Dependence of light-saturated photosynthesis on temperature and community structure

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Received 13 February 2004; received in revised form 16 September 2004; accepted 18 January 2005
Available online 27 April 2005

Abstract

Using data collected in the Arabian Sea and on the Nova Scotian Shelf we examined the relationships between temperature, phytoplankton taxonomic composition (indexed by pigment composition) and the size structure (indexed by chlorophyll-specific absorption coefficient at 676 nm), Chlorophyll-a biomass and the light-saturated photosynthesis parameter $P^B_m$. Our results show that changes in phytoplankton community structure for the Scotian Shelf closely follow changes in temperature. In the Arabian Sea the relationship between phytoplankton community structure and temperature was less striking and fluctuations in phytoplankton pigment composition were strongly related to Chlorophyll-a biomass. The light-saturated photosynthesis parameter $P^B_m$ was correlated with temperature for the Scotian Shelf. When we compared data collected on the Scotian Shelf with the temperature-dependent function of Eppley (1972. Fishery Bulletin 70, 1063–1085), the model fitted the data remarkably well. For the Arabian Sea data, however, only a weak temperature dependence in $P^B_m$ was observed, which may be a result of a strong negative correlation between ambient nitrate concentration and temperature. Our results also show that for both the Scotian Shelf and the Arabian Sea, diatom-dominated waters had similarly low $P^B_m$ values even though the temperatures of the two systems were markedly different. The absorptive characteristics of phytoplankton on the Scotian Shelf were well correlated with $P^B_m$, thus providing another potential predictor of $P^B_m$ that may, in the future, be routinely accessible by remote sensing. The contrasting relationships among community structure, temperature, and primary production observed in the two study regions suggest that primary production algorithms incorporating such information could be developed and applied on a domain-specific basis. These algorithms should be centred on knowledge of the relationships between physical forcing, community structure and phytoplankton photophysiology.

Keywords: Temperature; Community structure; Light-saturated photosynthesis; Marine phytoplankton; Nova Scotian Shelf; Arabian Sea

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1. Introduction

To compute primary production using ocean-colour data requires the assignment of values of the light-saturated photosynthesis parameter, $P_B^m$. Ideally, the assignment of $P_B^m$ values would be made using satellite data on the same spatial and temporal resolution as the pigment biomass field. Unfortunately, there is no direct way of obtaining this physiological parameter by remote sensing. Thus we must exploit information on the major determinants of phytoplankton photophysiology, such as temperature, phytoplankton size structure and taxonomic composition. Among these factors, sea-surface temperature is currently accessible directly by remote-sensing. Furthermore, information on phytoplankton size structure and taxonomic composition is potentially retrievable on large scales from ocean-colour data (Ciotti et al., 1999, 2002; Sathyendranath et al., 2004).

Eppley (1972) studied temperature dependence of $P_B^m$ and concluded that $P_B^m$ shows temperature dependence in some coastal regions, but that it fails to do so in open-ocean systems. Despite Eppley’s cautionary remarks (see also Kyewalyanga et al., 1998; Behrenfeld et al., 2002), several workers have used the Eppley model, or other temperature-dependent functions, to assign values of $P_B^m$ to produce global maps of primary production (Balch et al., 1992; Antoine and Morel, 1996; Behrenfeld and Falkowski, 1997).

A potential alternative to the use of temperature is the use of an index of the taxonomic structure of phytoplankton to predict photosynthetic performance, as first suggested by Margalef (1965). It has been shown in several field studies that $P_B^m$ varies with changes in both the taxonomic composition and size structure of natural assemblages (Yentsch and Ryther, 1957; Eppley, 1972; Platt and Jassby, 1976; Harris, 1978; Harrison and Platt, 1980; Côté and Platt, 1983, 1984). These results are perhaps not surprising, since culture studies have shown a size dependence of biomass-normalised photosynthetic rates (Taguchi, 1976; Geider et al., 1986) and since the size and taxonomic structure of phytoplankton communities are determined by the same abiotic forcing variables (temperature, light history, vertical mixing and nutrient availability) that influence algal photophysiology.

In this study we examine the utility of temperature, an index of phytoplankton taxonomic composition (pigment complement) and an index of phytoplankton size structure (phytoplankton absorption) as predictors of $P_B^m$ for two contrasting marine systems: the Scotian Shelf and the Arabian Sea. We begin by looking at the relationship of both phytoplankton community structure and size structure with temperature and Chlorophyll-a concentration in the two study areas and discuss how these relationships may be explained using our knowledge of the physical characteristics of the study areas. We then examine whether the strong relationship revealed between temperature and $P_B^m$ on the Scotian Shelf is in fact the result of a corresponding shift in phytoplankton community structure. Potential applications of the results for computation of primary production at large scales using remote sensing are discussed.

