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Energy content of Antarctic mesopelagic fishes: implications for the marine food web

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Abstract For a better understanding of the role of mesopelagic fish in the Southern Ocean food web, the energy and water content of *Bathylagus antarcticus*, *Electrona antarctica* and *Gymnoscopelus braueri* from the Lazarev Sea were investigated. Mean dry weight energy content of *B. antarcticus* (20.4 kJ g^{-1}) was significantly lower than in *E. antarctica* and *G. braueri* (both 29.4 kJ g^{-1}). In *E. antarctica*, an increase of dry weight energy density with age was evident from 26.9 kJ g^{-1} in juveniles of less than 1 year of age to 32.0 kJ g^{-1} in 3-year-old fish. Water content decreased with size in all three species. Abundant high-energy species such as *E. antarctica* are at a key position in the food web. Due to a marked influence of age on energy content, population structure can be an important variable in estimates of energy fluxes in the Southern Ocean ecosystem.

Introduction

Energy content of prey is a key factor controlling the structure of food webs and the relationships between their components. Accurate measurements of the caloric value of prey and predators allow estimates of food requirements and energy flux from lower to higher trophic levels. As such, they are valuable for the development of ecosystem models and play an important role in

ecosystem management. With increasing evidence that the classic diatom-krill-consumer model of the Southern Ocean is more complex than initially assumed, there is a need to better understand the role and position of other organisms, such as squid and mesopelagic fish (Ainley et al. 1992, 1994; van Franeker et al. 1997; Barrera-Oro 2002).

Lanternfishes (family Myctophidae) are the most abundant mesopelagic fish of the Antarctic Ocean, both in numbers and biomass (Kock 1992). They are major predators on mesozooplankton (Pakhomov et al. 1996; Pusch et al. 2004). Among them, *Electrona antarctica* (Günther, 1878) is considered a key species due to its high abundance and almost circumpolar distribution (Hulley 1990; Sabourenkov 1990; Hopkins et al. 1993; Barrera-Oro 2002). They display a diel migration between 300–650 m during the day and close to the surface layer at night. *E. antarctica* are an important prey for birds and seals (Lea et al. 2002a; Quillfeldt 2002; Casaux et al. 2003). The myctophid *Gymnoscopelus braueri* (Lönnerberg, 1905) exhibits a similar ubiquity, but appears to be less abundant than *E. antarctica* (Torres and Somero 1988; Lancraft et al. 1989; Sabourenkov 1990). Their role in the food web can be significant on a local scale (Ainley et al. 1991, 1994). *Bathylagus antarcticus* Günther, 1878 (family Bathylagidae) is widely distributed throughout the Antarctic Ocean. It is generally considered a deeper-dwelling midwater species mainly occurring between 950 and 170 m depth, with some vertical migration on a diel as well as seasonal basis (Lancraft et al. 1989; Gon 1990). Apart from sporadic occurrence in the diet of Antarctic fur seals (Casaux et al. 2004), *B. antarcticus* has not been reported to play a significant role in the diet of higher predators.

Energy content of Southern Ocean mesopelagic fish species has been estimated with respect to depth, season or region (Donnelly et al. 1990; Lea et al. 2002b; Tierney et al. 2002), or in the context of diet studies (Clarke and Prince 1980; Cherel and Ridoux 1992; Eder and Lewis 2005). Most studies were based on relatively small sample sizes.

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This paper contributes a new dataset for a region so far not sampled in the context of energetic analyses for ecosystem-based energy budget models. We discuss the influence of population structure on the energy budget based on the species-specific evolution of energy content with size and age. The ecological role of the three species investigated is evaluated in the light of their nutritional value, distribution, biology and function in the food web.

