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Impact of Effective Light Climate on Periphyton in the Nutrient Impacted River Ganges

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Abstract

Anthropogenic releases in large regulated rivers are overriding their organic load assimilation capacity and ability to rejuvenate. Effective light penetration in such water bodies are constrained by trade-off between organic load and benthic oxygen supply. We investigated the impact of light climate, as influenced by dissolved organic carbon (DOC) and phytoplankton shading effect, on periphyton biomass accrual in Ganges during summer low flows. Periphyton chlorophyll a decreased with increasing growth of phytoplankton and DOC. Periphyton biomass showed significant negative correlation with DOC (R^2=0.9483; p<0.0001) and phytoplankton biomass (R^2=0.9251; p<0.0001) and positive correlation with Secchi depth (R^2=0.9506; p<0.0001). Among taxonomic divisions, Chlorophyta, with 24-60% of total standing stock, showed higher biomass at sites characterized by moderate nutrients and DOC levels. Cyanophyta (39-74%) contributed large fraction at eutrophic sites and Bacillariophyta (2-5%) at moderately eutrophic sites. Cyanophycean alga *Phormidium* appeared dominant at sites enriched in nutrients. The study indicated that light attenuation driven by DOC and phytoplankton is leading to erode benthic primary producers and redistribution of taxonomic divisions in Ganges, which may, by implication, entail a similar shift in the trophic cascades.

1. Introduction

Urban-industrial release coupled with agricultural runoff and atmospheric deposition is causing large changes in Ganga River water quality along its 2525 km length. Reduction of nutrients and organic load to the river is considered as a key measure to reduce eutrophication and associated problems being demanded by National River Conservation Directorate (NCRD). Despite large efforts under Ganga Action Plan (GAP) targeted to reduce nutrients and organic load, the water quality of river is continuing to decline. Rapidly changing water quality and capacity to assimilate organic load necessitate long-term management efforts to rejuvenate the river. Nutrient supply in surface waters promotes algal growth and, as a long-term effect, causes a potential shift in ecosystem functions and trophic cascades (Bergstrom *et al*., 2008; Pandey, 2011; Pandey and Pandey, 2014). In lotic ecosystems, flow velocity and light climate of the channel also regulate algal growth.

For instance, decreased flow velocity increases the residence time of phytoplankton to proliferate (Hilton *et al*., 2006). The functional relationships between resource availability and algal growth may be complicated by hydrological disturbances (Lohman *et al*., 1992). Thus, the effect of resource availability on algal growth in rivers remains more apparent during low flows. Recent studies on tropical waters suggest that nutrient limitation is primary driver of phytoplankton productivity, whereas growth of epilithic periphyton is more effectively regulated by light attenuation (Carey *et al*., 2007; Pandey and Pandey, 2013). Periphetic algae take nutrients from sediments and also help supplying nutrients to phytoplankton while phytoplankton attenuate light limiting the growth of periphyton (Vadeboncoeur *et al*., 2003).

Epilithic algal periphyton, the submerged micro-floral community living attached to substrate, are important primary producers in surface waters. Periphyton growth in rivers is highly variable and serves signaling eutrophication (Chetelat *et al*., 1999), regulating trophic cascades and river ecology and, reducing the release of nutrients and greenhouse gases (Luijn *et al*., 1995; Flury *et al*., 2010). The wide-spread reliance of fishes and zoobenthos on carbon fixed by benthic algae cue the relative importance of taxonomic divisions in aquatic food webs (Vadeboncoeur *et al*., 2003). However, excessive growth of phytoplankton and/ or high levels of DOC shift surface waters from a clear to turbid state attenuating light to constrain

Table 1: Characteristics of sampling sites

Site	Code	Mean depth (m)	Substrate	Average flow (ms^{-1})	Characteristics
Adalpura	Adp	21	Sandy/ rocky	0.40	Least human interference; natural and agriculture runoff
Sultankeshwar Ghat	Stg	20	Muddy with pans	0.45	Less human interference; agricultural runoff
Bypass downstream	Bds	12	Sandy	0.40	Runoff from anthropogenic dredging
Nagwa discharge	Ngw	14	Muddy	0.27	Sewage outlets; urban surface discharge
Assi Ghat	Asg	14	Muddy/ sandy	0.26	Urban core; urban surface discharge
Shivala Ghat	Slg	16	Pans and pebbles	0.29	Urban core; municipal waste and small sewage outlet
Harishchandra Ghat	Hcg	16	Sandy with pebbles	0.37	Urban core; biomass burning
Rana Gat	Rng	20	Pans and pebbles	0.32	Urban core; cloth washing
Raj Ghat	Rjg	20	Muddy/ sandy	0.35	Urban core; sewage outlets
Raj Ghat downstream	Rds	18	Sandy with pebbles	0.32	Post-urban; downstream influence

periphyton growth (Pandey and Pandey, 2013). Colored humic substances of terrestrial origin, being optically dense, more effectively attenuate light penetration (Karlsson *et al*., 2009) and consequently, the periphyton growth. The DOC enrichment in surface waters is accelerated by anthropogenic activities in catchment and nutrient driven pulsed growth of phytoplankton (Evans *et al*., 2006; Eimers *et al*., 2008).

