LOW RES

OCEANOGRAPHIC VERSUS SEAFLOOR-HABITAT CONTROL OF BENTHIC MEGAFAUNAL COMMUNITIES IN THE S.W. ROSS SEA, ANTARCTICA

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Benthic megafaunal assemblages between 270 and 1173 m depth in the S.W. Ross Sea were characterized from analyses of fifty-five seafloor video transects. The shallow-water shelf community was dominated by high abundances of benthic suspension-feeders. Megafaunal density declined with increasing water depth, and deposit-feeding taxa were most abundant at the deepest sites. Five distinct faunal assemblages were identified from a cluster analysis of stations using taxon abundances. A "suspension-feeder rich" (SFR) group was typical of stations in shallow, high current areas where bryozoans, hydroids, and sponges were abundant. A "suspension-feeder poor" (SFP) assemblage found mainly on shallow banks was also dominated by suspension-feeders, with much lower bryozoan cover. The "mixed slope assemblage" (MSA) included suspension-feeders and deposit-feeders, with high abundances of bryozoans, ophiuroids, and holothurians. A deeper-living "ophiuroid—worm assemblage" (OWA) consisted of ophiuroids and maldanid polychaetes. The "depauperate basin assemblage" (DBA) had the lowest faunal density and included elements of the OWA and several sponge taxa. Benthic faunal patterns were associated more closely with seafloor habitat parameters and sediment organics than with the size and timing of ice cover or primary productivity. Thus, upper ocean factors appear less important than seafloor-habitat characteristics in regulating the spatial distribution of Ross Sea benthos, due to lateral advection and deposition of organic material at the seabed. Tight coupling between the upper ocean and benthos may instead be evident as temporal changes in the dynamics and productivity of Ross Sea benthos in response to seasonal and interannual variation in upper ocean production.

1. INTRODUCTION

Most marine benthos, and nearly all those inhabiting deep-sea environments except near hydrothermal vents and methane seeps, depend nutritionally on the sinking flux of organic debris from the overlying water column. Such trophic dependence requires some degree of coupling in space, time, or both, between benthic faunal patterns and hydrographic processes regulating primary production in surface waters, which, in turn, are influenced by climate variability. Depending upon the responsiveness of the upper ocean and the strength of coupling among ecosystem components, even remote deep-sea benthos are impacted by climate variability [e.g. *Smith and Kaufmann*, 1999].

Bentho-pelagic coupling has been investigated in many marine habitats, and has been considered to be stronger in nearshore and high latitude systems where a

high percentage of surface primary productivity sinks to the seafloor [*Atkinson and Wacasey*, 1987; *Grebmeier and Barry*, 1991]. Deep-sea and lower latitude benthic systems receive a smaller percentage of surface production, and may have weaker links between surface production and the structure and diversity of benthic communities [*Davies and Payne*, 1984; *Müeller and Suess*, 1979]. Recent studies of multiple sites in the world ocean have identified different scales of coupling between surface and benthic systems [see review by *Levin et al.*, 2001], with tight coupling in many environments, including abyssal equatorial regions [*Smith et al.*, 1998; *Smith et al.*, 2002]. Deep-sea benthos (particularly small size fractions) have been shown to respond rapidly (i.e. within days) to pulses of organic carbon [*Graf,* 1989; 1992; *Smith et al.*, 2002]. Longer time series observations have also established links between climate-driven variation in upper ocean productivity and benthic community processes [*Smith et al.*, 2002].

The ROAVERRS (Research On Atmospheric Variability and Ecosystem Response in the Ross Sea) project is a multidisciplinary investigation of ecosystem patterns and processes in the SW Ross Sea, Antarctica. The major focus of ROAVERRS is to evaluate links between climate variability and a cascade of ecosystem processes in the Ross Sea. These are initiated as climate-linked changes in sea ice cover and upper ocean hydrography that regulate phytoplankton productivity, sedimentation of organic debris, and benthic faunal dynamics. Variation in the intensity of the downslope wind field over the Antarctic ice cap is linked to changes in the size and persistence of polynyas in the SW Ross Sea [*Kurtz and Bromwich*, 1985; *Arrigo et al.*, 1998]. Because polynya formation can have large effects on regional phytoplankton productivity and sinking organic fluxes [*Dunbar et al.*, 1998; *Arrigo et al.*, 1994; 1998; 2000], the pattern of polynya development is expected to influence benthic community patterns and processes [*Barry and Dayton,* 1988; *Grebmeier and Barry*, 1991].

In this paper, we report the spatial distribution and abundance of benthic megafauna in the Ross Sea, and evaluate the relative importance of upper ocean processes (i.e. polynya formation, primary productivity) and seafloor habitat qualities (e.g. depth, current speed) in controlling benthic community structure.

Benthic megafauna have been described for several regions of the Antarctic continental shelf, particularly the Ross, Weddell, Lazarev, and Bellingshausen Seas, and areas along the Antarctic Peninsula. These surveys have been based on photographic, trawl, and benthic grab sur-

veys dating back to the 19th century [*see reviews by Hedgpeth*, 1969; 1971; *Dell*, 1972; *White*, 1984; *Dayton et al.,* 1994; *Arntz et al.*, 1994; *Gutt and Starmans*, 1998; *Starmans et al.*, 1999]. While there is some variability in the general structure of benthic megafaunal communities between regions and over smaller horizontal spatial scales [*e.g. White*, 1984; *Starmans et al.*, 1999], megafaunal distributions are generally considered to be circumpolar [*Arntz et al.*, 1994] along the "continental subregion" defined by Hedgpeth [1969].

The majority of studies have focused on shallow waters (<30 m) where faunal zonation is linked strongly to local physical processes influencing scour and uplift by ice, and light penetration. In shallow waters with persistent ice cover (e.g. southern McMurdo Sound), benthic algal cover is low and faunal zonation is produced by ice uplift [*Dayton et al.*, 1969; 1970; 1994].

Deeper assemblages exhibit eurybathy, presumably related to the weak thermal stratification of Antarctic waters [*Arntz et al.*, 1994], but are patchy over horizontal and vertical scales due to depth and substratum characteristics. Shelf and slope communities have been reported to include shallow assemblages of suspension-feeding invertebrates, a zone of mixed deposit- and filter-feeders, and a deeper assemblage of deposit-feeders best characterized by holothurian and ophiuroid echinoderms [*Bullivant and Dearborn*, 1967; *Gutt*, 1991; *Arntz et al.*, 1994; *Gutt and Starmans*, 1998 and references therein].

Although surface productivity in the Ross Sea must be fundamental to the development and maintenance of underlying benthic communities, several other factors may influence benthic community patterns and decrease the strength of coupling between the spatial patterns of upper ocean processes and seafloor community structure. Sediment heterogeneity, oxygen concentration, substratum type, currents, and disturbance have been shown to influence benthic community patterns over global, regional, and local scales [see review by *Levin et al.,* 2001]. The interaction of regional currents with the complex bathymetry of the Ross Sea, which includes several shallow banks, and deep, glaciated basins, very likely affects the advection and deposition (or resuspension) of sinking organic material and leads to a pattern of food availability for benthic consumers that differs from surface productivity. Thus, even though phytoplankton produced in the Ross Sea polynya can sink rapidly to the seafloor [*DiTullio et al.*, 2000] we expect, a *priori*, that benthic megafauna patterns may be linked more closely to factors near the seabed, based on the extreme bathymetric heterogeneity of the SW Ross Sea shelf.

We evaluate factors influencing faunal patterns in two ways. First, we establish groups of stations based on their similar faunal composition (*Faunal Groups*), and evaluate the magnitude of variation in physical parameters (e.g. depth,% carbon in sediments) among groups. If faunal patterns are controlled by physical factors, key factors should vary significantly among *Faunal Groups*. Second, we reverse this approach and establish groups of stations based on their similar environmental features, and then examine variation in faunal abundances among those groups. Environmental factors used to define groups of stations were; 1) the position and persistence of the Ross Sea polynya (*Polynya Groups*), 2) phytoplankton productivity in the upper ocean (*Productivity Groups*), 3) seafloor bathymetry and currents (*Habitat Groups*), and 4) the organic content of seafloor sediments (*Sediment Groups*). Because the distribution of animals in almost all ecosystems represents their integrated response (i.e. recruitment, growth, and survival) to multiple scales of environmental variability [*Barry and Dayton*, 1991], strong correlations between physical factors and faunal patterns suggests a key role for those factors. Thus, tight benthic-pelagic coupling in the Ross Sea would result in close correspondence between the distribution of faunal assemblages and the pattern of surface ice cover or productivity.

2. METHODS

2.1 Study Area

The SW Ross Sea is a high latitude Antarctic marine environment with a broad and deep continental shelf (Plate 1). The region is bounded in the northeast by the continental shelf break, to the west by the Victoria Land coast of Antarctica, and to the south by the Ross Ice Shelf. Isostatic depression of the Antarctic continent by the weight of the polar ice cap has deepened the Antarctic continental shelf [*Drewry et al.*, 1983], which averages 500 m deep in the Ross Sea. Bathymetry is complex in this region, with three shallow (~250–400 m) banks near the shelf break, and deep (<1200 m) glaciated troughs incising its western and southwestern margins.

Although sea ice covers the entire region during part of most years, three polynyas commonly develop in late winter or spring. The Ross Sea polynya forms along the terminus of the Ross Ice Shelf during November, driven by katabatic wind surges, thermal heating from below, or both [*Bromwich et al.*, 1994]. High phytoplankton pro-

ductivity occurs in the polynya during spring and summer [*Arrigo et al.*, 1994; 1998; 2000]. Two smaller polynyas near northern McMurdo Sound and Terra Nova Bay [*Kurtz and Bromwich*, 1985; *Van Woert*, 1999] also promote local phytoplankton growth [*Arrigo et al.*, 1998]. Phytoplankton productivity is greatest in the late spring and summer, with highest fluxes of sinking organic debris in late summer to early fall [*Dunbar et al.*, 1998; *Gardner et al.*, 2000]. Organic material may sink rapidly to the seafloor [*DiTullio et al.*, 2000] or drift laterally with the generally southwestward flow in the SW Ross Sea (see Van Woert in this volume). Advection toward the southwest leads to high rates of organic deposition in the western section of the Ross Sea polynya as well as beneath adjacent sea ice [*DeMaster et al.*, 1992; *Jaeger et al.*, 1996; *Dunbar et al.*, 1998].

Seafloor deposits in the Ross Sea vary from bedrock and cobble on some shallow banks, to mixtures of unsorted ice-rafted debris, siliceous biogenic material, calcareous shell debris, and terrigenous silts and clays [*Dunbar et al.*, 1985]. Terrigenous sediments are most common near the center of the Ross Ice Shelf front, with greatest concentrations of siliceous oozes toward the southwest. Organic content of the sediment varies from approximately 0.5 to 1.5% C, with highest values in deeper basins in the southwest.

Data from ROAVERRS cruises during the austral spring / summer periods of 1996/97 (NBP96-6), 1997/98 (NBP97-9), and 1998/99 (NBP98-7) were included in this paper. The distribution of biota was evaluated using a towed camera system on cruises NBP97-9 and NBP98-7. Features of the upper ocean (sea ice cover, primary production) and the seafloor (sediment organic qualities) were sampled during all three ROAVERRS cruises.

