Lipid content and composition of sub-Antarctic euphausiids and copepods from the Prince Edward Islands

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The lipid content, class composition and fatty acid composition of eight euphausiid and two large copepod species were investigated from samples taken in the sub-Antarctic in the region of the Prince Edward Islands. The lipid contents of the euphausiids were low compared to congeners from higher latitudes, especially considering that the samples were taken in late summer. The copepods were richer in lipids. Surface chlorophyll-a in the sub-Antarctic is low when compared to the oceanic fronts to the north and south, suggesting that this region is a less productive feeding environment for zooplankton. Most species in this region occur here at the extreme of their known ranges.

Thysanoessa vicina, T. macrura, Metridia lucens *and* M. gerlachei *were found to contain wax esters in abundance, whereas* Euphausia *spp.*, Nematoscelis megalops *and* T. gregaria *stored no wax ester. The fatty acid composition points to a herbivorous diet for all specimens examined, but it is likely that those lipid-poor species that do not store wax ester will switch to an alternative winter diet. Furthermore, the subtropical* Thysanoessa gregaria *and* Metridia lucens *contained less wax ester than their congeners of Antarctic origin, which presumably reflects the different feeding strategies associated with latitudinal differences.*

A herbivorous diet of sub-Antarctic euphausiids would imply that the large sea bird populations of this region, which feed largely on euphausiids, end a very short oceanic food chain, although the role of microzooplankton in this food chain remains unknown.

*Subantarktiese monsters van agt euphausiid- en twee groot kopepodespesies is geneem in die omgewing van die Prince Edward-eilande om die vetstofinhoud, klas- en vetsuursamestelling te ondersoek. Die vetstofinhoud van die euphausiide was laag in vergelyking met soortgelyke spesies van 'n hoër breedteligging, veral as in ag geneem word dat die monsters laat somer geneem is. Die kopepodes het 'n groter vetstofinhoud gehad. Oppervlakvlakchlorofil-*a *in die Subantarktiese streek was laag in vergelyking met die suidelike en noordelike oseaniese fronte. Dit is 'n aanduiding dat die gebied 'n minder produktiewe voedingsomgewing vir soöplankton is. Die meeste van die spesies kom hier voor op die verste bereik van hulle bekende verspreidingsgebied.*

Daar is gevind dat Thysanoessa vicina, T. macrura, Metridia lucens *en* M. gerlachei *baie was-ester bevat. Geen was-ester is in* Euphausia *spp.*, Nematoscelis megalops *en* T. gregaria *gevind nie. Die vetsuursamestelling dui op 'n herbivore dieet vir alle bestudeerde monsters. Dit is egter waarskynlik dat die vetstofarm spesies wat geen was-ester stoor nie na 'n alternatiewe winterdieet sal oorskakel. Die subtropiese* Thysanoessa gregaria *en* Metridia lucens *het minder was-ester bevat as soortgelyke Subantarktiese spesies. Dit weerspieël vermoedelik die verskillende voedingstrategieë wat met verskillende breedteliggings geassosieer word.*

'n Herbivore dieet van Subantarktiese euphausiide kan behels dat die groot seevoëlbevolking van die streek, wat hoofsaaklik van euphausiide leef, die einde van 'n kort oseaniese voedselketting is, hoewel die rol van mikrosoöplankton in dié ketting onbekend bly.

Introduction

The zooplankton of the sub-Antarctic supports large stocks of island-based planktivorous birds, yet the fauna of the sub-Antarctic are supported by very low *in situ* primary production. Logistic constraints to sampling the macrozooplankton in the vicinity of the Prince Edward Islands have left a relatively poor understanding of this part of the food web. Samples have not been taken repeatedly and have been limited to certain months of the year. The recent large sampling effort of the second cruise of the Marion Island Off-shore Ecological Survey (MOES II) provided estimates of zooplankton abundance. Grazing rates were estimated to be between 76 and 81% of oceanic primary production (Perissinotto 1992). This paper describes the lipid contents of the most abundant macrozooplankton species collected on MOES II, as it has relevance to aspects of zooplankton biology that are difficult to measure directly.

The variation in the quantity and composition of neutral lipids within copepod and euphausiid species can be explained in terms of their life cycle (e g Kattner & Krause 1987), breeding condition (e g Clark 1980), and integrated feeding history (e g Ohman 1988 & Willason *et al* 1986). The variation in the neutral lipid composition between species, and in some cases between populations that are geographically separated, concerns most notably the presence or absence of wax ester. It has been hypothesised that wax ester is synthesised as a long-term storage medium and is coupled to a particular life-history strategy of herbivorous zooplankton in strongly seasonal (i e polar) environments (Lee *et al* 1971). The synthesis

of triacylglycerol during short periods of high food concentration cannot proceed at a rate fast enough to create a large lipid store required for overwintering (see Sargent & McIntosh 1974). Planktonic herbivores that do not store wax esters are presumably switching to alternative winter food sources (zooplankton or detritus), or do not experience a short supply of phytoplankton in winter.

Certainly all copepod species seem to synthesise wax esters. Sargent & Henderson (1986) list 27 species from ten genera, of which all contained wax esters. They did, however, point out that polar copepods tend to contain a greater proportion of their lipids as wax esters than those of temperate and subtropical waters. The same trend is evident of euphausiid lipids. *Thysanoessa inermis* of the Arctic is richer in wax ester than its congener *T. raschii* with a more southerly distribution. The Antarctic herbivore, *Euphausia crystallorophias*, whose distribution extends to the ice-edge, is rich in wax ester, but the sympatric, omnivorous *E. superba*, which feeds all-year, entirely lacks wax ester (Clarke 1980). The omnivorous *Meganictyphanes norvegica* also lacks wax ester (Sargent & Falk-Peterson 1981).

