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Fatty acid composition of lipid-rich myctophids and mackerel icefish (*Champsocephalus gunnari*) – Southern Ocean food-web implications

Abstract The lipid content, fatty acid composition and calorific value of seven species of mesopelagic deep-sea fish of the family Myctophidae and the mackerel icefish, *Champsocephalus gunnari*, important in the diet of Southern Ocean marine predators, are presented. Fish were sampled at the Kerguelen Plateau (KP) and Macquarie Ridge (MR) in the Indian and Pacific sectors of the Southern Ocean respectively, to examine geographic variation in lipid compositon. All species of myctophid from KP and *Electrona antarctica* from MR were high in lipid content (6–18% wet mass), particularly *Gymnoscopelus nicholsi* (18%) and *E. antarctica* (15%). The mackerel icefish, and *G. fraseri* and *Protomyctophum tenisoni* from MR were generally lower in lipid content (3–5%) and varied significantly in fatty acid composition from KP species. KP myctophids were high in calorific content (9.3 kJ g^{-1} wet mass) when compared with icefish (5.4 kJ g^{-1} wet mass) and other published values for prey items of marine predators such as squid (1.7–4.5 kJ g^{-1}). KP myctophids were distinguished from each other and from *C. gunnari* and MR specimens by cluster and discriminant function analysis using six fatty acids (16:0, 18:1ω9, 20:1ω9, 22:1ω11, 20:5ω3, 22:6ω3).

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Findings presented here highlight trophic links between high-latitude fish and their prey and emphasise the importance of myctophids as a significant energy source for marine predators foraging in the Polar Frontal Zone.

Introduction

Myctophids (lanternfish) are the most widespread mesopelagic deep-sea fish family (Saito and Murata 1998), with more than 35 species occurring in the Southern Ocean (Hulley 1998). In addition, many of these species are circumpolar (Hulley 1990), their distribution being determined by the oceanographical structure of Antarctic waters, particularly in relation to the Antarctic Circumpolar Current (Sabourenkov 1990). Mesopelagic or pseudoceanic species often exhibit vertical migration from depths of 1,000 m (Marshall 1971) to 0–200 m at night (Hulley 1990; Duhamel et al. 2000) in search of prey, where they become accessible to vertebrate, marine predators. In regions of the Southern Ocean where krill, *Euphausia superba*, do not predominate, fish of the family Myctophidae constitute a significant proportion of the diet of Southern Ocean predators (penguins: Adams and Klages 1987; Cherel et al. 1993; Bost et al. 1997; Raclot et al. 1998; Hull 1999; seals: Sabourenkov 1991; Daneri and Coria 1993; Reid and Arnould 1996; Cherel et al. 1997; Goldsworthy et al. 1997; Green et al. 1997). The region around the Kerguelen Plateau, in the vicinity of the Kerguelen Archipelago and Heard Island, is one such area. The islands are situated within the Antarctic Polar Frontal Zone, a region of high and seasonal productivity, with zooplankton communities dominated by pelagic crustaceans such as euphausiids and amphipods (Pakhomov and Froneman 2000). Myctophids feeding on meso- and macrozooplankton including copepods, euphausiids and hyperiid amphipods, migrate vertically to within 50 m of the surface at night following the diel migration of the macrozooplankton (Duhamel et al. 2000). Guinet et al. (1996)

estimated that, in 1985, marine predators in the Kerguelen region consumed 460,000 tonnes of myctophids annually. Thus, their role in the ecosystems of the Southern Ocean is substantial.

Some notothenioid fish, such as the commercially harvested mackerel icefish, *Champsocephalus gunnari*, also feature in the diet of Antarctic fur seals (Green et al. 1991; North 1996; Reid and Arnould 1996; Cherel et al. 1997) and king penguins (Moore et al. 1998). Given the importance of these fishes to the ecology of many species in the sub-Antarctic, it is surprising that few studies have examined the lipid composition and energy content of lanternfish and the mackerel icefish. To date, studies of myctophid lipid composition have centred on North Pacific (Nevenzel et al. 1969; Neighbors 1988; Moku et al. 2000) and sub-Arctic species (Seo et al. 1996; Saito and Murata 1998), and in the Antarctic, Phleger et al. (1997, 1999) have studied several species from the Scotia Sea and East Antarctica, and Reinhardt and van Vleet (1986) analysed four species from the Antarctic Peninsula. In the southern Indian Ocean, Raclot et al. (1998) have recently conducted lipid analyses on four species of myctophid occurring in the diet of king penguins from the Crozet Archipelago in winter, and Nichols et al. (1994) described the fatty acid (FA) composition of two icefish from the Kerguelen Plateau. Such biochemical studies of prey species are required to complement concurrent studies examining the identification of dietary signature fatty acids in the milk and adipose tissue of marine mammals (Iverson 1993; Grahl-Nielsen and Mjaavatten 1995) and penguins (Raclot et al. 1998). In the last decade this technique has evolved as a tool in the identification of prey items to complement conventional methods, which identify hard parts, such as fish otoliths and squid beaks in faeces. Compositional profiles of the major prey species of myctophid predators, such as Antarctic fur seals, are necessary for comparisons with milk and blubber profiles (Iverson et al. 1997a, b; Kirsch et al. 2000; Walton et al. 2000) and may potentially yield greater knowledge concerning the diet of these predators.

Thus, we describe the lipid composition of Southern Ocean myctophids, particularly in the Kerguelen region, where little information is currently available. Seven species of Myctophidae known to occur in the diet of Antarctic fur seals at Îles Kerguelen (Cherel et al. 1997) were analysed: *Gymnoscopelus piabilis*, *G. nicholsi*, *G. fraseri*, *Electrona antarctica*, *E. subaspera*, *E. carlsbergi* and *Protomyctophum tenisoni*, in addition to mackerel icefish (*C. gunnari*). We present data for the species studied, which will compliment the FA spectra of prey available to Southern Ocean predators. These data are being incorporated into a study examining the efficacy of using FA signature analysis of fur-seal milk samples to identify prey species (see Lea et al., in press).

Secondly, we examined the geographical variation in lipid composition for three species of myctophid (*Electrona antarctica*, *G. fraseri* and *P. tenisoni*) from two sites, the Kerguelen Plateau and Macquarie Ridge, located in the southern Indian and Pacific Oceans, respectively. Phleger et al. (1997) noted a difference in lipid composition of *Electrona antarctica* from Elephant Island and East Antarctica, and thus it seems reasonable to assume that geographical variation in fatty acid composition of conspecific fish species may occur in response to regional and seasonal changes in marine productivity and associated changes in zooplankton community structure.

Finally, knowledge of the calorific content of such prey species is necessary for calculating energy flow rates through trophic levels of marine ecosystems (Goldsworthy et al. 2001) and in determining the energetic importance of particular prey species in the diet of marine predators (Cherel and Ridoux 1993; Kirkwood and Robertson 1997). Such information is scarce for many Southern Ocean species, and thus a further aim of this study was to determine the calorific value for each species analysed.

Materials and methods

Sample collection

Specimens of *P. tenisoni* ($n=3$), *Electrona subaspera* ($n=3$), *E. antarctica* ($n=2$), *Electrona carlsbergi* ($n=2$), *G. piabilis* ($n=3$), *G. nicholsi* ($n=3$) and *G. fraseri* ($n=3$) were collected by RV *La Curieuse* during bathypelagic trawls within the preferred foraging zone of female Antarctic fur seals (Guinet et al. 2001), to the northeast of the Kerguelen Archipelago (49°07′S, 70°45′E, Fig. 1) in June 1998 (Table 1). The samples were collected at night using an IYGPT net (International Young Gadoid Pelagic Trawl; opening: 12×7 m) with a 10-mm mesh size in the codend (Duhamel et al. 2000), and were sorted on deck and frozen. Frozen samples were transported by air to CSIRO Marine Research Laboratories where they remained frozen at –80°C until analysis within 2 months. The number of fish sampled was limited firstly by the logistical constraints of conducting such studies in the Southern Ocean, and secondly by the difficulties of transporting frozen samples from such remote locations. In addition, analyses of several similar species in previous studies have been performed on comparable sample sizes, with limited variation observed (Phleger et al. 1997, 1999; Raclot et al. 1998). Whilst comparisons have been made, we recognise the need for further sampling and analyses.

