

Abstract.—Demersal fish represent one of the most heavily exploited resources in the Antarctic ecosystem. The stocks around South Georgia Island have contributed a substantial portion of the annual catches and have declined over the past decade. Fishing has been implicated as the cause of this decline. However, a clear description of the community structure of this system, which is necessary to judge the influence of fishing accurately, has been lacking.

The spatial structure of the South Georgian fish community was investigated through the use of survey data collected over a three-year period. The results clearly indicated the absence of spatial structure in that community. The presence or absence of rare species at various stations was responsible for the weak structure found in the initial analysis. The general lack of structure was consistent from year to year.

The available data do not provide an explanation for this lack of structure. All surveys were conducted during the austral summer only. Events and community structure at other times of the year remain unknown. Although the data were representative of the fish community during the austral summer, no comparable data were available on the abundance and distribution of their prey items, especially krill (*Euphausia superba*). More extensive sampling, expanded to include other seasons, is necessary to properly address the questions of seasonal change in community structure and the role of competition in this Antarctic system.

Spatial structure and temporal continuity of the South Georgian Antarctic fish community

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The marine systems of the Antarctic are important both ecologically and economically. Many of the seasonal and long-term events that occur in this region have a significant impact on global environmental conditions (Gordon, 1975; Broecker and Peng, 1982; Kennett 1982, p. 249). The Antarctic is a large region physically isolated from the rest of the globe by the circumpolar circulation of the West Wind Drift Current (Kennett 1982, p. 725). The organisms of the Southern Ocean are unique and often highly productive. The waters south of the Antarctic convergence (about 5% of the world ocean) contribute a total production equivalent to 20% of that produced by all the oceans of the world (El-Sayed, 1968). In fact, it is believed that the evolution of the Mysticeti (baleen whales) depended on the development of the great production of this area (Fordyce, 1977).

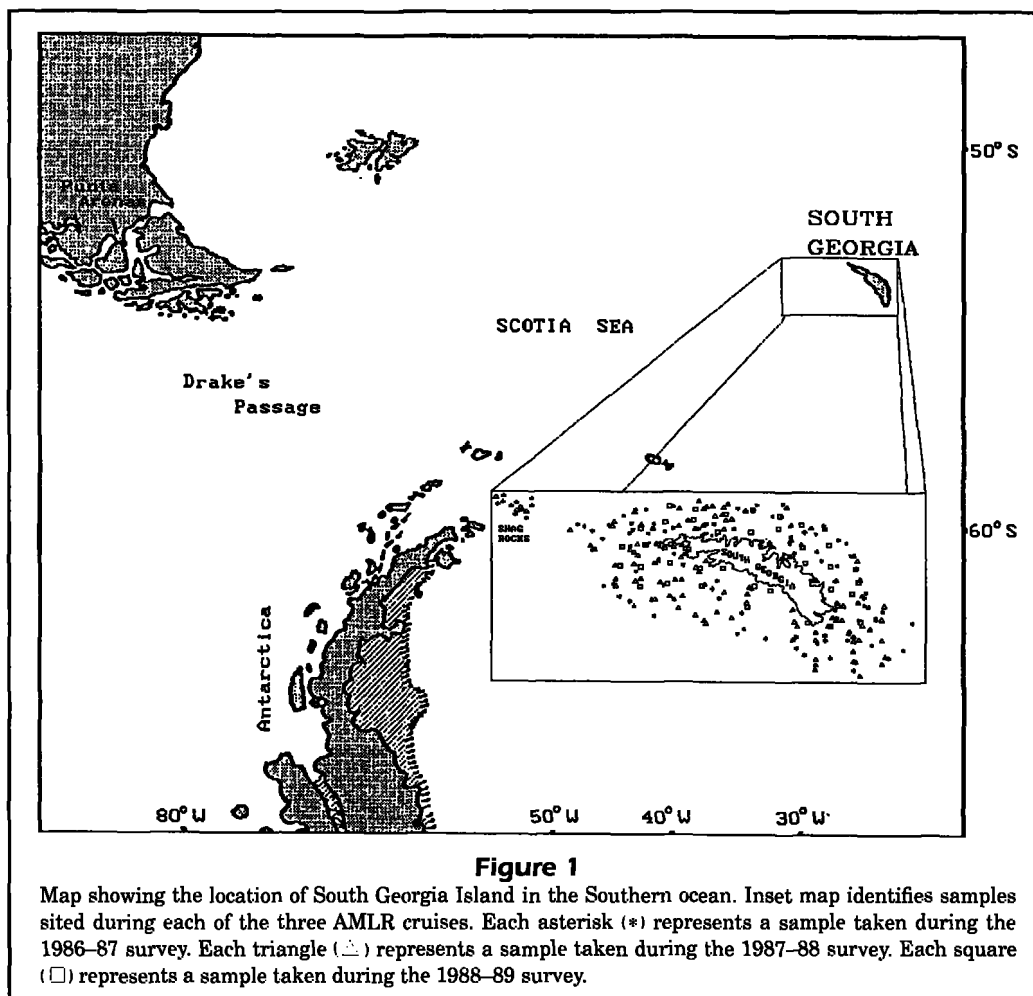
The environment of Antarctica and its associated islands has been established for a long time (ca. 37 million years), allowing a group of perciform fishes to radiate into a variety of niches and to dominate the fish fauna of this highly productive region (DeWitt, 1971; Targett, 1981; Eastman, 1985). Like other polar communities it is one of low species richness (Hedgepeth, 1969; Everson, 1984). Over 70% of the species and 90% of the individuals belong to four families in the suborder Notothenioidae and 95% of the species in this group are endemic to the Antarctic

region (DeWitt, 1971). The four dominant families are the Antarctic cods (Nototheniidae), dragonfish (Bathyracoonidae), icefish (Channichthyidae), and plunderfish (Harpagiferidae). These fish are generally sedentary, benthic forms found on the Antarctic continental shelves (Targett, 1981). Many of the species in this group have evolved to fill niches usually occupied by different families or orders of fish (Eastman, 1985).

Large stocks of demersal fish were discovered around some of the islands of the Scotia Arc in the late 1960's (Kock, 1986). A relatively intense and successful fishery developed around these stocks, especially those found at South Georgia Island (Fig. 1). However, the decline of those stocks over the past two decades has been evident (Kock, 1985a, 1986; Gabriel, 1987; McKenna and Saila, 1989; McKenna¹). This is especially true for the target species of this fishery, the marbled rockcod (*Notothenia rossii*) and the mackerel icefish (*Champsocephalus gunnari*). There is also evidence that a short-term (two to three years) shift in the species assemblage inhabiting the continental shelf around South Georgia has occurred (McKenna and Saila, 1991).

Although overfishing is suspected as the cause of the changes observed

¹McKenna, J. 1990. Status of the stocks of Antarctic demersal fish in the vicinity of South Georgia Island, January 1989. Antarctic Mar. Living Res. Contract Rep. Available from Dr. R. Holt, NOAA, NMFS, Southwest Fisheries Sci. Center, La Jolla, CA 92038.



in the demersal fish community (Kock, 1985b, 1986, 1991; Kock and Koster, 1989, 1990), there is a need for more basic information about the ecology of these fishes. The effects of natural (or anthropogenic) events on the populations of these animals cannot be accurately judged without a clear understanding of their basic community organization.

Analysis of Antarctic fish communities has generally been limited to descriptions of the species present and some investigations of their diets. Targett (1981) included some measures of diversity in his examination of the fish community at three different islands along the Scotia Arc. His research emphasized diets and resource partitioning, and gives some of the first descriptions of relationships between the species based on a quantitative analysis. However, his sampling was limited to one or two locations at each island. More extensive work has been conducted at Elephant Island by Tiedtke and Kock (1989). Their examination of the demersal fish assemblage around that Island found evidence of spatial structure associated with depth.

A survey program concentrating on the South Georgia area was established as part of the U.S. Antarctic Marine Living Resources (AMLR) project. The research described here used the data from that program to examine the spatial structure of the demersal fish community in the vicinity of South Georgia Island and its temporal consistency from 1986 to 1989.

Methods

Data used in this study consisted of species abundances (and associated length-frequency information) collected during three research survey cruises in the South Georgia area. The abundance of each species in the region was measured both numerically (number/standard tow) and on a biomass (kg/standard tow) basis.