2.2 Camera Tows

A camera system towed over the seafloor provided video sequences used to evaluate faunal distributions. The system has a torpedo-shaped PVC housing with a pressure case enclosing batteries, a hi-8 SONY camcorder to record imagery from the camera, and control electronics. A Deep-Sea Power & Light SeaCam 4000 camera with auto-focus was oriented orthogonal to the seafloor, thereby minimizing perspective distortion [*Wakefield and Genin*, 1987]. Two 250-watt lights (DSP&L SeaLite) illuminated the seafloor from the nose and tail sections of the system housing. The length of an anchor line towed from the tail of the camera system determined the distance of the camera above the seafloor (normally ~2 m).
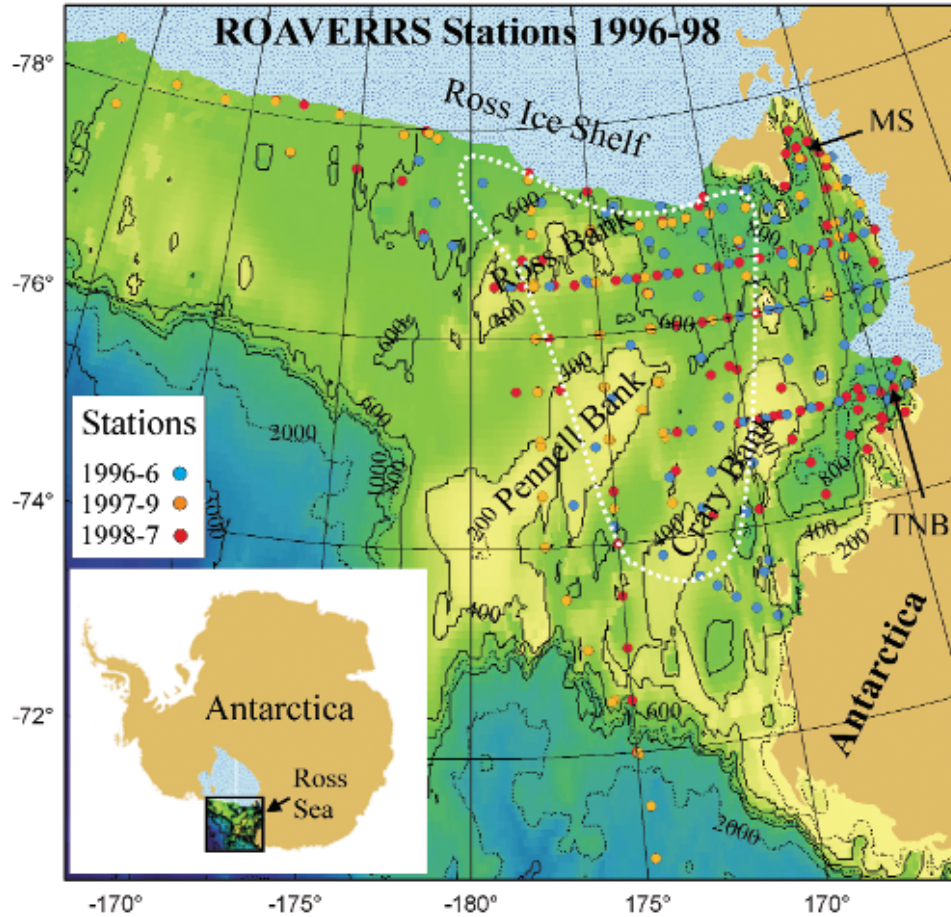
Plate 1. Map of S.W. Ross Sea. Dots indicate positions of ROAVERRS stations. Bathymetry in meters. TNB= Terra Nova Bay. MS= McMurdo Sound. Dotted white line indicates extent of Ross Sea Polynya during late spring / summer.

Irregularities in seafloor topography (e.g. erratic boulders) occasionally snagged the anchor line and temporarily decreased the distance above the bottom. A visual scale (one or two tennis balls attached to the ends of a ½ m stick) was hung from the front of the camera system so that it was positioned on the seafloor in the field of view. This scale allowed us to estimate the size of the field of view (normally ~1 m^2) and the distance towed. Camera tows consisted of deploying the system from the ship while underway at slow (0.25 to 0.5 kt) speed, allowing the system to reach the seafloor, then towing for fifteen to twenty minutes before recovery.

2.3 Physical and Biological Parameters

Water depth was recorded at each station and regional bathymetry was obtained from a gridded bathymetric database [*etopo5, www.ngdc.noaa.gov*]. Seafloor slope (degrees) was estimated at each station from analysis of the etopo5 bathymetry grid.

Current speed near the seafloor at each video station was estimated from the drift rate of particles in the video image at the beginning of each camera tow. Measurements were made after the camera system had arrived at the seafloor, but before tension on the tow-line caused movement over the bottom. The drift rate of particles (usually marine snow) suspended ~30 to 50 cm above the bottom was timed as they transited the field of view. An average current speed for each station was calculated from 3 to 5 particle drift measurements. Although these represent instantaneous measurements subject to variation due to the strong diurnal tidal periodicity of currents in the Ross Sea [*Pillsbury and Jacobs*, 1985*; Barry and Dayton*, 1988], they provide the only estimates of current near the seabed for each site.

The spatial pattern of primary production in surface waters was estimated from depth-integrated (100 m) carbon drawdown (the seasonal deficit in total dissolved inorganic carbon, ΣCO_2, from winter water values). The amount of seasonal ΣCO_2 drawdown, corrected for mixing as well as any invasive CO_2 flux from the atmosphere, corresponds to net community production through the date when the measurements are made. Since the air-to-sea invasive flux is generally small during the summer months [*Sweeney et al.*, 2000], here we use depth-integrated ΣCO_2 drawdown without an atmospheric replenishment correction as an indicator of variability in surface water production across our field area. ΣCO_2 was determined by analysis of CO_2 stripped from a known mass of seawater via acidification. A thermal conductivity detector was used during ROAVERRS cruise NBP 96-6 (precision of ~13μmol kg-1). A semi-automated coulometer system was used during NBP 97-9 and NBP98-7 (precision of ~1.6 μmol kg-1). Water samples from various depths were collected by CTD hydrocast at nearly 100 stations during three cruises (NBP96-6, NBP97-9, NBP98-7) in the Ross Sea. Salinity values are available for all samples analyzed for ΣCO_2. We have normalized all of our ΣCO_2 data to a value close to the mean salinity of the Ross Sea, 34.5 psu, to correct for variations in ΣCO_2 resulting from dilution by melting sea ice. Details of the analytical procedures are presented elsewhere [*Arrigo et al.,* 1999; *Takahashi et al.,* 2000].

Biogeochemical analyses of seafloor sediments were performed for most stations, based on samples collected using a Mark III ½ x ½ m box core. Sediment samples (1 to 3 samples of the top 1 cm per station) were processed upon retrieval of the box core to the surface. Organic carbon (OC) and total nitrogen (TN) content as well as OC $\delta^{13}C$ and TN $\delta^{15}N$ were analyzed using a Carlo-Erba NA-1100 elemental analyzer coupled to a Finnigan Delta+ continuous flow mass spectrometer. Samples were dried (60 °C), ground, and 4 to 20 mg weighed into silver boats. Weighed samples were acidified in-situ with 6% sulfurous acid to remove any carbonate phases prior to isotopic analysis. Isotopic compositions were calibrated against the NBS-21 and IAEA-N1 standards that were run before and after each set of 10 analyses. Isotopic reproducibility is on the order of 0.09 ‰. Sample analysis errors (1s) are generally <1% for C and N contents.

2.4 Analysis of Seafloor Video

Video recorded during camera tows at each station was used to quantify faunal abundance. Approximately 5 video subsamples (~1 minute each) selected from throughout each video transect, were chosen based on image quality, distance from the seafloor, and speed over the bottom. The total of all subsamples analyzed averaged between 3 to 5 min per station. Video with low clarity, too near or distant from the seabed, or moving to rapidly over the bottom, was rejected. The spatial dimensions of the field of view and tow speed were measured several times during each subsample analyzed, and were used to determine the total area of seafloor included in the analysis for each station.

Counts of megafauna consisted of enumerating all identifiable animals (as small as ~2-3 cm) and estimating the percentage cover of habitat types and megafauna in each video subsample. Lebenspurren, such as feeding

traces of echiuran worms, and burrows in the seafloor were counted. All animals were identified to the lowest possible taxon and assigned a tag name if their scientific name was not determined. An archival video frame-grab (still image) was recorded for each taxon or tag name observed.

Although it was often not possible to identify animals to a species level, tag names were assumed to be at the "species" level for analyses of faunal patterns. Thus, tag names belonging to different species may have been lumped in some cases. Alternatively, phenotypic variation within species (e.g. color or morphology) may have resulted in assignment of two or more tag names for a single species. Errors due to lumping multiple species within a single tag name are expected to be more common, especially for smaller species such as ophiuroids. Small individuals (<2-3 cm in maximum dimension) were usually not counted owing to low resolution of video images and difficulty in determining taxonomic assignment.

Percentage cover estimates based on point-contact methods [*Bohnsack*, 1979] were used as estimates of total faunal cover, the abundance of some colonial organisms (especially bryozoans and hydroids), and physical features (e.g. sediment or rocky substrata). A grid of 100 points was overlaid on 15 to 25 frame-grabs selected randomly from video sequences at each station. Physical features and megafaunal categories (animal, sponge, bryozoan / hydroid) underlying each point were recorded to determine an average percentage cover for each station. Ectoprocta and Hydroida were commonly indistinguishable and a bryozoan / hydroid complex was included in counts with the Ectoprocta, since this group was generally far more abundant than Hydroida.

Because counts of individual bryozoans were difficult, we estimated the density of bryozoans and hydroids as twice their percentage cover, similar to methods of Gutt and Starmans [1998]. All species were assigned to trophic guilds (suspension-feeder, deposit-feeder, or predator) according to information from the scientific literature concerning feeding habits. For taxa not identified to a species level, assignment was based on the closest known taxon.

2.5 Analysis of Faunal Patterns

Faunal assemblages in the Ross Sea were identified using cluster analysis and multidimensional scaling (MDS) techniques. Groups of stations with similar faunal composition, termed "Faunal Groups", were de-

termined by clustering stations based on taxon abundances (including the lowest taxonomic assignment possible), using hierarchical clustering techniques (Euclidean distance and Ward's averaging method; $SYSTAT_{10}$ *statistical package; SPSS Science Marketing, http://www.systat.com*). These clusters, hence termed *Faunal Groups*, were compared to those station groupings defined by MDS to evaluate the robustness of each *Faunal Group*, as recommended by Field et al. [1982]. A multidimensional scaling plot [MDS; *Systat_{10}*, 2001] was computed from a Bray-Curtis similarity matrix generated from pairwise comparisons of all species' abundances between stations. Multivariate analysis of this similarity matrix [ANOSIM; *Clarke and Warwick*, 1994] was used to detect significant variation among *Faunal Groups*. Taxa responsible for the greatest dissimilarity among *Faunal Groups* were determined from SIMPER analysis [*Clarke and Warwick*, 1994].

2.6 Environmental Characterization

Spatial variation in upper ocean factors was compared to the distribution of benthic megafauna in two ways. First, the size and location of the Ross Sea polynya was used to assign stations to categories, termed *Polynya Groups*, defined by the early, mid, and late seasonal development of the polynya. The abundances of benthic megafauna were then compared among *Polynya Groups*. All benthic video stations were assigned to early, mid, or late *Polynya Groups* by the estimated date of sea ice removal (polynya formation) at each station (Plate 2a), based on the satellite images indicating the extent of open water observed on November 15 and December 15 in 1996 and 1997. Development of the Ross Sea polynya by November 15 (early) represents roughly 10 percent of its normal full extent. By December 15 (mid), open water is roughly 50% of maximum. All other stations were assigned to the "late" polynya formation group. The areal extent of the Ross Sea polynya during these dates (Plate 2a) is similar to the recurring pattern identified by Kurtz and Bromwich [1985]. Variation in other physical parameters among *Polynya Groups* is presented in Table 1.

Second, we assigned stations to groups with similar levels of primary productivity in the SW Ross Sea, termed *Productivity Groups*, and then compared the degree of variation in megafaunal abundances between these groups. The pattern of primary production was estimated from depth-integrated (100 m) ΣCO_2 draw-
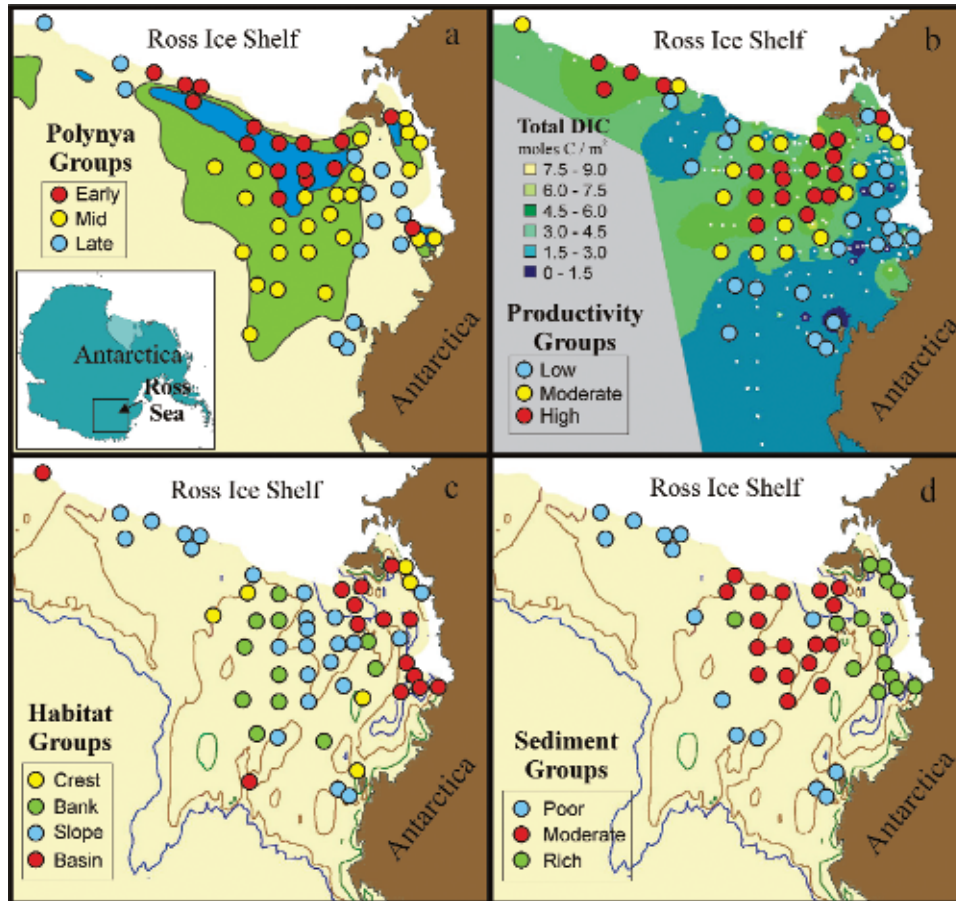
Plate 2. Map of stations assigned to environmental factor groups. A. *Polynya Group* categories. Dark blue and green areas represent early, and mid-state polynya development. Red dots= early, Yellow= mid, light blue= late season polynya formation groups. B. *Productivity Group* categories. Red circles= total dissolved inorganic carbon, Yellow= moderate, and blue= low. C. *Habitat Group* categories; Crest (yellow), Bank (green), Slope (blue), and Basin (red). Blue, brown, and green lines= 750, 500, and 250 m contours, respectively. D. *Sediment Group* categories. Blue= "poor", red= "moderate", green= "rich" (see text for explanation).

