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Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988)

Thomas M. Lancraft, Thomas L. Hopkins, Joseph J. Torres and Joseph Donnelly

Department of Marine Science, University of South Florida, 140 7th Avenue South, St. Petersburg, FL 33701-5016, USA

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Summary. Fifty-seven species of oceanic micronekton and macrozooplankton were collected under pack ice during the winter in the vicinity of the Weddell–Scotia Confluence with a modified opening-closing Tucker trawl. The majority of the 57 species did not vertically migrate and lived deeper during the winter than during the spring or fall. However, despite the short day length, several of the most common mesopelagic fish and crustaceans did migrate. Fish moved into shallower depths at night but apparently most did not continue into the near-freezing upper mixed layer, leaving that zone to the migratory crustaceans. In the upper 1000 m, the dominant species were, in order of decreasing biomass, *Euphausia superba*, the cnidarian *Atolla wyvillei*, the ctenophore *Beroe* sp., and the mesopelagic fish *Electrona antarctica*, *Bathylagus antarcticus* and *Gymnoscopelus braueri*. *Thysanoessa macrura* and *Salpa thompsoni* were biomass subdominants. The majority of the dominant species showed little seasonal differences in biomass. However, the biomass of gelatinous species varied considerably with *A. wyvillei* and *Beroe* sp. being most abundant and *S. thompsoni* least abundant during the winter. Incidence of food in the stomachs in several important species was low, suggesting a low impact on their zooplankton prey. Specimens of *S. thompsoni* had high quantities of food in their guts but this species was uncommon so its net impact would also have been low. *Euphausia superba* and the three common mesopelagic fish had significantly lower stomach fullness ratings during the winter than during the fall, suggesting an overall decrease in feeding activity of dominant species during the winter.

Introduction

The winter season is a critical period in the life histories of much of the Antarctic pelagic fauna. Long nights, severely curtailed primary production and the ubiquitous presence of sea-ice act in concert to influence the daily activities of species at every trophic level. Two activities that are particularly susceptible to the influence of the winter season are diel patterns of vertical migration, which are light cued, and visually mediated predation.

Data are scarce on distribution patterns in Antarctic pelagic fauna during the winter. A deeper winter distribution of important species among the Antarctic zooplankton (Foxton 1956; Hopkins 1971; Voronina 1973) changes the structure of the water column for secondary consumers; the biomass maximum is deeper and the probability of encounters with prey increases below 500 m.

This paper describes the diel vertical distribution, abundance and biomass of Antarctic macrozooplankton and micronekton in the Weddell–Scotia Confluence region during the winter season. Diet and gut fullness have been analyzed in the dominant species and compared with that of the austral fall in an attempt to discern the influence of the winter season on pelagic secondary consumers.

Methods

Sampling and treatment of specimens

Micronekton and macrozooplankton were collected in the southern Scotia Sea from the *RV Polar Duke* during the austral winter (20 June–14 August 1988) as part of the Antarctic Marine Ecosystem Research in the Ice Edge Zone (AMERIEZ) program (Fig. 1, study area C). Most of the samples were taken from below partially consolidated pack ice (8/10–10/10 coverage, up to 1 m thick floes); the resultant data are generally representative of a wintertime oceanic ice pack system. Hydrographic information was obtained and analyzed by Husby et al. (1989) using CTD and XBT casts on or near the stations we sampled.

Micronekton and macrozooplankton (> 20 mm in greatest dimension) were sampled using a modified opening-closing Tucker trawl with a 1.8 m^2 effective mouth opening towed at an average speed of 2 knots. The trawl mouth was opened and closed using a clock-actuated release device (Davies and Barham 1969). The main net was constructed of 4 mm mesh, tapering down to a 1 mm mesh cod-end net enclosed by a PVC jug-type cod-end (Lancraft et al. 1989). Volume of water filtered was measured only when the trawl was fishing by using dial type flowmeters mounted on the trawl frame (Hopkins and Baird 1975). Depth of tow was recorded by time depth recorders. Zooplankton were sampled concurrently with a collapsible 0.5 m, 163 μ mesh plankton net nested within the trawl (0.2 m^2 mouth area). Specimens larger than 20 mm captured in the plankton net were combined with the catch from the main trawl.

Twenty-six discrete depth tows (7 day and 19 night) were used (Table 1) to investigate patterns of diel vertical distribution, numerical abundance and biomass. Most of the tows were conducted under the ice pack (n = 16; 5 day, 11 night). Other discrete tows were taken in the open water (6) and ice edge (4) to complete the daytime vertical series and enlarge the overall data set (Table 1). Sampling was predominantly in the upper 1000 m but several tows sampled down to 1200 m. Supplementary oblique tows were used to establish a more complete species list.

Collections were preserved in a 10% buffered formalin solution, shipped to the laboratory and transferred to an aqueous solution immediately prior to analysis to remove the formaldehyde. After the analyses were complete the samples were stored in 50% isopropanol. All micronekton and macrozooplankton were identified to the lowest taxon, enumerated and their preserved wet weight (WW) measured (± 0.001 g). Since ctenophores do not preserve well, they were identified, counted and their volume estimated immediately after each tow. Ctenophore volume was converted to wet weight by assuming 1 l equals 1000 g. Dry weight (DW) was estimated by subtracting water content (determined by drying to constant weight at 60 °C) from wet weight.