Materials and methods

Sampling procedure

Samples were collected during the autumn SO-GLOBEC cruise of RV “Polarstern” (ANT XXI/4) in the Lazarev Sea (CCAMLR statistical subarea 48.6), between March 3 and May 5, 2004 (Fig. 1). The station grid consisted of four longitudinal transects between 0° and 6°W and 61°S–72°S, with a latitudinal spacing of 20 nautical miles between stations. Fish were caught using Rectangular midwater trawl nets (RMT 8 + 1),

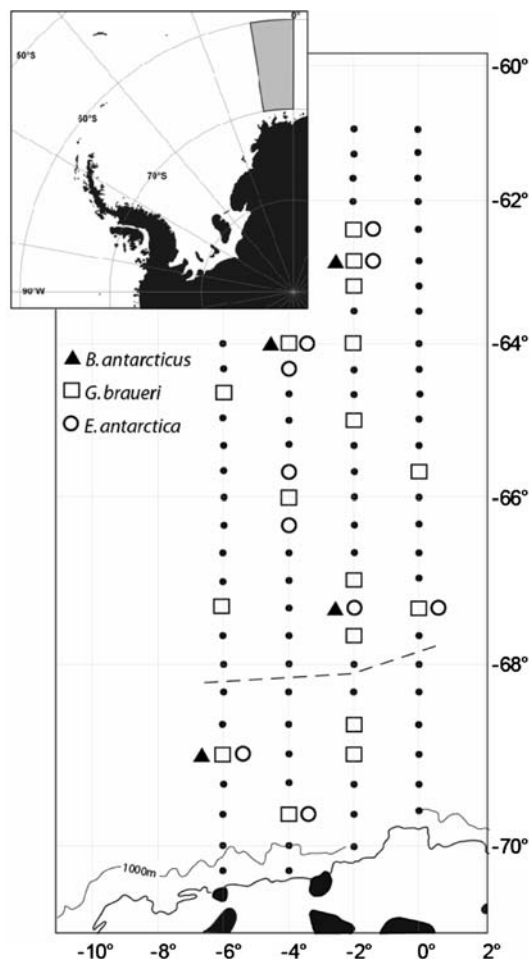


Fig. 1 Rectangular midwater trawl net sampling grid with geographic overview in upper left corner. Stations sampled for energy content are indicated with different markers for each species. Dashed line represents northern edge of the sea ice cover

consisting of an RMT 1 mounted above an RMT 8 with a mouth area of 1 and 8 m² and a cod end mesh size of 0.33 and 0.85 mm, respectively. Each haul consisted of a standard double oblique tow from the surface down to 200 m and back to the surface. Towing speed was approximately 2.5 knots. Further details on the sampling procedure are outlined in Siegel et al. (2004).

Fish were sorted from the total catch of the RMT 8 and identified to species level. Dry mass and energetic content was determined for three species: *E. antarctica*, *B. antarcticus* and *G. braueri*. Individuals were sampled from 21 stations distributed over the entire survey area where sufficient fish were caught to allow subsampling for energy measurements. From each of these stations, a subsample of up to 12 individuals per species covering the whole length range caught were stored at –20°C.

Water and energy content

To prevent errors due to the loss of body fluids during dissection, water and energy content were determined for whole individuals only. Frozen fish were thawed, blotted dry and their standard length (SL) was determined to the lower full mm. Total wet weight (WW) was determined to the nearest 0.1 mg. Fish were dried until complete desiccation (constant mass) in a drying oven at a constant temperature of 60°C. After drying, they were re-weighed to determine the total dry weight (DW). Water content was calculated as the difference between WW and DW, expressed as %WW.

Individual DW and WW energy content, expressed as kJ g⁻¹, was determined by an isoperibol bomb calorimeter calibrated with benzoic acid. After homogenizing, either the whole fish or a subsample (0.1–1.2 g) was used for calorimetry, depending on the size of the fish.

