

Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean

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ABSTRACT: This study describes the proximate composition (moisture, lipid, protein and ash content) and energetic value of 39 species (27 teleosts, 3 sharks, 7 rays and 2 squids) that are known as key prey or potential prey of top predators on the Patagonian continental shelf. Specimens were collected in the SW Atlantic Ocean in the area 39 to 51° S, 55 to 65° W. Fifty-two catches were performed at a depth range of 73 to 370 m: 27 catches in autumn and 25 in summer. A multivariate correspondence analysis showed an association between species identity and certain biochemical variables (main dimension = 83% of variance explained). Sharks and some demersal-pelagic teleosts were associated with lipids (9 to 18% wet mass). Teleosts constituted a higher source of protein (9–28% wet mass) than elasmobranchs. Rays were nutritionally poor, with the lowest lipid contents (2 to 10%) and energy values (3 to 7 kJ g⁻¹ wet mass), in agreement with the general biochemical characteristics of benthic fishes. Demersal-benthic and demersal-pelagic species did not change in their nutritional values with increasing size. However, demersal-benthic species increased seasonally in protein content from 11–16% in summer to 10–19% in autumn. The energetic value of teleosts from the SW Atlantic Ocean was not different from those of the Pacific or Indian Southern Ocean, but was higher than the energetic value of teleosts from the Northern Hemisphere. This study contributes to the understanding of the biochemical composition and energetic value of prey species over the seasons and their relevance as potential prey for top predators.

KEY WORDS: Nutritional quality · Energetic value · Teleosts · Elasmobranchs · Cephalopods · Southwestern Atlantic Ocean

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INTRODUCTION

The Patagonian shelf supports a rich and diverse community of resident top predators as well as seasonal migrants that either winter in the region or that travel to tropical and Northern Hemisphere wintering grounds (Croxall & Wood 2002). The Argentinean continental shelf system is strongly affected by different types of water masses that promote the recycling of nutrients, accounting for its high productivity (Podesta et al. 1991, Carreto et al. 1995). Several studies of marine mammals and seabirds highlighted the extraordinary importance of this system in sustaining populations breeding at the Patagonian coast, Malvinas/Falkland

Islands and South Georgia Island (Croxall & Wood 2002, Quintana & Dell'Arciprete 2002, Campagna & Croxall 2003). Regions visited by top predators during their foraging phase are assumed to be characterised by higher productivity (Bradshaw et al. 2004), but the energy content of potential food resources is currently unknown.

The nutritional quality of marine organisms is often estimated by the lean mass of commercial species, while nutritional information about whole specimens of commercial and non-commercial species is generally scarce. Therefore, there is a lack of knowledge about the energetic values of potential prey, which are needed, for example, to develop models of energy

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transfer between trophic levels. This study provides the relative dietary values of whole teleost, elasmobranch and cephalopod specimens from the SW Atlantic Ocean for the incorporation into trophic ecological studies, such as the foraging behaviour of predators, the assessment of energy transfer between trophic levels (Croxxall & Prince 1982, Tierney et al. 2002) and the shifting energetic values of the spectrum of prey species.

MATERIALS AND METHODS

The sampling area was located in the area 39 to 51°S, 55 to 65°W (Fig. 1). Fish and squid samples from the SW Atlantic Ocean were collected in autumn (May–June 2001) and summer (January–February 2002) by commercial fishing vessels operating with bottom trawls. Non-parametric Mann-Whitney *U* rank tests were performed to test for a difference in the depth of hauls between the 2 seasons (Siegel & Castellan 1995, Conover 1999). Collected material was frozen on board and later analysed in the laboratory. Thirty-nine species (27 teleosts, 3 sharks, 7 rays and 2 squids) were identified, weighed and measured. When smaller and larger specimens were observed, samples were sorted according to size, and size-classes were identified as juvenile or adults if appropriate literature was available (Brunetti et al. 1998, Bezzi et al. 2000, Cosseau & Perrota 2000). Besides, we assigned each species to an ecological

group (pelagic, demersal, demersal-pelagic, demersal-benthic, benthic) according to their habitat and vertical distribution (Brunetti et al. 1998, Bezzi et al. 2000, Cosseau & Perrota 2000).

Proximate composition and energetic value were determined for 76 samples (44 from autumn and 32 from summer). Samples were dried at 100°C until a constant weight was reached. Moisture content was calculated by the difference between wet and dry mass, and then expressed as a percentage of the original mass (Horwitz 1960). Total lipids were extracted with a Soxhlet equipment, using an ether-ethylic solvent. Protein content was determined by the Lowry method (Lowry et al. 1951). Ash content was measured using a muffle furnace at 550°C (AKE 1337 1100°C). Since carbohydrate content is generally low in fish and its contribution to the energetic value is practically zero (Márquez et al. 1996, Payne et al. 1999, Anthony et al. 2000), this component was not measured. The energetic value was determined indirectly—using Rubner's coefficients for aquatic organisms: 9.5 kcal g⁻¹ for lipids, 5.65 kcal g⁻¹ for proteins (Winberg 1971)—and expressed in kJ g⁻¹ wet mass. All presented nutritional values are means of triplicate determinations (average standard deviation was less than 3%).

