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Phytoplankton trends in the Great Lakes, 2001–2011

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ABSTRACT

We describe recent trends in phytoplankton composition and abundance in the Laurentian Great Lakes using synoptic spring (April) and summer (August) sampling events from 2001 through 2011, a period of rapid shifts in pelagic food webs and water quality. Data analysis identified qualitative and quantitative changes in algal densities, biovolume, and taxonomic composition of assemblages. Since 2001, Lake Superior has changed subtly with an increase in small-celled blue-green algae in spring and a recent decline in summer centric diatoms, possibly a result of lake warming and changes in water quality. Spring phytoplankton declines mainly attributed to diatoms occurred in Lakes Huron and Michigan, a probable result of invasions by non-native dreissenids that have reduced pelagic nutrients and selectively consumed certain taxa. The decline in Lake Huron's spring phytoplankton biovolume was earlier and more severe than that in Lake Michigan, despite a faster and more abundant dreissenid invasion in Lake Michigan. Lake Erie's central basin had a notable increase in spring centric diatoms (largely *Aulacoseira*), while the whole of Lake Erie shows a summer increase in cyanobacteria, complementing that found in coastal regions. The composition of Lake Ontario's species assemblage shifted, but little overall change in algal abundance was observed with the exception of higher summer densities of cyanophytes. Additional mechanisms for shifts in the pelagic primary producers are described or hypothesized in the context of concurrent shifts in water quality and invertebrate populations. Tracking these trends and explaining driving factors will be critical to the management of lake conditions.

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Introduction

Recent observations from the pelagic Laurentian Great Lakes have revealed rapid qualitative and quantitative changes in lake biology and water quality. Some of these rapid shifts include increases in chloride (all lakes; Chapra et al., 2009), declines (Lakes Huron and Michigan; Barbiero et al., 2011a) and blooms (uniquely in Lake Erie; Twiss et al., 2012) of phytoplankton, rapid propagation of non-native mussels (e.g. Lake Michigan; Nalepa et al., 2009), declines in zooplankton populations (e.g. Lake Huron; Barbiero et al., 2009), and changes in fish populations (e.g. Lake Huron; Schaeffer et al., 2006). In some cases these changes have apparent causation, such as the probable links between proliferation of profundal quagga mussels and the decline in spring phytoplankton (Vanderploeg et al., 2010) and zooplankton (Vanderploeg et al., 2012) populations in Lake Michigan. The unprecedented oligotrophication of Lakes Huron and Michigan has resulted in a convergence of the lower food webs of those lakes with Lake Superior (Barbiero et al., 2012). Lake Erie is experiencing increasing algal biovolume, and blooms of the blue-green alga *Microcystis* (Millie et al., 2009) and the diatom *Aulacoseira* (Twiss et al., 2012) in the lake are under study. No major shifts in algal abundance were observed in oligotrophic Lake Superior within a few decades prior to the 2000s (Barbiero and Tuchman, 2001), but the known warming of the atmosphere and lake (Austin and Colman, 2007) may be affecting the food web. Lake Ontario experienced a significant decline in phytoplankton biomass from the 1970s through the 1990s due to nutrient reductions and filtration by dreissenids (e.g. Millard et al., 2003), and a significant drop in the abundance of the invertebrate *Diporeia* (Lozano et al., 2001) in the late 1990s. In the last decade, any effects of continuing food web changes on Lake Ontario phytoplankton are poorly known. In many cases throughout the Great Lakes, linkages between human activities and these ecological shifts need resolution.

Anthropogenic activities often cause changes in phytoplankton abundance and community composition. For example, pelagic phytoplankton data from Lake Michigan were used to track shifts in algal abundance resulting from the mussel invasion (Fahnenstiel et al., 2010), but there has been no recent, comprehensive assessment of phytoplankton across the Great Lakes basin, and there has been little use of taxonomic information to provide potentially more refined reconstructions of community dynamics. Taxonomic details have provided robust

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environmental information, such as the increasing power of diatom–nutrient predictive models when refining from sub-division to species resolution (Rimet and Bouchez, 2012). Details of the phytoplankton assemblages and their temporal characteristics are particularly needed to monitor the impacts of human activities that are changing nutrient supplies, introducing non-native species, and altering climate. As a primary goal of the USEPA's biological monitoring program (USEPA, 2010), tracking long-term changes should be strongly supported by phytoplankton data because they are often the first group of organisms in the lower food web to respond to perturbations in pelagic ecosystems (Willen, 2000). Use of the latest biological collections may be beneficial in tracking changes and predicting trajectories of lake conditions for guiding management.

This study evaluated an 11-year record of algal assemblages in each of the Great Lakes. Major aims were to describe trends in biovolumes and cell densities and likely mechanisms for changes. Further, to clarify structural changes in the assemblages and possibly support mechanistic explanations, we evaluated changes in taxonomic composition of the phytoplankton over time using multivariate analyses. These analyses revealed lake-specific trends in pelagic primary producers; and where notable changes occurred, causes are described or suggested.

Materials and methods

We employed the most recently available 11 years of phytoplankton data collected as part of the Great Lakes monitoring program. The standard operating procedure for phytoplankton collection and analysis is described in detail in the published procedures (USEPA, 2010), but abbreviated details were as follows. The EPA data were based on twice-annual synoptic sampling ("spring" = typically the month of April, "summer" = typically the month of August) from standard stations throughout the Great Lakes basin (Fig. 1). Our analyses focused on samples collected from 2001 through 2011. Although additional data were available, data used in this report were analyzed by one team of taxonomists, and the data underwent identical quality assessment procedures for taxonomic and quantitative consistency. Some sampling stations had 11 years of data (the 14 "master stations") while all 72 stations had the most recent five years (2007 through 2011).

Whole water samples were collected from the rosette sampler onboard the Research Vessel Lake Guardian. Phytoplankton samples were composites of water sampled at discrete depths from the euphotic zone of the water column. For isothermal spring samples, the sample integrated equal volumes of water from 1, 5, 10, and 20 m. In shallower locations in Lake Erie, the 20-m sample was replaced by an above-bottom collection. If the total depth was less than 15 m, equal volumes were integrated from surface, mid-depth, and above-bottom samples. For the stratified (summer) water column, equal volumes were taken from 1 m, 5 m, 10 m, and the lower epilimnion and integrated. If the epilimnion was very shallow, equal volumes were integrated from a maximum of four and a minimum of two sampling depths. Samples were split and analyzed separately for the whole phytoplankton assemblage (i.e., "soft" algae) and diatoms. Analysis of soft algae used the quantitative Utermöhl method of counting preserved specimens in a settling chamber on an inverted microscope (Utermöhl, 1958). During soft algal analyses, diatoms containing cytoplasm were identified as centric or pennate forms. The second split sample was digested in nitric acid and subsequently in peroxide to isolate the diatom valves which were then plated on slides and counted using oil immersion (1000× or higher) to identify taxa. All counting included measurements of cell dimensions so that algal biovolumes could be calculated. Ultimately, analyses afforded detailed taxonomic resolution, and data were available in quantitative data formats [cell density (cells/ml) and biovolume (μm^3/ml)].

Because each lake has specific physical, chemical, and biological considerations, assessments were grouped according to nine major basins in the lakes: Superior, Michigan north, Michigan south, Huron north,

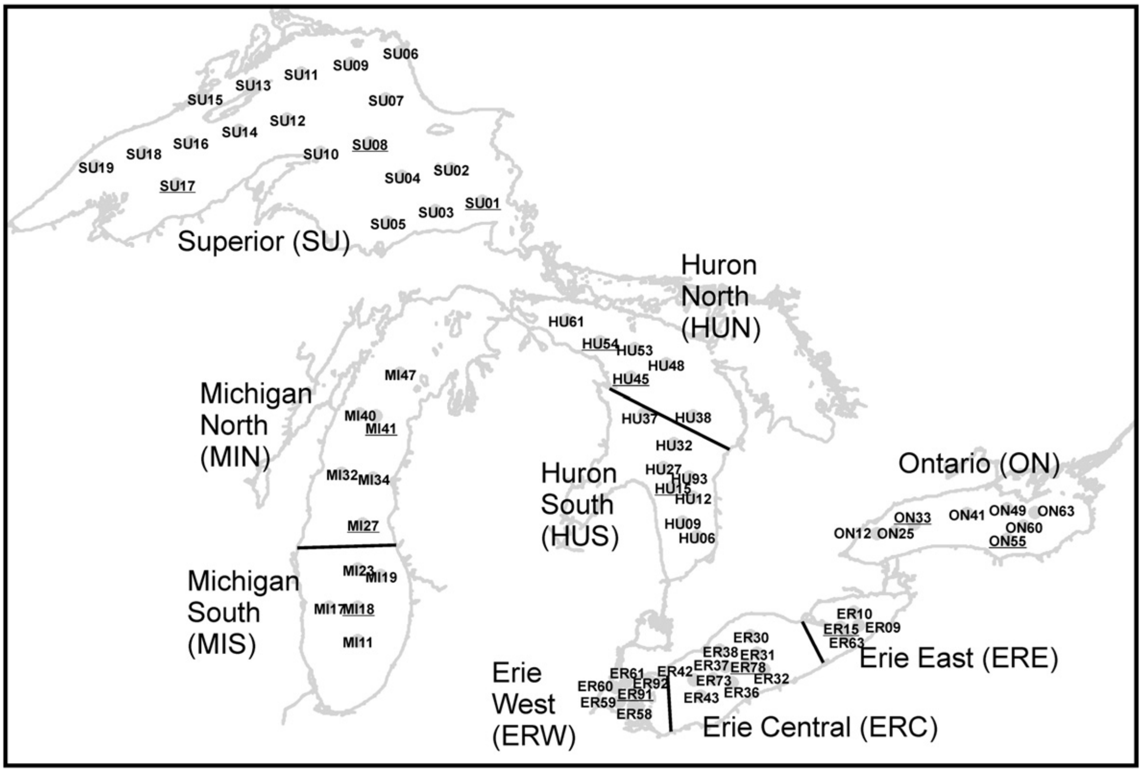

Fig. 1. Map of Great Lakes sample stations with master stations underlined. Lake regions within lakes used for data compilations are identified.

Table 1

Average lakewide spring biovolume (μm^3/mL) of dominant (more than 5% biomass at any site) phytoplankton taxa, 2007–2011. Numbered taxa have previously unpublished diagnostics. Taxon codes match those in NMDS figures. Taxon group codes are: BAC = centric diatoms, BAP = pennate diatoms, CHL = chlorophytes (green algae), CHR = chrysophytes, CRY = cryptophytes, CYA = cyanobacteria (blue-green algae), PYR = pyrrophytes (dinoflagellates), UNI = unidentified and unidentifiable entities.

DIV	Code	Taxon	Superior	Michigan	Huron	Erie	Ontario
BAC	ACYNORM	*Actinocyclus normanii* (Juhl.-Dannf.) Hust.	3756			11,334	
BAC	AULAMBI	*Aulacoseira ambigua* (Grun.) Simonsen	134	997	1030	12,793	91
BAC	AULDIST	*Aulacoseira distans* (Ehr.) Simonsen	92	741	348	2185	
BAC	AULGRAN	*Aulacoseira granulata* (Ehr.) Simonsen		86	405	16,930	
BAC	AULISLA	*Aulacoseira islandica* (O. Mull.) Simonsen	1069	6161	1365	1,645,148	5832
BAC	AULITAL	*Aulacoseira italica* (Ehr.) Simonsen	257	176		81,922	
BAC	CYCATOMF	*Cyclotella atomus* "fine form"	89	49	207	719	1929
BAC	CYCCOMES	*Cyclotella comensis* Grun.	474	121	3369	1142	288
BAC	CYCCOMRC	*Cyclotella comensis* "rough center with process"	469	253	1112	446	
BAC	CYCCOMT	*Cyclotella comta* (Ehr.) Kutz.	1996	531	6026		1291
BAC	CYCOCEL	*Cyclotella ocellata* Pant.	371	104	945	1712	164
BAC	CYCOPER	*Cyclotella operculata* (Ag.) Kutz.	68	28	904	625	81
BAC	CYCSP	*Cyclotella* spp.		35	1976	28,571	
BAC	STEALPI	*Stephanodiscus alpinus* Hust.	392	2525	3627	169,176	11,767
BAC	STEALP1	*Stephanodiscus alpinus* Type I Hust.	776	3401	2412	49,332	22,690
BAC	STEALP23	*Stephanodiscus alpinus* Type II/III Hust.	251	452	7876	70,353	6644
BAC	STEBIND	*Stephanodiscus binderanus* (Kutz.) Krieg.	58	214	234	54,266	1577
BAC	STEHANTH	*Stephanodiscus hantzschii* f. *hantzschii* Håk. & Stoerm.	6	1919	167	54,072	16,322
BAC	STEHANTT	*Stephanodiscus hantzschii* f. *tenuis* Håk. & Stoerm.	14	113	271	23,595	4309
BAC	STENIAG	*Stephanodiscus niagarae* Ehr.	1766	3784	21,977	84,621	598
BAC	STEPARV	*Stephanodiscus parvus* Stoerm. & Håk.	69	1542	86	50,584	40,636
BAC	STESP51	*Stephanodiscus* sp. 51	7	1511	81	4775	3753
BAC	STEPSBTR	*Stephanodiscus subtransylvanicus* Gasse	1091	1640	2639		
BAP	ASTFORM	*Asterionella formosa* Hass.	1152	4180	6818	13,722	4854
BAP	CYMSOLE	*Cymatopleura solea* (Breb. & Godey) W. Sm.	10,510	19,957	8126	130,411	6586
BAP	DIATENUE	*Diatoma tenue* var. *elongatum* Lyngb.	19	2140	146	26,963	1124
BAP	DIAVULG	*Diatoma vulgare* Bory.		459	600	7596	
BAP	FRACROT	*Fragilaria crotonensis* Kitton	223	4875	2530	6269	711
BAP	FRAPINN	*Fragilaria pinnata* Ehr.	53	26	229	1906	
BAP	GOMSP	*Gomphonema* spp.	54	206	53	1986	
BAP	GYRNODI	*Gyrosigma nodiferum* (Grun.) Reim.		712	5621	3976	
BAP	NAVTRIP	*Navicula tripunctata* (O.F. Mull.) Bory	350	1243	342	15,408	2527
BAP	NITACICS	*Nitzschia acicularis* W. Sm.	114	347	1634	2393	247
BAP	NITCLAU	*Nitzschia clausii* Hantz.				8795	
BAP	NITLAUE	*Nitzschia lauenburgiana* Hust.	444	2962	1061	9494	431
BAP	SUROVAL	*Surirella ovalis* Breb.			565	7218	
BAP	SUROVAT	*Surirella ovata* Kutz.		298	588	158,307	
BAP	SYNDELI	*Synedra delicatissima* W. Sm.		16,026	67		
BAP	SYNFILI	*Synedra filiformis* Grun.	225	465	2859	582	425
BAP	SYNOSTE	*Synedra ostenfeldii* (Krieg.) A. Cl.	556	888	1035	1726	352
BAP	SYNRADI	*Synedra radians* Kutz.	367	736	522	282	129
BAP	SYNULNAB	*Synedra ulna* var. *biceps* Kutz.	370	2322	226	2101	990
BAP	SYNULNAH	*Synedra ulna* var. *chaseana* Thomas	272	2602	534	188	1135
BAP	TABFLOC	*Tabellaria flocculosa* (Roth) Knud.	1007	699	994	9796	4979
CHL	ANKFALCM	*Ankistrodesmus falcatus* var. *mirabilis* (W. & G.S. West) G.S. West	34	855	94	308	
CHL	CHLSP	*Chlamydomonas* spp.	888	975	832	10,349	
CHL	CLOSPD	*Closterium* spp.	5685	1857			
CHL	COEMICR	*Coelastrum microporum* Nag. in A. Braun					14,185
CHL	COSPHAS	*Cosmarium phaseolus* Breb.	223		8134		
CHL	CRUQUAD	*Crucigenia quadrata* Morr.	440	107	46		
CHL	DICEHRE	*Dictyosphaerium ehrenbergianum* Nag.			3459		
CHL	GLOSPC	*Gloeocystis* spp.	581	2009	1616	1832	187
CHL	MOUSP	*Mougeotia* spp.	4277			16,054	
CHL	OOCBORG	*Oocystis borgei* Snow	751	442	483		377
CHL	OOCGIVIN	*Oocystis gigas* var. *incrassata* West & West sensu Skuja	3422				
CHL	PEDBORY	*Pediastrum boryanum* (Turp.) Menegh.				55,891	
CHL	PEDSIMP	*Pediastrum simplex* (Meyen) Lemm.				181,166	
CHL	PHASPE	*Phacus* spp.	839		2619	126,888	14,086
CHL	PLKSP	*Planktonema* spp.				6842	
CHL	SCESP	*Scenedesmus* spp.	60			12,417	
CHL	SLCELLI	*Sphaerellocystis ellipsoidea* Ettl			6710		
CHL	TRASP	*Trachelomonas* spp.				30,088	
CHR	CHMSPM	*Chromulina* spp.	587	758	1001	4018	1172
CHR	DINBAVA	*Dinobryon bavaricum* Imhof	674		2033		
CHR	DINCYLI	*Dinobryon cylindricum* Imhof	2331		5313	18,384	
CHR	DINSERT	*Dinobryon sertularia* Ehr.	4697		6018		
CHR	DINSOCI	*Dinobryon sociale* Ehr.	872		2199	12,033	
CHR	HAPSP	Haptophyceae	847	1571	2011	3681	1406
CHR	MALSP	*Mallomonas* spp.	867	1418	1800	28,356	4608
CHR	UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	2506	4126	4847	15,703	3860
CRY	CRYEROS	*Cryptomonas erosa* Ehr.	4055	6154	4111	15,108	8757
CRY	CRYPYRE	*Cryptomonas pyrenoidifera* Geitl.	2518	8081	3402	13,696	6217
CRY	CRYREFL	*Cryptomonas reflexa* Skuja	5445	9666	4226	14,336	12,290

