

The stable carbon isotope ratios of fish and their invertebrate prey in four New Zealand rivers

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SUMMARY. 1. Sources of carbon utilized by invertebrates and fish in four New Zealand streams were investigated using stable carbon isotope analysis. Complementary analyses were made to determine $\delta^{13}\text{C}$ alteration (fractionation) by fish reared on a known food and to examine the distribution of $^{13}\text{C}/^{12}\text{C}$ ratios in different tissues.

2. $\delta^{13}\text{C}$ values of hatchery-reared rainbow trout (white muscle tissue) were ^{13}C -enriched compared with their food (trout pellets) by an average of 1.7‰ . $\delta^{13}\text{C}$ values of different organs and tissues never differed by more than 1.8‰ in any fish species; white muscle always had an intermediate value.

3. $\delta^{13}\text{C}$ values of invertebrates ranged from -28.4 to -20.4‰ . At the more open sites invertebrates were ^{13}C -depleted, reflecting some use of algal carbon. However, invertebrates from the most heavily shaded stream site were unusually enriched in ^{13}C . An undetected carbon source of terrestrial origin, perhaps ^{13}C -enriched dissolved organic carbon in groundwater, may have been contributing indirectly to invertebrate biomass carbon.

4. $\delta^{13}\text{C}$ values for fish were not closely linked to aquatic invertebrate ratios; instead, at all sites their carbon was isotopically similar to terrestrial organic carbon. The reasons for this apparent anomaly are unclear.

Introduction

Stable carbon isotope analysis has been used successfully in New Zealand streams to document the differential utilization of allochthonous and autochthonous carbon by invertebrates (Rounick, Winterbourn & Lyon, 1982; Winterbourn, Cowie & Rounick, 1984; Winterbourn & Rounick, 1984). This has been

possible because $^{13}\text{C}/^{12}\text{C}$ ratios of aquatic algae (autochthonous inputs) are generally isotopically distinct from those of terrestrial plants (allochthonous inputs). Also, because only a small $^{13}\text{C}/^{12}\text{C}$ alteration (fractionation) has been found in animals relative to their food (DeNiro & Epstein, 1978), carbon isotope ratios can be used to identify their source of food.

An appealing advantage of stable carbon isotope analysis is that an animal's isotopic composition represents only its assimilated

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food, unlike gut content analyses which document ingested foods and not necessarily those incorporated into animal tissue. However, because potential foods must be isotopically distinct, the method can only resolve relatively coarse categories such as allochthonous or autochthonous carbon.

Fish have not hitherto been considered in $^{13}\text{C}/^{12}\text{C}$ studies on freshwaters in New Zealand or elsewhere. However, they have been examined in marine and estuarine studies (McConnaughey & McRoy, 1979; Fry & Parker, 1979). New Zealand freshwater fish are generally carnivorous and considerable information on their feeding behaviour and invertebrate foods exists (e.g. Cadwallader, 1975; McDowall, 1965).

In this study, the stable carbon isotope technique was used in an attempt to determine the primary source(s) of organic carbon utilized by fish taken from rivers which flow through pasture and forest catchments. To do this, we measured $^{13}\text{C}/^{12}\text{C}$ ratios in fish tissue, invertebrates upon which they feed and probable food sources of the latter. In addition, analyses were made to determine $^{13}\text{C}/^{12}\text{C}$ fractionation by fish fed on known food and to investigate variability of $^{13}\text{C}/^{12}\text{C}$ ratios in different tissues of the same fish.

Materials and Methods

(a) Study sites

Samples were collected from four streams in the Waikanae region of the southern North Island of New Zealand (Table 1). The sites were located within 32 km of each other. The streams drain Mesozoic greywacke sandstone

and land-use in the region is largely pastoral farming. However, pockets of native forest, dominated by species of beech, *Nothofagus*, occur in the region.

The Horokiri Back Branch (HBB) and Mangaone Stream (MS), second and third order streams respectively, drain largely pastoral catchments with no distinct riparian strips. The Horokiri Stream (formerly Horokiwi) is the site of Allen's (1951) classic trout production study. The stream bed at these sites is unconsolidated, consisting of rounded rocks and stones and to a lesser extent fine gravel and silt. The stream banks are undercut at both sites with some evidence of slumping.

The Horokiri Road Branch (HRB) is a second order stream which flows through a pocket of native beech forest and is heavily shaded. The bed consists of loosely packed fist-sized cobbles, and there is greater bank stability than at the MS and HBB sites.

