

The Wall of Green: The Status of *Cladophora glomerata* on the Northern Shores of Lake Erie's Eastern Basin, 1995–2002

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ABSTRACT. The biomass, areal coverage, algal bed characteristics, and tissue phosphorus concentrations of *Cladophora glomerata* were measured at 24 near shore rocky sites along the northern shoreline of Lake Erie's eastern basin between 1995–2002. Midsummer areal coverage at shallow depths (≤ 5 m) ranged from 4–100%, with a median value of 96%. *Cladophora* biomass began accumulating at most sites during early May, and achieved maximum values by mid-July. Peak seasonal biomass ranged from < 1 to 940 g/m² dry mass (DM), with a median value of 171 g/m² DM. Nearshore water concentrations of total phosphorus (TP) were lower than during pre-phosphorus abatement years. However, *Cladophora* biomass levels were similar to reported values in those years. The midsummer “die off” occurred shortly after the biomass peak, when water temperatures neared 22.5°C. Areal coverage declined after die-off to < 10%, mean filament lengths declined from 33 cm to < 1 cm, and mean biomass declined to < 1 g DM/m². Tissue phosphorus varied seasonally, with initial high values in early May (0.15 to 0.27% DM; median 0.23% DM) to midsummer seasonal low values during peak biomass (0.03 to 0.23% DM; median 0.06% DM). *Cladophora* biomass is sensitive to changes in phosphorus and light availability, and reductions in biomass previously achieved through phosphorus control may now be reversed because of increased water transparency and phosphorus availability to the benthos following establishment of dreissenids.

INDEX WORDS: *Cladophora*, benthic algae, Lake Erie, Dreissena, water quality.

INTRODUCTION

Cladophora glomerata is a filamentous green alga widely distributed throughout lentic and lotic freshwaters of the world (Blum 1956, Dodds 1991, Sheath and Cole 1992). In general, *C. glomerata* grows attached to hard substrates in nutrient rich alkaline freshwaters, and was first described in Lake Erie in 1848 (Taft 1975). The biology and ecology of *C. glomerata* have been reviewed elsewhere (see Whitton 1970, Dodds and Gudder 1992). Although high morphological plasticity makes classification to species level difficult (Bellis and McClarty 1967), the vast majority of researchers have identi-

fied *Cladophora* in the Laurentian Great Lakes region as *C. glomerata*. For the remainder of this paper all references to *Cladophora* infer *C. glomerata*. During the 1960s through to the early 1980s severe nuisance blooms of *Cladophora* were described throughout the rocky shorelines of Lake Ontario and Lake Erie, and in localized portions of Lake Michigan and Lake Huron (Herbst 1969, Shear and Konasewich 1975, Auer *et al.* 1982, Millner and Sweeney 1982, S. Malkin, University of Waterloo, unpublished data). Large blooms and subsequent “die-off” events of *Cladophora* severely reduced the aesthetic value of the nearshore waters where they occurred (Taft 1975). Beach accumulations of *Cladophora* were at times measured in

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tonnes of fresh material (Neil and Owen 1964, Shear and Konasewich 1975, Taft 1975). In the early stages of decay *Cladophora* releases noxious odors that deterred the recreational uses of beaches and shorelines (Shear and Konasewich 1975, DeJong 2000). Property values decreased in the areas where beach wash-ups occurred, and severe economic impacts were incurred by businesses in the tourism and recreational sectors (Taft 1975, DeJong 2000). When free-floating in the water column, these filaments clogged fishing nets, reducing their efficiency and increasing their down time when they must be cleaned, and caused problems for municipal and industrial water intakes (Taft 1975). Recent evidence indicates that shoreline mats of decaying *Cladophora* in Lake Michigan supported high concentrations of *Escherichia coli* (Byappanahalli et al. 2003).

Although the total socio-economic costs of the “*Cladophora* problem” have never been fully assessed in any of the Great Lakes (though see Taft 1975), the indication of *Cladophora* as a “serious problem” by the International Joint Commission led to a series of focussed studies aimed at understanding the factors that promoted growth and bloom occurrences (see Shear and Konasewich 1975, and *J. Great Lakes Res.* 8(1) 1982). These studies led to the conclusion that, although several important factors (e.g., light, temperature, phosphorus, nitrogen, CO₂) could be responsible for controlling growth rates (Canale and Auer 1982, Hoffman and Graham 1984), that elevated concentrations of soluble phosphorus were generally responsible for the bloom occurrences (Herbst 1969, Gerloff and Fitzgerald 1976, Auer and Canale 1980). Because *Cladophora* blooms and shoreline fouling occurred at the lake margins they were perhaps the most obvious signs of the extent of cultural eutrophication in Lake Erie from the 1960s through to the 1980s. Large public outcries about “the *Cladophora* problem,” in part, led to the multi-billion dollar investments in sewage treatment plant upgrades, and the removal of phosphates from detergents, to reduce phosphorus loadings. Total phosphorus concentrations in the offshore and nearshore zones of the Laurentian Great Lakes responded dramatically to the reduction of phosphorus loading (Stevens and Neilson 1987, Nicholls et al. 2001). While total phosphorus concentrations in the nearshore zones also decreased or remained unchanged after *Dreissena* colonization (Nicholls and Standke 1997, Nicholls et al. 1999), spring SRP concentrations have increased in all basins of Lake Erie post-*Dreissena*

(Makarewicz et al. 2000). Unfortunately, very little data exist on *Cladophora* in the Laurentian Great Lakes from 1983–1990, the period where phosphorus concentrations were dramatically reduced in the lower Great Lakes but prior to the invasion of *Dreissena polymorpha* (zebra mussel) and *D. bugensis* (quagga mussel). The little information that does exist for this period suggests that, at least in Lake Ontario, tissue phosphorus concentrations and bloom occurrences of *Cladophora* were somewhat reduced. Painter and Kamaitis (1987) indicated that mean tissue phosphorus declined from 0.49% AFDM to 0.20% AFDM from 1972–1983, a 59% reduction. Furthermore, over these same years mean biomass declined from 205.8 g DM m⁻² to 85.9 g DM m⁻², a 58% reduction (Painter and Kamaitis 1987).

Beginning in 1995 and through to 2002, the period following *Dreissena* establishment, a series of surveys for the investigation and surveillance of *Cladophora* shoreline fouling was undertaken in Lake Erie by the Ontario Ministry of the Environment (Howell 1998). Throughout the 1995–2000 period nuisance blooms were a regular occurrence in Lake Erie, and in 2001–2002 an intensive effort was undertaken to determine the seasonal and spatial distribution and physiological status of *Cladophora* in the eastern basin of Lake Erie. We bring together these datasets with the objective of assessing spatial and seasonal distribution, biomass, and nutrient status of *Cladophora* along the northern shoreline of Lake Erie’s eastern basin. We also estimate the total amount of phosphorus taken up by *Cladophora*, discuss its significance to littoral zone and basin-wide phosphorus dynamics, and provide preliminary estimates of how *Dreissena*-induced increases in water clarity influence *Cladophora* growth and biomass on a basin scale.

METHODS

1995 and 2002 Spatial Surveys

Cladophora samples were collected from 0.0625 m² quadrats over four depth zones (0–0.5 m, 0.5–1.0 m, 1.0–1.5 m, 1.5–2.0 m) at 20 sites during mid-summer (Table 1). At each survey location (Fig. 1) the percentage cover, and minimum, median, and maximum height of the *Cladophora* beds were determined for five randomly placed quadrats within each depth zone. For each site the data reported are the mean from all quadrats taken from 0–2 m depth, therefore at most sites a total of 20 quadrats was observed. In 1995, areal biomass was

TABLE 1. *Cladophora* bed characteristics for surveys in Lake Erie's eastern basin, 1995–2002. For sites with depth indicated as 0–2 m tissue P samples are the mean of four replicate samples, while remaining sites report the mean value of three replicate samples. Site names with (S) refer to locations where the 2002 seasonal survey was conducted (see text).

