

$^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure

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ABSTRACT: $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C/N were measured for each of 247 muscle tissue samples from 12 bird, 4 seal, and 4 fish species collected in the Weddell Sea primarily during March 1986. $\delta^{13}\text{C}$ values ranged from -31.3 to -22.0 ‰ and, in the case of fish and seal samples, varied inversely with C/N. This implied that lipid concentration significantly influenced these vertebrate $\delta^{13}\text{C}$ measurements. No such relationship was found between C/N and $\delta^{15}\text{N}$, where the latter values ranged from $+4.4$ to $+11.2$ ‰ with considerable overlap among many of the taxonomic groups measured. Notable exceptions to this were found in the Wilson's storm-petrel and the Kerguelan petrel, among which elevated $\delta^{15}\text{N}$ values of some individuals probably reflected feeding outside of the Weddell Sea. Significant feeding on vertebrate biomass was indicated by the ^{15}N enrichment of the southern giant fulmar and several snow petrel individuals. Some diet separation among crabeater, Antarctic fur, leopard, and Ross seals was also evident. Nevertheless, the overlap in $\delta^{15}\text{N}$ among most Weddell Sea vertebrates, coupled with an observed range of vertebrate values that was considerably narrower than that of their potential prey, supports the hypothesis that many of these higher consumers share a small number of common food resources and trophic levels.

INTRODUCTION

Due to present or potential human impact on populations of Antarctic krill, whales and other components of the Southern Ocean food web, considerable interest has focused on the trophic structure of this community. While Antarctic krill *Euphausia* spp. have long been reported to be an important food base for many higher consumers in these waters, the idea that a single invertebrate taxon provides the key nutritional link between primary production and higher consumers must now be tempered by observations that (1) primary production is consumed by micro- or macroplankton other than krill, (2) non-krill invertebrates are ingested in significant numbers by some higher consumers, (3) vertebrate prey can compose a significant fraction of some animals' diets, and (4) the diet for a given Antarctic taxa can change seasonally and spatially (e.g.

reviews by Nemoto & Harrison 1981, Everson 1984b, Laws 1984, Clarke 1985, Hempel 1985, 1990, Hewes et al. 1985, Ainley & DeMaster 1990, Ainley et al. 1991). A consensus on the nutritional interdependencies within the Antarctic marine food web has therefore been slow to emerge due in part to the logistical and interpretive difficulties imposed by the usual investigative methods employed.

In addition to observational techniques of studying animal diet such as stomach content analysis, measurement of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ in animal biomass has under certain circumstances proven useful in elucidating feeding relationships in a variety of marine settings. As reviewed by Fry & Sherr (1988) and Wada & Hattori (1990), the utility of such measurements for marine food web studies lies in the fact that stable isotope abundances of carbon and nitrogen in an animal are largely determined by the isotope abundance in the animal's food. Therefore, large differences in isotope abundances among animals within a community can provide evidence of significant differences in diet

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among those consumers. Conversely, similarities in isotope abundances among animals can signify similar diets provided that different combinations of isotopically contrasting food items have not by chance led to identical $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ among consumers.

Metabolic isotopic fractionations that occur within animals also need to be considered. It has been shown that marine vertebrates are measurably enriched in the heavier isotope (especially ^{15}N) relative to their food (e.g. Rau et al. 1983, Minagawa & Wada 1984, Schoeninger & DeNiro 1984). This is apparently the consequence of isotopically selective excretion or respiration of the lighter isotope. Elevations in an animal's $^{13}\text{C}/^{12}\text{C}$ and particularly $^{15}\text{N}/^{14}\text{N}$ relative to those of the community food base have thus been used to infer a consumer's trophic distance from that food base (e.g. Rau 1981, Minagawa & Wada 1984, Fry 1988, Hobson 1991). Indeed, Wada et al. (1987) used this approach to study lower animal trophic levels in the Antarctic Ross Sea. ^{13}C and ^{15}N natural abundances have also been used to investigate the ecology and biogeochemistry associated with high-southern-latitude seabird rockeries (Wada et al. 1981, Mizutani et al. 1985, 1986, 1991a, b, Mizutani & Wada 1988, Moors et al. 1988). Our intention was to use isotopic measurements to discern similarities and differences in vertebrate diets and trophic positions within the Weddell Sea.

