

NOTE

Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications

R. L. France

Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Quebec, Canada H3A 1B1

ABSTRACT: Previous work has shown freshwater macrophytes from lake littoral zones to be ^{13}C -enriched compared to the same species collected from fast moving rivers. It is thought that carbon fixation in aquatic plants having thicker, stagnant boundary layers, such as that which occurs within low turbulence lentic systems, will result in more positive $\delta^{13}\text{C}$ values due to greater diffusion resistance and subsequent assimilation of otherwise normally discriminated ^{13}C . The present study confirms this hypothesis by examining 876 algal $\delta^{13}\text{C}$ values collected from the literature. The average $\delta^{13}\text{C}$ value for benthic algae in lakes was -26‰ , whereas that for riverine benthic algae was -29‰ . The greater water turbulence to which planktonic algae are exposed is known to dramatically reduce boundary layer thickness and was found to cause even more severe ^{13}C depletion, resulting in an average value of -32‰ . This same effect also operates in coastal environments where the average $\delta^{13}\text{C}$ value for marine phytoplankton was -22‰ compared to -17‰ for marine benthic algae. When comparisons were made on an individual study basis, differences of 10‰ or greater in $\delta^{13}\text{C}$ were observed between planktonic and benthic algae in both oceans and lakes. These algal differences in $\delta^{13}\text{C}$ were found to be substantial enough to be reflected in the $\delta^{13}\text{C}$ values of consumers in marine coastal environments.

KEY WORDS: $\delta^{13}\text{C}$ · Marine · Freshwater · Benthic and planktonic algae

Ratios of stable carbon isotopes in aquatic plants such as marine macroalgae (Fry & Sherr 1984) and freshwater angiosperm macrophytes (Keeley & Sandquist 1992) are considerably more variable than are those of terrestrial plants. One possible reason that has been advanced to account for at least some of this variability is the major photosynthetic difference that exists between aquatic and terrestrial plants due to the diffusional resistance to CO_2 being 4 orders of magnitude greater in water than it is in air (Keeley & Sandquist 1992). The greater viscosity of water therefore creates a stagnant boundary layer around aquatic plants (up to $150\ \mu\text{m}$ in thickness for macrophytes), restricting the rate of CO_2 or HCO_3^- diffusion, and

thereby representing a major rate-limiting step in photosynthesis (Smith & Walker 1980). In effect, the carbon pool for aquatic plants is finite, producing a biochemical disequilibrium in isotopic discrimination between the stagnant boundary layer of progressively depleted carbon and the bulk solution of constantly mixed carbon (Andrews & Abel 1970, Smith & Walker 1980). Therefore, the fixation of carbon in aquatic plants with well-defined boundary layers leads to an entrapment of otherwise normally discriminated (expelled) ^{13}C . The result is a more positive $^{13}\text{C}/^{12}\text{C}$ ratio and subsequently higher $\delta^{13}\text{C}$ signature of plant tissue (Keeley & Sandquist 1992).

Given the importance of diffusion resistance to the degree of isotopic discrimination, the $\delta^{13}\text{C}$ signatures of aquatic plants should be influenced by the extent of mixing between inorganic carbon in boundary layers and that of the bulk solution. Indeed, Osmond et al. (1981) determined that freshwater macrophytes from low turbulence sites at the shores of lakes had more positive $\delta^{13}\text{C}$ values than those of the same species collected from fast moving water. Similarly, increased stand productivity and inferred decreased water circulation may have been responsible for the higher $\delta^{13}\text{C}$ observed within certain kelp beds (Simenstad et al. 1993) due to alterations in boundary layer thickness (cf. Wheeler 1980). Finally, laboratory experiments have shown that $\delta^{13}\text{C}$ values for individual algal species were decreased under conditions of high turbulence caused by rapid aeration (Degens et al. 1968a).

Because benthic algae are known to have diffusive boundary layers of over 1 mm in thickness (Jørgensen & Revsbech 1985, Riber & Wetzel 1987), their use for investigating the effects of water turbulence on plant $\delta^{13}\text{C}$ is appealing. The purpose of the present study was, therefore, to collate existing literature data on $\delta^{13}\text{C}$ for marine and freshwater benthic algae and to

compare these values with those determined for planktonic algae. Phytoplankton, exposed to highly turbulent conditions, are expected to have residual diffusive boundary layers in the order of only 10 μm thickness (Dainty in Smith & Walker 1980) and, as such, may therefore represent a $\delta^{13}\text{C}$ minimum for aquatic plants.

