Nutrient issues update 1995: metabolism in Boston Harbor, Massachusetts and Cape Cod Bays, MA (USA) during 1992-1994

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Nutrient Issues Update 1995: Metabolism in Boston Harbor, Massachusetts Bay, and Cape Cod Bay, MA (USA) during 1992-1994

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ABSTRACT

During 1992-1994, we made shipboard incubations suitable for determining rates of primary production in water from Boston Harbor, Massachusetts Bay, and Cape Cod Bay, MA. These measurements were part of an extensive baseline monitoring program developed by the Massachusetts Water Resources Authority in an effort to characterize water quality prior to diversion of effluent from Boston Harbor directly into Massachusetts Bay via a submarine outfall diffuser.

Whole-water samples were exposed to irradiance levels from ~5 to 2000 $\mu E\ m^{-2}\ sec^{-1}$. In each year, P-I incubations were performed on six surveys, spread over the year to capture seasonal features of production dynamics. The number of stations and depths examined varied between years. There were 10 stations and two depths sampled in 1992-1993. In 1994, we performed in-depth studies at two stations (Boston Harbor-edge and western Massachusetts Bay) by sampling 4 depths. In 1992, incubations used oxygen changes to estimate production and in 1993-1994, ^{14}C methods were used.

Using depth-intensive 1994 data, we present results in terms of parameters of P-I curves and compare these to previous studies. We were able to develop a simple empirical model to predict integrated primary production rates using information on chlorophyll biomass, incident daily light, and the depth of the photic zone. The resultant linear regression model was virtually the same as described for other estuarine and coastal waters, giving us confidence in our use of the model as an extrapolation tool. We used hydrographic surveys (with chlorophyll and light data) from a total of 16 surveys in 1994 to extrapolate production over the year. Results suggested primary production at the edge of Boston Harbor near Deer Island was ~266 $gC\ m^{-2}\ y^{-1}$, whereas western Massachusetts Bay was much higher, ~435-468 $gC\ m^{-2}\ y^{-1}$. Using the empirical model, we obtained favorable comparisons with production rates calculated from 1992-1993 P-I incubations. We therefore extrapolated from data in 1992 and 1993 to estimate annual production rates of 386 and 620 $gC\ m^{-2}\ y^{-1}$ for western Massachusetts Bay in 1992 and 1993 respectively, 416-555 and 486 $gC\ m^{-2}\ y^{-1}$ for the edge of Boston Harbor in 1992 and 1993.

Variability over time and across regions is discussed extensively and the many uncertainties inherent in production estimates and with different methodologies are detailed. We demonstrate that our high estimates of primary production are consistent with the literature on nutrient rich coastal shelf environments. Much of the variability in production on daily, seasonal, and annual timescales, as well as differences between Harbor and Bay may be ascribed to variations in light availability. Secondarily, production variability was related to integrated photic zone chlorophyll. Often, integrated water column production was higher in the Bay than the Harbor, even though the Harbor typically has higher nitrogen concentrations in the photic zone.

Using primary production estimates for an ~100 km^2 region in western Massachusetts Bay surrounding the future offshore outfall location, we constructed tentative metabolic budgets

for carbon. Budgets used measurements of respiration in the water column and sediments of this region and annual estimates were derived from empirical formulations of respiration rates in relation to temperature and organic matter. Results suggest that bottom sediments (32 m average water depth) consume ~5% of overlying production and that most of the production (~70%) is consumed in the photic layer of the water column (~20 m deep), which extends to the depth of the pycnocline during seasonal stratification.

Additionally, we compared rates of metabolism to trends in dissolved oxygen in western Massachusetts Bay. Seasonal and annual variations in bottom-water DO concentrations appear to be semi-independent of metabolism and cannot reliably be predicted by trends in production or respiration. Overall, a variety of results and calculations suggest that there is a somewhat weak linkage between surface layer autotrophic processes and bottom-layer heterotrophic processes and that dissolved oxygen in the future outfall area is strongly influenced by other, presumably physical, factors.

In view of our results, we examine the utility of primary production measurements in the context of a marine monitoring program for a shallow shelf-water environment. We conclude that primary production is a poor early-warning indicator of bottom-water DO problems. For that purpose, measurements of DO concentration trends during early phases of seasonal stratification should suffice. Primary production measurements should be considered to provide a metabolic framework for understanding the fate of organic matter in this environment. As such, we propose that use of the simple empirical model, rather than extensive series of incubations, will adequately provide that basis. Finally, our analysis of variations in influential factors and uncertainties with production estimates provide a strong basis for consideration of time-space sampling designs for any efforts to characterize primary production in our study region.

TABLE OF CONTENTS

Page

ABSTRACT iii

INTRODUCTION 1

METHODS 2

Field Procedures 2
Analyses 3

RESULTS 6

Production measurement and modeling in 1994 6
Production measurement and modeling in earlier years 9

DISCUSSION AND CONCLUSIONS 11

Empirical model 11
High annual production 15
Metabolic budgets: fate of production in western Massachusetts Bay 20
Implications of results: recommendations for monitoring and prediction 25

ACKNOWLEDGEMENTS 28

REFERENCES 29

LIST OF TABLES

Table 1. Average relative % error for production-related variables, summarized at different scales.

LIST OF FIGURES

Figure 1. Water quality sampling stations in Boston Harbor, Massachusetts Bay, and Cape Cod Bay in 1994.

Figure 2. Frequency distribution for P_{max} values from all 88 modeled P-I curves for stations F23P (Boston Harbor edge) and N16P(Nearfield) during 1994.

Figure 3. Frequency distribution for α values from all 88 modeled P-I curves for stations F23P (Boston Harbor edge) and N16P (Nearfield) during 1994.

Figure 4. Comparison of integrated water column production as calculated from near-surface and deepest depths of sampling for all incubations during 1994.

Figure 5. Production during 1994 for stations F23P (Harbor edge) and N16P (Nearfield).

Figure 6a. Empirical model for production based on 22 measurements in 1994.

Figure 6b. Empirical model for production based on survey averages at stations F23P (Harbor edge) and N16P (Nearfield) during 1994.

Figure 7. Production at station N16P during 1994.

Figure 8. Model-calculated production in the nearfield region during 1994.

Figure 9. Production in the nearfield region during 1993.

Figure 10. Production in the nearfield region during 1992.

Figure 11. Variability in modeled production and the I_0 and BZ_p terms of the empirical model at station N16P during 1994.

Figure 12. An example of fine-scale spatial variability in chlorophyll concentration as estimated by *in situ* fluorescence.

Figure 13. Surface chlorophyll concentration gradient from shore to sea across the 21 nearfield stations.

LIST OF FIGURES (Continued)

Figure 14. Modeled production for four western-edge (shoreward) and four eastern-edge (seaward) stations of the nearfield region during 1994.

Figure 15. Comparison of modeled production and incident daily irradiance for the nearfield during the monitoring period 1992-1994.

Figure 16. Depth distribution of DO (% saturation) at nearfield stations during the strongly stratified summer-fall season in 1994.

Figure 17. N input and production in different coastal and estuarine ecosystems.

Figure 18. Sediment oxygen uptake in Massachusetts Bay during 1993 and 1994.

Figure 19. Depth distribution of dark-bottle respiration from measurements during 1994.

Figure 20. Empirical models for normalized respiration as a function of temperature based on measurements during 1994.

Figure 21. DO concentrations and % saturation in nearfield surface and bottom water through the 1994 annual cycle.

Figure 22. DO in the nearfield bottom water from April to October 1994:
Comparison of observations to model projected-contributions of water and sediment respiration.

INTRODUCTION

Boston Harbor, Massachusetts, and Cape Cod Bays are adjacent estuarine and shallow shelf ecosystems that are linked ecologically through hydrodynamics and nutrient flows. Shallow shelf systems in general have not been extensively studied, and this is especially true in the context of inshore-offshore coupling. Our particular study region is of special interest not only because the Harbor presently appears to export most of its nutrient input to western Massachusetts Bay (Kelly, 1993), but also because the fundamental nature of the coupling is scheduled for an abrupt change. Effluent discharge (and most of the nutrient load) now going into the Harbor will be diverted directly to western Massachusetts Bay in the future via a submarine outfall in water ~32 m deep about 15 km offshore.

As part of an effort to characterize the present environment, inshore-offshore gradients and biogeochemical linkages between the Harbor and the Bay, it is of interest to develop understanding of existing rates of metabolism (primary production and respiration). Through conductance of a comprehensive baseline monitoring program prior to sewage effluent diversion, an extensive data set has been collected during the period 1992-1994. This paper summarizes monitoring results from measurements and modeling of primary production in Massachusetts Bay and Boston Harbor (and to a more limited extent, Cape Cod Bay). We offer a synthesis of production rates and patterns with results of measurements of respiration in water and sediments, and as related to three-year trends for dissolved oxygen concentrations in bottom waters in the region of the future outfall.

The objectives of the paper are 1) to provide estimates of annual primary production for western Massachusetts Bay using incubation measurement results and modeling, 2) to discuss factors influencing rates of primary production in the Bay and the Harbor, 3) to develop tentative metabolic budgets in western Massachusetts Bay that express the relation between autotrophic and heterotrophic processes, and 4) to comment on results in the context of monitoring, predicting, and understanding metabolic changes due to a major sewage diversion.

METHODS

Field Procedures

Metabolic studies were conducted during 1992-1994 as part of a three-year baseline monitoring program (Harbor and Outfall Monitoring Project) conducted by Battelle Ocean Sciences for the Massachusetts Water Resources Authority (MWRA). Each year, minor modifications were made in measurements and number of stations. There were a total of 14 hydrographic/nutrient surveys in 1992 and 16 surveys in 1993 and 1994. A series of comprehensive reports on water column monitoring are published in a technical report series publicly available from the MWRA (see acknowledgements). Standard measurements for profiling the water column included *in situ* sensing of conductivity, temperature, dissolved oxygen, beam transmissometry, fluorescence, and photosynthetically active irradiance; discrete bottle measurements for organic and inorganic carbon and nutrients, chlorophyll, suspended solids, and phytoplankton species; and vertical-oblique tows for zooplankton species. Except for a brief period early in 1992, when light profiles were measured with a Licor cosine sensor, light readings were made using a Biospherical QSP-200AL underwater sensor mounted on the top of the hydrocast rosette and a Biospherical QSR-240 cosine sensor for simultaneous on-deck irradiance measurements of incident light.

1994 studies. The 1994 data set forms a principal focus for the summary of water column production and respiration in this paper. Figure 1 shows the location of all water-quality sampling stations for 1994. Primary production measurements were made at two of these stations. Station F23P is at the edge of Boston Harbor near the major present MWRA effluent discharge. Station N16P is in the middle of a sampling region referred to as the "nearfield" and is located close to the eastern end of a 2-km long diffuser track that will discharge MWRA effluent into western Massachusetts Bay bottom water beginning in about 1998. For productivity, these two stations were sampled once in February. For each of five other surveys (March, April, June, August, October), the stations were resampled on a separate day. The six surveys covered the entire sampling region (Figure 1). Additional surveys for the year sampled only the nearfield region; during June to October, these surveys were approximately bi-weekly.

Primary production measurements in 1994 used the general ^{14}C method of Strickland and Parsons (1972) as practiced at the Marine Ecosystems Research Laboratory (MERL) at the University of Rhode Island. For samples taken at four depths, ^{14}C primary production was measured by exposing samples to a light gradient using an on-deck incubation box with temperature control and artificial illumination (250-watt metal halide lamp). Fifteen 300-mL BOD bottles were inoculated with 2.5 μCi of ^{14}C-sodium bicarbonate. Three bottles were incubated in the dark. The remaining 12 bottles were exposed to irradiance levels ranging from ~ 5 to 2000 $\mu E\ m^{-2}\ sec^{-1}$. Samples for dissolved inorganic carbon (DIC) were taken on each production-sample hydrocast and used in calculations (Strickland and Parsons, 1972).

Dark respiration measurements were made in 1994 using a time-series incubation approach. Water column respiration rates were estimated in April, June, August, and October at a

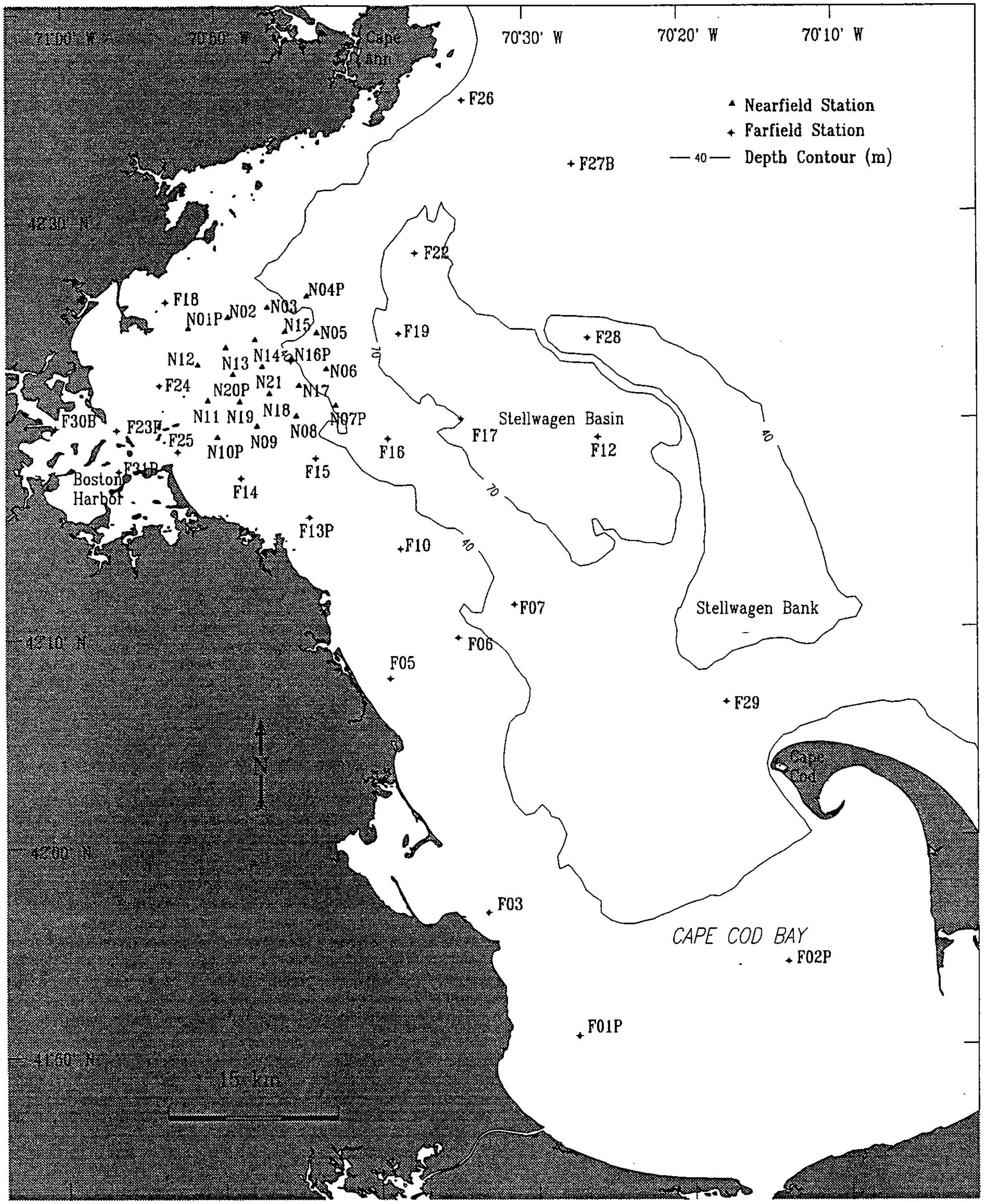

Figure 1. Water quality sampling stations in Boston Harbor, Massachusetts Bay, and Cape Cod Bay in 1994. The hydrographic and nutrient sampling station design was slightly different during 1992-1993, but all stations labeled "P" were sampled throughout the period. Productivity was measured at these ten stations during 1992-1993, but only at stations F23P and N16P during 1994.

series of stations representing a environmental gradient spanning the nearfield region from inshore to offshore. Sampling occurred at three depths (surface, mid-depth, and mid-bottom) at stations N20P and F19 and at the surface of station F24 (Figure 1). About twelve 300 ml-BOD bottles were filled with whole seawater and incubated at constant temperature near *in situ* conditions. Replicate (n=2 or 3) bottles were serially fixed (for automated Winkler titration using a Radiometer ABU-9 — Oudot *et al.*, 1988) at 5 time periods from 0 to 48 hours, or to 6 days for subpycnocline samples having lower temperature and with lower rates. Respiration rates were estimated by the slope of the DO concentration decrease over time as indicated by the slope obtained by linear regression analyses.

1992 and 1993 primary production measurements. In 1992 as well as 1993, production was estimated for 10 stations on six surveys in the same months as 1994. Stations (see Figure 1) included the Harbor-edge and coastal region (F23P and F13P), the nearfield region (N01P, N04P, N07P, N10P, N16P, and N20P), and Cape Cod Bay (F01P and F02P). Only two samples, from the near-surface and a mid-depth (the subsurface chlorophyll maximum if present) were incubated for each station. In 1993 the ^{14}C methodology described for 1994 was used. In 1992 the incubation procedures were the same as other years, but we used the oxygen light-dark technique (Strickland and Parsons, 1972), with a precise autotitration method (Oudot *et al.*, 1988). To convert oxygen to carbon we assumed a Photosynthetic Quotient (PQ) of 1.25 (e.g. Oviatt *et al.*, 1986). A total of 220 P-I incubations were completed in 1992 and 1993 (Kelly *et al.*, 1993; Kelly and Turner 1995a).

Analyses

A principal focus in the paper is to present results on production calculations for 1994; from these data we also develop estimates of production in previous years which are compared to measurement results in those years. In doing so, we used various statistical techniques including regression analysis and inference tests that are available on standard software packages (SAS, 1988; QuattroPro [Borland, 1993]).

The following briefly describes procedures for calculating integrated primary production for the 1994 data. Any significant differences in data treatment for 1992 and 1993 not detailed here are described when comparing results in later discussion. The data for light bottles were first corrected by subtracting uptake measured in dark bottles. The dark-bottle uptake was calculated as the mean of the three dark bottles, excluding samples where a value was an outlier, as determined by statistical testing using the Dixon Criterion (Natrella, 1963).

Dark-corrected values were normalized to chlorophyll [measured by extraction (*in vitro*); see Parsons *et al.*, 1984] at the sample depth from which incubation water was taken. Following this, a sequence of two models was used to fit the data. The first model fit three parameters, including a photoinhibition term, and followed the Platt *et al.* (1980) model to predict net production as

$$P_B = P_{SB}\,(1 - e^{-a})\,e^{-b}$$

where

P_B = production (chlorophyll-normalized)
P_{SB} = theoretical maximum production (chlorophyll-normalized) without photoinhibition
a = $\alpha\, I/P_{SB}$
b = $\beta I/P_{SB}$
α = initial slope of the rise in net production with light increasing from zero irradiance [units of (μgC μgChl^{-1} hr^{-1})/(μE m^{-2} sec^{-1})], calculated from I (light irradiance level, μE m^{-2} sec^{-1}) and P_{SB}.

The parameters were fit simultaneously by least squares using the NLIN procedure in SAS (1988) for each incubation series that measured paired P_B and irradiance. Fitting was accomplished where parameters were estimated if, within 50 iterations, the model converged on a suitable simultaneous fit (SAS, 1988). A derivative-free method was used that compares favorably with methods using partial derivatives (Frenette *et al.,* 1993). If the three-parameter model (Platt *et al.,* 1980) fitting did not converge on a fit, a two-parameter model (without photoinhibition, Webb *et al.,* 1974) was used. From the model

$$P_B = P_{max}\,[1 - e\,(-\alpha\, I/P_{max})]$$

where

P_{max} = light-saturated maximal productivity and
α = the initial slope for the curve where productivity is proportional to light intensity (I).

The second model was recommended by Frenette *et al.* (1993) to provide parameter estimates suitable for direct comparison as the two models are equivalent where the photoinhibition term (b) is zero. Note that P_{SB} must be converted to P_{max} to make a direct comparison of this parameter, often referred to as the assimilation number (Platt *et al.*, 1980; Falkowski, 1981). For 1992 data, we followed a convention prior to Frenette *et al.* (1993), which was to secondarily use a hyperbolic tangent model of Platt and Jassby (1976). For all models, use of as little as 12 observations to model the P-I curve can still result in near-optimum error in parameter estimation (cf. Zimmerman *et al.*, 1987), but our economic design with only 12 observations implicitly yielded more precise estimates of light-saturated rates (P_{max}) than it did of the initial rise in production at low light (α).

Model coefficients from chlorophyll-normalized P-I curves and vertical station profiles (0.5-m bin- averaged) for irradiance and *in situ* fluorescence were then used to calculate vertical profiles of production (on a volumetric basis). For each survey, *in situ* fluorescence was post-survey calibrated by regression against chlorophyll concentrations determined fluorimetrically [*in vitro*, after extraction in acetone; see Parsons *et al.*, 1984] in the laboratory for a set of 12-25 calibration samples taken from bottles on the hydrocasts. These were expressed as a rate per square meter of surface following the procedure next outlined.

