Change in biomass of benthic and planktonic algae along a disturbance gradient for 24 Great Lakes coastal wetlands

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Abstract: We quantified the chlorophyll *a* content of planktonic algae and benthic algae in periphyton on acrylic rods and in epiphyton growing on macrophytes in 24 coastal wetlands in all five Laurentian Great Lakes. Sites were selected to represent a wide range of environmental conditions ranging from nutrient-poor, clear-water marshes with abundant macrophytes to nutrient-enriched, turbid systems devoid of aquatic vegetation. Water quality and species and percent cover of submergent macrophytes were measured in each wetland. Principal components analysis (PCA) showed that total phosphorus, turbidity, and suspended solids, variables associated with human-induced degradation, were most strongly correlated with PC axis 1 (PC1), accounting for 69% of the total variation. The PC1 site score was significantly related to both periphyton and phytoplankton biomass, respectively accounting for 54 and 70% of the total variation in periphyton and phytoplankton data, whereas PC1 only accounted for 18% of the variation in epiphyton biomass. Periphytic and epiphytic biomass were negatively correlated with percent cover and species richness of submergent macrophytes, but phytoplankton biomass was not. We conclude that periphytic and planktonic chlorophyll *a* biomass are good indicators of human-induced water-quality degradation and recommend that both benthic and planktonic algal biomass should be routinely monitored as part of an effective wetland management program.

Résumé : Nous avons mesuré la concentration de chlorophylle *a* des algues planctoniques et benthiques, du périphyton poussant sur des tiges en acrylique et de l'épiphyton croissant sur des macrophytes dans 24 terres humides côtières des cinq Grands Lacs laurentiens. Les sites ont été choisis de façon à représenter une gamme étendue de conditions environnementales, allant de marécages à eau claire avec abondance de macrophytes jusqu'à des systèmes enrichis de nutriments, à eau turbide et sans végétation aquatique. Nous avons déterminé la qualité de l'eau, de même que la composition spécifique et le pourcentage de couverture des macrophytes submergés à chacun des sites. Une analyse en composantes principales (« PCA ») révèle que le phosphore total, la turbidité et les solides en suspension, des variables associées à la dégradation anthropique, sont en forte corrélation surtout avec l'axe PC1 et qu'ils expliquent 69 % de la variation totale. Les positions des sites sur PC1 sont significativement associées à la fois aux biomasses de périphyton et de phytoplancton et elles expliquent respectivement 54 et 70 % de la variation totale des données de périphyton et de phytoplancton; par ailleurs, PC1 n'explique que 18 % de la variation des biomasses de l'épiphyton. Les biomasses du périphyton et de l'épiphyton, mais non celle du phytoplancton, sont en corrélation négative avec le pourcentage de couverture et la richesse en espèces des macrophytes submergés. Nous concluons que les biomasses de la chlorophylle *a* dans le périphyton et le plancton sont de bons indicateurs de la dégradation anthropique de la qualité de l'eau et nous recommandons un suivi régulier de la biomasse des algues benthiques et planctoniques comme élément d'une gestion efficace des terres humides.

[Traduit par la Rédaction]

Introduction

Development of bioindicators to assess the quality of wetland communities has received a great deal of attention in the ecological literature over the past decade (see review by Adamus et al. (2001)). This heightened interest reflects the exceptional value of wetlands as habitat for recreationally important waterfowl, wildlife, and fish and also the great challenge to wetland managers to find appropriate tools to assess and monitor both the quality and quantity of such valuable habitat. A variety of multimetric indicators exist, incorporating the response of particular groups of organisms to environmental conditions (e.g., index of biotic integrity for fish and benthic invertebrates (IBI; Simon 1998; Helgen 2001) and wetland zooplankton index (WZI; Lougheed and Chow-Fraser 2002)).

The literature shows a historic bias towards heterotrophic versus autotrophic bioindicators, and of the autotrophs, vascular plants (emergent, submergent, and floating aquatic macrophytes) have been more often used to assess wetland quality (Adamus et al. 2001) than other primary producers. Only recently has there been interest in using algae as wetland bioindicators (McCormick and Stevenson 1998; Stevenson et al. 2001), even though they are commonly used as bioindicators

Received 9 August 2002. Accepted 29 March 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 17 July 2003.
J17039

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 doi: 10.1139/F03-054

of environmental quality in streams and rivers (Lowe and Pan 1996). This development is appropriate given that total algal production in wetlands varies widely and may be equal to or greater than that of vascular plant production under some conditions (Goldsborough and Robinson 1996; Wetzel 1996). Their high productivity, small size, and rapid turnover make algae an important food source at the bottom of many complex wetland food webs (Keough et al. 1996; Lamberti 1996).

Algae may be benthic (including periphyton that grow attached to any submerged surfaces and epiphyton that grow attached to aquatic plants) or planktonic (phytoplankton that are suspended in the water column) (Goldsborough and Robinson 1996). Unlike vascular plants, which obtain most of their nutrients from the sediment, algae respond directly to changes in nutrients in the water column, utilizing them directly (phytoplankton) or by scavenging nutrients in the benthic algal biofilm (Wetzel 1996). This makes them ideal organisms for monitoring nutrient enrichment resulting from altered land uses. Limnologists have capitalized on this and have developed useful indicators of lake trophic status by developing indices that measure planktonic chlorophyll *a* content in both algae-dominated (Dillon and Rigler 1974; Carlson 1977) and macrophyte-dominated systems (Canfield et al. 1983). In lotic environments, however, periphytic algae, often the dominant primary producers (Lamberti 1996), are the organism of choice because they are relatively immobile and respond quickly to environmental stress (Lowe and Pan 1996; U.S. Environmental Protection Agency (EPA) 2000). Similarly, a periphyton index of biotic integrity and a biological index of phosphorus availability have been proposed for the Florida Everglades because wetlands are hydrologically very dynamic and are subject to sudden influxes of sediment and nutrients (McCormick and Stevenson 1998).

To date, few algal studies have been carried out in coastal wetlands of the Laurentian Great Lakes. These ecosystems are important to study because of the tremendous biodiversity values associated with them (Chow-Fraser and Albert 1999) and because significant wetland destruction has already occurred along most of the Great Lakes shoreline, especially those associated with the lower lakes (Whillans 1982). Many of the remaining wetlands are degraded, having lost a substantial portion of their submergent plant community (Klarer and Millie 1992; Chow-Fraser et al. 1998; Lougheed et al. 2001). In such wetlands, planktonic algae make up a relatively large proportion of the net primary production (Goldsborough and Robinson 1996; Chow-Fraser 1999). By comparison, in undisturbed wetlands in which the submergent vascular plant community is diverse and robust, the planktonic algal component is relatively small and epiphytic algae are dominant (Goldsborough and Robinson 1996).

From Chow-Fraser's (1998) conceptual models of "healthy" and "degraded" wetland ecosystems, we offer the following generalizations. In healthy systems, there is abundant aquatic vegetation, which reduces turbidity by trapping sediment and provides substrata for epiphyton and habitat for benthic invertebrates. Nutrients entering the watershed are taken up by plants and algae, but planktonic and benthic algal biomass are kept low by zooplankton and benthic grazers. Grazer populations in these systems support a diverse fish community of planktivores and benthivores that are controlled by piscivorous fish. In contrast, degraded systems have little aquatic vegetation and are turbid and nutrient-rich, producing high planktonic and benthic algal biomass that further reduces light for germination of aquatic plants. Without aquatic vegetation, the habitat is suitable only for benthivores and planktivores, and as a result, grazers are kept in low numbers, and phytoplankton and periphyton proliferate. Epiphyton biomass is low because there are few vascular plants to serve as substrate. Based on these two models, we predict that benthic algal biomass (measured as chlorophyll *a* content in periphyton on artificial substrata and epiphyton on submergent vascular plants) and planktonic algal biomass (measured as chlorophyll *a*) will increase as wetlands become degraded (as measured by deterioration in water quality). Secondly, we predict that biomass of both epiphyton and periphyton will be inversely related to areal cover of submersed aquatic vegetation because Lougheed et al. (2001) found that submergent plant species richness and density were low in oligotrophic wetlands, increased as nutrients increased, but declined when light became limiting as the result of increased sediment loading.