The lipids of herbivorous and carnivorous copepods and euphausiids differ with respect to the fatty acid constituents. Herbivores are rich in 14:0 and 16:0 chains, monounsaturates (both $\omega 7$ and $\omega 9$) and a variety of long-chain $\omega 3$ polyunsaturates, which are derived from the glycolipids of algal chloroplasts. Schofield *et al* (1982) identified a fatty acid synthetase in *Calanus finmarchicus*, a herbivorous copepod, which implies additional *de novo* synthesis of 16:0, 18:0 and 20:0. Calanoid copepods have a Δ^9 desaturase enzyme and can synthesise 18:1 ($\omega 9$), 20:1 ($\omega 9$) and 22:1 ($\omega 11$) from unsaturated fatty acids by adding two carbon atoms and a double bond (Sargent & Henderson 1986). The fatty alcohols of wax esters of *Calanus* are predominantly long-chain saturates and monounsaturates, notably C_{18}, C_{20} and C_{22} chains (Lee 1974, 1975, Prahl *et al* 1984). These are converted from the equivalent fatty acids, which are synthesised *de novo*. The alcohols are then esterified with short-chain saturated, and long-chain unsaturated, fatty acids of phytoplanktonic origin to form wax ester. It has been suggested that wax ester formation is a means of allowing lipogenesis to proceed during a continuing input of dietery lipid (Sargent & Henderson 1986).

Neutral lipids of carnivorous zooplankton are typically triacylglycerols, the fatty acids of which are rich in long-chain monounsaturates, 18:0, 20:1 and 22:1. These are converted from the fatty alchohols of their herbivorous prey for, as fatty acids, these precursors are absent in phytoplankton, and are only an intermediate step in the synthesis of fatty alcohols in herbivores.

Other indicators of trophic position include the monounsaturates, 16:1 ($\omega 7$) and 18:1 ($\omega 7$). Both these molecules have their origin as 16:0, found in phytoplankton as the desaturase enzyme operates with a Δ^9 specificity (Sargent & Falk-Peterson 1981). Their strong presence would indicate a phytoplanktonic rather than an animal origin. Falk-Peterson *et al* (1987) showed that for *Metridia longa*, an omnivorous copepod, the levels of 16:1 ($\omega 7$) fatty acids decreased through winter, coinciding with a lower phytoplanktonic fraction in the diet.

The omnivorous euphausiid, *Meganyctiphanes norvegica*, on the other hand, has more of 18:1 ($\omega 9$), formed by the desaturation of 18:0 of animal origin, than the sympatric herbivorous euphausiids *Thysanoessa inermis* and *T. raschii* (Sargent & Falk-Peterson 1981). The ratio of these isomers of 18:1 is believed to be an indication of the diet.

While there are some inconsistencies among zooplankton as regards the simplified trends outlined above, the lipid composition can tell something about zooplankton life-history and trophic dynamics which are otherwise difficult to resolve. Are the macro-zooplankton predominantly herbivorous or carnivorous? How do the zooplankton overwinter? Are there differences between the lipids of zooplankton of subtropical and Antarctic origin? This paper presents the results of lipid analyses, including estimation of lipid fractions by densitometry and gas chromatography of the constituent fatty acids of sub-Antarctic zooplankton. Analyses were performed on specimens of eight species of euphausiids: *Euphausia vallentini* Stebbing; *E. similis v. armata* Hansen; *E. hemigibba* Hansen; *E. longirostris* Hansen; *Nematoscelis megalops* G.O. Sars; *Thysanoessa vicina* Hansen; *T. gregaria* G.O. Sars and *T. macrura* G.O. Sars, and two copepod species: *Metridia gerlachei* Giesbrecht and *M. lucens* Boeck, caught in the vicinity of the Prince Edward Islands in the southern Indian Ocean between the latitudes of 45° and 49° S. The specimens were collected in April/May (late summer, early winter) when it is to be expected that zooplankton is replete with lipids.

Material and methods

This study is based on material collected on the second cruise of the Marion Island Off-shore Ecological Study (MOES II), dated 30/03/1989 to 09/05/1989, between the latitudes of 45°17' S and 48°14' S, and the longitudes of 46°38' E and 40°30' E. Zooplankton were collected with a bongo net with mesh sizes of 300 μm and 500 μm. Daytime oblique hauls were extended to a depth of 300 m; nighttime hauls were extended to a depth of 100 m. Animals were carefully removed and identified in a petridish under a light-microscope. Once identified the specimens were sealed in plastic vials and frozen at −25° C. On return to Cape Town the samples were transfered to a −80° C freezer. The procedures outlined below were completed in the ensuing 12 months.

Prior to analysis, specimens were thawed and wet-weighed collectively for each species. There is no measure of variability of mass or lipid content within species. No attempt was made to differentiate the sexes. Immediately after weighing, total lipid was extracted by the method of Bligh and Dyer (1959) in chloroform-methanol. The final solution contained a 40 ml chloroform-lipid layer, 20 ml of which was pipetted into a pre-weighed flask and evaporated under vacuum in a water bath at 70° C. The flask with lipid was weighed again and the increase in mass was taken to be half the mass of the total lipid.

Lipid classes were separated by thin layer chromatography (TLC) using pre-coated TLC plates (Silica gel 60/Kieselguhr F254) and identified from standards. The solvent was a mixture of hexane (85 parts), diethyl ether (15 parts) and acetic acid (1 part). After development, the plates were immersed in a charring agent consisting of cupric acetate (3 parts), phosphoric acid (8 parts) and water (89 parts), and heated at 130° C for 15 minutes. The plates were scanned by a densitometer with an oscillating light beam and the output plotted graphically. The relative area under each peak represented the proportion of each lipid class.

