

Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988)

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Abstract—Zooplankton community structure and trophic ecology were investigated in the marginal ice zone of the Southern Scotia Sea during the austral winter of 1988 as part of the AMERIEZ program. In the study area, near the South Orkneys (34–49°W, 57–61.5°S), water emerging from the Weddell Sea mixed with Scotia Sea water to form a complex field of mesoscale eddies and meanders. Three primary zooplankton communities were identified: a shallow cold water assemblage typical of Weddell Sea water; a shallow/upper mesopelagic assemblage of subantarctic species introduced into the southern Scotia Sea with warm core eddies from the Polar Front; and a deep (>400 m) mesopelagic community with circumantarctic species. Zooplankton numerical dominants were cyclopoid copepods (mostly *Oithona* spp.); biomass dominants were four calanoid copepods, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus* and *Metridia gerlachei*. *Calanoides acutus* and *R. gigas* were undergoing winter diapause in the mesopelagic zone (>400 m) whereas *M. gerlachei* and *C. propinquus* were distributed throughout the water column. In the subantarctic eddies *M. gerlachei* was replaced by *M. lucens* as a dominant and *R. gigas* was more abundant than in cold water to the south.

Diet analysis of 35 dominant species revealed five feeding guilds among the zooplankton. One consisted primarily of small herbivorous copepods. Two closely related guilds consisting of copepods, krill and salps were omnivorous, feeding on phytoplankton, protozoans, metazoans and crustacean debris (molts). Two guilds were constituted by predatory copepods and chaetognaths. A sixth group, all copepods, which included important numerical and biomass dominants of the region, was trophically inactive. A comparison of gut fullness between winter 1988 and fall 1986 revealed that all but two of 19 small particle grazing species had significantly less food in their guts in winter. The exceptions were the biomass dominants *C. propinquus* and *M. gerlachei*, which were actively feeding in winter. Phytoplankton biomass was low in winter, averaging two-thirds that in fall.

Several major trophic pathways from phytoplankton through apex predators (birds and mammals) are proposed for winter in the southern Scotia Sea with zooplankton playing a central role in each.

INTRODUCTION

THE Antarctic marginal ice zone traverses an area equivalent in size to continental Antarctica ($\sim 20 \times 10^6 \text{ km}^2$) during its seasonal advance and retreat (ZWALLY *et al.*, 1983; LAWS, 1985). The retreating ice margin is the site of most of the region's yearly production (SMITH and NELSON, 1986; SMITH *et al.*, 1988). Zooplankton life cycles must be cued to the

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ebb and flow of the Antarctic pack ice and the highly pulsed seasonal production of the Antarctic pelagic system in order to grow and reproduce.

An important part of the life history of all Antarctic zooplankton is the strategy used in dealing with the food deprivation associated with the low productivity of the winter months. Potential strategies range from maintaining a normal activity level with no change in distribution or feeding activity to a state of dormancy or diapause (cf. CONOVER, 1988). Insufficient basic data exist on distribution, abundance, and feeding activity of winter Antarctic zooplankton populations to discern what strategies are being employed and how the zooplankton community interacts with the rest of the water column.

Historically, most of our information on oceanic zooplankton in the Southern Ocean has come from cruises in the spring, summer or fall, with sampling during the winter season being much less complete (e.g. FOXTON, 1956; HOPKINS, 1971; VLADIMIRSKAYA, 1978; ATKINSON, 1989). Complimentary winter data are essential if we are to understand seasonal dynamics in the marginal ice zone and develop predictive models for Southern Ocean ecosystem energy flow. As part of the AMERIEZ (Antarctic Marine Ecosystem Research in the Ice Edge Zone) program, sampling was conducted within the Weddell–Scotia Confluence region during the 1988 austral winter (June–August). Sampling was from the R.V. *Polar Duke* in a two-leg cruise which extended from well within the pack ice at 61.5°S to open water at 57°S, and within the longitudinal limits of 34°–49°W. In this paper we examine the community structure and trophic ecology of the zooplankton assemblage(s) in this hydrographically complex area, as well as the role of zooplankton in the pelagic ecosystem. Emphasis is on: (1) community composition in relation to water mass characteristics in the Southern Scotia Sea; (2) trophic structure and activity of the pelagic ecosystem in winter compared to fall; and (3) major trophic pathways through zooplankton to apex predators in the southern Ocean marginal ice zone.

METHODS

Sampling

Microzooplankton (<1 mm) was sampled with 30 l water bottles at the locations shown in Fig. 1. Eleven casts were made with 30 l bottles (137 samples) collecting at the surface, 10, 25, 50, 75, 100, 150, 200, 300, 400, 600, 800 and 1000 m horizons. Occasional samples were taken at depths of 500, 700 and 900 m. Sample water was passed through 30 µm gauze for quantitative sampling of metazoan microzooplankton (<1 mm).

Meso–macrozooplankton (1–20 mm) were collected in vertical series with 1 m², 162 µm mesh opening–closing plummet nets. Standard sampling zones (A–E) were 0–100, 100–200, 200–400, 400–600 and 600–1000 m. Nineteen vertical series were attempted yielding 105 collections. Oblique tows also were made with a collapsible 0.75 m², 162 µm mesh net mounted in the mouth of an opening–closing Tucker trawl. These collections provided supplementary material for diet analysis and information on the distributions of relatively uncommon species. Fifty-four oblique samples were obtained in various depth zones from the surface to 1000 m.

All material was fixed in buffered 10% v/v formalin–seawater and was transferred to 50% isopropanol after weighing. Wet weight biomass was obtained for all net collections. A wet weight (WW) to dry weight (DW) conversion was obtained by drying aliquots from selected samples to constant weight at 60°C.

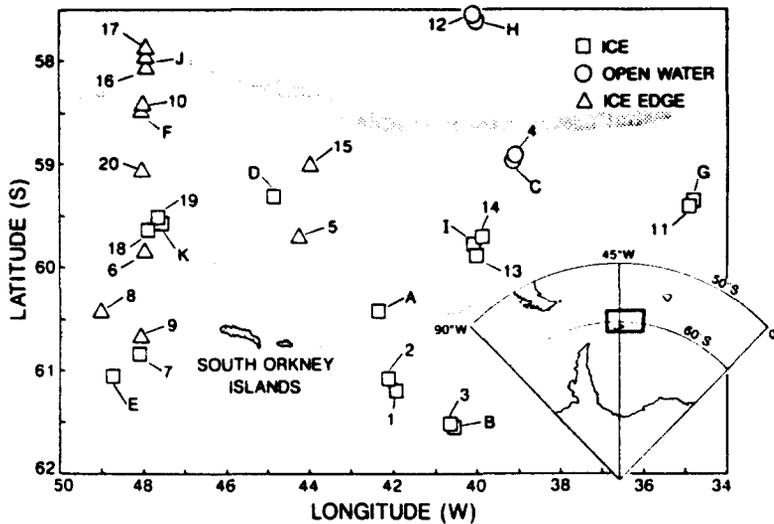


Fig. 1. Plummets (1-20) and bottle cast (A-K) station locations for AMERIEZ III, June-August 1988. Stippling represents approximate northern extent of pack ice during cruise legs I (~60.5°S) and II (~58.5°S).

Abundance data on meso-macrozooplankton were obtained from either entire or aliquoted plummets, depending on sample volume. Taxonomic analysis was to species level. The contribution of individual species to total biomass was estimated by measuring 20-30 specimens, then converting length to weight using size vs DW data (HOPKINS *et al.*, unpublished). Total sample biomass, calculated by summing data for individual species, agreed within $\pm 10\%$ of measured sample dry weights.

Taxonomic analysis of bottle-collected metazoan microzooplankton was less specific than for net-collected meso-macrozooplankton. Counts were of more general taxonomic categories and were taken to genus level only in the case of a few dominant taxa, e.g. *Oithona* and *Oncaea* cyclopoids. A minimum of 10-20 individuals in each category of microzooplankton were measured, with the biomass (DW) of certain groups such as copepodites being estimated with the appropriate size-DW regressions (unpublished AMERIEZ data). Biomass of other small metazoans such as nauplii was estimated by converting body measurements to volume (mm^3) using simple geometric formulas. A 1:1 ratio was assumed in converting mm^3 to mg WW, and DW was estimated at 0.15 WW (LOVEGROVE, 1966).

Data from plummets were analysed using clustering procedures to group samples according to faunal composition similarity (*Q*-mode analysis) as determined by species abundances. Species abundances expressed as no. 1000 m^3 were first root-root ($n^{1/4}$) transformed to reduce weighting of the abundant species (FIELD *et al.*, 1982). Next, a sample pairs-matrix consisting of BRAY and CURTIS (1957) dissimilarity indices was produced using the transformed data. The dissimilarity matrix was then hierarchically clustered using the agglomerative average distance linkage method (SAS PROC CLUSTER; SARLE, 1982). An average temperature and salinity value for each vertical plummets tow was next calculated from CTD data available in MEUNCH *et al.* (1990) so that physical characteristics associated with each of the sample clusters could be defined. The

transformed species abundance data also were ordinated in two dimensions to enable comparison with clustering results and to better graphically reveal spatial relationships between data points. This was done with correspondence analysis, a form of principal components analysis that assesses both sample and species associations (i.e. *Q*- and *R*-mode analysis combined) and is especially applicable to species abundance data (ORTNER *et al.*, 1989; SAS, PROC CORRESP).