Station name	Site-depth #	Depth (m)	Date sampled	n	% cover	Median Bed Height (cm)	Biomass (g DW/m ²)	Tissue P (% DW)
Port Ryerse	1	2	1-Jun-01	3	100	6.5	99	n/s
Port Dover	2	0–2	19-Jul-95	20	92	5.9	92	0.114
Nanticoke	3	0–2	19-Jul-95	20	73	7.4	49	0.065
Peacock Point (S)	4	0–2	17-Jul-95	20	100	12.0	320	0.043
	5	2	1-Jun-01	3	100	9.0	307	0.065
	6	2	8-Jul-02	3	100	15.7	156	0.040
	7	5	25-Jul-01	3	78	7.0	68	0.230
	8	5	8-Jul-02	3	97	4.4	68	0.120
	9	10	1-Jul-01	3	73	3.0	10	n/s
	10	10	14-Jun-02	3	10	1.0	0.74	0.200
Hoover Point (S)	11	2	8-Jul-02	3	100	10.3	185	0.050
Sandusk Creek mouth	12	0–2	19-Jul-95	20	99	11.0	150	0.050
Featherstone Point	13	0–2	13-Jul-95	20	99	19.0	600	0.045
West of Low Point	14	0–2	13-Jul-95	20	93	7.7	360	0.036
Grant Point (S)	15	0–2	13-Jul-95	20	96	14.0	440	0.062
	16	2	15-Jul-02	3	100	8.1	337	0.063
Splatt Bay (G. River)	17	0–2	12-Jul-95	20	98	18.0	180	0.095
Rock Point (S)	18	0–2	12-Jul-95	20	75	6.2	71	0.052
	19	2	8-Jul-02	3	100	11.6	162	0.230
Mowhawk Point	20	0–2	12-Jul-95	20	93	9.8	310	0.028
	21	0–2	2-Jul-02	20	100	15.0	319	0.063
Lowbanks	22	2	1-Jun-01	3	96	7.9	90	0.060
	23	5	1-Jun-01	3	100	7.3	28	0.129
	24	10	1-Jun-01	3	100	3.0	5	0.140
Long Beach	25	0–2	2-Jul-02	40	43	4.0	38	0.120
Grabel Point (west side)	26	0–2	2-Jul-02	20	4	1.0	1	0.061
Grabel Point (east side)	27	0–2	2-Jul-02	20	82	8.0	99	0.072
Morgans Point (west side)	28	0–2	2-Jul-02	20	24	2.0	<1	0.057
Morgans Point (east side)	29	0–2	11-Jul-95	20	87	7.9	390	0.060
	30	0–2	2-Jul-02	20	97	16.0	419	0.048
Rathfon Point (S)	31	0–2	11-Jul-95	20	87	8.0	220	0.040
	32	0–2	2-Jul-02	20	67	9.0	78	0.073
	33	2	8-Jul-02	3	100	11.6	52	0.098
Sugar Loaf Point	34	0–2	11-Jul-95	20	94	6.7	220	0.048
Whitemans Point	35	0–2	17-Jul-95	20	90	4.6	360	0.048
Point Abino	36	2	1-Jun-01	3	100	n/s	135	0.078
Windmill Point	37	0–2	17-Jul-95	20	93	6.5	330	0.046
Bertie Bay	38	0–2	10-Jul-95	20	91	5.7	340	0.045

estimated using a semi-quantitative approach that combined limited quantitative sampling for biomass with the results of the visual survey. At each site, five of the quadrats were cleared by hand of *Cladophora* and material was retained for determination of dry weight. A conversion factor was calculated for each site to convert estimated mean

areal volume (percent cover x median thickness x quadrat area) into biomass, and was determined by dividing the dry mass in a sample quadrat by the volume of *Cladophora* in the quadrat. In 2002, three 0.0625 m² quadrats were cleared of *Cladophora* in each depth zone, rinsed of debris, placed in bags, and stored on ice. The frozen sam-

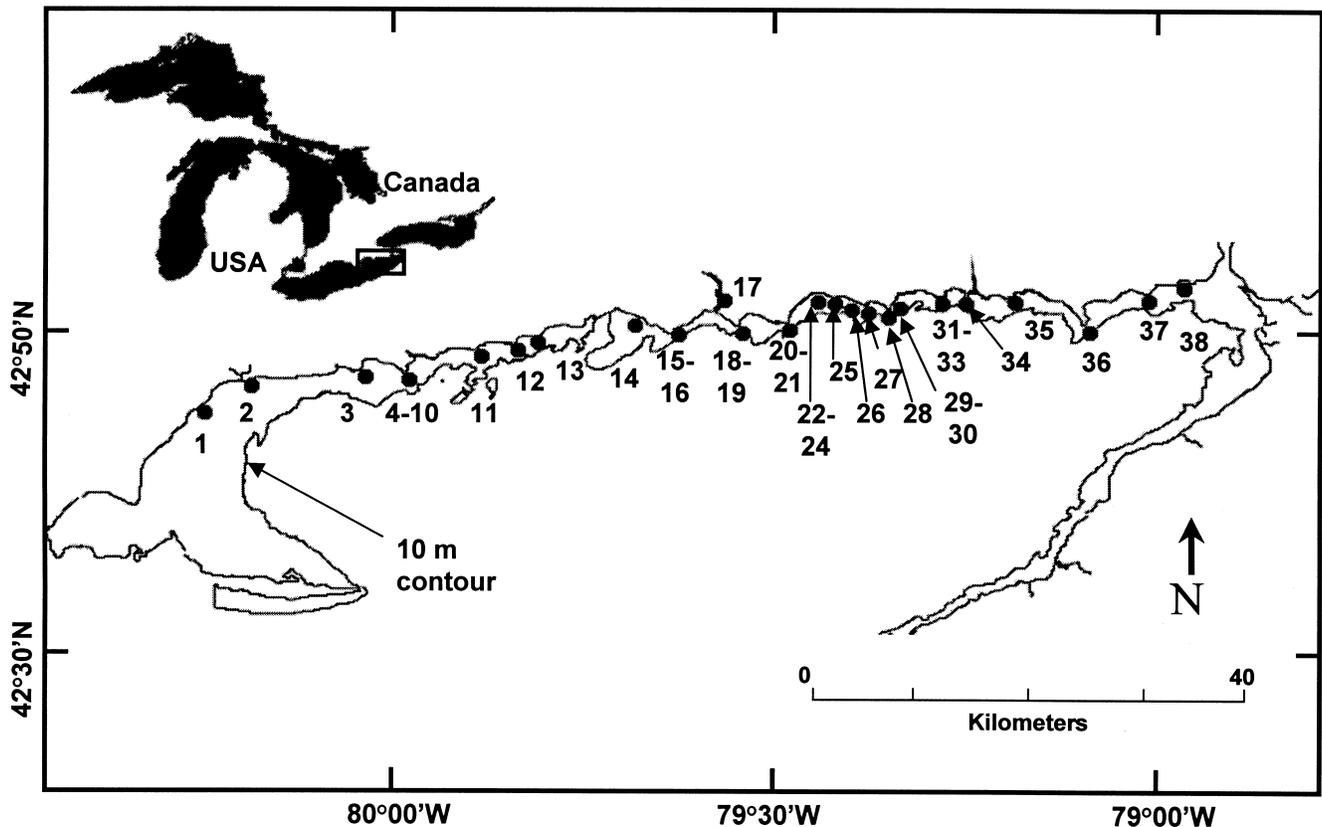


FIG. 1. Map of the northern shoreline of Lake Erie's eastern basin. Site numbers refer to locations of sites as indicated in Table 1.

ples were freeze dried and analyzed for loss-on-ignition (LOI), and total tissue phosphorus (% DM).

