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ORIGINAL PAPER

Phytoplankton and phytobenthos pigment strategies: implications for algal survival in the changing Arctic

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Abstract We compared phytoplankton and phytobenthos pigment strategies in 17 shallow lakes and ponds from northern Canada and Alaska, sampled during mid to late summer. Benthic chlorophyll *a* concentrations (8–261 mg m^{-2}) greatly exceeded those of the phytoplankton (0.008–1.4 mg m^{-2}) in all sites. Cyanobacteria dominated the phytobenthos, while green algae and fucoxanthin-groups characterized the plankton. Both communities had higher photoprotection in cold, UV-transparent, high latitude waters. Phytoplankton had higher concentrations of photoprotective carotenoids per unit chlorophyll *a* than the phytobenthos. The planktonic photoprotective pigments were positively correlated with UV-penetration, and inversely correlated with temperature and coloured dissolved organic matter. A partial redundancy analysis showed that the benthic pigments were related to latitude, area and temperature. The UV-screening compound scytonemin occurred in high concentrations in the phytobenthos and was inversely related to temperature, while benthic carotenoids per unit chlorophyll *a* showed much lower variability among sites. These differing pigment strategies imply divergent responses to environmental change between the phytobenthos and phytoplankton in high latitude lakes.

Keywords Algae · Carotenoids · CDOM · Climate change · Cyanobacteria · Lakes · Photoprotection · Pigments · UV

Introduction

In most shallow polar freshwater ecosystems, fast growing phytoplankton occur in sparse concentrations in the water column. This contrasts with the benthic communities in such waters, which often form well-developed, perennial mats and films. The benthic communities may be up to several millimetres thick and are often dominated by cyanobacteria (Vincent 2000; Hodgson et al. 2001; Sabbe et al. 2004). These interacting algal communities differ in composition, growth rates, loss processes, tolerance to nutritional stress and ability to optimize light use (Vézina and Vincent 1997; Bonilla et al. 2005). Such differences are likely to affect the algal sensitivity to various stressors, including climate change. Predicted future environmental changes in the Arctic include increased air temperatures, decreased duration of snow and ice cover, increased evaporation, changes in coloured dissolved organic matter (CDOM) and increases in exposure to ultraviolet radiation (UVR), and these will likely have broad impacts on Arctic freshwater ecosystems (Wrona et al. 2006; Smol and Douglas 2007a; Vincent and Laybourn-Parry 2008).

High latitude shallow water bodies are transparent and thus sensitive to high light and UVR exposure. Phytoplankton must optimize photosynthesis and avoid

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photo-oxidative damage to their photosynthetic apparatus due to light stress, which is exacerbated by cold temperatures that slow down the dark reactions of photosynthesis and cellular repair processes. Although phytobenthic communities are exposed to the same environmental constraints, light penetration can decrease rapidly through the mats, resulting in limiting conditions for photosynthesis in the bottom layers. Nutrient status also affects the photosynthetic/photoprotective balance and while polar freshwaters are typically oligotrophic, the phytobenthos habitat at the sediment-water interface is much richer in nutrients (Bonilla et al. 2005). Planktonic and benthic communities also differ in their taxonomic composition, which can result in differences in photosynthetic and photoprotective strategies. Microalgae and cyanobacteria have photoprotective carotenoids that mitigate photo-oxidative damage by quenching toxic reactive oxygen species (ROS) induced by UVR exposure (Goodwin 1980; Demmig-Adams and Adams 2000). In some benthic cyanobacteria, the pigment scytonemin provides additional protection by absorbing UV radiation (Garcia-Pichel and Castenholz 1991). Pigments can also play a role in conferring tolerance to other stress factors common in shallow polar freshwaters such as low temperatures and desiccation (Markager et al. 1999; Hodgson et al. 2001). Pigment analysis, therefore, provides information on the photophysiology of algal communities, as well as insights into community structure. Understanding pigment characteristics and strategies is also useful for paleolimnological reconstructions of past changes in autotrophic production and composition (Vinebrooke et al. 2002; Michelutti et al. 2005) and can aid in determining food web interactions (Andersson et al. 2003).

In the present study, we addressed the hypothesis that pigment strategies differ between planktonic and benthic algal communities in high latitude aquatic systems. Our objectives were to characterize the pigment signatures of both types of algal community and to evaluate their relationships with abiotic factors. We sampled shallow waterbodies at diverse sites to encompass a broad range of environmental conditions for empirical analysis: lakes and ponds in the Canadian subarctic, Alaskan low Arctic, and the Canadian High Arctic.

Materials and methods

A total of 17 shallow lakes and ponds were sampled in summer 2003 (Northern Quebec: 8–13 July, Cornwallis Island: 4–8 August) and 2004 (Alaska: 2–6 July, Ellesmere and Ward Hunt Islands: 30 July to 2 August) along a latitudinal gradient extending from 55°N to 83°N, and less than 100 m in altitude (Table S1, Fig. 1). All sites were fishless and were divided into five regions, according to their latitude and catchment vegetation: Northern Quebec (subarctic, forest tundra), Alaska (low arctic, shrub tundra), Cornwallis Island (arctic, polar desert), Ellesmere Island Lake Hazen area (Ellesmere-1; arctic, polar desert with well-vegetated wetland patches) and Ellesmere Island North and Ward Hunt Island (Ellesmere-2; arctic, polar desert). The Hazen Plateau region (Ellesmere-1) is an oasis region on Ellesmere Island that has unusually warm summers despite its high arctic location (Keatley et al. 2007; Fig. 1), and in the subsequent analyses is referred to as "oasis wetland". Water temperature, pH and conductivity were measured with a water analyser probe (Oakton, USA). Dissolved inorganic and organic carbon (DIC and DOC), and dissolved nutrients (nitrate and soluble reactive phosphorus) were analysed as in Bonilla et al. (2005) and Rautio and Vincent (2006) (Table S1).

