THE LIPID CONTENT AND COMPOSITION OF SOME ANTARCTIC MACROZOOPLANKTON

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ABSTRACT. The lipid content and composition of 24 species of macrozooplankton from seven phyla, collected mainly from the Southern Ocean around South Georgia, are reported. Some groups, notably cnidarians, ctenophores, chaetognaths, annelids and salps contained only small amounts of lipid (0.05–3.4% fresh weight) and the storage lipid was usually triacylglycerol. An exception was a ctenophore tentatively identified as *Pleurobrachia* sp., which contained a small wax ester droplet close to the gut. Crustaceans usually contained moderate or large amounts of lipid (1.3–19.4% fresh weight) of which a significant proportion was often wax ester, especially in copepods and some euphausiids. There was a significant positive correlation between total lipid content and the proportion of wax ester in the lipid. Freshwater zooplankton from Heywood Lake on Signy Island, South Orkneys, differed from marine species in storing triacylglycerol rather than wax ester, despite a strong seasonal variation in food availability.

INTRODUCTION

In the past 20 years there has been an increasing interest in the biochemistry of marine organisms. Zooplankton from many areas have now been analysed. Until recently, however, there has been no systematic investigation of the lipid composition of Antarctic zooplankton, although several workers have looked at zooplankton from the Arctic (Ikeda, 1972; Lee, 1975; Percy and Fife, 1981).

A series of oceanographic cruises by the British Antarctic Survey since 1978, mainly in the vicinity of South Georgia, has provided specimens of many species of macrozooplankton in net hauls. The lipid content and composition of 24 of the commoner species are reported in this paper.

MATERIALS AND METHODS

Zooplankton were sampled with a midwater trawl (RMT1+8; M. R. Clarke, 1969) from the surface waters of the Southern Ocean around South Georgia. A few specimens were collected further south, and some were taken from inshore waters at Grytviken, South Georgia, with a small hand net. All samples were collected in the latter half of the austral summer (January to April), and details are given in Table I. Freshwater zooplankton were collected by hand net from Heywood Lake on Signy Island, South Orkney Islands (60° 41′ S, 45° 36′ W), during the austral summer 1980–81.

A few species were analysed immediately, but most were carefully blotted free of excess water and frozen rapidly to −20°C. Transport to UK was at −40°C in sealed containers and specimens were stored at −50°C until analysed (up to nine months later). This treatment is believed not to have had any significant effect on either the amount or the composition of the lipid (Morris, 1972).

Lipid was extracted by homogenizing the sample in excess ice-cold, de-gassed methanol–chloroform (2:1 v/v). The homogenate was carefully filtered through a GF/C glass fibre filter paper. Calculated volumes of chloroform and water were

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Table I. Lipid content of macrozooplankton from the Southern Ocean; p – all individuals pooled for a single analysis, otherwise data is mean of stated number of individual analyses; species names in parentheses are tentative identifications.

Species	n	Lipid		Date	Ref.	Sample area and depth
		% fresh wt	mg per individual			
CNIDARIA						
Anthomedusae						
Sibogita borchgrevinki	16p	0.05	1.36	Mar 1980	L94	South Georgia, 200 m
Siphonophora						
Diphyes antarctica	14p	0.10	0.84	Mar 1980	L96	South Georgia, 200 m
CTENOPHORA						
Beroe sp.	p	2.89	—	8 Feb 1978	408	Northern Scotia Sea, 50 m
(*Pleurobrachia* sp.)	p	0.10	—	6 Jan 1978	1	King Edward Cove, SG, surface (dip-net)
PLATYHELMINTHES						
Turbellaria						
(species unknown)	1	2.74	15.2	14 Apr 1980	L139	South Georgia, 1500 m
ANNELIDA						
Polychaeta						
Tomopteris sp.	1	2.98	10.8	26 Jan 1978	7	South Georgia, 40 m
	p	2.91	—	8 Feb 1978	426	Northern Scotia Sea, 50 m
	p	3.45	—	8 Feb 1978	427	Northern Scotia Sea, 50 m
Vanadis antarctica	3p	0.99	15.5	9 Mar 1980	L86	Southern Scotia Sea, 200 m
CHAETOGNATHA						
(*Eukrohnia* sp.)	p	0.34	—	8 Feb 1978	412	Northern Scotia Sea, 50 m
	3p	0.28	2.83	29 Mar 1980	L136	South Georgia, 200 m
CRUSTACEA						
Amphipoda						
Brachyscelis sp.	19p	3.06	1.37	Mar 1980	L91	South Georgia, surface (neuston net)
Cyllopus sp.	11p	5.85	7.00	13 Mar 1980	L89	Southern Scotia Sea, 200 m
	16p	5.65	6.33	13 Mar 1980	L98	Southern Scotia Sea, 200 m
Eurythenes sp.	1	2.57	59.3	14 Apr 1980	L140	South Georgia, 1500 m
Parathemisto gaudichaudii	12p	4.84	1.83	26 Jan 1978	8	South Georgia, 40 m
	12p	4.53	2.60	26 Jan 1978	9	South Georgia, 40 m
	p	5.78	—	21 Feb 1978	409	South Georgia, 50 m
	p	6.10	—	21 Feb 1978	405	South Georgia, 50 m
	13p	7.43	4.04	Mar 1980	L92	South Georgia, 200 m
	5p	6.61	2.92	Mar 1980	L99	South Georgia, 200 m
	12p	5.24	3.40	Mar 1980	L109	South Georgia, 200 m
	28p	6.66	3.40	10 Apr 1980	L138	South Georgia, 70 m
Vibilia antarctica	[redacted]	4.66	1.60	31 Mar 1980	L124	South Georgia, 200 m
	6p	6.25	1.73	31 Mar 1980	L125	South Georgia, 200 m

