

## Spatial Patterns in Assemblage Structures of Pelagic Forage Fish and Zooplankton in Western Lake Superior

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**ABSTRACT.** We assessed abundance, size, and species composition of forage fish and zooplankton communities of western Lake Superior during August 1996 and July 1997. Data were analyzed for three ecoregions (Duluth-Superior, Apostle Islands, and the open lake) differing in bathymetry and limnological and biological patterns. Zooplankton abundance was three times higher in the Duluth-Superior and Apostle Islands regions than in the open lake due to the large numbers of rotifers. Copepods were far more abundant than Cladocera in all ecoregions. Mean zooplankton size was larger in the open lake due to dominance by large calanoid copepods although size of individual taxa was similar among ecoregions. Forage fish abundance and biomass was highest in the Apostle Islands region and lowest in the open lake ecoregion. Lake herring (*Coregonus artedii*), rainbow smelt (*Osmerus mordax*) and deepwater ciscoes (*Coregonus spp.*) comprised over 90% of the abundance and biomass of fishes caught in midwater trawls and recorded with hydroacoustics. Growth and condition of fish was good, suggesting they were not resource limited. Fish and zooplankton assemblages differed among the three ecoregions of western Lake

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*Superior, due to a combination of physical and limnological factors related to bathymetry and landscape position.*

**INDEX WORDS:** Lake Superior, zooplankton, lake herring, rainbow smelt, deepwater cisco, abundance, biomass.

## INTRODUCTION

Limnological assessments for Lake Superior were virtually absent prior to the Upper Lakes Reference Study of 1973 (Munawar 1978 and references therein), and unfortunately few comprehensive studies have followed to the present day. Fisheries assessment activities began much earlier, but were limited to commercially important species such as lake trout *Salvelinus namaycush* (Lawrie and Rahrer 1973, Hansen *et al.* 1995) and lake herring *Coregonus artedii* (Dryer and Beil 1964). More recent community-based fisheries assessments remain limited in their spatial extent, and are largely driven by management questions affecting top predators (trout and salmon). Bioenergetic models have been used to estimate prey supply from predator demand (Ebener 1995, Negus 1995, Johnson *et al.* 1998), and recent whole system ecological modelling (Kitchell *et al.* 2000) has provided aggregate estimates of biomass for many food web components. However, suitable information is not available to validate these results, nor do such modelling studies provide taxonomic resolution sufficient to describe species composition at lower trophic levels. Lack of suitable information describing fish and zooplankton communities will prevent scientists and managers from assessing the health of the ecosystem (Fabrizio *et al.* 1995) and addressing the ecological impacts of such factors as exotic species, climate change, and contaminants.

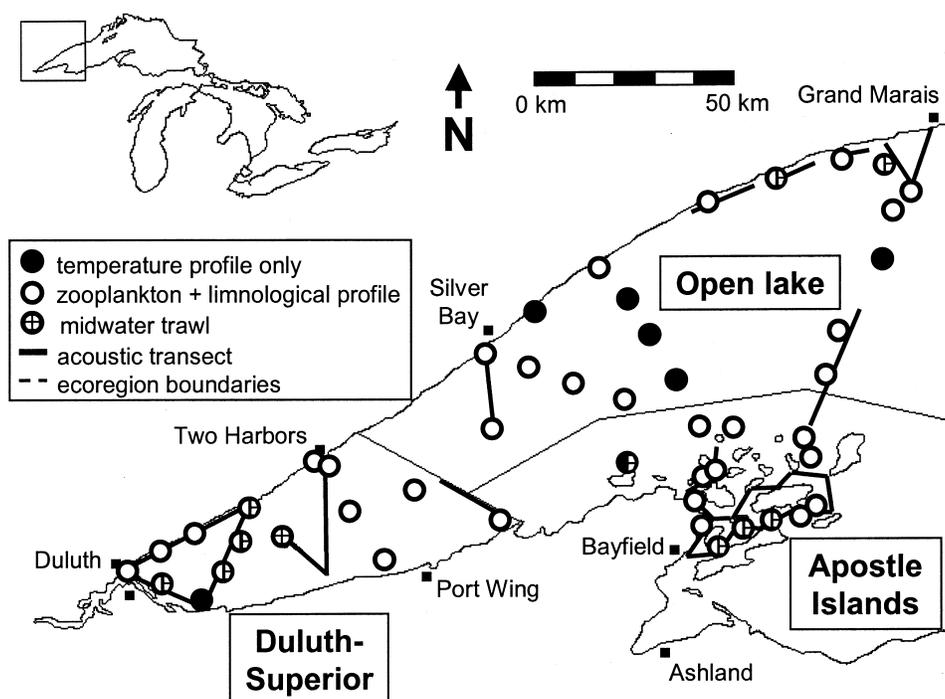
The species composition and abundance of resident taxa is the consequence of physical, chemical and biological factors. Productivity, biogeography, and habitat heterogeneity all influence the zooplankton and fish assemblages of aquatic ecosystems (Jackson and Harvey 1989, Benson and Magnuson 1992, Stemberger and Lazorchak 1994). Top down effects are largely size-based and influence the size, and therefore, the species composition of the fish and zooplankton community (Brooks and Dodson 1965, Tonn and Magnuson 1982). Physical and chemical properties create physiological barriers or act to modify the intensity of predator-prey interactions by shaping niche boundaries (Eadie and Keast 1984, Benson and Magnuson 1992, Stemberger *et al.* 2001). These

properties operate on differing spatial and temporal scales, making description of species assemblages difficult in natural systems. Designation of habitat zones (ecoregions) defined by large differences in physical, chemical, and biological properties is one way to simplify analyses of large systems, and provide a framework for description of the underlying assemblages (Benson and Magnuson 1992, Stemberger *et al.* 2001).

