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LAKE-WIDE BENTHIC SURVEYS IN LAKE MICHIGAN IN 1994-95, 2000, 2005, AND 2010: ABUNDANCES OF THE AMPHIPOD *DIPOREIA SPP.* AND ABUNDANCES AND BIOMASS OF THE MUSSELS *DREISSENA POLYMORPHA* AND *DREISSENA ROSTRIFORMIS BUGENSIS*

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1.0 INTRODUCTION

This technical report provides basic results of lake-wide, benthic surveys conducted in Lake Michigan in 1994-1995, 2000, 2005, and 2010 to assess temporal trends in the native amphipod *Diporeia* spp., the zebra mussel (*Dreissena polymorpha*), and the quagga mussel (*Dreissena rostriformis bugensis*). These surveys are an expansion of a continuing, monitoring program in the southern basin of the lake conducted by the Great Lakes Environmental Research Laboratory (GLERL) that examines trends in the abundance and composition of the entire macroinvertebrate community (Nalepa 1987, Nalepa et al. 1998). The GLERL program was initiated in 1980 with the original intent of assessing the response of the benthic community to phosphorus abatement efforts in the mid-1970s (Nalepa 1987). However, after *D. polymorpha* became established in the southwestern portion of the lake in 1989 (Marsden et al. 1993), the monitoring program detected several dramatic changes in the benthic community in the early 1990s. *Diporeia* began to systematically disappear, and *D. polymorpha* rapidly expanded and soon became dominant in the nearshore region (Nalepa et al. 1998). To determine if changes in the southern basin were also occurring throughout the lake, the monitoring program was greatly expanded in 1994-1995. Benthic sampling in these two years was conducted jointly with several other sampling programs in Lake Michigan: Environmental Monitoring and Assessment (EMAP) and Lake Michigan Mass Balance (LMMB). After 1994-1995, lakewide monitoring of *Diporeia* and *Dreissena* populations continued at 5-year intervals (i.e., 2000, 2005, and 2010) as part of a regular monitoring program at GLERL that supplemented the continued effort in the southern basin.

A technical report previously published (Nalepa et al. 2008) provided abundances of *Diporeia*, *D. polymorpha*, and *D. r. bugensis* at all sites sampled in 1994-1995, 2000, and 2005. In this report, we provide data collected in 2010 along with data collected in these previous surveys. We also include biomass estimates (ash-free dry weight) of *D. polymorpha* and *D. r. bugensis* for all four survey periods. As in the previous report, these data are presented with minimal analysis and interpretation; further, more-detailed analysis and discussion will be provided in other publications.

2.0 MATERIALS AND METHODS

2.1 Sampling Sites

Site locations and depths of sites sampled in 1994-1995, 2000, 2005, and 2010 are given in Table 1. For spatial comparisons on a regional basis, the sites were placed into five regions of the lake: southern, central, and northern regions of the main basin, Green Bay, and Grand Traverse Bay (Figure 1) (Nalepa et al. 2000). For the 1994-1995 period, samples were collected at 90 sites during two cruises in 1994 (late July and early September), and one cruise in 1995 (late August/early September). Sampling sites were part of either EMAP (n = 49), LMMB (n = 33), or various sampling programs at GLERL (n = 8). Site locations in EMAP were based on a random, probabilistic design (Stevens 1997) within the 85-m contour of the main lake, Green Bay, and Grand Traverse Bay, while site locations in LMMB were focused in offshore, depositional areas of the main lake. GLERL sites were located at various depths throughout the southern basin (Nalepa et al. 1985). In 2000, the number of sites sampled was expanded to 157. Sampled sites included 21 EMAP and 10 LMMB sites that were sampled in 1994-1995 and the 40 sites that were part of the GLERL monitoring program in the southern basin and regularly sampled since 1980. The other sites (n = 86) were added to provide broader spatial coverage of the lake than occurred in 1994-1995. These added sites were mostly along transects at 20, 30, 45, 60 m, and 80 m on both the east and west sides of the lake. In Green Bay, two of the five sites sampled in 1994-1995 were not sampled in 2000, but five sites were added in the outer bay. These sites were part of an assessment of food resources available to lake whitefish. In Grand Traverse Bay, only one site was sampled in 1994-1995; this site was re-sampled in 2000, along with 20 additional sites that were also part of the food resource assessment. All sites sampled in 2000 were also sampled in 2005 along with three additional sites (n = 160 total). All sites in the main lake that were sampled in 2000 and 2005 were re-sampled in 2010; however, no sites in Grand Traverse Bay or in inner Green Bay were sampled in 2010 because of time constraints. Locations of all sites sampled within each lake region regardless of year are given in Figures 2-6.

Table 1. Location and depth of sites sampled in 1994-1995, 2000, 2005, and 2010. Station designations and locations were associated with the following sampling programs: Environmental Monitoring and Assessment Program (EMAP); Lake Michigan Mass Balance (LMMB); Great Lakes Environmental Research Lab (GLERL) southern basin monitoring. GLERL* = Great Lakes Environmental Research Lab, 5-year lake-wide survey.
Link to excel file: http://www.glerl.noaa.gov/ftp/publications/tech_reports/glerl-164/tm-164_Table1.xlsx

Station	Program	Depth	Latitude	Longitude	1994	1995	2000	2005	2010
South Region									
A-1	GLERL	18	42°06.50	86°32.00			X	X	X
A-2	GLERL	35	42°06.00	86°37.00			X	X	X
A-4	GLERL*	74	42°03.50	87°06.50			X	X	X
B-2	GLERL	47	42°24.00	86°27.00			X	X	X
B-3	GLERL	68	42°24.00	86°35.50			X	X	X
B-4	GLERL	129	42°23.50	87°01.00			X	X	X
B-5	GLERL	108	42°23.50	87°21.00			X	X	X
B-6	GLERL	83	42°22.50	87°30.00			X	X	X
B-7	GLERL	45	42°22.00	87°40.00	X		X	X	X
C-1	GLERL	20	42°49.67	86°14.83			X	X	X
C-2	GLERL*	46	42°49.67	86°18.14			X	X	X
C-3	GLERL	77	42°49.17	86°28.42	X		X	X	X
C-5	GLERL	129	42°49.00	86°50.00			X	X	X
C-6	GLERL	93	42°47.67	87°26.83			X	X	X
C-7	GLERL	55	42°47.50	87°34.50	X		X	X	X
C-45	GLERL*	45	41°56.96	87°13.44			X	X	X
EG-12	GLERL	56	42°22.70	87°37.00			X	X	X
EG-14	GLERL	95	42°22.70	86°46.50			X	X	X
EG-18	GLERL	57	42°17.60	86°38.57	X		X	X	X
EG-22	GLERL	45	43°06.20	86°22.00			X	X	X
F-2	GLERL*	45	42°30.05	86°21.86			X	X	X
F-3	GLERL*	72	42°30.10	86°31.50			X	X	X
G-45	GLERL*	45	41°56.96	87°13.44			X	X	X
H-8	GLERL	19	42°23.92	87°46.25			X	X	X
H-9	GLERL	37	42°26.75	87°42.35			X	X	X
H-11	GLERL	73	42°33.25	87°35.83			X	X	X
H-13	GLERL	19	41°55.58	87°29.42			X	X	X
H-14	GLERL	37	42°04.33	87°27.17			X	X	X
H-15	GLERL	55	42°09.50	87°26.00			X	X	X
H-18	GLERL	19	41°59.00	86°36.00			X	X	X
H-19	GLERL	37	42°00.00	86°41.08			X	X	X
H-20	GLERL	55	42°00.00	86°41.08	X		X	X	X
H-21	GLERL	73	42°02.42	86°53.00			X	X	X
H-22	GLERL	46	42°08.35	86°39.83			X	X	X
H-24	GLERL	19	42°23.25	86°20.00			X	X	X
H-28	GLERL	19	42°37.80	86°15.92			X	X	X
H-29	GLERL	37	42°37.80	86°18.35			X	X	X
H-30	GLERL	73	42°37.80	86°26.00			X	X	X

Table 1. (Cont.)

