Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea

THOMAS L. HOPKINS* and JOSEPH J. TORRES*

Abstract—The structure of the food web in the vicinity of a marginal ice zone was investigated in the western Weddell Sea during austral autumn 1986. The diets of 40 species of zooplankton and micronekton occurring in the epipelagic zone were examined and compared using non-hierarchical clustering procedures. Over half the species were in three clusters of predominately small-particle (phytoplankton; protozoans) grazers. These included biomass dominants *Calanoides acutus*, *Calanus propinquus*, *Metridia gerlachei* and *Salpa thompsoni*. Six clusters contained omnivores that had diets consisting of small particles as well as a substantial fraction of metazoan food. Among these was *Euphausia superba*. Seven groups were carnivorous, including species of copepods (1), chaetognaths (3), and fishes (5). Copepods were the most frequent food of carnivores; however krill also were important in the diets of three fish species.

Among small-particle grazers, phytoplankton occurred more frequently in guts of individuals from open water; carnivory was more in evidence in samples collected under the pack ice. Regional comparisons of material taken on this and several previous cruises indicate that, in most of the dominant species, diets remain relatively consistent with respect to major food categories. Seasonal impact on feeding dynamics appears to be great: the guts of grazing species were generally much more full (visual evidence) during summer bloom conditions than during the autumn. The following trophic sequence is suggested for grazing zooplankton species in ice-covered regions of the Antarctic: (1) Active small-particle grazing during the summer bloom period; (2) reduced ingestion rates in autumn as primary production declines and the system becomes more oligotrophic, with some species augmenting grazing with carnivory; (3) descent of zooplankton biomass species into the mesopelagic zone in late autumn–early winter with feeding largely terminated. The sequence applies to the dominant zooplankton biomass species. Feeding dynamics and vertical distribution of several of the important larger sized grazing species, such as *Euphausia superba* and *Salpa thompsoni*, remain largely unknown

INTRODUCTION

MARGINAL ice zones are areas of concentrated biological activity responsible for a large fraction of the annual primary production of polar latitudes (cf. SMITH and NELSON, 1986; SMITH, 1987). For higher trophic levels, the ice edge is a diffuse boundary between the open-water and pack-ice systems. The influence of the ice edge is potentially profound. It may divide two distinct communities, one in the open water and one in the pack ice, or it may impact a single community by delimiting the extent of primary production in the water column. Thus far, evidence favors the latter, as the zooplankton species composition in the open water and in the ice pack are virtually identical when sampled synoptically (HOPKINS and TORRES, in press). However, the trophodynamics of the zooplankton community may be altered considerably by the presence of pack ice.

---

* Department of Marine Science, University of South Florida, 140 7th Avenue South, St. Petersburg, FL 33701, U.S.A.

The present research was conducted in the western Weddell Sea during the austral autumn (March) of 1986 as part of the AMERIEZ (Antarctic Marine Ecosystem Research at the Ice Edge Zone) program. It involved two vessels, one occupying stations in open water adjacent to the ice edge (R.V. *Melville*) and the other (U.S.C.G.C. *Glacier*) concurrently operating within the pack ice. Plankton and micronekton were sampled in both habitats and the resulting collections generated information on abundance and diel distributions (HOPKINS and TORRES, in press; LANCRAFT *et al.*, in press) and provided material for trophic analyses.

The physical and biological characteristics of the western Weddell Sea are summarized in CARMACK and FOSTER (1975), HUSBY and MUENCH (1988), and HOPKINS and TORRES (in press). At the time of sampling, the ice edge was near the average location of the maximum seasonal retreat (ZWALLY *et al.*, 1983). The water masses within the epipelagic zone included surface water (surface to 25–50 m), previous winter water (50 to ~ 100 m) and transition water overlying Weddell warm water, the latter with its core at 500 m. Temperature ranged from –1.8 to +0.2°C. In the upper 25 m, the water within the pack ice was more than 1°C colder than open water in the upper 25 m (HOPKINS and TORRES, in press; HUSBY and MUENCH, 1988 and unpublished AMERIEZ data). Current velocities in the central Weddell were characteristically low (KLEPIKOV, 1964; CARMACK and FOSTER, 1975; DEACON, 1979), and dynamic height calculations indicated negligible baroclinic flow at the time of sampling (HUSBY and MUENCH, 1988).

Standing crops of zooplankton and phytoplankton were low (SMITH, 1987; HOPKINS and TORRES, in press; SMITH and NELSON, unpublished AMERIEZ data), although micronekton biomass was comparable to that in other regions of the Southern Ocean and to that in temperate to subpolar latitudes in the northern hemisphere (LANCRAFT *et al.*, in press). The principal zooplankton biomass species were the characteristic dominants of the east wind circulation system, i.e. the copepods *Calanus propinquus*, *Calanoides acutus* and *Metridia gerlachei*. The principal biomass components of the micronekton were several midwater fishes (primarily *Electrona antarctica* and *Bathylagus antarcticus*), *Euphausia superba* and *Salpa thompsoni*.

This paper reports on the diet characteristics of the above species and 33 others common to abundant in the epipelagic zone. Synoptic samples collected on both sides of the ice edge allowed a comparison of diet in the pack ice and open water areas, as well as providing a strong data base on feeding habits of an Antarctic pelagic community during the austral fall.