Copepoda						
Calanoides acutus	p	12.65	—	2 Feb 1978	410	South Georgia, 50 m
Euchaeta antarctica	p	15.85	4.12	2 Feb 1978	411	South Georgia, 50 m
	26p	11.78	4.68	14 Apr 1980	L153	(Mature females) South Georgia, 1500 m
	31p	12.54	4.25	14 Apr 1980	L154	(Immature females) South Georgia, 1500 m
	6p	13.06	5.60	14 Apr 1980	L155	(Ovigerous females) South Georgia, 1500 m
	4p	15.17	4.00	5 Dec 1980	—	McMurdo Sound, 300 m
Rhincalanus gigas	10p	4.92	1.30	9 Jan 1978	2	King Edward Cove, SG, surface (dip-net)
	8p	8.72	2.08	10 Jan 1978	3	King Edward Cove, SG, surface (dip-net)
	8p	6.08	0.73	26 Jan 1978	5	South Georgia, 50 m
	10p	5.35	0.82	26 Jan 1978	6	South Georgia, 50 m
	10p	9.21	1.17	26 Jan 1978	406	South Georgia, 50 m
Euphausiacea						
Euphausia crystallorophias	35p	7.90	9.14	6 Feb 1980	L88	Prince Gustav Channel, 50 m
E. frigida	p	4.58	—	21 Feb 1978	404	South Georgia, 50 m
	14p	19.38	4.43	Mar 1980	L137	South Georgia, 200 m
E. superba	11	4.09	—	21 Jan 1978	—	(Immatures) South Georgia, 120 m
	2	6.49	—	1 Mar 1978	—	(Immatures) South Georgia, surface
	8	2.41	—	3 Feb 1978	—	(Mature males) Scotia Sea, 40 m
	12	5.33	—	1 Mar 1978	—	(Mature males), South Georgia, surface
	20	6.33	—	1 Mar 1978	—	(Gravid females), South Georgia, surface
	5	2.79	—	8 Feb 1978	—	(Spent females), South Georgia, surface
E. triacantha	1	7.77	12.1	20 Feb 1978	400	South Georgia, 1300 m
	1	6.67	18.2	20 Feb 1978	401	South Georgia, 1300 m
	1	6.56	18.5	20 Feb 1978	402	South Georgia, 1300 m
	1	7.31	26.5	20 Feb 1978	403	South Georgia, 1300 m
	8p	5.70	12.09	20 Feb 1978	413	South Georgia, 1300 m
	21p	4.03	9.40	6 Mar 1980	L87	Southern Scotia Sea, 200 m
	14p	4.37	7.08	6 Mar 1980	L102	Southern Scotia Sea, 200 m
	10p	4.03	12.56	14 Apr 1980	L144	South Georgia, 1500 m
Thysanoessa sp.	8p	15.20	9.11	26 Jan 1978	415	South Georgia, 40 m
	20p	14.20	8.34	26 Jan 1978	407	South Georgia, 40 m
	p	3.16	—	6 Mar 1980	L93	Southern Scotia Sea, 200 m
	20p	5.33	3.08	6 Mar 1980	L103	Southern Scotia Sea, 200 m
Mysidacea						
Antarctomysis ohlini	3	1.34	71.0	5 Dec 1980	—	McMurdo Sound, 300 m
A. maxima	10p	2.93	8.46	26 Jan 1978	414	South Georgia, 50 m
CHORDATA						
Thaliacea						
Salpa sp.	10p	0.13	5.17	Mar. 1980	L95	South Georgia, 200 m
	p	0.08	—	3 Feb 1978	416	Scotia Sea, 50 m
	p	0.05	—	3 Feb 1978	420	Scotia Sea, 50 m

added (Bligh and Dyer, 1959). Phase separation was allowed to take place overnight at 2°C. The chloroform layer was then removed, the solvent reduced under nitrogen in a rotary evaporator at 50°C and the amount of lipid determined gravimetrically, following removal of the solvent from a subsample in a tared vial with a stream of nitrogen. Lipid extracts were stored in chloroform in sealed vials at −40°C but without antioxidant since this interferes with quantitative thin-layer chromatography (TLC).