Specimens of *P. tenisoni* ($n=3$), *G. fraseri* ($n=3$) and *Electrona antarctica* ($n=2$) from Macquarie Ridge (54°35′S, 159°55′E) were included in the study to determine inter-site variation in fatty acid composition. These samples were collected by the CSIRO marine research vessel *Southern Surveyor* from 21 to 30 January 1999.

Mackerel icefish, *C. gunnari* ($n=3$), also preyed on by Antarctic fur seals (Cherel et al. 1997), were trawled on the southern Kerguelen Plateau at Gunnari Ridge, in the vicinity of Heard Island by MV *Austral Leader* during scientific research trawls of the Australian Antarctic Division. Species sampled and the trawl locations (Fig. 1) are listed in Table 1.

Lipid extraction

Fish were thawed, weighed and a standard length measurement taken. Whole fish, including gut contents, were macerated and the lipid quantitatively extracted overnight by a modified Bligh and Dyer (Bligh and Dyer 1959) one-phase methanol/chloroform/water extraction (1:2:0.8, by volume). The phases were separated the following day by the addition of chloroform, water and sodium chloride (final solvent ratio, 1:1:0.4, by volume, methanol/
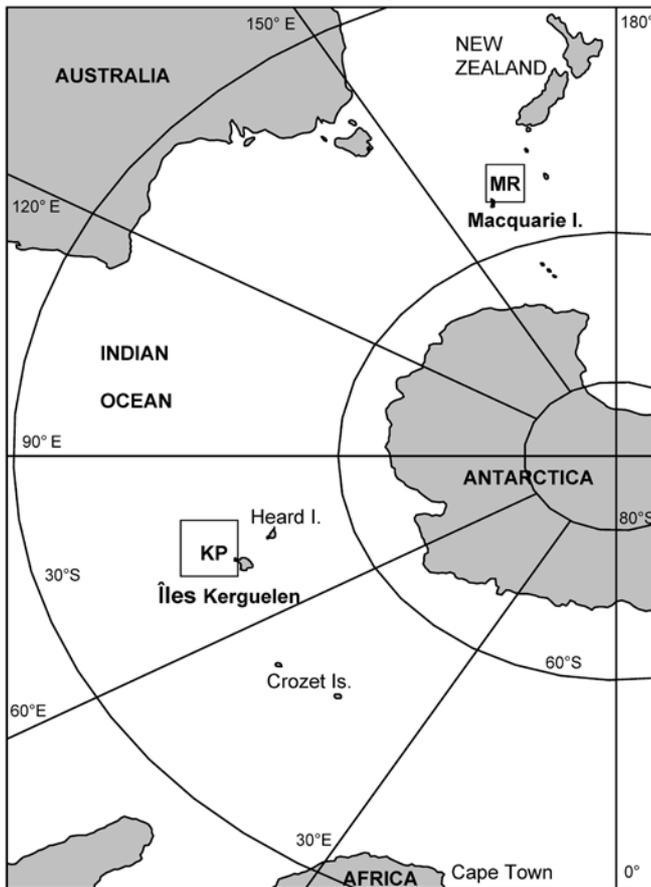
Fig. 1. The sampling regions of the Kerguelen Plateau (*KP*), Macquarie Ridge (*MR*), the Southern Ocean and surrounding sub-Antarctic islands

chloroform/water). Concentration of the total solvent extract (TSE) was obtained in vacuo by rotary evaporation at 40°C. A sub-sample of the extracted lipid was made up to a known concentration by the addition of chloroform and stored at –20°C. Lipid class analyses were conducted within 3 days.

An aliquot of the total lipid was analysed using an Iatroscan MK V TH10 thin-layer chromatography-flame-ionisation detector (TLC-FID) analyser (Tokyo, Japan) to determine the abundance of individual lipid classes (Volkman and Nichols 1991). Samples were applied in duplicate or triplicate to silica gel SIII chromarods (5 μm particle size) using 1-μl disposable micropipettes. Chroma-rods were developed in a glass tank lined with pre-extracted filter

paper. The solvent system used for the lipid separation was hex-ane/diethyl ether/acetic acid (60:17:0.2, by volume), a mobile phase resolving non-polar compounds such as wax esters (WE), triacyl-glycerols (TAG), free fatty acids (FFA) and sterols (ST). A second non-polar solvent system of hexane/diethyl ether (96:4 vol./vol.) was also used for selected samples to separate hydrocarbon from WE and TAG from diacylglyceryl ether (DAGE). After development, the chromarods were oven-dried and analysed immediately to minimise adsorption of atmospheric contaminants. The FID was calibrated for each compound class [phosphatidylcholine, cholesterol, cholesteryl ester, oleic acid, squalene, wax ester (derived from fish oil), triacyclglycerol (derived from fish oil) and DAGE (purified from shark liver oil); 0.1–10 μg range]. Peaks were quantified on an IBM compatible computer using DAPA software (Kalamunda, western Australia). Iatroscan results are generally reproducible to ±10% of individual component abundance (Volkman and Nichols 1991).

An aliquot of the total lipid was treated with methanol/hy-drochloric acid/chloroform (10:1:1, by volume; 80°C, 2 h). After cooling and the addition of MilliQ water (1 ml), fatty acid methyl esters (FAME) were extracted into hexane/chloroform (4:1, vol./vol., 3×1.5 ml) and the FAME mixture was treated with *N*,O-bis-(trimethylsilyl)-trifluoroacetamide (BSTFA, 50 μl, 60°C, 1 h) to convert sterols to their corresponding TMSi (trimethylsilyl) ethers.

Gas chromatographic (GC) analyses of FAME were performed with a Hewlett Packard 5890A GC (Avondale, Pa.) equipped with an HP-5 cross-linked methyl silicone fused silica capillary column (50 m×0.32 mm i.d.), an FID, a split/splitless injector and an HP 7673A autosampler. Hydrogen was the carrier gas. Following addition of methyl nonadecanoate and methyl tricosanoate internal standards, samples were injected in splitless mode at an oven temperature of 50°C. After 1 min, the oven temperature was raised to 150°C at 30°C min^{-1}, then to 250°C at 2°C min^{-1} and finally to 300°C at 5°C min^{-1}. Peaks were quantified with Waters Millenium software (Milford, Mass.). Individual components were identified using mass spectral data and by comparing retention time data with those obtained for authentic and laboratory standards. GC results are subject to an error of ±5% of individual component abundance. GC-mass spectrometric (GC-MS) analyses were performed on a Finnigan Thermoquest GCQ system (Austin, Tex.) fitted with an on-column injector. The GC was fitted with a capillary column similar to that described above.