These surveys were conducted during the austral summers of 1986-87 (29 Nov.-17 Dec. 1986), 1987-88 (19 Dec.-10 Jan.), and 1988-89 (17-28 Jan. 1989). The 1986-87 and 1987-88 surveys sampled the abundance

of fish from approximately 100 stations (Fig. 1) by thirty minute tows of a P32/36 otter trawl (mouth opening of 17.5 m, 43–52 mm mesh liner). These stations had been randomly located within three depth strata (50–150 m, 150–250 m, 250–500 m) (Gabriel, 1987; McKenna and Saila, 1989). The 1988–89 survey sampled 41 stations from a regular grid between 50-m and 250-m depth around South Georgia Island (Fig. 1). Collections of demersal fish during that survey were made with fifteen minute tows of a Christensen Bottom Trawl (wing spread of 4.6 m, 50-mm mesh codend with a 6-mm liner) (McKenna¹). Complete discussions of the methods and results of these surveys may be found in Gabriel (1987), McKenna and Saila (1989), and McKenna¹.

Species diversity has become a standard tool for describing natural communities. Three measures of diversity were calculated for each station sampled during the three surveys and for each survey as a whole based on the total catches. The first was species richness, which was simply the number of species caught at each station. The second was the Shannon-Wiener information index (H' , using \log_e) (Shannon and Weaver, 1949). The third index (V) was a measure of evenness (Pielou, 1977),

$$V = H' / \log(s^*),$$

where s^* is the total number of species in the region and was assumed to be 30.

Species associations give a more detailed description of a natural community than the simple summary provided by diversity indices. Species associations within each survey were identified by use of Spearman rank correlation (r') analysis (Freund, 1970, p. 311–313), and were based on the numerical abundance of fish caught during each survey. Species were arbitrarily designated as rare if they occurred at 5% or less of the sampled stations and uncommon if they occurred at 25% or less of the stations sampled. All pairwise combinations of common species (within each season) were examined. These correlation values were then used to generate Z -scores ($Z = r' \sqrt{(n-1)}$) to test the null hypothesis that the correlation was not significantly different from zero. Significance of associations was determined at the 0.01 level ($Z \geq 2.58$) (Freund 1970, p. 313).

Cluster analysis was used to examine the spatial structure of the community in an effort to identify significant subcommunities. This analysis method reduces the complex, multivariate data from field studies to a manageable level (Boesch, 1977) and often reveals the presence of important physical or biological factors affecting the distribution of the various species assemblages occupying the sampled region (Pielou,

1977). However, one of the major drawbacks of cluster analysis (and many other exploratory techniques) is the subjectivity associated with its application (Boesch, 1977; Pielou, 1984; Jain and Dubes, 1988).

The heterogeneity ratio (HR) was used in this analysis as the measure of similarity for the normal (R -mode) cluster analyses, because of the objectivity it provides. It is not affected by sample size or group size (the number of samples included in a cluster), measures the beta-diversity (McNaughton and Wolf, 1979a) existing among samples, and can be statistically tested for significance (Kobayashi, 1987).

$$HR = S_Q / E(S_Q),$$

where S_Q is the total number of species present in Q samples and $E(S_Q)$ is the expected number of species in the Q samples. $E(S_Q)$ is obtained by applying the mean number of species per sample to the logarithmic series distribution (Fisher et al., 1943), which is used as the model describing the relation between the sample size and number of species in the community. The logarithmic series describes communities which are dominated by one or a few species and contain numerous rare species. It is a common distribution in nature (Shepard, 1984; Dial and Marzluff, 1989) and is the most appropriate for this application (Kobayashi, 1987).

HR is robust to the requirement of good fit to the logarithmic series model (Kobayashi, 1987). However, the fit of the data to that distribution was tested for each station sampled during the three surveys with the aid of the BASIC program LOGSRFIT.BAS (Saila et al., 1991). This program generates values of X , Fisher's α , and K . X and α are the parameters of the logarithmic series model and α is also a diversity index (Fisher et al., 1943; Saila et al., 1991). Values of K measure the goodness-of-fit of the data to the logarithmic series model (Fisher et al., 1943). Values of K less than 1.0 indicate a reasonable fit to the model.

A normal (R -mode) clustering of the stations was performed for each survey. The clustering program, HRCLUSTER.BAS (written in Microsoft QuickBasic v. 4.5, Microsoft 1988), was developed for this purpose (available upon request). It was a modification of Kobayashi's² program and used the HR and an unweighted paired group method of averaging (UPGMA) linkage method (Sneath and Sokal, 1973). The null hypothesis of non-significant clusters was rejected at the 0.05 level (Kobayashi, 1987). Inverse (Q -mode) clustering was also performed on each survey's data to classify species into groups. This provides insight into

²Kobayashi, Faculty of Agriculture, Yamagata Univ., Tsuruoka, 997 Japan. Pers. commun. 1988.

their associations and distributions. The species were clustered with the correlation coefficient and an UPGMA linkage method (Jain and Dubes, 1988, p. 16). The results of these analyses were then combined through nodal analysis (Williams and Lambert, 1961; Lambert and Williams, 1962; Noy-Meir, 1971; Boesch, 1977) into two-way tables displaying the constancy and fidelity of the identified groups (Fager, 1963; Westhoff and van der Maarel, 1973).

Constancy describes how widespread a species group is within a given habitat and is expressed as

$$C_{ij} = a_{ij}/(n_i n_j),$$

where a_{ij} is the actual number of occurrences of members of species group i in collection (station) group j , and n_i and n_j are the number of entities in the respective groups. C_{ij} ranges from 0 to 1, where 1 indicates that all species occurred in all collections in the group (Boesch, 1977).

Fidelity describes the restriction of a species group to a given habitat and is expressed as

$$F_{ij} = (a_{ij} \sum_j n_j) / (n_j \sum_i a_{ij})$$

Values of this index greater than 2 suggest a strong preference of species in a group (i) for a collection group (j), and values much less than 1 suggest avoidance of a collection group (j) by a group of species (i) (Boesch, 1977).

The size structure of each species' population (1987–88 and 1988–89 surveys only) was also examined for patterns. Stations were clustered (using *HR* and UPGMA linkage) based on the abundance of individuals in each centimeter length class.

Natural communities may be aligned along environmental gradients, changing continuously from one end to the other (Whittaker, 1960). Skewer analysis uses multivariate correlations to measure the significance of linear trends in natural communities (Pielou, 1984; Saila et al., 1991). It was used in this study to examine the significance of trends in each community along suspected gradients of depth, longitude, latitude, and time (date within each survey). It was performed twice on each data set. The first application used the absolute measures of abundance, which detects trends that are a combination of changes in the species assemblage and the absolute abundances of individuals at each station. The second application used those abundance values converted to proportions, which is sensitive only to the changes in species composition along the gradient. Kendall's Tau provided the measure of correlation between each skewer and the observed data. The distribution of Tau was observed through the use

of ten classes (0–0.1, 0.1–0.2, etc.). Each data set was sorted in the order of the gradient being examined and probed with 500 skewers. Twenty random tables were generated during each analysis to provide a test of the null hypothesis that the assemblages were distributed randomly along the gradient at a 0.05 probability level (Pielou, 1984).

Although the change in an assemblage along an environmental gradient may be gradual, there may also be cases of rapid change. These ecotones may be due to rapid change in the environmental gradient or possibly a biological change for some other reason (Whittaker, 1960; McNaughton and Wolf, 1979b). Gradient analysis (Webster, 1973; Ludwig and Cornelius, 1987) was applied to the data sorted in order of each of the above potential gradients, to search for boundaries along the length of those gradients. The BASIC program, GRADSECT.BAS (written in Microsoft QuickBasic v. 4.5, Microsoft 1988), was developed for that purpose (available upon request). It used a moving split-window distance method of comparing moving averages (Whittaker, 1960). Each window contained nine stations and the multivariate distance measure was based on the squared Euclidean distance.

Results

The assemblage of demersal fish occupying the South Georgia region, during the three AMLR surveys, consisted of slightly more than two dozen (28) species, with representatives from thirteen families (Table 1). Seven of these species accounted for the vast majority (>85%) of fish biomass and individuals in the system (Fig. 2). Five are relatively large (>50cm), commercially valuable species. These included the three icefish (*Channichthyidae*) of the region (*Chaenocephalus aceratus*, *Champsocephalus gunnari*, and *Pseudochaenichthys georgianus*) and two species of rock cod (*Nototheniidae*: *Notothenia gibberifrons* and *Notothenia squamifrons*). The other two important species (*Nototheniops larseni* and *Nototheniops nudifrons*) are small but abundant members of the *Nototheniidae*. The distributions of these species with depth was similar to those described by Tiedtke and Kock (1989) for the fishes of Elephant Island.

Champsocephalus gunnari was the clear dominant both numerically and based on biomass (Fig. 2). One quarter of the biomass and nearly one third of the individuals were members of this species. It feeds almost strictly on krill (McKenna, 1991) and leads a more pelagic existence than the other icefish of the region (Kock, 1985b). *Notothenia gibberifrons* was a close second in biomass and was the third most abundant species. It is adapted to an epibenthic environ-

Table 1

Species codes and rareness designations. R = RARE (occurred at 5% or fewer of the stations sampled). U = UNCOMMON (occurred at 25% or fewer of the stations sampled). C = COMMON (occurred at more than 25% of the stations sampled). '—' indicates that that species was not caught during a particular survey.

