

Food web of an Antarctic midwater ecosystem

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Abstract

The diets of 93 species of plankton and micronekton taken in the upper 1 000 m of Croker Passage (Gerlache Strait) in the austral fall, 1983, were examined and the principal features of the food web were characterized. Most species were small particle feeders, with phytoplankton and debris (of phytoplankton and krill) being the principal diet components. Krill remains were found in the guts of the majority of species examined, with the krill playing a greater role in the form of molts and debris than as living prey. Carnivores fed mostly on copepods, coelenterates and salps. Some of the larger species fed on live krill. Non-hierarchical cluster analysis of diet information supported the concept of resource partitioning and determined the arrangement of the species into 21 feeding groups. Cluster analysis groupings tended to be along genetic lines with closely related and morphologically similar species having similar diets. These analyses were based on collections made in the austral fall (March–April, 1983) when phytoplankton standing crop was low, most zooplankton species had descended into the mesopelagic zone, and some of the more abundant species, such as *Calanoides acutus*, had ceased feeding. Because the trophodynamics of Antarctic ecosystems is strongly pulse-induced, it is essential to examine the food web at different periods in the seasonal cycle.

Introduction

Antarctic oceanic ecosystems south of the Polar Front are dominated by the krill *Euphausia superba*. In the East Wind Drift system, for example, krill can exceed the biomass of the rest of the pelagic community by over an order of magnitude (Hopkins, in press). Such large standing stocks of micronektonic-sized (1.5–20.0 cm) organisms result from a combination of factors including an effective

phytoplankton gathering mechanism, a large food supply at crucial periods during growth, a long life history, and an oceanic circulation pattern favoring population maintenance (Marr, 1962; Currie, 1964; Nemoto, 1968; Hamner *et al.*, 1983). The role of krill in the Southern Ocean trophic scheme has been intensively investigated and even modeled (Knox, 1970; El-Sayed, 1971; Green, 1977; Nemoto and Harrison, 1981). These models emphasize the importance of krill in shallow layers in the nutrition of Southern Ocean mammals, birds and fishes. Relatively little information is available, however, on the significance of krill to the trophodynamics of the midwater ecosystem, specifically of zooplankton, macroplankton and micronekton. This paper explores this relationship through diet analyses of most of the midwater species found in the upper 1 000 m of Croker Passage. This basin, which connects the Bransfield and Gerlache Straits, is an area with large krill standing stocks.

Material and methods

Sampling was conducted from the RV "Hero" in March–April of 1983. Specimens for diet analyses were collected with an opening-closing plankton net-Tucker trawl system in discrete zone hauls and oblique sweeps of the upper 1 000 m. The trawl net was 4.8 m² in mouth area and constructed of 1.1-cm (stretched) mesh netting. The plankton nets were 0.44 m² in mouth area, of 162- μ m mesh, collapsible, and suspended in the mouth of the trawl (see Hopkins and Baird, 1975). Nets were opened and closed in discrete zone hauls with clock-release mechanisms of Davies and Barham (1969) design. Trawling speed averaged two knots and flowmeters recorded water filtered. Depth was estimated by wire angle measurements and traced with time-depth recorders. Salinity at 12 horizons in the upper 700 m was determined with a conductivity salinometer using water from a 30-l bottle cast. Temperature to 700 m was profiled with expendable

bathythermograph probes. Details of sampling strategy and tow data are in Hopkins (in press). All material examined was initially preserved in 5 to 10% formalin, buffered with borax and subsequently transferred to 50% isopropyl alcohol.

Most specimens smaller than 15 mm used in diet analysis were from plankton net catches; organisms larger than 15 mm were mostly from trawl catches. The trawl catches were also searched for the rarer zooplankton species.

The maximal body dimension of all specimens used in the diet analyses was measured to the nearest 0.1 mm in the case of organisms < 15 mm in length, and to the nearest millimeter in organisms > 15 mm in length.

Digestive tracts were removed with iris scissors, fine point tweezers or teased out with insect pins, depending on the size of the organism. The gut contents of the larger organisms were examined in watch glasses with a dissecting microscope under 10 to 40× magnification. Gut contents of the smaller animals were examined on microscope slides in water at 45 to 600× magnification.

The sample size analyzed varied with species abundance. In cases where species were relatively abundant, at least 30 individuals were examined. When sample size was less than 30, it usually represented the total number of individuals encountered in a complete search of all the plankton and trawl samples. A total of 3 682 guts from 93 species were examined, with the contents and their frequency of occurrence included in Table 1. Diet results for 67 of the species in Table 1 were used in describing the structure of the food web with the criterion for inclusion being a minimum of four individuals of a species containing identifiable gut contents. Species (16) with only four to nine positive food instances were included in the food web structuring because of the high (usually) redundancy of food items in diets and the similarity of their diets to other members in the genus or family, or to the findings of others for the same species (see Results). Though in many instances the number of prey items per stomach could be determined, for the purpose of this study food types were graded either as present or absent without numerical tabulation.

Incidence of different food types in the 67 species was subjected to non-hierarchical cluster analysis (Sarle, 1982) in ordering the structure of the food web. The 20 categories of food used in the analysis were: (1) phytoplankton/detritus lacking diatoms, (2) phytoplankton with Coscinodiscineae diatoms, (3) phytoplankton with *Corethron* sp. diatoms, (4) phytoplankton with other types of diatoms, (5) dinoflagellates, (6) protozoans (tintinnids, radiolarians, foraminiferans), (7) *Euphausia superba* debris (molts and fragments), (8) *Euphausia superba* ingested as live prey, (9) salps, (10) coelenterates, as indicated by the presence of nematocysts, gonophores and calyophoran nectophores, (11) *Pelagobia longicirrata* (polychaete) and its debris (bristles), (12) *Calanoides acutus* (copepod), (13) *Metridia gerlachei* (copepod), (14) *Euchaeta* spp. (copepods, mostly *E. antarctica*), (15) *Microcalanus pygmaeus*

(copepod), (16) *Oncaea* spp. (copepods, mostly *O. curvata*), (17) *Oithona* spp. (copepods, mostly *O. similis*), (18) other copepods, (19) ostracods, and (20) chaetognaths. These categories accounted for all but a small fraction of the food observed in guts.

For the cluster analysis, the incidence of these food types in the guts of each of the 67 species was expressed as a percent of the total incidences of all types of food recorded. As an example, if food categories 1, 2, 4, 7 and 11 were found in an analysis of 30 guts for a particular species and they occurred, respectively, in 20, 10, 3, 15 and 2 guts (i.e. a total of 50 incidences), the percentages for each of these categories in the cluster analysis, for this species, would be 40, 20, 6, 30 and 4%, with the value for the remaining 15 food categories being recorded as 0%. The above food-incidence procedure was arbitrarily selected for use in place of one based on quantitative data on diet composition (e.g. numbers and biomass of food types), such data being unavailable. Despite limitations, the method proved satisfactory for arranging species into trophic groups which agreed well with feeding patterns obvious from the data set.

Diet diversity for copepod families (see Discussion) was calculated by substituting the above described incidence percentages into a variant of the information index, (Travers, 1971),

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

where

N = total incidences (= 100%) of all 20 food types within a copepod family (species results pooled),
 n_i = incidence (%) of a single food type, and $D = 0$ to 4.32.

The average-sized copepod in the diet diversity vs copepod size comparison in the Results was calculated by taking the mean of the median sizes of the species (Table 1) comprising each family.

Results

Crocker Passage in March–April, 1983. Crocker Passage is a deep water connection (1 200-m maximum depth) between the Bransfield and Gerlache Straits. The sampling zone was the upper 1 000 m of a 22 × 6 km area over one of the larger depressions in the passage (Fig. 1). Temperature and salinity showed little variation over the upper 700 m, with the mean trace for XBT profiles (12) made in April, when most of the discrete zone trawling was accomplished, being within ± 1°C of 0°C. The salinity range over this depth was 33.89 to 34.57 ‰.

