

Contrasting Zooplankton Community Structure in Sandusky Bay and Lake Erie

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Sandusky Bay와 Lake Erie의 상이한 동물 플랑크톤 군집의 구조에 대하여

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ABSTRACT

Zooplankton community structure and the factors correlated with community differences were examined in Sandusky Bay (SB) and the open water of Lake Erie (LE, U.S.A.). SB zooplankton communities differed from those in LE by having a greater rotifer density and species richness. *Keratella* spp., *Brachionus* spp., and *Pompholyx complanata* dominated SB rotifers; *Brachionus* and *Pompholyx* were rarely seen in LE. Of 19 rotifer species observed, nine species were found only at SB sites. Ordination of zooplankton species abundance by detrended correspondence analysis (DCA) showed an overlap between SB and LE sites, but indicated a portion of the space that was occupied by only SB communities. The seasonal trajectories of zooplankton dynamics in the ordination space at SB sites differed from that of LE. The zooplankton most important in forcing site separation along a DCA Axis I at SB sites were *Brachionus angularis*, *Pompholyx complanata*, *Keratella valga*, *Keratella quadrata*, *Filinia terminalis* (rotifers), and *Eubosmina coregoni* and *Daphnia* (cladocerans). These species had axis scores which were significantly correlated ($p < 0.01$) with bacterial density and bacterial phosphorus, total phosphorus, and algal density. Very high bacterial density and very abundant bacterivorous rotifers in SB suggest that the transport of bacterial carbon through rotifers may be a relatively important link to higher trophic levels. We believe that this "microbial carbon flow" from the base of the food web may be important in determining the suitability of SB as a spawning site and nursery for larval and juvenile fish.

Key words: Community structure, Sandusky bay, Zooplankton

INTRODUCTION

The zooplankton structure and their development in a certain environment is affected by many environmental parameters, yet they will only survive if they can find available organic matter to meet their nutritional requirements. Consequently, their development is closely related with the activities of autotrophic or heterotrophic producers. Zooplankton play an important role in aquatic food webs by linking energy flow both as grazers of bacteria, phytoplankton, and protozoans and by acting as prey for planktivorous fish (Janicki and DeCosta 1984, Martin *et al.* 1985, Sherr and Sherr 1987, Berninger *et al.* 1991, Carrick *et al.* 1991, Hwang 1995).

Because of the importance of zooplankton as a food web component, numerous studies of zooplankton ecology have been undertaken in many lakes including Laurentian Great Lakes (e.g., Patalas 1972, Krieger 1981, Evans and Jude 1986). However, very little is known of the ecology of zooplankton communities of the coastal wetlands, or of the extent to which those communities are influenced by the upland watershed. Recently, a few studies have reported that riverine coastal wetlands along the Great Lakes are subject to the frequent export of their resident water by the influx of storm runoff water from the tributary watersheds (Klarer 1983, Krieger and Klarer 1991). These events importing rich organic matter to coastal wetlands may support developments of bacteria and phytoplankton and, subsequently zooplankton (Hwang 1995).

The water of Great Lakes tributary wetlands is much more heterogenous compared with the open water of lakes. Brant and Herdendorf (1972) reported a gradient of increasing conductivity extending several kilometers upstream from the mouth of Lake Erie wetlands. More recently, chemical (conductivity, N and P) and biological (chlorophyll *a*) gradients have been described in coastal wetlands along Lake Erie, usually with higher concentrations in an upstream direction (Klarer 1988, Garono 1993). Therefore, relatively stable downstream zones of these wetlands appear to provide a habitat with chemical and physical characteristics intermediate between those of the upstream embayments and lake that may support different zooplankton communities.

Coastal wetlands are believed to provide important ecological roles to the lake biota by reducing or transforming the loading to the lakes of a variety of pollutants and nutrients transported by the wetlands (Heath 1987, Klarer 1988). As one of the most productive coastal wetlands of Lake Erie, Sandusky Bay is an important spawning site and nursery for the commercial and recreational fisheries in Lake Erie. It is dominated by the fish that feed on planktonic and benthic invertebrates rather than other fish (Johnson 1989). In contrast, the pelagic waters of Lake Erie support a different taxocene of fish that tend to be larger, older and piscivorous (Jude and Pappas 1992). Management of pelagic and coastal resources require an understanding of those factors that determine the quantity and quality of food available to the respective communities in those regions.

The purpose of this study was to examine the zooplankton community structure of Sandusky Bay and the pelagic waters of Lake Erie and to identify those factors that could explain community differences. Collected at monthly intervals, zooplankton populations were analyzed by detrended correspondence analysis (DCA). Correlation analysis was then used to identify factors salient in driving this ordination.

MATERIALS AND METHODS

Study sites

This study was conducted at four sites (three in Sandusky Bay and one in Lake Erie) along a 40 km transect from the upper reaches of Sandusky Bay (SB) to the pelagic zone

