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**Alexander E. Parker, Wim J. Kimmerer
& Ulrika U. Lidström**

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Alexander E. Parker · Wim J. Kimmerer ·
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Abstract Depth-integrated primary production (ΣP , in grams of carbon per square meter per day) was measured using ^{14}C in the northern San Francisco Estuary (SFE) from March through August of 2006 and 2007. Determinations of ΣP were then used to calibrate a published light-utilization model that relates ΣP to a composite parameter of chlorophyll, solar irradiance, and photic zone depth. The resultant calibration coefficient, ψ , varied by a factor of nearly two between 2006 and 2007 and was lower than determined in previous calibrations for the estuary. The now chronically low chlorophyll concentrations in the SFE have resulted in lower predictive power of the light-utilization model. The variation in ψ was likely the result of interannual variation in phytoplankton assimilation number. These results suggest that using a single ψ may yield large errors in estimated estuarine production when applied over-broad spatial and temporal scales. Given the food-limited condition of the SFE, it appears that direct measurements of primary production are necessary for accurately characterizing the base of the estuarine food web.

Keywords Primary production · Light-utilization model · San Francisco Estuary · Assimilation number · Carbon/chlorophyll

Introduction

Quantifying primary productivity is fundamental to understanding estuaries, which are considered among the most

productive marine ecosystems. For the past several decades, one approach used for estimating estuarine pelagic primary production has relied on empirical models of light-limited primary production based on variables that are more easily measured than either oxygen production (Gaarder and Gran 1927) or ^{14}C -labeled tracer bicarbonate uptake (Steemann Nielsen 1952). The “light-utilization” productivity model (Harding et al. 2002), developed during the 1980s for the light-limited San Francisco Estuary (SFE), provides estimates of depth-integrated primary production from measurements of chlorophyll, daily photosynthetically active radiation (PAR), and water column light attenuation (Cole and Cloern 1984). The original SFE model calibration was subsequently shown to be generally applicable to several light-limited estuaries (Cole and Cloern 1987) and invariant with time in the SFE (Alpine and Cloern 1992; Jassby et al. 2002). As a result, the model is routinely applied using data from water quality monitoring as a means of evaluating changes to the primary production cycle in the SFE and for comparison with other estuaries (Cole and Cloern 1987; Kimmerer 2005).

While the basic formulation of the light-utilization productivity model provides reasonable primary production estimates, model limitations, including those highlighted by its original authors (Cole and Cloern 1984, 1987), must be considered before relying solely on this approach for estimating estuarine productivity. One major limitation is that the model provides no information about the light physiology of the phytoplankton and relies on the assumption that it does not change in any meaningful way over space or time. Yet, physiological condition can vary with phytoplankton species composition (Tang 1997), solar irradiance, water temperature (Geider et al. 1986), nutrients (Falkowski and Raven 2002), contaminants (Cole and Cloern 1987), and probably other environmental variables.

A. E. Parker (✉) · W. J. Kimmerer · U. U. Lidström
 Romberg Tiburon Center, San Francisco State University,
 3152 Paradise Drive,
 Tiburon, CA 94920, USA
 e-mail: aeparker@sfsu.edu

Thus, care must be taken when interpreting primary production based on this model approach, and its use through time and across space requires periodic recalibration of the equation used to convert the proxy measurements to primary productivity rates. This may be especially true for systems known to be undergoing change in environmental condition or species composition.

Since development and initial calibration of the light-utilization model for the SFE, biomass and community structure of the phytoplankton have changed and water transparency has increased. At the time of the original model calibration, Suisun Bay, in the northern SFE, was characterized by low phytoplankton growth rates but high ($\sim 60 \mu\text{g}$ chlorophyll L^{-1}) summer phytoplankton biomass dominated by diatoms (Cloern 1979; Cole and Cloern 1984). In 1987 the invasive clam *Corbula amurensis* spread throughout the northern estuary, with grazing rates estimated to exceed phytoplankton growth (Alpine and Cloern 1992). Clam grazing is thought to have driven an abrupt decline in chlorophyll (now typically ~ 3 to $4 \mu\text{g}$ L^{-1}) in Suisun Bay; summer diatom blooms are now absent (Wilkerson et al. 2006), and summer silicic acid uptake, indicative of diatom production, is indistinguishable from zero (Kimmerer 2005). Smaller autotrophs including flagellates and cyanobacteria now appear to dominate the autotrophic community (Lehman 2000; Glibert et al. 2011). Phytoplankton community structure was likely altered via size-selective grazing by the clams (Werner and Hollibaugh 1993) although additional drivers, including pesticides (Brooks et al. 2012), changing nitrogen-to-phosphorus ratio (Glibert et al. 2011), and increased ammonium loads (Dugdale et al. 2007; Glibert et al. 2011; Parker et al. 2012) have also been implicated. At the same time, reduced sediment loads to the northern SFE, a consequence of damming upstream tributaries (Jassby 2008; Schoellhamer 2011) has resulted in increased water transparency and more favorable conditions for phytoplankton growth.

