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Dietary carbon sources for deep-sea organisms as inferred from their organic radiocarbon activities

P. M. WILLIAMS,* E. R. M. DRUFFEL† and K. L. SMITH, Jr*

Abstract—A small but significant depletion of radiocarbon activity (Δ^{14}C‰) is present in surface, meso-, bathy- and abyssopelagic fishes and crustaceans collected from depth in the North Central Pacific (NCP) and in the Northeast Pacific (NEP) in the 1960s and 1970s compared to average values for dissolved inorganic carbon (DIC) and zooplankton found in the euphotic zone during this period. These low ^{14}C activities are postulated to result from (1) the ^{14}C gradient in DIC in the euphotic zone, and (2) the incorporation of low activity, pre-bomb peak carbon (pre-1969) from the surface ocean into chronologically old organisms. Based on the relative increase of ^{14}C activity in surface and deep organisms, maximum estimates of the turnover times range from <1 to 9 years for the organic carbon in surface and mesopelagic animals and 4–18 years for bathy- and abyssopelagic animals from the NCP and NEP. These data suggest that the main source of dietary carbon for deep-sea organisms is from rapidly sinking organic detritus from the surface and from active (animal mediated) transport of living carbon. There may be a minor contribution (15%) to bathypelagic organisms from low ^{14}C activity chemolithotrophically derived organic carbon, from heterotrophic uptake of mid-depth DIC or from recycled carbon.

INTRODUCTION

IN A study of radiocarbon activities in marine organisms from the equatorial and North Pacific, WILLIAMS and LINICK (1975) concluded that bomb radiocarbon was removed more or less rapidly from the euphotic zone into the deep water depending upon particular food chain mechanisms. PEARCY and STUIVER (1983) reported a decrease with depth in the organic-^{14}C content of meso- and bathypelagic and abyssobenthic animals (500–5180 m) in the Northeastern Pacific Ocean off Oregon. They suggested that rapidly sinking, recently produced particles from the upper mixed layer (euphotic waters) are not the principal source of dietary organic carbon for deep-sea fishes and large benthic invertebrates. Instead, they concluded that "large and nutritious particles do indeed sink into the deep sea, but they are not from surface waters, and they do not have high ^{14}C levels because non-refractory organic carbon is regenerated and recycled many times in the euphotic zone, [and] fecal pellets that sink into deep-sea sediment traps are mainly produced by larger mesopelagic animals that consume such recycled and 'aged' carbon." They estimated a residence time of about 18–35 years for the dietary organic carbon pool for meso- and bathypelagic and abyssobenthic animals. We report here a re-analysis of their data, plus additional organic-^{14}C activities for meso-, bathy- and abyssopelagic fishes and crustaceans collected in the North Central Pacific (NCP) and the Northeastern Pacific (NEP). We conclude that the ^{14}C gradient in the dissolved inorganic carbon

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(DIC) in the mixed layer, combined with the chronological age of the organisms themselves are primarily responsible for the decrease in biocarbon-^{14}C activities with depth.

METHODS

Organic-^{14}C activities (Δ^{14}C‰) and δ^{13}C values measured at the SIO-La Jolla Radiocarbon Laboratory and not included in PEARCY and STUIVER's (1983) (hereon referred to as Pearcy and Stuiver) compilation are listed in Table 1, together with ancilliary information on each specimen. These more recent results are from LINICK (1979, 1980a, 1984). The error reported for Δ^{14}C is determined from counting statistics (1σ), and the precision of the δ^{13}C measurements is ±0.20‰. Δ^{14}C values are calculated in the standard manner (BROECKER and OLSON, 1961). Certain subjective judgements were made in ascribing specific habitat depths in Table 1. Generally, the actual or mean collection depth was taken for opening/closing (O/C) Bongo net samples, the shallowest depth of known occurrence for non-O/C Bongo or Isaacs–Kidd midwater trawl net samples, and the actual depth of collection for amphipods and grenadiers caught in baited traps or in baited gill nets. The collection locations of all of the samples discussed in this report are depicted in Fig. 1.

Table 1. Organic carbon-14 activity and carbon-13 content of fishes and crustacea from the North Central Pacific (NCP) and Northeast Pacific (NEP)

NCP	Location	Date collected (collector)*	Depth collected (m) (plotted depth)†	Δ^{14}C(‰)	δ^{13}C(‰)
Fishes					
9 *Lampanyctus* sp.	30°39′N 155°23′W	06/24/72 (MWT)	0–1350 (500)	177 ± 11	−19.8
1 *Lampadena* sp.	31°00′N 155°23′W	07/01/72 (o/cB)	700 (350)	161 ± 8	−21.1
1 *Cyclothone pallida*	28°00′N 155°00′W	09/01/73 (MWT)	0–1100 (300)	43 ± 6	−19.7
1 *Serrivamer* cf *sector*	28°00′N 155°00′W	09/02/73 (MWT)	0–1700 (300)	138 ± 9	−18.4
1 *Heterophotus ophistoma*	28°00′N 155°00′W	09/04-73 (MWT)	0–1700 (300)	134 ± 9	−21.9
1 *Serrivamer* cf *sector*	28°21′N 155°30′W	02/04/74 (MWT)	0–885 (300)	81 ± 9	−19.1
1 *Coryphaenoides yaquinae*	28°30′N 155°30′W	06/19/77 (HL)	5000 (5000) Bottom = 5800	37 ± 10	−18.7
1 *Coryphaenoides yaquinae*	30°57′N 158°59′W	08/28/79 (HL)	5185 (5185) Bottom = 5900	66 ± 10	−18.7
1 *Coryphaenoides yaquinae*	30°57′N 158°59′W	08/28/79 (HL)	5895 (5895) Bottom = 5900	85 ± 15	−19.3
1 *Coryphaenoides yaquinae*	30°57′N 158°59′W	08/28/79 (HL)	5595 (5595) Bottom = 5900	62 ± 17	−19.0