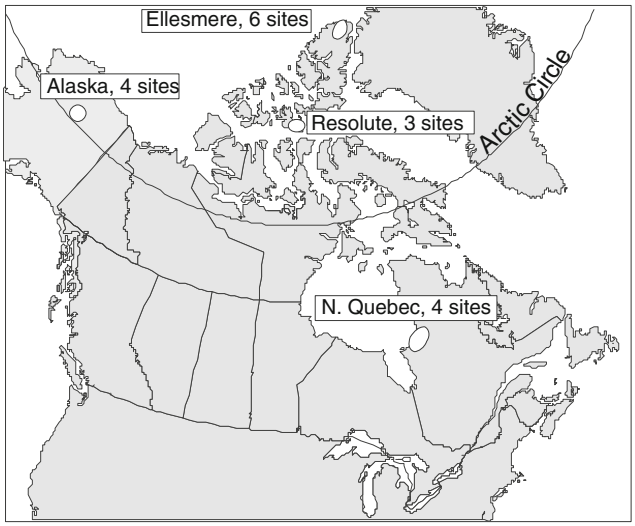

Fig. 1 Location map of the five studied regions: northern Quebec, Alaska, Cornwallis Island (Resolute), and the Ellesmere Island region, including Ward Hunt Island. The number of lakes and ponds studied in each region is also indicated

To estimate the algal exposure to UVR, we first measured the absorption spectrum of chromophoric dissolved organic matter (CDOM), the primary attenuator of solar UVR in high latitude waters (Laurion et al. 1997). Water samples were filtered through 0.2 μm Nuclepore membranes and then their absorbance was scanned relative to filtered MilliQ water in 5 cm cuvettes with a Varian Cary 300 spectrophotometer, as in Retamal et al. (2008). The absorption coefficient at 320 nm was calculated as an index of CDOM concentrations:

$$a_{\mathrm{CDOM}}(320) = 2.303 \times \text{ Absorbance at } 320\mathrm{nm}/(0.05\mathrm{m}).$$

The diffuse attenuation coefficient for ultraviolet radiation at 320 nm (K_{d320}, m^{-1}) in the lakes and ponds was calculated as:

$$K_{d320} = K_{d440} \exp[-S(320 - 440)],$$

where S was set to 0.0151 nm^{-1} and K_{d440} was estimated from the measured CDOM absorption coefficient at 440 nm [$a_{CDOM}(440)$], as in Laurion et al. (1997). The percentage of UV_{320} radiation reaching the bottom ($E_{d(z-max)}$) of the waterbody was estimated from K_{d320}, the depth of the water body (Z) at the sampling site (0.1–0.3 m), and the downward irradiance value at surface ($E_{d(0)}$) which was set as 100%:

$$E_{d(z-max)} = E_{d(0)} \exp[-K_{d320}(Z)].$$

One to five cores of benthic mats (10 mm diameter, top 1 mm) and subsurface phytoplankton samples (0.5–1.5 l) were taken from each water body. Phytoplankton samples were filtered onto 25 mm diameter GF/F glass-fibre filters. All samples were immediately frozen at −20°C and, within 3 weeks of sampling, transferred to a −80°C freezer until pigment extraction. Mat core samples were extracted in 90% acetone (−20°C overnight in the dark under argon gas) and phytoplankton in 95% methanol. High performance liquid chromatography (HPLC) protocols followed those described in Bonilla et al. (2005). Phytoplankton pigments were expressed as mg m^{-2} for the full water column depth of the sampling site. Mat pigments were directly converted to mg m^{-2} according to the sampled core area. Carotenoids were classified as photosynthetic (PSC = 19′-hexanoyloxyfucoxanthin + fucoxanthin + fucoxanthin-like + alloxanthin) or photoprotective (PPC = diadinoxanthin + diatoxanthin + echinenone + lutein + violaxanthin + zeaxanthin + canthaxanthin), after Porra et al. (1997). Some carotenoids have more than one role in the cells and were therefore excluded from our classification. These include myxoxanthophyll and β,β-carotene, a photosynthetic pigment only in prokaryotes (Porra et al. 1997). To assess changes in contributions to photosynthesis and photoprotection, two sets of pigment indices were calculated for both communities. To determine the main differences in photoprotective and photosynthetic strategies, ratios of specific pigments or pigment groups to total pigments (TP) were calculated for chlorophyll *a* (Chl a_{TP}), photoprotective pigments (PPT_{TP}), photosynthetic pigments (PSC_{TP}), accessory chlorophylls *b* and *c* (Chl acc_{TP}) and scytonemin (Scy_{TP}). To determine differences in pigment strategies in relation to the total phototrophic biomass, the pigment groups were also normalized to Chl *a,* the photosynthetic pigment common to all oxygenic phototrophs: PPT_{Chla}, PSC_{Chla}, Chl acc_{Chla} and Scy_{Chla} and total carotenoids to Chl *a* (TCar/Chl *a*). Finally, to compare the relative contribution of photosynthetic versus photoprotective pigment contribution, ratios of all photoprotective (PPC + SCY = PPP) to all photosynthetic (Chl *a* + Chl acc + PSC = PHOT) pigments were calculated.

Statistical analyses were made using SigmaStat (Version 3.1), Statistica (6.0) and CANOCO 4.5 for Windows. Statistical differences between indices were evaluated by standard parametric tests (*t* values), or if the distributions were non-normal, by Mann–Whitney tests (*U* values) for equal or unequal sample size. Linear regressions and one-way ANOVA were performed between pigment indices and abiotic variables (Table S1). A set of multivariate analyses was performed to further examine the pigment and abiotic data sets. To summarize the variation in physico-chemical water column environment among water bodies, a principal components analysis (PCA) was undertaken, with centred and standardized variables (lake area, lake depth, pH, temperature, conductivity, nitrate, dissolved reactive phosphorus, DIC, DOC and a_{320}). Nutrient data were not available for pond ACP, and this site was therefore not included in the analysis. Based on log-transformed matrices, an exploratory detrended correspondence analysis (DCA) was used to determine the gradient length in the pigment data and to choose between unimodal and linear methods for subsequent analyses (ter Braak and Šmilauer 2002). Accordingly, a linear method, partial redundancy analysis (partial RDA), was performed with manual selection to choose those environmental variables that were significantly (unrestricted Monte Carlo permutation test, 499 permutations, reduced model, $P \leq 0.05$) related to pigment indices. Then, the explained variation was partitioned by using combinations of the selected environmental variables as explanatory variables and covariables in subsequent partial RDA analyses, and their significance was tested with Monte Carlo permutation tests (reduced model, 499 permutations, $P \leq 0.05$; Borcard et al. 1992; Legendre 2008). Interstitial water in microbial mats at the water-sediment interface is rich in nutrients that are potentially available to the phytobenthos (Villeneuve et al. 2001; Rautio and Vincent 2006). Moreover, it has been demonstrated that the phytobenthos in an oligotrophic High Arctic lake (Ward Hunt Lake, Nunavut, Canada) was not limited by nutrients, despite low concentrations in the overlying water column (Bonilla et al. 2005). Thus, for the phytobenthos, nutrient concentrations for the water column (nitrate, phosphate, DIC and DOC) were not included in the multivariate analyses.

