
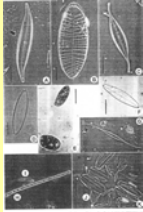
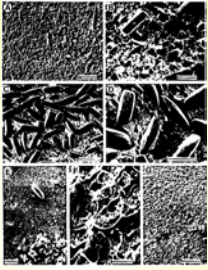
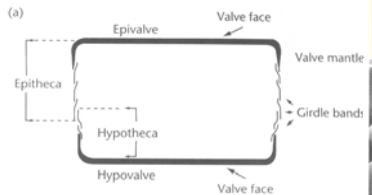
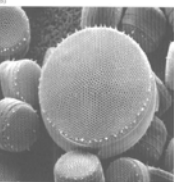
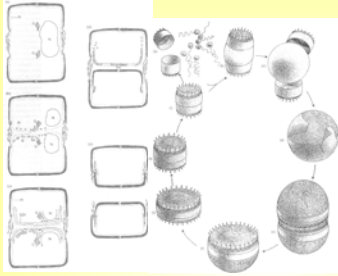
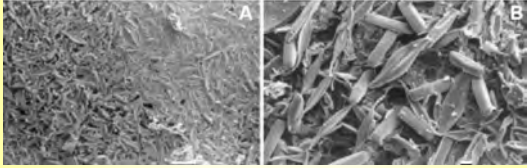

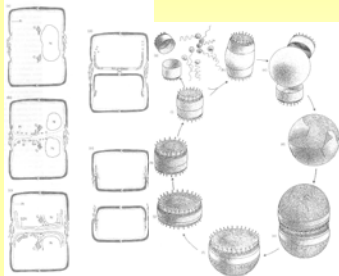


<div data-bbox="256 195 743 312" data-label="Section-Header"> <h2>Microphytobenthos, Especially Benthic Diatom Production</h2> </div> <div data-bbox="337 323 672 354" data-label="Text"> <p>Class 6: Th September 18, 2008</p> </div> <div data-bbox="531 497 786 541" data-label="Image"> </div>	<div data-bbox="816 132 1375 172" data-label="Section-Header"> <h3>Slide 1 Microphytobenthos, Especially</h3> </div> <div data-bbox="816 195 1180 228" data-label="Text"> <p>Benthic Diatom Production</p> </div> <div data-bbox="816 317 941 352" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="386 653 625 690" data-label="Section-Header"> <h2>Class schedule</h2> </div> <div data-bbox="430 699 579 728" data-label="Section-Header"> <h3>Order of topics</h3> </div> <div data-bbox="237 728 760 997" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Microphytobenthos today <ul style="list-style-type: none"> <li>• Chapter 3</li> <li>• 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. <i>Limnol. Oceanogr.</i> 35: 1757-1770.</li> </ul> </li> <li>• For Tuesday Benthic Population Biology <ul style="list-style-type: none"> <li>• Gallagher, E. D., G. B. Gardner and P. A. Jumars 1990. Competition among the pioneers in soft bottom benthic succession: field experiments and analysis of the Gilpin-Ayala competition model. <i>Oecologia</i> 83: 427-442.</li> <li>• Whittlatch, R. B. 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. <i>J. Mar. Res.</i> 38: 743-765.</li> </ul> </li> </ul> </div> <div data-bbox="531 984 786 1029" data-label="Image"> </div>	<div data-bbox="816 621 1143 657" data-label="Section-Header"> <h3>Slide 2 Class schedule</h3> </div> <div data-bbox="816 743 941 779" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="363 1144 649 1184" data-label="Section-Header"> <h2>Darwin's worms</h2> </div> <div data-bbox="303 1188 717 1218" data-label="Section-Header"> <h3>Earthworms: Oligochaetes (few bristles)</h3> </div> <div data-bbox="225 1213 758 1518" data-label="Image"> </div>	<div data-bbox="816 1108 1169 1146" data-label="Section-Header"> <h3>Slide 3 Darwin's worms</h3> </div> <div data-bbox="816 1232 941 1266" data-label="Text"> <p>NOTES:</p> </div>

<div data-bbox="347 165 669 203" data-label="Section-Header"> <h2>Nightcrawler burrows</h2> </div> <div data-bbox="393 214 605 241" data-label="Text"> <p>Can be up to 2 m deep</p> </div> <div data-bbox="237 245 509 497" data-label="List-Group"> <ul style="list-style-type: none"> <li>• Three types of earthworm feeding: <ul style="list-style-type: none"> <li>➢ Feeding on surface litter, dragging leaves and organic matter into burrows</li> <li>➢ Burrowing through the surface litter</li> <li>➢ Burrowing through deeper soils</li> </ul> </li> <li>• Nightcrawlers drag leaves into deep burrows <ul style="list-style-type: none"> <li>➢ Darwin: hundreds of leaf fragments per day</li> <li>➢ Produce middens, mounds of leaf material, at surface</li> </ul> </li> </ul> </div> <div data-bbox="509 241 776 541" data-label="Image"> <p>Fig. 4. Common earthworms (Lumbricus terrestris) in the soil. The worm (dark) is shown in the burrow (dark) in the soil. The burrow has a depth of approximately 1.5 m. The worm is a length of 1.5 m.</p> </div>	<div data-bbox="816 134 1248 170" data-label="Section-Header"> <h2>Slide 4 Nightcrawler burrows</h2> </div> <div data-bbox="816 256 940 291" data-label="Text"> <p>NOTES:</p> </div>
	<div data-bbox="816 621 919 657" data-label="Section-Header"> <h2>Slide 5</h2> </div> <div data-bbox="816 743 940 779" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="321 1144 696 1180" data-label="Section-Header"> <h2>Are earthworms harmful?</h2> </div> <div data-bbox="279 1188 747 1218" data-label="Text"> <p>Destroy the 'duff' layer, essential for native species</p> </div> <div data-bbox="241 1222 771 1518" data-label="Image"> </div> <div data-bbox="446 1428 511 1457" data-label="Text"> <p>Yes!</p> </div>	<div data-bbox="816 1108 1302 1146" data-label="Section-Header"> <h2>Slide 6 Are earthworms harmful?</h2> </div> <div data-bbox="816 1232 940 1266" data-label="Text"> <p>NOTES:</p> </div>