Procedures used to estimate vertically integrated numerical abundance and biomass were identical to those in Lancraft et al. (1989). However, abundance and biomass of *E. superba* were probably underestimated in this study due to their residence on or near the ice pack (Daly, 1990; Daly and Macaulay 1988) precluding capture by our trawl. Data from night tows were used to minimize bias due to visually mediated net avoidance. Integrated values for the 0–200 m and 0–1000 m depth strata were calculated using data from all discrete tows independent of habitat. This approach was necessitated by the patchy horizontal distribution patterns of the common species (e.g., *Euphausia superba*). The addition of data from open water and ice edge tows to pack ice data had a negligible effect on the estimates of integrated abundance and biomass. Depths of peak abundance (over 50% of the population) were calculated for dominant species.

Diets

The diets of 10 micronekton species, including most of the dominant species (coelenterates and *Thysanoessa macrura* excepted), were determined by gut analysis. Contents of digestive tracts were examined in water on microscope slides at 40 to 400 × magnification following procedures described by Hopkins (1985b, 1987) and Hopkins and Torres (1988).

To obviate bias from net feeding, the diet of *Euphausia superba* was examined only in specimens removed from the stomachs of 8 Adelie penguins captured within the pack ice. Diet analysis was restricted to krill foreguts because of the difficulty of removing the intestine. Only midguts of *Cyllopus lucasii* were examined as foreguts often contained food obviously ingested in the net. The 5 fish species investigated all showed evidence of net feeding hence only data from intestines are presented. Net feeding of *Thysanoessa macrura*, a common species, forced us to eliminate it from the data set. *Sagitta gazellae*, *Salpa thompsoni* and *Brachioteuthis picta* gave no indication of net feeding, therefore data from their entire digestive tracts are presented.

Results

Hydrographic setting

The study area was hydrographically complex (Fig. 1, area C). It was a region of mixing between water masses

Table 1. Wintertime trawl data from AMERIEZ cruise. N = Night, D = Day, I = Ice Pack, E = Edge, O = Open Water

Tow no.	Date	Habitat	Diel period	Depth (m)	Lat. (S)	Long. (W)	Local time		Vol. filt. (10^4 m^3)
							open	close	
3	20VI1989	E	N	0–40	60°10.4	42°01.6	2352	0025	0.5157
8	23VI1989	E	N	0–75	59°19.6	44°56.3	2129	2145	0.1900
21	25VII1989	O	N	0–50	57°41.5	35°44.4	0013	0053	0.1672
25	30VII1989	O	N	0–75	57°59.9	43°03.0	2013	2035	0.2417
28	3VIII1989	I	D	0–60	59°35.2	43°53.0	0949	1040	0.5056
29	3VIII1989	I	D	60–105	59°35.7	43°53.5	1205	1305	0.8361
30	3VIII1989	I	D	100–200	59°31.7	43°55.3	1412	1512	0.9091
31	3VIII1989	I	N	0–40	59°29.6	43°54.6	1924	2025	0.6048
32	3VIII1989	I	N	60–150	59°28.4	43°58.2	2100	2200	1.0045
33	3VIII1989	I	N	150–240	59°30.6	43°59.3	2301	0003	1.0380
34	4VIII1989	I	N	200–400	59°33.1	44°02.5	0110	0211	0.7924
37	4VIII1989	I	N	300–550	59°12.3	44°30.0	2200	0000	1.3920
38	5VIII1989	I	N	550–1000	59°14.5	43°57.6	0205	0438	1.3129
39	6VIII1989	I	D	300–500	58°51.1	44°13.2	1335	1435	0.7750
40	6VIII1989	I	D	200–300	58°51.4	44°12.3	1536	1638	1.0940
41	6VIII1989	I	N	> 1000	58°47.6	44°21.1	1825	2055	1.4010
42	6VIII1989	I	N	500–800	58°46.6	44°25.1	2230	2330	0.5365
43	7VIII1989	I	N	100–250	58°47.7	44°26.7	0102	0205	0.5574
44	7VIII1989	I	N	0–50	58°50.5	44°26.9	0233	0315	0.4471
45	7VIII1989	I	N	50–100	58°51.2	44°29.5	0352	0455	0.8277
46	7VIII1989	E	D	500–750	58°22.9	44°14.4	1125	1225	0.5813
47	7VIII1989	O	D	> 1000	58°24.1	44°12.1	1452	1656	1.4874
48	7VIII1989	O	N	300–500	58°29.5	43°59.8	2015	2115	0.8197
49	7VIII1989	O	N	100–400	58°25.3	44°07.8	2245	2347	0.7154
50	8VIII1989	O	N	0–60	58°20.8	44°13.3	0030	0117	0.6081
52	14VIII1989	E	N	0–75	58°56.2	48°14.8	0017	0116	0.6558

flowing northward from the Weddell Sea (Weddell–Scotia Confluence) and those flowing southeastward from the Drake Passage (Antarctic Surface Water) and Scotia Sea (Scotia Sea Warm Deep Water) (Husby et al. 1989). The present study area was a blend of Scotia Sea water (sampled in 1983, Fig. 1, area A) and Weddell Sea water (sampled in 1986, Fig. 1, area B). The depth of the upper mixed layer ranged from 80–140 m at all stations with the layer tending to be deeper and nearer the freezing point under the pack ice. The upper mixed layer was uniformly found above a layer of warmer water, which occurred below 200 m (Husby et al. 1989).

