

## ***Interactive comment on “Review: phytoplankton primary production in the world’s estuarine-coastal ecosystems” by J. E. Cloern et al.***

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We thank Dr. Gallegos, Dr. Harding and Dr. Murrell for their careful readings of our Discussion paper, their thoughtful and prompt evaluations. We considered each suggestion, and revised our manuscript as described below. Reviewer comments are in black and **authors’ responses in red.**

### **Referee 1**

The conceptual model used to discuss the source of variability in production among systems is not particularly well suited to the problem under consideration. It is certainly true that primary productivity is the product of plant biomass and growth rate, but the rate that this product gives is an instantaneous rate and a volumetric rate. This is a rate that varies from a maximum somewhere near the surface to near zero at depth in optically deep systems. The connection between the depth profile and the depth integral is not explicitly made, and similarly for the integration of instantaneous to annual rate. While we have a fairly good understanding of the controls on growth rate from culture studies, it is rarely measured (owing to difficulties) in field studies of coastal production, thereby providing little basis for cross-system comparison. I would suggest that the drivers of cross-system variability could be better discussed using a conceptual model for the quantity being discussed, i.e. depth-integrated production. Furthermore, the equations and approach for doing so are already explained in the paper. Please also note the supplement to this comment.

**This is a valid criticism and we could have resolved the problem by either (a) modifying the conceptual model so it matches the quantity we describe (annual phytoplankton primary production), or (b) explaining that the ultimate sources of APPP variability are the processes that drive variability of productivity measured in discrete samples. We chose path (b), adding this new introduction to the Conceptual Model Section: “The values of APPP reported here are the time integral of daily, depth-integrated primary productivity measured in discrete water samples. Primary productivity is the product of plant biomass times its turnover rate, so the variability of APPP described above is ultimately determined by processes that drive temporal and spatial variability of phytoplankton biomass and growth rate within estuaries (Fig. 6).”**

**We also thought it important to acknowledge this reviewer’s formal derivation of a conceptual model of primary productivity variability at the annual scale. At the end of section 4.1 we added text: “However, underlying all models is a strong empirical relationship between primary production and phytoplankton biomass. This relationship has been formalized by Reviewer 1 (<http://www.biogeosciences-discuss.net/10/C7574/2013/bgd-10-C7574-2013-supplement.pdf>) as an alternative conceptual model for understanding variability of APPP over time (Fig. 5B), within (Fig. 5A), and between (Fig. 4) estuarine-coastal ecosystems as a process tightly tied to processes of**

phytoplankton biomass variability. We use case studies to illustrate responses to four of these processes.”

I would also suggest that the magnitude of variability arising from the modeling of methodological factors is somewhat overstated. Aside from 2 numerical experiments made using 2 or 1 incubation depths (seldom employed and highly suspect in anything other than optically very shallow waters), the remaining 18 cases only span a factor of 2.

This is a valid comment. We made two changes: (1) we computed and reported the ratio MAD:median among results of the 17 simulated incubations so that variability across methods could be compared to variability across sites and time shown in Fig. 5; and (2) we modified the text to report that variability between commonly used methods is about a factor of two.

I am also puzzled why the exposition of the model ties grazing so specifically to mesozooplankton when grazing studies consistently show microzooplankton grazing to be a significant source of phytoplankton mortality in coastal systems (e.g. Table 7 in Strom et al. 2001, Mar. Biol. 138:355-368). The assumption appears to hinge on the experiment simulating screening through 202  $\mu\text{m}$  net, though the consequence of that practice could well be the release of microzooplankton from grazing control, resulting in declining rather than increasing phytoplankton populations. Such complexity is clearly beyond the scope and intent of the modeling exercise, and overall the modeling clearly demonstrates the need for some movement toward standardization of methods.

We did this experiment because in the 1960s, 1970s, and early 1980s it was thought that phytoplankton grazing was primarily by mesozooplankton (the Landry-Hasset paper describing the dilution technique for measuring microzooplankton grazing was published in 1982). A common practice in that era (e.g., Thayer 1976, Cole and Cloern 1984) was to screen samples to remove mesozooplankton prior to measuring phytoplankton production. We thought it would be instructive to estimate the effect of mesozooplankton removal as an example of a methodological variant. However, the reviewer is correct that there is uncertainty about what that effect was -- it could have been the opposite effect of what was intended, as explained by the reviewer. Therefore we removed this experiment from Table 1 and related discussion in the text.