Taxonomic diversity of plummet net samples was measured with a variant of the information index (TRAVERS, 1971),

$$D = \frac{1}{N} [\log_2 N - \sum n_i \log_2 n_i],$$

where D is the diversity index; N is the total number of individuals expressed as a percentage (=100%); and n_i is the percentage of the total of an individual species.

Evenness was calculated using PIELOU'S (1966) index (see also TRAVERS, 1971),

$$J = \frac{D}{D_{\max}},$$

where D is the diversity index as determined above and D_{\max} is the maximum possible diversity for the sample.

An information statistic was also used in identifying indicator species of clusters derived from sample faunal composition (*Q*-mode) analysis. This was accomplished with species presence or absence data using,

$$2\Delta I_i = 2(I_{Ti} - I_{1i} - I_{2i}),$$

where ΔI_i is the difference in information value of a species between two clusters; I_{Ti} is the total information content of that species in both clusters combined; and I_{1i} and I_{2i} are the information contents of that species in each of the two clusters (see FIELD *et al.*, 1982 for a more complete explanation). Since $2\Delta I_i$ values have distribution characteristics similar to the F -statistic, a value of $F < 0.05$ ($df = 1$) ≥ 4.0 (i.e. $2\Delta I_i \geq 4.0$) was arbitrarily used to determine indicator species.

Diet

Diet information for 35 of the more abundant zooplankton species was obtained through microscopic examination of gut contents. Food from guts was distributed as evenly as possible in water on a microscope slide, then identified and counted at 400 \times magnification. When feasible, the entire preparation was examined. When large numbers of food items (e.g. 10³ phytoplankton cells) were present, a smaller 60 mm² sub-area of the slide was quantitatively analysed. This protocol was consistent with that used in earlier AMERIEZ studies (HOPKINS and TORRES, 1989) enabling direct quantitative comparisons between the fall 1986 and present winter 1988 data sets.

Diet composition was recorded as presence or absence of a standard set of 20 food categories in each gut. Incidence of each food type in a species sample was calculated as a percentage of the total number of incidences of all food types found in that sample (see HOPKINS and TORRES, 1989). Diet diversity for a species sample was calculated with the diversity index, D , as defined above, but using the food incidence percentages instead of

species abundance percentages. The food incidence percentages were subjected to non-hierarchical cluster analysis (SAS FASCLUS; see also HOPKINS, 1985a, 1987; HOPKINS and TORRES, 1989) to determine zooplankton feeding guilds. Feeding guilds were then ordinated with the canonical analysis component of this same program. The food incidence percentages also were used in determining trophic indices (TI) for each species. This was done by assigning a trophic level value for each type of food eaten, then multiplying by the incidence percentage of that food in the diet. An average trophic value (TI) for each species was then calculated from these products. The arbitrary values for trophic levels for food were: 0 = non-feeding; 1.0 = phytoplankton; 2.0 = protozoans; 2.5 = grazing metazoans; and 3.0 = carnivorous metazoans.

The problem of post-capture feeding in nets was addressed in earlier studies wherein essentially the same field and laboratory techniques were used. For reasons cited in HOPKINS (1985a) and HOPKINS and TORRES (1989) we are convinced that the gut analysis data presented here represent natural diets which were relatively unbiased by net feeding.

RESULTS

Physical environment

The south central Scotia Sea is a hydrographically complex region where cold water emerging from the Weddell Sea mixes with warmer eastward flowing Scotia Sea water. In the winter of 1988 the Scotia Front, where these two water masses join, was a dynamic field of mesoscale eddies/meanders containing warm water from the Polar Front to the north. General trends were that of increased temperature and decreased salinity towards the north and of increased temperature and salinity with depth. Throughout the region the mixed surface layer extended to approximately 100 m. Surface temperatures ranged from near freezing, -1.8°C , in the south to 0°C in the north. Salinity decreased intermittently to the north, but the range was small, 33.9–34.2‰. The compressed transition zone, 50–100 m thick, immediately below the mixed surface layer showed strong salinity, temperature and density gradients. The underlying mesopelagic zone (>200 m) in the southern part of the study area was a mixture of cold Weddell shallow water and Antarctic Circumpolar Water, with temperatures less than 0.5°C . In the mesopelagic zone of the northern sampled area were the anticyclonic warm core eddies and meanders identified by temperatures $\geq 2^{\circ}\text{C}$. The overall surface current direction in the study area was to the northeast. Ice distribution was strongly influenced by local wind conditions but in general advanced from $\sim 60.5^{\circ}$ to 58°S during the period of mid-June to mid-August 1988, with the edge often roughly coinciding with the -1.0°C surface isotherm. For a more complete description of the hydrography of the study area during AMERIEZ 1988 see MUENCH *et al.* (1990).

Abundance, biomass

Typically, copepods were the most diverse group of zooplankton, accounting for over half (88 spp.) of the 160 species identified. A large fraction ($\sim 25\%$) of these were relatively uncommon, deep-dwelling species. Coelenterates ranked second (19 spp.), many of these being uncommon/rare hydromedusae taken in the trawl-mounted plankton nets which

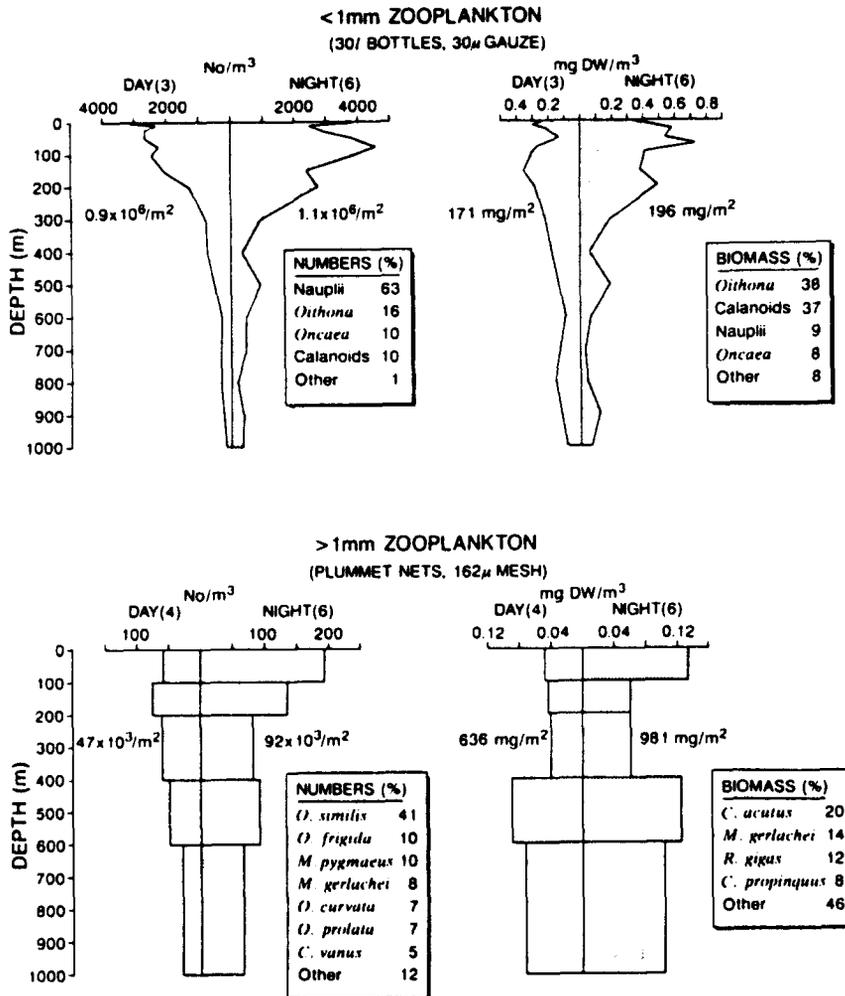


Fig. 2. Vertical distribution of zooplankton biomass in the southern Scotia Sea in winter 1988.

filtered relatively large volumes of water. Other moderately diverse groups in our catches were ostracods (11 spp.), amphipods (11 spp.) and polychaetes (10 spp.).

Vertical distribution data (Fig. 2) show that microzooplankton were most concentrated in the upper 200 m, with a maximum occurring shallower than 100 m. Numerically, the samples were dominated by nauplii (63%), mostly cyclopoid (W. A. CONLEY, personal communication). The remaining fraction was comprised mainly of copepodites, either of cyclopoids (*Oithona* and *Oncaea* = 26%) or of calanoids (10%). Overall numerical and biomass standing stocks of microzooplankton in the upper 1000 m were estimated at $0.9\text{--}1.1 \times 10^6$ individuals m^{-2} and $171\text{--}196$ mg DW m^{-2} . Within these ranges, night values were slightly greater than day values.

