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# MICROPHYTOBENTHIC PRODUCTION & CARBON LIMITATION

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# Assignment

## Topic

What limits the standing stock and production of benthic diatoms?

## Required papers

Gould, D. G. and E. D. Gallagher. 1990. Field measurement of specific growth rate, biomass and primary production of benthic diatoms of Savin Hill Cove, Boston. Limnol. Oceanogr. *35*: 1757-1770.

## Supplemental

Admiraal, W. 1984. The ecology of estuarine sediment-inhabiting diatoms. Prog. Phycol. Res. *3*: 269-322. *[Please read pages 269-287 {several pages are merely species lists} and pp. 296- 297]*

Admiraal, W., H. Peletier, and H. Zomer. 1982. Observations and experiments on the population dynamics of epipelic diatoms from an estuarine mudflat. Estuarine, Coastal and Shelf Science *14:* 471-487.

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Cahoon, L. B., G. R. Beretich, C. J. Thomas, and A. M. McDonald. 1993. Benthic microalgal production at Stellwagen Bank, Massachusetts Bay, USA. Mar. Ecol. Prog. Ser. *102*: 179-185.

Glud, R. N, M. Kühl, F. Wenzhöfer, and S. Rysgaard. 2002. Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production. Mar. Ecol. Prog. Ser. *238*: 15-29.

Ludden, E, W. Admiraal, and F. Colijn. 1985. Cycling of carbon and oxygen in layers of marine microphytes: a simulation model and its ecophysiological implications. Oecologia *66*: 50-59.

Redalje, D. G. and E. A. Laws. 1981. A new method for estimating phytoplankton growth rates and carbon biomass. Marine Biology *62*: 73-79.

Serôdio, J. and F. Catarino. 2000. Modelling the primary productivity of intertidal microphytobenthos: time scales of variability and effects of migratory rhythms. Mar. Ecol. Prog. Ser. 192: 13-30. *[Model of Tagus estuary Portugal using P vs. I curves and vertical migration. Variable fluorescence measured. 156 gCm$^{-2}$y$^{-1}$ production. Oxygen microelectrodes and fast repetition rate fluorescence measurements made on intact cores.] [4, 31]*

Comments on the readings & DIC Limitation

In shallow neritic waters, microphytobenthic production can often exceed water-column production. For example, **De Jonge (1994)** produced estimates of benthic and pelagic production for the shallow Dutch Ems-Dollard estuaries (Figure 1). A major loss term from the intertidal was erosion. Benthic diatoms continue to photosynthesize when eroded from the sediment-water interface by storms. He produced a carbon budget for the Dutch Ems-Dollard estuary (mean depth 1.2 m) showing that 25% of the total estuarine primary production is due to resuspended benthic diatoms, 53% by true phytoplankton, and 22% by benthic diatoms living on mudflats. **Jahnke et al. (2000)** found that microphytobenthic production on the Carolina shelf at depths of 14 to 40 meters was quite high 400 (±260) mgCm$^{-2}$d$^{-1}$ and comparable to pelagic production.

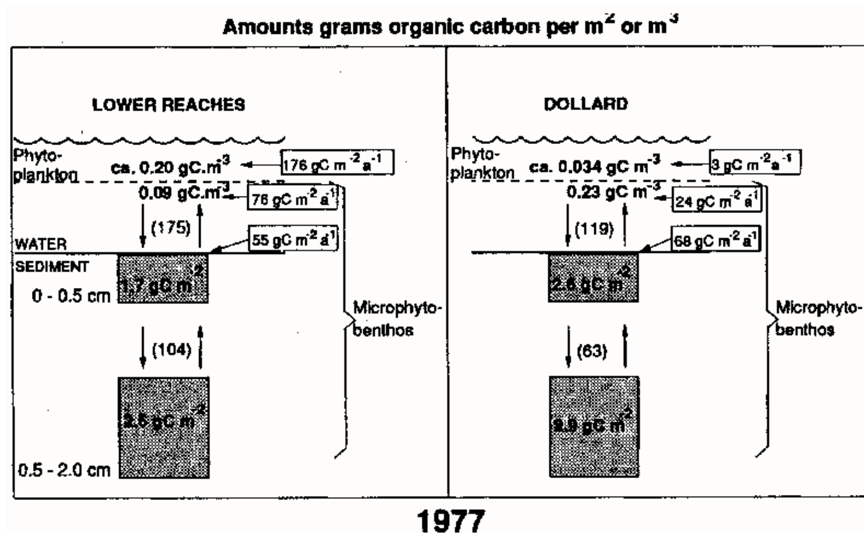


**Figure 1**. Primary production and average standing stocks in the lower reaches and Dollard portions of the Ems-Dollard estuary (from de Jonge 1994). In both regions, the microphytobenthos dominates biomass. In the shallow region, the production from the microphytobenthos (68 gC m$^{-2}$ y$^{-1}$) or resuspended microphytobenthos (24 gC m$^{-2}$ y$^{-1}$) is 31 times production by true phytoplankton (3 gC m$^{-2}$ y$^{-1}$).

Many surface and subsurface deposit feeders in shallow-water environments meet most of their food requirements by feeding on benthic diatoms. **Hentschel & Jumars (1994)** hypothesize that deposit feeders which can live on low-quality organic matter as adults may require nutritionally rich food, like benthic diatoms, as juveniles. Benthic diatom standing stock may be a better

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indicator of the nutritional quality of sediment than organic carbon concentration. Benthic diatoms—rich in the nitrogen, fatty acids, and essential amino acids required by many deposit feeders (**Phillips 1984**, **Marsh & Tenore 1990**)—are much more abundant in the intertidal than subtidal benthos.

## MODELING BENTHIC DIATOM PRODUCTION

**Serôdio & Catarino (2000)** present a truly remarkable field and modeling study of factors controlling epipelic diatom production. They measured the dark-level Chl *a* fluorescence ($F_o$) using a pulse-probe fluorometer. $F_o$ measures the increase in microphytobenthic biomass at the sediment-water interface as the epipelic diatoms vertically migrate to the surface. It also measures the shift up in the microphytobenthic photosystems as they acclimate to higher light intensities. Production was measured using the Revsbech & Jørgensen $O_2$ microelectrode method (**Revsbech et al. 1981** & **1986**, **Revsbech & Jørgensen 1983**) (see Figure 2).

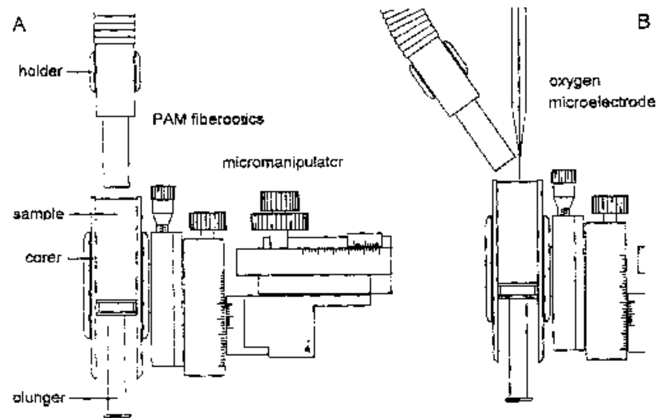


Fig. 1. The set-up used for (A) measuring chl *a* fluorescence, using a PAM fluorometer, and for (B) measuring photosynthesis, using oxygen microelectrodes, on undisturbed microphytobenthic samples. When measuring photosynthetic rates, the PAM fiberoptics is used to illuminate the sample surface

**Figure 2**. Fig. 1 from **Serôdio & Catarino (2000)**

**Serôdio & Catarino (2000)** modeled the P vs. I curves for epipelic diatoms and modeled the effects of both the diel and tidal vertical migrations of these diatoms. The combined effects of tides, diatom vertical migration and light on hourly production are shown in Figure 3.

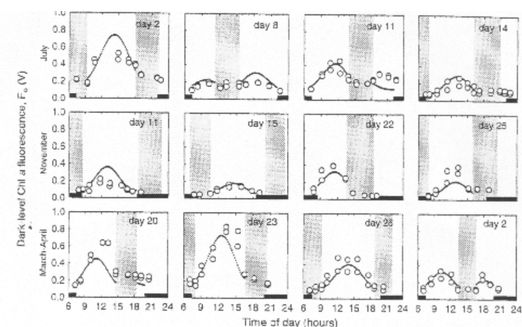


Fig. 5. Hourly variation of dark-level chl *a* fluorescence, $F_o$, during 3 spring-neap tidal cycles: observations (O) and model predictions (Eq. 1, -----). Shaded bars represent periods of high tide and black bars represent night periods

**Figure 3**. Fig. 5 from **Serôdio & Catarino (2000)**

**Serôdio & Catarino (2000)** used their model to predict that there is as much hourly and weekly variability in benthic primary production as there is seasonally. They calculated the annual primary production of the epipelic diatoms as 156 $gCm^{-2}y^{-1}$.

## A BRIEF OVERVIEW OF PAM FLUORESCENCE

The goal of the PAM fluorometric method is to estimate Chl *a* concentration and the rate of reaction of Photosystem II, the photosystem responsible for much of the fluorescent signal in intact phytoplankton cells.

The PAM fluorometer emits two different light signals from its fiberoptic probe. First there is a very low intensity red light measuring beam that is switched on and off rapidly (approximately 5-

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µs interval). The number of photons produced is insufficient to noticeably alter Photosystem II activity, but a fluorescent signal will be emitted in phase with the 'modulating' measuring light. The baseline fluorescence emitted is called $F_o$ and is usually linearly related to Chl *a* concentration.

In cells with low Photosystem II activity, the PSII reaction centers are 'closed,' and much of the absorbed light from the measuring beam is returned as fluorescent light (see Fig. 4). The fluorescent yield, or ratio of emitted fluorescent light to absorbed light, is high. In actively photosynthesizing cells, the electron transport rate is high in Photosystem II, and much of the absorbed light can be converted to chemical energy and not emitted as fluorescence, a process called photochemical quenching. The fluorescence yield is low.

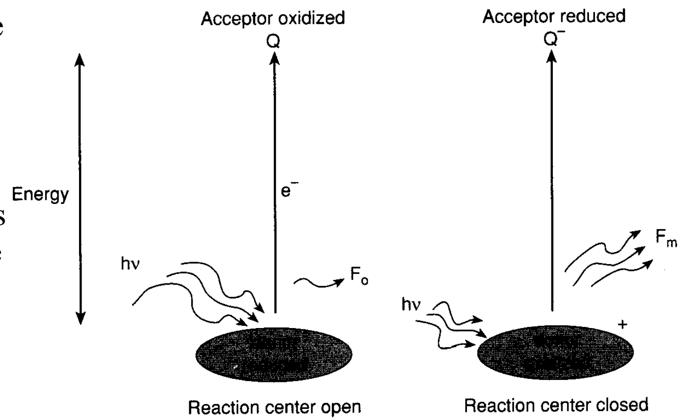


**Figure 4**. Fig. 3.11 from **Falkowski & Raven (1997)**

After measuring $F_o$ with the PAM fluorometer, a bright light is emitted from the fiber optic cable of the PAM fluorometer. The PSII reaction centers exposed to this high intensity bright white light (actinic light) will be reduced and unable to process and photochemically quench additional photons. Photons still being absorbed by the photosynthetic pigments will be emitted as fluorescent light. The fluorescent light emitted after the actinic light is added is called $F_m$.

Variable fluorescence, $F_v$, is defined as $F_v = (F_m - F_o)/F_m$. In senescent photoautotrophic cells, the PSII reaction centers were essentially closed to begin with, and there is little difference between $F_o$ and $F_m$, so $F_v$ will be low, usually much less than 0.75. In actively photosynthesizing cells, $F_v$ will be large. $F_v$ is generally linearly related to PSII activity and thus gross photosynthetic rate. $F_v$ * Photosynthetically available radiation is usually linearly related to photosynthetic rate.

## Is benthic diatom production limited by DIC flux?

Benthic diatoms evolved in a habitat with a thick molecular diffusive boundary: the sediment-water interface. The key physiological adaptation controlling the growth of benthic diatoms is their ability to fix carbon under conditions of very low $CO_2$ and high $O_2$ (**Admiraal 1984**, **Ludden *et al.* 1985**). The low $CO_2$ concentration is due both to highly alkaline pH at the sediment water interface, caused by microphytobenthic production, and depletion of total dissolved inorganic carbon (DIC) concentrations. Some of these physiological mechanisms, both biochemical and morphological, for coping with low $CO_2$ and high $O_2$ are also found in pelagic diatoms. These physiological mechanisms include a bicarbonate pump using carbonic anhydrase (CA), and high rates of β-carboxylation. Benthic diatoms are well adapted for coping with low $CO_2$ and high $O_2$ concentrations. The evidence is strong that high rates of $HCO_3^-$ uptake and β-carboxylation are the rule rather than the exception in the microphytobenthos (**Zimba *et al.* 1990**).

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While it is generally thought that DIC could never limit pelagic production, **Riebessel *et al.* (1993)** argue that DIC could be a limiting factor for large diatoms during spring blooms. The increase in atmospheric $CO_2$ concentrations since the last ice age could lead to conditions more favorable to diatom growth during blooms.

### *Evidence for DIC limitation of microphytobenthic production*

Admiraal and coworkers (e.g., **1982**, **1984**), **Ludden *et al.* (1985)** and **Gould & Gallagher (1990)** concluded that benthic diatom growth may be limited by the availability of inorganic carbon, or perhaps high $O_2$ leading to inhibition of photosynthesis (the Warburg effect). Conducting an experiment that can separate the effects of high $O_2$ concentrations from low DIC concentrations is very difficult. **Admiraal (1984, pp. 296-297)** briefly summarizes his evidence. **Admiraal *et al.* (1982)** and **DeJong & Admiraal (1984)** provide the most detailed discussion of the laboratory experiments, mostly bicarbonate enrichment of laboratory batch cultures of benthic diatoms, that led to the unorthodox conclusion that carbon, or the inhibitory effects of high $O_2$, limits microphytobenthic photosynthetic rates. Admiraal found that the growth rate and standing stock of benthic diatoms in laboratory cultures was a strong function of both pH and DIC concentration. The pH of the stagnant layer overlying cultured diatoms reached 9.9 (**DeJonge & Admiraal 1984, p. 270**). The additions of the traditional photoautotrophic macronutrients (N, P, and Si) did not affect growth.

To date, only the Dutch investigators have proposed the DIC limitation hypothesis. In the US, most investigators cite studies arguing for nitrogenous limitation of diatom growth. Van Raalte *et al.* (1976) found higher primary production and epibenthic Chl *a* concentrations in areas of Sippewissett marsh (MA) experimentally enriched in nitrogen (sewage sludge and urea). Most of this increased Chl *a* was probably due to increases in macroalgal standing stock (*e.g.*, green algae) and not microphytobenthic standing stock. **Nilsson *et al.* (1991)** also documented increases in phytobenthos in response to nitrogen enrichment in a laboratory mesocosm. Interestingly, the increased production in both studies was coupled mainly to increased growth of *Ulva* and *Enteromorpha* and not to benthic diatoms.

