^{15}N/^{14}N and ^{13}C/^{12}C in Weddell Sea invertebrates: implications for feeding diversity

Greg H. Rau[1], Thomas L. Hopkins[2], Joseph J. Torres[2]

[1] Institute of Marine Sciences, University of California, Santa Cruz, California 95064, USA
and
NASA-Ames Research Center, MS 239-4, Moffett Field, California 94035, USA

[2] Department of Marine Science, University of South Florida, St. Petersburg, Florida 33701, USA

ABSTRACT: Biomass δ^{13}C, δ^{15}N, and C/N were measured for each of 29 taxa of pelagic invertebrates sampled from the Weddell Sea in March 1986. The δ^{13}C values of these animals ranged from −33.2 to −23.9‰, and a significant negative logarithmic relationship was observed between these values and biomass C/N. This implies that the relative proportion of carbon-rich ^{13}C-depleted lipid in these animals significantly influenced the δ^{13}C of their bulk biomass. No such relationship with C/N is evident with respect to biomass δ^{15}N where values ranged from −1.2 to +7.3‰. This spread of values reflects a wide diversity of food sources and trophic positions among the species analyzed. Isotopic abundances within krill Euphausia superba varied with individual length, apparently reflecting dietary changes during growth. Isotope values within E. superba from the Weddell Sea overlap those of krill from other Southern Ocean locations in the Scotia Sea/Drake Passage, the Ross Sea, and Prydz Bay, Antarctica.

INTRODUCTION

Stable isotope abundances of carbon and nitrogen in animal biomass are largely determined by isotope abundances in the animal's food (Fry & Sherr 1989, Wada & Hattori 1990). Significant differences in isotope abundance among animals within a community have therefore been used as evidence of dietary differences among those animals. Furthermore, it may also be possible to determine the quantitative importance of potential food sources in an animal's diet by comparing isotope abundances within its biomass to that of the respective potential food sources. This approach can be problematic if many potential food sources exist, if the isotopic differences among these food sources are small, and/or if metabolic modifications to biomass isotope abundance are not considered. Regarding the last point, it has been shown that consumers are measurably enriched in the heavier isotope (especially ^{15}N) relative to their food, apparently the consequence of isotopically selective metabolism (e.g. Rau 1982, Minagawa & Wada 1984, Checkley & Entzeroth 1985). Elevations in animal ^{13}C/^{12}C and especially ^{15}N/^{14}N relative to those of the community's autotrophic food base have therefore been used to infer a consumer's trophic distance from that food base (e.g. Rau et al. 1983, Minagawa & Wada 1984, Fry 1988).

With the preceding in mind, we sought to measure isotopic differences among (and, to a lesser extent, within) a variety of invertebrate species collected from the upper water column of the Weddell Sea. The presumed simplicity of the autotrophic food base in this region – predominantly diatom primary production (Heywood & Whitaker 1984) with negligible organic inputs from land – suggested that isotopic differences among consumers could be interpreted in the context of feeding and trophic level differences without the complication of multiple and isotopically contrasting food bases often present in other marine environments (e.g. Rau et al. 1981, Peterson et al. 1985). In addition, earlier studies using gut content analyses have shown a wide diversity of diets among invertebrate consumers in the Weddell Sea (Hopkins 1985, Hopkins & Torres 1989). We anticipated that such diversity would be corroborated by the presence of large isotopic differences among the animal species sampled from this region.

METHODS

As part of the AMERIEZ expedition to the Weddell Sea in March 1986 (Sullivan & Ainley 1987), organisms for isotope analysis were collected using a 162 μm and 4 mm mesh opening-closing plankton and mid-water

trawl nets aboard the RV 'Melville' Trawls were con-
ducted to a depth of 200 m in the region bounded by 64
to 66° S latitude and 43 to 50° W longitude. Immediately
after arrival on deck animals were sorted by taxa, and a
subsample of each taxon stored frozen. Additional
samples of *Euphausia superba* were collected in and
outside of this area from a coarse mesh screen within
the 'Melville's' seawater intake system.

Upon return to the laboratory, the samples or sub-
samples of individuals from each taxon were prepared
and analyzed for total biomass $^{13}C/^{12}C$, $^{15}N/^{14}N$, and
C/N as described by Rau et al. (1989, 1990). By conven-
tion $^{13}C/^{12}C$ and $^{15}N/^{14}N$ are reported using 'δ' notation
as defined in the Fig. 1 legend.