Factor of 2 uncertainty is large, and we should reduce it as much as possible. Nevertheless, doubling the maximum and halving the minimum compiled values of annual production would not greatly increase the spread of values in Figure 4, reinforcing the conclusion that biomass and light attenuation are the main drivers of the variability.

This is another valid comment and we modified the text in section 5 to now read: “Variability between methods is small relative to the wide span of APPP between ecosystems (Fig. 4), consistent with the principle that phytoplankton biomass and light attenuation are the important drivers of primary production variability. However, variability among methods is large enough to confound comparisons across studies and the simulations presented here suggest that 2-fold differences of APPP across sites or over time (e.g., Parker et al., 2012) cannot be judged significant unless they are derived from common methods.

p. 17753 line 4, "ode" should be "code".

“ode” is correct – it’s the name of the solver in R package deSolve. We originally had it **bold**, to set it apart from standard text, but copy editor disallowed.

p. 17737, psi is better designated as a coefficient rather than a constant, which it is not  
yes we made this change

Einst. is not in the SI units.  
We replaced with mol quanta

## Referee 2

Discussion of the role of estuarine and coastal ecosystems in the global carbon cycle (p. 17728) is interesting, given the role of these ecosystems as a net source of CO<sub>2</sub>. But with significant uncertainties that attend to such estimates, it seems an overstatement to say that estuarine ecosystems constitute a “climate regulator”, based on an estimate of a 12% reduction of global CO<sub>2</sub> uptake by the oceans.

This is a valid point and we revised the sentence to read: “Therefore, sound understanding of ocean-atmosphere CO<sub>2</sub> exchange requires globally distributed measurements of primary production, external supplies of organic carbon, and respiration across the diversity of estuarine ecosystems.”

The data were assembled with several requirements for coverage and methodology (cf. p. 17731), although coverage appears to dominate decisions on inclusion or exclusion. I am not sure that was the right choice. One could argue that requiring monthly measurements might eliminate ecosystems whose annual cycles of PPP could be defined sufficiently to develop estimates of annual production with less highly resolved measurements. And it is certainly possible that empirical relationships, such as are discussed in some detail in the review, could be applied to remotely sensed data and thereby enrich coverage sufficiently to develop such estimates.

At the beginning of this (ambitious) undertaking we thought it important to set some criteria for which data sets would be included in the compilation for synthesis. Our criterion of at least monthly-frequency sampling is arbitrary. Others would argue the contrary view that even this is inadequate for accurate estimation of annual primary production, especially in estuaries where production is intense during blooms that can develop and disappear between monthly sampling periods. And, if the monthly-frequency criterion is too strict, then what is the ‘correct’ criterion? We read many papers where measurements were made 7, 8, 9, 10 times a year but the authors did not report APPP. We also decided at the beginning that we would only include results from studies where the authors reported annual primary production. Lastly, we certainly agree with the reviewer that there is potential to add to the compilation from empirical models and remote sensing. Maybe our paper will motivate others to take on this job.

The variety of approaches used to measure PPP is thoroughly presented, and Figure 1 identifies the measured properties. Attention to methods comparability nonetheless seems less well developed than would be desirable. All methods have strengths and limitations, an issue widely discussed throughout the literature for many years. But one might like to see a

fuller discussion of what is measured by particular approaches in the text, at least to the level of net or gross primary production (NPP, GPP). For example, what is being measured using simulated in-situ C-14 assimilation in part-day (4-5 h) incubations at a range of irradiances (probably close to GPP, when extrapolated to the photoperiod) is not explained sufficiently. This reasoning extends to other methods and is relevant to the simulation experiment presented late in the review. This is an area the authors understand quite well, having written about it extensively, it just strikes me as needing a fuller presentation here. **Much has been written about the challenge of interpreting <sup>14</sup>C assays and our intent was not to revisit that subject but, rather, to address issues that are less well understood: errors arise from inaccurate methods of integrating productivity over time or depth, and differences between short- and long-term incubations can result from biomass changes as incubations proceed. However, in response to this comment we added the following sentence to section 5.2: “Lastly, we remind readers of processes not included in our model - - respiration and subsequent refixation of assimilated <sup>14</sup>C -- that further confound interpretation of <sup>14</sup>C assays for measuring primary productivity (Marra, 2002b).”**

Cloern et al. correctly point out that inter-annual variability of PPP is poorly known for many estuarine and coastal ecosystems (p. 17736) because many data records are short. But given the magnitude of inter-annual variability of phytoplankton biomass (chl-a), we might expect high variability for PPP at the land margin.

