The Trophic Role of *Diporeia* (Amphipoda) in Colpoys Bay (Georgian Bay) Benthic Food Web: A Stable Isotope Approach

Karin R.R.A. Guiguer* and David R. Barton

Department of Biology
University of Waterloo
200 University Ave. West
Waterloo, Ontario N2L 3G1

ABSTRACT. In order to assess the trophic role of *Diporeia* in Colpoys Bay, amphipods were collected from depths of 30 and 50 m using an Ekman grab or a dredge. These were used to estimate the production dynamics, seasonal feeding patterns and lipid content. Stable isotope signatures of carbon and nitrogen were used to determine the sources of energy actually assimilated. Mean annual density of *Diporeia* was 1.7 times greater, and production was 2.7 times greater, at 50 m than at 30 m. Animals at both depths fed more or less continuously from April through November, but gut fullness was greatest in spring. Isotopic analyses suggested that, whereas *Diporeia* preferentially consumes freshly deposited diatoms when they are available, most of their carbon is derived from bacteria. The importance of littoral diatoms appeared to increase with proximity to shallow water.

INDEX WORDS: *Diporeia*, energy flow, POC, epilithon, Lake Huron.

INTRODUCTION

*Diporeia* is the most abundant macrobenthic organism in the profundal region of the Great Lakes (Johannsson *et al*. 1985, Nalepa 1987, Evans *et al*. 1990), commonly occurring at densities of about 7,000 individuals/m² (Nalepa *et al*. 1985). These amphipods usually inhabit the first two centimeters of soft sediments or fine sand with organic coatings (Robbins *et al*. 1979), and so can strongly affect sediment geochemistry through bioturbation and metabolic activities.

*Diporeia* is also an important food for Great Lakes fish. Primary predators include alewives (*Alosa pseudoharengus*), smelt (*Osmerus mordax*), deepwater sculpin (*Myoxocephalus thompsoni*) (Evans *et al*. 1990) and the commercially important lake whitefish *Coregonus clupeaformis* (Henderson and Paine 1988). Being abundant and high in lipid content, *Diporeia* is important in the transfer of energy, and organic contaminants, from the sediments to the fish community.

It has been suggested that *Diporeia* provides a direct link between the spring diatom bloom and fish in large lakes (Gardner *et al*. 1990), apparently because it feeds directly on diatoms after they settle to the lake bottom. Evans *et al*. (1990) noted that fragments of the diatoms *Cyclotella* spp. and *Melosira* spp. were the most common biological remains found in *Diporeia* guts. The frequency of full guts has been reported to be highest in the spring (Quigley 1988, Dermott and Corning 1988) and the lipid content of *Diporeia* increased after the spring diatom bloom in Lake Michigan (Gardner *et al*. 1985, 1990). These observations imply that *Diporeia* is largely dependent on energy from freshly sedimented diatoms.

Other reports suggest that *Diporeia* may have a different and more flexible diet. Marzolf (1965) found a strong correlation between the abundances of amphipods and bacteria in sediments from southern Lake Michigan. Siegfried (1985) attributed part of the very high production of *Diporeia* (nearly 15 g/m²/yr) at the south end of Lake George, USA, to detrital inputs from the nearby littoral zone. Littoral primary production may also be at least locally significant in offshore regions of larger lakes (Edsall *et al*. 1991).

The stable carbon isotope (¹³C/¹²C) signatures of planktonic and benthic algae are often quite different (Hecky and Hesslein 1995), so should be useful in evaluating the relative importance of these two
sources of energy to Diporeia. It is hypothesized here that dislodged epilithic algae would be an important component in the diet of Diporeia. To test this idea, and to more clearly define the biology of one of the most important benthic organisms in Georgian Bay, population dynamics, production rates, lipid content, and gut fullness for Diporeia were estimated at two depths in Colpoys Bay in southwestern Georgian Bay. Stable isotopes of carbon and nitrogen were analyzed in an attempt to define the ultimate sources of energy for this population.

