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Particulate amino acids in the sea: Effects of primary productivity and biological decomposition

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ABSTRACT

We measured the flux of amino acids associated with sinking particles collected by sediment traps at two Pacific Ocean sites. These results were compared with results from six other sites where we and others have measured amino acid fluxes. This comparison shows that the flux of amino acids on sinking particles is related to primary productivity. This relationship exists in spite of differences in the oceanic regimes sampled and in the sediment traps, bactericides, and amino acid analysis techniques used. The amount of particulate amino acids leaving the euphotic zone in areas of higher productivity is a higher proportion of the primary production than in less productive areas. And, a larger amount of particulate amino acids reaches deeper waters in more productive areas. However, the particulate amino acids leaving the euphotic zone decompose faster with depth in more productive areas. Faster decomposition below the surface waters in areas of high productivity suggests that (1) decomposition of particulate organic matter may be mediated more by zooplankton and less by microbial processes than in areas of lower productivity, or (2) phytoplankton growing in more productive areas are more easily remineralized than those growing in less productive areas.

1. Introduction

Particles in sea water can originate from a variety of sources. The largest of these sources is the formation of phytoplankton biomass by photosynthetic processes in the euphotic zone. Secondary consumers also produce living particulate biomass while recycling and dissipating the carbon, nitrogen and energy present in the primary producers. Resuspension of sediments, terrestrial inputs from rivers, and aeolian transport all add to the particulate load of sea water. The distribution of particulate organic matter in the open ocean is largely a function of *in-situ* production, which occurs mainly through photosynthetic processes in the euphotic zone, and heterotrophic decomposition, which occurs both in the euphotic zone and deeper in the water column. The composition of organic matter present in sinking and suspended particles varies with depth in the water column and with geographical location and can show the influence of individual types of organisms and the processes affecting those organisms (see Wakeham *et al.*, 1984 and references therein).

The balance between production and decomposition of sinking particulate organic

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matter determines the amount of material reaching the sea floor. Using sediment trap data, Suess (1980) has shown a correlation between organic carbon flux at any depth in the oceanic water column and surface primary production. Similar relationships have been shown to exist in coastal areas (Hargrave, 1980). Müller and Suess (1979) suggested that the rate of preservation of organic carbon in sediments is proportional to organic sedimentation rate, that is, the flux of organic matter reaching the sea floor. Proportionately more preservation (or proportionately less decomposition) was evident in sediments of higher accumulation rate. Similar processes are thought to occur in the water column. Most organic matter produced in the euphotic zone of the open ocean is remineralized in the upper several hundred meters (Menzel and Ryther, 1968). However, the proportion of organic matter which is remineralized in the upper several hundred meters varies with the surface productivity. Bishop *et al.* (1978) found that a smaller percentage of the organic matter production was decomposed in the upper 400 m of more productive regions (90%) than in less productive regions (99%) of the southeast Atlantic Ocean. In shallow coastal areas of very high productivity, as much as 30–40% of annual water column production may be transported to the sea floor (Steele and Baird, 1972; Davies, 1975).

In order to test these concepts further, we investigated the relationship between surface productivity and the flux of a major component of the organic carbon flux, the amino acids. Amino acids, the building blocks of protein molecules, can make up 25–50% of the particulate organic carbon in surface waters. By sinking in particles to the sea floor, amino acids can provide energy and nitrogen to benthic organisms. However, since they are more labile than other carbon compounds present in particulate matter, they become a smaller percentage of total particulate organic carbon with depth (Siezen and Mague, 1978; Lee and Cronin, 1982; Wefer *et al.*, 1982; Lee *et al.*, 1983; Wakeham *et al.*, 1984a; Ittekkot *et al.*, 1984a,b). We report here new data on fluxes of individual amino acids from sediment trap experiments 500 km off Mexico and 100 km off California. We then compare these fluxes with our previously published data from the Peru upwelling zones, the Panama Basin, and the central Pacific, as well as with data taken near Bermuda and from the Drake Passage and Panama Basin published by other laboratories (Table 1). These data allow a comparison of amino acid flux and define the relationship between decomposition and surface primary productivity. We also use relative concentrations of individual amino acids to illustrate qualitative changes in organic matter as a result of decomposition processes.

2. Methods

Suspended and sinking particles were collected from a variety of depths and sites (Table 1). Details of sample collection and handling for several of the stations (Peru, PARFLUX P, STIE) have been previously published. The Peru data were collected during February and March, 1978, in the 15S upwelling area using cylindrical,

Table 1. Sediment trap sampling and handling procedure.

Location sampled	Sediment trap used	Poison used	Time of deployment	Depth deployed (m)	Further description of traps and sampling
Peru*	Staresinic cylinder	None	6–12 hours	14–52	Lee and Cronin, 1982; Staresinic, 1978
Mexico* (VERTEX II)	Moss Landing Marine Lab cylinder	$CHCl_3$ or H_2CO	3 weeks	50–2000	(see Methods section) Martin *et al.*, 1983
California* (VERTEX I)	MLML cylinder	$CHCl_3$	2 weeks	50–2000	(see Methods section) Martin *et al.*, 1983
Panama Basin (STIE)*	Jannasch time-series cylinder	NaN_3	16 weeks	1200	Lee *et al.*, 1983 Honjo *et al.*, 1982
(PARFLUX)***	Honjo cone	NaN_3	8 weeks	890–3560	Ittekkot *et al.*, 1984a
Bermuda***	Deuser cone	None	8 weeks	3200	Ittekkot *et al.*, 1984b Deuser *et al.*, 1981
North Pacific* (PARFLUX P)	Honjo cone	NaN_3	12 weeks	400–5000	Wakeham *et al.*, 1984a; Honjo, 1980
Drake Passage**	Zeitzschel cone	$CHCl_3$ and $HgCl_2$	7 weeks	970–2500	Wefer *et al.*, 1982; Zeitzschel *et al.*, 1978

*analyzed by fluorescence HPLC in Woods Hole
**analyzed by amino acid analyzer in Kiel
***analyzed by amino acid analyzer in Hamburg

free-floating traps (Lee and Cronin, 1982). PARFLUX P samples were collected in the North Pacific using large, moored cone sediment traps (Wakeham *et al.*, 1984a). The Panama Basin data were collected as part of STIE, a Sediment Trap Intercomparison Experiment (Lee *et al.*, 1983).

