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Key Points:

- No single satellite algorithm or model reproduces seasonal and annual geochemically determined productivity rates throughout the North Pacific
- Discrepancies are particularly strong in the high-latitude regions during deep winter mixing, where few observational data are available
- Caution is needed when applying satellite- and model-based results to estimate current and future rates of the ocean's biological pump

Supporting Information:

- Supporting Information S1

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Discrepant estimates of primary and export production from satellite algorithms, a biogeochemical model, and geochemical tracer measurements in the North Pacific Ocean

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Abstract Estimates of primary and export production (PP and EP) based on satellite remote sensing algorithms and global biogeochemical models are widely used to provide year-round global coverage not available from direct observations. However, observational data to validate these approaches are limited. We find that no single satellite algorithm or model can reproduce seasonal and annual geochemically determined PP, export efficiency (EP/PP), and EP rates throughout the North Pacific basin, based on comparisons throughout the full annual cycle at time series stations in the subarctic and subtropical gyres and basin-wide regions sampled by container ship transects. The high-latitude regions show large PP discrepancies in winter and spring and strong effects of deep winter mixed layers on annual EP that cannot be accounted for in current satellite-based approaches. These results underscore the need to evaluate satellite- and model-based estimates using multiple productivity parameters measured over broad ocean regions throughout the annual cycle.

1. Introduction

Photosynthetic primary production generates the fixed organic carbon that supports nearly all marine food webs. A fraction of this carbon is exported from the surface ocean, sequestering it in the deep ocean and thus influencing the global carbon cycle. Given the scarcity of observational data to constrain both primary and export production (PP and EP), satellite-based algorithms and global biogeochemical models are widely used to fill these gaps and enable global-scale analysis of the rates and spatial patterns of marine PP and EP [e.g., *Laufkötter et al.*, 2013; *Siegel et al.*, 2014].

Satellite- and model-based global estimates of PP and EP are essential pieces of our understanding of the ocean's carbon cycle, but given the limited observational estimates available for validation, questions remain as to how well they represent true rates and spatial patterns of PP and EP. A number of previous studies have compared satellite-based PP with geochemical estimates based on ^{14}C-PP incubations [*Carr et al.*, 2006; *Saba et al.*, 2011; *Westberry and Behrenfeld*, 2014] and in situ triple oxygen isotopes [e.g., *Juranek and Quay*, 2013]. *Stukel et al.* [2015] recently compared export efficiency (e-ratio, defined as EP/PP) algorithms with observations at process study locations. However, global annual EP estimates from satellite-based approaches and global biogeochemical models range widely (~6–13 Pg C/yr) [*Laws et al.*, 2011; *Siegel et al.*, 2014; *Laufkötter et al.*, 2015], indicating that further work is needed to improve our consensus on current EP rates.

Recent work comparing geochemical and satellite-based EP estimates at Ocean Station Papa (OSP, 50°N, 145°W) in the eastern subarctic gyre and the Hawaii Ocean Time-series Station ALOHA (22.75°N, 158°W) in the subtropical gyre of the North Pacific indicated that a carbon-based PP model [*Westberry et al.*, 2008] combined with the *Laws et al.* [2000] e-ratio model matches geochemical EP estimates in both locations [*Emerson*, 2014]. However, no previous work to our knowledge has compared simultaneous year-round PP, EP, and EP/PP (e-ratio) observational-based estimates with satellite algorithm- or model-based estimates across broad ocean regions. We find that neither a biogeochemical model nor any single commonly used satellite-based algorithm matches the PP, EP, and e-ratio determined from geochemical measurements throughout the entire North Pacific over the full annual cycle.

2. Methods

We compare PP, EP, and e-ratios estimated from geochemical measurements, satellite-based algorithms, and a global biogeochemical model, with details of each approach described below. Comparisons are conducted