MATERIAL AND METHODS

Study Sites, Sampling, and Analytical Methods

Diporeia were collected with an Ekman grab (0.0225 m²) biweekly from May through November 1992 and March to July 1993, at 30 m depth off Mallory Beach (44° 48′ N, 81° 04′ W), and from July to November 1992 and May to July 1993, at 50 m off Gravelly Point (44°45′ N, 81°07′ W) (Fig.1). Thin ice made it impossible to reach the 30 m or 50 m depths in March 1993, so Diporeia were collected from depths of 20 to 25 m off Mallory beach. Five replicate samples were randomly taken at each depth on each sampling date, and preserved in 4% formaldehyde in the field. In the laboratory, Diporeia retained on 200 µm aperture netting were transferred to 70% ethanol for use in estimating production dynamics and gut fullness.

Diporeia for isotope and lipid analyses were collected on the same schedule using a dredge with a 500 µm aperture mesh collecting bag. In the field, amphipods were sorted from the sediment, placed in closed cages inside a cooler, and kept alive for 48 h to allow gut clearance, then stored frozen. One–third of the animals in each collection were dried for stable isotope analyses without further treatment; lipids were extracted from the remaining individuals prior to stable isotopes analyses. Potential foods for Diporeia were detritus from three major sources: epilithon scoured from rocks in shallow water, sedimenting pelagic particulate organic matter (POM), and allochthonous material of terrestrial origin. Epilithon samples consisted of material (algae, bacteria, and associated microbiota) scraped from rocks collected from depths of 0.5 to 1 m. The filamentous portion of this film often grows to a thickness of 2 cm or more during calm weather, then is scoured from the rock surfaces during storms. Samples collected along a steep rocky slope in Georgian Bay (Duthie and Jones 1990) suggest that this material is deposited in deeper water (D.R. Barton, unpublished data) where it would be available to Diporeia. Water for isotopic analysis of particulate organic matter (POM) was also collected on a monthly basis from May through October 1992 and March through August 1993, every 5 m from the surface to 30 m using a Van Dorn bottle. Large particles were removed by passing the water through a 40 µm aperture mesh prior to filtration. Three samples of 2 L of water from each depth were filtered through pre-combusted glass fiber filters (Whatman GF/F) using a peristaltic pump. Filters were frozen in the field. Each filter was washed with 10% HCL prior to isotope analysis.

Sediment samples were collected by scuba diving during the months of July, August and September 1992, along a 60 m transect line off Mallory beach beginning at the base of the rock area (3.5 m) to a depth of 25 m. A 10-cm long plexiglass core (5 cm i.d.) was used to collect sediment samples at 5 m intervals along this transect. Those cores were immediately placed upright in a cooler with dry ice in the field. At the University of Waterloo the first two centimeters of frozen water were discarded and the first centimeter of sediment was sliced off the top of the core and prepared for isotopic analysis.

Life Cycle and Production Estimates

Density was estimated from the numbers of Diporeia in all five replicate grab samples from each
sampling date. Preserved amphipods are often curved making body length measurements difficult, so maximum head dimensions (distance between the outer edges of the eyes (± 0.02 mm) were measured. Dry mass was estimated through linear regressions of the natural logarithm of dry mass on the natural logarithm of head dimensions. This relationship was based on 50 preserved animals comprising all size classes that were dried for 48 h at 60°C and weighed using a Cahn C-31 microbalance (model W/RS232). Head width (mm) was related to body length (mm) using the same 50 animals (carefully straightened and measured before drying), for comparison with other studies. Analysis of size frequency histograms allowed individuals to be assigned to seven size classes which were used to estimate production by the size-frequency method (Hynes and Coleman 1968, Hamilton 1969). Mean densities and mean individual weight were obtained for each size class. Mean biomass and production were then estimated for each size class, and total cohort production was the summation of all seven size classes. To obtain annual production these production values were corrected for the actual cohort production interval (CPI) (Benke 1979).

It should be noted that the estimates of production have not been adjusted for weight loss due to preservation. Such losses can range from 10 % to 40%, depending on the organism (Downing and Rigler 1984) but there do not appear to be any published conversion factors for Diporeia.