Samples of each lipid class were scraped from two-dimensional TLC plates for gas chromatography. Lipids were eluted into a flask with chloroform, filtered through a Whatman 41 filter to remove the silica and then the chloroform was evaporated. To the lipid residue, 5 ml 0.5 M NaOH in methanol was added. The solution was heated under reflux for five to ten minutes to saponify the fatty acids. Thereafter, 5 ml Boron trifluoride-methanol complex (20% in methanol) was added and the solution was refluxed for a further five minutes to prepare methyl esters. Hexane AR (5 ml) was finally added and the solution refluxed for a further five minutes and then allowed to cool before filling with saturated aqueous NaCl. The hexane layer was allowed to separate and

Table 1

Individual wet mass and lipid content (percent of wet mass) of pooled samples of euphausiid and copepod species from the sub-Antarctic

Species	Mean wet mass (mg)	% Lipid	n	Date and location of capture
Eupahausiids				
Euphausia vallentini	53.6	2.39	10	10-04-89; 46°53'S,37°07'E
			5	15-04-89; 45°17'S,37°48'E
			17	24-04-89; 46°49'S,38°01'E
			15	02-05-89; 46°40'S,37°42'E
E. similis v. armata	41.4	2.81	4	19-04-89; 46°05'S,40°28'E
			15	24-04-89; 46°49'S,37°55'E
			35	28-04-89; 46°38'S,37°37'E
			10	29-04-89; 46°53'S,37°07'E
			10	03-05-89; 46°40'S,37°42'E
E. hemigibba	44.8	2.04	9	08-04-89; 47°26'S,35°48'E
			3	10-04-89; 46°22'S,37°07'E
E. longirostris	214.6	1.33	4	17-04-89; 46°38'S,39°48'E
			2	28-04-89; 46°38'S,37°37'E
Nematoscelis megalops	86.9	1.50	10	08-04-89; 46°22'S,35°48'E
			3	16-04-89; 47°10'S,38°10'E
			7	09-04-89; 46°38'S,40°28'E
Thysanoessa vicina	6.5	3.19	20	16-04-89; 46°54'S,39°07'E
			13	17-04-89; 46°38'S,39°48'E
T. gregaria	32.7	3.40	4	15-04-89; 45°17'S,37°48'E
T. macrura	5.8	2.80	8	11-04-89; 48°14'S,37°48'E
			2	10-04-89; 46°53'S,37°07'E
Copepods				
Metridia gerlachei	0.76	14.09	15	08-04-89; 46°26'S,35°48'E
			15	15-04-89; 46°22'S,38°27'E
			20	24-04-89; 46°48'S,37°59'E
			25	28-04-89; 46°38'S,37°37'E
			15	02-04-89; 46°40'S,37°42'E
M. lucens	0.46	6.70	15	09-04-89; 46°10'S,36°28'E
			10	10-04-89; 46°53'S,37°07'E
			20	24-04-89; 46°49'S,37°59'E

Table 2

The lipid composition (expressed as a percentage of total lipid) of euphausiids and copepods from the sub-Antarctic, April/May 1989. PL = phospholipid, FFA = free fatty acids and alcohol, MG & DG = mono and diacylglycerol, CL = cholesterol, TG = triacylglycerol, WE = wax ester. tr = trace amount undetected by the oscilating densitometer scanner, but faintly visible

Species	PL	FFA	CL	MG & DG	TG	WE
Euphausiids						
Euphausia vallentini	25.2	42.0	12.9	1.7	18.2	0.0
E. similis v. armata	12.8	20.1	6.7	3.88	19.9	tr
E. hemigibba	29.7	41.9	21.4	tr	7.0	0.0
E. longirostris	41.9	32.8	14.8	9.4	1.1	0.0
Nematoscelis megalops	59.8	10.8	11.9	17.5	tr	0.0
Thysanoessa vicina	17.7	38.0	10.8	1.5	2.2	29.8
T. gregaria	41.4	34.1	10.1	8.1	6.3	tr
T. macrura	25.9	32.6	22.9	5.4	5.2	8.0
Copepods						
Metridia gerlachei	8.7	11.9	7.3	4.4	18.0	49.7
M. lucens	10.1	tr	13.5	2.7	47.9	25.8

this was transfered with a Pasteur pipette into a 5 ml sample bottle. The solvent was completely evaporated under a stream of nitrogen gas before 0.5 ml hexane was added. From this final solution 2μl was injected into a 5710A Hewlett Packard gas chromatograph with hydrogen as the carrier gas. The injection port temperature was 250° C, detector temperature 300° C and the temperature gradient was 150° C to 280° C at 4° C per minute. The column was a 40 m open tubular OV 73 capillary column. Peaks were integrated on a Spectra-Physics SP 4290 Integrator. The analytical precision of this particular instrument is good, the coefficient of variation of replicate samples being less than 5% (Wagener *et al* 1984).

Results

The wet mass and percentage lipid of each species are listed in Table 1. Studies on other species of euphausiids (Sargent & Falk-Peterson, Clarke 1980) have shown no marked differences with respect to these parameters between the sexes, provided females have not recently spawned. Being constrained by small sample sizes for at least five of the species, it was decided not to attempt separating sexes, but rather to pool individuals. The values listed are thus the mean of each sample.

Table 2 lists the total lipid composition as estimated by densitometry. On each TLC plate there were five samples, four of which were standards. These standards were respectively cholesterol, free fatty acid, orange roughy (*Hoplostethus atlanticus*) oil rich in wax ester and anchovy (*Engraulis capensis*) oil rich in triacylglycerol. The origin zone was taken as phospholipids, thereafter occurred mono- and diacylglycerol (the two were indistinguishable), cholesterol, free fatty acid, alcohol (these last two were indistinguishable), triacylglycerol and wax ester.