Lipid class composition was analysed by TLC on precoated plates of silica gel H (BDH Ltd, no added binder or fluorescent indicator) in the solvent system petroleum spirit (40–60°C)/peroxide-free diethyl ether/acetic acid (80/20/1, v/v). The relative amounts of the different lipid classes were determined by scanning densitometry after charring with 3% cupric acetate in 8% aqueous orthophosphoric acid at 180°C (Fewster and others, 1969). Peak areas were quantified electronically (HP 3390A) and correction factors applied to the phospholipid, free sterol and sterol ester components, based on calibration with marine invertebrate lipid. These correction factors were applied to all species and any unknown component was assumed to have a response similar to that of triacylglycerol. The method is described in detail by Clarke and Wickins (1980).

In a small number of samples, lipid phosphorus was assayed after digestion of a subsample with perchloric acid at 180°C (Clarke, 1979), and wax ester determined as the percentage of total lipid carbon following TLC and elution of the wax ester band from the silica gel. Blank corrections were applied for elution of non-lipid organic carbon from the TLC plates.

All solvents were double glass distilled (Rathburn Chemicals Ltd, Walkerburn, Peebles), and all other chemicals were of Analar standard (BDH Ltd). Standard lipids came from Sigma, and the secondary calibration standard for TLC densitometry was lipid isolated from the prawn *Penaeus merguiensis* (Clarke and Wickins, 1980).

Specimens were identified by consulting Mackintosh (1934), Hardy and Gunther (1935) (general zooplankton), Vervoort (1957) and Park (1978) (copepods), K. H. Barnard (1932), J. Barnard (1969), Bowman (1973) and Bowman and Gruner (1973) (amphipods) and for euphausiids, John (1936) and the key to antarctic euphausiids prepared for BIOMASS by J. Mauchline (SCAR/SCOR/IABO/ACMRR, Biomass Handbook 5, 4 pp., date of publication unknown).

Results and Discussion

Total lipid content

The total lipid contents of 24 species of macrozooplankton from the Southern Ocean are given in Table I. There was a wide range of total lipid contents, from 0.05% fresh weight in the anthomedusan *Sibogita borchgrevinki* to 19.4% in one sample of *Euphausia frigida*.

Low lipid contents were found in several groups of organisms, notably cnidarians, ctenophores, chaetognaths, annelids and salps. In some of these organisms (salps, ctenophores and siphonophores) a low lipid content on a wet weight basis is inevitable because so much of the body is either gelatinous or water. These groups are little known biochemically, but they are not generally believed to store large quantities of lipid. An interesting exception may be the ctenophore sampled from King Edward Cove and tentatively identified as a *Pleurobrachia* sp., where a clear lipid globule could be seen close to the gut in every individual examined (>30). The carnivorous worms *Eukrohnia* and *Vanadis* both had lipid contents <1%, although *Tomopteris* contained 2.9–3.5% lipid.

The crustaceans analysed contained moderate to high amounts of lipid. In general the amphipods contained between 2 and 7% lipid but euphausiids were much more variable, ranging from 2.4% in *E. superba* to almost 20% in one sample of *E. frigida*. Copepods were usually rich in lipid (4.9–16% fresh weight) and were frequently noted to have well developed oil droplets.

In two species lipid content was found to vary with sexual maturity. Immature and male *Euphausia superba* generally had low lipid contents, although there was some indication of an increase in lipid towards the end of summer (Clarke, in press). Female krill lipid content could be as high as 6.3% before spawning but was less than 3% afterwards (Table I; Clarke, 1980). In the copepod *Euchaeta antarctica*, females with maturing ovaries contained about 4.25 mg lipid, rising to about 4.7 mg when the ovaries were close to maturity. Females carrying egg sacs contained about 5.6% lipid.

Lipid class composition

Information on lipid class composition was obtained for 20 species, 19 of which were examined by TLC-scanning densitometry (Table II). The compositions observed were very variable, although certain trends were apparent. Zooplankton with relatively low lipid contents tended to have lipid class compositions dominated by phospholipid and free sterol. When storage lipids were present these tended to be triacylglycerol (TAG) rather than wax ester (WE). As before, an exception to this was the ctenophore *Pleurobrachia* sp., where the presence of a small oil sac raised the WE content to 47% total lipid, even though the total lipid content was only 0.1%. The high levels of phospholipid and free sterol in those species with very low lipid contents indicate that almost all the lipid present was structural membrane lipid, rather than depot lipid.

As has been found elsewhere, copepods were rich in wax ester (50–55% total lipid) and this was due to the presence of a discrete oil sac. The amphipods showed a fairly uniform pattern of storing both TAG and WE, together with small amounts of alkyldiacylglycerol (ADAG). Within this broad picture there were, however, variations both between species and, in *Parathemisto gaudichaudii*, also between different samples. The euphausiids had very variable lipid compositions, ranging from species that stored predominantly TAG (e.g. *E. superba*, which contains <1% WE), about equal amounts of TAG and WE (*E. triacantha*), to those storing almost exclusively WE (*E. crystallorophias, Thysanoessa* sp.).