Lipid Extraction and Gut Fullness

Lipid extraction was performed on amphipods from dredge collections grouped by year class (ages 0+, 1+ and 2+) to estimate total lipid relative to dry weight (Gardner et al. 1985). Ten to 20 pre-weighed dried amphipods from each year class were individually placed in centrifuge tubes with 3 mL of solvent (chloroform and methanol (2:1)) and left to stand for 30 minutes, after which the material was centrifuged at low speed and the solvent with lipids was decanted. This process was repeated three times. After drying for 24 h the animals were re-weighed and the difference in weight expressed as percentage of dried mass. These lipid-extracted amphipods were subjected to stable isotope analysis.

Gut fullness was estimated for Diporeia from three of the five replicate grab samples used for production for the months of May through November 1992, and March through July 1993. Amphipods were cleared overnight in 10% potassium hydroxide solution. This treatment allowed observation of the alimentary tract, measurement of gut content length (mm) and location of gut contents (fore, mid and hindgut). Gut fullness was expressed as the length of the gut contents divided by the total length of the gut (Dermott and Corning 1988).

Stable Isotope Analyses

Stable isotopes in samples (1 to 5 mg dry weight) of epilithon, POM and Diporeia (age 1+ and 2+, both with and without lipid extraction) were analyzed at the Environmental Isotope Laboratory, Department of Earth Sciences, University of Waterloo, Ontario using a Fisons Instruments VG Isocrom-EA continuous flow mass spectrometer with an analytic precision of ± 0.2 ‰ for carbon and ± 0.3 ‰ for nitrogen. Isotope ratios are universally reported as the deviation per mil (%e, i.e., parts per thousand) from the international standard reference materials VPDB (Vienna Peedee belemnite) for carbon, and N2 in the atmosphere (Mariotti 1983) for nitrogen, as follows:

\[
\delta^{13}C = \frac{[^{13}C/^{12}C_{\text{sample}}]/\left(^{13}C/^{12}C_{\text{standard}}\right) - 1} {10^3} \tag{1}
\]

The δ values are measures of the ratios between the heavy and the light isotopes (\(^{13}C/^{12}C\) and \(^{15}N/^{14}N\)) for carbon and nitrogen, respectively. Increases in these values denote an increase in the amount of the heavy isotope component and a reciprocal decrease in the light component.

Mean values for density and biomass are reported as ± 1 standard error (S.E.).

RESULTS

Life Cycle

Inspection of size frequency histograms over the sampling period allowed discrimination of three distinct year-classes (Fig. 2). Diporeia less than 1 year old (age 0+) ranged from 1.5 to 3.5 mm in body length, age 1+ individuals were 3.5 to 4.5 mm, and adults (age 2+) were larger than 4.5 mm (size of the smallest brooding female). Post-reproductive mortality appeared to be high. The largest individual collected was 8.0 mm in total length, so might have been 3 years old.

Brooding females were found at 30 m on the first sampling visit in early May 1992, newly released amphipods (hatchlings) were found from 20 May to 22 July 1992, and spent females were found as late
FIG. 2. Size frequency histograms (body length in mm) in Ekman grab samples from Colpoys Bay during 1992 to 1993 at depths of 30 m (top) and 50 m (bottom). Lines indicate approximate separation of age classes.
as August 1992. In the following year at 30 m, brooding females were found during March and April, and hatchlings from March through May. Brooding females were collected from mid-May through June at 50 m, but no hatchlings were collected at that station at any time.

Density, Biomass, and Production

The mean monthly density of Diporeia varied from 304 individuals/m² (March 1993) to 2,008 individuals/m² (September 1992) at 30 m, and from 881 individuals/m² (June 1993) to 3,437 individuals/m² (October 1992) at 50 m (Fig. 3 a,b). The annual mean densities from July 1992 to July 1993, were 1,415 ± 157 individuals/m² and 811 ± 132 individuals/m² at 50 m and 30 m, respectively.