Table 1 *continued*

NCP	Location	Date collected (collector)*	Depth collected (m) (plotted depth)†	$\Delta^{14}C(‰)$	$\delta^{13}C(‰)$
Crustacea					
1 *Acanthaphyra* sp.	31°00′N	07/01/72	700	133 ± 14	−20.6
1 *Systellaspis* sp.	155°23′W	(o/cB)	(350)		
1 *Pasiplea* sp.					
1 *Euphausid.* unidentified					
3 *Eurythenes gryllus*	28°30′N	06/19/77	5650	84 ± 11	−20.4
	155°30′W	(TUB)	(5650)		
			Bottom = 5700		
2 *Eurythenes* sp.	31°09′N	08/27/79	1 spec. 5060	110 ± 8	−20.4
	159°16′W	(TB)	1 spec. 5475		
			(5280 mean)		
			Bottom = 5780		
5 *Eurythenes* sp.	31°01′N	08/30/79	5865	67 ± 18	−21.0 (est.)
	158°57′W	(TB)	(5865)		
			Bottom = 5870		
1 *Eurythenes* sp.	31°01′N	08/30/79	4955	100 ± 9	−21.4
	158°57′W	(TB)	(4955)		
			Bottom = 5870		
NEP					
Fishes					
1 *Cetostoma regani*	31°00′N	08/13/75	1700–1800	−18 ± 7	−20.3
	120°45′W	(o/cB)	(1750)		
1 *Scopeloberyx robustus*	31°00′N	08/14/75	1450	66 ± 11	−22.0
	120°45′W	(o/cB)	(900)		
1 *Melamphaes* cf.	31°00′N	08/14/75	1450	28 ± 6	−21.7
acanthomus	120°45′W	(o/cB)	(1450)		
1 *Scopelogadus mizolepis*	31°00′N	08/14/75	1450	93 ± 9	−20.6
bispinosus	120°45′W	(o/cB)	(500)		
1 *Sagamichthys abei*	31°00′N	08/20/75	0–1500	117 ± 5	−19.5
	120°45′W	(o/cB)	(750)		
2 *Benthalbella dentata*	31°00′N	08/20/75	0–1500	127 ± 7	−23.3
	120°45′W	(o/cB)	(750)		
Coryphaenoides armatus	32°34′N	12/13/77	3400	45 ± 12	−18.4
	120°26′W	(HL)	(3400)		
			Bottom = 3800		
1 *Coryphaenoides armatus*	32°34′N	12/13/77	3500	27 ± 7	−18.3
	120°26′W	(HL)	(3500)		
			Bottom = 3800		
1 *Coryphaenoides armatus*	32°34′N	12/13/77	3750	37 ± 8	−19.7
	120°29′W	(HL)	(3750)		
			Bottom = 3800		
Crustacea					
1 *Caridean* sp.	31°00′N	08/14/75	1450	49 ± 6	−22.3
	120°45′W	(o/cB)	(1450)		
1 *Gnathophausia* (*zola?*)	31°00′N	08/14/75	1450	69 ± 9	−21.0
	120°45′W	(o/cB)	(900)		
2 *Gnathophausia ingens*	31°00′N	08/18/75	0–1350	153 ± 6	−21.6
	120°45′W	(o/cB)	(700)		

* MWT = Isaacs-Kidd midwater trawl, o/cB = opening/closing Bongo net, HL = baited gillnet, TB = baited trap, TUB = unbaited trap.

† Taken as shallowest or mean depth of known occurrence for MWT and Bongo samples. The actual depths of capture were used for the amphipod and rat-tails caught in traps or by baited gillnet.
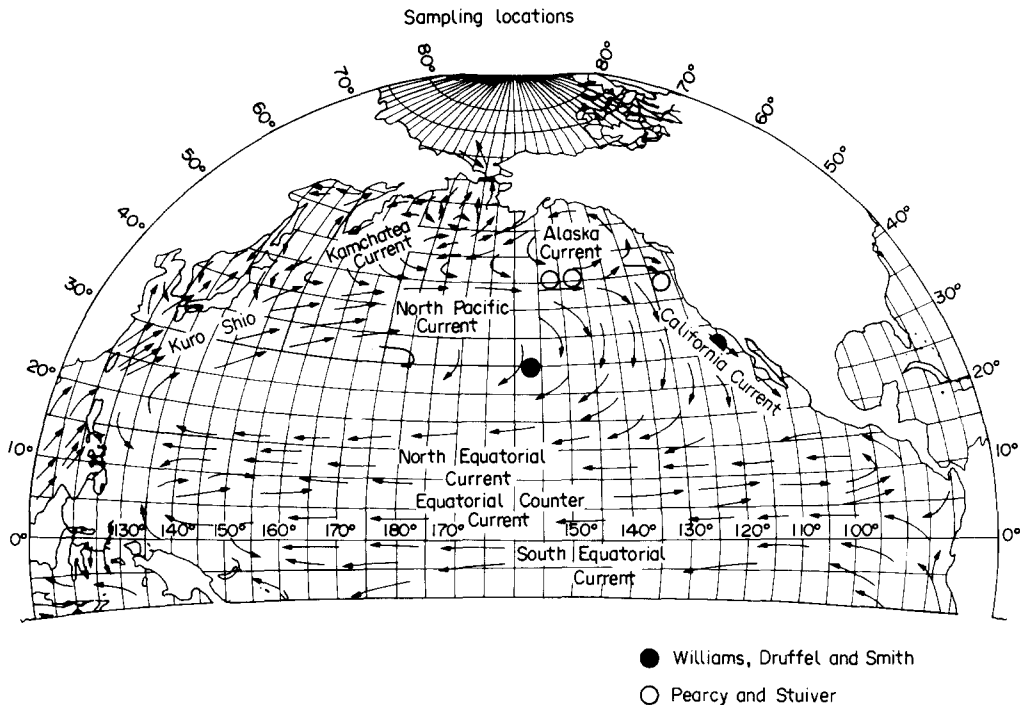
Sampling locations

Fig. 1.   Map of surface currents in the North Pacific Ocean. Sampling locations for the SIO study (●) and the PEARCY and STUIVER (1983) study (○) are shown.