METHODS

Organisms used in diet analyses were collected with opening–closing 162 μm mesh plankton and 4 mm mesh midwater trawl nets. Station locations and collecting techniques are described in HOPKINS and TORRES (in press), LANCRAFT *et al.* (in press) and TORRES and SOMERO (1988). Except for *M. gerlachei* and *C. acutus* sorted from several deep (>200 m) tows, all material used in diet analysis was from the upper 200 m. Samples were preserved initially in buffered formalin, then transferred to 50% v/v isopropanol. Animals used in diet analysis were first measured, then their gut contents were examined either suspended in water in small watch glasses or on slide preparations in water or glycerin. Examination was at ×40 to ×600 depending on gut and food size. Food organisms were identified and tallied; selected items were measured with an ocular

micrometer. Fragments of animal food useful in estimating total prey size, e.g. copepod and ostracod mandibles, were measured as well (HOPKINS, 1987). To enable interspecific diet comparisons, expecially in the case of small-particle grazers, gut contents were distributed as evenly as possible on microscope slides then examined in a 60 mm² center strip (= five adjacent passes at ×300 magnification from side to side of the preparation under a 22 × 22 mm coverslip). Counts were made of all types of food encountered within this standard area. The entire preparation was then scanned for large food items and for other types of food not encountered within the standard search area. For most zooplankton species, animals from four to six stations in open water and under ice were examined to minimize the effects of patchy food availability on diet. While potential bias from post-capture feeding in nets could not be assessed in most species (HOPKINS, 1985, 1987), it was minimized in the case of fishes by using only data obtained from intestines (i.e. not from stomachs). There was some indication of net feeding (carnivory) in *E. superba*, consequently only animals retrieved from the cooling water system of the R.V. *Melville* in open water and from seal stomachs in the pack ice were utilized in diet analyses.

Non-hierarchical cluster procedures (SARLE, 1982) were used to place animals into feeding groups. This was done by utilizing the data in Table 1 which is a tally of the incidences (i.e. presence or absence) of 30 food categories in guts of each species. The tally for each food type was then converted to a percentage of all the food types recorded for a species, and was used in this form in the cluster analysis. This method is detailed in HOPKINS (1985, 1987).

Diet diversity for each species was calculated with a variant of the information index (TRAVERS, 1971) using the food incidences in Table 1 converted to percent of total food occurrences as described above. The equation is

$$D = \log_2 N - 1/N \sum n_i \log_2 n_i,$$

where D is the diversity index with a range of $0-4.9$, N is total incidences ($=100\%$) of all 30 food types and n_i is incidence (%) of a single food type (HOPKINS, 1985, 1987).

The Kolmogorov–Smirnov (SOKAL and ROHLF, 1981) test was used to compare major diet characteristics in samples of selected species collected from open water and within the pack ice.

<div align="center">RESULTS</div>

Copepods

Nineteen species were common to abundant in the epipelagic zone. Most were small particle grazers feeding on phytoplankton and protozoans (Table 1). The five species, *Ctenocalanus citer*, *Microcalanus pygmaeus*, *Oncaea curvata*, *Oithona similis* and *Oithona frigida*, had only phytoplankton in their guts. In three other species, *Oncaea antarctica*, *Oncaea prolata* and *Scolecithreicella minor*, phytoplankton accounted for over 85% of the food occurrences. All of the above species were small, less than 2 mm in length, and diet diversity, *D* (Table 2) was low, ranging from 0 to 1.08. Grazing copepods that had moderate amounts of protozoans (>10% of food incidences, mostly tintinnids) were *Metridia gerlachei*, *Racovitzanus antarcticus*, *Rhincalanus gigas*, *Calanoides acutus*, *Calanus propinquus*, *Gaetanus tenuispinus* and *Scaphocalanus vervoorti*. The latter four occasionally had small metazoans in their guts. These copepods ranged in size from 1.6 to

Table 1.   *Gut contents of principal species of plankton and micronekton occurring in the upper* 200 m
whole animals were examined in most cases, with

Species	Sample size range (mm)†	No. of individuals used in diet analysis‡	Diatoms	Silicoflagellates	Dinoflagellates	Tintinnids	Radiolarians	Foraminiferans	Heliozoans (*Sticholonche*)	Mucous/debris
Copepoda										
Calanoides acutus	5.00–6.00(5.69)	30	29	9	7	8				
	4.30–5.60(4.88)	25 I	5			4				
	4.80–5.90(5.33)	18 D								
Calanus propinquus	5.30–6.10(5.76)	35	34	14	13	19			4	
	5.40–6.00(5.68)	33 I	13	1		5				
Ctenocalanus citer	1.02–1.36(1.13)	30	20	4	3					
Euchaeta antarctica (C-5)	6.00–7.00(6.46)	30	25	4	2	1				
Euchirella rostromagna	5.20–6.60(6.30)	30	29	14	10	26	14	7	2	
Gaetanus tenuispinus	3.08–3.40(3.23)	30	30	30	17	20	20		6	
Haloptilus ocellatus	7.40–9.50(8.50)	35	28	3		2	3		1	
Heterorhabdus austrinus	3.08–3.91(3.40)	53								
Metridia gerlachei	3.90–4.40(4.17)	31	24	2	5	5				
	4.00–4.40(4.12)	30 I	13			1				
	3.70–4.40(4.15)	18 D	3							
Microcalanus pygmaeus	0.61–0.70(0.65)	30	22		2					
Oithona frigida	1.05–1.28(1.15)	30	13	1						
	1.05–1.24(1.14)	30 I	7							
Oithona similis	0.73–1.00(0.85)	30	12	1						
	0.73–0.97(0.87)	30 I	1							
Oncaea antarctica	1.07–1.26(1.14)	25	22		1	1				
	1.04–1.16(1.11)	15 I	15	1						
Oncaea curvata	0.51–0.65(0.58)	30	8							
Oncaea prolata	0.60–0.69(0.64)	30	27		1					
Racovitzanus antarcticus	2.11–2.31(2.22)	30	30	29	12	14				
Rhincalanus gigas	8.20–9.50(8.74)	30	27	5	4	7				
Scaphocalanus vervoorti	1.53–1.72(1.60)	30	28	18	7	12	2			
Scolecithricella minor	1.22–1.34(1.27)	30	24		3	1				
Ostracoda										
Conchoecia hettacra	2.04–2.38(2.21)	30	24	4		10				20
Conchoecia isocheira	0.95–1.04(1.00)	30	26	9		6		1	2	23
Euphausiacea										
Euphausia superba (juv.–adult)	34.0–52.0(42.4)	31	29	2	14	17			2	
	40.0–52.0(41.1)	35 I	34	6	25	32	16			
Euphausia superba (calyptopis)	1.38–1.65(1.55)	30	29	4						
Thysanoessa macrura	15.0–21.0(17.2)	29	17	1		9	1	1		

*in the vicinity of the ice edge in the western Weddell Sea, March–April 1986. *Segments rather than segments always including the prostomium*

Frequency of occurrence (no. of guts)

