Sudden Disappearance of the Amphipod *Diporeia* from Eastern Lake Ontario, 1993–1995

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ABSTRACT. Diporeia, *Oligochaeta, and Sphaeriidae were sampled at three sites (28 to 35 m depth) in the east basin of Lake Ontario, and at one mid-lake site (125 m) from 1982 and 1996. In addition,* Diporeia *was sampled at 14 more sites located in the south and eastern part of the lake in 1990 and 1995. Before 1991, densities of all three macroinvertebrate taxa fluctuated with peaks occurring between 1988 and 1991. Between 1992 and 1995,* Diporeia *declined rapidly from > 6,000 per m² to 0 at all three sites in the east basin, while increasing from 1,050 to 5,230 per m² at the mid lake site. Samples from the south and eastern part of the lake confirmed the decline was extensive at depths < 100 m. Abundance and biomass of the Oligochaeta and Sphaeriidae also fluctuated, but remained more similar before 1991 and after 1993. Direct cause for the disappearance of* Diporeia *is unknown but declines occurred after establishment of nearshore* Dreissena *colonies. Lake circulation patterns suggest that the nearshore mussel populations may intercept diatoms and other material that had been consumed by* Diporeia *located further offshore. A substantial biomass of* Diporeia *(3 g/m² dry) has been lost from the food web of eastern Lake Ontario, with serious consequences to the coldwater fisheries of the lake.*

INDEX WORDS: *Amphipod,* Diporeia, *oligochaeta, Sphaeriidae, biomass, competition,* Dreissena, *offshore, Lake Ontario.*

INTRODUCTION

Off-shore areas of the Great Lakes, except central and western Lake Erie, support a similar profundal benthic community composed of a few species, dominated by the burrowing amphipod *Diporeia* spp. (Cook and Johnson 1974). Both *D. hoyi brevicornis* and *D. hoyi filicornis* are present in Lake Ontario. Since this genus may contain a species complex (Bousfield 1989), the designation *Diporeia* will be used in this study. This amphipod is the main benthic invertebrate in the offshore of the Great Lakes, and many large boreal lakes of North America (Dadswell 1974), while the related *Monoporeia affinis* and *Pontoporeia femorata* are key species of the Baltic (Elmgren *et al*. 1990). Offshore populations in Lake Ontario consist of two co-existing cohorts with a generation time of 2 years, so three size classes can be present: young (< 4 mm in length), juveniles (4 to 6 mm), and

adults (>7 mm) (Dermott and Corning 1988). Densities to 30,000/m² (Nalepa *et al*. 1985), high lipid levels to 50% of their dry weight (Gauvin *et al*. 1989), and high assimilation of deposited algae (Fitzgerald and Gardner 1993) make *Diporeia* an important link in the pelagic—benthic coupling between spring algal blooms and the fish community of the lakes (Wells 1980, McDonald *et al*. 1990). A large proportion of the offshore energy flow in the Great Lakes passes through *Diporeia* (Flint 1986).

Reduced phosphorous loadings to the Great Lakes in the 1980s improved water clarity, oxygen conditions, and reduced algae densities at many locations (Mullin 1980, Nalepa 1987, Charlton *et al*. 1993). Later zebra mussels (*Dreissena polymorpha*) invaded the Great Lakes, with *D. bugensis* colonizing sediments in deeper parts of Lakes Erie and Ontario (Mills *et al*. 1993). Filtering activity by the mussels have created ecological perturbations in nearshore areas causing increased water clarity (Holland *et al*. 1995), changing benthic populations and food-webs (Nalepa and Fahnenstiel 1995,

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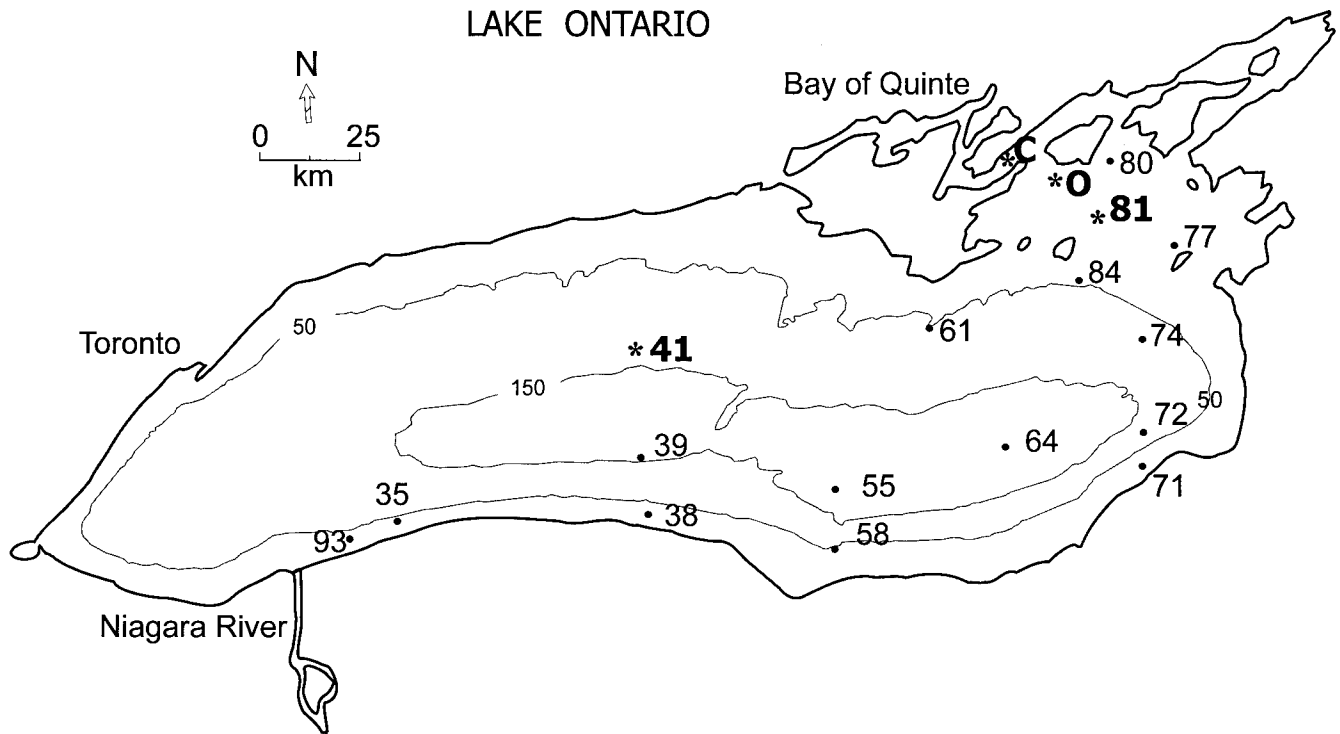
FIG. 1.   Location of long-term sampling sites at Bay of Quinte (C), Quinte outlet (O), east basin site #81, and mid lake site #41. Additional sites (#35 to #93) were sampled in 1990 and 1995. Depth contours are 50 and 150 m.