TABLE 1. Variation in physical parameters among *Polynya Groups*. Values are mean, standard deviation (SD), and sample size (N). P indicates the probability level for univariate ANOVA between groups and physical parameters. Letters listed under * indicated significant (p<0.05) differences for paired comparisons between groups (e.g. a vs. b= Early vs. Mid). See text for details concerning ΣCO_2.

Polynya Groups Parameter	P	Early (a) Mean	SD	N	*	Mid (b) Mean	SD	N	*	Late (c) Mean	SD	N	*
Latitude	0.24	−77.0	0.8	16		−75.7	1.0	25		−75.8	1.7	14	
Longitude	0.01	175.2	5.9	16	b,c	171.5	4.9	25	a	173.3	10.0	14	a
Slope (deg.)	0.56	0.2	0.1	16		0.3	0.4	25		0.3	0.3	14	
Current Speed (cm/s)	0.31	27.8	11.5	6		21.8	12.6	15		30.0	16.9	7	
Sediment Carbon (%)	0.36	0.7	0.3	2		0.8	0.3	9		0.7	0.3	4	
Sediment Nitrogen (%)	0.44	0.1	0.0	2		0.1	0.1	9		0.1	0.0	4	
Carbon / Nitrogen	0.42	8.1	0.5	2		8.9	1.6	9		8.5	0.5	4	
Carbon Isotope ($\delta^{13}C$)	0.15	−27.3	0.7	2		−26.1	2.2	9		−25.0	1.3	4	
Nitrogen Isotope ($\delta^{15}N$)	0.24	4.6	0.4	2		3.7	1.1	9		4.1	0.4	4	
Rock Substrata (%)	0.64	0.6	1.0	16		4.6	15.5	25		0.6	1.5	14	
Phytodetritus (%)	0.27	1.5	4.1	16		5.9	12.4	25		4.6	10.2	14	
Upper Ocean ΣCO_2	0.03	2456	1150	4		2844	813	8	c	1337	823	4	b

down measured during cruises NBP96-6 and NBP97-9. All video stations were assigned to *Productivity Groups* from a from cluster analysis of their ΣCO_2 values. Three *Productivity Groups* were defined with low, moderate, and high levels of ΣCO_2 drawdown that averaged 1940, 3154, and 4165 mmol / m², respectively (Plate 2*b*, Table 2).

Characteristics of seafloor habitats were also defined in two ways. Stations were assigned to *Habitat Groups* from cluster analysis of depth, seafloor slope, and current speed measurements, resulting in 4 major groups, generally associated with the banks, transition zones between banks and basins, and deep basins in the Ross Sea (Plate 2*c*). Six stations located near crests or abrupt margins of banks with high current speeds (mean=54 cm/s) clustered into a "Crest" group (Table 3). "Bank" stations, located more centrally on banks were characterized by shallow depths (mean=377 m), little seafloor slope, and moderate currents (25 cm/s). "Slope" stations were positioned at moderate depths between banks and basins, with moderate currents. The "Basin" group included deep (mean=808 m) stations with low current speeds (15 cm/s) and low seafloor slope.

Finally, variation in the organic content of seafloor sediments (*Sediment Groups*) in the study area was compared to benthic faunal patterns. Groups of stations with similar sediment organic content, termed *Sediment*

TABLE 2. Variation in physical parameters among *Productivity Groups*. See Table 1 for explanation of values.

Productivity Groups Parameter	p	Low (a) Mean	SD	N	*	Moderate (b) Mean	SD	N	*	High (c) Mean	SD	N	*
Latitude	0.01	−75.3	1.4	21	b,c	−76.3	1.1	15	a	−76.7	.8	19	a
Longitude	0.22	171.0	5.6	21		174.2	8.0	15		174.4	7.0	19	
Depth	0.10	621.3	210.8	21	b	500.1	147.4	15	a	599.4	139.3	19	
Slope (deg.)	0.14	0.4	0.4	21		0.2	0.2	15		0.2	0.2	19	
Current Speed (cm/s)	0.95	26.1	15.6	15		23.9	10.0	7		24.1	13.5	6	
Sediment Carbon (%)	0.28	0.7	0.3	10		0.8	0.2	3		1.1	0.1	2	
Sediment Nitrogen (%)	0.30	0.1	0.0	10		0.1	0.0	3		0.2	0.0	2	
Carbon / Nitrogen	0.77	8.5	1.0	10		9.7	2.3	3		8.4	0.1	2	
Carbon isotope ($\delta^{13}C$)	0.14	−25.6	1.7	10		−26.1	3.2	3		−27.6	0.5	2	
Nitrogen isotope ($\delta^{15}N$)	0.12	4.0	1.1	10		3.6	0.4	3		4.0	0.1	2	
Rock Substrata (%)	0.04	6.1	16.7	21	b,c	0.1	0.1	15	a	0.3	0.5	19	a
Phytodetritus (%)	0.14	7.8	15.1	21		2.5	4.7	15		1.9	3.7	19	
Upper Ocean ΣCO_2	0.07	1941	753	12	c	3154	554	2		4165	544	2	a

TABLE 3. Variation in physical parameters among *Habitat Groups*. See Table 1 for explanation of values.

Habitat Groups Parameter	p	Crest (a) Mean	SD	N	*	Bank (b) Mean	SD	N	*	Slope (c) Mean	SD	N	*	Basin (d) Mean	SD	N	*
Latitude	0.59	−76.1	1.4	6		−75.6	0.9	11		−76.2	1.4	24		−76.1	1.3	14	
Longitude	0.08	171.0	6.5	6		174.3	3.4	11		175.0	6.7	24		169.6	8.4	14	c
Depth	0.01	421.3	58.8	6	c,d	377.5	70.6	11	c,d	580.9	64.1	24	d	808.1	120.4	14	all
Slope (deg.)	0.01	0.6	0.2	6	b,c	0.2	0.1	11	a,d	23.7	10.3	11	all	14.9	4.2	7	all
Current Speed (cm/s)	0.01	53.5	8.3	3	all	25.4	9.0	7	a,d	23.7	10.3	11	a,d	14.9	4.2	7	all
Sediment Carbon (%)	0.48	0.5		1		0.6	0.4	3		0.8	0.3	7	a,d	0.9	0.3	4	
Sediment Nitrogen (%)	0.29	0.1		1		0.1	0.1	3		0.1	0.0	7		0.1	0.0	4	
Carbon / Nitrogen	0.01	7.8		1	b	10.6	2.0	3	all	8.4	0.4	7	b	8.1	0.1	4	b
Carbon isotope ($\delta^{13}C$)	0.14	−7.8		1		−24.7	2.0	3		−27.5	0.6	7	d	−23.8	0.2	4	c
Nitrogen isotope ($\delta^{15}N$)	0.02	3.6		1		2.7	1.4	3	c,d	4.1	0.5	7	b	4.5	0.7	4	b
Rock Substrata (%)	0.58	1.8	2.3	6		5.6	18.5	11		0.3	0.5	24		3.9	13.4	14	
Phytodetritus (%)	0.80	4.6	3.9	6		5.4	7.7	11		3.6	8.3	24		4.5	14.8	14	
Upper Ocean ΣCO_2	0.02	1163	920	3	b,c	2319	357	4	a	3189	916	6	a	2011	912	3	

Groups, were determined from a cluster analysis including organic constituents (%C, C/N ratio) and stable carbon isotopes ($\delta^{13}C$) of seafloor sediments at each station. Three well-defined *Sediment Groups* were defined (Table 4, Plate 2*d*). "Rich" stations had high (mean=1.0%) percent carbon and isotopically light carbon ($\delta^{13}C$=-27.5). "Carbon-poor" stations were low in organic carbon (mean%C=0.4%), with slightly heavier carbon ($\delta^{13}C$=-26.7). "Moderate" stations had intermediate%C (mean=0.8) and isotopically heavy carbon ($\delta^{13}C$=-24.3). This range in $\delta^{13}C$ is suggests a strong contribution of diatomaceous debris from ice edge blooms [*Villinski et al.,* 2000].

2.7 Comparison of Faunal Distributions with Environmental Factors

The association of faunal patterns with physical and biochemical features of the environment were evaluated by correlation, clustering and ordination techniques similar to those recommended by Field et al., [1982], coupled with univariate and multivariate analysis of variance. Pairwise correlation (product-moment correlation coefficient) measures were calculated for all combinations of physical parameters and densities of higher taxa (phyla, class, order). Faunal densities were transformed (sq. root (sq. root)) prior to analysis as recommended by Field et al., [1982]. The 'root-root' transformation reduces the weighting of very abundant species, and is also insensitive to spatial scale changes when similarity is measured using the Bray-Curtis index. Percent cover data were transformed using an angular transformation (arcsine (sq. root)) [*Sokal and Rohlf,* 1969]. Physical parameters were $\log_{10}$-transformed. Probability levels for correlation analyses were adjusted (Bonferroni adjustment) for the total number of paired comparisons.

Univariate and multivariate ANOVA were used to evaluate the relationship between environmental variability (*Polynya, Productivity, Habitat,* and *Sediment Groups*) and the abundance or species richness of major phyla, classes of echinoderms and cnidarians, trophic groups, and species, as well as the percentage cover and species richness for all animals. ANOVA methods were also used to assess the degree of variation in physical factors among station groups defined by *Faunal Groups.* Rare species (<2% occurrence among stations) were rejected from ANOVA species-level comparisons, but were included for analyses involving higher taxa. Taxa with fewer than five species were excluded from analysis of variance involving species richness.

TABLE 4. Variation in physical parameters among *Sediment Groups*. See Table 1 for explanation of values.

Sediment Organic Groups		Poor (a)				Moderate (b)				Rich (c)			
Parameter	p	Mean	SD	N	*	Mean	SD	N	*	Mean	SD	N	*
Latitude	0.85	−76.1	0.8	15		−76.3	0.7	17		−76.0	1.9	14	
Longitude	0.01	166.5	3.2	15	a,c	172.7	2.8	17	a,b	178.7	6.6	14	b,c
Depth	0.04	692.3	205.4	15	a	568.8	151.4	17		525.9	115.2	14	b
Slope (deg.)	0.01	0.5	0.5	15	a,c	0.2	1.1	17	b	0.2	0.2	14	b
Current Speed (cm/s)	0.01	30.6	14.4	6	a	14.9	4.8	6	a	17.4	6.5	8	b,c
Sediment Carbon (%)	0.01	0.4	0.1	6	a,c	0.8	0.2	11	a,b	1.0	0.2	8	b,c
Sediment Nitrogen (%)	0.01	0.1	0.0	6	a	0.1	0.0	11	a	0.1	0.0	8	b,c
Carbon / Nitrogen	0.87	8.5	1.3	6		8.3	1.4	11		8.2	0.4	8	
Carbon isotope ($\delta^{13}C$)	0.01	−26.7	0.7	6	a,c	−24.3	1.0	11	b	−27.6	0.5	8	b
Nitrogen isotope ($\delta^{15}N$)	0.38	4.9	1.3	6		4.0	0.6	11		4.0	0.3	8	
Rock Substrata (%)	0.47	3.7	12.9	15		0.4	0.8	17		0.6	1.5	14	
Phytodetritus (%)	0.71	6.0	14.3	15		2.6	4.9	17		3.7	9.9	14	
Upper Ocean ΣCO_2	0.18	1982	746	5		2138	735	5		3566	975	3	

3. RESULTS

3.1 General Megafaunal Patterns

Of 63 video camera deployments completed during cruises NBP97-9 and NBP98-7 in the SW Ross Sea, 57 were analyzed to estimate the densities of all identifiable megafauna. Six tows were rejected owing to camera failure, poor viewing orientation, or low water clarity. Results from two stations where camera tows were repeated during visits in 1997 and 1998 were averaged to represent faunal abundance and species richness at each station, reducing the total number of stations analyzed to fifty-five.