As part of a comprehensive 2-year study of food web structure and function in the northern SFE, we conducted surveys of primary production and phytoplankton abundance during the spring and summer of 2006 and 2007. A companion paper describes the temporal patterns of productivity and related variables (Kimmerer et al. 2012). Here we evaluate the light-utilization model and the generality of its calibration for the northern SFE with the goal of determining whether the model remains a robust approach for estimating estuarine production following the many changes to the system. Specifically, given the low chlorophyll conditions, we asked whether the model calibration developed during the 1980s is still accurate. Our hypothesis is that the changes in the phytoplankton physiological condition and community structure since the earlier studies should be reflected in changes in the model calibration efficiency factor ψ .

Methods

During 2006 and 2007, phytoplankton biomass, primary production, and water column light attenuation were measured from March through August in the northern SFE (Fig. 1). A detailed description of sampling design is provided in Kimmerer et al. (2012). Briefly, samples were collected weekly in 2006 and biweekly to weekly in 2007 from the Research Vessel *Questuary* at three stations during each cruise. Station locations were determined by surface salinity (nominally 0.5, 2, and 5) with a total of 114 stations sampled over the 2 years. During 2006, freshwater flow was high during spring and stations were located in Central and San Pablo Bays (Fig. 1). Starting in June 2006 and 2007 all of the stations were located in Suisun Bay and the western Delta (Fig. 1). At each station, a Seabird SBE-19 CTD was deployed for vertical measurements of temperature, salinity, and PAR using a Li-Cor 4π sensor. Water column light extinction coefficient (k , in per meter) was determined for most samples by linear fit of log-transformed vertical profiles of PAR or, in some cases, estimated from an empirically derived relationship between k and Secchi depth developed during this study (Kimmerer et al. 2012). In either case, it was assumed that k was invariant with depth through the photic zone. Measurements of daily PAR (I_0 , in einsteins per square meter per day) for each sampling date were obtained from a sensor at the Romberg Tiburon Center and calculated from data from pyranometers maintained by the California Irrigation Management Information System (Kimmerer et al. 2012; CIMIS, <http://www.cimis.water.ca.gov>). Solar radiation flux density averaged over 24 h (in watts per square meter) was converted to PAR (in microeinstein per square meter per second) assuming that photosynthetically active light comprises $\sim 45\%$ of the total quanta detected by a pyranometer (Morel and Smith 1974; Kimmerer et al. 2012).

Surface water was collected using a clean bucket, gently transferred to an acid-washed 20-L high density polyethylene carboy, and stored in a cooler in the dark for 3–4 h before processing. Because the water column was usually well mixed (Kimmerer et al. 2012), it was assumed that surface samples contained phytoplankton representative of the full water column. No attempt was made to remove phytoplankton grazers by prescreening. Samples were processed for chlorophyll using the extraction protocol of Arar and Collins (1992), modified for estuarine filtration volumes (Wilkerson et al. 2006). Aliquots of 50–100 mL were filtered under low vacuum (<250 mmHg) onto 25-mm GF/F (nominal pore size $0.7 \mu\text{m}$) and $5\text{-}\mu\text{m}$ Nuclepore polycarbonate filters. Filters were then placed in 90 % acetone and chlorophyll was extracted in the dark at -20°C for 24 h; the fluorescence was read on a Turner Designs AU-10 fluorometer (Holm-Hansen and Riemann 1978) calibrated with

Fig. 1 Map of the San Francisco Estuary (with inset map of estuary location within the state of California, USA). Sampling was conducted based on salinity with stations in Central Bay and San Pablo Bay during spring in 2006 and in Suisun Bay and the western Delta during summer in 2006 and spring and summer in 2007

commercially available chlorophyll standards (Turner Designs) and corrected for phaeophytin with the addition of 10 % hydrochloric acid.

Primary production was determined in ^{14}C -bicarbonate tracer experiments in 280 mL polycarbonate light/dark bottles following JGOFS protocols (JGOFS IOC 1996). After inoculation with $4.6 \mu\text{Ci NaH}^{14}\text{CO}_3$, single bottles were placed in neutral-density screen bags to simulate ten light levels from 0.1 to 100 % of surface in situ PAR. Incubations were terminated by filtering separate sample aliquots (50–100 mL) onto GF/F and 5- μm polycarbonate filters. Filters were acid fumed and then counted in a Wallac liquid scintillation counter after addition of 8 mL of HiSafe scintillation cocktail. Dissolved inorganic carbon concentrations, required for primary production calculations, were measured for each station using an MBARI-clone DIC analyzer with acid-sparging and nondispersive infrared analysis (Li-COR 6252) (Friederich et al. 2002).