Species code	Family and species	Rareness designation		
		86–87	87–88	88–89
ARTE	Artedidraconidae (Plunderfishes)			
	<i>Artedidracon mirus</i>	C	C	C
BATH	Bathydraconidae (Dragonfishes)			
	<i>Bathydraconidae</i> spp.	R	—	—
PARA	<i>Parachaenichthys georgianus</i>	C	C	C
PSIL	<i>Psilodracon breviceps</i>	U	U	U
MANT	Bothidae (Armless Flounders)			
	<i>Mancopsetta maculata</i>	U	U	R
CENT	Centrolophidae (Ruffs)			
	<i>Centrolophidae</i> spp.	—	R	—
ACER	Channichthyidae (Icelfishes)			
	<i>Chaenocephalus aceratus</i>	C	C	C
GUNN	<i>Champscephalus gunnari</i>	C	C	C
PSEU	<i>Pseudochaenichthys georgianus</i>	C	C	C
DIPL	Gempylidae (Snake Mackerels)			
	<i>Paradiplospinus antarcticus</i>	—	R	—
HARP	Harpagiferidae (Spiny Plunderfishes)			
	<i>Harpagifer georgianus</i>	—	R	—
CARE	Liparididae (Snailfishes)			
	<i>Careproctus georgianus</i>	—	R	—
LIPA	<i>Paraliparis</i> spp.	U	U	U
MICR	Muraenolepididae (Moray Cods)			
	<i>Muraenolepis microps</i>	C	C	C
ELEC	Myctophidae (Lanternfishes)			
	<i>Electrona antarctica</i>	R	—	R
MYCT	<i>Myctophidae</i> spp.	U	—	—
NICH	<i>Gymnoscopelus nicholsi</i>	U	R	—
ANGU	Nototheniidae (Antarctic Rock Cods)			
	<i>Notothenia angustifrons</i>	R	R	R
ELEG	<i>Dissostichus eleginoides</i>	C	C	R
GIBB	<i>Notothenia gibberifrons</i>	C	C	C
GUNT	<i>Patagonothoen brevicauda</i>	R	R	—
HANS	<i>Pagothenia hansonii</i>	C	C	U
KEMP	<i>Notothenia kempi</i>	R	R	—
LARS	<i>Nototheniops larseni</i>	C	C	C
NUDI	<i>Nototheniops nudifrons</i>	C	C	C
ROSS	<i>Notothenia rossii</i>	C	C	U
SQUA	<i>Notothenia squamifrons</i>	C	U	—
RAJA	Rajidae (Skates)			
	<i>Raja georgiana</i>	C	U	U
MELA	Zoarcidae (Eelpouts)			
	<i>Melanostigma gelatinosum</i>	—	R	—

ment (Daniels, 1982) and feeds on invertebrate infauna, primarily polychete worms (McKenna, 1991). *Nototheniops larseni* was the second most abundant species and is the most pelagically adapted of the common species (Targett, 1981). It is a relatively small fish (<25 cm) that feeds on krill and other pelagic invertebrates (McKenna, 1991). *Chaenocephalus aceratus* and *P. georgianus* are the other two icefish found in the vicinity of South Georgia Island. Both species are closely associated with the sea floor and feed heavily on other fish and krill (McKenna, 1991). *Notothenia*

squamifrons is a demersal rock cod that prefers the deeper strata of the region. It feeds on a wide variety of benthic invertebrates but has a preference for tunicates (McKenna, 1991). *Nototheniops nudifrons* is one of the smallest species in the region (10–5 cm). It lives in and among the sedentary megainvertebrates growing on the bottom (e.g., sponges). It feeds on benthic epifauna, but most of its diet consists of krill (McKenna, 1991). Other species collected by the AMLR surveys generally accounted for less than 2% of the fish in the region. For a more detailed description of this community see Gabriel (1987), McKenna and Saila (1989, 1991), and McKenna (1991).

Diversity values were moderate throughout the region and relatively consistent from year to year. The overall diversities (H') for each survey (1986–87–1988–89) were 1.51, 1.94, and 1.83 (based on numerical abundances) (Table 2). The value for any given station ranged from 0 to 2.097 (Fig. 3). Richness never exceeded 16 at a single station, but was as low as 1 (which accounts for the zero H' values) in a few cases. Survey-wide richness was nearly the same for 1986–87 and 1987–88 but declined in 1988–89 because of the lack of rare species collected during the survey. Overall evenness for each survey ranged from 1.02 to 1.35 and was greater in the latter two surveys.

Significant associations were found between species within each survey. However, all were weakly correlated (Table 3). Only three as-

sociations had r' values greater than 60% and none explained more than 70% of the variability in their distributions. None of the fifteen associations with r' values greater than 50% were consistent from year to year. However, three of these associations (*C. aceratus*–*P. georgianus*, *Artedidracon mirus*–*N. nudifrons*, *Muraenolepis microps*–*N. nudifrons*) persisted from 1986–87 to 1987–88. The inverse (Q -mode) cluster analysis appeared to classify the species into groups based on their relative rareness, but there were exceptions to such a classification in nearly every group.

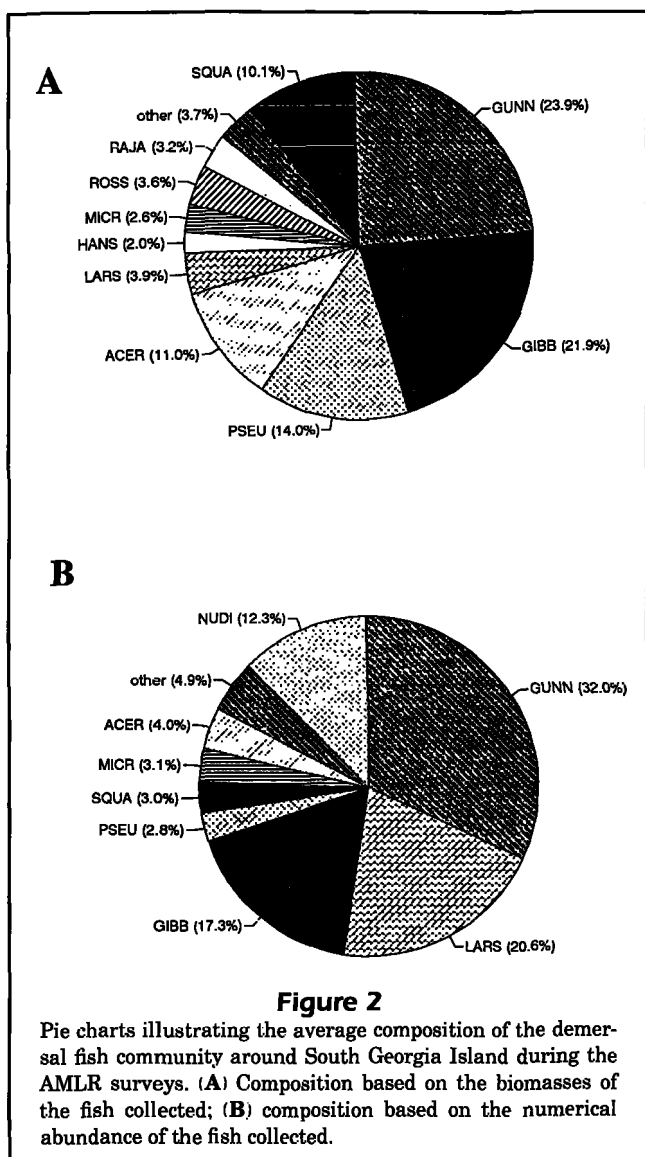


Figure 2

Pie charts illustrating the average composition of the demersal fish community around South Georgia Island during the AMLR surveys. (A) Composition based on the biomass of the fish collected; (B) composition based on the numerical abundance of the fish collected.

Table 2

Diversity of South Georgia Island Demersal Fish Community. R represents species richness. The # symbol indicates that the diversity values were calculated on a numerical abundance basis. The wt. symbol indicates that the diversity values were calculated on a biomass basis. H' is the Shannon-Wiener information index. V is an index of species evenness.

	1986-87		1987-88		1988-89	
	R-27		R-25		R-18	
	#	wt.	#	wt.	#	wt.
H'	1.51	1.91	1.94	1.94	1.83	1.99
V	1.02	1.29	1.31	1.31	1.24	1.35

The distribution of species abundances at most stations was described well by the logarithmic series model (Fig. 4). However, 27% of the stations (11) in the 1988-89 biomass data set fit the logarithmic series model poorly, while those of earlier surveys had less than half that proportion of poor fitting stations. The biomass data sets generally had more poor fitting stations than did the numerical data sets.