RESULTS AND DISCUSSION

Figure 2A shows $\Delta^{14}C$ values vs depth for the Scripps Institution of Oceanography (SIO, NCP and NEP), and Fig. 2B shows those values from Pearcy and Stuiver (P&S, NEP, 1983). Most of the depth adjustments made by Pearcy and Stuiver for the earlier SIO data (WILLIAMS *et al.*, 1970; WILLIAMS and LINICK, 1975) have been adopted in Fig. 2A. The only $\Delta^{14}C$ values for abyssobenthic organisms measured by Pearcy and Stuiver and included in Fig. 2B are those for the grenadiers, *Coryphaenoides armatus*, the same species as given in Table 1 and Fig. 2A. The other abyssobenthic organisms were excluded, because, as pointed out by Pearcy and Stuiver, they feed on ^{14}C-depleted sedimentary organic carbon (SOC) or on organisms that feed from this carbon source.

There is an apparent decrease in the bomb ^{14}C content of fishes and crustaceans from both the NEP and NCP in specimens caught and designated as inhabiting the >900–2100 m depth intervals (Figs 2A,B). There also appears to be an increase in the bomb radiocarbon content of the grenadiers (*Coryphaenoides* sp.) and amphipods (*Eurythenes* sp.) caught 5–915 m above the bottom in the NEP and NCP relative to that of the >900–2100 m organisms. However, the lack of any data from 1750 to 3400 m in the NEP and from 2100 to 5000 m in the NCP, coupled with uncertainties in habitat depths of the bathypelagic organisms, places serious constraints on the actual depth at which this increase occurs.
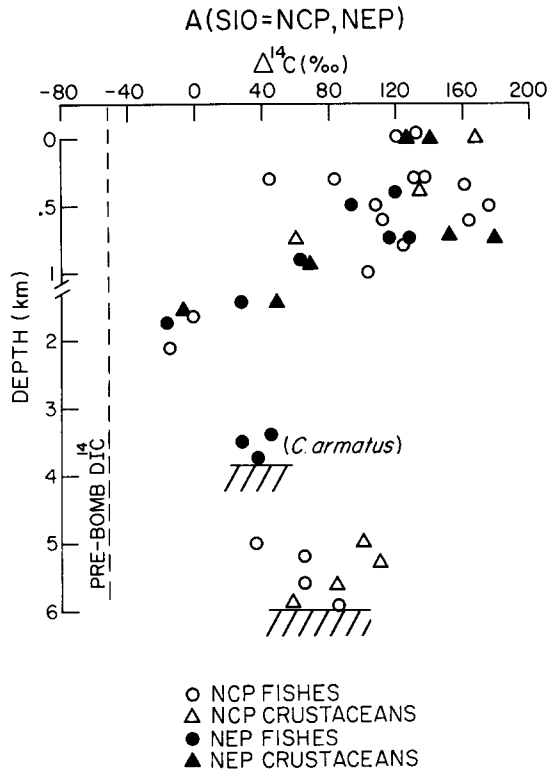
A(SIO=NCP,NEP)

O NCP FISHES
△ NCP CRUSTACEANS
● NEP FISHES
▲ NEP CRUSTACEANS

B(P+S=NEP)

● FISHES
▲ CRUSTACEANS } P+S
X COELENTERATES

Fig. 2. (A) $\Delta^{14}C$ vs depth for organisms collected in the NCP and NEP. Hatch marks are bottom depths: NCP = 5700–5900 m; NEP = 3800 m. Data taken from WILLIAMS *et al.* (1970), WILLIAMS and LINICK (1975), and LINICK (1979, 1980b, 1984). (B) $\Delta^{14}C$ vs depth for organisms collected in the NEP, redrawn from PEARCY and STUIVER (1983). Hatch marks are bottom depth at two sampling sites off Oregon: Cascadia Abyssal Plain, 2800–2900 m; and Tufts Abyssal Plain, 4883–5180 m.

The apparent decrease in organic-^{14}C activity from the surface to 2100 m (Figs 2A,B) is more evident from the SIO data than from the Pearcy and Stuiver data. There is, however, a wide range of ^{14}C activities in the fishes caught from the surface to 1000 m in our results (Δ^{14}C = 43–177‰) and those of Pearcy and Stuiver (Δ^{14}C = –33–188‰), with a lesser spread for the crustaceans (SIO: Δ^{14}C = 60–180‰; Pearcy and Stuiver: Δ^{14}C = 91–170‰) and coelenterates (Pearcy and Stuiver: Δ^{14}C = 102 and 170‰).

The fundamental question in interpreting the ^{14}C activities of the surface, meso-, bathy- and abyssopelagic organisms is: What are the sources of or processes leading to reduced ^{14}C activities in many of the organisms with respect to the ^{14}C activity of dissolved inorganic carbon (DI^{14}C) in the surface water? The two factors that we consider to be most important are: (1) the ^{14}C gradient in surface water DIC, and (2) the chronological age of the organisms, also postulated by Pearcy and Stuiver as a partial explanation.