Monthly mean biomass mirrored density at both depths (Fig. 3 c,d). At 30 m the mean total biomass was lowest in March 1993 (0.14 g/m²) and highest in August 1992 (0.50 g/m²). At 50 m, lowest values occurred in August 1992 (0.36 g/m²), with the highest value in October 1992 (0.91 g/m²). During the period July 1992 to July 1993, the annual mean biomass of YOY was virtually the same at 30 m and 50 m. Annual mean biomass of juveniles at depths of 30 m and 50 m were, respectively, 0.17 ± 0.03 g/m²

FIG. 3. Monthly mean densities (top) and biomass (bottom) of the three age classes of Diporeia at depths of 30 m and 50 m in Colpoys Bay, 1992 to 1993.
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The mean biomass of adult Diporeia was considerably greater at 50 m (0.31 ± 0.04 g/m²) than at 30 m (0.05 ± 0.004 g/m²).

Production at 30 m was 0.50 g/m²/y, with a total annual mean biomass of 0.25 ± 0.04 g/m² and annual P/B of 2.0. At the 50 m site, production was 1.34 g/m²/y, biomass 0.67 ± 0.04 g/m² and annual P/B 2.0 (Table 1).

**Lipid Content and Gut Fullness**

Lipid concentrations (% dry weight) for the period of July 1992 to July 1993 averaged 37.3 ± 4.1% and 35.6 ± 4.1% at depths of 30 m and 50 m, respectively (Fig. 4). Although monthly mean lipid concentration varied throughout the study period, spring concentrations (March/April) were considerably higher than autumn (September/October). Overall, there was a significant increase in lipid content with body size; this was best described by a curvilinear relationship between lipid concentration and amphipod dry weight (n = 200, r² = 0.79; Fig. 5).

Gut fullness also varied considerably throughout the study period, but the mean gut fullness was the same at 30 m (45.1 ± 1.6%) and 50 m (44.3 ± 2.2%). Gut fullness generally declined from spring through September, then increased in autumn (Fig. 6.a,b). The frequency of empty guts throughout the study period was slightly higher at the 50 m station (22.9 ± 3.0%) than at 30 m (18.5 ± 3.2%).

**Carbon and Nitrogen Stable Isotopes**

The mean isotopic signatures of entire Diporeia (before lipid extraction) at 30 m and 50 m were very similar: δ¹³C at 30 m for the period of May 1992 to July 1993 averaged −31.3 ± 0.4‰; the corresponding value at 50 m was −32.7 ± 0.3‰ (July 1992 to July 1993) (Fig. 7). The means for δ¹⁵N at 30 m and 50 m were 6.4 ± 0.3‰ and 6.2 ± 0.3‰, respectively. Heavier signatures occurred at 30 m in April 1993 (8.0‰), the lightest in June 1993 (4.3‰). δ¹³C signatures were enriched following lipid extraction, generally by 1 to 2‰, but slightly more in spring and autumn. Seasonal changes were more evident at 30 than 50 m. Diporeia were more

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**TABLE 1. Annual mean densities and biomass (± S.E.), annual production, CPI, cohort P/B and annual P/B of Diporeia for the period of July 1992 to July 1993 at 30 m and 50 m in Colpoys Bay. na = not applicable.**

