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Comparison of primary productivity estimates in the Baltic Sea based on the DESAMBEM algorithm with estimates based on other similar algorithms*

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Abstract

The quasi-synoptic view available from satellites has been broadly used in recent years to observe in near-real time the large-scale dynamics of marine ecosystems and to estimate primary productivity in the world ocean. However, the standard global NASA ocean colour algorithms generally do not produce good results in the Baltic Sea. In this paper, we compare the ability of seven algorithms to estimate depth-integrated daily primary production (PP, mg C m^{-2}) in the Baltic Sea. All the algorithms use surface chlorophyll concentration, sea surface temperature, photosynthetic available radiation, latitude, longitude and day of the year as input data. Algorithm-derived PP is then compared with PP estimates obtained from

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^{14}C uptake measurements. The results indicate that the best agreement between the modelled and measured PP in the Baltic Sea is obtained with the DESAMBEM algorithm. This result supports the notion that a regional approach should be used in the interpretation of ocean colour satellite data in the Baltic Sea.

1. Introduction

The quasi-synoptic view available from satellites makes it possible to observe the large-scale dynamics of marine ecosystems in near-real time. It is worth using these observations to quantify oceanic primary productivity (PP). Comparable, large-scale, observations cannot be achieved solely from ship-based PP measurements. Therefore, special efforts have been made in recent years to develop and evaluate algorithms for estimating primary productivity from satellite remote sensing products such as surface Chl *a* concentration (Chl), sea-surface temperature (SST) and photosynthetically available radiation (PAR) (e.g. Antoine et al. 1996, Behrenfeld & Falkowski 1997, Campbell et al. 2002, Carr et al. 2006, Friedrichs et al. 2009, Saba et al. 2011). Another way of assessing large-scale PP is to use coupled biogeochemical (BG) marine numerical models. With the enhanced computational capabilities of modern computers, BG models can now be run at appropriate horizontal and vertical resolutions to provide large-scale daily estimates of PP. Calculating accurate PP estimates over large areas is a crucial step in BG models, which are also used for assessing higher trophic dynamics, including zooplankton and even fish life cycles (e.g. Kiefer et al. 2011). BG models parameterize photosynthesis in much the same way as satellite PP algorithms. The main difference between the two approaches, however, is that satellite algorithms require satellite estimates of surface chlorophyll and temperature as input variables (e.g. O'Reilly et al. 1998, 2000, McClain 2008), whereas BG models explicitly compute these fields (although sometimes BG models can also assimilate satellite surface chlorophyll and SST data; see e.g. Gregg 2008). In addition, BG models simulate concentrations of nutrients, detritus, and often more than one functional or size groups of phytoplankton and zooplankton. They also incorporate mechanistic knowledge of nutrient uptake and physical transport of nutrients and biomass – information that is not derived directly from remote sensing PP algorithms.

Marine primary productivity is a large and highly variable component of the global carbon cycle and drives the oceanic biogeochemical cycles of other major chemical elements such as oxygen, iron, silicon, nitrogen and phosphorus. PP estimates from BG models and/or satellite data have been used for quantifying the air-sea flux of carbon dioxide (e.g. Bianchi et al. 2005), export production (e.g. Boyd & Trull 2007) and the production of climate-active gases such as dimethyl sulphide (e.g. Larsen 2005), as well as in research into the consequences of climate change for phytoplankton growth (Behrenfeld et al. 2006, Doney et al. 2009). Since PP estimates are crucial to our understanding of many vital oceanic processes, it is extremely important to validate the performance of the various PP algorithms with observations and to elucidate the reasons underlying the similarities/differences in model outputs. Such comparisons were carried out recently as part of the Primary Productivity Algorithm Round Robin (PPARR) series, funded by NASA (Campbell et al. 2002, Carr et al. 2006, Friedrichs et al. 2009, Saba et al. 2011). This activity provided an example of how the performance of primary productivity models could be compared. Such comparative results are valuable for those who wish to choose a single PP model to implement in a given study, and also to PP model developers, as they continue to improve their model formulations.

The PP models evaluated during PPARR were constructed with the aim of providing the best PP estimates at a global scale (e.g. Friedrichs et al. 2009, Saba et al. 2011). PPARR publications have stressed the fact that such global PP algorithms can produce significant over- or underestimates of primary productivity at regional/local scales (e.g. Campbell et al. 2002). At regional scales, regional algorithms should be derived for more accurate PP estimates. One example of such a challenging region is the Baltic Sea. It has been shown in the past that the standard NASA ocean colour algorithms generally do not produce good results in the Baltic Sea (e.g. Darecki & Stramski 2004). Consequently, significant efforts have been made to develop regional satellite remote sensing algorithms for the Baltic Sea (e.g. Woźniak et al. 2007, 2008, Darecki et al. 2008). The main objective of this paper is to compare the Baltic Sea PP DESAMBEM algorithm (e.g. Woźniak et al. 2008, Darecki et al. 2008) with six other PP models. Model-based PP estimates are also compared with in situ PP measurements. Our purpose is to improve the understanding of the similarities and differences between the models, and to verify which of them provides the most reliable PP estimates in the Baltic Sea region. In the near future, we plan to use these best models to study biological-physical interactions in the Baltic Sea. The comparative results presented in this paper will also be of interest to others who wish to implement satellite estimates of PP in the Baltic Sea region. In particular, this information will be of use to the participants in the SatBałtyk project (Satellite Monitoring of the Baltic Sea Environment, www.iopan.gda.pl/projects/SatBaltyk), who are working on improving the remote sensing PP DESAMBEM model formulations for the Baltic Sea.

2. Methods

2.1. Models

There is a range of different PP modelling approaches (see Campbell et al. 2002, Carr et al. 2006, Friedrichs et al. 2009, Saba et al. 2011 for model overviews and references). Model types have been broadly divided into wavelength- and depth-integrated (WIDI), wavelength-integrated and depth-resolved (WIDR), and wavelength- and depth-resolved models (WRDR) (Friedrichs et al. 2009). For our purpose we selected seven models. Four of them are satellite PP algorithms, of which only the DESAMBEM model belongs to the WRDR type, and only DESAMBEM is a regional model developed specifically for the Baltic Sea (Woźniak et al. 2008, Darecki et al. 2008). Additionally, we used three BG models in our calculations, two of which have frequently been used as regional Baltic Sea models (Neumann et al. 2002, Ołdakowski et al. 2005, Neumann & Schernewski 2005, 2008). Although the third one has been used for global simulations (Moore et al. 2002a,b, Moore et al. 2004), it is currently being adapted to Baltic Sea conditions by the members of our team. Note that the present comparison exercise did not attempt to assess the overall skill of the biogeochemical models; rather, its objective was to compare the potential of the BG models to accurately estimate PP, enabling them to be compared with satellite PP algorithms. In all of our calculations presented in the following sections we used the relationship between Chl and the spectral diffuse vertical attenuation coefficient for downwelling irradiance ($K_d(\lambda)$) taken from the DESAMBEM algorithm. Additionally, we assumed vertically uniform Chl in the water column in all of the calculations. This ensured that we had consistent light fields, water temperatures and Chl a concentrations in all our synthetic model situations. In all of the BG calculations carried out in this study we assumed a constant value of 30 for the C/Chl ratio. The selection of this particular value of the C/Chl ratio was justified by data collected in the Baltic Sea by IO PAN (Ostrowska, personal communication).

