Determination of Colpoys Bay (Georgian Bay) benthic community trophic structure and energy flow using stable isotopes and secondary production

by

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Abstract

In this thesis the energy flow through the benthic food web of an oligotrophic lentic system, Colpoys Bay, in Georgian Bay was described. Abundance, biomass, secondary production, species richness and diet of invertebrates in three contrasting habitats along a depth gradient were compared. Estimates of diet, obtained using stable isotopes of carbon and nitrogen and secondary production were combined to determine the dependence of each benthic community on autochthonous littoral versus pelagic sources and/or allochthonous inputs.

Among the three main zones studied, animals occupying charophyte beds made the most significant contribution (51.8%) to the total production of the bay. The site within the shallow littoral zone was more productive on a per unit area, but this habitat is found in less of the basin, so it accounted for slightly less secondary production than the charophyte bed. The profundal zone is largest in terms of area but supports a more restricted fauna and contributed only 9% of the benthic secondary production. The drastic decline at deeper depths (i.e. below the photic zone) suggests that benthic primary production determines the secondary production of Colpoys Bay. This study emphasized that a significant proportion of energy transfer between primary production and fish is through the benthic food chain.

The linkages between dissolved inorganic carbon (DIC) and particulate organic matter (POM) were investigated in the pelagic zone of Colpoys Bay. The results suggest that the temporal fluctuation in pelagic POM $\delta^{13}C$ is influenced by algal species changes in response to changes in the type (CO_2 or HCO_3^-) of aquatic DIC and seasonal intrusion of littoral matter. Inferences on the variation observed in

the zooplanktonic community were also made. The general trend in the isotope signatures of zooplankton followed those of POM.

The trophic structure of macroinvertebrate communities in the littoral (≤ 15 m) and profundal (≥ 30 m) zones was assessed using stable isotopes of carbon and nitrogen. Energy sources included periphyton, macrophytes, POM and allochthonous organic matter. Spatial and temporal isotopic variation were reported at the primary producer level and consequently primary consumers. Periphyton was the main energy source for benthic communities within littoral areas of Colpoys Bay. Littoral macrophytes, macroalga and allochothonous matter are not used as energy sources for invertebrates. Regardless of what feeding category an invertebrate was assigned, the vast majority of them are strongly dependent on the epilithic biofilm for food supply. This dependence on the epilithic biofilm diminishes with increasing water depth. Invertebrates at the sub-littoral site relied on a combination of epilithon, epiphyton and POM; those in the profundal region were dependent on autochthonous pelagic organic matter.

In order to assess the trophic role of *Diporeia hoyi* in Colpoys Bay, amphipods were collected from depths of 30 and 50 m These were used to examine the life cycle dynamics, estimate production, stomach fullness, lipid content and stable isotopes of carbon and nitrogen. In agreement with previous studies, *D.hoyi* collected in areas deeper than 30m seem to rely on pelagic primary production for energy sources as shown by increased feeding activity during spring followed by increased lipid content. Stable carbon isotopes showed that *D.hoyi* will also use littoral epilithon when it is available.

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Thanks

Dedication

This thesis is dedicated to my children, Camilla and Victor,

Love Mom

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Chapter 1: General introduction

Georgian Bay and the North Channel, together with Saginaw Bay and the main body of Lake Huron comprise the second largest of the Laurentian Great Lakes in total surface area. Georgian Bay and North Channel, with surface areas approximately 15 000 and 4 000 km^2 respectively, could very well be considered as large lakes in their own right (Herdendorf 1982; Munawar 1988).

As with many fisheries in Ontario, the sport fishery in southern Georgian Bay has become increasingly popular over the past decade. This area has long been a preferred destination for anglers due primarily to the diversity of the fishery. Anglers can fish for natural and stocked salmonids including chinook salmon (*Oncorhynchus tshawytscha*), brown trout (*Salmo trutta*), and lake trout (*Salvelinus namaycush*) and splake (*Salvelinus* sp.), naturalized species such as rainbow trout (*Oncorhynchus mykiss*), as well as indigenous species such as yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieu*), and lake whitefish (*Coregonus clupeaformis*) (Mohr and Nicol 1998).

In the Great Lakes of North America, as in other lake systems, zoobenthic populations represent a major link between primary producers and fish. These organisms may feed on detrital material settled from the water column and, in turn, are eaten by most species of fish. Published data on macroinvertebrate production for the Great Lakes is lacking or dated. Johnson and Brinkhurst (1971) estimated production of several taxonomic groups of benthic invertebrates for Lake Ontario. Johnson (1988) studied production of a single species (*Diporeia hoyi*) in Lake Huron. More recently Johnson et al. (1998) inferred production of *Mysis* sp. and *D.hoyi* from

patterns of fish predation in Lake Superior. Information about zoobenthic production of large lake systems is essential to four main conceptual themes: 1) elucidation of energy or material transfers within communities and ecosystems; 2) management of aquatic resources; 3) detection of pollution effects and 4) formation of general theories of biological productivity.

To date there has been no estimation of benthic invertebrate production in Georgian Bay. Chapter two of this thesis is an assessment of the production of benthic invertebrates along a depth gradient (i.e. littoral $\leq$ 20 m and profundal $\geq$30 m benthic communities) in Colpoys Bay, southern Georgian Bay.

Several features are common to most large lakes. They tend to be deep and have long water retention times; biogeochemical cycling is dominated by internal regeneration to a greater extent than by external inputs; and pelagic communities are thought to be more important than both littoral and bottom communities in the overall production process (Tilzer 1990). A common feature of large lakes is their two unique habitats: their remote offshore regions, and their wave-swept surf zones. The composition of the fauna in each of these habitats appears to be influenced more by physical factors that are related to the lake's size, wave action or distance from shore, than by the lake's water chemistry (Barton and Carter 1982). The coastal regions of lakes are characterized by a variety of littoral habitats, which support rich and abundant benthic communities, while the more uniform conditions in the profundal support a much less diverse benthic fauna.

Several factors can affect production rates of invertebrates in different habitats of a lake. Food availability will play a key role. In lakes, energy sources available for

littoral communities include allochothonous matter, phytoplankton, periphytic algae and macrophytic vegetation, whereas phytoplankton are usually considered to be most important offshore. Spring algal blooms can provide an important food source for profundal benthos (Gardner et al. 1985). With so many different sources of organic matter the analysis of specific pathways of energy flow in benthic food webs is very difficult. In this context stable isotopes can be valuable tools.

Stable isotopes have received attention recently in the field of ecology for its potential as a tracer of energy in ecological systems. Elements are a collection of isotopes, atoms with similar chemical properties but differing in nuclear structure. A small fraction of atoms of an element will have more neutrons than protons in the nucleus and may be described as radioactive or stable isotopes of the element. Stable isotopes react chemically in essentially the same manner as other isotopes of a particular element, but with subtle differences due to the difference in atomic weight. It is these differences in weight between isotopes that have allowed them to be used as tracers in biological reactions and as indicators of reaction conditions (Peterson and Fry 1987). Early investigations of the relative proportions of heavy and light isotopes contained in materials formed through different processes demonstrated changes in the relative proportions of heavy and light isotopes compared to source materials (Biegeleisen and Wolfsbeerg 1958). Further investigation has led to progress in understanding the differences in behavior of heavy and light isotopes with respect to chemical kinetics and bond energies. Ratios of heavy to light isotopes are expressed as δ signatures in units per mil ($^{o}/_{oo}$), which is the parts per thousand difference from a standard. An example is given for carbon:

$$\delta^{13}C = [(^{13}C/^{12}C_{sample})/ {}^{13}C/^{12}C_{standard}) - 1] \times 10^3$$

If the ^{13}C to ^{12}C ratio in the sample is lower than the ratio in the standard, the δ value will be negative. In comparing two samples, a more positive δ value indicates heavy isotope enrichment.

Natural stable carbon isotopes (^{13}C and ^{12}C) abundance in the aquatic environment has been used to quantify and characterize the carbon flux at different trophic levels (Fry 1991, Gu et al. 1997) and to identify organic carbon sources for animals (Haines and Montage 1979). Stable carbon isotope analysis (SCI) is a powerful technique for the elucidation of energy flow through consumer links in food webs provided that the sources of organic matter are isotopically distinct. The determination of primary energy sources (e.g. benthic vs pelagic) is possible because there is very little isotopic fractionation between an organism and its main food source, usually organisms are enriched in the heavier isotope by 1‰. The concentration and isotope signature of available dissolved inorganic carbon (DIC) determine the $\delta^{13}C$ of primary producers and organisms feeding on those primary producers. Chapter three is an overview of the factors that determine the isotopic signatures of DIC as well as particulate organic matter (POM) in Colpoys Bay.

Stable nitrogen isotopes (^{15}N and ^{14}N) have been utilized to determine the trophic position of lentic animals. Due to the relative retention of ^{15}N over ^{14}N, animals are usually +2 to +4 ‰ more enriched than their diets (Minigawa and Wada

1984, Owens 1987, Peterson and Fry 1987). By plotting the $\delta^{13}C$ vs. $\delta^{15}N$ from the various species inhabiting an ecosystem, a food web can be mapped. The trophic status of each organism can be inferred on the basis of where it lies on this plot in relation to the other organisms (Fry 1991). Hence, the use of stable isotopes of both carbon and nitrogen in food web studies can allow the identification of primary food sources, and pathways through which food energy is channeled. In chapter four I used the dual stable isotope approach to determine which sources of energy are most important to the dominant benthic macroinvertebrates in different habitats of Colpoys Bay, and also to describe the trophic structure within each habitat.

Diporeia spp 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 m^{-2} (Nalepa et al. 1985). *Diporeia* spp 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, *Dioporeia* is important in the transfer of energy, and organic contaminants, from the sediments to the fish community.

In the Great Lakes up to the present, there has been no study combining production rates and population dynamics with lipid content, gut fullness and stable isotopes of carbon and nitrogen to describe the energy flow through *Diporeia*. In chapter five I clarify the trophic status of *Diporeia* and its role as a link between planktonic, periphytic or allochthonous primary production and fish. The practical

application of this study is in examining relationships among growth, production and food supply and the possible impact on fish production.

Chapter six is a summary of the findings in the three previous chapters. The relationships among energy sources, trophic links and rates of benthic secondary production, as well as their role in fish production, are discussed.

Chapter 2: Description of the benthic community structure, life cycle dynamics and secondary production.

Abstract

This study was done to estimate benthic macroinvertebrate production along a depth gradient in Colpoys Bay, Georgian Bay. The more diverse and abundant littoral benthic community was dominated by collector-gatherers insects gradually changing to deposit-feeding invertebrates further offshore.

Among the three main zones studied, animals occupying charophyte beds made the most significant contribution (51.8%) to the total estimated macrobenthic production of the bay. The site in the shallow littoral zone was more productive per unit area, but such habitat is found in less of the basin, and so accounted for slightly less secondary production than the charophyte bed. The profundal zone is largest in terms of area but supports a more restricted fauna and contributed only 9% of the benthic secondary production.

Zoobenthic biomass estimates in Colpoys Bay were twice those reported for zooplankton in Georgian Bay. Several fishes are known to rely on macrobenthos in this system. Those include common white suckers, the commercially important lake whitefish, other deep-water ciscoes, and burbot. This suggests that a significant proportion of energy transfer between primary production and fish is through the benthic food chain.

2.1- Introduction

A major aspect of understanding the dynamics of aquatic ecosystems is quantification of energy and organic matter flow. Complete energy flow analyses require the determination of production at all trophic levels starting with primary production of autotrophs. Everything beyond the autotrophs falls in the realm of secondary production. Production is the most comprehensive representation of a population's success because it is a composite of other components of success: density, biomass, individual growth rate, reproduction, survivorship and development time (Benke 1993). The rate of secondary production within a system can be affected by several environmental factors. Among the most obvious environmental aspects directly affecting an animal's growth rate are temperature, food supply, substrate composition and dissolved oxygen concentration. Plant and Downing (1989) found a strong positive correlation among the mean annual biomass, individual body mass, annual production and mean annual water temperature.

When studying benthic secondary production in lakes it is necessary to account for the bathymetric variation in community structure. It is well known that density and diversity of benthic invertebrates usually decrease with distance from shore (Brinkhurst 1974). Because of great substrate heterogeneity and high concentrations of oxygen, the littoral zone allows for higher animal diversity than the more homogeneous profundal zone. Similarly, benthic invertebrates in the littoral zone are thought to be more productive and have higher production to biomass ratios.

In the Great Lakes of North America, as in other lake systems, zoobenthic populations represent a major link between primary producers and fish. Benthic organisms may feed on detrital material settled from the water column and, in turn, are eaten by most species of fish. Earlier studies on benthic invertebrates have focused to a large extent on community structure and distribution (Schneider et al 1969, Mozley & Allen 1973, Wesley 1972, and Barton & Hynes 1978), but there are also lake-wide estimates of macroinvertebrate biomass for Lake Superior (Cook 1975), Lake Huron (Shrivastava 1974) and Lake Michigan (Nalepa 1989). More site-specific specific data are available for Lake Ontario (Johannsson et al. 1985) and Lake Erie (Dahl et al. 1995). Published data on macroinvertebrate production for the Great Lakes is lacking or dated. Johnson and Brinkhurst (1971) were the first to report on production of several taxonomic groups of benthic invertebrates in Lake Ontario. Johnson (1988) estimated production of a single species (*D. hoyi*) in Lake Huron. More recently Johnson et al. (1998) estimated production of *Mysis* sp. and *D.hoyi* from patterns of fish predation in Lake Superior. To date there are no estimates of benthic invertebrate production in Georgian Bay. It is the purpose of this chapter to assess the production of benthic invertebrates along a depth gradient in Colpoys Bay, Georgian Bay.

2.2- Description of Colpoys Bay and the study sites

This study was conducted in Colpoys Bay, on the western shore of Georgian Bay. Colpoys Bay is a narrow inlet 1.8 to 18.2 km wide with a surface area of 37.9 km^2 along a 24 km NE-SW axis, partially separated from Georgian Bay proper by three islands (Fig. 2.1). The town of Wiarton (81°08'W, 44°45'N), located at the most southern perimeter of Colpoys Bay, has two marinas and several public docks. The town of Colpoys Bay (81°08'W, 44°47'N) also has a public dock. Considered an oligotrophic ecosystem (Maly 1992), basin geology and inputs from Georgian Bay and the atmosphere determine the water chemistry of Colpoys Bay. Runoff from the Niagara Escarpment (sandstone, shale and dolostone) produces a hard water environment with alkalinity levels as high as 75 mgL^{-1} (Weiler 1988). Total conductance is about 194 µS and pH 7.8 (Farwell 1993). The mean total phosphorus concentration prior to the stratification period is 5.2 ug/L, and 3.2 ug/L during stratification (Maly 1992).

In the coastal areas of Colpoys Bay, bottom-water temperatures during spring of 1992 (May and June) were 4 – 5°C, reaching a maximum of 15 – 20°C in August. By mid-November, temperatures were the same as spring (Table 2.1). Lakewide stratification occurred in early July and persisted until mid-October. The depth of the top of the thermocline varied between 15 m in July to about 30 m in September 1992. In the deeper areas (>30 m) bottom temperatures were usually around 4°C. During the winter of 1993, Colpoys Bay remained completely ice-covered from January until the end of March.

The area of the bay shallower than 9 m is 7.5 km^2, of which one third (2.5km^2) is covered by rocks and the rest is sand sparsely covered with macrophytes (Saffran 1993). The rocky shoreline and littoral fringe supporting *Cladophora glomerata* and associated epiphytes gives way to a narrow transitional zone of coarse sand and gravel, becoming progressively finer offshore. The most abundant aquatic macrophytes in Colpoys Bay are Characeae (*Chara globularis*, *Chara vulgaris*, *Nitella flexilis*, and *Tolypella nidifica*), covering an area of about 10.1 km^2 to a water depth of ca. 24 m (Farwell 1993). The most frequently occurring vascular macrophytes are *Potamogeton* spp, *Myriophyllum sibircum* and *Elodea canadensis*, limited to shallow depths (≤ 5.0 m). The deep portion of the bay has an area of about 20.3 km^2.

Vascular macrophyte stands in the southern region of the Bay are limited to depths of ≤ 5 m. Peverly and Brittain (1978) reported that *Myriophyllum* and *Potamogeton* species occurs throughout the Great Lakes at depths between 1 and 6 m where the sediments were soft, fine-textured and high in organic content. Spence (1982) concluded that substratum type and water movements probably determine the upper limit of vascular macrophytes, and placed the lower limit at 6.5 m. The difference in the vertical distribution of Characeae and vascular macrophytes may reflect anatomical differences. Wetzel (1975) hypothesized that due to the presence of intercellular gas systems (lacunae), vascular macrophytes are more sensitive to the increase in pressure with depth, but pressure was not considered a limiting factor in the depth distribution of non-flowering plants (cryptogams) such as Characeae (Andrews et al. 1984b)

Invertebrates were collected from three main sites (Fig 2.1). Site A (81°08'W, 44°46'N) was located near the western tip of the bay at a depth of 5 m and supported scattered macrophytes. Site B at Mallory beach (81°04'W, 44 °47'N) also situated along the western side about 6 km north of site A, was sampled at depths of 15m and 30 m. Benthic vegetation consisted of charophytes (at depths ≤ 24 m). The offshore site C (81°03'W, 44o49'N), approximately 6.5 km north of site B near Gravelly Point, supported no macrophytes at depths of 50m where invertebrates were collected. At site A (5 m) 75% of the sediment was fine sand and silt (< 0.125 mm), with small amounts of sand (0.125 – 0.5 mm) and a trace of gravel (> 2.00 mm). At site B (15 m and 30 m) fine sand and silt made up 95% of the sediment, with no gravel or coarse sand (Farwell 1993). The sediment at site C was also fine sand and silt.

2.3 Material and methods

2.3.1- Sampling scheme

Biological sampling started in May 1992 at sites A and B and in July 1992 at site C. Invertebrates were collected biweekly from May through November 1992, once in March and April 1993, and biweekly from May to July 1993. Appropriate sampling depths were located with the aid of an echo sounder. An Ekman grab (0.0225 m^2, height = 15 cm) was used to collect 5 samples from each depth, except in March 1993, when ice conditions made it impossible to reach the 50 m depth. Samples were

rinsed through a 200-μm aperture mesh in the field and preserved in 10% formalin. Only the Ekman grab samples that were at least half full (i.e., sediment penetration ≥ 7.5 cm) were retained. In the laboratory at the University of Waterloo, samples were rinsed with water through a 100-μm aperture net. The animals from each of the 300 grab samples were sorted from associated detritus under 12x magnification and stored in ethanol. All invertebrates were enumerated at the lowest practical taxonomic level, measured (maximum sclerotized head dimension or total body length ± 0.02mm), and stored in 70% ethanol.

The relationships between dry mass and head/body dimensions for each of the common taxa were established using animals from the stored samples. Head widths were measured for 25 to 50 specimens for each species of Insecta. I measured the distance between the outer edges of the eyes of amphipods, and body length for isopods. Shell length was used for bivalves. These individuals were then oven-dried for 48 h at 60°C and weighed (± 1 μg) using a Cahn C-31 microbalance (model W/RS232). The animals used covered the complete range of head or body dimensions found for each taxon of Colpoys Bay. Equations were developed using linear regressions of the natural logarithm of dry mass on the natural logarithm of head/body dimension (Downing and Rigler 1984). These equations were of the form:

Ln (dry mass) = a + b*Ln (head/body dimension)

where: a and b are regression coefficients for each taxon

2.3.2- Estimation of secondary production and analyses of community structure

Given that only some taxa produced recognizable cohorts, I applied the size frequency, or average cohort method (Hynes and Coleman 1968, Hamilton 1969) to be consistent in estimating production of all taxa. Each individual taxon was assigned into size classes, then mean annual density and mean individual weight for each class were determined. These values were used for estimation of annual mean biomass and annual production. Production estimates were corrected for the actual cohort production interval or CPI in days (Benke 1979) which is dependent on the voltinism (number of generations per year) of each species. When a species produced more than one cohort a year (i.e. spring and autumn cohorts) I used the mean CPI to estimate production. Unfortunately, gastropods shells were severely digested by formalin making identification and separation into size classes impossible, so I measured monthly biomass and used published P/B to estimate production method (Downing and Rigler 1984).

Diversity of sites was estimated as $H = - \sum P_i \ell_n P_i$, where P_i = proportions of total individuals in the ith taxon. Invertebrates were assigned to functional feeding groups according to Merritt and Cummins (1996) to facilitate comparison of the trophic structure of the benthic communities among sites.

The significance of temporal (monthly) variation in the densities distribuiton of the major groups was tested through one-way ANOVAs. The results of five

replicate ekmans were log-transformed and used in each month in the SYSTAT spreadsheet.

2.4- Results

2.4.1- Diversity and Density

From May 1992 to July 1993, a total of 69 taxa was collected and identified from all sites. Number of taxa decreased with depth (Table 2.2). Fifty-five taxa occurred only at 5 m and/or 15 m, of which 24 taxa were exclusive to 5 m, and five exclusive to 15 m. Of the other 14 taxa, four occurred at all depths, six at 5, 15 and 30m, one only at 30m and three at 30 m and 50 m. Consequently, community diversity was highest at site A (H = 3.93) and lowest at site C (H = 0.98).

The most frequently collected invertebrates were Chironomidae, represented by 38 genera. Fourteen were common to both 5 m and 15 m depths, of which *Micropsectra* was the most frequently collected (Table 2.3). *Protanypus*, *Pagastiella* and *Heterotrissocladius* were found exclusively at 30 and 50m.

Crustaceans were second in frequency of occurrence. Isopods were the dominant. Crustacea at the two shallower depths: *Lirceus lineatus* was more abundant at 15 m and *Caecidotea intermedius* was more abundant at 5 m. The amphipod, *Diporeia hoyi* was the most frequently collected and abundant animal at depths ≥ 30m. At the shallow sites *Hyalella azteca* was more frequent and abundant than *Gammarus pseudolimneaus*. Gastropods were the most numerous Mollusca but were limited to shallower depths. *Pisidium compressum* was found at all four depths but was most

abundant at 5 m. Tubificidae and Naididae (Oligochaeta) occurred at all depths; Enchytraeidae and Lumbriculidae were found only at depths ≤ 15 m. The Order Trichoptera was represented by eight genera at depths of 5 and 15 m: *Mystacides* was the most frequent and abundant; *Polycentropus* was also very frequently caught, but only at 5 m. Six genera of Ephemeroptera were collected at 5 m; *Ephemera simulans* was the only species also found at 15 m.

Total invertebrate densities were highest at the littoral sites and decreased with increasing depth. Mean annual densities were: 22232 ind.m^{-2} (5 m), 10384 ind.m^{-2} (15 m), 2041 ind.m^{-2} (30 m) and 1862 ind.m^{-2} (50 m).

The relative abundance of the major groups of invertebrates also varied with depth. Trichoptera (1.4%) and Ephemeroptera (1.3%) were most common at the 5 m depth. Molluscs were most abundant slightly deeper in the littoral with relative abundances of 11.4%, 16.6% and 9.1% at 5 m, 15 m and 30 m, respectively. The relative abundance of chironomids decreased from 67% at 5 m to 54.8% at 15m, 13.1% at 30 m and 2.6% at 50 m.

Crustaceans (amphipods, isopods and a few mysids) exhibited the opposite trend, becoming more important with increasing depth: 12.9% at 5 m, 23.3% at 15 m, 54.5% at 30 m and 77.6% at 50 m. Oligochaetes also became relatively more important with depth: 5.9% at 5 m and 5.2% at 15 m increasing to 23.3% at 30 m and 19.8% at 50 m.

The most frequent feeding group collected was collector-gatherers (37.0%), followed by deposit-feeders (21.7%), shredders (17.3%), scrapers (9.5%), predators (7.7%) and collector-filterers (6.9%). Representatives of all functional feeding groups

were found at 5m (Table.2.4). Collector-gatherers (mostly chironomids and a few ephemeropterans) were numerically dominant (38.7%), followed by shredders (19.6% isopods and trichopterans) and deposit feeders (15.5%, amphipods and oligochaetes). Scrapers (gastropods and a few trichopterans) contributed 10.8%; collector-filterers and predators accounted for 7.83% and 7.6% of the invertebrates at this site.

At site B (15m) collector-gatherers were again the most common (37.6%), followed by shredders (20.3%, all isopods) and scrapers (10.4%, gastropods). Collector-filterers and predators were equally abundant with 7.1% and 8.6%, respectively. Deposit feeders increased in relative abundance (16.0%). At 30 m depth deposit-feeders (*D.hoyi* and oligochaetes) were dominant (74.5%). There were no scrapers or shredders at 30 m and few collectors-gatherers (8.6%, chironomids), but filterers (16.9%) were more abundant that at the shallower depths. The fauna at 50 m was dominated (83.2%) by the deposit-feeders (*D.hoyi*, tubificids and naidids), with some collector-gatherers (9.1%) and filterers (7.7%).

In general, invertebrate abundance increased towards autumn at depths ≥ 15 m, but declined at 5 m (Fig 2.2). One-way ANOVA indicated that at 5 m the densities of all groups vary significantly among sampling dates (Table 2.5). At 15 m the densities of all groups except Trichoptera varied significantly among sampling dates. The densities of amphipods were strongly affected by season at 50m and to a less extent at 30m. Temporal variations were significant Chironomidae at both sites depper sites (Table 2.5).

2.4.2- Benthic community life history, biomass and production

Twenty-seven taxa were collected in sufficient numbers to permit analysis of life histories (Table 2.6). Except for *Chironomus annularis* (univoltine) and *Micropsectra* (trivoltine), chironomids at shallow depths produced two generations per year and had shorter cohort production intervals (CPI) than chironomids at greater depths. Both Trichoptera were univoltine. The mayfly *Caenis* sp produced two generations during the study period. Most bivoltine insects emerged in early spring (April-May), and first instar larvae (spring cohort) were present by late spring and/or early summer (May-June). This cohort emerged in late summer or early autumn (August-September) and first instar larvae (fall cohort) appeared in September-October. Univoltine insects emerged throughout the open water season (spring through summer). Amongst the amphipods, *Hyallela azteca* produced two broods, *Gammarus pseudolimneaus* one and *Diporeia hoyi* had a two-year life cycle. The life cycle of *Pisidium* spp. was estimated trough information from the literature and the life histograms for Colpoys Bay. The data showed that it grew slowly with a three-year life cycle at all depths.

As expected, secondary production by benthic macroinvertebrates was greatest at the shallow sites, steadily declining with increasing depth. From July 1992 to July 1993, production at 5 m was 21.75 $g.m^{-2}.y^{-1}$ with crustaceans making up 52.5%, followed by chironomids (29.0%) and molluscs including the shell mass (17.2%). Likewise, the mean biomass of 4.1$g.m^{-2}$ was the highest amongst the study sites (Table 2.7a).

Production at 15 m was 15.9 $g.m^{-2}.y^{-1}$ of which crustaceans (mostly isopods) made up 48.5%, followed by chironomids (30.1%) and molluscs 21.4%, mean annual biomass was 3.7 $g.m^{-2}$. Production dropped sharply at 30 m to 0.64 $g.m^{-2}.y^{-1}$. The amphipod *D. hoyi* was responsible for 68.7%, followed by the bivalve *P. compressum* (21.9%) and two species of chironomids (9.4 %). The higher density of *D. hoyi* at the most offshore site (50 m) resulted in an increase in biomass (0.67 $g.m^{-2}$) and production (1.34 $g.m^{-2}.y^{-1}$). The average annual P/B declined from 5.4 at 5 m depth to 2.0 at 50 m (Table 2.7b).

Shredders (isopods) made up 44% of the production at 5 m and 25% of the biomass; they accounted for 39% of the biomass and 46% of the production at 15 m. *Lirceus lineatus*, common at both shallow sites, produced two generations at 5 m depth but only one at 15 m. The higher density at 15 m resulted in higher biomass but only a marginal increase in production so that the P/B was considerably higher at 5 m than 15 m. *Caecidotea intermedius* was also common at both sites and produced two cohorts at each site. The higher densities at 5 m yielded greater biomass and production (0.50 $g.m^{-2}$, 4.99 $g.m^{-2}\,y^{-1}$ and P/B = 9.9) than at 15m.

Collector-gatherers (mostly chironomids, a few Trichoptera and Ephemeroptera) accounted for 19% of biomass and 27% of production at the 5m site, and 8.7% and 16% of biomass and production, respectively, at the 15 m depth.

Among the gatherers common to both shallow sites, annual P/B were generally higher at 15m. Higher densities of fourth instar larvae of *Microtendipes* at 15 m and a shorter CPI contributed to higher production and higher P/B. Similarly, the shorter CPI for *Gillotia alboviridis* at 15 m resulted in a higher P/B than at 5m. *Polypedilum*

had virtually the same P/B at both sites (7.5 at 5 m and 7.7 at 15 m). *Cladopelma lateralis* found only at 15 m had the lowest annual mean biomass (0.002 $g.m^{-2}$). *Micropsectra*, the only chironomid to produce three cohorts, was much more abundant at 5 m and had virtually same CPI at both 5 and 15 m, hence the observed differences in biomass and production but similar P/B at both depths.

Amongst the gathering caddisflies, only *Mystacides* was frequent enough to estimate production. Fifth instar larvae occurred from June through mid-August 1992. First instar larvae were present mostly in July 1992, with a few in August and September. CPI for this taxon was estimated to be 275 days. Annual mean biomass was 0.013 $g.m^{-2}$, and annual production was 0.08 $g.m^{-2}.y^{-1}$ with annual P/B = 6.2. The gathering mayfly *Caenis* had two generations, one from May to September 1992, the second from August 1992 through May 1993. Annual mean biomass was 0.015 $g.m^{-2}$, production 0.12 $g.m^{-2}.y^{-1}$ and P/B = 12.

Collector-gatherers chironomids at 30m site were *Protanypus* and *Heterotrissocladius*. Neither was very abundant, and both produced one cohort during the study period. Together they accounted for 6.3% of the biomass and 9.4% of production.

Collector-filterers included species of *Pisidium* and the caddisfly *Polycentropus*. Together they made up 32.6% and 14.5% of biomass at 5 and 15 m, respectively. The percentage of production was 10.4% at 5 m, and 5.3% at 15 m. There were six species of *Pisidium*: *P. compressum*, *P. fallax*, *P. ferrugineum*, *P. lilljeborgi*, *P. nitidium* and *P. rotundatum*. Only *P. compressum* and *P. lilljeborgi* were present in sufficient numbers to estimate individual production. Although *P. compressum* occurred at all

depths, production could be calculated only for 5 m, 15 m and 30 m. A three-year life span seems to predominate and annual mean biomass and production were highest at 5 m, and lowest at 30 m. Accordingly the P/B was lowest at 5 m and highest at 30 m. *P. lilljeborgi* also had a three-year life cycle; production was estimated for 5 m and 15 m. Annual mean biomass was 0.70 $g.m^{-2}$ (5 m) and 0.42 $g.m^{-2}$ (15 m); estimates of production and P/B values were 1.13 $g.m^{-2}y^{-1}$ and 1.6 at 5 m, and 0.59 $g.m^{-2}y^{-1}$ and 1.40 at 15 m.

Deposit–feeders in Colpoys Bay included three species of amphipods, *Hyallela azteca* and *Gammarus pseudolimnaeus* in the littoral areas and *D. hoyi* at depths ≥ 30 m. Percentage contribution to biomass and production increased with increasing depth. *H. azteca* and *G. pseudolimneaus* accounted for 4.9% and 8.6% of biomass and production, respectively, at 5 m. *H. azteca* was the only amphipod at 15 m, making up 1.9% of biomass and 2.8% of production. *H. azteca* produced two major cohorts at both sites. A large pulse of individuals of the smallest size class occurred in April and May 1992 and a second pulse was observed in August/September 1992. CPI at both sites was estimated to be 180.0 days. *D. hoyi* with a life cycle lasting for about 2 years was abundant at the 30 and 50 m sites. Percentage contribution to biomass and production were 78.1% and 68.8% at the 30 m site. Higher densities at the 50 m depth produced higher biomass, production and lower P/B ratio than at 30 m.

Although biomass and production were not calculated for Oligochaeta, also deposit-feeders, their numerical density was similar at both 5 m and 15 m, and lower at the deeper sites. Tubificid worms were present at all depths with annual mean densities of 969.m^{-2} (5 m), 324.m^{-2} (15 m), 415.m^{-2} (30 m) and 231.m^{-2} (50 m).

Naididae were less abundant with mean densities of 355.m^{-2} (5 m), 212.m^{-2} (15 m), 61.m^{-2} (30 m) and 147.m^{-2} (50 m).

The only scrapers other than insects were gastropods, which were present at the two shallow sites. Unfortunately identification of gastropods was not possible due to extensive decalcification caused by the use of unbuffered preservative. Annual mean densities and biomasses of gastropods, as a group, were, respectively, 746.m^{-2} and 0.69 g.m^{-2} at 5 m, and 1151.m^{-2} and 0.91 g.m^{-2} at 15 m. The only insect scraper was the chironomid *Phaenopsectra* found at 15 m. Scrapers made up, respectively, 17.0% and 7.2% of biomass and production at 5 m and 29.8% and 24.0% at 15 m.

2.5- Discussion

2.5.1- Faunal abundance, composition and vertical distribution

Over the past few decades several reports have described benthic macroinvertebrate communities in the Laurentian Great Lakes. Lake Huron and/or Georgian Bay were treated in the reports of Loveridge and Cook (1975), Shrivastava (1974), Barton and Carter (1979) and Barton and Griffiths (1984) but direct comparison of my results with these earlier studies is complicated by differences in sampling and sieving techniques. My results showed that in Colpoys Bay, chironomids were the most frequently occurring macroinvertebrate (43.3%), followed by Crustacea (29.2%), Mollusca (14.7%) and Oligochaeta (9.3%). The general pattern reported by Loveridge and Cook (1975) is quite different, probably because most of their sites were offshore and they did not survey the littoral areas. Nevertheless, my estimate of invertebrate abundance at 50m (1862 ind.m^{-2}) is remarkably similar to that at their closest site (st. 6E, 58m, 1871 ind.m^{-2}). Barton and Griffiths (1984) estimated invertebrate standing stocks of the nearshore zone of Lake Huron, Georgian Bay and North Channel during September and October 1980. Their estimate of 11,118 ind.m^{-2} along the east shore of Colpoys Bay is somewhat lower than the 15,198 ind.m^{-2} I reported in September-October. They concluded that density of macroinvertebrates was strongly associated with sediment type and that gravel supported the highest densities. My observations are in accordance with theirs. The same trend towards lower numbers at greater depths was observed.

The decrease in benthic invertebrate diversity and density with increasing water depth is typical of nearly all lentic ecosystems (Brinkhurst 1974). In eastern Georgian Bay, Barton and Carter (1982) demonstrated that exposure to wave action influences the composition of epilithic invertebrates. Jonasson (1978) summarized the effects of a number of factors such as concentration of oxygen, physiological adaptations, the ability of an individual to utilize the available food, type of substrate and competition.

The fauna of the littoral region of Colpoys Bay is dense and rich relative to the profundal region. My estimates of total abundance at 5m (22,232 ind.m^{-2}) and 15 m (10,384 ind.m^{-2}) for the year of 1992-1993 are very similar to Farwell (1993) obtained in 1991 (7.5 m, 24,970 ind.m^{-2} and 13.5 m, 10,007 ind.m^{-2}). Similar seasonal trends were also observed: although not as pronounced as in 1991, there was a tendency for densities to increase toward autumn for most invertebrate groups. For bivoltine insects this is probably a result of reproduction, since large numbers of first instar larvae of the following autumn/winter cohort appead at this time. The surprisingly drastic decline in numbers at 5m in October relative to September 1992 probably reflected very unsettled weather conditions; abundances recovered slightly by November (Fig.2.2).

The faunal assemblage in shallow water included representatives of all functional feeding groups. In terms of numerical frequency of occurrence collector-gatherers (48.2%) and shredders (19.8%) dominated and were followed by deposit-feeders, scrapers, collector-filterers and predators. While the littoral fauna is clearly distinct from that of the softer sediments further offshore, there was a gradual transition from a community of collector-gatherer insects to the typical open lake community

dominated by deposit-feeding amphipods and oligochaetes (78.8%) at deeper sites. Surprisingly, both scrapers (gastropods) and shredders (isopods) were most abundant at the 15m site, probably because of the presence of charophytes. Pereyra-Ramos (1981) and Hanson (1990) also reported that isopods and gastropods occurred in higher densities on charophytes than on rooted plants.

2.5.2- Life history, biomass, production and P/B

Secondary production of invertebrate populations is an important variable for understanding the structure and functioning of ecosystems, because it combines individual growth and population survivorship and is essential when attempting to quantify energy-flow pathways in ecosystem analysis. Over the years several factors have been suggested to explain the variability observed in production rates. Those can be intrinsic to the population under investigation (e.g. density, biomass, voltinism) or environmental factors which can directly affect the growth rates (e.g. temperature, food availability, predation).