Localized differences between regions can result in ambiguity as to the widespread generality of observed isotopic patterns (Fry & Sherr 1984). Because, on a global scale, a considerable variability exists in the $\delta^{13}\text{C}$ values of both benthic and planktonic marine algae in relation to environmental differences in light and temperature, as well as to algal differences in photosynthesis mechanisms, rates of primary production and species composition (e.g. Sackett et al. 1965, Deuser 1970, Raven 1970, Fontugne & Duplessy 1978, Fageneli et al. 1986, Wienke & Fisher 1990, Fry & Wainright 1991), it is difficult to reach consensus about whether benthic-planktonic differences exist in carbon pathways on the basis of individual studies only. This occurs because the true $\delta^{13}\text{C}$ variability of autotrophs may go unrecognized due to either inadequate sampling or presentation of data as mean values only. The objective of the present secondary analysis of literature results is to examine the complete range of $\delta^{13}\text{C}$ which has been recorded for benthic and planktonic algae and consumers collected from both littoral and pelagic sites on a global basis. Comparing the $\delta^{13}\text{C}$ frequency distributions originating from these 2 habitats should provide insight as to whether carbon flow in coastal regions is either tightly coupled or separated between benthic and planktonic sources.

Stable carbon isotope values were obtained for 876 algal samples directly from tables and from figures with use of a digitizing reader. Values for benthic algae represent periphyton (epipellic and epilithic forms), epiphyton, and haptobenthos from marine and both lotic and lentic freshwaters. Values for planktonic algae are particulate organic matter from the pelagic zones of oceans or lakes. Data sources are: Parker (1964), Sackett et al. (1965), Degens et al. (1968b), Deuser (1970), Haines (1976), Haines & Montague (1979), Rau (1980), Fry et al. (1982, 1983), Macko et al. (1982), McConnaughey & McRoy (1982), Rounick et al. (1982), Hughes & Sherr (1983), LaZerte (1983), Schwinghamer et al. (1983), Fry & Sherr (1984), Gearing et al. (1984), Rodelli et al. (1984), Estep & Vigg (1985), Nichols et al. (1985), Rounick & Hicks (1985), Simenstad & Wissmar (1985), Araujo-Lima et al. (1986), Winterbourn et al. (1986), Peterson & Howarth (1987), Wada et al. (1987), Yoshioka et al. (1988, 1989), Bunn et al. (1989), Kline et al. (1990), Rau et al. (1990), Sullivan & Moncreiff (1990), Takahashi et al. (1990a, b), Fry (1991), Hesslein et al. (1991), Shoto-Douglas et al. (1991), Hamilton et al. (1992), Hobson & Welch (1992),

Rosenfield & Roff (1992), Bunn & Boon (1993), Forsberg et al. (1993), Junger & Planas (1993), Kling (1994), and Milhuc & Toetz (1994).

If diffusion resistance is important to ^{13}C discrimination, then algal $\delta^{13}\text{C}$ should not only reflect the ultimate source of carbon for photosynthesis but also distinguish between different microenvironments within systems as well. In marine coastal areas (Fig. 1), benthic algae $[-17 \pm 4$ (SD) $\text{‰}]$ are on average ^{13}C -enriched by about 5 ‰ compared to planktonic algae $(-22 \pm 3\text{‰})$. In freshwaters (Fig. 2), benthic algae exhibited $\delta^{13}\text{C}$ values of $-26 \pm 3\text{‰}$, phytoplankton of $-32 \pm 3\text{‰}$, an average difference of about 6 ‰ . Further, as would be expected if the $\delta^{13}\text{C}$ difference between benthic and planktonic algae is due to water turbulence effects on boundary layer diffusion resistance, riverine benthic algae have $\delta^{13}\text{C}$ values $(-29 \pm 4\text{‰})$ intermediate between the 2 hydrodynamic endpoints. On an individ-

