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The Fatty Acids of Antarctic Phytoplankton and Euphausiids. Fatty Acid Exchange among Trophic Levels of the Ross Sea

N.R. Bottino

Department of Biochemistry and Biophysics, Texas A&M University; College Station, Texas, USA

Abstract

The fatty acids of 3 samples of *Euphausia superba*, 7 samples of *E. crystallorophias*, and 12 samples of phytoplankton collected in the Ross Sea, Antarctica, during Eltanin Cruise 51 were examined. The fatty acid profiles of the samples of *E. superba* resembled each other closely. The fatty acid profiles of the *E. crystallorophias* samples were also similar to each other but different quantitatively from those of *E. superba*. Phytoplankton fatty acid patterns varied with the geographical location and species composition of the samples. The fatty acids of euphausiids were compared to those of the phytoplankton from the corresponding locations. Rather similar fatty acid patterns in phytoplankton and *E. superba* corroborate the herbivorous nature of this euphausiid. On the other hand, phytoplankton and *E. crystallorophias* showed quite different fatty acid patterns. The differences were mostly due to the presence of waxes among the lipids of *E. crystallorophias*. It is not clear whether these waxes are of dietary origin or are synthesized endogenously.

Introduction

The study of krill has become intensive in recent times, perhaps as a result of its potential importance as food. A variety of organisms is usually included under that generic name, but in the Southern Oceans the name *Euphausia superba* has been considered almost a synonym for krill. However, due to a quite defined geographical distribution, there are certain areas in which *E. superba* is replaced by other members of the same genus. For example, *E. superba* is very seldom found in shallow waters close to ice, such as the Ross Ice Shelf, but the smaller *E. crystallorophias* predominates in such areas (Marr, 1962; Mauchline and Fisher, 1969).

The chemical composition of *Euphausia superba* is reasonably well known. Its fatty acids, in particular, have been the subject of several studies in the past few years (Nonaka and Koizumi, 1964; Tsuyuki *et al.*, 1964a, b; Hansen, 1969; Pierce *et al.*, 1969; Hansen and Meiklen, 1970; Sidhu *et al.*, 1970; Van der Veen *et al.*, 1971). On the other hand, very little is known about the lipids of *E. crystallorophias*, except that they increase in the late austral summer and decrease gradually during the winter (Littlepage, 1964). The present report describes studies on the fatty acids of *E. superba* and *E. crystallorophias* from various locations in the Ross Sea. The fatty acid patterns of the two euphausiids are compared to each other as well as to the fatty acids of phytoplankton from corresponding locations. An attempt is made to determine the flow of fatty acids through trophic levels.

Materials and Methods

Phytoplankton samples were collected with a 35 μ net, by vertical hauls to a depth of 200 m. After microscopic examination, samples containing less than 80% phytoplankton were discarded. Microzooplankton constituted the major contaminant. Euphausiids were collected with a 1 m mid-water trawl, at depths varying between 0 and 300 m. Shortly after being sorted by hand the samples were extracted for lipids with a chloroform:methanol (2:1, v/v) mixture (Folch *et al.*, 1957). Quantities of 5 to 10 mg total lipids were converted into fatty acid methyl esters by saponification, followed by reflux with methanol in the presence of boron trifluoride (American Oil Chemists' Society, 1970). The fatty acid methyl esters were studied by gas-liquid chromatography on a 6' 1/8" column of siliconized polyethylene glycol succinate (DGSS-X, Applied Science Co., State College, Pennsylvania) 10% w/w on Chromosorb (Johns-Manville, Denver, Colorado) at 170°C. A dual-flame model GC-5 Beckman gas chromatograph (Fullerton, California) was used connected to an Infotronics (Columbia Scientific Industries, Austin, Texas) digital integrator. Results are expressed as weight percent. Fatty acid methyl esters were identified by co-chromatography with known standards and by plotting relative retention times versus chain length before, and in most cases, after hydrogenation.

Results and Discussion

Fatty Acids of *Euphausia superba*

Samples of *Euphausia superba* were collected from Stations 8, 9 and 11 of Eltanin Cruise 51 (Fig. 1).

