

# Productivity and heterotrophy influences on zooplankton $\delta^{13}\text{C}$ in northern temperate lakes

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**ABSTRACT:** Although a range of over 30‰ in stable carbon isotope ratios has been recorded for freshwater plankton, no extensive synoptic survey has been undertaken to examine whether any environmental or ecophysiological determinants of  $\delta^{13}\text{C}$  exist. Here we reanalyze existing literature data on the seasonal variation in plankton  $\delta^{13}\text{C}$  from eutrophic lakes, and collect new data on mid-summer zooplankton  $\delta^{13}\text{C}$  from 52 Canadian Shield lakes, to demonstrate that plankton become enriched in  $^{13}\text{C}$  relative to  $^{12}\text{C}$  under conditions of high productivity and low  $\text{pCO}_2$ . Low zooplankton  $\delta^{13}\text{C}$  signatures in humic/dystrophic lakes of high DOC (dissolved organic carbon) concentration and colour, and in clear-water lakes with high rates of epilimnetic respiration and hypolimnetic metabolism, suggest that the  $^{13}\text{C}$ -depletion observed in oligotrophic lakes is probably due to heterotrophic activity.

**KEY WORDS:** Zooplankton  $\delta^{13}\text{C}$  · Lake productivity · Heterotrophy

## INTRODUCTION

The sources of organic matter that fuel foodwebs in lakes, and the trophic position of organisms in these webs, are 2 major questions in contemporary aquatic ecology that have been addressed with the use of stable isotope analysis. Although freshwater plankton display a considerable range of over 30‰ in stable carbon isotope ratios (France 1995a, b, del Giorgio & France 1996), the few attempts to relate cross-system differences to environmental conditions have been limited to data sets of 6 (McCabe 1985) or 11 (Gu et al. 1996) lakes. As a result, interpreting the sources of the differences in plankton  $\delta^{13}\text{C}$  among lakes is still largely conjectural.

Among the many factors thought to influence the  $\delta^{13}\text{C}$  values of organisms in pelagic foodwebs, the isotopic signature of phytoplankton is critical, as much of the variation in  $\delta^{13}\text{C}$  higher in the foodweb can be ascribed to variations in phytoplankton  $\delta^{13}\text{C}$ . Phytoplankton fractionate inorganic C during DIC (dissolved inorganic carbon) uptake and photosynthesis (Goer-

icke et al. 1994), and variations in  $\text{CO}_2$  concentrations and sources should have a large effect on the algal isotopic values, which will propagate throughout the pelagic foodweb. In marine systems, the variation in  $\delta^{13}\text{C}$  of POM (particulate organic matter) or phytoplankton is relatively minor, and a substantial portion of this variation can be explained by changes in phytoplankton biomass and production at small (Cifuentes et al. 1988, Fontugne et al. 1991), medium (Deuser 1970, Fisher 1991, Fry & Wainright 1991) and large (Sackett et al. 1965, Eadie & Jeffrey 1973, Rau et al. 1982, 1989, 1992, Fontugne et al. 1991, Francois et al. 1993) spatial scales. The plankton of lakes, in contrast, display a much larger range in  $\delta^{13}\text{C}$  than their marine counterparts, and it is perhaps unreasonable to expect that the majority of this variation could be explained by lake productivity alone.

A likely source for this difference between marine and freshwater systems is the more homogeneous isotopic composition of marine DIC compared to that of lakes (Oana & Deevey 1960, Hollander & McKenzie 1991). Respiration within the water column and sediments of lakes tends to yield  $\text{CO}_2$  that is depleted in  $^{13}\text{C}$ , and algal uptake of this light C should result in lower  $\delta^{13}\text{C}$  values of POM (Rau 1978). Studies have

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shown that many oligotrophic temperate lakes are strongly heterotrophic with extremely low community P/R (production/respiration) ratios (del Giorgio & Peters 1994) and high relative biomasses of planktonic heterotrophs (del Giorgio & Gasol 1995). Not coincidentally, oligotrophic temperate lakes are often supersaturated in  $\text{CO}_2$  which originates from respiration within the lake and from  $^{13}\text{C}$ -depleted DIC inputs from the drainage basin (Cole et al. 1994). These patterns suggest a predominance of recycled  $\text{CO}_2$  in the water column of many lakes, and further suggest that phytoplankton should become increasingly enriched in  $^{13}\text{C}$  as lakes become more productive (i.e. less heterotrophic).