Results

Environmental variables

Water bodies were mostly oligotrophic in terms of nitrogen (nitrate: 1–30 μg N l^{-1}) and soluble reactive phosphorus (SRP: <1–5.5 μg P l^{-1}) concentrations in the

Table 1 Pigment ratios to Chl *a* (average ± SE; μg μg^{-1}) in the phytoplankton for the studied water bodies grouped in the five regions, 4keto-myxo: 4keto-myxoxanthophyll-like

	Subarctic	Low Arctic	Arctic		
	NQuebec ($n = 4$) Forest tundra	Alaska ($n = 4$) Shrub tundra	Corn I ($n = 3$), Polar desert	Elles-1 ($n = 4$) Oasis wetland	Elles-2 ($n = 2$), Polar desert
Chl *b*	0.16 ± 0.02	0.21 ± 0.04	0.27 ± 0.11	0.13 ± 0.02	0.08 ± 0.08
Chl c_1	0.05 ± 0.03	ND	0.02 ± 0.01	0.29 ± 0.11	ND
Chl c_2	0.07 ± 0.02	0.05 ± 0.01	0.05 ± 0.03	0.21 ± 0.04	0.13 ± 0.07
Antheraxanthin	0.06 ± 0.02	0.01 ± 0.01	ND	0.02 ± 0.02	0.04 ± 0.04
Alloxanthin	0.05 ± 0.04	0.02 ± 0.02	0.11 ± 0.06	0.11 ± 0.07	ND
Canthaxanthin	ND	ND	0.06 ± 0.06	ND	0.07 ± 0.07
Diadinoxanthin	0.39 ± 0.12	0.04 ± 0.04	0.12 ± 0.12	0.17 ± 0.08	0.33 ± 0.07
Echinenone	ND	0.04 ± 0.02	0.29 ± 0.27	ND	ND
Fucoxanthin	0.53 ± 0.21	0.28 ± 0.05	0.95 ± 0.26	1.44 ± 0.25	0.70 ± 0.38
Myxoxanthophyll	ND	ND	ND	ND	ND
4keto-myxo	ND	ND	1.00 ± 1.00	ND	ND
Lutein	0.27 ± 0.12	0.31 ± 0.03	0.79 ± 0.39	0.37 ± 0.37	0.17 ± 0.17
Violaxanthin	0.16 ± 0.04	ND	0.45 ± 0.22	0.41 ± 0.10	0.57 ± 0.33
Zeaxanthin	0.06 ± 0.02	0.08 ± 0.04	0.12 ± 0.06	0.14 ± 0.04	0.26 ± 0.12
Scytonemin	ND	ND	ND	ND	ND
Red scytonemin	ND	ND	ND	ND	ND

ND not detected. The number of studied lakes (*n*) and the vegetation type per region are indicated

water column (Table S1). There were large differences in temperature and CDOM concentrations as measured by a_{320} among the five regions. The Subarctic and low Arctic waters had warmer temperatures (8.2–20.4°C), while high Arctic polar desert lakes had the lowest values (2.4–10.1°C; Table S1). CDOM was significantly lower in the polar desert regions CornI and Elles-2 ($t = 3.65$, $P < 0.05$). Consistent with this, the calculated UVR penetration (% surface UVR reaching the lake bottom) was highest ($t = 8.46$, $P < 0.001$) at the polar desert sites relative to other regions. The oasis wetland sites (Ells-1) had higher CDOM concentrations than the polar desert waters (Table S1), reflecting the greater development of terrestrial and semi-aquatic vegetation at the former.

The first two axes of the PCA explained 58.8% of the total variability in water chemistry and morphometry of the 16 lakes (Fig. 2). The PCA ordination revealed environmental gradients of temperature and CDOM, and conductivity and DIC (axis 1, 35.2% of total variance). The second PCA axis, which accounted for 23.6% of total variation, included gradients associated with morphometry (area and depth) and nutrients (NO_3^- and SRP). Subarctic and low arctic plotted close to each other on the negative side of axis 1. Most of the arctic sites (except two sites of

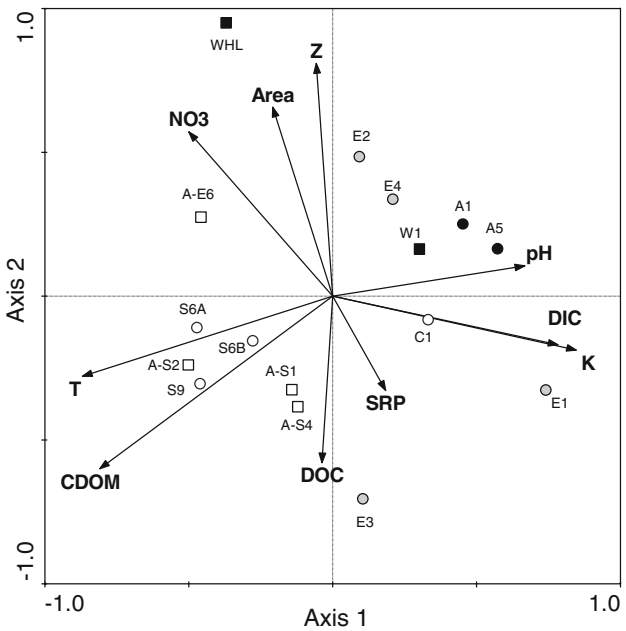

Fig. 2 Principal component analysis (PCA) of the physico-chemical characteristics of all lakes (except ACP), showing axes 1 and 2 (eigenvalues 0.352 and 0.237, respectively). Symbols refer to the regions as follow: *open circles* northern Quebec, *open squares* Alaska, *black circles* Cornwallis Island, *grey circles* Ellesmere-1 and *black circles* Ellesmere-2. Codes for variables as in Table S1

Table 2 Pigment ratios to Chl *a* (average ± SE; μg μg^{-1}) in the phytobenthos for the studied water bodies grouped in the five regions, 4keto-myxo: 4keto-myxoxanthophyll-like

