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Se-Jong Ju · K. Scolardi · K. L. Daly
H. Rodger Harvey

Understanding the trophic role of the Antarctic ctenophore, *Callianira antarctica*, using lipid biomarkers

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Abstract To better understand the trophic role of ctenophores in Antarctica during austral fall and winter, a major species of cydippid ctenophore, *Callianira antarctica*, was collected during April/May (fall) and August/September (winter) 2002 in the vicinity of Marguerite Bay. Lipid content, lipid classes, fatty acids, fatty alcohols and sterols were analyzed in animals, together with lipid biomarkers in krill and copepod species representing potential ctenophore prey. Lipid content in ctenophores collected in winter was slightly higher than from animals in fall (4.8 and 3.5% of dry weight, respectively). Polar lipids were the dominant lipid class in ctenophores, accounting for over half of the lipid content, with significant amounts of free fatty alcohols (more than 10% of total lipid content) detected. Lipid-class composition, however, differed significantly between seasons, with significant amounts of neutral lipid (wax esters and triacylglycerols) only detected in animals from fall. Although the dominant lipid classes in ctenophores varied between fall and winter, individual lipids (i.e., fatty acids, alcohols and sterols) showed only minor changes between seasons. Specifically, long-chain polyunsaturated fatty acids [20:5(*n*-3) and 22:6(*n*-3)] found in high abundance in larval krill were also elevated in ctenophores collected in winter. Very high amounts of monounsaturated fatty alcohols, particularly 20:1(*n*-9) and 22:1(*n*-11), known to be important components of wax esters in calanoid copepods, were also observed. Multivariate analysis using the suite of lipids found indicated that copepods are an important diet item for ctenophores in the study area. Results further suggest that *C. antarctica* feed actively year-round, with larval krill providing a food resource during austral winter.

S.-J. Ju · H. R. Harvey (✉)
Chesapeake Biological Laboratory,
University of Maryland Center for Environmental Science,
P.O. Box 38, Solomons, MD 20688, USA
E-mail: harvey@cbl.umces.edu
Tel.: +1-410-3267206
Fax: +1-410-3267341

K. Scolardi · K. L. Daly
College of Marine Science, University of South Florida,
140 Seventh Avenue, South, St. Petersburg, FL
33701, USA

Introduction

It is now recognized that ctenophores are quantitatively important predators of other zooplankton and fish eggs in pelagic food chains (Larson 1987; Mills 1995; Shiganova and Bulgakova 2002). For example, the cydippid *Mertensia ovum* accounts for the dominant biomass of macrozooplankton in the Canadian Arctic (Swanberg and Båmstedt 1991; Siferd and Conover 1992), and is an important predator on crustacean zooplankton. Elsewhere, field and laboratory studies have shown that the widely distributed cydippid ctenophore, *Pleurobrachia pileus*, has the potential to seriously impact zooplankton populations where it exists (Reeve et al. 1978; Frank 1986; Båmstedt 1998). Yet, our knowledge of Antarctic ctenophores and their role in Southern Ocean ecosystems remains sparse, largely due to the difficulties in sampling and preservation of fragile animals and in accessing Antarctic waters, especially in winter. These limitations have led to conflicting physiological and ecological hypotheses on survival and overwintering strategies of ctenophores. Ctenophore densities in coastal regions of Antarctic seas show substantial variation between seasons, possibly increasing during austral fall and winter (Lancraft et al. 1989, 1991). At times they appear to dominate total zooplankton biomass regionally (Pakhomov 1989; Pagès et al. 1996), and *Callianira* spp. have been observed to make up 30–35% of the zooplankton biomass on a dry-weight basis during early winter and spring 2000 in one embayment (Kaufmann et al. 2003). Among their prey, ctenophores have been observed to feed on larval krill, *Euphausia*

superba, under sea ice during fall and winter in the Scotia-Weddell seas, suggesting that they may be an important predator on larval krill (Hamner et al. 1989; Daly and Macaulay 1991) . Hamner and Hamner (2000) provided further detailed observations of ctenophore predatory behavior on larval krill.

As krill are a key species in Antarctic waters, the impact of ctenophore predation on krill populations could represent an important control over ecosystem function in this system. Recent evidence from gut-content analysis (Scolardi et al. 2004) suggests that ctenophores ingest a range of prey, including copepods, krill, and amphipods, with larval krill accounting for an important portion of the total diet in winter. Dietary information based on gut-content analysis alone, however, is difficult to interpret because of differences in digestion rates among prey, feeding patterns, and limitation in visual identification of digested prey.

We have applied detailed lipid analysis to the question of diet history in ctenophores, as a means to better understand their feeding ecology. Lipids are essential biochemical constituents of all organisms, and lipid composition can often be related to taxonomy and physiology. Lipid markers have been used as indices of feeding and metabolism for many gelatinous zooplanktons, including Ctenophora (Phleger et al. 1998; Nelson et al. 2000; Fukuda and Naganuma 2001; Falk-Petersen et al. 2002). In several cases, specific lipids (e.g., long-chain unsaturated fatty acids, dinosterol) have been applied to understand trophic relationships in Southern Ocean communities (Bottino 1974; Phleger et al. 1998; Cripps and Atkinson 2000; Graeve et al. 2001; Stübing et al. 2003) because such molecules are both taxon-specific and only obtained from dietary sources. In addition to detailed comparisons of lipid composition, multivariate statistics as principal components analysis (PCA) of individual lipids recently has shown promise as a tool for understanding trophic relationships in polar regions (Falk-Petersen et al. 2002; Ju and Harvey 2004). Here we used PCA of fatty acid and alcohol distribution to examine linkages between ctenophores and their potential prey collected from waters in the western Antarctic Peninsula (WAP) region.