Schloesser *et al.* 1996, Stewart *et al.* 1998). In offshore areas, decoupling of the algal-nutrient relationships, and community changes have occurred (Dermott *et al.* 1998, Millard *et al.* 1999), including reduced *Diporeia* density in eastern Lake Erie (Dermott and Kerec 1997).

This paper reports the rapid decline and disappearance of the amphipod *Diporeia* from several sites in eastern Lake Ontario. Data were from two long-term biological monitoring studies of Fisheries and Oceans: Project Quinte (1972–1999), and the Bioindex Program (1981–1995) (Johnson and Hurley 1986, Johannsson *et al.* 1998). Additional benthic samples were examined from lake-wide spatial surveys of Lake Ontario in 1990 and 1995.

METHODS

Benthic samples were collected yearly between 1982 to 1996 at three sites in eastern Lake Ontario (sites C, 0, and 81) and one mid-lake site (site 41) (Fig. 1). Two of the sites, C (–34 m depth; 44°06.5′N: 076°54.9′W) and O (–29m; 44°03.6′N: 076°46.6′W) were near the outlet from the Bay of Quinte. At these two sites, four or five Ekman samples (0.05/m^2) were taken each year during early August. These samples were washed on a 0.58 mm screen (#30 mesh), the residues preserved in 10% neutral formalin, and later transferred into alcohol, with all re-screening using a 0.25 mm screen. Location and methodology followed that of Johnson and Brinkhurst (1971), and Johnson and McNeil (1986). All macroinvertebrates were enumerated, but only data for the Amphipoda, Oligochaeta, and Sphaeriidae are presented in this study. After 1987, blotted wet biomass at sites C and O, and size frequency of *Diporeia* were also measured.

At site 81 in the middle of the east basin (–35 m, 43°58.9′N: 076°39.3′W), and at the mid-lake site 41 (–125 m at 43°43.0′N: 078°01.6′W), 3 to 5 replicate PONAR grabs (0.053/m^2) were collected in the spring (April) and fall (October), each year from 1982 to 1996. These samples were sieved on a 0.25 mm screen and preserved (Johannsson *et al.* 1985). Macroinvertebrates were enumerated and weighted (blotted wet biomass). *Diporeia* were sorted into size classes of 2 mm intervals and weighed. Biomass was converted to dry shell-free g/m^2 from
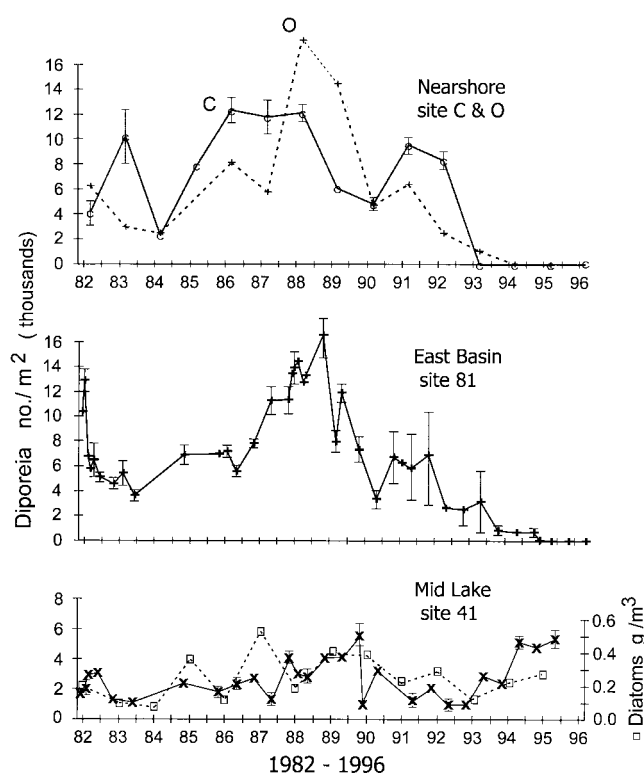
FIG. 2. *Density of* **Diporeia** *(thousands/m²) at nearshore sites C and O (top panel); east basin site 81; and mid Lake Ontario site 41 (bottom panel) between 1982 and 1996. Dashed lines in panel for site 41 are diatom biomass (g/m³ from Johannsson* **et al.** *1998).*

wet: dry weight relationships for each genera, and shell-free ratios of the Sphaeriidae.

An additional 14 sites were sampled with a PONAR in the eastern part and along south side of the lake during October 1990 and October 1995. These sites are part of the Canada Centre for Inland Waters (CCIW) surveillance program (L'Italien 1998). Only *Diporeia* density is presented from these spatial surveys.

RESULTS

Between 1982 and 1992 *Diporeia* averaged 8,240 ± 1,048/m² (mean ± SE) at site C. After August 1993, no *Diporeia* were collected at this site (Fig. 2). Although inter-annual variability was significant before 1993 (ANOVA, $p < 0.001$), *Diporeia* were always present. In 1994, 1 year after the disappearance at site C, density of *Diporeia* at site O dropped from an average of 6,170 ± 1,570/m² (1982 to

1992) to only 76 ± 38/m². No specimens were collected at this site after 1994. (Fig. 2).

Diporeia density at site 81 in the east basin of Lake Ontario averaged 8,084/m² ± 370 (n = 124) between 1982 and 1993, and declined to 330/m² ± 122 (n = 28) between April 1994 and 1995 (Fig.2). Although most replicates from site 81 in 1995 had no amphipods, specimens continued to be collected in April, 1995. By October 1995 and in 1996, no specimens were collected at this site. In contrast, over the same time period (1990 to 1995), *Diporeia* increased ($p < 0.001$) at the mid-lake site. Between 1982 and 1993, *Diporeia* at site 41 averaged 2,642/m² ± 208 (n = 40), but in 1994 and 1995 the average was 4,508/m² ± 370 (n = 14). At the 14 sites sampled in 1990 and 1995, *Diporeia* disappeared at most sites shallower than 50 m in the eastern part of the lake (Table 1). In 1995, densities at several deeper sites were reduced to < 10 % of the 1990 population.