Data analysis

Mean energy and water content with standard deviations were calculated for each species. Fish were divided into three size classes: small, medium and large. We used the maximum lengths reported in Hulley (1990) and Gon (1990) for each species and divided them by three to obtain size groups comparable for future studies. Reliable size–age data were available for *E. antarctica* (Greely et al. 1999). In order to obtain biologically more relevant categories, we calculated age in years based on the pooled length–age regression provided by Greely et al. (1999):

$$a = \frac{SL - 8.869}{0.063 \times 365} \quad (1)$$

where a = age in years.

Based on the results of Eq. (1), fish were divided into year groups 0 ($a < 1$), 1 ($1 \leq a < 2$), 2 ($2 \leq a < 3$), etc. Analysis of variance (ANOVA) was applied to

detect significant differences in energy and water content between species and their individual size classes and age groups. Tukey's Honestly Significant Difference test (Tukey's HSD) was used as a post-hoc test to discriminate species and single size classes and age groups from each other. Additionally, various regression analyses were performed in order to estimate the effect of size on energy and water content. Significance threshold α was 0.05 for all statistical tests.

Results

Species comparison

Electrona antarctica was abundant throughout the sampling area. A large and continuous part of the total size range was covered in this species. Both other species were caught infrequently. Only the upper portion of the natural size range was obtained for *G. braueri*. *B. antarcticus* was represented by a low number of samples spread over a wide size range, the bulk ranging from 36 to 95 mm, with only one larger specimen of 123 mm (Table 1).

While mean WW energy content of *B. antarcticus* (2.9 kJ g^{-1}) was significantly lower than that of *E. antarctica* (9.4 kJ g^{-1}) and *G. braueri* (8.9 kJ g^{-1}), no significant difference could be detected between the two myctophids in either WW or DW energy density. Conversely, the bathylagid's mean water content (86%) was significantly higher compared to that of *E. antarctica* (68%) and *G. braueri* (70%). The two myctophids showed no statistically significant difference in water content from each other (Table 2).

Size and age effects on energy content in *E. antarctica*

In *E. antarctica*, the number of samples and their widespread size distribution allowed the analysis of the effect of size, DW and WW on energy density.

Among the models tested, a linear regression of the ln-transformed data proved to deliver the statistically most robust results. The corresponding power function exhibits a steep increase of energy density with size, DW and WW in age group 0 and 1 fish, and a gradual increase in older fish (Fig. 2). The model parameters for energy content as a function of size, DW and WW are listed in Table 3.

Table 1 Known size ranges (Gon 1990; Hulley 1990), sampled size ranges and mean sizes of all three species investigated

Species	Known range (mm)	<i>n</i>	Size range (mm)	Mean size (mm)
<i>Bathylagus antarcticus</i>	0–170	12	36–123	71.6 (23.42)
<i>Electrona antarctica</i>	0–102	113	16–83	47.6 (15.90)
<i>Gymnoscopelus braueri</i>	0–132	20	64–132	87.3 (18.05)

Standard deviation in parentheses
n = sample size

Table 2 Mean water content, mean wet (WW) and dry weight (DW) energy density of all investigated species

Species	Water content (%)	WW energy density (kJ g^{-1})	DW energy density (kJ g^{-1})
<i>B. antarcticus</i>	85.6 (2.46)*	2.92 (0.421)*	20.36 (1.319)*
<i>E. antarctica</i>	68.4 (4.14)	9.35 (1.575)	29.40 (1.800)
<i>G. braueri</i>	69.5 (3.96)	8.86 (1.421)	29.37 (1.509)

Standard deviation in parentheses

Variation between species significant for all three variables (ANOVA: $P < 0.01$)

*Values significantly different from all other values in the same column (Tukey's HSD: $P < 0.05$)

Mean WW energy density increased from 7.5 kJ g^{-1} in small fish to 10.3 kJ g^{-1} in large specimens (Table 4). Small fish were significantly lower in DW and WW energy content than medium and large fish, which could not be statistically discriminated from each other. The opposite trend was significant in water content which decreased from 73% in small *E. antarctica* to 66–67% in the two larger size classes (Table 4).