To allow for the time to collect samples, all incubations were started at midday. During 2006, incubations were terminated after 6 h and during 2007 incubations were

maintained for 24 h, in part to account more fully for dark respiration and so more closely approximate net primary production (Eppley and Sharp 1975). The 24-h incubation period was also consistent with the majority of previous studies of primary production in the SFE (e.g., Cole and Cloern 1984; Alpine and Cloern 1992) making a direct comparison easier to interpret. Daily (24 h) estimates of primary production were calculated for 2006 by multiplying hourly uptake rates by day length omitting 1.5 h at dawn and dusk (the remaining day length is when 98 % of the solar irradiance strikes the Earth) and making no additional correction for dark respiration (Kimmerer et al. 2012).

Volumetric determinations of primary production (in milligrams of carbon per cubic meter per day) were fit to a three-parameter function of PAR (Macedo and Duarte 2006):

$$\Sigma P = \frac{\text{PAR}}{a\text{PAR}^2 + b\text{PAR} + c} \quad (1)$$

where PAR is photosynthetically active radiation (in einsteins per square meter per day); ΣP is depth-integrated

primary production (in milligrams per square meter per day); and a , b , and c are parameters. Because the overturning time scale of the water column is lower than photoinhibition time scales, photoinhibition is not likely to be important in the field (Kimmerer et al. 2012). Therefore, in incubations with apparent photoinhibition, the maximum primary production value from the three-parameter curve was used for the inhibited region. Removing apparent photoinhibition is also consistent with previous primary production studies in the SFE (Cole and Cloern 1984). Maximum chlorophyll-specific carbon assimilation rates ($P_{M(24)}^B$, in milligrams of carbon per (milligrams of chl- a) per day) were calculated from the maximum photosynthetic rate and chlorophyll concentrations. $P_{M(24)}^B$ should not be confused with the traditional instantaneous physiological parameter, P_M^B (Jassby and Platt 1976), measured under constant light (Pennock and Sharp 1986). $P_{M(24)}^B$ is based on 24 h incubations during which light intensities varied and chlorophyll content per cell may have changed. Some previous primary production studies also report $P_{M(24)}^B$, making direct comparisons possible.

Depth-integrated primary production from each sample was fit to the light-utilization model of Cole and Cloern (1984) and described by Jassby et al. (2002) as:

$$\sum P = \Psi B I_0 Z_p = -4.61 \Psi \frac{B I_0}{k} \quad (2)$$

in which $\sum P$ is the measured depth-integrated primary production, B is biomass as chlorophyll (in milligrams per cubic meter), I_0 is the daily surface PAR (in einstein per square meter per day), Z_p is the photic zone depth (in meter), and k is the extinction coefficient (in per meter). Cole and Cloern (1984) referred to the product $B \cdot I_0 \cdot Z_p$ as the “composite parameter” and we adopt that terminology here. Ψ is an “efficiency factor” as described by Jassby et al. (2002) and is determined empirically as the regression slope of $\sum P$ versus the composite parameter. The constant -4.61 is the natural log of 0.01 corresponding to the relationship between k and Z_p . We fitted the above model with zero intercept as suggested by Brush et al. (2002) and Cloern (1991).

To test for differences between years and between the two filter sizes, we included parameters as follows:

$$\sum P = (\Psi_y + \Psi_f) B I_0 Z_p \quad (3)$$

where the subscript y refers to year and Ψ_f is an offset for filter pore-size, where f is 1 for the GF/F filter and 2 for the 5- μ m filter. Estimates of variance were available for each estimate of integrated production (Kimmerer et al. 2012). Because variance was large for some measurements, it was important to take that variance into account in model fitting. We therefore fitted Eq. 2 using a Bayesian hierarchical model run in WinBUGS (Lunn et al. 2000). Since we lacked prior information on unknown parameters, they were assigned

uninformative prior probability distributions: normal (0, SD=100) for Ψ_y and Ψ_f , and uniform (0.1, 120) for process error (essentially the standard deviation of the residuals from the model). Data consisted of the individual measurements of the terms in the composite parameter, integrated production, and its measurement error. Model parameters were determined by running three Markov chains with tenfold thinning to reduce autocorrelation, 1,000 (post-thinning) iterations discarded to remove effects of initial values, and 10,000 iterations to obtain parameter values. Diagnostics used to ensure convergence included autocorrelation, MC error, and Gelman–Rubin statistics (Lunn et al. 2000), and a comparison of parameter values between the first and second half of the 10,000 iterations. In addition, because we sampled in different regions during spring of 2006 than during summer, for that year only we tested for a step change in Ψ by including two additional parameters in Eq. 1: the timing of a single step and the size of the step (Thomson et al. 2010).

