

The Zooplankton Community of Croker Passage, Antarctic Peninsula

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Summary. Zooplankton species composition, abundance and vertical distribution were investigated in the upper 1000 m of Croker Passage, Antarctic Peninsula during the austral fall (March–April, 1983). 106 species were identified, many being mesopelagic and reported previously from the Southern Ocean. The most numerous species ($>1000/100\text{ m}^3$) were the copepods *Metridia gerlachei*, *Microcalanus pygmaeus*, *Oncaea antarctica* and *Oncaea curvata*. *Oncaea curvata* alone constituted half the zooplankton population. Zooplankton biomass was dominated by three copepod species, *Metridia gerlachei*, *Calanoides acutus* and *Euchaeta antarctica*, which comprised 74% of the biomass. Size analysis revealed most of the zooplankton numbers were in the $<1\text{ mm}$ fraction. The biomass distribution was polymodal with major maxima in the $<1\text{ mm}$ and the 4–4.9 mm size classes. The $<1\text{ mm}$ peak, exclusive of protozoans, was primarily copepod nauplii and copepodites of *Oncaea*, *Metridia* and *Microcalanus*. The 4–4.9 mm peak was mostly *Calanoides acutus* and *Metridia gerlachei*.

All of the principal species had broad vertical distributions both day and night. There was some suggestion of diel vertical migration by *Metridia gerlachei* and *Euchaeta antarctica*, with segments of their populations migrating into the upper 100 m and 200 m, respectively, at night. Most of the dominant and subdominant species were concentrated below 200 m, with only the subdominant *Oithona similis* having its maximum in the epipelagic zone. The occurrence of zooplankton at winter depths appears to have been earlier in Croker Passage in 1983 than has been generally reported for waters south of the Polar Front.

Total standing stock of net-caught zooplankton ($<15\text{ mm}$) in the upper 1000 m was estimated at 3.1 gDW/m^2 , which is somewhat higher than values reported for the West Wind Drift and for open ocean areas of temperate to tropical latitudes. *Euphausia superba* (17–52 mm) dominated the pelagic biomass, exceeding zooplankton standing stock under a square meter of

ocean by a factor of 15. This is in contrast to lower latitudes where zooplankton biomass is usually greater than macrozooplankton-micronekton.

Introduction

With recognition of the economic potential in harvesting krill, the literature on the biology of *Euphausia superba* has grown exponentially in the last decade. The role of krill in the nutrition of birds, mammals and fishes in the Southern Ocean is especially well documented (see Nemoto 1968; El-Sayed 1971; Tranter 1982, for reviews). Much less attention has been focused on zooplankton and its interaction with krill dynamics. Hardy and Gunther (1935) recognized early on the importance of zooplankton in the Southern Ocean trophic scheme, their report being one of the few wherein plankton systematics, abundance, distribution, and seasonality were integrated.

The present paper reports on the zooplankton community in the upper 1000 m of Croker Passage, a connection between the Gerlache and Bransfield Straits adjacent to the Antarctic Peninsula. The location was chosen because of its large krill population, its considerable depth (max. $\sim 1200\text{ m}$) and its surrounding land masses (Fig. 1) which permitted continuous sampling by protection from weather. The information was to serve as a basis for a study of the food web at this location and to provide insight into zooplankton-krill interactions in particular. This initial paper provides an extensive species list for the region, data on zooplankton ($<15\text{ mm}$) abundance, biomass and size distribution, and information on diel vertical distribution.

Methods

Collections were made in March and April 1983 from the *RV Hero* using collapsible $66 \times 66\text{ cm}$, $162\text{ }\mu$ mesh nets mounted in the mouth of a 4.8 m^2 (mouth area) closing Tucker trawl (Hopkins and Baird 1975).