Our study seeks to remedy the lack of published information describing the zooplankton and forage fish assemblages of Lake Superior. Owing to the large size (82,414 sq km) and diversity of habitats within the lake, we designed a study that compared three ecoregions that are in relatively close proximity in the western arm of Lake Superior. We defined the ecoregions by differences in basin morphometry and limnological character that are expected to influence biological patterns, while also representing the three principal habitat types of Lake Superior—structurally complex nearshore areas (Apostle Islands), deep open water regions (open lake), and areas experiencing large anthropogenic influences (Duluth-Superior). Our objective was to compare the abundance, size and species composition of zooplankton and pelagic fishes in these three ecoregions of Lake Superior to help identify spatial patterns and scales needed to describe pelagic forage fish abundance and biomass at the lakewide scale.

## STUDY REGION

The study was conducted in the western arm of Lake Superior (Fig. 1). The western arm was divided into three ecoregions (Duluth-Superior, Apostle Islands, open lake) on the basis of lake morphometry and expected limnological and biological patterns. The Duluth-Superior ecoregion is characterized by simple bathymetry, shallow water (< 100 m) overlaying soft sand / silt substrates, and anthropogenic influences of Duluth-Superior and the St. Louis River (Munawar 1978, Minnesota Pollution Control Agency 1997). The Apostle Islands ecoregion is characterized by shallow water (< 100 m), sandy substrates with considerable habitat complexity owing to the 21 Apostle Islands and associated reefs and sandbars, and more dif-



**FIG. 1.** Location of sampling sites within the three ecoregions of the western arm of Lake Superior. Stations in both 1996 and 1997 are included. For clarity, stations used in both years, or those located close together are only marked once.

fuse anthropogenic influences. The open lake ecoregion was assumed to be more typical of the lake proper—deep water (up to 397 m) and steep rocky shorelines, with simple offshore physical structure, and comparatively few anthropogenic influences.

## METHODS

The study was conducted from 13–22 August 1996 and from 15–24 July 1997. In total, 74 physicochemical profiles, 40 vertical zooplankton hauls, 34 midwater trawls, and 585 km of hydroacoustic recording were collected across the 3 ecoregions in the 2 years. Limited sampling was done in the open lake ecoregion in 1996, and only in its south-western end (abutting the Duluth-Superior ecoregion). Technical problems with the hydroacoustic gear in 1996 restricted the processed data to the Duluth-Superior ecoregion. The R/V *Lake Explorer* (United States Environmental Protection Agency, U.S. EPA) served as the primary acoustic platform in both years, and also was used to collect zooplankton and water quality profiles. The R/V *Siscowet* (United

States Geological Survey, USGS) conducted midwater trawling, water quality sampling, and collected zooplankton samples. The R/V *Hack Noyes* (Wisconsin Department of Natural Resources, WDNR) collected acoustic data and temperature profiles in 1997, and Minnesota DNR collected temperature profiles in the Duluth-Superior and open lake ecoregions in 1997.

Zooplankton were sampled in single vertical hauls from 50 m to the surface (or from 2 m above the bottom in shallower water) with a 0.5-m, 63- $\mu$ m conical plankton net and preserved in 5% buffered formaldehyde solution. Vertical temperature profiles were collected with a SeaBird CTD (USGS and U.S. EPA), or Alec Electronics profiler (WDNR). The U.S. EPA CTD was also calibrated to collect profiles of oxygen, pH, conductivity, and fluorescence.

Fish were sampled using both midwater trawls and hydroacoustics. The midwater trawl (14.3-m box design, 6.4-mm cod-end mesh) was towed at approximately 4.8 km/hr, filtering approximately 4,072 m<sup>3</sup>/min trawled. All sampling was conducted at night (2100–0500) to optimize acoustic target

resolution resulting from expected diel patterns of fish behavior. Acoustic data were limited to the upper 100 m of the water column due to power limitations of the echosounder. The hydroacoustic gear (HTI 120 kHz split-beam system) was operated continuously for the duration of the sampling period, while trawls were conducted sporadically for 45-min duration. Initially, the trawls were aimed (with the aid of a SCANMAR® net mensuration system) at dense aggregations of acoustic targets reported by the Lake Explorer. However, due to the low catches in the trawl, this approach was abandoned after the first night in 1996 in favour of depth-stratified trawling at predetermined locations (Fig. 1).

The entire catch from each trawl was sorted by species, counted, sexed, and measured for length and weight. Fish age was determined from scales collected from a subset of all fishes using predetermined length categories. Fish diets are described elsewhere (Johnson *et al.* 2004).

