Hawaii long-term time studies, have described a domain-shift hypothesis. Productivity dramatically increased in the central North Pacific gyre in the 1980s and community composition became more dominated by prokaryotes. With increasing production, the gyre became increasingly phosphorus-limited. **Karl *et al.* (2001)** documented this pattern after **McGowan et al. (1998)** had documented patterns of dramatic decline in the abundance of *Calanus marshallae*, the dominant macrozooplankter in the California current system. There is now a well-documented pattern called the Pacific decadal oscillation (PDO) in which there are two phases: an anchovy phase in which productivity is higher in the California current and low in
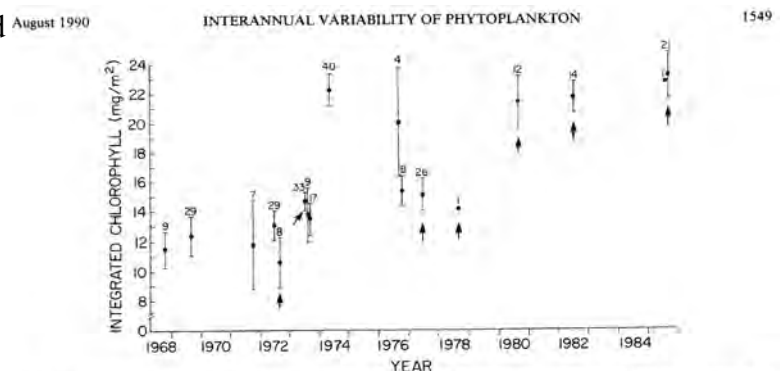
the gyres and the sardine phase in which productivity is lower in the California current and higher in the gyre.
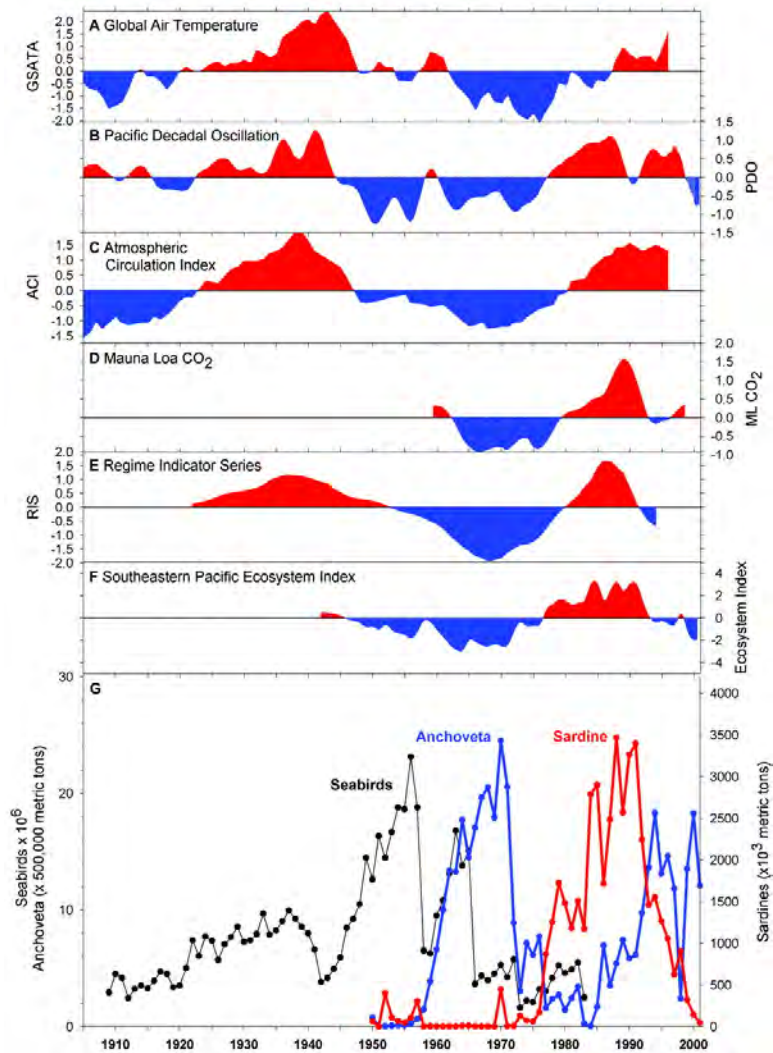
Figure 2. Phases of the Pacific decadal oscillation from **Chavez et al. (2003)**

Chavez *et al.* (2003), as shown in Figure 2, provide a recent review of the Pacific decadal oscillation, which is now strongly believed to have led to low Chl *a* concentrations, deep nutriclines and low productivities during the 1960s through 1975-1976. They call this 'the sardine regime.' There was a shift in climate patterns resulting in shallower depths to the nutricline (with higher nitrate flux to the euphotic zone), higher Chl *a* and higher productivity during the late 1970s, the 1980s, and up to the mid 1990s. There appears to have been another regime shift during the mid 1990s back to the 'sardine regime,' and this would be associated with lower productivities in the central North Pacific gyre.

monthly values for the PDO index: 1900 – September 2008
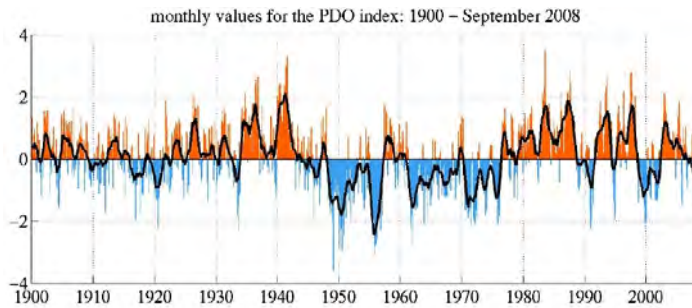
Figure 3. Phases of the Pacific decadal oscillation: 1900-2008. Updated monthly at
http://jisao.washington.edu/pdo/

PDO SST Index and Surface Height EOF's

Satellite altimeter sea level EOF1 (normalized by std dev)
Alaska Gyre dynamic height EOF1 (x3.5) [2]
PDO warm phase
PDO cold phase

1997-98 El Nino

[1]Mantua et al. (1997)
[2]Lagerloef (1995)
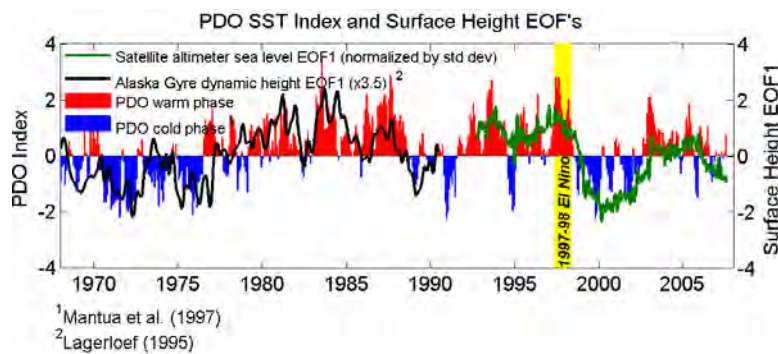
Figure 4. Phases of the Pacific decadal oscillation: 1965-2008, plotted with North Pacific satellite derived sea-Surface height. EOF1 is the first empirical orthogonal function (a form of PCA) of satellite altimetry Updated monthly at
http://www.esr.org/pdo_index.html
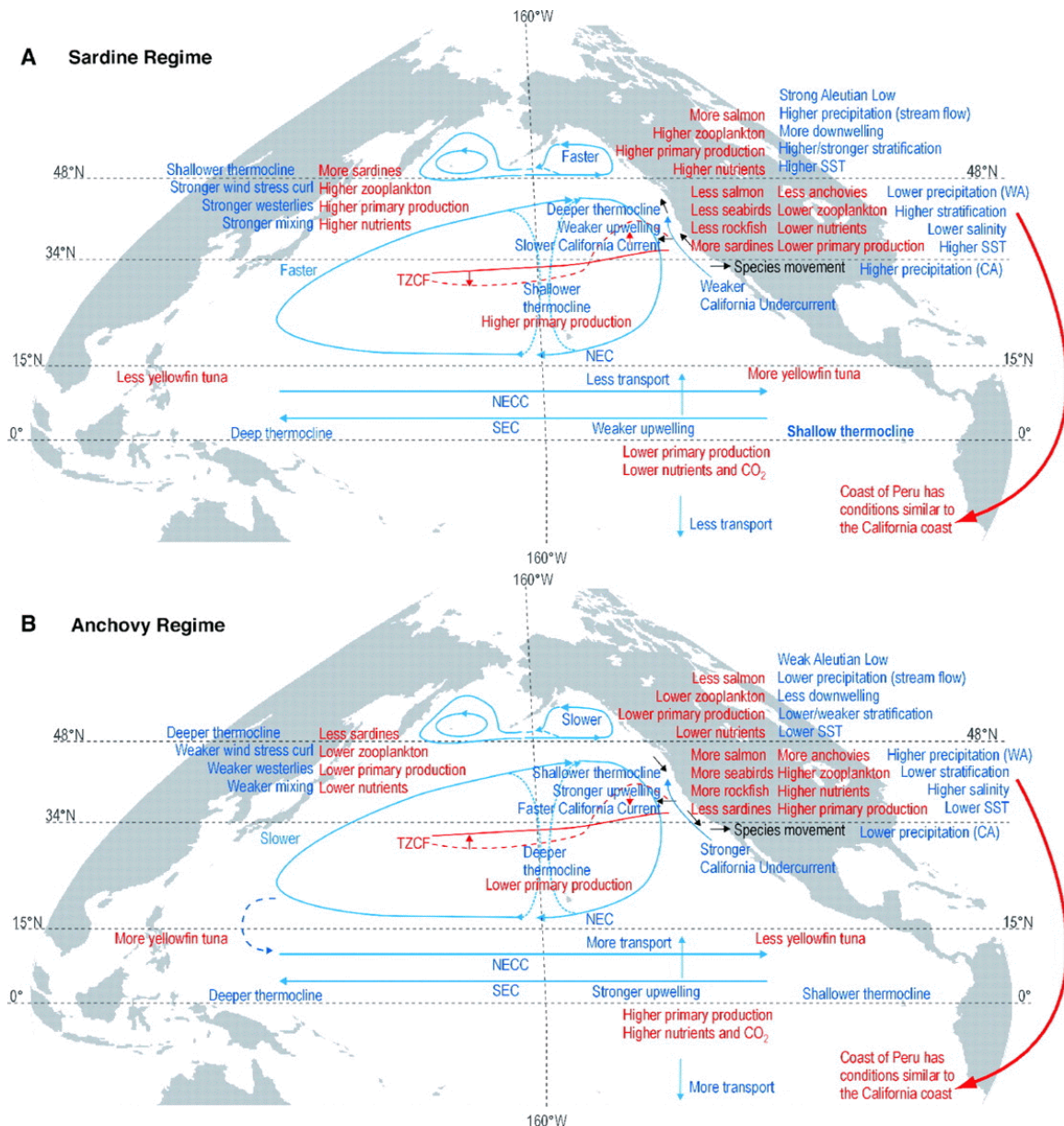
Figure 5. Oceanographic effects of the Pacific decadal oscillation from **Chavez et al. (2003)** Fig. 3

SOME KEY PAPERS THAT FRAMED THE GREAT DEBATE

Pro (High production):

Glover, H. E., B. B. Prezelin, L. Campbell, M. Wyamn, and C. Garside. 1988. A nitrate-dependent *Synechococcus* bloom in surface Sargasso sea water. Nature *331*: 161-163.