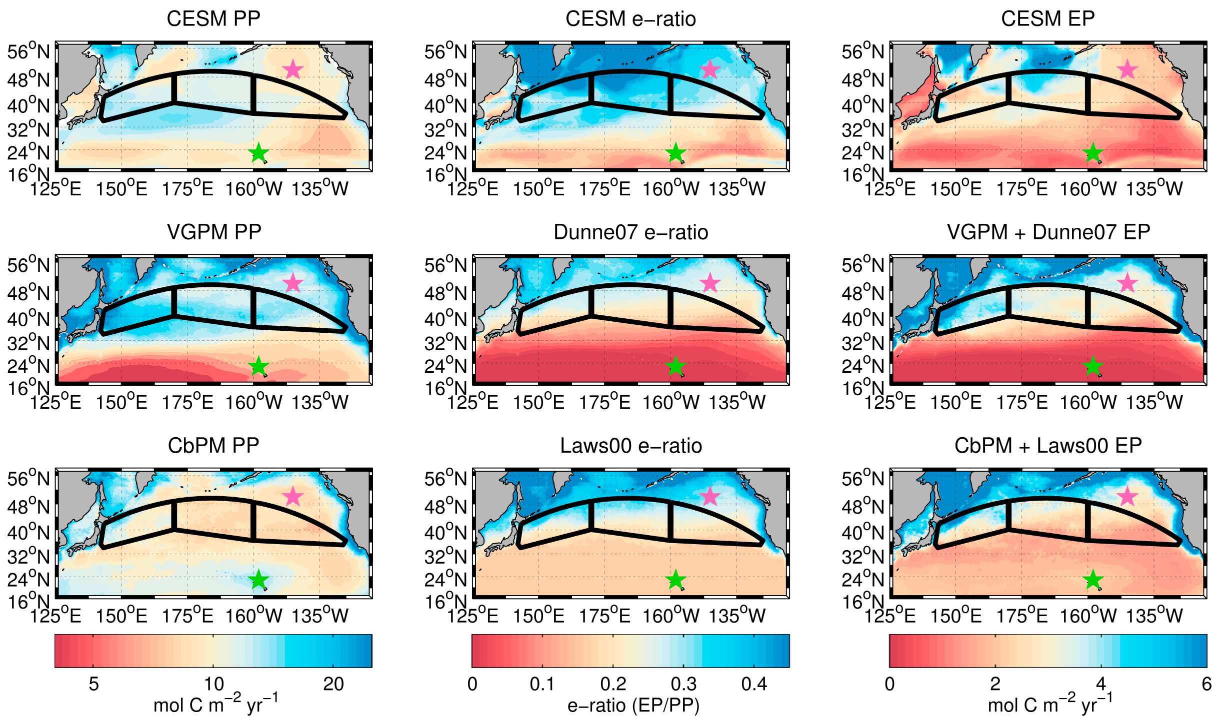

Figure 1. North Pacific annual (left column) PP, (middle column) e-ratio (EP/PP), and (right column) EP as predicted by (top row) CESM and satellite-based algorithms using (middle and bottom rows) MODIS 2003–2013 data. OSP (pink star), ALOHA (green star), and container ship regions (black outline; referred to from west to east as the Kuroshio, Western, and Eastern regions, respectively) are shown in all plots.

over the full annual cycle at two time series stations (OSP and ALOHA) and in three regions spanning the entire North Pacific basin in the transition zone and subarctic gyre (35°N–50°N, 142°E–125°W; Figure 1).

2.1. Productivity Estimation Approaches

Long-term sampling at OSP and ALOHA provides geochemical estimates of PP from ^{14}C-PP incubations (data sources in Table S1 in the supporting information) and of annual EP from oxygen, nitrate, and carbon isotope mass balance [*Emerson*, 2014]. Basin-wide geochemical PP, EP, and e-ratio estimates based on surface ocean triple oxygen isotope and O_2/Ar measurements ($n = 581$) collected during 16 container ship crossings of the North Pacific from 2008 to 2012 have recently been described in detail [*Palevsky et al*., 2016]. All PP estimates are converted to values equivalent to 24 h ^{14}C-PP incubations, representing net primary production (total photosynthesis minus autotrophic respiration) through the full euphotic zone (details in Table S1) [*Karl et al*., 1996]. EP (equivalent to net community production) is determined from the seasonally varying surface mixed layer and, for the container ship regions, also determined seasonally at the compensation depth (where gross photosynthesis and community respiration rates are equal) and annually at the winter ventilation depth. E-ratios are calculated from separate estimates of PP and EP.

Uncertainty in the geochemical estimates (ranging 13–36%) is quantified from the spread (1σ) among all existing estimates for the time series stations and from methodological uncertainty for the container ship regions (for further details, see the supporting information). For maximal comparability between geochemical estimates and other approaches, globally available satellite data and model output were extracted from a 2.5° box centered on each time series site in all months from 2003 to 2013, and for the container ship regions from a 1/3° box at the locations and months corresponding to each geochemical measurement and compiled for each region and season following the same procedure as the geochemical data compilation (results are not sensitive to spatial box size; see Table S2). Satellite- and model-based estimates are considered to match the geochemical estimates if they agree within the geochemical estimates' uncertainty bounds.

