CCAMLR Science, Vol. 4 (1997): 105-124

COMPARATIVE FEEDING ECOLOGY OF PATAGONIAN TOOTHFISH (*DISSOSTICHUS ELEGINOIDES*) IN THE SOUTHWESTERN ATLANTIC

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Abstract

The diet of Patagonian toothfish (*Dissostichus eleginoides*) was investigated in two offshore regions in the southwestern Atlantic: on the Argentinian continental shelf/slope between 46°–55°S and 60°–64°W, and around South Georgia between 53°–55°30′ and 35°–45°W. The South Georgia area was divided into two zones: the shelf zone and deep-water zone. On the Argentinian continental shelf/slope, the length of *D. eleginoides* ranged from 30 to 95 cm total length (TL) which corresponds to the juvenile stage. Around South Georgia, the size distribution included both juvenile and adult stages, and ranged between 18 and 212 cm TL. The diets of fish of various sizes and both sexes were compared, and the feeding status of this species is discussed. *D. eleginoides* is a mixed-species carnivore, feeding principally on fish and secondarily on crustaceans and cephalopods. The principal fish species in the diet of *D. eleginoides* on the Argentinian continental shelf were nototheniids (e.g. *Patagonotothen ramsayi*). Around South Georgia, adult *D. eleginoides* preyed mainly on fish (Zoarcidae, Moridae, Bathydraconidae, Channichthyidae) and on Decapoda, while juveniles in coastal waters consumed krill and, in deeper waters, various species of fish (Nototheniidae, Myctophidae, Channichthyidae). It was also found that the diet of *D. eleginoides* varied in relation to its size and water depth in both the shallow and deep-water zones.

Résumé

Étude du régime alimentaire de la légine australe (*Dissostichus eleginoides*) dans deux secteurs au large du sud-ouest de l'Atlantique : sur le plateau continental argentin et la pente entre 46°–55°S et 60°–64°W, et autour de la Géorgie du Sud entre 53°–55°30′ et 35°–45°W. Le secteur de la Géorgie du Sud est divisé en deux zones : celle du plateau et celle des eaux profondes. Sur le plateau continental argentin et la pente, la longueur totale (TL) de *D. eleginoides* variait de 30 à 95 cm, ce qui correspond au stade juvénile. Autour de la Géorgie du Sud, la distribution de tailles, de 18 à 212 cm de TL, comprenait les stades adulte et juvénile. L'auteur compare le régime alimentaire de poissons de diverses tailles et des deux sexes, et examine le statut alimentaire de cette espèce. *D. eleginoides* est un carnivore qui se nourrit d'espèces mixtes, principalement de poissons et à un moindre degré de crustacés et de céphalopodes. Les espèces de poissons prédominantes dans le régime alimentaire de *D. eleginoides* sur le plateau continental argentin sont les notothéniidés (*Patagonotothen ramsayi*, par ex.). Autour de la Géorgie du Sud, les adultes de *D. eleginoides* se nourrissent essentiellement de poissons (Zoarcidae, Moridae, Bathydraconidae, Channichthyidae) et de décapodes, alors que les juvéniles préfèrent le krill dans les eaux côtières et, dans les eaux plus profondes, diverses espèces de poissons (Nototheniidae, Myctophidae, Channichthyidae). Il est également apparu que le régime alimentaire de *D. eleginoides* varie en fonction de la taille de celui-ci et de la profondeur, tant dans les eaux profondes que peu profondes.

Резюме

Режим питания патагонского клыкача (*Dissostichus eleginoides*) изучался в двух районах юго-западной части Атлантического океана: на аргентинском континентальном шельфе/склоне между 46°-55°ю.ш. и 60°-64°з.д., и вокруг Южной Георгии между 53°-55°30'з.д. и 35°-45°з.д. Район Южной Георгии был подразделен на две зоны: шельфовую и глубоководную. На аргентинском континентальном шельфе/склоне общая длина (TL) клыкача колебалась в диапазоне 30-95 см, что соответствует стадии молоди. Вокруг Южной Георгии наблюдались взрослые особи и молодь рыбы длиной от 18 до 212 см TL. Был подвергнут сравнению рацион рыб обоего пола различной длины. Обсуждается степень наполнения желудков у особей *D. eleginoides*, который питается в основном рыбой, но иногда и ракообразными и головоногими. Главными рыбными компонентами рациона *D. eleginoides* на аргентинском континентальном шельфе являлись нототениевые (напр. *Patagonotothen ramsayi*). В районе Южной Георгии взрослые особи *D. eleginoides* питались в основном рыбой (бельдюговыми, моровыми, антарктическими плосконосыми и белокровными рыбами) и десятиногими, а молодь в прибрежных водах питалась крилем и, в более глубоких водах, различными видами рыб (нототениевыми, светящимися анчоусами и белокровными рыбами). Было обнаружено, что рацион *D. eleginoides* менялся в зависимости от размера особи и глубины как в мелких, так и глубоководных зонах.

Resumen

Se analizó la dieta del bacalao de profundidad (*Dissostichus eleginoides*) del Atlántico suroccidental, en la plataforma continental argentina (entre 46°–55°S y 60°–64°W), y alrededor de las islas Georgias del Sur (entre 53°–55°30′ y 35°–45°W), considerando en ésta última región una zona costera y otra de aguas profundas. En la plataforma continental argentina, el rango de longitudes (TL) de *D. eleginoides* se encuentra entre 30 y 95 cm, correspondiendo a estadios juveniles. Alrededor de las islas Georgias del Sur, la distribución de tallas comprende tanto juveniles como adultos, estando el rango de longitudes entre 18 y 212 cm. Se compara la dieta de los peces por sexo e intervalo de talla y se analiza la condición alimentaria de esta especie. *D. eleginoides* es una especie carnívora cuya dieta está compuesta de varios tipos de presa; su fuente principal de alimento son los peces y en segundo lugar los crustáceos y cefalópodos. El componente principal de la dieta de *D. eleginoides* de la plataforma continental argentina son las nototenias (*Patagonotothen ramsayi*). Alrededor de Georgia del Sur, los ejemplares adultos de *D. eleginoides* consumen principalmente peces (Zoarcidae, Moridae, Bathydraconidae, Channichthyidae) y Decapoda. Los juveniles consumen kril en la región costera y peces (Nototheniidae, Myctophidae, Channichthyidae) en la región de aguas profundas. La dieta de *D. eleginoides* varía de acuerdo con su tamaño y con el estrato de profundidad, tanto en aguas costeras como profundas.

Keywords: *Dissostichus eleginoides*, feeding ecology, Patagonian toothfish, southwestern Atlantic, CCAMLR

INTRODUCTION

Dissostichus eleginoides is widespread in the Southern Hemisphere, inhabiting waters near the Antarctic Convergence in the Pacific, Atlantic and Indian Oceans. Its geographic distribution ranges from 30°S in the Pacific, to the north of Chile, to Cape Horn (Fischer and Hureau, 1985; Oyarzún and Campos, 1987), along the coast of Argentina, in particular, off southern Patagonia, South Georgia, Malvinas/Falkland Islands, Shag Rocks and the islands of the Scotia Arc (Gon and Heemstra, 1990), to shelves and seamounts of the Indian sector, Kerguelen-Heard Ridge, Bouvet Islands and Macquarie Island (Lloris and Rucabado, 1991). Even though Yukhov (1972), based on data from the analysis of sperm whale stomach contents, reported the southern distribution limit of this species to be 55°S, Fischer and Hureau (1985) found juvenile *D. eleginoides* near the Antarctic Peninsula. Two biologically distinct populations of this species are recognised, one in the southwest Atlantic (Argentinian continental shelf/slope to South Georgia) and another in the sub-Antarctic region of the Indian Ocean (Hureau and Ozouf-Costas, 1980). These authors found that individuals in these populations had different maximum sizes and

growth rates. However, recent data indicate that the maximum size of individuals in both regions is similar, around 215 cm total length (TL) (Gon and Heemstra, 1990).