2. Description of the study areas

Seasonal changes in the size and taxonomic structure of marine phytoplankton, temperature and primary production were measured in two contrasting marine ecosystems, the Nova Scotian Shelf and the Arabian Sea. The two regions were chosen for the following reasons. First, the two systems experience strong seasonal shifts in phytoplankton community structure (Sathyendranath et al., 1999; Bouman, 2003). Both the Scotian Shelf and the Arabian Sea show a dominance of diatoms during periods of strong vertical mixing and bloom events, and a prevalence of smaller cells (prymnesiophytes and cyanobacteria) during stratified conditions (Sathyendranath et al., 1999; Bouman, 2003).

The Scotian Shelf and Arabian Sea are also extremely dynamic environments with highly predictable seasonal changes in their biological and physical properties. However, the two systems differ in the physical mechanisms driving these seasonal changes. As with most temperate systems of the North Atlantic, spring blooms on the Scotian Shelf are caused principally by the
formation of a shallow mixed layer consequent upon vernal warming and an increase in incident irradiance. Bloom events in the Arabian Sea, however, are caused by monsoon winds, resulting in upwelling of nutrient-rich water from depth into the euphotic zone (Barber et al., 2001).

Both study regions show strong seasonal variability in two factors that govern marine photosynthesis: nutrient concentration and mixed layer depth. In the North Atlantic, seasonal changes in solar heating and wind strength primarily regulate the depth of the mixed layer and the supply of nutrients from depth. The Arabian Sea also shows marked seasonal changes in the depth of the pycnocline and nutrient concentration, caused by wind-driven upwelling. The upwelling of nutrient-rich waters is particularly prevalent during the Southwest Monsoon, when winds blow parallel to the Arabian coastline causing Ekman transport of surface water offshore.

However, the regions markedly differ in the other two forcing factors: available irradiance and sea-surface temperature. In the North Atlantic, deep mixed layers tend to co-occur with low incident surface irradiance and temperatures, whereas in the Arabian Sea (a low-latitude region), deep mixed layers caused by wind mixing coincide with high temperatures and surface irradiance (Barber et al., 2001). Seasonal changes in sea-surface temperatures are also different between the two regions. Seasonal changes in sea-surface temperature on the Scotian Shelf tend to be gradual and follow an almost sinusoidal pattern, with maximum temperatures occurring during the late summer (August–September), and minimum temperatures occurring around February and March. The Arabian Sea, on the other hand, has a bimodal cycle in sea-surface temperature, with minimum temperatures occurring during the Southwest Monsoon and the Northeast Monsoon (Banse and English, 2000). The seasonal temperature in the surface waters of the Scotian Shelf varies between 1 and 20°C, whereas the range in the Arabian Sea is between 18 and 31°C. The differences in temperature excursions in the two regions allow the influence of temperature on $P_{\text{B}}$ to be assessed in two systems which show strong seasonal shifts in phytoplankton taxonomic and size structure.

3. Material and methods

The dataset consists of samples from nine cruises on the Scotian Shelf conducted over a five-year period (1997–2001) during spring and fall, and three cruises in the Arabian Sea during the SW monsoon (August–September 1994; June–July 1997) and intermonsoon periods (November–December 1994) (Fig. 1). Temperatures corresponding to the sample depths were obtained with in situ profiling conductivity, temperature,
depth (CTD) sensors. Chlorophyll-\(a\) concentrations were determined using both the standard fluorometric technique (Holm-Hansen et al., 1965) and reverse-phase, high-performance liquid chromatography analysis (HPLC). Accessory pigments were determined by HPLC as described in Head and Horne (1993).

To assess changes in the contribution of the three main phytoplankton size classes to total algal biomass, the ratios \(S_{\mu}, S_{n}\) and \(S_{p}\) were calculated according to Vidussi et al. (2001) as follows:

\[
S_{\mu} = (D_t + D_p)/D_t, \quad (1)
\]

\[
S_{n} = (D_a + D_h + D_b)/D_t, \quad (2)
\]

\[
S_{p} = (D_x + D_c)/D_t, \quad (3)
\]

