

Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983)

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Abstract. The structure of the food web was investigated in open waters adjacent to the marginal ice zone in the southern Scotia Sea in spring 1983. Diets were defined for dominant zooplankton, micronekton, and flying seabird species and then aggregated by cluster analysis into feeding groups. Most zooplankton were omnivorous, feeding on phytoplankton, protozoans, and in some cases, small metazoans (copepods). Only two species were found to be exclusively herbivorous: *Calanoides acutus* and *Rhincalanus gigas*. Micronekton were carnivores with copepods being the dominant prey in all their diets. The midwater fish *Electrona antarctica* was the dominant food item in seven of the nine seabird species examined. Cephalopods, midwater decapod shrimps and carrion were also important in the diets of a few seabird species. Comparison (cluster analysis) of diets in spring with other seasons (winter, fall) indicated that over half the species examined (18 of 31) had similar diets in all seasons tested. The significant intraspecific shifts in diet that did occur were attributable to regional, seasonal, and interannual effects. A scheme is presented that describes the major energetic pathways through the open water ecosystem from phytoplankton to apex predators. At the base are phytoplankton and protozoans which are the principal food resource for the biomass copepods and krill. Krill and the biomass copepods are the principal forage of the midwater fish *Electrona antarctica* which, in turn, is the central diet component of flying seabirds as well as important food for the Antarctic fur seal and cephalopods. Krill are a major diet element for the fur seal and cephalopods, and the principal food of the minke whale.

sons, spring (1983), fall (1986), and winter (1988) during the Antarctic Marine Ecosystem Research in the Ice Edge Zone (AMERIEZ) program. This paper describes the structure of the food web in open waters adjacent to the ice edge in the southern Scotia Sea in early spring. The trophic structure in fall and winter has been reported in earlier papers (Hopkins and Torres 1989; Ainley et al. 1991; 1992; Lancraft et al. 1991; Hopkins et al. 1993). The data set was based on collections from the RV *Melville* at open ocean locations north of 60° 45'S, the northern limit of the pack ice. Feeding in dominant zooplankton and micronekton species is described and the results integrated with data from other studies on top predators, i.e., birds and mammals, found in this region during spring. Feeding patterns in 1983 are also compared with those determined for other seasons in the Scotia-Weddell Sea region and major caloric pathways through the ecosystem from phytoplankton to apex predators are proposed.

Regional setting, spring

The physical characteristics and aspects of phytoplankton production and distribution in the study area have been presented in Nelson et al. (1987). Sampling was conducted in a hydrographically complex region of the southern Scotia Sea where water emerging from the Weddell Sea mixes with the eastward flow from the Bransfield Strait and Drake Passage. The northern extent of pack ice was encountered at approximately 60° 45'S (Fig. 1). The surface temperature showed a general gradient, with temperatures increasing from southeast to northwest. Temperatures south of 58° 30'S ranged from -1.6°C to 0°C while to the north the range was 0°C to +1°C.

Phytoplankton biomass (chl *a*) in the upper 150 m averaged 1.7 mg m⁻² which was 7 to 12 times that in fall and winter. Mean primary production, estimated at 590 mg C m⁻² d⁻¹, was twice that in fall and 20 times that in winter (unpublished data by Smith, and Smith and Cota). Standing crop and production were highest in the

The marginal ice zone in the southern Scotia Sea and the northwestern Weddell Sea was investigated in three sea-

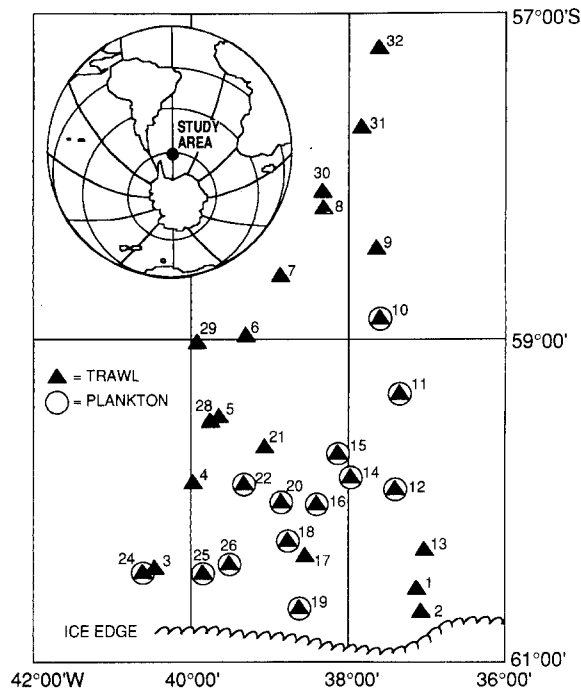


Fig. 1. Zooplankton and micronekton stations sampled from the RV *Melville* in the Scotia Sea, spring 1983

bloom encountered in the southwestern sector of the study area, west of $39^{\circ} 30' W$ and south of $59^{\circ} 15' S$.

Zooplankton biomass in spring (1.1 g DW m^{-2} ; $0\text{--}1000 \text{ m}$) varied little from that in the other two seasons ($1.0\text{--}1.3 \text{ g DW m}^{-2}$; Hopkins and Torres 1988; Hopkins et al. 1993). Total micronekton biomass was only slightly seasonal, ranging from $2.4\text{--}3.2 \text{ g DW m}^{-2}$ (Lancraft et al. 1991). Zooplankton and micronekton biomass dominants were the same as those in the marginal ice zone in other seasons, though relative abundances of dominants varied (Hopkins and Torres 1988; Lancraft et al. 1989, 1991; Hopkins et al. 1993). Also, the mammal dominants were the same in spring, fall and winter (Ribic et al. 1991). While biomass of birds in the pack ice did not vary seasonally, that in the open water was much reduced during winter (Ainley et al. 1993).