	Subarctic	Low Arctic	Arctic		
	NQuebec ($n = 4$) Tundra forest	Alaska ($n = 4$) Tundra, Shrubs	Corn I ($n = 3$), Polar desert	Elles-1 ($n = 4$) Oasis wetland	Elles-2 ($n = 2$), Polar desert
Chl *b*	0.05 ± 0.02	0.04 ± 0.03	0.03 ± 0.02	0.16 ± 0.11	0.02 ± 0.01
Chl c_1	ND	ND	ND	ND	ND
Chl c_2	0.03 ± 0.01	<0.01	0.01 ± 0.01	0.03 ± 0.02	0.01 ± 0.01
Antheraxanthin	ND	ND	ND	ND	ND
Alloxanthin	0.04 ± 0.02	ND	0.01 ± 0.01	0.02 ± 0.02	ND
Canthaxanthin	0.03 ± 0.01	0.03 ± 0.01	0.04 ± 0.03	0.05 ± 0.02	0.10 ± 0.02
Diadinoxanthin	0.28 ± 0.10	ND	ND	0.02 ± 0.01	0.07 ± 0.07
Echinenone	0.07 ± 0.04	0.14 ± 0.02	0.18 ± 0.04	0.11 ± 0.03	0.22 ± 0.03
Fucoxanthin	0.27 ± 0.12	0.01 ± 0.01	0.02 ± 0.02	0.09 ± 0.06	0.02 ± 0.02
Myxoxanthophyll	0.03 ± 0.02	0.02 ± 0.01	ND	0.04 ± 0.04	0.05 ± 0.05
4keto-myxo	0.05 ± 0.01	0.03 ± 0.02	0.05 ± 0.04	0.03 ± 0.01	0.24 ± 0.12
Lutein	0.06 ± 0.05	0.03 ± 0.02	0.01 ± 0.01	0.14 ± 0.12	0.01 ± < 0.01
Violaxanthin	0.08 ± 0.05	ND	ND	0.04 ± 0.01	0.09 ± 0.09
Zeaxanthin	0.04 ± 0.02	0.04 ± 0.02	0.03 ± 0.01	0.03 ± 0.01	0.04 ± 0.01
Scytonemin	0.53 ± 0.41	0.36 ± 0.21	10.49 ± 7.61	0.24 ± 0.14	11.85 ± 9.96
Red scytonemin	0.04 ± 0.04	ND	0.08 ± 0.06	ND	0.61 ± 0.61

ND not detected. The number of studied lakes (n) and the vegetation type per region is indicated

the Lake Hazen area and WHL) plot in the positive quadrant (on the positive side of both axes).

Major pigments and taxonomic groups

HPLC analyses revealed diverse pigment assemblages indicating the presence of fucoxanthin-groups (diatoms, prymnesiophytes and chrysophytes), green algae (Chl *b*, lutein and violaxanthin), cryptophytes (alloxanthin) and cyanobacteria (zeaxanthin, canthaxanthin, echinenone, myxoxanthophyll, 4-keto-myxoxanthophyll and scytonemin) (Tables 1, 2). The suite of major pigments indicated a diverse phytoplankton community in all regions (Table 1). Green algae had high pigment signals in low arctic as well as high arctic (Ellesmere-1) sites; high diadinoxanthin (euglenophytes and some chromophytes) signals appeared in the subarctic region, while fucoxanthin-groups were prominent in the three arctic regions (Table 1). Cyanobacterial pigments were more prominent in benthic mats, followed by minor concentrations of pigments from chlorophytes and other photosynthetic eukaryotes (i.e. Chl *b*, lutein, fucoxanthin and diadinoxanthin; Table 2). High levels of the cyanobacterial UV-screening pigment scytonemin were measured in most mats, and its reduced product, red scytonemin, was also present in some samples.

At all sites, the total ecosystem stock of autotrophic biomass, expressed as integral Chl *a* per unit area, was overwhelmingly dominated by benthic algae (8.3–260.5 mg Chl *a* m^{-2}) in comparison with phytoplankton (0.008–1.4 mg Chl *a* m^{-2}; Table 3). The phytobenthos on average represented more than 98% (up to 99.9%) of the total autotrophic biomass. Although the planktonic and benthic Chl *a* concentrations were variable among regions (Table 3), there were no significant differences between polar desert waters and waters that had vegetated catchments (forest tundra, shrub tundra and oasis wetland) (phytoplankton, $t = 1.27$, $P > 0.05$ and mats, $t = 1.05$, $P > 0.05$).

Pigment indices

The calculated pigment indices implied divergent strategies between the phytoplankton and the phytobenthic mats at all sites (Figs. 3, 4; Table 3). In general, phytoplankton had significantly higher mean concentrations of total carotenoids/Chl *a* ($t = 3.48$, $P < 0.05$) than mats (Table 3). Consistent with this, the pigment indices PPC_{TP}, PSC_{TP} and Chl acc_{TP} were significantly higher in the phytoplankton than in the mats (PPC_{TP}, $U = 29.00$; PSC_{TP}, $U = 27.00$ and Chl acc_{TP}, $t = 6.67$, $P < 0.0001$; Fig. 4). These differences were also evident in pigment to total phototrophic biomass (Chl *a*) ratios: the phytoplankton ratios were significantly higher than in the mats (Table 3: PPC_{Chla}, $U = 36.0$; PSC_{Chla}, $U = 20.00$ and Chl acc_{Chla}, $U = 15.00$; $P < 0.0001$). High variability was found in the all

Table 3 Phytoplankton and phytobenthos Chl *a* concentrations, ratios to Chl *a* of accessory chlorophylls (Chlacc), photosynthetic carotenoids (PSC), photoprotective carotenoids (PPC) and total carotenoids (TCar) and ratio of all photoprotective to all photosynthetic pigments (PPP_{PHOT}) (average ± SE) for lakes in northern Quebec (NQuebec), Alaska, Cornwallis Island (CornI), Ellesmere Island Lake Hazen area (Elles-1) and northern Ellesmere Island and Ward Hunt Island (Elles-2)

