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Nitrogen Regeneration and Glutamate Dehydrogenase Activity of Macrozooplankton in the Southeastern Sea of Korea

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韓國 東南海域에서의 動物性 浮游生物에 의한 窒素營養塩 再循環 및 Glutamate dehydrogenase의 生化學的 酵素 活性度에 關한 硏究

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Abstract

In southeastern sea of Korea, ammonium excretion rates of mixed macrozooplankton population ranged from 0.90 to 2.32 μg atoms NH^+_4-Nm^{-3} h^{-1} and zooplankton excretion contributed from 3 to 15% of total nitrogen requirement by phytoplankton. Wet weight specific excretion rate was averaged to be 3.45 μg atoms NH^+_4-N g^{-1} wet weight h^{-1}. Zooplankton biomass in wet weight and protein tended to increase toward outer shelf. GDH assay of macrozooplankton demonstrated a typical Michaelis-Menten kinetics with 5.1 mM of half saturation constant (K_m). Protein specific GDH activity in the present study ranged from 1.5 to 3.2 μg atoms NH^+_4-N mg^{-1} protein h^{-1}. Higher protein specific GDH activity in the outer shelf implies that zooplankters in the outer shelf were more active in nitrogen metabolism grazing higher primary production in the outer shelf. In the present study, averaged GDH/excretion ratio was 18.8 ± 2.6 (n = 6) showing high correlation between zooplankton GDH activity and direct ammonium excretion rate by zooplankton. GDH assay can be extremely useful in the future study for the ammonium regeneration by different size zooplankton fraction in various marine environments.

요약 : 본 연구 해역에서의 동물성 부유 생물에 의한 NH_4^+분비율은 0.90에서 2.32 μg atoms $NH_4^+ - N \cdot m^{-3} \cdot h^{-1}$의 범위를 보이며, 이에 의해 해양 기초생산에 필요한 총질소요구량의 3 내지 15%을 공급함을 밝혀졌다. 동물성 부유생물의 습중량 및 단백질량의 정량결과, 외부연안수로 갈수록 그 양이 증가되는 경향을 나타내었다. 동물성 부유생물의 가장 중심적인 생화학적 단위인 GDH의 활성도를 측정한 결과, 전형적인 Michaelis-Menten 효소기작을 보였다. 단백질 단위 GDH활성도는 본 연구 해역에서 1.5에서 3.2μg atoms $NH_4^+ - N$ mg^{-1} protein h^{-1}의 범위를 보였다. 외해수에서 동물성 부유생물의 GDH활성도가 높게 나타난 것은 조사당시의 외해수에서의 높은 기초 생산량을 포식하는 동물성 부유생물의 활발한 질소대사가 이루어지고 있음을 암시한다. 본 연구를 통하여 한국 동남해역의 동물성 부유생물의 GDH활성도와 NH_4^+분비율 사이에 매우 높은 상관관계가 밝혀졌으며 그 평균 GDH활성도 / NH_4^+분비율의 비율은 18.8±2.6 (n = 6) 이었다. 차후 GDH활성도 측정등을 통한 생화학적 효소연구방법은 여러 해양 환경에서 생물활동에 의하여 영향을 받는 비보전적인 해수원소의 동적 변화 및 해양생태계내에서의 각 생물군의 여러 생화학적 역할을 규명하는데 중요하게 이용될 것으로 판단된다.

INTRODUCTION

Zooplankton excretion has been recognized as an important nitrogen source for phytoplankton growth in most oceanic environments. Most marine zooplankton are known to be primarily ammonotelic (Corner and Newell, 1967; Mayzaud, 1976; Kremer, 1977; Park and Carpenter, 1986) excreting ammonium as a major end product from amino

acid and nucleic acid catabolism. Preference for the excreted nitrogen (ammonium and urea) over other forms of nitrogen (nitrate and nitrite) has been reported for phytoplankton (Carpenter et al., 1972; McCarthy et al., 1977). It has been demonstrated that nitrogenous nutrient uptake by phytoplankton is tightly coupled with zooplankton excretion in aquatic systems (McCarthy and Goldman, 1979).