Satellite-based EP estimates require two independent algorithms: one to estimate PP and a separate algorithm to estimate the e-ratio, where EP = PP × e-ratio. Each PP and e-ratio model can be combined to produce a unique EP model. All satellite-based PP and e-ratio estimates for this study use Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua R2014 monthly products (available from http://www.science.oregonstate.edu/ocean.productivity). The two most commonly used PP algorithms are the Vertically Generalized Production Model (VGPM) [*Behrenfeld and Falkowski*, 1997] and the Carbon-based Production Model (CbPM), [*Behrenfeld*, 2005; *Westberry et al*., 2008]. Both algorithms estimate integrated PP rates through the full euphotic zone. The VGPM combines measured surface chlorophyll concentrations and photosynthetically available radiation with an estimate of euphotic depth and an empirically determined relationship between sea surface temperature (SST) and carbon assimilation efficiency determined from ^{14}C-PP data. The CbPM uses backscattering-based estimates of phytoplankton biomass to produce a PP model that accounts for environmental condition-specific variations in carbon:chlorophyll ratios. E-ratio algorithms predict the fraction of PP exported from a given depth horizon based on satellite-measured SST, chlorophyll, and PP from the algorithms above. Here we consider three widely used e-ratio algorithms: (1) the pelagic food web model of *Laws et al*. [2000, hereafter Laws00], which includes both particulate and dissolved organic carbon (POC and DOC) export from the euphotic zone and was validated using geochemical data from 11 process study sites; (2) the empirical model of *Dunne et al*. [2005, 2007, hereafter Dunne07], based on a compilation of field measurements using a range of methods (sediment traps, ^{234}Th, $^{15}NO_3$ incubations, and nutrient, oxygen and carbon mass balance) adjusted to represent POC export from the euphotic zone; and (3) the empirical model of *Henson et al*. [2011, hereafter Henson11], based on a compilation of ^{234}Th measurements representing POC export below 100 m.

The global biogeochemical model used here is the ocean component of the Community Earth System Model (CESM) version 1.1.1, run with an embedded biogeochemistry and ecosystem module (the Biogeochemical Elemental Cycling model) [*Moore et al*., 2002, 2004]. The model includes three phytoplankton functional groups, multiple potentially limiting nutrients (N, P, and Fe), a single zooplankton class, and DOC and sinking POC pools. PP, EP, and e-ratios in previous and current versions of this model have been evaluated through comparison with existing data sets [*Moore et al*., 2002, 2004, 2013; *Doney et al*., 2009; *Friedrichs et al*., 2009]. However, the scarcity of direct observational estimates has limited previous comparisons of CESM output to process study locations or satellite-derived global PP (VGPM). CESM simulations presented here represent repeated normal year forcing run to equilibrium conditions in the surface ocean and thermocline after a 200 year spin-up (for full details, see *Nicholson et al*. [2014]). This CESM output includes depth-resolved photosynthesis and respiration rates, which were used to determine PP, e-ratio, and EP (calculated as net community production, directly equivalent to the geochemical approach) for a range of depth criteria (seasonal mixed layer, euphotic zone, compensation depth, and winter mixed layer) needed for optimal comparability to the geochemical estimates. Standard runs for model intercomparison projects such as the Coupled Model Intercomparison Project [*Taylor et al*., 2012] have not routinely archived the depth-resolved data needed for this type of comparison, limiting analysis across a wide range of models. We recommend that future model intercomparison projects extend standard output variables to enable monthly depth-resolved PP, EP, and e-ratio estimates.

2.2. Comparability Between EP and E-ratio Estimation Approaches

EP and e-ratio estimates vary with the integration depth criterion chosen. In stratified conditions when the mixed layer is shallower than the euphotic layer, PP can exceed respiration in the submixed layer euphotic zone and contribute additional EP excluded from mixed layer-based EP estimates. Seasonal EP integrated to the compensation depth represents the maximum EP of all possible depth criteria. In nearly all cases with shallow mixed layers, EP at the base of the euphotic zone (the Laws00 and Dunne07 depth criterion) will be greater than EP at the base of the seasonal mixed layer but less than EP at the compensation depth. E-ratios, however, are much more sensitive to the chosen depth criterion since they consistently decrease with depth, such that deeper depth criteria (i.e., 100 m for Henson11) produce lower e-ratios (illustrated in Figure S1).