First, variations in the Δ^{14}C of surface seawater DIC are considered. Figure 3 shows the time history of Δ^{14}C in the upper 10 m of the water column from available seawater and banded coral measurements in the NCP and NEP. Δ^{14}C Values rose from –55‰ (E. R. M. Druffel, unpublished data) during the pre-bomb period to about 185‰ by 1971. However, when the Δ^{14}C values of organisms are plotted vs year of collection (Figs 4A,B), virtually all of the values are lower than the Δ^{14}C trend found in surface DIC. Δ^{14}C Values for the surface (0–50 r.) organisms were 0–60‰ (SIO results, NEP and NCP) and 10–90‰ (P&S results, NEP, excluding one fish sample) lower than the mean DI^{14}C values. This suggests that DIC fixed into organic carbon during photosynthesis in the euphotic zone (0–100 m) had considerably lower ^{14}C activities than those found for DIC in the upper 10 m. This is most likely the result of reduced Δ^{14}C values in seawater
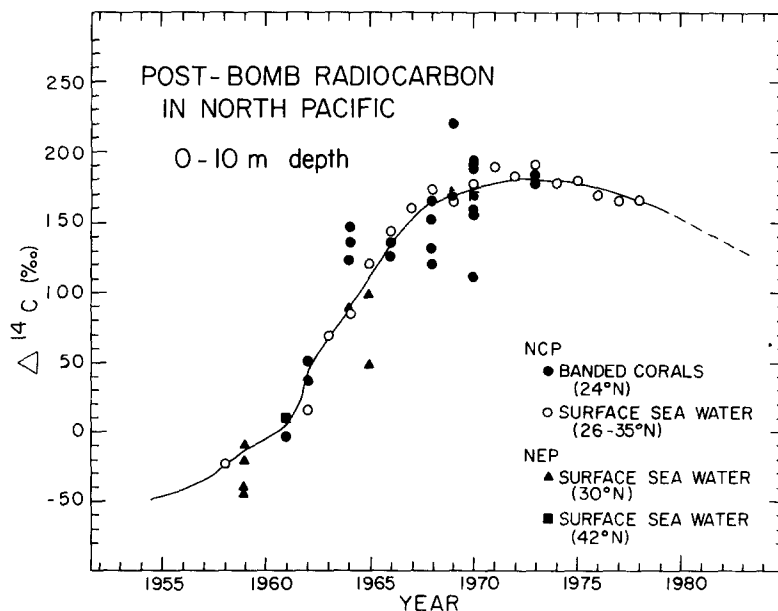

Fig. 3. Time history of bomb ^{14}C in surface North Pacific Ocean. Based on Δ^{14}C measurements of DIC from surface seawater between 26° and 37°N (Linick, 1975, 1980b; Östlund and Stuiver, 1980) and from corals at 24°N (Druffel, unpublished data).
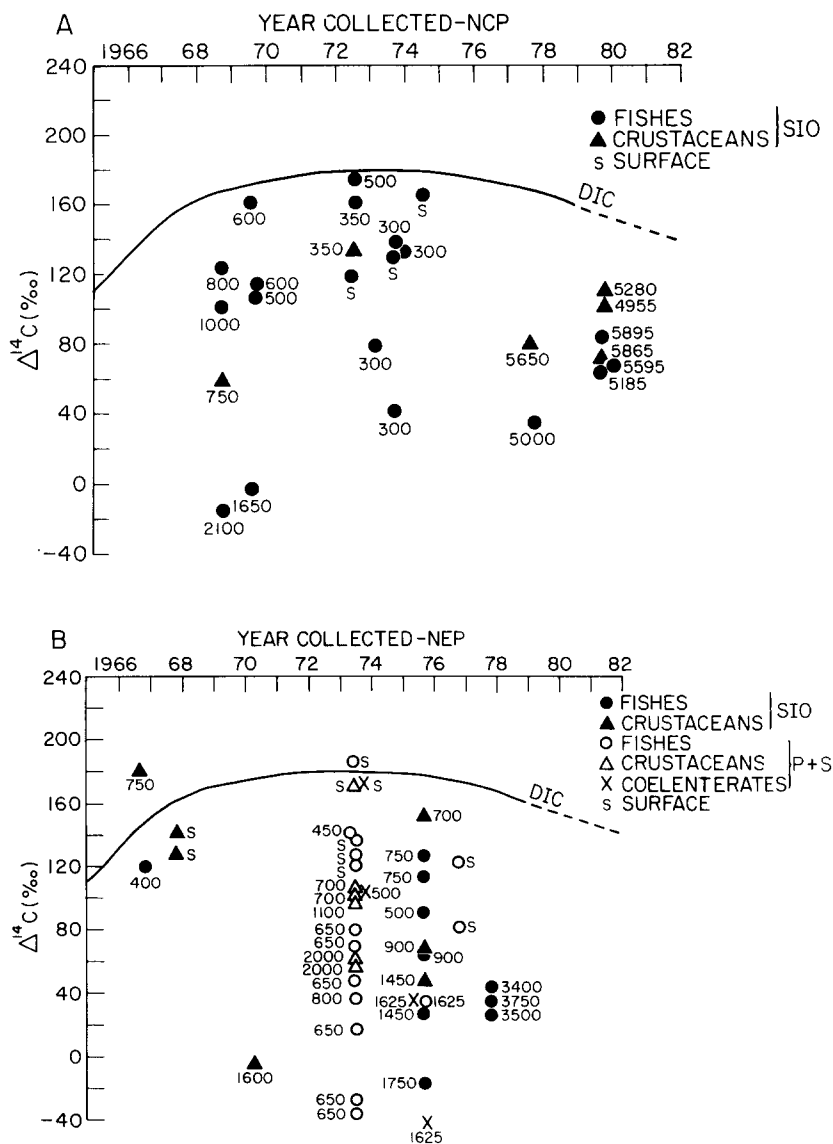
Fig. 4. (A,B) $\Delta^{14}C$ vs year collected for organisms collected in the (a) NCP and (b) NEP where the collection depths (m) are noted for each specimen; S = surface (0–50 m). No abyssobenthic organisms from PEARCY and STUIVER (1983) are included. The mean surface $DI^{14}C$ activity is the same as in Fig. 4.

