

PRIMARY PRODUCTION IN MASSACHUSETTS BAY, EUTROPHICATION, RED TIDES, AND SUBSURFACE CHLOROPHYLL MAXIMA

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Assignment

TOPICS

- ▶ What factors control primary production in harbors and bays, especially Boston Harbor and MA Bay?
- ▶ What is the Cole-Cloern relationship and why does it work so well in MA Bay?
- ▶ What factors control subsurface chlorophyll maxima in MA Bay?

REQUIRED READINGS

Cole, B. E. and J. E. Cloern. 1987. An empirical model for estimating phytoplankton productivity in estuaries. *Mar. Ecol. Prog. Ser.* 36: 299-305. [*Primary production is linearly related to the product of average water-column Chl a concentration * depth * light intensity (I₀).*]

McGillicuddy, D. J, R. P. Signell, C. A. Stock. B. A. Keafer, M. D. Keller, R. D. Hetland and D. M. Anderson. 2003. A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine. *J. Plankton Research* 25: 1131-1138. [*A model in which red tide blooms are seeded from offshore sediments, with blooms resulting from upwelling followed by downwelling winds*]{25}

SUPPLEMENTAL

- Adams, E. E., J. W. Hansen, R. L. Lago, P. Clayton, and X. Zhang. 1992. A simple box model of the Nitrogen cycle in Boston Harbor and the Massachusetts Bays. *Civil Engineering Practice* (Fall 1992): 91-103. *[This was an important early analysis of the effects of the MWRA outfall on Nitrogen cycling in MA Bay. The conclusion: with best case estimates, about 5% of the existing MWRA N loading is lost through denitrification in Boston Harbor sediments. Another 2.5% is lost through burial. About 25% of the nitrogen lost through denitrification comes from the Gulf of Maine or other MA Bay sources. Moving the outfall should result in only a 6% increase in nitrogen loading to MA Bay. Secondary treatment will reduce total N loading by 15%, resulting in a net 9% reduction in loading, about the same as occurred when sludge stopped being dumped in the harbor in December 1991]*
- Cullen, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Can. J. Fish. Aquat. Sci.* 39: 791-803. *[This was the best available synthesis and review prior to Longhurst & Harrison (1989). This review is more concise, hence we are using it instead of Longhurst & Harrison (1989).]* {30}
- Hauray, L. R., P. H. Wiebe, M. H. Orr, and M. G. Briscoe. 1983. Tidally generated high-frequency internal wave packets and their effects on plankton in Massachusetts Bay. *Journal of Marine Research* 41: 65-112. *[See especially their profiles of fluorescence with depth, which show crisp subsurface chlorophyll maxima [SSCM] in MA Bay and the effects of internal waves on these SSCM]*
- Kelly, J. 1997. Nutrients and human-induced change in the Gulf of Maine — “One, if by land, and two, if by sea”. Pp. 169-181 in G. T. Wallace and E. F. Braasch, eds., *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop*. RARGOM Report, 97-1. Hanover, NH: Regional Association on the Gulf of Maine.
- Kelly, J. R. and P. H. Doering. 1997. Monitoring and modeling primary production in coastal waters: studies in Massachusetts Bay 1992-1994. *Mar. Ecol. Prog. Ser.* 148: 155-168. *[Three years of monitoring data are described and fit to the Cole-Cloern model]*
- Lunven, M, J. F. Guillaud, A Youéno, M. P. Crassous, R. Berrie, E Le Gall, R. Kérouel, C. Labry, and A. Aminot. 2005. Nutrient and phytoplankton distributions in the Loire River plume (Bay of Biscay, France) resolved by a new fine scale sampler. *Est. Coastal Shelf Sci.* 65: 94-108. *[A fine scale sampler (≈10 cm resolution) used to document remarkable fine scale structure of light, Chl a, pheophorbide, diatoms, dinoflagellates and nutrients]* {?}
- Mann, K. H. and J. R. N. Lazier. 1996. *Dynamics of marine ecosystems: biological-physical interactions in the oceans*, 2nd Edition. Blackwell Scientific Publications. *[Classifies estuaries and describes tidal fronts]*
- Nixon, S. W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199-219. *[A general review of eutrophication, including a new definition, and estimates of nitrogen inputs into Narragansett Bay since 1800]* {?}
- Officer, C. B. and J. H. Ryther. 1977. Secondary sewage treatment versus ocean outfalls: an assessment. *Science* 197: 1056-1060. {12}
- Townsend, D. W. 1997. Cycling of carbon and nitrogen in the Gulf of Maine. Pp. 117-133 in G. T. Wallace and E. F. Braasch, eds., *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop*. RARGOM Report, 97-1. Hanover, NH: Regional Association for Research on the Gulf of Maine.

Comments

Parker's 1975 Ph.D. dissertation provides an excellent summary of the seasonal primary production cycle in MA Bay prior to the MWRA's intensive MA Bay monitoring program begun in 1992. Parker followed phytoplankton species composition at a site just outside the mouth of Boston Harbor, south of the proposed outfall site for 1 ½ years. He documented changes in production with simulated *in situ* incubations using the ¹⁴C technique and enumerated the major net phytoplankton species.

Based on his work, work by Loder, Smayda, Townsend *et al.*, **Kelly & Doering (1997)**, Craig Taylor, and Keller & Oviatt, we can describe the basics of the phytoplankton seasonal cycle in the Bay.

THE SEASONAL CYCLE OF PRIMARY PRODUCTION IN MA BAY

Primary production in MA Bay can be divided into five seasonal phases:

- **Winter**
 - From late October until March, the water column is usually strongly mixed by wind and tidal currents. Phytoplankton production rates are low and light-limited. DIN, mainly NO₃⁻, concentrations are high (≈ 15-20 μg atm l⁻¹). The increase in NO₃⁻ concentrations is probably due to both nitrification in the sediments and water column and the input of nitrate-rich water from the Gulf of Maine.
 - As our critical-depth calculations revealed (see Chapter 5), phytoplankton production is light-limited during the period from December 21, the day with the lowest solar insolation of the year, to mid-January (if I_c is about 40 langley's per day). After mid-January, Sverdrup critical-depth concept indicates a bloom should occur if the basal light attenuation coefficient - i.e., the light attenuation other than that due to Chl *a* - is about 0.2 m⁻¹, but phytoplankton production can increase only slightly before the phytoplankton again become light-limited due to self-shading. However, even slight water-column stratification can lead to small phytoplankton blooms during the November-March period. Water stratification can occur due to melting snow increasing freshwater input during this period. During this period, stratification occurs with a temperature inversion. The surface water is fresher and colder than the saltier and warmer bottom waters.
 - The following questions remain unanswered:
 - the rate of basal light attenuation (*i.e.*, not due to photosynthetic pigment absorption). **Parker (1975)** found winter-time PAR light attenuation coefficients of about 0.2 m⁻¹. The Massachusetts Bays model, now being run by Meng Zhou and Mingshun Jiang at UMASS/Boston uses a basal light attenuation coefficient for PAR of 0.15 m⁻¹ for MA Bay
 - the rates of wintertime zooplankton grazing and benthic suspension feeding
 - the extent of lateral transport of deposited organic matter by winter storms.

- **Winter-spring blooms**

- The spring bloom occurs when the critical depth exceeds bottom depth or the mixed-layer depth. If the water-column light attenuation coefficient is $k=0.2$ and the compensation light intensity is 40 ly/d, then the spring bloom should occur on about January 18. Very little increase in Chl *a* occurs after a brief period of phytoplankton increase, average light levels decrease to the point where the average light intensity through the water column equals the critical depth. During January and February, short blooms can occur due to water-column stratification from snow melt. This stratification is usually short-lived, being broken down by the frequent winter storm events.
- The water column can be well-mixed at the time of the spring bloom. That is, the bloom could occur when the critical depth exceeds MA Bay bottom depth. In Massachusetts Bay, critical depth probably exceeds bottom depth in January or early February, but the massive “bloom” doesn’t appear until March. Why?
- In Spring 1990 and 1991, Jim Shine (1993 UMASS/Boston Ph.D. dissertation) found that the spring bloom in March was associated with a short-term period of density stratification due to fresh-water input, largely from the Merrimack River. **Parker (1975)** also documents a March phytoplankton bloom. There is no published explanation of why applying **Townsend & Spinrad’s (1986)** estimates of k_z and the compensation light intensity (40 langleys/day) produce a January Massachusetts Bay bloom, when field studies show that the bloom doesn’t occur until March.
- In 1996, the spring bloom appears to have occurred in mid-January. The Winter 1996 period had the highest snowfalls in recent times, and the input of a lens of brackish water led to a short-term density stratification of MA Bay. This period was characterized by a temperature inversion in the water column, with colder, fresher water overlying slightly warmer but saltier deep water. This stratification led to a short-lived bloom. In Boston Harbor, turbidity and grazing pressure may delay the onset of the bloom, despite the shallow water depth.
- **Nelson & Smith (1991)** applied the critical depth concept to the Southern Ocean and may have hit on the key explanation for the March MA Bay bloom. They explained why Chl *a* concentrations were low year-round in the Southern Ocean despite abundant DIN. . “No need to invoke iron limitations as some had,” they argued. The Southern Ocean critical depth was only slightly deeper than the mixed layer depth. After only a slight increase in phytoplankton standing stock, the increased light attenuation reduced the critical depth to equal the mixed-layer depth. I would argue that the same analysis works for MA Bay. The spring bloom does occur in January or early February in MA Bay, but Chl *a* concentrations can only increase slightly before the critical depth, now reduced because of the chlorophyll-associated light attenuation, again equals the bottom depth. However, in March when density stratification due to the Merrimack River is established, reducing the mixed layer depth from 35 m to only 10-15m, a more massive bloom can result. Chlorophyll *a* concentrations can increase tremendously when the mixed layer depth is only 15 meters. It is the second

bloom, caused by the Merimack River Spring freshening that **Parker (1975)** and Shine (1993) observed.