As our data sets did not include any information on nutrient limitation, we assumed in the present comparison that PP was regulated only by light and temperature. A simple, first-order, approach for assessing potential nutrient limitation is to identify the periods of time when nutrient concentrations are below the theoretical half-saturation constant (Ks). Though crude, this approach has often been used to determine which nutrient is the most limiting in the Baltic Sea (e.g. Moisander et al. 2003). Note, however, that the concentrations of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphate (DIP) may be low and the primary production and phytoplankton biomass high, if the regeneration and/or inflow of DIN and DIP are high. Therefore, the approach to nutrient limitation based on nutrient concentrations is probably too simplistic, and there are still many inherent uncertainties in our understanding of when and what nutrients are limiting PP in a given season and region of the Baltic Sea. Nevertheless, the prevailing paradigm is that (e.g. Moisander et al. 2003): (1) the open Baltic Sea is N-limited at the end of the summer; (2) this favours N_2-fixing cyanobacterial blooms; and (3) the N_2-fixing cyanobacteria are P-limited. It is in this context that we decided to test whether the relationship between calculated and measured PP improved if we rejected summer and early autumn data, i.e. if the data collected between 15 May and 1 October of each year were excluded from the analysis.

Model 1. The DESAMBEM algorithm

The set of DESAMBEM algorithms (Woźniak et al. 2004, 2008, Darecki et al. 2008) makes it possible to estimate spatial distributions of numerous parameters and quantities of the Baltic Sea ecosystem from an upward flux of radiation recorded by the optical sensors operating on satellites. With the aid of these algorithms it becomes possible to derive information on sea surface temperature (SST), water transparency, radiation balance at the sea surface and in the upper layers of the atmosphere, the intensity of UV radiation, the Photosynthetically Available Radiation (PAR), concentrations of chlorophyll and other pigments, and the efficiency of photosynthesis. It is important to remember that the PP model in the DESAMBEM algorithm differs from the other PP models used in this study, as the DESAMBEM algorithm is the only model based on parameters that describe phytoplankton photophysiology. With the DESAMBEM algorithm, PP is computed as a function of irradiance, maximum photosynthetic quantum yield, photosystem II functional absorption cross-section, turnover time for carbon fixation, and pigment-specific light absorption. In our PP calculations we used the version of the algorithm described in Woźniak et al. (2008), assuming that the Chl *a* concentration, surface PAR and SST are given as input data.

Model 2. The Vertically Generalized Production Model (VGPM)

The Vertically Generalized Production Model (VGPM), developed by Behrenfeld & Falkowski (1997), is one of the most widely known and used WIDI PP models; it is one of the standard MODIS algorithms. This model estimates daily primary production in the euphotic layer from surface Chl *a* concentration, PAR, day length, euphotic depth, and the optimum photosynthetic rate (P^B_{opt}) of phytoplankton in the water column. The estimation of primary productivity in this model depends largely on the empirical relationship between SST and P^B_{opt}, represented by a seventh-order polynomial function. In our calculations the euphotic depth was estimated using the DESAMBEM formula for the relationship between Chl and $K_d(\lambda)$.

Model 3. The Vertically Generalized Production Model with Eppley parameterization of the temperature effect (VGPM/E)

This model differs from Model 2 in that P^B_{opt} is estimated as an exponential function of the water temperature following Eppley (1972).

Model 4. The Vertically Generalized Production Model modified by Kameda & Ishizaka (VGPM/KI)

This VGPM variant formulates P^B_{opt} as a function of SST and Chl (Kameda & Ishizaka 2005). The model is based on the assumptions that changes in chlorophyll *a* concentration depend on the relative abundance of large phytoplankton and that the chlorophyll-specific productivity is inversely proportional to phytoplankton size.

Model 5. The Baltic Sea Ecosystem Model (ERGOM)

This BG model, coupled to the Baltic Sea circulation model, has been successfully used to simulate many processes in the Baltic Sea (Neumann et al. 2000, 2002, 2005, 2008). The biogeochemical model consists of nine state variables and describes the nitrogen cycle. Primary production is due to three functional phytoplankton groups: diatoms, flagellates and cyanobacteria. Diatoms represent larger cells that grow fast in nutrient-rich conditions. Flagellates represent smaller cells with an advantage at lower nutrient concentrations during summer conditions. The cyanobacteria are able to fix atmospheric nitrogen, and phosphate is their only limiting nutrient. The role of light for primary production is parameterized in ERGOM according to Steele (1962). The value of the optimum irradiance I_{opt} is adopted from Stigebrandt & Wulff (1987), the minimum value $I_{min} = 25$ W m^{-2} was estimated from measurements in the Baltic Sea. Because diatoms develop in early spring, temperature does not limit their PP in the model. Flagellates, however, reach their highest abundances in summer and benefit from moderate temperatures, which is reflected in their temperature dependence included in the model. The growth rate of cyanobacteria has an even stronger dependence on water temperature. The vertical attenuation of light is parameterized in the original model in a very simple way, as the sum of attenuation by water and attenuation proportional to Chl. In our calculations we used the DESAMBEM formula for the relationship between Chl and $K_d(\lambda)$.

Model 6. The Production and Destruction of Organic Matter Model (ProDeMo)

The ProDeMo model is also a 3D coupled hydrodynamic-ecological model applicable to the entire Baltic Sea (Ołdakowski et al. 2005). The model describes nutrient cycles (phosphorus, nitrogen, silicon) through the food web with 15 state variables. The version of the model used in our calculations includes two functional groups of phytoplankton: diatoms and non-diatoms (Ołdakowski et al. 2005). The vertical attenuation of light is parameterized in the original model as the sum of attenuation by water and attenuation proportional to Chl. As in all the other cases, we used the DESAMBEM formula for the relationship between Chl and $K_d(\lambda)$. Note that this model assumes a relatively strong dependence of the phytoplankton growth rate on water temperature. Unlike in all the other models, PP is strongly favoured by a specific range of water temperatures.