The Waikanae River (WR) is a larger third order stream flowing through native beech forest. Substrata here are occasional boulders, with stones >35 cm predominating. The banks are formed of bedrock and stable consolidated alluvium. Because of the relatively wide stream channel (~10 m) the stream bed receives direct sunlight despite its forested banks.

(b) Sample collection and preparation

Collections were made at all four sites between December 1982 and February 1983. Fish were obtained by qualitative, pulsed, DC electric fishing along 40 m lengths of stream at each site. Invertebrates used for isotope analysis were taken with a 1.0 mm mesh net or were

TABLE 1. Environmental characteristics of the four study sites

	Mangaone Stream (MS)	Horokiri Stream Back Branch (HBB)	Horokiri Stream Road Branch (HRB)	Waikanae River (WR)
Location	40°43'S, 175°09'E	41°03'S, 174°57'E	41°03'S, 174°56'E	40°53'S, 175°08'E
Order	3	2	2	3
Mean summer discharge ($\text{m}^3 \text{s}^{-1}$)	0.7	0.9	0.8	1.5
Mean width (m)	5	5	6	10
Max. depth (m)	0.6	0.3	1.2	1.5
pH (at sampling time)	6.4	6.8	6.6	6.9
% shading*	10	0	80	50
Riparian vegetation	Pasture	Pasture	Forest	Forest

* Visually estimated.

caught on a seine net trailed behind the electric fishing probe. Fine particulate organic matter (FPOM, 0.45 μm to 1.0 mm) was obtained in sediment cores and passed through a 1 mm sieve. Algae and associated materials (surface organic layers) were scraped from stones. Finally, 500 ml samples of field-filtered (0.45 μm) stream water were collected for dissolved inorganic carbon (DIC) isotope analysis and prepared as described by Rounick *et al.* (1982).

Fish samples were kept fresh until their stomachs were dissected (less than 3 h after catching) for later contents enumeration. White muscle tissue from collected fish was removed (see Results) and frozen along with invertebrate, FPOM and stone-surface organic layer samples prior to preparation for isotope analysis. Before analysis, samples were thawed and guts were dissected from invertebrates to remove undigested food. Stone-surface organic layer samples were acidified with 1 N HCl for 24 h to remove carbonates. Up to twenty individuals of each invertebrate species from each site were pooled before being freeze-dried and pulverized. Fish tissue was also freeze-dried. Sub-samples (3–5 mg) were oxidized in quartz 'vycor' tubing as outlined by Rounick *et al.* (1982). The resulting CO_2 gas was purified and analysed in a Nuclide 6–60 ratio mass spectrometer. Results are reported as the relative difference per mille ($^0/_{00}$) between the isotope ratio of the sample and that of the international PDB standard (Craig, 1957), expressed as follows:

$$\delta^{13}\text{C} = \left[\frac{^{13}\text{C}/^{12}\text{C} \text{ sample}}{^{13}\text{C}/^{12}\text{C} \text{ PDB}} - 1 \right] \times 1000 \text{ per mille}$$

The more negative the $\delta^{13}\text{C}$ the greater the ^{13}C -depletion.

Eleven replicates of a graphite standard (NBS-21) were used to judge analytical preci-

sion over a 6-month period ($\bar{x} = -27.99$, $\text{SD} = 0.117$, range = 0.36). Replicates of fish samples never varied by more than 0.3 $^0/_{00}$. This included both replicate muscle tissue from the same fish and tissue from different fish of the same species at any given site. Replicates of other materials never differed by more than 0.4 $^0/_{00}$.

The distribution of $\delta^{13}\text{C}$ within the different tissues of four common fish (redfinned bully, *Gobiomorphus huttoni* (Ogilby); upland bully, *G. breviceps* (Stokell); longfinned eel, *Anguilla dieffenbachii* Gray; shortfinned eel, *A. australis* Richardson) was determined by analysing four replicate samples of heart, liver, anal fin, white muscle and scales (skin from eels) from two fish of each species collected in the nearby Hutt River during October 1982.

In order to document the ^{13}C -enrichment of fish tissue relative to fish food, three age classes (0+, 1+, 2+) of hatchery-reared rainbow trout (*Salmo gairdnerii* Richardson), and their sole food (trout pellets) were obtained from the Ngongotaha Fish Hatchery in Rotorua. Native fish raised on a known diet were unavailable. $\delta^{13}\text{C}$ values of pellets and four samples of muscle tissue dissected from each of four fish of each age class were determined.