**Höpner & Wonneberger (1985)** concluded that increased microphytobenthic production was directly coupled to increased diffusive flux of nitrogen and phosphorous and porewater. They estimated the concentration gradients of DIN and DIP in porewater, calculated the diffusive flux from Fick's 1st law and compared it with measurements of primary production. There was a strong positive association between them. They also measured the ratio of DIN and DIP supply from porewater and compared it to primary production rate (their Fig. 10). They state, based on their Fig. 10:

> *"We conclude, therefore, that nutrient effluxes from the sediment are patchiness-governing in such a way that epiphytobenthos-growth is favoured most when the N:P molar ratio fits the ratio needed for biomass formation. However data pairs fulfilling this condition are also pairs with the highest effluxes (P. 283)"*

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Their observations may appear to directly contradict Admiraal's DIC-limitation hypothesis, but in fact are consistent with it. Epipelic diatoms acquire most of their DIN and DIP from porewater, and influence the DIN and DIP gradients and fluxes (Sundback & Graneli 1981). Higher diatom production, caused by any process, depletes macronutrient concentrations at the sediment-water interface. The resultant concentration gradient drives higher fluxes of porewater DIN and DIP from porewaters to the sediment-water interface. When diatom production is high, these diatom-driven fluxes are more in accord with Redfield stoichiometry. Thus, **Höpner & Wonneberger's (1985)** close correlation of nutrient efflux with primary production rate is consistent with the DIC limitation hypothesis.

Another experiment conducted by **Höpner & Wonneberger (1985)** provides a more clear-cut test of the DIC theory. They added DIN and DIP in a subsurface layer in September 1982 and 1983. They observed a surface bloom of diatoms, relative to a disturbed but unfertilized control area, in 1982 but not in 1983. They discuss the 1982 fertilization experiment,

> *"...we had the pleasure to observe the formation of a magnificent diatom bed, which followed exactly the borders of the fertilized area. It had fully developed 14 days after fertilization (September 11, 1982) and remained visible for another 6 weeks, until it disappeared in a rich diatom bloom covering the whole neighborhood."*

Their nutrient enrichment facilitated the appearance of the fall bloom, which occurred throughout the mudflat. The DIC limitation theory predicts that such fall blooms in standing stock (not production) are characteristic features of temperate mudflats. Their fertilization experiment was not replicated, nor were surface production, cell numbers or composition, of Chl *a* measured. They summarized these two experiments in their abstract,

> *"The formation of a diatom bed at the fertilized area was observed once, but efforts to reproduce it failed, indicating the importance of other growth-determining conditions."*

The effect of nitrogen limitation on benthic diatom standing stock and production are important issues. Sundback *et al.* (in press) found that in laboratory mesocosm experiments N and P addition favors increases in large diatom cells. **Gould (1989)** found fall blooms of very large pennate diatoms (*Pleurosigma*, >300 µm). Such increases in large pennate diatoms, if they are less vulnerable to benthic grazing and have lower specific growth rates, could lead to increases of standing stock, as recorded by **Höpner & Wonneberger (1985)**, without increases in either specific or total production.

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### *Ludden et al.'s (1985) simulation model*

**Ludden *et al.* (1985)** analyzed the processes controlling benthic diatom growth with a computer simulation model. This model is highly unusual in biological oceanography, since DIC is the sole limiting nutrient. They assumed that benthic diatoms **must** have $C_4$-type (or C-4 like) metabolism, achieved through an active bicarbonate pump. **Ludden *et al.* (1985)** did not assume that $C_4$ compounds are the being fixed by PEPCase as in true $C_4$ Hatch-Slack or CAM metabolism. The microphytobenthos in their model are capable of taking up $HCO_3^-$, which is converted to $CO_2$ by intracellular CA. If the microphytobenthos take up $HCO_3^-$, they must achieve both intracellular charge and pH balance. High production of hydroxyl ion, resulting from high CA activity, could produce high intracellular pH, especially in cells with large volume: surface ratios. Alkaline intracellular pH can limit growth and is a potentially growth-limiting parameter in **Ludden *et al.* 's (1985)** model.

**Ludden *et al.*'s (1985)** model shows why benthic species using an active bicarbonate pump dominate on intertidal flats. Microphytobenthos using bicarbonate utilization can easily outcompete a true $C_3$ benthic diatom, using only $CO_2$ diffusion through the cell membrane, RuBPCO and the Calvin cycle. The microphytobenthic diatoms reduce drastically the seawater DIC pools and raise the pH to 9 or even 10.5, virtually eliminating any free $CO_2$ (aqu). Thus, not only can the species using both $CO_2$ and bicarbonate deplete the DIC supply for the $C_3$ species through exploitative competition, but they also excrete one hydroxyl ion ($OH^-$) for every $HCO_3^-$ incorporated, drastically reducing the percentage of DIC available as $CO_2$ (aqu) to true $C_3$ diatoms.

One part of **Ludden *et al.*'s (1985)** model of diatom production is probably wrong. When an anaerobic sediment layer is added, **Ludden *et al.*'s (1985)** model showed that most of the dissolved inorganic carbon (DIC) flux supplying microphytobenthic production is from the sediment porewater to the benthic diatom film. Only under high benthic diatom densities is there a flux from the overlying water to the film, but even then, this downward flux is less than that from the porewater. The source of DIC is very important to benthic productivity measurements. If most of the DIC flux fueling microphytobenthic production is from porewater, methods for estimating microphytobenthic production, that are based on $^{14}C$-labeled surface water, would underestimate production.

**Ludden *et al.* (1985)** assumed that the diffusive-layer thickness beneath the diatoms is only 1 mm. This thickness is far too small. Biologically enhanced molecular diffusion operates over the entire depth of the sediment surface, not 1 mm. **Aller (1982)** reviewed the diffusion geometry of sediments. Most workers model that vertical diffusion of solutes in cohesive sediments as a molecular diffusive process, accelerated by infaunal irrigation and reduced by sediment porosity. Users of one-dimensional diffusion models increase the apparent diffusion coefficient of solutes by 10 to 100-fold to simulate the effects of bio-irrigation. Without animals, solutes diffuse according to Fick's law (with molecular diffusion coefficients reduced by sediment porosity) over the entire depth of the sediment column, not 1 mm as modeled by **Ludden *et al.* (1985)**. This 1-mm diffusive sublayer thickness in sediments would have to produce tremendous

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overestimates of the contribution of porewater DIC flux to the diatoms photosynthesizing at the sediment surface.

## THE IMPORTANCE OF MOLECULAR DIFFUSIVE BENTHIC BOUNDARY LAYERS

The diffusive sublayer is always smaller than the viscous sublayer, since chemicals diffuse more slowly than does momentum. The ratio of kinematic viscosity ($\approx 10^{-2} cm^2 s^{-1}$) to chemical molecular diffusivity (for $CO_2$ about $10^{-5}$ $cm^2 s^{-1}$ at 0ºC, 1.77 x $10^{-5}$ at 25ºC) is known as the Schmidt number and is about 600-1000 for $CO_2$. The ratio of the diffusive sublayer to the viscous sublayer thickness scales linearly to the Schmidt number to the one third power (**Wimbush 1976, p. 8**). Thus the diffusive sublayer for $CO_2$ is roughly 1/8th to 1/10th the viscous sublayer thickness. Using $O_2$ microelectrodes, Jørgensen, Revsbech and co-workers (*e.g.*, Jørgensen & Revsbech **1985** & **1989**, **Revsbech et al. 1981**, **Revsbech & Jørgensen 1983**) have been able to directly measure the diffusive sublayer thickness.

Benthic diatoms live in a habitat where molecular diffusion through the diffusive sublayer at the benthic interface may be the limiting factor for the intracellular flux of inorganic carbon. The kinetic rate-limiting step in the recharging of the intracellular $CO_2$ pool is Fickean diffusion, probably through the 100-500 µm thick diffusive sublayer at the sediment water interface or through the much smaller capillary film surrounding diatoms completely exposed at low tide. Solutes must also diffuse through a relative thin mucopolysaccharide biofilm excreted by benthic diatoms. **Paterson (1989)** documented that the biofilm, produced by motile benthic pennate diatoms, is an extensive mucopolysaccharide matrix. This biofilm has extremely important effects on the critical entrainment velocity of cohesive sediments but is probably not that important as a kinetic barrier to DIC flux. This biofilm is relatively thin (far less than 10 µm as shown in **Paterson 1989**, Fig. 9D-F, Fig. 10B&F, see Fig. 5) compared to the thickness of diffusive water layer around the biofilm, which may range from 50-400 µm in moving water to 500 µm-1 mm in stagnant water (**Jørgensen & Revsbech 1985**).

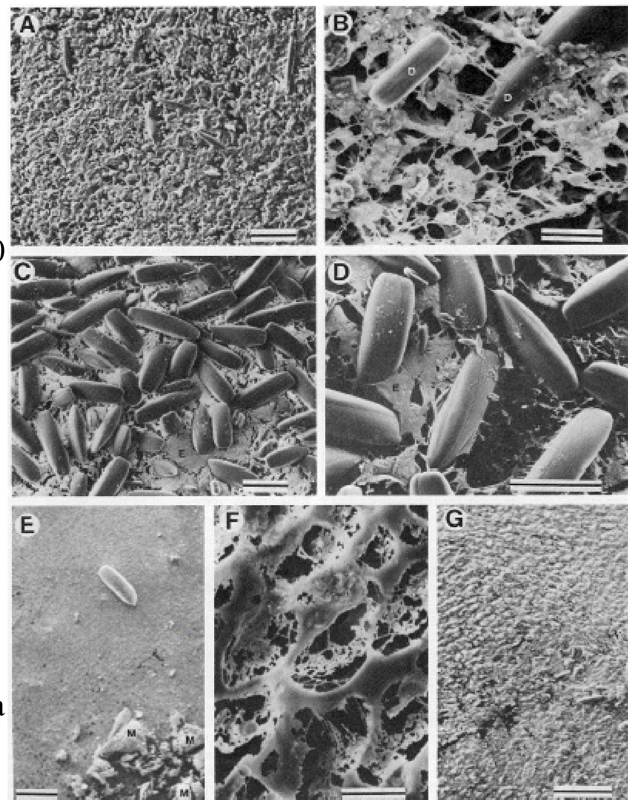


**Figure 5**. Figure 10 from Paterson 1989 showing the mucopolysacharide biofilm produced by benthic diatoms. The scale bar in frames B & F are 10 µm, the other scale bars are 100 µm.

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## *Stirring & production incubations*

Stirring and its effects on diffusional boundaries in benthic incubation chambers is an exceptionally important issue. **Gould & Gallagher (1990)** note that microphytobenthic production estimates with unstirred chambers are less than half those observed in stirred chambers. **Revsbech *et al.* (1981, p. 725)** also noted a two-fold increase in production with stirring. **Ludden *et al.* (1985)** modeled a 5-fold decrease in the thickness of the diffusive sublayer and also noted roughly a 2-fold increase in production of microalgae growing on solid surfaces.

The effect of stirring on diffusive flux estimates from chambers is crucial to the extrapolation of incubator estimates to the field (**Nowell & Jumars (1984, p. 312)**, but it is difficult to quantify the effects of stirring. The MANOP incubators, used to measure diffusive fluxes in the deep-sea benthos, are the only benthic flux chamber that have been calibrated. **Bucholtz-Ten Brink *et al.* (1989)** calibrated these chambers using alabaster dissolution and flush mounted hot-wire velocity sensors. Based on their work and an earlier flume study by **Opdyke *et al.* (1987)**, **Bucholtz-Ten Brink *et al.* (1989)** found a log-log relationship between $U_*$ diffusive sublayer thickness ($z_\delta$). Using their equation 8, the thickness of the diffusive sublayer ($z_\delta$ in µm) has the following relationship to $U_*$:

$$
\begin{aligned}
z_\delta &= a * U_*^{-.79}. \\
&\textit{where, a is calculated from molecular diffusion coefficient, D} \\
a &= 0.020 \ x \ 10^4 \ for \ D{=}1.7 \ x \ 10^{-5} cm^2 s^{-1}. \\
a &= 0.011 \ x \ 10^4 \ for \ D{=}1.0 \ x \ 10^{-5} cm^2 s^{-1}.
\end{aligned}
\qquad (1)
$$

As shown in Fig. 6, the diffusive sublayer thickness ($z_\delta$) declines rapidly as a function of $U_*$, and is relatively insensitive to increases in $U_*$ in excess of 1cm sec$^{-1}$. Depending on the molecular diffusivity (D), reduction of $U_*$ by stirring reduces the diffusive sublayer to a thickness of 100 to 200 µm at $U_*$ values of about 1.5 cm sec$^{-1}$. **Bucholtz-Ten Brink *et al.* (1989)** found a direct linear relation between stirring velocity (in r.p.m.) and $U_*$.

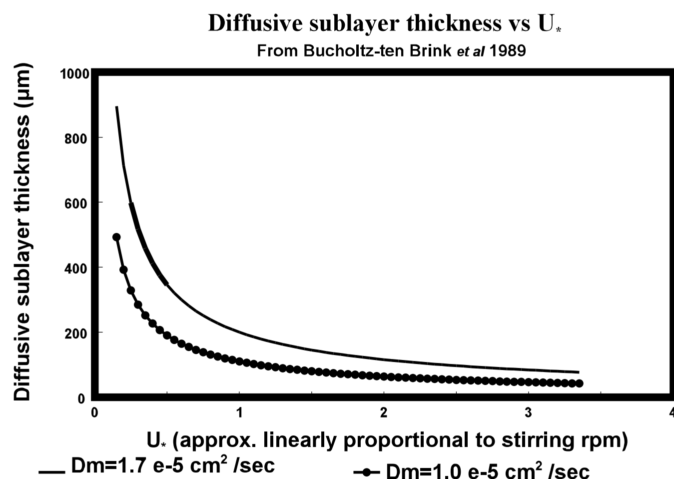


**Figure 6**. The relationship between $z_\delta$ (diffusive sublayer thickness) and $U_*$ (shear velocity) in the MANOP incubators.

Other studies confirm **Buchholtz-Ten Brink *et al.*'s (1989)** empirical relation between $z_\delta$ and $U_*$. Riber & Wetzel (1987) estimated the mass flux of radioactive phosphorous into lake periphyton (on microscope slides) as a function of water velocity. They noted that mass flux increased as a power function of water velocity, but the exponent was less

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than 1/3. Their documentation of exponents for increasing $PO_4$ flux in the range of 0.15 to 0.33 is consistent with a reduction of the diffusive sublayer to the -0.67 to -0.85 power, as found by **Bucholtz-Ten Brink (1989)**.

The geometry of the **Gould & Gallagher (1990)** incubator is considerably different than the MANOP incubator. With the present design, 5-mm plugs of sediment rest on petri dishes above the floor of the incubator. This undoubtedly creates smaller diffusive sublayers of varied thickness over the surface of the 5-mm plugs. As a slight improvement in this design, the plugs could be added to machined depressions in the bottom of the incubator. The goal of recessing the plugs would be to create more uniform boundaries over the surface of the diatom plugs, not thicker boundaries. Greater stirring speeds will be used to compensate for the differing plug geometries on the bottom of the incubators.

It is unlikely that the diffusive sublayer thicknesses in the **Gould & Gallagher (1990)** incubator could be decreased greatly by increased stirring. Sediment erosion sets the upper limit on stirring speeds in these incubators. Sandy-silt sediment will begin to erode at $U_{*cr}$ values greater than about 1.6 cm $sec^{-1}$ (**Nowell *et al.* 1981, Table II**). From these considerations and Fig. 3, I conclude that the diffusive sublayer overlying benthic diatoms films on smooth mud surfaces rarely decreases below about 100-200 µm. On hydrodynamically transitional boundaries, the enhanced shear produced by animal tubes and other roughness elements can create local patches of reduced diffusive boundary layer thickness (**Eckman & Nowell 1984**, **Eckman 1985**). The effect of these isolated tubes on the DIC flux to diatoms could provide the mechanistic explanation for the positive association between real and simulated tubes and macroinfaunal recruitment rates (**Eckman 1979**, **Gallagher *et al.* 1983**). The goal of stirring is to reduce the diffusive sublayer of approximately 500 µm-1 mm, which would occur in stagnant cores, to the range of 100-200 µm (and lower around tubes). The difference between stirred and stagnant film thicknesses could easily account for the 2-fold increases in production observed in stirred and unstirred incubators (**Gould & Gallagher 1990**, **Revsbech *et al.* 1981**). The thickness of this diffusive layer can probably not be reduced much below 100-200 µm without entraining sediment. **Gould & Gallagher (1990)** set the stirring rate at a point slightly below the stirring required to cause rocking or entrainment of biogenic particles on the sediment surface (≈1.2 cm $sec^{-1}$ in **Nowell *et al*. 1981**, Table II).

