Estimating phytoplankton productivity from light availability and biomass in the MERL mesocosms and Narragansett Bay

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ABSTRACT: Recent research has suggested that primary productivity in estuarine waters can be predicted as a function of phytoplankton biomass (chlorophyll a concentration) multiplied by light availability in the photic zone (photic depth times incident irradiance). The applicability of this function was confirmed using data from 1010 ^{14}C incubations (during 1978 to 1984) from 4 diverse mesocosm experiments and Narragansett Bay. For each experiment 70 to 80 % of the variation in productivity was explained by the composite function. A regression equation developed from all experiments explained 82 % of the variation in primary productivity and was not statistically different from a previously reported equation based on comparable data from 4 estuarine regions (North and South San Francisco Bay, Puget Sound, and New York Bight). Phytoplankton production was correlated with biomass alone on a seasonal basis (summer, $r = 0.87$; non-summer, $r = 0.77$), with chlorophyll-specific productivity higher during summer (June to September) than non-summer (October to May). The decline in the slope of the relation between production and biomass during non-summer periods corresponded to the seasonal switch from summer dominance by nanoplankton (primarily flagellates) to non-summer dominance by net plankton (primarily diatoms) and coincided with decreased light availability in the photic zone. Annual productivity was also highly correlated with the mean annual product of chlorophyll a, photic depth and incident light ($r = 0.96$).

INTRODUCTION

Attempts to determine the causal factors of temporal and spatial variability in estuarine phytoplankton productivity have focused primarily on nutrient or light availability (Riley 1967, Takahashi et al. 1973, Cadée & Hegeman 1974, Malone 1976). Despite considerable effort it has not been possible to generalize about the relation between nutrient concentration and productivity (Boynton et al. 1982, Nixon & Pilson 1983, Cole & Cloern 1984). Part of the problem is due to the general availability of nutrients in estuaries. When nutrient levels exceed growth-limiting concentrations, short-term rates of phytoplankton growth as measured by ^{14}C uptake may appear independent of inorganic nutrient concentration (Nixon et al. 1986). Additionally, internal storage and rapid cycling and regeneration of nutrients may obscure a quantitative relationship when ambient nutrient concentration is used as an index of nutrient availability. High rates of production may then occur when measured

nutrient concentrations are low. Because of these problems, no quantitative formulation describing a relation between nutrient concentration and primary productivity has been proposed for estuaries.

In turbid estuaries, biomass-specific production rates have long been associated with light (Flemer 1970, Malone 1976, Cadée 1978, Joint & Pomroy 1981). More recently, researchers have shown that much of the variability in phytoplankton production is highly correlated with a composite factor, the product of phytoplankton biomass and light availability (Falkowski 1981, Cole & Cloern 1984, 1987, Harding et al. 1986, Pennock & Sharp 1986). Experimental work in large-scale mesocosms at the Marine Ecosystem Research Laboratory (MERL) has concomittently established a strong linear relationship between nutrient loading level and phytoplankton biomass (Nixon & Pilson 1983, Nixon et al. 1984, 1986, Keller 1987a). Given this relationship, the predictive ability of an empirical model including both light availability and biomass is not

surprising. Phytoplankton biomass, measured as chlorophyll a, indirectly incorporates the effects of nutrient uptake rates, variations in growth rates, and community composition in the model.

Cole & Cloern (1987) showed that a single empirical function could be used to estimate productivity along gradients of phytoplankton biomass and turbidity in 4 estuarine systems. In this paper, I extend their approach using data from the MERL mesocosms and Narragansett Bay, Rhode Island, USA. A portion of these data were previously described using a somewhat different formulation (Keller 1986). I demonstrate here that a single equation successfully describes the relationship between primary productivity and Cole & Cloern's composite factor for the mesocosms and Bay over the annual cycle. By contrast, a relationship between productivity and chlorophyll a alone varied seasonally. In the absence of light or light extinction data, chlorophyll a is an adequate predictor of productivity on a seasonal basis. The seasonal difference in the relationship between rate of primary production and biomass coincides with a major change in phytoplankton species composition. The absence of seasonality when light was included in the analysis is discussed and implies a relationship between increased production per unit chlorophyll a and high light levels for nanoplankton. Finally, the correlation between yearly productivity and mean annual chlorophyll a multiplied by photic depth and light is also explored.

METHODS

The data used in the analysis (Table 1) were collected over a wide range of polluted and nutrient-enriched conditions in well-mixed, flow-through mesocosms and Narragansett Bay at the Graduate School of Oceanography (GSO Dock) station, USA. The control systems were designed to have regimes of temperature, mixing, turnover and light similar to relatively clean northeastern USA estuaries with no major sewage inputs (Pilson et al. 1979).

