Relationship between light absorption by pelagic particles and microplankton metabolic activity in the Gulf of Lions

Susana Agustí, Antonio Cruzado

Centre d'Estudis Avançats de Blanes, Camí de Santa Bárbara s/n, E-17300 Blanes, Girona, Spain

ABSTRACT: We examined the relative contribution of autotrophic and non-algal particles to light absorption in marine waters in the Gulf of Lions (NW Mediterranean), and the relationship between light absorption by sestonic particles and their gross biological activity, as measured by electron (ETS) transport activity. Our results showed that non-algal particles make an important, often dominant, contribution to light absorption by sestonic particles. The potential respiration rates (ETS activity) of seston were found to be remarkably related to the light absorption coefficient of sestonic particles, $a_{p\ (400)}$, as described by the equation ETS activity (μl $O_2\,l^{-1}\,h^{-1}$) = 14.1 $a_{p\ (400)}^{0.92}$ ($r^2 = 0.65$, n = 37, p < 0.001). This relationship was stronger than that to light absorption by either algal or non-algal particles alone, as would be expected from the contribution of both particle types to seston metabolism. Our findings suggest a potential for the assessment of gross metabolism of marine planktonic communities from remotely-sensed optical properties.

INTRODUCTION

The chlorophyll a concentration and primary production of marine waters are predictable from remotely-sensed optical properties. Similarly, the biogenic content of the photic zone of marine waters should be predictable from optical properties, because most light-absorbing materials there, whether particulate or dissolved, are of biological origin (Morel 1988). These comprise planktonic organisms, both photosynthetic and non-photosynthetic, and biogenic detritus, which may also have an important contribution to light attenuation in the sea (Iturriaga & Siegel 1989, Spinrad et al. 1989, Bricaud & Stramski 1990, Cho & Azam 1990). Thus, light absorption in the sea at certain wavelengths may be better related to the biomass of all light-absorbing particles than to that of photosynthetic organisms alone (Morel 1988, Spinrad et al. 1989).

Gross planktonic metabolism is also strongly related to total planktonic biomass, as demonstrated by strong relationships between particulate organic carbon (including that of detritus) and planktonic respiration (e.g. Williams 1981, Courties et al. 1989). Thus, we hypothesize a positive, indirect relationship between light absorption and the bulk metabolism of planktonic communities. This hypothetic relationship would, if

confirmed, extend the power of optical properties to monitor biological processes in the ocean even further.

Here we examine the relative contribution of autotrophic and non-algal (heterotrophic organisms and detritus) particles to light absorption in marine waters in the Gulf of Lions (NW Mediterranean), and test the hypothesized relationship between bulk metabolic activity and light absorption by pelagic particles.

METHODS

The optical properties of seston within the photic layer in the Gulf of Lions were examined on particles collected on filters. The bulk metabolic activity of sestonic particles was described by their potential respiration, as the electron transport activity of the particulate fraction (ETS activity; Packard 1971). ETS activity is closely related to realised respiration (Packard & Williams 1981), and can be measured at low biomass, where direct measurements of respiration may have large error (Packard & Williams 1981). The relative contribution of phytoplankton and non-algal particles to light absorption was assessed following the method of Bricaud & Stramski (1990). Phytoplankton abundance was represented by the chlorophyll a (chl a) concentration of the waters sampled.

Sampling at the Gulf of Lions was conducted during the Rhodiber-90 EROS 2000 cruise (14 to 29 September 1990) aboard the RV 'Garcia del Cid'. Water samples were collected using a 30 l Niskin bottle in the upper 120 m at Stations RA1, RA6b, RA7, RB2, RC2, RC4, RD2, RE1, RF2, and R1 (Cruzado et al. 1991), which comprise oceanic and coastal Mediterranean waters and riverine waters discharged by the Rhône river. Sampling depths were selected upon examination of the distributions of salinity and temperature (CTD). Aliquots of each sample were used to measure ETS activity, chl a concentration, and total-particle light absorption at fixed wavelengths across the PAR band. Samples for the different analyses were pre-filtered through a 240 μm net to exclude large zooplankton.

