Energy content of mesopelagic fish from Macquarie Island

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Abstract: The water and calorific content of fifteen species of mesopelagic sub-Antarctic fish from Macquarie Island were determined. Mean percent water content was 69–82%. Calorific content was highly variable between species, especially in the Myctophidae, where it ranged between 22.6–59.3 kJ·g^{-1} dry weight. The water and calorific content varied with size class within a species, with the smallest size classes generally having the lowest water content but highest calorific content. These values will be useful for future assessment of energetic transfer between trophic levels and energetic modelling of Southern Ocean ecosystems.

Introduction

Historically, the Southern Ocean has been described as a simple marine system consisting of a three-part linear food chain of diatoms–krill–consumers (for example Tranter 1982 in Clarke 1985). Recently, studies have revealed that the Southern Ocean is a much more complex and dynamic entity than previously believed. In some sectors of the Southern Ocean, for example in the South Atlantic, food webs are krill-based (Croxall *et al.* 1985, Ichii *et al.* 1996, Croll & Tershy 1998), whilst in others, particularly in the South Indian and Pacific sectors, it appears that fish and cephalopods play a more important role in the food web than pelagic crustaceans (e.g. Woehler & Green 1992, Adams *et al.* 1993, Guinet *et al.* 1996, Green *et al.* 1998, Goldsworthy *et al.* 2001). A common limitation to many food web models, however, is an inability to map energy flow through the system (Woehler & Green 1992). This is due, in part, to a paucity of existing data on the energy density of key Southern Ocean prey items that support higher order predators such as seals, seabirds, and cetaceans.

Reliable data on the energy density of prey species is essential for determining food and energy requirements for different components of the food web, in order to understand their role in the marine environment. In turn, this information can be used in management and conservation studies, particularly those concerned with the conservation of higher order predators and the potential impact of commercial fisheries on these populations (e.g. Balmelli & Wickens 1994, Mårtensson *et al.* 1996, Moore *et al.* 1998, Goldsworthy *et al.* 2001).

Energy density, or calorific value, has been calculated for a number of species of Southern Ocean squid (Clarke &

Prince 1980, Clarke 1985, Croxall *et al.* 1985, Cherel & Ridoux 1992) and fish (Clarke & Prince 1980, Cherel & Ridoux 1992, Gales *et al.* unpublished data in Green & Gales 1990), but studies are few and most have been based on small sample sizes (generally less than five). Some of these studies (Clarke & Prince 1980, Croxall & Prince 1982, Cherel & Ridoux 1992), and others on different species elsewhere (e.g. Balmelli & Wickens 1994, Mårtensson *et al.* 1996, Vondracek *et al.* 1996, Paul *et al.* 1998), have found that energy density can differ substantially between species, and even change within a species. These have been attributed to differences in relative status (size, age, reproductive state) and/or seasonal or geographical differences and influences. If these differences in calorific value of prey are not accounted for it can have serious repercussions on resultant energetic models. For example, Mårtensson (1996) determined that the food consumption estimates of minke whales in the north-east Atlantic, over the summer period, made by a previous study, should be increased by 10–15% (equating to *c*. 300 000 tonnes of food), based on a revision of prey calorific density. Therefore accurate measures of prey energy density for a range of species are important in generating realistic models of energy flow in marine ecosystems.

Here we present data on the water and calorific content of fifteen species of mesopelagic, sub-Antarctic fish, from the waters around Macquarie Island in the South Pacific Ocean. We also compare the water and calorific content of these species between different size classes, because these values may change within a species due to status (Croxall & Prince 1982, Sato *et al.* in Croxall & Prince 1982, Mårtensson *et al.* 1996, Paul *et al.* 1998), and because some predators are known to consume prey of significantly different size

Table I. Size class ranges (standard length, mm) for each species of fish used to calculate water and calorific content.

