The potential for improving remote primary productivity estimates through subsurface chlorophyll and irradiance measurement

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ABSTRACT

A 26-year record of depth integrated primary productivity (PP) in the Southern California Current System (SCCS) is analyzed with the goal of improving satellite net primary productivity (PP) estimates. Modest improvements in PP model performance are achieved by tuning existing algorithms for the SCCS, particularly by parameterizing carbon fixation rate in the vertically generalized production model as a function of surface chlorophyll concentration and distance from shore. Much larger improvements are enabled by improving the accuracy of subsurface chlorophyll and light profiles. In a simple vertically resolved production model for the SCCS (VRPM-SC), substitution of *in situ* surface data for remote sensing estimates offers only marginal improvements in model r^2 (from 0.54 to 0.56) and total $\log_{10}$ root mean squared difference (from 0.22 to 0.21), while inclusion of *in situ* chlorophyll and light profiles improves these metrics to 0.77 and 0.15, respectively. Autonomous underwater gliders, capable of measuring subsurface properties on long-term, long-range deployments, significantly improve PP model fidelity in the SCCS. We suggest their use (and that of other autonomous profilers such as Argo floats) in conjunction with satellites as a way forward for large-scale improvements in PP estimation.

1. Introduction

The satellite ocean color era began with the launch of the Coastal Zone Color Scanner (CZCS) in 1978. Several years later, with scientists using ocean color to estimate surface chlorophyll (chl_0), Eppley et al. (1985) examined relationships between chl_0 and euphotic zone integrated primary production (PP) in anticipation of attempts to quantify PP from satellites. In that paper they described variability in the ratio $F = PP/chl_0$ (see Table 1 for variable definitions), and suggested the simplest of satellite primary productivity algorithms (PPAs), where PP ($g\,C\,m^{-2}\,d^{-1}$) is approximated by the square root of chl_0 ($mg\,m^{-3}$). That model, which we refer to as the Eppley Square Root model (ESQRT), represents a baseline of both complexity and skill for PPAs.

In the subsequent decades, many PP models have been developed (see Saba et al., 2011 for 21 examples) in an effort to improve satellite productivity estimates. In addition to satellite estimates of surface chlorophyll (chl_0), they typically rely on satellite-derivable physical quantities such as sea surface temperature (SST) and photosynthetically available radiation (PAR), either directly or through the inclusion of physiological variables (*e.g.* quantum yield, carbon fixation rate) that are estimated from satellite-derived properties. A series of primary productivity algorithm round-robin (PPARR) comparisons (Campbell et al., 2002; Carr et al., 2006; Friedrichs et al., 2009; Saba et al., 2011) periodically evaluates satellite algorithms of wide-ranging complexity, from the ESQRT baseline to fully depth- and wavelength-resolved algorithms, and has produced several key findings: (i) model performance does not improve with model complexity, (ii) no particular model consistently outperforms the others, (iii) chl_0 captures primary productivity variability better than any other parameter, (iv) models typically underestimate observed PP variability and may fail to capture broad scale regime shifts, and (v) average model skill is significantly lower in coastal waters than pelagic waters, partly due to increased uncertainty in satellite chlorophyll estimates, and partly to limitations of the algorithms.

Though PPAs have been evaluated in some coastal systems (*e.g.* Saba et al., 2011), none of the PPARR experiments include data from the California Current System (CCS), nor do they include other major upwelling ecosystems (Humboldt, Canary, Benguela). Kahru et al. (2009) conducted a scaled-down PPARR-like comparison, evaluating five PPAs in the SCCS, and found little difference between the best performing algorithms. All were biased toward high productivity, and none captured more than 66% of the observed

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data variance. An empirically adjusted model was produced by fitting *in situ* data to remove the systematic bias, resulting in improved model skill (Kahru et al., 2009).

In this paper we explore PP in the southern CCS (SCCS) with the goal of informing improved satellite PPAs. First, we update the Eppley et al. (1985) analysis of *in situ* productivity data in the SCCS. Their study was based on ~270 stations occupied from 1974 to 1983 within a region bounded approximately by Los Angeles and San Diego to the north and south, respectively, and up to 100 km offshore. We use over 25 years of PP data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI), including over 1500 primary productivity casts from ~100 quarterly cruises since 1985, with spatial coverage throughout the southern California Bight and up to 600 km offshore. Next, we evaluate several existing PPAs for their performance against CalCOFI data and explore possibilities for improving their performance in the CCS. Finally, we provide suggestions for further improving PP estimates with the aid of autonomous subsurface platforms.

2. Methods

2.1. In situ data

Since 1984, on-deck ^{14}C incubations have been performed on quarterly cruises as a part of the CalCOFI program. Reported half-day (local noon to sunset) values, integrated over the euphotic depth, are multiplied by 1.8 to obtain equivalent 24 h productivity (Eppley, 1992). Station locations for the dataset used in this paper are shown in Fig. 1, totaling 1544 PP casts from 1985 to 2011. Additional parameters recorded on CalCOFI cruises and utilized here include SST, chlorophyll, light attenuation at depth, and distance from shore.
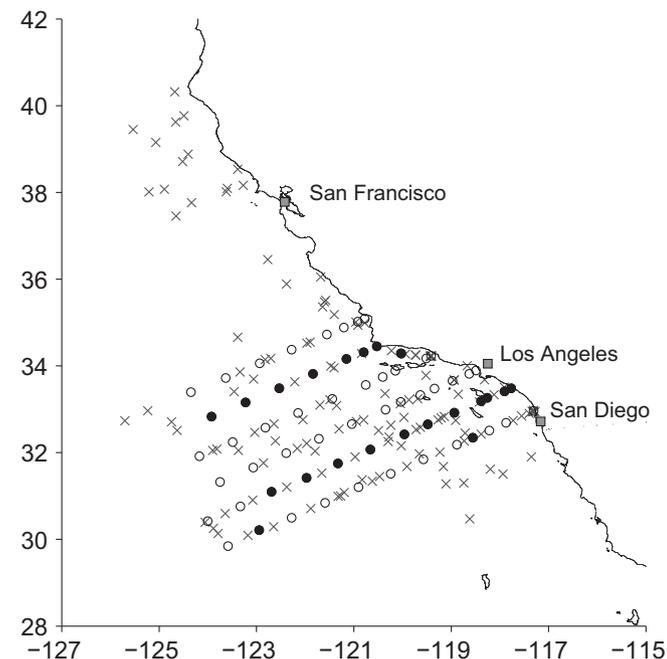
Fig. 1. Map of CalCOFI primary productivity survey coverage from late 1985 to early 2011. A total of 1544 PP casts make up the dataset. Circles indicate stations occupied more frequently during the study period (minimum of five times in this dataset, average of 22), while X's indicate stations occupied fewer than five times, typically only once or twice. Filled circles denote stations identified for match-ups with Spray glider profiles.

2.2. Satellite data

Where available, satellite estimates of chl_0, SST, and PAR have been obtained for comparison with CalCOFI data. Chl_0 was derived by applying a recently developed empirical algorithm (Kahru et al., 2012), based on over 10,000 *in situ* measurements from the CCS, to SeaWiFS Level-3 remote sensing radiance. This algorithm produces values very similar to those from the current standard OC4v6 algorithm for *in situ* $chl_0 < 1$ mg m^{-3} but significantly higher values for *in situ* $chl_0 > 1$ mg m^{-3}. PAR (mol quanta m^{-2} d^{-1}) was obtained from the standard SeaWiFS product (Frouin et al., 2003) for 1997–1999 and merged from multiple sensors (SeaWiFS, MODIS-Terra, MODIS-Aqua) for 2000–2010. For SST, we used the daily AVHRR Pathfinder 5 dataset described by Casey et al. (2010), and interpolated when measured SST values were missing. All three datasets were daily composites with 9 km global mapping. For each CalCOFI station, match-ups were sought for the nearest satellite pixel on the same day. If those data were not available, the search was continued forward and backward in time until the nearest valid dataset was found. Satellite match-ups were available for 723 CalCOFI PP stations.