Despite their significant roles, algal periphyton and environmental determinants of periphytic growth in Ganga River have received little attention (Pandey, 2013). There is a general dearth of studies explicitly addressing the effect of phytoplankton growth and DOC mediated light attenuation on periphyton growth in the Ganges. The present study was an effort to investigate variations in algal periphyton biomass accrual and the relative contribution of taxonomic divisions in relation to light attenuation driven by phytoplankton and DOC in Ganga River. Scientific information on these issues are essential assessing ecological status, establishing trans-boundary linkages of functional relationships, predicting climate change drivers and developing action plans for integrated river basin management.

2. Materials and Methods

2.1. Study area

Present study was conducted during four consecutive years (March, 2009 to 2012) at 10 selected sites along a 35 km stretch of Ganga River at Varanasi (25°18'N latitude, 83°1'E longitude and 76.19 m above msl), India. Each sampling site also represents a complementary site opposite to the city-side of the river and henceforth referred as off-side sampling locations. A description of different sampling stations is presented in Table 1. Climate of the region is tropical with distinct seasonality. The year can be divided into a hot and dry summer (March to June), a humid rainy season (July to October) and, a cold winter season (November to February). Mean annual rainfall varied between 870-1130 mm, relative humidity between 27 and 83% (summer) and 58 and 99% (rainy season). More than 90% of mean annual rainfall in the region occur during rainy season. During summer, day time temperature varied between 29 and 46.2°C. During winter, night temperature some time drops below 4°C. Wind direction shifts from predominantly westerly and south-westerly in October through April to easterly and north-westerly in remaining months. The soil in the region is alluvial fluvisol associated with recurrent floods or long wetness, recent sedimentation and high natural fertility. Catchment soils differ in terms of percentage of fine soils (silt and clay), total organic carbon (0.98 to 1.67% in upper 0-10 cm soil). Major parts of the river catchment witness intensified agriculture.

2.2. Methods

The experimental design consisted of three tiers of study; water chemistry, light attenuation and growth of phytoplankton and periphyton. We collected samples in summer low flows to ensure that periphytic communities have developed to a reasonably mature state for accurately reflecting local environment and effects of other variables being investigated. Periphytic growth varies season to season and with substrate.

However, flow-related factors override such patterns by washing away loosely attached species and the remaining taxa may not accurately able to reflect water chemistry and role of other variables (Biggs and Kilroy, 2000).

2.2.1. Water sampling and analysis

Composite water samples were collected from 15 m reach in summer low flows of four consecutive years. The distance between replicate sampling (n=3) was about 50 m. Water samples were collected from each site, directly below the surface (15-25 cm depth), in acid-rinsed 5L plastic containers for analysis of total dissolved solids (TDS), dissolved oxygen (DO), dissolved organic carbon (DOC), nitrate-N (NO_3^-) and orthophosphate (PO_4^{3-}). TDS was measured using a TDS meter and DO was estimated following Winkler's modified method (APHA, 1998). DOC was quantified using a $KMNO_4$ digestion procedure (Michel, 1984). For this purpose, water samples were mixed with acidified N/80 potassium permagnate and incubated at 37°C. Organic carbon was estimated by titrating to quantify oxygen after 4h of incubation (APHA, 1998). Nitrate-N was quantified using a brucine sulphanilic acid method (Voghe, 1971) and orthophosphate (dissolved reactive phosphorus, DRP) following ammonium molybdate stannous chloride method (APHA, 1998). Light attenuation in the river was measured using Secchi disk and intensity of light at depth was calculated using mid-summer surface light intensities (Vadeboncoeur *et al.*, 2003).

2.2.2. Algal biomass

Phytoplankton and periphyton biomass was measured in terms of chlorophyll a. Chlorophyll a constitutes approximately 1.5% of algal organic dry matter (APHA, 1998) and is considered among the most important indicators of algal biomass (US Geological Survey, 2007). Sub-samples taken for phytoplankton were preserved in Lugol's iodine and concentrated by centrifugation at 3500 rpm (APHA, 1998). Phytoplankton chlorophyll a, extracted using acetone, was determined spectrophotometrically and expressed as mg m^{-3}. For periphyton chlorophyll a, 35 mm plastic slides were laid in triplicate over experimental rock surface fixed in closed wire cage (basket sampler) of 15×15×15 cm size at 2m depth for one month during summer low flow (16th April to 15th May each year). Each replicate represents a composite sample of three independent slides placed at each collection point at a distance of 2m. The material within the slide area (scrub area = 2.3×3.5 cm = 8 cm^2) was pulled by vacuum onto a pre-ashed glass fiber filter (Whatman GF/A) for wet and dry weights. Enough care was taken to ensure complete recovery of algal assemblages attached to the surface. Chlorophyll a biomass was determined in fresh material following acetone extraction (Maiti, 2001) and expressed as mg m^{-2} by relating to area of exposed surface. Phycocyanin (PC) pigment was extracted in 0.05 M phosphate buffer (pH 6.8) and estimated following Bennett and Bogorad (1973). Autotrophic index (AI) was calculated by dividing ash free dry mass (AFDM) by the chlorophyll a concentration of periphyton (APHA, 1998). The AFDM was quantified by reweighing the sampled filter papers ashed at 500°C (Bowes *et al.*, 2012).