A multivariate analysis (correspondence analysis) was performed to investigate the association between species and nutritional variables (Digby & Kempton 1987, Ludwig & Reynolds 1988, Hair et al. 1999) using a statistical software package (STATISTICA; StatSoft 2001). Non-parametric Kruskal-Wallis and Mann-Whitney *U* rank tests were performed to test for seasonal differences, differences between adults and juveniles, and differences between ecological or taxonomic groups (Siegel & Castellan 1995, Conover 1999). In the case when more than 2 groups were compared, we performed post-hoc tests in order to determine in more detail how groups differed, using a pairwise comparison method that calculates a statistic (*T*) based on the differences of ranks of pairs and a critical value (CV; Conover 1999). If *T* > CV, pairs are assumed to be different (Conover 1999).

RESULTS

Fifty-two catches were performed at a depth range of 73 to 370 m (Fig. 2). Twenty-seven of these catches were done in autumn (82 to 370 m) and 25 in summer (73 to 119 m). There was no significant difference in the depth of catches between seasons (Mann-Whitney *U*-test,

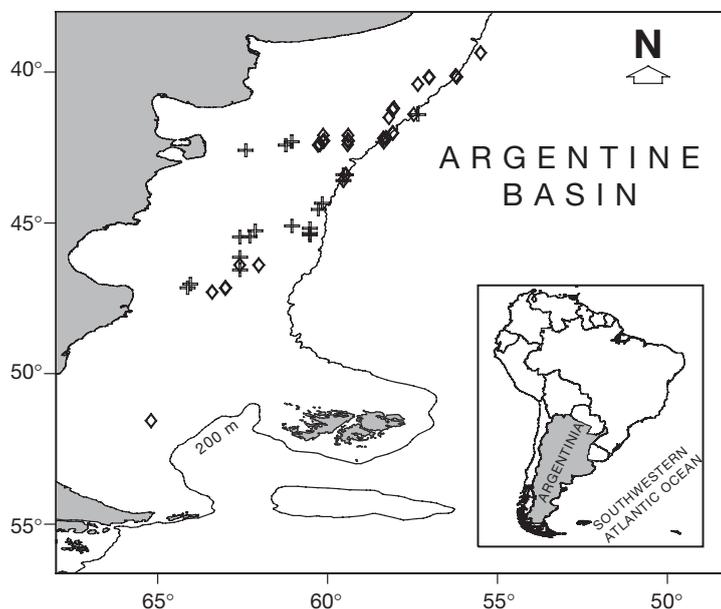


Fig. 1. Locations of catches of teleosts, elasmobranchs and cephalopods during autumn 2001 (◇) and summer 2002 (+) from vessels operating with bottom trawls

$U_{27,25} = 265.5$, $p > 0.05$). Of all observed species ($n = 39$), 51% was caught in both seasons ($n = 20$), 31% only in autumn ($n = 12$), and 18% only in summer ($n = 7$).

Wet mass ranged from 17 to 4475 g for teleosts, from 175 to 2425 g for sharks, from 260 to 3550 g for rays and from 72 to 1250 g for squids (Table 1). Total length was 14 to 99 cm for teleosts, 48 to 84 cm for sharks and 34 to 65 cm for rays (Table 1). Mantle length of squids ranged from 17 to 42 cm (Table 1).

Moisture content ranged from 60.5 to 82.5% and showed an inverse relation with lipid content ($n = 39$, Spearman $R = -0.8$, $p < 0.01$). Lipid and protein content varied among species (Table 2). Ash content was more constant; mean values were 3.1, 2.6 and 2% for teleosts, elasmobranches and squids respectively (Table 2).

The correspondence analysis showed an association of species with 3 biochemical variables. Two main groups associated with lipid (1) or protein (2), and 1 tiny group of teleosts (3) represented by *Prionotus nudigula* and *Cottunculus granulosis* stands out mostly due to the contribution of ashes (main dimension = 83% of variance explained; Fig. 3). The group of species closely associated with lipid is represented by *Dissostichus eleginoides*, *Stromateus brasiliensis*, *Parona signata*, *Seriola punctata*, *Bathyraxa brachyurops*, *Shroederichthys bivius*, *Squalus acanthias*, and *Macruronus magellanicus*. The group of species more associated with protein included teleost and ray species, the elasmobranch *Callorhynchus callorhynchus* and the squids *Illex argentinus* and *Moroteuthis ingens*. According to the results, lipid content was higher in the group of species associated with lipid (Kruskal-Wallis test $H_{2,39} = 19.18$, $p < 0.01$; Group 1 vs. Group 2: $T = 27.11$, $CV = 13.06$; Group 1 vs. Group 3: $T = 17.71$, $CV = 6.40$), but there

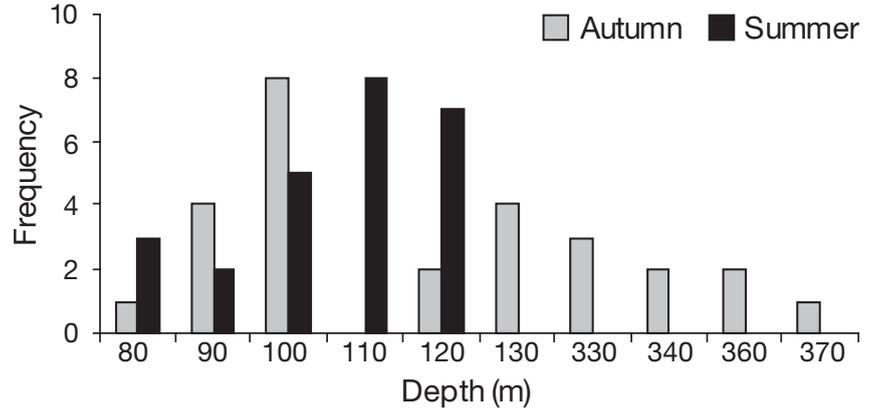


Fig. 2. Distribution of depths of geo-referenced hauls in autumn and summer in the SW Atlantic Ocean