DIC with depth, as shown by the GEOSECS data collected during August–September 1973 (Fig. 5) (ÖSTLUND and STUIVER, 1980). In the NCP, $\Delta^{14}C$ values decreased by about 40‰ by 60 m depth compared to surface values. In the NEP, the decrease was less (15‰) from surface to 70 m depth. As primary production takes place from the surface down to the subsurface chlorophyll maximum (50–150 m) (VENRICK et al., 1973; SHULENBERGER and REID, 1981; CULLEN, 1982), we expect $\Delta^{14}C$ values of organisms living in the surface

RADIOCARBON IN NORTH PACIFIC - 1973
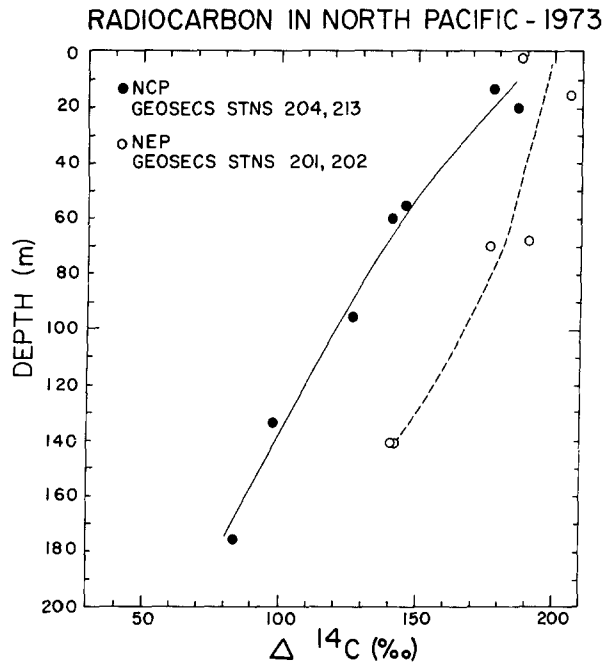

Fig. 5.   Decrease in $\Delta^{14}C$ with depth at four GEOSECS stations in the North Pacific Ocean
(ÖSTLUND and STUIVER, 1980).

mixed layer to be reduced significantly (15–40‰, average = 30‰) with respect to surface DIC (0–10 m) and coral (0–3 m) $\Delta^{14}C$ measurements. Thus, the $DI^{14}C$ values shown in Fig. 3 are maximum estimates of the ^{14}C activity of the carbon fixed by photosynthesis in the mixed layer.

A further consideration is the effect that wintertime mixing has on the $\Delta^{14}C$ values in surface waters. BROECKER and PENG (1980) noticed that surface water $\Delta^{14}C$ in the temperate North Atlantic was 35‰ higher in September, just before late autumn deepening of the mixed layer, than during March when the depth of the mixed layer was 200–400 m. They attributed the difference to the concentration of atmospheric bomb $^{14}CO_2$ into the thinner summer mixed layer (100 m deep). DRUFFEL et al. (1986) also observed a rise of at least 15‰ in surface $DI^{14}C$ in the Gulf of Alaska during the summer of 1984. At our Pacific locations, the depth of the mixed layer varies from about 30–50 m in the summer to 90–100 m during the winter (SHULENBERGER and REID, 1981). It is expected that winter $\Delta^{14}C$ values are lower throughout the surface water column than those reported from the GEOSECS study in summer (Fig. 5). Thus, the average $\Delta^{14}C$ values for organisms living in the surface waters are expected to be even lower in both the NCP and NEP if they utilize carbon fixed during winter mixing.

A second explanation for reduced ^{14}C activities in deep-sea organisms is the chronological age of the organisms themselves, such that they had been feeding on low ^{14}C activity pre-bomb carbon fixed in surface waters. That is, they incorporated and have still retained carbon fixed prior to the 1970–1974 peak in $DI^{14}C$ activities (Fig. 3). Pearcy and Stuiver reported life spans of certain mesopelagic and deep-sea fishes and crustaceans ranging from 8 to 17 years. BENNETT et al. (1982) estimated the longevity of the near-

bottom, shallow-water (200–500 m) rockfish (*Sebastes diploproa*) to be 50–80 years based on $^{210}Pb/^{226}Ra$ measurements in otoliths, and noted that more rapid growth occurred during the initial growth period of these rockfish. Thus, certain organisms caught during the years 1966–1976 (Fig. 4) whose life span exceeded 5–10 years could have incorporated low ^{14}C activity carbon initially and higher ^{14}C activity carbon subsequently. This would result in Δ^{14} values lower than those predicted from the sole utilization of rapidly sinking particles, even if a significant fraction of the carbon incorporated initially is replaced during the lifetime of the organism. STENHOUSE and BAXTER (1977) used the distribution of bomb ^{14}C in human tissue and various organs to estimate that the mean turnover time of soft tissue carbon in the human body is 6 years. Unfortunately, there are no data available for the mean turnover time of carbon in fishes.