To understand overall nitrogen cycle in the marine environment, it is imperative to quantify heterotrophic remineralization in the water column. Until now, measurements of macrozooplankton excretion were relied on time dependent bottle incubation. Many investigators reported artifacts of bottle incubation method such as overcrowding, starvation and other unkown bottle confinement effects (Mayzaud, 1973; Mullin et al., 1975; Takahashi and Ikeda, 1975; Szyper et al., 1976; Ikeda, 1977). To aviod those problems associated with direct measurements, several workers used enzymatic assays as alternative measurement of metabolic rates (Owens and King, 1976; Bidigare and King, 1981; Bidigare et al., 1982; Park et al., 1986). In most animals, glutamate dehydrogenase (EC 1.4.1.3) has been known to be primarily responsible for ammonium production from amino acid catabolism. McBean et al. (1966) found that glutamate dehydrogenase (GDH) activity of homogenized eel liver is closely related to ammonium excretion in eels. Recent studies on crustacean zooplankton GDH activity demonstrated that enzymatic assay of GDH can be successfully used for measuring ammonium regeneration and nitrogen metabolism of zooplankton in various oceanic environments (Bidigare et al., 1982; Park et al., 1986).

The primary purposes of the present study are to measure ammonium excretion rate of zooplankton and evaluate the importance of zooplankton excretion as a nitrogen source for phytoplankton production in the southeastern sea of Korea, and to establish a GDH/excretion ratio through the biochemical enzyme assay of GDH of zooplankton.

MATERIALS AND METHODS

Study area is located in the southeastern sea of Korea where the warm Tsushima current flow into the East Sea of Korea (Fig. 1). Mac-

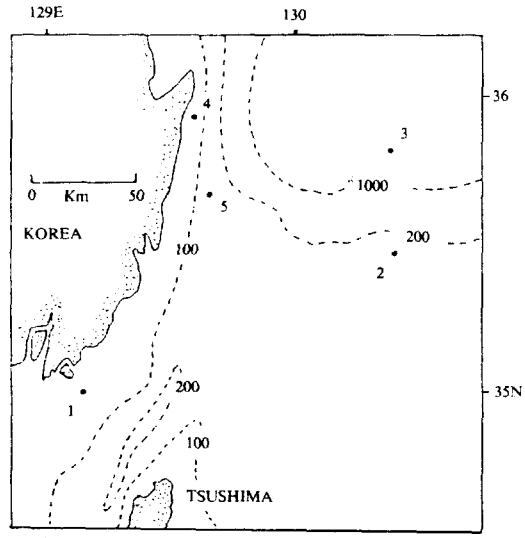

Fig. 1. Map showing sampling stations in the southeastern sea of Korea.

rozooplankton (>350μm) were collected by a vertical net (0.45 m dia., 350 μm mesh) haul from 40 m to surface with flowmeter attached. Collected zooplankton in the cod end jar were carefully transferred to 2 liter of polyethylene container and further diluted with ambient seawater. Quantified subsample was carefully concentrated on the 150 μm mesh screen and transferred to 1 liter of filtered ambient seawater with glass fiber filter paper (GF/C) in a large mouth glass container. After an hour for stabilization, time dependant ammonium excretion rates of zooplankton were determined for 4 hours by measuring duplicate 5 ml of medium hourly. Ammonium was determined colorimetrically immediately after termination of the incubation according to the method of Solorzano (1969). All the incubations were held at ambient seawater temperature (22 °C) on deck.

After termination of incubation, zooplankters were collected on a glass fiber filter paper (GF/C, 47 mm) and kept frozen on a dry ice for the later determinations of zooplankton GDH activity and extractable body protein. Concentrated zooplankton were homogenized for 2 min in 2 ml of 100 mM tris-acetate buffer (pH 8.5) and 0.2 % (v/v) Triton X-100 with glass-teflon homogenizer in an ice bath. Homogenates were centrifuged for 10 min at 1500 g in a RC 5 Superspeed Refrigerated Centrifuge (Dupont Instrument) at 0-4 °C. Supernatant was assayed for GDH activity

and protein. Reagents were purchased from Sigma Chemical Co. and freshly made before experiment. The standard GDH assay mixture was followed after Park et al. (1986).

The GDH activity was measured kinetically by the increase in absorbance at 340 nm for 3 min in a 1 cm path length quartz cuvette using a double beam recording spectrophotometer (Perkin-Elmer 552S) at an ambient seawater temperature. Routine GDH activity determination was measured at 50 mM of glutamate. Detailed procedure should be referred to Park et al. (1986). Extractable zooplankton protein was measured colorimetrically at 595 nm with a Bio-Rad protein assay reagent (Bradford, 1976).