- Nutrient depletion terminates the spring bloom in March, but grazers, especially meroplankton (the larval stages of benthic invertebrates), could play an important role. The role of mass sinking of the large diatoms, described by Smayda, Smetacek, and Alldredge in other ecosystems remains unknown. This mass sinking of diatoms might be due to Si depletion. The MWRA has documented a massive sinking event in their 1992 data, when a large *Phaeocystis* bloom sank to the bottom.
- **Spring transition**
 - There may be a brief transition period after the termination of the spring bloom, but before the onset of permanent summer stratification.
 - This transition may not be present if the winter-spring bloom occurs late in the year (March) with the onset of the major density stratification from the spring runoff from the Merimack river.
 - Often there is a bimodal spring bloom, with a large spring bloom in March followed by a smaller bloom event some weeks later. There is no adequate explanation for this phenomenon. One hypothesis might be that storms mixed the water column at the end of the first bloom, and then restratification led to the second bloom event. This riddle could be easily solved by closely spaced observations of water column stratification, light attenuation coefficients, primary production, and phytoplankton species composition.
- Late spring → Fall
 - From April through late September, Massachusetts Bay is stratified. It is stratified initially by the freshening of the surface water from the Merrimack River plume. After the water column has been partially stabilized by salinity differences, the surface is warmed and further stratifies. Bernie Gardner and Rocky Geyer have estimated the vertical eddy diffusion coefficients in MA Bay after density stratification has set in. They are approximately $0.1 \text{ cm}^2 \text{ sec}^{-1}$, a very low K_z .
 - During this period, the dominant phytoplankton are nanoplanktonic and motile. This transition matches the general phytoplankton succession pattern described by **Margalef (1978)** & **Bowman et al. (1981)**.
 - A pronounced subsurface chlorophyll maximum develops throughout MA Bay and the Gulf of Maine with the onset of strong density stratification. This subsurface Chl *a* maximum does not exist in the tidally mixed Boston Harbor and may not exist in weakly stratified water nearer shore. All forms of DIN are at nearly undetectable concentrations in the (relatively clear) surface waters of Massachusetts Bay, but nitrate concentrations increase in subsurface waters during this period (Loder 1988, MWRA report). The major unknown during this period is the level of primary production at and below the subsurface chlorophyll maximum. Another major unknown is the percentage of primary production that sinks to the benthos, and its rate of oxidation; these rates are needed to apply Officer's box models of benthic oxygen demand.

- **Fall bloom**
 - In September, density stratification begins to break down. This breakdown of the pycnocline is usually associated with a fall bloom. It is not known whether the onset of the fall bloom immediately follows the breakdown of the pycnocline. The temporal frequency of samples hasn't been high enough to resolve the factors associated with the onset of the fall bloom. In 1993, the MA Bay fall bloom was massive, with Chl *a* concentrations in excess of 20 µg/l. With a 35:1 C:Chl *a* ratio, some elementary math indicates that the phytoplankton biomass was well over 7 g C m⁻². In summer 1994, dissolved oxygen concentrations below 6 mg/l were observed in the Broad Sound area of Massachusetts Bay. The reasons for the massive 1993 fall bloom and the low dissolved oxygen levels observed in Massachusetts Bay in both 1994 and 1995 are huge unanswered and important questions now.
- Recent MWRA Results
 - The latest analysis of the MA Bay seasonal cycle, completed by Howes, Cibik and Craig Taylor provides the best analysis to date of the patterns and processes controlling the spring bloom. These investigators noted that the spring and fall blooms were associated with dramatic increases in the assimilation number of phytoplankton. The assimilation numbers often approached or exceeded 20 mg C (mg Chl *a* h)⁻¹, and were not associated with increases in phytoplankton production or standing stock. My interpretation of these data is that the onset of the spring and fall bloom is associated with the “seeding” of phytoplankton which were senescent or nearly so. These cells would have a very high C:Chl *a* ratio and would could have a very high assimilation number, even with a modest specific growth rate. Recall that:
$$\mu < \frac{\text{Assimilation number}}{C:\text{Chl } a}.$$
 - **MacIsaac et al. (1985)** call the stage where phytoplankton adapt to new P vs. I parameters as Stage II, or the “shift-up” phase in the typical upwelling sequence.

THE MALONE, COLE-CLOERN, PLATT REGRESSION

Cole & Cloern (1987) argue that primary production may be estimated with much greater precision and accuracy in estuaries and bays than in the open ocean. They review estimates of primary production from estuaries and produce a regression equation, using the composite variable $I_0 * B_p * z_{eu}$, which accounts for 82% of the variance in primary production in estuaries.

Dr Diane Gould applied this relationship for an October 1988 MWRA workshop on MA Bay eutrophication. Jim Shine (1993 Ph.D. dissertation) applied this equation to MA Bay and found that it gives a reasonable fit to **Parker's (1975)** data on MA Bay production. **Kelly & Doering (1997)** were unaware of these earlier applications of the Cole-Cloern model. They applied it to the 1992-1994 primary production data they collected during the first three years of the MWRA monitoring program for the MA Bay sewage effluent outfall.

Ironically, the Cole-Cloern equation does not include nutrient concentration as an independent (or predictor) variable. Thus it would seem to have limited predictive capability in analyzing the effects of nutrients on eutrophication. Does this mean nutrients are unimportant?

There are two reasons why nutrients don't need to be included. I call these the Wofsy and Platt explanations. **Wofsy (1983)** argued that in nutrient-rich lake, bay and estuarine environments, phytoplankton grow until they become light-limited. According to Wofsy, phytoplankton grow until the mixed layer is equivalent to five optical depths. An optical depth equals $(1/k)$, where k is the light-attenuation coefficient. Note that the 1% light depth is equivalent to 4.6 optical depths. Production is light-controlled, and nutrients are usually in excess. Such a process could account for Cole & Cloern's high R^2 in their regression.

The regression relationship also applies if nutrients are limiting. This is the Platt explanation. **Platt (1986)** found that the initial slope of the generalized P vs. I relationship, called Ψ (pronounced *psi*), was "relatively" constant, certainly less variable than many modelers might suppose. If there is a high positive correlation between nutrient supply and Chl *a*, and most phytoplankton are growing with high and relatively constant photosynthetic efficiencies (the initial slope in the P vs. I curve), then the Cole-Cloern relationship results. **Platt (1986)** proposed a similar relationship for the relationship between depth-averaged Chl *a* and primary production. **Platt et al. (1988)** argue that the Cole and Cloern relationship is identical to that used by **Platt (1986)**.

Shine (1993) showed that the Cole-Cloern relationship breaks down badly after the end of the spring bloom. During this period, there is a large biomass of apparently nutrient-depleted cells which sinks out of the euphotic zone. During this period, the Cole-Cloern model predicts primary production rates that are two to three times too high.

Cullen (1990) reviews mechanistic and descriptive models for phytoplankton growth and irradiance. He argues that the standard P vs. I model may be independent of growth rate and nutrient limitation. If the phytoplankton are nitrogen starved, they may produce less Chl *a*. Such a pattern could account for the utility of the Cole-Cloern and Platt relationships.

EUTROPHICATION OF MA BAY

I have listed as a supplementary reading **Officer & Ryther's (1977)** analysis of phytoplankton biochemical oxygen demand. The same argument is made in Stumm & Morgan's (1981, p. 707) Aquatic Chemistry textbook. There is a distinct possibility that the proposed MWRA secondary effluent discharge into MA Bay may produce a long-term and progressively worsening problem with low dissolved oxygen concentrations in bottom waters. Don't get bogged down in the details of the **Officer & Ryther's (1977)** diffusion model. The key element in the argument is that secondarily treated effluent is rich in DIN.

Both Ryther and Officer were members of the scientific advisory board that advised the MDC. This scientific advisory board, which also included Don Harleman from MIT and Willard Bascum, Director of the S. California Coastal Water Research Project, advised then Governor

Dukakis and the Secretary of Environmental Affairs Evelyn Murphy that the MDC should apply for a Section 301(h) waiver from the secondary treatment requirements of the Federal Clean Water Act. This advice led to the decision that Michael Deland, the Region I EPA Administrator, has called the most expensive Public Policy mistake in the history of New England. This decision also served as the basis for the influential Bush Boston Harbor commercial in the 1988 Presidential campaign.

THE PHYSICS OF MA BAY AND ITS EFFECTS ON EUTROPHICATION

The best available description of the physics of MA Bay is an October 1992 technical report by W. R. Geyer, G. B. Gardner, W. S. Brown, J. Irish, B. Butman, T. Loder and R. Signell, entitled, "Physical oceanographic investigations of Massachusetts and Cape Cod Bays". This report contains density profiles and nutrient profiles for transects taken throughout MA Bay.

Boston Harbor and MA Bay are a classic tidal front system. Boston Harbor can be classified as a well-mixed estuary (Riley 1967). Inner Broad Sound is also tidally mixed, but MA Bay is highly stratified during the late spring through early fall. **Haury *et al.* (1983)** and Gardner (in progress) have documented the stratified nature of the Bay. The combination of a well-mixed nearshore zone and a stratified offshore zone gives rise to a tidal-front (Mann & Lazier 1996).

There are two major problems created by the MWRA outfall. First, the DIN source is being moved from the well-mixed side of the front to the stratified side of the front. Second, the DIN source is being moved from an area with many silty depositional areas to one that is characterized as being more rocky in nature. This can have major consequences on the rates of denitrification in the system.

The net result of these changes could be eutrophication, which can be defined as an increase in the nutrient load to the system. The major problems associated with eutrophication of the Bay include anoxia in bottom waters and noxious phytoplankton blooms. The MWRA and USGS jointly found the development of a numerical simulation model of the currents and nutrient dynamics in the Bay. This model predicts that there will be less DIN available in the euphotic zone during the summer. The relatively high input of DIN will be trapped beneath the summertime pycnocline.

LAKE WASHINGTON EUTROPHICATION

Lehman (1986a) and **Edmondson (1991)** review the history of the eutrophication and recovery of Lake Washington. The example of Lake Washington indicates the extent to which an entire ecosystem can be affected by a single external variable, phosphorus loading in this case. Although canonical analysis hasn't been formally applied to the Lake Washington eutrophication dataset, it could be. The recovery of Lake Washington also provides a striking example of the limitation of the canonical approach. Many of the most dramatic changes in the biology of Lake Washington were driven by biological interactions that would be difficult to explain in terms of canonical models.

