Proximate composition of Antarctic mesopelagic fishes

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Abstract. Eleven mesopelagic fish species from the Weddell/Scotia Sea region of the Antarctic captured during the austral spring 1983, austral fall 1986, and austral winter 1988, were analyzed for proximate composition. Water, ash level, protein, lipid and carbohydrate were examined in relation to depth of occurrence and season. No depth-related trends were evident, primarily due to a low species diversity and minimal differences in those species' vertical distributions. The Antarctic species *Electrona antarctica* showed a significant increase in lipid level (% wet wt and % ash-free dry wt) between spring, fall and winter. The increase may signify an accumulation over the productive season, possibly as a reserve for the winter months. Lipid levels (% wet wt and % ash-free dry wt) were significantly lower in the Weddell Sea specimens examined in this study than in previously examined identical and congeneric species taken during the same season from a more productive near-shore Antarctic region. Comparisons with congeners and confamilials from tropical-subtropical and temperate systems revealed variable trends. The Antarctic species *E. antarctica* and *Cyclothone microdon* had lower water and protein (% wet wt) levels than similar species from tropical-subtropical or temperate regions. Lipid levels of the two species are similar to temperate individuals, while energy levels are slightly higher. In contrast, species of the genus *Bathylagus* show no trends in composition as a function of latitude. Differences in productivity, water-column temperature-structure, and seasonality are important considerations when examining trends among mesopelagic species.

Introduction

Compositional analyses of marine organisms provide a time-integrated set of attributes useful in evaluating a species' relationship with its habitat. In the short term, oscillations in compositional parameters can be indicative of changing nutritional or reproductive status (Love

1970). Short-term changes overlay a set of compositional characters that are habitat-specific.

Mesopelagic fishes show variability in proximate composition as a function of depth of occurrence (Childress and Nygaard 1973) and as a function of regional productivity (Bailey and Robison 1986). Deeper-living species (>200 m) contain a higher percentage of water than surface-dwelling counterparts, resulting in a predictable decline in protein (% wet wt) and lipid (% wet wt) with increasing depth of occurrence (Childress and Nygaard 1973). Individuals dwelling in oligotrophic regions exhibit higher protein levels (% wet wt) and lower lipid levels (% wet wt) than do members of the same species in areas of higher productivity (Bailey and Robison 1986). The trend toward higher protein level and lower lipid level demonstrated in Pacific mesopelagic fishes inhabiting the oligotrophic central gyre (Bailey and Robison 1986) has been corroborated by recent work in the Gulf of Mexico, an oligotrophic community with very different species make-up (Stickney and Torres 1989).

Mesopelagic fishes provide an excellent forum for examining latitudinal trends in chemical composition. Many of the midwater fish families enjoy a virtually world-wide distribution and analogous species within the families occupy similar niches in widely disparate regions. Yet, the pelagial is subject to latitudinal variation in temperature and seasonality in production, as are nearshore regions.

Classical midwater-fish families such as the Myctophidae, Gonostomatidae, and Bathylagidae are important components of the Southern Ocean ecosystem (Andriashev 1965, DeWitt 1970, Lancraft et al. 1989). Within the Weddell Sea pelagial, six species (*Bathylagus antarcticus, Cyclothone microdon, Electrona antarctica, Gymnoscopelus braueri, G. opisthopterus,* and *Notolepis coatsi*) account for greater than 95% of the biomass of mesopelagic fishes in the upper 1000 m (Lancraft et al. 1989). In the present study, we examine the proximate composition of the six species in relation to season and to minimum depth of occurrence (MDO, i.e., that depth below which 90% of the population lives; Childress and
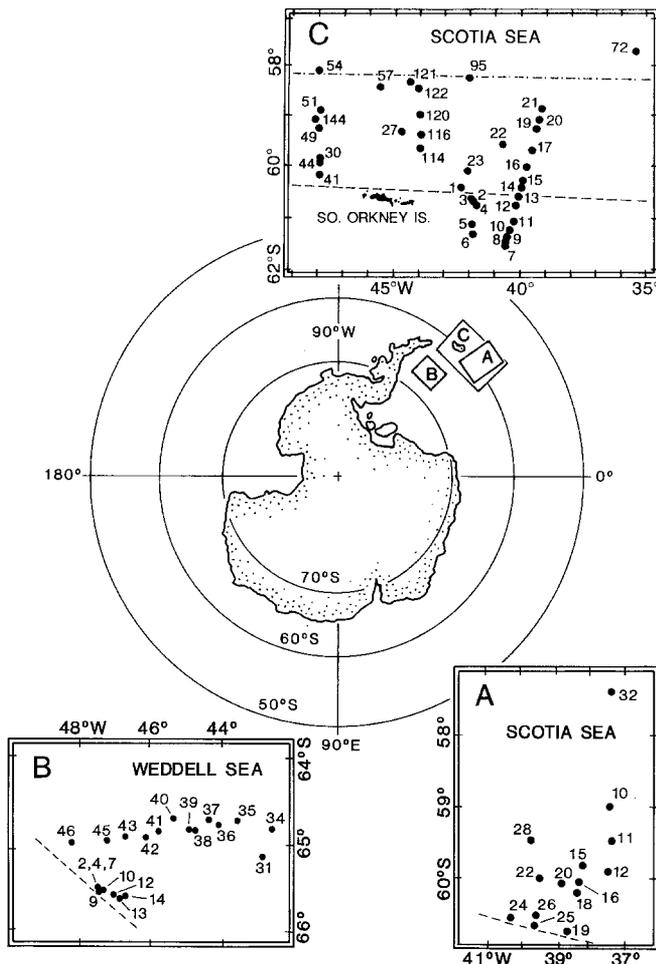
Fig. 1. Marginal ice-zone sampling locations in (A) southern Scotia Sea, November–December 1983; (B) northwest Weddell Sea, March 1986; (C) southern Scotia Sea, June–August 1988. Numbers in Insets A and B indicate open-water station locations; and in C, station locations for all three habitats (open-water, ice-edge and pack-ice); in A and B, dashed line indicates approximate relative location of ice-edge; in C, dashed line indicates approximate minimum and dot-dashed line maximum ice-edge locations

Nygaard 1973). Comparisons are made with mesopelagic species from tropical and temperate systems.