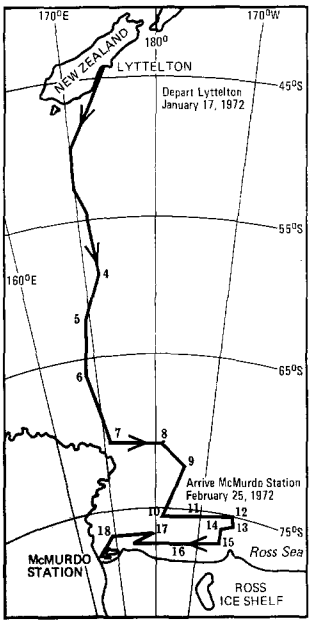

Fig. 1. Ross Sea, Antarctica: track of Eltanin Cruise 51, showing stations

These stations are located in an area in which two currents of water mix (Marr, 1962), thus providing the turbulent environment that *E. superba* seems to prefer for a habitat (Ivanov, 1970).

There is a remarkable similarity in the fatty acid compositions of the samples collected from the three stations (Table 1). In addition, these patterns resemble quite closely those reported by Hansen and Meiklen (1970) and by Sidhu *et al.* (1970). The present results, however, differ somewhat from those of Nonaka and Koizumi (1964) and of Van der Veen *et al.* (1971). Of all samples of *Euphausia superba* studied so far, only those of the present study were extracted immediately after capture. The others were frozen, transported and then extracted. This might explain some of the differences.

In two groups of krill (Stations 8 and 11), the hepatopancreas and stomach were excised and their fatty acids were studied separately from those of the whole animal. In one case (Station 11), the fatty acids of the remaining carcass were also studied. Since the stomachs were empty in all cases, the values in Table 1 under the heading hepatopancreas and stomach correspond essentially to hepatopancreas lipids only. The remarkable similarity among organ, remaining carcass, and whole

Table 1. *Euphausia superba*. Fatty acids (as weight per cent of total acids)

Fatty acid[a]	Station 8		Station 9	Station 11		
	Whole krill	HP+S[b]	Whole krill	Whole krill	HP+S	Remaining carcass
14:0	14.9	10.7	12.9	14.3	12.9	13.5
16:0	21.2	21.2	20.9	24.7	22.3	23.4
18:0	0.7	1.2	0.9	1.4	1.3	1.4
16:1(n-7)	9.0	6.7	10.7	8.9	8.2	8.0
18:1(n-9)	18.2	17.1	22.8	21.7	21.8	21.5
20:1(n-9)	0.6	0.9	1.1	0.9	1.2	1.1
18:2(n-3)	2.6	2.5	2.7	2.0	2.1	1.9
18:3(n-3)	1.1	1.2	1.4	1.0	1.0	1.1
18:4(n-3)	2.2	1.9	2.6	3.3	3.6	3.8
20:5(n-3)	16.0	22.2	11.8	11.4	13.9	11.6
22:6(n-3)	8.6	9.4	8.3	7.3	8.1	9.4
Minor fatty acids[c]	4.9	5.0	3.9	3.1	3.6	3.3

[a]The number preceding the colon gives the number of carbon atoms in the chain, the number following the colon the number of double bonds; (n-x): number of carbons in the chain minus number of carbons between the methyl end and the nearest double bond.

[b]Hepatopancreas plus stomach.

[c]Only those fatty acids present at a level of 1% or more are included.

body composition suggest that there is very little differentiation of organ lipids in *Euphausia superba*.

Fatty Acids of *Euphausia crystallorophias*

In contrast to *Euphausia superba*, which prefers turbulent waters, *E. crystallorophias* is usually found in shallow waters in the proximity of the Continental Shelf (Marr, 1962; Mauchline and Fisher, 1969). We know from Littlepage (1964) that *E. crystallorophias'* lipids decrease in amount at the end of the austral winter and rise in late summer. My own studies (Bottino, in press) show that 20 to 40% of the lipids of *E. crystallorophias* are waxes, the rest being mostly complex lipids and small amounts of neutral lipids.