Station	Program	Depth	Latitude	Longitude	1994	1995	2000	2005	2010
H-31	GLERL	46	43°02.47	86°19.99	X		X	X	X
M-25	GLERL*	25	43°12.00	86°22.67					X
M-29	GLERL*	29	43°12.08	86°23.46	X				
M-45	GLERL*	45	43°11.43	86°25.72	X		X	X	X
N-2	GLERL*	40	41°53.50	86°52.00			X	X	X
N-3	GLERL*	61	41°58.00	86°59.00			X	X	X
Q-13	GLERL*	13	42°50.63	87°47.92				X	X
Q-30	GLERL*	30	42° 50.61	87°39.24				X	X
R-20	GLERL*	20	42°45.04	87°41.78				X	X
R-45	GLERL*	45	42°45.00	87°36.33			X	X	X
S-2	GLERL	17	41°45.90	87°23.47			X	X	X
S-3	GLERL	25	41°51.00	87°19.20			X	X	X
S-4	GLERL	40	41°56.10	87°15.10			X	X	X
SAU-45	GLERL*	45	42°41.14	86°18.90			X	X	X
T-3	GLERL*	73	42°10.00	86°43.00			X	X	X
V-1	GLERL	16	41°41.80	87°00.80			X	X	X
V-2	GLERL	29	41°49.00	87°02.90			X	X	X
X-1	GLERL	36	43°08.25	86°21.70			X	X	X
X-2	GLERL	93	43°12.00	86°31.00			X	X	X
100	LMMB	100	43°01.02	86°37.02	X				
822	LMMB	52	42°08.52	86°39.72	X				
9211	LMMB	73	43°00.96	86°24.42	X				
9222	LMMB	124	42°29.76	86°49.74	X				
9224	LMMB	73	42°30.18	86°31.74	X				
9511	LMMB	87	42° 07.20	87°03.12		X			
9531	LMMB	145	42°40.14	87°15.06		X			
9534	LMMB	157	42°46.26	87°04.56		X			
9544	LMMB	93	42°57.12	87°18.54		X			
20148	LMMB	54	42°00.81	86°45.18	X				
31916	LMMB	26	41°49.98	86°54.36	X				
73452	EMAP	17	42°50.09	86°14.76	X				
73472	EMAP	45	42°22.02	86°26.58	X				
73492	EMAP	17	41°54.00	86°38.98	X				
75000	EMAP	28	43°06.72	86°19.74	X				
75010	EMAP	58	42°52.74	86°21.42	X				
75030	EMAP	59	42°23.10	86°35.46	X				
75040	EMAP	79	42°10.50	86°44.04	X				
75050	EMAP	47	41°56.58	86°49.74	X				
75060	EMAP	6	41°42.78	86°55.98	X				
76570	EMAP	104	43°03.54	86°39.72	X				
76580	EMAP	108	42°49.68	86°45.54	X				
76590	EMAP	145	42°35.22	86°51.36	X				
76611	EMAP	65	42°59.04	87°00.85	X				

Table 1. (Cont.)

Station	Program	Depth	Latitude	Longitude	1994	1995	2000	2005	2010
76620	EMAP	43	41°53.16	87°09.24	X				
76622	EMAP	20	41°47 40	87°17.58	X				
78150	EMAP	89	43°00.30	86°59.22	X				
78190	EMAP	51	42°03.96	87°22.80	X				
79752	EMAP	80	42°37.14	87°33.24	X				
79760	EMAP	88	42°28.86	87°30.60	X				
79781	EMAP	8	41°52.32	87°35.88	X				
81340	EMAP	46	42°53.70	87°38.46	X				
89195	LMMB	52	42°17.10	86°37.92	X				
Central Region									
E-1	GLERL*	44	44°37.50	86°18.20			X	X	X
K-2	GLERL*	45	43°20.10	86°29.80			X	X	X
KE-1	GLERL*	20	44°23.30	87°28.52			X	X	X
KE-2	GLERL*	30	44°23.30	87°27.64			X	X	X
KE-3	GLERL*	45	44°23.30	87°26.34			X	X	X
KE-5	GLERL*	80	44°23.30	87°23.98			X	X	X
L-220	GLERL*	20	43°30.05	86°30.14			X	X	X
L-230	GLERL*	30	43°30.05	86°31.12			X	X	X
L-245	GLERL*	45	43°30.05	86°31.88			X	X	X
L-260	GLERL*	60	43°30.05	86°33.29			X	X	X
L-280	GLERL*	80	43°30.05	86°36.22			X	X	X
LU-1	GLERL*	20	43°56.64	86°32.10			X	X	X
LU-3	GLERL*	45	43°56.64	86°36.49			X	X	X
LU-4	GLERL*	60	43°56.64	86°37.60			X	X	X
LU-5	GLERL*	80	43°56.64	86°39.00			X	X	X
MAN-1	GLERL*	20	44°24.78	86°16.93			X	X	X
MAN-2	GLERL*	30	44°24.78	86°17.18			X	X	X
MAN-3	GLERL*	45	44°24.78	86°19.91			X	X	X
MAN-4	GLERL*	60	44°24.78	86°20.37			X	X	X
MAN-5	GLERL*	80	44°24.78	86°20.82			X	X	X
PW-2	GLERL*	30	43°26.82	87°46.92			X	X	X
PW-3	GLERL*	45	43°26.82	87°46.19			X	X	X
PW-4	GLERL*	60	43°26.82	87°44.04			X	X	X
PW-5	GLERL*	80	43°26.82	87°41.90			X	X	X
SY-1	GLERL*	20	43°55.09	87°39.83			X	X	X
SY-2	GLERL*	30	43°55.09	87°38.86			X	X	X
SY-4	GLERL*	60	43°55.09	87°30.32			X	X	X
SY-5	GLERL*	80	43°55.09	87°22.54			X	X	X
9552	LMMB	86	43°11.10	87°12.54		X	X	X	X
9554	LMMB	114	43°14.28	86°53.22		X	X	X	X
9556	LMMB	71	43°18.30	87°46.32		X	X	X	X
9559	LMMB	80	43°25.14	87°06.54		X			
9561	LMMB	138	43°28.26	86°47.04		X			X

Table 1. (Cont.)

Station	Program	Depth	Latitude	Longitude	1994	1995	2000	2005	2010
9562	LMMB	129	43°30.00	87°37.02		X	X	X	X
9564	LMMB	140	43°36.06	87°20.46		X	X	X	X
9570	LMMB	174	43°53.16	86°54.48		X			X
9574	LMMB	137	44°04.08	87°08.82		X	X	X	X
9576	LMMB	175	44°09.06	86°37.26		X	X	X	X
9577	LMMB	75	44°14.58	87°22.44		X	X	X	X
9582	LMMB	128	44°24.48	86°22.14		X	X	X	X
9587	LMMB	207	44°37.26	86°21.18		X			X
19163	LMMB	116	43°12.00	86°42.00	X				
76560	EMAP	90	43°17.70	86°33.48	X				
78110	EMAP	30	43°56.64	86°34.72	X		X	X	X
78140	EMAP	112	43°14.35	86°53.18	X				
79730	EMAP	84	43°11.10	87°12.96	X				
79732	EMAP	67	43°05.34	87°21.48	X				
81330	EMAP	88	43°07.80	87°32.70	X				
82882	EMAP	60	44°23.30	87°25.40	X		X	X	X
82902	EMAP	40	43°55.09	87°37.44	X		X	X	X
82922	EMAP	8	43°26.82	87°48.54	X		X	X	X
North Region									
EA-7	GLERL*	40	45°16.80	85°26.20			X	X	X
FR-1	GLERL*	20	44°49.00	86°08.36			X	X	X
FR-2	GLERL*	30	44°49.00	86°09.31			X	X	X
FR-3	GLERL*	45	44°49.00	86°10.13			X	X	X
FR-4	GLERL*	60	44°49.00	86°11.07			X	X	X
FR-5	GLERL*	80	44°49.00	86°11.77			X	X	X
PET-1	GLERL*	17	45°26.74	85°04.26			X	X	X
PET-2	GLERL*	32	45°26.74	85°04.53			X	X	X
PET-3	GLERL*	43	45°26.74	85°11.21			X	X	X
SB-2	GLERL*	30	44°51.44	87°10.04			X	X	X
SB-3	GLERL*	45	44°51.44	87°09.06			X	X	X
SB-4	GLERL*	60	44°51.44	87°08.21			X	X	X
SB-5	GLERL*	80	45°45.37	86°06.32			X	X	X
SB-6	GLERL*	152	44°51.44	86°55.38					X
SC-2	GLERL*	30	45°50.47	86°06.32			X	X	X
SC-3	GLERL*	45	45°49.03	86°06.32			X	X	X
SC-4	GLERL*	60	45°47.41	86°06.32			X	X	X
SC-5	GLERL*	82	45°45.37	86°06.32			X	X	X
WI-1	GLERL*	20	45°14.85	86°54.30			X	X	X
WI-2	GLERL*	30	45°14.85	86°52.57			X	X	X
WI-3	GLERL*	45	45°14.85	86°49.80			X	X	X
WI-5	GLERL*	80	45°14.85	86°38.20			X	X	X
9597	LMMB	164	44°58.32	86°22.20		X	X	X	X
9599	LMMB	208	45°00.24	86°43.44		X			

Table 1. (Cont.)