**We modified text as follows:**

**Original text: “Phytoplankton biomass in estuarine-coastal ecosystems can fluctuate substantially from year-to-year (Cloern and Jassby, 2010).”**

**Revised text: “Phytoplankton biomass in estuarine-coastal ecosystems can fluctuate substantially from year-to-year (Cloern and Jassby, 2010), so we might expect comparably high interannual variability of APP.”**

Various empirical formulas to estimate PPP are discussed, and the essential properties are tracked nicely (p. 17737). Perhaps the range of outputs and what affects them might have been detailed a bit more fully. For example, in referring to global estimates (Behrenfeld et al., 2005) based on satellite data and a biomass-light model (VGPM – Behrenfeld and Falkowski, 1997) or something similar, Cloern et al. did not explicitly state that the model tends to overestimate PPP and has been adjusted elsewhere to improve retrievals. This bias high is due to the data used to develop the model (MARMAP) that had an uncommonly high psi value, leading to a coefficient in the model that others (including Harding et al., 2002 referenced by Cloern et al.) have adjusted. The general point is that specific data used to calibrate empirical approaches to estimate PPP strongly impact the outputs.

**We added text at the end of section 4.1: “Accurate estimates of primary production from all these model classes requires calibrations that capture seasonal and regional variations in photosynthetic efficiency expressed as  $p_{max}$  (Saux Picart et al.).”**

I would suggest that extending global PPP data for estuarine and coastal ecosystems to include satellite- or aircraft-derived data would be useful because they would be underpinned by improved biomass retrievals, with the caveat that this approach requires careful consideration of model type, accuracy, and applicability. Similar comments would apply to other empirical approaches, including the biomass-light model of Cole and Cloern (1987) that proves useful in some ecosystems and performs less well in others, or to those

based on psi that ranges at least two-fold.

We added the underlined text here for clarification:

“Thus, a second grand challenge is to organize and fund an international effort to use a common method and measure primary production regularly across a network of coastal sites that are representative of the world’s coastline to yield reliable estimates of global primary production, its influence on biogeochemical processes and food production, and its response to global change as it unfolds in the 21st century. Recent advances in development of bio-optical algorithms for turbid coastal waters (e.g. Son et al., 2014) indicate that remote sensing will play an increasingly important role in meeting this grand challenge.”

The importance of top-down regulation (p. 17743) is nicely presented, and it certainly is important in San Francisco Bay. But line 14 is confusing as the probable fate of phytoplankton production is often sedimentation, not consumption, given a spatial and temporal mismatch of production with grazing or filtering. Cloern et al. recognize the importance of ‘timing’ in this section, but some examples are incorrect. The role of once-abundant oysters in regulating phytoplankton biomass in Chesapeake Bay, for example, was refuted by Pomeroy et al. (2006) as the spring diatom bloom occurs months prior to maximal oyster filtration, and in areas of the estuary these bivalves did not occupy even in colonial times. The general point is, specifics of grazing vary greatly and this fate may or may not be important, depending on the ecosystem.

Thanks for reminding us of Pomeroy’s 2006 paper. We deleted our reference to Chesapeake Bay as an example where loss of bivalve grazing was a mechanism of increased phytoplankton biomass and production.

The analysis presented toward the end of the paper is quite interesting and useful, and one could wish for a stronger conclusion based on the findings. What method for measuring PPP would be encouraged by the results of the simulations? Can we eliminate some methods that emerge from the analysis as unreliable? Cloern et al. are well positioned to make such a recommendation, having synthesized and analyzed such a large amount of data for estuarine and coastal ecosystems, yet I don’t see one. The argument for more measurements is nicely made and well supported by the biased global representation of ecosystems, it could be paired with a value judgment on methods, especially with a clear statement of what is measured by those deemed most appropriate.

In response to this comment we added a new sub-section to the modeling section (5) giving Recommendations to others, based on our simulations of different methods for measuring primary productivity. We highlight the differences across methods in quantities measured, encourage authors to explicitly state the goals of their primary-production measurements and to tailor methods to those goals, and we explain why some commonly-used methods of integrating rates in bottles over time and depth produce errors that can be minimized with accurate integration techniques.

Gallegos’ review has addressed the simulation experiments in detail and I largely concur with his comments. I would add that an interesting exercise would be to use C-14 assimilation on the same water sample to determine both photosynthesis-irradiance (P-E) parameters (such as Cloern et al. used in the simulation) and gross (or net) PP from simulated in-situ sunlight incubations. This could be a simulation or actual measurements. Day-rates ( $\text{g C m}^{-2} \text{d}^{-1}$ ) derived from these two independent and quite different approaches

would help move toward consensus measurements. It is certainly true that many scientists who measure PPP have rather individual oddities in their approaches that make even interpretation of what they are measuring problematic, but P-E and simulated in-situ sunlight incubations are quite common, although infrequently compared (cf. Harrison et al., 1985; Lohrenz et al., 1992).