Additionally, EP estimates to the base of the euphotic zone or 100 m are only meaningful when the mixed layer is shallower than the chosen depth criterion. When the mixed layer is deeper, organic material must still sink out of the mixed layer to be seasonally exported from the surface ocean. For exported organic material to be effectively sequestered from the atmosphere on annual or multiannual time scales, it must sink deep enough to avoid being remineralized and ventilated to the atmosphere during deep winter mixing.

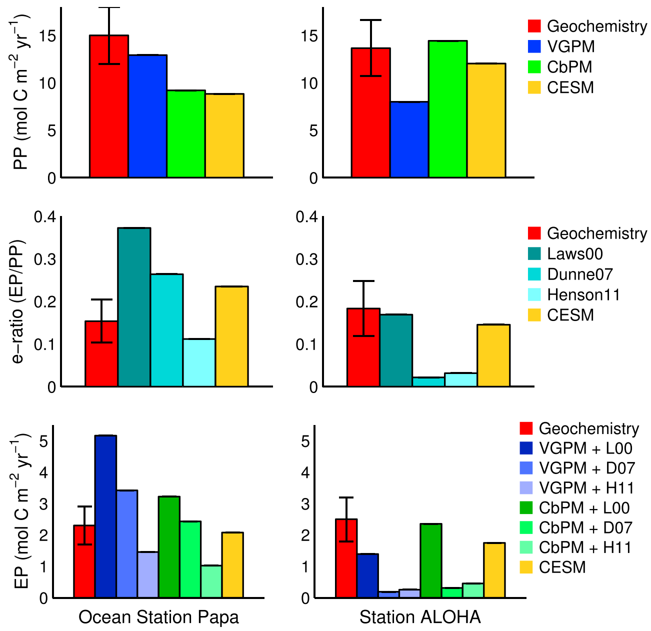

Figure 2. Annual (top row) PP, (middle row) e-ratio (EP/PP), and (bottom row) EP at OSP and ALOHA.

Geochemical and CESM EP estimates from the container ship regions account for winter ventilation; however, satellite-based EP cannot be evaluated to the winter ventilation depth using current e-ratio algorithms.

3. Results

3.1. Time Series Stations OSP and ALOHA

Geochemical, satellite algorithm, and CESM estimates of annual PP, e-ratio, and EP are compared at time series stations in the eastern subarctic (OSP) and subtropical (ALOHA) North Pacific (Figure 2). Geochemical estimates from ^{14}C-PP incubations yield comparable annual PP at OSP and ALOHA (15 ± 3 and 14 ± 3 mol C/m^2 yr, respectively). The two satellite-based algorithms predict conflicting relative PP between the two stations, with the VGPM estimating 38% lower annual PP at ALOHA, while the CbPM estimates 36% lower annual PP at OSP. CbPM PP agrees with geochemical PP at ALOHA, while VGPM-PP agrees with geochemical PP at OSP, but neither matches geochemical PP at both stations. CESM, similar to the CbPM, yields greater annual PP at ALOHA than OSP and only agrees with geochemical estimates at ALOHA.

Canonically, lower e-ratios are expected in the subtropics than the subarctic due to faster recycling in warmer waters and a phytoplankton community dominated by smaller cells [*Passow and Carlson*, 2012]. This canonical pattern is evident in lower e-ratios predicted by CESM and satellite-based e-ratio algorithms at ALOHA (0.02–0.17) than at OSP (0.11–0.37) (Figure 2). In contrast, geochemical-based e-ratios are slightly higher at ALOHA (0.18 ± 0.06) than OSP (0.15 ± 0.05). Although the geochemically based e-ratio is matched at ALOHA by the Laws00 algorithm and CESM and at OSP by the Henson11 algorithm, none of the three e-ratio algorithms nor CESM match geochemical e-ratios at both sites.

