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Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of larval krill, *Euphausia superba*, and two of its potential food sources in winter

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Abstract. Natural abundances of ^{13}C ($\delta^{13}C$) and ^{15}N ($\delta^{15}N$) were measured in larval krill (*Euphausia superba*), suspended particulate organic matter (POM) and ice-associated POM during early and late winter along the west coast of the Antarctic Peninsula. Larval krill were enriched in ^{13}C ($\delta^{13}C \geq 27‰$) relative to both larvae and adults sampled during summer months ($\delta^{13}C$ generally $\leq 27‰$). Elevated $\delta^{13}C$ values were also recorded in suspended POM ($\delta^{13}C \geq 21‰$) during early winter. These data imply that (i) seasonal shifts in the isotopic composition of larval krill need not result from changes in diet and (ii) mechanisms other than CO_2 limitation in the ice can account for ^{13}C enrichments in ice-associated POM. Stable carbon isotopes could not be used, in this study, to discern between suspended POM and ice-associated POM as alternative food sources for larval krill. During one early winter sampling period, larval krill were markedly depleted in ^{15}N ($\delta^{15}N < 1‰$), suggesting that they are primarily herbivorous prior to exploiting ice-associated food resources. Mechanisms are proposed to explain variation in the isotopic composition of POM and larval krill, and will be of particular interest to those investigating food web dynamics and biogeochemical processes in the region.

Introduction

Seasonal variation in ice coverage is thought to affect the winter-over survival and subsequent recruitment of larval and post-larval krill to the adult population (Ross and Quetin, 1991). Larval krill feed on ice-associated biota, algae in particular, and may be obligate consumers of this food resource during austral winter when phytoplankton levels in the water column are extremely low (Stretch *et al.*, 1988; Daly, 1990; Smetacek *et al.*, 1990; Quetin and Ross, 1991). Quantifying the role of ice biota in the early life history of *Euphausia superba* is necessary to understand more fully the effects of large-scale differences in ice cover on the population dynamics of krill.

Carbon and nitrogen stable isotope ratios might be useful to characterize the role of potential alternative food resources in the winter diet of *E.superba*. These isotope ratios in consumers largely reflect those assimilated, and can be used to trace and/or discriminate among dietary sources with distinct isotopic composition (Peterson and Fry, 1987). Reported measures of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in suspended particulate organic matter (POM) from the Southern Ocean and POM associated with sea ice, two alternate food sources, often differ (Fischer, 1991; Rau *et al.*, 1991b). This difference suggests that concurrent isotopic analyses of suspended POM, ice-associated POM and krill larvae collected at appropriate time and space scales might be used to resolve the relative importance of ice-associated food resources in the diet of larval krill.

During the austral summer, December–March, suspended POM in the Southern Ocean is characteristically depleted in ^{13}C (Sackett *et al.*, 1965; Rau *et al.*, 1982,

1989, 1991c; Wada *et al.*, 1987; Fischer, 1991; Fontugne *et al.*, 1991; Wada and Hattori, 1991) and is isotopically lighter than POM in or associated with sea ice. Explanatory mechanisms center on inorganic carbon and its availability as a substrate for photosynthesizing microalgae. Elevated levels of CO_2 (aq) in waters south of the polar front are thought to underlie low $\delta^{13}C$ in phytoplankton (see Rau *et al.*, 1989, 1991c), whereas algae growing in or associated with sea ice are often assumed to be CO_2 limited and, as a result, relatively enriched in ^{13}C (see Wada *et al.*, 1987; Fischer, 1989, 1991).

Less is known about stable nitrogen isotopes. Wada *et al.* (1987) confirmed a general pattern of ^{15}N enrichment with increased trophic level, but noted variable values in phytoplankton-dominated particulate matter. Rau *et al.* (1991b) also reported large $\delta^{15}N$ variations in POM. However, elevated values were found exclusively in POM in or associated with sea ice. The authors suggested that spatial and temporal changes in the concentrations and isotopic abundances of ammonium may underlie their observations. The reported isotopic variability within the food base provides an avenue for further investigating the coupling between larval krill and their ice-associated food resources.

Presented here are isotopic data and their interpretation from three winter cruises to a region west of the Antarctic Peninsula. The use of stable isotopes of carbon and nitrogen as indicators of ice-associated food resources in the diet of larval krill is evaluated and, in light of the findings, alternative mechanisms to explain temporal and spatial variation in the isotopic ratios of POM source material and krill are discussed.