Densities at site 81 were relatively low in November 1983 (3,621 ± 449/m²) and again in October 1990 (3,335 ± 744/m²), and were at a maximum in March 1982 (13,375 ± 497/m²) and April 1989

TABLE 1. *Density of* **Diporeia** *(indiv/m²) in southern and eastern Lake Ontario at the surveillance sites sampled in October 1990 and October 1995. Site locations are in Figure 1, n.s = no sample.*

CCIW Site	Depth m	1990	1995
South Shore			
35	23	19	97
38	20	38	0
39	150	1,984	2,865
93	70	15,806	1,544
South-east			
55	189	5,651	929
58	98	2,268	19
61	50	76	0
64	228	1,228	1,413
East			
71	12	n.s	0
72	107	4,007	19
74	65	6,426	2,032
77	25	n.s	0
81	35	3,572	0
80	20	1,115	0
84	36	2,683	0
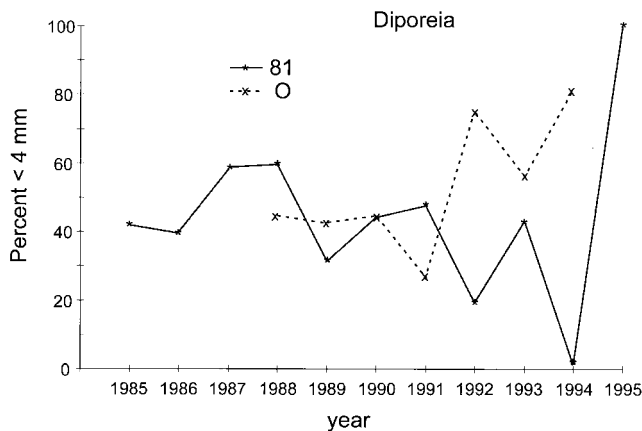
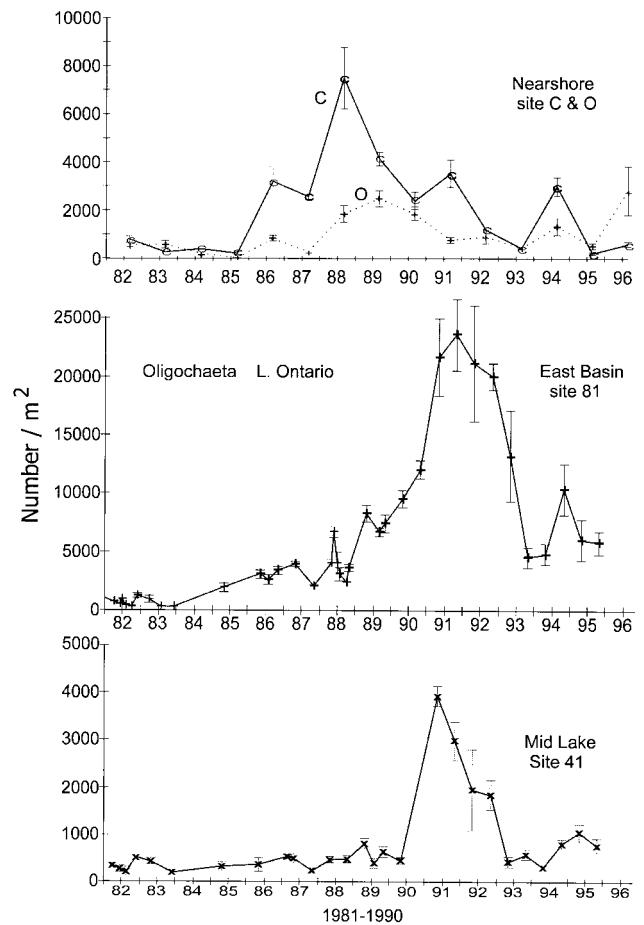**FIG. 3.   Percentage of young Diporeia < 4 mm length in the population at sites O and 81 in eastern Lake Ontario.**

FIG. 4.   Density of Oligochaeta (indiv/m²) at the Lake Ontario sites between 1982 and 1996.

(16,556 ± 1,822/m²), giving a periodicity of about 7 years. After 1989, densities decreased toward a low in the cycle. At site C, densities decreased rapidly to zero (Fig. 2), while at sites O and 81 the decrease was more gradual. At site 41, the population was low in 1983 (1,172 ± 58/m²), and reached a minimum (1,050 ± 238/m²) in April 1993. However, the mid-lake population increased again in 1995 to levels equal to that of the previous maximum in April 1990 (Fig. 2).

The percentage of young amphipods (< 4 mm) in the population at site 81 decreased gradually between 1987 and 1993, and was very low in 1994 (Fig. 3). In 1995 just prior to population disappearance, all *Diporeia* were < 4 mm. Conversely, the percent of young at site O remained between 44 and 74% from 1990 to 1992, suggesting higher mortality in the larger size classes. In the year just prior to disappearance, the percent of young increased to above 80%. Excluding the last year, the percent young before 1990 was not significantly different (ANOVA) from the percent after 1990 at either site.

Oligochaeta and Sphaeriidae (almost exclusively *Pisidium* spp.) densities peaked at sites O and 81 between 1989 and 1992 (Figs. 4 and 5), 1 to 2 years after the peak in *Diporeia*. But unlike *Diporeia*, Oligochaeta and Sphaeriidae densities after 1993 remained similar to or higher than densities prior to 1987. Oligochaetes at site 81 had the greatest increase to 23,530 ± 3,090/m² in 1991 (Fig. 4). Oligochaetes at mid-lake site 41 also peaked in 1991 before decreasing to < 500/m² in 1993. At site

81, Sphaeriidae density had a maximum in 1991, but densities before 1989 and after 1993 were more similar. Sphaeriidae at site O also peaked in 1991 but decreased to 480/m² in 1996. Sphaeriidae density was less variable at site C than at the other sites (Fig. 5).