In the Crocker Passage zooplankton assemblage, described by Hopkins (in press), the most abundant species (i.e. > 1 000/100 m³) were the copepods *Oncaea curvata*, *O. antarctica*, *Microcalanus pygmaeus* and *Metridia gerlachei*. The principal biomass species (> 40 mgDW/100 m³) were *M. gerlachei*, *Calanoides acutus* and *Eucha-*

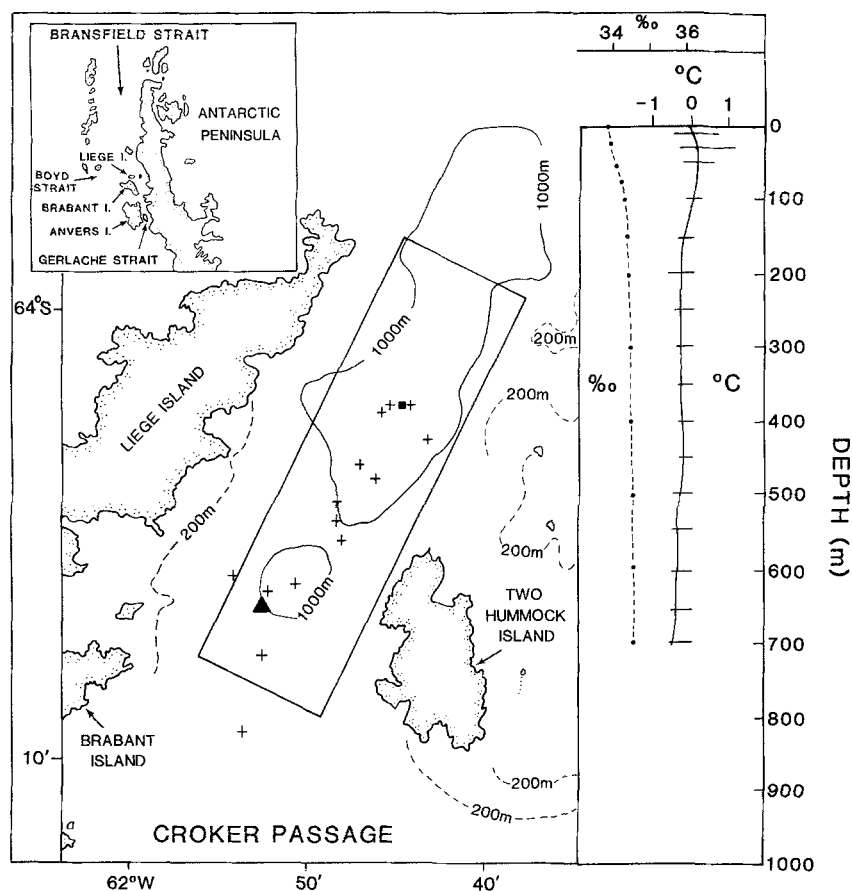


Fig. 1. The sampling area in Croker Passage along with vertical profiles of hydrographic parameters. + = XBT profiles; solid square = salinity station (8 April, 1983); solid triangle = 30-l bottle plankton cast. Horizontal lines in the vertical temperature plot are range bars for 12 XBT profiles made in the period 8–11 April, 1983

ta antarctica. The abundant zooplankton species showed broad vertical distributions, but most were centered below 200 m.

While quantitative information is unavailable for macroplankton and micronekton, the obviously abundant species (i.e. organisms > 15 mm in maximum dimension) in the trawl catch were the amphipods *Cyphocaris richardi*, *Parathemisto gaudichaudii*, *Eusirus propeperdentatus*, and *Orchomene plebs*; the euphausiids *Euphausia superba* and *Thysanoessa macrura*, the mysid *Antarctomysis ohlinii*; the polychaete *Tomopteris carpenteri*; the chaetognaths *Sagitta gazellae* and *Eukrohnia hamata*; the tunicate *Salpa thompsoni* and the siphonophores *Dimophyes arctica*, *Diphyes antarctica* and *Pyrostephos vanhoeffeni*. Other species which contributed significantly to wet weight biomass, if not to numbers, were the scyphomedusae *Periphylla periphylla* and *Atolla wyvillei*; the ctenophore *Callianira* sp., and the fishes *Electrona antarctica* and *Pleuragramma antarcticum*. Of these species, *Euphausia superba* was the overwhelming dominant, it being concentrated in the upper 100 m.

Total standing stocks in the upper 1000 m of Croker Passage were estimated at 0.7 gDW/m² and 2.9 gDW/m² for metazoan plankton < 1 mm and from 1 to 15 mm, respectively. In the macroplankton and micronekton size range (i.e. > 15 mm), *Euphausia superba* alone was 55 gDW/m² or 15 times the biomass of zooplankton (Hopkins, in press).

Thirty-micron gauze sievings from the 30-l bottle casts indicated that large diatoms of the *Coscinodiscineae* and *Corethron* sp. types were distributed throughout the water column, with the latter being the conspicuous dominant. Fluorescence analysis of water from Croker Passage in March, 1983 indicated that phytoplankton standing crop was quite low (R. Ross and L. Quetin, unpublished data). Three casts made on 4 April within the sampling area (Lat. 64°03.66'S, Long. 61°48.57'W) gave maximum values for chlorophyll *a* in the upper 100 m ranging from 0.330 to 0.496 µg l⁻¹. The phaeophytin maxima ranged from 0.076 to 0.140 µg l⁻¹, many values in the upper 100 m being near the limits of detection (5-cm light path).

Diet composition. The digestive tract contents and their incidence of occurrence in guts of 93 species of zooplankton, macroplankton and micronekton are given in Table 1; these results are presented in order of their occurrence in the table.

Copepods. Seven species of the family Aetidae were examined, four with sample sizes of 20 or more. The group was omnivorous, taking whole zooplankton as well as small particles. All species contained phytoplankton with a high incidence of large frustules of *Coscinodiscineae*. The incidence of *Euphausia superba* debris (in the form of bristles, fragments of appendages, pieces of the exoskeleton of the thorax and abdomen, and eye pigment and ommatidia) was high (> 75% incidence) in all species. The most common live prey were copepods, especially *Oncaea*

Table 1. Gut contents of Croker Passage species of plankton and micronekton. Code: A=amphipod, C=cephalopod; Co=*Corethron* sp. (diatom); Cs=*Coscinodiscineae* diatoms; D=debris; DO=other types of diatoms; E=*Eukrohnia hamata*; F=foraminiferan; G=gastropod; H=*Hyperiella* sp.; L=eaten as live prey; M=*Antarctomysis ohlinii*; N=nauplius; P=*Eusirus propeperdentatus*; Pm=*Primno macropa*; R=*radiolarian*; Sg=*Sagitta gazellae*; T=tintinnid; Tm=*Thysanoessa macrura*