RESULTS AND DISCUSSION

$\delta^{13}C$ measurements

Invertebrate $\delta^{13}C$ ranged from −33.2 to −23.9‰
(Fig. 1b), spanning the values previously reported for
Southern Ocean invertebrates (Eadie 1972, Sackett et
al. 1974, Wada et al. 1987, Fischer 1989). While we had
hoped to use such variations as evidence of dietary and
trophic differences among species, we noted that bio-
mass $\delta^{13}C$ is significantly and negatively related to
biomass C/N (Fig. 2). Such a relationship would be
expected if lipid concentration (rich in C, depleted in
^{13}C) was significantly influencing the $\delta^{13}C$ (and C/N) of
the bulk invertebrate biomass. In fact Wada et al.
(1987) suspected that lipid concentration was affecting
biomass $\delta^{13}C$ in the animals he analyzed from the Ross
Sea. Our data substantiate this idea, which clearly
complicates interpretation of animal $\delta^{13}C$ in the context
of feeding ecology, at least in this ocean province.

Elevated lipid content alone, however, cannot ex-
plain the general ^{13}C depletion observed in Antarctic
plankton. This is because no significant relationship
has been found between net plankton $\delta^{13}C$ and lipid
concentration in the Southern Ocean (Sackett et al.
1965, 1974), and because $\delta^{13}C$ and C/N did not co-vary
in suspended particulate organic matter (POM) sam-
pled from the Weddell Sea, the Scotia Sea, and Drake
Passage (Rau et al. 1991, in press).

$\delta^{15}N$ measurements

Biomass $\delta^{15}N$ values ranged from −1.2 to +7.3‰
(Fig. 1a), similar to those observed by Wada et al.
(1987) in the Ross Sea. Unlike the case with $\delta^{13}C$, we
found no systematic relationship between $\delta^{15}N$ and
C/N. This suggests that ^{15}N abundances here are inde-
pendent of variations in biochemical makeup, at least

as represented by variations in biomass C/N. We there-
fore interpret the range of $\delta^{15}N$ values present as
reflecting large dietary differences among these
species.

It has been repeatedly shown that biomass $\delta^{15}N$
increases in a systematic fashion as the trophic distance
from the base of the food web is increased (e.g. Rau
1982, Minagawa & Wada 1984, Checkley & Entzeroth
1985, Wada et al. 1987, Fry 1988). These studies found
a ca 3.5‰ increase in biomass $\delta^{15}N$ per trophic step.
Based on $\delta^{15}N$ measurements in surface-water-sus-
pended POM (Rau et al. in press), the $\delta^{15}N$ of the
phytoplankton food base in the Weddell Sea is esti-
mated to range from < −5‰ to perhaps as high as 0‰.
As in almost all studies of this type, pure phytoplankton
biomass was not isolated from bulk POM, and thus the
autotrophic food base of this system could not be accu-
rately characterized with respect to isotope abundan-
ces. Assuming an average phytoplankton value of
−4‰, the range of invertebrate $\delta^{15}N$ seen in the Wed-
dell Sea, ca −1 to +7‰, implies the presence of some 2
to 3 trophic levels (above the presumed food base)
within the invertebrate community sampled. A similar
number of trophic steps within the Weddell Sea
invertebrate community was inferred from gut content
analyses (Fig. 1d).