Phytoplankton biomass. At weekly intervals replicate chlorophyll a (mg m^{-3}) levels were measured (Strickland & Parsons 1972) from 10 ml aliquots of water collected at 0.1, 2.5 and 4.5 m from each mesocosm during the morning mixing cycle and the Bay. Samples were filtered onto 25 mm Whatman GF/F (or Gelman A/E) glass fiber filters, frozen and extracted within 2 wk using 90 % acetone. Precision was ± 5.0 %. For these well-mixed systems, chlorophyll a was assumed to be evenly distributed throughout the photic zone.

Light and light attenuation. Hourly light (Einst. m^{-2} h^{-1}) and daily light (Einst. m^{-2} d^{-1}) (photosynthetically active radiation, PAR 400 to 700 nm) were measured using LI-COR, LI-190S quantum sensors. Light attenuation coefficients (k, m^{-1}) were derived from data collected using a cosine-corrected LI-COR, LI-192S quantum sensor. The depth of the photic zone (depth of 1 % light) was calculated as $Z_p = 4.61/k$.

Productivity. Primary productivity was measured (weekly and fortnightly) using the ^{14}C method (Almquist 1983). Water samples were collected at 0.1, 2.5 and 4.5 m from the Bay and each mesocosm during the morning mixing cycle. Water collected from the 3 depths was pooled, then for each tank and the Bay, 5 light and 1 dark bottles were filled with samples and inoculated with 1 μCi of [^{14}C]HCO$_3$ solution (New England Nuclear). Glass bottles (60 ml) were used for sample incubation during the first 2 experiments and polypropylene bottles (85 ml) were used during the

Table 1. Mesocosm experiments 1978 to 1984. Each experiment incorporated 9 mesocosms, generally with 6 experimental systems and 3 controls, as well as Narragansett Bay

Experiment	Duration	Data collection schedule	Experiment description
Oil addition and recovery[a]	Mar 1978 –Jul 1978 Jul 1978 –Jul 1979	Fortnightly	Oviatt et al. (1982)
Sediment gradient[b]	Aug 1979–Apr 1981	Fortnightly	Oviatt et al. (1984)
Nutrient addition[c]	Jun 1981 –Sep 1983	Fortnightly	Oviatt et al. (1986)
Nutrient and sludge addition[d]	Jun 1984 –Sep 1984	Weekly	Oviatt et al. (1987)

[a] Twice weekly addition of No. 2 fuel oil to 3 mesocosms to maintain an average concentration of 90 ppb followed by recovery after long-term addition. Three additional mesocosms run primarily as controls with occasional short-term experiments

[b] Effects of 3 sediment sources (in triplicate) representing the pollution gradient in Narragansett Bay on water columns which originated from the same clean source (mid-Bay sediments = controls)

[c] Daily nutrient additions of NH$_4$Cl, KH$_2$PO$_4$ and NaSiO$_3$ (molar ratio, 12.8N : 1.0P : 0.91Si) in a logarithmic series (1×, 2×, 4×, 8×, 16×, 32×) to 6 mesocosms with the 1× loading level (2.88 mmol N m^{-2} d^{-1}, 0.23 mmol P m^{-2} d^{-1}, 0.19 mmol Si m^{-2} d^{-1}) representing the average daily sewage derived input to Narragansett Bay

[d] Daily nutrient additions (as above) of 1×, 4× and 8× to 3 mesocosms and sewage sludge additions with comparable levels of nitrogen (1×, 4×, 8×) to 3 additional mesocosms

latter two. The bottles were incubated in their respective mesocosms at 0.1, 0.5, 1.0, 2.5, and 4.5 m with the dark bottle at 4.5 m. Bay samples were incubated in a control mesocosm.

From March 1978 through May 1981 samples were incubated for 24 h from midmorning to midmorning. From June 1981, samples were incubated for 4 h around noon. After incubation samples were filtered through 25 mm Whatman GF/F (or Gelman A/E) glass fiber filters at < 125 mm Hg. Filters were rinsed twice with 20 ml filtered seawater to remove residual inorganic ^{14}C and placed in vials to which 3.5 or 10 ml scintillation fluid was then added depending on vial size. Samples were shaken for 3 h to aid penetration of the filters and to allow degassing of inorganic ^{14}C. Samples were then placed in the scintillation counter and counted after an 8 h dark-adaptation period.

Primary productivity at each depth was calculated following Strickland & Parsons (1972) and converted to integral productivity over the photic zone by numerically integrating (trapezoidal rule) these values over the photic depth (up top 5 m). Precision of bottle values was ± 10 %.