Water and energy content by age group are shown in Fig. 3. An increase in energy content was apparent from age group 0 (6.9 kJ g^{-1} WW) to age group 3 fish (11.7 kJ g^{-1} WW). The difference in DW and WW energy density between age classes 0, 1 and 2 was statistically significant. Mean water content declined from 74% in age class 0 to 64% in age class 3. However, only age group 0 fish could be statistically discriminated from older fish (Table 4).

Discussion

Inter-specific differences

Energy measurements on *E. antarctica* were at the higher end of the reported range, exceeded only by

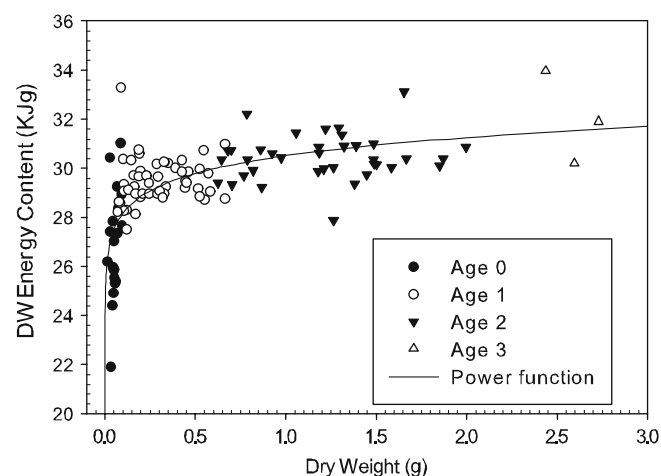


Fig. 2 *Electrona antarctica*. Relationship between dry weight (DW) and dry weight energy density with indicated age groups. Regression parameters of power function provided in Table 3

values reported by Lea et al. (2002b) (Table 5). Our values for *B. antarcticus* and *G. braueri* closely resemble autumn energy densities calculated from proximate composition by Donnelly et al. (1990) in specimens from the Weddell Sea.

Calorific values vary strongly among Southern Ocean fishes (Donnelly et al. 1990; Barrera-Oro 2002; Lea et al. 2002b; Tierney et al. 2002). Variation in energy content can be attributed to numerous factors, such as species, population, time of year, geographic location, sex and maturity stage, feeding condition, mode of life and size (Lawson et al. 1998; Saadettin et al. 1998; Eder and Lewis 2005).

The differences in energy/water content between the two myctophids compared to the bathylagid mirror the differences in life style and feeding regime. Both myctophids are strong diurnal migrators that feed mainly on euphausiids and copepods (Lancraft et al. 1991; Hopkins et al. 1993; Pakhomov et al. 1996; Pusch et al. 2004). In contrast, *B. antarcticus* remain at greater depth. They have a prey spectrum which includes many low-energy species such as coelenterates, polychaetes and chaetognaths which can affect the energy composition of the fish (Donnelly et al. 1990; Geiger et al. 2000).

Hartmann and Brandt (1995) provided a comprehensive collection of data on the relationship of energy content with proportional dry weight of fishes. Our values fit the results for a number of fishes, both in the Antarctic Ocean (Tierney et al. 2002) and worldwide (Hartmann and Brandt 1995; Anthony et al. 2000; Pedersen and Hislop 2001). The slopes of the regression

lines of *E. antarctica* and *G. braueri* closely resemble the combined model of Hartmann and Brandt (1995; Fig. 4). The elevated intercepts of the two myctophids are probably related to the body tissue being generally energy dense, which concurs with reported high lipid values in almost all tissue fractions of *E. antarctica* (Reinhardt and Van Vleet 1986; Phleger et al. 1997). A stable high proportion of lipids could explain the comparatively high energy density at low relative dry mass. The steady increase in energy density with decreasing water content could be explained by a replenishment of energy stores, replacing water with proteins and fat (Geiger et al. 2000).