In the southwestern Atlantic, *D. eleginoides* occurs widely within the Malvinas/Falklands current, south to 48°S. In this deep-water sector, mean catch rates of up to 5 tonnes/hour have been reported by Otero et al. (1982) during spring to the east of Isla de los Estados (55°S, 63°W). This species is also present to the north of 48°S up to 37°S, in the Malvinas/Falklands current, though reported mean catch rates are less than 0.3 tonnes/hour (Otero et al., 1982). Commercial catches of *D. eleginoides* in this region have increased markedly, from 133 tonnes in 1991 to 6 090 tonnes during January to October 1994 (Cassia and Perrotta, 1996). This increase reflects changes in the commercial status of this species, from a non-target species taken by Argentinian 'surimi' factory ships to target species in the longline fishery.

The life cycle of *D. eleginoides* includes a pelagic phase, in which it inhabits depths between 70 and 1 500 m (Fischer and Hureau, 1985; Gon and Heemstra, 1990), and in Chilean waters adult fish are found occasionally down to 2 500 m (Mora et al., 1986). Eggs, larvae and postlarvae are found around South Georgia during summer (December–January) (Efremenko, 1983) and on the south Patagonia shelf from October onwards (Ciechomski and Weiss, 1976). Ehrlich et al. (1996) found larvae in the Malvinas/Falklands current during spring (September–December), at depths of 100 to 200 m. Adult *D. eleginoides* feed on fish, macro-crustaceans and cephalopods (Tarverdiyeva, 1972; Lloris and Rucabado, 1991; McKenna, 1991), while postlarvae and juveniles consume zooplankton (*Euphausia similis*) and small fish (Duhamel, 1981).

We investigated the diet of *D. eleginoides* in two offshore areas (Argentinian continental shelf/slope and South Georgia), in relation to fish size and sex, and discuss the feeding ecology of this species.

MATERIAL AND METHODS

The data were obtained from *D. eleginoides* caught on the Argentinian continental shelf/slope (46°–55°S; 60°–64°W) at depths from 112 to 650 m during three cruises conducted by RV *Capitán Oca Balda*, Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), during 1994 and 1995. Data were also acquired from samples taken around South Georgia (53°–55°30'S; 35°–45°W) by RV *Dr Eduardo L. Holmberg* (INIDEP) during February 1994 at depths from 113 to 306 m (sampling zone SG1), and from a commercial longline vessel *Isla Sofia* at depths from 1 050 to 1 530 m (sampling zone SG2) during March and April 1995 (Table 1). The surveys on the Argentinian continental shelf/slope followed a random stratified sampling strategy; stratification was made by area and depth intervals. In all three cruises, samples were collected using an 'Engel' bottom trawl (33.5 m headline, 50 m groundrope, 32 mm codend mesh size) and the duration of each haul was 30 minutes. All fish were sampled from each haul.

The longliner *Isla Sofia* operated a main line of 20 000 m, with branch lines each with 90 hooks (model 'Ancora', 30 mm gap) spaced at 1 m

Table 1: Study details: vessels used, date, coordinates, mean depth sampled (m), fish number (n) and total length range (cm) in samples of *D. eleginoides*.

Study Area/Vessel	Date	Latitude (S)		Longitude (W)		Depth (m)	n	Length (cm)
South Georgia (SG1) RV *Eduardo L. Holmberg*	Feb 94	53°26′	55°26′	35°00′	42°23′	197.1	155	18 – 90
South Georgia (SG2) *Isla Sofia*	Mar 95	53°11′	55°12′	36°30′	45°00′	1197.5	3272	57 – 212
Argentinian continental shelf/slope RV *Capitán Oca Balda*								
Cruise 1	Feb 94	46°34′	49°43′	60°54′	62°15′	225.1	46	31 – 69
Cruise 2	Mar 94	51°12′	54°54′	60°18′	64°20′	358.6	169	29 – 95
Cruise 3	Feb 95	46°25′	49°43′	60°19′	62°39′	216.7	27	29 – 89

intervals. This fishing method is selective for *D. eleginoides* and allows the gear to be set at depths where the fish are known to occur. The samples for the diet study were collected from each of the 43 longline sets (total $n = 3\,272$ fish).

Length-frequency distributions were determined by grouping individuals in 10 cm total length (TL) classes. Fish were sorted by sex; individuals of indeterminate sex (<1%) were excluded from the analysis.

Food items present in the stomach were identified to the lowest possible taxonomic level, and when the degree of digestion permitted, measured and counted. The percentages of principal food items in the diet were calculated in terms of frequency of occurrence (%F), numbers (%N) and weight (%W) (Rosecchi and Nouaze, 1987). Lauzanne's (1975) alimentary index (AI) was calculated for samples taken in the Argentinian continental shelf/slope area because weight data were available for this area. Stomach fullness was also evaluated.

Spearman's correlation coefficient by ranges (Fritz, 1974; Woehler and Sánchez, 1994) and cluster analysis were used to characterise feeding preferences by sex and length categories in each study area and depth zone. Length groups by depth zones were classified hierarchically by cluster analysis, considering Euclidean distance measure and Ward linkage. The basic data matrix used was the frequency of occurrence of principal prey items. On the Argentinian shelf (AS), the overall size range (29 to 95 cm TL) was divided into five groups; in the South Georgia shelf zone (SG1) the range (18 to 95 cm TL) was divided into four size groups and in the South Georgia deep-water zone (SG2) the overall size range (57 to 212 cm TL) was divided into eight size groups. For Spearman analysis, differences were considered statistically significant when $P < 0.05$.

RESULTS AND DISCUSSION

Distribution and Size Structure of *D. eleginoides*

On the Argentinian continental shelf/slope, 66.6% of hauls containing *D. eleginoides* were made between depths of 112 and 300 m. In general, fish length ranged from 29 to 79 cm TL for males and 29 to 95 cm TL for females (Figure 1). 59.3% of fish caught were in the size interval from 40 to 49 cm TL. Females were relatively more abundant than males, and only females were larger than 80 cm TL. Argentinian research vessels found *D. eleginoides* during spring surveys conducted on the Argentinian continental shelf/slope, between 37°20′ and 55°S. The highest concentration found (>1 tonne/n mile^2) was between 53° and 55°S in depths greater than 200 m (Cotrina, 1981; Otero et al., 1982; Cassia and Perrotta, 1996). In the area between 53°–54°S and 60°–64°W, a nursery ground of the species was found during spring 1995, with fish varying from 38 to 66 cm TL, and a mean length of 52 cm TL (Cordo, 1995).