where the subscripts denote the size class as microplankton (\(\mu\)), nanoplanckton (\(n\)) or picoplankton (\(p\)). Fucoxanthin (\(D_t\), mg m\(^{-3}\)) and peridinin (\(D_p\), mg m\(^{-3}\)) are diagnostic pigments of diatoms and dinoflagellates, respectively, and typically fall within the microphytoplankton size range (> 20 \(\mu\)m) (Claustre, 1994; Jeffrey and Vesko, 1997; Vidussi et al., 2001). The carotenoids 19'-hexanoyloxyfucoxanthin (\(D_h\), mg m\(^{-3}\)) and 19'-butanoyloxyfucoxanthin (\(D_b\), mg m\(^{-3}\)), which are found predominantly in prymnesiophytes, are considered to be indicator pigments of the microphytoplankton size range (2–20 \(\mu\)m) (Claustre, 1994; Jeffrey and Vesko, 1997). Alloxanthin (\(D_a\), mg m\(^{-3}\)) is another indicator pigment of nanoflagellates and is commonly found in cryptophytes. Zeaxanthin (\(D_z\), mg m\(^{-3}\)) is a photoprotective pigment associated with picocyanobacteria, and total chlorophyll-b (\(D_c\), mg m\(^{-3}\)) is an indicator of both chlorophytes and Prochlorococcus sp., which are also in the picoplankton size range. The denominator (\(D_t\), mg m\(^{-3}\)) is simply the sum of the concentrations of the seven diagnostic pigments, which has been shown to be well correlated with total Chlorophyll-\(a\) concentration (Claustre, 1994). Thus, the three ratios described by Eqs. (1)–(3) can be viewed as proxies of the percentage contribution of the different size classes to the overall pigment biomass.

Particulate absorption was measured by the filter technique. Briefly, 0.25–1 L of seawater was filtered through a 25 mm GF/F filter, which was frozen immediately in liquid nitrogen and stored at \(-80^\circ\)C until analysed. The optical density of total particulates was measured with a Shimadzu UV-2101 dual-beam spectrophotometer with integrating sphere. Optical densities of total particulate matter were recorded at 1 nm spectral resolution from 350 to 750 nm. Phytoplankton pigments were extracted from samples with a mixture (6:4 vol:vol) of 90% acetone and dimethyl sulphoxide (DMSO) according to the method of Hoepffner and Sathyendranath (1992, 1993) for samples analysed prior to October 1998, or with hot methanol according to the method of Kishino et al. (1985) for samples analysed after October 1998. Unpublished data show no significant difference between extraction methods (Venetia Stuart, personal communication). The extracted filters were scanned from 350 to 750 nm to measure the optical density of the detrital component. Optical density measurements were corrected for pathlength amplification arising from scattering by the filter according to the method of Kyewalyanga et al. (1998). Corrected optical densities were then divided by the geometrical pathlength (the volume of seawater filtered divided by the clearance area of the filter) and multiplied by the constant 2.3, which converts from decimal to natural logarithms (Mitchell and Kiefer, 1988). Phytoplankton absorption coefficients were then normalised to fluorometrically-determined Chlorophyll-\(a\) concentrations to obtain Chlorophyll-\(a\) specific absorption coefficients of phytoplankton.

Photosynthesis–irradiance (\(P–E\)) experiments were performed on samples collected within the top 30 m of the photic zone. To obtain a \(P–E\) curve, 30 light bottles and three dark bottles, each containing 100 ml of seawater, were inoculated with 40 \(\mu\)Ci of sodium \(^{14}\)C-bicarbonate. Samples were placed in a light gradient ranging from approximately 8–2750 \(\mu\)mol quanta m\(^{-2}\) s\(^{-1}\) and incubated for 3 h. Experimental data were normalised to fluorometrically-determined Chlorophyll-\(a\) concentrations and were then fitted by the equation of Platt et al. (1980) to obtain values for the initial slope (\(z^B\)) and the photosynthetic rate at saturating irradiance (\(P^B_m\)).
4. Results and discussion

4.1. Variability in phytoplankton community and size structures

In this study we employed the pigment indices presented in Vidussi et al. (2001) to examine changes in the gross community composition of the algal cells. When values of $S_{\mu}$, $S_{n}$ and $S_{p}$ are plotted against temperature for samples collected on the Scotian Shelf, clear patterns are evident (Figs. 2a–c). As temperature increases there is a decrease in $S_{\mu}$ which indicates a decrease in the contribution of large cells (mainly diatoms) to total algal pigment biomass (Fig. 2a). The opposite is true in the cases of $S_{n}$ and $S_{p}$: both indices show increases with temperature, suggesting that smaller cells become more dominant at higher temperatures (Figs. 2b and c). For the Arabian Sea dataset the relationship between temperature and pigment composition was less pronounced, although a negative relationship between $S_{\mu}$ and temperature and a positive relationship between $S_{p}$ and temperature were found as in the case of the Scotian Shelf. A weak positive correlation between $S_{n}$ and temperature was observed for the Arabian Sea. Using flow cytometric counts of phytoplankton cell abundance, Shalapyonok et al. (2001) found a strong correlation between the abundance of Prochlorococcus and Eukaryotic phytoplankton and sea-surface temperature for data collected in the Arabian Sea during the Southwest and Northeast monsoon seasons. However, there appeared to be no relationship between the abundance of Synechococcus cells and temperature.