Little is known of the timing of the breeding cycle for any of the species examined in this study. None of the female *Euphausia* spp. nor *Thysanoessa gregaria* specimens examined were obviously gravid. Although the ovaries were visible through the cuticle in the live animals, they did not extend into the first abdominal segment and caused no marked swelling of the thorax. The ovaries of *Nematoscelis megalops* were not clearly visible.

The lipids of each genus will be presented separately. While all the major peaks of fatty acids were identified from standards (which include all major fatty acids found in zooplankton), there were many small unidentified peaks that totalled to substantial quantities in some species. Because only very small quantities of oil were available in certain species, the contribution of contaminants to the total might have been correspondingly large. Possibly, some of these unknown substances were contaminants, in which case the contribution of the known fatty acids would be underestimated.

Euphausia spp.

None of the four species contained wax ester, except for a trace amount in *E. similis v. armata*. Triacylglycerol content ranged from 1.1% wet mass in *E. longirostris* to 19.9% in *E. similis* v. *armata*. Free fatty acids were major components (20 to 40% wet mass). The mono and diacylglycerol levels were substantial and similar to those of some euphausiids (Sargent & Falk-Peterson 1981), but far greater than that reported for *E. superba* (Clarke 1980). Phospholipids ranged between 25% and 40%, while free sterols were generally less than half this value. Of the four species, *E. longirostris* had the lowest triacylglycerol content, but a high partial glyceride content. It also contained the least lipid of the four *Euphausia* species. A comparison between species shows a positive relationship between the percentage lipid and the triacylglycerol content.

Table 3

Fatty acid composition of the lipid classes of *Euphausia vallentini* and *E. similis* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids that constitute >1% of the total are listed. Blanks indicate absence

	Phospholipid	Free Fatty Acid	Triacylglycerol
	Euphausia vallentini		
14:0	4.7	13.6	4.9
15:0		2.9	1.2
16:1(ω7)	3.6	6.5	2.8
16:0	23.4	35.0	21.7
18:4			3.2
18:2			2.7
18:1(ω9)	12.2	9.6	9.7
18:1(ω7)		1.9	4.6
18:0	11.6	9.9	1.7
20:4(ω6)		2.2	1.6
20:5(ω3)	10.3	2.8	19.5
21:5	1.7		
22:6(ω3)	12.4	2.0	17.9
22:0	2.8	4.9	0.4
Total unknown of >1% occurrence	2.4		
	Euphausia similis		
14:04.8	2.9	14.2	
15:0	1.3	0.8	2.0
16:1(ω7)	0.8	1.9	2.4
16:0	17.7	14.4	24.5
18:4	1.0	2.5	2.0
18:2	9.8	2.4	3.7
18:1(ω9)	5.3	6.8	6.1
18:1(ω7)	6.6	3.5	10.9
18:0	6.4	0.7	2.9
20:4(ω6)	2.3	1.8	
20:5(ω3)	2.2	21.7	0.2
21:5	1.2		
22:6(ω3)	3.1	24.7	1.5
24:1	1.1		
24:0	1.6		
Total unknown of >1% occurrence	16.0	6.9	11.6

Table 3 lists the fatty acid composition of the phospholipid, free fatty acid and triacylglycerol fractions of *E. vallentini* and *E. similis* v. *armata*. The small sample sizes of *E. hemigibba* and *E. longirostris* did not provide sufficient of each of the lipid classes to analyse the fatty acid composition of these two species. In all lipid classes of both *E. vallentini* and *E. similis v. armata* 14:0 and in particular 16:0 were well represented. Of the long-chain saturates, 18:0 was more strongly represented in the phospholipids (>6%) of both species, and so too were 22:0 and 24:0 in *E. vallentini* and *E. similis v. armata* respectively.

The dominant monounsaturated fatty acids in both species were 16:1 (ω7), 18:1 (ω9) and 18:1 (ω7). The ratio 18:1 (ω9/18:1 (ω7) was <1 for *E. similis*, but >1 for *E. vallentini*. Long-chain monounsaturates, 20:1, 22:1 and 24:1, occurred only in very low concentrations, as they do in *E. superba* (Clarke 1980). Polyunsaturates were represented by 20:5 (ω3) and 22:6 (ω3). The triacylglycerol of *E. vallentini* was richer in these polyunsaturates than that of *E. similis* v. *armata*, which had free fatty acids rich in these polyunsaturates. Differences in the fatty acid composition of phospholipid and triacylglycerol were not substantial. For both species the unusual polyunsaturate 21:5 occurred only in the phospholipids in small amounts. Free fatty acid composition, however, did differ from that of phospholipid and triacylglycerol in *E. vallentini* by having more saturates, but in *E. similis* v. *armata* by having more polyunsaturates.

The stomachs of seven specimens of *E. vallentini* were dissected out and opened to estimate stomach fullness and gut contents. Table 4 lists these findings. Unidentified particulate matter was interpreted as detritus.

Nematoscelis megalops

About 60% of the lipid of this species consisted of phospholipids and only a trace of triacylglycerol was present. Correspondingly, the total lipid content was only 1.5% of wet mass. Partial glycerides constituted 17% of total lipid.

Table 5 lists the fatty acid composition of the phospholipid and only a trace of triacylglycerol was present. Correspondingly, the total lipid content was only 1.5% of wet mass. Partial glycerides constituted 17% of total lipid.

Table 5 lists the fatty acid composition of the phospholipid and free fatty acid fractions. The saturates of phospholipid were represented most strongly by 16:0, but also 14:0 and 18:0. The ω7 monounsaturate levels were low (<5%) compared to that of the 18:1 (ω9) isomer (14%). The 22:1 (ω11) isomer was possibly of copepod origin (Pascall & Ackman 1976, Sargent & Henderson 1986). Polyunsaturates were dominated by long-chain ω3 isomers.

