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Status of the Amphipod *Diporeia* spp. in Lake Superior, 1994–2000

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ABSTRACT. *The amphipod* Diporeia *spp. is the dominant component of the Great Lakes benthic macroinvertebrate fauna, and plays an important role in the ecosystem. The Great Lakes Water Quality Agreement of 1978 (GLWQA) calls for the use of* Diporeia *as an indicator of ecological condition, with a goal of 220 to 320/m*^{2} *at depths less than 100 m, and 30-160/m*^{2} *at greater depths. To ascertain the status of* Diporeia *in Lake Superior, a probability-based survey of 27 sites representing the U.S. nearshore (10 to 110 m) waters of Lake Superior was conducted in 1994, and again in 2000. During 1995 to 1998, ten nearshore non-depositional sites and five sites in major depositional basins in the western half of the lake were revisited yearly to examine variability of* Diporeia *abundance. In 1994, nearshore* Diporeia *abundance ranged from 550 to 5500/m*^{2}*, and the entire nearshore area met or exceeded the GLWQA ecosystem objective. In 2000, abundance ranged from less than 10 to 2,800/m*^{2}*, and 11% of the nearshore area did not meet the GLWQA objective. The area that did not meet the GLWQA objective was located in the eastern half of the lake. Examination of yearly abundance data in the western half of Lake Superior did not reveal a significant trend at nearshore or offshore sites. Although* Diporeia *abundance in the eastern half of the lake was lower in 2000 than 1994, the severe declines in* Diporeia *populations that have been observed in the lower Great Lakes are not evident in Lake Superior. Abundances of* Diporeia *observed in the present study are higher than those reported in the 1970s by a factor of seven.*

INDEX WORDS: *Lake Superior, benthic macro-inertebrates, amphipods,* Diporeia*, ecological status.*

INTRODUCTION

Abundance of the amphipod *Diporeia* spp. has been selected as an indicator of ecological condition for the Laurentian Great Lakes (Reynoldson 1993). Amphipods of the genus *Diporeia* are the dominant component of the Great Lakes benthic macroinvertebrate community, in terms of both numbers and biomass (Cook and Johnson 1974, Mozley and Howmiller 1977, Nalepa 1989). *Diporeia*, a glacial relict, is distributed throughout the Great Lakes in cold, clean waters of nearshore as well as offshore benthic zones. *Diporeia* is associated with the sediment-water interface, where it feeds on organic matter settling from the water column (Marzolf 1965, Gardner *et al.* 1985, Fitzgerald and Gardner 1993). This amphipod is an important component of the diets of numerous Great Lakes fishes, including sculpins, bloater, smelt, alewife, and juvenile burbot and lake trout (Owens and Weber 1995, Wojcik *et al.* 1986, Wells and Beeton 1963, Foltz and Norden 1977, Janssen and Brandt 1980, Fratt *et al.* 1997, Elrod 1983, Dryer *et al.* 1965). *Diporeia*'s prominence, its basin-wide distribution, and its role in benthic-pelagic coupling and food web dynamics suggest that changes in its abundance will reflect changes in ecological condition and will be accompanied by alterations in other ecosystem components of the Great Lakes.

The Great Lakes Water Quality Agreement (GLWQA) of 1978 (IJC 1978) established *Diporeia* abundance as an indicator of ecosystem health for the Great Lakes. Furthermore, the GLWQA set specific objectives for Lake Superior, calling for the maintenance of *Diporeia* throughout the lake at densities of 220 to 320/m^2 in nearshore waters

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(depths less than 100 meters), and 30 to 160/m^2 in offshore waters (depths greater than 100 meters). These objectives were based on maintaining *Diporeia* abundance at then-current levels. Recently, severe declines of *Diporeia* populations have been observed in the lower Great Lakes (Dermott and Kerec 1997, Nalepa *et al.* 1998, Lozano *et al.* 2001, Dermott 2001). However, data for Lake Superior are limited, with the most recent lakewide survey of sediment fauna conducted in 1973 by the Great Lakes Biolimnology Laboratory and reported by Cook (1975). The purpose of this study is to ascertain the status of *Diporeia* populations in U.S. nearshore waters of Lake Superior in relation to the GLWQA objective and the levels observed in 1973 (Cook 1975), and to determine whether *Diporeia* in Lake Superior are experiencing the declines observed in the lower lakes.