RESULTS

In the present study ammonium excretion by mixed macrozooplankton population, based on the time series incubation, presented a strong linear relationship ($r = 0.998$) throughout the short incubation period (Fig. 2). It is critical to measure excretion rates of zooplankton within at least 12 hours after the sample collection since starvation for 1 or 2 days can evidently decrease excretion rates (Mullin et al., 1975; Ikeda, 1977; Park, 1986). The wet weight specific ammonium excretion rates of zooplankton ranged from 4.41 to 2.64 μg atom N g^{-1} wet weight h^{-1} averaging 3.45 μg atom N g^{-1} wet weight h^{-1} (Table 1.).

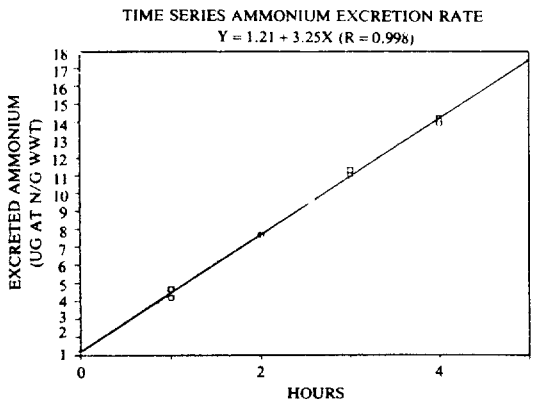

Fig. 2. A typical representation of ammonium excretion by macrozooplankton based on time series incubation.

Table 2. Zooplankton biomass distribution in wet weight and protein in the southeastern sea of Korea. Concentration of protein was measured from the superantant of extracted homogenates. All the values were averaged from triplicate meansurements.

Stations	Wet weight (g wwt/m^3)	Protein (mg protein/m^3)	Protein(mg) / Wet weight(g)
1	0.350	—	—
2	0.681	14.1	20.7
3	0.397	9.8	24.6
4	0.269	9.8	36.5
5	0.230	—	—

Wet weight specific biomass ranged from 0.68 to 0.23 g m^{-3} in the study area as shown in Table 2. Highest biomass was found at station 2 where highest primary production was reported in this area (Shim and Park, 1986). Protein contents per unit wet weight of zooplankton population near the coast were higher than those of outer shelf.

A typical Michaelis-Menten plot of GDH activity of mixed macrozooplankton at different glutamate concentrations is represented in Fig. 3 which was curve-fitted by double reciprocal transformation. Half saturation

Table 1. Ammonium excretion rates and GDH activities of mixed population of macrozooplankton in the southeastern sea of Korea.

Stations	Ammonium excretion rate		GDH activity			GDH/excretion ration
	μg at N/g wwt/h)	(μg at N/m^3/h)	(μg at N/g wwt/h)	(μg at N/mg protein/h)	(μg at N/m^3/h)	
1	4,41	1,54	—	—	—	—
	2.86	1.00	—	—	—	—
2	4.19	2.85	69.96	3.01	47.64	16.7
	2.64	1.79	55.97	3.10	38.12	21.2
3	3.25	1.29	52.76	2.29	20.95	16.2
	3.64	1.45	84.16	3.21	33.41	23.1
4	3.35	0.90	56.68	1.45	15.25	16.9
	3.30	0.89	62.12	1.84	16.71	18.8
Average	3.45		63.61	2.48		18.8
S.D.	0.57		10.72	0.67		2.7
C.V. (%)	16.49		16.85	27.04		13.6