Table 1. Mean wet mass (g) and length (cm) of species from the SW Atlantic Ocean. The ecological group for each species is shown in parentheses (D = demersal, DP = demersal-pelagic, DB = demersal-benthic, P = pelagic, B = benthic), n = number of specimens measured; for species with $n < 3$, wet mass and length are presented in the range column

Species	n	Wet mass (g)	Mean (range)	Length (cm)	Mean (range)
ELASMOBRANCHES					
Squalidae					
<i>Squalus acanthias</i> (DB)	22	893.2	(175–2425)	60.4	(47.5–75)
Scyliorhinidae					
<i>Schroederichthys bivius</i> (DB)	10	825.7	(447.7–1122.4)	67.2	(57.5–75.5)
Torpedinidae					
<i>Discopyge tschudii</i> (B)	1		795		41.2
Rajidae					
<i>Dipturus chilensis</i> (B)	8	630	(320–950)	50.4	(41–58.5)
<i>Psammobatis scobina</i> (B)	5	874	(260–2000)	47	(33.5–64.5)
<i>Psammobatis normani</i> (B)	8	627.5	(387.5–872.1)	45.7	(39.5–51.2)
<i>Bathyraxa brachyurops</i> (B)	2		(2900–3550)		(51.5–54)
<i>Bathyraxa macloviana</i> (B)	5	595	(300–800)	42.8	(34.5–48)
<i>Bathyraxa scaphiops</i> (B)	3	466.7	(350–600)	44.3	(40–50)
Callorhynchidae					
<i>Callorhynchus callorhynchus</i> (B)	1		1700		84
TELEOSTS					
Congridae					
<i>Bassanago albescens</i> (DB)	22	357.9	(212–625)	63.6	(56–71)
Moridae					
<i>Salilota australis</i> (DB)	5	1381.9	(295–4475)	54.4	(32.4–74)
<i>Austrophycis marginata</i> (DP)	3	38.9	(17–62)	17.8	(15–21)
Gadidae					
<i>Micromesistius australis</i> (DP)	4	943.8	(110.3–1375)	47.5	(27–57)
Macruronidae					
<i>Macruronus magellanicus</i> (DP)	5	1095	(300–1725)	71.7	(49–88)
Merlucciidae					
<i>Merluccius australis</i> (DP)	9	2447.8	(725–3625)	74.9	(61.5–86)
<i>Merluccius hubbsi</i> (DP)	20	536.7	(175–1457.3)	42	(33–64)
Macrouridae					
<i>Coelorhynchus fasciatus</i> (DB)	16	496.7	(187.3–1137)	45.9	(37–59)
Ophidiidae					
<i>Genypterus blacodes</i> (DB)	10	1303.3	(240–3500)	65.1	(42–98.5)

(Table 1 continued on next page)

Table 1 (continued)

Species	n	Wet mass (g)	Mean (range)	Length (cm)	Mean (range)
Scorpaenidae					
<i>Sebastes oculatus</i> (D)	8	486.6	(113.9–806.1)	33.3	(24.3–38.5)
Triglidae					
<i>Prionotus nudigula</i> (DB)	7	119.1	(113–140)	26	(25–28)
Congiopodidae					
<i>Congiopodus peruvianus</i> (D)	14	322.3	(50–727)	26.5	(18–35)
Serranidae					
<i>Acanthistius brasilianus</i> (DB)	7	603.6	(410–1000)	34.4	(31–41)
Bramidae					
<i>Brama brama</i> (DP)	9	3471.1	(3015–3920)	61.5	(57–63)
Zoarcidae					
<i>Ilucoetes fimbriatus</i> (D)	7	687.5	(450–925)	45.5	(41–53)
Bovichtidae					
<i>Cottopeca gobio</i> (D)	10	795.2	(353–2175)	38.7	(31–62)
Carangidae					
<i>Parona signata</i> (DP)	1		860		73.40
Cheilodactylidae					
<i>Nemadactylus bergi</i> (DB)	13	150.2	(43–400)	21.6	(16–33)
Nototheniidae					
<i>Dissostichus eleginoides</i> (DP)	1		3700		66.5
<i>Patagonotothen ramsayi</i> (DB)	23	154.1	(23.2–387.3)	23.4	(14–33)
Pinguipedidae					
<i>Pseudoperca semifasciata</i> (DB)	13	349.4	(95–900)	30.3	(21–43)
Scombridae					
<i>Scomber japonicus</i> (DP)	4	590	(380–725)	39.9	(35–43)
Centrolophidae					
<i>Seriola punctata</i> (DP)	8	771.8	(200–1281)	37.3	(28–44)
Stromateidae					
<i>Stromateus brasiliensis</i> (DP)	13	320.2	(191–380)	29.1	(25–32)
Psychrolutidae					
<i>Cottunculus granulatus</i> (D)	1		131.7		19
Paralichthyidae					
<i>Paralichthys patagonicus</i> (B)	1		491.4		37
Achiropsettidae					
<i>Mancopsetta maculata</i> (B)	4	384.6	(273.7–463.8)	34.5	(29.3–39)
CEPHALOPODS					
Ommastrephidae					
<i>Illex argentinus</i> (P)	22	316.9	(71.9–625)	24.7	(16.5–33)
Onychoteuthidae					
<i>Moroteuthis ingens</i> (P)	1		1250		41.5

were no significant differences in protein content between the group of species associated with protein and the other groups.

