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Does inorganic carbon assimilation cause ^{14}C depletion in deep-sea organisms?

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Abstract—The metabolic activities within and feeding relationships among deep-sea biota require that significant quantities of ^{14}C-depleted carbon be incorporated into their biomass. These processes cannot be ignored when interpreting the ^{14}C abundances of organisms and organic materials in the deep ocean.

INTRODUCTION

PEARCY and STUIVER (1983) reported that a variety of deep-sea animals were depleted in ^{14}C relative to surface water biota (Fig. 1). Similar isotopic depletions had also been encountered by WILLIAMS *et al.* (1970) and WILLIAMS and LINICK (1975). It was reasoned that the reduced ^{14}C abundances in deep-ocean organisms must be the consequence of a significant time lag between the production of the source organic matter in surface waters, and its eventual sedimentation, incorporation, and residence in deep-sea animal communities. Taking into account the addition of atomic bomb ^{14}C, Pearcy and Stuiver calculated the low $\Delta^{14}C$ values of mesopelagic and abyssobenthic animals to reflect organic carbon residence times of 18 to 35 years. Using several possible scenarios, they concluded that the biomass of these organisms must represent relatively 'old' organic carbon that has not been rapidly transferred to and utilized by deep-sea animal communities.

This conclusion, however, appears to be inconsistent with measured sinking rates (and hence, availability in the deep ocean) of surface-derived food sources (30 to 300 m day^{-1}; e.g. SMAYDA, 1970; SHANKS and TRENT, 1980; CARDER *et al.*, 1982; VINOGRADOV and TSEITLIN, 1983). Recent observations of marked seasonality of deep-sea sedimentation rates and of biological activity also imply a rapid (weeks to months) transfer and utilization of surface water organics in deep-sea biotic communities (e.g. LIGHTFOOT *et al.*, 1979; DEUSER *et al.*, 1981; HONJO, 1982; BILLET *et al.*, 1983; ITTEKKOT *et al.*, 1984; SMITH and BALDWIN, 1984). The amount of ^{14}C lost through radioactive decay during this expected transit time would probably not be detected by currently available methods. The large discrepancy in ^{14}C abundance between surface water biota and many deep-sea taxa is, therefore, a very significant discovery with profound implications for deep-sea ecology. Pearcy and Stuiver, and Williams and coworkers proposed the existence of complex particle cycling/sinking schemes, selective animal feeding, and/or lengthy

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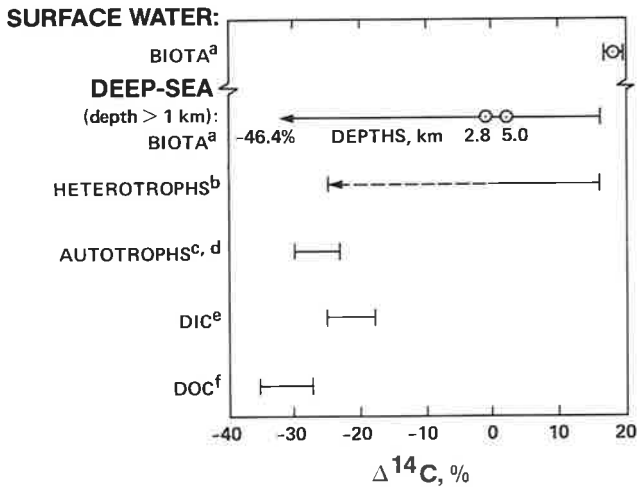


Fig. 1. Observed and predicted $\Delta^{14}C$ values of biota and other Pacific Ocean carbon pools where

$$\Delta^{14}C\ (\%) = \delta^{14}C - (2\delta^{13}C + 5)[1 + (\delta^{14}C/100)]$$

$$\delta^{13}C = [^{13}C/^{12}C(\text{sample})/^{13}C/^{12}C(\text{PDB standard}) - 1] \times 100,$$

$$\delta^{14}C = [^{14}C/^{12}C(\text{sample})/^{14}C/^{12}C(\text{oxalic acid standard}) - 1] \times 100.$$