Species	Minimum[†]	Size class (mm) Small ≤	Medium ≥–≤	Large ≥	Maximum[†]	Total *n*
Moridae						
Antimora rostrata (Günther)	227	-	-	-	255	2
Bathylagidae						
Bathylagus antarcticus (Günther)	57 (73)	89	90–120	121	196	30
Myctophidae						
Electrona antarctica (Günther)	30	40	41–54	55	73	30
Electrona carlsbergi (Taning)	26 (87)	-	-	-	97	10
Electrona subaspera (Günther)	70	-	-	-	117	6
Gymnoscopelus braueri (Lönnberg)	37	59	60–104	105	133	28
Gymnoscopelus fraseri (Fraser-Brunner)	35	49	50–64	65	78	30
Gymnoscopelus microlampus (Hulley)	84 (102)	-	-	-	122	10
Krefftichthys anderssoni (Lönnberg)	40	46	47–56	57	69	50
Lampanyctus archirus (Andriashev)	35	69	70–99	100	147	30
Protomyctophum andriashevi (Bekker)	23	30	-	45	51	18
Protomyctophum bolini (Fraser-Brunner)	29	39	40–51	52	61 (59)	30
Protomyctophum parallelum (Lönnberg)	20 (29)	-	-	-	48	10
Protomyctophum tenisoni (Norman)	43 (45)	-	-	-	51	10
Stomiidae						
Stomias gracilis (Garman)	130 (165)	194	195–249	250	278	30

[†]Numbers in parentheses indicate the minimum or maximum size of fish used for calorimetry, when different from that used to calculate percent water content.

classes at different times of the year (Hindell 1988, 1989, Daneri & Coria 1993, Balmelli & Wickens 1994, Goldsworthy *et al.* 1997).

Methods

Mesopelagic fish samples were collected from pelagic mid-water (top 1000 m) trawls (MIDOC multiple codend) undertaken by the Australian Commonwealth Science and Industrial Research Organization (CSIRO) Marine Research vessel RV *Southern Surveyor* in January 1999, in the vicinity of Macquarie Island and the Macquarie Ridge between 53°S–56°17'S and 158°30'E–159°30'E (see CSIRO Marine Research Cruise Report SS 01/99 for full details). The fish were frozen at -20°C immediately after capture, and later identified to species level in the laboratory. Where sufficient numbers of any particular species were available, samples were divided into three size classes (large, medium or small), based on standard length (tip of the snout to the end of the caudal vertebrae) (Cullen *et al.* 1992) (Table I).

Dry mass was taken after each fish had been completely desiccated (determined by having a constant mass) in a drying oven set at 60°C. Water content of each fish was calculated by the difference between wet and dry mass (± 0.0001 g), and then expressed as a percentage of original mass. It should be noted that the wet mass values are minimalistic due to any possible desiccation of samples during the freezing process.

Calorific value (kJ·g^{-1} dry mass) of each fish was determined by ballistic bomb calorimetry (custom made, University of Tasmania). Either the whole fish or a homogenized sub-sample (0.55g–0.62 g) of the fish was used in the calorimeter. Benzoic acid was used for calibration.

Mean percent water content (± SD) and mean calorific value (± SD) was calculated for each species, and size class

Table II. Mean (± SD) water (%) and mean (± SD) calorific (kJ·g^{-1} dry weight) content for each species of fish analysed.

Species	Mean water content ± SD (%)	Mean calorific content ± SD (kJ·g^{-1})	*n**
Moridae			
Antimora rostrata	80.1 ± 1.0	21.8 ± 2.3	2 (2)
Bathylagidae			
Bathylagus antarcticus	81.8 ± 1.8	21.5 ± 5.0	30 (18)
Myctophidae			
Electrona antarctica	69.9 ± 4.3	30.8 ± 9.7	30 (20)
Electrona carlsbergi	76.7 ± 5.2	21.7 ± 3.2	10 (6)
Electrona subaspera	72.1 ± 1.7	26.6 ± 1.15	6 (6)
Gymnoscopelus braueri	70.0 ± 7.1	39.0 ± 14.3	28 (18)
Gymnoscopelus fraseri	73.1 ± 4.0	29.3 ± 8.6	30 (18)
Gymnoscopelus microlampus	74.7 ± 1.3	22.6 ± 1.1	10 (6)
Krefftichthys anderssoni	69.8 ± 1.9	27.5 ± 2.8	50 (18)
Lampanyctus archirus	78.5 ± 3.4	28.5 ± 14.4	30 (18)
Protomyctophum andriashevi	75.7 ± 5.3	39.3 ± 21.5	18 (12)
Protomyctophum bolini	73.5 ± 3.9	28.0 ± 10.6	30 (18)
Protomyctophum parallelum	70.9 ± 3.6	28.3 ± 12.3	10 (6)
Protomyctophum tenisoni	73.2 ± 1.1	20.5 ± 0.7	10 (6)
Stomiidae			
Stomias gracilis	77.8 ± 3.1	23.2 ± 3.0	30 (18)
Total	74.1 ± 5.6	28.4 ± 11.1	324 (190)