Nauplii	Oithona spp.	Oncaea spp.	Other cyclopoids	Microcal (MP)/Ctenocal (CC)	Euchaeta (spp.)	Calanus (CP)/Calanoides (CA)	Metridia gerlachei	Other copepods	Ostracods	Calyptopis (C)/furcilia (F)	Euphausia superba	Euphausiid debris	Hyperiid amphipods	Limacina helicina	Clio (CP)/Clione (CA)	Salp (ST)/larvacean (OG)	Coelenterate fragments	Pelegobia longicirrata	Rhynchonereella bongraini	Eukrohnia hamata	Sagitta marri
1	1	1															1				
	7		1	1													2				
																	3				
1	7	14	1	6CC		1	7	11										1			
11	9		2	1CC			1	5		1F	1						2	7		2	
2		3							2								3	1			
1	1																2		9		
	6	8	1	3		1	1	3		1F							3				
	14	3															2				
1	1																				
	6	3															1				
	12	3	2				2	2			7					4ST	7	3			
	5								1								3				
3									2		3						23				
	8	5					2	5	1		5						34				
	6		1	2CC	1	4	1	7	3	1F							2	2			

Table 1.

Species	Sample size range (mm)†	No. of individuals used in diet analysis‡	Diatoms	Silicoflagellates	Dinoflagellates	Tintinnids	Radiolarians	Foraminiferans	Heliozoans (Sticholonche)	Mucous/debris
Decapoda										
Nematocarcinus lanceopes	26.0–43.0(34.3)	50	13	6		4	1		1	
Amphipoda										
Cyllopus lucasii	20.0–27.0(22.2)	36	14	3		4	2			
Eusirus antarcticus	15.0–18.0(16.6)	8								
Hyperiella dilatata	4.50–6.50(5.76)	30	19	4		2				
Polychaeta										
Pelagobia longicirrata	1.50–6.60(3.90)*	30	26							
Rhynchonereella bongraini	2.00–9.00(3.91)*	30	25	3						
Tomopteris septentrionalis	4.30–8.00(6.15)	30	26	1						
Pteropoda										
Clio pyramidata f. *sulcata*	16.0–23.0(17.9)	30	30	3	8	26		2		
Chaetognatha										
Eukrohnia hamata	15.0–27.0(19.8)	249								
Sagitta gazellae	40.0–82.0(60.4)	102								
Sagitta marri	9.0–19.0(12.4)	60								
Thaliacea										
Salpa thompsoni	38.0–58.0(45.0)	25	25	25	25	25	10	8	9	
	40.0–63.0(49.5)	22 I	22	19	20	22	19	2	7	
Pisces										
Bathylagus antarcticus	31.0–57.0(46.7)	7					4			
	61.0–82.0(70.9)	14					6			
	90.0–116.0(97.2)	14					1			
Electrona antarctica	31.0–59.0(44.5)	27								
	60.0–85.0(72.4)	33								
Gymnoscopelus braueri	90.0–125.0(95.7)	9								
Gymnoscopelus opisthopterus	85.0–137.05(109.1)	12								
Notolepis coatsi	36.0–58.0(42.4)	27								

† Average size in parentheses.
‡ I = pack ice, D = >200 m, night.

Continued

Frequency of occurrence (no. of guts)

Nauplii	Oithona spp.	Oncaea spp.	Other cyclopoids	Microcal (MP)/Ctenocal (CC)	Euchaeta (spp.)	Calanus (CP)/Calanoides (CA)	Metridia gerlachei	Other copepods	Ostracods	Calyptopis (C)/furcilia (F)	Euphausia superba	Euphausiid debris	Hyperiid amphipods	Limacina helicina	Clio (CP)/Clione (CA)	Salp (ST)/larvacean (OG)	Coelenterate fragments	Pelegobia longicirrata	Rhynchonereella bongraini	Eukrohnia hamata	Sagitta marri
2	4	3	2		1		2	4			3					7ST	10	2	11	1	
								3		5F											
1	1		1												2CA		29	3			
										1											
1	13			4CC			3												1	1	
					1		2	2													
				1			10														
	1	9		1MP			2	1		1F							2				
10	4	3	1	2	1		6				11						5				
18	11	4	1		1		3	17	2	2F	11			4			6		2		
1	7				1		7	2	4	2C							4	2		6	
1	13				1		13	3	14	5C	3						11	11		6	
1	11				3		11	4	12	6C	1				2CP	4OG,ST	5	10		5	
	1				6	9CP	14	7	6	1C	7			1	2CP	6OG,ST	5			5	
	2				2	16CP	12	6	3	1F	15			2	7CP	7OG	2			2	
					2	3CP	2	2	2	1C	4			1		3OG				1	
	1				1	1	3	4	6	2C	8			1		3OG			1	1	
17	7			4CC			12	6	6							2OG			1	17	3

*Table 2.   Feeding groups in the epipelagic zone of the western Weddell Sea, austral autumn 1986.
D = diet diversity; size is average for the species in the group; numbers in diet component column
represent average percent of food incidences for species in the group (see Methods). Metazoan food
types constituting 10% or more of total food incidences are listed in brackets; all numbers in
parentheses are data ranges*