METHODS

Vertebrates were sampled within a region bounded by 64° to 66°S latitude and 43° to 50°W longitude as part of the Antarctic Marine Ecosystem Research at the Ice-Edge Zone (AMERIEZ) Expedition to the Weddell Sea aboard the RV 'Melville' and the RV 'Glacier' during March 1986 (Sullivan & Ainley 1987). As part of a study of diet and morphology, birds were sacrificed at 15 locations within this region (Ainley et al. 1991), and a several-gram sample of breast muscle removed from each specimen. Fish were collected using a 4 mm mesh opening-closing midwater trawl (Hopkins & Torres 1989), and lateral muscle tissue was removed from each specimen. Abdominal muscle samples were taken from seals that had been sacrificed to determine stomach contents, demography, and reproductive history. Seal samples were also taken in a region ranging from 500 to 800 km NNE of the preceding study area during June and July 1988. The number of individuals sampled for any given species ranged from 1 (for the southern giant fulmar, the fish *Notolepis coatsi*, and the ross seal) to 32 individuals of Antarctic petrel. Common and Latin names for the taxa collected are listed in the legend to Fig. 1. All tissue samples were stored frozen prior to analysis.

In the laboratory each sample was prepared and analyzed for $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, and C/N as described by Rau et al. (1989a, 1990). By convention $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ are reported using 'δ' notation as defined in the Fig. 1 legend.

RESULTS AND DISCUSSION

$\delta^{13}\text{C}$ measurements

For the animals sampled, muscle $\delta^{13}\text{C}$ ranged from -31.3 to -22.0% with considerable overlap in values among taxa (Fig. 1B). Inverse and apparently nonlinear relationships between $\delta^{13}\text{C}$ and C/N were found within fish and seal species (Fig. 2), a feature also observed in Weddell Sea invertebrates (Rau et al. 1991a). This strongly suggests that biochemical makeup, in particular lipid content, had an important influence on these muscle $\delta^{13}\text{C}$ measurements. Lipid is both N- and ^{13}C -poor relative to other animal biochemical constituents, and its presence therefore increases C/N and depresses $\delta^{13}\text{C}$ as the lipid fraction in animal tissue increases (e.g. McConnaughey & McRoy 1979, Tieszen et al. 1983). Indeed, the trend in C/N observed among the fish species (Fig. 2) is mirrored by their lipid content (Donnelly et al. 1990). Lipid effects on animal $\delta^{13}\text{C}$ have been previously observed in a coastal Alaskan food web (McConnaughey & McRoy 1979), and were suspected by Wada et al. (1987) to influence carbon isotope abundances within Ross Sea animals.

In an attempt to remove lipid effects from our data, we used a C/N-based lipid correction, $\delta'^{13}\text{C}$ (see Fig. 1 legend), as suggested by McConnaughey & McRoy (1979). For many of the taxa these corrected values (range: -29.7 to -21.0%) were appropriately higher than the corresponding uncorrected $\delta^{13}\text{C}$ measurements of samples that had elevated C/N. The magnitude of these corrections was highest for several bird and fish species, while seal values were largely unaffected (Fig. 1B). As with uncorrected values, considerable overlap in $\delta'^{13}\text{C}$ is evident among many of the species.