Calorific content

Whole-fish samples of *P. tenisoni*, *Electrona subaspera*, *E. antarctica*, *E. carlsbergi*, *G. piabilis*, *G. nicholsi*, *G. fraseri* and *C. gunnari* were measured (SL), weighed and oven-dried at 50°C for several days until specimens maintained a constant dry mass. Once dried, the fish were homogenised with a mortar and pestle and either the whole fish or a 0.5-g sub-sample was taken. Calorific value (kJ g^{-1} wet and dry mass) of each fish was determined by ballistic bomb calorimetry using a custom-made bomb calorimeter, calibrated by

Table 1. Trawl locations and morphological characteristics of seven species of sub-Antarctic myctophid fish and the chan-nichthyid mackerel icefish (*KP* Kerguelen Plateau, *MR* Macquarie Ridge)

Species	n	Site	Date	Latitude	Longitude	Standard length (mm)	Mean body mass (g)
Protomyctophum tenisoni	3	KP	14/6/98	49°17′S	71°05′E	40.7±0.6	0.7±0.1
	3	MR	21–30/1/99	54°35′S	159°55′E	49.0±2.0	1.4±0.1
Electrona subaspera	3	KP	14/6/98	49°16′S	71°06′E	72.3±5.0	6.3±1.4
Electrona antarctica	2	KP	14/6/98	49°16′S	71°07′E	82.0±2.8	7.1±1.6
	3	MR	21–30/1/99	54°35′S	159°55′E	57.7±9.3	2.0±1.0
Electrona carlsbergi	2	KP	14/6/98	49°16′S	71°07′E	89.5±6.4	12.7±5.2
Gymnoscopelus piabilis	3	KP	14/6/98	49°16′S	71°07′E	103.5±10.6[a]	15.3±5.7
Gymnoscopelus nicholsi	3	KP	14/6/98	49°17′S	71°05′E	123.3±5.8	23.5±2.8
Gymnoscopelus fraseri	3	KP	14/6/98	49°16′S	71°07′E	71.7±5.8	4.4±1.4
	3	MR	21–30/1/99	54°35′S	159°55′E	50.7±1.2	1.0±0.1
Champsocephalus gunnari	3	KP	17/3/00	52°35′S	75°11′E	311.7±16.1	131.1±40.5

[a]Standard length available for two of the specimens

the combustion of pre-weighed benzoic acid thermochemical standard pellets (Vondracek et al. 1996).

Statistical analysis

All statistical analyses were conducted using the SYSTAT 9.0 package (SYSTAT, Evanston Ill.). Means are ±standard deviation unless otherwise stated. A cluster analysis evaluating the similarity of the different fish species was performed using a Bray Curtis dissimilarity matrix on arcsine-transformed (Phillips et al. 2001) proportional data of 29 fatty acids (>0.5%). Results are presented graphically by dendrogram. A backwards step-wise discriminant function analysis (DFA) was then used to determine how reliably the fatty acid profiles of the individual fish could be assigned to species cluster groups and which fatty acids were most influential. These analyses were conducted using proportions of the 10 most common fatty acids (14:0, 16:0, 16:1ω7, 18:1ω7, 18:1ω9, 20:1ω9, 20:5ω3, 22:1ω11, 22:6ω3, 24:1ω11) present in the compositional profiles. A jackknife analysis was used to verify the accuracy of the DFA (Tabachnick and Fidell 1996).

Results

Lipid content and composition

Those species containing notably high concentrations of lipid included *G. nicholsi* (18% wet mass-WM) and *Electrona antarctica* on the Kerguelen Plateau (14.3%) and the Macquarie Ridge (14.5%), *E. carlsbergi* (12.2%) and *G. fraseri* (11.6%; Table 2).

Two groups were apparent from lipid-class profiles. Samples of *Electrona antarctica* were rich in wax esters (Table 2), whilst the remaining myctophid samples and the mackerel icefish *C. gunnari* were characterised by high levels (51.3–90.9% of total lipid) of triacylglycerols although icefish also contained 1.0% WE. *G. fraseri* from the Macquarie Ridge and icefish were characterised by lower levels of TAG (45.3 and 40.0% WM, respectively) and elevated levels of polar lipid, in addition to particularly low percentages of total lipid (approximately 3.5% WM). *P. tenisoni* sampled at both sites also contained a relatively high proportion of polar lipid (Table 2).

Levels of free fatty acids were higher in the Macquarie Island samples of *G. fraseri* (13.1% cf. 8.2%) and *P. tenisoni* (20.4% cf. 7.1%). We propose that this variability may have resulted from differences either in onboard storage, differences in lipase activity, and/or varying proportions of visceral matter richer in FFA between the samples. Levels of PUFA (polyunsaturated fatty acids) in several of the species examined in this study were in the range previously determined for these species obtained from other regions (see Raclot et al. 1998; Phleger et al. 1999), indicating that the protocols used have not degraded individual fatty acids.

Fatty acid profiles

TAG-rich species

The eight species analysed were distinguished on the basis of their fatty acid profiles by cluster analysis (Fig. 2), identifying three groups: (1) the wax ester-rich myctophid *Electrona antarctica* from the Kerguelen Plateau and Macquarie Ridge; (2) other myctophid species, and (3) the icefish *C. gunnari*. Icefish differed considerably in fatty acid composition from that of the myctophid species, containing high levels of palmitoleic acid (16:1ω7) and eicosapentaenoic acid (EPA, 20:5ω3) in comparison to other species, and a generally greater proportion of polyunsaturated fatty acids (Fig. 3, Table 3) than other myctophids collected at the Kerguelen Plateau. The two TAG-rich species sampled at Macquarie Ridge, *G. fraseri* and *P. tenisoni*, were clustered together (Fig. 2).

Within the myctophid group, individual species were generally well separated on the basis of their fatty acid signatures (Fig. 2). All species of Myctophidae studied contained relatively high levels of monounsaturated fatty acids (MUFA; 33.8–53.5% of total FA). Of the two TAG-rich *Electrona* congeners, *Electrona carlsbergi* contained higher relative levels of 14:0, 16:1ω7, oleic acid (18:1ω9), 20:1ω9 and 20:5ω3 than *Electrona subaspera* (Table 3). The long-chain MUFA 22:1ω11,

Table 2. Lipid composition (% of total lipid) of seven myctophid species and the mackerel icefish, *Champsocephalus gunnari* (*KP* Kerguelen Plateau; *MR* Macquarie Ridge; *WE* wax ester; *TAG* triacylglycerol; *FFA* free fatty acid; *ST* sterol; *PL* polar lipid; *Other* includes *DAG* diacylglycerol)

Species	Site	WE	TAG	FFA	ST	PL	Other	Lipid (% wet mass)
Protomyctophum tenisoni	KP	0.0	59.6 ± 7.4	8.2 ± 1.7	1.1 ± 0.1	27.2 ± 5.9	3.9 ± 1.2	7.8 ± 1.5
	MR	0.1	51.3 ± 14.4	13.1 ± 6.0	5.1 ± 2.6	30.5 ± 5.9	0.0	5.2 ± 1.9
Electrona subaspera	KP	0.0	81.6 ± 6.1	4.1 ± 1.5	1.5 ± 0.2	12.8 ± 4.7	0.0	9.2 ± 1.6
Electrona antarctica	KP	71.6 ± 8.2	17.3 ± 10.3	2.1 ± 0.4	0.6 ± 0.4	7.9 ± 1.7	0.6 ± 0.2	14.3 ± 1.4
	MR	80.2 ± 4.6	2.0 ± 0.2	2.1 ± 0.3	0.6 ± 0.1	14.2 ± 4.7	0.9 ± 0.1	14.5 ± 1.1
Electrona carlsbergi	KP	1.0 ± 0.9	77.8 ± 6.7	3.1 ± 1.5	1.3 ± 0.4	16.5 ± 3.6	0.2 ± 0.3	12.2 ± 3.9
Gymnoscopelus piabilis	KP	0.0	72.7 ± 7.8	9.7 ± 3.3	2.0 ± 1.3	14.7 ± 4.0	1.0 ± 0.8	6.8 ± 1.1
Gymnoscopelus nicholsi	KP	0.0	90.9 ± 0.9	3.4 ± 0.4	0.8 ± 0.1	4.7 ± 0.2	0.2 ± 0.3	18.0 ± 2.3
Gymnoscopelus fraseri	KP	0.2 ± 0.2	78.1 ± 5.4	7.1 ± 1.4	2.2 ± 0.5	12.4 ± 4.0	0.0	11.6 ± 2.9
	MR	0.7 ± 0.2	40.0 ± 7.1	20.4 ± 3.0	8.5 ± 1.1	30.5 ± 3.1	0.0	3.6 ± 0.4
Champsocephalus gunnari	KP	1.0 ± 0.2	45.3 ± 5.9	13.2 ± 1.6	3.0 ± 0.6	37.5 ± 4.5	0.0	3.4 ± 0.4

