Deep-Sea Research, Vol. 34, Nos 5/6, pp. 807–827, 1987.
Printed in Great Britain.

0198-0149/87 $3.00 + 0.00

Geographical variation of the water column distribution of suspended particulate organic nitrogen and its ^{15}N natural abundance in the Pacific and its marginal seas

TOSHIRO SAINO* and AKIHIKO HATTORI*

(*Received* 21 *September* 1985; *in revised form* 25 *May* 1986; *accepted* 2 *June* 1986)

Abstract—The water column distribution of suspended particulate organic nitrogen (PON) and its natural abundance ratio of ^{15}N:^{14}N were investigated to a depth of ~4000 m at 13 stations in the North Pacific, and the South China, Philippine and Bering seas. At two stations in the northern North Pacific, sediment trap experiments were also carried out. The $\delta^{15}N$ of PON ranged from −1.5 to 23.3 per mil. The ^{15}N natural abundance of PON increased with depth between 0 and 200 m, while the PON concentration decreased sharply in the same depth range. In the vertical profiles, the PON in the deep water was, on an average, enriched with ^{15}N by approximately 6 per mil as compared with that in the euphotic zone. These findings imply that the vertical transport of organic matter is mediated primarily by rapidly sinking particles, and that most of the decomposition of organic matter takes place in the shallow layer beneath the bottom of the euphotic zone (<200 m) in a similar manner at all locations.

The average ^{15}N abundance of PON in the water column was higher in the eastern tropical and central gyre portions of the Pacific than in the western Pacific, the South China Sea, the Philippine Sea, and the Bering Sea. Year-round stratification, the influence of ^{15}N enriched nitrate produced during denitrification and the lack of significant nitrogen fixation in the surface layer probably caused the ^{15}N enrichment in the eastern tropical Pacific.

INTRODUCTION

PARTICULATE organic matter (POM) plays an important role in vertical transport of oceanic material. In the surface water of the open ocean, where input of organic matter from rivers and precipitation is not substantial POM arises mainly from primary production by phytoplankton, and consists of autotrophic and heterotrophic organisms and their detritus. While sinking towards the sea floor, much of the POM is decomposed and the organic materials are remineralized in the water column. Organic matter comprises the major part of the total particulate material in the sea surface (LAL, 1977). The POM acts as a source of organic matter and as a sink for some trace components such as heavy metals or artificial organic compounds (LAL, 1977; SACKETT, 1978; SIMPSON, 1982; and references therein) in the water column. The POM can be divided into two groups. One consists of larger particles such as fecal pellets and marine snow that sink rapidly and dominate the vertical transport of organic matter. The other is composed of slowly sinking smaller particles that dominate the standing stock of POM. Since the larger particles are rare, they are poorly collected by conventional water sampling; they are collected more effectively by sediment traps or by filtering large volumes of seawater at depth (MCCAVE, 1975).

* Ocean Research Institute, The University of Tokyo, 1-15-1 Minamidai, Nakano-ku, Tokyo 164, Japan.

The isotopic abundance of bioactive elements in various forms of biological material is determined by the isotope fractionation during the biochemical reactions that form or decompose these substances. Data on isotopic abundance of carbon and nitrogen in suspended particulate organic matter (POM) therefore provide useful information for understanding the production and decomposition of POM during its vertical transport. It is well documented that the carbon to nitrogen ratio of suspended POM generally increases with depth (ROMANKEVICH, 1984; GORDON, 1977; TANOUE and HANDA, 1979). This implies that nitrogen is more rapidly lost than carbon during degradation. SAINO and HATTORI (1980a) found that the ^{15}N abundance in PON below the euphotic layer increases with depth and attains a constant value in the deep water. The sharp increase below the euphotic layer has been confirmed by ALTABET and MCCARTHY (1986) in the shallow layers of the western Atlantic and the Sargasso Sea. Using data on ^{15}N abundance in PON, ALTABET and MCCARTHY (1985) further discussed the behavior of PON and the characteristics of the nitrogen cycle in a warm-core ring of the Gulf Stream.

We present here the water column distribution of suspended PON and its ^{15}N natural abundance extending to a depth of 4000 m over a widespread region in the North Pacific and in the South China, Philippine, and Bering seas. Geographical variations observed in the vertical profiles of PON and its ^{15}N abundance are discussed in relation to features of the nitrogen cycling in the respective areas.

MATERIALS AND METHODS

Sampling locations are shown in Fig. 1. Water samples were collected, during several cruises of the *Hakuho Maru* (University of Tokyo), using 23 l Niskin bottles (cruises

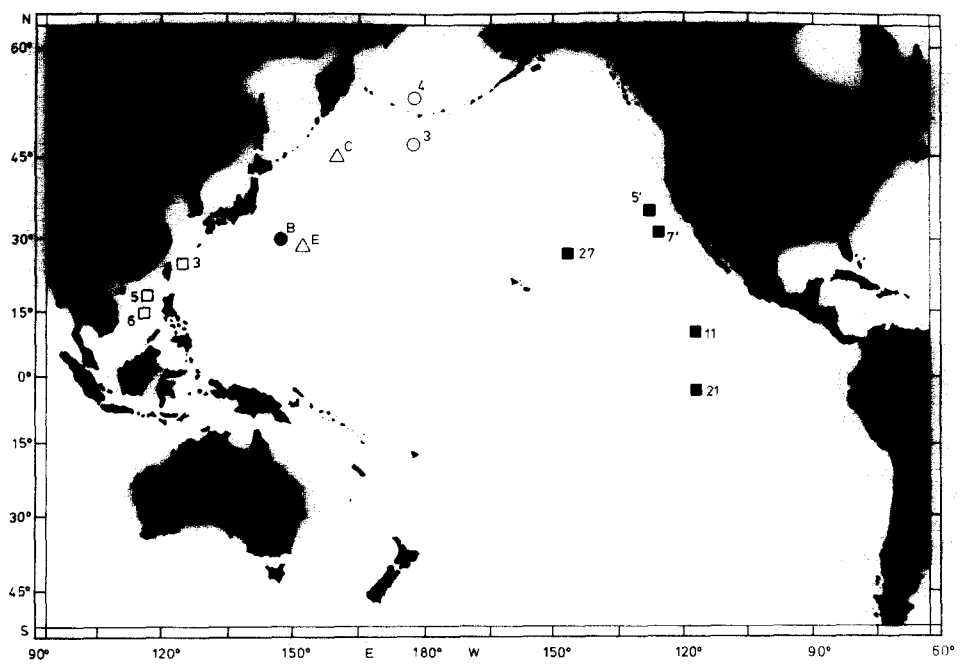

Fig. 1. Location of sampling stations. Open circles, KH-78-3 cruise; a filled circle, KH-78-4 cruise; open squares, KH-81-5 cruise; closed squares, KH-82-5 cruise; and open triangles, KH-83-3 cruise.

KH-78-3, KH-81-5, KH-82-5, and KH-83-3) or 25 l Van Dorn bottles (cruise KH-78-4). All of the seawater from each sampling bottle was transferred to a 25 l plastic container, and PON was collected on a precombusted (47 mm, 450°C, 4 h) Reeve Angel 984H (KH-78-3,4) or Whatman GF/F (KH-81-5, KH-82-5, and KH-83-3) glass fiber filter (GARDNER, 1977; CALVERT and MCCARTNEY, 1979). For the deep (>200 m) water samples of the KH-81-5, KH-82-5, and KH-83-3 cruises, the water samples were collected by using 2–4 Niskin bottles that had been attached to a hydrographic wire at 2–5 m intervals. The PON samples retained on the filters were frozen and brought back to the laboratory. Before analysis, these samples were freeze-dried and kept in a vacuum desiccator. The quantity and ^{15}N abundance of PON were measured by the method of WADA *et al.* (1977) using a Hitachi RMV-6 mass spectrometer for isotope ratio measurements. The ^{15}N abundance is expressed as per mil deviation from standard air nitrogen:

$$\delta^{15}N \text{ (per mil)} = [(^{15}N/^{14}N)_{smpl}/(^{15}N/^{14}N)_{std} - 1] \times 1000.$$

The 95% confidence limit of the ^{15}N isotope ratio determination was ~0.5 per mil.

Water temperature and salinity were measured by a CTD (Neil Brown MK III). Standard hydrocasts were also conducted at each station using the Rosette Multi Sampler (General Oceanics) or Niskin bottles fitted with reversing thermometers. Dissolved oxygen was determined by the Winkler method (JAPAN METEOROLOGICAL AGENCY, 1970). Nutrients were determined on board the ship using a Technicon Autoanalyzer II by the methods of WOOD *et al.* (1967) for nitrate, BENDSHNEIDER and ROBINSON (1952) for nitrite, and MURPHY and RILEY (1962) for phosphate as modified for the Autoanalyzer.

Sediment trap samples were obtained at Sta. 3 of the KH-78-3 cruise and Sta. C of the KH-83-3 cruise. Those experiments were conducted by S. Tsunogai and M. Uematsu of Hokkaido University, and N. Handa and E. Tanoue of Nagoya University on the KH-78-3 cruise and N. Handa and H. Matsueda of Nagoya University on the KH-83-3 cruise. The outlines of the experiment are described in the cruise reports (HATTORI, 1979, in press). The sediment trap materials of the KH-78-3 cruise were subjected to Kjeldahl digestion and steam distillation followed by wet oxidation to nitrogen gas by potassium hypobromite (SAINO, 1977). Samples of the KH-83-3 cruise were measured by the same procedure employed for the PON samples.