Methods

Zooplankton and micronekton were collected with a mouth-closing trawl-plankton net combination at the locations in Fig. 1. The trawl, 9 m^2 in mouth area, was of 4 mm mesh and terminated in a $500 \mu\text{m}$ mesh codend net. Opening and closing were effected with a pair of clock release devices similar to those described by Davies and Barham (1969). The collapsible plankton net was 0.2 m^2 in mouth area, of $162 \mu\text{m}$ mesh and fitted with a flowmeter which recorded only when the net was open (see Lancraft et al. 1989). The plankton net was suspended in the center of the trawl mouth as shown in Hopkins and Baird (1975). Collection data are in Table 1.

The catch of both nets was initially preserved in 5% buffered formalin-seawater solution then transferred to a 50% isopropyl-freshwater solution for storage. Zooplankton was identified and counted in sample aliquots, with the results prorated to volume of water filtered. Micronekton (trawl) collections were processed as described in Lancraft et al. (1989).

Diet analyses were performed on 28 common to abundant species of zooplankton and micronekton. Organisms used in the diet analyses were first measured (sample size ranges in Table 2), then had their gut contents examined in water in watch glasses or on microscope slides at 40 to 600X magnification. Food items in each preparation were identified and their incidence (presence or absence) assigned to one of 28 standard food categories (Table 2). To minimize the effects of patchiness on species diet characterization, animals from at least four different samples were examined. While there is potential bias from net feeding by zooplankton, we feel it does not strongly influence the results because of consistent differences in diets of an array of species taken in the same haul and for the reasons given in Hopkins (1985). Also, only the data from intestines (not stomachs) were used from midwater fishes.

The diet information for 26 of the zooplankton and micronekton species (*Haloptilus ocellatus* and *Eukrohnia hamata* not included) in Table 2 were converted to incidence percentages where the incidence percentage of each food type in a species sample is expressed as a percentage of the total incidences of all food types occurring in the diet. A sample pairs matrix consisting of Bray and Curtis (1957) dissimilarity indices was produced using the diet incidence percentage data. The dissimilarity matrix was then clustered to determine feeding groups, using average distance linkage hierarchical clustering procedures (Sarle 1982; Romesburg 1990). Diet information published by Ainley et al. (1991) on flying seabirds censused in spring 1983 in open waters adjacent to the marginal ice zone was also subjected to cluster analysis, as described above, for inclusion in the Results and Discussion sections in order to obtain a more comprehensive view of the food web. This required a separate analysis since bird diet components were expressed as percents of food biomass rather than percent incidence of occurrence.

Diets of selected important zooplankton and micronekton species taken in spring 1983 and on the AMERIEZ cruises (fall, winter; Hopkins 1989; Lancraft et al. 1989, 1991; Hopkins et al. 1993) were clustered as well to examine seasonal-geographical effects on diet composition of individual species. Again, it was necessary to run a separate analysis for bird interseasonal information. In all cluster analyses the level of diet separation was 40% dissimilarity ($= < 60\%$ diet similarity; see Zaret and Rand 1971; Berkes 1976; Hopkins and Gartner 1992).

Results

Cluster analysis of diets of 26 dominant zooplankton and micronekton species collected in spring yielded 12 feeding groups at the 40% diet dissimilarity level (Fig. 2). The first three clusters, containing over half the species, were composed of small-particle grazers having largely phytoplankton-protzoan-debris diets. The first springtime cluster (Sp-1) included the four copepod biomass dominants south of the Polar Front, *Calanus propinquus*, *Metridia gerlachei*, *Calanoides acutus* and *Rhincalanus gigas*. The latter two are winter diapause species which by November had migrated into the epipelagic zone (Fig. 3) to actively feed on phytoplankton. The two species in cluster Sp-2 were upper mesopelagic copepods separable from other small particle grazers in having a high incidence of euphausiid molt fragments in their guts. Cluster Sp-3, which included two macroplankton dominants, *Euphausia superba* and *Salpa thompsoni*, consisted of species with diverse omnivorous diets. The three species in cluster Sp-4 yielded high diet incidences of phytoplankton and invertebrate eggs. Cluster Sp-5 consisted of an apparently omnivorous hyperiid amphipod, *Vibilia stebbingi*, which is associated with salps (see Madin and Harbison 1977). Salp

Table 1. Collection data from AMERIEZ cruise on the RV *Melville* to the Scotia Sea in Spring 1983