METHODS

Diporeia were sampled at 27 sites in the U.S. nearshore waters of Lake Superior in August, 1994, and August to early October, 2000. Site selection followed a randomized, probability-based sampling design used in the Great Lakes Environmental Monitoring and Assessment Program (EMAP) (US EPA 1992, US EPA 1993, Stevens 1997). The target area was defined as waters of Lake Superior between the shoreline and the 150 m contour. The target area was delineated using bathymetric maps digitized on a 4 km grid. A three-fold enhancement of the EMAP base grid (US EPA 1993) was applied to the target area. Sampling sites were located at the intersections of the resulting hexagons. The point to point distance on the grid was 13.3 km, resulting in a density of one point per 155 km^2. Each site's sampling coordinate was verified using a differential global positioning system (DGPS). Sampling was limited to the portion of the target zone within U.S. waters and with depths between 10 and 110 meters, resulting in selection of 27 sampling locations (Fig. 1). Approximately half (n = 14) of the sites were located west of the Keweenaw Peninsula, and half (n = 13) to the east. In 1994, the depths of stations ranged from 22 to 110 m, with a mean of 59 m. In 2000, depths were 18 to 137 m, with a mean of 62 m.

To examine inter-annual variability in *Diporeia* abundance, 10 of the 27 nearshore, non-depositional sites were selected in the western half of the lake, along with 5 offshore sites in major depositional basins of western Lake Superior. The 15 sites extended from Duluth, at the western end of the lake, eastward to Keweenaw Bay (Fig. 4). *Diporeia* were sampled yearly at these 15 sites from 1995 to 1998, and again in 2000, during August to September. Nearshore stations ranged from 12 to 110 meters in depth with a mean of 54 m, and offshore stations from 110 to 301 meters with a mean of 203 m. Based on visual inspection, non-depositional, nearshore sediments included clay, sand, and gravel, whereas depositional, offshore sediments consisted of silt (mud) or soft glaciolacustrine clay. To examine seasonal variability, the five offshore stations were sampled in June, August, and September, 1995.

At each station, *Diporeia* were collected following the methods of Nalepa (1987). Sediment was collected using a Ponar grab with a sampling area of 0.046 m^2. Each sample consisted of three replicate grabs. The contents of each grab were placed into an elutriation device and rinsed through a 500 µ mesh sleeve. The organisms retained were preserved in 5% formalin containing rose bengal stain. In the laboratory, *Diporeia* were identified and enumerated under a dissecting microscope. The abundance for each sample was obtained by averaging the three replicate counts. Statistical analyses were performed using SYSTAT 9 (Wilkinson 1999).

RESULTS

Comparison of 1994 and 2000, U.S. Nearshore

Diporeia abundance in 1994 ranged from 554 to 5,507/m^2, with a mean (± SE) of 1,990 ± 208/m^2 (Fig. 1). In 2000, abundance ranged from 7 to 2,782/m^2, with a mean (± SE) of 1,301 ± 141/m^2 (Fig. 1). A paired sample t-test detected a significant difference in abundance between the two years (paired $t = 3.239$, d.f. = 26, $p = 0.003$). The greatest declines occurred in the eastern half of the lake (Fig. 2). Mean abundances in three depth ranges (10 to 39 m, 40 to 69 m, and 70 m and greater), in both eastern and western portions of the lake, were lower in 2000 as compared to 1994 (Table 1). However, the most substantial decrease was observed in the 10 to 39 m depth range in the eastern half of the lake. This eastern shallow zone had the highest mean abundance (2,993/m^2) in 1994 and the lowest (774/m^2) in 2000. In the eastern half of the lake, *Diporeia* abundance was significantly lower in 2000 than in 1994 (paired $t = 2.807$, d.f. = 12, $p = 0.016$), but in the western half, there was no signifi-