Materials and methods

Sampling area and collection

This study is one component of the US Southern Ocean GLOBEC field programs, which focused on Marguerite Bay and other environments along the WAP. Collections were made in late fall (7 April 2002–21 May 2002) and late winter (31 July 2002–18 September 2002). Methods used to collect ctenophores (*Callianira antarctica*) and potential diets— krill (*E. superba* and *E. crystallorophias*), copepods (*Paraeuchaeta antarctica*, *Metridia gerlachei*, *Calanoides acutus*, and *Calanus propinquus*), and mysids (*Anarctomysis ohlini*) included: a 1.5-m^2 Tucker trawl having a 0.25-in mesh graded down to a 707-μm mesh with a protected cod end, which was typically towed obliquely within the upper 200 m of the water column, and 1-m^2 and 10-m^2 multiple-opening/closing net and environmental sensing system (MOCNESS) equipped with 335-μm and 3-mm mesh nets, respectively, which were towed at discrete depth intervals through the water column. Nets were towed at a speed of 1.5–3 knots behind the ship, ice permitting. Significant ice cover was often a hindrance during winter 2002, but ctenophores and their potential prey were collected using a 1-m-diameter Reeve Net (333-μm-mesh net) with a 20-l protected cod end kept afloat with syntactic foam, and a 1-m-diameter Ring Net (333-μm mesh). The Reeve Net and Ring Net were deployed in tandem to about 10 and 15 m depth, respectively, while the propellers were run at 15–25% to keep water circulating into the nets, but with little forward ship movement or ice sweep-down into nets. This method retrieved animals in exceptionally good condition. Ctenophores collected by net tows were immediately separated from the catch once on board, and gently placed in a bucket of 0.1- or 0.2-μm filtered seawater at or near sea-surface temperature (−1.8 to 0°C). For lipid analysis, guts of ctenophores were removed to reduce bias, and samples immediately frozen and stored at −80°C until analysis at shore-based facilities.

Lipid extraction and analysis

Before lipid analysis, wet masses of all samples (ctenophore, krill, copepod, and mysid) were measured by thawing and briefly rinsing with Nano-pure water. A subset of ctenophore and prey samples were dried at 60°C for 48 h for measurement of water content, and were used to convert wet mass of animals to dry mass. The mean estimated water content of *Callianira antarctica* was 95.1% of the body wet mass, which is similar to reported values for other studies on Antarctic ctenophores (Clarke et al. 1992; Scolardi et al. 2004). Total lipids were extracted from freshly thawed animals three times with a mixture of CH_2CL_2:MeOH (1:1) in solvent-washed 25-ml screw-cap glass/Teflon-lined cap test tubes with probe sonication as previously described (Harvey et al. 1987). The three extracts were pooled, the solvent removed by rotary evaporation, and total lipid redissolved in CH_2CL_2:MeOH (2:1). Subsamples of lipid extracts from animals were used for lipid class analysis, with the remaining fraction used for measurement of individual lipid components.

Major lipid class composition was determined by thin-layer chromatography with flame ionization detection (TLC-FID) using an Iatroscan MK-V Analyzer (e.g., Volkman et al. 1986; Ju et al. 1997). Aliquots (1–2 μl) of total extracts were spotted onto replicate S-III Chromarods and developed in hexane: diethyl ether: formic acid (85:15:0.2) for separation of major lipid

classes. This solvent system allowed individual neutral lipid classes to be separated in a single development; phospholipids remained at the origin and were not identified individually. Lipid classes were identified and calibrated using a mixture of commercial standards (phosphatidyl choline for phospholipids, cholesterol for sterols, 1-octacosanol for free fatty alcohols, nonadecanoic acid for free fatty acids, triolein for triacylglycerol, and stearyl ester for wax esters; Sigma). Peak areas were integrated (HP ChemStation) and quantified using the standard mix run in parallel. Total lipid content was determined by summation of all lipid classes quantified by TLC-FID. Overall precision for total lipid and major classes was $\pm 10\%$ or better.

Quantification of individual components in neutral (alcohols and sterols) and polar (fatty acids) lipid fractions were essentially as previously described (e.g., Harvey 1994) with minor modifications. Internal standards (5α-cholestane for neutral and nonadecanoic acid for polar) were added to the remaining fraction (or subsamples) of the total lipid extract. Remaining solvent was dried under N_2 gas and the sample subjected to alkaline hydrolysis using 0.5 N methanolic KOH with gentle heating. After cooling and addition of water, neutral lipid fractions were partitioned three times with a mixture of hexane:diethyl ether (9:1). The neutral fraction was dried under N_2 gas and treated with 30 µl bis(trimethylsilyl) trifluoroacetamide (BSTFA) with 25% pyridine to convert free alcohols to their corresponding trimethylsilyl (TMS) esters. Polar lipid fractions containing fatty acids were partitioned similarly following acidification to pH 2, dried under N_2 gas, and converted to fatty acid methyl esters (FAMES) using BF_3–MeOH. FAMES were isolated from the final mixture by partitioning into hexane:diethyl ether (9:1). A subsample of FAMES was treated with dimethyl disulfide (DMDS) to determine double bond position of monounsaturated fatty acids (Nichols et al. 1986). Procedural blanks were processed in parallel with samples with similar internal standards. Polar and neutral lipids were quantified by capillary gas chromatography (HP-5890-II GC) equipped with a flame ionization detector. Separations were performed with DB-5MS fused silica column (60 m length×0.32 mm i.d.×0.25 µm film thickness) and hydrogen as carrier gas (e.g., Harvey and McManus 1991). Samples were injected in splitless mode at an initial oven temperature of 50°C and an injector temperature 225°C. The oven temperature was then ramped at 15°C min^{-1} to 120°C and thereafter 4°C min^{-1} to 300°C and held at 300°C for 10 and 20 min for polar and neutral lipids, respectively. All data were processed using a dedicated data system (HP ChemStation—Agilent Tech.) with quantification based on peak area response compared to the internal standards. Structural identification was made utilizing gas chromatography-mass spectrometry (GC-MS; Agilent 6870 GC with Agilent 5973 MSD) operating at 70 eV with mass range acquisition of 50–700 amu. The column and temperature programs for the GC-MS are similar to that described above, with helium used as a carrier gas and injector temperature of 250°C.