In Colpoys Bay, the most important environmental factors appearing to affect production vary with depth. Cooler temperatures and food supply most likely limit growth in deeper water populations, while competition and wave action are probably more significant in the littoral area.

The overall secondary production in the littoral was 21.75 g $m^{-2}y^{-1}$ at 5 m and 15.9 g $m^{-2}y^{-1}$ at 15 m, the result of the lower production of Chironomidae, Crustacea, Ephemeroptera and Trichoptera at 15 m. These communities also differed in terms of

functional organization. A decline in the relative importance of collector-gatherers, filterers and predators and a rise of scrapers was evident at the 15 m depth. The smallest decline in production was among shredders; scrapers were the only group showing an increase at 15 m.

The lower production at 30 m compared to 50 m was due to lower densities of *D.hoyi* at 30 m. At 50 m the higher densities of juvenile and adult amphipods promoted higher production. The reason for the difference in *Diporeia*'s production between those sites is not very clear, however temperature changes caused by oscillations in the depth of the thermocline may be more pronounced at 30 m than 50 m. This stress factor may depress *D.hoyi* populations, as explored in detail in chapter 4 of this thesis.

The annual turnover (P/B) at all sites mirrored the changes in production and biomass, being lowest at 50 m (lowest production and biomass). Annual P/B at littoral sites varied from a low of 1.6 for the slowly growing bivalve *Pisidium lilljeborgi* to a high of 15.0 for the bivoltine chironomid *Dicrotendipes*. Unlike the annual P/B, which can vary widely (Benke 1993), the cohort P/B usually ranges from 2 to 8 for freshwater invertebrates and is often close to 5 (Waters 1977). The differences observed in the annual P/B can be attributed to the length of aquatic life (for insects) or the CPI. In Colpoys Bay univoltine invertebrates had an average annual P/B of 4.3, bivoltine 8.0 and hemivoltione 2.6. Plante and Downing (1989) showed that when biomass reflects production, this is consistent with a turnover rate (P/B) set by environmental factors such as temperature. Higher temperatures and food supply in littoral sites enhance tissue growth, resulting in faster developmental times

and higher P/B ratios. On the other hand, lower temperatures slow growth rates at deeper sites, leading to lower turnover ratios.

Shredders the most productive functional feeding group, yield 4.2 $gm^{-2}y^{-1}$. In contrast, shredders tend to have the lowest production of all functional groups in running waters because they rely on poor quality food (Benke 1993). Contrary to shredders in running waters, the isopods of Colpoys Bay are relying on more nutritious food than decaying leaves (chapter 4). Isopods in Colpoys Bay were not only very numerous but also individually large, so had a large average total biomass (0.58 $g.m^{-2}$). This, coupled with a life cycle involving more than one generation per year, makes them the most productive animals in the system. Production by gathering-collectors (2.68 $g.m^{-2}y^{-1}$) was within the expected values reported by Benke (1993) and was greater than production by filtering-collectors even though the latter had a larger mean biomass. In stream ecosystems filtering collectors are amongst the highest producers; in Colpoys Bay they were fifth. Lotic filter-feeders normally include macrofiltering collectors such as hydropsychid caddisflies, which obtain a major energy subsidy from stream currents. While Colpoys Bay is a relatively energetic lentic habitat, the strength and predictability of water movements is much lower than in streams, also hydropsychid caddisflies in lakes are found on the rocky shore, which was not included in my study. *Pisidium* spp., although abundant, grow slowly (three years) and this decreases the rate of production. The high density of gastropods made scrapers the third most productive group. Those were followed by deposit-feeders (amphipods), which were also abundant in profundal areas. Least productive were the already mentioned filter-feeders and predators.

2.5.3- Role of benthic community in Colpoys Bay

To assess the contribution of each community to the total zoobenthic production of Colpoys Bay, total biomass and production were weighted according to the proportion of the three zones sampled relative to the total area of Colpoys Bay (i.e. littoral 13%, charophytes 27% and profundal 54%). For example, total production for the littoral was 21.75 $g.m^{-2}.y^{-1}$ x 0.13 x $37.9x10^6 m^2$ = $107.2x10^6$ $g.y^{-1}$. For charophyte beds I used the 15m values and for the profundal I used the mean values of 30 and 50 m. Total annual mean biomass of Colpoys Bay was $68.4x10^6$g and total annual zoobenthic production was $291.1x10^6 g.y^{-1}$ with the largest contribution from charophyte beds ($163.0x10^6$ $g.y^{-1}$) and the smallest from the profundal ($20.9x10^6 g.y^{-1}$).

These differences amongst the three zones are somewhat intuitive, since they reflect different benthic communities responding to shifts in physical features of the benthic habitat. At the shallowest depths, unstable substrates due to wave action might keep benthic standing stocks suppressed. The littoral was the most productive per unit area but occupies only 13% of the bay, so accounted for less of the total production than did the more extensive charophyte zone. Charophytes provide a large surface area for colonization by organisms (Farwell 1993) and are perennial, providing resources throughout the year. My observations suggest that benthic primary production plays a key role in determining the overall macrobenthic

productivity of Colpoys Bay. As depth increases further (below the photic zone) benthic secondary production declines drastically.

During thermal stratification temperature can vary widely because of internal currents and seiches that affect the depth of the thermocline on a daily or even hourly basis. Benthic invertebrates adapted to such wide variation in temperatures are not common, and this probably contributed to the low biomass and production values at 30 m. Temperature fluctuates less at the most offshore site (50 m), sediments are less influenced by storms and suspended particles from shallow areas settle providing food resources for the benthos, all of which contribute to higher biomass and production relative to the 30 m depth.

Studies providing data on biomass and production in benthic macroinvertebrate communities of the Great Lakes are so scarce that detailed synthesis and comparisons are very difficult. For comparison with other works, I converted my biomass and production values to ash-free-dry-weight (1g dry wt = 0.9 g ***AFDW***, Waters 1977). Cook and Johnson (1974) presented a good historical summary of standing stocks for the Great Lakes. Mean biomass (***AFDW***) was lowest in Lake Superior (0.081 $g.m^{-2}$) and highest in some enriched bays of the lower lakes (e.g. Toronto Harbour 3.87 to 42.3 $g.m^{-2}$). Average biomass in the other lakes was 3.06 $g.m^{-2}$ in Lake Michigan, 1.33$g.m^{-2}$ in Lake Huron and 4.17 $g.m^{-2}$ in Lake Erie. More recently Nalepa (1989) estimated benthic biomass for the major taxa in the profundal zone (> 90 m) of Lake Michigan to be 1.97 $g.m^{-2}$, at least 2.5 times greater that in the profundal zone of Lakes Superior, Huron or Ontario 0.05, 0.60 and 0.69 $g.m^{-2}$, respectively. Loveridge and Cook (1976) estimated that the biomass in Georgian Bay averaged 0.33 g

AFDW.m^{-2} at a mean depth of 59.7 m. My somewhat two-fold larger estimate of 0.60g AFDW.m^{-2} at 50m probably reflects the nearshore location of my sampling site.

Two sources of bias may have led to an underestimation of overall biomass and production. First, the rocky zone, representing 6.6% of the bay's total area, was not sampled and, second, the zoobenthic production estimates of Colpoys Bay do not include all of the organisms, especially the micro and meiofauna. These groups are included in very few lake ecosystem studies. In the Finnish oligotrophic Lake Paajarvi, Holopainen and Paasivirta (1977) used 100-μm aperture sieves to retain meiofauna and estimated that micro and meiofauna might contribute about 75 and 50% of total faunal production in the profundal and littoral zones, respectively. Strayer (1985) found that meiofauna made up 50% of total zoobenthic production in Mirror Lake. The meiofaunal groups not included in Colpoys Bay (Ostracoda, Cladocera, Copepoda, and Nematoda) made up only 15% of the production estimate in Mirror Lake. More significantly, I was not able to estimate production by Oligochaeta and Decapoda (crayfish). In oligotrophic Thingvallavatn, Lindegard (1992) found that tubificid, naidaid and enchytraeid worms together made up 23.7% of the total production on a lakewide basis. Therefore, the calculated invertebrate production in Colpoys Bay might be increased approximately 39% (23.7% + 15%), which brings the mean production of 8.9 g*AFDW*.$m^{-2}.y^{-1}$ to about 12.4 g*AFDW*.$m^{-2}.y^{-1}$, likewise the biomass of 2.0 g*AFDW*.m^{-2} could be 2.8 g*AFDW*.m^{-2}.

The range of zoobenthic production in lakes is considerable, from 0.43g*AFDW*.$m^{-2}.y^{-1}$ in a Russian Lake (Alimov et al. 1972) to 69.10g*AFDW*.$m^{-2}.y^{-1}$ for a shallow

lake in Australia (Paterson and Walker 1974). In the main basin of Lake Ontario, Johnson and Brinkhurst (1974) estimated a production of 2.63 g*AFDW*.$m^{-2}.y^{-1}$ which is considerably higher than the 0.92 g*AFDW*.$m^{-2}.y^{-1}$ at my offshore site in Colpoys Bay. Colpoys Bay ("corrected") zoobenthic production of 12.4 g*AFDW*.$m^{-2}.y^{-1}$ seems high at first glance, but includes part of the littoral community, which is usually overlooked in production studies of the Great Lakes. Clearly the littoral zone is of great significance to the ecosystem of Colpoys Bay.

What is the relative contribution of benthic invertebrate production to total secondary production of the Colpoys Bay? Estimates of zooplankton biomass are available for Georgian Bay proper (224.8 10^{-3} $g.m^{-3}$ (fresh weight); Sprules et al. 1988). To allow benthic and zooplankton biomass to be compared, the mean annual biomass reported in volumetric units ($g.m^{-3}$) was multiplied by the mean depth of Georgian Bay (44m), then converted to ash-free-dry-weight (6 g wet weight = 1 g dry weight = 0.9 g ash free dry weight) (Waters 1977). A final figure of 1.48 gAFDW.m^{-2} was obtained for Georgian Bay zooplankton biomass, which is about half the weighted mean benthic biomass estimated for Colpoys Bay (2.8 gAFDW.m^{-2}).

The actual importance of the benthic and pelagic food chains in the energy transfer between primary production and fish depends, of course, on production, not standing stock. To my knowledge there are no estimates of zooplankton production for Georgian Bay or Lake Huron. Borgmann et al. (1984) estimated P/B of several zooplankton taxa from Lake Ontario. To make a rough estimation of Georgian Bay zooplankton production, I multiplied their mean values of P/B for Cladocera (25), calanoid copepods (32) and cyclopoid copepods (10.2) by the estimated biomass for

Cladocera (0.13 gAFDW.m^{-2}), Calanoid copepods (0.3 gAFDW.m^{-2}) and Cyclopoid copepods (0.2 gAFDW.m^{-2}) from Sprules et al. (1988). This yielded an estimate of total zooplankton production of 14.89 gAFDW.m^{-2} y^{-1}. Although this is probably an underestimate since *Mysis* and rotifers were not considered, it is only slightly greater than benthic secondary production, suggesting that both zooplankton and zoobenthos are of equal importance to energy flow in Colpoys Bay.

Several researchers have tried to use zoobenthic biomass and/or production to predict fish yields and biomass (Matuszek 1978, Hanson and Leggett 1982). I applied the empirical relationship developed by Hanson and Leggett (1982) to estimate fish biomass using benthic macroinvertebrate biomass and the mean depth of Colpoys Bay. The relationship for fish biomass was described by FC=5.692(B/Z)+28.70 (r^2=0.83, n=20), where FC= fish standing crop (kg wet weight/ha), B = zoobenthic biomass (kg wet weight/ha) and Z = mean depth (m). The total benthic biomass in Colpoys Bay for the period of July 1992 to July 1993 of 68.4x10^3 kg dry weight was converted to 41.04x10^4 kg wet weight, or 1083 kg wet weight/ha. The resulting predicted fish biomass was 261.32 kg wet weight/ha or 99x10^3 kg wet weight for the entire bay.

There are no published figures for total fish biomass in Colpoys Bay, but several components of the community are monitored. The summary of creel survey data from southern Georgian Bay (Mohr and Nicol 1998) showed that in Colpoys Bay, total fish biomass harvested in 1992 was 9.08x10^3 kg, and 2.84x10^3 kg in 1993. These values are much less than the predicted fish stock, but only included four species of sports fish (i.e. rainbow trout, chinook salmon, brown trout and *Salvelinus* sp) and were

based on fish harvested, not the actual numbers present, or even caught. Data for the commercially important lake whitefish, chub and lake trout harvest are available for the management area including both the Colpoys Bay and Owen Sound areas (Mohr and Gile 1994; Gile et al. 1993) and amounted to 32.43×10^3kg in 1992, and 35.30×10^3kg in 1993. Colpoys Bay is also very popular for winter sports fishing; the estimated harvest consisted primarily of 2.14×10^3 kg of lake whitefish, 1.09×10^3 kg of lake trout, and 637 kg of rainbow trout (Mohr 1998).

The total fish harvest during 1992-1993 including angling (assuming the ice-fishing catch was similar to the succeeding year) was 43.70×10^3 kg about half of my estimate of 99.00×10^3 kg. Considering that many species present in Colpoys Bay (e.g. smelt, alewife, shiners, small mouth bass, yellow perch, carp, suckers, etc.) were not included in those surveys, and that most species are planktivorous at least during some part of their lives, my estimates are probably realistic. Overall then, my results emphasize the potential significance of benthic macroinvertebrate production in supporting the fish production of Colpoys Bay.

2.6- Conclusions

In summary, the benthic fauna of Colpoys Bay consists of a dense and rich littoral community characteristic of shallow sandy substrata and macrophytic vegetation, dominated by insects (mostly Diptera), isopods and gastropods with a gradual transition to the usual fauna of *D.hoyi, Pisidium* spp. and oligochaetes on soft sediments further offshore.

Unlike streams where filter-feeders have the highest rate of production (Benke 1993), shredders (isopods) were the most productive group because of their abundance and bivoltine life cycle. Shredders and gatherers dominated production at littoral sites; deposit-feeders accounted for most of production at depths $\geq$ 30 m.

As expected biomass and production were different in the three main zones studied, with the area covered by charophytes making the largest contribution to total production in Colpoys Bay. The shallow littoral zone (5 m) was more productive per unit area, but occupies much less of the basin, so it accounted for slightly less of the total production. The profundal zone is largest in terms of area, but supports a much more restricted fauna, at low densities, so it contributed only about 9% of total benthic secondary production in Colpoys Bay.

The mean zoobenthic biomass of Colpoys Bay is twice that of indirectly estimated biomass of zooplankton in Georgian Bay. Several species of fishes in Georgian Bay are benthivores during most of their lifetime, including species of the Coregoninae (the deep-water ciscoes and the commercially important lake whitefish), common white suckers and burbot. The final estimated fish biomass obtained from invertebrate

biomass further emphasizes the role of the benthic food chain in the energy transfer between primary producers and fish.

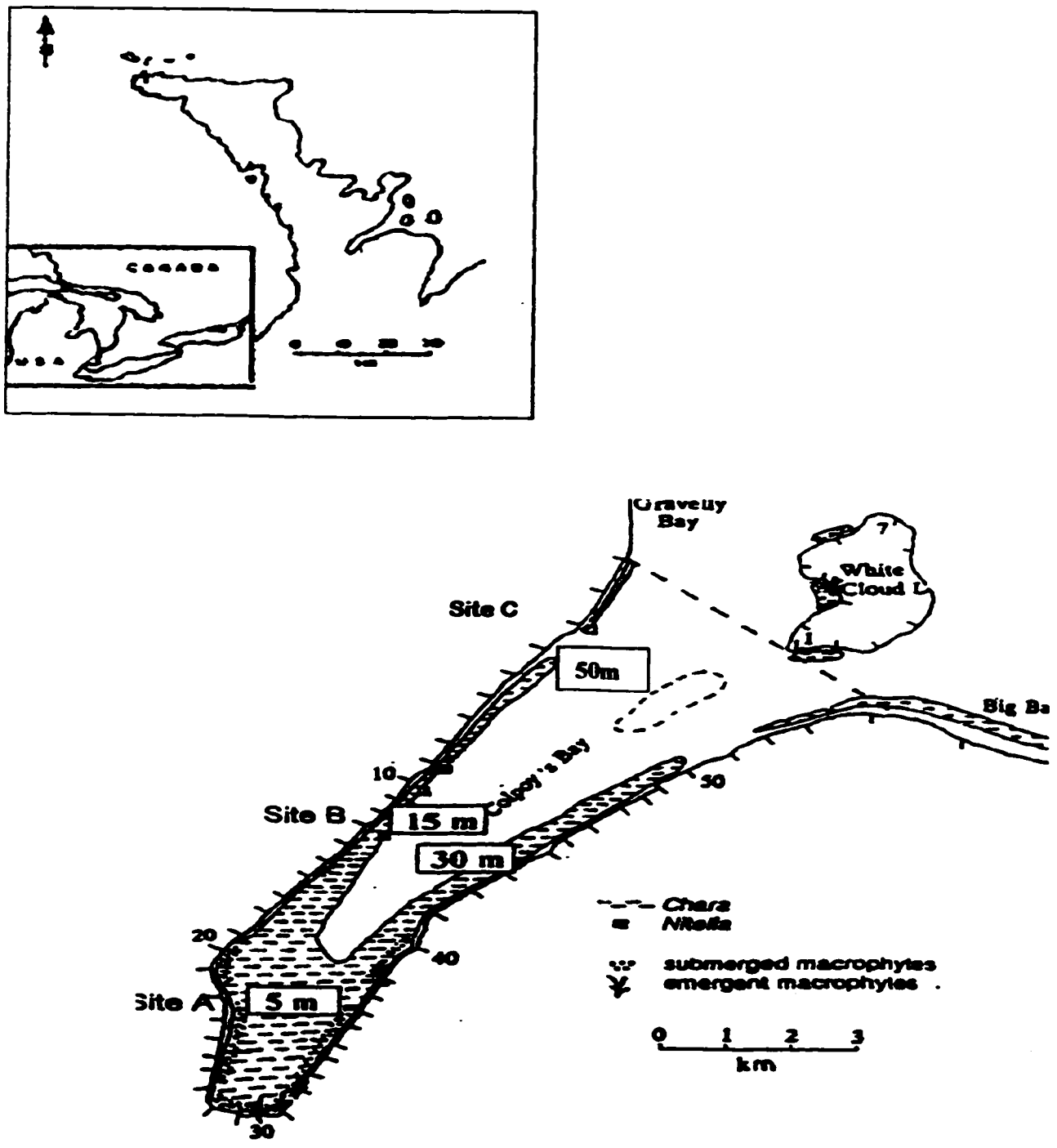


Figure 2.1:Locations of sampling sites in Colpoys Bay, Georgian Bay.

Table 2.1: Water temperature readings (°C) and total phosphorus (µg/L) for Colpoys Bay. na = not available, * data from Maly, J (1992).

Date/ 1992-1993	Surface	Sediment	TP (µg/L) *
May	6.5	4.5	4.5
June	7.8	5.0	4.6
July	13.0	5.5	4.3
August	15.0	5.5	3.8
September	15.0	6.0	5.2
October	7.0	5.0	3.9
November	6.0	5.0	na
December	na	na	na
January	na	na	na
March	na	na	na
March	1.0	2.0	na
April	2.0	2.0	na
May	6.0	4.5	na

Table 2.2: Total numbers of genera in each major group at each site for the period of May 1992 through May 1993.

Group	Family	site			
		A	B	B	C
		5m	15m	30m	50m
Diptera					
	Chironomidae	30	23	4	3
Ephemeroptera		6	1		
Trichoptera		8	2		
Crustacea					
	Amphipoda	2	2	1	1
	Isopoda	2	2		
Oligochaeta					
	Tubificidae	3	3	4	1
	Naididae	1	3		
	Enchytreidae	1	1		
	Lumbriculidae	1	1		
Hirudinea		1	1		
Mollusca					
	Bivalvia	6	5	3	1
	Gastropoda	2	2		
Total		63	45	12	5

Table 2.3: Invertebrates frequency of occurrence and functional feeding group (FFG; cg = collector-gatherers; cf = collector-filterers; df = deposit-feeders; pr = predators; sc = scrapers; sh = shredders). % Ind =% of individuals (all depths); F = number of dates out of 20 dates.

Taxa	Depth (m)	FFG.	%Ind	F	Taxa	Depth	FFG	%Ind	F
Chironomidae			43.3		**Trichoptera**			0.99	
Micropsectra	5,15	cg	7.87	14	*Mystacides*	5,15	cg	0.37	13
Procladius	5,15,30	pr	6.27	15	*Polycentropus*	5	pr;cf	0.35	12
Microtendipes	5,15,30	cg	5.77	16	*Oecetis*	5	pr	0.09	7
Polypedilum	5,15	cg	4.93	15	*Limnephilus*	5	sh	0.08	7
Tanytarsus	5,15,30	cg;cf	4.91	16	*Lepidostoma*	5,15	sh	0.08	5
Dicrotendipes	5,15	cg;cf	2.12	16	*Hydropsyche*	5	cf	0.01	2
Cladotanytarsus	5	cg;cf	1.89	16	*Triaenodes*	5	sh	0.01	2
Heterotrissocladius	30,50	cg	1.49	15	*Chematopsyche*	5	cf	0.00	1
Paralautherborniella	5,15	cg	1.36	12	**Crustacea**			29.2	
Gillotia alboviridis	5,15,30	cg	1.13	16	*Lirceus lineatus*	5,15	sh	9.51	14
Ablablesmia	5,15	pr	1.11	14	*Caecidotea intermedius*	5,15	sh	7.53	14
Phaenopsectra	15	sc	0.95	11	*Diporeia hoyi*	30,50	df	8.03	13
Chironomus annularis	5,15	cg;cf	0.68	10	*Hyallela azteca*	5,15	df	3.70	13
Cladopelma lateralis	15	cg	0.52	11	*G. pseudolimneaus*	5,15	df	0.47	14
Paracladius	15	cg	0.48	12	**Mollusca**			14.7	
Paratendipes	5,15	cg	0.37	6	**Bivalvia**				
Monodiamesa	5,15	cg	0.32	14	*Pisidium compressum*	5-50	cf	1.58	12
Protanypus	30,50	cg	0.31	13	*Pisidium lilljeborgi*	5-30	cf	1.28	10
Potthastia longimans	5,15	cg;sc	0.14	9	*Pisidium ferrugineum*	5,15	cf	1.06	8
Psectrocladius	5	cg	0.12	2	*Pisidium nitidum*	5-30	cf	1.02	7
Pagastiella	30	cg	0.09	5	*Pisidium fallax*	5,15	cf	0.99	7
Demicryptochironomus	5,15	cg	0.09	3	*Pisidium rotundatum*	5	cf	0.93	9
Chaetocladius	5	cg	0.07	2	**Gastropoda**	5,15	sc	8.80	15
Harnischia	all	cg	0.07	9	Oligochacta			9.3	
Glyptotendipes	5,15	sh	0.05	1	Tubificidae	5-50	df	7.96	18
Stictochironomus	5,15	cg;sh	0.03	2	Naididae	5-50	df	1.12	15
Corynoneura	5	cg	0.02	4	Lumbriculidae	5	df	0.19	8
Paratanytarsus	5,15	cf	0.02	3	Enchytracidae	5,15	df	0.02	6
Cryptotendipes	5	cg	0.02	1	**Hirudinea**	5,15	pr	0.22	11
Stempellina	5,15	cg	0.01	1					
Pseudochironomus	5	cg	0.01	2	Total				
Paracricotopus	5	cg	0.01	1	Collector-gatherers			37.0	
Epoicocladius	5	cg	0.01	1	Collector-filterers			6.9	
Cryptochironomus	5	pr	0.01	1	Deposit-feeders			21.7	
Rheotanytarsus	15	cf	0.00	1	Shredders			17.2	
Paracladopelma	15	cg	0.00	1	Scrappers			9.5	
Orthocladius	5	cg	0.00	1	Predators			7.7	
Omisus	5	cg	0.00	1					
Ephemeroptera			1.32						
Caenis latipennis	5	cg	0.58	9					
Caenis amica	5	cg	0.43	5					
Ephemera simulans	5,15	cg	0.19	13					
Paralaptophlebia	5	cg	0.06	2					
Baetis	5	cg	0.05	2					
Baetisca lacustris	5	cg;sc	0.01	3					

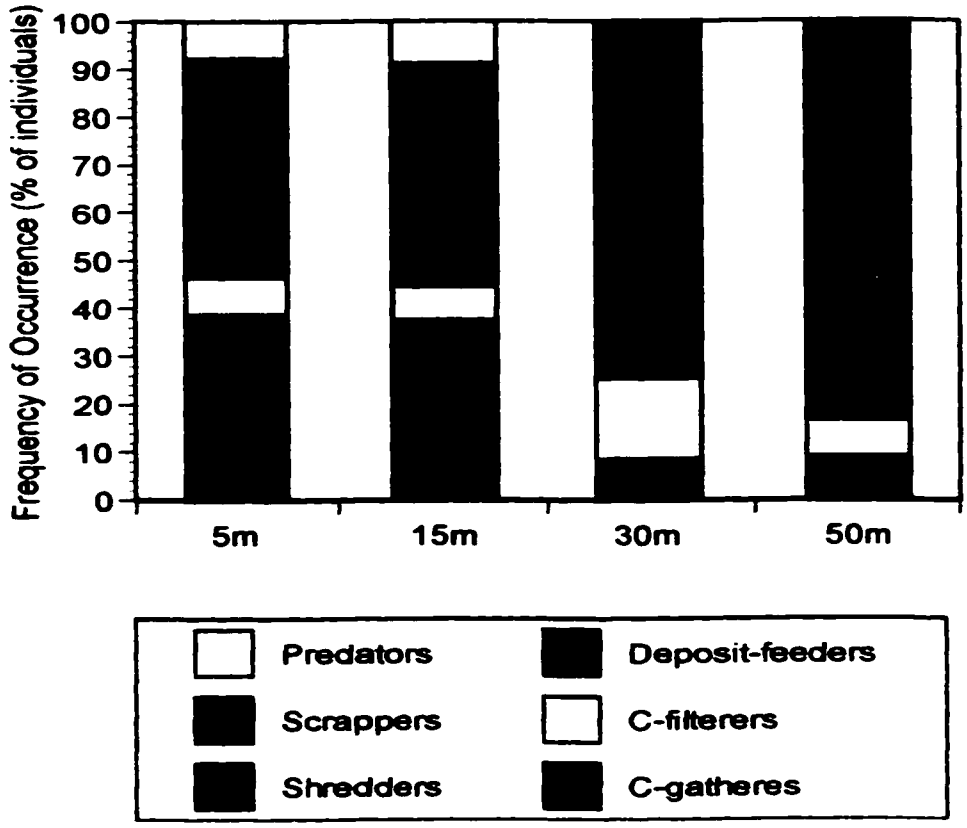


Figure 2.2: Functional feeding group frequency of occurrence as percent of individuals at each site.

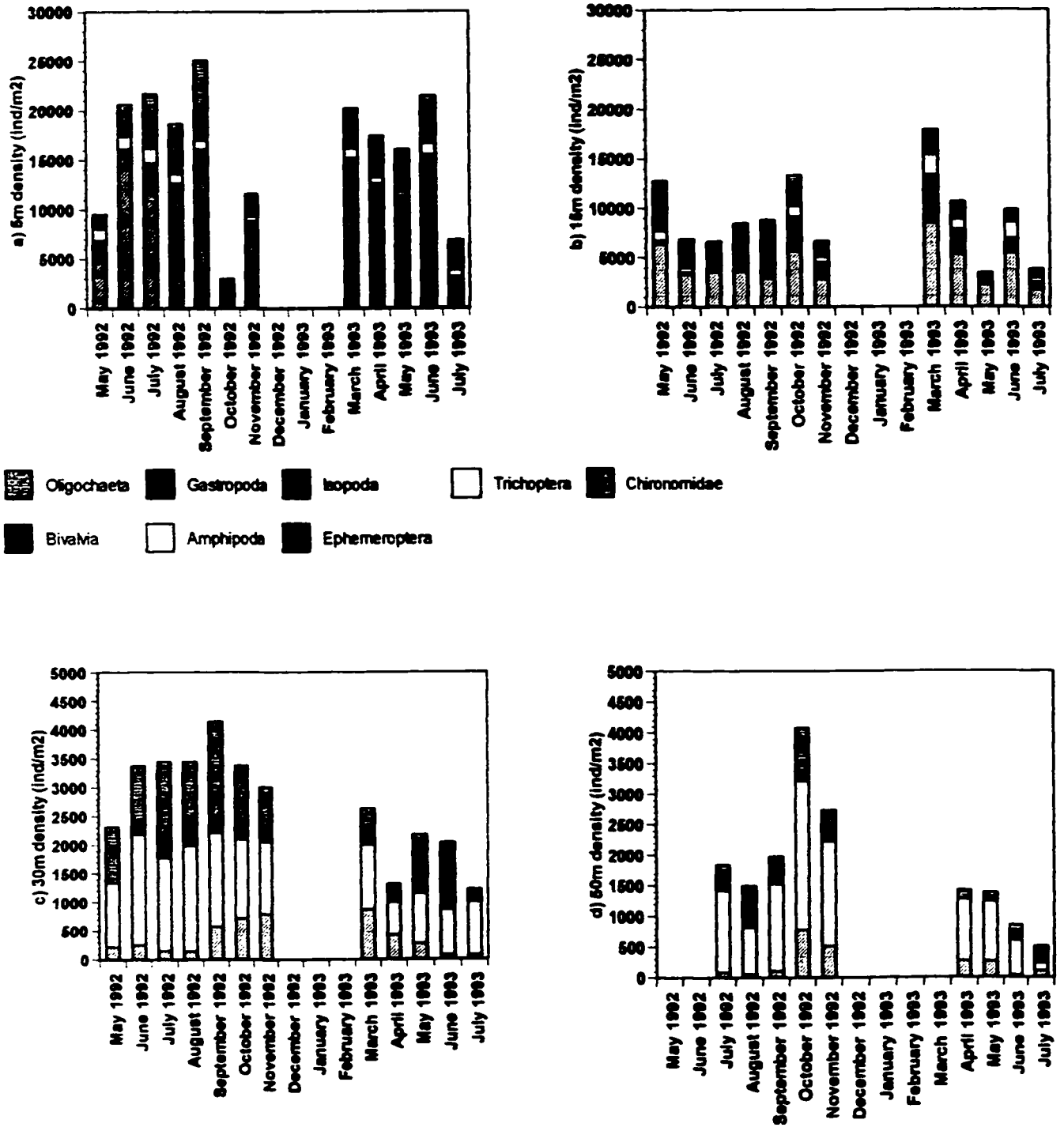


Figure2.3:Seasonal variation in density of the major groups in each site: a) 5m; b) 15m; c) 30m and d) 50m.

Table 2.4: Results of one-way ANOVA to test temporal effects on the density of major taxa at each depth.

Depth	5m					15m				
Taxon	**df**	**MS**	**F**	**p**	**r^2**	**df**	**MS**	**F**	**P**	**r^2**
Chironomidae	11	2.802	7.41	<0.00*	0.58	10	2.629	8.19	<0.00*	0.66
Trichoptera	11	1.52	2.40	0.015	0.36	11	0.234	0.621	0.800	0.15
Ephemeroptera	10	2.613	2.83	0.006*	0.33	11	1.043	6.06	<0.00*	0.63
Isopoda	11	3.706	2.576	0.010	0.32	11	7.020	7.04	<0.00*	0.66
Amphipoda	11	3.405	3.07	0.003*	0.36	10	2.319	3.404	0.003*	0.46
Gastropoda	11	2.552	3.31	0.001*	0.38	11	2.473	4.63	<0.00*	0.56
Bivalvia	11	4.754	4.87	<0.00*	0.48	11	1.691	2.67	0.012	0.42
Oligochaeta	11	4.269	7.76	<0.00*	0.58	11	2.911	4.45	<0.00*	0.53

Depth	30m					50m				
Taxa	**df**	**MS**	**F**	**P**	**r^2**	**df**	**MS**	**F**	**P**	**r^2**
Chironomidae	9	2.201	3.301	0.003*	0.36	9	2.266	6.29	<0.00*	0.57
Amphipoda	10	0.864	2.29	0.025	0.38	9	1.192	3.23	0.004*	0.55
Bivalvia	11	2.648	7.16	<0.00*	0.58	9	0.311	0.607	0.78	0.11
Oligochaeta	11	3.196	3.679	0.001*	0.41	9	1.840	2.52	0.02	0.26

Table 2.5: Voltinism (V) and cohort production interval (CPI) for each taxa during the study period. uni=univoltine, biv=bivoltine, semi-semivoltine, triv=trivoltine.

	5m		15m		30m		50m	
	V	CPI	V	CPI	V	CPI	V	CPI
Diptera								
Chironomidae								
Chironominae group								
Chironomus annularis	uni	295						
Cladopelma lateralis			biv	124				
Dicrotendipes	biv	137	biv	153				
Gillothia alboviridis	biv	169	biv	157				
Microtendipes	biv	207	biv	188				
Paralauterborniella	biv	123						
Polypedilum	biv	170	biv	163				
Phaenopsectra			biv	152				
Tanytarsini group								
Micropsectra	triv	112	triv	117				
Tanytarsus	biv	103	biv	135				
Cladotanytarsus	biv	141						
Diamesinae group								
Protanypus sp					uni	302		
Prodiamesinae group								
Monodiamesa	biv	138						
Tanypodinae group								
Ablabesmia	biv	127	biv	129				
Procladius	biv	119	biv	168				
Orthocladiinae group								
Heterotrissicladius					uni	318		
Paracladius			uni	298				
Ephemeroptera								
Caenis	biv	141						
Trichoptera								
Mystacides	uni	275						
Polycentropus	uni	291						
Crustacea								
Isopoda								
Caecidotea intermedius	biv	152	biv	165				
Lirceus lineatus	biv	166	uni	302				
Amphipoda								
Gammarus pseudolimneaus	uni	306						
Hyallela azteca	biv	180	biv	180				
Diporeia hoyi					semi	593	semi	593
Mollusca								
Bivalvia								
Pisidium compressum	semi	3 years	semi	3 years	semi	3years		
Pisidium lilljehorgi	semi	3 years	semi	3 years				
Gastropoda *	semi	2 years	semi	2 years				

* from literature

Table 2.6a: Annual mean density (ind m^{-2}), annual mean biomass (g m^{-2}), annual production ($gm^{-2}y^{-1}$) and P/B for the common taxa at sites 5 and 15m from July 1992 July 1993.

Taxa	Mean Density		5m		Mean Density		15m	
	(ind m^{-2})	B (g m^{-2})	P($gm^{-2}y^{-1}$)	P/B	(ind m^{-2})	B (g m^{-2})	P($gm^{-2}y^{-1}$)	P/B
Diptera								
Chironomidae		**0.82**	**6.31**	**7.6**		**0.78**	**4.80**	**6.2**
Chironominae group								
Chironomus annularis					248	0.24	1.08	4.5
Cladopelma lateralis					103	0.00	0.03	15.0
Dicrotendipes	411	0.03	0.45	15.0	155	0.02	0.12	6.0
Gillothia alboviridis	261	0.05	0.19	3.8	109	0.01	0.12	8.6
Microtendipes	1574	0.11	0.31	2.9	1152	0.12	0.87	7.3
Paralautherborniella	468	0.02	0.12	7.5				
Polypedilum	1030	0.15	1.13	7.5	167	0.03	0.23	7.7
Phaenopsectra					376	0.21	1.27	6.1
Tanytarsini								
Micropsectra	5804	0.25	2.23	8.9	751	0.04	0.39	9.8
Tanytarsus	1443	0.09	0.84	9.4	549	0.05	0.34	6.8
Cladotanytarsus	883	0.04	0.39	9.8				
Prodiamesinae								
Monodiamesa	50	0.01	0.03	3.0				
Tanypodinae								
Ablabesmia	216	0.01	0.09	9.0	103	0.00	0.06	15.0
Procladius	852	0.06	0.53	8.8	451	0.04	0.23	5.8
Orthocladiinae								
Paracladius					122	0.01	0.06	6.0
Ephemeroptera		**0.01**	**0.12**	**12**				
Caenis	179	0.01	0.12	12				
Trichoptera		**0.03**	**0.16**	**4.8**				
Mystacides	125	0.01	0.08	6.2				
Polycentropus	79	0.02	0.08	4.0				
Crustacea		**1.20**	**11.43**	**9.5**		**1.52**	**7.72**	**5.1**
Isopoda								
Caecidotea	991	0.50	4.99	9.9	481	0.33	2.57	7.8
Lirceus lineatus	764	0.50	4.56	9.1	1376	1.12	4.70	4.2
Amphipoda								
Gammarus	138	0.05	0.18	3.4				
Hyallela azteca	876	0.15	1.7	11.3	514	0.07	0.45	6.4
Mollusca		**1.99**	**3.73**	**1.9**		**1.45**	**3.41**	**2.4**
Bivalvia								
Pisidium compressum	1012	0.60	1.05	1.8	174	0.12	0.26	2.2
Pisidium lilljehorgi	574	0.70	1.13	1.6	369	0.42	0.59	1.4
Gastropoda	746	0.69	1.55	2.8	1213	0.91	2.56	2.8
Collector-gatherers		**0.77**	**5.89**	**7.5**		**0.52**	**3.24**	**6.2**
Collector-filterers		**1.32**	**2.26**	**1.7**		**0.54**	**0.85**	**1.6**
Deposit-feeders		**0.20**	**1.88**	**9.4**		**0.07**	**0.45**	**6.4**
Scrappers		**0.69**	**1.55**	**2.8**		**1.11**	**3.83**	**3.5**
Shredders		**1.00**	**9.55**	**9.6**		**1.45**	**7.27**	**5.0**
Predators		**0.07**	**0.62**	**8.9**		**0.04**	**0.29**	**7.3**
Total		**4.05**	**21.75**	**5.4**		**3.73**	**15.93**	**4.2**

Table 2.6b: Annual mean density (ind m^{-2}), annual mean biomass (g m^{-2}), annual production ($gm^{-2}y^{-1}$) and P/B for the common taxa at sites 30 and 50m from July 1992 July of 1993.