Method

Study area and sampling overview

Larval krill and two likely food sources were sampled during three separate cruises to an offshore region northwest of Adelaide Island along the west coast of the Antarctic Peninsula (Figure 1). From 26 to 29 May 1991 (early winter), larval krill and ice-associated POM were collected opportunistically by divers in areas of rapidly forming sea ice. Suspended POM was collected from ice-free surface water ~80 km north of a recognizable ice edge zone. During 13–29 September 1991 (late winter, early spring), samples of krill and POM were collected at selected stations along a transect originating in ice-free waters and penetrating into an area of heavy pack ice. Water samples were also collected at these stations for the determination of inorganic nutrient concentrations and isotopic measurements of dissolved inorganic carbon. Samples of krill and POM in both open and ice-covered waters were also collected during 9–23 June 1993 (winter).

Collection and preparation of samples

Krill. Animals in open waters and areas of 'light' pack ice were collected with either a 1.6 × 0.8 m trawl fitted with paired 505 μm mesh nets or a 1 m diameter ring net with the same mesh size. Nets were towed obliquely between 300 m and the surface. In 'heavy' pack ice, either a 60 cm diameter bongo net or a 1 m ring

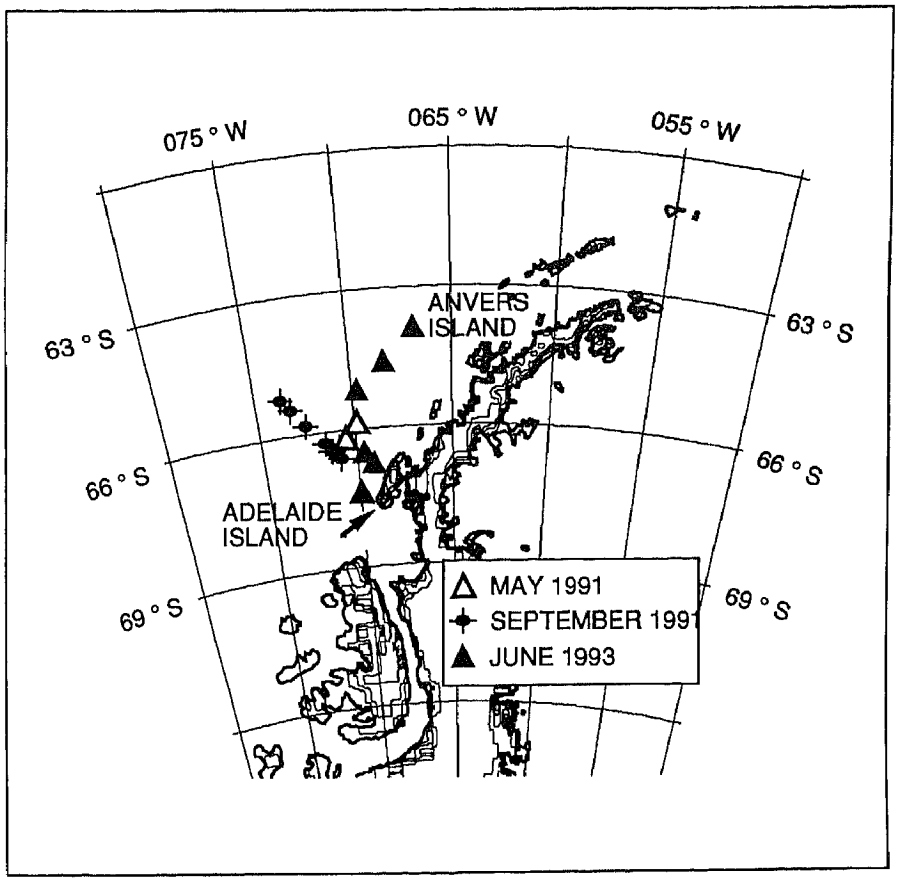

Fig. 1. Sampling stations occupied during each of the three winter cruises.

net (505 μm mesh) was towed vertically from the same depth. Krill closely associated with the undersurfaces of sea ice were collected by divers with hand-held aquarium nets. Larval krill were held in filtered seawater for 12–24 h after collection to allow the majority of food materials in their digestive systems to clear. Individuals were then staged (Fraser, 1936) and measured for total length (tip of rostrum to the end of uropods) under a dissecting microscope. Larvae of like stage were combined (five or more per sample), placed directly in glass vials and dried at 60°C in preparation for stable isotope analyses, i.e. $\delta^{13}C$ and $\delta^{15}N$.

Suspended particles. In May 1991, suspended POM was collected with a 10 cm diameter phytoplankton net (20 μm mesh) towed vertically between 0 and 100 m until clogged. Concentrated particulate matter was transferred to 20 ml glass scintillation vials via pipette, stored frozen (<–20°C) and subsequently dried at 60°C.