Hourly productivity measurements (June 1981 to September 1984) were converted to daily values by fitting the measured hourly rates and light data to the hyperbolic tangent equation (Platt & Jassby 1976):

$$P_z = P_m \tanh (\alpha I_z/P_m) \qquad (1)$$

where P_z = measured hourly productivity at each of 5 depths (mg C m^{-3} h^{-1}); I_z = light available at each depth (Einst. m^{-2} h^{-1}); P_m = maximum hourly production rate (mg C m^{-3} h^{-1}); and α = initial slope of the photosynthesis-light curve (mg C $Einst.^{-1}$ m^{-1}). Eq. (1) was appropriate for fitting the data since photoinhibition was rarely observed during the MERL experiments. Using the fitted parameters (P_m and α), the measured hourly PAR, and the attenuation coefficients, hourly production rates (P_z) were calculated for each hour of the day, integrated over the photic depth (P_h, mg C m^{-2} h^{-1}) and summed to give daily rates (P_d, mg C m^{-2} d^{-1}).

Model-derived daily productivity estimates approximate gross productivity since they were based on short-term ^{14}C incubations (Harrison et al. 1985) and do not account for night-time respiratory loss. Comparison of

Table 2. Linear regression analyses of productivity (P_d, mg C m^{-2} d^{-1}) versus the composite variable ($B Z_p I_o$) for Narragansett Bay, the controls, and treatment mesocosms from the individual MERL experiments, March 1978 to September 1984; m: slope; b: intercept

Experiment	m (± SE)	b (± SE)	r^2	n
Oil addition and recovery				
Bay	0.98 (0.12)	230 (102)	0.64	28
Controls	0.81 (0.05)	194 (35)	0.66	132
Treatments	0.70 (0.05)	369 (53)	0.69	82
Sediment gradient				
Bay	1.04 (0.09)	97 (49)	0.78	41
Controls	0.93 (0.07)	83 (28)	0.58	134
Treatments	0.99 (0.04)	37 (20)	0.72	268
Nutrient addition				
Controls	0.66 (0.05)	109 (28)	0.81	75
Treatments	0.66 (0.04)	454 (91)	0.81	151
Nutrient and sludge addition				
Controls	0.87 (0.14)	269 (120)	0.66	33
Treatments	0.66 (0.04)	325 (69)	0.83	66

Table 3. Linear regression analyses of productivity (P_d, mg C m^{-2} d^{-1}) versus the composite variable ($B Z_p I_o$) for the individual and combined MERL experiments, March 1978 to September 1984; m: slope; b: intercept

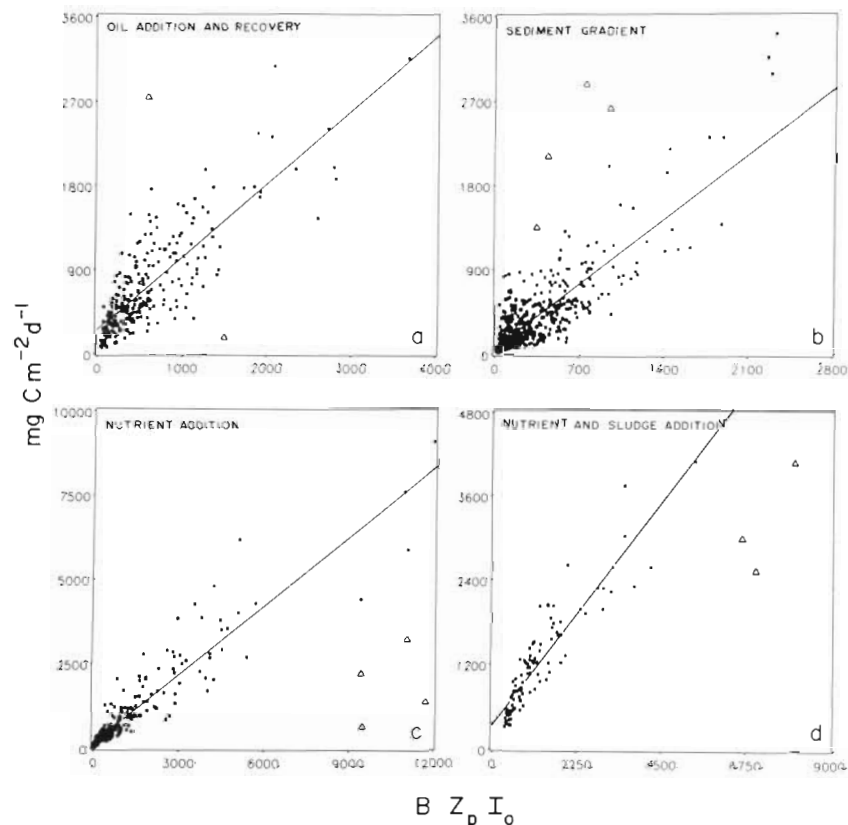| Experiment	m (± SE)	b (± SE)	r^2	n
Oil addition and recovery	0.78 (0.04)	254 (29)	0.67	242
Sediment gradient	0.98 (0.06)	55 (15)	0.70	443
Nutrient addition	0.66 (0.04)	235 (43)	0.81	226
Nutrient and sludge addition	0.85 (0.05)	282 (60)	0.82	99
Pooled experiments and Bay	0.70 (0.02)	220 (12)	0.82	1010