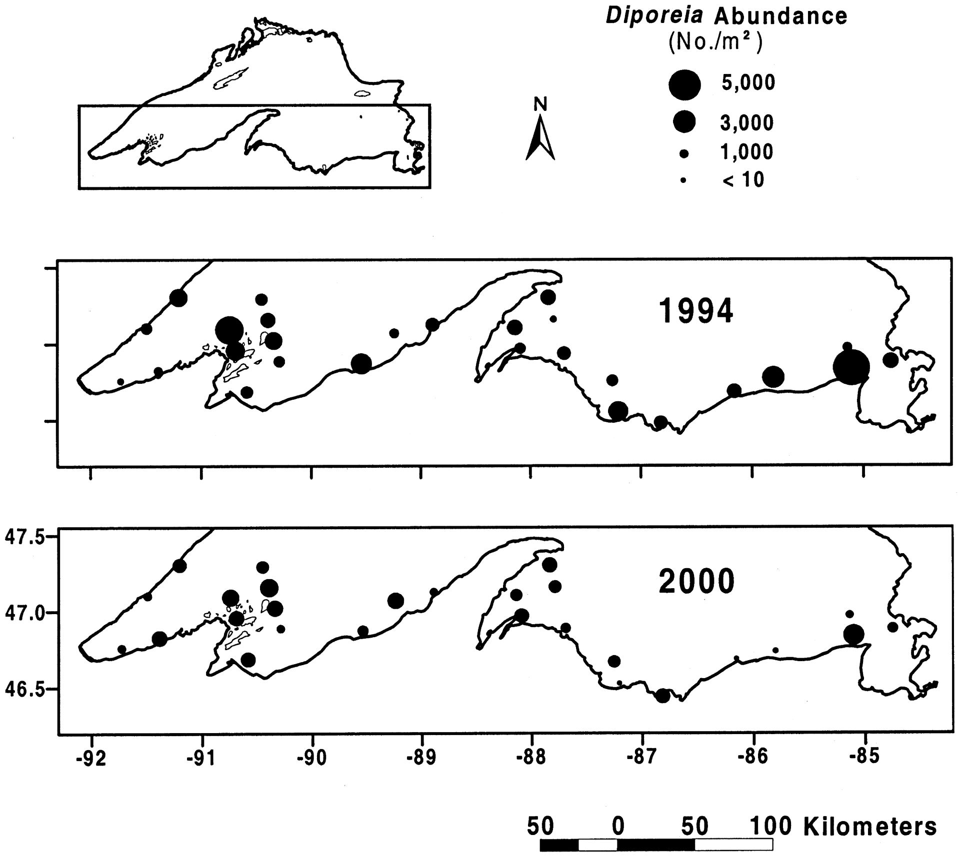

FIG. 1. Abundance of **Diporeia** *spp. in U.S. nearshore waters of Lake Superior, 1994 and 2000.*

cant difference in abundance between the two years (paired t = 1.728, d.f. = 13, p = 0.108).

The abundance of *Diporeia* across the entire area sampled can be summarized by a cumulative frequency distribution (Fig. 3). This plot shows the proportion of sites with *Diporeia* abundance at or below a given level. The proportion of sites represents the proportion of the area of the U.S. nearshore waters of Lake Superior. In 1994, the entire region exceeded the GLWQA objective of 220 to 320/m^2, and 11% of the area, represented by three sites, exceeded 3,000/m^2. In 2000, 11% of the area did not meet the GLWQA objective, and none of the area exceeded 3,000/m^2.

Inter-annual Variation, Western Lake Superior

Abundance of *Diporeia* at individual sites sampled annually from 1994 to 2000 exhibited considerable variability from year to year, with no consistent trends over time (Fig. 4). *Diporeia* abundance was significantly greater at nearshore sites than offshore sites (ANOVA, F = 51.984, d.f. = 1, 82, p = 0.000). The mean (± SE) density of *Diporeia* at nearshore sites was 1,742 ± 103/m^2, with a range of 254 to 4,478/m^2. Mean (± SE) density at offshore sites was 500 ± 85/m^2, with a range of 22 to 1,580/m^2. Comparison of *Diporeia* abundances for nearshore sites (Fig. 5) showed no significant effect of year (ANOVA, F = 0.655, d.f. = 5, 54, p = 0.659). Similarly, there was no significant effect of year for abundance at offshore sites (ANOVA, F = 2.476, d.f. = 4, 19, p = 0.079) (Fig. 5). Further examination of the 15 individual sites revealed no significant linear relationship between abundance and year, except one site (linear regression, F = 8.133, d.f. = 1, 4, p = 0.046, adjusted r^2 = 0.59) (Fig. 4).