The normal cluster analyses clearly demonstrated that there was little spatial structure in the demersal fish community. Extensive chaining (Boesch, 1977; Jain and Dubes, 1988), frequent reversals (crossovers) (Kobayashi, 1987), and low number of significant clusters were indicative of the absence of spatial structure (Fig. 5, page 484). The 1986-87 and 1987-88 communities displayed slightly more significant structure than that in 1988-89, but chaining and reversals were prevalent there as well. The nodal analyses demonstrated that the species groups occurred with similar constancy throughout the region and fidelity was not strong for any particular group (Fig. 6, page 484).

Species composition of significant clusters was basically the same as that for the region-wide species assemblage (Fig. 2), except for those clusters formed by a small number of samples with rare species (Fig. 7, page 485). Clusters containing samples from Shag Rocks had *Patagonothen brevicauda* as an additional component. Close examination of the clusterings revealed that the presence or absence of the rarest species was the basis for what little structure was present. When these rare species (those which occurred at 5% or fewer stations) were removed, all or nearly all significant structure disappeared. The lack of structure was consistent from year to year.

Clustering of the length distribution of each species revealed little structure there as well. *Nototothenia gibberifrons*, *C. gunnari*, and *N. larseni* showed a weak separation of large and small fish; large fish associated with deeper water and small fish with shallower stations during 1987-88 (Figures 8, A and B; 9A). Only *N. larseni* continued to show that trend in 1988-89 (Fig. 9B). *Nototothenia larseni* also displayed a temporal separation in size, with larger fish caught later in the cruise in both surveys (Fig. 9C). *Muraenolepis microps* showed a similar weak trend of larger fish later in the cruise during the 1988-89 survey (Fig. 8C).

The gradient analyses revealed several significant, but weak trends. Skewer analysis detected significant trends in longitude in all three years. Significant trends in latitude and depth were identified in 1987-88 and in 1988-89. In 1986-87 and 1988-89, significant tem-

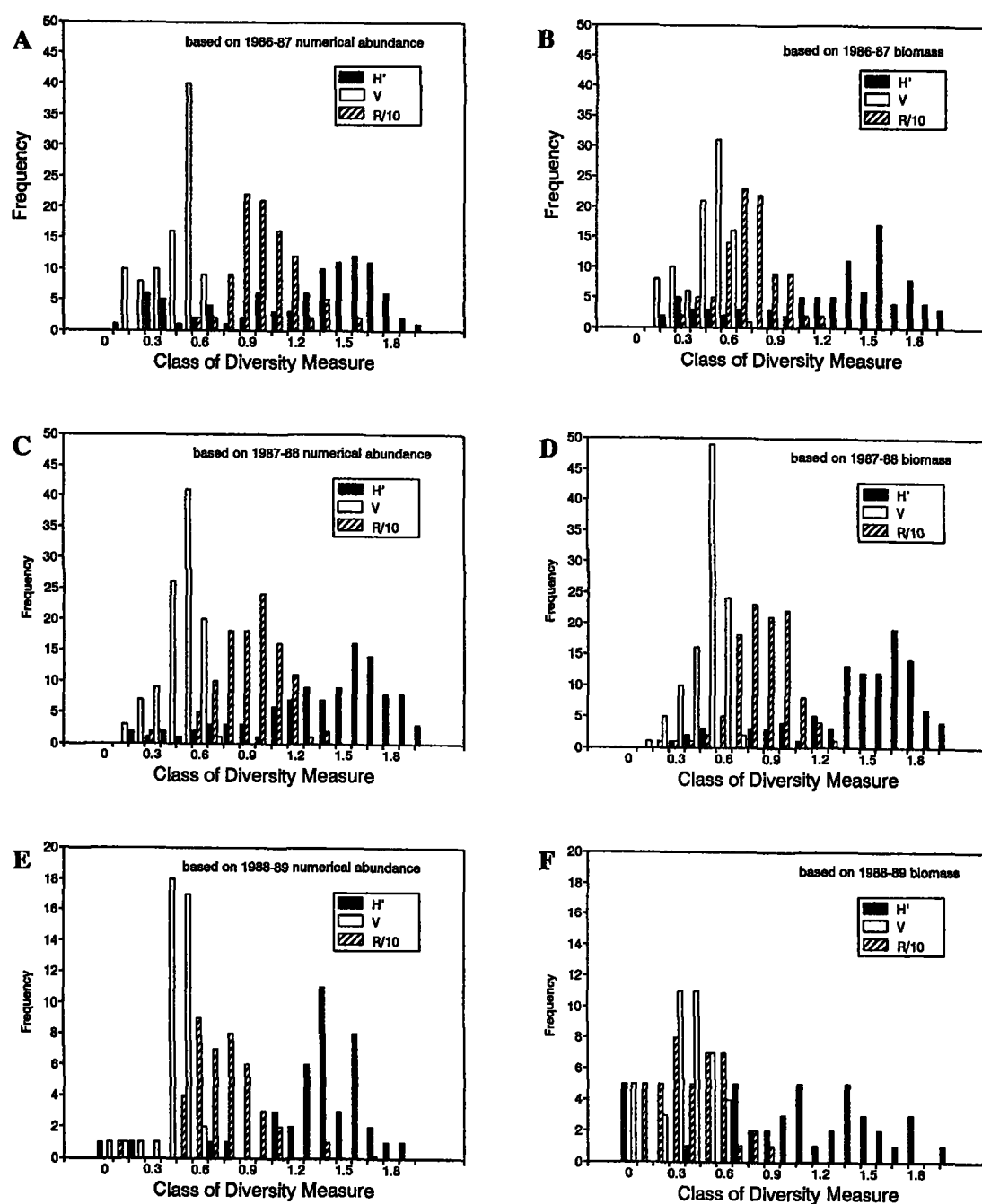


Figure 3

Distributions of diversity values for each AMLR survey. H' (SOLID BAR) represents the Shannon-Wiener Diversity index, and V (OPEN BAR) represents evenness, R (SHADED BAR) represents richness. (Richness was adjusted to the scale of the other indices by dividing by 10.) (A) Diversity of fish community at stations sampled during the 1986-87 survey, based on numerical abundance; (B) diversity of fish community at stations sampled during the 1986-87 survey, based on biomass; (C) diversity of fish community at stations sampled during the 1987-88 survey, based on numerical abundance; (D) diversity of fish community at stations sampled during the 1987-88 survey, based on biomass; (E) diversity of fish community at stations sampled during the 1988-89 survey, based on numerical abundance; (F) diversity of fish community at stations sampled during the 1988-89 survey, based on biomass.

Table 3

Results of spearman rank correlation analyses on common Antarctic demersal fish species associations. All correlation values in this table were significant at the 0.01 level when tested against the null hypothesis of zero correlation.

1986/87		1987/88		1988/89	
Species pair	r'	Species pair	r'	Species pair	r'
ACER-ARTE	-0.40	ACER-GUNN	+0.30	GIBB-LARS	+0.50
ACER-GIBB	+0.35	ACER-PSEU	+0.55	GIBB-MICR	+0.51
ACER-GUNN	+0.31	ACER-PSIL	+0.29	LARS-ACER	+0.54
ACER-NUDI	-0.33	ACER-RAJA	+0.33	LARS-MICR	+0.59
ACER-PSEU	+0.52	ARTE-ELEG	-0.38	MICR-ACER	+0.48
ARTE-MICR	-0.64	ARTE-GIBB	+0.26		
ARTE-NUDI	+0.70	ARTE-HANS	-0.39		
ARTE-PARA	+0.36	ARTE-MICR	-0.40		
ARTE-PSEU	-0.47	ARTE-NUDI	+0.60		
ARTE-RAJA	+0.35	ELEG-HANS	+0.40		
ARTE-SQUA	-0.49	ELEG-MANT	+0.43		
ELEG-ARTE	-0.36	ELEG-NUDI	-0.38		
ELEG-HANS	-0.47	GIBB-LARS	+0.28		
ELEG-NUDI	-0.37	GIBB-NUDI	+0.36		
ELEG-PSEU	-0.36	GIBB-PARA	+0.30		
ELEG-ROSS	-0.46	GIBB-PSIL	+0.26		
GIBB-LARS	+0.29	GIBB-ROSS	+0.34		
GIBB-NUDI	+0.33	GUNN-PSEU	+0.40		
GIBB-PARA	+0.30	GUNN-PSIL	+0.33		
GIBB-PSEU	+0.32	HANS-NUDI	-0.36		
GIBB-PSIL	+0.41	HANS-PSEU	+0.28		
GIBB-ROSS	+0.36	LARS-PARA	+0.30		
GUNN-PARA	+0.34	LARS-PSIL	+0.41		
GUNN-PSEU	+0.34	LARS-RAJA	+0.40		
HANS-PSIL	+0.36	MICR-MANT	+0.34		
LARS-PARA	+0.46	MICR-NUDI	-0.55		
LARS-PSIL	+0.36	MICR-PARA	-0.32		
MICR-MANT	+0.56	MICR-PSIL	+0.31		
MICR-NUDI	-0.63	MICR-RAJA	+0.35		
MICR-PARA	-0.39	PSEU-PSIL	+0.35		
MICR-SQUA	+0.59				
NUDI-RAJA	-0.29				
NUDI-SQUA	-0.37				
PARA-LARS	+0.46				
PARA-NUDI	+0.49				
PARA-SQUA	+0.35				
PSEU-NUDI	-0.41				
SQUA-MANT	+0.53				
SQUA-RAJA	-0.40				

peaks are real boundaries between communities (Fig. 11, page 488). Figure 12, page 488 summarizes the most pronounced boundaries from each of the gradients examined.

