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Zooplankton Communities in the Southern Weddell Sea (Antarctica)

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Summary. Standardized abundances of 40 frequently occurring macrozooplankton taxa collected by double-oblique bongo net hauls between the surface and 200 m depth were submitted to an agglomerative hierarchical cluster analysis, to characterize surface zooplankton communities in the southern and eastern Weddell Sea. The sensitivity of the analysis concerning reduction of the number of considered taxa (especially stages of species) was tested. Dominant taxa in the entire area over the whole period were copepods *Metridia gerlachei* and *Calanoides acutus*. *Calanus propinquus*, *Appendicularia* spp. and calyptopis-1 larvae of krill, *Euphausia superba* were abundant at 73 °S/19 °W. *Euphausia crystallorophias* and larval fish *Pleuragramma antarcticum* dominated at 77 °S/40 °W on the southern shelf. The cluster analysis revealed marked similarities between the southern shelf community and the January community further to the northeast. *E. crystallorophias*, and larval *Pleuragramma antarcticum* are thought to be transported in surface layers of the coastal current to the southwest. Oceanic species such as *Thysanoessa* sp. and *E. superba* are probably not transported in the same way. Possible mechanisms for the maintenance of the community structures are discussed. A simplified method of characterizing communities, based on analysis of euphausiids, is presented.

Introduction

The components of Antarctic pelagic systems have for long been known (e.g. Mackintosh 1934; Hardy and Gunther 1936; Baker 1954), but only recently have localized zoogeographical studies been attempted. Hopkins (1985) described zooplankton communities of Croker Passage west of Antarctic Peninsula. Rakusa-Suszczewski (1983) distinguished between "antarctic", "transitional", and "continental" zooplankton communities near Antarctic Peninsula, and Boysen-Ennen (1987) and Piatkowski (1987) described "oceanic", "eastern shelf", and "southern shelf" communities in the zooplankton of the Weddell Sea. These studies emphasized, that "the pelagic community" of the Weddell Sea is, in fact, a number of distinct communities.

The cyclonic Weddell Gyre, the largest of several gyre systems in the Southern Ocean, is dominated in the south by the Weddell Coastal Current, which flows from northeast to southwest along the edge of the continental shelf. The current system must be an important factor in the creation and maintenance of zooplankton communities, for example, in causing variability and large scale advection of zooplankton organisms.

This study investigated two geographically distinct plankton communities in the eastern and southern Weddell Sea, sampling in late January and mid February to identify possible effects of the current on both structure and stability. An important feature of this study was to identify key organisms by which the communities could be recognized, to reduce sorting effort and facilitate future ecosystem monitoring.

Methods

Zooplankton was collected from *RV POLARSTERN* during the 1985 "ANT III-3" cruise to the southern Weddell Sea at two locations (Fig. 1). Off Vestkapp (73 °S/19 °W), between January 23 and 29, samples were taken at 22 stations in a box grid of 50×50 nautical miles ("V-JAN" stations). The ship then proceeded 400 nautical miles south to sample at 11 stations over the Filchner Depression at 77 °S/40 °W, between February 3 and 9 ("Filchner" stations). On returning to Vestkapp, a further 24 stations were sampled between February 12 and 21 ("V-FEB" stations).

Details of sampling stations and the scientific work of the expedition appear in the cruise report (Hempel 1986).

Bongo nets with 300/500 µ mesh gauze were used in a total of 57 hauls. The opening of each net was 0.29 m^2. Nets were hauled in double oblique tows at 2 knots between 200 m and the surface. The wire was payed out at 0.3 m/s and retrieved at 0.5 m/s. Filtered volume was estimated from digital flowmeters attached to the nets, and from the ship's log. Mean filtered volume was 678 m^3 (sd = 164 m^3).