Conditions for each station varied and depended on which of the major water masses dominated at the time of sampling. Most of the trawling, conducted in the southern part of the study area under the pack ice, was in the colder Weddell–Scotia Confluence water (Fig. 1, area C). Samples taken from open water and at the ice edge were usually from the warmer Scotia Sea Warm Deep Water. However, because of rapid wind-forced ice movements, ice edges were often not congruent with water column conditions.

Species composition and vertical distribution patterns

Fifty-seven species of micronekton and macrozooplankton were collected (Table 2). Many species were rare, these being represented by fewer than 5 specimens. Mesopelagic fish were the most diverse group with a total of 17 species. The mesopelagic lanternfish (Myctophidae) accounted for nearly half of all fish species ($n = 8$). Cnidarians were also well represented with a total of 8 species. Among the crustaceans, amphipods were the most diverse group ($n = 6$) while euphausiids and decapods were each represented by 4 species. Cephalopods ($n = 3$) were probably under-represented because of their net-avoidance capabilities.

In winter much of the pelagic fauna in the study region resided deep in the water column, with some species only found below 1000 m (Table 2). With the exception of *Cyclothone microdon*, all of the common mesopelagic fish (*Bathylagus antarcticus*, *Electrona antarctica*, *Gymnoscopelus braueri*, *Notolepis coatsi*) vertically migrated (Table 2). *Cyclothone microdon* is a known non-migrator (Lancraft et al. 1989). In addition, the remaining two *Gymnoscopelus* species, the *Protomyctophum* species and *Krefftichthys anderssoni* have been shown to exhibit diel vertical migrations in other studies where they were more numerous (Hulley 1981; Lancraft et al. 1989; T.M. Lancraft et al., unpublished data). The daytime centers of distribution for most of the fish were greater than 1000 m. The nighttime (shallowest) centers of peak abundance for the fish were well below the near-freezing water of the mixed layer. In contrast, the vertically migrating crustaceans (*Euphausia superba*, *E. frigida* and *Cyllopus lucasii*) did inhabit the frigid surface mixed layer during the night. In fact, these three crustacean species and the ctenophore *Callianira antarctica* were the only common species to inhabit the mixed layer at any time of day.

Abundance and biomass

Euphausia superba was clearly the most numerous species in the study area with 11.5 individuals/m^2 in the water

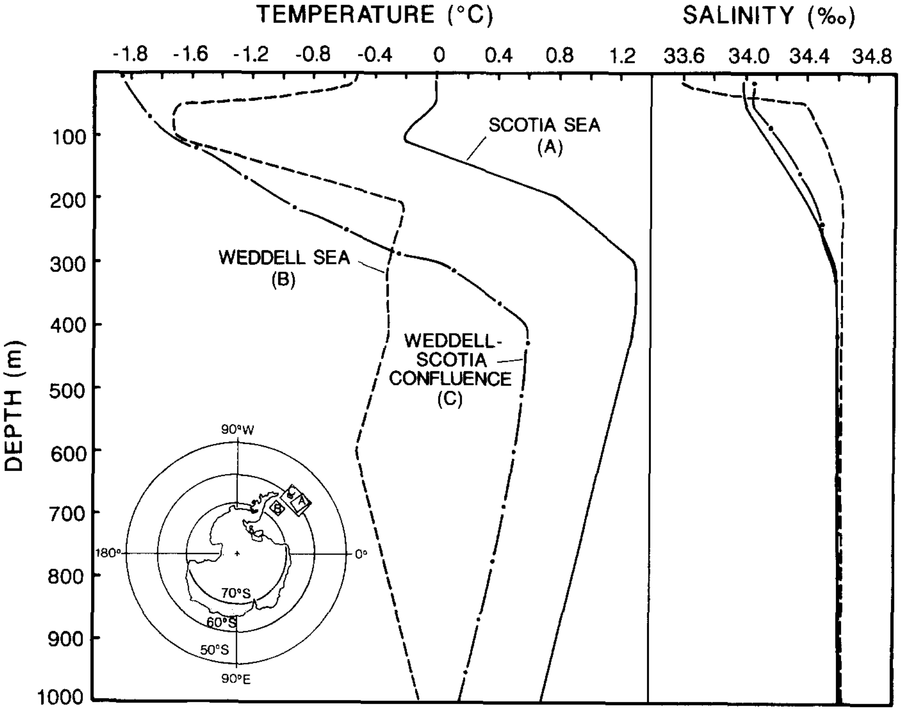

Fig. 1. Hydrographic conditions in three oceanic ice edge zones. Scotia Sea (*A*) and Weddell Sea (*B*) profiles represent open waters in spring 1983 and fall 1986, respectively (Lancraft et al. 1989). The Weddell–Scotia Confluence (*C*) represents the area of the present study during the winter in the ice pack

Table 2. Diel distribution patterns of micronekton and macrozooplankton collected during wintertime AMERIEZ cruise in ice covered seas