<table>
<thead>
<tr>
<th></th>
<th>30m</th>
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<th>50m</th>
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<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Age 0+</td>
<td>Age 1+</td>
<td>Age 2+</td>
<td>Total</td>
<td>Age 0+</td>
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<tr>
<td>Density</td>
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<tr>
<td>(ind/m²)</td>
<td>811 ± 132</td>
<td>362 ± 87</td>
<td>390 ± 49</td>
<td>59 ± 5</td>
<td>1415 ± 157</td>
<td>292 ± 87</td>
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<tr>
<td>Mean ind.</td>
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<tr>
<td>weight (mg/ind)</td>
<td>0.30 ± 0.01</td>
<td>0.07 ± 0.01</td>
<td>0.44 ± 0.01</td>
<td>0.81 ± 0.02</td>
<td>0.41 ± 0.01</td>
<td>0.09 ± 0.01</td>
</tr>
<tr>
<td>Biomass (g/m²)</td>
<td>0.25 ± 0.03</td>
<td>0.025 ± 0.01</td>
<td>0.172 ± 0.02</td>
<td>0.050 ± 0.01</td>
<td>0.67 ± 0.04</td>
<td>0.026 ± 0.01</td>
</tr>
<tr>
<td>Production (g/m²/y)</td>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
<td>1.34</td>
<td></td>
</tr>
<tr>
<td>CPI (days)</td>
<td>593</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>593</td>
<td>na</td>
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<tr>
<td>Cohort P/B</td>
<td>2.8</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>3.2</td>
<td>na</td>
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<tr>
<td>Annual P/B (y)</td>
<td>1.9</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>2.0</td>
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**FIG. 4. Monthly mean (± S.E.) lipid concentrations (% dry weight) in Diporeia at depths of 30 and 50 m in Colpoys Bay, 1992 to 1993.**
13C depleted than POM in all samples (Fig. 7 a,b). At 30 m, Diporeia became more 13C depleted from May through July 1992, then steadily more 13C enriched through October 1992. This trend was not observed during the shorter sampling period in the following summer. Seasonal or yearly changes were not evident at 50 m.

Despite the similarity in average δ13C signatures, entire Diporeia tended to be more depleted at 50 m than 30 m on any given sampling date (Paired t-test = 3.34, df = 6, p = 0.016) especially during summer and autumn of 1992. One-way ANOVA, followed by Tukey’s post-hoc test on data from March 1993 showed that the mean 13C-signatures of entire Diporeia collected at depths of 20, 25, 30, and 50 m to be significantly different from one another (F = 88.99, df = 3, 21, p < 0.001), becoming more depleted with increasing depth (Fig. 8). δ15N signatures did not vary systematically with depth.

The mean carbon isotope signatures of the potential food sources analyzed were significantly different from one another (One-way ANOVA, followed by Tukey’s post-hoc test: F = 8.91; df=2, 11; p = 0.005). Epilithon had the most enriched mean carbon signature (−22.3 ± 1.7‰), followed by POM (−25.7 ± 0.4‰) and allochthonous organic matter (−28.9 ± 0.6‰). Epilithon became 13C-enriched from spring (May to June, δ13C = −25‰ to −27‰) through autumn (September to October, δ13C = −20‰). Carbon signatures of POM in samples from the epilimnion, metalimnion and hypolimnion did not differ significantly (ANOVA: F = 0.561; df = 2, 109; p = 0.572), but seasonal changes were evident: POM became more 13C-enriched from July through October (Fig. 7). The average sediment carbon isotope value for the period of July to September 1992 was −24.6 ± 0.2‰. These values did not vary temporally or with depth.

δ15N values were similar among these sources of organic matter, with means ranging from 1.4 ±
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1.3‰ (allochthonous leaves) to 2.9 ± 0.4‰ (surficial sediment).

Carbon signatures of entire Diporeia were more depleted than any of the potential foods on most sampling dates (Fig. 7), while nitrogen signatures (Fig. 8) suggested that amphipods were 1 to 1.5 trophic levels above the potential primary producers. Diporeia's δ¹³C values roughly tracked those of POM in both years.

**FIG. 6.** Monthly mean gut fullness (as % of individuals) of Diporeia at depths of 30 m (a) and 50 m (b). Number of animals is indicated above each bar.

**FIG. 7.** δ¹³C (mean ± S.E.) of Diporeia before (solid circles) and after lipid extraction (open circles) and particulate organic matter (POM, squares) at depths of 30 m (top) and 50 m (bottom).

**DISCUSSION**

Life Cycle and Production Dynamics

The basic life cycle of Diporeia in Colpoys Bay was similar to that reported from other areas in the Laurentian Great Lakes (Johnson and Brinkhurst 1971, Dermott and Corning 1988). The majority of Diporeia had a life cycle of 2 years but a few survived up to 3 years at the 30 m depth. Similar variability is common among other Crustacea (crayfish; Corey 1988). At the 30 m site, reproductive activity took place during late winter and early spring, and recruitment to age 0+ was still occurring in May 1993. Brooding females were found at 50 m throughout the month of June but no newly released age 0+ were collected; larger age 0+ amphipods were present in June and early July 1993. Densities
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increased from spring through late summer, but were lower in 1993 than in 1992. Gut fullness was somewhat greater and growth was most rapid in spring (May and June) and autumn (October and November).