The *Euphausia crystallorophias* collected from Stations 11, and 13 through 17 during Eltanin Cruise 51 show closely similar fatty acid patterns (Table 2). Comparison of the fatty acids of the two euphausiids show (Table 3) that *E. crystallorophias* contains about twice as much oleic acid (average 44% of total fatty acids) as *E. superba* (average 21%). Most of this oleic acid comes from the waxes, since about 83% of the wax fatty acids is oleic acid (Bottino, in press). The levels of highly unsaturated fatty acids (HUFA), mostly 20:5(n-3) and 22:6(n-3) are quite similar in both euphausiids.

In conclusion, comparison of the fatty acids of both euphausiids shows that *Euphausia crystallorophias* lipids are more unsaturated than *E. superba* lipids on account of the larger amount of oleic acid in the former. This different degree of lipid unsaturation might be related to the different environment in which the two euphausiids live. Whereas *E. crystallorophias* dwells near the ice all year around, *E. superba* is probably in contact with the ice only during the winter months (Mackintosh, 1970).

Phytoplankton Fatty Acids

Phytoplankton samples from Stations 8, 9, 11, 13-15, and 18 were studied. According to microscopic and macroscopic observations[1], the nature of the phytoplankton population changes with the stations, and this is reflected in quantitative variations in the fatty acid patterns (Table 3). Qualitatively, however, the fatty acid patterns showed some common characteristics: (1) The presence in most samples of significant amounts (up to 15%) of C_8 to C_{13} fatty acids with both even and odd carbon chains (Table 3); most of these acids are not detected or are present at much lower levels in euphausiid lipids (Tables 1 and 2). (2) All phytoplankton samples contained HUFA, mainly 20:5(n-3) and 22:6(n-3) in levels ranging from less than 1% to about 23% (Table 3). This suggests that the

[1] Dr. S. El-Sayed provided qualitative and semi-quantitative microscopic data on the composition of the phytoplankton samples.

Table 2. *Euphausia crystallorophias*. Fatty acids (as weight per cent of total acids)

Fatty acid	Station 11	Station 13		Station 14	Station 15	Station 16	Station 17
		Adults	Juvenile				
14:0	2.3	2.2	2.4	2.6	2.6	2.2	2.6
16:0	15.3	12.1	13.3	17.2	15.5	13.1	16.0
18:0	0.3	0.4	0.6	0.3	0.5	0.5	0.8
16:1(n-7)	8.6	6.5	7.9	7.9	8.4	9.3	6.5
18:1(n-9)	39.6	49.8	48.8	47.8	49.0	47.6	40.7
18:2(n-3)	1.7	2.4	2.2	2.1	2.3	2.3	1.6
18:3(n-3)	1.0	1.0	1.0	1.0	0.8	0.7	0.8
18:4(n-3)	0.7	1.8	1.5	1.2	1.3	0.8	1.0
20:4(n-6)	0.9	-	-	0.7	0.4	-	1.0
20:5(n-3)	18.2	14.1	12.5	12.3	12.8	14.9	16.5
22:6(n-3)	9.9	7.2	7.7	6.0	5.3	5.6	11.1
Minor fatty acids[a]	1.5	2.5	2.1	0.9	1.1	3.0	1.4

[a] Except for stearic acid (18:0) only those fatty acids present at a level of 1% or more are included. -: not detected. See footnotes to Table 1 for further explanation.

Table 3. Fatty acids of Antarctic phytoplankton and euphausiids (as weight per cent of total acids)