However, the relationship between biomass $\delta^{15}N$
and previously estimated trophic level for selected
Weddell Sea invertebrates is weak (Fig. 1a, d), and the
correlation between these parameters is not statisti-
cally significant. This contrasts with the study by Wada
et al. (1987) where a highly significant correlation
between isotope abundance and independently esti-
mated trophic level was found among a broader taxo-
nomic group of vertebrate and invertebrate consumers
from the Ross Sea. Several reasons can be offered for
this discrepancy. First, it is likely that the base of the
food web in our study area is more complex than
anticipated. As discussed above, considerable error
may be associated with assigning a range of $\delta^{15}N$
values for phytoplankton based solely on measure-
ments of bulk POM. Additionally, much higher $\delta^{15}N$
values have now been found in POM collected from sea
ice (Rau et al. in press). Ice POM is suspected to be an
important food source for at least some Southern Ocean
invertebrates (e.g. Hamner et al. 1983, Marschall 1988,
Stretch et al. 1988, Daly 1990). Isotopic variability
within the food base(s) used by Weddell Sea inverte-
brates may therefore be contributing to the isotopic
variability observed among these organisms, thus
influencing invertebrate isotope abundances beyond
that attributable to metabolic and trophic effects alone.
It is also possible that considerable error exists in the
trophic level estimates based on gut content analysis,
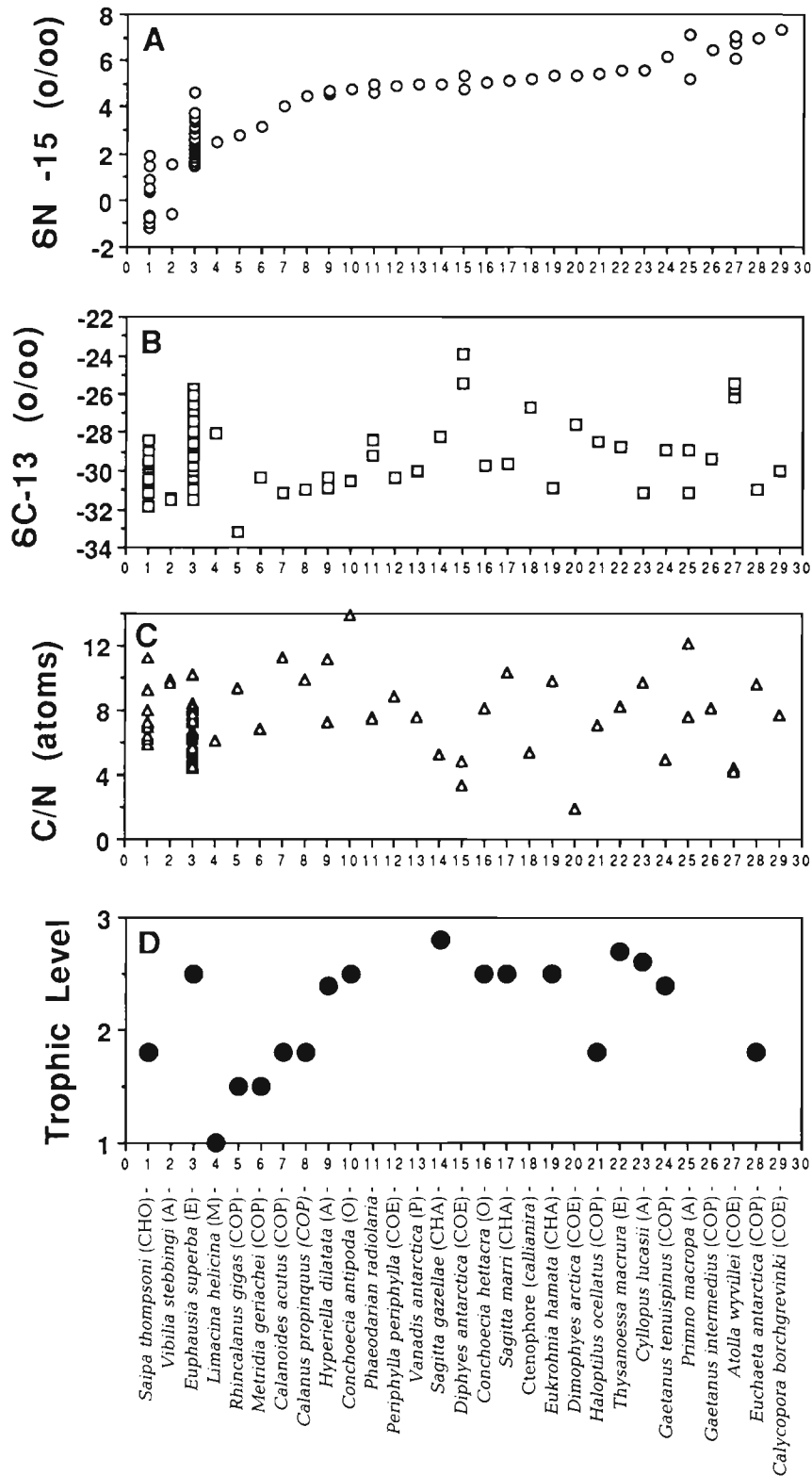due to difficulties in identifying gut contents and in