The free fatty acid composition differed in having proportionately more saturated than polyunsaturated fatty acids. The strong presence of 12:0 (30%) in the free fatty acids was unusual and might have been due to a contaminant in the sample. A large number of unidentified substances accounted for 28.2% of the free fatty acids.

Thysanoessa spp.

T. vicina and *T. macrura* specimens were late juveniles. *T. gregaria* specimens were all adults. Large fractions of the lipid of *T. vicina* and *T. macrura* (30% and 8%

respectively) were in the form of wax ester, while only a trace of wax ester was found in *T. gregaria*. Triacylglycerols were less important, except in *T. gregaria*. Free fatty acids (including, perhaps, fatty alchols) were major components in all three species. None of the species were particularly rich in total lipid (2.8 to 3.4% wet mass).

The fatty acid composition of the phospholipid, free fatty acid and wax ester fractions of *T. vicina* are listed in Table 6. These fatty acids were principally the saturates, 14:0 and 16:0, the monounsaturates 16:1 (ω7), 18:1 (ω7) and 18:1 (ω9), and ω3 polyunsaturates. The ratio of 18:1 (ω7): 18:1 (ω9) exceeded 1 in both the phospholipid and the wax ester. Long-chain saturated and monounsaturated fatty acids were absent.

Table 4

Stomach fullness and stomach contents of *Euphausia vallentini*. Stomach fullness index: 0 = empty, 1 = 1/4 full, 2 = 1/2 full, 3 = 3/4 full, 4 = full. Stomach content index: blank = absent, 1 = present, 2 = abundant, 3 = very abundant.

Date, time, position	Size mm	Stomach fullness	Stomach contents: Diatoms	Foraminifera	Tintinnids	Radiolarians	Detritus
23-04-1989	18.5	3	1				3
19h30	20.2	3	1	2	1	1	3
46°48' S, 38°00' E	20.0	3		2		1	3
24-04-1989	19.5	4	1	2			3
01h30	17.0	3		2			3
46°49' S, 38°01' E							
24-04-1989	19.0	3		2	1		3
04h30	16.5	4		2			3
46°49' S, 38°0' E							

Table 5

Fatty acid composition of the phospholipids and free fatty acids of *Nematoscelis megalops* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids that constitute > 1% of the total are listed. Blanks indicate absence.

	Phospholipid	Free fatty acid
12:0	0.5	30.8
14:0	3.2	1.6
15:0	1.0	
16:1(ω7)	4.0	2.5
16:0	25.2	4.1
18:4	0.6	
18:2	1.8	
18:1(ω9)	13.6	
18:1(ω7)	3.2	
18:0	3.3	
20:4(ω6)	1.3	
20:5(ω3)	12.2	
21:5	0.2	
22:6(ω3)	16.5	
22:1(ω11)	2.0	
Total unknown of > 1% occurrence	1.6	28.2

Table 6

Fatty acid composition of the lipid classes of *Thysanoessa vicina* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids that constitute > 1% of the total are listed. Blanks indicate absence.

	Phospholipid	Free fatty acid	Wax Ester
14:0	6.3	2.1	6.2
15:0	0.2	1.0	
16:1(ω7)	11.8	1.0	8.5
16:0	26.2	18.2	23.8
18:4(ω3)	1.2	1.0	0.8
18:2(ω6)	2.0	2.1	3.1
18:1(ω9)	7.3	7.1	8.2
18:1(ω7)	10.4	2.5	11.1
18:0	1.1	2.0	2.2
20:5(ω3)	12.9	17.3	14.9
22:6(ω3)	16.7	20.8	0.5
Total unknown of > 1% occurrence	3.6	19.5	0.9

***Metridia* spp.**

M. gerlachei and *M. lucens* were rich in wax ester (50% and 26% total lipid respectively) and triacylglycerol (18% and 48% total lipid respectivly). The 12% free fatty acid content of *M. gerlachei* might have included fatty alcohols as these two substances did not separate clearly. The relatively low phospholipid content is a reflection of the high total lipid content of these two copepods; *M. gerlachei* contained 14% lipid (wet mass) whereas *M. lucens* contained 6.7% lipid.

The fatty acid composition of the free fatty acids, triacylglycerols and wax esters of *M. gerlachei* are listed in Table 7. Because of the low levels of phospholipids, and the small sample of oil available for analysis, the phospholipid content could not be analysed accurately. The neutral lipids were rich in saturates, with 16:0 dominating. The monounsaturates were dominated by the ω9 isomer in all three lipid classes. Long-chain monounsaturates, 20:1 (ω9), 22:1 (ω11) and 24:1 (ω13), were present, but in low concentrations. Polyunsaturates were dominated in the neutral lipid by the ω3 isomer of 20:5 and 22:6.

Table 7

Fatty acid composition of the lipid classes of *Metridia gerlachei* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids that constitute > 1% of the total are listed. Blanks indicate absence.