The specific absorption coefficient of phytoplankton at 676 nm, $a_{p}^{676}$, was selected as an index of the size structure of the phytoplankton community. The 676 nm waveband corresponds to the red peak of Chlorophyll-4 absorption, where the influence of accessory pigments is considered to be minimal (Hoepffner and Sathyendranath, 1992, 1993; Allali et al., 1997; Bouman et al., 2000; Fujiki and Taguchi, 2002). Thus, variability in the specific absorption coefficient in this waveband is primarily a result of pigment packaging, which is governed by two properties of the cell: its intracellular pigment concentration and its size.

Fig. 2. Pigment ratios (a) $S_{\mu}$, (b) $S_{n}$ and (c) $S_{p}$ plotted as a function of temperature ($T$) for the Scotian Shelf ($S_{\mu} = -0.055T + 1.029, r^{2} = 0.74, p<0.001; S_{n} = 0.037T - 0.028, r^{2} = 0.68, p<0.001; S_{p} = 0.019T - 0.001, r^{2} = 0.47, p<0.001$) and the Arabian Sea ($S_{\mu} = -0.081T + 2.347, r^{2} = 0.44, p<0.001; S_{n} = 0.015T - 0.129, r^{2} = 0.071, p<0.001; S_{p} = 0.063T - 1.28, r^{2} = 0.40, p<0.001$). Circles and triangles denote samples collected on the Scotian Shelf and in the Arabian Sea, respectively. The computation of pigment ratios for the micro- ($S_{\mu}$), nano- ($S_{n}$) and picoplankton ($S_{p}$) size classes is described in Eqs. (1)–(3).

Fig. 3 shows $a_{p}^{676}$ plotted against temperature for samples collected on the Scotian Shelf and the Arabian Sea. As expected, there is a positive correlation between $a_{p}^{676}$ and temperature, adding further support to the view that the relative contribution of large cells to total phytoplankton biomass decreases with increasing temperature.
temperature is evident for the Arabian Sea.

No such relationship between \( a_p(676) \) and temperature is evident for the Arabian Sea.

Thus, two independent proxies of phytoplankton community structure (HPLC pigment and \( a_p(676) \)) are correlated with temperature for the Scotian Shelf. Although temperature itself may be responsible in part for the seasonal succession of phytoplankton, it is likely that other environmental changes associated with the vernal warming of surface waters, such as increases in water-column stratification and surface light, and a decrease in nutrient availability, also play important, if indirect, roles in determining these relationships (Bouman et al., 2003). Data from the Arabian Sea showed a weaker correlation between temperature and both phytoplankton pigment composition and specific absorption.

Since an increase in Chlorophyll-\(a\) concentration is often assumed to represent an increase in the relative contribution of large cells to the total phytoplankton biomass (Yentsch and Phinney, 1989; Chisholm, 1992; Bricaud et al., 1995), and Chlorophyll-\(a\) concentration is another ecological variable accessible to remote sensing, we also plotted the three pigment indices against Chlorophyll-\(a\) concentration (Fig. 4). On the Scotian Shelf the correlation between Chlorophyll-\(a\) concentration and the contribution of the various size classes to the total pigment biomass was markedly weaker (Figs. 4a–c) than the temperature–size–class relationship. Nevertheless, the plot shows that at high Chlorophyll-\(a\) concentrations (5–10 mg m\(^{-3}\)), the Scotian Shelf is generally characterised by high concentrations of accessory pigments associated with large cells (mainly diatoms) and relatively low concentrations of diagnostic pigments associated with nano- and picoplankton-sized cells. At intermediate-to-low Chlorophyll-\(a\) concentrations, however, there appears to be no discernible relationship between phytoplankton community structure and chlorophyll concentration. The relationship between the specific absorption coefficient at 676 nm and chlorophyll (Fig. 5a) supports this view: low
specific absorption coefficients are found at high chlorophyll concentrations, whereas at intermediate and low chlorophyll concentrations values of $a_C^p(676)$ are highly variable. Similar results have also been presented by Yentsch and Phinney (1989) and Bricaud et al. (1995).