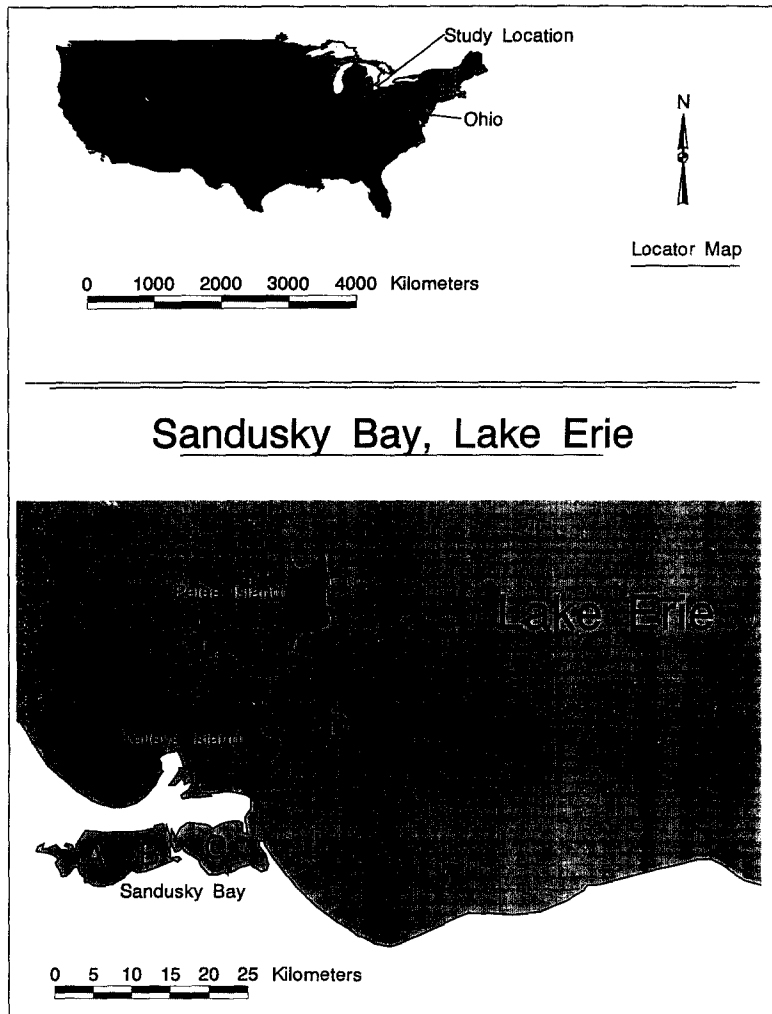


Fig. 1. Profile of Sandusky Bay and Lake Erie showing the locations of sampling sites.

of Lake Erie (LE) (Fig. 1). Study sites were located during each trip by satellite detection using a hand-held two dimensional Global Positioning System (GPS) unit. We visited these sites at approximately monthly intervals from May through September 1991.

The Sandusky River drains a large agricultural watershed, covering 3,678 km² and drains into the most productive coastal region of Lake Erie. Sandusky Bay, resulting from the drowned mouth of the river, has a mean depth of 2 m and is highly productive (Herdendorf 1975). It is turbid having both biogenic and abiotic suspended solids. During the summer, the algal community is dominated by cyanobacteria, predominantly *Oscillatoria*, with smaller numbers of *Anabaena* and *Aphanizomenon*. The pelagic site in the western basin is mesotrophic, and the dominant algal taxa are diatoms (notably *Cyclotella*, *Fragilaria*, and *Asterionella*) and also small cryptophytes (Hwang 1995).

Sample collection and fixation

Water samples were collected monthly between May and September in 1991 from the mid-epilimnion (1 m at SB sites and 4.5 m at the LE site). Triplicate water samples for water chemistry and chlorophyll *a* analysis were collected with a 4 L Van-Dorn sampler and stored in acid-rinsed 1 L plastic bottles at ambient temperature until being returned to the laboratory. One hundred milliliters of well mixed aliquots were placed in separate Whirl-Pak bags for algal and bacterial enumeration. Algae were preserved with 2 mL of Lugol's solution, and bacteria were preserved with 4% formalin (final conc.). Triplicate zooplankton samples were collected with a Schindler Patalas trap (64µm net size; 12 L volume). Zooplankton (both rotifers and microcrustaceans) were preserved with sucrose-formalin (4% formalin and 0.1% sucrose, final conc.).

Measurement of limnological and biological variables

Transparency was determined with a 20 cm white Secchi disk. Light intensity at the surface and 1.0 m was measured with Li-Cor LI-1000 photometer. Temperature and dissolved oxygen were measured *in situ* with a YSI Model 50 meter. Conductivity and pH were measured with a solution analyzer (Amber Science 4503A). Turbidity was measured with a Hatch ratio turbidimeter. Chloride concentrations and alkalinity (titrated to pH 4.5) were measured with a radiometer automatic end-point titration system (APHA 1989). Soluble reactive phosphorus (SRP) was determined on 0.45 µm filtrates using the colorimetric procedure of Murphy and Riley as modified by the USEPA (1971). Total phosphorus (TP) was determined by the same procedure as SRP, but after persulfate digestion (APHA 1989). Chlorophyll *a* concentration was determined by filtering 0.1~1.0 L sample aliquots onto GF/A glass fiber filters and using the standard dichromic spectrophotometric procedure in magnesium carbonate-saturated 90% acetone extract (APHA 1989). Measurements of algal particulate phosphorus and bacterial particulate phosphorus were described in Garono (1993). Algae were enumerated by the procedure of Utermohl (1958), and population densities were calculated from the counts as cells/mL

according to Lund *et al.* (1958). Bacterial densities were determined using the fluorometric acriflavine staining method (Bergstrom *et al.* 1986).

Zooplankton enumeration

Microzooplankton (rotifers and naupill) samples were concentrated to a known volume with a plastic bottle having a 20 μm mesh side window. Aliquots were settled in a counting chamber, and at least 300 animals or the entire chamber depending on densities, were counted at 80X on an inverted microscope.

Macrozooplankton (cladocerans and copepods) samples were concentrated in the same manner as the rotifer and nauplii samples, and enumerated at 20~40X magnification. All animals in the samples were counted and densities were determined as individuals /L.

Populations of each species were scored as dominant (D) if they represented greater than 15 percent of total individuals counted in that sample, common (C) if they represented between 5 and 15 percent, and rare (R) if they represented less than 5 percent of the total number of individuals counted.