Species	Size range (median size) mm	Sample size/ incidence of identifiable gut contents	Frequency of occurrence (No. of guts)				
			Diet component				
			Phytoplankton/ detritus	Diatoms		Dinoflagellates	Protozoans
COPEPODA							
Aetideidae							
<i>Aetideopsis minor</i>	4.2–4.8 (4.5)	30/30	29	29Cs	–	–	1T
<i>Euchirella rostromagna</i>	4.6–6.5 (6.2)	21/20	20	14Cs, 8DO	11	–	–
<i>Gaetanus antarcticus</i>	7.2	1/1	1	–	–	–	–
<i>Gaetanus intermedius</i>	3.7–5.9 (4.9)	30/29	27	27Cs, 4DO	6	–	1T
<i>Gaetanus tenuispinus</i>	3.5–4.0 (3.8)	30/30	30	29Cs	–	–	2T, 1F
<i>Pseudochirella hirsuta</i>	6.3	1/1	1	1Cs	–	–	–
<i>Pseudochirella mawsoni</i>	6.7	1/1	1	1Cs	–	–	–
Augaptilidae							
<i>Haloptilus ocellatus</i>	4.7–9.5 (8.4)	70/7	2	2Cs, 1DO	–	–	–
Calanidae							
<i>Calanoides acutus</i>	4.1–5.9 (4.9)	82/0	–	–	–	–	–
<i>Calanus propinquus</i>	5.0–6.5 (5.5)	30/14	13	13Cs, 8DO	2	–	2T
Eucalanidae							
<i>Rhincalanus gigas</i>	7.4–9.9 (8.7)	60/3	3	2Cs	–	–	–
Euchaetidae							
<i>Euchaeta antarctica</i>	8.6–9.8 (9.2)	47/18	1	1Cs	–	–	–
<i>Euchaeta rasa</i>	4.4–6.4 (5.1)	30/6	1	1Cs	–	–	–
<i>Euchaeta similis</i>	8.8–10.4 (9.8)	30/10	2	2Cs	–	–	–
Heterorhabdidae							
<i>Heterorhabdus austrinus</i>	3.2–3.9 (3.6)	75/7	1	1Cs	–	–	–
<i>Heterorhabdus farrani</i>	3.7–4.7 (4.0)	70/10	–	–	–	–	–
Lucicutiidae							
<i>Lucicutia macrocera</i>	3.7–4.0 (3.8)	4/3	3	2Cs	–	–	–
<i>Lucicutia ovalis</i>	1.1–2.0 (1.6)	40/23	23	2Cs	–	–	–
<i>Lucicutia wolfendeni</i>	4.9–7.0 (5.9)	8/6	4	3Cs, 1DO	1	–	–
Metridiidae							
<i>Metridia curticauda</i>	2.5–3.0 (2.7)	40/36	36	11Cs	2	–	–
<i>Metridia gerlachei</i>	2.3–4.6 (4.0)	125/125	125	3Cs, 1DO	2	–	8T
<i>Pleuromamma robusta</i>	3.4–4.7 (4.2)	28/24	21	14Cs, 6DO	22	–	6T
Oithonidae							
<i>Oithona frigida</i>	1.0–1.2 (1.1)	30/7	7	–	–	–	–
<i>Oithona similis</i>	0.7–0.9 (0.8)	100/14	14	–	–	–	–
Oncaeidae							
<i>Oncaea antarctica</i>	1.0–1.2 (1.1)	100/25	25	2DO	–	–	–
<i>Oncaea curvata</i>	0.6–0.8 (0.7)	100/17	17	1Cs	–	–	–
Phaennidae							
<i>Cephalophanes frigidus</i>	4.5–4.9	2/1	–	–	–	–	–
<i>Cornucalanus robustus</i>	3.9–7.5 (5.5)	10/0	–	–	–	–	–
<i>Onchocalanus wolfendeni</i>	5.1–7.2 (6.6)	24/8	1	–	–	–	–
<i>Xanthocalanus gracilis?</i>	2.0–3.0 (2.3)	34/5	3	3Cs, 1DO	–	–	–
Pseudocalanidae							
<i>Ctenocalanus citer</i>	1.0–1.6 (1.4)	40/9	8	2Cs	–	–	–
<i>Farrania frigida</i>	2.3–3.0	2/2	2	2DO	–	–	–
<i>Microcalanus pygmaeus</i>	0.8–1.2 (1.0)	100/10	10	–	–	–	–
Scolecithricidae							
<i>Racovitzanus antarcticus</i>	1.7–2.6 (1.9)	37/30	27	9Cs, 2DO	1	–	1T
<i>Scaphocalanus antarcticus</i>	4.2–6.0 (5.5)	20/15	10	5Cs, 2DO	–	–	–
<i>Scaphocalanus farrani</i>	2.7–3.2 (2.9)	30/22	6	3Cs	–	–	–
<i>Scaphocalanus parantarcticus</i>	5.5–5.8 (5.6)	3/2	1	–	–	–	–
<i>Scaphocalanus vervoorti</i>	1.6–2.1 (1.9)	44/26	14	2Cs	–	–	–
<i>Scolecithricella cenotelis</i>	1.7–2.5 (2.4)	30/29	18	5Cs, 1DO	–	–	1R
<i>Scolecithricella dentipes</i>	1.7–2.9 (2.3)	31/23	7	1Cs, 1DO	–	–	–

Table 1 (continued)

<i>Euphausia superba</i>	Salps	Coelenterates	<i>Pelagobia longicirrata</i>	<i>Calanoides acutus</i>	<i>Metridia gerlachei</i>	<i>Euchaeta</i> spp.	<i>Microcalanus pygmaeus</i>	<i>Oncaea</i> spp.	<i>Oithona</i> spp.	Other copepods	Ostracods	Chaetognaths	Fish debris	Other
23D	—	—	10	—	—	—	—	1	—	—	—	—	—	—
18D	—	3	9	—	7	—	—	6	—	3	1	1	—	—
1D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
26D	—	—	10	—	2	—	1	9	1	3	—	—	—	—
28D	—	2	5	—	1	—	—	3	—	—	—	—	—	—
1D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1D	—	—	1	—	—	—	—	—	1	1	—	—	—	—
1D	—	—	4	—	1	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3D	—	—	—	—	—	—	—	—	—	2	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1D	—	—	2	—	7	—	—	2	—	6	—	—	—	—
—	—	—	—	—	1	—	—	2	1	3	—	—	—	—
1D	—	—	—	1	5	—	—	3	—	4	—	—	—	—
—	—	—	3	—	1	—	—	—	—	2	—	—	—	—
—	—	—	9	—	—	—	—	—	—	—	1	—	—	—
1D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2D	—	—	—	—	—	—	—	1	1	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1D	—	—	1	—	—	—	—	—	—	—	—	—	—	—
19D	—	2	7	—	—	—	—	2	—	2	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
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—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	7	—	—	—	—	—	1	—	—	—	—	—	—
—	—	5	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
1D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4D	—	—	1	—	1	—	—	—	—	—	—	—	—	—
15D	—	2	6	—	1	—	—	—	—	—	—	—	—	—
13D	—	2	2	—	—	—	—	—	—	3	—	—	—	—
2D	—	—	1	—	—	—	—	—	—	—	—	—	—	—
3D	—	1	5	—	1	—	—	3	—	2	—	—	—	—
18D	—	4	5	—	—	—	—	—	—	—	—	—	—	—
14D	—	2	2	—	—	—	—	1	—	—	1	—	—	—

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Table 1 (continued)

Species	Size range (median size) mm	Sample size/ incidence of identifiable gut contents	Frequency of occurrence (No. of guts)			
			Diet component			
			Phytoplankton/ detritus	Diatoms	Dinoflagellates	Protozoans
<i>Scolecithricella emarginata</i>	3.4–4.8 (4.1)	14/13	5	3Cs	–	1T
<i>Scolecithricella minor</i>	1.2–1.6 (1.4)	30/22	22	–	–	–
Spinocalanidae						
<i>Mimocalanus cultrifer</i>	1.8	3/3	3	–	–	–
<i>Spinocalanus abyssalis</i>	1.5–2.5 (2.1)	30/18	17	17Cs	–	–
<i>Spinocalanus abyssalis</i> v. <i>pygmaeus</i>	0.9–1.3 (1.2)	30/24	24	8Cs, 5DO	1	–
<i>Spinocalanus magnus</i>	2.7–2.9 (2.8)	3/3	3	1Cs, 1DO	–	–
Stephidae						
<i>Stephos longipes</i>	0.6–0.8 (0.7)	30/6	6	1Cs	–	–
OSTRACODA						
<i>Conchoecia antipoda</i>	2.4–3.6 (3.3)	30/24	18	9Cs, 1DO	–	–
<i>Conchoecia belgicae</i>	1.8–2.9 (2.7)	30/28	23	10Cs, 1 Co, 2DO	–	–
<i>Conchoecia hettacra</i>	1.7–2.6 (2.4)	30/29	25	6Cs, 2DO	–	–
<i>Conchoecia imbricata</i>	3.3–4.9 (3.5)	7/7	6	4Cs, 1DO	1	–
<i>Conchoecia isocheira</i>	1.0–1.2 (1.1)	30/23	23	7Cs, 6DO	–	–
<i>Conchoecia skogsbergi</i>	1.2–1.8 (1.5)	30/28	21	8Cs, 1DO	–	–
AMPHIPODA						
Hyperiidea						
<i>Cylopus lucasii</i>	7–19 (10)	9/3	3	2Cs, 2Co, 3DO	–	1T
<i>Hyperiella dilatata</i>	5.1–7.2 (5.8)	30/23	1	1Cs	–	–
<i>Hyperiella macronyx</i>	7.0–9.2 (7.2)	5/5	2	1Cs	–	–
<i>Parathemisto gaudichaudii</i>	11–22 (18)	51/46	26	14Cs, 26Co, 15DO	–	–
<i>Primno macropa</i>	3–16 (8)	43/38	2	2Cs	–	–
<i>Vibilia stebbingi</i>	13–17 (15)	12/2	–	–	–	–
Gammaridea						
<i>Cyphocaris faurei</i>	23–27	2/2	–	–	–	–
<i>Cyphocaris richardi</i>	17–50 (40)	112/98	20	1Cs, 1Co, 2DO	1	1T
<i>Epimeriella macronyx</i>	15–30 (24)	24/22	8	4Cs, 1DO	–	–
<i>Eusirus microps</i>	17–55 (30)	16/16	2	1Cs	–	–
<i>Eusirus perdentatus</i>	17–20	2/2	2	2Cs, 1Co	–	–
<i>Eusirus propeperdentatus</i>	14–58 (33)	67/62	4	2Cs, 1Co	–	–
<i>Eurythenes gryllus</i>	24–96 (69)	10/8	1	1Cs	–	1T
<i>Eurythenes obesius</i>	33	1/1	–	–	–	–
<i>Orchomene plebs</i>	12–26 (20)	54/50	23	5Cs, 8Co	–	–
<i>Orchomene rossi</i>	17–35 (25)	22/22	7	5Cs, 5Co	–	–
<i>Parandania boeckii</i>	22–40 (30)	16/16	2	2Cs, 1DO	–	–
MYSIDACEA						
<i>Antarctomysis maxima</i>	47–93	2/2	1	1	–	–
<i>Antarctomysis ohlinii</i>	25–66 (54)	97/97	54	41Cs, 12Co, 18DO	6	1R, 1F, 6T
<i>Boreomysis</i> sp.	13–26 (19)	3/2	1	–	–	–
<i>Dactylamblyops hodgsoni</i> ?	8–25 (19)	23/23	22	6Cs, 1Co	–	–
<i>Mysidetes posthon</i>	17–25 (20)	8/8	7	2Cs, 1DO	–	–
<i>Pseudomma belgicae</i>	21–28 (27)	9/5	4	3Cs, 1DO	–	–
EUPHAUSIACEA						
<i>Euphausia superba</i>	29–44 (37)	57/32	52	10Cs, 3Co, 24DO	–	1R, 1T
<i>Thysanoessa macrura</i>	21–33 (26)	104/62	22	9Cs, 3Co, 6DO	–	1R, 1T
DÉCAPODA						
<i>Pasiphaea longispina</i>	29–37	2/1	–	–	–	–
THALIACEA						
<i>Salpa thompsoni</i>	30–62 (50)	25/25	25	25Cs, 25Co, 25DO	22	25T
CHAETOGNATHA						
<i>Eukrohnia hamata</i>	18–28 (23)	194/4	–	–	–	–
<i>Sagitta gazellae</i>	26–94 (67)	183/9	1	1Co	–	–
<i>Sagitta marri</i>	10–23 (17)	106/7	–	–	–	–