Because animal $\delta^{13}\text{C}$ is largely determined by the $\delta^{13}\text{C}$ of the diet, these inter-taxa overlaps in isotope abundances (with or without lipid correction) indicate isotopic similarity among the respective bulk diets of many of these species. This is most likely a consequence of the use of common food resources, as is more fully explored below in the interpretation of $\delta^{15}\text{N}$ measurements. We refrain, however, from emphasizing $\delta^{13}\text{C}$ or $\delta'^{13}\text{C}$ to infer similarities or differences in these animals' diets because (1) we cannot vouch for the effectiveness of the indirect corrections used in removing lipid bias in this case, and therefore (2) we cannot

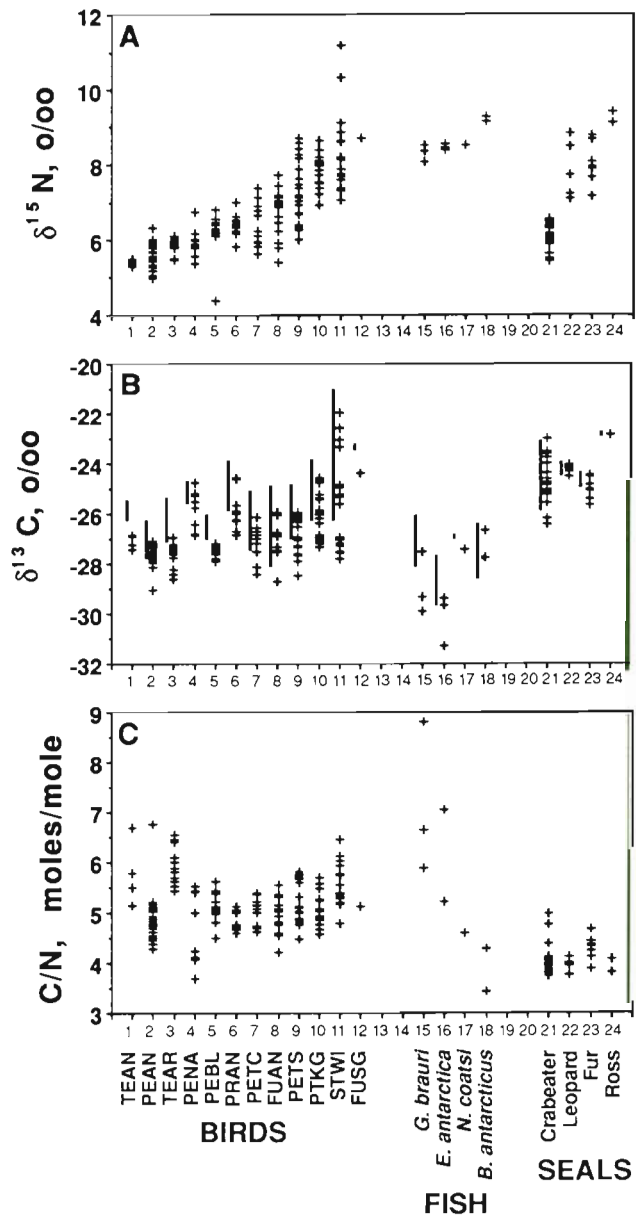


Fig. 1. (A) $\delta^{15}\text{N}$, (B) $\delta^{13}\text{C}$, and (C) C/N of muscle tissue from bird, fish, and seal species collected from the Weddell Sea. By convention, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are defined as $\delta x = [R(\text{sample})/R(\text{standard}) - 1] \times 1000$ (‰), where $x = {}^{13}\text{C}$ or ${}^{15}\text{N}$, $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ and 'standard' = PDB carbonate or air N_2 , respectively. That is, as δ values increase (or decrease) the relative abundances of the heavier isotopes, ${}^{13}\text{C}$ or ${}^{15}\text{N}$, increase (or decrease). The analytical precision of these measurements is typically ± 0.2 ‰. The range of lipid-corrected $\delta^{13}\text{C}$ values, $\delta'^{13}\text{C}$, for each species is denoted as a vertical line to the immediate left of the data points (+) for the respective $\delta^{13}\text{C}$ values: $\delta'^{13}\text{C} = \delta^{13}\text{C} + 6\{-0.207 + 3.9/[1 + 287(1 + 1/(0.246\text{C/N} - 0.775))]/93\}$ for $\text{C/N} > 4.0$ (McConnaughey & McRoy 1979). Within each animal group, species are arranged so that mean $\delta^{15}\text{N}$ increases from left to right. FUAN = Antarctic fulmar *Fulmarus glacialis*, FUSG = southern giant fulmar *Macronetes giganteus*, PEAN = Antarctic petrel *Thalassoica antarctica*, PEBL = blue petrel *Halobaena caerulea*, PENA = Adélie penguin *Pygoscelis adeliae*, PETC = cape petrel *Daption capense*, PETS = snow petrel *Pagodroma nivea*, PRAN = Antarctic prion *Pachyptila desolata*, PTKG = Kerguelan petrel *Pterodroma brevirostris*, STWI = Wilson's storm-petrel *Oceanites oceanicus*, TEAN = Antarctic tern *Sterna vitatta*, TEAR = Arctic tern *Sterna paradisaea*. Fish: *Gymnoscopelus braueri*, *Electrona antarctica*, *Notolepis coasti*, *Bathylagus antarcticus*. Seals: crabeater *Lobodon carcinophagus*, leopard *Hydrurga leptonyx*, Antarctic fur *Arctocephalus gazella*, Ross *Ommatophoca rossii*