2001–2002 Seasonal Surveys

Five sites that allowed shore access and were distributed across the northern shoreline were selected to sample the seasonal variability in biomass, tissue phosphorus, and algal bed characteristics. The seasonal sites are identified in Table 1 with (s) following the site name. At each site, algae was collected at 2 m depth, and at one of these sites (Peacock point) samples were collected at 2 m, 5 m, and 10 m depths. These same sites were also part of a separate study assessing seasonal growth rates and the contribution of *Dreissena* to *Cladophora* resurgence (Higgins 2005). Two other sites, Lowbanks and Point Abino (sites 22 and 36 in Table 1) were sampled in 2001 using the same methods. Samples were collected from three randomly placed 0.25 m² quadrats using SCUBA and an underwater airlifting device described by Barton and Hynes (1978). Prior to removing the biomass in each quadrat the percent

cover was estimated visually, and the bed height and maximum filament lengths were measured with a ruler at three locations within the quadrat and then averaged. *Cladophora* was collected using the airlifting device under very low suction into a 250 µm mesh bag. Algal material was washed of debris and placed in Whirl Pac bags and kept cool until return to the laboratory (1–4 h). Algal material was spun in a salad spinner for 20 s and the fresh mass (FM) determined. Sub-samples were taken for identification. Approximately 10 g FM was dried at 60°C for 24 h then reweighed to obtain the dry mass (DM) and the FM to DM conversion ratio. The dried material was then ground to a fine powder using a ball grinder, and a sub-sample was ashed at 440°C for 1 h and the Ash Free Dry Mass (AFDM) calculated. Ashed material was analyzed for tissue phosphorus using the methods of Planas *et al.* (1996) for phosphorus extraction, and Stainton *et al.* (1977) for soluble reactive phosphorus (SRP) measurement. Dried algal tissues were analyzed for tissue C and N using a CE-440 Elemental Analyzer (EAI).

Nearshore water samples were collected at each

site 1 m above the *Cladophora* bed using a Van Dorn sampler or while SCUBA diving and swimming up current from the sampling location (to minimize the potential for re-suspended material being collected in sample). The north shore 10-m bathymetry contour is typically 1.5 to 5.0 km from shore. Temperature was logged at each site, 0.1 m above the lake bottom, using HOBO tidbit temperature loggers (Onset Corporation) at 30 min discrete intervals for the majority of the ice-free season. Light extinction coefficients (kPAR) were calculated directly from profiles using a LICOR flat plate collector (Wetzel and Likens 1979), or from transmissometer deployments (during non-daylight hours) and a derived relationship between light extinction coefficients and transmissivity. "Offshore" Eplimnetic water samples were collected at multiple stations, ranging from 11 m to 65 m lake depth, throughout the eastern basin from the CSS *Limnos*. Soluble reactive phosphorus (SRP) and total phosphorus from unfiltered samples (TP) were sampled using the protocols of Charlton *et al.* (1999) and analyzed by the National Laboratory for Environmental Testing (NLET) at the National Waters Resource Institute (Environment Canada 1979).

Digitized bathymetric maps of Lake Erie (NOAA 1998) and bottom substratum composition (Rukavina and St. Jacques 1971, St. Jacques and Rukavina 1973) were used to calculate the area of rocky lake bottom within the 0–10 m contours of the eastern basin's northern shoreline. These maps were also used to calculate the volume of overlying water in the 0–10 m depth zone (north shore only), and the 11–67 m depth zone (offshore). In the offshore zone the upper 20 m of the water column was used for subsequent calculations of nutrient budgets for the epilimnion.

RESULTS

Physical and Chemical Environment

The northern shoreline of Lake Erie's eastern basin is dominated by bedrock (~80%), with smaller areas of glacial till and sand (Rukavina and St. Jacques 1971, St. Jacques and Rukavina 1973). All sites were located on rocky lake bottoms and shallow depths (0.5–10 m) (Table 1). The near shore rocky lake bottoms are typically large, flat expanses of limestone of low slope interspersed with smaller areas of cobbles and boulders. These shallow (≤ 10 m) rocky lake bottoms in the eastern basin currently have mean densities of *D. bugensis* between 4,000–11,000 ind/m² (Patterson *et al.*

2005). *Cladophora* typically grew attached to either rocky surfaces or living mussel shells, and was absent in small patches where the accumulation of sediment or dead shell material precluded their attachment to a hard, stable surface.

The northern shoreline of Lake Erie's eastern basin is a highly dynamic environment. The predominant winds are from the southwest with a resulting fetch exceeding 80 km. South-westerly winds of 10–15 km/h with corresponding 1–2 m waves are common, 15–25 km/h winds are not unusual, and physical forcing processes result in the re-suspension of organic and inorganic particles and a reduction in light penetration. As such, variability in light extinction coefficients (kPAR) increases at shallower depths due to increased potential for sediment resuspension (Fig. 2). Secchi depth readings were highly correlated to kPAR (Fig. 3). Seasonal epibenthic water temperatures fluctuated from near 0°C (winter) to approximately 25°C in August, then began declining in September (Fig. 4).

Mean SRP concentrations in north shore and offshore waters were high in spring (6–8 µg/L), and declined to seasonal low values (below the 0.2 µg/L

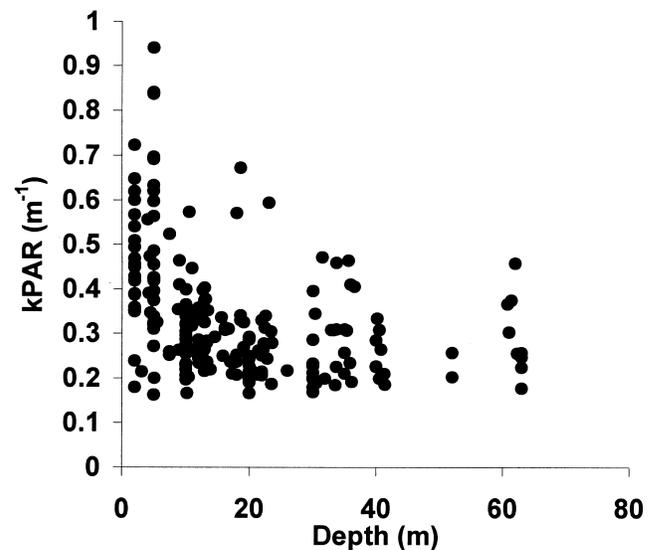


FIG. 2. Variability in light extinction coefficients (kPAR) with station depth. All measurements were conducted in situ during 2001–2002 (May–November) in the eastern basin of Lake Erie. The majority of near shore measurements (< 10 m lake depth) are from the Peacock Point to Hoover Point reach of shoreline, while offshore measurements (≥ 10 m lake depth) were made at numerous sites throughout the basin.

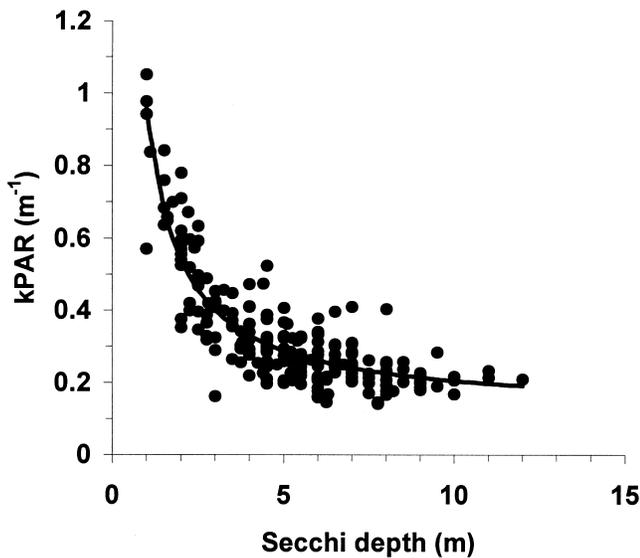


FIG. 3. Extinction coefficients (kPAR) vs. secchi depth (m) measured in eastern Lake Erie during 2001–2003 ($kPAR = 0.12 + (0.84 * (Secchi)^{-1})$, $R^2 = 0.79$, Fit Standard Error = 0.073, $n = 228$).