Fig. 2. A dendrogram based on a Bray-Curtis dissimilarity matrix for seven species of myctophids and the mackerel icefish, *Champsocephalus gunnari* (*Cg*) from the Kerguelen Plateau (*KP*) and Macquarie Ridge (*MR*). *highlights TAG-rich specimens from Macquarie Ridge (*Ea Electrona antarctica*, *Ec E. carlsbergi*, *Es E. subaspera*, *Gf Gymnoscopelus fraseri*, *Gn G. nicholsi*, *Gp G. piabilis*, *Pt Protomyctophum tenisoni*)
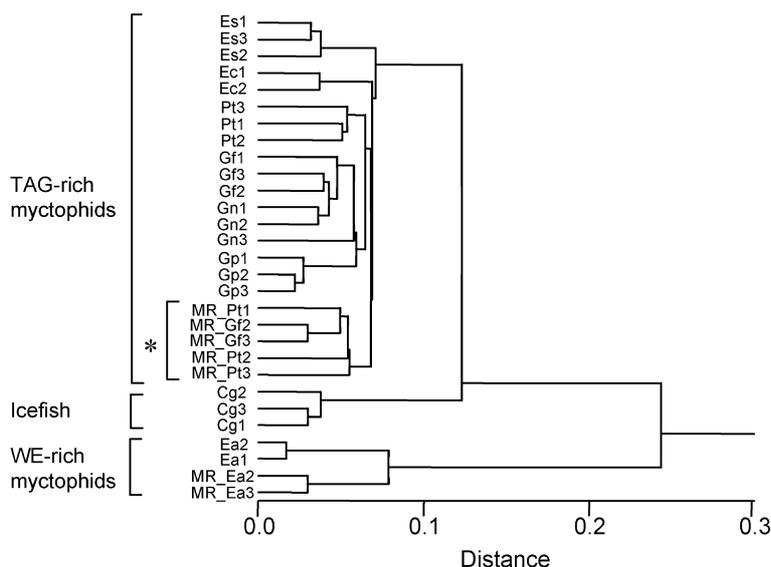
22:1ω9, 24:1ω11 and 18:4ω3 were more prevalent in *Electrona subaspera*. *P. tenisoni* from the Kerguelen Plateau was separated from the Macquarie Ridge specimens, and grouped with fish from the genus *Gymnoscopelus*. MR *P. tenisoni* contained a higher proportion of the essential PUFA decosahexaenoic acid (DHA, 22:6ω3), and lower relative levels of several MUFA: 16:1ω7, 22:1ω11 and 24:1ω11.

G. nicholsi, the largest and most lipid-rich of the *Gymnoscopelus* species studied, contained the highest levels of MUFA (53.5%) of all species analysed and, accordingly, the lowest proportion of PUFA (17.5%; Fig. 3). Levels of 20:1ω9 and 18:1ω7 were particularly elevated, whilst the proportion of 22:6ω3 was low in comparison to that of other myctophids (Table 3). *G. fraseri* appeared to be more similar to *G. nicholsi* (Fig. 2), containing high levels of MUFA (46.4%), although the PUFAs 20:5ω3 and 22:6ω3 were present in higher proportions. *G. piabilis*, also one of the larger myctophids, differed from the other two species of *Gymnoscopelus*, containing higher levels of saturated fatty acids (SFA), particularly 16:0 (Table 3). Proportions of 18:1ω9 (18.6%) were also the highest recorded in any of the fishes sampled (Table 3). Fish were generally high in ω3 fatty acids in comparison to ω6 fatty acids. TAG-rich specimens from Macquarie Ridge showed the highest ω3/ω6 ratio (11.6 and 13.3) with values of 5.1–9.0 observed for KP TAG-rich myctophids (Table 3).

Wax ester-rich species

Electrona antarctica specimens contained high levels of MUFA (65.4% and 67.5%) in comparison to other species (Tables 3, 4). The fatty acid profile of *Electrona antarctica* was characterised by particularly high proportions of 18:1ω9 (32–34%), followed by 16:1ω7, 22:6ω3, 20:5ω3 and 16:0. SFA composed only 9.1 and

11.1% of the total fatty acids for *E. antarctica* from KP and MR, respectively, values that are low in comparison to those of the TAG-rich species.

Overall, saturated and monounsaturated fatty alcohols occurred in similar proportions in *Electrona antarctica* collected from the two regions. However, a number of differences in the relative proportions of individual components were apparent. *Electrona antarctica* from the Kerguelen Plateau were highest in 16:0, 18:1ω9 and 16:1ω9 fatty alcohols (Table 4). Samples from Macquarie Ridge showed a similar profile, although 20:1ω9 was the major fatty alcohol present, and 14:0 and 18:1ω7 were also elevated. The ω3/ω6 fatty acid ratio was similar between sites although

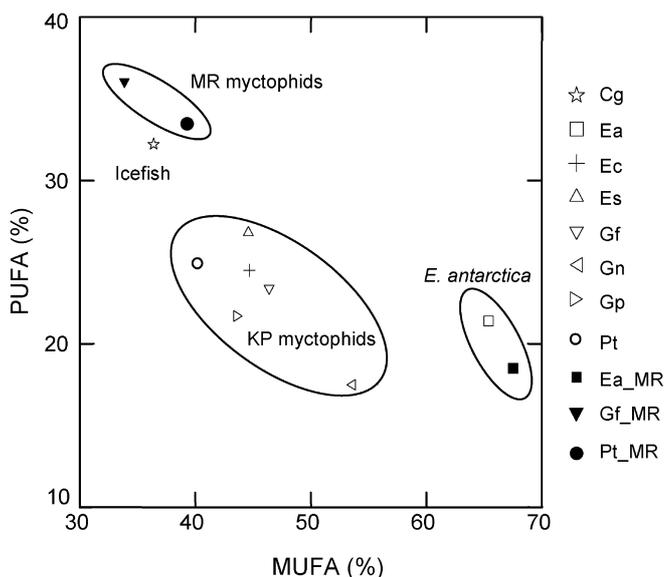**Fig. 3.** A plot of the percentage of monounsaturated fatty acids (*MUFA*) and polyunsaturated fatty acids (*PUFA*) present in myctophids and mackerel icefish from the Kerguelen Plateau (*KP*) and Macquarie Ridge (*MR*). Legend as for Fig. 2

Table 3. Fatty acid composition (% of total lipid) of seven myctophids *Protomyctophum tenisoni* (KP and MR), *E lectrona subaspera* (KP), *E. carlsbergi* (KP), *Gymnoscopelus piabilis* (KP), *G. nicholsi* (KP), *G. fraseri* (KP and MR) and the icefish *Champsocephalus gunnari* (KP). Values ± SD (*Other* < 0.5%: 14:1ω5, 4,8,12TMTD, iso15:0, a15:0, C₁₆PUFA, iso16:0, 16:1ω9, 16:1ω5, br17:1, i17:0, a17:0, 17:1ω8, 17:1ω6, 17:1, 17:0, 18:1ω7 t, 18:1, 19:1, 18:3ω6, 20:3ω6, C₂₀PUFA, 20:1ω5, C₂₁PUFA, 22:5ω6, 22:1ω7, 22:0, 24:0)