Fig. 1. Regression of daily primary productivity versus a composite variable (BZ_pI_o) for each of the 4 MERL experiments described in Table 1: (a) oil addition and recovery experiment, (b) sediment gradient experiment, (c) nutrient addition experiment, (d) nutrient and sludge addition experiment. ($\triangle$) Points not included in analysis (see text)

measured 24 h incubations with sequential short-term incubations over the daylight period suggested that 10 to 40 % of the daytime production was respired at night (Bender et al. 1987, Keller unpubl.) for the MERL mesocosms.

Differences thus exist between the modeled daily production rates and the measured 24 h rates. To compare data collected during different experiments, the 24 h measurements were converted to daytime rates by assuming that the night-time respiration rate was 25 % of the measured rate of production. For each experiment, daily productivity integrated over the photic depth (P_d, mg C m^{-2} d^{-1}) was then regressed against the composite function (BZ_pI_o) derived by Cole & Cloern (1987) where B is phytoplankton biomass (mg chlorophyll a m^{-3}), Z_p the photic zone depth (m) and I_o surface irradiance (Einst. m^{-2} d^{-1}).

RESULTS

Composite function

The relationship between photic zone productivity and Cole & Cloern's (1987) composite function BZ_pI_o was examined by least-squares linear regression techniques. Highly significant linear relations (p < 0.001) were found for all mesocosms and Narragansett Bay over the period studied (1978 to 1984). These relations were relatively consistent between the Bay, controls and treatment mesocosms for the individual experiments as demonstrated by the regression parameters and their error terms (Table 2).

For each of the 4 experiments, the data from the Bay water experiments, control and treatment mesocosms were pooled and the results from the 4 experimental periods compared (Fig. 1). The intercepts and slopes for the regression equations for the 4 experiments (Table 3) were generally not significantly different at the 95 % level of confidence. Despite the wide range of experimental conditions (oil addition, sediment sources, nutrient addition, sludge addition) and interannual variability, a single empirical function can be used to estimate phytoplankton production. Based on 1010 ^{14}C incubations, 82 % of the variation in photic zone productivity was explained by the composite variable BZ_pI_o using the equation:

$$P_d = 220 + 0.70 \ BZ_pI_o \tag{2}$$

Biomass

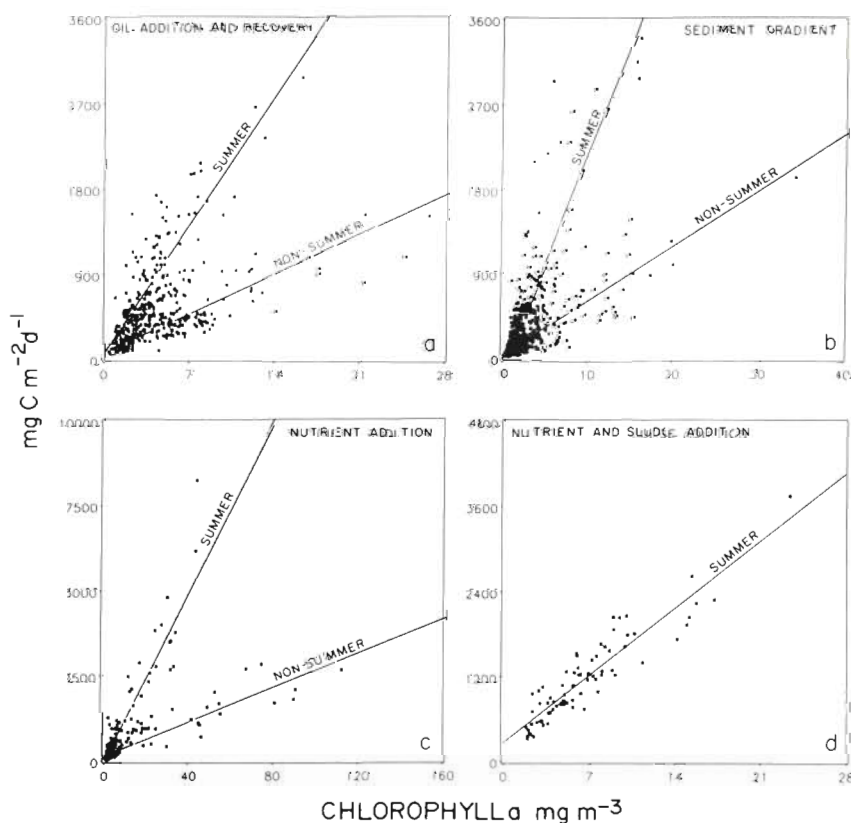The relation between productivity integrated over the water column and phytoplankton biomass meas-