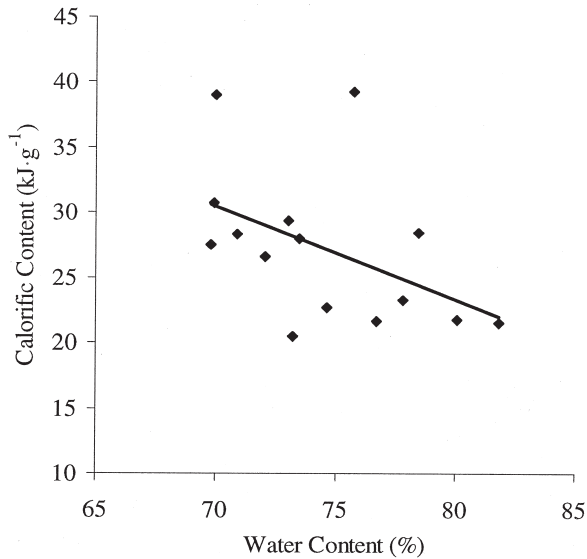*Numbers in parentheses indicates sample size used to determine calorific value

Fig. 1. Relationship between mean water content (%) and mean calorific value (kJ·g⁻¹) of all species analysed.

within a species, where applicable. Regression analysis (Zar 1984) was performed to investigate the relationship between mean energy content (kJ·g⁻¹) and mean water content (%) across all species on log-transformed data. We used Monte Carlo randomizations (Manly 1997) to test for differences between size classes within each species for water and calorific content. In each case, 10 000 random iterations (of the data set) were compared for each size class. For these tests, the *P*-value was equal to the proportion of iterations where differences were found. A significance value of $P < 0.05$ was set.

Results

Species analysis

Water content
The mean percent water content for each species was variable, ranging between 69.8% ± 1.9 (*Krefftichthys anderssoni*) and 81.8% ± 1.0 (*Bathylagus antarcticus*) water, with an average of 74.1% ± 5.6 (Table II). All

Table III. Mean (± SD) water (%) and mean (± SD) calorific (kJ·g⁻¹ dry weight) content for each size class (within a species) analysed. Significant differences ($P < 0.05$) between size classes within a species are indicated in bold.

Species	Size class	Water content (%)		Calorific content (kJ·g⁻¹)		$n^{\dagger}$
		Mean ± SD	P	Mean ± SD	P	
Moridae						
Bathylagus antarcticus	large	80.5 ± 2.5	**0.0072**	21.9 ± 8.8	0.8181	10 (6)
	medium	82.8 ± 0.5		20.3 ± 0.6		10 (6)
	small	82.1 ± 0.9		22.1 ± 0.7		10 (6)
Myctophidae						
Electrona antarctica	large	66.3 ± 1.1	**< 0.0001**	31.4 ± 2.6	**0.0415**	10 (6)
	medium	69.1 ± 3.3		25.8 ± 4.0		10 (7)
	small	74.4 ± 2.9		35.3 ± 15.6		10 (7)
Gymnoscopelus braueri	large	62.9 ± 1.5	**< 0.0001**	30.4 ± 1.4	**0.0001**	10 (6)
	medium	66.1 ± 2.3		29.2 ± 3.5		8 (6)
	small	80.2 ± 4.0		57.5 ± 8.3		10(6)
Gymnoscopelus fraseri	large	71.1 ± 2.4	0.1849	28.2 ±2.7	**0.0011**	10 (6)
	medium	74.6 ± 1.4		21.7 ± 1.9		10 (6)
	small	73.5 ± 6.2		38.1 ± 8.8		10 (6)
Krefftichthys anderssoni	large	70.3 ± 1.7	0.3487	28.7 ± 4.1	0.2823	20 (6)
	medium	69.2 ± 2.2		27.7 ± 1.9		20 (6)
	small	69.9 ± 1.7		26.2 ± 1.1		10 (6)
Lampanyctus archirus	large	76.7 ± 2.9	**0.0033**	26.9 ±2.4	**0.0022**	10 (6)
	medium	81.1 ± 1.7		19.0 ± 1.0		10 (6)
	small	77.6 ± 3.6		39.5 ± 16.2		10 (6)
Protomyctophum andriashevi	large	73.2 ± 1.4	0.2316	20.1 ± 2.6	**< 0.0001**	10 (6)
	medium	-		-		-
	small	78.9 ± 6.6		58.4 ± 11.4		8 (6)
Protomyctophum bolini	large	70.5 ± 1.2	**0.0001**	23.4 ± 1.2	**< 0.0001**	10 (6)
	medium	73.1 ± 1.8		20.9 ± 1.3		10 (6)
	small	76.9 ± 4.6		39.7 ± 11.7		10 (6)
Stomiidae						
Stomias gracilis	large	76.8 ± 3.7	**0.0250**	23.3 ± 2.9	0.7104	10 (6)
	medium	76.8 ± 2.5		24.8 ± 2.5		10 (6)
	small	79.9 ± 2.0		21.5 ± 3.9		10 (6)