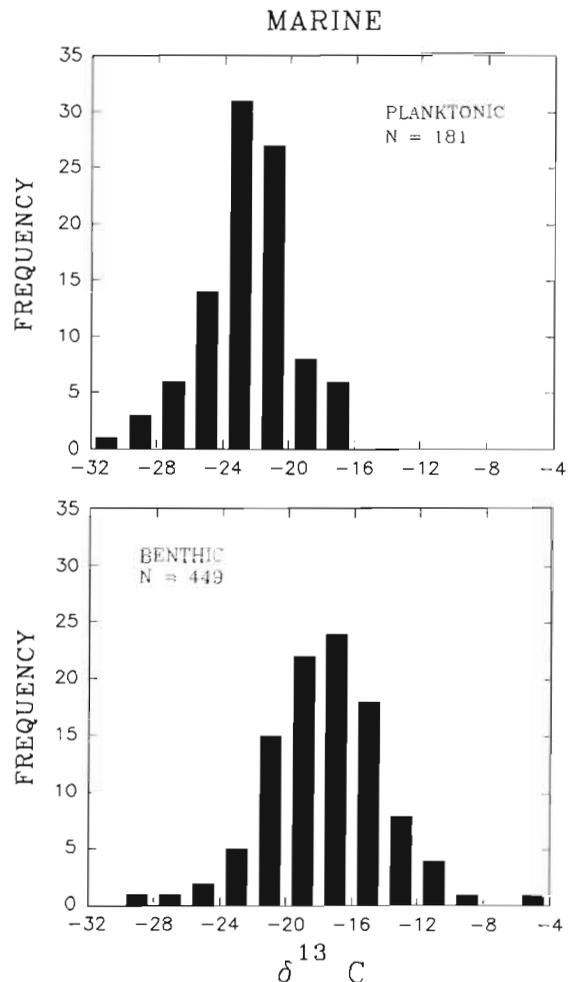


Fig. 1 Percentage frequency distributions of stable carbon isotope ratios for benthic and planktonic algae in marine environments

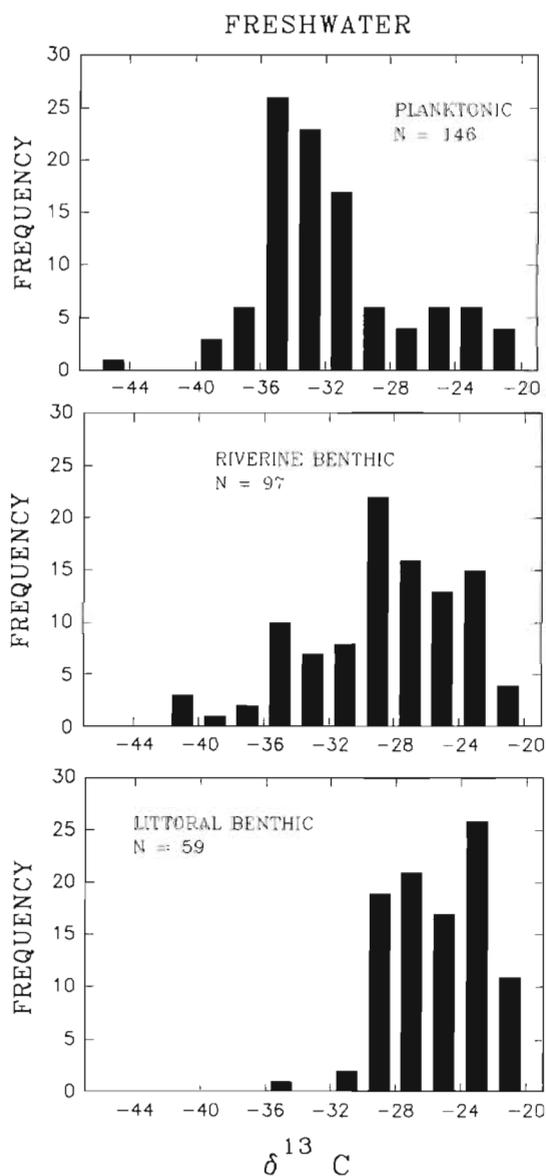


Fig. 2. Percentage frequency distributions of stable carbon isotope ratios for benthic algae in lake littoral zones and rivers and for planktonic algae in lake pelagic zones

ual study basis (Fig. 3), the $\delta^{13}\text{C}$ difference between benthic and planktonic algae ranged from 1 to 10‰ (mean = 6‰) for marine coastal areas, and from 3 to 12‰ (mean = 7‰) for lakes.