Goldman, J. C. 1980. Physiological processes, nutrient availability, and the concept of relative growth rate in marine phytoplankton ecology. Pp. 179-194 *in* P. G. Falkowski, ed, Primary

Productivity in the Sea. Plenum Press, New York.

Goldman, J. 1986. On phytoplankton growth rates and particulate C:N:P ratios at low light. Limnol. Oceanogr. *31*: 1358-1363.

Goldman, J. C. and P. M. Glibert. 1982. Comparative rapid ammonium uptake by four species of marine phytoplankton. Limnol. Oceanogr. *27*: 814-827.

Jenkins, W. J. 1982. Oxygen utilization rates in the North Atlantic subtropical gyre and primary production in oligotrophic systems. Nature *300*: 246-248.

Jenkins, W. J. and J. C. Goldman. 1985. Seasonal oxygen cycling and primary production in the Sargasso Sea. J. Marine Res. *43*: 465-491.

Kerr, R. A. 1983. Are the ocean's deserts blooming? Science *220*: 397-398.

Kerr, R. A. 1986. The ocean's deserts are blooming. Science *232*: 1395.

King, F. 1986. The dependence of primary production in the mixed layer of the eastern Tropical Pacific on the vertical transport of nitrate. Deep-Sea Res. *33*: 733-754.

Laws, E. A., D. G. Redalje, L. W. Haas, P. K. Bienfang, R. W. Eppley, W. G. Harrison, D. M. Karl, and J. Marra. 1984. High phytoplankton growth and production rates in oligotrophic Hawaiian waters. Limnol. Oceanogr. *29*: 1161-1169.

Laws, E. A., G. R. DiTullio, and D. G. Redalje. 1987. High phytoplankton growth and production rates in the North Pacific subtropical gyre. Limnol. Oceanogr. *32*: 905-918.

Reid, J. L and E. Shulenberger. 1986. Oxygen saturation and carbon uptake near 28ºN, 155ºW. Deep-Sea Res. *33*: 267-271.

Sheldon, R. W. 1984. Phytoplankton growth rates in the tropical ocean. Limnol. Oceanogr. *29*: 1342-1346.

Sheldon, R. W. and W. H. Sutcliffe. 1978. Generation times of 3 h for Sargasso Sea microplankton determined by ATP analysis. Limnol. Oceanogr. *23*: 1051

Shulenberger, E. and J. L. Reid. 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum and primary productivity, reconsidered. Deep-Sea Res. *28*: 901-919.

Spitzer, W. S. and W. J. Jenkins. 1989. Rates of vertical mixing, gas exchange and new production: estimates from seasonal gas cycles in the upper ocean near Bermuda. J. Mar. Res. *47*: 169-196.

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.

NO (The gyres are oligotrophic):

Cullen J. J, M. Zhu and D. C. Pierson. 1986. A technique to assess the harmful effects of sampling and containment for determination of primary production. Limnol. Oceanogr. *31*: 1364-1373.

Eppley, R. W. 1980. Estimating phytoplankton growth rates in the central oligotrophic oceans. Pp. 231-242 *in* P. G. Falkowsky, ed., Primary productivity in the sea. Plenum Press, New York.

Eppley, R. W. and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature *282*: 677-680.

Eppley, R. W., E. H. Renger, E. L. Venrick, and M. M. Mullin. 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. Limnol. Oceanogr. *18*: 534-551.

Eppley, R. W. and J. H. Sharp. 1975. Photosynthetic measurements in the central North Pacific: the dark loss of carbon in 24-hour incubations. Limnol. Oceanogr. *20*: 981-987.

Eppley, R. W., J. H. Sharp, E. H. Renger, M. J. Perry, and W. G. Harrison. 1977. Nitrogen assimilation by phytoplankton and other microorganisms in the surface waters of the Central North Pacific Ocean. Marine Biology *39*: 111-120.

Eppley, R. W. and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature *282*: 677-680.

Platt, T. 1984. Primary productivity in the central North Pacific: comparison of oxygen and carbon fluxes. Deep-Sea Res. *31*: 1311-1319. *[Platt criticizes the analysis of **Shulenberger & Reid (1981)**, who believed that O_2-flux measurements provided evidence for much higher rates of primary production than the ^{14}C method.]*

Platt, T., M. Lewis and R. Geider. 1984. Thermodynamics of the pelagic ecosystem: elementary closure conditions for biological production in the open ocean. pp. 49-84 *in* M. J. R. Fasham, ed., Flows of Energy and Materials in Marine Ecosystems, Plenum. *[They review the great debate and conclude that elementary thermodynamics preclude gross photosynthesis exceeding 197 mmol C $m^{-2}d^{-1}$ =2.3 g C $m^{-2}d^{-1}$, but a more likely value is .51 g C $m^{-2}d^{-1}$ (see Table 5, p. 73)]*

Platt, T. and W. G. Harrison. 1985. Biogenic fluxes of carbon and oxygen in the ocean. Nature *318*: 55-58.

Platt, T. and W. G. Harrison. 1986. Reconsideration of oxygen fluxes in the upper ocean. Deep-Sea Res. *33*: 273-276.

Sharp, J. H., M. J. Perry, E. H. Renger, and R. W. Eppley. 1980. Phytoplankton rate processes in the oligotrophic waters of the central North Pacific Ocean. J. Plankton Res. 2: 335-353.

Venrick, E. L., J. A. McGowan, D. R. Cayan and T. L. Hayward. 1987. Climate and Chlorophyll a: long-term trends in the central north Pacific Ocean. Science *238*: 70-72.

Williams, P. J. LeB., K. R. Heinemann, J. Marra, and D. A. Purdie. 1983. Phytoplankton production in oligotrophic waters: measurement by the ^{14}C and oxygen techniques. Nature *305*: 49-50.

Related Topics

THE VERTICAL FLUX OF ORGANIC MATTER:

The two-page article by **Pace *et al.* (1987)** describes a regression relationship between surface production and flux of organic material out of the euphotic zone. The primary production data were obtained using metal-clean ^{14}C-incubations as part of the VERTEX program. Predicted flux of organic carbon is 3x to 5x that of **Suess's (1980)** regression model.

These equations are of crucial importance in modeling the buffering capacity of the ocean for increasing concentrations of atmospheric CO_2. Also, these equations could be used, with a few assumptions, to estimate the magnitude of 'new' production in the euphotic zone. (What are the assumptions?). They are also important for assessing the degree of coupling between deep-sea benthic communities and primary production in the overlying euphotic zone. Deuser, in a series of papers, has shown that there is a seasonal trend in the flux of organic matter to the deep sea. This seasonal pulse may provide an important environmental cue to deep-sea species, leading to seasonal breeding cycles and other cycles with an annual periodicity.

One of the important issues in **Pace *et al.* (1987)** is how the composition of the pelagic zooplankton community affects the flux of organic matter out of the euphotic zone. Obviously the fraction of primary production consumed by microzooplankton would have a pronounced impact on the flux of organic matter out of the euphotic zone. There should be different flux equations for the North Atlantic and the North Pacific (Why?). Some of these issues are addressed by **Welschmeyer & Lorenzen (1985)**.

Welschmeyer & Lorenzen (1985) point out some fundamental differences in processes controlling the flux of material of the euphotic zone in Dabob Bay and the open ocean (pay particular attention to the conceptual model in Figure 8). **Welschmeyer & Lorenzen (1985)** use a pigment budget to estimate not only phytoplankton specific growth rates but also the extent of

net zooplankton and microzooplankton grazing. The basis for their pigment budget is **Shuman & Lorenzen's (1975)** study that documented that most of the chlorophyll *a* passing through a copepod's gut is converted to pheophorbide *a*. To estimate grazing rates, Welschmeyer & Lorenzen assumed that the conversion of Chl *a* to pheophorbide a was nearly complete, but **Conover *et al.* (1986)** criticized this assumption. In 2000, there remains an active debate in the literature over the validity of using pigment flux to estimate grazing rates.

Finally, all of these papers use sediment traps to estimate fluxes, and some use vertical arrays of traps to estimate the change in flux with depth. Most sediment traps follow designs, such as a 4:1 diameter to height ratio, that **Gardner (1977)** found to produce relatively unbiased estimates of the flux. Unfortunately, sediment traps **are** biased samplers: they underestimate or overestimate the flux of particles. A trap can underestimate the concentration of a particle with one settling velocity while overestimating the concentrations of particles with a higher settling velocity. Particles rarely sink into a trap as one might naively suppose from Stokes law. Sediment traps have complicated interactions with flow, and their trapping efficiencies vary as a function of their design (*e.g.*, cross section to height) and the flow velocity around the trap. Some designs work better than others, but there is no uniformly ideal sediment trap for organic particles of different settling velocities in different flow fields. **Butman (1986)** and **Butman *et al.* (1986)** address some of the important issues and point out that some of **Gardner's (1977)** trapping efficiencies apply only to a limited set of flow regimes.