ETS activity was measured on seston collected by filtering water (2 to 10 l, depending on seston concentration) through Whatman GF/F fibre-glass filters. Filters were immediately frozen in liquid nitrogen until enzymatic analysis at the laboratory. ETS activity, expressed as $\mu l\, O_2\, h^{-1}\, l^{-1}$, was measured at sea temperature (CTD) following the tetrazolium reduction technique (Packard 1971) as modified by Kenner & Ahmed (1975). Standardization of INT-formazan specific absorbance coefficient with NADH (Packard unpubl.) yielded a value of 0.2 for the INT-formazan specific absorbance coefficient at room temperature. The chl a concentration was measured in 250 ml aliquots filtered through Whatman GF/F filters. Filters were homogenized prior to chl a dark extraction for ca 4 h in acetone, and were kept refrigerated until measurement in a Turner Designs fluorometer (Parsons et al. 1984).

Measurement of light absorption by sestonic particles (phytoplankton, detritus, and other particles) followed Mitchell & Kiefer (1988). Seston was concentrated by filtering a variable volume of water (2 to 10 l) through Whatman GF/F filters. Filters were then placed on petri disks and kept wet and refrigerated in the dark until spectrophotometric measurements were made (within 4 h). The optical density of the filters (OD_f) was measured in a spectrophotometer (LKB) using a clean-water saturated Whatman GF/F filter as a blank. OD_f was measured at selected wavelengths within the PAR spectra (400, 440, 500, 520, 580, 625, 675, 700, 750 nm), representing those where peaks and valleys occur in most phytoplankton absorption spectra.

Particle light absorption (a_p, m^{-1}) was calculated following the equation,

$$a_{p(\lambda)} = 2.3\, OD_{f(\lambda)}\, C\, /\, V\, \beta_{(\lambda)} \qquad (1)$$

where λ = wavelength (nm); 2.3 is the factor to convert base 10 logarithms to natural logarithms; C = clearance area of the filter (m^2); V = volume of seawater filtered (m^3); and β = wavelength-dependent pathlength

amplification factor of the filters. The absorption attributable to phytoplankton and non-algal particles at the wavelengths measured was estimated by an indirect method described by Bricaud & Stramski (1990). The absorption coefficient by non-algal particles (a_d), was calculated as a negative exponential function of the wavelength (Bricaud & Stramski 1990). This method was modified to use light absorption at 400 nm to calculate the coefficients of the exponential equation instead of 380 nm as recommended by Bricaud & Stramski (1990). This modification was found, using an independent data set (Agustí unpubl.), to have no significant influence on the estimated absorption coefficients.

The light absorption coefficient for phytoplankton (a_{ph}) was then calculated (at each wavelength) following the expression,

$$a_{ph} = a_p - a_d \qquad (2)$$

We used light absorption at 675 nm, an absorption peak of chl a, to examine absorption by phytoplankton (e.g. Morel & Bricaud 1981). The measured particulate absorption coefficients at 400 nm were selected to examine the compound absorption of the different types of sestonic particles. This selection is based on the fact that the light absorption coefficients (PAR band) of different types of sestonic particles (e.g. bacteria, detritus) are greatest at 400 nm, which does not correspond to a pigment-related light absorption peak (e.g. Morel & Bricaud 1981, Morel & Ahn 1990, 1991).

The relationships between variables were described using least-squares linear regression analysis. Logarithmic (base 10) transformation of the variables was found to be necessary to avoid heteroscadicity (Draper & Smith 1966).

RESULTS

Chl a concentrations, particle light absorption, and potential respiration rates ranged greatly (Table 1), reflecting the high biological heterogeneity attributable to the discharge of the river Rhône in the Gulf of Lions (e.g. Cruzado & Velasquez 1990). Chl a concentrations, particle light absorption, and potential respiration rates were greatest at stations receiving a substantial discharge of river water.

Non-algal particles (e.g. detritus and heterotrophic organisms) made an important contribution to a_p in most samples (Fig. 1), and the contribution of phytoplankton to $a_{p(\lambda)}$ (i.e. $a_{ph(\lambda)}$) tended to be greater at 675 nm than at 400 nm (Wilcoxon sign-test, p < 0.01; Table 1). Thus, absorption by non-algal particles added considerable error to the relationship between chl a concentration and light absorption by particles. This rela-

Table 1 Maximum, minimum and mean values for biological and optical parameters measured in the Gulf of Lions. $a_p(\lambda)$: total particulate matter light absorption; $a_{ph(\lambda)}$: phytoplankton light absorption; $a_{d(\lambda)}$, non-algal matter light absorption; λ = 400 and 675 nm (wavelength); n = 37