The higher densities of Diporeia at 50 m than at 30 m are also consistent with bathymetric distributions reported from other portions of the Great Lakes (Robertson and Alley 1966, Nalepa 1987). Diporeia seems to prefer temperatures < 11°C (Siegfried 1985, Johnson 1988). Although measured bottom water temperatures in Colpoys Bay were always < 7°C at depths of 50 m (K.R.R.A. Guiguer, unpubl. data), temperatures were much more variable at 30 m. Frequent, strong westerly winds result in internal seiches which change the depth of the thermocline on a daily or even hourly basis (Tremain 1997). The lower density of Diporeia at 30 m likely reflects this thermal variability.

The higher densities of Diporeia at 50 m resulted in greater mean annual biomass and production for the period of July 1992 to July 1993. The age structure of the population at 50 m was unusual in that age 0+ were the least abundant size class. Johnson (1988) suggested that some adults migrate to shallower depths to release their young and observations during this study indicate that this may also occur in Colpoys Bay. Adult Diporeia were collected at depths of 25 to 20 m in March just prior to reproduction, and newly released young were found only at 30 m. If newly released Diporeia spend some time at shallower depths and start to migrate to deeper areas in mid to late summer as water temperatures rise, this would explain the occurrence of maximum densities of age 0+ amphipods in September at 30 m and in October at 50 m.

Overall, age 1+ amphipods dominated production at both sites in Colpoys Bay. Production at depths between 25 and 55 m in South Bay (Lake Huron) was estimated to be 1.15 g/m²/y (Johnson 1988), very similar to the mean production at the sites in Colpoys Bay (0.92 g/m²/y). These values are about half those reported by Siegfried (1985) from a depth of 32 m at the north end of Lake George.

Seasonality of Gut Fullness and Lipid Levels

Regardless of depth, Diporeia in Colpoys Bay did not fast during summer, although relative gut fullness was least in September at both 30 m and 50 m. Seasonal changes in lipid levels generally mirrored feeding intensity, with a lag of 1 month. A positive and significant relationship was established between lipid concentration (lc) and gut fullness (gf) in the previous month: lc = 0.5425gc + 6.7927 (r² = 0.45, p = 0.01). Feeding activity explained 45% of the variance observed in lipid concentration. The minimum lipid concentrations observed in October 1992 were preceded by the lowest feeding rates in the previous month.

As in Lake Michigan (Quigley et al. 1989), lipid concentrations tended to increase with size; this was most evident for ages 0+ and 1+. Adult Diporeia in Colpoys Bay seem to stabilize their lipid content after reaching 1.3 mg individual weight. Although sex ratios were not recorded, the adult amphipods almost certainly included both males and females at all stages of the reproductive cycle. This would account for much of the scatter in Figure 5 as adult male Diporeia have significantly less lipid than do females (Quigley et al. 1989), and females appear to stop feeding upon maturation.

Stable Isotopes

As a rule it is assumed that there is very little difference between the stable carbon isotope ratio of a
consumer and its main food source (DeNiro and Epstein 1978, Fry and Sherr 1984), although some studies have reported a slight (1‰) enrichment in $^{13}$C between trophic levels (Rau et al. 1983, Hobson and Welch 1992). When different food sources exhibit distinct $\delta^{13}$C values, the carbon isotope value of a consumer is indicative of the average $\delta^{13}$C of the carbon source, and organisms feeding on multiple sources will have intermediate values weighted according to the relative contribution of each source.