be certain that diet is the primary factor influencing the carbon isotope measurements we conducted on these animals. Future vertebrate studies in this region should use representative tissues of low lipid content (e.g. feathers, whiskers, scales, etc.) or chemically extracted proteinaceous sub-fractions of biomass that are common to all species under study (e.g. Schoeninger & DeNiro 1984, Hobson 1987, Mizutani et al. 1990, Collier & Lyon 1991, Hobson & Sealy 1991). If significant temporal or seasonal variation in isotope abundance within diet is known or anticipated, it is then also necessary to consider the turnover rate of the tissue to be analyzed. This is required so that such temporal changes in diet will either be ignored or integrated by

the isotope abundance of the tissue analyzed (e.g. Tieszen et al. 1983).

$\delta^{15}\text{N}$ measurements

The muscle $\delta^{15}\text{N}$ of the animals sampled ranged from +4.4 to +11.2‰ (Fig. 1A), and unlike $\delta^{13}\text{C}$ values, showed no significant relationship with C/N. Based on considerable evidence from other marine studies (review by Wada & Hattori 1990), we here interpret the $\delta^{15}\text{N}$ of our samples as a function of both diet and trophic position.

In the case of fish, the range of $\delta^{15}\text{N}$ values is remark-

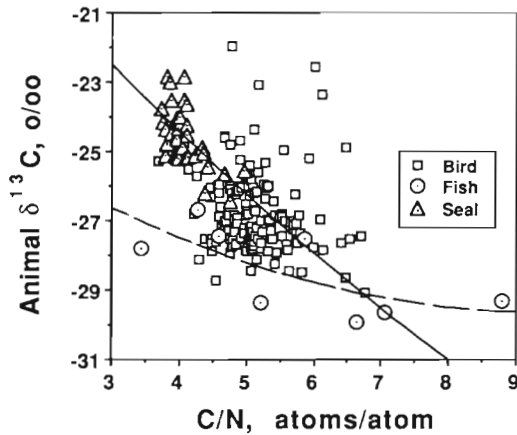


Fig. 2. $\delta^{13}\text{C}$ versus C/N measured in Weddell Sea vertebrate muscle. Data from Fig. 1B, C. Continuous line denotes best second-order polynomial fit to seal data ($y = -16.0 - 2.4x + 0.06x^2$; $r^2 = 0.37$; $r \neq 0$, $p = 0.05$, $n = 37$). Dashed line is best fit to fish data ($y = -23.1 - 1.4x + 0.07x^2$; $r^2 = 0.50$; $r \neq 0$, $p = 0.05$, $n = 8$)

ably narrow given both the intra- and inter-species ranges found among 29 invertebrate taxa from the Weddell Sea (see Fig. 3), encompassing most if not all potential fish prey in this region. While the small number of fish analyzed in our study precludes generalization, the existing isotopic data argue that dietary differences among these 4 fish species are small. Antarctic krill have been noted as a common food item for 3 of the 4 species reported here (Everson 1984a, Williams 1985), while Hopkins & Torres (1989) found that copepods dominated the gut contents of *Bathylagus antarcticus* examined from the Weddell Sea.