Multivariate analysis

Wax esters (WE) are a major storage lipid class in Antarctic zooplankton, comprising an equal number of fatty acids and alcohols (Albers et al. 1996; Ju and Harvey 2004). If ctenophores ingest copepods containing WE, those WE are typically hydrolyzed to free fatty acids and alcohols, which are then assimilated into several cellular compartments. PCA was performed using the summed relative abundance of the entire suite of fatty acid and alcohols present in ctenophores and potential prey using MINITAB statistic software package (Minitab). Fatty acids and alcohols of equivalent carbon length and unsaturation were combined to account for potential metabolic exchange. As a multivariate chemometric technique, PCA allows objective comparisons of large data sets to identify those variables that account for most of the variance. For this analysis, we included results from additional potential ctenophore prey collected in the same study area during winter 2001 (Ju and Harvey 2004) to reduce biased results due to limited prey items obtained in winter. Component scores were calculated from the first two principal components of each sample for evaluation.

Results and discussion

Lipid content and lipid class in ctenophore

Lipid content in *Callianira antarctica* was 3.5 and $4.8 \pm 0.6\%$ of dry mass from fall and winter, respectively (Fig. 1). The lipid concentrations observed in *Callianira antarctica* are within the range (2–7% of dry mass) reported for other Antarctic ctenophores (Nelson et al. 2000). The lipid content of *Callianira antarctica* is higher than those of mid-latitudinal forms such as *Aurelia aurita* and *Chrysaora quinquecirrha* (< 1% of dry mass; Joseph 1979; Kariotoglou and Mastronicolis 2001), but appear to have less lipid than Arctic gelatinous zooplankton (mean 8% of dry mass; Larson and Harbison 1989). Phospholipids (PL) were the dominant lipid class, accounting for more than 50% of the total lipid content in *Callianira antarctica*. The lipid-class composition of *Callianira antarctica* is similar to other Antarctic gelatinous zooplankton species (Nelson et al. 2000), with WE also appearing in Arctic ctenophores (Falk-Petersen et al. 2002). Lipid-class composition differed significantly between seasons, with significant amounts of WE and triacylglycerols (TAG) detected in animals from fall. The presence of these two neutral lipid classes may reflect active feeding on lipid-rich copepods, krill, or both. The absence of these neutral lipids in ctenophores collected during winter may be a consequence of

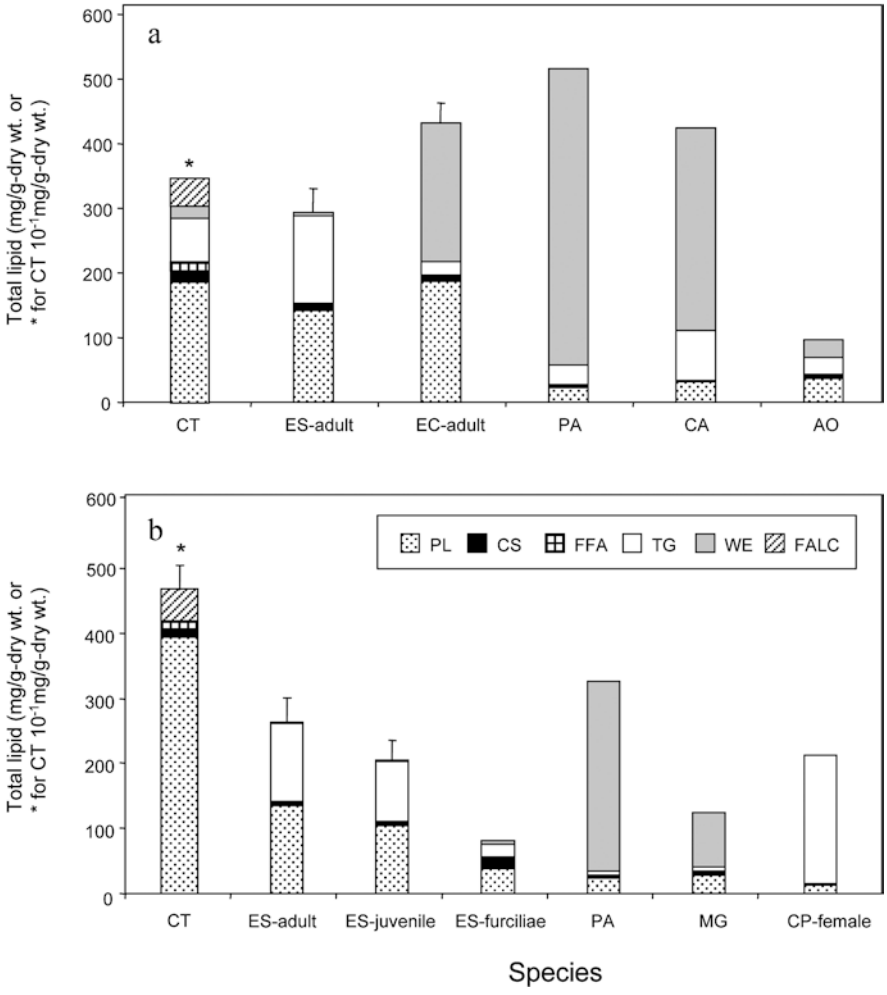

Fig. 1a,b Lipid content (% of dry mass or mg g^{-1} dry mass) and lipid-class compositions (*PL* polar lipids, *ST* sterols, *FFA* free fatty acids, *TAG* triacylglycerols, *WE* wax esters, *FALC* free fatty alcohols) of ctenophores and their potential prey sampled in fall and winter (***CT*** *Callianira antarctica*, ***ES*** *Euphausia superba*, ***EC*** *Euphausia crystallorophias*, ***PA*** *Paraeuchaeta antarctica*, ***CA*** *Calanoides acutus*, ***AO*** *Antarctomysis ohlin*, ***MG*** *Metridia gerachei,* ***CP*** *Calanus propinquus*). Data without *error bars* represent the composite samples.

decreased feeding and/or their mobilization and utilization for overwintering. Surprisingly high amounts (>10% of total lipids) of free fatty alcohols (FALC) were also detected (Fig. 1), which would support the suggestion for hydrolysis of dietary wax esters for metabolic needs.

Lipid contents and class compositions in potential ctenophore diets are summarized in Fig. 1. All potential prey contained relatively high lipid levels (≥10% of dry mass) with the exception of mysid and *E. superba* furciliae. While TAG were dominant storage lipids (>45% of total lipid) in *E. superba* and female *Calanus propinquus*, WE were dominant (>45% of total lipids) in *E. crystallorophias*, *Paraeuchaeta antarctica*, *Calanoides acutus*, and *Metridia gerlachei*. In the mysid *A. ohlili*, WE and TAG were both observed in equal amounts (27 and 26% of total lipids, respectively).