Regions	Subarctic	Low Arctic	Arctic		
	NQuebec	Alaska	CornI	Elles-1	Elles-2
Phytoplankton					
Chl *a* (mg m^{-2})	0.22 ± 0.11	0.47 ± 0.27	0.10 ± 0.05	0.54 ± 0.26	0.22 ± 0.18
Pigment ratios to Chla (μg μg^{-1})					
$Chlacc_{Chla}$	0.37 ± 0.05	0.26 ± 0.04	0.40 ± 0.14	0.79 ± 0.20	0.25 ± 0.05
PSC_{Chla}	0.58 ± 0.20	0.33 ± 0.04	1.05 ± 0.21	1.54 ± 0.27	0.70 ± 0.38
PPC_{Chla}	0.95 ± 0.15	0.48 ± 0.11	2.30 ± 0.80	1.34 ± 0.31	1.43 ± 0.18
$TCar_{Chla}$	1.56 ± 0.25	0.91 ± 0.19	4.62 ± 1.39	2.90 ± 0.56	2.18 ± 0.62
PPP_{PHOT}	0.81 ± 0.07	0.50 ± 0.08	1.39 ± 0.29	0.84 ± 0.08	1.07 ± 0.11
Phytobenthos					
Chl *a* (mg m^{-2})	154 ± 46.5	105.0 ± 52.5	74.8 ± 21.3	89.9 ± 34.1	86.8 ± 17.2
Pigment ratios to Chl*a* (μg μg^{-1})					
$Chlacc_{Chla}$	0.11 ± 0.03	0.06 ± 0.03	0.05 ± 0.02	0.20 ± 0.10	0.04 ± < 0.01
PSC_{Chla}	0.34 ± 0.10	0.01 ± 0.01	0.02 ± 0.02	0.12 ± 0.08	0.02 ± 0.02
PPC_{Chla}	0.56 ± 0.03	0.27 ± 0.04	0.32 ± 0.10	0.40 ± 0.08	0.54 ± 0.22
$TCar_{Chla}$	1.09 ± 0.07	0.62 ± 0.18	0.92 ± 0.30	0.80 ± 0.13	1.06 ± 0.36
SCY_{Chla}	0.57 ± 0.45	0.36 ± 0.21	11.16 ± 7.89	0.32 ± 0.21	12.46 ± 10.57
PPP_{PHOT} (μg μg^{-1})	1.00 ± 0.27	0.61 ± 0.21	10.96 ± 7.68	0.67 ± 0.17	12.16 ± 10.02

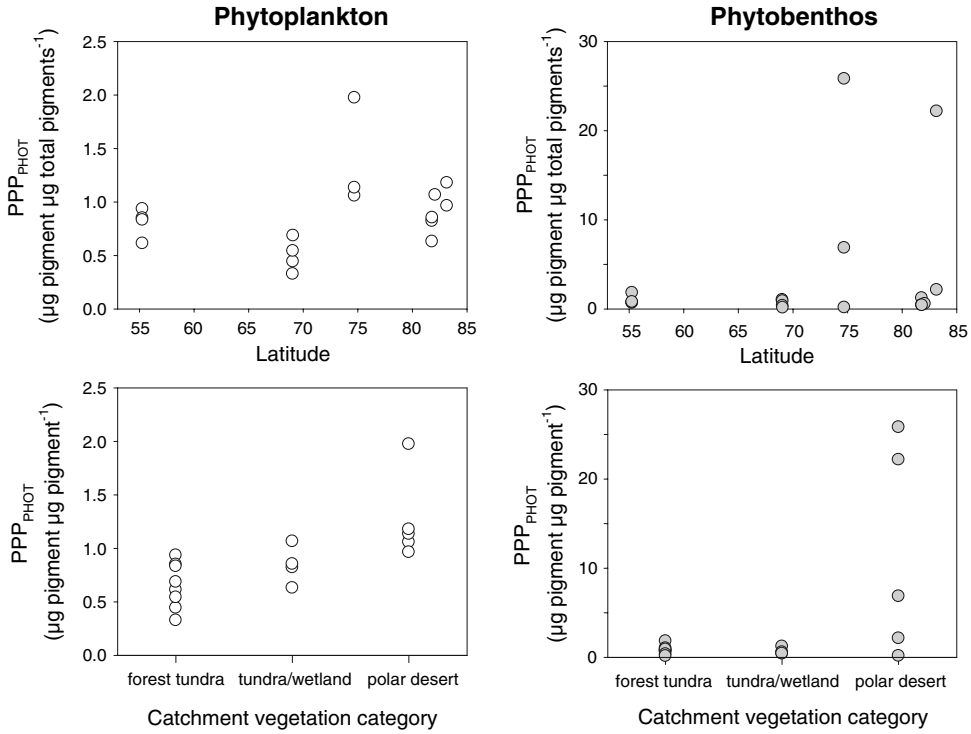

Fig. 3 The ratio of photoprotective to photosynthetic pigments (PPP_{PHOT}) for phytoplankton (*left*, *white circles*) and phytobenthos (*right*, *grey circles*) ordered according to latitude (*top*) and catchment vegetation type (*below*) for the 17 study sites

photoprotective to all photosynthetic pigment ratio (PPP_{PHOT}) for mats, and no significant differences ($P > 0.05$) were found for this index between plankton and benthic communities (avg ± SE of 0.88 ± 0.09 and 3.90 ± 1.88 for phytoplankton and mats, respectively; Table 3). No significant differences ($P > 0.05$) were found