Seasonal Variation, Western Lake Superior

Diporeia abundance sampled at five offshore stations in June, August, and September of 1995 showed little seasonal variation (Fig. 6). Analysis

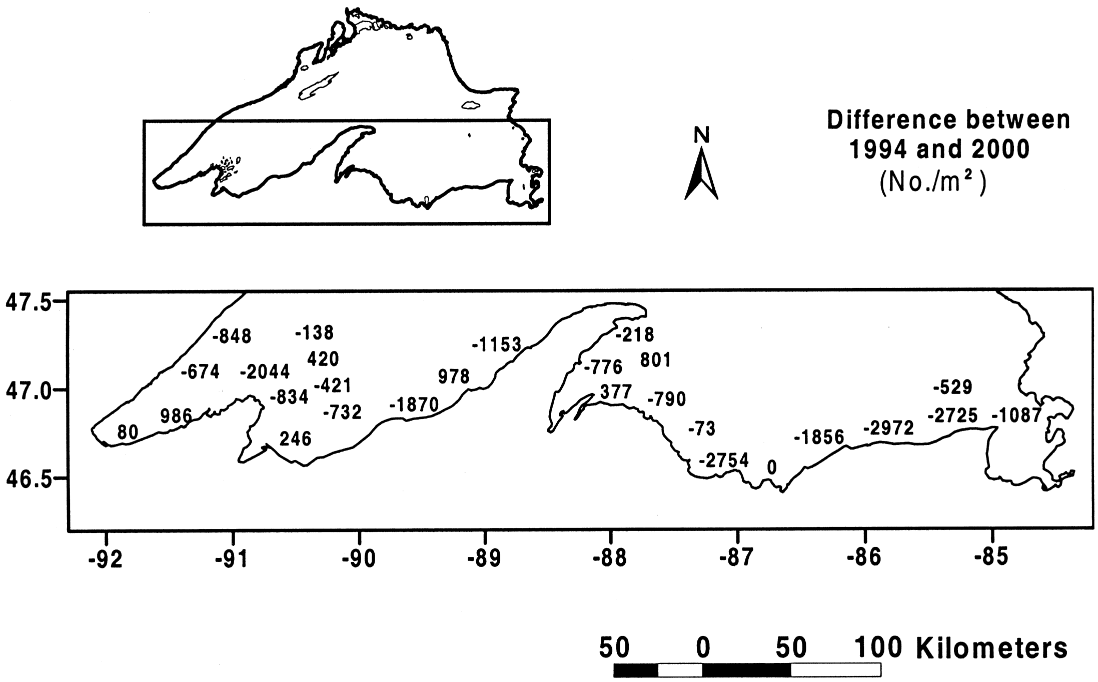

FIG. 2. Changes in* Diporeia *abundance from 1994 to 2000. Values are equal to: (abundance in 2000)—(abundance in 1994), expressed as number per square meter.

of variance detected no significant seasonal differences in abundance for the five stations (ANOVA, F = 0.174, d.f. = 2, 12, p = 0.842).

DISCUSSION

Abundance of *Diporeia* in the U.S. nearshore waters of Lake Superior was lower in 2000 than in 1994, and the decline appears to be limited to the eastern portion of the lake. In the western half of the lake, abundance did not differ significantly between 1994 and 2000. Yearly measures of abundance in western Lake Superior from 1994 to 2000 do not indicate a declining trend in either nearshore or offshore waters. Both lines of evidence support the conclusion that *Diporeia* populations in the western half of Lake Superior were not experiencing an ongoing reduction during 1994 to 2000. In the eastern half of the lake, abundance in 2000 was significantly lower than in 1994. Because abundance was not measured each year in this region of the lake, it is difficult to determine whether the observed decrease is within the range of normal year-to-year variability, or whether it is part of a long-term trend. This emphasizes the importance of using long-term sets of annual observations for detection of trends, rather than relying on isolated measures, and suggests that further examination of the eastern region of the lake is in order.

A lakewide survey of Lake Superior benthic

TABLE 1. Mean* Diporeia *abundance in eastern and western portions of U.S. waters of Lake Superior in 1994 and 2000, grouped by station depths. Values are mean ± SE expressed as number per square meter. N denotes number of stations.

	West of Keweenaw Peninsula			East of Keweenaw Peninsula		
Depth	n	1994	2000	n	1994	2000
10-39 m	5	1,983 ± 610	1,357 ± 297	5	2,993 ± 680	774 ± 532
40-69 m	2	2,529 ± 130	1,826 ± 109	4	1,786 ± 168	1,632 ± 121
70-110+ m	6	1,604 ± 209	1,500 ± 306	4	1,260 ± 316	1,038 ± 195
All depths	14	1,899 ± 257	1,470 ± 170	13	2,088 ± 339	1,119 ± 226