Near peak density in 1988, dry biomass of *Diporeia* was as high as 6.1 g/m² at site O and 5.9 g/m² at site 81 (Table 2). Prior to 1991, annual biomass of *Diporeia* in eastern Lake Ontario averaged 1.47 g/m², 3.44 and 3.04 g/m² at sites C, O and 81, respectively (Table 2). Beginning in 1993, the *Diporeia* biomass declined to zero progressively further offshore each year. Unlike *Diporeia*, biomass of the Oligochaeta and Sphaeriidae did not consistently decrease after 1991 (Table 2). Oligochaete biomass deceased significantly only at site C, but increased at site O from 0.18 g/m² in 1993 to
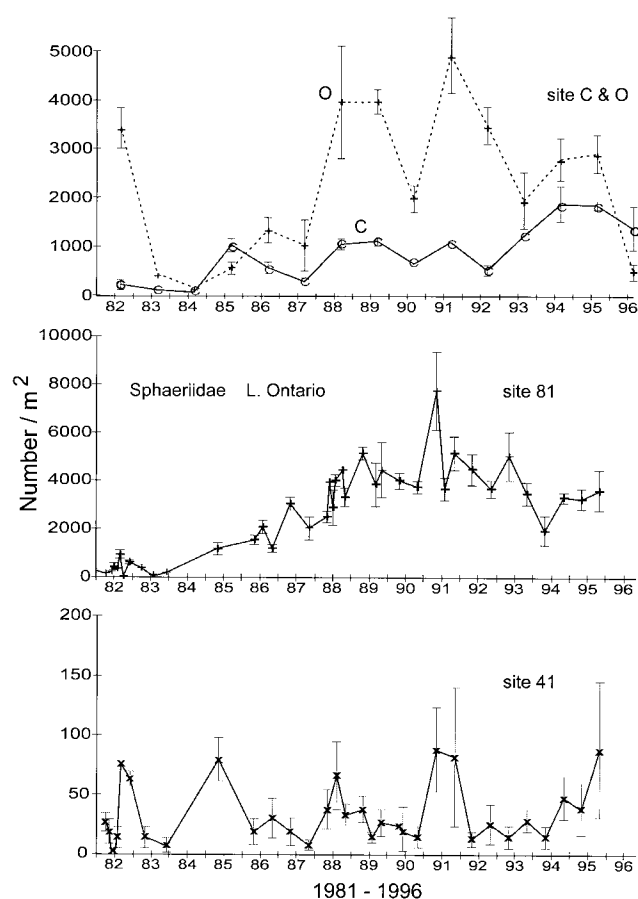
FIG. 5.   *Density of the Sphaeriidae (indiv/m²) at the Lake Ontario sites between 1982 and 1996.*

1.30 g/m² following the disappearance of *Diporeia*. At the same time, Sphaeriidae biomass decreased at inshore sites C and O from 0.14 and 0.17 g/m² to 0.6 and 0.01 g/m², respectively. At site 81, Sphaeriidae biomass changed little before or after 1991 (Table 2).

Spring diatom biomass peaked at site 81 in 1985 (1.2 g/m³) and again in 1990 (1.5 g/m³, Johannsson *et al*. 1998). Peak *Diporeia* biomass followed the diatom biomass peak by 2 to 3 years (Fig. 6). Lows in *Diporeia* biomass coincided with the lows in diatom biomass which occurred in 1983 and in 1986 (0.1 to 0.2 g/m³). At site 41, diatom biomass showed less annual variation, with no reduction after 1993 (Fig. 2). At site 81, mean seasonal diatom biomass decreased from 0.37 in 1991 to only 0.12 g/m³ in 1994 before the *Diporeia* population disappeared. However, seasonal total algal biomass at site 81 only gradually declined from 1.4 g/m³ in

1982 to 0.86 in 1995, with minor yearly variation (Fig. 6). Regression between *Diporeia* biomass and diatom biomass was poor (r² < 0.04), however amphipod biomass was correlated with total algal biomass (r² = 0.51, p = .006).

DISCUSSION

Two potential reasons for the rapid disappearance of *Diporeia* from eastern Lake Ontario are predation and decreased food supply caused by reduced nutrients and/ or competition with the exotic *Dreissena* spp. Johnson and McNeil (1986) suggested fish predation kept *Diporeia* density low (340 to 2,660/m²) in the Bay of Quinte prior to 1977. Lake whitefish feed extensively on *Diporeia*, selecting adult sized amphipods buried in the sediment (Larkin 1948, Christie *et al*. 1987). The increased whitefish populations in eastern Lake Ontario during the late 1980s (Casselman *et al*. 1996) could have reduced amphipod density, but at site 81, the percent of amphipods < 4 mm remained stable or decreased between 1988 to 1993 suggesting little change in predation pressure. The higher percent of young at site O suggested greater predation closer to shore. Coregonids and *Diporeia* have co-existed together since the evolution of the Great Lakes, so cycles in prey—predator densities have occurred previously without eliminating the prey from favorable habitats. Fish predation would reduce the *Diporeia* population with a few scattered areas of higher density, rather than complete removal of all prey over large areas. Sphaeriid clams are important coregonid prey (Larkin 1948, Tohtz 1993), so had whitefish predation been excessive, *Pisidium* biomass would also have been significantly reduced at the same time as *Diporeia*.

A secondary predator on *Diporeia* was the benthic Nemertea worm *Prostoma canadensis* which became common after 1988 at depths between 0.5 m to 125 m (Dermott unpublished data). Density of this 1.5 cm carnivorous worm increased rapidly in eastern Lake Ontario, reached a maximum of 156/m² in 1992, and 19/m² at the mid lake site. However, *P. canadensis* rapidly became rare again, averaging 20 ± 7/m² at site 81 in 1994. Marine nemertea prey on amphipods, feeding about once per week (McDermott 1993, Thiel and Reise 1993). Thus, at maximum density, *P. canadensis* could have reduced *Diporeia* at site 81 by 8,000/m²/yr. Although potentially high, it is unlikely excessive Nemertea or fish predation caused the complete disappearance of *Diporeia* from eastern Lake Ontario.

TABLE 2.   Mean dry biomass ± 1 S.E. (g/m² shell-free), minimum and maximum averages for macroinvertebrates at eastern Lake Ontario sites C, O, and 81 for periods before and after 1991. Data available at site 81 for 1985–1996.