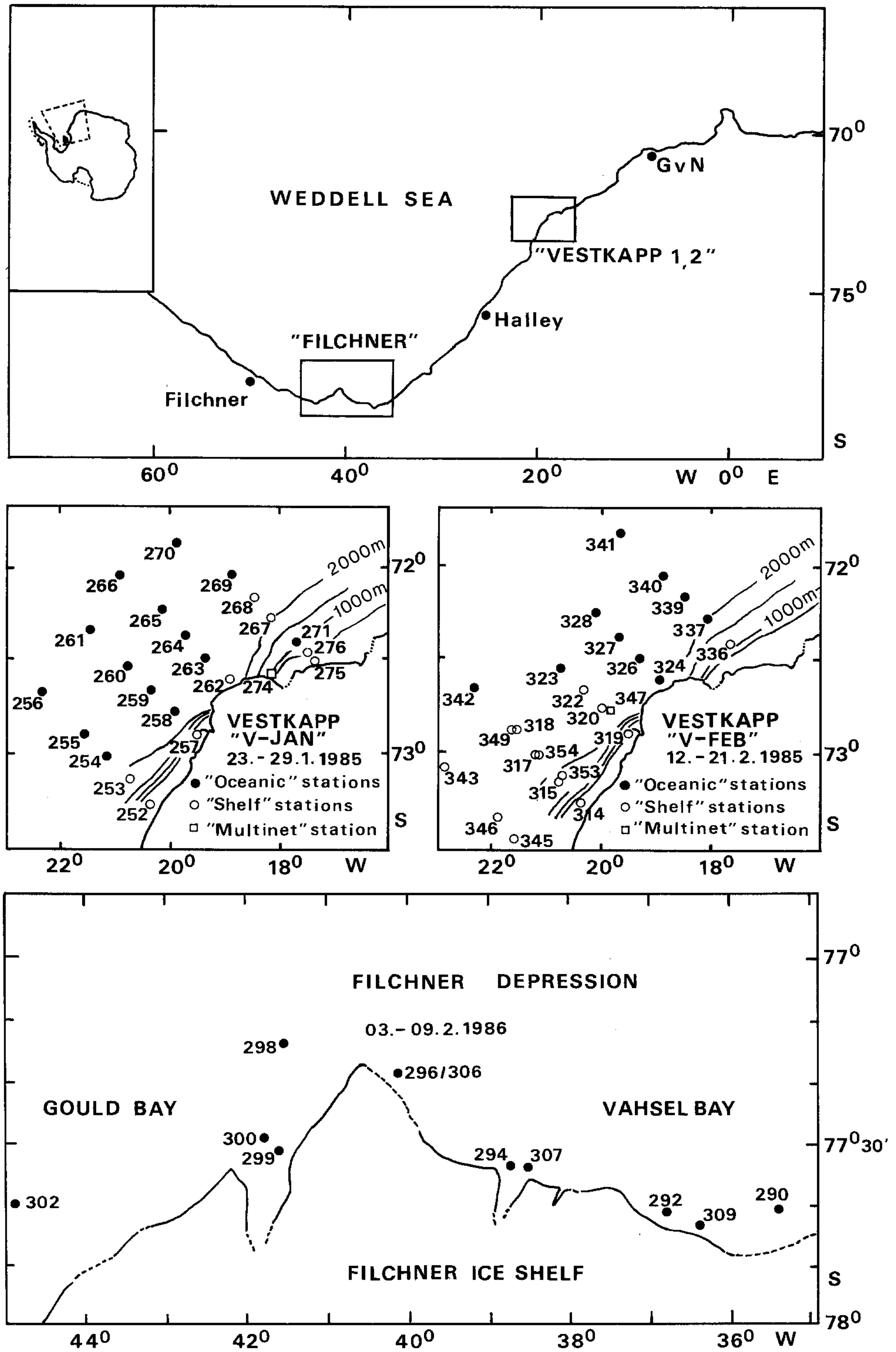

Fig. 1. Sampling stations and areas in the southern and eastern Weddell Sea

Bongo samples were analyzed from 300 μ nets except when these became clogged, mostly by *Phaeocystis* sp. Clogging occurred in the Filchner area and in "V-FEB". In these cases, the 500 μ net samples were used.

A test was made to assure the comparability of the nets. For 23 combined 300/500 μ bongo hauls the numbers of larval *Pleuragramma* (a notothenioid fish), taken from the two nets did not differ significantly in *t*-test. Furthermore, in the clusters, there was no systematic grouping according to mesh size of the bongo nets.

On two stations to the NE and SW of Vestkapp (Fig. 1), stratified vertical hauls were made by a multiple opening/closing net ("Multinet", Weikert and John 1981). On each station, six hauls were made over a period of 24 h. Each haul collected five separate samples in the depth strata 400–300 m, 300–200 m, 200–100 m, 100–50 m and 50–0 m. These hauls were taken as base for a cluster analysis of vertical stratification in "V-JAN" and "V-FEB".

To eliminate the influence of possible vertical migration, the standardized abundances in each depth layer from the 6 hauls (day and night) were averaged. The matrix for the cluster analysis thus consisted of the 2×5 depth strata (each stratum representing the mean of six day- and night hauls at each station).

The zooplankton was sorted into 58 taxa for shipboard processing. All taxa were larger than 500 μ. Thus, in the case of the copepods, small, but abundant species such as *Oithona* and *Oncaea*, as well as earlier developmental stages were not considered. Selected for ease of shipboard identification, the taxa included stages of species, species, genera, families and orders.

Except for the fish larvae, which were sorted from the unsplit samples, subsamples of between 1/10 to 1/100 were taken. In three cases, subsamples of less than 1/100 had to be used because of the great volume of phytoplankton collected by the 300 μ nets. These stations were localized in the clusters 5 and 7 in "V-JAN". Numbers of taxa were not correlated to size of the subsamples ($r^2 = 0.0008$; $n = 57$). In general, the abundance estimates for rare species must be considered as less reliable than those of the abundant taxa.

The data set was reduced to 40 regularly present taxa by eliminating very rare and unidentified taxonomic units. Standardized abundances (numbers per 100 m^3) of the 40 taxa and the 57 sampling stations were submitted to agglomerative hierachical cluster analysis. Calculations were made on a MZ 800 (Sharp) with "statistical block" programs (Bölter et al. 1980) adapted for personal computer.