Extensive analyses of zooplankton lipids from Arctic, temperate and tropical waters by many workers have been collated by Sargent (1976), who has shown that species that store large amounts of lipid usually do so as wax ester. This is particularly so in copepods. In Fig. 1 all available data from the lipid composition of Antarctic zooplankton are plotted, and a broadly similar pattern is evident. There is a positive correlation between total lipid content and the proportion of wax ester (Spearman rank correlation coefficient $r_s = 0.451$, $n = 30$, one-tailed, $P < 0.01$), and this correlation is even more marked if the point for *Pleurobrachia* sp. is excluded ($r_s = 0.539$, $n = 29$) or only crustaceans are included in the analysis ($r_s = 0.585$, $n = 20$).

Comparison with Arctic zooplankton

Previous analyses of the lipid composition of polar zooplankton have covered a taxonomic range similar to this study but all have been from the Arctic. Samples have come from the Bering Sea (53–56° N, 162–172° W; Ikeda, 1972), Fletcher's Ice Island

Table II. Lipid class composition of macrozooplankton from the Southern Ocean; SD, thin-layer chromatography followed by scanning densitometry; TLC, thin-layer chromatography followed by elution of bands; PCA, perchloric acid digest; PL, polar lipids (mostly phospholipid); MAG, monoacylglycerol; FS, free sterol; FFA, free fatty acid; DAG, diacylglycerol (both isomers combined); TAG, triacylglycerol; ADAG, alkyldiacylglycerol; WE, wax ester; SE, sterol ester; ukn, unknowns (number of components in parentheses); nd, not determined; –, not detected; tr, trace (<0.1%).

	Lipid			*Lipid class composition (% total lipid)*									
Species	*Ref*	*% fresh*	*Technique*	*PL*	*MAG*	*FS*	*FFA*	*DAG*	*TAG*	*ADAG*	*WE*	*SE*	*Ukn*
Sibogita borchgrevinki	L94	0.05	SD	44.0	—	17.6	1.1	0.8	25.0	1.8	9.2	—	0.2 (1)
Diphyes antarctica	L96	0.10	SD	40.6	—	21.5	1.4	1.2	21.0	0.8	—	12.5	0.9 (1)
Beroe sp.	408	2.89	SD	45.2	—	17.0	7.5	1.4	9.3	—	17.5	—	2.2 (2)
(*Pleurobrachia* sp.)	1	0.10	TLC	nd	nd	nd	nd	nd	nd	nd	46.9	nd	nd
	1	0.10	PCA	28.5	nd	nd	nd	nd	nd	nd	nd	nd	nd
Tomopteris sp.	7	2.98	PCA	55.2	nd	nd	nd	nd	nd	nd	nd	nd	nd
	426	2.91	SD	48.2	0.5	33.8	13.0	—	tr	—	4.6	—	—
	427	3.45	SD	49.1	0.5	32.4	12.6	—	tr	—	5.5	—	—
(*Eukrohnia* sp.)	412	0.34	SD	45.3	—	29.7	17.3	0.5	1.1	—	5.8	—	0.4 (1)
Brachyscelis sp.	L91	3.06	SD	33.2	—	19.5	11.3	1.3	22.5	5.5	3.7	—	2.9 (1)
Cyllopus sp.	L89	5.85	SD	43.4	—	21.4	2.8	—	22.0	2.6	6.5	—	1.3 (1)
Parathemisto gaudichaudii	405	6.10	SD	26.6	—	14.7	8.1	0.5	32.2	0.4	16.2	—	1.5 (2)
	409	5.78	SD	25.5	—	14.1	8.5	0.9	28.7	—	20.4	—	1.5 (2)
	L92	7.43	SD	17.3	0.4	21.1	6.4	—	46.7	3.7	3.0	—	1.5 (1)
	L99	6.61	SD	23.5	—	17.3	6.2	3.5	43.6	1.8	2.7	—	1.4 (1)
	L109	5.24	SD	22.4	—	17.5	7.3	3.3	40.4	5.9	2.0	—	1.3 (1)
Vibilia antarctica	L124	4.66	SD	25.3	—	13.9	10.3	—	32.9	5.8	9.6	—	2.2 (1)
Calanoides acutus	410	12.65	SD	30.8	—	4.3	6.3	0.5	3.8	—	54.1	—	0.1 (1)
Euchaeta antarctica	411	15.85	SD	26.1	—	6.2	4.2	tr	8.3	—	54.9	—	0.2 (1)
Rhincalanus gigas	406	9.21	SD	22.4	—	18.6	5.8	tr	2.8	—	50.0	—	—
	—	nd	TLC	6.5	nd	nd	nd	nd	nd	nd	53.0	nd	—
Euphausia crystallorophias	L88	7.90	SD	45.7	—	18.1	14.4	—	2.5	—	17.4	—	1.9 (1)
E. frigida	404	4.58	SD	4.39	—	30.5	14.4	0.5	8.2	tr	2.5	—	—
E. superba (male)	—	2.41	SD	41.3	1.4	16.2	14.4	0.4	21.5	—	1.9	2.8	
(female)	—	6.33	SD	39.3	1.6	16.9	11.4	0.6	29.2	—	tr	tr	
E. triacantha	403	7.31	SD	23.9	0.5	19.4	13.7	1.6	27.0	2.0	10.5	—	1.5 (1)
	402	6.56	SD	23.7	0.5	18.9	12.0	1.5	24.2	2.1	16.0	—	1.2 (1)
Thysanoessa sp.	407	14.20	SD	50.7	—	18.0	6.9	tr	tr	tr	23.1	—	0.9 (1)
	L93	3.16	SD	50.2	—	20.5	7.2	0.1	3.5	tr	18.0	—	0.6 (1)
Antarcticus maxima	414	2.93	SD	35.1	—	23.6	7.8	—	25.2	—	5.6	—	2.8 (1)
Salpa sp.	L95	0.13	SD	49.3	—	17.4	1.6	tr	14.4	—	1.1	—	3.4 (1)
	416	0.08	SD	54.6	—	21.0	13.5	0.2	3.6	—	3.3	—	3.9 (2)

