

EMPIRICAL RELATIONSHIPS BETWEEN PARTICULATE BEAM ATTENUATION COEFFICIENT, BACTERIA ABUNDANCE AND PRODUCTIVITY IN MARINE WATERS

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ABSTRACT

In this work we explore potential relationships between particle beam attenuation at 660 nm (c_p), chlorophyll a concentration (chl), heterotrophic bacteria abundance (BA) and carbon productivity (BCP) in oceanic waters of different latitudes, trophic levels, and upwelling conditions. It is hypothesized that c_p is positively related to BA and BCP if the dominant optically active component (detritus or phytoplankton) covary with heterotrophic bacteria. To test this possibility, surface data (0-20 m) of chl, BA, BCP, and c_p obtained from JGOFS (Joint Global Ocean Flux Study) and PAL-LTER (Palmer-Long-Term ecological Research) surveys were compared. In general, c_p values had a significant positive relationship with BCP in 64.7% of datasets analyzed. Dependency between c_p and BCP were mainly explained by phytoplankton-bacteria covariation (polar waters), and detritus-bacteria covariation (low/mid latitude waters). BA had only a significant contribution to c_p variability in non-polar waters.

INTRODUCTION

Heterotrophic marine bacteria (MHB) have a dual role (synthesis and degradation) on particulate organic carbon (POC) dynamics, and represent an important control of the biological ocean uptake ('biological pump') of atmospheric CO₂ (1). Unlike phytoplankton, global mapping of MHB across the oceans is more difficult due to three main facts. First, most of the MHB have not pigments (2) and can not be detected based on light absorption signatures and using large coverage satellite sensors. Second, field measurements are expensive or time-consuming (e.g., flow cytometry). Third, indirect estimation using phytoplankton parameters is not always reliable since phytoplankton biomass and productivity may not influence MHB variability (3,4).

The use of beam attenuation measurements (c) for global monitoring of MHB abundance (BA) and BA dependent parameters (e.g., carbon productivity or BCP) is probably feasible in oceanic waters. Theoretical calculations (Mie model) of scattering cross section of MHB (5) suggest a non-negligible contribution of MHB to particle beam attenuation ($c_p = c - c_w$, where c_w is the attenuation coefficient due to seawater). Likewise, field measurements in oceanic waters (Peruvian upwelling) pointed out a covariation between vertical distributions of BA and c_p values (6).

Despite these evidences no conclusions can be drawn *a priori* without testing *in situ* c_p -bacteria functionalities in diverse marine environments because two reasons. First, Mie model assumptions are not always met in nature (e.g., marine particles are not necessary spherical, 7), and second,

additional optical constituents (e.g., phytoplankton, detritus) not covarying with MHB may also have a comparable contribution to c_p (5, 8).

The objective of this study is to investigate empirical relationships between horizontal distributions of BA, BCP and c_p values on surface waters (0-20 m deep) of different oceans. The first part of this work is focussed on c_p -MHB functionalities in oceanic waters with different latitude, trophic level and upwelling conditions. The second part examines the contribution and effect of other optical targets (chl, detritus) on c_p -MHB relationships. The main hypothesis states that c_p is positively related to BA and BCP if the dominant optically active component (detritus or phytoplankton) covary with MHB.

Since c_p variability over large time and spatial scales is mainly driven by abundance of particles (9), the present contribution makes emphasis on c_p changes due to abundance of 'live' (MHB and phytoplankton cells) and 'death' (organic detritus) particles. The influence on c_p of other particle characteristics such as size, specific density and composition is out of scope of the present study.