Station depths ranged from 270 to 1137 m depth (mean=580 m). The average area of seafloor analyzed for camera tows at each of 55 stations was 103.6 m² (S.D.=28.7). From these video records, 107,684 individuals (including 66,789 based on percentage cover of bryozoans) from 141 taxa were counted on the surface of the substratum, yielding an average of 1956.3 ind. / 100 m² surveyed. In addition, 21,338 burrows of two principal sizes and shapes (oblong, aggregated holes ~5 x 8 cm, and small, ~3 cm, circular holes) were counted. Large and small burrows had densities averaging 61.8 and 283.1 ind. / 100 m², respectively. Examples of common benthic fauna are shown in Plates 3 & 4.

Percentage cover of all megafaunal organisms on the seafloor ranged from 0.06 to 84.93, with an average over all stations of 8.1 (S.D.=16.8). Total faunal cover decreased significantly with increasing depth (r=0.55, p<0.001), related largely to higher cover of bryozoans, sponges, hydroids, and other colonial species in shallow water. In contrast, the cover of non-colonial animals increased (r=0.36, p<0.01) with depth. Total faunal cover was also greater (r=0.47, p<0.01) at stations with in higher current speeds, associated with the higher cover of colonial organisms on current-swept banks. Slope of the seafloor explained little variation in total faunal cover.

3.2 Abundance and Distribution of Megafaunal Phyla

Ectoprocta, Echinodermata, Cnidaria, Annelida, and Porifera accounted for 77.6% of the total faunal density (excluding burrows) and 75% of the total species richness (number of taxa) enumerated from all camera tows (Table 5). Arthropoda and Chordata were significant components of the benthos, with 18 species and 2.6% of the total faunal density. Ctenophora, Hemichordata, Mollusca, and Echiura were minor contributors to the identifiable megabenthos, totaling 8 species and only 0.2% of total faunal density.

Ectoprocta was by far the most abundant phylum, with 62% of the total individuals counted, based on their estimated density as 2X their percentage cover (see methods). Percentage cover of ectoprocts averaged only 6.5%, but exceeded 50% at some stations. Because of the limited resolution of the video imagery and difficulty distinguishing some species, few taxa were identified (Plate 4*e*).

Echinoderms ranked second in abundance overall (3.6% of all individuals), with twice the faunal density of any phyla except ectoprocts, averaging 130 ind. / 100 m² (Table 5). Ophiuroids (83.2 ind. / 100 m²) were much more abundant than other echinoderm classes, with a group of depositing-feeding species (including *Ophionotus victoriae* (79.8 ind. / 100 m²), comprising 63% of the total echinoderms counted. Sixteen holothuroids species
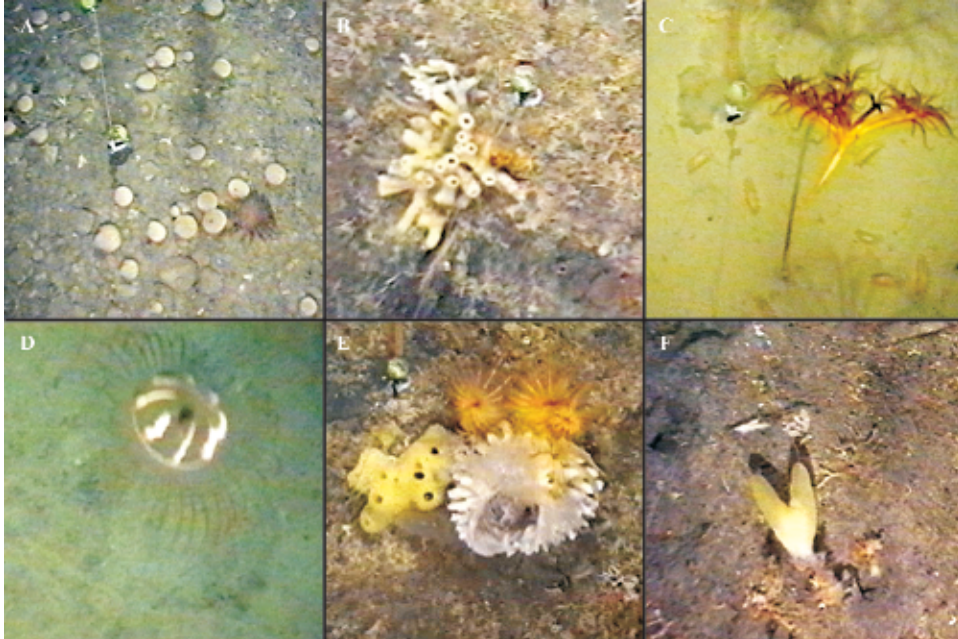
Plate 3. Benthic megafauna of the SW Ross Sea. A. *Polymastia* sp., common on deeper slopes. B. *Haliclona dancoi*, a common sponge on crests of shallow banks. C. The pennatulaceans *Umbellula pallida* and *U. magniflora* (shown) were common in various habitats. An unidentified holothurian is also visible. D. Unidentified benthopelagic trachymedusa. E. *Mycale acerata* (left), *Rosella nuda* (white), and comatulid crinoids, *Promachocrinus kerguelensis*. F. Benthic platyctenid ctenophore, *Lyrocteis flavopallidus.* Tennis ball provides scale in A, B, C, D.
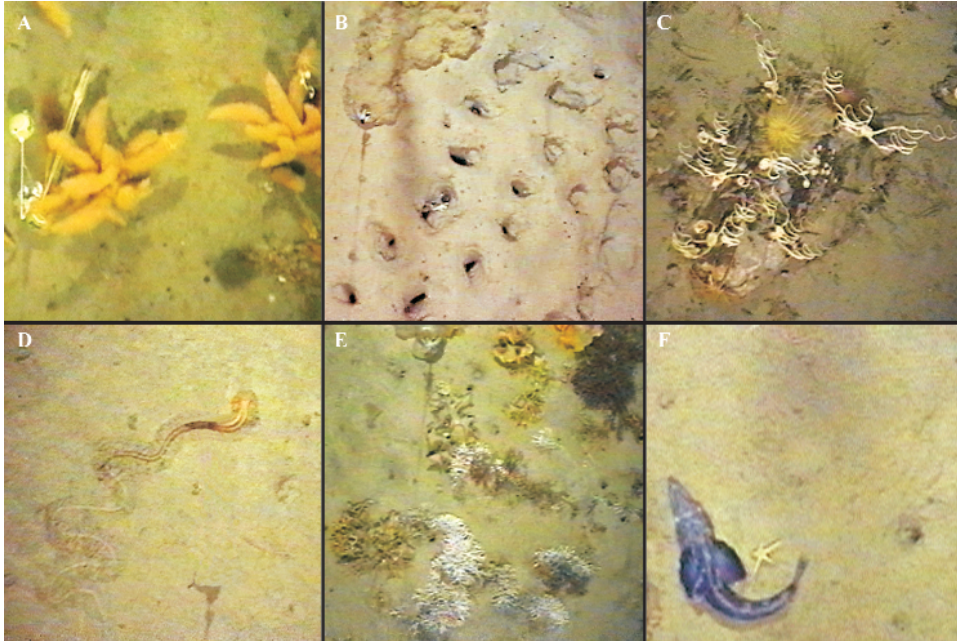
LOW RES

Plate 4. Megafauna from the SW Ross Sea. A. Gorgonacea, *Thouarella* sp. B. Complexes of large burrows, possibly excavated by crustaceans were common in most soft sediment habitats. C. The filter-feeding ophiuroid *Astrotoma agassizii* was observed frequently on rocks and sponges. D. This unidentified Lophenteropneust hemichordate was common in basin habitats. E. A mixed complex of bryozoans were the most abundant fauna of shallow banks. F. Notothenoid, Bathydraconidae?, and a small burrow on right. Echiuran worms were observed retracting into some of these burrows.

TABLE 5. Summary of megafaunal abundance for camera tow stations (n=55) in the Ross Sea. All taxa (a) includes two burrow types. All taxa (b) excludes burrows. Estimates are based on counts, except for All taxa (% cover from pt. contact estimate) and Ectoprocta (density estimated from 2X percent cover bryozoan / hydroid complex).

Taxon	Mean #/100 m^2	St. Err. #/100 m^2	Min. #/100 m^2	Max. #/100 m^2	% Freq.	Total #	Richness # Taxa
All taxa (% Cover)	8.1	2.3	0.1	84.9	100		
All taxa (a)	2301.1	310.3	83.1	16891.7	100.0	129022.2	
All taxa (b)	1956.3	263.8	83.1	16891.7	100.0	107684.4	143
Porifera	35.4	4.8	0.0	204.8	96.4	2082.4	44
Cnidaria	64.0	8.6	6.1	415.0	100.0	3913.3	30
Hydrozoa1	0.3	1.4	0.0	42.0	90.9	699.6	4
Trachymedusae	2.6	0.4	0.0	38.5	32.7	163.0	3
Anthozoa	51.2	6.9	1.5	385.4	100.0	3050.7	22
Hexacorallia	13.2	1.8	0.0	327.3	83.6	738.0	8
Octocorallia							
Alcyonacea	0.3	0.0	0.0	4.4	16.4	15.0	2
Gorgonacea	21.8	2.9	0.0	116.9	78.2	1251.1	2
Pennatulacea	15.9	2.1	0.5	44.4	100.0	1046.6	10
Ctenophora	0.4	0.2	0.0	12.3	14.5	23.0	1
Annelida	43.7	5.9	0.0	298.5	67.3	2973.5	5
Echiura	0.3	0.0	0.0	10.0	7.3	19.3	1
Mollusca	0.5	0.1	0.0	3.3	32.7	37.0	3
Arthropoda	21.0	2.8	1.6	73.1	100.0	1276.9	5
Echinodermata	129.9	17.5	9.4	771.1	100.0	7994.1	34
Asteroidea	2.1	0.3	0.0.	26.5	69.1	131.8	5
Ophiuroidea	83.2	11.2	0.0	749.8	98.2	5156.5	3
Crinoidea	14.8	2.0	0.0	78.4	92.7	911.2	4
Echinoidea	5.4	0.7	0.0	27.5	80.0	298.9	6
Holothuroidea	24.4	3.3	0.0	477.9	96.4	1495.7	16
Holo.-errant	24.1	3.3	0.0	477.9	96.4	1478.7	10
Holo.-sed	0.2	0.0	0.0	303	10.9	10.0	6
Ectoprocta	1297.1	174.9	0.0	16473.9	92.7	66789.3	2
Hemichordata	0.7	0.1	0.0	5.5	29.1	52.0	1
Chordata	14.6	2.0	0.0	46.3	98.2	964.2	14
Urochordata	7.0	1.0	0.0	38.5	89.1	479.9	7
Pisces	7.5	1.0	0.0	24.0	96.4	484.2	7
Deposit-Feeder	173.1	23.3	12.3	887.6	100.0	10830.5	28
Filter-Feeder	114.5	15.4	16.5	356.9	100.0	73847.0	82
Predators	27.7	3.7	0.8	335.8	100.0	1667.1	28

(24.4 ind. / 100 m^2, 7.7% of total density) were distributed widely among most habitats in the Ross Sea, and were common large megafauna, especially over relatively flat, soft sediments. Crinoid taxa (Plate 3*e*) were the fifth most abundant invertebrate class, averaging 14.8 ind. / 100 m^2. Echinoids, including 6 species, summed to densities to 27 ind. / 100 m^2 (mean=5.4).

The Cnidaria ranked third in faunal density among phyla, dominated by gorgonian and pennatulacean anthozoans, with densities of 21.8 and 15.9 ind. / 100 m^2,

respectively (12% of the total faunal abundance), third only to bryozoans and ophiuroids among all invertebrate classes. One gorgonian (*Thouarella* sp., Plate 4*a*) accounted for most of the gorgonian abundance. The species richness of cnidarians was relatively high, with 30 species (21% of megafaunal species richness). Ten pennatulaceans and eight anemones contributed the greatest species richness for the phylum.

Annelid worms, though low in species richness (5 taxa noted) ranked fourth in overall density among phyla, due

principally to the conspicuous agglutinated tubes housing maldanid polychaetes. Based on counts of their tube houses, maldanids were the second most abundant known taxon, occurring throughout carbon-rich sediments in the Ross Sea with an average density of 64 ind. / 100 m².

The Porifera was the most species-rich (44 taxa) phylum of benthic megafauna and represented 11.2% of all animals counted (35.4 ind. / 100 m²). The species richness and abundance of sponges was highest in shallow water, especially over rocky submarine terrain where the cover of sponges and colonial filter-feeders (e.g. bryozoans, hydroids) reached greater than 80%.

Several other phyla were lower in abundance and species richness, but were conspicuous members of the benthic community. Arthropods, especially decapod shrimps and pycnogonids (Colossendeidae), were common in most habitats, with somewhat higher densities in in slope and basin sediments. Shrimp (probably *Notocrangon* sp.), were indistinguishable on video and treated as a single taxon, were present in densities of 20 ind. / 100 m², with a maximum density of 73 ind. / 100 m².