Within a survey, the average incident irradiance (I_o) measured by the deck cell during a midday (1000 to 1400 h) period was used to standardize conditions. For each profile, an extinction coefficient (*k*) was determined by regressing ln (I_z/I_o) vs. depth, where I_z is the irradiance at depth *z*, I_o (in this case only) is the incident irradiance measured at the station during the hydrocast and the slope of the resultant line estimates *k*. The coefficient (*k*) was then used with the survey I_o to generate the standardized light profile using the model $I_z = I_o e^{-kz}$ and to determine $Z_{0.5\%\ Io}$, the depth where photosynthetically active radiation equals 0.5% I_o. Estimated rates were expressed per square meter of surface and integrated to $Z_{0.5\%\ Io}$. A 1% to 0.5% isolume is commonly accepted as the level to which net production (in excess of respiration) is achieved by plankton.

For each sample depth, the associated fitted P-I model was combined with the standardized light profile and multiplied by fluorescence to yield volumetric production rates (μg C L^{-1} h^{-1}) at 0.5-m intervals. For a profile, intervals were then appropriately summed over depth to $Z_{0.5\%\ Io}$ and converted to m^{-2} to yield depth integrated mid-day rates (μg C m^{-2} h^{-1}). Conversion to full day-time rates was made by multiplying by a factor of 7 which recognizes that about 55-60% of the production generally occurs during the 4 to 6-h period of our incubations (Vollenweider, 1966). Final modeled rates for *each P-I incubation* provide an estimate of daytime primary production as gC m^{-2} d^{-1}. For *each station*, an estimate of integrated water column production was calculated based on a composite of the four independent P-I incubations. The composite estimate was calculated by combining results from incubations, where the results from a given incubation were applied over a depth above and below the incubation sample's collection depth half-way to the next sample's collection depth. Thus, by using different P-I curves to extrapolate over appropriate portions of the water column, a composite production profile (by 0.5-m intervals) was developed. As for independent samples, rates for the composite profile were summed over depth and converted to day-time primary production rates (gC m^{-2} d^{-1}). In contrast to the computational scheme allowed by four P-I incubations over depth in 1994, there were only 2 depths sampled for P-I incubations in 1992 and 1993. For the 1992 and 1993 production data included in this paper, we use simple averages of integrated rates based on the two sample depths at a station.

RESULTS

Production measurement and modeling in 1994

P-I incubations. The frequency distribution for P_{max} modeled from incubations in 1994 (n=88) shows that 62% of the estimates were ≤ 8 μgC μgChl a^{-1} h^{-1} and 83% were ≤ 12 μgC μgChl a^{-1} h^{-1} (Figure 2). In general, P_{max} values in the range of 2-10 are typical of marine studies. However, values for marine plankton in batch culture have a wide range ($\sim$1 to 21 — e.g., Glover, 1980) and values have been reported for natural assemblages that approach or exceed 25 (a theoretical maximum — cf. Falkowski, 1981; Platt and Jassby, 1976; Malone and Neale, 1981). For the entire year, the mean P_{max} was similar at the two stations, 7-8 μgC μgChl a^{-1} h^{-1}; the median P_{max} was similar to the mean at station F23P (7.4), but was lower at station N16P (5.7).

Highest values for a given station and day often were noted for the surfacemost sample. There was no general trend of P_{max} with depth across the whole data set. During summer stratified conditions (e.g., June), P-I curves showed a decrease in P_{max} between surface and deep samples as expected when there is shade-adaptation at depth (e.g., Falkowski, 1981). There was considerable variability in P_{max} between station occupations on two different days within a survey and over depth within a given day. There were seasonal patterns nonetheless, but these patterns differed between stations. Data for station F23P showed a progressive increase from winter ($P_{max} \sim 2$ in February) to fall ($P_{max} \sim 11$-14 in October). In contrast, peaks in P_{max} (>10) at station N16P occurred in early spring (March) and summer (June) and values were in the general range of 2-7 at other times.

The frequency distribution for α's modeled from incubations in 1994 (n=88) shows that 78% of the estimates were ≤ 0.1 (μgC μgChl a^{-1} h^{-1})/μE m^{-2} sec^{-1} (Figure 3). The theoretical limit for α, expressed in our units, is approximately 0.1 to 0.115 (cf. Bannister, 1974; Platt and Jassby, 1976; Malone and Neale, 1981) although in practice, experiments often produce some data with α's above the theoretical maximum (e.g. Platt and Jassby, 1976; Malone and Neale, 1981). Modeling where multiple parameters are fit simultaneously can cause overestimates (Jassby and Platt, 1976) as sometimes could be seen in our results. The standard error of the estimate of α generally increased with increasing α and most P-I incubations with high α (>0.1) had a low R^2 for the P-I model fit. We chose to use the entire, unqualified data set in further calculations. But for a sensitivity exercise (see discussion) we excluded 23 P-I curves where $R^2<0.8$ and/or where $\alpha > 0.1$, unless the sample was at a light saturating depth. These criteria left 65 P-I curves: n=34 at station F23P and n= 31 and station N16P. An insert in Figure 3 shows the frequency distribution for the restricted data set. The mean for the restricted data was similar between stations and at 0.06 was 52-60% of the theoretical mean value and therefore $\sim$40% lower than the mean for the full set.

There was no seasonal pattern to α, nor an apparent difference between stations, but there was often a trend of decreasing values with sample depth at a station. High α's (>0.1) were often obtained in incubations of near-surface water; there were more cases (n=13) of high α

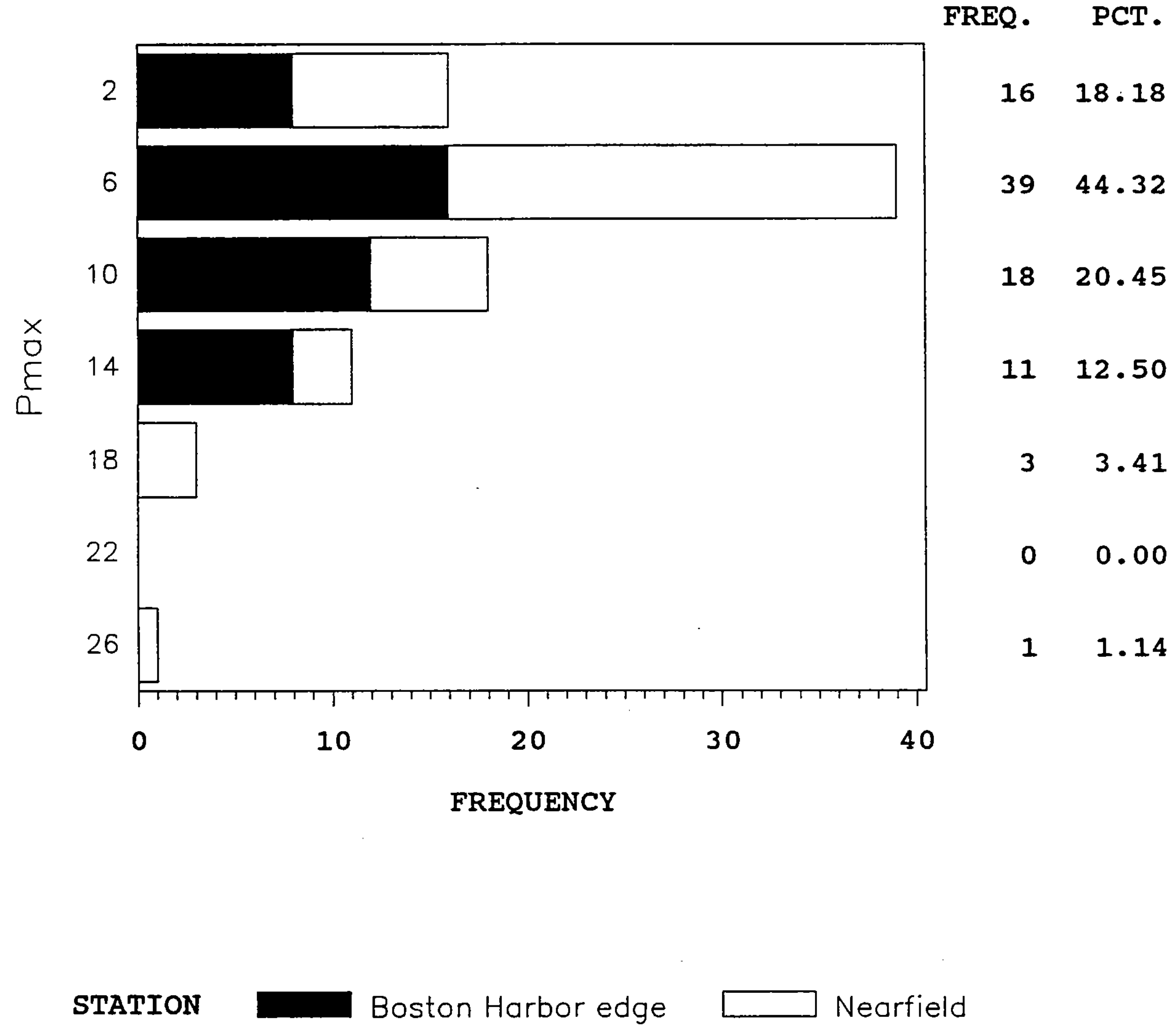

Figure 2. Frequency distribution for P_{max} values from all 88 modeled P-I curves for stations F23P (Boston Harbor edge) and N16P (Nearfield) during 1994. A theoretical maximum for P_{max} is 25 (Falkowski, 1981).

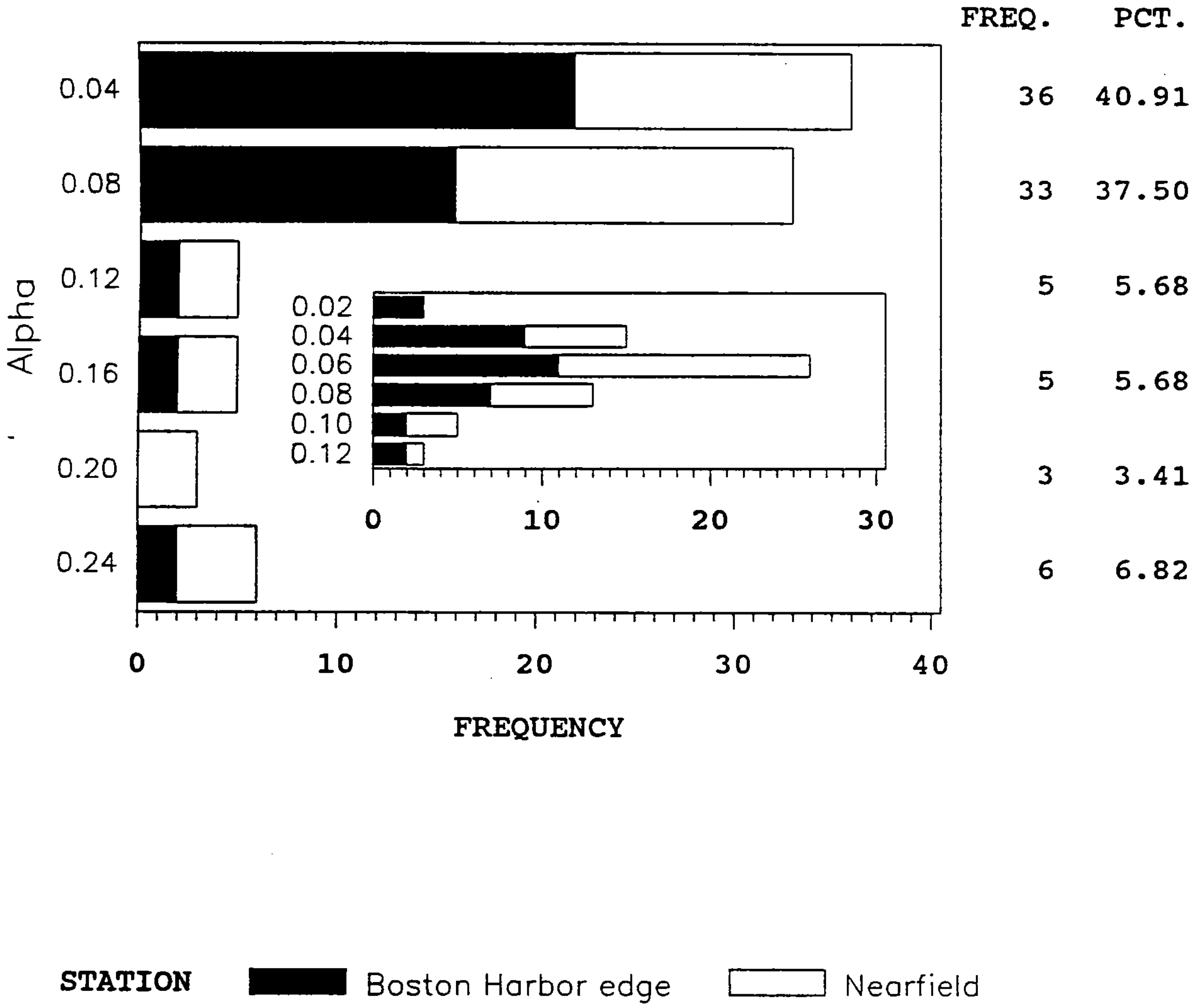

Figure 3. **Frequency distribution for ∝ values from all 88 modeled P-I curves for stations F23P (Boston Harbor edge) and N16P (Nearfield) during 1994. A theoretical maximum for ∝ is 0.1 to 0.115 as expressed in our units (cf. Bannister, 1974; Platt and Jassby, 1976; Malone and Neale, 1981). The insert shows the frequency distribution of ∝ for a subset of the data (n=65) that excluded poor model fits (see text).**

at station N16P than there were at station F23P (n=5). For surface samples, an imprecise estimate for α has minimal impact on the calculation of integrated water column production — light levels are high enough during midday (>200 μE m^{-2} sec^{-1}) over the upper few meters that the α term of the P-I curve does not affect the calculated rate because at saturating light levels P_{max} is the critical term.

Integrated ^{14}C production rates. Figure 4 shows integrated water column production calculated for the entire photic zone; the plot compares results of calculations based on the P-I modeling results for the surface sample incubation with results of calculations using P-I modeling results for the deepest sample at each station occupation (n=11). Often, the surface sample model overestimated integrated production as projected from the deep sample. The disparity between surface- and deep-sample based calculations at station N16P was quantitatively larger than at station F23P and was pronounced during early stages of the winter-spring bloom (March) and the entire period of strong physical stratification (April through August).

The sample depth "effect" on calculations of integrated water column production suggests a depth-related difference in plankton communities and/or physiology that may be expected during stratification (e.g. Falkowski, 1981). It also is a basis for deriving best estimates of integrated production by using the strategy of compositing of multiple incubations over depth. Viewing Figure 4, a compositing approach is more critical in the case of the stratified Massachusetts Bay water column. Integrated production rates calculated in 1994 from depth-composited results form the focus for further presentation.

Figure 5 summarizes integrated rates from depth-composited calculations for all measurements also shows the frequency distribution of daily production rates for 1994. Rates ranged from a low of 157 mgC m^{-2} d^{-1} at station F23P in February to a high of 3275 mgC m^{-2} d^{-1} at station N16P in March. The mean rate was 1.3 gC m^{-2} d^{-1} (n=22). In general, the repeated measurements at a station within a survey yielded rates within 25% of each other. For integrated rates, within-survey variability $\approx$50% was noted in three cases — station N16P in March and June and station F23P in June (Figure 5). In these three cases, the difference within a survey was not a function of between-day chlorophyll variations and instead arose due to differences in P-I curves.

Harbor-edge vs Bay comparison. Average production rates were lower at the edge of the Harbor than in the nearfield region in western Massachusetts Bay (two sample t-test, Pr < 0.03). Higher production at station N16P was achieved at the same annual average chlorophyll concentration as in the Harbor (2.09 vs 2.04 μg L^{-1}, respectively). Production averaged 0.96 gC m^{-2} d^{-1} at station F23P and 1.7 gC m^{-2} d^{-1} at station N16P. Omission of the higher value of the two visits to station N16P in March and June (see above) would lower that station's average rate to $\approx$1.4 gC m^{-2} d^{-1}.

Seasonal trends for production differed only slightly at the two stations (Figure 5). The principal difference in temporal pattern occurred in March, when station N16P had some of

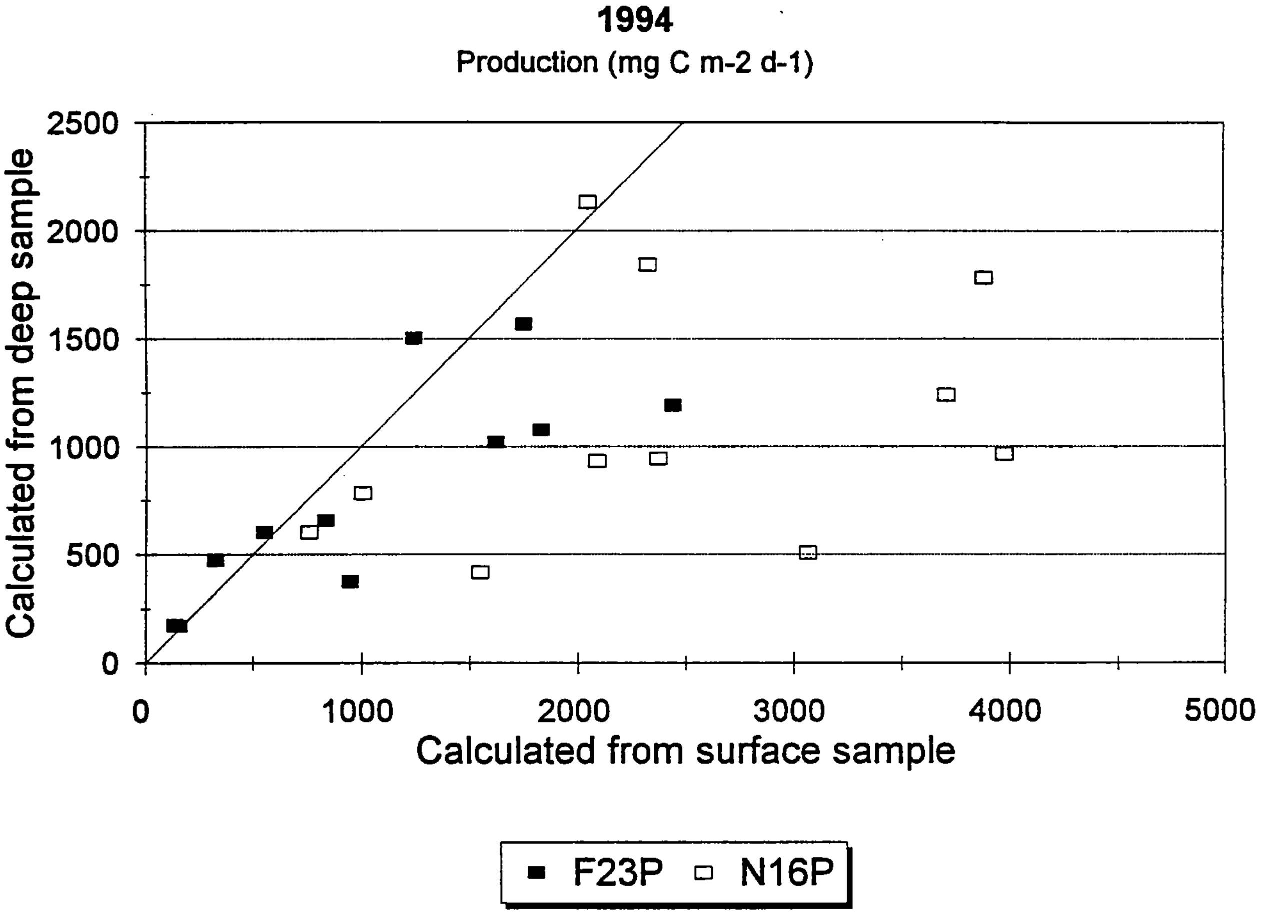

Figure 4. Comparison of integrated water column production as calculated from near-surface and deepest depths of sampling for all incubations during 1994.