ON THE FLUX OF PHOTOSYNTHETIC PIGMENTS & GRAZING BUDGETS:

Randy Shuman determined that calanoid copepods convert Chl *a* to pheophorbide *a* with strict stoichiometry. Thus, the flux of pheophorbide *a* in sediment traps could be used to estimate calanoid grazing rates. This technique was used by Nick Welschmeyer in his doctoral work. Some critiques of the approach are now emerging (*e.g.*, Conover *et al.* 1986).

Outlines of papers

ASSIGNED

Platt, T. *et al.* 1989. Biological production of the oceans: the case for a consensus. Mar. Ecol. Prog. Ser. *52*: 77-88. [2, 3, 8, 24]
1.   Abstract
    a.   Biological dynamics in the pelagic ocean are intermittent rather than steady
    b.   Proper averaging of NO_3^- supply and regenerated N is necessary to reconcile existing data on biogenic fluxes of O_2 and carbon
    c.   New production by NO_3^- is higher than previously thought.
2.   Introduction
        open ocean: 90% of surface area of the ocean and 80% of marine biological production
3.   **CONCEPTUAL BACKGROUND**
    a.   **Components of the carbon cycle**
        i.   net and gross production
        ii. net community production P_c is P_n – respiration from heterotrophs:
            P_g – Respiration = P_n (1)
    b.   **Components of the N cycle**

        i.   *f* ratio: ratio of new to total production
            (1) P_r is regenerated production
            (2) P_{new} is new production.
            (3)   The sum of P_{new} and P_r is P_T
        ii. P_t is equivalent to P_n since there is no evidence that phytoplankton remineralize N.

    c.   **Scales of measurement for primary production**
        i.   Each measurement technique in Table 1 has an intrinsic time scale
        ii.   The method of averaging can be very important [*cf.*, the fallacy
            of the average]

Table 1. Methods for estimating primary production [each has a characteristic time scale]
    In vitro
        ^{14}C
        O_2
        NO_3^-
    Bulk properties of seawater
        Sedimentation of organic matter below euphotic zone
        OUR
        Net O_2 accumulation in photic zone
        NO_3 flux to euphotic zone
    Upper limit
        optimal energy conversion of photons absorbed by phytoplankton pigments.
    Lower limit (depletion of winter NO_3^- above the seasonal thermocline)

    d.   **Comparing indices of primary production**
        i.   **Platt & Harrison (1986)**:
            (1)   Hypothesis 1:   indices of P_{new} are held to exceed *in vitro* measurements of P_t
            (2)   Hypothesis 2:   Bulk estimates of P_{new} when extrapolated to P_t exceed *in vitro*
                   measures of P_t
        ii.   **Hypothesis I**
            (1)   Shulenberger & Reid's (1981) oxygen data argument flawed.
            (2)   No ^{14}C data for the North Atlantic, therefore **Jenkins (1982)** model of AOU doesn't
                 need to be considered.
        iii.   the *f*-ratio and Hypothesis II
            (1) $P_t = f^{-1} * P_{new}$
                 <f>=double integral P_{new} /double integral P_T (2)
            (2)   Equ. 2 can be evaluated from a times series of f, provided that the covariance of P_t
                 and *f* is taken into account (**Platt & Harrison 1985**, **Vezina & Platt 1987**)
            (3)   **Eppley & Peterson's (1979)** *f* of 0.1 can't be extrapolated to <f>
            (4)   <f> may be 0.3 at the annual time scale.
            (5)   *"We can therefore expect that locally-enhanced nitrate flux will not be an*
                 uncommon feature of the pelagic ocean."
            (6)   Natural abundance of ^{15}N
                 Inverse correlation between sediment flux and surface temperature 1 month earlier
                 (p. 82)
            (7)   **f and P_t have positive covariance**
                      -the unweighted time average of f can underestimate <f>
            (8)   Emerson (1987) Station P. *In vitro* measures of new production with O_2
                 accumulation matched.
            (9)   **2-layer euphotic zone**

4.   **Ecological Energetics**
    a.   Estimates of primary production must respect known limits on the efficiency of photosynthesis
    b.   Fig. 2 shows how the implied conversion efficiency depends on <f> when P_{NEW}=5 mol O_2 m^{-2} y^{-1}
    c.   highest short-term yields in sugarcane < 0.5%

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} (Jenkins & Goldman 1985)**

5.   **Intermittency and sampling**

6.   Conclusions: The level of new production is higher than previously thought and these high rates are caused by intermittent inputs of $NO_3^{..}$

SUPPLEMENTAL

Eppley, R. W. 1980. Estimating phytoplankton growth rates in the central oligotrophic oceans. Pp. 231-242 *in* P. G. Falkowsky, *ed.*, Primary productivity in the sea. Plenum Press, New York. [2, 6, 15]

I.   Introduction
    A. $1/P \ dP/dt = \mu$ Equ (1)
Fig. 1.   Schematic of planktonic activities and flows of carbon during incubation of water samples in productivity experiments.
    B.   Some corroboration of ^{14}C method needed
    C.   Gyres are chemostats (the quasi-steady-state assumption)
    D.   Little annual variation in POC, Chl *a* (< factor of 2 over km's or days)
    E.   Goal of paper to review methods for calculating μ
II.   Measurements that shed light on μ
    A.   Microscopic observation of the frequency of cell division
        1.   Weiler
        2.   *[see later papers by McDuff and Chisholm, Rivkin, Carpenter]*
    B.   Isotope flux measurements
        1. ^{14}C method: 0.2 doublings per day
        2.   *"Koblenz-Mishke, Vedernikov & Shirshov (16) report typical growth rates of 6.6 doublings per day."*
            a.   similar ^{14}C incorporation estimates
            b.   disparities in estimates of phytoplankton standing stock
        3.   Maximum expected rates are 1 to 2 divisions per day based on temperature and light (Eppley 1972)
    C.   Elemental composition ratios
        1.   C/N ratio. Goldman, McCarthy & Peavey vs Sharp et al
            a.   GMP found 106:16:1
            b.   Sharp found that POC/PON was 13, indicating that $\mu/\mu_m = 0.3$ if phytoplankton carbon/nitrogen ratios were the same.
        2.   [DiTullio's ^{14}C-specific protein labeling provides an independent estimate of μ/μ_{max}. Laws et al. 1987 found relative growth$\approx$86%]
    D.   Turnover times: Jackson
        1.   grazing rate = primary production rate = ammonium turnover rate
        2.   calculations yield 0.2 doublings per day
    E.   Nucleotide content of particulate organic matter
    F.   rate of increase in particle volume
        1.   3 hour doubling times by Sheldon
        2.   large bottles include more zooplankton
        3.   large bottles yield higher ^{14}C values
    G.   light-dark O_2 method
        1.   Riley 1930's
        2.   Williams *et al* found no difference
    H.   Measurements in the open ocean
        1.   Schulenberger & Reid (1981)
        2.   Jenkins & Goldman (1985)
    I.   Collection of organic material sinking below the surface
        1.   Knauer, Martin & Bruland. 68 mg C $m^{-2}d^{-1}$, 6.1 mg N $m^{-2} \ d^{-1}$.
        2.   should be multiplied by 10 or 20 (Page 487 in Eppley 1979)
III.   Synthesis of existing data
    A. $1/P \ dP/dt = \mu + G+M+E+R$
        1. μ = net daily (24-h) increase in phytoplankton biomass
        2.   G = grazing loss
        3.   M = loss due to cell death (*e.g.*, bottle effects)

4.   E = extracellular release of fixed carbon

5.   R = dark loss of carbon due to community respiration

B.   Table 1 (page 239) Summary of rates = 550 mg C m^{-2}d^{-1}

Gieskes, W. W. and G. W. Kraay. 1984. State-of-the-art in the measurement of primary production. Pp. 171-190
_in_ M. J. R. Fasham, ed., Flows of Energy and Materials in Marine Ecosystems, Plenum.

I.   Introduction

A.   History of the ^{14}C technique

1.   Thousands of estimates

2.   few are reliable

B.   Gieskes' group compared and contrasted methods.

C.   Steeman-Nielsen's global production: 15 x 10^9 tons

1.   Riley: global production 126 x 10^9 tons

2.   Sieburth found food requirements of heterotrophs exceeded primary productivity estimates.

D.   In the North Sea the ^{14}C estimates don't seem so bad

E.   In the gyres there is a big problem with the ^{14}C method underestimating production.

II.   Problems

A.   enclosure in glass bottles too small and for too long

B.   leakage of metals from the glass

C.   metals in the ampules

D.   Schematic diagram:

Fig. 1   Carbon flow in a bottle

E.   If rates proceed through the entire loop, one does not get an estimate of real primary production

III.   Some results of recent measurements

A.   5 l bottles

B.   ultra-clean stock solution

C.   Standard addition: 2 mls from ampule to 100 mls of container

Fig. 2.   Primary production measured in tropical Atlantic

Fig. 3.   **Long incubations give better numbers than many short incubations**

Fig. 3.   A series of short incubations gave lower estimates than those with longer incubations. This discrepancy can possibly be explained by loss of ^{14}C to the DOM pool and subsequent recovery in particulate form after some time lag, namely through uptake by bacteria.

D.   "clean" techniques give higher rates of primary production

E.   Morris: algae accumulate carbohydrates in daytime that they use up in the night

F.   Postma found high rates of POC incorporation, but low changes in cell numbers or plankton pigment concentrations

G.   If one wants to estimate new production, one should use incubations that are not too short

IV.   Alternatives to the ^{14}C method

A.   sensitive Oxygen method

1.   differences between net and gross was rather small

2.   P. 180-181: PQ varies from 0.3-2.5

a.   PQ > 1 if lipids

b.   PQ < 1 if organic acids

3. ^{14}C and sensitive O$_2$ method close

matches Williams work

Fig. 5 Time course incubations show that the methods are close.

B.   Other methods

1.   track autoradiography

2.   counting dividing cells

3.   DCMU incubation

4.   Redalje & Laws Chl _a_ labeling procedure

a.   C:Chl _a_ ratios of 99.6 and 104 for North Sea populations in the late spring. p. 184

b.   C:Chl ratio of 107 for oligotrophic populations

c.   lower C:Chl at the Chl _a_ maximum zone, 64; surface 107

V.   Concluding remarks:

A.   diurnal variation important

B.   There is no standard procedure yet for estimating primary production

Grande, K. D., P. J. LeB. Williams, J. Marra, D. J. Purdie, K Heinemann, R. W. Eppley and M. L. Bender. 1989. Primary production in the North Pacific gyre: a comparison of rates determined by the ^{14}C, O$_2$ concentration and ^{18}O methods. Deep-Sea Res. *36*: 1621-1634.