Materials and methods

Sample collection

Specimens were collected during three cruises, one in November–December 1983, one in March 1986, and one in June–August 1988, as part of the AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone) program. Concomitant with the seasonal movement of the pack-ice edge, sampling locales were different for the three cruises. In the austral spring (1983) and winter (1988), sampling was conducted in the southern Scotia Sea. During the austral fall (1986), sampling was conducted in the northwest Weddell Sea (Fig. 1).

Sampling was conducted in the upper 1 000 m with both an opening-closing Tucker trawl (9 m^2 mouth area in 1983 and 1986; 2.25 m^2 mouth area in 1988) and a vertically-towed, opening-closing Plummet net (1 m^2 mouth area). Trawling procedures are described in detail in Lancraft et al. (1989).

On board, specimens were identified to species, measured to the nearest millimeter standard length, blotted dry, and individually sealed in either plastic freezer bags or polypropylene snap-cap vials and kept frozen at −20 °C until analysis in the laboratory. Prior to laboratory analysis, individual specimens were remeasured to the nearest millimeter and weighed to the nearest 0.001 g. Since the fishes were blotted dry before freezing, any water produced upon thawing was considered as part of the wet weight. Each fish was first cut up and then homogenized in a Brinkman Polytron homogenizer, with distilled water added to make a slurry of approximately 25 mg dry wt ml^{-1}. The slurry was transferred to a glass tissue-grinder for final homogenization. Samples were dispensed immediately from the slurry for the specific analyses.

Dry weight, ash-free dry weight and skeletal ash

Two samples of 0.4 ml were dispensed into individual, preweighed crucibles and dried at 60 °C to a constant weight. After weighing, samples were combusted at 500 °C for 3 h. Samples were reweighed to determine ash weight and ash-free dry weight (AFDW). Skeletal ash was determined by subtracting the estimated solute ash from the total ash. Solute ash was estimated by assuming that the internal fluids of the fishes had an ionic strength of 40% seawater, or 1.4% by weight, and that these salts would be left behind as ash after combustion. The ionic strength is equivalent to a solute concentration of 430 mM l^{-1}, a midrange value for marine teleosts (Holmes and Donaldson 1969). Intracellular and extracellular fluids were assumed to be isosmotic (Prosser 1973); any differences in concentration of inorganic solutes between intra- and extracellular fluids caused by organic molecules were assumed to be negligible.

Protein

One sample of homogenate per species (0.1 ml; 2.5 mg dry wt) was diluted 1:10 into deionized water, mixed, and 0.1 ml was placed into each of three test tubes for protein analysis. Samples were increased to 0.2 ml vol using deionized water; the standard (Sigma; human albumin and globulin) was treated in an identical manner. Samples and standards were hydrolyzed by adding 0.3 ml of 0.1 N NaOH to each tube and then heating at 100 °C for 10 min. The method of Lowry et al. (1951) was used for protein determination.

Lipid

Lipids were extracted from three 0.2 ml (5.0 mg dry wt) samples of homogenate according to the method of Bligh and Dyer (1959). Extracts were dried at 30 °C under a flow of nitrogen, and were analyzed for lipid content using the charring method of Marsh and Weinstein (1966), with stearic acid as the standard.

Carbohydrate

Two 0.4 ml (10 mg dry wt) samples each were dispensed into preweighed 5 ml centrifuge tubes and dried at 60 °C to a constant weight. The samples were washed consecutively with acetone and ether to remove lipids and re-dried. Trichloroacetic acid (10%) was added, and the samples were heated at 100 °C for 20 min to allow hydrolysis. The supernatant was analyzed for carbohydrate using the method of DuBois et al. (1956), with D-glucose as the standard.

Caloric content

Approximate caloric values were calculated using the following conversion factors: protein, 5.7 kcal g^{-1}; lipid, 8.7 kcal g^{-1}; carbo-

hydrate, 4.1 kcal g^{-1} (Brett and Groves 1979). Energetic density was calculated from these values by assuming 1 cal = 4.19 J.

Data presentation

Protein, lipid and carbohydrate components are expressed both as percent wet weight (% wet wt) and percent ash-free dry weight (% AFDW). Expressed as % wet wt, values show partitioning of components within the whole individual; expressed as % AFDW, values reflect compositional partitioning within the organic content of the individual. Minimum depth of occurrence values were determined from day and night vertical distributional ranges tabulated from both 1983 and 1986 cruises (Lancraft et al. 1989).

General variations in proximate composition were examined using only the 1986 data set. Data from 1983 and 1988 are addressed in "Results – Seasonal variations".

Results

Water level

Water level (as % wet wt) ranged from 59.6% in *Gymnoscopelus nicholsi* to 85.9% in *Bathylagus antarcticus* (Table 1). A regression of percent water on minimum depth of occurrence showed no significant trend (Student's t-test, $P < 0.50$).

Ash-free dry weight and skeletal ash

Ash-free dry weight (as % dry wt) showed no trends with depth. Values ranged from 81.9 to 97.1% and are in the range of values reported for temperate species (Childress and Nygaard 1973, Bailey and Robison 1986). Skeletal ash (% wet wt) ranged from 0.2% for *Cyclothone microdon* to 2.9% for *Gymnoscopelus braueri*. Skeletal ash values are within the range of values reported for temperate species (Childress and Nygaard 1973). No significant (Student's t-test, $P > 0.05$) changes in skeletal ash with depth were found.