2.2.3. Taxonomic and biomass partitioning

To understand per cent contributions of taxonomic divisions, we evaluated taxonomic and biomass partitioning in the algal community. Sites were sampled (n=3 per site) during summer low flow (16th April to 15th May each year from 2009 to 2012) and thus, did not reflect the effect of seasonality. A 50 ml of scraped homogenate was preserved in Lugol's iodine solution and identifications made from 0.5 ml aliquot and counted in a haemocytometer using an Olympus compound microscope. Identifications of benthic algae to genus level were made using Prescott (1973), Mizumo (1990) and Dillard (1991). Filaments, fragments and cell densities were measured and calculated for each recorded taxa. Cell dimensions were measured and cell volumes estimated by approximation to geometric shapes of known volume. Algal biomass was measured by converting the calculated cell volumes to biomass assuming a specific density of 1 g cm^{-3} (Chetelat *et al.*, 1999) and expressed as mg cm^{-2}. Relationships of taxonomic share to periphyton biomass were evaluated using locally weighted sequential smoothing technique (LOWESS) following Chetelat *et al.* (1999).

2.2.4. Statistical analysis

Mean estimates ($\bar{X}$) of water quality variables (TDS, NO_3^-, PO_4^{3-}, DO and DOC) and Secchi depth represent replication sites and temporal variability while that of Chl a, taxonomic and biomass partitioning and AI represent replication sites only. Significant effects of site and time were tested using analysis of variance (ANOVA). All repeated measurements (including replication sites), except a few that did not follow a normal distribution pattern, were considered in ANOVA model. Values were log-transformed when needed and interaction terms were included in the analysis. Coefficients of variation (CV) were computed for expressing data variability. Correlation coefficient

(R^2) and linear regression models were used to test linearity between variables. Relationships between percent contribution of taxonomic divisions and periphyton biomass were non-linear and evaluated using locally weighted sequential smoothing technique following Chetelat *et al*. (1999). SPSS package was used for statistical analysis.

3. Results

Concentrations of nutrients and TDS were high at downstream sites (Table 2). Values were high at city-side with NO_3^- ranging from 227.08 to 950.17 µg L^{-1} and PO_4^{3-}, 150.30 to 844.67 µg L^{-1}. Respective ranges at off-side locations were 217.10 to 568.45 µg L^{-1} and 134.22 to 467.10 µg L^{-1}. Dissolved oxygen (DO), on the other hand, remained high at upstream sites (Table 2). Site-wise differences in TDS, DO and nutrients were significant ($p<0.001$) (Table 3). DOC increased along the study gradient and at Rjg, the values were over 4-folds higher (Fig. 1). DOC concentrations at off-side locations were substantially low. River DOC increased over time and inter-annual variations were significant (Table 3).

Secchi depth declined over time and along the study gradient. At Rjg, Secchi depth declined by over 83%. Secchi disk transparency was higher at off-side compared to city-side locations irrespective of site and study year (Fig. 1). Phytoplankton Chl a biomass was high at downstream sites of both the sides (Fig. 1). Unlike phytoplankton, periphyton Chl a biomass declined along the gradient spanning over 4 to 6 orders of magnitude and was lowest at Rjg (Fig. 1). Spatial and temporal trends in periphyton Chl a were opposite to that of Secchi depth and phytoplankton production. At city-side, periphyton biomass varied between 23.24 and 79.86 mg m^{-2} in 2009 and between 11.25 and 66.34 mg m^{-2} in 2012. The relative contributions of taxonomic divisions varied along the study gradient. Chlorophyta, with 24-60% of total standing stock, showed high biomass at sites containing moderate amount of nutrients (Fig. 2). Cyanophyta, with 39-74% share

Table 2: Variation in total dissolved solids (TDS) and concentrations of nitrate (NO_3^-), orthophosphate (PO_4^{3-}) and dissolved oxygen (DO) measured at city-side and off-side in Ganga River along the study gradient. Values are mean (n= 24) ±1 SE