The original model calibration (Cole and Cloern 1984) used a slightly different approach to calculate integrated production and lumped data from all regions to estimate Ψ . To ensure that differences between their results and ours were not due to analytical methods, we recalculated primary productivity estimates used in their original model calibration from raw data gathered throughout the SFE during 1980–1981 (Fig. 1). Data were transcribed from computer printouts, although three pages out of 89 were illegible. Incubations on clear days used additional screening to prevent photoinhibition, which was never observed (Cole and Cloern 1984). Raw data comprising individual measurements of carbon uptake at each light level were fitted to a hyperbolic tangent curve of two parameters (Jassby and Platt 1976) using the nonlinear fitting function gnls in Splus (Venables and Ripley 2003) as with our data, except that variance was held constant. The resulting integrated production values were fitted in WinBUGS as described above, except that the variance in individual values was estimated using the median coefficient of variation of 15 %. The model was similar to that in Eq. 3

$$\sum P = \Psi_r B I_0 Z_p \quad (4)$$

but allowed for differences among the three regions (r) of the estuary included in the analysis (South Bay, San Pablo Bay, and Suisun Bay; Fig. 1). To ensure that the difference in fitting functions did not bias results, we also fitted our raw data using a hyperbolic tangent after removing data at light levels >36 % of incident PAR to remove photoinhibition introduced by our experimental design.

In all of the estimates of Ψ that have been determined, the model fitting method has been some variant on least-squares regression for which the x variable is assumed to be determined without error (or with small error). The alternative is to fit a geometric mean or major axis regression but that can

result in biased predictions and would have been inconsistent with previous model fitting practices (e.g., Jassby et al. 2002). We therefore fitted our raw data from the three-parameter curve using an alternative Bayesian model in which the composite parameter was estimated with error. For each data point and each of the three components B , I_0 , and k , the model sampled from a normal distribution with the individual value and standard error, and estimated the composite parameter based on the sample, for each of the 11,000 model iterations.

Results

Details of spatial and temporal variability in these data are presented in Kimmerer et al. (2012). The frequency distribution of chlorophyll concentration in the GF/F size fraction was skewed toward lower values in both years, and the overall range of values for chlorophyll concentrations was narrower in 2007 than in 2006 (Fig. 2a, b). In 2006, over 80 % of chlorophyll concentrations measured were between 2 and 7 $\mu\text{g L}^{-1}$ whereas, during 2007, >80 % of chlorophyll measurements were $\leq 3 \mu\text{g L}^{-1}$. Chlorophyll concentrations

greater than 10 $\mu\text{g L}^{-1}$ represented <10 % of observations made during 2006 and were never observed in 2007. Chlorophyll in cells $>5 \mu\text{m}$ was similar for both years, with over 80 % of chlorophyll in the size fraction $\leq 3 \mu\text{g L}^{-1}$ (Fig. 2a, b).

Individual primary production rates in the GF/F fraction varied from 17 to 503 $\text{mg C m}^{-2} \text{ day}^{-1}$ in 2006 and 24 to 250 $\text{mg C m}^{-2} \text{ day}^{-1}$ during 2007. The range of primary production in the $>5 \mu\text{m}$ size fraction was more similar between years, varying between 9 to 194 $\text{mg C m}^{-2} \text{ day}^{-1}$ and 17 to 200 $\text{mg C m}^{-2} \text{ day}^{-1}$ during 2006 and 2007, respectively (Kimmerer et al. 2012). Within these ranges, primary production was more frequently found on the lower end of these values. During 2006, >80 % of all ΣP values in the GF/F fraction and 97 % of ΣP in the $>5 \mu\text{m}$ fraction were $<150 \text{ mg C m}^{-2} \text{ day}^{-1}$. During 2007, ΣP was similarly skewed toward lower values, with >70 % of all values in the GF/F fraction and 100 % of values in the $>5 \mu\text{m}$ size fraction $<150 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Fig. 2c, d).

The depth of the photic zone was remarkably similar for 2006 and 2007 (Table 1, Fig. 2e, f) considering that spring freshwater discharge during 2006 was roughly sevenfold higher than in 2007. Monthly mean depth of the photic zone

Fig. 2 Frequency distributions for 2006 (top row) and 2007 (bottom row) of (a, b) extracted chlorophyll for the whole water (GF/F) size fraction (filled bar) and $>5 \mu\text{m}$ size fraction (dark bar); c, d depth-integrated primary production with bars as in a, b; e, f photic zone depth

Table 1 Monthly averaged values during the study period and for two earlier periods for parameters in Eq. 2: photosynthetically active radiation (PAR), photic zone depth (Z_p), and chl-*a* (>0.7 μm)