Discussion

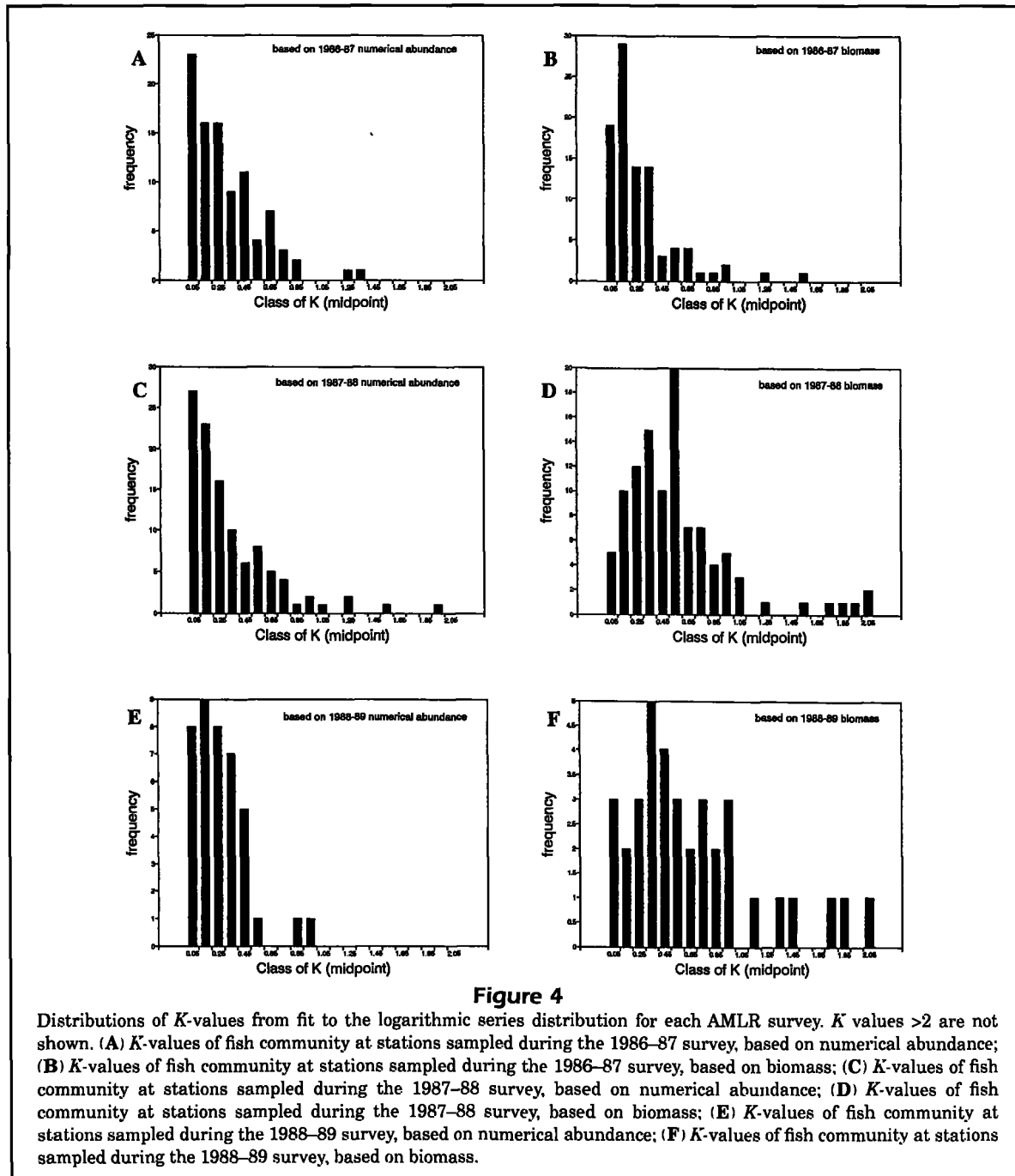
The diversity values for the South Georgian fish community were generally greater than those reported by Targett (1981) for the same region. They were within the range of those reported for demersal fish in tropical estuarine areas (Yanez-Arancibia et al., 1980). These values place the South Georgia fish community on the relative, global diversity continuum, but the wide range of values demonstrates that diversity alone is a poor model of this community.

The richness component of diversity was low and similar to that reported by Targett (1981), but the evenness was considerably larger than had been reported for this region. This observation is consistent with the finding that a significant shift in the species assemblage from 1986-87 to 1987-88 was associated with an increase in diversity because of an increase in the evenness component of that index (McKenna and Saila, 1991). The increasing number of stations that poorly fit the logarithmic series distribution with time also supports the hypothesis that the

community was changing toward one which was less dominated by a small number of species. This apparent change in the community was compounded in 1988-89 by the use of different sampling techniques and gear. The sampling during that season was insufficient to accurately represent the abundance of the rarest species. A bias was also introduced by the small gear used for that survey. In all previous AMLR surveys the mackerel icefish (*C. gunnari*) was the most abundant species. The smaller individuals of this species tends to be more pelagic than many of the others

poral trends also existed. However, all of the trends revealed by skewer analysis were weak; the primary mode fell into either the smallest or second smallest class interval of Tau (Fig. 10, page 487). Gradient analysis, using GRADSECT.BAS, measures the rate of change of the species assemblage along the gradient of interest. However, it offers no objective decision about the value that the rate must reach in order to be considered significant. Thus, it will identify ecotones along any gradient and it is a matter of subjective judgment to determine which (if any) of the

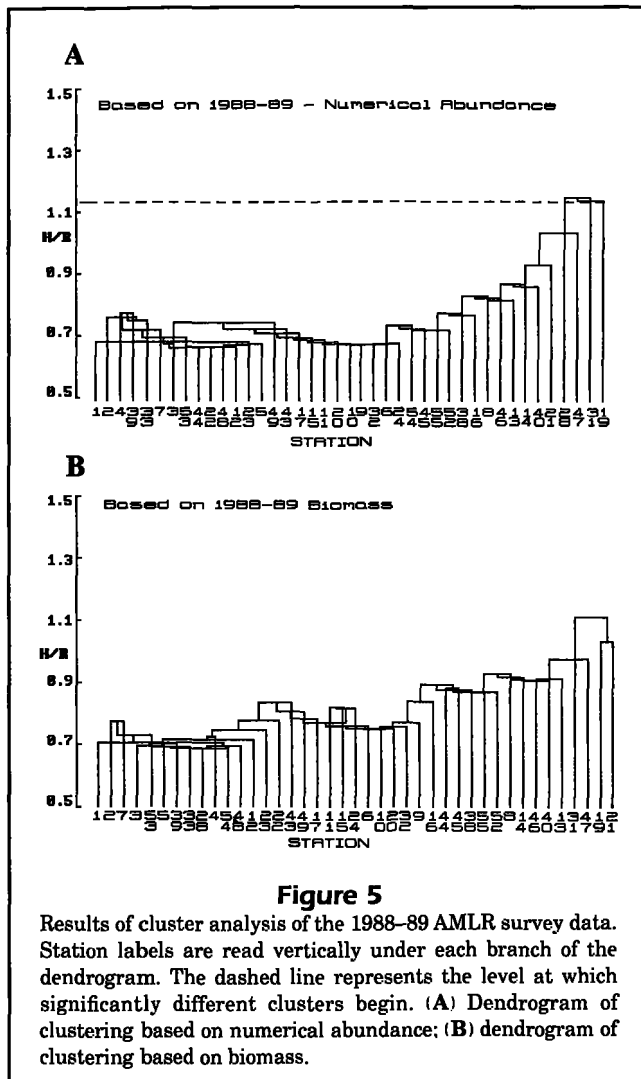
community was changing toward one which was less dominated by a small number of species. This apparent change in the community was compounded in 1988-89 by the use of different sampling techniques and gear. The sampling during that season was insufficient to accurately represent the abundance of the rarest species. A bias was also introduced by the small gear used for that survey. In all previous AMLR surveys the mackerel icefish (*C. gunnari*) was the most abundant species. The smaller individuals of this species tends to be more pelagic than many of the others



in this system (Slosarczyk, 1983). The smaller gear might have missed some concentrations of this species, thus underestimating its population and diminishing the apparent dominance of the community.