The VERTEX samples from the coasts of Mexico and California were collected as part of the Vertical Transport and Exchange program. Both experiments used a free-floating MULTITRAP array which allows 12 small cylinders (0.0039 m^2 collection area) to be placed at each depth (Knauer *et al.*, 1979). The VERTEX I array was deployed about 100 km off Point Sur, California (35°45'N, 123°45'W) for 13 days during August and September, 1980. Further discussion of this site is presented in Martin *et al.* (1983), Broenkow and Greene (1981), and Karl and Knauer (1984). We collected trap material from nine depths as well as suspended particles from 16 depths at the VERTEX I site. About 16 cm of chloroform was placed in the bottom of each sediment trap cylinder used for amino acid collection to minimize decomposition of organic matter during the 13-day collection period. After recovery of the traps, half of the water was siphoned from the top of the cylinder and discarded. The remaining water and the chloroform were filtered through combusted Gelman AE glass-fiber filters and the retained particles returned frozen to Woods Hole for analysis. The chloroform was evaporated and the residue analyzed for amino acids as discussed later. The amount of amino acid extracted into the chloroform was less than 0.1% that of the particulate material, even in the deepest traps. Suspended particles were collected by pressure (<0.7 atm N_2) filtration of water caught in Niskin bottles through combusted Gelman AE glass-fiber filters, which were returned frozen to Woods Hole.

The VERTEX II array was deployed off Manzanillo, Mexico (18N, 108W) for 22 days during October and November, 1981. This study site is an area of merging surface waters from the California Current, the Equatorial Countercurrent, and the Gulf of California (Broenkow and Krenz, 1982; Wyrtki, 1967) and is characterized by a strong oxygen minimum zone extending from 100 to 800 m (Goering, 1968; Cline and Richards, 1972). Duplicate trap samples recovered from nine depths were preserved with either formalin in a dense salt solution (Knauer *et al.*, 1979) or chloroform. Samples were filtered and frozen as described above for VERTEX I. Suspended particles were filtered from Niskin bottles and frozen as described above.

Suspended and trap particles were hydrolyzed with 6N HCl for 19 hours to free amino acids in peptide bonds (protein) or adsorbed onto the particles (Lee and Cronin, 1982). Free amino acids were then measured by high-performance liquid chromatography using a modification (Jones *et al.*, 1981) of the Lindroth and Mopper (1979) fluorescent o-phthaldialdehyde derivative technique for sea water. Analytical replication of subsamples of the acid hydrolyzate was ±5%.

Estimates of primary productivity for the nine sites were taken from various sources. Productivity was measured at the time of trap deployment for most of the sites: VERTEX I (Karl and Knauer, 1984), VERTEX II (Knauer, pers. comm.), Peru

Table 2. Amino acid flux (μmol amino acid/m^2 day) in chloroform-poisoned traps collected at VERTEX I California site.

	Depth (m)								
	50	100	200	300	500	600	700	1700	1950
asp	85	150	59	34	30	7.3	6.2	9.3	7.3
glu	23	51	14	7.8	7.9	2.5	1.4	2.8	1.8
ser	19	36	99	15	19	3.1	3.2	4.2	3.6
thr + gly	47	43	32	24	27	5.9	4.6	6.8	4.8
arg	4.6	9.0	2.9	1.4	2.7	0.8	0.2	0.6	0.3
β-ala	1.1	5.0	0.3	0.6	0.1	0.7	0.1	0.1	0.1
ala	21	41	14	7.9	11	2.5	1.6	3.0	1.8
γ-aba	5.2	11	3.5	1.6	0.5	1.0	0.3	0.6	0.4
met	6.5	7.0	7.9	7.4	0.9	2.8	2.4	0.9	2.0
val	16	30	9.3	4.6	8.0	2.7	1.1	1.3	1.1
phe	13	22	6.9	3.2	6.0	2.1	0.4	1.0	0.8
ile	17	30	10	5.7	0.4	2.9	1.1	1.7	1.2
leu	23	41	13	5.9	0.4	4.3	1.1	2.3	1.4
orn	3.1	4.8	4.7	4.8	6.2	2.6	1.5	1.7	1.2
lys	29	42	12	7.6	0.6	5.9	1.0	3.2	2.2
TOTAL	320	520	290	130	120	47	27	40	30
TOTAL (mg/m^{2}day)	40	66	35	16	14	6.0	3.3	4.9	3.7

upwelling area (Staresinic, 1978), Panama Basin (Marra *et al.*, 1984), and the Drake Passage (Wefer *et al.*, 1982). Productivity was assumed to be the same for the Panama Basin PARFLUX samples of Ittekkot *et al.* (1984b) in 1980 as for the 1979 STIE experiment. Literature values of primary productivity were used for the Sargasso Sea near Bermuda (Deuser *et al.*, 1981) and for the oligotrophic North Pacific (Eppley *et al.*, 1973) since measurements were not made at the time of trap deployment.

3. Results and discussion

a. Distribution of amino acids in particles. The concentrations and fluxes of individual amino acids in suspended and sinking particles are shown in Tables 2 and 3 for VERTEX I and Tables 4, 5, and 6 for VERTEX II. At both stations, the total amount of amino acid generally decreases with depth. Suspended particles show greater variation in both concentration and composition than the sinking particles collected in sediment traps, probably due in part to the time-integration during sediment-trap sampling as compared to the instantaneous nature of suspended particle sampling. Sediment traps average much of the temporal and spatial variability present in the water column. Both suspended and sinking particles have gross amino acid compositions similar to those reported by Degens (1970) and Siezen and Mague (1978) for suspended particulate organic matter.

Aspartic acid, glycine, and serine are the most abundant amino acids at all depths,

Table 3. Concentration (nmol/liter) of suspended particulate amino acids from the VERTEX I California site.