RESULTS

Suspended PON

The vertical profiles of PON and its ^{15}N abundance are shown in Figs 2–14, together with σ_t, saturation percentage of dissolved oxygen, and nitrate concentration. The highest concentration of PON was 4.06 μg-at. N l^{-1} (KH-78-3, Sta. 3; 0 m), and the lowest was 0.024 (KH-83-3, Sta. E; 3940 m). PON decreased rapidly in the top 100–200 m of the water column, where gradients of density, nutrients, and oxygen saturation percentage were the highest. Except for Sta. 11 of the KH-85-2 cruise, the ^{15}N abundance of PON generally increased with depth between 100 and 200 m. At Sta. 11 of the KH-82-5 cruise, where the intermediate water was extremely oxygen-depleted, a significant increase of $\delta^{15}N$ in the PON was observed below 300 m. The $\delta^{15}N$ of PON ranged from –1.5 (Sta. C, KH-83-3; 35 m) to 23.3 per mil (Sta. 27, KH-82-5; 2477 m).

Figure 15 shows the frequency distributions of $\delta^{15}N$ and the concentration of PON in three depth ranges: 0–100 m, 100–200 m, and >200 m. Increases in $\delta^{15}N$ and decreases

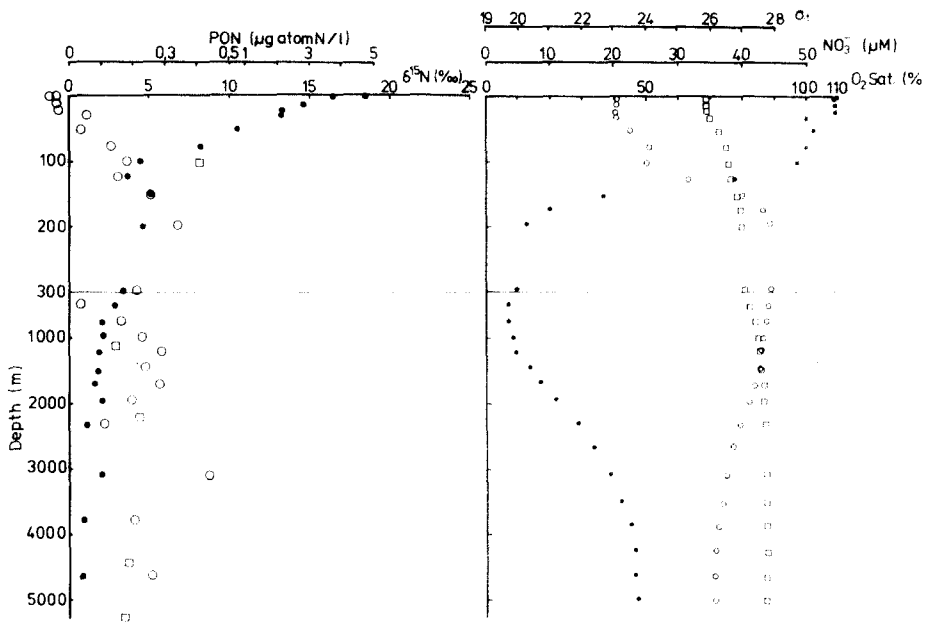

Fig. 2. Vertical profiles of PON (●) and its $\delta^{15}N$ values (○), and $\delta^{15}N$ of material collected in sediment traps (□) (left), and σ_t (□), nitrate (○), and saturation percentage of dissolved oxygen (●) (right) at Sta. 3 of the KH-78-3 cruise (11 July 1978; 47°57′N:176°25′E; ○ 3 in Fig. 1) in the northern North Pacific. Depth scale changes at 300 m, and PON scale changes at 0.5 μg-at. N l^{-1}.

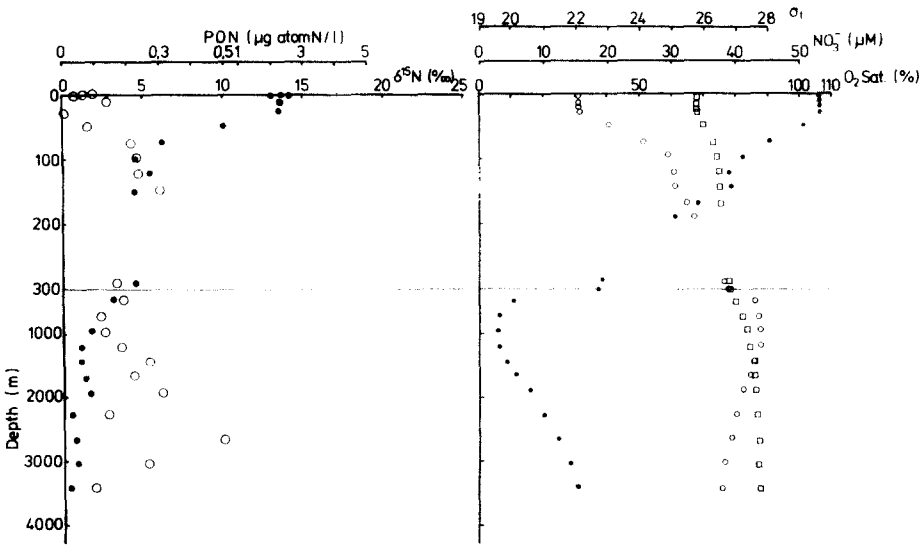

Fig. 3. Vertical profiles of PON and its $\delta^{15}N$ values (left) and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 4 of the KH-78-3 cruise (15 July 1978; 53°34′N:177°10′E; ○ 4 in Fig. 1) in the Bering Sea. Symbols and scale changes are the same as in Fig. 2.

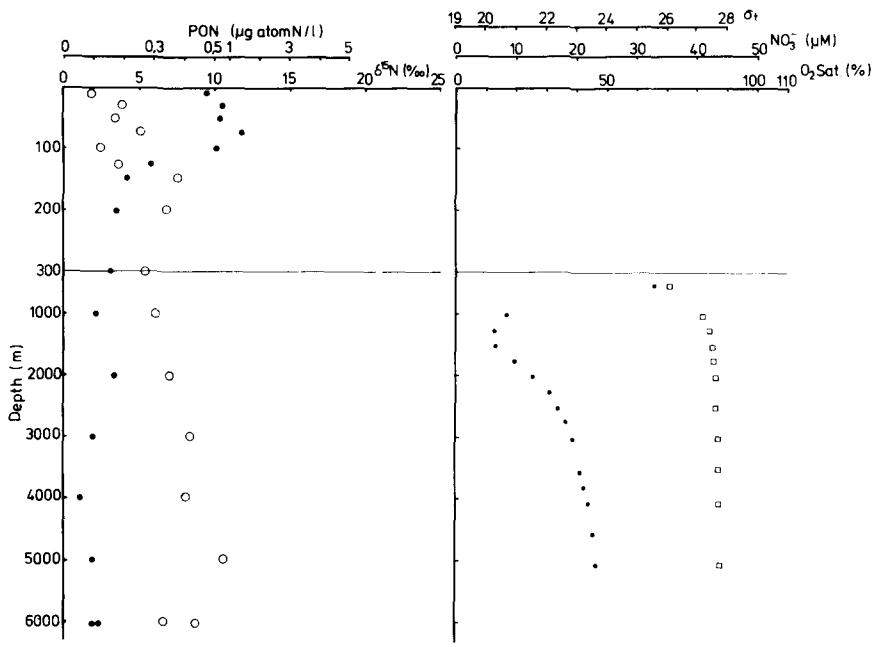

Fig. 4. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, and saturation percentage of dissolved oxygen (right) at Sta. B of the KH-78-4 cruise (30 September 1978; 29°36′N:146°40′E; ● B in Fig. 1) in the western subtropical Pacific. Symbols and scale changes are the same as in Fig. 2.

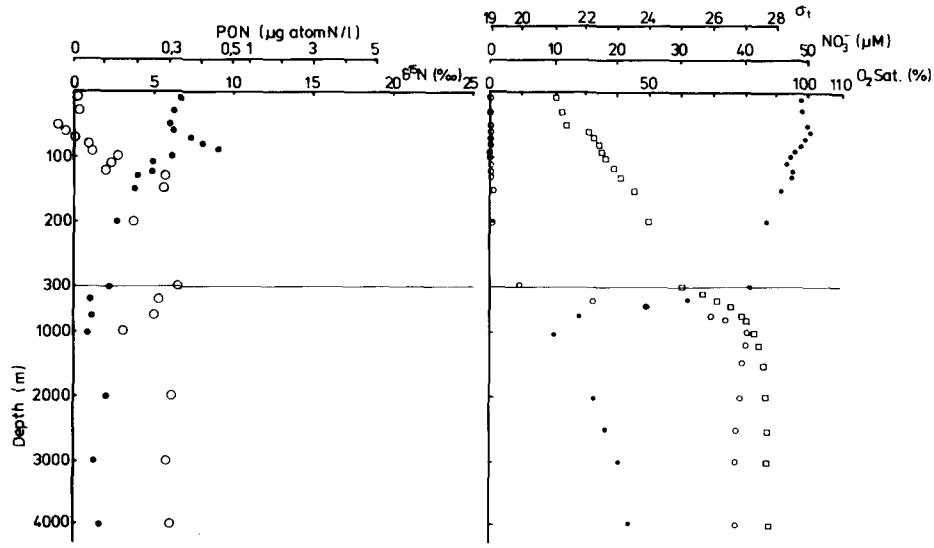

Fig. 5. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 3 of the KH-81-5 cruise (16 September 1981; 21°59′N:125°00′E; □ 3 in Fig. 1) in the Philippine Sea. Symbols and scale changes are the same as in Fig. 2.

