

Abstract.— Knowledge of trophic relationships is vital to understanding any ecological community. The trophic relationships of Antarctic demersal fish are poorly known and have been described quantitatively by only a few researchers.

Gut contents were analyzed on over 300 stomachs from fish collected during the 1987–88 AMLR ground fish survey of South Georgia I., Antarctica. All fish were collected with a bottom trawl during the austral summer. Fifteen species of demersal fish (including those of commercial value) were collected. Similarity analysis was applied to the diet information to describe trophic relationships in the South Georgia community.

The most abundant species of the South Georgia demersal fish community were classified into three groups based on summer diets. The largest group contained species heavily dependent on krill *Euphausia superba*, and included *Champscephalus gunnari* and *Notothenia rossii*. The second group was comprised of piscivores. Three of the four members of this group (*Dissostichus eleginoides*, *Chanocephalus aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The food of their prey often consisted of krill. The third group contained a loose association of species which feed on benthic organisms more than did other fish species in the community. *Notothenia gibberifrons* and *Notothenia squamifrons* were the important commercial species in this group.

Krill was found to be the most important prey species to the fish in the South Georgia system. However, based on the analysis of diet overlap, competition appeared to be unimportant in this community during the austral summer.

Selective reduction of populations within the fish community by fishing may have widespread repercussions. Many of the commercially valuable species feed on other fish species which in turn feed on krill or benthic organisms. The relatively simple but highly interconnected food web in the South Georgia system may have a lower potential for fish yield than previously thought.

Trophic Relationships within the Antarctic Demersal Fish Community of South Georgia Island

James E. McKenna Jr.

Graduate School of Oceanography, University of Rhode Island
Narragansett, Rhode Island 02882

Present address: Florida Marine Research Institute
100 8th Avenue SE, St. Petersburg, Florida 33701

The Antarctic ecosystem has been physically isolated from the rest of the world for at least the last 30 million years, since the Drake passage opened as South America moved away from Antarctica (Kennett 1982: 726) and probably longer (Regan 1914). The fish assemblage of this region appears to be the result of evolutionary radiation from a limited fauna that was present in the region when Antarctica separated from Australia (Eastman 1985, Kock 1985b). Over 60% of the species and 90% of the individuals belong to four families in the suborder Notothenioidei, and 95% of the species in this group are endemic to the Antarctic region (DeWitt 1971, Kock 1985b). The four dominant families are the Antarctic cods (Nototheniidae), dragonfish (Bathydraconidae), icefish (Channichthyidae), and spiny plunderfish (Harpagiferidae). These fish are generally sedentary, benthic forms found on the Antarctic continental shelves (Norman 1938). An international fishery has developed for larger members of these families, especially in the region around South Georgia I. (Fig. 1) (Kock 1986).

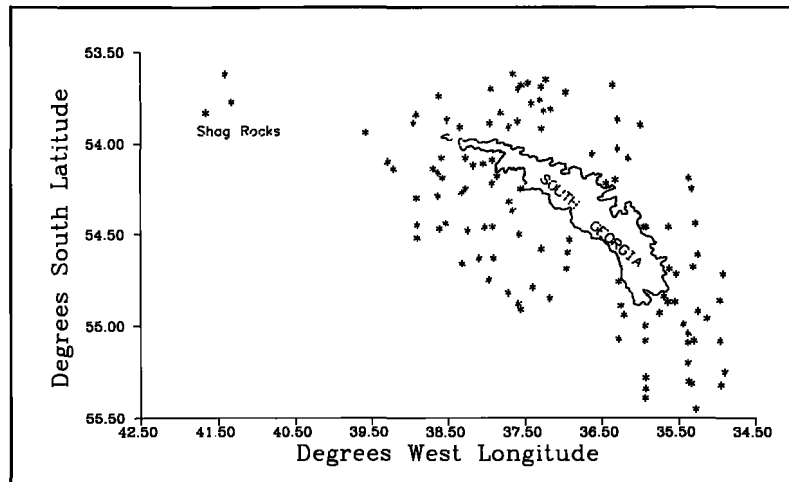
South Georgia is located just south of the Antarctic Convergence and is surrounded by a narrow, relatively shallow continental shelf. The physical oceanography of the region is very complex (Foster 1984) and may contribute to the high productivity and abundance of krill (Hempel 1985).

There is a high degree of endemism in Antarctic fishes (DeWitt 1971). The assemblage of fish species that has evolved in the Southern Ocean is well adapted to the Antarctic environment (Eastman 1985). However, the fish community in the South Georgia area appears to be changing, possibly in response to the fishing pressure that it has experienced over the past two decades (Kock 1985b and 1986, McKenna and Saila 1991). Exploited South Georgian stocks have been declining since the late 1970s (Kock 1985b and 1986, Gabriel 1987). In the early 1970s, the commercial trawl fishery was supported mostly by the catch of marbled rockcod *Notothenia rossii*, which yielded hundreds of thousands of tons each season (Kock 1986). By 1985, the stock was estimated to be less than 10% of its pristine size (Kock 1985b). The fishery is presently supported by catches of mackerel icefish *Champscephalus gunnari*, but its decline is also evident (Kock 1986, McKenna and Saila 1989). Abundance estimates of other species in the South Georgia region decreased by as much as two orders of magnitude between 1975–76 and 1980–81 (Kock et al. 1985a).

The community structure has changed with decreases in stock sizes (McKenna and Saila 1991). There has been a significant shift from a community dominated by a few large-bodied species to fewer, mostly small-bodied species with more equitable abundances.

Figure 1

Location of stations sampled around South Georgia I., Antarctica, by the 1987–88 AMLR demersal fish survey.



To effectively manage fish stocks, it is necessary to understand the impact of fishing on the fish community. This includes understanding interspecific relationships among fish and with other organisms in their environment. Knowledge of trophic relationships is necessary to describe these ecological links (Edwards and Bowman 1979, Grosslein et al. 1980, Langton 1983, Sissenwine 1984).

A number of other studies have examined the diets of Antarctic fish (Holloway 1969, Permitin and Tarverdieva 1979, Yukhov 1971, Rakusa-Suszczewski and Piasek 1973, McCleave et al. 1977, Moreno and Osorio 1977). Everson (1984b) reviews the feeding ecology of Antarctic fishes. However, few of these studies have quantitatively measured the interspecific overlap of diets. The most extensive work is that of Targett (1981) who gave a quantitative description of the community structure and trophic relationships of demersal fish around three Antarctic islands. However, his collections were made with a small net (3m) (not easily compared with those used commercially, (17–18m)) and only two stations were sampled in the South Georgia I. region late in the autumn of 1975.