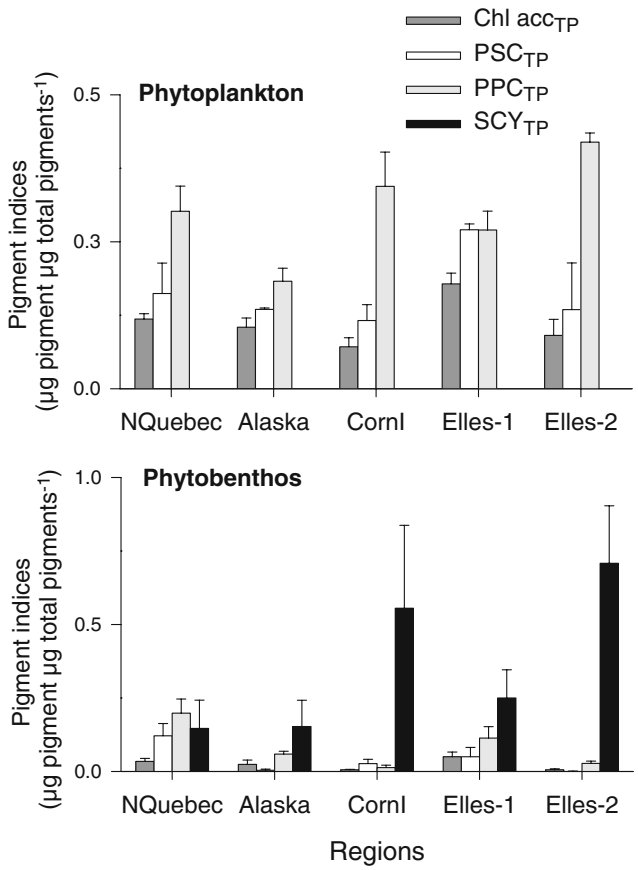

Fig. 4 Pigment indices for the phytoplankton (above) and phytobenthos (below) in each region. Accessory chlorophylls (Chl acc$_{TP}$, dark *grey bars*), photosynthetic carotenoids (PSC$_{TP}$, *white bars*), photoprotective carotenoids (PPC$_{TP}$, *grey bars*) and scytonemins (SCY$_{TP}$, *black bars*). Vertical lines indicate standard errors. The regional codes are given in Table S1

in mean Chl a_{TP} (0.30 ± 0.03 and 0.35 ± 0.04 for phytoplankton and mats, respectively, average ± SE for all sites).

The relative contribution of photosynthetic and photoprotective pigments in the phytoplankton and phytobenthos differed according to latitude and catchment vegetation (Figs. 3, 4). Phytoplankton photoprotective to photosynthetic pigment ratios, PPP$_{PHOT}$, were significantly higher in arctic waters (Cornwallis Island, Ellesmere-1 and 2) than in subarctic and low arctic waters (Northern Quebec and Alaska) ($t = 2.78$, $P < 0.05$) which was due to the significantly higher Chl*a* contribution to total pigment budget (Chla_{TP}) in subarctic and low-arctic waters and higher carotenoid contribution in the arctic waters (PPC$_{Chla}$ $t = 2.74$, $P < 0.05$ and PSC$_{Chla}$ $t = 3.22$, $P < 0.05$). Although mat photoprotection (PPP$_{PHOT}$ ratios) was higher in arctic waters (Fig. 3), the differences were not significant relative to lower latitude regions. The ratio of mat photoprotective pigments to total pigments (PPC$_{TP}$) was higher in subarctic and low-arctic freshwaters ($U = 97.00$, $P < 0.05$); however, there was no similar pattern in photoprotective carotenoids to biomass (PPC$_{Chla}$).

Some pigment indices also showed differences between vegetated (tundra forest, shrub tundra, oasis wetland) and non-vegetated (polar desert) regions. The accessory chlorophyll indices (Chl acc$_{TP}$) were significantly higher in vegetated regions relative to the polar desert sites in phytoplankton (avg ± SE, vegetated: 0.126 ± 0.010 and polar desert sites: 0.069 ± 0.013; $U = 6.00$, $P < 0.05$) and mats (avg ± SE, vegetated: 0.036 ± 0.008 and polar desert sites: 0.005 ± 0.002; $U = 3.00$, $P < 0.05$), respectively. Photoprotective pigments in phytoplankton (PPC$_{TP}$) were significantly higher in polar deserts relative to other regions (vegetated: 0.343 ± 0.118 and polar deserts: 0.261 ± 0.126, $t = -4.8$, $P < 0.001$; Fig. 3). The same pattern was found in the phytobenthos (PPC$_{TP}$ for vegetated sites: 3.73 ± 1.18 and polar desert sites: 2.03 ± 0.94, $t = 2.515$, $P < 0.05$). The scytonemin to total pigment ratio in mats was also higher in the polar desert sites relative to other regions (Scy$_{TP}$ for vegetated sites: 0.182 ± 0.053 and polar desert sites: 0.616 ± 0.170, $U = 10.5$, $P < 0.05$). Phytobenthos pigment indices calculated *per* Chl*a*, showed significant differences between regions for SCY$_{Chla}$ (vegetated: 0.42 ± 0.17 and polar desert sites: 11.46 ± 5.47, $U = 11.00$, $P = 0.0484$).

The pigment indices were statistically related to specific environmental variables. Phytoplankton photoprotective indices PPP$_{PHOT}$, PPC$_{TP}$ and PPC$_{Chla}$ were inversely related to temperature (PPP$_{PHOT}$, $r^2 = 0.44$, ANOVA $F_{1,16} = 10.97$, $P < 0.05$ and PPC$_{TP}$, $r^2 = 0.42$, ANOVA, $F_{1,16} = 10.08$, $P = 0.006$; PPC$_{Chla}$, $r^2 = 0.42$, ANOVA $F_{1,16} = 10.983$, $P < 0.05$; Fig. 5a, b, e). Phytoplankton PPC$_{TP}$ was also inversely related to CDOM (a_{320}) ($r^2 = 0.44$, ANOVA, $F_{1,12} = 7.184$, $P = 0.02$; Fig. 5c) and positively with UV penetration ($r^2 = 0.50$, ANOVA, $F_{1,12} = 11.05$, $P = 0.006$; Fig. 5d). This variable was derived from a_{320}, and consequently cross-correlated (Spearman correlation coefficient, r_s, a_{320} vs. UV% = −0.74, $P < 0.05$). Moreover, these two variables also cross-correlated with temperature (Spearman correlation coefficient, r_s, for temperature vs. $a_{320} = 0.64$ and temperature vs. UV penetration = −0.69, $P < 0.05$). The inclusion of other abiotic variables (nutrients) in multiple linear regressions did not improve the prediction obtained with simple regressions. Phytobenthos SCY$_{TP}$ was inversely related to temperature ($r^2 = 0.25$, ANOVA, $F_{1,16} = 5.03$, $P = 0.04$; Fig. 5f). No significant linear relationships were found between the other mat indices and environmental factors.