We reserve the use of the term zooplankton to mean crustacean zooplankton unless noted to include rotifers. For the large taxa (e.g., *Mysis*, *Lepidodora*) total counts were made per sample, whereas abundances of smaller taxa were determined by averaging the counts in triplicate subsamples. Zooplankton size distributions were generated by measuring from the anterior margin of the head to the base of the tail spine (cladocerans) or caudal rami (copepods) for up to 15 individuals of each zooplankton taxon from each sample, and convert-

ing the results to counts per 0.1-mm size categories. Zooplankton biomass was estimated for dominant taxa using published length-weight relationships (McCauley 1984, Culver *et al.* 1985) by converting the mid-point of the size-category to dry weight, and multiplying by the density. Analysis of variance on appropriately transformed data ( $\log(x-1)$ ) was used to test for differences ( $\alpha < 0.05$ ) between years and ecoregions. Tukey's *post hoc* test was used to identify which pair-wise differences were significant.

We used an agglomerative, hierarchical clustering analysis to examine the patterns in zooplankton communities (sites) sampled in 1996 and 1997. Clustering was done using a complete linkage method (Lance and Williams 1967, Fisher and Van Ness 1971) with percent similarity as the distance measure (Pielou 1984). Those zooplankton sites with the greatest similarity in percent species composition clustered closest together.

## RESULTS

### Limnology

As expected, significant limnological differences were found among ecoregions: the Apostle Islands ecoregion was the warmest, whereas the Duluth-Superior ecoregion had the highest mean epilimnetic fluorescence (our surrogate for algal standing crop) (Table 1). The open lake ecoregion was the coolest, and was characterised by a much greater euphotic depth.

**TABLE 1.** Mean limnological characteristics observed in each ecoregion during the 1996 and 1997 cruises in the western arm of Lake Superior. Surface area, mean depth, and percent area < 30 m based on NOAA bathymetric data for Lake Superior. Values marked with different superscripts indicate significant differences ( $\alpha = 0.05$ ) within a row. — indicates that no light profile data were collected in the open lake ecoregion in 1996

Parameter	Duluth-Superior		Apostle Islands		Open lake	
	1996 (n=15)	1997 (n=12)	1996 (n=12)	1997 (n=17)	1996 (n=6)	1997 (n=16)
Surface area (km <sup>2</sup> )	1,562		2,757		4,261	
Mean depth (m)	71		57		159	
% area < 30m	27.6		37.9		2.2	
Water temperature at 1-m depth (°C)	14.0 <sup>a</sup>	12.4 <sup>ab</sup>	17.7 <sup>c</sup>	16.5 <sup>c</sup>	12.9 <sup>a</sup>	9.0 <sup>b</sup>
Thermocline depth (m)	10.0 <sup>d</sup>	8.1 <sup>d</sup>	8.0 <sup>d</sup>	6.4 <sup>d</sup>	6.5 <sup>d</sup>	4.4 <sup>e</sup>
Epilimnetic dissolved oxygen (mg/L)	12.1 <sup>fgh</sup>	10.8 <sup>fij</sup>	11.2 <sup>fj</sup>	9.9 <sup>i</sup>	12.5 <sup>gh</sup>	11.3 <sup>fgj</sup>
Epilimnetic temperature (°C)	13.6 <sup>k</sup>	11.9 <sup>kl</sup>	16.6 <sup>m</sup>	16.0 <sup>m</sup>	12.6 <sup>kl</sup>	10.4 <sup>l</sup>
Hypolimnetic dissolved oxygen (mg/L)	15.3 <sup>n</sup>	13.2 <sup>o</sup>	15.6 <sup>n</sup>	13.1 <sup>o</sup>	15.6 <sup>n</sup>	13.5 <sup>o</sup>
Euphotic depth (m)	49.1 <sup>pq</sup>	25.8 <sup>q</sup>	43.7 <sup>pq</sup>	22.9 <sup>q</sup>	—	80.7 <sup>p</sup>
Mean epilimnetic fluorescence (mV)	2.2 <sup>r</sup>	1.4 <sup>s</sup>	1.0 <sup>s</sup>	0.8 <sup>t</sup>	1.4 <sup>s</sup>	0.8 <sup>t</sup>

**TABLE 2.** Mean zooplankton abundance (#/m<sup>3</sup>) by ecoregion (1996 and 1997 combined). Only the most common taxa are listed individually, but all taxa observed are reflected in the totals. Other Cladocera species found were *Diaphanosoma birgei* and *Bythotrephes cederstroemii*. Other copepods found were *Senecella calanoides*, *Limnocalanus minutus*, *Leptodiptomus ashlandi*, *Mesocyclops edax*, and calanoid or cyclopoid juveniles for which species identification could not be made. Other rotifer genera found were *Asplanchna*, *Chromogaster*, *Gastropus*, *Lepadella*, *Locane*, *Monostyla*, *Ploesoma*, *Synchaeta*, and *Trychocerca*. Values marked with different superscripts indicate significant differences ( $\alpha = 0.05$ ) within a row.