Comparisons of these lipid-class results with other published work require a caveat. It has been suggested that detector response for TLC-FID used in lipid-class determination is affected by the degree of lipid unsaturation (Volkman and Nichols 1991; Ohman 1997; Miller et al. 1998). As a consequence, the lipid content and class distribution of marine organisms with highly unsaturated lipid components (i.e., polyunsaturated fatty acids) could be significantly underestimated when commercial lipid standards composed of more saturated lipids are used for calibration. In contrast, other studies have not found significant differences of TLC-FID responses between highly unsaturated TAG versus saturated TAG (Fraser and Taggart 1988). Here we elected to use commercial standards routinely used for lipid-class calibration by ourselves and others, including previous work on polar samples (Hagen 1989; Hagen et al. 1993; Albers et al. 1996; Kattner and Hagen 1998) . Those previous reports find comparable lipid values for the same species seen here using TLC-FID, with the calibration based on the commercial lipid standards. Although the absolute lipid amount presented here may provide a conservative measure of lipid content, it does not significantly affect the outcome of this study. It does, however, highlight the need

for careful comparison among methods used for lipid-class analysis.

Fatty acids and alcohols in ctenophores and their potential diets

Ctenophores contained a wide range of saturated (SFA), monounsaturated (MUFA), polyunsaturated (PUFA), and branched fatty acids ranging from C_{12} to C_{24} (Table 1). Total fatty-acid concentrations were substantially higher in winter collections (19.3 and 34.3 mg g^{-1} dry mass from fall and winter, respectively). The 16:0, 16:1(*n*-7), 18:1(*n*-9), 20:1(*n*-9), 20:5(*n*-3), and 22:6(*n*-3) acids were the major acids observed, with only minor differences between two sampling seasons. These fatty-acid profiles are also very similar to those in other Antarctic Ctenophora species with high PUFA content (about 40% of total fatty acids) (Nelson et al. 2000). Small quantities of fatty alcohols were also found, mainly composed of the 20:1(*n*-9) and 22:1(*n*-11). These long-chain MUFA and alcohols are present in large amounts in calanoid copepods (Table 2). The presence of long-chain MUFA and alcohols supports the evidence for ctenophore carnivory on copepods, as seen from gut-content analyses.

The fatty acid and alcohol distributions among potential ctenophore prey (e.g., krill, copepods, and mysids) are shown in Table 2. In adult krill, 16:0, 18:1(*n*-9), and 20:5(*n*-3) fatty acids accounted for over 55% of total fatty acids with minor seasonal changes. Significant abundance of 22:6(*n*-3) was only observed in larval krill from winter. Alcohols were minor or absent in *E. superba*, but adult *E. crystallorophias* contained significant amounts of fatty alcohols with the dominance of saturated moieties (i.e., 14:0 and 16:0) (> 70% of total fatty alcohols). Although only a limited number of krill samples were available for lipid analysis in this study, results for krill agree well with those from other previous works (Clark 1984; Kattner and Hagen 1998; Falk-Petersen et al. 1999; Hagen et al. 2001).

All copepod species (*Paraeuchaeta antarctica*, *Calanoides acutus*, *Metridia gerlachei*, and *Calanus propinquus*) contained fatty acids ranging from C_{12} to C_{22}, with a dominance of MUFA (> 40% of total fatty acids) and minor differences between species and sampling seasons. Among MUFA, the major acids included the 16:1(*n*-7), 18:1(*n*-9), and 20:1(*n*-9) with the 22:1 acid (equal abundance of the (*n*-11) and (*n*-9) isomers) dominant (> 46% of total fatty acids) in female *Calanus propinquus*. These fatty acid and alcohol distributions in Antarctic copepods support previous reports (Hagen et al. 1993; Kattner et al. 1994; Kattner and Hagen 1995; Albers et al. 1996; Falk-Petersen et al. 1999), which also provide detailed information on lipid dynamics and biosynthesis in Antarctic copepods. In the mysid *Antarctomysis ohlini*, 16:0, 18:1(*n*-9), 20:5(*n*-3), and 22:6(*n*-3) were dominant fatty acids (60% of total fatty acids). Significant amounts of fatty alcohols were also present in all potential prey with the exception of female *Calanus*

Table 1 Fatty acid and alcohol composition in abundance in ctenophores sampled in fall and winter 2002 [– not detected; *Tr* trace amount (< 0.1% of total concentration)]

	Fall[a] ($n = 5$)		Winter ($n = 2$)	
	Acid	Alcohol	Acid	Alcohol
n-Saturates				
14:0	6.6	2.8	5.6 ± 0.8	–
16:0	15.5	2.2	16.3 ± 1.0	–
18:0	1.5	0.1	1.4 ± 0.1	–
Other[c]	0.1	Tr	1.4 ± 0.7	0.3 ± 0.1
Monounsaturates				
16:1(*n*-7)	7.6	0.4	6.4 ± 0.6	–
16:1(*n*-5)	0.2	–	0.2 ± 0.0	–
18:1(*n*-9)	14.4	0.9	10.2 ± 0.9	–
18:1(*n*-7)	5.1	–	5.9 ± 1.2	–
18:1(*n*-5)	0.4	–	0.5 ± 0.1	–
20:1[b]	11.6	24.7	3.5 ± 0.6	38.6 ± 0.2
22:1[b]	1.2	68.1	0.7 ± 0.1	59.1 ± 0.6
Other[d]	0.2	–	0.2	0.5 ± 0.1
Polyunsaturates				
16:2(*n*-6)	0.6	–	0.9 ± 0.0	–
16:4(*n*-1)	0.4	–	Tr	–
18:3(*n*-3)	0.1	–	0.2 ± 0.1	–
18:4(*n*-3)	1.0	–	1.8 ± 0.8	–
18:2[b]	1.1	–	2.4 ± 0.4	–
20:4(*n*-3)	0.3	–	0.6 ± 0.2	–
20:4(*n*-6)	0.5	–	0.7 ± 0.1	–
20:5(*n*-3)	21.4	–	26.0 ± 1.3	–
22:6(*n*-3)	9.3	–	12.1 ± 0.9	–
Other[e]	0.5	–	1.2 ± 0.4	
Branched and odd chain	0.5	Tr	1.6 ± 0.3	1.5 ± 0.5
Total concentration (mg g^{-1} dry mass)	19.3	3.8	34.3 ± 2.5	6.9 ± 0.5

[a]Composite samples were used for analysis.
[b]Indicate all isomers combined. Others indicate the sum of minor amounts (≤ 0.5% of total concentration) of fatty acids and alcohols [[c]includes 12:0, 20:0, and 22:0; [d]is 14:1(*n*-5), 16:1(*n*-9), 16:1(*n*-3), and 24:1(*n*-9); [e]is 16:3(*n*-4), 20:2(*n*-6), 22:4(*n*-3), and 22:5(*n*-6)].