		1980	1988	2006	2007
PAR	March	—	—	27.9	25.6
E m ⁻² day ⁻¹	April	34.5	—	24.9	46.5
	May	18.6	54.8	53.7	48.0
	June	52.3	59.5	52.4	62.4
	July	43.7	55.6	57.2	54.1
	August	35.2	53.6	51.9	43.1
Z _p	March	—	—	1.10	1.32
m	April	0.90	—	1.15	0.92
	May	0.64	1.55	1.44	0.94
	June	0.79	1.85	1.21	1.18
	July	0.60	1.58	1.64	1.64
	August	0.69	1.57	1.24	1.77
Chl- <i>a</i>	March	—	—	6.0	1.7
μg L ⁻¹	April	2.0	—	4.8	3.5
	May	7.1	1.6	4.3	2.1
	June	11.2	1.6	4.7	2.6
	July	21.5	2.1	3.5	2.1
	August	35.4	1.7	4.3	2.3
ΣP	March	—	—	57	88
mg Cm ⁻² day ⁻¹	April	89	—	40	115
	May	143	143	147	60
	June	349	206	138	97
	July	338	149	107	131
	August	526	88	111	171
P ^B _{M(24)}	March	—	—	15.2	75.7
mg C (mg chl- <i>a</i>) ⁻¹ day ⁻¹	April	51.1	—	14.7	60.8
	May	43.6	114.5	28.2	51.8
	June	41.1	143.5	31.1	74.0
	July	28.3	105.8	28.9	68.1
	August	30.0	88	27.3	62.6

Monthly values for 1980 from Cole and Cloern (1984) using values reported for USGS station 6 in Suisun Bay. Data for 1988 was from Table 2 in Alpine and Cloern (1992), monthly mean for all stations in the navigational channel of Suisun Bay

varied from 0.9 to 1.8 m (Table 1); annual mean depths of the photic zone were virtually identical (1.42 and 1.45 m for 2006 and 2007, respectively; Kimmerer et al. 2012) and were never greater than the water column depth. Roughly 25 % of photic zone estimates were >2 m and ~10 % were <1 m (Fig. 2e, f). Photosynthetically active radiation was also similar between years except during cloudy conditions in April 2006 (Table 1).

Depth-integrated primary production measurements were positively correlated with the composite parameter $B \cdot I_0 \cdot Z_p$ (Fig. 3). The overall root-mean-square prediction error was 35 mg C m⁻² day⁻¹, and the absolute value of the prediction

error was 27 % (median) of the predicted value. Estimates of ψ for the GF/F and >5 μm fractions were not significantly different from one another: the filter offset (ψ_f in Eq. 2) was smaller (0.015 ± 0.022) compared to values of ψ_y (Fig. 3a–d). The pooled ψ , derived from both size fractions, differed substantially between the 2 years: ψ determined for 2006 was just over half of the value for 2007 (Table 2). However, there was a step increase at 37 ± 4 km from the mouth of the estuary (the Golden Gate), close to the boundary between San Pablo Bay and Carquinez Strait (Fig. 1), at which ψ increased from 0.23 ± 0.017 to 0.33 ± 0.012 .

The values of ψ determined from tanh fits to our data after high-light values were deleted (see “Methods” section) were 0.27 ± 0.02 for 2006 and 0.57 ± 0.05 for 2007, not different from the values in Table 2. Values calculated by including error in the composite parameter were 0.30 ± 0.02 for 2006 and 0.60 ± 0.04 for 2007. As with geometric mean regression, these are higher than the estimates without error in the independent variable, but not by much and the confidence intervals overlapped with those in Table 2. Substituting carbon biomass estimates for phytoplankton based on counts (Lidström 2009) in place of chlorophyll in the composite parameter results in ψ values of 0.0221 ± 0.005 and 0.0252 ± 0.0022 (95 % Bayesian credible interval) for 2006 and 2007, respectively.

Seasonal and interannual variation in assimilation number ($P^B_{M(24)}$) for the GF/F fraction was evident (Fig. 4). In 2006 $P^B_{M(24)}$ averaged 24 ± 3 mg C (mg chl-*a*)⁻¹ day⁻¹ (± 95 % CI) but varied between 9 and 53, with a clear increasing pattern from spring to summer (Fig. 4). In contrast, mean $P^B_{M(24)}$ during 2007 was 65 ± 6 mg C (mg chl-*a*)⁻¹ day⁻¹ (± 95 % CI) and varied substantially but with no clear seasonal pattern (Fig. 4).

Discussion

Like many other urbanized estuaries around the world, the SFE has experienced perturbations in key ecosystem drivers, including sediment and nutrient loads (Schoellhamer 2011; Jassby 2008), quantity and diversity of toxic pollutants (Brooks et al. 2012), decreased phytoplankton biomass, and a loss of diatoms (e.g., Alpine and Cloern 1992; Kimmerer 2004; Dugdale et al. 2007), and changes in zooplankton and fish (Mueller-Solger et al. 2002; Kimmerer 2005). Although the original authors of the light-utilization model for the SFE (Cole and Cloern 1984) predicted that the empirical efficiency factor ψ would likely respond to such changes, this parameter has been previously recalculated for the northern estuary only twice (Alpine and Cloern 1992; Jassby et al. 2002). In both cases the value of ψ was similar to the previously estimated value. Given the current, chronically food-limited conditions for zooplankton and fish