Fig. 1. (A) $\delta^{15}N$, (B) $\delta^{13}C$, and (C) C/N of bulk animal biomass for each of 29 taxa of invertebrates sampled from the western Weddell Sea in March 1986. $\delta^{13}C$ and $\delta^{15}N$ are defined as:

$$\delta X = [R(\text{sample})/R(\text{standard}) - 1] \times 1000\ (‰)$$

where $X = {}^{13}C$ or ${}^{15}N$, $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ and 'standard' = PDB carbonate or air N_2, respectively. That is, as 'δ' values increase (or decrease) the relative abundances of the heavier isotopes, ${}^{13}C$ or ${}^{15}N$, increase (or decrease). The analytical precision of these measurements is typically $\pm 0.2‰$. (D) Estimated consumer trophic levels (the number of consumer steps above primary production) for selected species from Hopkins & Torres (1989). Species are arranged in order of ascending mean $\delta^{15}N$. Higher taxonomic groupings are indicated by the following: A, amphipod; CHA, chaetognath; CHO, chordate; COE, coelenterate; COP, copepod; E, euphausiid; M, mollusc; O, ostracod; P, polychaete
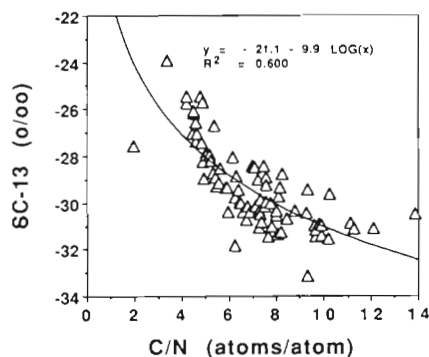
Fig. 2. Biomass $\delta^{13}C$ versus C/N for Weddell Sea invertebrate species as shown in Fig. 1

obtaining adequate numbers of individuals to determine temporal, spatial, and within-species variations in diet.

Nevertheless, among the taxa measured, coelenterates have many of the highest $\delta^{15}N$ values (Fig. 1a), in keeping with their observed role as predators (e.g. Biggs 1977, Purcell 1984). A number of copepod and amphipod species also show significant ^{15}N enrichment. With regard to the latter group, the range of $\delta^{15}N$ values is considerable (−0.6 to +7.1‰), reflecting diverse feeding strategies and trophic roles within this group. In contrast, the 3 chaetognath species measured fell within a narrow range of +5.0 to +5.3‰ (Fig. 1). The $\delta^{15}N$ of salps occupies the low end of the range with values of −1.2 to +1.9‰, consistent with observed herbivory (e.g. Harbison & Gilmer 1976, Hopkins & Torres 1989, Huntley et al. 1989).

The euphausid species analyzed differ in their $\delta^{15}N$, with *Thysanoessa macrura* possessing the higher value, +5.5‰, in contrast to mean of +2.3‰ for *Euphausia superba* (Fig. 1a). This apparently reflects the higher trophic position of *T. macrura* as indicated by gut analysis (Hopkins & Torres 1989). The $\delta^{15}N$ range of *E. superba*, +1.5 to +4.6‰, laces it in the lower third of the invertebrate $\delta^{15}N$ range, implying a trophic position slightly above that of a primary consumer such as salps (Fig. 1). While omnivory has been previously observed in this species (Price et al. 1988, Hopkins & Torres 1989), some controversy has arisen over its food preferences and trophic position (reviews by Daly [1990] and Quetin & Ross [1991]). Our data support its assignment as an omnivore, but clearly show that its diet does not overlap the more ^{15}N-enriched and therefore the more predatory consumers in our study (Fig. 1a).

Some evidence for changes in diet during the growth of *Euphausia superba* is evident in our data. When graphed as a function of individual length, the intermediate-sized individuals (ca 30 to 40 mm) display the lowest $\delta^{15}N$, with higher values present in