1. Abstract.
    a. ^{18}O method based on rate at which ^{18}O-labeled O$_2$ is produced
    b. ^{14}C productivity ranges from 60% to 100% of ^{18}O gross production
    c. *"However, in samples incubated on board ship (with neutral density filters at 35% of incident light intensity and at surface temperatures), the rates of gross oxygen production measured with ^{18}O were up to two times the rates measured with light/dark bottles, and 2-3 times the rates of ^{14}C production."* Spectral quality of light

2. Introduction
    a. *"It is now generally believed that the ^{14}C method gives a good approximation of the rate of primary production. (Williams et al., , Platt 1984, Davies & Williams 1984, Bender et al., 1987)"* [Statement criticized in 1991 L & O article on dark-bottle problems]
    b. ^{18}O method
    $H_2^{18}O + CO_2 -> CH_2O + ^{18}O^{16}O$
        i. $\delta^{18}O$ raised to +2000ppt to 3000ppt
        ii. ^{18}O method measures gross production.

3. Materials & Methods
    a. **Fitzwater et al. (1982)** trace metal clean methods.
    b. neutral density P vs. I incubations.
    c. *in situ* incubations.
    d. PQ assumed to be 1.25 since NO$_3^-$<100 nm

4. Results
    - no apparent effect of bottle type

5. Discussion
    a. *In situ* incubations
    turnover time varies from 1 day at surface to infinity at the base of the euphotic zone.
    b. Simulated in situ incubations
    -no mid-depth maximum
    c. "shipboard incubations"
    There are 2 striking differences between the shipboard incubation results and those observed in the *in situ* incubations.
        i. ^{18}O gross production rates exceed other measures of productivity by a greater amount than in the *in situ* experiments. The rates of ^{18}O gross production in the shipboard experiments are 2.2 times greater than the rates of ^{14}C production, while in the *in situ* experiment they are 1.4 times higher. The ^{18}O gross production rates in the shipboard experiments are on average 2.0 times greater than gross O$_2$ production rates measured with light/dark bottles, in the *in situ* experiments, the two rate terms are nearly equal. In the shipboard experiments, the rate of respiration in the light is higher than the rate in the dark, by a factors of 3-8. In contrast, light and dark respiration rates are roughly equal in the *in situ* experiments.
        ii. absolute rates of metabolic activity are higher in the shipboard experiments. For example ^{14}C production rates are systematically higher in the shipboard incubations than for mixed layer samples incubated by the *in situ* technique.
    d. Discrepancy between productivity measures by "shipboard" and *in situ* incubation procedures.
        i. anomalous high rates of ^{14}C assimilation and ^{18}O gross production and (2) anomalous high rates of respiration for samples incubated on board ship.
        ii. temperature is identical
        iii. N$_2$ gas bubbled through the shipboard incubators.
        iv. UV light not a factor, since Pyrex used.
        v. spectral quality of light can affect photosynthetic response. Keifer & Strickland
        vi. spectral quality can affect redox transformations
                -can change the concentrations of essential and toxic trace metals

Laws, E. A., G. D. DiTullio, K. L. Carder, P. R. Betzer, and S. Hawes. 1990. Primary productivity in the deep blue sea. Deep-Sea Res. *37*: 715-730. *[Clean techniques used to estimate production. Light quality is important in estimating production. Simulated in situ incubations may underestimate production]*

1. Abstract
2. Introduction
    light-quality important
3. Materials & methods.
    a. clean sampling and incubations
    b. Time-zero controls used.*"Dark bottles were not used as corrections for non-photosynthetic processes, because it is clear that non-photosynthetic ^{14}C uptake may occur at very different rates in the light and dark. (Hecky & Fee 1981)*"
4. **Results**
    a. average photoperiod production of 777 ± 219 mg C m^{-2}
    b. disturbing fact (Laws *et al.*, 1990, p. 719): initial slope of the P vs. I curve = 14 g C m^2 g^{-1} Chl *a* Ein^{-1}, if we assume a mean k_c value of 16 m^2 g^{-1} Chl *a*, the implication is that the absorption of 1.0 Ein of visible light yields 14/16=0.875 g C in very dim light. The quantum requirement therefore becomes 12/0.875=13.7 Ein mol^{-1}C. Based on the widely accepted Z-scheme of photosynthesis (Hill & Bendall, 1986), the **minimum quantum requirement** is expected to be at least 8.0 Ein mol C^{-1}, and the minimum quantum requirements are more in the range of 10-20 or higher (Falkowski 1985) *[See Raven & Lucas (1985) for additional discussions of the quantum requirements, which range between 8-14-20 Ein/mol C]*
Fig. 3.   Median quantum requirements vs. percent surface irradiance calculated assuming k_c =16 m^{2}g-1Chl *a*
    c. Quantum requirements=(Ik_c X)/P, where I is irradiance, k_c is the Chl *a* specific absorption coefficient, X is the concentration of Chl *a* and P is the photosynthetic rate (Fig 3. Legend).
    d. Recent criticisms of primary production take the attitude that the ^{14}C method underestimates production. However if our quantum requirements are too low, the implication is that the production numbers are too high rather than too low.
    e. **Grande et al (1989)** found excellent agreement between ^{14}C and ^{18}O methods at irradiance at less than 35% of surface values. Thus we feel the low quantum requirements are not the result of measurement inaccuracy.
    f. could changes in k_c account for differences?
        (Chl *a*)k_c I=Integral K(x)Q(x)dx   (1)
        where,   Chl *a* is concentration in g Chl *a*m^{-3}, k_c is the Chl *a*-specific absorption coefficient in m^{2}g^{-1} Chl *a*, I is the quantum flux of visible light in Ein m^{-2}h^{-1}. Q(x) is the quantum flux of visible light between wavelengths x and x+dx, and K(x) is the absorption coefficient in m^{-1} for all photosynthetically active pigments. The integral is taken over the range 400-700 nm. Note that I – Integral Q(x)dx.

        k_c =Integral k_c (x)f(x) dx,   (2)
        where, k_c(x)=K(x)/(Chl *a*)=Chl *a* specific absorption at wavelength x due to all photosynthetically active pigments., and f(x)=Q(x)/I=fraction of visible quanta in wavelength range x to x+dx.
Fig. 4.   Relationship between k_c using equation (1) and data from extracted pigments (abscissa) and k_c (x) from particulate material collected on filters (R=0.88)
    g. The k_c values are 3 times higher for than surface values from samples taken at or below the 14% light levels. All of this increase is due to changes in f(x).
        k_c in the blue wavelengths is between 40 and 80, not 16
    h. Using our estimates of k_c, we have replotted in Fig. 3, the quantum requirements.. all values exceed quantum requirement of 8 Ein mole^{-1}C median of 20 Ein mol^{-1} C in the limit of dim values
5. **Discussion**
    a. Neutral density filters (p. 726)
        i.   *"Based on the results shown in Fig. 7, this practice could lead to a substantial underestimation of primary production. For example, the 2-fold difference in k_c for white and blue light at quantum flux equal to 33% of surface value (Fig. 7) means that phytoplankton incubated at the 33% light level in white light would be absorbing light at a rate equal to that of in situ cells at the 16.5% light level. In the upper portion of the water column the difference in k_c between whit and submarine light will have little effect on measured photosynthetic rates because of the hyperbolic relationship between photosynthetic*

rate and light intensity. However, photosynthetic rates and k_c become almost directly proportional to each other at greater depths, where production is truly light limited."

b.   Areal production from neutral density filters was 350 ± 79 mg c m^{-2} for photoperiod or 45% of the 717 ± 219 mg Cm^{-2} estimated from the simulated *in situ* incubations. The former figures is comparable to the 414 ± 34 mg C m^{-2} obtained by PRPOOS (Laws *et al.*, 1987). PRPOOS used white light.

    factor of 2 underestimation with neutral density filters.

c.   Morel *et al.* (1987) review: More recently, Morel *et al.*, (1987) examined the photosynthetic characteristics of the diatom *Chaetoceros protuberans* to changes in light intensity and color. *et al.*, They found that the initial slope of the P vs. I curve was 81% higher when the cells were grown in blue light vs white or green light and commented that (p. 1077):

"The enhanced absorption capacities of algae in the blue part of the spectrum obviously account for this expected difference." In fact, if their results were recalculated in terms of absorbed radiation rather than incident radiation, the initial slopes were identical, independent of light color. This result is consistent with the conclusions reached in the present study."

6.   bottles should be incubated in situ

Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. Chapter 10.

References

ON GYRE PRODUCTION

Altabet, M. 1989. A time-series study of the vertical structure of nitrogen and particle dynamics in the Sargasso Sea. Limnol. Oceanogr. *34*: 1185-1201.

Benitez-Nelson, C. and D. M. Karl. 2002. Phosphorus cycling in the North Pacific subtropical gyre using cosmogenic ^{32}P and ^{33}P. Limnol. Oceanogr. 47: 762-770. [?]

Bienfang, P. K. 1985. Size structure and sinking rates of various microparticulate constituents in oligotrophic Hawaiian waters. Mar. Ecol. Prog. Ser. *23*: 143-151. *[Documents the small size of oligotrophic phytoplankton. 80% of Chl a, and 60% of C, N, P, and Si in phytoplankton less than 5 µm. Sinking loss rates are of minor importance (<7% of total loss)]*

Campbell, L and H. A. Nolla. 1994. The importance of Protochlorococcus to community structure in the central North Pacific Ocean. Limnol. Oceanogr. *39*: 954-961.

