Seasonal variation of lipid composition, weight, and length in juvenile *Diporeia* spp. (Amphipoda) from lakes Michigan and Ontario[1,2]

Joann F. Cavaletto, Thomas F. Nalepa, Ronald Dermott, Wayne S. Gardner, Michael A. Quigley, and Gregory A. Lang

Abstract: Benthic amphipods, *Diporeia* spp., were collected during 1988 and 1989 at four sites to compare size and lipid levels of animals living in Lakes Michigan and Ontario: sites were at depths of 45 and 100 m in Lake Michigan and 35 and 125 m in Lake Ontario. In Lake Michigan, the mean length, mass, and lipid levels of individual *Diporeia* from 45 m were significantly different from those collected from 100 m in 1988; in 1989, only mass and lipid levels were significantly different between depths. In contrast, regardless of the year, the Lake Ontario *Diporeia* from 35 m were similar in mass and length to those from 125 m, but lipid levels were significantly different between depths. Combined means for total lipid for each lake over similar months revealed higher levels in Lake Ontario than in Lake Michigan *Diporeia*. Triacylglycerols were the dominant lipid class in all the amphipods, with mean levels reaching a maximum of 84% of the total lipid in individuals from Lake Ontario at 35 m. Trophic state, food-web, and (or) genetic differences are probably responsible for the occurrence of higher lipid levels in Lake Ontario *Diporeia* than in Lake Michigan *Diporeia*.

Résumé : Des amphipodes benthiques, Diporeia spp., ont été prélevés en 1988 et 1989 dans quatre sites pour comparer la taille et la teneur en lipides des animaux vivant dans les lacs Michigan et Ontario. Les sites de prélèvement se situaient à 45 et 100 m dans le cas du lac Michigan et à 35 et 125 m dans le cas du lac Ontario. Dans le lac Michigan, les longueurs, masses et concentrations en lipide moyennes des *Diporeia* individuels vivant à la profondeur de 45 m différaient de manière statistiquement significative de celles des organismes prélevés à 100 m en 1988; en 1989, seules la masse et la concentration en lipide différaient de manière significative d'une profondeur à l'autre. À l'opposé, peu importe l'année, les *Diporeia* du lac Ontario prélevés à une profondeur de 35 m étaient semblables par leur taille et leur masse à ceux qui ont été prélevés à 125 m, mais leur concentration en lipide était différente de manière significative. Les moyennes combinées des lipides totaux pour chacun des lacs au cours des mêmes mois ont révélé des concentrations plus élevées dans les *Diporeia* du lac Ontario que dans ceux du lac Michigan. Les triacylglycérols constituaient la classe de lipide dominante chez tous les amphipodes, les concentrations moyennes atteignant un maximum de 84 % des lipides totaux chez les animaux du lac Ontario vivant à 35 m. L'état trophique, le réseau alimentaire et (ou) des différences génétiques expliquent probablement les concentrations en lipide plus élevées observées chez les *Diporeia* du lac Ontario comparativement à ceux du lac Michigan.
[Traduit par la Rédaction]

Introduction

The amphipods *Diporeia* spp. are the most abundant macrobenthic organisms in the slope and profundal zones of the Great Lakes (Johannsson et al. 1985; Nalepa 1987; Evans et al. 1990) and are a direct link between spring primary production and fish. Previous studies have shown that *Diporeia* feeds directly on the spring diatom bloom after it settles to the lake bottom. For instance, fragments of the diatoms *Cyclotella* spp. and *Melosira* spp. are the most common biological remains found in *Diporeia* guts (Evans et al. 1990) and the frequency of full guts is highest in the spring, implying active feeding on fresh food inputs at this time (Quigley 1988; Dermott and Corning 1988). *Diporeia* lipid levels increase after

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J.F. Cavaletto, T.F. Nalepa, W.S. Gardner, M.A. Quigley, and G.A. Lang. National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, U.S.A.
R. Dermott. Department of Fisheries and Oceans, Great Lakes Laboratory for Fisheries and Aquatic Science, Canada Centre Inland Waters, P.O. Box 5050, Burlington, ON L7R 4A6, Canada.

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Table 1. Summary of sample collections from Lakes Michigan at 45 and 100 m and Lake Ontario at 35 and 125 m during 1988 and 1989.