Protein

Protein content showed no trends with depth of occurrence either as % wet wt or % AFDW. Values (as % wet wt) ranged from 5.8% for *Bathylagus antarcticus* to 12.1% for *Cyclothone microdon*. Values as % AFDW ranged from 28.6% for *Gymnoscopelus nicholsi* to 66.5% for *B. antarcticus*. For all species examined, protein content (% AFDW) showed a strong inverse correlation with lipid. Variability among sample replicates was uniformly less than 5% of the mean.

Lipid

Lipid (% wet wt) ranged from 0.8% for *Bathylagus antarcticus* to 23.9% for *Gymnoscopelus nicholsi*. As % AFDW, values ranged from 6.3% for *B. antarcticus* to 64.7% for *G. nicholsi*. Lipid, expressed either as % wet wt

or % AFDW, showed no trend with depth of occurrence. Between-replicate variability for individual lipid samples was less than 10% of the mean value.

Carbohydrate

Carbohydrate (% wet wt and % AFDW) showed no trends with depth. Values were consistently low, ranging from 0.1 to 0.2% wet wt and 0.2 to 1.0% AFDW. Replicate variability was less than 15% of the mean.

Energy level

Energy level expressed as kJ 100 g^{-1} wet wt showed no trends with depth of occurrence. Values ranged from 172 to 1 175 kJ 100 g^{-1} wet wt. Nine of the eleven species examined had caloric values > 420 kJ 100 g^{-1} wet wt, indicating that they are high-energy food items. In all cases, recovery of organic matter was less than 100% of the AFDW ($x = 78.5 \pm 8.8$). Comparisons with data from other authors are made only on the basis of recovered organic matter (Table 6). However, corrected energy levels for all species are provided (Table 1) based on the assumption that any unrecovered organic matter is due to refractory protein (Sibuet and Lawrence 1981).

Composition and size

Two species, *Bathylagus antarcticus* and *Electrona antarctica*, had large size ranges and were broken down into size groups for resolution of possible size-related changes in water, protein and lipid (Tables 2 and 3). Variability between size groups was examined using one-way analysis of variance with significance at $P < 0.05$. For *B. antarcticus*, the general trend was of decreasing protein (% wet wt and % AFDW) with increased size and increasing lipid (% wet wt and % AFDW) and water with increased size. For *E. antarctica*, both water and protein (% wet wt and % AFDW) showed a decreasing trend, while lipid (% wet wt and % AFDW) increased with increased size. For both species, the respective patterns were consistent within individual years, although not significantly so in all cases.

As a consequence of the observed changes in water, protein and lipid content with increased size for both species, regional and latitudinal comparisons were made using only values from the larger size classes.

Seasonal variations

Variations in proximate composition between spring (Scotia Sea), fall (Weddell Sea) and winter (Scotia Sea) were examined in two species, *Bathylagus antarcticus*, and *Electrona antarctica*. Although individuals of *Gymnoscopelus braueri* were analyzed from all three cruises, the limited sample size in 1983 (spring) and 1986 (fall) precludes any rigorous examination of seasonal

Table 1. Standard lengths (SL), wet weights and proximate composition for Antarctic mesopelagic fishes. Where applicable, data for austral spring 1983, fall 1986, and winter 1988 are given. MDO: minimum depth of occurrence. AFDW: ash-free dry weight. SA: skeletal ash. Standard deviations are given in parentheses.