Craig, H. and T. Hayward. 1987. Oxygen supersaturation in the ocean: biological versus physical contributions. Science *235*: 199-201. *[72-86% of O_2 supersaturation due to net photosynthetic production. Discusses **Shulenberger & Reid's (1981)** analysis and finds fault with **Platt's (1984)** critique of Shulenberger & Reid] [7]*

Cullen J. J, M. Zhu and D. C. Pierson. 1986. A technique to assess the harmful effects of sampling and containment for determination of primary production. Limnol. Oceanogr. *31*: 1364-1373. *[Using DCMU-induced fluorescence, Cullen et al. show that bottled phytoplankton from oligotrophic areas have the same photosynthetic rate as in situ phytoplankton, and that rate is slow.]*

Eppley, R. W. 1980. Estimating phytoplankton growth rates in the central oligotrophic oceans. Pp. 231-242 *in* P. G. Falkowski, ed., Primary productivity in the sea. Plenum Press, New York. *[A review of methods for calculating µ, and a discussion of the great productivity debate. This paper provides the most complete summary of the view that gyres had low productivity - a view now greatly modified. See **Platt et al. (1989)**2, 3, 8, 24]* [**2**, **6**, **15**]

Eppley, R. W. 1989. New production: history, methods, problems. Pp. 85-97 *in* W. H. Berger, V. S. Smetacek and G. Wefer, eds. Productivity of the Ocean: Present and Past. Wiley, New York.

Eppley, R. W., E. H. Renger, E. L. Venrick, and M. M. Mullin. 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. Limnol. Oceanogr. *18*: 534-551. *[In this classic paper, Eppley et al. describe the gyres as chemostats (run with D=μ=0.13 d^{-1}). The upward vertical NO$_3^-$ flux (and N fixation & rain input) is balanced by sedimenting organic matter. Regenerated N from grazers is the major nitrogen source.]*

Eppley, R. W. and J. H. Sharp. 1975. Photosynthetic measurements in the central North Pacific: the dark loss of carbon in 24-hour incubations. Limnol. Oceanogr. *20*: 981-987. *[There is a 4-5% hourly loss from POC in the dark due to phytoplankton respiration. Eppley & Sharp's recommendation of longer incubations is in conflict with* **Peterson's (1980)** *recommendations.* **Harris et al. (1989)** *have readdressed this issue.]*

Eppley, R. W., J. H. Sharp, E. H. Renger, M. J. Perry, and W. G. Harrison. 1977. Nitrogen assimilation by phytoplankton and other microorganisms in the surface waters of the Central North Pacific Ocean. Marine Biology *39*: 111-120. *[One of a series of papers documenting low specific growth rates and production in the Central N. Pacific gyre. These papers led to the model that the gyre could be likened to a chemostat.]*

Eppley, R. W. and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature *282*: 677-680. *[They argue that the annual rate of new to total production is only 5-10%.* **Platt et al. (1989)** *argue that 30-40% is more likely.]*

Eppley, R. W., E. Swift, D. G. Redalje, M. R. Landry and L. W. Haas. 1988. Subsurface chlorophyll maximum in August-September 1985 in the CLIMAX area of the North Pacific. Mar. Ecol. Prog. Ser. *42*: 289-301. *[There is a pronounced chl maximum throughout the gyre with low growth (μ=0.11d^{-1})]*

Fuhrman, J. A., T. D. Sleeter, C. A. Carlson, and L. M. Proctor. 1989. Dominance of bacterial biomass in the Sargasso Sean and its ecological implications. Mar. Ecol. Prog. Ser. *57*: 207-217. *[Bacterial biomass>>eucaryotic biomass]*

Gieskes, W. W. C., G. W. Kraay and M. A. Baars. 1979. Current ^{14}C methods for measuring primary production : gross underestimates in oceanic waters. Neth. J. Sea Res. *13*: 58-78.

Glover, H. E., A. E. Smith and L. Shapiro. 1985. Diurnal variations in photosynthetic rates: comparisons of ultraphytoplankton with a larger phytoplankton size fraction. J. Plankton Res. *7*: 519-535. *[Transects from the Gulf of Me to the Sargasso Sea, the ultraphytoplankton (<3 μm) were separated into cyanobacteria and eukaryotes by the presence of phycoerythrin in the former. In the Sargasso Sea, small cyanobacteria dominated in surface waters, larger cyanobacteria below the mixed layer, and eukaryotes dominated in the chl max.]*

Glover, H. E., B. B. Prezelin, L. Campbell, M. Wyman, and C. Garside. 1988. A nitrate dependent *Synechococcus* bloom in surface Sargasso sea water. Nature *331*: 161-163. *[They document a very short-lived (3 d) Synechococcus bloom after a rainfall. As discussed by* **Platt et al. (1989)***, intermittent NO$_3^-$ pulses and blooms may reconcile short-term incubuation results with bulk measurements of primary production.]* {**2**, **6**, **15**}

Goldman, J. C. 1980. Physiological processes, nutrient availability, and the concept of relative growth rate in marine phytoplankton ecology. Pp. 179-194 *in* P. G. Falkowski, ed, Primary Productivity in the Sea. Plenum Press, New York. *[Phytoplankton only have RKR ratios when μ/μ$_m$ is roughly 1. DiTullio now has a rapid method for estimating relative growth based on ^{14}C activity in protein.]*

Goldman, J. 1986. On phytoplankton growth rates and particulate C:N:P ratios at low light. Limnol. Oceanogr. *31*: 1358-1363. *[C:N:P ratios are a function of μ/μ$_m$, not of light level. The observed C:N:P ratios near the RKR ratios lead to the prediction that relative growth of oceanic phytoplankton is one.]*

Goldman, J. C., J. J. McCarthy, and D. G. Peavey. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature *279*: 210-215. *[A very important paper! The C:N and C:P ratios from chemostat studies are reviewed and it is shown that phytoplankton only grow with Redfield ratios at high relative growth rates 0.9 < μ/μ$_{max}$ < 1. They introduce the controversial hypothesis that patches of nutrients from zooplankton excretion explain high relative growth rates in the field]*

Goldman, J. C. and P. M. Glibert. 1982. Comparative rapid ammonium uptake by four species of marine phytoplankton. Limnol. Oceanogr. *27*:

814-827. *[Gyre phytoplankton apparently have the ability to exploit short-lived nutrient micropatches. cf. references on Handout 9.]*

Grande, K. D., P. J. LeB. Williams, J. Marra, D. J. Purdie, K Heinemann, R. W. Eppley and M. L. Bender. 1989. Primary production in the North Pacific gyre: a comparison of rates determined by the ^{14}C, O_2 concentration and ^{18}O methods. Deep-Sea Res. *36*: 1621-1634.

Hayward, T. L. 1987. The nutrient distribution and primary production in the central North Pacific. Deep-Sea Res. *34*: 1593-1627.

Hayward, T. L. 1991. Primary production in the North Pacific gyre: a controversy with important implications. Trends in Ecology and Evolution *6*: 281-284.

Iturriaga, R. and J. Marra. 1988. Temporal and spatial variability of chroocococcoid cyanobacteria *Synechococcus* spp. specific growth rates and their contribution to primary production in the Sargasso Sea. Mar. Ecol. Prog. Ser. *44*: 173-181.

Jackson, G. A. and P. M. Williams. 1985. Importance of dissolved organic nitrogen and phosphorous to biological nutrient cycling. Deep-Sea Res. *32*: 223-235. *[DOC and DON were grossly underestimated until the mid-1980's. Many estimates of gyre nutrient fluxes could be inaccurate]*

Jenkins, W. J. 1982. Oxygen utilization rates in the North Atlantic subtropical gyre and primary production in oligotrophic systems. Nature *300*: 246-248. *[^{3}H:^{3}He used to date water and to provide a time reference for O_2 utilization below the pycnoclline. New production ≈ 5 moles $O_2 m^{-2} y^{-1}$]* [6]

Jenkins, W. J. 1988. The use of anthropogenic tritium and helium-3 to study subtropical gyre ventilation and circulations. Phil. Trans. R. Soc. London A *325*: 43-61. *[Jenkins uses tracers to estimate vertical NO_3^- flux in the Sargasso sea. These rates match those determined earlier using O_2 utilization]*

Jenkins, W. J. and J. C. Goldman. 1985. Seasonal oxygen cycling and primary production in the Sargasso Sea. J. Marine Res. *43*: 465-491. *[Hydrographic data from Station S in the Sargasso Sea is used to compute new production from observed seasonal increases in O_2 concentration. New production is 50 g C $m^{-2} yr^{-1}$. They propose that there are 2 distinct zones in the oligotrophic ocean, with the upper zone characteristic of chemostat and the lower zone more dependent on new production.]*

Karl, D. M., R. Letelier, L. Tupas, J. Christian and D. Hebel 1997. The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. Nature 388: 533-538 .

Kerr, R. A. 1983. Are the ocean's deserts blooming? Science *220*: 397-398. *[A popular science review of some of the issues]*

Kerr, R. A. 1986. The ocean's deserts are blooming. Science *232*: 1395. *[Based on preliminary results from PRPOS, Kerr answers his (1983) question. Metal contamination may have led to underestimates of production in earlier studies in the gyres.]*

King, F. 1986. The dependence of primary production in the mixed layer of the eastern Tropical Pacific on the vertical transport of nitrate. Deep-Sea Res. *33*: 733-754. *[Primary production is roughly proportional to algal standing stocks with specific rates of 1 doubling per day. Nitrate supply may be the key*. Cf. *Lewis et al. 1986.]*

King, F. D. and A. H. Devol. 1979. Estimates of vertical eddy diffusion through the thermocline from phytoplankton nitrate uptake rates in the mixed layer of the eastern tropical Pacific. Limnol. Oceanogr. *24*: 645-651. *[^{15}N-NO_3^- uptake is combined with vertical NO_3^- gradients to calculate K_z's through the thermocline. The approach, similar to Eppley et al. 1979, produces K_z's of .05-1.1 $cm^2 s^{-1}$. A log-log relationship between $d\sigma/dz$ and K_z is used to predict NO_3^- flux. An indirect estimate of the f ratio is produced ranging from 4.3 to 75.3%]*

Laws, E. A., D. G. Redalje, L. W. Haas, P. K. Bienfang, R. W. Eppley, W. G. Harrison, D. M. Karl, and J. Marra. 1984. High phytoplankton growth and production rates in oligotrophic Hawaiian waters. Limnol. Oceanogr. *29*: 1161-1169.