To test these predictions, we sampled 24 wetlands spanning a range of environmental conditions from extremely clear, nutrient-poor systems with abundant submersed aquatic vegetation to turbid, nutrient-enriched systems devoid of submergent plants, and we compare how the chlorophyll *a* biomass of periphyton (CHL_{peri}), epiphyton (CHL_{epi}), and phytoplankton (CHL_{phyto}) change across this disturbance gradient. By selecting wetlands that occur in all five Great Lakes, we hope that results from this study will be widely applicable and become an important contribution to the development of basin-wide bioassessment tools for Great Lakes coastal wetlands.

Methods and materials

Study sites

Twenty-four coastal wetland complexes throughout the Great Lakes were sampled (Fig. 1). Sites were deliberately chosen to represent a gradient from degraded to pristine based on water-quality information collected in previous years (Lougheed et al. 2001; P. Chow-Fraser, unpublished data). Wetlands from all five Great Lakes are represented, 13 in Canada and 11 in the U.S. There are 11 sites from the upper lakes (Superior, 4; Michigan, 3; Huron, 4) and 13 from the lower lakes (Ontario, 8; Erie, 5) representing a variety of hydrogeomorphic wetland types (Table 1; Chow-Fraser and Albert 1999). Differences in environmental conditions and site types were purposely included so that any significant trends that emerge from this study could be widely applicable throughout the Great Lakes shoreline, without qualification to site type.

Field methods

All field sampling was completed between 24 May and 16 August in 2000 and 2001 between 1000 and 1600 hours. The time period for sampling each wetland is shown in Table 1.

Benthic algae: periphyton

We followed the methods outlined in Goldsborough et al. (1986) to sample periphyton with artificial substrata (clear

Fig. 1. Map of the Laurentian Great Lakes of North America showing the location of the 24 wetlands sampled for this study in 2000 and 2001. Two-letter codes identify each wetland location and are listed in Table 1. Two wetlands are located at Long Point in Lake Erie (LP), Long Point Inner Bay (LPIB), and Long Point Big Rice Bay (LPBR), but only LP is shown on the map.

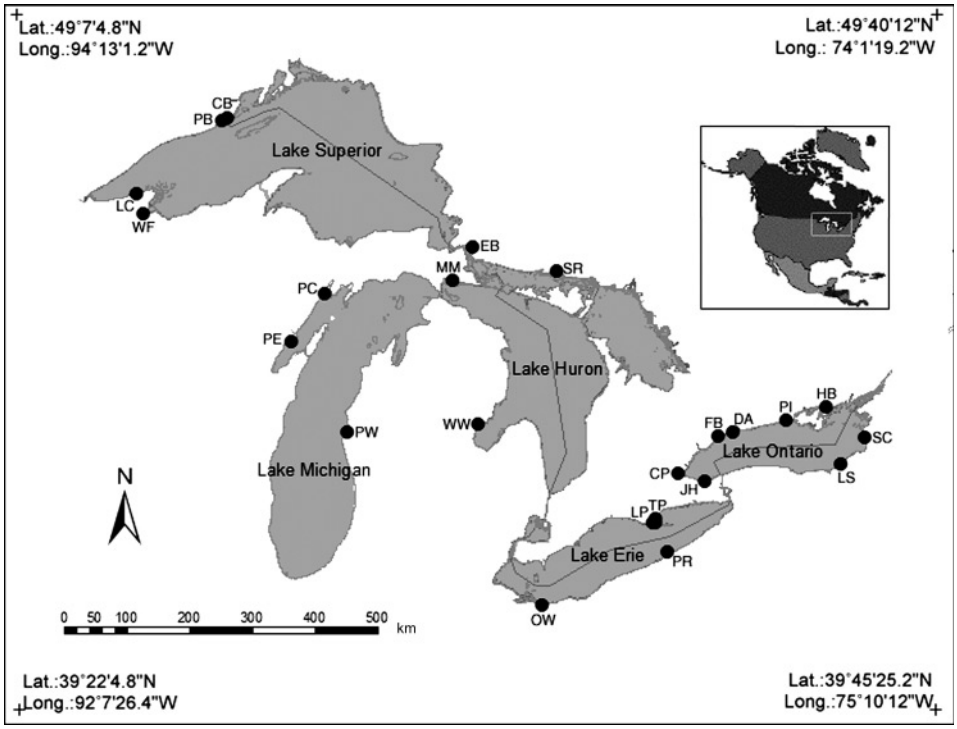


Table 1. Summary of 24 wetlands and sampling period included in this study.

				Sampling period	
Lake	Wetland, state or province	Wetland code	Wetland type	Start	Finish
Superior	Cloud Bay, Ont.	CB	Lacustrine	07/17/01	08/13/01
Superior	Pine Bay, Ont.	PB	Lacustrine	07/19/01	08/14/01
Superior	Lost Creek, Wis.	LC	Estuarine	07/17/01	08/16/01
Superior	West Fish Creek, Wis.	WF	Estuarine	07/17/01	08/16/01
Michigan	Portage Creek, Wis.	PC	Lacustrine	06/15/01	07/10/01
Michigan	Peshtigo Marsh, Wis.	PE	Estuarine	06/14/01	07/10/01
Michigan	Pentwater, Mich.	PW	Estuarine	06/16/01	07/11/01
Huron	Echo Bay, Ont.	EB	Riverine	07/16/00	08/15/00
Huron	Spanish River, Ont.	SR	Riverine	07/15/00	08/15/00
Huron	Mismer Marsh, Mich.	MM	Lacustrine	07/16/00	08/16/00
Huron	Wigwam Bay (Pine River), Mich.	WW	Lacustrine	06/17/01	07/12/01
Ontario	Hay Bay, Ont.	HB	Lacustrine	06/19/00	07/13/00
Ontario	Presqu'Ile, Ont.	PI	Lacustrine	05/29/01	06/27/01
Ontario	Darlington, Ont.	DA	Lacustrine	05/30/01	06/28/01
Ontario	Frenchman's Bay, Ont.	FB	Lacustrine	05/30/01	06/28/01
Ontario	Sandy Creek, N.Y.	SC	Estuarine	06/21/01	07/18/01
Ontario	Little Sodus, N.Y.	LS	Estuarine	06/19/01	07/18/01
Ontario	Cootes Paradise, Ont.	CP	Estuarine	06/27/00	07/24/00
Ontario	Jordan Harbour, Ont.	JH	Estuarine	06/30/00	07/31/00
Erie	Turkey Point, Ont.	TP	Lacustrine	06/07/01	07/05/01
Erie	Long Pt., Big Rice Bay, Ont.	LPBR	Lacustrine	06/06/01	07/04/01
Erie	Long Pt., Inner Bay, Ont.	LPIB	Lacustrine	06/06/01	07/05/01
Erie	Presque Isle, Pa.	PR	Lacustrine	05/23/01	06/20/01
Erie	Old Woman Creek, Ohio	OW	Estuarine	05/24/01	06/21/01

Note: Wetland types are according to Chow-Fraser and Albert (1999). Sampling period dates provided in month/day/year format.

acrylic rods, 0.6 cm diameter, 90 cm long). Each rod was prescored at 5-cm intervals (to allow subsamples from various depths to be easily taken) and then cleaned with alcohol to remove oils deposited through handling. At each wetland, rods were inserted vertically into the sediment in either four blocks of five rods each or five blocks of four rods each (rods approximately 1 m apart, arranged in a line). Blocks were distributed throughout the wetland area within submergent macrophyte beds if submergent plants were present. Rods were placed in areas of water depth from 40 to 70 cm and at least 3 m from emergent vegetation to prevent shading effects. Samples were collected after ~4 weeks of colonization time. Earlier experiments showed that periphyton chlorophyll *a* biomass reached a peak between 3 and 5 weeks at the test sites and then began to senesce (S. McNair, unpublished data). One 5-cm sample was collected from each rod at a depth of 10–15 cm using cutting pliers. Each sample was wrapped in foil, stored on ice in the field, and then frozen until analyzed for chlorophyll *a* content back in the lab.