Table 2 Fatty acid (*Acid*) and alcohol (*ALC*) compositions and distribution present in potential prey of ctenophores (***ES*** *Euphausia superba*, ***EC*** *Euphausia crystallorophias* , ***PA*** *Paraeuchaeta antarctica* , ***CA*** *Calanoides acutus*, ***AO*** *Anarctomysis ohlini*, ***MG*** *Metridia gerlachei*, ***CP*** *Calanus propinquus*). None or only trace amounts (< 0.mg g^{-1} dry wt.) of fatty alcohols [20:1 (all isomers combined)] were found in *ES*-adult, *ES*-juvenile, and *CP* (– not detected; *Tr* trace amount; < 0.1% of total concentration)

Species	ES-adult ($n=4$)		EC-adult ($n=3$)		PA[a] ($n=20$)		CA[a] ($n=50$)		AO[a] ($n=2$)	
	Acid	ALC	Acid	ALC	Acid	ALC	Acid	ALC	Acid	ALC
Fall 2002										
n-Saturates										
14:0	11.6 ± 0.7	11.0 ± 9.7	1.7 ± 0.3	66.5 ± 1.8	1.1	39.0	4.5	14.8	5.1	18.5
16:0	24.4 ± 1.1	5.9 ± 8.1	17.9 ± 0.7	5.9 ± 8.1	2.9	25.1	10.1	20.0	17.0	24.3
18:0	1.4 ± 0.2	–	1.1 ± 0.1	–	0.1	0.7	0.6	0.9	1.1	0.9
Others[c]	Tr	–	1.3 ± 0.1	–	Tr	0.2	0.2	–	1.4	0.8
Monounsaturates										
16:1(*n*-7)	7.2 ± 0.7	–	6.0 ± 0.7	1.7 ± 0.2	27.0	4.9	9.3	3.7	9.1	3.1
16:1(*n*-5)	0.2 ± 0.0	–	0.1 ± 0.0	–	0.2	–	0.3	–	0.2	–
18:1(*n*-9)	13.2 ± 1.4	76.5 ± 20.5	38.6 ± 2.0	Tr	27.0	7.3	6.2	5.3	16.9	10.5
18:1(*n*-7)	7.6 ± 0.4	–	13.4 ± 1.5	–	2.5	Tr	4.6	Tr	6.4	Tr
18:1(*n*-5)	0.1 ± 0.0	–	0.1 ± 0.0	–	0.7	–	1.1	–	0.7	–
20:1[a]	1.5 ± 0.1	–	–	–	8.4	12.9	10.3	44.3	6.7	24.3
22:1[a]	0.8 ± 0.1	2.5 ± 4.9	–	–	1.2	6.1	9.2	9.7	–	13.7
Others[d]	0.3 ± 0.1	–	0.2 ± 0.0	–	0.4	1.0	0.1	0.1	0.2	2.4
Polyunsaturates										
16:2(*n*-6)	0.9 ± 0.1	–	1.0 ± 0.1	–	0.5	–	0.9	–	0.6	–
16:4(*n*-1)	0.7 ± 0.0	–	0.1 ± 0.0	–	1.7	–	4.5	–	0.3	–
18:4(*n*-3)	1.2 ± 0.3	–	0.9 ± 0.1	–	1.9	–	2.7	–	0.6	–
18:2[a]	0.7 ± 0.0	–	1.6 ± 0.2	–	1.0	–	1.3	–	0.9	–
20:4(*n*-3)	0.2 ± 0.1	–	0.1 ± 0.0	–	0.2	–	0.7	–	1.3	–
20:5(*n*-3)	21.3 ± 1.2	–	13.2 ± 1.2	–	13.6	–	20.0	–	15.1	–
22:6(*n*-3)	3.9 ± 0.5	–	0.9 ± 0.2	–	6.2	–	7.3	–	11.4	–
Others[b]	0.3 ± 0.1	–	0.2 ± 0.0	–	2.4	–	2.8	–	1.3	–
Branched and odd chain	2.4 ± 0.1	–	1.7 ± 1.1	1.5 ± 0.3	1.9	3.0	2.6	1.0	1.7	1.5
Total concentration (mg g^{-1} dry mass)	236.2 ± 32.8	0.2 ± 0.1	217.7 ± 12.5	79.5 ± 8.6	222.9	118.4	190.7	148.0	56.9	8.0