The species associations and distribution of species groups were weak and inconsistent. The association between *A. mirus* and *N. nudifrons* was the strongest and still only accounted for, at most, 70% of the variability in their distributions (Table 3). Both of these

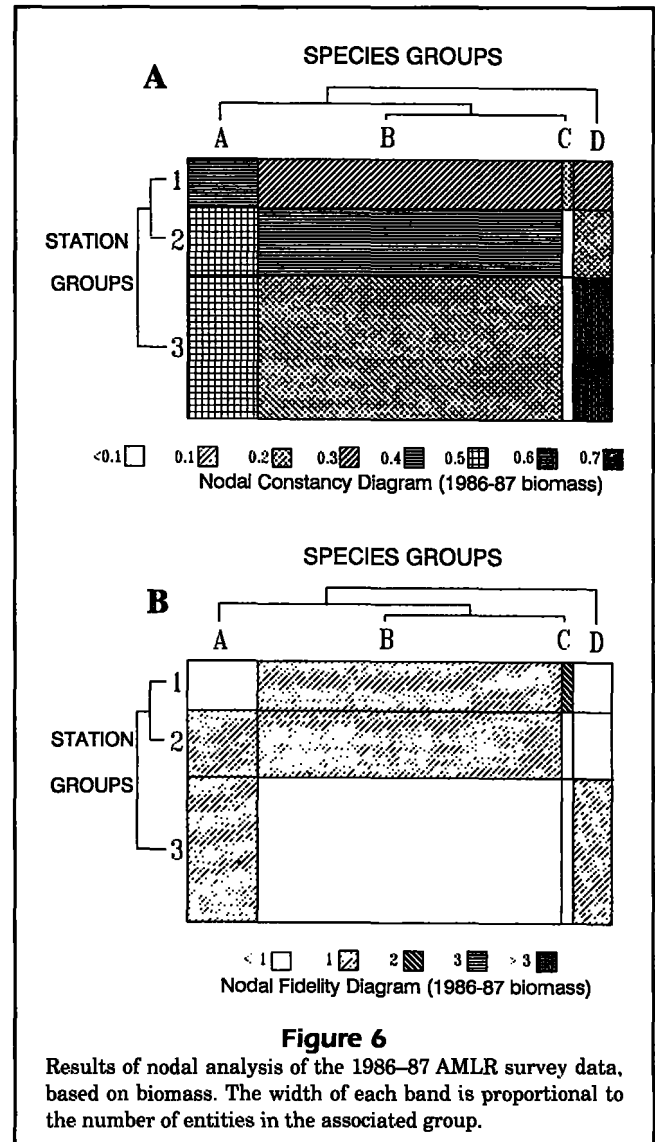
fish are small (<15 cm), benthic species; however, their diets overlapped only slightly (38%) (McKenna, 1991). They were often removed from within sponges and other large invertebrates that formed a major part of the catch. They were not numerically dominant, but they were ubiquitous in the region. Although their distributions may have been linked, the association is probably more indicative of how widespread their preferred habitat is (i.e. habitat containing an abundance



of large, epibenthic invertebrates: branching sponges, corals, tunicates, crinoides, etc.).

The *C. aceratus*-*P. georgianus* association is most likely a result of the similar feeding behavior and habitat preferences of these species. Both are relatively sedentary, benthic fish which feed heavily on krill and other fish. Their diets strongly overlap (64%, McKenna, 1991) and their distribution may well reflect the distribution of their prey.

Significant associations suggest some biological interactions between the species involved. However, little can be said about the cause of these associations. Two species may display a negative association owing to distinct habitat requirements; they may have similar habitat requirements but experience a niche shift because of competition (McNaughton and Wolf, 1979b); or they may not coexist because of predation by one on the other. Most of the significant negative associations in this study involved one piscivorous member



(McKenna, 1991), which suggests predator-prey relationships. The strongest of these negative associations were between *M. microps* and two of the smallest species in the region, *N. nudifrons* and *A. mirus* (Table 3). These three species are found close to the bottom and much of their diet consists of benthic organisms (37% overlap, McKenna, 1991). However, *M. microps* grows to over twice the size of the other two (Fischer and Hureau, 1985) and will feed on fish (McKenna, 1991) (though its small mouth probably limits any predation on the other two species to juveniles). Information about available habitats and the diets of the individuals within each habitat are necessary before these relationships may be more clearly defined for the South Georgia system.

The classification of the species into groups (by inverse clustering) and their distributions were not

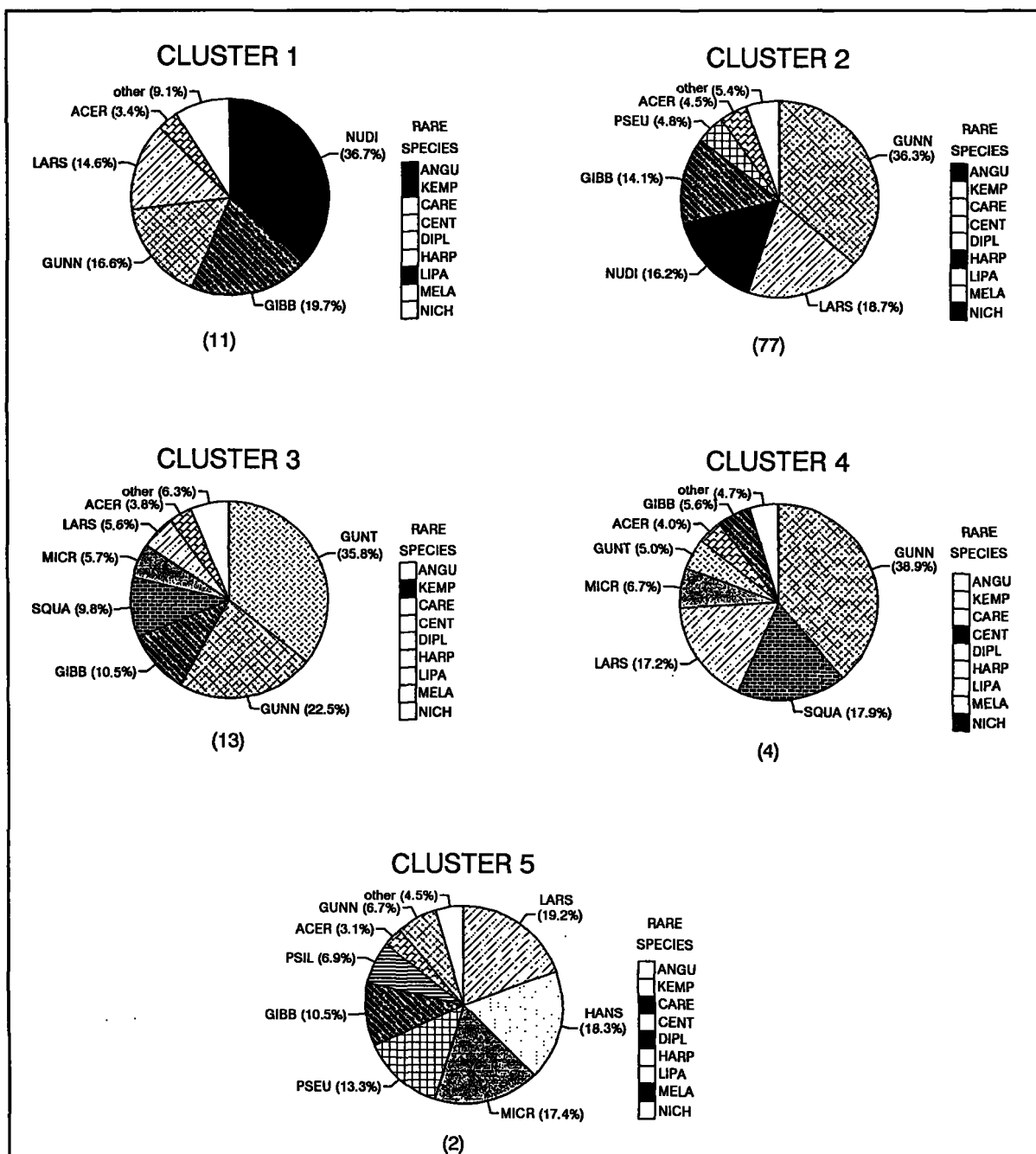


Figure 7

Charts describing the composition of the communities identified by cluster analysis of the 1987–88 AMLR survey data, based on numerical abundance. Pie charts depicting the composition of each community. Stations comprising each cluster are listed horizontally below each chart. The species which accounted for at least 10% of the community are listed to the left of each chart. Bars depicting the presence/absence of the rarest species in each community. Shaded boxes indicate presence. Stations comprising each cluster are listed horizontally below each chart. Species codes are read vertically under each box of a given bar.

clearly defined. The weakness of the pairwise associations and the nebulous basis for the classification of species into groups suggests the lack of stronger ecological ties between some species than others in the community.