There are four rare specimens (3 fish, 1 crustacea) in the SIO data set that have unusually low $\Delta^{14}C$ values (range = –1 to –18‰, Fig. 1A), all of which were collected from 1600 to 2100 m depth. These results appear, at first, to be too low, even if the two mechanisms described above were taken into account. However, three of these samples were collected between late 1968 and early 1970 (WILLIAMS *et al.*, 1970; WILLIAMS and LINICK, 1975), very soon after the input of bomb radiocarbon to the ocean (about 1959) and before peak $\Delta^{14}C$ values had been attained in the surface ocean. Thus, these specimens were drawing from a pool of carbon with a lower average $\Delta^{14}C$ than had other samples that were collected later. In addition, these specimens would have had to have been only a few years old in order for them to have incorporated pre-bomb carbon into their bodies. The fourth sample, a fish (*Cetostoma regani*) collected in 1975 (Table 1), was much larger (20 cm long) than the other three specimens (<10 cm long) and as a result was probably significantly older.

However, the other 10 samples collected during the early years of 1966–1969 contained much higher levels of bomb radiocarbon (range = +60–180‰). Only the four samples collected at mid-depths (1600–2100 m) were severely depleted in ^{14}C. Thus, it appears that there is some mechanism limited to a certain depth range that is causing unusually low $\Delta^{14}C$ values in organisms. We are unable to determine whether this mechanism is selective toward certain species, since not enough measurements were made to be statistically significant.

Is is possible that low ^{14}C activity particulate organic matter, produced by chemolithotrophic fixation of DIC at mid-depth levels in the water column (KARL and KNAUER, 1984; KARL *et al.*, 1984), is being utilized by meso-, bathy- and abyssopelagic organisms. The chemolithotrophic production of particulate microbial carbon was greatest in the oxygen minimum zones (500 and 900 m in the NEP and NCP, respectively) and was estimated to be 0.4 mg C m^{-2} d^{-1} at 500 m in the NEP (15°55′N, 107°12′W) or 5% of the total amount of sinking particulate organic matter collected in a particle trap deployed at the same depth (KARL *et al.*, 1984). Alternatively, it is possible that low ^{14}C activity DIC is directly utilized heterotrophically by these subsurface organisms via anapleurotic carboxylations (RAU *et al.*, 1986). They also suggest that heterotrophic uptake of low ^{14}C activity DIC could occur incrementally at successive food chain consumer levels resulting in $\Delta^{14}C$ reductions of about 200‰ between photosynthetically fixed surface DIC ($\Delta^{14}C$ = 180‰) and deep-sea biocarbon ($\Delta^{14}C$ = –10 to +20‰). This assumes a 5% incorporation of DIC at each of 11–14 trophic levels, with an initial $\Delta^{14}C$ of –200‰ for the DIC utilized at depth. However, there is no direct evidence for either heterotrophic uptake of DIC by marine animals nor for simple multi-level food chains in the deep sea.

In any case, it is necessary to invoke only a small amount of old carbon from this (these) mechanism(s) in order to obtain even the lowest $\Delta^{14}C$ values (–6‰ average) we observed in the three bathypelagic organisms collected in 1968–1970. To make this calculation, we have constructed a simple mass balance model, that neglects food chain amplification. We assume that the three organisms had maximum ages of 10 years. During this period, the $\Delta^{14}C$ value of DIC in the mixed layer (0–60 m) of the North Pacific rose about 190‰ (165 – 30 – [–55]) by early 1970 (with an average $\Delta^{14}C$ value of about 35‰ between 1960 and 1970). This is the $\Delta^{14}C$ value we would expect to find in an organism that lived from 1960 to 1970, whose diet consisted exclusively of freshly produced particles from the euphotic zone. To obtain the observed average $\Delta^{14}C$ value of –6‰, it is necessary to invoke an input of 15% old carbon that had been produced at mid-depths, assuming a $\Delta^{14}C$ value for mid-depth DIC (1300–3000 m) of –240‰ (ÖSTLUND and STUIVER, 1980) for both the NEP and NCP locations. Percent old carbon incorporation is inversely proportional to the fish age estimate, that is if the average age of the three organisms was only 5 years then 30% old carbon is needed to lower the calculated average surface value from 100‰ (average mixed layer $DI^{14}C$ from 1965 to 1970) to –6‰. Thus, it appears that the main source of dietary carbon is ultimately from rapidly sinking organic detritus produced in the surface ocean even at the depths where the lowest $\Delta^{14}C$ values for organisms were found (1600–2100 m).

It is certain that utilization of "old", low ^{14}C activity sedimentary organic matter by abyssobenthic organisms significantly lowers their organic-^{14}C activities (Pearcy and Stuiver). Direct utilization of resuspended, "old" particulate SOC by abyssopelagic organisms feeding within the benthic boundary layer is less likely than the indirect incorporation of "old" SOC into these organisms via their feeding on abyssobenthic animals which utilize sedimentary organic matter as a carbon source. The mean organic ^{14}C activity ($\Delta^{14}C$) of SOC was –336 ± 10‰ in the upper 0–1 cm of the sedimentary column at 2800–2900 m depth in the NEP in 1973 (Pearcy and Stuiver) and –640 ± 23‰ in the NCP in 1970 and 1977 at 5800–5900 m (WILLIAMS *et al.*, 1978; DRUFFEL *et al.*, 1984). Thus, incorporation of a relatively small quantity of SOC into the biocarbon of abyssopelagic organisms—whose main carbon source is "recent" carbon sinking or actively transported down from the surface waters—could appreciably reduce their organic ^{14}C activities. However, there was no direct correlation of the ^{14}C activities of the abyssopelagic organisms with surface $SO^{14}C$. Mean $\Delta^{14}C$ values of NCP grenadiers (*C. yaquinae*) and amphipods (*Eurythenes* sp.) in the NCP (63 ± 13 and 92 ± 22‰, respectively, Table 1), were higher than the mean values of the grenadiers (*C. armatus*) in the NEP (36 ± 9‰, Table 1; and 34 ± 7‰, Fig. 2B, Pearcy and Stuiver), a reverse effect to that expected from the lower ^{14}C activities of sedimentary organic matter in the NCP. The wide scatter in the $\Delta^{14}C$ values for the grenadiers and amphipods in the NCP (37 ± 10 to 110 ± 8‰) and NEP (–56 ± 18 to 79 ± 6‰), although unrelated to specimen size, suggests that some individual specimens may reflect an ontogenetic shift in diet with benthic food contributing a greater fraction of juvenile carbon intake. Alternatively, some individuals may consume sediment-feeders which others do not.