Species	*n*	Day range (m)	Peak (m)	*n*	Night range (m)	Peak (m)
Pisces						
Bathylagus antarcticus	2	> 1000		10	300–1000	500–1000
Benthalbella elongata[a]				2	0–1800	
Borostomias antarcticus[a]	1	0–1000				
Electrona antarctica	13	500– > 1000	> 1000	38	0–1000	100–400
E. carlsbergi				1	300–500	
Gymnoscopelus braueri	3	> 1000		18	100–550	200–400
G. opisthopterus[a]				2	0–400	
G. nicholsi[a]				3	0–1100	
Protomyctophum bolini	3	200–500		6	300– > 1000	400–500
P. tenisoni				10	0–400	
Krefftichthys anderssoni				1	500–800	
Cyclothone pallida[a]				1	0–890	
C. microdon	2	> 1000		6	300– > 1000	> 1000
Cyclothone sp.[b]	1	500–750		1	500–800	
Notolepis coatsi	1	> 1000		13	150–1000	200–400
Paradiplospinus gracilis				3	0–240	
Muraenolepis microps	1	> 1000				
Crustaceans						
Euphausia superba	35	0– > 1000	200–350	9626	0– > 1000	0–40
E. triacantha	41	200– > 1000	200–350	65	0– > 1000	100–500
E. frigida	1	200–350		9	0–100	50–100
Thysanoessa macrura	40	200–350		296	0– > 1000	50–550
Cyllopus lucasii	1	300–500		21	0–150	0–40
Cyphocaris richardi	2	500 > 1000		2	100–400	
C. faueri				1	> 1000	
Parandania boecki	3	500– > 1000		1	> 1000	
Themisto gaudichaudi				7	0–70	
Megalanceola stephensi[a]				1	0–1800	
Nematocarcinus lanceopes				3	150–400	
Pasiphaea scotiae	1	> 1000		2	> 1000	
Petalidium foliaceum				2	> 1000	
Gennadas kempi	1	> 1000		1	> 1000	
Gigantocypris mulleri	1	500–750				
Gnathophausia gigas	1	> 1000		1	> 1000	
Boreomysis rostrata[a]	1	> 1000		2	550– > 1000	
Eucopia australis				2	> 1000	
Molluscs						
Brachioteuthis picta	1	– 1000		3	150–400	
Galiteuthis glacialis	1	500–750		3	100–400	
Psychroteuthis glacialis[a]					0–650	
Clio pyramidata				1	0 70	
Macrozooplankton						
Salpa thompsoni	103	0– > 1000	> 1000	157	0– > 1000	500–1000
Sagitta gazellae	122	100– > 1000	> 1000	244	0– > 1000	300– > 1000
S. marri	6	> 1000				
Eukrohnia hamata	47	300– > 1000	> 1000	87	0– > 1000	550– > 1000
Calycopsis borchgrevinki				16	100–1000	300–550
Crossota brunnea[a]				1	0–890	
Halicreas minimum	1	> 1000		7	> 1000	
Pandea rubrum[a]	1	0–1000				
Diphyes antarctica	54	0–500	100–200	61	0–1000	100–300
Atolla wyvillei	4	> 1000		8	550– > 1000	
Periphylla periphylla	2	500– > 1000		1	300–500	
Stygiomedusae gigantea				1	500–800	
Callianira antarctica	2	0–105		6	0–240	0–60
Beroe sp.	1	100–200		4	0–70	
Tomopteris carpenteri	7	200– > 1000	> 1000	19	0–550	50–100
Vanadis antarctica				2	0–550	
Travisiopsis coniceps[a]				1	0–890	
Pelagonemertes rollestoni[a]				1	0–890	

[a] From oblique tows not listed in Table 1

[b] Described as *Cyclothone sumiae*, Kobayashi, unpublished 1973

column (0–1000 m) (Table 3) despite its probable underestimation. Other common species included, in decreasing abundance, *Thysanoessa macrura*, *Sagitta gazellae*, *Eukrohnia hamata* and *Salpa thompsoni*. These five species comprised 88.5% of the total numbers of all species for the 0–1000 m zone. However, *Euphausia superba* was abundant only in the upper 200 m, while the other 4 species were frequently collected below that depth (Tables 2, 3). The sixth most common species in the upper 1000 m was *E. triacantha*, a deeper living euphausiid.

Total nighttime integrated biomass for the 0–1000 m zone under the ice pack was 2978 mg DW/m^2 (Table 3). Mesopelagic fish were the most important group providing 39% of the total biomass. They were followed closely by euphausiids (principally *E. superba*) with 32% and coelenterates (25%). Salps, represented exclusively by *Salpa thompsoni*, contributed only slightly (2%) to the total dry weight biomass.

Nighttime biomass in the 0–200 m zone (1515 mg DW/m^2) was 51% of the 0–1000 m zone total. *Euphausia superba* provided most (56%) of the biomass in the upper 200 m with the ctenophore *Beroe* sp. contributing a large fraction (23%). The mesopelagic fish *Electrona antarctica* (8.5%) and *Paradiplospinus gracilis* (3.5%) provided moderate biomass in that zone, mainly between 100 to 200 m.

Integrated nighttime biomass in the zone between 200 and 1000 m (1463 mg DW/m^2) was dominated by three common mesopelagic fish (*Electrona antarctica*, *Bathylagus antarcticus* and *Gymnoscopelus braueri*) and the large scyphomedusa *Atolla wyvillei*. These comprised 24%, 17%, 13% and 22% of total nighttime biomass in that zone, respectively. Biomass subdominants in the 200–1000 m zone were *Thysanoessa macrura*, *Protomyctophum bolini* and *Salpa thompsoni*.

