Depth-dependence in stable isotope ratio $\delta^{15}N$ of benthic POM consumers: The role of particle dynamics and organism trophic guild

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Abstract

The stable nitrogen isotope ratio ($\delta^{15}N$) is an established indicator of trophic hierarchy in marine food-web studies. Most of these studies presume that spatial variation in the primary food source is negligible, although a water-depth-related increase in $\delta^{15}N$ of particulate organic matter (POM) has been found in many systems. We used the high-Antarctic Weddell Sea shelf and slope ecosystem to test whether such a depth-related change in $\delta^{15}N$ is reflected at higher trophic levels, i.e., benthic consumers of POM. In suspension feeders (SF) we found a significant increase in $\delta^{15}N$ with water depth of up to 9.8‰, whereas in deposit feeders (DF) a depth effect was barely detectable. Particle-size preferences of the two feeding guilds combined with particle-size-dependent sinking velocities and biogeochemical reworking of POM are discussed as the major causes of these differences. It is essential to marine food-web studies to take into account the general depth effect on POM $\delta^{15}N$ as well as potential feeding-guild-specific differences in the response of POM consumer tissue $\delta^{15}N$ to avoid serious bias and misinterpretation of stable-isotope-based trophic information.
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1. Introduction

Analyses of trophic hierarchy based on stable nitrogen isotope ratio ($^{15}N/^{14}N = \delta^{15}N$) are an integral part of state-of-the-art food-web studies in marine ecosystems. The underlying principle is the enzymatic selection for the heavier isotope ^{15}N with each assimilation step in the food chain. Fractiona-

tion of ^{15}N is variable but averages a $\delta^{15}N$ increase of 3.3‰ per trophic level (e.g., Minagawa and Wada, 1984). Recently, within-population variability in $\delta^{15}N$ was additionally proposed as a descriptor of omnivory (Sweeting et al., 2005). Most studies of metazoan consumers rely on one important *a priori* presumption, namely that within-system spatial variation in $\delta^{15}N$ of the primary food source is negligible. This, however, may not necessarily hold true in systems of substantial water depth, where particulate organic

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matter (POM) originating from the euphotic-zone food web is considered to be the primary food source.

Composition and production of the euphotic-zone community are the principal determinants of formation and fate of POM. The origin of particles contributing to bulk POM in this water layer is obviously reflected in a $\delta^{15}N$ signature that tends to increase with particle size (3 to $>150\,\mu m$; Wada et al., 1987; Altabet, 1988; Rau et al., 1990; Wu et al., 1997). The POM particle-size spectrum at any water depth is a function of various interacting processes (see model in Stemmann et al., 2004), in particular (i) sinking velocity as determined by particle size and density (Stokes's law), (ii) coagulation and fragmentation, and (iii) consumption by zooplankton and by microorganisms (Kiørboe, 2000, 2001; Lee et al., 2004). These processes result in the rapid decrease of bulk POM and the alteration of biochemical POM composition (Suess, 1980; Wakeham and Lee, 1993; Boyd and Stevens, 2002).

In particular, biological and biochemical processes discriminate against individual organic components, as is evident in the increase of the C/N ratio of POM with depth (Tanoue and Handa, 1979; Wefer et al., 1982; Smith et al., 1992). The rapid loss of nitrogen compared to carbon is attributed mainly to hydrolytic enzymatic activity and microbial consumption, since bacteria primarily degrade nitrogen-rich compounds (Smith et al., 1992; Lee et al., 2004). However, microbial activity alters not only the general organic composition of POM, but also its isotopic composition. Biochemical processes during bacterial degradation result in the release of nitrogen depleted in ^{15}N and a corresponding enrichment in ^{15}N of the residual material (Saino and Hattori, 1980; Wada, 1980; Macko and Estep, 1984; Macko et al., 1986). Microbial consumption is thus reflected in an increase of POM $\delta^{15}N$ with depth, as observed in several oceanic areas. The overall increase in $\delta^{15}N$ may amount to 5 to $>10\permil$ between 0 and 1000 m depth (Saino and Hattori, 1980; Biggs et al., 1987; Rau et al., 1991; Altabet and Francois, 2001).