In zone SG1 (<300 m deep), data from the South Georgia shelf and Shag Rocks area were pooled (Figure 2). In this zone, females ranged from 18 to 90 cm TL and males from 30 to 60 cm TL, with most fish around 60 cm TL. Sampling on the South Georgia shelf was conducted at a mean depth of 240.5 m, and 80% of the trawls in which this species occurred were made between 247 and 306 m. Small fish from 18 to 39 cm TL group were caught in only a few trawls taken around 53°30′S and 40°–42°30′W (Shag Rocks area) at a mean depth of 176 m. Duhamel and Pletikosic (1983) mentioned that *D. eleginoides* has been caught around the Crozet Islands, at depths of 90 to 1 020 m, with catches being more frequent at depths of 150 to 200 m. The same study also found that fish commonly ranged between 22 and 45 cm TL, while larger fish of up to 122 cm TL were only found in catches taken on the continental slope and in abyssal waters.

Samples in zone SG2 were taken at a mean depth of 1 197.5 m. In this zone, 74.4% of the longline sets in which *D. eleginoides* were caught were set between 1 100 and 1 290 m. Fish of 80 to 89 cm TL were most frequent and sizes ranged from 60 to 144 cm TL for males and 57 to 212 cm TL for females. At lengths greater than 120 cm TL, females were more abundant, and all fish with TL of more than 140 cm were female. Larger females up to 212 cm TL were caught only north and south of the island (Figure 2).

Zhivov and Krivoruchko (1990), using data from South Georgia, found that males matured at lengths of 64 to 94 cm TL (7 to 11 years old) and females matured at lengths of 85 to 115 cm TL (9 to 12 years old). This means that the size range we observed on the Argentinian continental shelf/slope corresponds only to juvenile stages. This finding supports those of Cotrina (1981) and Cassia and Perrotta (1996). However, *D. eleginoides* sampled in the South Georgia area include both juvenile and adult stages. The commercial longliner *Isla Sofia* caught adult *D. eleginoides* and some juveniles over 50 cm TL in

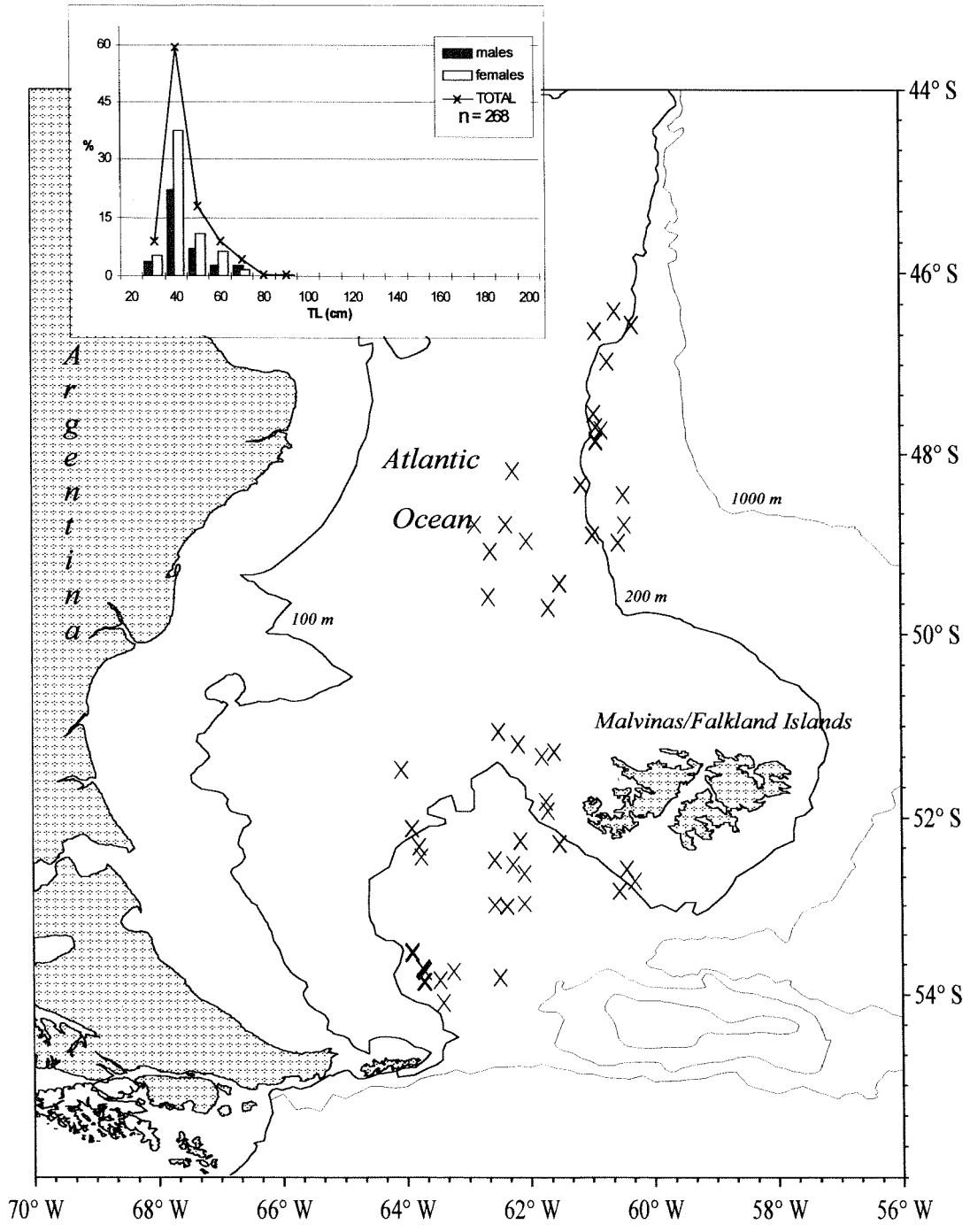

Figure 1: Positions of sampling (X) on the Argentinian continental shelf/slope, and size distribution (total and by sex) for *D. eleginoides* caught during the 1994/95 summer.