Normal (*R*-mode) clustering of sample sites based on both species assemblages and size structure of each species' population indicated the lack of spatial structure in the community, as well. The movement of fish towards deeper water as they grow larger offers a pos-

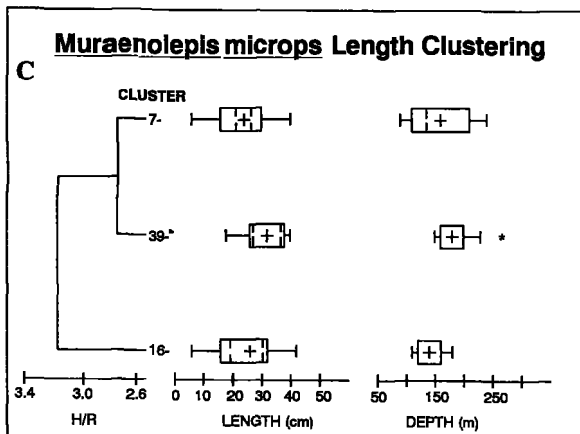
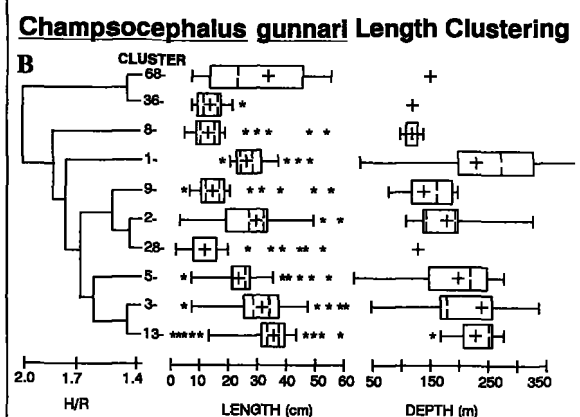
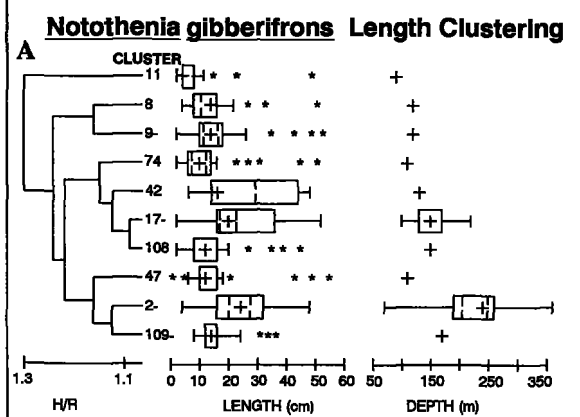
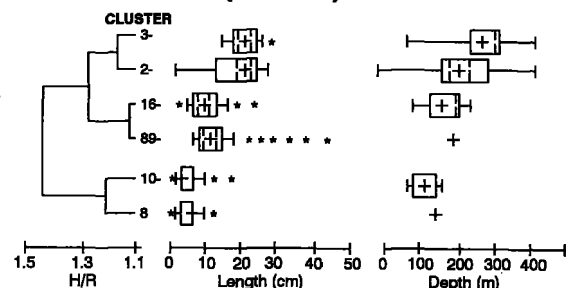


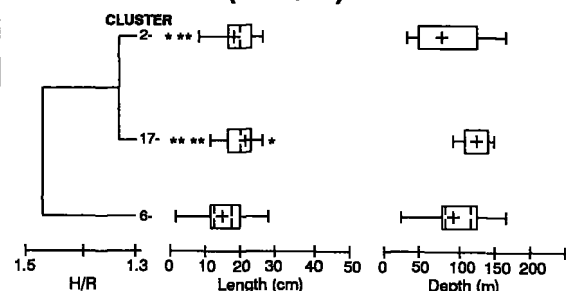
Figure 8

Results of cluster analysis of the size structure of three fish populations around South Georgia Island. Each dendrogram depicts the classification of samples according to the size composition of the associated fish population. Box plots describe the location and spread of the total length of fish in each cluster and the depth or sequential order of the stations that comprise each cluster. The broken verticle lines within each box represent the upper and lower notches and provide a rough measure of the significance of differences between medians (Hoaglin et al., 1983). **A** = *N. gibberifrons* during 1987-88 survey compared with depth; **B** = *C. gunnari* during 1987-88 survey compared with depth; **C** = *M. microps* during 1988-89 survey compared with sample order.

***Nototothenlops larseni* Length Clustering (1987/88)**



***Nototothenlops larseni* Length Clustering (1988/89)**



***Nototothenlops larseni* Length Clustering (1988/89)**

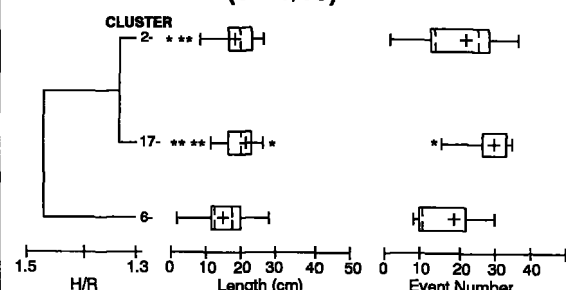
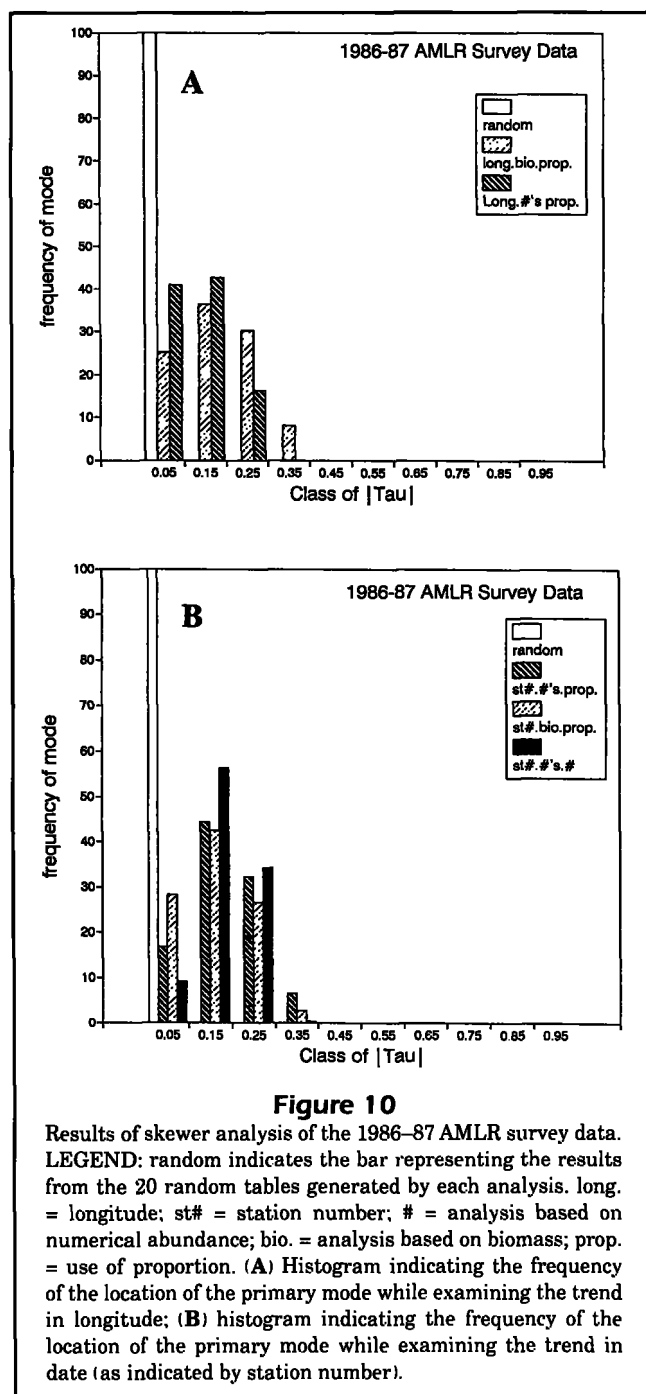


Figure 9

Results of cluster analysis of the size structure of the *N. larseni* fish population around South Georgia Island. Each dendrogram depicts the classification of samples according to the size composition of the associated fish population. Box plots describe the location and spread of the total length of fish in each cluster and the depth or sequential order of the stations that comprise each cluster. The broken verticle lines within each box represent the upper and lower notches and provide a rough measure of the significance of differences between medians (Hoaglin et al., 1983). **A** = Comparison of 1987-88 population with depth; **B** = comparison of 1988-89 population with depth; **C** = comparison of 1988-89 population with sample order.