	Lake Michigan		Lake Ontario	
Date	45 m	100 m	35 m	125 m
1988				
19 Apr.			d,f,b	d,b
21 Apr.	d,b,f,l	d,b,l		
10 May			d,f,b	
12 May	d,b,f,l	d,b,l		
01 June			d,b,f,l	l
08 June	d,b,f,l	d,b,l		
21 June			d,b,f,l	l
29 June	d,b,f,l	d,b,l		
12 July	d,b,f,l	d,b,l		
20 July			d,b,f,l	d,b,l
17 Aug.			l	l
19 Aug.	l			
29 Aug.	d,b,f,l	d,b,l		
12 Sept.			d,b,f,l	l
12 Oct.			d,b,f,l	d,b,l
14 Nov.	d,b,l	d,b,l		
1989				
18 Apr.	d,b,l	d,b,l		
25 Apr.			d,b,f,l	d,b,l
15 May	d,b,l	d,b,l		
18 May			l	l
14 June			l	l
15 June	d,b,l	d,b,l		
02 Aug.			d,b,l	d,b,l
23 Aug.	d,b,l	d,b,l		
11 Oct.			d,b,l	d,b,l

*d, density; b, biomass; f, frequency distribution; l, lipid.

the diatom bloom in Lake Michigan, suggesting their use of this high-quality food source (Gardner et al. 1985*a*, 1990). In turn, *Diporeia* is fed upon by numerous species of fish (Wells 1980; McDonald et al. 1990).

A direct link between primary production and benthic biomass often occurs in temperate large lakes (Gardner et al. 1990; Johnson and Wiederholm 1992). Although primary production and sedimentation rates are higher in Lake Ontario than in Lake Michigan, benthic biomass is greater in Lake Michigan (Nalepa 1991). This inconsistency between Lakes Michigan and Ontario has caused some speculation about the nature of the pelagic–benthic coupling systems in these two lakes. Differences in fish predation, levels of persistent contaminants, and SiO_2 concentrations have all been suggested to explain differences in benthic biomass between the two lakes (Nalepa 1991; Sly and Christie 1992). Because lipid levels and lipid classes are an excellent indicator of the nourishment available to *Diporeia*, we conducted a seasonal study of lipids in *Diporeia* in Lakes Michigan and Ontario to examine pelagic–benthic coupling in the two lakes. *Diporeia* were examined at a sublittoral and profundal site in each lake.

Diporeia spp. were formerly known as one species, *Pontoporeia hoyi*, in the Great Lakes ecosystem; however, the genus *Diporeia* contains at least two and perhaps as many as eight species (Bousfield 1989). Because this study was under taken when these amphipods were all classified as *Pontoporeia hoyi* we will simply group them under the genus *Diporeia* with no specific designation.

Methods

Diporeia were collected spring through fall in 1988 and 1989 from a 45-m site (43°1′N, 86°20′W) and a 100-m site (43°1′N, 86°37′W) in southern Lake Michigan offshore from Grand Haven, Mich., and a 35-m site (43°59′N, 76°39′W) in Lake Ontario's eastern basin off Main Duck Island and a 125-m site (43°43′N, 78°02′W) in the middle of Lake Ontario. On dates specified in Table 1, benthic organisms were collected with a Ponar grab, washed through a 500-μm screen for the Lake Michigan samples or a 250-μm screen for the Lake Ontario samples, and preserved in 10% formalin for later enumeration and length measurements to determine *Diporeia* areal density and biomass. As many as 75% of newly hatched young-of-the-year (YOY) may pass through a 500-μm screen (Johnson 1988); hence, we corrected for the different screen sizes used in each lake by subtracting the proportion of 1–2 mm amphipods determined for each month. Lengths were converted to biomass using an empirical relationship that was derived from a subset of unpreserved *Diporeia*. The Lake Michigan biomass estimates are conservative because they were based on the non-normalized 500-μm screen densities. *Diporeia* size–frequency distributions (1-mm size categories excluding the

Fig. 1. Mean lengths of *Diporeia* from Lake Michigan and Lake Ontario that were examined for total lipid and lipid classes. Error bars are SEs.