Fig. 2. Seasonal regression of daily primary productivity versus phytoplankton biomass (measured as chlorophyll a) for (a) oil addition and recovery experiment, (b) sediment gradient experiment, (c) nutrient addition experiment, and (d) nutrient and sludge addition experiment. The 4×, 8×, 16×, and 32× treatments were excluded from the non-summer regression for the nutrient addition experiment and the 8× nutrient and 8× sludge addition mesocosms were excluded from the nutrient and sludge addition experiment (summer only)

ured as chlorophyll a for experiments longer than an annual cycle revealed significant seasonal differences (Fig. 2). These differences were not evident in the data collected during the short-term (4 mo) nutrient-sludge addition experiment conducted during the summer in 1984. Subsequently, the data for the remaining 3 experiments were separated into summer (June to September) and non-summer (October to May) periods and analyzed using regression techniques.

For each experiment, individual regressions were calculated for each mesocosm and Narragansett Bay during the summer and non-summer periods (data not shown). In most cases, the seasonal regression equations for the individual mesocosms and Narragansett Bay were not significantly different within experiments. However, during the non-summer period of the nutrient addition experiment, the regression slopes for data from high level nutrient addition mesocosms (4×, 8×, 16× and 32×)

Table 4. Linear regression analyses of production (P_d, mg C m^{-2} d^{-1}) versus phytoplankton biomass (B, mg chl a m^{-3}) for the individual and combined MERL experiments. Data are separated by period, with summer being June to September and non-summer being October to May; m: slope; b: intercept

Period	Experiment	m ($\pm$ SE)	b ($\pm$ SE)	r^2	n
Summer	Oil addition and recovery	172.0 (9.8)	192.2 (42.7)	0.67	153
	Sediment gradient	196.4 (7.9)	45.2 (27.6)	0.81	137
	Nutrient addition	124.3 (6.2)	67.3 (85.8)	0.82	107
	Nutrient and sludge addition[a]	135.1 (6.6)	279.5 (50.7)	0.85	77
	Pooled[a]	125.2 (3.2)	253.0 (24.4)	0.76	459
Non-summer	Oil addition and recovery	47.4 (2.5)	153.1 (15.6)	0.63	215
	Sediment gradient	54.1 (2.7)	100.2 (13.9)	0.56	311
	Nutrient-addition[b]	53.9 (4.0)	24.4 (23.9)	0.82	40
	Pooled[b]	52.7 (1.8)	116.3 (10.4)	0.60	566

[a] Highest level nutrient (8×) and sludge (8×) treatments excluded
[b] Upper level nutrient (4×, 8×, 16×, 32×) treatments excluded

were significantly lower than the controls and low level nutrient treatments (1× and 2×). Also, during the nutrient-sludge addition experiment (summer only) the slopes of the regressions between productivity and chlorophyll a in the 8× nutrient and 8× sludge treatments were significantly lower than the other treatments.

After excluding the noted exceptions, for each experiment the data from the individual mesocosms and the Bay were pooled and analyzed seasonally (Table 4). There was a distinct seasonal shift in the productivity-to-biomass relation with the slope of the regression equations significantly higher in the summer than the non-summer period. A single regression was developed for each period (summer versus non-summer). During the summer, chlorophyll a accounted for 76 % of the variation in primary productivity, while during the non-summer period 60 % of the variation in productivity could be explained as a function of biomass (Table 4).

Annual production

Yearly primary production (P_y, g C m^{-2} yr^{-1}) was calculated by integrating the measured production values over an annual cycle. Estimates of annual productivity in the control mesocosms and GSO Dock station in Narragansett Bay varied by a factor of 2 within years (Table 5). Between years, annual productivity in these systems varied by a factor of 3, ranging from a low of 82 g C m^{-2} yr^{-1} to a high of 273 g C m^{-2} yr^{-1}. Estimated productivity in the control tanks and Bay averaged 155 g C m^{-2} yr^{-1} for the 1978 to 1983 period.