In September 1991, seawater was collected at 60 m with either 5 or 10 l Niskin bottles. Suspended particles were concentrated via filtration (vacuum ≤7 p.s.i.) on

pre-combusted (500°C, 4 h) glass fiber filters (GF/F, 2.5 cm, 0.7 μm pore size), stored frozen (<–20°C) and subsequently dried at 60°C.

In June 1993, suspended POM was collected with a phytoplankton net (15 cm diameter, 20 μm mesh) towed vertically to 100 m and also with 10 l Niskin bottles. In the latter case, water from four discrete depths (20, 40, 60 and 80 m) was taken in equal amounts and combined to obtain enough material for analysis. In all instances, particulate matter was concentrated on pre-combusted glass fiber filters via filtration (see above) and dried at 60°C.

Ice-associated particles. Particulate matter was collected from sea ice surfaces where krill were observed feeding. Methods of collection differed in May, June and September due to the physical nature of sea ice. In May, unconsolidated ice crystals often formed a loose substrate, i.e. frazil ice, in which concentrations of entrained microalgae were readily visible (see Garrison *et al.*, 1983). The unconsolidated ice layer, while irregular in thickness (zero to tens of centimeters), was easily sampled with the same aquarium nets used for krill collection. Sampled material was stored in the dark at ~1°C and allowed to thaw (<24 h). Settled particles were concentrated, stored frozen and subsequently dried at 60°C prior to analysis.

During September, ice was generally hard to the touch and particulate matter was suctioned from ice surfaces and the immediate (estimated ≤5 cm) underlying substrate by divers with a pneumatically driven pump. Ice surfaces were agitated with a rigid section of PVC pipe and loose material evacuated through connected tubing. Samples (a mixture of loose ice crystals, associated particles and adjacent seawater; the proportion of each was not quantified) were housed in opaque plastic bags and immediately prepared for analyses aboard ship. Particles were concentrated on pre-combusted glass fiber filters and prepared for isotopic analysis in the same manner as described above for suspended materials.

In June 1993, ice was again hard to the touch and particulate matter was suctioned from ice surfaces where krill were feeding. Ice surfaces were agitated with a rigid section of pipe and loose material evacuated into a polyethylene flask through connected tubing. Suction was created by releasing vacuum pressure in the 500 ml flask. Particles from the flask were concentrated on glass fiber filters and prepared for subsequent analyses as described above.

Water samples. In September 1991, water from 60 m was collected with either 5 or 10 l Niskin bottles. Interstitial water was drawn from the underside of annual sea ice by divers with hand-held syringes (50 cc, $n \geq 10$ at each station). Water from each selected station was passed through a pre-combusted (500°C, 4 h) glass fiber filter (GF/F, 4.25 cm, 0.7 μm pore size), subdivided, and then prepared for subsequent determination of inorganic nutrient concentrations and $\delta^{13}C$ of total dissolved inorganic carbon. Subsamples for inorganic nutrients were stored frozen (≤–20°C) in 20 ml plastic scintillation vials for up to 4 months. Water to be used for the measurement of dissolved inorganic carbon parameters (250 ml) was transferred to glass jars, poisoned with 1 ml $HgCl_2$, sealed with electrical tape and refrigerated in the dark prior to analyses.

Isotopic analyses. Measurements of carbon and nitrogen stable isotope ratios were made at the Stable Isotope Laboratory of the Marine Biological Laboratory (MBL) in Woods Hole, MA. Results are reported in standard δ notation and were calculated as follows:

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = [(R_{sample}/R_{standard}) - 1)] \times 1000$$

where $R = (^{13}C/^{12}C)$ or $(^{15}N/^{14}N)$, respectively. PeeDeeBelemnite and atmospheric dinitrogen served as reference standards. The analytical precision of the reported measures is ≤0.3‰.

Krill collected during all three cruises and POM collected during the May cruise were dried directly in glass vials and homogenized prior to analysis. Suspended POM and ice-associated POM samples concentrated onto pre-combusted glass fiber filters in September 1991, and June 1993, were combusted in their entirety and subsequently blank corrected. Samples were not acidified as part of the preparation procedure. All organic samples were analyzed with an automated system for coupled $\delta^{13}C$ and $\delta^{15}N$ measurements (Fry *et al.*, 1992). Procedures for the isotopic analysis of dissolved inorganic carbon are described by Kroopnick (1974).

Nutrient analyses. Concentrations (micromolar) of inorganic nitrate, nitrite and silicate were measured with a flow injection system (Johnson *et al.*, 1985) at the Marine Science Institute's analytical facility at the University of California, Santa Barbara. Concentrations of total dissolved inorganic carbon (μmol C kg^{-1}) from poisoned water samples were determined at MBL simultaneously with measures of isotopic composition ($\delta^{13}C$).