Benthic algae: epiphyton

Epiphyton on submergent macrophytes were sampled at the end of the periphyton field incubation period, described above at all sites, and 17 of the 24 sites were also sampled at the beginning of the incubation period. One sample of leaf and (or) stem tissue was collected at each periphyton block from a depth of 10–20 cm and stored in the dark at 5°C before returning to the lab for analysis. If no submergent plants were present, stems of floating or emergent species were collected for epiphyton analysis.

Planktonic algae: phytoplankton

Phytoplankton samples were collected at each wetland complex at the end of the periphyton incubation period using a 1-L Van Dorn bottle in an area devoid of submergent plants. Water samples collected at mid-depth were stored in brown polyethylene bottles and kept at 5°C before processing.

Submergent vascular plants

The submergent macrophyte community was surveyed within each periphyton block using a 0.75 m × 0.75 m floating PVC (polyvinyl chloride) quadrat. Percentage cover of submergents within the quadrat was estimated one time by direct observation at the surface and by raking the bottom if the vegetation was dense or if water turbidity was high. All plant species present in the quadrat and within the periphyton blocks (approximately 1 m × 5 m) were noted. Plants were identified to species where possible and always to genus using Voss (1972) and Newmaster et al. (1997). Species that could not be identified in the field were collected and dried in a plant press for later identification. Several *Potamogeton* species with slender leaves that were not identified to species because of absence of flowering or fruiting structures were grouped into *Potamogeton* spp.

Physico-chemical conditions in wetland

Water samples for nutrient and suspended solids analysis were collected at the end of the incubation period using a 1-L Van Dorn bottle at mid-depth in a vegetation-free area. Samples were stored in acid-washed Nalgene® bottles and kept in the dark at 5°C before returning to the lab for analysis. Physical measurements of ambient water were made at the beginning and end of the field incubation period at each wetland complex. Measurements made at the same time as the water collection for nutrient analysis were used in statistical analyses. Turbidity was measured with a Hach 2100P turbidimeter (Hydrolab-Hach, Loveland, Colo.). Temperature, pH, dissolved oxygen (DO), conductivity, and total dissolved solids (TDS) were measured with Hydrolab multiparameter probes (Hydrolab-Hach; H20 sonde or Mini sonde 4a with a Surveyor; or Quanta). Light measurements were made with a LI-COR photometer (Lincor, Lincoln, Nebr.) equipped with spherical submersible sensor at 19 sites in a vegetation-free area. Rain prevented accurate measurement at the other five wetlands. Sediment samples were collected using an Ekman grab sampler for determination of organic material, total phosphorus, and exchangeable ammonia content.

Laboratory methods

CHL_{peri}, CHL_{epi}, and CHL_{phyto} were determined by pigment extraction in 90% acetone and spectrophotometry (American Public Health Association 1992). Periphyton rod sections were placed in 90% acetone in the freezer for 24–96 h. Samples were centrifuged, and chlorophyll *a* content was determined by measuring absorbance with a Milton Roy 301 spectrophotometer (Fisher Scientific, Toronto, Ont.) before and after acidification (to account for phaeophytin pigments). Epiphyton was removed from vascular plant samples by shaking in 250 mL of distilled water in a 500-mL Nalgene® bottle for 5 min at a rate of 80 beats/min (method after V. Gosselain, GRIL, Departement de Sciences Biologiques, Université de Montréal, C.P. 6128, succursale Centre Ville, Montreal, QC H3C 3J7, Canada, personal communication). The resulting suspensions were filtered through 0.45-µm GF/C filters, wrapped in aluminum foil, and kept frozen for chlorophyll *a* analysis. Surface areas of the plant samples were estimated using a ruler, and biomass was calculated as chlorophyll *a* per unit area (cm^2). Phytoplankton samples (3/wetland) were filtered through 0.45-µm GF/C filters and then stored frozen in aluminum foil until analysis. Chlorophyll *a* from natural (plant) substrata and phytoplankton from the water column were extracted from frozen filters and analyzed as above. Chlorophyll *a* content for both CHL_{epi} and CHL_{peri} were expressed as $\mu g \cdot cm$ substrate $sampled^{-2}$, whereas values for CHL_{phyto} were expressed as $\mu g \cdot L$ water $sampled^{-1}$. Because the time period for colonization of periphyton was known, CHL_{peri} is expressed as a rate, standardized to 28 days ($\mu g \cdot cm^{-2} \cdot 28\ days^{-1}$).

Water samples for all nutrients were analyzed for soluble reactive phosphorus (SRP) and total phosphorus (TP) following standard methods (APHA 1992). Following digestion by potassium persulfate, TP was analyzed according to Murphy and Riley (1962) and measured on a Milton Roy 301 spectrophotometer. Total Kjeldahl nitrogen (TKN), total nitrate nitrogen (TNN), and total ammonia nitrogen (TAN) were measured with Hach protocols and reagents (Hach Company 1989) using a Hach DR2000 spectrophotometer (Hach, Loveland, Colo.). Total nitrogen (TN) was calculated by addition of TKN and TNN. Samples that had been preserved for Winkler titration in the field were processed within 4–6 h of collection, with a Hach digital titrator to

confirm dissolved oxygen (DO) values measured in situ. Water samples for total suspended solids (TSS) determination were filtered through preweighed GF/C filters and frozen until processing. Filters were first dried at 100°C for 1 h, dried in a dessicator with calcium sulphate for another hour, and then weighed to determine TSS. Loss on ignition was determined after combustion at 550°C for 20 min followed by drying in the dessicator for an hour. Weight of the combusted filter was assumed to be total inorganic suspended solids (TISS), whereas difference in the weight of the filter before and after combustion was total organic suspended solids (TOSS).

Sediment samples for analysis of sediment total phosphorus (Sed TP), inorganic content (Sed Inorg) and exchangeable ammonia (Sed NH_4) were frozen within 12 h of collection. To determine the percentage of inorganic material in the sediment, the sample was dried at 40°C and then placed in a desiccator and weighed to determine the starting amount. This sample was then combusted at 550°C for 1 h and weighed again, and loss on ignition was calculated as Sed Inorg. Sediment phosphorus was determined using the ignition method described by Andersen (1976) and is expressed as milligrams per gram of combusted sediment. For determination of Sed NH_4, the sediment was first dried overnight at 40°C. The ammonium was then extracted from approximately 1.5 g of sediment using 25 mL of 2 M potassium chloride. This mixture was shaken vigorously for 30 s and allowed to sit overnight. On the next day, the samples were again shaken for 30 s and filtered through GF/C filters. The ammonium content of the sample was determined by addition of Nessler reagent and subsequent colorimetric analysis using the Hach DR2000 spectrophotometer. Two replicates were carried out for most sites; however, those with very high Sed NH_4 values needed to be diluted and time only permitted one replicate in these cases.

Statistical methods

Statistical analyses were performed using SAS JMP software version 3.5 for the Macintosh (SAS Institute Inc., Cary, N.C.). Data were standardized (to mean of zero and standard deviation of 1) before a principal components analysis (PCA; Digby and Kempton 1987). All environmental and algal data were $\log_{10}$-transformed to normalize the data before conducting regression and correlation analyses. Percent cover of submergent vegetation data were arcsin-transformed before analysis.

Results

Environmental gradient

Degraded wetlands had high nutrient concentrations, poor water clarity (high suspended solids, turbidity, light extinction coefficient), and high conductivity. At the other end of the gradient, pristine wetlands exhibited low nutrient levels and good water clarity. Because the wetlands were not randomly selected, the range of values are not representative of general wetland quality for the lakes in question; on the contrary, we made a deliberate effort to include a selection of high-quality and poor-quality wetlands in each Great Lake. Nevertheless, there was an obvious bias towards more degraded wetlands in the lower lakes compared with those in the upper lakes, and this tendency was also reflected in nutrient data for respective water column and sediment samples. Latitude, longitude, and variables associated with water clarity (turbidity, light extinction, TSS, TISS, TOSS) and those related to anthropogenic disturbance (conductivity, TDS; Lougheed et al. 2001) are presented, along with the nutrient data, on a lake-by-lake basis in Appendix A. It is noteworthy that wetlands with the lowest nutrient levels and clearest water were located in the Lake Superior basin, in areas characterized by relatively minimum human influence (Cloud Bay), whereas those with the highest nutrient levels and most turbid water were located in one of the most heavily impacted areas of Lake Erie, the western basin (Old Woman Creek; Lougheed et al. 2001).