some of the smaller and larger individuals (Fig. 3a). Similarly, krill $\delta^{13}C$ and C/N also appear to synchronously change with krill length (Fig. 3b, c). It was anticipated that $\delta^{15}N$ would increase with increasing size, reflecting the transition to larger, and therefore trophically higher, food/prey as the krill grow (e.g. Rau et al. 1981, Minagawa & Wada 1984). Instead, the presence of elevated values in both small and large (young and old) adults indicates a more complicated feeding history, possibly reflecting seasonal and life-history changes in diet as previously hypothesized for *E. superba* in this region (e.g. Daly 1990, Quetin & Ross 1991). Analysis of various size classes of *E. superba*
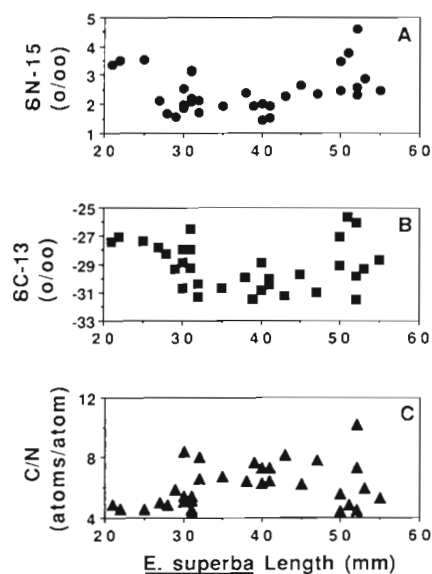

Fig. 3. *Euphausia superba*. (A) $\delta^{15}N$, (B) $\delta^{13}C$, and (C) C/N versus individual length (anterior carapace to tail) for krill sampled from the Weddell Sea, March 1986

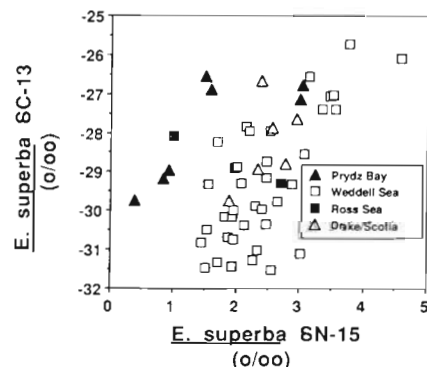Fig. 4. *Euphausia superba*. $\delta^{13}C$ versus $\delta^{15}N$ for individuals from: the Weddell Sea in March 1986 (this study); the Ross Sea (Jan 1984; Wada et al. 1987); the Drake Passage/Scotia Sea (March 1986; Rau unpubl.); and Prydz Bay, Antarctica (Jan–Feb 1985; Rau & J.-C. Miquel unpubl.)

collected at different times during the year would be useful in addressing temporal changes in krill diet. With regard to geographic variation in invertebrate isotope abundance, the δ^{13}C and δ^{15}N of Weddell Sea *E. superba* overlap those from the Drake Passage/ Scotia Sea, the Ross Sea, and Prydz Bay, Antarctica (Fig. 4). This implies that there is considerable dietary overlap among krill from different regions of the Southern Ocean.

In conclusion, large differences in biomass δ^{13}C and δ^{15}N were observed among upper-ocean invertebrate consumers from the Weddell Sea. While invertebrate δ^{13}C in this region appears to be significantly influenced by lipid content, the large range of δ^{15}N present in these animals provides a clear indication of the diversity of feeding strategies among species. Further isotopic measurements may prove useful in elucidating the diets and trophic positions of Southern Ocean invertebrates.

LITERATURE CITED

Biggs, D. C. (1977). Field studies of fishing, feeding and digestion in siphonophores. Mar. Behav. Physiol. 4: 261–274

Checkley, D. M., Entzeroth, L. C. (1985). Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. J. Plankton Res. 7: 553–568

Daly, K. L. (1990). Overwintering development, growth and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. Limnol. Oceanogr. 53: 1564–1576

Eadie, B. J. (1972). Distribution and fractionation of stable carbon isotopes in the Antarctic ecosystem. Thesis, Texas A & M Univ.

Fry, B. (1988). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. 33: 1182–1190

Fry, B., Sherr, E. (1989). δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. In: Ehleringer, J., Rundel, P. (eds.) Stable isotopes in ecological research. Springer-Verlag, New York, p. 196–229

Fischer, G. (1989). Stabile Kohlenstoff-Isotope in partikularer organischer Substanz aus dem Südpolarmeer (Atlantischer Sektor). Thesis, Univ. of Bremen

Hamner, W. M., Hamner, P. P., Strand, S. W., Gilmer, R. W. (1983). Behavior of antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. Science 220: 433–435

Harbison, G. W., Gilmer, R. W. (1976). The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps. Limnol. Oceanogr. 21: 517–527

Heywood, R. B., Whitaker, T. M. (1984). The marine flora. In: Laws, R. M. (ed.) Antarctic ecology, Vol. 2. Academic Press, London, p. 373–419