Integrated wet weight biomass for the 0–1000 m range was 22894 mg WW/m^2 (Table 3). The coelenterates, though rare, contributed more wet weight biomass than

Table 3. Integrated abundance, wet weight (WW) and dry weight (DW) biomass for important species. Data from nighttime discrete depth tows taken during winter Ameriez 1988 cruise. Dash indicates < 1 mg/m^2

Species	0–200 meter zone			0–1000 meter zone		
	No./m^2	mgWW/m^2	mgDW/m^2	No./m^2	mgWW/m^2	mgDW/m^2
Pisces						
B. antarcticus				0.180	1742	249
E. antarctica	0.079	411	129	0.310	1534	481
G. braueri	0.041	162	54	0.127	736	247
P. bolini				0.050	189	49
N. coatsi	0.007	–	–	0.102	37	7
P. gracilis	0.002	177	53	0.003	282	85
C. microdon				0.036	48	16
Others	0.008	19	4	0.063	101	27
Subtotal	0.137	769	240	0.871	4669	1161
Euphausiacea						
E. superba	11.463	3125	854	11.527	3171	866
E. triacantha	0.125	8	2	0.576	48	13
E. frigida	0.021	1	–	0.021	1	–
T. macrura	0.551	44	13	2.341	228	67
Subtotal	12.160	3178	869	14.465	3448	947
Thaliacea						
S. thompsoni	0.228	329	13	1.004	1427	59
Coelenterata						
A. wyvillei				0.115	7312	322
D. antarctica	0.155	77	1	0.391	206	3
Other Cnidaria	0.013	38	1	0.177	806	35
Beroe sp.	0.007	3573	347	0.007	3573	347
C. antarctica	0.013	335	32	0.016	501	49
Subtotal	0.188	4023	381	0.706	12398	755
Other						
S. gazellae	0.214	60	3	2.175	824	40
E. hamata	0.035	–	–	1.254	32	2
Others	0.126	58	9	0.198	96	14
Subtotal	0.375	118	12	3.627	952	56
Total	13.088	8417	1515	20.673	22894	2978

Table 4. The diets of common micronekton and macrozooplankton species in the ice edge zone during winter. Values under dietary taxa within the body of the table are frequency of occurrence (number of guts)

	E. superba	*C. lucasii*	*S. gazellae*		*S. thompsoni*	*B. picta*	*B. antarcticus*		*E. antarctica*			*G. braueri*		*P. bolini*	*P. tenisoni*
Size range (mm)	32–47	11–27	30–60	60–90	40–56	20–50	60–90	90–120	30–60	60–90	90–120	60–90	90–120	30–60	30–60
Sample size	30	26	192	103	15	11	11	17	46	70	11	40	13	11	22
Incidence of identifiable food	21	21	5	9	15	10	10	17	30	36	5	39	10	11	21
Dietary taxa															
Diatoms	18				15										
Dinoflagellates	3				15										
Silicoflagellates					11										
Foraminifera					10										
Radiolarians	1				15										
Tintinnids	15				15							2			
Oithona	1				11							2			
Oncaea							8	11	2	2		1			
Calanidae			1					2			1	2	1	4	3
Aetideidae								2		1		3	1	2	
Euchaeta										1		1		2	
Metridia			1				3	5	7	1			1	4	11
Pleuromamma									1	2		3		1	
Heterorhabdus							3	4		2		5	1		1
Other copepods	1				14		6	5	3	1		23	5	1	
Copepod nauplii					12										
Conchoecia							5	12	15	19	3			10	
Euphausia			1	4										1	
Thysanoessa			1	2											
Euphausiids	3[a]		1	4		1			16	21	2	23	3	4	15
Euphausid larvae								2							1
Hyperids							1	5		2		2			
Siphonophores		12					6	8	2	2					
Pelagobia	1	1					4	5	1	4		6	7	7	4
Limacina					2										2
Oikopleura							1		6	1		4	2		
Salpa		8						4					1		
Gelatinous tunicates		1					2	4		1		3			
Eukrohnia										2			1	1	1
Chaetognaths				1					2	1				1	2
Others					2[b]					1[c]					

[a] molts; [b] eggs; [c] polychaete

any other group (54% of the total) because of their large size and high water content.

Diets

Little food was observed in the foreguts of *Euphausia superba*; 26 of 30 foreguts were less than 25% full. Food items were almost exclusively diatoms, usually fragmented, and tintinnids (Table 4). Little other food was recorded with only 10 incidences of all other types of food in 30 foreguts. *Salpa thompsoni*, the other principal small particle consumer among the macroplankton, contained a wide variety of food which ranged from phytoplankton to copepods. Based on visual estimates, the principal food, in terms of biomass, was phytoplankton. Salps examined from shallow water (0–50 m) within the pack ice contained tisbid harpacticoid copepods, which are dominant in ice pore water (Lang 1948; Hopkins and Torres 1988). *Cyllopus lucasii*, a predatory hyperiid amphipod, generally had full guts which contained gelatinous food (siphonophores and salps). *Sagitta gazellae*, the dominant chaetognath, had low food incidence in that only 14 of 295 individuals contained food. The principal prey were euphausiids, including both *E. superba* and *T. macrura*. Eleven *Bathyteuthis picta* were examined but 10 had empty digestive tracts. The gut of one individual contained euphausiid debris.