In the early 1950s, Lake Washington began to undergo changes due to eutrophication from the increased phosphorus input to the lake. As shown in Figure 1, Secchi disk transparency decreased from nearly 4 m to about 1 m during the period of peak phosphorus loading. *Oscillatoria rubescens* an indicator of eutrophication in European lakes appeared in Lake Washington in 1955. Edmondson in 1956 began his participation in the public policy process that led to the creation of Washington's METRO. This public super agency provided the means for diverting sewage from Lake Washington to Puget Sound. When the sewage effluent was diverted to Puget Sound starting in February 1963 (with complete diversion by 1968), lake transparency responded dramatically, increasing to the early 1950s levels. The Lake Washington recovery from eutrophication could be hailed as the hallmark of the Vollenweider approach to understanding aquatic systems.

In 1976, Lake Washington sprang a surprise on the limnologists by becoming more transparent than it had been in any time in recorded history (Edmondson 1991, p. 38). As shown in Fig. 2, Secchi disk transparency increased to over 9 meters during some seasons. With NSF support, Edmondson and his graduate students were able to document that the change was due to the reestablishment of *Daphnia* in Lake Washington. These cladocera grazed the phytoplankton to low levels, increasing water transparency. With NSF funding, Edmondson and his doctoral students explained the reemergence of *Daphnia* in the lake. The mysid *Neomysis mercedis*, a voracious invertebrate predator on *Daphnia*, decreased from 10% of its former abundance between 1962 and 1967. The *Daphnia* populations did not become reestablished until the disappearance of *Oscillatoria* in 1976.

The "bottom up" canonical approach could not explain the drastic decline of *Neomysis*, the predator of *Daphnia*. *Neomysis* declined because of the reintroduction in the 1960s of the sockeye salmon and the longfin smelt in the Cedar River. But why did the smelt and salmon return to Lake Washington and the Cedar River? In a chain of connections that James Burke (host of the PBS series Connections) would be impressed with, Edmondson (1991, p. 45) describes the chain of events: the smelt and salmon had declined from 1916 on because home owners built homes on the lower reaches of the Cedar River. To prevent flooding and erosion of the sediment near the shore, the channel from the Cedar River was

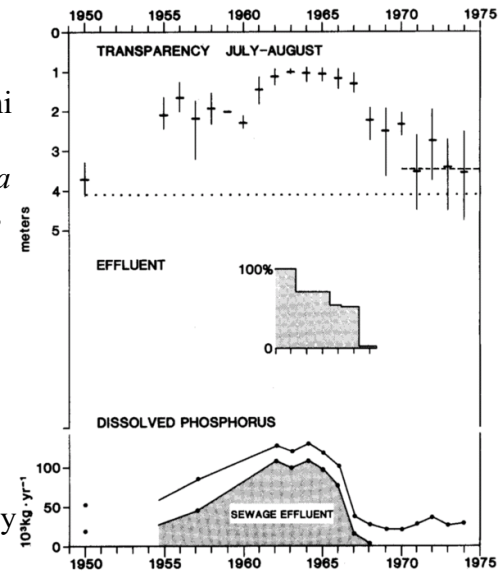


Figure 1. Change in Secchi disk transparency (top) and phosphorus loading (bottom, metric tons per year). (Based on Fig. 1.4 in Edmondson (1991)).

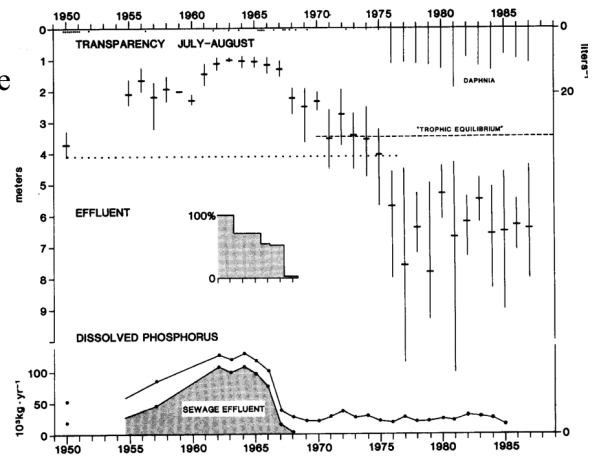


Figure 2. Same as Fig. 1, but extended through 1987 to show the *Daphnia* era. The summer abundance of *Daphnia* is shown in the upper right. (Based on Fig. 1.8 in Edmondson (1991)).

dredged and the dredged material was deposited on the beds used for fish spawning. The dredge broke in 1947 and between 1960 and 1965, revetments were built to reduce erosion and reduce the need for dredging.

... the probable explanation of the success of Daphnia involved a chain of circumstances. Between 1933 (the first detailed study of the lake) and about 1967 Daphnia was suppressed by predation by Neomysis. Between 1955 and 1976 Daphnia was suppressed by interference with its feeding by Oscillatoria. Between 1955 and 1967 it was suppressed by both. Oscillatoria decreased between 1964 and 1967 as a predicted result of the diversion of sewage. After 1967 -Neomysis was reduced by predation by an increased population of long-fin smelt. Both the smelt and the salmon were able to increase after spawning conditions in the Cedar River improved.

DID CHANGES IN POLLUTANT LOADING IN LAKE WASHINGTON HARM PUGET SOUND?

Lehman (1986a) and **Edmondson (1991)** describe a situation somewhat analogous to Boston Harbor: the recovery of an impacted ecosystem resulting from the reduction of pollution loading. One of the major scientific questions facing scientists studying Boston Harbor and Massachusetts Bay is whether the diversion of sewage effluent to Massachusetts Bay will cause impacts there.

Tommy **Edmondson (1991)** devoted a chapter of his book to the problems of Puget Sound, concluding “the problems of Puget Sound are more complex, and particularly, the solutions are less straightforward than those for Lake Washington.” To give some indication of the complexity of the processes controlling Puget Sound, there is an interesting pattern documented for the 100-fathom hole in the deep basin of Puget Sound.

Ulf Lie began sampling the hundred-fathom hole in Puget Sound about 1960. Fred Nicholls sampled this site for his M.Sc. and Ph.D. dissertations at the University of Washington in the mid 1960s. Nicholls continued to sample the 100-fathom hole throughout the 1970s and 1980s, finally publishing his work in 1985.

Nichols (1985a) concluded that the main basin of Puget Sound had been degraded by the introduction of sewage since the 1960s. One of the dominant species during the 1960s, the ice-cream-cone worm *Pectinaria californiensis* had declined dramatically since the 1960s. This species, which feeds on subsurface deposits, is the type of species that Pearson & Rosenberg (1976, 1978) and **Rhoads et al. (1978)** had predicted should decline as the result of increasing organic enrichment. After publishing 20 years of long-term data in 1985, Nichols was forced to retract his major hypothesis when *Pectinaria* returned. **Nichols (1988)** concluded that the benthic community in the main basin of Puget Sound may change as the result of a long-term change in the flushing characteristic of the Sound, a process which is now known as the Pacific long-term oscillation.

Definitions of terms

Phytoplankton biochemical oxygen demand [PBOD] The oxygen required to respire the photoautotrophic biomass produced by the addition of a limiting amount of nutrient. **Officer & Ryther (1977)** noted that secondary sewage treatment in Boston Harbor and elsewhere would reduce **biochemical oxygen demand [BOD]**, the amount of oxygen required to respire the organic matter in sewage effluent, but secondary treatment doesn't reduce the amount of dissolved nutrients, which fuel increased primary production. They defined the oxygen required to respire this new production **PBOD**. Hence PBOD remains high with secondary treatment, and tertiary treatment might be required to reduce both BOD and the concentration of limiting nutrient that leads to PBOD.

Web pages on Boston Harbor and the Gulf of Maine

Table 1. Web resources on Boston Harbor, MA Bay, and the Gulf of Maine.	
Description	URL
Bigelow Laboratory for Ocean Sciences	http://www.bigelow.org
Center for Coastal Studies Provincetown	http://www.coastalstudies.org/
Dartmouth Gulf of Maine Home Page. Includes circulation models of the Gulf of Maine	http://www-nml.dartmouth.edu/circmods/gom.html
Dartmouth WWW Server www-nml.dartmouth.edu	http://www-nml.dartmouth.edu
Environmental, Coastal & Ocean Sciences; UMASS/Boston	http://www.umb.edu
EPA Region 1 MA Bay Outfall Monitoring Scientific Advisory Panel	http://www.epa.gov/region01/omsap/
The Marine Biological Laboratory	http://www.mbl.edu

Table 1. Web resources on Boston Harbor, MA Bay, and the Gulf of Maine.	
Description	URL
Massachusetts Water Resources Authority	http://www.mwra.com
MIT SEA GRANT	http://web.mit.edu/seagrant/
MWRA ENQUAD, Environmental Quality Division (Includes a listing of all MWRA Technical Reports)	http://www.mwra.state.ma.us/harbor/enquad/trlist.html
NOAA Review of the Great Whales, including the Northern Right Whale	http://spo.nwr.noaa.gov/mfr611/mfr611.htm
Northeast Fisheries Center, Woods Hole, NOAA's National Marine Fisheries Service	http://www.nefsc.noaa.gov/
Stellwagen Bank National Marine Sanctuary	http://stellwagen.nos.noaa.gov/
New England Aquarium	http://www.neaq.org
Woods Hole Oceanographic Institution WWW Server	http://www.whoi.edu/
USGS analysis of Boston Harbor/MA Bay	http://woodshole.er.usgs.gov/project-pages/bostonharbor/index.html
USGS analysis of Boston Harbor sediments (Mike Bothner)	http://marine.usgs.gov/fact-sheets/fs150-97/

Outlines of readings

ASSIGNED

Cole, B. E. and J. E. Cloern. 1987. An empirical model for estimating phytoplankton productivity in estuaries. *Mar. Ecol. Prog. Ser.* 36: 299-305. [Primary production is proportional to Chl a conc, depth, and light intensity.]