Chordates were diverse and relatively abundant, with seven species of both fishes and tunicates, and were found in highest concentrations in areas of high sponge abundance (chordate vs. sponge density; r=0.37, p<0.005). Hemichordates were common, especially in transition zones between banks and basins, where a single species of lophenteropneust worm was often observed with its characteristic sinusoidal feeding trace (Plate 4*d*). The benthic platyctenean ctenophore *Lyrocteis flavopallidus* (Plate 3*f*) was observed rarely, principally on shallow banks.

Small circular burrows (<2-3 cm diameter) were common features on the seafloor (Plate 4*f*), present in densities as high as 1000 ind. / 100 m² (mean=283 ind. / 100 m²). Although it was not possible to determine the species occupying such burrows, echiuran worms were observed retracting into some of these holes. Larger, oblong burrows (Plate 4*b*) created and maintained by an unknown organism are similar to those produced by burrowing shrimps or other decapod crustaceans [*Gage and Tyler*, 1991]. These burrows were often aggregated and were very abundant (mean=62 ind. / 100 m²) in most shallow sloped, sediments.

3.3 Faunal Associations

Statistically significant correlations in the abundance of several pairs of major taxa were detected. The most robust faunal association was a correlation between Porifera and crinoid echinoderms (r=0.55, p<0.05). Comatulid crinoids were observed frequently on sponges (Plate 3*e*), where their feeding efficiency was presumably improved by their position higher in the boundary layer flow. Bryozoan / hydroid densities were also correlated with crinoids, and both groups declined in abundance with depth. The bryozoan / hydroid group was correlated negatively with deposit-feeding holothurians, as expected for groups feeding on suspended and deposited material, respectively.

Several additional faunal associations were detected, largely related to the feeding modes of species. Gorgonians exhibited significant associations with chordates and holothurians. *Thouarella* sp., the dominant gorgonian, was common in areas of high chordate density (r=0.44, p<0.1), but less abundant amongst deposit-feeding holothurians (r=0.41, p<0.05). Densities of chordates (tunicates and fishes) and pennatulaceans (sea pens) were also correlated positively (r=0.41, p<0.1).

3.4 Ross Sea Megafaunal Assemblages

Five *Faunal Groups* were identified from cluster analysis of stations among all individual taxa (Figure 1).
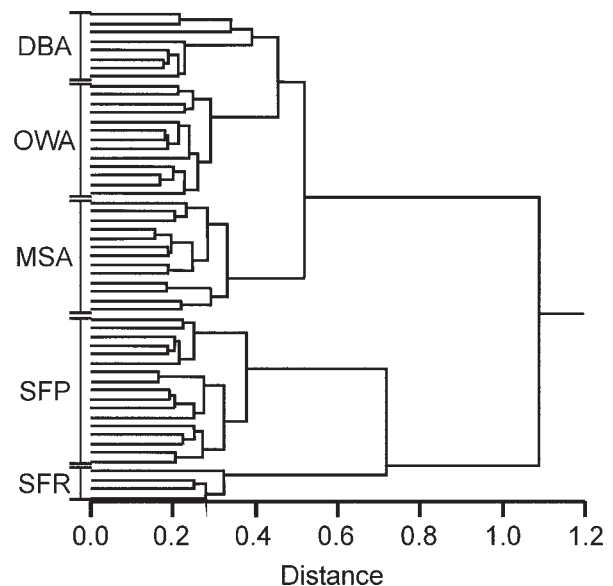

Fig. 1. Results from clusters analysis of all stations using faunal abundances for all species. *Faunal Groups* characterizing benthic megafaunal assemblages for station clusters are listed. SFR= suspension-feeders, rich. SFP= suspension-feeders, poor. MSA= mixed slope assemblage. OWA= ophiuroid / worm association. DBA= depauperate basin association.

These faunal assemblages represented a gradient from shallow-living suspension-feeders to deeper deposit-feeders (Figure 2). Total faunal density decreased greatly among *Faunal Groups* from shallow to deep waters (Figure 3). Four stations represented a "suspension-feeder-rich" (SFR) *Faunal Group* dominated by bryozoan / hydroid cover. SFR included the highest total percentage cover (64%) and density (12,846 ind. / 100 m²) of animals (Table 6, 7). Other notable taxa were filter-feeding ophiuroids (*Astrotoma agassizii*), the gorgonian *Thouarella* sp., and decapod shrimps (*Notocrangon* sp. and others). Hemichordates, echiurans, and mollusks were absent from SFR, with low densities of annelids and elasipodid holothurians.

The suspension-feeder-poor (SFP) assemblage was similar to SFR, but with much lower total cover (7%) and abundance (1,718 ind. / 100 m²), due largely to lower bryozoan / hydroid abundance. Cnidarians,

Fig. 3. Variation in faunal density and species richness among *Faunal Groups*. Mean (+/– standard error) abundance (# / 100 m²) of all megafauna by group (filled circles) - note $\log_{10}$ scale. Mean (+/– standard error) number of species per station by *Faunal Group* (open squares).

annelids, echinoderms and chordates increased in abundance in the SFP group. The SFR and SFP were characteristic of the shallower, current-swept areas with high cover of rock and low cover of soft sediments (Table 8).

A "mixed slope assemblage" (MSA) had a transitional fauna intermediate between shallow banks and deep basins. Most MSA stations were located between banks and basins (Plate 5), where elements of the suspension-feeding assemblages (e.g. bryozoans, crinoids) from shallow water, as well as an increased abundance of deposit-feeders (167 ind. / 100 m²). Elasipodid and other deposit-feeding holothurians were present in their highest densities (59 ind. / 100 m²) in the MSA, more than twice the abundance observed in other *Faunal Groups*.

Thirteen stations distributed along the deeper slopes of the SW Ross Sea clustered together to form an "ophiuroid / worm assemblage" (OWA), with peak densities of deposit-feeding ophiuroids and the highest abundance of maldanid polychaetes tubes, hemichordates, echiurans, and mollusks.

The "depauperate basin assemblage" (DBA), found principally in the deepest basins (Table 8), had the lowest cover, density, and species richness of megafauna (Table 6, Figure 3). The DBA also includes species inhabiting glacial erratic boulders, often with relatively high densities of sponges and crinoids, resulting in some-
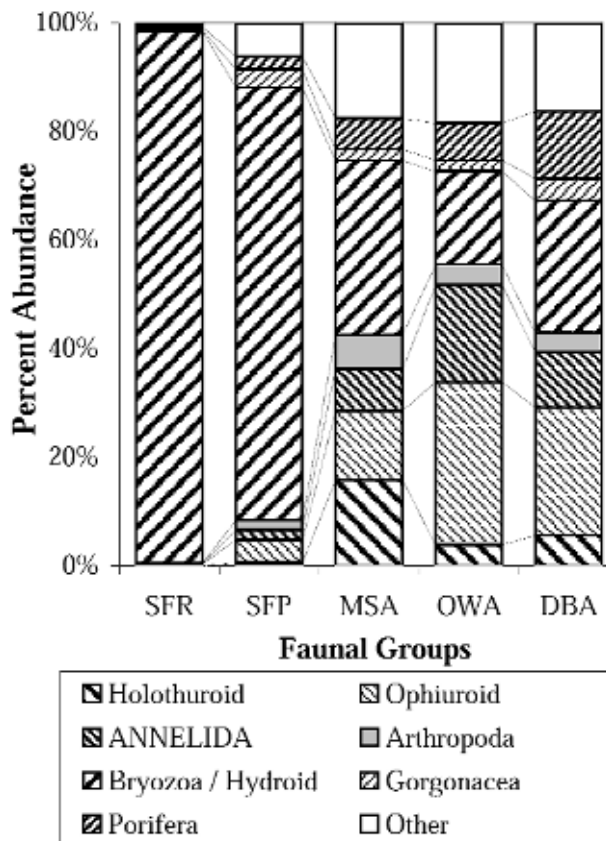
Fig. 2. Variation in faunal dominance among *Faunal Groups*. Fill for suspension-feeding groups slants up from left side. Fill for deposit-feeders slopes down from left. Acronyms for *Faunal Groups* as in Figure 1.
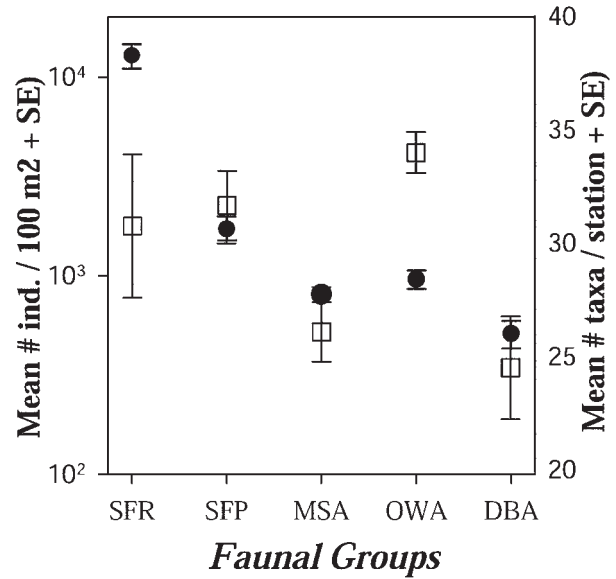
TABLE. 6. Variation in megafaunal distributions among *Faunal Groups*. Sample size for groups were SFR (4), SFP (17), MSA (13), OWA (13), and DBA (8). Means represent faunal density (# / 100 m²). See Table 1 for explanation of values and abbreviations.

Fauna Clusters	P	SFR (a) Mean	SD	*	SFP (b) Mean	SD	*	MSA (c) Mean	SD	*	OWA (d) Mean	SD	*	DBA (e) Mean	SD	*
Megafauna (%)	0.01	64.1	18.6	All	7.1	5.0	All	1.9	0.9	a,b	2.5	1.0	a,b	1.6	0.9	a,b
Sp. Richness (# taxa)	0.01	31	6	All	32	6	c,e	26	5	b,d	34	3	c,e	25	6	b,d
Megafauna (#/100 m²)	0.01	12943.9	3548.9	All	2105.6	1279.3	All	1233.4	436.5	a,b,e	1330.7	545.6	a,b,e	707.2	364.4	All
Porifera	0.05	81.6	72.7	c,e	31.8	37.6		21.8	34.3	a,d	39.7	27.3	c	35.1	69.1	a
Cnidaria	0.14	57.0	35.1		80.1	39.9	c	41.9	16.2	b	79.1	103.5		44.7	34.2	
Hydrozoa	0.01	4.5	5.2	b,c,d	8.2	8.5	a,e	15.6	11.8	a,e	13.7	10.5	a,e	3.2	3.7	b,c,d
Trachymedusae	0.01	0.0	0.0	e	0.7	2.3	d,e	0.3	0.8	c,e	1.7	2.0	b,c,e	13.1	14.5	All
Anthozoa	0.01	52.5	34.4		71.2	40.1	c,e	26.0	16.2	b	63.7	99.4		28.4	32.3	b
Hexacorallia	0.23	8.3	5.9		7.0	7.4		5.3	11.8	d	33.3	89.3	c	8.6	18.7	
Octocorallia	0.01	0.4	0.3	e	0.6	0.4	c,d,e	0.2	0.1	b	0.3	0.2	b	0.2	0.3	a,b
Alcyonacea	0.31	0.0	0.0		0.6	1.2		0.0	0.0		0.3	0.5		0.2	0.5	
Gorgonacea	0.02	26.6	26.7		43.9	38.8	c,d,e	7.8	8.9	b	11.8	13.0	b	11.6	28.2	b
Pennatulacea	0.07	17.7	17.8		19.7	9.3	c,e	12.9	7.3		18.3	12.8		7.9	5.4	b
Ctenophora	0.04	3.1	6.2	d	0.4	0.6	d,e	0.1	0.3		0.0	0.0	a,b	0.0	0.0	b
Annelida	0.01	2.9	5.1	d	24.9	38.6	d	28.9	52.1	d	104.6	82.9	All	29.0	49.9	d
Echiura	0.01	0.0	0.0	d	0.0	0.0	d	0.0	0.0	d	1.4	2.9	All	0.0	0.0	d
Mollusca	0.76	0.2	0.4		0.6	1.0		0.3	0.6		0.5	0.6		0.6	1.1	
Arthropoda	0.11	22.2	34.2		23.0	16.7	e	24.1	14.4	e	21.9	8.6	e	9.9	6.3	b,c,d
Echinodermata	0.16	97.2	72.5		93.1	69.4	d	124.3	132.5	d	219.5	204.9	b	88.0	71.7	
Asteroidea	0.03	7.0	13.0		2.6	2.0	c,e	0.8	1.1	b	1.7	1.5		1.2	1.9	b
Ophiuroidea	0.04	47.3	26.8	e	55.5	61.7	d	48.0	54.2	d	175.8	198.7	b,c	66.9	65.8	
Crinoidea	0.01	31.9	33.0	c,e	22.2	18.3	c,e	8.1	10.7	a,b,e	14.6	14.2	e	1.7	2.3	All
Echinoidea	0.33	9.6	12.1		4.7	4.2		7.6	8.6		4.8	5.2		2.2	4.2	
Holothuroidea	0.01	1.4	1.9	All	8.0	8.3	a,c,d	59.8	127.8	a,b,e	22.7	20.5	a,b	15.9	16.3	a
Holo. - errant	0.01	0.5	0.6	All	7.7	8.3	a,c,d	59.7	127.8	a,b,e	22.7	20.5	a,b	15.2	16.8	a,c
Holo. - sed.	0.73	0.8	1.6		0.1	0.4		0.1	0.4		0.0	0.2		0.1	0.4	
Ectoprocta	0.01	12469.0	3720.8	All	1061.8	1006.9	All	121.1	166.9	a,b,e	101.1	77.1	a,b,e	69.3	164.3	All
Hemichordata	0.01	0.0	0.0	d	0.0	0.0	d,e	0.7	1.8	d	1.8	1.5	All	0.7	1.1	b,d
Chordata	0.01	13.6	16.4		15.9	7.0	e	14.6	9.7	e	16.5	12.6	e	6.6	5.9	b,c,d
Urochordata	0.13	10.2	14.5		5.2	5.6		6.5	6.5	e	9.7	12.2	e	3.3	4.7	c,d
Pisces	0.01	3.4	2.3	b	10.7	6.9	a,e	8.1	5.3	e	6.7	2.9	e	3.3	3.7	b,c,d
Deposit-feeder	0.02	74.7	68.8	d	107.3	84.5	d	166.7	146.4		301.8	247.0	a,b,e	122.9	96.5	d
Filter-feeder	0.01	12652.8	3701.8	All	1201.6	997.9	All	195.5	168.7	a,b	208.1	100.4	a,b	162.2	254.3	a,b
Predator	0.12	20.2	15.0		22.7	9.3		15.6	13.4	d	49.0	87.4	d	27.4	25.6	