Feeding group	Diet diversity and animal size	Principal diet components
I		
Ctenocalanus citer	*D*: 0.5(0−1.4)	Phytoplankton: 97(86−100)
Metridia gerlachei	Size: 2.0(0.6−6.2) mm	
Microcalanus pygmaeus		
Oithona frigida		
Oithona similis		
Oncaea antarctica		
Oncaea curvata		
Oncaea prolata		
Calyptopis (E. superba)		
Pelagobia longicirrata		
Rhynchonereella bongraini		
Tomopteris septentrionalis		
II		
Calanoides acutus	*D*: 1.8(0.7−2.5)	Phytoplankton: 77(64−84)
Racovitzanus antarcticus	Size: 9.0(1.3−34.3) mm	Protozoans: 16(8−24)
Rhincalanus gigas		
Scaphocalanus vervoorti		
Scolecithricella minor		
Nematocarcinus lanceopes		
III		
Calanus propinquus	*D*: 2.8(2.2−3.5)	Phytoplankton: 52(36−71)
Euchirella rostromagna	Size: 15.8(1.8−45.7) mm	Protozoans: 31(27−35)
Gaetanus tenuispinus		Metazoans: 18(2−30)
Clio pyramidata f. *sulcata*		
Salpa thompsoni		
IV		
Haloptilus ocellatus	*D*: 2.1	Phytoplankton: 66
	Size: 8.5 mm	Metazoans: 22
		[*Pelagobia longicirrata*: 18]
V		
Conchoecia hettacra	*D*: 2.8(2.5−3.2)	Phytoplankton: 42(38−46)
Conchoecia isocheira	Size: 1.6(1.0−2.2) mm	Metazoans: 27(12−42)
		[*Oithona* spp: 10; mucous/debris: 25]
VI		
Euphausia superba	*D*: 3.2	Phytoplankton: 48
	Size: 42.4 mm	Protozoans: 20
		Metazoans: 32
		[coelenterates: 24]
VII		
Euchaeta antarctica	*D*: 3.2(3.0−3.4)	Phytoplankton: 34(30−39)
Thysanoessa macrura	Size: 11.8(6.5−17.2) mm	Protozoans: 10(1−19)
		Metazoans: 57(53−60)
		[*Oithona* spp: 10; *Oncaea* spp: 15]

Table 2. *Continued*

Feeding group	Diet diversity and animal size	Principal diet components
VIII *Hyperiella dilatata*	*D*: 2.1 Size: 5.8 mm	Phytoplankton: 37 Metazoans: 60 [coelenterates: 46]

IX
Cyllopus lucasii
	D: 3.9
	Size: 22.2 mm
		Phytoplankton: 24
		Metazoans: 68
		[coelenterates: 13;
		  Rhynchonereella
		  bongraini :15]

X
Heterorhabdus austrinus
	D: 2.8
	Size: 3.4 mm
		Metazoans: 100
		[*Oithona* spp: 22;
		  Oncaea spp: 29;
		  Pelagobia longicirrata: 11]

XI *Eukrohnia hamata*	*D*: 1.5 Size: 19.8 mm	Metazoans: 100; [Calanidae: 20; *Metridia gerlachei*: 40]
XII *Sagitta gazellae*	*D*: 0.4 Size: 60.4 mm	Metazoans: 100 [*Metridia gerlachei*: 91]
XIII *Sagitta marri*	*D*: 1.9 Size: 12.4 mm	Metazoans: 100 [*Oncaea* spp: 59; *Metridia gerlachei*: 13]

XIV
Bathylagus antarcticus
	D: 3(3.0−3.4)
	Size: 71.6(30−120) mm
		Metazoans: 93
		[*Oncae* spp: 17;
		  Metridia gerlachei: 17;
		  Ostracoda:14;
		  coelenterates: 10;
		  Pelagobia longicirrata: 10]

XV
Electrona antarctica
Gymnoscopelus braueri
Gymnoscopelus opisthopterus
	D: 3.2(3.1−3.3)
	Size: 80.4(30−120) mm
		Metazoans: 100
		[Calanidae: 13;
		  Metridia gerlachei: 14;
		  Ostracods: 11; *Euphausia*
		  superba: 18; tunicates: 10]

XVI
Notolepis coatsi
	D: 3.1
	Size: 42.4 mm
		Metazoans: 100
		[*Oithona* spp: 23;
		  Metridia gerlachei: 16;
		  Eukrohnia hamata: 23]

8.7 mm, with most being 3–6 mm in length. Diet diversity in this group reflected a more diverse food array (D = 1.43–2.88) than in the previous group of small copepods. Measurement of diatoms in guts of small particle grazers showed an overall increase in the fraction of large diatom species (>30 µm) in the diet with increasing copepod size (Table 3). This increase appeared to be linear; the percent of diatoms >30 µm in guts regressed on copepod length yielded an r^2 value of 0.87. A large share of the diatoms in the diets of all of the grazing copepods also consisted of very small diatoms (<15 µm) (Table 3), with these being mostly small pieces of *Nitzschia* and *Thalassiosira*.

Four of the 19 copepod species can be grouped as predominantly large particle feeders. *Euchaeta antarctica* preyed largely on the copepods *Oncaea* spp., *Oithona* spp. and *M. gerlachei*, but also had a high incidence of phytoplankton in the guts. *Euchirella rostromagna* was broadly omnivorous, with a diet having high frequencies of phytoplankton, protozoans and copepods. *Haloptilus ocellatus* yielded a high incidence of polychaetes as well as phytoplankton, though some of the latter, as in *E. antarctica*, may have been secondary food. *Heterorhabdus austrinus* was exclusively carnivorous. Most of its prey was cyclopoid copepods. The four large-particle feeders were moderate to large

Table 3. *Size distribution of diatoms in the diets of the principal grazing species in the upper* 200 m (*open water*). *Number in parentheses is fraction* (%) *smaller than* 15 µm

Species	Average size (mm)	% of diatoms in diet	
		<30 µm	>30 µm
Copepoda			
Oncaea curvata	0.58	100(74)	–
Oncaea prolata	0.64	99(66)	1
Microcalanus pygmaeus	0.65	93(63)	7
Oithona similis	0.85	100(75)	–
Ctenocalanus citer	1.13	95(48)	5
Oncaea antarctica	1.14	98(67)	2
Oithona frigida	1.15	95(34)	5
Scolecithricella minor	1.27	94(61)	6
Scaphocalanus vervoorti	1.60	93(55)	7
Racovitzanus antarcticus	2.22	90(38)	10
Gaetanus tenuispinus	3.23	78(23)	22
Metridia gerlachei	4.17	93(65)	7
Calanoides acutus	5.69	76(30)	24
Calanus propinquus	5.76	78(40)	22
Euchirella rostromagna	6.30	77(47)	23
Rhincalanus gigas	8.74	65(39)	35
Euphausiacea			
Euphausia superba (calyptopis)	1.55	80(30)	20
Euphausia superba (juv.–adult)	42.4	94(43)	6
Tunicata			
Salpa thompsoni	45.7	72(44)	28
Mollusca			
Clio pyramidata f. *sulcata*	17.9	72(37)	28
Polychaeta			
Pelagobia longicirrata	3.90*	68(34)	32
Rhynchonereella bongraini	3.91*	62(40)	38
Tomopteris septentrionalis	6.15	82(40)	18

* Mostly fragments bearing the prostonium; few whole animals.

in size, and all but *H. austrinus* (3.4 mm) exceeded 6 mm in length. Diet diversity in this group was relatively high, ranging from 2.11 to 3.52.