Fatty acid	Phytoplankton at Stations[a]												*Euphausia superba* (average of 3 stations)	*Euphausia crystallorophias* (average of 7 stations)
	8	9a	9b	11a	11b	13	14	15a	15b	15c	18a	18b		
8:0	-	-	-	0.4	-	1.2	1.0	-	-	0.7	-	-	-	
9:0	0.2	0.3	2.9	0.9	0.2	1.4	2.5	1.5	0.1	1.7	-	-	-	0.2
10:0	-	1.5	-	1.7	-	0.9	4.0	2.4	0.1	2.2	-	-	-	
11:0	-	-	-	0.7	1.3	1.2	1.9	1.1	trace	0.3	-	-	-	
12:0	1.3	2.3	2.3	1.9	0.4	2.0	2.2	2.5	0.4	0.8	0.2	-	0.2	0.1
13:0	-	1.1	-	-	-	0.4	3.0	0.8	-	-	-	-	-	0.1
14:0	9.7	22.5	11.5	15.9	22.9	25.5	20.7	17.4	19.3	5.1	13.0	9.5	14.0	2.4
15:0	1.9	0.3	1.6	2.6	1.7	2.6	-	3.4	0.7	1.1	0.3	-	0.4	0.1
16:0	20.4	20.1	19.9	16.0	18.8	21.7	18.5	18.7	17.2	16.1	17.3	14.9	22.3	14.6
18:0	7.0	2.1	3.3	2.0	2.0	2.6	2.2	1.9	1.8	5.2	1.7	1.5	1.0	0.5
10:1(n-?)	0.6	2.2	2.5	-	0.8	-	-	-	-	-	0.2	-	-	-
11:1(n-?)	-	-	-	0.7	-	1.9	2.0	1.3	0.1	0.9	-	-	-	-
12:1(n-?)	-	2.8	1.5	1.6	2.4	0.7	1.2	1.6	0.2	0.9	1.5	0.3	-	-
13:1(n-?)	-	0.5	-	1.0	-	0.6	1.8	1.4	0.1	1.1	-	-	-	-
15:1(n-?)	0.5	0.7	0.6	1.3	0.6	1.2	1.0	2.7	0.4	0.7	1.8	-	trace	-
16:1(n-?)	12.4	8.3	7.5	6.2	5.7	5.3	3.4	7.8	3.6	3.2	13.1	10.3	9.5	7.9
17:1(n-?)	1.6	0.3	0.9	0.6	0.3	0.2	-	0.3	0.3	trace	1.4	0.9	0.5	0.3
18:1(n-9)	12.1	16.0	15.6	16.2	18.3	16.3	24.8	11.4	20.2	12.5	17.3	18.7	20.8	46.2
20:1(n-9)	0.4	-	0.8	trace	-	1.7	-	0.1	trace	-	0.3	0.3	0.9	0.2
18:2(n-6)	2.1	0.1	0.3	0.2	0.1	-	-	-	0.1	-	4.1	3.8	0.2	-

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18:2(n-3)	3.7	3.3	2.4	3.1	3.3	3.0	2.7	2.1	7.1	12.0	1.2	1.7	2.4	2.1
22:2(n-6)	-	-	-	-	-	0.8	0.9	1.6	2.0	-	-	-	-	-
22:2(n-3)	-	0.6	0.7	1.4	1.4	-	-	-	-	-	-	-	-	-
18:3(n-6)	0.3	0.3	0.3	0.2	0.2	-	-	-	0.2	0.3	0.2	0.3	0.2	0.1
18:3(n-3)	0.9	0.7	0.6	0.7	0.7	0.7	0.3	0.2	0.1	0.2	0.2	0.3	1.2	0.9
20:3(n-6)	0.4	0.2	-	trace	0.9	trace	-	0.3	2.6	0.1	-	0.1	-	-
20:3(n-3)	0.2	0.2	0.3	-	-	-	-	trace	0.9	1.0	-	0.2	0.5	0.3
16:4(n-1)	-	-	0.5	-	-	-	-	-	-	6.3	-	-	-	-
18:4(n-3)	2.0	3.1	3.5	5.2	6.0	3.0	2.7	3.2	6.2	0.9	2.2	2.5	2.7	1.2
20:4(n-6)	-	-	-	0.4	-	-	-	-	-	4.7	-	-	0.4	0.4
20:4(n-3)	0.2	-	0.3	0.2	-	-	-	0.1	trace	-	-	0.2	0.4	0.1
22:4(n-6)	-	-	-	-	-	-	-	-	-	trace	-	-	0.2	-
22:4(n-3)	1.3	-	trace	-	-	-	-	trace	-	trace	-	-	-	-
20:5(n-3)	11.4	4.8	9.2	7.0	6.4	1.7	2.1	5.3	6.0	2.1	18.4	23.4	13.1	14.4
22:5(n-6)	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-
22:5(n-3)	0.3	0.3	-	-	-	-	-	0.1	-	2.1	-	-	0.2	-
22:6(n-3)	6.1	4.9	7.9	8.4	5.5	0.9	0.8	7.1	7.8	16.5	5.5	11.0	8.1	7.5
Minor fatty acids[b]	3.3	1.5	4.3	4.6	1.0	3.2	0.6	4.0	2.8	1.8	0.5	0.9	0.8	0.4