Site	City-side				Off-side			
	TDS (mgL^{-1})	NO_3^- (µgL^{-1})	PO_4^{3-} (µgL^{-1})	DO (mgL^{-1})	TDS (mgL^{-1})	NO_3^- (µgL^{-1})	PO_4^{3-} (µgL^{-1})	DO (mgL^{-1})
Adp	470.10 ±27.45	227.08 ±20.05	150.30 ±11.05	9.30 ±0.52	457.00 ±26.10	217.10 ±13.22	134.22 ±9.38	9.35 ±0.47
Stg	472.20 ±29.05	267.30 ±21.11	174.18 ±11.67	8.50 ±0.53	462.00 ±28.67	222.10 ±13.76	138.20 ±9.57	8.82 ±0.49
Bds	751.34 ±49.10	396.22 ±26.17	271.57 ±15.10	7.25 ±0.41	492.81 ±28.96	236.17 ±14.05	148.36 ±10.28	7.82 ±0.42
Ngw	840.20 ±58.76	796.81 ±48.45	532.20 ±31.46	6.63 ±0.36	518.21 ±32.25	391.23 ±15.96	260.33 ±14.59	7.51 ±0.40
Asg	846.52 ±63.18	850.41 ±61.72	676.76 ±49.75	6.41 ±0.37	529.67 ±36.18	408.35 ±20.67	311.20 ±17.92	7.42 ±0.41
Slg	852.46 ±61.72	887.32 ±73.22	705.72 ±58.23	6.15 ±0.32	568.37 ±36.58	430.18 ±21.05	342.67 ±24.05	7.31 ±0.37
Hcg	858.63 ±70.34	896.30 ±78.40	750.67 ±57.20	5.84 ±0.30	576.13 ±35.92	452.46 ±23.30	371.71 ±23.97	7.11 ±0.36
Rng	866.37 ±71.46	905.72 ±77.39	788.61 ±64.10	5.12 ±0.28	580.28 ±35.87	470.27 ±26.45	390.37 ±25.87	6.94 ±0.33
Rjg	888.24 ±74.90	950.17 ±81.46	844.67 ±71.15	4.21 ±0.26	592.44 ±37.05	568.45 ±31.28	467.10 ±29.15	6.05 ±0.34
Rds	882.20 ±73.14	932.16 ±84.10	831.00 ±74.28	4.40 ±0.24	590.86 ±37.16	567.11 ±30.49	458.00 ±31.86	6.00 ±0.30