Data analysis

Zooplankton data matrices were ordinated with detrended correspondence analysis (DCA) using DECORANA (Hill 1979). The species abundance data matrix (including both species identification and their densities) was made for each taxon at each site for each date. Our intent in ordinating these data was to determine whether the SB communities differed from LE community in such a way that they could be separated in two-dimensional ordination space, permitting us to identify those species that illustrate differences among sites and those environmental factors that correlate with community differences. DCA performed eigen analysis in which ordination scores were derived from a data matrix to provide a four-axis ordination space that was drawn in two most important axes of space (first two axes; axis I and II). Equivalent distances in DCA ordination space represent equivalent differences in community composition because DCA reduced certain artifacts characteristic of other multivariate analytic procedures (Gauch 1982). When placing samples in ordination space, the sample variance accounted for by each axis was expressed as a percentage of the eigenvalue of each axis with respect to eigenvectors derived for all axes; thereby, providing an estimate of the amount of variance "explained" by each axis.

Correlation analysis, SAS Stat Version (SAS Inst. 1989) was used to determine correlations between DCA axis scores and each of limnological variables investigated. Correlation between DCA axis scores and each variable were made one variable at a time. Significant correlations were defined as $p < 0.05$. The differences of limnological variables and zooplankton densities among sites were compared by paired t-tests.

A similarity index was calculated based on species composition (Sorenson 1948) within bay sites and between bay and lake sites. The Shannon diversity index (Shannon 1949)

Table 1. Limnological variables and their means (\pm SD), maximum, and minimum values at Sandusky Bay sites (A, B, and C), and Lake Erie site (D) from May through September

Variables	site A	site B	site C	site D
Temperature ($^{\circ}$ C)				
Mean	24.3 \pm 1.2	22.8 \pm 2.0	22.7 \pm 1.7	21.33 \pm 3.5
MAX	25.4	24.6	24.4	23.9
MIN	22.3	19.6	19.7	15.3
Secchi depth (m)				
Mean	0.33 \pm 0.04	0.50 \pm 0.18	0.78 \pm 0.23	3.32 \pm 0.42
MAX	0.38	0.87	1.21	3.74
MIN	0.27	0.28	0.59	2.82
Surface light (μ E/S/M)				
Mean	848 \pm 319	922 \pm 389	809 \pm 384	672 \pm 289
MAX	1163	1600	1390	936
MIN	410	450	400	270
% light at 1.0m				
Mean	5 \pm 5	7 \pm 8	18 \pm 12	36 \pm 15
MAX	11	22	36	48
MIN	0	0	5	15
Turbidity (NTU)				
Mean	51.8 \pm 7.2	27.2 \pm 8.2	14.4 \pm 3.7	1.5 \pm 0.2
MAX	60.5	38.0	20.0	1.8
MIN	43.0	19.0	9.7	1.1
Conductivity (mhos)				
Mean	625 \pm 73	460 \pm 80	349 \pm 37	250 \pm 21
MAX	708	610	400	271
MIN	530	383	297	222
Chloride (mg/L)				
Mean	38.2 \pm 0.4	28.8 \pm 1.5	19.5 \pm 1.0	11.4 \pm 1.3
MAX	38.6	30.2	20.8	12.2
MIN	37.8	26.7	18.3	9.5
Dissolved oxygen (mg/L)				
Mean	12.44 \pm 1.59	11.82 \pm 2.72	10.55 \pm 1.51	10.56 \pm 0.67
MAX	14.32	16.22	12.82	11.40
MIN	10.41	8.14	8.40	9.89
Alkalinity (mg CaCO ₃ /L)				
Mean	2.15 \pm 0.26	1.51 \pm 0.18	1.64 \pm 0.17	1.82 \pm 0.11
MAX	2.40	1.84	1.90	1.96
MIN	1.79	1.35	1.44	1.69
Total phosphorus (μ g/L)				
Mean	190.1 \pm 6.8	206.7 \pm 95.9	146.5 \pm 0.6	54.6 \pm 19.2
MAX	268.6	341.4	206.7	79.2
MIN	110.9	64.7	95.2	26.6
Soluble reactive P (μ g/L)				
Mean	7.3 \pm 9.7	11.2 \pm 8.1	11.0 \pm 7.2	10.9 \pm 5.1
MAX	23.9	24.7	19.9	16.7
MIN	0.0	1.7	0.0	3.3

Table 1. Continued

Variables	site A	site B	site C	site D
Bacterial P ($\mu\text{g/L}$)				
Mean	20.0 \pm 11.6	38.5 \pm 14.9	31.4 \pm 12.0	14.6 \pm 7.9
MAX	36.7	57.9	44.8	22.7
MIN	4.1	9.80	9.3	2.2
Algal P ($\mu\text{g/L}$)				
Mean	113.1 \pm 68.5	102.8 \pm 60.0	57.4 \pm 41.5	6.46 \pm 0.2
MAX	217.2	182.6	132.9	6.8
MIN	26.8	22.5	18.3	6.3
Chlorophyll <i>a</i> ($\mu\text{g/L}$)				
Mean	134.1 \pm 52.0	66.6 \pm 31.4	42.1 \pm 30.8	5.9 \pm 4.8
MAX	180.4	116.3	85.5	10.7
MIN	61.5	29.4	18.7	1.1
Algal density (10^4 cells/mL)				
Mean	7.40 \pm 5.84	9.05 \pm 8.14	3.06 \pm 3.10	0.91 \pm 0.84
MAX	13.24	20.56	7.41	1.75
MIN	1.55	2.84	0.39	0.07
Bacterial density (10^6 cells/mL)				
Mean	10.44 \pm 2.44	13.85 \pm 4.40	10.10 \pm 3.19	4.96 \pm 2.14
MAX	14.50	22.39	15.94	7.27
MIN	7.95	7.75	6.37	1.46

was calculated and the statistical difference of index values was determined according to Zar (1984).