The central question for any food-web study is whether this depth-related change will cause a detectable depth trend in $\delta^{15}N$ of consumer species. The first indication for such a depth-related $\delta^{15}N$ increase owing to degeneration of the basal food source was found in higher trophic level consumers (fish and crustaceans) on the western Mediterranean slope (Polunin et al., 2001) and in the northeast

Atlantic Ocean (Rau et al., 1989). The effect of depth on $\delta^{15}N$ might, moreover, differ between small particles suspended in the water column and large, fast sinking particles depositing on the sea floor. The smaller the particle, the longer the residence time in the water column and the higher the rate of microbial alteration and the corresponding increase in $\delta^{15}N$. Since benthic suspension feeders (SF) depend on small suspended food particles, preferably well below $100\,\mu m$ in diameter (Reiswig, 1971; Ribes et al., 1998; Orejas et al., 2003), the depth-related increase in $\delta^{15}N$ of POM should be reflected within this trophic guild. In contrast, deposit-feeding organisms (DF) rely on material deposited on the sea floor and can handle particles across the whole size range of POM (see e.g., Massin, 1982). Since organic matter in the sediment mainly originates from larger and faster sinking particles which are supposed to be less exposed to microbial alteration during vertical transport, $\delta^{15}N$ increase with depth should be less pronounced within this trophic guild. We therefore hypothesize that:

(i) $\delta^{15}N$ of benthic POM consumers will increase with water depth, and
(ii) SF will show this effect more clearly than DF.

On the basis of a large dataset of $\delta^{15}N$ values referring to benthic species from the Weddell Sea shelf and slope, we present the first attempt to demonstrate a depth-related increase in $\delta^{15}N$ of primary POM consumers. The results are discussed in respect of known POM dynamics. If our hypotheses prove true, sampling and analysis strategies would have to be adjusted accordingly in order to avoid serious bias in estimates of organisms' trophic level or the degree of omnivory within populations.

2. Methods

Samples considered in this study were taken by means of trawls and grabs during three RV "Polarstern" expeditions into the northeastern Weddell Sea (expeditions ANT XIII/3 in 1996, ANT XV/3 in 1998, ANT XXI/2 in 2003). All samples were collected between December and February in the ice-free zone ranging from $70°30'S$ to $75°00'S$ and from $010°00'W$ to $027°20'W$ (Fig. 1). Benthic SF and DF were collected from the shelf and slope between 50 and 1600 m water depth.
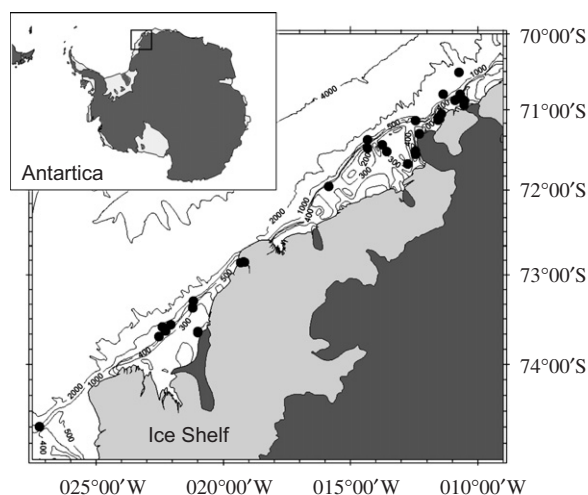
Fig. 1. Study area on the northeastern Weddell Sea shelf with sampling locations (●). Depth contours are in meters.