Fatty acids	*Protomyctophum tenisoni*		*Electrona subaspera*	*E. carlsbergi*	*Gymnoscopelus piabilis*	*G. nicholsi*	*G. fraseri*		*Champsocephalus gunnari*
	KP ($n=3$)	MR ($n=3$)	KP ($n=3$)	KP ($n=2$)	KP ($n=3$)	KP ($n=3$)	KP ($n=3$)	MR ($n=3$)	KP ($n=3$)
14:0	5.4 ± 1.2	2.7 ± 0.5	2.7 ± 0.2	4.9 ± 0.4	4.8 ± 0.2	5.5 ± 0.3	5.6 ± 0.2	3.3 ± 0.3	5.8 ± 1.0
15:0	0.7 ± 0.1	0.5 ± 0.1	0.5 ± 0.0	0.3 ± 0.1	0.6 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.3 ± 0.0
16:0	20.0 ± 0.7	17.4 ± 0.5	17.1 ± 0.6	17.8 ± 1.2	19.2 ± 0.6	14.5 ± 0.6	15.8 ± 0.9	17.5 ± 1.2	19.8 ± 0.5
18:0	2.5 ± 0.4	3.1 ± 0.3	3.1 ± 0.4	3.1 ± 0.3	4.1 ± 0.1	3.8 ± 0.3	3.0 ± 0.3	3.3 ± 0.2	1.5 ± 0.3
20:0	0.3 ± 0.0	0.2 ± 0.0	0.5 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.1 ± 0.0	0.03 ± 0.0
Total SFA	28.9 ± 2.4	23.9 ± 1.4	23.9 ± 1.3	26.3 ± 2.0	28.9 ± 1.0	24.3 ± 1.4	25.1 ± 1.6	24.7 ± 1.8	27.4 ± 1.8
16:1ω7	6.5 ± 1.0	4.5 ± 0.8	5.4 ± 0.5	8.6 ± 0.1	5.8 ± 0.6	5.3 ± 0.4	5.6 ± 0.8	3.6 ± 0.1	11.5 ± 0.7
16:1ω7t[a]	0.3 ± 0.2	0.1 ± 0.2	0.6 ± 0.1	0.3 ± 0.5	0.6 ± 0.1	0.5 ± 0.1	0.4 ± 0.3	0.5 ± 0.0	1.0 ± 0.1
18:1ω9	14.8 ± 0.6	14.0 ± 1.0	15.0 ± 3.2	17.8 ± 0.4	18.6 ± 1.3	16.6 ± 3.4	13.7 ± 0.8	13.3 ± 0.4	13.5 ± 1.0
18:1ω7	3.3 ± 0.7	4.4 ± 0.3	2.8 ± 0.3	3.2 ± 0.2	5.3 ± 0.4	8.2 ± 0.6	5.9 ± 1.4	4.3 ± 0.3	5.4 ± 0.2
18:1ω5	0.9 ± 0.1	0.7 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.7 ± 0.0	0.9 ± 0.0	0.6 ± 0.1	0.3 ± 0.0
20:1ω9	3.9 ± 1.4	7.7 ± 2.4	1.8 ± 0.4	4.3 ± 1.3	7.3 ± 0.7	14.5 ± 0.7	9.1 ± 0.9	7.2 ± 1.9	2.5 ± 0.4
20:1ω7	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.0	0.5 ± 0.2	0.6 ± 0.0	0.7 ± 0.1	0.6 ± 0.1	0.4 ± 0.0	0.3 ± 0.0
22:1ω11	4.1 ± 0.4	2.3 ± 0.5	8.5 ± 1.3	4.2 ± 0.2	1.9 ± 0.2	3.3 ± 1.8	4.9 ± 1.1	1.1 ± 0.3	0.2 ± 0.2
22:1ω9	2.1 ± 0.2	1.2 ± 0.2	3.7 ± 0.5	2.2 ± 0.1	1.1 ± 0.0	1.6 ± 0.6	2.2 ± 0.4	0.7 ± 0.1	0.4 ± 0.1
24:1ω11	2.3 ± 0.2	0.9 ± 0.3	4.0 ± 0.6	1.4 ± 0.1	0.7 ± 0.2	1.1 ± 0.1	1.5 ± 0.5	0.4 ± 0.1	0.1 ± 0.2
24:1ω9	1.7 ± 0.1	1.3 ± 0.3	1.5 ± 0.1	1.4 ± 0.2	1.1 ± 0.2	1.0 ± 0.4	1.6 ± 0.2	1.7 ± 0.2	0.4 ± 0.1
Total MUFA	40.3 ± 5.0	37.4 ± 6.2	44.6 ± 7.1	44.7 ± 3.4	43.7 ± 3.8	53.5 ± 7.9	46.4 ± 6.5	33.8 ± 3.4	35.6 ± 3.0
18:2ω6	1.4 ± 0.1	1.3 ± 0.3	1.7 ± 0.0	1.4 ± 0.1	1.7 ± 0.1	1.7 ± 0.5	1.5 ± 0.1	1.4 ± 0.1	1.8 ± 0.4
18:4ω3	1.7 ± 0.3	1.2 ± 0.3	2.3 ± 0.4	1.3 ± 0.0	1.3 ± 0.1	1.0 ± 0.1	1.6 ± 0.2	1.3 ± 0.1	1.1 ± 0.1
20:4ω6	0.5 ± 0.0	0.7 ± 0.1	0.5 ± 0.1	0.8 ± 0.0	0.6 ± 0.1	0.4 ± 0.1	0.5 ± 0.0	0.9 ± 0.0	0.9 ± 0.2
20:5ω3	7.9 ± 0.5	9.6 ± 1.1	8.5 ± 0.5	10.2 ± 0.5	7.0 ± 0.4	6.7 ± 1.1	8.6 ± 0.4	9.8 ± 0.5	16.5 ± 0.2
20:4ω3	0.5 ± 0.4	0.8 ± 0.1	1.2 ± 0.1	0.5 ± 0.0	1.2 ± 0.2	0.8 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	0.4 ± 0.0
20:2ω6	0.4 ± 0.3	0.1 ± 0.1	0.6 ± 0.0	0.2 ± 0.0	0.5 ± 0.1	0.4 ± 0.1	0.2 ± 0.2	0.4 ± 0.1	0.3 ± 0.1
22:6ω3	12.2 ± 0.1	18.9 ± 2.9	11.0 ± 1.1	9.4 ± 0.3	8.3 ± 1.8	5.5 ± 0.2	8.8 ± 1.2	20.5 ± 0.1	10.7 ± 0.5
22:5ω3	0.7 ± 0.0	1.4 ± 0.8	1.0 ± 0.1	0.7 ± 0.1	1.1 ± 0.0	1.0 ± 0.2	1.1 ± 0.1	1.2 ± 0.1	0.6 ± 0.0
Total PUFA	25.3 ± 1.7	34.0 ± 5.7	26.8 ± 2.3	24.5 ± 1.0	21.7 ± 2.8	17.5 ± 2.4	23.4 ± 2.3	36.6 ± 1.1	32.2 ± 1.5
Other	5.5 ± 1.5	4.7 ± 1.0	4.7 ± 1.2	4.5 ± 0.7	5.7 ± 0.8	4.7 ± 1.6	5.1 ± 0.7	4.9 ± 0.4	4.8 ± 1.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Total (ω3FA)	21.6	30.5	22.0	20.6	18.0	13.9	19.5	32.6	29.2
Total (ω6FA)	2.4	2.3	2.9	2.6	3.0	2.7	2.4	2.8	3.4
Ratio ω3/ω6	9.0	13.3	7.6	7.9	6.0	5.1	8.1	11.6	8.6

[a]16:2 celutes with 16:1ω7 t

absolute percentages of ω3 and ω6 fatty acids differed (Table 4).