Intense recycling of  $\text{CO}_2$  in the water column is not the only factor likely to affect the isotopic values of the plankton community in lakes. Many oligotrophic lakes have a large pool of dissolved and particulate organic matter of terrestrial origin. Planktonic heterotrophs are capable of utilizing some of this carbon (Jones 1992) which maintains the relatively constant ( $-29$  to  $-26\text{‰}$ )  $\delta^{13}\text{C}$  signature of temperate terrestrial vegetation. The proportion of allochthonous detrital organic matter in the total carbon pool tends to decline with lake productivity (Jones 1992, del Giorgio & Gasol 1995, del Giorgio & France 1996), so that the relative importance of this allochthonous pool to the C isotopic values of the plankton community should also decline with lake productivity. Thus, there are 2 fundamental but contrasting processes which might shape the  $\delta^{13}\text{C}$  values of freshwater plankton: (1) increased utilization of respiratory  $\text{CO}_2$  in oligotrophic lakes, leading to  $^{13}\text{C}$ -depleted phytoplankton; and (2) increased utilization of  $^{13}\text{C}$ -enriched allochthonous organic matter which should lead to  $^{13}\text{C}$ -enriched planktonic heterotrophs. The extent to which these 2 processes propagate upwards in the pelagic foodwebs of lakes depends both on the magnitude of each process and the relative importance of detrital versus algal carbon in zooplankton nutrition. If lake zooplankton overwhelmingly consume phytoplankton, then the effect of  $\text{CO}_2$  recycling should be most evident and there should be a strong relationship between  $\delta^{13}\text{C}$  and lake productivity. Conversely, if zooplankton consume variable amounts of phytoplankton, detritus and planktonic heterotrophs, then the outcome in terms of  $\delta^{13}\text{C}$  should be less predictable.

In this paper we investigate some of the factors that may influence plankton  $\delta^{13}\text{C}$ , and focus on zooplankton (organisms  $< 1$  mm to  $> 150$   $\mu\text{m}$ ) for several reasons. First, the  $\delta^{13}\text{C}$  value of phytoplankton can seldom be reliably measured because of dilution with the large detrital component present in many lakes (Hamilton & Lewis 1992, del Giorgio & France 1996). Second, phytoplankton are not the sole food source to zoo-

plankton in lakes, and planktonic heterotrophs together with detritus can often form a variable and yet unquantified fraction of zooplankton diet (Jones 1992). We assume here that zooplankton integrate some of the changes in the food base of pelagic communities among lakes. Third, zooplankton are the direct link between the pelagic food base composed of algae, a variety of planktonic heterotrophs, and detritus, and organisms higher in the foodweb which are of economic or management value.

Here we hypothesize a link between zooplankton  $\delta^{13}\text{C}$  and the degree of heterotrophy in the plankton of lakes. We measured zooplankton  $\delta^{13}\text{C}$  in 52 Canadian Shield lakes and attempted to explain the variation in  $\delta^{13}\text{C}$  with measured factors that are related both to plankton productivity and to the degree of heterotrophy in the pelagic foodweb. The first factor includes chlorophyll *a* concentration and total phosphorus as surrogate measures of phytoplankton production. The second category includes planktonic P/R ratios, DOC (dissolved organic carbon) or water colour, and partial pressure of  $\text{CO}_2$ , all variables that have been previously related to the degree of heterotrophy in the system. We report that only a moderate portion of the among-lake variation in zooplankton  $\delta^{13}\text{C}$  can be explained by any combination of these variables, although there is indication that zooplankton in oligotrophic temperate lakes are generally depleted in  $^{13}\text{C}$ , suggesting a role of heterotrophy.

## MATERIALS AND METHODS

Cross-system comparisons in mid-summer zooplankton  $\delta^{13}\text{C}$  were obtained from: (1) 24 lakes in southern Quebec and 4 in northwestern Ontario as the 250  $\mu\text{m}$  size fraction from pumped epilimnion samples (del Giorgio & France 1996); (2) 4 northwestern Ontario lakes as daytime tows using a 250  $\mu\text{m}$  plankton net and nighttime tows and hauls using a 400  $\mu\text{m}$  *Mysis* net (France 1995b, c); and (3) 24 central Ontario lakes as daytime hauls using a 363  $\mu\text{m}$  plankton net with later hand-sorted selection of filter-feeding cladocerans (Westcott 1995). In all cases, these size fractions represent macrozooplankton (del Giorgio & Gasol 1995). France et al. (1996) present stable nitrogen isotope data for these same zooplankton samples.