Table 1

Analysis of covariance (ANCOVA) of the effect of feeding guild (DF vs. SF) and covariate log(depth) on δ^{15}N

Source	df	Sum of squares	Mean square	p
Analysis of variance				
Model	3	315.640	105.213	<0.001
Error	178	681.894	3.831	
Total	181	997.534		
Effect tests				
log(depth)	1	86.081	22.470	<0.001
Feeding guild	1	4.946	1.291	0.257
log(depth)∗feeding guild	1	56.832	7.004	0.009

df = degrees of freedom.

Sampled taxa include amphipods, anthozoans, ascidians, bivalves, bryozoans, crinoids, pterobranchs, hydrozoans, sponges (Porifera), holothurians, irregular echinoids, sipunculan worms and echiuroid worms. Body tissue samples were thoroughly cleaned with seawater and stored deep-frozen at −30 °C until further preparation.

Back in the laboratory, the frozen samples were lyophilised for 24 h, ground to fine powder, and treated with $1 \, mol \, l^{-1}$ hydrochloric acid to remove inorganic carbon. Afterwards, samples were dried in an oven at 60 °C and ground again. Mass-spectrometric analysis of stable isotope composition was carried out in the GeoBioCenter in Munich (Thermo/Finnigan Delta plus, precision ⩽0.15‰), with stable isotope ratio of ^{15}N/^{14}N expressed as δ^{15}N in ‰ (for details on stable isotope terminology and measurement see, e.g., Peterson and Fry, 1987).

Analysis of covariance (ANCOVA) was applied to identify the effect of (log transformed) water depth, of feeding guild, and of taxon on individual δ^{15}N. Finally, the relation of δ^{15}N to water depth within feeding guilds was described by regression models.

3. Results

Our data set of POM consumers includes 42 data points of DF and 140 data points of SF. Body tissue δ^{15}N and log(depth) are significantly related ($p < 0.001$), but this relationship differs in slope between SF and DF, as indicated by the significant interaction term ($p = 0.009$, Table 1).

The DF data set comprises δ^{15}N values referring to seven species and four major taxa and covers the depth range 165–1600 m. δ^{15}N values range from about 6‰ to 9‰, except the two shallowest (165 m) data points, which have distinctly lower values (3.89‰ and 4.78‰, Fig. 2A). Taxon effects on δ^{15}N are not detectable. The fit of the regression model

$$\delta^{15}N_{DF} = 3.510 + 1.462 \times \log(depth);$$
$$N = 42, \quad r^2 = 0.090, \quad p = 0.049$$

is poor, and becomes insignificant ($p = 0.504$) if the two data points at 165 m water depth are excluded.

The SF data refer to 26 species and 10 major taxa, which were sampled in water depths between 65 and 880 m (Fig. 2B). δ^{15}N in SF increases significantly with log(depth). The relationship differs significantly in intercept between sponges and the remaining taxa, i.e., sponge δ^{15}N signatures are generally higher:

$$\delta^{15}N_{SF} = -8.580 + 6.506 \times \log(depth)$$
$$+ 1.552 \times Taxon;$$
$$N = 140, \quad r^2 = 0.530, \quad p < 0.001;$$
$$Taxon = [1, -1] \quad for \quad [Porifera, Others].$$