Distance indices were calculated with the Canberra Metric (Lance and Williams 1967), which considers the abundances of elements in the matrix in a more moderate way than the Euclidean distance method. Grouping followed the "complete linkage" method, which links each new element with the most distant element of the existing cluster ("farthest neighbour technique"): This best detects clusters in a relatively homogeneous matrix (Lance and Williams 1967). Clustering was done by stations (station clusters 1 to 11) and by taxa (taxa clusters A to G).

Results

Clusters of Stations

Similarities between the standardized abundances of the zooplankton taxa at each station are plotted as a dendrogram (Fig. 2). In spite of the shortcomings of the estimates for rare species, and the mixture of very different taxonomic levels, the analysis produced meaningful clusters of stations of similar geographical and temporal origin.

Two main groups are separated on the 0.57 distance level: The Filchner stations and "V-JAN" on one side, and the "V-FEB"stations on the other.

The 0.38 level was chosen to describe 11 sets of similar stations within the two major groups. On this level, the two Filchner clusters (2 and 3) separated from all Vestkapp stations. Three stations (Cluster 1) of "V-JAN" were more similar to the Filchner stations than to the rest of "V-JAN". These stations were located very close to the coast at Vestkapp. Within the five "V-JAN" clusters, station 257 (Cluster 4) was distinguished from Cluster 5, consisting of a group of three other shelf stations (276, 267, 262). Two distinct sets of oceanic stations were found (266–265, and 261–258) as Cluster 6 and 7.

"V-FEB" includes four distinct clusters. The single station of Cluster 8 was different from the rest. This station was made at the same site close to the ice shelf as station 257 (Cluster 4 in "V-JAN"). Cluster 9 contains the coastal and slope stations of "V-FEB", and Cluster 11 the offshore stations. The samples grouped as Cluster 10 were mostly collected one week after the grid of "V-FEB".

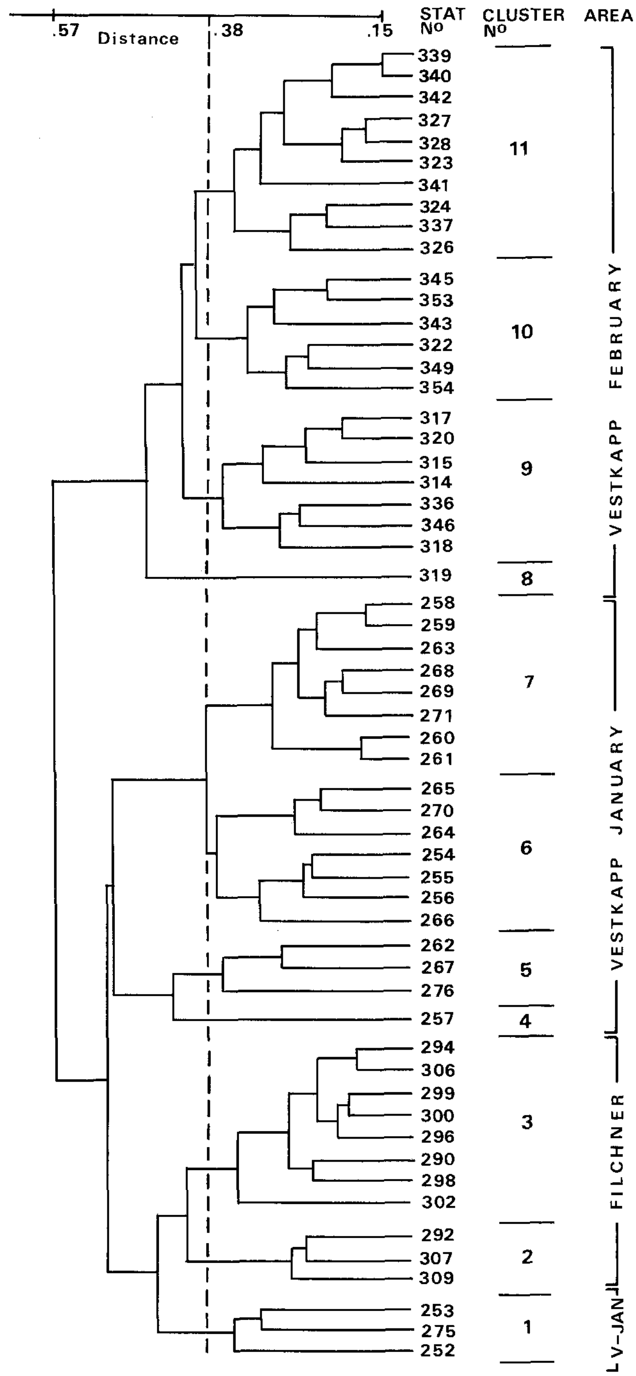

Fig. 2. Cluster diagram of sampling stations derived from standardized abundances of zooplankton species

Clusters of Taxa

To detect similarities between taxa and their geographical and temporal distribution pattern, and hence co-occurrence, the taxa were grouped in a second dendrogram according to their occurrence and abundance at the sampling sites (Fig. 3).