In contrast to the fish values, seal $\delta^{15}\text{N}$ ranged more widely (from +5.4 to +9.4‰; Fig. 1A), with some dietary diversity indicated among the 4 seal taxa as denoted by interspecies differences in $\delta^{15}\text{N}$. For example, crabeater seal values clustered near +6‰, while replicate measurements of a single Ross seal individual yielded values near +9‰ (Fig. 1A). This isotopic difference between these species is consistent with observed differences in diet. In a review of Antarctic seal nutrition, Laws (1984) lists krill as the primary food (> 90%) of the crabeater species, compared to < 10% of the Ross seal diet, with squid noted as the principle food item for the latter species.

Both Antarctic fur seal and leopard seal $\delta^{15}\text{N}$ values clearly fall between those of the Ross and crabeater seals (Fig. 1A), and their overlap implies that they share similar trophic positions if not common food resources. In contrast to this conclusion, leopard seals are regarded as significant predators on other vertebrates, principally penguins, while Antarctic fur seals are reported to feed primarily on krill and squid (Laws

1984, Siniff & Stone 1985, Green & Williams 1986, Lowry et al. 1988). However, fur seals are known to also feed on penguins (Bonner & Hunter 1982, D. Ainley pers. obs.).

Bird $\delta^{15}\text{N}$ exhibited a much larger range (+4.4 to 11.2‰) than that of the other taxa (Fig. 1A), but with considerable overlap in values among many of the bird species. Such overlap again implies that trophic positions and food resources are commonly shared. This is corroborated by gut content analyses of many of the same bird individuals used in this study, where 19 of the 26 interspecies diet overlaps shown by $\delta^{15}\text{N}$ are also indicated by the presence of common prey items within gut contents (Ainley et al. 1991) of the 10 species common to both studies (Table 1). A notable discordance between the 2 methods in identifying diet similarity is present for the Wilson's storm-petrel and the Kerguelan petrel. Only one diet overlap with other taxa is indicated by $\delta^{15}\text{N}$ data for each of these 2 species, whereas stomach content analyses show diet similarity with 8 to 9 other species (Table 1).

In the case of the Wilson's storm-petrel, some individuals had $\delta^{15}\text{N}$ (and $\delta^{13}\text{C}$) values that were clearly higher than those of the other taxa (Fig. 1A, B). This may reflect considerable feeding and biomass formation outside of the Weddell Sea, consistent with their known migration to the lower Northern Hemisphere during austral winter (Watson 1975). The Kerguelan petrel is also known to spend much of its annual cycle north of the Antarctic Convergence (Watson 1975). Elevated bird $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values would be anticipated in such species, given that lower-latitude plankton food bases tend to be enriched in ^{13}C and ^{15}N relative to those in Antarctic waters (e.g. Rau et al. 1982, 1989b, 1991c, Wada et al. 1987). The relatively large range of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ among the Wilson's storm-petrel individuals, however, shows that a large intra-species variation in diet/migration is present (Fig. 1A, B).

Another significant migrator in our study is the Arctic tern. However, unlike the Wilson's storm-petrel, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of this tern overlap many of the bird species endemic to the Southern Ocean (Fig. 1a, b). This may corroborate speculation that little or no low-latitude feeding is conducted by Arctic terns during their journey between residences in the high-latitude Northern and Southern Hemispheres (Watson 1975), where ^{13}C - and ^{15}N -depleted food bases are characteristic (e.g. Rau et al. 1982, 1991a, Wada et al. 1987, Schell & Ziemann 1988, Saupe et al. 1989).