Taxa	Mean Density	30m			Mean Density	50m		
	(ind m^{-2})	B (g m^{-2})	P($gm^{-2}y^{-1}$)	P/B	(ind m^{-2})	B (g m^{-2})	P($gm^{-2}y^{-1}$)	P/B
Diptera								
Chironomidae		**0.020**	**0.06**	**3.0**				
Diamesinae								
Protanypus	70	0.01	0.02	2.0				
Orthocladiinae								
Heterotrissocladius	182	0.01	0.04	2.7				
Crustacea		**0.25**	**0.50**	**1.9**		**0.67**	**1.34**	**2.0**
Amphipoda								
Diporeia hoyi	811	0.25	0.50	1.9	1415	0.67	1.34	2.0
Mollusca		**0.05**	**0.14**	**2.8**				
Bivalvia								
Pisidium compressum	185	0.05	0.14	2.8				
Collector-gatherers		**0.02**	**0.06**	**3.0**				
Collector-filterers		**0.05**	**0.14**	**2.8**				
Deposit-feeders		**0.25**	**0.50**	**1.9**		**0.67**	**1.34**	**2.0**
Total		**0.32**	**0.70**	**2.2**		**0.67**	**1.34**	**2.0**

Chapter 3: Carbon cycle dynamics in the pelagic zone

Abstract

The linkages between dissolved inorganic carbon (DIC) and particulate organic matter (POM) were investigated in the pelagic zone of Colpoys Bay. Water for analysis of stable carbon isotopes in DIC and POM was collected from the epiliminion, metaliminion and hypoliminion. POM was also separated into three size fractions in an attempt to isolate different components of the algal community.

The results suggest that the temporal fluctuation in pelagic POM $\delta^{13}C$ is influenced by algal species changes in response to changes in the type (CO_2 or HCO_3^-) of aquatic DIC and seasonal intrusion of littoral matter. The seasonal isotopic variation observed in bulk zooplankton and *Mysis relicta* followed the general trend of POM.

If isotopes of carbon and/or nitrogen are to be used for inferences regarding energy sources for secondary consumers in the pelagic zone, it is essential to understand the system biogeocheochemistry, including phytoplankton species composition, inorganic nutrient concentrations and inputs from the watershed and their influence on DIC isotopic signatures on a temporal and spatial scale.

3.1 – Introduction

In a lake ecosystem most of the organic matter sequestered into the sediments is ultimately derived from organic matter synthesized by organisms inhabiting the surface waters and transported to the lake floor as particulate organic matter (POM). Some of the organic matter produced in the water column will be recycled (Wetzel 1983) especially during thermal stratification, so only a fraction of the particulate organic matter produced will sink to the lake bottom. When extensive alteration of POM occur in the water column and at the sediment–water interface the sedimentary organic matter may have a chemical composition markedly different from that of the original material. All those processes can affect the carbon isotope signatures of POM and, consequently, organisms feeding upon it. Therefore an understanding of the factors that alter the isotopic signatures of POM is imperative if stable carbon isotope analysis is to be used to make inferences about energy and material flow within lentic food webs.

Temporal studies of the $\delta^{13}C$ of particulate organic matter in relation to inorganic carbon suggest that the carbon isotope composition is a function of the system biogeochemistry (Leggett 1998). About 1% of the carbon dioxide in the atmosphere is $^{13}CO_2$ while 99% is $^{12}CO_2$. $^{13}CO_2$ diffuses more slowly, reacts more slowly and has a greater tendency toward bicarbonate formation than $^{12}CO_2$. Carbon isotopes have been used by plant physiologists to develop an understanding of the mechanisms of carbon uptake by algae (Sharkey and Berry 1985). Of particular interest is the rather larger discrimination against ^{13}C (ca. 28 parts per mil) that occurs

in the enzymatic fixation of CO_2 by RUBISCO. Essentially all net fixation of carbon by aquatic photosynthetic organisms occurs by this reaction, so organic carbon derived from photosynthesis tends to be depleted in ^{13}C relative to the inorganic carbon of the environment.

In aquatic ecosystems, the amount and composition of available DIC is influenced by biological processes of respiration and photosynthesis as well as equilibrium kinetics and atmospheric gas exchange. DIC is the sum of bicarbonate (HCO_3^-), dissolved carbon dioxide ($CO_{2(aq)}$) (which is approximately equal to H_2CO_3) and carbonate (CO_3^{2-}) in the system. These different components of the DIC pool of aquatic systems will move towards a state of chemical equilibrium with each other and with atmospheric CO_2 (Stumm and Morgan 1981). The carbon isotope signature, $\delta^{13}C$, of DIC is determined by the relative magnitudes of the forms of DIC and the processes influencing the chemical and isotopic equilibrium between components of the lake carbonate system.

The fractionation between source carbon and primary producers is dependent on; (1) the chemical speciation of the carbon; and (2) which of these species are taken up by the photosynthetic organisms. For example, blue-green algae (*Microcystis*) have been reported to be able to efficiently use HCO_3^-, whereas some diatoms (e.g. *Asterionella, Melosira, Fragilaria*) are thought to be inefficient HCO_3^- users (Maberly and Spence 1983) and chrysophytes are believed to be obligate CO_2 users (Sandgren 1988). The isotopic signature of POM is, therefore, a weighted average of all different algal types plus associated bacteria, detritus and even small zooplankton. Temporal variations are influenced based on phytoplankton succession. It would be

expected that POM composed mostly of blue-green algae would be more enriched in ^{13}C than POM dominated by chrysophytes.

This chapter is a description of the processes influencing the isotope signatures of dissolved inorganic carbon (DIC) in Colpoys Bay and its subsequent role in determining the isotope signatures of particulate organic matter (POM) and organisms feeding upon it.

3.2 - Material and Methods

During the 1992 field season the thermal structure of the water column was determined using a SeaTech transmissometer combined with a Richard Brancker Research Ltd. TD-400 logging/profiling system equipped with temperature and depth sensors.

Water samples for isotopic analyses of dissolved inorganic carbon (DIC) were collected once a month from June through October 1992, March and May 1993. One liter of water was collected every 10m from the surface to 30m, preserved with mercuric chloride and stored in dark glass bottles inside coolers with ice in the field. In the environmental isotope laboratory at the University of Waterloo, DIC was extracted from the water under vacuum by acidification with phosphoric acid, and the evolved CO_2 gas was trapped and purified cryogenically. Isotopic analyses of DIC was performed using a VG ISOGAS (Prims Series II) stable-isotope-ratio mass spectrometer with an analytic precision of $\pm 0.2‰$. Dissolved $\delta^{13}CO_2$ signatures were

calculated from the $\delta^{13}C$ DIC values, assuming equilibrium conditions, using estimates of CO_2 and HCO_3^- concentrations from pH readings and temperature (Stumm and Morgan 1981) and temperature-related hydration isotope fractionation effects (Mook et al. 1974).

Water for isotopic analyses 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 opaque Van Dorn bottle. In 1992 large particles (mainly zooplankters) were removed by passing the water through a 40-μm aperture mesh prior to filtration; in 1993, to include larger algae, water was screened through a 60-μm mesh prior to filtration. Three 2 l water samples were filtered from each depth. In an attempt to separate the bacterial fraction from algae, those water samples were filtered through a series of three pre-combusted glass fiber filters of decreasing pore size (Whatman GF/D = 2.7-um; GF/C = 1.2-um; GF/F = 0.7-um) using a peristaltic pump. Filters were frozen in the field. Prior to isotope analysis each filter was acidified with 10% HCl.

For isotopic analyses, zooplankton were collected from depths of 0 to 10 m using vertical hauls of a plankton net (64-um mesh size) in May, June, July, August and October 1992, and April and May of 1993. A few mysids were collected by dredging the lake bottom and removed from sediments under a dissecting microscope. For estimation of zooplankton composition, samples were collected from May to August 1992. Water samples were taken with a 4 liter opaque Van Dorn bottle. Zooplankton retained in a 40 μm screen was preserved in 5% sugar formalin. Three

replicate samples were taken every 5 m from surface to a maximum depth of 30 m. Those samples were obtained by Karen Barry as a part of her undergraduate thesis (Berry 1992).

Isotopic analyses for POM, zooplankton and mysid samples containing 1 to 5mg of organic matter were performed at the Environmental Isotope Laboratory, Department of Earth Sciences, University of Waterloo, Ontario using a Fisons Instruments VG Isochrom-EA continuous flow mass spectrometer with an analytic precision of $\pm$ 0.2‰ for carbon and $\pm$ 0.3‰ for nitrogen. Isotope ratios are expressed as parts per mil deviation from the international standard reference materials VPDB (Vienna Peedee belemnite) for carbon (Coplen 1996), and N_2 in the atmosphere (Mariotti 1983) for nitrogen as follows:

$$\delta^{13}C = [(^{13}C/^{12}C_{sample})/ {}^{13}C/^{12}C_{standard}) - 1] \times 10^3$$

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

3.3 – Results

3.3.1 - Thermodynamics and Water Chemistry

In the first field season, during the months of May and June 1992, the water column was isothermal with mean temperatures of 4°C and 6°C, respectively. Thermal stratification occurred around July 23 with a 10 m thick thermocline starting at 15 m (top of the thermocline). Water temperature was always 5°C at 50 m, except that in mid-September it rose to 7°C and the thermocline was much deeper, top starting at 30 m (10 m thick). The water column was isothermal again by mid-October 1992. Transmissometer readings first revealed a particle peak at 5 m (from surface) on 26 June 1992. Two other particle peaks were observed on each of 9 July (5 to 10 m and 20 to 25 m) and on 23 July (20 and 35 m). Single peaks also occurred in August (15 m) and September 1992 (30 m). In 1993 thermal stratification was established by July 22 and remained until mid-October. Hypolimnetic water temperature varied from 4.3°C on June 10 to 5°C on August 12 (Furgal 1995).

The relative concentration of dissolved CO_2 (CO_2 aq), bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) were calculated using equations describing equilibration of the carbonate systems in fresh water (Stumm and Morgan 1981). Measured data included the DIC concentration, pH and temperature. Estimated concentrations of bicarbonate were always much higher than those of carbonate or dissolved carbon dioxide (Table 3.1). Differences in the percentage contribution of HCO_3^- were minimum from 96.60

% to 97.04 %, and dissolved CO_2 from 2.61 % to 3.14 %, with carbonates being negligible.

3.3.2 - $\delta^{13}C$ and $\delta^{15}N$ of POM and - $\delta^{13}C$ of DIC

The DIC pool is composed of bicarbonate (HCO_3^-), hydrated and dehydrated dissolved carbon dioxide (CO_2) and carbonate (CO_3^{2-}) in a state of equilibrium with the atmosphere and each other such chemical equilibrium however, may not be met under conditions of intense photosynthesis. The carbon isotope signature of DIC is determined by the relative concentrations of the different forms of DIC and biochemical processes influencing the isotopic equilibrium of the lake carbonate system. Under conditions of atmospheric equilibrium, HCO_3^- will have a $\delta^{13}C$ signature in the range of 0 to 1‰. In Colpoys Bay, $\delta^{13}C$ DIC ranged from -2.1‰ to +0.7‰ for most of the year (Table 3.1). Fractionation in the formation of dissolved CO_2 from HCO_3^- varies between -12.0‰ to -8.4‰ depending on temperature (Mook et al. 1974). In Colpoys Bay $\delta^{13}C$ of HCO_3^- were calculate to vary from +0.9‰ to -1.8 ‰, and $\delta^{13}C$ of CO_2 (aq) signatures ranged from -9.3 ‰ to -12.8 ‰, with a mean of -10.7 ‰ (Table 3.1). In general, there was no pattern of variation with depth (Fig. 3.1). The $\delta^{13}C$ DIC from the epilimnion and metalimnion remained fairly constant throughout the sampling period. DIC in the hypolimnion was less consistent with a minimum (mean= -1.67 ‰) in July 1992

POM was separated into three size fractions. Paired t-tests revealed significant differences in the signatures of particles sizes ≤ 1.2μm and 1.2μm to 2.7μm (df=23; p=0.015), and significant seasonal changes occurred in all size fractions (Table 3.2.a). Paired t-tests showed no significant differences in POM among the three depth strata. Strong, significant, seasonal changes occurred in the carbon signatures of particles from the metalimnion and hypolimnion (Table 3.2b).

Annual mean signatures were –25.5°/$_{oo}$ (1992) and –25.8°/$_{oo}$ (1993). A paired T-test including only the months for which the data were available in both years showed no significant differences between the two years (df=18, p=0.36). In the first year (May to October 1992), monthly mean POM isotope signatures within all sizes fractions and depth strata tended to become more enriched from spring through autumn. During the second year (March to August 1993) POM signatures remained fairly stable (Fig. 3.2 a, b, c). Overall, there was some isotopic enrichment with depth in the first year (Table 3.3). Mean signatures for 1992 and 1993 were, respectively –26.4 °/$_{oo}$ and –25.9 °/$_{oo}$ in the epilimnion, –25.4 °/$_{oo}$ and –26.1 °/$_{oo}$ in the metalimnion and -24.5 °/$_{oo}$ and –25.4 °/$_{oo}$ in the hypolimnion.

Particulate organic nitrogen (PON) $\delta^{15}N$ signatures were most enriched in May (3.9 °/$_{oo}$± 0.2) and depleted in August (2.5 °/$_{oo}$± 1.3) (1992), and in 1993, they were most enriched in April (4.4 °/$_{oo}$ ± 0.3) and depleted in August (1.9 °/$_{oo}$ ±0.9).

3.3.3 - Zooplankton and *Mysis relicta*

The mean $\delta^{13}C$ signature of zooplankton from May 1992 to July 1993 was $-26.2\,^{\circ}/_{oo} \pm 1.2$, but signatures varied among sampling dates (Fig.3.3). Signatures were most enriched in July 1993 ($-24.9\,^{\circ}/_{oo} \pm 0.6$) and depleted in May 1993 ($-27.4\,^{\circ}/_{oo} \pm 0.3$). $\delta^{15}N$ values ranged from $3.1\,^{\circ}/_{oo}$ in May 1992 to 8.1 in April 1993, with a mean of $6.1\,^{\circ}/_{oo} \pm 1.3$.

Zooplankton included species of Cladocera (*Bosmina*, *Daphnia*, *Leptodora*, *Diaphanosoma*, *Holopedium*, *Bythotrepes*, *Chydorus*), copepods (Calanoida, Cyclopoida, nauplii) and rotifers (*Keratella*, *Asplancha*, *Brachionus*). The numerical composition of zooplankton in the top 10 m of the water column was dominated by nauplii in May 1992 and June 1992 (57.20% and 68.77% respectively), followed by cyclopoid copepods (22.13%) in May 1992 or rotifers (14.00%) in June 1992. Rotifers were most abundant on 15th July (49.7%) and 19th August (70.37%), followed by nauplii at both times. Below 15m the dominant organisms were nauplii and Cyclopoida in May, and nauplii and rotifers in June. In July, nauplii made up 53.45% and calanoid copepods 29.6%. Rotifers reached 51.15% followed by nauplii (25.97%) in August.

The omnivorous planktonic crustacean *Mysis relicta* had $\delta^{13}C$ values most depleted in May 1992 ($-27.2 \pm 1.0\,^{\circ}/_{oo}$) and most enriched in September 1992 ($-24.8\,^{\circ}/_{oo} \pm 0.4$). $\delta^{15}N$ signatures varied little with a mean of $8.7\,^{\circ}/_{oo} \pm 0.9$.

3.4 - Discussion

3.4.1 – DIC and POM

Carbon isotope signatures of POM varied temporally and spatially. The relative DIC delta values, its concentration, and mode of photosynthetic uptake (Shelske and Hodell 1991; Fogel and Cifuentes 1993) influence POM signatures. DIC isotope signatures remained fairly constant throughout the year, with a slight enrichment observed towards autumn. Physical parameters such as temperature and light directly affect the metabolism and isotopic signatures of algae, which may be reflected in changes in the remaining substrate DIC.

Temperature influences the DIC pool in two ways. First, the lower temperatures during isothermal periods should enhance CO_2 (aq) solubility, as confirmed by my observation that CO_2 (aq) contributes more in spring (= 3.15%) and less in summer (= 2.75%). This higher concentration of CO_2 in spring lowers the isotopic signatures of the DIC since CO_2 (aq) is depleted relative to bicarbonate (Mook et al. 1974). Accumulation of biogenic CO_2 during winter ice cover should add to the DIC pool as shown by the more depleted signatures in March 1993. In the summer CO_2 contributes less to the total DIC pool, hence more enriched signatures are to be expected. Second, warmer water temperatures as the season progresses increases photosynthetic rates and, if CO_2 is not limiting, discrimination against ^{13}C will occur leaving the substrate DIC more enriched.

Changes in the DIC signatures influence the delta values of photosynthetically fixed carbon. During the 1992 field season, bulk POM exhibited no real change from May through July, after which a steady strong enrichment in the signatures was observed from August until October.

In aquatic ecosystems, photosynthesis produces organic matter depleted in ^{13}C relative to the inorganic source. This is mainly due to isotopic discrimination by RUBISCO. Under conditions of CO_2 saturation this enzyme has been shown to exhibit a large discrimination against ^{13}C (ca. 28 $^{o}/_{oo}$, Guy et al. 1987). Therefore, if POM in Colpoys Bay were dominated by algae that are obligate CO_2 (aq) users, it would have a carbon signature around -38.0 $^{o}/_{oo}$. Such depleted signatures were never observed during the study period. Given the observed isotopic range of POM, the fractionation associated with photosynthesis was more likely to be around -15 $^{o}/_{oo}$. Sharkey and Berry (1985) suggested that a diffusion resistance resulting in low concentrations of CO_2 at the site of enzymatic activity would lessen carbon discrimination since most of the carbon will be utilized before it can leak out of the cell. The discrimination observed in Colpoys Bay may be in part due to in situ carbon limitation which would result in elevated isotope signatures. However, utilization of HCO_3^- is also associated with more enriched signatures.

Phytoplankton species differ in their ability to use CO_2 or HCO_3^-. While I did not identify the algae present in 1992-1993, data from May through October 1991 are available in Maly (1992). Total phytoplankton abundance was highest in May and June, with an irregular but persistent decline from early stratification until mid-October. The phytoplankton was dominated by Bacillariophycea from May until late

June (isothermal conditions), with a short-lived maximum in the abundance of Cryptophycea at the end of June. Such a spring bloom could cause some temporary carbon limitation.

During the period of thermal stratification in 1991, phytoplankton was dominated by species of Chlorophyceae in the metalimnion and Chrysophyceae in the epilimnion (Maly 1992). In general, diatom abundance decreased from spring to autumn as the abundances of Cyanophyceae and Chlorophyceae steadily increased. Some of the diatom genera found in Colpoys Bay (e.g *Asterionella, Melosira, and Fragilaria*) are thought to be inefficient HCO_3^- users (Maberly and Spence 1983). Therefore, those diatoms were probably carbon-limited to some extent, in which case carbon isotope discrimination is decreased. In addition, the subsequent dominance of blue-green and green algae, which have been reported to use HCO_3^- during late summer through autumn, would further enrich POM carbon signatures.

Another alternative is that autumn storms act to resuspend littoral sediments and scour shoreline substrates, introducing periphytic material to the water column. In Colpoys Bay littoral diatoms can contribute 26% to the total diatom flux sedimenting out of the metalimnion (Maly 1992). The maximum flux of littoral matter corresponded to periods of very unsettled weather in September and October. Climate data obtained from Environment Canada showed the frequency of days with strong winds (≥20 km/h) to increase from August to November for 1992 and 1993. If periphytic matter is also enriched during autumn, and in combination with more enriched DIC signatures in September, the inclusion of littoral seston would contribute to further enrichement of POM signatures in October. In spring, slightly

depleted DIC signatures and high enzymatic discrimination against ^{13}C caused POM to be more depleted than in autumn.

In aquatic ecosystems, fractionation by biological processes can lead to changes in the nitrogen isotope ratios in the dissolved pools of nitrogen (Horrigan et al. 1990). Such processes include assimilation of nitrogen by primary producers, nitrification, denitrification and reduction of nitrate to ammonium (Wada and Hattori 1978; Mariotti et al. 1981, Horrigan et al. 1990). Denitrification leads to a ^{15}N enrichment of the residual nitrate while ^{15}N enrichment of the residual ammonia occurs during nitrification; hence nitrates produced by this processes are ^{15}N depleted (Mariotti et al. 1984). The isotopic signature of PON during 1993 varied seasonaly, with relatively more enriched signatures in April and May. It has been suggested that the $\delta^{15}N$ of POM increases with increasing productivity of the lake basin (Gu et al. 1996). If a spring bloom dominated by diatoms is followed after stratification by an increase in blue-green and green algae [as reported by Maly (1992)], this would contribute to a shift from more enriched spring signatures to more depleted in summer, if those blue-green algae were utilizing N_2 from atmospheric nitrogen.

3.4.2 – Zooplankton and *Mysis relicta*

As with POM, signatures of zooplankton seem likely to reflect seasonal changes in species composition. There was a departure, with signatures more depleted than POM, in October 1992. The reason for this is not very clear; however, the numerical composition of zooplankton was dominated by nauplii and cyclopoid

copepods in spring and rotifers in summer. Those different types of zooplankton were probably grazing selectively on different phytoplankton. Another potential confounding factor is lipid accumulation; Leggett (1998) reported that lipid-extracted zooplankton were 1 to 2 $^{o}/_{oo}$ more enriched than unextracted, which could account for some of the observed departure.

Nitrogen signatures of zooplankton were between 4 $^{o}/_{oo}$ and 8 $^{o}/_{oo}$ for most of the year. Unexpectedly, the zooplankton signature in May 1992 was only slightly more enriched than POM. Graham (1997), in a study of zooplankton and POM, demonstrate that *Diacyclops thomasi* actively selected for N_2 fixing blue-greens which dropped its $\delta^{15}N$ signature below that of *Daphnia* sp feeding on other primary producers in the same lake. It is probable that selective grazing upon different algal assemblages is occurring in Colpoys Bay.

Mysids are omnivorous crustaceans that migrate between the sediment surface and the metalimnion of lakes. They both compete with, and prey on, zooplankton (Johannson et al. 1994). Leggett (1998) estimated that *Mysis relicta* could have a diet of roughly 50:50 mixture of diatoms and copepods in Lake Ontario. The seasonal change in $\delta^{13}C$ $^{o}/_{oo}$ is similar to zooplankton during most of the first year and the nitrogen data suggest that it is relying mostly on zooplankton.

3.5. Conclusions

Several processes influence the $\delta^{13}C$ of DIC and POM at any given point in the season. Among those, both physical (e.g temperature) and biological (e.g. algal species) parameters seem to be key. The observed $\delta^{13}C$ signature depends on which process is dominant at any given time.

The results of my work suggest that the level of fluctuation in the $\delta^{13}C$ of POM is influenced by algal species changes in response to changes in the type of aquatic DIC and seasonal intrusion of littoral matter.

The seasonal fluctuations observed at the primary producer level were at least partially responsible for the variability observed in zooplanktonic community. A more through investigation of the zooplankton community is needed in order to clarify its linkages with primary producers and DIC.

Therefore, an understanding of system biogeocheochemistry and its potential influence on the $\delta^{13}C$ of primary producers should be an essential part of any study where carbon isotopes are used to make suppositions regarding carbon sources.

Table 3.1: Seasonal changes in carbonate chemistry of Colpoys Bay. Ct total carbon concentration

Date	Depth (m)	T °C	Ct (μmol/L)	HCO_3 (μmol/L)	CO_{2aq} (μmol/L)	CO_3^{2-} (μmol/L)	HCO_3 %	CO_{2aq} %	CO_3^{2-} %	$\delta^{13}DIC$ ‰	$\delta^{13}CO_2$ ‰
12/Jun/92	0	8.5	3285.0	3180.3	94.7	9.96	96.81	2.88	0.30	0.06	-10.56
12/Jun/92	5	7.6	1609.1	1557.4	46.9	4.78	96.78	2.92	0.30	0.12	-10.59
12/Jun/92	10	7.1	999.5	967.2	29.4	2.94	96.77	2.94	0.29	0.04	-10.73
12/Jun/92	15	6.4	1813.2	1754.1	53.86	5.25	96.74	2.97	0.29	-0.39	-11.24
12/Jun/92	20	6.4	1016.8	983.6	30.2	2.94	96.74	2.97	0.29	-0.56	-11.4
12/Jun/92	25	6.3	1745.5	1688.5	51.9	5.04	96.74	2.97	0.29	-0.33	-11.19
25/Jun/92	0	10.4	3282.9	3180.3	92.16	10.39	96.88	2.81	0.32	-1.47	-11.87
25/Jun/92	5	6.0	1610.1	1557.4	48.09	4.62	96.73	2.99	0.29	-1.30	-12.19
25/Jun/92	10	5.9	1000.0	967.2	29.93	2.86	96.72	2.99	0.29	-1.35	-12.25
25/Jun/92	15	5.7	1813.7	1754.1	54.43	5.16	96.71	3.00	0.28	0.46	-10.47
25/Jun/92	20	5.1	1017.3	983.6	30.8	2.86	96.69	3.03	0.28	0.28	-10.71
15/Jul/92	0	13.9	1960.7	1901.6	52.3	6.73	96.99	2.67	0.34	0.36	-9.64
15/Jul/92	5	11.3	1776.3	1721.3	49.2	5.74	96.91	2.77	0.32	0.43	-9.87
15/Jul/92	10	10.6	2131.9	2065.6	59.64	6.78	96.88	2.80	0.32	0.33	-10.04
15/Jul/92	15	9.7	1777.2	1721.3	50.39	5.54	96.85	2.84	0.31	0.23	-10.25
15/Jul/92	20	8.6	2031.9	1967.2	58.51	6.18	96.82	2.88	0.30	0.38	-10.23
15/Jul/92	25	7.5	2066.5	2000.0	60.41	6.13	96.78	2.92	0.30	-2.13	-12.84
15/Jul/92	30	6.4	2033.5	1967.2	60.40	5.88	96.74	2.97	0.29	-1.22	-12.06
19/Aug/92	0	15.6	895.4	868.9	23.35	3.18	97.04	2.61	0.36	-0.41	-10.23
19/Aug/92	10	14.9	1585.7	1538.4	41.78	5.55	97.02	2.63	0.35	0.35	-9.56
19/Aug/92	15	14.6	1842.0	1786.9	48.75	6.40	97.01	2.65	0.35	0.61	-9.33
19/Aug/92	20	12.9	1724.6	1672.1	46.69	5.78	96.96	2.71	0.34	-0.55	-10.67
19/Aug/92	25	10.9	1678.4	1626.23	46.81	5.37	96.89	2.79	0.32	-0.38	-10.72
19/Aug/92	30	8.2	1795.1	1737.71	51.99	5.41	96.80	2.90	0.30	-0.93	-11.57
24/Sep/92	0	14.9	1282.5	1244.26	33.79	4.49	97.02	2.63	0.35	0.24	-9.66
24/Sep/92	5	14.9	1409.3	1367.21	37.12	4.93	97.02	2.63	0.35	0.47	-9.44
24/Sep/92	10	14.8	1424.5	1381.96	37.55	4.98	97.01	2.64	0.35	0.51	-9.4
24/Sep/92	15	14.7	1265.7	1227.87	33.42	4.41	97.01	2.64	0.35	0.67	-9.25
24/Sep/92	20	12.9	1401.7	1359.01	37.94	4.7	96.96	2.71	0.34	0.58	-9.54
24/Sep/92	25	9.9	1413.2	1368.85	39.96	4.42	96.86	2.83	0.31	0.33	-10.13
24/Sep/92	30	8.1	1407.3	1407.34	40.82	4.23	96.80	2.90	0.30	0.34	-10.32
29/Oct/92	0	7.1	1515.4	1466.39	44.6	4.45	96.76	2.94	0.29	0.07	-10.71
29/Oct/92	10	7.0	1679.8	1625.41	49.47	4.93	96.76	2.94	0.29	0.34	-10.44
29/Oct/92	20	6.5	1625.9	1572.95	48.22	4.71	96.74	2.97	0.29	-0.04	-10.87
29/Oct/92	30	6.0	1593.9	1541.8	47.61	4.57	96.73	2.99	0.29	-0.25	-11.14
11/Mar/93	0	2.5	1748.0	1688.52	54.86	4.63	96.60	3.14	0.26	-1.29	-12.57
11/Mar/93	10	2.5	1934.7	1868.85	60.72	5.13	96.60	3.14	0.27	-0.21	-11.48
11/Mar/93	20	2.5	1849.8	1786.88	58.06	4.9	96.60	3.14	0.26	-0.18	-11.45
11/Mar/93	30	3.0	1781.6	1721.31	55.52	4.77	96.62	3.12	0.27	-0.42	-11.64
10/May/93	0	6.0	1745.7	1688.52	52.14	5.01	96.73	2.99	0.29	nd	nd
10/May/93	15	5.2	1729.2	1672.13	52.24	4.87	96.70	3.02	0.28	nd	nd
10/May/93	30	5.0	1729.4	1672.13	52.39	4.85	96.69	3.03	0.28	nd	nd

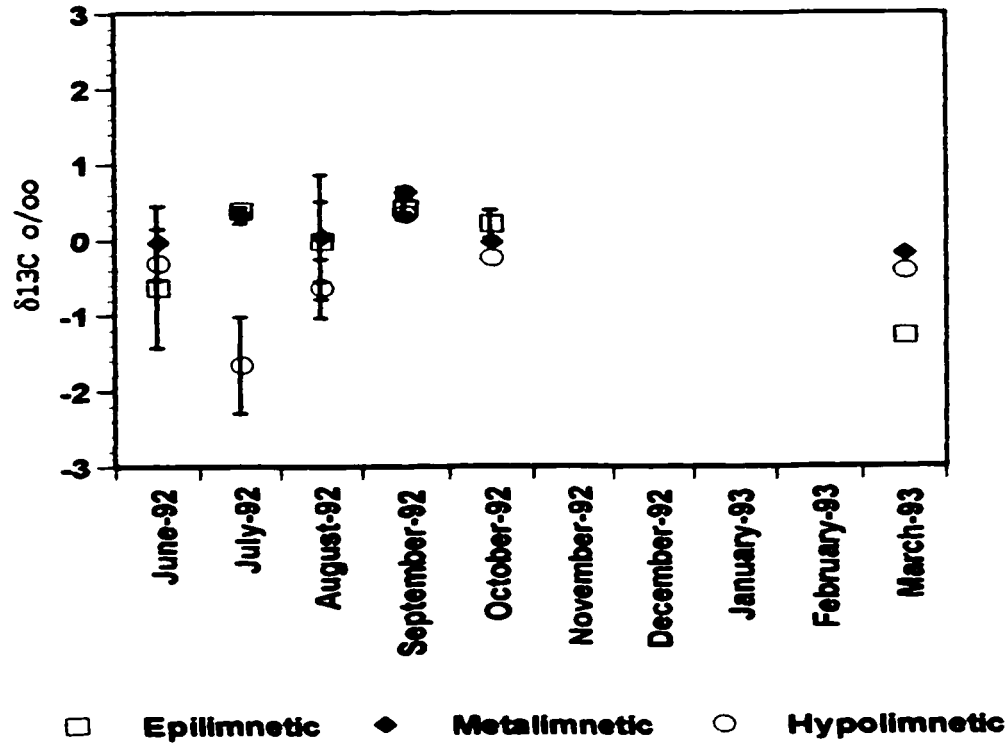


Figure 3.1: DIC $\delta^{13}C$ seasonal variation for each depth stratum. Bars are standard deviations from the mean of samples obtained at different depths within the epilimnion., metalimnion or hypolimnion.

Table 3.2a: Results of one-way ANOVAs to detect temporal differences in the $\delta^{13}C$ of POM at each size fraction.

Size Fraction	df	MS	F	P	r^2
0.7 ≥ 1.2μm	8	4.710	3.850	0.006	0.58
1.2 ≥ 2.7μm	10	3.024	3.919	0.004	0.64
2.7 ≥ 40μm	9	5.585	5.280	0.001	0.63

Table 3.2b: Results of one-way ANOVAs to detect temporal differences in the $\delta^{13}C$ of POM at each depth stratum.

Depth strata	df	MS	F	P	r^2
Epilimnion	8	3.279	1.607	0.2	0.45
Metalimnion	11	4.729	5.705	<0.000	0.53
Hypolimnion	7	14.668	6.909	<0.000	0.64

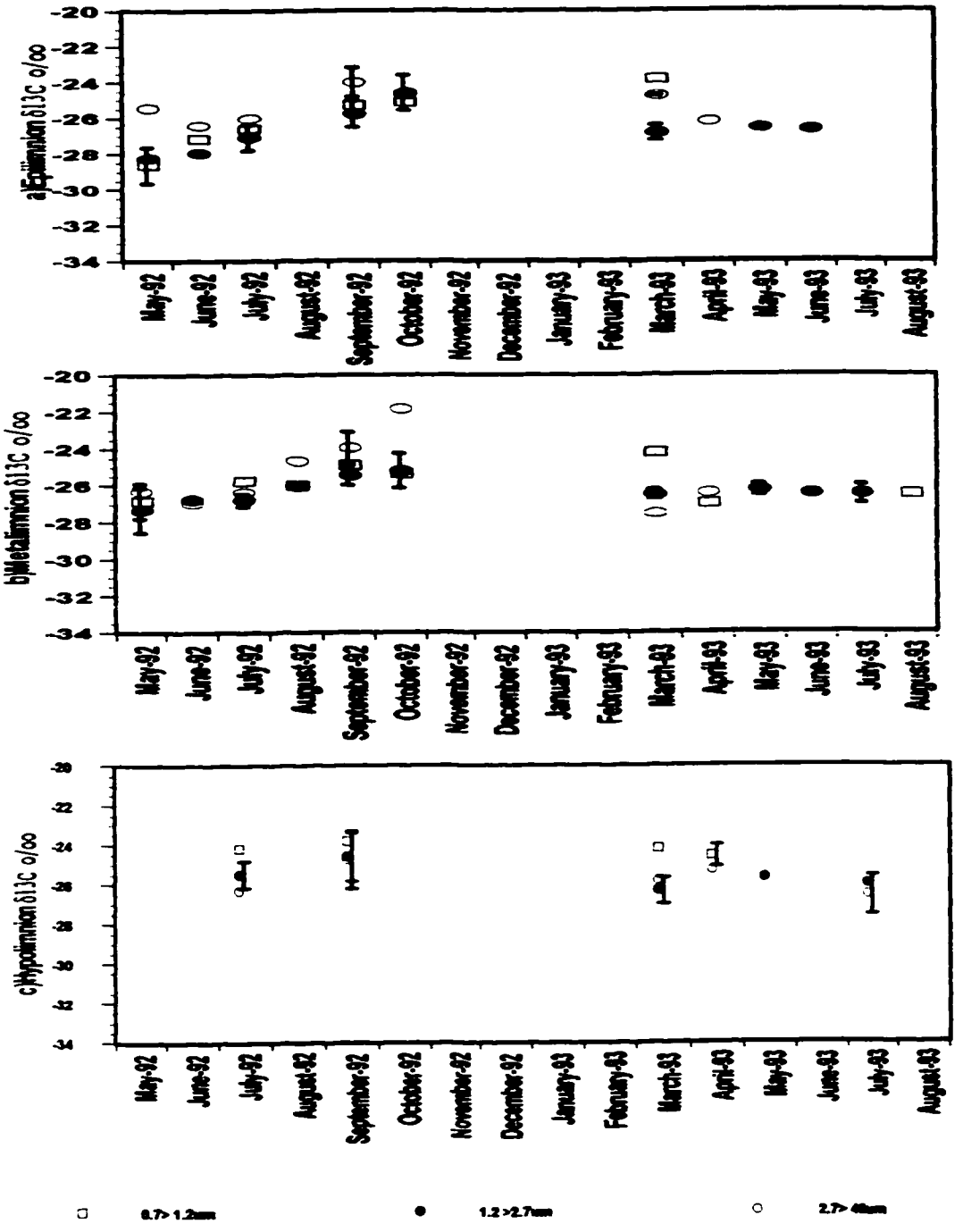


Fig 3.2: Seasonal variation of POM $\delta^{13}C$ ‰ signatures at a) Epilimnion; b) Metalimnion and c) Hypolimnion for each size fraction from May to October 1992 and March to August 1993. * indicates not enough material for analysis.