Other crustaceans

Seven crustacean species other than copepods were examined. The two ostracods had similar diets, but the larger *Conchoecia hettacra* had a somewhat more diverse food array than the smaller *C. isocheira* ($D = 3.21$ vs 2.45). Their gut contents included phytoplankton, tintinnids (*C. hettacra*), small copepods, euphausiid fragments and debris of gelatinous plankton. Both species showed high incidences of mucous/membranous-like debris. Many of the food fragments were from organisms larger than the ostracods themselves (e.g. *E. superba*), and it is undetermined whether this material was from molts scavenged from the water column, normal predation on live prey or from post-capture feeding in the net (HOPKINS, 1985, 1987).

Two life stages of *E. superba* were examined. The calyptopis (I–II) diet consisted exclusively of phytoplankton ($D = 0.53$), whereas late juvenile–adult *E. superba* had a more diverse diet ($D = 3.16$) which included protozoans, some copepods and a large fraction of non-crustacean metazoan food (mostly coelenterate debris). The other common euphausiid, *Thysanoessa macrura*, also had a diverse diet ($D = 3.36$), but with copepods, cyclopoids in particular, accounting for much more of the gut contents than was the case in *E. superba*.

Nematocarcinus lanceopes was the only decapod shrimp in our collections from the upper 200 m and was in the epipelagic zone day and night (LANCRAFT *et al.*, in press). Its diet was limited in range ($D = 1.78$), consisting entirely of phytoplankton and protozoans.

The two pelagic amphipods, *Cyllopus lucasii* and *Hyperiella dilatata*, were essentially predaceous, although phytoplankton and protozoans were frequently observed in the guts. Much of the phytoplankton, however, may have been secondary food. In *C. lucasii*, the crustacean element of the diet was mostly copepods of the genera *Oithona, Oncaea, Calanus* and *Calanoides*. The non-crustacean food, which accounted for most of the diet bulk, was largely salp and coelenterate fragments and the alciopid polychaete *Rynchonereella bongraini*. The diet of *H. dilatata*, in terms of biomass, consisted of little other than coelenterate fragments.

Eusirus antarcticus was collected exclusively by SCUBA divers in the interstices underneath pack ice. Its diet consisted of copepods and euphausiid furciliae.

Other invertebrates

The three polychaetes, *Pelagobia longicirrata, Rhynchonereella bongraini* and *Tomopteris septentrionalis*, had exclusively phytoplankton diets. The pteropod, *Clio pyramidata* f. *sulcata*, also fed primarily on small particles, i.e. phytoplankton and protozoans, but ingested some copepods, mostly *Oithona* spp., as well. While this pteropod grazed on a wide range of diatom species, a conspicuous fraction of the food biomass was accounted for by the centrate diatom *Schimperiella* spp. All specimens of *Clio* examined were from a single tow and their diets may have reflected patchiness in food availability. The diet of *Salpa thompsoni*, predictably, was mostly phytoplankton and protozoans. However, this species was omnivorous and ingested metazoans such as cyclopoid copepods, small pteropods (*Limacina helicina*) and polychaetes. Thick muscle bands were frequently apparent in ingested copepods, which indicates salps were ingesting live copepods and

not only molted exoskeletons. The three chaetognath species had low incidences of food in their guts. Their diets were exclusively crustacean and primarily copepods. The few *Eukrohnia hamata* that had ingested prey contained *C. propinquus*, *C. acutus* and *M. gerlachei*. *Sagitta gazellae* fed predominately on *M. gerlachei*, whereas *S. marri*, the smallest chaetognath species, ingested mostly small cyclopoids, with *Oncaea* spp. alone accounting for half the food occurrences.

Fishes

Five fish species occurred in the epipelagic zone at night. They fed primarily on crustacean zooplankton which accounted for 60% of the food incidences in all fish samples. *Bathylagus antarcticus* fed heavily on copepods, e.g. *Oncaea* spp. and *M. gerlachei*, though other common diet items were ostracods, the polychaete *P. longicir-rata*, coelenterate fragments, and large radiolarians. Little difference was perceived in the food composition of three fish size classes examined. Prey size in all *Bathylagus* size groups was generally small, with median prey size occurring in the 1–2 mm fraction. The crustacean component of the *Electrona antarctica* diet was largely *C. propinquus*, *M. gerlachei* and *E. superba*. Non-crustacean food included *Clio pyramidata* f. *sulcata* and *Oikopleura gaussica*. While the two size classes examined showed no major taxonomic shifts in diet, *E. superba* was proportionately more abundant in the food of the larger size class. Median prey size occurred in the 4–5 mm size fraction for both *E. antarctica* size classes.

The two species of *Gymnoscopelus* fed on a broad spectrum of zooplankton and, although fish sample size was small, their diets appeared similar. Copepods were prevalent food items, but the most frequently encountered prey species was *E. superba*. Gelatinous plankton was poorly represented, though remnants of *O. gaussica* were found in a number of guts. Median prey size for both species, as in *E. antarctica*, was in the 4–5 mm size fraction. *Notolepis coatsi*, the smallest of the fishes, fed largely on cyclopoids (mostly *Oithona* spp.), *M. gerlachei*, ostracods, and chaetognaths, with the latter being primarily *Eukrohnia hamata*. Median prey size was small, 1–2 mm, as in *B. antarcticus*. All of the fish species, with the exception of *N. coatsi*, occasionally had deep mesopelagic copepod species, e.g. *Spinocalanus magnus*, *Arietellus simplex*, *Pseudochirella* spp. and species of Augaptilidae, in their intestines, which indicates that some feeding occurred in daytime at mesopelagic residence depths.