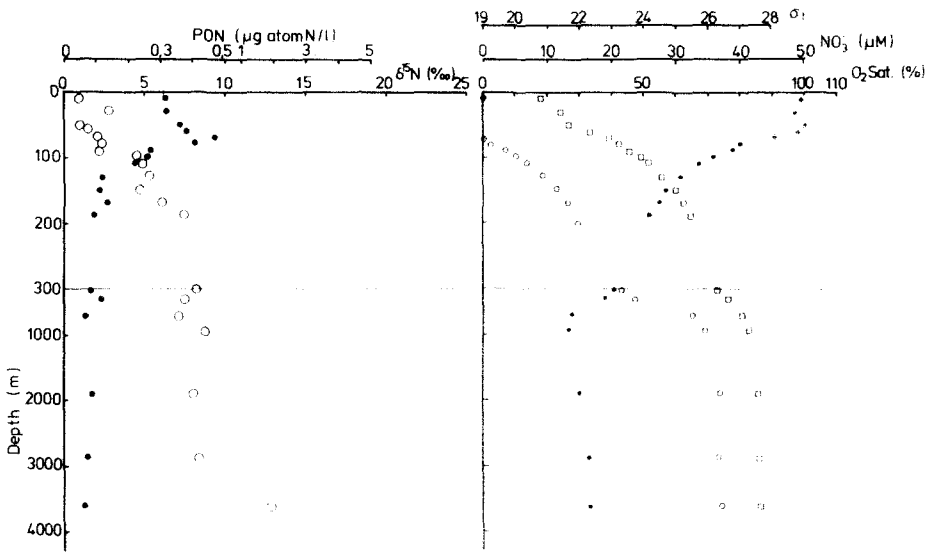

Fig. 6. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 5 of the KH-81-5 cruise (27 September 1981; 18°05′N:117°00′E; □ 5 in Fig. 1) in the South China Sea. Symbols and scale changes are the same as in Fig. 2.

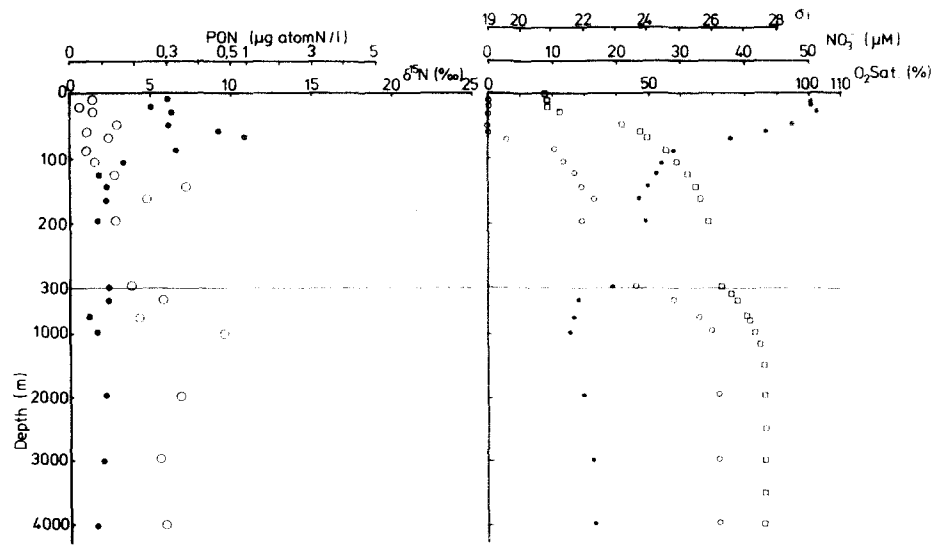

Fig. 7. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 6 of the KH-81-5 cruise (29 September 1981; 14°40′N:114°10′E; □ 6 in Fig. 1) in the South China Sea. Symbols and scale changes are the same as in Fig. 2.

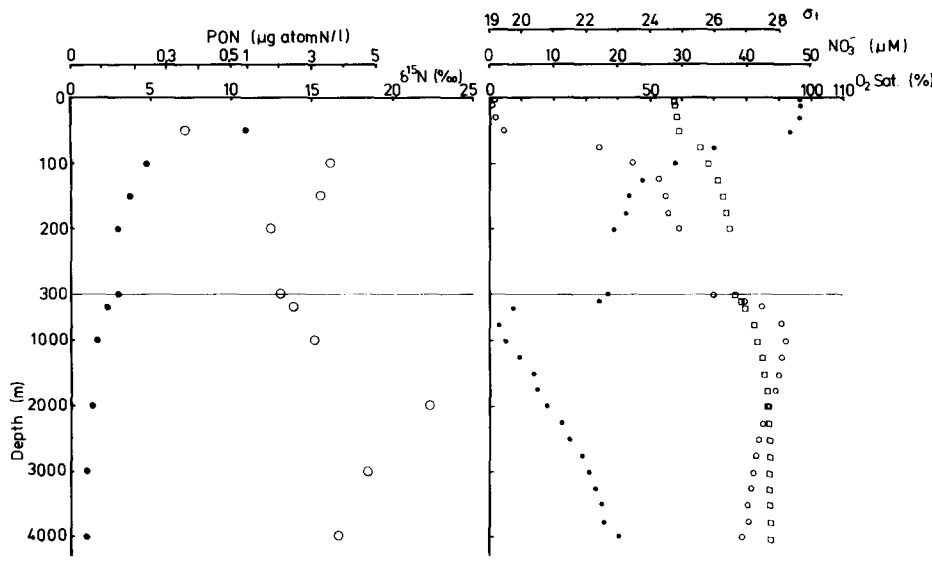

Fig. 8. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 5′ of the KH-82-5 cruise (17 December 1982; 36°56′:127°31′W; ■ 5′ in Fig. 1) in the eastern Pacific Ocean off San Francisco. Symbols and scale changes are the same as in Fig. 2.

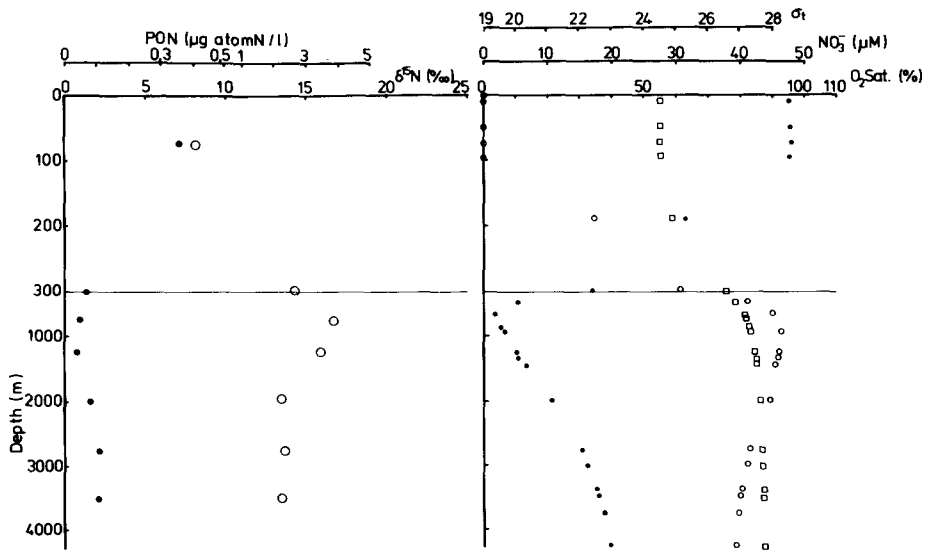

Fig. 9. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 7′ of the KH-82-5 cruise (28 January 1983; 31°40′N: 124°22°W; ■ 7′ in Fig. 1) in the eastern Pacific off San Diego. Symbols and scale changes are the same as in Fig. 2.

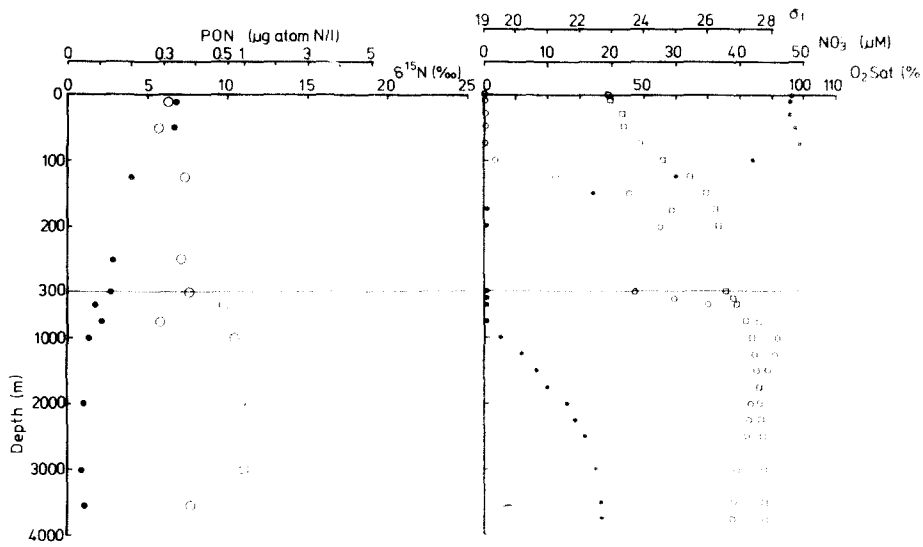

Fig. 10. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 11 of the KH-82-5 cruise (24 December 1982; 17°27′:117°00′W; ■ 11 in Fig. 1) in the eastern tropical Pacific. Symbols and scale changes are the same as in Fig. 2.