Table 3.3. $\delta^{13}C$ of POM during the first field season (May to October 1992) and during second field season (March to August 1993).

Depth stratum	Particle size	First year $\delta^{13}C$
	0.7-1.2 μm	-26.9±1.9
Epilimnion	1.2-2.7 μm	-26.9±1.6
	2.7-40 μm	-25.4±1.0
	0.7-1.2 μm	-25.4±0.9
Metalimnion	1.2-2.7 μm	-25.9±1.1
	2.7-40 μm	-24.7±1.7
	0.7-1.2 μm	-23.9±0.6
Hypolimnion	1.2-2.7 μm	-24.5±0.6
	2.7-40 μm	-24.8±1.4
Depth stratum	**Particle size**	**Second year $\delta^{13}C$**
	0.7-1.2 μm	-23.8
Epilimnion	1.2-2.7 μm	-26.7±0.1
	2.7-60 μm	-25.7±0.9
	0.7-1.2 μm	-25.1±1.3
Metalimnion	1.2-2.7 μm	-26.5±0.2
	2.7-60 μm	-26.8±1.1
	0.7-1.2 μm	-24.3±0.2
Hypolimnion	1.2-2.7 μm	-26.0±0.3
	2.7-60 μm	-25.9±0.6

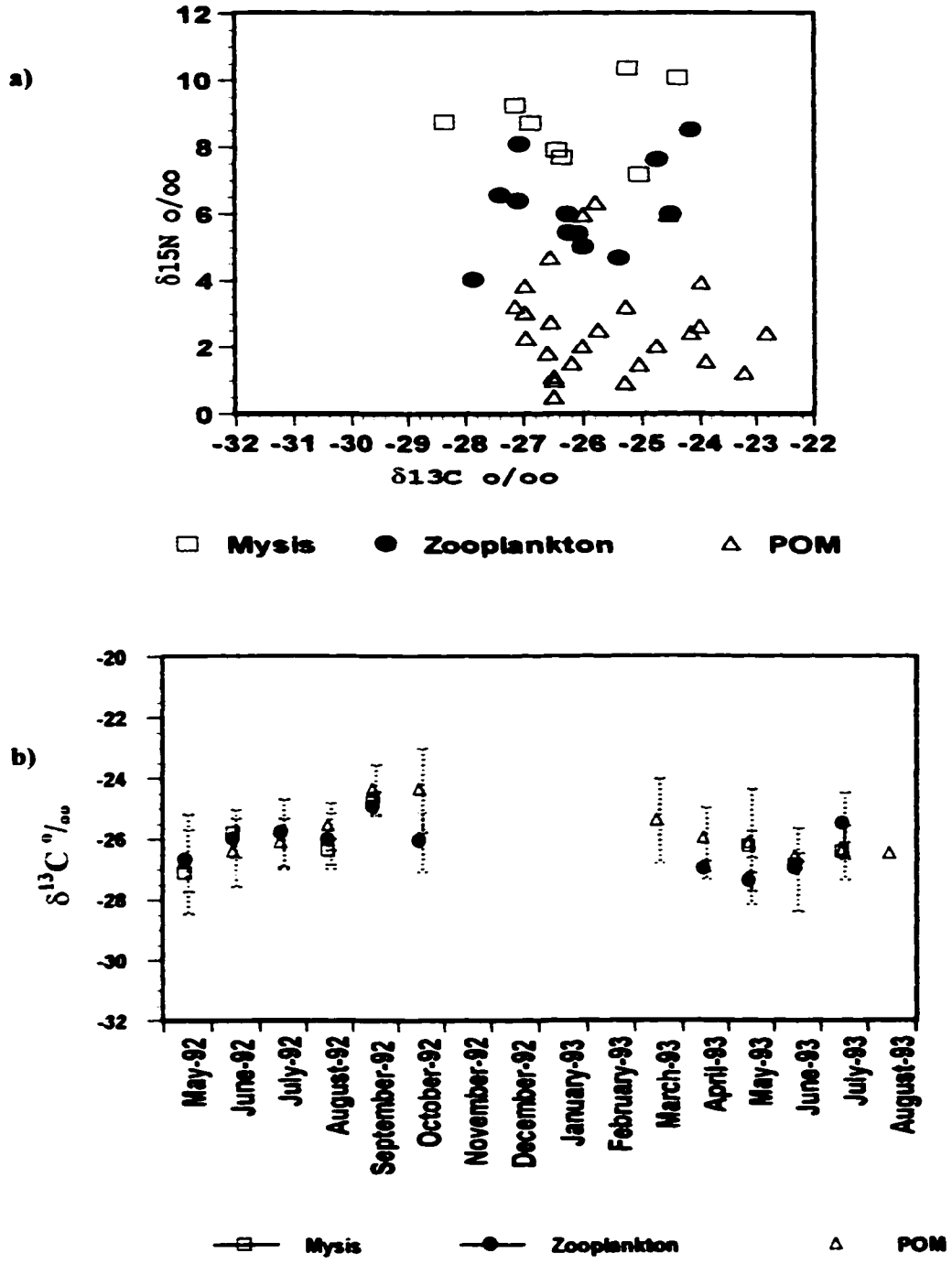


Figure 3.3: a)$\delta^{13}C$ °/$_{oo}$ and $\delta^{15}N$ °/$_{oo}$ for POM, zooplankton and *Mysis* and b)$\delta^{13}C$ °/$_{oo}$ seasonal variation for POM, zooplankton and *Mysis* POM error bars are standard deviations from the means of epilimnion, metalimnion and hypolimnion. Error bars for *Mysis* and zooplankton are standard deviation from means of replicate samples

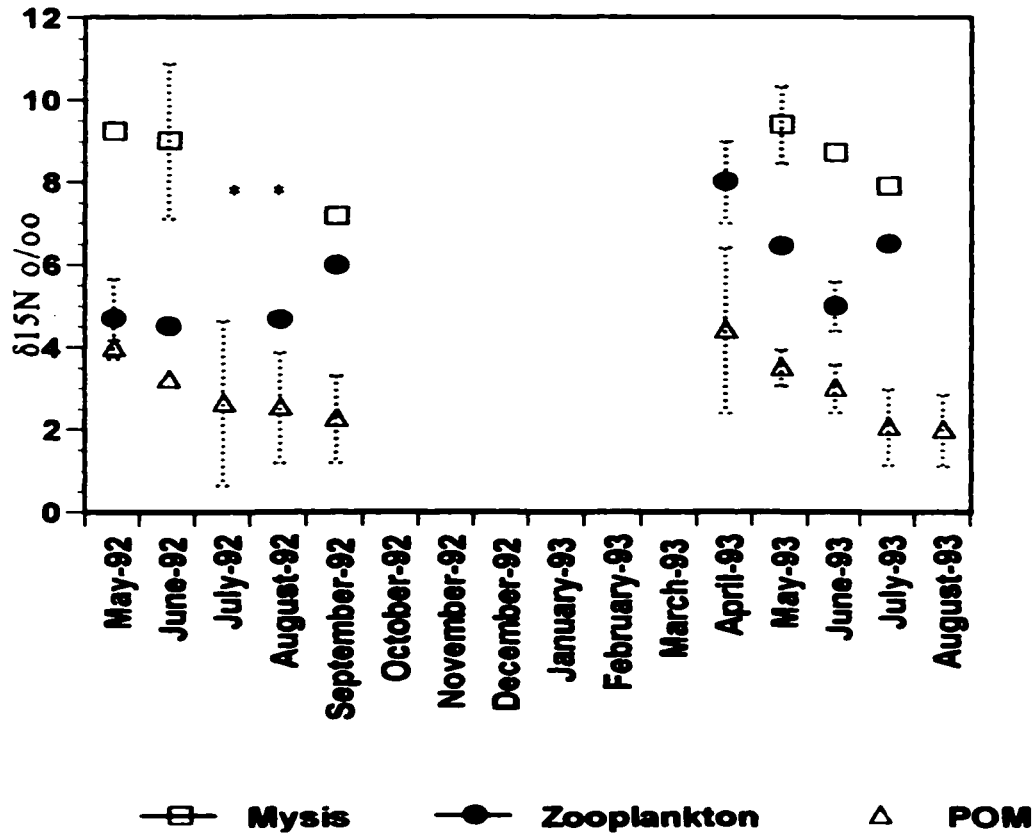


Figure 3.4: $\delta^{15}N$ ‰ of seasonal variation for *Mysis*, zooplankton and bulk POM. Error bars are standard deviation from the means of replicate samples. * Denotes not available for analysis.

Chapter 4: Benthic Community Trophic Structure Using Carbon and Nitrogen Stable Isotopes

Abstract

The trophic structure of benthic macroinvertebrate communities in littoral (≤ 15m) and profundal (≥ 30m) areas of Colpoys Bay, Georgian Bay was assessed using stable isotopes of carbon and nitrogen. Invertebrates were collected with a dredge from depths of 5, 15, 30 and 50m. Potential energy sources included periphyton, macrophytes, POM and allochthonous organic matter.

Spatial and temporal isotopic variations were observed among both primary producers and primary consumers. Lower trophic levels tend to respond quickly to abiotic changes in the environment and are therefore isotopically very variable.

Periphyton was the most important source of energy to benthic animals within littoral areas of Colpoys Bay. Vascular macrophytes and macroalgae may be important as refugia against predation, but are not directly consumed by invertebrates. Although other works have suggested that allochothonous matter could be important in oligotrophic lakes, my observations did not support this hypothesis. Invertebrates in the profundal region appear to rely almost exclusively on sedimenting organic matter (POM).

Overall the results of my work suggests that benthic primary production is the main energy source for the benthic invertebrates of Colpoys Bay.

4.1 - Introduction

The distribution, abundance and diversity of benthic invertebrates in lakes are directly affected by the complexity of the habitat. The littoral regions of lakes are characterized by a variety of habitats supporting a rich and abundant benthic community. The more uniform conditions in the profundal support a much less diverse benthic fauna. Jonasson (1984) used a community and habitat approach to describe the bathymetric distribution of invertebrates in Lake Esrom. Herbivores dominated only in the surf zone; their importance was markedly reduced in the macrophyte zone. Filter feeders occurred mostly in the sublittoral but also in the littoral. Species diversity was much greater in the littoral than in the sublittoral and profundal, where detritivores dominated entirely. Potential energy sources for littoral communities include allochothonous matter, periphythic algae, POM and macrophytic vegetation. Phytoplankton is more important offshore; spring algal blooms can provide an important food source for profundal benthos (Gardner et al. 1985). With so many different sources of organic matter, the analysis of specific pathways of energy in benthic food webs can be very difficult.

Food web investigations have traditionally been based upon gut analyses. The functional feeding group concept, widely used in aquatic ecology (Merrit and Cummins 1996), is useful to specify how an animal captures its food; but assigning an obligate trophic status is risky since a given taxon can change its feeding mode and trophic state during its life cycle. Stomach content analyses can indicate specific foods consumed at a certain point in time, representing a static measure of a dynamic

process which is not necessarily representative of foods assimilated over the longer term. In this context stable isotopes of carbon and nitrogen can be valuable tools.

Natural carbon isotope (^{13}C and ^{12}C) abundance in the aquatic environment has been used to study the carbon cycle on a global scale, to quantify and characterize the carbon flux at different trophic levels (Fry 1991, Gu et al. 1997) and to identify organic carbon sources for animals (Haines and Montage 1979). Stable carbon isotope analysis (SCIA) is a powerful technique for the elucidation of energy flow through consumer links in food webs provided that the sources of organic matter are isotopically distinct. The determination of primary energy sources (i.e. benthic vs pelagic) is possible because there is very little carbon isotope fractionation between an organism and its main food source, usually 0 to 1‰. It is not uncommon however, for the signatures of aquatic primary producers at a site to vary by up to 10‰ for carbon (Kline et al. 1990, Fogel et al. 1992, Bunn and Boon 1993). Very few researchers have conducted a thorough analysis of the variation in autotrophic stable isotope signatures. This casts doubt on the conclusions drawn from some studies and can limit the resolving power of SIA (France 1995). The factors that influence the isotope signatures of benthic primary producers in Colpoys Bay, with an emphasis on biogeochemical processes, are reviewed in this chapter.

Stable nitrogen isotopes (^{15}N and ^{14}N) have been utilized to determine the trophic position of lentic animals. Due to the relative retention of ^{15}N over ^{14}N, animals are usually +2 to +5 ‰ more enriched than their diets (Minigawa and Wada 1984; Owens 1987; Peterson and Fry 1987). The use of stable isotopes of both carbon and nitrogen in food web studies can allow the identification of primary food sources,

and pathways through which food energy is channeled. The primary objectives of this chapter are to determine which sources of energy are most important to the dominant benthic macroinvertebrates in different habitats of Colpoys Bay, and also to describe the trophic structure within each habitat.

4.2 - Study Sites

The substrate in Colpoys Bay, southwestern Georgian Bay consists of a combination of dolostone, shale and sandstone along the shore to depths up to 7.5m (Farwell and Duthie 1993) with sand and glacio lacustrine mud in deeper water. Invertebrates were collected from 3 main sites (Fig.4.1). Site A (81°08'W, 44°46'N) was located near the western tip of the bay at a depth of 5m. A rock substrate extended 15m to 20m from the shoreline to a depth of 3.5m, giving way to a transitional zone of gravel and coarse sand. This is followed by a silt and sand substrate which supports a sparse growth of charophytes and scattered vascular macrophytes, mainly *Potamogeton* spp. and *Myriophyllum* sp. Site B at Mallory beach (81°04'W, 44°47'N) was also situated along the western side about 6 km north of site A. The rocky substrate extended approximately 20 m offshore to a depth of 5 m, followed by sand then a charophyte zone (about 40 m offshore) beginning at a depth of 7.5m. Samples were collected at 15 m and 30 m depths. Site C (81°03'W, 44°49'N) was approximately 6.5 km north of site B near Gravelly Point. It was the most exposed site, the shoreline had the steepest slope and there were no

macrophytes. Invertebrate samples were collected from postglacio-lacustrine sediment at a depth of 50 m.

These sites were chosen because of their differences in habitat complexity and potential sources of energy for benthic communities. At the more littoral sites (5 and 15 m), submerged vascular macrophytes, charophytes, periphytic matter and POM could be important sources locally. The significance of periphyton should decrease with increasing distance from shore. POM input should increase with thickness of water column, hence this material was expected to be fueling the communities at the deeper sites. Allochthonous organic matter should be more important near shore and at the head of the bay.

4.3 - Material and Methods

Samples of two charophytes (*Chara* spp. and *Nitella flexillis*) were collected from depths 5 and 15m by hand while scuba diving on a monthly basis from May through October 1992, and March 1993. Several vascular macrophytes were collected in July, August, September and October 1992. Periphyton was epilithic material (mostly diatoms, detritus and some Chlorophycea) scraped from the surface of rocks collected near the shore, epiphytic material (mostly filamentous Chlorophycea) removed from *Chara* and macrophytes; both were collected from May through October 1992. The filamentous green algae *Cladophora glomerata* was collected on

the same occasions as periphyton. Allochthonous material was collected in September and October 1992, by handpicking leaves from dominant tree species along the shore.

Sediment samples were also collected by scuba diving during the months of July, August and September 1992, along a 60 m transect line from 3.5 to 25 m in depth off Mallory beach beginning at the base of the rock area. Ten cm long plexiglas tubes (5 cm i.d.) were used to collected 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 top two centimeters of frozen water were discarded and the first cm of sediment was sliced off the top of the core and used for isotopic analysis. Prior to isotopic analysis sediment samples were acidified with 10% HCL at 70° C for 48 h, then distilled water was added until pH reached 6. Those samples were dried and stored until analysis.

Macroinvertebrates were collected with a dredge during the open water season, or with an Ekman grab during the winter. A few hydropsychid caddisflies were removed from the rocks used for epilithon samples. Invertebrates were sorted to the family level and held alive for 24 to 48 h in mesh cages in lake water to allow clearance of stomach contents, then were bagged and frozen for further analysis. In the laboratory at the University of Waterloo, all animals were measured (either length or head width) and identified to genus, then oven dried at 60°C, pulverized and stored in a desiccator.

Autochthonous plant samples were identified to genus and cleared of debris with the aid of a dissecting microscope. Samples were washed with 10% HCL to

remove inorganic carbon, then oven dried (60°C) for 48h, pulverized and kept in a desiccator until needed.

Isotopic analyses for primary producers, macroinvertebrate and sediment samples containing 1 to 5mg of organic matter were performed at the Environmental Isotope Laboratory, Department of Earth Sciences, University of Waterloo, Ontario using a Fisons Instruments VG Isochrom-EA continuous flow mass spectrometer with an analytic precision of $\pm 0.2^{o}/_{oo}$ for carbon and $\pm 0.3^{o}/_{oo}$ for nitrogen. Isotope ratios are expressed as parts per mil deviation from the international standard reference materials VPPDB (Vienna Peedee belemnite) for carbon, and N_2 in the atmosphere (Mariotti 1983) for nitrogen as follows:

$$\delta^{13}C = [(^{13}C/^{12}C_{sample})/ {}^{13}C/^{12}C_{standard}) - 1] \times 10^{3}$$

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

4.4 – Results

4.4.1 - $\delta^{13}C$ and $\delta^{15}N$ of Benthic Community

4.4.1a - Primary Producers

Mean carbon isotope signatures from May 1992 to May 1993, of aquatic primary producers ranged from –26.1 °/₀₀ (epiphyton) to –10.1 °/₀₀ (vascular macrophytes) (Fig.4.2).

Mean carbon isotope signatures of epilithon were most ^{13}C depleted in May 1993 (-27.7 °/₀₀) and enriched in October 1992 (-20.1 °/₀₀, Table 4.1). *Cladophora* signatures showed the same pattern of enrichment towards autumn but seasonal differences were very small. Epiphytic algae were most depleted in summer (Fig. 4.3).

Mean nitrogen isotope values for epilithon varied from +0.2°/₀₀ (spring 1993) to +2.2°/₀₀ (summer 1992). Epiphyton nitrogen signatures varied little amongst seasons: +1.7°/₀₀ (spring), +1.2 °/₀₀ (summer) and +1.6 °/₀₀ (autumn) *Cladophora* nitrogen values varied from +0.1 °/₀₀ in spring 1993 to +2.8 °/₀₀ in summer 1992 (Table.4.2).

Carbon and nitrogen isotopes were obtained for four taxa of aquatic vascular macrophytes and two charophytes. Vascular macrophyte carbon isotope values ranged from -7.3°/₀₀ to -15.5°/₀₀ (mean = -10.1 °/₀₀) and did not differ between summer and autumn (T-test, df=16, t=0.58, p=0.57). Of the two charophytes *Chara*

globularis (mean = -13.2°/$_{oo}$) was more enriched than *Nitella flexillis* (mean = -24.8°/$_{oo}$). One-way-ANOVA showed significant carbon isotope changes over the seasons for both characean species (i.e. *Chara* F=4.47, p=0.05, r^2=0.66; *Nitella* F=55.01, p<0.000, r^2=0.96) with summer signatures more enriched than other seasons. Nitrogen signatures varied little amongst macrophytes: mean values were +1.4°/$_{oo}$ for vascular macrophytes, -0.3°/$_{oo}$ for *C. globularis* and +2.6°/$_{oo}$ for *N. flexillis*.

Allochthonous matter was represented by five plant species collected during September and October of 1992. Carbon signatures varied from -25.6°/$_{oo}$ to -30.2°/$_{oo}$, with a mean of -28.9 °/$_{oo}$. The mean of nitrogen signatures was +1.4°/$_{oo}$, and individuals species ranged from -2.2°/$_{oo}$ to +5.9°/$_{oo}$.

A 2 x 2 factorial ANOVA showed a significant depletion in the sediment carbon signatures with increasing depth (df = 4, f = 8.48, p = 0.001). There was no temporal variation as monthly means ranged from -23.9°/$_{oo}$ to -24.5°/$_{oo}$. Organic nitrogen was +2.45°/$_{oo}$, +2.87°/$_{oo}$ and +2.7°/$_{oo}$ in July, August and September, respectively (Table 4.3).

4.4.1b – Primary Consumers

Carbon and nitrogen signatures were determined for the most common taxa of Insecta (Diptera, Trichoptera and Ephemeroptera), Crustacea (Amphipoda, Isopoda and Decapoda) and Mollusca (Bivalvia and Gastropoda). These signatures were compared with the mean signatures of potential foods during the period of maximum growth of each invertebrate prior to collection, based on life history data described in Chapter 2. For example, animals collected in October, which had been growing rapidly since July, were compared with the mean signatures of epilithic algae, POM, etc. from July, August, September and October. Patterns of energy assimilation were investigated both by taxonomic classification (individual taxa) as well as by functional feeding groups (Merrit and Cummins 1996). If the functional feeding group concept is applicable to lentic invertebrates, isotopic signatures were expected to be similar within groups regardless of taxonomic classification.

Overall there was ^{13}C depletion and ^{15}N enrichment with increasing depth (Fig.4.4). This trend was most evident among the groups occurring at all sites (i.e. Amphipoda, Chironomidae and Tubificidae) and to a lesser extent within groups found only at littoral sites (i.e. Trichoptera, Ephemeroptera, Isopoda, Bivalvia and Gastropoda).

Within the littoral communities, all groups were slightly more ^{13}C depleted at 15 m than at 5 m (Figure 4.5 a,b). Significant differences in the carbon isotope signatures between the two depths were found for Bivalvia (Two sample T-test $t=5.29$, $df=2$, $p=0.034$), Chironomidae ($t=2.13$, $df=39$, $p=0.039$), Ephemeroptera ($t=2.26$, $df=8$, $p=0.05$) and Trichoptera ($t=2.36$, $df=13$, $p=0.035$). Bivalves (*Pisidium* spp.) were the most depleted group

at both sites, with annual means at 5 and 15 m of –22.3 °/₀₀ and –26.3 °/₀₀, respectively, followed by Trichoptera at 5m (-21.4°/₀₀) and Ephemeroptera at 15 m (-24.6 °/₀₀). The most enriched group at 5 m was Tubificidae (-18.1°/₀₀) and the crayfish *Orconecties propinquus* at 15m (-19.9 °/₀₀).

Annual mean nitrogen signatures were more ^{15}N enriched at 15m than at 5m. Chironomids were the most enriched group at 5m (+5.3°/₀₀) and crayfish *Orconectes propinquus* at 15m (+6.6°/₀₀). The most depleted group at both depths was Tubificidae with signatures at 5m and 15m respectively of, +3.1°/₀₀ and +3.4°/₀₀.

Carbon isotope signatures of most littoral invertebrates at 5 m became significantly more $\delta^{13}C$ enriched from spring through autumn 1992 (Figs: 4.6 a,b,c). This temporal variation was strong and significant for Chironomidae (One-way ANOVA, df=3, f=5.97, p=0.01, r^2=0.64) and Amphipoda (ANOVA, df=2, f=7.32, p=0.046, r^2=0.79) and, to a lesser extent, Trichoptera (ANOVA, df=2, f=4.18, p=0.08, r^2=0.63). Amphipods (*Hyallela azteca* and *Gammarus pseudolimneaus*) became 2 to 5 °/₀₀ more enriched in autumn relative to spring (Table 4.3). Chironomids showed a steady enrichment from spring (-22.2°/₀₀) to autumn (-18.5°/₀₀). The same pattern was observed among isopods (*Caecidotea and Lirceus*) and tubificids.

Hydropsychid caddisflies, collected from the rocky shore in autumn, were in their fourth larval instar, so their isotope signatures reflected long term feeding or summer growth. While these are generally thought to be filter-feeders, carbon signatures varied somewhat: *Cheumatopsyche* was the most depleted (-27.1°/₀₀), followed by *Hydropsyche recurvata* (-25.8 °/₀₀) and *H.bifida* (-24.9 °/₀₀).

The mean carbon signatures of Chironomidae, Ephemeroptera, Amphipoda and Isopoda at 15 m were also more enriched in autumn than spring, but the seasonal change was not as strong or significant as at 5 m (Fig. 4.7.a,b,c) Opposite to the general trend were the chironomids *Gillotia*, *Chironomus* and *Polypedilum* and the isopod *C. intermedius*, with autumn signatures more depleted than spring. No seasonal changes were observed for nitrogen signatures at either 5 or 15 m.

At the deeper sites primary consumers were more ^{13}C-depleted at 50 m than 30 m. *D. hoyi*, tubificids and a few genera of chironomids were more depleted at 50 m than at 30 m. *D. hoyi* was on average 8.5 $^{o}/_{oo}$ more ^{13}C-depleted than tubificids, and 6.7 $^{o}/_{oo}$ more ^{13}C-depleted than chironomids. In contrast, mean nitrogen signatures were more enriched at the deeper site for most taxa except *Diporeia*.

4.5 - Discussion

4.5.1 - Benthic Primary Producers Isotope Variability

In Colpoys Bay, benthic primary producers displayed a wide range of variation in both carbon and nitrogen isotopes. Differences were observed according to species and sample date. The factors that dictate such variability are complex. In order to interpret the inevitable isotope variability at higher trophic levels it is necessary to understand the controlling factors acting on primary producers.

The variability in annual mean $\delta^{13}C$ signatures of benthic primary producers in Colpoys Bay is a reflection of differences in the mode of carbon uptake by the different plants. The ambient concentration of DIC suggests that carbon is not limiting, and, with a mean estimated $CO_2(aq)$ signature of -10.7 $^{o}/_{oo}$, the fractionation observed for some primary producers in this lake can not solely be attributed to the enzyme (RUBISCO) pathway. For the periphytic community, such a discrepancy between the theoretical and observed fractionation can be attributed to carbon concentration at the site of the enzymatic activity: Sharkey and Berry (1985) showed that when inorganic carbon concentrations are low, discrimination will be reduced since most of the carbon will be utilized before it can leak out of the cell.

This suggests that the discrimination observed in the benthic primary producers of Colpoys Bay is mostly due to diffusive resistance, especially within the epilithic community. The delta change from spring to autumn was about +6.0$^{o}/_{oo}$. Although the ambient DIC concentration is supersaturated high cell densities during the course of summer, will increase the thickness of the periphytic layer, hindering CO_2 diffusion, and in addition, higher temperatures will increase rates of algal growth resulting in carbon limitation, thus more enriched signatures (less fractionation) should occur as the season progress towards autumn (older benthic algal matrix).

It is also possible (as discussed in Chapter 3) that species succession and differences in the mode of carbon acquision affect isotope signatures to some degree, but *Cladophora* signatures showed the same seasonal trend observed for epilithon. Raven et al. (1982) suggested that *Cladophora* can complement CO_2 diffusion with HCO_3^- uptake under conditions of carbon limitation, and this could explain the more

enriched signatures in autumn. Therefore, I suggest that the combination of carbon limitation at the site of RUBISCO activity and bicarbonate uptake was responsible for the observed enrichment.

Epiphytic algae removed from the leaves of macrophytes or *Chara* experienced similar light and temperature conditions, but had signatures considerably more depleted than their hosts. This suggests that they are not carbon limited and perhaps that bicarbonate uptake by epiphytes is not very efficient. The small temporal variation observed was not statistically significant and likely reflects changes in growth rate and carbon species supply at localized scale.

The more enriched $\delta^{13}C$ signatures of vascular macrophytes and *Chara globularis* likely reflect uptake of HCO_3^-. The ability to directly or indirectly take up bicarbonate is important in alkaline waters where the rate of supply of CO_2 compared to relatively unbuffered waters may fall below the photosynthetic demand on a daily or seasonal basis. Two models have been proposed to explain HCO_3 uptake by *Chara* spp. and *Potamogeton* spp. Lucas (1985) proposed a H^+– HCO_3^- co-transport system in *Chara* which involves an enzyme, ATPase, providing a supply of protons to the outer surface of the plasmalemma. H^+ reacts with HCO_3^- to produce CO_2 which (assuming an appropriate gradient) can diffuse into the cell membrane. The active transport of HCO_3^-, therefore, has an associated energy cost (Raven and Lucas 1985). It is interesting to note that the other charophyte in Colpoys Bay, *Nitella flexillis*, did not show the same capacity to utilize bicarbonate (mean isotope signature of -24.65 $^o/_{oo}$). This result is not unexpected: Hutchinson (1975) classified species of Characeae according to pH preference, and *Nitella flexillis* was listed in the acidic

group. At pH above 7.3 most *Nitella* spp. are limited by the availability of dissolved carbon dioxide (Wetzel 1975). *N. flexillis* prefers slightly acidic waters (Wile et al. 1985, Sheath and Burkholder 1985; Burknolder and Sheat 1985), hence species of *Chara* are more abundant in Colpoys Bay.

Elzenga and Prins (1989) report that leaf polarization, and consequently bicarbonate uptake, in *Potamogeton* sp. is induced by increased light or reduced carbon availability. This is in accordance with my results: enriched carbon signatures in the summer when growth rates and carbon demand were likely to be greatest.

As with carbon, fractionation between source DIN (N_2, NO_3, NO_2, NH_4) and organic nitrogen depends on the form of nitrogen used, its concentration and the flux of nitrogen entering and exiting the cell (Handley and Raven 1992). Total inorganic nitrogen values for Georgian Bay were reported to be around 270 µg/L, with nitrate levels showing a minimum in the epilimnion during July (Weiler 1988). The most common form of nitrogen available to primary producers would likely be dissolved molecular nitrogen from atmospheric origin, and nitrate as a result of ammonium nitrification.

The $\delta^{15}N$ signatures of epilithon and *Cladophora* exhibited a similar pattern of seasonal change to that observed with carbon. Lower signatures, close to atmospheric nitrogen ($\cong 0.0$ $^{o}/_{oo}$), during spring suggest some utilization of dissolved molecular nitrogen and/or high rates of enzymatic discrimination against ^{15}N. The enrichment observed in summer implies utilization of nitrate as well. During summer higher temperatures will result in increased algal metabolism and growth rates. As with

carbon, higher photosynthetic rates will decrease enzymatic discrimination resulting in heavier isotopic signatures (Mariotti et al. 1984, Macleod and Barton 1998).

Nitrogen values for epiphytic algae were fairly constant. The moderately lower values in the summer are probably due to fractionation associated with nitrogen fixation. It is unlikely that the slightly enriched fall signatures were due to a change of the inorganic source (i.e. ammonia), but probably reflect lower enzymatic discrimination.

Of the two charophytes, *Nitella* had similar spring and autumn enriched values with a strong depletion in the summer (-1.7‰). The reason for such a change is not clear. *Chara* didn't show such a seasonal change. The depleted signature in winter is consistent with lower metabolic rates and increased enzymatic discrimination.

Vascular macrophytes can obtain nitrogen from sediments and from the water column. A large range of values was observed (from -3.5 ‰ to +2.5 ‰). All macrophytes were collected from the same site and so were subject to similar light and temperature regimes suggesting that this isotopic variability is a result of intrinsic differences amongst the species analyzed. Lake sediments are characterized by the accumulation of NH^{+}_{4} (Reddy et al. 1989). Ammonium can be taken up directly by aquatic vascular macrophytes, and can be oxidized to NO^{-}_{3}, which may also be taken directly or be denitrified in the adjacent anaerobic zone. Plants relying on sediment nitrogen (ammonium) are usually more enriched than those relying on dissolved inorganic nitrogen.

Such spatial and temporal isotopic variation amongst primary producers complicates the assignment of trophic levels to describe energy pathways in lake food webs.

4.5.2 - Benthic macroinvertebrates energy sources: littoral vs profundal communities

The use of stable isotopes to define trophic relationships depends upon two assumptions. First is that there is very little fractionation between ^{13}C and ^{12}C in each trophic transfer, so the carbon signature is consistent between a consumer and the food which it assimilates. Second is that there is a consistent level of enrichment of the heavier isotope of nitrogen, approximately, 3.4 $^{o}/_{oo}$ at successive trophic levels (Peterson and Fry 1987, Minagawa and Wada 1984, Cabana and Rasmussen 1994). Five potential food sources (i.e. macrophytes, charophytes, periphyton, POM and allochothonous matter) were analyzed. Carbon signatures were distinctive amongst macrophytes, *Chara* and allochthonous matter, but those of the periphytic community (i.e. epilithon, epiphyton and *Cladophora*), *Nitella* and POM exhibited some degree of overlap depending on the season. In order to clarify what energy sources were consumed by secondary producers it was necessary to concentrate on periods of rapid growth for each invertebrate under investigation. A summary of most probable energy sources consumed by each taxon is presented in tables 4.4 to 4.6.

The second assumption of consistency in the level of nitrogen isotope enrichment between trophic levels is only an approximation. Field studies in which

stable isotopes have been applied to discern trophic relationships show a range in trophic fractionation from 2 to 5 $^{o}/_{oo}$. (Minigawa and Wada 1984, Owens 1987). My results showed fractionation to be as low as 2 $^{o}/_{oo}$ (some invertebrates at littoral sites) and as high as 7 $^{o}/_{oo}$ (some invertebrates at profundal areas). This variability can be attributed to varying degrees of omnivory among the benthos of Colpoys Bay. As with carbon, consideration of the isotope variability among the primary producers is necessary to account for the observed variability among primary consumers.

Different components of the periphytic community were the primary energy source for benthic communities within littoral areas of Colpoys Bay. Littoral macrophytes and macroalgae known to be important refugia against predation were not directly consumed by invertebrates. Although it has been suggested that allochothonous matter can be important in oligotrophic lakes (Wissmar et al. 1977), this does not seem to apply to Colpoys Bay. Except for some Hydropsychidae, the vast majority of littoral invertebrates were strongly dependent on the periphytic biofilm for food supply. The increased $\delta^{13}C$ depletion and $\delta^{15}N$ enrichment in the communities offshore implied that the dependence on periphyton diminishes with increasing depth. Invertebrates found in areas deeper than 30 m rely on autochthonous sedimenting organic matter.

Given the nitrogen isotope variability observed at the primary producer level, primary consumers could be assimilating any of the five major food categories. However, it is clear from the carbon isotope results that vascular macrophytes were not assimilated by benthic invertebrates; likewise, the macroalga *Chara* sp. is far too enriched to be of any significance in the diets. Benthic invertebrates at littoral sites

were also too ^{13}C enriched to have used significant amounts of allochthonous matter. Most primary consumers in the littoral zone at 5 m displayed increasing enrichment from the spring growing season through the autumn growing season, the same trend observed in epilithon. Invertebrates at 15 m had isotope signatures very similar to sediment. Epilithic primary production was shown to occur at depths up to 18 m in Dyer's Bay, just north of Colpoys Bay (Duthie and Jones 1990). It is likely that invertebrates at 15 m were grazing on epipsammic algae (algae growing on fine sediments).

Amongst Hydropsychidae, *Cheumatopsyche* had the most depleted signatures for both carbon and nitrogen isotopes. This genus may be filter-feeding on particles from allochthonous origin. According to Ferrier and Wissing (1979), detritus (both from allochthonous and autochonous sources) is the main food source for *Cheumatopsyche analis* from mid July through early November. Another possibility is that *Cheumatopsyche* was feeding on epilithon on the lower surfaces of the rocks where less light leads to lower growth rates allowing for greater discrimination between carbon isotopes and resulting in more depleted signatures than the epilithon growing on top. The other two species of Hydropsychidae, *H. recurvata* and *H. bifida*, were more ^{13}C enriched than *Cheumatopsyche*. Studies of the feeding ecology of *Hydropsyche* species (Fuller and Mackay 1980, Gray and Ward 1979) reported that larval *Hydropsyche* graze on epiphytic diatoms growing on *Cladophora* mats and rarely ingest the filamentous green algae. My carbon and nitrogen signatures of *H. recurvata* and *H. bifida*, however, suggest utilization of POM. Fuller and Mackay (1980) also noted seasonal differences in diet, with more animal detritus in summer

and a diet dominated by diatoms in autumn. The elevated nitrogen signatures of *H. bifida* imply a higher degree of omnivory than *H. recurvata.*

In the other more herbivorous Trichoptera, *Phryganea* and *Nectopsyche,* the carbon assimilated during spring growth (-21.6°/$_{oo}$) was more depleted than during summer and autumn (-18.7°/$_{oo}$). For both species, carbon and nitrogen results indicate consumption of epilithon. Species of *Lepidostoma* have a role in processing large particulate allochthonous organic material in lotic systems (Grafius and Anderson 1980). However the carbon signature of *Lepidostoma* (-21.6°/$_{oo}$) in Colpoys Bay suggests usage of epiphytic matter. *Limnephilus* and *Mystacides* are relying on epilithon, however the nitrogen isotope signatures of the later during spring imply a high degree of omnivory

Among the Ephemeroptera, abundances of *Baetis* have been found to be positively correlated with density of periphyton (Richards and Minshall 1988). My carbon data suggest assimilation of epiphyton at 5 m during spring 1992, but nitrogen was enriched by only 2°/$_{oo}$. *Baetis* collected in May 1993 were assumed to reflect feeding during the previous winter; at 5 m the closest signature was to that of *Cladophora* collected in spring. However, except for two highly specialized Hydroptilidae caddisflies (Keiper et al. 1998) the general belief is that most invertebrates do not assimilate *Cladophora* (Fuller and Mackay 1980, Scrimgeour et al. 1991, Berg 1995). At this time the slightly elevated nitrogen signature may suggest assimilation of other sources of detritus. I'm leery of accepting the idea of *Cladophora* consumption. Species of *Baetis* are considered herbivorous grazers of periphyton (Scrimgeour et al. 1991) and as such they were probably consuming

attached diatoms. *Stenonema* was analyzed only in autumn and, like the other mayflies, SI signatures indicated a dependence on epilithon. Edwards and Meyer (1990) suggested that this genus actually consumes the bacterial biomass associated with the substrate.