Targett's work emphasized the degree of resource partitioning by demersal fish. In general, he found a low degree of overlap in food utilization. In the case of commercial species, however (*Champocephalus gunnari*, South Georgia icefish *Pseudochaenichthys georgianus*, and painted notie *Nototheniops larseni*), there was a relatively high degree of overlap. This group consists mostly of predators on krill. At one South Georgia station, all fishes preyed on krill.

The present study reports on a quantitative examination of the trophic relationships within the demersal fish community on the continental shelf (~5 km offshore) around South Georgia I.

Methods

The specimens for this study were collected from the research vessel RV *Professor Siedlecki* using commercial fishing gear, and represent the fishable community that was present during December 1987–January 1988. Fish were collected by 30-minute tows of a P32/36 otter trawl (mouth opening of 17.5 m, 43–52 mm mesh

liner) as part of the 1987–88 Antarctic Marine Living Resources (AMLR) survey of the fish stocks around South Georgia I. Successful trawls were made at 108 stations within about 5 km of the island (Fig. 1). These stations were randomly located over the continental shelf within three depth strata (50–150 m, 150–250 m, 250–500 m) (Gabriel 1987, McKenna and Sails 1989). The collection methods are described in detail by McKenna and Sails (1989).

This sampling provided a substantial size range of individuals from the common species and at least a few representatives of most of the rare species (Table 1; McKenna 1990, app. C). A total of 321 stomachs were collected from 15 species of fish. Three of the fifteen species from which stomachs were collected belonged to the icefish family (Channichthyidae; *Champocephalus gunnari*, black-finned icefish *Chaenocephalus aceratus*, *Pseudochaenichthys georgianus*). Eight species were Antarctic cods (Nototheniidae; *Notothenia rossii*, gray rockcod *Notothenia squamifrons*, striped rockcod *Pagothenia hansonii*, *Nototheniops larseni*, yellowfin notie *Nototheniops nudifrons*, humped rockcod *Notothenia gibberifrons*, Patagonian rockcod *Patagonothen brevicauda guntheri*, and Patagonian toothfish *Dissostichus eleginoides*). Two species of Bathydraconidae (South Georgia icedragon *Parachaenichthys georgianus*, and bronze icedragon *Psilodraco breviceps*) were represented. The remaining two were members of some of the less-common families of the region (Arteidraconidae: fancy plunderfish *Arteidraco mirus*, Mureanolepididae: smalleye morey cod *Muraenolepis microps*).

Length (TL and SL) and weight measurements were taken for fish from each trawl. A stomach index value was also recorded for each fish. This index ranged from zero (empty stomachs) to five (full stomach). Individuals with a stomach index (Permitin and Tarverdieva 1979)

Table 1

Number of stomachs from each fish species collected at South Georgia I., used in diet analyses. *n* = number of stomachs which contained identifiable prey. Pooled *n* category = number of replicates used in the community-wide cluster analysis. # = number of stomachs used in the determination of numerical abundance of prey items.

Fish species	Species code	Number of stomachs					
		<i>n</i>			Pooled <i>n</i>		Empty
		#	Wet wt.	Dry wt.	#	Dry wt.	
<i>Artedidraco mirus</i>	ARTE	4	4	4	4	4	1
<i>Chaenocephalus aceratus</i>	ACER	19	19	19	7	7	16
<i>Champscephalus gunnari</i>	GUNN	41	43	41	15	15	2
<i>Dissosticus eleginoides</i>	ELEG	50	50	50	18	18	0
<i>Muraenolepis microps</i>	MICR	6	6	6	2	2	0
<i>Notothenia gibberifrons</i>	GIBB	22	23	21	8	7	0
<i>Notothenia rossii</i>	ROSS	25	25	25	9	9	1
<i>Notothenia squamifrons</i>	SQUA	13	13	13	5	5	0
<i>Nototheniops larseni</i>	LARS	7	8	7	3	3	3
<i>Nototheniops nudifrons</i>	NUDI	12	14	12	4	4	0
<i>Pagothenia hansonii</i>	HANS	9	9	9	3	3	0
<i>Parachaenichthys georgianus</i>	PARA	9	9	9	3	3	0
<i>Patagonothen brevicauda</i>	GUNT	8	10	7	4	3	0
<i>Pseudochaenichthys georgianus</i>	PSEU	27	27	27	9	9	7
<i>Psilodraco breviceps</i>	PSIL	3	3	3	3	3	0

greater than zero were selected arbitrarily from the catch for gut content analysis. The sex of each fish was also noted. These data were recorded and the stomach was assigned an identification number for correlation with station information.

Stomachs were removed, taking care to prevent loss of any contents. Each stomach was preserved by injection with 10% formalin and wrapped in gauze or paper towels. Large stomachs were soaked in a 10% formalin solution for at least 24 hours. Stomachs were sealed in plastic ziplock bags and stored until they could be examined.

Examination of stomach contents

In the laboratory, the weights of all fish and stomach contents were measured to within 0.001 g on an electronic balance. Objects weighing more than 160 g were measured on a triple-beam balance. Before contents were removed from the stomach, the total formalin-preserved wet weight was measured. The stomach was then opened with a longitudinal incision through the stomach lining from esophagus to intestine. The contents were removed and sieved through a 0.5 mm mesh screen. Wet weight of the empty stomach lining was then measured. This allowed back-calculation of the wet weight of unidentifiable material (GORP) by the difference between total wet weight and the sum of the weights of the separate, identifiable items plus stomach

lining. Empty stomachs and those containing only unidentifiable material were not used in the analysis of similarity.

Items remaining on the sieve screen were sorted into general taxonomic groups (e.g., fish, amphipod, isopod) and then identified to family or species where possible. Each group was enumerated and weighed. Specimens were then placed in a drying oven at 60°C and dried to constant weight.

Analysis of the diet data

Frequency of occurrence and dietary coefficients (Linkowski et al. 1983) were determined as simple measures of the importance of each potential prey item in the diet of each species (Table 2). To remove the biases due to varying stomach size and total number of items contained in each stomach, all diet data were converted to percent composition. Percent composition of the diet was determined for each stomach based on numerical abundance, wet weight, and dry weight of the prey items. Results refer to the use of percent composition by dry weight unless stated otherwise. Average percent composition of the diet was then calculated for each of the 15 species of fish for which stomachs had been collected (Table 3). Only stomachs which contained identifiable prey items were included in the diet analysis.