2.3. Glider data

Spray gliders (Sherman et al., 2001) deployed on CalCOFI lines 80 and 90 as a part of the Southern California Coastal Ocean Observing System (SCCOOS) provided vertical fluorescence profiles. All available glider data were filtered to find profiles in proximity to CalCOFI PP stations, subject to a range of spatial and temporal constraints. For each station, a mean fluorescence profile was obtained by averaging all glider profiles within the match-up criteria. Fluorescence was converted to chlorophyll according to Lavigne et al. (2012) assuming that euphotic zone depth exceeds mixed layer depth, the predominant condition off the California coast (Frolov et al., 2012b). The Lavigne et al. (2012) algorithm uses measured surface chlorophyll to calibrate the fluorescence profile, reducing uncertainty due to detector variability, drift on long deployments, and fluctuations in the relationship between fluorescence and chlorophyll. Nonetheless, we assume that there is unquantified variability in the fluorescence data due to these factors.

2.4. Satellite primary productivity algorithms

It is not our intention to replicate the PPARR comparisons specifically for the CCS. Instead, we evaluate several well-known models that we consider representative of the larger set of available PPAs in both methodology and performance. Each of the models tested includes physiological variables that may be tuned for the CCS as a first step toward improving model-data agreement.

The model described by Marra et al. (2003) (MARRA) is depth-resolved, and uses inputs of chl_0, SST, and PAR. It is based on chlorophyll-specific absorption, which is parameterized by SST, and maximum quantum yield, which is assumed constant for a given region. The vertical chlorophyll profile is estimated from surface concentration and is used along with non-photosynthetic absorption coefficients to calculate light attenuation with depth.

The widely used vertically generalized production model (VGPM) of Behrenfeld and Falkowski (1997) requires the same three inputs as MARRA, and uses latitude and time of year to calculate day length. It relates productivity to the optimal chlorophyll-specific carbon production rate (P_{OPT}^B), which is estimated by a seventh-order polynomial fit to SST. A number of VGPM variants have been proposed with alternate methods of estimating P_{OPT}^B, and we evaluate one proposed by Kameda and

Ishizaka (2005) (VGPM-KI), which assumes the chlorophyll concentration is made up of a small, stable component and a large, fluctuating component.

2.5. Statistics

To quantify model performance, we present a suite of statistical measures that have been employed routinely in past PPA comparisons. They are the determination coefficient (r^2), total root mean square difference (RMSD), centered-pattern RMSD (RMSDcp), and bias. All statistics are calculated on log-transformed data, and the total RMSD summed over n data points is

$$\text{RMSD} = \left(\frac{1}{n} \sum_{i=1}^{n} [\log(\text{PP}_M(i)) - \log(\text{PP}_I(i))]^2 \right)^{1/2} \qquad (1)$$

where PP_M and PP_I denote modeled and *in situ* primary productivity (mg C m^{-2} d^{-1}), respectively. RMSD is a measure of total model skill, and captures a model's ability to accurately represent both the mean and the variability of *in situ* data. We therefore also

divide RMSD into two components

$$\text{RMSD}^2 = \text{RMSDcp}^2 + \text{Bias}^2 \qquad (2)$$

where Bias is the difference between log-transformed model and data means, and RMSDcp captures model-data differences in variability.

To avoid evaluating new PPAs against the data with which they were developed, we divide the CalCOFI-satellite match-ups into one period for model development (1997–2004, $n=399$) and one for model validation (2005–2010, $n=324$). Statistics for PPA comparisons are calculated on the latter.

3. Results

3.1. Properties of the CalCOFI dataset

We begin with an examination of the full *in situ* primary productivity dataset. Data are available year-round, with 72–254PP casts available per month (mean is 154), except for June and December, which had five casts and none, respectively, during our
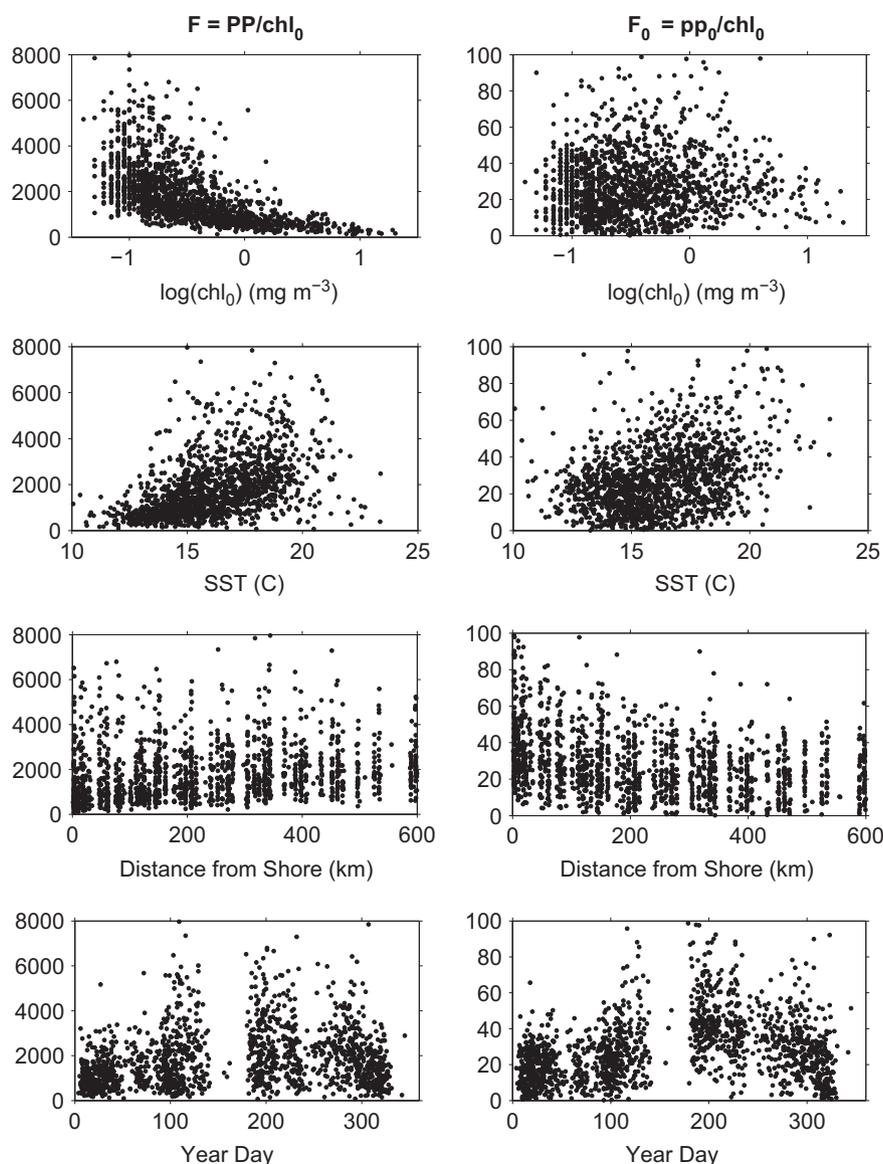
Fig. 2. Ratios of integrated PP to surface chlorophyll (F, left panels) and surface PP to surface chlorophyll (F_0, right panels) plotted against four parameters: surface chlorophyll, sea surface temperature, distance from shore, and time of year.

26-year analysis window. Mean monthly PP over the entire CalCOFI domain exhibits seasonal variability with lower values from late fall to early spring (PP$=450$–$600\ \mathrm{mg\,C\,m^{-2}\,d^{-1}}$ from September to March), higher values in the spring and late summer (800–$850\ \mathrm{mg\,C\,m^{-2}\,d^{-1}}$ for April, July, and August), and maximum productivity in May ($\sim 1400\ \mathrm{mg\,C\,m^{-2}\,d^{-1}}$) during peak upwelling season.

As in Eppley et al. (1985), we examine properties of the ratio $F=\mathrm{PP}/\mathrm{chl}_0$, a parameter of particular interest for remote sensing applications. Correct representation of F is the necessary link between satellite estimates of chl_0 and accurate PP estimates from depth-integrated PPAs. An analogous ratio for surface primary productivity (pp_0), $F_0=\mathrm{pp}_0/\mathrm{chl}_0$, may be of greater interest for depth-resolved PPAs that aim to relate PP and chlorophyll at discrete depths. Unlike F, F_0 is not impacted by the subsurface distribution of productivity.