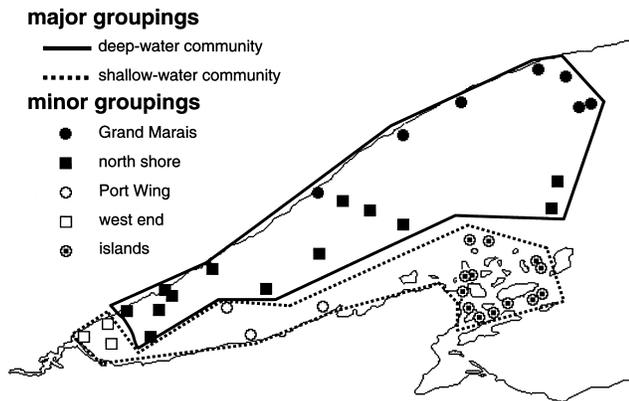
Taxa	Duluth-Superior		Apostle Islands		Open lake	
	1996 (n = 4)	1997 (n = 9)	1996 (n = 8)	1997 (n = 6)	1996 (n = 3)	1997 (n = 10)
All Cladocera	305 <sup>ab</sup>	1,212 <sup>a</sup>	530 <sup>a</sup>	647 <sup>a</sup>	24 <sup>b</sup>	<1 <sup>b</sup>
<i>Bosmina longirostris</i>	133	666	168	170	13	0
<i>Daphnia galeata mendotae</i>	116	43	112	215	10	<1
<i>Daphnia retrocurva</i>	30	448	50	40	1	<1
<i>Holopedium gibberum</i>	25	51	196	218	0	0
All copepods	10,063 <sup>c</sup>	14,703 <sup>c</sup>	10,487 <sup>c</sup>	14,925 <sup>c</sup>	9,090 <sup>c</sup>	8,765 <sup>c</sup>
Adult and juvenile calanoids	1,332 <sup>de</sup>	1,689 <sup>de</sup>	2,201 <sup>e</sup>	2,618 <sup>e</sup>	1,108 <sup>de</sup>	859 <sup>d</sup>
<i>Diaptomus sicilis</i>	241	161	66	83	382	171
<i>Epischura lacustris</i>	< 1	16	11	33	0	21
<i>Limnocalanus macrurus</i>	93	144	29	38	147	227
Adult and juvenile cyclopoids	718 <sup>f</sup>	3,453 <sup>f</sup>	1,265 <sup>f</sup>	3,143 <sup>f</sup>	343 <sup>fg</sup>	179 <sup>g</sup>
<i>Diacyclops thomasi</i>	108	362	220	566	29	24
nauplii	8,013 <sup>h</sup>	9,562 <sup>h</sup>	7,021 <sup>h</sup>	9,164 <sup>h</sup>	7,639 <sup>h</sup>	7,727 <sup>h</sup>
All crustacean zooplankton	10,368 <sup>i</sup>	15,916 <sup>i</sup>	11,017 <sup>i</sup>	15,573 <sup>i</sup>	9,115 <sup>i</sup>	8,765 <sup>i</sup>
All rotifers	9,448 <sup>j</sup>	38,883 <sup>j</sup>	23,650 <sup>j</sup>	43,873 <sup>j</sup>	5,532 <sup>jk</sup>	2,779 <sup>k</sup>
<i>Conochilus</i> sp.	3,977	13,027	8,307	21,097	1,426	159
<i>Kellicottia longispina</i>	3,578	18,722	5,258	12,118	2,024	1,788
<i>Keratella</i> sp.	432	855	4,387	7,361	405	129
<i>Polyarthra</i> sp.	666	4,135	3,955	1,740	369	58
All zooplankton	19,816 <sup>lm</sup>	54,799 <sup>l</sup>	34,667 <sup>l</sup>	59,446 <sup>l</sup>	14,646 <sup>lm</sup>	11,544 <sup>m</sup>

### Zooplankton

Zooplankton (including rotifers) densities in the Duluth-Superior and Apostle Islands ecoregions were approximately 45,000 / m<sup>3</sup>, whereas zooplankton densities were substantially lower in the open lake (~12,000 / m<sup>3</sup>, Table 2). Rotifers composed about 70% of the zooplankton in the Duluth-Superior and Apostle Islands ecoregions but only about 28% in the open lake. Copepods substantially outnumbered Cladocera in all three ecoregions, and calanoids were more abundant than cyclopoids in the open lake. According to Johannsson *et al.*'s (1999) zooplankton index for classification of trophic state (ratio of calanoids to (cladocerans + cyclopoids)) the Duluth-Superior (index = 0.44) and the Apostle Islands (0.90) ecoregions were considerably more productive than the open lake (4.09).

The hierarchical classification of zooplankton

sites revealed similar patterns to our *a priori* separation of ecoregions. In 1996, there were two zooplankton communities: one associated with the open lake and the other with the Apostle Islands. In the open lake area, the zooplankton community was dominated by copepod nauplii (40%) and *Kellicottia longispina* (25%). Within the Apostle Islands, the zooplankton community was dominated by two genera of rotifers (*Conochilus*, *Kellicottia* – 45%) and copepod nauplii (35%). In 1997, more sites were sampled over a much greater geographical area. There were again two main zooplankton groupings but the associations were more complex (Fig. 2). Within the open lake, the area along the northern coastline of Minnesota was dominated by copepod nauplii (89%) whereas deeper sites in the Duluth-Superior ecoregion were dominated by copepod nauplii (55%) and *Kellicottia longispina* (28%). The second large grouping in 1997 included



**FIG. 2.** Spatial delineation of zooplankton communities in western Lake Superior in 1997 showing two major and five minor communities. Groupings based on hierarchical clustering analysis.

the shallower sites of the Duluth-Superior ecoregion and the Apostle Islands ecoregion. Similar to results in 1996, two genera of rotifers (*Conochilus*, *Kellicottia*—52%) and copepod nauplii (19%) dominated the zooplankton community at the shallower sites along the south shore of Lake Superior.