Station	Program	Depth	Latitude	Longitude	1994	1995	2000	2005	2010
74880	EMAP	23	45°54.54	85°01.50	X		X	X	X
74900	EMAP	55	45°26.74	85°13.31	X		X	X	X
76442	EMAP	20	46°00.06	85°24.60	X		X	X	X
76451	EMAP	17	45°43.36	85°19.89	X		X	X	X
76462	EMAP	55	45°32.10	85°38.16	X		X	X	X
76471	EMAP	32	45°14.52	85°33.36	X		X	X	X
76482	EMAP	28	45°04.14	85°51.42	X		X	X	X
78030	EMAP	35	45°48.72	85°43.08	X		X	X	X
79612	EMAP	21	45°54.00	86°06.32	X		X	X	X
81220	EMAP	39	45°42.60	86°24.54	X		X	X	X
81240	EMAP	57	45°14.85	86°40.11	X		X	X	X
82851	EMAP	81	45°03.01	86°55.36	X		X	X	X
82862	EMAP	12	44°51.44	87°11.40	X		X	X	X
95116	LMMB	94	45°24.00	85°35.46		X			
95118	LMMB	89	45°28.32	86°31.02		X			
95120	LMMB	140	45°31.44	86°10.14		X			X
95122	LMMB	92	45°34.44	85°49.50		X			
95126	LMMB	96	45°45.36	86°03.48		X			
Green Bay									
BBDN-1	GLERL*	12	45°42.00	86°44.50			X	X	X
BBDN-2	GLERL*	24	45°37.25	86°44.50			X	X	X
BBDN-3	GLERL*	24	45°32.50	86°44.50			X	X	X
LBDN-2	GLERL*	15	45°30.00	87°00.00			X	X	X
LBDN-3	GLERL*	25	45°30.00	87°05.83			X	X	X
82842	EMAP	37	45°19.62	87°00.54	X		X	X	X
84450	EMAP	11	45°36.18	87°05.82	X		X	X	X
84470	EMAP	23	45°08.04	87°18.36	X		X	X	
86101	EMAP	16	44°56.40	87°36.12	X				
86112	EMAP	8	44°44.82	87°53.70	X				
Grand Traverse Bay									
EA-1	GLERL*	45	44°47.00	85°31.00			X	X	
EA-2	GLERL*	45	44°47.00	85°33.00			X	X	
EA-3	GLERL*	40	44°51.00	85°27.80			X	X	
EA-4	GLERL*	40	44°54.00	85°26.12			X	X	
EA-5	GLERL*	47	44°54.00	85°29.00			X	X	
EA-6	GLERL*	20	45°02.00	85°23.65			X	X	
EA-61	GLERL*	45	45°02.00	85°24.43			X	X	
EA-62	GLERL*	70	45°02.00	85°25.01			X	X	
GT-1	GLERL*	98	44°50.00	85°37.00			X	X	
GT-3	GLERL*	112	44°59.00	85°34.80			X	X	
GT-11	GLERL*	60	44°50.00	85°38.48			X	X	
GT-12	GLERL*	45	44°50.00	85°38.63			X	X	
GT-13	GLERL*	30	44°50.00	85°38.70			X	X	

Table 1. (Cont.)

Station	Program	Depth	Latitude	Longitude	1994	1995	2000	2005	2010
GT-31	GLERL*	75	44°59.00	85°35.30			X	X	
GT-32	GLERL*	55	44°59.00	85°35.45			X	X	
GT-33	GLERL*	45	44°59.00	85°35.49			X	X	
GT-34	GLERL*	25	44 59.00	85°35.50			X	X	
GT-35	GLERL*	17	44°59.00	85°35.62			X	X	
SG-5	GLERL*	120	44°57.40	85°34.00			X	X	
SG-38	GLERL*	115	45°01.75	85°32.80			X	X	
74920	EMAP	51	45°07.86	85°27.24	X		X	X	

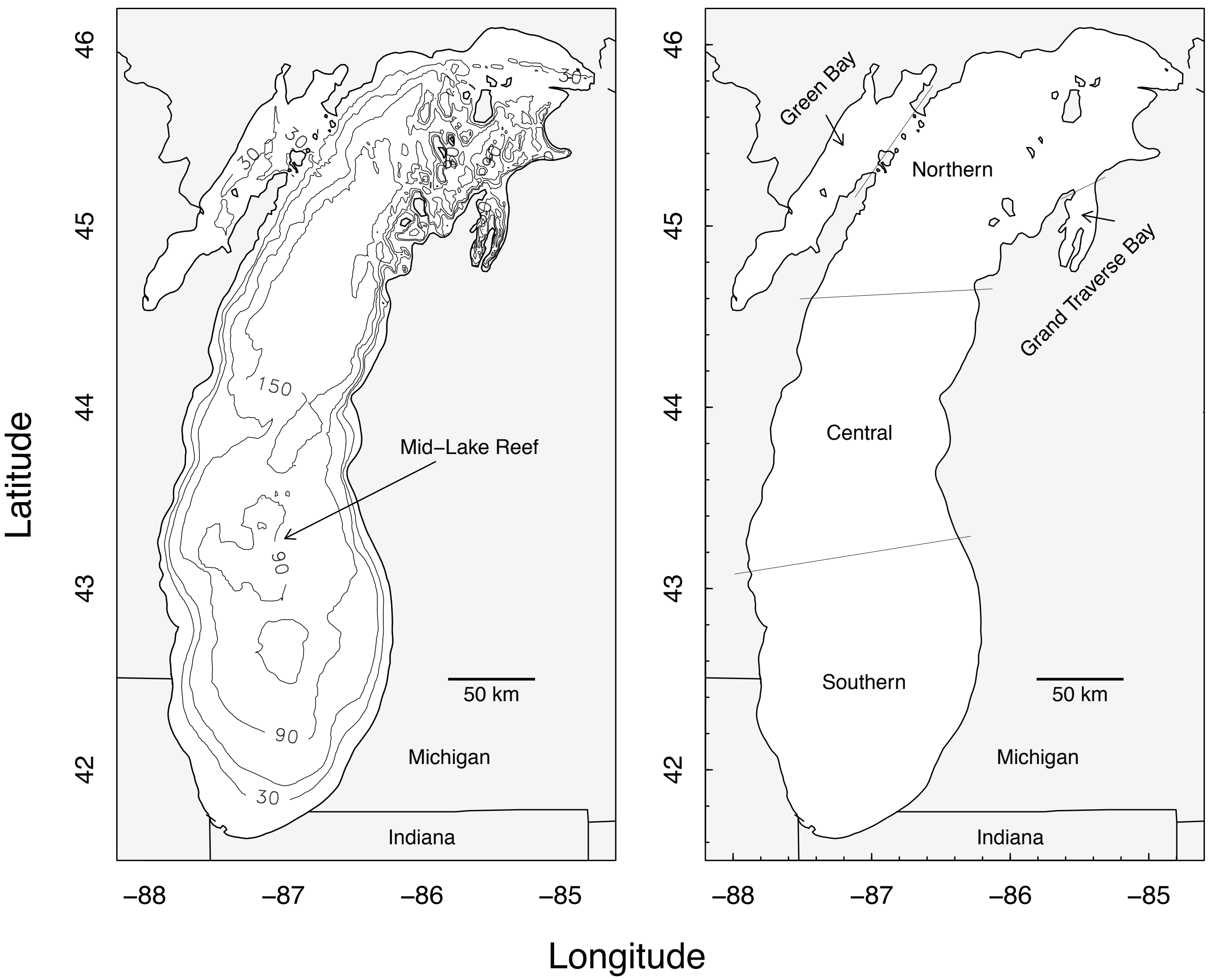

Figure 1. Bathymetric contours (left panel; in meters) and designated regions (right panel) of Lake Michigan.

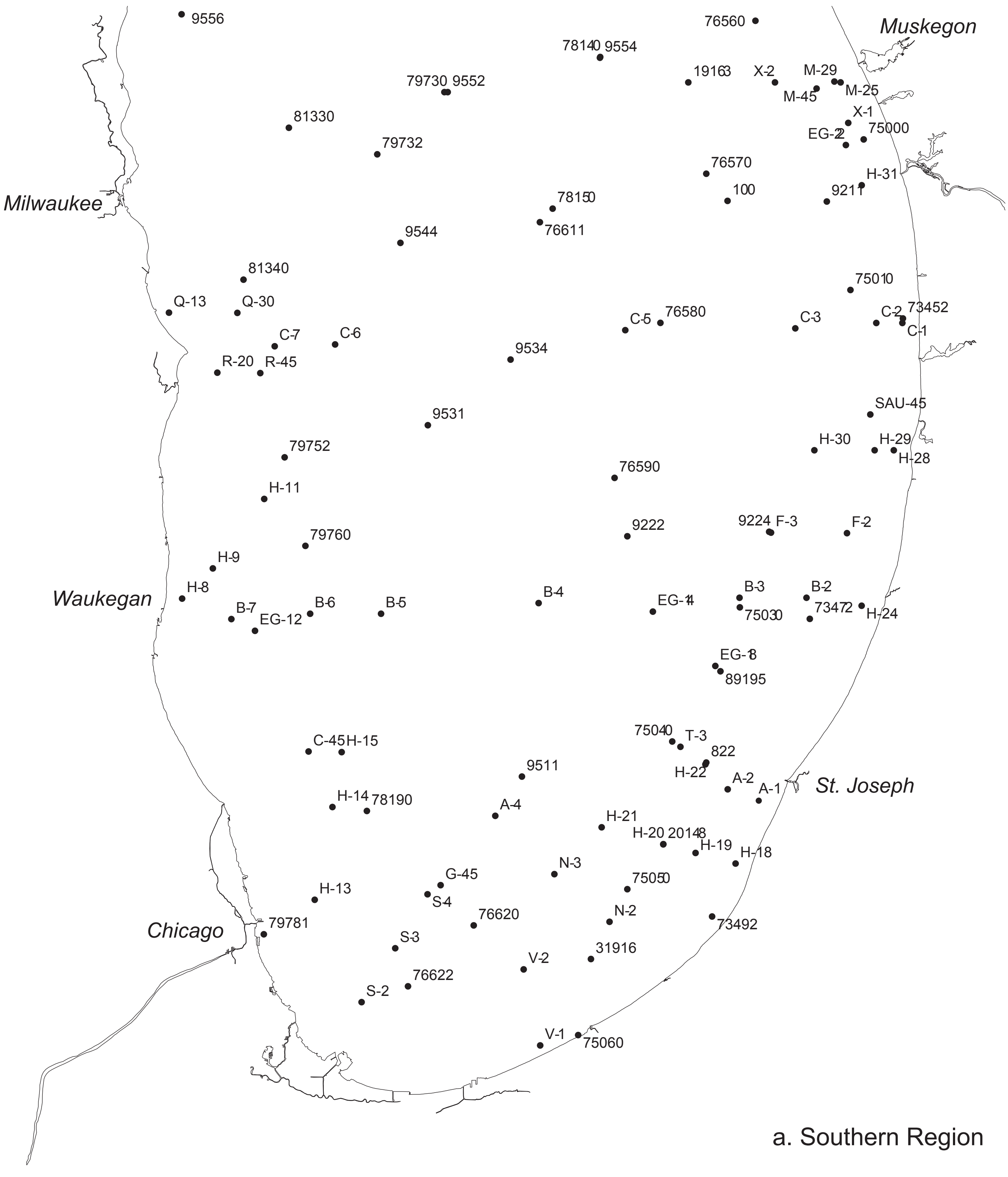

Figure 2. Station designations of sites located in the southern region of Lake Michigan that were sampled in 1994-1995, 2000, 2005, or 2010. Station coordinates are given in Table 1.