Model 7. The Biogeochemical Elemental Cycling (BEC) Ocean Model

We used the version of the model described in Moore et al. (2002a,b), which is a global BG model with four nutrients (nitrogen, phosphorus, silicon and iron) and three phytoplankton groups (diatoms, diazotrophs and a generic small phytoplankton class). Growth rates are limited by available nutrients and/or light levels. A newer version of this model has been developed more recently (Moore et al. 2004, Doney et al. 2009) and is included in a coarse-resolution ocean component of the Community Climate System Model (Yeager et al. 2006), forced by time-varying atmospheric fluxes. In our calculations we used the DESAMBEM formula for the relationship between Chl and $K_d(\lambda)$.

2.2. Data sets

For evaluating the PP models we used the data set collected in the Baltic Sea by IO PAN (Darecki et al. 2008) and by the Sea Fisheries Institute (MIR). In total, this joint data set included 570 measured PP values. In addition, we used the in situ global PPARR4 data (Saba et al. 2011), comprising 1157 stations located in eutrophic and oligotrophic oceanic waters. All the in situ PP data used in our paper were based on ^{14}C techniques (Longhurst et al. 1995, JGOFS 1996). Productivity measurements were integrated to the 1% light depth to estimate water-column-integrated PP.

It needs to be borne in mind that ^{14}C-based estimates are subject to errors (Peterson 1980, Fitzwater et al. 1982, Richardson 1991, JGOFS

2002). The ^{14}C incubation technique measures photosynthetic carbon fixation within a confined volume of seawater, and there are no methods for the absolute calibration of bottle incubations (e.g. Balch et al. 1992). Furthermore, there is no universally accepted method for measuring and verifying vertically integrated production derived from discrete bottle measurements. For brevity, in this paper, we refer to ^{14}C-based estimates as 'measured' and to the differences between algorithm-derived and ^{14}C-derived estimates as 'errors'. We have to remember, however, that both estimates are subject to error.

2.3. Statistical measures

The formulas used for calculating the error statistics provided in the Tables are as follows.

1) The absolute average error (AAE) is a quantity used to measure how close model predictions (P_n) are to the observations (O_n). The absolute average error was estimated according to the formula:

$$\mathrm{AAE} = \frac{1}{N}\sum_{n=1}^{N} |\mathrm{O}_n - \mathrm{P}_n|. \tag{1}$$

2) Bias (B) is defined as the mean difference between the modelled PP (P_n) and the measured PP (O_n):

$$\mathrm{B} = \frac{1}{N}\sum_{n=1}^{N} \mathrm{P}_n - \frac{1}{N}\sum_{n=1}^{N} \mathrm{O}_n = \bar{\mathrm{P}} - \bar{\mathrm{O}}. \tag{2}$$

3) The percentage of model bias (P_{bias}) was estimated as follows:

$$\mathrm{P_{BIAS}} = 100\frac{\sum_{n=1}^{N}(\mathrm{P}_n - \mathrm{O}_n)}{\sum_{n=1}^{N}\mathrm{O}_n}. \tag{3}$$

4) The mean absolute percentage error (MPE) was calculated using the following formula:

$$\mathrm{MPE} = 100\frac{1}{N}\sum_{n=1}^{N} |\frac{\mathrm{P}_n - \mathrm{O}_n}{\mathrm{O}_n}|. \tag{4}$$

5) The root mean square error (statistical error) was calculated as:

$$\mathrm{RMSE} = \left[\frac{1}{N-1}\sum_{i=1}^{N}(\mathrm{P}_i - \mathrm{O}_i)^2\right]^{1/2}. \tag{5}$$

3. Results

3.1. Modelled PP as a function of light and temperature

Estimates of PP as a function of surface irradiance (PAR) and water temperature calculated using all the models are shown in Figures 1–5.

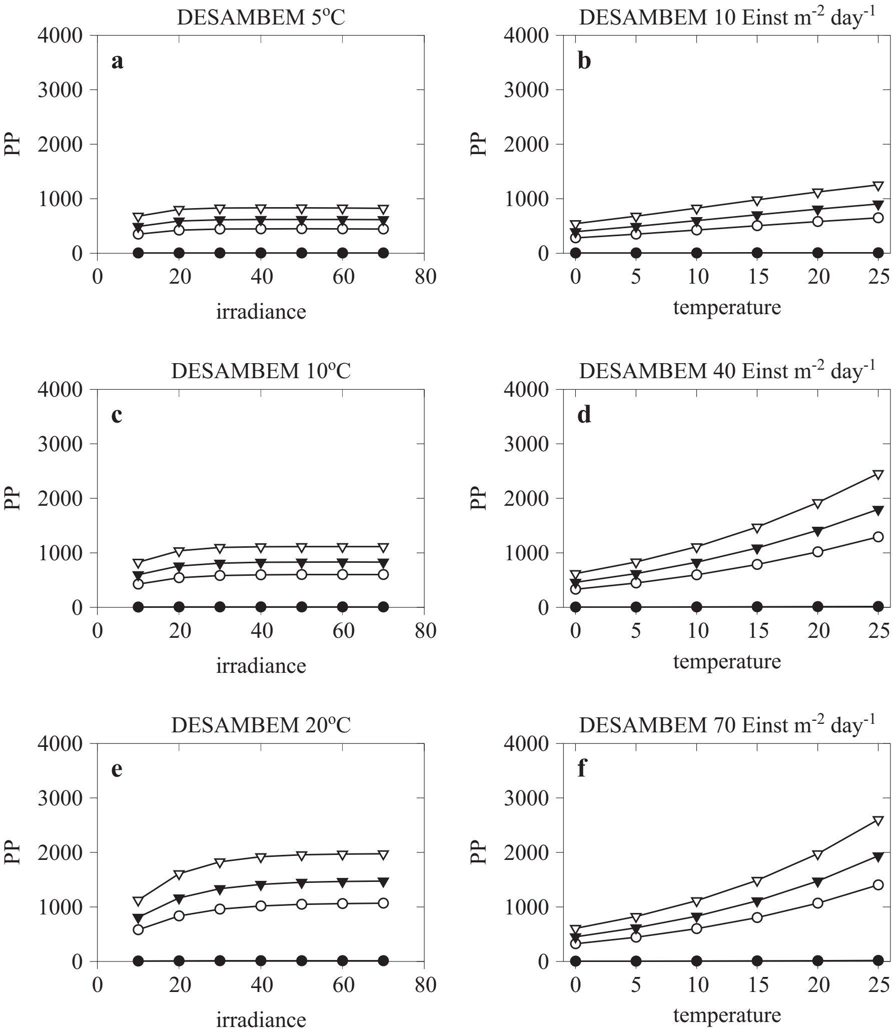

Figure 1. Water column integrated primary production (PP, mg C m^{-2}) estimated with the DESAMBEM algorithm as a function of downwelling irradiance PAR (Einst m^{-2} day^{-1}) for water temperatures of 5, 10 and 20°C (plots in panels a, c, e) and as a function of water temperature for surface PAR of 10, 40 and 70 Einst m^{-2} day^{-1} (plots in panels b, d, f). Chlorophyll concentrations of 0.1, 3.0, 5.0, and 9.0 mg m^{-3} are indicated by black circles, white circles, black triangles and white triangles respectively