Table 1 (continued)

<i>Euphausia superba</i>	Salps	Coelenterates	<i>Pelagobia longicirrata</i>	<i>Calanoides acutus</i>	<i>Metridia gerlachei</i>	<i>Euchaeta</i> spp.	<i>Microcalanus pygmaeus</i>	<i>Oncaea</i> spp.	<i>Oithona</i> spp.	Other copepods	Ostracods	Chaetognaths	Fish debris	Other
13D	—	2	5	—	—	—	—	2	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1D	—	—	1	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22D	—	2	1	—	—	—	—	4	—	—	—	—	—	—
23D	—	2	—	—	—	—	1	3	1	1N	—	—	—	1G
24D	—	1	9	—	—	—	—	2	—	2	—	—	—	—
7D	—	—	—	—	—	—	—	1	—	—	—	—	—	—
17D	—	—	—	—	1	—	—	—	—	—	—	—	—	—
23D	—	—	4	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3D	—	20	5	—	—	—	—	—	—	—	—	—	—	—
1D, 2L	—	2	2	—	1	—	—	—	1	2	—	—	—	—
20D, 13L 24	—	10	6	2	4	1	1	5	1	9	—	4E, 2	9	—
13D, 18L	—	—	3	8	—	1	—	3	1	3	—	1	—	—
2D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
95D, 1L	5	2	4	2	6	9	—	1	—	7	—	—	—	2M
6D	1	19	12	—	9	—	2	3	—	—	—	—	—	—
11D	2	1	3	—	3	3	—	—	—	1	—	1E	6	—
2D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
34D, 2L	—	4	10	—	41	34	—	1	—	17	10	3	—	7M, 4A
—	—	5	—	—	—	—	—	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
15D, 9L	14	8	18	—	15	1	5	15	5	15	—	2E, 1SG, 5	29	—
11D, 6L	5	—	9	1	7	5	4	7	—	9	—	1E, 1	12	—
1L	2	16	1	—	—	—	—	—	—	—	—	1Sg, 1	2	—
—	—	—	—	—	1	—	—	—	—	—	—	1	—	—
97D	1	21	26	13	30	22	1	15	—	17	24	5E, 2	3	1A
2D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
23D	—	—	1	—	1	1	—	5	1	1N, 1	—	—	—	—
8D	—	4	—	—	—	—	—	—	—	1	—	—	—	—
5D	—	3	—	—	—	—	—	—	—	—	—	—	—	—
40D	—	—	1	—	—	—	—	—	—	2	—	—	—	—
9D	—	6	14	28	27	9	—	5	2	13	2	1E	1	—
—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
12D	—	—	—	—	—	—	—	—	—	1	—	—	—	—
—	—	—	—	—	—	4	—	—	—	—	—	—	—	—
3D	—	2	1	—	1	9	—	—	—	2	—	—	—	1P, 1M
—	—	—	1	—	4	—	—	3	—	—	—	—	—	—

continued on next page

Table 1 (continued)

Species	Size range (median size) mm	Sample size/ incidence of identifiable gut contents	Frequency of occurrence (No. of guts)			
			Diet component			
			Phytoplankton/ detritus	Diatoms	Dinoflagellates	Protozoans
POLYCHAETA						
<i>Maupasia caeca</i>	2.4–13.0 (4.0)	19/3	2	1Co	–	1R
<i>Pelagobia longicirrata</i>	2.2–4.5 (3.2)	144/12	10	2Cs, 1DO	–	–
<i>Tomopteris carpenteri</i>	17–67 (26)	40/10	3	3Cs, 2Co, 1DO	1	–
<i>Tomopteris planktonis</i>	4.6–9.2 (6.2)	56/17	17	9Cs, 1Co, 1DO	–	1T
<i>Tomopteris septentrionalis</i>	7.5–13.5 (9.6)	10/2	2	2Cs, 2Do	–	–
MOLLUSCA						
<i>Clione antarctica</i>	5.4–12.0 (9.0)	28/0	–	–	–	–
<i>Spongiobranchaea australis</i>	1.0–9.2 (1.7)	40/0	–	–	–	–
<i>Auillroteuthis antarcticus</i>	100	2/2	–	–	–	–
<i>Crystalloteuthis glacialis</i>	64–104 (84)	3/3	–	–	–	–
PISCES						
<i>Electrona antarctica</i>	54–101 (82)	186/172	–	–	–	–

spp., and the polychaete *Pelagobia longicirrata*. Dinoflagellates were found in guts of two species and tintinnids in three. Of the more commonly occurring Aetidae, *Euchirella rostromagna* and *Gaetanus intermedius* had the most diverse diets and *Aetideopsis minor* the least. The data for Aetidae in Croker Passage are not at variance with the findings of others for this family, with phytoplankton debris, protozoans and small crustaceans having been recorded from their guts (Esterly, 1916; Heinrich, 1958; Chindonova, 1959; Wickstead, 1962; Mullin, 1966; Arashkevich, 1968; Harding, 1974).

A single augaptilid species *Haloptilus ocellatus* was examined, but relatively few specimens (10% incidence) contained any food. As in the Aetidae, this species appeared to be omnivorous, ingesting phytoplankton and small euphausiid debris as well as *Pelagobia longicirrata* and copepodites of *Metridia Gerlachei*. Other studies (Heinrich, 1958; Harding, 1974) on this group have shown the family to be comprised largely of small particle feeders which ingest phytoplankton and protozoans.

The Calanidae and Eucalanidae include important biomass species in Croker Passage (Hopkins, in press). In March–April, two of three species in this group, however, had evidently ceased feeding for the year, with all of the guts of *Calanoides acutus* being empty and only a few guts (3) of *Rhincalanus gigas* containing food (phytoplankton). Approximately half the *Calanus propinquus* had food in their guts, which was mostly phytoplankton with a high incidence (43%) of Coscinodiscineae diatoms. Several individuals contained dinoflagellates, tintinnids and euphausiid fragments. Two had fed on calanoid copepodites. The extensive literature on these families (e.g. Marshall

and Orr, 1955; Heinrich, 1958; Andrews, 1966; Mullin, 1966; Arashkevich, 1968; Harding, 1974) shows them to be primarily herbivorous. Also, the present data on *C. acutus* are in agreement with the observations of Andrews (1966), who reported that this species ceased feeding with the onset of winter.