When viewed against environmental variables, qualitative differences between F and F_0 are readily apparent (Fig. 2). F is negatively correlated with chl_0 and weakly positively correlated with SST. In contrast, F_0 is uncorrelated to chl_0, and has even weaker temperature dependence. One explanation for this discrepancy is the relationship of surface chlorophyll to the vertical chlorophyll profile. As reported previously off central California (Frolov et al., 2012b), the relationship between chl_0 and depth-integrated chlorophyll is piecewise linear, with distinct slopes above and below $\mathrm{chl}_0 \cong 1\ \mathrm{mg\,m^{-3}}$. However, low chl_0 is associated with a deep chlorophyll max while high chl_0 is characteristic of surface-intensified phytoplankton blooms. Productivity is distributed to greater depths in the case of low chl_0, resulting in generally high values of F with large scatter, while the opposite is true for high chl_0. This paradigm indicates that the decrease of F with increasing chl_0 is a proxy for changes in the vertical distribution of phytoplankton, not a physiological effect, and explains why a similar pattern is not seen in F_0. The same explanation can be invoked for the increasing trend of F toward higher temperatures, since cold, upwelled waters near shore in the CCS are associated with higher chl_0. It should be noted, however, that increased growth rates at higher temperatures are expected outside of upwelling systems as well (Eppley, 1972; Behrenfeld and Falkowski, 1997), and we do see weak temperature dependence in F_0.

Though noisy, opposite trends are visible in F and F_0 when viewed as functions of distance from shore. F is on average higher farther from shore, in line with a trend toward low chl_0 and deep chlorophyll maxima offshore. F_0 decreases with distance from shore, and the mean offshore value is approximately half that near the coast. In contrast to the trend in F, this result is likely a physiological response driven by a combination of nutrient availability and phytoplankton community composition. Seasonal variability is present in both F and F_0, though more strongly for F_0, with a minimum in winter, increase in the spring, and peak in late summer/fall. Attributing seasonality in these ratios to a specific cause is difficult, as time of year is a proxy for day length and generally for PAR as well, but may also reflect changes in community structure, specifically the relative abundance of diatoms and dinoflagellates.

3.2. Performance of existing PPAs

Model statistics for common PPAs (ESQRT, MARRA, VGPM, VGPM-KI) are given in Table 2 for both *in situ* and satellite chl_0 and SST inputs. Differences between the *in situ* and remote sensing statistics can be attributed to inaccuracies in satellite chlorophyll estimates, as differences in model performance using *in situ* rather than remotely sensed SST are negligible. The models are less sensitive to SST than chl_0, and *in situ*-satellite correlations are better for SST than for chl_0 ($r^2=0.81$ and 0.59, respectively). Satellite PAR is used in all cases, as surface PAR is not reliably available on CalCOFI cruises.

Outside of the simplistic ESQRT model, none of the PPAs tested here is clearly superior to the others. All are biased high and capture just less than 60% of the total $\log_{10}$ data variance. MARRA and VGPM-KI have comparable RMSD, though MARRA represents the mean slightly better and the variability slightly worse than VGPM-KI. VGPM is even more biased than the others but has the lowest RMSDcp and ties for the best r^2, making it the ideal candidate for a purely empirical adjustment of model output (Kahru et al., 2009). VGPM-KI is most sensitive to inaccuracies

Table 2
Model statistics for CalCOFI stations with satellite match-ups, 2005–2010 ($n=324$). Statistics are shown for NPP estimates using *in situ* chl_0 and SST (left) and for estimates from remote sensing data (right). In both cases, PAR is from satellite.

Model	In situ				Satellite			
	r^2	RMSD	RMSDcp	Bias	r^2	RMSD	RMSDcp	Bias
ESQRT	0.488	0.246	0.223	0.105	0.475	0.248	0.224	0.106
MARRA	0.586	0.245	0.232	0.080	0.561	0.249	0.235	0.083
VGPM	0.586	0.289	0.205	0.204	0.555	0.296	0.212	0.207
VGPM-KI	0.566	0.238	0.207	0.118	0.514	0.247	0.217	0.119
VGPM-SC	0.620	0.193	0.193	0.013	0.585	0.202	0.201	0.013

Table 1
Notation for environmental and physiological variables.

P_z^B	Carbon fixation rate at depth z (mg C (mg chl)$^{-1}$ h^{-1})
P_{OPT}^B	Maximum carbon fixation rate within a water column (mg C (mg chl)$^{-1}$ h^{-1})
$P_{OPT,VGPM}^B$	P_{OPT}^B calculated according to Behrenfeld and Falkowski (1997) (mg C (mg chl)$^{-1}$ h^{-1})
$P_{OPT,CALC}^B$	P_{OPT}^B calculated from *in situ* PP, according to Eq. (3) (mg C (mg chl)$^{-1}$ h^{-1})
PP	Depth integrated primary productivity (mg C m^{-2} d^{-1})
PP_I	*In situ* measured PP (mg C m^{-2} d^{-1})
PP_M	Model estimated PP (mg C m^{-2} d^{-1})
pp_z	Primary productivity at depth z (mg C m^{-3} d^{-1})
pp_0	Primary productivity at depth nearest the surface (mg C m^{-3} d^{-1})
chl_z	Chlorophyll concentration at depth z (mg chl m^{-3})
chl_0	Chlorophyll concentration at depth nearest the surface (mg chl m^{-3})
d_{irr}	Day length (h)
PAR	Photosynthetically available radiation (mol quanta m^{-2} d^{-1})
PAR_z	PAR at depth z (mol quanta m^{-2} d^{-1})
F	chl_0-specific PP (mg C m (mg chl)$^{-1}$ d^{-1})
F_0	chl_0-specific pp_0 (mg C (mg chl)$^{-1}$ d^{-1})
z_{eu}	Euphotic zone depth (m)
k_z	Optical attenuation coefficient for PAR at depth z (m^{-1})

Table 3
Seasonal performance of VGPM and MARRA models, run with *in situ* chl$_0$ and SST. Unlike in Table 2, the full set of CalCOFI-satellite match-ups (1997–2010) was used to calculate statistics.

Season	VGPM				MARRA			
	r^2	RMSD	RMSDcp	Bias	r^2	RMSD	RMSDcp	Bias
Winter	0.530	0.312	0.188	0.249	0.532	0.258	0.230	0.118
Spring	0.760	0.293	0.197	0.217	0.744	0.247	0.219	0.114
Summer	0.675	0.271	0.200	0.182	0.710	0.205	0.203	0.027
Fall	0.472	0.263	0.202	0.168	0.473	0.231	0.225	0.051
All	0.645	0.285	0.200	0.203	0.639	0.236	0.223	0.076

in chl$_0$, incurring the most significantly reduced determination coefficient when satellite chl$_0$ is used in place of *in situ* data.

VGPM and MARRA exhibit seasonally dependent performance when evaluated within winter (December–February), spring (March–May), summer (June–August), and fall (September–October) periods (Table 3). While both models are biased high year-round, they are more so in the winter/spring, and less in the summer/fall. Neither model appears to fully capture the seasonal variability in chlorophyll-specific phytoplankton growth evident in Fig. 2. Consequently, model bias is highest when chlorophyll-specific productivity is relatively low. Coefficients of determination range widely among seasons, with values highest values in spring (~0.75) and lowest in fall (~0.47). However, RMSD and RMSDcp do not follow the same pattern, and r^2 values are likely high in the spring largely due to it being the season of greatest PP variance.