Table 1 (*continued*)

DIV	Code	Taxon	Superior	Michigan	Huron	Erie	Ontario
CRY	CRYROST	*Cryptomonas rostratiformis* Skuja	5111	2760	15,625	12,203	12,500
CRY	UNICRYP	*Cryptomonas* spp.	2015	2435			
CRY	RHOLENS	*Rhodomonas lens* Pasch. & Rutt.	1766	6904	4461	5364	6400
CRY	RHOMINU	*Rhodomonas minuta* Skuja	1414	3292	2097	17,387	5470
CYA	ANBSP	*Anabaena* spp.			4575	2040	679
CYA	APHFLOS	*Aphanizomenon flos-aquae* (Lyngb.) Ralfs			174,081	16,036	
CYA	APASP	*Aphanocapsa* spp.	714	531	550	1183	341
CYA	APOSP	*Aphanothece* spp.	737	34	1649	364	
CYA	MICSPA	*Microcystis* spp.	2127				
CYA	OSCAGAR	*Oscillatoria agardhii* Gom.			3013	38,213	
CYA	OSCLIMN	*Oscillatoria limnetica* Lemm.	844	986	859	3491	1112
CYA	OSCMINI	*Oscillatoria minima* Gick.	387	1772	1190		1080
CYA	RHASP	*Rhabdoderma* spp.		13,417			7533
CYA	UNICOCCY	Unidentified coccoid Cyanophyta	542	1051	702	4168	313
PYR	GLESP	*Glenodinium* spp.	2607	4762	4866	18,637	5502
PYR	GYMHELV	*Gymnodinium helveticum* Pen.	18,803	28,356	17,975	142,756	46,736
PYR	GYMSP	*Gymnodinium* spp.	4622	2637	2052	20,246	12,423
PYR	PERSP	*Peridinium* spp.	4861		4652	93,675	51,993
UNI	UNICOCCS	Unidentified coccoid spherical	3092	136	429	393	513
UNI	UNIFLAGO	Unidentified flagellate — ovoid	3984		1415	2059	297
UNI	UNIFLAGF	Unidentified flagellate fusiform	160	1685		849	149

Huron south, Erie west, Erie central, Erie east, and Ontario. Herein, multiple sample stations within each basin are treated as replicates to capture within-basin variability that may result from actual assemblage differences and error associated with sampling and analytical methods. Eleven-year trend analyses were performed for each basin and for each season. Temporal trends in algae densities and biovolumes were evaluated non-parametrically using Kendall tests of the relationship between total algal abundance (cell density or biovolume) in all sample observations and year. Positive or negative trends over the sample period were deemed significant at $P < 0.05$. Phytoplankton were further considered as basin averages from 2007 through 2011 to characterize and compare current phytoplankton abundance and taxonomic composition within and among lakes.

Ordination

While addressing trends in overall algal abundance is important for management, more detailed assessment of the algal assemblage composition can provide details on biodiversity, food web dynamics, and problem species. In our analyses we condensed the complex algal assemblage data using nonmetric multidimensional scaling (NMDS) in order to track changes that may not be visible via bulk trends. NMDS compared sample assemblages based on distance metrics (Rabinowitz, 1975). While preliminary analyses of the algae and diatom assemblages using detrended correspondence analysis (ter Braak and Prentice, 1988) revealed that the algae respond unimodally along environmental gradients, NMDS is based on rank orders and therefore does not require nonlinear assumptions. NMDS was performed using the R package "vegan" (Oksanen et al., 2011; R Development Core Team, 2010). NMDS ordinated the phytoplankton data using Bray–Curtis dissimilarity on relative biovolume data. All taxa known to be strictly benthic were assumed to be allochthonous and were removed from analyses. Post-processing of sample scores included plotting on two NMDS axes using gray-scaled colors for each period and application of a summary ellipse for each year using the "dataEllipse" function in the R package "car" (Fox et al., 2012). Ellipses were configured to capture the 75th percentile of the spread of sample scores in each year. This approach enabled us to assess year-to-year movements of assemblages through the changes in locations of ellipses. Analyses were performed on six basins considered to have unique assemblages and physicochemical conditions: Superior, Michigan, Huron, Erie west, Erie central and east combined, and Ontario.

Results

A total of 485 unique taxa was encountered in the 2001 through 2011 phytoplankton dataset. The assemblages comprised centric diatoms (56 taxa), pennate diatoms (192 taxa), chrysophytes (59 taxa), green algae (126 taxa), cryptomonads (8 taxa), blue-green algae (29 taxa), euglenoids (3 taxa), dinoflagellates (7 taxa), and some unknown entities (5 taxonomic categories). Several of these taxa were rarely observed, some were species or genera not identifiable to the species level (a genus followed by "spp."), and others were members of known divisions but with few diagnostic characteristics (e.g., "unidentifiable chrysophyte ovoid"). Table 1 (spring) and 2 (summer) present the taxa encountered with the highest biovolumes throughout the Great Lakes, based on average biovolumes recorded in the 2007 through 2011 phytoplankton collections. Electronic supplementary material (ESM) provides a similar set of common taxa based on cell densities in spring (ESM Table S1) and summer (Table S2). While these tables are a good representation of modern taxonomic composition in the lakes, some anomalies were identified as follows. A high spring biovolume of *Aphanizomenon flos-aquae* in Lake Huron was based on a sporadic bloom observed largely at two sites in 2009. *Surirella ovata*, a large benthic diatom, had a high biovolume in shallow western Lake Erie likely due to suspension of specimens into the water column. Similarly in Lake Erie, high biovolumes of *Pediastrum boryanum*, *Pediastrum simplex*, and *Phacus* spp. were based on sporadic occurrences of entities with large colonies or cells, so we caution against any interpretation that these taxa are typically abundant.

A comparison of phytoplankton abundance across the lake basins (Fig. 2; Tables 1, 2) clearly demonstrates the high biovolumes and cell densities (ESM Tables S1 and S2) in Lake Erie compared to the other lakes. Spring biovolumes in Lake Erie's central basin were particularly high, whereas phytoplankton in the western basin was especially high in the summer due to high abundances of cyanobacteria. In summer, Lake Ontario had an algal biovolume similar to Lake Erie's eastern basin. The substantially lower algal abundances of the upper lakes (Superior, Michigan, and Huron) are apparent from cell densities and biovolumes in spring and summer. While the several-fold difference in phytoplankton abundance between the upper and lower (Erie and

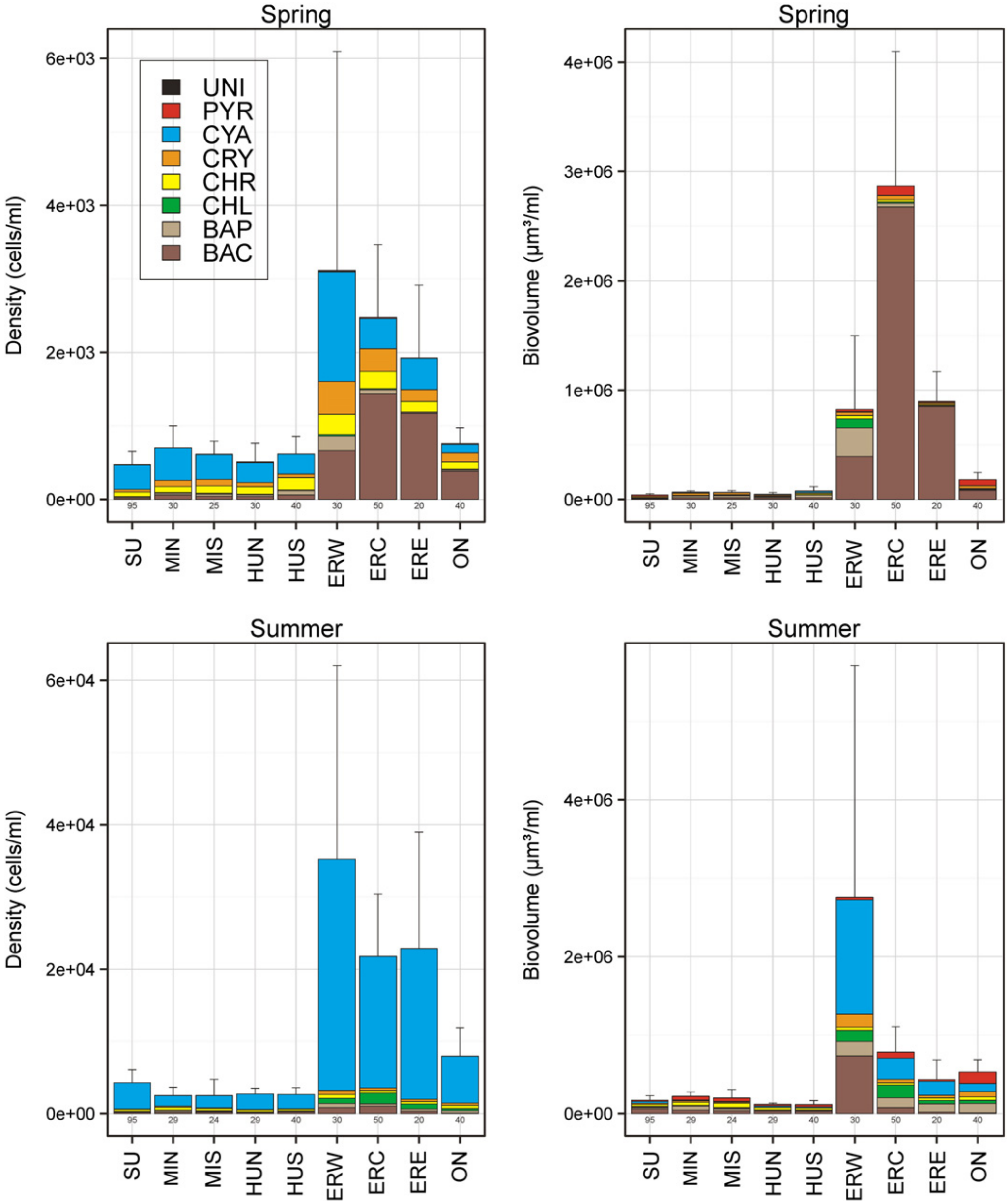

Fig. 2. Basin-wide averages of phytoplankton abundance in spring (top) and summer (bottom), from 2007 through 2011 in the major lake basins: Superior (SU), Michigan north (MIN), Michigan south (MIS), Huron north (HUN), Huron south (HUS), Erie west (ERW), Erie central (ERC), Erie east (ERE), Ontario (ON). Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of every bar indicate the number of samples considered in each stacked bar. Error bars are based on the standard deviation of sample totals. Taxon group codes are: BAC = centric diatoms, BAP = pennate diatoms, CHL = chlorophytes (green algae), CHR = chrysophytes, CRY = cryptophytes, CYA = cyanobacteria (blue-green algae), PYR = pyrrophytes (dinoflagellates), UNI = unidentified and unidentifiable entities.

Ontario) lakes is clearly apparent from a comparison of cell densities, the difference in biovolumes is especially remarkable due to the numeric dominance of small-celled cyanobacteria which account for a very small biovolume in the upper lakes.

High spring biovolumes in Lake Erie are overwhelmingly dominated by the centric diatom *Aulacoseira islandica* (Table 1), in line with recent findings regarding blooms of this taxon (Twiss et al., 2012). Summer abundance tends to be highest for the blue-green alga *Microcystis aeruginosa* in Lake Erie (Table 2). Although algal abundance was much lower in Lake Ontario, there were some high spring abundances of diatoms including *Stephanodiscus alpinus* and *Stephanodiscus parvus* and the dinoflagellates *Peridinium* and *Gymnodinium helveticum*. Other spring dominants include several diatom taxa (e.g., *Aulacoseira*, *Stephanodiscus*) which make use of abundant nutrients, such as phosphorus and silica, before nutrient limitation is established later in the year, as observed in Lake Michigan (Parker et al., 1977). In terms of cell densities, blue-green algae dominated the upper lakes in the spring and all of the lakes in the summer (Fig. 1), but the upper lakes tended to have a much more even biovolume distribution in the other phytoplankton divisions (diatoms, chrysophytes, dinoflagellates, cryptophytes, and green algae). These data also clearly illustrate how some taxa with low density and large cell size (e.g., *Ceratium hirundinella* in summer Lake Ontario) can comprise an important component of algal biovolume. In the summer the upper lakes are dominated by diatoms such as *Cyclotella*, the chrysophyte *Chrysosphaerella longispina,* and the large-celled dinoflagellates *Peridinium* and

Table 2
Average lakewide summer biovolume (μm^3/mL) of dominant (more than 5% biomass at any site) phytoplankton taxa, 2007–2011. Numbered taxa have previously unpublished diagnostics. Taxon codes match those in NMDS figures and taxon group codes match those in Table 1.