†Numbers in parentheses indicates sample size used to determine calorific value

Table IV. Comparison of water (%) and calorific (kJ·g^{-1}) content (both wet and dry weight, where available) determined for fish in this study, with those available in the literature.

Species	This study				Clarke & Prince (1980)			Cherel & Ridoux (1992)				Green & Gales (1990)		Lea *et al.* (unpublished data)			
	water content %	dry weight kJ·g^{-1}	wet weight kJ·g^{-1}	n[†]	water content %	wet weight kJ·g^{-1}	n	water content %	dry weight kJ·g^{-1}	wet weight kJ·g^{-1}	n	wet weight kJ·g^{-1}	n	water %	dry weight kJ·g^{-1}	wet weight kJ·g^{-1}	n
Electrona antarctica	69.9	30.76	9.04	20 (30)	-	-	-	-	-	-	-	9.11	6	60.8	34.3	13.3	5
Electrona carlsbergi	76.7	21.67	5.37	6 (10)	71.23	6.57	3	70.2	23.5	7.00	3	-	-	67.0	25.9	8.6	6
Electrona subaspera	72.1	26.56	7.42	6 (6)	-	-	-	-	-	-	-	-	-	72.3	26.6	7.4	3
Gymnoscopelus braueri	70.0	39.03	10.91	18 (28)	66.10	9.06	3	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus fraseri	73.1	29.32	8.26	18 (30)	-	-	-	-	-	-	-	-	-	62.6	27.0	10.2	5
Krefftichthys anderssoni	69.8	27.54	8.36	18 (50)	-	-	-	69.3	26.4	8.10	2	10.12	5	-	-	-	-

[†]Numbers in parentheses indicates sample size used to determine calorific value

myctophid species had similar percent water contents, ranging between 69.8% ± 1.9 and 78.5% ± 3.4.

Calorific content
Calorific content (kJ·g^{-1}), calculated on a dry mass basis, was variable, ranging from 22.5 ± 5.0 kJ·g^{-1} (*Bathylagus antarcticus*) up to 39.3 ± 21.5 kJ·g^{-1} (*Protomyctophum andriashevi*) (Table II). The average across all species was 28.4 ± 11.1 kJ·g^{-1}. Calorific content within the Myctophidae was highly variable, incorporating both the highest and second lowest values recorded. There was a significantly negative relationship between the mean energy content and the mean water content for each species (data log transformed: $F_{1,13} = 6.861$, $P = 0.021$, $r^2 = 0.345$, n = 15; Fig. 1).

Size comparison

Water content
Percent water content was significantly different between size classes in six of the nine species analysed (Table III). Generally the percentage water content decreased with increasing size for those species with water content differences between size classes.