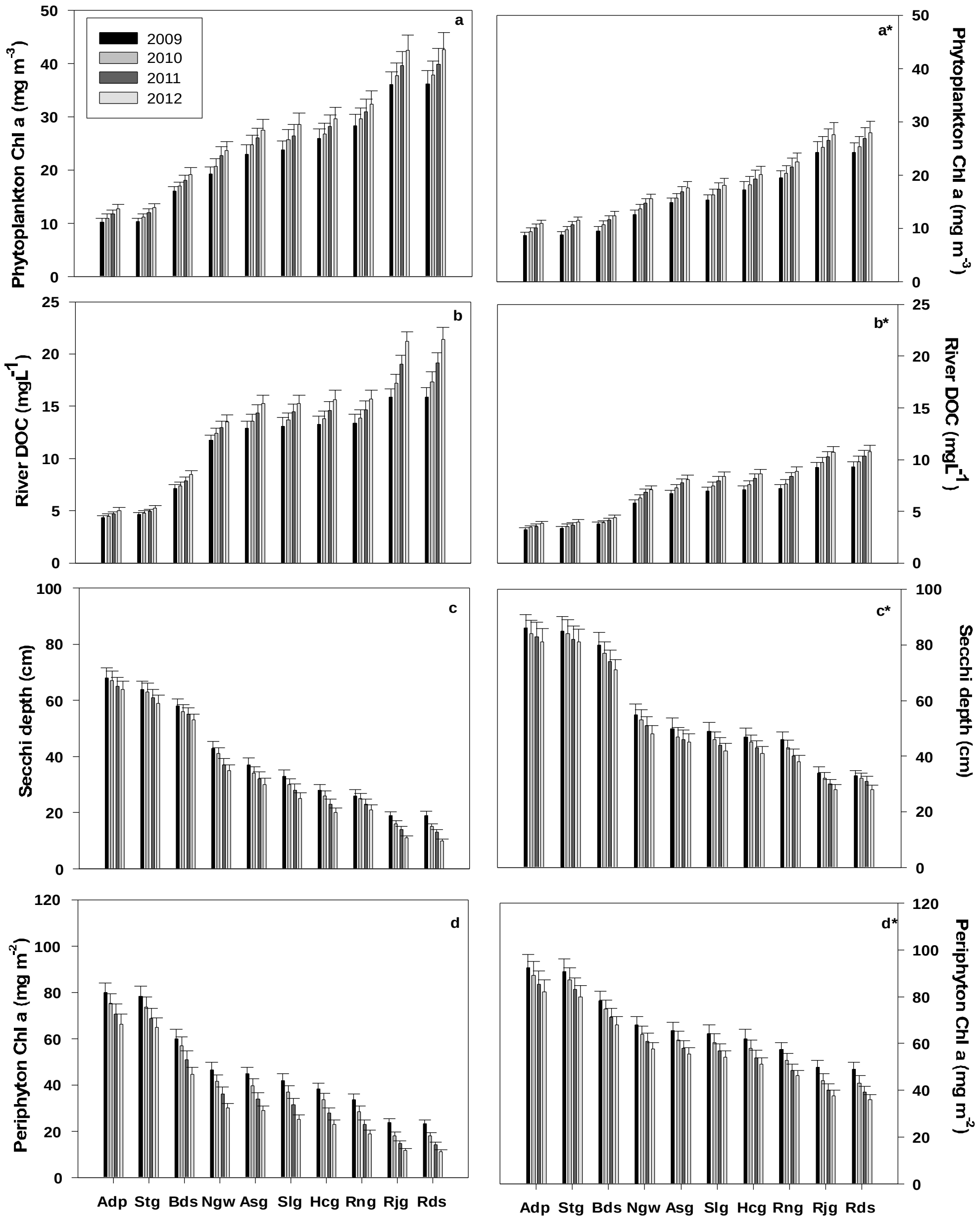

Fig. 1: Phytoplankton chlorophyll a biomass (a), dissolved organic carbon (b, DOC), Secchi depth (c) and periphyton chlorophyll a biomass (d) measured at city- side and off-side in Ganga River along the study gradient. Values are mean (n= 24 for DOC and Secchi depth and n=12 for Chl a biomass) ±1SE. Boxes with alphabets marked with * represent complementary sites at off-side of the river

acquired larger fraction at eutrophic sites and, Bacillariophyta, with 2-5% share, at moderately eutrophic sites. Periphyton biomass showed positive correlation with Secchi depth (R^2=0.9506; $p<0.0001$) and negative correlation with DOC (R^2=0.9483; $p<0.0001$) and phytoplankton biomass (R^2=0.9251; $p<0.0001$). Secchi depth was found negatively related with DOC (R^2=0.9608; $p<0.0001$) and phytoplankton biomass (R^2=0.9390; $p<0.0001$) (Table 4, Fig. 3). Autotrophic index (AI) showed a trend similar to phytoplankton biomass (Fig. 4). Phycocyanin to chlorophyll a (PC: Chl a) ratio varied between 2.00 and 3.44 (city-side) and, 2.10 and 2.67 (off-side). The ratio showed an initial decrease with rise in nutrients but an increasing trend with further rise in nutrients (Fig. 4). Spatial and temporal differences in DOC, Secchi depth, periphyton Chl a, phytoplankton Chl a and AI were significant (Table 3).

Table 3: F-ratios obtained from analysis of variance (ANOVA) to indicate significant effects of site (s), side (S), year (Y) and their interactions on water quality variables and chlorophyll a biomass along the study gradient of Ganga River

Variable	s	S	Y	s×S	s×Y	S×Y	s×S×Y
TDS	712.50***	183.20***	ns	74.05***	7.05*	17.68**	4.93*
NO_3^-	387.43***	364.05***	12.84*	126.32***	118.50***	156.70***	17.85**
PO_4^{3-}	583.76***	417.30***	19.00*	105.18**	113.75***	127.12***	56.98***
DO	102.33***	216.20***	ns	30.11**	38.15**	56.11***	4.87*
DOC	406.15***	375.18***	38.00**	156.59***	137.52***	186.40***	112.76***
Secchi depth	311.50***	417.00***	37.70**	117.22***	96.87***	194.35***	102.15***
Phytoplankton Chl a	874.67***	258.70***	69.54***	68.90***	105.20***	209.18***	205.67***
Periphyton Chl a	637.82***	307.15***	58.47***	79.20***	92.54***	237.50***	198.72***
AI	349.27***	192.87***	57.28***	65.00***	41.07**	74.23***	32.10**

Note: TDS: total dissolved solids; DO: dissolved oxygen; DOC: dissolved organic carbon; AI: autotrophic index. Values significant at: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns: not significant.

4. Discussion

Periphyton contributes substantially to ecosystem productivity and large changes in these benthic producers may lead to shift the trophic cascades (Vadeboncoeur *et al.*, 2003; Hilton *et al.*, 2006). Nutrient enrichment enhances phytoplankton production whereas benthic algal growth is directly limited by light climate. Both, phytoplankton and DOC reduce benthic algal growth through light attenuation (Karlsson *et al.*, 2009; Pandey and Pandey, 2013). We observed a marked increase in DOC over time and along the study gradient. A corresponding decrease in DO along the gradient further indicates rising level of oxygen demanding organic substances. Nutrient driven increase in pelagic production (Pandey and Pandey, 2009; Pandey, 2011) together with increased terrestrial C inputs associated with climate, hydrology and human activities (Evans *et al.*, 2006; Monteith *et al.*, 2007; Pandey and Pandey, 2013) enhance DOC in surface waters. Large agricultural catchment of Ganges and sewage discharge from the city enhances DOC of terrestrial origin (Pandey *et al.*, 2014a). Reduced overall stream flow due to damming of the river could further enhance DOC. During recent years, the water discharge in Ganga River in reduced by over 70% from its pre-damming stage (Pekárová *et al.*, 2003).