However, teleost fishes showed higher protein values than elasmobranchs (Kruskal-Wallis test $H_{3,76} = 14.88$, $p < 0.01$; teleosts vs. rays: $T = 25.49$, $CV = 13.84$; teleosts vs. sharks: $T = 20.83$, $CV = 16.15$). Rays presented the highest moisture contents ($H_{3,76} = 15.53$, $p < 0.01$; rays vs. teleosts: $T = 28.32$, $CV = 13.77$; rays vs. sharks: $T = 33.37$, $CV = 19.71$; rays vs. squids: $T = 32.00$, $CV = 21.91$) and the lowest lipid contents ($H_{3,76} = 10.86$, $p < 0.05$; rays vs. teleosts: $T = 17.85$,

$CV = 14.30$; rays vs. sharks: $T = 31.81$, $CV = 20.41$; rays vs. squids: $T = 30.10$, $CV = 22.75$). Comparing ecological groups (Table 1), benthic species showed the lowest lipid contents ($H_{3,66} = 12.67$, $p < 0.05$; benthic vs. demersal-pelagic: $T = 23.08$, $CV = 12.44$; benthic vs. demersal-benthic: $T = 12.56$, $CV = 11.90$; benthic vs. pelagic: $T = 22.05$, $CV = 18.55$), the lowest energetic values ($H_{3,66} = 15.91$, $p < 0.01$; benthic vs. demersal-pelagic: $T = 26.77$, $CV = 12.04$; benthic vs. demersal-benthic: $T = 16.64$, $CV = 11.52$; benthic vs. pelagic $T = 21.56$, $CV = 17.96$) and the highest moisture contents ($H_{3,66} = 15.43$, $p < 0.01$; benthic vs. demersal-pelagic: $T = 26.17$, $CV = 12.10$; benthic vs. demersal-benthic: $T = 18.55$, $CV = 11.58$; benthic vs. pelagic: $T = 21.87$, $CV = 18.05$). Demersal-benthic species showed lower lipid values than demersal-pelagic species ($T = 10.52$, $CV = 10.26$).

Lipid contents of demersal-benthic and demersal-pelagic groups did not differ between adults and juveniles: 5 vs. 4 % in demersal-benthic (Mann-Whitney U -test, $U_{9,9} = 29.00$, $p > 0.05$), 10 vs. 7 % in demersal-pelagic ($U_{5,5} = 10.00$, $p > 0.05$). Although formal statistical testing was impossible with only 2 samples, it was striking that *Nemadactylus bergi* adults showed a lipid content of 22 %, while juveniles showed a lipid content of only 5 %. Protein content was similar between adults and juveniles: 16 vs. 14 % in demersal-benthic ($U_{9,9} = 23.00$, $p > 0.05$) and 13 vs. 14 % in demersal-pelagic ($U_{5,5} = 12.00$, $p > 0.05$). Demersal-benthic species showed an increase in protein content in autumn ($U_{9,9} = 18.00$, $p < 0.05$; Table 3).

DISCUSSION

This work reports the nutritional values of several species cited as prey of some marine mammals and seabirds from the Patagonian coast (Table 4) and that are more frequently caught by commercial fishing vessels. Despite the diversity of potential prey and