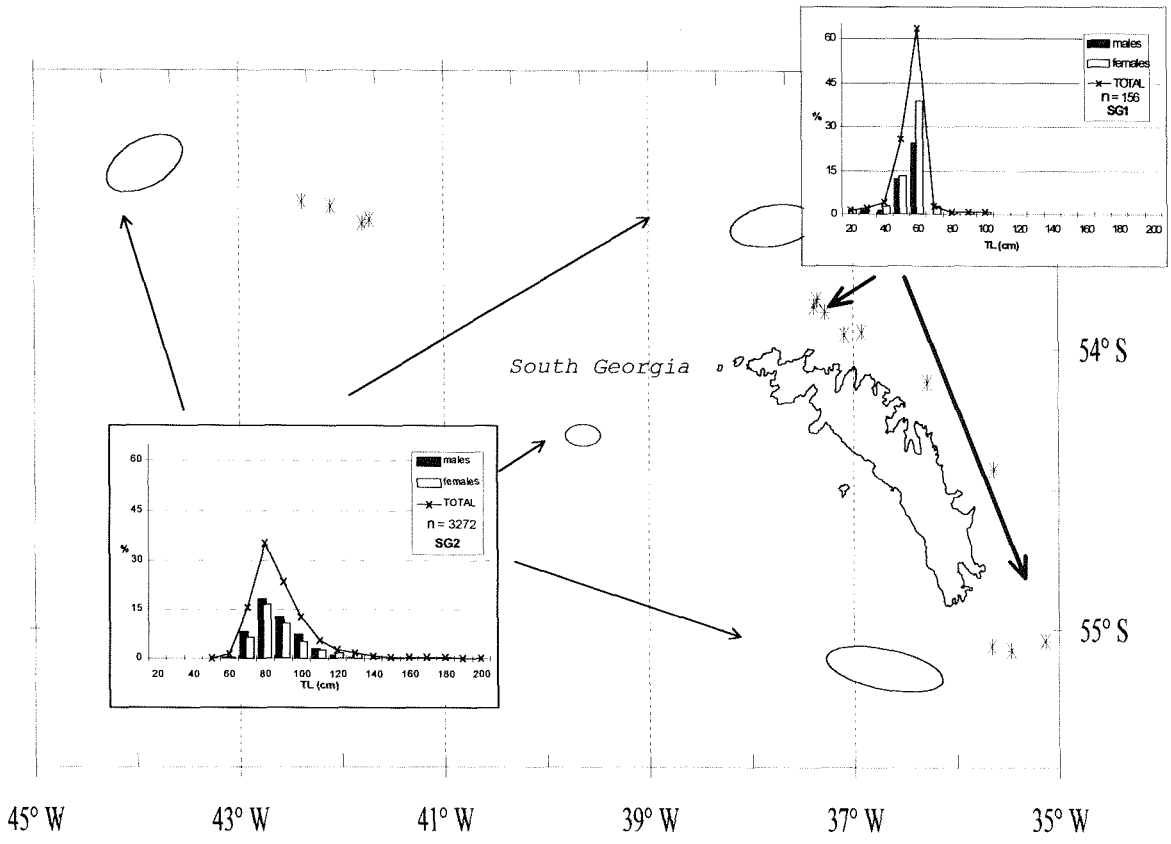

Figure 2: South Georgia (Subarea 48.3). Positions of sampling on the shelf zone (SG1) (*) and in the deep-water zone (SG2) (shaded), and size distribution (total and by sex) for *D. eleginoides* caught during the study.

deep waters around South Georgia. Juveniles of 40 to 95 cm TL were caught in research trawls near the edge of the South Georgia shelf, but smaller fish between 18 to 39 cm TL were caught only in the few trawls taken around the Shag Rocks area.

Diet of *D. eleginoides*

Principal Prey Items

The feeding pattern of *D. eleginoides* varied between the areas investigated, and its diet included a wide diversity of prey items (Table 2). In the Argentinian shelf/slope area the percentage of full stomachs was 58.4%, and in coastal waters in zone SGl feeding intensity was higher, as reflected in the percentage of full stomachs (83.1%), while in zone SG2, only 6.9% of the fish sampled had full stomachs (Tables 3, 4 and 5). A similar low percentage of full stomachs (11%) had been found by Martinez (1975) for fish caught on longlines in Chilean waters (33°S) at depths around 500 to 1 020 m. The fish were around 51 to 127 cm TL.

Some authors have reported *D. eleginoides* as a primarily ichthyophagous species, preying secondarily on macrocrustaceans and cephalopods, with juvenile stages feeding on euphausiids and other zooplankters (Hart, 1946; Tarverdiyeva, 1972; Duhamel and Pletikosic, 1983; Lloris and Rucabado, 1991; McKenna, 1991; Cassia and Perrotta, 1996).

The principal prey items in the diet of *D. eleginoides* from the three study areas were fish, with crustaceans and cephalopods being secondary prey items (Tables 3, 4 and 5). The occurrence of fish in the diet was between 60 and 95%F; for krill, present only in zone SG1, this was 20%F, while cephalopods ranged from 1 to 15%F. Another prey group, macrocrustaceans, was found only in stomachs of fish taken in zone SG2 (22%F).

The most frequent fish prey species on the Argentinian continental shelf/slope were Nototheniidae (25.7%F), including *Patagonotothen ramsayi*, eelpouts (*Iluocoetes fimbriatus*) – 5.6%F, southern blue whiting (*Micromesistius australis*) – 4.9%F and Merlucciidae (3.5%F) such as

Table 2: Diet composition of *D. eleginoides* on the Argentinian continental shelf/slope (AS) and in the South Georgia shelf (SG1) and deep-water (SG2) zones.

Prey Items			AS	SG1	SG2
Mollusca	Cephalopoda				
	Sepiolidae				
		Semirossia tenera	X		
	Ommastrephidae				
		Illex argentinus	X		
	Onychoteuthidae				
		Kondakovia longimana			X
	Loliginidae				
		Loligo gahi	X		
	Octopodidae			X	X
		Octopus tehuelchus	X		
Crustacea	Isopoda *				X
	Myscidacea *				X
	Decapoda				
	Lithodidae *				X
	Euphausiacea				
		Euphausia superba		X	
Thaliacea	Salpidae *		X		
Pisces	Myctophiformes				
	Myctophidae *		X	X	X
	Gadiformes				
	Macrouridae				
		Coelorhynchus fasciatus	X		X
		Macrourus holotrachys	X		X
	Moridae				
		Antimora rostrata			X
		Austrophysis marginata	X		
	Gadidae				
		Micromesistius australis	X		
	Merlucciidae				
		Macruronus magellanicus	X		
		Merluccius hubbsi	X		
	Ophidiiformes				
	Ophidiidae				
		Genypterus blacodes	X		
	Scorpaeniformes				
	Agonidae				
		Agonopsis chiloensis	X		
	Perciformes				
	Zoarcidae				
		Iluocoetes fimbriatus	X		
		Pachycara brachycephalum			X
		Lycodapus spp.			X
	Nototheniidae *				X
		Patagonotothen ramsayi	X		
		Patagonotothen guntheri			X
		Gobionotothen gibberifrons		X	
		Nototheniops nudifrons		X	
	Bathydraconidae				
		Bathydraco spp.			X
	Channichthyidae				
		Chaenocephalus aceratus		X	
		Champsocephalus gunnari		X	
		Pseudochaenichthys georgianus		X	
		Chionodraco spp.			X

* Unidentified species

Table 3: Diet of *D. eleginoides* grouped by size class and for all fish, on the Argentinian continental shelf/slope (<650 m deep).

Length range (cm):	Overall	30–39	40–49	50–59	60–95	70–95
Total *n*	231	21	144	34	20	12
% Stomach contents	58.4	52.4	53.5	58.8	70.0	100.0
Prey Items	Frequency of Occurrence (%F)					
Pisces						
Fish remains	50.7	61.5	50.7	45.0	42.9	50.0
Merluccidae	3.5		2.5	11.5		
Gadidae	4.9		5.1	3.8	7.1	8.3
Nototheniidae	25.7	7.7	24.1	35.0	28.6	25.0
Zoarcidae	5.6	15.4	5.1	3.8		8.3
Moridae	2.1		3.8			
Macrouridae	2.1		3.8			
Myctophidae	0.7		1.3			
Total fish	95.1	81.8	97.4	100.0	78.6	91.7
Molluscs						
Loligo gahi	2.8	7.7	2.5		7.1	
Illex argentinus	2.8	7.7	2.5		7.1	
Semirossia tenera	0.7	7.7				
Octopus tehuelchus	0.7					8.3
Total Cephalopods	6.9	23.1	5.1		14.3	8.3
Salpidae	0.7				7.1	

Table 4: Diet of *D. eleginoides* grouped by size class and for all fish in the South Georgia shelf zone (SG1) (<300 m deep).