The average size of zooplankton taxa was larger in the open lake ecoregion than in the other two ecoregions ( $F = 11.37$ ,  $p < 0.001$ ) (Table 3). However, the average size of any given species of zooplankton was similar among ecoregions.

Consequently, zooplankton size differences among ecoregions reflected differences in species composition. The open lake ecoregion was dominated by calanoid copepods, which were significantly larger than either cyclopoid copepods or Cladocera (Fig. 3).

Despite the much lower zooplankton abundance in the open lake, biomass estimates were only somewhat lower there than in the Duluth-Superior or Apostle Islands ecoregions (Fig. 4). Cladocera dominated the biomass in the Duluth-Superior and Apostle Islands ecoregions, whereas calanoid copepods dominated in the open lake.

In addition to differences in zooplankton community composition at the family level, there were differences among ecoregions at the species level. *Holopedium gibberum* was more abundant in the Apostle Islands than in the Duluth-Superior ecoregion, and was absent in the open lake at the time of our samples (Table 2). *Daphnia retrocurva* was more abundant than *D. galeata mendotae* in the Duluth-Superior ecoregion, but less abundant than *D. g. mendotae* in the other ecoregions (Table 2). *Alona* sp. and *Mesocyclops edax* were only found in the Apostle Islands, *Ceriodaphnia* spp. and *Leptodiptomus ashlandi* were only found in the Duluth-Superior ecoregion, and *Diaphanosoma birgei*, *Leptodora kindtii*, and *Limnocalanus minutus* were absent from the open lake.

The mesh size of our zooplankton nets was too large to quantitatively sample the entire rotifer

**TABLE 3.** Mean length (mm) of selected zooplankton taxa by Lake Superior ecoregion. Lengths based on adult individuals only. "n/a" means there were too few organisms of that taxa measured to develop a good size distribution and "—" means that taxa was not found in that ecoregion. Note the lengths were measured from the anterior margin of the head to the base of the tail spine (cladocera) or caudal rami (copepoda).

Taxa	Duluth-Superior		Apostle Islands		Open lake	
	1996	1997	1996	1997	1996	1997
Cladocera						
<i>Bosmina longirostris</i>	0.35	0.35	0.38	0.37	0.30	n/a
<i>Daphnia galeata mendotae</i>	1.55	1.27	1.55	1.37	1.50	n/a
<i>Daphnia retrocurva</i>	0.90	1.02	0.89	0.89	n/a	n/a
<i>Holopedium gibberum</i>	0.77	0.92	0.86	0.81	—	—
Calanoid copepods						
<i>Diaptomus sicilis</i>	0.91	0.91	0.97	0.94	0.95	0.96
<i>Epischura lacustris</i>	n/a	1.04	1.10	1.07	n/a	n/a
<i>Limnocalanus macrurus</i>	1.47	1.47	1.52	1.56	1.48	1.49
Cyclopoid copepods						
<i>Diacyclops thomasi</i>	0.51	0.52	0.47	0.51	n/a	0.58
All crustacean zooplankton	0.86	0.72	0.82	0.73	1.10	1.24

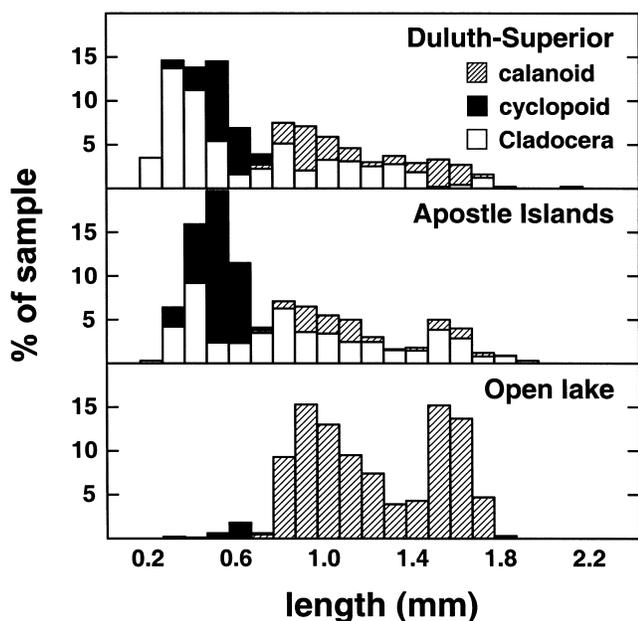


FIG. 3. Length-frequency distribution for zooplankton taxonomic groups by ecoregion. Data for both 1996 and 1997 cruises are combined.

community, and catches under represent the smaller taxa, but differences among ecoregions were apparent nonetheless. Of the 13 rotifer taxa found, *Conchilus* sp. and *Kellicottia longispina* were the most abundant, followed by *Polyarthra* and *Keratella* sp. *Conchilus* sp. and *Polyarthra* composed a much smaller percentage of rotifers in the open lake than in the other two ecoregions, whereas *Keratella* was much more abundant in the Apostle Islands than