The analysis separated a group of 7 taxa (Cluster A) from the rest on a level of 0.96. This group includes the orders Appendicularia and Chaetognatha, as well as

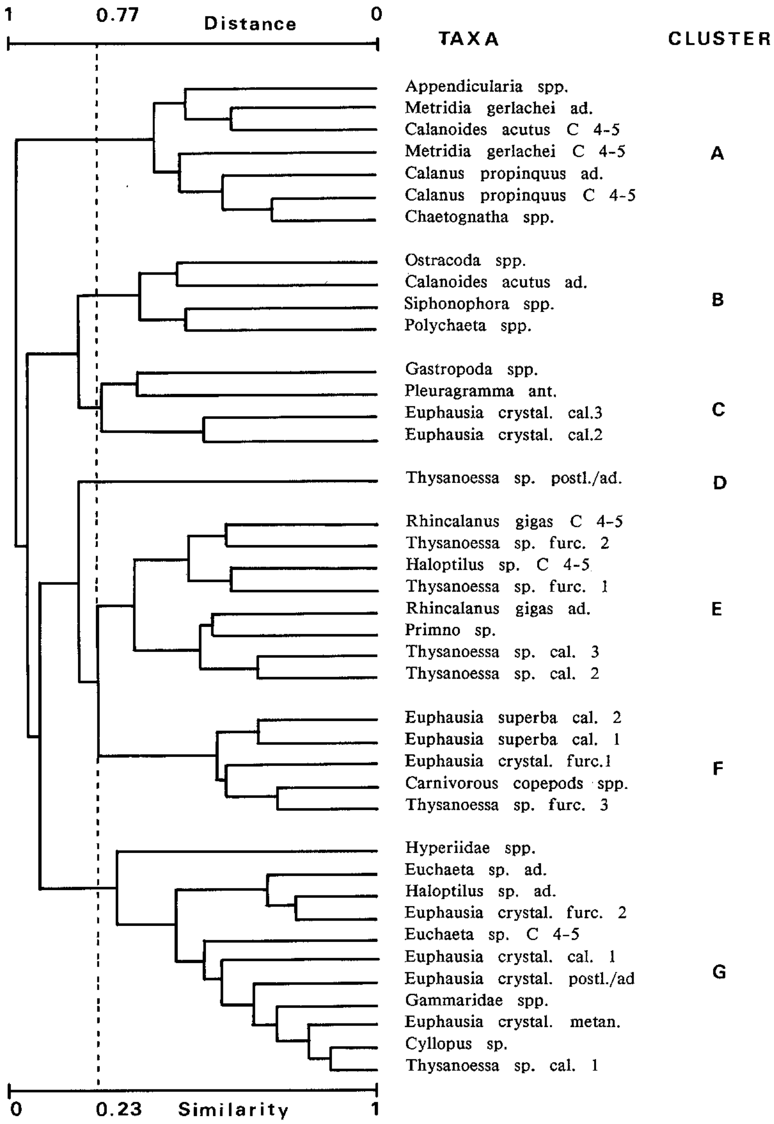

Fig. 3. Cluster dendrogram for 40 taxa collected in the southern and eastern Weddell Sea

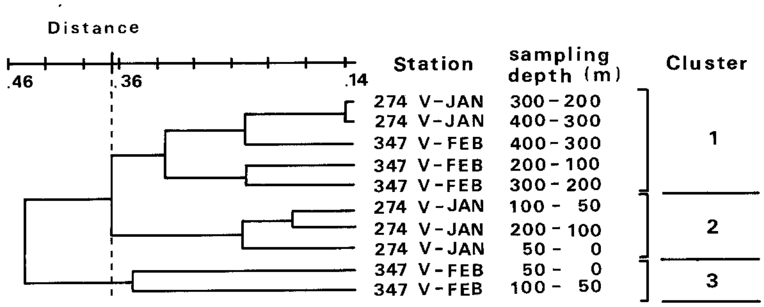

Fig. 4. Cluster diagram of 2 times 5 depth layer Multinet hauls with 35 evaluated taxa of zooplankton. The 0.36 distance level separates three main clusters

species and the copepodite (C 4–5) stage of calanoid copepods. At the 0.77 distance level, chosen for the grouping of the taxa, Cluster B consists of Ostracoda, adult *Calanoides acutus*, Siphonophora and Polychaeta.

Gastropoda, larval fish *Pleuragramma antarcticum* and calyptopis 2 and 3 of *Euphausia crystallorophias* form Cluster C. Postlarvae and adults of *Thysanoessa* sp. also separate from all others on this level (Cluster D).

Cluster E contains copepods and the euphausiid *Thysanoessa* sp., and in Cluster F we find the calyptopis-1 and -2 stages of krill (*E. superba*), and unidentified carnivorous copepods.

Cluster G includes the hyperiid amphipods as a somewhat isolated taxon, and copepods in two different stages (adults and C 4–5), as well as three stages of *E. crystallorophias*.

Mean Abundances of Zooplankton in the Geographical Areas

The taxa were listed according to the clusters (0.77 level), and the mean abundances were calculated per station cluster (0.38 level) (Table 1).

Of the taxa considered, the copepod *Metridia gerlachei* was most abundant. A maximum of 2597 ind/100 m^3 (C 4–5 and adults combined) was found as a mean of 6 offshore stations in "V-JAN" (Cluster 6). Adults showed varying, but generally high abundance in most cluster groups, and may serve as the model of an abundant generalist species.