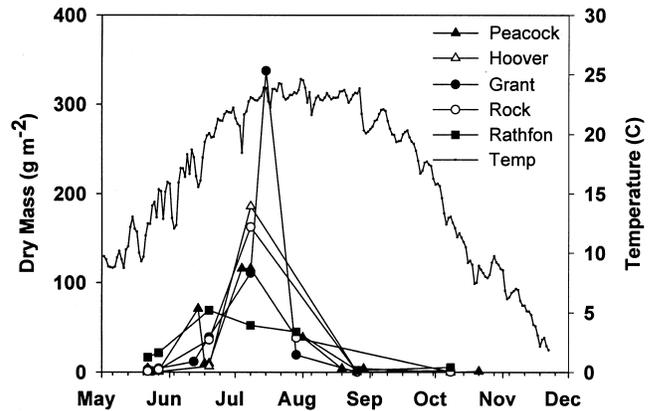


FIG. 4. Seasonal changes in water temperature and *Cladophora* biomass at five sites in the eastern basin of Lake Erie during 2002. All sites were at 2 m depth. At peak biomass the standard error ranged from 6–42% of the mean biomass at each site. Reported daily mean temperatures were recorded using in situ Tidbit© temperature loggers at 0.25 m from the lake bottom and averaged among the five sites.

limit of detection) in September, then increased in the autumn (~3 µg/L)(Table 2). The north shore depth zone (0-10 m), and the epilimnion of the offshore zone (11-67 m), have water volumes of 1.3 km³ and 94 km³ respectively. Total SRP ranged from 0.25 to 7.8 tonnes P in the north shore waters, and 18 to 700 tonnes in the offshore waters (Table 2). Mean TP, from unfiltered samples, ranged from 7.4 to 12.5 µg/L in the north shore waters, and 7.0 to 13.6 µg/L

in offshore waters. Total TP ranged from 9.3 to 15.8 tonnes in the north shore waters, and from 650 to 1,300 tonnes in offshore waters (Table 2).

Cladophora Distribution and Bed Characteristics

Seasonally, the areal coverage of *Cladophora* achieved its maximum by mid June to early July 2002 at sites of shallow depth (≤ 2 m). This maxi-

TABLE 2. Ambient phosphorus concentrations in north shore and offshore waters in the eastern basin of Lake Erie during 2002.

Month	n	North shore (0–10 m)						Offshore (11–65 m)						
		Mean SRP (ug/L)	sd	Total SRP Nshore (tonnes)	Mean TP (ug/L)	sd	Total TP Nshore (tonnes)	Mean SRP (ug/L)	sd	Total SRP Offshore (tonnes)	Mean TP (ug/L)	sd	Total TP Offshore (tonnes)	
Apr	11	6.21	2.89	7.83	12.5	1.55	15.8	18	7.59	2.02	701	13.6	1.23	1256
May	8	2.34†	0.75	2.94	10.46†	1.38	13.2	8	4.56†	2.57	421	12.31†	1.43	1137
Jun	11	1.70	0.98	2.14	9.1	1.90	11.4	16	1.36	0.65	125	9.7	2.19	896
Jul	11	1.20	0.30	1.51	7.4	2.37	9.3	16	1.19	0.69	110	7.0	2.08	647
Aug	3	0.93	0.12	1.18	9.7	3.59	12.2	4	1.28	0.25	118	8.9	1.16	823
Sept	10	nd	n/a	0.25	9.8	4.16	12.3	15	nd	n/a	18	9.1	2.14	844
Oct	9	2.82	1.29	3.55	10.7	2.47	13.5	13	2.96	1.68	274	10.2	0.86	944

Note: “n” refers to the number of stations sampled and averaged. “nd” refers to samples at or below the limit of detection of 0.2 µg/L. For Sept. dates total SRP was calculated using the 0.2 µg/L detection limit. † refers to a significant difference between nearshore and offshore SRP or TP concentration assessed using a two sample student T test (p < 0.05).

imum areal coverage was maintained until the mid-summer die-off period (between the 15 July and 29 July sampling dates) when areal coverage began to decline. By 26 August, areal coverage had declined from nearly 100% at most sites to 2–5%, then increased once again at most sites by September. Combining our 1995, 2001, and 2002 data, *Cladophora* had a median areal coverage estimate of 95% at our rocky near shore sites during the peak-growing season (data from Table 1). Some sites, particularly those in shallow zones (≤ 2 m) on the west sides of peninsulas (sites 26 and 28 in Table 1), had reduced areal coverage. Our sampling design did not allow us to empirically determine the causes of this phenomenon, however we hypothesize that algal coverage in these shallow westerly facing littoral zones may be lower due to the prevalent southwesterly winds that increase turbulence and sloughing. At depths 2 m or greater we saw no effects of water turbulence on early summer coverage patterns, although we noted qualitatively that areal coverage less than 100% occurred primarily where small (cm^2) or large (m^2) patches of previously sedimented material (including shells of dead *Dreissena*) on the lake bottom that prevented the attachment of filaments. Areal coverage at most of the 5 and 10 m sites was at or near 100% by early summer (Table 1).

The maximum filament lengths at all sites during 2002 followed a similar pattern to coverage, increasing throughout the spring until the end of July, when much of the algal material had been sloughed. *Cladophora* at 2-m sites achieved maximum filament lengths of approximately 30–35 cm by mid July 2002 (data not shown). After the sloughing period, *Cladophora* at some sites showed increasing filament lengths in the autumn, although little biomass accumulated during that time (Fig. 4). Maximum filament lengths declined greatly with increasing depth beyond 2 m, such that at 10 m only 0.5–2 cm filaments were present at our sites. The median height of the *Cladophora* bed from the lake bottom was 8.0 cm at depths ≤ 2 m during the peak-growing season (Table 1).

Areal Biomass

Seasonally, biomass at most of our 2-m sites (2002) increased slowly until late June, then rapidly until mid July (Fig. 4). These sites showed a range of seasonal maximum biomass from 78 g DM/m² at Rathfon Point to 337 g DM/m² at Grant Point (Fig. 4). Biomass declined dramatically after daily aver-

aged water temperatures reached 22.5°C (Fig. 4), and by 29 July all sites had biomass values < 50 g DM/m². The importance of short sampling intervals is highlighted by our increased sampling effort at the Grant Point site. The *Cladophora* biomass at Grant Point tripled within 7 days in mid July to reach a maximum value of 340 g DM/m² (Fig. 4). Because other sites were not sampled as frequently, we likely did not observe the maximum biomass present at these sites, and biomass values presented in Table 1 possibly under-represent true seasonal maximum values. The midsummer sloughing event began between 15 July and 29 July as water temperatures approached 22.5°C. By the end of July areal biomass was reduced to levels < 45 g DM/m² and had decreased even further to < 2 g DM/m² by September (Fig. 4). Although filament length increased during the autumn, there was only a small increase in biomass (Fig. 4) because of low areal coverage. Highest biomass levels were reported from the Featherstone to Grant Point (site-date #'s 13–16), Morgans Point (#29–30), and Whitemans Point (#35) shorelines (Table 1). Overall, 21 of the 32 shallow water site-date combinations had biomass values over 100 g DM/m² by midsummer, and 13 of these sites had over 300 g DM/m² (Table 1). *Cladophora* biomass declined with increasing depth and, although coverage was often high, very little biomass existed at 10 m at any of the sites during the season (Table 3). The mean seasonal peak biomass for each depth stratum (Table 3) was highly correlated with estimates of daily mean PAR reaching each depth (Fig. 5). PAR values at depth were calculated using surface irradiance values generated for 1 July 2002, which was approximately the mid-point during the peak growing period (Fig. 4), under cloudless conditions (Fee 1990), and a negative linear relationship between light extinction and station depth from 0–12 m (Fig. 2).