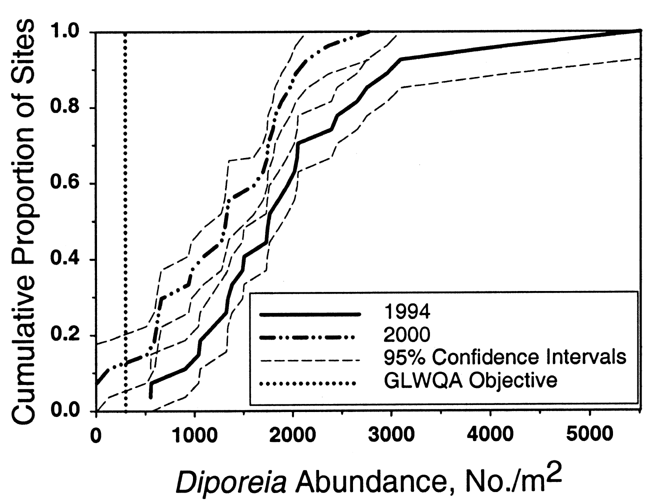

FIG. 3. Cumulative frequency distributions of **Diporeia** *abundance at 27 stations in U.S. nearshore waters of Lake Superior, 1994 and 2000. The 1978 Great Lakes Water Quality objective of 300/m² is shown for comparison.*

fauna was conducted in 1973 by the Great Lakes Biolimnology Laboratory (Cook 1975). For comparison with the current study, we selected 26 sites from Cook's survey with locations close to, and with depths similar to, the sites we visited in 1994 and 2000. Comparison of the cumulative frequency distribution for *Diporeia* abundance during 1973 with distributions from the present study reveals a substantial increase in *Diporeia* abundance in U.S. nearshore waters of Lake Superior since 1973 (Fig. 7). In 1973, the mean abundance of *Diporeia* at the 26 sites was 243 ± 55/m² (Table 2), and 70% of the sites did not meet the GLWQA objective of 220 to 320/m² for nearshore sites (Fig. 7). The seven-fold increase in *Diporeia* abundance from the 1970s to the present overshadows the relatively small changes observed between 1994 and 2000.

Differences in sampling methodology may partially account for lower abundances in Cook's survey compared with the present study. Cook used a Shipek grab at more than half of the sites and a