METHODS

Data of c_p ($\lambda = 660$ nm), BA, BCP and chlorophyll *a* concentration (chl) were obtained from JGOFS (Joint Global Ocean Flux Study, <http://www1.who.edu/>) and Pal-LTER (Palmer-Long Term Ecological Research, <http://pal.lternet.edu/data/>) projects. Detailed protocols and methods are also described in these web pages. 24 datasets corresponding to low (Equatorial current, Sargasso Sea, North Pacific Central Gyre), mid (Arabian Sea, North Atlantic), and high (Antarctic Polar Front or APF, Ross Sea, Western Shelf of Antarctic Peninsula or WAP) latitude oceanic environments, and representing different trophic levels (oligotrophic vs eutrophic), and upwelling conditions were analyzed. Additional optical data (absorption spectra) were processed when available to characterize contribution of detritus and phytoplankton to c_p . All measurements were averaged within the first 20-m of the water column and comparisons between optical and MHB parameters were performed with samples obtained simultaneously (time difference less than 4 hours). Values of c_p were calculated by subtracting seawater contribution from c measurements, and assuming a minimum influence of yellow substances on c and water/salinity effects on c_w . Detritus absorption was determined spectrophotometrically (pad technique) after degrading phytoplankton pigments with methanol. Although BA was determined by two methods (flow cytometry or microscopic counts), both estimates are not consistently different (10). BCP estimations consisted in radioactive leucine and thymidine uptake incubations following standard methods (protocols details in JGOFS and Pal-LTER websites). Values of chl were measured using fluorometry. The partial contribution of BA to c_p was estimated from spectral curves of c_p obtained in (2) for marine bacteria and assuming non-pigmented cells. To quantify dependency of c_p on BA and BCP, and the contribution of other optical targets (phytoplankton, detritus) to c_p , multiple regression analysis was conducted using individual or groups of datasets. The influence of detritus on c_p was estimated from detritus absorption measurements at 412 nm (a_{d412}) using spectrophotometry. Final values (a_{d412}^*) were corrected by MHB absorption contribution (detritus - bacteria) at the same wavelength (2).

RESULTS

Empirical relationships between c_p and BCP

The linear increase of BCP with c_p was the most typical behavior found in most of the datasets under study (Table 1). Only 35.3% of comparisons had not a significant regression line ($P>0.05$) between c_p and BCP values. In general, c_p -BCP regression slopes were lower in polar waters (thymidine: 0.6-1.6 picomol $l^{-1} h^{-1} m$, leucine: 1.7-51.9 picomol $l^{-1} h^{-1} m$) with respect to low/mid latitude waters (thymidine: 5.3-18.1, leucine: 276.4-596.6). Likewise, lower c_p -BCP slopes were characteristic of oligotrophic (e.g., non-monsoon climate regime in Indian Ocean, non-El Niño condition in Equatorial Pacific waters) conditions with respect to eutrophic (e.g., monsoon, El Niño) conditions. For each c_p -BCP fitting curve, determination coefficient (r^2) was generally greater for leucine-based (0.50-0.73) with respect to thymidine-based (0.33-0.65) BCP measurements. Better adjustment between c_p and BCP values were observed in datasets where BCP/BA were the largest (e.g., ARAB-1, PAL-LTER2, and AESOPS-1, Table 1). Linear regression intercept values were in most cases no significantly different from zero ($P>0.05$).

Contribution of bacteria, phytoplankton and detritus to c_p magnitude and variability

For individual cruises, c_p values were always, not always (Sargasso Sea, Ross Sea during April-May 1997), and never related with organic detritus (a_{d412}^*), chl, and BA, respectively (data not shown). In general, BA contribution to c_p was highly variable (5.6 and 53.5%) and there was not a systematic trend between waters located at different latitudes, or with diverse trophic status and upwelling conditions (e.g., monsoon vs non-monsoon, El Niño vs non-El Niño). Seasonal contribution of BA to c_p was comparable to latitudinal differences. Based on multiple regression between c_p (independent variable), chl (dependent) and BA (dependent) values of polar and non-polar waters, BA only explained a significant fraction of c_p in low/mid latitude waters (20% of partial correlation, Table 2). Unlike BA, phytoplankton was the main optical component affecting c_p , and accounted for 80 and >90% of partial correlation in low/mid and polar waters, respectively (Multiple regression, Table 2). Notice that the influence of detritus on c_p variability of polar vs non-polar waters was not assessed using multiple datasets due to the scarcity of data. The importance of organic detritus on c_p variability was also evaluated but with a reduced number of cruises due to the lack of a_{d412} measurements (Table 3). Organic detritus was a major term driving c_p variability in oceanic waters, and generally had a greater contribution to a_{d412} (>50%) magnitude than MHB. Multiple regression of c_p as a function of a_{d412}^* , BA, and chl (Table 3) evidenced that organic detritus and BA had a minor contribution to c_p in polar waters (<1%) compared to non-polar waters (a_{d412}^* : 28.4%, BA: 22%).