<p><b>Don't release earthworms into forests!</b></p> 	<p><b>Slide 7 Don't release earthworms into forests!</b></p>
	<p>NOTES:</p>
	<p><b>Slide 8 All New England earthworms wiped out by the Pleistocene Glaciation (&gt;13,000 years ago)</b></p>
	<p>NOTES:</p>
	<p><b>Slide 9 Big topics for today's class</b></p>
	<p>NOTES:</p>

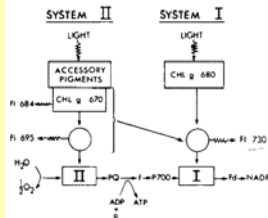
<p style="text-align: center;"><b>Microphytobenthos</b></p> <p style="text-align: center;"><math>20\ \mu\text{m} - 1\ \text{mm length}, 5 \times 10^6\ \text{cells}/\text{cm}^2, .5\text{-}20\ \text{g C m}^{-2}</math></p> <div style="display: flex; justify-content: space-around;">   </div> <div style="display: flex; justify-content: space-between;"> <p>Brotas &amp; Plante-Cuny (1998, MEPS), Scale bars: 20 <math>\mu\text{m}</math></p> <p>Paterson (1989)</p> </div>	<p><b>Slide 10 Microphytobenthos</b></p> <p>NOTES:</p>
<p style="text-align: center;"><b>Diatom frustules</b></p> <p style="text-align: center;">Miller (2004) Fig. 2.1, <i>Thalassiosira</i></p> <div style="display: flex; align-items: center;">   </div>	<p><b>Slide 11 Diatom frustules</b></p> <p>NOTES:</p>
<p style="text-align: center;"><b>Diatom cell division, can be used to estimate <math>\mu</math> specific growth rate</b></p> <p style="text-align: center;">Miller (2004) Figs. 2.4 &amp; 2.6</p> <div style="display: flex; align-items: center;">  <div style="margin-left: 20px;"> <p>Frequency of dividing cells can be used to estimate <math>\mu</math> (McDuff &amp; Chisholm equations)</p> </div> </div>	<p><b>Slide 12 Diatom cell division, can be used to estimate <math>\mu</math> specific growth rate</b></p> <p>NOTES:</p>

<p><b>Microphytobenthic motility</b></p> <p>Defew et al. (2002) Right: 10-<math>\mu</math>m scale</p>  	<p><b>Slide 13 Diatom cell division, can be used to estimate <math>\mu</math> specific growth rate</b></p> <p>NOTES:</p>
<p><b>Diatom cell division, can be used to estimate <math>\mu</math> specific growth rate</b></p> <p>Miller (2004) Figs. 2.4 &amp; 2.6</p>  <p>Frequency of dividing cells can be used to estimate <math>\mu</math> (McDuff &amp; Chisholm equations)</p>	<p><b>Slide 14 Microphytobenthic motility</b></p> <p>NOTES:</p>
<p><b>Methods for estimating benthic diatom standing stock, production &amp; specific growth rate (<math>\mu</math>)</b></p> <ul style="list-style-type: none"> <li>• Estimating standing stock: <ul style="list-style-type: none"> <li>• Cell numbers</li> <li>• Biomass using Chl <i>a</i> extraction (measured using fluorescence in laboratory)</li> </ul> </li> <li>• Estimating production <ul style="list-style-type: none"> <li>• <math>^{14}\text{C}</math> incorporation into organic matter</li> <li>• <math>\text{O}_2</math> production <ul style="list-style-type: none"> <li>■ Bell jars</li> <li>■ Microelectrodes</li> </ul> </li> <li>• Fluorescence: fast-repetition and pulse amplitude modulated fluorescence (FRR &amp; PAM)</li> </ul> </li> <li>• Estimating <math>\mu</math>: Redalje-Laws Chl <i>a</i>-specific <math>^{14}\text{C}</math> activity</li> </ul>	<p><b>Slide 15 Methods for estimating benthic diatom standing stock, production &amp; specific growth rate (<math>\mu</math>)</b></p> <p>NOTES:</p>

<div data-bbox="313 163 711 201" data-label="Section-Header"> <h2>Chlorophyll a fluorescence</h2> </div> <div data-bbox="280 212 730 258" data-label="Text"> <p>Lorenzen (1966) excite at 430 nm (blue), measure fluorescence at 650-680 nm (red)</p> </div> <div data-bbox="238 256 680 529" data-label="Chemical-Block"> <p>(a)</p> <p>Chlorophyll a, R = CH<sub>3</sub> Chlorophyll b, R = CHO</p> </div>	<div data-bbox="820 130 1326 168" data-label="Section-Header"> <h2>Slide 16 Chlorophyll a fluorescence</h2> </div> <div data-bbox="820 252 941 287" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="380 653 618 690" data-label="Section-Header"> <h2>Lorenzen (1966)</h2> </div> <div data-bbox="303 699 714 724" data-label="Text"> <p>Linear relation between Chl a &amp; fluorescence</p> </div> <div data-bbox="277 722 641 1029" data-label="Figure"> <p>Fig. 1. Linear relationship between relative chlorophyll, serial dilutions of a single population with PH Millipore® filtered seawater, and in vivo fluorescence. Curve A, IX sensitivity scale, and B, IX sensitivity scale.</p> <p>the blank readings are probably the result of light scattering and/or light leakage through the color filter.</p> <p>ECOS630</p> </div>	<div data-bbox="820 619 1182 657" data-label="Section-Header"> <h2>Slide 17 Lorenzen (1966)</h2> </div> <div data-bbox="820 739 941 774" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="280 1136 753 1218" data-label="Text"> <p>In situ fluorometry allows an analysis of fine scale pattern in phytoplankton biomass, in real time</p> </div> <div data-bbox="238 1224 633 1520" data-label="Figure"> <p>Fig. 2. A portion of the trace obtained on cruise TO-45-1 showing variables in chlorophyll a concentrations and temperature as the ship proceeded from 26° 33' N, 112° 45' W to 26° 52' N, 112° 45' W.</p> </div>	<div data-bbox="820 1108 1356 1220" data-label="Text"> <p>Slide 18 In situ fluorometry allows an analysis of fine scale pattern in phytoplankton biomass, in real time</p> </div> <div data-bbox="820 1302 941 1337" data-label="Text"> <p>NOTES:</p> </div>