Tow no.	Depth zone sampled (m)	Long. (S)	Lat. (W)	Date (mo./day)	Fishing time	Light conditions	Volume filtered	
							Trawl	Plankton net
1	70-150	60 33.8	37 06.4	11/11	0551-0621	Day	17,568 ^a	
2	0-570	60 40.9	37 02.0	11/11	1253-1529	Day	107,829	
3	0-760	60 28.4	40 33.9	11/14	1749-2200	Dusk	171,153	
4	200-300	59 54.8	39 59.4	11/15	1420-1520	Day	49,086 ^a	
5	0-430	59 29.8	39 41.0	11/16	0246-0410	Dawn	42,732	
6	0-750	58 59.4	39 17.2	11/16	1152-1353	Day	92,133	
7	0-260	58 36.2	38 51.6	11/17	0129-0348	Dawn	45,612	
8	0->1000	58 11.1	38 18.3	11/17	0958-1528	Day	124,605	
9	0-400	58 26.9	37 37.7	11/18	0737-1123	Day	116,725	
10	270-400	58 52.4	37 35.6	11/19	2315-0115	Night	71,969	4,215
11	430-500	59 21.6	37 20.4	11/19	1240-1404	Day	112,077	5,320
12	0-90	59 56.8	37 24.8	11/20	0046-0120	Night	15,390	731
13	0->1000	60 18.5	37 00.1	11/20-21	1946-0319	Day, Night	155,385	
14	400-900	59 50.9	37 59.5	11/22	1009-1209	Day	91,692	4,353
15	600-900	59 43.3	38 06.8	11/23	2200-0000	Night	74,016	3,514
16	0-100	60 01.6	38 21.2	11/23	0846-0938	Day	23,706	1,126
17	0-640	60 21.6	38 30.6	11/23-24	2234-0114	Night	102,600	
18	100-170	60 15.5	38 45.6	11/24	1057-1157	Day	46,611	2,213
19	100-200	60 40.9	38 35.7	11/24-25	2311-0011	Night	47,448	2,252
20	200-290	60 01.6	38 49.1	11/25	0828-0928	Day	40,545	1,924
21	310-410	59 39.7	39 04.3	11/25	2000-2130	Dusk	60,012	
22	390-530	59 56.1	39 18.5	11/26	1212-1342	Day	50,184	2,382
24	190-280	60 28.2	40 32.9	11/27	1009-1139	Day	83,295	3,954
25	350-550	60 28.1	39 48.5	11/27	1828-1958	Night	51,372	2,439
26	250-370	60 24.5	39 29.0	11/29	0004-0134	Night	45,657	2,167
28	500-980	59 30.7	39 44.7	11/30	1022-1222	Day	31,400	
29	470-700	59 02.4	39 55.6	12/01	0050-0250	Night	31,300	
30	150-250	58 07.0	38 21.0	12/02	0225-0325	Dawn	21,816	
31	0-860	57 43.0	37 56.3	12/02	1116-1540	Day	55,296	
32	0-125	57 12.4	37 36.7	12/02-03	2340-0045	Night	21,816	

^a Non-quantitative samples; net damaged

fragments were commonly found in guts, consequently the phytoplankton consumed by *V. Stebbingi* may have been secondary food derived from the salp filtration-digestive system.

The remaining seven clusters had predatory species and, except for cluster Sp-6, consisted of single species. Copepods were the dominant prey in all seven clusters in percent incidence but not necessarily in biomass. Species in these clusters were different in the kinds of copepods in their diets and in varying percentage of other invertebrate prey. Cluster Sp-6 grouped two species with diverse diets, *Electrona antarctica* and *Gymnoscopelus braueri*. These mesopelagic fishes had high diet incidences of the copepod dominants *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* and of ostracods and euphausiids. *Sagitta gazellae* (cluster Sp-7) ingested copepods, larvaceans and euphausiids while *Notolepis coatsi* (cluster Sp-8), another common midwater fish, had cyclopoid copepods, chaetognaths (mostly *Eukrohnia*) and euphausiids as its most frequent diet items. Clusters Sp-9 and Sp-10 consisted, respectively, of *Euchaeta antarctica* and *Heterorhabdus austrinus*, two predatory copepods which fed on a variety of other copepods. *Bathylagus antarcticus* (cluster Sp-11), a midwater fish, most frequently ingested copepods

and gelatinous prey. *Sagitta marri* (cluster Sp-12) fed exclusively on copepods, with *Metridia* being the dominant prey genus.

Cluster analysis of bird diets (Fig. 4) resulted in nine predator species clustering into four groups. Cluster Sp-1B, the largest, consisted of six species: five petrels (Blue, Cape, Wilson's storm and Snow petrel, and the Antarctic prion) and the Arctic tern, which grouped together due to the predominance of *Electrona antarctica* in diets. The Antarctic petrel (cluster Sp-2B) partitioned its diet between *Electrona* and the midwater shrimp *Pasiophaea scotiae*, and the Antarctic fulmar (cluster Sp-3B), between *Electrona* and the squid *Galiteuthis glacialis*. The Southern giant fulmar was a carrion feeder (cluster Sp-4B) exclusively.

Table 3 shows the results of clustering 22 zooplankton/micronekton midwater fauna and nine bird species' dietary information from different seasons and habitats (i.e. covered vs open waters) within the northwestern Weddell and southern Scotia Seas. There are eight midwater and five bird clusters, using data from all seasons (AS cluster). Of the 31 species clustered, 22 were analyzed in all three seasons (spring, fall and winter). Of these 22 species, 12 showed no major seasonal variation in diet, two