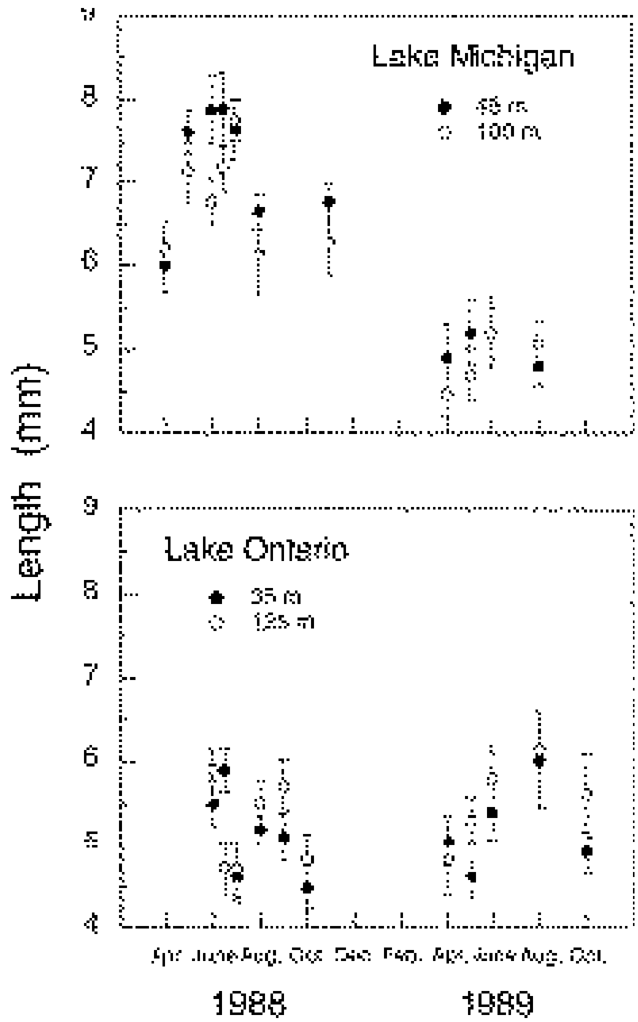
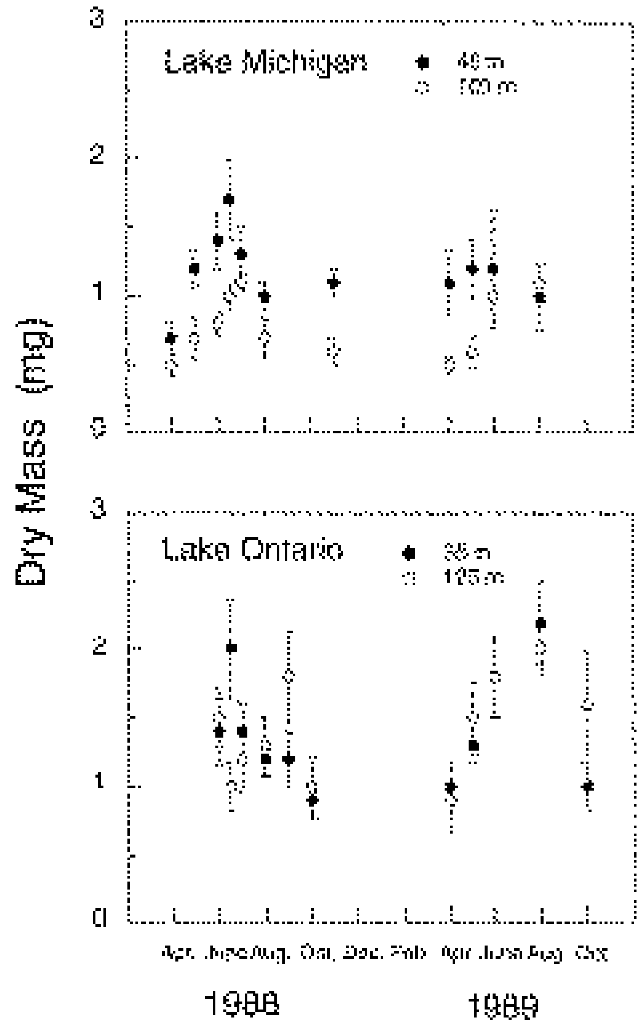


Fig. 2. Mean dry masses of *Diporeia* from Lake Michigan and Lake Ontario that were examined for total lipid and lipid classes. Error bars are SEs.



1–2 mm class) were determined from preserved samples collected at the shallower depths on dates indicated in Table 1.