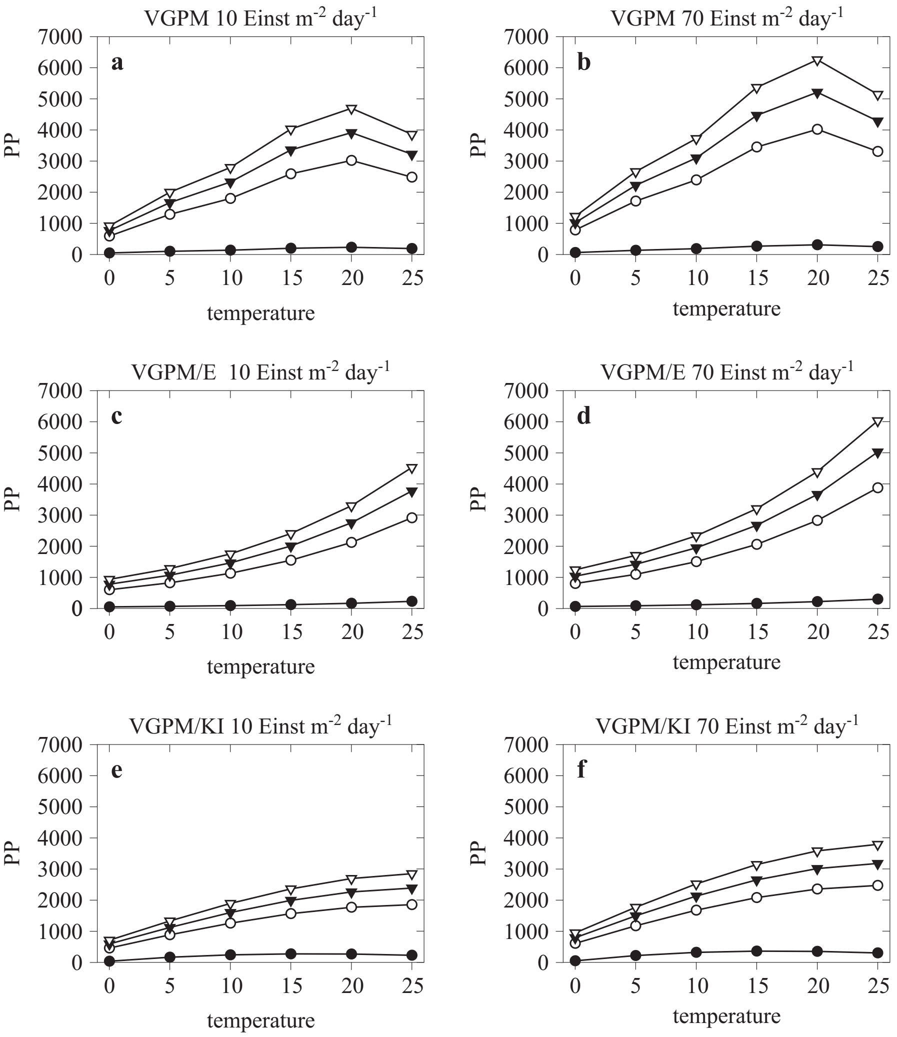

Figure 2. Water column integrated primary production (PP, mg C m^{-2}) estimated with the following algorithms: VGPM (panels a and b), VGPM/E (panels c and d) and VGPM/KI (panels e and f). PP is shown as a function of water temperature for surface PAR of 10 Einst m^{-2} day^{-1} (plots a, c, e) and 70 Einst m^{-2} day^{-1} (plots b, d, f). Chlorophyll concentrations of 0.1, 3.0, 5.0, and 9.0 mg m^{-3} are indicated by black circles, white circles, black triangles and white triangles respectively

In Figure 1, we present the results for the DESAMBEM algorithm. In this case, because the DESAMBEM algorithm is of special interest to us, we decided to show PP as a function of surface irradiance for specific water temperatures (left-hand column in Figure 1) and as a function of