Results

Larval krill sampled during winter were generally enriched in ^{13}C relative to krill sampled during summer months (Figure 2). During one early winter sampling period (June 1993), larvae were also markedly depleted in ^{15}N (Figure 2). Comparative summer data are from T.K.Frazer *et al.* (unpublished data) and Rau *et al.* (1991a).

$\delta^{13}C$ of larvae sampled during the three winter cruises (Table I) did not differ among cruises (ANOVA, $F = 0.96$, d.f. = 2, $P > 0.05$). $\delta^{15}N$ of larvae sampled during June 1993, on the other hand, were significantly lower than those collected during May or September 1991 (Table I; ANOVA, $F = 55.99$, d.f. = 2, $P < 0.01$). The isotopic composition of larvae collected in the water column showed essentially the same distribution as those collected from ice surfaces in September 1991 and June 1993. Thus, no effort was made to separate data on the basis of habitat type.

There was no statistical relationship between krill total length and $\delta^{13}C$ for animals collected in winter (Figure 3; Pearson $r = 0.07$). There was, however, a weak positive correlation between total length of larvae (mm) and $\delta^{15}N$ for animals collected in winter (Figure 4; Pearson $r = 0.58$). Within sampling periods, the isotopic composition of krill larvae was independent of size or life history stage (Figure 5).

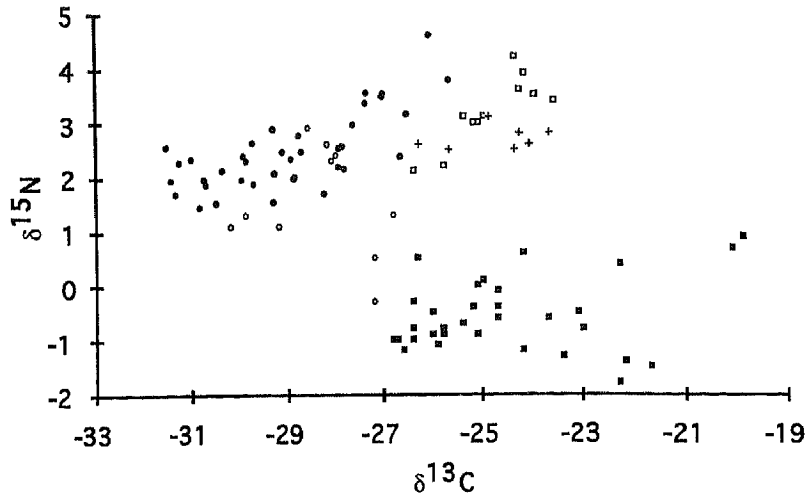

Fig. 2. $\delta^{13}C$ versus $\delta^{15}N$ for krill irrespective of size: June 1993 (■), September 1991 (□) and May 1991 (+). Summer measurements are from T.K.Frazer *et al.* (unpublished data) and Rau *et al.* (1991a) for larvae (○) and adults (●), respectively. The latter data are provided as a comparative reference.

Table I. Sample sizes and mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ for suspended POM, ice-associated POM and larval krill collected during each of the three winter cruises. In those instances where $n \leq 4$, data for individual samples are reported immediately below the summary statistics

	Suspended POM			Ice-associated POM			Larval krill		
	n	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$
May 1991	3	–20.9 (0.0)	–1.0 (0.1)	4	–22.1 (0.1)	1.9 (0.2)	8	–24.9 (0.9)	2.7 (0.2)
		–20.9	–0.9		–21.9	2.1			
		–20.9	–1.0		–22.2	1.9			
		–20.9	–0.9		–22.0	1.8			
					–22.4	1.7			
Sept. 1991	2	–32.0 (1.4)	6.35 (0.1)	3	–24.7 (0.3)	5.2 (1.1)	10	–24.7 (0.9)	3.3 (0.7)
		–31.0	6.4		–24.6	4.0			
		–33.0	6.3		–24.5	5.6			
					–25.0	6.1			
June 1993[a]	8	–27.3 (1.0)	4.4 (2.4)	2	–25.2 (1.8)	14.0 (5.6)	32	–24.5 (1.9)	–0.6 (0.7)
					–26.5	17.9			
					–23.9	10.0			

[a] Additional information is provided in Table II.