Tissue Phosphorus, Tissue Nitrogen, and Potential Growth

Seasonally, tissue phosphorus concentrations were high during the spring (0.20–0.35 % DM), and then decreased as the biomass increased until the midsummer die-off event. (Fig. 6a). Following the midsummer die-off event, tissue phosphorus concentrations increased to 0.16–0.25% DM, and then declined to 0.10–0.16% DM by mid-August. The exception to this general trend at our seasonal sites was Rock Point, a site that is adjacent to the outlet of the Grand River and is often enriched by its high

TABLE 3. The depth distribution, biomass, and algal bed characteristics of *Cladophora* during the peak growth period in the eastern basin of Lake Erie during 2001–2002. “n” refers to the number of stations where *Cladophora* parameters were sampled and averaged. n/s refers to “no sample” available for analysis.

Depth (m)	n	Areal cover (%)	Median Bed ht (cm)	Biomass (g DW/m ²)					%N	%P
				Max	Min	Mean	Median	Std dev		
0.5	12	62	8.2	939.2	<1	196.1	113.9	268.4	n/s	n/s
1	12	94	9.2	780.8	<1	175.3	70.6	230.8	1.9	0.063
1.5	12	88	9.3	486.7	<1	138.5	69.6	156.3	n/s	n/s
2	15	100	10.3	341.7	52.8	146.4	122.8	83.7	2.5	0.070
5	6	96	7.4	111.1	25.4	54.4	53.8	34.4	2.1	0.129
10	5	73	2.9	4.7	0.5	1.9	0.5	2.4	3.1	0.230

nutrient and sediment-laden plume (T. Howell, Ontario Ministry of the Environment, unpublished data). *Cladophora* at Rock Point maintained high tissue phosphorus concentrations throughout the 2002 growing season, and exhibited the highest total areal phosphorus values of the five seasonal sites (Fig. 6b). At all seasonal sites other than Rock Point, tissue phosphorus declined to 0.05–0.1% DM (Fig. 6a) by early July. The low midsummer tissue phosphorus concentrations indicated by the sea-

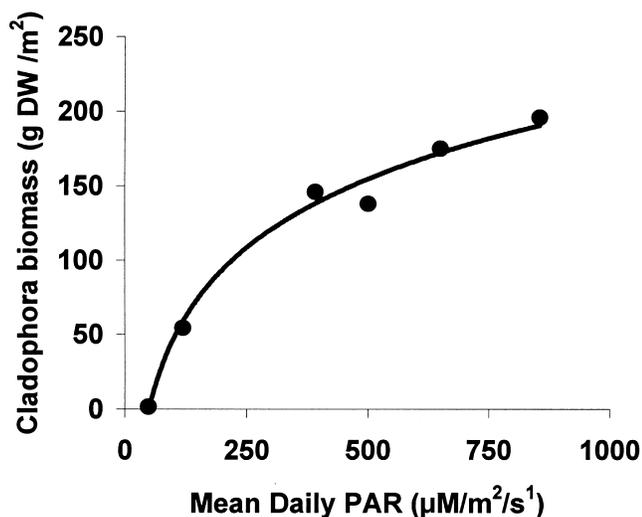


FIG. 5. *Cladophora* biomass in eastern Lake Erie as a function of mean daily PAR. *Cladophora* biomass values are mean values from Table 3. See text for calculations of mean daily PAR at depth. The regression *Cladophora* biomass and PAR ($\text{Biomass (g DW/m}^2) = 66.82 \ln(\text{Mean Daily PAR}) - 260.53$ ($R^2 = 0.99$, $n = 6$)) was fitted using the least squares method.

sonal surveys are similar to values reported in our larger mid-summer spatial dataset (Table 1). The mean midsummer tissue phosphorus concentration at shallow depths (1 m) was 0.06% DM, increasing to 0.23% DM at our deepest sites (10 m). Seasonally, tissue nitrogen concentrations did not follow a consistent pattern between sites (data not shown). However, tissue nitrogen concentrations were always in excess of the 1.1% critical concentration reported by Gerloff and Fitzgerald (1976). During the midsummer period when N limitation might be expected mean tissue nitrogen concentrations ranged from 1.9 to 3.1 % DM (Table 3).

The relationship between tissue phosphorus and specific growth of Lake Huron strains of *Cladophora* has been determined under laboratory conditions, and maximal rates are approximately 0.77/day (Auer and Canale 1982). The Droop equation has been used to model specific growth as a function tissue phosphorus concentration (Auer and Canale 1982), and the resulting curve has an inflection point at a tissue phosphorus value near 0.10% DM. Therefore, at tissue phosphorus concentrations below 0.10% DM the model predicts that specific growth becomes increasingly sensitive to small shifts in internal phosphorus stores. Wong and Clark (1976) indicate that phosphorus-limited growth begins below 0.16% DM. The critical concentration of tissue phosphorus required for positive growth is 0.06% DM (Gerloff and Fitzgerald 1976, Auer and Canale 1982). Using this approach of relating tissue phosphorus concentrations to potential growth, we considered tissue phosphorus concentrations below 0.06% DM to be “critically” phosphorus limited, concentrations between 0.06–0.10% DM to be “severely” phosphorus limited, concentrations between 0.10–0.16% DM to be

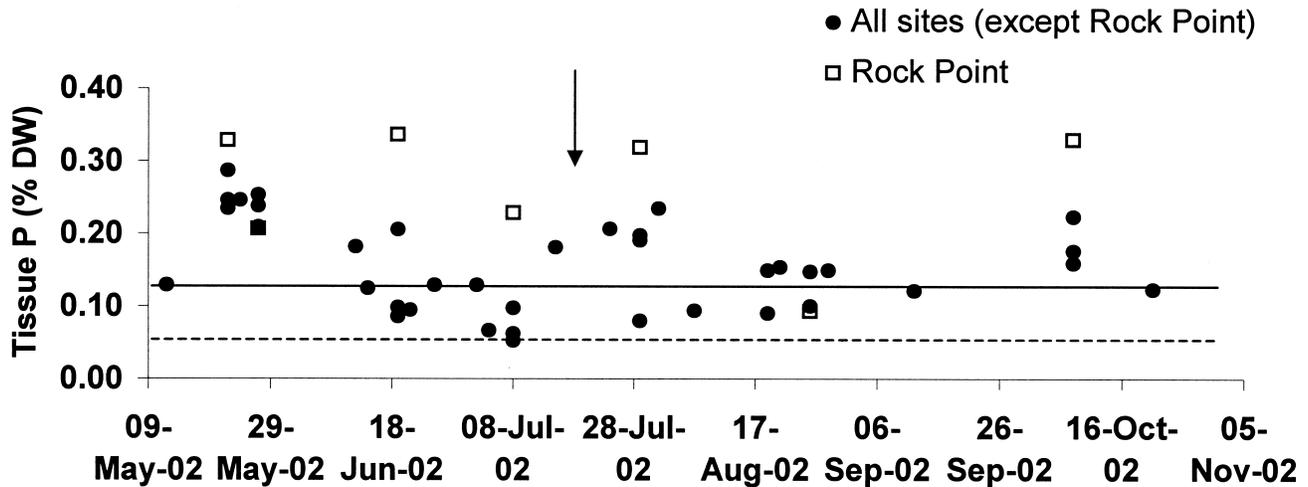


FIG. 6a. Seasonal changes in internal P concentrations in Cladophora tissues measured at 5 shallow (2 m) sites in the eastern basin of Lake Erie during 2002. The Rock Point site is located adjacent to the outlet of the Grand River and is considered to be enriched site (see text). The arrow indicates the approximate date when the major sloughing, or “die-off,” period began. The upper solid line represents the tissue P concentration (0.16% DW) where P limitation of growth begins (Wong and Clark 1976). The lower dashed line represents the tissue P concentration (0.10% DW) where severe P limitation is expected (see text).

