Journal of Oceanography (2005)

An Ecosystem Model Including Nitrogen Isotopes: Perspectives on a Study of the Marine Nitrogen Cycle

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(Received 15 September 2004; in revised form 21 February 2005; accepted 6 March 2005)

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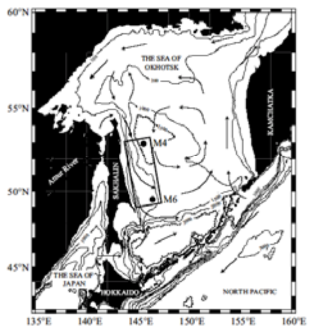
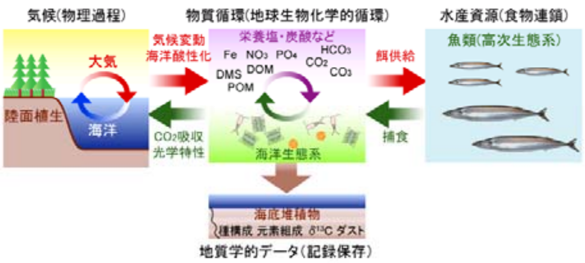
研究対象地域



生態系モデル



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1. Introduction

Incubation experiments with the artificial addition of ^{15}N tracers have been widely conducted to estimate the various marine biogeochemical fluxes and rates of nitrogenous nutrients. For example, uptake rates of nutrients and nitrogen *f*-ratios, defined as the ratio of nitrate assimilation by phytoplankton to total nitrogenous nutrient assimilation, have been estimated with on-deck and/or in-situ incubation experiments through assimilations of ^{15}N-nitrate, ^{15}N-ammonium or ^{15}N-urea by phytoplankton (e.g., Dugdale and Wilkerson, 1986; Sambrotto and Mace, 2000; Wilkerson *et al.*, 2000; Sambrotto, 2001). Nitrification rates have been measured in in-situ incubation experiments through ^{15}N-ammonium oxidation (Sutka *et al.*, 2004). These fluxes and rates are usually estimated with small bottles for a few hours, or up to two days at most. That is, the condition of the incubation experiment is restricted to a small space and a short time. Moreover, these experiments are difficult to conduct under the condition of the actual concentration of substrate, because artificial ^{15}N addition changes this concentration. In a strict sense, these are reasons why the

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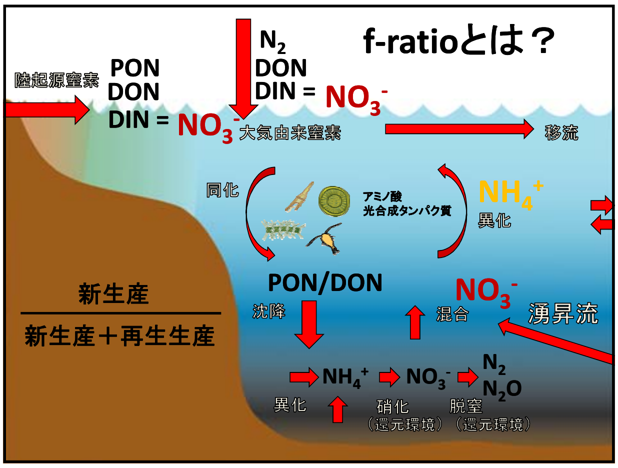
様々な窒素化合物のd15Nを分析することで、海洋の窒素循環について明らかにする試みがなされてきている。

室内実験系データを、自然環境で起きていることに応用することの問題性



incubation experiments cannot simulate a natural ecosystem. On the other hand, the natural abundance of nitrogen isotopes has also been observed to understand marine biogeochemical processes. For example, $\delta^{15}N$ values of nutrients in the surface water usually show the degree of nutrient utilization (e.g., Miyake and Wada, 1971; Altabet *et al.*, 1991; Waser *et al.*, 1998), and the relationship among $\delta^{15}N$ values of phytoplankton, zooplankton, fishes, marine mammals, etc., indicates the degree of trophic level (Minagawa and Wada, 1984; Wu *et al.*, 1997; Adams and Sterner, 2000). Moreover, $\delta^{15}N$ of nitrogenous components in a special region indicate the source of nutrients affected by denitrification or nitrogen fixation (Ostrom *et al.*, 1997; Altabet *et al.*, 1999), although these processes do not occur in the Sea of Okhotsk. These estimations are made under natural ecosystem conditions. However, little quantitative estimation has been done, since natural abundances of nitrogen isotopes are determined by complex biogeochemical processes. In this study, we not only use actual observed data of $\delta^{15}N$, but also an ecosystem model including various biogeochemical processes and nitrogen isotopes to quantitatively understand nitrogen isotopic dynamics. Furthermore, we suggest a new potential of natural abundance of nitrogen isotopes as a tracer instead of the incubation experiment.