Additional samples were taken at each site for measurement of total lipid and lipid classes. These unpreserved samples were transported at or below ambient temperature (4–8°C) to Ann Arbor, Mich., as soon as possible after collection (1–3 days). In the laboratory, juvenile *Diporeia* 4–8 mm long were selected at random. Juveniles were selected to eliminate variation in lipid content that occurs between adults. For example, in one study total lipid of dry mass averaged 23% in female and 9% in male *Diporeia* (Quigely et al. 1989). Selected *Diporeia* were rinsed with distilled water, blotted dry, measured with a digitizing system (Quigley and Lang 1989), and placed in miniature test tubes (6 × 50 mm) for drying (under N_2, at 50°C) and lipid extraction (Folch et al. 1957; Gardner et al. 1985*b*). For every lipid sample collection date, length, dry mass, and total lipid were determined on 8–13 individuals from each site in each lake, while lipid classes were determined on only a portion of these individuals (n = 2–6). Total lipids were extracted using chloroform:methanol (2:1, v/v), and quantified gravimetrically. Lipid classes were analyzed by thin layer chromatography with flame ionization detection (TLC-FID). Lipid classes were separated by spotting a portion of the lipid extract onto silica-coated Chromarods-SII or -SIII (RSS Inc.) and sequentially developing them in solvent systems of increasing polarity. Chromarods were scanned after each group separation in an Iatroscan Mark IV (Iatron Labs, Tokyo, Japan). A mixed lipid standard, containing one compound from each of the following lipid classes: hydrocarbon, sterol ester, triacylglycerol, free fatty acid, alcohol (aliphatic), sterol (alicyclic), and phospholipid, was used for TLC-FID calibration and quantification. Calibration curves were determined over a range of 0.15–30 μg for each standard compound (Parrish 1986, 1987).

Statistical differences were determined using a two-tailed t-test (SYSTAT, Inc. 1992). Variances were tested for homogeneity using the F-statistic.

Results

Mean lengths of *Diporeia* used for lipid analysis were 5.2 ± 0.1 (mean ± SE) and 5.3 ± 0.1 mm from both depths in Lake Ontario in 1988 and 1989, respectively. In Lake Michigan, the mean lengths of amphipods from both depths were 7.3 ± 0.1 mm in 1988, and 4.9 ± 0.1 mm in 1989 (Fig. 1, Table 2). Mean dry masses were 1.2 ± 0.1 mg in 1988 and 1.0 ± 0.1 mg in 1989 for *Diporeia* from Lake Michigan. In Lake Ontario, *Diporeia* mean dry masses were 1.3 ± 0.1 mg and

Table 2. Summary of means (± SEs) for 1988 and 1989 *Diporeia* from Lakes Michigan and Ontario, with *n* given in parentheses.

	Density (individuals·m^{-2})	Biomass (g·m^{-2})	Dry mass (mg)	Length (mm)	Total lipid (% of DM)	TG (% of TL)
			1988			
Lake Michigan						
45 m	7 831 ± 521 (7)	6.0±0.4	1.4±0.1 (48)	7.6±0.2	28.2±1.0	82.5±2.5 (14)
100 m	5 311 ± 243 (7)	1.9±0.1	0.9±0.1 (39)	7.0±0.2	20.4±0.9	66.0±3.4 (14)
Combined	6 572 ± 445 (14)	4.0±0.6	1.2±0.1 (87)	7.3±0.1	24.7±0.8	73.5±2.6 (28)
Lake Ontario						
35 m	7 378 ± 431 (6)	3.0±0.1	1.3±0.1 (53)	5.1±0.1	35.7±1.1	81.0±2.7 (20)
125 m	3 185 ± 365 (3)	0.9±0.1	1.3±0.1 (57)	5.3±0.1	32.4±1.2	72.3±3.6 (20)
Combined	5 980 ± 768 (9)	2.0±0.3	1.3±0.1 (110)	5.2±0.1	34.0±0.8	76.7±2.3 (40)
			1989			
Lake Michigan						
45 m	9 787 ± 789 (4)	11.4±0.9	1.1±0.1 (40)	5.0±0.2	25.7±1.2	76.0±2.9 (18)
100 m	5 176 ± 410 (4)	4.2±0.5	0.8±0.1 (41)	4.9±0.2	17.9±1.2	56.4±5.4 (16)
Combined	7 482 ± 964 (8)	7.8±1.5	1.0±0.1 (81)	4.9±0.1	21.7±1.0	67.4±3.3 (34)
Lake Ontario						
35 m	10 006 ± 1202 (3)	3.1±0.5	1.4±0.1 (39)	5.2±0.1	37.4±1.1	84.2±1.2 (15)
125 m	2 971 ± 480 (3)	1.1±0.2	1.4±0.1 (39)	5.4±0.1	32.5±1.3	76.9±3.4 (16)
Combined	6 488 ± 1676 (6)	2.1±0.5	1.4±0.1 (78)	5.3±0.1	34.9±1.2	80.6±1.9 (31)

Note: The *n* given for density is the same for biomass and the *n* for dry mass (DM) is the same for length and total lipid (TL). The triacylglycerol (TG) *n* is given separately. Density and biomass means were determined from the same months as in Fig. 4. To compare a similar season, the annual means for DM, length, TL, and TG were determined from Lake Ontario collection dates from June through the middle of September and from Lake Michigan dates from June through late August in 1988. In 1989 the means were determined from the collection dates from April through August in both lakes (see Table 1 for exact dates).