Yearly productivity (P_y) was regressed against annual mean values of $B Z_p I_0$ for the mesocosms and the Bay over the 1978 to 1983 period (Fig. 3). The resulting equation:

$$P_y = 25 \ (\pm \ 10) + 0.30 \ (\pm \ 0.02) \tag{3}$$

with $n = 32$ was highly significant ($p < 0.001$) and accounted for 92 % of the variation in annual production. The values in parentheses are the standard errors for the regression parameters.

DISCUSSION

Composite factor

Cole & Cloern (1987) demonstrated a strong linear correlation between integral productivity and $B Z_p I_0$ for 7 estuarine regions. Similarly good correlations between phytoplankton productivity and biomass coupled with light availability were reported by Falkowski (1981) and Cole & Cloern (1984). The general applicability of this relationship was confirmed here using an
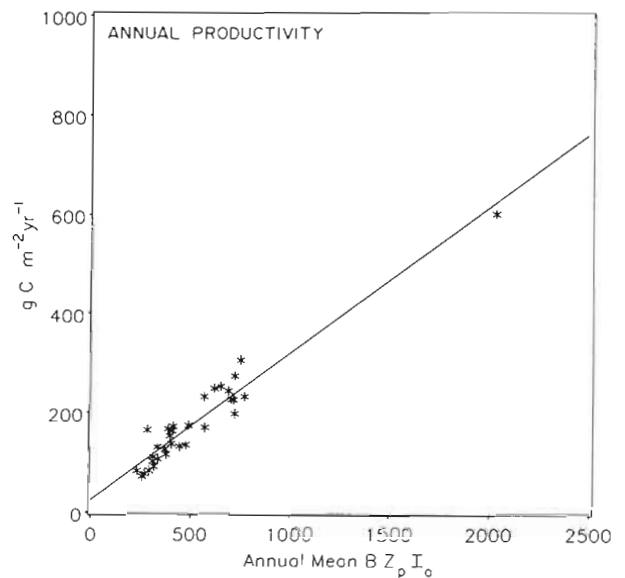
Fig. 3. Annual water column productivity plotted as a function of mean annual $B Z_p I_0$ for the MERL mesocosms and Narragansett Bay (GSO Dock Station). The annual periods are listed in Table 5

extensive data set from Narragansett Bay and the MERL experimental ecosystems. For the wide range of experimental conditions encountered over the study period, the slopes of the equations relating productivity to $B Z_p I_0$ varied remarkably little (0.66 to 1.04) and did not differ seasonally (summer versus non-summer). Cole & Cloern (1987), using data with similar units of

Table 5. Annual productivity (P_y, g C m^{-2} yr^{-1}) for the control mesocosms and Narragansett Bay (GSO Dock Station). Numbers in parentheses are Julian dates (e.g. 78045 = Day 45 of 1978)

Tank	1978 (78045–79044)	1979 (79001–79365)	1980 (80001–80365)	1982–83 (82181–83180)
1	134	173	110	82[a]
5	273	231	82	121
8	131	166	162	121
Bay	250	164	152	98

[a] Tank 0

measurement, reported a range in slope of 0.67 to 1.14 for 4 independent studies while Platt (1986) found a similarly small range in slope for the regression of biomass specific productivity on I_o over a wide range of oceanic waters. Frequently, the intercepts of these equations are not significantly different from 0.

In the above cases, greater than 80 % of the variability in productivity was commonly explained by variation in the composite parameter. The consistency of these results confirms that much of the large-scale variation in productivity in nutrient-rich estuaries can be explained as a function of phytoplankton biomass and light availability.

Incubation length

The principal problem encountered in considering the mesocosm experiments as a single data set was adjusting 24 h ^{14}C incubations to approximate daytime measurements derived from 4 h incubations. The 4 h incubations used for the model were considered to estimate gross daytime productivity (Davies & Williams 1984, Harrison et al. 1985, Bower et al. 1987) since not much respiratory loss of fixed ^{14}C occurs until the dark period.