Zooplankton samples were frozen, dried, pulverized, and measured for carbon isotope ratios on a Europa Tracermass spectrometer interfaced with a Roboprep-CN analyzer which produced an average SD of  $\pm 0.3\text{‰}$  for 2 to 3 replicates per sample after correction for weight-related bias as in Hall (1995). Samples were run in 12 sequences of 5 per tray, each sequence being separated by paired standards (i.e. a blank to clear the

combustion tube followed by an identical reference), with duplicates or triplicates never occurring in the same run sequence. Differences among zooplankton  $\delta^{13}\text{C}$  values in Canadian Shield lakes probably reflect environmental influences on feeding diversity rather than metabolic fractionations due to differences in either lipid content or trophic position (France 1995c, France & Peters 1997). Our mass spectrometer was unable to measure inorganic aqueous  $\delta^{13}\text{C}$ , and this must be recognized as a shortcoming to many of our subsequent interpretations which are consequently based on inferred alterations in atmospheric-aqueous fractionations.

Colour was measured in the 24 central Ontario lakes as Hazen Units. Colour in the remaining lakes was measured as absorbance at 440 nm. All colour units are expressed in  $\text{mg Pt l}^{-1}$  following conversion procedures in Cuthbert & del Giorgio (1992). Dissolved organic carbon concentrations were measured in the 24 southern Quebec and 4 northwestern Ontario lakes from filtered ( $0.45 \mu\text{m}$  membrane) and acidified water samples using a Dohman carbon analyzer. Total phosphorus (TP) concentrations in all the lakes were measured using the ascorbic acid method following persulphate digestion. Partial pressures of  $\text{CO}_2$  ( $\text{pCO}_2$ ) were calculated from total alkalinity, pH and temperature in these lakes by Cole et al. (1994). Plankton P/R ratios are from del Giorgio & Peters (1994).

## RESULTS AND DISCUSSION

### Influence of lake productivity and $\text{pCO}_2$

Reanalysis of literature data for 3 eutrophic lakes revealed that POM and zooplankton communities became  $^{13}\text{C}$ -enriched during bloom periods of high biomass and primary productivity (Fig. 1; see also Hollander & McKenzie 1991). Together, this limnological work supports marine studies that have demonstrated laboratory cultures of algae to display less (water-cell) isotopic fractionation at high cell densities or growth rates (Degens et al. 1968, Deuser et al. 1968, Pardue et al. 1976, Wong & Sackett 1978, Fry & Wainright 1991), and temporal data for estuaries (Gearing et al. 1984, Fry & Wainright 1991, Fogel et al. 1992), coastal regions (Fry & Wainright 1991, Nakatsuka et al. 1992, Canuel et al. 1995, Kopczynska et al. 1995), the open ocean (Rau et al. 1992), and sediment cores (Arthur et al. 1985, Schemesh et al. 1993), which have all indicated that plankton collected during blooms are  $^{13}\text{C}$ -enriched compared to those sampled at times of low productivity.

Compilation of temporal data from McCabe (1985) and other freshwater studies (Fig. 2) indicates that, like

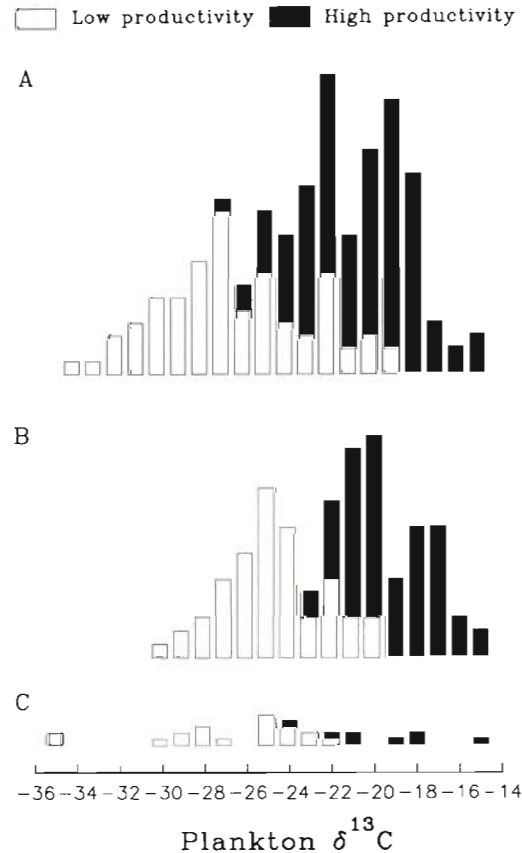


Fig. 1. Carbon-13 enrichment in plankton communities of lakes (A) Suwa (Takahashi et al. 1990, Yoshioka et al. 1994), (B) Kinneret (Stiller & Nissenbaum 1980, Zohary et al. 1994), and (C) Kizaki (Yoshioka et al. 1989) during high productivity seasonal blooms (solid bars) compared to non-bloom (open bars) conditions. Smallest bar indicates frequency of one. Compare these data with those for oceans in Fry & Wainright (1991)