4. Discussion

All samples considered in this study were taken during the same season (austral summer) to avoid potential effects of seasonality in POM composition on consumer δ^{15}N. In order to ensure a clear
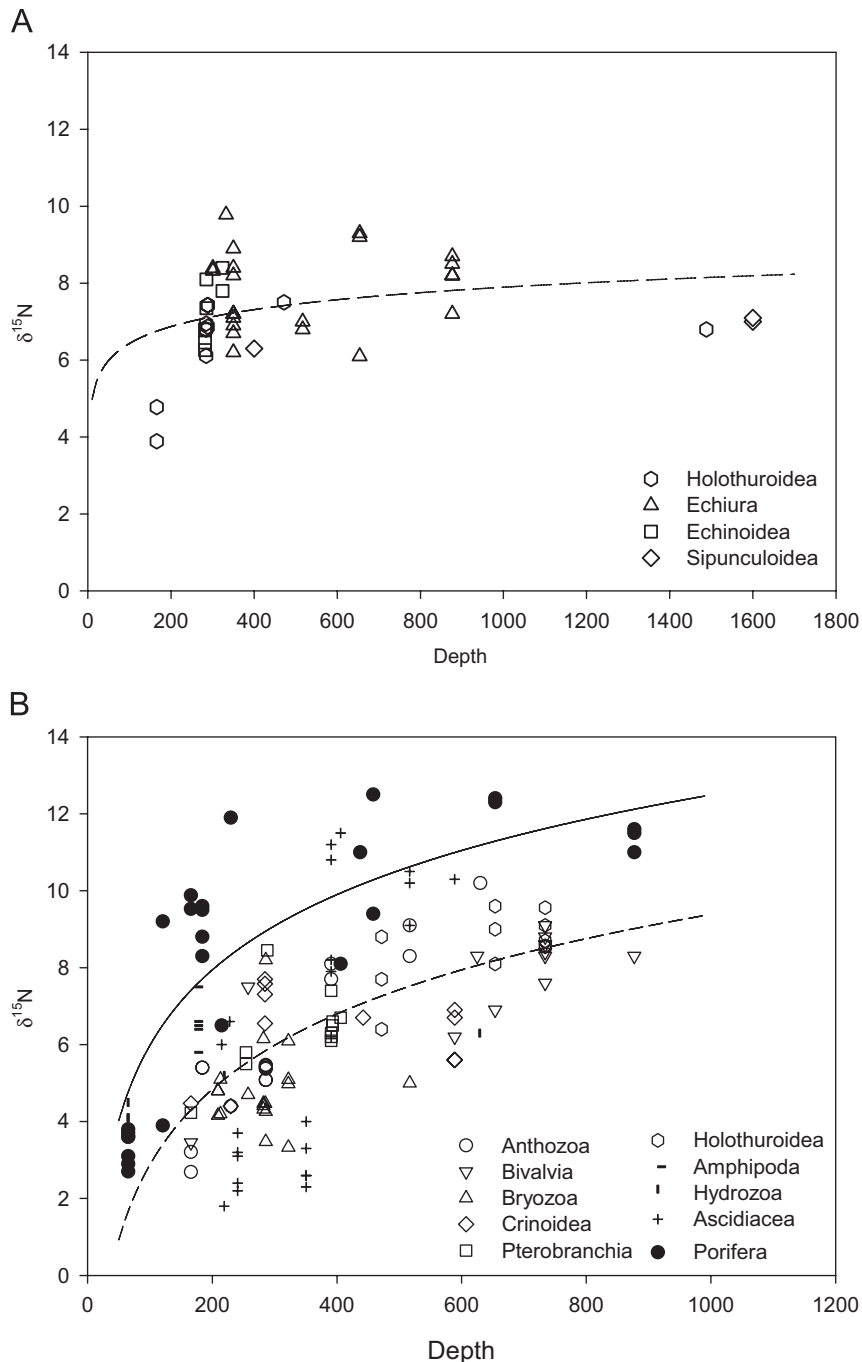
Fig. 2. Relationship between $\delta^{15}N$ [‰] and water depth [m] in (A) deposit feeders, DF, and (B) suspension feeders, SF, and adapted logarithmic regression models. Particular taxa are marked by different symbols. (A) DF: $\delta^{15}N = 3.510 + 1.462 \times \log(\text{depth})$ ($N = 42$, $r^2 = 0.09$, $p = 0.049$); (B) SF: $\delta^{15}N = -8.580 + 6.506 \times \log(\text{depth}) + 1.552 \times \text{Taxon}$; Taxon $= 1$ for Porifera (filled cycles, solid line), -1 for pooled remaining taxa (open symbols, dashed line) ($N = 140$, $r^2 = 0.53$, $p < 0.001$). Note different depth ranges in A and B.

separation of the two feeding guilds, SF and DF, we restricted our analysis to obligate DF (subsurface feeders and those that are morphologically constrained to feeding from the sediment surface) and to obligate SF (taxa that are morphologically constrained to feeding from the water column), i.e., we excluded taxa capable of both suspension-feeding and deposit-feeding (e.g., spionid polychaetes; Taghon

and Greene, 1992), as well as facultative predators of zooplankton, such as some suspension-feeding hydroids and octocoralls (Orejas et al., 2001).