Species, year	(n)	MDO (m)	SL, mm (range)	Wet wt, g (range)	% H₂O	AFDW (% dry wt)	SA (% wet wt)	Protein % wet wt	Protein % AFDW	Lipid % wet wt	Lipid % AFDW	Carbohydrate % wet wt	Carbohydrate % AFDW	kcal 100 g⁻¹ wet wt	kJ 100 g⁻¹ wet wt	kJ 100 g⁻¹ wet wt (corrected)
Bathylagus antarcticus																
1983	(8)	170	99.4 (44–145)	5.82 (0.2–11.9)	85.1 (2.1)	85.1 (2.3)	1.0 (0.4)	7.6 (1.1)	62.9 (14.5)	0.8 (0.3)	6.3 (2.0)	0.1 (0.0)	0.5 (0.2)	53	220	312
1986	(32)	170	77.2 (32–143)	3.78 (0.1–23.9)	85.9 (2.0)	83.9 (5.)	1.2 (0.8)	7.7 (1.1)	66.5 (5.6)	0.9 (0.3)	8.1 (3.0)	0.1 (0.0)	0.7 (0.2)	53	224	294
1988	(16)	300	90.0 (51–150)	7.77 (0.8–37.7)	88.4 (1.4)	81.9 (1.9)	0.9 (0.3)	5.8 (0.7)	62.3 (2.1)	0.8 (0.3)	8.5 (3.0)	0.1 (0.0)	0.7 (0.1)	41	172	237
Benthalbella elongata																
1988	(2)	–ᵃ	248.5 (245–252)	97.60 (95–99.8)	77.0 (8.4)	90.8 (3.5)	0.7 (0.1)	6.6 (1.8)	34.5 (4.5)	9.8 (4.4)	47.3 (3.0)	0.1 (0.0)	0.3 (0.1)	127	533	623
Cyclothone microdon																
1986	(4)	500	60.5 (57–64)	1.04 (0.8–1.2)	67.0 (1.6)	97.1 (1.0)	0.2 (0.2)	12.1 (0.7)	39.4 (3.8)	10.4 (1.2)	33.8 (2.7)	0.1 (0.0)	0.4 (0.0)	167	699	901
1988	(4)	500	56.5 (51–67)	0.90 (0.7–1.4)	66.9 (2.2)	90.5 (1.5)	2.2 (0.3)	10.4 (0.8)	35.7 (2.4)	15.4 (1.7)	52.7 (4.0)	0.1 (0.1)	0.4 (0.1)	199	832	913
Electrona antarctica																
1983	(16)	5	66.1 (33–98)	3.80 (0.6–9.7)	69.0 (3.7)	92.0 (3.3)	1.5 (0.9)	10.6 (0.9)	38.1 (3.3)	8.9 (2.3)	31.3 (4.6)	0.1 (0.0)	0.4 (0.1)	140	586	793
1986	(27)	5	61.9 (29–101)	3.89 (0.3–13.3)	68.7 (3.4)	88.4 (7.5)	2.5 (2.0)	10.5 (1.9)	39.3 (8.1)	10.9 (2.3)	40.8 (9.3)	0.1 (0.1)	0.4 (0.2)	161	673	802
1988	(35)	100	68.3 (29–101)	5.64 (0.2–15.9)	69.6 (3.7)	92.1 (2.9)	1.4 (0.6)	10.3 (0.9)	38.2 (5.7)	13.7 (3.7)	50.3 (10.3)	0.1 (0.1)	0.5 (0.3)	184	771	845
Gymnoscopelus braueri																
1983	(3)	160	110.3 (106–114)	9.16 (8.2–10.4)	64.2 (2.5)	93.7 (0.4)	1.3 (0.3)	11.7 (1.0)	36.2 (0.7)	11.1 (2.4)	34.5 (5.6)	0.1 (0.0)	0.3 (0.0)	170	714	946
1986	(3)	160	101.3 (88–124)	8.74 (4.6–16.7)	66.6 (2.2)	88.6 (0.6)	2.9 (0.5)	11.3 (0.5)	39.6 (3.4)	13.7 (1.3)	47.5 (2.2)	0.1 (0.0)	0.3 (0.1)	189	794	883
1988	(23)	200	81.2 (45–123)	5.83 (0.5–18.4)	67.2 (2.3)	91.5 (1.8)	1.8 (0.5)	10.2 (0.7)	35.0 (2.1)	13.0 (2.7)	45.6 (6.3)	0.1 (0.0)	0.3 (0.1)	179	752	888
G. nicholsi																
1988	(1)	–ᵃ	148	37.60	59.6	95.5	1.0	10.6	28.6	23.9	64.7	0.1	0.2	280	1175	1 235
G. opisthopterus																
1986	(6)	250	108.8 (81–140)	12.29 (4.2–22.1)	80.1 (3.3)	86.1 (9.7)	1.4 (1.3)	6.0 (2.0)	36.6 (13.4)	8.7 (2.9)	49.1 (5.7)	0.1 (0.0)	0.3 (0.1)	110	458	515
Notolepis coatsi																
1986	(5)	100	62.4 (57–66)	0.25 (0.2–0.3)	82.2 (2.7)	91.9 (3.0)	0.5 (0.4)	9.1 (1.4)	56.7 (2.1)	1.1 (0.4)	6.8 (1.8)	0.2 (0.0)	1.0 (0.0)	63	265	404
1988	(5)	150	63.4 (40–88)	0.42 (0.04–1.0)	79.4 (3.4)	83.2 (2.3)	2.4 (1.0)	9.3 (1.4)	55.5 (2.3)	2.0 (1.4)	14.7 (4.5)	0.1 (0.0)	0.8 (0.1)	77	322	440

Table 1 (continued)

Species, year	(n)	MDO (m)	SL, mm (range)	Wet wt, g (range)	% H₂O	AFDW (% dry wt)	SA (% wet wt)	Protein % wet wt	Protein % AFDW	Lipid % wet wt	Lipid % AFDW	Carbohydrate % wet wt	Carbohydrate % AFDW	kcal 100 g⁻¹ wet wt	kJ 100 g⁻¹ wet wt	kJ 100 g⁻¹ wet wt (corrected)
Paradiplospinus gracilis																
1988	(2)	—[a]	325.5 (315–336)	44.95 (39–51.2)	69.1 (2.4)	90.0 (2.3)	2.1 (0.4)	10.0 (0.3)	37.5 (2.4)	14.4 (2.5)	53.4 (4.3)	0.7 (0.0)	0.3 (0.0)	189	792	850
Protomyctophum bolini																
1988	(6)	—[a,b]	48.3 (43–53)	1.51 (1–1.9)	74.6 (1.4)	85.9 (2.1)	2.5 (0.6)	11.5 (0.2)	54.3 (2.7)	4.0 (0.9)	18.8 (3.9)	0.1 (0.0)	0.5 (0.1)	104	434	572
P. tenisoni																
1988	(3)	—[a]	47.0 (44–51)	1.61 (1.2–1.8)	72.2 (0.6)	86.5 (1.7)	2.7 (0.4)	11.8 (0.5)	50.2 (3.6)	5.0 (1.6)	21.0 (6.1)	0.1 (0.0)	0.6 (0.1)	113	475	637

[a] Frequency of capture insufficient for generation of minimum depth of occurrence
[b] Specimens of *Protomyctophum* spp. were recorded from stomach contents of surface-feeding seabirds (D. G. Ainley personal communication)

variability. There were no significant (ANOVA, $P < 0.05$) changes in wet weight, AFDW as % dry wt, or skeletal ash for either species. Percent water increased slightly in the winter only for *B. antarcticus*; however, this increase may have been a consequence of both the absence of any smallest-size-class individuals and the inclusion of one very large specimen from the winter data set. Percent water for *E. antarctica* showed no significant changes.

With the exception of % wet wt in *Bathylagus antarcticus*, protein (% wet wt and % AFDW) showed no significant changes for either species. The observed decline in protein (% wet wt) for *B. antarcticus* in the winter, since it was not accompanied by a similar change in % AFDW, may only be a reflection of the changes in water content for that same data set. Lipid (% wet wt and % AFDW) showed no changes in *B. antarcticus*. Contrastingly, in *Electrona antarctica*, lipid (% wet wt and % AFDW) showed a steady, significant increase from spring to fall to winter. In conjunction with increasing lipid, energy levels increased by approximately 15% from both spring to fall and fall to winter.