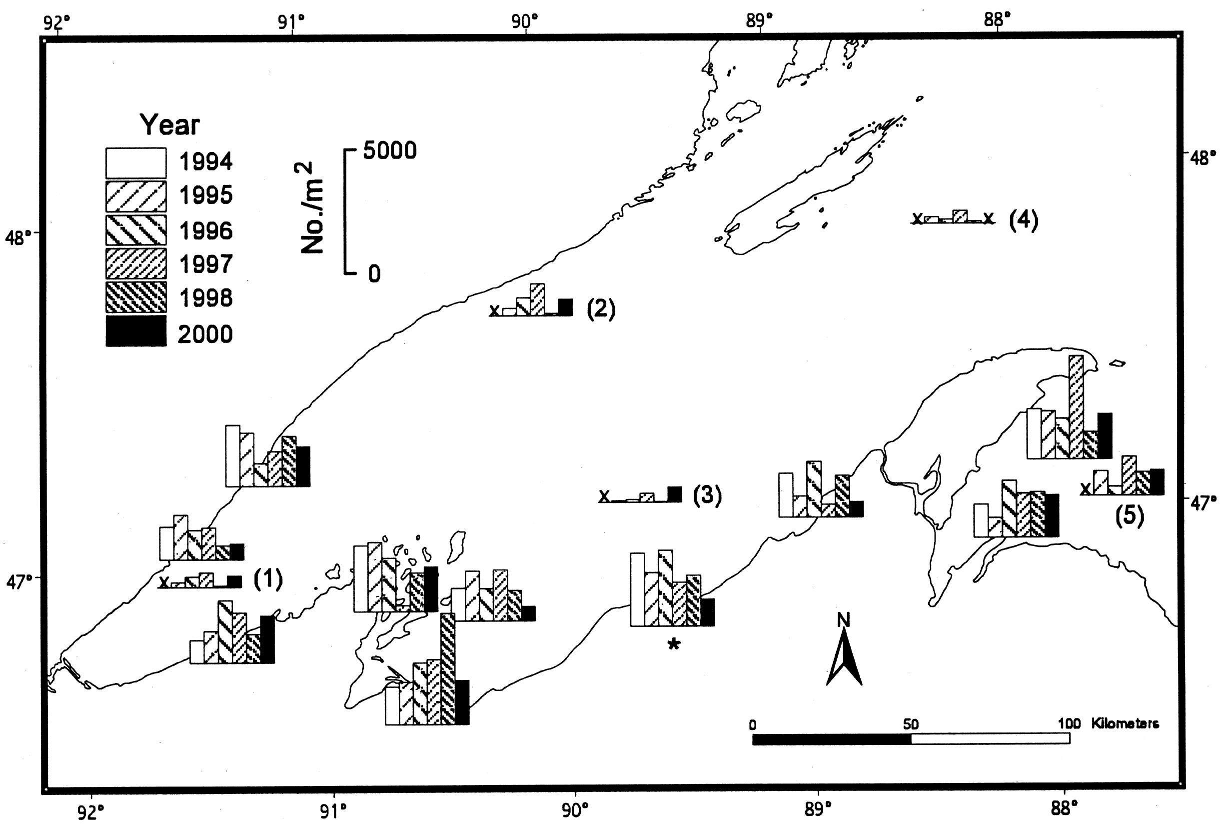

FIG. 4. Annual measures of **Diporeia** *abundance in western Lake Superior, 1994–2000. Offshore sites, located in major depositional basins, are indicated by numerals: 1) Duluth sub-basin, 2) Apostle sub-basin, 3) Chefswet sub-basin, 4) Isle Royale sub-basin, 5) Keweenaw basin. × indicates not sampled. The only station exhibiting a significant relationship between year and abundance is indicated by an asterisk.*

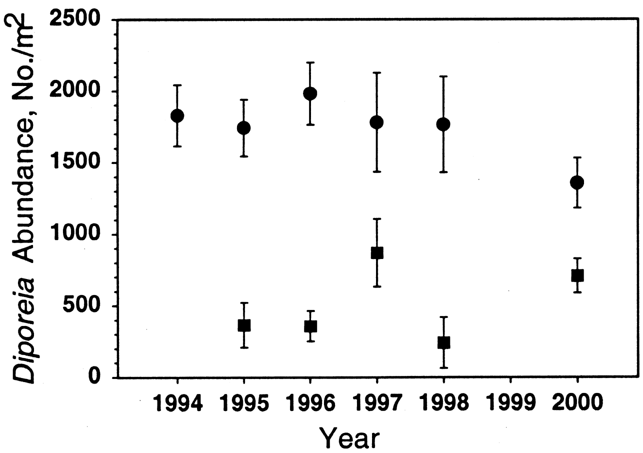

FIG. 5. Mean annual abundance of Diporeia in western Lake Superior, 1994 to 2000: • Nearshore (≤ 110 m); ■ Offshore (≥ 110 m). Error bars are ± one standard error. N is 10 nearshore sites for all years, 5 offshore sites during 1995–1998, and 4 offshore sites in 2000.

Ponar grab at the remainder. Although subsequent comparisons between the two dredges revealed no significant differences in sampling efficiency (Cook 1975), Flannagan (1970) reported that the Shipek and Ponar grabs performed similarly in sand and gravel, but that the Shipek collected only one third to one half as many animals/m^2 as the Ponar in mud. However, the increases from 1973 to the present in the Duluth basin and eastern quarter, where a Ponar grab was predominantly used, are similar to those in the remaining zones, where a Shipek grab

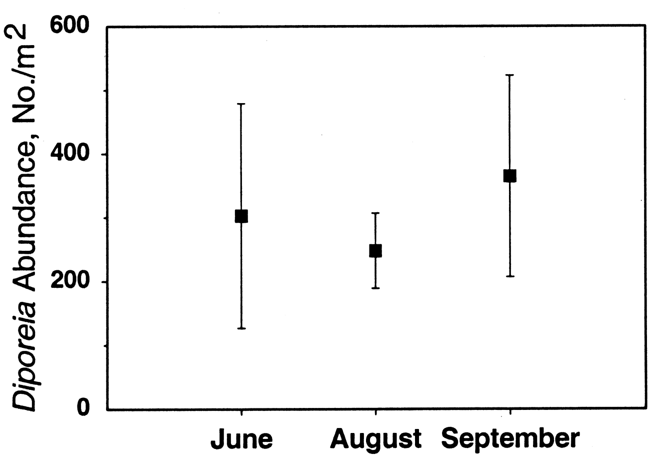

FIG. 6. Mean seasonal abundance of* Diporeia *at five offshore stations in western Lake Superior, 1995. Error bars are ± one standard error.

was used (Table 2). Another factor to consider is the timing of sampling relative to seasonal abundance patterns. Cook's survey took place in late April to early June, whereas we sampled during August to early October. No seasonal effect on *Diporeia* abundance was evident at the five offshore sites we sampled in June, August, and September of 1995. Previous studies of seasonal abundance of *Diporeia* in Lakes Michigan and Huron at depths of 30-100 m reported lower abundances during April-June than during August-September, by factors ranging from 1.2 to 2.9 (Winnell and White 1984, Evans *et al.* 1990, Guigauer and Barton 2002). However, the magnitude of the increase in abundance from 1973 to the present (approximately 7-fold) suggests that the increase is not an artifact related to sampling equipment or seasonality.