Table 2

Frequency of occurrence (%), dietary coefficient (Q), and diversity values for the diets of 15 Antarctic demersal fish species collected off South Georgia I. SPP = fish species code (see Table 1 for key to specific identification); %f = percent frequency of occurrence; Q = average number of prey \times average dry weight of prey; H = Shannon-Wiener diversity index using average percent composition of the diet of each species; var(H) = variance of Shannon-Wiener index (Hutcheson 1970).

	SPP: ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
Fish															
%f	84.62	0.00	96.00	0.00	0.00	37.50	11.11	0.00	33.33	0.00	77.78	62.96	0.0	52.00	0.00
Q	6.92	0.00	7.65	0.00	0.00	0.48	0.00	0.00	0.09	0.00	1.91	6.65	0.0	7.27	0.00
Krill															
%f	15.38	25.00	18.00	50.00	100.00	100.00	100.00	42.86	16.67	83.33	22.22	59.26	100.0	76.00	30.77
Q	0.91	0.01	0.01	0.08	58.89	15.01	7.96	0.07	0.00	0.19	0.13	64.11	1.8	165.14	0.00
Tunicate															
%f	0.00	0.00	0.00	31.82	0.00	0.00	11.11	28.57	16.67	0.00	0.00	3.70	0.0	44.00	84.62
Q	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.17	5.73
Amphipod															
%f	0.00	25.00	2.00	68.18	0.00	0.00	11.11	28.57	50.00	25.00	0.00	0.00	0.0	32.00	61.54
Q	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.02	0.01	0.02	0.00	0.00	0.0	5.12	0.01
Isopod															
%f	0.00	50.00	0.00	36.36	0.00	0.00	11.11	0.00	0.00	8.33	0.00	0.00	0.0	20.00	38.46
Q	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Polychaete															
%f	0.00	50.00	0.00	86.36	2.44	0.00	0.00	0.00	33.33	16.67	0.00	0.00	0.0	8.00	23.08
Q	0.00	0.00	0.00	6.56	0.00	0.00	0.00	0.00	0.01	0.04	0.00	0.00	0.0	0.03	0.01
Shrimp															
%f	15.38	0.00	6.00	9.09	0.00	0.00	0.00	0.00	16.67	0.00	66.67	0.00	0.0	28.00	0.00
Q	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.09	0.00	0.0	0.19	0.00
Echiura															
%f	0.00	0.00	0.00	22.73	0.00	0.00	0.00	0.00	16.67	8.33	0.00	0.00	0.0	0.00	7.69
Q	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Gastropod															
%f	0.00	0.00	0.00	45.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	8.00	7.69
Q	0.00	0.00	0.00	36.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Rocks															
%f	0.00	0.00	4.00	13.64	0.00	0.00	0.00	0.00	33.33	16.67	0.00	0.00	0.0	0.00	7.69
Q	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Diversity															
H	0.988	1.464	0.198	1.772	0.00	0.573	0.389	1.296	1.701	1.148	0.96	0.677	0.0	1.306	1.613
var(H)	0.0107	0.0018	0.0042	0.0143	0.00	0.0022	0.0092	0.0019	0.004	0.0086	0.0028	0.0004	0.0	0.0101	0.017

Similarity analysis was used to classify fish species into distinct trophic groups based on their diets. Two techniques were used. The first, based on the work of Smith (1985), generated a matrix of similarity coefficients and associated variances for each pair of species being compared. Similarity was measured with the proportional similarity coefficient (PS) for each pair of fish species being compared. This analysis was based on the average percent composition for each species.

The second method applied cluster analysis to these data. I used the clustering methods of Nemec and Brinkhurst (1988), which use a bootstrap technique applied to replicate samples to determine the significance of clusters. The Bray-Curtis similarity coefficient was used and, where replicates were available, significance was tested using 50 bootstrap simulations. For each species, a separate cluster analysis was performed to

determine if there were significant intraspecific subgroups by size, sex, or depth of habitat (McKenna 1990, app. D). Although the variability in diet of each species was obvious, no significant subgroups were identified.

Cluster analysis was then applied to examine the structure of the community. There is virtually no spatial structure to the South Georgia fish community at this season (McKenna 1990:178-251) and, since no significant intraspecific structure was found, each stomach examined was used as a replicate sample of the diet of the predator species (Table 1). These data were used in the SIGTREE cluster analysis program (Nemec and Brinkhurst 1988). Due to a limitation of the program (a maximum of 110 observations [sum of replicates per species] are allowed), the data were pooled into groups of three and averaged to reduce the number of observations from 264 to 97 (Table 1).

Table 3

Average percentages of total diet contributed by each prey species for 15 Antarctic demersal fish species collected around South Georgia I. Asterisk (*) = prey item accounted for <0.1% of the diet. See Table 1 for key to species code identifications.