Diet comparisons in open water and pack ice

Major diet components of dominant grazing species from both environments are compared in Table 4. All but one species, *S. thompsoni* (we were unable to obtain reliable quantitative results on phytoplankton from this species without standard counting techniques), had measurably more phytoplankton in their guts in open water than under the pack ice. Differences were not statistically different in *Oithona frigida*, *O. similis* and *E. superba*. The chlorophyll data indicate that phytoplankton standing crop was 6 times greater in open water than under ice. Within the pack ice, four species, *E. superba*, *S. thompsoni*, *M. gerlachei* and *C. propinquus*, had a significantly greater zooplankton component to their diets. The most frequent zooplankton food encountered in *E. superba* was cyclopoid copepods (primarily *Oithona*), coelenterate fragments and tintinnids. In *M. gerlachei* and *C. propinquus* the zooplankton food was primarily *Oithona* spp., and in *S. thompsoni*, both *Oithona* spp. and *Oncaea* spp. Tintinnids have

Table 4. *Major diet variations in dominant grazing species in open water and within pack ice. Differences were tested with the Kolmogorov–Smirnov test. Number in parentheses compares the total numbers (see Methods) of that consumed diet item in one habitat relative to the other. The relative abundance of chlorophyll in both areas is indicated at the bottom of the table*

	Diet items	
	Open water	Pack ice
Euphausia superba	Diatoms (2.5×) NS	Copepods (20×)**
		Tintinnids (2.8×)***
		Coelenterate fragments (3×)***
Salpa thompsoni		Copepods (8×)***
Metridia gerlachei	Diatoms (5×)*	Copepods (26×)**
Calanus propinquus	Diatoms (28×)***	Copepods (10×)***
Calanoides acutus	Diatoms (70×)*	
Oithona similis	Diatoms (9×) NS	
Oithona frigida	Diatoms (3×) NS	
Oncaea antarctica	Diatoms (7×)**	
Chl *a* (mg m^{-2})	(6×)***	

* $P <0.05$; ** $P <0.01$; *** $P <0.001$.
NS = not significant at $P <0.05$.

proven to be excellent habitat indicators, as the proportions of dominant tintinnid species were significantly different in the diets of *E. superba* and *S. thompsoni* taken from both environments (BUCK *et al.*, 1987).

M. gerlachei and *C. acutus* collected at depths below 200 m at night within the pack ice were examined to compare diets in populations living within and below the epipelagic zone. As Table 1 indicates, except for a few diatoms found in three *M. gerlachei* individuals, their guts were empty.

DISCUSSION

The data set

Many of the sources of bias discussed in our recent papers on Antarctic food webs (HOPKINS, 1985, 1987) potentially impact the present data set. As in all food-web studies based on net collections, results can be influenced by post-capture feeding in nets. However, plankton nets and cod ends are turbulent environments for small zooplankton, and the trauma induced there almostly certainly inhibits extensive net feeding. Further, in the present study most small to medium-sized species (<1 cm) usually had little food in their guts and diets were intraspecifically consistent (see also HOPKINS, 1987). These results would not be expected were there extensive net feeding. As discussed in Methods, precautions were taken to minimize bias from net feeding in the larger organisms such as fish and krill.

Resolution of diet components improved with increasing food size with the result that diets of groups such as fishes were better described taxonomically than diets of the small-particle grazers (most copepods, krill, salps). Missing from diet results, for example, is information on athecate types of phytoplankton and single-cell heterotrophs (MARCHANT and NASH, 1986) and on the detrital component of diets.

The present results are from organisms occurring in the upper 200 m. While most species examined were found in the epipelagic layer throughout the diel cycle (HOPKINS

and TORRES, in press), some of the larger species, the fishes in particular, migrated into the mesopelagic zone during the day and some apparently fed there. However, prey species typical of the mesopelagic zone (mostly deep-dwelling copepods) were readily separable from epipelagic prey. Except for fishes, where several size classes were examined, diet analysis was limited to late juvenile–adult individuals and diet changes with ontogeny were not considered (HOPKINS, 1987). Also missing from our analysis is information on gelatinous carnivores, i.e. coelenterates and ctenophores, which are an important component of pelagic biomass and in the Southern Ocean (LANCRAFT et al., in press). As in previous studies (HOPKINS, 1985, 1987), gelatinous carnivores were too fragmented in our collections for diet analysis. Micronektonic squids occur in the epipelagic zone of the Weddell Sea, a fact documented by the occurrence of squid beaks in the guts of sea birds taken during AMERIEZ 1986 (AINLEY, unpublished data). Squids were poorly sampled by our trawls and information on their diets is lacking.

Cluster analysis was used for arranging organisms into feeding groups (Table 2). Its usefulness lies in its capability of comparing and grouping elements within complicated data sets. In our investigation complexity comes from the large number of species used in the analyses, many of which have diverse diets. Cluster analysis lacks a universally accepted null hypothesis (SARLE, 1982), and in the present study it proved especially sensitive to "outliers", i.e. single-species groups specializing on relatively few types of prey. After numerous computer runs, the results that agreed best with our subjective evaluation of the data set in Table 1 were obtained through runs made subsequent to combining all phytoplankton food types into one category, combining all of the protozoan categories into one, and excluding the obvious "outliers" (the three chaetognath groups). It should be noted here that non-hierarchical clustering procedures group organisms with similar but not necessarily identical diets. For example, Group I in Table 2 contains grazing copepods which vary in size. From Table 3 it is apparent that the larger copepod species ingest a wider size range of phytoplankton than do the smallest species; hence their diets are not identical. As applied here, cluster analysis is useful in grouping organisms with partially overlapping diet patterns but obscures subtle differences which may be important in defining specific niche parameters. An examination of raw tallies reveals, in fact, that while much overlap occurs, the diets of no two species were precisely the same.

Despite the foregoing caveats, these results present a realistic pattern of much of the structure of the food web in the epipelagic zone of the western Weddell Sea in austral autumn, 1986, and describe the natural diets of the species that constitute all but a small fraction of the numbers and biomass of the metazoan component of the ecosystem.