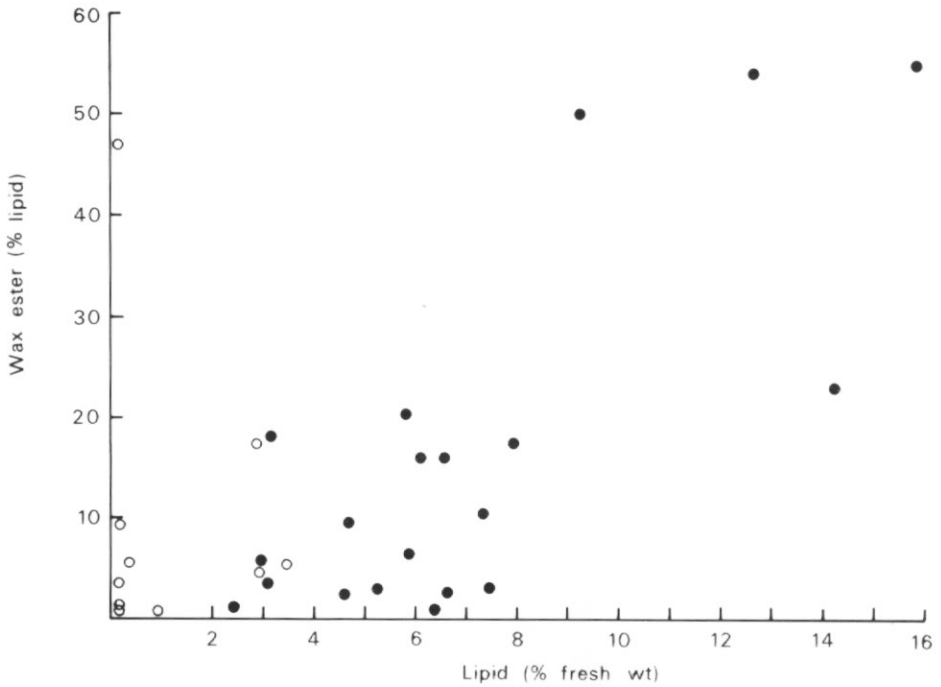

Fig. 1. Relationship between total lipid content (% fresh weight) and wax ester content (% of the total lipid) for 20 species of Southern Ocean zooplankton. Data are from Table II: ●, 13 species of crustaceans; ○, all other taxa (the point at 0.01% lipid, 47% wax ester is for the ctenophore tentatively identified as *Pleurobrachia* sp.). The relationship is significant (Spearman rank correlation coefficient, r_s=0.451, n=30, one-tailed P<0.01).

Station (83–88° N, 112–85° W; Lee, 1975), and Frobisher Bay (63° N, 68° W; Percy and Fife, 1981).

With the exception of a single specimen of *Hybocodon prolifer*, all medusae analysed have contained <1% fresh weight lipid. Even when expressed on a dry weight basis to allow for the high water content, lipid contents are still quite low (3–22% dry wt). Low lipid contents have also been reported for the ctenophores *Beroe cucumis* (4.4–6.0% dry wt) and *Mertensia ovum* (5.3–14.4% dry wt) by Percy and Fife (1981). These are equivalent to 0.15–0.2% fresh wt and 0.24–0.65% fresh wt respectively. Medusae and ctenophores are mostly water and frequently have very high contents of mineral ash (50–60% dry wt; Percy and Fife, 1981). Nevertheless, even allowing for this, relatively little of the organic matter is lipid, which would suggest that most of the lipid is structural, with little depot fat. The analyses of *Beroe*, *Sibogita* and *Diphyes* from the Southern Ocean reported here would support this, since phospholipid and free sterol together totalled 61–62% of the total lipid in all three species. Storage lipid was usually triacylglycerol, although *Beroe* lipid did contain 17.5% wax ester. These analyses would suggest that, in polar waters, neither medusae nor ctenophores rely on a lipid store to survive any periods of low food availibility (both groups are carnivores). In a recent study of the temperate water ctenophore *Bolinopsis infundibulum*, Morris and others (1983) found 16% dry weight lipid, of which 67% was phospholipid and 19% TAG. They suggested that the major energy reserve was protein (38% dry wt, compared with a

range of 7.7–31% reported for arctic medusae and ctenophores by Percy and Fife, 1981). During four weeeks starvation the gut was observed to shrink by over one-third.