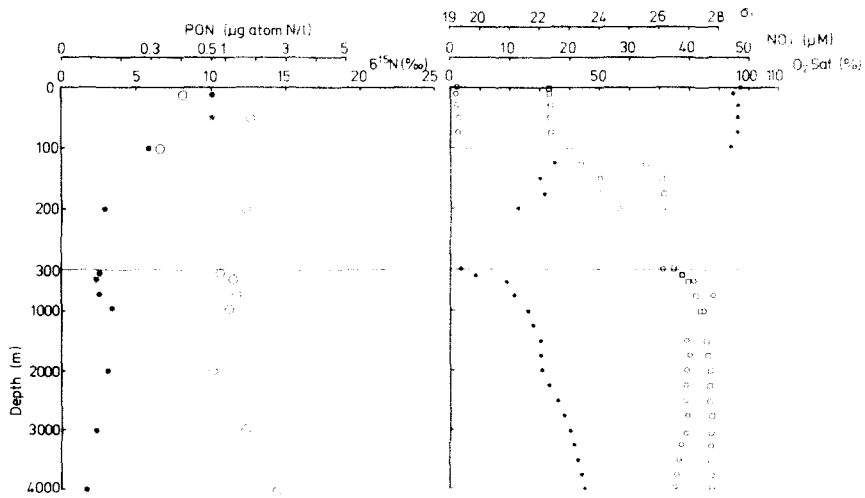

Fig. 11. Vertical profiles of PON and its $\delta^{15}N$ values (left), and δ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 21 of the KH-82-5 cruise (10 January 1983; 2°46′:117°01′W; ■ 21 in Fig. 1) in the eastern equatorial Pacific. Symbols and scale changes are the same as in Fig. 2.

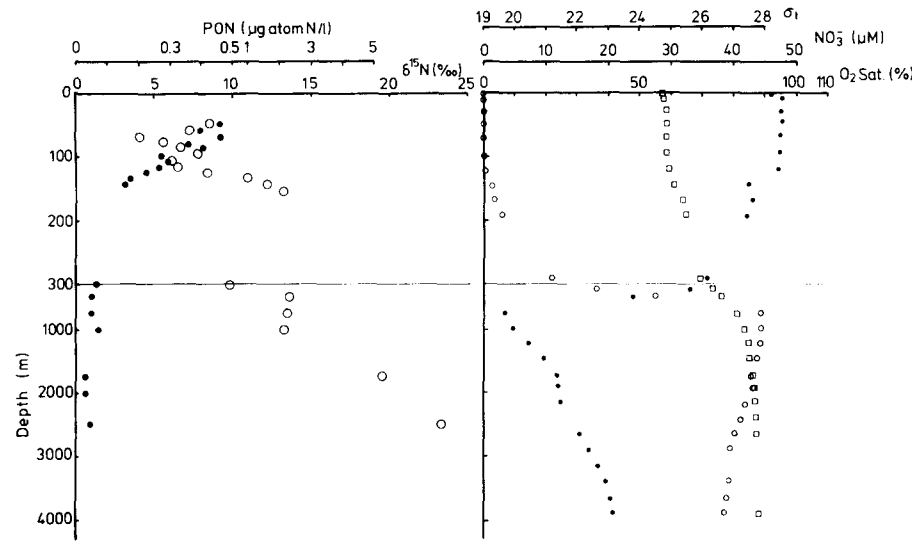

Fig. 12. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. 27 of the KH-82-5 cruise (3 February 1983; 26°45′N:146°46′W; ■ 27 in Fig. 1) in the North Pacific Central Gyre. Symbols and scale changes are the same as in Fig. 2.

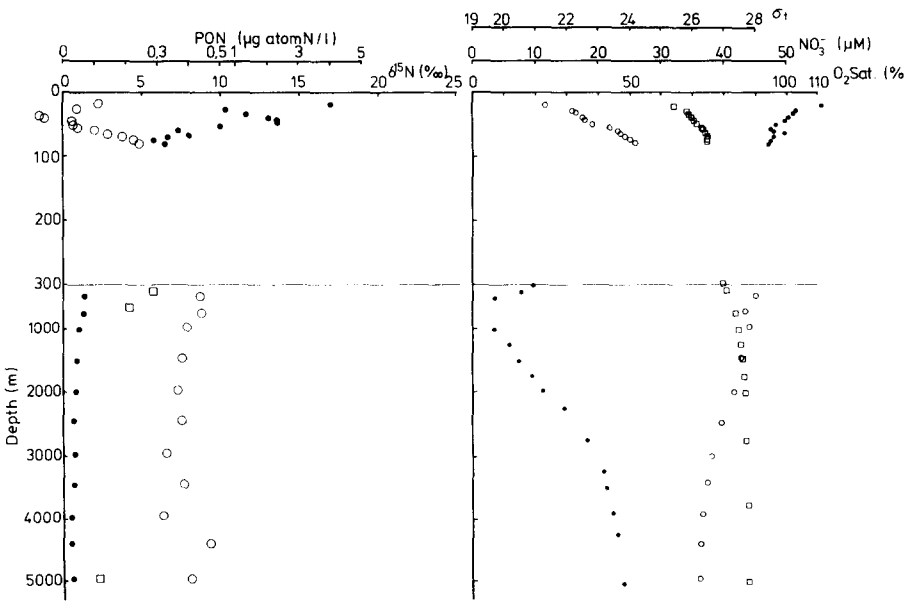

Fig. 13. Vertical profiles of PON and its $\delta^{15}N$ values, and $\delta^{15}N$ of material collected in sediment traps (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. C of the KH-83-3 cruise (18–23 August 1983; 45°N160°E; △ C in Fig. 1) in the northwestern North Pacific. Symbols and scale changes are the same as in Fig. 2.

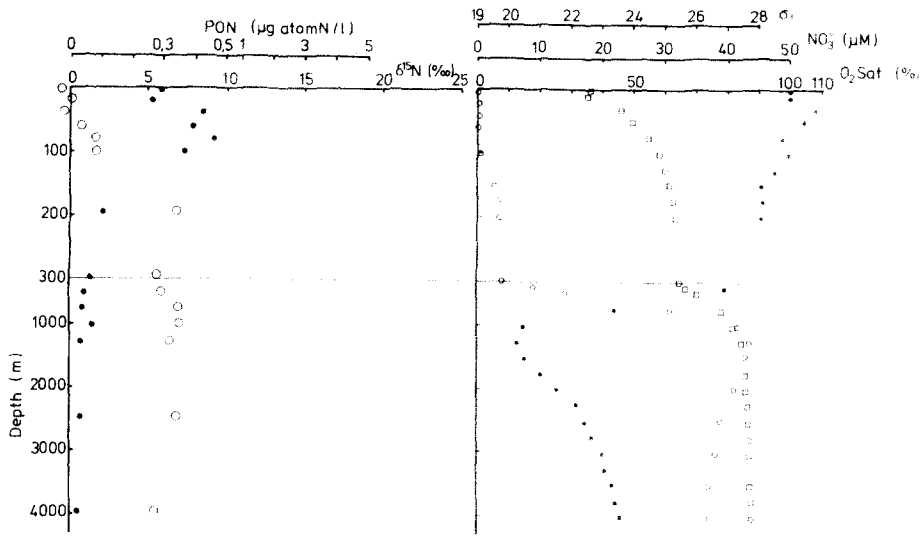

Fig. 14. Vertical profiles of PON and its $\delta^{15}N$ values (left), and σ_t, nitrate, and saturation percentage of dissolved oxygen (right) at Sta. E of the KH-83-3 cruise (7–9 September 1983; 28°N:153°N E; △ E in Fig. 1) in the western subtropical Pacific. Symbols and scale changes are the same as in Fig. 2.

in PON with depth are clearly seen. The concentration of PON in the top 100 m varied from 0.2 to 4.1 μg-at. N l^{-1}. The variation of PON concentration was relatively small in the deeper layers, but the variation of $\delta^{15}N$ of PON was greatest in this zone. In Fig. 15, data from the east and west Pacific are separated to illustrate the regional differences in concentration and ^{15}N abundance of PON. The $\delta^{15}N$ of PON was consistently higher in the eastern Pacific, but the concentration of PON fell within the range of the other values. Table 1 summarizes some hydrographic features. The maximum concentration of

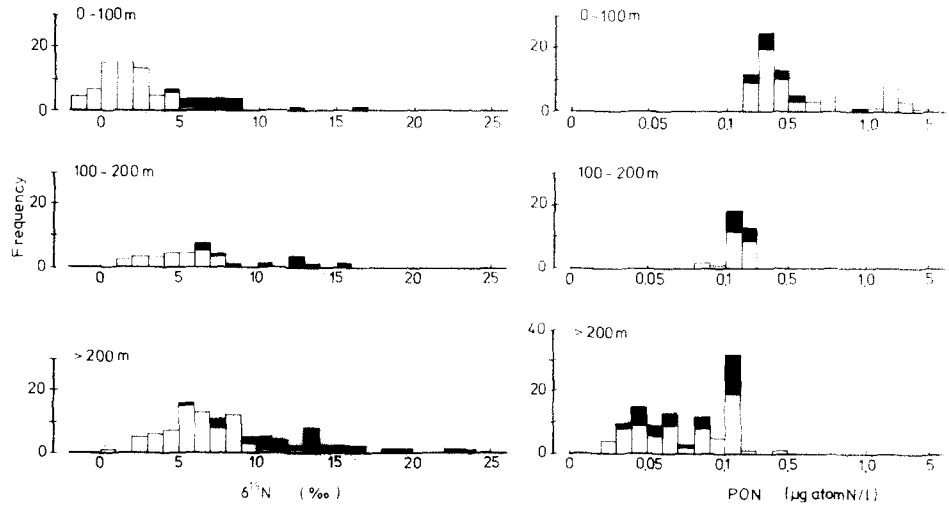

Fig. 15. Frequency distributions of $\delta^{15}N$ and concentrations of suspended PON measured in this study. Filled bars; data from the eastern Pacific, open bars; data from the other areas except the eastern Pacific. Note the scale changes in PON concentration.