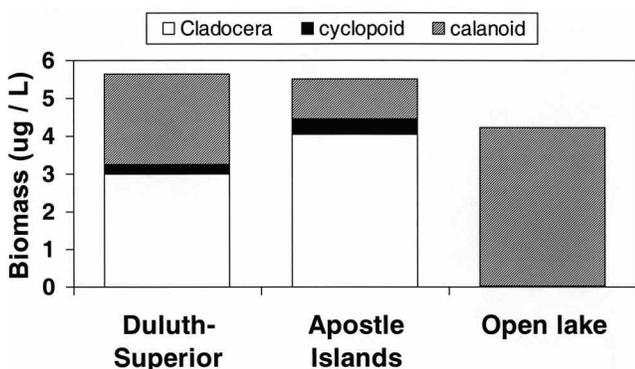


FIG. 4. Estimated biomass ( $\mu\text{g/L}$  dry weight) of zooplankton taxonomic groups in the three ecoregions of western Lake Superior. Data for both 1996 and 1997 were combined prior to estimating the biomass.

elsewhere (Table 2). *Chromogaster*, *Locane*, and *Monostyla* sp. were found only in the Apostle Islands, *Lepadella* was found only in the open lake, and *Pleosoma* was absent from the open lake.

### Fish

Nine species of fish were caught in midwater trawls (Table 4). Over 98% of the number, and 92% of the total midwater trawl biomass was composed of lake herring, rainbow smelt, and deepwater ciscoes (*Coregonus kiyi*, *C. hoyi*). Catch-per-unit-effort was highest for all three fish groups in the Apostle Islands; rainbow smelt and lake herring catches were lowest in the open lake, whereas deepwater cisco catches were lowest in the Duluth-Superior ecoregion (Table 5). More species and significantly more lake herring ( $t = 1.76$ ,  $p < 0.02$ ) were caught in midwater trawls in 1996 than in 1997 (Table 4), in part due to the greater number of trawl tows conducted in the Apostle Islands ecoregion.

Mean length and weight of lake herring caught in midwater trawls were largest in the open lake ecoregion, intermediate near Duluth-Superior, and smallest in the Apostle Islands ecoregion ( $F_{\text{length}} = 103.8$ ,  $p < 0.001$  and  $F_{\text{weight}} = 78.94$ ,  $p < 0.001$ ). For deepwater ciscoes, the largest individuals were caught in the Apostle Islands, with no size difference between the other two ecoregions ( $F_{\text{length}} = 12.9$ ,  $p < 0.001$  and  $F_{\text{weight}} = 19.5$ ,  $p < 0.001$ ). There were no significant differences in the size of rainbow smelt among ecoregions.

Acoustic estimates of fish biomass were highest in the Apostle Islands (Fig. 5). Approximately 90% of the biomass in each ecoregion was composed of lake herring and deepwater ciscoes, with the remainder composed of rainbow smelt. Insufficient midwater trawls and overlapping size and spatial distribution precluded differentiating between lake herring and deepwater ciscoes in the acoustic data.

### DISCUSSION

We began this study with the *a priori* expectation of differences in biological assemblages among ecoregions based on bathymetry, substrate, and characteristics of the surrounding watershed, and indeed, found such differences. The Apostle Islands was the warmest and shallowest ecoregion (Table 1), and contained the highest biomass of zooplankton and fish. The open lake was the coldest and deepest ecoregion, and contained the lowest densi-

**TABLE 4.** Total catch composition from midwater trawls towed in western Lake Superior in 1996 and 1997. Data are provided by number and total weight.

Species	1996 (n = 15)		1997 (n = 19)	
	number	weight (g)	number	weight (g)
Rainbow smelt <i>Osmerus mordax</i>	42	757	45	714
Lake herring <i>Coregonus artedii</i>	470	64,596	58	13,889
Kiyi <i>Coregonus kiyi</i>	7	347	12	594
Bloater <i>Coregonus hoyi</i>	9	877	18	1,644
Unidentified coregonines	6	420	3	186
Lake trout <i>Salvelinus namaycush</i>	2	3,357	1	635
Lake whitefish <i>Coregonus clupeaformis</i>	3	1,768	0	0
Walleye <i>Sander vitreus</i>	1	752	0	0
Spoonhead sculpin <i>Cottus ricei</i>	2	8	0	0
Total	542	72,882	137	17,662

**TABLE 5.** Catch statistics (means  $\pm$  S.D.) for dominant fish species collected from midwater trawls in three ecoregions of western Lake Superior in 1996 and 1997. Superscripts indicate significant differences ( $\alpha = 0.05$ ) within a row.