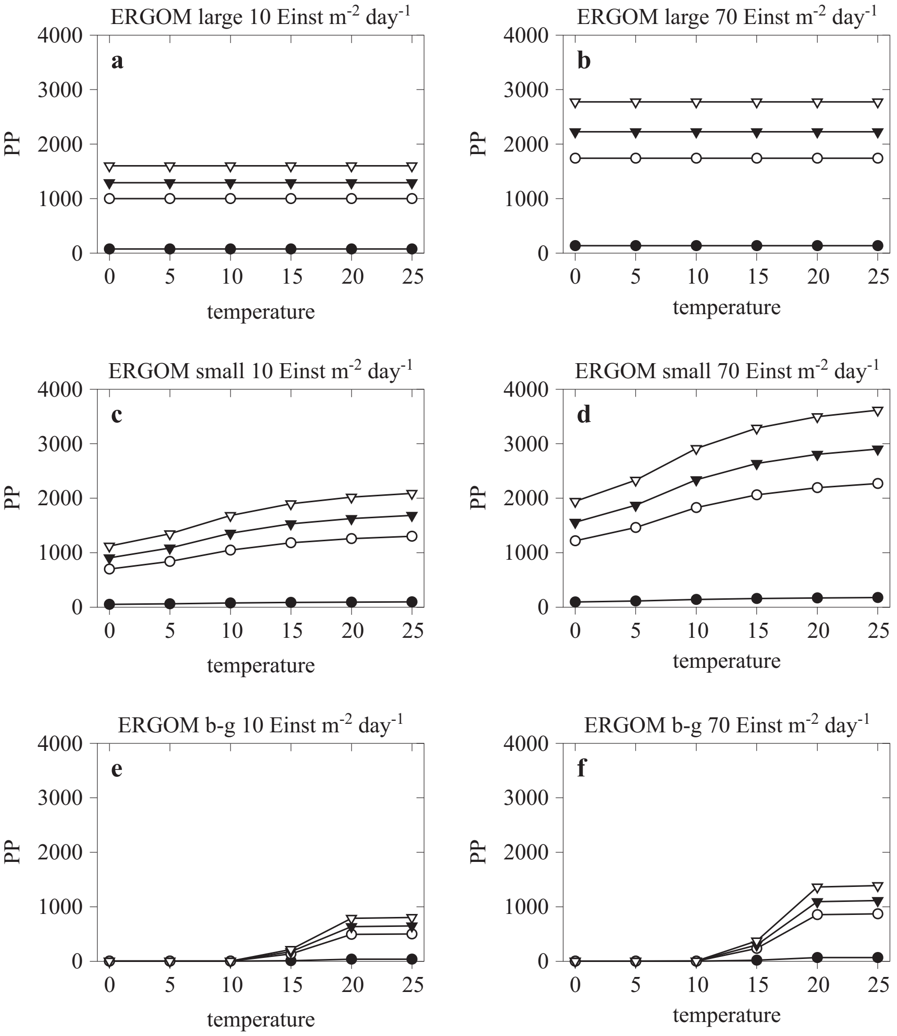

Figure 3. As in Figure 2, but for calculations carried out with the ERGOM model. The results are shown for large phytoplankton (panels a and b), small phytoplankton (panels c and d) and blue/green algae (panels e and f)

water temperature for selected levels of surface PAR (right-hand column in Figure 1). In all other cases, i.e. for calculations based on other models, PP is shown for only two surface irradiances (10 and 70 Einst m^{-2} day^{-1}) as a function of water temperature (Figures 2–5). The results for the ERGOM, BEC and ProDemo models are displayed separately for different phytoplankton groups, as parameterized in the models.

The results shown in Figures 1–5 highlight the differences between the models. (The vertical scales on Figures 1–5 vary because of the different

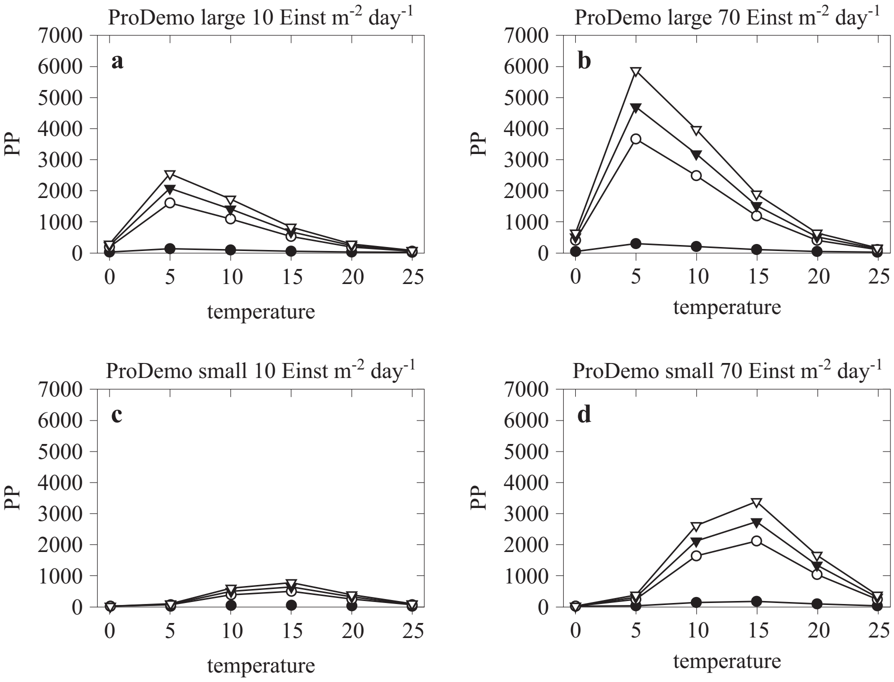

Figure 4. As in Figure 3, but for calculations carried out with the ProDemo model. The results are shown for large phytoplankton (panels a and b) and small phytoplankton (panels c and d)

ranges of PP values in the models). In general, for the range of light levels, Chl and water temperatures considered, the PP estimates achieve the largest values in the global models (VGPM and BEC). Recall that the VGPM model and its derivatives (VGPM/E and VGPM/KE) are designed for use with remotely sensed ocean colour data, as is the DESAMBEM algorithm. However, the application of any of the VGPM algorithms leads to higher estimates of PP than when using the DESAMBEM algorithm, particularly at higher light levels and water temperatures. Importantly, the values of PP obtained with the original global version of the VPGM algorithm (not shown here) are even greater than the values shown in Figure 2, because the VGPM calculations are based on the standard global Chl ocean colour product, which gives significant overestimates for the Baltic Sea. In addition, the rate of increase of PP with concurrent increase in water temperature in the VGPM and the VGPM/E models (results shown in Figure 2) seems to be more pronounced when compared to the rate of increase in the DESAMBEM model for the same conditions. For example, for Chl = 5 mg m^{-3}, surface PAR = 70 Einst m^{-2} day^{-1} and a water temperature change from 0°C to 20°C, the VGPM model shows a three-

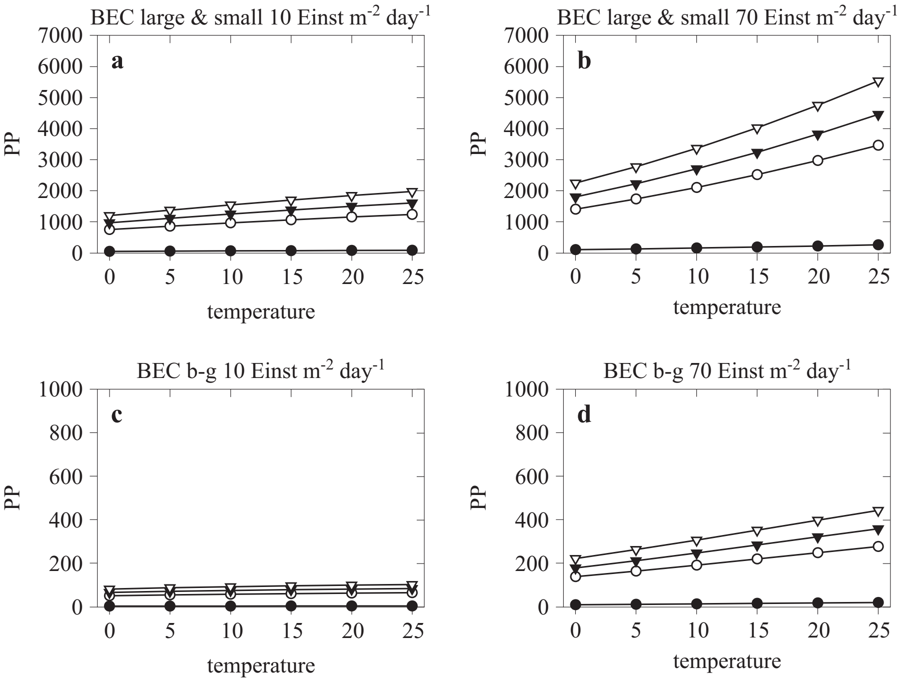

Figure 5. As in Figure 4, but for calculations carried out with the BEC model. The results are shown for large and small phytoplankton (panels a and b) and for blue-green algae (panels c and d)