Geochemical estimates of annual EP from the seasonally varying mixed layer are comparable at OSP and ALOHA (2.3 ± 0.6 and 2.5 ± 0.7 mol C/m^2 yr respectively) [*Emerson*, 2014]. The many potential permutations combining individual satellite-based PP and e-ratio algorithms provide a wide range of annual EP estimates (Figure 2). At ALOHA, however, the only combination that agrees with geochemically determined EP is the CbPM PP + Laws00 e-ratio. Since the CbPM and Laws00 algorithms also agree with geochemical observations at ALOHA for PP and e-ratio, respectively, this is an appropriate approach to estimate EP at ALOHA and perhaps more broadly in the subtropical North Pacific. At OSP, the CbPM + Laws00 combination yields annual EP (3.2 ± 0.7 mol C/m^2 yr; 2003–2013 mean ± 1σ) that, accounting for interannual variability, agrees within uncertainty with geochemical estimates (2.3 ± 0.6 mol C/m^2 yr), as previously observed by *Emerson* [2014]. However, this agreement is a fortuitous combination of underestimated PP from the CbPM and overestimated e-ratio from Laws00 for OSP. Other approaches (CbPM + Dunne07, VGPM + Henson11, or CESM) more closely match annual EP at OSP, but no single combination successfully matches geochemical-based estimates of PP, EP, and e-ratio at both OSP and ALOHA.

3.2. Basin-Wide Comparisons Across the North Pacific

Geochemical, satellite algorithm, and CESM estimates for PP, e-ratio, and EP are compared to geochemical estimates [*Palevsky et al.*, 2016] in three broad container ship-sampled regions (boundaries shown in Figure 1) across the basin both throughout the seasonal cycle (Figure 3) and annually (Figure 4). In all three regions, satellite- and CESM-based PP estimates are generally lower than the geochemical-based PP

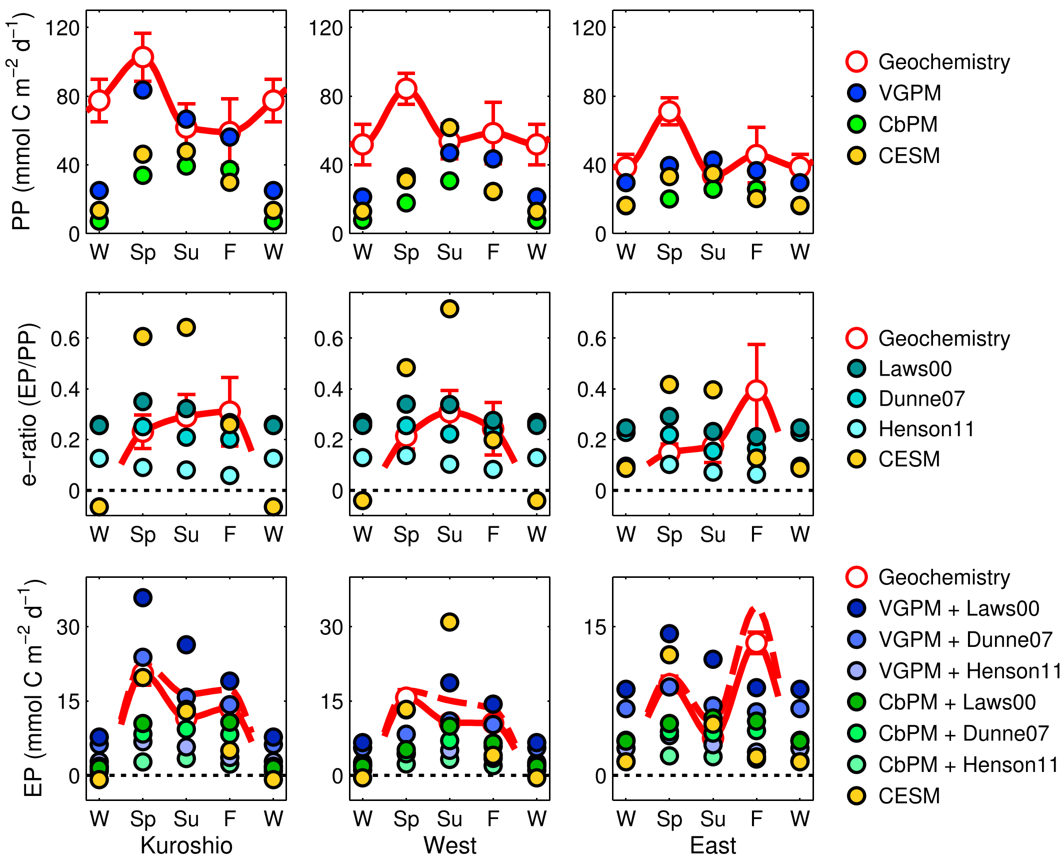

Figure 3. Seasonal (top row) PP, (middle row) e-ratio, and (bottom row) EP for each container ship region. For EP, dashed red lines indicate geochemical EP extended to the compensation depth. Geochemical EP is not presented in winter due to high uncertainty. Note the 2 times change in *y* axis scale for EP in the East.