Taxa mean $\Delta^{14}C$ values are denoted by circles. (a) Observed by PEARCY and STUIVER (1983). (b) Predicted values for deep-sea heterotrophs are derived from consideration of heterotrophic DIC incorporation and food chain transfer processes as discussed in the text and illustrated in Fig. 2. (c) Observed by WILLIAMS *et al.* (1981). (d) Predicted by assuming deep-sea autotroph carbon biomass is totally derived from deep-ocean DIC as discussed in the text. (e) Observed by STUIVER *et al.* (1983) and OSTLUND and STUIVER (1980). (f) Observed by WILLIAMS *et al.* (1969, 1978).

animal life histories and low animal carbon turnover in order to reconcile the apparent 'old age' of many deep-sea biota relative to contemporary surface water organisms.

This interpretation assumes, however, that the low $\Delta^{14}C$ values (relative to newly-produced, surface water biomass) provide a direct measure of the time elapsed since the production of that organic matter, if the original ^{14}C level, the isotopic decay rate and atomic bomb ^{14}C additions are known. We believe other mechanisms for reducing ^{14}C levels in the deep-ocean biota warrant consideration, in particular, biological uptake and incorporation of deep-sea dissolved inorganic carbon (DIC).

HETEROTROPHIC DIC UPTAKE

It is known from ^{14}C-labeled bicarbonate uptake experiments (e.g. SEKI and ZOBELL, 1967; SOROKIN, 1971, 1978; TUTTLE and JANNASCH, 1979; KARL *et al.*, 1984) that measurable quantities of DIC are nonphotosynthetically incorporated into the deep-ocean organic carbon pool via biological assimilation. Uptake mechanisms may include chemoautotrophic fixation of DIC as well as heterotrophic uptake via anapleurotic carboxylations. As reviewed by WOOD and UTTER (1965) and KORNBERG (1966), hetero-

trophic carbon fixation occurs primarily via the carboxylation of pyruvate to produce malate, an intermediate in the tricarboxylic acid cycle which is a major biosynthetic pathway present in most organisms. A number of other carbon fixation pathways are also known to exist. Thus, inorganic carbon is heterotrophically incorporated into biomass and is, indeed, essential for the growth and metabolism of all biota (Wood and Utter, 1965; Kornberg, 1966). Inorganic carbon incorporation into heterotrophic cells can provide up to 10% of total carbon biomass, although higher percentages may occur (reviews by Sorokin, 1978; Van Es and Meyer-Reil, 1982).

The incorporation of inorganic carbon into living biomass at depth in the Pacific Ocean has significant implications for the ^{14}C content of the biota and organic carbon residing there. This is because the ambient DIC in the deep Pacific is very depleted in ^{14}C (Ostlund and Stuiver, 1980; Stuiver *et al.*, 1983; Fig. 1). Even a small incorporation of this carbon into the biomass/organic carbon pool will have a measurable effect on that pool's radiocarbon content. For example, if we assume that deep-sea carbon biomass is derived from the assimilation of some proportion of organic carbon (food) and deep-sea DIC, both carbon sources of known ^{14}C content, then the Δ^{14}C of the resultant deep-sea biota can be calculated using the following equation:

$$\Delta^{14}\text{C(deep biota)} = A \times \Delta^{14}\text{C(food)} + B \times \Delta^{14}\text{C(deep DIC)}, \quad (1)$$

where A is the proportion of deep biota carbon derived from food, B is the proportion of deep biota carbon derived from deep inorganic carbon, and $1 = A + B$. Assuming that (a) 5% of deep-sea heterotrophic carbon uptake will be in the form of CO_2 or HCO_3^-, (b) the inorganic carbon assimilated is in isotopic equilibrium with the ambient DIC pool (Δ^{14}C = –20%, Fig. 1), and (c) the remaining heterotrophic carbon requirement (95%) is met by assimilation of surface-derived organic carbon (Δ^{14}C = 18%, Fig. 1), then the Δ^{14}C of 'deep biota' is calculated to equal 16.1%.