Table 1. Summary of the characteristic features in the vertical distributions of PON, $\delta^{15}N$ of PON, nitrate, and dissolved oxygen, and of nitrate and phosphate concentrations at the surface

		PON		$\delta^{15}N$		Nitrate			Phosphate	Depth range of	Minimum oxygen	
Cruise	Station	max. avg. (μg-at. N l^{-1})	>200 m	min. (‰)	max.	0 m	max. (μM)	(depth) (m)	0 m (μm)	NO_3^->40 μM (m)	sat. %	(depth) (m)
KH-78-3	3	4.06	0.080	−1.1	8.8	20.2	44.3	(292)	1.70	150–2000	7.1	(486)
	4	2.30	0.047	0.1	10.0	15.7	43.6	(959)	1.46	500–2300	5.8	(959)
KH-78-4	B	1.38	0.104	1.8	10.6	ND	42.4	(1250)	ND	1000–2000	13.2	(1250)
KH-81-5	3	0.45	0.006	−1.1	6.5	0.0	40.4	(1000)	0.00	1000	20.6	(994)
	5	0.47	0.070	0.9	12.9	0.2	37.0	(3607)	0.09	None	26.9	(942)
	6	0.54	0.088	0.6	9.6	0.0	36.5	(3978)	0.09	None	25.7	(993)
KH-82-5	5′	0.99	0.063	7.1	22.3	0.9	46.2	(1000)	0.67	500–3750	3.2	(750)
	7′	0.36	0.082	8.1	16.8	0.0	46.2	(1241)	0.32	500–3500	3.7	(668)
	11	0.34	0.051	5.7	11.0	0.1	45.8	(1000)	0.21	750–2750	0.9	*
	21	0.56	0.131	6.6	14.4	1.3	44.0	(750)	0.34	500–1750	3.8	(300)
	27	0.46	0.051	4.0	23.3	0.1	44.2	(750)	0.08	750–2700	6.9	(733)
KH-83-3	C	3.98	0.034	−1.5	9.3	1.1	44.2	(1000)	0.27	300–2500	6.9	(750)
	E	0.47	0.044	−0.5	7.0	0.0	43.3	(1250)	0.00	1000–2000	12.7	(1250)

ND = not determined.

* Oxygen depleted water 150–750 m.

nitrate in the water column of each station was higher in the eastern North Pacific than at the other stations. The depth range of nitrate higher than 20 μM was largest at Stas 5′ and 7′. In the South China Sea, the maximum concentration of nitrate appeared near the bottom, but the concentration was lower than 40 μM. Regional trends in oxygen concentration are best shown by comparing saturation percentages. The minimum percentage of dissolved oxygen in the water column was low (<5%) at the eastern stations (Stas 5′,7′,11,21; KH-82-5), intermediate (5–13%) at the rest of the Pacific stations, and high (21–27%) in the Philippine and South China seas. Phosphate at the sea surface was almost depleted in the western low latitude stations, but not at the eastern stations.

Sediment trap material

Table 2 summarizes the ^{15}N abundance data from the materials collected by sediment traps. At Sta. 3 of the KH-78-3 cruise, the $\delta^{15}N$ values were almost constant (2.9–4.4 per mil) below 1000 m, and similar to those of the suspended PON. At 100 m, the settling material was more enriched with ^{15}N (8.1 per mil) than the suspended PON (3.7 per mil). At Sta. C of the KH-83-3 cruise, the settling materials were taken from three layers. The $\delta^{15}N$ of the settling materials decreased with depth. At this station, the settling material was significantly less enriched with ^{15}N than the suspended PON. It should be noted that no preservative was added to the sediment traps, and that the duration of the sediment trap deployment was one month on the KH-78-3 cruise and 5 days on the KH-83-3 cruise. From the fatty acid analysis, TANOUE and HANDA (1980) concluded that bacterial biomass in the trapped materials of the KH-78-3 cruise is negligibly small. However, their observation does not necessarily exclude the possibility of a biological reworking. Consequently, some alteration in the ^{15}N abundance may have occurred in the sediment traps.

DISCUSSION

PON in the shallow layer

The PON concentration in the euphotic zone is controlled by the gain by primary production and the loss by sinking and decomposition. According to DUGDALE and GOERING (1967), primary production can be classified into new production (usually supported by nitrate uptake or nitrogen fixation) or regenerated production (usually

Table 2. Summary of sediment trap experiments

Cruise	Period	Depth (km)	N-flux (mg N m^{-2} d^{-1})	$\delta^{15}N$ (‰)
KH-78-3	13 Jul.	0.1	0.36*	8.1
Sta. 3	to	1.1	2.23	2.9
	14 Aug.	2.2	1.23	4.4
		4.4	0.78	3.7
		5.25	0.22	3.5
KH-83-3	18 Aug.	0.39	6.89	5.7
Sta. C	to	0.62	3.81	4.2
	23 Aug.	4.92	0.83	2.3

* A part of the sample was lost upon recovery.

supported by ammonium uptake). In a steady-state, the input of new nitrogen from underlying water and from the atmosphere by nitrogen fixation into the euphotic zone equals the loss of organic nitrogen from the euphotic layer by sinking (EPPLEY and PETERSON, 1979). The suspended PON in the shallow layers is comprised mainly of phytoplankton, microzooplankton, bacteria and detritus. It contains a small amount, if any, of large sized particles such as fecal pellets, marine snow, and zooplankton (MCCAVE, 1975). The ^{15}N abundances of PON in the euphotic layer are therefore affected by the mode of the primary productivity (relative contribution of new and regenerated production), isotope fractionation during the nitrogen uptake processes, and vertical flux of organic matter and its ^{15}N abundance.

A subsurface minimum in the $\delta^{15}N$ vertical profile was observed near the bottom of the euphotic zone at Stas 4 (KH-78-3), B (KH-78-4), 3 (KH-81-5), 27 (KH-82-5), and C (KH-83-3). On the other hand, the minimum $\delta^{15}N$ appeared at or near the sea surface at Stas 3 (KH-78-3), B (KH-78-4), 5 (KH-81-5), 6 (KH-81-5), and E (KH-83-3). At the other stations, we cannot identify the depth of the minimum $\delta^{15}N$ due to scarcity of data.

The depth of the subsurface minimum of PON $\delta^{15}N$ often coincides with the depth where the saturation percentage of dissolved oxygen shifts from supersaturation to undersaturation. We (SAINO and HATTORI, 1980a) previously interpreted the low $\delta^{15}N$ of PON as resulting from isotope fractionation in nitrate uptake under light limited conditions. In the northern North Pacific and in the Bering Sea, where a subsurface ammonium maximum exists in summer, the subsurface minimum in $\delta^{15}N$ (Fig. 13) probably resulted from ammonium utilization and the isotope fractionation associated with it (SAINO and HATTORI, 1985).

The occurrence of *Trichodesmium*, a nitrogen fixing cyanobacterium, is significant in the South China Sea and the northern part of the Philippine Sea and the western Pacific near the Kuroshio (SAINO, 1977; SAINO and HATTORI, 1980b; CARPENTER, 1983). Isotope fractionation during nitrogen fixation is small (HOERING and FORD, 1960; WADA, 1980), and *Trichodesmium* has a low $\delta^{15}N$ value, between −2 and 1 per mil (WADA and HATTORI, 1976; and unpublished data of T. SAINO from the South China Sea and the South Atlantic Bight). Thus nitrogen fixation by *Trichodesmium*, or by other nitrogen fixers if any, introduces "new" nitrogen with near zero $\delta^{15}N$ values. The near zero values for $\delta^{15}N$ of PON in the shallow layers of Stas 3, 5, and 6 of the KH-81-5 cruise and Sta. E of the KH-83-3 cruise suggest that nitrogen fixation is substantial in these areas. This view contradicts previous estimates of the contribution of nitrogen fixation by *Trichodesmium* to the total nitrogen budgest based on rate measurements and algal biomass estimates; it was estimated as ~6% in the East China Sea (SAINO and HATTORI, 1980b) and as ~8% in the Carribean Sea (CARPENTER and PRICE, 1977). This contradictory situation probably results from the inadequacy in rate measurement; the rate of nitrogen fixation by *Trichodesmium* is highly susceptible to environmental conditions (CARPENTER and PRICE, 1976; SAINO, 1977; SAINO and HATTORI, 1980b). It is also likely that nitrogen fixing organisms other than *Trichodesmium* contribute significantly to nitrogen fixation in these areas.

The low $\delta^{15}N$ value in the surface layer at Sta. 3 (KH-78-3) cannot, however, be explained by nitrogen fixation and may instead reflect one stage of a seasonal progression. Stations 3 and 4 of KH-78-3 and Sta. C of KH-83-3 are located in an oceanic region characterized, in summer, by the presence of a subsurface temperature minimum, or dichothermal water (UDA, 1963). In winter, the water column is mixed down to the depth

of the temperature minimum zone but no further because of the presence of a well developed halocline at mid-depth (UDA, 1963; REID, 1973). This mixing transports nitrate from the subsurface layer to the euphotic zone. At the beginning of the spring, the water column starts to stratify, the surface nitrate decreases, and phytoplankton increases. In summer, a part of the nitrate transported to the surface in winter is converted to ammonium and contributes to the formation of the subsurface ammonium maximum (SAINO *et al.*, 1983). SAINO and HATTORI (1985) showed a linear inverse relationship between the surface nitrate concentration and the $\delta^{15}N$ of the suspended PON in the surface layer. They explained that the observed inverse correlation resulted from an isotope fractionation in nitrate uptake by phytoplankton (WADA and HATTORI, 1978). The regional difference in $\delta^{15}N$ of the shallow PON will, therefore, be partly explained by this relationship. Temporal changes in population composition, or food chain structure, and their influence on the transport of organic materials through the pycnocline also affect the ^{15}N abundance of PON; organisms of higher trophic levels (MINAGAWA and WADA, 1985) and zooplankton fecal pellets (CHECKLEY and ENTZEROTH, 1985) might be enriched with ^{15}N.