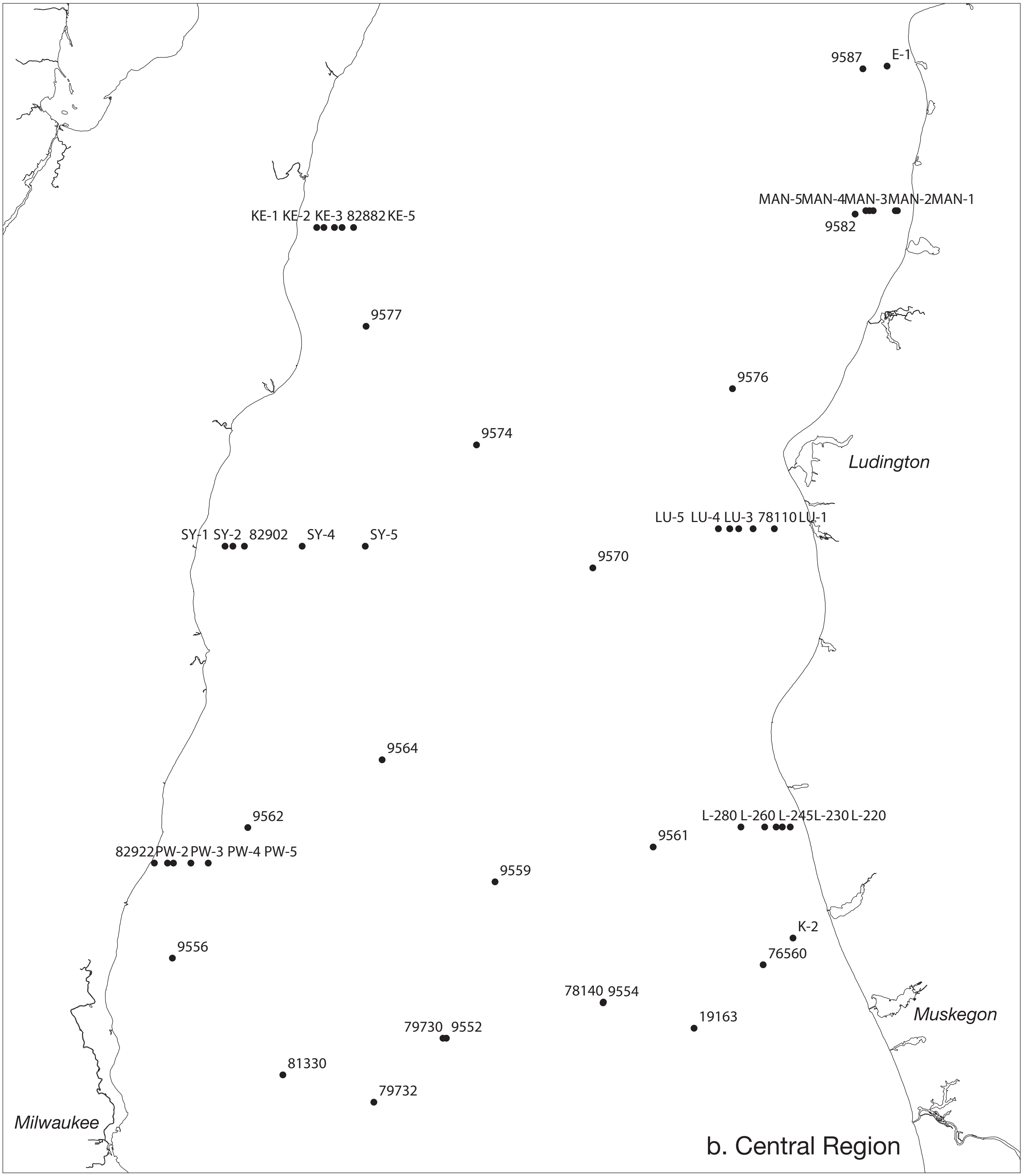

Figure 3. Station designations of sites located in the central region of Lake Michigan that were sampled in 1994-1995, 2000, 2005, or 2010. Station coordinates are given in Table 1.

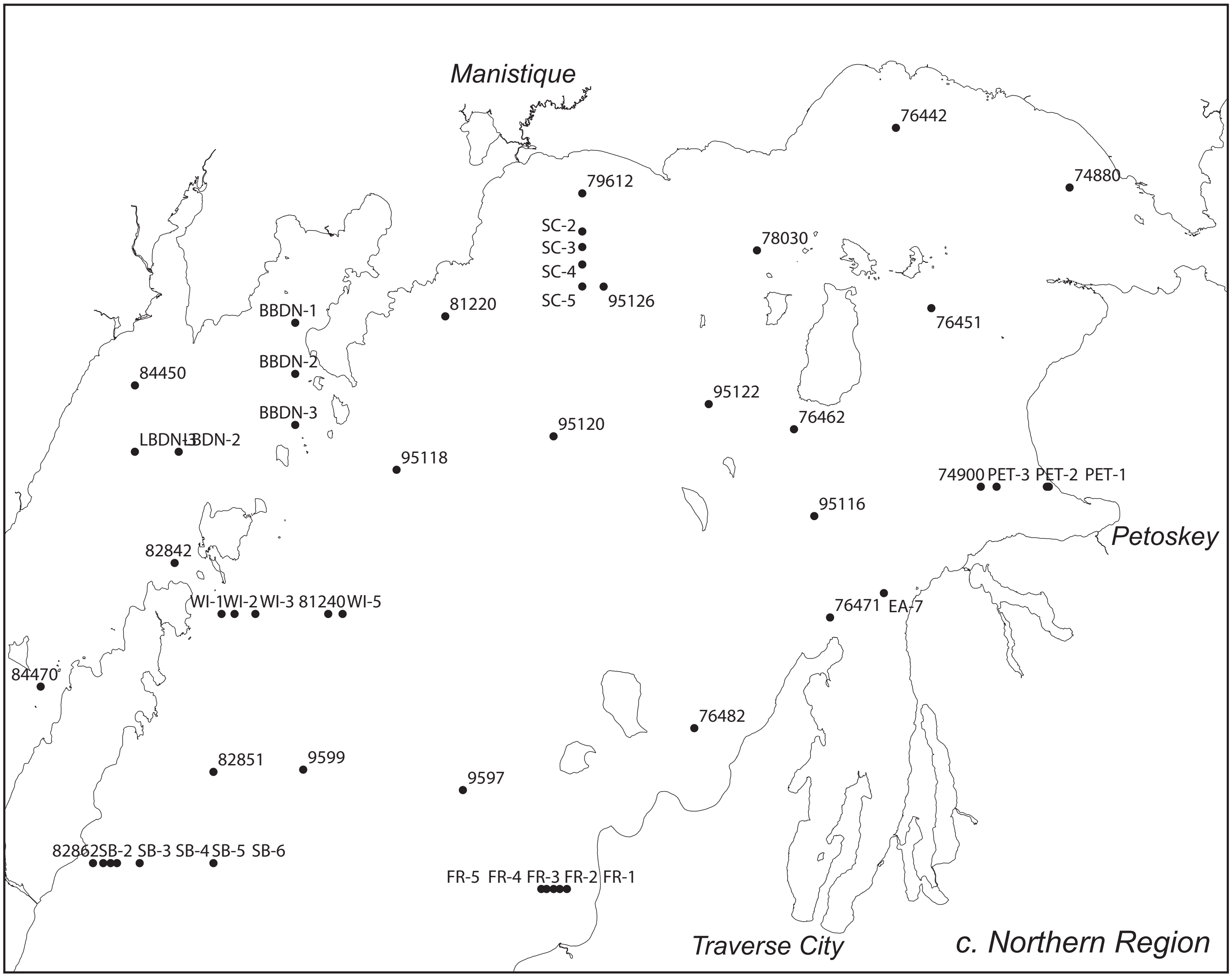

Figure 4. Station designations of sites located in the northern region of Lake Michigan that were sampled in 1994-1995, 2000, 2005, or 2010. Station coordinates are given in Table 1.

Figure 5. Station designations of sites located in Green Bay, Lake Michigan that were sampled in 1994-1995, 2000, 2005, or 2010. Station coordinates are given in Table 1.