fourfold increase in PP, while with the DESAMBEM for the same conditions PP increases less than twofold. There are also significant differences in the PP temperature dependence between the DESAMBEM and the biogeochemical models. In particular, for large phytoplankton (diatoms), the ERGOM model assumes no dependence of PP on water temperature but does include the effect of water temperature for small phytoplankton cells. The BEC model (designed for phytoplankton simulations in the global ocean) uses the same temperature dependence for PP of large and small phytoplankton. Strikingly different temperature effects on PP are prescribed in the ProDemo model (developed for simulating the Baltic Sea ecosystem). In this case, in contrast to all the other models considered here, maximum PP for large phytoplankton is reached at a relatively low water temperature of about 5°C (Figures 4a and b). This parameterization of PP is quite different from other frequently used temperature parameterizations and was most likely introduced into the model in order to obtain better agreement between the observed in situ and the simulated biomass of phytoplankton in the Baltic Sea. Note that the temperature parameterization of PP most commonly used in the literature is probably the one derived by Eppley (1972). Eppley (1972) compiled a database of culture studies in which growth rates of approximately 130 species or clones of phytoplankton were measured at a variety of temperatures under 24 hours of continuous illumination and conditions of nutrient sufficiency. When growth rates were plotted against temperature, Eppley found that the data fell below an envelope, which was exponential in shape. This exponential function has become known as the 'Eppley curve' and is routinely used to define the maximum attainable daily growth rate under non-limiting conditions of light and nutrients in many phytoplankton models (see also Brush et al. 2002). We are not aware of any phytoplankton culture experiments that confirm the temperature dependence used in the ProDemo model. Note also that, in comparison to the Baltic Sea BG models, the global BG model used in our work (BEC model, Moore et al. 2002a,b) gives significantly higher PP estimates than the DESAMBEM algorithm for large and small phytoplankton classes at high light levels (70 Einst m^{-2} day^{-1}) and water temperatures $> 15°C$. In contrast, the PP values for blue-green algae in the BEC model are significantly lower than the PP values for blue-green algae in the ERGOM model at water temperatures $> 15°C$.

3.2. Comparison between modelled and measured PP data

In Tables 1, 2, and 3, we present comparisons between:

1) modelled and measured PP in the Baltic Sea during all seasons (Table 1, all data, i.e. 570 PP stations);

2) modelled and measured PP in the Baltic Sea with data collected between 15 May and 1 October of each year being omitted (Table 2); and

3) comparisons of modelled PP with PP estimates from the global PP data set (Table 3).

The formulas used for calculating the error statistics are provided in the Methods section.

It is clear from the results presented in Table 1 that the best agreement between the modelled and measured PP in the Baltic Sea (when all data points are considered, $N = 570$) is obtained using the DESAMBEM algorithm. The error statistics for BG models improve somewhat if we exclude the data collected between 15 May and 1 October (Table 2). However, the error statistics in this case are also the best for the DESAMBEM algorithm. The global remote sensing algorithms (VGPM, VGPM/E, and VGPM/KI) significantly overestimate PP in the Baltic Sea. Although the bias and P_{BIAS} are significantly larger in the BG models than in the DESAMBEM algorithm, these models show relatively high

Table 1. Estimates of the absolute average error (AAE), bias, percentage of model bias (P_{bias}), mean absolute percentage error (MPE), r^2 coefficient and root mean square error (RMSE) obtained for comparisons of calculated water column integrated primary production (PP, mg C m^{-2}) with the Baltic Sea in situ data set (all seasons, $N = 570$). The r^2 indicates the coefficient of determination for the linear regression

	AAE	Bias	MPE [%]	P_{bias} [%]	r^2	RMSE
DESAMBEM	284.56	−75.41	64.26	−11.22	0.46	460.85
ProDemo large	969.65	748.25	295.42	111.35	0.20	1443.65
ProDemo small	443.40	−103.90	77.76	−15.46	0.17	664.28
ERGOM large	683.25	642.89	233.57	95.67	0.50	850.15
ERGOM small	738.32	699.19	212.79	104.10	0.47	952.07
ERGOM blue-green	534.90	−506.74	84.79	−75.41	0.11	772.50
BEC small large	825.16	789.73	229.26	117.53	0.45	1082.29
BEC blue-green	567.76	−566.81	81.83	−84.35	0.43	797.47
VPGM	1704.39	1695.92	405.05	252.39	0.38	2213.23
VGPM/KI	876.50	832.90	243.52	123.95	0.41	1129.62
VGPM/E	884.03	838.26	235.61	124.75	0.38	2582.96

Table 2. Estimates of the absolute average error (AAE), bias, percentage of model bias (P_{bias}), mean absolute percentage error (MPE), r^2 coefficient and root mean square error (RMSE) obtained for comparisons of calculated water column integrated primary production (PP, mg C m^{-2}) with the Baltic Sea in situ data set (data collected between 15 May and 1 October have been excluded, $N = 285$). The relevant data are shown in Figures 6 and 7

	AAE	Bias	MPE [%]	P_{bias} [%]	r^2	RMSE
DESAMBEM	221.16	−133.34	79.77	−26.36	0.64	439.46
ProDemo large	1266.76	1245.95	474.02	246.27	0.54	1818.10
ProDemo small	408.56	−335.08	82.59	−66.23	0.12	693.81
ERGOM large	587.16	557.04	324.21	110.10	0.61	323.04
ERGOM small	453.37	406.23	247.54	80.30	0.59	624.97
ERGOM blue-green	500.00	−499.02	98.73	−98.63	0	814.17
BEC small large	512.79	475.46	268.24	93.98	0.60	696.47
BEC blue-green	434.35	−432.47	83.73	−85.48	0.58	734.77
VPGM	785.63	769.33	390.30	152.07	0.51	1082.62
VGPM/KI	441.99	370.34	258.95	73.20	0.52	621.15
VGPM/E	410.25	337.19	244.92	66.65	0.54	585.24

Table 3. Estimates of the absolute average error (AAE), bias, percentage of model bias (P_{bias}), mean absolute percentage error (MPE), r^2 coefficient and root mean square error (RMSE) obtained for comparisons of calculated water column integrated primary production (PP, mg C m^{-2}) with the PP from the global data set (Saba et al. 2011)