RESULTS

Limnological and biological variables

Most chemical or biological variables at SB sites (A, B, and C) had higher values than those at the LE site D ($p < 0.05$, t-test) (Table 1). The highest turbidity, conductivity, and chloride values at site A, and their decreasing gradients from upstream site A to the open water site D likely were a function of sediment loading from the Sandusky River. Secchi disk transparency and percent light transmission at 1 m showed an increasing gradient from site A to site D, reflected by the negative correlation with turbidity. Chlorophyll *a* concentration showed a decreasing gradient from site A to site D. Both algal and bacterial densities did not show a gradient, but were much higher at SB sites than LE site ($p < 0.01$, t-test), which likely reflected by much high TP and chlorophyll *a* concentration at SB sites ($p < 0.01$, t-test). Both particulate algal and bacterial P showed a very similar trend to that of algal and bacterial densities. Overall, SB sites were much more eutrophic, and accordingly, contained significantly higher algal and bacterial biomass than LE site.

Zooplankton density

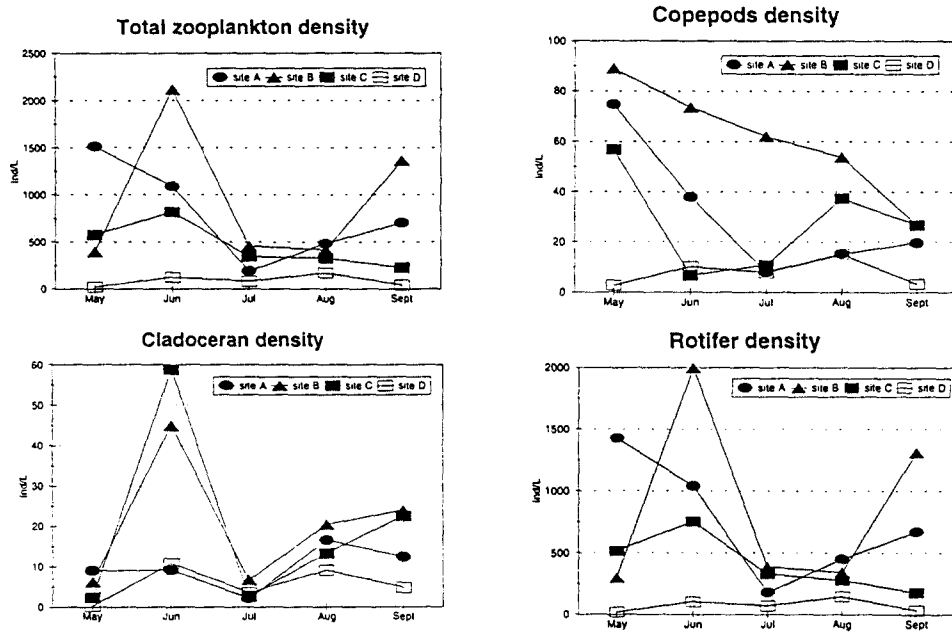


Fig. 2. Total zooplankton, cladoceran, copepod, and rotifer densities (individuals /L) at study sites between May and September.

Total zooplankton density, including cladocerans, copepods, and rotifers, were much higher at SB sites (A, B, and C) (ranged: 226~2,113 ind /L) than at LE site (D) (range: 21~170 ind /L) during the study period ($p < 0.01$, t-test) (Fig. 2). Mean cladoceran density was always higher at SB sites (ranged: 2~59 ind /L) than at LE site (<1~11 ind /L), with the largest difference occurring in June between site C and site D. Changes in cladocerans were most dramatic at site D (range: 0.1~11 ind /L) and site C (range: 2~59 ind /L) during the study. Despite high monthly variabilities, mean seasonal cladoceran densities were not significantly different between SB sites and LE site ($p > 0.05$, t-test). Monthly variation of copepod densities was smaller than that displayed by cladocerans and rotifers. The highest copepod density was always observed at site B (range: 27~89 ind /L), resulting in a significant difference between sites B and D at all times ($p < 0.01$, t-test) (Fig. 2). The seasonal mean copepod density at only site B significantly differed from that of site D ($P < 0.01$, t-test). Seasonal mean rotifer densities were always significantly higher (between 5~10 fold higher) at sites A, B, and C (range: 177~1,995 ind /L) than at site D (21~170 ind /L) ($p < 0.01$, t-test) (Fig 2). Monthly variation was most significant at site B (range: 299~1,995 ind /L).

Zooplankton composition in Sandusky Bay and Lake Erie

During this study, 29 species of zooplankton were identified in SB; 7 cladocerans, 3

Table 2. Zooplankton taxa and their occurrences in Sandusky Bay (pooled from sites A, B, and C) and Lake Erie (site D). * are species found only in Sandusky Bay. M, JN, JL, A, S indicates May, June, July, August, and September. Species abundance is indicated as D=dominant, C=common, or R=rare