Cole & Cloern (1987) included both 24 h ^{14}C incubations and half-day (noon to sunset) incubations in their composite data set. They made no attempt to account for night-time respiration. However, their Fig. 2 suggested that the half-day incubations (adjusted by a factor of 2 to give daytime measurements) from Puget Sound are important in controlling the slope of the final regression equation for the assembled data set. For comparison with their equation, I adjusted the 24 h values to daytime production measurements rather than vice versa. Their final equation for 211 incubation experiments using pooled data from San Francisco Bay, Puget Sound and the Hudson River Plume:

$$P = 150 + 0.73\, B Z_p I_o \tag{4}$$

is very similar to the final equation for pooled data over all experiments ($N = 1010$) seen in the above analysis (Table 3). When no adjustments are made for respiration, the slope of the mesocosm regression for 24 h production versus $B Z_p I_o$ is lower (0.63 ± 0.03). Thus the length of the ^{14}C incubation should be considered in comparing the results since daytime measurements may approximate gross primary production while 24 h measurements may be closer to net (Peterson 1980).

Model considerations

Given the wide range of experimental conditions, the close agreement in regression equations emphasizes the general applicability of this empirical approach to predicting productivity in other estuaries with similar properties and behavior. As suggested by Cole & Cloern (1987) the technique will allow increased temporal and spatial coverage of productivity in diverse estuarine systems. After calibration by a few measures of productivity, large-scale surveys of the more readily measured chlorophyll a and light availability should improve our knowledge of productivity throughout an estuary.

In all experiments, a few data points deviated widely from the observed relation (Fig. 1). Although these points are shown in the figures they were not included in the regression analysis. During the nutrient addition experiment (Fig. 2c), abnormally low levels of measured versus predicted productivity were confined to the higher level (16× and 32×) treatment mesocosms. Nutrient limitation was not a problem in these measurements. The low productivity was traced to dense algal growth on the outside of incubation bottles lowering light availability. In other instances over- or underprediction of productivity might be measurement error, nutrient limitation, toxicity effects or high assimilation rates. Deviations from predicted values might indicate when factors other than biomass and light are important in controlling productivity (Cole & Cloern 1987).

Table 6. Annual primary productivity (P_y, g C m^{-2} yr^{-1}) for selected estuaries and coastal regions of the USA

Area		P_y	Source
Narragansett Bay	Mid-Bay	308	Furnas et al. 1976
	GSO Dock	221	Oviatt et al. 1981
	GSO Dock	189	This study
Hudson Estuary	Bight	370	Malone 1976
	Lower Bay	200	Malone 1977
Chesapeake Bay	Mid-Bay	335–780	Boynton et al. 1982
Delaware Bay		190–400	Pennock & Sharp 1986
San Francisco Bay		95–150	Cole & Cloern 1984

Biomass

For the MERL mesocosms and Narragansett Bay, the relationship between primary productivity and chlorophyll a alone showed a marked seasonal difference. Productivity and chlorophyll a were significantly correlated ($p < 0.01$) during both summer ($r = 0.87$) and non-summer ($r = 0.77$) periods. For each experiment, and overall, chlorophyll-specific production rate (slope of the regression line) was significantly higher during the summer compared with the non-summer period by a factor of ca 2.5.

Chlorophyll a has been considered a poor indicator of phytoplankton productivity over a wide range of environmental conditions or aquatic environments (Cadée & Hegeman 1974, Boynton et al. 1982, Cole & Cloern 1984, Côté & Platt 1984). And yet, within specific embayments in San Francisco Bay, Cole & Cloern (1984) found good correlations ($r = 0.53$ to 0.92) between production and chlorophyll a. Malone et al. (1986) reported similarly high correlations ($r = 0.97$ to 0.98) for distinct geographic areas within Chesapeake Bay. Côté & Platt (1983) noted shifts in the relation between maximum phytoplankton production rates and chlorophyll a which correlated with major changes in phytoplankton species composition. Pennock & Sharp (1986) showed a marked seasonal change in the relation between productivity and a variable composed of biomass and light availability, with the slope of the relation being greater during the summer. They attributed this shift to either periodic nutrient limitation, zooplankton grazing or changes in species composition from diatoms to nanoplankton.

In the mesocosms and Narragansett Bay, the increase in the slope of the equation relating primary productivity to biomass corresponded with the change in species composition from net plankton (primarily diatoms) to nanoplankton (primarily flagellates) (Pratt 1959, Durbin et al. 1975, Furnas et al. 1976). In Narragansett Bay, the nanoplankton ($< 20 \mu m$) are most important during the summer when over 75 % of the chlorophyll a is in this size class (Durbin et al. 1975). During this period the productivity-to-chlorophyll a ratios (slope of regression, Table 4) were significantly higher than the non-summer periods when net plankton dominate. These results, thus, support the basic hypothesis that small cells have higher rates of productivity per unit chlorophyll a than do large cells.