FOOD CHAIN EFFECTS

Deep-sea consumer Δ^{14}C values near 16% were among the highest found by Pearcy and Stuiver, with average values for deep-sea taxa near 0% (Fig. 1). The cause of these lower Δ^{14}C values, however, may also lie in the nature of deep-sea heterotrophy. This is because the carbon biomass of many deep-sea consumers has probably not come directly from sea surface production, but rather has passed through one or more intermediate deep-sea microbial or metazoan consumers. The isotopic consequence of the indirect transfer of surface production through deep-sea food webs is that in addition to the isotopic effects of DIC uptake occurring at the consumer level under consideration, that consumer also 'inherits' the sum of ^{14}C depletions incurred by DIC incorporation at all preceding consumer levels. That is, if our above-mentioned consumer with Δ^{14}C = 16.1% became food for a secondary consumer, the Δ^{14}C of this secondary consumer would equal 14.3% using equation (1) [A = 0.95, B = 0.05, Δ^{14}C(food) = 16.1%, and Δ^{14}C(deep DIC) = –20%]. Using this model, the progressive ^{14}C depletions at successive consumer levels are predicted in Fig. 2.

While feeding behavior and trophic relationships among animals in the deep sea are poorly understood, it is clear from existing observations that predation and carcass scavenging is a common mode of feeding there. Consumers feature many special

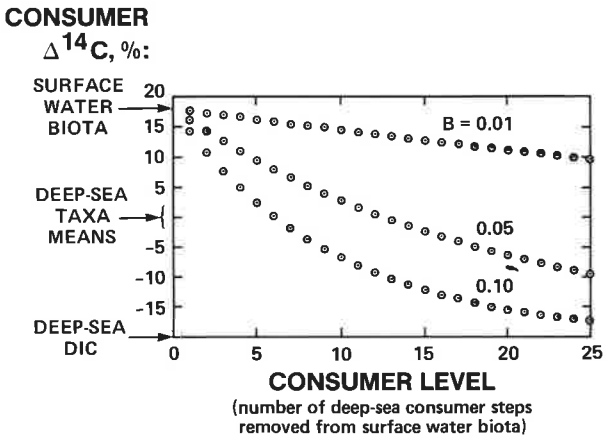


Fig. 2. Predicted deep-sea consumer $\Delta^{14}C$ based on varying degrees of heterotrophic incorporation of deep-ocean DIC, and the number of deep-sea consumer steps removed from surface water production. Values are generated using the equation:

$$\Delta^{14}C\ (n\text{th consumer}) = A \times \Delta^{14}C(n\text{th-1 consumer}) + B \times \Delta^{14}C(\text{deep DIC}),$$

where A is the proportion of biomass C derived from nth-1 consumer, B is the proportion of biomass derived from deep DIC, and $A + B = 1$. $\Delta^{14}C$(0th consumer) = 18‰, and $\Delta^{14}C$(deep DIC) = –20‰. B values of 0.01, 0.05, and 0.1 correspond to 1, 5, and 10% of biomass derived from deep-sea DIC. See text for further discussion.

adaptations for luring and capturing prey, ingesting prey larger than themselves, and locating large carcass falls from great distances (e.g. PEARCY and AMBLER, 1974; ISAACS and SCHWARTZLOSE, 1975; SMITH and BALDWIN, 1982; STOCKTON and DELACA, 1982; INGRAM and HESSLER, 1983; VINOGRADOV and TSEITLIN, 1983). Assuming that the observed mean $\Delta^{14}C$ of deep-sea taxa (–1 to 2‰, Fig. 1) results entirely from DIC uptake and food chain transfer processes, such values then imply a mean consumer level for these taxa of 11 to 14 using the $B = 0.05$ curve in Fig. 2. A higher or lower mean consumer level would, respectively, result from lower or higher DIC incorporation per consumer (lower or higher B values, Fig. 2).