Considerable variation in the isotopic composition of POM samples was evident and there were few similarities with krill larvae collected during like sampling periods (Table I). Suspended POM sampled during May 1991 was slightly enhanced in ^{13}C relative to ice-associated POM and more so relative to larval krill collected on the same cruise. Suspended POM in September 1991 was significantly depleted in ^{13}C relative to ice-associated POM and larval krill, and tended also to

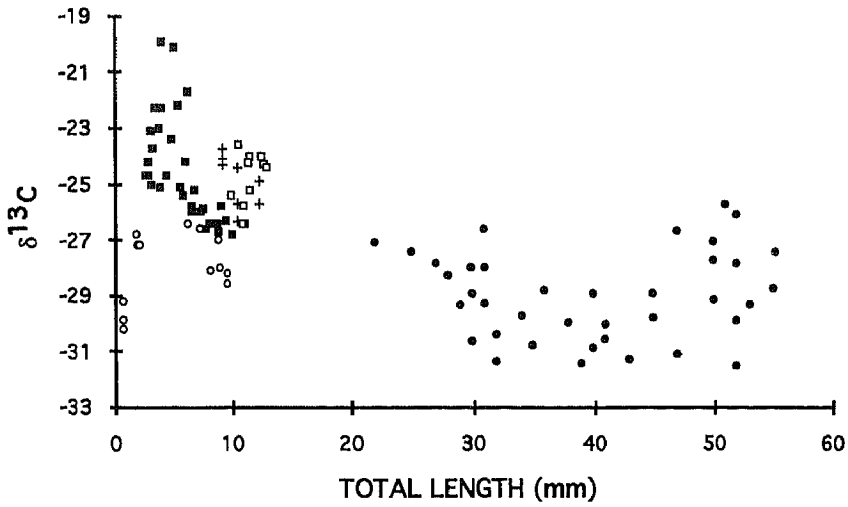

Fig. 3. $\delta^{13}C$ of krill as a function of total length (mm). Symbols are defined in Figure 2. Larval sizes during summer are approximations based on life history size distributions at the time of collection (T.K.Frazer *et al.*, unpublished data). Eggs were collected during January and February 1993, and size approximated according to Hoffman *et al.* (1992). Data for animals >20 mm are from Rau *et al.* (1991a).

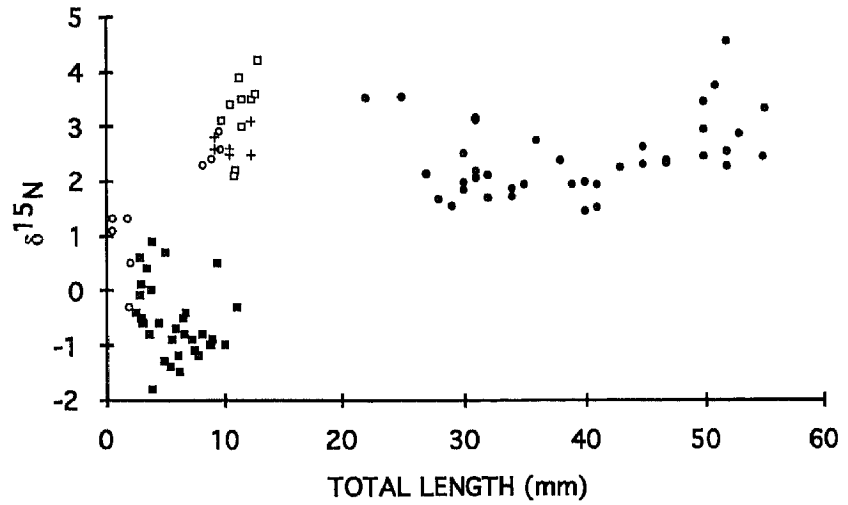

Fig. 4. $\delta^{15}N$ of krill as a function of total length (mm). Symbols are defined in Figure 2. Larval sizes during summer are approximations based on life history size distributions at the time of collection (T.K.Frazer *et al.*, unpublished data). Eggs were collected during January and February 1993, and size approximated according to Hoffman *et al.* (1992). Data for animals >20 mm are from Rau *et al.* (1991a).

be enriched in ^{15}N relative to the latter two. During June 1993, POM samples varied widely with respect to $\delta^{15}N$ and measures were dependent on habitat type as well as collection method. POM sampled with phytoplankton nets was isotopically lighter, with respect to nitrogen, than POM sampled with Niskin bottles