	Depth (m)															
	1	10	30	50	100	200	300	400	500	600	700	900	1100	1400	1700	2000
asp	30	69	61	33	35	28	11	58	9.9	14	12	21	26	10.4	21	13
glu	19	37	17	16	12	9.0	5.9	17	3.3	3.5	3.4	5.3	0.6	3.3	0.6	3.5
ser	16	24	11	15	15	9.0	10	19	3.8	5.8	3.9	22	9.7	4.5	7.1	5.3
thr + gly	39	34	32	18	17	13	8.7	28	5.3	4.3	6.9	22	13	6.8	11	5.1
arg	5.0	22	12	5.8	4.1	2.8	3.3	4.2	1.0	1.0	0.9	3.2	2.2	0.9	2.0	1.0
β-ala	5.8	11	0.9	1.9	1.2	0.5	1.0	0.9	—	—	0.1	0.6	—	0.1	—	—
ala	28	32	22	15	10	7.4	5.8	9.4	2.1	3.9	2.3	10	6.6	2.4	5.7	2.7
γ-aba	—*	—	3.8	2.0	—	—	—	4.7	0.1	—	0.7	1.3	—	0.7	—	0.9
val	14	29	12	9.1	5.3	4.4	4.1	5.8	1.2	0.9	2.8	2.9	2.5	1.4	1.8	1.2
phe	8.4	17	11	7.9	4.9	4.2	2.6	6.1	1.2	1.3	2.2	3.3	3.1	1.2	2.5	1.3
ile	9.6	18	11	18	5.0	4.2	3.4	7.8	1.0	1.0	2.4	3.7	2.5	1.5	2.3	1.3
leu	17	30	17	13	9.1	8.2	5.7	12	1.9	1.9	3.3	5.2	5.0	2.4	4.1	3.1
orn	3.3	6.8	0.2	1.8	0.9	2.0	2.4	8.1	0.6	2.7	0.9	0.9	0.2	1.3	1.0	1.2
lys	12	4.7	12	3.7	5.2	1.8	0.8	4.7	0.1	0.3	2.0	5.4	3.4	3.1	2.1	0.7
TOTAL	210	340	230	150	120	97	69	190	32	41	45	110	76	41	63	40
TOTAL (μg/l)	25	43	28	18	15	12	8.3	23	4.0	5.0	5.6	13	9.2	5.0	7.6	4.9

*A dash (—) indicates concentrations below the detection limit.

Table 4. Amino acid flux (μmol amino acid/m^2 day) in formalin-poisoned traps collected at VERTEX II Mexico site.

	Depth (m)								
	30	110	200	400	700	800	900	1400	1950
asp	1400	620	470	190	140	26	83	16	6.2
glu	1900	590	420	140	110	18	75	14	5.4
ser	710	410	150	89	54	12	28	6.7	2.8
thr + gly	1800	740	380	190	150	26	94	16	3.1
arg	1400	270	170	50	49	18	32	6.9	2.4
β-ala	3.0	0.2	2.0	0.1	0.1	0.02	0.02	0.01	0.01
ala	1100	470	330	160	88	17	49	9.0	3.7
tyr	1.7	11	0.1	0.1	0.1	1.1	0.9	0.1	0.5
val	3100	650	260	150	120	20	72	15	5.5
phe	2000	260	120	120	48	9.7	30	4.8	2.9
ile	790	210	91	57	66	11	39	8.4	3.1
leu	1600	240	240	110	66	9.9	37	7.5	6.3
orn	110	200	240	36	2.6	0.1	0.1	0.5	2.2
lys	1400	270	270	42	50	0.2	23	5.1	0.5
TOTAL	17300	4900	3100	1300	950	169	560	110	42
TOTAL (mg/m^2 day)	2300	610	390	160	120	21	70	14	5.7

Table 5. Amino acid flux (μmole amino acid/m^2 day) in chloroform-poisoned traps collected at VERTEX II Mexico site.

	Depth (m)								
	30	110	200	400	700	800	900	1400	1950
asp	210	35	21	13	20	8.1	9.4	8.0	3.4
glu	250	39	25	11	23	6.8	8.6	7.5	2.2
ser	160	21	9.8	5.3	12	3.1	4.2	2.9	1.7
thr + gly	160	22	14	8.9	16	4.1	6.4	6.6	2.5
arg	270	29	10	5.3	14	3.2	4.1	3.0	1.1
β-ala	—*	0.4	—	0.1	0.01	—	0.01	0.02	—
ala	270	35	17	8.5	22	4.8	6.6	4.9	1.8
tyr	1.2	—	—	1.9	5.9	1.2	1.7	1.0	0.4
val	580	13	35	14	34	8.5	11	9.7	2.5
phe	350	7.8	20	6.2	14	3.5	5.2	3.1	0.8
ile	180	5.3	24	7.3	19	4.8	6.1	5.4	1.3
leu	340	11	24	5.0	17	4.4	5.3	4.9	1.3
orn	21	15	25	8.0	—	1.9	0.9	1.1	0.7
lys	290	1.6	24	2.1	8.2	1.0	1.8	0.6	0.7
TOTAL	3100	240	250	97	210	55	71	59	20
TOTAL (mg/m^{2}day)	390	29	31	12	26	6.9	8.9	7.4	2.5

*A dash(—) indicates concentrations below the detection limit.

Table 6. Concentration (nmol/liter) of suspended particulate amino acids from the VERTEX II Mexico site.

	Depth (m)									
	50	110	200	300	400	500	750	1000	1250	2000
asp	33	9.4	4.8	7.5	2.9	2.7	3.4	3.5	2.0	0.7
glu	38	11	5.1	6.5	2.5	3.2	4.7	3.2	2.7	0.3
ser	29	11	7.6	6.5	2.4	3.9	5.7	4.3	3.9	1.0
thr + gly	41	13	6.8	5.5	0.8	3.5	6.5	2.5	2.5	0.6
arg	9.4	3.3	1.4	1.8	0.7	1.1	1.6	0.3	0.2	0.1
β-ala	4.1	—*	—	—	—	—	0.2	0.1	—	0.1
ala	40	9.2	2.8	5.0	1.4	2.5	2.6	0.6	1.3	0.7
tyr	4.9	1.5	0.2	0.5	—	0.1	0.1	—	—	—
val	26	8.0	3.5	5.0	1.3	2.1	1.8	0.6	1.2	0.4
phe	6.9	4.3	2.0	1.3	0.6	1.4	1.0	0.1	0.2	—
ile	9.3	3.0	1.3	1.7	0.7	0.8	0.9	0.5	0.2	0.3
leu	16	5.0	1.9	2.6	1.2	1.6	2.8	0.4	0.4	0.3
orn	2.8	—	—	—	1.4	—	—	0.1	0.1	0.2
lys	12	4.1	—	5.1	1.6	1.9	1.0	0.2	0.1	0.2
TOTAL	270	83	37	49	18	25	32	16	15	4.9
TOTAL (μg/l)	33	10	4.5	6.1	2.3	3.1	3.9	2.0	1.7	0.6