Plummet net results also show the numerical importance of small cyclopoids, particularly *Oithona* spp., with *Oithona similis* alone constituting 41% of the >1 mm zoo-

Table 1. Comparison of abundances (no. m⁻²) in the upper 200 m based on 30 l bottle (30 µ gauze) and plummet net (162 µ gauze) catches

	30 l bottle	Plummet net
Nauplii	392,725	327
<i>Oithona</i>	67,766	24 229
<i>Oncaea</i>	5675	581
<i>Microsetella rosea</i>	7083	0
Small calanoids*	29,371	3975

**Ctenocalanus*, *Stephos* and *Microcalanus*.

plankton. While the same genera were numerically dominant in both the bottle and net catches, the bottles gave much higher estimates of microzooplankton abundances, particularly nauplii. Abundance comparisons (Table 1), show that nauplii were underestimated by three orders of magnitude by the plummet nets. Small cyclopoid and calanoid species were also seriously underestimated (3 to >10×) and the small harpacticoid *Microsetella rosea*, moderately abundant in some bottle collections, was not seen at all in the plummet net catches.

In the plummet net samples, all of the major (>5% of total) 0–1000 m biomass components were copepods. The four dominants, *Calanoides acutus*, *Metridia gerlachei*, *Rhincalanus gigas* and *Calanus propinquus*, combined were 54% of the standing stock. Three plummet net series taken within warm core eddies (Stas 12, 16 and 17 in Fig. 1), however, revealed a markedly different composition than that of the other series collected to the south (Fig. 3). In these, *Metridia lucens* replaced *M. gerlachei* as a dominant in the 1–3 mm size fraction and *Thysanoessa macrura* and *Euphausia frigida* replaced *Euphausia superba* (larvae/juveniles) as biomass principals in the 9–15 mm fraction. Also, *Rhincalanus gigas* was proportionately more important in the 5–9 mm fraction of the warm core eddy samples.

The vertical distribution pattern from plummet net samples (Fig. 2) shows a higher biomass concentration in the upper 100 m at night than during the day. Meaningful statistical comparisons of diel vertical differences were precluded, however, by the small number of sample replicates taken within areas of different physical conditions (e.g. ice cover, open water). Regional day–night meso–macrozooplankton numbers and biomass in the 0–1000 m zone were, respectively, 47–92 × 10³ individuals m⁻² and 640–980 mg DW m⁻².

It is apparent from Fig. 2 that much of the zooplankton biomass was deeper than 400 m (see also FOXTON, 1956; HOPKINS, 1971). Mesopelagic (200–1000 m) biomass was largely constituted by the four copepod dominants, *Calanoides acutus*, *Metridia gerlachei*, *Calanus propinquus* and *Rhincalanus gigas*, with *R. gigas* increasing in importance towards the Polar Front. Vertical distributions of these four species exhibited one of two patterns (Fig. 4): a broad distribution throughout the water column, (*M. gerlachei* and *C. propinquus*), or a distribution restricted to mostly deeper than 400 m (*C. acutus* and *R. gigas*). Size data indicate that proportionately more early copepodites were present in the populations of the two broadly distributed species and, in general, the fraction of later copepodites in the population of all four species increased with depth.

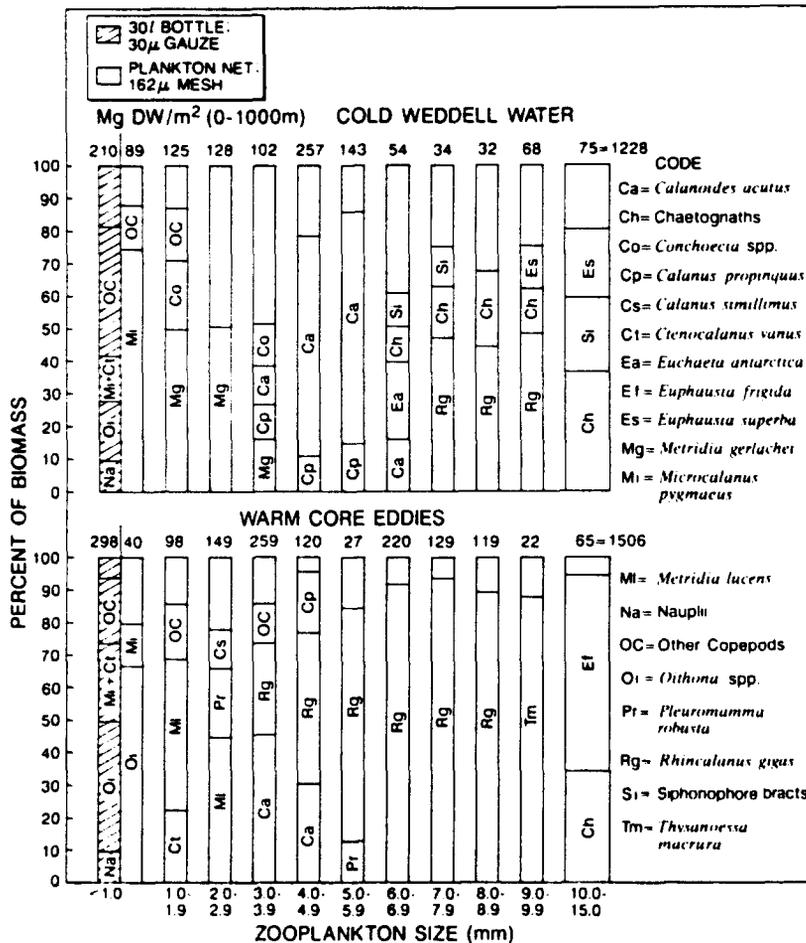


Fig. 3. Size and taxonomic distribution of zooplankton in Weddell Sea water and warm core eddies in the Southern Scotia Sea, winter 1988.

Community structure

Several water masses are juxtaposed and mix in the southern Scotia Sea, consequently biological complexity would be predicted in the study area. Cluster analysis indicates at the 60% dissimilarity level (=0.82 on the average distance between cluster scale), six groups of samples can be identified based on faunal composition (Fig. 5A). The physical volume occupied in the study area by these six sample clusters is shown in Fig. 5B, and physical and biological characteristics defining these clusters are in Table 2.

Cluster I consisted of four shallow (0–100 m) samples from stations centrally located in the study area between the southern and northern ice edge limits encountered during cruise legs 1 and 2. Water in this area was cold and moderately saline. Species diversity was low, though evenness indices were unexpectedly high given the general preponderance of *Oithona similis* in the epipelagic zone. Species of this cluster were those most abundant

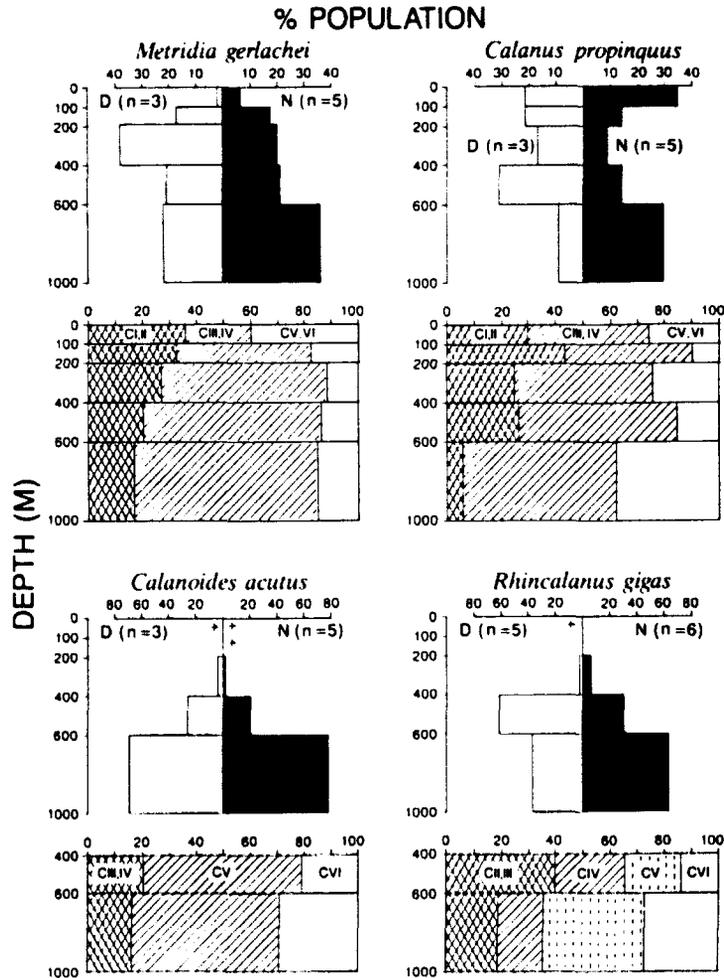


Fig. 4. Vertical distribution and copepodite composition of four biomass dominant copepods in the Southern Scotia Sea, winter 1988.

south of the Polar Front, with little admixture of subantarctic species. Cluster II grouped three samples from the epipelagic zone between 58° and 59.5°S at the eastern edge of the study area, and, as in cluster I, between the southern and northern limits of the ice edge. Physical characteristics associated with this cluster were similar to those for cluster I in that samples were taken from relatively cold, low salinity water ($<34\text{‰}$). Species diversity and evenness indices were quite low, this again largely the result of the relative abundance of *O. similis*. The species defining this cluster were those predominating in cold shallow water south of Polar Front, though species proportions differed from those of cluster I. There was little contribution from subantarctic species.