Among the highest $\delta^{15}\text{N}$ values for endemic bird species were those of the southern giant fulmar and the snow petrel (Fig. 1A). Such ^{15}N enrichment is consistent with the fulmar's known role as a predator/scavenger on bird, seal, and whale biomass. The snow

Table 1. Determination of isotopic and diet similarity among Weddell Sea bird species sampled during March 1986. Species codes as in Fig. 1. Within the matrix vertices, 'I' denotes diet similarity as indicated isotopically by failure to reject the hypothesis that the $\delta^{15}\text{N}$ means of 2 species are equal. A critical difference, D_{crit} , was calculated for each comparison of 2 means such that $D_{\text{crit}} = Q_{0.05} s_x (n_i^{-1} + n_j^{-1})^{0.5}$, where $Q_{0.05}$ (= 4.6) is the Studentized Range statistic for $p = 0.05$, for 11 treatments and with 177 degrees of freedom; s_x is the pooled standard deviation (= 0.64); and n_i and n_j are the number of individuals analyzed within any 2 species i and j , respectively ('n' values in table). The hypothesis that the mean $\delta^{15}\text{N}$ of species i , x_i , was equal to the mean of species j , x_j , was rejected if $|x_i - x_j| > D_{\text{crit}}$. These tests did not include the species FUSG because only one individual of this species was analyzed. 'N' denotes that diet similarity was found by Ainley et al. (1991) based on numbers of common prey taxa found in stomachs of most of the same bird individuals analyzed for $\delta^{15}\text{N}$ (above). 'W' identifies diet similarity among the same birds based on consideration of the weight contribution of each prey taxon found in bird stomachs (Ainley et al. 1991). These stomach content analyses did not include TEAN species. Otherwise, an asterisk denotes that significant differences in both $\delta^{15}\text{N}$ and stomach contents were found between indicated bird taxa

Species	$\delta^{15}\text{N}$	n	FUSG	FUAN	PEAN	PEBL	PETC	PETS	PRAN	PTKG	STWI	TEAR	PENA	TEAN
			8.7	6.7	5.6	6.3	6.5	7.2	6.4	7.8	8.3	5.9	5.9	5.4
			1	15	32	15	12	22	11	19	17	11	9	4
FUSG	8.7	1												
FUAN	6.7	15			N	I	IN	W	I	N	N	IN	IN	I
PEAN	5.6	32				I	IN	•	IN	N	N	IN	IN	I
PEBL	6.3	15					I	IN	W	•	W	I	I	I
PETC	6.5	12						I	IN	N	N	IN	IN	I
PETS	7.2	22							IN	IN	W	•	•	•
PRAN	6.4	11								N	N	W	IN	I
PTKG	7.8	19									IN	N	N	•
STWI	8.3	17										N	N	•
TEAR	5.9	11											IN	I
PENA	5.9	9												I
TEAN	5.4	4												I

petrel has been reported to consume significant quantities of fish (e.g. Ainley et al. 1991). Parenthetically, we assume that the effect of extreme aridity in increasing animal $\delta^{15}\text{N}$ reported for African land mammals (e.g. Ambrose & DeNiro 1987, Sealy et al. 1987) is not relevant to our interpretation of the $\delta^{15}\text{N}$ variations found among endemic Weddell Sea bird and seal taxa. If these or other metabolic effects were variably operating within certain taxa we would expect to see some higher $\delta^{15}\text{N}$ values and greater intra- and interspecific isotopic variations than encountered.

Food web implications

The smaller range of $\delta^{15}\text{N}$ values for Weddell Sea vertebrates relative to that of invertebrates implies less trophic and diet diversity in the former animal group (Fig. 3). Indeed, the overlap in $\delta^{15}\text{N}$ values between these 2 groups indicates that many vertebrate and invertebrate species share common trophic positions if not food sources. It has been repeatedly demonstrated that marine animal $\delta^{15}\text{N}$ increases by 3 to 4‰ per trophic level (e.g. Rau 1982, Minagawa & Wada 1984, Schoeninger & DeNiro 1984, Wada et al. 1987, Fry 1988, Goering et al. 1990). Applying a per-trophic-level $\delta^{15}\text{N}$ increase of 3.3‰ found by Wada et al. (1987) in the Ross Sea, the isotopic range expected in the diet of the endemic Weddell Sea vertebrates can be calculated