*A dash (—) indicates concentrations below the detection limit.

while glutamic acid is also prominent in surface waters. Siezen and Mague (1978) found glycine and serine to increase more with depth relative to other amino acids. We also found this trend, but more for serine than for glycine, and more at VERTEX II than VERTEX I. The average relative mole % of serine and glycine (plus threonine) was higher in the suspended than the sinking particles, and more disparate at VERTEX II than VERTEX I (Table 7). Siezen and Mague (1978) suggested that the presence of serine and glycine on particles found deeper in the water column might be due to the persistence of a protein-silica complex in diatom cell walls proposed by Hecky *et al.* (1973). Two nonprotein amino acids, β-alanine and γ-aminobutyric acid, were present in both the suspended and sinking particles. As reported earlier (Wakeham *et al.*, 1984; Lee *et al.*, 1983), these amino acids do not increase in relative concentration with depth. Therefore, formation on sinking particles probably does not account for the predominance of these two compounds in deep-sea sediments.

Degens (1970) suggested that the presence of ornithine in particulate matter indicated that dead plankton cells in the particles had begun to decompose. Siezen and Mague (1978) found no ornithine in suspended particles from oceanic and coastal waters of the Pacific. Ittekkot *et al.* (1984b) found very little ornithine in Panama Basin sediment-trap samples. However, we found ornithine in both suspended and sinking particles at most depths. At both VERTEX stations, there was an inverse relationship between the relative molar concentration of ornithine and the oxygen

Table 7. Average mol% values for serine and glycine + threonine for VERTEX I and II suspended and sinking particles.

	mol% ser	mol% gly + thr
VERTEX I		
suspended	11	15
trap	10*	14
VERTEX II		
suspended**	18	15
trap (chloroform)	6.0	8.6

*200 m trap deleted from this average.

**The mol% ser was lower than mol% gly in samples taken above 200 m, but mol% ser increased more rapidly with depth.

concentration (Fig. 1). This relationship is more clear at the VERTEX II Mexico site where the oxygen minimum is well defined.

The inverse relation between ornithine and oxygen is most likely microbial in origin. Wakeham *et al.* (1984) observed alterations in particulate organic matter due to decomposition in the oxygen minimum at this same location; they noted the unusual presence of sterenes, unsaturated steroidal hydrocarbons, which are microbial decomposition products of sterols. Since more decomposition occurs in the oxygen minimum, more ornithine may be produced in sinking particles. Arginine, one of the major precursors of ornithine, shows no decrease in relative concentration in the oxygen minimum but does decrease rapidly in absolute concentration and thus could serve as a source of ornithine. Mopper and Lindroth (1982) observed an increase in dissolved ornithine with increasing depth and decreasing oxygen content in the Baltic Sea, which they attributed to a depth-related increase in heterotrophic activity. In addition to being a product of microbial decomposition, ornithine may also be a constituent of microorganisms which inhabit low oxygen zones. Holm-Hansen and Lewin (1965) reported the presence of bound ornithine in some marine bacteria and blue-green algae. Garfield *et al.* (1983) reported the occurrence of high microbial activity associated with a particle maximum at 200 m in the same area as VERTEX II. Their geographically more extensive survey of the site off Mexico suggested an advective origin for the particle maximum and associated chemical and biological variations. Horizontal advection of water depleted in oxygen by microbial activity could be a source of particulate ornithine produced by microbes at another location. Advected particles might also be rich in ornithine-containing microbes.

Although the relative composition of particulate amino acids in the formalin- and chloroform-poisoned "replicate" traps at VERTEX II were similar, a very obvious difference exists between the amount present in the traps. The traps poisoned with formalin collected 2–10 times more amino acids than the traps poisoned with chloroform. This discrepancy may be due to a difference in the number of living

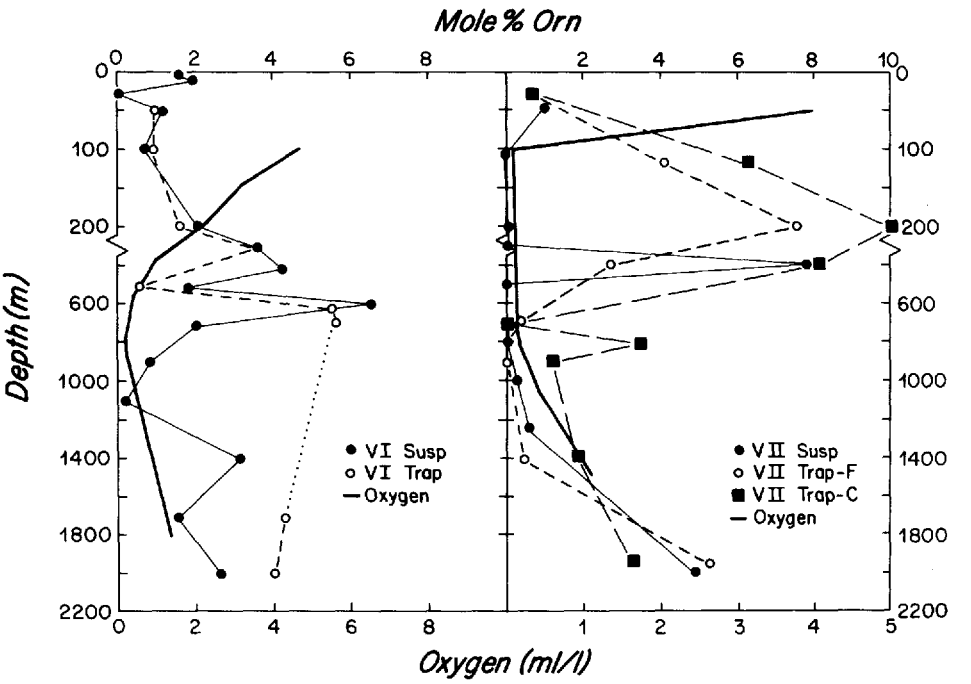

Figure 1. Relative molar concentration of ornithine as a function of depth in both suspended and sinking particles at VERTEX I (a) and VERTEX II (b). Oxygen concentrations were those measured at the time of the sediment trap experiments (Broenkow and Krenz, 1982; Broenkow and Greene, 1981).

organisms, or "swimmers", which were collected by the two traps. In the chloroform-poisoned traps, the chloroform sits in the bottom of the glass cylinder and forms a distinct interface with the water. In fact, much of the particulate material is lying at this interface when the trap is recovered. The overlying water contains some dissolved chloroform, as determined by smell. In the formalin-poisoned traps, the formalin is dissolved in a salt gradient and probably permeates the water in the trap more completely. Therefore, an organism which is attracted to the sediment trap array and which swims a short distance into a trap might be more likely to come into contact with formalin than with chloroform. Thus, the formalin traps could collect more swimmers than the chloroform traps. Organisms which may have swum into the traps were not removed prior to analysis because of the difficulty we have in distinguishing between swimmers and only slightly decomposed organisms which fell dead into the traps.