The preceding calculation of a mean deep-sea consumer level is, however, probably a considerable overestimate. This is because of our (and Pearcy and Stuiver's) assumption that $\Delta^{14}C$ values averaged over deep-sea taxa generate a mean $\Delta^{14}C$ value that is representative of deep-sea animal biomass as a whole. Such mean values do not, however, take into account animal biomass and abundance within taxa, and therefore underweigh the ^{14}C content of the most abundant species and overweigh the ^{14}C content of the least abundant taxa. An ideal assessment of the average deep-sea biomass $\Delta^{14}C$ values [and, hence, average DIC uptake (or time-dependent ^{14}C addition/decay effects)] would require information about the standing stock of each taxa. Unfortunately, this information is not known, yet we can derive a feeling for the relative abundance of the taxa analysed by Pearcy and Stuiver by examining catch-per-unit effort from trawl samples taken in the same general area they sampled (Fig. 3). Of all the taxa Pearcy and Stuiver surveyed, the most abundant species generally show the highest ^{14}C levels. Species with lower $\Delta^{14}C$ values are among the least common forms. Therefore, a $\Delta^{14}C$

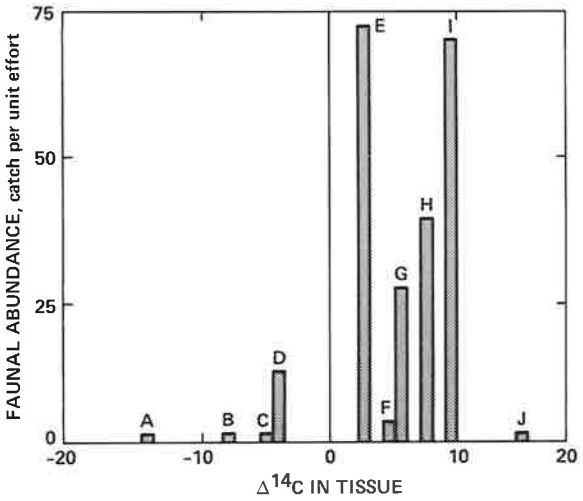


Fig. 3. $\Delta^{14}C$ vs abundance of the deep-sea taxa indicated. $\Delta^{14}C$ data from PEARCY and STUIVER (1983). 'Abundance' refers to number of individuals captured per 2 h of trawling as reported by CARNEY (1977 and unpublished data), CARNEY and CAREY (1982), and CAREY (unpublished data). All trawling was conducted on the Cascadia Abyssal Plain, 1970 to 1976. Species and additional data: (A) *Molpadia musculus* (holothuroid), [mean abundance ≐] 1.1, [individuals/2 h of trawling], [range =] 0 to 16, [number of trawls =] 76; (B) *Sperosoma giganteum* (urchin), 1.2, 0 to 11, 70; (C) *Dysaster gilberti* (starfish) 1.2, 0 to 6, 70; (D) *Coryphaenoides filifer* (fish), 12.0, 0 to 48, 79; (E) *Paelopatides confundens* (holothuroid), 74.4, 1 to 257, 76; (F) *Coryphaenoides leptolepis* (fish), 3.8, 0 to 15, 79; (G) *Coryphaenoides armatus* (fish), 26.0, 0 to 104, 79; (H) *Scotoplanes globosa* (holothuroid), 38.5, 0 to 172, 76; (I) *Peniagone intermedia (holothuroid)*, 72.9, 0 to 263, 76; (J) *Paraliparis rosaceus* (fish), 0.8, 0 to 6, 79.

value representative of average deep-sea animal biomass must be considerably higher than the average value of deep-sea animal taxa, –1 to 2%. In turn, less DIC incorporation per consumer and/or fewer consumer levels, is then required to explain the true average ^{14}C content of deep-sea biomass.