Six fatty acids (16:0, 18:1ω9, 20:1ω9, 22:1ω11, 20:5ω3, 22:6ω3) were identified by a backwards-stepwise DFA (see Methods) as distinguishing the fatty acid profiles of the ten species cluster groups (Wilks' Lambda$_{6,9,19}$ = 0.000; $F_{54,75}$ = 47.115, $P < 0.001$). A jackknife classification matrix reassigned individual profiles to the species cluster groups in 97% of cases, indicating that these 6 fatty acids were strong predictors of the species cluster groups (Fig. 4).

Geographic variation in fatty acid composition

The fatty acid profiles of TAG-rich *P. tenisoni* and *G. fraseri* from Macquarie Ridge were more similar to each other than to conspecifics from the Kerguelen Plateau (Fig. 2) and contained higher levels of PUFA (Fig. 3). Interestingly, *G. fraseri* from Macquarie Ridge had much lower lipid levels (3.6%) than those from the Kerguelen Plateau (11.6%, Table 2), which may have been due to the disparity in size of specimens from the two sites. *G. fraseri* specimens from Macquarie Ridge were smaller in length and mass (Table 1). Both species also contained considerably higher levels of 22:6ω3 and 20:5ω3 fatty acids at Macquarie Ridge than on the Kerguelen Plateau (Table 3).

The fatty acid and fatty alcohol composition of *Electrona antarctica* from the two sites differed in that specimens from Macquarie Ridge had higher proportions of 20:1ω9, 18:1ω7 and 14:0 fatty acids and fatty alcohols, while those from the Kerguelen Plateau contained higher levels of 16:0 and 18:1ω9 fatty alcohols (Table 4).

Water and calorific content

The water content of the eight species of fish varied considerably, ranging from 60.8 to 76.7% of wet mass. The wax ester-rich *Electrona antarctica* contained the

849

Table 4. Fatty acid and fatty alcohol composition of *Electrona antarctica* from the Kerguelen Plateau and Macquarie Ridge (*SFA* saturated fatty acids, *MUFA* monounsaturated fatty acids, *PUFA* polyunsaturated fatty acids; *Other* <0.5%: 14:1ω5, a15:0, iso15:0, C₁₆PUFA, 17:0, a17:0, iso17:0, 17:1, 18:1, 18:3ω6, 20:0, 20:1ω5, 20:1ω11, 20:2ω6, 20:3ω6, 22:5ω6, 22:0, 22:1ω7, 4,8,12TMTD)

	Alcohols		Fatty acids	
	KP	MR	KP	MR
14:0	7.9 ± 0.5	10.8 ± 0.2	1.7 ± 0.2	2.7 ± 0.1
15:0	0.8 ± 0.1	0.6 ± 0.0	0.1 ± 0.1	0.1 ± 0.0
16:0	37.0 ± 1.7	33.9 ± 1.6	5.3 ± 0.3	6.7 ± 0.1
18:0	2.2 ± 0.1	1.9 ± 0.3	2.0 ± 0.2	1.6 ± 0.0
Total SFA	47.7 ± 2.4	47.2 ± 2.1	9.1 ± 0.8	11.1 ± 0.2
16:1ω9	5.7 ± 0.6	4.9 ± 0.1	0.3 ± 0.0	0.3 ± 0.0
16:1ω7	0.9 ± 0.1	0.9 ± 0.1	17.2 ± 0.9	16.2 ± 0.1
16:1ω5	0.8 ± 0.1	0.9 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
18:1ω9	27.3 ± 1.8	19.8 ± 2.4	34.4 ± 0.8	32.1 ± 1.5
18:1ω7	5.3 ± 0.2	6.8 ± 0.6	3.9 ± 0.3	5.8 ± 0.4
18:1ω5	1.2 ± 0.1	1.3 ± 0.1	0.6 ± 0.0	0.2 ± 0.0
20:1ω9	3.4 ± 0.1	10.5 ± 2.6	2.9 ± 0.5	7.4 ± 0.7
20:1ω7	0.4 ± 0.0	0.4 ± 0.0	0.7 ± 0.0	0.7 ± 0.0
22:1ω11	0.8 ± 0.0	1.6 ± 0.1	2.0 ± 0.4	2.0 ± 0.2
22:1ω9	0.9 ± 0.2	0.9 ± 0.2	1.5 ± 0.2	1.3 ± 0.1
24:1ω7	0.4 ± 0.0	0.5 ± 0.3	1.7 ± 0.4	1.2 ± 0.2
Total MUFA	47.1 ± 3.2	48.5 ± 6.5	65.4 ± 3.5	67.5 ± 3.2
18:4ω3	0.0	0.0	2.0 ± 0.1	1.6 ± 0.0
18:2ω6	0.0	0.0	1.5 ± 0.0	1.4 ± 0.1
20:4ω6	0.0	0.0	0.7 ± 0.0	0.5 ± 0.0
20:5ω3	0.0	0.0	6.0 ± 0.0	6.8 ± 0.1
20:4ω3	0.0	0.0	0.6 ± 0.0	0.4 ± 0.0
22:6ω3	0.0	0.0	10.0 ± 0.1	7.3 ± 0.2
22:5ω3	0.0	0.0	0.6 ± 0.0	0.5 ± 0.0
Total PUFA	0.0	0.0	21.4 ± 0.2	18.5 ± 0.4
Other	5.2 ± 0.4	4.3 ± 0.4	4.1 ± 0.6	2.9 ± 0.4
Total	100.0	100.0	100.0	100.0
Total ω3 FA	.	.	19.2	16.6
Total ω6 FA	.	.	2.2	1.9
Ratio ω3/ω6	.	.	8.7	8.7

content (kJ g⁻¹ wet mass) was highly, negatively significant (Fig. 5; $P < 0.0001$, $n = 8$, $r^2 = 0.902$). A positive relationship between size and calorific content was present for some species, such as *G. piabilis* and *E. carlsbergi*, whilst for other species there was no trend, although sample size was limited.

Calorific content per gramme wet mass ranged between 5.4 kJ g⁻¹ and 13.3 kJ.g⁻¹ for *C. gunnari* and *Electrona antarctica*, respectively. Calorific values per gramme dry mass were also variable (23.2–34.3 kJ) as a result of the variability in water content for the various species. The mean calorific value for myctophids from the Kerguelen Plateau was high at 9.3 kJ g⁻¹ wet mass.

Discussion

Total lipid, lipid classes and calorific value

Myctophids from the Kerguelen Plateau examined in this study were generally rich in lipid levels (7.8–18.0% WM) whilst the mackerel icefish was relatively lipid-poor (3.4% WM). *G. nicholsi* and *Electrona antarctica* were particularly oily fishes, with 18.0% and 14.5% WM respectively. Species examined from the Macquarie Ridge area were generally lower in lipid content, except for *E. antarctica*, which exhibits some of the highest lipid levels for any species of fish regardless of location (East Antarctica: Reinhardt and van Vleet 1986; Phleger et al. 1997; Kerguelen Plateau and Macquarie Ridge: this study). Values are comparable to those reported by Seo et al. (1996) and Saito and Murata (1998) for myctophids of the sub-Arctic (6.7–21.7% and 4.4–26.1% WM, respectively).