Length range (cm):	Overall	18–39	40–49	50–59	60–95
Total *n*	155	11	27	109	7
% Stomach contents	83.1	72.7	77.8	96.3	85.7
Prey Items	Frequency of Occurrence (%F)				
Pisces					
Fish remains	7.6	66.7	4.8	2.9	
Channichthyidae	39.5	33.3	28.6	34.3	50.0
Nototheniidae	37.8	50.0	42.9	30.5	75.0
Myctophidae	1.9			1.9	
Total fish	86.5	100.0	76.2	69.5	100.0
Molluscs					
Cephalopoda, Octopodidae	0.8			0.8	
Crustacea					
Euphausia superba	20.1		23.8	17.1	25.0
Unidentified crustaceans	2.9			2.9	
Total crustaceans	22.7		23.8	20.0	25.0

Table 5: Diet of *D. eleginoides* grouped by size class and for all fish in the South Georgia deep-water zone (SG2) (1 050 to 1 530 m deep).

Length range (cm):	Overall	50–79	80–89	90–99	100–109	110–119	120–129	130–149	150–200
Total *n*	3272	552	1153	763	418	180	83	79	44
% Stomach contents	6.9	7.1	6.5	6.8	6.0	5.6	10.8	6.3	20.5
Prey Items	Frequency of Occurrence (%F)								
Pisces									
Fish remains	54.0	43.6	49.3	65.4	60.0	60.0	55.6	60.0	55.6
Moridae	1.3	5.1				10.0			
Zoarcidae	2.2	5.1	2.7		4.0				
Bathidraconidae	0.9			1.9	4.0				
Macrouridae	0.9			1.9		10.0			
Nototheniidae	0.5								11.1
Channichthyidae	0.5								11.1
Total fish	60.3	53.8	52.0	69.2	68.0	80.0	55.6	60.0	83.3
Molluscs									
Kondakovia longimana	14.7	17.8	20.0	7.7	20.0	10.0		40.0	
Crustacea									
Reptantia									
Lithodidae	7.1	2.6	2.7	3.8	4.0	10.0	33.3	20.0	55.5
Natantia	2.7		4.0	3.8	4.0			20.0	
Isopoda	11.6	10.3	14.7	15.4	8.0	10.0			
Unidentified crustaceans	0.5	12.8	5.3	1.9			11.1	20.0	
Total Crustaceans	21.8	25.6	26.7	25.2	16.0	20.0	44.4	40.0	55.5

Macruronus magellanicus and *Merluccius hubbsi*. Other fish (Moridae, Macrouridae and Myctophidae) occurred occasionally in the diet – below 3%F (Tables 2 and 3).

In zone SG1 the principal fish prey items were Channichthyidae (*Chaenocephalus aceratus, Champsocephalus gunnari* and *Pseudochaenichthys georgianus*) and Nototheniidae (*Gobionotothen gibberifrons, Nototheniops nudifrons* and *Patagonotothen guntheri*) with occurrences of 39.5 and 37.8%F, respectively. Myctophidae had occurrences below 2%F (Tables 2 and 4). Koslov (1995) found that myctophids were a secondary prey item in the diet of fish species inhabiting island shelf waters.

In zone SG2, other fish species found in stomachs included Zoarcidae (*Pachycara brachycephalum* and *Lycodapus* spp.), Moridae (*Antimora rostrata*), Macrouridae (*Coelorhynchus fasciatus* and *Macrourus holotrachys*), Bathydraconidae (*Bathydraco* spp.), Nototheniidae and Channichthyidae (*Chionodraco* spp.), all with occurrences below 3%F (Tables 2 and 5). Myctophidae were absent in the diet of *D. eleginoides* in this deep-water area, though Konforkin and Koslov (1992) reported this species as a regular dietary component of *D. eleginoides* in South Georgia waters. In many cases, *D. eleginoides* stomach contents were in an advanced stage of digestion, making taxonomic identification difficult; unidentified fish occurred frequently in both areas. Around South Georgia, remains of *D. eleginoides*, discarded by commercial fishing vessels after processing, were found as prey and were included as fish remains. This predation behaviour is frequently observed in commercial fishing areas and is similar to that of other large piscivorous fish (Macpherson, 1983).

Principal cephalopods found in the diet of *D. eleginoides* on the Argentinian continental shelf/slope were shortfin squid (*Illex argentinus*) and longfin squid (*Loligo gahi*), both having occurrences of 2.8%F, while *Octopus tehuelchus* and *Semirossia tenera* were occasionally ingested (Table 3). In contrast, only single specimens of cephalopods (Octopodidae) were found in samples from zone SG1. Around South Georgia in zone SG2, the only cephalopod found as prey was *Kondakovia longimana* with an occurrence of 14.7%F and a high percentage by weight in the diet due to the large size of these squids (Table 5).

The macrocrustaceans present in zone SG2 consisted of isopods, mysids and Anomura decapods belonging to Lithodidae. As indicated in López Abellán and Balguerías (1994), the area studied is on the southernmost limit of distribution for the species of the family Lithodidae in the Atlantic Ocean where only two crab species of the genus *Paralomis* were found. In zone SG1, the principal macrocrustacean prey item was krill (*Euphausia superba*) with an occurrence of 20.1%F (Tables 4 and 5).

Some gelatinous plankton species belonging to the Salpidae were an occasional food item off the Argentinian shelf, with an occurrence of 0.7%F (Table 3).

Dietary Differences between Males and Females

The sex ratio (male : female) of *D. eleginoides* on the Argentinian continental shelf/slope and zone SG1 was 1.5 : 1; and individuals larger than 70 cm TL were exclusively females. In zone SG2, the sex ratio was almost 1 : 1, but fish smaller than 60 cm TL or larger than 144 cm TL were exclusively females (Figures 1 and 2).

On the Argentinian continental shelf/slope, the occurrence of fish prey was 94.3%F for males and 95.6%F for females and consisted mainly of fish remains and nototheniids. By weight (W), these groups represented about 98.3 and 94.6%W of the diet respectively (Table 6a and Figure 3a).

In zone SG1, the fish prey also comprised nototheniids and channichthyid species, with occurrences of 95.8%F for males and 87.3%F for females, and 93.2%W and 96.3%W, respectively. Krill (*E. superba*) is another important prey item in this area with low weight in the diet but with high number values of 99.2%N for males and 98.3%N for females (Table 6b and Figure 3b).

In zone SG2, the occurrence of fish prey totalled 63.2%F for males and 55.9%F for females, and represented by weight about 73.1%W and 13.2%W, respectively. Females in this area fed mainly on cephalopods with an occurrence by weight of 83.4%W. Crustaceans (Isopoda and Decapoda) were also present, with similar occurrences for both sexes of around 25.5%F for males and 27.9%F for females, representing by weight about 23%W and only 3.3%W, respectively (Table 6c and Figure 3c).