1.4 ± 0.1 mg in 1988 and 1989, respectively (Fig. 2, Table 2). In Lake Michigan, *Diporeia* from the 45-m depth differed ($P < 0.05$) in mean length and mass from individuals collected at 100 m in 1988 (Table 2). In 1989, *Diporeia* from 45 m were heavier on average ($P < 0.05$) than those from 100 m; however, the mean lengths from both depths were not different ($P > 0.05$). In contrast, regardless of year, the Lake Ontario *Diporeia* from 35 and 125-m depths were similar ($P > 0.05$) in mean mass or length (Table 2).

Length–mass relationships of *Diporeia* were determined for each lake, year and depth combination (Table 3). The best relationship was $\ln(\mathrm{DM}) = a + b\ln(L)$, where DM is amphipod dry mass (milligrams) and L is length (millimetres). All relationships were significant ($P < 0.001$), and there were no significant differences among the variances of the residuals (Cochran's test: Beyer 1991) or slopes (GLM test for equality of slopes) of the eight regressions. However, based on a common slope of 2.602, there were significant differences among the intercepts (analysis of covariance; Hald 1967; SYSTAT, Inc. 1992). A post-hoc Tukey HSD multiple comparison test revealed that five of the intercepts were similar while three were significantly different from each other and also different from the other five. The order of mass per given length of these three was 100-m Lake Michigan 1988 < 45-m Lake Michigan 1988 < 100-m Lake Michigan 1989. Dry masses of all of the Lake Ontario *Diporeia* and those from Lake Michigan at 45 m in 1989 were not significantly different from each other but had the greatest dry masses for a given length.

Mean total lipid levels of *Diporeia* (as percentage of dry mass) from Lake Ontario were higher ($P < 0.05$) in 1988 and 1989 than in Lake Michigan individuals from both years (Table 2). This difference between lakes was especially apparent at the deep sites in August 1988 when *Diporeia* total lipid levels were over twice as high in Lake Ontario than in Lake Michigan (Fig. 3). Triacylglycerol (TG), the energy reserve lipid, was the most abundant lipid class in *Diporeia* from both lakes; it paralleled seasonal changes in total lipid. The most pronounced seasonal changes in TG occurred at the 125-m site in Lake Ontario in 1988 (Fig. 3). The largest TG, and therefore total lipid increase, occurred in August and September of that year; however, this late summer TG peak was not apparent in 1989. In Lake Michigan, the largest TG levels occurred during summer at both sites, in both 1988 and 1989 (Fig. 3). Phospholipid (PL; structural cell membrane lipid) constituted between 2 and 53% of the total lipids present in *Diporeia*. A high percentage of PL occurred when storage lipids (TG) were low. Other lipid classes that were analyzed occurred at relatively low levels and were combined; these classes include hydrocarbons, methyl esters, sterol esters, sterols, and the operationally defined acetone mobile polar lipids (including monoacylglycerols, glycolipids, and chlorophyll pigments; Parrish 1986).

Diporeia densities (based on >2 mm amphipods) were similar in both lakes at the shallow depths; at the deeper sites, *Diporeia* densities were higher in Lake Michigan than in Lake Ontario (Fig. 4A, Table 2). Nevertheless, *Diporeia* biomass in Lake Michigan was higher than in Lake Ontario at the shallow depth in 1988, and at both depths in 1989 (Fig. 4B, Table 2). This was due principally to the frequency of larger animals in Lake Michigan (Fig. 5).

Fig. 3. *Diporeia* mean percent total lipid and lipid classes in Lake Ontario from the 35- and 125-m sites and in Lake Michigan *Diporeia* from the 45- and 100-m sites. Error bars are SEs of the mean total lipid. Lipid classes are represented as triacylglycerols (TG), phospholipids (PL), and other lipids (OL). *Diporeia* were analyzed in both early and late June 1988. See Table 1 for exact dates.