	AAE	Bias	MPE [%]	P_{bias} [%]	r^2	RMSE
DESAMBEM	534.86	−526.35	84.36	−80.89	0.33	714.76
ProDemo large	591.97	−219.10	108.37	−33.67	0.24	858.25
ProDemo small	594.58	−580.98	90.66	−89.28	0.17	819.65
ERGOM large	356.34	−62.55	77.71	−9.61	0.42	484.85
ERGOM small	320.15	−163.08	64.31	−25.06	0.43	464.79
ERGOM blue-green	609.72	−607.54	92.02	−93.36	0.01	828.74
BEC large small	317.00	−88.92	67.14	−13.66	0.40	472.12
BEC blue-green	603.77	−603.68	91.27	−92.77	0.43	809.11
VPGM	395.15	73.63	89.49	11.31	0.29	601.56
VGPM/KI	299.89	−55.97	64.52	−8.60	0.38	462.22
VGPM/E	315.79	−13.50	68.08	−2.07	0.38	514.23

r^2 coefficients for modelled PP by large and small phytoplankton and measured PP. Relatively low r^2 coefficients are noted for blue green algae. The performance of the ERGOM and BEC models seems to be better than that of the ProDemo model, which has a significantly larger bias and RMSE than the other two BG models. The scatter of the data points for the relationship between measured and calculated PP is shown in Figures 6 and 7. For brevity, we display only the results from the runs included in Table 2 (without the data collected between 15 May and 1 October). It seems that the DESAMBEM underestimates PP for the largest values of measured PP. In our database there are only relatively few data points with such high measured PP values, and at present it is impossible to speculate on the reason for this discrepancy. We need to collect more PP data to verify this issue. If this tendency is confirmed, we shall have to make an adjustment to the DESAMBEM so that it can perform better in such conditions. At present our PP database does not contain any information about the dominant phytoplankton functional groups present in the water column at the time the PP measurements were made. Therefore, it is impossible to assign measured PP values to specific functional groups of phytoplankton. We hope that in the near future, with further improvements to the DESAMBEM, we shall develop a capability to derive information about the phytoplankton community composition in the Baltic Sea from

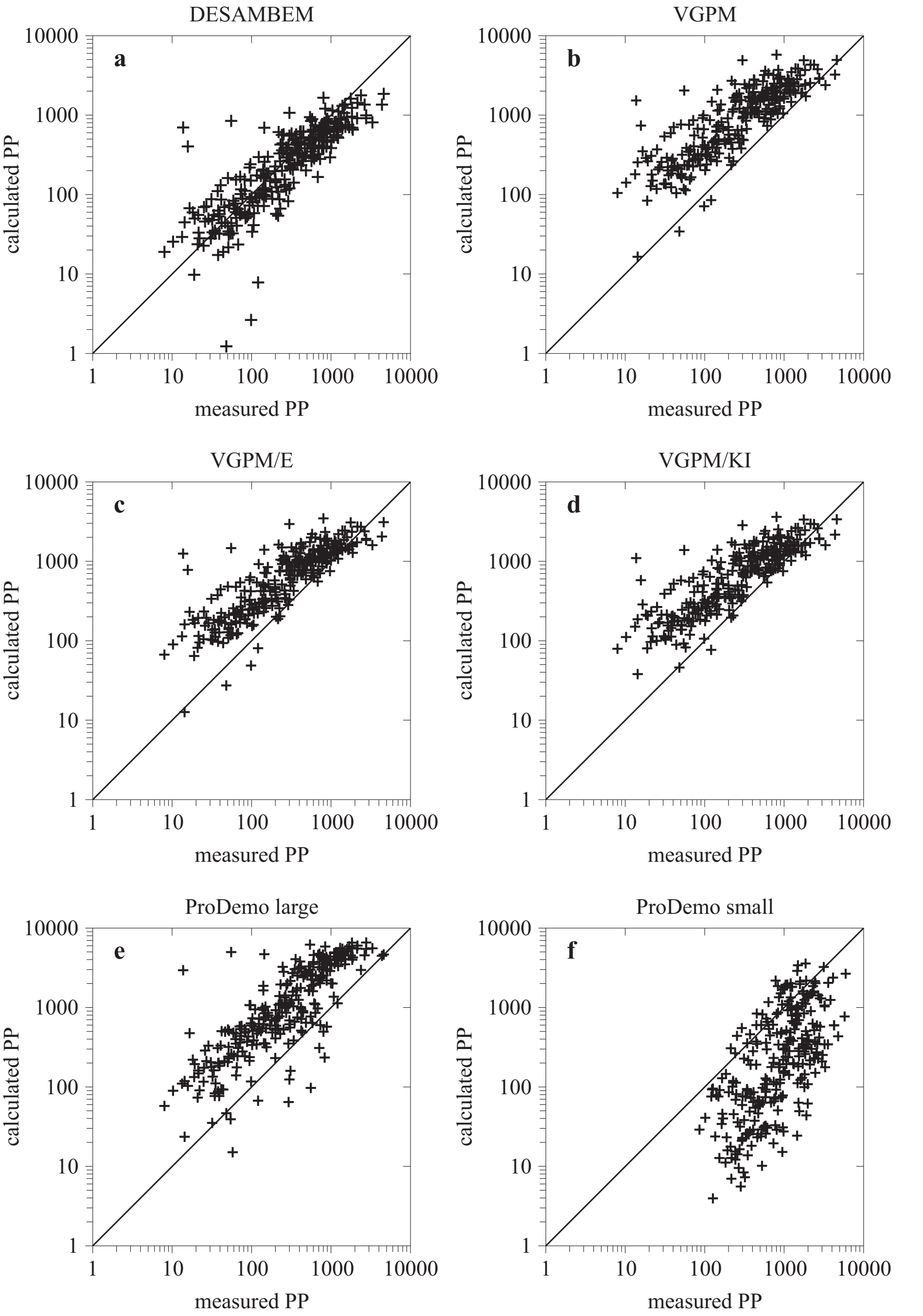

Figure 6. Comparison of model-estimated water column integrated primary production (PP, mg C m^{-2}) with in situ data collected in the Baltic Sea. The statistical metrics are summarized in Table 1. The solid line indicates the $Y = X$ line