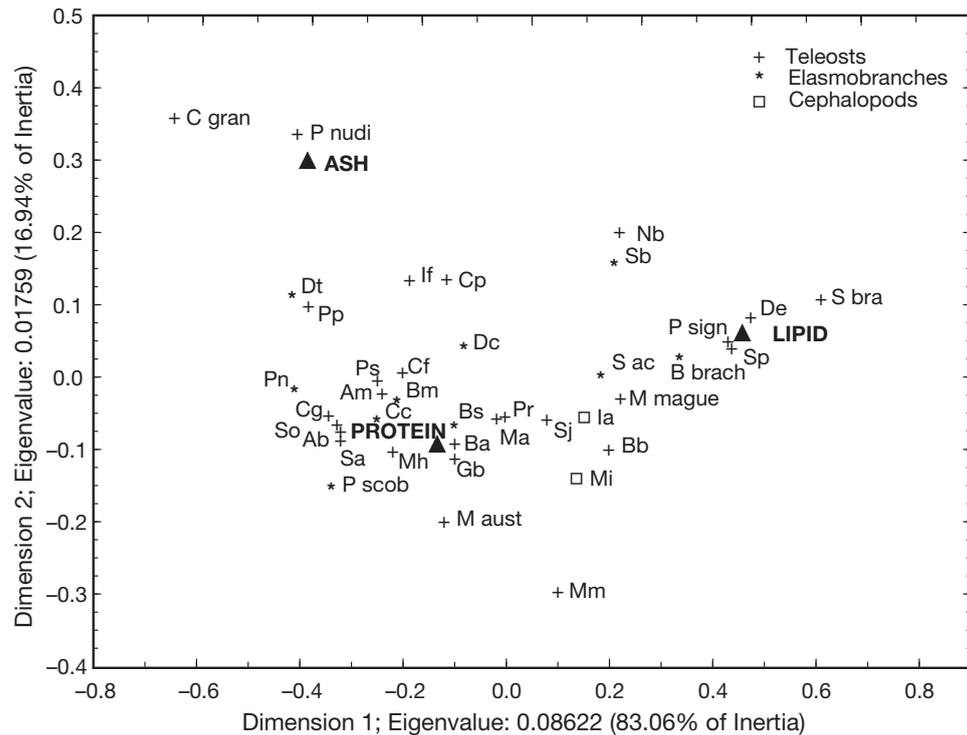


Fig. 3. Results of a multivariate correspondence analysis between some nutritional components and species identity. Samples from summer and autumn, and adults and juveniles, were averaged for each species. Species identity labels: Ab, *Acanthisitius brasiliensis*; Am, *Austrophycis marginata*; Ba, *Bassanago albescens*; B brach, *Bathyraja brachyurops*; Bb, *Brama brama*; Bm, *B. macloviana*; Bs, *B. scaphiops*; Cc, *Callorhynchus callorhynchus*; Cf, *Coelorhynchus fasciatus*; C gran, *Cottunculus granulosus*; Cg, *Cottoperca gobio*; Cp, *Congiopodus peruvianus*; Dc, *Dipturus chilensis*; De, *Dissostichus eleginoides*; Dt, *Discopyge tschuddi*; Gb, *Genypterus blacodes*; Ia, *Illex argentinus*; If, *Iluocoetes fimbriatus*; M mague, *Macruronus magellanicus*; Mm, *Mancopsetta maculata*; M aust, *Merluccius australis*; Ma, *Micromesistius australis*; Mi, *Moroteuthis ingens*; Mh, *M. hubbsi*; Nb, *Nemadactylus bergi*; P nudi, *Prionotus nudigula*; Pn, *P. normani*; Pp, *Paralichthys patagonicus*; P scob, *Psammobatis scobina*; P sign, *Parona signata*; Pr, *Patagonotothen ramsayi*; Ps, *Pseudoperca semifasciata*; S ac, *Squalus acanthias*; Sa, *Salilota australis*; Sb, *Schroederichthys bivius*; S bra, *Stromateus brasiliensis*; Sj, *Scomber japonicus*; So, *Sebastes oculatus*; Sp, *Seriolella punctata*

the nutritional quality of different species in the SW Atlantic Ocean system, only the Argentine hake *Merluccius hubbsi* and the Argentine shortfin squid *Illex argentinus* were described as important contributors to the diet of most predators, with a relative importance index greater than 10% (Table 4).

Thirty-eight percent of the species analysed here are commercially important. Only the Argentine hake *Merluccius hubbsi* was a target species for bottom trawler vessels, and the remaining 62% of the species are by-catch (Bezzi et al. 2000, Cosseau & Perrotta 2000). Seasonal migration of some species and the seasonal distribution of catches may explain why some species were sampled in only 1 season, e.g. *Dissostichus eleginoides* and *Moroteuthis ingens*, which are targeted in autumn with specific fishing gear, or *Micromesistius australis*, whose summer distribution is

Table 2. Mean proximate composition (% wet mass) and energetic value (kJ g^{-1} wet mass) of species from the SW Atlantic Ocean

Species	Moisture	Ash	Lipid	Protein	Energetic value
ELASMOBRANCHES					
Squalidae					
<i>Squalus acanthias</i>	72.79	2.31	8.55	12.79	6.42
Scyliorhinidae					
<i>Schroederichthys bivius</i>	72.21	3.35	9.36	11.12	6.34
Torpedinidae					
<i>Discopyge tschuddi</i>	82.50	3.05	1.58	8.67	2.68
Rajidae					
<i>Dipturus chilensis</i>	78.06	2.75	4.42	10.51	4.23
<i>Psammobatis scobina</i>	77.73	2.36	2.05	12.56	3.79
<i>Psammobatis normani</i>	77.90	3.31	1.87	12.13	3.61
<i>Bathyraja brachyurops</i>	75.41	1.92	10.00	11.66	6.72
<i>Bathyraja macloviana</i>	77.64	2.69	3.22	11.68	4.04
<i>Bathyraja scaphiops</i>	78.39	2.65	2.97	11.79	3.97
Callorhynchidae					
<i>Callorhynchus callorhynchus</i>	77.18	2.09	3.89	10.79	4.09
TELEOSTS					
Congridae					
<i>Bassanago albescens</i>	75.78	2.58	4.76	14.14	5.25

Table 2 continued on next page

Table 2 (continued)