Bathylagus antarcticus fed mainly on crustaceans (Table 4) but gelatinous prey (tunicates and siphonophores) were a substantial fraction of the diet. Most intestines contained some food (about 6–8 items/intestine) though they were rarely full. Crustaceans also predominated as food for all three size-classes of *Electrona antarctica*. The most abundant prey were copepods, ostracods and euphausiids. Gelatinous food was a minor constituent. Intestines of this species contained few items (average 1.1 items/intestine). The food of *Gymnoscopelus braueri* was primarily copepods and euphausiids with a notable absence of ostracods in the diet. Some gelatinous food was present, mainly from relatively small species (larvaceans and pelagobid polychaetes). Nearly all the intestines of *G. braueri* contained food but the number of prey in each intestine was low (average 1.9 items/intestine). *Protomyctophum bolini* primarily ingested copepods, ostracods and euphausiids and the polychaete *Pelagobia longicirrata*. All intestines contained some food with an average of 4.5 items/intestine. *Protomyctophum tenisoni*, a less abundant congener, had a similar diet but with proportionally more euphausiids. The average number of food items per intestine for this species was 3.7.

Discussion

This is the first examination of a wintertime micronekton/macrozooplankton community in an oceanic Antarctic ice pack system. The few other winter studies which included micronekton and macrozooplankton investigated near-continent (Siegel 1988, 1989) or near-island areas (Atkinson and Peck 1988). Lancraft et al. (1989) examined the southern Scotia Sea during the spring and the northern Weddell Sea during the fall. Both study areas were in open water in the vicinity of marginal ice zones close to the present study area (Fig. 1). Comparisons between vertical distribution, abundance, biomass and diet of the macrozooplankton/micronekton communities at the three study areas allow us to examine the effect of environmental conditions (ice cover and season) on oceanic pelagic systems.

Diversity in the study area was high and increased with depth. Undoubtedly the complexity of the oceanographic conditions enhanced the diversity of the region. In the present study, fish species also found in subtropical-temperate regions, e.g. *Cyclothone pallida* (Badcock 1984) and *Borostomias antarcticus* (Gibbs 1964), as well as those with subantarctic distributions (*Electrona carlsbergi*, *Krefftichthys anderssoni* and *Protomyctophum tenisoni*, Hulley 1981; *Benthalbella elongata*, Johnson 1982) were collected under the pack ice in Antarctic water masses. We also collected *Gennadas kempi*, a subantarctic decapod (Kensley 1971; Kirkwood 1984), under the pack ice well south of its usual range. Previous studies have shown that horizontal migrations of both *E. superba* larvae (Rakusa-Suszczewski 1984) and pelagic shrimps (Iwasaki and Nemoto 1987) were not prohibited by oceanic fronts associated with water masses. The majority of micronektonic species live at greater depths where the oceanic fronts are not sufficiently well developed (Husby et al. 1989) to preclude transport between water masses.

Ice conditions have been shown to affect community structure. During the spring, deep dwelling mesopelagic species were collected nearer to the surface under pack ice than in the open water (Ainley et al. 1986). In addition, Ainley et al. (1988) and Daly and Macaulay (1988) report *E. superba*, *E. antarctica* and squid to be most prevalent near the ice or in the ice pack. In contrast, *E. frigida*, *S. thompsoni* and the amphipods *Cyllopus* and *Vibilia* were found by Ainley et al. (1988) and Daly and Macaulay (1988) to be less abundant in the water column under the ice pack. Daly and Macaulay (1988) further demonstrated that population size of *T. macrura* was less under the pack ice. The above observations of distributional modifications by these species were substantiated by comparisons with estimates of biomass in open water (Lancraft et al. 1989) and pack ice (Table 5, 0–1000 m zone).

A seasonal comparison of vertical distribution patterns in important micronektonic and macrozooplanktonic species (Fig. 2) shows that wintertime patterns often varied from those observed during the fall and spring (Lancraft et al. 1989). Peak abundance at night for *B. antarcticus*, *C. microdon*, *S. thompsoni*, *S. gazellae* and *E. hamata* were much deeper in the winter than during the spring and fall. Depths of maximum nighttime abundance were also greater for *E. antarctica* and *E. triacantha* during winter, though seasonal differences in vertical distribution were less pronounced. Both species were rare at the surface only during winter. *Thysanoessa macrura*, *G. braueri* and *N. coatsi* did not exhibit different seasonal vertical patterns. *Euphausia superba* inhabited shallower depths during the winter. The close relationship between the distribution patterns of these species and their prey

Table 5. Seasonal comparison of integrated nighttime biomass (mg DW/m^2) for important micronekton and macrozooplankton species. Data taken from Lancraft et al. (1989) and discrete tows in present study. S, F and W represent spring, fall and winter, respectively

Species	0–200 meters			0–1000 meters		
	Open water		Ice	Open water		Ice
	S 1983	F 1986	W 1988	S 1983	F 1986	W 1988
B. antarcticus	0	60	0	216	283	249
E. antarctica	74	132	129	314	273	481
G. braueri	1	17	54	128	86	247
N. coatsi	< 1	1	< 1	1	9	7
C. microdon	0	0	0	31	20	16
Total fish	130	296	240	773	1015	1161
E. superba	773	616	854	1077	667	866
E. triacantha	3	0	2	8	0	13
T. macrura	7	8	13	15	27	67
Total euphausiids	783	624	869	1100	694	947
C. lucasii	1	< 1	2	17	3	2
S. thompsoni	105	137	13	1156	159	59
A. wyvillei	0	2	0	1	32	322
Ctenophores	0	99	379	0	99	396
Total	1027	1447	1515	3132	2377	2978