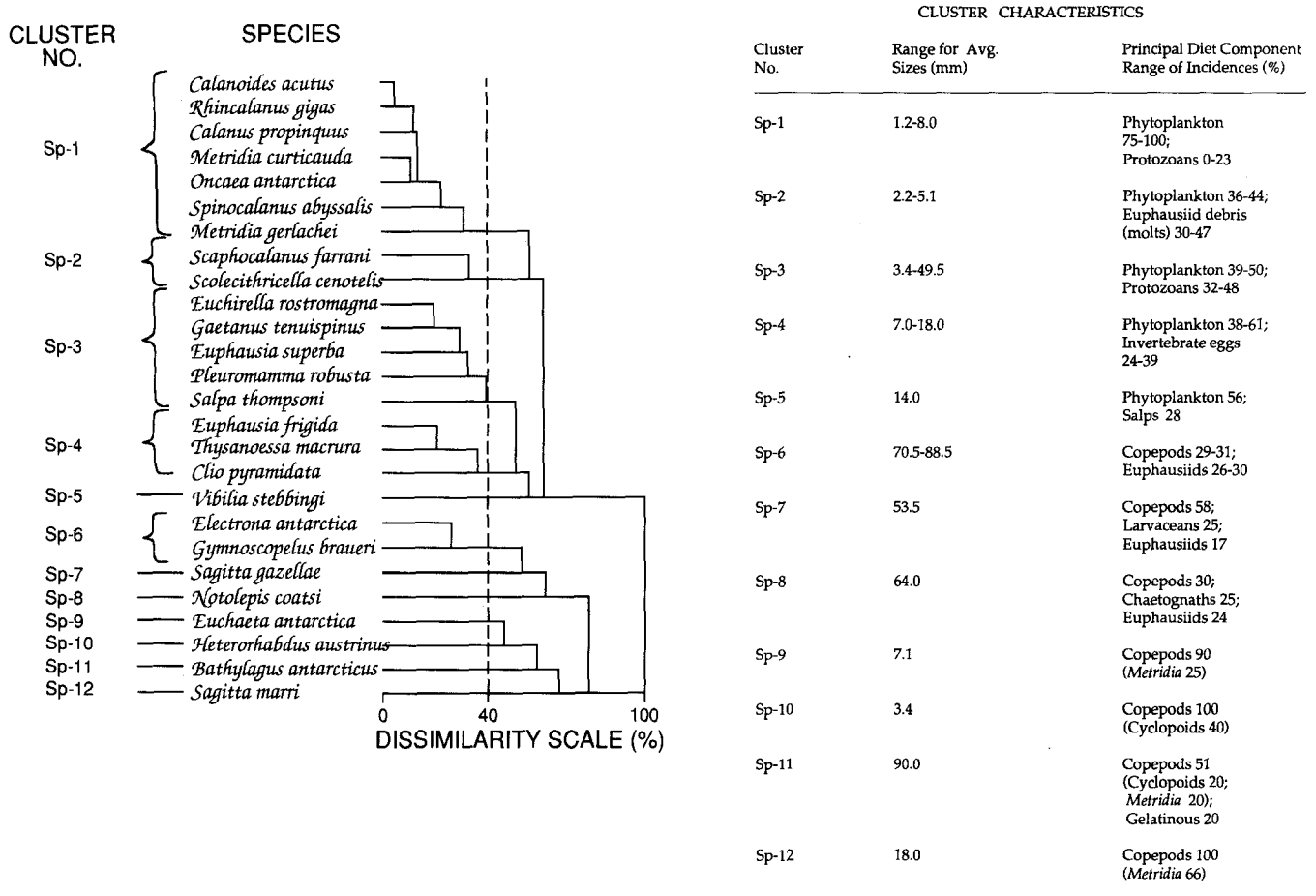


Fig. 2. Cluster analysis dendrogram of diets of zooplankton and micronekton species from the southern Scotia Sea, spring 1983

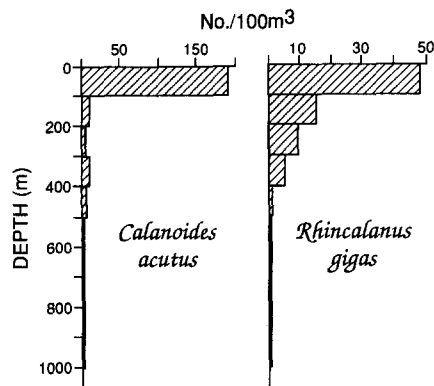


Fig. 3. Vertical distribution of the two winter diapause species *Calanoides acutus* and *Rhincalanus gigas* in the southern Scotia Sea in spring (1983)

(*Calanoides acutus* and *Rhincalanus gigas*: the winter diapause species) showed no change when they were feeding and six (*Oncaea antarctica*, *Metridia gerlachei*, *Calanus propinquus*, *Euchaeta antarctica*, *Fulmarus antarcticus*, *Daption capense*) had similar diets in two of three seasons.

Two species, *Sagitta gazellae* and *Thalassoica antarctica*, had diets which were significantly different in all three seasons. The remaining nine species were analyzed for only two seasons and six of these (*Metridia curticauda*, *Spinocalanus abyssalis*, *Pleuromamma robusta*, *Sterna Paradisaea*, *Oceanites oceanicus*, *Pachyptila vitatta*) had similar diets in those seasons. Therefore, 18 of the 31 species (12 midwater and six bird) had no major dietary changes in the seasons for which data were available.

Those species that showed significant variations in diet included three smaller particle-grazing species in inter-seasonal clusters AS-1 and AS-2, *Oncaea antarctica*, *Metridia gerlachei* and *Calanus propinquus*, with these having a more carnivorous diet in winter than in other seasons. *Thysanoessa macrura* and *Clio pyramidata* (cluster AS-3) had diets which varied significantly in spring and fall (cluster AS-2, AS-4), reflecting the high incidences of invertebrate eggs in their diets in spring. The diet of *Euchaeta antarctica* in fall (cluster AS-4) differed from that in winter and spring (cluster AS-5) especially in the regular occurrence of phytoplankton in guts of specimens collected in fall. The midwater fish *Notolepis coatsi* had significantly more gelatinous prey in its diet in spring (cluster AS-7) than in fall (cluster AS-5), and similarly, *Sagitta gazellae* fed more on gelatinous food in spring (cluster AS-6) than fall (cluster AS-5).