	Free fatty acid	Triacylglycerol	Wax Ester
14:0	4.2	6.4	2.9
15:0		0.6	0.3
16:4		1.1	0.7
16:1(ω7)	4.4	5.0	10.6
16:0	18.2	21.2	9.3
18:4	1.9	1.5	2.6
18:2	2.1	1.1	1.4
18:1(ω9)	10.4	7.0	24.9
18:1(ω7)	2.2	4.4	1.6
18:0	4.2	4.2	2.0
20:4(ω6)	0.6	0.5	0.6
20:5(ω3)	15.1	11.7	13.0
20:1	1.6	2.2	1.1
22:6(ω3)	16.6	7.3	9.0
22:5	1.6	1.7	1.5
22:1(ω11)	1.1	0.8	0.5
24:1	1.7	0.8	0.5
Total unknown of > 1% occurrence	11.3	4.9	1.3

Discussion

The strong presence of free fatty acids in many of the species examined could be due to deterioration of lipids after death (autolysis) or due to metabolic breakdown of lipids prior to death. According to temperature-dependent rates of hydrolysis of phospholipids and neutral lipids in hake (*Merluccius capensis*) (De Koning & Mol 1990), at −40° C, free fatty acid is formed at a rate of 0.00023 mmoles kg^{-1} day^{-1} from phospholipid and 0.0073 mmoles kg^{-1} day^{-1} from neutral lipid. For a mixture of 60% phospholipid and 40% neutral lipid, 0.0031 mmoles free fatty acid are formed per kg lipid per day (or 0.87 oleic acid kg^{-1} day^{-1}). In 1 000 days this amounts to <0.01% autolysis. As this rate decreases exponentially with temperature, at −80° C the rate of free fatty acid formation while in storage should have been negligible. Autolysis would have occurred in the freshly caught animals while these were being identified, as autolysis in freshly caught krill can proceed very rapidly (Eddie 1977). Further autolysis would have occurred during the weighing process prior to extraction, although this was done as rapidly as possible. Free fatty acids and cholesterol values were higher than is usually the case for euphausiids (Clarke 1980, Reinhardt & Van Vleet 1986, Falk-Peterson *et al* 1987). The high free fatty acids in some species might simply reflect a paucity of neutral lipid and it is possible that this result reflects a condition prior to death. Although variation in the amount of lipase between species might account for some variation in rates of lipid deterioration, the possibility that a total absence of wax ester, or of triacylglycerol, in certain species is due to deterioration after death can be discounted, since some species contained an abundance of these lipid classes, and all specimens were treated in the same way.

As with the free fatty acids, the interpretation of high levels of partial glycerides might be ambiguous. The concentrations of free fatty acids were greatest for the lipid-poor species. The coincidence of low total lipid and a high occurence of breakdown products of neutral lipid suggests that the four *Euphausia* species, *Nematoscelis megalops* and *Thysanoessa gregaria* were in poor nutritional condition and that lipid deterioration is not the primary cause of a high proportion of free fatty acids and partial glycerides.

The fatty acid composition of phospholipid is understood to be less variable than that of neutral lipid, which might be attributable to the specific functional role of phospholipid as a structural element (Clarke 1980). Indicators of diet should thus be sought among the fatty acids of neutral lipid. Phytoplankton is known to be rich in 14:0, 16:0, 16:1 (ω7) and ω3 polyunsaturates (Sargent *et al* 1985). These featured strongly in the triacylglycerols and free fatty acids of the two *Euphausia* species and particularly in the wax ester and triacylglycerol of *Thysanoessa vicina* and *Metridia gerlachei*, suggesting a phytoplanktonic diet for these species. Considering the paucity of long-chain saturated or monounsaturated fatty acids, likely to have been derived from the alcohol moiety of crustacean prey wax ester, the four species examined (*E. vallentini, E. similis v. armata, T. vicina* and

M. gerlachei) were likely to have been herbivorous in the preceeding summer months. Of these, it might be expected that the *Euphausia* species at least, being rather poor in lipid, would turn to an alternative winter diet. Given a lack of neutral lipid in *Nematoscelis megalops*, nothing can be said about its diet. Both phytoplankton and copepod fatty acids were present in the phospholipids.

In two of the four species examined, *E. vallentini* and *M. gerlachei*, the ω9 isomer of 18:1 predominated, suggesting that carnivory might have been an important source of this isomer for these species. Alternatively, domination of the ω9 isomer could be a result of considerable *de novo* synthesis of lipid, despite a phytoplanktonic input of the ω7 isomer. This interpretation is ambiguous.

Mauchline's (1980) review of the biology of the euphausiids lists the known dietery items of several species. *T. gregaria* is listed as a filter-feeder/omnivore; *Nematoscelis megalops* is listed as an omivore/predator; *E. similis* is known to eat coccolithophores and tintinids, but this list is surely incomplete. Diatoms, foraminifera, tintinids and radiolarians were found in the stomachs of the seven specimens of *E. vallentini* examined. *M. gerlachei* shows great efficiency at handling large-sized diatoms (46 μm), although based on 'edge-indices' of the mandibles, this species is a potential omnivore (Schnack 1983).

Compared to records from the Antarctic, the lipid content of the *Euphausia* spp. examined in this study (1.3 to 2.8%) was low. For mature *E. superba*, *E. frigida* and *E. triancantha* the known lipid contents are 5 to 8%, 19.4% and 4% respectively (Clarke 1980). However, compared to tropical and warm-temperate species these low levels are normal; *E. americana* and *E. krohni* from 20° N had 0.8% and 1.0% lipid (Morris 1971), *E. pacifica* off southern California had 3.1% lipid (Childress & Nygaard 1974), *E. gibboides* from 22° N and 28° N had 1.2% lipid (Morris 1971) and *E. similis* off Japan had 2.1% lipid (compared to 2.8 for *E. similis v. armata* from this study). The mature *T. gregaria* (3.4% lipid) can be compared to its north Atlantic congeners *T. inermis* (7 to 8% lipid) and *T. raschii* (18% lipid) (Hopkins *et al* 1984) and the north Pacific congener *T. longiceps* (7.7%) (Sameoto *et al* 1975). The equally low lipid contents of *T. vicina* and *T. macrura* late juveniles might, however, be more typical of immature *Thysanoessa* specimens (Hopkins *et al* 1984). *Metridia gerlachei* had 14.1% lipid, and *M. lucens* 6.7%, which is similar to autumn values for *M. longa* from the Arctic 11.5% (assuming that dry mass = 0.2 wet mass) (Lee 1975) and to *R. gigas* from the Antarctic 13.8% (Lee & Hirota 1973).