DIV	Code	Taxon	Superior	Michigan	Huron	Erie	Ontario
BAC	ACYNORM	*Actinocyclus normanii* (Juhl.-Dannf.) Hust.				34,059	
BAC	AULGRAN	*Aulacoseira granulata* (Ehr.) Simonsen		569		677,772	3418
BAC	AULISLA	*Aulacoseira islandica* (O. Mull.) Simonsen	811			14,411	
BAC	AULITAL	*Aulacoseira italica* (Ehr.) Simonsen				33,089	
BAC	CYCCOMES	*Cyclotella comensis* Grun.	792	2406	5232	23,287	756
BAC	CYCCOMRC	*Cyclotella comensis* “rough center with process”	21,050	20,633	6913	3454	349
BAC	CYCCOME1	*Cyclotella comensis* var. 1	655	3298	5792	3283	2125
BAC	CYCCOMT	*Cyclotella comta* (Ehr.) Kutz.	32,090	8789	15,165	44,103	6589
BAC	CYCMICH	*Cyclotella michiganiana* Skv.	296	5170	1513	1951	36
BAC	CYCOCEL	*Cyclotella ocellata* Pant.	3233	1766	732	23,107	1135
BAC	CYCOPER	*Cyclotella operculata* (Ag.) Kutz.	1922	437	2258	1200	138
BAC	CYCOPERU	*Cyclotella operculata* var. *unipunctata* Hust.	1011	798	442	3716	3208
BAC	CYCPSEU	*Cyclotella pseudostelligera* Hust.	1125	2969	2397	3549	489
BAC	CYCSTEL	*Cyclotella stelligera* (Cl. & Grun.) V.H.	134	534	1360	2911	255
BAC	CYCTRIP	*Cyclotella tripartita* Pant.	1070	1209	255	77	
BAC	RHILONG	*Rhizosolenia longiseta* Zach.	588	394	223	635	498
BAC	STEALPI	*Stephanodiscus alpinus* Hust.	3874	1968	1369	17,397	1581
BAC	STEALP1	*Stephanodiscus alpinus* Type I Hust.	1175	2067	2027	7184	438
BAC	STENIAG	*Stephanodiscus niagarae* Ehr.	28,296			75,853	
BAP	ASTFORM	*Asterionella formosa* Hass.	4430	3691	1043	3331	1857
BAP	DIATENUE	*Diatoma tenue* var. *elongatum* Lyngb.	243	2466	141	1812	23,807
BAP	FRACROT	*Fragilaria crotonensis* Kitton	2072	20,905	1295	139,981	71,226
BAP	SYNDELIA	*Synedra delicatissima* var. *angustissima* Grun.	1303	961	675	413	6226
BAP	SYNDELI	*Synedra delicatissima* W. Sm.		7199	153		2380
BAP	SYNFILI	*Synedra filiformis* Grun.	588	12,891	5974	3706	2970
BAP	SYNOSTE	*Synedra ostenfeldii* (Krieg.) A. Cl.	3682	2029	398	704	23,735
BAP	SYNRADI	*Synedra radians* Kutz.	1496	1282	439	699	1408
BAP	SYNULNAB	*Synedra ulna* var. *biceps* Kutz.	3683	4332	322		1765
BAP	SYNULNAH	*Synedra ulna* var. *chaseana* Thomas	2255	3590	1648	4702	3580
BAP	TABFLOC	*Tabellaria flocculosa* (Roth) Knud.	5182	543	2621	300	4444
CHL	BOTBRAU	*Botryococcus braunii* Kutz.	55,459				
CHL	CHLSP	*Chlamydomonas* spp.	5801	681	827	25,965	2335
CHL	CRLSP	*Chlorella* spp.	7503			23,681	
CHL	CLOLONG	*Closteriopsis longissima* (Lemm.) Lemm.		17,670		2611	
CHL	COEASTR	*Coelastrum astroideum* De-Not	17,892	6806		43,133	64,285
CHL	COEMICR	*Coelastrum microporum* Nag. in A. Braun	34,334	11,850		181,900	30,249
CHL	COESPHA	*Coelastrum sphaericum* Nag.					120,157
CHL	COSPHAS	*Cosmarium phaseolus* Breb.	5314		3861	178,996	7956
CHL	COSSPD	*Cosmarium* spp.	7342		1174	35,370	6249
CHL	CRURECT	*Crucigenia rectangularis* A. Braun				64,081	
CHL	EUDSP	*Eudorina* spp.	19,639			14,061	
CHL	EUGSP	*Euglena* spp.		47,261			
CHL	EUTSPC	*Eutetramorus* spp.	15,824				
CHL	FRADROE	*Franceia droescheri* (Lemm.) G.M. Sm.	4210		1214	13,720	9268
CHL	GLOPLAN	*Gloeocystis planktonica* (W. & G.S. West) Lemm.			874	22,364	
CHL	GLOSPC	*Gloeocystis* spp.	3089	20,840	2019	88,255	13,479
CHL	GONPECT	*Gonium pectorale* Mull.				49,035	
CHL	MITPUSI	*Micractinium pusillum* Fres.				21,430	12,095
CHL	MOUSP	*Mougeotia* spp.				49,554	26,779
CHL	OOCBORG	*Oocystis borgei* Snow	5045	2861	2397	22,449	9522
CHL	OOCGIVIN	*Oocystis gigas* var. *incrassata* West & West sensu Skuja	12,441		26,873	70,588	3475
CHL	OOCPARV	*Oocystis parva* W. & G.S. West	1259	849	264	4797	720
CHL	OOCPUSI	*Oocystis pusilla* Hansg.	810	157	349	2708	
CHL	OOCSP	*Oocystis* spp.	858			12,412	
CHL	PEDBORY	*Pediastrum boryanum* (Turp.) Menegh.				22,725	6812
CHL	PEDDUPLG	*Pediastrum duplex* var. *gracillimum* W. & G.S. West				129,196	
CHL	PEDTETR	*Pediastrum tetras* (Ehr.) Ralfs	2038			19,065	
CHL	SCEBIJU	*Scenedesmus bijuga* (Turp.) Lag.	223	518	1002	3846	2931
CHL	SPYSCHR	*Sphaerocystis schroeteri* Chod.	1153			78,298	
CHL	STASPD	*Staurastrum* spp.				23,725	12,837
CHL	TRASP	*Trachelomonas* spp.		24,154		3744	
CHR	CHMSPM	*Chromulina* spp.	2559	4065	2531	4645	5844
CHR	CSLLONG	*Chrysosphaerella longispina* Laut. emend. Nich.	102,923	118,000	65,695		21,135
CHR	DINBAVA	*Dinobryon bavaricum* Imhof	1912	1682	974	9836	2390
CHR	DINBAVAV	*Dinobryon bavaricum* var. *vanhoeffenii* (Bachm.) Krieg.	2948	771			
CHR	DINCYLI	*Dinobryon cylindricum* Imhof	6461	17,328	35,903		3369
CHR	DINCYLIA	*Dinobryon cylindricum* var. *alpinum* (Imhof) Bachm.			10,955		
CHR	DINDIVE	*Dinobryon divergens* Imhof	10,433	3666	2273	10,487	27,299
CHR	DINSERT	*Dinobryon sertularia* Ehr.	10,691	44,792	29,945		
CHR	DINSERTP	*Dinobryon sertularia* var. *protuberans* (Lemm.) Kreig.	807	1810	9159		
CHR	DINSOCI	*Dinobryon sociale* Ehr.	1647	1445	1244	4379	4156
CHR	DINSOCIA	*Dinobryon sociale* var. *americanum* (Brunnth.) Bachm.	1571	2858	1370	8668	8699
CHR	DINSOCIS	*Dinobryon sociale* var. *stipitatum* (Stein) Lemm.	1947	849	1995	4783	3030

(continued on next page)

Table 2 (*continued*)

DIV	Code	Taxon	Superior	Michigan	Huron	Erie	Ontario
CHR	HAPSP	Haptophyceae	1039	1763	1457	3395	3150
CHR	MALSP	*Mallomonas* spp.	2206	6607	5248	8113	
CHR	OCHSPOV	*Ochromonas* spp. — ovoid	1454	3795	1306	3376	2559
CHR	STCSP	*Stichogloea* spp.	1370	16,287	6533	34,447	
CHR	UNCFLAG	Unidentified chrysophyte flagellate	1208	1379	930	3146	5049
CHR	UNCOVO	Unidentified chrysophyte ovoid (nonflagellate)	11,797	20,568	12,290	17,033	26,834
CHR	UROLIND	*Uroglena lindii* Bourr.					12,713
CHR	UROSP	*Uroglena* spp.	4518	831	6929	471	1360
CRY	CRYEROS	*Cryptomonas erosa* Ehr.	8386	7578	6799	44,767	30,206
CRY	CRYPYRE	*Cryptomonas pyrenoidifera* Geitl.	6632	14,231	7714	38,892	21,362
CRY	CRYREFL	*Cryptomonas reflexa* Skuja	12,540	14,222	3840	66,948	41,144
CRY	CRYROST	*Cryptomonas rostratiformis* Skuja	19,266			43,672	59,911
CRY	UNICRYP	*Cryptomonas* spp.			8219	5244	5127
CRY	RHOLENS	*Rhodomonas lens* Pasch. & Rutt.	1409	4905	787	5813	5797
CRY	RHOMINU	*Rhodomonas minuta* Skuja	2627	4366	1955	10,216	10,202
CYA	ANBCIRC	*Anabaena circinalis* Rabh.				182,037	15,100
CYA	ANBFLOS	*Anabaena flos-aquae* (Lyngb.) Breb.	4781	5302		100,578	179,760
CYA	ANBSP	*Anabaena* spp.	391,826	3604	10,239	14,028	2305
CYA	APHFLOS	*Aphanizomenon flos-aquae* (Lyngb.) Ralfs	2123	1677	20,286	296,580	6369
CYA	APHSP	*Aphanizomenon* spp.	285,889			83,575	
CYA	APASP	*Aphanocapsa* spp.	14,548	7940	9637	224,078	23,440
CYA	APOSP	*Aphanothece* spp.	1416	380	1944	14,315	4786
CYA	CROLIMN	*Chroococcus limneticus* Lemm.	5885	31,435	47,864	74,089	71,175
CYA	COEDUBI	*Coelosphaerium dubium* Grun.				581,165	
CYA	GMALACU	*Gomphosphaeria lacustris* Chod.		629	8636	23,891	
CYA	MERSP	*Merismopedia* spp.	47	258	84	15,259	1045
CYA	MICAERU	*Microcystis aeruginosa* (Kutz.) emend. Elenkin				3,248,149	
CYA	OSCAGAR	*Oscillatoria agardhii* Gom.				102,905	
CYA	OSCLIMN	*Oscillatoria limnetica* Lemm.	2789	1306	963	35,273	15,320
CYA	OSCSP	*Oscillatoria* spp.	1474			10,158	7853
CYA	PHOSP	*Phormidium* spp.				32,618	
CYA	UNICOCCY	Unidentified coccoid Cyanophyta	910	1617	2460	4279	2544
PYR	CERHIRU	*Ceratium hirundinella* (O.F. Mull.) Schr.	9367	20,541	18,663	85,907	130,345
PYR	GLESP	*Glenodinium* spp.	7793	11,983	11,253	21,607	17,492
PYR	GYMHELV	*Gymnodinium helveticum* Pen.	52,169	196,242	71,737		241,543
PYR	GYMSP	*Gymnodinium* spp.	9031	13,571	8318	11,663	31,440
PYR	PERSP	*Peridinium* spp.	14,856	75,765	33,104	72,973	30,298
UNI	UNIFLAGO	Unidentified flagellate — ovoid	2013	596	596	3021	2315

Gymnodinium helveticum. Lake Superior was dominated by a high relative density of summer blue-green algae including *Anabaena* and *Aphanizomenon*.

Lake Superior

In terms of cell densities, Lake Superior is dominated by blue-green algae throughout the year (Fig. 3). Dominant taxa include entities comprising many small cells such as *Aphanizomenon* and *Aphanocapsa* in the summer (ESM Table S2). However, phytoplankton biovolume in Lake Superior is dominated by diatoms, chrysophytes, cryptophytes and dinoflagellates in the spring, and more so by diatoms in the summer. Over the sampling period a significant increase in spring algal density was observed. Although the change is not obvious based on annual averages for the 11 years, the apparent increase from 2007 through 2011 was based on higher sample numbers (19 samples/y) so those years governed the nonparametric trend analysis. Similarly, a significant decline was observed for summer algal biovolumes, largely based on what appears to be a monotonic decline in average biovolume from 2007 through 2011.

The Lake Superior NMDS plots (Fig. 4) clearly indicate the differences in assemblages between spring and summer, and the imbalance of dominant taxa on the right side of the diagram reveals how summer biovolume is substantially higher than that in spring. However, tracing the year-to-year movement of assemblage characteristics reveals some similarities in spring and summer trends. There was little variation in assemblages for 2001 through 2006, but 2007 assemblages were suddenly different. Although 2007 was an anomalous year, since then algal assemblages have had a higher axis 2 score than pre-2007 assemblages. Changes in assemblage structure observed over the decade were largely due to shifts in non-diatom algae such as cyanobacteria [e.g. *Anabaena* (ANBSP) and *Aphanocapsa* (APASP)]. However, the placement of taxon scores reveals that summer assemblages after 2007 contained a higher relative amount of centric diatoms such as *Cyclotella* (e.g., CYCCOMT).

Lake Michigan

Cell densities in Lake Michigan are dominated by blue-green algae such as *Oscillatoria minima*, *Aphanocapsa,* and *Oscillatoria limnetica*, but in terms of biovolume, spring is dominated by diatoms (e.g., *A. islandica*), albeit less so in more recent years. Spring biovolume in the southern basin has significantly declined since 2001 (Fig. 5). A decline was also apparent in the northern basin, but it was not significant for the period. Since 2007 there has been a greater spring relative dominance by cryptophytes (*Cryptomonas* and *Rhodomonas*) as diatoms continued to decline. The main years of spring algal biovolume decline were 2002 and 2003 in the northern basin and 2005 in the southern basin. A similar decline was not observed for summer phytoplankton; summer algal biovolume has been erratic, with 2009 and 2010 being years with somewhat higher summer biovolumes in the southern basin owing to atypically high chrysophyte and dinoflagellate abundance. In the most recent three years, the summer phytoplankton assemblage was dominated by dinoflagellates (e.g., *Peridinium*), pennate diatoms (e.g., *Fragilaria*), centric diatoms (e.g., *Cyclotella*), and chrysophytes in the northern basin and by colonial chrysophytes (e.g., *Chrysosphaerella*) and centric and pennate diatoms in the southern basin.