## Photosystem II is the source of most fluorescence

Light-dependent rate of electron flow to terminal electron acceptors (Falkowski & Raven, 1997 p 264)



Figures from Parsons et al. (1984)

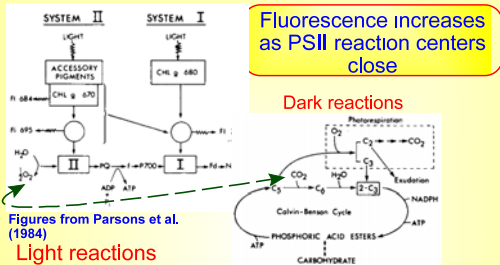


## Slide 19 Photosystem II is the source of most fluorescence

NOTES:

## Gross primary productivity

Light-dependent rate of electron flow to terminal electron acceptors (Falkowski & Raven, 1997 p 264)



Figures from Parsons et al. (1984)

Light reactions

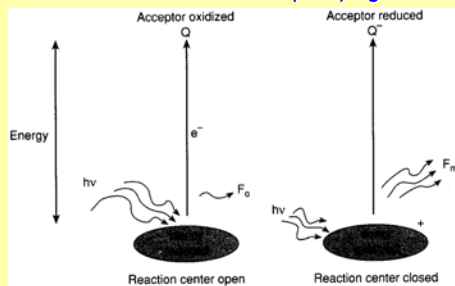
Dark reactions

## Slide 20 Gross primary productivity

NOTES:

## Fluorescence yield not constant: open & closed reaction centers


Falkowski & Raven (1997) Figure 3.11



## Slide 21 Fluorescence yield not constant: open & closed reaction centers

NOTES:



<p><b>Specific growth rate, 'mu' <math>\mu</math> and little 'r'</b></p> <p><math>\mu</math> is the specific growth rate, (per capita growth rate);  <math>\mu_{\max}</math> is max growth rate, intrinsic growth rate, Malthusian parameter</p> $\frac{dN}{dt} = \mu N.$ $\mu = \frac{1}{N} \frac{dN}{dt}.$ $\frac{dN}{dt} = \mu_{\max} N, \text{ with no resource limitation.}$ $\mu_{\max} = \frac{1}{N} \frac{dN}{dt}.$ 	<p><b>Slide 22 Specific growth rate, 'mu' <math>\mu</math> and little 'r'</b></p>
	<p>NOTES:</p>

**The Malthusian parameter:  $r_{\max}$**

Maximum growth rate. no density-dependent limitation

$$\frac{dN}{dt} = r N.$$

$$\frac{dN}{dt} = r_{\max} N, \text{ with no resource limitation.}$$

$$N_t = N_0 e^{\mu_{\max} t},$$

$$N_t = N_0 e^{r_{\max} t},$$

$$\ln \left( \frac{N_t}{N_0} \right) = \mu_{\max} t.$$

$$\ln \left( \frac{N_t}{N_0} \right) = r_{\max} t.$$

**ECOS630**

**Specific growth rate,  $\mu$ , and doublings per day (archaic)**

$\mu$ : Units of inverse time

$$\ln \left( \frac{N_t}{N_0} \right) = \ln(2) = \mu t_d.$$

$$t_d = \frac{\ln(2)}{\mu} \approx \frac{0.693}{\mu}.$$

$$\text{Specific growth rate} \left[ \frac{\text{doublings}}{\text{day}} \right] = \frac{1}{t_d}.$$

$$= \frac{\mu}{\ln(2)}.$$

$$\approx \frac{\mu}{0.693}.$$



### Biomass-specific production, $\mu$

Estimating biomass, in carbon, the key problem in estimating  $\mu$ . Estimating photoautotrophic Carbon:Chl *a* ratio difficult

$$\begin{aligned}\mu &= \frac{\text{specific production}}{\text{biomass}} = \frac{P}{B} \\ &= \frac{\frac{dC}{dt}}{B}\end{aligned}$$

ECOS630

### Slide 25 Biomass-specific production, $\mu$

NOTES:

### Bell jars used to estimate $O_2$ flux

Uthicke & Klumpp (1998), MEPS

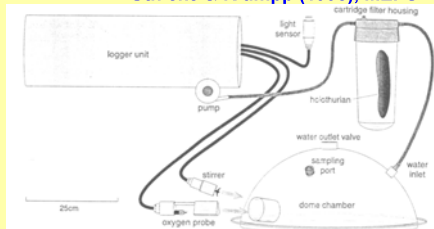


Fig. 1. Schematic diagram of the components of the respirometer with dome chambers as used in nutrient enhancement experiments. In routine respirometry measurements, the filter housing with holodurian was omitted. See Klumpp et al. (1987) for details on respirometer components

### Slide 26 Bell jars used to estimate $O_2$ flux

NOTES:

### The oxygen method

Separating Gross vs. Net production.