		Maximum	Minimum	Mean
Chl a (mg m^{-3})		5.2	0.03	0.6
ETS activity (μl O$_2$ l^{-1} h^{-1})		19.0	0.14	1.18
$a_{p(400)}$	(m^{-1})	0.418	0.008	0.052
$a_{p(675)}$	(m^{-1})	0.144	0.002	0.020
$a_{d(400)}$	(m^{-1})	0.238	0.000	0.030
$a_{d(675)}$	(m^{-1})	0.090	0.000	0.007
$a_{ph(400)}$	(m^{-1})	0.180	0.003	0.022
$a_{ph(675)}$	(m^{-1})	0.116	0.0007	0.012

tionship was, therefore, stronger (r = 0.92 and 0.84, at 675 and 400 nm, respectively) when examining light absorption by phytoplankton ($a_{ph(\lambda)}$) than that to bulk light absorption by sestonic particles ($a_{p(\lambda)}$, r = 0.81 and 0.67 at 675 nm and 400 nm, respectively). These results
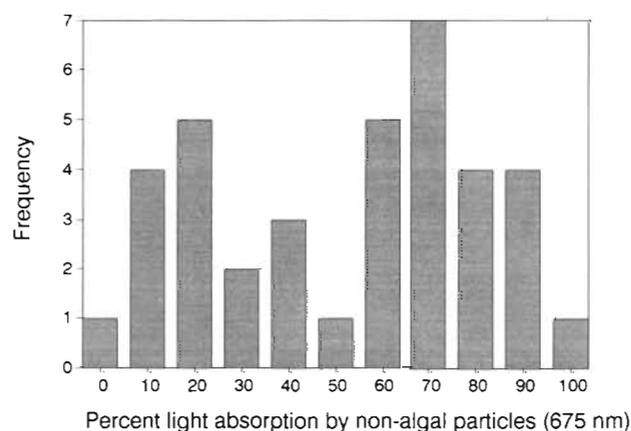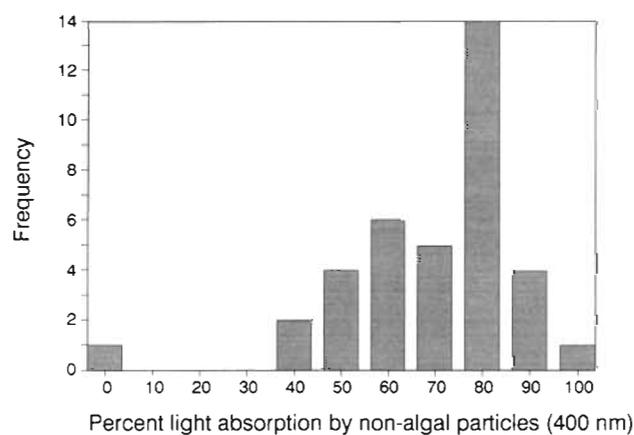

Fig. 1. Frequency distribution of light absorption percentages at 400 and 675 nm by non-algal particles in the Gulf of Lions

support the adequacy of the empirical method used to partition the total absorption coefficient into an algal ($a_{ph(\lambda)}$) and detrital ($a_{d(\lambda)}$) component (Bricaud & Stramski 1990).

The relationship between chl a concentration and ETS activity was weak (r = 0.65, p < 0.05). The weakness of this relationship may reflect the importance of non-algal particles (e.g. heterotrophic organisms) in these waters, which should also contribute to seston metabolic activity. Thus, seston metabolic activity was significantly related to the light absoption coefficients (400 nm) of both algal (r = 0.75) and non-algal (r = 0.69) particles (Fig. 2). Yet, the potential metabolic
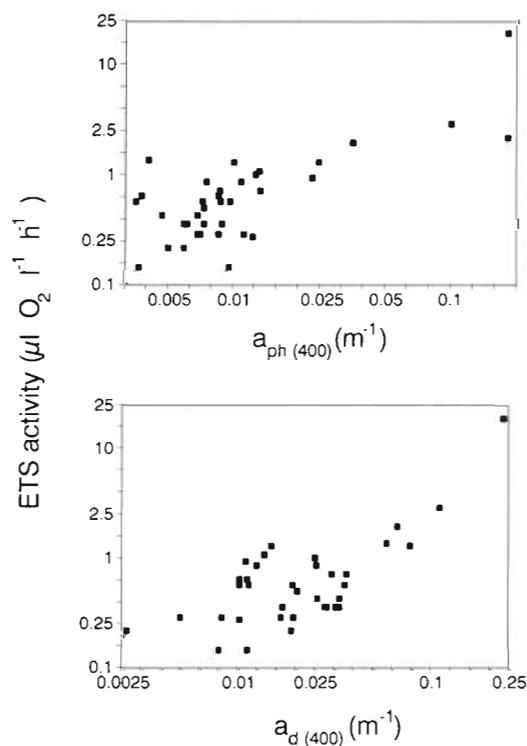