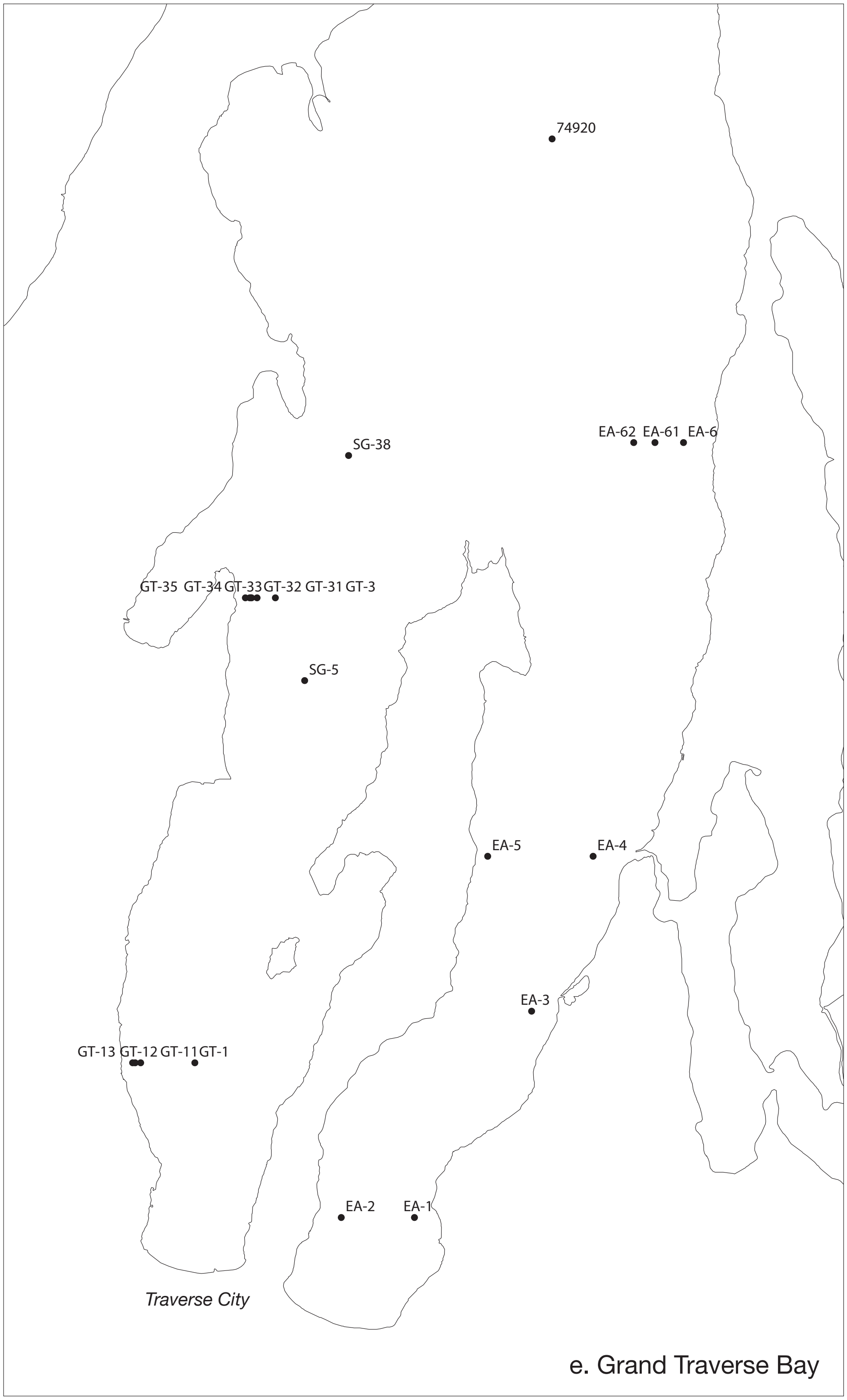

Figure 6. Station designations of sites located in Grand Traverse Bay, Lake Michigan that were sampled in 1994-1995, 2000, 2005, and 2010. Station coordinates are given in Table 1.

2.2 Sample Collection and Processing

Sampling procedures were the same at all sites on all sampling dates. Samples were taken in triplicate at each site with a Ponar grab (sampling area = 0.046 m2). Sediments were washed through an elutriation device fitted with a 0.5-mm mesh net, and retained residue was preserved in 5-10% buffered formalin containing rose bengal stain. In the laboratory, all *Diporeia* and *Dreissena* were picked and counted under a low-power magnifier lamp (1.5 x) or under a binocular microscope (10 x). In replicates with high numbers of individuals, the sample was randomly subdivided and only a portion of the total sample counted. For *Diporeia*, the sample was split using a folsom plankton splitter. For *Dreissena*, the sample was randomly placed into a divided tray (4 quadrants), and all individuals in one or more quadrants were counted. For both taxa, at least 100 individuals were counted in a given replicate. *Diporeia* and all dreissenids with a shell length > 5 mm were placed into labelled vials containing 10 % buffered formalin. Dreissenids with a shell length < 5 mm were counted but were not picked and placed into vials.

2.3 Determination of *Dreissena* Biomass

Biomass (ash-free dry weight) of *Dreissena* was determined from size frequencies and derived length-weight regressions. Since the abundance and distribution of *Dreissena* increased dramatically between 1994-1995 and 2010, the approach to determining size-frequencies varied by survey year. All dreissenids collected in 1994-1995 were measured (shell lengths). Dreissenids collected in 2000 were not measured, while dreissenids collected in 2005 and 2010 were measured only at representative sites (Table 2). These sites were located mostly along depth transects on the east and west sides of the lake and in three of the regions in the main basin of the lake (south, central, and north). For determination of size frequencies and subsequent calculation of biomass, sites were first binned into four depth intervals: < 30 m, 31-50 m, 51-90 m, and > 90 m. To measure shell lengths, individuals were placed on a scanner and lengths of the scanned images were determined with a calibrated software program that also binned lengths of the images into 1-mm intervals. Size frequencies at the > 90 m interval were only obtained in 2010 because dreissenids were rarely found at these deep depths prior to that year. In all years, size-frequencies for *D. polymorpha* and *D. r. bugensis* were determined separately.

Length-weight relationships for *D. polymorpha* and *D. r. bugensis* were obtained in 2004 and 2010. In 2004, mussels were collected at two sites on the east side of the lake (M-25, depth = 25 m; M-45 depth = 45 m), and at two sites on the west side of the lake (H-8, depth = 18 m; B-7, depth = 45 m). Mussels were collected on seven dates at the east sites (20 April, 3 June, 23 June, 21 July, 31 August, 21 September, and 27 October), and on four dates at the west sites (27 May, 1 July, 25 August, and 20 September). After collection with a Ponar grab, mussels were kept cool, and weights determined on live mussels within 48 h. In 2010, extra mussels for determination of length-weights were collected at 24 sites during the population survey (see Table 3). These 24 sites were representative of different depths and regions of the lake. Mussels for

Table 2. Stations where shell lengths of all collected *Dreissena* were measured in 2005 and 2010. *measured in 2010 only; ** binned in the 31-50 m interval in 2005.

Depth (m)	Stations
≤ 30	C-1, FR-1, FR-2, H-8*, H-13, H-18, H-24*, L-220, L-230, R-20, SB-2, SC-2, SY-1, SY-2
31-50	B-2*, B-7*, C-2, FR-3, H-14, H-19, H-31*, L-245, R-45, SB-3, SC-3, 82902
51-90	B-3*, B-6*, C-3, FR-4, FR-5, H-15, H-20, H-21, L-260, L-280, SB-4, SB-5, SC-4**, SC-5, SY-4
> 90	B-4*, B-5*, C-6*, EG-14*, X-2*, 9554*, 9562*, 9574*, 9576*, 9597*, 95120*

Table 3. Stations where additional *Dreissena* was collected for determination of length-weight relationships in 2010.

Depth (m)	Stations
≤ 30	H-18, MAN-2, PW-2, SB-2, SC-2
31-50	B-7, H-19, MAN-3, PW-3, SB-3, SC-3
51-90	EG-12, H-20, H-21, MAN-4, MAN-5, PW-4, PW-5, SB-4, SB-5, SC-4, SC-5, 82851
> 90	9582

determination of a length-weight relationship were collected at only one site > 90 m, since other sites at this depth interval did not have mussel populations with a wide range of sizes needed for an accurate determination of the relationship. Upon collection, all mussels were immediately frozen and kept frozen until analysis.

In the laboratory, mussels were placed into five size categories (9-12 mm, 13-15 mm, 16-18 mm, 19-21 mm, and > 22 mm), and the soft tissue of five individuals within each size category was removed, placed separately into pre-weighed aluminum planchets, dried at 60º C for at least 48 h, and then weighed. Tissues were ashed at 550º C for 1 h, cooled in a dessicator to room temperature, and then re-weighted to obtain ash-free dry weight. The shell length (SL) of each corresponding mussel was measured to the nearest mm.

The AFDW:SL relationship was determined as: LnAFDW = a +bLnSL, where LnAFDW = natural log of the ash-free dry weight in mg; LnSL = natural log of the shell length in mm; a and b = regression constants. In 2004, two relationships were determined for each species (four total). A relationship was determined from individuals collected at H-8 and M-25 (combined all dates at the two sites), and another relationship were determined from individuals collected at M-45 and B-7 (combined all dates at the two sites). It was assumed that these relationships reflected conditions above (≤ 30 m) and below (> 30 m) the thermocline, respectively (Nalepa et al. 2009). In 2010, a length-weight relationship was determined from individuals collected within each of the four depth intervals by combining data from all sites within that depth interval. Depth-specific relationships were obtained only for *D. r. bugensis* since *D. polymorpha* was rarely found in 2010. Table 4 gives the length-weight relationship by year, depth interval, and species. Preliminary results indicate that AFDW derived from frozen rather than live mussels may be underestimated by up to 15 % (Fanslow, unpublished data). Reasons for lower weight in the frozen samples are unclear, but may be related to cell lyses and the loss of water-soluble constituents during the thawing process and subsequent removal of tissue from the shell. At any rate, biomass determined for 2010 (see below) may potentially be underestimated and values should be considered as conservative.