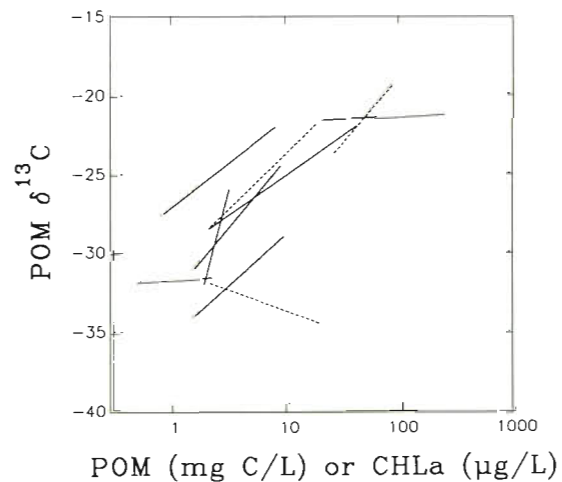


Fig. 2. Temporal relationships between phytoplankton biomass (POM as solid lines, chlorophyll *a* as dotted lines) and  $\delta^{13}\text{C}$  in 10 lakes from the literature (LaZerte 1983, McCabe 1985, Yoshioka et al. 1989, Takahashi et al. 1990, Zohary et al. 1994)

the marine situation (Kopczynska et al. 1995), system-specific empirical relationships can be developed between the abundance of POM or phytoplankton and its  $\delta^{13}\text{C}$  signature. The considerable inter-lake variability among these [POM]- $\delta^{13}\text{C}$  relationships indicates, however, that as in the oceans (Francois et al. 1993), a combination of both algal physiological and environmental influences can modify the carbon isotopic composition of plankton communities (Goerick et al. 1994).

McCabe (1985) believed that because the  $\delta^{13}\text{C}$  of POM in lakes is closely dependent upon that of DIC, any effect on the latter of for example temperature, groundwater seepage, pH, or air-water carbon exchanges will limit the possibility of observing a general relationship of plankton  $\delta^{13}\text{C}$  across lakes. Despite this prediction, we observed systematic differences in the  $\delta^{13}\text{C}$  values of mid-summer zooplankton communities grouped in relation to the trophic categorization of Canadian Shield lakes. Zooplankton were found to be  $^{13}\text{C}$ -enriched in meso-eutrophic compared to oligo-mesotrophic and especially oligotrophic lakes (Fig. 3). POM in eutrophic lakes (which should be isotopically equivalent to zooplankton; del Giorgio & France 1996) from the literature displayed even further  $^{13}\text{C}$  enrichment in comparison to zooplankton in the present less-productive study lakes.

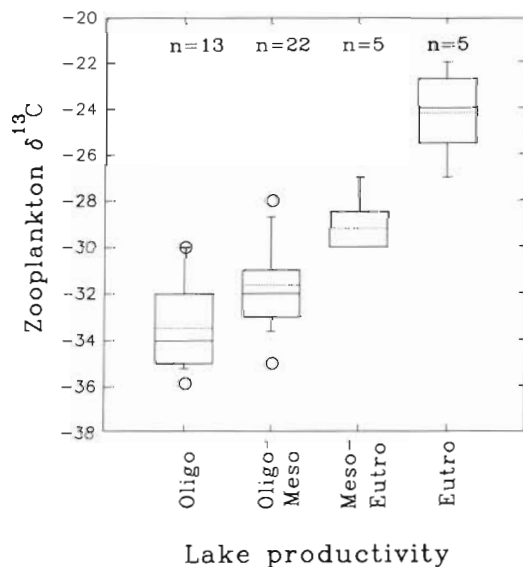


Fig. 3. Box and whisker plots (10, 25, 50, 75 and 90 percentiles indicated; means = dashed lines; O: extreme values) of the stable carbon isotope ratios of zooplankton in clearwater Canadian Shield lakes. Oligotrophic lakes: total phosphorus concentrations  $[\text{TP}] < 10 \mu\text{g l}^{-1}$ ; oligo-mesotrophic lakes:  $10 \mu\text{g l}^{-1} < [\text{TP}] < 20 \mu\text{g l}^{-1}$ ; meso-eutrophic lakes:  $[\text{TP}] > 20 \mu\text{g l}^{-1}$ ; compared to POM in eutrophic lakes from the literature (those in Fig. 1 and 3 of those in Fig. 2)

The aforementioned marine studies have interpreted the observation of a productivity-linked  $^{13}\text{C}$ -enrichment as being due to  $\text{CO}_2$  diffusion becoming increasingly rate limiting at high rates of primary production, thereby causing less isotopic fractionation, exacerbated by the possibility of a resulting shift to greater active uptake of  $\text{HCO}_3^-$ . Because of this, empirical relationships have been described between the  $\delta^{13}\text{C}$  of marine POM and either  $[\text{CO}_2\text{aq}]$  (Rau et al. 1992) or  $\text{pCO}_2$  (Francois et al. 1993).