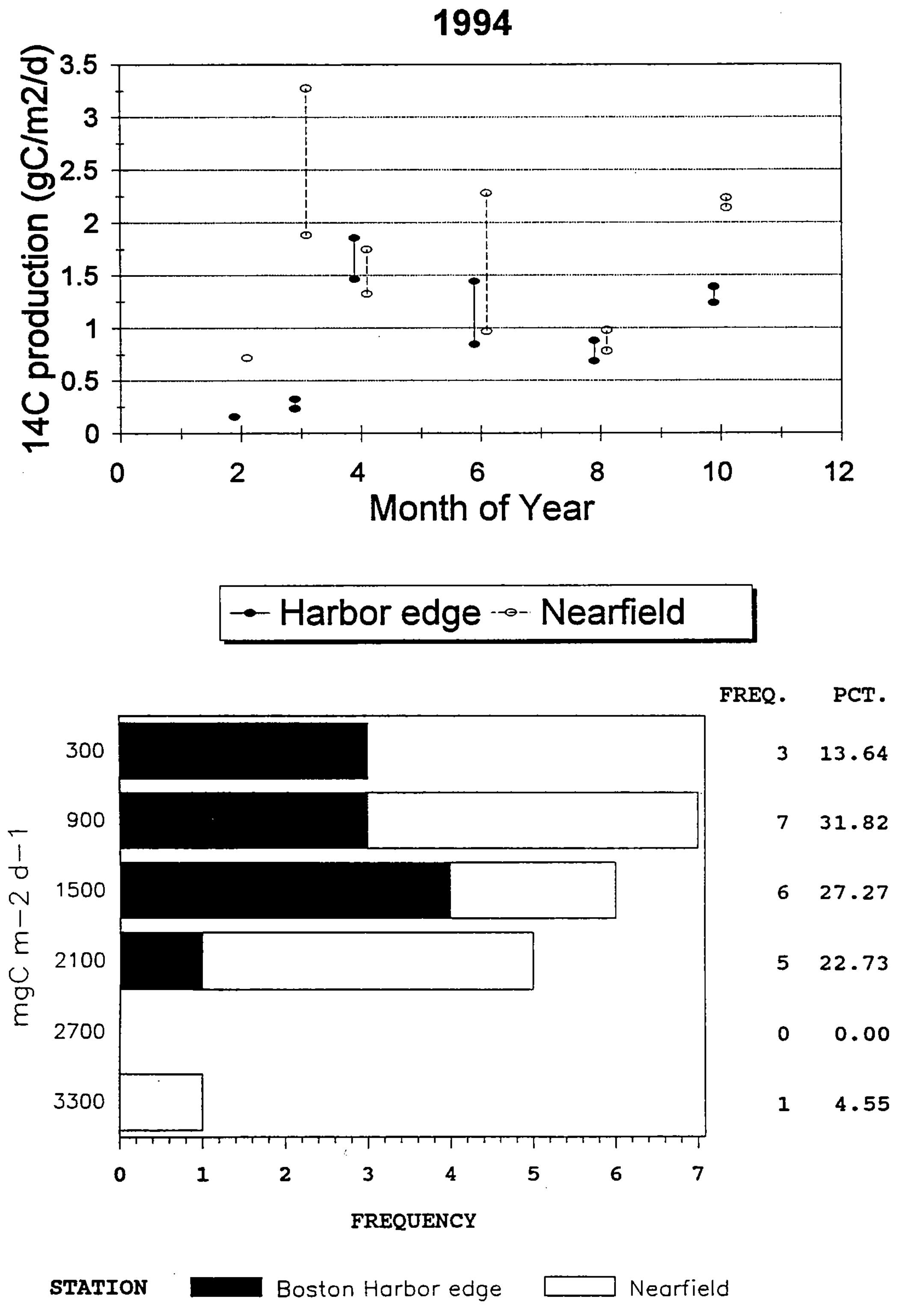

Figure 5. **Production during 1994 for stations F23P (Harbor edge) and N16P (Nearfield). Top: Replicate measurements within a survey were completed in March, April, June, August, and October. Bottom: Frequency distribution of production (n=22).**

its highest rates of the year; at this time a spring bloom had not yet begun in the Harbor. Otherwise, temporal patterns for the two stations were coherent: substantial rates for both stations (≥ 0.75 gC m^{-2} d^{-1}) were noted during the April to October period and, with a late summer minima prior to higher rates in a fall bloom.

Empirical model. Previous modeling efforts (cf. Cole and Cloern, 1987; Keller, 1988) have related integrated production to a composite parameter, BZ_pI_o, where B = the average chlorophyll concentration (μg L^{-1}) in the photic zone, Z_p = the depth of the photic zone (m), and I_o = the daily incident photosynthetically active radiation (PAR) to the water surface (E m^{-2} d^{-1}). An intent of the sampling design in 1994 was to develop such an empirical model for Boston Harbor-Massachusetts Bay. Moreover, if production in the two different environments followed a common empirical model, it would enable generalized extrapolation of results over space and time throughout the region of interest from relatively few measurements.

There was a significant relationship between integrated production rates and BZ_pI_o for the 22 data points for 1994 (Figure 6a). Two points were well above the main trend, the high production estimates for N16P in March and June that were pointed out above. With or without these points, a linear correlation was significant ($R^2=0.53$, n=22; vs. $R^2=0.80$, n=20). A functional regression (Ricker, 1973) for all points provided the following regression model:

$$Y = 0.61\,X - 94 \qquad \text{[Equation 1].}$$

Production was calculated using a survey-specific I_o (not day-specific) and, having replicate measurements for each station during a survey, we further developed the regression model using survey averages, thus limiting the data to 6 points per station (Figure 6b). A functional regression provided a significant model:

$$Y = 0.56\,X + 20 \; (R^2 = 0.73,\ n=12) \qquad \text{[Equation 2].}$$

The result is similar to the first regression, but has a better fit without discarding points. More importantly, the pattern shown in Figure 6b confirms that the two stations follow the common formulation. Average station rates were different and there are many environmental differences between the inshore and offshore environments, but nonetheless there appears to be a fundamental underlying relationship between production, biomass, and light availability.

Annual production in western Massachusetts Bay in 1994. The empirical model allows extrapolation in time and space. Production measurements were made at station N16P on only 6 surveys in 1994, but simultaneous measurements of each parameter of the empirical model (BZ_pI_o) were available from surveys at station N16P for 28 individual days (sometimes three separate days within a given survey), providing more extensive coverage of the year. Using the survey-average regression [Equation 2] we calculated production at station N16P for each of these 28 days (Figure 7). The exercise does not test the empirical model, for the

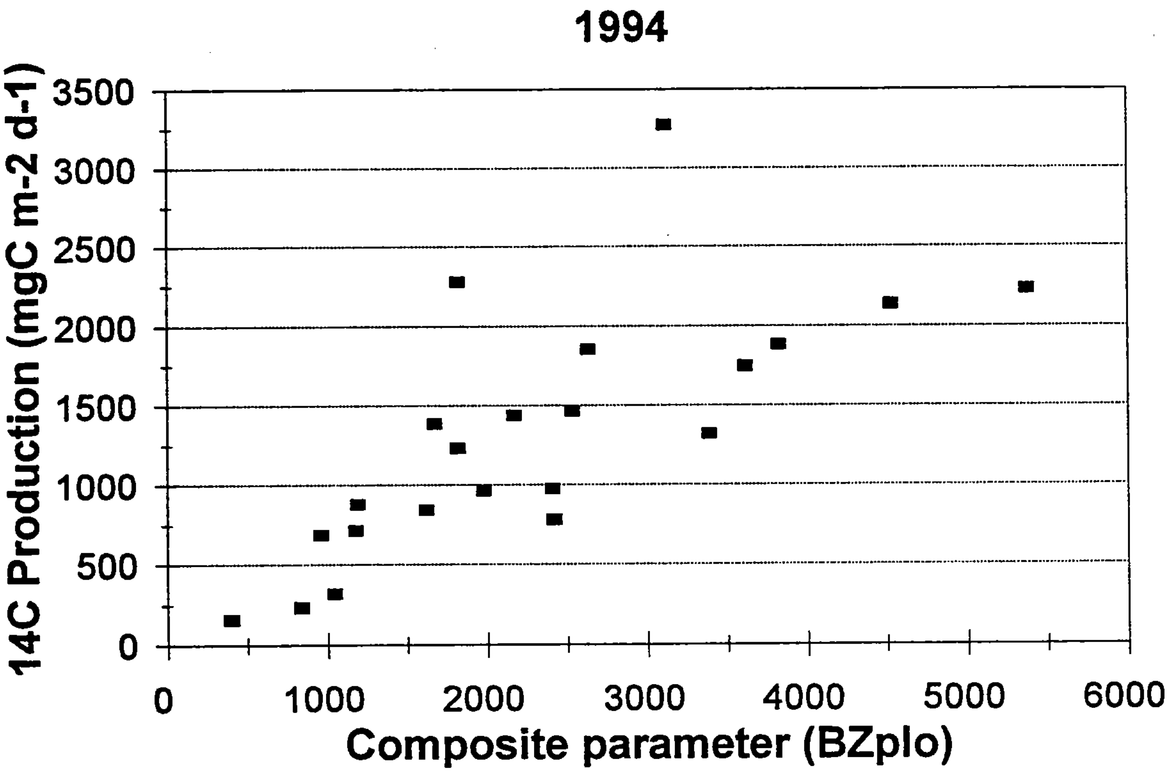

Figure 6a. Empirical model for production based on 22 measurements in 1994.

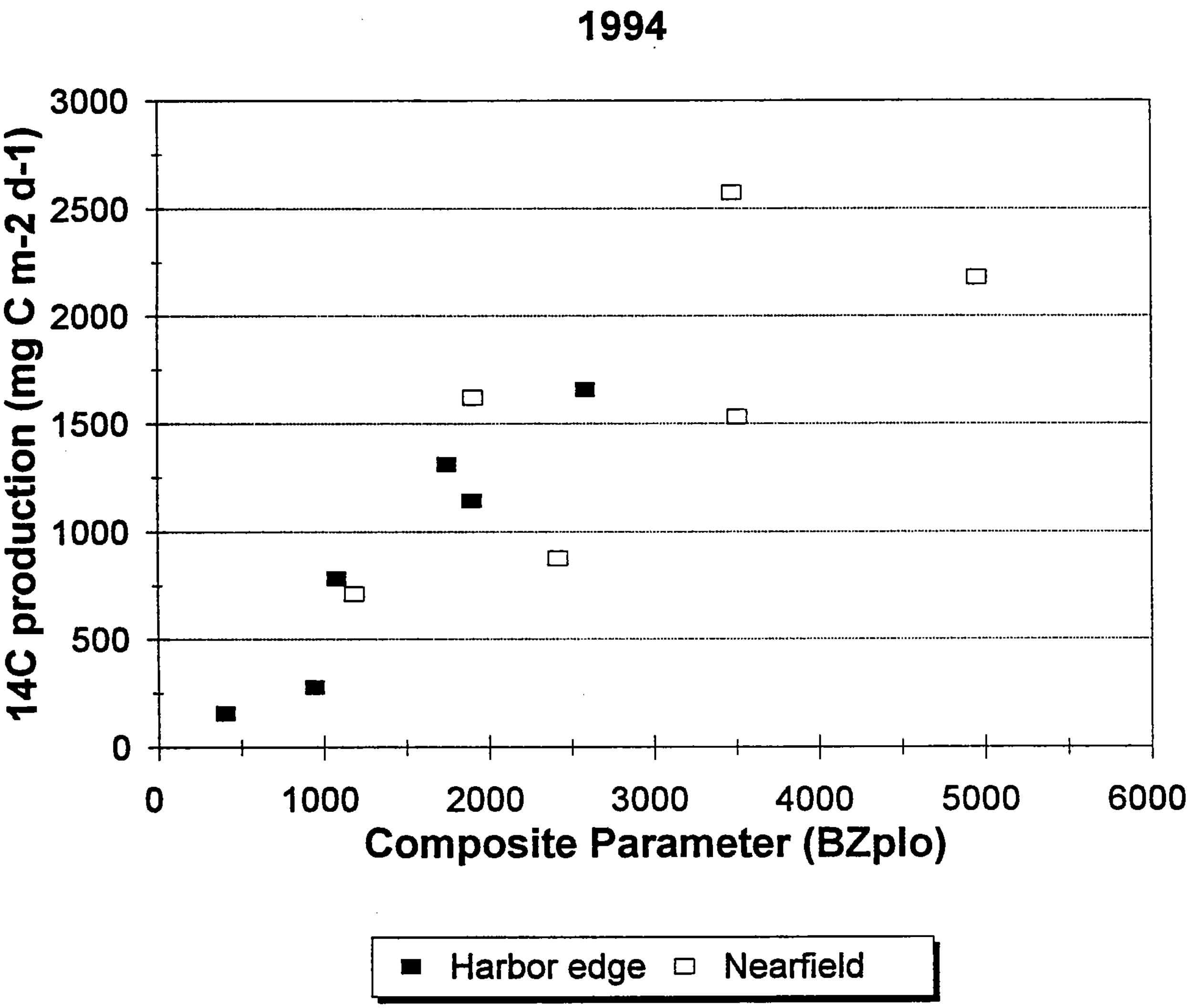

Figure 6b. Empirical model for production based on survey averages at stations F23P (Harbor edge) and N16P (Nearfield) during 1994.

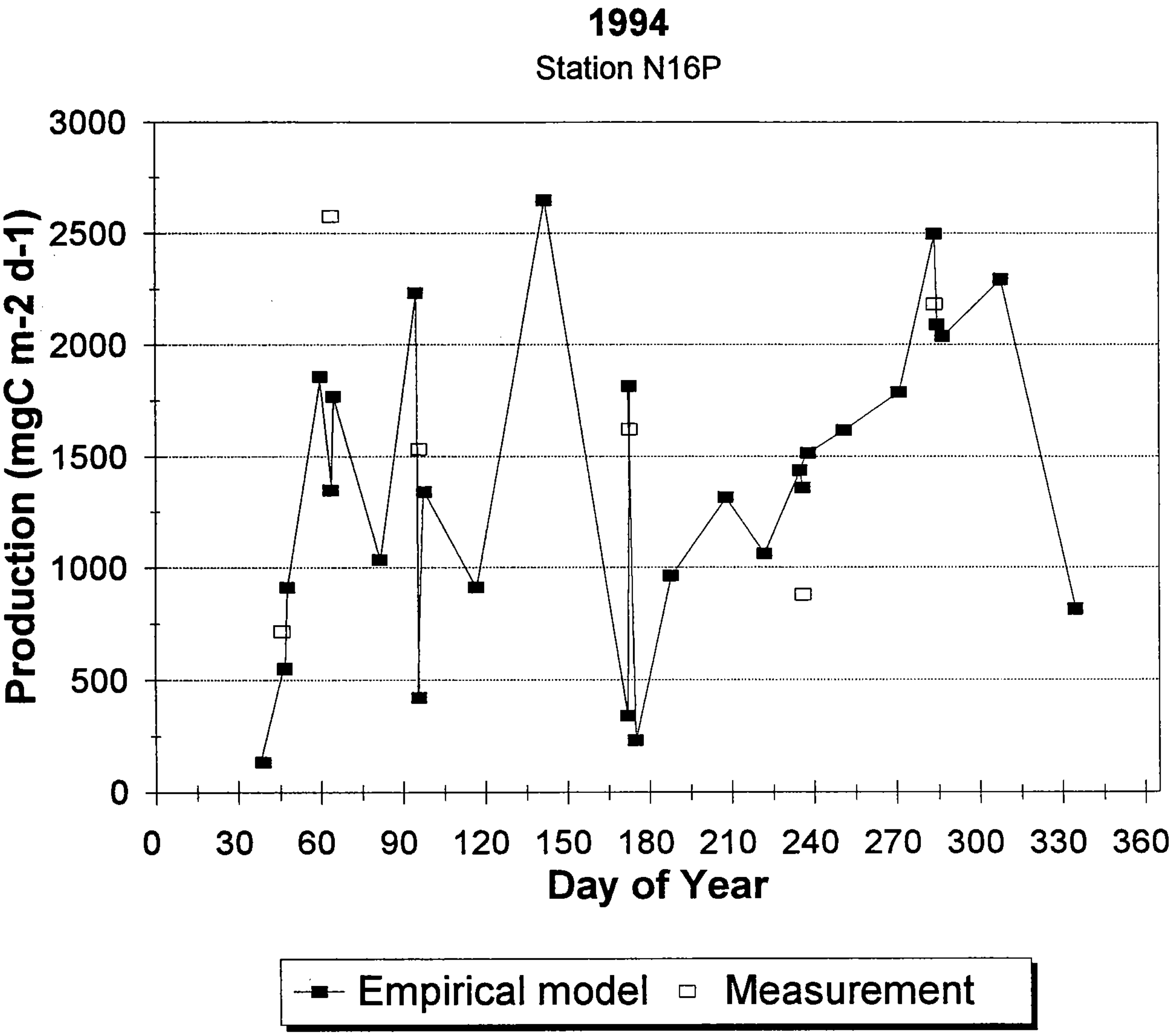

Figure 7. Production at station N16P during 1994.

model arises in part from these data, but for general comparison the figure displays survey-averages from measurements. Some variance between the model and measurements arises because the model used a day-specific I_o and the measurement used a survey-average I_o. Interestingly, the modeling suggests significant short-term variability in many cases where three near-consecutive days were surveyed; primarily this model variability comes from sharply different light (cloudy vs. sunny days), but some variation is due to daily variations in chlorophyll — there is significant spatial patchiness and the region is physically dynamic.

Recognizing small-scale variability, the empirical model was also applied at a larger scale for the purpose of estimating annual production for the entire nearfield region ($\approx$100 km^2) that has been of prime interest for monitoring. For each of 16 surveys in 1994, 21 stations in this region had suitable data for the BZ_pI_o formulation. For each survey, the average B (n=21, summarized from 0.5-m bin averaged data to the limit of the photic zone), Z_p (n=21), and I_o (1-3 days) were calculated; the high density of data provide rather precise estimates for these parameters in a manner that recognizes and includes existing short-scale spatial and temporal variability but provides a spatially-averaged result. Resultant projections of integrated production are shown in Figure 8. Results are similar to those for station N16P (Figure 7) because that station is near the center of the region and often represents a near-average condition. We believe that late spring ($\approx$day 150) projection may be overestimated. Assuming the winter, low productivity, months not sampled had production of 250 mgC m^{-2} d^{-1}, time-integration of model rates yield an annual production in the nearfield of 435 to 468 gC m^{-2} y^{-1}, depending on inclusion or omission of the late spring peak.

For the Harbor station, we do not have 16-survey data for modeling production throughout the year and must extrapolate to annual values from measurements made only 6 times. From the nearfield results, the average daily rate from the annual integration was 1.3 gC m^{-2} d^{-1}, or 76% of the average based on 6-survey measurements at station N16P. Assuming this 76% conversion factor also applied to the set of six measurements at station F23P, the resulting annual production at the edge of the Harbor is estimated as 266 gC m^{-2} y^{-1} (vs. 350 gC m^{-2} y^{-1} if the factor is not applied).

Production measurement and modeling in earlier years

1993. Using the empirical model (Equation 2) from 1994, production was estimated for all 16 nearfield surveys of the nearfield in 1993 (Figure 9). Comparing Figures 8 and 9, one notes that production in 1993 was higher on average than in 1994. Primarily this was true because of generally higher summer rates and very high rates (>5 gC m^{-2} d^{-1}) in an immense September-October bloom of *Asterionellopsis glacialis* (~1.2 to 6.5 million cells L^{-1} and total chlorophyll a concentrations averaging ~10-12 μg L^{-1}). The integration of 1993 data suggest an annual nearfield production of 620 gC m^{-2} y^{-1}, based on an average daily rate of 1.7 mg m^{-2} d^{-1} from the model.