1. Abstract
 - a. Primary production in San Francisco Bay is highly correlated with phytoplankton biomass B, and an index of light availability in the photic zone $Z_p I_0$ (photic depth times surface irradiance)
 - b. compared the generality of this relation with 5 other estuaries
 - c. daily production regressed against the composite parameter $B * Z_p I_0$.
 - d. One regression line fit all 4 estuaries.
 - e. Physiological variability is a secondary control on phytoplankton productivity in nutrient-rich estuaries.
2. Introduction
 - a. Contention: Photosynthetic carbon assimilation may be more amenable to prediction in estuaries than in oligotrophic areas.
 - b. Evidence:
 - i. many estuaries have horizontal gradients of increasing productivity with decreasing turbidity
 - ii. estuarine sites with low suspended sediments have areal production
 - iii. in many estuaries phytoplankton biomass and production increase during stratification events
 - iv. productivity of the whole phytoplankton and 3 size fractions in San Francisco bay is highly correlated with biomass and light availability.
 - c. phytoplankton can exhibit short-term variability in production which may not be important long term.
 - d. Cites Platt's remote sensing paper.
 - e. 6 diverse estuaries fit the picture.
3. Methods
 - a. 27 sites in 6 US estuaries of 3 types: fjord, river-dominated (partially mixed), and lagoon, as well as an estuarine plume.
 - b. total production regressed against $B Z_p * I_0$, where Z_p is the photic depth and irradiance I_0 (variable units).
 - c. Photic depth = 1% light depth, calculated from light attenuation coefficient. $Z_p = 4.61/k$; $k = 0.4 + 1.09/\text{Secchi depth}$, data derived from SF Bay.
 - i. assume phytoplankton homogeneously distributed in the photic zone.
 - ii. B = mean Chl concentration in the photic zone.
 - iii. B and Z_p are not totally independent variables, because phytoplankton can control the attenuation coefficient
 1. contribution to k of phytoplankton small relative to sediments
 2. 5% of light attenuation in SF bay due to chlorophyll a concentration
 - iv. Chl a measured fluorometrically or spectrophotometrically.
 - v. PAR measured (350 - 700 nm ??)
 - vi. 0.47 conversion factor to convert Puget sd and Hudson River data to PAR
 - vii. radiometric PAR ($\text{gcal cm}^{-2} \text{d}^{-1}$) converted to quantum values $\text{E m}^{-2} \text{d}^{-1}$) using a conversion factor of 0.192 Colijn (1982)
4. Results
 - a. A linear relation was found from each of 6 systems
 - b. there were no significant differences with seasons.
 - c. mean $r^2 = 0.82$
 - d. for pooled data, there was a highly significant relationship. $r^2 = 0.82$
 - e. Thus, a single regression equation can be used to estimate production in a wide range of temperate estuarine environments.
5. Discussion.
 - a. There is a strong correlation between production and light.
 - b. Fits with Wofsy (1983) and Platt (1986) that primary productivity, normalized to phytoplankton biomass is largely dependent on light availability

- c. Wofsy (1983): developed a mechanistic model to estimate water-column primary production in rivers and estuaries based on light attenuation partitioned between phytoplankton and detritus.
 - d. Platt (1986) explains the mechanistic basis of such an approach concludes that biomass-specific production in the ocean is a linear function of light intensity.
 - e. We know that P_m^B and α of the P vs I curve vary with
 - i. recent light history
 - ii. spectral quality of light
 - iii. temperature
 - iv. salinity
 - f. Such studies may not be relevant over time scales of weeks to years.
 - g. Model implications and utilities:
 - i. Because a single formulation gives reasonable estimates of productivity, large-scale spatial variability of productivity can be determined from a few measures of productivity and many measures of B and Z_p over a large geographic area.
 - ii. Remote sensing.
 - iii. Airborne color imager. sensors for wavebands specifically required for turbidity and chlorophyll
 - iv. the model is also useful for determining when factors other than biomass and light are important controls on productivity.
 - v. Predictions in Table 2 assume nutrient-replete systems.
 - vi. Hudson River plume estimates where quite high.
 - h. Summary:
 - i. the linear relation and high degree of similarity between regressions of productivity has 2 implications
 - 1. a simple empirical equation can be used to estimate daily production
 - 2. instances when measured productivity differs widely from that predicted using the composite parameter model m may indicate that secondary factors are significantly affected in the measured rates.
6. Overall conclusion: $Z_p * I_o * B$ explains 82% of the variation in estuarine production
"This implies that physiological variability is a secondary control on phytoplankton production in nutrient-rich estuaries, and that one empirical function can be used to estimate seasonal variations in productivity or to map productivity along estuarine gradients of phytoplankton biomass and turbidity."

SUPPLEMENTAL

Cullen, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. Can. J. Fish. Aquat. Sci. 39: 791-803. [This was the best available synthesis and review prior to **Longhurst and Harrison (1989)**. This review is more concise, hence we are using it instead of Longhurst and Harrison (1989). I will refer to Longhurst & Harrison in class.] {30}

Haury, L. R., P. H. Wiebe, M. H. Orr, and M. G. Briscoe. 1983. Tidally generated high-frequency internal wave packets and their effects on plankton in Massachusetts Bay. Journal of Marine Research 41: 65-112. "See especially their profiles of fluorescence with depth."

- 1. Abstract
 - a. internal waves form at Stellwagen bank and propagate into MA Bay.
 - b. dominant wave packets have lengths of 300 m, period of 8-10 min, and have amplitudes of up to 30 m
 - c. Longhurst-Hardy plankton recorder used.
 - d. light levels from 0.1% to 26% of surface light, 30 m displacement
 - e. the nutrient input to surface layers can be enhanced (so too, can oxygen flux)
- 2. Materials and Methods:
 - sampling locations A & P located far away from inner Mass. Bay.
- 3. Results
 - a. New wave packet generated every 12.4 hours
 - b. Wave packets dissipate on the shoal waters of the Western side of the Bay
 - c. some internal waves can break in 80 m of water.

- d. Figure 7 documents the passage of an internal wave, 15 - 20 m displacement of the Chl maximum
4. Discussion
- a. at depths less than 30 m, the breaking internal waves are capable of scouring the bottom.
 - b. intense mixing at the pycnocline.

Kelly, J. R. and P. H. Doering. 1997. Monitoring and modeling primary production in coastal waters: studies in Massachusetts Bay 1992-1994. Mar. Ecol. Prog. Ser. 148: 155-168. [Three years of monitoring data are described and fit to the Cole-Cloern model]

I. Abstract

- A. 1992-1994 sampling.
- B. P vs. I approach
 1. 6 surveys per year
 2. 10 stations, 2 depths in 1992-1993
 3. 2 stations in 1994 4 depths.
- C. Annual primary production estimated 386-486 gCm⁻²d⁻¹
- D. Cape Cod 527-613 gCm⁻²d⁻¹
- E. Production coupled directly to irradiance, less to Chl *a*

II. Introduction

- A. Outfall 15 km offshore in 32 m water
- B. Cole & Cloern (1987), Keller
 1. $B Z_p I_o$
 - a. B average chlorophyll concentration in the photic zone
 - b. Z_p =depth of the photic zone
 - c. I_o =daily incident PAR

III. Methods

- A. Field procedures
 1. In situ fluorescence was regressed against chlorophyll concentration.
 2. R²=0.7
- B. 1994 studies
 1. P vs. I incubations doen at 2 stations.
 2. ¹⁴C method
 - a. 4 depths
 - b. Temperature maintained to 3°C
 - c. 15 300-ml BOID bottles
 - d. 3 dark bottles
 - e. DIC
- C. 1992-1993 studies
 1. 10 stations
 2. 1992: O₂ method used
- D. Analyses.
 1. Subtract dark bottles
 - a. Remove outliers using the Dixon criterion
 2. Dark-corrected values normalized to Chl *a*

$$P^B = P_s^B \left(1 - e^{\left(\frac{-\alpha I}{P_s^B} \right)} \right) e^{\frac{-\beta}{P_s^B}}$$

where, α = Initial slope of P vs. I curve.
 β = Photoinhibition parameter.
 = Negative slope at high light intensity.
 P_s^B = Max. photo. rate without photoinhibition.

$$P^B = P_s^B \left(1 - e^{\left(\frac{-\alpha I}{P_s^B} \right)} \right).$$

where, α = *Initial slope of P vs. I curve.*
 = *Negative slope at high light intensity.*
 P_s^B = *Max. photo. rate without photoinhibition.*

3. For 1992 data, used Platt & Jassby (1976)
4. Determined extinction coefficient
5. Used 2-5 day average light
6. Euphotic zone: 0.5% I_0
7. Multiply mid-day rates by 7 (Vollenweider 1966)
8. For 1992-1993 data, calculated the average production

IV. Results & Discussion

- A. Production measurement and modeling in 1994
 1. P-I incubations.
 - a. $83\% \leq 12 \mu\text{g C } \mu\text{g Chl a h}^{-1}$
 - b. Summer, decrease in P_{max} between surface and deep samples
 - c. Progressive increase from 2 to 11-14 in October
 - d. α : $78\% \leq 0.1$
 2. Integrated ^{14}C production rates at the 2 stations.
 3. Modeling depth-integrated production
 4. Fig. 5a 22 data for 1994: Very high production in March
 5. Common formulation for both stations
- B. Annual production in W. MA Bay in 1994
 1. 1994: Late bloom production might be overestimated.
- C. Empirical production model for 1994
 1. Comparison to previous formulations
 2. $Y=0.073X+15$ ($R^2=0.82$)
 3. $Y=0.70X+220$ ($R^2=0.82$)
 4. Cole & Cloern and IKeller used 12%, they used 0.5%
 - a. Only 3% change
 - b. $Y=0.79X+285$
- D. Interannual comparisons of measurements and modeling in our study region.
 1. Fall 1993 bloom $10-12 \mu\text{g Chl a l}^{-1}$
 2. 1992: daily production 1.06 gCm d^{-1} , $386 \text{ gC m}^{-2}\text{y}^{-1}$
 3. Used a PQ of 1
 4. Model based on 1994, fits 1992 data if PQ near 1
- E. Modeling uncertainty and sensitivity analysis
 1. P-I modeling
 - a. Anomalously high α values.
 - b. Model not sensitive to imprecisions of α
 - c. Light intensity is the prime determinant of production
 - d. Chl *a* and N are strongly related
 2. Production remains about 1 across MA Bay
- F. Comparison of annual production ranges

Lunven, M, J. F. Guillaud, A You  nou, M. P. Crassous, R. Berrie, E Le Gall, R. K  rouel, C. Labry, and A. Aminot. 2005. Nutrient and phytoplankton distributions in the Loire River plume (Bay of Biscay, France) resolved by a new fine scale sampler. *Est. Coastal Shelf Sci.* 65: 94-108. [A fine scale sampler (≈ 10 cm resolution) used to document remarkable fine scale structure of light, Chl *a*, pheophorbide, diatoms, dinoflagellates and nutrients]{?}

Nixon, S. W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199-219. [A general review of eutrophication, including a new definition, and estimates of nitrogen inputs into Narragansett Bay since 1800] [?]