Lacustrine data from the present study support these marine results. Zooplankton in our meso-eutrophic lakes with high POM biomass and consequently low  $\text{pCO}_2$  were found to exhibit less isotopic fractionation compared to those in lakes with medium or high  $\text{pCO}_2$ , which in turn did not differ (Fig. 4). Isotopic fractionation has been shown to decrease during blooms within individual eutrophic lakes due to low  $[\text{CO}_2\text{aq}]$  (McCabe 1985, Hollander & McKenzie 1991). Our results support findings of Gu et al. (1996) in showing that these fractionation differences may be substantial enough to be reflected by greater  $^{13}\text{C}$  enrichment in such lakes compared to those differences in lakes of lower trophic status and higher  $\text{pCO}_2$  values. In other words, zooplankton  $\delta^{13}\text{C}$  in high productivity lakes more closely reflects atmospheric DIC sources whereas zooplankton  $\delta^{13}\text{C}$  in oligotrophic lakes may be affected by microbial processes (see below).

Both our study and that of Francois et al. (1993) record a considerable range of  $\delta^{13}\text{C}$  values for plankton at the same  $\text{pCO}_2$ . One of the reviewers suggested that the present observation of invariate zooplankton  $\delta^{13}\text{C}$  in lakes of either medium or high  $\text{pCO}_2$  may be due to

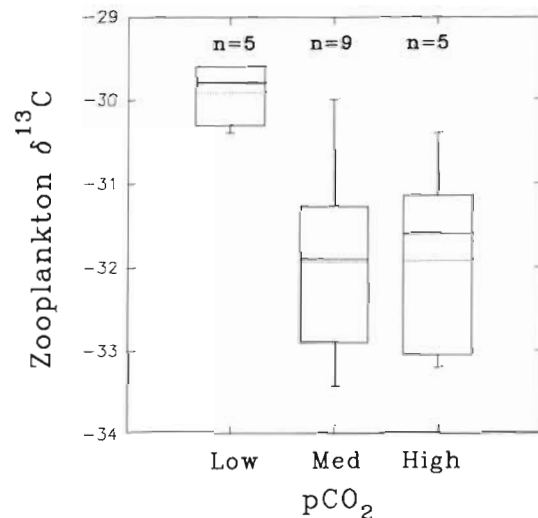


Fig. 4. Box and whisker plots (as in Fig. 3) of stable carbon isotope ratios of zooplankton from Quebec lakes of ranging  $\text{pCO}_2$ . Low:  $< 600 \mu\text{atm}$ ; med: 600 to 900  $\mu\text{atm}$ ; high:  $> 900 \mu\text{atm}$

the low sensitivity of fractionation to  $\text{CO}_2$  under such high ambient conditions as found by Francois et al. (1993) in a marine system. This, however, seems counter to the close empirical relationship found by Hollander & McKenzie (1991) between fractionation and  $[\text{CO}_2\text{aq}]$  in a Swiss lake. Obviously, considerably more research has to be undertaken to understand the breadth of the complete ramifications of  $\text{pCO}_2$  influences on plankton  $\delta^{13}\text{C}$  in lakes.

### Influence of plankton respiration

When the subset of our carbon isotope data was examined for those lakes in which plankton P/R ratios had been simultaneously determined or empirically predicted using equations (del Giorgio & Peters 1994), indication of an inferred respiration-induced  $^{13}\text{C}$ -depletion became apparent (Fig. 5). In the present oligotrophic lakes with very high plankton respiration rates relative to those of primary production, zooplankton are much more likely to exhibit  $^{13}\text{C}$ -depleted values than in oligo-mesotrophic and meso-eutrophic lakes wherein the 2 rates move closer toward equality and were not found to differ. Unusually low  $\delta^{13}\text{C}$  values of DIC are thought to be the result of net-heterotrophic activity which can have a marked influence on POM  $\delta^{13}\text{C}$  in estuaries (Coffin et al. 1994) and the open ocean (Fontugne et al. 1991). In particular, during coastal algal blooms, a rapid DOC release occurs followed by its selective uptake by bacteria, and consequent isotopic modification (Norrman et al. 1995).