Algal $\delta^{13}\text{C}$ therefore displays the same relationship to water movement as found previously for angiosperm macrophytes (Osmond et al. 1981) and suggested for marine macroalgae (Simenstad et al. 1993). The boundary layer which develops over benthic algae in littoral zones may be a key factor in regulating benthic community metabolism through internal recycling of both nutrients (Conover 1968, Riber & Wetzel 1987)

and carbon (this data compilation). Because the boundary layers for benthic algae are reduced in thickness with faster water movement (Jørgensen & Revsbech 1985), the exchange with the bulk solution of both nutrients (e.g. Lock & John 1979, Riber & Wetzel 1987, Stevenson & Glover 1993) and carbon (this study) increases in such situations. Moreover, the even greater water turbulence to which planktonic algae are exposed functions to maintain still lower diffusion resistances, thereby supplying the cells with fresh carbon at higher rates and promoting even greater ^{13}C -depletion.

A notable distinction was found to exist between the $\delta^{13}\text{C}$ values of benthic, seagrass-dominated foodwebs (which are based on algae, not vascular plants; France 1995a) and pelagic, planktonic foodwebs (Fig. 4). Separation between these 2 foodwebs was more evident for the generally sessile invertebrates than it was for the mobile fishes. Seagrass invertebrates exhibited a unimodal distribution in $\delta^{13}\text{C}$ with a considerable range from -24 to -5‰, centered about a mode of -14‰. By comparison, the range in $\delta^{13}\text{C}$ displayed by offshore invertebrates was much reduced (-24 to -14‰), centered about a mode of -20‰. Offshore fishes ranged in $\delta^{13}\text{C}$ from -20 to -11‰, centered about a mode of -17‰. Seagrass fishes showed a greater range in $\delta^{13}\text{C}$ from -20 to -8‰, and displayed a bimodal frequency distribution with modes at -18 and -13‰. Obviously, a substantial proportion of the fishes collected from seagrass meadows ultimately derive their carbon from the plankton-based, rather than the benthic-based, foodweb. Similarly, compilation of $\delta^{13}\text{C}$ data for such non-seagrass, non-estuarine

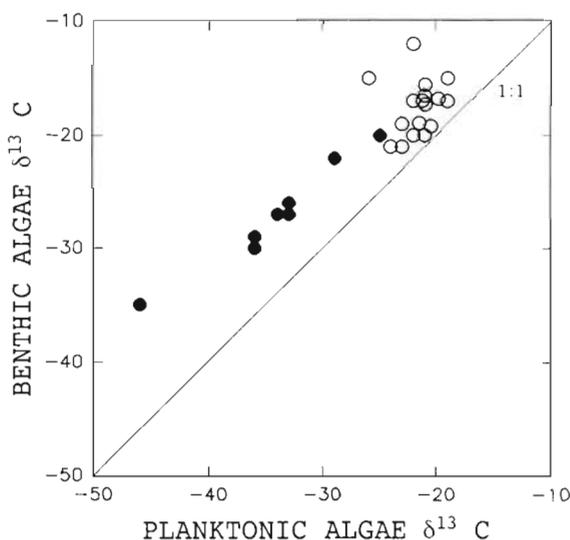


Fig. 3. Study-specific differences in stable carbon isotopes between benthic and planktonic algae for (●) freshwater and (○) marine environments