Reinhardt and van Vleet (1986) noted that percentage lipid increased with depth in many Antarctic fish species. It appears that this may not necessarily be the case for myctophid species in waters surrounding the Kerguelen Archipelago. The more lipid-rich species such as *G. nicholsi*, *G. fraseri*, *E. antarctica* and *E. carlsbergi* were

least water, in addition to the highest calorific value of 34.3 kJ per gramme of dry mass (Table 5). This value is in accordance with the high lipid content (14.3%) reported earlier for *E. antarctica* (Table 2). The relationship between percentage water content and mean energy

Fig. 4. Relative proportions of the six most common fatty acids found in the ten species cluster groups identified by MDS. Legend as for Fig. 2 (*MR* Macquarie Ridge)
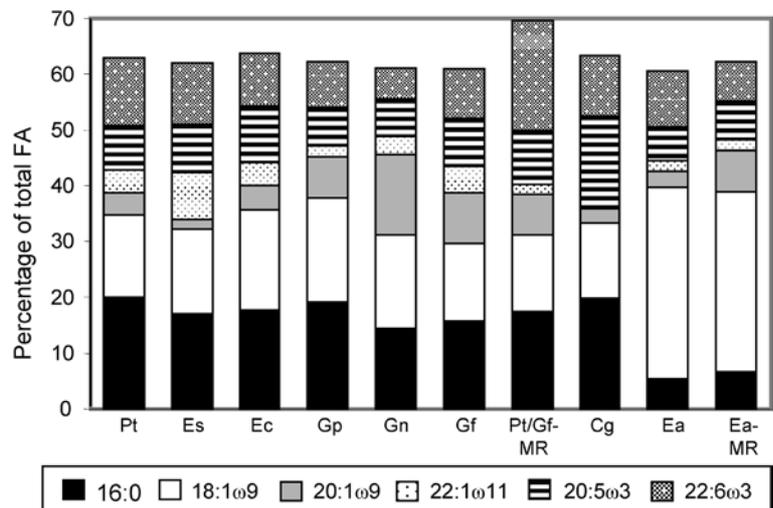
Table 5. Calorific content of seven species of myctophid fish and the mackerel icefish, *Champsocephalus gunnari*, from the Îles Kerguelen region

Species	n	Standard length (mm)	Wet mass (g)	Water content (%)	kJ g^{-1} dry mass	kJ g^{-1} wet mass
Protomyctophum tenisoni	1	45	0.9	74.6	24.2	6.1
Electrona subaspera	3	92.7 ± 7.5	11.8 ± 4.3	72.3 ± 1.6	26.6 ± 2.1	7.4 ± 1.0
Electrona antarctica	5	64.5 ± 8.6	3.2 ± 1.8	60.8 ± 8.8	34.3 ± 3.8	13.3 ± 2.6
Electrona carlsbergi	6	84.7 ± 3.6	8.7 ± 2.2	67.0 ± 3.2	25.9 ± 3.2	8.6 ± 1.2
Gymnoscopelus piabilis	5	187.6 ± 32.0	74.6 ± 30.7	68.5 ± 3.0	30.0 ± 2.6	9.5 ± 1.7
Gymnoscopelus nicholsi	1	128	22.0	66.8	28.0	9.8
Gymnoscopelus fraseri	5	66.2 ± 7.1	3.0 ± 1.7	62.6 ± 10.1	27.0 ± 2.9	10.2 ± 3.5
Champsocephalus gunnari	3	311.7 ± 16.1	130.1 ± 40.5	76.7 ± 2.0	23.2 ± 0.6	5.4 ± 0.3

all present in 300-m trawls during the day, whilst *E. subaspera* and *G. piabilis* (9.2 and 6.8% lipid, respectively) were only detected during night trawls, indicating they inhabit depths in excess of 300 m during the day (Duhamel et al. 2000). Further targeted sampling and lipid analyses are necessary to examine such a trend.

TAG was the primary lipid class in all species except *E. antarctica*, which was rich in WE (71.6–80.2% of total lipid). Specimens of *E. antarctica* from Elephant Island, the Antarctic Peninsula and East Antarctica were also found to be high in WE, which are thought to play a role in buoyancy and long-term energy storage (Reinhardt and van Vleet 1986; Phleger et al. 1997, 1999). Myctophids characterised by high levels of WE in the sub-Arctic generally tend to be stationary species, inhabiting deep water, and not undergoing the diurnal vertical migration typical of many myctophids (Seo et al. 1996). Our findings of WE-rich *E. antarctica* in surface waters of the Polar Frontal Zone (KP) and at Macquarie Ridge support the observations of Phleger et al. (1999) that both TAG-rich and WE-rich species are successful in all regions of the Antarctic Ocean.

In terms of calorific value, myctophids exhibit some of the highest values for any fish species. In this study, values ranged from 6.1 to 13.3 kJ g^{-1}WM for species from the Kerguelen Plateau. Tierney et al. (2002) reported similar values for Southern Ocean myctophids from the Macquarie Ridge (5.4–10.9 kJ g^{-1}), as have Cherel and Ridoux (1993) who recorded values of 7.0 and 8.1 kJ g^{-1} for *E. carlsbergi* and *Krefftichthys anderssoni*, respectively, from the Crozet Archipelago. *C. gunnari*, however, was relatively low in energy content (5.4 kJ g^{-1}WM) and more comparable to the calorific content of the majority of fish species eaten by Cape fur seals in South Africa (3.7–7.7 kJ g^{-1}), as studied by Balmelli and Wickens (1994). Squid, also a preferred food item of many Southern Ocean marine predators (Slip 1995; Rodhouse et al. 1996; Cherel and Weimerskirch 1999), are remarkably low in energy content when compared to the lipid-rich Myctophidae, with the majority of species ranging from 2.0 to 4.0 kJ g^{-1}WM (Croxall and Prince 1982).

Fatty acid and alcohol composition

MUFA composed the majority of FA of all myctophids (40.3–65.4%) from the Kerguelen Plateau, as was reported by Saito and Murata (1998) for 13 sub-Arctic species, who suggested that high monoene content be considered characteristic of this family. However, the two TAG-rich species from the Macquarie Ridge, *G. fraseri* and *P. tenisoni*, contained similar levels of MUFA and PUFA (33.8–37.4%), perhaps indicating a difference in dietary intake between the two regions. The levels of MUFA present in mackerel icefish more closely approximated those of myctophids from Macquarie Ridge than any species sampled from the Kerguelen Plateau, and were twofold higher than levels reported for specimens from Heard Island, further south on the Kerguelen Plateau (Nichols et al. 1994).

All fish contained relatively high levels of 16:0, 18:1ω9, 22:6ω3, 20:5ω3 and 20:1ω9 fatty acids. *G. nicholsi* contained notably higher levels of 20:1ω9 fatty acid than other species (14.5% cf. 1.8–9.1%). Raclot et al. (1998) found *G. piabilis* from the Crozet Archipelago to be rich in 20:1ω9, whereas in 1998 on the Kerguelen Plateau, *G. piabilis* was particularly high in 16:0 and 18:1ω9. Raclot et al. (1998) also reported that the major fatty acids in the four species of myctophid they studied (*G. piabilis*, *Lampichthys procerus*, *Metelectrona ventralis* and *P. bolini*) were consistently 18:1ω9, 16:0, 22:6ω3 and 20:1ω9.