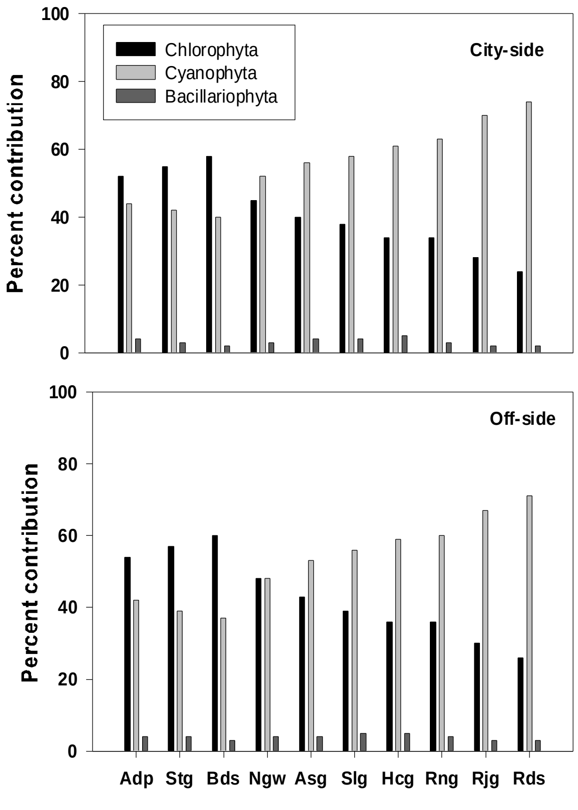

Fig. 2: Percent contribution of taxonomic divisions (Chlorophyta, Cyanophyta and Bacillariophyta) to overall periphyton Chl a biomass. The percent taxonomic division biomass was computed following a model-free locally weighted sequential smoothing technique

Despite the fact that nutrient enrichment enhances growth of phytoplankton (Bergstrom *et al.*, 2008; Pandey *et al.*, 2014b) and periphyton (Chetelat *et al.*, 1999), we found significant negative relationships between phytoplankton and periphyton growth. Phytoplankton Chl a biomass increased while that of periphyton declined with increasing N and P concentrations along the study gradient. Since benthic algae derive sediment-associated nutrients, light limitation more strongly influence benthic primary production in surface waters (Karlsson *et al.*, 2009). Here we hypothesize that an increase in DOC and/ or phytoplankton growth reduces benthic algal biomass accrual through light attenuation. Our results showed that nutrient enrichment and associated growth of