Results

(a) Fish isotope relationships

$\delta^{13}\text{C}$ values of tissues collected from the redfinned bullies, *Gobiomorphus huttoni* collected from the Hutt River ranged from -20.4 to -19.8 $^0/_{00}$. Scales were most ^{13}C -enriched (-19.8 $^0/_{00}$) whereas heart and liver were most ^{13}C -depleted (-20.4 $^0/_{00}$). Anal fin and white muscle had intermediate $\delta^{13}\text{C}$ values (-20.1 $^0/_{00}$ and -20.3 $^0/_{00}$, respectively) (Table 2). The range of $\delta^{13}\text{C}$ values found in the same tissues in three

TABLE 2. Mean $\delta^{13}\text{C}$ ($^0/_{00}$) of various tissues from four species of New Zealand fish collected from the Hutt River ($n=4$ samples from two fish of each species). 1 SD never exceeded 0.2 $^0/_{00}$.

Tissue	<i>Gobiomorphus huttoni</i>	<i>Anguilla dieffenbachii</i>	<i>Anguilla australis</i>	<i>Gobiomorphus breviceps</i>
Scales	-19.8	-19.5	-19.8	-18.9
Heart	-20.4	-21.3	-21.2	-19.9
Liver	-20.4	-21.0	-21.1	-19.7
Muscle	-20.3	-20.7	-20.6	-19.3
Anal fin	-20.1	-20.4	-20.7	-19.6
Total range	0.6	1.8	1.4	1.0

TABLE 3. $\delta^{13}\text{C}$ of muscle tissue and food (trout pellets) of hatchery-reared rainbow trout, *Salmo gairdnerii* Richardson

Year class	Fish muscle ($\delta^{13}\text{C} \pm 1 \text{ SD}$)	Food ($\delta^{13}\text{C} \pm 1 \text{ SD}$)	Difference ($^0/_{\text{‰}}$)
0+	-19.8 \pm 0.3	-21.5 \pm 0.3	1.7
1+	-20.0 \pm 0.2	-21.3 \pm 0.5	1.3
2+	-20.4 \pm 0.3	-21.3 \pm 0.5	0.9

other native fish species was never more than 1.8 $^0/_{\text{‰}}$ (Table 2). White muscle tissue dissected from all fish species was always intermediate in value for the range of tissues analysed. Because of this and because it was easy to collect, white muscle tissue was used for all subsequent $\delta^{13}\text{C}$ determinations. Fry & Parker (1979) also found that muscle tissue was representative of overall fish $\delta^{13}\text{C}$ in marine environments.

The difference between $\delta^{13}\text{C}$ of muscle tissue of hatchery-reared rainbow trout and their food ranged from 0.9 to 1.7 $^0/_{\text{‰}}$ (Table 3), within the 2 $^0/_{\text{‰}}$ ^{13}C enrichment range expected (DeNiro & Epstein, 1978).

(b) Invertebrate abundance

Larval Ephemeroptera, Trichoptera and Coleoptera dominated the benthic fauna at all four study sites. Large particle detritivores (shredders) generally were absent from all sites with the fauna being dominated by collector-browsers and predators. The species composition of the benthos was similar at all four sites with a common core of species predominant.

These core species and other invertebrates that were well represented in dissected fish stomachs were used for $\delta^{13}\text{C}$ analysis.

(c) Fish stomach contents

All fish examined were carnivorous. Stomach contents consisted entirely of invertebrate material and in most cases were identifiable to the generic level (Table 4). The long- and shortfinned eels, *A. dieffenbachii* and *A. australis*, had variable numbers of terrestrial invertebrates (mainly oligochaetes) in their stomachs. In the other fish, only aquatic invertebrates were found with Ephemeroptera, Trichoptera and to a lesser extent Diptera and Plecoptera dominating. The ephemeropteran *Deleatidium* was the most abundant food item in most of the fish examined. This was also found by Hopkins (1970). While our sample size was small and limited to one time period, the studied fish have rather similar feeding habits throughout the year (Cadwallader, 1975; McDowall, 1965). Therefore, our gut analyses should be a reasonable indicator of general food relations in these streams.

TABLE 4. Stomach contents of fish from the four study sites. MS=Mangaone Stream; HBB=Horokiri Back Branch; HRB=Horokiri Road Branch; WR=Waikanae River. Terrestrial material was estimated visually.