Officer, C. B. and J. H. Ryther. 1977. Secondary sewage treatment versus ocean outfalls: an assessment. *Science* 197: 1056-1060.

1. Environmental scientists and engineers alike have argued that secondary treatment of wastewater is unneeded and ineffective if discharges are made into open coastal waters, where there is adequate mixing.
2. Secondary treatment removes 80 - 90 % of BOD
3. WBOD = 400 mg O₂/l
4. Oxygen to N ratio is 276:15.5 by atoms or 20:1 by weight (RKR ratio)

5. PBO
 D : phyto

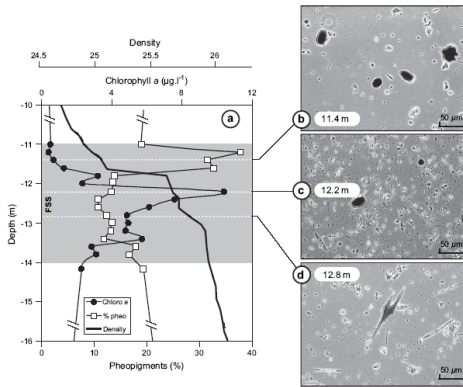


Fig. 7. Vertical profiles of density, chlorophyll and pheopigments (a) around the pycnocline and examples of microscopic observations from samples taken around the phytoplankton peak (b), (c), (d) on 23 June 2003. The thin layer was located below the pycnocline and was dominated by colonies of *Chaetoceros socialis* (c). The water above the pycnocline mostly contained individual diatoms and the maximum number of *Dinophysis* was observed in this layer (b). Detrital aggregates, senescent diatoms and dinoflagellates were observed below the maximum of chlorophyll a (d).

9. $\tau = \tau_a$
 u' is the residence or flushing time [d]

Figure 4. Lunven Fig. 7

- 9.1.1. volume averaged concentration is given in terms of τ as $C/(V/\tau)$ where C is the input
- 9.1.2. enters the first order reaction terms in the form of $k*\tau$, where k is first-order reaction constant
 - 9.1.2.1. large $k*\tau$: complete reaction
 - 9.1.2.2. low $k*\tau$: incomplete reaction

9.2. Table 1 residence times for various rivers, with dilution potential.

10.

Waste oxidation model

- 10.1. W is the combined waste discharge oxygen demand
- 10.2. WDOD waste dissolved oxygen demand
- 10.3. oxygen replenishment proportional to the Oxygen deficit.
 - k_2 is the reaeration coefficient.

$$PDOD = [(P/V)/\tau] * (1 - (1 - (e^{-k_p\tau})/k_p\tau) * (\beta/\alpha)$$

(3)

where,

PDOD= Phytoplankton dissolved oxygen deficit (in bottom waters) [g O₂ m⁻³]

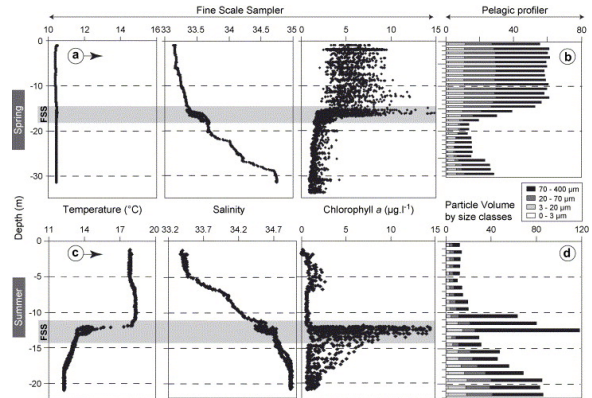


Figure 3. Lunven Fig. 4

plankton biochemical oxygen demand

6. WBOD has organic nitrogen of 20 mg/l
7. Thus, secondary effluent may have twice the oxygen demand of a straight waste effluent
8. Assimilation characteristics of rivers, estuaries and coastal waters.

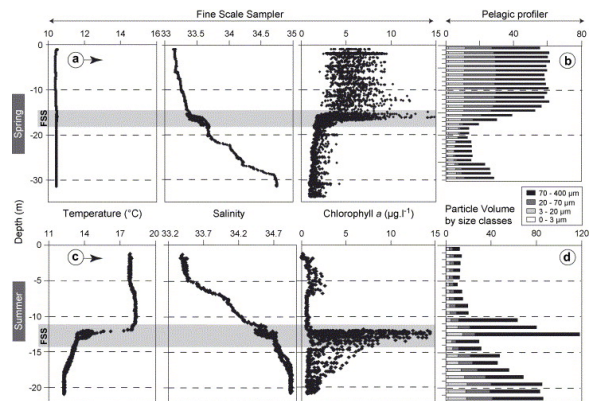


Figure 5. Lunven Fig. 4

P	is the oxygen utilization rate [g O ₂ d ⁻¹]
V	total volume [m ³]
τ	(<i>tau</i>) is the flushing time. [d]
k _p	phytoplankton production coefficient, assumed to be [1 d ⁻¹] [k _p =μ/0.693]
β	(<i>Beta</i>) is the fraction of the phytoplankton bloom that is retained and decays within the system out of the euphotic zone (assumed to be 0.5 for Fig. 1)
α	(<i>alpha</i>) is the ratio of the volume of the bottom waters to the total volume, V. (assumed equal to 0.5 for Fig. 1)

For large values of k_p*τ, Equation (3) approaches (P/V)*τ*(β/α).

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ON NERITIC PRODUCTION

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- Smith, S. V., J. T. Hollibaugh, S. J. Dollar and S. Vink. 1989. Tomales Bay, California: a case for carbon-controlled nitrogen cycling. *Limnol. Oceanogr.* 34: 37-52.
- Townsend, D. W. and R. W. Spinrad. 1986. Early phytoplankton blooms in the Gulf of Maine. *Cont. Shelf Res.* 6: 515-529. [*Spring blooms near shore occur when the critical depth reaches the bottom. The bloom occurs when the water column is well mixed.*]
- Townsend, D. W., J. P. Christensen, D. K. Stevenson, J. J. Graham, and S. B. Chenoweth. 1987. The importance of a tidally-mixed water to the biological oceanography of the Gulf of Maine. *J. Mar. Res.* 45: 699-728.
- Turner, J. T. 1994. Planktonic copepods of Boston Harbor, Massachusetts Bay and Cape Cod Bay, 1992. *Hydrobiologia* 292/293: 405-413.
- Welsh, B. L., R. B. Whitlatch, and W. F. Bohlen. 1982. Relationship between physical characteristics and organic carbon sources as a basis for comparing estuaries in Southern New England. Pp. 53-67 in V. S. Kennedy ed. *Estuarine Comparisons*. Academic Press, New York.

GRAY LITERATURE ON PRIMARY PRODUCTION IN BOSTON HARBOR/MASS. BAY¹

- Fitzgerald, M. C. 1980. Anthropogenic influence on the sedimentary regime of an urban estuary-Boston Harbor. Ph.D. thesis. MIT-Woods Hole Ocean. Inst. [*He collected plankton data in Boston Harbor from 1977-1979. The 1978 spring bloom was dominated by Thalassiosira, with Coscinodiscus and Chaetocerus sp. also abundant. In May 1979, Coscinodiscus and Skeletonema costatum were dominant and Thalassiosira secondary.*]

- Frankel, S. and B. Pierce. 1973. Determination of water quality parameters in the Mass. Bay (1970-1973). MIT Sea Grant Project Office [MITSG 74-8], Cambridge, 342 pp. [*Field data were collected from Nov. 1970 through Aug. 1973 on NO_2^- , NO_3^- , PO_4^- , SiO_2 , NH_3 and dissolved oxygen. There was a linear gradient in nutrients away from Boston Harbor, indicating a Boston Harbor nutrient source (or increased vertical diffusion nearshore). Nitrogen is virtually undetectable in MA Bay after the spring bloom, whereas phosphorus remains at approx. 1.5-3.5 μ Molar.]*
- Karpen, J. 1973. Dissolved nutrient-seawater density correlations and the circulation in Boston Harbor and Vicinity. Part II in Spring run-off and nutrient-seawater density correlations in Massachusetts Bay. MIT, Cambridge.
- Marshall, H. G. and M. Cohn. 1982. Seasonal phytoplankton assemblages in Northeastern coastal waters of the United States. NOAA Technical Memorandum NMFS-F/NEC-15. Woods Hole MA, 34 pp. [*This is one of the earlier studies on MA Bay phytoplankton composition **Parker (1975)** provides the best description of phytoplankton species composition. The 1982 301(h) waiver contains additional data, as does the 1987 MWRA Environmental Impact Report on the secondary outfall siting.]*
- Martin, C. and C. S. Yentsch. 1973. Monitoring of the "foul area" dumping area in Massachusetts Bay for effects of dredge spoil disposal on phytoplankton growth. Rept to U.S. Army Corps of Engineers, Cont DACW 33-74-M-0190.
- MWRA. March 31, 1988. Secondary Treatment Facilities Plan. Volume V, Appendix A. [*Section 4.9.2 briefly discusses the far-field modeling of nutrients. The concentrations after 7 d are plotted (a large area will have a concentration of 40 μ g/l) The DO simulations are described on p. 5-101. Flow rates of the diffuser will vary from 13.14 m^3 /sec (300 mgd) to 55.64 m^3 /sec (1270 mgd). The median flow is 400-500 mgd.]*
- MWRA. March 31, 1988. Secondary Treatment Facilities Plan. Volume V, Appendix B. Chemical and Biological Oceanography "The phytoplankton and primary productivity results are summarized on p. B-35
- MWRA. March 31, 1988. Secondary Treatment Facilities Plan. Volume V, Appendix H. Far-field modeling results.
- MWRA. March 31, 1988. Secondary Treatment Facilities Plan. Volume V, Appendix Y (Nutrients) and Appendix Z (Primary Production) [*Appendix Z Includes primary production estimates, species composition and nutrient pulse experiments performed by T. Smayda (Mackerel Cove Associates) on samples taken on 4 cruises from early July - September 1987. The proposed diffuser site has production ranging from .2 to over 1 g C $m^{-2}day^{-1}$. A subsurface Chl maximum was not found in 2 of the cruises at the proposed diffuser site.]*
- MDC. 1979. Application for modification of secondary treatment requirements for its Deer Island and Nut Island Effluent discharges into marine waters. Vol. 5, Sept. 13, 1979. [*Plankton samples were taken in July 1979 in Boston Harbor and at the proposed diffuser site in MA Bay.]*
- Mulligan, H. F. and G. C. McLeod. 1974. Phytoplankton Productivity in Mass. Bay Jan-June 1974. Final Report to New England Aquarium.
- New England Aquarium. 1973a. Vol. I. Water quality measurements of Boston Harbor. G. C. McLeod, Director of Research. September 1973. [*Includes measurements of nutrients and Chl a in Boston Harbor. There is a rather late spring bloom in April-May, followed by a decline in Chl a , with highly variable small-scale late summer and fall blooms from late July through October.]*
- New England Aquarium. 1973b. Vol. III. Experimental analysis of Boston Harbor water quality data with the model Bio-Dyn III. H. V. Rice and G.C. McLeod.