Zooplankton	Sandusky Bay					Lake Erie				
	M	JN	JL	A	S	M	JN	JL	A	S
CLADOCERA										
<i>Daphnia</i> spp.	C	D	C	C	D		D	D	C	C
<i>Bosmina longirostris</i>	D	R	R	R	C	C		R	R	
<i>Eubosmina coregoni</i>	C	D	D	D	D		D	D	D	D
<i>Chydorus sphaericus</i>	R	R	R	R	C		R		R	R
<i>Diaphanosoma birgei</i>		C	D	R	R		R	C	R	R
* <i>Alona</i> sp.		R								
<i>Leptodora kinditii</i>		R	R				R			
COPEPODA										
Nauplii	D	D	D	D	D	C	D	D	D	C
Cyclopoids	C	C	C	C	C	D	C	C	C	R
Calanoids	C	C	C	C	C	R	C	C	R	R
ROTIFERA										
<i>Keratella cochlearis</i>	D	D	C	D	D			D	C	C
<i>Keratella quadrata</i>	R	C	C	R	D			R	R	C
* <i>Keratella valga</i>		R	R							
<i>Brachionus angularis</i>	R	D	C	C	C		R		R	
* <i>B. quadridentatus</i>	D	R	D	R						
* <i>Brachionus havanensis</i>	R	D	R							
* <i>Brachionus caudatus</i>			C							
* <i>Brachionus rubens</i>	R									
<i>Pompholyx complanata</i>		D	C	D	D		R			
<i>Asplanchna herricki</i>	C	R	C	C	C	D			D	
<i>Polyarthra vulgaris</i>	R	C	D	C	C			C	C	C
* <i>Lecane</i> sp.		R								
* <i>Trichocerca</i> sp.	R	C	C	R	R					
<i>Synchaeta</i> sp.	D	R	C	C		D	D	C	C	
* <i>Monostyla</i> sp.			R							
<i>Ascomorpha</i> sp.	R	R	R	C			C	C		
<i>Anuraeopsis fissa</i>		R	R					C		
<i>Filinia terminalis</i>			R	R				R		
* <i>Notholca</i> sp.	R	R								
No. of species in each month	19	25	25	18	15	6	12	14	14	10
Total species	29					19				

copepods, and 19 rotifers (Table 2). The greatest number of species was found in June and July, while species richness decreased toward the end of the summer. *Eubosmina coregoni* and *Daphnia* spp. numerically dominated cladocerans during the study period. Copepods occurred throughout the season and nauplii were always dominant. *Keratella*

Table 3. Shannon diversity index for zooplankton at each site and statistical difference between indices in pair-wise comparison. Significant differences among the values are shown as alphabetical letters (a>b>c: a<0.001, b<0.01, and c<0.05). Number of species is indicated in parentheses

	Sandusky Bay			Lake Erie
	site A	site B	site C	site D
May	0.73	0.57	0.46	0.40
	(14)	(11)	(9)	(6)
	a	b	c	c
June	0.86	0.72	0.67	0.71
	(19)	(13)	(15)	(12)
	a	b	b	b
July	0.83	0.90	0.85	0.87
	(12)	(14)	(14)	(14)
	a	a	a	a
August	0.65	0.60	0.63	0.71
	(10)	(11)	(9)	(14)
	b	b	b	a
September	0.64	0.68	0.82	0.71
	(11)	(14)	(11)	(10)
	b	b	a	b

spp., *Brachionus* spp., and *Pompholyx complanata* were the dominant rotifers of SB, while *Brachionus* sp. and *Pompholyx* sp. were seen in LE only rarely. *Monostyla* sp., *Anuraeopsis fissa*, *Filinia terminalis*, *Notholca* sp., *Lecane* sp., *Brachionus rubens*, and *Keratella valga* were found in SB throughout the study period but only as minor constituents of the community. Of 19 rotifer species we identified, nine species were observed only in SB (Table 2).

Overall, we found 19 of the 29 SB zooplankton species in LE: six cladocerans, three copepods and ten rotifers (Table 2). *Eubosmina coregoni* and *Daphnia* spp. also were the dominant cladocerans in Lake Erie. Species composition and occurrence of copepods were very similar in SB and LE. Rotifer species with the greatest abundance in Lake Erie were *Polyarthra vulgaris*, *Ascomorpha* sp., and *Synchaeta* sp.

Community indices

Community diversity of both the SB and LE sites varied from month to month (Table 3). Community diversity at the SB sites was significantly higher than at the LE at all times examined, except in July when the reverse was observed. The highest community diversity developed earliest in the upper reaches of SB, perhaps resulting from the very shallow depth, permitting rapid warming in those regions. Generally, sites within the SB had a more diverse zooplankton community.

Community similarity was compared between each pair of sites for a given date (Table 4). Community similarity at sites within SB was always higher (range: 0.69~0.89) than those (range: 0.44~0.84) between SB sites and the LE site. A combined comparison of

Table 4. Similarity index of pair-wise comparison of zooplankton species composition at each site. A, B, C, and D indicate sampling sites. SB indicates pooled data from sites A, B, and C.

	Within Bay				Bay-Lake		Whole SB-LE
	A-B	B-C	A-C	A-D	B-D	C-D	
May	0.80	0.90	0.78	0.44	0.53	0.61	0.42
June	0.81	0.78	0.76	0.55	0.52	0.72	0.58
July	0.69	0.85	0.61	0.54	0.50	0.58	0.55
August	0.80	0.80	0.76	0.67	0.69	0.76	0.75
September	0.88	0.88	0.82	0.63	0.73	0.84	0.73

pooled data from all sites within SB and the LE site indicated that communities within SB and LE became more similar as the season progressed.

DCA of zooplankton communities

Ordination of sample sites based on species abundance accounted for 67.5%, 20.0%, 9.8%, and 2.5% of sample variances by Axis I, Axis II, Axis III and Axis IV, respectively. The species abundance matrix ordinated in two-dimensional space showed some overlap between LE and SB sites but indicated a portion of the space occupied by SB communities and not LE communities (Fig. 3).