Feeding groups

Most of the biomass and numbers and half of the species of the open water epipelagic fauna are small-particle grazers (Table 2). These are contained in feeding Groups I–III. The trend within these three groups is for increasing frequency of protozoans in the diet. Small metazoans first make their appearance as an important food item in Group III. Included in these three groups are biomass dominants such as *M. gerlachei, C. propinquus, C. acutus* and *S. thompsoni* and the numerical dominants, *Oncaea* spp. and *Oithona* spp. With a few exceptions, species in these groups are small to moderate in size.

Groups IV–IX consist of species with omnivorous diets containing moderate to high

incidences of both small particles and metazoan food. Most of the metazoan food is small copepods (primarily cyclopoids), polychaetes, and coelenterate fragments. Among these groups (VI) is the biomass dominant *E. superba* (VI). The remaining seven groups (X–XYI) are carnivorous and include the copepod *Heterorhabdus austrinus*, chaetognaths and midwater fishes. Most of these feeding groups consist of a single species because they feed on unique combinations of the prevalent prey species. Copepods are the most frequently occurring prey items in these carnivorous groups, their percent incidence in diets ranging from 43 to 100%. The species that feed most heavily on krill were those in Group XV, *Electrona antarctica* and the two *Gymnoscopelus* species. *E. antarctica* has been recorded as a krill predator by other investigators (SOLYANIK, 1967; ROWEDDER, 1979), and we found, as did ROWEDDER (1979), that large *E. antarctica* had a higher incidence of krill in their guts than did smaller individuals. The diet of *B. antarcticus*, as noted for the family Bathylagidae in general (GORELOVA and KOBYLYANSKY, 1987), and that of *Notolepis coatsi* contained a substantial fraction of non-crustacean food (coelenterates, polychaetes, chaetognaths).

The patterns of trophic groups determined by this study are largely predictable from our previous research. A survey of the diet literature on the species found in the western Weddell Sea (HOPKINS, 1985, 1987) reveals that broadly distributed Southern Ocean species in open water occupy approximately the same trophic position irrespective of region during summer and autumn. Table 5 demonstrates this by comparing the diets of 15 species abundant in each of three Antarctic areas, the western Weddell, Croker passage adjacent to Brabant Island in the Gerlache Strait, and in McMurdo Sound. While some regional variation in diet is apparent, for example, metazoan food is important in the diet of *Oncaea antarctica* only in McMurdo Sound, the diets of these 15 species are generally consistent from region to region.

Ecosystem dynamics

It is apparent from Table 2 that the trophic scheme presented for open water would not be directly applicable for epipelagic waters under the pack ice without important modifications. The feeding activity of small-particle grazers on the basis of gut fullness was, in general, lower under the pack ice for a number of important species (Table 4). Metazoan food, especially small cyclopoids, increased in importance in the diets of several dominant small-particle grazers, e.g. *M. gerlachei, C. propinquus, E. superba* and *S. thompsoni*. A shift to zooplankton prey when phytoplankton becomes scarce has been recorded for small-particle grazing species in other oceanic regions as well (LANDRY, 1981). Metazoan food was common in the guts of *S. thompsoni* in both habitats and considering their abundance (LANCRAFT *et al.*, in press), and the volume of water they potentially filter (e.g. HARBISON and GILMER, 1976), salps should be included among the more important consumers of small metazoan plankton in the Southern Ocean.

Feeding dynamics at high latitudes undoubtedly reflect the seasonal primary production cycle. In the summer in open water there is typically a 60-day bloom period initiated in the marginal ice zone as the ice retreats (SMITH and NELSON, 1985). Primary production declines after the bloom period (e.g. EL-SAYED, 1971; TRANTER, 1982; SAKSHAUG and HOLM-HANSEN, 1984), and by autumn the high latitude system approaches oligotrophy. In winter under the ice, primary production presumably ceases. This cycle was mirrored to a certain degree in our feeding data from different seasons. Samples from McMurdo Sound were collected during the summer bloom period (SMITH and

Table 5. Comparison of diets of abundant species common to three contrasting areas of the Antarctic: western Weddell Sea; McMurdo Sound; Croker Passage (Antarctic Peninsula). Data for the latter two areas are from Hopkins *(1985, 1987). Comparisons apply to open water communities. Percentages are for incidence of food occurrences calculated as described in Methods*

Diet composition	Western Weddell Sea March 1986	McMurdo Sound February 1983	Croker Passage March–April 1983
Phytoplankton >85%	*Ctenocalanus citer* *Metridia gerlachei* *Microcalanus pygmaeus* *Oithona frigida* *Oithona similis* *Oncaea antarctica* *Oncaea curvata* *Pelabogia longicirrata*	*Ctenocalanus citer* *Microcalanus pygmaeus* *Oithona frigida* *Oithona similis* *Oncaea curvata* *Pelagobia longicirrata*	*Ctenocalanus citer* *Metridia gerlachei* *Microcalanus pygmaeus* *Oithona frigida* *Oithona similis* *Oncaea antarctica* *Oncaea curvata*
Phytoplankton and Protozoans >90%	*Calanoides acutus* *Calanus propinquus*	*Calanoides acutus* *Calanus propinquus* *Metridia gerlachei*	*Calanus propinquus* *Pelagobia longicirrata*
Metazoans 20–40%	*Conchoecia isocheira*	*Conchoecia isocheira* *Oncaea antarctica* *Thysanoessa macrura*	*Conchoecia isocheira*
Metazoans 40–80%	*Thysanoessa macrura*		*Thysanoessa macrura*
Coelenterates >40%	*Hyperiella dilatata*	*Hyperiella dilatata*	*Hyperiella dilatata*
Metazoans 100%	*Eukrohnia hamata* *Sagitta gazellae*	*Eukrohnia hamata* *Sagitta gazellae*	*Eukrohnia hamata* *Sagitta gazellae*
Not feeding			*Calanoides acutus*

Nelson, 1985; Hopkins, 1987) and guts of the dominant small-particle feeders were full of phytoplankton. In contrast, Croker Passage and the western Weddell were sampled in the autumn when phytoplankton levels were low (Hopkins, 1985; Smith, 1987). The low productivity was manifested in lower levels of gut fullness (visual ranking) and a higher incidence of carnivory among small-particle grazers, especially under the ice (western Weddell Sea). By autumn some species terminated grazing as noted for *C. acutus* and *Rhincalanus gigas* in Croker Passage and in the deeper elements of the *C. acutus* and *M. gerlachei* populations (>200 m) under the ice in the Weddell Sea. Evidence for reduced ingestion rates during the winter comes from sediment-trap results from the central Weddell Sea (S. Honjo, personal communication). During the winter few fecal pellets occurred in traps, whereas in other seasons they were abundant.