Year	n	*Diporeia* g/m² ± S.E.	Oligochaeta g/m² ± S.E.	Sphaeriidae g/m² ± S.E
Site C				
1987–91	15	1.468 ± 0.164	0.463 ± 0.051	0.074 ± 0.011
	min.	0.609 ± 0.045	0.240 ± 0.048	0.009 ± 0.003
	max.	2.332 ± 0.106	0.706 ± 0.131	0.122 ± 0.010
1992–96	15	0.200 ± 0.107	0.165 ± 0.022	0.095 ± 0.012
	min.	0.000 ± 0.000	0.088 ± 0.018	0.031 ± 0.007
	max.	1.002 ± 0.055	0.310 ± 0.043	0.143 ± 0.033
F-value.		41.79	28.65	1.76
p df 1,28		< 0.0001	< 0.001	0.19
Site O				
1987–91	15	3.444 ± 0.425	0.263 ± 0.053	0.172 ± 0.028
	min.	1.550 ± 0.289	0.030 ± 0.008	0.027 ± 0.011
	max.	6.153 ± 1.218	0.592 ± 0.155	0.308 ± 0.105
1992–96	15	0.176 ± 0.059	0.455 ± 0.129	0.104 ± 0.016
	min.	0.000 ± 0.000	0.121 ± 0.041	0.013 ± 0.004
	max.	0.443 ± 0.176	1.302 ± 0.563	0.167 ± 0.054
F-value.		57.86	1.90	4.29
p df 1,28		< 0.0001	0.18	< 0.05
Site 81				
1985–91	58	3.040 ± 0.197	1.213 ± 0.101	0.153 ± 0.009
	min.	1.164 ± 0.068	0.374 ± 0.063	0.070 ± 0.013
	max.	5.924 ± 0.223	2.655 ± 0.492	0.315 ± 0.064
1992–96	27	0.975 ± 0.234	1.035 ± 0.145	0.181 ± 0.010
	min.	0.000 ± 0.000	0.428 ± 0.068	0.109 ± 0.013
	max.	3.562 ± 0.667	2.421 ± 0.630	0.257 ± 0.050
F-value.		38.9	2.52	3.25
p value. df 1,83		< 0.0001	0.12	0.07

Decrease from Reduced Food

In Europe, *Monoporeia affinis* has shown longterm oscillations in density, with periodicity of 5 to 10 years (Sarvala 1986, Johnson and Wiederholm 1989). These population oscillations have been attributed to inter-generation interaction (Hill 1992) and interannual variability of the diatom food source (Johnson and Wiederholm 1992). In Lake Ontario, cycles were similar at site 81 and at site 41 until 1992. But after 1992, density in the east basin continued to drop, while the mid-lake population increased again to a peak in 1995 in phase with an expected population cycle.

Reduced food supply could be partly responsible for the decline of *Diporeia*. Total phosphate levels dropped by about 50%, from 14.3 μg/L in 1981 to 7.9 μg/L in 1995 (Johannsson *et al*. 1998). This reduced total phytoplankton biomass in eastern Lake Ontario by 34% (from 1.4 to 0.86 g/m³) between 1982 and 1995. A similar reduction in phosphorous loadings to the Bay of Quinte resulted in a decline of phytoplankton biovolume from 13.1 mm³/L in 1977 to 6.7 in 1986 (Nicholls and Hurley 1989).
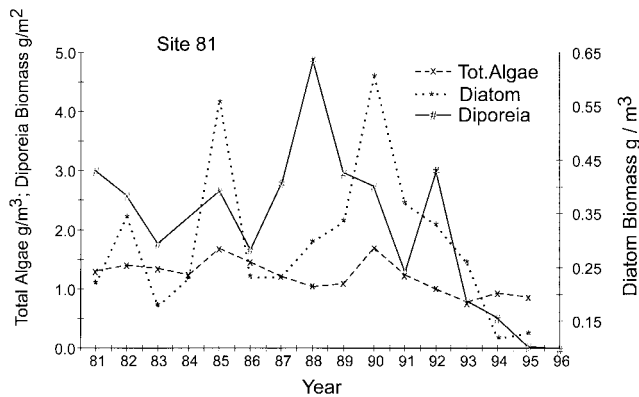
FIG. 6. *Seasonal (April–Oct.) total algal biomass and diatom biomass (g/m³ from Johannsson et al. 1998) and dry biomass of* Diporeia *(g/m²) at site 81 between 1982 and 1996.*

This algal reduction could account for a gradual decline in *Diporeia* biomass of 35 to 50 %, but not the sudden disappearance of the species.

Recent increased spring silica levels in Lake Ontario, from 190 to 351 µg/L (1992 to 1995) suggest reduced diatom production (Johannsson *et al*. 1998). *Diporeia* are known to rely on the spring diatom bloom for much of their annual energy requirement and increased lipid reserves (Gardner *et al*. 1985, 1989). Peaks in diatom biomass in 1985 and again in 1990 (Johannsson *et al*. 1998) were about 2 years or 1 generation ahead of the high *Diporeia* densities in eastern Lake Ontario. Correlation with seasonal diatom biomass at site 81 was poor in spite of correcting for a 2 year lag. However, the decrease in seasonal diatom biomass from 0.6 g/m³ in 1990 to 0.1 g/m³ in 1994 and 1995 (Johannsson *et al*. 1998 and Fig. 6) coincided with the decline of *Diporeia*. This could account for a *Diporeia* biomass decline of 80%, but again not their complete absence.

All three macroinvertebrates responded to the same favorable abiotic and food conditions in eastern Lake Ontario since densities of all three peaked between 1988 and 1991. Oligochaetes feed deeper in the sediments than *Diporeia* and use more of the sediment bacterial production (Robbins 1982, Van de Bund *et al*. 1994). Likewise, *Pisidium* spp. feed extensively on interstitial bacteria in the sediments (Lopez and Holopainen 1987) as an alternate to settling algae. Thus both would rely less on freshly settled algae than the surface feeding amphipods, and have a delayed response to reduced phyto-

plankton abundance. Both the oligochaetes and *Pisidium* took advantage of the food resources in 1990 to 1992, following the decreased amphipod populations in 1989. However after the disappearance in 1994, oligochaetes increased little in the absence of amphipods. Like fish predation, declining algal biomass should not eliminate the *Diporeia*, but reduce all the macroinvertebrates to densities similar to that in oligotrophic Lake Superior (250/m², Cook 1975).