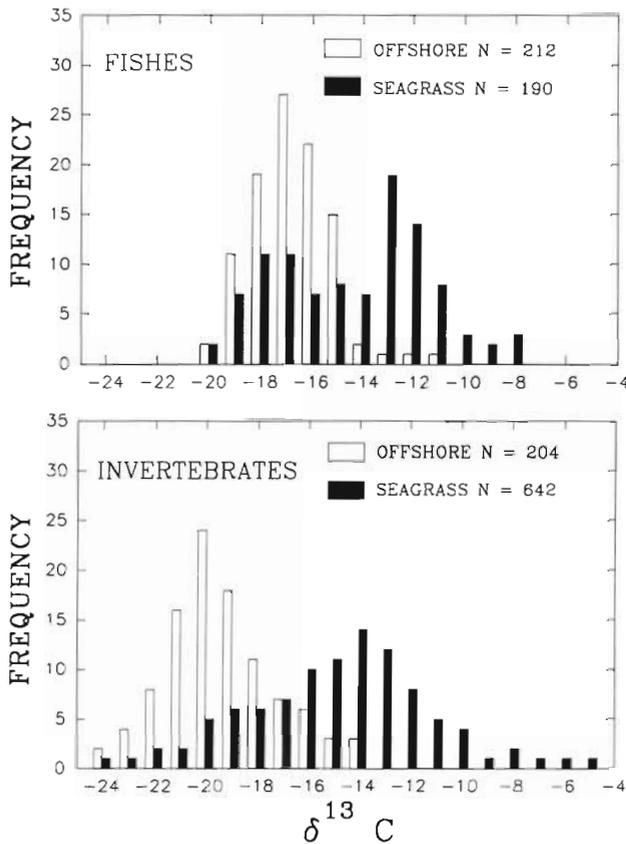


Fig. 4. Percentage frequency distributions of stable carbon isotope ratios for consumers collected from seagrass meadows and offshore coastal regions around the world. Data sources available upon request

systems as rocky shores, kelp beds, coral reefs, mangrove swamps and many other coastal regions worldwide, indicated that the same separation between benthic and planktonic foodwebs existed in these habitat types as well (Fig. 5).

In summary, the ^{13}C -enrichment of benthic compared to planktonic algae, as a possible consequence of reduced water turbulence, is substantial enough to be reflected in the isotopic values of benthic consumers. Coastal fauna utilizing benthic carbon sources are on average enriched in ^{13}C by about 5‰ compared to animals deriving their carbon from phytoplankton. Carbon isotope analysis can, therefore, be used as a rapid procedure for distinguishing between benthic and planktonic food sources for coastal animals (e.g. Hobson 1993, Hobson et al. 1994). For example, seagrass fishes having $\delta^{13}\text{C}$ values more negative than -15‰ are probably components of the planktonic foodweb, while those displaying $\delta^{13}\text{C}$ values more positive than -14‰ almost certainly derive their carbon from benthic algae. Seagrass invertebrates exhibiting $\delta^{13}\text{C}$ values less than -18‰ are probably dependent

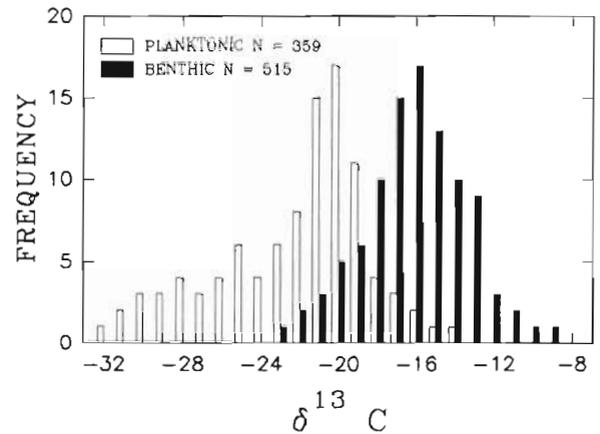


Fig. 5. Percentage frequency distributions of stable carbon isotope ratios for consumers collected from non-seagrass, non-estuarine coastal regions around the world. Data sources available upon request

upon phytoplankton, whereas those having $\delta^{13}\text{C}$ values greater than -16‰ are most likely components of a benthic foodweb. Other coastal consumers in non-seagrass regions that rely upon phytoplankton for sustenance will generally display $\delta^{13}\text{C}$ values below -20‰ , whereas those individuals dependent upon benthic algae most commonly will have $\delta^{13}\text{C}$ signatures enriched above -19‰ .

The present demonstration of different carbon isotopic signatures for benthic and planktonic algal food sources as the likely reason for the relative ^{13}C -enrichment of benthic consumers provides a counter hypothesis to that of Fry & Sherr (1984), who supposed that the ^{13}C -enrichment present in continental shelf foodwebs may be caused by an increased number of trophic levels and, therefore, further isotopic fractionation steps. Finally, it has recently been shown that such a discrimination between planktonic and benthic foodwebs, as a result of observed differences between the carbon isotopic ratios of attached algae and phytoplankton, also exists in freshwaters as well (France 1995b).

Acknowledgements. This study was funded by a Canadian NSERC Strategic Grant for work on ecotonal coupling in lake littoral zones. Conversations about carbon isotopic variability with R. Peters, G. Cabana, P. del Giorgio, J. Blais, and especially R. Hesslein were beneficial to the ideas contained herein. R. Peters is thanked for reviewing the manuscript.

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This note was submitted to the editor

Manuscript first received: July 5, 1994

Revised version accepted: March 2, 1995