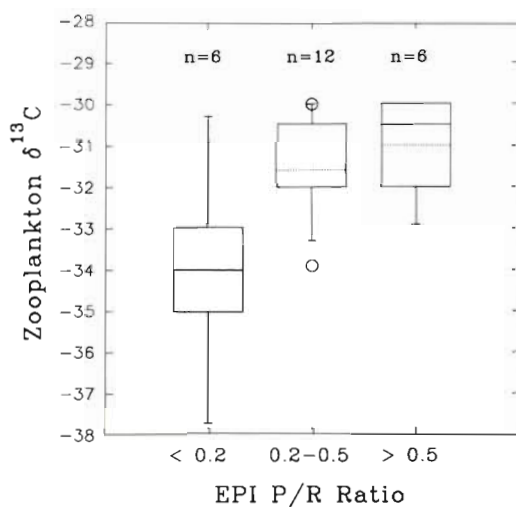


Fig. 5. Box and whisker plots of stable carbon isotope ratios of zooplankton from Quebec lakes of ranging epilimnetic planktonic production:respiration (P/R) ratios (data from del Giorgio & Peters 1994)

Fogel et al. (1992) believed that at times of low primary productivity in estuaries, such heterotrophic activity was maximal and the DOC excreted by phytoplankton will become metabolized by bacteria and then released during the latter's mineralization. Uptake of this respired carbon will then cause phytoplankton to become isotopically depleted in  $^{13}\text{C}$  compared to algae assimilating fresh carbon directly from the water

Similar respiration-induced depletions in zooplankton  $^{13}\text{C}$  will probably be even greater in lakes than in estuaries due to the greater influence of ecotonal boundary effects in the former type of system (del Giorgio & France 1996). Comparative analyses of plankton metabolism (del Giorgio & Peters 1993) have shown that rates of respiration exceed those of photosynthesis in oligotrophic lakes, which would explain the pattern observed in our zooplankton  $\delta^{13}\text{C}$  data. The dominance of heterotrophy in the plankton communities of oligotrophic lakes (del Giorgio & Gasol 1995) may therefore lead to  $\text{CO}_2$  oversaturation (Cole et al. 1994) and consequently a depletion in the  $\delta^{13}\text{C}$  signatures of resident zooplankton either by direct assimilation of  $^{13}\text{C}$ -depleted algae or by assimilation of planktonic heterotrophs which may also be depleted in  $^{13}\text{C}$  (cf. Coffin et al. 1989). In support of this hypothesis, both McCabe (1985) and Gu et al. (1994) recorded lower  $\delta^{13}\text{C}$  values for POM or zooplankton sampled during mid-winter at times of high  $\text{CO}_2$  availability compared to animals sampled during the ice-free season. Coffin et al. (1994) caution, however, at least for estuaries, that the  $\delta^{13}\text{C}$  signature of DIC is dependent not only on the rate and isotopic ratio of respiration, but also on the extent of atmospheric exchange (cf. Mizutani & Wada 1982).

### Influence of DOC and colour

Our contention of a heterotrophic-regulated  $^{13}\text{C}$ -depletion in oligotrophic lakes is supported by the observation that zooplankton  $\delta^{13}\text{C}$  was generally lower in high DOC lakes than in clearwater lakes in Quebec and northwestern Ontario (Fig. 6A), and that zooplankton exhibited less  $^{13}\text{C}$  enrichment per unit [TP] in coloured compared to clearwater lakes in central Ontario (Fig. 6B).

Humic or dystrophic (i.e. high colour, high DOC) lakes are known to be heterotrophically dominated with a considerable decomposition of allochthonous organic matter. As a result, such systems exhibit high respiration rates (Salonen et al. 1983, Hessen 1992) and low P/R ratios (del Giorgio & Peters 1994), and consequently might also be expected to have  $^{13}\text{C}$ -depleted plankton communities. In agreement with the present findings, McCabe (1985) found  $\delta^{13}\text{C}$  values of