The ctenophore identified tentatively as *Pleurobrachia* sp. appears to be an exception to this general pattern in that, although the lipid content was low, almost 50% of the lipid was wax ester. The wax was located in a single oil sac close to the gut. Ctenophores are important predators of copepods and it is possible that this wax came directly from the food. Although 17.5% wax ester was detected in *Beroe* and Lee (1974) reported 13% and 9% wax ester in *Beroe cucumis* and *Pleurobrachia pileus* respectively from the cold temperate waters of Bute Inlet, Canada, it would seem that, as a general rule, ctenophores and medusae do not store large quantities of wax ester. The siphonophore *Diphyes antarctica* was notable in having 12.5% sterol ester.

Chaetognaths appear to be variable in lipid content. Those analysed here (probably *Eukrohnia hamata*) contained <0.05% lipid and a low lipid content (0.57%) was also found by Ikeda (1972) in *Sagitta elegans* from the Arctic. Elsewhere however, the same species contained 1.7–2.2% lipid in late summer (Percy and Fife, 1982) and *E. hamata* from the high Arctic in autumn contained about 1.7% lipid (Lee, 1974). Because of the large water content of chaetognaths (about 90%), these differences are even more pronounced when expressed on a dry weight basis (about 6% dry wt in lipid-poor, and 17–24% in lipid-rich individuals).

Although the absolute sizes of lipid reserves in chaetognaths are small, the available evidence suggests that they store wax ester rather than TAG. Lee (1975) found 12% wax ester in arctic *Eukrohnia hamata* and specimens from around South Georgia that were low in lipid contained about 6% wax ester (Table II) and only about 1% TAG; TAG was not detected in the Arctic specimens. These results suggest that chaetognaths do not make extensive use of lipid as a reserve material; this is confirmed by field and laboratory data on the composition of *Sagitta hispida*, which indicate that the major reserve material is probably protein and arrow-worms appear to survive periods of poor feeding by a decrease in body size and a general utilization of body material (Reeve and others, 1970) rather than a specific lipid store.

The lipid content and composition of the amphipods examined were quite variable, although they were broadly similar to those reported for arctic amphibods. Both wax ester and TAG are stored, with usually TAG > WE, as well as small but significant amounts of alkyldiacylglycerol (ADAG), usually 1–6% total lipid. Samples of the predatory hyperiid *Parathemisto gaudichaudii* taken in successive years were strikingly different in composition. In 1978 the lipid contained roughly 30% TAG, only a trace of ADAG and 16–20% wax ester; in 1980 there was 20–47% TAG, 1.8–5.9% ADAG and only 2–3% wax ester (Table II). These differences were repeatable from sample to sample for each year, and were not obviously related to total lipid content. The reason for this variation is unclear.

The euphausiids examined were also very variable in lipid content and composition, with a similar range in composition to that found in arctic species (see Falk-Petersen and others, 1981). Thus some species store only TAG (*Euphausia superba, Meganyctiphanes norvegica*), some both TAG and wax ester (*Thysanoessa inermis, T. raschii, Euphausia frigida, E. triacantha*) and some almost exclusively wax ester (*Thysanoessa* sp., *Euphausia crystallorophias*).

Are polar zooplankton rich in lipid?

The first well-documented suggestion that polar zooplankton might be richer in lipid than related organisms in warmer waters was that of Littlepage (1964), although

several previous authors had noted that many cold water organisms were particularly rich in lipid (Klem, 1932; Sheard, 1953; MacGinitie, 1955). Working at McMurdo Sound, Littlepage found that the total lipid contents of the copepod *Euchaeta antarctica* and the euphausiid *Euphausia crystallorophias* varied seasonally, but were generally high (*Euchaeta*: 28.1–46.1% dry wt; *E.crystallorophias*: 9.4–35.5% dry wt). These Antarctic species were richer in lipid than other euchaetids (Orr, 1934) and euphausiids (Fisher and others, 1952, 1954, 1955; Sheard, 1953) for which data were available. Since then several analyses have demonstrated a striking tendency for an increase in the total lipid content of copepods from the tropics to the poles (Lee and others 1971; Lee and Hirota, 1973; Clarke, 1983). In euphausiids the pattern is less clear, but many polar species are notably rich in lipid. Littlepage (1964) suggested no reason for this but some subsequent workers have proposed that cold water *per se* may result in a high lipid content (e.g. Steeves, 1969). The data in Table I, together with several surveys of the lipid content of Arctic zooplankton (Ikeda, 1972; Lee, 1975; Percy and Fife, 1981), and data for many benthic polar marine invertebrates (Clarke, 1983), indicate that this cannot be so for many of these species are quite low in lipid.