A diversity of feeding modes, types of food and feeding behaviours exist among subfamilies, tribes, genera and even species of chironomids. Based on larval feeding modes, chironomids can be grouped in six categories (e.g.collectors gatherers and filterers, scrapers, shredders, engulfers and pierces), but most chironomids are not restricted to one feeding mode. A variety of factors including larval size, food quality and quantity and sediment composition can influence feeding behavior (Berg 1995). Food items include algae (Johannsson and Beaver 1983), detritus and associated microorganisms, macrophytes, woody debris and other invertebrates (Merrit and Cummins 1996). Diets may change as larvae mature or because of seasonal changes in food availability. Given the diverse feeding modes and the variety of food items ingested by chironomids at any given time, carbon and nitrogen isotope signatures were expected to encompass a large range of values.

At the littoral sites, chironomid carbon signatures ranged from -17.7‰ to -24.8‰. It is evident that allochthonous matter, macrophytes and *Chara* were not important foods. Generally chironomids collected in early spring were third or fourth instar larvae, as opposed to summer when most were small first or second instar individuals. Large, late instar, chironomids can ingest large food items and often exhibit more flexible diets than smaller early instar larvae. Spring signatures are therefore reflective of longer-term feeding on a more variable diet as opposed to

summer when signatures should reflect recent feeding on a more restricted diet. A general seasonal trend toward carbon enrichment was evident for chironomids at 5 m and followed that observed in epilithon and *Cladophora*.

The two tube-dwelling chironomids, *Polypedilum* and *Chironomus*, are thought to be non-selective consumers of detritus (Titmus and Badcock 1981). Unlike most chironomids, *Polypedilum* at 15 m became more depleted from spring through autumn suggesting assimilation of POM. *Microtendipes*, *Micropsectra* and *Gillotia* had more ^{13}C enriched signatures towards autumn and/or summer following the general trend of epilithon. *Monodiamesa* was analyzed only in summer and its signatures suggest assimilation of epilithon. Mihuc and Toetz (1994) used SI analysis to show the dependence of *Phaenopsectra* on periphyton; my data confirms this dietary dependence.

Food items of the two predatory Tanypodinae *Ablabesmyia* and *Procladius* include small Crustacea (Titmus and Badcock 1981), oligochaetes and other chironomids (Berg 1995). However, despite studies demonstrating the importance of animal matter, detritus and algae have also being reported in the diets of *Procladius* and other Tanypodinae (Hershey 1986). Their nitrogen signatures confirm that they aren't obligate carnivores.

Pisidium spp. (bivalves) filter interstitial water. Their signatures following the spring growing season suggest utilization of epilithon at 5 m, perhaps material washed off the rocks and deposited nearby. These bivalves seemed to utilize POM at 15 m.

Gastropods are supposed to be scrapers of attached algae and associated material. The abundance of *Valvata* sp. was positively correlated with epiphyton development on charophyte beds in *Chara* dominated lakes (van den Berg et al. 1997). The carbon signatures of *Valvata* and *Helisoma* closely mirrored the signatures of epiphyton. According to Jonasson (1996) *Valvata piscinalis* has two modes of nutrition: it is a scraper of epiphytes on littoral macrophytic vegetation at depths of about 2 m, but is a filter-feeder at depths of ≤ 15 m. Its relatively more depleted carbon signature during the winter at 15m supports this hypothesis. Gastropods have high cellulase activities (Monk 1976) giving them the ability to digest cellulose: *Helisoma* and *Valvata* nitrogen signatures suggest mostly a herbivorous diet. In contrast, the more depleted carbon and enriched nitrogen signatures of *Physa* imply a less selective omnivorous diet.

The isopods *L. lineatus* and *C. intermedius* at 5 m had carbon and nitrogen signatures consistent with utilization of epilithon. At 15 m, however, the signatures suggest some use of epiphytic algae growing on *Chara*. As mentioned in Chapter 2, isopods have been reported to occur in higher densities in charophyte beds (Pereyra-Ramos 1981, Hanson 1990).

MacNeil et al. (1997) reported that *Gammarus* spp. may be mainly shredders in one habitat in one season, collector-gatherers in the same habitat in a different season, generalist-detritivores in a different habitat and even predators. This trophic flexibility allows success throughout a diverse range of freshwater habitats. In Colpoys Bay *Gammarus pseudolimneaus* seems to rely primarily on epiphyton and or epilithon, depending on season, and the nitrogen signatures imply mostly a

herbivorous diet. Likewise *Hyallela azteca* also seems to rely on epilithon or epiphyton, but perhaps is slightly more omnivorous.

All profundal invertebrates analyzed were more carbon 13 depleted and nitrogen 15 enriched than animals from the littoral zone. This has also been reported for several lakes in Ontario (Vander Zanden and Rasmussen 1998). Primary producers in profundal areas have access to biogenically depleted hypolimnetic carbon and lower rates of photosynthesis, both of which allow greater carbon discrimination resulting in ^{13}C signatures more depleted than those of littoral species. Conversely, remineralized nitrogen from the hypolimnion is likely to be enriched relative to more epilimnetic and/or littoral, nitrogen.

Profundal benthic communities are thought to be dependent on pelagic sedimentation for their food supply (Brinkhurst 1974). However, it is unknown whether profundal macroinvertebrate growth is supported directly by nutrients in fresh or decaying algae, or indirectly via microbial utilization of accumulated refractory detritus. In Colpoys Bay energy sources likely to reach deeper sediments include epilithic material washed from rocks in shallower water, allochthonous matter from surrounding land and planktonic primary production settling out of the water column. My carbon isotope results showed that epilithic matter maybe utilized by some macroinvertebrates at 30 m. Allochthonous organic matter from terrestrial plants does not appear to be important.

Profundal invertebrates were chironomids, tubifids and amphipods. Carbon signatures of *Heterotrissocladius, Protanypus, Pagastiella,* and *Gillotia* suggested dependence on sedimenting POM with some occasional consumption of epilithon.

Their nitrogen signatures were, however, about 7.5 $^{o}/_{oo}$ higher than POM. This does not imply that those insects aren't primary consumers of sedimenting POM. As mentioned earlier, in sediments, isotopic fractionation during decomposition is thought to result in residual material having an isotopically heavy composition (Fogel and Cifuentes 1993). In these instances, the residual, isotopically heavy ammonium may be incorporated into microbial biomass. Therefore, chironomids assimilating decomposing sedimented POM will have enriched nitrogen signatures. Likewise, the carbon isotope signatures of tubificids, subsurface deposit feeders, imply a diet of sedimenting POM (i.e. detritus and associated microbiota), Tubificids also dwell in sub-surface sediments and rely on food particles affected by diagenetic processes, therefore their nitrogen signatures were relatively enriched.

It has been suggested that *Diporeia* rely heavily on spring diatom blooms (Gardner et al. 1990). *Diporeia* had carbon signatures considerably more depleted than chironomids or tubificids. Depleted carbon signatures ($\cong -31^{o}/_{oo}$) were also observed for *D. hoyi* in Lake Ontario (Leggett 1998). This is a result of lipid accumulation (Gardner et al. 1985), since lipids tend to retain more of the lighter carbon. After lipid extraction *Diporeia* from Lake Ontario fell in the range of –27 to 29 $^{o}/_{oo}$ (Leggett 1998). The nitrogen signatures of *D. hoyi* were also relatively more depleted than chironomids or tubificids and can be attributed to the fact that *D. hoyi* dwell mostly on the sediment surface and consume freshly deposited material. Chapter 5 is a detailed study of the biology and energy requirements of *Diporeia*.

In summary, littoral invertebrates were mostly dependent upon periphytic sources, while the profundal benthos rely primary on pelagic primary production. The

extent to which individual components of the periphytic community were assimilated is not known. Most researchers agree that *Cladophora* is indigestible. Stomach content analysis would greatly enhance the ability to distinguish among isotopically similar sources.

4.6. - Conclusions

Complex processes influence assimilation of several different sources of energy by invertebrates in lake food webs. I tried to simplify this problem by blocking my results within littoral and profundal communities knowing however that they are affected by one another. For both communities spatial and temporal changes were observed among primary producers and consequently primary consumers. Therefore, if isotopes are to be used to infer energy sources and pathways to consumers, the need to consider the temporal variation in growth rates of consumers as well as intense sampling and investigation of the factors that control the isotopic signatures of primary producers cannot be overemphasized.

My study highlighted the importance of epilithon fueling benthic communities at most littoral areas of oligotrophic ecosystems such as Colpoys Bay. The clear waters of Colpoys Bay probably make periphytic primary production possible at greater depths than in more eutrophic systems. Duthie and Jones (1990) showed that epilithic primary production can occur at depths of 18 m in Dyer's Bay, just north of Colpoys Bay. Littoral macrophytes and macroalgae are not used as energy sources but appear to be important as habitat for large numbers of invertebrates. Although other works suggest that allochothonous matter can be important in oligotrophic lakes, my data do not support this hypothesis.

As expected, this dependence on the epilithic biofilm diminishes with increasing water depth. Invertebrates at the sub-littoral site rely on a combination of epilithon, epiphyton and POM. Given the presence of the extensive charophyte

growth in the system, epiphytic attached algae seem to play a more important role than at the littoral site.

Invertebrates in the profundal region seem to rely on autochthonous pelagic organic matter. The communities in the profundal region could be separated in two components on the basis of isotopes. Chironomids and tubificid worms that dwell in sub-surface sediment had access to refractory nitrogen and, as a consequence, were more enriched than *Diporeia* which dwell on the sediment surface.

Assigning invertebrates to functional feeding guilds played a minor role in identifying energy sources for different taxa. Most invertebrates exploit more than one feeding mode throughout their life cycle, so food assimilation was controlled more by supply and demand than by mode of acquisition.

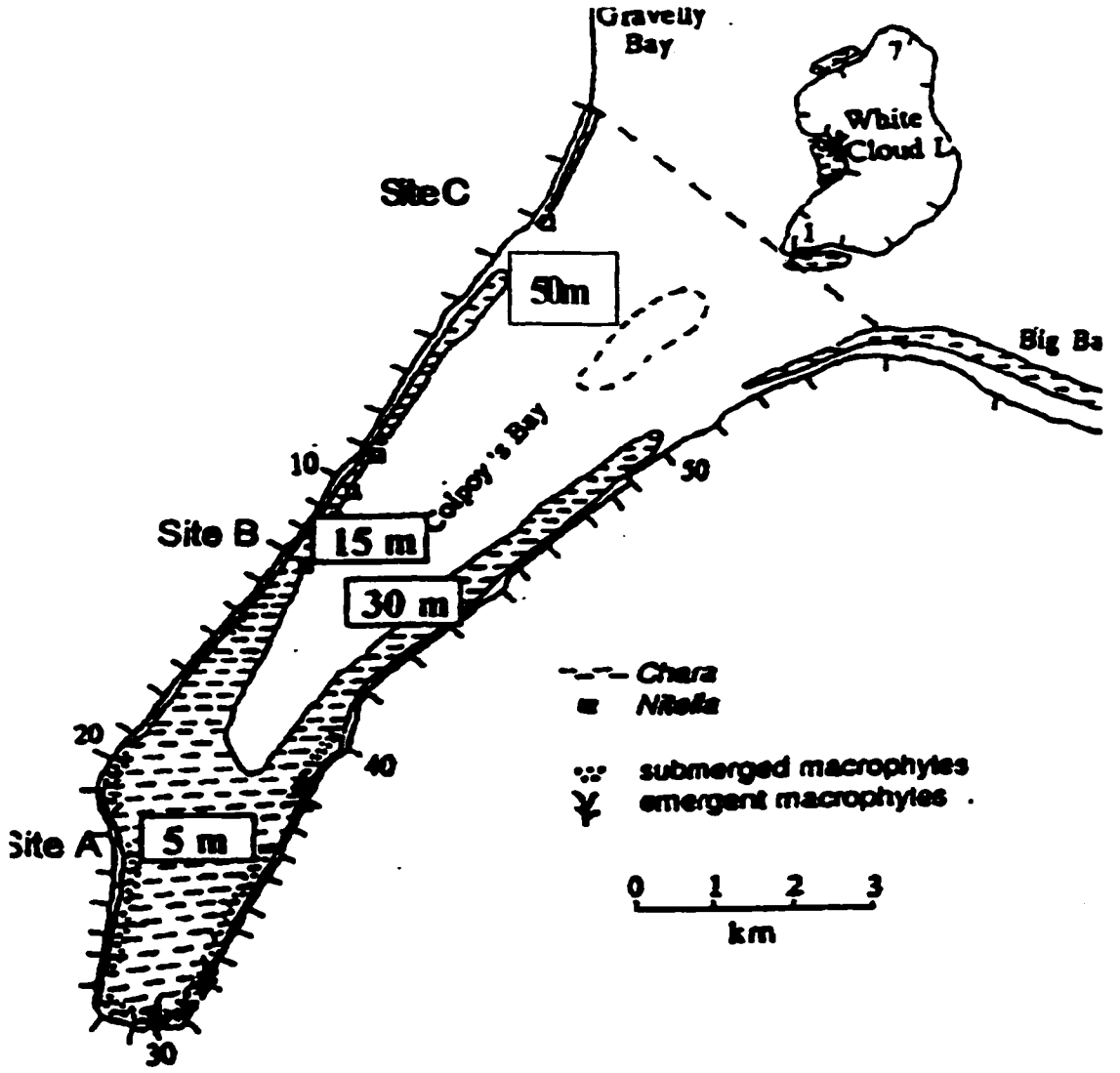


Fig 4.1: Site locations within Colpoys Bay. Benthic primary producers were periphyton, vascular macrophytes and charophytes at site A; periphyton and charophytes at B and phytoplankton at site C. Invertebrates were collected at 5m (site A), 15m and 30m (site B), and 50m (site C).

Table 4.1: $\delta^{13}C$ (‰) VPDB of primary producers and standard deviation from the mean of replicate samples. Number of samples in parenthesis. nd= not available for analysis.

	May-June 92	July-Aug 92	Sept-Oct. 92	March 93	May-June 93	Min	Max	Average
Macrophytes								10.1
Ranunculus	nd	-7.4±0.8 (4)	-7.2±0.5 (4)	nd	nd	-7.6	-6.8	-7.3
Potamogeton	nd	-8.7±0.9 (4)	-9.9±0.6 (4)	nd	nd	-10.6	-7.9	-9.1
Elodea	nd	-15.5 (1)	nd	nd	nd			-15.5
Myriophyllum	nd	-8.7±1.0 (4)	-8.3±0.9 (4)	nd	nd	-9.8	-7.6	-8.6
Macroalgae								
Chara	-12.7±0.5 (4)	-11.0±0.6 (4)	-16.1±1.1 (3)	-11.9±0.2 (3)	-13.1(1)	-17.9	-10.6	-13.2
Nitella	-26.9±0.1 (2)	-21.9±0.3 (4)	-24.0±0.9 (3)	-28.7±0.2 (2)	-26.9±0.1(2)	-28.9	-21.6	-24.8
Periphyton								
Epilithon	-25.4±0.3 (6)	-22.8±0.6 (6)	-20.1±2.6 (8)	nd	-27.7±0.4(3)	-28.0	-14.8	-22.3
Epiphyton	-22.3±0.2 (3)	-28.8±1.5 (2)	-26.5±0.6 (3)	nd	nd	-29.9	-22.2	-26.1
Cladophora	-23.0±0.4 (5)	-22.5±1.9 (4)	-21.3±0.2 (4)	nd	-24.8±2.9 (3)	-26.8	-20.7	-23.6
Terrestrial								-28.98
Vitus riparia	nd	nd	-26.9±0.5 (3)	nd	nd	-27.5	-26.5	-26.9
T.occidentalis	nd	nd	-26.8±0.9 (3)	nd	nd	-27.4	-25.6	-26.8
L.perene	nd	nd	-29.9 (1)	nd	nd			-29.9
Amelanchier	nd	nd	-29.0±0.9 (3)	nd	nd	-30.0	-28.5	-30.0
F. americana	nd	nd	-29.5±0.9 (2)	nd	nd	-30.2	-28.8	-30.2
POM	-26.7±1.5(19)	-26.1±0.8(37)	-24.3±1.0(11)	-25.4±1.4(15)	-26.4±0.4(10)	-30.6	-20.7	-25.6

Table 4.2: $\delta^{15}N$ (‰) of primary producers and standard deviation from the mean of replicate samples. Number of samples in parentheses. nd= not available for analysis.

	May-June 92	July-Aug 92	Sept-Oct 92	March 93	May-June 93	Min	Max	Average
Macrophytes								
Ranunculus	nd	1.5±0.0(2)	1.5±0.0(2)	nd	nd	1.5	1.5	1.5
Potamogeton	nd	1.4±0.8(3)	2.0±2.5(3)	nd	nd	0.2	3.8	1.7
Elodea	nd	1.1	nd	nd	nd			1.1
Myriophyllum	nd	2.6±0.0(3)	-0.44±4.3(3)	nd	nd	-3.5	2.6	1.1
Macroalgae								
Chara	0.2±0.0(3)	-0.74±0.0(4)	0.1±0.0(3)	-0.2±0.0(2)	0.7	-0.7	0.2	-0.3
Nitella	3.0±0.1(3)	1.7±0.0(4)	3.1±0.0(4)	2.6±0.0(3)	3.0±0.1(2)	1.7	3.1	2.6
Periphyton								
Epilithon	0.2±0.2(6)	2.2±1.1(4)	2.2±1.2(10)	nd	0.2(1)	0.1	4.0	1.8
Epiphyton	1.7±0.12(2)	1.2±0.3(2)	1.6±1.6(2)	nd	nd	0.9	2.9	1.7
Cladophora	0.2±0.1(4)	2.8±1.0(4)	1.7±1.9(4)	nd	0.1±0.1(2)	0.1	3.4	1.7
Terrestrial								
Vitus riparia	nd	nd	5.2±0.6(3)	nd	nd	4.8	5.9	5.2
T. occidentalis	nd	nd	1.3±0.2(3)	nd	nd	-1.4	1.1	1.3
L.perene	nd	nd	4.53	nd	nd			4.5
Amelanchier	nd	nd	-0.3±1.1(3)	nd	nd	-1.5	0.7	-0.3
F. americana	nd	nd	-1.7±0.8(2)	nd	nd	-2.2	-1.1	-1.7
POM	3.6±0.2(3)	2.6±2.1(3)	2.3±1.1(5)	3.8±0.9(4)	3.2±0.5(11)	6.5	0.5	2.7

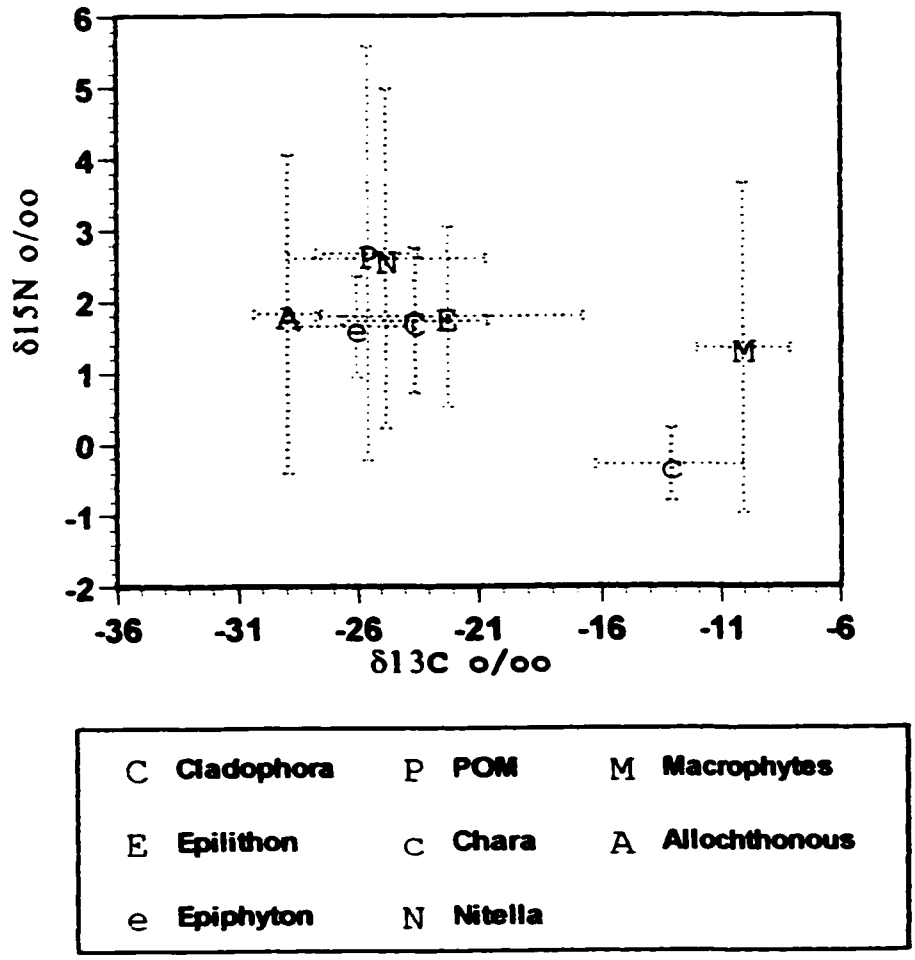


Figure 4.2: Average (and standard deviation) for $\delta^{13}C$ ‰ and $\delta^{15}N$‰ of each primary producer.

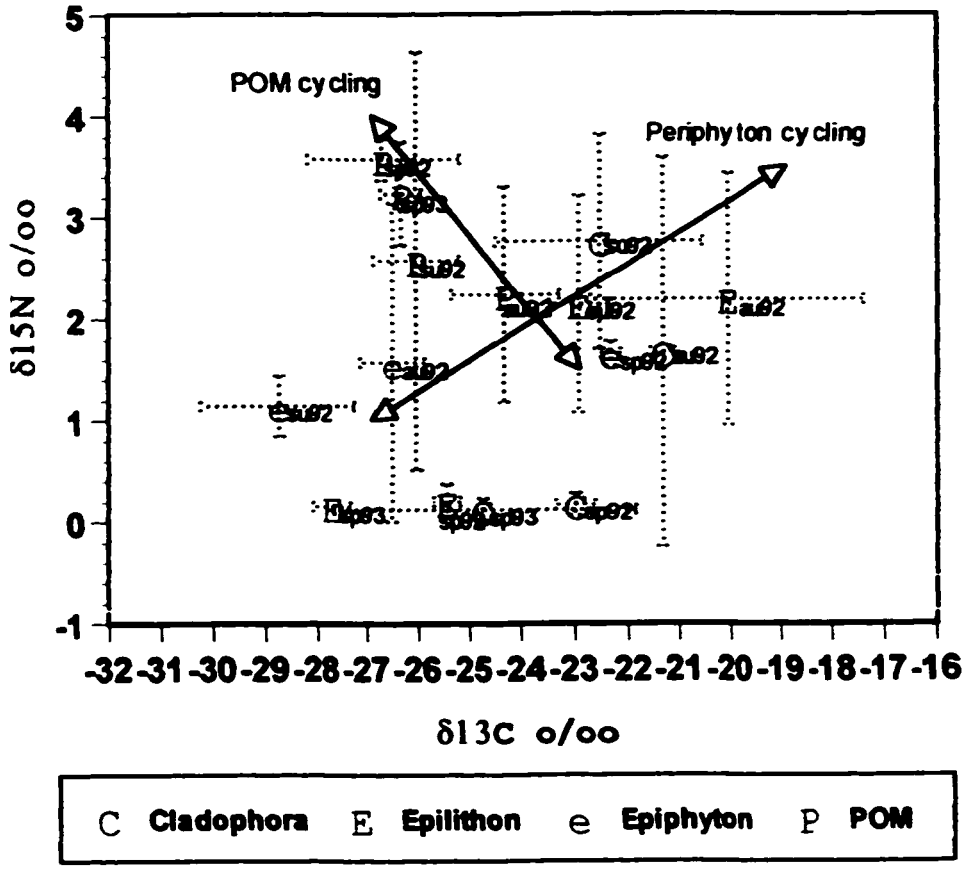


Figure 4.3: Seasonal means (and standard deviation) of POM and periphytic community $\delta^{13}C$ °/₀₀ and $\delta^{15}N$ °/₀₀. Subscripts are: sp92 (spring 92), su92 (summer 92), au92 (autumn 92) and sp93 (spring 93).

Table 4.3: $\delta^{13}C$ ‰ and $\delta^{15}N$‰ sediment transects for the period of July, August and September 1992. Length is the distance from the base of the rock shore.

Month	Length (m)	Depth (m)	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰
July	0	3.5	-23.1	nd
	15	7.5	-23.6	nd
	30	10	-23.5	2.8
	45	15	-24.7	1.6
	55	20	-24.8	2.9
August	0	3.5	-24.3	4.6
	15	7.5	-22.2	1.2
	30	10	-23.7	1.6
	45	15	-25.0	3.4
	55	20	-24.6	3.6
September	0	3.5	-24.7	3.9
	15	7.5	-24.3	3.4
	30	10	-24.4	3.3
	45	15	-24.6	2.9
	55	20	-24.6	3.6

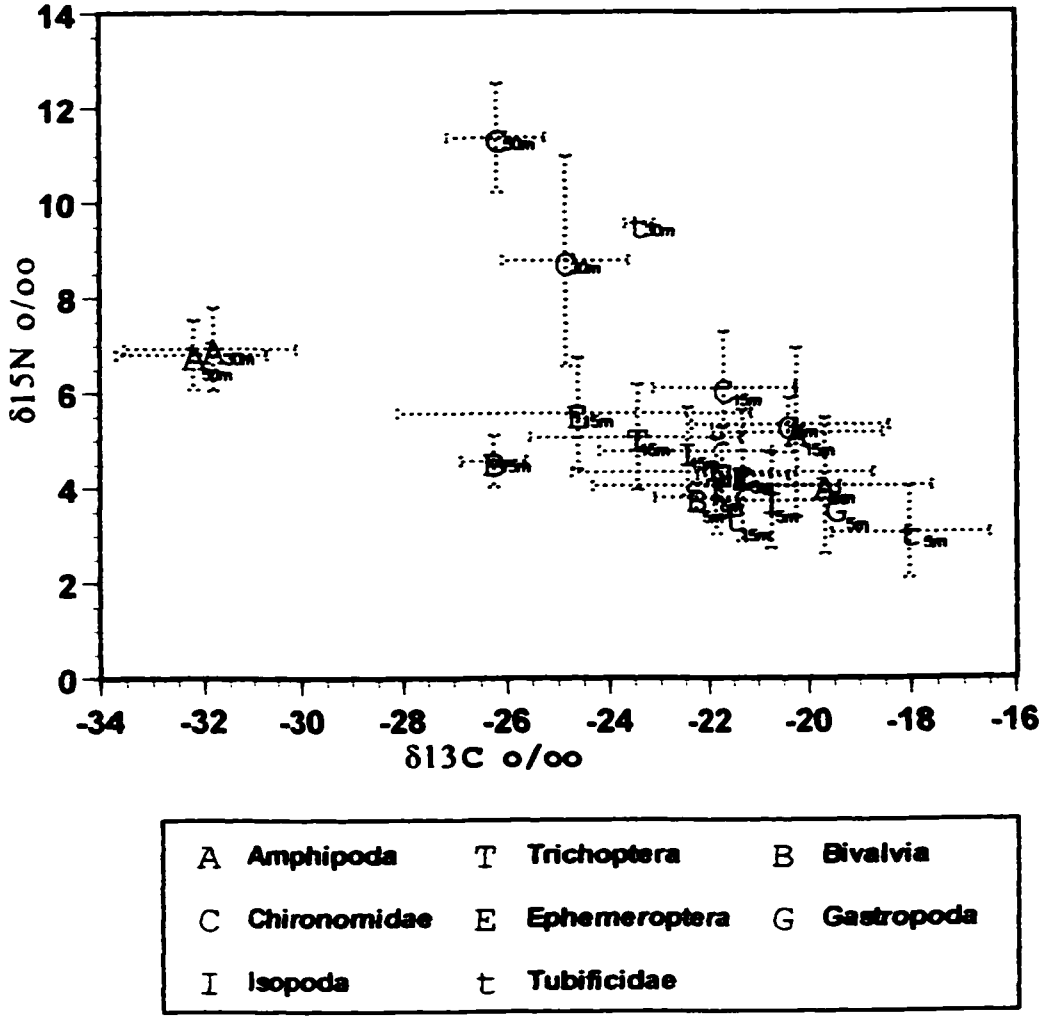


Figure 4.4: Mean $\delta^{13}C$ and $\delta^{15}N$ signatures for major taxa. Subscripts depict depths 5,15, 30 and 50m. Bars are standard deviation from the mean over the entire study period.

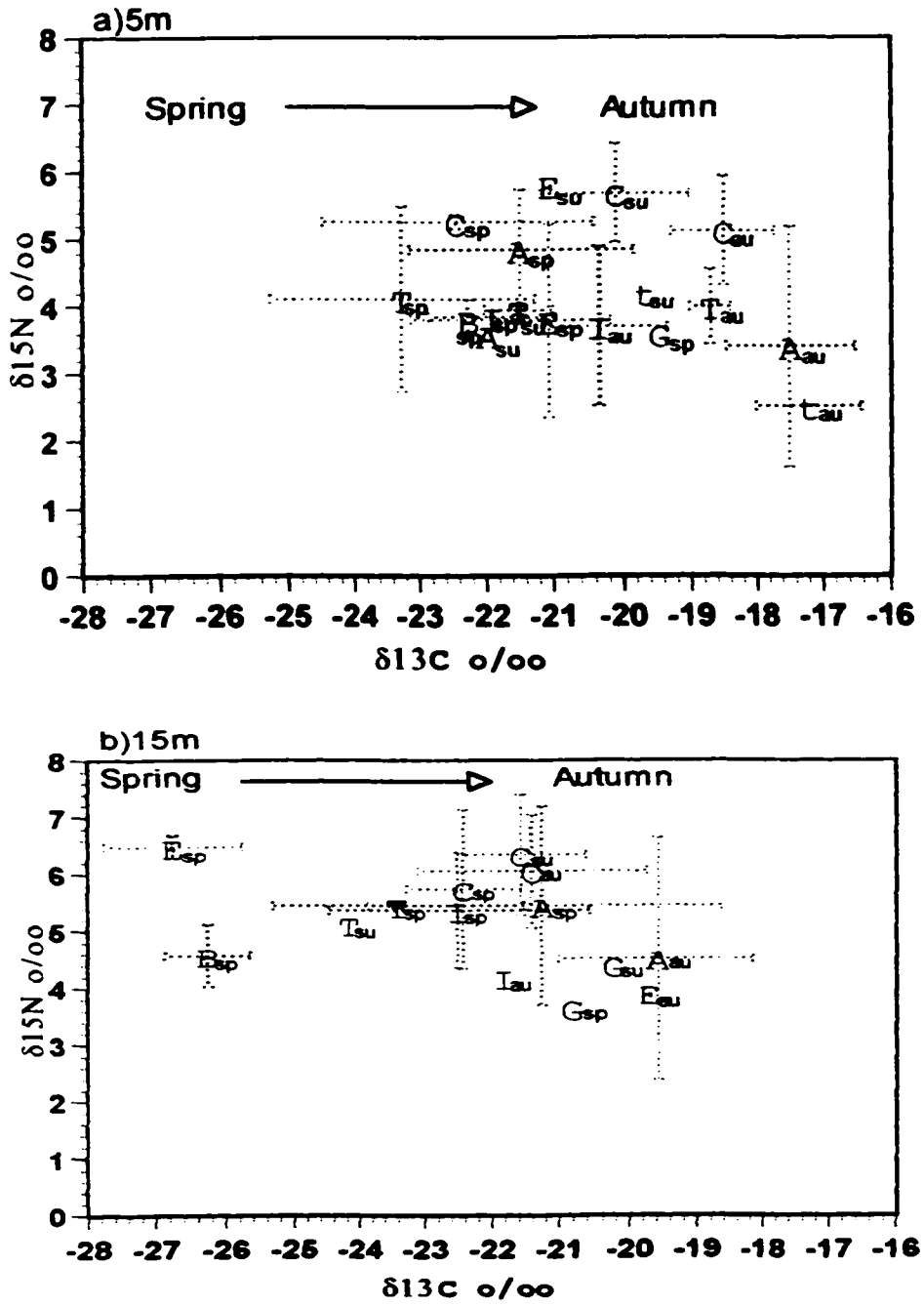


Figure 4.5: $\delta^{13}C$ and $\delta^{15}N$ signatures for major taxa collected at a) 5m and b)15 m depths. Each data point represents a seasonal mean and standard deviation (sp=spring, su=summer and au=autumn).

Figure 4.6: Isotopic signatures $\delta^{15}N$ ‰ and $\delta^{13}C$ ‰ of littoral benthos at 5 m and potential foods grouped by animals' growing season: a) spring, b)summer and c)autumn.