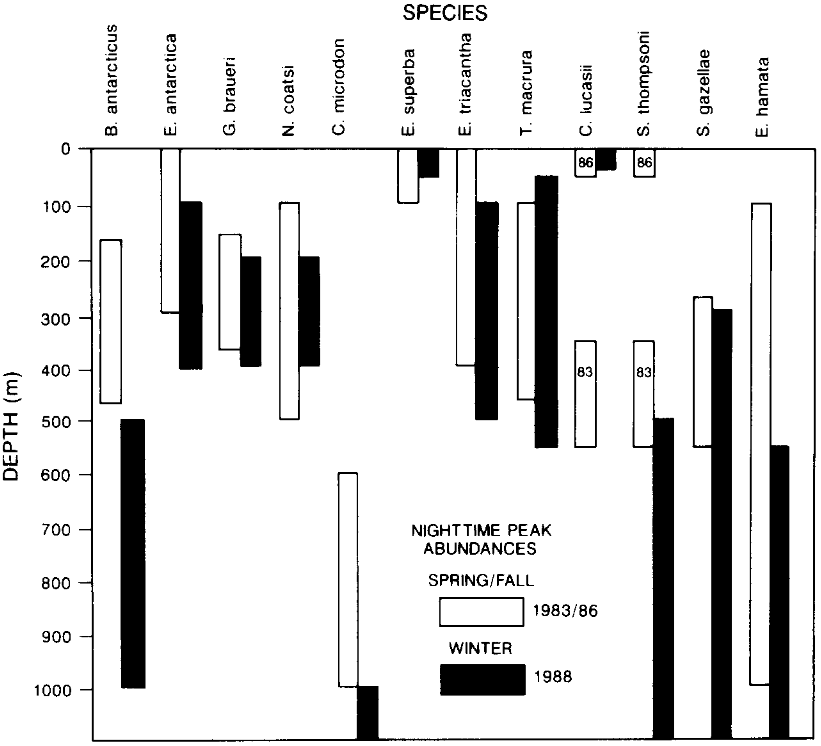

Fig. 2. Peak abundance (> 50% of the population) at night for important micronekton and macrozooplankton. *Filled bars* represent winter (1988) distributions and *open bars* indicate spring/fall (1983/1986) distributions

(Hopkins and Torres 1988, 1989; T.L. Hopkins, unpublished data) suggest that predator-prey interactions, in combination with vertical temperature structure, are a driving force for the horizontal and vertical distribution patterns of micronekton within and between seasons.

A comparison of the oceanic regions investigated in this study and Lancraft et al. (1989) showed little seasonal variation in total micronekton/macrozooplankton biomass despite the differences in ice conditions sampled; the biomass of all three sampling periods ranged from 2377 to 3132 mg DW/m^2 (Table 5). These differences are small when compared to the biomass of a nearshore, krill dominated system (over 50 g DW/m^2, Hopkins 1985a, b; T.M. Lancraft et al., unpublished data). In all seasons for the oceanic regions, *Euphausia superba* dominated the 0–200 m layer and the mesopelagic fish (*E. antarctica*, *B. antarcticus* and *G. braueri*) dominated the 200–1000 m layer (Table 5). The standing stocks of individual species of fish and euphausiids, as well as total fish and total euphausiid biomass, also varied little seasonally. On the other hand, the biomass of *S. thompsoni* was variable with lowest values occurring during the winter. This species is capable of rapid population expansion through asexual production during bloom periods.

Differences in number of prey consumed were most pronounced between the winter and fall in the diets of the two small-particle grazers (*E. superba* and *S. thompsoni*). *Euphausia superba* foreguts were relatively empty reflecting the lower phytoplankton availability during winter than during fall (mean chl a/m^3 over 1–100% light zone: winter 1988 = 0.18 mg; fall 1986 = 0.38 mg; Nelson et al. 1989; W.O. Smith, unpublished data). Counts of the mean number of diatom fragments/foregut indicate that krill foreguts were significantly (Student's t-tests, $P = 0.01$–0.001) less full in winter than in late fall in the western Weddell Sea (Table 6). The wintertime reduction in feeding is supported by experimental data on krill grazing rates (Schnack 1985) which show that carbon intake falls off sharply with decreasing phytoplankton availability.

On the other hand, the digestive tracts of *S. thompsoni* were quite full and yielded the same high food diversity noted in the fall (1986) in the western Weddell Sea (Hopkins and Torres 1989). This species difference in feeding intensity probably results because salps have a lower metabolic rate than krill (Ikeda and Mitchell 1982) and yet can filter similar volumes (Harbison and Gilmer 1976; Morris 1984) thereby making high levels of feeding energetically more feasible during periods of decreased food availability. Zooplankton were again noted to be abundant in salp guts, confirming our earlier observations that salps are consumers of small zooplankton (Hopkins and Torres 1989). Since salps contributed only 2% of the total micronekton/macrozooplankton biomass during the winter their impact on small zooplankton was probably minor. Their predation impact may be more during other seasons when their abundance and biomass are much greater (e.g., Lancraft et al. 1989, T.M. Lancraft et al., unpublished data).