Also shown in Figure 9 are the average rates measured for six stations (see methods) in the nearfield at each of six surveys in 1993. Model and measurements compare favorably, and the range for individual measurements at each survey includes the model result. A functional

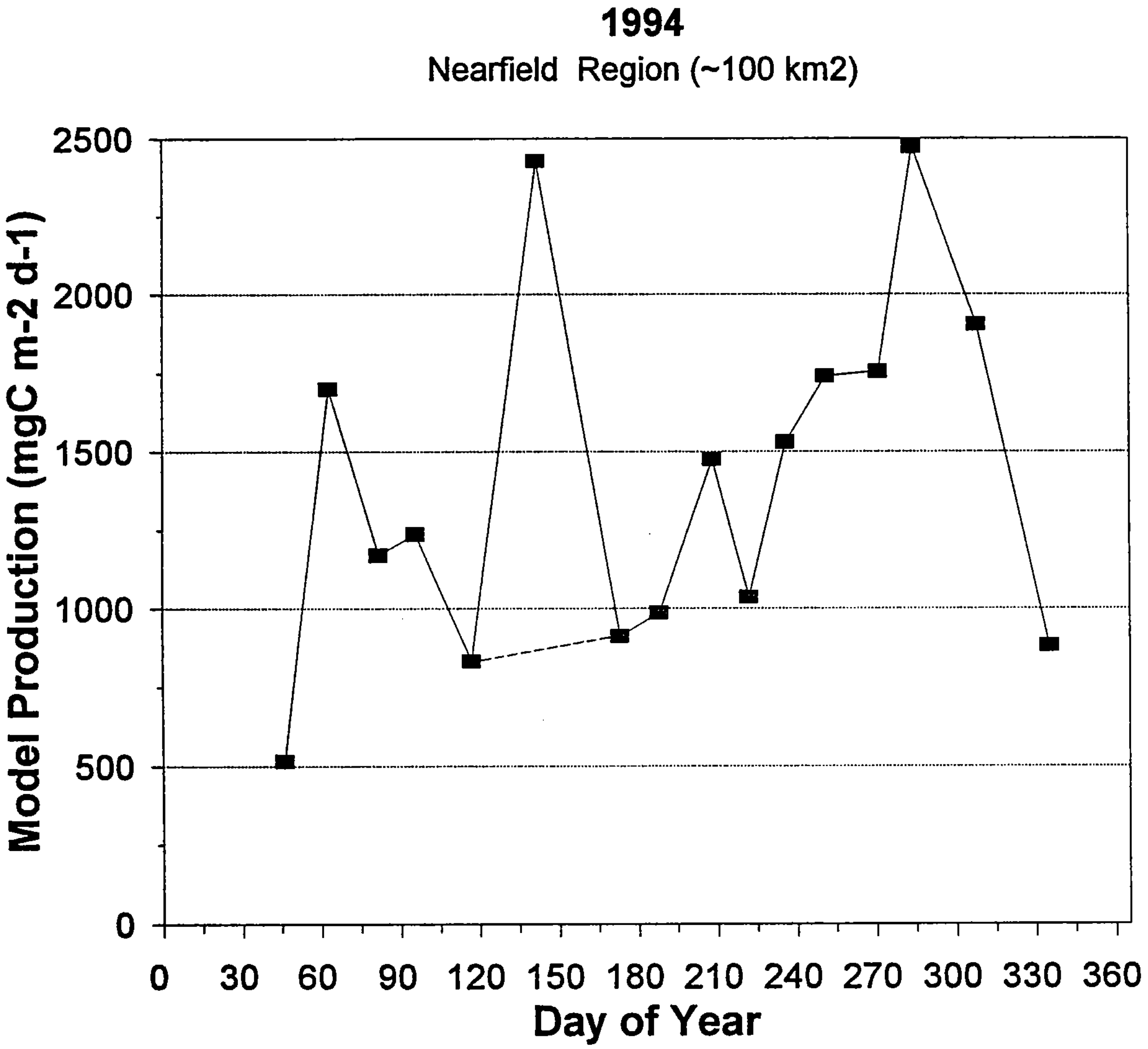

Figure 8. Model-calculated production in the nearfield region during 1994.

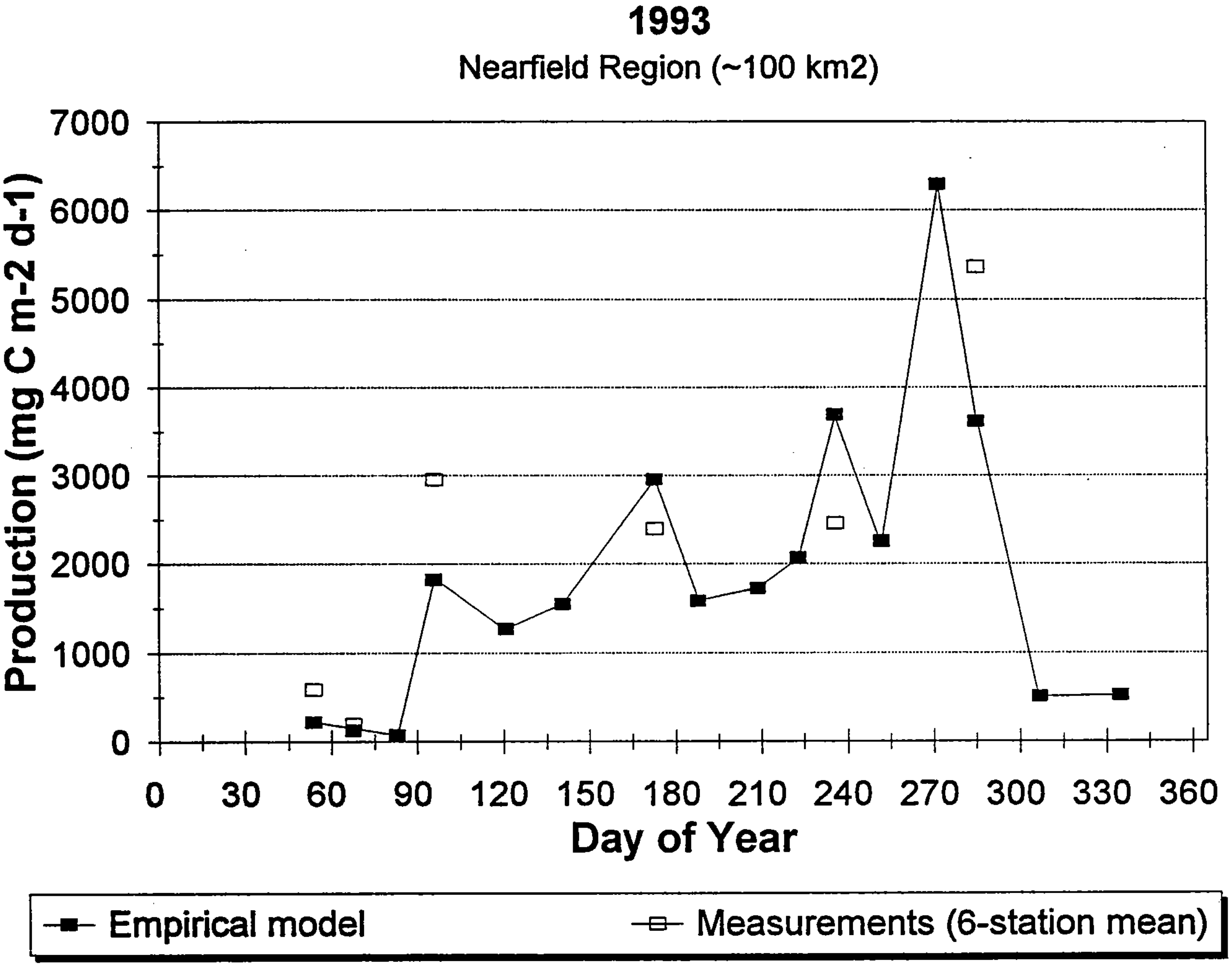

Figure 9. Production in the nearfield region during 1993.

regression of model and measurement yielded a significant relation (R^2=0.66, n=6), in which the slope (±stnd.err) was 0.87(±0.25) and not different from 1. This result implies that the model formulated from 1994 data applies without modification to 1993.

The average daily rate from nearfield measurements on six surveys in 1993 was 2.3 mg m^{-2} d^{-1}, or 74% of the model results, a percentage essentially the same as calculated for station N16P in 1994 (above). In 1993, station F23P and two stations in central Cape Cod Bay were also sampled for productivity on six surveys. Using the mean daily rates for those measurements and assuming the same 74% factor applies, annual production is estimated as 486 gC m^{-2} for station F23P (mean = 1.8 gC m^{-2} d^{-1}, n=6) and 527 gC m^{-2} for central Cape Cod Bay (mean = 1.95 gC m^{-2} d^{-1}, n=12). Consistently, ^{14}C production measurements in 1993/1994 indicated that the Harbor-edge region was less productive than the nearfield region.

1992. Using the 1994 empirical model (Equation 2), production was estimated using data on B, Z_p, and I_o that was available for 11 surveys in 1992 (Figure 10). The integration of 1992 data give an annual nearfield production of 386 gC m^{-2} y^{-1}, based on a projected average daily rate of 1.06 gC m^{-2} d^{-1}.

Also shown in Figure 10 are the average rates measured for six stations in the nearfield at each of six surveys. In this year P-I incubations were oxygen- rather than ^{14}C-based and the modeling effort differed slightly from 1993-94. Model and measurements compared favorably, and as in previous years, the model appeared to underestimate some measurements during the winter-spring bloom. Overall, however, the model tended to overestimate the measurements. Comparison of model and measurement yielded strong correlations (R^2=0.46, n=6; or omitting the March measurement, R^2=0.92, n=5). The functional regression slope (±stnd. error) for the former case was 1.25 (±0.45). The functional regression slope (±stnd. error) for the latter case was 1.40 (±0.21). This analysis implies that the model formulated from 1994 data (^{14}C-based studies) slightly overestimated (roughly 25%) 1992 results based on O_2 and an assumed PQ of 1.25.

The average daily rate from 6-survey results in 1992 was 1.06 gC m^{-2} d^{-1}, or the same as model results. Note that conversions of 6-point averages to an annual value in 1992 would adhere to the ~75% factor for 1993-1994 if the model had not overestimated measurements by about 25%. In 1992 as in 1993, station F23P and two stations in central Cape Cod Bay were sampled for productivity on six surveys. Using the mean daily rates for those measurements and assuming a conversion factor from six measurements to an annual rate is not needed, annual production is estimated as 555 gC m^{-2} for station F23P (mean=1.5 gC m^{-2} d^{-1}, n=6) and 613 gC m^{-2} for central Cape Cod Bay (mean=1.7 gC m^{-2} d^{-1}, n=11 with one anomalous point omitted).

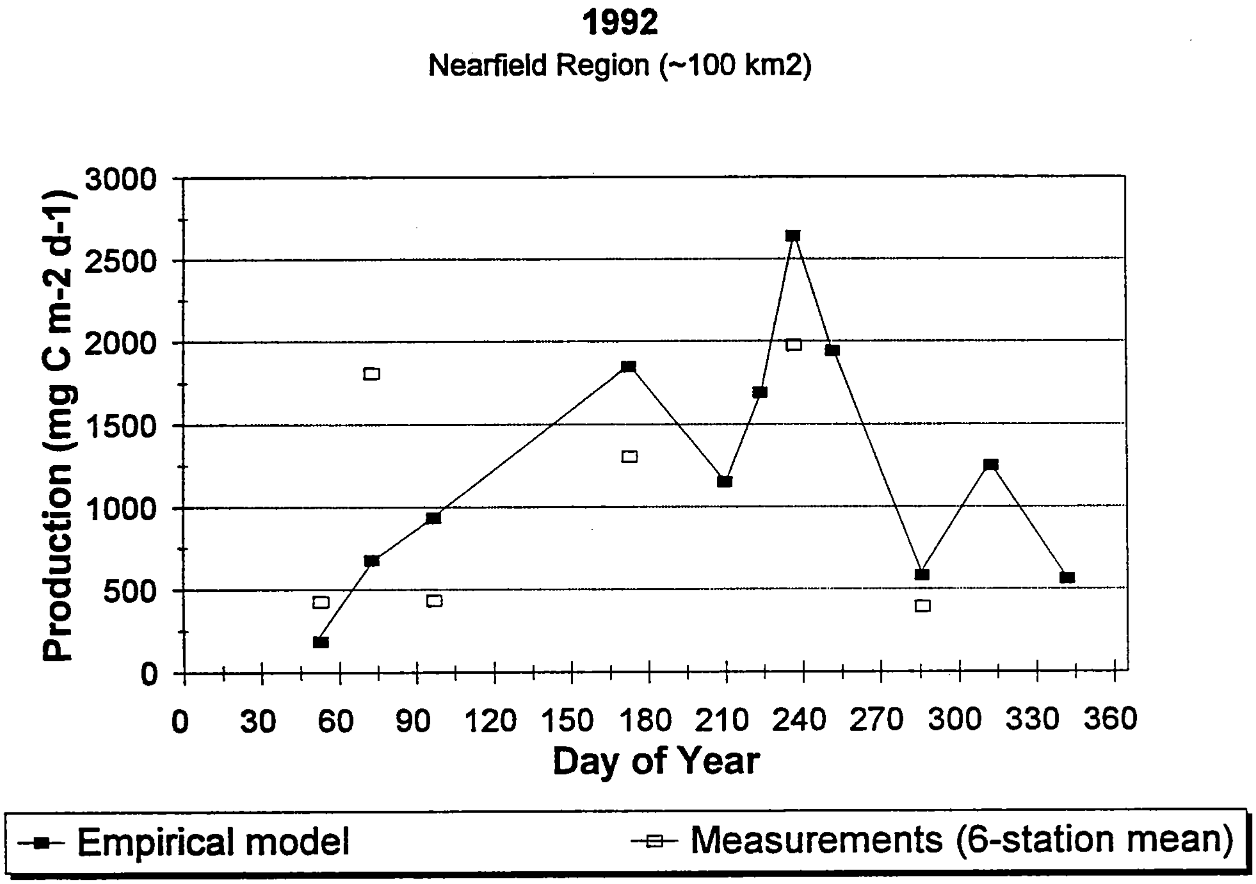

Figure 10. Production in the nearfield region during 1992.

DISCUSSION AND CONCLUSIONS

Empirical model

Comparison to previous model formulations. Cole and Cloern (1987) derived an equation for photic zone production (*Y*) and BZ_pI_0 (*X*) measurements (n=211, same units as this study) from Puget Sound, New York Bight, South and North San Francisco Bays:

$$Y = 0.73\, X + 15 \qquad \text{[Equation 3].}$$

Keller (1988) derived an similar equation for measurements (n=1010, same units as this study) from a variety of MERL mesocosm experiments and data for Narragansett Bay:

$$Y = 0.70\, X + 220 \qquad \text{[Equation 4].}$$

The intercept of the suite of previous regression models often has not been different from zero (cf. Keller, 1988) and in any event usually has a minor influence on the level of predicted annual production. The slope of models for different estuaries and experiments in estuarine/coastal regions varies within a rather small range, about 0.66 to 1.14 and may be sensitive (±10%) to variations in the length of incubation between 4 to 24 h (cf. Keller 1988).

For direct comparison to results of this study, note that using a functional, rather than predictive regression, the slopes for equations 3 and 4, would be 0.81 and 0.77, respectively. Although the ^{14}C technique was used to derive equations 2-4, there are a number of differences in methodological details among the set of studies summarized by Cole and Cloern (1987) and Keller (1988), and also in comparison to this study. One difference that generically affects the model's slope is the presumed depth of the photic zone, because thus differentially affects the production calculation and the composite parameter (BZ_pI_0). Both Cole and Cloern (1987) and Keller (1988) used the 1% PAR level, not the 0.5% routinely used in our calculations. To enable direct comparison of model results, we recalculated integrated water column production and BZ_pI_0 to the 1% PAR level for the 1994 data set. The functional regression for survey-averaged data (as with equation 2) was significant ($R^2=0.66$, n=12) and the resulting model was:

$$Y = 0.79\, X + 285 \qquad \text{[Equation 5].}$$

Therefore, the 1994 Harbor-Bay model is virtually indistinguishable from formulations developed for a variety of other locations and conditions. There is a theoretical basis for projecting integrated production from knowledge of photic biomass and light availability (e.g. Ryther and Yentsch, 1957; Falkowski, 1981; Cole and Cloern, 1987) and the Boston Harbor—Massachusetts Bay region is no exception to the general empirical finding on the relationship between production, biomass, and light.

This is one of the first efforts to use the model construct in a marine monitoring context, a general approach suggested decades ago (Ryther and Yentsch, 1957) and more recently promoted by Cole and Cloern (1987). The empirical model developed from Harbor-Bay measurements in 1994 is appropriate as a time-space extrapolation tool, including extrapolation across different years. Each individual measurement will not be predicted accurately by the empirical model — there are sampling and measurement errors in part related to small-scale environmental variability, there is uncertainty regarding the assumptions necessary to convert short-term bottle measurements into integrated production rates, and, moreover, assumptions of the underlying theory may be inapplicable over the range of physiological states, plankton communities, physical mixing conditions, and water quality status encountered in nature. Regardless, the need for extrapolation and the utility of the empirical model both increase as the time-space scales of interest broaden.

Implications of the model concept regarding time-space variability in production. The simple empirical formulation allows one to think in an elementary way about factors influencing production rates and their time-space variability. In practice, the parameters B and Z_p may be combined, for they are not independent — increases in B decrease Z_p (e.g. Bannister, 1974). For example, using the nearfield data averaged for each survey in 1994, there was a significant negative linear correlation between B and Z_p ($R^2 = 0.65$, $n=16$). Multiplied, the term (BZ_p) calculates photic zone mass of chlorophyll (mg m^{-2}). Figure 11 displays variations in BZ_p and I_o for station N16P in 1994, along with the model result for production. Of the two terms, I_o has the greater range and can experience more rapid and extreme fluctuations when sunny and cloudy days are juxtaposed (see three-day series near day 95 and also day 175). On a daily to weekly basis, variations in incident irradiance are a prime determinant of the level of production, as suggested by the similarly high level of variability in I_o and production at this timescale (Table 1). Over seasonal and annual timeframes, the terms BZ_p and I_o were roughly comparable in magnitude. Except for late fall, I_o was the larger term in the model, but chlorophyll concentrations (B and BZ_p terms) were the most variable at the seasonal-annual timescale (Table 1). An interpretation from Figure 11 and Table 1 is that incident light is always a major factor determining production, while fluctuations in chlorophyll have a strong role in establishing seasonal and annual patterns of production in the Harbor-Bay region.

Much as daily fluctuations in cloud cover can control production, spatial chlorophyll variability (B and BZ_p) at fine scales (meters to 100's of meters) in the western Massachusetts Bay area (Figure 12) will also influence real and measured production at a localized scale (e.g., at a fixed sampling station location). The effect of this spatial variability is brought into focus when considering that P-I incubations are done on small volumes (<1 L); both the practice of normalization of production to chlorophyll in incubations and the subsequent extrapolation using adequately characterized chlorophyll concentrations in nature are critical assumptions at fine space scales. At broader scales (kilometers and seasons), the influence of chlorophyll variability on integrated production has significance if there are persistent spatial gradients, either in chlorophyll concentrations or the degree of patchiness. To examine this, we can use the oft-noted chlorophyll

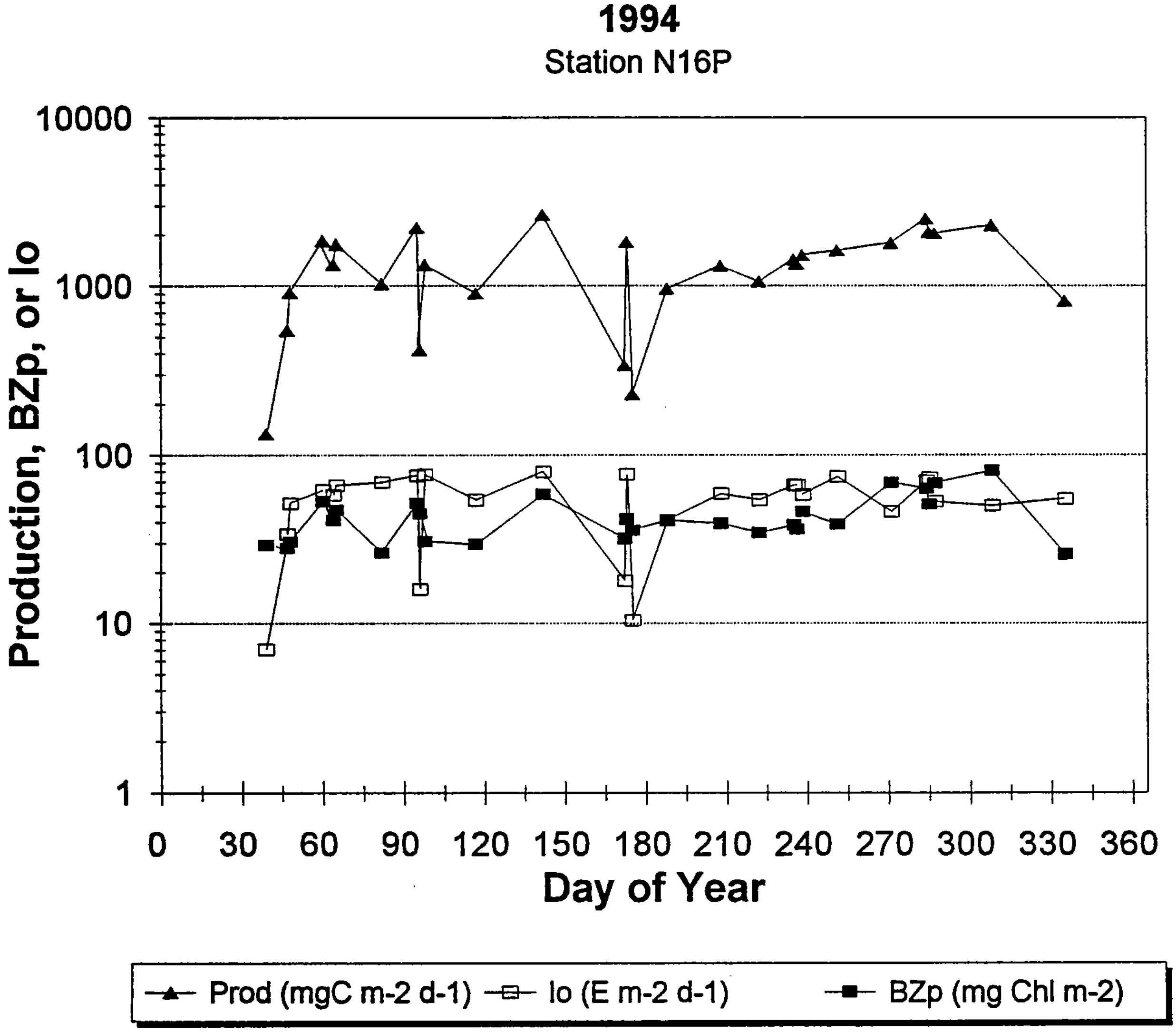

Figure 11. Variability in modeled production and the I_0 and BZ_p terms of the empirical model at station N16P during 1994. Production is the same as presented in Figure 7, but is shown on a log scale.