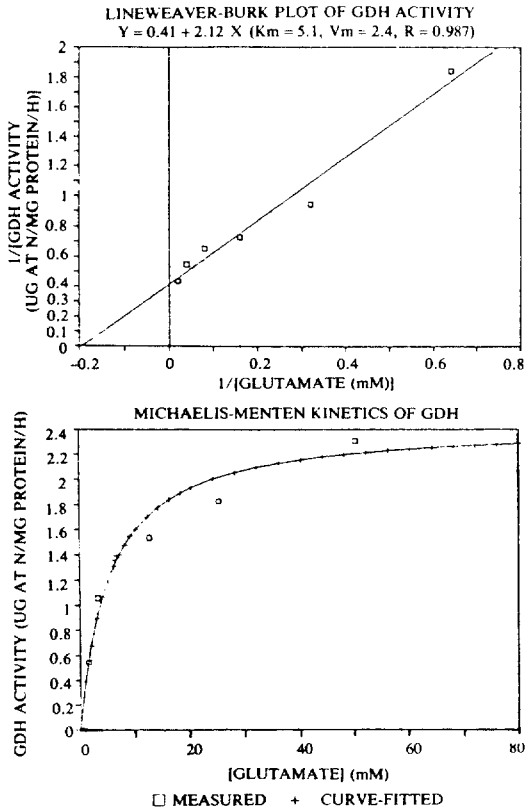

Fig. 3. A typical representation of macrozooplankton GDH kinetics in southeastern sea of Korea. K_m was 5.1 mM. At 50 mM of glutamate, standard GDH assay condition accounted 90% of V_{max}.

constant (K_m) was around 5.1 mM which is consistent with Park et al. (1986). Protein specific GDH activies in the present study ranged from 1.5 to 3.2 μg atoms NH_4^+-N mg^{-1} protein h^{-1}. These values are approximately same order with those of estuarine zooplankton population. Protein specific GDH activities in the outer shelf (stations 2 and 3) were higher than those of inner coastal water (station 4). Highest GDH activity was found at station 2 averaging 42 μg atoms NH_4^+-N m^{-3} h^- and lowest was 16 μg atoms NH_4^+-N m^{-3} h^{-1} at station 4. Volume specific GDH activities in the present study are 2 or 3 times lower than those of estuarine waters. This is due to the lower zooplankton biomass in the coastal water comparing to that in the estuarine waters such as in Great South Bay near Long Island (Park et al., 1986).

Among the kinetic parameters of ammonium excretion by mixed zooplankton, the lowest coefficient of variation was found in GDH activity/excretion rate (13.6%). Coefficients of variation of wet weight specific GDH activity, protein specific GDH activity and wet weight specific excretion rate were 16.8, 27.0 and 16.5%, respectively in the present study.

DISCUSSIONS

The result presented in this study demonstrate that GDH is the responsible key enzyme in oxidative deamination of zooplankton amino acid metabolism. In biochemical aspects, phytoplankton proteins ingested by zooplankton must be proteolyzed into amino acids before they can be used as fuel or directly incoporated into building blocks of biomolecules of zooplankton. As shown in Fig. 4, when amino acids are used as fuel source, they undergo transamination and successive oxidative deamination. In transamination, the

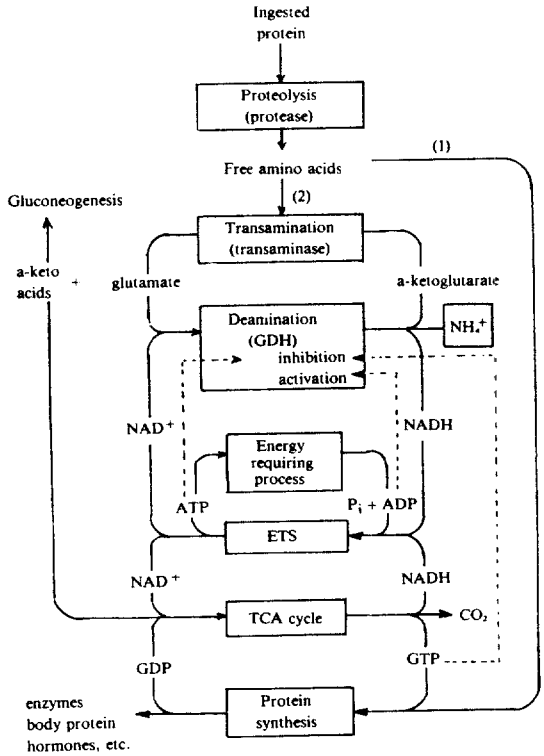

Fig. 4. Biochemical pathways for the protein metabolism in zooplankton. (1) Incorporation of free amino acids into biomolecules of zooplankton. (2) Utilization of amino acids as a fuel sources. Broken lines represent regulatory functions of ADP, ATP and GTP.