There were no significant differences between the diets of males and females within the same area (Table 7).

Table 6: Frequency of occurrence (%F), number (%N) and weight (%W) of principal prey items in the diet of male and female *D. eleginoides* caught: (a) on the Argentinian continental shelf/slope, (b) on the South Georgia shelf, and (c) in deep waters around South Georgia.

(a) Argentinian shelf/slope

	Males			Females		
Medium size (cm)	54.2			55.4		
Total number of stomachs	94			138		
% of full stomachs	54.2			60.9		
	%F	%N	%W	%F	%N	%W
Total fish	94.12	92.31	98.30	95.24	91.50	94.60
Total cephalopods	5.70	5.98	0.92	7.69	8.60	5.32
Salpidae	1.90	1.80	0.78	-	-	-

(b) South Georgia shelf

	Males			Females		
Medium size (cm)	49.6			50.2		
Total number of stomachs	62			93		
% of full stomachs	83.4			82.8		
	%F	%N	%W	%F	%N	%W
Total fish	95.83	0.83	93.20	87.32	1.64	96.30
Total cephalopods		-	-	1.41	-	0.17
Total crustaceans	25.00	99.20	6.80	22.54	98.40	3.50
Krill (*Euphausia superba*)	22.92	99.15	6.60	18.31	98.26	3.20

(c) South Georgia deep waters

	Males			Females		
Medium size (cm)	90.2			99.2		
Total number of stomachs	1671			1549		
% of full stomachs	6.3			11.1		
	%F	%N	%W	%F	%N	%W
Total fish	63.21	55.56	73.10	55.93	55.30	13.20
Total cephalopods	13.21	11.11	3.16	16.10	15.15	83.42
Total crustaceans	25.47	33.40	23.10	27.90	29.50	3.30
Lithodidae	4.72	4.76	19.18	9.32	8.33	3.08
Natantia	3.77	3.17	1.06	1.69	1.52	-
Isopoda	14.15	23.02	2.48	9.32	10.61	0.08

Table 7: Results of Spearman's correlation rank analysis by sex of *D. eleginoides* caught on the Argentinian continental shelf/slope (AS) and off South Georgia (SG). Significant correlations are indicated (**).

	Argentinian Continental Shelf/Slope		South Georgia	
	Males	Females	Males	Females
AS males	1.00			
AS females	0.852**	1.00		
SG males	0.02	-0.02	1.00	
SG females	-0.03	0.05	0.627**	1.00
R (23 ; 0.01) = 0.505				

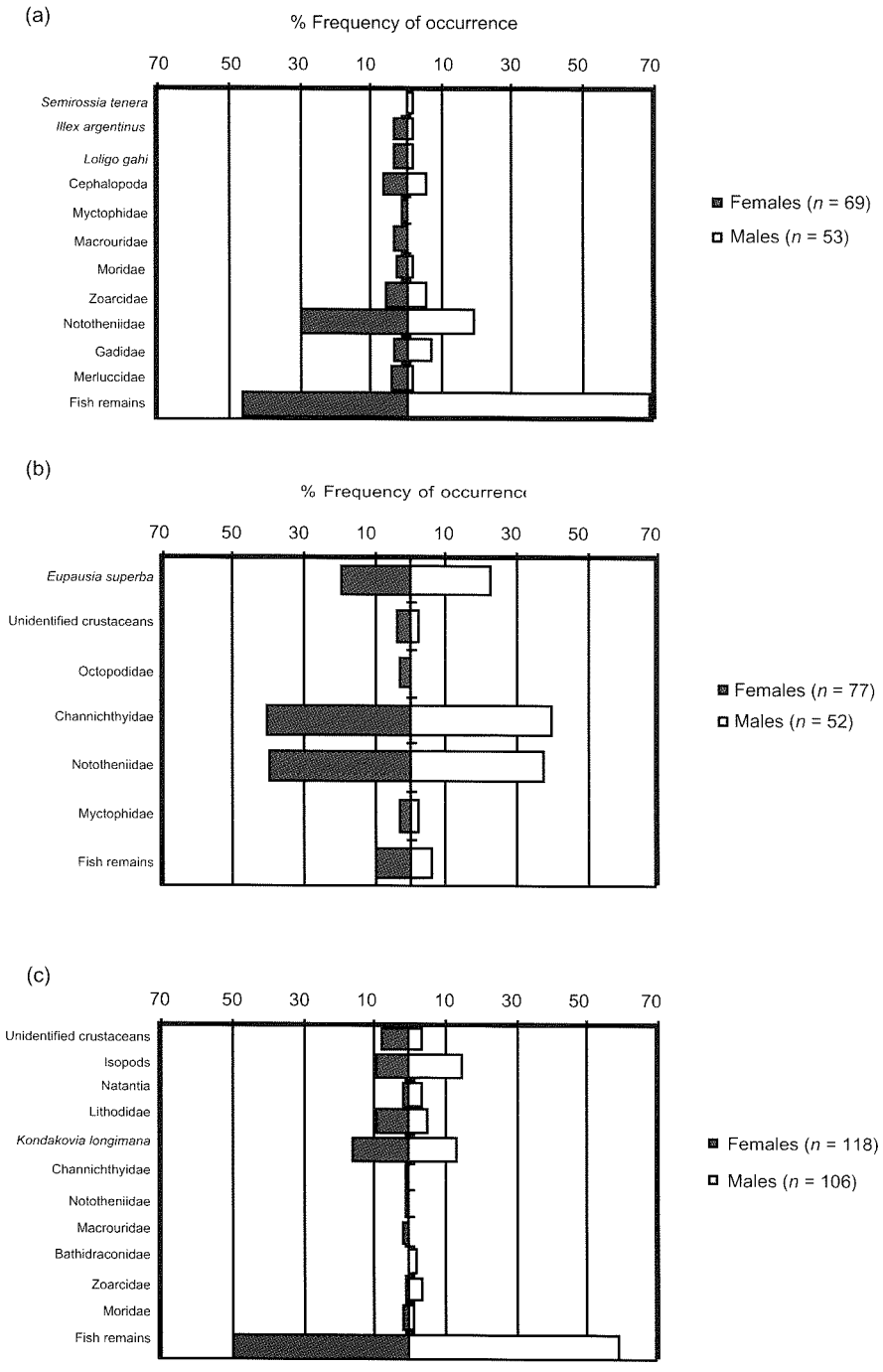

Figure 3: Frequency of occurrence of principal prey items in the diet of male and female *D. eleginoides* caught: (a) on the Argentinian continental shelf/slope, (b) on the South Georgia shelf, and (c) in deep waters around South Georgia. The number (*n*) of full stomachs is given in brackets.