DCA ordination indicated that zooplankton dynamics among sites were seasonally variable (Fig. 4). Monthly behavior of the zooplankton community among SB sites was similar in the ordination space, except in site C in September. A similar pattern of community change was shown in the earlier season (May through July) at site D, but changes in

Ordination of sites

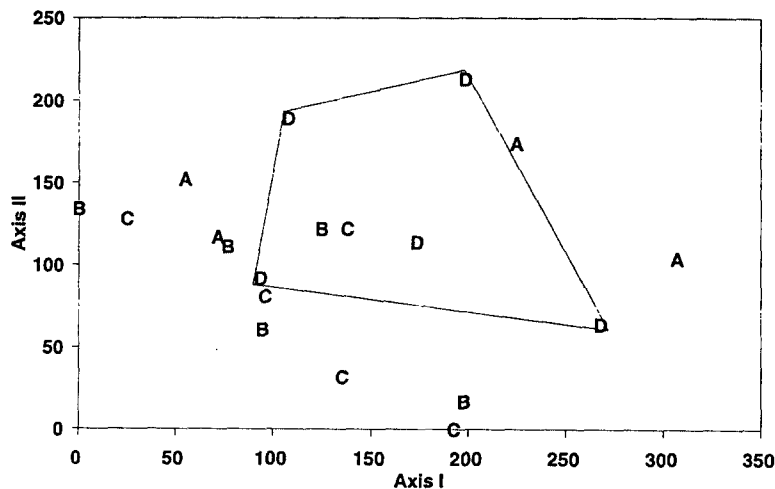


Fig. 3. Distribution of different sites in two dimensional DCA space. A, B, and C are Sandusky Bay sites and D is Lake Erie. Lake Erie site D is enclosed by a polygon.

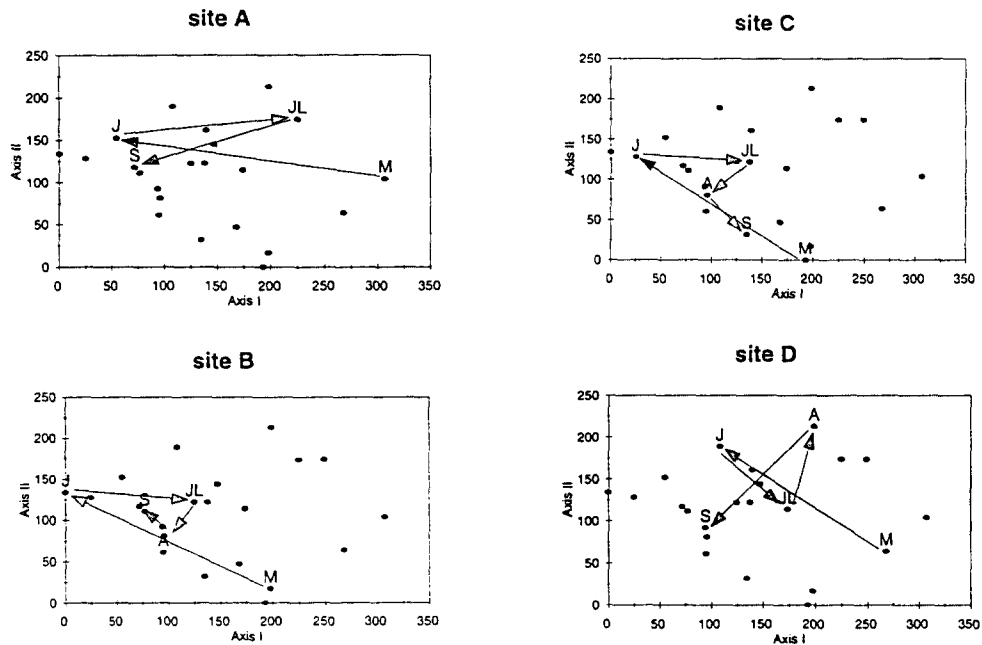


Fig. 4. Monthly trajectory of zooplankton dynamics in DCA ordination, M=May, J=June, JL=July, A=August, and S=September.

Table 5. Pearson correlation coefficients between limnological variables and DCA Axis scores of species ordination. Only significant correlations are shown. * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

Axis	Variables	correlation coefficients
Axis I	Algal density	-0.78**
	Alkalinity	0.80**
	Bacterial density	-0.75**
	Bacterial phosphorus	-0.71**
	Dissolved oxygen	0.73**
	Total phosphorus	-0.63**
Axis II	Chlorophyll-a	0.73*

separation along DCA Axis I (i.e., those species abundances that forced a low Axis I score) at SB sites were *Brachionus angularis*, *Pompholyx complanata*, *Keratella valga*, *K. quadrata*, *Filinia terminalis* (rotifers), *Eubosmina coregoni* and *Daphnia* spp. (cladocerans).

Correlation of limnological variables and species abundance DCA Axis scores

Pearson correlation coefficients were calculated to describe the strength of correlations

August and September were quite different from those of SB sites.