by subtracting 3.3‰ from the extremes of these species' $\delta^{15}\text{N}$ range, +4.4 to +9.4‰. This yields an estimated vertebrate diet $\delta^{15}\text{N}$ range of +1.1 to +6.1‰, values that lie in the center of the $\delta^{15}\text{N}$ range observed for 29 invertebrate species from this same region (Fig. 3). Antarctic krill $\delta^{15}\text{N}$ values lie conspicuously in the middle of this span of values (Fig. 3) that also include the $\delta^{15}\text{N}$ of several species of copepods and amphipods. This feature may be consistent with observations that these species, in particular krill, are the dietary staple of many Antarctic vertebrate consumers (e.g. Ainley et al. 1991, Ainley & DeMaster 1990). A similar isotopic study in the high Arctic also recently found considerable dietary overlap among marine invertebrates, with strong dependence on invertebrate prey (Hobson & Welch 1992).

While squid were not measured by our study, Wada et al. (1987) reported $\delta^{15}\text{N}$ values of +7.0 and +7.2 for 2 individual *Kondakovia longimama* from the northern Weddell Sea. These values occupy the extreme high end of the $\delta^{15}\text{N}$ range found for other Weddell Sea invertebrates and are within the range of values we found for vertebrate consumers (Fig. 3). This suggests that rather than being predator and prey, respectively, vertebrates and squid share common prey/food resources. Again, using a per-trophic-level enrichment factor of 3.3‰, animals preying exclusively on such squid would be expected to have $\delta^{15}\text{N}$ values in excess of +10‰, clearly above values found in endemic verte-