The trawl-plankton net system was opened and closed with mechanical clock-release mechanisms identical to that described by Davies and Barham (1969). For discrete depth-zone hauls (19), nets were lowered to depth, opened, then undulated through the selected sampling zone by paying out and retrieving wire. The trawl was closed off prior to return to the surface. Discrete zone towing was attempted using wire angle measurements and triangulation; consequently there was a lack of precise depth control during sampling and some overlap in zonal boundaries. For 0–1000 m oblique biomass hauls (5), the open trawl was slowly lowered and retrieved in a “v” path through the water column, with 1000 m being the maximum depth attempted. A time-depth recorder was attached to the trawl to provide a depth trace for each tow. Fishing time (i.e., trawl open) for tows <100 m depth was 28 min and for tows at depths >100 m, 76 min. The five 0–1000 m oblique tows averaged 230 min. Ship's speed for all towing was approximately 2 knots. Flow through plankton nets was recorded with mechanical dial-type flowmeters suspended in the center of the net. Zooplankton was initially preserved in 10% v/v borax buffered formalin, and later transferred to 50% isopropyl alcohol. Tow information is in Table 1.

Zooplankton counts and measurements were made in aliquots obtained with a Motoda box splitter (Motoda 1959). Aliquots ranged from 1/4–1/64 of the sample, though all but five analyses were of 1/32 or 1/64 splits. The zooplankton in two aliquots from each sample was counted and the results were averaged. The sample splits were analyzed in 10×10 cm plastic microorganism medium trays with a 144 square grid ruled on the bottom. Prior to counting, all organisms >15 mm in maximum body dimension were removed and added back to the trawl collections, the macroplankton and micronekton to be reported on elsewhere. Partial aliquots were counted for very abundant

species with the number of grid squares counted varying with species abundance. The entire aliquot was examined for less abundant species and the entire preserved catch of both the plankton and the trawl nets was searched for rare zooplankton species. The search procedure for rare species was to examine the collections trayfull at a time using the 10×10 cm plastic medium trays until each entire sample was processed. The average number of individual zooplankters counted for each aliquot was 700, with a coefficient of variation among counts of 16%.

When abundance permitted, the maximum body dimension of 25 individuals of every species was measured in each sample. The anatomical dimensions measured for each major type of zooplankton are described in Hopkins (1982). Size-weight regressions were established for dominant species and for selected species which were morphologically representative of other less abundant types of zooplankton (106 species were found, many of them rare). Specimens of each species were sorted into several size groups covering the entire size range and dried to a constant weight at 60°C. Dry weight (DW) was recorded to the nearest 0.01 mg. The regressions were used to determine the contribution of individual species by size class in 1 mm increments. Total sample biomass was estimated by cumulating individual species weights as derived from the size-weight regressions. A check of this method was made by comparing total biomass determinations obtained in this manner with direct dry weight measurements (of 1/4 splits) of the five 0–1000 m oblique samples. The averages of both methods were within 4% of one another. All dry weights may be biased to some degree through losses of organic matter from zooplankton stored in preservatives (e.g., Omori 1978). Abundance and biomass data were calculated using the appropriate net mouth-area and flowmeter calibration factors and expressed