Prey item	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
Based on numerical abundance of prey items															
Fish	59.6	0.0	83.6	0.0	0.0	15.5	2.8	0.0	13.9	0.0	39.1	43.9	0.0	14.2	*
Krill	18.5	15.0	11.1	5.2	99.3	84.5	86.1	33.3	4.2	65.3	22.2	56.1	100.0	64.6	5.6
Tunicate	0.0	0.0	0.0	5.1	0.0	0.0	5.6	16.7	8.3	0.0	0.0	*	0.0	9.5	47.5
Amphipod	0.0	16.7	*	10.9	0.0	0.0	2.8	38.9	20.8	10.1	0.0	0.0	0.0	3.6	32.8
Isopod	0.0	30.0	0.0	1.4	0.0	0.0	2.8	0.0	0.0	1.4	0.0	0.0	0.0	*	5.0
Polychaete	0.0	13.3	0.0	52.3	0.6	0.0	0.0	0.0	16.7	11.4	0.0	0.0	0.0	0.6	3.9
Shrimp	16.2	0.0	3.1	*	0.0	0.0	0.0	0.0	5.6	0.0	38.7	0.0	0.0	5.4	0.0
Echiura	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	16.7	8.3	0.0	0.0	0.0	0.0	*
Ctenophora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2
Cumacid	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropod	0.0	0.0	0.0	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	*
Hydroid	1.0	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	0.0	0.0	*	0.0
Crust. spp.	4.8	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rocks	0.0	0.0	1.7	*	0.0	0.0	0.0	0.0	13.9	3.5	0.0	0.0	0.0	0.0	2.2
Based on wet weight of prey items															
GORP	18.8	48.0	6.1	41.5	12.4	42.7	26.0	34.7	30.9	26.9	9.6	14.3	6.6	21.2	19.6
Fish	60.3	0.0	88.7	0.0	0.0	10.3	0.0	0.0	15.8	0.0	49.9	50.0	0.0	27.1	0.0
Krill	7.9	16.5	4.7	1.4	85.4	46.9	71.2	31.9	2.1	49.8	21.2	35.5	93.4	38.6	1.5
Tunicate	0.0	0.0	0.0	4.9	0.0	0.0	2.3	12.1	3.1	0.0	0.0	*	0.0	7.7	66.6
Amphipod	0.0	2.6	*	2.1	0.0	0.0	*	8.7	5.0	4.7	0.0	0.0	0.0	1.7	3.0
Isopod	0.0	27.3	0.0	*	0.0	0.0	*	0.0	0.0	*	0.0	0.0	0.0	*	2.0
Polychaete	8.0	4.4	0.0	28.6	*	0.0	0.0	0.0	25.1	10.6	0.0	0.0	0.0	*	1.7
Shrimp	0.1	0.0	*	3.3	0.0	0.0	0.0	0.0	1.2	0.0	19.3	0.0	0.0	2.0	0.0
Echiura	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	15.5	6.9	0.0	0.0	0.0	0.0	4.2
Gastropod	0.0	0.0	0.0	12.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	*
Hydroid	*	0.0	0.0	0.0	0.0	0.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	*	0.0
Based on dry weight of prey items															
Fish	63.4	0.0	95.2	0.0	0.0	37.8	4.4	0.0	25.5	0.0	58.6	58.9	0.0	36.1	*
Krill	10.3	18.5	4.3	4.8	99.6	62.2	90.7	33.3	2.0	62.1	21.9	41.0	100.0	45.5	3.8
Tunicate	0.0	0.0	0.0	7.5	0.0	0.0	3.6	22.8	9.5	0.0	0.0	*	0.0	6.2	48.8
Amphipod	0.0	3.2	*	5.3	0.0	0.0	*	32.8	9.6	12.7	0.0	0.0	0.0	4.0	10.0
Isopod	0.0	30.2	0.0	1.5	0.0	0.0	1.2	0.0	0.0	*	0.0	0.0	0.0	*	9.0
Polychaete	0.0	23.1	0.0	48.4	*	0.0	0.0	0.0	31.1	12.2	0.0	0.0	0.0	*	2.2
Shrimp	17.5	0.0	*	4.5	0.0	0.0	0.0	0.0	5.6	0.0	19.1	0.0	0.0	3.2	0.0
Echiura	0.0	0.0	0.0	5.4	0.0	0.0	0.0	0.0	16.7	8.3	0.0	0.0	0.0	0.0	5.1
Gastropod	0.0	0.0	0.0	14.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	5.7
Hydroid	*	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	0.0	0.0	*	0.0
Crust. spp.	4.8	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rocks	0.0	0.0	*	3.0	0.0	0.0	0.0	0.0	*	4.2	0.0	0.0	0.0	0.0	6.9
Other	5.0	0.0	1.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	8.0

Results

Krill and fish were the dominant items in the diets of these fish (Table 2). In addition to these items, 26 types of invertebrates and plant material were represented in the guts (Sponges, Ctenophores, Cnidarians, Nematodes, Nematodes, Bivalves, Cephalopods, Picozonids, Cumacids, Tanaiids, Copepods, Mysids, Bryozoans, and Echinoderms accounted for less than 1% of the diet). Of the 321 stomachs examined, 26 were discarded because they were not properly preserved, 30 were empty, and 13 contained only unidentifiable material. The highest proportion of unidentifiable

material (among the stomachs used in the similarity analysis) was 48% (on a wet weight basis) and occurred in *Artedidraco mirus* (Table 3). The ratio of dry weight to wet weight of unidentifiable material averaged 22%. This is within the range of values for identifiable prey items in the diets and was most similar to the same ratio for fish (Table 4). Despite the problems of differential digestion, it was assumed that the proportions of identifiable material were accurate representations of the diet of these fish.

Every species examined ate some krill (Table 2). However, most pairwise comparisons of species diets

Table 4

Dry- to wet-weight ratios for the most common prey items in the diets of 15 species of Antarctic demersal fish.

Prey taxon	Identified species	Dry:Wet (%)
Amphipod	<i>Vibilia antarctica</i>	18.62
	<i>Parathemisto gaudichaudii?</i>	
	Hyperiidae	
	<i>Hyperoche medusarum?</i>	
Echirua		24.01
Fish	<i>Chaenocephalus aceratus?</i>	23.79
	<i>Arteididrao mirus?</i>	
	<i>Dissosticus eleginoides</i>	
	<i>Champscephalus gunnari</i>	
	<i>Patagonothen brevicauda?</i>	
	<i>Pagothenia hansonii</i>	
	<i>Nototheniops larseni</i>	
	<i>Muraenolepis microps</i>	
	<i>Nototheniops nudifrons?</i>	
	<i>Parachaenichthys georgianus</i>	
<i>Trematomus</i> spp.?		
Gastropod	<i>Atlantica</i> spp.?	12.66
Isopod	<i>Arcturus</i> spp.?	15.42
Krill	<i>Euphausia superba</i>	17.76
Polychaete	<i>Sternopsis</i> spp.?	17.58
	Maldanidae	
	Lumbrineridae?	
	Terribellidae?	
Philodocidae?		
Shrimp	<i>Crangon antarcticus?</i>	18.42
Tunicate		9.76
GORP		22.06

showed less than 50% overlap (Tables 5, 6), suggesting that in most cases resource partitioning was occurring. This is supported by the cluster analysis which showed that there was more than one significant cluster (Figs. 2, 3). The species or groups of species distinguished by the cluster analysis were feeding on different sets of prey. There were three groups of species in the community: fish-eaters, krill-eaters, and benthic invertebrates feeders.