Durbin et al. (1975) suggest that dominance of nanoplankton during the summer in Narragansett Bay is favored by the high temperatures and low nutrient levels present at that time, while Furnas et al. (1976) suggest that the summer phytoplankton dynamics in the Bay are primarily influenced by nutrient regulation and grazing. The data presented here show a signifi-

cant increase in the productivity-to-chlorophyll a ratio during the summer when nanoplankton predominate. There was no significant difference in the production to $B Z_p I_o$ relationship on a seasonal basis. Since the average photic depths were greater in the summer than the non-summer periods, the higher slope for the nanoplankton-dominated community might be due to increased ambient light level.

Bruno et al. (1983) found no significant differences for productivity per unit chlorophyll a between net plankton and nanoplankton fractions during periods of clear dominance of either size fraction. They noted, however, that their net plankton could really be considered nanoplankton if chain length were ignored. Malone (1980) indicated that both high temperature and light were important in the observed seasonal differences in production efficiencies between size fractions in estuaries during summer. The mesocosm and Bay data suggest that high ambient light is a major factor controlling the production to biomass ratio ($P : B$) for summer phytoplankton (primarily nanoplankton) populations. However, the importance of temperature in controlling $P : B$ cannot be ruled out since temperature and light were significantly correlated ($r = 0.59$, $p < 0.001$) on an annual basis.

Twice, regressions from individual mesocosms had slopes which were significantly lower than expected relative to the overall seasonal regressions (Table 4). In both cases these were high nutrient concentration or sludge treatment tanks. As noted previously, low rates of primary production were occasionally found in mesocosms with high nutrient concentrations, and are believed to be due to shading caused by algal growth on the outside of the incubation bottles. The phytoplankton in these mesocosms may have had changes in their size and/or species composition. Sanders et al. (1987) reported large changes in dominant phytoplankton species and patterns of succession during nutrient enrichment experiments in the Patuxent River, Chesapeake Bay, USA. They concluded that nutrient enrichment promoted diatom dominance particularly during the summer and early fall.

No increase in total diatom abundance (in the $> 10 \mu m$ size fraction) was noted in the upper level sludge and nutrient treatment tanks during summer 1984 (Keller 1987b). However, these mesocosms had higher abundances of dinoflagellates than the controls and lower level treatments (Keller 1987b). In the highest level nutrient treatment tank 32 % of phytoplankton biomass (measured as in vivo fluorescence) was in the $> 10 \mu m$ size fraction compared with 18 % in mesocosms with low nutrient concentrations. The alterations in species composition and size distribution, away from the expected summer dominance by small phytoplankton (Durbin et al. 1975) with high productivity (Furnas et al.

1976), may thus explain the observed decrease in chlorophyll *a* specific production rates in these upper level treatment mesocosms.

Annual productivity

The range in annual productivity (Table 5) for the control mesocosms and Narragansett Bay is at the mid- to lower range of values reported for other estuaries (Table 6) but represents a single location in lower Narragansett Bay. Furnas et al. (1976) estimated annual productivity for a mid-Narragansett Bay station as 308 g C m^{-2} yr^{-1}. Oviatt et al. (1981) noted a decreasing down-Bay gradient in primary productivity with the lowest values in the West Passage of Narragansett Bay at the GSO Dock station.

Annual values of productivity for the mesocosms and Bay during the experimental period (1978 to 1983) were highly correlated with mean annual values of $B Z_p I_o$. Smayda (1983) attributed variation in productivity between years to variation in insolation. The data presented here demonstrate that variability in annual productivity is due not only to light but also to annual variations in the mean values of biomass and photic zone depth. Mean annual $B Z_p I_o$ may prove useful for estimating annual productivity, with a minimum expenditure of effort, for estuarine systems.

In summary, the mesocosm results and Narragansett Bay data lend considerable support to the empirical model proposed by Cole & Cloern (1987) for predicting primary productivity in estuaries. The success of the approach is tied to the indirect incorporation of nutrient loading, growth rate, grazing rate, sinking and many associated processes in the model through biomass combined with the importance of light availability in controlling productivity in these turbid environments. The relationship was consistent over the annual cycle. On a seasonal basis, production was seen to be highly correlated with biomass alone measured as chlorophyll *a* concentration. The decline in chlorophyll-specific production rate during the non-summer period coincided with the switch in predominance from primarily nanoplankton (flagellates) during the summer to primary net plankton (diatoms) during the rest of the year and also coincided with decreased irradiance. Annual levels of primary productivity in the control mesocosms and lower Narragansett Bay were comparable and at the mid to lower range of values reported for other estuarine systems. Yearly production for all mesocosms and the Bay was highly correlated ($p < 0.001$) with mean annual $B Z_p I_o$.

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