CLUSTER CHARACTERISTICS

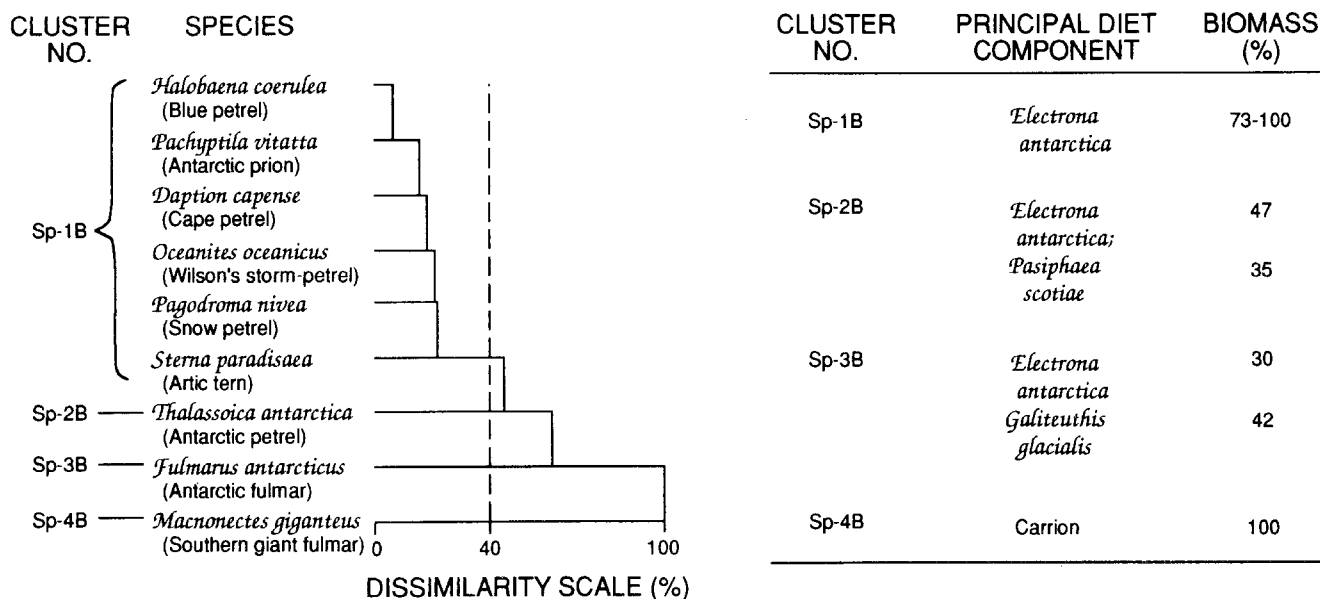


Fig. 4. Cluster analysis dendrogram of diets of flying seabirds predominant in the southern Scotia Sea in spring (1983)

Among birds, seasonal shifts occurred in the diet of *Thalassoica antarctica*, which fed predominantly on *Electrona antarctica* in all three seasons, but fed heavily as well on the shrimp *Pasiphaea scotiae* in spring (cluster AS-2B) and cephalopods in fall (cluster AS-3B). *Fulmarus antarcticus* took little but *Electrona* in winter (cluster AS-1B) but added cephalopods to this diet in spring and fall (cluster AS-4B). The diet of *Daption capense* shifted from predominantly *Electrona* in spring and winter (cluster AS-1B) to one including cephalopods in fall (cluster AS-4B).

Discussion

Spring 1983

Bloom conditions prevailed in the southern Scotia Sea in November 1983, with highest chlorophyll biomass in the southwestern sector of the study area. Spring conditions were reflected in the zooplankton community, with the appearance of the winter diapause species, *Calanoides acutus* and *Rhincalanus gigas*, in the epipelagic zone where they were actively feeding on phytoplankton. Also, *Salpa thompsoni*, which was only moderately represented in fall and winter collections, was abundant in spring. As in other seasons, biomass south of the Polar Front was dominated by the small-particle grazers occurring in clusters Sp-1 and Sp-3 (Fig. 2; see also Hopkins and Torres 1988; Boysen-Ennen et al. 1991; Lancraft et al. 1989, 1991; Hopkins et al. 1993). These clusters include the four biomass species, *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei*, and the two macroplankton dominants, *Salpa thompsoni* and *Euphausia superba*. Strict herbivory, despite the increase in phytoplankton availability in spring, was uncommon among small-particle

grazers. Only two species, *Calanoides acutus* and *Rhincalanus gigas*, had exclusively phytoplankton diets. Exclusive herbivory in this pair of species has been reported by Andrews (1966) and Voronina and Sukhanova (1976), though in other seasons (e.g. fall) they can ingest protozoans (Hopkins and Torres 1988). In the Ross Sea, *Calanoides acutus* will even take metazoans (Hopkins 1987). The other small-particle grazers in spring were omnivorous at least to the extent that they ingested protozoans along with phytoplankton, and in cluster Sp-2 and Sp-3 species, small metazoans (copepods; see Table 2) as well. Some of the species in clusters Sp-1, 2, and 3 had mesopelagic distributions (e.g., *Euchirella rostromagna*, *Spinocalanus abyssalis*, *Gaetanus tenuispinus*, *Scaphocalanus farrani*, *Scolecithricella cenotelis*). The mesopelagic species center in layers below 200 m (Hopkins and Torres 1988) yet were successful in grazing phytoplankton. As this was reported for winter and fall as well as spring (Hopkins and Torres 1989; Hopkins et al. 1993), it is apparent that an appreciable fraction of the phytoplankton is advected or settles out of the euphotic zone regardless of season, thus helping to sustain a deep dwelling array of small-particle grazers. Major vertical transport of bloom phytoplankton out of the euphotic zone, with much reaching bottom, has been reported in the Ross Sea by Smith and Nelson (1985).