Table 1: Summary of bio-optical relationships between particulate beam attenuation (c_p) and bacteria carbon productivity (BCP) in different oceanic regions; BCP (picomol $l^{-1} h^{-1}$) = $m c_p$ (m^{-1}) + b ; for each cruise, first and second row correspond to regression parameters obtained from leucine and thymidine incubations, respectively; n is number of measurements, r^2 is the regression coefficient of the linear fitting, Nd means no data; statistical significance (m , b and r^2 different from zero) at 95% () and 99% (**) of confidence limits. AESOPS: Ross Sea (1: January 1996, 2: January 1997, 3: April 1997, 4: November 1997), PAL-LTER: Western Shelf of the Antarctic Peninsula (1: January 2003, 2: January 2005), KIWI: Antarctic Polar Front (1: October 1997, 2: December 1997, 3: January 1998, 4: February 1998), NABE: North Atlantic (1: April-June 1989, 2: June-July 1989), ARAB: Arabian Sea (1: January 1995, 2: March 1995, 3: July 1995, 4: August 1995, 5: October*

1995, 6: November 1995), EQPAC: Equatorial Pacific (1: February-March 1992, 2: March-April, 3: August 1992, 4: September 1992), HOTS: North Pacific Central Gyre (1992-1995), BATS: Sargasso Sea (1992-1997). In Arabian Sea, June to September coincide with 'monsoon' climate regime whilst August-September 1992 corresponded to non-El Niño conditions.

Cruise	<i>m</i>	<i>B</i>	<i>n</i>	<i>r</i> ²
AESOPS-1	6.56**	-0.02	18	0.73*
	1.58**	0.02	18	0.68*
AESOPS-2	30.51**	18.40*	14	0.60*
	Nd	Nd	Nd	Nd
AESOPS-3	51.90*	-0.35	8	0.56*
	1.10*	-0.01	8	0.65*
AESOPS-4	1.72**	2.11**	20	0.50*
	0.55**	0.38**	33	0.70*
PAL-LTER1	12.11**	-0.58	35	0.66*
	0.95*	-0.06	37	0.36*
PAL-LTER2	3.62	14.48	33	0.01
	0.62	0.30	33	0.16
KIWI-1	Nd	Nd	Nd	Nd
KIWI-2	0.75	4.09	9	0.01
	-0.12	0.59	11	0.01
KIWI-3	Nd	Nd	Nd	Nd
KIWI-4	8.87	0.91	17	0.27
	0.15	0.48	17	0.01
NABE-1	66.40	59.32	12	0.07
	-6.93	11.10	20	0.17
NABE-2	Nd	Nd	Nd	Nd
	-13.20	19.33	4	0.20
ARAB-1	276.4**	8.21	15	0.61*
	14.01*	2.25	13	0.45*
ARAB-2	106.88	34.51	14	0.08
	77.59	-5.73	14	0.13
ARAB-3	510.72**	12.2	7	0.58*
	23.3	3.82	7	0.13
ARAB-4	Nd	Nd	Nd	Nd
ARAB-5	Nd	Nd	Nd	Nd
ARAB-6	Nd	Nd	Nd	Nd
EQPAC-1	398.4**	2.71	12	0.63*
	14.7**	0.14	26	0.33*
EQPAC-2	196.14	32.42	17	0.08
	6.92	2.54	17	0.03
EQPAC-3	596.6**	-20.8	20	0.59*
	18.12**	-0.17	10	0.50*
EQPAC-4	51.37	24.31	20	0.03
	13.21	1.27	20	0.29
HOTS	Nd	Nd	Nd	Nd
BATS	Nd	Nd	Nd	Nd
	5.27**	-1.73	15	0.51*