Species	ES-adult ($n=6$)	ES-juvenile ($n=4$)	ES-furciliae[a] ($n=4$)		PA[a] ($n=10$)		MG[a] ($n=20$)		CP-female[a] ($n=10$)
	Acid	Acid	Acid	ALC	Acid	ALC	Acid	ALC	Acid
Winter 2002									
n-Saturates									
14:0	13.4 ± 1.9	11.6 ± 1.8	3.2	37.6	1.4	32.3	0.5	37.5	2.6
16:0	24.5 ± 1.9	25.1 ± 1.4	19.3	35.4	2.8	33.2	5.6	34.1	13.1
18:0	1.3 ± 0.2	1.7 ± 0.3	1.0	2.5	0.3	1.6	0.4	2.8	1.0
Other[c]	Tr	1.9 ± 1.3	3.3	0.3	2.2	1.4	0.9	0.1	1.6
Monounsaturates									
16:1(*n*-7)	9.5 ± 1.2	9.4 ± 1.2	4.3	0.7	26.4	3.1	9.4	3.7	4.5
16:1(*n*-5)	0.3 ± 0.2	0.3 ± 0.1	0.1	0.5	0.2	1.0	0.1	0.9	0.2
18:1(*n*-9)	13.2 ± 0.8	12.1 ± 0.7	10.5	1.4	33.9	6.4	25.4	8.9	1.6
18:1(*n*-7)	7.7 ± 1.2	6.8 ± 0.6	8.5	–	2.7	1.9	3.1	1.2	1.4
18:1(*n*-5)	0.1 ± 0.1	0.2 ± 0.0	0.3	–	0.7	–	0.4	0.2	2.0
20:1[a]	1.3 ± 0.5	0.9 ± 0.0	1.2	3.8	3.3	5.7	12.0	0.8	4.6
22:1[a]	0.6 ± 0.4	–	–	11.8	0.2	4.2	–	0.3	45.6
Other[d]	0.3 ± 0.1	0.2 ± 0.1	0.2	0.4	0.1	3.0	0.1	2.8	2.4
Polyunsaturates									
16:2(*n*-6)	1.0 ± 0.2	1.4 ± 0.1	0.8	–	0.6	–	0.8	–	0.5
16:4(*n*-1)	0.7 ± 0.1	1.3 ± 0.3	0.5	–	0.4	–	0.7	–	Tr
18:4(*n*-3)	1.7 ± 0.4	2.7 ± 0.6	1.6	–	3.0	–	2.7	–	0.4
18:2[a]	1.8 ± 0.7	1.7 ± 0.6	1.9	0.7	2.0	0.4	3.2	0.4	0.7
20:4(*n*-3)	0.3 ± 0.2	Tr	0.2	–	0.3	–	0.6	–	0.9
20:5(*n*-3)	13.6 ± 1.1	14.5 ± 2.3	24.4	–	9.4	–	18.4	–	5.7
22:6(*n*-3)	4.0 ± 1.2	2.6 ± 0.6	12.6	–	7.6	–	12.6	–	0.6
Other[e]	1.0 ± 0.4	0.8 ± 0.3	1.5	–	1.3	0.2	2.0	–	5.3
Branched and odd chain	3.8 ± 0.8	8.0 ± 0.1	4.7	5.1	1.3	5.8	1.1	6.4	2.3
Total concentration (mg g^{-1} dry wt.)	223.4 ± 61.0	210.0 ± 17.0	59.5	2.5	188.4	93.7	108.1	55.6	194.5

[a]Indicate all isomers combined; [b]Composite samples were used for analysis. Others indicate the sum of minor amounts (≤ 0.5% of total concentration) of fatty acids and alcohols [[c]includes 12:0, 20:0, and 22:0; [d]is 14:1(*n*-5), 16:1(*n*-9), 16:1(*n*-3), and 24:1(*n*-9); [e]is 16:3(*n*-4), 20:2(*n*-6), 22:4(*n*-3), and 22:5(*n*-6)].

propinquus. Alcohol distributions were similar among other copepods and the mysid, dominated by 14:0, 16:0, and the 20:1 [mainly the (*n*-9) isomer], which accounted for >70% of total fatty alcohols. The relative abundance of long-chain monounsaturated fatty alcohols (20:1 and 22:1) was highly varied between season and species.

Sterols in ctenophores and their potential diets

Sterol concentration and distribution in ctenophores for the two sampling seasons are shown in Table 3 . Cholesterol was the major sterol (more than 73% of total sterols) in ctenophores with minor differences between sampling seasons. This is in contrast to Nelson et al. (2000) who found that phytoplankton-derived sterols were the dominant sterols in most of the other Antarctic Ctenophora species. Minor amounts of a number of sterols (less than 1.4 mg g^{-1} dry mass) were also present and diverse in distribution. The ability of ctenophores to synthesize cholesterol de novo has not been established, but similar abundances are present among all analyzed crustaceans. The high amount of cholesterol is consistent with the belief that *Callianira antarctica* is largely carnivorous. The second most abundant sterol was desmosterol (cholesta-5, 24-dienol), which is produced from phytosterol dealkylation and common in marine microalgae, such as *Nitzschia closterium* and *Rhizoselenia setigera* (Goad 1978; Barrett et al. 1995). The presence of this algal sterol could be from direct algal ingestion or obtained indirectly by feeding on herbivores.

In addition to cholesterol, sterol distributions in potential prey, particularly krill, were similar to those in ctenophores, and included desmosterol as the second most abundant sterol (Table 3). Significant amounts of cholest-7-en-3β-ol were present only in adult *E. crystallorophias* and *Calanoides acutus*. Additional sterols [i.e., dehydrocholesterol (cholesta-5,22-dien-3β-ol)] not seen in adult and juvenile krill were also present and accounted for a significant fraction of the total sterols in copepods and larval krill (Table 3). Dehydrocholesterol

Table 3 Composition and distribution of sterols (% of total concentration) in ctenophores and their potential diets [***CT*** *Callianira antarctica*, ***ES*** *Euphausia superba*, ***EC*** *Euphausia crystallorophias*, ***PA*** *Paraeuchaeta antarctica* , ***CA*** *Calanoides acutus*, ***AO*** *Antarctomysis ohlini*, ***MG*** *Metridia gerachei*, ***CP*** *Calanus propinquus*; – not detected; *Tr* trace amount (<0.1% of total concentration)]

Sterols	Species					
	CT[a] ($n=5$)	ES-adult ($n=4$)	EC-adult ($n=3$)	PA[a] ($n=20$)	CA[a] ($n=50$)	AO[a] ($n=2$)
Fall 2002						
24-Norcholesta-5,22-dien-3β-ol	0.4	–	–	13.1	9.6	0.2
Cholesta-5,22-dien-3β-ol (Dehydrocholesterol)	2.7	0.5 ± 0.1	–	7.7	14.3	1.0
5α-Cholest-22-en-3β-ol (Dehydrocholestanol)	0.4	–	–	1.9	–	1.8
Cholest-5-en-3β-ol (Cholesterol)	73.0	71.3 ± 3.9	55.7 ± 9.0	46.8	36.3	88.2
5α-Cholestan-3β-ol (Cholestanol)	0.8	3.6 ± 4.2	–	–	–	1.5
Cholesta-5,24-dien-3β-ol (Desmosterol)	22.0	24.6 ± 2.9	28.4 ± 9.2	30.5	25.6	5.7
Cholest-7-en-3β-ol	0.1	–	15.9 ± 1.3	–	14.1	1.7
24-Methylcholesta-5,24(28)-dien-3β-ol	0.6	–	–	–	–	–
24-Methylcholest-5-en-3β-ol	0.1	–	–	–	–	–
Total sterols (mg g^{-1} dry wt.)	0.3	1.8 ± 0.7	2.5 ± 1.0	2.1	1.6	4.6