3.3. Empirical adjustment of PPAs

The simplest method of improving an existing PPA is an empirical adjustment of the model output to match *in situ* data (Kahru et al., 2009). The adjustment has no ecological basis, but improves performance. A next step is to improve the model's parameterizations of physiological variables, for example the quantum yield and chlorophyll-specific absorption terms in MARRA or the optimal carbon fixation rate term (P^B_{OPT}) in VGPM. The latter has been done before, with the original seventh-order fit to SST replaced by alternate functions of SST, chl$_0$, or a combination of the two (Friedrichs et al., 2009). Here, we rearranged the original VGPM algorithm (Eq. (10) of Behrenfeld and Falkowski, 1997) and used measured PP and chl$_0$ to calculate P^B_{OPT} values that give perfect model-data agreement for each data point:

$$P^B_{OPT,CALC} = \frac{PP}{0.66125 \cdot (PAR/PAR+4.1) \cdot z_{eu} \cdot chl_0 \cdot d_{irr}} \quad (3)$$

We estimated euphotic zone depth (z_{eu}) from chl$_0$ (Morel and Berthon, 1989) and day length (d_{irr}) from latitude and time of year (Forsythe et al., 1995). We then searched for correlations of $P^B_{OPT,CALC}$ with environmental variables including chl$_0$, SST, PAR, latitude, and distance from shore. As in Eppley et al. (1985), SST did not offer significant improvement of the parameterization. PAR is strongly correlated with the already included d_{irr}, and offered no additional gains. We also found no significant relationship between $P^B_{OPT,CALC}$ and latitude. A clear relationship with chl$_0$ does exist, as expected from the upper left panel of Fig. 2, and we find that for a given chl$_0$, $P^B_{OPT,CALC}$ is higher closer to shore, likely due to increased nutrient availability and a different phytoplankton community composition. Fig. 3 illustrates this relationship, the basis for a southern California-specific VGPM variant (VGPM-SC). All CalCOFI PP casts from 1997 to 2004 were divided into three regimes based on their distance from the coast – near shore (< 50 km), transition (50–250 km), and offshore (> 250 km), and $P^B_{OPT,CALC}$ was fit as a power law function of chl$_0$ within each
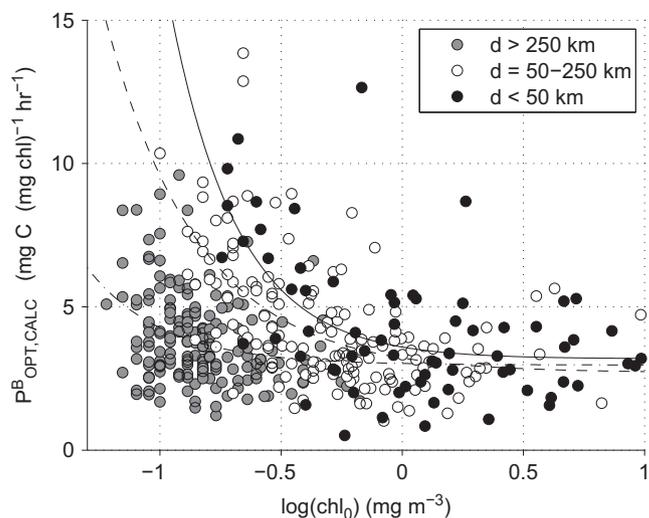
Fig. 3. P^B_{OPT} values for VGPM calculated from *in situ* data according to Eq. (3). Stations are divided into three regions by distance from shore, *d*. Solid, dashed, and dash-dot lines used for the development of VGPM-SC are power law fits ($y=ax^b+c$) to near shore (< 50 km, $a=0.054$, $b=-1.38$, $c=2.97$), transition (50–250 km, $a=0.513$, $b=-1.13$, $c=2.70$), and offshore (> 250 km, $a=0.410$, $b=-1.54$, $c=3.19$) regions, respectively. Data shown here is limited to 1997–2004, the period designated for model development.
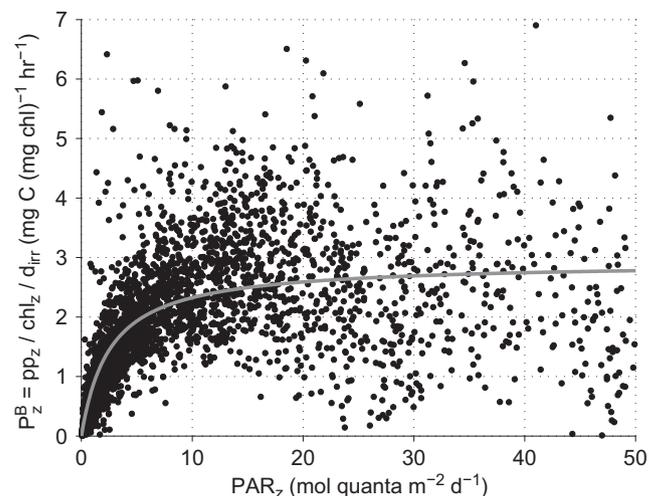
Fig. 4. Dependence of carbon fixation rate at all depths, P^B_z, on PAR for CalCOFI stations with satellite match-ups from 1997 to 2004. The gray line fit, used to develop the VRPM-SC algorithm, is described by $P^B_z=2.9 \cdot PAR_z/(PAR_z+2.6)$.

cross-shore region. When tested in the 2005–2010 period, VGPM-SC improves all model statistics relative to the original VGPM and other models tested here (Table 2).

3.4. Vertically resolved production model

Given the availability of vertically resolved *in situ* primary productivity measurements from the CalCOFI dataset, model-data productivity comparisons are possible at discrete depths as well for the euphotic zone integrated value. We take advantage of that resource here to examine the potential for the development of a vertically resolved production model for the SCCS (VRPM-SC). Again, we start with the depth integrated VGPM, which performed well when initially developed in a vertically resolved form (Behrenfeld and Falkowski, 1997). We discard factors related to vertical generalization of the productivity profile to obtain a

simple expression for depth-dependent productivity (pp_z)

$$pp_z = P_z^B \cdot chl_z \cdot d_{irr} \qquad (4)$$

where P_z^B and chl_z are the carbon fixation rate and chlorophyll concentration, respectively, at depth z. PAR is assumed to be the next most important factor influencing depth-dependent productivity, as we expect photoinhibition at high light levels and light limitation at depth. Though PAR profiles are not consistently available for CalCOFI data, productivity measurements are accompanied by reported light levels, expressed as a percentage of the surface value. To estimate the vertical PAR profile, CalCOFI *in situ* light percentages are multiplied by the SeaWiFS/MODIS remote sensing surface PAR.

Fig. 4 shows the dependence of P_z^B on PAR at discrete depths (PAR_z), most significantly the light limitation below $\sim$10 mol quanta m^{-2} d^{-1}. At higher light levels, P_z^B is noisy and ranges from 0 to 5 mg C mg chl^{-1} h^{-1}. Photoinhibition is difficult to discern for the full dataset, though maximum P_z^B values for individual profiles occur between 0 and 1.5 optical depths, consistent with previous analysis (Behrenfeld and Falkowski, 1997). We fit P_z^B to capture decreased carbon fixation rates at low light levels and the mean rate at higher light levels, resulting in the final form of VRPM-SC:

$$pp_z = 2.9 \cdot chl_z \cdot d_{irr} \cdot \frac{PAR_z}{PAR_z + 2.6} \qquad (5)$$

while further parameterization of P_z^B could be attempted with the use of SST, latitude, or distance from shore, we focus on the impact of the vertical chlorophyll and PAR profiles, as outlined in the next section.

3.5. Importance of chlorophyll and light profiles

The value of providing *in situ* chlorophyll and light profiles to PPAs is illustrated by incrementally improving the quality of input data to VRPM-SC. The base level of performance is that achieved with solely remote sensing inputs (Fig. 5a). The vertical chlorophyll profile is estimated from chl_0 according to Woźniak et al. (2003) and light attenuation at depth is calculated from an empirically derived, chlorophyll dependent extinction coefficient, k_z (Parsons et al., 1984)

$$k_z = 0.04 + 0.0088 chl_z + 0.054 chl_z^{0.67} \qquad (6)$$

while it is possible from the CalCOFI data to develop an *ad hoc* chl_z–k_z relation for the SCCS, we find that correlation between the two is weak and tuning Eq. (6) offers negligible improvement in resultant model performance. By all metrics, VRPM-SC performance with only satellite data input is slightly worse than that of VGPM-SC, but comparable to previously established PPAs (Fig. 5a and Table 2). This outcome is not surprising as those models include just one additional variable, SST, which does not significantly improve model performance in the SCCS (Eppley et al., 1985, this study).

Model performance with CalCOFI chl_0 substituted in place of SeaWiFS estimates represents the best performance achievable as satellite chlorophyll estimates improve, converging on perfect agreement with *in situ* data. However, comparison of statistics in Table 2 indicates that uncertainty in satellite data is a relatively small contributor to model error, and the same holds true for VRPM-SC (Fig. 5b). With *in situ* chl_0 replacing satellite data, total log_{10} RMSD and RMSDcp are reduced by just 2–3%, while r^2 improves marginally from 0.537 to 0.564. Additional performance gains may be possible with improved satellite PAR estimates, though they are likely to be small particularly for VGPM variants, which are inherently insensitive to PAR except at very low light levels.