For diatoms growing in very thin water layers, the diffusive boundary at the sea-air interface, the sea-surface microlayer, becomes the key boundary. With thin overlying water layers, the recharging of the DIC pool through air-sea exchange must be considered as an important flux. The air-sea flux is controlled by Fickean diffusion through the air-sea microlayer. This diffusion is linearly related to the $\Delta pCO_2$ gradient times the microlayer thickness. **Frankignoulle (1988, Table 3)** estimated the air-sea surface microlayer thickness, in which diffusion is governed by Fick's law, as 48-200 µm in the Bay of Calvi and North Sea. Most of his microlayer thickness estimates ranged from 50 to 100 µm, close to the oceanic mean value of 40 µm quoted by **Broecker & Peng (1982)** based on ocean-atmosphere distributions of $^{222}Rn$ and $^{14}C$. Erikson (1989) found transfer velocities or piston velocities similar to those documented by **Broecker & Peng (1982)**. These microlayers are oceanic values; the air-surface microlayer on mudflats has apparently not been estimated.

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**Darley *et al.* (1976)**, **Darley *et al.* (1981)** and **Whitney & Darley (1983)** introduced techniques for estimating the production of microphytobenthic production through the air-water interface. By adding radioactively labeled $CO_2$ gas to incubators containing a fan, they estimated primary production rates of up to 245 mg C $m^{-2}$ $h^{-1}$. Their rates are among the highest ever recorded on mudflats and are more than double the maximum production rate noted by **Gould & Gallagher (1990)**. Their observed rate of air-to-sea carbon flux of 5.7 x $10^{-6}$ mol $m^{-2}s^{-1}$, with a $\Delta CO_2$ gradient of 340µatm $CO_2$, would require a gas exchange coefficient or piston velocity of 4.3 x $10^{-4}$ m/sec, using the following equation from **Frankignoulle (1988)**:

$$\begin{aligned} Flux &= K\ \alpha\ \Delta P. \\ where,\ K &= \text{"}piston\ velocity\text{"} \\ &= \frac{mol.\ diffusion\ coef.}{diff.\ layer\ thickness}. \\ \alpha &= CO_2\ solubility\ coefficient. \\ &\approx 39\ mol\ m^{-3}\ atm^{-1}. \\ \Delta P &= difference\ in\ CO_2\ partial\ pressure. \end{aligned} \qquad \textbf{(2)}$$

The effective molecular diffusive boundary associated with an air-to-diatom flux of 245 mgC$m^{-2}h^{-1}$ is only 4 - 10 µm thick. This boundary is approximately that shown by **Paterson (1989)** for the mucous biofilm surrounding pennate diatoms on mud. This 4-10 µm thick layer is only a fraction of the 40 µm thick molecular diffusive layer that occurs at the air-sea interface (Broecker & Peng 1974).

**Whitney & Darley (1983)** modified the air$^{14}C$-$CO_2$ incubator so that desiccation would be less of a problem. Their estimates of summertime production ranged from 4.1 mg $Cm^{-2}d^{-1}$ to 143.2 mg $Cm^{-2}d^{-1}$ on a Sapelo Island Georgia salt marsh. This latter estimate from a Creek bank may reflect the production of diatoms exposed directly to air, growing with an effective diffusive layer thickness of 7 to 14 µm.

If there is a water film overlying the sediments, the Darley technique can underestimate production, since with a typical air-sea microlayer thickness of 40 µm, a molecular diffusion coefficient of 2 x $10^{-9}$ $m^2$ $sec^{-1}$, an air-to-sea flux of only 36 mg C $m^{-2}h^{-1}$ is possible. Thus if there is a water layer of even fractions of a millimeter overlying the mudflat surface and zone of production, the Darley incubator would probably underestimate production. The surface of Savin Hill Cove is wet when the tide goes out, but the surface of Southern salt marshes and even Massachusetts salt marshes are relatively dry. Air incubation should be used if the sediment surface is dry during low tide. However, it probably should not be used if there is overlying water as is typical of Savin Hill Cove.

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## Redalje-Laws Chl *a*-specific labeling to estimate μ & C:Chl *a*

**Redalje & Laws' (1981)** Chl *a* specific labeling procedure is a very clever method for estimating two of the three major growth variables: μ and the C:Chl *a* ration. **Laws (1984)** provides one mathematical and biochemical model for the method.

**Table 1** shows the variables used in the calculation of the specific growth rate, using the Redalje-Laws procedure.

**Table 1.** Definitions and variables used in applying the Redalje-Laws approach (from **Gould & Gallagher 1990**)

| Variable | Units | Description |
|---|---|---|
| ΔC | $\frac{\mu g C}{sample \times time}$ | C fixed during incubation |
| μ | $\frac{1}{h}$ | specific growth rate |
| 1.05 | Dimensionless | Factor to account for isotope discrimination |
| $A^*$ | $\frac{dpm}{sample}$ | $^{14}C$ activity of total particulate matter |
| $C_p$ | $\frac{\mu g C}{sample}$ | Microalgal C at the end of the incubation |
| $I^*$ | $\frac{dpm}{\mu g C}$ | Specific activity of DIC |
| $R^*_{chl}$ | $\frac{dpm}{\mu g C}$ | Specific activity of C in Chl *a* molecule |
| t | h | duration of incubation in hours. |

A standard $^{14}C$ incubation is run, just as if the goal were merely to measure primary production. Usually the phytoplankton population would be split into two fractions after the incubation. One half of the sample would be used to estimate the radioactivity of the total phytoplankton fraction, called $A^*$ in Table 1. With $A^*$ and $I^*$, the specific activity of the dissolved inorganic carbon (DIC) in the incubation vessel, the amount of primary production can be determined using Equation 3:

$$\Delta C = \frac{1.05\ A^*}{I^*\, t} . \qquad \textbf{(3)}$$

Equation 3 is the same equation used for a standard $^{14}C$ incubation to estimate primary production (covered in the next class). To estimate μ, the radioactivity in the Chl *a* molecule must be determined. This was first done by using thin-layer chromatography of the photosynthetic pigments, but now the pigments are separated using HPLC. The Chl *a* fraction is

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removed, its mass estimated, and the amount of radioactivity is determined to estimate $R^*$. The amount of microalgal carbon at the end of the incubation can be determined from Equ 4.

$$C_p = \frac{A^*}{R^*}. \qquad \textbf{(4)}$$

The specific growth rate assuming a 12-h photic period to convert the hourly incubation timescale can be estimated using Equ. 5:

**Box 1** Derivation of the Redalje-Laws equation to estimate μ as $h^{-1}$. The equation multiplies the hourly rate by 12 to obtain the daily specific growth rate.

$$\mu = \frac{1}{C_p}\frac{dC}{dt}.$$

$$C_p = C_o\, e^{\mu t}.$$

$$ln\left(\frac{C_p}{C_o}\right) = \mu t.$$

$$\mu = \frac{-ln\left(\frac{C_o}{C_p}\right)}{t}.$$

$$\mu = \frac{-ln\left(\frac{C_p - \Delta C\, t}{C_p}\right)}{t}.$$

$$\mu = \frac{-ln\left(1 - \frac{\Delta C\, t}{C_p}\right)}{t}.$$

$$\mu = \frac{-ln\left(1 - \frac{\left(\frac{\frac{1.05\,A^*}{I^*}}{t}\right)t}{\frac{A^*}{R^*}}\right)}{t}.$$

$$\mu = \frac{-ln\left(1 - \frac{1.05\;R^*}{I^*}\right)}{t}.$$

$$\mu = \frac{-ln\left(1 - \left(\frac{1.05\,R^*}{I^*}\right)\right)}{t} \times 12. \qquad \textbf{(5)}$$

Equation 5 certainly looks daunting. It is based on the balanced growth assumption, which states that new Chl *a* is being labelled at the same rate as the total microalgal carbon pool. **Redalje (1983)** and **Goericke & Welschmeyer (1993a)** tested this assumption, finding it is not true if the microalgae are switched from low to high light, or when sun-adapted microalgae are switched to lower light. Shade adapted algae, with a low C:Chl *a* ratio, drastically curtail the synthesis of Chl *a* when placed in high light and the Redalje-Laws method can grossly underestimate μ. If the balanced growth assumption is true, then the amount of microalgal carbon in the incubation vessel, $C_p$, can be estimated from Equ. 4. With this estimate of $C_p$, Equation 16 can be readily derived from **Equation 1**. This derivation is shown in the text box to the left.

Redalje & Laws (**1981**, **Laws 1984**) derived the equation originally under the assumption that the Chl *a* molecule turns over rapidly so that Chl *a* would have the same specific activity as the total phytoplankton carbon pool. **Welschmeyer & Lorenzen (1984)** derived a mathematically equivalent expression, under the less restrictive assumption that the new Chl *a* that is synthesized during an incubation matches the specific activity of the total pool of organic carbon synthesized during the incubation. This assumption is called the balanced growth assumption. If this 'balanced growth' assumption is met, the Redalje-Laws method can estimate μ, phytoplankton carbon content, and

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the C:Chl *a* ratio. **Goericke & Welschmeyer (1993a)** experimentally showed that the Chl *a* molecule does not turn over at a significant rate during the course of an incubation, invalidating one of the original assumptions of the method, but not the equation (Equation 16). They derived a more complicated expression for estimating μ using the Chl *a* labeling method. Their major recommendation is to use long incubations (24 h) to estimate μ with Chl *a*-specific labeling. **Jesperson *et al.* (1992)** found that the Chl *a* molecule was labeled at a higher rate than the total phytoplankton carbon pool. Thus Equation 16 would produce an overestimate of the phytoplankton specific growth rate.

The Redalje-Laws labeling method has been used by many investigators, most notably **Welschmeyer & Lorenzen (1984)** and Gieskes & Kraay (**1986**, **1989**). **Laws *et al.* (1987)** used the technique to show that phytoplankton in the oligotrophic open ocean were growing at very high specific growth rates. **Gould & Gallagher (1990)** adapted the Redalje-Laws Chl *a* labeling procedure to obtain the first field estimates of the specific growth rates for benthic diatoms.

### Taxon-specific μ

**Gieskes & Kraay (1989)** modified the Redalje-Laws method to estimate the specific growth rate of different phytoplankton groups (*e.g.*, diatoms *vs.* cyanobacteria) by estimating the radioactivity in $^{14}C$ incorporation into different carotenoids. This technique was used to great effect by **Strom & Welschmeyer (1991)** who estimated the specific growth rate of diatoms in the subarctic Pacific. **Goericke & Welschmeyer (1993b)** provide more details on this labeling method.

# Outlines of Papers

## Required & supplemental

**Admiraal, W. 1984. The ecology of estuarine sediment-inhabiting diatoms. Prog. Phycol. Res. *3*: 269-322.** *[Please read pages 269-287 [several pages are merely species lists] and pp. 296 & 297]* {**5**, **6**, **24**, **25**}

1. Introduction
2. The estuarine habitat
    - i. diatoms can grow at depths greater than 40 m in clear tropical waters (Plante-Cuny 1974)
   - b. *Diatom growth on sediment*
      - i. most are pennates (having symmetrical lanceolate cells)
      - ii. in plankton, centric (radially symmetrical cells) predominate
      - iii. types
         - (1) species that can move up into water column
         - (2) motile species, also called epipelon (Round 1971), pennates belonging to the biraphid section
         - (3) immobile fixed diatoms
      - iv. other divisions: epipsammon and epipelon
      - v. *"motile diatoms are able to position themselves in the top-layer of the sediments by their photo, geo-, and chemo-taxis, combine with rhythmic responses to tidal and light cycles (Harper 1977)"* P. 271
      - vi. nothing known about energy expenditure

**Figure 3. Vertical migration rhythm**

      - vii. motile diatoms dominant on sheltered sediments

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**Figure 4.** Depth distribution of chlorophyll from sediment cores. can go from near the surface to greater than 15 cm depth.

c. **Environmental parameters [sic].**

i. strong vertical zones.

**Figure 5.** Diagrammatic representation of distribution of populations in sand in Barnstable Harbor (Massachusetts) during period when the tide is out. "Round (1979a) found a two-layered structure in diatom assemblages from sand, with species migrating up and down in the top-layer and non-motile species living at more than 3 mm depth."

ii. parameters

(1) salinity

(2) light, 1% light depth 140 µm in mud (**Colijn 1982**)

**Fig. 6**. Seasonal fluctuation of daylight from **Colijn 1982**

(3) tides: increased growth during neaps when emersion greater (Riazu 1982)

(4) strong oxygen gradient, Revsbech & Jørgensen

**Figure 7.** "profile of oxygen and photosynthetic oxygen production measured with micro-electrodes."

(5) pH

Terry & Edvyvean (1981) measured the daily fluctuation in the pH under a diatom cover and found pH values up to 9.5 to 10 during illumination . **Fig. 8.**

**Figure 8. Time course of pH change from Terry and Edyvean 1981, fluctuations up to 9.5-10**

The photosynthetic activity of diatoms increases the pH (through the uptake of $HCO_3^{-}$) to values over 9.

d. **The distribution of species.**

Fig. 10. Seasonal distributions of diatom species from **Admiraal *et al.* 1984**

3. **SURVIVAL STRATEGIES OF BENTHIC DIATOM SPECIES.**

a. *Adaptation to variable conditions.*

i. *irradiance and daylength*

(1) little photoinhibition observed

(2) certain diatom species adapt to wide ranges in light conditions

(3) several species of intertidal diatoms occur throughout the year.

ii. *temperature*

(1) temperature response not that much different from phytoplankton (Eppley 1972)

iii. *salinity*

iv. **Oxygen, pH and inorganic carbon**.

(1) endowed with significant β-carboxylating activity

(2) DIC is depleted. Oxygen concentrations rise to values equaling saturation with pure oxygen (Fig. 7)

Benthic diatoms are endowed with significant B-carboxylating enzyme activity.

(3) Schwinghamer *et al*. 1983. A del C-13 of -18 was found in sparse populations and -13 in dense assemblages.

(4) Ludden *et al*. used a simulation model. Could it be that the migration of diatoms in the top-layers of the sediment provides the cells alternatively with abundant inorganic carbon supply or abundant illumination, thereby allowing the metabolism to function according to the Crassulacean-type? (p. 296)

v. **Nutrients.**

(1) only modest stimulation from nutrients, in contrast to phytoplankton

(2) determine Redfield ratios using the lens-tissue technique

b. **Exposure to toxic substances**

c. *Autotrophic and heterotrophic metabolism*

high half-saturation coefficients relative to bacteria

d. Competition for space and nutrients

i. **Jong & Admiraal (1984)** showed that insufficient supply of DIC and too much $O_2$ affected dominance of species in culture.

ii. inverse relationship between diversity and population density

iii. Lee (1975) antibiotic substances

iv. **Jong & Admiraal (1984)** document severe antibiosis

e. Niches of diatom species

4. **Population growth and production.**

a. *Note on methodology.*

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i. bell jars
ii. air incubation: **Holmes & Mahall (1982)** noted that overlying water had a big effect on rates.
iii. microelectrodes
produce much higher rates: photorespiration implicated

b. *Photosynthesis and growth in natural populations*
i. The primary controlling factor is the biomass of the algal populations.