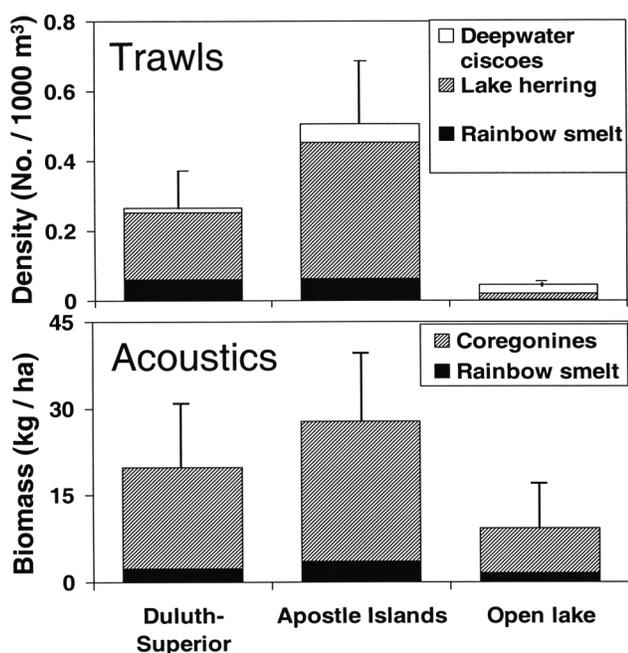
Species	Parameter	Duluth-Superior	Apostle Islands	Open lake <sup>1</sup>	Overall
rainbow smelt	CPUE (#/1,000 m <sup>3</sup> )	0.0614	0.0636	0.0032	0.0518
	total length (mm)	152 $\pm$ 30 <sup>a</sup>	147 $\pm$ 29 <sup>a</sup>	83 <sup>b</sup>	148 $\pm$ 30
	weight (g)	25 $\pm$ 17 <sup>a</sup>	17 $\pm$ 9 <sup>b</sup>	1 <sup>c</sup>	20 $\pm$ 14
	age (yr) <sup>2</sup>	2.1	2.3	no data <sup>1</sup>	2.1
lake herring	CPUE (#/1,000 m <sup>3</sup> )	0.1916	0.3887	0.0162	0.2395
	total length (mm)	296 $\pm$ 26 <sup>a</sup>	261 $\pm$ 30 <sup>b</sup>	362 $\pm$ 38 <sup>c</sup>	273 $\pm$ 34
	weight (g)	187 $\pm$ 66 <sup>a</sup>	131 $\pm$ 49 <sup>b</sup>	335 $\pm$ 132 <sup>c</sup>	150 $\pm$ 64
	age (yr) <sup>2</sup>	6.0	5.3	no data <sup>1</sup>	5.5
deepwater ciscoes	CPUE (#/1,000 m <sup>3</sup> )	0.0133	0.0547	0.0258	0.0336
	total length (mm)	197 $\pm$ 43 <sup>a</sup>	241 $\pm$ 20 <sup>b</sup>	207 $\pm$ 22 <sup>a</sup>	227 $\pm$ 32
	weight (g)	47 $\pm$ 25 <sup>a</sup>	88 $\pm$ 19 <sup>b</sup>	52 $\pm$ 19 <sup>a</sup>	74 $\pm$ 27
	age (yr) <sup>2</sup>	4.8	5.3	no data <sup>1</sup>	5.2

<sup>1</sup>No trawls were towed in the open lake ecoregion in 1996.

<sup>2</sup>Ages based on 1996 fish only.

ties and biomass of zooplankton and forage fish. Hoff (In review) studied the structure of benthic fish communities in western Lake Superior, and found that three discrete communities existed in that region of the lake. Those communities were structured by depth, so bathymetric differences among the three ecoregions would result in different proportions of the basin in each ecoregion being inhabited by these communities. Morphological attributes (Hoff 2004) and parasite communities (Hoff *et al.* 1997) of lake herring have also been used to differentiate stocks in the western arm of Lake Superior, which indicates that individual species adapt to local habitats and conditions.

The zooplankton community of western Lake Superior has changed structurally since the 1970s. The zooplankton densities we found were 2-4 fold greater than the July-August values reported by Watson and Wilson (1978) for comparable regions of the lake. The numerical dominance by copepods that we found was evident in previous studies (Patalas 1972, Selgeby 1974, Watson and Wilson 1978), although the cyclopoid fraction increased in our study relative to the previous work. We also observed a greater contribution of nauplii in our samples than was found previously. We do not think this was simply related to lake temperature, as seasonal life cycles for all taxa should have favoured



**FIG. 5.** Density from midwater trawls (top) and biomass from acoustics (bottom) for dominant pelagic fishes in the three ecoregions of western Lake Superior during 1996 and 1997. 95% confidence intervals are for total catch. Deepwater ciscoes include bloater chub *Coregonus hoyi* and kiyi *C. kiyi*; coregonines include lake herring and deepwater ciscoes.

adults and copepodites over nauplii by the July–August period when we were sampling.

Despite the greater zooplankton abundance we found, our estimates of zooplankton biomass were half of those reported by Watson and Wilson (1978). Further, the relative biomass proportions shifted in favour of cladocerans at the expense of calanoid copepods in the Duluth-Superior and Apostle Islands ecoregions. While some of this difference in reported biomass may be due to our omission, but Watson and Wilson's inclusion, of nauplii in the estimates, our lower reported biomass also reflects a shift towards smaller cyclopoids over larger calanoids. This shift in size composition may have resulted from increased size-selective predation by lake herring, which were more abundant in the 1990s than during the early 1970s.

Watson and Wilson (1978) did not find any differences in zooplankton abundance or biomass among their ecoregions based on hierarchical cluster analyses. Differences were evident when they assigned samples to *a priori* zones based on tem-

perature patterns, and the relative abundances were similar to what we observed in our study. Both Watson and Wilson (1978) and Patalas (1972) sampled the entire lake, but with low spatial coverage for any one area, which prevented them from discriminating regional differences such as we detected among ecoregions.