Observed $\delta^{15}N$ values of nitrogenous components record information concerning the marine biogeochemical cycle, as described above. However, $\delta^{15}N$ of nitrogenous components are hard to observe frequently throughout the

d15Nによって明らかにされてきた、様々な海洋の窒素循環プロセス

興味深い事象の列挙・レビュー
↓
問題の提起
↓
問題の解決がもたらす利益
↓
着眼点
↓
何をやるのか？(取り組んだテーマ)

どのようなイントロの構成が好ましいか？

例36　なぜ、ベガルタ仙台は強いのか：勝利を呼ぶ牛タン定食仮説の検証

ベガルタ仙台は強い。サポーターの熱狂的な声援に支えられて、向かうところそんなには敵無しである。

ベガルタ仙台の強さの秘密の一つは、選手の身体能力が非常に高いことにある。その運動量とスピードは、90分間衰えることがない。**なぜ、身体能力がこのように高いのであろうか。**（取り組んだ問題）その理由を解明できれば、ベガルタ仙台の継続的強化に役立てることができるであろう。（問題意識）

ベガルタ仙台の選手は牛タン定食が好きで、頻繁に食べているらしい
牛タンは非常に良質なタンパク質で栄養価が高い。もしかしたら牛タンは、サッカー選手の体調維持に役に立つのかもしれない。ベガルタ仙台が強い理由の一つは、牛タン定食を食べて超人的身体能力を手にしているからであろうか。（着眼点）

本研究では、牛タン定食を食べているからベガルタ仙台は強いという仮説の検証を試みる。（何をやるのか）

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year. To validate our model comparing the simulated $\delta^{15}N$ values and the observed data set, we are also in need of another recorder. Information of $\delta^{15}N$ in surface water is transmitted to $\delta^{15}N$ of sinking particles. Seasonal variations in $\delta^{15}N$ of the sinking particles obtained from sediment trap experiments can reproduce the seasonal variations in biogeochemical processes in surface water. $\delta^{15}N$ values of sinking particles reflect the proportion in the components of sinking particles, which consist of dead phytoplankton and zooplankton bodies, as well as fecal pellets (Voss *et al.*, 1996; Wu *et al.*, 1999; Peña *et al.*, 1999), and the state of nutrients in the surface water, such as the degree of nutrient utilization (Altabet and Deuser, 1985; Altabet *et al.*, 1991; Altabet and Francois, 1994, 2001; Voss *et al.*, 1996; Nakatsuka and Handa, 1997; Peña *et al.*, 1999). In this study we also compare the simulated $\delta^{15}N$ values of sinking particles with those observations in order to confirm our model's consistency with real seasonal variations in $\delta^{15}N$ of nitrogenous components.

We have developed an ecosystem model including nitrogen isotopes based on recent ecosystem models, which successfully simulated several time series observations in high latitudes (Kawamiya *et al.*, 1997, hereafter KKYS; Fujii *et al.*, 2002; Yamanaka *et al.*, 2004, hereafter YYFANK). We apply this model to the region off the east coast of Sakhalin in the Sea of Okhotsk (Fig. 1; 49–53°N, 144–146°E). The Sea of Okhotsk is located at the northwestern rim of the North Pacific, where the maximum primary production reaches 5000 mgC/m^2/day, which is much higher than typical values of the northwestern Pacific (Sorokin and Sorokin, 1999). CTD observations and water sampling were taken in the Sea of Okhotsk during three research cruises by R/V Professor Khromov. Sediment trap experiments were also carried out at two mooring stations off the east coast of Sakhalin for two years (Table 1), where a seasonal variation in fluxes of sinking particles has been observed (Yoshikawa *et al.*, 2001; Nakatsuka *et al.*, 2004). These observations provide us with enough data (e.g., $\delta^{15}N$ of sinking particles and nitrate, fluxes of sinking particles, concentrations of nitrate, ammonium and chlorophyll-a) to construct and validate the ecosystem model (Yoshikawa *et al.*, 2001, 2005; Nakatsuka *et al.*, 2004).