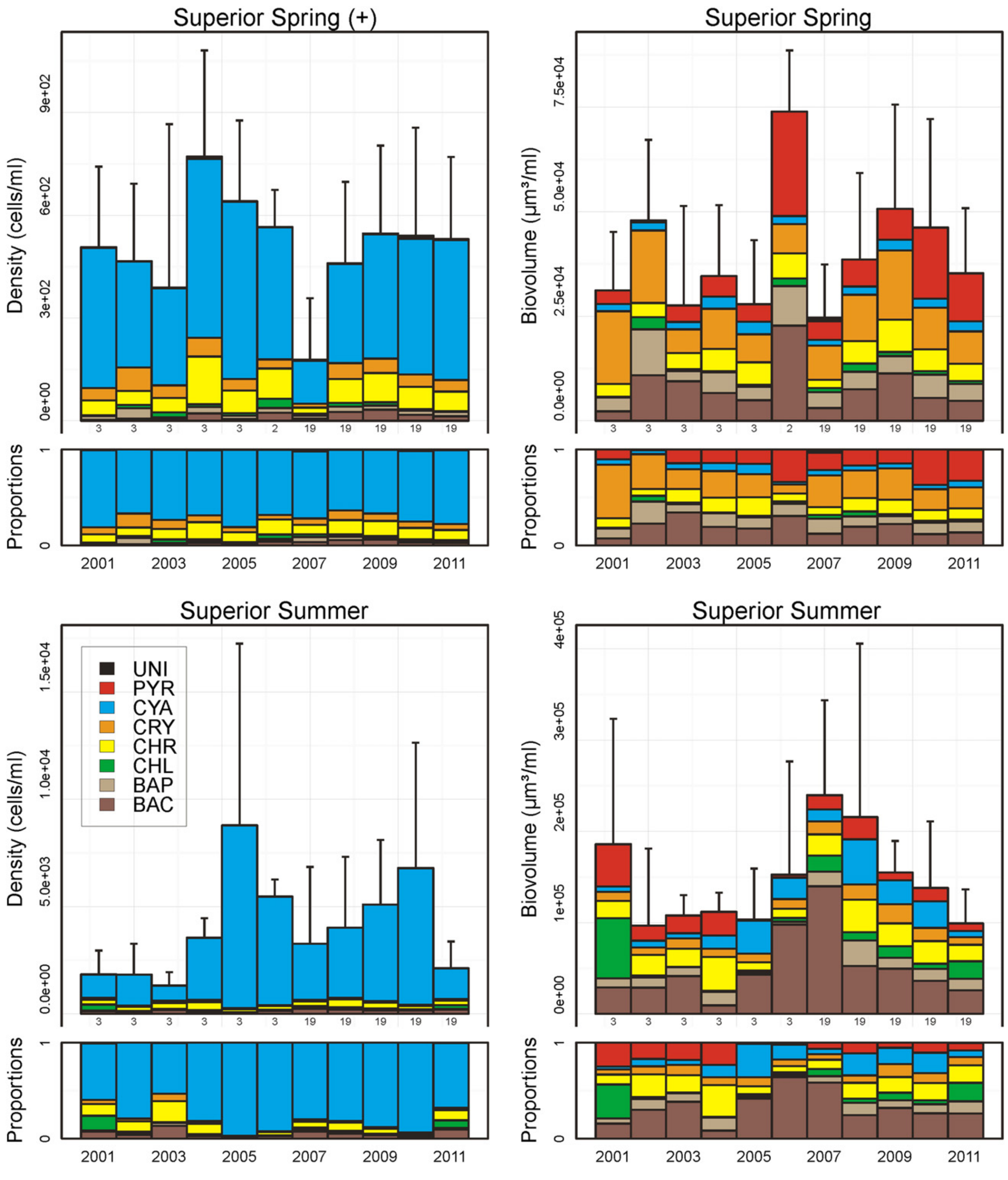

Fig. 3. Basin-wide averages of phytoplankton abundance in spring (top) and summer (bottom), from 2001 to 2011 in Lake Superior. Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of each absolute abundance bar indicate the number of samples averaged, and below that the relative abundances are shown as proportions. Error bars represent a standard error of the sample totals. A significant increasing (+) or decreasing (−) trend (Kendall's rank correlation test, $P < 0.05$) for the 11-year period is indicated in the respective heading at the top of each figure panel. Taxon group codes match those from Fig. 2.

Analysis of species assemblages (Fig. 6) clearly separates the seasons by dominant species such as *A. islandica* (AULISLA) and *Stephanodiscus alpinus* (STEALP1) in spring and *Peridinium* (PERSP), *Cyclotella* (e.g., CYCCOMT, CYCCOMRC), and *Synedra filiformis* (SYNFILI) in the summer. NMDS plots for both seasons track a shift from positive to negative values on axis 2 from 2001 through 2007, owing to higher relative biovolumes of *A. islandica* (AULISLA), *Cryptomonas reflexa* (CRYREFL), and *Cryptomonas erosa* (CRYEROS) in spring and *Cyclotella* (e.g. CYCCOMRC) in summer. Since 2007 it is apparent that the species assemblages have partly returned to patterns similar to those in the early 2000s.

Lake Huron

Blue-green algae (*Aphanocapsa* and other cyanophytes) dominate Lake Huron's phytoplankton in terms of cell densities (Fig. 7), but in

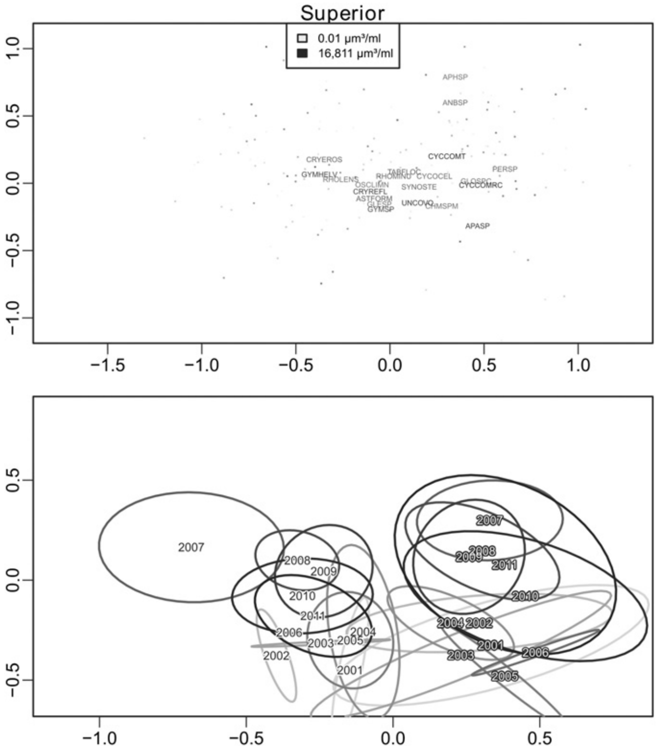

Fig. 4. Species (top) and sample (bottom) scores from NMDS analysis of phytoplankton biovolume assemblages from Lake Superior. Darker species scores indicate higher average abundance for the 10-year period. The 20 most abundant taxa for the period are labeled by their species code (Tables 1 and 2) while rarer taxa are indicated by dots. The legend at the top of each species ordination indicates the lowest and highest taxon average abundance. The lower plot illustrates supplementary plotting of all samples which are summarized by annual ellipses for each season (more recent samples have darker ellipses) with the year plotted at each period centroid. Annual centroids for spring ellipses are in black text and centroids for summer ellipses are in white (black bordered numbers) text.

terms of biovolume Lake Huron is dominated by the blue-green alga *Aphanizomenon*, diatoms (e.g., *Asterionella*, *Cyclotella*), and chrysophytes in the spring and by centric diatoms (e.g., *Cyclotella*), chrysophytes, and dinoflagellates (e.g., *Peridinium* and *G. helveticum*) in the summer (Tables 1 and 2). Since 2001 Huron has experienced a decline in spring biovolume with the major transition occurring from 2002 to 2003, a decline that has been recorded in satellite-inferred chlorophyll data for the north and south basins (Barbiero et al., 2011a). Based on the Kendall test, this decline in phytoplankton biovolume was not significant for the 11-year period, likely a result of lower sample numbers in earlier years in the decade. This transition was marked in the northern and southern basins by a decline in pennate diatoms. Trend analyses for the southern basin suggest a significant increase in spring cell densities and a significant decline in summer biovolume. These trends likely apply to the recent period (2007 through 2011) which had a higher sampling intensity of eight samples/yr, as otherwise there are no apparent trends for the decade based on annual averages. A high summer 2001 biovolume in the north basin may also be an abnormal result of small sample size as satellite data did not suggest a particularly high chlorophyll *a* concentration for the basin in August 2001 (Barbiero et al., 2011a).

NMDS ordination reveals that a persistent change in phytoplankton assemblages has occurred in spring (Fig. 8). Spring assemblage scores indicate that conditions in 2001 through 2005 were quite different than the more recent period (2007 through 2010), representing a shift from diatoms such as *Tabellaria flocculosa* (TABFLOC, which represents more than half of the post-2002 pennate diatom loss illustrated in Fig. 7) to taxa such as *Asterionella formosa* (ASTFORM) and a high biovolume of *A. flos-aquae* (APHFLOS) in 2008. For summer phytoplankton, there is little overall trend in scores for the 11-year period.

Lake Erie west

Lake Erie's western basin biovolume was typically dominated by centric diatoms in the spring (e.g., *A. islandica*, *Stephanodiscus*). The 11-year period exhibited erratic spring fluctuations in algal abundance and composition, but mid-decade (2005 through 2008) saw a temporary high biovolume of centric diatoms. A significant increasing trend was observed for spring cell densities and for summer densities and biovolumes (Fig. 9). The summer data revealed a recent increase in blue-green algae (dominated by *Aphanocapsa* and *Microcystis*) coinciding with recent nearshore cyanobacteria blooms (Wynne et al., 2010). We acknowledge that fragmented colonies of *Microcystis aeruginosa* may be misidentified as *Aphanocapsa* due to the similarly small size of individual cells and difficulties identifying taxonomic diagnostics such as gas vacuoles in *Microcystis*. Hence, pelagic collections of both taxa probably complement nearshore observations of *Microcystis* (Michalak et al., 2013).

NMDS ordinations (Fig. 10) show little evidence of a major trend over the decade despite changes in total phytoplankton biovolume. One notable observation is the large ellipse for summer 2011 centered high on axis 2 which indicates substantial variation among sample assemblages but also a tendency for high abundance of *M. aeruginosa* (MICAERU).

Lake Erie central and east

Spring phytoplankton communities in Lake Erie's central basin were overwhelmingly dominated in biovolume by the filamentous centric diatom *A. islandica* (Table 1) which largely contributed to a significant increase for the 11-year period (Fig. 11). At some stations, 2005 through 2011 saw biovolumes of *Aulacoseira* higher than 3,000,000 μm^3/ml, much higher than typical pre-2005 biovolumes. A similar increase in spring centric diatom blooms was not observed in the eastern basin. Summer assemblages reveal a significant increase in algal biovolume in the last 5 years in the central basin; the highest abundances in the eastern basin during our data series were also seen during this period although no significant increasing trend was found. A large proportion of this increase was from blue-green algae in the central basin (e.g., *Aphanocapsa*, possibly misidentified as or mixed with *Microcystis*) and a higher biovolume of chlorophytes (e.g., *Gloeocystis*) especially in 2010.

NMDS for phytoplankton indicates that the composition of spring species assemblages centered around a persistent dominance of *A. islandica* (AULISLA) with occasional years favoring other species such as *S. alpinus* (STEALPI) in 2007 (Fig. 12). Similarly, summer 2007 had unique assemblages, but the dominant summer trend was that the algae from 2005 through 2010 were farther to the right on the plot than 2001 through 2004, due to greater dominance by blue-green algae such as *Aphanocapsa* (APASP) and the dinoflagellate *C. hirundinella* (CERHIRU) in recent years. Despite changes in abundance for the period (Fig. 11), ordinations indicate little shift in species composition.

Lake Ontario

Summer cell densities exhibited a significant summer increase, but otherwise Lake Ontario phytoplankton sample abundance had no apparent change over the sampling period (Fig. 13). Spring relative densities of blue-green algae declined while centric diatom densities increased. The summer density increase was largely attributable to blue-green algae (e.g., *Aphanocapsa*). No notable temporal shifts in composition were apparent in the biovolume data. A single instance of high

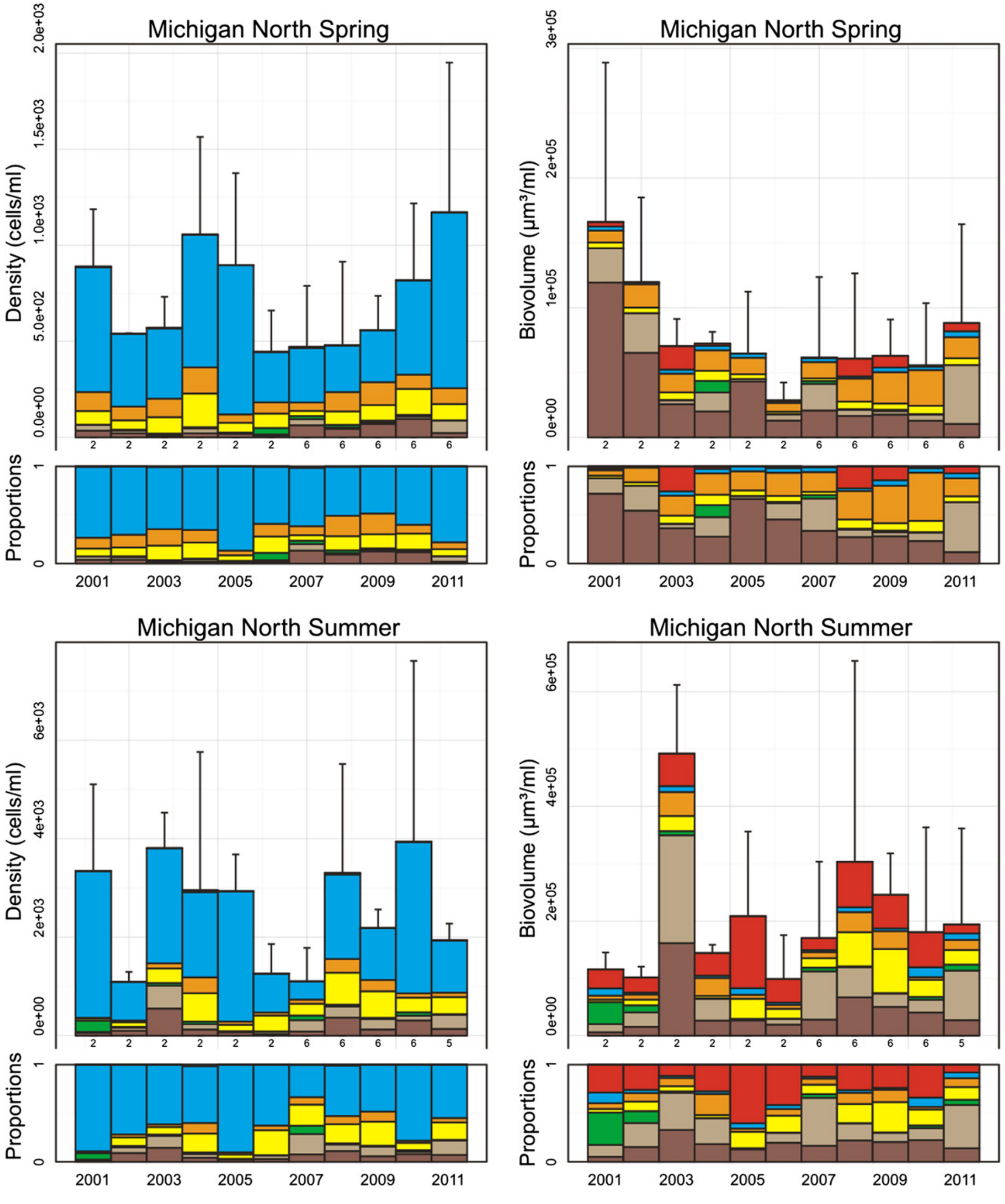

Fig. 5. Basin-wide averages of phytoplankton abundance in Lake Michigan northern (upper) and southern (lower) basins. Abundance data are summarized for spring and summer, from 2001 to 2011. Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of each absolute abundance bar indicate the number of samples averaged, and below that the relative abundances are shown as proportions. Error bars represent a standard error of the sample totals. A significant negative trend (Kendall's rank correlation test, $P < 0.05$) for the 11-year period (−) is indicated at the top of each figure panel in the respective heading. Taxon group codes match those from Fig. 2.

green algal biovolume (mainly *Phacotus*) occurred in 2006, but this was probably an artifact of an atypical observation and low sample size for that year.