Fig 1 shows the known latitudinal distributions of the species in this study. No species occurs at both the Subtropical Convergence (STC) and the Antarctic Polar Front (APF), as might be expected from the strong temperature gradient. *E. vallentini* can be considered as a sub-Antarctic species that occurs at or near the APF. *E. similis v. armata* and *E. longirostris* are also common in the in the sub-Antarctic, but their distributions clearly overlap the STC. *N. megalops* is common between 30° and 45° in both hemipsheres. The *Thysanoessa* spp. show a clear geographical separation; *T. gregaria* is subtropical, *T. vicina* is Antarctic/sub-Antarctic, *T. macrura* is high Antarctic (Nemoto 1966). *M. lucens* is abundant in sub-Antarctic water between Marion and Crozet Islands and also appears in the cold upwelled water of the Benguela current in the south-east Atlantic (De Decker 1984). *M. gerlachei* is a common Antarctic species (Raymont 1983). The presence of Antarctic and subtropical elements in sub-Antarctic water can be explained by the interaction of the west-wind drift with the irregular bottom topography in these longitudes, which causes a mixing of surface water across the circumpolar fronts (Deacon 1983).

The low lipid content observed in many of the sub-Antarctic species may perhaps be explained by the poor feeding conditions encountered in this biogeographic region. Chlorophyll-*a* measured at 89 stations on the same cruise of the mv *SA Agulhas* (April/May) did not exceed 0.4 mg Chl-*a*.m^{-3} over five weeks (mean 0.19 mg Chl-*a*.m^{-3}) at least 50% of which was in the picoplankton size fraction (< 2.0 μm cell size). The mid-summer chlorophyll-*a* values are not much greater. A synthesis of data collected on 11 Japanese Antarctic Research Expedition (JARE) voyages from Fremantle to the Japanese Antarctic base (Syowa) in early summer, and the return voyages to Cape Town in mid/late summer (Fig 2) show that the average Chlorophyll-*a* concentration in the sub-Antarctic region, 45-49° S, of the Indian ocean in summer is low and invariable when compared to the STC and to the APF. The weak and poorly understood sub-Antarctic Front (SAF) (Lutjeharms *et al* 1985) is seldom

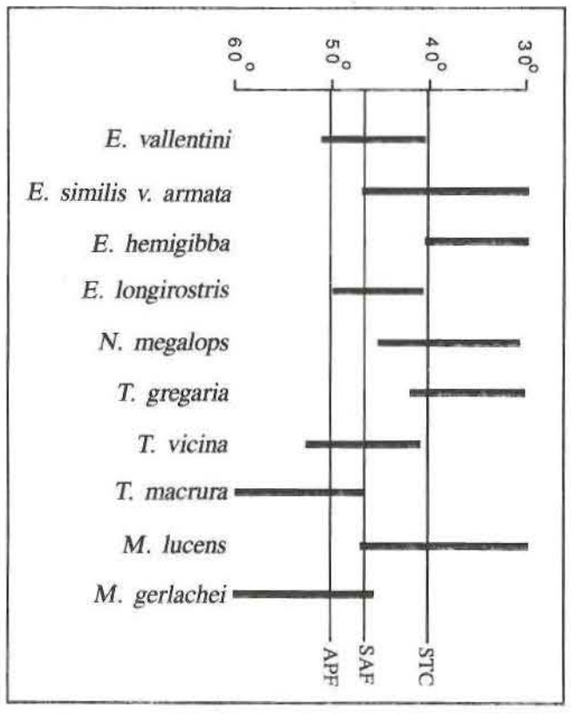

Fig 1: *The known distribution of the ten zooplankton species in the southern Indian Ocean considered in this study. The information comes from Boden (1954), Mauchline and Fischer (1964), Nemoto (1966), Raymont (1983) and De Decker (1984)*