Cluster III included a group of three epipelagic samples taken near the northern boundary of the study area. Water temperatures here were above 0°C and salinities were low. Species diversity and evenness indices were also low. The salient biological feature of

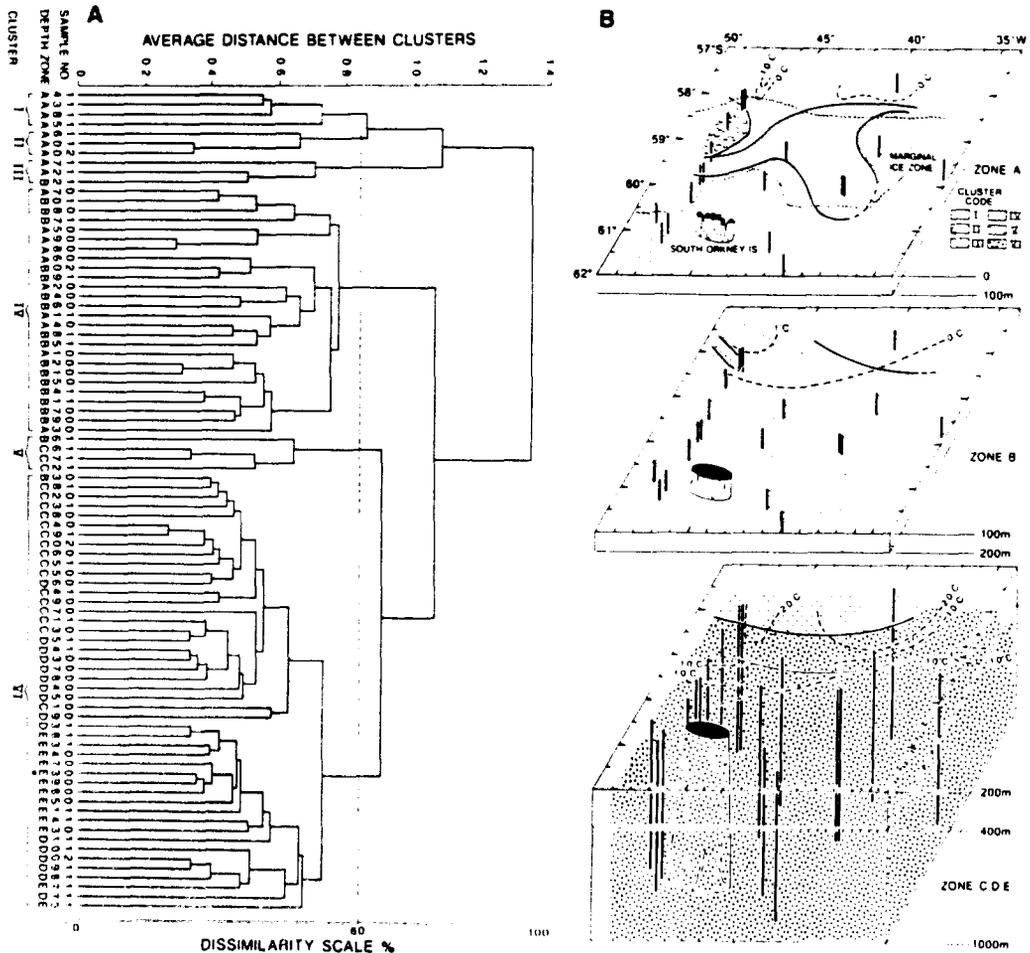


Fig. 5. Cluster analysis dendrogram of plummet net tows based on zooplankton species composition (left) and location of these clusters in a three-dimensional projection of study area (right). Dashed line is selected level of cluster definition. Temperature isopleths for the three water column sections are at 50, 150 and 300 m (from MÜENCH *et al.*, 1990). Vertical bars represent vertical sampling zones of plummet nets at each station. Vertical bars in top section represent the A series of tows; those in the second section, B series; and those in the bottom section, C–E series (see Methods). * = a replicate E series tow taken near Sta. 3.

this cluster was the large component of subantarctic species. Cluster IV, the second largest (26 samples), was also epipelagic, occupying the 0–200 m zone in the southern half of the study area and the 100–200 m layer throughout the central and much of the northern sectors. Diversity and evenness indices were moderately low as in cluster I and cold water species were predominant as in clusters I and II.

Cluster V grouped four shallow mesopelagic (100–400 m) samples from stations located near the northern extent of the study area. Water temperatures and salinities were comparatively high, with the median water temperature, 1.66°C, indicating the presence of Polar Front water. Faunal composition was a mixture of epi/mesopelagic species and

Table 2. Physical and biological characteristics associated with sample clusters (see Fig. 5). Ranges are in parentheses

Cluster no.	No. samples	Primary depth zone (m)	Median temp. (°C)	Median sal. (‰)	Median no. species	Median diversity (D)	Median evenness (J)	Median no. subantarctic spp.	Median no. subantarctic individuals 10 ³ m ⁻³
I	4	0-100	-1.50 (-1.25 to -1.65)	34.19 (34.15-34.19)	16 (7-18)	1.67 (0.92-2.23)	0.53 (0.26-0.59)	0 (0-2)	40 (0-120)
II	3	0-100	-1.00 (-1.25 to +0.30)	33.95 (33.93-34.00)	9 (7-10)	0.52 (0.33-0.56)	0.16 (0.12-0.18)	1 (1-2)	40 (40-120)
III	3	0-100	+0.30 (+0.25 to +0.65)	33.95 (33.95-33.99)	20 (12-22)	1.16 (0.67-1.84)	0.27 (0.19-0.41)	7 (6-8)	11 130 (5540-14 380)
IV	26	0-200	-0.98 (-1.80 to +0.63)	34.29 (34.05-34.48)	18 (11-31)	1.69 (0.49-2.76)	0.39 (0.12-0.59)	0 (0-4)	0 (0-1070)
V	4	200-400	+1.66 (+0.63 to +1.91)	34.51 (34.25-34.57)	27 (24-29)	2.71 (1.15-2.79)	0.56 (0.25-0.59)	5 (3-6)	3410 (5540-14 380)
VI*	46	200-1000	+0.25 (-0.31 to +1.81)	34.63 (34.48-34.69)	35 (24-62)	3.11 (2.04-3.96)	0.59 (0.43-0.70)	1 (1-5)	3 (0-11 135)

*Physical data not available for 12 samples in Cluster VI.

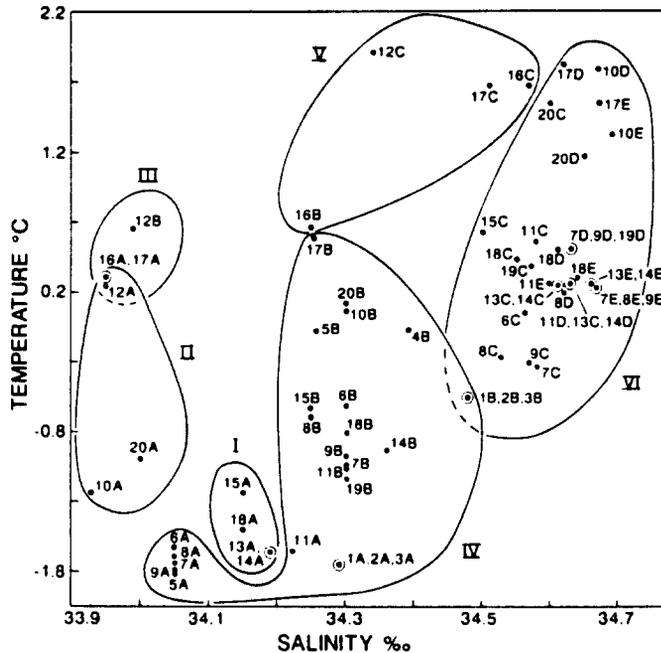


Fig. 6. Distribution of plummet net tows with respect to average temperature and salinity values recorded for each vertical tow zone (see Methods). Samples grouped by cluster analysis are encircled (see Fig. 5).

warm water subantarctic species. The latter were introduced with warm core eddies and meanders from the Polar Front. This mixing of faunas, along with the reduced dominance of *O. similis* in the mesopelagic zone, yielded high diversity and evenness indices. Cluster VI, the largest (46 samples), was entirely mesopelagic and occupied most of the 200–400 m and all of the 400–1000 m volume of the study area. Water temperatures were mostly above zero and salinity values were consistently high (>34.5‰). Species diversity was the greatest of any cluster, which is attributable to the large number of circumantarctic copepod species inhabiting the mesopelagic zone (see VERVOORT, 1957; HERON, 1977; PARK, 1978, 1980, 1982). Diversity and evenness indices were high as well. Subantarctic species were encountered in cluster VI samples from the northern half of the study area, but with one or two exceptions, their populations were usually small. Also encountered in these samples were dominant biomass species (e.g. *Calanoides acutus*, *Rhincalanus gigus*) which overwinter in the mesopelagic zone.