Congeneric variation

Within same-year data sets, differences in proximate composition were examined between *Gymnoscopelus braueri* and *G. opisthopterus* (1986 only) as well as between *G. braueri* and *G. nicholsi* (1988 only). Percent water was significantly higher in *G. opisthopterus* than in *G. braueri* (80.1% vs 66.6%). Although a greater number of large *G. opisthopterus* were analyzed, the difference in mean wet weight between the two species was not significant. Expressed as % AFDW, protein and lipid values were similar for both species. However, as a consequence of the higher percent water in *G. opisthopterus*, both components (% wet wt) were significantly higher in *G. braueri*. Caloric values, also as a consequence of dissimilar percent water, were higher for *G. braueri*.

When *Gymnoscopelus braueri* and *G. nicholsi* were compared, water and protein (% AFDW) were significantly lower in *G. nicholsi*. However these differences may be a consequence of the significantly different mean wet weights of the two species. Lipid, expressed both as % wet wt and % AFDW, was significantly greater in *G. nicholsi*.

Discussion

Minimum depth of occurrence

The absence of any significant trends in proximate composition as a function of depth of occurrence differs from previous studies reporting depth-related changes in composition (Childress and Nygaard 1973, Bailey and Robison 1986, Stickney and Torres, 1989). However, the Antarctic mesopelagic community exhibits a low fish-species diversity, together with vertical distribution patterns skewed towards shallower minimum depths. Interspecific variability combined with a low number of spe-

Table 2. *Bathylagus antarcticus*. Composition by size group. Variability between size groups examined using analysis of variance; SL: standard length. NS, not significant at $P>0.05$; S, significant at $P<0.05$

Size class (mm SL)	(n)	Wet wt, g (range)	% H$_2$O (SD)	Protein % wet wt (SD)	% AFDW (SD)	Lipid % wet wt (SD)	% AFDW (SD)
1983, spring							
25– 49	(1)	0.202	82.8	8.99	64.37	0.91	6.52
50– 74	(1)	0.634	86.7	7.77	70.00	0.64	5.72
75– 99	(2)	2.559 (1.5–3.7)	84.2 (1.3)	6.59 (0.5)	51.99 (8.4)	0.56 (0.1)	4.33 (0.2)
100–124	(2)	9.135 (7.4–11)	87.6 (1.1)	7.41 (1.4)	74.86 (21.1)	0.76 (0.4)	7.21 (2.8)
125–149	(2)	11.154 (10.4–12)	83.9 (1.3)	7.97 (0.5)	57.38 (0.6)	1.04 (0.3)	7.38 (1.5)
Significance:			NS	NS	NS	NS	NS
1986, fall							
25– 49	(3)	0.305 (0.11–0.56)	83.3 (1.3)	8.33 (0.6)	64.41 (8.9)	0.77 (0.1)	5.96 (1.1)
50– 74	(12)	1.181 (0.56–1.7)	84.5 (1.7)	8.54 (1.0)	67.92 (4.2)	0.81 (0.2)	6.43 (1.7)
75– 99	(12)	3.917 (1.2–7.2)	87.2 (1.2)	7.03 (0.7)	67.74 (5.4)	0.84 (0.3)	8.02 (2.4)
100–124	(4)	8.780 (6.7–9.8)	86.9 (1.3)	6.80 (0.3)	58.72 (3.2)	1.60 (0.2)	13.82 (1.5)
125–149	(1)	23.885	89.2	6.15	71.00	0.99	11.58
Significance:			S	S	S	S	S
1988, winter							
50– 74	(4)	1.176 (0.77–1.6)	88.5 (1.8)	5.74 (1.0)	63.55 (2.5)	0.59 (0.1)	6.60 (0.6)
75– 99	(7)	4.104 (2.5–6.9)	87.7 (1.3)	6.17 (0.6)	62.10 (1.6)	0.76 (0.3)	7.54 (2.1)
100–124	(3)	10.784 (10–12.1)	89.3 (1.3)	5.38 (0.7)	62.26 (2.5)	1.04 (0.5)	11.60 (4.9)
125–149	(2)	29.283 (21–37.7)	89.6 (1.2)	5.10 (0.5)	60.25 (2.0)	0.94 (0.2)	11.00 (1.3)
Significance:			NS	NS	NS	NS	NS
All years							
25– 49	(4)	0.279 (0.11–0.56)	83.2 (1.1)	8.50 (0.6)	64.40 (7.3)	0.81 (0.1)	6.10 (1.0)
50– 74	(17)	1.148 (0.56–1.7)	85.6* (2.4)	7.84* (1.5)	67.02 (4.2)	0.75 (0.2)	6.43 (1.4)
75– 99	(21)	3.85 (1.2–7.2)	87.1* (1.6)	6.70 (0.8)	64.36* (6.9)	0.78 (0.3)	7.51 (2.4)
100–124	(9)	9.527 (6.7–12)	87.9 (1.6)	6.45 (1.2)	63.49 (12.7)	1.23 (0.5)	11.61 (4.0)
125–149	(5)	20.952 (10.4–38)	87.2 (3.3)	6.46 (1.5)	61.25* (5.7)	0.99 (0.2)	9.67 (2.5)
Significance:			S	S	NS	S	S

* Seasonal compositional variability significant (ANOVA, $P<0.05$)

cies and a uniformly shallow minimum-depth range resulted in the absence, or at least masking, of any depth-related trends.

Seasonal variation

The increase in total lipid content (% wet wt) from spring (Scotia Sea) to fall (Weddell Sea) to winter (Scotia Sea) for *Electrona antarctica* could be accounted for by: (1) variations in the relative amount of other compositional components such as water or protein, resulting in an arti-factual increase in lipid as a percent of the total; (2) regional differences in food availability and productivity between the sampling sites; (3) seasonal changes related to reproductive patterns and/or feeding patterns.