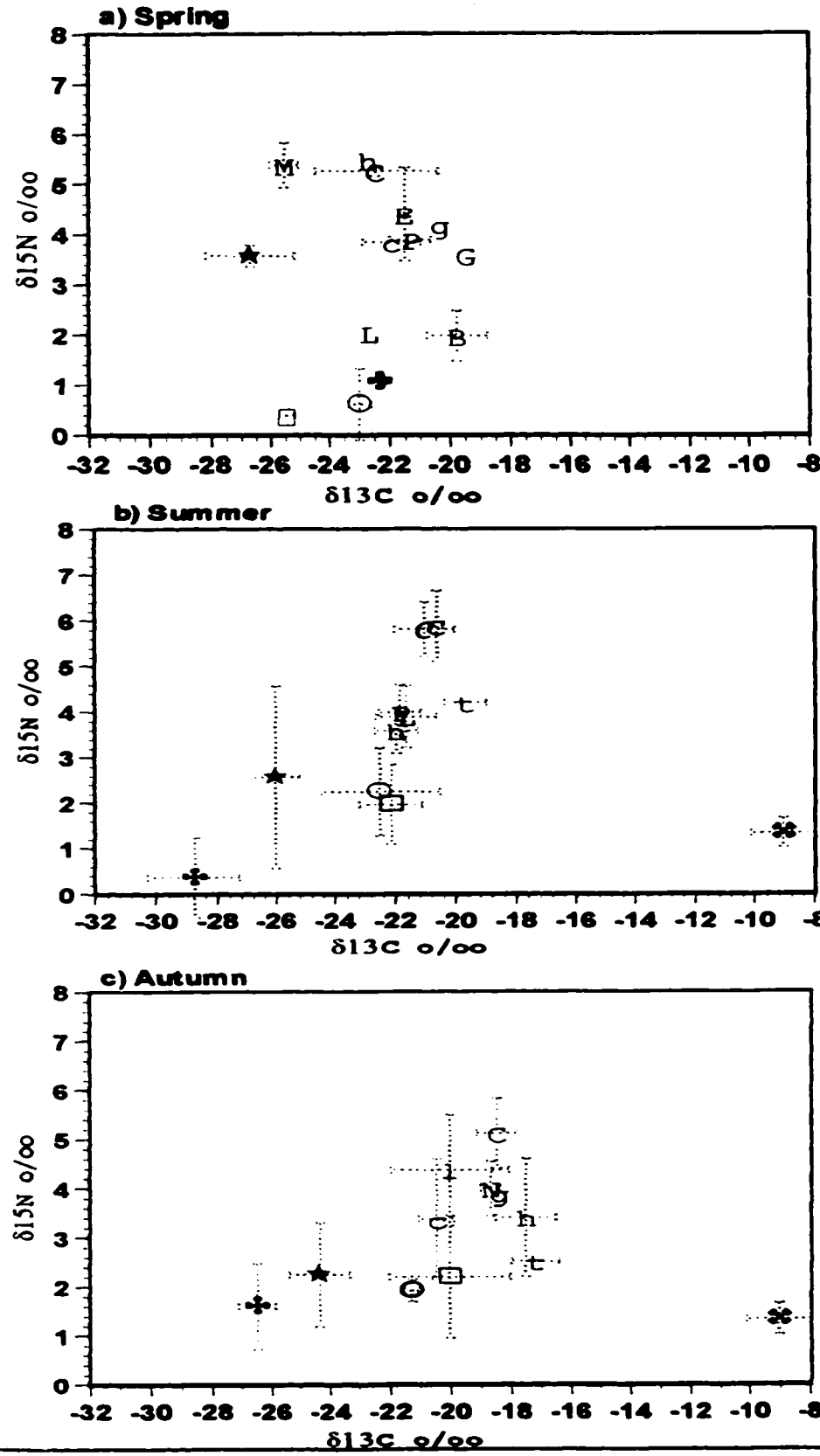
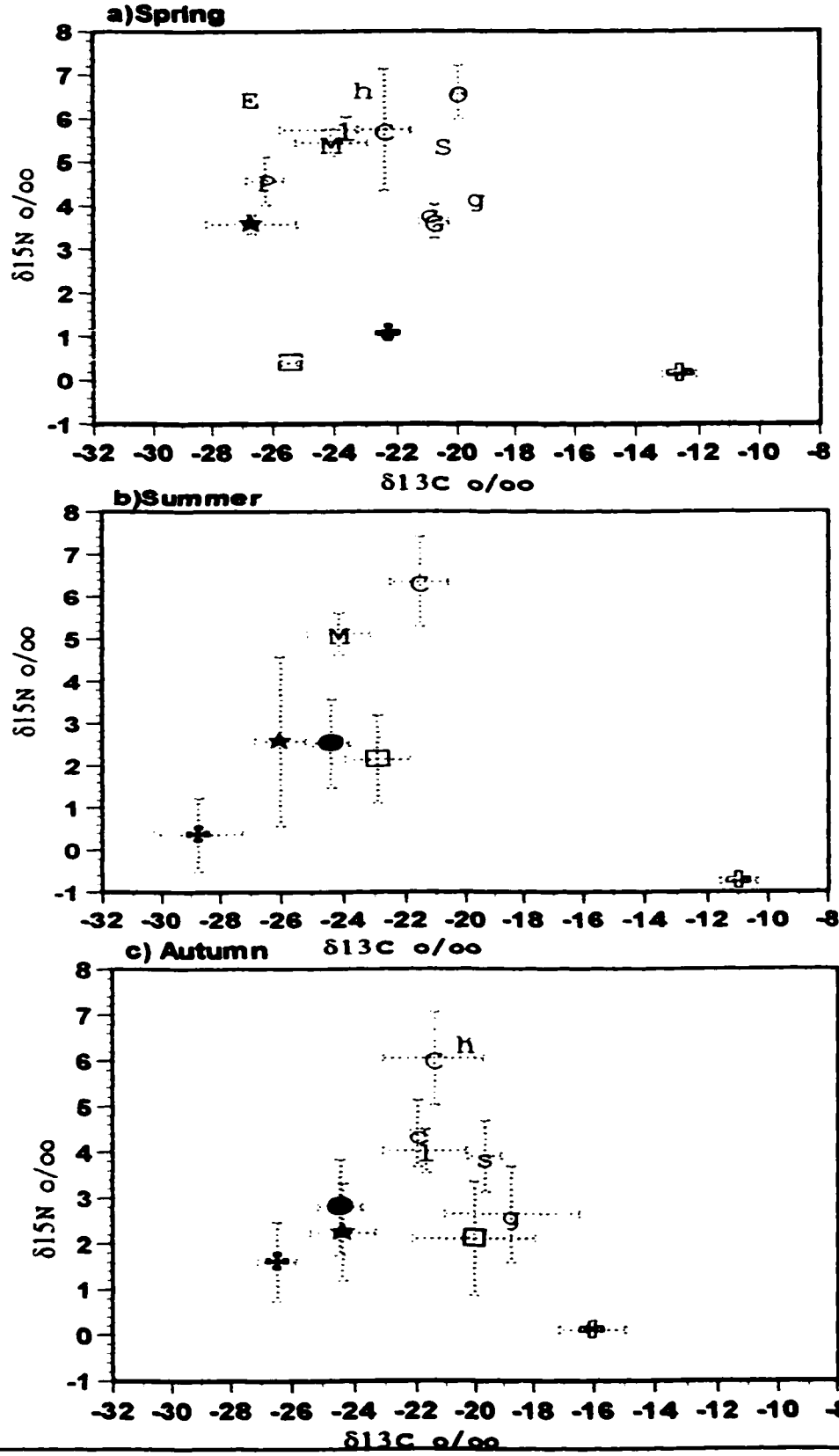

a) Spring
δ15N o/oo
δ13C o/oo
b) Summer
δ15N o/oo
δ13C o/oo
c) Autumn
δ15N o/oo
δ13C o/oo
B Baetis
C Chironomidae
h Hyallela
M Mystacides
t Tubificidae
Epiphyton
C Caenis
G Gastropoda
L Limnephilus
N Nectopsyche
Cladophora
POM
c Caecidotae
g Gammarus
l Lirceus
P Phryganea
Epilithon
Macrophytes

Figure 4.7: Isotopic signatures ($\delta^{15}N$ ‰ and $\delta^{13}C$ ‰) of littoral benthos at 15 m and potential foods grouped by animals' growing season: a) spring, b)summer and c)autumn.



c	Caecidotae	G	Gastropoda	l	Lirceus	P	Pisidium	□	Epilithon	★	POM
C	Chironomidae	g	Gammarus	M	Mystacides	S	Setodes	✣	Epiphyton	●	Sediment
E	Ephemera	h	Hyalella	O	Orconectes	s	Stenonema	✣	Chara		

Table 4.4: Isotope signatures, feeding guilds (FFG), growing season (GRS) and primary diet for invertebrates in the littoral community (depth=5m); cg=collector-gatherers; df=deposit-feeders; ff=filters-feeders; pr=predators; sc=scrapers; sh=shredders.

Taxa	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰	FFG	GRS	Primary Diet
Chironomidae					
Chironomus	-20.7	5.25	c.g	Winter92	Epiphyton?
	-20.5	6.4		Summer92	Epilithon
Gillotia	-18.5	5.9	c.g	Autumn92	Epilithon
Micropsectra	-22.9	5.2	c.g	Spring92	Epiphyton?
	-18.5	5.1		Autumn92	Epilithon
Microtendipes	-22.6	5.4	c.g	Winter92	POM
	-20.9	6.3		Summer92	Epilithon
	-18.3	5.5		Autumn92	Epilithon
Phaenopsectra	-17.7	4.0	s.c	Autumn92	Epilithon
Polypedilum	-19.6	5.1	c.g	Autumn92	Epilithon
Procladius	-21.5	5.4	p.r	Spring92	Animal/detritus?
	-20.6	5.0		Summer92	Animal/detritus?
Ephemeroptera					
Baetis pygmaeus	-19.8	1.9	c.g	Spring92	Epiphyton?
	-22.7	4.6		Winter93	POM
Caenis	-21.1	5.8	c.g	Summer92	Epilithon
Ephemera	-21.4	4.1	c.g	Spring92	Epiphyton
Trichoptera					
Cheumatopsyche *	-27.1	4.6	f.f	Summer92	POM
Hydropsyche bifida *	-24.9	7.1	f.f	Summer92	POM
Hydropsyche recurvata *	-25.8	4.5		Summer92	POM
Limnephilus	-22.7	2.0	s.h	Spring92	Epiphyton
	-21.2	3.9		Summer92	Epilithon
Mystacides	-25.6	5.4	c.g	Spring92	Epilithon
Nectopshyche	-18.7	4.0	s.h	Autumn92	Epilithon
Phyragnaea	-20.8	3.9	s.h	Spring92	Epiphtyon
	-21.9	4.0		Summer92	Epilithon
Amphipoda					
Gammarus	-20.4	4.2	d.f	Spring92	Epiphyton?
	-18.5	3.9		Autumn92	Epilithon
Hyallela azteca	-22.7	5.5	d.f	Spring92	Epiphyton
	-22.0	3.6		Summer92	Epilithon
	-17.6	3.4		Autumn92	Epilithon
Isopoda					
Caecidotae intermedius	-21.9	3.8	s.h	Spring92	Epiphyton
	-20.5	3.4		Autumn92	Epilithon
Lirceus lineatus	-20.1	4.4	s.h	Autumn92	Epilithon
Bivalvia					
Pisidium	-22.3	3.8	f.f	Autumn92	Epilithon/POM?
Gastropoda					
Valvata	-19.5	3.6	s.c	Spring92	Epiphyton
Oligochaeta					
Tubificidae	-19.7	4.2	d.f	Summer92	Sediment-detritus
	-17.2	2.5		Autumn92	Sediment detritus

* Collected at the rock shore.

Table 4.5: Isotope signatures, feeding guilds (FFG), growing season (GRS) and primary diet for invertebrates in the littoral community (depth=15m); cg=collector-gatherers; df=deposit-feeders; ff=filters-feeders; pr=predatos; sc=scrapers; sh=shredders.

Taxa	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰	FFG	GRS	Primary Diet
Chironomidae					
Ablabesmia	-21.3	4.8	p.r	Spring92	Animal/detritus
Chironomus	-21.3	5.2	c.g	Winter92	POM
	-23.2	7.8		Spring92	Epilithon/epiphyton
	-23.8	6.9		Winter93	POM
Dicrotendipes	-21.8	4.8	c.g	Summer92	Epilithon
Gillotia	-21.3	6.9	c.g	Summer92	Epilithon
	-22.2	6.1		Autumn92	Epilithon
Micropsectra	-22.6	5.2	c.g	Spring92	Epilithon
	-19.3	5.1		Autumn92	Epilithon
	-24.8	3.6		Spring93	POM
Microtendipes	-21.5	6.4	c.g	Winter92	POM
	-21.2	7.4		Summer92	Epilithon
	-20.9	6.7		Autumn92	Epilithon
	-22.9	7.9		Winter93	POM
Monodiamesa	-22.1	6.4	c.g	Summer92	Epilithon
Phaenopsectra	-23.3	6.8	s.c	Summer92	Epilithon
	-21.6	5.7		Autumn92	Epilithon
	-22.2	5.9		Winter93	POM
Polypedilum	-19.2	7.9	c.g	Spring92	Epiphyton?
	-23.3	6.8		Summer92	POM
	-24.1	6.7		Autumn92	POM
Procladius	-20.3	7.3	p.r	Summer92	Animal/detritus?
	-20.2	5.2		Autumn92	Animal/detritus?
Ephemeroptera					
Baetis pygmeaus	-26.1	5.9	c.g	Winter93	Epilithon
Ephemera	-26.8	6.5	c.g	Spring92	Epilithon
Stenonema	-19.7	3.9	c.g	Autumn92	Epilithon
Trichoptera					
Lepidostoma	-21.6	5.7	s.h	Winter93	Epiphyton?
Mystacides	-24.1	5.5	c.g	Spring92	Epilithon
	-24.2	5.1		Summer92	POM
	-26.8	2.4		Winter93	POM
Setodes	-20.5	nd	c.g	Spring92	Epiphyton
Amphipoda					
Gammarus pseudolimneaus	-19.4	4.2	d.f	Spring92	Epiphyton?
	-18.8	2.7		Autumn92	Epilithon
Hyallela azteca	-23.1	6.7	d.f	Summer92	POM
	-20.4	6.4	d.f	Autumn92	Epilithon
Isopoda					
Caecidotea intermedius	-20.9	3.9	s.h	Spring92	Epiphyton
	-21.9	4.4		Autumn92	Epiphyton/Epilithon
Lirceus lineatus	-23.0	5.9	s.h	Spring92	Epiphyton
	-21.7	4.0		Autumn92	Epilithon
	-25.6	5.3		Winter93	POM?

Table 4.5: con't.

Taxa	$\delta\ ^{13}C$ ‰	$\delta^{15}N$ ‰	FFG	GRS	Primary Diet
Decapoda					
O.propinquus	-19.9	6.6	s.h	Spring92	?
Gastropoda					
Valvata	-23.0	3.6	s.c	Winter92	POM?
Valvata	-20.8	3.7		Spring92	Epiphyton
Valvata	-20.2	4.4		Summer92	Epilithon
Helisoma	-19.6	4.8	s.c	Winter92	Epiphtyon?
Physa	-26.0	5.9	s.c	Winter92	Epilithon/POM
Bivalvia					
Pisidium	-26.3	4.6	f.f	Spring92	POM
Oligochaeta					
Tubificidae	-21.5	3.4	d.f	Summer92	Sediment/detritus

Table 4.6: Isotope signatures, depth (m), feeding guilds (FFG), growing season (GRS) and primary diet fort invertebrates in the profundal community; cg=collector-gatherers; df=deposit-feeders; ff=filters-feeders; pr=predatos; sc=scrapers; sh=shredders.

Taxa	$\delta^{13}C$ °/₀₀	$\delta^{15}N$ °/₀₀	Depth	FFG	GRS	Primary Diet
Amphipoda						
Diporeia	-29.4	6.3	30	d.f.	winter92	POM
	-33.1	6.1	30	d.f	spring92	POM
	-32.4	6.0	30	d.f.	summer92	POM
	-30.5	7.4	30	d.f.	winter93	POM
	-32.4	6.9	50	d.f.	summer92	POM
	-32.8	6.7	50	d.f.	spring92	POM
Chironomidae						
Gillotia	-24.6	9.9	30	c.g	spring92	POM
	-24.7	6.3	30	c.g	summer92	POM
Heterotrissocladius	-22.8	9.9	30	c.g	spring92	POM
	-26.0	7.7	30	c.g	summer92	POM
	-26.5	12.7	50	c.g	spring92	POM
	-26.9	10.5	50	c.g	summer92	POM
Pagastiella	-25.7	9.9	30	c.g	spring92	POM
Protanypus	-25.3	11.2	30	c.g	summer92	POM
	-25.1	12.6	50	c.g	spring92	POM
	-25.7	11.0	50	c.g	summer92	POM
Tubificidae						
	-23.5	9.6	30	d.f.	summer92	POM
	-24.5	9.0	50	d.f.	summer92	POM

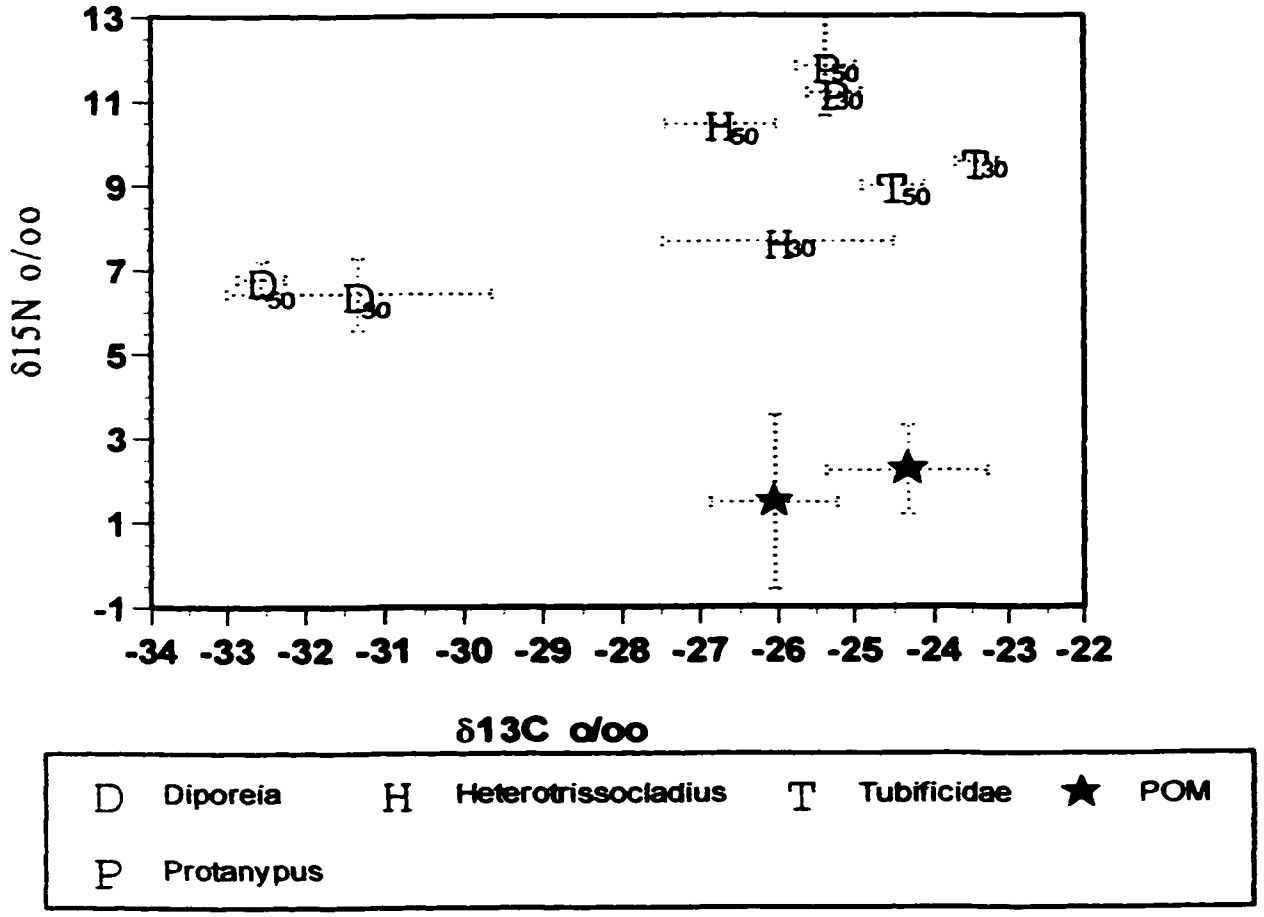


Figure 4.8) $\delta^{13}C$ and $\delta^{15}N$ signatures for POM and primary consumers collected at 30 m and 50 m.

Chapter 5: The trophic role of *Diporeia hoyi* in Colpoys Bay benthic food web

Abstract

In order to assess the trophic role of *Diporeia hoyi* in Colpoys Bay, amphipods were collected from depths of 30 and 50m using an Ekman grab or a dredge. These were used to estimate the life cycle, production dynamics, stomach fullness, lipid content and measure stable isotopes of carbon and nitrogen.

In agreement with previous studies, *D.hoyi* collected in areas deeper than 30m seems to rely on pelagic primary production as shown by increased feeding activity during spring followed by increased lipid content. Stable carbon isotopes showed that *D.hoyi* living at depths ≤ 25 m assimilate littoral benthic algae as well. The role of deeper populations as a trophic link between pelagic primary production and fish was emphasized by stable nitrogen analyses.

5.1-Introduction

Diporeia hoyi 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 m^{-2} (Nalepa et al. 1985). *Diporeia hoyi* usually inhabits the first two centimeters of soft sediments or fine sand with organic coatings (Robbins et al. 1979). The high densities of this amphipod, combined with its restriction to the thin surface layer, strongly affect sediment geochemistry through bioturbation and metabolic activities.

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

It has been suggested that *D. hoyi* provides a direct link between the spring diatom bloom and fish in large lakes (Gardner et al. 1990). *D. hoyi* 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, and the frequency of full guts has been reported to be highest in the spring, implying active feeding on fresh food inputs at this time (Quigley 1988; Dermott and Corning 1988). The lipid content of *Diporeia* was shown

to increase after the diatom bloom in Lake Michigan, suggesting consumption and assimilation of this high quality food source (Gardner et al. 1985, 1990).

In a previous study (Guiguer 1990), stable carbon isotopes (SCI) were used to determine the major energy sources for profundal benthos in a set of ten small lakes in southern Ontario. The results showed a strong isotopic seasonality for *D. hoyi* with enriched carbon values in spring and fall similar to POM, suggesting that both spring and fall blooms were assimilated by the amphipods. However, summer signatures were much more depleted than POM. Gardner et al. (1985) reported an increase in lipid content during spring with a peak in June and a decline from July through December. Plant lipids are known to be carbon-depleted relative to other major components such as proteins and carbohydrates, as well as the total plant (Fritz and Fontes 1980). Therefore lipid content can dominate the isotopic signature of *Diporeia*.

In this chapter, I combine production rates, population dynamics, lipid content, gut fullness and stable isotopes of carbon and nitrogen to describe the flow of energy to *D. hoyi* in Colpoys Bay. The results of this study will clarify the relationships among growth, production and food supply and the possible impact on fish production. The emphasis is on the trophic status of *Diporeia hoyi* and its role as a link between planktonic, periphytic or allochthonous primary production and fish.

5.2. Material and Methods

5.2.1 -Study Sites, Sampling and Analytical Methods

Diporeia hoyi for the study of production dynamics and gut fullness were collected with an Ekman grab (0.0225 m^2) biweekly from May to 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). Thin ice made it impossible to reach the 30 m or 50 m depths in March 1993, so *Diporeia* were collected from depths of 20-25 m off Mallory beach. Five replicates were taken on each sampling date. Samples were preserved in 10% formaldehyde in the field. In the laboratory at the University of Waterloo, *Diporeia* retained on 200 μm aperture netting were transferred to 70 % ethanol until needed.

Diporeia for isotope and lipid analyses were also collected on the schedule described above using a dredge. In the field, amphipods were removed from the sediment with the aid of forceps, placed in closed cages inside a cooler and kept alive for 48 h to allow gut clearance, then stored frozen until needed. Potential foods for *Diporeia* were detritus from three major sources: epilithon, 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 near the shore. Water for particulate organic matter (POM) isotopic analysis 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. In 1992 large particles (mainly zooplankters) were removed by passing the water through a 40 μm aperture mesh prior to filtration. In 1993, to include larger algae, water was screened through a 60 μm prior to filtration. Three samples of 2 l of water were filtered from each depth. In an attempt to separate the bacterial fraction from algae, the water samples were filtered through a series of three pre-combusted glass fiber filters of decreasing pore size (Whatman GF/D = 2.7um; GF/C = 1.2um; GF/F = 0.7um) using a peristaltic pump. Filters were frozen in the field. Prior to isotope analysis each filter was acidified with 10% HCL.

Sediment samples were also 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 collected 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 was discarded and the first centimeter of sediment was sliced off the top of the core and prepared for isotopic analysis.

5.2.2-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 I measured maximum head dimensions (distance between the outer edges of the eyes (± 0.02 mm). Dry mass was estimated through linear regressions of the natural logarithm of dry mass on the natural logarithm of head dimensions. In total, approximately 50 preserved animals encompassing all size classes were dried for 48 h at 60°C and dry mass was obtained using a Cahn C-31 microbalance (model W/RS232). Head width (mm) was also converted to body length (mm) for comparison with other studies. *Diporeia*'s life cycle has been reported to range from 1 to 3 years, with between 9 and 14 molts. Analysis of size frequency histograms allowed me to assign individuals to seven size classes. Production was estimated 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. This production value was further corrected for the Cohort Production Interval (CPI) to obtain the annual production.

5.2.3-Lipid Extraction and Gut Fullness

Lipid extraction was performed on amphipods from dredge collections grouped by year class (e.g. 0+, 1+, and 2 years old) 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 animals were subjected to stable isotope analysis.

Gut fullness was estimated for *D.hoyi* 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). The average gut fullness was calculated by measuring gut content length and dividing by the total gut length.

5.2.4- Stable Isotopes

Stable isotopes in samples of epilithon, POM and *Diporeia* (1+ and 2 years old) containing 1 to 5 mg of organic matter were analyzed at the Environmental Isotope Laboratory, Department of Earth Sciences, University of Waterloo, Ontario using a Fisons Instruments VG Isochrom-EA continuous flow mass spectrometer with an analytic precision of $\pm$ 0.2‰ for carbon and $\pm$ 0.3‰ for nitrogen. Isotope ratios

are expressed as parts per mil deviation from the international standard reference materials VPDB (Vienna Peedee belemnite) for carbon, and N_2 in the atmosphere (Mariotti 1983) for nitrogen as follows:

$$\delta^{13}C = [(^{13}C/^{12}C_{sample})/ {}^{13}C/^{12}C_{standard}) -1] \times 10^3$$

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

5.3. Results

5.3.1- Life Cycle

Inspection of size frequency histograms over the sampling period allowed discrimination of 3 distinct year-classes at each site (Fig 5.1). At the 30 m station young of the year (YOY, i.e. 0+ year class) ranged from 1.5 to 3.5 mm in body length, juveniles (age 1+) were 3.5 to 4.5 mm and adults (age 2+) were larger than 4.5mm (size of smallest brooding female). The maximum size attained was 8.0 mm. Brooding females were found in early May, newly-hatched amphipods were found from 20 May to 22 July 1992, and spent females were found as late as August 1992. In the following year, brooding females were found as early as March and hatchlings

from March through May. The majority of amphipods took 2 years to attain sexual maturity, but a few were mature after one year.

Sampling at 50 m started only in July 1992. Hatchlings were not present at this time, only YOY and a few spent females were found. Brooding females were first collected in early June 1993, but no newly-hatched amphipods were collected in either year. YOY and juveniles were of similar sizes at both sites. The smallest brooding female was 4.5 mm, the largest was 5.8 mm in length.

5.3.2- Density, biomass, production and P/B

The mean monthly density of *D. hoyi* varied from 881m^{-2} (June 1993) to 3437 m^{-2} (October 1992) at 50 m, and from 304 m^{-2} (March 1993) to 2008 m^{-2} (September 1992) at 30m (Fig. 5.2a,b). The annual mean densities of *D. hoyi* from July 1992 to July 1993, were 1415 m^{-2} and 811.m^{-2} at 50m and 30m, respectively.

Monthly mean biomass mirrored density at both depths (Fig.5.2 c.d). At 30 m the mean total biomass was lowest in March 1993 (0.14 $g.m^{-2}$) and highest in August 1992 (0.50 $g.m^{-2}$). At 50m, lowest values occurred in August 1992 (0.36 gm^{-2}), with the highest value in October 1992 (0.91$g.m^{-2}$). During the period of July 1992 to July 1993, the annual mean biomass of YOY was virtually the same at 30 m and 50m. Annual mean biomass of juveniles at depths of 30 m and 50 m were, respectively, 0.17 $g.m^{-2}$ and 0.33 $g.m^{-2}$. The mean biomass of adult *D. hoyi* was considerably greater at 50 m (0.31 $g.m^{-2}$) than 30m (0.05 $g.m^{-2}$).

Production at 30 m was 0.50 $g.m^{-2}.y^{-1}$, with a total annual mean biomass of 0.25 $g.m^{-2}$ and annual P/B of 1.9. At the 50 m site, production was 1.34 $g.m^{-2}.y^{-1}$, biomass 0.67 $g.m^{-2}$ and annual P/B 2.0 (Table 5.1).

5.3.3-Lipid content and gut fullness

Annual mean lipid concentrations (% dry weight) for the period of July 1992 to July 1993 were very similar around 40% at both depths (Fig.5.3). Lipid content varied seasonally, with maximum values in early spring (March/April) and minimum concentrations in October at both 30 m and 50 m. Overall there was a significant increase in lipid content with size ($n=200$, $p < 0.000$, $r^2=0.78$) (Fig.5.4).

Mean gut fullness from July 1992 to July 1993 was virtually the same at 30 m (45.1%) and 50 m (44.3%). The seasonal trend was also very similar at both sites (Fig. 5.5 a,b) with gut fullness generally declining from spring through September, then increasing in autumn. The frequency of empty guts throughout the study period was slightly higher at the 50 m station (22.9%) than at 30 m (18.5%).

5.3.4- Carbon and Nitrogen Stable Isotopes

$\delta^{13}C$ signatures of *D. hoyi* became more depleted from 20 m to 30 m, with signatures 2 to 3 $^{o}/_{oo}$ more depleted at the deeper station than the shallower. Mean

$\delta^{15}N$ signatures were similar at 30 and 50 m sites but more enriched than those at 20 m (Fig.5.6).

The mean $\delta^{13}C$ at 30m for the period of May to October 1992 was -30.5 $^{o}/_{oo}$, and -30.2$^{o}/_{oo}$ from April to July 1993. At 50 m, mean signatures were -32.5$^{o}/_{oo}$ (July 1992 to October 1992), and -32.6 $^{o}/_{oo}$ (May to July 1993). $\delta^{15}N$ means at 30 m were 6.0 and 6.7$^{o}/_{oo}$ for 1992 and 1993 respectively. Mean $\delta^{15}N$ signatures at 50 m were 6.5 and 6.1 $^{o}/_{oo}$ for 1992 and 1993, respectively. Enriched signatures occurred at 30 m in April 1993 (8.0 $^{o}/_{oo}$), the most depleted in September 1992 (4.9 $^{o}/_{oo}$).

Carbon isotope values for *Diporeia* after lipid extraction were 1 to 2$^{o}/_{oo}$ more ^{13}C-enriched. Seasonal changes were similar at both depths (Fig.5.7 a,b). *Diporeia* became more ^{13}C depleted from May through July 1992, then steadily more enriched through October 1992.

Of the food sources analyzed, epilithon had the most enriched mean carbon signature followed by POM and allochthonous organic matter (Chapter 4). Mean annual carbon and nitrogen isotope δ values of epilithon were -22.3$^{o}/_{oo}$ and 1.8$^{o}/_{oo}$. Since no significant differences were observed among the three POM size fractions or depth (Chapter 3), *Diporeia's* signatures were compared with mean POM for the entire water column. Allochthonous organic matter was collected only in 1992, with values ranging from -30.2$^{o}/_{oo}$ to -27.5$^{o}/_{oo}$ (mean of -28.9$^{o}/_{oo}$) for carbon and from –2.2$^{o}/_{oo}$ to +5.9$^{o}/_{oo}$ (mean of 1.4$^{o}/_{oo}$) for nitrogen. Mean sediment carbon and nitrogen isotope values for the period of July to September 1992 were, respectively, -24.6$^{o}/_{oo}$ and 2.9$^{o}/_{oo}$. *D. hoyi* signatures roughly tracked those of POM in both years

5.4. Discussion

4.4.1- Life Cycle and Production Dynamics

The length of the life cycle of *Pontoporeia affinis* was shown to be one year at depths ≤ 20 m in mesotrophic Lake Erken (Johnson 1987). *Diporeia hoyi* formerly known as *Pontoporeia hoyi*, most commonly has a two year life cycle (Johnson 1988), with these differences contributed to separating the two genera. In Colpoys Bay, the majority of *Diporeia* had a life cycle of two years at both sites. However, at the 30 m depth a few survived up to three years. Similar variability is common among other Crustacea (e.g crayfish; Corey 1988). At the 30 m site, reproductive activity took place during late winter and early spring, and recruitment of YOY was still occurring in May 1993. At the 50m site brooding females were found throughout the month of June, however hatchlings were not collected at this site. Older YOY were present in June and early July 1993.

Growth rates are influenced by both food supply and temperature. The molt increment (e.g. the increase in size occurring at a molt) may be unchanged or reduced with a rise in temperature but an increase in temperature can shorten the intermolt period, so growth may be faster. *D. hoyi* seems to prefer temperatures < 11°C (Siegfried 1985; Johnson 1988). Although in Colpoys Bay measured bottom water temperatures were always lower than 8°C at depths ≥ 30 m (Chapter 3, Table 3.1), strong westerly winds are frequent, resulting in dynamic patterns of water movement. Internal seiches change the depth of the thermocline on a daily or even hourly basis,

so *Diporeia* at 30 m are subject to a very different thermal regime than those at 50 m and this thermal variability likely accounts for the lower density of *D.hoyi* at 30 m.

The absence of larger *D.hoyi* at 50m is puzzling. A reduction in food supply can either reduce the molt increment and consequently reduce the size attained at maturity, or lengthen the intermolt period so that it would take longer to reach a given size (Hartnoll 1982). The annual mean gut fullness was similar at both depths suggesting that food supply is about the same at 30 and 50m. This was also confirmed by lipid concentrations.

A second possible explanation for the absence of large *D. hoyi* at 50 m is greater predation pressure by sculpins or other fish. Evans et al. (1990) reported that the mean size of *D. hoyi* consumed by deepwater sculpins was about 2-3 mm larger than those collected directly from the sediments. *D. hoyi* become increasingly more vulnerable to sculpin predation after reaching a length of 5 mm. Sly and Christie (1992) also suggested that density differences between Lakes Michigan and Ontario can be attributed to different forms of predator-prey interactions between the two lakes. In Colpoys Bay, larger amphipods ($\geq$6 mm) were found occasionally, but only at the shallower station. The dense charophyte bed at this site may provide protection from predation.

Despite the absence of large individuals, the higher densities of *Diporeia* at 50 m gave rise to greater mean annual biomass and production for the period of July 1992 to July 1993. Production of *D. hoyi* was about 63% higher at 50 m, of which juveniles (51%) and adults (44%) make up the bulk. Adults at 30 m had slightly lower mean individual weight and were less abundant, so contributed only 18.0% to

the total production, whereas juveniles contributed 68.3%. YOY contributed relatively more at 30 m (9.6%) than 50 m (5.0%). The age structure of the population at 50 m is surprising: YOY had the lowest density. This may reflect reproductive failure in 1993, or migration. Johnson (1988) suggested that some adults migrate to shallower depths to release their young. My results confirm this hypothesis: I collected adult *Diporeia* at depths of 25-20 m in March just prior to reproduction, and hatchlings were collected only at 30 m. Hence, it is possible that YOY spend some time at shallower depths and start to migrate to deeper areas in mid to late summer as water temperatures rise. This migration pattern would also explain the maximum densities of YOY in September at 30 m and in October at 50 m.

Overall, juvenile amphipods dominated the 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 $gm^{-2}y^{-1}$ (Johnson 1988), very similar to the mean production at my sites in Colpoys Bay (0.92 $gm^{-2}y^{-1}$). The slightly (14%) greater production in South Bay may reflect sediment focussing in that smaller, shallower basin.

5.4.2- Seasonality of gut fullness and lipid levels

Regardless of depth, the amphipod *D. hoyi* in Colpoys Bay fed heavily on freshly sedimented material during spring and/or autumn diatom blooms (Dermott and Corning 1988; Quigley 1988), but did not fast during summer. Throughout the study period the frequency of > 75% full guts was similar (≅ 37%) at both stations. The guts of about 18% to 23% of animals were < 25% full throughout the study

period at both sites. Seasonal feeding patterns were also similar at both stations, but the frequency of full or empty guts was subtly different at the two depths. In general, at 30 m, the majority of guts ≥ 75% full occurred in spring and early summer, whereas at 50 m, more guts were ≥ 75% full during mid summer through autumn. This difference could be an artifact of different sample sizes, or may reflect temporal variation in food availability at both sites. It is obvious that particles will settle to the bottom sediment sooner at 30 m than 50 m, but this might be a difference measured in days, not weeks.

Despite apparent temporal differences in feeding patterns, annual mean lipid levels were very similar at both sites. The seasonal changes in lipid levels mirrored to some extent feeding intensity, with a month lag (Fig 5.8). The minimum lipid concentrations observed in October 1992 were preceded by the lowest feeding rates in the previous month.

As expected, lipid concentrations tended to increase with size (Fig. 5.4); this was most evident for YOY and juveniles. This increase in lipid dry weight with size in juvenile *D.hoyi* was also observed for amphipods in Lake Michigan (Quigley et al. 1989) Adult amphipods of Colpoys Bay seem to stabilize their lipid gain after reaching 1.3 mg individual weight. Those adult amphipods were a composite of males and females, either during reproductive activity or spent. According to Quigley et al. (1989), adult male *Diporeia* have significantly less lipid than do females and females appear to halt all feeding upon maturation, which should deplete lipid levels.

5.4.3- Diporeia's energy sources: stable isotopes

The changes observed in feeding activity, lipid levels and physiological processes during *Diporeia*'s life cycle were all reflected in the amphipod's stable carbon isotope signatures. 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 an intermediate $\delta^{13}C$ value weighted according to the relative contribution of each source. I analyzed three energy sources potentially available to *Diporeia*: epilithon, suspended POM and allochthonous organic matter. Of these, epilithon was more ^{13}C enriched on average than all other sources. 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 ($1^{o}/_{oo}$) enrichment between trophic levels (Rau et al. 1983, Hobson and Welch 1992). *Diporeia*'s carbon signatures became increasingly more enriched at shallower depths (Fig.5.6). Maly (1992) showed that in Colpoys Bay, littoral diatoms accounted for about one-quarter (26%) of the contents of sediment traps placed below the metalimnion during periods of thermal stratification. My results suggest that detached epilithon contributes significantly to the nutrition of *D. hoyi* at depths of 20-25 m: amphipod signatures were similar to those of sediment, which, in turn, were intermediate between epilithon and POM. Signatures of animals from depths $\geq$ 30 m were more depleted suggesting that organic matter produced in the shallow littoral is not consumed in significant amounts.