Laws, E. A., G. R. DiTullio, and D. G. Redalje. 1987. High phytoplankton growth and production rates in the North Pacific subtropical gyre. Limnol. Oceanogr. *32*: 905-918.*[Growth rates off Oahu of 1-2 d^{-1}, close to μ_{max} = 1.63 (2.35 doublings/day) predicted for 27°C water using Eppley (1972). The Redalje-Laws Chl a and DiTulio-Laws protein labeling procedures used.] {?}*

Legendre, L. and M. Gosselin. 1989. New production and export of organic matter to the deep ocean: consequences of some recent discoveries. Limnol. Oceanogr. *34*: 1374-1380. *[Nitrification and denitrification in low O_2 regions, as well as DON transport may play key roles in interpreting oceanic N fluxes. A nice conceptual model is proposed for gyre production. The Eppley-Peterson steady-state assumption model is evaluated and found wanting.]* [**27**]

Legendre, L. and J. Le Fevre. 1989. Hydrodynamic singularities as controls of recycled versus export production in oceans. Pp. 49-63 in W. H. Berger *et al.*, eds., Productivity of the Ocean: Present and Past. Wiley.

Lewis, M. R., W. G. Harrison, N. S. Oakey, D. Herbert and T. Platt. 1986. Vertical nitrate fluxes in the oligotrophic ocean. Science *234*: 870-873. *[They estimated K_z using turbulent kinetic energy fluctuations, the N gradients, and ^{15}N uptake. They calculate low rates of new production (.14 mmol $Nm^{-2}d^{-1} \approx 1$ mmol C $m^{-2}d^{-1}$). This is in accord with "older" estimates of gyre production. The vertical nitrate flux is not sufficient to account for the newly proposed high gyre production rates.]*

Li, W.K.W., D. V. Suba Rao, W. G. Harrison, J. C. Smith, J.J. Cullen, B. Irwin and T. Platt. 1983. Autotrophic picoplankton in the tropical ocean. Science *219*: 292-295. *[Both biomass and production are dominated by the picoplankton (< 2 μm diameter)]*

Longhurst, A. R., A. Bedo, W. G. Harrison, E. J. Head, E. P. Horne, B. Irwin, and C. Moreles. 1989. NFLUX: a test of vertical nitrogen flux by diel migrant biota. Deep-Sea Res. *36*: 1705-1719. *[Zooplankton which ingest phytoplankton at the surface and respire at depth could affect the vertical nitrogen flux]* [**8**]

Marra, J. and K. R. Heinemann. 1987. Primary production in the North Pacific central gyre: new measurements based upon ^{14}C. Deep-Sea Res. *34*: 1821-1829.

Martin, J. H., G. A. Knauer, D. M. Karl, and W. W. Broenkow. 1987. VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Res. *34*: 267-285.

Nelson, D. M. and M. A. Brzezinski. 1997. Diatom growth and productivity in an oligotrophic midocean gyre: a 3-yr record from the Sargasso Sea near Bermuda. Limnol. Oceanogr. *42*: 473-486. *[Si-30 used to estimate production. Diatom production is 20-45 $gCm^{-2}y^{-1}$, ≈15-25% of total production. 80% of silica dissolves in upper 150 m. Diatoms account for 30% of annual POC flux, but nearly 100% during the winter/spring bloom. Fe not limiting]*

Perry, M. J. 1972. Alkaline phosphatase activity in subtropical central North Pacific waters using a sensitive fluorometric method. Marine Biology *15*: 113-119. *[She wasn't able to detect phosphatase activity initially, but after a few hours on board ship, activity appeared. This may indicate that the cells were zinc-limited]* {?}

Perry, M. J. 1976. Phosphate utilization by an oceanic diatom in phosphorous-limited chemostat culture in the oligotrophic waters of the central North Pacific. Limnol. Oceanogr. *21*: 88-107. *[Only a few gyre samples had detectable alkaline phosphatase activity]*

Peterson, B. 1980. Aquatic primary productivity and the ^{14}C-CO_2 method: a history of the productivity problem. Ann. Rev. Ecol. Syst. *11*: 359-385. *[A superb review of the controversy over the ^{14}C method]* {**4**, **24**}

Platt, T. 1984. Primary productivity in the central North Pacific: comparison of oxygen and carbon fluxes. Deep-Sea Res. *31*: 1311-1319. *[Platt critiques the analysis of **Shulenberger & Reid (1981)**, who believed that O_2-flux measurements provided evidence for much higher rates of primary production than the ^{14}C method.. **Reid & Shulenberger (1986)** wrote a rebuttal.]* [**7**, **27**]

Platt, T., D.V. Subba Rao, and B. Irwin. 1983. Photosynthesis of picoplankton in the oligotrophic ocean. Nature *301*: 702-704.

Platt, T., M. Lewis and R. Geider. 1984. Thermodynamics of the pelagic ecosystem: elementary closure conditions for biological production in the open ocean. *Pp*. 49-84 *in* M. J. R. Fasham, ed., Flows of Energy and Materials in Marine Ecosystems, Plenum. *[They review the great debate and conclude that elementary thermodynamics preclude gross photosyntheses exceeding 197 mmol C $m^{-2}d^{-1}$ =2.3 $gCm^{-2}d^{-1}$, but a more likely value is .51 $gCm^{-2}d^{-1}$ (see Table 5, p. 73). This paper includes some nice applications of dimensionless primary production plots.]*

Platt, T. and W. G. Harrison. 1985. Biogenic fluxes of carbon and oxygen in the ocean. Nature *318*: 55-58.{**18**}

Platt, T. and W. G. Harrison. 1986. Reconciliation of carbon and oxygen fluxes in the upper ocean. Deep-Sea Res. *33*: 273-276. *[A critique of **Shulenberger & Reid (1981)**] [7]*

Prakash, A., R. W. Sheldon, and W. H. Sutcliffe. 1991. Geographic variation of ^{14}C dark uptake. Limnol. Oceanogr. *36*: 30-39 *[A 20-y old data set is used to show that dark uptake, normally about 10% of light, increases to over 50% in gyres and southern ocean. Absolute dark uptake rates increase as well.]*

Quinones, P. A. and T. Platt. 1991. The relationship between the *f*-ratio and the P:R ration in the pelagic ecosystem. Limnol. Oceanogr. *36*: 211-213.

Reid, J. L and E. Shulenberger. 1986. Oxygen saturation and carbon uptake near 28ºN, 155ºW. Deep-Sea Res. *33*: 267-271. [A defense of the **Shulenberger & Reid (1981)** hypothesis that O_2 supersaturation at the pycnocline in gyres indicates high total production - a rebuttal of **Platt (1984)**] [**26**, **27**]

Sahlsten, E. 1987. Nitrogenous nutrition in the euphotic zone of the Central North Pacific gyre. Marine Biology *96*: 433-439.

Sharp, J. H., M. J. Perry, E. H. Renger, and R. W. Eppley. 1980. Phytoplankton rate processes in the oligotrophic waters of the central North Pacific Ocean. J. Plankton Res. *2*: 335-353.

Sheldon, R. W. 1984. Phytoplankton growth rates in the tropical ocean. Limnol. Oceanogr. *29*: 1342-1346. [**6**]

Sheldon, R. W. and W. H. Sutcliffe. 1978. Generation times of 3 h for Sargasso Sea microplankton determined by ATP analysis. Limnol. Oceanogr. *23*: 1051- .

Shulenberger, E. and J. L. Reid. 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum and primary productivity, reconsidered. Deep-Sea Res. *28*: 901-919. *[Primary production was estimated by O_2 concentration and the rate was found to be much higher than that of the C-14 method. The methods are criticized by **Platt (1984)**, and this criticism was addressed by **Reid & Shulenberger (1986)**]* [**7**, **15**, **27**]

Smith, R. E. H., R. J. Geider, and T. Platt. 1984. Microplankton productivity in the oligotrophic ocean. Nature *311*: 252-254.

Spitzer, W. S. and W. J. Jenkins. 1989. Rates of vertical mixing, gas exchange and new production: estimates from seasonal gas cycles in the upper ocean near Bermuda. J. Mar. Res. *47*: 169-196. *[Their new estimates match the earlier **Jenkins-Goldman ('85)** estimates.]*

Toggweiler, J. R. 1989. Is the downward DOM flux important in carbon transport? Pp. 65-83 *in* W. H. Berger *et al.*, eds, Productivity of the ocean: present and past. Wiley. *[Cited by **Legendre & Gosselin 1989**. DOM flux at high latitudes may control open-ocean vertical N fluxes. About half of new production may end up as long lived DOM, with half-lives of 1200 y.]*

Venrick, E. L. 1982. Phytoplankton in an oligotrophic ocean: observations and questions. Ecol. Monogr. *52*: 129-154.

Venrick, E. L. 1988. The vertical distributions of chlorophyll and phytoplankton species in the North Pacific central environment. J. Plankton Res. *10*: 987-998. *[Two species groups distinguished.]*

Venrick, E. L. 1990. Phytoplankton in an oligotrophic ocean: species structure and interannual variability. Ecology *71*: 1547-1563. *[Variation on the annual to decade time scale is analyzed in the diverse (300-500 spp) oligotrophic ocean. Chl* a *concentration has doubled over the decadal time scale. The rank order of species composition has changed dramatically, especially the diatom assemblage in deeper water. The increase in Chl a documented in this paper can now be explained by the phases of the Pacific decadal oscillation, see* **Chavez et al. (2003)***]* {**10**, **28**}

Venrick, E. L. 1997. Comparison of phytoplankton species composition and structure in the Climax area (1973-1985) with that of station ALOHA (1994) Limnol. Oceanogr. *42*: 1643-1648. *[Using Kendall's tau to show among year variation, the new ALOHA data shown to be comparable in species composition with the Climax area]*

Vezina, A. and T. Platt. 1987. Small-scale variability of new production and particulate fluxes in the ocean. Can. J. Fish Aquat. Sci. 44: 198-205. *[A nonlinear model predicts that organic matter flux to sediment traps, a measure of the f ratio if the system is in steady state, may be 30%-40% of total production.]* {**18**}

Villareal, T. A. and E. J. Carpenter. 1989. Nitrogen fixation, suspension characteristics, and chemical composition of *Rhizosolenia* mats in the central North Pacific gyre. Biol. Oceanogr. *6*: 327-345.

Villareal, T. A., M. A. Altabet, and K. Culver-Rymsza. 1993. Nitrogen transport by vertically migrating diatom mats in the North Pacific Ocean. Nature *363*: 709-710. *[Bouyant Rhizoselenia mats have high [NO$_3^-$]. ^{15}N analyses indicate that the N source is beneath the pycnocline, and thus vertical migration by these mats can contribute a substantial portion of the vertical N flux (2-27% of estimated flux from turbulent diffusion).]* [**8**]

Vinogradov, M. E., I. I. Gitelson, and Y. I. Sorokin. 1970. The vertical structure of a pelagic community in the tropical ocean. Marine Biology *6*: 187-194. *[Vertical migration, documented here, can be extremely important sources of nitrogen flux.]*

Vinogradov, M. E., V. V. Menshutkin, and E. A. Shushkima. 1972. On mathematical simulation of a pelagic ecosystem in tropical waters of the ocean. Marine Biology *16*: 261-268. *[Horizontal diffusion of nutrients.]*

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.