[a]Microscopic examination indicated that the following genera predominated in each station. Station 9: *Eudorina, Pandorina;* Station 10: *Thalassiosira, Fragilaria, Nitzchia, Corethron,* Silicoflagellates; Station 11: *Corethron, Fragilaria, Chaetoceros,* Silicoflagellates; Station 12: *Corethron, Fragilaria, Nitzchia,* Tintinnids; Station 13: Complex mixture; Station 14: *Phaeocystis;* Station 15: *Phaeocystis, Chaetoceros, Nitzchia, Thalassiosira, Fragilaria;* Stations 17 and 18: *Fragilaria, Nitzchia, Coscinodiscus,* Dinoflagellates, Tintinnids.

[b]Only those fatty acids present at a level of 1% or more are included. See footnotes to Tables 1 and 2 for further explanation.

HUFA of the marine food-chain originate in phytoplankton. Holz (1969) has reached a similar conclusion from studies on laboratory-grown Protozoa.

Comparison of Trophic Levels

Whereas most euphausiids are considered omnivores, there is good evidence that *Euphausia superba* feeds on phytoplankton (Mauchline and Fisher, 1969). Whether the preferred food is *Fragilaria* as stated by many (Raymont, 1963; Nemoto, 1968), or whether *E. superba* has a wider range of selectivity (Pavlov, 1970), is still in doubt. Although generally considered a phytoplankton feeder (Andriashev, 1968; Knox, 1970), the evidence on the food preference of *E. crystallorophias* seems to be only of indirect nature, e.g. the finding by Littlepage (1964) of parallel changes in seasonal phytoplankton abundance and the lipid content of *E. crystallorophias*, and the study by Mauchline (1967) showing striking similarities between the feeding appendages of *E. crystallorophias* and *E. superba*.

It was of interest, therefore, to compare the fatty acid patterns of *Euphausia superba* and *E. crystallorophias* collected during Eltanin Cruise 51 with the fatty acids of phytoplankton from the corresponding stations. It was hoped that the feeding habits would be reflected in similarities in the fatty acid patterns of the related trophic levels. This obviously assumes that euphausiids add very little endogenously-made fatty acids to those they acquire from the diet. Since the lipid content of phytoplankton is relatively high, between 2 and 20% of their dry weight (Parsons *et al.*, 1961; Andriashev, 1968), their ingestion by zooplankton should markedly diminish the lipogenetic activity of the zooplankton. Recent experiments by Jeffries (1972) show that the dietary origins of the body lipids of omnivorous fish can be determined with a simple budget of fatty acid flow from diet to body lipids. The feasibility of these determinations is supported by the findings of Owen *et al.* (1972) who, confirming previous work by others, have shown that the fatty acid composition of fish lipids reflects the composition of the dietary lipids. Additional support is given by experiments in my laboratory (Warman and Bottino, 1974) which indicate that, in salt-water fish-liver the degree of lipogenesis is equally low whether the animals are starved, fed fat, or fed a fat-free diet. Most probably, the same is true for other marine organisms including euphausiids.

It is possible that certain fish-lipid classes such as triglycerides may reflect changes in dietary lipids better than other classes of a more structural nature. It is shown below that this is not true in the present case. Finally, the similar fatty acid composition of euphausiid whole body and hepatopancreas (shown above) rules out the possibility of a preferential incorporation of dietary fatty acids into certain tissues. Owen *et al.* (1972) reached the same conclusion while studying the ingestion of polyunsaturated fatty acids by fish.