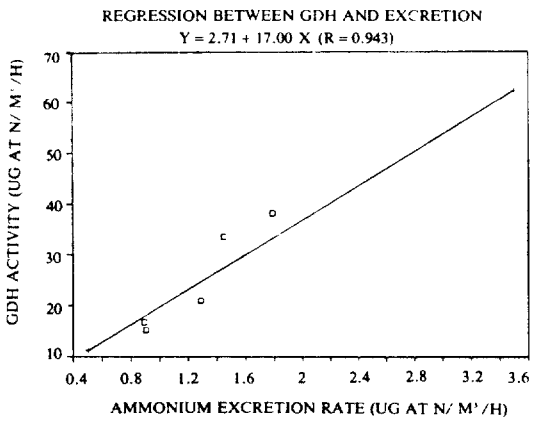

Fig. 5. Correlation between GDH activity and ammonium excretion rate of macrozooplankton collected from southeastern sea of Korea. Correlation coefficient was 0.943.

amino groups of various amino acids are usually transferred to a-ketoglutarate forming glutamate. Then glutamate undergoes oxidative deamination catalyzed by NAD(P)-specific GDH producing ammonium as excretory end-product which readily diffuses into the surrounding waters. GDH catalyzes a reversible reaction and its activity is stimulated in the direction of deamination of high ADP concentrations. Logically speaking, when energy charge (0.5 ([ADP] + 2[ATP]) / ([AMP] + [ADP] + [ATP]) becomes low, energy yielding processes such as oxidative deamination are activated through allosterism. However, when *in vivo* GTP concentration increases, GDH activity is strongly inhibited. GTP is the essential energy form in the elongation cycle of protein synthesis. Park et al. (1986) showed zooplankton GDH activation by additon of excessive ADP into the GTP inhibited enzyme reaction. In general, GDH is known to fuction with either NAD or NADP as a coenzyme. However, zooplankton GDH activity in the direction of oxidative deamination was found to be NAD-specific (Park et al., 1986).

In the present study, I found a high correlation (=0.943) between ammonium excretion rates and GDH activity of the mixed zooplankton population as shown in Fig. 5. The GDH/excretion ratio found in this study is 18.8 ± 2.6 (n = 6) which is favorably consistent with others (Table 3). This implies that nitrogenous nutrient regeneration by zooplankton can be quantified by the use of GDH assay in most oceanic environments. As previously discussed by Bidigare and King (1981), GDH assay can avoid labor and time consuming bottle incubation and other artifacts from bottle incubation. Rapid uptake of microzooplankton excreted ammonium by phytoplankton hampered direct determination of ammonium excretion rates of smaller zooplankton by the conventional bottle incubation method since smaller zooplankters are frequently in the same size fraction of phytoplankton. The most important implication of GDH assay in the marine environment is the determination of ammonium excretion rates by micro- and nanozooplankton. Glibert (1982), using N-15 dilution method, demonstrated the importance of the micro- and nano-fraction heterotrophic organisms as a major remineralizer in the oceanic waters. As NAD-specific phytoplankton GDH could not be detected, ammonium excretion rates of similar size fraction of protozoa and heterotrophic flagellates could be measured with GDH assay (Park et al., 1986). GDH assay has another advantage of biochemical work, that is, kinetic parameters (V_{max} and K_m) can be useful to investigate the nutritional status and nitrogen metabolism of zooplankton.

In the present study, it is evident that ammonium excretion rates by mixed zooplankton population closely follow the variation of zooplankton biomass. Primary productivity measurement reported by Shim and Park (1986) demonstrated higher primary proudction in the outer shelf in this area where the ammonium excretion by zooplankton was highest. Considering tight coupling between phytoplankton and zooplankton in terms of

Table 3. Comparison of GDH/excretion ratios (±S.D.) determined in the southeastern sea of Korea with others.