We can estimate the extent to which swimmers may have contributed to material caught in the traps (Table 8). Organic carbon flux was measured in traps deployed at the VERTEX stations (Karl and Knauer, 1984; Knauer, pers. comm.). Swimmers were manually removed from the filters for these analyses. Fluxes of amino acids in the

Table 8. Weight ratio of amino acid carbon to organic carbon* in suspended and sinking particles.

	VERTEX I		VERTEX II		
Depth	Suspended (g aaC/g orgC)	Trap (g aaC/g org C)	Suspended (g aaC/g org C)	Chloroform trap (g aaC/g org C)	Formalin trap
50		0.08	0.27		
100	0.33	0.39			
110			0.23	0.34	7.1
200	0.36	0.35	0.11	0.59	7.4
300	0.53	0.23	0.18		
400	0.93		0.08	0.37	5.0
500	0.24	0.26	0.14		
600	0.25	0.12			
700	0.31	0.09		1.6	7.3
750			0.20		
800				0.42	1.3
900	0.77			0.54	4.2
1000			0.08		
1100	0.37				
1250			0.08		
1400	0.21			0.73	1.4
1700	0.34	0.15			
1950		0.11		0.24	0.53
2000	0.32		0.03		

*Organic carbon values are from Karl and Knauer (1984) and Knauer (pers. comm.). Swimmers were manually removed from trap samples before organic carbon measurements but not before amino acid measurements. Values of organic carbon in suspended material were estimated for some depths since amino acids and organic carbon samples were not always taken at the same depth. Sampling for amino acids and organic carbon were about two weeks apart for both VERTEX cruises.

chloroform-poisoned traps were about 30–40% of the organic carbon flux (measured with swimmers removed), only slightly higher than we have found in other areas (Lee and Cronin, 1982; Wakeham *et al.*, 1984). However, the amino-acid carbon fluxes calculated for the shallow formalin-poisoned traps were over seven times higher than the total organic carbon flux (again measured with swimmers removed). Deeper in the water column (2000 m), half of the carbon flux could still be attributed to the amino acids. The large ratios of amino-acid carbon to organic carbon in the formalin traps likely reflects the contribution from unpicked swimmers in the amino acid traps, especially since this ratio is lower where swimmer abundances are lower. Similar large contributions from swimmers in formalin-poisoned sediment-trap material have been observed previously (Knauer and Martin, 1982; Knauer *et al.*, 1984). Some of the

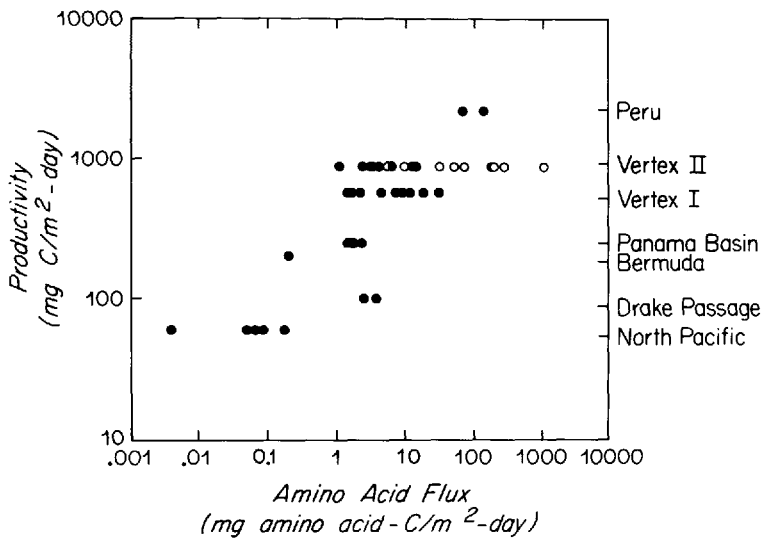

Figure 2. Relationship between the flux of amino acids on large particles and the primary productivity at seven locations, coastal Peru upwelling area, coastal California off Point Sur, Eastern Tropical North Pacific off Mexico, Panama Basin, Sargasso Sea near Bermuda, Drake Passage, Antarctica, and central North Pacific. Each point reflects the flux at a particular depth measured and not variability in sampling or analysis. Open circles at VERTEX II are for formalin-poisoned trap fluxes which were not used in any correlation calculations. Flux usually decreased with depth, and the clusters of points usually show the more shallow depths towards the right and deeper depths towards the left. The correlation coefficient for the data shown using geometric linear regression is 0.83.

variation in the suspended particle data in Table 8 is probably due to samples for amino acids being collected about two weeks after the organic carbon samples. We saw considerable variation (±100%) in suspended-particle amino acid concentrations in samples taken from the same depth several days apart. This variation was always less in deeper waters.

b. Relationship between flux and productivity. The flux of particulate amino acids as measured by sediment traps can be compared for eight locations in the world oceans. Samples from the eight sites were obtained using very different methods of collection, preservation, handling, and analysis (Table 1). In spite of these considerable differences as well as the problems associated with the measurement of primary productivity (Peterson, 1980), there is a relationship between amino acid flux and the surface primary productivity for the sites (Fig. 2). Amino acid flux increases with productivity as a power function; for every 10-fold increase in productivity, the flux of amino acids increases by about 250-fold. Figure 2 shows the amino acid flux measured at every depth sampled at each of the eight sites. For each site, the different points are