Fig. 15. Chl *a* and daily production from **Colijn & de Jonge (1984)**.

ii. Assimilation numbers are low 0.1 to 1
iii. Admiraal & Peletier measured observed rate in real and *in situ* cultured diatoms in the field

c. *Carbon budgets of populations.*
i. "The utilization of photosynthetic products and the biomass of diatoms in the benthic ecosystem has hardly been analyzed"
ii. Admiraal's (1980) summary of losses
(1) Burial and vertical migration
(2) respiration mortality and excretion
(3) herbivory
(4) Heterotrophic utilization of organic substrates
(5) transport by tidal currents.

Fig. 16: on organically polluted mudflats, most of the photosynthate is lost as respiration, mortality and excretion.

5. **BENTHIC DIATOMS AS A FOOD SOURCE FOR HERBIVORES.**
a. nematodes, oligochaetes, harpacticoids, turbellarians and ciliates all eat diatoms
i. Steele & Frost (1977) to illustrate effects of grazers on size composition of diatoms
b. Quantitative effects of grazing
i. freshwater ciliates exert only a low grazing pressure
ii. Davis & Lee (1983): macrofauna can control diatoms
iii. macrofauna affect microalgae strongly (Admiraal *et al.* 1983)

6. **Concluding remarks.**

**Cahoon, L. B., G. R. Beretich, C. J. Thomas, and A. M. McDonald. 1993. Benthic microalgal production at Stellwagen Bank, Massachusetts Bay, USA. Mar. Ecol. Prog. Ser. *102*: 179-185.** *[Significant benthic diatom production at 30-40 m depth]* **{?}**

1. Abstract:
a. Chl *a* and production measured at 3 sites on Stellwagen Bank during August 1991
b. microalgal Chl *a* averaged 40 mg/m$^2$ vs average phyotplankton Chl *a* of 26
c. Primary production measured from oxygen exchange: 21 mg C m$^{-2}$ h$^{-1}$
i. light levels never exceeded 1% of $I_o$

2. Methods & Materials
a. Stellwagen Bank
b. Benthic microalgal production measured *in situ*
c. Plastic domed chambers with whirling cup rotors

3. Results

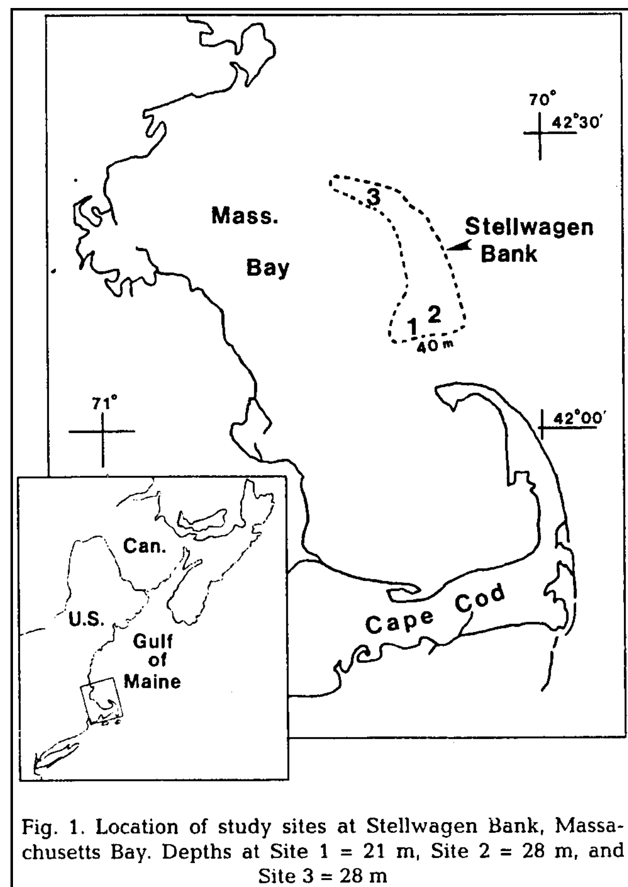


Fig. 1. Location of study sites at Stellwagen Bank, Massachusetts Bay. Depths at Site 1 = 21 m, Site 2 = 28 m, and Site 3 = 28 m

**Figure 7**. Location of Study sites at Stellwagen Bank

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a. Microphytobenthic Chl *a* exceeded phytoplankton Chl *a* 6 of 7 times
b. Gross benthic production about 21 mg C $m^{-2}h^{-1}$
c. Phytoplankton production 240 mg C $m^{-2}$ $h^{-1}$ or 2.9 g C $m^{-2}$ $d^{-1}$ (12-hour day)
d. Net benthic production always negative
   i. Light intensities 0.52% of surface irradiance

4. Discussion
   a. Benthic production was only 6% of water column production and was negative
   b. Benthic respiration high due to high zooplankton fecal pellet flux.

**Gould, D. G. and E. D. Gallagher. 1990. Field measurement of specific growth rate, biomass and primary production of benthic diatoms of Savin Hill Cove, Boston. Limnol. Oceanogr. *35*: 1757-1770. {6, 10, 11, 12, 13, 15, 31}**

1. Chl *a* labeling

Table 1. Definitions and equations used in the $^{14}$C-Chl *a*-labeling technique (adapted for sediment from Redalje and Laws 1981; Redalje 1983; Welschmeyer and Lorenzen 1984).

| | |
|---|---|
| $A^*$ | Activity of total particulate matter, dpm $core^{-1}$ |
| $R^*$ | Specific activity of C in Chl *a* molecule, dpm $\mu g^{-1}$ C |
| $I^*$ | Specific activity of DIC, dpm $\mu g^{-1}$ C |
| ΔC | C fixed during the incubation, $\mu g$ C $core^{-1}$ $incubation^{-1}$ converted to mg C $m^{-2}$ $h^{-1}$ |
| Cp | Microalgal C present at the end of the incubation, $\mu g$ C $core^{-1}$ converted to g C $cm^{-2}$ |
| $\mu$ | Specific growth rate per day assuming 12 h growth per day |
| 1.05 | Factor to account for isotope discrimination |
| $t$ | Duration of incubation in hours |

Equations:

$$\Delta C = 1.05\ [(A^*/I^*) \times (1/t)] \quad (1)$$

$$Cp = A^*/R^* \quad (2)$$

$$\mu = \frac{-\ln[1 - (1.05\ R^* \times I^{*-1})]}{t} \times 12 \quad (3)$$

**Figure 7**. Table 1 from Gould & Gallagher (1990)

*"The $^{14}$C-Chl a labeling technique assumes that the specific activity of Chl a C ($R^*_{chl}$) and total cell C($R^*_{Cp}$) are equal after a given period of growth in labeled medium"*

My derivation:

$\mu=1/C_p\ dC/dt$

$C_p=C_o\ e^{\mu t}$
$ln(C_p/C_o)=\mu t$
$\mu=-\ln(C_o/C_p)/t$
$\mu=-\ln([C_p-\Delta Ct]/C_p)/t$
$\mu=-ln(1-\Delta Ct/C_p)/t$
$\mu=-ln(1-\{1.05(A^*/I^*)t/t\}/[A^*/R^*])/t$
$\mu=-ln(1-\{1.05(R^*/I^*)\})/t$

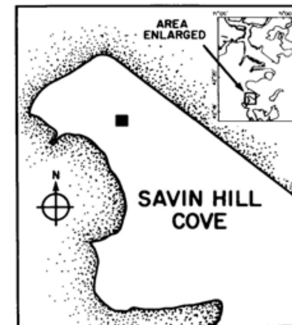

Fig. 1. Savin Hill Cove with inset map of Boston Harbor. Area sampled—■.

**Figure 8**. Figure 1 from Gould & Gallagher (1990)

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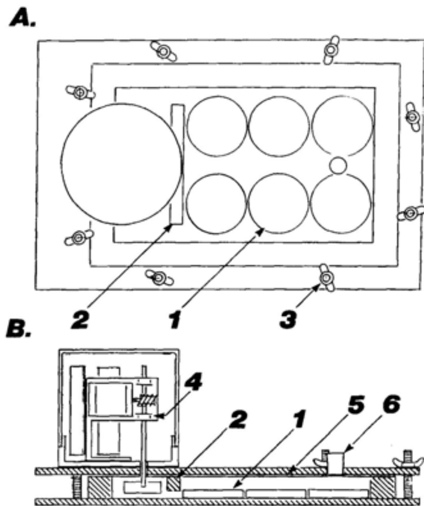


Fig. 2. A. Overhead view of the incubation chamber with the lid in place. Interior dimensions of the water chamber are 21.5 cm long × 13 cm wide × 2 cm deep. B. Midline cross-sectional view: 1—50-mm plastic Petri dish lid; 2—Plexiglas baffle; 3—bolt and wing-nut assembly; 4—stirring device consisting of a 1.5-V motor, resistors, paired AA batteries, worm gear drive, plastic-coated drive shaft, and Plexiglas paddle; 5—gasket made of silicone aquarium sealant; 6—port.

**Figure 9**. Figure 2 from Gould & Gallagher (1990)

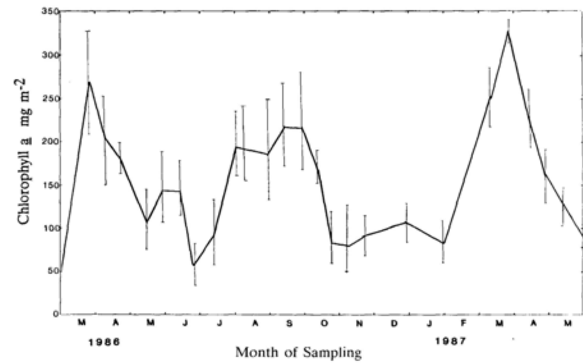


Fig. 3. Relationship between Chl $a$ concentration and date of sampling. Letters indicate the beginning of each month. The 95% confidence limits (based on ±1.96 SD, $n$ = 5) are indicated.

**Figure 10**. Figure 3 from Gould & Gallagher (1990)

Table 3. Results of stirred vs. unstirred incubation of mixed field populations collected 3 August 1987. SD in parentheses ($n$ = 3). Units given in Table 1.

| $t$ | $A^*$ (×10[illegible]) | $P^*$ (×10[illegible]) | $R^*$ | ΔC | Cp (×10[illegible]) | $\mu$ |
|---|---|---|---|---|---|---|
| Stirred | | | | | | |
| 3.0 | 16.87(2.17) | 1.41 | 764(43) | 75(5) | 4.16(0.82) | 0.23(0.02) |
| Unstirred | | | | | | |
| 3.0 | 10.62(0.19) | 1.34 | 356(32) | 47(1) | 5.62(0.67) | 0.11(0.02) |

**Figure 11**. Table 3 from Gould & Gallagher (1990)

Table 2. Results of $^{14}$C-Chl $a$-labeling experiments done in the laboratory to compare effects of (A) length of incubation on specific growth rate of laboratory cultures, (B) length of incubation on specific growth rate of mixed field populations, and (C) substrate (natural sediment vs. glass-fiber filter) on specific growth rate. In each case, $\mu$ was calculated with Eq. 3 (Table 1). SD in parentheses.

| $t$(h) | $\mu$(d$^{-1}$) |
|---|---|
| A. Laboratory cultures | |
| 3.0 | 0.13 |
| 5.25 | 0.13 |
| 8.0 | 0.11 |
| B. Mixed field population collected 21 Feb 88 | |
| 3.5 | 0.03 (0.00, $n$ = 2) |
| 13:11 | 0.03 (0.00, $n$ = 3) |
| Mixed field population collected 25 Feb 88 | |
| 2.0 | 0.05 (0.00, $n$ = 2) |
| 7.5 | 0.05 (0.00, $n$ = 2) |
| Mixed field population collected 29 Feb 88 | |
| 4.0 | 0.06 |
| 8.0 | 0.06 (0.00, $n$ = 2) |
| C. Laboratory cultures grown on natural sediment | |
| 8.0 | 0.11 (0.01, $n$ = 2) |
| Laboratory cultures grown on GFC filters | |
| 8.0 | 0.10 (0.00, $n$ = 2) |

**Figure 12**. Table 2 from Gould & Gallagher (1990)

Table 4. Results of field incubations done in Savin Hill Cove and laboratory incubation of Duxbury Beach sediment. C:Chl ratio is based on Cp calculated via $^{14}$C-Chl $a$ labeling and on fluorometrically determined Chl $a$ values. SD in parentheses. Spearman's rank correlation coefficients calculated for Savin Hill Cove data as follows: C:Chl ratio and $\mu$, $r_s$ = −0.94, $P$ < 0.01; Cp and C:Chl, $r_s$ = 0.89, $P$ < 0.05; Cp and $\mu$, $r_s$ = −0.78, $P$ < 0.05. Units given in Table 1. Temperature (°C) in the incubation chamber at the end of the incubation—T; doubling time (d)—DT.

| | $T$ | $t$ | $A^*$ (×10[illegible]) | $P^*$ (×10[illegible]) | $R^*$ | ΔC | Cp (×10[illegible]) | $\mu$ | DT | C:Chl |
|---|---|---|---|---|---|---|---|---|---|---|
| Savin Hill Cove | | | | | | | | | | |
| 14 Aug 87 | | | | | | | | | | |
| Low tide | 31 | 2.75 | 8.35(1.85) | 8.56 | 489(31) | 70(15) | 3.23(0.98) | 0.27(0.02) | 2.6 | 21.3 |
| 30 Aug 87 | | | | | | | | | | |
| High tide | 20 | 3.0 | 15.62(3.42) | 7.60 | 346(11) | 136(34) | 8.51(2.21) | 0.18(0.01) | 3.9 | 32.5 |
| 11 Sep 87 | | | | | | | | | | |
| Low tide | 28 | 3.0 | 3.76(0.41) | 5.62 | 321(20) | 44(03) | 2.21(0.42) | 0.24(0.02) | 2.0 | 18.7 |
| 6 Mar 88 | | | | | | | | | | |
| Low/high | 5 | 10.0 | 48.38(6.95) | 8.59 | 593(06) | 112(16) | 15.40(0.36) | 0.09(0.01) | 7.7 | 54.4 |
| 19 Mar 88 | | | | | | | | | | |
| Low/high | 7 | 11.0 | 28.49(5.43) | 7.86 | 413(27) | 65(13) | 13.00(3.57) | 0.06(0.01) | 11.6 | 60.4 |
| 4 Jul 88 | | | | | | | | | | |
| Low tide | 30 | 2.5 | 7.13(0.56) | 5.75 | 192(08) | 98(08) | 6.19(0.89) | 0.17(0.01) | 3.6 | 42.5 |
| 4 Jul 88 | | | | | | | | | | |
| Low/high | 20 | 10.5 | 18.55(0.20) | 5.08 | 608(100) | 69(04) | 5.75(1.21) | 0.15(0.03) | 4.6 | |
| Duxbury Beach | | | | | | | | | | |
| 7 Aug 88 | | | | | | | | | | |
| Lab | 26 | 3.0 | 5.84(0.81) | 7.14 | 95(09) | 54(07) | 11.60(3.00) | 0.06(0.01) | 11.6 | 55.4 |

**Figure 13**. Table 4 from Gould & Gallagher (1990)

Table 5. Estimation of loss rate using biomass and specific growth rate. A. For the 14–30 August loss rate, $\mu$ = 0.21 is based on high and low tide rates and mean tidal exposure. B. Loss rate between 19 March and 19 April 1988 is based on Cp determined via $^{14}$C-Chl $a$ labeling for 19 March 1988 and an estimated C biomass for 19 April 1988. This estimate is based on analysis of 10 sediment samples (Chl $a$ = 56.6 μg core$^{-1}$) and C:Chl = 20.