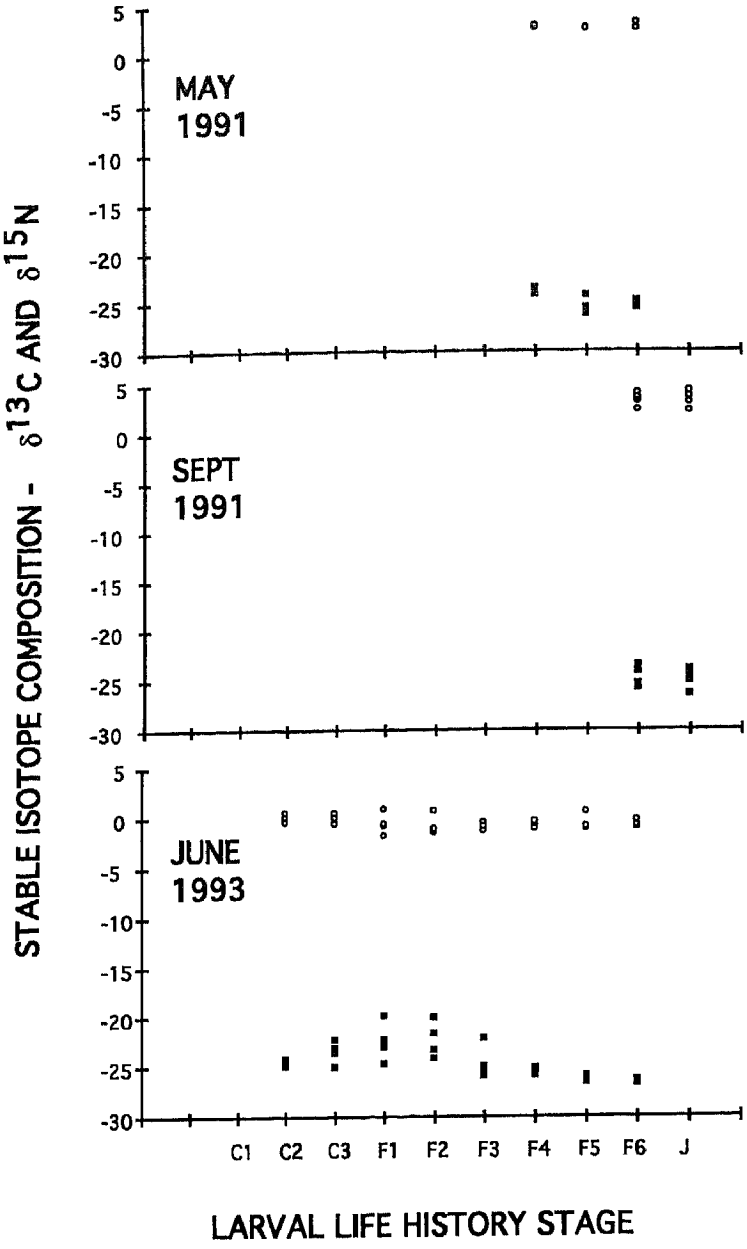

Fig. 5. $\delta^{13}C$ (■) and $\delta^{15}N$ (○) for calyptopis (C) and furcilia (F) stage larvae collected during three winter cruises.

Table II. Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ for POM sampled with Niskin bottles and phytoplankton nets (20 μm mesh) at four stations during June 1993. Data for individual samples are reported immediately below the summary statistics

	Niskin bottle		Phytoplankton net	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
	–26.9 (1.3)	6.6 (0.5)	–27.7 (0.5)	2.2 (0.2)
Station 1	–25.2	7.0	–27.5	2.0
Station 2	–28.2	5.9	–27.8	2.5
Station 3	–26.7	6.7	–28.4	2.1
Station 4	–27.3	6.9	–27.2	2.3

Table III. Concentrations (μmol/kg) and isotopic composition ($\delta^{13}C$) of total dissolved inorganic carbon in seawater and sea ice during September 1991

	[Total CO_2]	$\delta^{13}C$
Seawater		
Median value	2196	1.3
Sample #1	2188	1.6
Sample #2	2198	1.4
Sample #3	2202	1.3
Sample #4	2196	1.4
Sample #5	2219	1.3
Sample #6	2187	1.3
Sample #7	2183	1.3
Sea ice		
Median value	2162	1.7
Sample #1	2176	1.2
Sample #2	2140	1.7
Sample #3	2162	1.8

(Table II). Comparisons among winter sampling periods are suggestive of a similar pattern (see Table I).

Concentrations of total dissolved inorganic carbon in the interstices of sea ice were less than those in the water column during September 1991 (Table III; Mann-Whitney rank sum test, $P = 0.008$). $\delta^{13}C$ of total dissolved inorganic carbon in water samples from ice and open-water habitats did not differ (Table III; Mann-Whitney rank sum test, $P = 0.258$). Water column measures of nitrate, nitrite and silicate were similar to those from the interstices of sea ice (Table IV). Nitrate and silicate concentrations, though variable, were generally greater than 10 and 30 μM, respectively. Nitrite concentrations were at or below the limit of detection, i.e. 0.1 μM.