TABLE 7. Summary of dominant species for Ross Sea megafaunal assemblages. Codes for *Faunal Groups* indicate bryozoan / hydroid complex, Ophiuroidea, Gorgonacea, Decapoda, Porifera, Cerianthidae, Holothuroidea, and animal burrows. Values are mean abundance per 100 m^2. Taxa accounting for greater than 5% of the total faunal abundance within the assemblage are in bold. *= dominant species for multispecies taxon.

Taxon	SFR	SFP	MSA	OWA	DBA
Bryozoa / Hydroidea	**12469.0**	**161.8**	**121.8**	**118.0**	**69.3**
Ophiuroidea	41.0	**48.0**	**46.5**	**174.9**	**66.1**
Thouarella sp.	22.1	**43.4**	7.8	11.7	11.6
Notocrangon sp.*	20.9	**22.3**	**23.0**	19.4	9.6
Haliclona sp.	20.9	2.5	8.7	1.7	1.0
Cerianthidae	0.3	0.2	0.2	27.7	0.8
Holothuroidea sp. 1	0.2	3.7	**41.8**	10.5	1.2
Porifera sp. 1	0.0	0.1	0.0	0.0	**22.8**
Polymastia invaginata	0.0	0.0	0.0	0.0	**28.5**
Maldanidae tubes	0.0	**24.6**	**28.9**	102.8	29.0
Burrow, large	3.9	**69.1**	**82.7**	74.4	20.3
Burrow, small	94.2	**317.9**	**345.0**	299.1	177.1

what higher densities of suspension feeders. Ophiuroids, maldanid polychaetes, and sponges were the most abundant taxa (Table 7).

Average species richness per station varied little among faunal assemblages (27 to 35 sp. / st.) compared to the differences in faunal density (Figure 3), due at least partially to the limited taxonomic detail available for some organisms (e.g. bryozoans).

MDS analysis revealed groups of stations with faunal abundances very similar to the *Faunal Groups* identified from cluster analysis (Figure 4). All *Faunal Groups* were separated along two MDS axes (stress=0.2, R^2=0.85) except DBA. This deep-basin assemblage of eight stations included two minor clusters (Figure 1) with three stations that separate in both analyses.

Variation in the abundance of megafauna among *Faunal Groups* was statistically significant (ANOSIM; global R=0.51; p<0.001). Pairwise *Faunal Group* comparisons were all significant. R-values ranged from 0.39 to 0.99 with probability levels (Bonferroni correction applied) less than 0.01 for all comparisons except DBA vs. SFR (p<0.05). The abundances of most higher taxa varied significantly (multivariate and univariate ANOVA) among *Faunal Groups* (Table 6). Variation in the abundance of the hydroid-bryozoan complex, small burrows, and ophiuroids abundances were responsible for the greatest dissimilarity (average dissimilarities of 49 to 60% determined by SIMPER analysis).

3.5 Faunal Correlations with Environmental Factors

3.5.1 Correlation analysis of faunal abundance and physical factors. *Faunal Groups* identified by cluster

analysis were correlated significantly to several physical parameters. Environmental parameters (especially depth) explained the greatest amount of variance in the abundance of various taxa, indicating decreasing faunal density with depth for total fauna density (r=–0.59, p<0.05), the bryozoan / hydroid complex (r=–0.72, p<0.05), and filter-feeders (r=–0.72, p<0.05). Trachymedusae were most common in deeper areas (r=0.60, p<0.05) with reduced currents (r=0.47, p<0.1), and were also correlated with longitude (r=–0.51, p<0.1), most likely due to longitudinal differences in depth among stations.

Although the influences of depth and current speed are at least partially confounded due to the decrease in current speeds with depth (r=0.45), the abundances of several taxa were correlated with current speed. The density of suspension-feeders (r=0.47, p<0.10) was correlated positively with current speed, due largely to ectoprocts (r=0.47, p<0.05). In contrast, the density of deposit-feeders was negatively correlated to current speed (r=0.39, p<0.05), supporting the notion of higher food availability for deposit feeders in areas of low flow.

Sediment organic parameters were correlated with the abundances of several taxa. Although densities of gorgonaceans (sea fans) were correlated negatively with %C (r=–0.69, p<0.05) and %N (r=-0.49, p<0.05), these relationships likely derive from the influence of currents on sediment characteristics. In contrast, deposit-feeders as a whole, holothurians, and echiurans were more abundant in carbon-rich sediments, although these relationships were not statistically significant.

Faunal densities were largely uncorrelated with features of the upper water column. Suspension-feeding

TABLE 8. Variation in physical factors among clusters of stations forming *Faunal Groups*. Overall significance levels indicated by P. Significant (p<0.05) differences for pairwise comparisons (*) listed for each *Faunal Group*. Clusters include SFR (suspension-feeder rich), SFP (suspension-feeder poor), MSA (mixed slope assemblage), OWA (ophiuroid / worm assemblage), and DBA (depauperate basin assemblage).

Fauna Group		SFR (a)				SFP (b)				MSA (c)				OWA (d)				DBA (e)			
Factor	P	Mean	SD	N	*	Mean	SD	N	*	Mean	SD	N	*	Mean	SD	N	*	Mean	SD	N	*
Latitude	0.61	−75.3	1.3	4		−76.1	1.2	17		−76.4	1.6	13		−76.2	0.8	13		−75.8	1.4	8	
Longitude	0.01	173.4	5.3	4		173.0	6.2	17	c,e	178.0	8.9	13	b,d,e	171.6	4.4	13	c	167.3	2.9	8	b,c
Depth (m)	0.01	359.5	104.7	4	All	503.5	164.9	17	a,d,e	573.8	120.8	13	a,e	644.5	88.6	13	a,b	762.6	216.5	8	a,b,c
Slope (deg.)	0.33	0.4	0.3	4		0.4	0.5	17		0.2	0.3	13		0.2	0.2	13		0.2	0.1	8	
Current Speed (cm/s)	0.05	42.8	10.4	4		23.6	17.7	7	a	18.3	2.9	4	a	27.3	11.6	7		17.0	3.5	6	a
Sediment Carbon (%)	0.63	0.5		1		0.6	0.3	5		0.8	0.3	4		0.8	0.3	4		0.9	0.3	6	
Sediment Nitrogen (%)	0.54	0.1		1		0.1	0.1	5		0.1	0.0	4		0.1	0.0	4		0.1	0.1	6	
Carbon / Nitrogen	0.32	7.8		1		9.3	2.2	5		7.9	0.5	4		8.2	0.3	4		8.0	0.6	6	
Carbon Isotope ($\delta^{13}C$)	0.15	−27.8		1		−24.9	1.9	5	d	−25.8	1.6	4		−26.8	1.5	4		−25.1	1.4	6	b
Nitrogen Isotope ($\delta^{15}N$)	0.09	3.6		1		3.1	1.2	5	c,d,e	4.1	0.3	4	b	4.1	0.4	4	b	4.2	0.7	6	b
Rock Substrata (%)	0.50	1.7	2.8	4		3.4	12.1	17		0.1	0.1	13		0.4	0.8	13		7.8	21.7	8	
Phytodetritus (%)	0.01	6.0	6.1	4	b,c,e	3.0	4.5	17	e	0.1	0.3	13	e	2.5	4.5	13	e	15.8	22.3	8	b,c,d
Upper Ocean ΣCO_2	0.57	1444		2		2106	1018	4		2041	206	2		2985	1253	6		2307	82	2	

holothuroids were correlated negatively with upper water column ΣCO_2 (r=0.69, p<0.05), perhaps due to statistical chance. Alternatively, this may be a confusing relationship between high phytoplankton production and low holothurian abundance.

3.5.2 ANOVA comparisons of faunal assemblages versus physical factors. Several factors, particularly depth, longitude, and near-bottom current speed, were associated with the distribution and abundance of benthic megafauna. Depth varied significantly among *Faunal Groups*, ranging from a mean of 360 m for the SFR group to 762 m for DBA stations (Table 8). Variation in longitude among *Faunal Groups* was also highly significant, likely due to the deeper depths in the western Ross Sea. Currents were highest at stations in the SFR group (42.8 cm/s) compared to other groups where mean speeds were all lower than 28 cm/s. Significant variation in the isotopic signatures of both carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in the sediment may be related to different sources of surface productivity among *Faunal Groups*.

3.6 Faunal Abundance among Polynya, Productivity, Habitat, and Sediment Groups

3.6.1 Faunal patterns beneath the Ross Sea polynya. The position and extent of the Ross Sea polynya was largely unrelated to the patterns of megabenthos abundance on the seafloor (Table 9). Species richness of benthic megafauna did not vary significantly among *Polynya Groups*, though univariate analyses (not shown) indicated significant variation among the number of annelid and arthropod species. The average number of annelid species per station was highest in regions of early ice breakout (1.2 sp. / station), and significantly lower in other regions (<0.76 sp. / st., p<0.05). Similarly, arthropod species richness was significantly higher beneath early ice breakout stations (1.9 vs. <1.6 sp. / st., p<0.05).