$Cp_t = Cp_0^{(\mu - L)t}$
$Cp_t$ = microalgal biomass at time $t$
$Cp_0$ = initial microalgal biomass
$\mu$ = specific growth rate
$L$ = loss rate
$t$ = days

A.
$\mu$ = 0.21 d$^{-1}$ (14 Aug 87)
$Cp_0$ = 1,710 μg C core$^{-1}$ (14 Aug 87)
$Cp_t$ = 4,520 μg C core$^{-1}$ (30 Aug 87)
$L$ = 0.15 d$^{-1}$

B.
$\mu$ = 0.06 d$^{-1}$
$Cp_0$ = 6,900 μg C core$^{-1}$ (19 Mar 88)
$Cp_t$ = 1,100 μg C core$^{-1}$ (19 Apr 88)
$L$ = 0.12 d$^{-1}$

**Figure 14**. Table 5 from Gould & Gallagher (1990)

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**Ludden, E, W. Admiraal, and F. Colijn. 1985. Cycling of carbon and oxygen in layers of marine microphytes: a simulation model and its eco-physiological implications. Oecologia *66*: 50-59.**{?}

1. SUMMARY
   - 1.a. Mathematical simulation model
   - 1.b. validated using available data
   - 1.c. simulated oxygen concentration and pH
   - 1.d. model predicted upper limits of primary production and biomass.
   - 1.e. limits set by a combination of oxygen accumulation and depletion of inorganic carbon resulting from diffusion limitations and the recirculation of organic carbon in photosynthetic, respiratory and excretory processes.
2. Introduction.
   -Three issues merit consideration
   - 2.a. bell jar methods unsatisfactory
     - 2.a.i. Revsbech & Jørgensen (**1981**, **1983**) found discrepancies among bell jars and microelectrode methods.
     - 2.a.ii. Gradients of $O_2$ crucial
   - 2.b. transfer of carbon indicate that only a fraction of the fixed carbon serves as food for the micro and meiofauna.
     -Does the rate of respiration and photorespiration in dense populations account for a considerable drain?
   - 2.c. Conditions for algal growth are extreme.
     - 2.c.i. pH up to 10
     - 2.c.ii. Glover *et al.* (now published) indicate various patterns of carbon fixation.
3. **Theory and description of the model.**
   - 3.a. *Outline of the method:*

**Fig. 1**. Diagram of carbon and oxygen flow in the model.

     - 3.a.i. Oxygen transfer across cell membrane immediate, carbon complicated.
     - 3.a.ii. algal film connected with the seawater via a diffusion gradient
     - 3.a.iii. P, Si and N not included int he model.
     - 3.a.iv. simulation run with various modifications
       -connected with an underlying sediment layer.
   - 3.b. *The carbonate system.*
     - 3.b.i. Hydration of $CO_2$ and dehydration of $HCO_3^-$ are fairly slow processes (Johnson 1972). The carbonate system may not be in equilibrium
     - 3.b.ii. Equilibrium not assumed: transient dynamics modeled
     - 3.b.iii. *"We used a variable step, variable order, Gear method from NAG to do the integration."*
     - 3.b.iv. pK1 and pK2 taken from Buch (1960), $kCO_2$ and $kHCO_3^-$ taken from Johnson (1982)
   - 3.c. *Algal metabolism*: 6 parts
     - 3.c.i. $CO_2$ fixation
       - 3.c.i.1. fixation exclusively by RuBPCO
       - 3.c.i.2. half saturation constant for Rubisco is 30 micromoles/l
     - 3.c.ii. Photorespiration
       - 3.c.ii.1. controlled by $O_2$:$CO_2$ ratios (Laing *et al.* 1974)
       - 3.c.ii.2. half the glycolate was converted to serine and half was excreted.
       - 3.c.ii.3. 3 different $K_mO_2$ values assumed: 300, 1000, and 2000μmoll$^{-1}$, 400 is $K_m$ of pure enzyme
     - 3.c.iii. Uptake of bicarbonate ions
       - 3.c.iii.1. active uptake of bicarbonate ions.
       - 3.c.iii.2. $K_m$ never measured, assumed 10-100μmol l$^{-1}$
       - 3.c.iii.3. maximum internal DIC 6mmol l$^{-1}$ (Colman & Colman
         - 3.c.iii.3.a. feedback inhibition of DIC uptake
       - 3.c.iii.4. carbonic anhydrase: instantaneous equilibrium of carbonate system
       - 3.c.iii.5. internal pH control, affected at high pH
         - 3.c.iii.5.a. 2 different methods used
     - 3.c.iv. $CO_2$ leakage out of cells
       - 3.c.iv.1. slow leakage out of cells
     - 3.c.v. dark respiration
       - 3.c.v.1. ≈ 10% of primary production.

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3.c.v.2. small biomass-dependent term and photosynthesis dependent term

3.c.vi. Excretion

3.c.vi.1. low excretion (3% of biomass per day)

3.c.vi.2. excretion coupled to photorespiration

3.c.vii. Three types of algal DIC metabolism simulated.

3.d. *the diffusion equations.*

3.d.i. some runs exchanges with the underlying water

3.d.ii. Fick's first law

3.d.iii. *"The thickness of the diffusion barrier was taken to equal half the variable thickness of the algal film plus the depth of a stagnant boundary layer (Table 1)"* p. 53

3.d.iv. "We chose a thickness of 1 mm for the stagnant layer and later check the effect of a fivefold reduction in the diffusion barrier.

Table 1. Equations variables and constants in the model.

4. **Results and discussion.**

4.a. *Results of the photosynthesis submodel*

**Table 3.** Parameters of three different algal types.

Case 1: C3 type diatom, Case 3: C4 type diatom(large $K_m$ for $O_2$ 2000µmol $l^{-1}$, low $K_m$ for $HCO_3^-$. Case 2: Admiraal's guess for *Navicula salinarum*. STANDARD RUN.

**Fig. 2.** Photosynthetic oxygen production per unit biomass as a function of extracellular concentrations of inorganic carbon (DIC) and oxygen.

4.a.i.Three different algal species modeled.

4.a.ii. Rasmussen's sandflat algae are like type 1.

4.a.iii. *N. salinarum* like case 2.

4.a.iv. Standard alga chosen (Type 2)

4.b. *Development of a growing microalgal film: a standard run.*

4.b.i. Type 2 diatom, Table 3

**Fig. 3.** Fluctuation in the state variables.

4.b.ii. time resolution comparable to microelectrodes

4.b.iii. $O_2$ increased to 1200 µmol $l^{-1}$ (comparable to **Revsbech & Jørgensen 1983**)

4.b.iv. pH rises to 10 when the light is switched on.

4.b.v. Next step: Development of an algal mat over a scale of weeks.

4.b.v.1. starts with a few cells

**Fig. 4.** Simulated development of an algal mat on an inert substrate

4.b.v.2. Sparse populations doubled at 0.5 $d^{-1}$

4.b.v.3. biomass stabilized at 18 mg C $dm^{-2}$=18 g C $m^{-2}$

4.b.v.4. peak production 0.05 mmol C $dm^{-2}h^{-1}$=60mgC$m^{-2}h^{-1}$

4.b.v.5. *"These rates are probably set by the maximum transport rate across the diffusion barrier, since similar photosynthetic rates have been measured in compact biological material such as the thallus of macroalgae"* p. 55

4.b.v.6. The amount of inorganic carbon within the algal mat decreased and mainly consisted of carbonate, whereas the concentrations of photosynthetically available bicarbonate and carbon dioxide were reduced to levels that are assumed to be limiting.

**Fig. 5.** **Total DIC is less than 0.1 mmolar** (100 µM) c. 15% grazing per day. biomass decreased slightly. A: standard run stippled, solid line is Type 1 algal. B as in A but solid line is type 3 ($C_4$ alga). C: 15% grazing $d^{-1}$

4.b.v.7. oxygen as high as 1200µmol $l^{-1}$ inhibit fixation of carbon

4.b.v.8. significant loss of DOM during later stages of the model

4.b.v.9. Photosynthetic quotient decreased from 1.4 to 0.6 from photorespiration, dark respiration and excretion of organic matter.

4.c. *Biological effects*

4.c.i. 3 physiology types

4.c.i.1. Type 1: full C3 metabolism,

4.c.i.2. Type 3: full C4 metabolism

4.c.i.3. Type 2: mixture of C3 and C4.

4.c.ii. Type 1 algae competitively displaced

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4.c.iii. Type 1 algae are able to form a mat but would not be able to survive under the conditions created by an invading alga of the Type 3 type.
4.c.iii.1. competition for DIC
4.c.iv. 15% grazing modeled.
4.c.iv.1. Grazing had hardly any effect on the oxygen concentration and oxygen flux
4.c.iv.2. altered the standing stock
4.c.iv.3. grazing doesn't alter productivity
4.c.iv.4. Grazing altered the allocation between growth and dissipating processes.
4.c.iv.5. *"Grazing by large herbivores might have additional repercussions such as the reworking of sediment and the burial of algal cells in the sediment and in altering structure and porosity of the sediment top layer."* p. 57

4.d. *Physical effects:*
4.d.i. anaerobic sediment added: "anaerobic, pH 7.5, DIC of 3 mmol $l^{-1}$. **THE DIFFUSION LAYER IN THE SEDIMENT WAS TAKEN AS 1 MM**. The porosity of the sediment was assumed to be 0.7" p. 57

**Fig. 6.** Physical effects. A algal mate on sediment layer. B algal mat exposed to air. C standard run with stagnant boundary layer reduced 5-fold. Standard run with light period doubled to 16 h.

4.d.ii. sedimentary oxygen removal and increase in $CO_2$ resulted in 40% increase in biomass.
4.d.iii. measurement of $O_2$ flux to water layer may grossly underestimate primary production.
4.d.iv. air flux: biomass increased, carbon supply more difficult, $O_2$ less of a problem. ph increased to 11.5 (improbable), above pH 10.5 carbonates are precipitated.
4.d.v. With stirring and reduction of diffusive sublayer, the production doubled: 20% increase in biomass.

4.e. *Carbon fluxes and carbon budgets.*

**Fig. 7**. predicted net flux of DIC. A: low biomass. B: biomass=8 mg C $dm^{-2}$ (=80 g C $m^{-2}$ . from sediment to overlying water.

4.e.i. Methodological problems: $CO_2$ flux from the overlying water is not a representative measure of production.
4.e.ii. sparse: 70% of production is net, dense: 50% net production

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Varela, M. and E. Penas. 1985. Primary production of the benthic microalgae in an intertidal sandflat of the Ria de Arosa, N. W. Spain. Mar. Ecol. Prog. Ser. *25*: 111-119. *[Used **Whitney & Darley (1979)** hexane extraction and found 15% active chl a, 12% chlorophyllide a, 54% pheophytin a and 19% pheophorbide a.]*

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## Flux chambers & diffusive boundary layers (and effects of boundaries on photosynthesis)

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Aller, R. C. and J. E. Mackin. 1989. Open-incubation, diffusion methods for measuring solute reaction rates in sediments. J. Mar. Res. *47*: 411-440.

Booij, K, W. Helder, and B. Sundby. 1991,. Rapid redistribution of oxygen in a sandy sediment induced by changes in the flow velocity of the overlying waters. Neth. J. Sea Res. *28*: 149-165. *[This tea-leaves effect, thicker diffusive sublayer at the center of a stirred chamber, may invalidate the use of stirred flux chambers to estimate diffusive fluxes from sediments]*

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Carpenter, R. C., J. M. Hackney, and W. H. Adey. 1991. Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnol. Oceanogr. *36*: 40-49 *[Growth increases as diffusive sublayer thickness decreases]*

Eckman, J. E. 1985. Flow disruption by an animal-tube mimic affects sediment bacterial concentrations. J. Mar. Res. *43*: 419-435. *[Four $U_*$ (0.12 to 1.2 cm $sec^{-1}$) and boundary roughness regimes were created and the bacterial colonization of Nitex. At the 2 higher regimes, tube height exceeded the viscous sublayer thickness (<0.2 cm) and bacterial growth was enhanced.]*

Eckman, J. E. and A. R. M. Nowell. 1984. Boundary skin friction and sediment transport about an animal-tube mimic. Sedimentology *31*: 851-862. *[Flush-mounted hot-film anemometers used to document the areas of enhanced and decreased $U_*$ around a single simulated tube]* {**11**}

Glud, R. N. S. Forster, and M. Huettel. 1996. Influence of radial pressure gradients on solute exchange in stirred benthic chambers. Mar. Ecol. Prog. Ser. *141*: 303-311. *[Bromide used a consiervative tracer of flux. Stirring enhances diffusive flux. An example of the tea-leaf effect]*

Jørgensen, B. B. 2001. Life in the diffusive boundary layer, Pp. 348-373. in B. P. Boudreau and B. B. Jørgensen, eds., The benthic boundary layer: transport processes and biogeochemistry. Oxford University Press, Oxford.

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Opdyke, B. N., G. Gust and J. R. Ledwll. 1987. Mass transfer from smooth alabaster surfaces in turbulent flows. Geophysical Research Letters *14*: 1131-1134. *[Provides an equation relating $U_*$ to diffusive sublayer thickness: $\log(z_\delta) = -.79 \log(U_*) + 3.06 + \log(Dm) \approx -.79 \log U_* - 1.7$, where Dm is $1.7 x 10^{-5}$ or $z_\delta = 0.02 * U_*^{-.79}$]* {**10**}

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Riber, H. H. and R. G. Wetzel. 1987. Boundary layer and internal diffusion effects on phosphorous fluxes in lake periphyton. Limnol. Oceanogr. *32*: 1181-1194. *[Radioactive phosphate used to measure flux into diatom films on slides. Flux is a power function of velocity and is greater at the leading edge of films. Periphyton production is probably limited by the diffusional flux of phosphorous.]*

Røy, H, M. Hüttel and B. B. Jørgensen. 2002. The role of small-scale sediment topography for oxygen flux across the diffusive boundary layer. Limnol. Oceanogr. *47*: 837-847. *[Calculation of the 3-d diffusive flux through the diffusive boundary layer, but only a 10% difference in flux between 3-d and 1-d models. A new topographic scaling parameter is introduced]*[?]

Santschi, P. H., P. Bower, U. P. Nyffeller, A. Azevedo and W. S. Broecker. 1983. Estimates of the resistance to chemical transport posed by the deep-sea boundary layer. Limnol. Oceanogr. *28*: 899-912.

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## MICROPHYTOBENTHIC PRODUCTION AND NUTRIENT FLUX

Andersen, F. O. and E. Kristensen. 1988. The influence of macrofauna on estuarine benthic metabolism: a microcosm study. Marine Biology *99*: 591-603. *[Cited by* ***Sundback et al. (1991)*** *as showing inverse relation between nutrient efflux and microphytobenthic production]*

Asmus, R. 1986. Nutrient flux in short term enclosures of intertidal sand communities. Ophelia 26: 1-18 *[Cited by* ***Nilsson et al. (1991)*** *cited by* ***Sundback et al. 1991.****]*

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Kelderman, P., H. J. Lindeboom, and J. Klein. 1988. Light-dependent sediment-water exchange of dissolved reactive phosphorous and silicon in a producing microflora mat. Hydrobiologia *159*: 137-147. *[Cited in* ***Nilsson et al. (1991)****]*

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Ludden, E, W. Admiraal, and F. Colijn. 1985. Cycling of carbon and oxygen in layers of marine microphytes: a simulation model and its eco-physiological implications. Oecologia *66*: 50-59. *[These authors assume a thin diffusive sublayer beneath diatoms on mudflats, which produces an upward flux of DIC. They are wrong.]* {?}

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Pomeroy, L. R., W. M. Darley, E. L. Duan, J. L. Gallagher, E. B. Harris and D. M. Whitney. 1981. Primary production. Pp. 39-67 *in* L. R. Pomeroy and R. G. Wiegert, eds., The ecology of a salt marsh. Springer-Verlag, Heidelberg & New York.