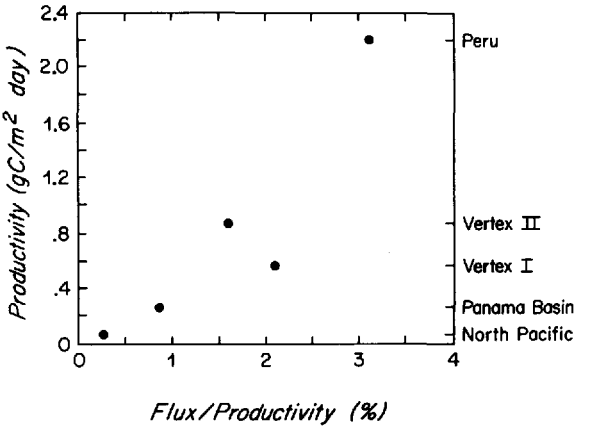

Figure 3. Relationship between productivity and the amount of material remaining undecomposed which passes out of the euphotic zone. F_{ED}/P is calculated as the ratio of flux in mg amino acid C m^{-2} day^{-1} to productivity in gC m^{-2} day^{-1}. Flux data are from 52 m for Peru, 200 m for VERTEX I, 200 m for VERTEX II, 380 m for North Pacific, and 890 m for Panama Basin.

individual depths, and the effect of depth is quite regular, with points to the right (higher flux) being surface samples and points to the left (lower flux) being deeper samples.

A relationship between particulate amino acid flux and primary production is not particularly surprising for a class of compounds synthesized by all organisms and used as a major structural component. This correlation has been seen with temporal variations in productivity as well as with the spatial variations shown in Figure 2. Ittekkot *et al.* (1984a,b) measured amino acid flux in sediment-trap material from the Sargasso Sea near Bermuda and from the Panama Basin. Amino acid flux peaked seasonally with the peak in surface production, just as Deuser *et al.* (1981) reported earlier for organic carbon.

From data in Figure 2, we can calculate the proportion of primary-produced amino acids which falls through the euphotic zone to deeper waters. The ratio of flux at any depth to primary productivity (F_z/P) represents the proportion of material produced in the surface waters which remains undecomposed and sinks past that depth. Figure 3 shows the relationship between productivity and F_{ED}/P (ED is the euphotic depth, which varies with location) calculated for the four stations for which flux data from just below the euphotic zone exist, and for the shallowest trap depth (890 m, Ittekkot *et al.*, 1984b) at the Panama Basin site. This graph shows that in areas of higher productivity, the amount of material falling out of the euphotic zone is a higher proportion of the primary production than in less productive areas.

The proportion of primary production sinking out of the euphotic zone as amino acids (the ratio F_{ED}/P shown in Fig. 3) can be compared to the "new" production

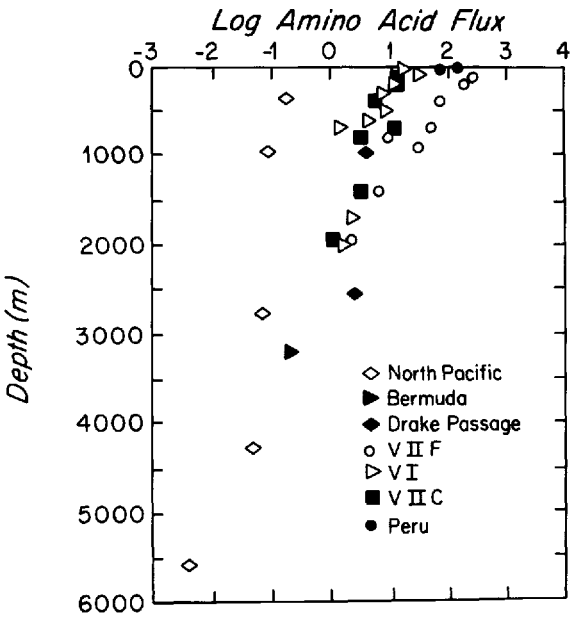

Figure 4. Particulate amino acid flux as a function of depth. Locations are the same as in Figure 2.

discussed by Eppley and Peterson (1979). New production is defined as primary production resulting from allochthonous nutrient inputs to the euphotic zone rather than from nutrients regenerated in the euphotic zone during the decomposition of organic matter. If the euphotic zone is not to become gradually depleted of particulate organic matter, the flux of organic matter out of the euphotic zone can only be as much as is "newly" produced. Eppley and Peterson showed that new production, and thus the extent of nutrient recycling within the euphotic zones, varies regionally with the total production rate. New production, calculated from the assimilation of ^{15}N-labelled nitrate and ammonium, increases asymptotically with increasing productivity until new production is about half of total production. The proportion of primary productivity sinking out of the euphotic zone as amino acids also increases (asymptotically?) with productivity (Fig. 3). The similarity of the relationships of new production and downward flux of amino acids with productivity suggests that inorganic nitrogen recycling and amino acid decomposition are tightly coupled. This might be expected since amino acids usually make up 40–60% of the organic nitrogen in sinking particles.

Areas of higher productivity usually have shallower euphotic zones, at least partially because the plankton reduce the amount of light which can pass through the water (Parsons *et al.*, 1977). An increase in productivity which reduces the depth of the euphotic zone thus reduces the depth (time) available for particulate decomposition and concomitant nutrient recycling within the euphotic zone. More productive areas

Table 9. First-order decay rate constants (k) calculated from fitting amino acid flux data from below the euphotic zone to the exponential function $F/F_o = e^{-kz}$.

Station	k (m^{-1})	Correlation coefficient[a]	Productivity ($mgC\ m^{-2}\ day^{-1}$)	F/F_o evaluated at z = bottom[c]
Peru	0.018	—[b]	2200	$1.2\ (10)^{-4}$
VERTEX IIC	0.0013	0.89	860	$9.3\ (10)^{-3}$
VERTEX I	0.0012	0.80	560	$1.2\ (10)^{-2}$
PARFLUX P	0.00058	0.88	60	$4.0\ (10)^{-2}$

[a]The correlation coefficient was calculated by applying least-squares linear regression analysis to $\ln F = \ln F_o - kz$.

[b]The flux was measured at only two depths (14 m and 52 m) at the Peru site so no coefficient of correlation could be calculated. However, calculations using both HEA and FEA amino acid flux data for this and two other sediment-trap experiments from the Peru site (Lee and Cronin, 1982) gave almost identical rate constants.