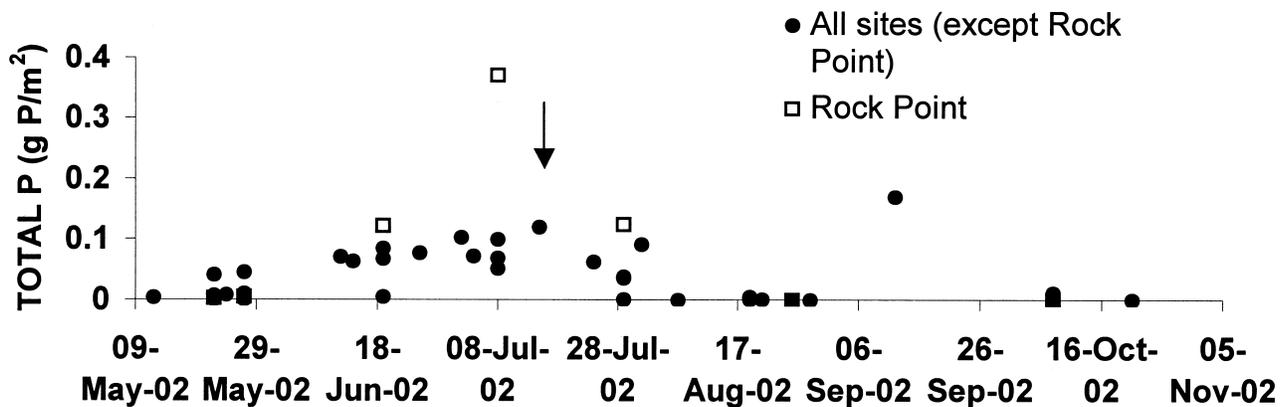


FIG. 6b. Seasonal changes in areal P of Cladophora tissues at five shallow (2 m) sites in the eastern basin of Lake Erie during 2002. The Rock Point site is located adjacent to the outlet of the Grand River and is considered to be enriched (see text). The arrow indicates the approximate date when the major sloughing, or “die-off,” period began.

“moderately” phosphorus limited, and values exceeding 0.16% DM to be “non-phosphorus” limited. In general, our seasonal data show two distinct patterns: high tissue phosphorus concentrations in the spring where specific growth rates would not be strongly affected by internal phosphorus stores, and low midsummer tissue phosphorus concentrations where maximum potential growth rates would be

reduced and strongly affected by small shifts in internal phosphorus (Fig. 6a). At our seasonal sites “non-phosphorus” limited growth occurred in the early spring period prior to the onset of rapid growth, and immediately after the midsummer die-off event (Figs. 4, 6a). “Moderate” phosphorus-limitation occurred between 14 June 2002 and 4 July 2002, and growth was then considered “severely”

phosphorus limited until the midsummer die-off event that occurred between 20–29 July. “Moderate” phosphorus limitation persisted from early August to early October. *Cladophora* tissues from Rock Point did not follow the general trends outlined above and growth, with the exception of one date in late August, was non-phosphorus limited throughout the season (Fig. 6a).

We had tissue phosphorus data from 31 shallow water (≤ 2 m) sites sampled during mid-summer (Table 1). Twenty-eight of these sites had tissue phosphorus values below the 0.10% DM inflection point, indicating “severe” phosphorus limitation. The median specific growth rate from the overall mid-summer dataset (Table 1), as predicted from tissue phosphorus via the Droop model, is $0.11/\text{day}^1$. This value is only 14% of the maximum specific growth rate of $0.77/\text{day}^1$ (Auer and Canale 1982), and suggests that low tissue phosphorus concentrations can dramatically reduce the upper limit to growth during the midsummer period. Furthermore, *Cladophora* at 17 of these shallow (≤ 2 m) sites had tissue phosphorus concentrations below the “critical” value of 0.06% phosphorus (DM) and would not be expected to exhibit any positive growth during this midsummer period (Table 1). The only shallow (≤ 2 m) sites that did not show “severe” phosphorus limitation in the midsummer were Port Dover, Rock Point, and Long Beach. *Cladophora* tissues from deeper (5 and 10 m) sites indicated either “moderately” phosphorus limited or “non-phosphorus” limited growth.

DISCUSSION

Distribution

Perhaps the most obvious and important observation of our surveys is that dense stands of *Cladophora* are now a consistent feature across eastern Lake Erie’s northern shoreline. Our sites encompassed a wide geographical distribution, and for all years sampled (1995, 2001, 2002) areal coverage approached 100% in shallow (≤ 5 m) rocky zones by early summer. The spatial distribution of *Cladophora* was limited by the availability of hard substrata for attachment, and therefore dominated on exposed rocky peninsulas and shorelines rather than in depositional zones (deep embayments or sand beaches) where hard lake bottoms were overlain by eroded materials (Rukavina and St. Jacques 1971, St. Jacques and Rukavina 1973). In general, the sites that showed the least areal cover were either from very shallow depths (0.5 m) on shorelines

exposed to the predominant southwesterly winds where we expect that high turbulence and scour increased sloughing rates, or included deposits of unconsolidated material (sand, or empty *Dreissena* shells) that overlaid suitable substratum. In the 1–5 m depth zone it was rare to find suitable substratum that was not completely overgrown by early summer. The midsummer areal biomass (≤ 5 m) was highly variable among sites, with mean values near $100 \text{ g DM}/\text{m}^2$ (Table 3), and was almost always above $50 \text{ g DM}/\text{m}^2$ (Table 1). Maximum biomass, up to $940 \text{ g DM}/\text{m}^2$, was associated with the shallowest depth zone (Table 3), and may indicate localized nutrient enrichment. These biomass levels are similar to those in Lake Erie during the 1970s (Table 4) when *Cladophora* blooms were deemed a “serious problem” by the International Joint Commission (Shear and Konasewich 1975).

Phosphorus Limitation

Although a number of factors have contributed to the success and dominance of *Cladophora* in the Laurentian Great Lakes, the majority of studies conducted in the 1970s indicated that the high dissolved phosphorus concentrations had promoted high growth rates and bloom occurrences (e.g., Shear and Konasewich 1975, Gerloff and Fitzgerald 1976, Canale and Auer 1982, Lorenz and Henderdorf 1982, Neil and Jackson 1982). By the early 1980s the aggressive phosphorus abatement strategies initiated in the 1970s had significantly reduced phosphorus loading and offshore total phosphorus concentrations in the lower Great Lakes (Dolan 1993, Charlton *et al.* 1999), and significant declines in both tissue phosphorus concentrations and areal biomass of *Cladophora* were noted in Lake Ontario (Painter and Kamaitis 1987). Although there is a lack of published studies on *Cladophora* from the other lower Great Lakes, presumably tissue phosphorus and biomass of *Cladophora* declined in these systems as well. However, as early as 1995 (our initial survey) *Cladophora* had once again reached nuisance levels in Lake Erie. *Cladophora* blooms and shoreline fouling have recently been noted in Lake Ontario (S. Malkin, University of Waterloo, unpublished data), Lake Michigan (Byapanahalli *et al.* 2003), and localized shorelines of Lake Huron (T. Howell, Ontario Ministry of the Environment, unpublished data). Despite the large reductions in phosphorus loadings and concentrations it is troubling to note that large stands of *Cladophora* are currently widespread in the lower

TABLE 4. Peak seasonal biomass in Lake Erie 1967–2002 (0–3 m depths). Maximum, minimum, and median values are from *n* number of sites indicated within the study. References are as follows 1. Mantai et al. 1982, 2. Neil and Jackson 1982, 3. Kishler in Taft 1975, 4. Lorenz and Herdendorf 1982, and 5. Monaco 1985.

Location	Year	n	Biomass (g DW/m ²)				Reference
			Max	Min	Median	Std Dev	
L. Erie (east basin)	1977	1	420	420	420	n/a	1
	1979	11	983	4	65	300	2
	1995	58	781	24	280	165	This study
	2001	4	307	28	117	118	This study
	2002	42	939	0	84	205	This study
L. Erie (west basin)	1967	15	268	55	111	58	3
	1979	2	102	100	101	1	4
	1980	2	214	184	199	21	4
	1982	14	235	15	63	60	5

Great Lakes, especially in oligotrophic systems such as the eastern basin of Lake Erie. Although a significant modeling effort is ongoing to discern which variables were most important to growth, and the relevance of *Dreissena* to the “resurgence” of *Cladophora*, our present data indicate that increases in spring soluble phosphorus concentrations and shifts in water clarity may be largely responsible for the overall increase biomass post *Dreissena*.