2. Model Description

The ecosystem model in this study has six compart-

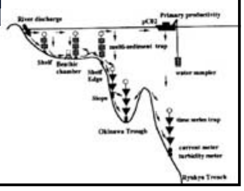
海洋表層においてd15N分析に十分なN化合物を季節的に得ることは難しい。

↓

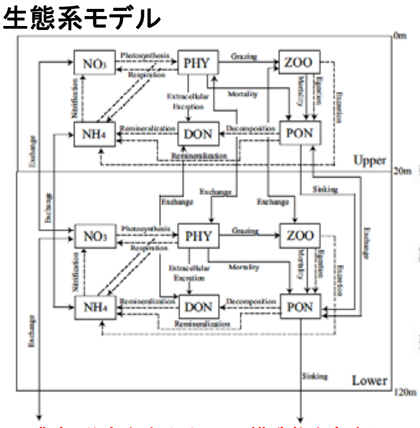
沈降粒子（多くのプロセスを反映している）のd15Nを利用

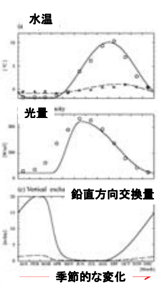
セジメントトラップとは？

セジメントトラップ



生態系モデル





（N濃度・分布を決める6つの構造物を考慮）

生態系モデル　*e*NEMURO（北大＋東北水研）

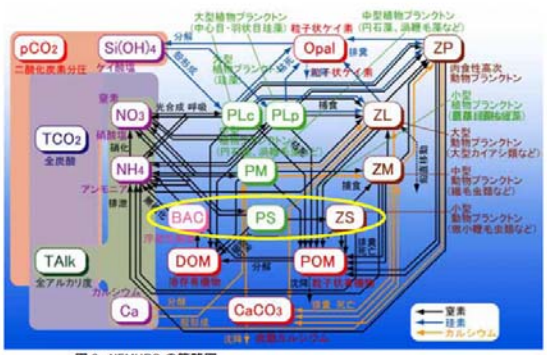
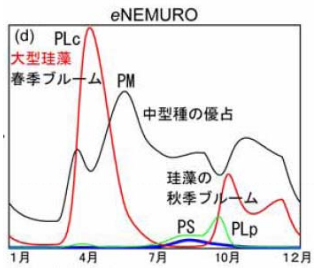


図 3 *e*NEMURO の簡略図
黄色で囲んだ部分は亜熱帯域で優占する小型生物グループ

生態系モデルで予想される植物プランクトン季節変化



PL: 大型植物プランクトン
PM: 円石藻や鞭毛藻などの中型植物プランクトン
PS:原核緑藻などの小型植物プランクトン
PLc: 亜寒帯域で優占するグループ（鉄に敏感）
PLp: 世界中に広く分布するグループ（鉄に無反応）

吉江直樹

ments, the prognostic variables being concentrations of nitrogen (N). Figure 2 illustrates the six compartments, phytoplankton (PHY), zooplankton (ZOO), particulate organic nitrogen (PON), dissolved organic nitrogen (DON), nitrate (NO_3) and ammonium (NH_4). The equations for the nitrogen cycle are the same as those in KKYS and are presented in detail in Appendix A.1. Photosynthesis is formulated as a function of light intensity, temperature and concentrations of nitrate and ammonium. The other biological processes are formulated as functions of temperature and nitrogen concentrations. The PON in this model consists of dead phytoplankton and zooplankton bodies and fecal pellets of zooplankton. The parameters are based on those in YYFANK applied to the northwestern Pacific, since the ecosystem there is similar to that in the Sea of Okhotsk (Table 2). As YYFANK has two classes of phytoplankton and two species of zooplankton, parameters for planktons in our model are set to the mean values of those of the small and large classes.

We added the ^{15}N (nitrogen isotope) cycle to the nitrogen cycle in KKYS. The ^{15}N concentrations of the six compartments are also prognostic variables, and their equations are presented in detail in Appendix A.2. Isotopic fractionation of each process has been studied as follows. Phytoplankton assimilates mainly nitrate and ammonium as its nitrogen source. Since $^{14}NO_3^-$ and $^{14}NH_4^-$ are more readily assimilated than $^{15}NO_3^-$ and $^{15}NH_4^-$, the $\delta^{15}N$ of nitrate and ammonium in the surface water increase as phytoplankton takes up these nutrients (e.g., Miyake and Wada, 1971; Altabet et al., 1991; Waser et al., 1998). The isotopic fractionation during uptake of nitrate by phytoplankton is estimated to be from −4 to