Species	Moisture	Ash	Lipid	Protein	Energetic value
Moridae					
<i>Salilota australis</i>	77.40	3.15	2.62	14.39	4.44
<i>Austrophycis marginata</i>	73.48	3.95	4.15	16.26	4.91
Gadidae					
<i>Micromesistius australis</i>	73.88	2.47	5.55	13.42	5.38
Macruronidae					
<i>Macruronus magellanicus</i>	72.82	2.07	8.59	13.14	6.51
Merlucciidae					
<i>Merluccius australis</i>	76.08	2.03	4.48	15.66	5.48
<i>Merluccius hubbsi</i>	77.27	2.84	3.65	14.65	4.91
Macrouridae					
<i>Coelorhynchus fasciatus</i>	76.44	3.44	4.00	13.34	4.74
Ophidiidae					
<i>Genypterus blacodes</i>	76.67	2.59	5.02	15.28	5.60
Scorpaenidae					
<i>Sebastes oculatus</i>	73.88	3.85	2.99	16.61	5.12
Triglidae					
<i>Prionotus nudigula</i>	70.29	6.94	3.62	13.36	4.63
Congiopodidae					
<i>Congiopodus peruvianus</i>	74.33	4.00	5.26	12.21	5.00
Serranidae					
<i>Acanthistius brasiliensis</i>	76.36	2.79	2.27	12.41	3.82
Bramidae					
<i>Brama brama</i>	67.66	2.09	10.85	18.38	8.65
Zoarcidae					
<i>Ilucoetes fimbriatus</i>	78.15	3.00	3.22	8.82	3.36
Bovichtidae					
<i>Cottopectera gobio</i>	74.78	3.36	2.49	13.93	4.28
Carangidae					
<i>Parona signata</i>	62.43	2.49	16.24	16.23	10.27
Cheilodactylidae					
<i>Nemadactylus bergi</i>	62.83	4.98	13.25	15.13	8.83
Nototheniidae					
<i>Dissostichus eleginoides</i>	61.42	2.50	17.06	15.64	10.46
<i>Patagonotothen ramsayi</i>	73.06	3.10	7.36	17.07	6.88
Pinguipedidae					
<i>Pseudoperca semifasciata</i>	73.94	3.70	3.84	14.56	4.97
Scombridae					
<i>Scomber japonicus</i>	69.66	2.62	8.13	16.23	7.06
Centrolophidae					
<i>Serirolella punctata</i>	63.96	2.15	14.78	14.83	9.36
Stromateidae					
<i>Stromateus brasiliensis</i>	67.25	1.86	17.48	12.48	9.92
Psychrolutidae					
<i>Cottunculus granulosus</i>	77.76	6.08	0.97	11.01	2.99
Paralychthyidae					
<i>Paralichthys patagonicus</i>	76.17	4.05	2.27	12.11	3.77
Achiropsettidae					
<i>Mancopsetta maculata</i>	60.55	1.06	11.29	27.90	11.45
CEPHALOPODS					
Ommastrephidae					
<i>Illex argentinus</i>	72.52	2.05	7.90	13.88	6.42
Onychoteuthidae					
<i>Moroteuthis ingens</i>	77.24	1.34	6.54	12.81	5.64

centred around the Falkland Islands, but whose distribution during autumn–winter is much wider (Cosseau & Perrotta 2000). Another case is *Scomber japonicus*, which migrates to coastal waters during summer (Cosseau & Perrotta 2000), coinciding with the displacement of the catches during summer (see Fig. 1). Besides their temporally variable geographic distribution, these species have the capacity to move vertically between intermediate and superficial water layers, making them potential prey of both deep-water-feeding and surface-water-feeding predators. Many of these species are distributed in close relation to the cold waters of the Malvinas/Falkland Current, which is also where petrels, albatrosses and elephant seals forage (Campagna et al. 1998, 1999, Nicholls et al. 2002, Quintana & Dell'Arciprete 2002, Campagna & Croxall 2003).

One of the 2 main prey species for top predators, *Merluccius hubbsi*, is one of the most abundant resources in the area, but also one of the most targeted species by fisheries. In fact, it is an over-fished resource that is near to collapse (Bezzi et al. 2000). Hence, it is useful to have data on nutritional values of other species, since it can help us to understand changes in trophic responses of predators as consequence of seasonal changes in food availability. Trites & Donnelly (2003) have shown strong evidence for a relationship between the decline of Steller's sea lions *Eumetopias jubatus* in the Gulf of Alaska and Aleutian Islands between the late 1970s and 1990s and the reduced availability of suitable prey, which may have been caused by a reduced abundance of several key species of high nutritional quality. In the SW Atlantic Ocean, there is no evidence for declining populations of top predators, perhaps because this system is offering a broader spectrum of prey of high energetic value. Teleost fish species in the SW Atlantic Ocean have higher energetic values than those from the Gulf of Alaska in the Northern Pacific Ocean (Kruskal-Wallis test $H_{2,61} = 11.16$, $p < 0.05$; $T = 11.15$, $VC = 9.46$; Table 5). Our energetic values for teleosts were similar to values of Myctophidae species reported in other Southern Ocean studies (Atlantic Ocean: 6.6 to 9.1 kJ g^{-1} , Clark & Prince 1980; Indian Ocean: 7.4

Table 3. Seasonal comparison of mean proximate components (% wet mass) and energetic values (kJ g⁻¹ wet mass) of demersal-benthic and demersal-pelagic species (n = total number of specimens included in the samples); ns = not significant