Patterns in the species assemblages for spring and summer consistently indicated a shift from a 2001 through 2005 assemblage to a new assemblage starting in 2007 (Fig. 14). Summer assemblages from 2010 and 2011 suggest a reversion to early 2000s conditions. The NMDS plot clarifies that the spring shift in the late 2000s was due to increases in the relative biovolume of taxa such as the small centric diatom *Stephanodiscus parvus* (STEPARV) and the

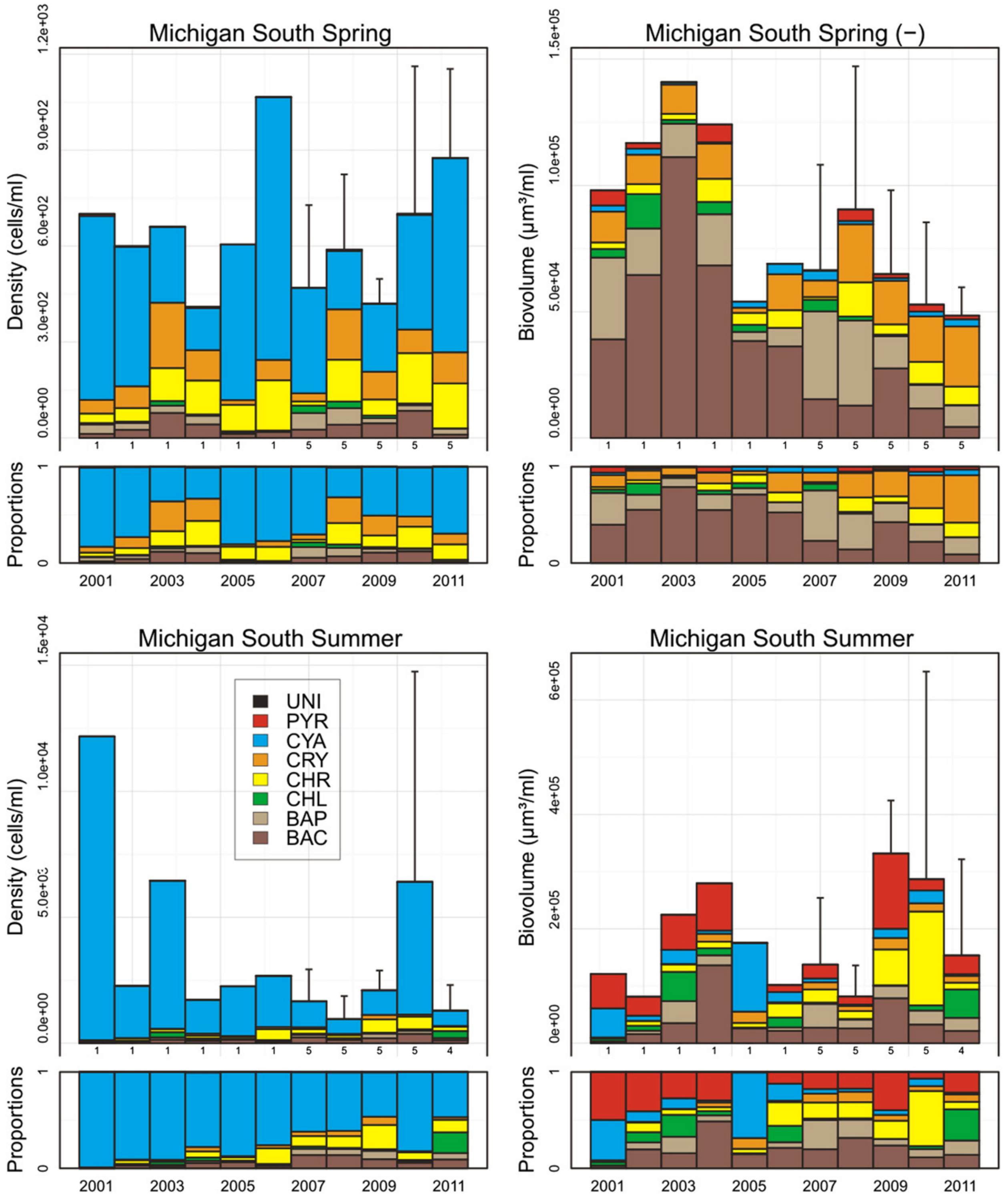

Fig. 5 (*continued*).

dinoflagellate *Gymnodinium helveticum* (GYMHELV). The summer transition from the early to late 2000s was due to an increased relative dominance of dinoflagellates such as *Ceratium hirundinella* (CERHIRU), pennate diatoms such as *Fragilaria crotonensis* (FRACROT), and blue-green algae such as *Aphanocapsa* (APASP) and *Anabaena flos-aquae* (ANBFLOS).

Discussion

In the 11 years covered in this report, certain phytoplankton taxa in certain lake basins have flourished while others have declined. Likely reasons for these changes include nutrient and other water quality shifts, size-specific preferences of food organisms by successful grazers,

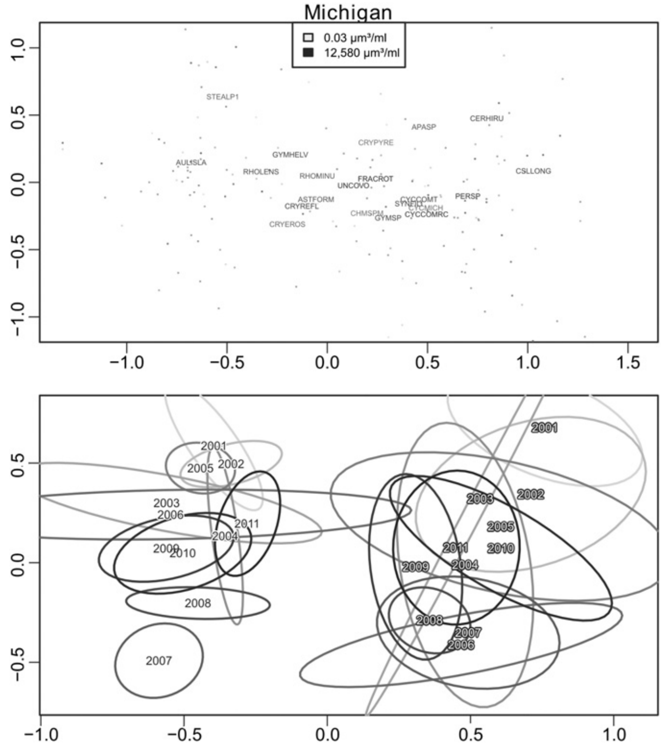

Fig. 6. Species (top) and sample (bottom) scores from NMDS analysis of phytoplankton biovolume assemblages from Lake Michigan. Darker species scores indicate higher average abundance for the 10-year period. The 20 most abundant taxa for the period are labeled by their species code (Tables 1 and 2) while rarer taxa are indicated by dots. The legend at the top of each species ordination indicates the lowest and highest taxon average abundance. The lower plot illustrates supplementary plotting of all samples which are summarized by annual ellipses for each season (more recent samples have darker ellipses) with the year plotted at each period centroid. Centroids for spring ellipses are in black text and centroids for summer ellipses are in white text.

and changes in physical properties of the lakes due to climate-related variables. In some cases, the causes for changes remain speculative, but we summarize the trends and likely drivers as follows.

Lake Superior

Little change in phytoplankton was observed during our period of study on Lake Superior, but current conditions reflect a changed system, as supported by previous studies. Of the five lakes, Lake Superior is probably closest to its pre-anthropogenic impact condition although human influences such as nutrient enrichment have degraded water quality in the past (Fahnenstiel et al., 1990; Stoermer et al., 1985). Two major transitions in the paleolimnological record were observed by Stoermer et al. (1985) and Chraïbi et al. (in press): (1) an early 20th century increase in *A. islandica* that was attributed to increased nutrient flux, followed by a decline likely resulting from agricultural abatement; and (2) a recent increase in *Cyclotella* taxa attributed to lake warming and other water quality shifts. Summer diatom (and overall algal) abundance is much higher than in spring (Fig. 3), so paleolimnological observations of increasing diatom taxa (e.g., *Cyclotella*) in the last few decades match our observations of typical summer taxa in the phytoplankton. However, Barbiero and Tuchman (2001), in an investigation of survey data from 1998, determined that algal conditions in the lake had remained relatively unchanged over the previous two decades.

Current phytoplankton conditions in Lake Superior do not suggest impairment by nutrients (Reavie and Allinger, 2011), but there is subtle evidence that changes in water quality variables have occurred over the last decade. Recently, increases have been reported in chloride, nitrates, turbidity, and alkalinity as well as declines in silica (Osantowski et al., 2010), which may be driving relative increases in certain species of algae. For instance, higher nitrates and changing epilimnion thickness may be favoring greater abundances of *Cyclotella comta* (*bodanica*) and *Cyclotella comensis*, common summer diatoms in Superior (Table 2) which may be able to exploit the new physicochemical environment. Such was observed by Saros et al. (2012) for these two taxa by examining their growth in nutrient enrichment incubations and through paleolimnological observations from lakes including one located on Isle Royale, Lake Superior. Due to climatic drivers, winter ice cover has also decreased in extent and period during recent decades, and it is known that the physical properties of the lake are responding (Munawar and Munawar, 2009), particularly that the summer epilimnetic temperatures are warming faster than the atmosphere (Austin and Colman, 2007). While our 11-year record of monitoring data does not track a strong decadal change in the phytoplankton, and examination of the data do not suggest relative increases in *Cyclotella*, the coupled effect of nutrients and climate-driven modification of stratification will continue to be evaluated as mechanisms of the long-term change in pelagic organisms. The recent decline in summer algal biovolume since 2007 is not yet explained and may be a short-term fluctuation, but it is noted that matching water quality changes, including a prevailing increase in alkalinity and chloride, occurred over those five years (unpublished data).

Lake Michigan

To aid in interpretation, we put the recent decline and change in assemblage structure we observed in Lake Michigan phytoplankton in the context of several previous investigations. Lake Michigan experienced progressive eutrophication since European settlement through the early 1980s (Stoermer et al., 1990); however, measurements since 1980 suggest abatement of the nutrient load (Dolan and Chapra, 2012) and a reduction in in-lake TP (Barbiero et al., 2002). Historical accounts that Michigan was always dominated by diatoms (Davis, 1966) apply to most of our spring biovolume observations, but summer data indicate greater contributions by other algal groups, usually phytoflagellates such as chrysophytes and dinoflagellates, as noted by Makarewicz et al. (1998). Summer dominance of phytoflagellates matches that observed by Scavia and Fahnenstiel (1987) from the 1980s. Further, there has been a spring relative increase in cryptophytes (*Cryptomonas* and *Rhodomonas*). Diatoms tend to have higher sinking rates (Scavia and Fahnenstiel, 1987), particularly heavily silicified taxa such as *Aulacoseira*, which may have enhanced feeding efficiency by dreissenids, therefore more effectively reducing diatom populations relative to other taxa. However, one would expect that diatoms sinking to the profundal zone (whether or not mussels are present) are nevertheless removed from the epilimnetic system so preferential sinking mechanism as a cause for the spring diatom decline remains hypothetical.

Declines in benthic invertebrates (Nalepa et al., 2009) and phytoplankton biomass and productivity (Fahnenstiel et al., 2010) have coincided with the expansion of dreissenid populations, in particular the deep-living *Dreissena rostriformis bugensis*. The exact time course of the reductions in phytoplankton in Lake Michigan has not been clear. Fahnenstiel et al. (2010) reported an 87% decline in average spring isothermal period phytoplankton biomass at two stations in southern Lake Michigan between 1995–1998 and 2007–2008, although the timing of onset of the decrease was unknown due to the decade-long gap between sampling periods. Further, Kerfoot et al. (2010) noted a decline in late-winter, satellite-inferred and directly measured chlorophyll *a* in the southern basin from 2001 through 2008. Our data suggest spring declines in the northern basin of Lake Michigan might have occurred by 2002, although there was no statistically significant long-term trend in that basin, while in the southern basin a significant decrease occurred,