Parker, J. 1974. Phytoplankton primary productivity in Massachusetts Bay. Ph.D. Thesis, U. New Hampshire. [*The spring bloom is dominated by Porosira glacialis, Thalassiosira nordenskoldii, T. gravida, Chaetocerus debile, Thalassiosira spp., Skeletonema costatum reaches peak abundances during the summer and fall. The summer community is dominated by Chlamydomonas and dinoflagellates (Amphidinium sp., Gonyaulax sp. and Ceratium sp.. Parker also estimated primary production seasonally at 1 station in MA Bay, and Chl. concentrations at a number of stations.]*

Trapper, C. 1970. Identification of phytoplankton from three stations in Boston Harbor: Research Report. New England Aquarium, April 1970. [*A 1970 sampling program revealed a late-March to early-April spring bloom of Thalassiosira nordenskoldii. In 1971, the dominant species in the Boston Harbor spring bloom was Skeletonema costatum [New Eng. Aqu. 1973a]]*

MODELS OF PRIMARY PRODUCTION IN ESTUARIES

Chang, J. and E. J. Carpenter. 1985. Blooms of the dinoflagellate *Gyrodinium aureolum* in a Long Island estuary: box model analysis of bloom maintenance. *Marine Biology* 89: 83-93.

Cole, B. E. and J. E. Cloern. 1987. An empirical model for estimating phytoplankton productivity in estuaries. *Mar. Ecol. Prog. Ser.* 36: 299-305. [*Primary production is linearly related to the product of average water-column Chl a concentration * depth * light intensity (I₀). This model updated in **Jassby et al. 2002**] [24]*

Dwyer, R. L. and J. N. Kremer. 1983. Frequency-domain sensitivity analyses of an estuarine simulation model. *Ecol. Model.* 18: 35-54.

Jassby, A. D., J. E. Cloern and B. E. Cole. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnol. Oceanogr.* 47: 698-712. [Sacramento-San Joaquin River Delta. Uses the Cole-Cloern model] [24]

Kremer, J. N. and S. W. Nixon. 1978. A coastal marine ecosystem. Simulation and analysis. Springer-Verlag, Berlin.

Kremer, J. N. and P. Kremer. 1983. Ecological

circulation model of Los Angeles Harbor. *Env. Man.* 7: 239-252.

Officer, C. B. and J. H. Ryther. 1977. Secondary sewage treatment versus ocean outfalls: an assessment. *Science* 197: 1056-1060. [*This should have been a key paper in the debate over Boston Harbor's application for a Section 301(h) waiver document — the application for a waiver from the secondary sewage treatment requirements of the 1972 Federal Clean Water Act. After writing this paper, Officer and Ryther joined the MDC's scientific advisory board which advised the Dukakis and King administrations that Boston Harbor should apply for a waiver. This paper was never cited in any of the subsequent reports and decisions on the 301(h) waiver — strange*]

Peterson, D. H. and J. F. Festa. 1984. Numerical simulation of phytoplankton productivity in partially mixed estuaries. *Est. Coast. & Shelf Sci.* 19: 563-589.

Winter, D. F., K. Banse, and G. C. Anderson. 1975. The dynamics of phytoplankton blooms in Puget Sound, a fjord in the northwestern United States. *Marine Biology* 29: 139-176. [*Nutrients are rarely limiting in the main basin of Puget Sound. Primary production is controlled largely by physical factors. This situation may apply to many temperate and arctic waters if Harrison & Platt's 1986 analysis in Polar Biology is borne out*]

Wofsy, S. C. 1983. A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. *Limnol. Oceanogr.* 28: 1144-1155. [*The optical depth in nutrient-rich systems is between 5 and 10. Phytoplankton standing crops and production can be predicted if the extinction of light by nonliving material is known. To estimate the potential effects of eutrophication, one needs to know: 1) mixing depth, total light extinction, and extinction due to nonliving and refractory materials. This model was later refined by **Cole & Cloern (1987)***]

HARMFUL ALGAL BLOOMS

[I'm just starting this listing of papers on noxious species with an emphasis on those known to occur in MA Bay. Most of the key papers are listed on the harmful algae web page: <http://www.redtide.who.edu/hab/>. Volume 42, No. 5, part 2 is a full issue of *Limnol. Oceanogr.* devoted to harmful algal blooms]

Anderson, D. M. 1994. Red tides. *Scientific American* 271: 62-68 .

Anderson, D. M. 1997. Bloom dynamics of toxic *Alexandrium* species in the northeastern U. S. *Limnol. Oceanogr.* 42: 1009-1022.

Burkholder, J. M., H. B. Glasgow and C. W. Hobbs. 1995. Fish kills linked to a toxic ambush-predator dinoflagellate: distribution and environmental conditions. *Mar. Ecol. Prog. Ser.* 124: 43-61.

Donaghay, P. L., and T. R. Osborn. 1977. Toward a theory of biological-physical control of harmful algal bloom dynamics and impacts. *Limnol. Oceanogr.* 42: 1283-1296.

Franks, P. J. S. 1997. Models of harmful algal blooms. *Limnol. Oceanogr.* 42: 1273-1282.

Franks, P. J. S. 1997. Spatial patterns in dense algal blooms. *Limnol. Oceanogr.* 42: 1297-1305.

Franks, P. J. S. and D. M. Anderson. 1992a. Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. *Marine Biology* 112: 153-164. [Proposes that the source of MA Bay *Alexandrium* blooms are Maine coastal rivers with transport by a coastal buoyant plume. The hypothesis tested by **Franks & Anderson 1992b** and revised by **McGillicuddy et al. 2003**] {25}

Franks, P. J. S. and D. M. Anderson. 1992b. Toxic phytoplankton blooms in the southwestern Gulf of Maine: testing hypotheses of physical control using historical data. *Marine Biology* 112: 165-174. [Test of the buoyant plume hypothesis proposed by **Franks & Anderson 1992a**. See **McGillicuddy et al (2003)** for a modified model] [25]

Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32: 79-99 .

Matsuyama, Y, T. Uchida, and T. Honjo. 1997. Toxic effects of the dinoflagellate *Heterocapsa circularisquama* on clearance rate of the blue mussel *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.* 146: 73-80.

McGillicuddy, D. J, R. P. Signell, C. A. Stock, B. A. Keafer, M. D. Keller, R. D. Hetland and D. M. Anderson. 2003. A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine. *J. Plankton Research* 25: 1131-1138. [Revises the coastal bloom hypothesis proposed by **Franks & Anderson 1992a** and **1992b**] {25}

National Research Council 2000. Clean coastal waters: understanding and reducing the effects of nutrient pollution. National Academy Press, Washington D. C. [?]

Smayda, T. J. 1997. What is a bloom? A commentary. *Limnol. Oceanogr.* 42: 1132-1136.

Smayda, T. 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.* 42: 1137-1153.

Townsend, D. W., N. R. Pettigrew, and A. C. Thomas. 2001. Offshore blooms of the red tide dinoflagellate, *Alexandrium* sp., in the Gulf of Maine. *Continental Shelf Research* 21: 347-369. [Documents an offshore source and bloom of dinoflagellates. See **McGillicuddy et al. 2003** for a model of blooms] {?}

Turner, J. T. and P. A. Tester. 1997. Toxic marine phytoplankton, zooplankton grazers and pelagic food webs. *Limnol. Oceanogr.* 42: 1203-1214.

Valiella, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological consequences. *Limnol. Oceanogr.* 42: 1105-1118.