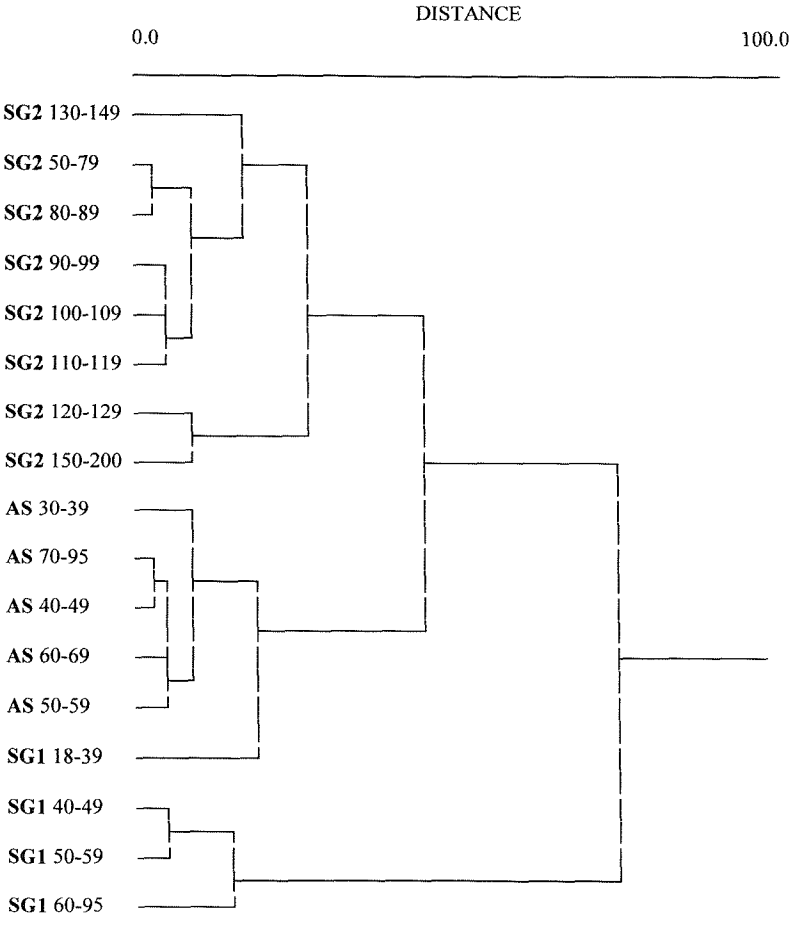

Figure 4: Dendrogram identifying size groups of individuals of *D. eleginoides* by areas. AS – Argentinian shelf/slope, SG1 – South Georgia shelf zone, SG2 – South Georgia deep waters. Size ranges are indicated in centimetres.

Size-Related Differences in the Diet

Cluster analysis identified three major groups of fish, each comprising individuals belonging to the same geographical area (Figure 4).

The Argentinian shelf (AS) group showed a high degree of diet overlap, with cluster distances smaller than 10 (Figure 4). The smallest size group (30 to 39 cm TL) was distinguished from other groups from this area by having the highest consumption of fish remains (61.5%F), Zoarcidae (15.4%F) and Cephalopoda (23.1%F), and a minimal consumption of Nototheniidae (7.7%F). The other size groups (40–49 cm, 50–59 cm, 60–69 cm and 70–95 cm TL) were ranked closely on a cluster dendrogram due to intermediate values in the diet of fish remains (42 to 51%F), and similar rates of consumption of nototheniids and other fish. Individuals of less than 60 cm TL had similar percentages of full stomachs for all study areas and zones (52.4, 53.5 and 58.8%). Larger fish had higher values of full stomachs, up to 100% (Table 3). This group also included the smallest size class from zone SG1 (18 to 39 cm TL), because fish of this size fed only on fish and also on fish remains (66.7%F). This was not common for other sizes of fish from zone SG1, but individuals belonging to this smallest group were caught around Shag Rocks (Table 4).

The South Georgia shelf (zone SG1) group comprised three individual size groups (40–49 cm, 50–59 cm and 60–95 cm TL) with distance values smaller than 20 (Figure 4). These size groups consumed crustaceans (20 to 25%F) – mainly krill – as well as fish (69.5 to 100%F), but consumption of fish remains was low (Table 4). Medium-sized fish had the highest percentage of full stomachs (96.3%), although fish from other size groups showed values of between 77.8 and 85.7%.

The South Georgia deep-water (zone SG2) group revealed three distinct size groups (Figure 4). The first one included individuals between 50 and 119 cm TL with similar

frequencies of consumption of fish, crustaceans and cephalopods. Among crustaceans, isopod consumption was exclusive to this group. The second group (130–149 cm TL) was closely linked to the former group, due to a high intake of cephalopods (40%F) and Natantia crustaceans (20%), a prey item which is absent in the remaining third group. This third group comprised individuals of 120–129 cm TL and of 150–200 cm TL, which were grouped together due to the same frequencies in the diet of fish remains and Lithodidae crustaceans (33.3 to 55.5 %F) (Table 5). The percentages of full stomachs in this group were very low in comparison with values observed on the Argentinian shelf/slope area, the maximum value being 20.45% for individuals larger than 150 cm TL. The other size groups had full stomach values of between 5 and 11% (Table 5). Individuals smaller than 70 cm TL or larger than 181 cm TL had empty stomachs.

The degree of stomach fullness was evaluated only for fish sampled in zone SG2. The index of stomach fullness was higher in larger fish. 60% of fish of 70 to 89 cm TL had stomachs with an index of 1 (25% full), and less than 10% had stomachs with an index of 3 (100% full), while about 40% of fish between 110 and 180 cm TL had stomachs with an index of 3 (Figure 5). This observation could be related to prey type, meal size, size of the predator itself and its rate of food digestion, which is slower in larger fish (Bromley, 1994).

Depth-related Differences in the Diet

On the Argentinian continental shelf/slope, the highest feeding intensity of fish (65% full stomachs) was at depths of 200 to 300 m; the percentage of full stomachs above or below this depth range was less than 49%. Principal prey items at depths less than 200 m were nototheniids (*P. ramsayi*) with an alimentary index (AI) of 10.92, meanwhile other fish species had AI values under 2. Shortfin squid (*I. argentinus*) and Salpidae had AI values of 0.72 and 0.96 respectively. At depths of 200 to 299 m, the importance of nototheniids abruptly decreased to values of 0.92, and fell to almost zero at depths of 300 to 650 m. In deep water, long-tailed hake and shortfin squid became important, with AI values of 3.17 and 1.34, respectively. In depths of 300 to 650 m, the most important prey items were salps (Salpidae) (2.55) and fish remains (3.92) (Figure 6).

In zone SG2, nototheniids and Channichthyidae were the only fish prey items found in stomachs of fish taken deeper than 1 250 m. It is important to note that remains of *D. eleginoides* (heads and tails) were found in numbers only in stomachs of fish taken at depths of less than 1 250 m. This may be due to large numbers of heads and tails discarded by commercial fishing vessels operating in the area. The benthic food items, Lithodidae and 'all crustaceans' (isopods, mysids and decapods) were predominant at depths from 1 250 to 1 530 m. McKenna (1991) mentioned the presence of rocks in some *D. eleginoides* stomach contents, indicating that this species also feeds close to the bottom. In zone SG1, the same fish species were present as in zone SG2, but with higher %F values. In this zone, the principal crustacean in stomach contents was krill (20%F). Krill are transported over long distances by prevailing water currents. The Antarctic Circumpolar Current and the Weddell–Scotia Confluence contribute to the formation of krill aggregations around South Georgia (Fedoulov et al., 1996). However, in the areas away from the shelf and over deep water, low densities of krill were observed (Trathan and Everson, 1994). Krill is the most important prey item of fish in the South Georgia area. All species of fish feed directly or indirectly on krill and most species are specialised krill consumers (McKenna, 1991).