However, there appears to have been considerable incorporation of SOC into the abyssobenthic organisms reported by Pearcy and Stuiver, which is the reason we eliminated these values from Fig. 2A and from subsequent calculations. The $\Delta^{14}C$ values of these organisms were low in comparison to those for abyssopelagic organisms, and

these values must therefore not be used in models that calculate the major dietary carbon sources to the meso-, bathy- and abyssopelagic organisms.

It is useful to estimate the turnover time of biocarbon in the meso-, bathy- and abyssopelagic zones with respect to transfer of particulate organic carbon from the euphotic zone to subsurface organisms. We have divided the $\Delta^{14}C$ measurements into two groups based on the time of collection (1966–1970, 1972–1979), because the length of the collection period (13 years) is significant compared to the turnover time of biocarbon in the deep sea. Assuming an average $\Delta^{14}C$ value of 175‰ in the upper 10 m during the 1970s (Figs 3 and 5) and the 15–40‰ reduction with depth in the mixed layer (Fig. 5), the rise in the surface ocean $DI^{14}C$ by 1970–1980 was 190‰ $(175 - [40] - [-55])$ in the NCP and 215‰ $(175 - [15] - [-55])$ in the NEP. Maximum estimates of the turnover times of biocarbon in four depth zones of the ocean are listed in Table 2. For example, the average $\Delta^{14}C$ value of mesopelagic organisms collected from 1972 to 1980 in the NEP is 112‰. This reflects a rise above surface pre-bomb values (−55‰) of 167‰ or 78% of the rise in the mixed layer by this time. From Fig. 3, we observe that $\Delta^{14}C$ values in the North Pacific had been approximately the same since 1969, a period of seven years to the average time of collection (1976). Therefore, a maximum estimate of the turnover time is 9 years (7 years/.78) for biocarbon at subsurface depths (400–900 m). The turnover times of biocarbon in the surface of the NEP and NCP and those in the mesopelagic zone of the NCP and pre-1969 NEP are less than 1 year (see Table 2). This is because the average $\Delta^{14}C$ values of organisms at these depths were indistinguishable from those in the surface water DIC. Note that the turnover times of the NEP grenadiers, *C. armatus*, are virtually identical for both the SIO (17 years) and Pearcy and Stuiver (15 years) measurements and that the abyssobenthic organisms (from Pearcy and Stuiver) have a

Table 2. Calculation of turnover times of organic carbon in meso- bathy- and abyssopelagic organisms

	NCP (SIO)		NEP (SIO)		NEP (P&S)
Collection period	1966–1970	1972–1979	1966–1970	1972–1979	1973–1976
Average $\Delta^{14}C$ in mixed layer	110	135	135	160	160
$\Delta^{14}C_{1950}$ mixed layer	−55	−55	−55	−55	−55
$\Delta^{14}C_{org.\ surface}$	ND	140 (3)	134 (2)	ND	140(8)
$\Delta^{14}C_{org.\ mesopel.}$ *	112 (6)	124 (7)	150 (2)	112 (5)	58 (11)
$\Delta^{14}C_{org.\ bathypel.}$ *	−8 (2)	ND	−4 (1)	31 (4)	40 (6)
$\Delta^{14}C_{org.\ abyssopel.}$ *	ND	76 (8)	ND	36 (3)	34 (8)† 1 (51)‡
No. years at peak $\Delta^{14}C$ values (since 1969)	1	7	1	7	6
$J_{org.\ surface}$	—	<7	<1	—	<6.6
$J_{org.\ mesopel.}$ *	<1	<7.4	<1	9.0	11
$J_{org.\ bathypel.}$ *	3.5	—	3.7	18	14
$J_{org.\ abyssopel}$ *	—	10	—	17	15† 23‡

$$ J = \frac{\text{Years } [\Delta^{14}C_{aver.\ M.L.} - \Delta^{14}C_{1950}]}{\Delta^{14}C_{org.} - \Delta^{14}C_{1950}} $$

ND, no data; ( ), number of samples.

* Depths (m): NCP (SIO) = 300–1000 (mesopelagic), >1000–2100 (bathypelagic), >2100 (abyssopelagic). NEP (SIO) = 400–900 (mesopel.), >900–1750 (bathypel.), >1750 (abyssopel.). NEP (P&S) = 300–800 (mesopel.), >800–2000 (bathypel.), >2000 (abyssobenthic).

† Values for the grenadiers *C. armatus* only.