We examined the contribution of each species to each ordination as a way of determining those species that were most important in driving the DCA ordination (Fig. 5). We identified those species at the extremes of Axis I with other parameters that were significantly correlated with the axis scores because it was along that axis that explained most of variation in site separation. Zoo plankton groups most important in forcing site

Ordination of species

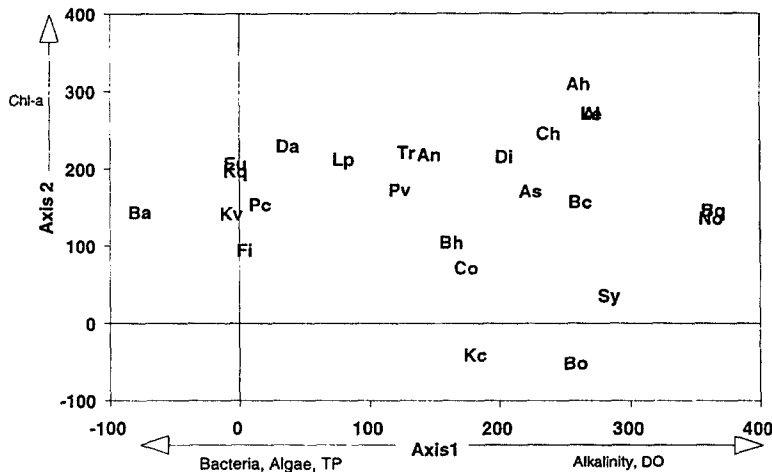


Fig. 5. Distribution of zooplankton species important in distinguishing sites and times based on the ordination (Da=*Daphnia* spp., Eu=*Eubosmina coregoni*, Bo=*Bosmina longirostris*, Ch=*Chydorus sphaericus*, Di=*Diaphanosoma birgei*, Al=*Alona* sp., Lp=*Leptodora kindtii*, Co=Copepods (including cyclopoids, calanoids, and nauplii), Kc=*Keratella cochlearis*, Kq=*Keratella quadrata*, Kv=*Keratella valga*, Ba=*Brachionus angularis*, Bq=*Brachionus quadridentatus*, Bh=*Brachionus havanensis*, Bc=*Brachionus caudatus*, Pc=*Pompholyx complanata*, Ah=*Asplanchna herricki*, Pv=*Polyarthra vulgaris*, Le=*Lecane* sp., Tr=*Trichocerca* sp., Sy=*Synchaeta* sp., As=*Ascomorpha* sp., An=*Anuraeopsis fissa*, Fi=*Filinia terminalis*, No=*Notholca* sp.)

made between DCA axis scores and limnological and chemical variables (Table 5). Alkalinity and dissolved oxygen were significantly positively correlated with Axis I scores ($p < 0.01$), while algal density, bacterial density, bacterial phosphatase, and total phosphorus were negatively correlated with Axis I scores ($p < 0.01$). Chlorophyll *a* concentration was positively correlated with Axis II scores ($p < 0.05$).

DISCUSSION

We found that the zooplankton communities in Sandusky Bay (SB) differed from those in Lake Erie (LE) in two ways by having a greater rotifer density and species richness. Almost half of the 19 rotifer species found in SB were not observed in LE. Except for *Keratella cochlearis* which was common in both SB and LE, dominant rotifers in SB (*Brachionus angularis*, *Keratella quadrata*, and *Pompholyx complanata*) were uncommon in LE, and those that were dominant in LE (*Synchaeta* sp., *Asplanchna herricki*, and *Ascomorpha* sp.) were less important constituents of the SB communities. The ordination of DCA

showed only a partial separation between SB and LE communities.

Like other Great Lakes coastal embayments at drowned river mouths, SB is characterized by high sediment and nutrient loading, sediment resuspension induced by wind and wave action, and exchange of nutrient-rich sediment water (Krieger 1989). The relatively high turbidity and suspended sediment concentrations in SB resulting from agricultural erosion (Richards and Baker 1985) may exert important selective forces on zooplankton physiology. A high concentration of suspended organic and inorganic particles can adversely effect feeding, growth and reproduction of certain zooplankton (Arruda *et al.* 1983, Kirk and Gilbert 1990, Krieger and Klarer 1991). Rotifers are generally favored over cladocerans in the presence of suspended sediments (Kirk and Gilbert 1990). The reproductive strategy and relatively long generation times of cladocerans and copepods are better adapted to less turbid, more stable environments (Allan 1976).

The flushing action of storm events may also be important in determining differences between SB and LE zooplankton communities (Krieger and Klarer 1991). Pace *et al.* (1992) reported that zooplankton biomass differed among lakes, estuaries, and rivers, suggesting that advective losses appear to be important in explaining differences between planktonic communities in lentic and lotic environments. Rotifers are considered to be opportunistic r-strategists with a great reproductive potential (Allan 1976, Pontin 1989), capable of rapidly restoring populations following storm events. Accordingly, Sprules and Jin (1990) found that natural systems with high flushing rates favored the growth of smaller zooplankton (e.g., rotifers).

Zooplankton communities in lakes having more eutrophic conditions generally have a higher percentage of rotifers (Radwan and Popiolek 1989). Rotifer abundances differed greatly under different trophic conditions of Lake Huron and Lake Michigan, indicating rotiferan preference for more productive systems containing abundant food sources (Evans 1986). *Brachionus* spp. and *Pompholyx complanata*, which were very abundant in SB, tend to occur in nutrient-rich environments and have used as indicators of eutrophic conditions (Stemberger 1979). Nutrient-rich conditions of SB also favor high densities of filamentous cyanophytes, which are relatively inedible to rotifers (Dumont 1977) and microcrustaceans (Webster and Peters 1978), but are capable of supporting large bacterial populations through release of dissolved organic compounds. In many aquatic environments, algal-released DOC significantly supported bacterial growth (Cole *et al.* 1982, Sondergaare *et al.* 1985, Sondergaard *et al.* 1988). In addition to autochthonous algal-released DOC, allochthonous DOC inputs may also support large bacterial populations as a food source for rotifers.