Williams, P. J. LeB., K. R. Heinemann, J. Marra, and D. A. Purdie. 1983. Phytoplankton production in oligotrophic waters: measurement by the ^{14}C and oxygen techniques. Nature *305*: 49-50.

PACIFIC INTERDECADAL OSCILLATION (PDO)

Chavez, F P., Ryan, J, Lluch-Cota, S. E., Miguel Niquen C.. 2003. From Anchovies to Sardines and Back: Multidecadal Change in the Pacific Ocean. Science *299*: 217-221. *[A review of the Pacific decadal oscillation]* {*10*, *11*, *13*, *28*, *29*}

Hare, S. R. And N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. *47*: 103-145. *[100 Oceanographic time series are analyzed using PCA, and 2 regime shifts are identified.]* {?}

Karl, D. M., R. R. Bidigare and R. M. Letelier. 2001. Long-term changes in plankton community structure and productivity in the North Pacific subtropical gyre: the domain shift hypothesis. Deep-Sea Res. 48: 1449-1470. *[Over 30 years, Chl* a *and primary production in the North Pacific subtropical gyre doubled while silicate and phosphorus decreased. This domain shift towards prokaryotes has altered geochemistry & food webs]* {**10**}

Mantua, N. J., S. R. Hare, Y Zhang, J. M. Wallace, R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Amer. Meteorological Soc. *78*: 1069-1079. *[Principal components analysis reveals decadal patterns of change in oceanographic, especially ecological, time series.* **Roemmich & McGowan (1995)** *had earlier documented changes in CA current macrozooplankton and temperature][?]*

McGowan, J. A, D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science *281*: 210-217. {**10**}

Roemmich, D. and J. McGowan. 1995.Climatic warming and the decline of zooplankton in the California Current. Science *267*: 1324-1326. *[Since 1951 an 80% decline of macrozooplankton biomass and a 1.5°C increase in temperature]* [**28**]

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature *413*: 591-596. *[Gradual changes in climate, with PDO being one of the better examples, can lead to abrupt changes in ecosystems]{?}*

Venrick, E. L., J. A. McGowan, D. R. Cayan and T. L. Hayward. 1987. Climate and Chlorophyll *a*: long-term trends in the central north Pacific Ocean. Science *238*: 70-72. *[Chl a concentration has nearly doubled between 1968 and the early 1980's due to changes in atmospheric and physical oceanographic forcing of nutrient flux. The higher rates of production observed in the 1980's may reflect real changes in production, not changes in methodology.]* {**10**}

Williams, J. G. 2003. Sardine Fishing in the early 20th century. Science *300*: 2003. *[A letter to the editor in response to **Chavez et al. (2003)** Chavez had stated low sardines in the 1920s. Williams disagrees.]*

FLUX OF ORGANIC MATTER

Altabet, N. H., W. G. Deuser. 1985. Seasonal variations in natural abundance of ^{15}N in particles sinking to the deep Sargasso Sea. Nature *315*: 218-219. *[The flux of ^{15}N particles can be used to monitor the upward nitrate flux.]*

Altabet, M. A. 1989. Particulate new nitrogen fluxes in the Sargasso Sea. J. Geophys. Res. *94*: 12771-12779.

Altabet, M. A. 1989. A time-series study of the vertical structure of nitrogen and particle dynamics in the Sargasso Sea. Limnol. Oceanogr. *34*: 1185-1201.

Asper, V. L, W. G. Deuser, G. A. Knauer, and S. E Lohrenz. Rapid coupling of sinking particle fluxes between surface and deep ocean waters. Nature *357*: 670-672. *[100 m per day sinking rates]*

Baker, E. T., R. A. Feeley, M. R. Landry, and M. Lamb. 1985. Temporal variations in the concentration and settling flux of carbon and phytoplankton pigments in a deep fjordlike estuary. Est. Coastal and Shelf Science *21*: 859-877. *[Fluxes in the main basin of Puget Sound]*

Betzer, D. R., W. J. Showers, E. A. Laws, C. D. Winn, G. R. DiTullio and P. M. Kroopnick. 1984. Primary productivity and particle fluxes on a transect of the equator at 153° W in the Pacific Ocean. Deep-Sea Res. *31*: 1-11. *[A free-drifting sediment trap is used to estimate that: flux = surface production**1.4 * depth**0.63.]*

Billett, D. S. M., R. S. Lampitt, A. L. Rice, and R. F. C. Mantoura. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature *307*: 520-522.

Burns, K. A. and G.-P. Villeneuve. 1983. Biogeochemical processes affecting the distribution and vertical transport of hydrocarbon residues in the coastal Mediterranean. Geochim. Cosmochim. Acta *47*: 995-1006.

Buscail, R. and C. Germain. 1997. Present-daay organic matter sedimentation on the NW Mediterranean margin: importance of off-shelf transport. Limnol. Oceanogr. *42*: 217-229. *[200-2300 m depth, fluff layer found throughout Types of organic matter measured in surface sediments (sugars, amino acids)*

Cadee, G. C. 1986. Organic carbon in the water column and its sedimentation, Fladen Ground (North Sea), May 1983. Neth. J. Sea Res. *20*: 347-358.

Cole, J. J., S. Honjo, and N. Caraco. 1985. Seasonal variation in the flux of algal pigments to a deep-water site in the Panama Basin. Hydrobiologia *122*: 193-197.

Cowie, G. L. and J. I. Hedges. 1984. Carbohydrate sources in a coastal marine environment. Geochim. Cosmochim. Acta *48*: 2075-2087.

Deuser, W. G. and E. H. Ross. 1980. Seasonal change in the flux of organic matter to the deep Sargasso Sea. Nature *283*: 364-365.

Deuser, W. G. , E. H. Ross, and R. F. Anderson. 1981. Seasonality in the supply of sediment to the deep Sargasso Sea and implications for the rapid transfer of matter to the deep ocean. Deep-Sea Research *28*: 495-505.

Deuser, W. G., F. E. Muller-Karger, R. H. Evans, O. B. Brown, W. E. Esaias, and G. C. Feldman. 1990. Surface-ocean color and deep-ocean carbon flux: how close a connection? Deep-Sea Res. *37*: 1331-1343. *[The (expected) temporal lag between increased Chl a in the surface and the flux to sediment traps is documented]*

Graf, G. 1989. Benthic-pelagic coupling in a deep-sea benthic community. Nature *341*: 437-439.

Hargrave, B. T. 1980. Factors affecting the flux of organic matter to sediments in a marine bay. Pp. 243-264 *in* K. R. Tenore and B. C. Coull, *eds*. Marine Benthic Dynamics. U. S. Carolina Press, Columbia.

Harrold, C, K. Light, and S. Lisin. 1998. Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. Limnol. Oceanogr. *43*: 669-678. *[Marcoalgae can account for 20-83% of POC reaching the 400-m seafloor]*

Hedges, J. I., W. A. Clark, and G. L. Cowie. 1988a. Organic matter sources to the water column and surficial sediments of a marine bay. Limnol. Oceanogr. *33*: 1116-1136.

Hedges, J. I., W. A. Clark and G. L. Cowie. 1988b. Fluxes and reactivities of organic matter in a marine bay. Limnol. Oceanogr. *33*: 1137-1152. *[Dabob Bay WA]*

Honjo, S., S. J. Manganini, and C. J. Poppe. 1982. Sedimentation of lithogenic particles in the deep ocean. Marine Geology *50*: 199-219.

Honjo, S., S. J. Manganini, and J. C. Cole. 1982. Sedimentation of biogenic matter in the deep ocean. Deep-Sea Res. *29*: 609-625.

Ittekkot, V., W. G. Deuser, and E. T. Degens. 1984. Seasonality in the fluxes of sugars, amino acids, and amino sugars to the deep ocean: Sargasso Sea. Deep-Sea Res. *31*: 1057-1069.

Knauer, G. A., D. G. Redlaje, W. G. Harrison and D. M. Karl. 1990. New production at the VERTEX time-series site. Deep-Sea Res. *37*: 1121-1134.

Lampitte, R. S. 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Res 32: 885-897.

Longhurst, A. R., A. W. Bedo, W. J. Harrison, E. J. Herd, and D. Sameoto. 1990. Vertical flux of respiratory carbon by diel migrant biota. Deep-Sea Res. *37*: 685-694. *[20-430 mg C m^{-2}d^{-1} or 13-58% of computed particulate sinking flux]*

Lorenzen, C. J. and N. A. Welschmeyer. 1983. The in-situ sinking rates of herbivore fecal pellets. J. Plankton Research *5*: 929-933. *[w$_s$=31 to 122 m d^{-1}, with mean=87 m d^{-1}]*

Lorenzen, C. J., N. A. Welschmeyer, and A. E. Copping. 1983. Particulate organic carbon flux in the subarctic Pacific. Deep-Sea Research *30*: 639-643. *[7% of primary production leaves the euphotic zone; only 3.7% reaches the seafloor; and only 0.04% incorporated into sediments.]*

Lorenzen, C. J., N. A. Welschmeyer, A. E. Copping, and M. Vernet. 1983. Sinking rates of organic particles. Limnol. Oceanogr. *28*: 766-769. *[9.2 m d^{-1}]*

Michaels, A. F. and M. W. Silver. 1988. Primary production, sinking fluxes and the microbial food web. Deep-Sea Res. *35*: 473-490.

Michaels, A. F. and M. W. Silver. 1988. Primary production, sinking fluxes and the microbial food web. Deep-Sea Res. *35*: 473-490.

Pace, M. L., G. A. Knauer, D. M. Karl, and J. H. Martin. 1987. Primary production and vertical flux in the eastern Pacific Ocean. Nature *325*: 803-804. *[Primary production measured with trace-metal clean methods and coupled to POC flux to sediment traps]*

Prahl, F. G. and R. Carpenter. 1979. The role of zooplankton fecal pellets in the sedimentation of polycyclic aromatic hydrocarbons in Dabob Bay, Washington. Geochim. Cosmochim Acta *43*: 1959-1972.