Among food items prevalent in the food web in spring but not in the other two seasons were invertebrate eggs, with these most closely resembling the eggs of *Metridia gerlachei* (H.G. Franz, personal comm.). Eggs occurred in the guts of at least ten species, some (e.g. *Euchirella rostromagna*, *Metridia curticauda*) being mesopelagic. The eggs also appeared in diets of large species such as *Euphausia superba* and *Salpa thompsoni* which are capable of high grazing and filtration rates (Boyd et al. 1984;

Table 3. Results of cluster analysis of seasonal composition of diets of principal midwater and flying seabird species. Cluster separation based on 40% diet dissimilarity. Sp = spring, F = fall, W = winter. * = species with similar diets ($\geq 60\%$ similarity) for all seasons tested, AS = all seasons, B = Bird, Rn = range

Feeding Cluster	Principal Diet Component %: \bar{x} (Rn)	Feeding Cluster	Principal Diet Component %: \bar{x} (Rn)
AS-1 <i>Calanoides acutus</i> SpF <i>Rhincalanus gigas</i> SpF * <i>Metridia curticauda</i> SpW <i>Oncaea antarctica</i> SpF * <i>Spinocalanus abyssalis</i> SpW <i>Metridia gerlachei</i> SpF <i>Calanus propinquus</i> SpF	Phytoplankton 83 (71–100)	AS-5 * <i>Heterorhabdus austrinus</i> SpFW * <i>Sagitta marri</i> SpFW <i>Euchaeta antarctica</i> SpW <i>Notolepis coatsi</i> F <i>Oncaea antarctica</i> W <i>Sagitta gazellae</i> F	Metazoans 98 (91–100) (copepods 88 (61–100))
AS-2 * <i>Gaetanus tenuispinus</i> SpFW * <i>Euchirella rostromagna</i> SpFW * <i>Pleuromamma robusta</i> SpW * <i>Euphausia superba</i> SpWF * <i>Salpa thompsoni</i> SpFW <i>Clio pyramidata</i> F <i>Calanus propinquus</i> W <i>Metridia gerlachei</i> W	Phytoplankton 46 (33–56); Protozoans 32 (15–45); Metazoans 21 (7–40)	AS-6 * <i>Electrona antarctica</i> SpFW * <i>Gymnoscopelus braueri</i> SpFW * <i>Bathylagus antarcticus</i> SpFW <i>Sagitta gazellae</i> Sp	Metazoans 99 (94–100) (Copepods 42 (20–58); Other Crustaceans 31 (15–61); gelatinous prey 26 (19–35))
AS-3 <i>Thysanoessa macrura</i> Sp <i>Clio pyramidata</i> Sp	Phytoplankton 46 (31–61); Invertebrate eggs 35 (32–39)	AS-7 <i>Notolepis coatsi</i> Sp	Metazoans 100 (Crustaceans 57; gelatinous 43)
AS-4 <i>Thysanoessa macrura</i> F <i>Euchaeta antarctica</i> F	Phytoplankton 34 (29–39); metazoans 56 (52–60) (Copepods 49 (39–59))	AS-8 <i>Sagitta gazellae</i> W	Metazoans 100 (Euphausiids 60; copepods 40)
AS-1B * <i>Halobaena coerulea</i> SpFW * <i>Sterna paradisaea</i> SpF <i>Fulmarus antarcticus</i> W * <i>Pagodroma nivea</i> SpFW * <i>Oceanites oceanicus</i> SpF * <i>Pachyptila vitatta</i> SpF <i>Daption capense</i> SpW <i>Thalassoica antarctica</i> W	<i>Electrona</i> 85 (62–100)	AS-3B <i>Thalassoica antarctica</i> F	<i>Electrona</i> 40; cephalopods 37
AS-2B <i>Thalassoica antarctica</i> Sp	<i>Electrona</i> 47; <i>Pasiphaea</i> 35	AS-4B <i>Fulmarus antarcticus</i> SpF <i>Daption capense</i> F	Cephalopods 76 (46–96)
		AS-5B * <i>Macronectes giganteus</i> SpFW	Carrion 100

Huntley et al. 1989). Small particle grazers may ingest a considerable fraction of ecosystem egg production, and may in turn account for much of the mortality in the early life stages of zooplankton and micronekton (see also Huntley et al. 1989). This may possibly influence life history strategies in the Southern Ocean pelagic ecosystem.

Seven of the spring clusters of midwater species were composed of predatory species (Fig. 2). While the range of prey was taxonomically diverse, copepods consistently dominated their diets, underscoring the importance of copepods in intermediate levels of the food web. The genera occurring most frequently in diets were the cyclo-poids *Oithona*, *Oncaea* and the calanoids *Calanoides*,

Calanus and *Metridia*. Copepod species in these genera were either numerical or biomass dominants in all seasons and their availability was reflected in ecosystem feeding patterns. As an important example, *Electrona antarctica*, the principal micronektonic predator in the epipelagic zone at night in spring (Lancraft et al. 1989), had the biomass species *Calanus propinquus*, *Calanoides acutus* and *Euphausia superba* as primary dietary constituents (Table 2). In spring these forage species were concentrated in the epipelagic zone at night.