The relationship between pigment composition and total Chlorophyll-a concentration is more striking in the Arabian Sea (Figs. 4d–f) than on the Scotian Shelf, for comparable ranges in chlorophyll concentrations. The plot shows a clear increase in $S_m$ values and decline in $S_p$ values with increasing Chlorophyll-a concentration. Values of $S_n$ appear to peak at a Chlorophyll-a concentration of approximately 0.7 mg m$^{-3}$. Upon examination of the plot of $a_C^p(676)$ against Chlorophyll-a concentration, the pattern is not as obvious (Fig. 5b). When the data are separated by cruise (Fig. 6), the relationship between pigment composition and $a_C^p(676)$ is not as tightly linked for the Arabesque cruises as for the Sonne 1997 cruise. Values of $a_C^p(676)$ remain relatively low over a range of $S_n$ values in the Arabesque-1 data, which would suggest that the absorptive properties of the phytoplankton are independent of phytoplankton community structure. One explanation may be that the various pigment indices used in this analysis are unsatisfactory proxies of phytoplankton size structure in the region. Sathyendranath et al. (1999) examined the relationship between the specific absorption coefficient at 440 nm and the percentage of the Chlorophyll-a biomass that was attributed to cells less than 2 μm in diameter for the Arabesque-1 cruise. The plot showed no discernible relationship between $a_C^p(440)$ and the percent contribution of picoplankton cells to the total biomass, which also indicates that the absorptive properties of the phytoplankton cells are not strongly related to the size structure of the microalgal community. We cannot offer any explanation for these anomalous results except to suggest that photoadaptation and resultant changes in intracellular concentrations of Chlorophyll-a may be modifying $a_C^p$ in these waters. At any rate, they do suggest that the absorptive properties of phytoplankton are not a good proxy for phytoplankton size structure in the Arabian Sea.

One might ask why temperature is the best indicator of phytoplankton community structure (as indexed by pigment composition) on the Scotian Shelf, whereas in the Arabian Sea Chlorophyll-a concentration is a more reliable predictor of phytoplankton taxonomic composition. The dissimilarity in the kinds of abiotic and biotic factors regulating phytoplankton taxonomic composition may in part explain this disparity. As mentioned in Section 1, the onset of the spring bloom on the Scotian Shelf is caused by the formation of a shallow mixed layer and an increase in solar radiation, exposing cells to sufficient light for rapid cell growth. When stratification intensifies as the temperature of the mixed layer increases, nutrients become limiting, leading to the dominance of smaller nanoflagellates (typically...
The overall range of temperatures in such temperate systems is relatively large (approximately 20°C). In these waters, temperature may be considered to be a good proxy of the turbulent properties of the water column, which are principally responsible for variation in nutrient availability and consequently for phytoplankton species succession (Margalef et al., 1979; Cullen et al., 2002). Chlorophyll-\(a\) is not a satisfactory indicator of phytoplankton community structure because low pigment biomass may be a result of light or nutrient limitation, zooplankton grazing or the sinking of algal cells from the photic zone. Before the onset of the spring bloom, light is limiting to algal cells because of low irradiance incident on the sea surface and deep vertical mixing. Strong mixing conditions result in the entrainment of nutrients from depth into the surface waters and allow large cells to remain in the upper water column. These conditions of high nutrient availability and turbulence tend to favour the presence of diatoms. In post-bloom, stratified conditions, light levels are high and nutrient concentrations are greatly diminished, resulting in a dominance of smaller cells. Theoretical studies have established that reducing cell size increases a phytoplankter’s ability to utilise low nutrient concentrations (Raven, 1998) and to minimise its sinking rate (Smayda, 1970). It is therefore not surprising that in the field, shifts in phytoplankton community structure have been correlated with the stability of the water column (Li, 2002; Bouman et al., 2003), turbulence (Rodriguez et al., 2001) and nutrient status (Yentsch and Phinney, 1989).

In the Arabian Sea, however, the physical mechanism responsible for the initiation of blooms is the upwelling of nutrient-rich waters by the SW monsoon winds. The intermonsoon season, characterised by highly stratified, nutrient poor conditions, is associated principally with smaller cells, in particular picoplanktonic cyanobacteria. The introduction of nutrients into the euphotic zone via upwelling (both along the western coast and offshore) by monsoon winds results in the dominance of diatoms. Unlike the temperate regions however, the seasonal mixing of waters by monsoon winds does not lead to a large change in sea-surface temperature.

It should be noted that during the Northeast monsoon, which occurs during the months of November–February, large heat losses in the Northern Arabian Sea by evaporative cooling, combined with cool winds result in convective mixing offshore. These conditions also cause a decline in sea-surface temperature. Shalapyonok et al. (2001) found a strong relationship between temperature and the abundance of various phytoplankton groups using data collected during both the Southwest and Northeast monsoon seasons. In addition, the study found a strong correlation between both nitrate concentration and salinity, which can be considered with temperature as indices of freshly-upwelled waters.

The strong correlation between the proxies for the three size classes of phytoplankton (based on pigment data) and chlorophyll concentration for the Arabian Sea can be viewed as an increase in the contribution of large cells as phytoplankton biomass increases. Goericke (2002) also observed the strong relationship between diagnostic pigments and Chlorophyll-\(a\) concentration in a study of the Arabian Sea. In his study, zooplankton grazing was considered to be the principal mechanism controlling both Chlorophyll-\(a\) biomass and community structure. Although our study contains no direct evidence to implicate zooplankton grazing as the main factor responsible for the observed patterns between total Chlorophyll-\(a\) concentration and pigment composition, we cannot rule out this biotic factor as a potential cause.