The widespread nature of dense *Cladophora* stands (> 50 g DM/m²) across our sites indicates that phosphorus concentrations in the north shore waters (Table 2) were sufficient to produce bloom occurrences. Furthermore, the majority of tissue phosphorus was accumulated by mid-June (Fig. 6b), prior to the rapid growth phase that began in mid-June and continued to early July (Fig. 4), indicating that spring and early summer phosphorus concentrations were most important to growth. With only a few exceptions, tissue phosphorus concentrations were drawn down to extremely low values by early summer (Table 1, Fig. 6a) at all our shallow sites (≤ 2 m). These tissue phosphorus values were generally well below the 0.16% DM value where growth becomes increasingly sensitive to internal phosphorus stores (Planas et al. 1996), and often close to the critical 0.06% DM value required for positive growth. Such low tissue phosphorus concentrations indicate that growth likely became strongly phosphorus-limited as stands approached peak biomass.

Light Limitation

While *Cladophora* at shallow water sites showed signs of phosphorus limitation by early summer,

those at depths of 5 m or greater maintained high tissue phosphorus concentrations, and had lower areal biomass, indicating that other factors potentially controlled growth at these deeper depths. The potential for photosynthetically active radiation (PAR) to limit growth and accumulated biomass was investigated by assessing photosynthetic light response curves of *Cladophora* vs. estimates of available PAR *in situ* in the same fashion as Lorenz et al. (1991). The photosynthetic response to light in *Cladophora*, as with other algae, follows a hyperbolic (or similar) response to increasing irradiance (e.g., Graham et al. 1982). At low light levels, growth is directly proportional to PAR and growth is considered light limited. As PAR increases past the inflection point (I_k) of the photosynthesis vs. PAR curve, photosynthesis becomes light saturated and increasing PAR has little positive effect on growth rates. Because PAR declines exponentially with depth, the degree to which can be determined from measured PAR extinction coefficients (kPAR), at some depth photosynthetic rates are linearly dependent on available PAR and are termed light limited. The depth (Z_{lim}) where light limitation of *Cladophora* will occur can be estimated using the equation:

$$Z_{lim} = (\ln I_0 - \ln I_k) / kPAR$$

where I_0 is the mean surface irradiance during daylight hours, I_k is the inflection point of the photosynthesis vs. PAR curve, and kPAR is the extinction coefficient of PAR through the water column. Due to the high variability in kPAR along the north

shore of Lake Erie (Fig. 2), we chose to estimate Z_{lim} over a range of kPAR values that encompassed most of the variability noted *in situ* (0.2–0.6/m), and a mean surface irradiance (I_0) of 807 $\mu\text{E}/\text{m}^2/\text{s}$ determined by Lorenz *et al.* (1991) for 39 cloud-free days (April–November) over western Lake Erie. I_k values for naturally growing *Cladophora* at our seasonal sites had a mean value of 205 $\mu\text{E}/\text{m}^2/\text{s}$ ($n = 35$, $sd = 175$, Higgins unpublished data). These I_k values are below those determined by Graham *et al.* (1982) for Lake Huron strains of *Cladophora*, where I_k values were approximately 300 $\mu\text{E}/\text{m}^2/\text{s}$. Using our estimate of I_k , we estimate Z_{lim} to be 6.9 m, 3.4 m, and 2.3 m at kPAR values of 0.2/m, 0.4/m, and 0.6/m respectively. Because *in situ* kPAR values are typically between 0.4–0.6/m (Fig. 2), the depth of Z_{lim} would generally be expected to fall between 2.3–3.4 m depth, below which growth rates would be light limited. Using the I_k value of Graham *et al.* (1982) Z_{lim} would fall between 1.6–2.5 m at kPAR values 0.4–0.6/m.

The seasonal peak biomass of *Cladophora* over depth (Table 3) was highly correlated to estimates of available PAR (Fig. 5), and allowed us to estimate: 1) the areal biomass of the *Cladophora* beds, and the total P contained within them, at depths other than those we directly sampled; and 2) how shifts in water clarity (i.e., kPAR) could affect the depth distribution and biomass of *Cladophora* across the northern shoreline (Table 5). Because sloughing (Canale *et al.* 1982) and potentially grazing by *Gammarus fasciatus* (R. Johnson, Dept. of Biology, University of Waterloo, unpublished data) can be significant loss terms and our estimates of areal phosphorus are based only on the standing crop and the amount of phosphorus contained therein, the estimates presented should be conservative. Overall, by early summer, the *Cladophora* beds along eastern Lake Erie's northern shoreline would have a total mass of approximately 12,000 tonnes by dry mass (Table 5). This biomass of *Cladophora* would have contained approximately 15 tonnes of phosphorus, most of which would have been removed from the water over a 31 d period (12 May 2002–12 June 2002, Fig. 6b) at a mean rate of 0.49 tonnes/day. The mass removal rate of SRP by *Cladophora* (8 tonnes) during May exceeds the nearshore decline in SRP (6 tonnes) during this period, and is likely an important factor in causing the large SRP gradient between nearshore and offshore (Table 2, Student T-test, $p = 0.03$). The amount of SRP contained within the north shore water mass, however, would have been

insufficient to maintain the P demand by *Cladophora* over the 30-d period, and additional phosphorus from underlying *Dreissena* beds, from surface runoff, or from the offshore water mass would be required. By June however, both nearshore and offshore water masses had low SRP concentrations ($< 2 \mu\text{g}/\text{L}$) that were not significantly different from one another (Table 2, student T-test, $p = 0.28$). It is during this period (June to July) when *Cladophora* tissue phosphorus concentrations declined rapidly to values considered “severely limiting” to growth (Fig. 6a).

The invasion and proliferation of *Dreissena* within the Laurentian Great Lakes has resulted in environmental conditions that are conducive to the growth of *Cladophora*. In the somewhat isolated bays of Lakes Huron, Ontario, and Erie, where water quality parameters were studied intensively pre- and post-*Dreissena* colonization, large increases in water clarity and ambient phosphorus were noted. For example, declines in kPAR over *Dreissena* invasion were approximately 0.3/m in western Lake Erie (Holland 1993) and between 0.4–0.8/m in Saginaw Bay of Lake Huron (Fig. 9b in Fahnenstiel *et al.* 1995). In the north shore waters of eastern Lake Erie, where current mean mussel densities are 4×10^3 to 11×10^3 ind./ m^2 (Patterson *et al.* 2005), we calculated a decline in kPAR of 0.08/m over the invasion period based on the increase in secchi depth (4–6 m) noted by Howell *et al.* (1996) and the relationship between secchi depth and kPAR (Fig. 3). Howell *et al.*'s (1996) measured increases in water transparency should be conservative since they were taken at a 10 m index station, and *Dreissena* should have a larger effect on water clarity at shallower depths with a reduced overlying water column.