Feeding in birds censused during spring 1983 and in other seasons, described in Ainley et al. (1991) and Ainley et al. (1992, 1993) and further analyzed for the present paper, clearly demonstrated the crucial role of *Electrona*

antarctica in their diets. As Ainley et al. (1991; 1992) note, it is midwater fishes rather than krill which have the central position in trophic dynamics of flying seabirds feeding in open waters near the ice edge. Midwater decapod shrimps and cephalopods were also important diet components in spring for a few species (e.g., Antarctic petrel and Antarctic fulmar). *Electrona* was the major food element for seven of the nine dominant species examined. In spring *Electrona antarctica* ranked 5th ($0.1/m^2$) in numbers in the epipelagic zone (0–200 m), well behind *Salpa thompsoni* ($17.5/m^2$), *Euphausia superba* ($3.1/m^2$) *Thysanoessa macrura* ($0.4/m^2$) and *Sagitta gazellae* ($0.4/m^2$), but was second in biomass ($74 \text{ mg DW}/m^2$) only to *E. superba* ($774 \text{ mg DW}/m^2$) (Lancraft et al. 1989). While *E. antarctica* was distributed throughout the upper 200 m at night, some obviously reached the surface where they were taken by seabirds in preference to the more abundant but smaller (therefore less energetically rewarding) macrozooplankton (see also Ainley et al. 1992).

All Seasons

Some variability in species' diet composition is to be expected as the three AMERIEZ studies occurred in different seasons, locations, and ice conditions. For example, *Rhincalanus gigas*, and *Metridia lucens* were more common in diets of predators taken near the Polar Front than further south in the Weddell Sea because these species are more abundant at lower latitudes in the Southern Ocean (Hopkins and Torres 1988; Hopkins et al. 1993). Seasonal variation was markedly apparent in the phytoplankton signal which was much stronger in spring than in the other two seasons (Nelson et al. 1987; AMERIEZ cruise reports). Spring phytoplankton abundance was especially reflected in the diets of the two diapause species, *Calanoides acutus* and *Rhincalanus gigas* (Hopkins and Torres 1989; Hopkins et al. 1993; present paper). Invertebrate eggs were a more prevalent food resource in spring than in fall or winter, and seasonal shifts in vertical distribution of the midwater fauna (Lancraft et al. 1989, 1991) altered prey availability in surface layers to seabirds (Ainley et al. 1991). The impact of ice conditions on feeding was most apparent in the fall; the important midwater biomass species had less food in their guts and were more carnivorous under the ice than in open waters (Hopkins and Torres 1989).

While regional and temporal variation in feeding does occur in the northwestern Weddell Sea-Scotia Sea Confluence region, there is nevertheless much consistency in diets. Over half the species tested exhibited little diet variation. This was apparent in midwater species and particularly in bird species.

Trophic pathways

Top predators other than birds that were abundant in the marginal ice zone in Spring 1983 were the Antarctic fur seal (*Arctocephalus gazella*) and the minke whale (*Balaenoptera acutorostrata*). Both mammals were most abundant

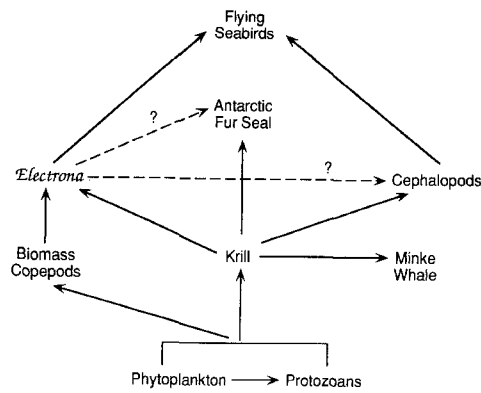


Fig. 5. Principal trophic pathways in open water adjacent to the marginal ice zone in the southern Scotia Sea in spring 1983

at the ice margin. Other dominants such as the crabeater seal and all species of penguins occurred either deeper in the pack or farther at sea (Ribic et al. 1991; Ainley et al. 1992) than in our study area. Diet information for the fur seal and minke whale was not available from AMERIEZ 1983. Other investigations confirm that minke whales are primarily krill feeders (Bushuev 1986; Ichii 1990; Ichii and Kato 1991); Antarctic fur seals at South Georgia forage on krill, cephalopods and fish (Doidge and Croxall 1985; Laws 1985).

Our data suggest that the major energetic pathways from phytoplankton to apex predators in open waters of the southern Scotia Sea in spring are as presented in Fig. 5. The basic pathways are quite similar to those we observed in this region in winter (Hopkins et al. 1993). The simplified food web illustrates the principal routes for energy through the ecosystem to the top predators, and highlights the importance of the intermediate trophic levels, the fish and cephalopods, to energy flow through the pelagic system. In addition, it strongly suggests that relatively few taxa account for most of the biomass and energy flow through this region of the Southern Ocean. Lower latitudes, in contrast, are characterized by higher biological diversity; dominance is more evenly shared. For example, the upper 600 m of low latitude "gyre" ecosystems have over 200 copepod species, 25 to 30 euphausiid species, 30 to 40 decapod shrimp species, approximately 50 cephalopod species and more than 250 species of midwater fishes (Boden et al. 1955; James 1971; Walters 1976; Hayward and McGowan 1979; Heffernan and Hopkins 1981; Hopkins et al. 1989; Passarella and Hopkins 1991; Flock and Hopkins 1992). The combined diversity in those groups exceeds that in the Scotia-Weddell Confluence region by more than a factor of six. Our data indicate that most of the biomass and energy flow at intermediate and top trophic levels in the Scotia-Weddell region can be accounted for by less than 20 species. These key species are predominant throughout the West Wind Drift south of the Polar Front, hence the simplified food web presented in Fig. 5 pertains to an immense area of the Southern Ocean.