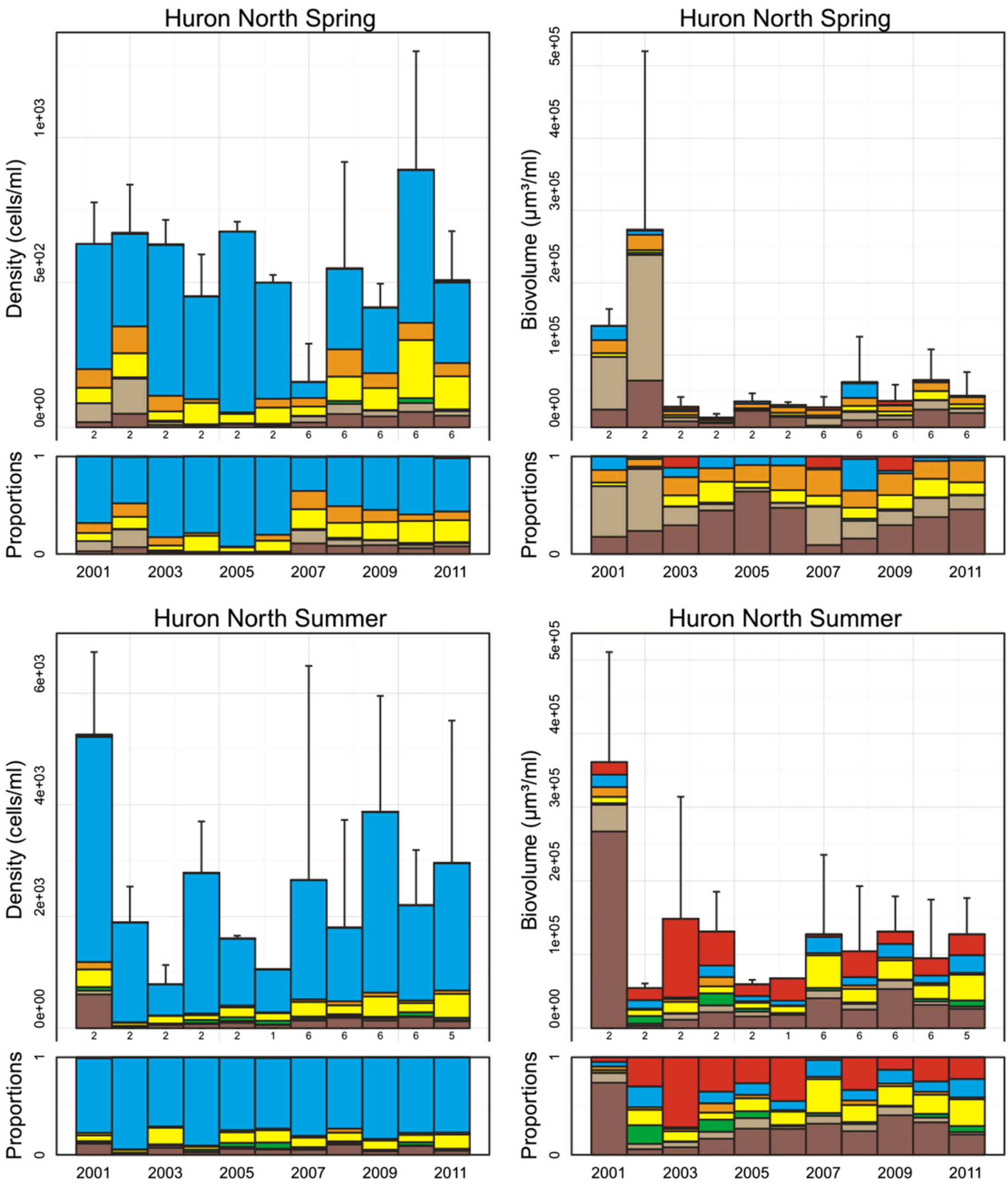

Fig. 7. Basin-wide averages of phytoplankton abundance in Lake Huron northern (upper) and southern (lower) basins. Abundance data are summarized for spring and summer, from 2001 to 2011. Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of each absolute abundance bar indicate the number of samples averaged, and below that the relative abundances are shown as proportions. Error bars represent a standard error of the sample totals. A significant positive (+) or negative (−) trend (Kendall's rank correlation test, $P < 0.05$) for the 11-year period is indicated in the respective headings. Taxon group codes match those from Fig. 2.

largely defined by a drop in biovolume between 2004 and 2005. It should be noted that the GLNPO sampling typically occurs prior to the spring maximum in the lake (Barbiero et al., 2012). Multivariate analyses suggest that species assemblages were especially different in 2007 and 2008, a brief period when pennate diatoms dominated, but the more recent trend of increasing relative dominance of phytoflagellates suggests an increasing similarity to Lake Superior which has a greater tendency towards spring cryptophytes (Fig. 3; Barbiero and Tuchman, 2001).

Lake Huron

The substantial decline in Lake Huron's spring phytoplankton was accompanied by a change in assemblage structure. Based on numerous

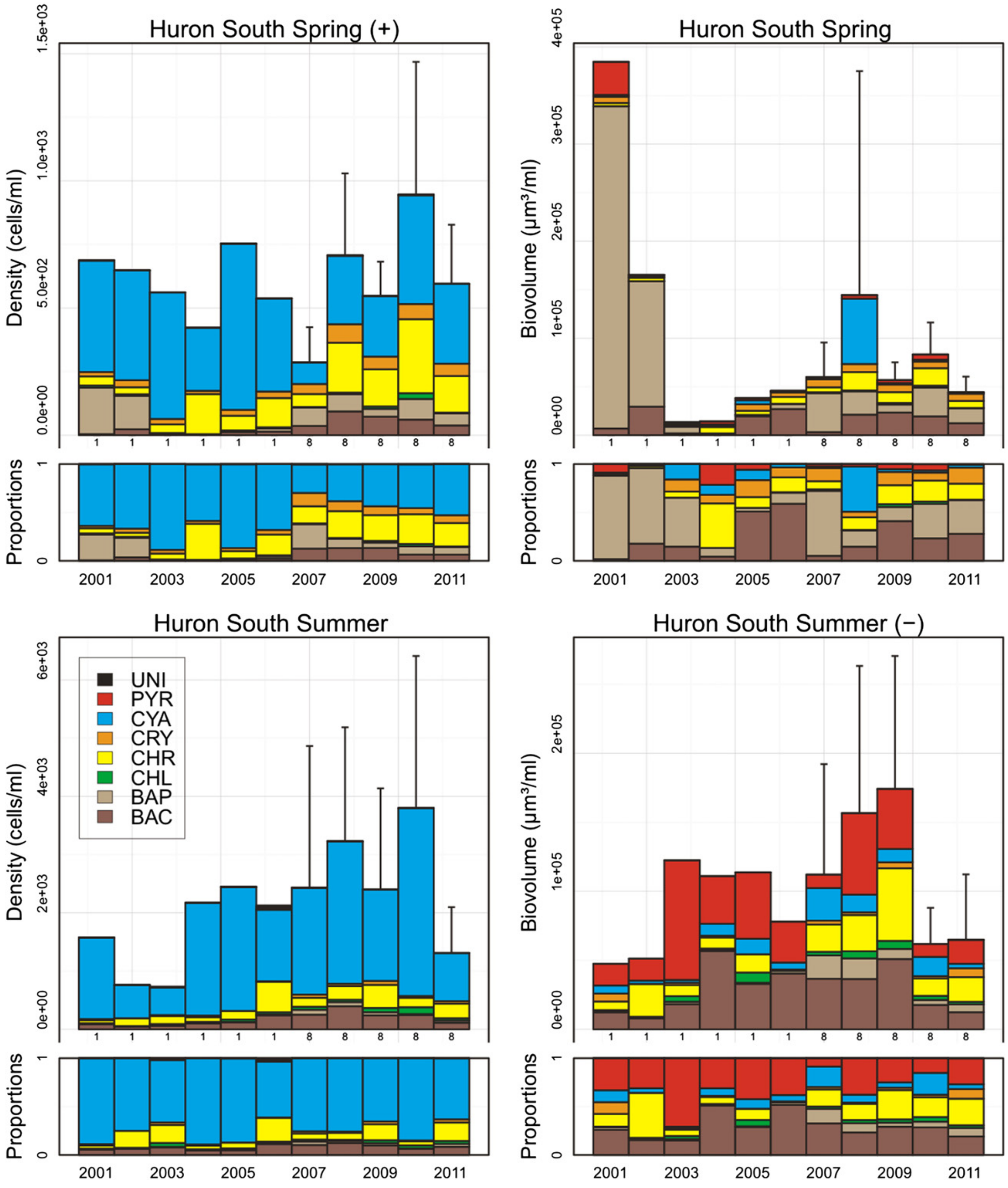

Fig. 7 (*continued*).

historical accounts, diatoms tended to dominate the phytoplankton biomass of Lake Huron (Makarewicz and Bertram, 1991; Munawar and Munawar, 1982, 1986; Schelske et al., 1974). For post-2002 collections, this was not necessarily the case as chrysophytes and cryptophytes typically comprised a large portion of the spring population and chrysophytes and dinoflagellates often exceeded diatom abundance in summer (Fig. 7). These summer abundances of phytoflagellates concur with observations from 1998 (Barbiero and Tuchman, 2001), in which the authors suggested that the increase in phytoflagellates may be indicative of a new, "disturbed" community.

A major shift in the lower pelagic food web of Lake Huron was first noted with the near complete loss of cladocerans in 2003 (Barbiero et al., 2009). It was subsequently determined that a dramatic reduction in the size of the spring phytoplankton maximum had occurred in that

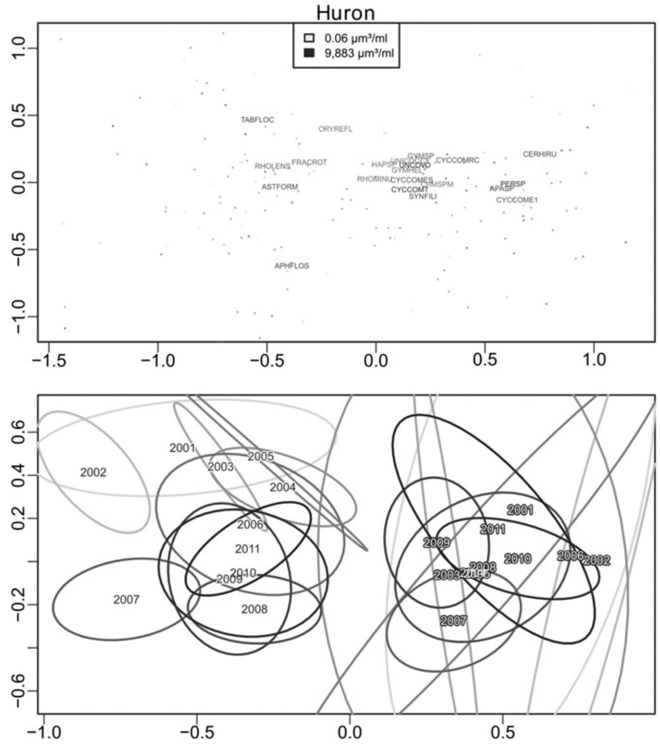

Fig. 8. Species (top) and sample (bottom) scores from NMDS analysis of phytoplankton biovolume assemblages from Lake Huron. Darker species scores indicate higher average abundance for the 10-year period. The 20 most abundant taxa for the period are labeled by their species code (Tables 1 and 2) while rarer taxa are indicated by dots. The legend at the top of each species ordination indicates the lowest and highest taxon average abundance. The lower plot illustrates supplementary plotting of all samples which are summarized by annual ellipses for each season (more recent samples have darker ellipses) with the year plotted at each period centroid. Centroids for spring ellipses are in black text and centroids for summer ellipses are in white text.

year, with much of the decline due to reductions in the populations of *Tabellaria flocculosa* and *A. islandica* (Barbiero et al., 2011a). In addition, a reduction in average cell sizes of certain dominant taxa was noted (Reavie and Barbiero, 2013), suggesting selective grazing of larger cells by filter-feeders (i.e., mussels). The species composition in Lake Huron remains different from assemblages observed in the early 2000s, particularly during spring. A reduction in spring diatoms, especially *A. islandica*, has similarly been observed in paleolimnological data from Lake Superior, where it was suggested that nutrient abatement largely caused a stratigraphic reduction in *A. islandica* in the mid-20th century (Stoermer et al., 1985). While *A. islandica* has some well-known autecological characteristics in the Great Lakes, such as high silica requirements and a tendency for winter and spring blooms during colder, isothermic conditions (Twiss et al., 2012), this taxon has been noted elsewhere to prosper in more mesotrophic environments (e.g., Canter and Haworth, 1991). Bottom-up controls due to shifting nutrients and ionic composition are very likely to be important drivers (e.g., Barbiero et al., 2011a) and may be favoring a limited number of algae species that are tolerant of these revised and still-changing conditions.

Lakes Huron and Michigan experienced significant expansion of dreissenid populations during the 11-year period, so it is not surprising there are some similarities in phytoplankton changes. A number of possible mechanisms have been invoked to account for the interaction between dreissenid populations and declines in phytoplankton biomass, including sequestration of nutrients by dreissenids in the nearshore (Hecky et al., 2004), nutrient retention in mid-depths by deeper-living mussels (Vanderploeg et al., 2010), and direct filtration of phytoplankton during periods of isothermy (Fahnenstiel et al., 2010). Lower pelagic nutrients may also be a result of reductions in external loading (Barbiero et al., 2012).

It is not known why phytoplankton reduction was more substantial in Lake Huron despite a slower expansion of the dreissenid population in that lake. However, between-lake similarities in phytoplankton shifts suggest parallel, dreissenid-driven mechanisms for the decline. Most notable is the spring loss of diatoms in both lakes, although in Lake Huron this loss was more attributed to pennate diatoms such as *Fragilaria crotonensis*. During the mid- to late-20th century, these lakes experienced progressive eutrophication; sediment records manifested this change as an increase in accumulation of *Aulacoseira* (often identified as *Melosira*) taxa, particularly *A. islandica* (Parker and Edgington, 1976; Stoermer et al., 1990) as well as other taxa (*Fragilaria*, *Tabellaria* and *Asterionella*) in Huron (Wolin et al., 1988). Although comparisons between synoptic phytoplankton samples and sedimentary assemblages can be challenging because sediments integrate year-round deposition, the recent decline in these taxa suggests a reversion to an earlier condition, at least in terms of spring diatom abundance. However, relative dominance of *Cyclotella* species in summer diatoms equates with a late 20th century increase in the stratigraphic record from Lake Michigan (Stoermer et al., 1990) and Lake Huron (Wolin et al., 1988), well before establishment of dreissenids. Overall, the modern phytoplankton changes in these lakes reflect oligotrophication, perhaps to a standing crop like that prior to European settlement, but it is still a modified condition supporting an assemblage that has been reorganizing for more than 100 years.

Simultaneous changes have been observed over our sampling period for other water quality variables, notably increasing chloride (Chapra et al., 2009) and silica (Barbiero et al., 2012) and decreasing phosphorus loading (Dolan and Chapra, 2012). Salinity is a strong determinant of phytoplankton (e.g. Fritz et al., 1993), but the potential effects of chloride, which may or may not be related to anthropogenic inputs such as road salt (Chapra et al., 2009), on phytoplankton community size and composition in the Great Lakes are not known. The decline in pelagic nutrients appears to be the major driver of these declines; higher silica is likely due to a lack of use in response to a reduced spring diatom population. This is a fair contrast to the central basin of Lake Erie which is experiencing a decline in spring silica concentrations due to uptake by larger diatom populations.

Compared to more recent years, spring phytoplankton around the turn of the 21st century were higher in Lake Huron based on biovolumes (Figs. 5 and 7) and chlorophyll measurements (Barbiero and Tuchman, 2001). Since 2006 spring biovolumes are now similar in Lakes Huron and Michigan, generally ranging between 40,000 and 100,000 μm^3/mL, suggesting that other environmental factors may be ensuring some minimum algal production despite greater dreissenid abundance in Lake Michigan. Based on water quality acquired simultaneously with our phytoplankton collections, increases in Lake Michigan nitrate concentrations have been observed in spring and summer (unpublished data), a similar trend to that observed for Lake Superior due to a purported combination of the lake's nitrogen cycle actively producing nitrate and a conservative build-up of atmosphere-derived nitrates (Sterner, 2011). No trend in nitrates was observed for Lake Huron, suggesting that phytoplankton may also be determined by differential nutrient limitation. While there has been some convergence of biovolume among Lakes Michigan, Huron, and Superior, as concurrently observed for satellite-inferred chlorophyll data (Barbiero et al., 2012), Lake Superior remains less productive with average spring biovolumes ranging between 25,000 and 50,000 μm^3/mL.