The relationship of the six sample clusters to temperature and salinity (Fig. 6) shows a rather clear separation of station clusters on the basis of these two key physical properties. The plot helps explain the faunal groupings resulting from cluster analysis in that it demonstrates the relationship of faunal composition to water types in the southern Scotia Sea. Ordination of sample data through correspondence analysis also indicates the spatial distance in two dimensions between individual samples based on species composition (Fig. 7). Along the horizontal axis (Dimension 1) is a depth principal component as apparent from the occurrence of the shallow zone series A and B samples on the right side of the plot and the concentration of the deeper series C, D and E in the left half of the figure. The

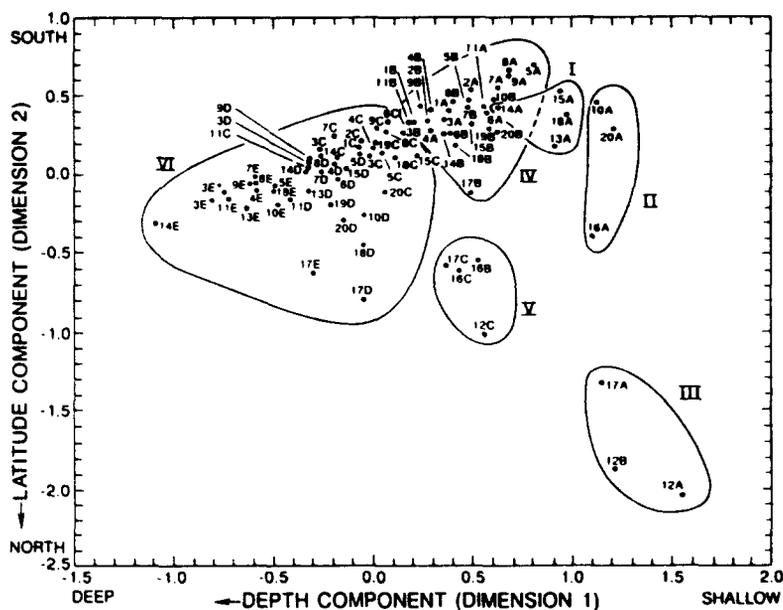


Fig. 7. Plot of correspondence analysis of species composition of plummet net tows. Samples grouped by cluster analysis (see Fig. 5) are encircled.

vertical (Dimension 2) principal component is latitude, with most of the samples rich in subantarctic species occurring in the bottom two-thirds of the figure. The sample groups derived from cluster analysis (encircled) show little overlap. These two analytical procedures then, are complementary and together reveal the spatial and therefore faunal relationships among the six clusters.

Indicator species for the six clusters based on $2\Delta I_1$ values (Table 3) show that clusters III, IV and VI have the clearest definition. Clusters III and IV are shallow clusters centered at opposite ends of the study area (III to the north and IV to the south), and cluster VI is the deepest. Clusters I and II in the transitional ice zone and V in the upper mesopelagic zone in the north appear to be admixtures of the faunas found in the "core" clusters (III, IV and VI) and consequently were less defined and separable by indicator species. Cluster III, rich in subantarctic species, had three or four indicator repeats out of five possible cluster pairings of *Pleuromamma robusta*, *Conchoecia elegans* and *Euphausia frigida*. Cluster IV, containing samples from cold shallow waters having a large Weddell Sea component, had the cold water dominant *Metridia gerlachei* as an indicator in four cluster pairings. Cluster VI had the mesopelagic species *Oithona frigida*, *Oncaea prolata*, *Scaphocalanus vervoorti* and *Pelagobia longicirrata* as indicators in three or four cluster pairings. Many of the less common mesopelagic species probably would have been excellent indicators for this cluster as well had our deep plummet net tows sampled larger volumes of water.

Feeding

Through cluster analysis, 35 of the most abundant species were grouped into five guilds (Table 4). Guild one grouped nine species, eight small to medium sized copepods and an

Table 3. Indicator species of clusters from Fig. 5 dendrogram. Numbers in parentheses are number of samples for clusters A and B in which species occur. The minimum information ($2\Delta I$) cut-off value above which a species is considered a cluster indicator is 4.0 (see Methods)

Cluster pair A,B	No. samples in A,B	Indicator species		Range of $2\Delta I$, values for A,B ≥ 4.0
		A	B	
1,2	4,3	—	—	(all <4.0)
1,3	4,3	Tm(4,0)	Cs(0,3), Pr(0,3) Ce(0,3)	4.2
1,4	4,26	—	Mp(0,26), Eh(0,21), Oc(0,20)	4.4–15.1
1,5	4,4	Sl(4,0), Mg(4,0)	Rg(0,4), Sg(0,4), Oc(0,4), Mp(0,4), Eh(0,4), Ho(0,4), Sm(0,4), Op(0,4)	4.8
1,6	4,46	—	Of(0,46), Oc(0,45), Eh(0,45), Op(0,45), Oa(0,44), Sv(0,43)	8.0–12.1
2,3	3,3	Tm(3,0)	Ml(0,3), Pr(0,3), Ce(0,3), Ef(0,3)	6.5
2,4	3,26	Cl(3,0)	Mg(1,26), Ch(1,26), Eh(0,21)	4.3–8.4
2,5	3,4	—	Ci(0,4), Oc(0,4), Mp(0,4), Eh(0,4), Of(0,4), Ml(0,4), Ho(0,4)	4.2
2,6	3,46	—	Of(0,46), Oc(0,45), Eh(0,45), Op(0,45), Pl(0,44), Ci(0,43), Mp(0,43), Sv(0,43)	6.2–9.8
3,4	3,26	Ef(3,2), Ce(3,1), Cs(3,0), Cl(3,0), Pr(3,3), Ea(2,0), Lr(2,0)	Mg(1,26), Mp(1,26)	4.7–8.4
3,5	3,4	—	—	(all <4.0)
3,6	3,46	Cl(3,4), Ef(3,4), Ea(2,0), Lr(2,0), Ce(3,7)	Ha(0,44), Pl(0,44), Sv(0,43), Of(1,46), Sm(0,40), Ca(0,39), Sp(0,39)	4.5–6.9
4,5	26,4	Mg(26,0)	Rg(1,4), Cs(0,3), Ce(1,3)	4.6–15.1
4,6	26,46	—	Op(2,45), Sp(1,39), Sm(2,40), Ck(0,34), Sa(0,32), Cp(1,34), Rg(1,33)	15.8–30.1
5,6	4,46	Sg(4,7), Ea(2,0), Ls(2,0)	Ha(0,44), Mg(0,43), Pl(1,44), Sv(1,43), Tx(0,34), Cp(0,34), Ck(0,34)	4.3–8.8

Species code: Ca = *Calanoides acutus*; Ce = *Conchoecia elegans*; Ch = *Conchoecia hettacra*; Ci = *Conchoecia isocheira*; Ck = *Conchoecia skogsbergi*; Cl = *Clausocalanus laticeps*; Cp = *Conchoecia antipoda*; Cs = *Calanus similimus*; Ea = *Euaetideus australis*; Eh = *Eukrohnia hamata*; Ef = *Euphausia frigida*; Ha = *Heterorhabdus austrinus*; Ho = *Haloptilus oxycephalus*; Lr = *Limacina retroversa*; Mg = *Metridia gerlachei*; Ml = *Metridia lucens*; Mp = *Microcalanus pygmaeus*; Oa = *Oncaea antarctica*; Oc = *Oncaea curvata*; Of = *Oithona frigida*; Op = *Oncaea prolata*; Pl = *Pelagobia longicirrata*; Pr = *Pleuromamma robusta*; Rg = *Rhincalanus gigas*; Sa = *Spinocalanus abyssalis*; Sg = *Sagitta gazellae* (juv.); Sl = *Stephos longipes*; Sm = *Sagitta marri*; Sp = *Spinocalanus abyssalis* v. *pygmaeus*; Sv = *Scaphocalanus verwoortii*; Tm = *Thysanoessa macrura*; Tx = *Typhloscolex mulleri*.