Discussion

Elevated $\delta^{13}C$ in suspended POM and larval krill during early winter implies that seasonal shifts in the isotopic composition of larval krill need not result from changes in diet. Because $\delta^{13}C$ of larval krill collected during May 1991 and June 1993 (early winter sampling periods) was not statistically different from $\delta^{13}C$ of

Table IV. Concentrations (μM) of nitrate, nitrite and silicate in seawater and sea ice during September 1991

	Nitrate	Nitrite	Silicate
Seawater			
Median value	13.4	[a]	32.5
Sample #1	13.1	[a]	31.1
Sample #2	11.2	[a]	34.3
Sample #3	18.9	[a]	38.4
Sample #4	17.3	[a]	32.5
Sample #5	24.8	[a]	55.1
Sample #6	10.7	[a]	24.9
Sample #7	13.4	0.1	28.9
Sea ice			
Median value	11.8	[a]	30.0
Sample #1	11.0	[a]	30.0
Sample #2	23.1	0.1	45.2
Sample #3	11.8	[a]	26.0

[a] Below the limit of detection.

larvae collected during September 1991 (late winter), stable carbon isotopes, in this study, failed to distinguish suspended POM from ice-associated POM as alternative food sources for larval krill.

Stable nitrogen isotope ratios shed little light on the relative roles of suspended POM and ice-associated POM in the winter diet of larval krill. $\delta^{15}N$ of larval krill differed significantly between the two early winter sampling periods and, moreover, the isotopic signatures of larvae sampled in early winter and later winter of the same year did not differ.

Data reported here do support the contention that larval krill, prior to encountering sea ice, are primarily herbivorous. Larvae collected during summer months in the region of this study (T.K.Frazer *et al.*, unpublished data) were isotopically comparable to adult krill sampled during summer in other regions of the Southern Ocean (Wada *et al.*, 1987; Rau *et al.*, 1991a). By early winter, however, larval krill were relatively enriched in ^{13}C and often markedly depleted in ^{15}N. This latter observation is inconsistent with a shift to a carnivorous mode of feeding as increases in trophic level are generally associated with a stepwise enrichment in ^{15}N (DeNiro and Epstein, 1981; Wada *et al.*, 1987). Since detrital material, too, is enriched in the heavy nitrogen isotope relative to phytoplankton-dominated POM (B.Fry, personal communication), it is unlikely that detritivory by larval krill accounts for the observed pattern. These data lead to the suggestion that isotopic variation within the phytoplankton component of POM is the primary determinant of isotopic composition in larval krill.

Although there was some evidence for a positive relationship between $\delta^{15}N$ and total length of larval krill sampled in winter, there was a clear clustering of data based on time of collection. This is further support for pronounced seasonal variation in the isotopic composition of algal food resources exploited by krill. However, the extent to which geographical differences in the isotopic composition of food and/or consumer might be represented in these data is not known.

The relative depletion of ^{15}N in krill larvae sampled during early winter (June 1993, see above) suggests that the animals had been feeding on an isotopically light component of the particulate pool for an extended period of time. Rates of isotopic turnover and accumulation in tissues of larval krill have not been measured, but are essential information for a complete interpretation of field-collected data. Fry and Arnold (1982) demonstrated, in the laboratory, that brown shrimp, *Panaeus aztecus*, reflected the $^{13}C/^{12}C$ ratios of a new diet after a 4-fold increase in wet tissue weight. Growth-related parameters for krill larvae during winter are not well established, but reported values often equate to ≤5% of wet weight per day (see Quetin *et al.*, 1994) and suggest that isotopic shifts for furcilia stage krill larvae occur on a time scale of months.

Rau *et al.* (1989) argued that abundant CO_2 (aq) underlies characteristic ^{13}C depletion in suspended particles from the Southern Ocean. Elevated $\delta^{13}C$ in suspended POM during early winter (this study) suggests that other factors may, at times, control the stable carbon isotope composition of suspended POM. Elevated $\delta^{13}C$ could result from changes in the carbon fixation pathways of the dominant microalgae. High rates of β-carboxylation will increase $\delta^{13}C$ of algae (Goericke *et al.*, 1994) and low light levels during the austral fall and/or early winter probably induce such activity. Fontugne *et al.* (1991) reported significant β-carboxylase activity (PEPC+PEPCK) in POM samples from the Weddell sector of the Southern Ocean, i.e. the pathway exists, and Mortain-Bertrand (1988) found that an Antarctic diatom, *Nitzschia tugiduloides*, exhibited increased rates of β-carboxylation under low-light regimes, providing support for the mechanism proposed above. Moreover, recent work by Thompson and Calvert (1994) showed that carbon isotope discrimination by a marine diatom, *Thalassiosira pseudonana*, varied with daylength and irradiance; discrimination (against ^{13}C) was minimal at low irradiances (25–50 μmol photons m^{-2} s^{-1}). Thompson and Calvert (1994) suggest that their results 'demonstrate a substantial role for irradiance rather than $[CO_2]$ (aq) in the physiology of ^{13}C incorporation of a marine diatom'.