Our diet analyses also included a number of biomass dominants among the larger carnivores. The stomach contents of the hyperiid *Cyllopus lucasii* were gelatinous food items also frequently encountered in the guts of Antarctic pelagic amphipods (Hopkins 1985b, 1987; Hopkins and Torres 1989) and it is suggested that the prey were salps and siphonophores with which the amphipods probably associate (Lancraft et al. 1989). The present results for *Sagitta gazellae* are similar to earlier studies examining chaetognath diets (David 1955; Hopkins 1985b, 1987; Hopkins and Torres 1989) in that few digestive tracts contained food. The low incidence of guts with food relative to the total number of chaetognaths examined (4.7%) argues for a small daily ration and a relatively low metabolic rate as demonstrated by Ikeda and Kirkwood (1989). The diet of *Brachioteuthis picta* remains relatively unknown, although one individual did contain euphausiid remains. Two other mesopelagic Southern Ocean cephalopods, *Alluroteuthis antarcticus* and *Galiteuthis* (= *Crystalloteuthis*) *glacialis* are also known to feed on krill (Hopkins 1985b).

The five midwater fish species examined fed predominantly on crustaceans (see also Solyanik 1967; Rowedder 1979). *Bathylagus antarcticus*, as characteristic of the Bathylagidae (Gorelova and Kobylyansky 1985), also contained moderate amounts of gelatinous prey. In general, intestines (and stomachs, except in obvious cases of net feeding) had moderate to low amounts of food. Mean numbers of prey/intestine for *B. antarcticus*, *E. antarctica* and *G. braueri* were less in winter, at the Weddell–Scotia Confluence, than during the fall in the western Weddell Sea – significantly so in the first two species (Table 6). Much of the population of *E. antarctica* and *G. braueri*

Table 6. Comparisons (Student's t-tests) of dietary parameters between specimens collected during fall (AMERIEZ 1986) and winter (AMERIEZ 1988). The parameters examined for the fish and krill were mean No. prey/intestine and mean No. diatoms (fragments)/foregut, respectively

Species	Cruise (yr)	Size (mm)	n	Dietary parameter	t	df	P
E. antarctica	1986	30–60	26	3.46	3.29	70	< 0.01– > 0.001
	1988	30–60	46	1.54			
	1986	60–90	33	4.09	5.99	101	< 0.001
	1988	60–90	70	0.94			
B. antarcticus	1986	60–90	13	33.85	5.41	22	< 0.001
	1988	60–90	11	7.90			
	1986	90–120	14	24.29	4.89	29	< 0.001
	1988	90–120	17	6.60			
G. braueri	1986	90–120	9	3.44	1.85	20	< 0.1– > 0.05
	1988	90–120	13	1.54			
E. superba	1986	35–52	35	268	3.11	63	< 0.01– > 0.001
	1988	32–47	30	77			

were found between 100 and 400 m at night which, in winter, has the lowest concentration of zooplankton of any time of the year (Foxton 1956; Hopkins 1971). Thus, food would be comparatively scarce for fishes feeding in this zone at night after upward migration. Those fish feeding on krill probably made short forays into the upper 100 m thereby exposing themselves to potentially fatal low temperatures (Torres and Somero 1988) as well as intense predation by surface feeding and diving birds (D.G. Ainley, personal communication). *Bathylagus antarcticus* intestines contained somewhat more food than did *E. antarctica* and *G. braueri*. This is not surprising since *B. antarcticus* remains mostly below 300 m at night where zooplankton is more abundant in winter (Hopkins 1971, T.L. Hopkins, unpublished data). The gut fullness data for these three fishes, and that for krill, support the evidence of our analyses on zooplankton feeding in the ice edge at the Weddell–Scotia Confluence (T.L. Hopkins, unpublished data) which show reduced feeding during the winter for important oceanic species.

In conclusion, from the data we suggest that the structure of the Antarctic oceanic community is dependent on several factors including hydrographic and ice conditions, season, life history and feeding patterns. Despite seasonal differences in ice conditions that affect vertical and horizontal patterns of micronekton and macrozooplankton distribution (Ainley et al. 1986; Daly and Macaulay 1988) there was no concomitant seasonal change in biomass of the longer lived dominant species of micronekton; this is consistent with multi-year survival. During the more productive seasons ice pack habitats and particularly the ice edge retain micronektonic species, possibly taking advantage of better feeding opportunities than in open water (Ainley et al. 1988; Daly and Macaulay 1988). During the less productive winter season carnivores may descend to the greater winter depths of their zooplankton prey (T.L. Hopkins, unpublished data) to feed, though feeding activity is apparently reduced in a number of species. Obviously, this is not the case for the herbivorous *E. superba* which may use the pack ice as a nursery area during the winter (Daly and Macaulay 1988). In addition, the near-freezing upper mixed layer during the winter may present life-threatening cold temperatures to mesopelagic fish (Torres and Somero 1988) thus preventing them from taking full advantage of the large numbers of krill in the ice pack. Lastly, seasonal differences in feeding intensities probably result from the influence of ice habitat and water masses on prey and predator concentrations and distributions.

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