- Use light and dark bottles
- Dark bottle measures respiration (but not photorespiration)
  - Photorespiration may not be too important
  - In the absence of grazers, light bottle measures net production.
  - In the absence of grazers, Light-Dark measures gross production.
- Photorespiration and heterotrophic respiration create large problems

### Slide 27 The oxygen method

NOTES:

<div data-bbox="425 165 570 205" data-label="Section-Header"> <h3><math>O_2</math> vs. <math>^{14}C</math></h3> </div> <div data-bbox="248 218 745 340" data-label="Text"> <p> <math>n CO_2 \xrightarrow{\text{light}} \text{Particulate organic } C_1 + \text{Dissolved organic } C_2 + n O_2_3</math>  <math>O_2</math> method measures <math>O_2</math> production, = measuring 1 + 2.  <math>^{14}C</math> method measures only 1 if only filtered POC is counted.         </p> </div> <div data-bbox="259 350 737 531" data-label="List-Group"> <ul style="list-style-type: none"> <li>■ In theory, the <math>O_2</math> method can estimate gross and net production             <ul style="list-style-type: none"> <li>▸ Increase in light bottle is net</li> <li>▸ Dark bottle decrease is respiration</li> <li>▸ Light-dark = gross production</li> </ul> </li> <li>■ The <math>^{14}C</math> activity of dissolved organic matter should be determined</li> </ul> </div>	<div data-bbox="816 132 1107 168" data-label="Section-Header"> <h3>Slide 28 <math>O_2</math> vs. <math>^{14}C</math></h3> </div> <div data-bbox="816 256 940 291" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="267 651 753 707" data-label="Section-Header"> <h3><math>O_2</math> flux used to measure Stellwagen Bank microphytobenthic production</h3> </div> <div data-bbox="311 716 698 743" data-label="Text"> <p>Cahoon et al. 1993 Figure 1 &amp; Conclusion</p> </div> <div data-bbox="235 749 401 984" data-label="Image"> </div> <div data-bbox="420 770 756 972" data-label="Text"> <p>The importance of benthic microalgal production at Stellwagen Bank derives from the apparent ability of the distinctly benthic microalgal assemblage there to sustain significant production at light levels consistently below 1% surface incident PPFD. If this ability is common, benthic microalgae may be widely distributed in continental shelf habitats. Benthic habitats underlying clearer, less productive water columns than at Stellwagen Bank may support relatively higher benthic microalgal production. Benthic microalgal production may therefore be a significant, if infrequently considered, fraction of total production in continental shelf ecosystems.</p> </div> <div data-bbox="652 1001 773 1029" data-label="Text"> <p>ECOS630</p> </div>	<div data-bbox="816 623 1326 735" data-label="Section-Header"> <h3>Slide 29 <math>O_2</math> flux used to measure Stellwagen Bank microphytobenthic production</h3> </div> <div data-bbox="816 821 940 854" data-label="Text"> <p>NOTES:</p> </div>
<div data-bbox="347 1218 669 1255" data-label="Section-Header"> <h3>Sub-aerial production</h3> </div> <div data-bbox="271 1264 751 1293" data-label="Text"> <p>Whitney &amp; Darley's surveys of Georgia Salt marshes</p> </div> <div data-bbox="246 1306 539 1583" data-label="Image"> </div> <div data-bbox="565 1312 709 1556" data-label="Text"> <p>Georgia salt marshes Highest benthic diatom production ever measured! diffusive sublayer thickness &lt; 10 <math>\mu m</math></p> </div>	<div data-bbox="816 1184 1261 1222" data-label="Section-Header"> <h3>Slide 30 Sub-aerial production</h3> </div> <div data-bbox="816 1306 940 1341" data-label="Text"> <p>NOTES:</p> </div>

## Redalje-Laws Chl a labelling

HPLC separation of Chl a to determine  $^{14}\text{C}$  activity  
Gould & Gallagher (1990)

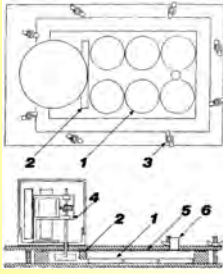


Table 1. Definitions and equations used in the  $^{14}\text{C}$ -Chl a labelling technique (adapted for sediment from Redalje and Laws 1981; Redalje 1983; Woloszewicz and Linzen 1984).

$A^*$	Activity of total particulate matter, dpm
$R^*$	Specific activity of C in Chl a molecule, dpm $\mu\text{g}^{-1}\text{C}$
$P^*$	Specific activity of DMC, dpm $\mu\text{g}^{-1}\text{C}$
$\Delta C$	$^1\text{C}$ fixed during the incubation, $\mu\text{g C core}^{-1}$ incubation $\times$ converted to $\mu\text{g C m}^{-2}\text{d}^{-1}$
$C_p$	Microalgal C present at the end of the incubation, $\mu\text{g C core}^{-1}$ converted to $\mu\text{g C cm}^{-2}$
$\mu$	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:	
$\Delta C = 1.05 [(A^*/P^*) \times (1/f)]$	(1)
$C_p = A^*/R^*$	(2)
$\mu = \frac{-\ln(1 - 1.05 R^* \times P^* \times t)}{t} \times 12$	(3)

## Slide 31 Redalje-Laws Chl a labelling

NOTES:

## Gould & Gallagher (1990)

Estimates of diatom standing stock,  $\mu$ , and production

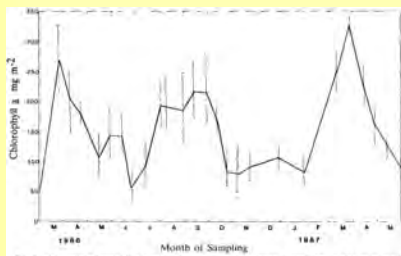


Fig. 1. Relationship between Chl a concentration and date of sampling. Letters indicate the beginning of each month. The 95% confidence limits (based on  $n=136$  SD,  $n=21$  per month).



## Slide 32 Gould & Gallagher (1990)

NOTES:

TABLE 2. RESULTS OF CHL INCUBATIONS DONE IN SAVIN HILL COVE AND LABORATORY INCUBATION OF LUXURANT SEDIMENT. C: Chl ratio is based on  $C_p$  calculated via  $^{14}\text{C}$ -Chl a labelling 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  $\mu$ ,  $r_s = -0.94$ ,  $P < 0.01$ ;  $C_p$  and C: Chl,  $r_s = 0.89$ ,  $P < 0.05$ ;  $C_p$  and  $\mu$ ,  $r_s = -0.78$ ,  $P < 0.05$ . Units given in Table 1. Temperature ( $^{\circ}\text{C}$ ) in the incubation chamber at the end of the incubation— $T$ ; doubling time (d)—DT.