To explore the contribution of sets of variables to explain the variation of pigment indices, a partial RDA was performed. This analysis showed that temperature plus CDOM explained 54% of variability in the PPP$_{PHOT}$

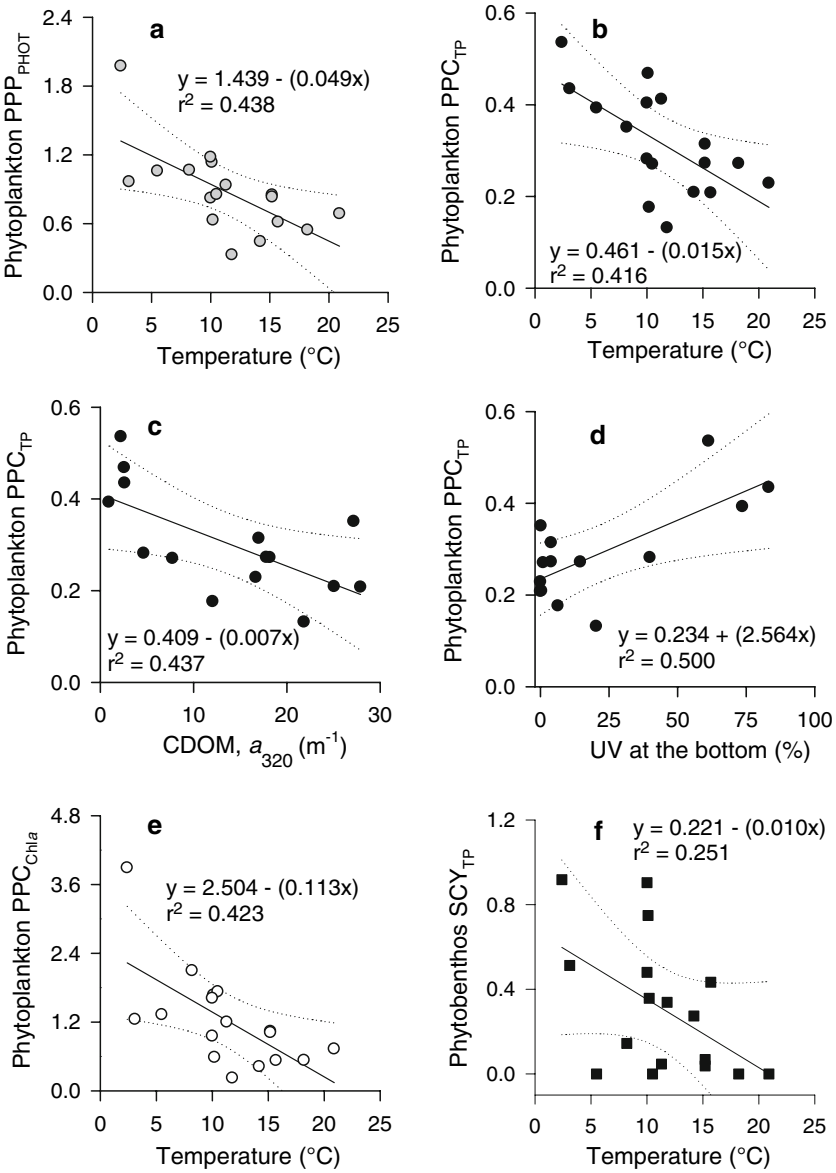

Fig. 5 Relationship between the phytoplankton photoprotection indices PPP_{PHOT} (*grey circles*), PPC_{TP} (*black circles*) and PPC_{Chla} (*white circles*) and the mat SCY_{Chla} index (*black squares*) and individual environmental variables: phytoplankton **a** PPP_{PHOT} versus temperature; **b** PPC_{TP} versus temperature, **c** PPC_{TP} versus CDOM absorption at 320 nm, **d** PPC_{TP} versus UV penetration (in percentage), **e** PPC_{Chla} versus temperature and **f** phytobenthos SCY_{TP} versus temperature. *Solid lines*: least-squares regression curve; *dotted lines* confidence intervals (99%); regression coefficients, r^2 and significance (P) are also given

phytoplankton index, with a significant interaction effect (Table 4). Temperature and CDOM also emerged as the explanatory variables for phytoplankton PPC_{TP} (Table 4). The partial RDA also showed that latitude and area explained 45% of the variance of the phytobenthos PPC_{TP} index, with an interaction effect (Table 4). The variability in scytonemin per unit biomass in the phytobenthos (SCY_{Chla}) was related to temperature and area (64% of total variation; Table 4).

Discussion

The set of lakes in the present study encompassed a variety of limnological conditions and showed differences in their abiotic environment among regions. In general, the greatest differences between low and high latitude waters were in temperature and CDOM, and the correlation between these two variables is consistent with more catchment vegetation and thus greater inputs of allochthonous, UV-absorbing CDOM at the warmer sites. Higher concentrations of CDOM can also result in greater absorption of photosynthetically available radiation (PAR) and faster warming (Caplanne and Laurion 2008).

Benthic mats dominated the total phototrophic biomass at all sites in our study. This is consistent with shallow freshwaters in many other parts of the polar regions (Vincent 2000). Cyanobacterial dominance was evident in the pigment signatures of benthic mats as commonly found in high latitude phytobenthos (Bonilla et al. 2005; Mueller et al. 2005; Toro et al. 2007). Although low in biomass concentrations, the phytoplankton pigment analyses

Table 4 Significant results of the partial redundancy analysis (RDA) of the effect of environmental variables, and their interactions, on phytoplankton and phytobenthos pigment indices (total and Chl *a* based)

Explained variables	Explanatory variables	Covariables	Explained variation (%)	*F*	*P*
Phytoplankton					
PPP_{PHOT}	T, a_{320}		53.7	8.11	0.006
	T	a_{320}	16.7	5.05	0.048
PPC_{TP}	T, a_{320}		42.1	5.09	0.030
Phytobenthos					
PPC_{TP}	Lat, Area		44.7	5.67	0.014
	Lat	Area	39.8	10.10	0.006
SCY_{TP}	Lat		49.6	4.93	0.038
SCY_{Chla}	Area, T		63.7	7.89	0.030
	Area	T	36.3	8.99	0.012
	T	Area	20.3	5.03	0.032

T temperature, *Lat* latitude

revealed a flora with representation from diverse algal classes, notably cryptophytes, diatoms, chlorophytes and cyanobacteria, as found in high latitude freshwaters elsewhere (Vézina and Vincent 1997; Izaguirre et al. 1998; Vincent 2000; Bonilla et al. 2005; Toro et al. 2007).