CHECKLEY and ENTZEROTH (1985) observed that during the grazing of a nitrogen limited population of particle grazing copepods, the bodies (+6 per mil) and feces (+8 per mil) of the animals were enriched with ^{15}N relative to the suspended particulate matter. This might cause ^{15}N enrichment in the deep water PON. They speculated further that, as a result of enrichment of ^{15}N in fecal materials, the surface water of the oligotrophic area could become depleted with ^{15}N. This mechanism can be an alternate to nitrogen fixation for lowering ^{15}N abundance in the surface water of the oligotrophic ocean. However, there is a process that has an opposite effect. This situation arises because nitrate near the bottom of the euphotic layer in the oligotrophic ocean is enriched with ^{15}N (CLINE and KAPLAN, 1975) and nitrate uptake by phytoplankton in the euphotic layer is in balance with the input from depth (KING and DEVOL, 1979; EPPLEY *et al.*, 1979). Nitrate uptake by phytoplankton under light limited conditions is associated with isotope fractionation, but the isotope fractionation diminishes when nitrate limits uptake (WADA and HATTORI, 1978). During the upward transport of nitrate by turbulent mixing, nitrate will be enriched with ^{15}N as a result of isotope fractionation during nitrate uptake in the lower euphotic zone. Nitrate transported higher, into the upper euphotic zone, will be taken up completely and transformed into PON which then enters into rapid cycling between PON, (DON?), and ammonium. This mechanism would operate so as to increase the ^{15}N abundance in the shallow layer.

At Sta. 27 (KH-82-5) in the North Pacific Central Gyre, the water column is permanently stratified, and the contribution of nitrogen fixation may not be substantial (MAGUE *et al.*, 1974, 1977), although nitrogen fixing cyanobacteria sometimes flourish (VERNICK, 1974; MAGUE *et al.*, 1974, 1977). The minimum $\delta^{15}N$ was 4.0 per mil at 68 m (Fig. 12). We do not have data within the upper 50 m, but the deeper values suggest that the $\delta^{15}N$ value for the surface PON at this station could be as high as 8 per mil. MULLIN *et al.* (1984) reported $\delta^{15}N$ values of 4.4–4.6 and 1.9–3.8 per mil for Chaethognaths and for Copepods (*Neocalanus*), respectively, in the North Pacific Central Gyre. Since the ^{15}N abundance is known to increase along with trophic level (MINAGAWA and WADA, 1984), we cannot explain the low $\delta^{15}N$ value of zooplankton presented by MULLIN *et al.* (1984) based on our $\delta^{15}N$ number for PON. Year to year or seasonal variations in the surface populations and the co-occurring changes in the contribution of nitrogen fixation should be investigated.

The vertical profiles (Figs 2–14) commonly show sharp increases with depth in ^{15}N abundance of suspended PON in the upper discontinuity layer. The increase of ^{15}N abundance is concomitant with the decrease in PON, an increase in nitrate, and a decrease in dissolved oxygen. The increase in $\delta^{15}N$ of PON in this depth zone probably results from isotope fractionation during the oxidative degradation of PON as suggested by SAINO and HATTORI (1980a). In that process the ^{15}N abundance of PON may vary due to isotope fractionation during ammonification (MACKO and ESTEP, 1983; MINAGAWA and WADA, 1984). In addition, ammonium oxidizing bacteria produce isotopically lighter nitrite (MIYAKE and WADA, 1971; MARIOTTI *et al.*, 1981) and utilize, together with other heterotrophic bacteria, ^{15}N enriched ammonium to form PON (SAINO and HATTORI, 1985).

PON in the deep layer

In the deep layer, suspended PON is supplied from above by rapidly sinking large particles (settling materials) such as fecal pellets (e.g. WIEBE *et al.*, 1976; BISHOP *et al.*, 1977; ISEKI, 1981), and marine snow (SILVER *et al.*, 1978; ALLDREDGE, 1979; SHANKS and TRENT, 1980), by slowly sinking small particles, or by horizontal advective transport of small particles. PON in the deep layer is thus an admixture of newly produced small particles originating from settling fecal material fragmented at depth, and old small particles which slowly descend from above or are advected horizontally. In other words, the slowly sinking suspended PON is diluted by rapidly sinking particles fragmented at depth. If the rapidly sinking particles are not directly converted to dissolved nitrogenous compounds (most probably nitrate in oxygenated seawater), we can calculate the apparent residence time of suspended PON from PON concentrations (Figs 2 and 13) and the change with depth of the vertical flux of settling materials (Table 2). For Sta. 3 (KH-78-3), the apparent residence time of PON between 1.1 and 5.3 km was calculated at about 2100 days, and for Sta. C (KH-83-3) the PON residence time was 70 days at 0.4–0.6 km and 750 days at 0.6–4.9 km. In this calculation, only the PON supply by rapidly sinking particles was taken into account. The differences in PON residence times with depth imply that seasonal variations in the surface are reflected only in the shallow to mesopelagic PON, not in the bathypelagic PON. If we assume that the horizontal and vertical velocities of abyssal water movement are 3×10^{-2} cm s^{-1} (STOMMEL, 1958; CHUNG and CRAIG, 1980) and 3–5 m y^{-1} (STOMMEL, 1958; FIADEIRO and CRAIG, 1978), respectively, then PON travels *ca.* 50 km (horizontally) or *ca.* 20–30 m (vertically) during its estimated residence time of 2000 days in the deep water.

The average $\delta^{15}N$ of PON in the deep water is correlated with the minumum δ^{15} number in the shallow layer (Fig. 16), suggesting that the ^{15}N abundance in the deep water PON is closely coupled with the ^{15}N abundance of the source PON in the surface layer. Vertical transport mediated by rapidly sinking fecal pellets of amorphous material like marine snow is probably responsible for this close coupling. More than 90% of the particles sinking out of the upper discontinuity layer are comprised of fecal pellets or material derived from the fecal pellets (BISHOP *et al.*, 1977). Most of these settling materials are fragmented and produce the suspended PON in the deep water. The relationship in Fig. 16 further suggests that decomposition which is responsible for an increase of $\delta^{15}N$ in PON, takes place in a similar manner at all locations and causes an approximately 6 per mil increase in the $\delta^{15}N$ of deep water PON.

The $\delta^{15}N$ value for materials collected with sediment traps was similar to that of the suspended PON at Sta. 3 of the KH-78-3 cruise (Fig. 2), and lower at Sta. C of the KH-

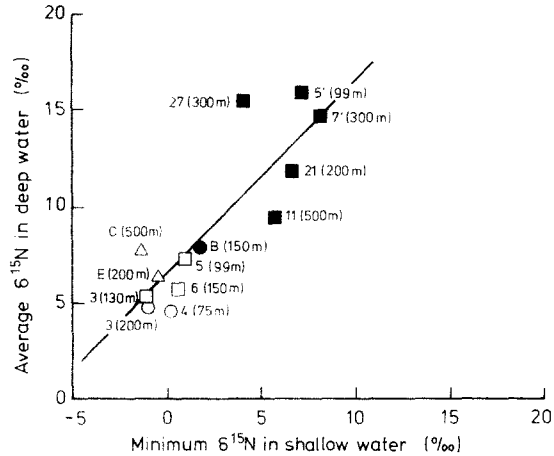

Fig. 16. Relationship between the minimum $\delta^{15}N$ in or near the euphotic zone and the average $\delta^{15}N$ in the deep layer for each vertical profile of $\delta^{15}N$ of PON. Symbols are the same as in Fig. 1. Depths in parentheses denote the uppermost depth below which the average $\delta^{15}N$ in the "deep" layers are calculated (see Figs 2–14). The regression equation is [deep water average $\delta^{15}N$] = 6.5 + 1.02 × [shallow water minimum $\delta^{15}N$] with $r = 0.85$.

83-3 cruise (Fig. 13). Since no preservative was applied to our sediment traps, we will discuss only Sta. C (KH-83-3; 5-day deployment). The average sinking velocity of the settling material collected in sediment traps is approximately 100 m day^{-1} (DEUSER and ROSS, 1980; SHANKS and TRENT, 1980; LORENZEN *et al.*, 1983). Thus sinking particles at 600 and 4900 m are calculated to have left the surface 6 and 49 days ago, respectively. The seasonal variability in the $\delta^{15}N$ value of the surface PON in these sea areas, as mentioned previously, may, in part, explain the vertical variation in $\delta^{15}N$ of the trapped materials. ALTABET and DEUSER (1985) found a seasonal variation in $\delta^{15}N$ of the sediment trap material in the deep (3200 m) Sargasso Sea. The $\delta^{15}N$ covaried with the magnitude of the particle flux; the higher the flux the lower the $\delta^{15}N$. Although biological reworking of the settling particles is well-known (e.g. KARL *et al.*, 1984; ANDREWS *et al.*, 1984; WAKEHAM *et al.*, 1984), little is known about the alteration of their ^{15}N abundance in the water column. The difference in $\delta^{15}N$ values between the suspended PON and the settling materials should be evaluated on time scales similar to or longer than the residence time of PON. Seasonal and annual variation of ^{15}N abundance of the settling materials should therefore be investigated.

High $\delta^{15}N$ values in PON (>15 per mil) were found at Stas 5′, 7′, and 27 of the KH-82-5 cruise located in the eastern North Pacific Ocean. At Stas 5′ and 27, the vertical profiles of PON and $\delta^{15}N$ in the depth range of 500–2500 m are quite similar. The intermediate water of the eastern North Pacific is the oldest in the global circulation of abyssal water. This is reflected in the low concentration of oxygen and high concentration of nitrate (Table 1). The old PON component enriched with ^{15}N after extensive oxidative decomposition and reworked in the process of early diagenesis might have accumulated in this old water. To date the existence of such a substance, however, is not known.