Sterols	Species						
	CT ($n=2$)	ES-adult ($n=6$)	ES-juvenile ($n=4$)	ES-furciliae[a] ($n=4$)	PA[a] ($n=10$)	MG[a] ($n=20$)	CP-female[a] ($n=10$)
Winter 2002							
24-Norcholesta-5,22-dien-3β-ol	0.3 ± 0.2	0.6 ± 0.6	1.6 ± 1.4	0.4	–	6.2	2.1
Cholesta-5,22-dien-3β-ol (Dehydrocholesterol)	1.7 ± 0.4	0.8 ± 0.2	0.8 ± 0.1	4.9	12.8	12.7	17.9
5α-Cholest-22-en-3β-ol (Dehydrocholestanol)	0.1 ± 0.1	Tr	Tr	–	–	–	-
Cholest-5-en-3β-ol (Cholesterol)	80.7 ± 1.3	82.3 ± 4.8	85.4 ± 2.1	78.6	71.8	61.8	37.4
5α-Cholestan-3β-ol (Cholestanol)	1.0 ± 0.6	0.6 ± 0.8	Tr	2.4	9.5	3.7	-
Cholesta-5,24-dien-3β-ol (Desmosterol)	15.9 ± 0.4	15.7 ± 4.8	12.1 ± 1.8	13.7	5.3	15.7	32.8
Cholest-7-en-3β-ol	–	–	–	–	–	–	9.1
24-Methylcholesta-5, 24(28)-dien-3β-ol	0.2 ± 0.0	–	–	Tr	0.7	–	0.7
24-Methylcholest-5-en-3β-ol	Tr	–	–	–	–	–	-
Total sterols (mg g^{-1} dry wt.)	1.2 ± 0.2	2.8 ± 1.2	1.9 ± 0.4	4.6	4.8	0.4	0.7

[a]Composite samples were used for analysis.