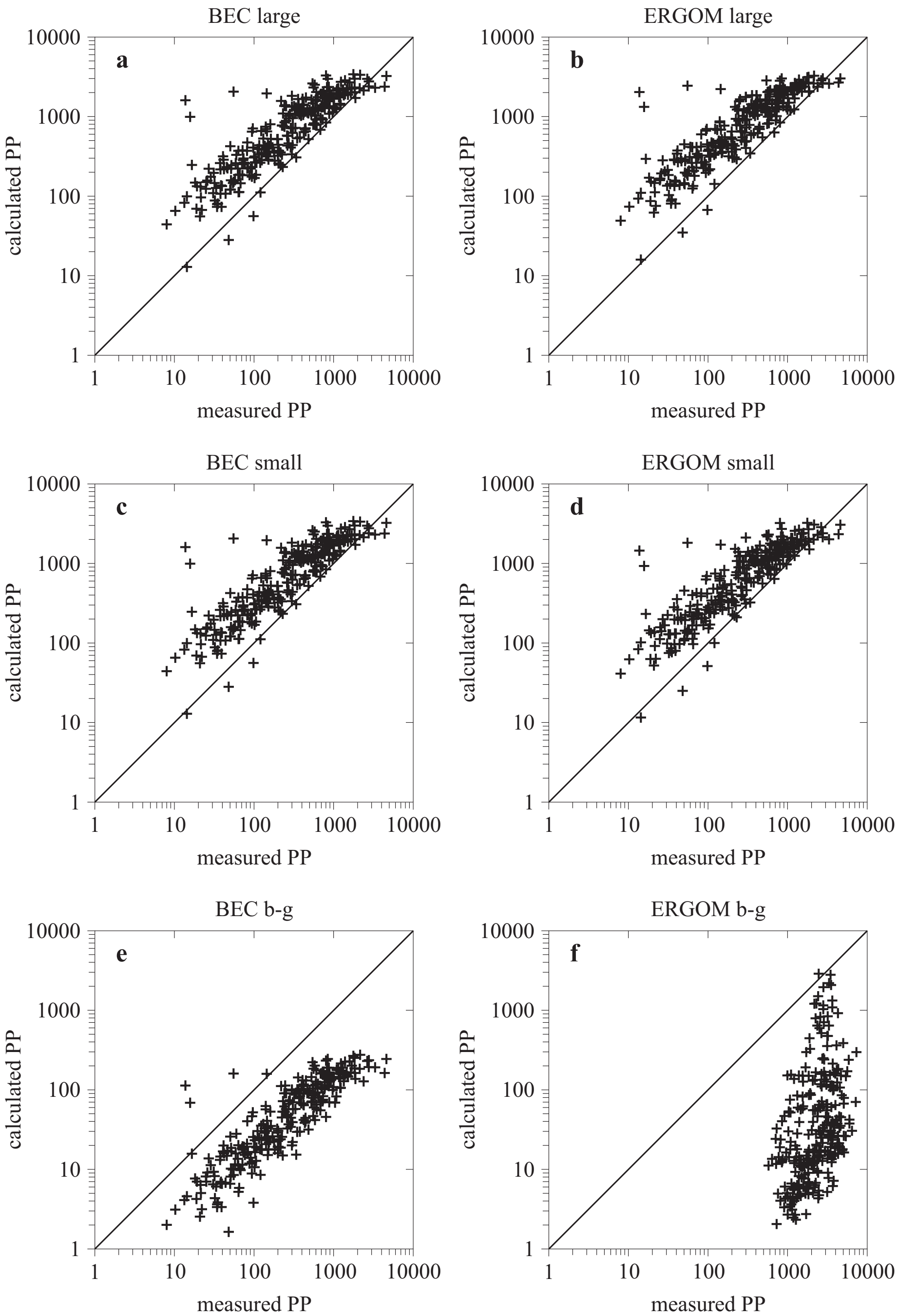

Figure 7. As in Figure 6, but the comparison is for the BEC and ERGOM models

ocean colour and that our new in situ PP measurements will be accompanied by observations of phytoplankton functional types.

The comparison between the global PP data set and PP calculated with our models (see Table 3) clearly indicates that the DESAMBEM model is tuned to the Baltic Sea, but does not perform so well in the global scenario. Comparison of Table 3 with Tables 1 and 2 shows that the performance of PP models can be improved by applying the regional approach to PP modelling in the Baltic Sea.

4. Discussion

The assessment of regional and larger-scale quantities characterizing ecosystems in the ocean from a limited number of in situ data has been a significant challenge in the past. In recent years, ocean colour remote sensing has provided a powerful means of improving our understanding of ocean biogeochemistry and ecosystems. Although some quantities critical to the understanding of biogeochemical cycles and ecosystems are not directly accessible to satellite detection, they can be assessed through a combination of approaches. We are currently developing such an approach for the Baltic Sea within the framework of the SatBałtyk project (Satellite Monitoring of the Baltic Sea Environment, www.iopan.gda.pl/projects/SatBaltyk). Our approach will be based on blending numerical ecosystem models with satellite data products derived using regional algorithms. In this approach we want to describe many important ecosystem functions, such as nutrient cycling, carbon fluxes and oxygen dynamics. With this aim in mind it is crucial that we accurately simulate rate processes as well as state variables. The basic information needed in our approach is a reliable estimate of primary production. In this paper, we have shown that in our future work we can rely on the PP estimates from the DESAMBEM algorithm, because they agree reasonably well with in situ PP determinations.

While biogeochemical models often produce realistic predictions of phytoplankton biomass, they can simultaneously underestimate or overestimate phytoplankton production (e.g. Brush et al. 2002). This apparent paradox is due to generally limited knowledge of phytoplankton loss processes (such as respiration, flushing, sinking, and grazing by various size fractions of zooplankton and benthic filter feeders). Such losses are characterized by a large spatial and temporal variability. Many of the loss terms are poorly constrained or need to be assumed a priori due to insufficient data (or a complete lack of data) in the literature (e.g. Broekhuizen et al. 1995, Ebenhöh et al. 1995). Moreover, there are simply far more loss processes operating in a system than can be included in any model, so crude approximations are inevitable (e.g. Hofmann & Lascara 1998). As a result, parameter values are often guessed during the calibration of BG models in order to achieve an acceptable fit between predicted and observed biomasses. As simultaneous errors in production and loss rates can result in correct estimates of biomass, we may remain unaware of the problems affecting rate estimates. Since phytoplankton production occurs at the base of the food web, the accurate prediction of phytoplankton production and biomass is critical for making correct predictions of concentrations and processes in the system. Incorrect estimates of phytoplankton production weaken the conclusions drawn from models as well as their utility in management applications. These arguments justify our interest in examining the way in which existing BG Baltic models calculate phytoplankton production. Our analysis shows that both the ERGOM and BEC models appear to provide consistent results, the main difference between them being the way in which blue-green algae are modelled. Both ERGOM and BEC calculate PP, which is significantly correlated with measured PP, but they seem to overestimate these measured PP values. We plan to use these two models with some modifications in our future work.

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