Table 1. Average Relative % Error for Production-Related Variables, Summarized at Different Scales[1].

Data Summary	Relevant Time Scale	Parameter				
		I_o	B	Z_p	BZ_p	Production (Modeled)
Paired days of P-I incubations (n=5 pairs)	~Days	27%	10%	7%	9%	33%
Sets of 4 days within 6 major surveys (n=5 sets)	~Week	22%	12%	6%	8%	26%
Sets of 8-12 days within 4 seasons (n=4 sets)	~Season	10%	24%	6%	19%	24%
Set of 28 days on 16 surveys (n=28)	~Annual	6%	10%	4%	6%	9%

[1] Data are for measurements at station N16P in 1994. Comparisons are valid across rows, but comparison down columns have different "n" and should be made with caution.

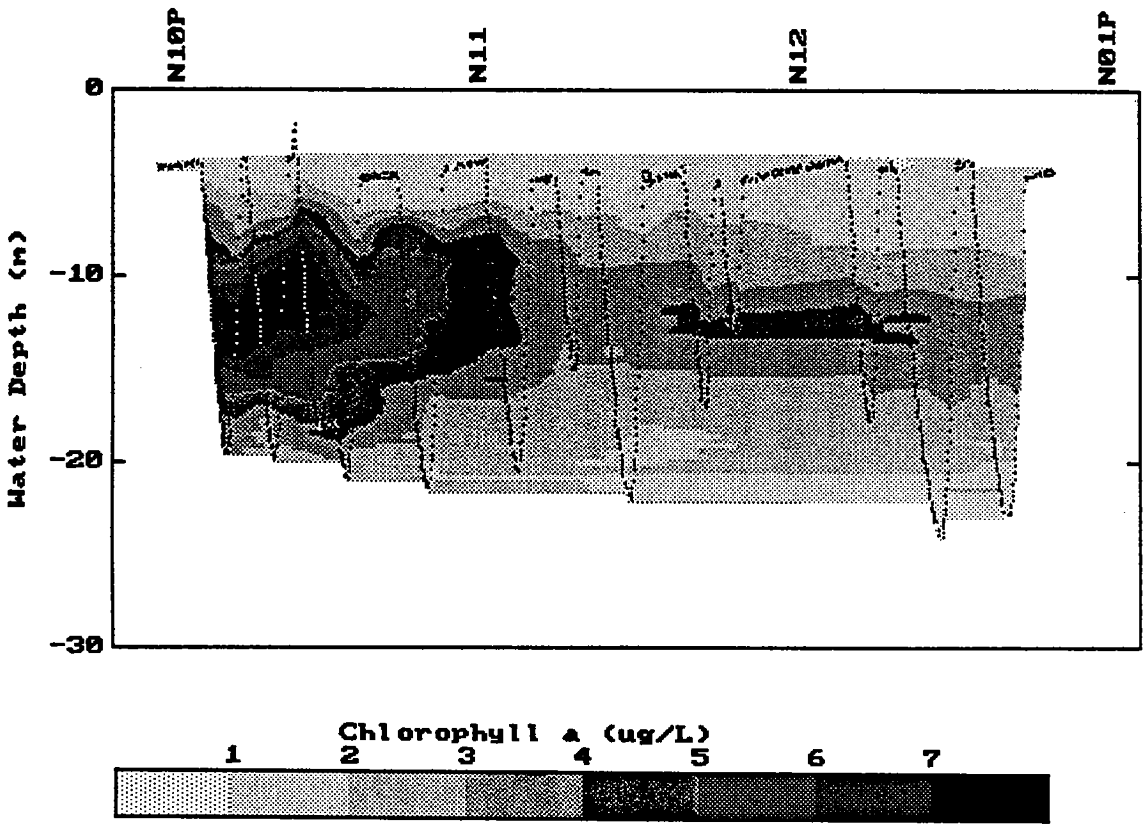

Figure 12. An example of fine-scale spatial variability in chlorophyll concentration as estimated by *in situ* fluorescence. Data were collected by profiling with an *in-situ* fluorometer oscillating from near-surface to near-bottom at vessel speeds from 4-7 kt. From Kelly (1993).

concentration gradient (e.g., the "B" term of the model) across the nearfield sampling stations (Figure 13).

The conceptual model is that production = f ($I_o \cdot [BZ_p]$). Each station sampled on a nearfield survey had equal daily light, so by comparing stations or groups of stations across the nearfield we effectively can remove the effect of I_o and ask how the observed gradient from shore relates to production. We calculated the BZ_p term for the group of four stations on the west side of the nearfield (high chlorophyll, ≥ 2.5 ug L^{-1} as an annual average) and the group of four stations the east side of the nearfield (low chlorophyll, ≈ 1.5 ug L^{-1} as an annual average). Previous statistical assessments have shown these groups of stations to differ with respect to their surface chlorophyll concentrations (Kelly and Turner, 1995a,b). Using the measured light for 1994 surveys, Figure 14 shows calculated production for the two groups. B and Z_p terms essentially counterbalance each other, and production between the groups is similar within 10-15% (e.g., not different by one tailed t-test on 16 surveys, $df=30$, $P<0.18$). Summaries of measured production in 1993 and 1992 at the six nearfield stations also confirm the similarity of average production across the field (Kelly *et al.*, 1993; Kelly and Turner, 1995a).

Our exercise suggests that similar production levels may be achieved where roughly constant photic biomass (BZ_p) results from opposing gradients in B and Z_p, since Z_p increases at about the pace per kilometer from shore that B decreases. This result may arise from unusual circumstances. The deepening of Z_p was faster than could be predicted from changes in chlorophyll alone (the effect on k, the extinction coefficient, is expected to be ~ 0.016 m (ug Chl *a*/L)$^{-1}$ — cf. Bannister, 1974). From the linear relationship between B and Z_p (noted above) we estimate an effect on k equivalent to 0.035 m (ug Chl *a*/L)$^{-1}$. We therefore attribute the deepening in Z_p to approximately equal parts decrease in chlorophyll and non-chlorophyll turbidity from west to east across the nearfield.

The broadest scale addressable in the context of controlling factors on production is interannual, and at this scale too there may be an influence of fluctuations in irradiance. Model-estimated production for the nearfield region 1992-1994 (Figure 15) shows that 1993 in general had high production for most of the summer, culminating in the peak production event in early fall 1993. 1994 had the highest winter-spring production, but in general for each year the seasonal cycle portrayed high rates (>1 gC m^{-2} d^{-1}) for most of the stratified period and often peak production rates in the fall bloom. Figure 15 also shows daily light measurements for the 1992-1994 period. Lowest average light was recorded in 1992 (47.5 E m^{-2} d^{-1}), followed by 1994 (55 E m^{-2} d^{-1}), and 1993 (64 E m^{-2} d^{-1}). Model production is determined in part by I_o, so the annual production as calculated by the model must reflect this interannual variability in light; thus production was estimated as 386, 468, and 620 gC m^{-2} y^{-1} in 1992, 1994, and 1993, respectively. For nearfield stations, note that not only the modeled, but also the measured production (June-October), was highest in 1993. An interesting aspect shown in Figure 15 is that, in 1993, incident light in early summer and through most of the fall was higher than the other years. From these observations, the hypothesis is that unusually high chlorophyll concentrations (>10 μg L^{-1}) that were observed

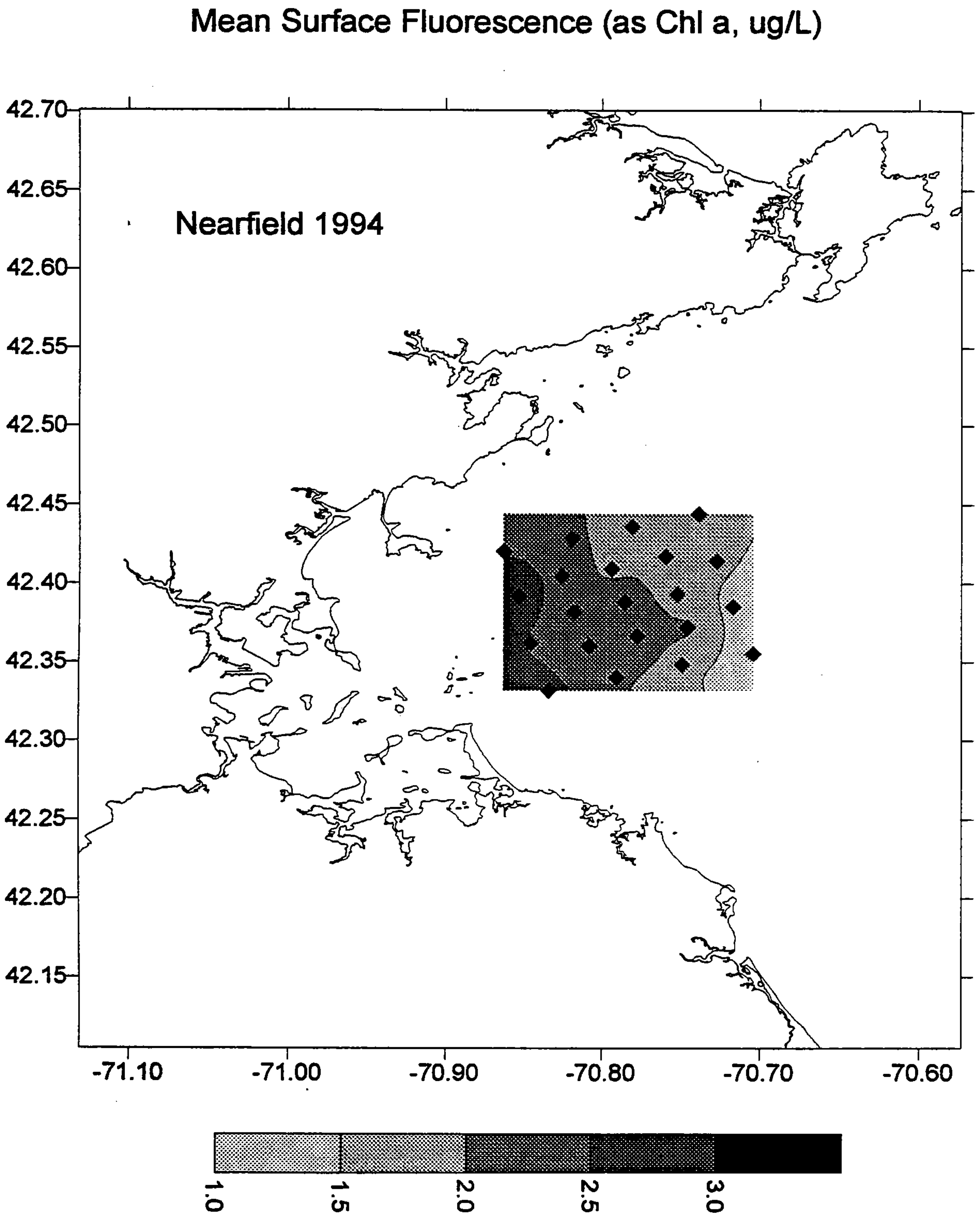

Figure 13. Surface chlorophyll concentration gradient from shore to sea across the 21 nearfield stations.

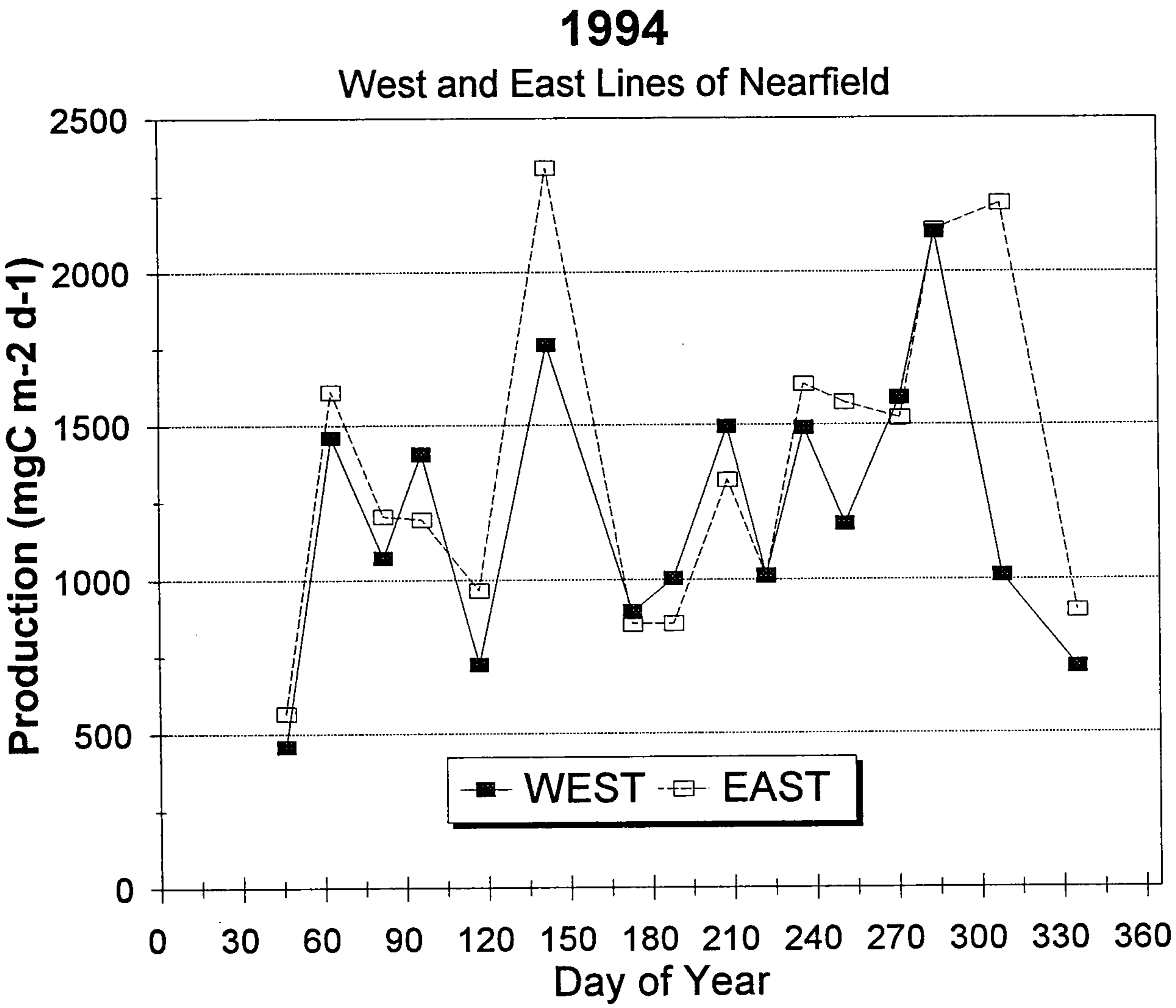

Figure 14. Modeled production for four western-edge (shoreward) and four eastern-edge (seaward) stations of the nearfield region during 1994.

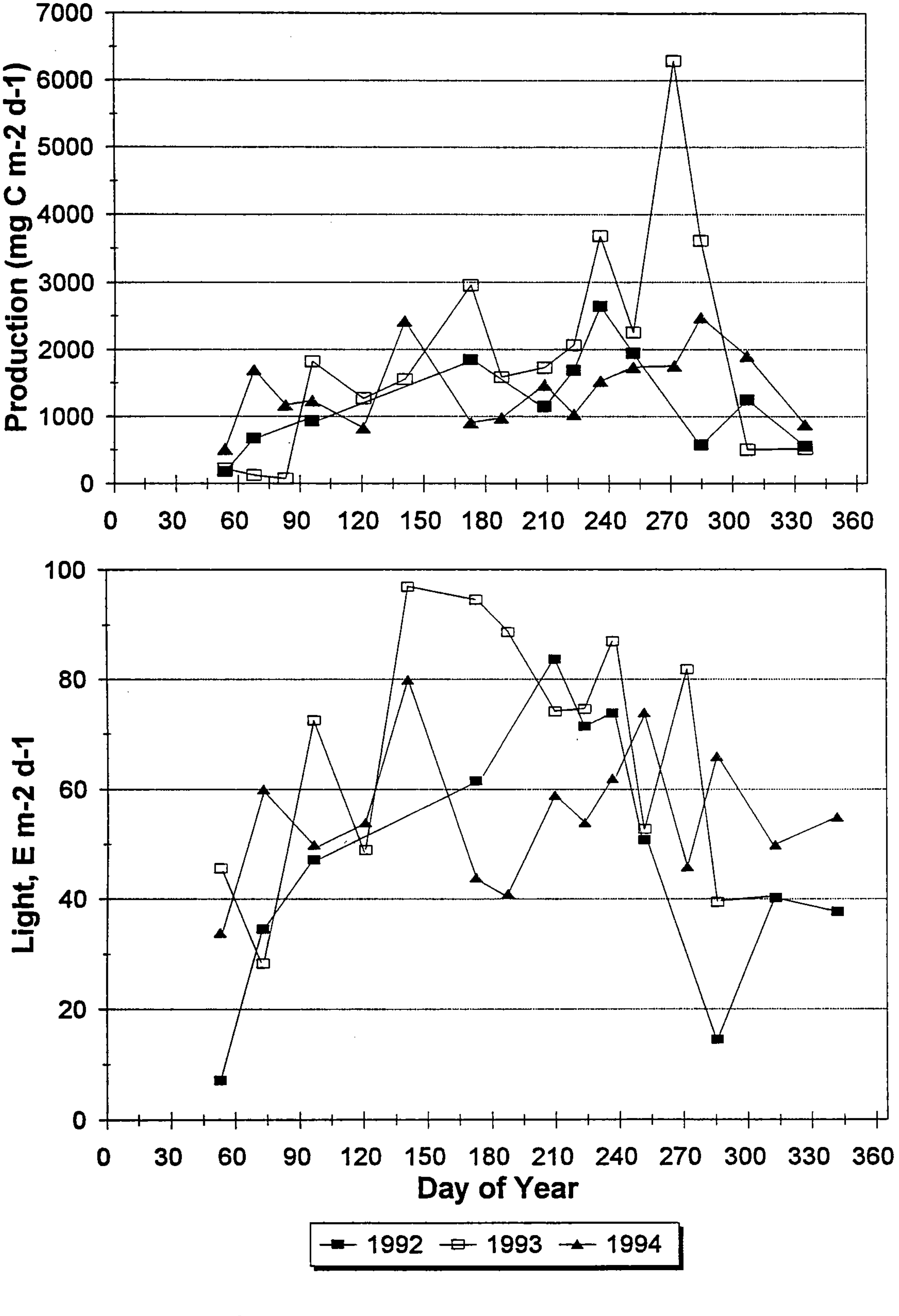

Figure 15. Comparison of modeled production and incident daily irradiance for the nearfield during the monitoring period 1992-1994.

in summer-fall 1993 (Kelly and Turner, 1995a), and the concomitantly high production that was modeled for that period (Figure 15), were in part a consequence of relatively high irradiance in summer-fall 1993. For future tests of this hypothesis, it would be helpful to have daily measurements of cloud cover or irradiance rather than the more limited frequency available from surveys.

Implications of model/data comparisons regarding different methods of measuring production. ^{14}C-based model projection was compared with production calculations based on oxygen metabolism (1992 data). Net daytime production, as measured by oxygen change, and assuming a PQ (O_2/CO_2) of 1.25, underestimated ^{14}C-based model production by roughly 25-40%. Indeed, it is tempting to use the regression for the 1994 model and the 1992 oxygen measurements (not converted to C) to estimate an "effective" PQ. The result would be $\approx$ 1, within the range commonly used for such conversions (e.g., Parsons *et al.* 1984). In October 1992, we measured P_{max} by both O_2 and ^{14}C methods. About 50% of the tests ($n=11$) gave a PQ $\approx$ 1 at saturating light conditions, but the PQ range was 0.7 to 2.7, similar to many previous studies. In the two cases where full P-I curves were compared, α values for O_2 and ^{14}C were the same even when the implied PQ's at P_{max} were ≥ 2. Oviatt *et al.* (1986) saw even wider variability in PQ in individual measurements ($n>100$), but showed a median PQ of 0.9 although a regression slope suggested an average of 1.24. Our conclusion, like Oviatt *et al.* (1986), is that individual incubations cannot be predicted accurately with a constant PQ. Over an annual timeframe an average PQ is a reasonable simplifying assumption, but the annual integration results will be sensitive to it. For example, our *a priori* choice of PQ=1.25, rather than 1, could explain the underestimation of annual production in 1992 described above. We cannot assess whether the empirical suggestion of an effective PQ of 1 reflects phytoplankton physiological processes within in our incubations. However, we believe annual production estimates given in results for Boston Harbor and Cape Cod Bay in 1992 may be 25% high and therefore suggest an appropriate estimated range for that year is 416-555 gC m^{-2} y^{-1} for the Harbor and 460-613 gC m^{-2} y^{-1} for central Cape Cod Bay.