4.2. Variability in light-saturated photosynthesis

When the photosynthetic capacity, \(P^m_b\), of phytoplankton collected on the Scotian Shelf is plotted against temperature, a clear positive correlation is observed (Fig. 7a) for \(P^m_b\) values that range from 0.3 to 10.5 mgC (mg Chl-a\(^{-1}\)) h\(^{-1}\). In contrast, the relationship between \(P^m_b\) and temperature is less clear (Fig. 7b) for the Arabian Sea, where assimilation numbers range between 1.3 and 11.6 mgC (mg Chl-a\(^{-1}\)) h\(^{-1}\). We also plotted values of \(P^m_b\) against total Chlorophyll-\(a\) concentration, which is considered a useful index of trophic status (Yentsch and Phinney, 1989;
The plots for both the Scotian Shelf (Fig. 7c) and the Arabian Sea (Fig. 7d) are similar, in that values of $P_m^B$ tend to be lower and less variable at moderate to high chlorophyll concentrations (>2 mg Chl-a m$^{-3}$), whereas at low pigment concentrations, assimilation numbers are highly variable.

Since high Chlorophyll-$a$ concentrations correspond to a dominance of diatoms for both locations (see previous section) we examined the relationships of $P_m^B$ with the two indices of phytoplankton community structure: $S_m$, which can be considered an index of the relative contribution of large cells to the algal biomass, and $a_p^*(676)$. Both study areas show that high values of $S_m$ correspond to low values of $P_m^B$ (Figs. 8a and b). We see a relatively weak relationship between the phytoplankton absorption and light-saturated photosynthesis for the Arabian Sea region, whereas for the Scotian Shelf a clear positive correlation exists (Figs. 8c and d). The poor correlation between $a_p^*(676)$ and phytoplankton taxonomic structure for the Arabian Sea shown in Fig. 6 may be a potential cause for this weak relationship between $P_m^B$ and $a_p^*(676)$.

### 4.3. Relationship between $P_m^B$ and temperature: correlation or causation?

Eppley (1972) was the first to assess systematically the utility of temperature as an indicator of light-saturated photosynthesis. His paper attempted to draw comparisons between field observations and culture experiments that examined the influence of temperature on phytoplankton growth and photosynthesis. The temperature-dependent function derived from these laboratory experiments
represented the maximum rates of growth and photosynthesis under nutrient-replete conditions. His overall conclusion was that temperature may be a useful predictor of $P_{B_m}$ in shallow, eutrophic coastal and estuarine environments.

There is evidence from field data to support Eppley's deduction. Numerous studies conducted in temperate marine and freshwater coastal ecosystems have shown a strong correlation between light-saturated photosynthesis and temperature (Harris, 1978; Harrison and Platt, 1980; Côté and Platt, 1983, 1984). A recent study of the variability of the photosynthesis-irradiance parameters in the Black Sea also showed a significant correlation between $P_{B_m}$ and temperature (Fienko et al., 2002). When we compare the results from the Scotian Shelf with Eppley's model, using a carbon to chlorophyll (C:Chl) ratio of 60 (Fig. 9a), the Eppley model fits the Scotian Shelf data remarkably well.

One could argue that the Scotian Shelf does not match Eppley's criterion of a eutrophic, shallow-water system. During stratified periods on the Shelf, nutrient concentrations were often low (<0.5 μM) and in some cases reached undetectable levels. Our results from the Scotian Shelf suggest that confining the relationship between temperature and light-saturated photosynthesis to shallow coastal estuarine systems may be too conservative. This view is supported by the work of Kyewalyanga et al. (1998), which showed from multiple-linear regression analysis that temperature was the best single environmental predictor of $P_{B_m}$ for samples collected over a range of open-ocean conditions in the North Atlantic.

Twenty-five years after the publication of Eppley's paper, another temperature-dependent model of light-saturated photosynthesis was presented in a study by Behrenfeld and Falkowski.
Their empirical model was based on an extensive dataset of $P_{\text{opt}}$ values (the maximum observed rate of carbon fixation within the water column (mg C [mg Chl-a]$^{-1}$ h$^{-1}$). The parameters $P_{\text{opt}}^B$ and $P_{\text{m}}^B$ are used in models of primary production to represent the biomass-normalised, maximum rate of carbon fixation. However, it is important to note that the parameters are obtained by different experimental means: $P_{\text{opt}}^B$ is obtained from 6 to 24 h in situ $^{14}$C incubations, whereas $P_{\text{m}}^B$ is derived from short-term ($\sim 3$ h) $^{14}$C experiments conducted in an incubator onboard a ship. Since in situ experiments are conducted over a much longer time-frame than $P-E$ experiments, they might be strongly influenced by zooplankton grazing, respiration and excretion of labelled carbon by algal cells. Moreover, the value of $P_{\text{opt}}^B$ is the maximum biomass-normalised production rate observed for a given in situ profile, whereas values of $P_{\text{m}}$ are obtained by fitting a non-linear function to data obtained from photosynthesis-irradiance experiments conducted over a range of light intensities. In situ incubations usually consist of around 5–10 samples spaced evenly throughout the photic zone, whereas $P-E$ experiments are typically conducted over 20–30 light intensities. Another important distinction between the two methods is that available light is variable during in situ incubations, whereas irradiance levels are held constant in a $P-E$ incubation experiment.