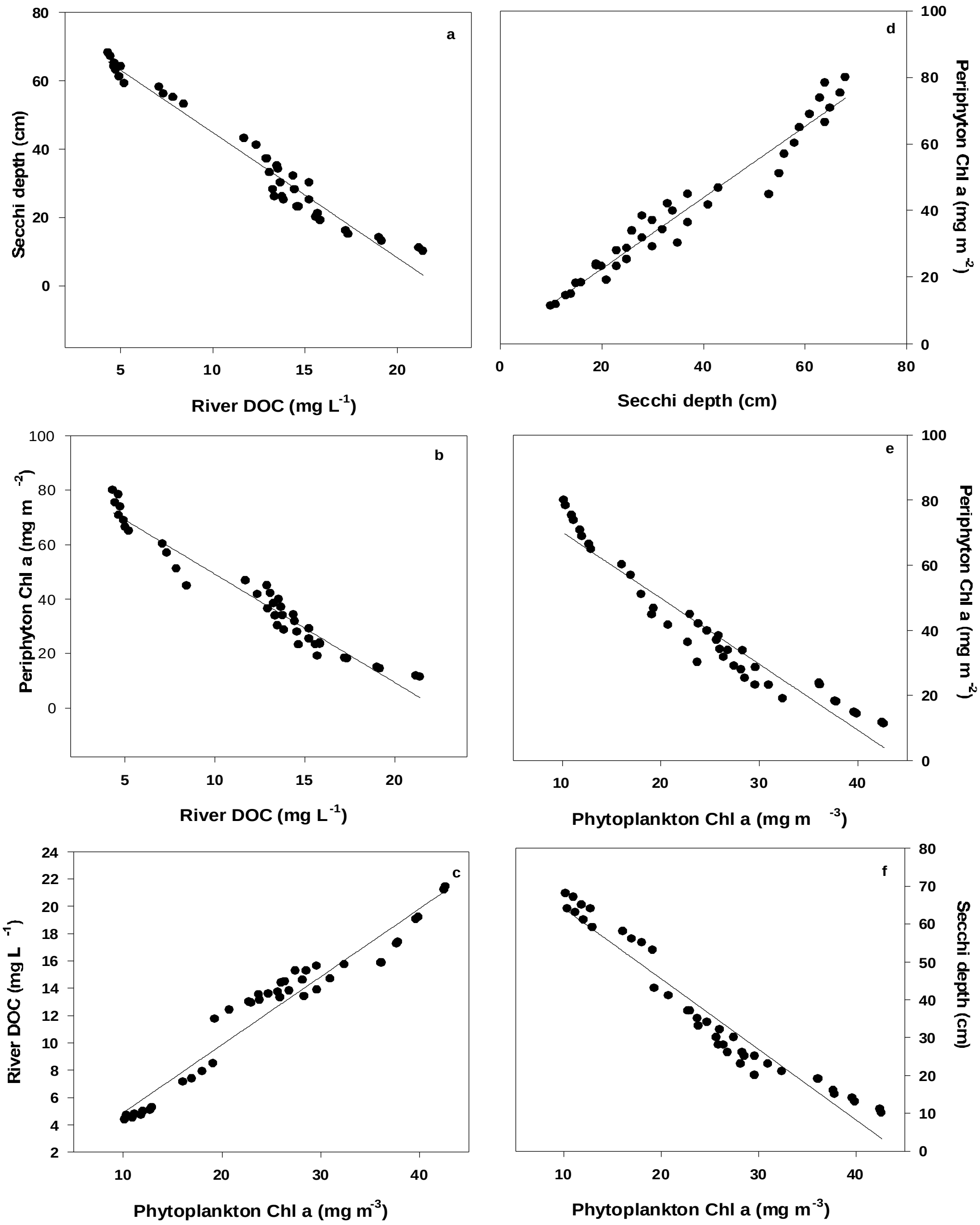

Fig. 3: Significant relationship between (a) river DOC and Secchi depth, (b) river DOC and periphyton Chl a, (c) phytoplankton Chl a and river DOC, (d) Secchi depth and periphyton Chl a, (e) phytoplankton Chl a and periphyton Chl a and, (f) phytoplankton Chl a and Secchi depth

phytoplankton together with enhanced DOC of terrestrial origin reduced periphyton biomass accrual in Ganga River. Among the nutrients, P is a common limiting nutrient associated with freshwater eutrophication. Vadeboncoeur *et al*. (2003) observed that phytoplankton blooms and associated light attenuation along a gradient of P input in Greenland and Danish lakes caused significant loss of benthic growth. Although the growth limiting concentrations of phosphorus vary greatly from river to river ranging from less than 20 µg L^{-1} soluble reactive-P (Chambers *et al*., 2006) to greater than 100 µg L^{-1} (Bowes *et al*., 2007), data in this study and the published records (Pandey *et al*., 2014b) show that P is not a limiting nutrient in Ganga River. Under such condition, anthropogenic releases would likely lead towards N-driven eutrophication. Decrease in periphyton biomass along the gradient could be related to light attenuation caused

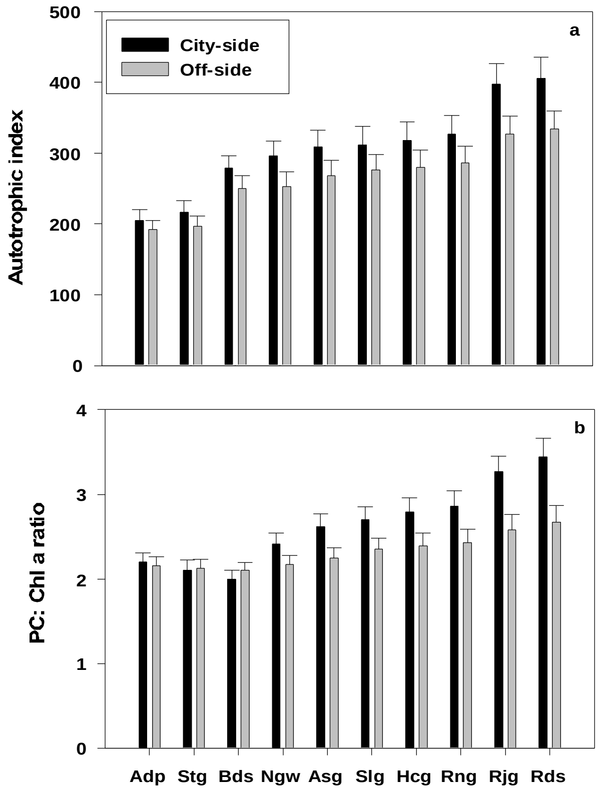

Fig. 4: Autotrophic index (a) and phycocyanin (PC) to Chl a ratio (b) estimated at city-side and off-side locations in Ganga river along the study gradient. Values are mean (n= 12) ± 1SE

by DOC and phytoplankton (Carey *et al*., 2007). Benthic algal biomass was positively correlated to depth of light penetration and the latter was negatively correlated to DOC and phytoplankton biomass indicating that DOC and phytoplankton both reduced benthic algal growth through light attenuation.