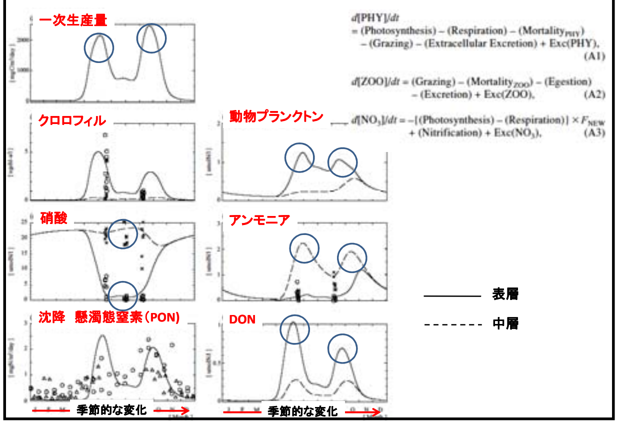
−8‰ in the field (Wada, 1980; Horrigan et al., 1990; Wu et al., 1997; Sigman et al., 1999; Altabet et al., 1999) and from −2 to −15‰ in culture (Montoya and McCarthy, 1995; Waser et al., 1998). As for ammonium, the isotope fractionation is estimated to be from −6.5 to −9.1‰ in the field (Cifuentes et al., 1989; Montoya et al., 1991) and from −5 to −29‰ in culture (Pennock et al., 1996; Waser et al., 1998). The ammonium excreted by zooplankton is lighter, by 2 to 8‰, than the concentration of their bodies (Checkley and Miller, 1989), but their fecal pellets are roughly 1‰ heavier than the diet (Altabet and Small, 1990; Montoya et al., 1990). The net result of these two processes is an increase in $\delta^{15}N$ of animal tissue relative to the animal's diet. An average increase of 3.4‰ (ranging from 0 to 6‰) per trophic level was estimated in previous studies (Minagawa and Wada, 1984; Wu et al., 1997; Adams and Sterner, 2000). The enrichment in $\delta^{15}N$ of PON associated with microbial degradation has been inferred in many studies (Saino and Hattori, 1980, 1987; Altabet and McCarthy, 1985; Ostrom et al., 1997). PON is known to be decomposed to ammonium by microbial processes. The fractionation of ammonification is estimated to be from 0 to −5‰ (Miyake and Wada, 1971; Hoch et al., 1996; Ostrom et al., 1997; David, 2001). Ammonium is oxidized to nitrate by nitrifying bacteria. The fractionation for nitrification is estimated to be from −5 to −38‰ (Miyake and Wada, 1971; Horrigan et al., 1990; Casciotti et al., 2003), which is larger than the other indicated values. The isotopic fractionation effect (ε (‰)) for each process is set to a mean value within the range of the following effects, as in previous studies (Table 3). For the representation and discussion in this paper, we use the traditional notation, $\delta^{15}N$, converted from ^{15}N concentrations, although these values are calculated in the model. The $\delta^{15}N$ value is defined as $\delta^{15}N$ (‰) = $((^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{atmospheric\ N2} - 1) \times 1000$ using ^{15}N and ^{14}N of each compartment.

We applied the box model including the biological processes described above to regions off the east coast of Sakhalin in the Sea of Okhotsk (Fig. 1). This model has two vertical layers (Fig. 2). In this region, mixed layer depths, which are given in reference to the observed ver-