Dermott and Munawar (1993) hypothesized competition with the exotic *Dreissena* species for settling algae caused the disappearance of *Diporeia* from eastern Lake Erie. Unlike Lake Ontario, *D. bugensis* is present on the sediment surface throughout the deeper eastern basin of Lake Erie (Dermott and Kerec 1997, Dermott *et al*. 1998). There, mussels directly competed for settling algae with the amphipods burrowing beneath them. The feeding habits and niche of *Diporeia* are unlike that of the scavenging amphipods *Gammarus fasciatus* and *Echinogammarus ischnus* which have benefited from the *Dreissena* colonies on nearshore substrates in depths < 20 m (Stewart *et al*. 1998). *Diporeia* feed on settled plankton, organic detritus, and bacteria in soft sediments, while the Gammaridae, which live on rocks and macrophytes, use their well developed gnathopods to tear algae, animal and plant material. (Larkin 1948, Segerstråle 1959).

Although *D. polymorpha* and *D. bugensis* were present along the east shore of Lake Ontario in 1991, densities in the east basin remained low in 1992 (Wormington *et al*. 1993). Prior to 1993, *Dreissena* was rare in the Bay of Quinte, but became common in the lower Bay in 1993, the year *Diporeia* disappeared at site C, and mussel density increased rapidly in 1994 (Wormington *et al*. 1995). However, on the soft sediments at all the sites in the east basin (C, O, and 81), *Dreissena* was very rare, averaging 0.1/m² between 1990 and 1995. Numerous rocky islands and gravel ridges are present throughout the east basin (Sly 1984), which support dense populations of mussels. Wormington *et al*. (1995) found *Dreissena* populations of 18,000/m² at the entrance to the Bay of Quinte in 1993, while Mills *et al*. (1999) found high densities along the south shore of Lake Ontario above 50 m, with greatest biomass at 35 m. *Dreissena* on these shoals can intercept algae that would otherwise have settled in deeper depositional zones inhabited by *Diporeia*. This may explain why the disappearance occurred first at sites closest to shore, and later progressed further out into the lake, while populations

at mid-lake, located far from the mussels colonies, did not decline.

Most areas in the Great Lakes where *Diporeia* populations have recently disappeared are influenced by longshore currents which transport particles from elsewhere. In Lake Ontario, the Niagara plume (Masse and Murthy 1992) moves material past *Dreissena* along the south shore (Mills *et al.* 1999), and then into the east basin of Lake Ontario across the shoals and ridges near the eastern islands (Fig. 1). In Lake Erie, the Long Point current sweeps material from the central basin into the deepest part of the lake (Thomas *et al.* 1976), where dense *D. bugensis* populations exist (Dermott *et al.* 1998). The southern Lake Michigan gyre moves water from Chicago toward the east shore (Beletsky *et al.* 1999) past abundant *Dreissena* populations nearshore (Nalepa *et al.* 1998). Nalepa *et al.* (1998) found *Diporeia* densities approached zero at most sites above 50 m in the south east region the lake. In this manner, the *Dreissena* populations may be long-range competitors with the depositional feeding *Diporeia* in the offshore profundal zone. However, even when combined, decreasing algal resources, and indirect competition with nearshore zebra mussel colonies should reduce *Diporeia* populations, but cannot explain the total elimination from favorable habitats. This study cannot address if an unknown factor, perhaps associated with *Dreissena*, may be the direct cause of the *Diporeia* decrease.

Consequences of *Diporeia* Declines

The absence of *Diporeia* from its most productive zone (25 to 60 m depth; Johannsson *et al.* 1985, Sly and Christie 1992), will have serious consequences to food web structure and energy transfer efficiency in the Great Lakes. Where absent, the major link in the benthic-pelagic coupling between spring diatom blooms to offshore benthos has been broken. Lakewide *Diporeia* production in Lake Ontario was calculated as 34 kilotonnes/yr dry weight in 1981 (Johannsson *et al.* 1985). Elimination of the *Diporeia* populations between the 20 and 60 m contours of Lake Ontario (area = 4.3 E^9 m^2) would remove 9.9 kilotonnes, or 29% of the lake-wide amphipod production. Flint (1986) calculated *Diporeia* represented 86% of the total benthic production in Lake Ontario and up to 94% of the amphipod production was consumed by fish each year. Hence, this decline represents a major loss of food for the cold-water fish of Lake Ontario.

The lake whitefish populations in eastern Lake Ontario (Casselman *et al.* 1996) supported 50% of the lake's total commercial harvest of all fish species in the 1990s. Since 1993, Hoyle *et al.* (1999) found a significant decrease in whitefish body condition, decreased juvenile and adult abundance, poor survival, and reduced production in eastern Lake Ontario. *Diporeia* had been the major diet item of the whitefish, but since their disappearance, *Dreissena* were present in 90% of the whitefish stomachs. A similar reduction in production can be expected in forage fish that fed heavily on *Diporeia*, especially alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) which attained 40% and 11% of their energy budget from *Diporeia*, respectively (Flint 1986). These two fish support a large part of the salmonid stocks in the Great Lakes.

The absence of *Diporeia* in the upper profundal zone has altered food-web structure and left vacant the niche of surface feeding detritivore. The profundal benthos of eastern Lake Ontario is now a simplified community of oligochaetes, a few *Pisidium*, ostracods, and nematods (Johannsson *et al.* 1985). The disappearance of *Diporeia* from eastern Lake Ontario has not resulted in a corresponding increase in other benthic macroinvertebrates (Table 2). This is very different from Lake Erie, where *D. bugensis* has utilized all the habitat previously occupied by *Diporeia*, resulting in an increase in total biomass (Dermott and Kerec 1997).

Regardless of the direct cause, the vacancy of the niche of the deepwater amphipod in eastern Lake Ontario, disappearance of *Diporeia* from Lake Erie, a 60% decline in southern Lake Michigan at depths < 50 m (Nalepa *et al.* 1998), and perhaps a similar decline in southern Lake Huron, will uncouple the linkages between algal production and cold-water fishes (Wells 1980, Flint 1986, Gardner *et al.* 1990). This will lead to a significant reduction in fish carrying capacity in a large area of the Great Lakes.

REFERENCES

Beletsky, D., Saylor, J.H., and Schwab, D.J. 1999. Mean circulation in the Great Lakes. *J. Great Lakes Res*. 25: 78–93.