Organisms	Temperature (°C)	GDH/excretion ratio	Sources
Calanus finmarchicus	10	16.8 ± 0.3 (n = 5)	Bidigare and King (1981)
Mexed zooplankton (Gulf of Mexico)	25	18.7 ± 4.3 (n = 11)	Bidigare et al. (1982)
Mixed zooplankton (Great South Bay)	3-27	20.4 ± 3.5 (n = 10)	Park et al. (1986)
Mixed zooplankton (Southeastern sea of Korea)	22	18.8 ± 2.6 (n = 6)	Present study

prey-predator relationship, high zooplankton biomass might be found where phytoplankton growth is active and standing crop is high. Goldman (1984) advocated spinning wheel hypothesis implying that standing crop may not be neccessarily high to support high zooplankton biomass. He suggested that magnitude of kinetic rates such as nutrient uptake and grazing is more directly related to the population size of photosynthetic organisms and heterotrophic grazers in a steady state conditon. Assuming collected population were equally composed of herbivores and carnivores with ecological efficiency of 10% and daily food requirement for the basal metabolism is 66%, grazing rate by zooplankton can be virtually balanced by photosynthetic rate establishing a steady state in this area. The present result support the above hypothesis since I could find better correlation between nutrient regeneration rate by zooplankton and photosynthetic rate ($r = 0.92$) than between nutrient regeneration rate by zooplankton and standing crop of phytoplankton ($r = 0.42$).

Ammonium regeneration by zooplankton in this area amounts 3.5 mg atoms N m^{-2} d^{-1}. Daily nitrogen requirement by phytoplankton was estimated to be 15.6 mg atoms N m^{-2} d^{-1} and upward flux of nitrate by diffusion through thermocline amounted o.45 mg atoms N m^{-2} d^{-1} in the same area (Shim and Park, 1986). In the the present study, ammonium excretion by mixed zooplankton contributes a significant fraction of the nitrogen demand for primary production in the southeastern sea of Korea. Contribution by zooplankton excretion ranges from 3.2 to 14.8% averaging 13.1%. In various marine environments, macrozooplankton contributes less than 50% of nitrogen requirement by phytoplankton (Table 4). In oligotrophic ocean, macrozooplankton exerts less than 2% (Eppley et al., 1973; Bidigare et al., 1982). In upwelling region, where the vertical flux from nutrient rich bottom water is more important, contribution ranges from 1 to 36% (Whitledge and Packard, 1971; Smith and Whitledge, 1977). In coastal waters, Ikeda and Motoda (1978) reported that macrozooplankton contributed from 11 upto 44% in the Kuroshio and adjacent seas, and Dagg et al. (1982) reported 2-22% in the Bering Sea. The present result is very consistent to others. It is interesting to note that volume specific zooplankton excretion and its contribution to phytoplankton nitrogen demand in outer shelf are higher than in inner shelf. Dagg et al. (1982) found similar result in Berring Sea (Table 4). Low contribution of zooplankton excretion to primary production in inner shelf seems primarily due to higher dependence of phytoplankton growth upon coastal mixing in inner shelf than in outer shelf. However, still the large portion of nitrogen demand by primary production is not explained in this area. Glibert (1982) and Park et al. (1986) demonstrated that smaller zooplankton, protozoa and bacteria are the major remineralizer in the

Table 4. Comparison of macrozooplankton excretion rates and contribution to primary production in various marine environments (After Bidigare (1983) in "Nitrogen in the marine envirnment". Carpenter and Capone ed.).

Areas	Ammonium excretion rate (ug at N/m³/h)	Contribution to phytoplankton nitrogen demand (%)	Sources
Esturaine waters			
Long Island Sound	4.54-8.42	43-66	Harris (1959)
Narragansett Bay	3.27	4	Vargo (1979)
Great South Bay	0.29-6.50	1-13	Park and Carpenter (1986)
Upwelling			
Northwest Africa	2.25	12-36	Smith and Whiteledge (1977)
Peru	0.02-0.35	1	Whiteledge and Packard (1971)
Costa Rica Dome	0.03-0.94	1-12	〃
Coastal waters			
Kurohio and adjacent seas	0.08-0.48	11-44	Ikeda and Motoda (1978)
Berring Sea (inner shelf)	0.14-0.18	2	Dagg et al. (1982)
(mid-shelf)	0.85-2.18	16	〃
(outer shelf)	0.53-0.99	6-22	〃
Southeastern sea of Korea	0.90-2.32	3-15	Present study
Oligotrophic oceanic waters			
Gulf of Mexico	0.10-0.26	17	Bidigare et al. (1982)
North Pacific Central Gyre	0.04-0.24	16-20	Eppley et al. (1973)

coastal waters. Therefore I suggest that further studies such as N-15 dilution technique or GDH activity of smaller zooplankton and micro-sized heterophic organisms are necessary for the complete elucidation of nitrogenous nutrient recycling in the coastal waters in the future.

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