To determine biomass, the number of individuals in each 1-mm size category from the size-frequencies was multiplied by the AFDW of an individual within that category (mid-category shell length) as derived from the derived length weight relationship, and then all category weights were summed. For 1994-1995 and 2005, derived relationships from 2004 were used to determine biomass for the two species at all sites ≤ 30 m and > 30 m where size frequencies were obtained. Similarly, derived relationships from 2010 were used to determine biomass of *D. r. bugensis* at all sites in the ≤ 30 m, 31-50 m, 51-90 m, and > 90 m intervals where size frequencies were obtained. Biomass at sites where size frequencies were not obtained (mussels not measured) in 2005 and 2010 was estimated by first determining the mean weight of an individual within each depth interval from sites where mussels were measured, and then multiplying this mean weight by the total number of mussels found at each of the non-measured sites within each depth interval. Since dreissenids were not measured in 2000, we used depth-specific mean weights of individuals as determined in 1994-95 and 2005. After the sites sampled in 2000 were placed into the four depth intervals, means of interval- specific weights of individuals in 1994-1995

Table 4. Relationship between shell length (SL in mm) and tissue ash-free dry weight (AFDW in mg) for *D. polymorpha* and *D. r. bugensis* at various depth intervals in 2004 and 2010. Regression constants (a, b) derived from the linear regression: LnAFDW = a +bLnSL; n = total number of mussels used to derive the relationship.

Year/Depth Interval	Species	a	b	n	R^2
2004					
≤ 30 m	*D. polymorpha*	-5.256	2.672	242	0.76
> 30 m	*D. polymorpha*	-5.255	2.652	242	0.80
≤ 30 m	*D. r. bugensis*	-6.095	2.968	244	0.85
> 30 m	*D. r. bugensis*	-6.969	3.316	247	0.90
2010					
≤ 30 m	*D. r. bugensis*	-5.857	2.814	122	0.63
31-50 m	*D. r. bugensis*	-5.528	2.617	172	0.85
51-90 m	*D. r. bugensis*	-5.601	2.683	269	0.87
> 90 m	*D. r. bugensis*	-5.993	2.854	24	0.98

and 2005 were then multiplied by the number of individuals at each site. Mean weights used in the calculation for biomass in 2005 were determined from only those sites where size frequencies were obtained.

Figures of density distributions of *Diporeia*, *D. polymorpha*, and *D. r. bugensis* were produced using natural neighbor spatial interpolation (Sibson 1981). This technique uses spatial proximity to predict/depict density at locations distant from actual observations. Because of fewer sampling sites in deeper regions (> 90 m), and the expansion of *D. r. bugensis* from shallow to deep regions in 2005 and 2010, the tendency of such interpolations was to overestimate *Dreissena* densities in the deep regions in the middle of the lake. Hence, figures in 2005 were manipulated to more realistically depict densities in the middle of the lake as based on actual observations (Nalepa et al. 2009). Figures produced for 2010 were not manipulated, and thus may depict densities in the deep, middle region that are slightly overestimated. Figures of biomass distributions of *Dreissena* were produced using a recently-developed geostatistical model (Rowe et al. submitted). The geostatistical model simulates the spatial correlation structure of collected data while using bathymetry and spatial coordinates as predictor variables that define large-scale spatial trends (Obenour et al. 2013). Thus, the model uses lake bathymetry in addition to spatial proximity to predict biomass at locations distant from sites actually sampled.

3.0 RESULTS AND DISCUSSION

Data collected in each survey period are given in Appendix 1 (excel file). In the file, densities (no./m^2) of *Diporeia*, *D. polymorpha*, and *D. r. bugensis* are given under the coded variables DIPO, DPOL, and DBUG, respectively, and biomass (mg AFDW/m2) of *D. polymorpha* and *D. r. bugensis* are given under the coded variables BIODPOL and BIODBUG, respectively. Biomass of *Diporeia* was not included in the file, but summaries can be found in other publications (Nalepa et al. 2000, 2009).

To summarize temporal trends, sites in the main basin (i.e. not within Grand Traverse Bay or Green Bay) were placed into the four depth intervals (< 30 m, 31-50 m, 51-90 m, > 90 m), and mean densities of *Diporeia*, *D. polymorpha*, and *D. r. bugensis*, and biomass of *D. polymorpha* and *D. r. bugensis*, were determined for each interval. Sites in Grand Traverse Bay and Green Bay were excluded from the analysis since the number of sites varied and most were not sampled over all four survey periods. Densities of *Diporeia* declined dramatically over the 15-year period at each of the four depth intervals (Table 5). In 1994-95, mean densities at the < 30 m and 31-50 m intervals were 3,907/m^2 and 6,111/m^2, respectively. These mean densities were likely already depressed since *Diporeia* in the southern region of Lake Michigan began to decline at depths < 50 m in the early 1990s (Nalepa et al. 1998). By 2010, mean densities of *Diporeia* had declined to < 1/m^2 at both intervals. Severe declines were also evident at the deeper intervals. In 1994-95, mean densities at the 51-90 m and > 90 m intervals were 6,521/m^2 and 4,547/m^2, but in 2010 mean densities had declined to 98/m^2 and 429/m^2, respectively. Overall, *Diporeia* was collected at 98.9% of the sites sampled in 1994-95 (89 of 90), but in 2010 it was collected at only 16.7% of the sampled sites (24 of 144). Declines were most evident in the southeastern, eastern, and northern portions of the lake between 1994-1995 and 2000, while declines in the western portion of the lake were most severe between 2000 and 2010 (Figure 7).

Densities of *D. polymorpha* increased between 1994/1995 and 2000, but then decreased thereafter such that by 2010 it was rarely found (Table 5; Figure 8). Over the entire 15-year sampling period, it tended to be most abundant in the northern portion of the lake and at depths < 50 m. The maximum mean density was 2,113/m^2 in the < 30 m interval in 2000. In 2000, when *D. polymorpha* was most widespread and abundant, it was collected at 67 of 97 sites in these two shallower intervals, but in 2010 it was only collected at one 1 of 85 sampled sites in these two intervals.

In contrast to the noted declines in both *Diporeia* and *D. polymorpha*, densities of *D. r. bugensis* increased between 1994-1995 and 2010. It was not found at any site in 1994-1995, and mean densities in 2000 were only 57/m^2, 11/m^2, 0/m^2, and 0/m^2 at the four intervals, respectively. However, in 2010 mean densities increased to 9,717/m^2, 12,739/m^2, 14,811/m^2, and 1,881/m^2 (Table 5, Figure 9). *D. r. bugensis* was first reported in Lake Michigan in the northern region of the lake near the Straits of Mackinac in 1997 (Nalepa et al. 2001). During the lakewide survey in 2000, it was only found in the northern region of the lake, but by 2005 it had expanded southward and was collected in all lake regions. In 2010, mean densities of *D. r. bugensis* within the < 30 m and 31-50 m intervals increased minimally, or slightly decreased compared to 2005, indicating that at least at depths < 50 m the population may be stabilizing or may perhaps be in the early stages of decline. On the other hand, mean densities at the 51-90 m and > 90 m intervals were 2.3x and 156.8x greater in 2010 than in 2005, indicating the population was still expanding in deep, offshore regions.

Table 5. Mean (± SE) density (no./m^2) of *Diporeia*, *Dreissena polymorpha*, and *Dreissena r. bugensis* at four depth intervals (< 30 m, 31-50 m, 51-90 m, and > 90 m) in each of the survey periods. n = number of stations sampled. Values are for the main basin of the lake (excluding Green Bay and Grand Traverse Bay).

	Survey Period			
Depth Interval/Taxa	1994-95	2000	2005	2010
≤ 30 m	n = 16	n = 38	n = 41	n = 42
Diporeia	3,907 ± 1,005	853 ± 315	104 ± 88	1 ± 1
D. polymorpha	730 ± 510	2,113 ± 539	258 ± 86	0 ± 0
D. r. bugensis	0 ± 0	51 ± 26	7,547 ± 1,566	9,717 ± 1,582
31-50 m	n = 11	n = 36	n = 36	n = 36
Diporeia	6,111 ± 1,377	2,116 ± 563	24 ± 16	<1 ± <1
D. polymorpha	252 ± 239	1,021 ± 511	427 ± 109	1 ± 1
D. r. bugensis	0 ± 0	11 ± 9	15,838 ± 2,860	12,739 ± 1,129
51-90 m	n = 32	n = 41	n = 41	n = 41
Diporeia	6,521 ± 562	3,469 ± 464	548 ± 131	98 ± 49
D. polymorpha	< 1 ± <1	16 ± 8	38 ± 29	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	6,472 ± 1,704	14,811 ± 1,310
>90 m	n = 25	n = 13	n = 13	n = 18
Diporeia	4,547 ± 385	2,804 ± 453	1,244 ± 217	429 ± 122
D. polymorpha	0 ± 0	0 ± 0	<1 ± <1	0 ± 0
D. r. bugensis	0 ± 0	0 ± 0	12 ± 7	1,881 ± 907

Trends in mean biomass of *Dreissena* (total of *D. polymorpha* and *D. r. bugensis*) basically followed trends in mean densities (Table 6). As discussed by Rowe et al. (submitted), spatial patterns in biomass derived from the geostatistical model provided a more refined depiction of distributions than the nearest neighbor technique (Figure 10). After *D. r. bugensis* became widespread in 2005 and 2010, of note was the focused region of high biomass in the mid-depth region (31-50 m and 51-90 m intervals), and the high biomass in the mid-lake reef region (for reef location see Figure 1).