CONCLUSIONS

The three study areas considered in this paper have different oceanographic characteristics (depth profile, salinity and temperature). The size distribution, abundance and feeding habits of *D. eleginoides* reflect these differences between areas.

D. eleginoides is not a frequently-caught species on the Argentinian shelf/slope. 66.6% of the hauls which contained this species were taken between depths of 112 and 300 m. The fish in these hauls had a length distribution of 29 to 95 cm TL, corresponding to juvenile stages. The highest abundance was found at depths of between 257 and 474 m, although this species was found down to 650 m. The size and abundance of *D. eleginoides* increases with increasing depth. This observation supports the findings of Duhamel (1992) for the same species. The exact reason for the apparent absence of fish larger than 95 cm TL on the Argentinian continental shelf/slope is not known. All studies carried out in this area have only dealt with the younger part of the population.

South Georgia is an area subject to commercial fishing where both juvenile and adult stages of *D. eleginoides* are present. Juveniles (18 to 80 cm TL) with a modal length of around 60 cm TL are

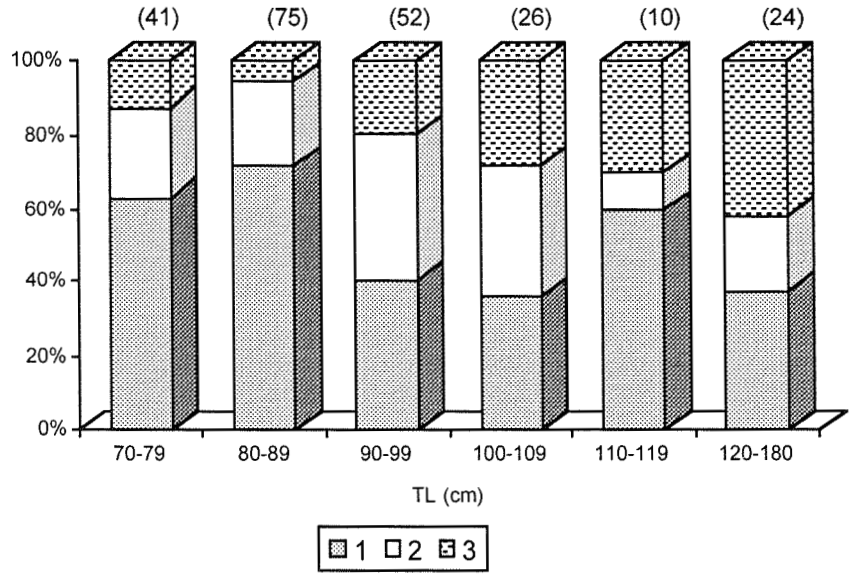

Figure 5: Stomach fullness degree versus size of *D. eleginoides* caught in the South Georgia deep-water zone (SG2). Sample size given in brackets.

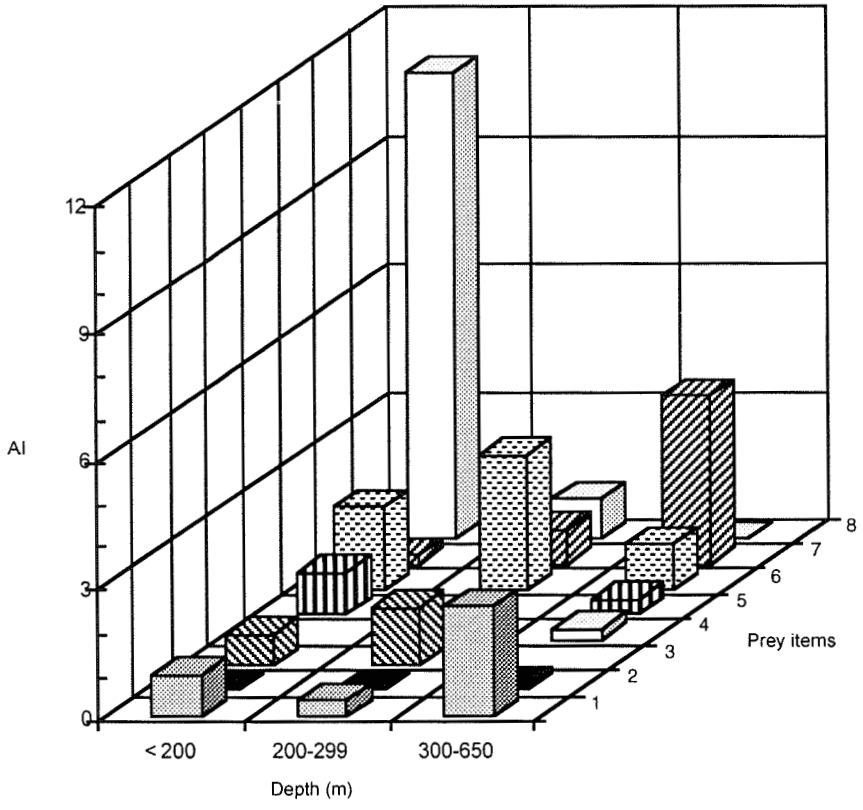

Figure 6: Alimentary index (AI) of principal prey items of *D. eleginoides* on the Argentinian continental shelf by three depth ranges. Prey items: 1 Salpidae, 2 *Octopus tehuelchus*, 3 *Illex argentinus*, 4 *Merluccius hubbsi*, 5 *Agonopsis chiloensis*, 6 *Macruronus magellanicus*, 7 fish remains, 8 *Patagonotothen ramsayi*.

caught in zone SG1 at depths of 113 to 300 m. Both juveniles and adults (57 to 212 cm TL) are found in zone SG2, at depths of 1 050 to 1 530 m. The most frequent size groups in the catches are those between 80 and 89 cm TL.

D. eleginoides demonstrated differences in feeding between the areas studied. On the Argentinian shelf, feeding intensity was high as reflected by the percentage of full stomachs of 58.4%. In the South Georgia region, this percentage increases to 83.1% in zone SG1 but only reaches 6.9% in zone SG2. This species is characterised as a mixed-species carnivore feeding principally on fish and secondarily on crustaceans and cephalopods. However, crustaceans were missing from the diet of fish in the Argentinian shelf/slope area and cephalopods were an occasional food item in the South Georgia shelf area. There may be a replacement of prey belonging to the same trophic level in the food web or an addition of other prey items, reinforcing the hypothesis that *D. eleginoides* is an opportunistic feeder.

We found no significant differences in the diet and feeding intensity of *D. eleginoides* between males and females in the same area. However, the differences between areas were noticeable.

Juvenile fish are pelagic predators, while adults are benthic feeders capable of undertaking feeding migrations in pelagic waters. The overlap of diet between fish of different size groups was correlated with changes in their feeding strategies. Cluster analysis by size groups identified three major groups whose diets overlapped, each group consisting of individuals belonging to the same geographical area.

At all depth ranges considered in this study, *D. eleginoides* fed mainly on fish, with regional differences in the fish species consumed. They fed on krill only in the South Georgia shelf area where krill is abundant. Over deep waters in the South Georgia area, krill abundance is low and krill do not constitute an important food item for *D. eleginoides*.

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