Table 2: Multiple regression analysis of c_p as a function of bacteria and phytoplankton variability; polar waters (AESOPS, PAL-LTER, KIWI cruises), low/mid latitude waters (HOTS, BATS, NABE, ARAB, EQPAC cruises); c_p (m^{-1}) = β_{chl} chl + β_{BA} BA + α , chl = chlorophyll a concentration ($mg\ m^{-3}$), BA: bacteria abundance (cells l^{-1}), β_{chl}^ and β_{BA}^* are standardized weights (partial correlation coefficients) for phytoplankton and bacteria contributions, respectively; n is number of data, F is the F-test value of the multiple regression, r^2 is the coefficient of determination. For each regression parameter, statistical significance at 95% (*) and 99% (**) of probability level.*

	Polar	Non-polar
N	179	236
Adjusted r^2	0.80	0.37
F	342.5**	84.9**
α	0.22**	0.07**
β_{BA}	$9.44\ 10^{-12}$	$4.89\ 10^{-11*}$
β_{chl}	0.18**	0.12**
β_{BA}^*	0.012	0.13*
β_{chl}^*	0.89**	0.53**

Table 3: Multiple regression analysis of c_p as a function of bacteria, phytoplankton and detritus variability; non-polar waters: ARAB-2 and ARAB-6 cruises, polar waters: AESOPS-4, KIWI-3 and KIWI-4 cruises, c_p (m^{-1}) = β_{chl} chl + β_{BA} BA + β_{det} a_{d412}^ + α , chl: chlorophyll a concentration ($mg\ m^{-3}$), BA: bacteria abundance (cells m^{-3}), a_{d412}^* : absorption coefficient of organic detritus at 412 nm corrected by bacteria contribution (detritus-bacteria). β_{chl}^* , β_{BA}^* and β_{det}^* are standardized weights (partial correlation coefficients) for phytoplankton, bacteria, and detritus contributions, respectively; n is number of data, F is the F-test value of the multiple regression, r^2 is the coefficient of determination. For each regression parameter, statistical significance at 95% (*) and 99% (**) of probability level.*

	Polar	Non-polar
N	34	38
Adjusted r^2	0.90	0.77
F	100.27**	41.33**
α	0.10	0.037*
β_{BA}	$1.60\ 10^{-10}$	$3.18\ 10^{-11*}$
β_{chl}	0.16*	0.06**
β_{det}	4.40	1.66**
β_{BA}^*	0.08	0.27*
β_{chl}^*	0.77*	0.61*
β_{det}^*	0.16	0.35*

CONCLUSIONS

This study attempts for first time to evaluate the potential application of c_p to derive BCP and BA in different oceanic waters given the widely use of c_p in past and present oceanographic projects. A common pattern observed in oceanic waters of different latitudes, trophic levels and upwelling conditions was the positive covariation between c_p and BCP. For individual cruises, this relationship was not explained by BA changes but was instead very often related to modifications of chl (index of phytoplankton biomass) and a_{d412}^* (index of organic detritus) values. Phytoplankton is a 'live particle' that provides dissolved and particulate carbon to MHB metabolism affecting indirectly

BCP (11). The covariation between c_p and BCP could also be attributed to the availability of organic 'death particles'. A preliminary set of a_{d412} measurements underlined the importance of organic detritus, a substrate for MHB, to explain the observed c_p -BCP functionality. Since MHB can be associated to particles (12) and BCP/BA of particle-attached population is greater than free-living population (13), it is suggested that part of the variability embedded on c_p -BCP curves could be attributed to concomitant variations of organic detritus and particle-attached bacteria. In this work, correspondence between better fitting (greater r^2) of c_p -BCP curves and greater BCP/BA values supported this idea.

The original hypothesis of this study was valid for the data analyzed, thus two types of ecological systems explaining dependency between c_p and BCP are proposed: (1) waters with phytoplankton-bacteria covariation (typical of polar waters), and (2) waters with detritus-bacteria covariation (typical of low/mid latitude waters). Although these two bio-optical systems were present in most of the datasets processed, there were some cases where c_p was not a reliable proxy of BCP (e.g., PALTER2, NABE-1, Table 1). This 'occasional' poor coherence between c_p and BCP variability deserves future investigation.

ACKNOWLEDGEMENTS

This work was supported by the National Science Foundation (OPP-90-11927, OPP-96-32763, OPP-02-17282) and NASA funding (NNG04GL55G; KLC).

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