By contrast, the second most abundant taxon, calyptopis larvae of krill (*E. superba*) were caught almost exclusively in "V-FEB", with a maximum of 2143 ind/100 m^3 in the coastal and slope stations off Vestkapp (Cluster 9). First calyptopis were by far the most numerous.

Notably varying abundance was found also in the copepod *Euchaeta* sp. C 4–5 stage appeared at mean abundance of 60/100 m^3 and adults at 28/100 m^3 in "V-JAN", but were virtually absent in "V-FEB".

About 1500 ind/100 m^3 of *E. crystallorophias* larvae (various stages) were obtained in the Filchner area. One third (427/100 m^3) of this abundance was found in "V-JAN", and less than one tenth (140/100 m^3), in "V-FEB". A similar relation was found for the abundances of *Pleuragramma antarcticum*, which occurred with 135 ind/100 m^3 in the Filchner area, and 13 ind/100 m^3 in "V-JAN"; only 2 ind/100 m^3 were found in "V-FEB" samples.

Regional Zooplankton Variability

Large Scale Geographical Variability. The main differences in the zooplankton communities between Vestkapp and Filchner, which led to the observed clusters of stations were due rather to changes in abundance than to clear presence or absence.

No species occurred exclusively at the Filchner stations. Adult copepods *Metridia gerlachei*, larval *Pleuragramma antarcticum*, and calyptopis 1 and 2 and adults of *Euphausia crystallorophias*, as well as the orders Polychaeta and Gastropoda occurred in higher numbers in the south than at Vestkapp. In contrast, several Vestkapp species were rare or absent in the south, including all stages of *Thysanoessa* sp., *E. superba*, copepods *Rhincalanus gigas* and *Haloptilus* sp., amphipods *Primno* sp., as well as furciliae 2 of *E. crystallorophias* and adults of copepods *Euchaeta* sp.

Small Scale Geographical Variability. In each of the sections of "V-JAN", "shelf" stations (Clusters 1, 4 and 5) can be clearly distinguished from "oceanic" stations (Clusters 6 and 7) by the analysis. Shelf and oceanic stations as defined by the clusters are indicated in the station maps of Fig. 1. The three stations of "V-JAN", which grouped with the Filchner stations are nearshore stations on the shallower areas to the SW and NE of Vestkapp.

In "V-FEB", the "oceanic" station 324 was located close to the coast over the deep trench off Vestkapp (water depth >2600 m, Fig. 1). The "coastal" and "shelf" stations were grouped in the clusters 8, 9 and 10. In the southwest, these clusters also include offshore stations over water depths exceeding 2800 m.

Temporal Zooplankton Variability

"V-JAN" and Filchner Area. The time lag between "V-JAN" and Filchner stations was approximately 11 days. In spite of the later sampling, younger developmental stages of zooplankton organisms were found in the south. This is consistent with the generally delayed development of summer conditions in this southern-most part of the Weddell Sea.

"V-JAN" and "V-FEB". Although the "V-JAN" and "V-FEB" samples were taken in the same area in almost identical sections of stations, the stations of "V-FEB" were separated from the rest of the collection in a distinct cluster.

The abundances of 31 taxa decreased from "V-JAN" to "V-FEB". These taxa are found in all clusters except Cluster F. The taxa involved are earlier stages of euphausiids and copepods, and the generalist species of the clusters A to D (Table 1). The earlier stages of species may have disappeared due to their development in the course of three weeks. Ten taxa showed increased abundances in "V-FEB". Amongst these, dramatic change is observed for the species of cluster E. Krill (*E. superba*) calyptopis 1 and 2 stages were almost absent in "V-JAN" and accounted for over 2000 ind/100 m^3 in parts of "V-FEB".

The moderate increase found in the numbers of C 4–5 of *Rhincalanus gigas, Thysanoessa* sp. furciliae 2, adult *Haloptilus* sp., *E. crystallorophias* furciliae 2, and in the gammarids, may be an artefact due to the low numbers in the subsamples.

Temporal Variability Within "V-FEB". One week after the start of "V-FEB" sampling, three stations of the southwesterly section of the grid were sampled again (st. no. 349 = 318, 354 = 317, 353 = 315 in Fig. 1). Four additional hauls were made farther to the southwest of section 1 (st. no. 342, 343, 345, 346).

Five of the seven later stations were grouped separately with one earlier station (322) from farther east as cluster 10, indicating a variability of the Vestkapp zooplankton at a time scale of only one week.

Vertical Zooplankton Variability

In contrast to the Bongo stations, the clusters of the Multinet catches mixed the two sets of temporally and geographically different hauls, and grouped them according to the sampled depth strata (Fig. 4).