The generally accepted hypothesis is that the amount of storage lipid is related to the pattern of food availability experienced by the organism (Sargent, 1976). Species that can feed year round or throughout their life cycle do not require large lipid stores since they are unlikely to have to survive long periods without food. These are generally carnivores or omnivores. In contrast, species that must overcome long periods of starvation and must therefore make maximal use of food when it does become available, store large amounts of lipid. Often, and particularly so in copepods, this is wax ester. Primary productivity in polar regions is strikingly seasonal, being confined almost exclusively to the summer months, and so food for the herbivorous zooplankton is itself limited to the summer months. This seasonality of primary production is more severe than in temperate areas and, in consequence, lipid stores in the herbivorous zooplankton are larger than in warmer waters.

Comparison with freshwater zooplankton

The limited data available on the lipids of freshwater zooplankton suggest that, unlike marine species, copepods in lakes store TAG rather than wax ester (Sargent, 1976). Opportunity was therefore taken to examine the lipid content and composition of the three species of crustacean zooplankton found in Heywood Lake on Signy Island. The species examined were the small herbivorous copepod *Pseudoboeckella poppei*, the larger predatory copepod *Parabroteas sarsi* and the anostracan (fairy shrimp) *Branchinecta gaini*. The results are given in Table III.

Adults of both copepod species overwinter in the lakes, mainly close to the bottom, and probably feed very little (Weller, 1977). In the males of both species, lipid content increased as winter approached, suggesting that lipid is used as an overwintering reserve. This lipid, however was exclusively triacylglycerol. In only a few cases were traces detected of components with TLC mobilities typical of wax ester but the amounts were always too small for further characterization. Adult *Branchinecta* do not survive the winter and their lipid contents were very low (<1%, even in ovigerous females). The lipid contents of female copepods, both gravid and ovigerous, varied throughout the summer, with a suggestion of a peak in mid-summer (February/March).

There was surprisingly little correlation between amount of lipid stored and proportion of triacylglycerol in the total lipid (Table II), except at the very broadest level, comparing *Branchinecta* (lipid <1% fresh wt, TAG 1–23% lipid) with the two

Table III. Lipid content and composition of crustacean zooplankton from Heywood Lake, Signy Island. Total neutral lipids includes FFA, TAG and all other minor components.

			Lipid class composition (% total lipid)				
Species	*Date*	*Lipid % fresh wt*	*PL*	*FS*	*FFA*	*TAG*	*Total neutral lipids*
COPEPODA							
Pseudoboeckella poppei							
males	16 Feb 81	2.38	20.7	15.0	14.8	45.2	61.2
	17 Mar 80	7.41	29.3	15.7	18.5	31.7	50.2
	8 Apr 80	11.59	24.8	11.6	16.8	42.9	59.7
mature females	16 Feb 81	2.42	36.9	16.7	28.9	12.5	41.4
	17 Mar 80	9.27	38.4	13.8	21.7	21.8	43.5
	8 Apr 80	3.61	35.5	14.5	14.8	31.5	46.3
ovigerous females	16 Feb 81	5.84	21.5	13.2	9.5	52.0	63.1
	17 Mar 80	25.34	41.4	14.4	17.7	22.8	40.5
	8 Apr 80	5.53	30.9	12.7	14.8	37.2	52.0
Parabroteas sarsi							
males	16 Feb 81	4.16	25.6	12.0	8.4	46.9	60.7
	8 Apr 80	13.97	25.4	12.4	9.5	50.0	59.5
ovigerous females	16 Feb 81	15.60	25.2	9.9	7.3	54.2	63.2
	8 Apr 80	4.57	24.7	12.4	6.5	53.7	60.2
ANOSTRACA							
Branchinecta gaini							
males	20 Feb 81	0.34	42.3	31.9	17.2	3.4	24.3
	8 Apr 80	0.34	45.3	38.5	13.7	1.3	15.9
ovigerous females	20 Feb 81	0.63	38.2	26.8	14.4	16.1	33.4
	8 Apr 80	0.57	33.8	28.9	12.4	23.5	35.9

copepods (lipid 2–25% fresh wt, TAG 13–54% lipid). This would suggest that both TAG and phospholipids are being stored in males and females. The picture may be further complicated by changes in the size of the copepods in response to environmental conditions.

Although the data in Table III are sparse, they do make ecological sense in terms of food supply. In mesotrophic lakes such as Heywood Lake, the summer growth of phytoplankton provides a rich source of food for zooplankton herbivores (mainly *Pseudoboeckella poppei* and the larval stages of *Branchinecta gaini*), which in turn are consumed by the predatory *Parabroteas sarsi*. When surface ice forms in autumn, the water column stabilizes and most of the phytoplankton cells settle out to the bottom, where they are decomposed by bacteria (Ellis-Evans, 1982). During this winter period the water column can become anoxic and there are virtually no phytoplankton in the water column. Total algal volume and chlorophyll-*a* are particularly low in between May and September and adult and juvenile copepods (both are present in Heywood Lake over winter), therefore, have very little phytoplankton food available (Light and others, 1981). Although a few copepods may be found in the water column during winter, most congregate close to the bottom, where they may feed on detritus (Heywood, 1979; Weller, 1977). Both *Pseudoboeckella poppei* and *Parabroteas sarsi* appear to utilize a lipid store to survive this winter period, whereas *Branchinecta*, which overwinters as an egg, has no need of such a store.