The fatty acid composition of the nocturnally benthopelagic icefish differed from that of the myctophids, being high in 16:0, 16:1ω7, 20:5ω3 and 22:6ω3 fatty

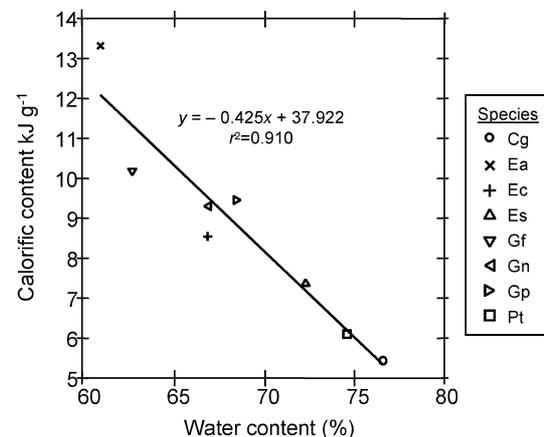**Fig. 5.** A regression of water and energy content (kJ g^{-1} wet mass) of seven species of myctophid and mackerel icefish from the Kerguelen Plateau. Legend as for Fig. 2

($y = -0.425x + 37.922$, $r^2 = 0.910$)

acids. The diet of *C. gunnari* at Kerguelen consists primarily of the crustacean, *Euphausia vallentini*, the hyperiid amphipod, *Themisto gaudichaudii*, and occasional fish (Duhamel 1987). The small proportion of WE (1.0%) recorded in the lipid composition of *C. gunnari* may represent the consumption of occasional *Electrona antarctica* or *G. braueri*, also high in WE (Phleger et al. 1999). *T. gaudichaudii* constitutes an important local component of the macrozooplankton community, where it is the main prey for many planktivorous seabirds inhabiting the Kerguelen Archipelago (Bocher et al. 2001). Nelson et al. (2001) reported high levels of 16:0, 20:5ω3 and 22:6ω3 fatty acids (51.7% of total fatty acids) in *T. gaudichaudii* from the Elephant Island region, Antarctica, as did Phleger et al. (1998). The presence of the diatom trophic-marker fatty acid 16:1ω7, as found in *C. gunnari*, is usually indicative of phytoplankton ingestion in zooplankton communities (Hagen et al. 2001). The cnidarian, *Calycopsis borchgrevinki*, and the chaetognath, *Sagitta gazellae*, both displayed high levels of 16:1ω7 in comparison to other zooplankton studied (Phleger et al. 1998). A recent study by Gurney et al. (2001) of the trophic position of euphausiids in the vicinity of the subantarctic Prince Edward Islands indicates that juveniles of *Electrona vallentini* are in fact herbivorous, which may explain the higher proportion of diatom-derived lipids found in *Champsocephalus gunnari* relative to other fishes analysed.

Trophic relationships and spatial variation in fatty acid composition

Myctophids primarily consume herbivorous zooplankton (Kozlov and Tarverdiyeva 1989), which include copepods, euphausiids and hyperiid amphipods. The diet may also be dependent upon intra-species variation in fish size; for example, smaller individuals of *Electrona antarctica* may subsist on a diet primarily composed of copepods and hyperiid amphipods while larger fish are capable of consuming euphausiids (Kozlov and Tarverdiyeva 1989).

It is clear from the results of this study that species of Myctophidae, while similar in general lipid composition, may be distinguished from each other on the basis of fatty acid composition. Variations observed represent real inter-species differences arising from dietary differences and, based on the use of common methodologies are, we believe, not artifacts due to sampling or analytical techniques. Saito and Murata (1998), in their study of the FA spectra of sub-Arctic myctophids and their prey, noted a relationship between the high monoene levels of myctophid stomach contents and their tissues, suggesting that prey lipids may be incorporated into tissue FA with little modification. Several species from the Kerguelen Plateau (*E. subaspera*, *G. nicholsi* and *G. fraseri*) contained particularly high levels of the fatty acids 20:1ω9 and 22:1ω11, which are indicative of a diet containing copepods (Dahl et al. 2000).

Specimens of a species collected from different sites may also vary significantly in their fatty acid composition, as was the case in this study where *P. tenisoni* and *G. fraseri* from the Kerguelen Plateau contained higher levels of lipid and different proportions of major fatty acids than conspecifics trawled on Macquarie Ridge. These differences may relate to variability in food availability between the sites (Fig. 2, Phleger et al. 1997) and/or to the age, size and condition of fish, as has been demonstrated by Wilson and Nichols (2001) for Patagonian toothfish, *Dissostichus eleginoides*. Proportions of 16:0, 16:1ω7, 22:1ω9 and 22:1ω11 FA (and 20:1ω9 in *G. fraseri*) were also higher in specimens inhabiting waters east of the Kerguelen Archipelago, while fish from the Macquarie Ridge contained higher levels of 20:5ω3 (EPA) and 22:6ω3 (DHA), which are known to be typical of crustaceans such as hyperiid amphipods and polychaetes (Phleger et al. 1998, 2000; Nelson et al. 2001). EPA and DHA are useful as biomarkers as they cannot be synthesised by marine zooplankton and must be obtained from the diet (Phleger et al. 2000).

Interestingly, the fatty acid and fatty alcohol profiles of *Electrona antarctica* from Kerguelen and the Macquarie Ridge, while appearing similar overall, differed in levels of 20:1ω9 fatty acid and alcohol, which were higher at Macquarie Ridge. Phillips et al. (2001) also noted 20:1ω9, along with 18:1ω9, as being the major fatty acids found in the squid, *Moroteuthis ingens*, at Heard and Macquarie Islands, and highlighted the existence of a copepod-myctophid-*M. ingens*-higher predator food chain. A similar food chain had previously been proposed for the ommastrephid squid, *Martialia hyadesi*, at South Georgia by Rodhouse et al. (1992). It would seem that copepods constitute an important dietary component of all three species sampled from Macquarie Ridge. *Electrona antarctica* is also known to be an important predator of krill (Greely et al. 1999), which are high in 18:1ω9 (Hagen et al. 2001). The notably high levels of 18:1ω9 found in specimens of *Electrona antarctica* from both the Kerguelen Plateau and Macquarie Ridge also confirm this trophic link.

Levels of 18:1ω9 fatty alcohol were higher in fish from the Kerguelen Plateau. Phleger et al. (1997), studying *Electrona antarctica* in the Antarctic, noted differences in fatty acid and alcohol composition for specimens from two locations. The same methodology was used in our study, indicating that real variation in composition is apparent between studies. Whether this relates to the size and age of specimens, the site or year of capture and associated dietary differences presently remains unclear.

Inter-annual shifts in fatty acid composition may also occur, as is evidenced by differences in profiles of mackerel icefish (*C. gunnari*) FA profiles from the same location, the vicinity of Heard Island, in the early 1990s (Nichols et al. 1994) and during this study. The combined level of the essential FA, EPA and

DHA was twofold higher in samples analysed by Nichols et al. (1994), with EPA/DHA composing 52.5% of fatty acids, while the specimens examined in this study contained considerably higher proportions of 16:1ω7 (11.5% cf. 4.3%) and 18:1ω9 (13.5% cf. 6.4%). It appears, based on the FA composition of fish examined in this study, that significant inter-annual variations in dietary composition may occur for *C. gunnari* on the Kerguelen Plateau. This could indicate higher proportions of hyperiid amphipods, such as *T. gaudichaudii*, may compose a large proportion of the diet in some years (e.g. elevated EPA and DHA), or in other years, crustaceans such as *Electrona vallentini*, the juveniles of which are known to be herbivorous (Gurney et al. 2001), may predominate. A recent study by Hunt et al. (2001) of the zooplankton community structure within the Polar Frontal Zone at the Prince Edward Islands confirms that the composition of zooplankton communities is highly spatially and temporally variable. Differences were due to hydrodynamic variability of the region, biological interactions and inter-annual variability in the timing of the biological season.

Conclusions

Myctophids constitute an important, energy-rich contribution to the diet of many Southern Ocean species and, to date, many studies examining their composition have been limited by access to specimens and resultant low sample sizes. The findings presented here provide a basis, through the use of a signature lipid approach, for greater understanding of trophic links and energy transfer in the Southern Ocean, particularly in sub-Antarctic regions. It is evident from this study that much spatial and temporal variability exists in the biochemical composition of high-latitude fish species and that further, broad-scale studies are required if we are to understand the links between more wide-ranging marine predators, such as whales and many seal species over the winter period, and their dynamic prey resources.

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