The Euchaetidae and Heterorhabdidae were predatory, though traces of phytoplankton were found in a small percentage of the guts with food. Among the Euchaetidae the most frequently occurring prey was *Oncaea* spp. and copepodites of *Metridia gerlachei*. Debris of *Euphausia superba* (molt fragments) was found in the guts of two *Euchaeta* (one each of *E. antarctica* and *E. similis*) individuals. The food of *Heterorhabdus farrani* was almost exclusively *Pelagobia longicirrata*, while *H. austrinus* ingested about an equal percentage of *P. longicirrata* and copepods. The incidence of food in copepods of these two families was moderate to low (9 to 38%). Other investigations as well have shown these two families to be predators on small crustaceans, especially copepods (Heinrich, 1958; Chindonova, 1959; Wickstead, 1962; Mullin, 1966; Arashkevich, 1968; Harding, 1974; Shuert, 1984).

Members of the genus *Lucicutia* were uncommon in our collections, with a large sample size (40) only in the case of *L. ovalis*. This species apparently fed on phytoplankton, which occurred in digestive tracts as amorphous greenish-brown debris that contained few diatoms. Only four individuals of *L. macrocera* were found, these also containing phytoplankton, and in one instance, euphausiid debris. The largest species, *L. wolfendeni*, ingested copepods as well as phytoplankton and euphausiid debris. The literature indicates that the Lucicutiidae show a size-

Table 1 (continued)

<i>Euphausia superba</i>	Salps	Coelenterates	<i>Pelagobia longicirrata</i>	<i>Calanoides acutus</i>	<i>Metridia gerlachei</i>	<i>Euchaeta</i> spp.	<i>Microcalanus pygmaeus</i>	<i>Oncaea</i> spp.	<i>Oithona</i> spp.	Other copepods	Ostracods	Chaetognaths	Fish debris	Other
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3D	1	1	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1D	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-	-	1C
-	-	-	-	-	-	1	-	-	-	-	-	-	1	1Tm
145L	1	-	1	-	18	24	-	-	-	4	23	-	-	1Pm, 1Tm 2P, 2H

related trend, with the smaller species being reported as utilizing phytoplankton and detritus and the larger species as being more omnivorous (Heinrich, 1958; Chindonova, 1959; Harding, 1974). This is reflected to a certain extent in the present data, with the largest species, *L. wolfendeni*, being the only one to ingest copepods.

The Metridiidae in Croker Passage include *Metridia gerlachei*, the principal biomass species in our zooplankton collections, the much less abundant *M. curticauda* and the rare *Pleuromamma robusta*. *M. curticauda*, the smallest species, had the least diverse diet and fed on phytoplankton. The diet of *M. gerlachei* was broader, and was composed of phytoplankton, tintinnids and in two instances, euphausiid and *Pelagobia longicirrata* debris. *Pleuromamma robusta*, the most omnivorous of the three, had a diet similar to that of the aetidid *Gaetanus intermedius*, and consisted of phytoplankton (with a high incidence of dinoflagellates), protozoans, euphausiid fragments, *P. longicirrata* debris, and copepods. The Metridiidae in general appear to be omnivorous (Esterly, 1916; Heinrich, 1958; Chindonova, 1959; Wickstead, 1962; Arashkevich, 1968; Harding, 1974), feeding on protozoans and crustaceans as well as phytoplankton.

Cyclopods of the genera *Oncaea* and *Oithona*, while extremely abundant, had a low (14 to 25%) incidence of food in their guts. All of this group fed on small particles which appeared as amorphous green-brown debris containing relatively few diatoms and devoid of recognizable animal fragments. Others have also reported these genera as being small particle feeders and as ingesting mostly phytoplankton and small debris (Lebour, 1922; Heinrich, 1958).

The species of Phaennidae taken in Croker Passage were moderate- to large-sized copepods. The largest sample sizes were for the species *Onchocalanus wolfendeni* and *Xanthocalanus gracilis* (?). Both species fed primarily on coelenterates though *X. gracilis* (?), the smaller of the two, ingested phytoplankton as well. The ingestion of coelenterates by *Xanthocalanus* species has also been reported by Chindonova (1959).

The Pseudocalanidae were represented by three small species, with one, *Microcalanus pygmaeus*, being a dominant. As in the case of cyclopoids, the food was mostly an amorphous greenish-brown debris poor in diatoms. Bristles of *Pelagobia longicirrata* and euphausiid debris were encountered in a few specimens. Excluding *Farrania frigida*, which was represented by only two specimens, incidence of food in guts was low (10 to 23%). The one member of this family examined by Lebour (1922) and Zagorodnyaya (1974), *Pseudocalanus elongatus*, also fed on phytoplankton.

Nine species of the Scolecithricidae were examined, seven with sample sizes in excess of 20 individuals. Food incidence in guts was relatively high, exceeding two-thirds of the individuals examined in all but one species (*Scaphocalanus verwoorti*; 59%). The prevalent foods were phytoplankton and euphausiid debris, though the latter was absent from the diets of *Scolecithricella minor* and *Racovitzanus antarcticus*. Omnivory appeared to be characteristic of the group, with the debris of *Pelagobia longicirrata* being found in the guts of all but one species, and coelenterate remains in all but two species. Omnivory is also indicated by the literature on the family. Phytoplankton, protozoans and detritus have been reported

from guts, with the last usually being a primary diet component (Esterly, 1916; Heinrich, 1958; Wickstead, 1962; Mullin, 1966; Arashkevich, 1968; Harding, 1974).

The Spinocalanidae had five representatives, all rather small in size. As others have found (Lebour, 1922; Heinrich, 1958), they were small particle feeders and the food debris had a moderate to high incidence of diatoms.

While many of the points are statistically inseparable because of differences in sample size and incidence of food in guts, the overall pattern for copepods shown in Fig. 2 is for an increase in food diversity with copepod size. Diversity in the present case, however, was based on a more accurate separation of types of food particles at the upper end of the diet size spectrum than at the lower end. The amorphous greenish-brown debris category was undoubtedly composed of a variety of particle sizes and types which offered potential for selective grazing. For example, the same greenish-brown material was reported as the principal diet component for *Oncaea curvata*, *O. antarctica* and *Microcalanus pygmaeus*, yet in reality they each might have been selecting a unique particle array.

Ostracods. Six species of *Conchoecia* were found, of which only *C. imbricata* was rare. The most conspicuous and frequently occurring food in stomachs was debris of *Euphausia superba* usually in the form of strips of exoskeletons. A considerable amount of phytoplankton which often contained diatoms, with the Coscinodiscineae being prevalent, was also present. Omnivory in this group of crustaceans was apparent in that *Pelagobia longicirrata* and coelenterate remains occurred in three species, and copepods were found in the diets of all but *C. skogsbergi*. In a survey of feeding in conchoecid ostracods, which included *C. skogsbergi*, a Croker Passage species, Angel (1972) indicated that detritus is important in the diets of many species. He cautioned, however, that much of what had been reported could have resulted from net feeding. This seemed a doubtful source of bias in the present data set because most of the specimens examined were from discrete tows well beneath the krill zone, and were from catches containing relatively few krill individuals or molts. The data suggest, then, that ostracods were able to locate and feed on molts settling through the water column.

Amphipods. Diet information was obtained on six hyperiids and 11 gammarids. A sample size of ten or more individuals was available for 12 of these species. Diet diversity was high in most of this group, though variety was to some extent related to sample size. Amphipods, more than any other group examined, contained a significant fraction of soft bodied prey. All species, for example, fed on coelenterates and *Pelagobia longicirrata*, and salps and fish remains were found in the guts of a third of the species. *Parathemisto gaudichaudii* had the most diverse diet, having fed on an array of soft-bodied organisms (salps, coelenterates, fish) and various types of crustaceans including *Euphausia superba*. Euphausiid gill fragments were common items in guts of this amphipod and of *Primno macropa* as well.