PON in the oxygen depleted water column

Dissolved oxygen was extremely depleted (<0.1 ml l^{-1}) at Sta. 11 (KH-82-5) in the eastern tropical Pacific from 175 to 750 m (Fig. 10). Judging from the nitrate deficit (CLINE and RICHARDS, 1972) or from the nitrite profile (data not shown), denitrification actively proceeds from 175 to 500 m, and is centered at ~300 m. From 250 to 500 m, PON decreases with depth and the $\delta^{15}N$ increases by 2.7 per mil (Fig. 10). During denitrification POM is decomposed but nitrogen liberated from PON remains in the reduced state, such as organic materials or ammonium. Nitrification does not take place in the extremely oxygen depleted water (KAPLAN, 1983; YOSHIDA *et al.*, 1984). The isotope fractionation during the liberation of the dissolved form of organic nitrogen or ammonium from PON probably causes the ^{15}N enrichment of PON in the denitrification layer.

A PON maximum and a minimum of $\delta^{15}N$ (5.8 per mil) occurs at 750 m, the lower boundary of the anoxic zone (Fig. 10). This might result from the *in situ* production of particulate matter at this depth by chemolithotrophic bacteria (KARL *et al.*, 1984). The VERTEX III sediment trap experiment of KARL *et al.* (1984) was conducted in November 1982 at 15°55'N, 107°12°W; nearly at the same time and in the same water mass as our observation (23 December 1982, 17°23'N; 117°00'W). They observed that ammonium is transported with the settling materials in the denitrification layer, and subsequently utilized for chemolithotrophic production of organic matter associated with nitrification in the underlying zone where dissolved oxygen is available. If the isotope fractionation occurs during ammonification, the ammonium transported through the oxygen depleted denitrifying zone with settling materials is less enriched with ^{15}N than the nitrogen in the settling materials. PON produced by chemolithotrophy utilizing ammonium will therefore have low $\delta^{15}N$ values.

Comparison between the eastern and western North Pacific

The most obvious geographical trend in the ^{15}N abundance is that the ^{15}N in the suspended PON is higher in the eastern North Pacific than in the western North Pacific. Since the ^{15}N abundance of the suspended PON in the deep water is correlated with its source, the shallow water PON (Fig. 16), the cause of the geographical variation can be attributed to the variation of the shallow water PON.

As previously discussed, nitrogen fixation is probably responsible for the low surface $\delta^{15}N$ value of PON in the low to mid-latitude areas of the western North Pacific. When nitrogen fixation occurs, nitrogen is no longer a limiting element of primary productivity in the water column. Phosphate in the surface water is relatively higher in the eastern North Pacific than in the western North Pacific, and the South China and Philippine seas (Table 1). This indicates that phosphate is not limiting nitrogen fixation in the eastern North Pacific. It is likely that some other element (e.g. Fe or Mo) limits the growth of nitrogen fixing organisms (for Fe; J. G. RUETER, personal communication). The aeolian input of Fe (or Mo) by Asian continental dust, an important pathway of air–sea material transport in the Pacific (UEMATSU *et al.*, 1983), is larger in the western Pacific than in the eastern Pacific. This might explain the east–west regional variation of nitrogen fixation in the Pacific.

Denitrification occurs in the oxygen depleted intermediate water of the eastern tropical Pacific. Isotope fractionation during denitrification causes ^{15}N enrichment in nitrate and ^{15}N depletion in the nitrogen gas that is produced (CLINE and KAPLAN, 1975). Thus, the oxygen depleted intermediate water in the eastern tropical Pacific forms a

source of ^{15}N enriched nitrate, which is transported to the surrounding water mass by advection or eddy diffusion (LIU, 1979). PON in the euphotic zone produced by utilizing the nitrate rich in ^{15}N would have higher $\delta^{15}N$ value. The relationship in Fig. 16 implies that horizontal transport of suspended PON is of minor importance when compared with the vertical transport mediated either by rapidly sinking or by slowly sinking particles. Therefore, the selective loss of ^{15}N depleted nitrogen gas (–22 per mil; CLINE and KAPLAN, 1975) by denitrification in the eastern tropical Pacific and input of ^{15}N depleted nitrogen gas (0 to –2 per mil; WADA, 1980) by nitrogen fixation in the western North Pacific is in accordance with the geographical trend observed in ^{15}N abundance in PON.

CONCLUSIONS

The ^{15}N abundances of the suspended PON in the deep layer are generally higher by approximately 6 per mil than those in the euphotic layer of each station. This implies that the vertical transport of organic materials is primarily mediated by rapidly sinking particles, and the decomposition of organic matter in the water column takes place in a similar manner irrespective of location. Geographically, the suspended PON is richer in ^{15}N in the eastern North Pacific than in the western North Pacific. Nitrogen fixation in the low to mid-latitude surface waters in the western Pacific and the uptake of nitrate, that is replenished by winter convection in the northern North Pacific are probably responsible for the low $\delta^{15}N$ numbers in the western North Pacific. Denitrification in the oxygen depleted intermediate water in the eastern tropical Pacific produces ^{15}N enriched nitrate. The nitrate rich in ^{15}N is advected to the surrounding water. If the ^{15}N enriched nitrate is transported into the euphotic zone, PON enriched with ^{15}N will be produced. This mechanism is probably responsible for the higher $\delta^{15}N$ for PON in the eastern Pacific.

The ^{15}N abundance data as such are not sufficient to identify and quantify each process causing variation of ^{15}N abundance, but they can offer unperturbed and at least qualitative information on the processes responsible for ^{15}N variation under *in situ* conditions. For example, the trend in the geographical variation of $\delta^{15}N$ of PON observed in this study highlighted the importance in the low latitude western Pacific of nitrogen fixation, which has been thought of as a minor contribution to the nitrogen economy in that area. Thus, studying the natural abundance of ^{15}N will complement ^{15}N tracer studies.

Acknowledgements—We thank the scientists, Captain, officers, and crew aboard the *Hakuho Maru* cruises KH-78-3, KH-78-4, KH-81-5, KH-82-5, and KH-83-3 for help in the water sampling. Thanks are also due to L. A. Codispoti for helpful comments. This work was partly supported by grants-in-aid (574216, 58740258, 60740300) to T.S. from the Ministry of Education, Science, and Culture, Japan.

REFERENCES

ALLDREDGE A. L. (1979) The chemical composition of macroscopic aggregates in two neritic seas. *Limnology and Oceanography*, **24**, 855–866.

ALTABET M. A. and W. G. DEUSER (1985) Seasonal variation in natural abundance of ^{15}N in particles sinking to the deep Sargasso Sea. *Nature*, **315**, 218–219.

ALTABET M. A. and J. J. MCCARTHY (1985) Temporal and spatial variations in the natural abundance of ^{15}N in PON from a warm-core ring. *Deep-Sea Research*, **32**, 755–722.

ALTABET M. A. and J. J. MCCARTHY (1986) Vertical patterns in ^{15}N natural abundance of PON from the surface waters in warm-core rings. *Journal of Marine Research*, **44**, 185–201.

ANDREWS C. C., D. M. KARL, L. F. SMALL and S. W. FOWLER (1984) Metabolic activity and biolumniescence of oceanic faecal pellets and sediment trap particles. *Nature*, **307**, 539–541.

BENDSHNEIDER D. and R. L. ROBINSON (1952) A new spectrophotometric method for the determination of nitrite in sea water. *Journal of Marine Research*, **11**, 87–96.

BISHOP J. K. B., J. M. EDMOND, D. R. KETTEN, M. P. BACON and W. B. SILKER (1977) The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. *Deep-Sea Research*, **24**, 511–548.

CALVERT S. E. and M. J. MCCARTNEY (1979) The effect of incomplete recovery of large particles from water samplers on the chemical composition of oceanic particulate matter. *Limnology and Oceanography*, **24**, 532–536.

CARPENTER E. J. (1983) Nitrogen fixation by marine *Oscillatoria (Trichodesmium)* in the world's oceans. In: *Nitrogen in the marine environment*, E. J. CARPENTER and D. G. CAPONE, editors, Academic Press, New York, pp. 65–103.

CARPENTER E. J. and C. C. PRICE IV (1976) Marine *Oscillatoria (Trichodesmium)*: Explanation for aerobic nitrogen fixation without heterocyst. *Science*, **191**, 1278–1280.

CARPENTER E. J. and C. C. PRICE IV (1977) Nitrogen fixation, distribution and production of *Oscillatoria (Trichodesmium)* spp. in the western Sargasso and Caribbean Seas. *Limnology and Oceanography*, **22**, 60–72.

CHECKLEY, D. M., Jr and L. C. ENTZEROTH (1985) Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. *Journal of Plankton Research*, **7**, 553–569.

CHUNG Y. and H. CRAIG (1980) ^{226}Ra in the Pacific Ocean. *Earth and Planetary Science Letters*, **49**, 267–292.

CLINE J. D. and F. A. RICHARDS (1972) Oxygen deficient conditions and nitrate reduction in the eastern tropical North Pacific Ocean. *Limnology and Oceanography*, **17**, 885–900.

CLINE J. D. and I. R. KAPLAN (1975) Isotopic fractionation of dissolved nitrate during denitrification in the eastern tropical Pacific Ocean. *Marine Chemistry*, **3**, 271–299.

DEUSER W. G. and E. H. ROSS (1980) Seasonal change in the flux of organic carbon to the deep Sargasso Sea. *Nature*, **283**, 364–365.

DUGDALE R. C. and J. J. GOERING (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography*, **12**, 196–206.

EPPLEY R. W. and B. J. PETERSON (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677–680.