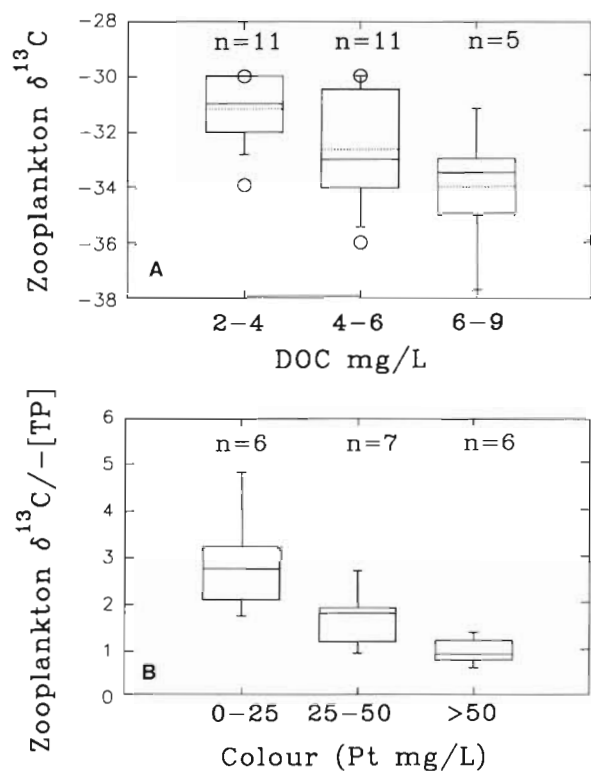


Fig. 6. Box and whisker plots of stable carbon isotope ratios of (A) zooplankton from Quebec and northwestern Ontario lakes in relation to DOC concentration, and (B) zooplankton standardized for lake trophic status (i.e. per [TP]) in central Ontario lakes in relation to colour

POM to be on average 5‰ lower in 2 dystrophic lakes compared to 3 clearwater lakes of similar nutrient concentration.

The present lacustrine results for north-temperate humic lakes therefore support (sub)tropical marine research which has indicated that as a result of the copious generation of respiratory  $\text{CO}_2$  from the mineralization of mangrove detritus, sediments (Hemminga et al. 1995), seagrasses (Zieman et al. 1984, Fleming et al. 1990, Lin et al. 1991), POM (Hemminga et al. 1994), attached benthic algae (France & Holmquist unpubl.), and molluscs (Lin et al. 1991) are all depleted in  $\delta^{13}\text{C}$  compared to like material distant from the region of heterotrophic decomposition.

#### Influence of hypolimnetic metabolism

The hypolimnetic metabolism of sedimented allochthonous (Schallenberg 1992) and autochthonous (McCabe 1985) organic matter produces  $\text{CO}_2$  in stratified bottom waters that is  $^{13}\text{C}$ -depleted relative to that in mixed surface waters (McCabe 1985, Quay et al. 1986,

Herczeg 1987). Therefore, as occurs in the understory layer of many forests (Schelser & Jayasekera 1985, Medina et al. 1986, Da Silveira et al. 1989, France 1995d), photoassimilation of this recycled  $\text{CO}_2$  will produce lower  $\delta^{13}\text{C}$  values of autotrophs (Rau 1978, McCabe 1985, Hollander & McKenzie 1991, del Giorgio & France 1996).

There has only been 1 previous attempt to compare inter-lake differences in the effects of biogenic respiration from the hypolimnion on plankton  $\delta^{13}\text{C}$ . Oana & Deevey (1960) recorded progressive  $^{13}\text{C}$ -depletions in plankton in relation to metabolic  $\text{CO}_2$  production within the hypolimnia of 4 lakes. Combining data from McCabe (1985), del Giorgio & France (1996), and France (unpubl. data) on differences between epilimnetic and either meta- or hypolimnetic  $\delta^{13}\text{C}$  of POM revealed a pattern in relation to lake trophic status (Fig. 7). Because euphotic zones in high nutrient eutrophic lakes are shallow, the likelihood that POM will be able to assimilate deepwater recycled  $\text{CO}_2$  will be restricted to the autumn period of weakening thermal stratification (e.g. Hollander & McKenzie 1991). In contrast, because of the increased water transparency in oligotrophic lakes, metalimnetic biomass peaks of POM can often develop (e.g. Fee 1976) which will rely to some degree upon this recycled  $\text{CO}_2$ . As a result, zooplankton which graze upon such metalimnetic POM (e.g. Kettle et al. 1987) and then migrate back up into the epilimnion will assume some of the deepwater  $\delta^{13}\text{C}$  signature (del Giorgio & France 1996). Alternatively, McCabe (1985) believed that as the period of stratification persists and the [DIC] in the hypolimnion

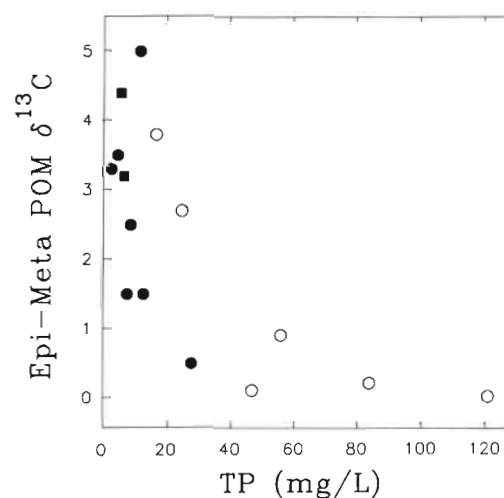


Fig. 7 Carbon isotopic differences in POM from surface and deep waters of stratified lakes in Quebec (●; del Giorgio & France 1996), northwestern Ontario (■; France unpubl. data), and New Zealand (○; McCabe 1985) in relation to system productivity measured by [TP]

increases, the  $\delta^{13}\text{C}$  of surface waters and POM become more negative due to the transport of  $^{13}\text{C}$ -depleted DIC to the surface through diffusion or the short-term breakdown of stratification from mixing events. If this process persists, it will result in a homogenization of  $\delta^{13}\text{C}$  values between surface and deepwater POM in such shallow eutrophic lakes.