There are, however, other reasons our oxygen-based measurements could underestimate production compared to ^{14}C (cf. Bender *et al.*, 1987). A complete consideration of this complex topic is far beyond the scope of this paper, but two aspects are briefly mentioned. First, oxygen and ^{14}C methods do not measure the same processes. It is generally acknowledged that, while oxygen measures net production, ^{14}C often measures between net and gross production. There is not a constant relationship between the two and short incubations (hours), such as ours, more closely approximate gross production than longer incubations (Peterson, 1980; Leftley *et al.*, 1983; Davies and Williams, 1984; Bender *et al.*, 1987). In theory, our 1992 measurements thus should provide lower estimates. Second, in our calculations, a correction was applied for dark ^{14}C uptake, but for O_2 a fourth term (R=respiration, a constant) was included in the P-I modeling. This approach, although not always providing a precise R term due to scatter in P-I curves at low light, did provide an estimate of the compensation light intensity, where respiration exceeded production and no net production occurred (cf. Jassby and Platt, 1976, Cote and Platt, 1983). In the resulting modeling over depth, this compensation depth was often reached at depths shallower than the 0.5% light level, and depth-integrations were stopped at this point (because net production became negative), rather than carried out to a constant isolume. There are cases where this difference in modeling procedure for 1992 (independent of the issue of differences in what O_2 and ^{14}C measure) would tend to underestimate integrated production.

High annual production

That the empirical model for Massachusetts Bay is virtually the same as for other areas is one strong argument that our measured and projected rates are valid. Nonetheless, annual integrations indicate very productive waters and we next address the validity of this principal result. Our examination involves a summary of uncertainties related to developing primary production estimates and includes consideration of 1) uncertainties and sensitivities related to P-I incubations and parameter modeling, and 2) assumptions on converting incubation data to depth- and daily-integrated rates. Moreover, we also present some ancillary monitoring data on oxygen dynamics that confirms some production results. Finally, we compare our annual estimates of production to other coastal waters and show that the rates are commensurate with nitrogen loading to Boston Harbor and western Massachusetts Bay.

Sensitivity/uncertainties concerns with P-I measurements and modeling. A number of P-I incubations for 1994 data yielded poor model fits and concomitantly high α values that visibly overestimated the data and often were also well above a theoretical maximum. Similarly, in 1992 and 1993, about 21% of the total incubations (n=216) had unreliably high α values, the majority being from 1992 when less-sensitive oxygen methods were employed. High α values may arise from simultaneous fitting of parameters (e.g. Jassby and Platt, 1976); where the data were well fit by the model, overall P-I results might be acceptable, but in most instances with high α, this was not the case. Re-fitting an α parameter independent of the full P-I model is one approach that might reduce some high α's, but this approach usually is not recommended (cf. Frenette *et al.*, 1993). We approached the issue through a sensitivity exercise on a restricted data set (Figure 3), in which high α's were eliminated and the mean α was reduced by 40% compared to the full data set. For this selected subset, we then recalculated integrated daily rates for each station and computed an annual average by station to compare with those calculated for the full set. For station F23P, recalculation gave an annual average that was 98% (i.e., 2% lower) of the previous value and for station N16P, recalculation gave an annual average that was 84% of the previous value. The lower percentage at station N16P occurred because the subsetting procedure omitted one day with anomalously high rates (June, Figure 5); note that recalculated rates for the selected subset of data at station N16P were identical to the annual average obtained when two anomalous high values (Figure 6a) were excluded, as discussed earlier.

Using recalculated rates, we again obtained a significant regression of ^{14}C production on BZ_pI_o ($R^2=0.77$, n=12). Compared to the full set, the functional regression slope was 0.51, or <10% lower than the one (Equation 2) used for extrapolations in this paper. Recalculation of the annual rate for the nearfield in 1994 gave an estimate of 419 gC m-2 y-1, or at least 90% of that based on the full data set.

Unlike α, the P_{max} values were in expected ranges and similar to representative values for other studies (cf. Platt and Jassby, 1976; Falkowski, 1981; Malone and Neale, 1981; Laws *et al.* 1990). For all years combined, <3% of the modeled P-I curves (n=304) produced P_{max} values above a theoretical maximum. We performed studies to address whether chlorophyll *a* concentrations changed during incubations and whether chlorophyll was adequately measured by our small volume sampling (10 mL). Results showed that neither small sample volumes nor the standard practice of normalization of ^{14}C rates with the *initial* chlorophyll *a* concentrations (rather than a concentration determined at the end of the incubation) introduced a strong or consistent bias upon P_{max}. Therefore, we have no reason to assume that the study's P_{max} values were unreasonably high (as a basis for explaining high production) and we did not further screen the P-I data.

Uncertainties related to spectral quality during incubations. Our incubations did not provide environmental levels of UV-radiation, nor did they attempt to simulate a differential spectral decay with depth. The effect of virtual exclusion of UV-B in incubations is difficult to extrapolate to integrated *in situ* production rates, but *in situ* rates are probably overestimated by 5-15%, and maybe substantially more (e.g., Smith and Baker, 1982; Smith *et al.*, 1992; Cullen *et al.*, 1992). UV-B effects diminish with depth. On the other hand, Laws *et al.* (1990) suggest that use of neutral density filters (as in our studies) rather than simulations that mimic the spectral quality at depth in clear ocean water may *underestimate* integrated water column production by a factor of two. The spectral effect that Laws *et al.* (1990) describe is minor in the upper water column and only significantly applies to light levels below which P_{max} is maintained. In most cases of our studies, the upper water column was the most productive, and the spectral effect would likely underestimate integrated production by a factor far less than two even if the lower depths of the photic zone are twice as productive as indicated by our incubations.

Sensitivity and uncertainties with integrated calculations. Two particular assumptions of the computational scheme are mentioned with regard to their potential to over- or underestimate rates. First, the use of $Z_{p0.5\%}$, rather than $Z_{p1\%}$, disregarding any spectral effects, only leads to marginally higher production. Calculations for all 1994 incubation data using the 1% light level lowered the integrated rate only an average of 3% (range=0 to 10%, n=22) compared to the assumed 0.5% light level. The lower few meters (1% to 0.5% isopleths) of a potentially net photosynthetic zone contribute a small fraction of the integrated water column production in Massachusetts Bay and other shelfwater systems (cf. O'Reilly and Bush, 1984; J. O'Reilly, NOAA, pers. comm.).

Second, the length of incubation may bias rate estimates, resulting in higher rates with shorter incubations (e.g. Malone, 1984; Keller, 1988). The reasons for this bias may include "bottle effects", nutrient depletion, tracer-related (^{14}C) uptake dynamics that lead to estimates closer to gross production in short incubations and net production in longer incubations. Because of this bias, shorter term incubations have been the norm for marine studies and Vollenweider (1966) describes derivation of the factor we used to convert short-term rates to daily production. In mesocosm studies having a range of environmental conditions similar to those within the Boston Harbor-Massachusetts Bay gradient, Oviatt *et al.* (1986) confirmed empirically Vollenweider's hour-to-day conversion factor. If measured by 4-6 hour incubations during midday, at any season, Vollenweider calculated that there was an uncertainty on the order of ±10% associated with use of the conversion factor.

Summary of quantifiable uncertainties. Overall, the select subset analysis with reduced α suggested that annual integration results presented for the nearfield during 1992-1994 could be roughly 10% high. This uncertainty is lower than that generally observed in P-I modeling. We summarized uncertainty in P-I modeling by calculating the average % error (standard error/parameter estimate x 100) for parameters of curves described by oxygen changes (1992 stations), the ^{14}C technique in 1993 (same stations as 1992), and incubations for the two stations sampled using the ^{14}C technique in 1994. Confirming what is well established (cf. Peterson, 1980; Leftley *et al.*, 1983), ^{14}C was much more precise than oxygen for estimating both P_{max} and α, but not for the P_{SB} or β terms of the model with photoinhibition (see methods). For example, for oxygen, the error was 36% (P_{max}) and 69% (α), whereas for ^{14}C in 1993 it was 4% (P_{max}) and 19% (α) and was 38% for α in 1994. The average R^2 for curve fits was 0.7 for oxygen, whereas it was 0.9 for ^{14}C in 1993 and 0.8 in 1994. If non-significant fits (or, at 95% probability, where $R^2 < 0.33$ for df=10) for the comparable 1992 and 1993 data sets were excluded, the oxygen and ^{14}C compare more favorably; these non-significant cases, not surprisingly, usually occurred at low production rates. For either technique, P_{max} was more precisely estimated than α. For more precise estimates of α, one would need more points in the linear portion of the P-I curve, i.e., where $I = 0$ to $150\ \mu E\ m^{-2}\ sec^{-1}$. However, below we argue this may not be our largest source of uncertainty in deriving production rates.

Phytoplankton studies have identified considerable short-term (hours to days) variability in P-I model parameters (e.g. Neale and Marra, 1985). Cote and Platt (1983) measured three-fold variations in model parameters, P_{max} and α, from day to day. For our 1994 data set, parameter values for a given station and depth at replicate days within a survey were usually within a factor of two to three of each other. We again summarized variability by calculating the average relative % error for surface sample incubations at two sampling days within surveys. Results showed a relative % error (n=10) of 23 and 40% for P_{max} and α, respectively. There was often more variability in model parameters over depth on a given day than there was between similar depths on different days. For comparison, we calculated the relative % error for integrated production rates for the same replicate station pairs (n=10) to be ~17%, or substantially lower. The error for production, as for the P-I modeling, does not include day-to-day variation in incident light because a standard light was used in calculations for each survey. This simple comparison suggests non-linearity in the relationship between variation in model parameters, especially α, and integrated production rates.

We can address this issue of non-linearity another way. For example, when we screened the 1994 P-I data to remove for poorly-fitted curves, this reduced the mean α by 40%. (Note that this value approximates the average error for α during 1992, 1993, and 1994 [69%, 19%, 38%, respectively], as well as the average error between days in 1994 [40%]). In contrast to α, the value for P_{max} for the full set (n=88) and the restricted set (n=65) was essentially unchanged (<5% different). Using the empirical regression approach to model production, the annual production estimates for the screened and full data sets varied only by ~10%. This modest difference, compared to that in α can be explained because the majority of the production occurs at light saturation near the surface (i.e., at P_{max}) and, moreover, since we composited four incubations over depth, an individual α has limited influence. Therefore, high variability in α can produce modest effects on integrated rates. The design of our incubations, which provided more precise estimates of P_{max} than of α, appears not to be a major shortcoming for the present sampling design, and we estimate that the imprecision of P-I modeling may result in errors of near 10%, on average, in depth-integrated rates.

Beyond P-I modeling uncertainties, it is more difficult to estimate the additive effects of other production calculation assumptions and methodological features mentioned here, which themselves are not a full set of the possible factors affecting production estimates. Without further study, we must regard these as *unquantifiable* uncertainties. However, a major source of *quantifiable* uncertainty that has a direct influence on production rates is incident light. Calculations for 1994 show that daily light levels within short periods have a relative % error near 25% (Table 1), or larger than that apparent from sensitivity analysis of P-I modeling. Intuitively, we thus believe that the production estimates can be representative of *in situ* rates to no better than ±25%, a level coincidentally approximated by the confidence associated with empirical model regression slopes.

Ancillary information from the monitoring program: DO variability in time and space. Measured production during stratification was often high enough to hypothesize that, if real, there 1) might be detectable DO changes in the water column throughout the day under normal advection and wind conditions and 2) that diurnal changes in DO should become progressively smaller with depth.

Kelly *et al.* (1994) examined daytime trends in DO concentrations in the nearfield for a survey in June 1993. They treated the nearfield as a unit sampled twenty-one times (each station) from near dawn to late afternoon. At depth strata from the surface to 15 m daytime trends of DO indicated a net increase in % saturation. In contrast, no net change in % DO saturation was suggested for depths from 15 m to the bottom. Net production was therefore implied in the surface layer, and for the entire water column as a whole. Rough calculations of net production (uncorrected for diffusion from the air to the sea — values were above 100% saturation for the whole day in the surface layer) were made based on these free-water changes in DO and compared to rates derived from ^{14}C incubations at six stations in the nearfield several days earlier. The comparison was made for this survey because (1) there was strong stratification and low winds, (2) the nearfield was fairly uniform in water quality parameters including chlorophyll, and (3) ^{14}C production rates were substantial, ~2-3 gC m^{-2} d^{-1}. These conditions seemed nearly ideal for asking whether diurnal free-water changes could be detected; based on ^{14}C and assuming a PQ of 1 to 1.25, we expected changes to be on the order 0.5 mg O_2 L^{-1} in surface waters. Integrated water column production rates were virtually identical between the two methods of calculation. We have not tested further for concordance between incubations and free-water DO change to determine the limits for detection, nor was the survey sampling specifically designed to support such exercises. The example simply illustrates a case where high rates of production (about twice the average ^{14}C-measured daily rates) were associated with commensurate changes in DO at expected depths; this provides additional confirming evidence, on a nearfield-wide basis, for high primary production.

Throughout the monitoring program we have noted that during stratified summer periods DO characteristically drops below 100% saturation near the base of the average photic zone (~20 m) (e.g., Figure 16). There often occurs a mid-depth peak in absolute concentration and % saturation at depths of the 0.5 to 1.0% light levels (generally 10 to 25 m). The mid-depth DO peak regularly was at the top of the pycnocline or within the pycnocline, but virtually never below it, and when present coincided with a subsurface chlorophyll maximum. A peak in DO (% saturation) at this depth must be taken as unequivocal evidence for *in situ* production near the base of the photic zone. This data speaks to the issue of inclusion of production to low light levels and adds validity to our choice of a deep photic zone in initial calculations, even though we have calculated a minimal (3%) contribution of deep-water zones to integrated production rates. However, if deep production has been underestimated due to a lack of spectral simulation in low-light incubations, then integrated production indeed may be underestimated by our results.

Comparison with other coastal ecosystems. Production estimates for the nearfield region on the shallow inner shelf of Massachusetts Bay, 386-620 gC m^{-2} y^{-1} during 1992-1994, suggest a highly productive system. Rates are at the high end of the range reported for a number of coastal shelf and estuarine systems (e.g. Kelly and Levin, 1986; Nixon, 1990). Some other shelfwater systems have production between 400-600 gC m^{-2} y^{-1} (e.g., Hopkinson, 1985). O'Reilly and Bush (1984) published an extensive compilation of production for shelf waters from the Mid-Atlantic Bight to the Gulf of Maine, finding rates from 280-470 gC m^{-2} y^{-1} across large geographic sectors. They noted that highest daily rates were measured in the NY Bight apex area that receives outflow from the Hudson River and nutrients from New York City; Malone (1984) reported production of 590 gC m^{-2} y^{-1} for the Hudson River plume extending into coastal shelf water.

Based on very high nitrogen inputs to Boston Harbor and subsequent high export to western Massachusetts Bay (Kelly, 1991, 1993), substantial production is expected. Unlike the Harbor, where turbidity is high and light can be a strong limiting factor, light availability is higher in shelf waters and continuous input of nutrients should support high production. Kelly (1993) estimated that about 4.5 moles N m^{-2} y^{-1} may be expelled to the nearfield region (~100 km^2) from the Harbor area; inputs from coastal circulation and advection could increase the total N loading. The Harbor input occurs principally to the surface layer of the nearfield. If we assume the surface mixed layer above the thermocline (including $Z_{p0.5\%}$) is, on average, about 20 m deep, the volumetric input is 225 mmol m^{-3} y^{-1}. Examining Nixon's

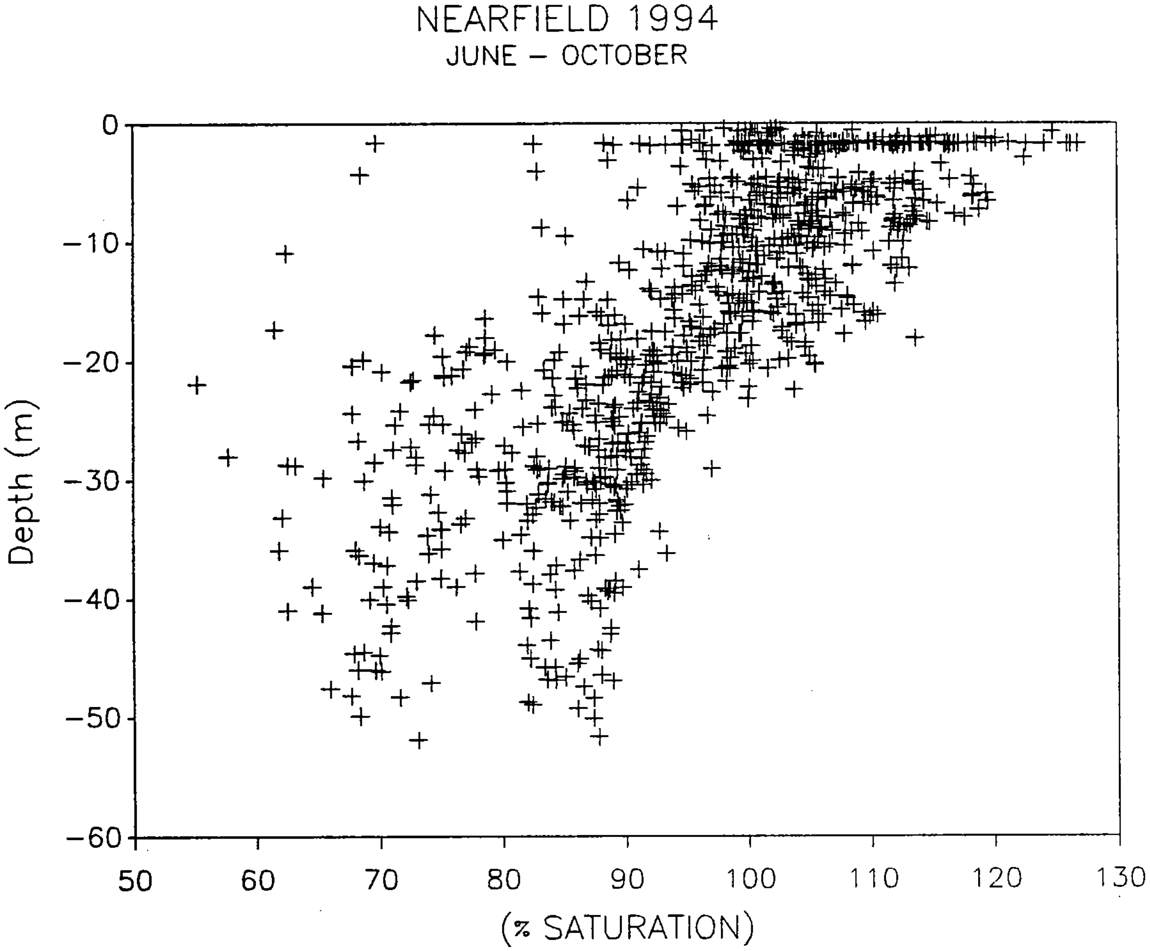

Figure 16. Depth distribution of DO (% saturation) at nearfield stations during the strongly stratified summer-fall season in 1994.

(1990) empirical relationship between annual primary production and nutrient input, it is apparent that the few coastal ecosystems with DIN (dissolved inorganic nitrogen) inputs of ~2 to 5 moles m^{-2} y^{-1} (or ~200 to 500 mmol m^{-3} y^{-1}) have production in the almost the same range as the nearfield in Massachusetts Bay during 1992-1994 (Figure 17). A substantial fraction of the N input from the Harbor is held within organic forms (including phytoplankton), some of which will be readily available as DIN, but the nearfield input as DIN only (as used by Nixon) has not been determined. The scatter in Nixon's relationship makes it useful only as a very coarse predictive tool; nevertheless an appropriate conclusion is that our results are consistent with the general pattern for marine systems and western Massachusetts Bay is an enriched system with commensurately high primary production.

Compared to the nearfield and the overall trend summarized by Nixon, Boston Harbor tends to be slightly low with respect to production for its nitrogen load. We have previously ascribed some ecological differences between the Harbor and the Bay to high turbidity and stronger light limitation of phytoplankton in the Harbor (cf. Kelly, 1993; Kelly and Turner, 1995b). Insufficient availability of light, as well as a short water residence time in the Harbor (Kelly, 1991; Signell and Butman, 1992), may contribute to the pattern in Figure 17, for inputs have not been normalized for flushing times.

Metabolic budgets: Fate of production in western Massachusetts Bay

Other aspects of the metabolism of western Massachusetts Bay, i.e. respiration in water and sediments, have been examined during 1992-1994. Overall, the data supports the notion that a relatively minor fraction of the annual production in surface waters is metabolized in sub-pycnocline waters and bottom sediments (e.g. Kelly, 1991, 1993; Kelly and Turner, 1995) and such evidence is summarized next.