Bousfield, E.L. 1989. Revised morphological relationships within the amphipod genera *Pontoporeia* and *Gammaracanthus* and the "glacial relict" significance of their postglacial distributions. *Can. J. Fish. Aquat. Sci*. 46:1677–1688.

Casselman, J.M., Hoyle, J.A., and Brown, D.M. 1996. Resurgence of lake whitefish, *Coregonus clupeaformis*, in Lake Ontario in the 1980s. *Great Lakes Fisheries Review* 2:20–28.

Charlton, M.N., Milne, J.E., Booth, W.G., and Chiocchio, F. 1993. Lake Erie offshore in 1990: restoration and resilience in the central basin. *J. Great Lakes Res*. 19:291–309.

Christie, W.J., Scott, K.A., Sly, P.J., and Struss, R.H. 1987. Recent changes in the aquatic food web of eastern Lake Ontario. *Can J. Fish. Aquat. Sci*. 44 (Suppl. 2):37–52.

Cook, D.G. 1975. *A preliminary report on the benthic macroinvertebrates of Lake Superior*. Environ. Canada, Fisheries and Marine Service, Tech. Rep. 572.

_____, and Johnson, M.G. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. *J. Fish. Res. Board Can*. 31:763–782.

Dadswell, M.J. 1974. *Distribution, ecology, and postglacial dispersal of certain crustaceans and fishes in eastern North America*. National Museum of Natural Sciences Publications in Zoology, No 11. National Museums of Canada.

Dermott, R.M., and Corning, K. 1988. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. *Can. J. Fish. Aquat. Sci*. 45:1886–1895.

_____, and Kerec, D. 1997. Changes to the deep-water benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979 to 1993. *Can. J. Fish. Aquat. Sci*. 54: 922–930.

_____, and Munawar, M. 1993. Invasion of Lake Erie offshore sediments by *Dreissena*, and its ecological implications. *Can. J. Fish. Aquat. Sci*. 50:2298–2304.

_____, Munawar, M., and Lorimer, J. 1998. Submersible confirmation of the profuse abundance of *Dreissena* on sediments in Lake Erie: implications to food web. *Verh. Internat. Verein. Limnol*. 26:2044–2047.

Elmgren R., Ankar, S., and Ejdung, G. 1990. Amphipods of the genus *Pontoporeia* as key elements in the Baltic benthos. *Ann. Zool. Fennici* 27:303–304.

Fitzgerald, S.A., and Gardner, W.S. 1993. An algal carbon budget for pelagic-benthic coupling in Lake Michigan. *Limnol. Oceanogr*. 38:547–560.

Flint, R.W. 1986. Hypothesized carbon flow through the deepwater Lake Ontario food web. *J. Great Lakes Res*. 12:344–354.

Gardner, W.S., Nalepa, T.F., Frez, W.A., Cichocki, E.A., and Landrum, P.F. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. *Can. J. Fish. Aquat. Sci*. 42:1827–1832.

_____, Eadie, B.J., Chandler J.F., Parrish, C.C., and Malczyk, J.M. 1989. Mass flux and "nutritional composition" of settling epilimnetic particles in Lake Michigan. *Can. J. Fish. Aquat. Sci*. 46:1118–1124.

_____, Quigley, M.A., Fahnenstiel, G.L., Scavia, D., and Frez, W.A. 1990. *Pontoporeia hoyi*—a direct trophic link between spring diatoms and fish in Lake Michigan. In *Large lakes: Structure and functional properties*, pp. 632–644, ed. M.M. Tilzer and C. Serruya. Springer.

Gauvin, J.M., Gardner, W.S., and Quigley, M.A. 1989. Effects of food removal on nutrient release rates and lipid content of Lake Michigan *Pontoporeia hoyi*. *Can. J. Fish. Aquat. Sci*. 46:1125–1130.

Hill, C. 1992. Interactions between year classes in the benthic amphipod *Monoporeia affinis*: effects on juvenile survival and growth. *Oecologia* 91:157–162.

Holland, R.E., Johengen, T.H., and Beeton, A.M. 1995. Trends in nutrient concentrations in Hatchery Bay, western Lake Erie, before and after *Dreissena polymorpha*. *Can. J. Fish. Aquat. Sci*. 52:1202–1209.

Hoyle, J.A., Schaner, T., Casselman, J.M., and Dermott, R. 1999. Changes in lake whitefish (*Coregonus clupeaformis*) stocks in eastern Lake Ontario following *Dreissena* mussel invasion. *Great Lakes Research Review* 4:5–10.

Johannsson, O.E., Dermott, R.M., Feldkamp, R., and Moore, J.E. 1985. Lake Ontario Long Term Biological Monitoring Program: Report for 1981 and 1982. *Can. Tech. Rep. Fish. Aquat. Sci*., 1414.

_____, Millard, E.S., Ralph, K.M., Myles, D.D., Graham, D.M., Taylor, W.D., Giles, B.G., and Allen, R.E. 1998. The changing pelagia of Lake Ontario (1981 to 1995): A report of the DFO Long-term Biomonitoring (Bioindex) Program. *Can. Tech. Rep. Fish. Aquat. Sci*., 2243.

Johnson, M.G., and Brinkhurst, R.O. 1971. Associations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. *J. Fish. Res. Board Can*. 28:1683–1697.

_____, and Hurley, D.A. 1986. Overview of Project Quinte—1972–82. *Can. Spec. Publ. Fish. Aquatic Sci*. 86:1–6.

_____, and McNeil, O.C. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–84. *Can. Spec. Publ. Fish. Aquatic Sci*. 86:177–189.

Johnson, R.K., and Wiederholm, T. 1989. Long-term growth oscillations of *Pontoporeia affinis* Lindström (Crustacea: Amphipoda) in Lake Mälaren. *Hydrobiologia* 175:183–194.

_____, and Wiederholm, T. 1992. Pelagic-benthic coupling—The importance of diatom interannual variability for population oscillations of *Monoporeia affinis*. *Limnol. Oceanogr*. 37:1596–1607.

Larkin, P.A. 1948. *Pontoporeia* and *Mysis* in Athabaska, Great Bear, and Great Slave Lakes. *Bull. Fish. Res. Bd. Can*. 88:1–33.