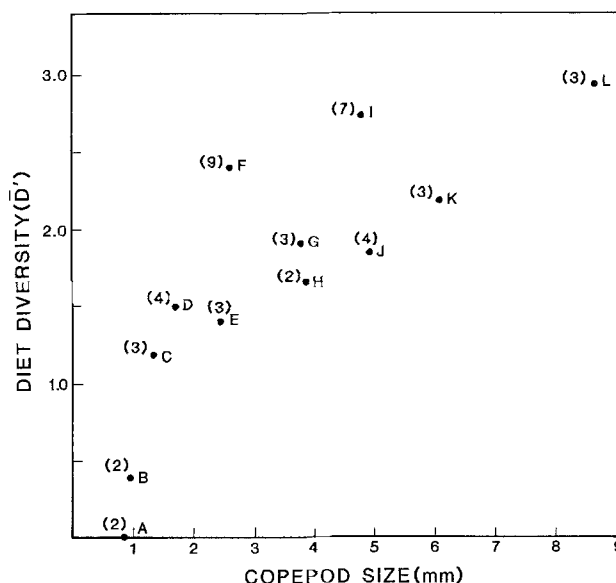


Fig. 2. Plot of the relationship between size of copepods examined in Croker Passage and the diversity of their diet (see Material and methods). Points represent mean values for copepod families, and the value above each point, the number of species included in the averages. Code: A = Oithonidae; B = Oncaeidae; C = Pseudocalanidae; D = Spinocalanidae; E = Lucicutiidae; F = Scolecithricidae; G = Metridiidae; H = Heterorhabdidae; I = Aetidiidae; J = Phaenidae; K = Calanidae + Eucalanidae; L = Euchaetidae

Coelenterates were the principal food of four species, *Hyperietta dilatata*, *Epimeriella macronyx*, *Eurythenes gryllus* and *Parandania boeckii*. The diet of *Cyphocaris richardi* consisted primarily of euphausiid molts (85% incidence), though this species took live prey as well, copepods in particular. *Eusirus propeperdentatus* fed mostly on small crustaceans, of which copepods were the major diet item. Euphausiid molts were important (57% incidence) in its diet as well. *Orchomene plebs*, the most abundant of the two representatives of this genus, contained soft bodied prey (e.g. coelenterates, salps, *Pelagobia longicirrata*, fish), euphausiid debris and copepods. The genus *Oncaea* was especially prevalent among the copepod food. *Orchomene rossi*, the larger of the two species, had a diet similar to its congener, though lacking a coelenterate component.

From the above it is apparent that while essentially predaceous, amphipods ingested detritus as well, particularly as euphausiid molts. Their diets also reflected their probable association with gelatinous organisms in Croker Passage (e.g. see Madin and Harbison, 1977; Harbison *et al.*, 1977). Four species fed predominantly on coelenterates and several species ingested salps. As noted above, included with salp food in the diet of the two *Orchomene* species were large numbers of *Oncaea* spp. cyclopoids and the polychaete *Pelagobia longicirrata*. *Oncaea* spp. and *P. longicirrata* were small in relation to *Orchomene* spp. and its feeding apparatus would seem poorly adapted for capturing prey in this size range. Some association between *Oncaea* spp., *P. longicirrata* and *Salpa thompsoni* is

therefore suggested to explain the frequent appearance of these small zooplankters in the *Orchomene* "diet". The association between *Oncaea* spp. cyclopoids and tunicates has been reported previously, Alldredge (1972) having observed them browsing on larvacean houses.

Four of the species examined contained remnants of fresh krill. The krill population in Croker Passage at the time of sampling had a size range of 17 to 52 mm (mean = 31 mm) the lower limit of which exceeded the length of most of the *Parathemisto gaudichaudii* and *Primno macropa* examined, and was equivalent to the size of most of the *Orchomene* spp. analyzed. While *P. gaudichaudii* feeds on euphausiids and copepods (Hardy and Gunther, 1935; Nemoto and Yoo, 1970) in the Antarctic, it was uncertain if krill remains (frequently gill material) in Croker Passage individuals were an artifact of net feeding or part of their diet.

While all but three amphipod species (*Cylopus lucasii* and the two *Eurythenes* species) included debris of *Euphausia superba* in their diets, this food was the principal gut contents of *Cyphocaris richardi*. *C. richardi* was reported by Chindonova (1959) as having white material with a black outer coat (fish remains?) in their guts, and by Andres (1979) as containing crustacean debris. Andres (1979) found the guts of *Eusirus propeperdentatus* to contain calanoid copepods, bristles of crustaceans, and polychaetes and nematocysts, which constitute many of the elements of the diet of this species in Croker Passage.

Mysids. Six species of these crustaceans occurred in our collections with two, *Antarctomysis ohlinii* and *Dactylamblyops hodgsoni* (?), providing large sample sizes. All species contained phytoplankton and five of the six fed on euphausiid molts. Omnivory was apparent as five species also ingested copepods and three, coelenterates. An omnivorous diet for pelagic mysids has also been reported by Chindonova (1959).

Euphausiids. *Euphausia superba* fed mostly on phytoplankton, though many guts contained euphausiid debris as well. Other types of food were rare. The phytoplankton was characterized by a relative scarcity of diatoms, with the prevalent frustules being those of small *Nitzschia* spp. or *Fragilariopsis* spp. types.

Euphausia superba has been classified essentially as a small particle feeder (e.g. Nemoto, 1968) and this was substantiated by the present results. Most guts examined in the present study, however, were usually only partially full and often contained little food. Everson and Ward (1980) suggested that this species reduces feeding activity and tends to swarm when concentrations of phytoplankton are too low for energetically profitable grazing. Indications (see first section of Results) are that phytoplankton levels were low in March–April, 1983 in Croker Passage. Food in guts was amorphous greenish-brown material containing relatively few diatoms. Further, *E. superba* in Croker Passage occurred in dense swarms as indicated by the ship's depth recorder and by our enormous catches in short

duration hauls in the upper 100 m. The relationship between feeding activity and swarming has not been clearly resolved, however, with Antezana and Ray (1984) offering alternative explanations for observed distributions of phytoplankton and krill.

Thysanoessa macrura, the other abundant euphausiid, contained a variety of food which included some phytoplankton and euphausiid molts, but was essentially a predator on small zooplankton, especially crustaceans. The copepods *Calanoides acutus* and *Metridia gerlachei* were its most common food items. Other reports (e.g. Nemoto and Harrison, 1981) have suggested that this species feeds on phytoplankton.

Tunicates. *Salpa thompsoni*, one of the major components of macroplankton and micronekton biomass, was the only tunicate examined. Its gut contained a wide range of small particle food types including amorphous greenish-brown debris (mostly bristle fragments). The most abundant diatom in guts was *Corethron* sp., with species of the Coscinodiscineae ranking second.

The filter feeding mechanism of this group has been well described (e.g. Madin, 1974; Harbison and McAlister, 1979) and in the present study, *Salpa thompsoni* gut contents mirrored the particle composition of our 30- μ m gauze sievings from the 30-l bottle casts. Guts were invariably full, indicating that *S. thompsoni*, in contrast to *E. superba*, was able to continue feeding successfully in Croker Passage despite the low concentrations of phytoplankton. This was likely possible because of the capability of salps to pump large volumes of water through an effective small particle retention system (see Harbison and Gilmer, 1976).

Chaetognaths. Copepods were the most frequent prey of this group. *Sagitta marri*, the smallest species, took mostly *Oncaea* spp. and copepodites of *Metridia gerlachei*. Few *Eukrohnia hamata* contained food (2%) though *Euchaeta* spp. copepods were the prey in all positive instances. *Sagitta gazellae* the largest species, had the most varied diet, and, while *Euchaeta* spp. was the principal diet item, several immature *Antarctomysis ohlinii* and *Eusirus propeperdentatus* appeared in guts as well. Few *S. gazellae* contained food (5%).

Eukrohnia hamata has been reported as feeding on copepods and radiolarians (Chindonova, 1959) and *Sagitta gazellae* on copepods and euphausiids (David, 1955). As in the present study, David (1955) noted that the incidence of food in *S. gazellae* from RV "Discovery" collections was low.

Polychaetes. The five polychaete species all contained phytoplankton and little else. Occurrences (8) of protozoans, euphausiid bristles, salp debris and nematocysts were also noted. Diatoms were frequent components of the ingested phytoplankton, though they were uncommon in the food of the most abundant species, *Pelagobia longicirrata*. The gut content of this species, in fact, resembled that of cyclopoid and pseudocalanid copepods.

Most accounts of feeding in pelagic polychaetes refer to tomopterids (e.g. Lebour, 1923; Åkesson, 1962; Rakusa-Suszczewski, 1968). Species in this family, while ingesting other zooplankton whole (e.g. fish larvae, larvaceans and chaetognaths), may obtain a significant portion of their nutrition by sucking out body fluids from other soft-bodied forms, such as chaetognaths (Rakusa-Suszczewski, 1968). One of the Croker Passage tomopterids, *Tomopteris carpenteri*, did contain salp remnants and it is possible that the phytoplankton observed in guts of this species could have been secondarily obtained through some association with *Salpa thompsoni*. The phytoplankton noted in both *Maupasia caeca* and the very abundant *Pelagobia longicirrata* may have been obtained similarly. As noted previously, the latter species often co-occurred with the salp remains in guts of *Orchomene* spp. amphipods, though the *P. longicirrata* contained virtually no *Corethron* sp. diatoms, which were predominant in salp food.