Polar algae must contend with a wide range of temperature and irradiance conditions over the year, including high PAR and nearly continuous UV exposure during summer. The algal communities must also cope with water stress due to freeze-up, with impacts on internal osmotic pressure and cellular processes (Sabbe et al. 2004, Vincent 2007). The different adaptive strategies of phytoplankton and mats were reflected in their pigment indices. Our results showed that photoprotection in both planktonic and benthic communities was most developed in arctic waters in general and particularly in the clear, low-CDOM waters of the polar deserts. These lakes had low concentrations of UV-screening CDOM, with DOC concentrations below the threshold value of 5 mg l^{-1} (Vincent and Pienitz 1996), implying strong exposure to UV-B as well as UV-A radiation.

The planktonic communities were rich in ROS-quenching carotenoids that were significantly correlated with decreased temperatures and the increased UVR exposure. The increment in carotenoid concentration under total irradiance stress is a cellular photoprotective response against reactive oxygen species (Goodwin 1980; Porra et al. 1997). However, the accumulation of carotenoids can be also be induced by low-temperature stress, as for example observed in *Dunaliella* cultures (Król et al. 1997). It has been demonstrated that carotenoid/Chl *a* ratios in Antarctic cyanobacteria strains are enhanced by the combination of UV and temperature, implying a photoprotective response to high excitation pressure in cold waters (Roos and Vincent 1998). Consequently, in shallow polar lakes, low-temperature and high-irradiance exposure are likely to induce photoprotective strategies, consistent with the phytoplankton PPC_{TP} trends found in the present study.

A different pigment strategy was observed in slow-growing benthic mats, where scytonemin and red scytonemin accumulated in high concentrations. UV-absorbing scytonemins are stable compounds, synthesized under UVR stress (Cockell and Knowland 1999), and their concentration can be the result of slow accumulation over time, as suggested for ice shelf cyanobacterial mats (Mueller et al. 2005). We found significantly higher indices of benthic scytonemin to total pigments in the more UVR exposed (polar desert) waters than at the lower latitude sites where carotenoid-photoprotection was higher. However, only marginally significant differences were found when scytonemin concentrations were standardized to Chl*a* (SCY_{Chla}) suggesting a high variability in the scytonemin content in relation to the bulk biomass. Moreover, no significant differences were found for photoprotective carotenoids when standardized to Chl *a*, suggesting that scytonemin dominated the total pigment signal. Thus the main changes in mat pigment strategies were related to the increase and accumulation of scytonemin, independently of total biomass (as measured by Chl *a*).

There was no simple relationship between benthic pigment indices and the measured abiotic variables, except for temperature, suggesting that an ensemble of climate-related factors is responsible for the observed pattern. For scytomenin, a combination of local (area) and regional (temperature and latitude) factors appeared to influence its accumulation in the phytobenthos. Desiccated metabolically inactive cells are more protected from UVR and recover faster if they have higher concentrations of scytonemin in their sheaths (Fleming and Castenholz 2007). Consequently, accumulated scytonemin in benthic mats may also play a role in withstanding desiccation, a common stress factor in shallow polar desert freshwaters (Smol and Douglas 2007b). Polar desert lakes have low precipitation to evaporation (P/E) ratios and their water levels can fluctuate rapidly, resulting in intermittent desiccation

stress. Similar osmotic stresses may also be imposed during the complete freeze-up of these shallow waters, and cells may similarly benefit from the protective effects of scytonemin during these periods.

A factor that can affect the bulk pigment stocks and pigment strategies of algae is their nutritional status (Rücker et al. 1995; Porra et al. 1997; Fleming and Castenholz 2008). Benthic and planktonic algal communities occupy different habitats in this respect, with the planktonic environment typically poor in nutrients, while the phytobenthos experience an environment that may be replete in nitrogen, phosphorus and dissolved inorganic carbon (Vincent 2000), up to three orders of magnitude higher than the water column (Villeneuve et al. 2001; Rautio and Vincent 2006). In a previous study carried out in one of the polar desert lakes sampled in the present study (Ward Hunt Lake), low-nutrient concentrations were a major constraint for phytoplankton, which incremented its biomass 19-fold after 2 weeks of experimental enrichment (Bonilla et al. 2005). The same study found that benthic mats did not respond to nutrient enrichment, at least over timescales of days to weeks.

Arctic freshwater ecosystems must increasingly contend with climate change. Predictions of future conditions include increased air temperatures, with changes in snow and ice cover dynamics, and increased PAR and UV exposure as a result of earlier ice melting and longer open water conditions. Earlier ice melting has dramatic effects on the irradiance regime, with order of magnitude increases in UV exposure as a consequence of ice cover removal (Vincent et al. 2007). Our results show that phytoplankton photoprotection via pigments is greater under conditions of higher UVR exposure. Over longer timescales of vegetation change and permafrost degradation, an increase in the amount of CDOM is predicted, which can have opposing consequences for phototrophs: UV-filtration and PAR-shading (Wrona et al. 2006; Vincent et al. 2007). These factors can affect the production and the species composition of the communities. Based on fossil pigment reconstructions, Leavitt et al. (2003) found an algal biomass decline of 10 to 25-fold corresponding to periods of natural increase in UVR, implying sensitivity to climate-mediated changes in UV exposure. In contrast, slow-growing cyanobacterial mats in the Arctic could be less affected in terms of total biomass, due to their capacity to synthesize and accumulate scytonemin to tolerate bright PAR, high UVR exposure and desiccation. Similar survival strategies also operate in antarctic cyanobacterial mats (Hodgson et al. 2004).

Increases in temperature as a consequence of climate change are another factor that can affect algal biomass production of high latitude lakes, as has been inferred by fossil pigment reconstructions (Antoniades et al. 2007). These authors found abrupt increases in bulk pigment concentrations and striking changes in pigment structure in the upper strata of the sediments that indicated recent, large-scale shifts in community biomass and composition in response to changes in ice cover. Moreover, warming can also affect the trophic structure of cold fishless lakes, favouring the dominance of small phytoflagellates and small predators, as experimentally demonstrated by Strecker et al. (2004). Projected temperature increases for the Arctic will result in a longer open-water period, water heating and consequently higher evaporation losses (Prowse et al. 2006), with associated changes in water level and volume (Vincent et al. 2007). These changes may expose the perennial benthic mats to desiccation, and a combination of UVR and water stresses. The scytonemin-based strategy in the phytobenthos will likely confer some resilience to these climate-mediated environmental changes. In contrast, the phytoplankton community may be more vulnerable to future changes; however, increases in their photoprotective carotenoids, as observed here in the most transparent waters, will mitigate these effects.

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