alciopid polychaete (*Rhynchonerella bongraini*), which were small particle grazers having diets of low diversity ($D = 1.1$), predominately phytoplankton and low trophic index values ($TI = 1.0-1.4$). The 13 species in guilds 2 and 3, also mostly copepods (10 spp.), were more omnivorous, having protozoans, some metazoans and crustacean debris (euphausiid molt debris; guild 2) in their diets. Canonical analysis (Fig. 8) shows these two guilds were spatially nearest neighbors and can perhaps be considered as two subunits of one large cluster. Diets in these guilds were relatively diverse, ($D = 2.4-2.7$), and trophic indices were intermediate to moderately high ($TI = 1.3-2.3$). Guild 4 was comprised of three copepod and two chaetognath species which were carnivorous and essentially predators on small copepods. Diet diversity in this guild was intermediate in range ($D = 1.1-2.4$), whereas trophic indices were high, ($TI = 2.3-2.8$). Guild 5 consisted of a single carnivorous copepod, *Haloptilus ocellatus*, which mostly ingested polychaetes and copepods. A sixth group not included in the cluster analysis was made up of seven species that had little or no food in their guts and were classified as trophically inactive. In this important group were four small cyclopoids, three of which were numerical dominants (*Oithona similis*, *O. frigida*, *Oncaea curvata*), two calanoid biomass dominants (*Calanoides acutus*, *Rhincalanus gigas*) and a mesopelagic carnivorous copepod (*Heterorhabdus farrani*; see HOPKINS, 1985a). All totalled, the 35 species examined for diet analysis accounted for 97% of the numbers and 86% of the biomass of the plummet net zooplankton samples.

DISCUSSION

Standing stocks

Net-caught biomass in the Weddell-Scotia Confluence region exhibited the general winter-time vertical distribution pattern evident in earlier studies (e.g. FOXTON, 1956;

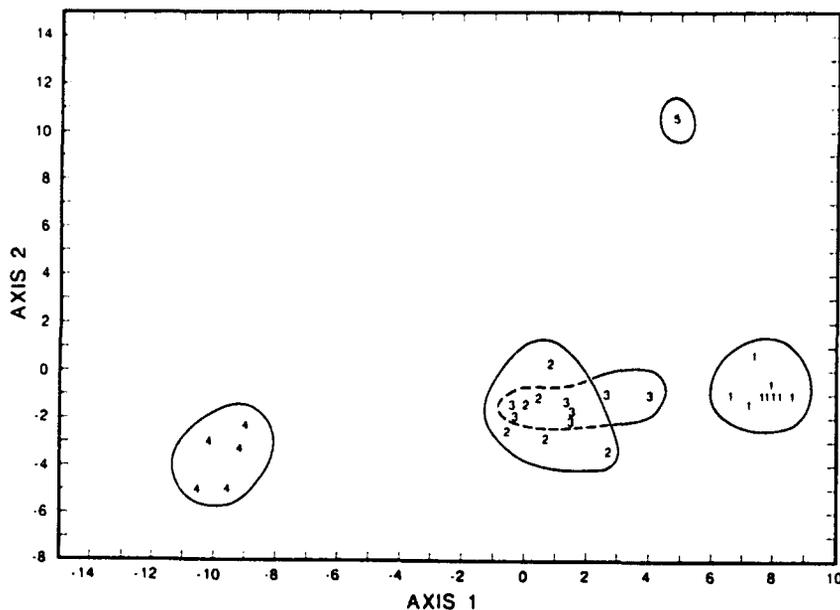


Fig. 8. Two-dimensional plot of species relationships based on diet composition. Guilds were determined by cluster analysis (see Table 4).

Table 4. Feeding groups based on cluster analysis. Median size and size range of species analysed in each cluster in mm; proportions of principal food types are expressed as median and range of food incident per cents in diets (see Methods); D and TI values are medians and ranges for diversity and trophic indices, respectively

<p>Guild 1</p> <p>Size: 2.0 (0.6–3.0)</p> <p>Phytoplankton: 86 (72–100)%</p> <p>Protozoans: 11 (0–27)%</p> <p>Metazoans: 3 (0–17)%</p> <p>D = 1.1 (0–2.2)</p> <p>TI = 1.2 (1.0–1.4)</p> <p><i>Calanus simillimus</i></p> <p><i>Ctenocalanus vanus?</i></p> <p><i>Metridia curticauda</i></p> <p><i>Metridia lucens</i></p> <p><i>Microcalanus pygmaeus</i></p> <p><i>Oncaea prolata</i></p> <p><i>Rhynchonerella bongraini</i></p> <p><i>Spinocalanus abyssalis</i></p> <p><i>Spinocalanus abyssalis</i> var. <i>pygmaeus</i></p>	<p>Guild 4</p> <p>Size: 8.4 (1.1–16.0)</p> <p>Phytoplankton: 4 (0–9)%</p> <p>Protozoans: 1 (0–4)%</p> <p>Metazoans: 95 (91–100)%</p> <p>D = 1.9 (1.1–2.4)</p> <p>TI = 2.6 (2.3–2.8)</p> <p><i>Euchaeta antarctica</i></p> <p><i>Eukrohnia hamata</i></p> <p><i>Heterorhabdus austrinus</i></p> <p><i>Oncaea antarctica</i></p> <p><i>Sagitta marri</i></p>
<p>Guild 2</p> <p>Size: 8.9 (3.3–37.0)</p> <p>Phytoplankton: 31 (20–49)%</p> <p>Protozoans: 30 (5–47)%</p> <p>Metazoans: 24 (0–52)%</p> <p>Euphausiid debris: 15 (7–37)%</p> <p>D = 2.7 (2.2–3.0)</p> <p>TI = 1.9 (1.3–2.3)</p> <p><i>Actideopsis minor</i></p> <p><i>Euchirella rostromagna</i></p> <p><i>Euphausia superba</i> (juv.)</p> <p><i>Gaetanus tenuispinus</i></p> <p><i>Racovitzanus antarcticus</i></p> <p><i>Scolecithricella cenotelis</i></p>	<p>Guild 5</p> <p>Size: 8.0</p> <p>Phytoplankton: 8%</p> <p>Metazoans: 92%</p> <p>D = 2.0</p> <p>TI = 2.5</p> <p><i>Haloptilus ocellatus</i></p> <p>Trophically inactive</p> <p><i>Calenoides acutus</i></p> <p><i>Heterorhabdus farrani</i></p> <p><i>Oithona frigida</i></p> <p><i>Oithona similis</i></p> <p><i>Oncaea curvata</i></p> <p><i>Oncaea englishi</i></p> <p><i>Rhincalanus gigas</i></p>
<p>Guild 3</p> <p>Size: 2.1 (1.4–49.0)</p> <p>Phytoplankton: 48 (34–60)%</p> <p>Protozoans: 21 (0–40)%</p> <p>Metazoans: 29 (9–46)%</p> <p>Euphausiid debris: 2 (0–18)%</p> <p>D = 2.4 (1.7–3.2)</p> <p>TI = 1.7 (1.5–1.9)</p> <p><i>Calanus propinquus</i></p> <p><i>Metridia gerlachei</i></p> <p><i>Pelagobia longicirrata</i></p> <p><i>Pleuromamma robusta</i></p> <p><i>Salpa thompsoni</i></p> <p><i>Scaphocalanus verwoorti</i></p> <p><i>Scolecithricella minor</i></p>	

HOPKINS, 1971; VLADIMIRSKAYA, 1978) where much of the biomass resides below 400 m. This contrasts with distributions in the austral summer when biomass is concentrated in the epipelagic zone (FOXTON, 1956). Much of the biomass in the deeper layers in winter is constituted by four copepod species, *Metridia gerlachei*, *Calanoides acutus*, *Calanus propinquus* and *Rhincalanus gigas*. VORONINA *et al.* (1978), MARIN (1988), SCHNACK-SCHIEL *et al.* (1991) and ATKINSON (1991) have shown that these species, especially the latter two, have different annual vertical migration cycles, the timing of which is species- and/or water mass-dependent. Sampling data from this study is consistent with the two contrasting winter strategies suggested for these species (see MARIN, 1988; SCHNACK-SCHIEL *et al.*, 1991). *Calanoides acutus* and *Rhincalanus gigas* were undergoing winter diapause during which the majority of the population had migrated below 400 m and showed no sign of feeding activity. Copepodite distribution (Fig. 4) indicated that the population, as assessed by 162 μ mesh nets, was composed largely of CIV–VI stages, suggesting the absence of recent egg release. We did find, however, moderate percentages of male *Calanoides acutus* (up to 18% of the population in one sample) which supports the suggestion of MARIN (1988), SCHNACK-SCHIEL *et al.* (1991) and ATKINSON (1991) that this species mates in winter.

Metridia gerlachei and *Calanus propinquus*, in contrast to the other two species, were broadly distributed throughout the upper 1000 m, with a large fraction of their populations occurring shallower than 400 m. These two species were actively feeding, and recent reproduction was evident from the moderately high percentages of CI–II stages in the population, particularly in the epipelagic zone.