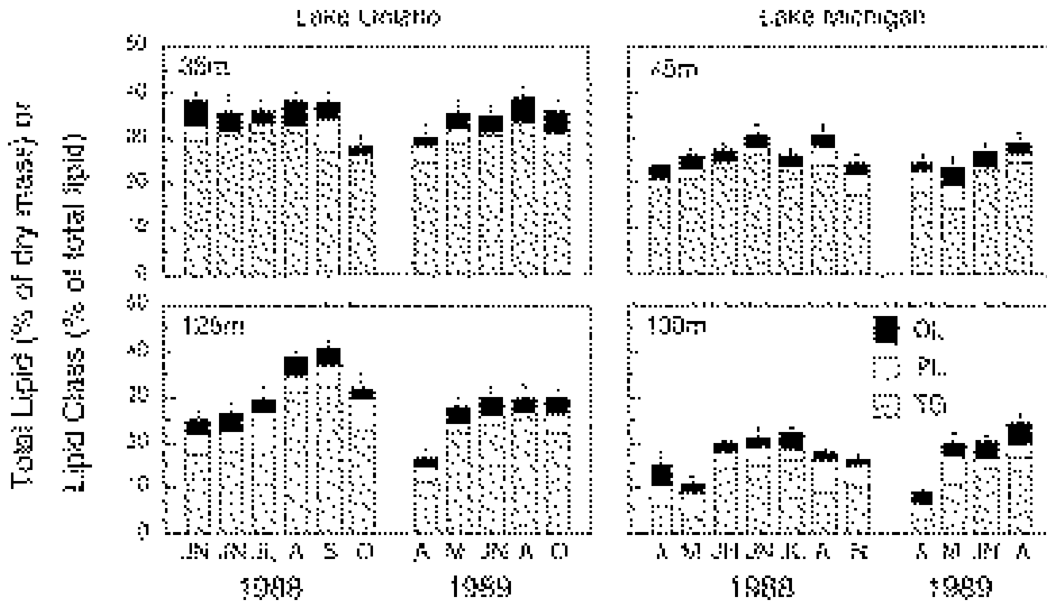


Table 3. Summary of regression analyses for *Diporeia* dry mass (mg) versus length (mm).

Lake	Year	Depth (m)	*a*	*b*	R^2	*n*
Michigan	1988	45	−4.946	2.556	0.831	77
	1989	45	−3.695	2.300	0.892	40
Ontario	1988	35	−3.974	2.544	0.760	65
	1989	35	−3.625	2.371	0.717	49
Michigan	1988	100	−5.071	2.471	0.688	67
	1989	100	−4.704	2.752	0.765	41
Ontario	1988	125	−4.387	2.718	0.789	68
	1989	125	−4.843	3.005	0.861	48

Note: Both variables were first log transformed using the model: $\ln(DM) = a + b \ln(L)$, where DM is dry mass and *L* is length. All slopes (*b*) and intercepts (*a*) are significantly different from zero ($P < 0.001$). All regressions are significant ($P < 0.001$).

Discussion

Lakes Michigan and Ontario are different in many limnological respects, and *Diporeia* populations reflect these differences. The higher total lipid levels of Lake Ontario *Diporeia* relative to those in Lake Michigan regardless of depth, suggests that food inputs are more abundant in Lake Ontario even in the profundal region. This finding was unexpected given low SiO_2 concentrations that could perhaps reduce the spring diatom bloom in Lake Ontario as compared with Lake Michigan (Sly and Christie 1992; Johengen et al. 1994). However, Lake Ontario is more productive than Lake Michigan, and the majority of spring phytoplankton are large diatoms such as *Melosira* spp. that remain abundant until early June and July at the 35- and 125-m sites, respectively (Johannsson et al. 1985; Gray 1987; Johengen et al. 1994). Lipids in diatoms and other phytoplankton increase under stress (i.e., nutrient limitation) (Roessler 1988; Shifrin and Chisholm 1981). SiO_2 limitation may induce greater lipid production in diatoms in Lake Ontario than in Lake Michigan. Upon their settling to the benthos, lipid-rich diatoms would be a direct high energy food source to *Diporeia*. In addition, Lake Ontario is dominated by small zooplankton such as rotifers and cyclopoid copepods (Johannsson et al. 1991; Mazumder et al. 1992) that may not consume large diatoms, thus allowing a high proportion of cells to settle to the bottom and become available to benthic organisms.