In contrast to the relatively small error induced by uncertainty in chl_0, accurate representation of the subsurface chlorophyll profile improves model performance significantly (Fig. 5c). RMSD drops from 0.215 for PP estimates based on satellite chl_0 to 0.177
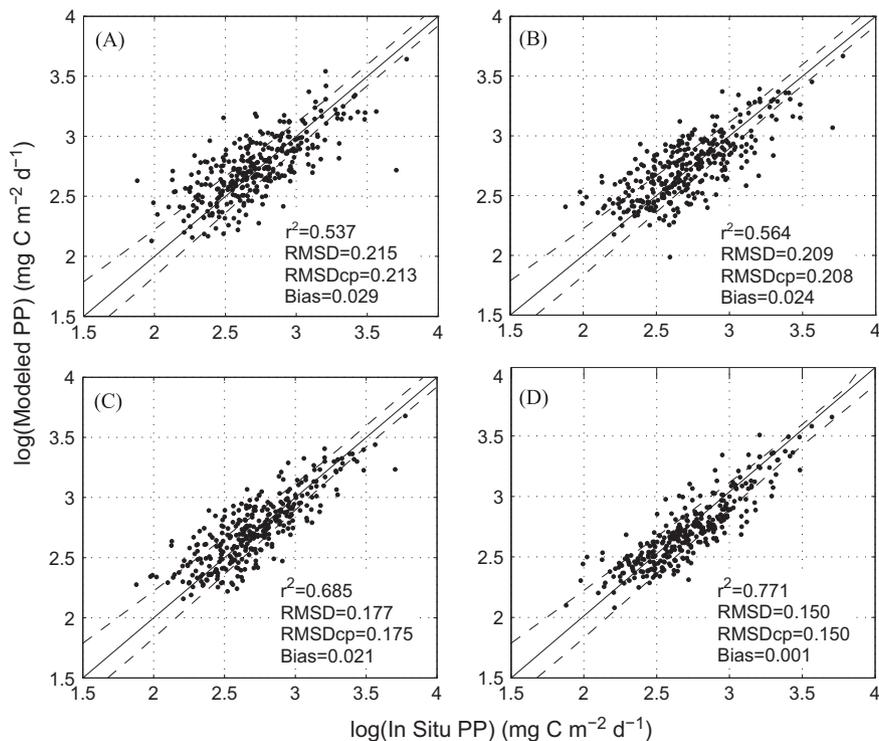

Fig. 5. Dependence of VRPM-SC performance on available input data for all 2005–2010 CalCOFI-satellite match-ups. In all cases, surface PAR comes from satellite. Additional inputs are (a) satellite chlorophyll and SST, (b) *in situ* surface chlorophyll and SST, (c) *in situ* chlorophyll profile, (d) *in situ* chlorophyll and light profiles. Dashed lines indicate uncertainty bounds for *in situ* primary productivity measurement, estimated according to Saba et al. (2011).
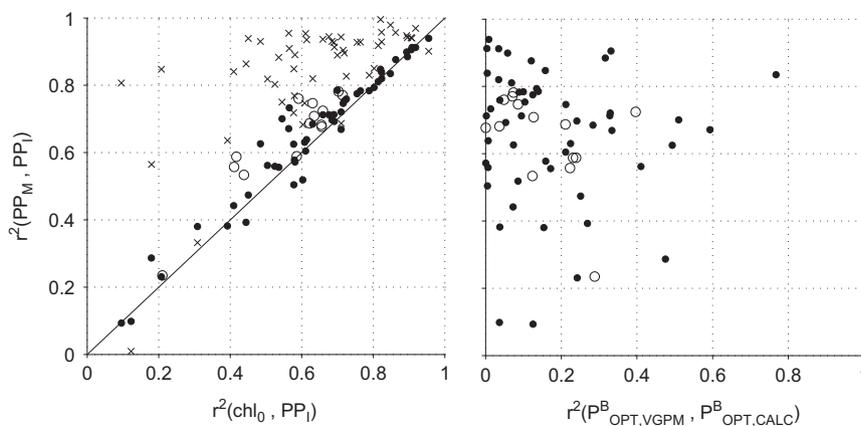
Fig. 6. Impact of individual model components on PPA performance. On the horizontal axes are r^2 values for (left) surface chlorophyll correlation with PP, calculated on log-transformed data, and (right) P^B_{OPT}, with the VGPM predicted value compared to the calculated value that would give perfect model-data agreement. In each panel, the vertical axis shows model performance as indicated by r^2 between modeled and measured PP. The model-data comparisons are calculated on each quarterly cruise for VGPM (solid dots) and VRPM-SC (X's), and on each year (1997–2010) for VGPM (open circles).

with known chlorophyll profiles – an improvement six times larger than that obtained by substituting *in situ* chl$_0$ for satellite data. RMSDcp and r^2 also improve dramatically, to 0.175 and 0.685 respectively, while bias remains small.

Finally, we explore model performance as influenced by uncertainty in the vertical light profile. CalCOFI reports light levels coincident with PP measurements as percentages of the surface value. We combine these subsurface light percentages with satellite surface PAR to obtain *in situ* PAR profiles. With *in situ* PAR profiles substituted for the empirical estimate of Eq. (6), VRPM-SC performance experiences yet another jump comparable to that achieved through inclusion of the chlorophyll profile (Fig. 5d). As P^B is relatively insensitive to PAR above ∼10 mol quanta m^{-2} d^{-1}, model improvements must be forced primarily by capturing light limitation at depth. RMSD and RMSDcp drop to 0.150, bias is negligible, and r^2 improves to 0.771. Accurate representation of chlorophyll and light profiles together represent a potential improvement in total model skill (RMSD) an order of magnitude greater than that possible from improved satellite chlorophyll estimates (Fig. 5). Furthermore, much of the discrepancy between *in situ* and VRPM-SC PP estimates lies within the uncertainty of the *in situ* measurements. Saba et al. (2011) assumed uncertainties decreasing as a linear function of log(PP), from 50% for PP $\leq$ 50 mg C m^{-2} d^{-1} to 20% for PP $\geq$ 2000 mg C m^{-2} d^{-1}. In the best-case scenario, given these uncertainties, model statistics for VRPM-SC (Fig. 5d) improve to $r^2 = 0.943$ and RMSD = 0.070.

The performance of satellite PPAs, relying solely on observable surface properties, is regulated by the relationship between chl$_0$ and PP, captured by the ESQRT model. More complex formulations employing additional parameters (SST, PAR) offer only modest improvements in the SCCS (Kahru et al., 2009). In fact, when model performance is assessed individually for quarterly CalCOFI cruises, VGPM captures no more variance than that associated with chl$_0$ (Fig. 6). Extending the model-data evaluation over a year or more results in improved r^2 for VGPM due to the inclusion of day length, which captures seasonal variability in chlorophyll-specific productivity. VRPM-SC, on the other hand, is weakly influenced by the chl$_0$–PP relationship, and model performance is excellent on nearly all cruises ($r^2 > 0.8$ for 42 of 52 cruises, as compared to 12 of 52 for VGPM). While efforts to improve VGPM typically focus on tuning P^B_{OPT}, we find no correlation between model performance and the accuracy of P^B_{OPT} prediction (Fig. 6). Accordingly, we turn our attention to improving our knowledge of vertical profiles.

Table 4

VRPM-SC statistics for CalCOFI stations with glider and satellite match-ups within 10 days and 10 km ($n = 38$).

Chlorophyll data	PAR Data	r^2	RMSD	RMSDcp	Bias
CalCOFI surface	SeaWiFS/MODIS	0.521	0.200	0.199	0.016
Glider profile	SeaWiFS/MODIS	0.585	0.188	0.186	0.027
CalCOFI profile	SeaWiFS/MODIS	0.586	0.182	0.182	0.017
CalCOFI profile	CalCOFI profile	0.735	0.142	0.141	−0.015

3.6. Potential for improving chlorophyll profiles

The potential of vertically resolved PPAs to improve productivity estimates, detailed above, is evident. However, these models suffer from one clear limitation: the scarcity of *in situ* vertical chlorophyll and PAR profiles. As a result, in large scale comparisons they demonstrate no clear performance edge over vertically integrated models (Friedrichs et al., 2009; Saba et al., 2011). Chlorophyll at depth is typically estimated from the surface value based on empirical relationships (Marra et al., 2003; Woźniak et al., 2003; Ostrowska et al., 2007), which assume that a deep chlorophyll maximum accompanies low chl$_0$ and high surface chlorophyll is associated with a relatively uniform vertical distribution in the surface mixed layer. While qualitative structural agreement with *in situ* data is good, any discrepancies in the position or concentration of subsurface chlorophyll features influence PP estimates significantly.