Species	n	Season	Moisture	Ash	Lipid	Protein	Energetic value
ELASMOBRANCHES							
<i>Squalus</i>	15	Autumn	71.47	2.43	9.20	13.51	6.85
<i>acanthias</i>	7	Summer	74.11	2.18	7.92	12.07	5.99
<i>Schroederichthys</i>	5	Autumn	71.83	3.49	11.62	10.44	7.07
<i>bivius</i>	5	Summer	72.59	3.20	7.11	11.80	5.61
TELEOSTS (DEMERSAL-BENTHIC)							
<i>Bassanago</i>	15	Autumn	74.18	2.99	5.23	17.63	6.27
<i>albescens</i>	7	Summer	77.39	2.16	4.29	10.66	4.22
<i>Salilota</i>	1	Autumn	76.02	3.69	3.88	16.41	5.42
<i>australis</i>	3	Summer	79.67	2.83	1.17	11.37	3.15
<i>Genypterus</i>	1	Autumn	75.55	2.72	9.99	13.69	7.20
<i>blacodes</i>	4	Summer	78.22	3.15	1.23	12.48	3.44
<i>Nemadactylus</i>	1	Autumn	60.08	5.52	13.41	17.57	9.47
<i>bergi</i>	4	Summer	56.32	4.58	21.63	15.94	12.34
<i>Patagonotothen</i>	11	Autumn	71.30	3.33	10.44	18.9	8.46
<i>ramsayi</i>	12	Summer	75.14	2.86	4.27	15.24	5.30
Mann-Whitney U-test, U _{9,9}			20.00	26.00	22.00	18.00	16.00
Significance			ns	ns	ns	p < 0.05	p < 0.05
TELEOSTS (DEMERSAL-PELAGIC)							
<i>Merluccius</i>	5	Autumn	74.74	1.15	6.68	15.02	6.20
<i>australis</i>	2	Summer	77.43	2.91	2.28	16.29	4.76
<i>Merluccius</i>	12	Autumn	76.4	2.36	5.36	12.91	5.18
<i>hubbsi</i>	8	Summer	78.14	3.26	1.94	16.38	4.64
<i>Brama brama</i>	7	Autumn	67.61	2.06	10.96	17.59	8.51
	2	Summer	67.71	2.12	10.74	19.16	8.79
<i>Seriolella</i>	4	Autumn	60.98	2.20	15.13	15.93	9.76
<i>punctata</i>	4	Summer	66.93	2.11	14.44	13.72	8.96
<i>Stromateus</i>	7	Autumn	65.56	1.94	17.09	12.13	9.64
<i>brasiliensis</i>	3	Summer	65.09	1.63	22.28	11.80	11.76
Mann-Whitney U-test, U _{5,5}			9.00	5.00	10.00	12.00	11.00
Significance			ns	ns	ns	ns	ns

to 13.3 kJ g⁻¹, Lea et al. 2002; Pacific Ocean: 5.4 to 10.9 kJ g⁻¹, Tierney et al. 2002).

We found that rays had the lowest nutritional value, due to their lower lipid and energy contents. Compared with teleosts and in correspondence with the rest of the elasmobranchs, rays also showed a poor protein content. This low nutritional value fits well with the low index of relative importance of elasmobranchs in the diet of marine mammals (0.4%; Koen Alonso et al. 2000). However, and with relevance to biases associated with the techniques commonly implemented in diet reconstruction, shark species had lipid and energetic values that were as high as teleosts and squids.

Typical lean fish species are those that are associated with the sea floor, while pelagic fishes are usually referred to as 'fatty fishes' due to their high lipid content (Murray & Burt 1969). Our results agree with this

general picture. Benthic species were the lowest in lipid content and consequently had the lowest energetic values and highest moisture contents (although most of them were rays); demersal-pelagic fishes were higher in lipid and energetic values. An exception to this pattern is the benthic flounder *Mancopsetta maculata*, which showed a high lipid content but a low moisture content. In all cases, we found a general inverse relationship between moisture and lipid content. Some studies have reported this same trend (Clarke et al. 1994, Márquez et al. 1996, Anthony et al. 2000) and have related this to buoyancy adjustments in some cases, but the main reason for the relationship could be the fact that, unlike proteins and carbohydrates, lipids can be stored almost 'dry' (Stryer 1995).

For marine organisms, body composition is variable with respect to geographical location, time of year, size, maturity condition, sex, and feeding regime or ecological habits (Saadettin et al. 1988, Lawson et al. 1998). Some authors have found a reduction of the protein component during the spawning season (Ando & Hatano 1986). Since spawning is a process of high energy demand and fish generally do not feed during spawning, lipid stores fall as spawning progresses, and the protein component can also be depleted for this purpose. During intensive feeding seasons, the protein

levels rise back to normal values. Reinitz et al. (1979) consider that the nutritional composition of food is the most important factor affecting the proximal composition of fish. Unfortunately, knowledge is not complete for all species from the SW Atlantic, and available information is still insufficient to relate autumnal increases in protein and energetic values in demersal-benthic species with spawning or feeding regimes. Another factor affecting proximal components is the gravid condition. Croxall & Prince (1982) have found in krill that lipid and energetic value was 42% higher for gravid females than for mature males. The flounder *Mancopsetta maculata* showed high average lipid, protein and energetic values: this can be explained by the fact that it was the only benthic species whose sample included gravid specimens. In some studies, larger size (or adult) categories tended to have higher lipid