The relationship between *Cladophora* biomass and available PAR (Fig. 5):

$$\text{Peak Biomass} = 66.82 \text{ Ln} (\text{Mean daily PAR}) - 260.53 \\ (R^2 = 0.99, n = 6)$$

can be used to estimate how shifts in mean daily PAR would affect the seasonal peak biomass of *Cladophora* at different depths. Mean daily PAR at each depth is a function of daily mean surface irradiance, depth, and kPAR. To simplify our calculations, and negate the potential effect of different atmospheric conditions pre and post *Dreissena*, we considered surface irradiance under cloudless conditions, using a constant value pre and post *Dreissena*. kPAR values for each depth were calculated

TABLE 5. *The biomass and P content of Cladophora glomerata along the northern shoreline of Lake Erie's eastern basin pre- and post-Dreissena colonization. Pre-mussel conditions were assumed to represent an increase in mean kPAR by 0.08/m from current, post-mussel conditions (see text).*

Depth strata (m)	Total Area (km ²)	Bedrock Area (km ²)	Est Kd		Est Kd		Estimated Biomass (tonnes/N shore)			Estimated Phosphorus (tonnes/N shore)			Difference as % of total
			Pre-Mussels	Post-Mussels	Pre-Mussels	Post-Mussels	Pre-Mussels	Post-Mussels	Difference	Pre-Mussels	Post-Mussels	Difference	
0-1	20.3	18.0	0.64	0.56	3,381	3,429	48	1.8	2.70	2.74	0.04	0.8	
1-2	13.2	13.0	0.62	0.54	1,907	2,011	104	4.0	1.53	1.61	0.08	1.7	
2-3	16.7	15.0	0.59	0.51	1,638	1,839	200	7.6	1.59	1.78	0.19	3.9	
3-4	20.0	16.0	0.56	0.48	1,207	1,506	299	11.4	1.85	2.31	0.46	9.2	
4-5	23.8	18.0	0.53	0.45	815	1,248	433	16.4	1.71	2.62	0.91	18.2	
5-6	25.9	18.0	0.51	0.43	339	868	529	20.1	0.72	1.84	1.12	22.4	
6-7	25.4	18.0	0.48	0.40	0	554	554	21.0	0.00	1.19	1.19	23.7	
7-8	22.3	19.5	0.45	0.37	0	332	332	12.6	0.00	0.72	0.72	14.3	
8-9	26.5	19.3	0.42	0.34	0	134	134	5.1	0.00	0.29	0.29	5.8	
9-10	32.7	19.2	0.40	0.32	0	2	2	0.1	0.00	0.00	0.00	0.0	
Total	226.8	174.0			9,287	11,924	2,637		10.10	15.10	5.00		

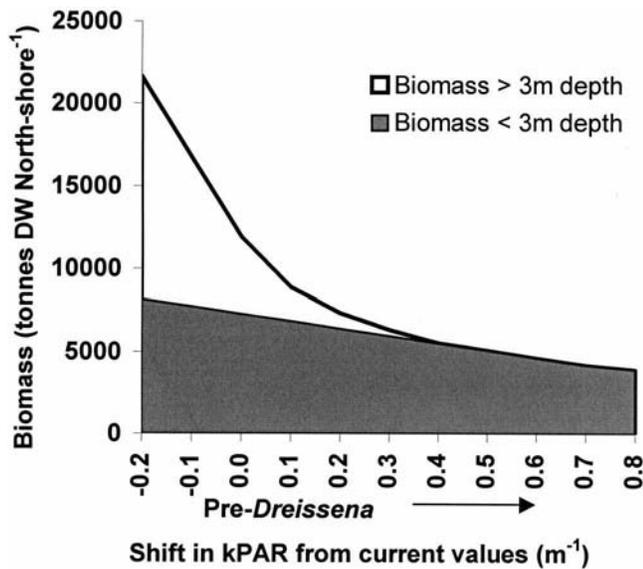


FIG. 7. Dependence of maximum standing *Cladophora* biomass along eastern Lake Erie's northern shoreline on deviation of mean kPAR from current conditions. Current kPAR values (0) are depth dependent and are presented in Figure 2.

from the relationship between kPAR and water depth (Fig. 2) and then increased by 0.08/m to represent pre-*Dreissena* conditions. Because this approach is based solely on shifts in water transparency, it would not be expected to provide accurate predictions of how *Cladophora* biomass would change where light does not limit growth (i.e., above I_k or approximately 3 m). Previous studies on Lake Erie (see Table 4 for references) limited their surveys to ≤ 3 m and our model suggests that, based on an increase in kPAR of 0.08/m from current conditions, depths > 3 m would have contained 25% of the depth integrated biomass pre-*Dreissena* (Table 5). Our surveys indicate that *Cladophora* below 3 m now contributes approximately 40% of the depth-integrated biomass (Table 5). Furthermore, when we modeled depth-integrated biomass by shifting kPAR over a range conditions seen in other systems, we noted that although biomass at depths < 3 m were not strongly affected (light saturated under most likely scenarios), biomass at depths > 3 m was strongly influenced by shifts in kPAR equal to that caused by *Dreissena* in Lake Erie and other systems (Fig. 7).

Management Implications

Increases in overall water clarity and spring concentrations of SRP attributed to *Dreissena* (Howell et al. 1996, Makarewicz et al. 2000) have undoubtedly increased the habitat and overall biomass of *Cladophora* in eastern Lake Erie. Increases in benthic algal production post-*Dreissena* were also noted in Saginaw Bay of Lake Huron (Lowe and Pillsbury 1995). Unfortunately, our assessment of *Cladophora* in the western and central basins of Lake Erie is hampered by a lack of data on biomass and distribution. *Cladophora* blooms were a serious problem in the western basin of Lake Erie from the late 1960s to the early 1980s (Table 4), however we expect that these blooms subsided in the 1980s, as was the case in Lake Ontario (Painter and Kamaitis 1987), as SRP concentrations were reduced through phosphorus abatement. Increases in water clarity (Holland 1993) and SRP (Makarewicz et al. 2000) in the western basin post-*Dreissena* would likely have a similar positive effect on *Cladophora* distribution and biomass as noted in the eastern basin.

Previous *Cladophora* surveys in Lake Erie during the late 1970s restricted their observations to depths ≤ 3 m, and our current estimates of biomass within this depth range are similar (Table 4). During the 1970s and early 1980s, as management strategies were being designed to control *Cladophora* biomass, there was no reason to expect increases in nearshore water clarity. While our data indicate that phosphorus remains the key nutrient controlling bloom occurrences, the increases in water clarity due to *Dreissena* have increased the overall habitat of *Cladophora*, which is now found growing at much deeper depths (Table 5). The potential for management of *Cladophora* biomass will ultimately depend on controlling available phosphorus during the spring and early summer. While *Dreissena* have likely increased available phosphorus (to the benthos) through metabolic wastes, feces, and pseudo-feces production (Hecky et al. in press), the rapidly declining tissue phosphorus concentrations of *Cladophora* from May-July (Fig. 6a) indicate that phosphorus from *Dreissena* and the overlying water column was insufficient to overcome the growth dilution effect and maintain high growth rates during this time period. Other researchers (Makarewicz et al. 2000) have noted significant increases in spring SRP in all basins of Lake Erie post-*Dreissena* invasion. We hypothesize that mixing of nearshore waters with offshore waters during the early spring (April-May), when a large SRP gradient exists,

provides most of the phosphorus required by the *Cladophora* and is therefore critical to controlling biomass accrual. During the period of maximum growth (mid-June to mid-July) the offshore waters had low SRP concentrations (1.2–1.4 µg/L), and the SRP gradient that had existed between the near-shore and offshore waters during April and May had disappeared (Table 2). At most of the shallow water sites tissue phosphorus values are near the critical concentration required for positive growth by early summer (Table 1) suggesting that further reductions in dissolved P would reduce *Cladophora* biomass. Conversely, due to the increase in habitat and depth of light saturated growth, increases in local or basin-wide ambient P could accentuate the “*Cladophora* problem” even further.

The offshore zone of the eastern basin of Lake Erie is considered oligo-mesotrophic (Table 2, Wetzel 1983). However, the widely distributed nearshore blooms of *Cladophora* indicate that the northern coastal areas are experiencing severe eutrophication. The underlying causes of this eutrophication remain unclear, but appear linked to increased water clarity and bioavailability of phosphorus attributable to the dense communities of *Dreissena*. The implications of the *Cladophora* blooms, and their subsequent die-off and decomposition, are wide ranging and include those discussed for years prior to phosphorus abatement. Also highly important, although largely unknown, are the implications of these widespread blooms to nutrient cycling, and the density and diversity of nearshore food web members; and the implications of the die-off, transport, and decomposition of the large amounts of organic material to rates of hypolimnetic oxygen consumption, the deep water anoxia phenomena noted in the central basin of Lake Erie, and the use of *Escherichia coli* as an indicator of fecal bacteria in locations where *Cladophora* accumulates on shorelines (Byappanahalli *et al.* 2003).

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