Fig. 2. Relationship between the ETS activity of microplankton and the light absorption coefficients of phytoplanktonic (a_{ph}) and non-algal (a_d) particles at 400 nm

activity of seston (ETS activity) was better correlated with the total particulate light absorption (r = 0.81) than with its separate algal and non-algal components (Fig. 3). This relationship was best described by the regression equation,

$$\text{ETS activity } (\mu l\ O_2\ l^{-1}\ h^{-1}) = 14.1\ a_{p(400)}^{0.92} \quad (3)$$

which reveals a remarkable, linear tendency (H0: slope = 1, p > 0.10) for the potential respiration of seston to increase as the particulate light absorption at 400 nm increases (Fig. 3). The strength of the relationship between potential seston metabolic activity and light
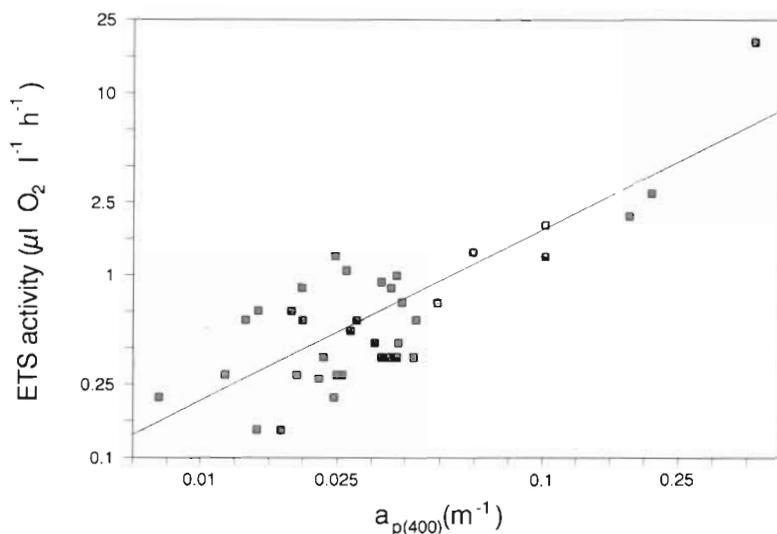
Fig. 3. Relationship between the ETS activity of microplankton and the light absorption by bulk particulate matter at 400 nm ($a_{p(400)}$). Solid and dotted lines: Eq. (3) with 95 % confidence limits

absorption decreased significantly (r = 0.57) when particulate light absorption was measured at 675 nm. The reason for this is probably that light absorption at this wavelength, which corresponds to an absorption peak by chl a, overestimates the presence of phytoplankton relative to heterotrophs, which may dominate planktonic metabolism (e.g. Williams 1981).

DISCUSSION

Our results show that non-algal particles make an important, often dominant, contribution to particulate light absorption in the oligotrophic waters of the Gulf of Lions (Fig. 1). This observation is in agreement with the increased importance of microheterotroph biomass (Bird & Kalff 1984, Fuhrman et al. 1989) and bacterial particulate organic carbon (Cho & Azam 1990) relative to phytoplankton biomass in oligotrophic waters.

The hypothesis that the optical properties of waters should allow the prediction of their bulk biological activity was supported by the significant relationship observed between the potential respiration rates and light absorption by sestonic particles (Eq. 3, Fig. 3). Detritic particles should not interfere with this relationship because detritus increases particulate light absorption but is also the focus of much microbial and heterotrophic activity (e.g. Fenchel 1970, Sorokin 1981).

Both respiration and light absorption by seston may be modelled as a combination of biomass-specific respiration and absorption, and biomass. Biomass-specific respiration rates and light absorption coefficients are influenced by many factors, such as habitat conditions and particle size and nature (e.g. Agustí 1991a, b, Ahrens & Peters 1991). Yet, seston biomass is expected to be related both to seston respiration (Packard et al.

1981, Williams 1981, Iriarte et al. 1991) and light absorption (Morel 1988) when comparing waters across a broad range of seston biomass. This explains the remarkable, indirect relationship between light absorption and seston metabolism reported here (Fig. 3).

In summary, the results presented here demonstrate that the study of optical properties of marine particles allows inferences on the relative composition and gross metabolism of planktonic communities. Whether the relationship between particulate light absorption and seston metabolism reported here holds elsewhere needs be tested. If confirmed, this relationship would allow assessment of gross metabolism of planktonic communities from remotely-sensed optical properties.

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