In response to this and comments from Reviewer 1 we revised the simulation experiments and added clarity to our discussion of those simulations. In particular, we added text to explain that differences between P-E and simulated in-situ incubations are determined in part by the balance between phytoplankton biomass growth and loss during long term incubations. Reviewer 1 correctly noted that the P-E approach can yield values either smaller or larger than values derived from long-term incubations, so there is no simple scaling relationship between the two. And, our benchmark method and experiment 2 are the exercise suggested above. The key point is that outcomes of this exercise will be highly variable depending upon sign and magnitude of biomass change during incubations. We tried to make this key point clearer in our revision.

The terminology is sometimes mixed in the paper and the property, i.e., net, gross, being discussed can be confusing.

This is an inherent problem with the subject because, for example, different authors have a different meaning of net production, which can mean net phytoplankton production in the photic zone or net phytoplankton production in the water column or net pelagic production. We carefully proofed the manuscript with this comment in mind to add clarity where terminology was potentially confusing.

And abbreviations are sometimes used and other times omitted, further complicating the presentation. Given the wide variety of methods used to generate the data presented by Cloern et al., clarity is essential.

We carefully proofed the manuscript with this comment in mind to ensure that each abbreviation is defined when first introduced and that use of each abbreviation is consistent throughout the paper.

p. 17729, lines 4-7 – seasonal is not episodic, these sentences are confusingly written, although understandable.

We modified text as follows:

The original text: “The rate of phytoplankton production is highly variable in space and time because algal cells divide daily (or faster) under optimal growth conditions. Dynamics of phytoplankton production are characterized by seasonal periods or episodic bursts of rapid photosynthesis as blooms develop. These events are transformative as phytoplankton photosynthesis exceeds total system respiration and estuaries shift temporarily to a state of autotrophy”

Revised text: “Much of the annual production occurs during seasonal or episodic blooms when phytoplankton photosynthesis exceeds total system respiration and estuaries shift temporarily to a state of autotrophy”

p. 17739, line 16 – reference should be Harding and Perry (1997).

We made this correction, thanks

Also in references section, p. 17767, line 4, authors should read Harding, L.W., Jr. and E.S. Perry.

We made this correction, thanks

p. 17745, line 15 – should be ‘seasonal and interannual variability is’ for correct tense.

We made this correction, thanks

p. 17746, line 12 – should be ‘a large fraction of the nutrients delivered to the Hudson River Estuary is exported’ for correct tense.

We made this correction, thanks

### Referee 3

My main critique of this manuscript is that the overall tone, anchored by the Grand Challenges section, tended to overshadow the accomplishments of this paper in particular and the scientific field in general. The overwhelming message appeared to be that our current understanding of coastal zone productivity is hopelessly hampered by unacceptably high variability, however this summary demonstrated that median APPP varied by ~10X, of which ~3X is potentially attributable to methods. One might argue that this range of variability is sufficiently small to constrain global budgets given the small collective area of the coastal zone relative to global surface area.

Although estuaries, bays, lagoons, river plumes, fjords etc. occupy a small fraction of the ocean surface they do provide disproportionately important functions such as metabolism, nutrient cycling and fish production. Recall our citation of Borges (2005) that inclusion of CO<sub>2</sub> emission from estuaries “reverses the function of the coastal ocean from being a net sink to a net source of CO<sub>2</sub>, and this term reduces the calculated global ocean CO<sub>2</sub> uptake by 12%”. Our intention here was not to dismay readers but rather inspire them to launch new measurement programs in the vast under-sampled regions of the planet so we can collectively reduce the uncertainties in global estimates of photosynthesis and respiration in coastal waters influenced by connectivity to land. Note that Reviewer 2 had a different view, writing, “The argument for more measurements is nicely made and well supported by the biased global representation of ecosystems.” We are sensitive to the reviewer’s comment about the overall tone of our paper, so we followed his advice and added text (see below) to highlight key advances since the last review of this topic.

What we have learned from many individual studies, and from this synthesis, is that phytoplankton production is highly variable in space and time and the available data suggests a clear central tendency (i.e. median APPP of ~185 g C m<sup>-2</sup> y<sup>-1</sup>). It is unclear to me whether a global sampling program would fundamentally change these estimates of the magnitude of variability or the magnitude of the central tendency. Perhaps the authors could speculate, based on our current understanding of the environmental drivers, how far and in which direction a true global median might deviate from our current best estimates.