No significant (ANOVA $P>0.05$) differences between 1983, 1986 and 1988 individuals were found in size, percent water, AFDW as % dry wt, or protein content. Thus, the increase in lipid does not represent a relative change in content as a consequence of decreases in some other component.

As shown by Bailey and Robison (1986), conspecific fish from areas of different productivity may contain sig-

Table 3. *Electrona antarctica*. Composition by size group. Variability between size groups examined using analysis of variance. NS, not significant at $P > 0.05$; S, significant at $P < 0.05$

Size class (mm SL)	(n)	Wet wt, g (range)	% H$_2$O (SD)	Protein		Lipid	
				% wet wt (SD)	% AFDW (SD)	% wet wt (SD)	% AFDW (SD)
1983, spring							
25– 49	(3)	0.469 (0.24–0.64)	70.6 (3.8)	10.81 (0.9)	40.99 (2.3)	7.35 (0.7)	27.91 (1.2)
50– 74	(8)	2.374 (1.1–4.1)	70.4 (2.8)	10.40 (0.8)	39.37 (0.2)	7.87 (0.8)	29.88 (2.7)
75– 99	(5)	8.089 (5.1–11)	65.7 (3.9)	10.84 (1.1)	34.19 (2.1)	11.4 (2.8)	35.48 (6.1)
Significance:			NS	NS	S	S	NS
1986, fall							
25– 49	(9)	0.652 (0.25–1.1)	68.4 (4.7)	11.68 (1.3)	45.46 (9.0)	9.67 (3.0)	36.99 (10.6)
50– 74	(9)	2.704 (1.0–4.7)	69.8 (2.3)	10.37 (1.7)	39.66 (3.8)	11.17 (1.5)	43.52 (8.7)
75– 99	(8)	7.703 (6–10.8)	68.1 (3.2)	9.67 (2.4)	33.44 (6.2)	11.78 (1.9)	41.67 (9.5)
100–124	(1)	13.319	66.8	8.59	28.68	12.75	42.56
Significance:			NS	NS	S	NS	NS
1988, winter							
25– 49	(6)	0.986 (0.21–1.6)	72.1 (2.5)	10.28 (0.8)	43.27 (9.6)	10.01 (4.2)	39.86 (15.0)
50– 74	(17)	3.519 (1.7–5.5)	71.2 (3.2)	10.07 (0.8)	39.23 (2.0)	12.56 (2.3)	49.96 (9.5)
75– 99	(10)	9.896 (6–14.5)	66.3 (3.0)	10.67 (0.5)	35.03 (3.3)	16.92 (2.6)	54.87 (4.5)
100–124	(2)	16.235 (16–16.5)	67.2 (1.6)	9.73 (3.4)	31.72 (10.4)	16.52 (0.2)	59.00 (6.8)
Significance:			S	NS	S	S	S
All years							
25– 49	(18)	0.733 (0.21–1.6)	70.1 (4.1)	11.07 (1.2)	43.98 (8.3)	9.39 (3.2)	36.43 (11.7)
50– 74	(34)	3.02 (1.0–5.5)	70.6 (2.9)	10.23 (1.1)	39.38 (2.5)	11.04* (2.6)	43.34* (11.5)
75– 99	(23)	8.525 (5–14.5)	66.8 (3.3)	10.37 (1.5)	34.32 (4.2)	14.05* (3.5)	46.43* (10.4)
100–124	(3)	15.263 (13–16.5)	67.1 (1.1)	9.35 (2.5)	30.71 (7.6)	15.26* (2.2)	53.52 (10.6)
Significance:			S	NS	S	S	S

* Seasonal compositional variability significant (ANOVA, $P < 0.05$)

nificantly different levels of lipid, with higher values generally found in individuals from the more productive region. Primary production within the Scotia Sea is greater than in open ocean areas within the Weddell Sea (El-Sayed 1968). Chlorophyll *a* concentrations and overall primary productivity values measured in the marginal ice-zone during all three AMERIEZ cruises showed that both phytoplankton biomass and primary production were highest in the Scotia Sea during the spring and lowest in the same area during the winter. Mean values for chlorophyll *a* concentrations were 3.1 μg l^{-1} in the spring compared to 0.18 μg l^{-1} in the fall and 0.11 μg l^{-1} in the winter (Smith 1987, G. F. Cota and W. O. Smith unpublished data). Measurements of mean primary production were 571 mg C m^{-2} d^{-1} in the spring, 200 mg C m^{-2} d^{-1} in the fall and only 30 mg C m^{-2} d^{-1} in the winter (Smith

1987, Cota and Smith unpublished data). Data from previous investigators on zooplankton biomass within the upper 1 000 m from similar locations in the Scotia Sea show a relatively high value for the spring season (approximately 3 to 5 g dry wt m^{-2}; Foxton 1956, Vladimirskaya 1976). Contrastingly, zooplankton biomass measured during the fall and winter AMERIEZ cruises was low. Values integrated over the upper 1 000 m were 1.2 g m^{-2} in the Weddell Sea in the fall (Hopkins and Torres 1988), and 0.9 g dry wt m^{-2} in the Scotia Sea in the winter (Hopkins unpublished data). Measurements of krill biomass during all three cruises also showed a similar pattern, with values highest in the spring and decreasing through the fall and winter (Daly and MacCaulay 1988, Daly unpublished data). As a consequence, the observed higher lipid levels in the fall (Weddell Sea)

Table 4. *Electrona antarctica.* Proximate composition and caloric content of excised gonads in relation to total body lipid (1988 individuals only). GSI: gonadal-somatic index

SL (mm)	Total body wet wt (g)	Gonad wet wt (g)	GSI	Max. egg size (mm)	Gonad composition					Gonad lipid (g)	Total body lipid (g)	Gonad lipid as % body lipid	Gonad cal as % total body cal
					H₂O (%)	Protein % wet wt	% AFDW	Lipid % wet wt	% AFDW				
61	2.6686	0.0239	0.90	0.1	79.1	6.49	49.47	3.24	18.15	0.00078	0.3686	0.21	0.41
62	3.3518	0.0379	1.13	0.1	79.1	6.49	49.47	3.24	18.15	0.00125	0.4129	0.30	0.54
83	6.8715	0.2083	3.03	0.5	80.8	7.83	45.83	4.64	27.15	0.00983	1.0234	0.96	1.40
98	10.9993	0.3821	3.47	0.5	79.4	8.23	44.01	5.02	26.87	0.01956	2.2067	0.89	1.30
103	14.1378	1.3720	9.70	0.8	84.1	6.13	41.84	4.83	32.99	0.06713	2.7752	2.42	3.20

and winter (Scotia Sea) specimens cannot be attributed to differences in regional productivity.