海洋の窒素循環に伴う同位体分別

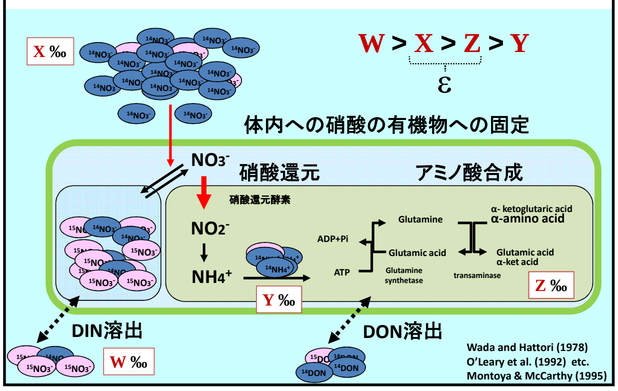
Process	ε (‰)	Remarks
NO_3^- assimilation by phytoplankton (植物プランクトンの硝酸取り込み時)	$\varepsilon_1 = -5$	in field −5 (Wada, 1980) −7 (Horrigan et al., 1990) −5∼−6 (Wu et al., 1997) −4∼−6 (Sigman et al., 1999) −5 (Altabet et al., 1999) −6∼−8 (Altabet et al., 2001) in culture 0∼−15 (Montoya and McCarthy, 1995) −2∼−6 (Waser et al., 1998)
NH_4^- assimilation by phytoplankton (植物プランクトンのアンモニア取り込み時)	$\varepsilon_2 = -10$	in field −9 (Cifuentes et al., 1989) −7∼−8 (Montoya et al., 1991) in culture −5∼−29 (Pennock et al., 1996) −16∼−26 (Waser et al., 1998)
Excretion by zooplankton	$\varepsilon_3 = -5$	−2∼−8 (Checkley and Miller, 1989)
Egestion by zooplankton (動物プランクトンの排泄時)	$\varepsilon_4 = -2$	no data
Nitrification (アンモニア硝化時)	$\varepsilon_5 = -14$	−5∼−21 (Miyake and Wada, 1971) −12∼−17 (Horrigan et al., 1990) −14∼−38 (Casciotti et al., 2003)
Remineralization (PON to NH_4^-)	$\varepsilon_6 = -1$	no data
Remineralization (DON to NH_4^-)	$\varepsilon_7 = -1$	no data
Decomposition (PON to DON) (無機化、分解時)	$\varepsilon_8 = -1$	0∼−2 (Miyake and Wada, 1971)

各要素のシミュレーションモデル値と実測値（1）

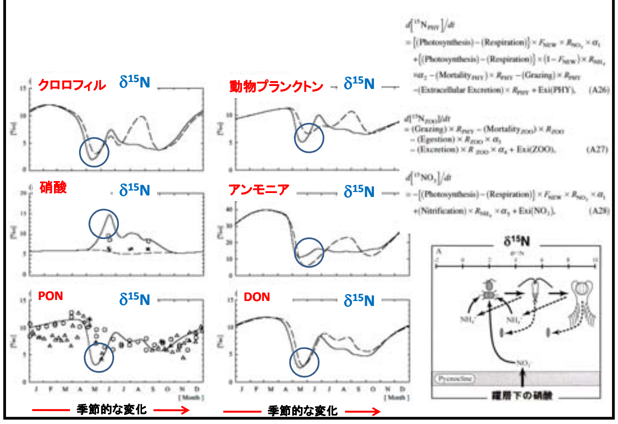


硝酸の取り込みに伴う同位体分別の模式図

（膜透過と同化反応時）

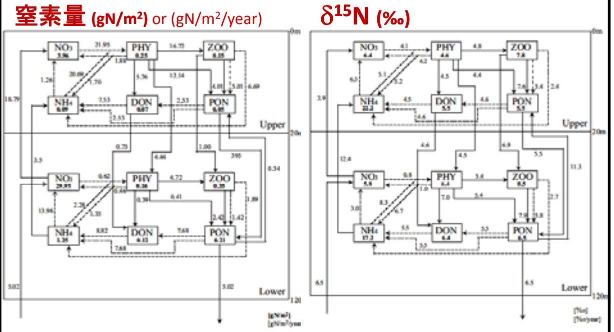


各要素のシミュレーションモデル値と実測値（2）



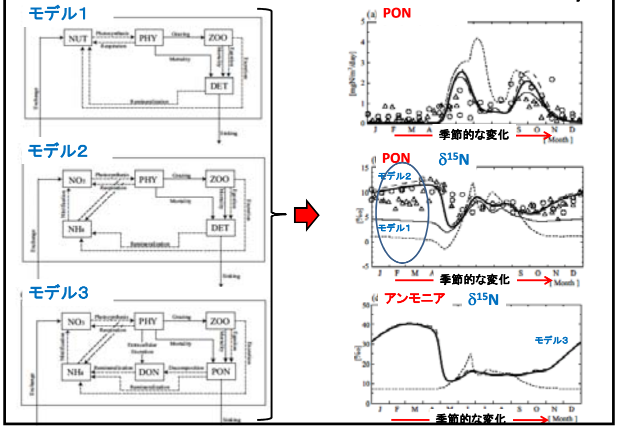
窒素量、$\delta^{15}N$のボックス収支モデル

窒素量 (gN/m²) or (gN/m²/year)　　$\delta^{15}N$ (‰)