[c]Bottom depths were 500 m for Peru, 3600 m for VERTEX I, 3600 m for VERTEX II, and 5600 m for PARFLUX P.

would therefore lose a larger proportion of their primary production (and associated nitrogen) to waters below their shallower euphotic zone. Our results suggest that in areas of higher productivity, either a smaller proportion of the material produced is being decomposed within the shallower euphotic zone, or more of the primary production is dissolved rather than particulate. Different proportions of organic matter remineralized in areas of different productivity could also depend on the assimilation efficiency of the major decomposing organisms. For example, Landry *et al.* (1984) suggest that marine zooplankton consume organic matter with variable assimilation efficiencies which are high when the animals are acclimated to low food availability and lower when the animals are acclimated to higher concentrations of food. They suggest that zooplankton acclimated to low food availability will conserve nutrients within the surface food web by producing fecal pellets lower in nitrogen than those from zooplankton feeding in richer areas.

c. Relationship between flux and depth. As expected, the flux of particulate amino acids decreases with depth at the sites sampled (Fig. 4). However, the rate of decrease is different for the different sites. Areas of higher productivity, and hence higher flux, show a faster rate of decrease in amino acid flux. This can be seen more clearly if we fit the amino acid flux values to a single-exponential decay function (Olson, 1963; Wieder and Lang, 1982). A similar approach has been applied to fatty acid data from the PARFLUX P sediment traps (De Baar *et al.*, 1983). Calculation of the decay rate constant (k) at four different sites using only data from below the euphotic zone shows that the decomposition of particulate amino acids is a function of productivity (Table 9).

Since we have derived a mathematical relationship between flux and depth, it is tempting to calculate the proportion of surface flux which reaches the sea floor. By

applying the exponential decay model described in the previous section, we can calculate F/F_o at z = bottom depth (Table 9), bearing in mind that the quantitative value of the results reflects uncertainties due to curve fitting only two points in the case of Peru and five points at PARFLUX P. Qualitatively, the calculations show that the proportion of amino acid *flux* out of the euphotic zone which reaches the sea floor is greater in areas of lower productivity than in areas of higher productivity. This result stems, both mathematically and intuitively, from the observed differences in decomposition rate between the areas of different productivity. This result may also explain the uniformity of flux in deeper waters seen in our amino acid data (Fig. 4) and in flux data for other organic compounds such as fatty acids, wax esters, and triacylglycerides (Wakeham *et al.*, 1984). Although more material is produced and sinks out of the euphotic zone in areas of higher productivity, this material is decomposed faster with depth, resulting in similar bathypelagic-zone fluxes regardless of the surface productivity of an area.

As mentioned earlier, Steele and Baird (1972) and Davies (1975) found that a large proportion of annual water-column productivity was transported to the sea floor in a highly productive, shallow sea loch. We cannot determine the proportion of surface *productivity* which reaches the sea floor from our data. Although F/F_o may be higher in lower productivity areas, the proportion of surface productivity which initially sinks as large particles, F_o/P, is probably lower in less productive areas. Thus, in areas of higher productivity, the flux reaching the seafloor can indeed be a higher proportion of surface productivity, especially in shallow seas.

Why might the rate of decomposition of particulate amino acids vary with the productivity of the surface waters of a region? Decomposition of organic matter in the sea occurs through the action of macro- and microheterotrophs. However, the relative importance of zooplankton versus microbes in remineralizing organic matter is not clear (e.g. see Sorokin, 1978; Harrison, 1980; Williams, 1981; Azam *et al.*, 1983, among others). Microbes rapidly remineralize dissolved organic matter, while their role in decomposition of sinking particulate matter is less clear, as discussed later. On the other hand, zooplankton are clearly efficient at consuming particulate matter and are not known to take up dissolved material from seawater. Whether microbes or zooplankton are the dominant decomposers may therefore depend on the proportion of primary production partitioned between dissolved and particulate pools.

The variation we observed in amino acid decomposition rate with productivity could be explained in several ways. The first explanation supports the idea that zooplankton consume detrital particles and are more important than bacteria in remineralizing particulate organic matter. The rate of particulate organic matter decomposition by zooplankton is dependent on particle feeding rate and the percent of each particle which is respired. Zooplankton feeding rates are dependent on the density of food (Parsons *et al.*, 1977). The ingestion rate increases with food density up to a point at which ingestion rate remains constant or decreases (Mullin, 1963; McAllister, 1970). And, below a certain threshold concentration of food, grazing may not occur (Frost,

1975). Beneath the euphotic zone in areas of lower productivity such as the PARFLUX P site in the central Pacific gyre, the concentration of large, sinking particles is lower than in more productive areas and thus zooplankton grazing rates should also be lower. The variation with surface productivity of amino acid decomposition rate beneath the euphotic zone may result from lower particle-grazing and therefore lower decomposition rates in areas of lower productivity and higher grazing and decomposition rates in areas of higher productivity.

Steele (1965) and Paffenhöfer and Strickland (1970) have argued against Riley's (1963) assertion that detrital particles are a major food source for copepods. Steele (1965) suggested that the very abundance of detritus in sea-water is an argument against heavy grazing on it. Paffenhöfer and Strickland (1970) failed to get *Calanus* to eat non-fecal detrital particles in laboratory experiments. However, Paffenhöfer and Strickland (1970) and later Paffenhöffer and Knowles (1979) showed that zooplankton readily consume fecal material and dead phytoplankton cells. Our proposed mechanism of control of large particle concentration by zooplankton grazing thus assumes that most of the particles are edible materials such as fecal pellets and dead phytoplankton cells. Such a composition has been observed (Bishop *et al.*, 1978; Urrere and Knauer, 1981).

Microbes are present on or within sinking particles (Gowing and Silver, 1983) and do not have to actively seek them like zooplankton must. Thus, microbial decomposition is dependent only on the percent of each particle which can be consumed and not on particle feeding rate. Microbial decomposition is therefore not dependent on the concentration of sinking particles but on the substrate concentration within the particle. Since the concentration of amino acids in sinking particles does not vary much between different sites, concentration differences cannot explain the differences in decomposition rate we observed. Substrate quality, or the availability of the amino acids in particles, may have an effect on decomposition rate, as discussed later. The small decrease in particulate amino acid flux with depth at the PARFLUX P site suggests that microbial decomposition of large sinking particles is small. Gardner *et al.* (1983) have shown that fresh organic material is rapidly colonized by bacteria when incubated in the deep sea. They observed rapid loss of dried lobster shells, squid pens, and zooplankton in poisoned as well as unpoisoned sediment traps. However, they made no attempt to prevent losses from grazing by microzooplankton or similar <200 μ-sized organisms. Lee *et al.* (1983) found that the bulk composition of detrital particles collected at 1200 m in the Panama Basin was not greatly changed by *in-situ* microbial decomposition in closed jars over a period of several months. In any case, rapidly sinking particles presumably have a shorter residence time in the water column (<60 days, Deuser *et al.*, 1981) and are thus subjected to microbial action for a shorter time. Hence, bacterial decomposition on large particles is not the most likely explanation for the variation of decomposition rate with productivity observed in our amino acid flux data.