Data on the reproductive strategies of Antarctic mesopelagic fish are sparse. Based on the seasonal occurrence and distribution of eggs and larvae, data from Efremenko (1986) suggest that reproduction occurs year-round for *Electrona antarctica,* with a maximum egg size of 1.2 to 1.4 mm and a peak spawning time in summer–early fall. With the exception of possibly moving up the period of maximum spawning to late spring–summer, examinations of *E. antarctica* gonads from all three AMERIEZ cruises indicate a reproductive pattern consistent with that proposed by Efremenko (Lancraft unpublished data). In the spring, 78.6% of the gonads contained eggs ≥0.8 mm and only 10.7% consisted of eggs 0.3 mm or smaller (specimens >80 mm standard length only). Conversely, in the fall for the same size-class individuals, only 5.6% of the gonads contained eggs ≥0.8 mm, while eggs ≤0.3 mm constituted 88.9% of the total. In the winter, 56% of the eggs were ≥0.8 mm and 16.0% were ≤0.3 mm (Lancraft unpublished data). In order to approximate the effect of gonad development on the observed increase in total lipid for the winter (1988) data set, individual gonads were weighed and egg size recorded for all frozen specimens of *E. antarctica.* In addition, proximate composition of selected gonads over a size range was determined and examined in relation to the total body lipid and caloric content (Table 4). The relationship between egg size (S) and gonad wet-weight (W) can be expressed by the regression: $W = 0.984\ S^{2.116}$ ($n = 28$, $r = 0.882$). From this, a maximum egg size value of 1.4 mm yields an approximate maximum gonad wet-weight of 2.0 g for a 110 mm, 16.4 g fish. Furthermore, the relationship between gonad caloric content as a percent of the total body (C) and gonad wet-weight (W) is best expressed by the regression: $C = 2.575\ W^{0.485}$ (Table 4; $n = 5$, $r = 0.986$). Combining the results from these two equations produces an estimated caloric value for a ripe gonad with 1.4 mm eggs of 3.6% of the total caloric value of the fish. Were gonad caloric percentage versus gonad weight expressed in exponential terms ($W = 0.624\ e^{1.29C}$, $n = 5$, $r = 0.880$), with an exaggerated gonad weight of 2.5 g for a 113 mm, 17.0 g fish, the resultant gonad caloric percentage would only be 15.7%. Thus, it does not appear that, even under maximum conditions, the precentage of total body calories tied up in the gonads constitutes a large fraction of the total.

Seasonal increases in lipid have previously been associated with herbivorous invertebrates which are unable to feed sufficiently during the winter (Littlepage 1964, Raymont et al. 1971, Sargent 1976). Concomitant with increased lipid stores are high levels of wax esters (as % of total lipid) which serve as the predominant long-term reserve material (Lee and Hirota 1973, Lee 1974, Bottino 1975, Sargent 1976, Clarke 1984). For *Electrona antarctica,* wax esters are the predominant lipid fraction (Reinhardt and Van Vleet 1986). Furthermore, gut fullness (stomach and intestine) was moderate to low in *E. antarctica* collected during the winter relative to the fall and spring AMERIEZ cruises (Lancraft et al. in preparation). Thus, the observed increase in lipids for this species

may be an accumulation of reserves against subsequent decreases in food availability and/or changes in feeding strategies during the winter and early spring months.

Interspecific variability

The significant difference in water content between *Gymnoscopelus braueri* and *G. opisthopterus* is not readily explained. *G. opisthopterus* is more common at greater depths (McGinnis 1974, Hulley 1981). However, minimum depths of occurrence and overall vertical distributions for the two species display considerable overlap (Lancraft et al. 1989). Diet analyses reveal a strong similarity in dominant prey items (Hopkins and Torres 1989). Previous compositional studies involving congeneric species (Childress and Nygaard 1973, Neighbors and Nafpaktitis 1982, Stickney and Torres 1989) show that species with similar depth distributions and life habits usually have similar water contents. Significant differences in composition are evident only in congeners dissimilar in vertical distribution or life history (e.g. *Lampanyctus regalis* and *L. ritteri*; Childress and Nygaard 1973). Although hydrographic conditions are considerably more uniform in the vertical plane in high-latitude systems, it is possible that the observed differences between *G. braueri* and *G. opisthopterus* are a consequence of more subtle environmental cues that are sufficient to separate the two species ecologically.

Comparisons of *Gymnoscopelus braueri* and *G. nicholsi* are hindered by the fact that only a single, very large individual of *N. nicholsi* was examined. The slightly lower percent water and protein (% AFDW) observed in *G. nicholsi* could be accounted for solely as a consequence of the large size-differential between the two species. Lipid (% wet wt and % AFDW), however, is significantly greater in *G. nicholsi*. and it is unlikely that a difference of such magnitude can be attributable entirely to size-related variability. A more probable explanation is the difference in distributional patterns between the two species. *G. braueri* is strictly pelagic, while large *G. nicholsi* exhibit a benthopelagic life style within Antarctic shelf and slope waters (Hulley 1981, Linkowski 1985) and thus are exposed to more highly productive areas resulting in increased lipid content. In support of this, *G. nicholsi* sampled within the Croker Passage (Bransfield Strait, vicinity of Palmer Peninsula) showed very high lipid values (72.8% dry wt, Reinhardt and Van Vleet 1986). Increased lipid as a result of reproductive stage is not a factor, as *G. nicholsi* are not reproductive south of the Antarctic convergence (Efremenko 1986) and thus represent an expatriate population.