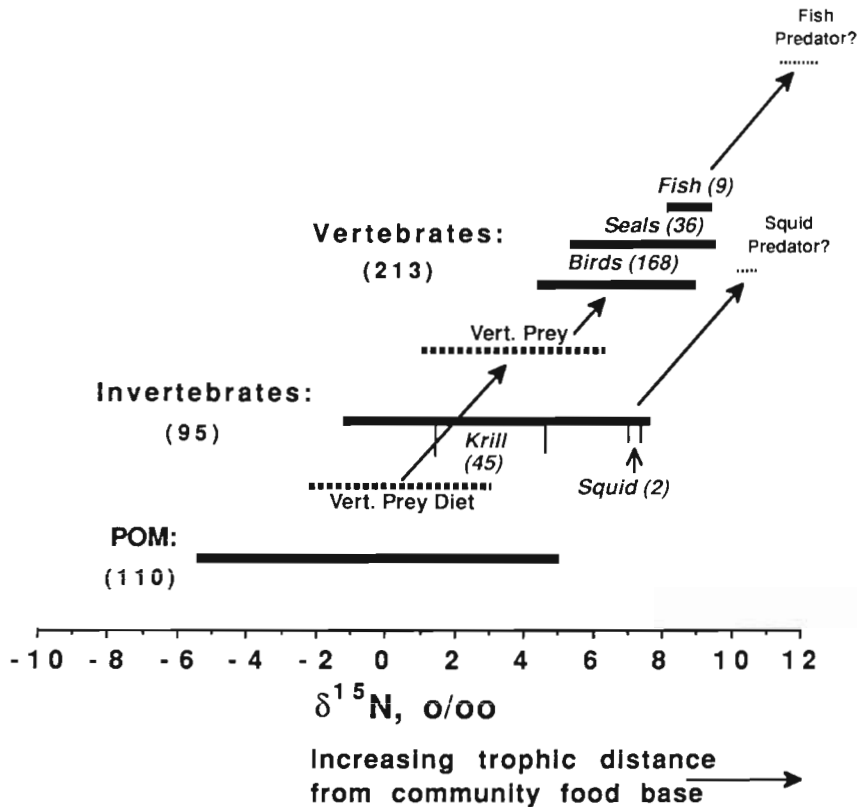


Fig. 3. Observed and predicted $\delta^{15}\text{N}$ ranges for Weddell Sea: suspended particulate organic matter (POM, retained on Whatman GF/F filters; Rau et al. 1991b); invertebrates (29 taxa including krill; Rau et al. 1991a); squid (Wada et al. 1987); vertebrates (excluding migrators Wilson's storm-petrel and Arctic tern; present study). Categories are arranged so that mean $\delta^{15}\text{N}$ increases from bottom to top. Numbers of analyses for each group are in parentheses. $\delta^{15}\text{N}$ range of vertebrates' prey was estimated by subtracting 3.3‰ from the total vertebrate $\delta^{15}\text{N}$ range (Wada et al. 1987). Similarly, the potential $\delta^{15}\text{N}$ range for the diet of vertebrates' prey is also estimated. The ranges of $\delta^{15}\text{N}$ expected for exclusive predators of either squid or fish are each estimated by adding 3.3‰ to the squid or fish $\delta^{15}\text{N}$ ranges, respectively. Diagonal arrows link selected prey/diet $\delta^{15}\text{N}$ ranges with respective predator $\delta^{15}\text{N}$ ranges. Based on numerous observations in other marine ecosystems (Wada & Hattori 1990), increasing animal $\delta^{15}\text{N}$ values are assumed to represent increasing trophic distance from the community food base. See text for discussion

brate species (Fig. 3). Further measurements of relevant Antarctic squid taxa are obviously needed to confirm these conclusions.

Nor do $\delta^{15}\text{N}$ measurements indicate that fish are the major food item for vertebrate consumers. Applying the same '+3.3‰ per trophic level' rule as used for the squid data above, exclusive fish predators should exhibit $\delta^{15}\text{N}$ values substantially above +10‰ (Fig. 3). It is again surprising that no endemic animal had $\delta^{15}\text{N}$ values higher than this, given that fish and other vertebrate remains were commonly observed in the stomachs of many of the same individuals analyzed in this present study (Ainley et al. 1991). Hempel (1990) also emphasized the importance of pelagic fish in the diet of Weddell Sea higher consumers.

We can offer several possible explanations for such discrepancies in diets implicated by $\delta^{15}\text{N}$ and by gut analyses. First, the numbers of $\delta^{15}\text{N}$ measurements for both fish and squid are small and may not be representative of the Weddell Sea populations available for predation. Secondly, the '+3.3‰ increase in $\delta^{15}\text{N}$ per trophic level' rule may not be applicable to the animals or tissues analyzed in this study. This could be due to nitrogen metabolism and associated isotope fractionation(s) within Weddell Sea animals that differ in some way from those generally observed elsewhere. Lastly, the long-term importance of squid and fish in vertebrate diets may have been overestimated by previous,

seasonally restricted stomach content analyses. An important difference between the isotope and the stomach content approach to diet studies is the time scale each method addresses. While stomach contents of an animal may reflect its diet for the last several meals, the isotope abundance in the animal's tissues are affected by the isotope abundances in its diet integrated over months or years depending on growth and biomass turnover of the animal tissue analyzed (e.g. Tieszen et al. 1983).

In conclusion, given the taxonomic diversity of the vertebrates analyzed and the isotopic variability among their potential invertebrate (and vertebrate) prey, it is noteworthy that vertebrate $\delta^{15}\text{N}$ values do not range more widely and that higher ^{15}N enrichment is not present in the non-migratory species sampled. This feature is consistent with a food web whose number of trophic steps is small and where a small subset of the available prey species are nutritionally important to most vertebrate consumers. The similarity between the anticipated range of vertebrate-diet $\delta^{15}\text{N}$ and the $\delta^{15}\text{N}$ of Antarctic krill is consistent with other studies showing krill to be the key trophic intermediary between primary production and many higher vertebrate consumers in this region. Further research on temporal, spatial, and taxonomic variations in isotope abundances within Southern Ocean animals would be helpful in addressing these issues.

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