Prahl, F. G., G. Eglinton, E. D. S. Corner. and S. C. M. O'Hara. 1984. Copepod fecal pellets as a source of dihydrophytol in marine sediments. Science *224*: 1235-1237.

Prahl, F. G., G. Eglinton, E. D. S. Corner, and S. C. M. O'Hara. 1985. Faecal lipids released by fish feeding on zooplankton. J. mar. biol. Ass. U.K. *65*: 547-560.

Reimers, C. E. and E. Suess. 1983. The partitioning of organic carbon fluxes and sedimentary organic matter decomposition rates in the ocean. Marine Chemistry *13*: 141-168.

Shanks, A. L. and J. D. Trent. 1980. Marine snow: sinking rates and potential role of vertical flux. Deep-Sea Research *27*: 137-143.

Suess, E. 1980. Particulate organic carbon flux in the oceans – surface productivity and oxygen utilization. Nature *288*: 260-263.

Thunnell, R. C., W. B. Curry, and S. Honjo. 1983. Seasonal variation in the flux of planktonic Foraminifera: time series sediment trap results from the Panama Basin. Earth planet. Sci. Letts. *64*: 44-55.

Tromp, T. K., P. van Capellen and R. M. Key. 1995. A global model for the early diagenesis of organic carbon and organic phosphorus in marine sediments. Geochim. Cosmochim. Acta *59*: 1259-1284. *[A general diagenetic model is presented incorporating organic matter input, advection, particle mixing by bioturbation, porewater diffusion, organic matter degradation by aerobic respiration, sulfate reduction and methanogenesis]*

Vezina, A. F. and T. Platt. 1987. Small-scale variability of new production and particulate fluxes in the ocean. Can. J. Fish Aquat. Sci. *44*: 198-205. *[A non-linear model of sedimentation; particulate losses amount to 30-40% of production in oligotrophic systems. This rate is much higher than the 5% to 10% rate implied by Eppley's New: Total production estimates and the analogy that the gyres are chemostats.]* {**18**}

Wakeham, S. G. 1982. Organic matter from a sediment trap experiment in the equatorial North Atlantic: wax esters, steryl esters, triacylglycerols, and alkyldiacylglycerols. Geochim. cosmochim. Acta *46*: 2239-2257.

Wakeham, S. G., J. W. Farrington, R. B. Gagosian, C. Lee, H. DeBaar, G. E. Nigrelli, B. W. Tripp, S. O. Smith and N. M. Frew. 1980. Organic matter fluxes from sediment traps in the equatorial Atlantic Ocean. Nature *286*: 798-800.

ON THE FLUX OF PHOTOSYNTHETIC PIGMENTS & GRAZING BUDGETS

Comment:

Randy Shuman and Carl Lorenzen, his doctoral advisor, discovered that Chl *a* is converted to pheophorbide *a* as phytoplankton cells are processed in the guts or phagocytic vesicles of grazers. Since macrozooplankton feces sink and microzooplankton feces do not, the sediment-trap flux of pheophorbide *a* provides an estimate of macrozooplankton grazing. Nick Welschmeyer and Jan Downs (Downs and Lorenzen 1985) continue to work on balancing the pelagic grazing budget using pigment fluxes. (Welschmeyer & Lorenzen (1985) estimated the grazing budget of a coastal system, Dabob Bay WA state, and the N. and South Central Pacific gyres. Conover *et al.* (1986) have questioned the stoichiometric conversion of Chl *a* to pheophorbide *a* assumed in much of this work.

Carpenter, S. R., P. R. Leavitt, J. J. Elser, and M. M. Elser. 1988. Chlorophyll budges: response to food web manipulation. Biogeochemistry *6*: 79-90. *[The Shuman-Welschmeyer-Lorenzen method is used to study grazing rates after fish are added to an aquatic system.]*

Conover, R. J. R. Duvasula, S. Roy, and R. Wang. 1986. Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton and some of the consequences. Limnol. Oceanogr. *31*: 878-886.

Downs, J. N. and C. J. Lorenzen. 1985. Carbon: pheopigment ratios of zooplankton fecal pellets as an index of herbivorous feeding. Limnol. Oceanogr. *30*: 1029-1036.

Emerson, C. W. and J. C. Roff. 1987. Implications of fecal pellet size and zooplankton behavior to estimates of pelagic-benthic carbon flux. Mar. Ecol. Prog. Ser. *35*: 251-257.

Shuman, F. R. and C. J. Lorenzen. 1975. Quantitative degradation of chlorophyll *a* by a marine herbivore. Limnol. Oceanogr. *20*: 580-586.[?]

Shuman, F. R. 1978. The fate of phytoplankton chlorophyll in the eupotic zone: Washington coastal waters. Ph.D. dissertation, U. of Washington. 250 p. *[Shuman, under Lorenzen's direction, introduced the use of the pheophorbide flux method for estimating macrozooplankton grazing.]*

Welschmeyer, N. A. and C. J. Lorenzen. 1985. Role of herbivory in controlling phytoplankton abundance: annual pigment budget for a temperate marine fjord. Marine Biology *90*: 75-86.

ON SEDIMENT TRAPS

Comments

Many of the above papers use sediment traps. Garnder's Ph.D. dissertation and subsequent papers analyzed the hydrodynamics of sediment traps. **Butman *et al.* (1986)** reevaluated this work. There are many other potential sources of systematic errors in sediment-trap work including animals which choose to feed near traps. These papers present some of the problems and guidelines for use of these sampling devices:

Butman, C. A., W. D. Grant, and K. D. Stolzenbach. 1986. Predictions of sediment trap biases in turbulent flows: a theoretical analysis based on observations from the literature. J. Mar. Res. *44*: 601-644. *[Sediment traps are inherently biased sampling devices, oversampling or undersampling particle flux based on the interaction of the trap with mean water flow and turbulence and the fall velocities of the particles. At a slow flow velocity, a trap could oversample slow sinking particles. At a higher flow velocity, the trap might undersample both fast- and slow-sinking particles].*

Butman, C. A. 1986. Sediment trap biases in turbulent flows: results from a laboratory flume study. J. Mar. Res. *44*: 645-693.

Gardner, W. D. 1977. Fluxes, dynamics and chemistry of particulates in the ocean. Ph.D. dissertation, WHOI/MIT.

Gardner, W. D., K. R. Hinga, and J. Marra. 1983. Observations on the degradation of biogenic material in the deep ocean with implications on the accuracy of sediment trap fluxes. J. mar. Res. *41*: 195-214.

N$_2$ FIXATION IN THE GYRES

Fuhrman, J. A. and D. G. Capone. 2001. Nifty nanoplankton. Nature *412*: 593-594. *[A news comment on the discovery by **Zehr et al. (2001)** of a nanobacterial sized (3-10 μm) nitrogen fixer identified using a gene probe. The bacterial groups include nanoplanktonic cyanobacteria and proteobacteria]*

Zehr, J. P., J. B. Waterbury, P. J. Turner, J. P. Montoya, E. Omoregie, G. F. Steward, A. Hansen, and D. M. Karl. 2001. Unicellular cyanobacteria fix N$_2$ in the subtropical North Pacific. Nature *412*: 635-638. *[In addition to large mats of the cyanobacterium Trichodesmium, there are abundant nanoplanktonic-sized nitrogenase containing cyanobacteria at the ALOHA time series site in the North Pacific gyre.]* {?}

MESOSCALE EDDIES, CYCLONES, HURRICANES & GYRE PRODUCTION

Jenkins, W. J., D. J. McGillicuddy, and D. E. Lott. 2008. The distributions of, and relationships between, ^{3}He and nitrate in eddies. Deep-Sea Research II *55*: 1389-1397. *[A cyclonic and anticyclonic eddy are evaluated. The cyclonic eddy has enhance vertical nitrate flux]*

McGillicuddy, D. J., Jr., R. Johnson, D. A. Siegel, A. F. Michaels, N. R. Bates, and A. H. Knap. 1999. Mesoscale variations of biogeochemical properties in the Sargasso Sea, J. Geophys. Res., 104(C6), 13381-13394.[?]

McGillicuddy, D. J., Jr., A. R. Robinson, D. A. Siegel, H. W. Jannasch, R. Johnson, T. D. Dickey, J. McNeil, A. F. Michaels, and A. H. Knap. 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. Nature *394*: 263-266.[?]

McNeil, J. D., H. W. Jannasch, T. Dickey, D. McGillicuddy, M. Brzezinski, and C. M. Sakamoto. 1999. New chemical, bio-optical and physical observations of upper ocean response to the passage of a mesoscale eddy off Bermuda, J. Geophys. Res., 104(C7), 15537-15548.[?]

MISCELLANEOUS

Comment:

Several of these papers deal with methodological problems with the ^{14}C method. A fuller set of papers can be found in Gallagher's Chapter 8.

Fitzwater, S. E., G. A. Knauer, and J. H. Martin. 1982. Metal contamination and its effect on primary production estimates. Limnol. Oceanogr. *27*: 544-551. *[Small concentrations of metals (200 ng/l) were shown to have drastic effects on production estimates. The major source appeared to be `dirty' sampling procedures and contaminated stock solutions of chemicals. Note that* **Marra & Heineman (1984)** *and* **Cullen *et al.* (1986)** *Were unable to detect a toxic heavy metal effect in their gyre productivity studies]* {**3**, **21**}

Harris, G. P, F. B. Griffiths, and D. P. Thomas. 1989. Light and dark uptake and loss of ^{14}C: methodological problems with productivity measurements in oceanic waters. Hydrobiologia *173*: 95-105. *[Dark uptake ≈ light uptake in oligotrophic waters. Therefore, investigators should subtract the dark bottle. Banse had noted this earlier in the 1989 ASLO meeting in Alaska.]* {**4**, **24**}

Prakash, A., R. W. Sheldon, and W. H. Sutcliffe. 1991. Geographic variation of ^{14}C dark uptake. Limnol. Oceanogr. *36*: 30-39 *[A 20-y old data set is used to show that ^{14}C dark uptake, normally about 10% of light, increases to over 50% in gyres and southern ocean. Absolute dark uptake rates increase as well. Many of the excessivelyh high estimates of gyre production might have been due to a failure to subtract the blank.]* {?}

Index