A PCA was used to produce the three synthetic axes that best capture overall variation in the data set and to identify the environmental variables that contribute most to these axes. Of 21 measured environmental variables, 10 were found to be most significant in explaining the variation in the data and were included in this analysis (Table 2). The only direct measure of light availability, the light extinction coefficient, was not included in the PCA because of missing data for five wetlands. However, light extinction was strongly related to turbidity ($r^2 = 0.93$, $p < 0.0001$) in the 19 wetlands in which both were measured. Initial analysis included all 24 wetlands in the PCA, but Jordan Harbour appeared to be an outlier because of extremely high inorganic suspended solids in the water (134.4 $mg \cdot L^{-1}$ compared with 67.23 $mg \cdot L^{-1}$ at Old Woman Creek, the next highest measurement). This site is located in the highly agricultural Niagara Peninsula, and it was sampled immediately after an extremely heavy rainstorm when sediment loading from the watershed was high. We removed this site from the PCA because it did not reflect the same type of disturbance regime as the other wetlands and then reanalyzed the data including 23 wetlands. The first three principal components accounted for almost all variation in the data set (91%). PC1 accounted for 69% of the variation in the data and was highly correlated with TP and water clarity variables (turbidity, suspended solids) and more weakly correlated with conductivity, TDS, and nitrogen (TKN, TN, TAN). All of these variables are associated with degraded aquatic environments in Great Lakes wetlands (Lougheed et al. 2001; Lougheed and Chow-Fraser 2002). A further 13% was accounted for by PC2, which was primarily correlated with nitrogen variables (TN, TKN) and negatively correlated with conductivity. Another 9% was explained by PC3, which was positively correlated with TDS and negatively correlated with TISS.

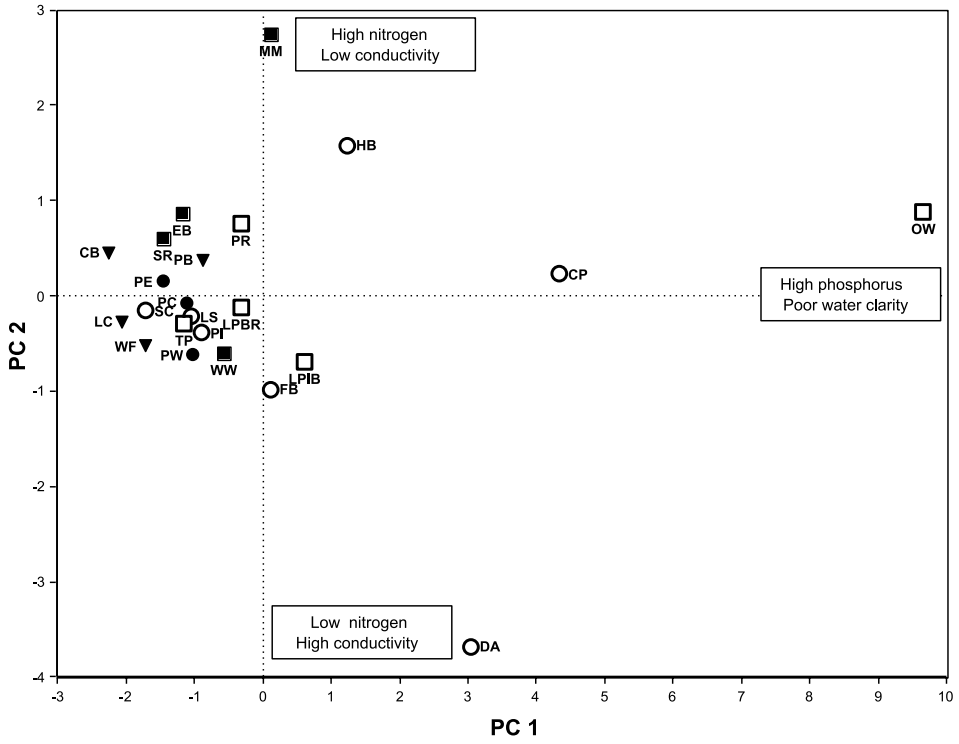
The PCA biplot illustrates the distribution of coastal wetlands along the two major environmental axes (Fig. 2). Sites with high PC1 values (Old Woman Creek of Lake Erie and Cootes Paradise of Lake Ontario) had correspondingly high water turbidity and TP concentrations. Sites with low PC1 values had clear water and low TP concentrations and included all sites in the upper lakes as well as several better-quality sites in the lower lakes (e.g., Cloud Bay, Lost Creek, and West Fish Creek of Lake Superior, Sandy Creek of Lake Ontario, and Turkey Point of Lake Erie). PC2 separated wetlands along a nitrogen and conductivity axis, with Mismer

Table 2. Results of principal components analysis (PCA) of environmental data for 23 wetland sites and correlations between environmental variables and principal components axes.

Principal components axis	Variance explained, %	Environmental variable	Correlation coefficient *r*	*p* value
PC1 (eigenvalue = 6.9)	69	TP	0.95	<0.0001
		TSS	0.93	<0.0001
		TOSS	0.93	<0.0001
		Turbidity	0.91	<0.0001
		TISS	0.89	<0.0001
		Conductivity	0.76	<0.0001
		TDS	0.75	<0.0001
		TKN	0.73	0.0001
		TN	0.72	0.0001
		TAN	0.64	0.0010
PC2 (eigenvalue = 1.3)	13	TN	0.61	0.0020
		TKN	0.59	0.0028
		Conductivity	–0.50	0.0163
		TDS	–0.45	0.0292
PC3 (eigenvalue = 0.9)	9	TDS	0.44	0.0361
		TISS	–0.42	0.0484

Note: TP, total phosphorus; TSS, total suspended solids; TOSS, total organic suspended solids; TISS, total inorganic suspended solids; TDS, total dissolved solids; TKN, total Kjeldahl nitrogen; TN, total nitrogen; TAN, total ammonia nitrogen.

Fig. 2. Plot of PC1 versus PC2 scores for 24 coastal wetlands. Open symbols are wetlands in the lower lakes (Lake Erie, open squares; Lake Ontario, open circles), solid symbols indicate wetlands in the upper lakes (Lake Huron, solid squares; Lake Michigan, solid circles; Lake Superior, solid triangles). Letter codes shown in the plot for each wetland are listed in Table 1.



Marsh at one end (high nitrogen levels, average conductivity) and Darlington at the other (high conductivity, relatively low nitrogen levels).

Interpretation of how water quality in our wetlands responds to anthropogenic stressors is premised on the assumption that these variables are unaffected by large-scale regional differences relating to latitude or climate. We tested for this confounding effect by including latitude in the PCA, but found latitude to be more weakly correlated with PC1 than the other environmental variables ($r = –0.56$, $p = 0.0055$) and to have no significant correlation with the other two PC axes. Because mean August temperature was a significant

Table 3. Mean chlorophyll *a* biomass for periphyton (CHL_{peri}) on plastic rods, epiphyton (CHL_{epi}) on submergent plants, and phytoplankton (CHL_{phyto}) at each wetland site.