The seasonal cycle in feeding dynamics of small-particle grazing zooplankton inhabiting the ice-covered oceanic zone of the Antarctic is proposed below:

austral summer	austral autumn	austral winter
During the bloom period most food derived from small-particle grazing.	Reduced ingestion from grazing; carnivory supplementing diets in some species.	Descent from epipelagic zone for many species (e.g. Voronina, 1973); feeding virtually terminates.

Little is known about the seasonal distribution and feeding dynamics of larger-sized small-particle grazers such as *S. thompsoni* and *E. superba* during the winter. Both apparently can supplement their diets with small zooplankton such as cyclopoid copepods during the autumn when phytoplankton is scarce (present results; PRICE *et al.*, 1988). If the small cyclopoids remain in the epipelagic zone, in contrast to the larger zooplankton which seasonally migrate, a potential food resource is available in the epipelagic zone during the winter. It is important, then, to extend zooplankton distribution and trophic studies into the winter season within the ice-covered zone of the Antarctic.

REFERENCES

BUCK K. R., D. L. GARRISON and T. L. HOPKINS (1987) Abundance and distribution of tintinnids in an ice edge zone: An AMERIEZ study. Abstract 51E-10 *EOS. Transactions of the American Geophysical Union*, **68**, 1173.
CARMACK E. C. and T. D. FOSTER (1975) On the flow of water out of the Weddell Sea. *Deep-Sea Research*, **22**, 711–724.
DEACON G. E. R. (1979) The Weddell Gyre. *Deep-Sea Research*, **26**, 981–995.
EL-SAYED S. Z. (1971) Dynamics of trophic relations in the Southern Ocean. Research in the Antarctic. American Association for the Advancement of Science, pp. 73–91.
GORELOVA T. A. and S. G. KOBYLYANSKY (1985) Feeding of deepsea fishes of the Family Bathylagidae. *Voprosy Ikhtiologii*, **2**, 264–274 (English translation).
HARBISON G. R. and R. W. GILMER (1976) The feeding rates of the pelagic tunicate, *Pegea confederata*, and two other salps. *Limnology and Oceanography*, **21**, 517–527.
HOPKINS T. L. (1985) Food web of an Antarctic midwater ecosystem. *Marine Biology*, **89**, 197–212.
HOPKINS T. L. (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology*, **96**, 93–106.
HOPKINS T. L. and J. J. TORRES (1988) The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. *Polar Biology*, in press.
HUSBY D. M. and R. D. MUENCH (1988) Hydrographic observations in the northwestern Weddell Sea marginal ice zone during March 1986. NOAA technical memorandum NMFS, NOAA-TM-NMFS-SWFC-106, 33pp.
KLEPIKOV V. V. (1964) Warm deep waters in the Weddell Sea. *Soviet Antarctic Expedition*, Vol. 2, Elsevier, Amsterdam, pp. 194–198.
LANCRAFT T. M., J. J. TORRES and T. L. HOPKINS (1988) Micronekton and macrozooplankton in the ocean waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biology*, in press.
LANDRY M. R. (1981) Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. *Marine Biology*, **65**, 77–82.
MARCHANT H. J. and G. V. NASH (1986) Electron microscopy of gut contents and faeces of *Euphausia superba* Dana. *Memoirs. National Institute of Polar Research. Speical Issue*, **40**, 167–177.
PRICE H. J., K. R. BOYD and C. M. BOYD (1988) Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. *Marine Biology*, **97**, 67–77.
ROWEDDER V. (1979) Feeding ecology of the myctophid *Electrona antarctica* (Gunther, 1878) (Teleostei). *Meeresforschung*, **27**, 252–263.
SAKSHAUG E. and O. HOLM-HANSEN (1984) Factors governing pelagic production in Polar Oceans. In: *Lecture notes on coastal and estuarine studies. Marine phytoplankton and productivity*, O. HOLM-HANSEN, L. BOLIS and R. GILLES, editors, Springer-Verlag, Berlin, pp. 1–18.
SARLE W. S. (1982) Introduction to SAS clustering procedures. In: *SAS user's guide: statistics*, A. A. RAY, editor, SAS Inst., Inc. Gary, North Carolina, pp. 432–447.
SMITH W. O. (1987) Phytoplankton dynamics in marginal ice zones. *Oceanography and Marine Biology Annual Review*, **25**, 11–38.
SMITH W. O. and D. M. NELSON (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea. Spatial coherence with the density field. *Science*, **277**, 163–166.

SMITH W. O. and D. M. NELSON (1986) The importance of ice-edge phytoplankton productivity in the southern Ocean. *Bioscience*, **36**, 251–257.

SOKAL R. R. and F. J. ROHLF (1981) *Biometry*. W. H. Freeman, San Francisco, 766 pp.

SOLYANIK G. A. (1967) The food of the Antarctic *Electrona antarctica. Soviet Antarctic Expedition Information Bulletin*, **6**, 443.

TRANTER D. J. (1982) Interlinking of physical and biological processes in the Antarctic Ocean. *Oceanography and Marine Biology Annual Review*, **20**, 11–35.

TORRES J. J. and G. N. SOMERO (1988) Metabolism, enzymic activities and cold adaptation in Antarctic mesoplagic fishes. *Marine Biology*, **98**, 169–180.

TRAVERS M. (1971) Diversité du microplancton du Golfe de Marseille en 1964. *Marine Biology*, **8**, 308–343.

VORONINA N. M. (1973) Vertical structure of a pelagic community in Antarctica. *Oceanology*, **12**, 415–420 (English translation).

ZWALLY H. J., J. C. COMISO, C. L. PARKINSON, W. J. CAMPBELL, F. D. CARSEY and P. GLOERSEN (1983) Antarctic Sea Ice 1973–1976 from satellite passive microwave observations. NASA special publication, Vol. 459, 244 pp.