Fig. 3 Depth-integrated primary production (ΣP , in milligrams of carbon per square meter per day) versus the composite parameter, $BloZ$ for whole water (GFF) size fraction during: **a** 2006 and **b**

2007 and $>5\text{ }\mu\text{m}$ size fraction during **c** 2006 and **d** 2007. Dotted line is model fit with slope, the efficiency factor (ψ). Statistics given in inset with 95 % confidence limits of ψ

($<10\text{ }\mu\text{g L}^{-1}$ chlorophyll; Mueller-Solger et al. 2002; Kimmerer 2008; Gould and Kimmerer 2010) that characterize the northern estuary, accurate primary production measurements are critical for understanding and managing the ecosystem. Our results indicate that: (1) substantial spatial and temporal variation in ψ occurred interannually (in the 2 years of this study) and over the past three decades that are not likely attributable to differences in experimental approach; (2) at the low chlorophyll concentrations now typical for the northern SFE, confidence in the predicted rates derived from the model is lower than in the past even with a recently calibrated model; and (3) a long-term decline in ψ may have occurred which likely reflects

ecosystem-level changes in the phytoplankton community in the SFE.

The light-utilization model provided a good fit (although with a lower squared correlation coefficient than previously reported for the SFE when chlorophyll-*a* was higher, Table 2) to the data for primary production for the northern SFE during 2006 and 2007 (Table 2, Fig. 3). However, the original calibration efficiency factor ψ determined by Cole and Cloern (1987) and corroborated by Alpine and Cloern (1992) and Jassby et al. (2002) was not substantiated by our results. Re-examination of ψ previously reported or recalculated using data from previous reports from the SFE since the early 1980s reveals considerable variability

Table 2 Estimates of the efficiency factor (ψ) for the San Francisco Estuary reported in this study, including recalculated values, and reported in previous studies

Year	Location	Season	Incubation period, h	ΣP , mg C m ⁻² day ⁻¹	ψ	r^2	N	Reference
1980	South Bay San Pablo	Annual	24	24–2,200	0.99±0.09	0.82	33	Refit data from Cole and Cloern 1984
				25–922	1.22±0.15	0.85	26	
	Suisun Bay			9–663	0.66±0.09	0.86	27	
1988	Suisun Bay	May–Oct	24	19–298	0.81±0.10	0.62	33	Alpine and Cloern 1992, from data in Table 2
1997	Delta	May–Nov	0.5	9–2,500	0.73±0.05	0.95	51	Jassby et al. 2002 as reported
2004–2005	Central Bay	Annual	6	35–540	0.37±0.04		50	Lorenzi 2006 as reported
2006	LSZ (San Pablo–Suisun)	Mar–Aug	6	9–500	0.29±0.03	0.81	117	This study
2007	LSZ (~Suisun)	Mar–Aug	24	17–250	0.56±0.04	0.49	82	This study

Values are presented with 95 % confidence intervals and r^2 calculated as the squared correlation coefficient between integrated values and predicted values. All incubations were performed under natural light except for those reported by Jassby et al. (2002). Locations within the SFE can be found in Fig. 1. Data from three dates during 2006 were excluded due to anomalously low chlorophyll concentrations (see Kimmerer et al. 2012)

among values that greatly exceeds the confidence limits of the estimates.

During this single study, estimates of ψ varied by a factor of nearly two between the 2 years. The four ψ determinations made prior to 2004 (Table 2) are high compared to estimates from other marine systems (Jassby et al. 2002), whereas ψ determined for 2006 and reported by Lorenzi (2006) are more consistent with typical marine values (~0.40, Platt 1986; Falkowski and Raven 2002). Spatial patterns are discernable among the ψ determinations for the SFE presented in Table 2. Previous estimates of ψ for Suisun Bay and the Delta ranged from 0.66 to 0.77 (Fig. 1, Table 2); ψ determined during 2007 was similar when our

sampling remained in Suisun Bay and the western Delta. In contrast, during 2006, the mean value of ψ was considerably lower (0.29) and more similar to the value (0.37) reported by Lorenzi (2006) for Central Bay (Fig. 1, Table 2). In addition, when sampling was in Central Bay and San Pablo Bay for about a third of the sampling period, ψ was still lower (0.23) than later in the summer in Suisun Bay. Aside from Lorenzi (2006), no estimates of ψ exist for Central Bay, but Cole and Cloern (1984) reported relatively high ψ values in the adjacent San Pablo Bay (Table 2). This analysis, along with the temporal variation in ψ described above, suggests that applying a single model calibration across broad spatial or temporal scales within the SFE will lead to substantial error in estimates of actual primary production (Table 2, Fig. 5).