Wetland code	CHL_{peri}, $\mu g \cdot cm^{-2} \cdot 28\ days^{-1}$	*n*	SD	CHL_{epi}, $\mu g \cdot cm^{-2}$	*n*	SD	CHL_{phyto}, $\mu g \cdot L^{-1}$	*n*	SD
OW	166.13	20	56.69	20.27	10	23.71	100.35	3	3.28
CP	65.24	34	39.36	72.19	9	37.84	65.37	12	22.16
FB	32.05	12	14.09	12.87	8	13.76	7.42	6	4.00
JH	23.13	19	14.39	5.34	10	4.61	2.84	3	0.00
LPIB	22.19	16	24.47	8.37	9	11.61	4.02	6	2.37
PW	20.63	20	9.65	6.28	10	6.18	2.70	3	0.62
LS	17.12	18	12.40	1.89	10	1.67	5.05	3	1.79
PE	15.82	15	12.39	8.98	10	11.84	1.89	3	1.08
DA	13.85	12	16.72	1.75	7	1.33	9.56	3	7.41
PR	11.41	15	14.39	3.86	9	3.38	9.28	3	6.02
SC	11.28	18	9.72	6.87	10	10.16	5.30	3	0.38
LC	10.33	20	6.36	10.15	4	13.22	2.25	3	0.74
MM	9.41	20	5.50	6.84	4	4.20	0.27	3	0.23
HB	8.55	21	6.82	17.12	18	17.66	13.44	6	11.28
PB	6.57	8	6.15	38.86	6	62.70	2.46	3	0.33
PC	4.83	12	3.55	1.02	6	0.78	3.98	3	1.61
LPBR	3.90	16	1.93	3.22	8	3.19	4.24	8	3.30
PI	3.15	19	2.92	1.63	9	2.27	1.28	3	0.33
TP	2.80	20	2.49	0.94	10	1.01	2.49	6	2.28
SR	2.51	18	2.22	3.27	5	0.57	4.92	3	0.87
CB	1.63	19	1.24	8.65	10	7.02	0.09	3	0.08
WW	1.49	17	2.44	4.65	10	4.92	3.98	3	0.28
EB	1.23	18	0.74	1.05	5	0.16	1.08	3	0.62
WF	0.85	18	0.55	2.95	4	2.59	0.46	3	0.42

Note: Data are ordered by decreasing periphyton biomass. SD, standard deviation.

predictor of growing season length ($r^2 > 0.95$, $p < 0.001$), we substituted mean August temperature and reran the PCA but still found no change in the outcome of the PCA (data obtained from Agriculture and Agri-Food Canada 2002; Midwest Regional Climate Center 2002). Therefore, we are confident that the results of the PCA using water-quality variables alone can be interpreted as the response of wetlands to varying degree of anthropogenic stress.

Phytoplankton, epiphyton, and periphyton biomass

We have organized the algal data for the 24 wetland complexes in descending order according to CHL_{peri} (Table 3). Incubation periods for periphyton varied from 24 to 31 days, so we have standardized the data to $\mu g \cdot cm^{-2}$ for a 28-day period to ease comparison. Although 20 rods were installed at each site (except Cootes Paradise, which had 35 rods), some were lost before collection, and between 8 and 34 samples were collected at each site (as shown in Table 3). Mean CHL_{peri} for all wetlands was 19.18 ± 7.02 (± SE) $\mu g \cdot cm^{-2} \cdot 28\ days^{-1}$, with values ranging from a low of 0.85 in relatively undisturbed West Fish Creek wetland to a high of 166.12 $\mu g \cdot cm^{-2} \cdot 28\ days^{-1}$ in the heavily disturbed Lake Erie wetland, Old Woman Creek. Because the colonization period for epiphyton could not be determined, we expressed the values simply as $\mu g \cdot cm^{-2}$. For the majority of the wetlands, ~10 epiphyton samples were obtained on two sampling occasions (sample numbers for each site are shown in Table 3). Mean CHL_{epi} was 10.34 ± 3.18 (±SE) $\mu g \cdot cm^{-2}$, with a range of 0.94 $\mu g \cdot cm^{-2}$ in Turkey Point, a high-quality Lake Erie marsh, to 72.19 $\mu g \cdot cm^{-2}$ in degraded Cootes Paradise Marsh of Lake Ontario. These values are higher than the range reported in Goldsborough and Robinson (1996) of 0–37 $\mu g \cdot cm^{-2}$ for epiphyton in freshwater marshes. Mean CHL_{phyto} was 10.61 ± 4.71 (±SE) $\mu g \cdot L^{-1}$, with values ranging from 0.09 $\mu g \cdot L^{-1}$ in pristine Cloud Bay wetland of Lake Superior to 100.35 $\mu g \cdot L^{-1}$ in heavily impacted Old Woman Creek, and fall within the range of values reported for Great Lakes wetlands by Lougheed et al. (2001).

We can compare the trends in CHL content for each algal group across the striking degradation gradient, as indicated by the PC1 site score (Fig. 3*a*). Mean CHL_{peri} decreased predictably as wetlands changed from poor-quality (Old Woman Creek and Cootes Paradise) to high-quality marshes (Lost Creek and Cloud Bay) (Fig. 3*b*). CHL_{epi} (Fig. 3*c*) and CHL_{phtyo} (Fig. 3*d*) showed similar decreases.

To test the relationship between each of the algal variables with water-quality degradation, we regressed CHL_{peri}, CHL_{phtyo} (Figs. 4*a*, 4*b*, respectively), and CHL_{epi} against PC1 site scores. Consistent with our first hypothesis, we found significant relationships between PC1 score and CHL_{peri} and CHL_{phyto}, respectively accounting for 54 and 70% of the variation in periphyton and phytoplankton data ($p < 0.001$ for both; Fig. 4). Poor-quality wetlands with high turbidity and nutrients supported high biomass of phytoplankton and rapid colonization by periphyton. By comparison, PC1 was not a significant predictor of CHL_{epi} ($r^2 = 0.19$, $p = 0.039$).

Correlations between each of the environmental variables used in the PCA and the three algal groups were performed

Fig. 3. Values of (*a*) PC1 score and chlorophyll *a* biomass (mean ± 1 standard error) of (*b*) periphyton (CHL_{peri}), (*c*) epiphyton (CHL_{epi}), and (*d*) phytoplankton (CHL_{phyto}) for each of 24 coastal wetlands. In each plot, wetlands are ranked according to PC1 value or chlorophyll *a* biomass, decreasing from left to right.