Suspended POM, collected as part of this study, was not acidified prior to isotopic analysis and a potential for inflated ^{13}C in the samples is recognized. However, a qualitative microscopic examination of the particles provided little evidence that $CaCO_3$-containing organisms, e.g. Foraminifera, contributed substantially to the biomass of the samples, regardless of collection period. In fact, all POM samples appeared to consist primarily of diatoms and prymnesiophytes with a smaller detrital component (T.K.Frazer, unpublished data). On one occasion (September 1991), this qualitative assessment of the algal make-up was corroborated with a subsequent characterization of the pigment composition using HPLC analysis (T.K.Frazer, unpublished data).

With respect to nitrogen isotope ratios, Wada and Hattori (1991) noted that $\delta^{15}N$ of diatoms cultured under low-light intensities were less than those grown under high light intensities. Light is the most significant environmental factor affecting the growth and physiology of planktonic algae in the Southern Ocean, and light-limited growth of phytoplankton during the austral fall may result in large isotope fractionations associated with the uptake of nitrate that are not observed during the primary growth season (see Wada *et al.*, 1987; Altabet and

Francois, 1994; Goericke *et al.*, 1994). An alternative explanation for low $\delta^{15}N$ in phytoplankton during late fall and/or winter is a greater reliance on ammonium (see Rau *et al.*, 1991b), a more reduced nitrogenous nutrient, for growth. Even though nitrate concentrations generally exceed those of ammonium by more than an order of magnitude in the region of this study, the energy cost associated with nitrate metabolism in extreme low-light environments may restrict its use by phytoplankton. Additional information on the isotopic compositon of nitrate and ammonium in Antarctic surface waters is necessary to investigate this possibility further.

Broad scale shifts in the isotopic signature of phytoplankton may also result from changes in species composition. Phytoplankton assemblages in the Southern Ocean are extremely diverse with regard to both taxonomy and size (Smith and Sakshaug, 1990), and both variables can influence the isotopic signature of a sample (Montoya, 1990; Rau *et al.*, 1990). It is not unreasonable to expect that the $\delta^{15}N$ of a fall bloom consisting primarily of diatoms and/or other large species would differ appreciably when compared to a community dominated by small flagellates. A more quantitative characterization of the species assemblages associated with the POM samples collected as part of this study (see the discussion above) would have been needed to address this possibility.

It is difficult to reconcile the differences reported here in $\delta^{15}N$ from POM sampled with Niskin bottles and phytoplankton nets. Rau *et al.* (1990) found that large particles were isotopically heavier than small ones and it does not seem likely that nets would discriminate against large particles or that Niskin bottles would discriminate against small particles. Either of these two scenarios would have to occur to explain the relative abundance of $\delta^{15}N$ in net-collected particulate matter. Isotopic differences in suspended particles collected with different methods are of obvious concern, and data reported here are interpreted with caution. Future investigators are advised to recognize the potential for isotopic variation in suspended POM as a result of sampling methodology.

Low concentrations of total CO_2 in sea ice during September 1991 (Table III) are consistent with a hypothesis that algae growing in or associated with sea ice may at times become CO_2 limited and, as a consequence, exhibit elevated $\delta^{13}C$ (see Wada *et al.*, 1987; Fisher, 1989, 1991). However, suspended POM can clearly be enriched in ^{13}C prior to its incorporation into annual sea ice (May 1991), and other mechanism(s) can explain elevated $\delta^{13}C$ in ice-associated POM (see the discussion above). The above observation calls into question the generality of the aforementioned hypothesis. High nitrate concentrations, both in the ice habitat and water column, do not support the idea of nitrogen limitation. However, ammonium concentrations were not measured, and it is possible that relative differences in the concentrations and uptake rates of the two nitrogen species account for temporal and spatial variation in $\delta^{15}N$ of POM (see Rau *et al.*, 1991b). Other explanations, e.g. increased heterotrophy and/or changes in the microbial assemblage, remain to be explored.

In summary, stable carbon isotopes in larval krill were found to be a poor indicator of the significance of ice-associated food resources in its diet. The measure of stable nitrogen isotopes, however, did provide evidence for herbivory over

alternative modes of feeding (carnivory and/or detritivory) prior to winter. Spatial and temporal variations in the isotope ratios reported here, and mechanisms posited to explain them, are compelling from both a biological and geochemical perspective and deserving of further investigation.

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