Both DOC and phytoplankton biomass increased over time and along the gradient while light penetration and periphyton biomass showed an opposite trend. For majority of sampling stations, autotrophic index (AI) remained above 250 and reached over 406 indicating that the biofilm community was relatively unbalanced between heterotrophic and autotrophic conditions (Ameziane *et al*., 2002). Although DOC and phytoplankton shading effect did not rule out one from the other, former could be more crucial than the latter reducing periphyton growth. Terrestrially derived DOC, being optically dense, reduces light penetration more effectively (Karlsson *et al*., 2009). The C: N ratios in the study stretch were >15 indicating allochthonous influences (Elser *et al*., 2000). The magnitude of effect of DOC on light attenuation observed in this study was similar to the results from previous studies. Our results showed, a 7 mg L^{-1} increase in DOC caused light penetration to decline by 42%. Further increase in DOC showed a consistently increasing light attenuation. McEachern *et al*. (2000) have shown that a 9% increase in DOC caused Secchi disk transparency to decline by 46%. Bergstrom *et al*. (2001) observed that a 7 mg L^{-1} increase in DOC correspond to approximately 37% decrease in light climate. Luijn *et al*. (1995) have reported that even 15 to 20% attenuation in Secchi depth can significantly alter the benthic growth. Similar effects of light limitation on periphyton biomass accrual have been reported by Bowes *et al*. (2012) in Thames River and by Pandey and Pandey (2013) in a freshwater tropical lake of India.

To understand per cent contributions of taxonomic divisions, we evaluated taxonomic and biomass partitioning in the algal community. Periphyton biomass coupled taxonomic partitioning is an important indicator of water quality in rivers (Chetelet *et al*., 1999). We found a marked shift in the relative contribution of taxonomic divisions of benthic primary producers. Initially, with rise in nutrients, Chlorophyta contributed the major share, latter however, with further increase in nutrients; Cyanophyta represented the larger fraction of community biomass. A synchrony in PC: Chl a ratio

Table 4: Summary of regression model relating periphyton Chl a biomass (mg m^{-2}) to the determinants of light climate in the study river

Equation	n	R^2	p
DOC = -0.1009 Phy Chl a + 0.4981	40	0.9385	<0.0001
Secchi depth = 81.3665 DOC - 3.6589	40	0.9608	<0.0001
Secchi depth = 82.6700 Phy Chl a -1.8600	40	0.9390	<0.0001
Per Chl a = 1.084 Secchi depth + 1.0693	40	0.9506	<0.0001
Per Chl a = 89.0063 DOC - 3.9867	40	0.9483	<0.0001
Per Chl a = 90.3783 Phy Chl a - 2.0248	40	0.9251	<0.0001

Note: DOC: dissolved organic carbon; Phy: phytoplankton; Per: periphyton; Chl a: chlorophyll a biomass; n: number of observations indicated the dominance of Cyanophyta towards eutrophic sites. Further, there was a shift in dominance among blue green algal taxa from *Oscillatoria, Gloeocapsa* and *Tolypothrix* to *Phormidium* along the gradient. Increasing dominance of *Phormidium* along the gradient indicate its ability to exploit nutrient enriched conditions. Our previous studies have shown gradual replacement of sensitive species by more opportunistic invasive species which rapidly capitalize over available nutrients (Pandey and Pandey, 2002, 2013; Pandey, 2013). Chetelat *et al*. (1999) observed that nutrient enriched rivers sites in southern Ontario and western Quebec were associated with high periphyton standing crop but dominated by particular filamentous taxa. In the present study, on further increase in DOC however, light driven constraints did offset the influence of nutrient enrichment even for aggressive species causing overall biomass to decline. These observations suggest that DOC enrichment may affect periphyton standing crop and also cause a shift in community composition towards particular algal taxa. It is possible that, for the whole ecosystem productivity, the net reduction in benthic production may partly be offset by an enhanced pelagic production, a large shift in benthic primary production however, may lead to long-term changes in the river ecosystem functioning. Since DOC is an important component of global carbon cycle, our observations on rising DOC in an oceanic river like Ganges have relevance from climate perspective as well.

5. Conclusions

The river gradient considered in this study showed a switchover from benthic to pelagic dominance of primary productivity. The study concludes that light limitation resulting from rising concentrations of DOC and enhanced growth of phytoplankton, driven by the anthropogenic causation, are leading to erode benthic primary producers and redistribution of taxonomic divisions of periphyton. A shift in relative importance of primary production from periphyton to phytoplankton as well as in taxonomic groups of periphyton may entail a similar shift in the diets of zoobenthos. Since benthic algae help supporting higher trophic levels, sequestering nutrients, maintaining bottom oxygenation and reducing the release of phosphorus and greenhouse gases from bottom sediments, a shift in benthic primary producers may lead to long-term changes in trophic cascades as well as in waste assimilation capacity and ecosystem resilience of the river. Scientific information on these issues would help understanding ecosystem energetics and climate change drivers and establishing integrated river basin management strategies.

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