We wrote in the original manuscript: “Much higher phytoplankton production has been measured in some tropical-subtropical systems, such as Cienaga Grande de Santa Marta, Golfo de Nicoya and Huizache-Caimanero Lagoon, suggesting that our current assessments might substantially underestimate primary production in the world’s estuarine-coastal ecosystems because we have greatly under-sampled tropical and subtropical sites.”

While I agree that consistent methods, and more comprehensive global coverages are desirable goals, I also think the authors should emphasize how this compilation provided a valuable update to the Boynton review, and expanded and reinforced the key patterns observed in the earlier paper. This might provide a bit more hopeful outlook to balance out the current emphasis on pointing out the inadequacies of the available data.

We changed the title of section 6 and added new text (underlined):

#### **“6. Advances Since 1982 and Two Grand Challenges for the Future**

Our goal was to compile and synthesize measurements of annual phytoplankton primary production in estuarine-coastal waters as a key Earth-system process that drives variability of water quality, biogeochemical processes, and production at higher trophic levels. Most primary production measurements in estuaries have been made since the 1982 review of Boynton et al. when APPP was available for 45 estuaries – most (32) from North America. The record now includes APPP measurements from 131 estuaries and its geographic coverage has expanded, particularly in Europe. Increased sampling has captured a larger range of variability: mean APPP across 45 estuaries ranged between 19 and 547 g C m<sup>-2</sup> yr<sup>-1</sup> (Boynton et al. 1982) compared to -105 and 1890 g C m<sup>-2</sup> yr<sup>-1</sup> in the latest compilation (Fig. 4). Enhanced sampling has led to discoveries that: APPP can vary up to tenfold within estuaries and fivefold from year to year (this is probably an underestimate); some tropical-subtropical estuaries sustain very high rates of primary production (so global upscaling of APPP from measurements in temperate estuaries might have substantial errors); synthesis of estuarine APPP is confounded by the use of many methods that can yield results that differ ~twofold; and daily depth-integrated primary productivity is strongly correlated with the product of phytoplankton biomass times light availability (but the specific relationship is variable so site-specific and seasonally adjusted model calibrations are essential). In the past three decades we have also developed a deeper understanding that variability of phytoplankton production at the land-sea interface cannot be explained by a single factor, such as nutrient loading rate (Cloern, 2001). Contemporary conceptual models now recognize that nutrient loading sets the potential for biomass production in estuaries, but the realization of that potential changes over time (Duarte et al., 2008) and is shaped by variability of hydrology, optical properties, transport processes, inputs of heat, light and mixing energy, and top-down control of phytoplankton biomass growth (Fig. 6).”

We also added text (underlined) in section 3: “We found only 8 APPP series longer than a decade, but these represent notable advances since the 1980s when none were available (Boynton et al. 1982).”

I offer some specific suggestions on a couple of figures to enhance the information content:

Fig 1. This is a nice summary of the distribution of sampling effort. However, would it be possible to add an identical set of panels to show mean/variance estimates of APPP along these different categories? Such a modified figure would be more informative because it would simultaneously show the distributions of both the sampling effort and the magnitude of APPP in each of these bins.

We considered this suggestion but had a difficult time understanding how the results would be interpreted. For example, comparing mean APPP across regions would not be very



informative because the sample size is too small in most regions to develop meaningful indicators of mean and variance of APPP.

Fig 2: It might be more intuitive to remove the left hand panel and simply annotate the right hand panel with the number of observations in each latitude bin.

We did redraft the figure as suggested, but prefer the original graphical presentation of effort. We did, however, make the left panel smaller and the right panel (containing much more data) wider.

Fig 4: I am curious about how this cumulative distribution, would compare to Figure 3 in Boynton et al. 1982? How would Boynton's 45 values (properly normalized), expressed as a ranked cumulative distribution, overlay with the ~160 or so values in this figure? My guess is that the two curves would be very similar; the differences between them would be a way to represent what we have learned in the intervening 30 years.

We added the 45 values from Boynton et al. (1982) to Fig. 4 and added text in section 3.3: "We also show in Fig. 4 the ranked distribution of APPP reported for 45 estuaries by Boynton et al. in 1982, which averaged  $190 \text{ g C m}^{-2} \text{ yr}^{-1}$  and ranged from 19 to  $547 \text{ g C m}^{-2} \text{ yr}^{-1}$ ." We also added text (see above) to specifically highlight key advances since the last review by Boynton et al.