L'Italien, S. 1998. *Lake Ontario surveillance activities including sampling strategies for 1981–1998*. Environmental Conservation Branch, Ecosystem Health Division, Ontario Region, Environment Canada. Rep.: ECB/EHD-OR/98-09/I.

Lopez, G.R., and Holopainen, I.J. 1987. Interstitial suspension-feeding by *Pisidium* spp. (Pisidiidae: Bivalvia): a new guild in the lentic benthos? *Am. Malacol. Bull*. 5:21–30.

Masse, A.K., and Murthy, C.R. 1992. Analysis of the Niagara plume dynamics. *J. Geophysical Res*. 97 (C2):2403–2420.

McDermott, J.J. 1993. Nemertea inhabiting the *Haploops* (Amphipoda) community of the northern Oresund with special reference to the biology of *Nipponnemertes pulcher* (Hoplonemertea). *Hydrobiologia* 266:15–28.

McDonald, M.E., Crowder, L.B., and Brandt, S.B. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan :a response to shifts in the fish community. *Limnol. Oceanogr*. 35 :220–227.

Millard, E.S., Fee, E.J., Myles, D.D., and Dahl, J.A. 1999. Comparison of phytoplankton photosynthesis methodology in Lakes Erie, Ontario, the Bay of Quinte and the Northwest Ontario Lake Size Series. In *State of Lake Erie (SOLE)—Past, Present and Future*, pp. 441–468, ed. Munawar, M., Edsall, T., and Munawar, I.F. Ecovision World Monograph Series, Backhuys Publishers, Leiden, The Netherlands.

Mills, E.L., Dermott, R.M., Roseman, E.F., Dustin, D., Mellina, E., Conn, D.B., and Spidle, A. 1993. Colonization, ecology and population structure of the "quagga" mussel in the lower Great Lakes. *Can. J. Fish. Aquat. Sci*. 50:2305—2314.

_____, Chrisman, J.R., Baldwin, B., Owens, R.W., O'Gorman, R., Howell, T., Roseman, E.F., and Raths, M.K. 1999. Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *J. Great Lakes. Res*. 25 :187–197.

Mullin, M.D. 1980. Lake Erie nutrient control: effectiveness regarding assessment in eastern basin. U.S. Environmental Protection Agency, Washington D.C. EPA-600/3-80-067: 63–84.

Nalepa, T.F., 1987. Long-term changes in the macrobenthos of southern Lake Michigan. *Can. J. Fish. Aquatic. Sci*. 44:515–524.

_____, and Fahnenstiel, G.L. 1995. *Dreissena polymorpha* in the Saginaw Bay, Lake Huron Ecosystem: overview and perspective. *J. Great Lakes Res*. 21: 411–416.

_____, Quigley, M.A., Childs, K.F., Gauvin, J.M., Heatlie, T.S., Parker, M.P., and Vanover, L. 1985. *Macrobenthos of southern Lake Michigan, 1980–81*. NOAA Data Report. ERL-GLERL-28. Great Lakes Environ. Res. Lab., Ann Arbor, Michigan.

_____, Hartson, D.J., Fanslow, D.L., Lang, G.A., and Loranzo, S.J. 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. *Can. J. Fish. Aquatic Sci*. 55:2402–2413.

Nicholls, K.H., and Hurley, D.A. 1989. Recent changes in the phytoplankton of the Bay of Quinte, Lake Ontario: the relative importance of fish, nutrients, and other factors. *Can. J. Fish. Aquat. Sci*. 46:770–779.

Robbins, J.A. 1982. Stratigraphic and dynamic effects of sediment reworking by Great Lakes zoobenthos. *Hydrobiologia* 92:611–622.

Sarvala, J. 1986. Interannual variation of growth and recruitment in *Pontoporeia affinis* (Lindström) (Crustacea: Amphipods) in relation to abundance fluctuations. *J. Exp. Mar. Biol. Ecol*. 101:41–59.

Schloesser, D.W., Nalepa, T.F., and Mackie, G.L. 1996. Zebra mussel infestation of unionid bivalves (Unionidae) in North America. *Amer. Zool*. 36:300–310.

Segerstråle, S.G. 1959. Synopsis of data on the crustaceans *Gammarus locusta*, *Gammarus oceanicus*, *Pontoporeia affinis* and *Corophium volutator* (Amphipoda Gammaridea). Soc. Scient. Fenn. Comment. Biol. 20, 5:1–23.

Sly, P.G. 1984. Sedimentology and geochemistry of modern sediments in the Kingston basin of Lake Ontario. *J. Great Lakes Res*. 10:358–374.

_____, and Christie, W.J. 1992. Factors influencing densities and distributions of *Pontoporeia hoyi* in Lake Ontario. *Hydrobiologia* 235/236:321–352.

Stewart, T.W., Miner, J.M., and Lowe, R.L. 1998. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. *J. Great Lakes Res*. 24:868–879.

Thiel, M., and Reise, K. 1993. Interaction of nemertines and their prey on tidal flats. *Neth. J. Sea Res*. 31: 163–172.

Thomas, R.L., Jaquet, J.M., and Kemp, A.L. 1976. Surficial sediments of Lake Erie. *J. Fish. Res. Board Can*. 33:385–403.

Tohtz, J. 1993. Lake whitefish diet and growth after the introduction of *Mysis relicta* to Flathead Lake, Montana. *Trans. Amer. Fish. Soc*. 122:629–635.

Van de Bund, W.J., Goedkoop, W., and Johnson, R.K. 1994. Effects of deposit-feeding activity on bacterial production and abundance in profundal lake sediment. *J. N. Am. Benthol. Soc*. 13:532–539.

Wells, L. 1980. Food of alewives, yellow perch, spottail shiners, trout-perch, and slimy and four-horn sculpins in southeastern Lake Michigan. *U.S. Fish. and Wild. Serv. Tech. Paper* 98.

Wormington, A., Timmins, C.A., and Dermott, R.M. 1993. *Distribution of zebra mussels on Canadian navigation buoys on the Great Lakes and Upper St. Lawrence River, December 1992*. Can. Manuscr. Rep. Fish. Aquat. Sci. 2186.

_____, Timmins, C.A., Johnston, H., and Dermott, R.M. 1995. *Distribution of zebra mussels on Canadian navigation buoys on the Great Lakes, December 1993*. Can. Manuscr. Rep. Fish. Aquat. Sci. 2281.