Hopkins, T L. (1985). Food web of an antarctic midwater ecosystem. Mar Biol. 89: 197–212

Hopkins, T L., Torres, J. J. (1989). Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. Deep Sea Res. 36: 543–560

Huntley, M. E., Sykes, P. F., Marin, V (1989). Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicate: Thaliacea) near the Antarctic Peninsula in the austral summer, 1983–1984. Polar Biol. 10: 59–70

Marschall, H.-P. (1988). The overwintering strategy of antarctic krill under the pack ice of the Weddell Sea. Polar Biol. 9: 129–135

Minagawa, M., Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim. Cosmochim. Acta 48: 1135–1140

Peterson, B. J., Howarth, R. W., Garrit, R. H. (1985). Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science 227: 1361–1363

Price, H. J., Boyd, K. R., Boyd, C. M. (1988). Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. Mar. Biol. 97: 67–77

Purcell, J. E. (1984). The function of nematocysts in prey capture by epipelagic siphonophores (Coelenterata, Hydrozoa). Biol. Bull. mar. biol. Lab., Woods Hole 166: 310–327

Quetin, L. B., Ross, R. M. (1991). Behavioral and physiological characteristics of the antarctic krill, *Euphausia superba*. Am. Zool. 31: 49–63

Rau, G. H. (1981). Low ^{15}N/^{14}N in hydrothermal vent animals: ecological implications. Nature, Lond. 289: 484–485

Rau, G. H. (1982). The relationship between trophic level and stable isotopes of carbon and nitrogen. In: Bascom, W. (ed.) Coastal Water Research Project – Bienial Report for the Years 1981–1982. Southern California Water Research Project, Long Beach, p. 143–148

Rau, G. H., Heyraud, M, Cherry, R. D. (1989). ^{15}N/^{14}N and ^{13}C/^{12}C in mesopelagic shrimp from the northeast Atlantic Ocean: evidence for differences in diet. Deep Sea Res. 36: 1103–1110

Rau, G. H., Mearns, A. J., Young, D. R., Olson, R. J., Schafer, H. A., Kaplan, I. R. (1983). Animal ^{13}C/^{12}C correlates with trophic level in pelagic food webs. Ecology 64: 1314–1318

Rau, G. H., Sullivan, C. W., Gordon, L. I. (in press). δ^{13}C and δ^{15}N variations in Weddell Sea particulate organic matter Mar. Chem.

Rau, G. H., Sweeney, R. E., Kaplan, I. R., Mearns, A. J., Young, D. R. (1981). Differences in animal ^{13}C, ^{15}N, and D abundance between a polluted and an unpolluted coastal site: likely indicators of sewage uptake by a marine food web. Estuar. coast. Shelf Sci. 13: 701–707

Rau, G. H., Takahashi, T., Des Marais, D. J., Sullivan, C. W. (1991). Particulate organic matter δ^{13}C variations across the Drake Passage. J. Geophys. Res. 96: 15131–15135

Rau, G. H., Teyssie, J.-L., Rassoulzadegan, F., Fowler, S. (1990). ^{13}C/^{12}C and ^{15}N/^{14}N variations among size-fractionated marine particles: implications for their origin and trophic relationships. Mar. Ecol. Prog. Ser. 59: 33–38

Sackett, W. M., Eadie, B. J., Exner, M. E. (1974). Stable isotope composition of organic carbon in recent Antarctic sediments. Adv. org. Geochem. 1973: 661–671

Sackett, W. M., Eckelmann, W. R., Bender, M. L., Be, A. W. H. (1965). Temperature dependence of carbon isotope composition in marine plankton and sediments. Science 148: 235–237

Stretch, J. J., Hamner, P. P., Hamner, W. M., Michel, W C.,

Cook, J., Sullivan, C. W. (1988). Foraging behaviour of antarctic krill *Euphausia superba* on sea ice microalgae. Mar. Ecol. Prog. Ser. 44: 131–139

Sullivan, C. W., Ainley, D. G. (1987). AMERIEZ 1986: a summary of activities on board the R/V Melville and USCG Glacier. Antarct. J. U.S. 22: 167–169

Wada, E., Hattori, A. (1990). Nitrogen in the sea: forms, abundances, and rate processes. CRC Press, Boca Raton

Wada, E., Terazaki, M., Kabaya, Y., Nemoto, T (1987). ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. Deep Sea Res. 34: 829–841

This article was submitted to the editor