Rotifers are capable of feeding on suspended solids and benthic detritus, bacteria, small phytoplankton, and protozoans (Bogdan *et al.* 1980, Starkweather 1980, Bogdan and Gilbert 1982, Pejler 1983, Lair and Ali 1990). Although rotifers affect phytoplankton assemblages in freshwater environments (Scheda and Cowell 1988), they are important bacterial grazers in certain environments (Sanders *et al.* 1989, Hwang 1995). Species that survive in

hypereutrophic systems consist mostly of highly-efficient bacterivores and species that can alter the relative proportions of bacteria and phytoplankton in their diet to include a larger fraction of bacteria (Pejler 1983). The ordination of SB communities to regions of the DCA space not occupied by LE communities was due to the relative species abundance of the rotifers *Brachionus angularis*, *Pompholyx complanata*, *Keratella quadrata*, *K. valga*, and *Filinia terminalis*. The DCA axis separating these characteristic SB species from LE was significantly correlated with bacterial abundance and bacterial P, and all of these species were active bacterial grazers (Hwang 1995). These results suggest that microbial interactions may be active and that bacterial carbon flux may be relatively important in SB communities.

Currently much attention is focused on the significance of bacteria in planktonic food webs and whether bacteria are important in retrieving and retaining reduced carbon compounds that otherwise would be lost from the trophic web (e.g., Azam *et al.* 1983). Traditionally, the only C-link considered to be important was that from algae to microcrustaceans (algal food chain). Recent studies indicate that C-link from DOC to bacteria-protzoa-zooplankton (the microbial food web) can be significant in certain cases, and the relative importance of the algal food chain, on the one hand, and the microbial web, on the other, may differ in different habitats (Sherr and Sherr 1988, Carrick *et al.* 1991, Hwang and Heath 1996). In habitats such as SB that support large populations of inedible cyanophytes and large populations of bacteria, the microbial link may be relatively more important than the algal link in providing C to higher trophic levels. However, theoretical considerations imply that as the microbial C-link becomes stronger, the energetic efficiency of C-flow to higher trophic levels decreases due to the respiratory losses (Pomeroy and Wiebe 1988).

Trophic conditions that lead to a greater relative importance of the microbial link may support fundamentally different fish communities. Stockner and Shortreed (1989) reported that different fish communities and production level existed in lakes differing in structure at the base of the food web. They observed an inefficient energy transfer and a decreased production of small fish resulted in an ultra-oligotrophic lake that supported a picoplankton-based food chain with an abundance of protozoans and rotifers. Conversely, a greater production of larger fish and higher production were observed in a more productive oligotrophic lake, where nano- and microphytoplankton supported large-bodied zooplankton. A more direct and efficient carbon transfer through the food web is thought to be the cause of the differences in fish and zooplankton assemblages.

Indeed, fish communities of coastal embayments differ from those of the open water of the Great Lakes (Jude and Pappas 1992). Coastal embayment wetlands were characterized by a diverse fish community that was tolerant of silt and turbidity, that used wetlands for spawning, and as a nursery or shelter area. Larval and young fish can consume rotifers as readily as they consume cladocerans and copepods in rotifer-dominated environments (Hammer 1985, Hewitt and George 1987). Although coastal habitats are often ch-

characterized by their physical and chemical differences, we believe that the structure of the base of the trophic web may fundamentally differ in coastal and offshore habitats and may be an important factor determining the structure and productivity of fish communities characteristic of those regions.

적 요

오대호(The Great Lakes)의 하나인 Lake Erie (LE)와 이와 연결된 부영양화된 coastal wetland인 Sandusky Bay(SB)에서 동물 플랑크톤 군집의 구조를 분석하여, 이들의 차이점을 비교하고 서로 다른 군집형성에 관여하는 요인들을 조사하였다. 군집 구조의 분석을 위해, 동물 플랑크톤의 종과 밀도를 이용한 다중변이분석(multivariate analysis)인 Detrended Correspondence Analysis (DCA)를 수행하였다.

이 두 생태계에 있어서, 동물 플랑크톤 군집의 가장 큰 차이는 Sandusky Bay에서 윤충류(rotifer)의 훨씬 높은 종 풍부도와 밀도에 기인하였다. *Keratella* spp., *Brachionus* spp., 그리고 *Pompholyx complanata* 등이 SB 윤충류의 우점종들이었으며, LE에서는 *Brachionus*와 *Pompholyx*의 밀도가 상대적으로 매우 낮았다. 동물 플랑크톤 군집의 DCA 배열공간(ordination space)에서, LE 지역이 SB의 범위에 중복되어, SB 동물 플랑크톤 dynamics의 변이가 더 큼을 시사하였다. 그러나, ordination 공간에서 LB와 중복되지 않는 SB 지역의 배열은 두 지역의 동물 플랑크톤 군집이 상이함을 나타내며, *Brachionus angularis*, *Pompholyx complanata*, *Keratella valga*, *Keratella quadrata*, *Filinia terminalis*, *Notholca* sp. (이상 윤충류), *Eubosina coregoni*, *Daphnia* spp. (이상 지각류: cladocera) 등이 두 군집의 차이를 나타내는데 중요한 역할을 하였다. LE와 SB 동물 플랑크톤 군집의 상이함을 일차적으로 설명하는 DCA ordination Axis I은 박테리아의 밀도, 인산의 농도, 그리고 식물 플랑크톤의 밀도 등과 유의한 상관관을 보였다.

본 연구는 부영양상태의 연안 습지 생태계인 Sandusky Bay에서의 독립적인 동물 플랑크톤의 구조가 풍부한 유기 물질로 인한 박테리아의 높은 밀도와 이들을 섭식하는 많은 윤충류들에 의해 큰 영향을 받음을 보여주며, 이 윤충류가 박테리아 에너지를 상위 food web (즉, 고기)에 전달하는 중요한 연결단계가 됨을 시사한다. 이러한 미생물 에너지원이 Sandusky Bay가 어류의 산란 장소와 치자어의 양육지(nursery area)로서 역할을 하는데 중요한 요인이 되는 것으로 사료된다.

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