Metazoan microzooplankton, as assessed from bottle catches, showed a different vertical distribution pattern than the meso–macrozooplankton in that both numbers and biomass were concentrated within the upper 200 m. The numerical and biomass dominants of the microzooplankton were cyclopoids and their nauplii, particularly the genus *Oithona*. This genus was also numerically dominant in plankton net collections, as has been previously reported by ourselves and others investigating Southern Ocean zooplankton (e.g. JAZDZEWSKI *et al.*, 1982; CHONJACKI and WEGLENSKA, 1984; SCHNACK *et al.*, 1985; HOPKINS, 1985b; FRANZ, 1988; HOPKINS and TORRES, 1988). The abundance of cyclopoid nauplii in the bottle collections indicates reproductive activity in this group during the winter season. Winter-time reproduction is not easily explained in light of the fact that chlorophyll at most stations was at trace level concentrations (0.07–0.17 mg m⁻³ in upper 150 m) and the principal cyclopoid species, *Oithona similis*, *O. frigida* and *Oncaea curvata*, were trophically inactive. Also, no cyclopoid egg sacs were encountered in our collections. Nevertheless, support for the possibility of winter-time reproduction comes from FRANSZ'S (1988) observation that *Oithona* appears to reproduce prior to the spring bloom when food concentrations are low.

Zooplankton standing stock in the Weddell–Scotia Confluence region is comparable to what we have recorded for the northwestern Weddell Sea (HOPKINS and TORRES, 1988) and is equivalent to that in low latitude areas, oligotrophic boundary currents in particular (HOPKINS, 1971, 1982). The area sampled is similar to one of the three major types of habitat south of the Polar Front described by HEMPEL (1985), this particular one being the ice-free oceanic habitat dominated by herbivorous copepods, salps (seasonally) and small euphausiid species. *Euphausia superba*, the largest euphausiid species, is also an important component of the system in the Weddell–Scotia Confluence region, but its biomass contribution is difficult to assess. In the upper 1000 m water column its biomass is matched by midwater fishes and by gelatinous “megaplankton” (i.e. large salps, ctenophores,

scyphomedusae; LANCRAFT *et al.*, 1991), and except when occasional patches were sampled, *E. superba* did not dominate our plummet net catches. Our nets, though, underestimated krill biomass, especially in the pack ice because a substantial portion of larvae and juveniles are associated with the ice under-surface in winter (DALY, 1990). The role of krill, then, in the open ocean ecosystem in this region remains to be defined.

Community structure

Zooplankton diversity, while not comparable to that in low latitude systems (HOPKINS, 1985b), is moderately high in the southern Scotia Sea. This is a consequence of the area being an ecotone where several water masses, each with its representative fauna, are mixing, and because sampling extended well into the mesopelagic zone. The southern extent of the study area was characterized by water with major faunal contributions from the Weddell Current, which is populated by cold water species predominant south of the Polar Front. Towards the northern extent were warm core eddies containing water from the Polar Front which introduced subantarctic species. Underlying these was a highly diverse, deep mesopelagic fauna. These three communities were discernible from both cluster analysis and ordination through correspondence analysis (Figs 5 and 7). They were most clearly represented in sample clusters III, IV and VI, these being the most consistently separable from other cluster units by indicator species (Table 3).

The relationship (Fig. 9) of cluster physical parameters (median values) to most probable source areas (e.g. Weddell Sea; subantarctic/Polar front) reflects the extensive mixing that occurs in the southern Scotia Sea and suggests that the faunas defined by most of the clusters were composites from several source areas. Of the three clusters (I, II and IV) with shallow cold water characteristics, only cluster I falls within the N.W. Weddell Sea salinity-temperature envelope. Median values for clusters II and IV lie above the envelope and are representative of Weddell Sea water that has mixed with southern Scotia Sea water. Species composition in these three clusters is little different from that in the N.W. Weddell Sea (HOPKINS and TORRES, 1988) because the predominant epipelagic (0–200 m) species south of the Polar Front have broad latitudinal distributions. It is the proportions of the dominant species common to the area that separates these clusters. The proportions vary between clusters because of the mixing of Weddell Current water with different sources of Scotia Sea water or possibly from mixing with a common source of Scotia Sea water, but with the extent of mixing varying geographically.

The other "source" water curve in Fig. 9 is from the Scotia Sea Polar Front. The water column at this location generally has much warmer temperatures, especially in the epipelagic zone and below 500 m, than do the stations from which cluster III and V samples were taken, these having sampled the warm core intrusions. The location of these two clusters with respect to the Polar T-S curve (from PATTERSON and SIEVERS, 1980) indicates that warm Polar Front water had mixed to some degree with cooler Scotia Sea water from south of the Polar Front. Admixture of Antarctic with subantarctic species, then, would be expected, which is the case. Also, cluster VI, the largest mesopelagic cluster underlying the study area, falls between the Polar Front T-S curve and the NW Weddell envelope (Fig. 9), which is indicative of a mixed water mass and fauna. Samples in this cluster, in varying proportions, had elements of the circumpolar mesopelagic fauna, many species of which extend south into the Weddell Sea (HOPKINS and TORRES, 1988), the subantarctic

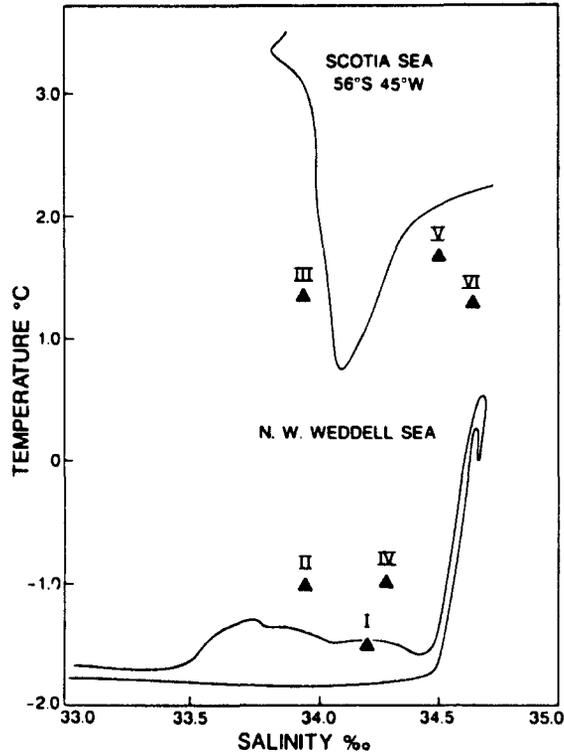


Fig. 9. Plot of median temperature and salinity characteristics for each sample cluster (see Table 2). Included as reference points are a T-S envelope for the NW Weddell Sea based on AMERIEZ II, fall 1986 data (MUENCH *et al.*, 1990) and a T-S curve from the Polar Front (PATTERSON and SIEVERS, 1980).

fauna and the shallow cold water fauna prevalent south of the Polar Front. Given that the southern Scotia Sea is a dynamic region of mixing and that the geographic and depth distributions of many of the abundant species are broad (e.g. *Calanoides acutus* and *Rhincalanus gigas* occur on both sides of the Polar Front; KANAYEVA, 1968; ATKINSON, 1991), it is difficult to identify precisely geographical source areas for the zooplankton sampled at each station. MUENCH *et al.* (1990) note that potentially all Bransfield Strait, Bellingshausen Sea, Antarctic Circumpolar and Western Weddell water types can occur in the southern Scotia Sea, each with its own physical and presumably, biological signatures.

The effect of ice cover on community structure in the south Scotia Sea in winter is not clear. The extent of ice cover changed significantly during each cruise, and, at any one location, could vary widely over the period of a day because of local wind conditions. Ice, then, was often moving at a faster rate than the currents transporting the plankton. Except for the increased abundances of a few ice-habitat species (e.g. *Stephos longipes*, tishid harpacticoids, larval and juvenile *Euphausia superba*; see LANG, 1948; KACZMARUK, 1983; DAHMS and DIECKMANN, 1987; HOPKINS and TORRES, 1988) in shallow samples taken near ice, no major effect of ice cover on zooplankton community structure was discernible, especially when considering a 0–1000 m water column.