Therefore, because surface and deepwater differences in POM  $\delta^{13}\text{C}$  are more pronounced in low-nutrient lakes (Fig. 7), zooplankton in such oligotrophic basins will be more  $^{13}\text{C}$ -depleted compared to those in higher-nutrient lakes (Fig. 3). For example, the most  $^{13}\text{C}$ -depleted zooplankton that have ever been recorded ( $-40$  to  $-47\%$ ) came from situations where POM  $\delta^{13}\text{C}$  minima could develop, as for example in an ultra-oligotrophic lake (Rau 1978), a meromictic lake (Fry 1986), and during mid-winter in a subarctic lake (Gu et al. 1994). In all 3 cases, a repeated recycling of carbon through biogenic respiration in the deepwaters was thought to produce the exceptionally low  $\delta^{13}\text{C}$  values.

### Conclusions and implications for stable isotope research

To quantitatively summarize the above results, we attempted to develop an empirical model relating zooplankton  $\delta^{13}\text{C}$  to lake characteristics, which included DOC, colour, TP,  $\text{pCO}_2$ , temperature, lake and drainage basin morphometry, pH and alkalinity, and the estimated primary production and respiration rates in the water column. The multivariate regression model which explained the greatest variation in zooplankton  $\delta^{13}\text{C}$  had colour and TP as independent variables:

$$\text{zooplankton } \delta^{13}\text{C} = -32.93 + 0.13 [\text{TP}] - 0.02 [\text{Colour}]$$

$n = 52, r^2 = 0.40, p < 0.0001, \text{SE of estimate} = 1.70$

Zooplankton, therefore, tend to become enriched in  $^{13}\text{C}$  either as lake TP (and productivity) increases, or as lake humic content (and heterotrophy) decreases. Considerable variation remains to be explained, most likely related to phytoplankton and zooplankton species composition, unmeasured water chemistry parameters, hydrologic patterns, and other as yet unrecognized determinants, many of which may be occurring within the watersheds rather than the lakes themselves (e.g. Schiff et al. 1990). It is significant, however, that the 2 factors known to most strongly influence plankton metabolism in lakes, TP and DOC (cf. del Giorgio & Peters 1994), also underlie the observed pattern in zooplankton  $\delta^{13}\text{C}$ . A recent study by Gu et al. (1996) found POM  $\delta^{13}\text{C}$  in 11 Florida lakes to be positively correlated to chl *a* ( $r = 0.82$ ) and TP ( $r = 0.77$ ), and negatively correlated to  $\text{CO}_2\text{aq}$  ( $r = -0.60$ ) as would be expected from our model results.

The present findings and interpretation of previous literature data support Smith & Kroopnick's (1981) belief, based on their work with coral reef organisms, that the magnitude of carbon isotopic fractionation can be used as a convenient measure of aquatic metabolism, particularly the balance between the production of new compared to the recycling of old organic matter (cf. Rosenfield & Mackay 1991).

Because the  $\delta^{13}\text{C}$  values of consumers closely match those of their food sources (DeNiro & Epstein 1978), animals residing in habitats characterized by extensive heterotrophic activity may often be quite  $^{13}\text{C}$ -depleted due to assimilation of respired  $\text{CO}_2$  (forests: Ambrose & DeNiro 1986, Bada et al. 1990; mangrove swamps: Lin et al. 1991; lakes: Rav 1980, this study) relative to animals from habitats where photosynthesis predominates. Our work suggests that in certain lakes the metabolism of organic carbon generates inorganic carbon that is depleted in  $^{13}\text{C}$  relative to inorganic carbon in equilibrium with the atmosphere. The  $^{13}\text{C}$ -enrichment of plankton in high nutrient/high productivity lakes may therefore be a serious impediment to the often intended use of stable carbon isotope analysis in freshwater ecology: if other planktivorous consumers reflect this  $^{13}\text{C}$ -enrichment, as they are likely to do (France 1995b), it will therefore be difficult if not outright impossible to identify the importance to such foodwebs of either littoral or terrestrial derived carbon, both of which also have  $\delta^{13}\text{C}$  values enriched above  $-30\%$  (France 1995a, e).

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