In situ vertical chlorophyll profiles are sparse, though they are becoming more widely available thanks to vertical profiling floats and underwater gliders. The latter are capable of autonomous, long-range operation for several months while carrying a variety of oceanographic instruments including CTD sensors (conductivity, temperature, depth) and fluorometers. We explore here the potential of using glider data to improve PP estimates from a vertically resolved production model.

Application of glider data to PP estimates was initially constrained to glider profiles with available satellite match-ups and within 10 km and 10 days of CalCOFI sampling, similar to decorrelation scales reported for the SCCS (4–8 km and ∼17 days, Frolov et al., 2012a). A total of 38 CalCOFI PP stations had corresponding glider profiles within the 10 km/10 day window; locations for successful match-ups are shown in Fig. 1. For this small sample we find that inclusion of glider chlorophyll profiles in VRPM-SC, in comparison to chl$_0$ alone, improves model performance. RMSD drops from 0.200 to 0.188 and r^2 increases from 0.521 to 0.585

(A)

(B)
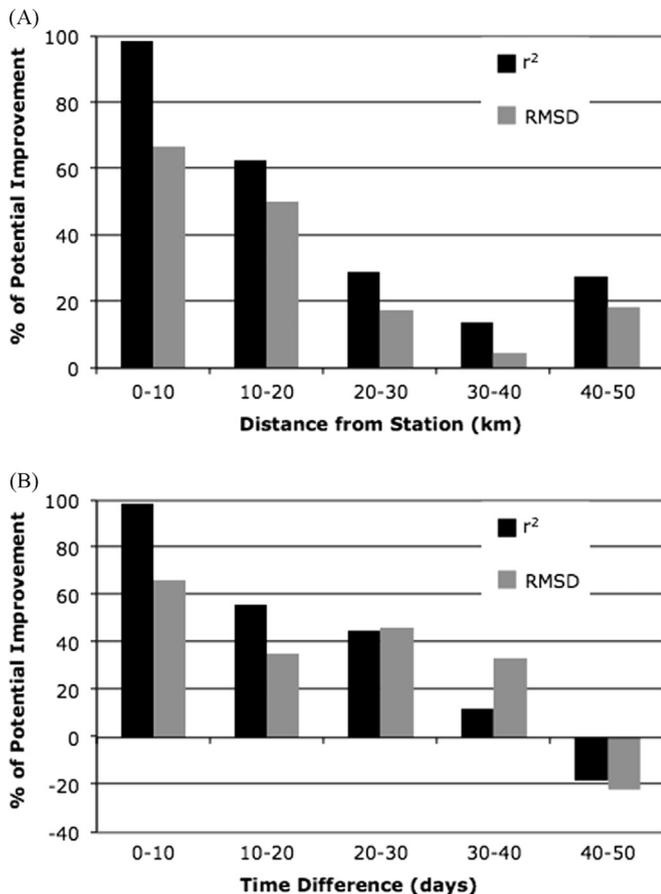
Fig. 7. Efficacy of incorporating glider chlorophyll profiles to improve PP estimates as a function of distance and time between glider and PP estimates. (Top) Match-ups were constrained within 10 days, while distance between CalCOFI and glider data increased in 10 km increments. The numbers of match-ups in each bin were 38, 45, 55, 57, and 58, from closest to farthest. (Bottom) Match-ups were constrained within 10 km, while increasing temporal disparities were considered. The numbers of match-ups in each bin, from shortest time to longest, were 38, 61, 56, 55, and 58. In each case, model improvements were measured relative to the case where only chl_0 was known, with vertical structure based on empirical relationships. The y-axis represents improvement in VRPM-SC performance achieved with glider chlorophyll profiles relative to improvement achieved with CalCOFI chlorophyll profiles (*i.e.* |Row2–Row1|/|Row3–Row1| in Table 4). Note that much more improvement is possible with the addition of known PAR profiles.

(Table 4). This is a substantial portion of the gain realized when chlorophyll is known at the exact location and depth of the productivity data, indicating the high quality of glider match-ups within the 10 km/10 day window (Fig. 7). As match-up constraints are relaxed, the power of gliders to effect positive change in model performance is reduced, though a modest improvement is seen even at time and space scales significantly longer than 10 days and 10 km. Although these gliders did not include light profiles, commercially available PAR sensors are routinely deployed on gliders and profiling floats; addition of that data would further improve the PP estimates.

4. Discussion

4.1. Limitations of satellite NPP algorithms

We examined properties of a 26-year primary productivity record, composed of over 1500 stations throughout the SCCS. The ratio of integrated primary productivity to surface chlorophyll, a value of key significance for nearly all satellite PPAs (Lee et al., 1996 is one exception), correlated strongly to chl_0. The ratio of

surface productivity to surface chlorophyll did not, however, indicating that the former is a proxy for variability in the vertical structure of productivity, not in phytoplankton physiology. The same appeared to be true for correlations with other variables, often used in PPAs to parameterize the relationship between chl_0 and PP. These models seem to rely heavily on surface variables to implicitly represent subsurface features, and inherent limitations in that process may explain why we found similarly restricted model performance for a range of PPAs (MARRA, VGPM, and VGPM-KI). Increased model skill was obtained using a VGPM variant relating P_{OPT}^B to chl_0 and distance from shore (Fig. 3), with higher chlorophyll-specific productivity near shore presumably due to nutrient availability and phytoplankton community structure. The new model (VGPM-SC) improved model-data r^2 by about 6% over the best-performing existing PPAs, and a larger reduction of total RMSD (19%) was due mostly to elimination of a systematic model-data offset. While VGPM-SC is a useful tool for the SCCS, and a similar approach may be valuable in other eastern boundary current systems, it is worth noting that the use of distance from shore in NPP models is less than ideal. For example, upwelled water that separates from the coast at Pt. Conception may be offshore in terms of position but biologically more representative of coastal water. Also, static variables such as distance from shore have no ability to capture change in the system over time.

Regardless of the method used to relate chl_0 to PP, satellite PPAs are inherently limited by their ignorance of vertical structure in the water column. Most of their power for PP estimation comes from the correlation of chl_0 to PP. This was noted at the outset of the satellite PP era by Eppley et al. (1985), whose observations produced the elegant but clearly limited ESQRT model, in which PP is a function of chl_0 alone. Several decades later, numerous models of varying complexity and regional specificity are available. However in the round robin comparison of Friedrichs et al. (2009), with 30 participating satellite and biogeochemical models, ESQRT was best in total model skill (RMSD) by just one. Saba et al. (2011) found ESQRT to be among the best performing models in 5 of 10 regions across the globe. In our SCCS analysis, we find that VGPM performance is driven almost entirely by the correlation of PP and chl_0, and accurate prediction of P_{OPT}^B, the model's key physiological parameter, provides no clear improvement to PP estimates (Fig. 6). It makes sense then that model fidelity would be enhanced more by accurate representation of the vertical structure than by further refinement of surface-based calculations.

4.2. Subsurface data for NPP estimates

We used a very simple vertically resolved production model (VRPM-SC) to explore the utility of *in situ* subsurface measurements, and found that even without capturing any physiological variability (*i.e.* assuming P_z^B is constant unless light limited), substantially improved PP estimates are achieved by including *in situ* chlorophyll and light profiles (Fig. 5). Relative to model statistics with only satellite data available, chlorophyll and light profiles enable a 44% increase in model r^2 (from 0.537 to 0.771) and a 30% reduction in total RMSD (from 0.215 to 0.150). In contrast, the evolution of satellite PPAs over several decades has produced an 18% increase in r^2 (from 0.475 for ESQRT to 0.561 for MARRA) and negligible improvement in total RMSD (from 0.248 for ESQRT to 0.247 for VGPM-KI). Friedrichs et al. (2009) suggested that with continued model improvement, satellite PPA performance might soon fall within the uncertainty of *in situ* measurements (RMSD=0.070). Reaching that metric in the SCCS by satellite alone appears to be far away if possible at all, based on past progress. The addition of *in situ* profiles with VRPM-SC immediately provides a large step forward, and we suggest that it is presently the best way to improve remote PP estimates.