In *B. antarcticus*, the relationship of energy density and proportional dry weight follows a different pattern. Its high intercept and small slope imply a comparatively high energy content in body tissues at high water content. Energy density only slowly rises when water content declines (Fig. 4). This suggests that the tissue replacing water is relatively poor in energy, which agrees with low lipid contents reported by Reinhardt and Van Vleet (1986) and Donnelly et al. (1990).

Electrona antarctica has a lipid class composition which is very different from both *B. antarcticus* and *G. braueri* (Reinhardt and Van Vleet 1986; Lea et al. 2002b). Although differences in lipid class composition are often correlated to differences in biology, they have limited effects on energy content. It has been proposed that *E. antarctica* stores lipids to survive periods of low food supply, whereas *B. antarcticus* probably relies on a short-term use of energy reserves which implies the need

Table 3 *Electrona antarctica*. Energy density (y) of dry weight (DW) and wet weight (WW) as a function of size, WW and DW (x)

x	y (kJ g ⁻¹)	a	b	P	r^2	e^a
Size (mm)	DW	2.9361	0.1164	< 0.01	0.40	18.8422
	WW	0.7942	0.3745	< 0.01	0.47	2.2127
WW (g)	DW	3.3778	0.0367	< 0.01	0.44	29.3062
	WW	2.2154	0.1165	< 0.01	0.50	9.16507
DW (g)	DW	3.4181	0.0347	< 0.01	0.46	30.5114
	WW	2.3500	0.1160	< 0.01	0.58	10.4856

Regression parameters a and b , adjusted r^2 and P value for linear regressions of ln-transformed data [$\ln(y) = a + b \ln(x)$], and corresponding power function [$y = x^b e^a$]

Table 4 *Electrona antarctica*. Mean energy and water content of size classes and age groups

Class/group	Size range (mm)	n	Water content (%)	DW energy content (kJ g ⁻¹)	WW energy content (kJ g ⁻¹)
Small	0–34	32	73.1 (3.84)*	27.76 (2.235)*	7.49 (1.36)*
Medium	35–68	68	66.4 (2.21)	29.92 (0.887)	10.05 (0.79)
Large	69–102	14	66.7 (3.25)	30.69 (1.541)	10.25 (1.42)
Age group 0	0–31	21	74.4 (3.92)*	26.94 (2.156)*	6.89 (1.231)*
Age group 1	32–53	52	67.6 (2.57)	29.49 (0.922)*	9.56 (0.826)*
Age group 2	54–77	37	66.3 (2.56)	30.45 (0.919)	10.27 (0.959)
Age group 3	78–102	3	63.6 (1.60)	32.01 (1.885)	11.66 (1.197)

Standard deviation in parentheses

n = sample size

Variation between species significant for all three variables (ANOVA: $P < 0.01$)

*Values significantly different from all other values in the same column (Tukey's HSD: $P < 0.05$)

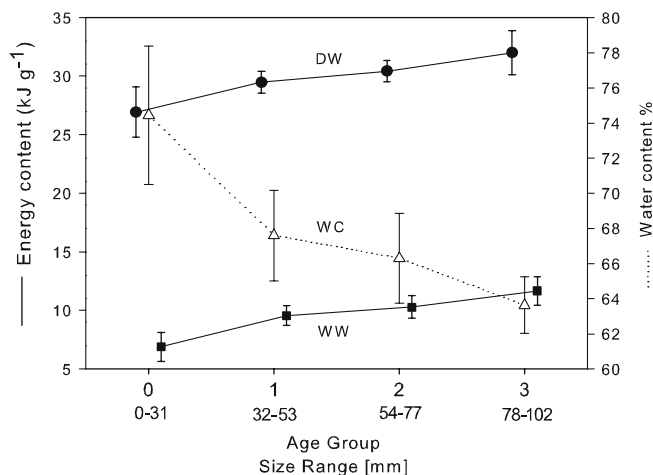


Fig. 3 *Electrona antarctica*. Mean water content (WC), DW and wet weight (WW) energy content by age group. Error bars indicate 95% confidence intervals

to feed constantly (Reinhardt and Van Vleet 1986; Geiger et al. 2000).