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Sundbäck, K. and P. Snoejis. 1991. Effects of nutrient enrichment on microalgal community composition in a coastal shallow-water system: an experimental study. Botanica Marina 34: (galleys) *[Observed as N flux increased, increased filamentous cyanobacteria, diatoms and flagellagetes, rapid growth of Enteromorpha. Data analyzed with CANOCO]*

Sundbäck, K., V. Enoksson, W. Graneli and K. Petterson. 1991. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous-flow study. Mar. Ecol. Prog. Ser. *74*: 263-279. *[Microphytobenthos from 15 m depth influence pore water fluxes of N and P.]* [**28**, **30**]

Sundbäck, K., F. Linares, F. Larsen, and A. Wulff. 2004. Benthic nitrogen fluxes along a depth gradient in a microtidal fjord: the role of denitrification and microphytobenthic production. Limnol. Oceanogr. *49*: 1095-1107. *[MPB assimilation exceeds and inhibits denitrification. MPB assimilation exceeded denitrification at all depths surveyed from 1 to 15 m]{?}*

Van Raalte, C. D., I. Valiela, and J. M. Teal. 1976. Production of epibenthic salt marsh algae: light and nutrient limitation. Limnol. Oceanogr. *21*: 862-872. *[Nutrients affect macroalgal production, not much effect on microalgae]*

## EFFECTS OF TEMPERATURE & LIGHT

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Admiraal, W. and H. Peletier. 1979. Influence of organic compounds and light limitation on the growth rate of estuarine benthic diatoms. Br. Phycol. J. *14*: 197-206.

Admiraal, W. and H. Peletier. 1980. Influence of seasonal variation of temperature and light on the growth rate of cultures and natural populations of intertidal diatoms. Marine Ecology Progress Series *2*: 35-43. *[Documents very slow growth of in situ cultured diatoms and 3-10 times slower doubling of Chl a on mudflats. Their Chl a doubling is comparable to the slowest doubling times in* ***Gould & Gallagher (1990)****]*

Barranguet, C. and J. Kronkamp. 2000. Estimating primary production rates from photosynthetic electron transport in esutarine microphytobenthos. Mar. Ecol. Prog. Ser. *204*: 39-52. *[Like* ***Serôdio & Catarino 2000****, they use PAM fluorescence to measure* $F_o$*, which they relate to primary production ]* {?}

Colijn, F. 1982. Light absorption in the waters of the Ems-Dollard estuary and its consequences for the growth of phytoplankton and microphytobenthos. Neth. J. Sea Res. *15*: 196-216. *[The spring bloom is cued by tidal emersion cycles and occurs from January to March, with lower mudflats blooming later]* {**16**}

Colijn, F. and G. van Buurt. 1975. Influence of light and temperature on photosynthetic rate of marine benthic diatoms. Marine Biology *31*: 209-214. *[Cited by Rasmussen et al. 1983 as showing a 10% increase in potential photosynthesis for every 1 °C change in temperature from 4 °C to 20 °C. This matches the increase in μ from Gould and Gallagher 1990]*

**Colijn & de Jonge (1984)**

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**de Jonge (1994)**

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## GRAZING, PRIMARILY ON BENTHIC DIATOMS

*"Grazers are usually lumped into the larger category of deposit feeders, or occasionally as 'selective surface deposit feeders'. Sometimes they are called herbivores. However, many benthic species are either facultative or even obligate predators of the microphytobenthos. Grazers in the Fauchald-Jumars scheme might be termed microphagous surface-feeding herbivores."*

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Montagna, P. A., B. C. Coull, T. L. Herring, and B. W. Dudley. 1983. The relationship between abundances of meiofauna and their suspected microbial food (diatoms and bacteria). Est. Coast. Shelf Science *17*: 381-394. *[Regression analyses show a positive correlation between meiofaunal abundance and diatom standing stock (but not bacterial standing stock). At the gross taxonomic level, total meiofauna do not respond to changes in the food level, even when time lags are considered. Other factors may control meiofaunal abundance (e.g., predation).]*

Montagna, P. A. and J. E. Bauer. 1988. Partitioning radiolabeled thymidine uptake by bacteria and meiofauna using metabolic blocks and poisons in benthic feeding studies. Marine Biology *98*: 101-110.

Montagna, P. A., G. F. Blanchard and A. Dinet. 1995. Effects of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. J. exp. Mar. Biol. Ecol. *185*: 149-165.

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Pace, M. C. and K. R. Carman. 1996. Interspecific differences among meiobenthic copepods in the use of microalgal food resources. Mar. Ecol. Prog. Ser. *143*: 77-86. *[Pelagic and benthic microalgae labeled and fed to 2 harpacticoids species. Both feed on both food types but at different rates]*

Phillips, N. W. 1984. Role of different microbes and substrates as potential suppliers of specific essential nutrients to marine detritivores. Bull. Mar. Sci. *35*: 283-298. *[Bacteria lack essential fatty acids required for metazoan growth. Benthic diatoms are excellent sources for these essential dietary components.* cf., *Marsh and Tenore 1990.]* {4}

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Pinckney, J. and R. Sandalli. 1990. Spatial autocorrelation analysis of meiofaunal and microalgal populations on an intertidal sandflat: scale linkage between consumers and resources. Est. Coastal & Shelf Sci. *30*: 341-353. *[Work done on Barnstable Harbor as part of the 1987 MBL Marine Ecology course. Moran's I statistics calculated between meiofauna and Chl a]*

Raven, J. A. and A. M. Waite. 2004. The evolution of silicification in diatoms: inescapable sinking and sinking as escape? New Phytologist *162*:1-45. *[A nice history of diatom evolution. Coevolution with parasites and grazers may have played a role in the adaptive radiation of silicified diatoms]* {?}

Rieper, M. 1985. Some lower food web organisms in the nutrition of marine harpacticoid copepods: an experimental study. Helg. wiss. *39*: 357-366. *[Rieper studies an odd mix of harpacticoids and food sources. Little evidence is provided that the food sources are appropriate for the copepods in the field. Growth on bacteria, 2 ciliate species and Skeletonema costatum are compared.]*

Smith, D, R. G. Hughes and E. J. Cox. 1996. Predation of epipelic diatoms by the amphipod *Corophium volutator* and the polychaete *Nereis diversicolor*. Mar. Ecol. Prog. Ser. *145: 53-61. [Experimental removal of Corophium using an insecticide produced enhanced diatom densities. Corophium eats 2150 to 3767 cells per day N. diversicolor eats 5476 to 12184 cells per day {nice sig. figs!} n.b. benthic diatoms can reach* $5\times10^6$ *cells per* $cm^2$*. These feeding rates seem too low to cause much of an effect]*

Sommer, U. 1997. Selectivity of *Iothea chlipes* (Crustacea: Isopoda) grazing on benthic micoalgae. Limnol. Oceanogr. *42*: 1622-1628. *[The specific grazing rates of different periphyton on microscope slides. Small single diatoms eaten more readily than other groups]*

Stuart, S. V., E. J. H. Head, and K. H. Mann. 1985. Seasonal changes in the digestive enzyme levels of the amphipod *Corophium volutator* (Pallas) in relation to diet. J. Exp. Mar. Biol. Ecol. *88*: 243-256.

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Wagner, M. and K. Foreman. 1981. Response of benthic diatoms to removal of macroconsumers. Indiana Acad. Sci. *91*: 237-266. *[Caging experiments from Sippewissett marsh]*

White, D. C., R. H. Findlay, S. D. Fazio, R. J. Bobbie, J. S. Nickels, W. M. Davis, G. A. Smith, and R. F. Mertz. 1980. Effects of bioturbation and predation by *Mellita quinquiesperforata* on sedimentary microbial community structure. Pp. 163-171 *in* V. S. Kennedy, *ed*., Estuarine Perspectives. Academic Press, New York. [Mellita is an echinoid echinoderm or sand dollar]

## STABLE ISOTOPIC ANALYSES

Altabet, M. A. 1988. Variations in nitrogen isotopic composition between sinking and suspended particles: implications for nitrogen cycling and particle transformation in the open ocean. Deep-Sea Res. *29*: 1035-1039.

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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.

Altabet, M. A. and W. B. Curry. 1989. Testing models of past ocean chemistry using Foraminifera $^{15}N/^{14}N$. Global Biogeochem. Cycles 3: 107-119.

Altabet, M. A. and L. F. Small. 1990. Nitrogen isotopic ratios in fecal pellets produced by small zooplankton. Geochim. Cosmochim. Acta *54*: 155-163.

Beardall, J., H. Griffiths, and J. A. Raven. 1982. Carbon isotope discrimination and the $CO_2$ accumulating mechanism in *Chlorella emersonii*. J. Exp. Bot. *33*: 729-738. *[*$HCO_3^-$ *uptake induced by nitrogen limitation. High* $HCO_3^-$ *utilization produces high intracellular* $CO_2$*, reducing the loss of* $NH_3$ *resulting from the conversion of glycine into serine in the photorespiratory carbon-oxidation cycle.]*

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Berner, R., M. L. Fogel, E. K. Sprague, and R. E. Hodson. 1987. Depletion of $^{13}C$ in lignin and its implications for stable carbon isotope studies. Nature *329*: 708-710.

Bouton, T. W., M. A. Arshad, and L. L. Tieszen. 1983. Stable isotope analysis of termite food habits in East African grasslands. Oecologia *59*: 1-6.

Boyle, E. A. 1988. Vertical oceanic nutrient fractionation and glacial/interglacial $CO_2$ cycles. Nature *331*: 55-56.

Brooks, J. M. *et al.* 1987. Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. Science *238*: 1138-1142.

Chanton, J. and F. G. Lewis. 2002. Examination of coupling between primary and secondary production in a river-dominated estuary: Apalachicola Bay, Florida, U.S.A. Limnol. Oceanogr. 47: 683-697. *[$^{13}C$ and S-34 measured in sources and benthic animals (polychaetes -22 to -26)]*

Chisholm, B. S., D. E. Nelson, and H. P. Schwartz. 1982. Stable-carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. Science *216*: 1131-1132.

Cifuentes, L. A., J. H. Sharp, and M. L. Fogel. 1988. Stable carbon and nitrogen isotope biogeochemistry in the Delaware estuary. Limnol. Oceanogr. *33*: 1102-1115. *[An excellent paper; diatom $\delta^{13}C$ values are at their heaviest during the bloom, when $CO_2$ (aqu) may be depleted]*

Cloern, J. E., E. A. Canuel, and D. Harris. 2002. Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. Limnol. Oceanogr. 47: 713-729.*[Variability in N and C made identification of food sources difficult. Caution advised. Benthic diatoms $^{13}C$ -20 to -26]* [**40**, **41**]

Coffin, R. B, B. Fry, B. J. Peterson, and R. T. Wright. 1989. Carbon isotopic compositions of estuarine bacteria. Limnol. Oceanogr. 34: 1305-1310. *[Bacteria are within 2 ‰ of their food]*

Couch, C. A. 1989. Carbon and nitrogen stable isotopes of meiobenthos and their food resources. Est. Coast. Shelf Sci. 28: 433-441. *[Total sed=-19.54; Spartina=-16.31; microalgae=-12.76 {with no seasonal change}, cited by* ***Cloern et al. 2002****. Diatoms isolated in a gel]*

Currin, C. A. S. Y. Newell, and H. W. Paerl. 1995. The role of standing dead Spartina alterniflora and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Mar. Ecol. Prog. Ser. *121*: 99-116.

Dansgaard, W. and H. Tauber. 1969. Glacier Oxygen-18 content and Pleistocene ocean temperatures. Science *166*: 499-502. *[$\delta^{18}O$ is a function of both oceanic temperatures and ice volume]*

Dauby, P. 1989. The stable carbon isotope ratios in benthic food webs of the Gulf of Cavi, Corsica. Cont. Shelf Res. *9*: 181-195. *[Posidinia (seagrass)=-9; brown algae=-19; phytoplankton=-23]*

Deegan, L. A. and R. H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. Mar. Ecol. Prog. Ser. *147*: 31-47. [Cited by **Cloern et al. 2002**]

Delaney, M. L. 1989. Geological boundaries: extinctions and carbon cycling. Nature *337*: 18-19. *[Summary of Gruszczynnksi and a summary of the functional relationship between primary production and $\delta^{13}C$]*

DeNiro, M. J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta *42*: 495-506.

Duggins, D. O., C. A. Simenstead, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science *245*: 170-174. *[phytoplankton=-24; kelp=-17.7; microphytobenthos not measured]*

Ember, L. M. and D. F. Williams. 1987. Processes that influence carbon isotope variations in salt marsh sediments. Mar. Ecol. Prog. Ser. *36*: 33-42. *[Surface organic matter $\delta^{13}C$=-22 to -17]*

Emiliani, C. 1966. Isotopic paleotemperatures. Science *154*: 851-857. *[The $\delta^{18}O$ signal is now known to be more a function of ice volume rather than temperature on the millennial time scale; see Dansgaard and Tauber]*

Estep, M. F. and H. Dabrowski. 1980. Tracing food webs with stable hydrogen isotopes. Science *209*: 1537-1538.

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Findlay, S. and K. Tenore. 1982. Nitrogen source for a detritivore: detritus substrate versus associate microbes. Science *218*: 371-372. *[A flawed study using spiked $\delta^{15}N$]*

Fisher, C. R., M. C. Kennicut and J. M. Brooks. 1990. Stable carbon isotopic evidence for carbon limitation in hydrothermal vent vestimentiferans. Science 247: 1094-1096. *[Their $\delta^{13}C$ looks like Spartina or the microphytobenthos. Normally chemoautotrophic bacteria have pronounced enzyme kinetic discrimination producing $\delta^{13}C$ values of -26. These vestimentiferans have enriched ratios indicating severe DIC limitation]*

Fontugne, M. R. and J.-C. Duplessey. 1981. Organic carbon isotopic fractionation by marine plankton in the temperature range -1 to 31ºC. Oceanol. Acta *4*: 85-90. *[Temperature reduces isotopic discrimination by 0.35 ‰ per degree C. Two different plankton populations are identified, with a distinct break at 25C. Not a particularly good paper. The authors did not separate the phytoplankton from zooplankton and pleuston.]*

France, R. L. 1995. Critical examination of stable carbon isotope analysis as a means for tracing carbon pathways in stream ecosystems. Can. J. Fish Aquat. Sci. *52*: 651-656.

France, R. L. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnol. Oceanogr. *40*: 1310-1313. *[Plants with boundaries will assimilate normally discriminated $^{13}C$. Benthic algae enriched by 7 ‰. Epilithon scraped from rocks had $\delta^{13}C \approx -17 \pm 2$; bimodal distribution observed between pelagic and littoral foodwebs.]*

France, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar. Ecol. Prog. Ser. *124*: 307-312.

Fry, B. 1986. Sources of carbon and sulfur nutrition for consumers in three meromictic lakes of New York State. Limnol. Oceanogr. *31*: 79-88.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. *33*: 1182-1189.

Fry, B. 1996. $^{13}C/C^{12}$ fractionation by marine diatoms. .Mar. Ecol. Prog. Ser. *134*: 283-294. *[External $CO_2$ is the biggest factor controlling isotopic discrimination]*

Fry, B. and P. L. Parker. 1979. Animal diet in Texas seagrass meadows: $\delta^{13}C$ evidence for the importance of benthic plants. Est. Coastal Mar. Sci. *8*: 499-509.