The substantial increase in *Diporeia* abundance since 1973 does not appear to result from an increase in food supply. Lake Superior exhibits low productivity, and although nitrogen levels have been increasing for decades (Bennett 1986), phosphorus levels have remained low and limiting, and primary production and phytoplankton abundance have not changed appreciably (Williams and Kuntz 1999, Fahnenstiel *et al.* 1986).

A decrease in predation may have allowed *Diporeia* populations to increase. In nearshore waters

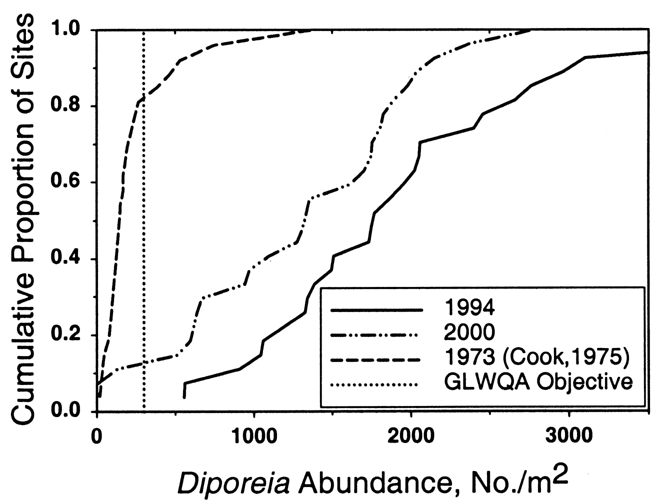

FIG. 7. Cumulative frequency distribution of* Diporeia *abundance in U.S. nearshore waters of Lake Superior from the survey of Cook (1975) compared with cumulative frequency distributions for 1994 and 2000 from the present study. The 1978 Great Lakes Water Quality Agreement objective of 300/m^2 is shown for comparison.

TABLE 2. **Diporeia** ***abundance in nearshore Lake Superior in 1994 and 2000 (present study) and 1973 (Cook 1975), grouped by the regions of Cook (1975): Zone 1, Duluth basin; Zone 2, Apostle Islands; Zone 3, southwest shore; Zone 4, Keweenaw to Grand Island; Zone 5, eastern quarter. Values are mean ± SE, expressed as number per square meter. N is number of stations. Z is mean depth in meters.***

	1994			2000		1973		
Zone	n	z	Abundance	z	Abundance	n	z	Abundance
1	4	60	1,315 ± 413	54	1,201 ± 322	4	78	90 ± 32
2	7	64	2,218 ± 379	74	1,718 ± 223	6	89	234 ± 66
3	3	49	1,930 ± 556	51	1,248 ± 471	3	48	136 ± 56
4	8	57	1,697 ± 228	64	1,268 ± 208	8	84	298 ± 78
5	5	54	2,714 ± 771	54	881 ± 504	5	60	350 ± 257
All zones	27	58	1,990 ± 208	62	1,301 ± 141	26	80	243 ± 55