estimates, with the largest discrepancies during winter and spring. The geochemically determined rates show a spring PP maximum in each region and lower, even PP in summer, fall, and winter. In contrast, the satellite algorithms and CESM generally produce PP seasonal cycles with a winter minimum and summer maximum, consistent with light-limited growth conditions in the subarctic [*Matsumoto et al.*, 2016; *Sasai et al.*, 2016]. However, in nutrient-limited conditions in the subtropics, winter shoaling of the nitracline can lead to maximum annual PP rates in winter [*Matsumoto et al.*, 2016]. The geochemically determined PP is consistent with mixed nutrient and light limitation at the boundary between the subtropics and subarctic.

Due largely to discrepancies in winter and spring, both the satellite algorithms and CESM predict lower annual PP than the geochemical-based estimates in all regions (Figure 4), with the least discrepancy in the VGPM and the greatest in the CbPM. The VGPM, CbPM, and CESM all reproduce the geochemically observed westward increase in annual PP across the basin, though the magnitude of the trend is matched only by the VGPM, while the CbPM and CESM predict a smaller westward increase. Integrated across all three regions, mean annual PP rates determined from geochemical observations are significantly higher than those estimated by other approaches (1.5 × VGPM, 2.7 × CbPM, and 1.7 × CESM).

Dunne07 and Laws00 e-ratios at the base of the euphotic zone both are frequently within the range of geochemical e-ratio estimates at the base of the seasonal mixed layer (Figure 3), with Dunne07 predicting e-ratios 15–35% lower than Laws00 (consistent with the Dunne07 algorithm excluding DOC, which is on order ~20% of total export [*Hansell and Carlson*, 1998]). In contrast, Henson11 e-ratios (representing ^{234}Th-based estimates of POC export at 100 m) are significantly lower than geochemically determined e-ratios at the base of the mixed layer, which in part would be expected from POC flux attenuation between the base of the mixed layer and 100 m. All e-ratio algorithms predict relatively constant e-ratios throughout the year, whereas CESM predicts much higher e-ratios in spring and summer than in fall and e-ratios (and EP)

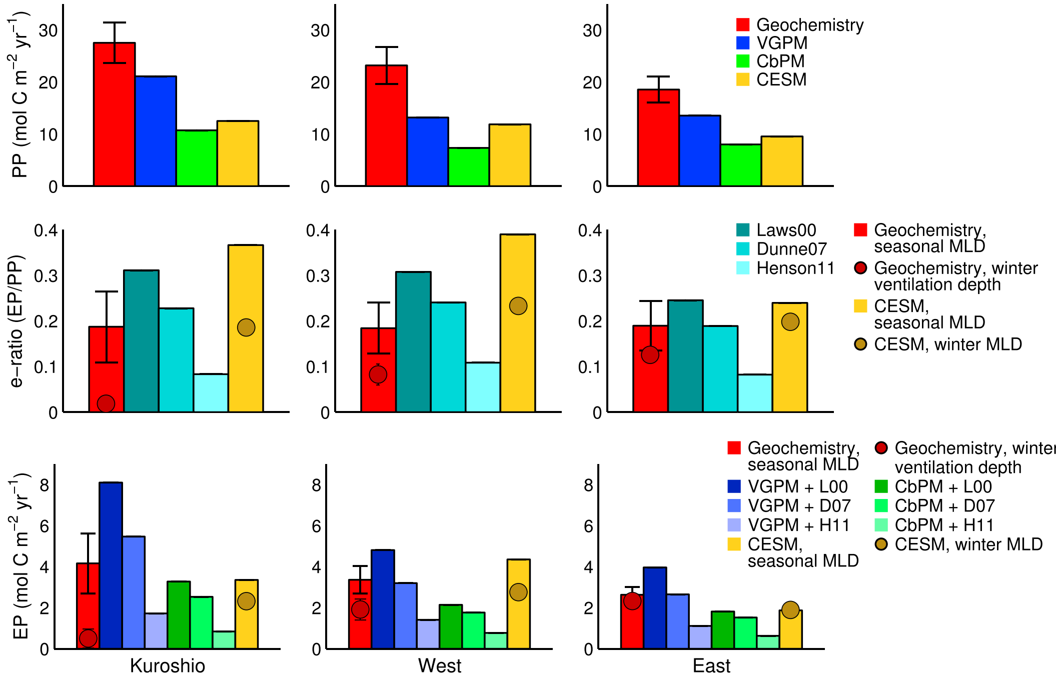

Figure 4. Annual (top row) PP, (middle row) e-ratio (EP/PP), and (bottom row) EP for each container ship region. For e-ratio and EP, geochemical and CESM estimates are presented both to the seasonally varying mixed layer depth (bars) and the winter ventilation depth (colored circles).