During most months the 3–5 mm amphipods were more abundant in Lake Ontario while 6–11 mm individuals were more abundant in Lake Michigan (Fig. 5). The predominance of smaller individuals in Lake Ontario may reflect differences in fish predation rather than food limitation because lipid reserves in juvenile *Diporeia* were relatively high. In Lake Ontario, significant correlations suggest that slimy sculpin (*Cottus cognatus*) suppress *Diporeia* biomass (Sly and Christie 1992). In addition, large juvenile (>5 mm) and adult *Diporeia* are most commonly found in deepwater sculpin (*Myoxocephalus thompsoni*) guts (Evans et al. 1990). This implies that fish predation will reduce the larger size-classes of *Diporeia*. Lake whitefish (*Coregonus clupeaformis*) also prey on *Diporeia*, and their relative abundances have increased recently in eastern Lake Ontario (Christie et al. 1987; Casselman and Scott 1992). In Lake Michigan, benthic predation is dominated by adult bloater (*Coregonus hoyi*) that appear to feed in a narrower prey size range (>4 to <8 mm) than whitefish or sculpin. These gape-limited foragers may permit the largest *Diporeia* to escape predation in Lake Michigan (McDonald et al. 1990).

Differences in *Diporeia* areal biomass and lipid levels may reflect different lower food-web interactions in Lake Michigan and Lake Ontario. The Lake Michigan spring diatom bloom is coupled to benthic organisms, especially *Diporeia*,

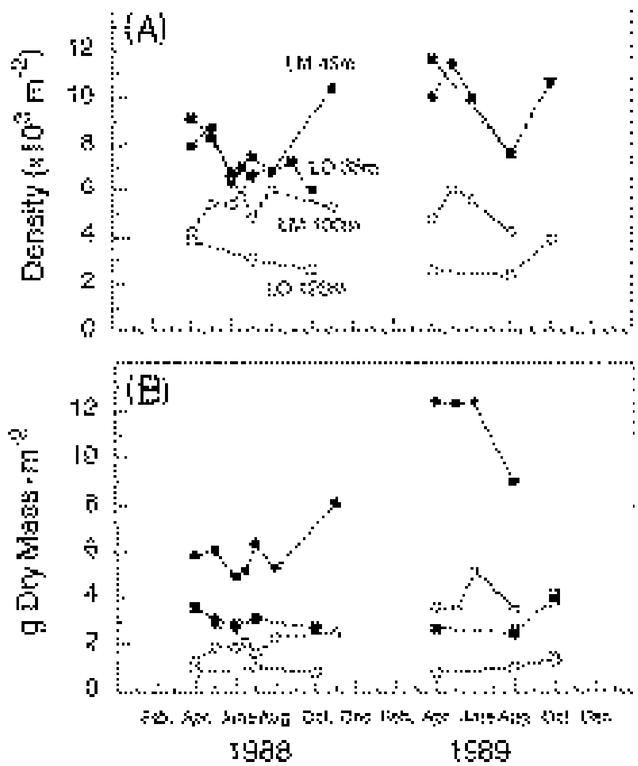


Fig. 4. Mean *Diporeia* densities (A) and biomasses (B) from two depths in lakes Ontario (LO) and Michigan (LM) in 1988 and 1989.

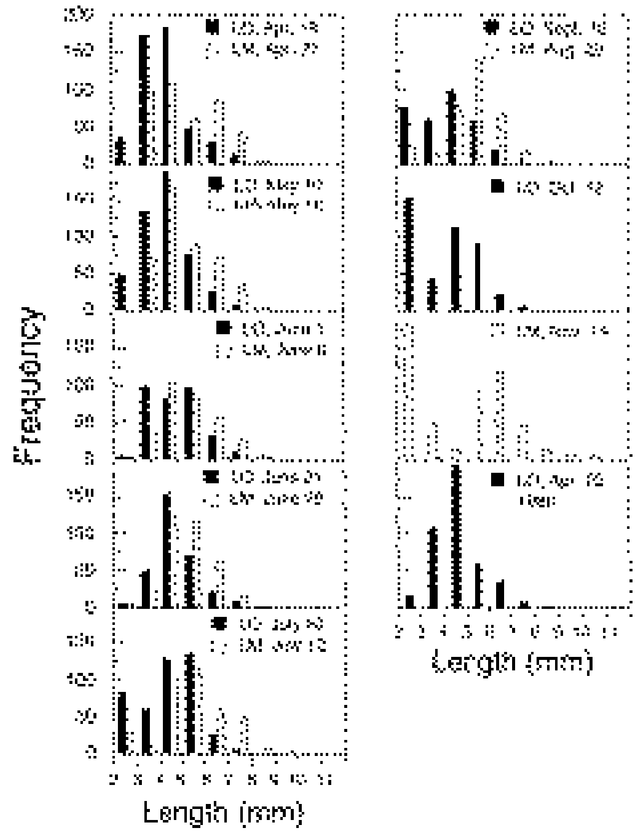


Fig. 5. *Diporeia* size-class frequency distributions from the Lake Ontario (LO) 35-m and Lake Michigan (LM) 45-m sites.