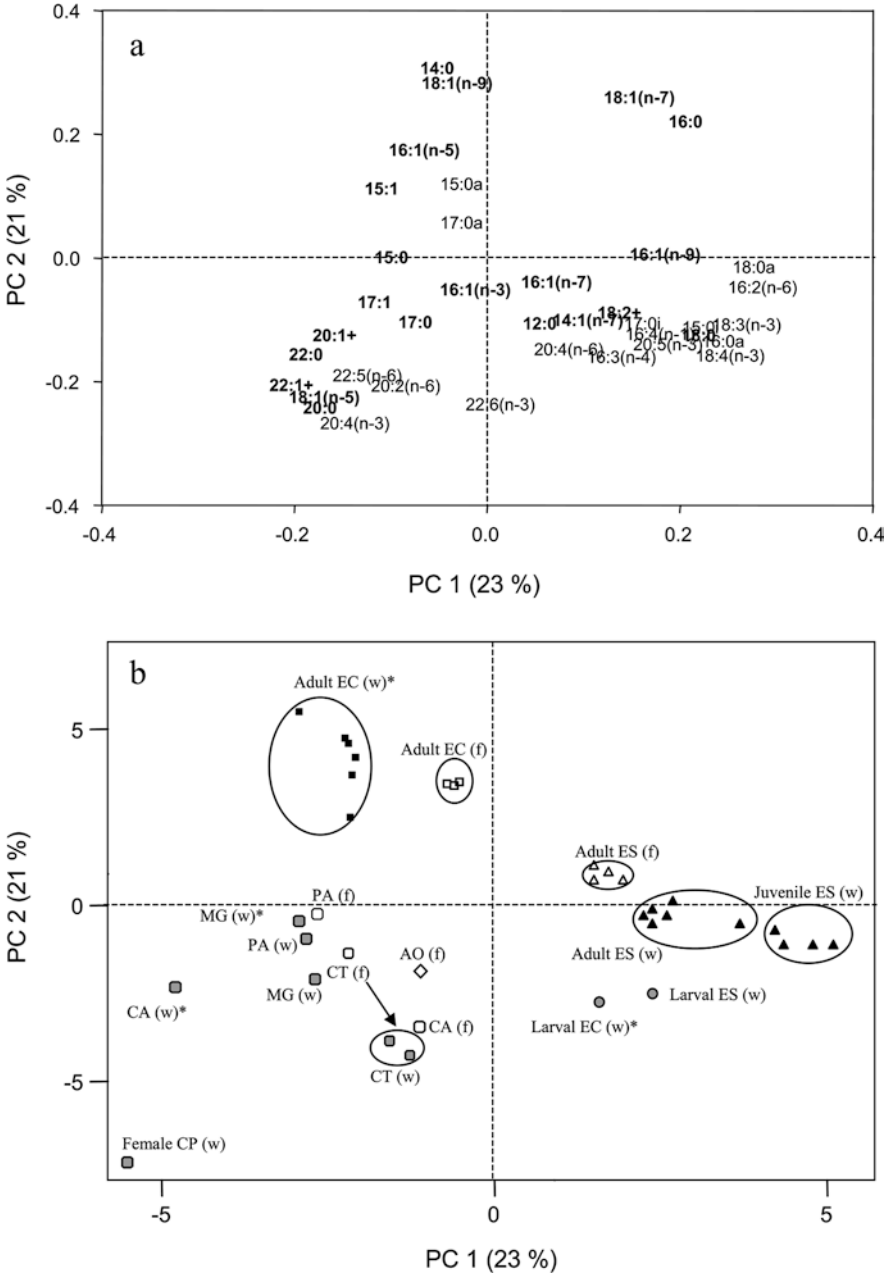

Fig. 2a,b Two-dimensional PCA loading (**a**) and score (**b**) plot of the first two principal components observed for ctenophores and potential ctenophore prey based on combined fatty acid/alcohol profiles. Additional data (indicated as *) taken from recent work (Ju and Harvey 2004) are included for this analysis. **Bold symbols** indicate combined fatty acid and alcohol moieties of identical chain length and unsaturation (***CT*** *Callianira antarctica*, ***ES*** *Euphausia superba*, ***EC*** *Euphausia crystallorophias*, ***PA*** *Paraeuchaeta antarctica*, ***CA*** *Calanoides acutus*, ***AO*** *Antarctomysis ohlini*, ***MG*** *Metridia gerachei*, ***CP*** *Calanus propinquus*). *w* samples were collected in winter 2002 and *f* samples were collected in fall 2002; + indicates all isomers combined, *a* and *I* indicate anti-iso and iso branched fatty acid/alcohol units, respectively

was noted as the major sterol in the Antarctic ice diatom *N. cylindrus* (Nichols et al. 1986) and in marine particulate matter from Antarctica (Mühlebach et al. 1999). It is well known that ice-associated algae are a major food source for herbivorous copepods and larval krill in Antarctica (Daly 1990). The appearance of dehydrocholesterol in ctenophores indicates that herbivorous copepods (i.e., *Calanoides acutus*) and larval krill may be a significant food source for *Callianira antarctica* during winter.

Principal component analysis using lipid biomarkers

In this study, we consider fatty alcohols as additional indicators of dietary history, because animals preying on WE-rich prey (i.e., Antarctic calanoids) can either convert ingested fatty alcohols to fatty acids, or alternatively deposit dietary fatty alcohols in WE (Sargent and

Falk-Peterson 1981; Sargent and Henderson 1986). PCA was applied to the combined suite of fatty acids and alcohols encountered in individual animals and potential prey to allow a more robust examination of trophic links among prey and predators. Loading and score plot for the first two principal components for these units seen in individual animals and potential prey are shown in Fig. 2. The first principal component (PC 1) accounted for 23% of the total variation, with the second principal component (PC 2) accounting for 21% of the variation. Loadings among individual carbon chains with identical unsaturation (fatty acid + alcohol) showed that the first component was mainly due to monounsaturated and polyunsaturated units. These lipids (positive in PC 1) are associated with *E. superba*, which were likely obtained from ingestion of ice-associated organisms or seston in the water column (Fig. 2a). Negative displacements in PC 1 were mainly due to 20:1 and 22:1 isomers. These two fatty acids and alcohols are commonly found in copepods. Positive displacement in PC 2 included saturated and monounsaturated units [e.g., 14:0, 18:1(*n*-9)], which were found in the alcohol fraction of lipid in *E. crystallorophias* and copepods, while negative loadings were found for long-chain units [e.g., 20:1 and 22:1 isomers, 20:5(*n*-3), 22:6(*n*-3)]. All copepods have negative displacement in PC 1 and PC 2 and were well separated from krill because of their high concentration of 20:1 and 22:1 isomers. Using the suite of fatty acids and alcohols, it is apparent that ctenophores were most closely linked with copepods, with the exception of *Calanus propinquus*. *Calanus propinquus* was isolated from the ctenophore in PCA plot (Fig. 2b) due to the absence of the long-chain MUFA 22:1(*n*-9) in ctenophores, but presence in high abundance in *Calanus propinquus*. Although *Calanus propinquus* is one of the dominant Antarctic copepod species, this substantial difference in composition suggests they may not be a major prey item for ctenophores. Ctenophores from winter shift to more negative values in PC 2 (more PUFA) and more positive PC 1 (Fig. 2b). This suggests that although copepods were still a major prey item for ctenophores, larval krill (high PUFA) become a significant portion of their diets during winter. Visual gut-content analysis of ctenophores collected during this study was conducted by Scolardi et al. (2004). Although only a small fraction ($<20\%$ of total gut contents) of the gut contents were recognizable, copepods appeared to be the major components (89 and 62% of recognizable gut contents during fall and winter, respectively) of the ctenophore diet during 2002. These observations agree well with observations from lipid analysis. A recently conducted study using lipid markers by Falk-Petersen et al. (2002) suggested that marine copepods (particularly *Calanus* sp.) were the major prey items for Arctic ctenophores, with little dietary different preferences between species. Their findings correspond well with our findings for Antarctic ctenophores. Despite these similarities, several issues are still relevant to the use of lipid markers to further interpret the feeding ecology of ctenophores in polar waters. First, lipid content and prey composition could alter overall digestive rates, as suggested by Scolardi et al. (2004). For example, TAG are dominant storage lipid classes in *E. superba* and *Calanus propinquus*, while WE are dominant storage lipid classes in *E. crystallorophias*, *Paraeuchaeta antarctica*, and *Calanoides acutus*. As a result, changes in prey have the potential to strongly impact the distribution of lipid available for metabolism. Second, the prey fields of Antarctic ctenophores appear to vary spatially and temporally, and long-term integration of the lipid signal is unknown. For example, gut contents of ctenophores collected during winter 2001 were dominated by larval krill (83% of total recognizable gut contents), and coincided with the higher abundance of larval krill during winter 2001, but were very different in the winter of 2002 (Daly 2004). Additional sampling over more extended time periods is needed to elucidate the inter-annual and intra-annual differences in ctenophores and their potential prey.

Conclusions

The application of multivariate analysis of lipid markers significantly improves our knowledge of the feeding ecology of Antarctic ctenophores and provides new insight into the ecological role of *Callianira antarctica*. Results of individual lipid profiles, together with multivariate analysis of lipid markers, suggest that copepods compose the primary diet of *Callianira antarctica* in both fall and winter seasons. Lipid distributions suggest that larval and juvenile krill are a minor component of ctenophore diets. Nevertheless, Antarctic ctenophores may still play a significant role in krill population dynamics. This might be a direct influence through predation when larval krill are abundant during winter, or indirectly through competition with adult krill for limited food sources during winter when phytoplankton (the primary food source for krill) are scarce.

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