POM included any particles smaller than 40-60 μm and these can be from allochthonous sources, autochthonous littoral or pelagic matter. The relative input from each source is difficult to quantify. In Colpoys Bay, the overall POM carbon signature during the study period of –25.6 ‰ was intermediate between epilithon (-22.1 ‰) and allochothonous matter (-28.9 ‰). It is unlikely that allochthonous material made a significant contribution to POM; rather, the seasonal change towards enrichment in autumn suggests intrusion of another source (e.g. epilithon). As mentioned in Chapter 3, maximum flux of littoral diatoms corresponded to periods of very unsettled weather in September and October. Those results suggest that POM was dominated by pelagic primary production, with substantial littoral inputs in some seasons or years.

D. hoyi displayed an isotopic seasonality similar to pelagic POM, but its signatures were more depleted than POM at both depths (Fig.5.7a). Factors other than differences in the isotope composition of source carbon can produce variability in the $\delta^{13}C$ of aquatic organisms. Of particular significance is the fractionation of carbon isotopes that occurs in the formation of lipids, resulting in lower values in this biological component (DeNiro and Epstein 1978). If an organism has a high lipid content relative to its body mass, it may have an artificially low $\delta^{13}C$ (Tieszen et al. 1983), so temporal differences in lipid content will cause fluctuation in the $\delta^{13}C$ of an organism that are not related to changes in diet.

The isotopic depletion observed at both sites may be partially associated with seasonal lipid loads (Fig. 5.7a). The accumulation of lipids from June to July at 30 m was reflected in more carbon depleted signatures. At 50 m, lipid loads were

maximum in August 1992, but carbon isotope signatures were most depleted in September 1992. Amphipods at both sites were more enriched in October 1992 coinciding with a drop in lipid concentrations. POM signatures also became more enriched.

The seasonality of lipid loads only partially explains *Diporeia*'s carbon depletion relative to POM. After the removal of the lipid fraction, amphipod isotopic values shifted upwards 1 to 3 ‰ (Fig. 5.7b), but were still sometimes depleted relative to POM. As mentioned in Chapter 3, alteration and degradation of organic matter while sinking to the lake bottom can modify the overall character of sedimented organic matter, therefore the isotopic signatures at the water-sediment interface can be quite different from the original source. Additionally, organic matter produced by hypolimnetic algae should be depleted relative to epilimnetic algae, because they have access to more biogenic CO_2 and have lower photosynthetic rates allowing for higher carbon discrimination. In Colpoys Bay phytoplankton densities in the hypolimnion increase during mid to late stratification (Maly 1992). Throughout the summer, the hypolimnetic phytoplankton was dominated by Bacillariophyceae, followed by Cryptophyceae and Crhysophyceae. It is possible that my samples of POM did not include the material actually available to *Diporeia*. However, the similarity in seasonal variation suggests that *D.hoyi* relies on pelagic POM which becomes more depleted before reaching the sediment.

Is *Diporeia* a direct trophic link between spring diatoms and fish in Colpoys Bay? Gardner et al. (1990) suggested that *Diporeia* in Lake Michigan must obtain a large portion of its annual energy directly from the spring diatom bloom, partially

because summer sedimentation rates were not sufficient to support the observed annual production. I estimated the minimal detrital food required for *Diporeia* to achieve the production measured in Colpoys Bay using the same approach described in Gardner et al. (1985). Assuming growth efficiencies (food used for growth and reproduction/food assimilated) of 0.3 to 0.6 [based on *D.hoyi* in Lake Ontario and the Bay of Quinte (Johnson and Brinkhurst 1971)] and my mean production for Colpoys Bay of 0.83 $gAFDWm^{-2}y^{-1}$ (average of rates at 30m and 50m), *Diporeia* would have to assimilate ≈1.5 to 3.0 $gAFDWm^{-2}$ during the period of July 1992 to July 1993. The amount of food ingested was then estimated based on literature-derived values for ecological efficiencies (Benke and Wallace 1980). Since assimilation efficiency (assimilation/ingestion) was assumed to be 30% for diatoms, *D. hoyi* would have to ingest 5 to 10 $gAFDW.m^{-2}$.

Estimates of sedimentation rates as (ash-free-dry-weight) from the metalimnion into the hypolimnion of Colpoys Bay were obtained from Maly (1992). For the period of July to October of 1991, the mean sedimentation rate was 395.5 mg $m^{-2}d^{-1}$ which amounts to 48.3 $g.m^{-2}$ during the stratification period. The contents of traps placed below the metalimnion showed approximately 26% of the diatoms present to be of littoral origin, which, as demonstrated by isotope results can be assimilated by *Diporeia* at depths ≤ 30 m. The remaining 35.7 gm^{-2} of organic matter of pelagic origin available only during the period of thermal stratification is enough to support the annual production of *D .hoyi* at 50m observed in Colpoys Bay.

My nitrogen isotope data also suggest that *D. hoyi* rely on POM throughout the summer. It is usually assumed that there is a consistent level of enrichment of the

heavier isotope of nitrogen in each successive trophic level. A predator will on average have a nitrogen isotope signature 2.5 to 3.0‰ (Owens 1987; Peterson and Fry 1987) or 3.4 ‰ more enriched than its prey (Minagawa and Wada 1984; MacLeod 1998). The mean difference between *Diporeia* and POM in the spring of 1992 was 2.5 ‰ (30 m) and during stratification 3.4 ‰ (30 m) to 4.1 ‰ (50 m). If I assume a 3.4‰ difference between successive trophic levels with POM as "primary producer" *Diporeia* is a primary consumer about 0.8 (spring) to 1.3 (summer) trophic levels up from pelagic POM throughout the year.

My results show that *D.hoyi* in this "low-nutrient", deep, temperate aquatic system feeds more or less continuously throughout the year. It does utilize spring and autumn blooms, which are stored as lipids, but it also uses pelagic sources during periods of thermal stratification. There is no need for *D. hoyi* to starve during summer since pelagic inputs are more than enough to support the population in Colpoys Bay Furthermore, *Diporeia* inhabiting shallower areas can exploit other sources such as algae from littoral areas.

5.4. Conclusions

The majority of *Diporeia*'s population takes two years to develop, although some may be sexually mature within a year. Migration of adult amphipods to shallower waters in late winter to release their young was evident, and accounted for the lower YOY density at the deeper site. Juvenile amphipods were responsible for most of the production at both sites.

Analysis of lipid concentrations and gut fullness showed *Diporeia* feeds more or less continuously and also that spring and fall blooms were readily assimilated. The seasonal changes in feeding activities, hence lipid content, were reflected in changes in the carbon isotope signatures.

D. hoyi collected at areas deeper than 30 m seem to depend on pelagic primary production; in shallower areas (20-25 m) *Diporeia* will use epilithic production as well. Nitrogen isotope analyses showed that only one intermediate trophic step is required to convert photosynthetically fixed energy into a form sufficiently large to be eaten by fish. In agreement with previous studies, *D. hoyi* has the capacity to accumulate energy from spring diatom blooms in the form of lipids, however *D. hoyi* does not fast during summer months in Colpoys Bay where pelagic inputs are enough to support its population.

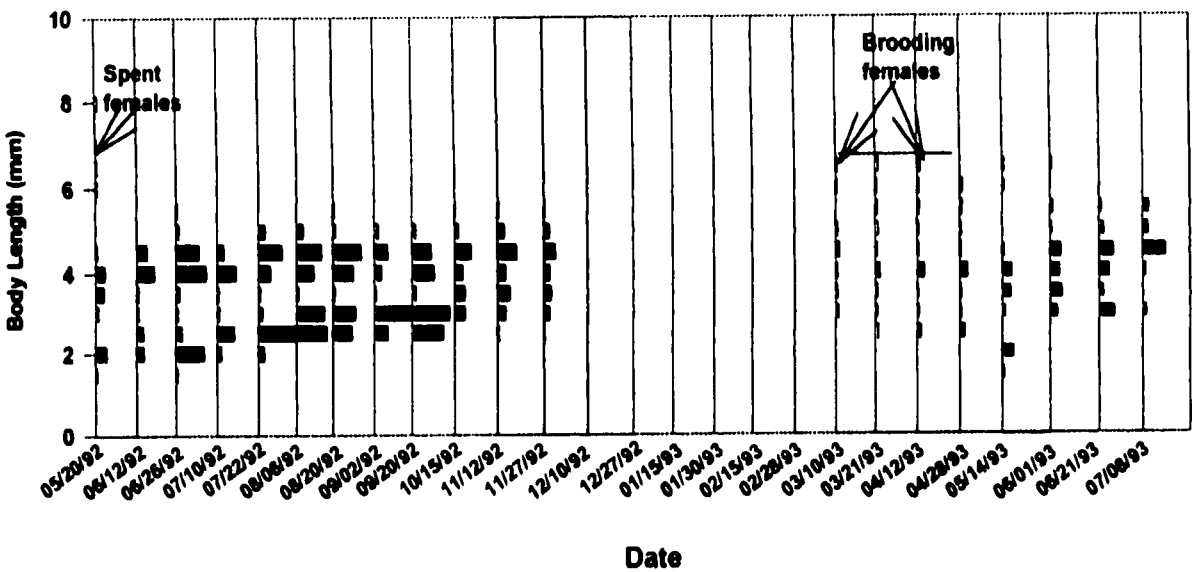


Figure 5.1a) Size frequency histograms (number of individuals vs body length in mm) over sampling period at 30 m.

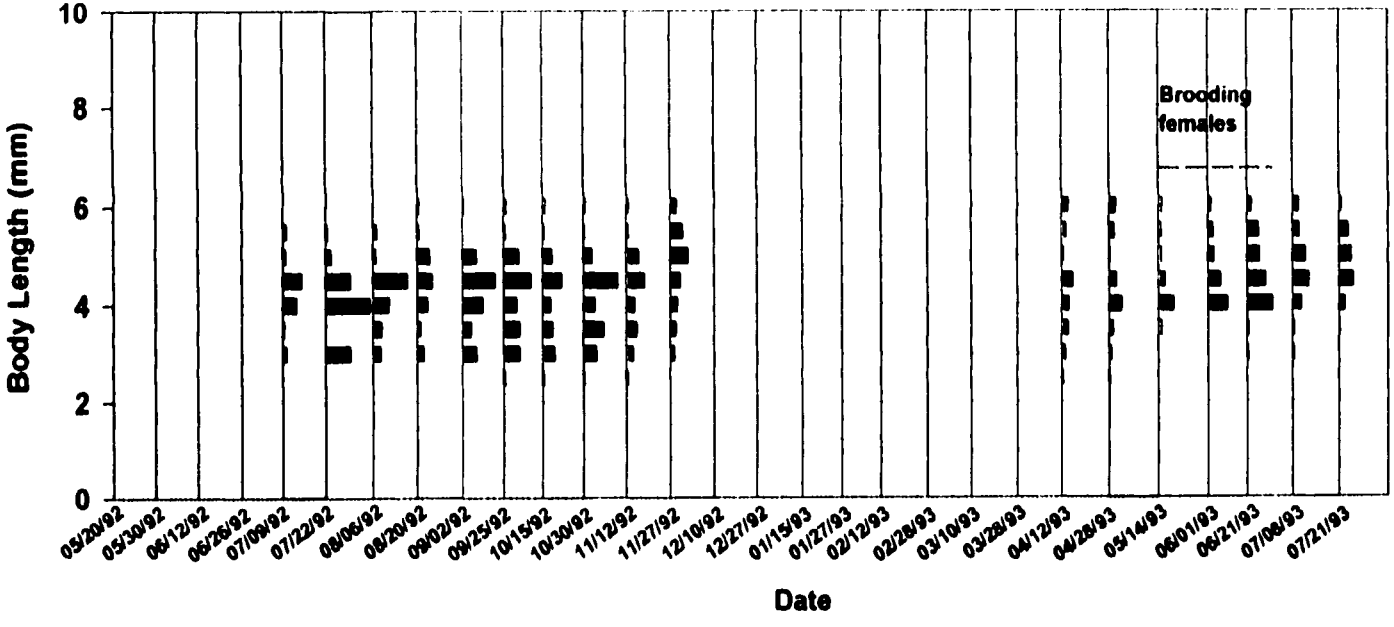


Figure 5.1 b) Size frequency histograms (number of individuals vs body length in mm) over sampling period at 50 m.

Table 5.1: *Diporeia's* annual mean densities, annual mean biomass, annual production, CPI, cohort P/B and annual P/B. na=not applicable.

	30m				50m			
	Total	YOY	Juveniles	Adults	Total	YOY	Juveniles	Adults
Density ($indm^{-2}$)	811	362	390	59	1415	292	808	315
Mean ind.weight (mg/ind)	0.30	0.068	0.440	0.809	0.41	0.088	0.413	0.970
Biomass (gm^{-2})	0.25	0.025	0.172	0.050	0.67	0.026	0.333	0.305
Production ($gm^{-2}y^{-1}$)	0.50				1.34			
CPI (days)	593	na	na	na	593	na	na	na
Cohort P/B	2.8	na	na	na	3.2	na	na	na
Annual P/B (y^{-1})	1.9	na	na	na	2.0	na	na	na

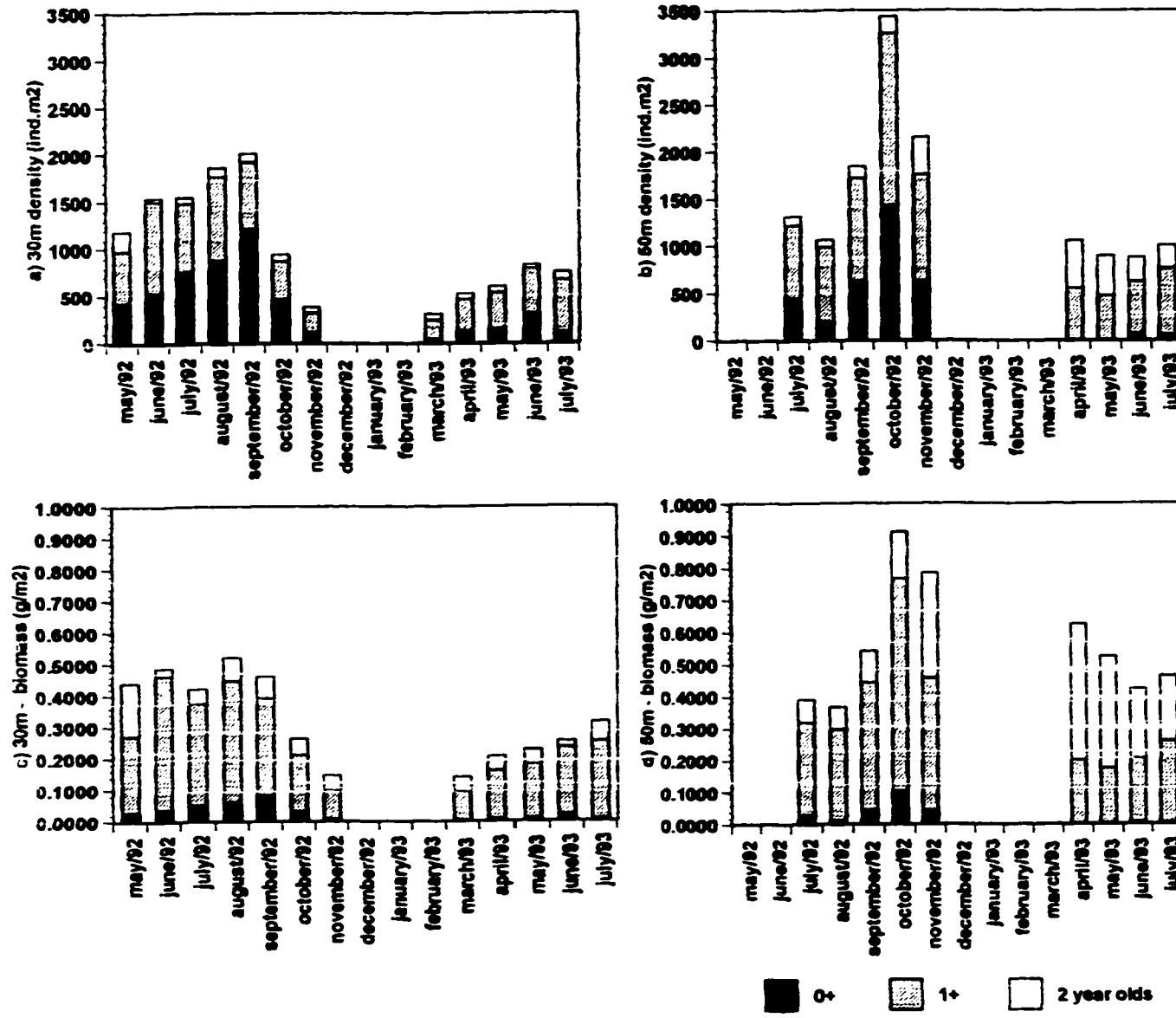


Fig 5.2: a) Monthly mean densities at a) 30 m; b) 50 m and monthly mean biomass at c) 30 m and d) 50 m.

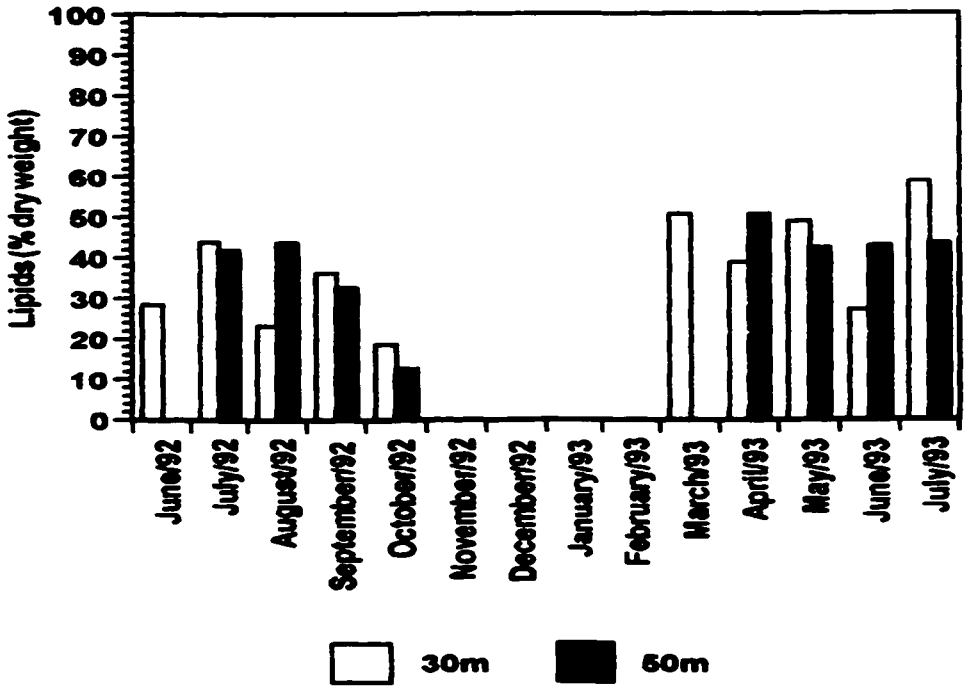


Figure 5.3. Mean lipid concentrations (% dry weight) in *D.hoyi* over the study period at 30 and 50 m.

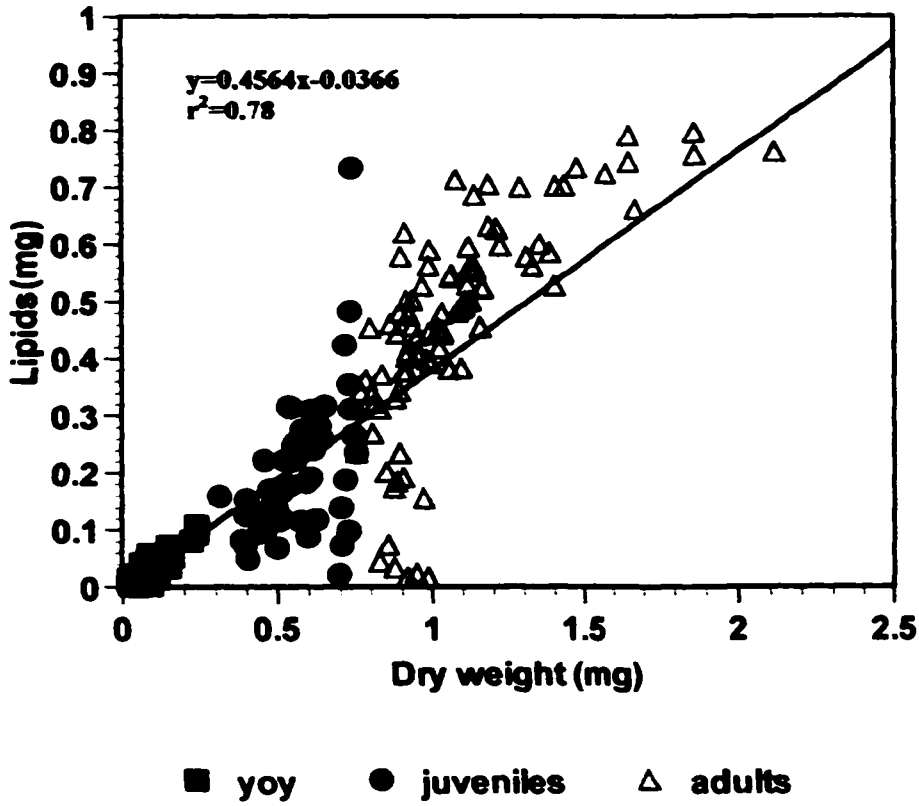


Figure 5.4. Relationship of lipid concentration (as the difference between dry weight before and after extraction in mg) and dry weight (mg) of *D.hoyi*.

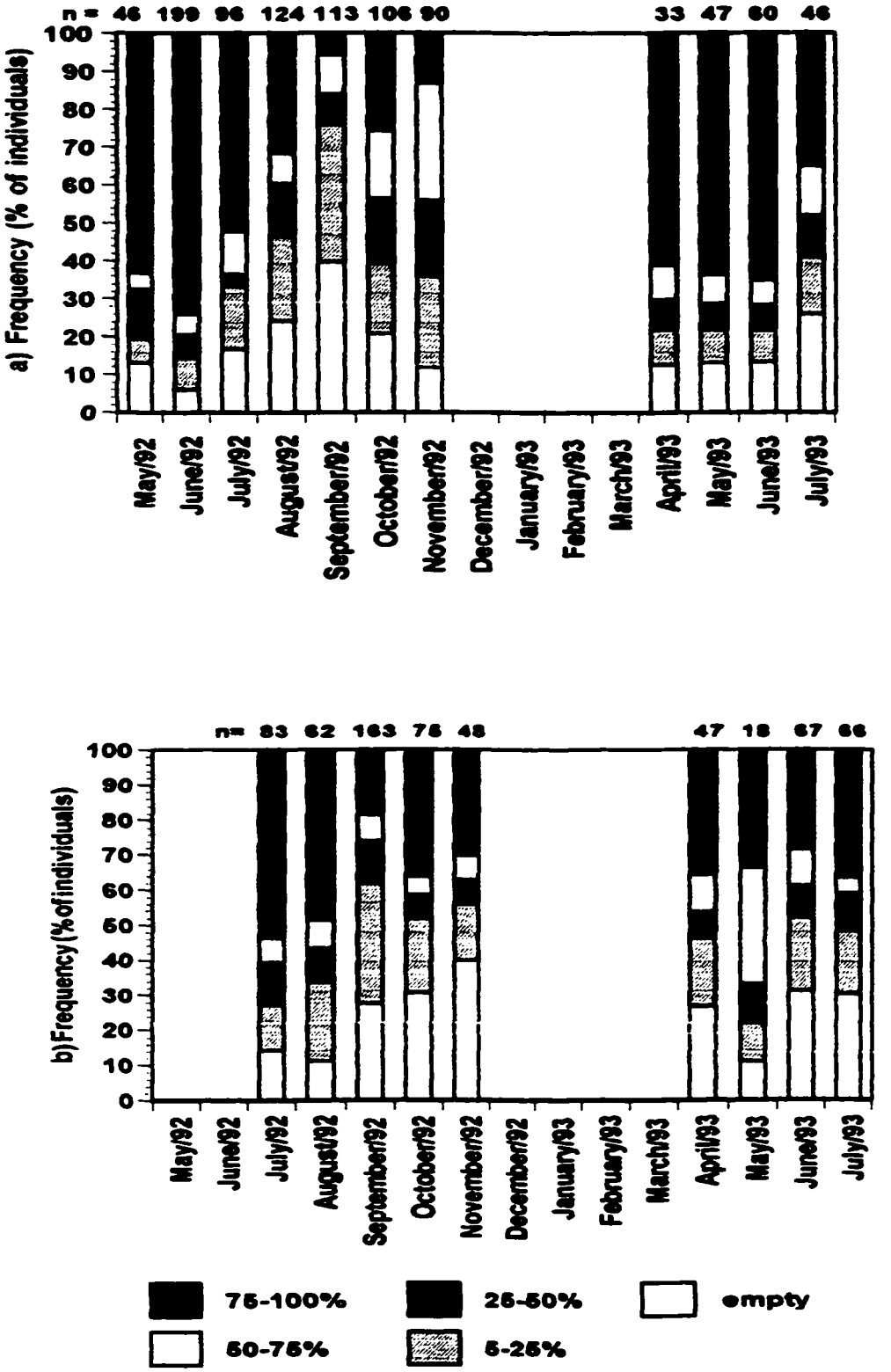


Figure 5.5: Gut fullness (as% of individuals) on each sampling date at depths of a) 30m and b) 50m. Number of animals is indicated above each bar.

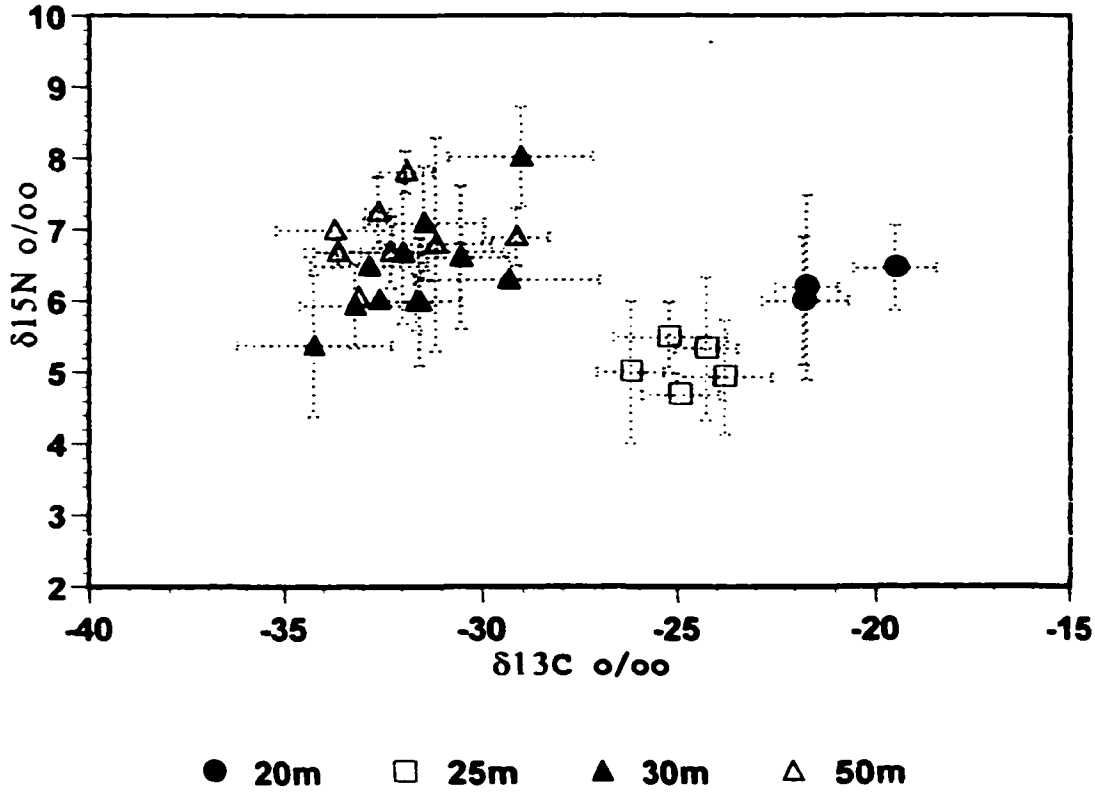


Figure 5.6:Carbon and nitrogen isotopes signatures for *Diporeia* at four depths during the study period. Error bars are standard deviations from the mean in 2 or 3 replicate samples.

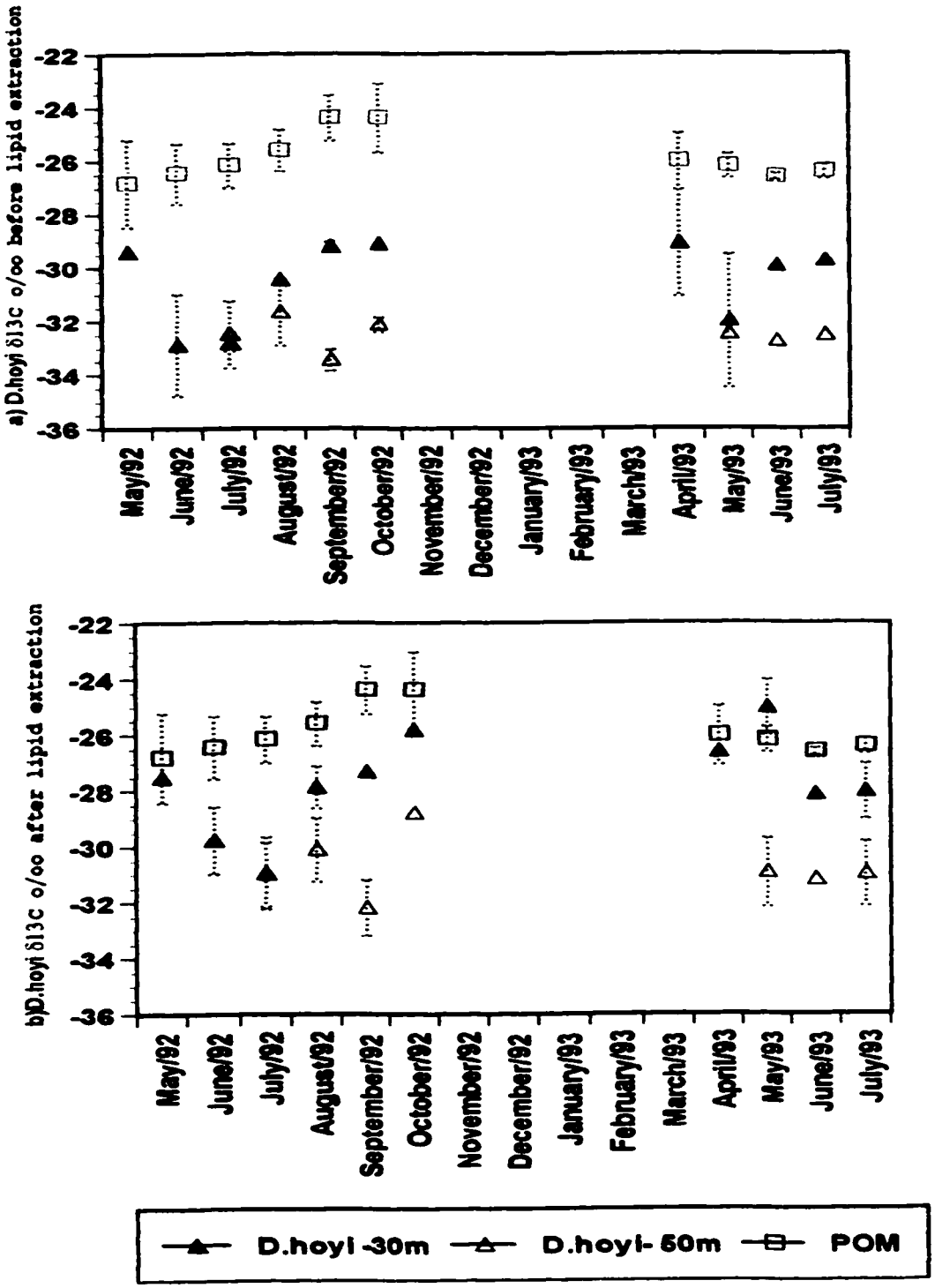


Figure 5.7 $\delta^{13}C$ seasonal variation for *Diporeia* at 30 and 50 m and POC; a) before lipid extraction and b) after lipid extraction. Error bars are standard deviation from themean of replicate samples for *Diporeia*.

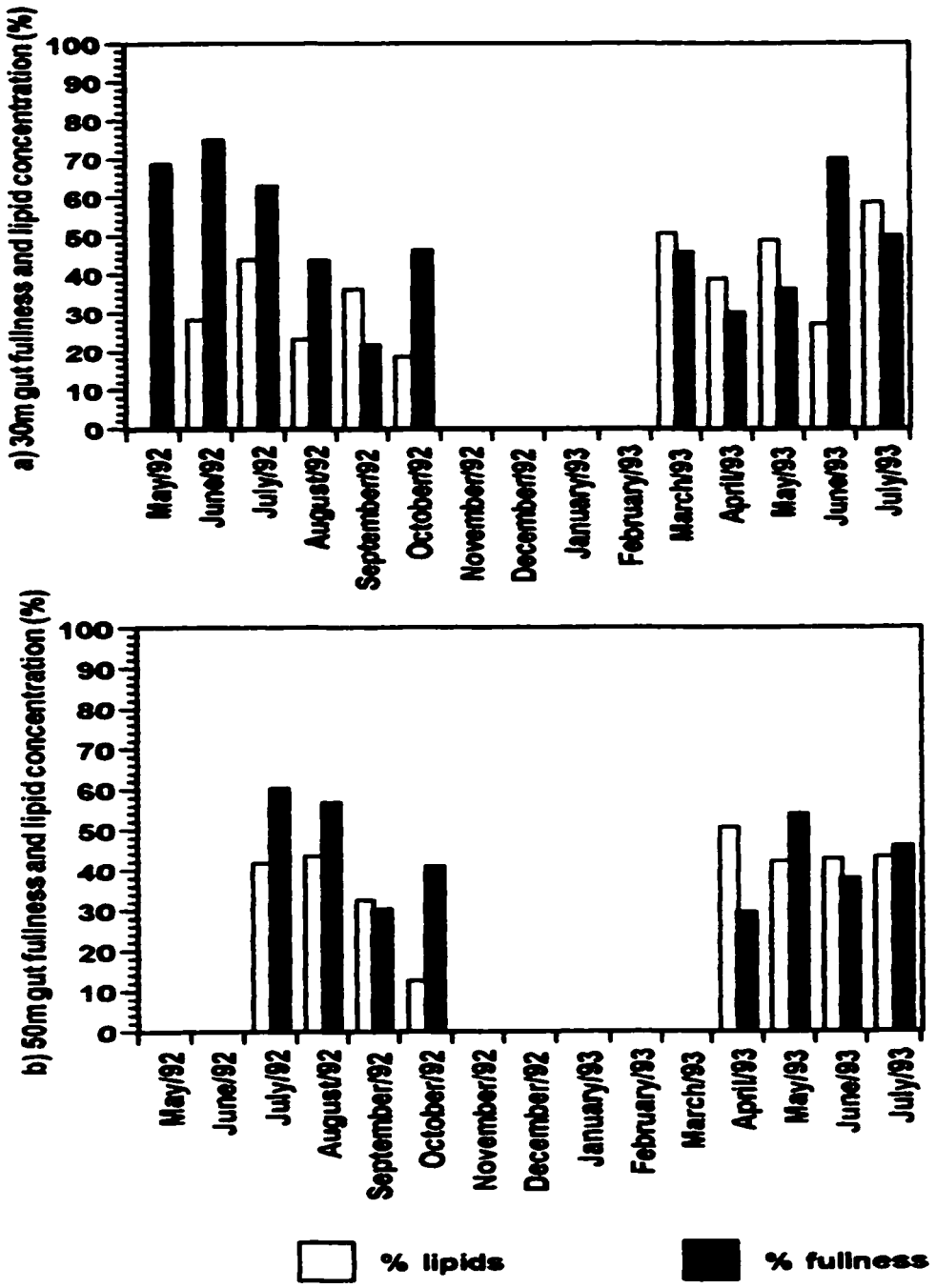


Figure 5.8: Seasonal variation of gut fullness and lipid concentration of *Diporeia* during the study period.

Chapter 6: General Conclusions: Benthic Community Energy Requirements

In this thesis the assimilation of several different sources of energy by benthic invertebrates was examined. The diversity, abundance, biomass, production and diet of benthic communities were compared in habitats of different complexity (e.g. littoral, charophytes and profundal areas). Estimates of diet, obtained using stable isotopes of carbon and nitrogen, and secondary production were combined to determine the dependence of individual taxa in each habitat on different sources of energy.