Fish	Site	Fish		Terrestrial material	Total food items
		n	Primary gut content (% by numbers)		
<i>Gobiomorphus breviceps</i>	MS	5	<i>Deleatidium</i> (48), <i>Nesameletus</i> (38)	0	21
<i>Galaxias brevipinnis</i>	WR	6	<i>Beraeoptera</i> (48), <i>Zelandoperla</i> (14)	0	29
<i>Anguilla dieffenbachii</i>	MS	7	Terrestrial Oligochaetes (59), <i>Aoteapsyche</i> (15)	High	101
	HBB	4	<i>Ichthyobus</i> (24), <i>Deleatidium</i> (16)	High	23
	HRB	13	Muscidae (62), <i>Archichauliodes</i> (12)	High	517
	WR	9	<i>Pycnocentroides</i> (37), <i>Olinga</i> (12)	Low	59
<i>A. australis</i>	MS	1	Chironomidae (75)	0	4
	HBB	2	Terrestrial Oligochaetes, <i>Deleatidium</i>	High	2
	HRB	5	Trichoptera, <i>Archichauliodes</i>	Low	10
<i>Gobiomorphus huttoni</i>	MS	1	Ephemeroptera	0	1
	HBB	9	<i>Deleatidium</i> (47), <i>Coloburiscus</i> (16)	0	32
	HRB	8	Chironomidae (55), <i>Oxyethira</i> (18)	0	109
	WR	10	<i>Deleatidium</i> (27), other Ephemeroptera (14)	0	44
<i>Cheimarrichthys fosteri</i>	WR	1	<i>Deleatidium</i> (75)	0	72

TABLE 5. $\delta^{13}\text{C}$ values for dissolved inorganic carbon, potential foods, invertebrates, and fish muscle tissue at the study sites. (MS=Mangaone Stream; HBB=Horokiri Back Branch; WR=Waikanae River; HRB=Horokiri Road Branch)

	MS	HBB	WR	HRB
Dissolved inorganic carbon	-13.1		-15.5	-13.0
Stone-surface scrapings	-34.3	-35.8	-34.3	-24.3
Fine particulate organic matter	-26.8	-26.9	-26.4	-24.1
INVERTEBRATES				
Herbivores-detritivores				
<i>Coloburiscus humeralis</i> (Walker)	-26.1	-25.6	-25.8	-20.6
<i>Nesameletus ornatus</i> (Eaton)	-23.3	-27.7	-25.3	-22.8
<i>Pycnocentroides</i> sp.			-24.1	-20.4
Elmidae	-24.9	-26.6	-24.2	-20.9
<i>Deleatidium</i> spp.	-27.1	-28.4	-27.2	-22.6
Predators				
<i>Stenoperla prasina</i> (Newman)	-25.0	-27.2	-24.1	-20.9
<i>Archichauliodes diversus</i> (Walker)	-23.2	-26.9	-23.3	-20.8
<i>Aoteapsyche colonica</i> (McLachlan)	-24.1	-27.3		
<i>Aphrophila neozelandica</i> (Edwards)				-20.2
VERTEBRATES (predators)				
<i>Gobiomorphus hutoni</i> (Ogilby)	-21.0	-24.9	-23.3	-20.3
<i>Gobiomorphus breviceps</i> (Stokell)	-20.7			
<i>Cheimarrichthys fosteri</i> Haast			-23.4	
<i>Galaxias brevipinnis</i> Günther			-23.1	
<i>Anguilla dieffenbachii</i> Gray	-22.3	-23.7	-23.5	-21.7
<i>Anguilla australis</i> Richardson	-19.6	-24.7		-21.5

(d) $\delta^{13}\text{C}$ of invertebrate foods

Terrestrial coarse particulate organic matter which falls into the stream and can serve as a direct carbon source for shredders, was not analysed because of the virtual absence of shredders in either fish stomachs or benthic samples. As the fauna was dominated by collector-browsers at these sites FPOM and stone-surface organic layers were considered as their potential foods.

$\delta^{13}\text{C}$ of stone scrapings from the MS, HBB and WR sites were similar and ranged from -35.8 to $-34.3^{0/00}$ (Table 5). These values indicate that algal carbon makes an important contribution to the stone-surface organic layers. This was confirmed by microscopic observations of scrapings which showed that pennate diatoms were abundant at the MS and WR sites and filamentous diatoms were prevalent at the more open HBB site. In contrast, $\delta^{13}\text{C}$ of organic layers from the HRB site were relatively enriched in ^{13}C ($-24.3^{0/00}$). Organic layers at this well-shaded site included few algal cells and were apparently allochthonous-based.