BENTHIC-PELAGIC COUPLING

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- Boynton, W. R. and W. M. Kemp. 1985. Nutrient regeneration and oxygen consumption by sediments along an estuarine salinity gradient. *Mar. Ecol. Prog. Ser.* 23: 45-55.
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- Czytrich, H. U. Eversberg, and G. Graf. 1986. Interaction between pelagial and benthic during autumn in Kiel Bight. II. Benthic activity and chemical composition of organic matter. *Ophelia* 26: 123-133. [Diatoms are not utilized, since bacteria apparently can not break down intact frustules.]
- Dame, R., R. Zingmark, H. Stevenson, and D. Nelson. 1980. Filter feeder coupling between the estuarine water column and benthic subsystems. Pp. 521-526 in: V. S. Kennedy, ed. *Estuarine Perspectives*. Academic Press, New York.
- D'Elia, C. F., D. M. Nelson, and W. R. Boynton. 1983. Chesapeake Bay nutrient and plankton dynamics: III. The annual cycle of dissolved silicon. *Geochim. Cosmochim. Acta* 47: 1945-1955. [The benthic nutrient flux is 5 times that of riverine input]
- Emerson, C. W., J. C. Roff, and D. J. Wildish. 1986. Pelagic-benthic coupling at the mouth of the Bay of Fundy. *Ophelia* 26: 165-180. [Phytoplankton production is relatively low ($130 \text{ g C m}^{-2}\text{y}^{-1}$) compared to the Gulf of Maine ($300 \text{ g C m}^{-2}\text{y}^{-1}$). Water-column heterotrophy is far more important than benthic. But, they conclude: "However, the very high macrobenthic production on the Scotian Shelf drift (Wildish and Peer 1983) indicates that the lateral transport of carbon by tidal energy may be very significant within the Bay of Fundy...Production at higher trophic levels within the bay should thus not be viewed as a simple consequence of the proportion of the vertical energy loss from the pelagic to the benthic realm.(p. 177)"]
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EUTROPHICATION IN THE SEA

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- Ryther, J. H. and W. M. Dunstan. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* 171: 1008-1013. [Bioassay experiments indicate N limitation in the New York bight]
- Smith, S. V. and J. T. Hollibaugh. 1989. Carbon-controlled nitrogen cycling in a marine macrocosm: an ecosystem-scale model for managing cultural eutrophication. *Mar. Ecol. Prog. Ser.* 52: 103-109. [The nitrogen flux in a lagoon is controlled by the rate of carbon input (e.g., increased organic carbon input can lead to increased denitrification)]

EUTROPHICATION IN LAKES (WITH AN EMPHASIS ON LAKE WASHINGTON)

- Chapro, S. and K. Beckhow. 1983. Comment on "the effect of changes in the nutrient income on the condition of Lake Washington. *Limnol. Oceanogr.* 28: 792-795. [The authors critique an empirical relationship of Edmondson & Lehman [1981]]

- Edmondson, W. T. 1970. Phosphorus, nitrogen, and algae in Lake Washington after diversion of sewage. *Science* 169: 690-691.
- Edmondson, W. T. 1991. The uses of ecology: Lake Washington and Beyond. University of Washington Press, Seattle. [This book, based on the U. Washington Danz lectures, discusses the politics and science in the cleanup of Lake Washington. Lehman 1986a also provides a good summary of the science and politics of Lake Washington's recovery.]
- Edmondson, W. and J. Lehman. 1981. The effect of changes in the nutrient income on the condition of Lake Washington after diversion of sewage. *Science* 169: 690-691.
- Harris, G. P. 1986. Phytoplankton ecology. Chapman & Hall, London & New York. [Pp. 143-165 and 275-285 provide summaries of Vollenweider's mass loading relationships to lake chlorophyll. Harris suggests that, in general, phytoplankton are not nutrient limited; succession occurs so that the species present are adapted to grow near their maximal growth rates, given the nutrient input (including regeneration). He further suggests that both nitrogen and phosphorus are important in the oceans.]
- Lehman, J. T. 1986. Control of eutrophication in Lake Washington. Pp. 301-316 in *Ecological knowledge and environmental problem-solving: concepts and case studies*. National Academy Press, Washington D.C. 388 pp. [Lehman provides an excellent discussion of the politics and science involved in the clean-up of Lake Washington. The article is a panegyric to the efforts of W. T. Edmondson]
- Lehman, J. T. 1986. The goal of understanding in limnology. *Limnol. Oceanogr.* 31: 1160-1166. [This written as rebuttal to Peters 1986. Eutrophication is covered on p. 1162-1165. Lehman is not a fan of the Vollenweider/Harris approach of using log-log empirical relationships to assess the effects of eutrophication.]
- Peters, R. H. 1986. The role of prediction in limnology. *Limnol. Oceanogr.* 31: 1143-1159. [Follows Vollenweider in advocating a predictive limnology based on regression, not population dynamics.]

- Schindler, D. W. 1978. Predictive eutrophication models. *Limnol. Oceanogr.* 23: 1080-1081. [*A critique of Thomann 1977 and support for Vollenweider's [1976] empirical relationship.*]
- Thomann, R. V. 1977. Comparison of lake phytoplankton models and loading plots. *Limnol. Oceanogr.* 22: 370-373.
- Thoman, R. V. 1978. Reply to comment by D. W. Schindler. *Limnol. Oceanogr.* 23: 1082-1083.
- Vollenweider, R. A. 1976. Advances in defining critical loading levels in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* 33: 53-83. [*Derives empirical relationships (i.e., regression equations) between nutrient input and lake response (e.g., Chl a concentration).*]

SUBSURFACE CHLOROPHYLL MAXIMA

Comments

Massachusetts Bay has a well developed subsurface chlorophyll maximum in the summer (**Haury et al., 1983**). **Holligan et al. (1984)** have shown that this maximum is found throughout the Gulf of Maine and is a phytoplankton carbon maximum as well. Subsurface chlorophyll maxima occur in many areas of the world's ocean. **Longhurst and Harrison (1989)** provide the most recent summary.

Subsurface chlorophyll maxima (SSCM's) in Southern California waters have been shown to be critical for the first-feeding larvae of the Northern anchovy (**Lasker 1975**). They are particularly dependent on the abundances of the large (40-50 µm) dinoflagellate *Gymnodinium splendens*, which is often dominant in the SSCM. Lasker proposed the "stable-ocean hypothesis" to explain the Interannual variability in larval anchovy. In years with high wind stress during the key 1-wk feeding period of the first-feeding larvae, the SSCM is weak and the fish starve.

This short reading list contains some very difficult papers. The key paper in the list is **Haury et al. 1983**, which describes the subsurface chlorophyll maximum in Mass. Bay, detected by pump sampling water through a Turner fluorometer. **Cullen (1982)** provides a good summary of the literature on subsurface chlorophyll maxima. Cullen points out that a subsurface chlorophyll maximum does not necessarily mean that there is a subsurface phytoplankton carbon maximum. Harrison, Platt & Lewis (1985) provide an exceptionally powerful approach to estimating primary production in the field.

Understanding the MA Bay SSCM

- Harrison, W. G., T. Platt, and M. K. Lewis. 1985. The utility of light-saturation models for estimating marine primary productivity in the field: a comparison with conventional simulated in situ methods. *Can. J. Fish. Aquat. Sci.* 42: 864-872. [*Their P vs I model breaks down at the 1% light depth. In their subarctic sites, little total production occurs at the subsurface Chl maximum, but that is probably not the case in MA Bay. There may also be a physiologically different assemblage of phytoplankters (probably different species) at the subsurface chlorophyll maximum*]
- Haury, L. R., P. H. Wiebe, M. H. Orr, and M. G. Briscoe. 1983. Tidally generated high-frequency internal wave packets and their effects on plankton in Massachusetts Bay. *Journal of Marine Research* 41: 65-112. [*See especially their profiles of fluorescence with depth.*]
- Holligan, P. M., W. M. Balch, and C. M. Yentsch. 1984. The significance of subsurface chlorophyll, nitrite, and ammonium maxima in relation to nitrogen for phytoplankton growth in the stratified waters of the Gulf of Maine. *J. Mar. Res.* 42: 1051-1073. [*The SSCM is a biomass maximum, sometimes contains toxic Gonyaulax tamarensis, and may be a new production maximum. Primary production above the SSCM is heavily dependent on regenerated N. The importance of pelagic nitrification is discussed; benthic nutrient regeneration is impeded by a layer of G. of Me intermediate water.*]
- Townsend, D. W., T. L. Cucci and T. Berman. 1984. Subsurface chlorophyll maxima and vertical distribution of zooplankton in the Gulf of Maine. *J. Plankton Res.* 6: 793-802.

Other readings on subsurface chlorophyll maxima

- Abbott, M. R., K. L. Denman, T. M. Powell, P. J. Richerson, R. C. Richards, and C. R. Goldman. 1984. Mixing and the dynamics of the deep chlorophyll maximum in Lake Tahoe. *Limnol. Oceanogr.* 29: 862-878.