of Lake Superior, bottom trawl surveys conducted by the United States Geological Survey (USGS) revealed substantial declines in bottom fishes, specifically slimy sculpins (*Cottus cognatus*) and burbot (*Lota lota*), from 1978 to the present, with low and stable abundance of bloater (*Coregonus hoyi*) (Gorman *et al.* 2002). Slimy sculpins, bloaters, and burbot are important predators of *Diporeia*. *Diporeia* dominate the diets of slimy sculpins in nearshore waters (less than 100 m) of Lake Ontario (Brandt 1986, Owens and Weber 1995) and Lake Superior (Selgeby 1988, Hudson *et al.* 1995), accounting for 65-93% of stomach contents. *Diporeia* is a major prey item of bloaters larger than 170 mm in nearshore waters of Lake Michigan, averaging 51% dry weight of stomach contents (Wells and Beeton 1963). *Diporeia* is an important food item for burbot as well, comprising 17% of stomach contents by volume for Lake Michigan burbot less than 350 mm long (Fratt *et al.* 1997), and 12% for Lake Superior burbot of all sizes (Bailey 1972). Previous studies have suggested that *Diporeia* abundance in Lake Michigan is influenced by fish predation. McDonald *et al.* (1990) found that *Diporeia* abundance in southeastern Lake Michigan declined 50% from years of low benthivore abundance (1979-80) to years of high benthivore abundance (1984-85) and concluded that the decreases in *Diporeia* abundance resulted from increased predation by bloaters. Nalepa (1987) reported an increase in *Diporeia* populations by a factor of two to five in southern nearshore Lake Michigan from 1964-67 to 1980-81, and attributed the increased *Diporeia* abundance to reduced fish predation rather than nutrient enrichment. The high densities of *Diporeia* we observed in 1994-2000, relative to low levels in 1973, coincident with reductions in abundance of benthivores, suggests that predation may be a factor limiting abundance of *Diporeia* in Lake Superior.

Another factor contributing to increases in *Diporeia* populations from the 1970s to the 1990s in specific areas, particularly in the western arm of Lake Superior, could be reductions in harmful substances released into the lake. Taconite mining operations discharged an estimated 500 million tons of tailings into Lake Superior at Silver Bay, MN, starting in 1956 and ending in 1980 (Cook *et al.* 1985). The lowest amphipod abundances reported by Cook (1975) were located in the Duluth basin (Table 2) and he suggested heavy metal ions and siltation as causal factors. This zone also showed the greatest increase in *Diporeia* abundance (approximately 14- fold) between 1973 and 1994-2000 (Table 2).

In the more productive lower Great Lakes, nearshore *Diporeia* densities have historically been higher than in Lake Superior, but have recently declined dramatically following establishment of the dreissenid mussels, *Dreissena polymorpha* and *Dreissena bugensis* (Dermott and Kerec 1997, Nalepa *et al.* 1998, Lozano *et al.* 2001, Dermott 2001). In southeastern Lake Michigan, mean *Diporeia* densities at nearshore sites dropped from 3,000–8,000/m^2 during 1980–87 to fewer than 100/m^2 in 1993 (Nalepa *et al.* 1998). In the Kingston basin of Lake Ontario, mean abundance declined from 6,000-8,000/m^2 during 1982-1992 to zero by 1995 (Dermott 2001). *Diporeia* abundance has declined by 90% in the entire nearshore area of Lake Ontario (Lozano *et al.* 2001), and all of Lake Erie (Dermott and Kerec 1997). These reductions in *Diporeia* populations have been proposed to result from the filtering activities of *Dreissena* spp. removing phytoplankton from the water column, thereby reducing the proportion of primary production reaching the bottom as detritus, and limiting the food supply for *Diporeia* (Nalepa *et al.* 1998, Lozano *et al.* 2001). Clearly, the decimation of *Di-*

poreia populations that has been observed in the lower lakes during the 1990s is not occurring throughout Lake Superior. Although *Dreissena* spp. has been found in some Lake Superior harbors, it has not become established in the lake proper (Griffiths *et al.* 1991). This supports the hypothesis that the severe declines observed in Lakes Michigan, Ontario and Erie result from influences specific to the lower lakes, such as colonization by *Dreissena*, rather than from Great Lakes basin-wide influences.

The 1978 Great Lakes Water Quality Agreement identified *Diporeia* abundance as an indicator of ecosystem quality for Lake Superior, and called for maintenance of "present" (i.e., 1978) levels of *Diporeia* throughout the lake (IJC 1978). Our results show that *Diporeia* populations in Lake Superior are in good condition as measured by the GLWQA criteria. Almost 90% of the U.S. nearshore waters met or exceeded the objectives in both 1994 and 2000. Furthermore, current densities are much higher than those in the 1970s, by a factor of seven. We found no evidence of lakewide population declines on the scale observed in the lower Great Lakes. Additional studies are planned to determine whether the reduction observed in the eastern half of the lake is indicative of an ongoing trend. As an indicator of condition for Great Lakes ecosystems, it appears that *Diporeia* abundance is responsive to community level influences, including competition (zebra mussels) and predation (fish), as well as to anthropogenic stressors (taconite tailings). As an important trophic link between phytoplankton and benthivorous fish (Flint 1986, Fitzgerald and Gardner 1993), changes in this amphipod's status are expected to impact other components of the Great Lakes ecosystem.

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