near or below zero in winter. In contrast, geochemically determined e-ratios do not show elevated spring values. On an annual basis, Dunne07 e-ratios agree with geochemically based e-ratios from the seasonal mixed layer in all three regions whereas the Laws00 estimates are consistently higher and Henson11 estimates are consistently lower (Figure 4).

No single satellite algorithm combination nor CESM matches geochemical estimates of EP from the mixed layer (or compensation depth) in all seasons and regions (Figure 3). Because it underestimates PP, the CbPM produces EP rates that are significantly lower than geochemical estimates in both spring and fall when combined with any e-ratio algorithm. Similarly, since Henson11 estimates lower e-ratios than the geochemical approach, it produces EP rates that are consistently lower than geochemical estimates in all seasons, whether combined with VGPM or CbPM PP. CESM EP estimates show stronger spring to fall seasonality than the geochemical and satellite-based estimates, mainly a result of consistently underestimated EP in fall. The only approach that agrees with geochemically determined annual EP from the mixed layer in all three regions is the VGPM + Dunne07 combination (Figure 4).

4. Discussion

4.1. Primary Production

The VGPM comes closest to reproducing geochemically observed PP rates at OSP and in the container ship regions, while the CbPM underestimates PP as compared to the geochemically determined rates. Similarly, a previous study in the Gulf of Alaska showed that VGPM-based EP matched O_2/Ar-based EP in a springtime high-productivity hot spot, whereas it was not detected in CbPM-based EP [*Palevsky et al.*, 2013]. However, the VGPM significantly underestimates PP in the subtropics (Figure 2) and also underestimates winter and spring PP in the container ship regions (Figure 3). This may reflect an inability of the VGPM's single empirical relationship between SST and photosynthetic assimilation efficiency to represent all phytoplankton physiological variations across regions and throughout the seasonal cycle [*Westberry and Behrenfeld*, 2014].

CbPM underestimates of PP in the transition zone and subarctic North Pacific may reflect physiological effects of photoacclimation and iron stress not accounted for in existing satellite models [*Behrenfeld et al.*, 2009, 2015; *Westberry et al*., 2016]. The CbPM photoacclimation model underestimates PP when mixed layers extend below the euphotic zone during winter and early spring because it does not account for the effect of total darkness below the euphotic zone on phytoplankton carbon:chlorophyll ratios [*Behrenfeld et al*., 2015; *Westberry et al*., 2016]. This is consistent with the larger discrepancy between CbPM and geochemical PP estimates in winter and spring, particularly in regions of deep winter mixing in the western basin (Figure 3). Additionally, iron limitation in high nutrient-low chlorophyll regions increases cell carbon: chlorophyll ratios [*Behrenfeld et al*., 2009; *Westberry et al*., 2016] but is not accounted for in the CbPM, which could also bias PP estimates in the transition zone and subarctic regions throughout the year. At ALOHA, where the mixed layer is shallower than the euphotic depth year round and phytoplankton are not iron limited, the CbPM matches geochemical PP estimates.

CESM, though more mechanistically sophisticated than the VGPM or CbPM, also underestimates PP as compared to geochemical estimates throughout the subarctic and transition zone in all seasons except summer. This may be a result of model physics, which underestimates maximum annual mixed layer depths in the northwest Pacific and, in turn, underestimates surface nutrient concentrations throughout the subarctic [*Moore et al*., 2013], which could suppress PP. Further analysis of model output separately evaluating physical and ecological impacts on PP would help understand the discrepancies with geochemical-based PP estimates.