Table 3 includes in the columns to the right averages of the *Euphausia superba* and *E. crystallorophias* fatty acids to facilitate comparisons. Comparisons can be made quantitative by determining the "distance" between fatty acid profiles with the formula (McIntire *et al.*, 1969; De Mort *et al.*, 1972):

$$D_{jh} = \left[\sum_{i=1}^{n} (P_{ij} - P_{ih})^2 \right]^{1/2},$$

where D_{jh} is the degree of difference between the jth and hth species and P_{ij} is the percentage of the total fatty acid content represented by the ith fatty acid in the jth species. For example, the distance between the results of two gas-chromatographic analyses of the same sample of marine fatty acids is about 2.2 ± 1.8 (average ± 1 standard deviation). The average distance between the 3 samples of *E. superba* fatty acids (Table 1) was 6.3 ± 1.2. The average distance among the 6 samples of *E. crystallorophias* fatty acids (Table 2) was 7.7 ± 3.5. The distance between the average of *E. superba* and the average of *E. crystallorophias* (Table 3) was 29.0.

In comparing the euphausiids with the phytoplankton samples of the corresponding stations, the distances between the average of *Euphausia superba* and the phytoplankton profiles (Stations 8, 9a and 9b) ranged between 10 and 15, which are reasonably low values. The distances between the average of *E. crystallorophias* and phytoplankton (Stations 11, 13, 14, 15 and 18[2]) were in the 30 to 40 range. Thus, the fatty acids of *E. superba* compare well both in nature and concentration with those of phytoplankton of the corresponding locations. However, there are marked quantitative differences between the fatty acid profiles of *E. crystallorophias* and those of phytoplankton. It was mentioned earlier that the lipids of *E. crystallorophias* differ from those of *E. superba* in that they contain 20 to 40% waxes very rich in oleic acid (Bottino, in press). Thus, the difference in fatty acid profiles between the two euphausiids and between *E. crystallorophias* and phytoplankton may be due to the presence of these waxes. To assess this possibility, the average fatty acid profile of *E. crystallorophias* was recalculated eliminating the oleic acid contributed by the waxes, and distances were determined between the new set of values and those of *E. superba* and phytoplankton. The distance between the corrected average of *E. crystallorophias* and the average of *E. superba* was 14.1. The distances between the corrected values of *E. crystallorophias*

[2] Despite the fact that no samples of *Euphausia crystallorophias* from Station 18 were analyzed, the phytoplankton data from that station are included in view of the short distance between Stations 18 and 17.

and phytoplankton ranged between 22 and 32 for Stations 11 to 15 and between 10 and 15 for Station 18. These results indicate that the presence of waxes in *E. crystallorophias* is what makes the fatty acid profile of this euphausid different.

It is possible that certain lipid classes such as triglycerides may be more susceptible than, for example, complex lipids to changes in dietary lipids. In fact, it has been accepted for many years that depot lipids are more sensitive than structural lipids to changes in dietary fats. To test this possibility, distances were determined between the major lipid classes of both euphausiids and the total lipids of the phytoplankton obtained in corresponding stations. The results showed that the waxes of *Euphausia crystallorophias* were the most distant from phytoplankton (average D = 76). The complex lipids of both euphausiids and the steroid esters of *E. crystallorophias* showed an average distance of about 30 with respect to phytoplankton. The triglycerides of *E. superba* were the closer to phytoplankton with an average D = 17, a value which is in the same range as that of *E. superba* total lipids versus phytoplankton. These results show that, in the present case, measuring distances between diet lipids and individual lipid classes is not better than comparing the total lipid fatty acids of the diet with those of total body lipids. In addition, the data seem to indicate that neither the complex lipids nor the steroid esters, and even less the waxes of *E. crystallorophias* reflect very well the composition of the dietary fatty acids.

The similarity between the corrected values for *Euphausia crystallorophias* and some of the phytoplankton values suggest that *E. crystallorophias* may be, in fact, herbivorous. Since most of the phytoplankton samples contained relatively small amounts of waxes, it is possible that *E. crystallorophias* may be able to incorporate and concentrate dietary waxes. Alternatively, waxes could have been synthesized, partially or totally by the euphausiid. Holtz *et al.* (1973) and Sargent *et al.* (1974) have recently characterized wax synthesizing systems in copepods.

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Dr. N.R. Bottino
Department of Biochemistry and Biophysics
Texas A & M University
College Station, Texas 77843
USA

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