3.6.2 Upper ocean productivity. Carbon drawdown in the upper water column, a proxy for primary production, was related to the abundance or species richness of few megafauna groups (Table 9). The abundance of echinoderm classes varied significantly among *Productivity Groups* (MANOVA; p<0.02). Asteroids and alcyonarians were twice as abundant at stations within the low *Productivity Group*, than at high productivity stations. Ophiuroids showed the opposite pattern, with higher densities under the most productive waters.
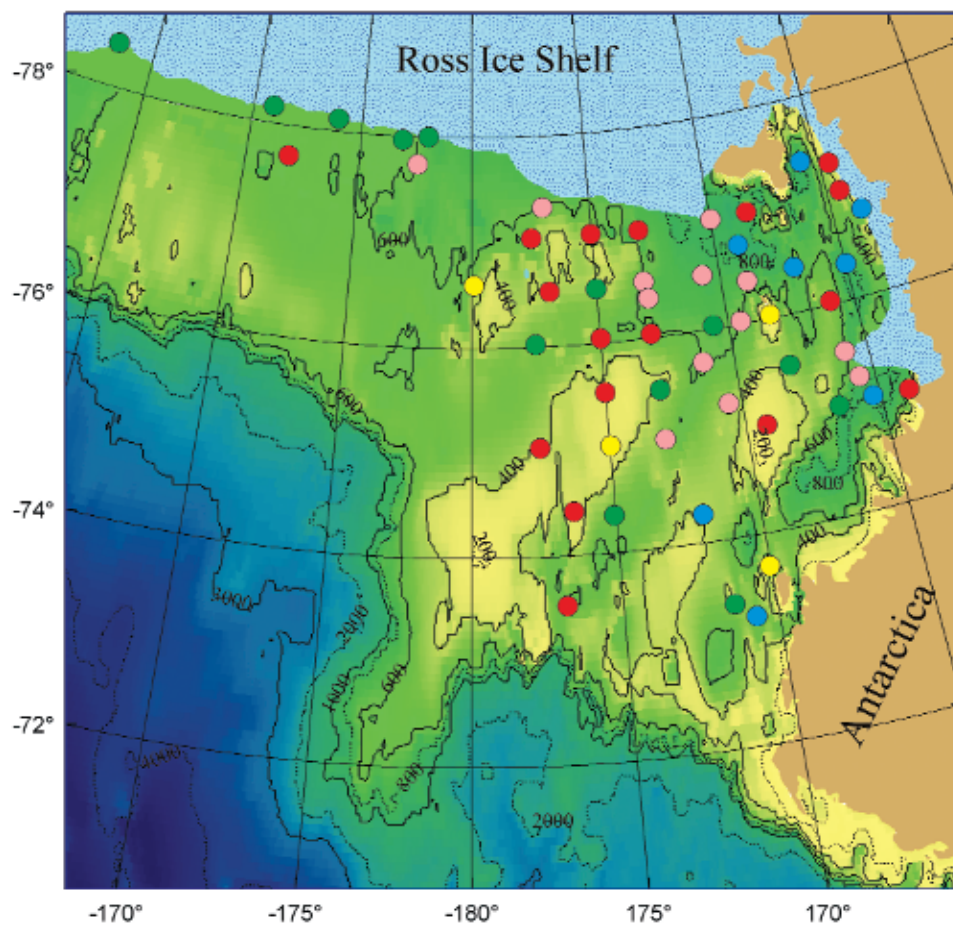
Plate 5. Map of stations belonging to *Faunal Groups* defining Ross Sea megafaunal assemblages. Yellow circles= SFR, red= SFP, green= MSA, pink= OWA, blue= DBA. Acronyms for *Faunal Groups* as in Figure 1.
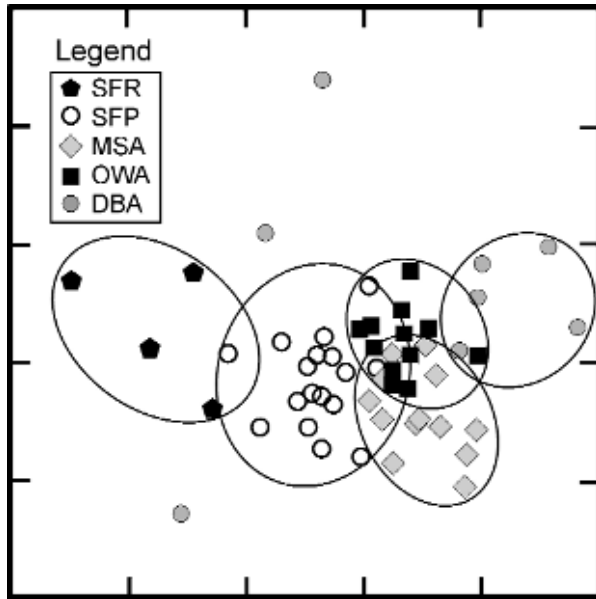
Fig. 4. Multidimensional scaling of species distributions, coded by *Faunal Group* clusters. Different symbols represent *Faunal Groups* determined by cluster analysis (see Figure 1 for explanation).

Species richness overall or within major taxa was generally invariant among groups of stations defined by *Productivity Groups*. Asteroids, however, were significantly ($p<0.05$) more species-rich at stations beneath areas of low productivity (1.3 sp. / st. versus <0.8 sp. / st.), explaining ~12% of the variance in asteroid species richness among stations. Species richness within trophic guilds also varied among regions of surface productivity, with more deposit-feeding species (8.1 sp. / st.) in the low *Productivity Groups*, than in medium (6.8 sp. / st., $p<0.05$) or high (6.6 sp. / st., $p<0.02$) groups.

As expected, primary productivity was related to the pattern of sea ice cover (ANOVA; $p<0.05$; $R^2=0.43$) in the SW Ross Sea. Regions of the Ross Sea polynya that opened in early to mid-spring had higher carbon drawdown than those under more persistent ice cover [*see Arrigo et al.*, 1998, 2000]. Because of this correlation, the effects of ice cover and carbon drawdown represented by categories of *Polynya* and *Productivity* are partially confounded.

3.6.3 Habitat Group characteristics. Benthic megafaunal patterns varied greatly among groups of stations (*Habitat Groups*) defined by depth, slope, and current speed immediately above the seabed (Table 9, 10). The mean percentage cover of animals (summed over all megafaunal taxa) varied significantly among *Habitat Groups* (F=7.03; $p<0.0001$; $R^2=0.29$), and was six times greater at stations on the shallow peaks and edges of shallow areas (crests and banks) than on slopes or basins (Table 10), due mainly to the bryozoans / hydroid complex, sponges, and cnidarians (Table 7). Total megafau-

TABLE 9. Summary of ANOVA analyses comparing faunal density and species richness with *Polynya, Productivity, Habitat, Sediment, and Faunal Groups*. Comparisons of total # species, total density, and all species were univariate ANOVA. All others were multivariate ANOVA. Levels of significance (p) and estimated proportion of variance explained (Eta) by each factor listed. Statistically significant values ($p<0.05$) presented in bold.

Factor	Polynya		Productivity		Habitat		Sediment		Faunal	
	p	Eta	p	Eta	p	Eta	p	Eta	p	Eta
Faunal Abundance										
Total% Cover	0.42	0.03	0.28	0.05	**0.01**	0.29	0.39	0.04	**0.01**	0.88
Total Density	0.93	0.01	0.22	0.06	**0.01**	0.30	0.29	0.06	**0.01**	0.76
All Species	0.32	0.99	0.44	0.99	0.30	0.98	0.13	0.14	0.08	0.99
All Phyla	0.42	0.20	0.56	0.18	**0.01**	0.48	**0.01**	0.40	**0.01**	0.58
Cnidarian Classes	0.33	0.07	0.63	0.04	**0.01**	0.21	0.14	0.11	**0.01**	0.29
Anthozoan Orders	0.90	0.04	0.16	0.11	0.26	0.09	0.24	0.12	0.06	0.12
Echinoderm Classes	0.28	0.11	**0.02**	0.21	**0.01**	0.31	0.09	0.18	**0.01**	0.29
Trophic Groups	0.67	0.04	0.28	0.07	**0.01**	0.21	**0.01**	0.18	**0.01**	0.50
Faunal Richness										
Total # species	0.85	0.01	0.49	0.03	0.06	0.13	0.88	0.01	**0.01**	0.31
All Phyla	0.11	0.17	0.37	0.12	**0.01**	0.22	0.35	0.25	**0.01**	0.25
Cnidarian Classes	0.84	0.03	0.26	0.03	**0.01**	0.16	0.06	0.14	**0.01**	0.21
Anthozoan Orders	0.38	0.08	0.07	0.13	0.19	0.10	0.69	0.07	**0.01**	0.18
Echinoderm Classes	0.65	0.06	0.09	0.15	**0.01**	0.16	0.76	0.08	**0.01**	0.29
Trophic Groups	0.87	0.02	**0.04**	0.12	**0.01**	0.20	0.29	0.08	**0.01**	0.44

TABLE 10. Variation in megafaunal abundance among *Habitat Groups*. Sample sizes were, Crest (6), Bank (11), Slope (24), and Basin (14). See Table 1 for explanation of values.

Habitat Groups Parameter	P	Crest (a) Mean	SD	*	Bank (b) Mean	SD	*	Slope (c) Mean	SD	*	Basin (d) Mean	SD	*
Megafauna (%)	0.01	20.0	22.5	c,d	20.4	29.9	c,d	2.8	2.7	a,b	2.5	2.1	a,b
Sp. Richness (# taxa)	0.06	35	4	b,d	27	7	a	31	6		28	6	a
Megafauna (# / 100 m2)	0.01	4645.2	4261.8	c,d	4722.0	5725.1	c,d	1325.6	577.2	a,b	1066.7	556.1	a,b
Porifera	0.61	39.5	52.4		24.7	40.5		40.9	48.3		32.6	39.5	
Cnidaria	0.12	89.5	45.4		43.1	19.3	a	73.6	78.1		53.2	38.4	
Hydrozoa	0.06	6.7	4.3		10.4	10.0		13.1	11.3	d	6.7	8.6	c
Trachymedusae	0.01	0.0	0.0	d	0.0	0.0	d	1.6	4.9	d	7.5	11.2	All
Anthozoa	0.08	82.8	45.4	b,d	32.7	19.7	a	58.8	75.3	a	39.0	40.7	a
Hexacorallia	0.05	9.8	7.0	d	4.1	4.8		24.5	66.4	d	2.2	2.4	a,c
Octocorallia	0.10	0.7	0.5	All	0.3	0.2		0.3	0.3		0.4	0.4	a
Alcyonacea	0.98	0.7	1.8		0.2	0.5		0.2	0.5		0.3	0.8	
Gorgonacea	0.20	48.0	40.9	b,c	12.6	12.9	a	18.7	25.2	a	23.3	37.0	a
Pennatulacea	0.19	24.3	12.0	d	15.7	10.7		15.4	9.9		13.3	10.7	a
Ctenophora	0.01	2.5	4.9	b,c,d	0.1	0.2	a	0.2	0.4	a	0.1	0.2	a
Annelida	0.12	38.1	54.2		16.6	33.4	c	55.6	64.4	b	46.9	82.6	
Echiura	0.15	0.0	0.0		0.0	0.0		0.7	2.2		0.0	0.0	
Mollusca	0.81	0.3	0.5		0.4	0.9		0.5	0.8		0.6	1.0	
Arthropoda	0.07	12.7	9.9	b	30.9	22.9	a,d	21.3	10.9		16.5	14.1	b
Echinodermata	0.07	105.0	56.0		102.4	137.1	d	108.3	102.8	d	199.2	186.5	b,c
Asteroidea	0.07	7.0	9.8	b,c	1.4	1.8	a	1.2	1.2	a	2.0	2.1	a
Ophiuroidea	0.01	50.5	35.8	c,d	33.7	40.1	d	71.0	87.6	d	157.2	183.5	b,c
Crinoidea	0.12	33.3	25.6	c,d	13.3	15.9		12.1	12.4	a	12.7	19.4	a
Echinoidea	0.01	9.4	10.2	d	5.0	8.0	d	6.9	5.6	d	1.4	1.6	a,c
Holothuroidea	0.11	4.8	4.4	c,d	49.0	142.4		17.1	16.3	a	25.9	25.1	a
Holo. - errant	0.07	3.9	4.2	c,d	48.8	142.5		16.8	16.5	a	25.8	25.1	a
Holo. - sed	0.01	0.9	1.3	All	0.0	0.0	a	0.1	0.3	a	0.1	0.3	a
Ectoprocta	0.01	3608.7	4494.2	c,d	3841.3	5929.6	c,d	238.9	412.9	a,b	123.4	308.7	a,b
Hemichordata	0.02	0.0	0.0	d	0.0	0.0	c,d	0.7	1.0	b	1.5	2.1	a,b
Chordata	0.29	19.7	12.0		10.9	6.4		14.8	9.8		13.3	11.8	
Urochordata	0.41	8.2	11.8		3.1	2.3		7.6	7.6		7.3	11.1	
Pisces	0.35	11.6	8.1		7.9	5.7		7.2	4.4		6.0	6.0	
Deposit-feeder	0.12	98.6	91.0		133.3	153.4		153.4	145.0		246.9	221.0	a
Filter-feeder	0.01	3787.0	4533.7	c,d	3942.8	5952.7	c,d	349.2	436.1	a,b	222.1	390.1	a,b
Predator	0.14	31.0	10.0		14.8	6.8		38.1	66.2		18.7	9.9	

nal density exhibited a similar pattern, with approximately four times greater density on crest and bank stations than in other areas (F=7.4; p<0.0001; R^2=0.30).

Species richness within major phyla varied significantly among *Habitat Groups*, with patterns of variation linked to feeding types. Filter-feeders (bryozoan / hydroid =95% of total) were thirteen times more abundant in crest and bank habitats than on slopes or basins (Table 10). Exclusion of the bryozoan / hydroid complex reduces this difference to only 140 vs. 105 ind. / 100 m². Unlike most deeper-living ophiuroids, *Astrotoma agassizii* (Plate 4c) feeds on benthopelagic zooplankton [*Dearborn et al.*, 1986], and was far more abundant on current-swept crest habitats than elsewhere. Like *A. agassizii*, comatulid crinoids were two to three times more abundant on crests (33.2 ind. / 100 m², p<0.05) than in slope or basin areas. Overall, Cnidarians were somewhat more abundant on crests than on either bank or basin stations, due to the locally high density of *Thouarella* sp. and some sea pens (Pennatulacean 1, *Umbellula* sp.), compared to other habitats. Suspension-feeding holothurians also were most abundant in crest habitats (p<0.0001). The Ctenophora, represented by the benthic platyctenean, *Lyrocteis flavopallidus*, were far more abundant (p<0.01) on crests than in basins (Table 10). The relatively high cnidarian density on slopes resulted from high densities of cerianthid anemones (15 ind. / 100 m²) and hydroids (*Corymorpha* sp., 7.4 ind. / 100 m²).