These data clearly support our initial hypotheses: the increase of $\delta^{15}N$ in POM with depth is reflected in POM consumer tissue, in particular in suspension-feeding taxa. However, variability in $\delta^{15}N$ remains high, particularly in SF, even if effects of depth and of major taxon (Porifera versus remaining taxa) are taken into account. Most likely this variability is taxon related, as the SF data set contains at least 26 species that may differ in $\delta^{15}N$ enrichment rates (Minagawa and Wada, 1984; Lovvorn et al., 2005) or in feeding preferences such as selection for specific items (e.g., cnidarians; Orejas et al., 2003) or for a narrow particle-size range (e.g., sponges; Reiswig, 1971). Unfortunately, the limited number of data/species does not allow for a thorough statistical analysis.

The generally higher $\delta^{15}N$ values of sponges may be related to either (i) the restriction of sponge diet to the smallest particles (e.g., Gili et al., 2001), which are the most degraded (see Section 1), or (ii) the heavy colonization of sponge surfaces and interstices by bacteria (e.g., Webster et al., 2004), which are most likely included in the analysed tissue samples.

Our data indicate that in suspension-feeding POM consumers $\delta^{15}N$ increases with water depth in a non-linear way; i.e., the rate of change decreases with depth, with the major shift in $\delta^{15}N$ of up to 9.8‰ (sponges) occurring apparently in the upper 500 m. It remains questionable, however, whether such a depth effect exists in deposit-feeding POM consumers (Fig. 2A, B).

This consumer $\delta^{15}N$ distribution reflects what has been observed previously for particulate nitrogen (PN) $\delta^{15}N$ and may be linked to the dynamics of POM production and sedimentation. Overall POM dynamics in the Southern Ocean are comparable to those in other marine systems: bulk POM decreases with depth (Biggs et al., 1987; Bathmann et al., 1997; Carlson et al., 2000), and POM $\delta^{15}N$ increases simultaneously (Biggs et al., 1987; Rau et al., 1991). In Fig. 3 $\delta^{15}N$ values of small suspended and large sinking particles from the Sargasso Sea (Altabet, 1988) and the northeastern Indian Ocean (Saino and Hattori, 1980) are shown as an example. Depth-related changes in $\delta^{15}N$ of fast sinking PN that will be deposited on the sea floor are minor. $\delta^{15}N$ of suspended PN consumed by SF, in contrast, distinctly increases with depth, mainly within the upper 100–500 m of the water column.

This pattern is attributed to rapid POM turnover and degradation in the upper mesopelagial, especially
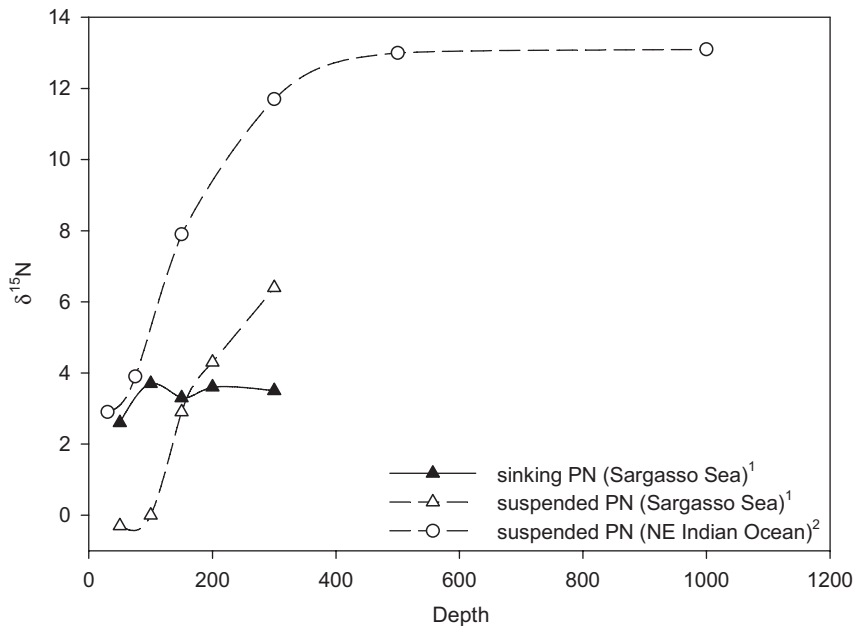