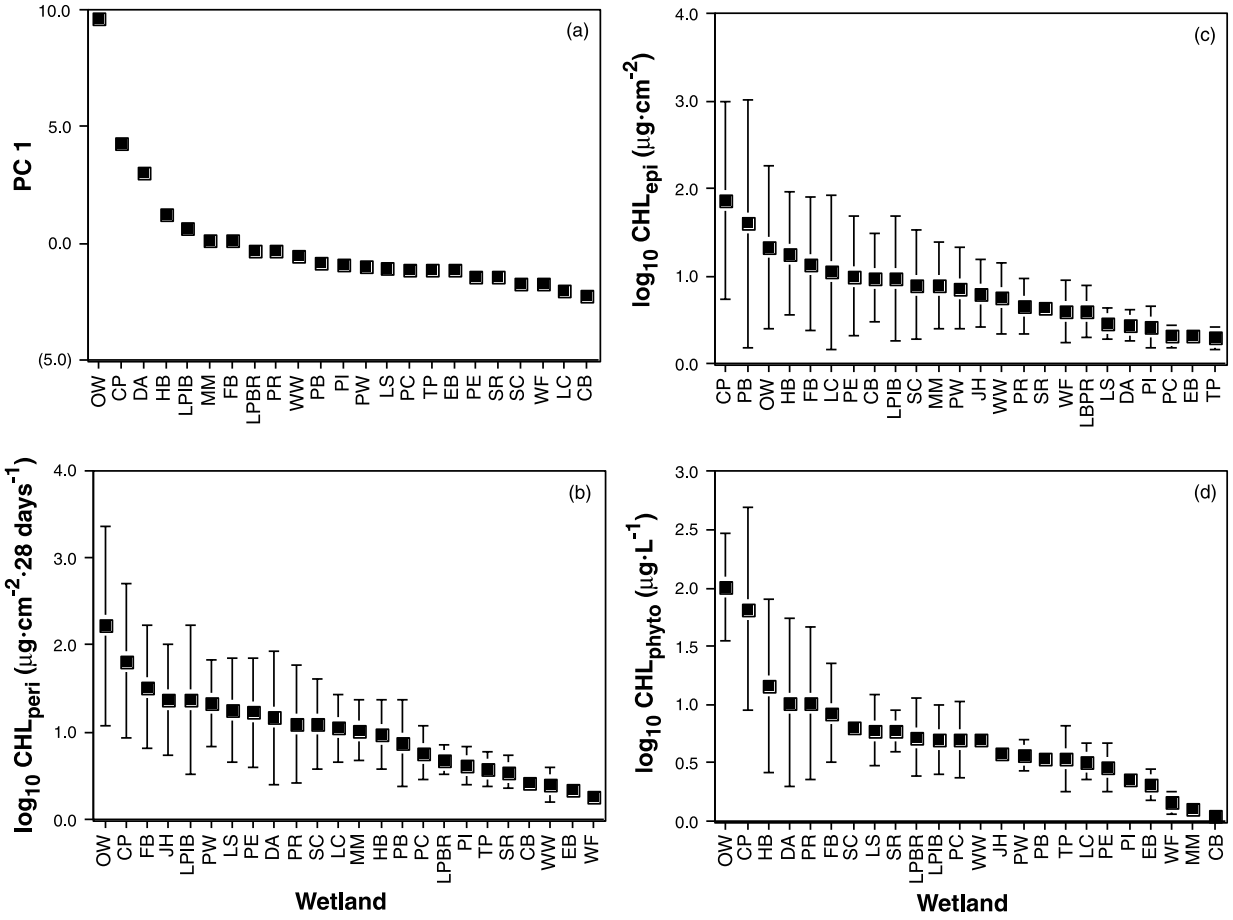
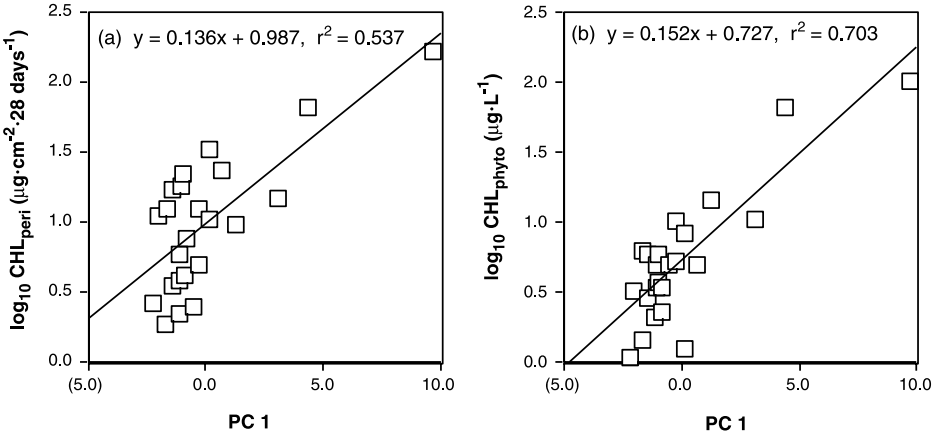


Fig. 4. Chlorophyll *a* biomass for (*a*) benthic algae (CHL_{peri}) and (*b*) planktonic algae (CHL_{phyto}) plotted against water quality (PC1 scores).



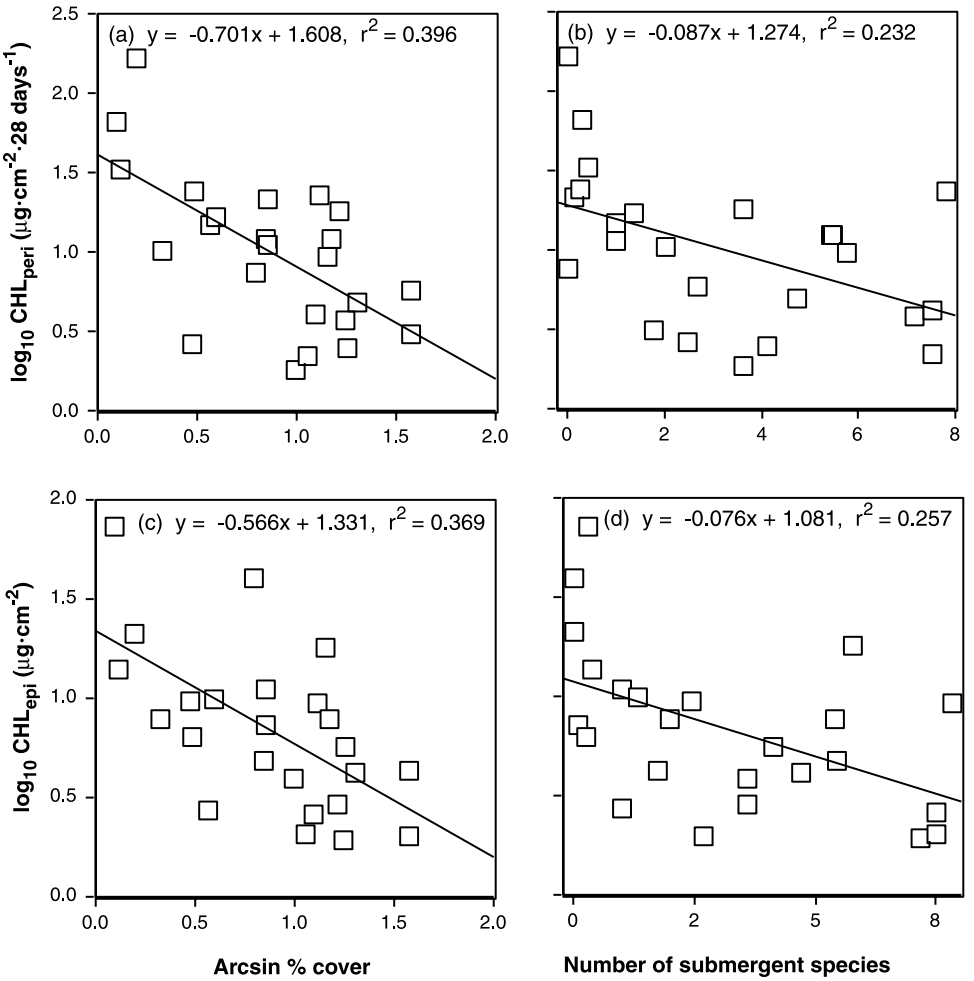
using log_{10}-transformed data (Table 4). CHL_{phyto} was significantly correlated with all environmental variables ($p < 0.05$), whereas CHL_{peri} was significantly correlated with all but TISS, and CHL_{epi} was only significantly correlated with turbidity and TAN. CHL_{peri} was positively correlated with TOSS, conductivity, TDS, and TP, suggesting that high nutrient concentrations stimulate the colonization rate of attached algae, even though light penetration of the water column is reduced. The strong relationship between CHL_{phyto} and TOSS, conductivity, TSS, TDS, TP, and nitrogen (TKN, TN, TAN) may be spurious because phytoplankton are included in the measurement of five of these parameters (TOSS, TSS, TP, TKN, and TN). Both CHL_{peri} and CHL_{phyto} were negatively correlated with latitude ($r = –0.57$, $p = 0.004$ and $r = –0.68$, $p = 0.0004$, respectively); the most northern sites in Lake Superior generally had very low algal biomass, but these

Table 4. Correlations between benthic (CHL_{peri} and CHL_{epi}) and planktonic (CHL_{phyto}) chlorophyll *a* biomass and PC1 and the environmental variables associated with PC1.

	CHL_{peri}		CHL_{phyto}		CHL_{epi}	
	r	*p* value	*r*	*p* value	*r*	*p* value
PC1	0.73	0.0001	0.84	<0.0001	0.43	0.0400
Turbidity	0.54	0.0076	0.62	0.0014	0.44	0.0349
TSS	0.53	0.0100	0.71	0.0001	0.38	0.0800
TOSS	0.68	0.0004	0.84	<0.0001	0.35	0.1005
TISS	0.34	0.1119	0.53	0.0093	0.34	0.1157
Conductivity	0.63	0.0013	0.72	0.0001	0.13	0.5650
TDS	0.62	0.0015	0.70	0.0002	0.16	0.4679
TP	0.59	0.0032	0.70	0.0002	0.24	0.2776
TKN	0.51	0.0138	0.58	0.0038	0.37	0.0826
TN	0.51	0.0122	0.56	0.0053	0.35	0.0971
TAN	0.54	0.0074	0.69	0.0003	0.64	0.0010
CHL_{peri}			0.75	<0.0001	0.58	0.0034
CHL_{phyto}	0.75	<0.0001			0.47	0.0229
CHL_{epi}	0.58	0.0034	0.47	0.0229		

Note: TSS, total suspended solids; TOSS, total organic suspended solids; TISS, total inorganic suspended solids; TDS, total dissolved solids; TP, total phosphorus; TKN, total Kjeldahl nitrogen; TN, total nitrogen; TAN, total ammonia nitrogen.