Size and age effects on energy content in *E. antarctica*

An increase in energy content was significant with increasing size classes and age groups (Table 4). These trends correspond with the size effect found by Donnelly et al. (1990). In contrast, Tierney et al. (2002) found the highest energy content in the smallest size class. Within specimens of uniform species, geographic location, time of year and size, there can still be considerable variation

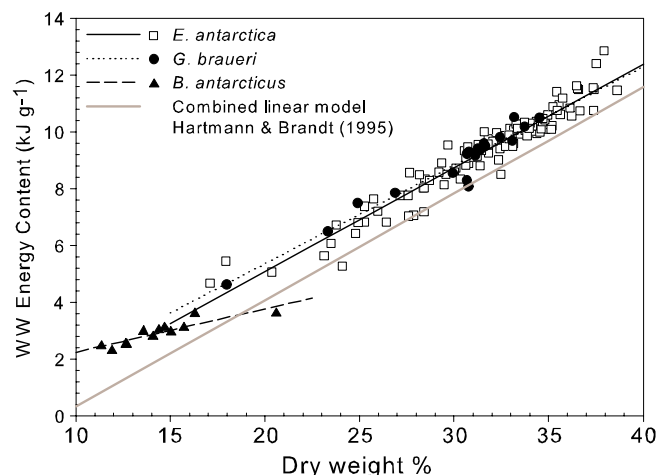


Fig. 4 Correlation between percentage dry weight and energy content per gram wet weight. Individual data from this study were added to the combined linear model of Hartmann and Brandt (1995). *E. antarctica*: $y = -2.2077 + 0.3650x$ ($r^2 = 0.93$; $P < 0.01$); *G. braueri*: $y = -1.5583 + 0.3467x$ ($r^2 = 0.94$; $P < 0.01$); *B. antarcticus*: $y = 0.7136 + 0.1532x$ ($r^2 = 0.8003$; $P < 0.01$)

in energy content due to undetermined random factors (Paul et al. 1998). For example, Tierney et al. (2002) used 6–7 specimens per size class. They could not exclude possible outliers which could have led to an overestimate of the reported mean value in small fish (M. Tierney, personal communication).

The energy content of *E. antarctica* strongly increases with size in age group 0. From the second year on, size-related increase in energy content slows down considerably, while variation increases. Part of this variation

Table 5 Review of mean water and energy contents of *B. antarcticus*, *E. antarctica* and *G. braueri* by season and region of the Southern Ocean