Fig. 3. Relationship between $\delta^{15}N$ [‰] and water depth [m] in suspended PN and sinking PN in the Sargasso Sea ([1]redrawn from Altabet, 1988, pp. 545–546, Tables 2 and 3, with permission from Elsevier Ltd.), and the northeastern Indian Ocean ([2]redrawn from Saino and Hattori, 1980, p. 753, Fig. 1, with permission from Macmillan Publishers Ltd.).

by mesozooplankton (Kiørboe, 2000, 2001) and by microorganisms that show highest abundance and activity in this zone of enhanced POM alteration (e.g., Lochte et al., 1997; Aristegui et al., 2002). $\delta^{15}N$ of SF from <100 m water depth was on average 3.6‰ (see Fig. 2B), which is about one trophic step above $\delta^{15}N$ of bulk POM observed in Southern Ocean surface waters during austral summer (0.4–1.6‰ between November and February; Biggs et al., 1987; Wada et al., 1987).

Large diatoms are not considered a principal food for benthic SF because of their large size and short period of availability (short-term blooms and rapid sedimentation; e.g., Scharek et al., 1999). Instead organisms of this trophic guild preferably consume particles from the pico- to nanoplankton fraction that are present year round, albeit in low concentrations during winter (Barnes and Clarke, 1995; Detmer and Bathmann, 1997).

If lost from the mixed layer, POM of this size exhibits extremely low sinking velocities (in general <1 m d^{-1}; Wakeham and Lee, 1993), owing to small size and low density (~ 1.1 g cm^{-3}; van Ierland and Peperzak, 1984). The rate of microbial alteration of these particles will be correspondingly high, which results in rapid loss of ^{14}N and the distinct changes in $\delta^{15}N$ observed in POM and its suspension-feeding consumers above 500 m water depth. The aggregation to marine snow can increase the sinking velocity of small particles but simultaneously accelerate degradation because of intensive colonization by bacteria and sometimes even by protozoans (see review in Kiørboe, 2001). Accordingly, the POM size spectrum will shift towards larger, rapidly sinking particles with increasing depth. Faecal material of zooplankton origin, for example, exhibits sinking velocities of up to 800 m d^{-1} (Cadée et al., 1992) due to large particle size and high particle density (1.22 g cm^{-3}; Komar et al., 1981) and thus provides an important food source for benthic consumers at greater depth (see e.g., Iseki, 1981; Fortier et al., 1994). In fact, Weddell Sea POM flux is dominated by krill faecal strings, faecal pellets and large diatom cells at depth greater than 250 m (Nöthig and von Bodungen, 1989; Bathmann et al., 1991). These particles make up the major part of organic matter that is deposited in the sediment.