Calorific content
Calorific value (kJ·g^{-1}) was also significantly different in six of the nine species (Table III), although some of these differed from those that had significantly different percent water contents. The calorific contents between size classes in five of these six species (*G. braueri, G. fraseri, Lampanyctus archirus, P. andriashevi,* and *P. bolini*) were strongly significant ($P < 0.0001$, $P = 0.0011$, $P = 0.0022$, $P < 0.0001$, and $P < 0.0001$, respectively). The smallest size classes had the highest calorific values for all species where there was a significant difference between size classes.

Discussion

The range of calorific values varied considerably (20.5–39.3 kJ·g^{-1}) between species, confirming the need to use species-specific values for energy density when calculating energy consumption or energy flow rates in marine ecosystems. Even within a single family (e.g. the Myctophidae) mean calorific content varied twofold between species. Several of these species, for example *K. anderssonii, E. antarctica* and *G. braueri* would be a rich energy source for predators, (with 27.5 kJ·g^{-1}, 30.8 kJ·g^{-1}, and 39.0 kJ·g^{-1}, respectively), and are known to feature predominantly in the diet of some seals (Daneri & Coria 1993, Green & Burton 1993, Slip 1995, Goldsworthy *et al.* 1997) and seabirds (Clarke & Prince 1980, Croxall *et al.* 1985, Hindell 1988, 1989, Cherel & Ridoux 1992, Moore *et al.* 1998).

As with the inter-specific differences in energy content, the intra-specific differences also varied as much as twofold (e.g. *P. bolini, G. braueri, P. andriashevi,* and *G. fraseri*), introducing another level of complexity when attempting to use the most appropriate values for energy based calculations. For most species, smaller size classes had both a higher water (%) and calorific (kJ·g^{-1}) content. This is in contrast to other studies (Mårtensson *et al.* 1996, Paul *et al.* 1998), where larger fish tended to have high calorific content. Determining why these trends exist is beyond the scope of this study, but we suggest (as has been found in other studies e.g. Balmelli & Wickens 1994, Mårtensson *et al.* 1996, Vondracek *et al.* 1996, Paul *et al.* 1998) that both inter- and intra-specific differences in calorific content, are most likely associated with seasonal changes in chemical composition, particularly lipid content, which may be due, in turn, to reproductive status, age or condition. It is now possible, by identifying and measuring fish otoliths, to determine the size, and therefore approximate age and/or reproductive status of some prey items taken from diet samples of predators (Hecht 1987, Williams & McEldowney 1990, Adams *et al.* 1993, Reid 1996).

Therefore, having energy density values for particular size classes, as opposed to a single value for a whole species, may assist in making studies of energetic requirements and transfer through the ecosystem more realistic, particularly where predators are known to target prey of different sizes at different times of the year. It should be noted, though, that the data presented here, represents a 'snapshot' of the energy density of these species in one place and time. Further analysis of samples collected over a number of different seasons, and from different locations are required to gauge how the energy content of these prey species many change both temporally and spatially. Measuring parameters of age, condition and reproductive status of each sample will also enable a more detailed insight into any variability detected in the data.

There are few comparative studies available that have analysed Southern Ocean species of fish for water and calorific content, and none have compared these values between different size classes. However, water (%) and calorific (kJ·g^{-1}) content obtained in this study for *E. antarctica*, *E. carlsbergi*, *G. braueri*, and *K. anderssoni* were similar to those determined by Clarke & Prince (1980), Cherel & Ridoux (1992), and Gales *et al.* (unpublished data in Green & Gales 1990) (Table IV). In comparison to those analysed by Lea *et al.* (unpublished data) from Îles Kergeulen, the samples in this study generally had considerably lower energy densities, except those for *E. subaspera* (Table IV). Differences between the present study and others may be attributable to a number of factors, including size (which was not reported in these other studies, except for Lea *et al.* unpublished data), age, reproductive state, or sample size. Geographic variation, particularly for samples collected in the same season, may also account for differences observed. For example, the same species of fish may exhibit different energy densities between regions due to differences in their diet. These factors should be taken into account, or at least acknowledged, if energy density values of a species from one region are used for energy based calculations in another location.

The data presented here should be useful to future trophodynamic modelling of the Southern Ocean marine ecosystems. This information can, in turn, be used for future management and conservation issues and research.

Acknowledgements

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