that are in turn preyed upon by fish (Gardner et al. 1990; Fitzgerald and Gardner 1993). However, it appears that *Diporeia* lipid levels have declined slightly in Lake Michigan at the 45-m site from a mean of 33.7 ± 3.3% of dry mass in 1984 to 28.2 ± 1.0% of dry mass in 1988, and then to 25.7 ± 1.2% of dry mass in 1989 (Gardner et al. 1985*a*; Table 2). The relatively low lipid levels in Lake Michigan *Diporeia* suggest that the Lake Michigan spring diatom bloom is not as great as that in Lake Ontario or that the diatoms are being intercepted by zooplankton before they settle to the benthos. Spring NO_3 and SiO_2 uptake rates suggest that diatoms contribute more to total springtime production in Lake Michigan than in Lake Ontario (Johengen et al. 1994). In 1988, mean springtime algal biomasses were 1.5 g·m^{-3} at the 100-m site in Lake Michigan (G.L. Fahnenstiel, Lake Michigan Field Station, NOAA, Great Lakes Environmental Research Laboratory, Muskegon, Mich., unpublished data) and 1.0 g·m^{-3} at the 125-m site in Lake Ontario (O.E. Johannsson, DFO, Great Lakes Laboratory for Fisheries and Aquatic Science, Canada Centre for Inland Waters, Burlington, Ont., unpublished data). It is possible that spring diatoms are being intercepted before they can reach the benthos by hypolimnetic calanoid copepods that are dominant in Lake Michigan. Calanoid copepods are a minor component of the zooplankton community in Lake Ontario (Mazumder et al. 1992; Johannsson et al. 1985). Recently, the calanoid copepods *Diaptomus sicilis* and *Limnocalanus macrurus* have been increasing in numbers in Lake Michigan (G.L. Pernie, NOAA, Great Lakes Environmental Research Laboratory, Ann Arbor, Mich., personal communication) and will probably increase grazing pressure on spring diatoms. Early spring feeding experiments with *D. sicilis* revealed that high feeding rates occurred during under-ice and post-ice phytoplankton blooms in Grand Traverse Bay, Lake Michigan (Vanderploeg et al. 1992*a*). The decline in *Diporeia* lipid levels since 1984 may also suggest that the settling of high quality food to the benthos has been reduced in offshore Lake Michigan. In addition, the longer settling time required for diatoms to reach greater depths would allow for more zooplankton grazing and microbial decomposition that would cause a lower percentage of total diatoms to reach the profundal zone (Eadie et al. 1984). This may explain the greater range in *Diporeia* lipid reserves between the shallow (slope) and deep sites in Lake Michigan than in Lake Ontario (Table 3).

The higher lipid levels of *Diporeia* from Lake Ontario, compared with Lake Michigan *Diporeia*, may indeed reflect differences in the food web of the two lakes. However, the different populations may also have genetic explanations for their modes of food assimilation and lipid storage patterns, as do two sympatric species of amphipods from the Baltic Sea, *Monoporeia affinis* and *Pontoporeia femorata*. Although they dwell in the same sediments, *M. affinis* has a higher respiration and feeding rate than *P. femorata*, and thus has faster lipid accumulation and turnover rates than the more seasonally stable lipid storage pattern of *P. femorata* (Hill et al. 1992). Whereas eight or more species of *Diporeia* may be found in North America, exact species identifications have not been determined in the Great Lakes region (Bousfield

1989). Ideally, further morphological and genetic studies are necessary to clarify species within *Diporeia*.

Finally, lipid storage patterns can reveal a great deal about an organism's life history. For example, many invertebrates need to accumulate a certain percentage of lipids before they can reproduce or metamorphose into adults as is the case for some insects (Hill et al. 1992; Vanderploeg et al. 1992*b*; Cargill et al. 1985). Adult *Diporeia* females have higher lipid levels than males or juveniles (Quigley et al. 1989). Most of the lipids are then transferred from the gravid females to their brooded young to give them an advantage in their first few days of life. In addition, lipid-rich females may produce large broods. In support of this idea, Lake Ontario gravid female *Diporeia* brooded a mean of 29 eggs (R. Dermott, unpublished data) while gravid females from Lake Michigan brooded a mean of 17 eggs (Winnell and White 1984).

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