Fig. 5. Log_{10} chlorophyll *a* biomass of periphyton (CHL_{peri}) and epiphyton (CHL_{epi}) plotted against (*a* and *b*) arcsin % cover of submergent plants and (*c* and *d*) number of submergent plant species.



sites also have lower anthropogenic impacts (consequently lower nutrient and sediment levels). There was a strong positive correlation between CHL_{phyto} and CHL_{peri} ($r = 0.75$, $p < 0.0001$), whereas CHL_{epi} was more weakly correlated with CHL_{phyto} ($r = 0.47$, $p = 0.02$) and CHL_{peri} ($r = 0.58$, $p = 0.0034$).

Submergent macrophytes

Our second hypothesis predicts that both epiphyton and periphyton will be inversely related to areal cover of submersed aquatic vegetation. We regressed algal biomass against both percent cover and species richness of submergent plants (Fig. 5). CHL_{peri} and CHL_{epi} biomass decreased with percent cover of aquatic plants ($r^2 = 0.40$, $p = 0.001$ and $r^2 = 0.37$, $p = 0.0016$, respectively) and with species richness of macrophytes ($r^2 = 0.23$, $p = 0.017$ and $r^2 = 0.26$, $p = 0.0115$, respectively), whereas there was no significant correlation between CHL_{phyto} and either macrophyte variables. These results reveal that high rate of colonization by attached algae, low species richness, and low percent cover of submergents are found in degraded wetlands.

Discussion

The 24 wetlands in this study represent a very large disturbance gradient that was accurately reflected in the synthetic axis, PC1. There was a highly significant linear relationship between the water quality of wetlands and PC1 scores, and previous studies have demonstrated that variation in PC1 scores can be attributed to alteration in land uses in wetland watersheds (Crosbie and Chow-Fraser 1999; Lougheed et al. 2001; P. Chow-Fraser, unpublished data). From this study, it is clear that regional variation in climate and bedrock geology did not contribute a significant amount to the variation in water-quality characteristics of these wetlands.

That CHL_{peri} and CHL_{phyto} are both strongly related to PC1 scores bodes well for using these as indicators of wetland degradation. In undisturbed wetlands, both periphyton and phytoplankton biomass are limited by low nutrient availability, whereas in highly disturbed wetlands, excessive nutrient loading results in high CHL_{peri} and CHL_{phyto}. By comparison, the relationship between CHL_{epi} and disturbance is complicated by the fact that when nutrients become limiting in the water column, epiphytic algae may be able to obtain nutrients leaked from the vascular plants they colonize or from nutrients recycled within the epiphytic matrix of living and detrital material attached to the plant surface (Burkholder 1996; Wetzel 1996).

It is not possible to conduct a meaningful numerical comparison of all three variables because periphyton and epiphyton do not share the same colonization periods, and phytoplankton data are expressed volumetrically, whereas the other two are expressed on an areal basis. Nevertheless, the utility of each type of algae for biomonitoring can be compared in other ways. Periphyton grown on artificial substrata allow for standardization of both time and substrate characteristics, reducing the variation found in epiphyton and phytoplankton samples and providing for more meaningful site-to-site comparisons. The acrylic rods used in this study are easily installed, collected, and processed. The chief disadvantage to using this method is that two trips to each site are required. Epiphyton samples are most representative of the natural benthic algae community, but many unquantified factors such as successional stage, senescence, or seasonal internal community changes could be influencing the biomass estimates. Epiphyton samples require more processing time at collection, and chlorophyll *a* biomass estimates may be confounded by incomplete removal of algae from the vascular plant material or by inclusion of macrophyte chlorophyll *a* in the sample. In addition, estimating surface area of submergent plants is difficult and subject to greater measurement error compared with artificial substrata. Although phytoplankton samples are easily collected and processed, their spatial and temporal variability in degraded wetlands (Chow-Fraser 1999) make them difficult to sample accurately without a great deal of effort or without the use of expensive in situ probes. In this study, periphyton grown on artificial substrata provided the most precise data because of the higher degree of control and the relative ease of collecting a large number of samples.

The main external factors that regulate the biomass of algae in wetlands include light availability, primary nutrient concentrations, and grazing pressure from benthic and planktonic herbivores. Compared with benthic algae that are sessile and that obtain their nutrients from the biofilm attached to substrate (Burkholder 1996), planktonic algae obtain all of their nutrients from the water column. Hence, phytoplankton are less constrained by low light availability when there is abundant nutrient in the water column because they can move towards the light and shade out other primary producers. However, they are vulnerable to grazing because they reside in the same medium in which zooplankton grazers live (Borchardt 1996). In this regard, benthic algae may have an advantage in enriched environments, because the community of benthic invertebrates that graze on periphyton and epiphyton tend to be depressed, presumably because of the presence of a large number of benthivorous fish (Chow-Fraser 1998). Thus, even though benthic algae can be limited by light, their biomass is unconstrained by grazing pressure in degraded wetlands. In contrast, when benthic algae occur in good-quality marshes that have abundant macrophytes, benthic grazers tend to be abundant and keep the benthic algal biomass at low levels (Goldsborough and Robinson 1996).

The large site-to-site differences in the biomass of phytoplankton, epiphyton, and periphyton measured in this study are most likely due to the combined effects of nutrient limitation, light availability, and grazing pressure rather than to a single factor. The limiting factor for a particular site must be deduced experimentally. The decline of submergent macrophytes in degraded wetlands has been attributed to high epiphytic and planktonic algal biomass resulting from nutrient enrichment of freshwater ecosystems (Hough et al. 1989; Chow-Fraser 1998; Lougheed et al. 2001). The relationship between both areal cover and species richness of submergent plants found in this study is in agreement with these previous studies. There is a strong negative association between high benthic algal biomass and presence of submergent plants. Although it is not possible to state whether the benthic algae are the cause of macrophyte decline in degraded wetlands, it is clear that a suite of measurable factors are implicated in the loss of significant wetland habitats.

We have shown that the biomass of periphyton grown on acrylic rods can be used to indicate the degree of wetland degradation relating to anthropogenic nutrient loading and concomitant alterations in water clarity. The standardized protocol that we used provides a relatively precise measure of wetland quality and is better for this purpose than phytoplankton or epiphyton growing on vascular plant material. Information regarding the taxonomic affiliation of the planktonic and benthic algae should provide further insight into wetland algal ecology and enhance the use of these organisms as bioindicators. We recommend that both planktonic and benthic algal biomass be included in routine monitoring and management of coastal wetlands.

Acknowledgements

This study was funded by a research grant from the Great Lakes Fishery Commission to P.C-F. We thank Dennis Albert for his assistance with plant identification in the field. We acknowledge the field and laboratory assistance of 25 summer students, friends, and colleagues who helped with the project and, in particular, Maria Strack, who also provided all of the sediment nutrient data as part of an undergraduate honours thesis. We are grateful to two anonymous reviewers whose comments improved this manuscript.

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Appendix A

Appendix appears on the following page.

Table A1. Location of wetland sites and measured environmental variables for 24 Great Lakes coastal wetlands included in this study.