With regard to DIC incorporation in deep-sea macrofauna, successive predator–prey or scavenger biomass transfer, possibly involving progressively larger consumers, may bring into question the isotopic equilibrium between the DIC assimilated by those heterotrophs and the DIC in ambient deep-ocean seawater. As consumer volume and volume-to-surface-area ratios increase, the likelihood that the internal DIC pool (available for carboxylation) is in equilibrium with the surrounding seawater DIC should decrease. This means that the isotopic abundance of DIC available for heterotrophic carboxylation will become more influenced by DIC generated internally (via respiration) than by the DIC external to the consumer. We point out, however, that brief incubations (≤ several minutes) of whole invertebrates and vertebrate tissues in ^{14}C labeled bicarbonate solutions result in rapid incorporation of DIC label into amino acids, proteins, and other cell constituents of these organisms/tissues (ANFINSEN *et al.*, 1949; BUCHANAN, 1951; HAMMEN and OSBORNE, 1959; HAMMEN and LUM, 1962; WOOD and UTTER, 1965; KORNBERG, 1966; ZEBE, 1975; DE ZWAAN and WIJSMAN, 1975; FELBECK, 1983). While it is difficult from these experiments to calculate accurately the percent biomass derived from DIC, it is nevertheless clear that measurable quantities of external DIC were incorporated and, therefore, appropriate B values for these consumers must

be greater than 0. Consumer $\Delta^{14}C$ trends resulting from DIC incorporation as low as 1% of total consumer biomass (i.e. $B = 0.01$) are presented in Fig. 2.

MICROBIOTA

Carbon transfer by microheterotrophs may also be relevant to the observed ^{14}C depletions. By interaction of the detrital–microbial-detrital carbon biomass cycle, the end product of such cycling will reflect the summation of DIC uptake effects on the $\Delta^{14}C$ incurred by each intervening microbial consumer. The isotopic composition of the internal DIC pool of these organisms will be influenced more readily by the ^{14}C content of the surrounding water than will larger volume macroconsumers discussed above. The proportion of consumer biomass derived from ambient DIC could reach 10% (or higher as previously mentioned), with the resulting precipitous decrease in $\Delta^{14}C$ per detrital–microbial carbon cycle, 'consumer level' (Fig. 2; $B = 0.10$). Eventual incorporation of this biomass into macroconsumers would obviously serve to decrease their ^{14}C content relative to surface water biota. We note that while varying the values of B will vary the amount of ^{14}C depletion incurred by each consumer step, it does not change the $\Delta^{14}C$ value asymtotically approached by the nth deep-sea consumer level (i.e. the $\Delta^{14}C$ value of deep-sea DIC, –20%; Fig. 2). Thus, both individual and collective DIC uptake by deep-sea micro- and macroconsumers, however small that uptake is per consumer, forces their carbon biomass toward partial isotopic equilibrium with the ambient DIC.

In addition to DIC assimilation, microbial uptake and incorporation of deep-sea dissolved organic carbon (DOC) could also lead to reduced ^{14}C levels in biota. The $\Delta^{14}C$ of bulk DOC in the deep Pacific has been measured to be below –27% (WILLIAMS *et al.*, 1969, 1978; Fig. 1). While the size and ^{14}C content of the biologically labile portion of this total DOC is presently unknown, biological incorporation of ^{14}C-depleted dissolved organics could provide another way of diluting the ^{14}C present in deep-sea communities. In turn, if DOC is produced by deep-sea biological activity, then the low $\Delta^{14}C$ values of this carbon pool may be in part the result of a DIC→Biota→DOC transformation and subsequent ^{14}C dilution. The existence of DOC $\Delta^{14}C$ values significantly below those of deep-water DIC (Fig.1), however, obviously cannot be explained entirely by such a pathway.