Of course, the inherent obstacle in realizing potential gains described in Fig. 5 is the provision of subsurface data. Autonomous technologies, including AUVs, profiling floats, and underwater gliders, are platforms that today are capable of that task. Gliders, first envisioned by Henry Stommel (1989), have achieved widespread use in long-range, months-long deployments. In 2012 alone, Scripps Institution of Oceanography used Spray gliders to collect over 10 glider-years of data including over 23,000 dives to depths of up to 1000 m. Two gliders continuously trace CalCOFI lines 80 and 90 (yielding over 6000 dives in 2012), and we searched for the glider profiles nearest CalCOFI PP casts. For 38 stations, CalCOFI and Spray data were found within 10 days and 10 km of each other. Improvements in VRPM-SC performance enabled by glider data were nearly equal to those attained using CalCOFI chlorophyll measured coincident with primary productivity (Table 4 and Fig. 7). In this study, glider fluorescence was converted to chlorophyll by the algorithm of Lavigne et al. (2012), which implicitly accounts for several sources of uncertainty in chlorophyll estimation from gliders. Alternatively (or in addition), uncertainty in glider-based measurements due to instrument drift (Cetinić et al., 2009) and daytime fluorescence quenching (Sackmann et al., 2008) may be reduced by pre- and post-deployment calibrations, anti-fouling strategies, and use of night-time measurements to avoid quenching effects.

Fig. 7 illustrates the spatial and temporal extent of improvements in PP estimation around glider profiles. The improvement in model performance enabled by glider fluorescence data, as a percentage of the increase with a known chlorophyll profile at the exact place and time of PP estimation, decreases as the distance between glider and PP estimation increases, especially beyond 20 km. However, even at separation distances up to 50 km, model performance is improved by glider fluorescence profiles. Time lag between glider data and PP estimation also limits performance gains, with a fairly consistent decline as separation increases. Beyond 40 days, inclusion of glider profiles actually resulted in worse model performance than an empirical estimation of the profile. For comparison, spatial and temporal decorrelation scales reported for surface chlorophyll in the SCCS are 4–8 km and ~17 days, respectively (Frolov et al., 2012a). In all cases, the gliders available for these comparisons were not equipped with PAR sensors, which appear to represent substantial potential improvement beyond that provided by fluorometers alone (Table 4). Though we were unable to assess the efficacy of glider-based PAR sensors, which must contend with operational issues such as self-shading and hull reflection, their use is not unprecedented (*e.g.* Rudnick et al., 2004).

Another useful platform is the autonomous profiling float, as in the global Argo program. Approximately 3000 Argo floats are deployed at any time, covering the ocean at ~3° resolution and performing vertical profiles of the ocean's upper 2000 m at 10-day frequency. While the core Argo measurements are temperature, salinity, and position, small numbers of "Bio-Argo" floats have been deployed with optical sensors for downward irradiance and chlorophyll-a fluorescence (Xing et al., 2011). Addition of fluorometers and PAR sensors to a greater portion of the Argo fleet could supplement and ground-truth satellite PP models, improving global productivity estimates.

4.3. Uncertainty in the CalCOFI PP data

As described in recent PPA round robin comparisons (Friedrichs et al., 2009; Saba et al., 2011), observational uncertainty in PP measurements is a considerable contributor to model-data discrepancies. The CalCOFI dataset is not different, and Munro et al. (2013) suggest that CalCOFI PP measurements are consistently biased low, likely due to $DO^{14}C$ excretion and limitations of simulated on-deck incubations. It is likely that *in situ* data uncertainty is to blame for at least part of the substantial positive bias reported for PPAs in this study (Table 2). Friedrichs et al. (2009) found that the models with greatest skill were generally those with lowest bias, indicating that biased PP observations may significantly affect the outcome of a model comparison. Similarly, empirically tuned models such as VGPM-SC and VRPM-SC inherently carry the biases of the data used to develop them.

However, the CalCOFI record is consistent over 25+ years, any underestimation of productivity does not appear to be related to the magnitude of productivity (Munro et al., 2013), and there is no indication that the variance is incorrect. Improvements in model performance may therefore be more accurately assessed with the centered-pattern RMSD (RMSDcp) and r^2, which are independent of bias, than with total RMSD. In either case, the key findings of this study are unchanged: for the SCCS, satellite PPAs have improved little over recent decades (Table 2) and vertical profiles hold substantial value for improving model performance (Fig. 5).

4.4. Considerations for further study

While the analysis here demonstrates the feasibility of glider- or float-aided PP estimates in the SCCS, it is restricted to locations of synchronized glider and shipboard sampling. Expansion of coordinated profiler and shipboard sampling programs to additional physically and biologically distinct regions would further inform the true potential and limitations of autonomous vertical profilers for improving our understanding of PP. Similarly, determination of the optimal method to combine high vertical resolution *in situ* data with synoptic satellite surface coverage is beyond the scope of this study. Efforts of this nature have been carried out to improve the quality of subsurface chlorophyll estimation (Boss et al., 2008; Lavigne et al., 2012), and a similar effort for productivity is likely to be valuable.

The CCS, like other eastern boundary current systems, is an extremely dynamic environment, with spatially and temporally variable phytoplankton populations. Vertical chlorophyll structure at any time may reflect surface-dominated diatom blooms, vertically migrating dinoflagellates, low-light cyanobacteria, and a host of other communities. Vertically migrating species represent a particular challenge for satellites, and fundamental alteration of the PP to chl_0 ratio through changes in vertical phytoplankton distribution may accompany shifts in community structure (*e.g.* the 2004–2006 "age of dinoflagellates" in Monterey Bay, Jester et al., 2009). Moreover, empirical algorithms for estimating chlorophyll at depth have no chance of capturing unexpected subsurface chlorophyll due to subduction of upwelled waters, a pervasive feature of the CCS that may impact a substantial portion of upwelling-derived productivity (Washburn et al., 1991; Barth et al., 2002). Similarly, estimation of subsurface PAR is particularly difficult in an optically complex (case 2) environment, where light attenuation is significantly influenced by constituents that do not co-vary with chlorophyll. In the open ocean, reduced optical complexity enables better modeling of PAR absorption, and good success has been found estimating chlorophyll profiles from surface measurements (*e.g.* Morel and Berthon, 1989). It may therefore be expected that vertical profiles are less important in these regions and PP models are capable of performing relatively well with satellite data alone. However, oligotrophic regions are notably problematic for satellite PPAs, and particularly for depth resolved PPAs (Friedrichs et al. 2009), so a study similar to ours in an open ocean environment would be a valuable one.

Finally, even with complete knowledge of subsurface chlorophyll and light profiles, our ability to determine net primary productivity ultimately depends on understanding the factors governing phytoplankton growth, respiration, and mortality. Fortunately, the suite

of satellite PPAs already available, through their functional forms and parameterizations, encompass an enormous body of knowledge surrounding those processes. Reducing uncertainty in subsurface chlorophyll and PAR simply enables a focus on representing those physiological effects, rather than finding proxies for vertical structure.

Acknowledgments

References

Barth, J.A., Cowles, T.J., Kosro, P.M., Shearman, R.K., Huyer, A., Smith, R.L., 2002. Injection of carbon from the shelf to offshore beneath the euphotic zone in the California Current. J. Geophys. Res. 107 (C6), 3057.

Behrenfeld, M., Falkowski, P., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. 42 (1), 1–20.

Boss, E., Swift, D., Taylor, L., Brickley, P., Zaneveld, R., Riser, S., Perry, M., Strutton, P., 2008. Observations of pigment and particle distributions in the western North Atlantic from an autonomous float and ocean color satellite. Limnol. Oceanogr. 53, 2112–2122.

Campbell, J., Antoine, D., Armstrong, R., Arrigo, K., Balch, W., Barber, R., Behrenfeld, M., Bidigare, R., Bishop, J., Carr, M.-E., Esaias, W., Falkowski, P., Hoepffner, N., Iverson, R., Kiefer, D., Lohrenz, S., Marra, J., Morel, A., Ryan, J., Vedernikov, V., Waters, K., Yentsch, C., Yoder, J., 2002. Comparison of algorithms for estimating ocean primary production from surface chlorophyll, temperature, and irradiance. Global Biogeochem. Cycles 16, 1035.