Table 1. Mean abundances (n/100 m^3) of zooplankton caught in the Vestkapp and Filchner areas during Jan-Feb 1985. Station clusters are separated on the 0.38 level, taxon clusters on the 0.77 level

Code	Taxon	Area	Filchner	"V-JAN"						"V-FEB"				
		Cluster	2+3	1	4	5	6	7	Total	8	9	10	11	Total
55	Appendicularia spp.	A	198	23	2863	774	415	2143	1150	578	717	907	1284	907
45	Metridia gerlachei ad.		789	311	15	867	477	724	577	6	640	515	429	515
42	Calanoides acutus C 4–5		386	765	104	617	980	826	805	15	206	240	297	240
46	Metridia gerlachei C 4–5		90	513	390	220	2120	1553	1357	1	113	126	140	126
39	Calanus propinquus ad.		32	17	5	95	284	284	209	0	32	124	216	124
40	Calanus propinquus C 4–5		177	150	39	220	350	352	291	73	92	139	168	139
32	Chaetognatha spp.		49	68	242	280	236	363	274	56	163	210	232	210
54	Ostracoda spp.	B	36	26	25	31	243	196	157	2	26	43	38	43
41	Calanoides acutus ad.		58	32	0	231	77	210	137	0	8	20	40	20
58	Siphonophora spp.		10	12	20	2	30	40	30	2	9	13	21	13
56	Polychaeta spp.		112	12	5	46	46	77	51	7	17	26	27	26
57	Gastropoda spp.	C	162	5	133	88	18	64	48	14	22	16	10	16
03	Pleuragramma antarcticum		135	4	0.3	41	11	10	13	0	2.2	2.3	1.1	2.3
18	Euphausia crystallorophias cal 3		155	27	49	128	135	520	256	8	106	42	6	42
17	Euphausia crystallorophias cal 2		782	74	35	157	58	180	117	1	49	17	0.1	17
31	Thysanoessa sp. postlarv/ad.	D	0.3	1	0.3	3	3	6	4	0	1	2	3	2
44	Rhincalanus gigas C 4–5	E	0	5	10	27	36	9	20	0	17	30	23	30
29	Thysanoessa sp. furc. 2		0	0	5	30	23	26	21	7	46	45	42	45
51	Haloptilus sp. C 4–5		0	0	5	19	109	73	64	1	3	9	15	9
28	Thysanoessa sp. furc. 1		0	22	29	147	63	108	84	5	22	26	24	26
43	Rhincalanus gigas ad.		1	7	0	41	19	30	23	0	11	7	8	7
36	Primno sp.		0	0	0	0	11	72	30	4	12	8	9	8
27	Thysanoessa sp. cal. 3		0	6	49	50	57	97	63	4	8	4	3	4
26	Thysanoessa sp. cal. 2		2	7	29	50	38	48	38	0	0	0	0	0
08	Euphausia superba cal. 2	F	0	0	5	0	0	5	2	14	70	161	3	161
07	Euphausia superba cal. 1		1	0	0	0	0	0	0	679	2073	1358	30	1358
19	Euphausia crystallorophias furc. 1		6	0	5	13	0	0	2	5	156	73	15	73
47	Carnivorous copepods spp.		11	0	0	0	0	0	0	28	45	30	25	30
30	Thysanoessa sp. furc. 3		0	0	0	0	0	0	0	1	30	34	29	34
34	Hyperiidae spp.	G	7	4	0.1	0.2	43	0.1	14	0	0.2	9	17	9
48	Euchaeta sp. ad.		1	0	0	32	28	41	28	0	0	0.5	0	0.5
50	Haloptilus sp. ad.		0	0	5	2	4	2	2	0	1	3	5	3
20	E. crystallorophias furc. 2		0	0	0	0	0	0	0	0	3	7	2	7
49	Euchaeta sp. C 4–5		18	42	99	0	81	65	60	0	0	0	0	0
16	E. crystallorophias cal. 1		491	119	64	169	4	6	46	0	5	1	0	1
22	E. crystallorophias postlarv./ad.		53	7	0	0.3	0	0.4	1	0	0.3	0.1	0	0.1
37	Gammaridae spp.		3	0	0	0	0	0	0	0	3	9	0	9
15	E. crystallorophias metan.		6	24	15	7	0	0	5	0	0	0	0	0
35	Cyllopus sp.		0	7	0	0.2	0	1	0.2	0	0	0	0	0
25	Tysanoessa sp. cal. 1		0	2	20	0	4	3	4	0	0	0	0	0

Three clusters were distinguished on the 0.36 distance level: Deeper samples (400 to 100 m depth layers) from both stations (cluster 1); surface samples (200–0 m) from "V-JAN" (cluster 2), and surface samples (100–0 m) from "V-FEB". This grouping indicates a lower variability in the deeper layers off Vestkapp than in the surface.

Due to the smaller amount of water filtered (100 m^3), the vertical Multinet catches differ in several aspects from bongo net catches (e.g. they lack larger organisms like fish larvae). Furthermore, the 12 hauls do not give a representative depth distribution of all taxa. Nevertheless, species analysis revealed that certain taxa could be allocated to the surface layers (200–0 m); others occurred both at the surface and in deeper layers (Table 2).

Typical representatives of the surface layer were most of the developmental stages of *E. crystallorophias*. Larval *P. antarcticum*, not recorded in the Multinet catches, were also confined to the upper 50–100 m layer (Hubold 1985).