Benthic respiration (1993-1994). Seasonal patterns of sediment oxygen demand for fine-grained depositional sediments in the western portion of the nearfield have been presented for 1993-1994 (Giblin *et al.*, 1994, 1995). Figure 18 displays benthic respiration as a function of bottom-water temperature for the two years, based on six measurements at 3-5 stations each year (Feb/March, May, July, August, and October). Overall, the data for the two years could be fit by a common flux-temperature model. There is a slight suggestion that high-temperature (>10 °C) fluxes in 1993 tended to higher than 1994, but the overlap of flux rates makes 1993 and 1994 indistinguishable statistically.

Giblin *et al.* (1994,1995) compared nearfield benthic respiration with primary production rates during the summer stratified period. Assuming an RQ (Respiratory Quotient=$C0_2/O_2$) of 1, sediment oxygen uptake rates were calculated to consume ~10-23% of summertime primary production in 1993 and 7-17% in 1994. The higher value of the range for each year is based on measurements in depositional sediments only and the lower value is based on an extrapolation of results at western nearfield depositional sediments to the rate across *all* bottom types of the nearfield. Unlike the *western* nearfield, most of the bottom (about 71%, Knebel, 1993) is non-depositional (e.g., sand, gravel, cobble, or hard-bottom) and, moreover, the average temperature for the field is generally lower than that measured on the

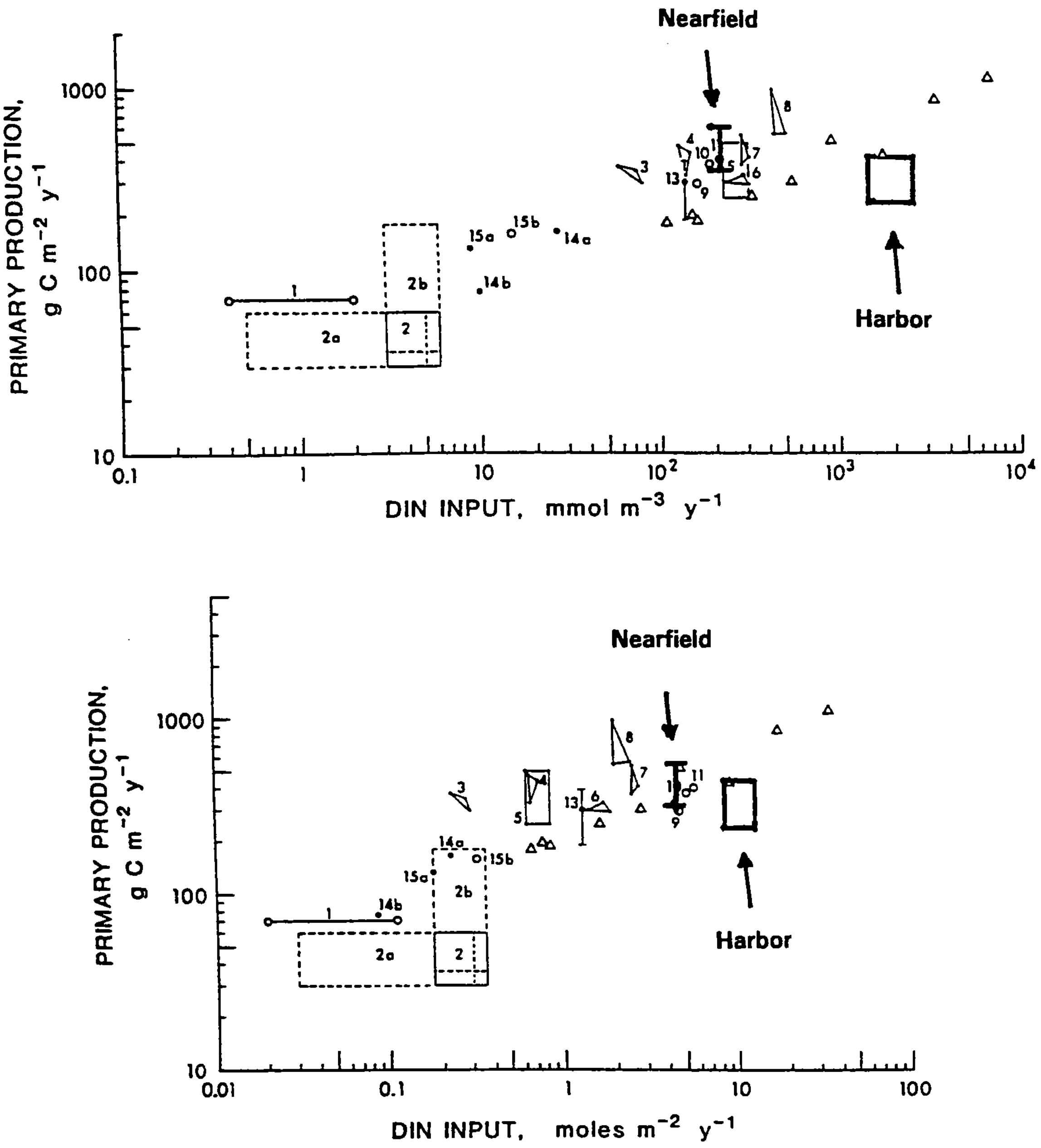

Figure 17. N input and production in different coastal and estuarine ecosystems. Modified from Nixon (1990). Production variability for the Harbor and nearfield are given in this paper. Estimates for N input are given in Kelly (1993) and Kelly and Nowicki (1993) and include total N. DIN inputs are ~50% of total N inputs.

shallower western side. The percentages above likely provide maximum estimates of the role of benthos in consumption of primary production of the nearfield region in the stratified season.

With respect to estimating annual averages, we used the simple linear temperature-flux relationship of Giblin *et al.* (1994). Their linear regression

$$O_2 \text{ flux } (\text{mmol m}^{-2}\text{ d}^{-1}) = 1.38\ (^\circ\text{C}) + 6.76 \qquad \text{[Equation 6]}$$

suggested a tripling of rates for a 10 °C rise in temperature (from 0-10°C, or close to the annual range). The model was coupled with the average nearfield near-bottom temperature for surveys throughout 1993 and 1994. Annual benthic respiration was estimated as ~60 and ~69 gC m^{-2} y^{-1} for 1993 and 1994, with 1994 being higher because of higher bottom-water temperatures in summer and fall. Without decrementing rates by a factor >2 to account for the preponderance of non-depositional bottom, benthic respiration would account for ~10 to 15% of the annual primary production (1993 to 1994). Extrapolating to the entire nearfield by recognizing variations in bottom types, we estimate this range to decrease to 4-6%. Interestingly, the modeling exercise also suggested that ~50% of the annual benthic respiration occurs from about August through November, coinciding with the period of high bottom-water temperature. Thus, the period of peak sediment metabolism may slightly lag the period of peak primary production.

Water column respiration patterns (1994). In 1994, we estimated water column respiration in dark 300-mL BOD bottles from three stations along a transect from inshore to offshore. The inshore station (F24) is about halfway between the Harbor and the nearfield, the middle station (N20P) lies in the middle of the nearfield, and the offshore station (F19) is in the deepwater of Stellwagen Basin ~10 km east of the nearfield. DO declines were significant in most cases; we limited the data set to cases where R^2 for linear regressions on 0-48 h (or 0-168 h) data were >0.5 (23 of 27 incubations, the excluded data being primarily from April when temperatures were lowest.

Figure 19 shows dark respiration rates from bottle incubations as a function of the depth of the sample. In general, rates were highest in surface samples, especially those nearest the Harbor, and declined to reach lowest rates at depth, especially in deepwater in Stellwagen Basin. Variability at given depths relates in part to variations in organic matter and temperature across the stations and months of measurement. This conclusion is supported by the patterns shown in Figure 20, where rates have been normalized to chlorophyll and particulate organic carbon (POC) and then plotted as a function of incubation temperature. Both trends in Figure 20 suggest an exponential rise with increasing temperature with a Q_{10} (factor of increase in rate for each 10 °C rise in temperature) near 2, which is expected for metabolic processes.

Interestingly, normalized rates (Figure 20) suggest the three stations are similar and follow the same general pattern. These stations bracket the gradient of conditions of temperature,

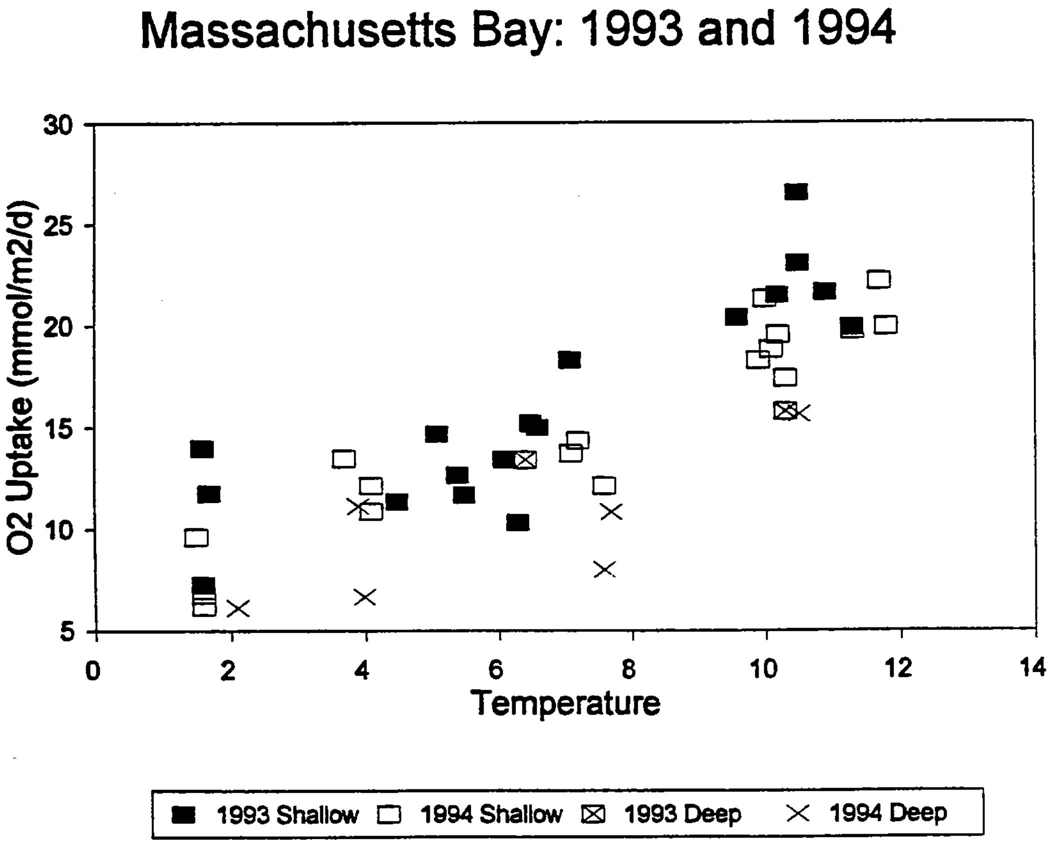

Figure 18. Sediment oxygen uptake in Massachusetts Bay during 1993 and 1994. Shallow stations are located at ~30 m water depth and represent depositional sediments in western Massachusetts Bay. Deep stations are not considered in this paper. From Giblin *et al.* (1995).

chlorophyll, and POC across the nearfield, so we used all the data to develop a generalized empirical model describing the decline of respiration with depth for nearfield conditions (Figure 19). This was obtained by regressing the ln(rate) on depth ($R^2=0.5$, $n=23$, $P<0.01$) to derive the following:

$$\text{Respiration } (\text{mgO}_2\ \text{L}^{-1}\ \text{d}^{-1}) = 0.23\ e^{-0.034\ \text{Depth (m)}} \qquad \text{[Equation 7].}$$

The model, shown in Figure 19, underestimates highest rates near the Harbor and some cases where there were high subsurface chlorophyll maxima offshore (20-35 m), but appears to describe the general decline over depth. Using the model results, one can calculate that the average rate for the upper 20 m (~the average photic zone for the nearfield) as 0.17 $\text{mgO}_2\ \text{L}^{-1}\ \text{d}^{-1}$, or, converted to carbon on an areal basis (assuming an RQ of 1), about 1.3 $\text{gC m}^{-2}\ \text{d}^{-1}$. In contrast, the rate for the sub-euphotic, subpycnocline lower layer of the water column (20 m to the bottom, on average ~15 m) is calculated as 0.08 $\text{mgO}_2\ \text{L}^{-1}\ \text{d}^{-1}$, or 0.5 $\text{gC m}^{-2}\ \text{d}^{-1}$. These are approximate average rates and have substantial uncertainty, but they nonetheless are derived from the data and illustrate the basic point that respiration declines with depth. Using the model heuristically, it is suggested that the surface layer contributed 72%, and the bottom layer about 28%, of the total water column respiration (average=1.8 $\text{gC m}^{-2}\ \text{d}^{-1}$) during the stratified period encompassed by these measurements in 1994. While both the respiration estimates and the production estimates have substantial and acknowledged uncertainties, it is worth carrying the heuristic exercise further to outline some fundamental notions on the metabolic functioning of the nearfield region.

Using the incubation data at N16P and BZ_pI_0 modeling for the entire nearfield (above), the production during the April-October 1994 period averaged 1.3 to 1.6 $\text{gC m}^{-2}\ \text{d}^{-1}$. This range includes the implied respiration in the upper water column (1.3 $\text{gC m}^{-2}\ \text{d}^{-1}$). The fact that near-surface water is slightly, but consistently supersaturated, in DO during the stratified season (Figure 21 and 16) is strong evidence that production slightly exceeds respiration during the period and that there is net ecosystem production in surface waters.

On the other hand, estimated photic zone production (1.35 to 1.55 $\text{gC m}^{-2}\ \text{d}^{-1}$) is *less* than the respiration calculated for the *entire* water column (1.8 $\text{gC m}^{-2}\ \text{d}^{-1}$). This could occur for at least two reasons. First, with the export of nutrients from inshore comes a substantial particulate organic matter export, especially during summer (Kelly, 1993) and this material (an allochthonous input), as well as primary production (an autochthonous input), is available for metabolism and will contribute to O_2 respiration (cf. Hopkinson, 1985). Thus, a focus only on primary production will somewhat underestimate the total organic matter supply in the nearfield. Second, with the seasonal rise in bottom-water temperatures, bottom waters and bottom sediments increasingly consume organic matter. Peak respiration occurs with a slight seasonal lag relative to the production cycle. The lag provides another mechanism for having excess respiration (above production) over select periods of the year. Note that if a portion of stratified season sediment respiration was due to prior organic deposition, then the direct quantitative linkage of surface production and sediment metabolism *during the most productive season of the year* is less than implied by calculations above.

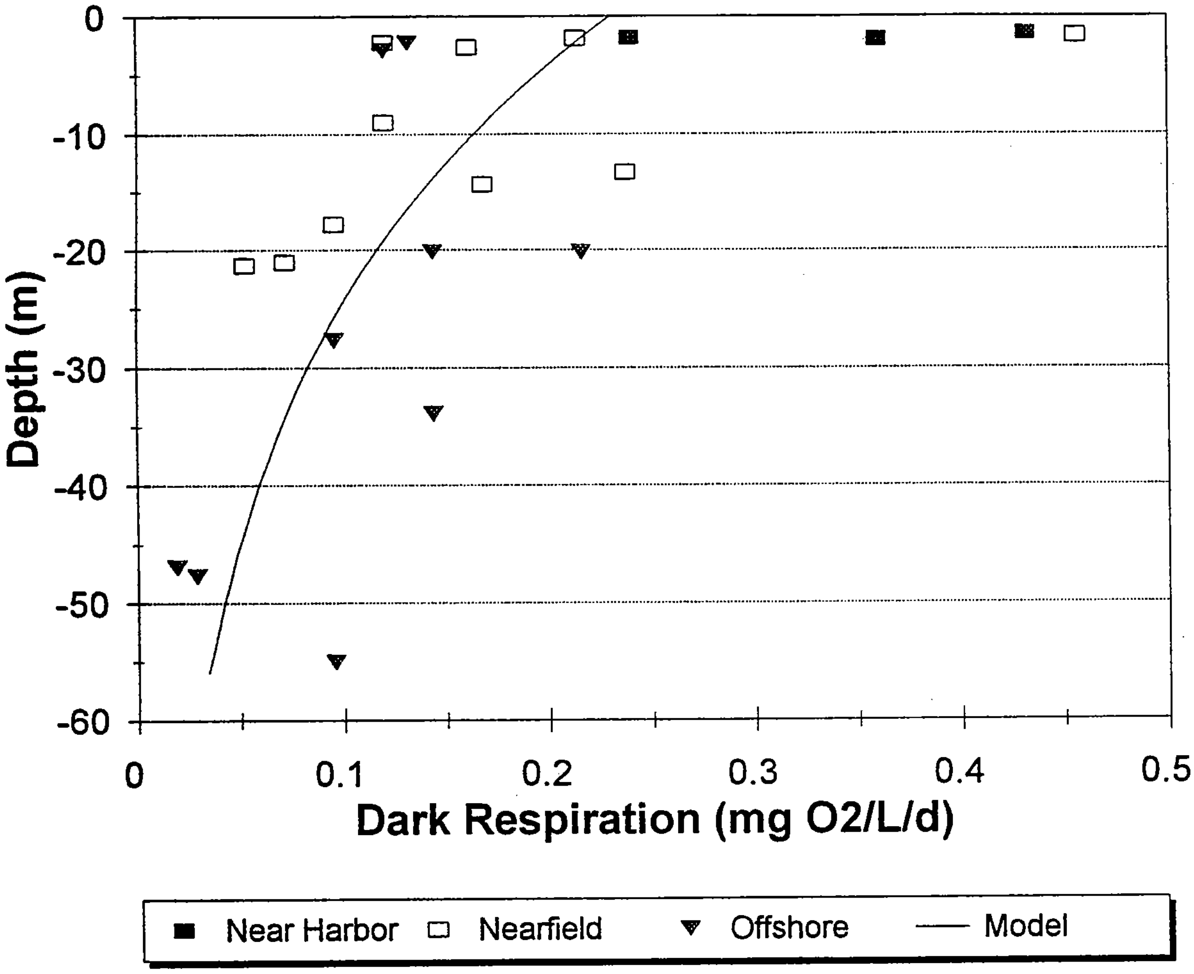

Figure 19. Depth distribution of dark-bottle respiration from measurements during 1994.

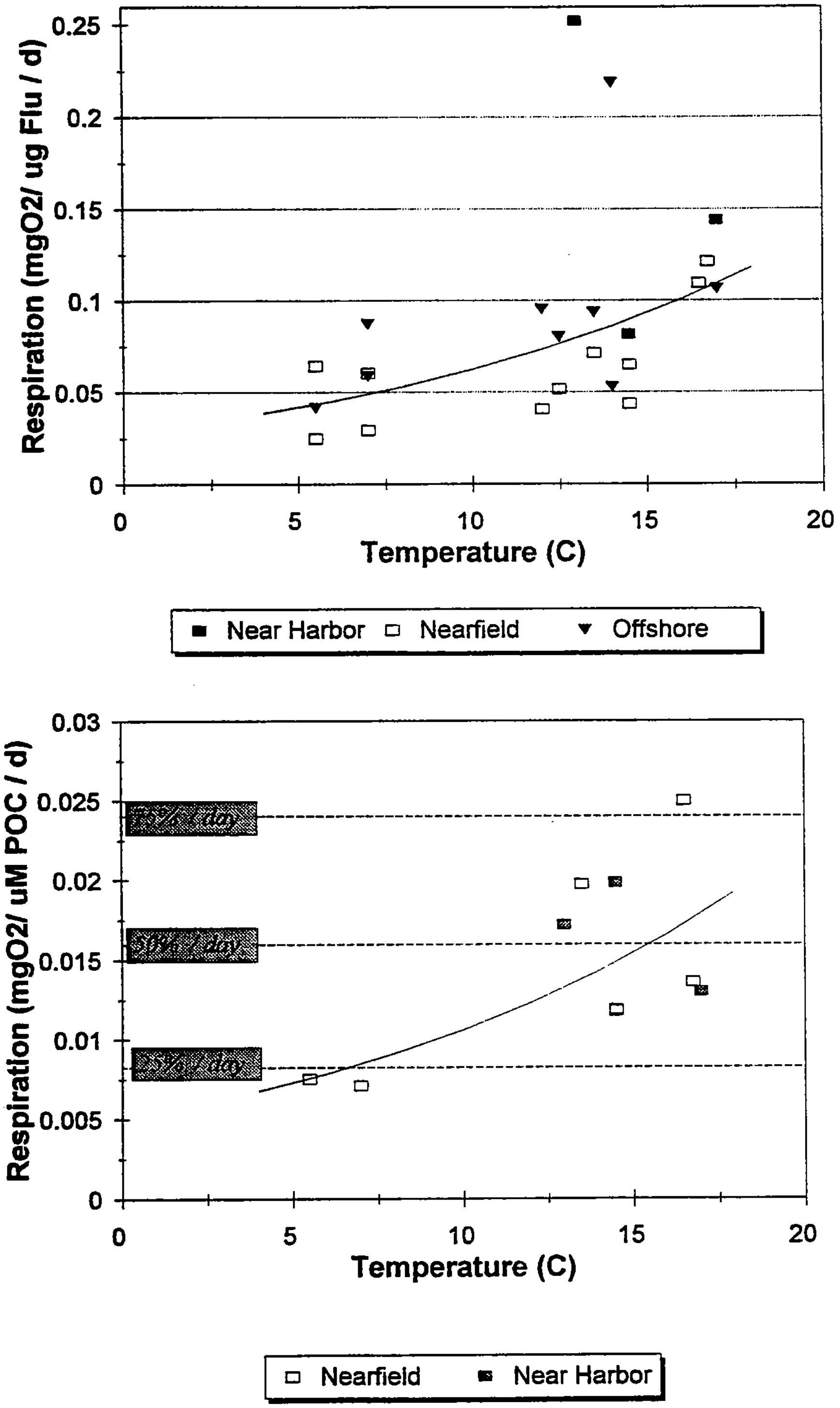

Figure 20. Empirical models for normalized respiration as a function of temperature based on measurements during 1994. Top: normalized to chlorophyll, as *in situ* fluorescence (Flu). Bottom: normalized to particulate organic carbon (POC). There were fewer cases where POC was measured. Approximate daily turnover rates of carbon (RQ = 1) are indicated.