Molluscs. Two species each of gymnosome pteropods and decapod squids were examined. The pteropods *Clione antarctica* and *Limacina helicina* contained no recognizable food. The genus *Clione* appears to consist of highly specialized predators on thecosomatous pteropods, especially on the Limacinidae (Lebour, 1931; Conover and Lalli, 1974). *Limacina helicina*, a phytoplankton feeder (Morton, 1954; Paranjape, 1968), was rare which might account for the small size and empty digestive tracts of the *Clione antarctica* in our collection.

The squid *Alluroteuthis antarcticus* (2 specimens) contained *Euphausia superba* and squid beaks. *Crystalloteuthis glacialis* (3 specimens) contained a euchaetid copepod, a *Thysanoessa macrura* individual and some fish debris.

Fishes. Three species of midwater fishes were examined, but only the results for *Electrona antarctica* were reported because of evidence of a considerable degree of net feeding in *Pleuragramma antarcticum* and *Gymnoscopelus nicholsi* (see Discussion). *E. antarctica* was essentially a predator on *Euphausia superba*, with most stomachs containing one to several krill. Copepods, mostly *Euchaeta antarctica* and *Metridia gerlachei*, also appeared to be part of the normal diet as they occurred in intestines as well as in stomach. Amphipods and *Thysanoessa macrura* were occasional food items.

Rowedder's (1979) data also indicate that *Electrona antarctica* feeds primarily on *Euphausia superba* and, in fish 50 mm and larger, over half the food biomass in this species in the Scotia Sea was constituted by krill. In Croker Passage nearly all of the *E. antarctica* exceeded 50 mm in length. While the diet information for *Pleuragramma antarcticum* from Croker Passage could not be used, other studies indicate that large juveniles and adults also feed heavily on krill (e.g. DeWitt and Hopkins, 1977). In Croker Passage, then, it is the micronektonic fishes and possibly the squids (undoubtedly poorly sampled with our nets) which are the principal predators on live krill among the midwater fauna.

Table 2. Occurrence of major food types in the food web of Croker Passage March–April, 1983

Food type	No. of species
Phytoplankton/detritus lacking diatoms	78
Phytoplankton/ <i>Coscinodiscineae</i>	64
<i>Euphausia superba</i> (molts, debris)	56
<i>Pelagobia longicirrata</i> (Polychaete)	42
Phytoplankton/other diatom types	37
Coelenterates	32
Other copepods	29
<i>Metridia gerlachei</i>	28
<i>Oncaea</i> spp.	28
Protozoans	18
Phytoplankton/ <i>Corethron</i> sp.	17
<i>Euchaeta</i> spp.	15
Dinoflagellates	13
<i>Oithona</i> spp.	11
Chaetognaths	11
<i>Euphausia superba</i> (as live prey)	8
Salps	7
<i>Calanoides acutus</i>	7
<i>Microcalanus pygmaeus</i>	7
Ostracods	7

Discussion

Elements of bias. The problems inherent in investigations of this nature warrant discussion. A major potential source of bias is post-capture feeding in the nets. It was possible to assess this in fish species through the use of bogus prey, which in the present case was small styrofoam balls introduced in the trawl cod end (see Lancraft and Robison, 1980). These occurred in considerable numbers in the stomachs of *Pleuragramma antarcticum* and in all of the *Gymnoscopelus nicholsi* examined, but were uncommon in *Electrona antarctica* (8% incidence). Consequently, reasonable confidence can be placed in the diet information for the latter species. Crustaceans, however, constituted most of the array of species examined, and they usually masticate rather than swallow food whole. Therefore, styrofoam balls were of no use in making judgments on net feeding in this group. Observations were made, though, as to which organisms arrived on deck alive and on their behavior in the catch. Amphipods were especially hardy and individuals of *Orchomene* spp. were frequently seen chewing on larger animals, fish in particular. The chunks of fresh fish muscle and skin often observed in their guts were, therefore, not considered a natural part of the diet. Also, euphausiid gills were frequent diet items in *Parathemisto gaudichaudii* and *Primno macropa*, and it is uncertain whether these were browsed off krill in the catch or were bitten off under natural conditions.

While definitive proof is lacking, the following lines of evidence suggest that net feeding did not obscure the natural diet patterns of most of the species examined: (1) most crustacean species and non-crustacean invertebrates arrived at the surface moribund; many species appeared to be fragile and it is surmised that they did not survive

long in the cod end after capture; (2) during towing the cod end was undoubtedly a turbulent environment, generating a well mixed population, yet gut contents of individual species and species groups consistently differed (e.g. among copepods, compare the diets of the Phaenidae, Scolecithricidae, Aetidae and Euchaetidae and among the amphipods, *Cyphocaris richardi*, *Orchomene* spp. and *Parandania boeckii*); (3) in some of the larger species where comparisons were made (e.g. *Orchomene rossi*, *C. richardi*, *Antarctomysis ohlinii*, *Electrona antarctica*) food types found in foreguts (stomachs, gastric mills) usually also appeared in hind guts or intestines; (4) krill molts were frequent and often dominant food of organisms (e.g. *C. richardi*, species of Scolecithricidae, ostracods and mysids) examined from catches made well below the krill zone (upper 100 m) and in catches which contained few live krill or molts; and (5) though all studies based on net collections are subject to bias from net feeding, the present results are in general agreement with the findings of others for many groups and show the same types of specialization in feeding (see references in diet comparison section of Results).

Assessment of the greenish-brown or greenish-grey debris was difficult. In omnivorous groups and in deep-dwelling species in particular, it was uncertain whether the food in guts represented freshly gathered phytoplankton or was secondary food in the form of fecal pellets, secondary food trapped in mucous strands, or was attached to ingested appendages and other parts of molts. This type of debris was found in all but a few species, even occurring in predatory species (e.g. amphipods). Also, the contribution of fragile athecate phytoplankton and protozoans to this amorphous material could not be determined with the techniques used. This material becomes unrecognizable in herbivore-omnivore guts as a result of mastication and digestion. Nematocysts may have occurred secondarily in the guts of many species as well, since they may have been discharged on prey species or debris (e.g. euphausiid molts) which came in contact with coelenterate tentacle arrays prior to ingestion.

Another important potential source of bias was sample size. Sample size was uneven, and high diet diversity within a group often was associated with large sample size (Table 1). Analysis of most species was usually restricted to a relatively narrow size range of specimens and therefore could not reveal possible changes in diet with ontogeny. Finally, the food web structure proposed here was based on incidence and not the volume of food types in guts, hence it is non-quantitative *sensu stricto*.

Food web structure. The species occurring in Croker Passage can readily be divided into small- and large-particle feeders. However, with information on 20 food categories available, a more sophisticated grouping through cluster analysis suggests a food web constituted by 21 feeding clusters (Fig. 3). There was much commonality apparent in the diets of most species examined from Croker Passage, particularly with respect to phytoplankton

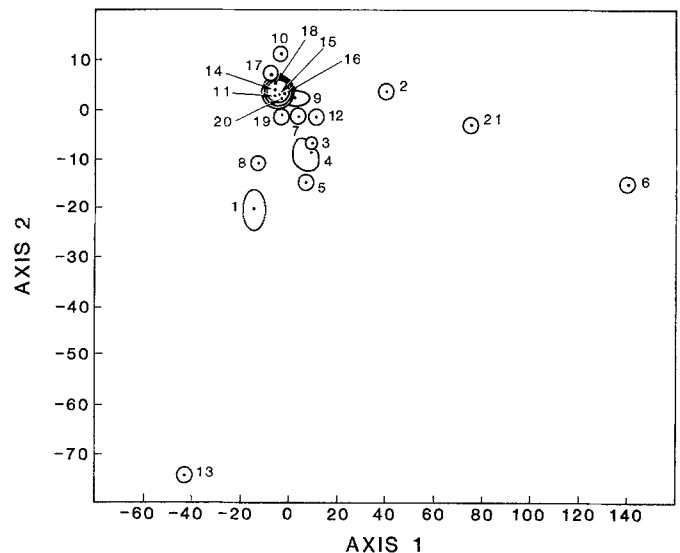


Fig. 3. Non-hierarchical cluster analysis plot on canonical axes of class means for 21 feeding groups of midwater organisms in Croker Passage (see Material and methods; Searle, 1982)

and debris of *Euphausia superba* as food; consequently most of the clusters of small-particle feeders are clumped towards the upper left of the plot. The large-particle feeders, i.e. the carnivores, are distributed around the periphery of this group of clusters.