Lake	Wetland, state or province	Wetland code	Latitude	Longitude	Turbidity (FTU)	Light extinction	Conductance ($\mu S \cdot cm^{-1}$)	TDS ($g \cdot L^{-1}$)	DO ($mg \cdot L^{-1}$)	pH	Temperature (°C)
Superior	Cloud Bay, Ont.	CB	48.0828	–89.4372	2.89	2.62	73.5	0.039	8.77	7.83	15
Superior	Pine Bay, Ont.	PB	48.0333	–89.5195	17.19	2.47	101.1	0.045	8.05	7.98	18
Superior	Lost Creek, Wis.	LC	46.8586	–91.1358	4.87	3.40	102.1	0.065	4.21	7.15	20
Superior	West Fish Creek, Wis.	WF	46.5869	–90.9458	11.03	2.06	102.6	0.066	9.30	7.72	16
Michigan	Portage Creek, Wis.	PC	45.7062	–87.0800	7.06		267.4	0.212	9.91	8.37	22
Michigan	Peshtigo Marsh, Wis.	PE	44.9840	–87.6607	2.06	3.44	247.2	0.164	7.43	8.15	25
Michigan	Pentwater, Mich.	PW	43.7628	–86.4078	4.95	2.80	383.4	0.269	10.10	8.63	22
Huron	Echo Bay, Ont.	EB	46.4944	–84.0761	16.99		84.0	0.054	8.82	8.31	23
Huron	Spanish River, Ont.	SR	46.1850	–82.3306	4.06		145.3	0.093	8.81	8.05	23
Huron	Mismer Marsh, Mich.	MM	46.0051	–84.4606	3.12		215.5	0.140	9.73	8.34	22
Huron	Wigwam Bay (Pine River), Mich.	WW	43.9702	–83.8543	4.42	2.54	425.1	0.249	10.32	9.27	24
Ontario	Hay Bay, Ont.	HB	44.1750	–76.9250	5.78	1.63	495.3	0.333	6.18	7.73	22
Ontario	Presqu'Ile, Ont.	PI	44.0154	–77.7306	4.33	2.21	298.3	0.363	9.09	8.07	23
Ontario	Darlington, Ont.	DA	43.8730	–78.7970	21.65	5.00	1171.5	0.664	6.21	8.47	21
Ontario	Frenchman's Bay, Ont.	FB	43.8123	–79.0947	30.35	2.70	426.3	0.270	8.88	8.66	25
Ontario	Sandy Creek, N.Y.	SC	43.7009	–76.1965	1.95	1.72	217.2	0.149	10.15	9.01	24
Ontario	Little Sodus, N.Y.	LS	43.3390	–76.6944	2.32	2.67	319.9	0.233	8.25	8.14	24
Ontario	Cootes Paradise, Ont.	CP	43.2800	–79.8980	42.12	6.65	676.9	0.511	10.28	8.21	25
Ontario	Jordan Harbour, Ont.	JH	43.1600	–79.3700	116.73	13.17	488.0	0.311	6.06	7.74	22
Erie	Turkey Point, Ont.	TP	42.6485	–80.3417	3.96	2.05	315.7	0.203	7.83	8.33	22
Erie	Long Pt., Big Rice Bay, Ont.	LPBR	42.5893	–80.3355	3.29	1.87	301.4	0.172	8.91	8.43	21
Erie	Long Pt., Inner Bay, Ont.	LPIB	42.5867	–80.3877	16.70		313.1	0.348	7.24	8.20	20
Erie	Presque Isle, Pa.	PR	42.1590	–80.0985	4.70	3.22	273.4	0.163	7.39	8.41	23
Erie	Old Woman Creek, Ohio	OW	41.3822	–82.5145	90.56	11.01	774.5	0.495	5.04	8.05	22

Note: Data are ordered by decreasing latitude by lake. TDS, total dissolved solids; DO, dissolved oxygen.

Table A2. Nutrients and dissolved solids for water column and sediment samples from each wetland site.

Wetland code	TP ($\mu g \cdot L^{-1}$)	SRP ($\mu g \cdot L^{-1}$)	TKN ($mg \cdot L^{-1}$)	TNN ($mg \cdot L^{-1}$)	TAN ($mg \cdot L^{-1}$)	TN ($mg \cdot L^{-1}$)	TN:TP	TSS ($mg \cdot L^{-1}$)	TISS ($mg \cdot L^{-1}$)	TOSS ($mg \cdot L^{-1}$)	Sed TP ($mg \cdot L^{-1}$)	Sed NH_4 ($mg \cdot g^{-1}$)	Sed Org ($g \cdot g^{-1}$)	Sed Inorg ($g \cdot g^{-1}$)
CB	19.80	2.60	1.25	0.13	0.02	1.38	69.9	0.82	0.02	0.80	0.45	0.010	0.03	1.0
PB	56.26	6.25	1.25	0.27	0.10	1.52	27.0	16.88	13.68	3.20	0.47	0.023	0.08	0.9
LC	49.49	8.86	0.42	0.23	0.01	0.65	13.1	4.20	0.96	3.25	0.24	0.020	0.15	0.8
WF	59.91	10.42	0.00	0.03	0.10	0.03	0.6	9.28	6.18	3.10	0.13	0.001	0.01	1.0
PC	58.87	5.21	1.25	0.93	0.04	2.18	37.1	3.58	0.98	2.60	0.27	0.014	0.02	1.0
PE	45.84	0.52	1.67	0.30	0.02	1.97	42.9	2.08	0.00	2.08	0.10	0.001	0.01	1.0
PW	40.63	0.52	1.25	0.67	0.00	1.92	47.2	4.84	0.91	3.93	0.63	0.005	0.01	1.0
EB	76.60	4.15	1.67	0.63	0.04	2.30	30.1	6.17	4.57	1.60	0.55	0.029	0.06	0.9
SR	41.85	6.17	1.67	0.60	0.03	2.27	54.2	5.76	4.06	1.70	0.52	0.003	0.02	1.0
MM	117.14	5.16	5.00	0.57	0.07	5.57	47.5	3.64	3.37	0.27	0.52	0.175	0.11	0.9
WW	49.49	0.00	1.67	0.07	0.03	1.73	35.0	10.78	5.58	5.20	0.04	0.007	0.01	1.0
HB	133.47	6.93	5.00	0.47	0.06	5.47	41.0	9.17	5.05	4.13	0.81	0.356	0.37	0.6
PI	93.00	10.11	1.67	0.03	0.02	1.70	18.3	1.38	0.39	0.99	0.33	0.009	0.01	1.0
DA	158.36	3.65	1.25	0.10	0.01	1.35	8.5	33.12	15.52	17.60	0.91	0.165	0.20	0.8
FB	68.50	1.04	1.25	0.10	0.09	1.35	19.7	12.24	4.44	7.80	1.53	0.097	0.68	0.3
SC	44.28	1.56	1.25	0.01	0.01	1.26	28.5	2.38	0.00	2.38	0.26	0.021	0.09	0.9
LS	66.68	5.73	1.67	0.17	0.02	1.83	27.5	4.07	0.88	3.19	0.66	0.095	0.12	0.9
CP	145.60	4.85	3.95	0.53	0.75	4.48	30.8	27.95	13.78	14.17	0.71	0.038	0.07	0.9
JH	341.88	166.29	2.19	0.80	0.22	2.99	8.7	146.90	134.40	12.50	0.97	0.151	0.18	0.8
TP	41.73	2.47	1.46	0.12	0.05	1.58	37.8	5.96	2.99	2.97	0.58	0.014	0.04	1.0
LP BR	89.03	4.42	1.67	0.07	0.04	1.73	19.5	19.96	15.58	4.38	0.70	0.039	0.08	0.9
LPIB	66.42	7.29	1.46	0.85	0.05	2.31	34.8	26.51	18.45	8.06	0.56	0.011	0.02	1.0
PR	94.21	9.13	2.92	0.13	0.08	3.05	32.4	6.36	0.08	6.28	1.15	0.367	0.33	0.7
OW	398.05	14.80	6.25	0.53	0.32	6.78	17.0	91.30	67.23	24.07	0.74	0.116	0.08	0.9

Note: Site codes are the same as in Table 1A; data are ordered by decreasing latitude by lake. TP, total phosphorus; SRP, soluble reactive phosphorus; TKN, total Kjeldahl nitrogen; TNN, total nitrate nitrogen; TAN, total ammonia nitrogen; TN, total nitrogen; TSS, total suspended solids; TISS, total inorganic suspended solids; TOSS, total organic suspended solids; Sed. TP, sediment total phosphorus; Sed. NH_4, sediment ammonia; Sed. org., sediment organic content; Sed. inorg., sediment inorganic content.