With uncertainties, the bounds of a preliminary metabolic budget for the nearfield are established by our summaries of production and respiration. Roughly 70% of production appears to be consumed in surface layers, while the remaining 30% or so is consumed in the lower water column and bottom sediments. We must ask the fundamental question as to how this substantial metabolic understanding contributes to understanding of the dynamics of DO, which, after all, is the ecological endpoint of concern and the basis for measuring and monitoring metabolic parameters. This question is complex, but in part may be addressed by considering metabolic rates and trends relative to DO concentrations and trends in the region.

Trends in bottom-water DO (1992-1994). Kelly and Turner (1995b) examined trends for DO in subpycnocline waters during three annual cycles. Their conclusion: interannual differences in bottom-water DO were more related to physical factors, including bottom-water temperature, than to organic matter and metabolic factors, like variations in chlorophyll and primary production. For example, lowest DO concentrations were detected in 1994, not 1993 when chlorophyll concentrations and production rates were much higher (see also above).

A progressive decline in DO concentration in bottom water during the stratified season has been characteristic of the nearfield and deeper Bay waters. Moreover, rates of decline have been quite similar for each year of the monitoring period (1992-1994; Kelly and Turner, 1995b) and there has been evidence for a non-linear decline in DO, with rates of decline increasing as temperatures rise over the period. Here we compare the DO decline in 1994 to projections from metabolic data (Figure 22). Observed mean DO concentrations for measurements of nearfield bottom water (>20 m) decreased from 11.5 mg L^{-1} in April to 6.7 mg L^{-1}, a period covering 11 surveys. We used the mean bottom-layer temperature and fluorescence concentrations (as chlorophyll *a*) for each survey and the relationships given above for sediment and water (normalized to fluorescence) respiration as a function of temperature (e.g., Figures 18 and 20) to predict the change in DO from initial conditions in April that might be due to respiratory processes, based on bottle and flux chamber measurements. For the projections, note that DO decline was slightly faster over the period.

For the sediments, we used the method of areal extrapolation from depositional rates presented in Giblin et al. (1994, 1995). The projection suggests that the observed decline of DO cannot be due to sediment respiration alone (Figure 22). In contrast, the projection for water respiration (with or without sediments) far exceeds the observed drop in DO. Expressed as an average DO loss rate for the bottom-layer during the period, the observed decline was ~ 0.025 $mgO_2\,L^{-1}\,d^{-1}$, whereas sediments (projected) had a rate of ~ 0.016 $mgO_2\,L^{-1}\,d^{-1}$. The water (projected) had a rate about 3 times the sediments, ~ 0.049 $mgO_2\,L^{-1}\,d^{-1}$, which was similar, perhaps low in comparison to the observed rates shown in Figure 19. Projected total respiratory demand on DO was therefore >2 times the observed decline.

In evaluating the validity of our water respiration rates, we found that our bottle-derived rates were rather low, not high, compared to similar measurements reported in the literature,

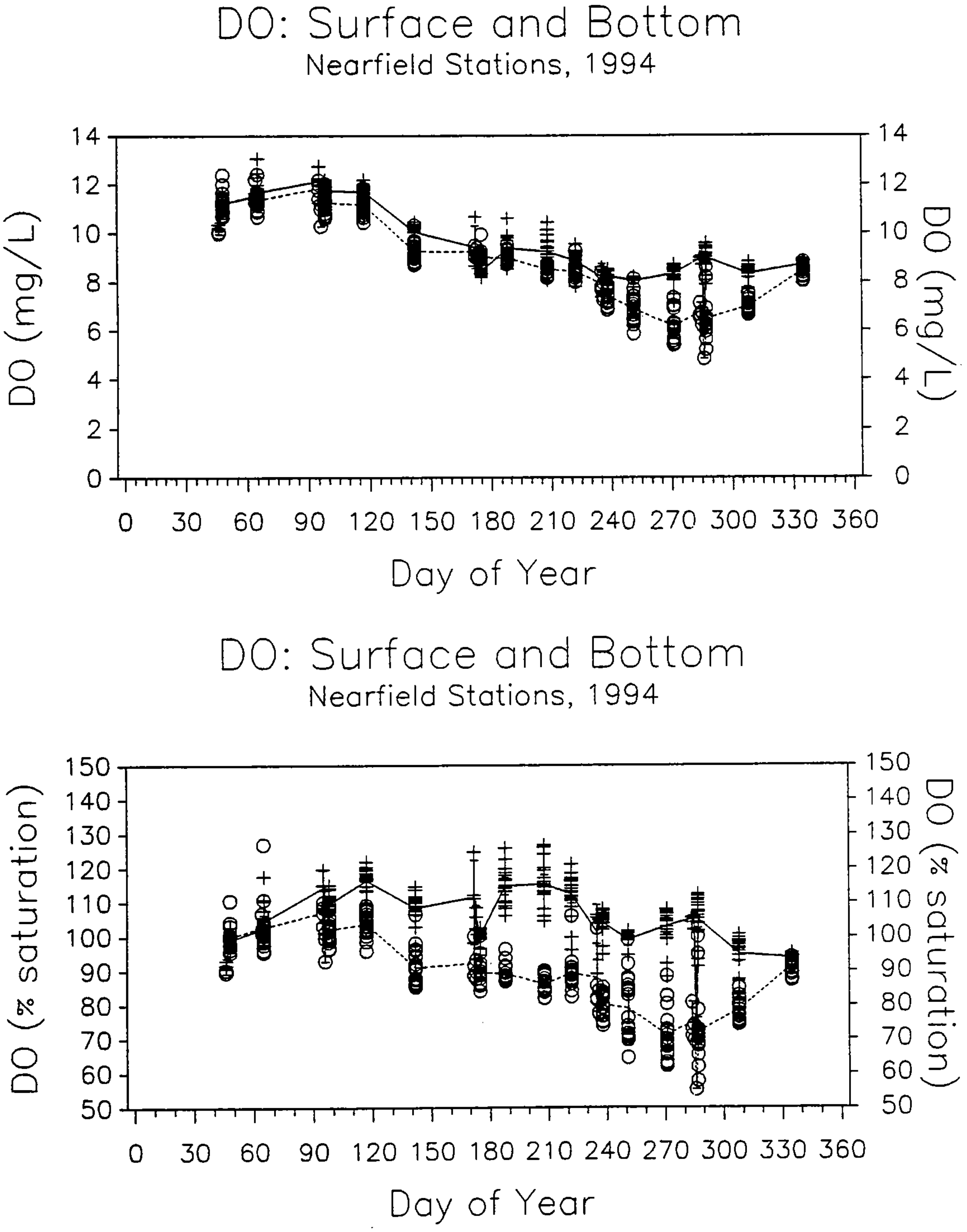

Figure 21. **DO concentrations and % saturation in nearfield surface and bottom water through the 1994 annual cycle. Surface data are represented by the plus symbol and solid lines. Bottom data are represented by circles and dotted lines. Lines pass through mean values for each day of sampling. Vertical lines with bars indicate standard error of the mean. From Kelly and Turner (1995b).**

such as for Chesapeake Bay and coastal waters off Georgia (cf. Sampou and Kemp, 1994; Hopkinson *et al.*, 1989). Assuming our water respiration rates are valid, one must conclude that additional factors besides metabolism help regulate DO concentrations in nearfield bottom waters. Further study on this is warranted, but logically one assumes that these factors are physical. They could include a eddy-diffusive flux into the depleted bottom-water layer from the DO-rich upper layers during stratification (e.g. Figure 21) and/or advective exchanges with other Bay waters. For example, following Kelly (1993) and based on Okubo (1971), a rough calculation for eddy-diffusive flux of DO to the bottom layer can be calculated. We assumed a very low range for the eddy-diffusion coefficient (k) of 0.5 to 1 cm^2 sec^{-1} during strong summer stratification (based on Geyer, pers. comm.). Using observed DO summertime gradients between the surface and bottom layer (1-2.5 mg L^{-1}, Figure 21) and a boundary thickness of 5 m, one can calculate flux of DO into the bottom layer of 0.01 to 0.02 mgO_2 L^{-1} d^{-1}. Such a process is of the correct order of magnitude to nearly balance observed rates of DO decline and projected respiratory demands summarized above. If correct, this notion provides a physical means of partially "ventilating" bottom waters without upwelling or destratification, and one which must be sensitive to primary production and maintenance of DO concentrations near the base of the photic zone.

Summary. We offer several conclusions on estimated production and metabolic budgets of the nearfield region, the most intensively monitored region of our studies.

- Substantial rates of primary production occur in western Massachusetts Bay. This conclusion is consistent with high nutrient availability as export from Boston Harbor, with patterns of DO in space and time, and with estimates of respiration.

- Variability in production over seasons and years is a function of fluctuations in surface irradiance, chlorophyll, and the clarity of the water as defined by the depth of the photic zone. Production during 1992-1994 was generally highest during summer and the fall bloom, although substantial rates can occur in a spring bloom.

- Budgets indicate that a quantitatively small role is played the benthic community in consumption of primary production. A more precise definition of the benthic role can only be accomplished with additional information on the metabolism of sandy and hard-bottom non-depositional areas of the nearfield.

- Measured rates of water column respiration decline with depth, being related to the general decline with depth of both suspended organic matter and water temperature. Tentative budgets suggest that the vast majority of the primary production of the photic layer (generally just above the pycnocline) is consumed within that same layer during the stratified season. Some organic matter may be advected out of the nearfield, but budgets suggest that perhaps only ~25-35% of primary production is consumed in underlying water or sediments.

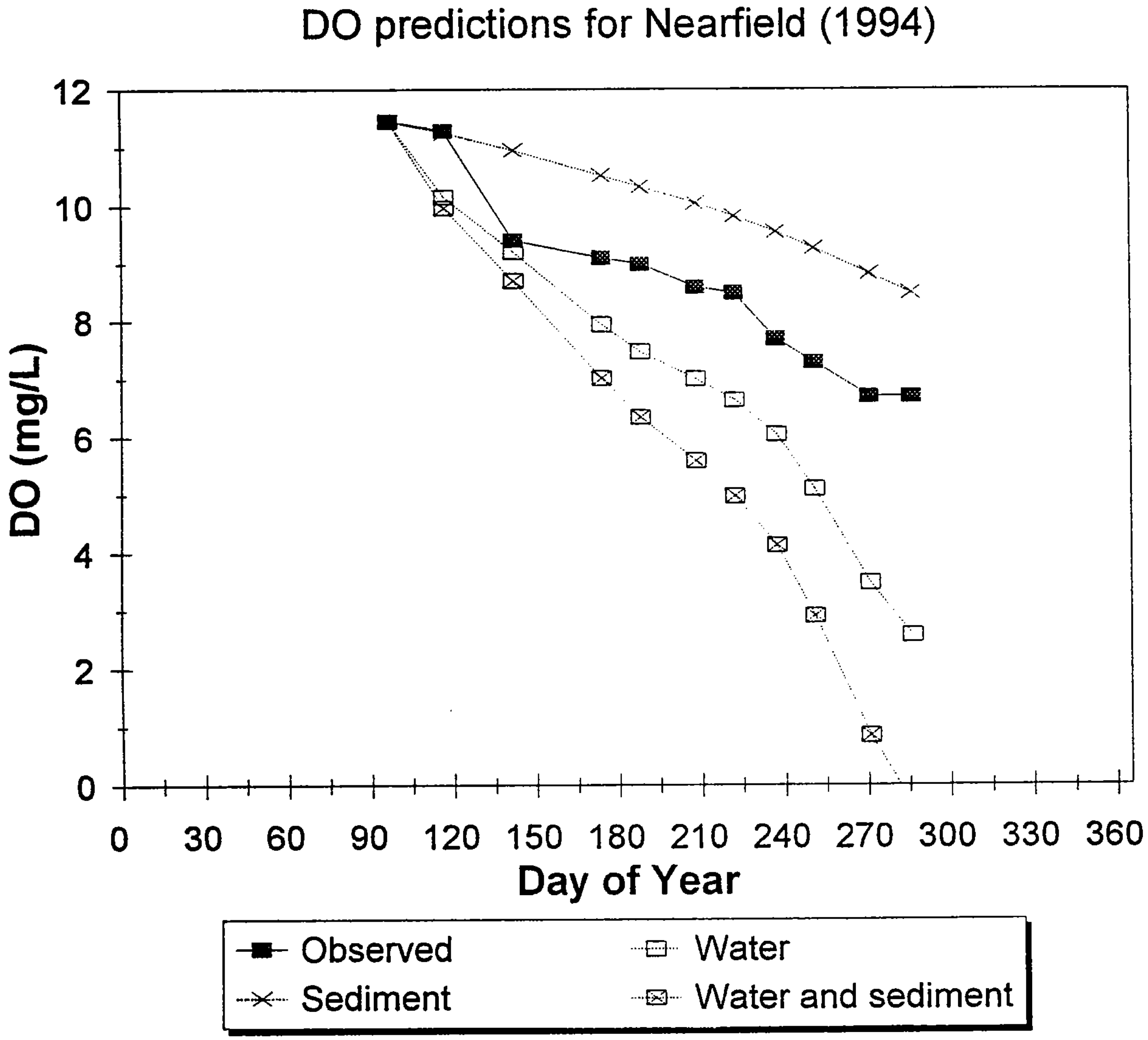

Figure 22. DO in the nearfield bottom water from April to October 1994: Comparison of observations to model projected-contributions of water and sediment respiration.

- It is presumed that the limited metabolic role for sub-pycnocline water and sediments is in part a function of generally strong and stable two-layer thermal stratification during the warm season of the year. Temperature partially regulates respiratory activity in both water and sediments. Variations in organic matter secondarily moderate temperature effects on metabolism.

- Seasonal and annual variations in bottom-water DO concentrations appear to be semi-independent of changes expected by metabolism. Consequently, it is suggested that the near-bottom environment of the nearfield modulates metabolic demands through other, presumably, physical processes.

Implications of results: recommendations for monitoring and prediction
Two major points are emphasized and supported below:

- Evidence is lacking to support the use of integrated primary production rates as the most suitable early-warning indicator for hypoxic conditions in western Massachusetts Bay. This conclusion is independent of the measurement technique. Instead, measurements of trends of DO itself generally has provided a sensitive, reliable, and economical indicator of annual DO minima.

- For broad characterization of primary production, which is still valuable information relevant to understanding fundamental functioning of the ecosystem, the use of an empirical model approach as the primary tool for estimating production has many attractive features.

A measurement of concentration or of an ecological process may be used as an indicator of specific endpoints of concern with respect to water quality, like DO concentrations. In principle, indicators should be chosen to serve specified purposes, on the basis of criteria such as signal-to-noise ratio, sensitivity and fidelity of response, economy, and ability to provide useful feedback to management options (cf. Kelly and Harwell, 1990). One intention of the monitoring program was that metabolic measures might offer an early-warning indicator of hypoxia or anoxia. The available data described here and in Kelly and Turner (1995b) provide little evidence to establish the link between variations in primary production and DO minima in bottom waters. This is not to say the two are unrelated, just that physical and biological factors involved in the linkage are complex and the majority of observed seasonal and interannual variability in DO is not easily ascribed to metabolism. To be a useful harbinger of lowered DO concentrations, the relationship between DO trends and metabolism has to be fully established. Lacking full understanding of the linkage between intended indicator and endpoint, one does not have a reliable harbinger of the endpoint of concern.

Luckily, the experience of three years of monitoring has shown that simple measurements of DO concentrations in bottom-waters in late spring/early summer offer an economical and apparently reliable early warning indicator of the annual DO concentration minima in early fall. In general, the progression of DO concentration decrease during stratification is slow and easily tracked by bi-monthly surveys. *In situ* DO measurements provide instant feedback with substantially less uncertainty than is associated with production measurements. In this case, direct measurement of the endpoint itself is possible, preferable, and easier to use since action levels are simpler to establish (indeed there are even state standards established).

It not a simple task to establish what one could consider a meaningful level of change for primary production. Variations in annual production between about 400 and 600 gC m^{-2} y^{-1} (i.e., ±50%) during the three-year baseline period seem easily distinguishable, and are within rough limits of predictability (~25%) for either production measurements or the empirical models used here. At this level of baseline variation, for example, it has been possible to distinguish between Harbor and nearfield stations within seasons and years. Analyses conducted in this study as related to the empirical model illustrated key aspects to consider in designing sampling for primary production, independent of method. For example, one should control biases that will increase uncertainties in any station-station, region-region, or year-to-year data comparisons. Therefore, care should be taken to avoid unintentional biases to cloudy or sunny days and generally recognize the strong effects of irradiance on net production estimates at daily, seasonal, and annual scales. Equally, measurements should avoid sampling bias to patches of high or low chlorophyll, for this has secondary influence on production estimates. Finally, the exercise comparing west and east sides of the nearfield illustrated that comparable integrated rates can be achieved at different levels of chlorophyll and nutrient concentrations. It suggests the possibility that some change in the underlying structure of the system can occur without changes in integrated production; many integrated ecological processes can be maintained at a given level even as the underlying species composition and component processes fluctuate. Clearly, this well-established notion of process redundancy (e.g. Schindler, 1987) is a conclusion at odds with an intended use of integrated production as a sensitive, early-warning indicator.

On the other hand, it seems fair to say that a meaningful change in the indicator must be greater than that presently detectable by the measurements because interannual differences can be established in spite of the fact that extreme years for production did not result in extreme years with respect to DO minima. Considering the problem this way, modeling production using data on light and chlorophyll from vertical profiles seems sufficient. Making ever more extensive field measurements that seek greater precision (usually at smaller and smaller, less relevant scales) seems a path not necessary to follow even if direct measurement of DO were not an option, because variability in influential features of the environment (especially light) that is greater than precision in modeling is already encountered.

Having argued the evidence presently does not support use of integrated primary production as a warning indicator, we suggest an alternate relevant purpose in the context of the monitoring program. First of all, knowing fundamental rates of carbon transfer can be helpful in examining fate and transport of organic matter and contaminants from a discharge. Moreover, it is of interest to examine some of the expected changes in the metabolic structure of the nearfield ecosystem (e.g., relationship between surface and bottom-layer metabolism), especially in the context of future delivery of effluent directly to the nearfield bottom-water layer via the offshore outfall. For example, with the offshore outfall, it is reasonable to expect less primary production in the nearfield than in the current situation (Kelly, 1993; HydroQual, 1995). It is also reasonable to presume that the vertical gradients in nutrients will be altered and the vertical distribution of primary production and water column respiration may shift, perhaps to result in greater significance of metabolism at mid-depth near the top of the thermocline. The outfall discharge may alter the thermal regimes slightly; given the sensitivity of respiration in water and sediments to temperature as suggested by the data in this summary, temperatures could affect DO (see also Kelly and Turner, 1995b). Additionally, the future situation will provide allochthonous particles (having BOD demand) delivered directly to bottom layers at rates higher than present. While projections (HydroQual, 1995) do not suggest large or widespread depression of DO from this change, one can project that the future role of the benthos in metabolism of organic matter in the system may become enhanced relative to the limited present role, and continued measurements of benthic metabolism are necessary to confirm such a response.

Towards the purpose of using metabolic measures in the monitoring program to provide fundamental metabolic understanding of the ecosystem, we argue that "indirect" estimates of production, using the BZ_pI_o approach, complimented with relatively few direct field measurements to reveal vertical patterns of production and respiration (water and sediments), will suffice for characterizing the system. This approach requires high-quality data on light, extinction, and chlorophyll, which are all relatively easy to obtain at high frequency and spatial density. It is economical and preferable to extensive field measurements which likely will never adequately cover the space and time scales of interest and, just as the indirect method, require multiple assumptions and carry large uncertainties in extrapolation.

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