Trophic structure

Trophic activity in the pelagic ecosystem of the Weddell–Scotia Confluence region was lower in the winter than in fall, the only other season for which feeding data are available. A statistical comparison of zooplankton gut fullness between the fall of 1986 and winter of 1988 (Table 5) shows that all but two of 19 small particle grazers (herbivorous and omnivorous grazers) had significantly less food in their digestive tracts in winter. Seven of the 19 species had little or no food in their guts at all in winter and were considered trophically inactive (none were trophically inactive in fall). This group included most of the numerical and biomass dominants of the region. The two exceptions were *Calanus propinquus* and *Metridia gerlachei*, biomass dominant species, which were well represented in the upper 200 m and actively feeding. Of the four species of carnivorous zooplankton (two copepods; two chaetognaths) tested, two had less food in their guts in winter. Among the larger midwater fauna, *Euphausia superba* and the two dominant micronektonic fishes, *Electrona antarctica* and *Bathylagus antarcticus*, all contained less food in winter (LANCRAFT *et al.*, 1991). The above comparisons all point to reduced feeding activity in the pelagic ecosystem in winter, especially at lower trophic levels. This would be expected considering that wintertime phytoplankton standing crop based on chlorophyll concentrations, was low and averaged only two-thirds of that in fall (Table 5). In spite of the limited winter phytoplankton availability, some of the epipelagic production and/or ice-melt released phytoplankton does reach mesopelagic layers. This can be in the form of unincorporated cells or perhaps phytoplankton aggregated in fecal pellets or marine snow. Evidence for transport out of the epipelagic zone is the occurrence of phytoplankton and protozoans in guts of mesopelagic species, e.g. *Spinocalanus abyssalis*, *Euchirella rostrata*, *Gactanus tenuispinus* and *Aetideopsis minor* (see Table 4).

The dominant zooplankton species in the southern Scotia Sea were grouped into five feeding guilds (Table 4). As in our previous studies on Southern Ocean pelagic food webs (HOPKINS 1985a, 1987; HOPKINS and TORRES, 1989), most of the species were small particle grazers occurring in guilds 1, 2 and 3. The trophically inactive species, on the basis of

Table 5. Gut content comparisons of zooplankton taken in the marginal ice edge zone in fall 1986 and winter 1988. *t*-tests: $P < 0.05$. Chlorophyll averages calculated from unpublished AMERIEZ II, III data reports by Smith, and Smith and Cota

No. species with less food in guts in winter	No. species with less food in guts in fall	No. species showing no differences in gut fullness
Small particle grazers		
17	0	2
Carnivores		
2	0	2
Chl mg m^{-3} (0–150 m):		
Fall	0.17	
Winter	0.11	

earlier work (op. cit), would be included in these guilds in other seasons. Trophic information thus far indicates relative consistency in geographic and seasonal patterns in diets of many southern ocean species (op. cit.), with variations in food percentages probably being regulated by seasonal and geographic resource availability. Also apparent is the role of omnivory in zooplankton trophic dynamics. Most of the small particle grazers examined were omnivorous to some degree, with this being especially evident in guild 2 and 3 species in the present study. An abundant component in diets of these omnivorous species is protozoans. This points to the potentially important role of metazoan zooplankton in the Southern Ocean microbial loop. Lacking, however, is quantitative information on the grazing impact of metazoan zooplankton on microheterotroph populations.

In order to gain a broader perspective of food web structure in the Weddell–Scotia confluence region, cluster analysis was rerun (Fig. 10) to include winter diet information for principal micronektonic fishes and invertebrates. Dominant sea bird, mammal and cephalopod (principal species in sea birds diets) predators censused during the winter 1988 cruises (AINLEY *et al.*, 1991; RIBIC *et al.*, 1991) are included in the trophic scheme as well. Diet information on micronekton and the top predators was obtained from LAWS (1985), DOIDGE and CROXALL, 1985, BUSHUEV (1986), ICHII (1990), KLAGES and COCKCROFT (1990), AINLEY *et al.* (1991) and LANCRAFT *et al.* (1991), and the zooplankton feeding guilds are identical to those in Table 4.

What emerges from our results and the sources cited above are three major trophic pathways to dominant apex predators in winter:

(1) phytoplankton + protozoans → copepods (the four biomass spp.; only two actively feeding) + krill → *Electrona antarctica* → flying seabirds (five petrels, one fulmar);

(2) phytoplankton + protozoans → krill → mammals (crabeater and fur seals, minke whale), and;

(3) phytoplankton + protozoans → krill → cephalopods (3 spp.) → penguins (adelie, emperor) + fur seal.

AINLEY *et al.* (1991) find that the midwater fish *Electrona antarctica* is a more important prey item than *Euphausia superba* for flying seabirds, a result that runs counter to the usual perception of krill as the overwhelmingly dominant prey item in the Southern Ocean ecosystem. Clear definition of the third pathway is lacking because of the inadequacy of sampling techniques: birds catch squids much more efficiently than do trawls. The few available data indicate that Southern Ocean squids are predators on krill (e.g. LAWS, 1985; NEMOTO *et al.*, 1985) and on smaller zooplankton (HOPKINS, 1985a).

The role of zooplankton in each of the above pathways is crucial in converting phytoplankton and microheterotrophs into larger organic units, which can be effectively utilized by micronekton. In turn, micronektonic fishes, cephalopods and krill are the major prey of apex predators in the northern Weddell–southern Scotia Sea region. The marginal ice zone is the center of interaction and therefore carbon flow between water column biota and top predators in the Antarctic pelagial (AINLEY and DEMASTER, 1990). The ice margin may be viewed as a magnet for increased abundance of apex predators and a generator for increased carbon flow through the trophic pyramid that shifts seasonally with the advance and retreat of the Antarctic pack ice.

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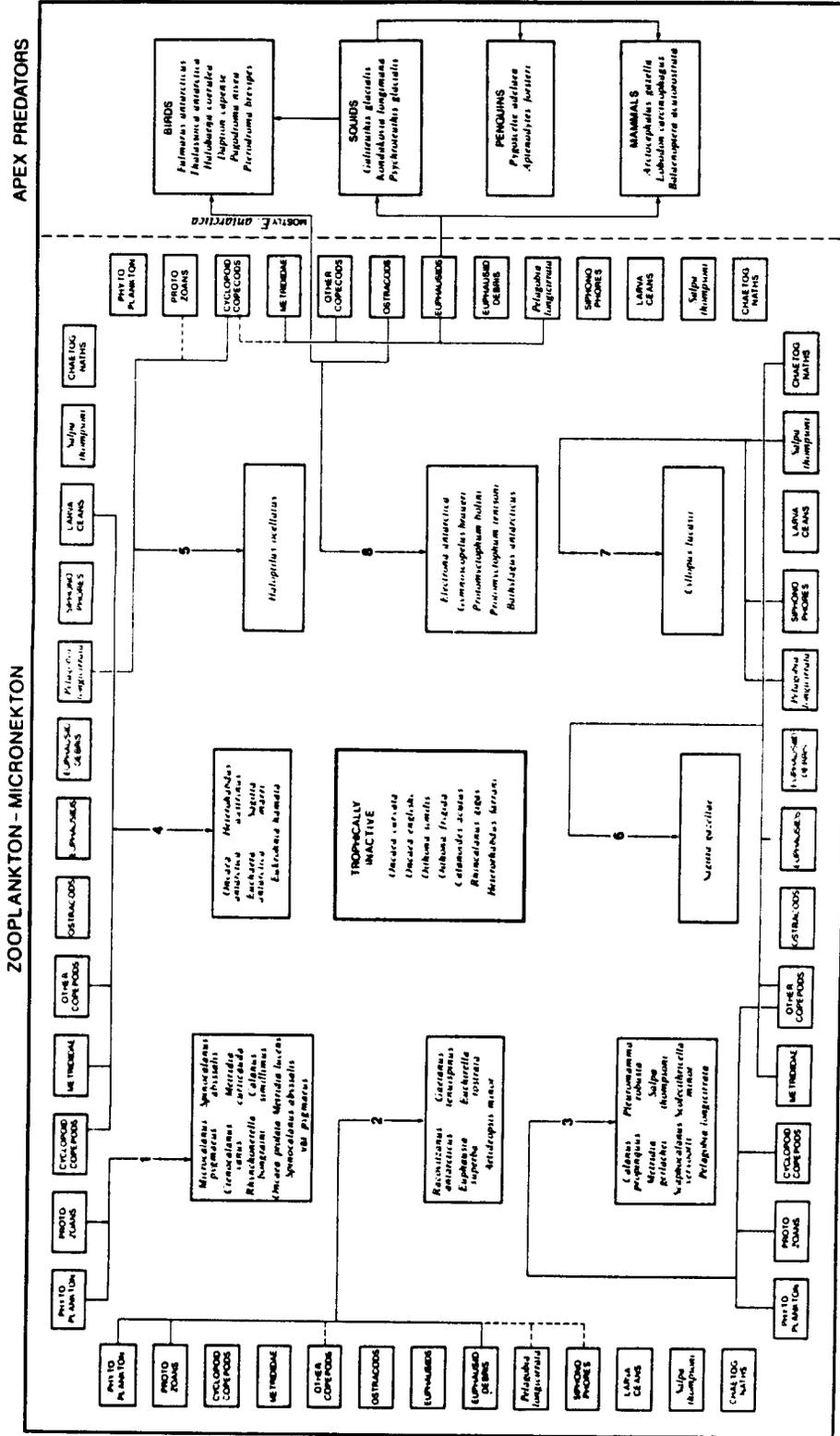


Fig. 10. Food web in the marginal ice zone of the Weddell-Scotia Sea Confluence region, austral winter 1988.

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