Table 4. Top predators in the SW Atlantic Ocean and their key prey species

Predators	Prey species	Sources
MARINE MAMMALS		
Cetaceans		
<i>Cephalorhynchus commersonii</i> (Commerson's dolphin)	<i>Merluccius hubbsi</i> <i>Patagonotothen ramsayi</i> <i>Stromateus brasiliensis</i> <i>Illex argentinus</i>	Bastida et al. (1988), Crespo et al. (1997) Crespo et al. (1997) Bastida et al. (1988), Crespo et al. (1994, 1997)
<i>Lagenorhynchus obscurus</i> (Dusky dolphin)	<i>Macruronus magellanicus</i> <i>Merluccius hubbsi</i> <i>Stromateus brasiliensis</i> <i>Notothenia</i> sp. <i>Illex argentinus</i>	Bastida et al. (1988) Koen Alonso et al. (1998) Crespo et al. (1994), Koen Alonso et al. (1998) Crespo et al. (1994)
<i>Delphinus delphis</i> (Common dolphin)	<i>Illex argentinus</i> <i>Moroteuthis ingens</i>	Crespo et al. (1994)
<i>Globicephala melaena</i> (Long-finned pilot whale)	<i>Illex argentinus</i>	Crespo et al. (1994)
<i>Physeter macrocephalus</i> (Sperm whale)	<i>Illex argentinus</i> <i>Moroteuthis ingens</i>	Clarke et al. (1980), Crespo et al. (1994) Crespo et al. (1994)
Pinnipeds		
<i>Otaria flavescens</i> (South American sea lion)	<i>Merluccius hubbsi</i> <i>Genypterus blacodes</i> <i>Pseudopercis semifasciata</i> <i>Stromateus brasiliensis</i> <i>Acanthistius brasilianus</i> <i>Seriolella punctata</i> <i>Lucooetes fimbriatus</i> <i>Nemadactylus bergi</i> <i>Illex argentinus</i>	Koen Alonso et al. (2000)
MARINE BIRDS		
<i>Diomedea exulans</i> (Wandering albatross)	<i>Illex argentinus</i>	Croxall & Prince (1994)
<i>Spheniscus magellanicus</i> (Magellanic penguin)	<i>Merluccius hubbsi</i> <i>Illex argentinus</i>	Scolaro et al. (1999) Clarke et al. (1980), Scolaro et al. (1999)
SHARKS		
<i>Galeorhinus galeus</i> (Tope shark)	<i>Stromateus brasiliensis</i>	Cosseau & Perrotta (2000)

and energetic values than smaller size (or juvenile) categories (Croxall & Prince 1982, Clarke et al. 1994, Anthony et al. 2000). However, other studies have not found such a relationship between size and proximate composition (Payne et al. 1999), and yet another even found the opposite pattern: smaller size-classes showed higher energy contents (Tierney et al. 2002). It seems that we cannot use general rules, and proximal composition depends strongly on the conditions for each species.

The data presented in this study cover a broad spectrum of species and give practical and useful information about the nutritional values of regional species. Since differences in lipid and protein contents have important implications for digestive efficiency, foraging behaviour and dietary preferences of predators (Lawson et al. 1998), further sampling of individual species is needed for the establishment of detailed standards for composition of potential prey.

Feeding habits, foraging movement patterns, and energy and time expenditure are a predator's inte-

gration of its requirements and perceptions of the nutritional resources (Robbins 1983). It is also well known that the distribution of marine predators at sea is closely related to food availability and productivity conditions. Bathymetry has been shown to strongly affect the amount and types of fish available for some top predators, and shelves with a higher surface area offer a greater opportunity for demersal foraging (Green & Burton 1993). These circumstances, plus high productivity conditions such as frontal zones, could help explain why, even while breeding at South Georgia, wandering albatross, giant petrel and white-chinned petrel forage over the Patagonian shelf (Croxall & Wood 2002). Predators can compensate for variation in prey availability through adjusted selection of prey as a function of their nutritional quality (Krebs & Davies 1978, Anthony et al. 2000). Knowledge of the nutritional value of food items turns into an important tool when trying to comprehend these adjustments.

Table 5. Energy content (kJ g⁻¹ wet mass) of teleost species of the Northern Pacific Ocean calculated from the lipid and protein values in Payne et al. (1999). Energetic values were calculated using the same coefficients as used in this study (see 'Materials and methods')

Species	Northern Ocean	
	Pacific (Gulf of Alaska)	Pacific (Bering Sea)
Osmeridae		
<i>Thaleichthys pacificus</i>	10.05	10.90
<i>Mallotus villosus</i>	5.30	6.50
<i>Hypomesus pretiosus</i>	7.25	–
<i>Osmerus mordax</i>	–	6.90
Ammodytae		
<i>Ammodytes hexapterus</i>	5.23	6.12
Trichodontidae		
<i>Trichodon trichodon</i>	5.11	5.30
Stichaeidae		
<i>Lumpenus</i> spp.	5.40	–
Gadidae		
<i>Theragra chalcogramma</i>	3.93	–
Zaproridae		
<i>Zaproa silenus</i>	3.00	–
Hexagrammidae		
<i>Pleurogrammus monopterygius</i>	4.94	–
Clupeidae		
<i>Clupea pallasii</i>	3.43	–

Acknowledgements. We would like to express our gratitude to the Harengus S.A. fishing company for the samples provided, and to Centro Nacional Patagónico (CONICET) and Universidad Nacional de la Patagonia for institutional support. We thank Dr. A. Gosztonyi for his help with fish identification, Lic. N. De Vido for technical assistance in the chemical analyses, and Dr. P. Edelaar for improving the English language of this paper. We also thank the editor and 2 anonymous reviewers for their comments and suggestions.

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: April 5, 2004; Accepted: January 27, 2005
 Proofs received from author(s): March 30, 2005