Fish-eaters

The four members of the fish-eating group included most of the large carnivorous species in the region. The diets of *C. aceratus* and *Parachaenichthys georgianus* showed the greatest similarity (Figs. 2, 3) within the fish-eating group and overlapped by 78% (Table 6). They fed predominantly on fish, but each species also consumed roughly similar proportions of krill *Euphausia superba* and shrimp *Notocrangon antarcticus* (Table 3). Although little is known about the life history of *Parachaenichthys georgianus*, both it and *C. aceratus* appear to be epibenthic in their behavior.

Chaenocephalus aceratus is the largest species of icefish found in the South Georgia region, growing up to 75 cm (Fischer and Hureau 1985). It is an ambush predator (Kock 1985b). Heavily calloused pelvic fins of older individuals indicate that it spends much of its time sitting on the bottom. Fish prey included *Parachaenichthys georgianus* and *N. larseni*, which were as much as 58% of its body size (TL).

Table 5

Proportional prey overlap in the diets of 15 Antarctic demersal fish species collected off South Georgia I., based on the numerical abundance of prey items in each diet. Proportional similarity coefficient values are given in the upper subdiagonal of the matrix. Variance of the proportional similarity coefficient values are given in the lower subdiagonal of the matrix. Values of ≥ 0.5 have been underlined.

	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
ACER	—	0.2026	<u>0.8118</u>	0.0594	0.2043	0.2864	0.2321	0.2148	0.2362	0.2043	<u>0.6687</u>	<u>0.6430</u>	0.2043	0.4170	0.0614
ARTE	0.1773	—	<u>0.1250</u>	0.3013	0.1567	0.1500	0.2056	0.3167	0.3417	0.3785	0.1500	0.1500	0.1500	0.2420	0.3559
ELEG	0.3547	0.1094	—	0.0672	0.1200	0.2021	0.1528	0.1250	0.2372	0.1433	<u>0.5440</u>	<u>0.5587</u>	0.1200	0.3117	0.0847
GIBB	0.0559	0.2553	0.0633	—	0.0638	0.0571	0.1557	0.2089	0.4070	0.3248	0.0594	0.0573	0.0571	0.2101	0.3062
GUNN	0.1626	0.1342	0.1056	0.0605	—	<u>0.9179</u>	<u>0.8611</u>	0.4286	0.0484	<u>0.6601</u>	0.2222	<u>0.5612</u>	<u>0.9922</u>	<u>0.5853</u>	0.0681
GUNT	0.2379	0.1275	0.1810	0.0538	0.0754	—	<u>0.8889</u>	0.4286	0.1238	<u>0.6534</u>	0.3043	<u>0.6433</u>	<u>0.9179</u>	<u>0.6607</u>	0.0614
HANS	0.1896	0.1800	0.1364	0.1435	0.1196	0.0988	—	<u>0.5120</u>	0.1529	<u>0.6951</u>	0.2500	<u>0.5892</u>	<u>0.8611</u>	<u>0.6970</u>	0.1726
LARS	0.1687	0.2164	0.1094	0.1653	0.2449	0.2449	0.3213	—	0.3333	<u>0.5296</u>	0.2222	0.4288	<u>0.4286</u>	<u>0.6104</u>	0.4051
MICR	0.1804	0.2500	0.2014	0.3241	0.0466	0.1153	0.1388	0.2222	—	0.3743	0.2362	0.1808	0.0417	0.4043	0.3767
NUDI	0.1626	0.3038	0.1228	0.2696	0.2331	0.2265	0.2490	0.3357	0.2619	—	0.2222	<u>0.5612</u>	<u>0.6534</u>	<u>0.6706</u>	0.2510
PARA	0.4388	0.1275	0.3679	0.0559	0.1728	0.2482	0.1999	0.1728	0.1804	0.1728	—	<u>0.6129</u>	0.2222	0.4334	0.0614
PSEU	0.4088	0.1275	0.3518	0.0540	0.2463	0.3216	0.2733	0.2451	0.1482	0.2463	0.2373	—	<u>0.5612</u>	<u>0.7148</u>	0.0616
PSIL	0.1626	0.1275	0.1056	0.0538	0.0077	0.0754	0.1196	0.2449	0.0400	0.2265	0.1728	0.2463	—	<u>0.5786</u>	0.0614
ROSS	0.3300	0.2110	0.2631	0.1878	0.2505	0.3192	0.3415	0.3937	0.2950	0.2209	0.3394	0.3761	0.2438	—	0.2574
SQUA	0.0576	0.2923	0.0804	0.2484	0.0643	0.0576	0.1565	0.3205	0.2977	0.2193	0.0576	0.0578	0.0576	0.2152	—

Table 6

Proportional prey overlap in the diets of 15 Antarctic demersal fish species collected off South Georgia I., based on the dry-weight abundance of prey items in each species diet. Proportional similarity coefficient values are given in the upper subdiagonal of the matrix. Variance of the proportional similarity coefficient values are given in the lower subdiagonal of the matrix. Values of ≥ 0.5 have been underlined.

