Status of the Amphipod \textit{Diporeia} spp. in Lake Superior, 1994–2000

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ABSTRACT. The amphipod \textit{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 \textit{Diporeia} as an indicator of ecological condition, with a goal of 220 to 320/m\textsuperscript{2} at depths less than 100 m, and 30-160/m\textsuperscript{2} at greater depths. To ascertain the status of \textit{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 \textit{Diporeia} abundance. In 1994, nearshore \textit{Diporeia} abundance ranged from 550 to 5500/m\textsuperscript{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\textsuperscript{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 \textit{Diporeia} abundance in the eastern half of the lake was lower in 2000 than 1994, the severe declines in \textit{Diporeia} populations that have been observed in the lower Great Lakes are not evident in Lake Superior. Abundances of \textit{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-invertebrates, amphipods, \textit{Diporeia}, ecological status.

INTRODUCTION

Abundance of the amphipod \textit{Diporeia} spp. has been selected as an indicator of ecological condition for the Laurentian Great Lakes (Reynoldson 1993). Amphipods of the genus \textit{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). \textit{Diporeia}, a glacial relict, is distributed throughout the Great Lakes in cold, clean waters of nearshore as well as offshore benthic zones. \textit{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). \textit{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 \textit{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 \textit{Diporeia} throughout the lake at densities of 220 to 320/m\textsuperscript{2} in nearshore waters.

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The 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 Bioluminology 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 km². 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 m². Each sample consisted of three replicate grabs. The contents of each grab were placed into an elutriation device and rinsed through a 500 µm 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/m², with a mean (± SE) of 1,990 ± 208/m² (Fig. 1). In 2000, abundance ranged from 7 to 2,782/m², with a mean (± SE) of 1,301 ± 141/m² (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/m²) in 1994 and the lowest (774/m²) 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-
cantly different 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
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.

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

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**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.

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**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 subbasin, 2) Apostle sub-basin, 3) Chefsweet sub-basin, 4) Isle Royale sub-basin, 5) Keweenaw basin. x indicates not sampled. The only station exhibiting a significant relationship between year and abundance is indicated by an asterisk.
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/m² as the Ponar in mud. However, the increases 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 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.

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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/m² during 1980–87 to fewer than 100/m² in 1993 (Nalepa *et al.* 1998). In the Kingston basin of Lake Ontario, mean *Diporeia* densities at nearshore sites dropped from 3,000–8,000/m² during 1980–87 to fewer than 100/m² in 1993 (Nalepa *et al.* 1998). In the Kingston basin of Lake Ontario, mean abundance declined from 6,000-8,000/m² 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

### 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.

<table>
<thead>
<tr>
<th>Zone</th>
<th>1994</th>
<th>2000</th>
<th>1973</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>z</td>
<td>Abundance</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>60</td>
<td>1,315 ± 413</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>64</td>
<td>2,218 ± 379</td>
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<tr>
<td>3</td>
<td>3</td>
<td>49</td>
<td>1,930 ± 556</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>57</td>
<td>1,697 ± 228</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>54</td>
<td>2,714 ± 771</td>
</tr>
<tr>
<td>All zones</td>
<td>27</td>
<td>58</td>
<td>1,990 ± 208</td>
</tr>
</tbody>
</table>
poreia populations that has been observed in the lower lakes during the 1990s is not occurring in the lower lakes. 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 Lake Superior 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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