Discussion

The surface zooplankton off Vestkapp contains representatives of both the "Southern Shelf Community" and the "Oceanic Community" (Boysen-Ennen 1986; Piatkowski 1987), distributed roughly according to water depth. The "Southern Shelf" taxa occurred mainly over the shelf and

Table 2. Groups of zooplankton taxa and their occurrence in water layers between 400 and 0 m in Multinet catches during "V-JAN" and "V-FEB" sampling

Taxon	Ocurred only in layer:
Euphausia crystallorophias cal. 1, 3, furc. 2 *Euphausia superba* cal. 3 Hyperiidae	50–0 m
Euphausia superba metan. *Thysanoessa* sp. cal. 3, postlarv. *Rhincalanus gigas* ad. Amphipoda	100–0 m
Euphausia crystallorophias cal. 2 *Thysanoessa* sp. metan., cal. 1, furc. 2 Syphonophora Gastropoda	100–50 m
Euphausia superba cal. 1 *Euphausia crystallorophias* furc. 1 *Thysanoessa* sp. cal. 2 *Rhincalanus gigas* C 4–5 Unidentified carnivorous copepods	200–0 m
Taxon	Occurred in all depth layers:
Ostracoda spp. Appendicularia spp. *Metridia gerlachei* C 4–5 *Metridia gerlachei* ad. *Calanoides acutus* C 4–5 *Calanoides acutus* ad. *Calanus propinquus* C 4–5 *Calanus propinquus* ad. Chaetognatha spp. Polychaeta spp. *Thysanoessa* sp. cal. 2 *Thysanoessa* sp. furc. 1 *E. crystallorophias* metan. *E. superba* cal 2	400–0 m

continental slope, and oceanic taxa dominated beyond the slope. This pattern was consistent during both collection periods as suggested by the cluster groups of "V-JAN" and "V-FEB" stations, even when profound changes took place in the zooplankton. The "V-FEB" stations grouped separately from the "V-JAN" collection, which as a whole, was more similar to the Filchner collection (Fig. 2).

The existence of two well defined surface zooplankton communities over the narrow continental shelf of the eastern Weddell Sea, the similarity of the coastal zooplankton to the southern shelf community 400 miles apart, and the pronounced variability within only three weeks are the striking observations of this analysis. Both advective and developmental processes have to be considered to explain the changes in spatial and temporal distribution of the organisms.

The Southern Shelf Community

The zooplankton of the southern Weddell Sea shelf lives year round in water of below $-1.8\,°C$ (Eastern and Western Shelf Water). In summer, the 50–100 m thick surface layer of -1.5 to $-1\,°C$ is the preferred environment for the larval forms of these animals.

In the present analysis, characteristic taxa of this community were the fish *Pleuragramma antarcticum*, various developmental stages of the euphausiid *E. crystallorophias*, and the orders Polychaeta and Gastropoda. Among the polychaetes, larvae of *Bylgides pelagica* dominate (Boysen-Ennen 1987). Gastropods are mostly *Limacina helicina.*

The Oceanic Community

Typical taxa of the oceanic community encountered off Vestkapp were *Thysanoessa* sp., *Rhincalanus gigas*, *Haloptilus* sp., *Primno* sp., *E. superba*, and *Cyllopus* sp., among others. These taxa are widely distributed in the Weddell Sea. In winter, they are concentrated in the "Warm Deep Water" below 500 m depth. In summer, they ascend into the surface layer and penetrate onto the shelf.

Transport in the Coastal Current

The water masses off Vestkapp are transported southwest in the Weddell Sea Coastal Current, which is the southern branch of the Weddell Gyre. Current velocity was calculated as 0.1–0.3 m/s (Gill 1973) with a maximum over the slope of the continental shelf. Transport of a thin surface layer is determined by Ekman drift mostly in direction of the coastal current due to the predominant easterly windfield. From 27 °W, to coastal part of the current follows the coastline to the south, terminating in a cyclonic gyre over the Filchner Depression (Carmack and Foster 1975). The deeper and offshore portion of water is carried along the slope of the continental shelf to the western Weddell Sea and finally to the tip of Antarctic Peninsula (Carmack and Foster 1977).

Downstream transport of organisms in the coastal current can explain the similarity between the geographically distant locations (Filchner-Vestkapp) as well as part of the dissimilarity between the temporally distinct samples of "V-JAN" and "V-FEB".

Planktonic species living in surface waters over the shelf and slope are transported at higher rates than deeper-living and offshore taxa. Typical taxa of both coastal and surface occurrence are the younger developmental stages of the euphausiid *E. crystallorophias* and larval fish *Pleuragramma antarcticum*, i.e. characteristic members of the southern shelf community.

Due to downstream transport, these developmental stages tend to accumulate in the south. The dominant stage of *E. crystallorophias*, the first calyptopis, were 10 times more abundant in the Filchner area, than off Vestkapp ("V-JAN"). A very similar relation was found for the larval stages of *Pleuragramma antarcticum* (Table 1).

The oceanic taxa of the Vestkapp zooplankton are not likely to be transported to the Filchner area. Transport in the offshore parts and in deeper layers is less pronounced than near the surface. Seasonal vertical migration into deeper layers may reduce transport of these taxa. At the divergence of the coastal current at 27 °W, the offshore community follows the continental slope to the west in the circulation of the Weddell Gyre.