‡ Value for all abyssobenthic organisms excepting *C. armatus* and one pyenogonid (−464‰).

longer average turnover time due to their grazing on low ^{14}C activity SOC. The turnover times in the bathy- and abyssopelagic depth ranges (NCP and NEP, SIO results) are slower than those in the mesopelagic zone, suggesting an input of old, low ^{14}C activity carbon to the deep sea possibly by chemotrophic or heterotrophic utilization of mid-water DIC. We believe, however, that the chronological age of these animals is the principle factor resulting in the low ^{14}C activities.
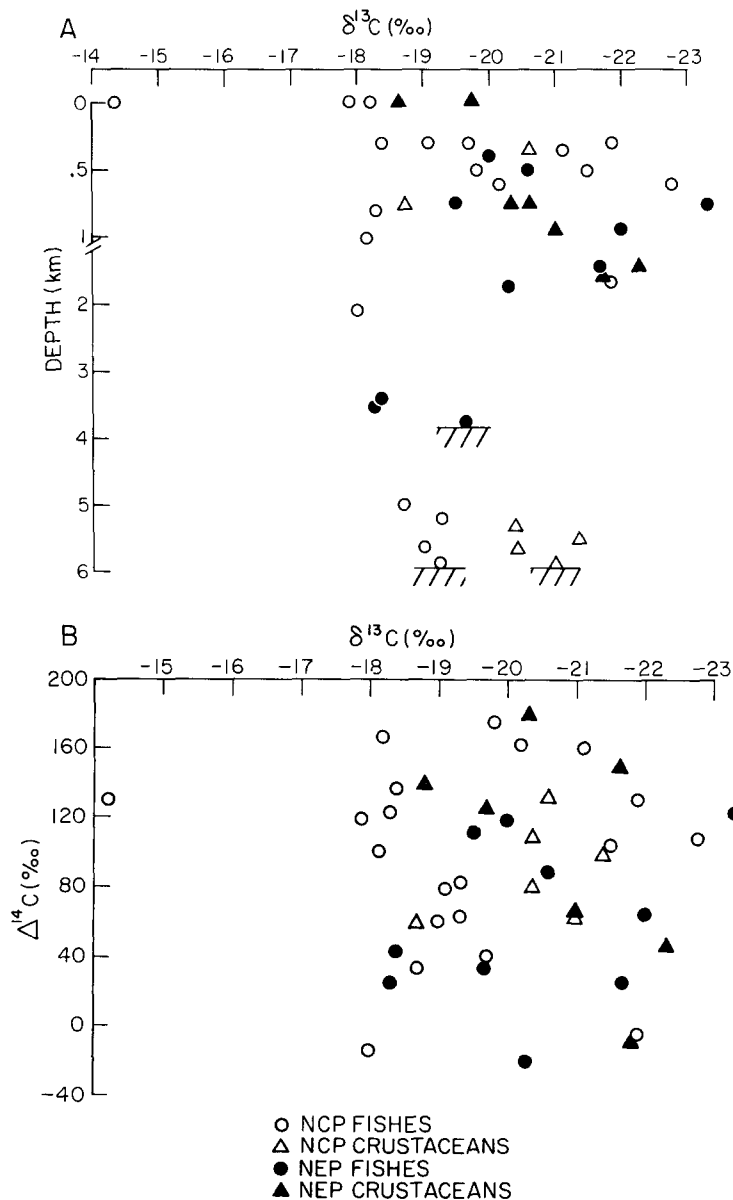

Fig. 6. (A) δ^{13}C vs depth for organisms collected in the NCP and NEP. Legend and data sources same as in Fig. 1 plus T. W. LINICK and P. M. WILLIAMS (unpublished data). (B) δ^{13}C vs Δ^{14}C for organisms used in this (SIO) study.

Many of the organisms collected from 1966 to 1979 and examined in these two studies could be 1–2 decades old (R. BACKUS, personal communication) and have thus incorporated a significant amount of pre-1970 carbon fixed in the euphotic zone. However, the scatter of the individual results indicates that there is a wide range in the chronological age and/or mean turnover time of carbon in the deeper organisms and further studies of this problem are needed to understand the bomb ^{14}C signal in marine organisms.

All of the δ^{13}C values for the NEP and NCP (SIO results only, no δ^{13}C values were given by Pearcy and Stuiver) organisms are plotted vs depth and vs Δ^{14}C in Figs 6A and B. These data do not appear to provide any insights into dietary carbon sources, reflect isotopic fractionation, or show any obvious correlation between δ^{13}C and Δ^{14}C values. Some of the scatter in the δ^{13} values might have been due to variations in the lipid content of the various organisms, since δ^{13}C values for marine lipids are 3–6‰ lower than for the corresponding protein and carbohydrate fractions. The δ^{13} values of the four samples with the lowest Δ^{14} measurements were not different from the other results, which suggest that these bathypelagic organisms had not ingested significantly greater quantities of chemolithotrophically fixed organic matter.

We conclude that the major source of dietary carbon to meso-, bathy- and abysso-pelagic organisms is recently formed carbon transported rapidly down through the water column from its origin in the euphotic zone. We do not support the hypothesis that the recycling of organic matter in the euphotic zone over a time period of years resulting in low activity particles and subsequent repackaging and utilization by subsurface organisms is an important mechanism for diminished biocarbon activities in these subsurface organisms. First, photosynthetically fixed carbon is rapidly utilized and oxidized to CO_2 or sinks out of the surface water rapidly (EPPLEY et al., 1983). Second, if multiple dissolution and repackaging of particles in the euphotic zone over ten's of years results in a lower ^{14}C activity dietary carbon source in surface waters, then both surface and deep-sea organisms should have similar Δ^{14}C values with little or no diminution of biocarbon ^{14}C activities with depth.

Our studies suggest that the principal source of dietary carbon for most meso-, bathy- and abyssopelagic organisms is "recent" carbon fixed in the euphotic zone which sinks or is actively transported into deeper water, and that there may be a source (e.g. chemolithotrophic and/or heterotrophic utilization of mid-water DIC) of old carbon to the mid-depth organisms (1000–3000 m). However, we maintain that the diminished ^{14}C activity of the subsurface organisms is due (1) to the initial low ^{14}C activity of the photosynthetically derived particulate matter arising from the strong ^{14}C gradient in the upper 100 m of the water column during the 1970s, and (2) to the longevity (1–2 decades) of certain primarily bathy- and abyssopelagic organisms which incorporated low ^{14}C activity particulate matter during the period prior to 1970.

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