$\delta^{13}\text{C}$ of FPOM was similar at the MS, HBB

and WR sites (-26.9 to $-26.4^{0/00}$), whereas at the HRB site FPOM was slightly more ^{13}C -enriched ($-24.1^{0/00}$). These values suggest that all FPOM samples were composed primarily of allochthonous carbon. The catchment vegetation consists of C_3 plants whose $\delta^{13}\text{C}$ are $\sim -25^{0/00}$ in New Zealand (Troughton & Card, 1972).

(e) Invertebrate $\delta^{13}\text{C}$

$\delta^{13}\text{C}$ of invertebrates from the four sites ranged from -28.4 to $-20.2^{0/00}$ (Table 5). The mayfly *Deleatidium* was the most ^{13}C -depleted animal at all sites indicating incorporation of some algal-derived carbon into biomass carbon through either selective assimilation of algae (Rounick *et al.*, 1982) and/or through utilization of leaked algal exudates incorporated into stone-surface organic layers (Winterbourn *et al.*, 1984; Winterbourn & Rounick, 1984).

$\delta^{13}\text{C}$ of invertebrates at the MS, HBB and WR sites were all similar. However, the same invertebrate species from the HRB site were in most cases at least $4^{0/00}$ more ^{13}C -enriched compared with animals taken from other sites. In general, at specific sites invertebrate pre-

dators were ^{13}C -enriched relative to their herbivore-detritivore counterparts (Table 5).

(f) Fish $\delta^{13}\text{C}$

$\delta^{13}\text{C}$ of white muscle from fish collected at the four study sites ranged from -24.9 to -19.6 ‰ (Table 5). Within sites, fish $\delta^{13}\text{C}$ values were not as variable between species as invertebrate values despite variations in diet (indicated by stomach contents). Further, no fish species was found to be consistently either depleted or enriched in ^{13}C at any one site. The most ^{13}C -depleted fish were found at the open pasture HBB site ($\bar{x} = -24.4$ ‰), whereas the most ^{13}C -enriched were found, surprisingly, at the open MS site ($\bar{x} = -20.9$ ‰). Although invertebrates showed some ^{13}C -depletion, corresponding to an increase in abundance of algal inputs at the more open sites, fish $\delta^{13}\text{C}$ values did not show this pattern. The closest links between fish and invertebrate $\delta^{13}\text{C}$ occurred at the HRB and WR sites. Fish from HBB and particularly MS were more ^{13}C -enriched than expected.

Discussion

A prerequisite for the use of stable isotope techniques in food-chain studies is an understanding of the amount of ^{13}C -fractionation (either enrichment or depletion) which normally occurs between food source and consumer. Generally it is assumed there is approximately 2‰ ^{13}C -enrichment (following DeNiro & Epstein, 1978). Recently, however, Macko, Lee & Parker (1982) showed slight ^{13}C -depletion, rather than enrichment, of marine amphipods fed algal diets. As the amount of ^{13}C -fractionation has not been reported for fish, we measured this using hatchery-reared trout. The mean ^{13}C alteration was $+1.7$ ‰ which indicates that fish muscle tissue $\delta^{13}\text{C}$ should match closely the $\delta^{13}\text{C}$ values of natural invertebrate prey.

A second prerequisite for studies of this kind is that a measurable isotopic distinction exists between potential food sources, e.g. allochthonous and autochthonous inputs. Rounick *et al.* (1982) and Winterbourn & Rounick (1984) demonstrated such a difference between New Zealand C_3 plants (~ -25 ‰) and aquatic algae

(~ -35 ‰), and this was found also in the present study.

Utilization of carbon inputs by invertebrates showed some variation; at the open pasture-lined sites and the wide, forested WR site, animals were more ^{13}C -depleted than those at the shaded HBB site, reflecting at least some use of algal carbon. This concurs with the findings of Rounick *et al.* (1982) who found that in a small forest stream allochthonous inputs (^{13}C -enriched) were the major sources of energy used by most benthic invertebrate species whereas in a nearby tussock grassland stream, algae assumed greater significance in invertebrate diets. It is interesting to note, however, that the shift to lighter $\delta^{13}\text{C}$ values in the more open streams in the present study was not as pronounced as reported by Rounick *et al.* (1982).