Due to the different time scales of transportation in the current, the oceanic community gains influence over the shelf and dominates the zooplankton off Vestkapp later in summer.

Developmental Processes

Besides the effect of downstream transport, developmental processes of stages of species also affected the composition of the communities in "V-JAN" and "V-FEB".

The three abundant stages of *E. crystallorophias* in "V-JAN" were cal. 1, 2, and 3 (Table 3). In "V-FEB", cal. 2, 3 and furc. 1 were found. Thus, in three weeks, a mean developmental advance of one stage took place. In the same time, the three abundant stages of *Thysanoessa* sp. in "V-JAN" (cal. 2, 3, and furc 1) developed to furc 1, 2, and 3, i.e. advanced two stages. Of both species younger stages were found off Filchner, indicating a generally delayed development in the south.

Of *E. superba*, only two developmental stages (calyptopis 1 and 2) were caught mostly in "V-FEB" samples, with cal. 1 predominant. Krill therefore appears last of the euphausiids, towards the end of summer, accompanied by carnivorous copepods and furciliae of *E. crystallorophias* and *Thysanoessa* (species cluster F).

It cannot be decided whether the *E. superba* calyptopis were carried horizontally from the northeast into the area, or whether the nauplii hatched in the deep trench near Vestkapp and appeared in surface samples at the end of their developmental ascent. Nauplii, however, were not caught in any of the deep Multinet catches during "V-JAN", which supports a transportation hypothesis. Taking an approximate age of 15–20 days for a calyptopis-2 larva (Makarov 1979), spawning may have occurred only a few miles upstream, e.g. near Cape Norvegia, where relatively high concentrations of adult krill, as well as krill larvae have been found in earlier years (Hempel and Hempel 1982; Piatkowski 1987).

E. superba is considered a typical species of the Weddell Gyre and so far has rarely been recorded in net catches over the shelf of the southern Weddel Sea (Fevolden 1979, 1980; Piatkowski 1987). Recent observations during late winter indicate, however, that adult krill lives abundantly in and under sea ice in the southern Weddell Sea (Hempel, in press). Thus, this species must be considered as a member of a cryopelagic shelf community at least in winter. The drift of larvae in the neritic part of the coastal current off Vestkapp indicates a krill population in the southern Weddell Sea, with its reproduction tuned to the late summer zooplankton community of the coastal current.

A Simplified Analysis

Overall need to reduce sorting time led us to compare results from these matrices with simpler versions in which (a) all copepod stages and species (> 500 μ) were lumped in the order Copepoda, or (b) all euphausiid stages were lumped in the respective species. By restricting the analysis on the size fraction > 500 μ, the copepod communities were not represented adequately in our material. For the considered size fraction, results (Table 4) suggest that the present analysis of macrozooplankton is not influenced to a high degree by the stages and species of Copepoda but is strongly influenced by the distribution of the euphausiid developmental stages. When lumped in the respective species, the share of lower distance levels increased markedly.

Table 3. Developmental stages of two euphausiid species off Vestkapp and in the Filchner area in percentage (100% = abundance of all stages of the species in each area; [a] based on very low abundances)

Species/stage		V-JAN	Filchner	V-FEB
		%	%	%
E. crystallorophias	metan.	1.2	0.4	0.0
	cal. 1	10.8	32.9	0.7
	cal. 2	27.4	52.4	12.1
	cal. 3	60.0	10.4	30.0
	furc. 1	0.5	0.4	52.1
	furc. 2	0.0	0.0	5.0
	postlarv./adult	0.2	3.6	0.1
Thysanoessa sp.	cal. 1	1.9	0.0	0.0
	cal. 2	17.8	87.0[a]	0.0
	cal. 3	29.4	0.0	3.6
	furc. 1	39.3	0.0	23.4
	furc. 2	9.8	0.0	40.5
	furc. 3	0.0	0.0	30.6
	postlarv./adult	1.9	13.0[a]	1.8
E. superba	cal. 1	0.0	100.0[a]	11.6
	cal. 2	100.0[a]	0.0	89.4

Table 4. Frequency distribution of distance coefficients of the data matrix used for the present cluster analysis, as well as two reduced versions. a) lumping the copepod stages and species as order Copepoda and b) lumping the stages of the euphausiids as species

Coefficients of distance	All taxa	Copepods lumped as order	Euphausids lumped as species
$d < 0.1$	0	0	0
$0.1 < d < 0.2$	0	0	0
$0.2 < d < 0.3$	0	0	4
$0.3 < d < 0.4$	4	7	33
$0.4 < d < 0.5$	49	52	141
$0.5 < d < 0.6$	159	155	337
$0.6 < d < 0.7$	374	304	425
$0.7 < d < 0.8$	595	565	438
$0.8 < d < 0.9$	382	443	198
$0.9 < d < 1.0$	33	70	20
$d = 1.0$	0	0	0

For a practical approach of macrozooplankton community analysis for monitoring purposes, we recommend concentrating the sorting and identification effort on a detailed analysis of euphausiid species and developmental stages, which are more adequately sampled as a population than the copepods.

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