It is generally assumed that *Diporeia* feeds primarily on freshly sedimented organic matter, particularly diatoms (Quigley 1988, Dermott and Corning 1988). *Diporeia* displayed an isotopic seasonality somewhat similar to pelagic POM, but its signatures were $^{13}$C-depleted relative to POM on nearly all sampling dates. In part, this reflects the high lipid content of *Diporeia* and the strong fractionation of carbon isotopes that occurs in the formation of these compounds (DeNiro and Epstein 1978). Lipid-rich organisms tend to have low overall $\delta^{13}$C (Tieszen et al. 1983), so temporal differences in lipid content will cause fluctuations in $\delta^{13}$C of an animal that are not directly related to changes in diet.

Removal of the lipid fraction from the amphipods resulted in isotopic values which were enriched by 1 to 3‰, but most were still depleted relative to POM. A similar pattern was observed in Lake Ontario where carbon signatures of *D. hoyi* also increased slightly as the season progressed, but remained consistently below values of epilimnetic POM (Leggett et al. 1999).

Three hypotheses may explain those results. First, alteration and degradation of organic matter while sinking to the lake bottom can modify the overall character of sedimented organic matter, so isotopic signatures at the water-sediment interface might be different from the original source. Second, hypolimnetic algae should be depleted relative to epilimnetic algae, because they have access to more biogenic CO$_2$ and lower photosynthetic rates, allowing for greater discrimination against $^{13}$C (MacLeod and Barton 1998). Phytoplankton densities in the hypolimnion of Colpoys Bay increase during mid to late stratification and are dominated by Bacillariophyceae, followed by Cryptophyceae and Chrysophyceae (Maly 1992). However, samples of POM from the hypolimnion were slightly $^{13}$C-enriched relative to epilimnetic POM.

A third hypothesis is that *Diporeia* assimilate substantial quantities of bacteria from the surficial sediments where they normally burrow. This is not a new idea: Marzolf (1965) demonstrated a strong correlation between the abundances of amphipods and bacteria in sediments in southern Lake Michigan. In lake sediments the $\delta^{13}$C of biogenic methane ranges from $-52$ to $-61‰$ (Woltemate et al. 1984) suggesting that methane-oxidizing bacteria should be highly depleted. The highest rates of methane oxidation normally occur during summer stratification in the lower metalimnion (Wetzel 1983). It is possible that bacteria growing at low temperatures on sedimented organic matter have an essentially unlimited source of carbon, so are able to discriminate strongly against $^{13}$C. Preliminary laboratory data support this idea (K.R.R.A. Guiguer et al., unpublished). If *Diporeia* rely on a combination of freshly sedimented POM and bacterial carbon throughout the year, this would yield the observed isotopic signatures.

The different seasonal changes in the $\delta^{13}$C of *Diporeia* at 30 m and 50 m confirm the original hypothesis that littoral epilithic primary production is more important to the diet of amphipods in shallower water. *Diporeia* became more $^{13}$C-enriched through the summer of 1992 at 30 m, but changed little at 50 m. The pattern was similar in 1993, but much less obvious due to the shorter sampling period. If these signatures were simply tracking pelagic POM, the seasonal changes should have been the same at both sites. Little is known about the production and fate of epilithic algae in the Great Lakes, but dislodgement and transport must be strongly affected by weather. This could account for the somewhat less $^{13}$C-depleted signatures of *Diporeia* at 30 m in 1993, relative to 1992. Maly (1992) reported that hypolimnetic phytoplankton densities increase during mid to late stratification, and that littoral diatoms accounted for up to 26% of material caught in sediment traps, especially during periods of stormy weather. Deposition of littoral benthic algae at the bottom of steep slopes in deep water has been reported in the Great Lakes (Edsall et al. 1991) and Mediterranean Sea (Bavestrello et al. 1991). The slope of the bottom of Colpoys Bay is fairly gentle, so the rate of deposition of dislodged material would be expected to decrease with increasing distance from shore.

These results show that *Diporeia* in this deep, oligotrophic, temperate system feeds more or less continuously throughout the open-water season. There is no need for *Diporeia* to starve during sum-
mer since pelagic inputs are more than enough to support the population in Colpoys Bay. Its basic diet is probably bacteria growing on sedimented organic matter, but it feeds preferentially on freshly deposited diatoms when they are available. The importance of littoral diatoms appears to increase with proximity to shallow water.

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