Although there is general agreement in ψ values for several light-limited, nutrient-replete system (Brush et al. 2002), investigators working in other estuaries have also reported significant spatial and temporal variation in ψ (e.g., Pennock and Sharp 1986; Kromkamp et al. 1995; Falkowski and Raven 2002; Harding et al. 2002). For example, Harding et al. (2002) found that the light-utilization model was a poor predictor of primary production from samples taken throughout the Chesapeake Bay during 1982–2000, whereas Kromkamp et al. (1995) reported variation in ψ of more than threefold across locations in the Scheldt Estuary during a single sampling date. The spatial and temporal variability of ψ observed here for the SFE suggests that other factors besides those captured by the composite parameter may play a previously underappreciated role in determining ΣP in the SFE.

One challenge in interpreting apparent long-term trends in ψ is the potential that differences arose as a result of differences in methods (Jassby et al. 2002). Based on previously reported values of ancillary data (i.e., PAR, chl-*a*, ΣP , and Z_p ; Table 1), there is no indication of gross analytical differences

Fig. 4 Time series of phytoplankton assimilation number ($P^B_{M(24)}$ (±SD)) for 2006 (filled circles) and 2007 (open circles). $P^B_{M(24)}$ as reported by Cole and Cloern (1984) (dotted line) shown for comparison

Fig. 5 Depth-integrated primary production (ΣP) for individual sampling dates during 2006 determined by ^{14}C incubations (filled diamonds) and calculated ΣP for 2006 based on ψ determinations by Cole and Cloern (1984) (open circles) and ψ determined during this study for 2007 (open squares)

in the individual variables that make up the composite parameter. ψ calculated from studies employing 24-h incubation periods for primary production measurements were higher than values from studies that used 6 h incubations (Table 2), a counterintuitive result as one would expect greater respiration of labeled carbon during the longer incubation periods which should lead to lower ψ , all else being equal. The greatest differences in incubation period (between Jassby et al. 2002 and Cole and Cloern 1984) did not result in a large discrepancy in ψ (although Jassby et al. did correct for the difference in net and gross primary production). Together, these results provide no evidence of a systematic bias in ψ due to incubation period.

The choice of three-parameter or tanh formulations for the dependence of productivity on irradiance (P vs. I) also varied across studies. However, this difference in analytical approach produced only small differences in ψ when we compared our results calculated using the two alternative formulations. Similarly, the use of a simple regression model only slightly underestimated ψ when compared to a model in which the independent variable was assumed to be measured with error. We have retained the results of the former model because it is more directly comparable to the previous results, and because predictions using the more complex model would require simulations of the error terms in the components of the composite parameter.

In the original derivation of the light-utilization model for the SFE (Cole and Cloern 1984), it was found that while the composite parameter provided the best model fit, chlorophyll alone explained more than 80 % of ΣP . Similarly,

Goebel et al. (2006) found that chlorophyll explained 59 % of the variability in ΣP in Long Island Sound. In contrast, under the present condition of chronically low chlorophyll in the northern SFE (e.g., Alpine and Cloern 1992; Wilkerson et al. 2006; Kimmerer et al. 2012; Fig. 2) chlorophyll alone had no predictive power for ΣP (Fig. 6a). Photic zone depth or irradiance alone was also not significant determinants of ΣP (Fig. 6b, c). The much lower ranges of both chlorophyll and rates of primary production measured during this study resulted in lower squared correlation coefficients for ψ than previously reported (Table 2; Cole and Cloern 1984; Alpine and Cloern 1992; Jassby et al. 2002) and indicate that the ability of the model to accurately estimate primary production is now diminished. This result suggests that, with low autochthonous production in the LSZ, direct determinations of primary production may be more appropriate for investigations of food web dynamics in this region of the estuary.

Our analysis suggests a long-term decline in values of ψ in the northern SFE since the original model calibration made during the early 1980s. Notably, values of ψ reported from studies prior to 1997 were substantially higher than those reported from observations made in Central Bay by Lorenzi (2006) and ψ reported here during 2006. Complicating this interpretation, our determination of ψ during 2007 is higher and is more consistent with the pre-1997 ψ values. Still, changes in abiotic and biotic drivers of light-limited primary production have been documented for the northern SFE in the decades since the original model calibration which have the potential to change ψ .

Fig. 6 Depth-integrated primary production during 2006 and 2007 in the GF/F size fraction (*open circles*) and $>5 \mu\text{m}$ size fraction (*filled circles*) versus **a** extracted chlorophyll, **b** Photoc zone depth (Z_p); **c** photosynthetically active radiation (PAR)