	$T$	$\mu$	$P^* \times 10^3$	$P^* \times 10^3$	$R^*$	$\Delta C$	$C_p \times 10^3$	$\mu$	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	15.6(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(3)	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(66)	112(16)	15.40(3.36)	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(8)	58(8)	6.19(0.89)	0.17(0.01)	3.6	42.5
4 Jul 88										
Low-high	20	10.5	18.55(0.20)	8.08	608(100)	69(94)	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(99)	54(7)	11.60(3.00)	0.06(0.01)	11.6	55.4

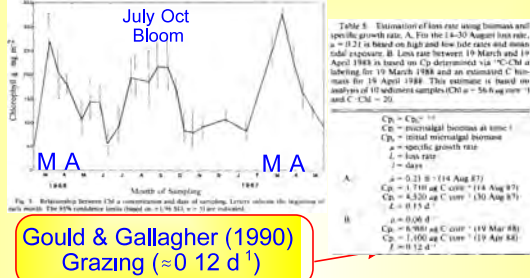
Doubling time =  $\ln(2)/\mu \approx 0.69/\mu$

## Slide 33

NOTES:

## What causes the crash of the spring bloom?

Gould & Gallagher (1990) Figure 3



## Slide 34 What causes the crash of the spring bloom?

NOTES:

## Serôdio & Catarino (2000)

$\text{O}_2$  microelectrodes & pulse amplitude modulated (PAM) fluorescence, diver-PAM, <http://www.walz.com/>

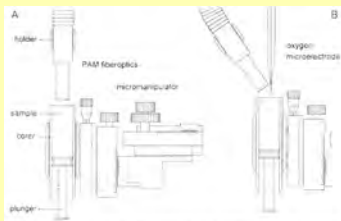


Fig. 1. The setup used for (A) measuring  $\text{Chl } a$  fluorescence, using a PAM fluorometer, and for (B) measuring photosynthesis, using oxygen microelectrodes, on undisturbed microphytobenthic samples. When measuring photosynthetic rates, the PAM fluorometer is used to illuminate the sample surface.

## Slide 35 Serôdio & Catarino (2000)

NOTES:

## Jørgensen & Revsbech (1985)

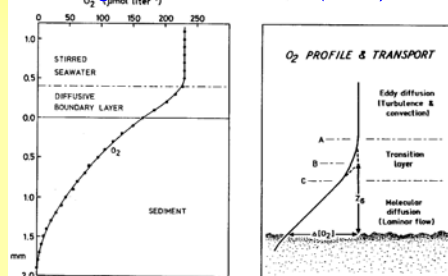


Fig. 1. Left. Oxygen microprofile in sediment collected from Aarhus Bay at 20-m water depth, July 1982. A transition (broken line) is seen above the sediment surface between the stirred seawater with homogeneous  $\text{O}_2$  distribution and the diffusive boundary layer with a steep  $\text{O}_2$  gradient. Right. The boundary layer at the sediment-water interface as determined by chemical transport processes and gradients. The oxygen microgradients are here used to define the outer limit (A) of the diffusive boundary layer as well as the true (C) and the effective (B) diffusive boundary layer.

## Slide 36

NOTES:

**Benthic boundaries****Ekman layer****Log layer****Viscous sublayer****Molecular diffusive sublayers****Ox c zone****Ox d zed zone****Sulfidogenic zone****Methanogenic zone****Slide 37**

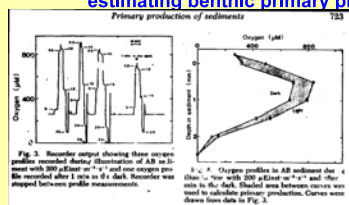
NOTES:

**Thicknesses of benthic boundaries**

Parameter	Deep-Sea	Shelf	Description
$U$ (cm/s)	3	30	average water velocity
$U_*$ (cm/s)			Boundary shear velocity (the square root of boundary shear stress/water density)
$\nu$ (cm <sup>2</sup> /s)	0.1	1	characteristic eddy viscosity
$z_i$ (cm)	500	5000	Ekman depth
$z_l$ (cm)	100	1000	log layer thickness
$z_v$ (cm)	2	0.2 to 1	viscous sublayer thickness
			diffusive sublayer thickness $z_d = \sqrt{\nu / S_c}$ , where $S_c$ = Schmidt number $\nu \approx 0.600$ for $O_2$ or $CO_2$ $\bar{D}$ = molecular diffusivity
$z_d$ (cm)	0.2	0.02-0.1	

**Slide 38 Thicknesses of benthic boundaries**

NOTES:

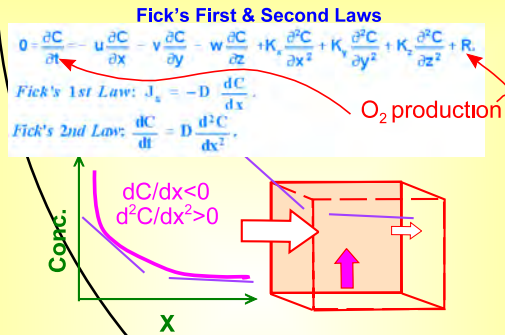
**Revsbech & Jørgensen (1983)** **$O_2$  microelectrode profiles of the best methods for estimating benthic primary production**

$O_2$  primary production obtained by subtracting the integrated light & dark profiles (after 1 min in dark)

**Slide 39 Revsbech & Jørgensen (1983)**

NOTES:

## Advection-diffusion equation



## Slide 40 Advection-diffusion equation

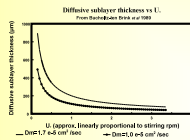
NOTES:

## Stirring effects on diatom production

Stirred  $0.23 \text{ d}^{-1}$  (3-d doubling), Unstirred  $0.14 \text{ d}^{-1}$  (6 d)

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.