In summary, *Diporeia* and *D. polymorpha* declined, while *D. r. bugensis* increased in Lake Michigan between 1994-1995 and 2010. In the main basin of Lake Michigan in 2010, *Diporeia* was rarely collected at depths < 50 m and was collected at relatively low densities (< 500/m^2) at depth > 50 m. Similar declines have been documented in Lake Huron, Lake Ontario, and eastern Lake Erie (Dermott and Kerec 1997, Nalepa et al. 2007, Watkins et al. 2007, Barbiero et al. 2011). The decline of *Diporeia* throughout the Great Lakes has been temporally coincident with the increase and expansion of *Dreissena*, exact mechanisms for the negative response are not entirely clear (Nalepa et al. 2006). Lower densities of *D. polymorpha* after 2000 coincided with the increase in *D. r. bugensis*; similar declines relative to *D. r. bugensis* have been documented in Lake Ontario (Mills et al. 1999). Based on laboratory experiments, *D. polymorpha* has a lower assimilation rate (Baldwin et al. 2002) and a higher respiration rate (Stoeckmann 2003) compared to *D. r. bugensis*, and therefore is likely to be outcompeted by *D. r. bugensis* for available food resources. In comparing mean densities and biomass in 2010 relative to 2005, *D. r. bugensis* in Lake Michigan appears be stable or in the early stages of decline at depths of < 50 m, but still expanding at depths > 50 m.

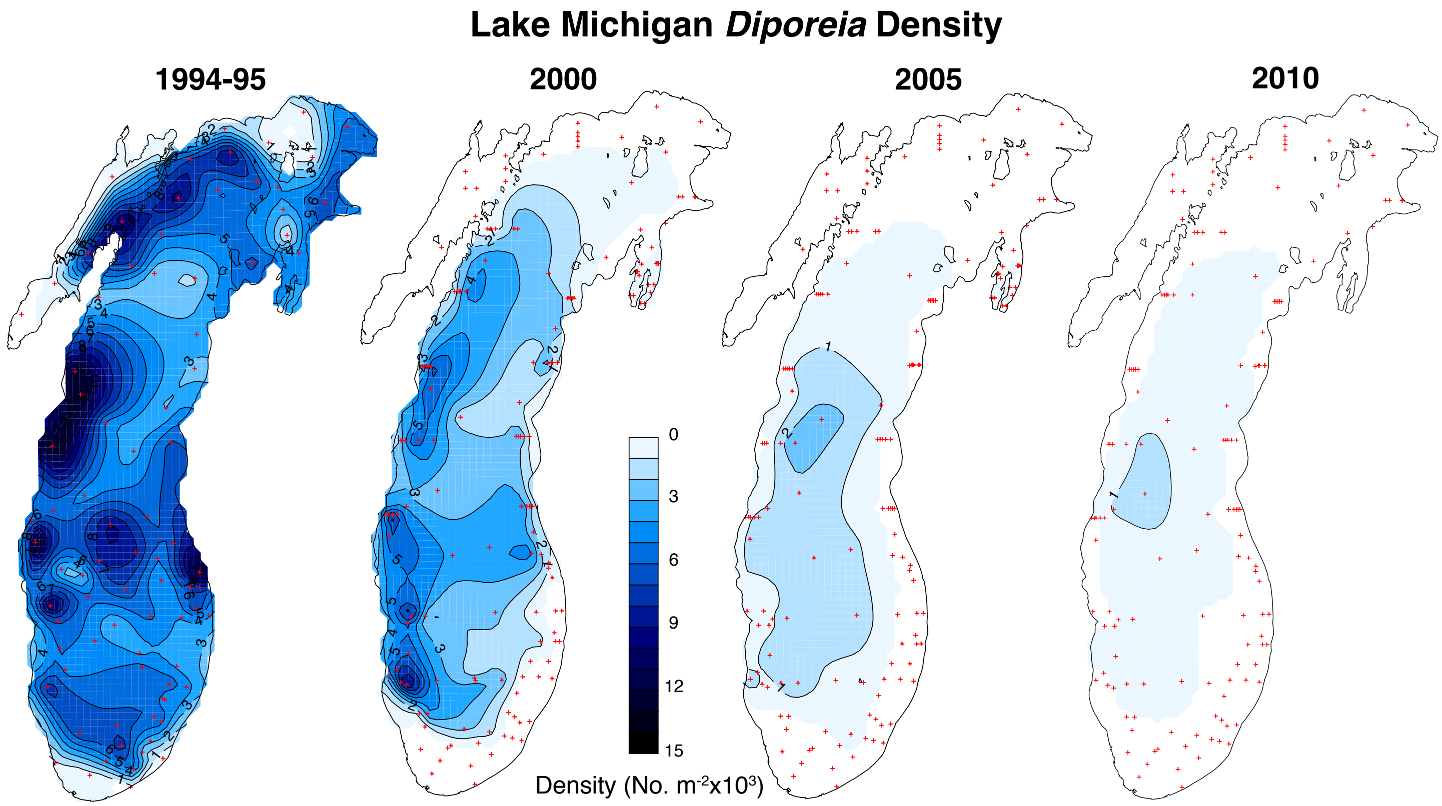

Figure 7. Mean density (no./m^2) distribution of *Diporeia* in Lake Michigan in 1994-1995, 2000, 2005, and 2010. Values given as mean density (no./m^2). Small red crosses denote sampling sites.

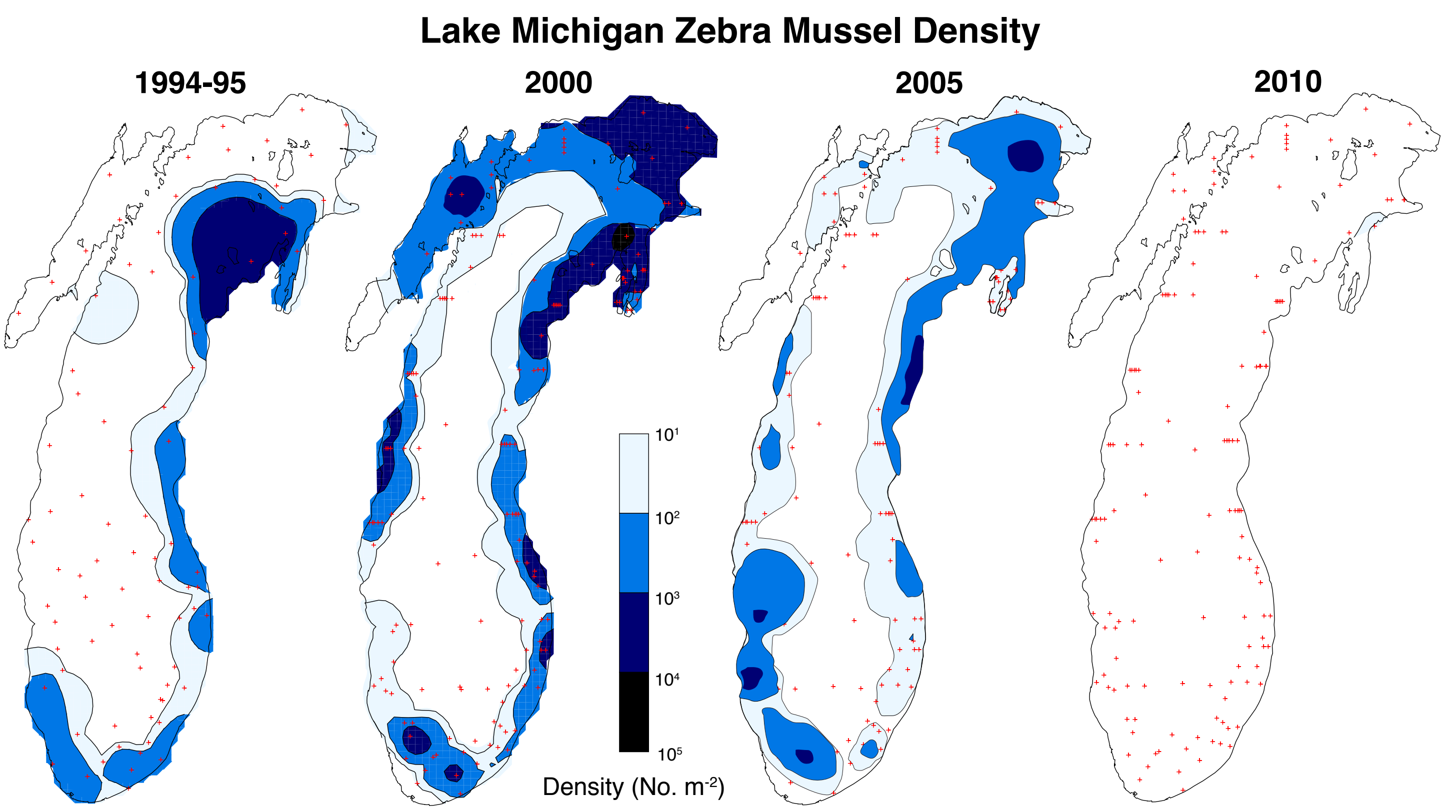

Figure 8. Mean density (no./m^2) distribution of *Dreissena polymorpha* in Lake Michigan in 1994-1995, 2000, 2005, and 2010. Small red crosses denote sampling sites.