Large OM particles originating from surface waters have *a priori* higher $\delta^{15}N$ values and experience less enrichment in ^{15}N by microbial decomposition during sinking (see Section 1 and Sargasso Sea data in Fig. 3). Once settled on the sea

floor, this fresh material is rapidly mixed into sediments by active bioturbation, and degraded slowly (Mincks et al., 2005), thus providing a "long-term" storage of high nutritive organic matter (Isla et al., 2006; Mincks et al., in press). Combined with sediment associated microorganisms, particle accumulation adds up to the rather consistent $\delta^{15}N$ of 4–6‰ measured in bulk surface sediment from various sites and depths in the Southern Ocean south of 60°S (e.g., Wada et al., 1987; Altabet and Francois, 1994; Mincks et al., in press). Accordingly, deposit-feeding consumers of this material exhibit about 3‰ higher $\delta^{15}N$ values (6–9‰) at all depths within the range considered here. Depth-independent $\delta^{15}N$ variability within this trophic guild is most likely caused by differences in the degree of particle selectivity or due to feeding in different sediment layers (Mincks et al., in press). Moreover, the probability of small, low $\delta^{15}N$ particles reaching the sea floor decreases exponentially with depth. Therefore, shallow water (above ~ 200 m) DF may show lower $\delta^{15}N$ values, as indicated by the two data points at 165 m (Fig. 2A).

In contrast to DF, SF are restricted mostly to the fine POM fraction (see above). At greater depth, SF therefore depend on small particles originating from fragmentation of large particles either in the water column or on the sediment surface (made available by resuspension). $\delta^{15}N$ of SF changes little at greater depth but is up to one trophic level higher than $\delta^{15}N$ of DF (see Fig. 2A, B). This indicates that the proposed particle fragmentation process involves a distinct increase in $\delta^{15}N$, possibly due to the intense microbial activity in the benthic boundary layer (e.g., Lee et al., 2004).

$\delta^{15}N$ of suspended and sinking POM in the surface layer might vary depending on season: Lourey et al. (2003) observed a decrease in PN $\delta^{15}N$ during summer due to the uptake of recycled ^{15}N-depleted ammonium. During winter and spring (after sea-ice melting), mean POM $\delta^{15}N$ might significantly increase as ice-associated POM exhibits values much higher than POM originating from the free water column (Rau et al., 1991). Hence, surface water POM $\delta^{15}N$ values ranging from -5‰ to $+6$‰ were found in the Weddell Sea (Rau et al., 1991). However, such "short-term" variability in ephemeral water column POM $\delta^{15}N$ is integrated in tissues of long-living consumers, and obviously buffered in the sediment (Lovvorn et al., 2005; Mincks et al., in press).

The observed depth effects on δ^{15}N of benthic POM consumers are unlikely to be restricted to the Weddell Sea, as POM is subject to comparable physical, biological and biogeochemical processes in all marine systems. δ^{15}N signatures might vary between oceanic regions; the general pattern of δ^{15}N depth dependence, however, should remain the same (see e.g., Fig. 3). Indirect evidence from higher trophic level consumers in bathyal communities (Polunin et al., 2001; Rau et al., 1989; see Section 1), moreover, points towards the propagation of the depth-related increase in δ^{15}N along the food chain.

5. Conclusion

Our data confirm previous observations of depth-related changes in PN δ^{15}N and provide strong evidence for a trophic-guild-specific depth-dependence of δ^{15}N in benthic POM consumers. The depth-related change in δ^{15}N of POM causes a distinct bias in range and average of δ^{15}N in benthic SF and their consumers, and thus has serious implications for marine food-web studies that integrate data over a wider depth range: (i) The observed δ^{15}N range of up to 9.8‰ in certain SF taxa is well above the average enrichment per trophic step, 3.3‰ (Minagawa and Wada, 1984), and this bias would shift affected taxa one or more levels up in the trophic hierarchy, thus affecting the whole trophic structure. (ii) Depth-dependent shifts in δ^{15}N strongly affect estimates of consumer omnivory based on δ^{15}N variability (see Sweeting et al., 2005). There are two possible methods of compensating for the depth effect on δ^{15}N: If both the δ^{15}N-to-depth relationship for all SF taxa as well as all trophic links originating from these taxa are known, then a numerical correction could be applied to the affected δ^{15}N values. This, however, seems to be quite a complex and costly method. Therefore, we propose a depth-stratified approach towards systems with a wide vertical extension, in order to minimise depth effects on consumer δ^{15}N.

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