Year	Season	Region	Method	<i>N</i>	Mean size (mm)	Size range (mm)	Water content (%)	DW energy content (kJ g ⁻¹)	WW energy content (kJ g ⁻¹)	Source
<i>B. antarcticus</i>										
1983	Spring	Scotia Sea	PCA	8	99.4	44–145	85.1 (2.3)		3.12	Donnelly et al. (1990)
1986	Autumn	Weddell Sea	PCA	32	77.2	32–143	85.9 (2.0)		2.94	Donnelly et al. (1990)
1988	Winter	Scotia Sea	PCA	16	90.0	51–150	88.4 (1.4)		2.37	Donnelly et al. (1990)
1999	Summer	Macquarie Ridge	BC	18	116.8	73–196	81.8 (1.8)	21.5 (5.0)		Tierney et al. (2002)
2004	Autumn	Lazarev Sea	BC	12	71.6	36–123	85.6 (2.5)	20.4 (1.32)	2.92 (0.42)	This study
<i>E. antarctica</i>										
1983	Spring	Scotia Sea	PCA	16	66.1	33–98	69.0 (3.7)		7.93	Donnelly et al. (1990)
1986	Autumn	Weddell Sea	PCA	27	61.9	29–101	68.7 (3.4)		8.02	Donnelly et al. (1990)
1988	Winter	Scotia Sea	PCA	35	68.3	29–101	69.6 (3.7)		8.45	Donnelly et al. (1990)
1998	Winter	Kerguelen Plateau	BC	5	64.5		60.8 (8.8)	34.3 (3.8)	13.3 (2.6)	Lea et al. (2002b)
1999	Summer	Macquarie Ridge	BC	20	50.4	30–73	69.9 (4.3)	30.8 (9.7)	9.04	Tierney et al. (2002)
2004	Autumn	Lazarev Sea	BC	113	47.0	16–83	68.4 (4.14)	29.4 (1.80)	9.35 (1.58)	This study
<i>G. braueri</i>										
1983	Spring	Scotia Sea	PCA	3	110.3	106–114	64.2 (2.5)		9.46	Donnelly et al. (1990)
1986	Autumn	Weddell Sea	PCA	3	101.3	88–124	66.6 (2.2)		8.83	Donnelly et al. (1990)
1988	Winter	Scotia Sea	PCA	23	81.2	45–123	67.2 (2.3)		8.88	Donnelly et al. (1990)
1999	Summer	Macquarie Ridge	BC	18	78.2	37–133	70 (7.1)	39.0 (14.3)	10.91	Tierney et al. (2002)
2004	Autumn	Lazarev Sea	BC	20	87.3	64–132	69.9 (4.0)	29.4 (1.51)	8.86 (0.61)	This study

Standard deviation in parentheses

n = sample size, BC bomb calorimetry, PCA proximate composition analysis

may be related to differences in gender and maturation condition. Another source of variation might be the time of spawning. Since *E. antarctica* is believed to be a batch spawner (Hulley 1990), different batches within the same year class may encounter very different food availability which can have a strong influence on the energetic composition of the fish.

Energy data in relation to age groups rather than to arbitrary size classes can be a practical tool to estimate ecosystem energy budgets. The results of this study indicate that using distinct energy contents for each age group in *E. antarctica* could significantly improve energy budget estimates: The total energy budget of a population would strongly be influenced by the proportion between age group 0 juveniles and older fish.

Ecological implications

The size–energy density relationship of *E. antarctica* suggests that the smallest fish invest proportionally more energy in growth and locomotion than older individuals. This view agrees with the common notion that there is a strong need for young fish to grow quickly in order to escape predation pressure (Anthony et al. 2000). The need of an abundant species such as *E. antarctica* to build up high energy reserves over a short period of time may partly explain the high predatory impact of mesopelagic fishes, which has been suggested to reach up to 40% of the secondary production in the Antarctic Ocean (Pakhomov et al. 1996).

Through its pelagic mode of life, abundance and high lipid content, *E. antarctica* could be seen as the off-shelf counterpart of Antarctic silverfish *Pleuragramma antarcticum*, the primary prey of many top predators in High-Antarctic shelf waters (Hubold 1985; Arnould and Whitehead 1991; Creet et al. 1994). Stocks of *E. antarctica* represent a large reserve of energy through their high abundance and circumpolar distribution (Lancraft et al. 1989; Kock 1992). The myctophid has an energy density more than twice that of Antarctic krill *Euphausia superba* (Clarke and Prince 1980; Torres et al. 1994). Although being usually much lower in biomass than krill (Lancraft et al. 1989), they represent a valuable prey for top predators: the average lanternfish is significantly larger than an average krill and would thus optimize the energy yield per prey item of a potential predator. In fact, the proportional mass of myctophid fish often dominates, or at least equals euphausiids in the diet of many Antarctic top predators (e.g. van Franeker 2001; Bost et al. 2002; Quillfeldt 2002; Osman et al. 2004).

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