4.2. Export Production and Efficiency

Previous analysis at OSP and ALOHA found that annual EP from the CbPM PP + Laws00 e-ratio algorithms agreed with geochemically determined annual EP in both the subtropics and subarctic [*Emerson*, 2014]. However, neither the CbPM PP nor the Laws00 e-ratio agrees with geochemical estimates in the transition zone and subarctic North Pacific, such that annual EP agreement at OSP is the fortuitous result of offsetting biases in the PP and e-ratio algorithms. No single e-ratio algorithm matches geochemical e-ratio estimates throughout the North Pacific, with Dunne07 best fitting geochemical estimates at OSP and in the container ship regions, while Laws00 best fits geochemical estimates at ALOHA. These algorithms represent e-ratio variations based only on SST, chlorophyll, and PP and therefore may not be applicable in locations or seasons where few or no calibration data were available. A potential benefit of CESM is that it employs a mechanistic ecosystem model to determine the fraction of PP that is recycled versus exported. However, the seasonality and magnitude of CESM e-ratios does not match geochemical estimates. Recent development of a mechanistic ecosystem-based e-ratio model using satellite products provides a promising step forward [*Siegel et al*., 2014], although further work is needed to validate and expand upon such approaches [e.g., *Stukel et al*., 2015; *Siegel et al*., 2016], particularly in high-latitude regions in fall and winter where observational data are lacking.

Satellite-based estimates of annual EP face the additional challenge that existing e-ratio algorithms are based on single time point estimates of EP/PP and therefore cannot account for effects of seasonal physical dynamics on the annual e-ratio. Geochemical-based annual EP estimates demonstrate that 40–90% of seasonally exported organic carbon is ventilated during deep winter mixing in the Kuroshio and Western regions of the North Pacific [*Palevsky et al*., 2016] yielding significantly lower estimates for EP determined to the winter ventilation depth than the seasonally varying mixed layer depth (Figure 4). Satellite-based e-ratio models cannot account for wintertime ventilation or net heterotrophy, both of which reduce annual EP. In order to quantify the influence of EP on the global carbon cycle, annual EP rates need to account for these wintertime processes to avoid overestimating carbon sequestration. New e-ratio models should be developed to account for these physical processes and existing e-ratio algorithms should be evaluated with this context in mind.

Global biogeochemical models explicitly resolve depth-dependent production, remineralization, and ventilation. CESM shows significantly reduced EP (30–40%) to the winter mixed layer depth as compared to the base of the seasonally varying mixed layer in the Kuroshio and Western regions (Figure 4), with the fraction of seasonally exported material ventilated comparable to geochemical estimates in the Western region but lower in the Kuroshio. Importantly, both the geochemical observations and CESM output demonstrate that annual EP and e-ratio to the winter ventilation depth (i.e., export that sequesters carbon from the atmosphere) are substantially lower than EP and e-ratio integrated to the seasonally varying mixed layer depth in regions with deep winter mixing. These results emphasize the role of physics in the ocean's biological pump. Furthermore, the ability of CESM to capture winter ventilation effects on EP is promising for our ability to model the ocean's biological pump over annual and longer time scales.

5. Conclusions

This study represents a rare opportunity to compare geochemical, satellite, and global biogeochemical model estimates of PP, e-ratio, and EP across broad spatial scales throughout the annual cycle. The results demonstrate that no combination of the satellite-based PP and e-ratio algorithms nor CESM can reproduce geochemical observation-based estimates of PP, EP, and e-ratio at the ALOHA and OSP time series stations and across the North Pacific basin. These results emphasize that caution is needed in applying ecosystem models or satellite-based algorithms for global-scale analysis of the ocean's biological pump since no single approach accurately represents spatial and temporal trends in productivity across multiple biogeochemically and ecologically distinct regions. Caution is especially warranted in the strongly seasonal and more physically dynamic high-latitude ocean, which is less well validated than the subtropics in model and algorithm development and likely undersampled from late fall through early spring. Both geochemical- and model-based estimates of export highlight the importance of deep winter mixing at high latitudes in significantly reducing annual export rates, indicating a need for new e-ratio algorithms that account for physical as well as biological processes. Additional observational data, especially from high-latitude regions and during seasons with deep mixed layers that may confound models designed for stratified conditions, are needed to better calibrate model and satellite-based estimates of export and improve their skill in estimating the current magnitude and predicting future changes in the global ocean's biological pump.

Acknowledgments
All data sources are cited in section 2, with additional details provided in Table S1. We thank Michael Behrenfeld, Steve Emerson, Edward Laws, and two anonymous reviewers for constructive feedback that improved the manuscript. This work was funded by a NDSEG Fellowship from the Office of Naval Research, a NSF Graduate Research Fellowship, and an ARCS Foundation Fellowship to H.I.P.

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