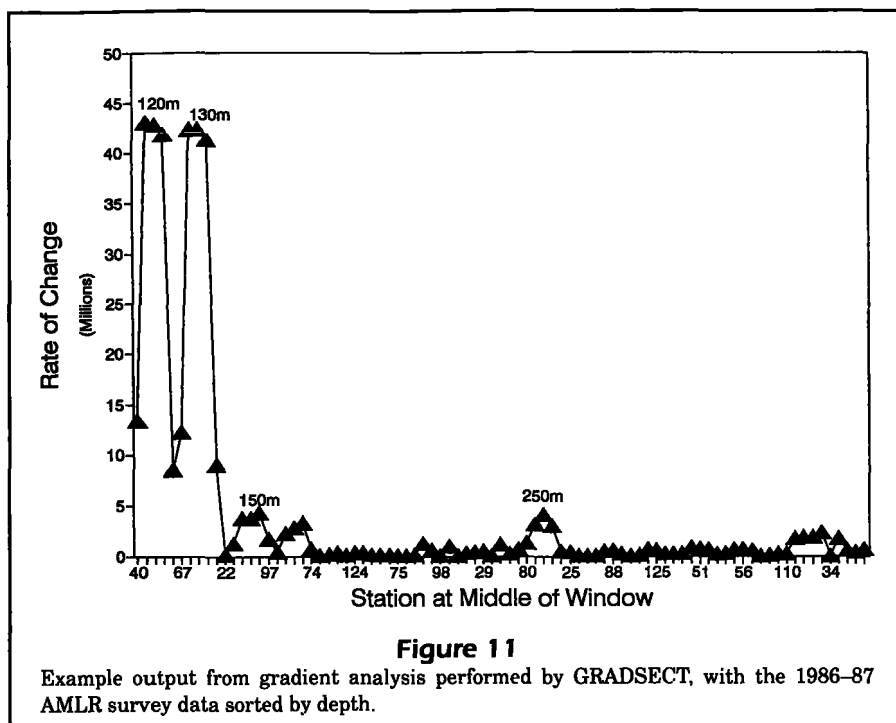


sible explanation for changes in size structure of some of the species within a survey. However, those trends were all weak and inconsistent. In general the results indicate that there was little or no structure to the demersal fish community of South Georgia Island. No areas that could be considered nurseries were identified. Nor were there areas of particularly high abundance of only the most valuable commercial species. Variability in the abundance of each species was evident. However, essentially the same assemblage

with similar dominant species was found at nearly every sampled location on the continental shelf. This consistency in the species assemblage has been noted in the South Georgia region before (Targett, 1981).

The absence of spatial structure is unusual in natural communities and it is unclear why this situation exists in the South Georgia Island system. The species within this community can be classified into three trophic groups: krill-eaters (e.g., *C. gunnari* and *N. larseni*), piscivores (e.g., *C. aceratus* and *P. georgianus*), and benthic invertebrate feeders (e.g., *N. gibberifrons* and *N. squamifrons*) (McKenna, 1991). One would expect these animals to be distributed according to the availability of their prey or appropriate habitat (or both). Although the trophic groups are clear, they are closely linked and the distribution of all these species may be dependent on the abundance and distribution of krill (*Euphausia superba*). If krill was superabundant then, even if it were patchy, it might have more than met the demands of the krill-eaters, explaining their uniform distribution. The piscivores will follow their fish prey, which fed either on krill or some benthic resource. The benthic invertebrate feeders were also uniformly distributed. Little is known about the benthic community around South Georgia Island. However, it has been shown that most of the organisms of that habitat are inedible to fish (Belyaev and Ushakov, 1957). It might be expected then that the edible benthic resources are distributed in patches within this habitat. That was not apparent from the distribution of the fish and may have been concealed by the fact that even the benthic feeders ate krill (McKenna, 1991), including *N. gibberifrons* and *N. nudifrons*. These two species are highly adapted to feeding on benthic organisms and yet their diets included krill. Targett (1981) also observed krill in the diet of these benthic-feeding species and suggested that a shoal of krill had moved into shallow water and was forced close to, or in actual contact with, the bottom. This would seem to be an indication of the great abundance of krill in the vicinity of South Georgia Island.

The results of this research imply that during the austral summer there was, in general, a uniform distribution of the necessary resources throughout the sampled region, at scales of 10 km to 100's of km. It must be emphasized that these surveys took place only in the summer and little is known about this community at other times of the year. The strong seasonality of this environment may present the inhabitants with an annual 'boom' and 'bust' cycle, having abundant resources in the summer and a 'bottleneck' period (when resources are less available than at other time of year) during the winter (Wiens, 1977; DuBow, 1988). The abundance of available resources during the summer may allow different species to feed on the same



the populations of these species than will those of the summer. To better understand this ecosystem, information on the seasonal dynamics of the community and its constituent populations (including krill and benthic invertebrates) is needed.

Acknowledgments

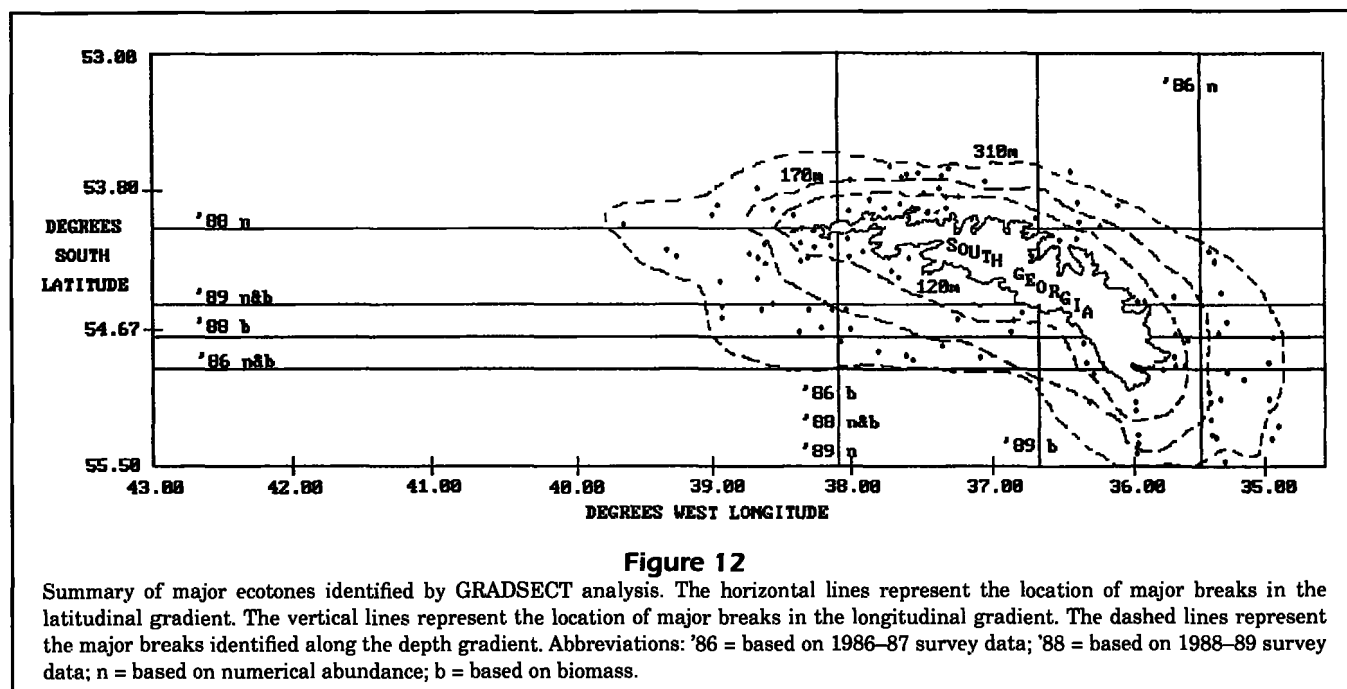
My thanks go to S. Saila, J. Heltsh, and K. Sherman for their technical and editorial assistance. Supporting research for this study was funded by grants from the National Oceanic and Atmospheric Administration through the Antarctic Marine Living Resources Project of the National Marine Fisheries Service.

resource (e.g., krill) without experiencing competition (McKenna, 1991). However, during the long winter, resources may be limiting, causing strict resource partitioning, and more highly defined community structure may develop. If this is the case, the events of the austral winter will be more important to regulation of

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