To describe the relationship between $P_{\text{opt}}^B$ and temperature, Behrenfeld and Falkowski (1997) fitted a seventh-order polynomial to median values of $P_{\text{opt}}^B$ computed for every 1°C interval. The empirical model of Behrenfeld and Falkowski (B–F) is similar to the Eppley model within the low-to-intermediate temperature range (0–12°C), and for this range this model also fits our data well (Fig. 9). For higher temperatures (12–22°C), the median $P_{\text{opt}}^B$ values obtained by Behrenfeld and Falkowski (1997) match our data and the Eppley model better than does the seventh-order polynomial (Fig. 9). This agreement is facilitated by the high proportion (over 88%) of the data points used to derive the Behrenfeld and Falkowski model that were obtained in the Western North Atlantic (Behrenfeld and Falkowski, 1997, Table 1). Extrapolations of the results to regions other than the NW Atlantic, therefore, should be approached with caution, as is seen in the case of the Arabian Sea.

In the Arabian Sea, large variability in $P_{\text{m}}^B$ values was observed at high temperatures, which the temperature-dependent functions of both Eppley (1972) and Behrenfeld and Falkowski (1997) failed to describe (Fig. 9). A possible explanation for the weak correlation between $P_{\text{m}}^B$ and temperature in the Arabian Sea is that the relationship between temperature and nutrient availability is weak compared with that observed in temperate waters. Yet when we plot temperature against ambient nitrate concentration, it appears that the opposite is true: the relationship between temperature and nitrate concentration is
much stronger for the Arabian Sea than for the Scotian Shelf (Fig. 10a). These results are consistent with those reported by Goericke (2002), who also found a strong negative correlation between nitrate concentration and temperature for the Arabian Sea. When we plot $P_B^m$ against nitrate for the two study areas we see no discernible relationship between ambient nitrate concentration and $P_B^m$ (Fig. 10b). Barber et al. (2001) also found a poor relationship between ambient nitrate concentration and $P_B^m$ for data collected during the Northeast and Southwest Monsoons. Although it can be argued that ambient nitrate concentration may not be the best indicator of nutrient supply, these results do suggest that nitrate availability alone cannot explain the spatial and temporal variability in photosynthetic performance observed in this study.

There is little doubt that the wide variation in phytoplankton taxonomic composition observed in the Arabian Sea, which is similar to that observed in temperate regions such as the Scotian Shelf, is responsible in part for the large variation in the physiological properties found in the Arabian Sea. In both regions, $P_B^m$ tends to be low when $S_m$ is high (i.e. when diatoms are dominant) (Figs. 8a and b) despite the large differences in ambient temperature between the two regions (1–5°C for the Scotian Shelf compared with 25–30°C for the Arabian Sea). Figs. 8a and b also show that variation of $P_B^m$ increases with decreasing $S_m$. This pattern of increased variability in $P_B^m$ as one moves from large-cell to small-cell dominated systems is also shown in the plot of Chlorophyll-$a$ as an indicator of $P_B^m$ for the Scotian Shelf and the Arabian Sea (Figs. 7c and d). At the high chlorophyll concentrations, commonly associated with diatom blooms, $P_B^m$ values are relatively low in both of the regions studied, whereas at low Chlorophyll-$a$ concentrations, where algal community structure can be mixed, $P_B^m$ values are highly variable. The explanation for both of these trends may be that low pigment biomass can be a result of many factors, such as low growth irradiance, nutrient limitation, zooplankton grazing, and sinking, acting singly or in concert. Each of these factors will impact the photophysiological properties of the phytoplankton cells differently, either by altering the physico–chemical properties of the marine environment or shifting the phytoplankton community structure. In the case of high pigment biomass, however, environmental conditions are constrained: only with ample light and nutrient availability and low losses by grazing pressure and sinking relative to algal growth can high pigment biomass persist.