Lake Erie

Spring and summer sampling revealed recent, rapid increases in phytoplankton abundance in Lake Erie, a trend that is probably at least

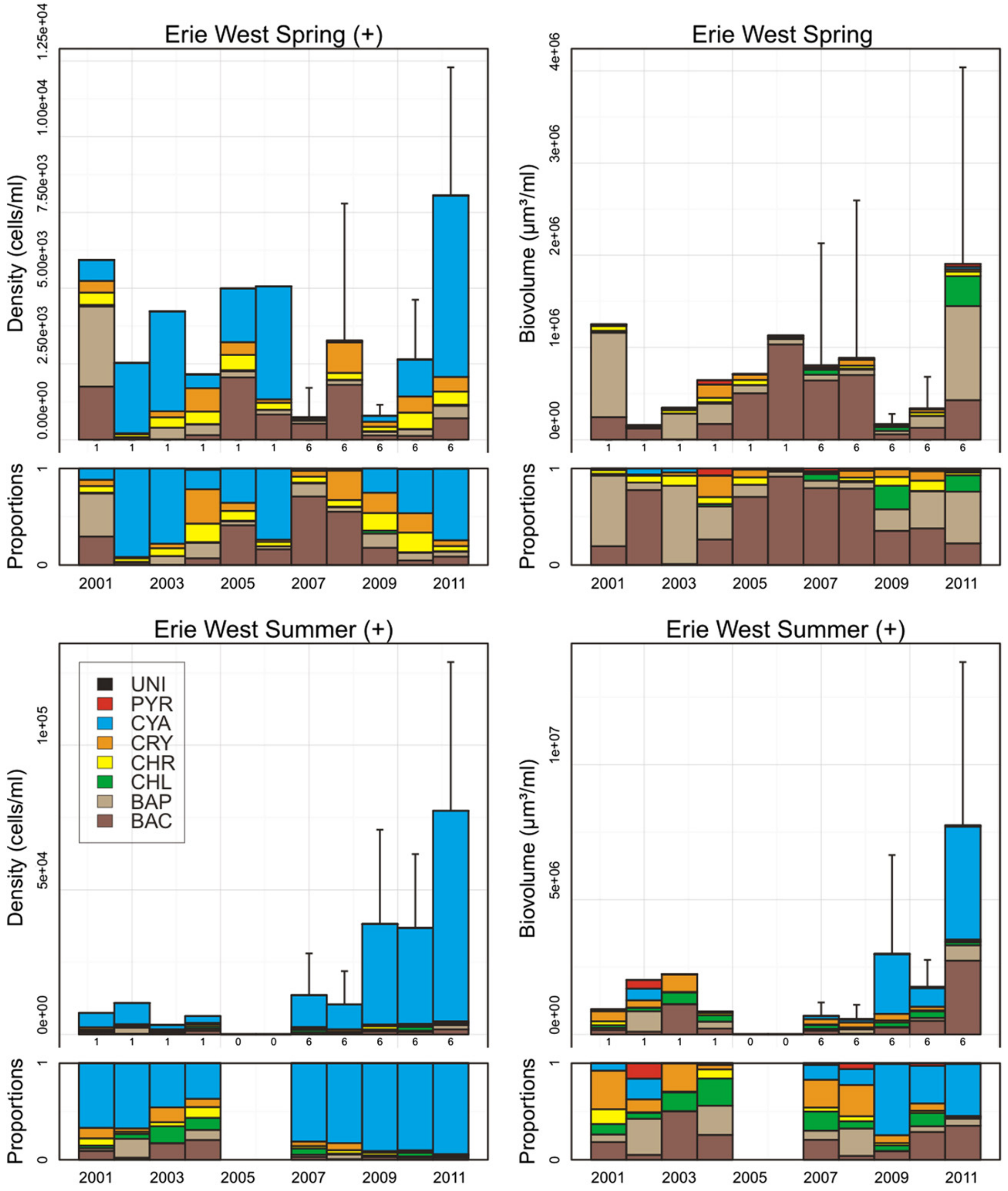

Fig. 9. Basin-wide averages of phytoplankton abundance in spring (top) and summer (bottom), from 2001 to 2011 in the Lake Erie western basin. Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of each absolute abundance bar indicate the number of samples averaged, and below that the relative abundances are shown as proportions. Error bars represent a standard error of the sample totals. A significant increasing (+) trend (Kendall's rank correlation test, $P < 0.05$) for the 11-year period is indicated in the respective headings. Taxon group codes match those from Fig. 2.

partly associated with anthropogenic drivers that have determined the lake's algal community for several decades. It is well known that long-term anthropogenic influences on Lake Erie resulted in changes to phytoplankton community composition (Allinger and Reavie, 2013). Prior to the 1950s, the lake was usually dominated by diatoms, but increases in chlorophytes and summer cyanophyte blooms, especially in the western basin, were prominent in the 1960s and 1970s. Beginning in the 1960s, there has been a substantial reduction in the nutrient load to Lake Erie (Allinger and Reavie, 2013; Dolan and McGunagle, 2005) and a corresponding reduction in algal blooms (Makarewicz,

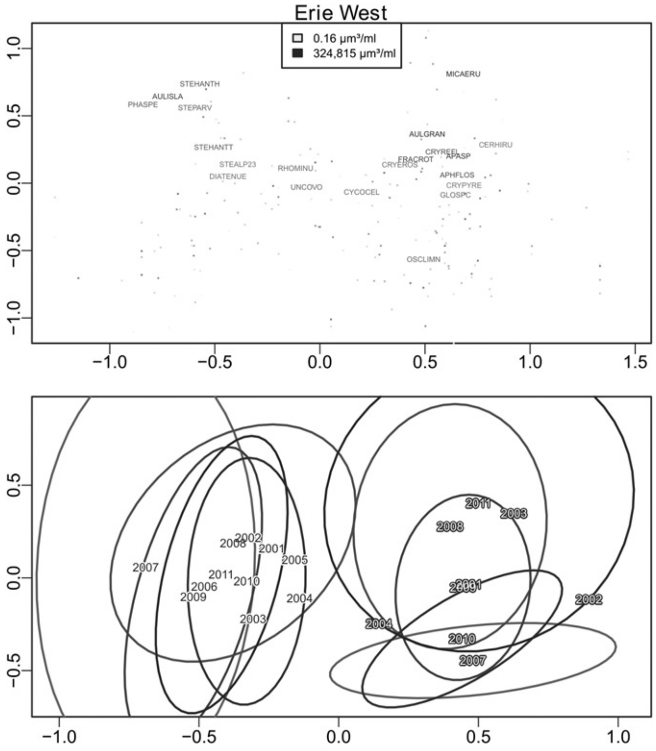

Fig. 10. Species (top) and sample (bottom) scores from NMDS analysis of phytoplankton biovolume assemblages from the Lake Erie western basin. Darker species scores indicate higher average abundance for the 10-year period. The 20 most abundant taxa for the period are labeled by their species code (Tables 1 and 2) while rarer taxa are indicated by dots. The legend at the top of each species ordination indicates the lowest and highest taxon average abundance. The lower plot illustrates supplementary plotting of all samples which are summarized by annual ellipses for each season (more recent samples have darker ellipses) with the year plotted at each period centroid. Centroids for spring ellipses are in black text and centroids for summer ellipses are in white text. Years with no ellipses had fewer than three samples.

1993; Nicholls and Hopkins, 1993) and populations of the invertebrate *Diporeia* in the eastern basin (Barbiero et al., 2011b). However, since phytoplankton minima were reached in approximately the mid-1990s (Dahl et al., 1995), monitoring data through 2002 revealed an increase in phytoplankton biomass in all basins (Conroy et al., 2005). Since then, the shallow western basin of Lake Erie had an increase in blue-green algae, concurring with similar nearshore increases (Michalak et al., 2013). (It is worth noting that our August collections may have captured the blue-green algae blooms before they peaked.) Nutrient loads to coastal waters have been periodically high, favoring nearshore summer blooms (Michalak et al., 2013), but measurements from the pelagic stations do not suggest a nutrient increase. The small-celled blue-green algae in our summer samples may have been allochthonous algae that were carried from nearshore locations, as suggested by satellite photographs that connect coastal blue-green algae blooms with pelagic regions (Michalak et al., 2013). Also, the recent decline in the Redfield (nitrogen:phosphorus) ratio in western and central Lake Erie (unpublished data) may be favoring cyanobacteria such as *Microcystis aeruginosa* (Marinho, 2007). Selective feeding by dreissenids may also be allowing for higher abundances of blue-green algae, but such a trend would not be expected in the deeper central and eastern basins (Makarewicz et al., 1998).

There may be an allochthonous component to the recent increases in blue-green algae in the central and eastern basins of Lake Erie, but the recent increase in biomass of filamentous centric diatoms are known to be derived from sub-ice developments prior to spring sampling (Twiss et al., 2012). Further, cell-size analyses revealed an increase in the average size of algal cells largely attributed to *A. islandica* (Reavie and Barbiero, 2013). It is conjectured that silica availability and winter mixing to supply nutrients and propagules have caused the recent diatom blooms, which continue to flourish immediately following ice melt. Currently we have no explanation for the relatively high biovolume of *A. islandica* since the mid-2000s; a longer time series is needed to evaluate relationships with other environmental variables.

There were changes in phytoplankton during the decade, but NMDS analyses suggest there has not been a permanent change in relative assemblage structure since 2001. The spring and summer blooms may be contributing to the low-oxygen “dead zone” in the central basin, more so due to the filamentous diatoms which comprise a substantially higher total biovolume than summer algae. An updated evaluation of the year-to-year dynamics of the dead zone magnitude and extent (Burns et al., 2005) should be related to these trends in phytoplankton biovolume.

Lake Ontario

Over our 11-year sampling period in Lake Ontario, we did not observe significant changes in phytoplankton biovolume. A significant decline in Lake Ontario's phytoplankton biomass from the 1970s through the 1990s (Millard et al., 2003; Munawar and Munawar, 2003) was associated with concomitant declines in zooplankton (e.g., Holeck et al., 2008). Significant declines in the invertebrate *Diporeia* occurred between 1994 and 1997 (Lozano et al., 2001), and more recent data indicate that this decline is continuing (Barbiero et al., 2011b). In addition to decreasing nutrient loads (Dove, 2009), non-native dreissenid grazing may be reducing the offshore nutrient load, and the removal of phytoplankton is likely contributing to the zooplankton decline between 1987 and 2005 (Stewart et al., 2010). Although trends from 2001 through 2011 suggest no significant change in algal biovolume, changes are taking place in the composition of the phytoplankton assemblages. More recent data reveal relatively greater numbers of spring diatoms and dinoflagellates, and blue-green algae comprise more of the summer assemblage. The increasing abundance of blue-green algae may be a result of the selective effect of the still growing dreissenid population, as suggested by Vanderploeg et al. (2001) in Lake Erie. As of summer 2008, a substantial population of dreissenids occupies Lake Ontario's nearshore regions (Pennuto et al., 2012), and they are also abundant in deeper waters (Rudstam et al., 2012), as similarly observed by Nalepa et al. (2009) in Lake Michigan. Additional studies are needed to confirm whether dreissenid abundance is continuing to increase. In addition, nitrates are increasing, in-lake phosphorus has remained steady (unpublished data), and phosphorus load is decreasing (Dolan and Chapra, 2012). It is also possible that phytoplankton are being affected by shifts in nutrient limitation, as has been suggested for *Microcystis* in western Lake Erie (Chaffin et al., 2011), but additional empirical studies are required to establish such a relationship across additional Great Lakes taxa.

Summary

By multiple accounts, the Great Lakes are developing new water quality conditions, in many cases undoubtedly a result of food web modification. The recent shift to low-nutrient algal assemblages in Lakes Michigan and Huron is likely due to the direct and indirect effects of the dreissenid advance. However, contemporary changes in non-infested lakes are due to lesser-known drivers. While not clearly visible in our recent dataset, longer-term changes in Lake Superior are likely due to shifts in water quality and physical characteristics related to atmospheric and lake warming. In Lake Erie, ascribing assemblage–environmental relationships is problematic because the phytoplankton are being affected by multiple

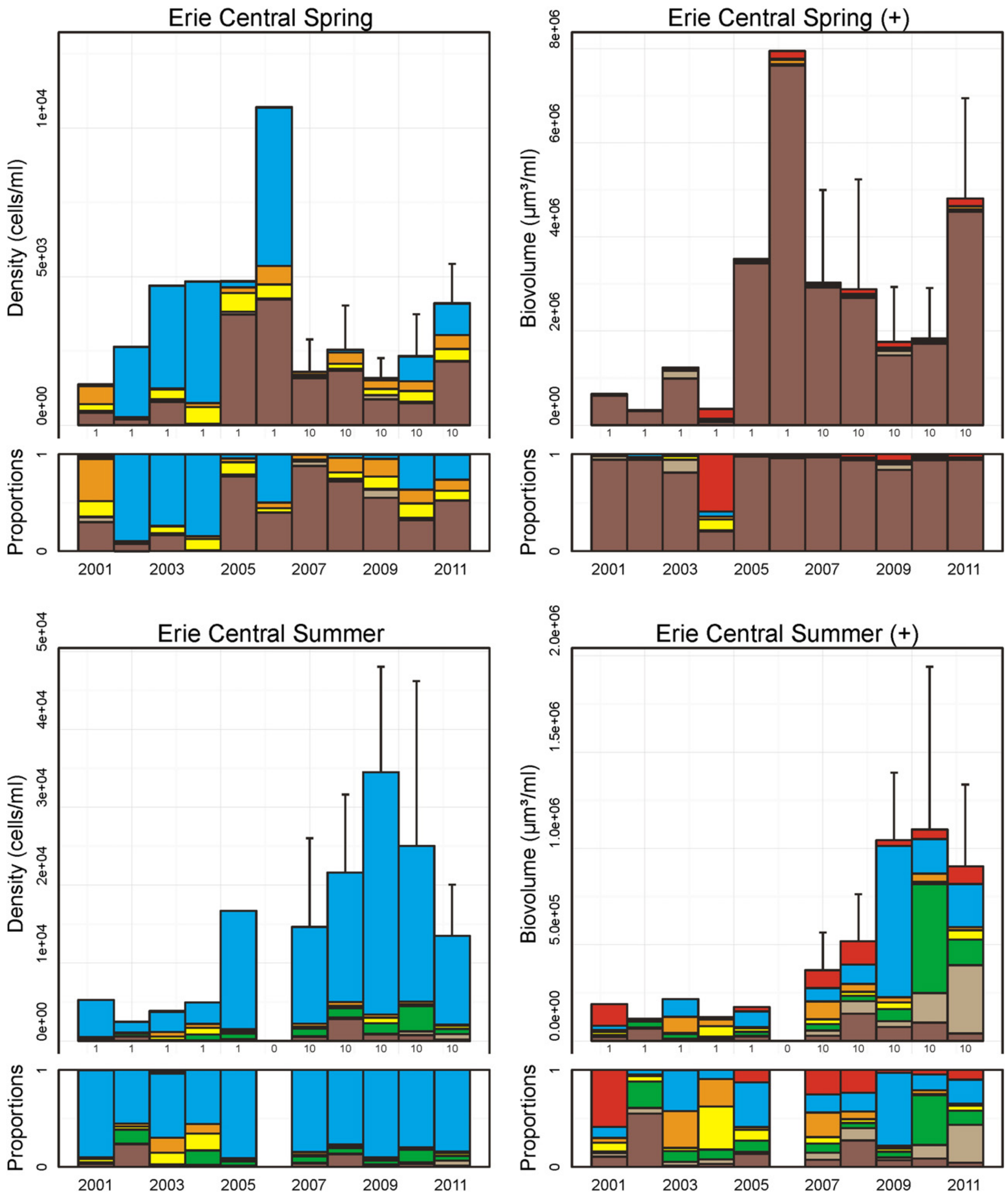

Fig. 11. Basin-wide averages of phytoplankton abundance in Lake Erie central (upper) and eastern (lower) basins. Abundance data are summarized for spring and summer, from 2001 to 2011. Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of each absolute abundance bar indicate the number of samples averaged, and below that the relative abundances are shown as proportions. Error bars represent a standard error of the sample totals. A significant positive (+) trend (Kendall's rank correlation test, $P < 0.05$) for the 11-year period is indicated in the respective headings. Taxon group codes match those from Fig. 2.

interacting variables with dominant influences being unknown or shifting throughout a year. Other variables that may be determining patterns in the phytoplankton communities include changing physical conditions (especially stratification), the amount of time since ice-out (i.e., age of spring population), and the presence of pelagic grazers, all of which need to be better characterized and analyzed in an integrated way with phytoplankton data if we are to better understand changes.