Carr, M.E., Friedrichs, M.A. M., Schmeltz, M., Aita, M.N., Antoine, D., Arrigo, K.R., Asanuma, I., Aumont, O., Barber, R., Behrenfeld, M., Bidigare, R., Buitenhuis, E.T., Campbell, J., Ciotti, A., Dierssen, H., Dowell, M., Dunne, J., Esaias, W., Gentili, B., Gregg, W., Groom, S., Hoepffner, N., Ishizaka, J., Kameda, T., Le Quéré, C., Lohrenz, S., Marra, J., M´elin, F., Moore, K., Morel, A., Reddy, T.E., Ryan, J., Scardi, M., Smyth, T., Turpie, K., Tilstone, G., Waters, K., Yamanaka, Y., 2006. A comparison of global estimates of marine primary production from ocean color. Deep-Sea Res. Part II 53, 741–770.

Casey, K.S., Brandon, T.B., Cornillon, P.R., Evans, R., 2010. The past, present and future of the AVHRR Pathfinder SST program. In: Barale, V., Gower, J.F. R., Alberotanza, L. (Eds.), Oceanography from Space: Revisited. Springer, Netherlands, pp. 273–287.

Cetinić, I., Toro-Farmer, G., Ragan, M., Oberg, C., Jones, B, 2009. Calibration procedure for Slocum glider deployed optical instruments. Opt. Express 17, 15420–15430.

Eppley, R., 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. 70, 1063–1085.

Eppley, R., Steward, E., Abbott, M., Heyman, U., 1985. Estimating ocean primary production from satellite chlorophyll: introduction to regional differences and statistics for the Southern California Bight. J. Plankton Res. 7, 57–70.

Eppley, R.W., 1992. Chlorophyll, photosynthesis and new production in the Southern California Bight. Prog. Oceanogr. 30, 117–150.

Forsythe, W.C., Rykiel Jr., E.J., Stahl, R.S., Wu, H.-I., Schoolfield, R.M., 1995. A model comparison for daylength as a function of latitude and day of year. Ecol. Model. 80 (1), 87–95.

Friedrichs, M.A. M., Carr, M.-E., Barber, R.T., Scardi, M., Antoine, D., Armstrong, R.A., Asanuma, I., Behrenfeld, M.J., Buitenhuis, E.T., Chai, F., Christian, J.R., Ciotti, A.M., Doney, S.C., Dowell, M., Dunne, J., Gentili, B., Gregg, W., Hoepffner, N., Ishizaka, J., Kameda, T., Lima, I., Marra, J., Mélin, F., Moore, J.K., Morel, A., O'Malley, R.T., O'Reilly, J., Saba, V.S., Schmeltz, M., Smyth, T.J., Tjiputra, J., Waters, K.,

Westberry, A., Winguth, A., 2009. Assessing the uncertainties of model estimates of primary productivity in the tropical Pacific Ocean. J. Mar. Syst. 76, 113–133.

Frolov, S., Kudela, R.M., Bellingham, J.G., 2012a. Monitoring of harmful algal blooms in the era of diminishing resources: a case study of the U.S. West Coast. Harmful Algae 21 and 22, 1–12.

Frolov, S., Ryan, J.P., Chavez, F.P., 2012b. Predicting euphotic-depth-integrated chlorophyll-a from discrete-depth and satellite-observable chlorophyll-a off central California. J. Geophys. Res. 117, C05042.

Frouin, R., Franz, B. A., Werdell, P. J., 2003. The SeaWiFS PAR product, in: Hooker, B. S., Firestone, E.R. (Eds.), Algorithm Updates for the Fourth SeaWiFS Data Reprocessing. NASA/TM-2003-206892, p. 22.

Jester, R., Lefebvre, K., Langlois, G., Vigilant, V., Baugh, K., Silver, M.W., 2009. A shift in the dominant toxin-producing algal species in central California alters phycotoxins in food webs. Harmful Algae 8, 291–298.

Kahru, M., Kudela, R.M., Manzano-Sarabia, M., Mitchell, B.G., 2009. Trends in primary production in the California Current detected with satellite data. J. Geophys. Res. 114, C02004.

Kahru, M., Kudela, R.M., Manzano-Sarabia, M., Mitchell, B.G., 2012. Trends in the surface chlorophyll of the California Current: merging data from multiple ocean color satellites. Deep-Sea Res. Part II 77–80, 89–98.

Kameda, T., Ishizaka, J., 2005. Size-fractionated primary production estimated by a two-phytoplankton community model applicable to ocean color remote sensing. J. Oceanogr. 61, 663–672.

Lavigne, H., D'Ortenzio, F., Claustre, H., Poteau, A., 2012. Towards a merged satellite and in situ fluorescence ocean chlorophyll product. Biogeosciences 9, 2111–2125.

Lee, Z.P., Carder, K.L., Marra, J., Steward, R.G., Perry, M.J., 1996. Estimating primary production at depth from remote sensing. Appl. Opt. 35 (3), 463–474.

Marra, J., Ho, C., Trees, C., 2003. An Alternative Algorithm for the Calculation of Primary Productivity from Remote Sensing Data. LDEO Technical Report #LDEO-2003-1.

Morel, A., Berthon, J.F., 1989. Surface pigments, algal biomass profiles, and potential production of the euphotic layer: relationships reinvestigated in view of remote-sensing applications. Limnol. Oceanogr. 34 (8), 1545–1562.

Munro, D.R., Quay, P.D., Juranek, L.W., Goericke, R., 2013. Biological production rates off the Southern California coast estimated from triple O_2 isotopes and O_2:Ar gas ratios. Limnol. Oceanogr. 58, 1312–1328.

Ostrowska, M., Majchrowski, R., Stoń-Egiert, J., Woźniak, B., Ficek, D., Dera, J., 2007. Remote sensing of vertical phytoplankton pigment distributions in the Baltic: new mathematical expressions. Part 1: total chlorophyll a distribution. Oceanologia 49 (4), 471–489.

Parsons, T.R., Takahashi, M., Hargrave, B., 1984. Biological Oceanographic Processes. Pregamon Press, New York.

Rudnick, D.L., Davis, R.E., Eriksen, C.C., Fratantoni, D.M., Perry, M.J., 2004. Underwater gliders for ocean research. Mar. Tech. Soc. J. 38 (2), 73–84.

Saba, V.S., Friedrichs, M.A. M., Antoine, D., Armstrong, R.A., Asanuma, I., Behrenfeld, M.J., Ciotti, A.M., Dowell, M., Hoepffner, N., Hyde, K.J. W., Ishizaka, J., Kameda, T., Marra, J., Mélin, F., Morel, A., O'Reilly, J., Scardi, M., Smith Jr., W.O., Smyth, T.J., Tang, S., Uitz, J., Waters, K., Westberry, T.K., 2011. An evaluation of ocean color model estimates of marine primary productivity in coastal and pelagic regions across the globe. Biogeosciences 8, 489–503.

Sackmann, B.S., Perry, M.J., Eriksen, C.C., 2008. Seaglider observations of variability in daytime fluorescence quenching of chlorophyll-a in Northeastern Pacific coastal waters. Biogeosci. Discuss. 5, 2839–2865.

Sherman, J., Davis, R.E., Owens, W.B., Valdes, J., 2001. The autonomous underwater glider 'Spray'. IEEE J. Ocean. Eng. 26, 437–446.

Stommel, H., 1989. The Slocum mission. Oceanography 2, 22–25.

Washburn, L., Kadko, D.C., Jones, B.H., Hayward, T., Kosro, P.M., Stanton, T.P., Ramp, S., Cowles, T., 1991. Water mass subduction and the transport of phytoplankton in a coastal upwelling system. J. Geophys. Res. 96, 14927–14945.

Woźniak, B., Dera, J., Ficek, D., Majchrowski, R., Ostrowska, M., Kaczmarek, S., 2003. Modelling light and photosynthesis in the marine environment. Oceanologia 45 (2), 171–245.

Xing, X., Morel, A., Claustre, H., Antoine, D., D'Ortenzio, F., Poteau, A., Mignot, A., 2011. Combined processing and mutual interpretation of radiometry and fluorimetry from autonomous profiling bio-Argo floats: chlorophyll a retrieval. J. Geophys. Res. 116, C06020.