	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
ACER	—	0.1665	<u>0.7514</u>	0.0924	0.1139	0.3723	0.1575	0.1145	0.3311	0.1139	<u>0.7878</u>	<u>0.7033</u>	0.1139	0.4819	0.0458
ARTE	0.1388	—	0.0460	0.3253	0.1862	0.1846	0.1980	0.2166	0.2827	0.3434	0.1846	0.1846	0.1846	0.2229	0.2043
ELEG	0.2576	0.0439	—	0.0514	0.0459	0.3043	0.0896	0.0460	0.2798	0.0468	<u>0.6373</u>	<u>0.6353</u>	0.0459	0.3833	0.0444
GIBB	0.0839	0.2522	0.0488	—	0.0491	0.0475	0.0966	0.1757	<u>0.5578</u>	0.3111	0.0930	0.0482	0.0475	0.1918	0.3132
GUNN	0.1009	0.1521	0.0438	0.0468	—	<u>0.7416</u>	<u>0.9073</u>	0.4286	0.0213	<u>0.6224</u>	0.2194	0.4099	<u>0.9961</u>	0.4929	0.0451
GUNT	0.2926	0.1505	0.2354	0.0452	0.1916	—	<u>0.7852</u>	0.4286	0.2751	<u>0.6208</u>	0.4778	<u>0.6683</u>	<u>0.7416</u>	<u>0.7497</u>	0.0435
HANS	0.1426	0.1637	0.0856	0.0919	0.0841	0.2333	—	0.4661	0.1008	<u>0.6275</u>	0.2630	0.4542	<u>0.9073</u>	<u>0.5799</u>	0.0926
LARS	0.1014	0.1697	0.0439	0.1448	0.2449	0.2449	0.2810	—	0.2107	<u>0.5561</u>	0.2194	0.4106	0.4286	<u>0.5165</u>	0.2948
MICR	0.2215	0.1231	0.2041	0.3968	0.0209	0.1994	0.0938	0.1663	—	0.3212	0.3311	0.2758	0.0197	0.4079	0.2566
NUDI	0.1009	0.2804	0.0446	0.2611	0.2370	0.2354	0.2360	0.3561	0.2656	—	0.2200	0.4099	<u>0.6208</u>	<u>0.5270</u>	0.2170
PARA	0.4035	0.1505	0.2904	0.0845	0.1713	0.3629	0.2130	0.1713	0.2215	0.1716	—	<u>0.8056</u>	0.2194	<u>0.5872</u>	0.0470
PSEU	0.3429	0.1505	0.2858	0.0459	0.2419	0.4335	0.2837	0.2420	0.2001	0.2419	0.1566	—	0.4099	<u>0.7433</u>	0.0442
PSIL	0.1009	0.1505	0.0438	0.0452	0.0039	0.1916	0.0841	0.2449	0.0193	0.2354	0.1713	0.2419	—	0.4913	0.0435
ROSS	0.3335	0.1874	0.2701	0.1687	0.2515	0.4416	0.3245	0.3251	0.3146	0.2544	0.4038	0.4640	0.2499	—	0.1531
SQUA	0.0437	0.1736	0.0425	0.2610	0.0432	0.0416	0.0883	0.2472	0.2233	0.1720	0.0451	0.0423	0.0416	0.1393	—

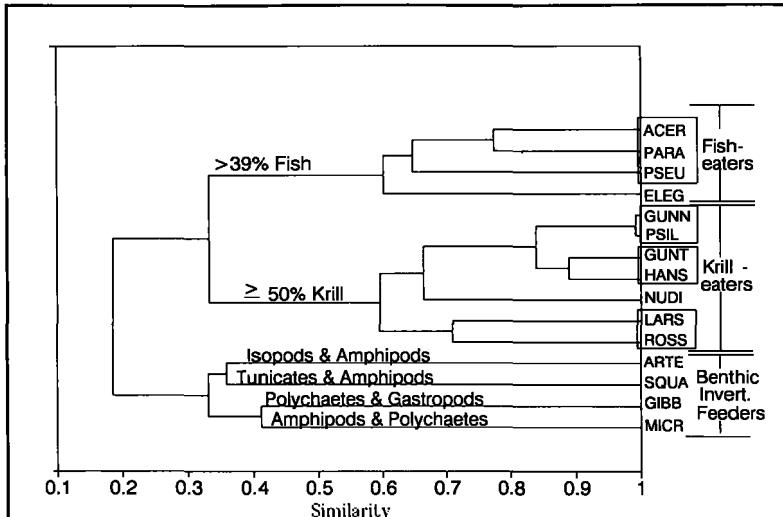


Figure 2

Dendrogram representing the classification of Antarctic demersal fish into trophic groups based on numerical abundance of prey items in their guts. Refer to Table 1 for key to species codes. Species grouped together within a box were identified as having significantly similar diets.

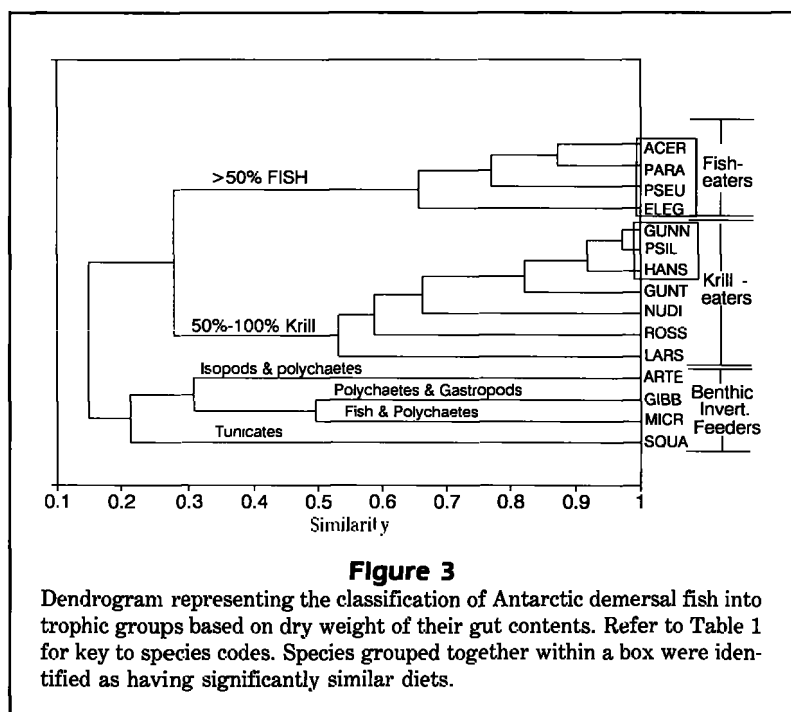
Parachaenichthys georgianus has a scaleless, elongate body. Its mouth is tube-shaped and probably functions like a slurp gun. It may be an ambush predator like the *C. aceratus*. Its diet consisted mainly of fish (59%) and roughly equal proportions of krill and shrimp

(Table 3). None of the fish it consumed were identifiable. Its diet overlapped most (80%) with that of the *Pseudochaenichthys georgianus* (Table 6).

Pseudochaenichthys georgianus also preyed heavily on other fish (59%) (Table 3). Like *C. aceratus*, it has a large mouth. However, it tended to feed on smaller fish and more krill than *C. aceratus* and did not eat shrimp. It fed on a variety of other fish species including *N. larseni*, *C. gunnari*, *M. microps*, and *Parachaenichthys georgianus*. Its diet overlapped most (80%) with that of *Parachaenichthys georgianus*.

D. eleginoides is the largest of all Antarctic demersal fish, growing to over 2m, and is an active predator (Fischer and Hureau 1985). It is known to be pelagic during some stages of its life (Fischer and Hureau 1985), but the presence of rocks in a few stomachs indicates that some had been feeding close to the bottom. It fed almost exclusively on fish (97%) (Table 3). Based on identifiable fish in the guts, it preyed

on *M. microps*, *N. larseni*, *Parachaenichthys georgianus*, and its own young. Stomachs from this species often contained a single fish that was as much as 53% of the size (TL) of the predator. Its diet overlapped most (75%) with that of *C. aceratus*.