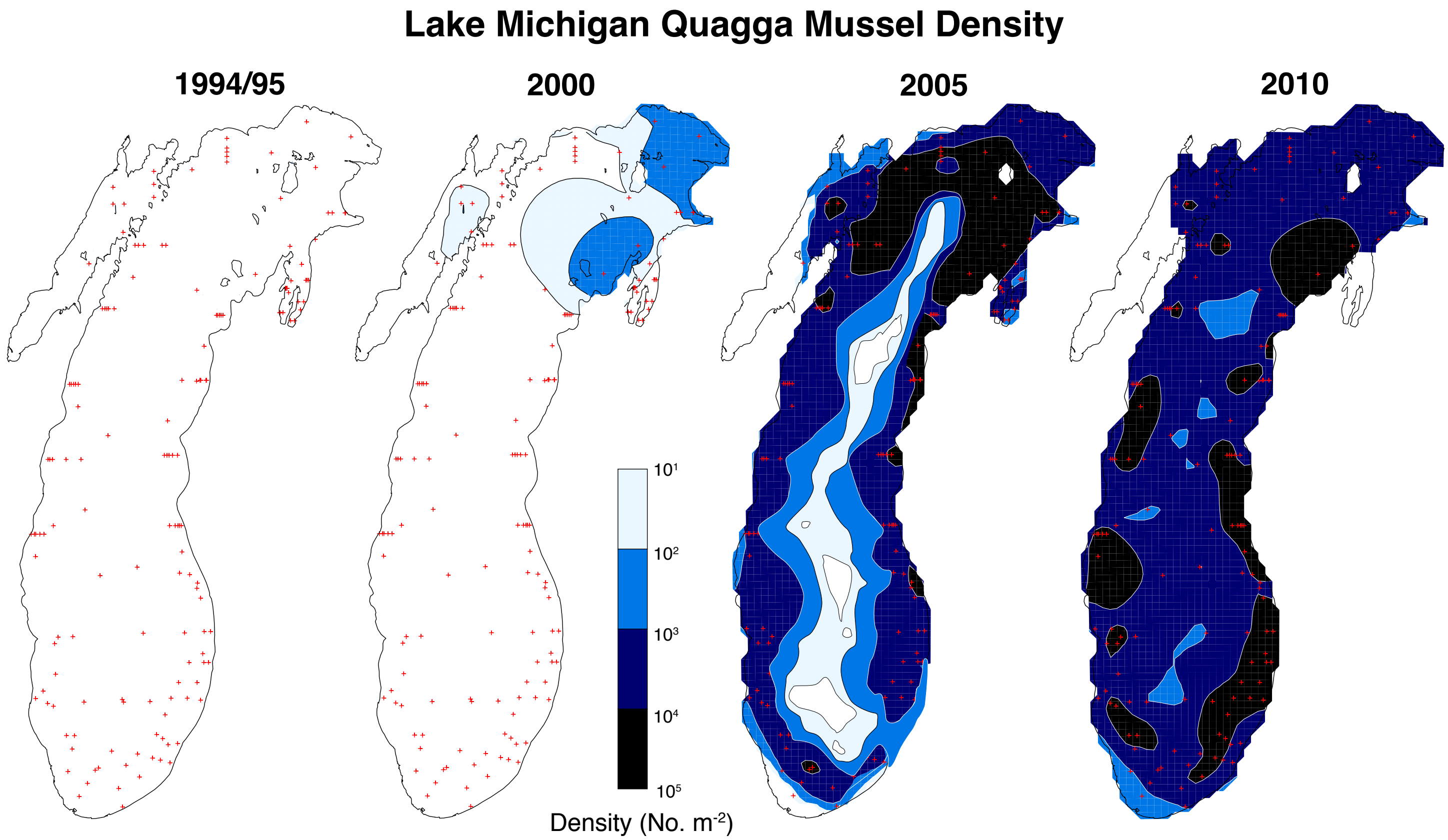

Figure 9. Mean density (no./m²) distribution of *Dreissena rostriformis bugensis* in Lake Michigan in 1994-1995, 2000, 2005, and 2010. Small red crosses denote sampling sites.

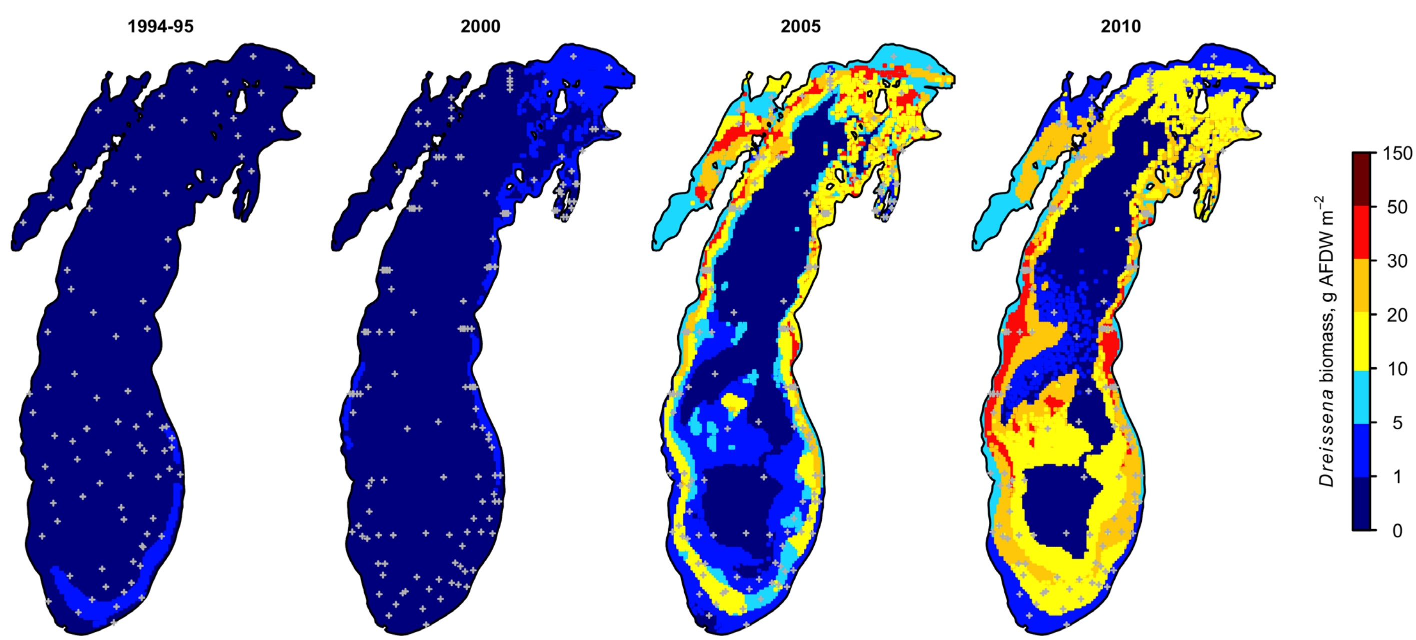

Figure 10. Mean biomass (g AFDW/m²) of *Dreissena* in Lake Michigan in 1994-1995, 2000, 2005, and 2010. Small white crosses denote sampling sites.

Table 6. Mean (± SE) biomass (g AFDW/m^2) of *Dreissena polymorpha*, and *Dreissena r. bugensis* at four depth intervals (< 30 m, 31-50 m, 51-90 m, and > 90 m) in each of the survey periods. n = number of stations sampled.

	Survey Period			
Depth Interval/Taxa	1994-95	2000	2005	2010
≤ 30 m	n = 16	n = 38	n = 41	n = 42
D. polymorpha	0.61 ± 0.26	1.11 ± 0.28	0.80 ± 0.25	0.00 ± 0.00
D. r. bugensis	0.00 ± 0.00	0.07 ± 0.04	11.43 ± 2.57	11.64 ± 2.23
31-50	n = 11	n = 36	n = 36	n = 36
D. polymorpha	0.03 ± 0.02	0.72 ± 0.36	1.12 ± 0.31	< 0.01 ± <0.01
D. r. bugensis	0.00 ± 0.00	0.02 ± 0.01	24.89 ± 4.13	24.31 ± 1.99
51-90	n = 32	n = 41	n = 41	n = 41
D. polymorpha	<0.01 ± <0.01	0.12 ± 0.06	0.28 ± 0.22	0.00 ± 0.00
D. r. bugensis	0.00 ± 0.00	0.00 ± 0.00	10.96 ± 2.45	25.41 ± 2.26
>90 m	n = 25	n = 13	n = 13	n = 18
D. polymorpha	0.00 ± 0.00	0.00 ± 0.00	< 0.01 ± <0.01	0.00 ± 0.00
D. r. bugensis	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.01	1.58 ± 0.79

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APPENDIX 1. EXCEL DATA FILES

http://www.glerl.noaa.gov/ftp/publications/tech_reports/glerl-164/tm-164_Appendix1.xlsx

Densities (no./m^2) of *Diporeia, D. polymorpha*, and *D. r. bugensis* are given under the coded variables DIPO, DPOL, and DBUG, respectively, and biomass (mg AFDW/m^2) of *D. polymorpha* and *D. r. bugensis* are given under the coded variables BIODPOL and BIODBUG, respectively.