*Leptodiaptomus ashlandi* and *Senecella calanoides* remain rare in western Lake Superior. *L. ashlandi* was very abundant in 1971 (Selgeby 1974), but abundance had declined dramatically by 1973 (Watson and Wilson 1978) and further still by 1979–80 (Balcer *et al.* 1984), and we found *L. ashlandi* only rarely in our plankton hauls, and never in fish stomachs. *S. calanoides* are only found in deep, cold water masses (Conway *et al.* 1973) and often at low density ( $< 1/m^3$ , Balcer *et al.* 1984). Our net sampling protocol (hauls from 50 m to surface) may have reduced our likelihood of encountering this species. Low numbers of *S. calanoides* were seen in lake herring stomachs, but only in the Duluth-Superior ecoregion, suggesting this taxon remains scarce in western Lake Superior.

Few independent surveys exist to compare with the abundance and species composition of the fish community sampled in our study, but changes in abundance, biomass, and species are evident over time. Annual lakewide bottom trawl surveys conducted by the USGS Lake Superior Biological Station since 1978 (Bronte *et al.* 2003), show that mean biomass of rainbow smelt, lake herring and deepwater ciscoes were all lower during our study years than the long-term (1978–1999) mean. Relative contributions of the three taxa have varied through the USGS time series owing to variable recruitment (strong lake herring year classes in 1984, 1988–90, and 1998; and rainbow smelt in 1983, 1986, and 1994) and changes in survival (high rainbow smelt mortality in 1979 and 1980 reduced rainbow smelt biomass by 90% from 1978 to 1981) (Selgeby *et al.* 1994). Bottom trawl surveys conducted in the Duluth-Superior and Apostle Islands regions in the 1960s (Reigle 1969) were dominated by deepwater ciscoes, although deepwater ciscoes were largely absent from tows  $< 30$  m. In Reigle's surveys, as with our trawl data, deepwater cisco catches were over twice as high in the Apostle Islands region compared with Duluth-Superior, and lake herring were caught only rarely.

We estimated that approximately 10% of the acoustic biomass was rainbow smelt and the balance was coregonids, whereas Heist and Swenson (1983) estimated that rainbow smelt composed

75–99% of the 1978–79 pelagic fish biomass in the upper 30–50 m, and 50% of the pelagic biomass in the upper 30–100 m of three of the same areas that we sampled. Our estimates of rainbow smelt biomass (1.58–3.58 kg/ha) were substantially lower than those reported by Heist and Swenson (3.23–5.61 kg/ha averaged across all three ecoregions, and 4.31–17.78 kg/ha in the Duluth-Superior ecoregion). In contrast, our total fish biomass estimates from acoustics equaled (Duluth-Superior) or exceeded (average of all ecoregions) the Heist and Swenson estimate for rainbow smelt, and probably would exceed their total fish biomass given the low incidence of non-rainbow smelt targets they observed in the upper 50 m of the water column.

On the basis of the hydroacoustic estimates, the pelagic fish biomass of Lake Superior is 4 to 11 times lower than Lake Michigan (68.8 kg/ha), Green Bay (97.7 kg/ha), or Lake Ontario (179.7 kg/ha) (Mason *et al.* 2000). When appropriately scaled to other Lake Superior studies, our estimates of pelagic forage exceeded those used by Negus (1995) for Minnesota waters, but are comparable to those used by Ebener (1995) for the western half of Lake Superior. If predator demand has remained comparable to these earlier studies, then our results support the conclusions of Negus (1995) and Ebener (1995)—prey supply is inadequate to satisfy predator demand.

Our study demonstrated large differences in the composition, abundance, and biomass of zooplankton and fish assemblages among ecoregions. Spatial variability within ecoregions was also high, whereas fish and zooplankton abundance was low, which indicates that any comprehensive survey must be spatially intensive to adequately describe community composition. The ecoregion differences we found support the development of whole-lake scale biological assessments and habitat surveys stratified by such regions, and the three ecoregion types we investigated (gently sloping shallower areas (Duluth-Superior); bathymetrically complex regions around islands and underwater ridges (Apostle Islands); and steep-sided, bathymetrically simple, open coastline (open lake)) provide useful divisions for much of the Lake Superior shoreline. On finer scales, sample designs considering river plumes, small embayments, and similar local features should be considered. Acoustic transects revealed that most fish were concentrated inside the 80 m bathymetric contour regardless of ecoregion, suggesting sampling effort should consider proximity to shore or to longshore thermal bars. Similar

spatial descriptors could not be generated for the zooplankton because of absence of continuous sampling; an optical plankton counter or high-frequency acoustic system calibrated to zooplankton target size would greatly improve our understanding of zooplankton community dynamics. Vertical plankton hauls and midwater trawling must remain part of any survey to supplement data collected by acoustical and optical instrumentation to enable species separation. While depth-stratified trawling caught more fish than trawls aimed at acoustic scatter, we still felt too few trawl tows were taken to provide adequate information to develop relationships among acoustic target strength, fish size, and species separation. Our findings should help to guide future assessments of zooplankton and fish assemblages in Lake Superior.

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