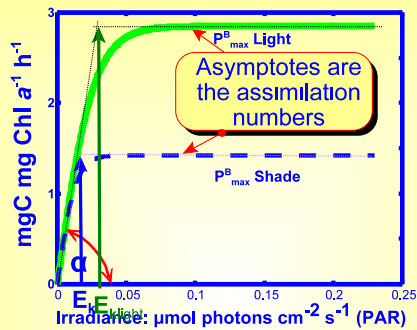
	$P^B (\times 10^3)$	$P^B (\times 10^3)$	$P^B$	$P^B$	$C/D (\times 10^3)$	$\mu$
Stirred						
3.0	16.87(2.17)	1.41	764(43)	75(5)	4.16(0.82)	0.23(0.02)
Unstirred						
3.0	10.62(0.19)	1.34	356(32)	47(1)	5.62(0.67)	0.14(0.02)



## Slide 41 Stirring effects on diatom production

NOTES:

## Chl a-specific gross productivity

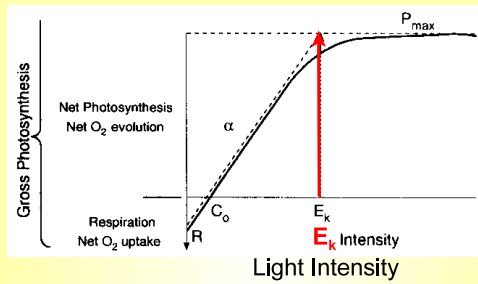


## Slide 42

NOTES:

## Falkowski & Raven P vs. E curves

**Falkowski & Raven (1997, p. 196, Fig 7.2)**

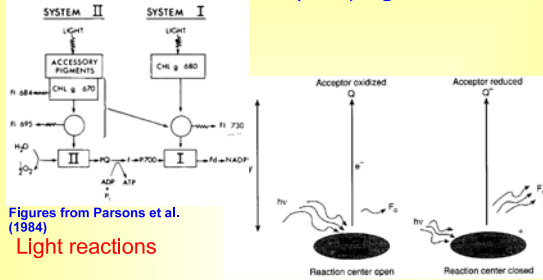


## Slide 43 Falkowski & Raven P vs. E curves

NOTES:

## Fluorescence yield and open & closed PSII reaction centers

Falkowski & Raven (1997) Figure 3.11

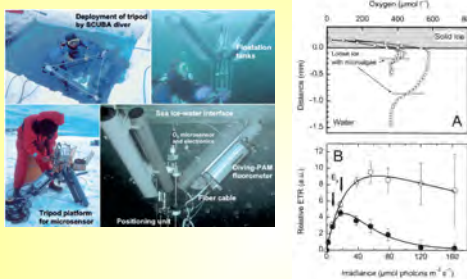


## Slide 44 Fluorescence yield and open & closed PSII reaction centers

NOTES:

## PAM Fluorometer & O<sub>2</sub> microsensor

Kühl et al. 2002 MEPS 223: 1-14



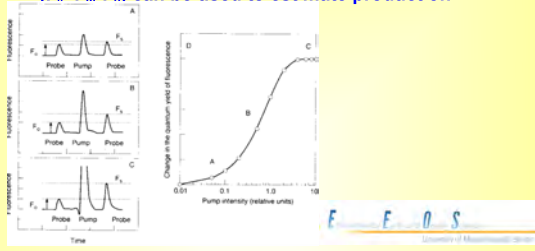
## Slide 45 PAM Fluorometer & O2 microsensor

NOTES:



## $F_o$ , minimal Chl a fluorescence (dark fluorescence)

Falkowski & Raven (1997): Pump intensities close PSII reaction centers.  $F_o$  & differences in fluorescence ( $F_m - F_o$ ) can be used to estimate production

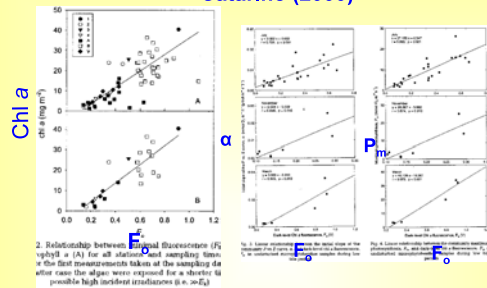


## Slide 46 $F_o$ , minimal Chl a fluorescence (dark fluorescence)

NOTES:

## $F_o$ linearly related to Chl a, $\alpha$ , & $P_{max}$

Barranquet & Kromkamp (2000), Serôdio & Catarino (2000)

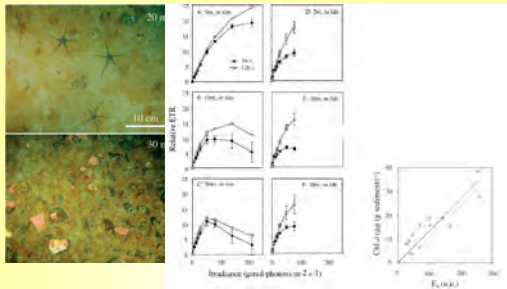


## Slide 47 $F_o$ linearly related to Chl a, $\alpha$ , & $P_{max}$

NOTES:

## Measuring Production using fluorescence by SCUBA

Glud et al. 2002

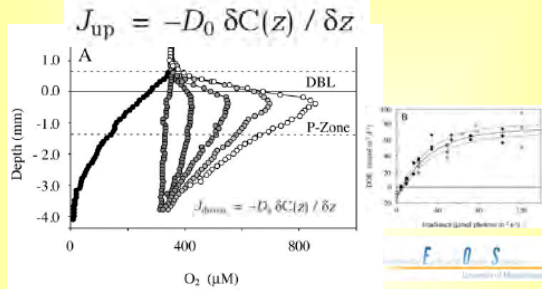


## Slide 48 Measuring Production using fluorescence by SCUBA

NOTES:

## Comparing production using fluorescence & O<sub>2</sub> flux by SCUBA

Glud et al. (2002) Figure 7

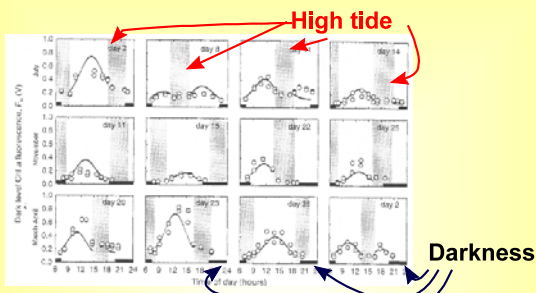


## Slide 49 Comparing production using fluorescence & O<sub>2</sub> flux by SCUBA

NOTES:

## Modeled effects of tide & light

Serôdio & Catarino (2000) Estimates of production



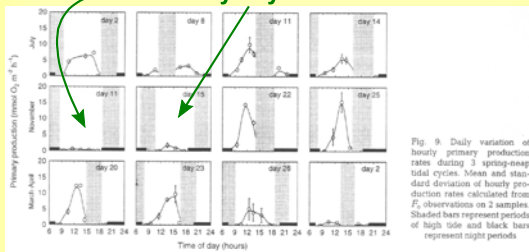
## Slide 50 Modeled effects of tide & light

NOTES:

## Modeled effects of tide & light

Serôdio & Catarino (2000)

Cloudy days



## Slide 51 Modeled effects of tide & light

NOTES:

## Rates of diatom production

Epipellic: about 100-200 gCm<sup>-2</sup>y<sup>-1</sup>

Location/Source	Technique	g C/m <sup>2</sup> /yr*	Author
<b>Benthic microalgae:</b>			
Georgia salt marsh	O <sub>2</sub> , CO <sub>2</sub>	280	Pomeroy (1959)
Delaware salt marsh	O <sub>2</sub>	38-99	Callagher and Dunbar (1973)
California salt marsh	O <sub>2</sub>	217-409	Zedler (1980)
Massachusetts salt marsh	<sup>14</sup> C (shaded)	106	Van Raaij et al. (1976)
marsh	(unshaded)	165	
Intertidal sandflat	O <sub>2</sub>	143-226	Pennelmar (1968)
Intertidal sandflat	O <sub>2</sub>	0-325	Rizyck and Phlips (1972)
Intertidal sandflat	<sup>14</sup> C	4-9	Steele and Rinal (1968)
Intertidal mudflat	<sup>14</sup> C	31	Leach (1970)
Intertidal mudflat	<sup>14</sup> C	116	Crofford (1969)
Estuarine subtidal	<sup>14</sup> C	90	Marshall (1970)
	<sup>14</sup> C	189	Jost (1978)
	<sup>14</sup> C	95-177	Cade (1980)
<b>Wadden Sea sand flat</b>			
<b>Sea and marsh grasses:</b>			
Thalassia test	O <sub>2</sub>	520-640	Wentlake (1963)
Spartina (Georgia)	O <sub>2</sub>	257-897	Tall (1962)
(North Carolina to Nova Scotia)	cropping	130-256	Mann (1972b)
(Massachusetts)	cropping	1100-2300*	Valiela et al. (1976)
<b>Mangrove swamps:</b>			
Florida (not prod.)	O <sub>2</sub> (+ litter)	400	Mann (1972b)
<b>Reefs:</b>			
Laminaria (Nova Scotia)	cropping	1909	Wentlake (1963)
(England)	cropping	1225	Belamy et al. (1968)
(Nova Scotia)	biotic renewal	1750	Mann (1972b)
Microcystis	cropping	400-820	Clelland (1972)
<b>Littoral seaweeds:</b>			
Fucus	O <sub>2</sub>	<3000*	Kanwisher (1966)

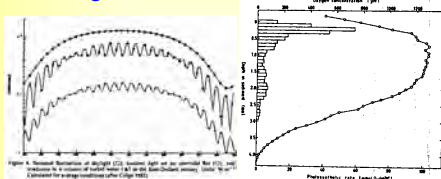
## Slide 52 Rates of diatom production

NOTES:

## What limits benthic production?

Light In winter, DIC In summer

- Production limited by light in winter
- Production may be limited by inorganic carbon in North temperate mudflats throughout the remainder of the year



## Slide 53 What limits benthic production?

NOTES:

## DIC limitation in diatoms mats

pH from Terry & Edyvean (1981)

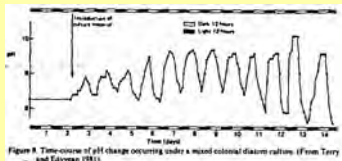
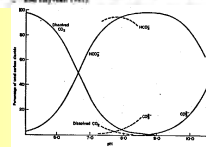


Figure 5 Time-course of pH change occurring under a mixed colonial diatom mat (from Terry and Edyvean 1981)

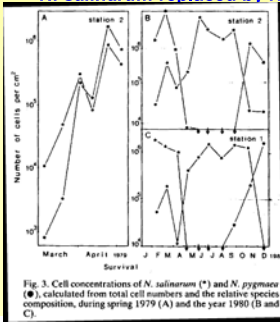


## Slide 54 DIC limitation in diatoms mats

NOTES:

## pH & species composition

*N. salinarum* replaced by *N. pygmaea*

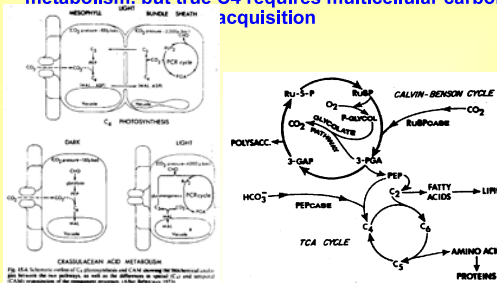


## Slide 55 pH & species composition

NOTES:

## Acclimation to low DIC

C3 & C4 photosynthesis; diatoms have a C4-like DIC metabolism, but true C4 requires multicellular carbon acquisition

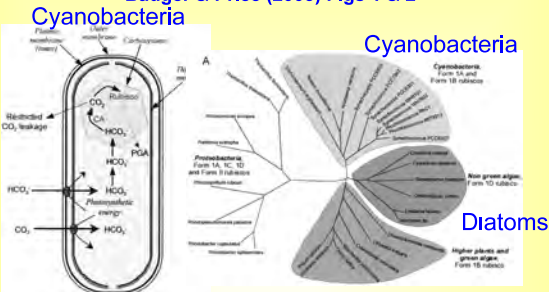


## Slide 56 Acclimation to low DIC

NOTES:

## Evolutionary History of DIC Concentrating mechanisms

Badger & Price (2003) Figs 1 & 2



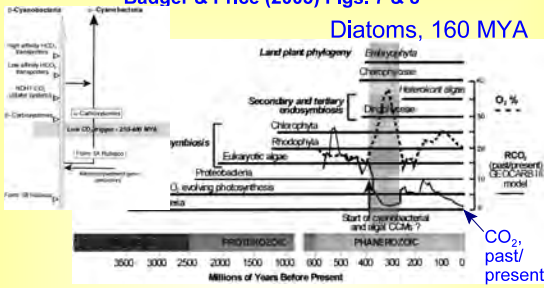
## Slide 57 Evolutionary History of DIC Concentrating mechanisms

NOTES:

## Cyanobacterial evolution & DIC concentrations; the end of nature?

Badger & Price (2003) Figs. 7 & 8

Diatoms, 160 MYA

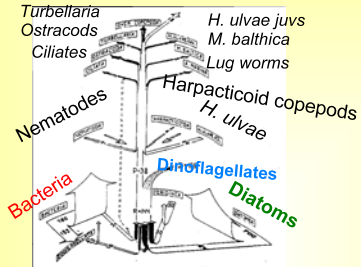


## Slide 58 Cyanobacterial evolution & DIC concentrations; the end of nature?

NOTES:

## Microphytobenthos: dominates benthic food supply

Slava Epstein's White Sea food web



ECOS630

## Slide 59 Microphytobenthos: dominates benthic food supply

NOTES:

## Herman et al. 2000

Linear relation between microphytobenthic production and infaunal biomass

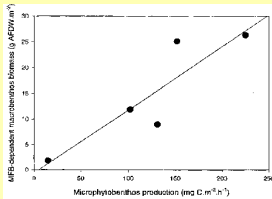
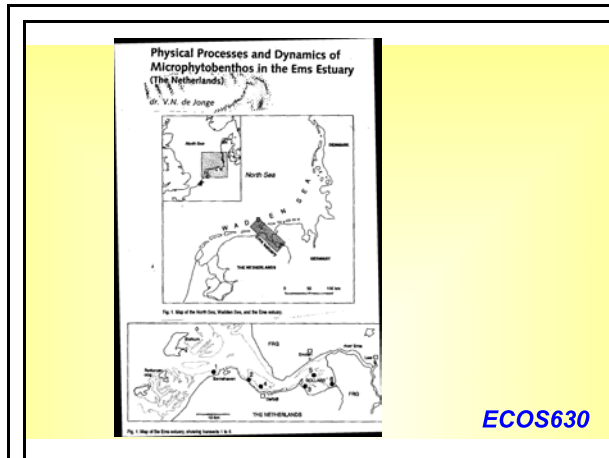


Fig. 8. Relation between microphytobenthic primary production (Hauke et al. 1998, C. Buzzaquet unpubl. data) and infaunal biomass that is calculated to be directly dependent on microphytobenthos (MPB) (see Table 2 for parameters and Discussion) for calculation. Linear regression coefficient is 0.94 ( $p = 0.004$ ). AFDW: ash-free dry wt.

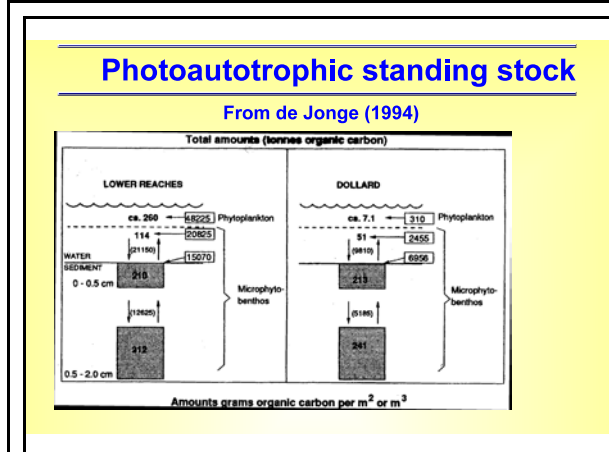
## Slide 60 Herman et al. 2000

NOTES:



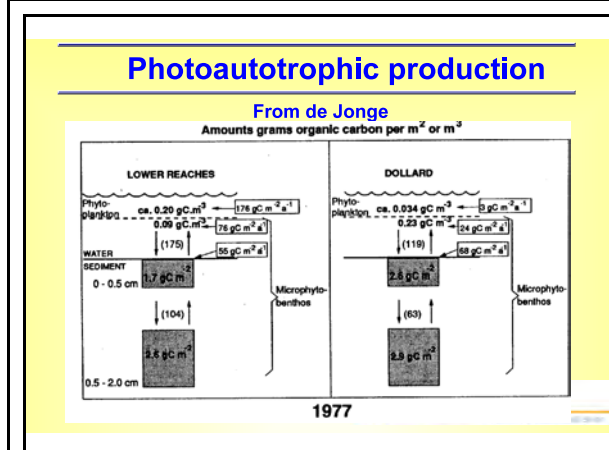
## Slide 61

NOTES:




## Slide 62 Photoautotrophic standing stock

NOTES:



## Slide 63 Photoautotrophic production

NOTES:

<h2>Microphytobenthos &amp; phytoplankton</h2>	<h2>Slide 64 Microphytobenthos &amp; phytoplankton</h2>
<ul style="list-style-type: none"> <li>● Ems Dollard                             <ul style="list-style-type: none"> <li>▸ Microphytobenthic production 60-250 mgC m<sup>-2</sup> d<sup>-1</sup></li> <li>▸ 30% of phytoplankton are resuspended microphytobenthos</li> </ul> </li> <li>● Dollard (about 1 m deep)                             <ul style="list-style-type: none"> <li>▸ 92% of Chl a from microphytobenthos</li> <li>▸ Production                                     <ul style="list-style-type: none"> <li>■ 25% of total production from resuspended benthic diatoms</li> <li>■ 53% from true phytoplankton</li> <li>■ 22% from tidal flat production</li> </ul> </li> </ul> </li> </ul> 	<p>NOTES:</p>