The very low levels of lipid found for *Bathylagus antarcticus* and *Notolepis coatsi* may be related to diet. A considerable portion of prey items for both species include coelenterates, polychaetes, and chaetognaths (Hopkins and Torres 1989), organisms generally low in total lipid content (Reinhardt and Van Vleet 1986, and unpublished AMERIEZ data). Individual lipid components may or may not be associated with diet (Kayama and Nevenzel 1974, Sargent 1976, Reinhardt and Van

Vleet 1986); however, specific data correlating total lipid levels between predator and prey are not available. The suggestion that prey items low in lipid contribute to low total lipid levels in predator species has been made previously by Reinhardt and Van Vleet (1986) and Stickney and Torres (1989).

Regional and latitudinal variations

Comparison of data between different regions within the Antarctic reveals that higher lipid levels are associated with more productive areas. Values (% wet wt and % AFDW) for identical species from the more productive Croker Passage region (Reinhardt and Van Vleet 1986) are markedly higher than those from Weddell Sea individuals (Table 5 of present study). The finding underscores the importance of considering the pertinent physical and biological characteristics of ocean systems and their resident species when examining trends among mesopelagic communities.

These data, together with previous data from the tropical-subtropical Gulf of Mexico (Stickney and Torres 1989), temperate California Current (Childress and Nygaard 1973), and temperate eastern North Pacific Gyre (Bailey and Robison 1986), allow for preliminary examination of trends in proximate composition between different systems. To best elucidate trends in composition with respect to such broad parameters as latitude or hydrography, comparisons need be confined to species exhibiting similar depth distributions and life styles. Three species (*Bathylagus antarcticus, Cyclothone microdon,* and *Electrona antarctica*) from this study can be compared to congeneric or confamilial species from tropical-subtropical and temperate systems (Table 6). For the myctophid *E. antarctica* and its ecological equivalents *Lampanyctus alatus* and *L. ritteri,* water content and protein (% AFDW) tend to decrease progressively from low-latitude to high-latitude species. Lipid and caloric values increase considerably between species living in the Gulf of Mexico and those in the North Pacific Gyre, even though both systems are similarly oligotrophic. Species

Table 5. Regional comparisons of lipid (% wet wt and % AFDW) for conspecific fishes in the fall season

Region	*Bathylagus antarcticus*		*Electrona antarctica*	
	% wet wt	% AFDW	% wet wt	% AFDW
Weddell Sea (present study; 1986 data)[a]	1.3	12.7	12.3	42.1
Croker Passage (Reinhardt and Van Vleet 1986)	3.3[b]	27.5[c]	20.7	70.6[c]

[a] Values taken from largest size groups only
[b] Values converted from % dry wt originally reported; % H_2O values from present study used for conversion purposes
[c] Values converted from % dry wt originally reported; AFDW as % dry wt values from present study used for conversion purposes

Table 6. Latitudinal Comparisons of proximate composition and caloric value for congeneric or confamilial fishes. M: strong migrator; WM: weak migrator; NM: nonmigrator

System	MDO (m)	Migratory habit	% H_2O	Protein (% AFDW)	Lipid (% AFDW)	kcal 100 g^{-1} wet wt	kJ 100 g^{-1} wet wt
Gulf of Mexico (Stickney and Torres 1989)							
Bathylagus longirostris	200	WM	86.7	64.6	9.1	45	189
Cyclothone pallida	500	NM	81.6	75.3	8.9	58	243
Lampanyctus alatus	75	M	78.9	77.3	7.8	92	385
California Current (Childress and Nygaard 1973)							
Bathylagus milleri	550	NM	87.1	49.4	28.5	60	251
Bathylagus wesethi	25	M	83.3	62.4	17.3	68	285
Cyclothone acclinidens	500	NM	79.4	51.1	35.5	94	394
Lampanyctus ritteri	75	M	70.6	43.6	44.3	166	696
Eastern North Pacific Gyre (Bailey and Robison 1986)							
Cyclothone acclinidens	500	NM	77.2	43.9	36.2	115	482
Lampanyctus ritteri	75	M	75.4	40.2	41.1	135	566
Weddell Sea (present study; 1986 data)							
Bathylagus antarcticus	200	WM	85.9	66.5	8.1	53	224
Cyclothone microdon	500	NM	67.0	39.4	33.8	167	699
Electrona antarctica	50	M	68.7	39.3	40.8	161	673

living in the Weddell Sea are similar in lipid content to those living in the North Pacific Gyre or the more productive California Current. Because of similar lipid levels and slightly lower water content, caloric values in the Weddell Sea species are similar to or slightly higher than in species from the California Current or Gyre. The three Cylothone species show trends parallel to those observed for the myctophid E. antarctica and Lampanyctus spp.

In contrast, the Bathylagus species exhibit a different pattern. Excluding those changes associated with differences in lifestyle, Bathylagus species show no significant latitudinal variations in proximate composition. Compositional values for B. antarcticus are essentially identical to its tropical-subtropical congener B. longirostris. Water protein and content are high, while lipid and caloric values are very low. Direct comparison with congeners from the temperate systems is complicated by the fact that eastern Pacific Bathylagus species display different vertical distributions and migratory habits. Although similar in body shape and appearance to B. antarcticus, B. milleri is deeper living and non-migratory, which may account for its much lower protein content. In support of this, B. wesethi, a shallow-living, migratory Pacific species, shows high protein values similar to B. antarcticus and B. longirostris, both of which are also migratory. The considerably higher lipid levels in temperate congeners may be related to the high productivity levels within the California Current system.

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