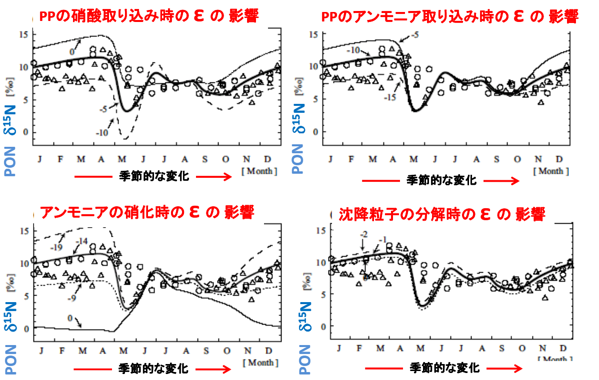


オホーツクの生産量はとても大きい。 PONの8割は、120mより上層にて分解される。
一次生産に対する移出量(export ratio)は0.11F-ratioは0.5
120mより上の層での硝化と、下層からの硝酸流入量は、同化された窒素の89%。表層でのregenerationだけでなく、下層も含めたトータルでのregenerationの寄与が重要。

使用したモデルの妥当性検査Ⅰ（考慮する項目）

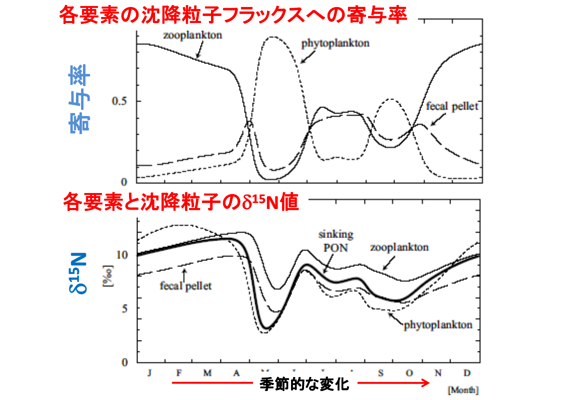


使用したモデルの妥当性検査Ⅱ（同位体分別係数）



・硝酸やアンモニアの植物プランクトン取り込み時の同位体分別、アンモニアの硝化時の同位体分別を考慮しないと、現場の値を説明できない。

沈降粒子量とそのδ15Nへの各要素の寄与率

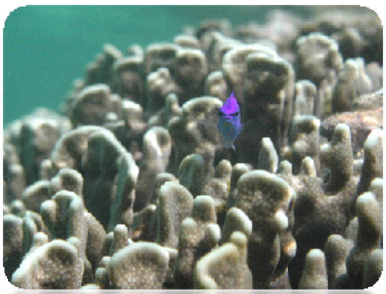


本論文のまとめ

- 窒素同位体比を導入した生態系モデルを構築し、観測データと比較することで、オホーツク海で得られた沈降粒子試料などの観測データをほぼ再現することができた。
- 植物プランクトンの硝酸、アンモニア取り込み時の同位体分別の大きさは、沈降粒子の同位体比を大きく左右する要因である。
- 冬季は、硝化によって重たくなったアンモニアの選択的な利用によって（f-raioは0.2-0.3まで低下する）、有機物、及び、沈降粒子も重たくなっている。
- 春と秋のブルーム時のアンモニア、硝酸、植物プランクトンの窒素安定同位体比を測定することができれば、植物プランクトンによる栄養塩の選択性（f-ratio）を見積もることができる。

論文の感想

- 優秀な二人の指導教官の成果を十二分に活用した、まとめ論文
- それぞれの過程での同位体分別のレビューとしても価値がある。
- 用いられている数式の妥当性や使われている生データは別論文にあるのでやや不完全燃焼。
- 4章で、他のシンプルなモデル、またその拡張型、本研究のモデルと比較して、モデルのバリデーションを行っている。この章がなくても、論文として成り立つと思われるが、この章によって、論文の質が高められている。
- 5章のディスカッションで、最初のアンモニアの議論は余計であると思う。なぜなら、十分に議論されている内容だから。しかも、アンモニアの同位体比は実測値がほとんどない。 それに続く他のディスカッションも、繰り返しのような気がする。
- JOのIFは0.8程度。しかし、この論文は、もっとレベルの高い別雑誌でも受け入れられると思う。



ご静聴、ありがとうございました。
ご質問、コメントをお願いします。