In a study of suspended particles in the Bering Sea, Nakajima and Nishizawa

(1972) found exponential decreases in carbon concentration in surface waters which they also attributed to a combination of zooplankton grazing and bacterial consumption. They found that the rate of decrease in carbon concentration was higher when the concentration of particles was higher. These results are similar to our findings for amino acids on larger, sinking particles. Based on zooplankton biomass and an assumed rate of particle clearance by each zooplankton, Nakajima and Nishizawa calculated that zooplankton could account for one third of the carbon loss they observed. Their calculated carbon "elimination" by zooplankton varied directly with rate of carbon decrease and with carbon concentration, thus demonstrating density-dependent feeding. Nakajima and Nishizawa calculated that only one third of the suspended particulate carbon loss was due to zooplankton grazing, while we suggest that zooplankton are the dominant consumers of sinking particulate amino acids (and carbon). This is entirely reasonable considering the feeding studies mentioned earlier which showed that zooplankton prefer the fecal pellets and dead plankton cells more commonly found in sinking particulate matter rather than amorphous detrital particles associated with suspended particulate material.

A second explanation (which does not preclude the processes described above from also occurring) for the variation in particulate amino acid decomposition rate with surface productivity is a variation in production rather than decomposition of particulate organic matter. Using a sediment-trap approach similar to ours, Stabel (1984) found that turnover of particulate organic carbon is faster in more eutrophic than in less productive lakes. He suggested that due to differences in chemical resistance or settling rate, certain organisms such as the dinoflagellates and blue-green algae produced in eutrophic lakes were more completely remineralized than the diatoms produced in more oligotrophic lakes. Algae containing more resistant cell-wall organic material would very likely be decomposed more slowly, whether through microbial or zooplankton heterotrophy. Such an explanation for the presence of serine, threonine, and glycine on deep particles was discussed earlier. A similar difference in the resistance of organic material in different species of phytoplankton growing in areas of low or high productivity in the ocean could help explain the data presented here.

To summarize some of the concepts discussed, we present a conceptual model of particulate amino acid decomposition (Fig. 5). The flux of particulate amino acids is proportional to primary production in the surface waters. In areas of higher productivity, both the surface flux (F_o) and the flux of material passing out of the euphotic zone (F_{ED}) are a higher proportion of the surface production than in areas of lower productivity. The rate of loss of particulate amino acids beneath the euphotic zone (k), effectively the decomposition rate, is higher in more productive areas due either to (1) increased particle-concentration-dependent feeding by zooplankton in more productive areas, or (2) a higher proportion of resistant amino acids produced in areas of lower productivity. In more productive waters, the flux of amino acids deeper in the water

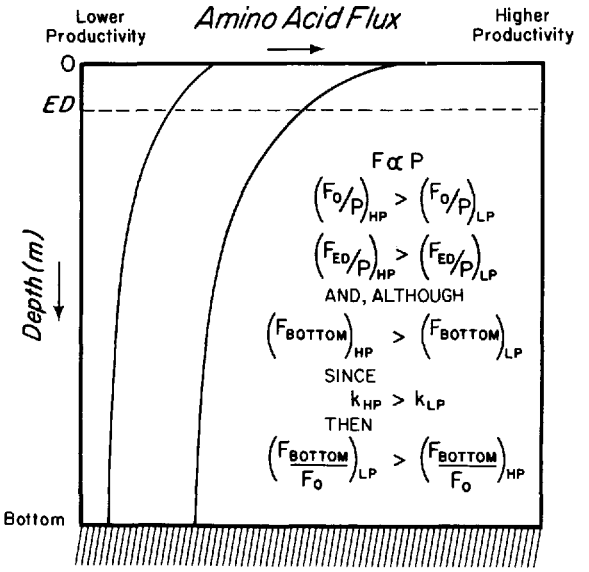

Figure 5. Conceptual model of particulate organic matter decomposition. F is the flux of material at the surface (F_o), out of the euphotic zone (F_{ED}), and to the bottom (F_{BOTTOM}) in areas of higher productivity (HP) and lower productivity (LP). P is the primary productivity integrated over the euphotic zone. The decomposition rate constants, k, are from the first-order exponential decay equation.

column is a smaller proportion of the surface flux because of the larger decomposition rate. This would cause a greater uniformity in flux in deeper waters than in surface waters for areas of different productivities.

4. Conclusions

Amino acid flux measurements from eight geographical locations show a relationship with primary productivity. The eight sets of samples were collected using different trap designs, different preservation techniques, and different lengths of deployment. The samples were analyzed in three different labs by different techniques. The close relationship of amino acid flux with productivity as well as the similarity of amino acid distribution are consistent with the assumption that either the sediment trap techniques used approximate the true flux of particles sinking through the water column, or all the different traps had a similar systematic trapping bias. Trapping of live organisms seemed to be a problem especially at the VERTEX II station. Formalin-poisoned traps apparently caught more swimmers than chloroform-poisoned traps of the same design.

The extent of decomposition of amino acids varied in areas of different productivity. The amount of amino-acid carbon falling below the euphotic zone was a higher

proportion of the primary production in areas of higher productivity than in less productive areas. However, once below the surface waters, the particulate amino acid flux decreased with depth faster in areas of higher productivity, possibly due to more efficient zooplankton feeding in more productive areas, or to the production of amino acids in more resistant organic matrices in less productive areas. The amino acids, a nutritious source of energy and nitrogen, disappeared from the water column faster than total organic carbon, presumably due to biological decomposition.

Possible evidence of decomposition on sinking particles was shown by changes in the relative concentration of ornithine with depth. In areas of the water column where decomposition is presumed to be greater than production, such as in the oxygen minimum zone and in deeper waters, the relative molar concentration of ornithine was comparatively high. Ornithine may also be a component of microorganisms living in oxygen-depleted waters.

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