The open streams in the present study (MS, HBB and WR) were less stable physically than the tussock-grassland stream as indicated by geomorphic features including stream bed structure and mass-wasting into the channel, and also by the composition of the invertebrate fauna (see Rounick & Winterbourn, 1982). Algal standing crops can vary in response to flow patterns (Rounick & Gregory, 1981) and in these unstable North Island streams, algae may be unavailable to the benthos at certain times of the year despite their open nature. In terms of autochthonous carbon source availability therefore, these streams appear to lie somewhere between the extremes represented on one hand by the large, open (40 m wide) flood-prone Inangahua River on the West Coast of the South Island where invertebrates sampled had allochthonous based (^{13}C -enriched) stable carbon ratios (Winterbourn *et al.*, 1984), and the stable, lake-fed Grasmere Stream, which supports a high autochthonous standing crop all year round (Rounick *et al.*, 1982).

$\delta^{13}\text{C}$ values of invertebrates from the shaded HRB site were unusually enriched in ^{13}C relative to those from other studied forest-streams in New Zealand. The cause of this additional ^{13}C -enrichment relative to local C_3 vegetation is unclear, but it is likely that an additional unknown ^{13}C -enriched carbon source is contributing (either directly or indirectly) to the diet of the resident invertebrates. One possible source could be isotopi-

cally enriched dissolved organic matter entering in groundwater (see Hynes, 1983) and being incorporated into stone-surface organic layers (Rounick & Winterbourn, 1983) which are grazed by the benthic species. This is likely considering that stone surface scrapings from this site were enriched in ^{13}C ($\delta^{13}\text{C} = -24.3\text{‰}$).

Recent work on food webs using the $\delta^{13}\text{C}$ technique work has demonstrated that carbon becomes more ^{13}C -enriched as it progresses through a food chain (McConnaughey & McRoy, 1979). This is because consumers generally are more enriched than their food source, and therefore top predators should be the most ^{13}C -enriched animals in the food web. Our data support this idea since carnivorous fish were generally the most ^{13}C -enriched animals at individual sites. However, comparisons of $\delta^{13}\text{C}$ values obtained for fish and their potential invertebrate prey (especially at MS) showed a greater than expected difference between the two trophic levels (Table 5).

It is illustrative to compare $\delta^{13}\text{C}$ of the mayfly *Deleatidium* with that of *G. huttoni*, the redfinned bully. *Deleatidium* is a major food ingested by this fish (as shown in this study and by McDowall (1965) in a similar, nearby stream). *G. huttoni* from the HRB site was 2.3‰ enriched relative to *Deleatidium*, a 'classic' ^{13}C fit supporting the observation that *Deleatidium* is a major food of the species. However, at HBB and WR *G. huttoni* was 3.5 and 3.9‰ enriched, respectively, relative to *Deleatidium* and at MS the difference between predator and prey $\delta^{13}\text{C}$ was 6.1‰ . Similar disparities were evident between the $\delta^{13}\text{C}$ values of other fish from these sites and their observed (or inferred from the literature) diets.

A possible explanation for these 'excessive' enrichments that may be applicable to the two eel species, *A. dieffenbachii* and *A. australis* is that terrestrial invertebrates which are relatively ^{13}C -enriched (e.g. Oligochaeta, -22.7‰ ; authors' unpubl. data) are being incorporated into biomass carbon. Some eel stomachs contained 100% terrestrial invertebrates showing they can be significant dietary items.

Such an explanation cannot explain the highly enriched $\delta^{13}\text{C}$ values of the other fish found at the disparate sites, however, and no obvious alternative explanation is forthcoming.

Logically, it would seem likely that the

excessive ^{13}C -enrichment found in fish must be caused by an unrecognized carbon source, probably of terrestrial origin. This material was not apparent in the fish stomachs examined but could well represent carbon not available at the time of the study which is held in 'isotopic memory' in fish tissue. No estimates of $\delta^{13}\text{C}$ turnover time are available for fish so it is difficult to predict how long tissue retains the $\delta^{13}\text{C}$ of previously assimilated foods.

Stable carbon isotope analysis is coarse in its resolving power as it requires potential foods to be isotopically distinct. In order to increase its usefulness in studies of carbon flow further work on carbon turnover time in animals, especially carnivores, is needed.

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