Krill-eaters

Seven species were grouped as krill-eaters. The hierarchical cluster analysis places *C. gunnari*, *P. breviceps*, and *P. hansonii* in a single cluster and identifies others within this group as distinct clusters. The cluster analysis arranged these species in order of decreasing proportion of krill in the diet (Fig. 3, from top to bottom). These species are probably more pelagic in nature than other members of the community, with the possible exception of *N. nudifrons* (Permitin and Tarverdiyeva 1972, Targett 1981).

C. gunnari and *P. breviceps* had the most similar diets (Table 6), feeding almost exclusively (>97%) on krill. *Psilodraco breviceps* diet consisted 100% of krill (Table 3), but only three specimens were examined and the true variability of this species' diet may not be accurately represented here.

Champocephalus gunnari is the most important commercial species around South Georgia (Kock 1986, Gabriel 1987, McKenna and Saila 1989). It leads a more pelagic existence than its local relatives (*C. aceratus*, *P. georgianus*) (Kock 1985b). Its heavy dependence on krill has been documented (Targett 1981, Permitin and Tarverdiyeva 1972, Permitin and Tarverdieva 1979, Tarverdiyeva and Pinskaya 1980, Kock 1981). In this sample, its diet was composed almost entirely (99%) of krill (Table 3).

Little is known about the life history of *P. hansonii*, except for its heavy dependence on krill (Targett 1981).

In 1987-88, its diet consisted primarily of krill (91%), but it also fed on fish and tunicates (Table 3). Its diet overlapped those of *C. gunnari* and *P. breviceps* by more than 90% (Table 6).

Patogonothothen breviceauda is endemic to a shallow shelf region west of South Georgia known as Shag Rocks. Its diet consisted of 80% krill and 20% fish (Table 3). Its diet overlapped that of four other species (*C. gunnari*, *P. hansonii*, *P. breviceps*, and *N. rossii*) by more than 70%, due to the heavy dependence on krill (Table 6).

Nototheniops nudifrons is thought to be benthic in nature (Targett 1981, Permitin and Tarverdiyeva 1972, Permitin and Tarverdieva 1979). However, in 1987-88, 66% of its diet consisted of krill (Table 3) and the remainder was composed of epibenthic invertebrates. Rocks accounted for about 0.5% of the average dry-weight contents. Its diet overlapped that of four other species (*C. gunnari*, *P. breviceauda*, *P. hansonii*, and *P. breviceps*) by 62% (Table 6).

Notothenia rossii is a large (90 cm) species that was the mainstay of the commercial catch during the early 1970s (Kock 1986). Its diet was diverse, but it was grouped with the krill-eaters because 46% of its food was krill (Table 3). Fish was the second-most-important item in its diet and included *Parachaenichthys georgianus*, *M. microps*, *P. hansonii*, and *N. larseni*. *Notothenia rossii*'s diet overlapped most (74%) with those of *Pseudochaenichthys georgianus* and *P. breviceauda* (Table 6).

Nototheniops larseni is considered to be one of the most pelagically adapted of the nototheniids (Targett 1981). Previous work has shown that its diet is often dominated by krill (Permitin and Tarverdiyeva 1972 and 1979, Targett 1981, Daniels 1982). In this study, krill comprised only one-third of its diet, and 56% was pelagic tunicates and amphipods (Table 3). Its diet overlapped that of *N. nudifrons* by 55% (Table 6).

Consumers of benthic invertebrates

All of the members of the 'benthic invertebrate feeders' group had diets which were distinct from one another as well as from members of the other major groups. However, these fish all seemed to be closely associated with the bottom.

Notothenia squamifrons diet was the most unusual of all the species examined. It included a large proportion (49%) of tunicates (salps) (Table 3). The remainder of its diet consisted almost entirely of benthic invertebrates. Krill made up only 4%. The preponderance

of salps is also a feature of the diet of *N. squamifrons* found at Kerguelen I. (Duhamel and Hureau 1985). *Notothenia squamifrons* diet displayed the least amount of overlap of all the species examined. It reached a maximum of 32% when compared with that of *N. gibberifrons* (Table 6).

Polychaetes were a major component (>23%) of the diets of the three remaining species. *Notothenia gibberifrons* is an important commercial species. It was the dominant species (numerically and by biomass) during the 1988–89 AMLR survey of the South Georgia region (McKenna 1989). It is a benthic species, which uses its relatively small, subterminal mouth to 'slurp up' benthic epi- and infauna (Daniels 1982). It had the most diverse diet of the species examined (Table 2); however, over 50% of its diet consisted of polychaetes. The remainder was comprised of invertebrate epifauna and a small amount of krill (5%, Table 3). Its diet overlapped most (56%) with that of *M. microps* (Table 6).

Mureanolepis microps is a scaleless, eel-like species with a diverse diet (Table 2). It was the only 'benthic invertebrate feeder' to eat fish (Table 3). Nine percent of its diet consisted of salps and 2% of krill. The other items in the diet were benthic organisms. Polychaetes were the dominant prey item. Its diet overlapped most (56%) with that of the *N. gibberifrons* (Table 6).

Artedidraco mirus was the smallest species (~8 cm TL) consistently caught in the trawl. Its diet was composed mostly of isopods and polychaetes (Table 3). This species was represented by only four stomachs, which may not accurately display the true diet of this species at South Georgia. The greatest overlap of its diet (34%) occurred with *N. nudifrons* (Table 6).

Discussion

These results support the conclusions of earlier workers, in that the most abundant species (including those of commercial value) of the South Georgia demersal fish community can be classified into three groups based on their summer diets. The largest group contained those fish that depended heavily on krill and included *C. gunnari* and *N. rossii*. Fish-eaters represented a second distinct group. Three of the four members of this group (*D. eleginoides*, *C. aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The third group contained a loose association of species which tended to feed mostly on benthic invertebrates. *Notothenia gibberifrons* and *N. squamifrons* are the commercially important members of this group. *Notothenia gibberifrons* is one of the most abundant species in the region, while *N. squamifrons* is rare on

the continental shelf around South Georgia (<500 m) (McKenna and Saila 1989, McKenna 1989).