DEEP-SEA AUTOTROPHY

Heterotrophic processes are not the only means whereby ^{14}C-depleted carbon could be incorporated into the living organic carbon pool in the deep ocean. A number of researchers, finding relatively high DIC uptake rates as well as other evidence in localized pelagic and benthic deep-sea environments have indicated the presence of chemoautotrophic production of organic carbon (e.g. SOROKIN, 1978; JANNASCH and WIRSEN, 1979; KARL *et al.*, 1980, 1984; FELBECK, 1981). If autotrophic microorganisms are indeed present in the deep Pacific, the $\Delta^{14}C$ of their biomass carbon will likely be lower than that of the surrounding ambient DIC, namely $\Delta^{14}C$ values $\leq$ –20% (Fig. 1). This is because nearly 100% of their biomass will be derived from this inorganic carbon source, with additional isotope fractionation (^{14}C depletion) resulting from kinetic isotope effects during carbon fixation via the Calvin–Benson cycle (O'LEARY, 1981; WIGLEY and MULLER, 1981). $\Delta^{14}C$ values below –20% are present in chemoautotrophi-

cally based hydrothermal vent organisms (WILLIAMS *et al.*, 1981), and significant ^{14}C depletions have been reported in other contemporary aquatic animals as a consequence of apparent autotrophic uptake of ^{14}C-depleted DIC and subsequent food chain transfer (e.g. DAMON *et al.*, 1966; HAYNES *et al.*, 1964; RIGGS, 1984). Additionally, symbiotic associations between chemoautotrophic bacteria and invertebrates have been shown to exist in a variety of benthic environments (SOUTHWARD *et al.*, 1981; FELBECK *et al.*, 1981, 1983; FELBECK, 1983). Autotrophy occurring at depth in the ocean and subsequent food chain incorporation will cause significant ^{14}C depletions in those organisms as has been found in hydrothermal vent biota (WILLIAMS *et al.*, 1981).

POC FLUX VS DIC UPTAKE

Finally, how important is biological uptake of DIC in influencing the Δ^{14}C of the total living and dead POC (particulate organic carbon) pool in the deep Pacific Ocean? From data on deep-sea bacterial productivity (SOROKIN, 1978) one can back-calculate the DIC uptake rates that Sorokin and others measured radioisotopically in their attempt to estimate heterotrophic bacterial production. That is, multiplying estimated bacterial production (0.4 to 5×10^{-2} mg C m^{-3} day^{-1}) by 0.05 yields measured DIC uptake rates of 0.2 to 2.5×10^{-3} mg C (as DIC) m^{-3} day^{-1}. In a deep-ocean water column (say 4 km in length, between water depths of 1 to 5 km), total DIC uptake in such a column would then equal 0.8 to 10 mg C m^{-2} day^{-1}. The input of POC to the deep Pacific Ocean from waters above 1000 m in depth ranges from 4 to 35 mg C (as POC) m^{-2} day^{-1} (KNAUER and MARTIN, 1981; SMITH and HINGA, 1983; KARL and KNAUER, 1984). Thus, the proportion of deep POC derived from deep DIC uptake potentially ranges from $0.8/(0.8 + 35) = 0.02$ to $10/(10 + 4) = 0.71$. Inserting these proportions, 0.02 and 0.71, for B values in equation (1), and assuming the Δ^{14}C of sedimenting POC to equal 18% and the Δ^{14}C of deep DIC to equal –20% (as previously discussed), the calculated range of deep POC Δ^{14}C is –9.0 to 17.2%. Clearly, biologically mediated DIC→ POC transformations can substantially dilute the ^{14}C content of the bulk POC pool in the deep Pacific under conditions of high DIC incorporation relative to the delivery rate of euphotic zone POC to the deep ocean.

CONCLUSION

Because heterotrophic and chemoautotrophic processes occur at depth in the ocean, significant quantities of ^{14}C-depleted carbon must be incorporated into resident biomass. These processes should be considered in interpreting the ^{14}C abundances of deep-sea organisms and organic materials.

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