Insight into the apparent downward trend in ψ may be obtained by looking at the phytoplankton assimilation

number, $P^B_{M(24)}$ which varied between twofold and fourfold during 2006 and 2007, consistent with the differences observed for ψ . $P^B_{M(24)}$ is a function of both the light-saturated growth rate and carbon to chlorophyll-*a* ratio and is implicit in ψ (which has units of milligrams of carbon per (milligrams of chl *a* einstein)). Cole and Cloern (1984) reported a seasonal downward trend in $P^B_{M(24)}$ in Suisun Bay from spring to summer (Fig. 4), indicating relatively low light-saturated growth rates in summer. They attributed summer diatom blooms in Suisun Bay prior to 1987 to accumulation of phytoplankton biomass rather than a high growth rate (Cloern 1979; Cole and Cloern 1984). Our $P^B_{M(24)}$ estimates for 2006 are consistent with the low summer $P^B_{M(24)}$ reported by Cole and Cloern (1984); the slight seasonal increase that we observed for $P^B_{M(24)}$ occurred in parallel with the movement of the sampling area from Central Bay to Suisun Bay and the western Delta (Kimmerer et al. 2012). The higher $P^B_{M(24)}$ values observed during 2007 were similar to values reported by Cole and Cloern (1984) for spring. It has been hypothesized that growth rates of phytoplankton in the northern SFE have potentially decreased as a result of increased NH_4 loading (Dugdale et al. 2007; Parker et al. 2012), contaminants (Brooks et al. 2012), and shifts in phytoplankton community composition (Lehman 2000; Glibert et al. 2011). The decline in both $P^B_{M(24)}$ and ψ in 2006 supports the idea that changes in phytoplankton physiology may have occurred.

$P^B_{M(24)}$ reported by Alpine and Cloern (1992) was much higher than other estimates of $P^B_{M(24)}$ reported for the SFE (Table 1) but similar to values reported for some other estuaries (e.g., Pennock and Sharp 1986). The higher assimilation number in 1988 implies a substantial increase in light-saturated growth rate for phytoplankton immediately following the collapse of summer chlorophyll in Suisun Bay. It is unclear why this may have occurred but appears to have offset any change in ψ , maintaining the model calibration at levels similar to those reported before chlorophyll declined.

The analysis above, suggesting that variation in $P^B_{M(24)}$ reflect changes in light-saturated growth, assumes a constant carbon to chlorophyll ratio. Kimmerer et al. (2012) reported low phytoplankton carbon to chlorophyll ratios (ca. 12/20) during the study period, based on extracted chlorophyll and carbon biomass estimates from microscopy. Our estimates of $P^B_{M(24)}$ presented here, and based on the same chlorophyll determinations but ^{14}C carbon uptake estimates, independently corroborate the Kimmerer et al. (2012) observations of unusually low carbon/chlorophyll ratio. ψ did not differ between the two size classes (GF/F and $>5.0 \mu\text{m}$) either in this study or that of Cole et al. (1986). Using estimates of carbon biomass in place of chlorophyll in the composite parameter resulted in efficiency factors that differ significantly from each other because of tight confidence intervals but are quantitatively

more similar to each other than ψ values for the 2 years using chlorophyll. This strongly suggests that variation in chlorophyll content of cells is an important determinant of the observed trends in ψ .

As with light-saturated growth rates, it is known that carbon/chlorophyll varies as a function of species composition (Tang 1997). Lidström (2009) examined phytoplankton community composition on samples collected in parallel with our rate measurements. The author noted a seasonal shift in phytoplankton community composition during 2006 from centric diatoms and microflagellates during the spring to picoplankton and pennate diatoms during the summer. During 2007, pennate diatoms represented a significant fraction of the phytoplankton community during both seasons. These shifts in phytoplankton community composition are consistent with the timing of variations in observed for $P_{M(24)}^B$ (Fig. 4) and carbon/chlorophyll by Kimmerer et al. (2012). As noted by others (e.g., Pennock and Sharp 1986; Keller 1988; Shaw and Purdie 2001; Brush et al. 2002), seasonal, interannual, and long-term shifts in phytoplankton community composition from diatoms to smaller flagellates (as has occurred in the northern SFE, Lehman 1996, 2000; Glibert et al. 2011) are a potentially important driver of the observed changes in carbon/chlorophyll, $P_{M(24)}^B$, and ψ .

Accurate estimates of pelagic primary production are critical for effective management of resources in any highly perturbed coastal ecosystem, but particularly critical for the northern SFE, where several populations of pelagic fishes have collapsed (Sommer et al. 2007). Food limitation has been implicated in the declines of populations at higher trophic levels, including threatened and endangered fishes (Mueller-Solger et al. 2002; Kimmerer et al. 2005; Bennett 2005; Sommer et al. 2007; but see Thomson et al. 2010). Many of the current estimates of primary production for the SFE are based on the light-utilization model and rely on the early determinations of ψ . As such, the actual primary production in the estuary may be overestimated, obscuring the actual scale of the problem. For example, using the light-utilization model with ψ originally determined by Cole and Cloern (1984) overestimates actual depth-integrated primary production for 2006 by nearly 50 % on average (Fig. 5); in some cases the model estimate is nearly threefold higher than actual ΣP . Using the model calibration (ψ) based on 2007 data also grossly overestimates actual ΣP (Fig. 5). These results indicate that interannual variation in model calibration is substantial.

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