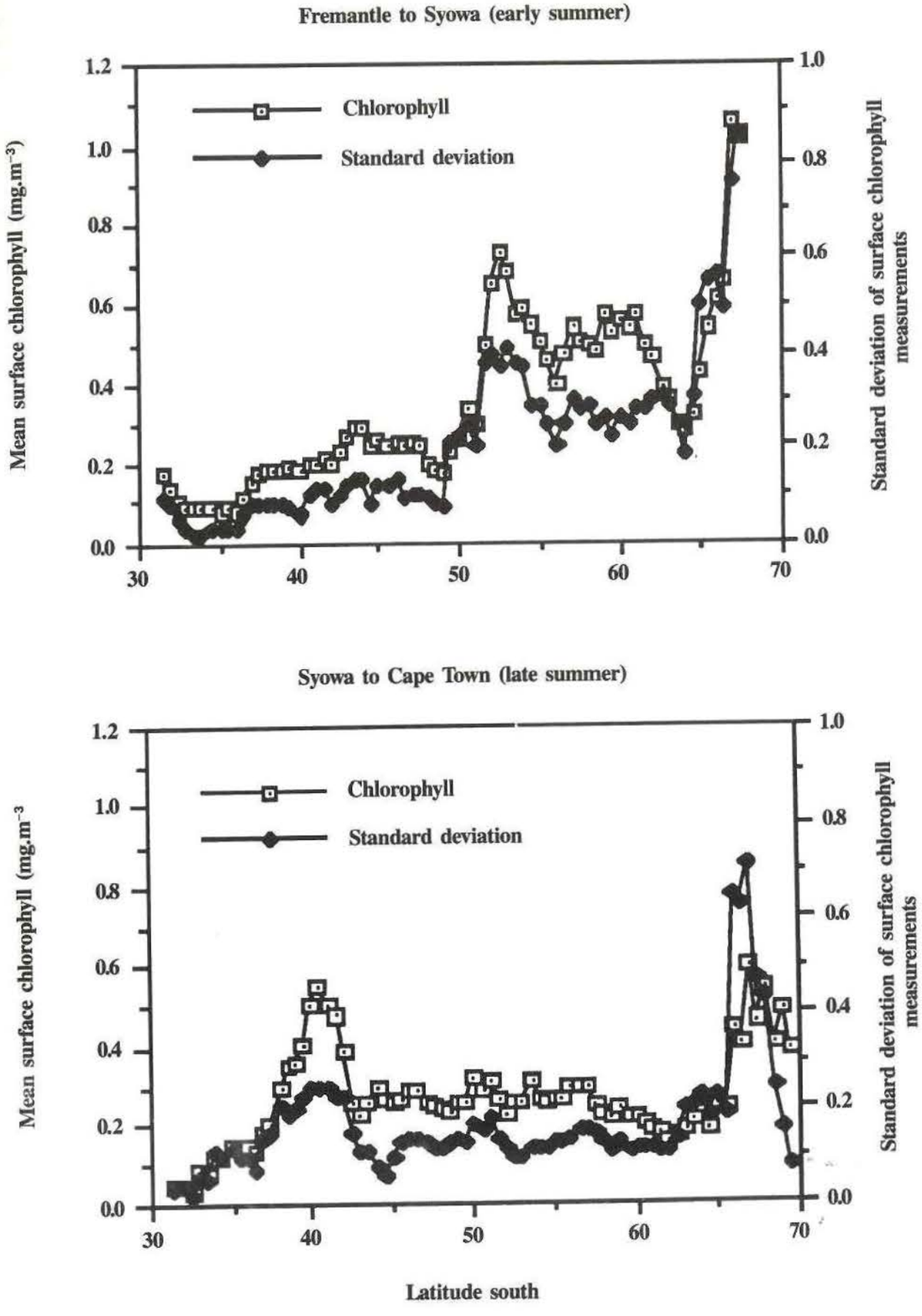

Fig 2: *A synthesis of surface chlorophyll-a measurements taken on 11 cruises from Fremantle to Syowa (68°22' S; 44°08' E) in the months December and January, and again from syowa to Cape Town in the months Febraury and March. The data points are means for each half degree, but smoothed with a running mean spanning 1.5 degrees. Data come from Tomanaga (1971), Nishiwaki (1972), Hoshimo (1974), Ohyama and Mayama (1976), Ohno (1976), Fukuchi (1977), Kuroda (1978), Tanimura (1981). Yamagata and Fukui (1981), Fukuchi and Tamura (1982) and Watanabe and Nakajima (1983)*

associated with elevated chlorophyll concentrations. No data are available to compare the winter situation. It is likely that in winter chlorophyll is scarce due to low light levels south of the APF, and both poor light and unstable water between the STC and APF. Both sub-Antarctic and Antarctic zooplankton are five to six times more abundant, measured volumetrically, in summer than in winter (Foxton 1956). A moderate winter north of the STC would afford this region some winter production. The sub-Antarctic region, integrated over a period of one year, is perhaps the least productive area within the respective ranges of the species under consideration. The frontal zones either side of the sub-Antarctic are far more productive. Correspondingly, the zooplankton biomass in the sub-Antarctic is two to three times lower than that of the APF and further south, but not less than the tropical water to the north (Foxton 1956, Vladimirskaya 1976).

Although a low lipid content (1 to 3% wet weight) might be normal for (sub)tropical euphausiids, the sub-Antarctic is not subtropical but strongly seasonal. Such low values for the end of summer would suggest that the species examined in this study would feed carnivorously on organisms with a long generation time that persists during winter. Alternatively, the subtropical species were too far south to maintain a herbivorous diet in winter. In the case of the Antarctic species, *T. vicina* and *T. macrura*, these specimens might have been too far north to accumulate a large lipid store for winter, as other polar herbivorous species generaly have >10% of wet weight as lipid at the close of summer. The two copepod species were richer in lipid and it is possible that these harvest the available phytoplankton more efficiently, perhaps by selecting smaller algae. Coccolithophores, radiolarians and tintinids do seem to constitute a significant fraction of euphausiid diet. Microzooplankton might provide a better food source where phytoplankton is dominated by the pico-size fraction as many euphausiids cannot filter small particles (<5 μm) efficiently (Boyd *et al* 1984, Quetin & Ross 1985, Stuart 1989). Unfortunately the seasonal availability, nutritional contribution and lipid characteristics of these protozoans are unknown.

The lack of wax ester and the low neutral lipid levels in the *Euphausia* spp., *Nematoscelis megalops* and *T. gregaria* indicates that no rapid synthesis of neutral lipid occurred in preparation for a non-feeding winter in these species. *T. vicina* and *T. macrura* both stored wax esters in contrast to *T. gregaria*, which is a subtropical species. Similary, *M. gerlachei* of Antarctic affinity stored more wax ester than *M. lucens* of a more temperate distribution. These latitudinal differences fit the hypothesis of Lee *et al* (1971). The wax ester storing species could be entirely herbivorous.

Thysanoessa vicina and *T. macrura* are the dominant prey items of penguins from Marion Island and Gough Island (Williams & Laycock 1981). Three representative species of the sea bird community at Marion, a penguin, an albatross and a petrel, are able to rapidly digest wax ester and triacylglycerols (Jackson & Place 1990). If the *Thysanoessa* prey species are indeed herbivorous, then these tertiary predators end a rather short food chain (plant — herbivore — bird) in an oceanic environment that is traditionally expected to be characterised by long food chains (Ryther 1969). It is however acknowledged that microzooplankton, as an intermediate step between phytoplankton and zooplankton, may be an important component the chlorophyll-poor waters of the sub-Antarctic. Microzooplankton may substantially increase the mean food chain length.

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