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References

- Ainley DG, Fraser WR, Smith WO Jr, Hopkins TL, Torres JJ (1991) The structure of upper level pelagic food webs in the Antarctic: effect of phytoplankton distribution. *J Mar Systems* 2:111-122
- Ainley DG, Ribic CA, Fraser WR (1992) Does prey preference affect habitat choice in Antarctic seabirds? *Mar Ecol Prog Ser* 90:207-221
- Ainley DG, Ribic CA, Fraser WR (1993) The ecological structure of seabird communities in the Scotia-Weddell Confluence region of the Southern Ocean. *Oecologia* (in press)
- Andrews KJH (1966) The distribution and life history of *Calanoides acutus* (Giesbrecht). *Discovery Rep* 34:117-162
- Berkes F (1976) Ecology of euphausiids in the Gulf of St. Lawrence. *J Fish Res Bd Canada* 33:1894-1905
- Boden BP, Johnson MW, Brinton E (1955) The Euphausiacea (Crustacea) of the North Pacific. *Bull Scripps Inst Oceanogr Univ California* 8:287-390
- Boyd CM, Heyraud M, Boyd CN (1984) Feeding of the Antarctic krill *Euphausia superba*. *J Crust Biol* 4:123-141
- Boysen-Ennen E, Hagen W, Hubold G, Piatkowski U (1991) Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. *Mar Biol* 111:227-235
- Bushuev SG (1986) Feeding of minke whales, *Balaenoptera acutorostrata*, in the Antarctic. *Rep Int Whaling Comm* 36:241-245
- Davies IE, Barham EG (1969) The Tucker opening-closing micronekton net and its performance in a study of the deep scattering layer. *Mar Biol* 2:127-137
- Doidge DW, Croxall JP (1985) Diet and energy budget of the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. Antarctic cycles and food webs. 4th SCAR Symp on Antarctic Biol Springer Berlin, Heidelberg, New York pp 543-550
- Flock ME, Hopkins TL (1992) Species composition, vertical distribution, and food habits of the sergestid shrimp assemblage in the eastern Gulf of Mexico. *J Crust Biol* 12:210-223
- Hayward TL, McGowan JA (1979) Pattern and structure in an oceanic Zooplankton Community. *Am Zool* 19:1045-1055
- Heffernan JJ, Hopkins TL (1981) Vertical distribution and feeding of the genera *Gennadas* and *Bentheogenemema* (Decapoda: Penaeidea) in the eastern Gulf of Mexico. *J Crust Biol* 4:461-474
- Hopkins TL (1985) Food web of an Antarctic midwater ecosystem. *Mar Biol* 89:197-212
- Hopkins TL (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Mar Biol* 96:93-106
- Hopkins TL, Baird RC (1975) Net feeding in mesopelagic fishes. *Fish Bull US* 73:908-914
- Hopkins TL, Gartner JV Jr (1992) Resource partitioning and predation impact of a low latitude myctophid community. *Mar Biol* 114:185-197
- Hopkins TL, Torres JJ (1988) The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. *Polar Biol* 9:79-87
- Hopkins TL, Torres JJ (1989) Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. *Deep-Sea Res* 36:543-560
- Hopkins TL, Gartner JV Jr, Flock ME (1989) The caridean shrimp (Decapoda: Natantia) assemblage in the mesopelagic zone of the eastern Gulf of Mexico. *Bull Mar Sci* 45:1-14
- Hopkins TL, Lancraft TM, Torres JJ, Donnelly J (1993) Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). *Deep-Sea Res* 40:81-105
- Huntley ME, Sykes PF, Marin V (1989) Biometry and Trophodynamics of *Salpa thompsoni* Foxton (Tunicata: Thaliacea) near the Antarctic Peninsula in austral summer, 1983-1984. *Polar Biol* 10:59-70
- Ichii T (1990) Distribution of Antractic krill concentrations exploited by Japanese krill trawlers and Minke whales. *Proc NIPR Symp. Polar Biol (No. 3) Natl Inst Polar Res Tokyo, March 1990* 3:36-56
- Ichii T, Kato H (1991) Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biol* 11:479-487
- James BM (1970) Euphausiacean Crustacea. In: Pequenat WE, Chace FA Jr (eds) Contributions to the biology of the Gulf of Mexico. Texas A & M Univ Oceanogr Stud 1:205-229
- Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biol* 9:225-233
- Lancraft TM, Hopkins TL, Torres JJ, Donnelly J (1991) Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). *Polar Biol* 11:157-167
- Laws RM (1985) The ecology of the Southern Ocean. *Am Scientist* 73:26-40
- Madin LP, Harbison GR (1977) The associations of Amphipoda Hyperiidea with gelatinous zooplankton. I. Associations with Salpidae. *Deep-Sea Res* 24:449-463
- Nelson DM, Smith WO Jr, Gordon LI, Huber BA (1987) Spring distributions of density, nutrients and phytoplankton biomass in the ice edge zone of the Weddell-Scotia Sea. *J Geophys Res* 92:7181-7190
- Passarella KC, Hopkins TL (1991) Species composition and food habits of the micronektonic cephalopod assemblage in the eastern Gulf of Mexico. *Bull Mar Sci* 49:638-659
- Ribic CA, Ainley DG, Fraser WR (1991) Habitat selection by marine mammals in the marginal ice zone. *Antarctic Sci* 3:181-186
- Romesburg HC (1990) Cluster analysis for researchers. Robert E Krieger Pub Co Malabar, Florida USA 334 pp
- Sarle WS (1982) Introduction to SAS clustering procedures. In: Ray AA (ed) SAS user's guide: statistics SAS Inst., Cary, North Carolina USA pp 432-447
- Smith WO Jr, Nelson DM (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea. Spatial coherence with the density field. *Science* 277:163-166
- Voronina NM, Sukhanova IN (1976) Composition of food of massive species of herbivorous Antarctic copepods. *Oceanology* 16:614-616
- Walters JF (1976) Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae). *Fish Bull US* 74:799-836
- Zaret TM, Rand AS (1971) Competition in tropical stream fishes: support for the competitive exclusion principal. *Ecol* 52:336-342