- Anderson, G. C. 1969. Subsurface chlorophyll maximum in the Northeast Pacific ocean. *Limnol. Oceanogr.* 14: 386-391. [*Anderson's '69 and '72 papers describe one of the most pronounced deep subsurface Chl maxima, the dynamics of which were modeled by Jamart et al. (1977)*] {31}
- Anderson, G. C. 1972. Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum. Pp 219-240 in A. T. Pruter and D. L. Alverson, eds., *The Columbia River Estuary and adjacent ocean waters*. University of Washington Press, Seattle, U.S.A.
- Banse, K. 1987. Clouds, deep chlorophyll maxima and the nutrient supply to the mixed layer of stratified water bodies. *J. Plankton Res.* 9: 1031-1036.
- Cox, J. L., P. H. Wiebe, P. Ortner and S. Boyd. 1982. Seasonal development of subsurface chlorophyll maxima in slope water and the northern Sargasso Sea of the northwestern Atlantic Ocean. *Biol. Oceanogr.* 1: 271-285.
- Cullen, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Can. J. Fish. Aquat. Sci.* 39: 791-803. [*This was the best available synthesis and review prior to Longhurst & Harrison (1989)*] {30}
- Cullen, J. J. and R. W. Eppley. 1981. Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance. *Oceanol. Acta* 4: 23-32. [*Detailed observations of primary production rate, fluorescence, Chl a, and phytoplankton biomass are combined to explain the processes controlling the S. Cal. SSCM. Grazing isn't assessed*]
- Cullen, J. J., F. M. H. Reid, and E. Stewart. 1982. Phytoplankton in the surface and chlorophyll maximum off Southern California in August 1978. *J. Plankton Res.* 4: 665-694.
- Dortch, Q. 1987. The biochemical composition of plankton in a subsurface chlorophyll maximum. *Deep-Sea Res.* 34: 705-712.
- Eppley, R. W., E. Swift, D. G. Redalje, M. R. Landry and L. W. Haas. 1988. Subsurface chlorophyll maxima in August-September 1985 in the CLIMAX area of the North Pacific. *Mar. Ecol. Prog. Ser.* 42: 289-301.
- French, D. P., M. J. Furnas, and T. J. Smayda. 1983. Diel changes in nitrite concentration in the chlorophyll maximum in the Gulf of Mexico. *Deep-Sea Res.* 30: 707-722.
- Haury, L. R., P. H. Wiebe, M. H. Orr, and M. G. Briscoe. 1985. Tidally generated high-frequency packets and their effects on plankton in Massachusetts Bay. *J. Mar. Res.* 41: 65-112.
- Holligan, P. M. 1978. Patchiness in subsurface phytoplankton populations on the northwest European continental shelf. Pp. 221-238 in J. H. Steele (ed) *Spatial Pattern in Plankton Communities*. Plenum Press, New York. [*The SSCM in the British Isles is described. It persists for 2 to 4 months. With weak stratification, diatoms are dominant but are replaced by dinoflagellates with increasing stratification.*]
- Holligan, P. M., W. M. Balch, and C. M. Yentsch. 1984. The significance of subsurface chlorophyll, nitrite and ammonium maxima in relation to nitrogen for phytoplankton growth in stratified waters of the Gulf of Maine. *J. Mar. Res.* 42: 1051-1073.
- Jamart, B. M., D. F. Winter, K. Banse, G. C. Anderson, and R. K. Lam. 1977. A theoretical study of phytoplankton growth and nutrient distribution in the Pacific Ocean off the northwestern U. S. coast. *Deep-Sea Research* 24: 753-777. [*The seasonal development of the subsurface Chl *a* maximum documented by Anderson (1969) is theoretically modeled. This model includes a strong role for zooplankton grazing, which speeds the development of the SSCM. The role of zooplankton grazing is discounted in many later models (mathematical and conceptual) for the SSCM. Tittel et al. (2003) invoke grazing by mixotrophs as key to the development of the SSCM*] {31, 33}
- Jamart, B. M., D. F. Winter, and K. Banse. 1979. Sensitivity analysis of a mathematical model of phytoplankton growth and nutrient distribution in the Pacific Ocean off the northwestern U.S. coast. *Journal of Plankton Research* 1: 267-290. [*A mathematical sensitivity analysis of the 1977 Deep-Sea Research model*]
- Jenkins, W. J. and J. C. Goldman. 1985. Seasonal oxygen cycling and primary production in the Sargasso Sea. *J. Mar. Res.* 43: 465-491.
- Kiefer, D. A. and J. N. Kremer. 1981. Origins of vertical

- patterns of phytoplankton and nutrients in the temperate, open ocean: a stratigraphic hypothesis. *Deep-Sea Res.* 28: 1087-1105.
- Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *U. S. Fish. Bull.* 73: 453-462. [*Anchovy larvae were added to different water masses. They require dinoflagellates (Gymnodinium splendens) which grow at the subsurface chlorophyll maximum. Lasker's stable ocean hypothesis ties Interannual variability in anchovies to the strength of subsurface chlorophyll maxima. Windy years produce poor recruitment.*]
- Lasker, R. 1988. Food chains and fisheries: an assessment after 20 years. Pp. 173-182 in B. J. Rothschild, ed., *Toward a theory of biological-physical interaction in the World Ocean*. B. J. Rothschild, ed., Kluwer, Dordrecht.
- Longhurst, A. R. and W. G. Harrison. 1989. The biological pump: profiles of plankton production and consumption in the upper ocean. *Prog. Oceanogr.* 22: 47-123. [*The best available synthesis and review. L & H discuss the relationship between the SSCM, primary production and devote major emphasis to the vertical profiles of zooplankton and inferred grazing pressure*] {3, 15, 30, 31}
- Lunven, M., J. F. Guillaud, A. Youénu, M. P. Crassous, R. Berrie, E. Le Gall, R. Kérouel, C. Labry, and A. Aminot. 2005. Nutrient and phytoplankton distributions in the Loire River plume (Bay of Biscay, France) resolved by a new fine scale sampler. *Est. Coastal Shelf Sci.* 65: 94-108. [*A fine scale sampler (≈ 10 cm resolution) used to document remarkable fine scale structure of light, Chl a, pheophorbide, diatoms, dinoflagellates and nutrients*] {?}
- Napp, J. M., E. R. Brooks, F. M. H. Reid, P. Matrai, and M. M. Mullin 1989. The vertical distribution of marine particles and grazers. I. Their vertical distribution of food quality and quantity. *Mar. Ecol. Prog. Ser.* 50: 45-58. II. Absence of grazer control upon the vertical distribution of phytoplankton. *Mar. Ecol. Prog. Ser.* 50: 59-72
- Parker, R. A. 1986. Simulating the development of a chlorophyll maxima in the Celtic Sea. *Ecol. Modelling* 33: 1-11.
- Platt, T. and C. L. Gallegos. 1980. Modelling primary production. Pp. 339-362 in P. G. Falkowski, ed., *Primary productivity in the sea*. Plenum, New York, U.S.A.
- Reid, F. M. H., E. Stewart, R. W. Eppley and D. Goodman. 1978. Spatial distribution of phytoplankton species in chlorophyll maximum layers off Southern California. *Limnol. Oceanogr.* 23: 219-226. [*The phytoplankton species composition of the SSCM was analyzed to test three hypotheses: 1) the phytoplankton species composition in more similar in samples taken from the SSCM from different areas, than the surface and SSCM from the same area, 2) the species composition of the SSCM from area to area will be more similar than the surface phytoplankton from area to area, and 3) species composition change should be more abrupt in the offshore than onshore direction. Cluster analysis and PCA used to test the hypothesis. All 3 hypotheses were refuted by some analyses*]
- Reid, J. L. and E. Shulenberger. 1986. Oxygen saturation and carbon uptake near 28°N, 155°W. *Deep-Sea Res.* 33: 267-271. [*This is an important paper in the Great Debate over primary production in oligotrophic gyres. Part of the debate centers on whether the gyres are 2-layered systems, with the subsurface Chl maximum acting with different dynamics, particularly less Nitrogen regeneration, than the surface layer.*]
- Roman, M. R., C. S. Yentsch, A. L. Gauzema, and D. A. Phinney. 1986. Grazer control of the fine-scale distribution of phytoplankton in warm-core Gulf Stream rings. *J. Mar. Res.* 44: 795-813. [*There is a subsurface primary production maximum, overlying a subsurface Chl. maximum. Both layers are below the layer of maximum grazing.*]
- Shulenberger, E. and J. L. Reid. 1981. The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity reconsidered. *Deep-Sea Res.* 28: 901-919.

- Taguchi, S., G. R. DiTullio and E. A. Laws. 1988. Physiological characteristics and production of mixed layers and chlorophyll maximum phytoplankton populations in the Caribbean Sea and western Atlantic Ocean. *Deep-Sea Res.* 35: 1363-1377. [The Redalje-Laws Chl a specific labeling procedure is used to estimate specific growth rates and C:Chl ratios.]
- Tittel, J., Bissinger V, Zippel B, Gaedke U, Bell E, Lorke A, Kamjunke N. 2003. Mixotrophs combine resource use to outcompete specialists: implications for aquatic food webs. *Proc Natl Acad Sci U S A.* 100(22):12776-81. [An interesting new hypothesis for the seasonal development of SSCM, which they argue result from mixotrophic predation. **Jamart et al. (1977)** had earlier invoked predation as important for the creation of the SSCM] {31}
- Townsend, D. W., T. L. Cucci, and T. Berman. 1984. Subsurface chlorophyll maxima and vertical distribution of zooplankton in the Gulf of Maine. *J. Plankton Res.* 6: 793-802.
- Woods, J. D. and R. Onken. 1982. Diurnal variation and primary production in the ocean-preliminary results of a Lagrangian ensemble model. *Journal of Plankton Research* 4: 735-756. [A really superb paper. They show that the dynamics of phytoplankton growth are best modeled by following a consortium of individual cells as they are advected vertically through the water column. Phytoplankton growth doesn't occur with assemblages of cells being layered vertically, and perhaps it shouldn't be modeled as if it were.]
- Lie, U. 1974. Distribution and structure of benthic assemblages in Puget Sound, Washington, U.S.A. *Marine Biology* 26: 203-223. [Includes ternary plots of community structure, which appears to fit the continuum model.]
- Nichols, F. H. 1979. Benthic polychaete assemblages and their relationship to the sediment in Port Madison, Washington. *Mar. Biol.* 6: 48-57. [A paper from Fred Nichols M.Sc. dissertation.]
- Nichols, F. H. 1985. Abundance fluctuations among benthic invertebrates in two Pacific estuaries. *Estuaries* 8: 136-144. [Comparison of a shallow subtidal community in San Francisco Bay, and a community in the deepest part of Puget Sound (the 100-fathom hole in Elliot Bay). The latter community changed dramatically in 20 years, with the change attributed here to organic enrichment. **Nichols (1988)** recanted this conclusion]
- Nichols, F. H. 1988. Long-term changes in a deep Puget Sound benthic community: local or basin-wide? Pp. 65-71 in *Proceedings of the 1st Annual Meeting on Puget Sound Research*. Puget Sound Water Quality Authority, Olympia WA. [*Pectinaria*, among the dominants in the 1960s had disappeared by the early 80s, leading Nichols 1985 to conclude that organic enrichment had led to a Pearson-Rosenberg successional replacement. After **Nichols (1985)** published this conclusion, *Pectinaria* returned, leading Nichols to argue for long-term cycles]
- Pearson, T. H. and R. Rosenberg. 1976. A comparative study of the effect on the marine environment of wastes from cellulose industries in Scotland and Sweden. *Ambio* 5: 77-79.
- Pearson, T. H. and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 16: 229-311
- Rhoads, D. C., P. L. McCall, and J. L. Yingst. 1978. Disturbance and production on the estuarine seafloor. *American Scientist* 66: 577-586.

MISCELLANEOUS

- Giblin, A.E., C.S. Hopkinson, and J. Tucker. 1997. Benthic metabolism and nutrient cycling in Boston Harbor, Massachusetts, U.S.A. *Estuaries* 20:346-364. {?}

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