In low-chlorophyll, high-temperature environments it has been observed that a large variation in primary productivity may occur with limited alteration in the overall phytoplankton size structure (Marañón et al., 2003). This may be the result of the presence of different functional groups of small cells within the picoplankton cell range that are highly specialised to respond to short-term fluctuations in nutrient conditions. For
example, the presence of nitrogen-fixing, single-celled cyanobacteria in the oligotrophic ocean (Zehr et al., 2001) adds complexity to the classical foodweb paradigm, which associates small unicellular cyanobacteria with regenerated production. Moreover, in the Arabian Sea, the link between the size structure of the phytoplankton community and the absorptive properties of the phytoplankton appears to be highly variable between seasons (Fig. 6). This being the case, the assignment of $P_B^m$ values based on the size structure of phytoplankton communities may not be reliable, particularly if picoplankton cells dominate (Fig. 8d). However, in temperate marine ecosystems, such as the Scotian Shelf, the use of absorptive properties of algal cells as an indicator of $P_B^m$ shows much promise (Fig. 8c).

The picture that emerges from this study favours a partitioning of oceanic domains based on the principal forcing mechanisms that regulate marine photophysiology (Platt and Sathyendranath 1988; 1999), if temperature is to be used as a predictor of $P_B^m$. This study and others have shown that regions where temperature and community structure are correlated are also regions where the use of these two properties of the aquatic environment are strongly correlated with $P_B^m$ (Eppley, 1972; Harris, 1978; Harrison and Platt, 1980; Côté and Platt, 1983, 1984). The use of the optical properties of marine phytoplankton may hold great promise as a predictor of the photosynthetic parameters, especially in temperate oceanic regions that experience large fluctuations in phytoplankton size structure over an annual cycle. Presently, optical models are being developed to retrieve information on the size and taxonomic structure of marine phytoplankton (Ciotti et al., 1999, 2002; Sathyendranath et al., 2004). Maps of taxonomic composition in addition to sea-surface temperature generated from remote-sensing data may in the future improve our estimates of primary production.

5. Concluding remarks

Phytoplankton community structure and primary productivity are ecological features of marine systems that are known to change in response to the prevailing physical and chemical conditions (Margalef, 1965). In temperate regions, the evolution of phytoplankton communities from early to mature stages of succession is accompanied by transitions in the physicochemical properties of the marine ecosystem, from vertically-mixed, nutrient-rich cooler waters to stratified, nutrient-poor, warmer waters (Margalef, 1978; Margalef et al., 1979; Cullen et al., 2002).

Temperature has been shown to be correlated with the size structure of phytoplankton communities (Carder et al., 1999; Bouman et al., 2003). In addition, numerous studies of temperate freshwater and marine systems have shown a strong relationship between light-saturated photosynthesis and temperature (Platt and Jassby, 1976; Harrison and Platt, 1980; Côté and Platt, 1983, 1984; Kyewalyanga et al., 1998). It is likely that the strong relationship between $P_B^m$ and temperature is due, in part, to the seasonal changes in the taxonomic and size structures of phytoplankton communities, which often coincide with the vernal warming of surface waters in temperate marine waters. In the Arabian Sea, however, temperature is not correlated with the seasonal fluctuations in $P_B^m$, which is likely the result of a poor correlation between temperature and phytoplankton community structure.

Eppley (1972) suggested that our ability to predict $P_B^m$ from temperature is restricted to shallow, coastal and estuarine environments, where the influence of nutrient limitation on algal photophysiology is minimal. Although it is clear from this, and other studies, that temperature cannot be used indiscriminately as an indicator of light-saturated photosynthesis, our results do suggest that Eppley’s own opinion of temperature as indicator of light-saturated photosynthesis may have been too conservative. We propose that especially in temperate oceanic regions, where strong seasonal fluctuations in both temperature and community structure occur, temperature might be a viable predictor of $P_B^m$.

Results of this study show that indices of the taxonomic composition of natural phytoplankton assemblages show similar relationships with $P_B^m$ for both the Scotian Shelf and the Arabian Sea. This suggests that, in the future, ocean-colour algorithms developed to discriminate between
different phytoplankton groups may be used to aid in the assignment of photosynthetic parameters used in the computation of marine primary production. However, regional differences in the optical properties of phytoplankton groups may impose the need for regional algorithms for discrimination.

Acknowledgements

H.A.B. was supported by a NSERC research grant to T.P. and a Dalhousie Graduate Scholarship. This work was carried out as part of the Canadian contribution to the Surface Ocean - Lower Atmosphere Study (SOLAS). We thank Hervé Claustre, Erica Head and two anonymous reviewers for comments which improved the manuscript and Brian Irwin, Jeff Anning and Tim Perry for the collection and processing of the photosynthesis-irradiance experiments and the high-performance liquid chromatography pigment data. We also thank Carla Caverhill and Heidi Maass for data management support.

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