Continuing studies include refined analyses of relationships among pelagic phytoplankton, water quality, stressors (e.g., atmospheric

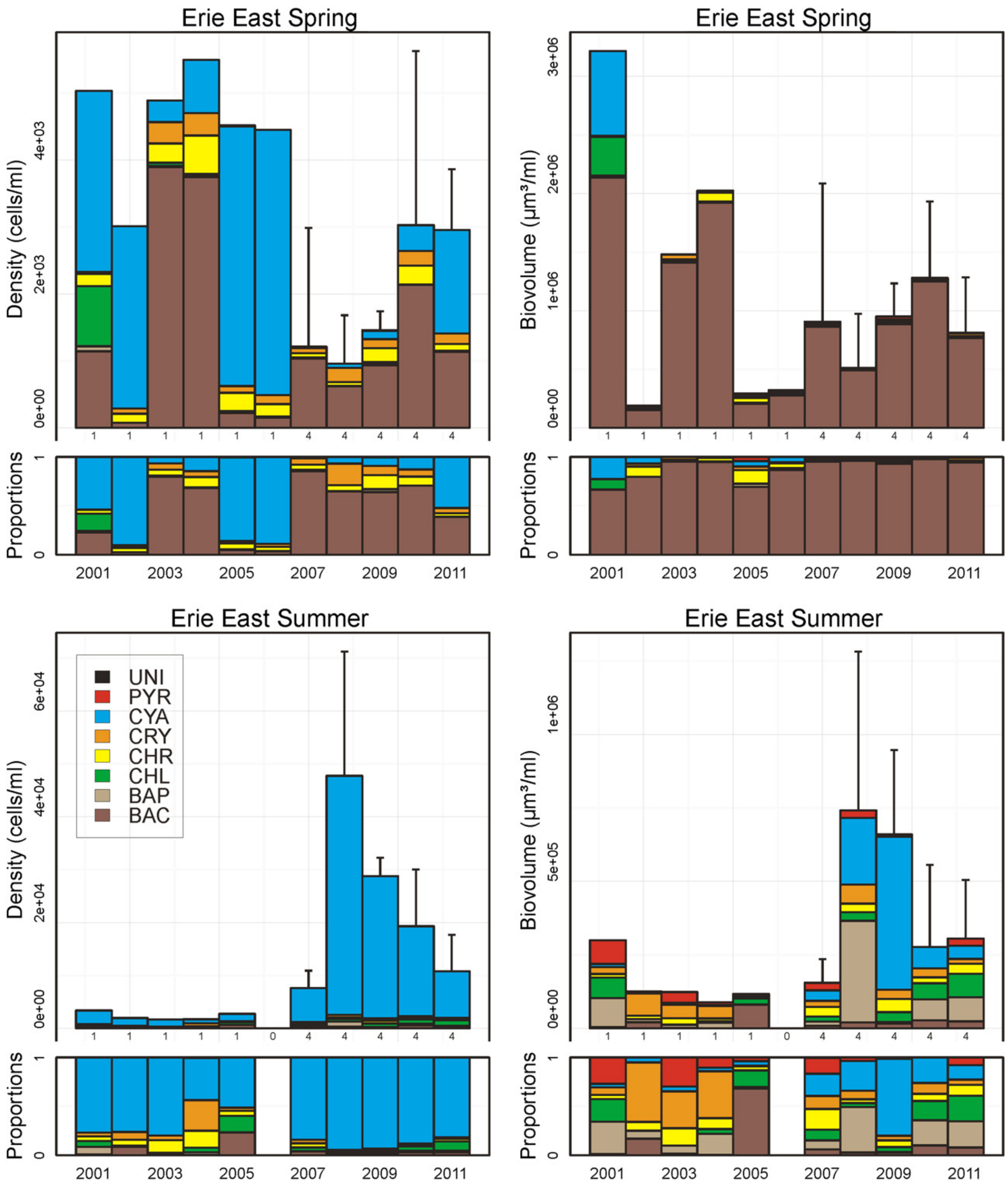

Fig. 11 (*continued*).

effects, agriculture, urban development), and zooplankton. New, concurrent paleolimnology studies are underway to better place modern phytoplankton assemblages in a long-term context for the lakes. For instance, a recent sedimentary study of diatom fossils in Lake Superior revealed that major recent determinants of phytoplankton include warming and suggested that assemblages are evolving to something unlike any previously observed in the lake (Chraïbi et al., in press). Also, the nature and importance of late-summer deep chlorophyll maxima (DCM) are poorly understood, but we know that the depth and algal content of the DCM has changed (e.g., Lake Superior; Barbiero and Tuchman, 2001) and that it is probable that this aspect of the algal crop should not be ignored if we are to better understand overall phytoplankton dynamics.

These ecological trend and trajectory data have the potential to guide management of lake quality through contemporary evaluation of changing lake conditions. Ultimately, better characterizing and

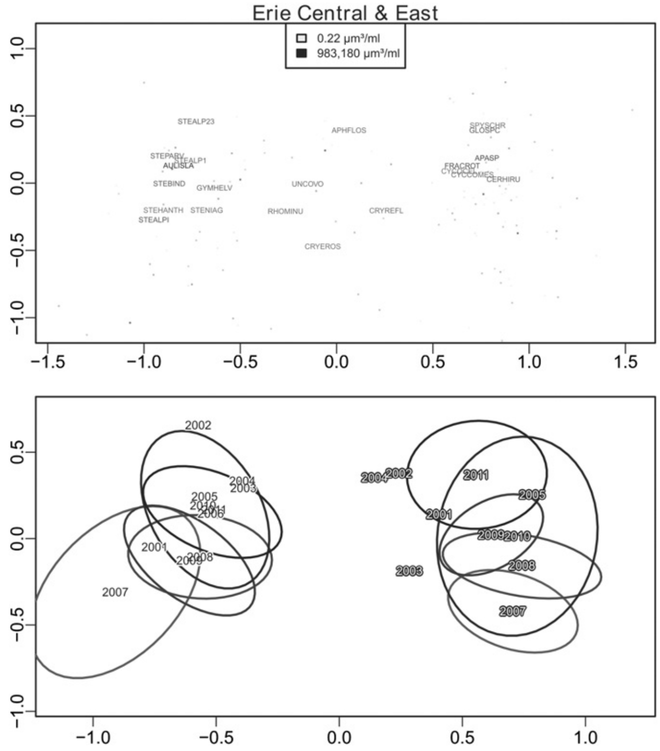

Fig. 12. Species (top) and sample (bottom) scores from NMDS analysis of phytoplankton biovolume assemblages from the Lake Erie central and eastern basins. Darker species scores indicate higher average abundance for the 10-year period. The 20 most abundant taxa for the period are labeled by their species code (Tables 1 and 2) while rarer taxa are indicated by dots. The legend at the top of each species ordination indicates the lowest and highest taxon average abundance. The lower plot illustrates supplementary plotting of all samples which are summarized by annual ellipses for each season (more recent samples have darker ellipses) with the year plotted at each period centroid. Centroids for spring ellipses are in black text and centroids for summer ellipses are in white text. Years with no ellipses had fewer than three samples.

explaining mechanisms determining phytoplankton shifts will be critical to managing the causes and impacts of changes in the lakes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2014.04.013.

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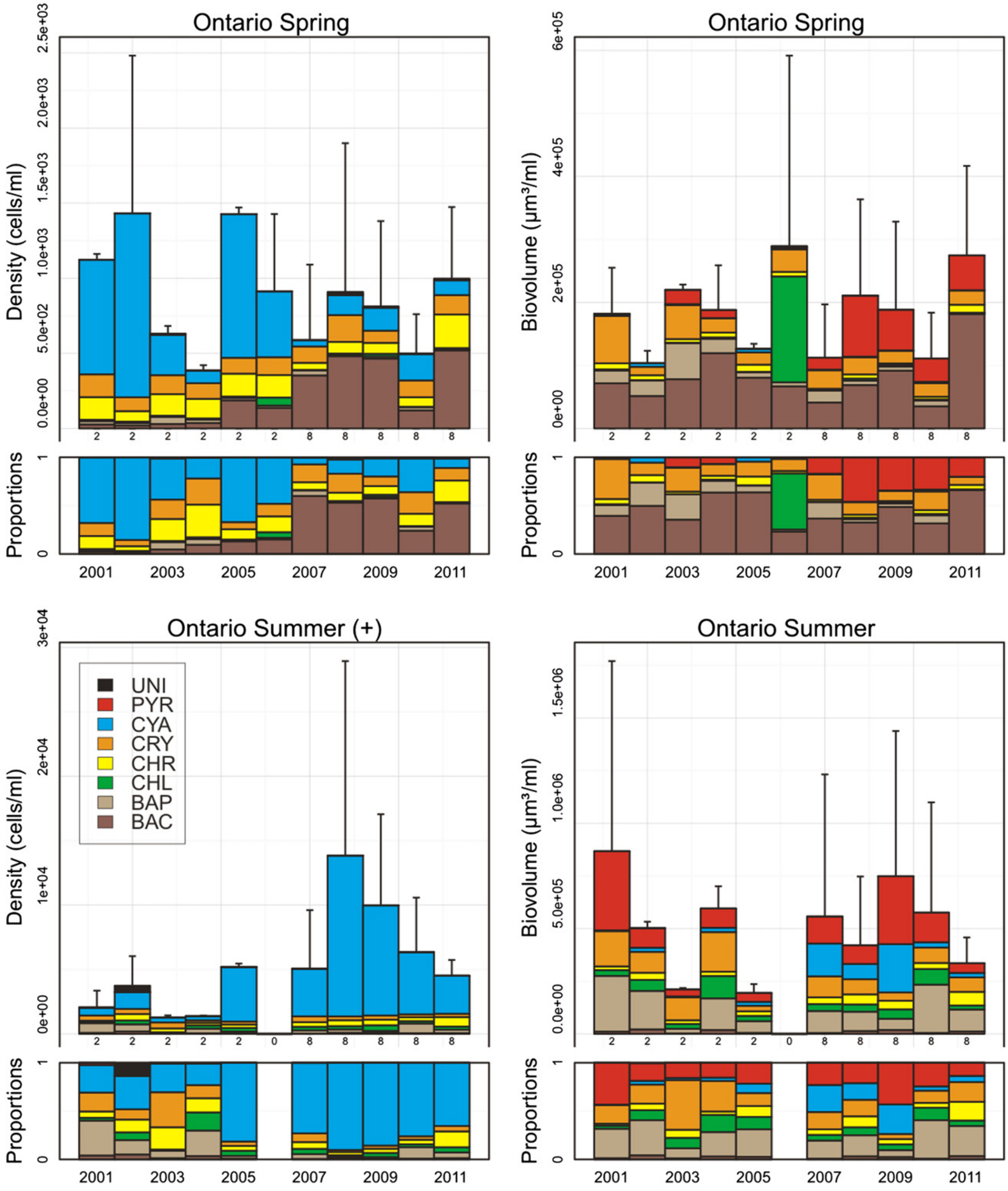

Fig. 13. Basin-wide averages of phytoplankton abundance in spring (top) and summer (bottom), from 2001 to 2011 in Lake Ontario. Algal cell densities (left) and biovolume (right) are presented. Numbers at the bottom of each absolute abundance bar indicate the number of samples averaged, and below that the relative abundances are shown as proportions. Error bars represent a standard error of the sample totals. A significant increasing (+) trend (Kendall's rank correlation test, $P < 0.05$) for the 11-year period is indicated in the respective headings. Significant positive trends for the 11-year period (+) are indicated in the respective heading. Taxon group codes match those from Fig. 2.

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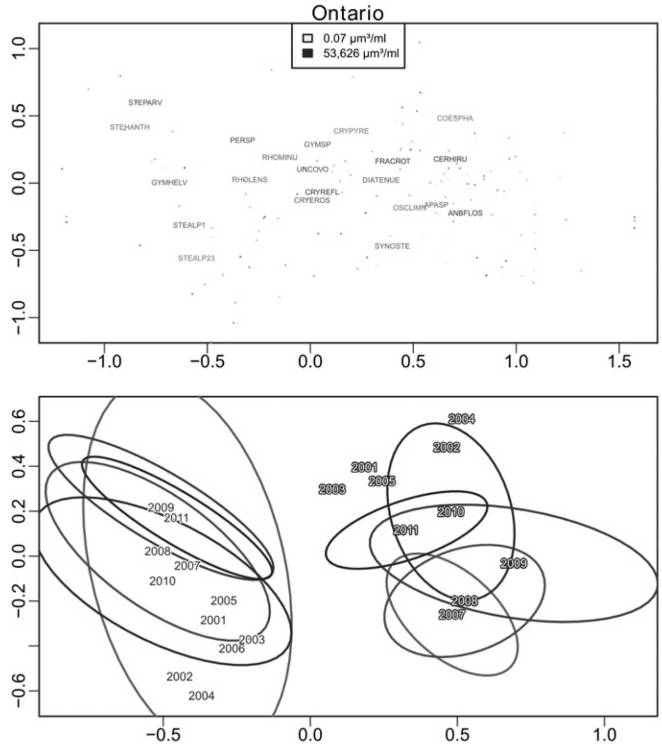

Fig. 14. Species (top) and sample (bottom) scores from NMDS analysis of phytoplankton biovolume assemblages from Lake Ontario. Darker species scores indicate higher average abundance for the 10-year period. The 20 most abundant taxa for the period are labeled by their species code (Tables 1 and 2) while rarer taxa are indicated by dots. The legend at the top of each species ordination indicates the lowest and highest taxon average abundance. The lower plot illustrates supplementary plotting of all samples which are summarized by annual ellipses for each season (more recent samples have darker ellipses) with the year plotted at each period centroid. Centroids for spring ellipses are in black text and centroids for summer ellipses are in white text. Years with no ellipses had fewer than three samples.

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