The fluctuation in female copepod lipid during the summer may reflect the variation in fecundity with the availability of phytoplankton food; total algal cell volume in the water column is frequently greatest about February/March (Light and others, 1981) and this corresponds well with the period of peak female lipid content (Table III).

The patterns of lipid storage in male and female copepods are thus very different, as is often the case with marine copepods. Males appear to exploit the summer food by steadily synthesizing a large store of lipid to supply energy during winter starvation, whereas female copepods rapidly utilize the phytoplankton for egg production. These strategies are slightly different from those of marine copepods, and this may explain their differing biochemistries.

Lipid, food and reproduction

It is generally believed that the cycles of lipid storage and utilization during the life history of an organism are dictated by the pattern of food availability experienced by that organism and the energetic demands of reproduction (Sargent 1976; Clarke, 1983). As with many such broad ecological hypotheses, however, a critical test of this relationship is not possible.

Carnivores are likely to be able to feed year round and hence have no need of a large lipid store. Thus analyses of ctenophores, medusae, annelids and chaetognaths usually reveal relatively low lipid contents (even when allowance is made for high water and ash contents). Storage lipids are usually a relatively small fraction of the total and, although wax esters may be present, they never predominate. Euchaetid copepods are an exception to this rule.

The opposite end of the spectrum is occupied by marine copepods. For herbivorous species, food is believed to be available only in the short summer months. In many of these species, however, the gonad matures over winter, allowing larvae to hatch the following spring when food is once more available. This vitellogenesis is fuelled by the wax ester store synthesized the previous summer as a stage V copepodid. Gatten and others (1980) have shown that, in the temperate species *Calanus helgolandicus*, the amount of wax ester stored by the stage V copepodid, and hence the subsequent fecundity, is dictated by the abundance of particulate matter in the water during the summer. Not all of this wax ester is converted directly to yolk, suggesting that there is a high metabolic cost to egg production.

Euchaetid copepods appear to be an exception to this picture in that, although they are carniverous, many species (e.g. *Euchaeta japonica, E. norvegica, E. antarctica*) synthesize wax ester as late as copepodids and use this to produce eggs. Perhaps food is scarce in winter for these small organisms too, despite their being carnivorous.

The proposed relationship between lipid storage and biology makes ecological sense but it does not explain why marine copepods synthesize a store of wax ester rather than triacylglycerol. The food contains little or no wax and, in many cases, the production of eggs involves the resynthesis of triacylglycerol.

Freshwater copepods also are subject to a seasonal variation in food availability but they store TAG rather than wax (Table III). There are no observations of oil droplets in Antarctic freshwater copepods, although these have been noted in some stages of copepods in high alpine lakes (E. Gnaiger, pers. comm.). A possible reason for the difference in lipid biochemistry between marine and freshwater copepods lies in the pattern of reproduction. In lakes on Signy Island, South Orkneys, both copepod species may breed year round, although there is a decrease in reproductive

activity in winter. Where food is scarce reproduction is largely confined to summer but, in contrast to marine copepods, there is no winter production of eggs. Rather, egg production proceeds whenever there is food and several batches of eggs may be produced in summer when food is abundant (R. B. Heywood, pers. comm.). Thus in freshwater copepods the reproductive output responds to immediate conditions, whereas, in the sea, female copepod fecundity is related to feeding conditions during the copepodid V stage during the previous summer (Gatten and others, 1980).

If wax ester is the preferred storage lipid for longer term depots, but TAG used in normal short-term stores (Sargent, 1976), then this would explain the difference between the lipid compositions of marine and freshwater copepods. It is also possible, however, that there are subtle differences between the marine and freshwater environments of which we are as yet unaware.

Interpretation of the lipid biochemistry of Antarctic euphausiids is made difficult by our relatively thin knowledge of their general feeding biology. As with copepods, it is likely that the type of lipid stored will be related to the food and feeding ecology of the particular organism. Only when we have more data on both the seasonal changes in lipid composition, and the biology of the organisms concerned (such a[illegible] are now available for arctic euphausiids: Falk-Petersen, 1981; Sargent and Falk-Petersen, 1981; Falk-Petersen and others, 1981, 1982) will we be in a position to try to relate these two together.

We are in an even poorer position with amphipods. The predatory hyperiid *Parathemisto gaudichaudii*, for example, stores wax ester and TAG, as well as small amounts of ADAG. Also, the composition is variable from sample to sample (Tables I and II). It is possible that this reflects recent feeding history or possibly sexual maturation but interpretation of this variability will require further sampling and a much fuller understanding of the biology of the organism in question.

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