Deposit-feeding megafaunal taxa were far more abundant in the quieter depositional environments of basins than over crests or banks (Table 10). Ophiuroids were the most abundant echinoderm class, with nearly 160 ind. / 100 m² in basin habitats, representing two to three times the densities found in shallower groups (p<0.003). This pattern is related principally to the distribution of several species lumped with *Ophionotus victoriae*, which account for most (>90%) ophiuroids observed. Lophenteropneust hemichordate worms, represented by a single taxon, were relatively low in abundance, but were observed only in basin and slope habitats (1.5 ind. / 100 m²; p<0.02). Deposit-feeding holothurians were lower in abundance on crests than either slopes (p<0.026) or basins (p<0.044).

Decapod shrimp accounted for the majority of arthropods observed, and were more abundant on banks than on crests or basins. It is possible that lower counts on crests were due partly to the high cover of other biota, which may limit detection of shrimps and other small organisms.

The number of species varied significantly among *Habitat Groups*. The number of taxa per station within echinoderms and chordates was higher on crests and slopes than over banks and basins (p<0.05). Holothurian species richness was high overall (16 species), and was greatest in slope habitats (p<0.05). Variation in the species richness of trophic guilds among *Habitat* categories was similar to faunal density (p<0.001, Table 9). Filter-feeders were more species-rich on crests (21.5 sp. / st.) than other areas (p<0.01). Deposit feeders were most diverse in slope habitats (8.4 sp. / st.), significantly greater than all other habitats (p<0.01).

3.6.4 Variation in megafaunal patterns among Sediment Groups. Though to a lesser extent than observed among *Habitat Groups,* the abundance and species richness of several taxa varied significantly among stations defined by *Sediment Groups* (Table 9). Deposit-feeder densities were higher at stations with carbon-poor sediments than at stations in "rich" or "moderate" organic content sediments (ANOVA, p<0.001).

The densities of several phyla (4 of 11) varied significantly among *Sediment* categories. Annelid (mainly maldanid tubes), echiuran worms, and ophiuroids were the most abundant taxa in carbon-rich sediments (Univariate ANOVA results not shown). Urochordates were most abundant in carbon-poor areas (p<0.025), while fishes were more common (p<0.01) in carbon-rich sediments. Although variation within phyla and trophic groups were significant, abundances of individual species overall did not vary among *Sediment* groups (MANOVA; p<0.88). The densities of few species (6 of 99) varied significantly (univariate ANOVA) among *Sediment* groups.

Species richness did not vary significantly among *Sediment* divisions for either univariate comparisons of all species or multivariate and univariate comparison among phyla, classes, or trophic guilds.

4. DISCUSSION

4.1 Megafaunal Assemblages in the High Antarctic

The depth-related shift from shallow suspension-feeding assemblages to deeper deposit-feeder groups documented here (Figure 2) very similar to the faunal transition documented in the Weddell and Lazarev Seas by Gutt and Starmans [1998; their Figure 3a]. High resolution camera surveys in the Weddell and Lazarev Seas [*Gutt and Starmans, 1998*; *Starmans et al., 1999*] have produced a comprehensive inventory of megafauna in these areas and

have defined faunal associations that vary among depth and substratum characteristics, elaborating on the more general assemblages defined by earlier studies [*Voß,* 1988; *Piepenburg et al.,* 1997]. Bullivant and Dearborn's [1967] analysis of drop-camera photographs identified megafaunal assemblages that were associated principally with sediment type and presence of hard substrata (cobbles or erratic boulders). Their "McMurdo glass sponge assemblage" is similar to the very high cover of sponges, bryozoans, and hydroids of the SFR group detected in this study and by Gutt and Starmans [1998]. In slightly deeper water, the "McMurdo Sound mixed assemblage" overlaps with the SFP [this study and *Gutt and Starmans,* 1998] and MSA groups in which deposit-feeders play in increasing role. The OWA of deep shelf waters corresponds to Bullivant and Dearborn's [1967] "Deep shelf mixed assemblage". Deeper zones with more sluggish currents have lower faunal densities and a more complete transition to deposit-feeders. Analogs in the Weddell and Lazarev Seas to these assemblages are the "suspension feeders deep" and "detritus feeders shallow" defined by Gutt and Starmans [1998].

4.2 Ecosystem Structure and Faunal Associations

The high degree of correlation among various taxa suggests that biological interactions may influence the structure of the Antarctic benthos, an idea promoted by several investigators. In particular, the effects of large sponges and other taxa that increase the structural complexity of the seafloor environment may enhance habitat quality for some species. Porifera were correlated positively with the abundance of several groups, most strongly with comatulid crinoids (*Promachocrinus kerguelensis*), known to climb on rocks or other animals to position themselves in the optimal flow conditions for feeding efficiency [*Fabricius,* 1994; *Fujita et al.,* 1987]. Their association with sponges in Antarctic waters is well known [*Picken,* 1985; *Gutt and Schickan,* 1998]. Several other species exhibit similar behaviors, also apparently linked to feeding efficiency. Most notably, we observed the gorgonocephalid *Astrotoma agassizii* on sponges, rocks (Plate 4*c*), gorgonians, and other species, as examined in detail by Dearborn et al., [1986].

Although these associations may result from direct biological interactions, high correlations may also arise from similar responses of species to environmental factors without interaction among species. Passive suspension-feeders like *Promachocrinus kerguelensis* and

Astrotoma agassizii may benefit from sponges solely via a feeding platform. Fishes (correlated positively with sponges) and other taxa may use complex biogenic habitats for refugia and feeding. Thus, fishes appear to depend not only on the physical effects of "multistoried habitats [*Gutt,* 1996], but also on a related increase in species richness and productivity.

4.3 Oceanographic Versus Seafloor-Habitat Control of Antarctic Megabenthos

Other than the physical effects of ice uplift and iceberg scour [*Lenihan and Oliver*, 1995; *Gutt et al.*, 1996; *Peck et al.,* 1999], links between environmental parameters and the distribution and abundance of benthic megafauna on Antarctic continental shelves are reported to be weak, especially compared with Arctic shelf and slope communities. Starmans et al., [1999] documented strong depth zonation of the megabenthos off Northeast Greenland, including gradients in species composition, abundance, species richness, and evenness, but found much weaker patterns in the Weddell and Amundsen / Bellingshausen Seas. Faunal gradients from shallow suspension feeders to deeper deposit-feeders in the Weddell and Lazarev Seas defined by Gutt and Starmans [1998] were correlated most closely to a combination of geographic gradients, water depth, stone abundance, and phytodetritus.

Our results indicate strong seafloor-habitat control over the spatial distribution of benthic megafauna in the Ross Sea. Whether comparing the level of habitat variability observed among groups of stations clustered by species abundances, or the reverse (the degree of faunal variability among habitat clusters), it is clear that faunal patterns and habitat characteristics are closely linked. This is supported by the much stronger relationship between *Habitat Groups* and Ross Sea megabenthic patterns (Table 9), than between megafauna and *Sediment Groups* or any upper water column factors.

Although our determination of *Habitat Groups* incorporated depth, current speed, and slope of the seafloor, depth was most commonly correlated with faunal distributions. However, depth alone is an unlikely candidate for the regulation of faunal patterns. It is much more likely that factors which covary with depth, such as current speed and sinking organic flux, play a much larger role, since these both influence the level and availability of food for consumers. Levin and Gage [1998] also note the importance of organic input on the structure of continental slope benthos.

The strength and interaction of currents with seafloor relief (estimated partially by seafloor slope) determine whether a site will be dominated by resuspension or deposition, and may determine the availability of food among trophic guilds [e.g. *Genin et al.,* 1992]. Because our instantaneous current measurements fail to characterize the average current regime for each station, it is somewhat surprising that such a strong role of current speed was detected. Likewise, our measure of seafloor slope were very coarse, since they based on the ETOPO5 worldwide bathymetric grid, estimated from sea surface deformation over a grid spacing of 5 min. More accurate measurements of the slope of the seafloor for each video station would have allowed a more rigorous estimation of its link to faunal patterns.

Another weakness of our analysis is the similar pattern of variation for several factors. In particular, depth is correlated with several factors including; current speed ($r=0.55$, $p<0.05$),% nitrogen ($r=0.45$, $p<0.05$), and C/N ($r=0.55$, $p<0.01$). As noted above, the pattern of polynya formation is tied closely to water column productivity. Moreover, areas of high productivity are located mainly over banks and slopes, rather than basins, partially confounding our comparisons of productivity with depth.

4.4 Pelagic—Benthic Coupling

Pelagic and benthic systems can be coupled over spatial scales, temporal scales, or both. The spatial distribution of abundance, biomass, or diversity of benthic assemblages may mimic the pattern of surface productivity in some systems, with little variation in seafloor habitat features. This condition is likely where lateral advection is relatively unimportant to the sinking flux of organic material and the seabed is relatively homogeneous. Seafloor relief, currents, episodic disturbances, and other factors can modify patterns of deposition and/or resuspension of organic material, reducing the spatial conformity between surface productivity and seafloor food availability, leading to decoupling in the spatial patterns of surface and seafloor systems.

Regardless of the strength of spatial coupling between the surface and the seafloor community, benthic and pelagic systems may be linked tightly over temporal scales. Variation in surface productivity over time that leads to seasonal, interannual, or other pulses or organic flux toward the seafloor, are known to result in peaks of benthic secondary production. Responses of the benthic community to organic pulses can include very rapid uptake by bacteria [e.g. *Graf,* 1992] to modified reproductive output and recruitment of megafauna [see review by *Gooday and Turley,* 1989]. Over longer periods, changes in upper ocean production may produce shifts in the composition and distribution of benthic megafauna. We were not able to measure reproduction or recruitment of megafauna in this study, and thus, cannot evaluate the influence of temporal changes in organic flux due to variation in upper ocean production. Smaller size fractions (infaunal polychaetes and crustacea) in the Ross Sea do show evidence of short-term (i.e. interannual) responses to the magnitude of organic carbon input from the Ross Sea polynya [*Barry et al.,* manuscript in preparation, 2002]. Megafaunal patterns observed in the SW Ross Sea during this study were largely unrelated to the distribution of sea ice (*Polynya*) and had a relatively weak link with upper ocean productivity (*Productivity*). Except in very shallow areas, the distribution of sea ice itself is not expected to have a large effect on benthic faunal patterns. However, the role of polynyas in the Ross Sea in enhancing productivity [*Arrigo and McClain,* 1994; *Arrigo et al.,* 1998] may indirectly influence seafloor megafaunal patterns.

Considering that the shelf and slope fauna of the Antarctic beneath ~50-100 m depends entirely on the productivity of the surface waters, failure to detect strong coupling between benthic faunal patterns and upper ocean productivity is somewhat counterintuitive. Productivity in the upper ocean undoubtedly influences the Antarctic benthos—but the local to regional influence of advection and bathymetry redistributes sinking organic debris and obscures the footprint of surface productivity among benthic communities in the Ross Sea. From a temporal perspective, however, secondary production by benthic megafauna (not measured in this study), may be coupled tightly to variation in primary production in the Ross Sea.

Weak coupling in the spatial patterning of surface and seafloor systems observed in the Ross Sea during this study provide partial support for the notion that coupling between upper water column processes and benthic megafaunal patterns of distribution is stronger on Arctic shelves than in Antarctic systems [*Grebmeier and Barry,* 1989; *Dayton et al.,* 1994]. The great depth of the Antarctic continental shelf alone, may promote decoupling between surface and benthic systems, compared to the shallower shelves of the Arctic. In contrast, organic deposition in the vicinity of Arctic polynyas leads to tight trophic coupling between megabenthos and surface waters, as observed near the St. Lawrence Island polynya [*Grebmeier and Cooper*, 1995] and the Northeast Water polynya [*Gallagher et al.,* 1998].

At bathyal depths, however, spatial coupling in surface and seafloor community patterns may depend on local to regional processes, with little difference between polar systems. Resuspension and lateral advection of material in the Ross Sea can transport organic material westward toward deep basins where the organic content of the sediment is highest [*Dunbar et al.,* 1985], leading to nutritional dependence of benthic fauna near McMurdo Sound on primary productivity in the Ross Sea polynya [*Barry,* 1988, *Barry and Dayton,* 1988]. Spatial patterns of Antarctic seafloor communities in more homogeneous, less energetic shelf / slope systems may mimic more closely the pattern of surface production.

Of four factors that could play a strong role in the distribution of benthic megafaunal assemblages in the Ross Sea, seafloor habitat features and processes (*Habitat*, *Sediment*) were linked far more intimately with faunal patterns than upper ocean patterns of polynya formation and productivity. The spatial distribution of banks and basins, coupled with regional currents, define erosive and depositional current regimes across seafloor environments, which, coupled with variation in sinking organic debris from surface waters, determine environmental quality for potential species assemblages. Although the level of primary production in the upper ocean must be a fundamental determinant of benthic community production, patterns of sea ice cover and hydrographic variability play a secondary role in benthic faunal patterns over the deep Ross Sea Shelf.

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