The benthic fauna of Colpoys Bay consists of a dense and rich littoral community characteristic of shallow sandy substrata and macrophytic vegetation, dominated by insects (mostly Diptera), isopods and gastropods with a gradual transition to the usual fauna of *D. hoyi*, *Pisidium* spp and oligochaetes typical of soft sediments further offshore.

Isopods were the most productive group because they are very numerous, individually large and have a bi-voltine life cycle. Chironomids were the second most productive group at littoral sites. *Diporeia hoyi* accounted for most of production at depths $\geq$ 30 m.

As expected, biomass and production were different in the three main zones studied (i.e. littoral, charophytes and profundal) with the area covered by charophytes making the largest contribution to total production in Colpoys Bay. The shallow littoral zone (5 m) was more productive per unit area, but occupies much less of the basin, so accounted for slightly less of total production. The profundal zone is largest in terms of area, but supports a much more restricted fauna, at low densities, and

contributed only about 9% of accountable benthic secondary production in Colpoys Bay.

While pelagic communities are thought to be more important than both littoral and bottom communities in the overall production process in large lakes (Tilzer 1990), my estimates of mean zoobenthic biomass of Colpoys Bay were twice those of zooplankton biomass and the estimated zooplankton production only slightly greater than zoobenthos. Those results emphasize the significance of littoral areas in the overall production processes of Colpoys Bay.

Most species of fish in Georgian Bay are benthivores during at least part, if not most, of their lifetimes. The similarity between predicted fish production based on benthic invertebrate biomass and reported harvests further emphasises the potential importance of benthic invertebrates in energy transfer between primary producers and fish.

I used the dual stable isotope (carbon and nitrogen) approach to determine which sources of energy are most important to the dominant benthic macroinvertebrates in different habitats of Colpoys Bay, and also to describe the trophic structure within each habitat. The processes that influence assimilation of different sources of energy by invertebrates in lake food webs are very complex, so I tried to simplify this problem by blocking my results within littoral, profundal and pelagic communities, knowing, however, that they interrelate. For all three communities, carbon and nitrogen signatures of primary producers and primary consumers varied both spatially and temporally.

Most of the organic matter in the sediments of lakes is ultimately derived from organic matter synthesized by organisms inhabiting shallow waters and transported to the lake floor as particulate organic matter (POM). Most of the organic matter produced in the water column can be recycled, especially during period of thermal stratification so only a fraction of the particulate organic matter produced will reach the bottom. Processing within the water column will also affect the carbon isotope signatures of POM, and the organisms which subsequently feed upon it.

Carbon isotope signatures of POM varied temporally and spatially. The isotopic signature and concentration of DIC, and the mode of photosynthetic uptake all influence POM signatures. In Colpoys Bay, most of the DIC is in the form of HCO_3^-, therefore the $\delta^{13}C$ of DIC is dominated by the $\delta^{13}C$ of HCO_3^-. DIC isotope signatures remained fairly constant throughout the year, with a slight enrichment toward autumn. Changes in the DIC signatures influence the delta values of photosynthetically fixed carbon. POM exhibited no real change during periods of isothermal conditions, after which a steady strong enrichment in the signatures was observed from late summer until fall overturn. This enrichment in POM signatures was attributed to an intrusion of periphytic littoral sources and perhaps, some in situ carbon limitation.

In Chapter four, temporal variations among energy sources and macroinvertebrates were examined, and trophic dependencies determined. I originally hypothesized that submerged vascular macrophytes, charophytes, epiphytic and epilithic matter could be important sources at littoral sites (5 and 15 m). The significance of epilithon should decrease with increasing depth and distance from

shore. POM input should increase with thickness of the water column, so was expected to be fueling the communities at the deeper sites. Allochthonous organic matter should be more important near shore and at the head of the bay.

My results emphasized the importance of epilithon as the major energy source for benthic communities within littoral areas of Colpoys Bay. Regardless of feeding guilds, littoral invertebrates are strongly dependent on the epilithic biofilm, therefore caution must be taken when assigning the widely used functional feeding group concept to lentic invertebrates. The dependence on periphyton diminishes with increasing depth. Invertebrates found in areas deeper than 30 m rely mostly on autochthonous sedimenting organic matter and some seasonal littoral inputs.

In Chapter 5 the trophic role of *Diporeia hoyi* in Colpoys Bay was assessed. Production rates, population dynamics, lipid content, gut fullness were combined with information on stable isotopes of carbon and nitrogen to describe the flow of energy to *D. hoyi* in Colpoys Bay. The majority of *Diporeia* take two years to develop, although some may be sexually mature within a year. Juvenile amphipods were responsible for most of the production at both sites. Lipid concentrations and gut fullness showed *Diporeia* feeds more or less continuously throughout the summer and also that spring and fall blooms were readily assimilated. *D. hoyi* collected at areas deeper than 30 m seem to depend on pelagic primary production; in shallower areas (20-25 m) *Diporeia* uses epilithic production as well. Nitrogen isotope analyses showed that only one intermediate trophic step is required to convert photosynthetically fixed energy into a form sufficiently large to be eaten by fish. In agreement with previous studies, *D. hoyi* has the capacity to accumulate energy from

spring diatom blooms in the form of lipids; however, *D. hoyi* does not fast during the summer months in Colpoys Bay where pelagic inputs are enough to support its population.

To estimate minimum inputs of each food source to the total benthic production of the bay I used the same procedure described in Benke and Jacobi (1994) based on literature-derived values for ecological efficiencies (Benke and Wallace 1980) (Table 6.1). These were net production efficiency (annual production/assimilation) of 40%, assimilation efficiencies (assimilation/ingestion) were assumed to be 30% for diatoms and 70% for animals and gross efficiencies (annual production/ingestion) of 12% and 28%, respectively, for diatoms and animals. Minimum inputs to support *D. hoyi* populations were obtained in Chapter 5.

Table 6.1: Estimates of food sources required to support benthic production of Colpoys Bay.

Production supported by each food item ($g.m^2y^{-1}$)	Minimum food inputs ($g.m^2y^{-1}$)
Site:5m total production = 21.75	
Benthic algae = 12.25	102.08
Epiphyton = 6.54	54.50
POM = 2.34	19.50
Animal = 0.62	2.21
Site:15m total production 15.93	
Benthic algae = 3.22	26.83
Epiphyton = 7.27	60.58
POM = 5.15	131.37
Animal = 0.29	1.04
Site: 30 and 50 total production 1.12*	
POM = 1.12	28.00
Total Benthic algae	**128.91**
Total Epiphyton	**115.08**
Total POM	**90.42**
Total Animal	**3.25**

* Production of *Pisidium* and chironomids added to the mean production of *D. hoyi*.

Epilithic primary production rates in 1984 and 1985 (Duthie and Jones, 1990) from Dyer's Bay, just north of Colpoys Bay, were 35 and 50 $mgC.m^{-2}.h^{-1}$. Assuming the growing season lasts from mid-April to mid-December, minimum yearly estimates would be 100 and 144 $gC.m^{-2}$, which amounts to 200 and 288 g dry $weight.m^{-2}.y^{-1}$ ($1gC \approx 2g$ dry weight). While there are no measurements of primary production for benthic algae growing on the sediment, a rough estimation may be made: Rosenfeld and Roff (1991) found primary production on fine sediments in streams to be 20% of that on rock surfaces, which gives a range of 40 to 57.6 $g.m^{-2}.y^{-1}$. Therefore, primary production for benthic algae weighted according to the realtive proportions of rock and sand areas to a maximum depth of 18m may range from 140 to 201 $g.m^{-2}.y^{-1}$, which just enough to support the invertebrate production dependent on this food source. Similarly, phytoplankton production for Georgian Bay was 76 $gC.m^{-2}.y^{-1}$ or 152 g dry weight. $m^{-2}.y^{-1}$, more than adequate to support the secondary production dependent on POM. I have found no measurements of the production of epiphytic algae growing on *Chara*, but, given that charophytes cover a large area in Colpoys Bay, the quantities must be large.

Although those estimates are only approximations, they support the conclusions drawn from Chapters 2 and 4 that benthic primary production determines the overall secondary productivity of benthic invertebrates in Colpoys Bay. At depths below the photic zone, invertebrate production declined drastically.

In summary, the combination of stable isotope methods and measurement of secondary production allowed me to describe carbon flow through individual benthic taxa and within a lake ecosystem. The success of the stable isotope method is

dependent upon isotopically distinct signatures among potential dietary components. The fact that carbon signatures of aquatic primary producers are dependent on growth rates demands a sampling procedure that detects both seasonal and microhabitat variation within this food source. Additionally, it is imperative that animal life cycles (e.g. periods of maximal growth and reproduction) are known.

References

Andrews, M., I.R. Davison, M.E. Andrews and J.A. Raven. 1984b. Growth of *Chara hispida* I. Apical growth and basal decay. Journal of Ecology. 72: 873-884.

Allimov, A.F., V.V. Boullion, N.P. Finogenova, M.B. Ivanova, N.K. Kuzmitskaya, V.N. Nikulina, N.G. Ozeretskovskaya, and T.V. Zharowa. (1972). Biological productivity of Lakes Krivoe and Krugloe – In: Kajak, Z and Hillbricht-Ilkowska, A. (eds). Productivity problems of freshwaters. PWN Pol. Sci. Publ., Warsaw, pp. 39-56.

Barton, D.R., and H.B.N. Hynes. 1978. Wave-Zone macrobenthos of the exposed canadian shores of the St. Lawrence Great Lakes. Journal of Great Lakes Research 4 (1): 27- 45.

Barton, D.R., and J.C.H. Carter. 1979. Benthic macroinvertebrates from southern Georgian Bay. Waterloo Res. Inst., Report No. O1SU.KF 714-8-0045.

Barton, D.R., and J.C.H. Carter. 1982. Shallow–water epilithic invertebrate communities of eastern Georgian Bay, Ontario, in relation to exposure to wave action. Canadian Journal of Zoology 60: 984-993.

Barton, D.R., and M. Griffiths. 1984. Benthic invertebrates of the nearshore zone of eastern Lake Huron, Georgian Bay and North Channel. Journal of Great Lakes Research 10(4): 407-416.

Barton, D.R. and S.M. Smith. 1984. Insects of extremely small and extremelly large aquatic habitats. In: The ecology of aquatic insects. V.H. Resh. and D.M. Rosenberg (eds). Praeger. NY.NY. 623pp.

Benke, A.C., 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnology and Oceanography 24 (1): 168-171.

Benke, A.C. 1993. Concepts and patterns of invertebrate production in running waters. Edgardo Baldi Memorial Lecture. Verhandlungen International Verein. Limnologie 25:15-38.

Benke, A.C. and D.I. Jacobi. 1994. Production dynamics and resource utilization of snag-dwelling mayflies in a blackwater river. Ecology 75 (5): 1219-1232.

Benke, A.C and J.B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology 61: 108-118.

Berg, M.B. 1995. Larval food and feeding behaviour. *In*: The Chironomidae. The biology and ecology of non-biting midges. Armitage, P., P.S. Cranston and L.C.V. Pinder. (eds). Chapman and Hall

Biegeleisen, J. and M. Wolfserbeerg. 1958. Theoretical and experimental aspects of isotope effects in chemical kinetics. Advances in Chemical Physics 1: 210-216.

Borgman. U., H. Shear and J. Moore. 1984. Zooplankton and potential fish production in Lake Ontario. Canadian Journal of Fisheries and Aquatic Science 41: 1303-1309.

Brinkhurst, R.O. 1974. The benthos of lakes. Macmillan Press Ltd., London 150 pp.

Burkholder, J.M. and R.G. Sheath. 1985. Characteristics of softwater streams in Rhode Island. I. A comparative analysis of physical and chemical variables. Hydrobiology 128: 97-108.

Bunn, S.E. and P.I. Boon. 1993. What sources of organic carbon drive foodwebs in billabongs? A study based on stable isotope analysis. Oecologia 96: 85-94.

Cabana, G. and J.B. Rasmussen. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotope. Nature 372: 255-257.

Cavaletto, J.F., T.F. Nalepa., R. Dermott., W.S. Gardner., M.A. Quigley., & G.A. Lang. 1996. Seasonal variation of lipid composition, weight, and length in juvenile *Diporeia* spp. (Amphipoda) from lakes Michigan and Ontario. Canadian Jouranl of Fisheries and Aquatic Science 53: 2044-2050.

Cook, D.G. 1975. A preliminary report of the benthic macroinvertebrates of Lake Ontario. Journal of Fisheries Research Board Canada Tech. Rep. 449.

Cook, D.G., & M.G. Johnson. 1974. Benthic macroinvertebrates of the St. Lawerence Great Lakes. Journal of Fisheries Research Board Canada 31: 763-789.

Corey, S. 1988. Comparative histories of four populations of *Orconectes propinquus* (Girard, 1852) in Southwestern Ontario, Canada (Decapoda, Astecidea). Crustaceana 54: 128-138.

Dahl, J.A., D.M. Graham, R. Dermot, O.E. Johannson, E.S. Millard and D.D. Myles. 1995. Lake Erie 1993, western, west central and eastern basins: Changes in trophic status, and assessment of the abundance, biomass and

production of the lower trophic levels. Canadian Technical Report of Fisheries and Aquatic Sciences. No. 2070.

DeNiro, M.J., & S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.

Dermott, R., and K. Corning. 1988. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in lake Ontario. Canadian Journal of Fisheries and Aquatic Science 45: 1886-1895.

Downing, J.A. and F.H. Rigler 1984. A manual on methods for the assessment of secondary productivity in fresh waters. Downing and Rigler (eds). 2nd edition. Blackwell Scientific Publications. 501pp.

Duthie H.C. and D.K. Jones 1990. Epilithic algal productivity on the submerged Niagara Escarpment, Georgian Bay, Canada. Verhandlungen International Verein. Limnologie 24: 411-415.

Edwards, R.T and J.L. Meyer. 1990. Bacterivory by deposit-feeding mayfly larvae (Stenonema spp). Freshwater Biology 24(3): 453-462

Elzenga, J.T.M. and H.B.A. Prins. 1989. Light induced polar pH changes in leaves of *Elodea canadensis*. Plant Physiology 91: 68-72.

Evans, M.S., M.A. Quigley and J.A. Wojcik. 1990. Comparative ecology of *Pontoporeia hoyi* populations in southern Lake Michigan: The profundal region versus the slope and shelf regions. Journal of Great Lakes Research 16(1): 27-40.

Farwell, A.J.C. 1993. The ecology of characeae in Colpoy's Bay, Georgian Bay. M.Sc. thesis. University of Waterloo. Waterloo. Ontario. Canada.

Farwell, A.J.C. and H.C. Duthie. 1993. Distribution, biomass and seasonality of charophytes in Georgian Bay, Lake Huron, Canada. Verhandlungen International Verein. Limnologie 25: 350-354.

Ferrier, M.D. and T.E. Wissing. 1979. Larval retreat and food habits of the net-spinning Trichopteran *Cheumatopsyche analis* (Trichopetera: Hydropsychidae). The Great Lakes Entomologist 12(4): 157-164.

Fogel, M.L., L.A. Cifuentes., D.J. Velisnky and J.H. Sharp. 1992. Relationship of carbon availability in estuarine phytoplankton to isotope composition. Marine Ecology Progress Series 82: 291-300.

Fogel, M.L. and L.A. Cifuentes 1993. Isotope fractionation during primary production, p.73-98 In: M.H. Engel and S.A. Macko [eds], Organic Geochemistry. Plenum. N.Y.N.Y.

France, R. 1995c. Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. Canadian Journal of Fisheries and Aquatic Science 52: 651-656.

Fritz. P., & J.Ch. Fontes. 1980. Handbook of environmental isotope geochemistry. Elsevier Scietific Public Company.

Fry, B., and E.B. Sherr. 1984. $\delta^{13}C$ measurements as indicator of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science. 27: 13-47.

Fry. B. 1991. Stable isotope diagrams of freshwater foodwebs. Ecology 72 (6): 2293-2297

Fuller, R.L. and R.J. Mackay 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Canadian Journal of Zoology 58: 22392251.

J.H. Furgal. 1995. Effects of major environmental variables and ultrviolet light on phtosynthetic carbon assimilation and allocation in a natural assemblage of Great Lakes phytoplankton. MSc. Thesis. University of Waterloo.

Galimov, E.M. 1985. The Biological Fractionation of Isotopes. Eds: Meinschein.W.G. Academic Press Inc 261pp.

Gardner, W.S., T.F. Nalepa., W.A. Frez., E.A. Cichocki. and P.E. Landrum. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. Canadian Journal of Fisheries and Aquatic Science 42: 1827-1832.

Gardner, W.S., M.A. Quigley., G.L. Fahnenstiel., D. Scavia. and W.A. Frez. 1990. *Pontoporeia hoyi*-a direct trophic link between spring diatoms and fish in Lake Michigan. In: Large Lakes: Ecological structure and function M.M.Tilzer and C.Serruya (eds). Springer-Verlag.

Gile, S.R., A.P. Liskauskas., F.I. McNeil., E.J. deLaplante and S. Mannonen. 1993. Status and Outlook for the Major Commercial Fish Species of Lake Huron, 1993. Lake Huron Fisheries Management Unit Report 1-93. O.M.N.R.

Goericke, R., J.P. Montoya and B. Fry. 1994. Physiology of isotopic fractionation in algae and cyanobacteria. In: Lajtha,K., Michener, R.H. (eds), Stable Isotopes in Ecology and Environmental Science. Blackwell, Oxford, pp. 187-221.

Grafius. E. and N.H. Anderson.1980. Population dynamics and role of two species of *Lepidostoma* (Trichoptera: Lepidostomatidae) in an Oregon Coniferous Forest Stream. Ecology. 6(14):808-816.

Gray, L.J. and J.V. Ward. 1979. Food habits of stream benthos at sites of different food availability. American Midland Naturalist 102: 157-167.

Graham, M. 1997. Influence of omnivory and selective feeding on $\delta^{15}N$-determined trophic position of zooplankton along a gradient of lake production. Dissertation. U. of Regina. Regina, Sask. Canada.

Gu. B., C.L. Schelske and M. Brenner. 1996. Relationship between sediment and plankton isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) and primary productivity in Florida Lakes. Canadian Journal of Fisheries and Aquatic Science 53: 875-883.

Gu. B., V. Alexander and D.M. Schell. 1997. Stable isotopes as indicators of carbon flows and trophic structure of the benthic food web in a subartic lake. Archiv fur Hydrobiologie 138 (3): 329-344.

Guiguer, K.R.R.A. 1990. Relative contribution of allochthonous and autochthonous food sources to the profundal benthos: A stable isotope application. MSc Thesis. 67pp. University of Waterloo. Waterloo. Ontario. Canada.

Guy, R.D., M.F. Fogel, J.A. Berry and T.C. Hoering. 1987. Isotope fractionation during oxygen production and consumption by plants. Progress in Photosynthesis Research 3: 597-600.

Haines, B.E. and C.L. Montague. 1979. Food sources of estuarine invertebrates analyzed using ^{13}C /^{12}C ratios. Ecology 60 (1): 48-56.

Hamilton, A.L. 1969. On estimating annual production. Limnology and Oceanography 14: 771-782.

Handley, L.L. and J.A. Raven. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. Plant, Cell and Environment 15: 965-985.

Hanson, J.M. 1990. Macroinvertebrate size-distribution of two contrasting freshwater macrophyte communities. Freshwater Biology 24: 481-491.

Hanson, J.M. & W.C. Leggett. 1982. Empirical estimation of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Science 39 (2): 257-263.

Hartnoll, R.G. 1982. Growth. *In*: The Biology of Crustacea volume 2: embryology, morphology and genetics. L.G.Abele (ed.) Academic Press.

Hein, M. 1997. Inorganic carbon limitation of photosynthesis in lake phytoplankton. Freshwater Biology 37: 545.552.

Henderson, B.A., and N.R. Payne. 1988. Changes in the Georgian Bay Fish community, with special reference to lake trout (*Salvelinus namaycush*) rehabilitation. Hydrobiology 163: 179-194.

Hershey, A.E. 1986. Selective predation by *Procladius* in an Artic Alaskan lake. Canadian Journal of Fisheries and Aquatic Science 43: 252-328.

Hobson, K.A. and H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84: 9-18.

Holopainen, I.J., & L. Paassivirta. 1977. Abundance and biomass of the meiozoobenthos in the oligotrophic and mesohumic Lake Paajarvi, southern Finland Annals of Zoology Fennici 14: 124-134.

Horrigan, S.G., J.P. Montoya., J.L. Nevins. and J.J. McCarthy. 1990. Natural isotopic composition of dissolved inorganic nitrogen in the Chesapeake Bay. Estuarine, Coastal and Shelf Science 30: 393-410.

Hutchinson, G.E. 1975. A treatise on Limnology. Vol. III. Limnological Botany. John Wiley and Sons. New-York. Pp. 1-70.

Hynes H.B.N. and M.J. Coleman 1968. A simple method of assessing the annual production of stream benthos. Limnology and Oceanography 13: 569-575.

Johannsson, O.E and J.L. Beaver. 1983. The role of algae in the diet of *Chironomus plumosus f. semireductus* from the Bay of Quinte, Lake Ontario. Hydrobiologia 107: 237-47

Johannsson, O.E., Dermott, R.M., Feldkamp, R., and J.E. Moore. 1985. Lake Ontario long term biological monitoring program, 1981, 1982, Data base. Canadian Data Report of Fisheries and Aquatic Science No: 552.

Johannsson, O.E., R.M. Dermott., R. Feldcamp and J.E. Moore. 1985. Lake Ontario long term biological monitoring program: report for 1981 and 1892. Canadian Technical Report of Fisheries and Aquatic Science No: 1414.

Johannsson, O.E., L.G. Rudstam and D.C. Lasenby. 1994. *Mysis relicta* Assessment of metalimnetic feeding and implications for competion with fish in Lakes Onatrio and Michigan. Canadian Journal of Fisheries and Aquatic Science 51 (11): 2591-2602.

Johnson, M.G., and R.O. Brinkhurst. 1971. Production of benthic invertebrates of Bay of Quinte and Lake Ontario. Journal of Fisheries and Research Board of Canada 28: 1699 – 1714.

Johnson, M.G. 1988. Production by the amphipod *Pontoporeia hoyi* in South Bay, Lake Huron. Canadian Journal of Fisheries and Aquatic Science 45: 617 – 624.

Johnson, R.K. 1987. Seasonal variation in the diet of *Chironomus plumosus* (L.) and *C.anthracinus* Zett. (Diptera:Chironomidae) in mesotrophic Lake Erken. Freshwater Biology 17: 525-532.

Jonhson, R.K. 1987. The life history, production and food habits of *Pontoporeia affins* Lindstrom (Crustacea: Amphipoda) in mesotrophic Lake Erken. Hydrobiology 144: 277-283.

Johnson, T.B., D.M. Mason., C.R. Bronte., and J.F. Kitchell. 1998. Estimation of invertebrate production from patterns of fish predation in western Lake Superior. Trans-American Fisheries Society 127(3): 496-506.

Jonasson, P.M. 1978. Zoobenthos of lakes. Int. Verh. Theo. Agnew.Limnol. Verh. 20: 13-37.

Jonasson, P.M. 1984. The ecosystem of eutrophic Lake Esrom. pp:177 – 204. In: F.B. Taub. Ecosystems of the World – Lakes and Reservoirs. 643p. Elsevier Science Publisher. Amsterdam.

Jonasson, P.M. 1996. Limits for life in the lake ecosystem. Verhandlungen International Verein. Limnology 26: 1-33

Keiper, J.B., D.A. Casamatta & B.A. Foote. 1998. Use of algal monocultures by larvae of *Hydroptila waubesiana* and *Oxyethira pallida* (Trichoptera: Hydroptilidae). Hydrobiology 380: 87-91.

Kinney, W.L. 1972. The macrobenthos of Lake Ontario. Journal of Great Lakes Research Progress Report No 15: 53 – 79.

Kline Jr.T.C., J.J. Goering, O.A. Mathisen, P.H. Poe and P.L. Parker. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. $\delta^{15}N$ and $\delta^{13}C$ evidence in Sashin creek, southern Alaska. Canadian Journal of Fisheries and Aquatic Science 47: 136-144.

Kwiatkowski, R.E. 1984. Comparison of 1980 Lake Huron, Georgian Bay, North Channel surveillance data with historical data. Hydrobiology 118: 255-266.

Legget, M.F. 1998. Food-Web dynamics of Lake Ontario as determined by carbon and nitrogen isotope analysis. Ph.D. thesis. University of Waterloo. Waterloo. Canada.

Lindegaard, C. 1992. Zoobenthos ecology of Thingvallavatn: vertical distribution, abundance, population dynamics and production. Oikos 64: 257-304.

Loveridge, C.C., and D.G. Cook. 1976. A preliminary report on the benthic macroinvertebrates of Georgian Bay and North Channel. Environment Canada, Fisheries and Marine Service Research Division Tec. Rep. 610.

Lucas , W.J. 1985. Bicarbonate utilization by *Chara*: A re-analysis. Pp 229-254. *In*: W.J. Lucas and J.A. Berry. (eds), Inorganic carbon uptake by aquatic photosynthetic organisms. American Society of Plant Physiologists, N.Y.N.Y.

Maberly S.C. and D.H.N. Spence. 1983. Photosynthetic inorganic carbon use by freshwater plants. Journal of Ecology. 71:705-724.

MacLeod, A.N. 1998. Trophic structure and the effects of agriculture in a headwater stream in southern Ontario using stable isotopes and secondary production. Ph.D. thesis: 138pp. University of Waterloo. Waterloo. ON. Canada.

MacLeod, A.N. and D.R. Barton. 1998. Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotopes ratios in periphyton. Canadian Journal of Fisheries and Aquatic Science Vol. 55: 1919-1925.

Macneil, C., Jaimie, T.A. Dick and W.E. Robert. 1997. The trophic ecology of freshwater *Gammarus* spp. (Crustacea:Amphipoda): problems and perspectives concerning the functional feeding group concept. Biology Review 72: 349-364.

Maly. J.A . 1992.Vertical distribution and flux of phytoplankton and other suspendend particles in a nearshore zone of western Georgian Bay (Colpoys Bay). M.Sc thesis. University of Waterloo. Ontario. Canada.

Mariotti. A., J.C. Germon, P. Hubert, P. Kaiser and R. Letolle.1981. Experimental determination of nitrogen kinetic isotope fractionation: some principles: illustration for denetrification and nitrification processes. Plant and Soil 62: 413-30.

Mariotti, A., C. Lancelot., and B. Gilles. 1983. Natural isotopic composition of nitrogen as a tracer of origin for suspended organic matter in the Scheldt estuary. Geochimica et Cosmochimica Acta. 48: 549-555.

Matuszek, J.E. 1978. Empirical predictions of fish yields of large North American lakes. Trans-American Fisheries Society 107: 385-394

Merritt, R.W. and K.W. Cummins. 1996. An Introduction to the Aquatic Insects of North America. Third Edition. Kendall/Hunt Publishing Company.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48: 1135-1140.

Mihuc, T. and D. Toetz. 1994. Determination of diets of alpine aquatic insects using stable isotopes and gut analysis. American Midland Naturalist 131: 146-155.

Mohr, L.C. 1998. Winter sport fishery Creel in Owen Sound and Colpoys Bay, 1994. Lake Huron management Unit Report 04-98. O.M.N.R

Mohr, L.C. and M.L. Nicol. 1998. Summary of creel survey data from soutern Georgian Bay, 1989 to 1994. Lake Huron Management Unit Report 02-98. O.M.N.R.

Mohr, L.C. and S.R.Gile. 1994. Status and outlook for the major commercial fish species of Lake Huron, 1994. Lake Huron Management Unit Report 1-94. O.M.N.R.

Monk, D.C. 1976. The distribution of cellulase in frshwater invertebrates of different feeding habits. Freshwater Biology 6: 471-475.

Mook, W.G., J.C. Bommerson and W.H. Staverman. 1974. Carbon isotope fractionation between dissolved and gaseous carbon dioxide. Earth Planet Science Letters 22: 169-176.

Mozley, S.C., and P.A. Wayne. 1973. Distribution of benthic invertebrates in the south end of Lake Michigan. Journal of Great Lakes Research Progress Report No 16: 87 – 96.

Munawar, M. and I.F. Munawar. 1979. Phytoplankton of Georgian Bay and North Channel, 1974: A preliminary study. Fisheries and Marine Service Technical Report No 918.

Munawar. M. 1988. Limnology and Fisheries of Georgian Bay and the North Channel Ecosystems. Developments in Hydrobiology 46. M. Munawar (ed). Kluewer Academic Publishers.

Nalepa, T.F., M.A. Quigley, K. Childs, J. Gauvin, T. Heatlie, M. Parker, and L. Vanover 1985. Macrobenthos of southern Lake Michigan 1980-1981. NOAA Data Report, Environmental Research Laboratories, Great Lakes Environmental Research Laboratory, Ann Arbor, MI., 273pp.

Nalepa, T.F. 1987. Long-term changes in the macrobenthos of southern Lake Michigan. Canadian Journal of Fisheries and Aquatic Science 4: 515-524.

Nalepa, T.F. 1989. Estimates of macroinvertebrate biomass in Lake Michigan. Journal of Great Lakes Research 15 (3): 437 – 443.

Owens, N.J.P. 1987. Natural variations in ^{15}N in the marine environment. Advances in Marine Biology 24: 388-397.

Paterson, C.G. and K.F. Walker. 1974. Seasonal dynamics and productivity of *Tanytarsus barbitarsis* Freeman (Diptera: Chironomidae) in the benthos of a shallow saline lake. Australian Journal of Marine and Freshwater Research 25: 151-165

Pereyra-Ramos, E. 1981. The ecological role of Characeae in the lake littoral. Ekol. pol. 29(2): 167-209.

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. American Review of Ecology Syst. 18: 293-320.

Peverly, J.H. and J. Brittain. 1978. Effect of Milfoil (*Myriophyllum spicatum* L.) on phosphorus movement between sediment and water. Journal of Great Lakes Research 4 (1): 62-68.

Plante, C., and J.A. Downing. 1989. Production of freshwater invertebrate population in lakes. Canadian Journal of Fisheries and Aquatic Science 46(9): 1484-1488.

Quigley, M.A. 1988. Gut fullness of the deposit feeding amphipoda, *Pontoporeia hoyi*, in southeastern Lake Michigan. Journal of Great Lakes Research 14: 178-187.

Quigley, M.A., J.F. Cavaletto and W.S. Gardner. 1989. Lipid compositon related to size and maturity of the amphipod *Pontoporeia hoyi*. Journal of Great Lakes Research 15(4): 601-610.

Raven, J., J. Beardall and H. Griffiths. 1982. Inorganic C-sources for *Lemanea*, *Cladophora* and *Ranunculus* in a fast-flowing stream: Measurements of gas exchange and of carbon isotope ratio and their ecological implications. Oecologia. 53: 68-78.

Raven, J.A. and W.J. Lucas. 1985. Energy costs of carbon acquisition. Pp. 305-324. *In:* W.J.Lucas and J.A.Berry (eds), Inorganic carbon uptake by aquatic

photosynthetic organisms. American Society of Plant Physiologists, N.Y. N.Y.

Rau, G. H., A.J. Mearns, D. R. Young, R.J. Olson, H. A. Schafer, and I. R. Kaplan. 1983. Animal 13C/12C correlates with trophic level in pelagic food webs. Ecology 64: 1314-1318.

Reddy, K.R., W.H. Patrick,Jr. and C.W. Lindau 1989. Nitrification-denitrification at the plant root-sediment interface in wetlands. Limnolology and Oceanography 34(6): 1004-1013.

Richards, C. and G.W. Minshall. 1988. The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. Journal of North American Benthological Society 7: 77-86.

Robbins, J.A., P.L. McCall., J.B. Fisher. and J.R. Krezoski. 1979. Effects of deposit feeding on migration of ^{137}Cs in lake sediments. Earth Planet Science Letters 42: 277-287.

Rosenfeld, J.S. and J.C. Roff. 1991. Primary production and potential availablity of autochthonous carbon in Ontario streams. Hydrobiology 224: 99-109.

Sandgren, C.D. 1988. The ecology of chrysophyte flagellates: their perennation strategies as freshwater phytoplankton. In: Growth and Reproduction strategies as freshwater phytoplankton (ed. C.D.Sandgren), pp.9-104. Cambridge University Press, Cambridge.

Saffran, K.R. 1993. Trophic ecology of the crayfish *Orconectes propinquus* in Colpoys Bay. M.Sc. thesis. University of Waterloo. Waterloo. Ontario.

Schelske, C. and D.A. Hodell. 1991. Recent changes in productivity and climate of Lake Ontario detected by isotope analysis of sediments. Limnology and Oceanography 36: 961-975.

Scrimgeour, G.J., M.C. Joseph, M.L. Bothwell, F.J. Wrona and M.H. M^{c}Kee. 1991. Mechanisms of algal patch depletion: importance of consumptive and non-consumptive losses in mayfly-diatom systems. Oecologia 85: 343-348.

Sharkey, T.D. and J.A. Berry. 1985. Carbon isotope fractionation of algae as influenced by an inducible CO_2 concentrating mechanism. Pp. 389-401. *In:* W.J.Lucas and J.A.Berry (eds), Inorganic carbon uptake by aquatic photosynthetic organisms. American Society of Plant Physiologists, N.Y. N.Y.

Sheath, R.G. and J.M. Burkholder. 1985. Characteristics of softwater streams in Rhode Island II. Composition and seasonal dynamics of macroalgal communities. Hydrobiology 128: 109-118.

Shrivastva, H. 1974. Macrobenthos of Lake Huron. Fisheries Research Board Canada Technical Report No. 449.

Shneider, J.C., F.F. Hooper., and A.M. Beeton. 1969. The distribution and abundance of benthic fauna in Saginaw Bay, Lake Huron. Proc. 12th Conference of Great Lakes Research, International Association of Great Lakes Research. Pp. 80-90.

Siegfried, C. A. 1985. Life history, population dynamics and production of *Pontoporeia hoyi* (Crustacea, Amphipoda) in relation to the trophic gradient of Lake George, New York. Hydrobiology 122: 174-180.

Sly. P.G. and W.J. Christie. Factors influencing densities and distributions of *Pontoporeia hoyi* in Lake Ontario. Hydrobiology 235/236:321-352.

Spence, D.H.N. 1982. The zonation of plants in freswater lakes. Advances in Ecological Research 12:37-125.

Sprules, W.G., M. Munawar and E.H. Jin. 1988. Plankton community structure and size spectra in the Georgian Bay and North Channel ecosystem. p: 135-140. In: M.Munawar (ed.), Limnology and Fisheries of Georgian Bay/North Channel Ecosystems. Kluwer Academic Publishers.

Strayer, D.R. 1985. The benthic micrometazoans of Mirror Lake, New Hamphshire. Archiv fur Hydrobiologie Supplement 72:282- 426.

Stumm, W. and J.J. Morgan. 1981. Aquatic Chemistry: An Introduction Emphasizing Chemical Equilibria in Natural Waters. J. Wiley and Sons, Tor. ON. Canada.

Tieszen, L.L.,T.W. Boulton and K.G. Tesdahl. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32-37.

Tilzer, M.M. 1990. Specific properties of large lakes. In: Large lakes: Ecological Structure and Function. Tilzer, M.M. and C. Serruya. (eds). Springer-Verlag. NY.NY. 691pp.

Titmus, G. and M. Badcock. 1981. Distribution and feeding of larval Chironomidae in a gravel pit lake. Freshwater Biology 11(3): 263-272.

Van den Berg, M.S., H. Coops., R. Noordhuis., J.van Schie en J. Simons. 1997. Macroinvertebrate communities in relation to submerged vegetation in two Chara-dominated lakes. Hydrobiology 342/343: 143-150.

Vander Zanden, M.J. and J.B. Rasmussen. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology. 80: 1395-1404.

Wada, E. and A. Hattori. 1978. Nitrogen isotope effects in the assimilation of inorganic nitrogenous compounds by marine diatoms. Geomicrobiology Journal 1: 85-101.

Waters, T.F. 1977. Secondary production in inland waters. Advances in Ecological Research 10:91-164.

Watson, N.F.H., L.R. Culp and H.F. Nicholson. 1976. Chlorophyll-a and primary production in Georgian Bay, North Channel and Lake Huron, Apr. to Dec., 1974 – Environment Canada, Fisheries and Marine Service, Technical Report 600, 40pp.

Weiler, R.R. 1988. Chemical limnology of Georgian Bay and the North Channel. Hydrobiology 163: 77-83.

Wetzel,R.G. 1975. Limnology. W.B. Saunders Company. Toronto. pp. 355-418.

Wile, I., Miler, G.E., Hitchin, G.C. and Yan, N.D. 1985. Species composition and biomass of the macrophytes vegetation of one cidified and two acid-sensitive lakes in Ontario. Canadian Field-Naturalist 99 (3): 308-312.

Wissmar. R.C., J.E. Richey., and D.E. Spyridakis. 1977. The importance of allochthonous particulate carbon pathways in a subalpine lake. Journal of Fisheries Research Board Canada 34: 1410-1418.