The fishes at South Georgia were using two different food resources: pelagic organisms (mostly krill) and benthic organisms. The large benthic biomass of the Antarctic appears incapable of supporting a large or diverse fish fauna because most of it is in the form of non-food species (e.g., sponges, sea stars) (Belyaev and Ushakov 1957, Andriashev 1965). This may explain why *N. gibberifrons*, and a few less-common species, were the only fish that depended heavily on benthic organisms. To survive in this environment, these fish have had to diversify their diets and draw upon more prey species than the pelagic fish of the region.

The majority of fish in the vicinity of South Georgia I. relied on the pelagic food resource. The adaptations of many of these basically benthic fishes to pelagic feeding (Nybelin 1947, Permitin 1970, Eastman 1985, Kock 1985b) indicate the relative superiority, in quality and/or availability, of food in the pelagic realm. Krill was the only food resource consumed by all species of Antarctic fish examined in this study. Five of the fifteen species examined relied on krill for greater than 50% of their diet.

There were direct and indirect trophic links between krill and piscivores. All piscivores ate some krill, and most of the identifiable fish that they ate were krill-eaters. However, most of the fish consumed by piscivores in this study were unidentifiable, and a strong link between a piscivore (*N. rossii*) and the benthos (*N. gibberifrons*) has been demonstrated at Kerguelen I. (Linkowski et al. 1983). Thus, the relative magnitudes of links between piscivores and krill or the benthos remain unknown.

Diet overlap and Interspecific competition

In paired comparisons, there was at least some overlap in the diets, especially in those species relying heavily on krill. However, in most cases the overlap was less than 50%, indicating that resources were effectively partitioned within the South Georgia community during the austral summer.

Despite the heavy dependence on krill and high overlap (90%) of the diets of a few species, competition is probably not important in the Antarctic demersal fish community during the summer (Targett 1981, Daniels 1982). Competition occurs only when the resource in common use is limiting (Larkin 1963). The availability of krill to Antarctic fish varies (Permitin and Tarverdieva 1979), but whether it is limiting is unknown. In some years, krill is abundant enough to come in contact with the bottom and is then available to even strict benthic feeders like *N. gibberifrons* (Targett 1981).

This study suggests that resources are effectively partitioned in the austral summer. However, the Antarctic undergoes strong seasonal changes, which affect the abundance and availability of krill as well as other aspects of the ecosystem. Krill spawn in summer and the larvae migrate vertically from great depths (>500m) as they develop over the winter, recruiting to the population the next summer (Marshall 1979). Adult and juvenile krill do most of their growing in summer when they may be superabundant, occurring in dense 'swarms' (Everson 1984a). During the unproductive winter, krill grow little or may even shrink in size (Ikeda and Dixon 1982), but their distribution at that time is poorly known.

The trophic structure of the Antarctic fish community may change in response to these seasonal events. Prey switching and niche shifts offer two mechanisms to deal with these seasonal changes. Although diet diversities were low for South Georgia fishes, all species (with the exception of *P. breviceps*) consumed at least one alternative food resource regularly. This indicates that there is the potential for prey switching according to the availability of the prey resources in the environment. Seasonal prey switching has been inferred from changes in the diets of related species living along the Antarctic Peninsula (Daniels 1982).

Niche shifts may occur to reduce competition at times when krill is limiting. As krill becomes more limiting, behavioral changes, such as a shift to more specialized feeding on alternative prey or in specific habitats, may occur. To test these hypotheses a seasonal time series of diets and the availability of prey is needed.

Possible effects of commercial fishing

Selective removal of species by fishing will effect the demersal fish community. Prey of removed predators may benefit from reduced predation, as has been suggested for *Champocephalus gunnari* at Kerguelen I. (Duhamel and Hureau 1985). One competitor may benefit by increased fecundity if the other is removed by fishing (Beddington and May 1982). Competition may be intensified at a lower trophic level if a predator on one species of a competing pair is reduced (Miller and Kerfoot 1987, Abrams 1987, Boisclair and Leggett 1989). If a niche shift had taken place in the past to reduce competition, a species may expand to occupy more of a niche when its competitor is removed (Connell 1980, Beddington and May 1982). However, it is difficult to predict the response of the community without more data on the life histories and seasonal dynamics of these fish and their prey.

Ecological efficiency is another topic to be considered when harvesting an Antarctic community. The South Georgia community is highly productive (Hempel 1985).

The diversity of the system is low and the food web is relatively simple (Beddington and May 1982). However, the cost of activity and survival in the Antarctic is high (Hempel 1985) and the loss of energy at each trophic transfer places a limitation on the biomass of fish available for harvest. Many of the commercially valuable species are large piscivores (*Chaenocephalus aceratus*, *Pseudochaenichthys georgianus*, *Dissostichus eleginoides*, *Notothenia rossii*) one or more steps removed from secondary production. The availability of krill to these fish and their prey, and the fish's ability to emphasize krill in their diets, will strongly influence the yield of fish from the South Georgian community.

Conclusions

The most abundant species of the South Georgia demersal fish community were classified into three groups based on their summer diets. Species that depended heavily on krill comprised the largest group, including *Champocephalus gunnari* and *Notothenia rossii*. The second group was comprised of piscivores. Three of the four members of this group (*Dissostichus eleginoides*, *Chaenocephalus aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The food of their prey often consists of krill. The third group contained a loose association of species which fed mainly on benthic organisms. *Notothenia gibberifrons* and *Notothenia squamifrons* are the important commercial species in this group.

Krill is the most important prey species to the fish in the South Georgia system during the austral summer. It was consumed either directly or indirectly by all of the fish in this study. However, it is unknown whether the krill resource is limiting to these fish at that time or in any other season. More information on the seasonal dynamics and behavior of these fish and their prey is necessary to conclusively determine the role of competition for food in this system.

The potential for change in this community due to fishing is evident. Selective reduction in populations within the fish community may have widespread repercussions. The relatively simple, but highly interconnected, food web in the South Georgia system may have a lower potential for fish yield than previously thought (Hempel 1985).

Acknowledgments

This work was supported by a grant from the Antarctic Marine Living Resources Program of the National Marine Fisheries Service. I am grateful to S. Saila for technical and editorial assistance and S. Pratt for aid

with some invertebrate identifications. For their assistance in collecting stomachs, thanks go to the members of the crew and scientific parties on the RV *Profesor Siedlecki* during the 1987-88 survey of the South Georgia fish community.

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