Fry, B. and E. Sherr. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contr. Mar. Sci. *27*: 13-47.

Fry, B. and S. C. Wainright. 1990 (abstract). Carbon isotopic fractionation by marine phytoplankton. Field results from George's Bank. *[A talk presented at the March 1990 AGU meeting in New Orleans. GA Bank phytoplankton fall in the range of -20 to -25 ‰. There is an isotopic discrimination from DIC to POC of 22 to 28 ‰. One bloom of the large diatom Coscinodiscus in August was observed with $\delta^{13}C$ values of -15.]*

Fry, B. and S. C. Wainright. 1991. Diatom sources of $\delta^{13}C$-rich carbon in marine food webs. Mar. Ecol. Prog. Ser. *76*: 149-157. [GA Bank spring bloom diatoms have $\delta^{13}C$ ratios of -15 ‰ to -19‰, whereas other phytoplankton had $\delta^{13}C$ values of -21 ‰ to -25 ‰. 40% of carbon for zooplankton from diatoms] {?}

Gearing, J. N., P. J. Gearing, D. T. Rudnick, A. G. Requejo and M. J. Hutchins. 1984. Isotopic variability of organic carbon in a phytoplankton-based, temperate estuary. Geochim. Cosmochim. Acta *48*: 1089-1098. *[Diatoms -20.3, nanoplankton is -22.2, benthos -16 to -20, meiofauna -19.7]*

Gervais, F. and U. Riebesell. 2001. Effect of phosphorus limitation on elemental composition and stable carbon isotope fractionation in a marine diatom grown under different $CO_2$ concentrations. Limnol. Oceanogr. *46*: 497-504 .[Cited by **Cloern et al. 2002**]

Goering, J., V. Alexander, and N. Haubenstock. 1990. Seasonal variability of stable carbon and nitrogen isotope ratios of organisms in a North Pacific Bay. Est. Coast. Shelf Sci. *30*: 239-260 *[Macoma nasuta., bloom diatoms settle out intact and ungrazed; $CO_2$ limitation]*

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Grande, K. D., J. Marra, C. Langdon, K. Heinemann and M. L. Bender. 1989. Rates of respiration in the light measured in marine phytoplankton using $^{18}O$ isotope-labelling technique. J. exp. Mar. Biol. Ecol. *129*: 95-120. *[$^{18}O$ labeling can separate light from dark respiration and can be used to estimate gross photosynthesis. The $^{14}C$ technique produces production estimates less than gross, but greater than community $O_2$ production. In incubations performed with $N_2$ bubbling, rates of production were twice as high as when incubations were performed in situ. This result would be consistent with Gould and Gallagher's (1990) hypothesis that stirring is necessary to limit the diffusional constraints on production. The bubbled simulated in situ incubators produce diffusional boundaries around the cells that are probably more like field conditions.]*

Gruszczynski, M., S. Halas, A. Hoffman, and K. Malkoski. 1989. A brachiopod calcite record of the oceanic carbon and oxygen isotopic shifts at the Permian/Triassic transition. Nature *337*: 64-68.

Haines, E. B. 1976. Stable carbon isotope rates in the biota, soils and tidal water of a Georgia salt marsh. Est. Coastal Marine Science *4*: 609-616.

Haines, E. B. 1977. The origins of detritus in Georgia salt marsh estuaries. Oikos *29*: 254-260.

Hedges, J. I, W. A. Clark and G. L. Cowey. 1988. Organic matter sources to the water column and surficial sediments of a marine bay. Limnol. Oceanogr. *33*: 1116-1136. *[Stable C ratios in traps varied from -23.6 to -19.3, with higher values in the spring.]*

Hemminga, M. A. and M. A. Mateo. 1996. Stable isotopes in seagrasses: variability in ratios and use in ecological studies. Mar. Ecol. Prog. Ser. *140*: 285-298. *[$\delta^{13}C$ of -10 to -11 with high range. Negative correlation between $\delta^{13}C$ and latitude, with temperate seagrasses more $^{13}C$ depleted than tropical]*

Herczeg, A. L. 1987. A stable carbon isotope study of dissolved inorganic carbon cycling in a softwater lake. Biogeochemistry *4*: 231-263.

Herman, P. M. J., J. J. Middelburg, J. Widdows, C. H. Lucas, and C. H. R. Heip. 2000. Stable isotopes as trophic tracers: combining field sampling and manipulative labelling of food resources for macrobenthos. Mar. Ecol. Prog. Ser. *204*: 79-92. *[Benthic diatoms have $\delta^{13}C$ of -15 other sources in low 20s. The dependence on microphytobenthos of the various species calculated]*

Hughes, J. E., L. A. Deegan, B. J. Peterson, R. M. Holmes and B. Fry. 2000. Nitrogen flow through the food web in the oligohaline zone of a New England estuary. Ecology *81*: 433-452.

Incze, L. S., L. M. Mayer, E. B. Sherr. and S. A. Macko. 1982. Carbon inputs to bivalve mollusks: a comparison of two estuaries. Can. J. Fish. Aquat. Sci. *39*: 1348-1352. *[Macoma balthica which is undoubtedly feeding on benthic diatoms has a stable isotope ratio similar to Spartina. This study offers indirect evidence for C-4 type metabolism in benthic diatoms.]*

Jasper, J. P. and J. M. Hayes. 1990. A carbon isotope record of $CO_2$ levels during the late quaternary. Nature *347*: 462-464. *[Isotope-ratio-monitoring GC/MS is used to analyze the $\delta^{13}C$ values alkadienones from prymnesiophytes (*e.g., coccolithophorids*) in cores in the N. Gulf of Mexico. Coccolithophorids lack a $CO_2$ concentrating mechanism. After correlation, using Popp et al.'s (1989) model with the Vostok ice core, they predict atmospheric $CO_2$ to 100 ky.]*

Kneib, R. T., A. E. Stiven, and E. B. Haines. 1980. Stable carbon isotope ratios in *Fundulus heteroclitus* (L.) muscle tissue and gut contents from a North Carolina *Spartina* marsh. J. exp. Mar. Biol. Ecol. 46: 89-98. *[Gut content $\delta^{13}C$=-16 to -18; muscle -14 to -16]*

Korb, R. E., J. A. Raven, A. M. Johnston and J. W. Leftley. 1996. Effects of cell size and specific growth rate on stable carbon isotope discrimination by two species of marine diatom. Mar. Ecol. Prog. Ser. *143*: 283-288. *[A large and small diatom were grown with the faster growing diatom is enriched in $\delta^{13}C$. Measure the source $\delta^{13}C$-DIC to get consistent results]*

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Korb, R. E, J. A. Raven, and A. M. Johnston. 1998. Relationship between aqueous $CO_2$ concentrations and stable carbon discrimination in the diatoms *Chaetoceros calcitrans* and *Ditylum brightwelli*. Mar. Ecol. Prog. Ser. *171*: 303-305. *[An inverse relation between $CO_2$(aq) and $\delta^{13}C$]*

Kwak, J. T. and J. Zedler. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110: 262-277.

Laws, E. A., B. N. Popp, R. R. Bidigare, M. C. Kennicutt, and S. A. Macko. 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aqu}$: theoretical considerations and experimental results. Geochim. Cosmochim. Acta *59*: 1131-1138.

Laws, E. A., R. R. Bidgare and B. N. Popp. 1997. Effect of grwoth rate and $CO_2$ concentration on carbon istopic fractionation by the marine diatom Phaedactylum tricornutum. Limnol. Oceanogr. *42*: 1552-1560. *[Experimental data and modeling reveal that the $\delta^{13}$ C ratio is a function of both specific growth rate and external nutrient supply. They discount active bicarbonate uptake, but propose other mechanisms for increasing the CO2 to O2 ratio at the RUBISCO active site]*

LeBlanc, C. G., R. A. Bourbonniere, H. P. Schwarcz, and M. J. Risk. 1989. Carbon isotopes and fatty acids of the sediments of Negro Harbour, Nova Scotia Canada. Est. Costal Shelf Sci. *28*: 261-276. *[plankton $\delta^{13}C$=-21.2; Zostera=-14.9; S. alterniflora=-12.2]*

Maberly, S. C. J. A. Raven and A. M. Johnston. 1992. Discrimination between $^{13}C$ and $^{12}C$ by marine plants. Oecologia 91: 481-492.

Macko, S. A., W. Y. Lee, and P. L. Parker. 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. J. Exp. Mar. Biol. Ecol. *63*: 145-149.

Macko, S. A., M. L. F. Estep, and W. Y. Lee. 1983. Stable hydrogen isotope analysis of foodwebs on laboratory and field populations of marine amphipods. J. Exp. Mar. Biol. Ecol. 72: 243-249.

Matson, E. A. and M. M. Brinson. 1990. Stable carbon isotopes and the C:N ration in the estuaries of the Pamlico and Neuse Rivers, North Carolina. Limnol. Oceanogr. *35*: 1290-1300.

McLelland, J. W., I. Valiella, and R. H. Michener. 1997. Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. Limnol. Oceanogr. *42*: 930-937.

McConnaughey, T. and C.P. McRoy. 1979. Food web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology *53*: 257-262. {cited by Rau 90}

McConnoughey, T. 1989. $^{13}C$ and $^{18}O$ isotopic disequilibrium in biological carbonates. I. Patterns. Geochim. Cosmochim. Acta 53: 151-162. II. In vitro simulation of kinetic isotope effects. *Ibid* 53: 163-171.

Middleburg, J. J., C. Barranguet, H. T. S. Boschker, P. M. J. Herman, T. Moens, and C. H. R. Heip. 2000. the fate of intertidal microphytobenthos carbon: an in situ $^{13}C$ -labeling study. Limnol. Oceanogr. 45: 1224-1234 . [Cited by **Takai et al. 2002**]

Moncreiff, C. A. and M. J. Sullivan. 2001. Trophic importance of epiphytic algae in subtropical seagrass beds. Evidence from multiple stable isotope analysis. Mar. Ecol. Prog. Ser. *215*: 93-106 .

Moncreiff, C. A., M. J. Sullivan and A. E. Daehnick. 1992. Primary production dynamics in seagrass beds of Mississippi Sound. The contributions of seagrass, epiphyte algae, sand microflora and phytoplankton. Mar. Ecol. Prog. Ser. *87*: 161-171.

Montero, P. M. S., A. G. James, A. D. Shalto-Douglas and J. G. Field. 1991. The $\delta^{13}C$ trophic position isotope spectrum as a tool to define and quantify carbon pathways in marine foodwebs. Mar. Ecol. Prog. Ser. *78*: 33-40. *[The argue for isotopic enrichment with trophic level, but they have not cleanly accounted for the isotopic enrichment of large diatoms which may produce enriched $\delta^{13}C$ ratios in larger grazers]*

Mook, W. G., J. C. Bommerson, and W. H. Staverman. 1974. Carbon isotope fractionation between dissolved bicarbonate and gaseous carbon dioxide. Earth Plan. Sci. Lett. *22*: 169-176. *[-8 to 10 ‰ fractionation between $CO_2$ and $HCO_3^-$]*

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Peters, K. E., R. E. Sweeney, and I. R. Kaplan. 1978. Correlation of carbon and nitrogen isotope ratios in sedimentary organic matter. Limnol. Oceanogr. *23*: 598-604.

Peterson, B. J., R. W. Howarth, F. Lipschultz, and D. Ashendorf. 1980. Salt marsh detritus: an alternative interpretation of stable carbon isotope ratios and the fate of *Spartina alterniflora*. Oikos *34*: 173-177.

Peterson, B. J., R. W. Howarth, and R. H. Garritt. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science *227*: 1361-1363. *[They argue that mussels feed on Spartina but they don't have estimates of the isotopic composition of the benthic diatoms in their salt marsh.]*

Peterson, B. J., R. W. Howarth, and R. H. Garritt. 1986. Sulfur and carbon isotopes as tracers of salt-marsh organic matter. Ecology *67*: 865-874.

Peterson, B. J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Ann. Rev. Ecol. Syst. *18*: 293-320. *[$\delta^{13}C$ for benthic diatoms of -17ppt, p. 313. They acknowledge that benthic microalgae have been inadequately characterized]*

Peterson, B. J. and R. W. Howarth. 1987. Sulfur, carbon and nitrogen isotopes used to trace organic matter flow in salt-marsh estuaries of Sapelo Island Georgia. Limnol. Oceanogr. *32*: 1195-1213. *[$\delta^{13}C$,$\delta^{15}N$,and $\delta^{34}S$ used to distinguish upland $C_3$ plants, Spartina alterniflora and plankton. The plankton $\delta^{13}C$=-21.3, Spartina was -12.9. Most of the marsh and estuarine macrofauna are similar neither to plankton or Spartina. Benthic diatoms, with a $\delta^{13}C$=-16.9 may have been the food source]*

Popp, E. A., R. Takiglku, J. M. Hayes, J. W. Louda, and E. W. Baker. 1989. Am. J. Sci. *289*: 841-844. *[Using the equation $\varepsilon_p$=a logc+b, where c is dissolved $CO_2$, and a and b are fitted constants, one can determine c from a isotopic fractionation in phytoplankton. $\varepsilon_p$ is the fractionation of phytoplankton carbon in an open system. Applied by Jasper and Hayes (1990) to estimate Quaternary $CO_2$[atm]]*

Popp, B. N. R. Takigiku, R. Hayes, J. W. Louda, and E. W. Baker. 1989. The post paleozoic chronology and mechanism of $\delta^{13}C$ depletion in primary marine organic matter. Am. J. Sci. *289*: *[Produced the model, used by Jasper and Hayes (1990) to predict the isotopic fractionation due to photosynthesis]*

Quay, P. D., B. Tilbrook, and C. S. Wong. 1992. Oceanic uptake of fossil fuel $CO_2$: carbon-13 evidence. Science *256*: 74-79. *[Models of $^{13}C$- and bomb-$^{14}C$-profiles confirms Tans et al.'s result that the open ocean is a major sink of atmospheric $CO_2$, but that there is a major sink not accounted for in current carbon budgets.]*

Rau, H. G. and J. I. Hedges. 1979. Carbon-13 depletion in a hydrothermal vent mussel: suggestion of a chemosynthetic food source. Science *203*: 648-649.

Rau, G. H. and N. H. Anderson. 1981. Use of $^{13}C/^{12}C$ to trace dissolved and particulate organic matter utilization by populations of an aquatic invertebrate. Oecologia *48*: 19-21.

Rau, G. H., R. E. Sweeney, and I. R. Kaplan. 1981. Differences in animal $^{13}C$, $^{15}N$, and D abundance between a polluted and an unpolluted coastal site: likely indicators of sewage uptake by a marine food web. Estuar. cst. Shelf Sci. *13*: 701-707. {cited by Rau 90}

Rau, G. H., R. E. Sweeney, and I. R. Kaplan. 1982. Plankton $^{13}C$:$^{12}C$ ratio changes with latitude: differences between northern and southern oceans. Deep-Sea Res. *29*: 1035-1039. *[The latitudinal asymmetry in $\delta^{13}C$ values is a true mystery. These authors didn't see it, but the only area where phytoplankton utilizing C-3 metabolism with no diffusional constraints is in the Antarctic; phytoplankton in all other areas experience some diffusional constraints or use C-4 type metabolism.]*

Rau, G.H., A. J. Mearns, D. R. Young, R. J. Olson, H. A. Schaffer and I. R. Kaplan. 1983. $^{13}C$ /$^{12}C$ correlates with trophic level in pelagic food webs. Ecology *64*: 1314-1318.