The structure of the food web based on the cluster analysis is given in Fig. 4. The principal food types have been repeated around the four sides of the diagram to minimize congestion from the arrows representing feeding relationships (arrow direction is from the consumer to the type of food consumed). Again, small-particle feeding groups, which accounted for the majority of the species examined (clusters 11, 14, 16, 17, 18), are arranged to the left of the figure while the large-particle feeders (carnivores) are across the bottom and to the center and right.

From the taxonomic composition of the clusters and from species-size information in Table 1, several trends are apparent. Predictably, the small-particle feeders, *Euphausia superba* and *Salpa thompsoni* excluded, were smaller in size on the average than the large particle feeders. The mean sizes and size ranges for the species in each of these two groups, here compared as those species in clusters 11, 14, 16, 17, and 18 versus those in the remaining clusters, were 6.3 mm (Rn: 0.7–54.0 mm) and 22.8 mm (Rn: 2.3–82.0 mm), respectively, and were significantly different (Student's *t*-test; $p < 0.01$). Also, while many of the feeding clusters are closely grouped and there is commonality of certain abundant food types among many species clusters, the concept of resource partitioning receives support among both the small- and large-particle feeders. It is also apparent, however, on examining species composition of clusters, that closely related species had similar diets. This has been reported in other types of ecosystems. Orians and Horn (1969), for example, noted the similarity in diets of co-occurring species of closely related birds. Among the

THE MIDWATER FOOD WEB IN CROKER PASSAGE, ANTARCTIC PENINSULA, AUSTRAL FALL (MARCH-APRIL), 1983

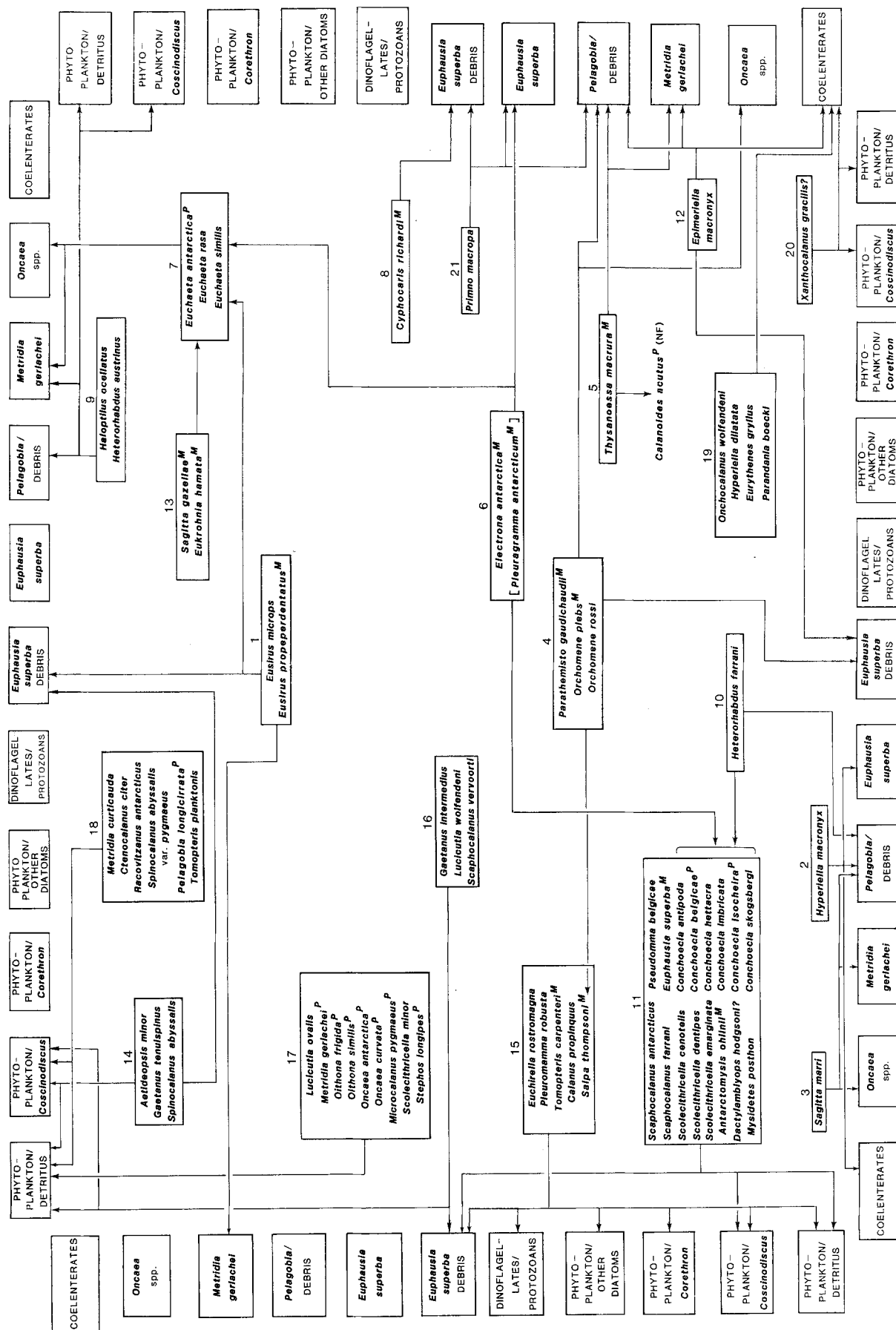


Fig. 4. The food web in Croker Passage based on cluster analysis; number over boxes represent feeding cluster number (see Fig. 3). P and M indicate that these species are dominant, respectively, in the plankton and in the macroplankton; NF=all guts empty (not feeding). Arrows run from the consumer towards the type of food consumed, and indicate food types which have an incidence rate in guts of > 10%

small-particle feeders this was especially noticeable in Croker Passage in the Scolecithricidae, the cyclopoid copepods and the conchoecid ostracods; and among the large-particle feeders, in the euchaetid copepods and the *Eusirus* spp. and *Orchomene* spp. amphipods.

In fact, resource partitioning becomes increasingly difficult to resolve below the level of family. This is not to say that the diets of closely related species were identical; analytical techniques were too coarse to permit much resolution among types of small particulate food in stomachs. "Fine tuned" resource partitioning may not be a necessary characteristic of the ecosystem in any event, because in the spring more than sufficient phytoplankton may be available to the entire midwater community so as to ensure adequate energy for reproduction, most of the yearly growth and the build-up of fat reserves. Later in the year (late summer–fall), when the ecosystem becomes more oligotrophic (Currie, 1964; Walsh, 1969; Holm-Hansen and Huntley, 1984), species such as *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus* and *Euphausia superba* may terminate (e.g. see Andrews, 1966) or significantly reduce their level of feeding in anticipation of winter conditions. Other species in Croker Passage apparently supplement their diets during this period with the probable abundant supply (e.g. krill standing crop ~ 55 g DW/m²) of krill debris.

While the preceding seems a logical scenario for the trophic sequence in Croker Passage, the proposed scheme requires substantiation through the examination of the food web structure at other times in the year in this strongly pulse-induced ecosystem (Currie, 1967; Knox, 1970; Nemoto and Harbison, 1981). For example, feeding patterns in the spring when phytoplankton is abundant may contrast significantly with the trophic picture in the fall. Also, the role of gelatinous predators, such as scyphomedusae and ctenophores, requires investigation (e.g. using SCUBA techniques; Hamner *et al.*, 1975, 1983) to obtain a clearer image of how this ecosystem functions. Heavy predator pressure from gelatinous plankton (e.g. Fraser, 1962; Miller and Williams, 1972; Rogers *et al.*, 1978; Clifford and Cargo, 1978; Reeve and Walter, 1978), in combination with that reported from non-gelatinous organisms in the present investigation would, as Hayward and McGowan (1979) suggested, conceivably allow many prey species which spatially co-occur to subsist on similar diets with a minimum of competition.

Krill debris ranked third in diet incidence and was found in 56 of the 93 species examined among the species analyzed from Croker Passage (note that live krill remains were found in only eight species). The pervasiveness of krill debris throughout the food web, i.e. from the diets of small copepods to those of large-particle feeding crustaceans, invites studies on the frequency of molting, the persistence of molts in the water column, the time sequence and pattern of molt disintegration, and on the nutritional worth of krill debris. At present it is not certain as to how *Euphausia superba* debris enters the diets of so many species. For instance, among the copepods it re-

mains to be determined if these organisms capture krill debris directly as it settles, obtain it secondarily by ingesting fecal pellets, or by actually browsing on molts.

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