EPPLEY R. W., E. H. RENGER and W. G. HARRISON (1979) Nitrate and phytoplankton production in southern California coastal waters. *Limnology and Oceanography*, **24**, 483–494.

FIADEIRO M. E. and H. CRAIG (1978) Three-dimensional modeling of tracers in the deep Pacific Ocean: I. Salinity and oxygen. *Journal of Marine Research*, **36**, 323–355.

GARDNER W. D. (1977) Incomplete extraction of rapidly settling particles from water samplers. *Limnology and Oceanography*, **22**, 764–768.

GORDON D. C., Jr (1977) Variability of particulate organic carbon and nitrogen along the Halifax–Bermuda section. *Deep-Sea Research*, **24**, 257–270.

HATTORI A., editor (1979) *Preliminary Report of the* Hakuho Maru *Cruise KH-78-3*. Ocean Research Institute, University of Tokyo, 87 pp.

HATTORI A., editor (in press) *Preliminary Report of the* Hakuho-Maru *Cruises KH-83-3 and KH-85-2*. Ocean Research Institute, University of Tokyo.

HOERING T. C. and H. T. FORD (1960) The isotope effect in the fixation of nitrogen by *Azotobacter*. *Journal of the American Chemical Society*, **82**, 376–378.

ISEKI K. (1981) Vertical transport of particulate organic matter in the deep Bering Sea and Gulf of Alaska. *Journal of the Oceanographical Society of Japan*, **37**, 101–110.

JAPAN METEOROLOGICAL AGENCY (1970) *Manual of oceanographic observations*. The Oceanographical Society of Japan, Tokyo, 427 pp.

KAPLAN W. A. (1983) Nitrification. In: *Nitrogen in the marine environment*, E. J. CARPENTER and D. G. CAPONE, editors, Academic Press, New York, pp. 139–190.

KARL D. M., G. A. KNAUER, J. H. MARTIN and B. B. WARD (1984) Bacterial chemolithotrophy in the ocean is associated with sinking particles. *Nature*, **309**, 54–56.

KING F. D. and A. H. DEVOL (1979) Estimates of vertical eddy diffusion through the thermocline from phytoplankton nitrate uptake rates in the mixed layer of the Eastern Tropical Pacific. *Limnology and Oceanography*, **24**, 645–651.

LAL D. (1977) The oceanic microcosm of particles. *Science*, **198**, 997–1008.

LIU K.-K. (1979) Geochemistry of inorganic nitrogen compounds in two marine environments; the Santa Barbara Basin and the ocean off Peru. Thesis, University of California, Los Angeles, 354 pp.

LORENZEN C. J., N. A. WELSCHMEYER, A. E. COPPING and M. VERNET (1983) Sinking rates of organic particles. *Limnology and Oceanography*, **28**, 766–769.

MACKO S. A. and M. L. F. ESTEP (1983) Microbial alternation of stable nitrogen and carbon isotopic composition of organic matter. *Annual Report of the Director, Geophysical Laboratory, Carnegie Institution, 1982–1983*, pp. 394–398.

MAGUE T. H., N. M. WEARE and O. HOLM-HANSEN (1974) Nitrogen fixation in the North Pacific Ocean. *Marine Biology*, **24**, 109–119.

MAGUE T. H., F. C. MAGUE and O. HOLM-HANSEN (1977) Physiology and chemical composition of nitrogen fixing phytoplankton in the central North Pacific Ocean. *Marine Biology*, **41**, 213–227.

MARIOTTI A., J. C. GERMON, P. HUBERT, P. KAISER, R. LETOLLE, A. TARDIEUX and P. TARDIEUX (1981) Experimental determination of nitrogen kinetic isotope fractionation: some principles; illustration for the denitrification and nitrification processes. *Plant and Soil*, **62**, 413–430.

MCCAVE I. N. (1975) Vertical flux of particles in the ocean. *Deep-Sea Research*, **22**, 491–502.

MINAGAWA M. and E. WADA (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et Cosmochimica Acta*, **48**, 1135–1140.

MIYAKE Y. and E. WADA (1971) The isotope effect on the nitrogen in biochemical oxidation–reduction reactions. *Records of Oceanographic Works in Japan*, **11**, 1–6.

MULLIN M. M., G. H. RAU and R. W. EPPLEY (1984) Stable nitrogen isotopes in zooplankton: Some geographic and temporal variations in the North Pacific. *Limnology and Oceanography*, **29**, 1267–1273.

MURPHY J. and J. P. RILEY (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31–36.

REID J. L. (1973) *Northwest Pacific Ocean waters in winter*. The Johns Hopkins Oceanographic Studies, No. 5. The Johns Hopkins University Press, Baltimore, 96 pp.

ROMANKEVICH E. A. (1984) *Geochemistry of organic matter in the ocean*. Springer-Verlag, Berlin, 334 pp.

SACKETT W. M. (1978) Suspended matter in sea-water. In: *Chemical oceanography*, Vol. 7. J. P. RILEY and R. CHESTER, editors, Academic Press, London, pp. 127–172.

SAINO T. (1977) Biological nitrogen fixation in the ocean with emphasis on the nitrogen fixing blue-green alga, *Trichodesmium*, and its significance in the nitrogen cycling in the low latitude sea areas. Thesis, University of Tokyo, 153 pp.

SAINO T. and A. HATTORI (1980a) ^{15}N natural abundance in oceanic suspended particulate matter. *Nature*, **283**, 752–754.

SAINO T. and A. HATTORI (1980b) Nitrogen fixation by *Trichodesmium* and its significance in nitrogen cycling in the Kuroshio area and adjacent waters. In: *The Kuroshio IV*, A. Y. TAKENOUTI, editor, Saikon Publishing, Tokyo, pp. 697–709.

SAINO T. and A. HATTORI (1985) Variation of ^{15}N natural abundance of suspended organic matter in shallow oceanic water. In: *Marine and estuarine geochemistry*, A. C. SIGLEO and A. HATTORI, editors, Lewis Publishers, Chelsea, MI, pp. 1–13.

SAINO T., H. OTOBE, E. WADA and A. HATTORI (1983) Subsurface ammonium maximum in the northern North Pacific and the Bering Sea in summer. *Deep-Sea Research*, **30**, 1157–1171.

SHANKS A. L. and J. D. TRENT (1980) Marine snow: sinking rates and potential role for vertical flux. *Deep-Sea Research*, **27**, 137–144.

SILVER M. W., A. SHANKS and J. TRENT (1978) Marine snow: microplankton habitat and source of small scale patchiness in pelagic populations. *Science*, **201**, 371–373.

SIMPSON W. R. (1982) Particulate matter in the oceans–sampling methods, concentration, size distribution and particle dynamics. *Oceanography and Marine Biology Annual Review*, **20**, 119–172.

STOMMEL H. (1958) The Abyssal circulation. *Deep-Sea Research*, **5**, 80–82.

TANOUE E. and N. HANDA (1979) Distribution of particulate organic carbon and nitrogen in the Bering Sea and the northern North Pacific Ocean. *Journal of the Oceanographical Society of Japan*, **35**, 47–62.

TANOUE E. and N. HANDA (1980) Vertical transport of organic materials in the northern North Pacific as determined by sediment trap experiments. Part 1. Fatty acid composition. *Journal of the Oceanographical Society of Japan*, **36**, 231–245.

UEMATSU M., R. A. DUCE, J. M. PROSPERO, L. CHEN, J. T. MERRILL and R. L. MCDONALD (1983) Transport of mineral aerosol from Asia over the North Pacific Ocean. *Journal of Geophysical Research*, **88**, 5343–5352.

UDA M. (1963) Oceanography of the subarctic Pacific Ocean. *Journal of the Fishery Research Board of Canada*, **20**, 119–179.

VENDRICK E. L. (1974) The distribution and significance of *Richelia intracellularis* Schmidt in the North Pacific Central Gyre. *Limnology and Oceanography*, **19**, 437–445.

WADA E. (1980) Nitrogen isotope fractionation and its significance in biogeochemical processes occurring in marine environments. In: *Isotope marine chemistry*, E. D. GOLDBERG, Y. HORIBE and K. SARUHASHI, editors, Uchida Rokakuho, Tokyo, pp. 375–398.

WADA E. and A. HATTORI (1976) Natural abundance of ^{15}N in particulate organic matter in the North Pacific Ocean. *Geochimica et Cosmochimica Acta*, **40**, 249–251.

WADA E. and A. HATTORI (1978) Nitrogen isotope effects in the assimilation of inorganic nitrogenous compounds by marine diatoms. *Geomicrobiology Journal*, **1**, 85–101.

WADA E., T. TSUJI, T. SAINO and A. HATTORI (1977) A simple procedure for mass spectrometric microanalysis of ^{15}N in particulate organic matter with special reference to ^{15}N-tracer experiments. *Analytical Biochemistry*, **80**, 312–318.

WAKEHAM S. G., C. LEE, J. W. FARRINGTON and R. B. GAGOSIAN (1984) Biogeochemistry of particulate organic matter in the oceans: results from sediment trap experiments. *Deep-Sea Research*, **31**, 509–528.

WIEBE P. H., S. H. BOYD and C. WINGET (1976) Particulate matter sinking to the deep-sea floor at 2000 m in the Tongue of the Ocean, Bahamas, with a description of a new sediment trap. *Journal of Marine Research*, **34**, 341–354.

WOOD E. D., F. A. ARMSTRONG and F. A. RICHARDS (1967) Determination of nitrate in sea water by cadmium-copper reduction to nitrite. *Journal of the Marine Biological Association of the United Kingdom*, **47**, 23–31.

YOSHIDA N., A. HATTORI, T. SAINO, S. MATSUO and E. WADA (1984) $^{15}N/^{14}N$ ratio of dissolved N_2O in the eastern tropical Pacific Ocean. *Nature*, **307**, 442–444.