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Rau, G. H., T. Takahashi, and D. J. Des Marais. 1989. Latitudinal variations in plankton $\delta^{13}C$: implications for $CO_2$ and productivity in past oceans. Nature *341*: 516-517. *[Due to temperature dependence in the Henry's Law coefficient, $CO_2$ (aq) is far more abundant in cold Antarctic waters than in the tropics. There is an inverse relationship between $CO_2$ (aq) concentration and $\delta^{13}C$ ratio of the phytoplankton. Rau et al. confirm model predictions that the $CO_2$ concentrations in the Cretaceous atmosphere may have been over twice that of even today's fossil-fuel enriched $CO_2$ (atm) concentrations.]*

Rau, G. H., J.-L. Teyssie, F. Rassoulzadegan, and S. W. Fowler. 1990. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ variations among size-fractionated marine particles: implications for their origin and trophic relationships. Mar. Ecol. Prog. Ser. *59*: 33-38. *[Smaller particles (1-8μm) at a coastal Mediterranean site have lower $\delta^{13}C$ and $\delta^{15}N$ ratios. Interpretation is fuzzy because detritus, heterotrophs and autotrophs are all analyzed within each size class]*

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Riera, P, P. Richard, A Grémare, and G. Blanchard. 1996. Food source of intertidal nematodes in the Bay of Mareenes-Oléron (France), as determined by dual stable isotope analysis. Mar. Ecol. Prog. Ser. *142*: 303-309. *[Nematodes eat microphytobenthos] [Cited by **Takai et al. 2002**]*

Schwinghamer, P., F. C. Tan and D. C. Gordon. 1983. Stable carbon isotope studies on the Pecks Cove mudflat ecosystem in the Cumberland Basin, Bay of Fundy. Can. J. Fish. Aquat. Sci. *40*: 262-272. *[Spartina and benthic diatoms have similar $\delta^{13}C$ values for most of the year (-13 and -14 ‰). The benthic diatom $\delta^{13}C$ values usually ranged from -13.2 to -14.2 ‰; one sample in May had a $\delta^{13}C$ of -17.6 to -18.5ppt). The benthic macrofauna, Macoma, Corophium, and Heteromastus had $\delta^{13}C$ values of -13.1, -14.6 and -15.1 respectively. Interestingly, none of the benthic macrofauna appear to be deriving their carbon from the isotopically lighter bulk POC.]*

Sharkey, T. D. and J. A. Berry. 1985. Carbon isotope fractionation of algae as influenced by an inducible $CO_2$ concentration mechanism. Pp. 389-401 in W. J. Lucas and J. A. Berry, eds., Inorganic carbon uptake by photosynthetic organisms. Amer. Soc. Plant Physiol., Rockville MD. *[Gas blowing over $HCO_3^-$ only cultures was collected. The 28ppt fractionation observed due to RuBPCO; isotopically heavy phytoplankton with DIC pump, a model is proposed.]*

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Spies, R. B. H. Kruger, R. Ireland, and D. W. Rice. 1989. Stable isotope ratios and contaminant concentrations in a sewage-disturbed food web. Mar. Ecol. Prog. Ser. *54*: 157-170.

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Sullivan, M. J. and C. A. Moncreiff. 1990. Edaphic algae are an important component of saltmarsh food webs: evidence from multiple stable isotope analysis. Mar. Ecol. Prog. Ser. *62*: 149-159.

Takahashi, K., E. Wada, and M. Sakamoto. 1990. Carbon isotope discrimination by phytoplankton and photosynthetic bacteria in monomictic Lake Fukami-ike. Arch. Hydrobiol. *120*: 197-210.

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Van Dover, C. L. and B. Fry. 1989. Stable isotopic composition of hydrothermal vent organisms. Marine Biology *102*: 257-263.

Wada, E. and A. Hattori. 1978. Nitrogen isotope effects in the assimilation of inorganic nitrogenous compounds by marine diatoms. Geomicrobiology *1*: 85-101.

Wada, E., M. Terazaki, Y. Kabaya and T. Nemoto. 1987. $^{15}N$ and $^{13}C$ abundances in the Antarctic ocean with emphasis on the biogeochemical structure of the food web. Deep-Sea Res. *34*: 829-841. *[The $\delta^{13}C$ of phytoplankton is a very low -26.9 (for oceanic phytoplankton), about 10 ‰ enriched compared to the maximum isotopic fractionation for the RuBPCase system {strangely, they assume that diatoms are using $HCO_3^-$ or their description is wrong}. The $\delta^{15}N$ value is also low indicating maximal kinetic isotope fractionation using $NO_3^-$ ($\delta^{15}N$ =7ppt, phytoplankton POM $\delta^{15}N \approx 0.1$). One 3870 m core had isotopically enriched $\delta^{13}C$ indicative of ice algae.]*

Wainright, S. C. and B. Fry. 1990 (abstract). Carbon isotope comparisons of planktonic algae grown is seawater enrichment cultures. New Orleans AGU meeting. *[Field isotope fractionation from GA Bank approached 30 ‰ in some areas. Phytoplankton grown in culture exhibited less fractionation 17.6 ‰ to -23ppt, especially if silicate was added. Fractionation was independent of pH, indicating a lack of direct coupling to $CO_2$[aqu]]*

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## BENTHIC DIATOMS AS INDICATORS

Birks, H. J. B, S. Juggins, and J. M. Line. 1990. Lake surface-water chemistry reconstructions from palaelimnological data. Pp. 301-313 *in* B. J. Mason, ed., The surface waters acidification program. Cambridge University Press, Cambridge. *[Surface water acidification (SWAP) program: Diatom counts from 178 surface samples in lakes from England (5), Norway (51), Scotland (60), Sweden (30) and Wales (32). Canonical correspondence analysis used for constrained ordination. Distinct diatom gradient correlated with alkalinity, Ca and pH, and a significant gradient associated with DOC. A paleolimnology history of lake pH and DOC is constructed, stretching back 10,000 years]*

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Birks, H. J. B., J. M. Line S. Juggins, A. C. Stevenson, and C. J. F. ter Braak. 1990. Diatoms and pH reconstruction. Phil. Trans. R. Soc. Lond. B 327: 263-278. *[Maximum likelihood estimation used to fit pH to diatom species composition profiles. A Gaussian unimodal response model fit with logit regression]*

ter Braak, C. J. F. and S. Juggins. 1993. Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia **269/270:** 485-502. *[PLS, developed by Wold for chemometrics, applied for the 1st time to develop a transfer function to predict environmental composition (pH) using diatom species composition]* {}

ten Cate, J. H., R. Maasdam and R. M. M. Roijackers. 1993. Perspectives for the use of diatom assemblages in the water management policy of Overijssel (The Netherlands). Hydrobiologia 269/270: 351-359.

Chmura, G. L., A. Santos, V. Pospelova, Z. Spasojevic, R. Lam, and J. S. Latimer. 2004. Response of three paleo-primary production measures to development of an urban estuary. Science Total Environment. *320*: 225-243. *[Benthic & pelagic diatoms measured in cores to assess New Bedford Harbor eutrophication: pigments, biogenic silica (BSi), and cysts of autotrophic dinoflagellates, palynological signals of land clearance, changes in the ratio of centric and pennate diatoms, sedimentary organic carbon and stable carbon isotopes to constrain our interpretations. Nutrient loading from watershed clearance and urban sewage on the estuarine ecosystem shifted not only levels of primary production, but also the nature of the production from benthic-dominated to pelagic-dominated. Water column production (by diatoms and dinoflagellates) rapidly increased as soil nitrogen was released following forest clearance. Stabilization in rates of forest clearance is reflected as a decline in production. A new sewer outfall near the core site and changes in estuarine hydrography due to construction of a hurricane barrier across the mouth of the harbor are reflected by renewed water column production, but decreases in the population of diatoms and dinoflagellates..]{?}*

Pienitz, R. and J. P. Smol. 1993. Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest-tundra ecotone near Yellowknife, Northwest Territories, Canada. Hydrobiologia 269/270: 391-404. *[Canonical correspondence analysis used to infer DIC and DOC from diatom composition]*

## REDALJE-LAWS CHL -SPECIFIC LABELING

Calliau, C., H. Claustre, F. Vidussi, D. Marie, and D. Vaulot. 1996. Carbon biomass, and gross growth rates as estimated from $^{14}$C pigment labeling, during photoacclimation in *Prochlorococcus* CCMP 1378. Mar. Ecol. Prog. Ser. *145*: 209-221. *[Lab studies indicate that $^{14}$C incorporation into zeaxzanthin better than into Dv-chl a to estimate prochlorophyte μ]*

DiTullio, G. R. and E. A. Laws. 1986. Diel periodicity of nitrogen and carbon assimilation in five species of marine phytoplankton: accuracy of methodology for predicting N-assimilation rates and N/C composition ratios. Mar. Ecol. Prog. Ser. *32*: 123-132. *[Estimates of the percentage of $^{14}$C incorporated into protein after 24 h (12L:12D) can provide estimates of the relative rates of C and N assimilation and hence relative growth rates] [?]*

DiTullio, G. R., D. A. Hutchins, and K. W. Bruland. 1993. Interaction of iron and major nutrients controls phytoplankton growth and species composition in the tropical North Pacific Ocean. Limnol. Oceanogr. 38: 495-508. *[Chl-a specific labeling used to estimate the specific growth rate of pico-, nano- and microplankton at 9º N in the Pacific. Large diatoms are limited by Fe; prochlorophyte specific growth {measured by specific activity of divinyl Chl a labeling} limited by macronutrients. Picoplankton appeared to be controlled by grazers, but diatoms were controlled by Fe limitation]*

Eppley, R. W., E. Swift, D. G. Redalje M. R. Landry and L. W. Hass. 1988. Subsurface chlorophyll maximum in August-September 1985 in the CLIMAX area of the North Pacific. Mar. Ecol. Prog. Ser. *42*: 289-301.

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 Press, New York. *[To be discussed and outlined in the class on Gyre productivity]*

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Gieskes, W. W. and G. W. Kraay. 1986. Floristic and physiological differences between the shallow and the deep nanophytoplankton community in the euphotic zone of the open tropical Atlantic revealed by HPLC analysis of pigments. Marine Biology *91*: 567-576. *[Primary production incubations done on deck with neutral density filters. Reverse-phase HPLC used to analyze the floral composition of the surface and deep communities off Africa. Diatoms have high concentrations of fucoxanthin, cyanobacteria have high concentrations of zeaxanthin, and Prymnesiophyscea (Coccolithophorids) have 19'- hexanolyloxyfucoxanthis). The* ***Redalje-Laws (1981)*** *technique is also applied to estimate phytoplankton carbon concentration and specific growth rates. High assimilation numbers were observed (15), despite having relatively low dark-bottle $^{14}C$ incubations.]*

Gieskes, W. W. and G. W. Kraay. 1989. Estimating the carbon-specific growth rate of the major algal species in eastern Indonesian waters by $^{14}C$ labeling of taxon-specific carotenoids. Deep-Sea Res. *36*: 1127-1139. *[The* ***Redalje-Laws (1981)*** *technique is expanded to analyze the specific growth rate of different floral groups based on the specific activity in Chl a and taxon-specific accessory pigments]* {?}

Goericke, R. 1998. Response of phytoplankton community structure and taxon-specific growth rates to seasonally varying physical forcing of the Sargasso Sea off Bermuda. Limnol. Oceanogr *43*: 921-935.

Goericke, R. 1998. Response of Sargasso Sea phytoplankton biomass, growth rates and primary production to seasonally varying physical forcing., J Plankton Res *20*: 2223-2249.

Goericke, R. and N. A. Welschmeyer. 1993a. The chlorophyll-labeling method: measuring specific rates of chlorophyll *a* synthesis in cultures and in the open ocean. Limnol. Oceanogr. *38*: 80-95.

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Gould, D. M. 1989. Epipelic diatoms of Savin Hill Cove: an analysis of species composition, biomass, specific growth rates and primary production. Ph.D. dissertation, Environmental Sciences Program, UMASS/Boston.

Gould, D. G. and E. D. Gallagher. 1990. Field measurement of specific growth rate, biomass and primary production of benthic diatoms of Savin Hill Cove, Boston. Limnol. Oceanogr. *35*: 1757-1770. *[The* ***Redalje-Laws (1981)*** *technique adapted for benthic diatoms: high biomass and production, low μ (6-8 day doubling times)]*

Jesperson, A.-M., J. Nielsen, B. Riemann, and M. Søndergaard. 1992. Carbon-specific phytoplankton growth rates: a comparison of methods. J. Plankton Res. *14*: 637-648. *[Axenic cultures used. Problems in all methods.* ***Redalje-Laws (1981)*** *$^{14}C$ method labels Chl* a *higher than total algal C, producing too high an estimate of μ]*

Laws, E. A. 1984. Improved estimates of phytoplankton carbon based on $^{14}C$ incorporation into chlorophyll *a*. J. Theor. biol. *110*: 425-434.{**13**, **14**}

Laws, E. A., D. J. 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 coastal waters. Limnol. Oceanogr. *29*: 1161-1169.

Laws, E. A., G. R. DiTullio, and D. J. Redalje. 1987. High phytoplankton growth and production rates in the North Pacific subtropical gyre. Limnol. Oceanogr. *34*: 905-918.

Redalje, D. G. 1983. Phytoplankton carbon biomass and specific growth rates determined with the labeled chlorophyll a technique. Marine Ecology Progress Series *11:* 217-225.{?}

Redalje, D. G. and E. A. Laws. 1981. A new method for estimating phytoplankton growth rates and carbon biomass. Marine Biology *62:* 73-79. *[A landmark paper describing the Chl a-specific labeling procedure for estimating μ]* {**13**, **48**}

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Strom, S. L. and N. A. Welschmeyer. 1991. Pigment-specific rates of phytoplankton growth and microzooplankton grazing in the open subarctic Pacific Ocean. Limnol. Oceanogr. *36*: 50-63. *[48 h, clean bottle, incubations with dilution grazing experiments (* ***Landry & Hassett 1982****) and pigment-specific µ determinations (by HPLC)]* {?}

Taguchi, S., G. R. DiTullio and E. A. Laws. 1988. Physiological characteristics and production of mixed layer and chlorophyll maximum phytoplankton populations in the Caribbean Sea and western Atlantic Ocean. Deep-Sea Res. *35*: 1363-1377. *[Chl a and DiTullio's protein specific labeling are used to estimate absolute and relative growth rates, respectively, using clean techniques. Surprisingly, 23% of inorganic carbon fixation occurred at night and by phytoplankton. Taguchi et al. attribute this to the incorporation of DOM produced during the day, but fixation via C4-type pathways may provide an alternate explanation. The chl maximum is neither a biomass nor production maximum]*

Waterhouse, T.Y. and N.A. Welschmeyer. 1995. Taxon-specific analysis of microzooplankton grazing rates and phytoplankton growth rates. Limnol. Oceanog. *40*: 827-834

Welschmeyer, N. A. and C. J. Lorenzen. 1984. Carbon-14 labeling of phytoplankton carbon and chlorophyll a carbon: determination of specific growth rates. Limnol. Oceanogr. *29*: 135-145.{**14**, **15**}

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Eckman, J. E. 1979. Small-scale patterns and processes in a soft-substratum intertidal community. Journal of Marine Research *37*: 437-457. *[An important study introducing the use of spatial cross correlation statistics to ecology. Tanaids respond to sewing needles and animal abundances are correlated with ridge-crest topography on the Skagit flats]* {**11**}

Falkowski, P. G. and J. A. Raven. 1997. Aquatic Photosynthesis. Blackwell Science, Malden MA. 375 pp. *{**5**}*

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Wimbush, M. 1976. The physics of the benthic boundary layer. Pp. 3-10 in I. N. McCave, ed., The Benthic Boundary Layer. Plenum Press, New York. {**9**}

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