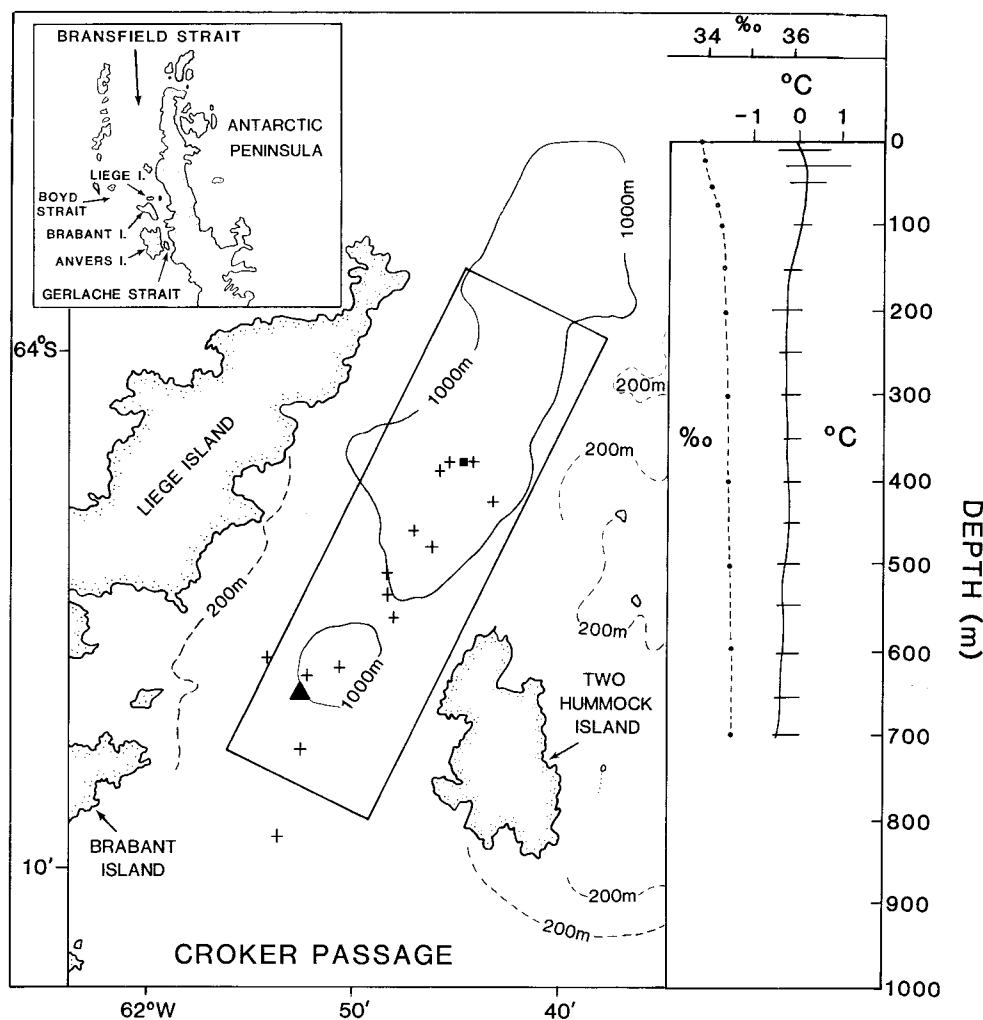


Fig. 1. The sampling area in Croker Passage with vertical profiles of salinity and temperature. + = XBT profiles; solid square = salinity station (8 April, 1983); solid triangle = 301 bottle plankton cast (12 March, 1983). Horizontal lines in the vertical temperature plot are range bars for 12 XBT profiles made in the period 8–11 April, 1983

30 l bottle was collected with 30 l water bottles on 12 March (0624–1620 h) from depths of surface, 25, 50, 75, 100, 150, 200, 300, 400, 600, 800 and 1000 m. The surface samples were destroyed during transit. Water was strained through 30 μ gauze and the sievings preserved in 5% buffered formalin. Counts were made in the square microbiology trays described above, with tallies being kept on metazoans, tintinnids and radiolarians. At least 10 of each type of metazoan, which were virtually all copepod nauplii and copepodites of cyclopoids and calanoids, were measured. Dry weights of the copepodites were estimated with the appropriate size-weight regressions, while nauplius biomass were determined through body measurements converted to a volume (mm^3) using simple geometric formulas. A one-to-one ratio was assumed in converting mm^3 to mg wet weight (WW) and dry weight was assumed to be 0.15 WW (Lovegrove 1962). The conversion factor used in Fig. 6B for relating zooplankton biomass to caloric content was 1 mg DW \approx 5 cal (Ostapenya and Shuskina 1973).

Salinity in the sampling area was determined with a conductivity salinometer using water from an 8 April (1927–2105 h) 30 l bottle cast. Temperature was profiled throughout the sampling period with expendable bathythermograph probes.

Results

Sampling Locale

Croker Passage is one of the principal connections between the Gerlache and Bransfield Straits. Our collecting was in the upper 1000 m of a 22 \times 6 km rectangle over one of the large central depressions in the passage (Fig. 1). Minimum depths through Boyd Strait immediately to the north and the Bransfield Strait to the northeast exceed 500 m and thus offer access for mesopelagic waters from the open Southern Ocean to Croker Passage. Temperature profiles (12) for the period 8–11 April when most of the discrete zone sampling was done showed as much as 1.6 $^{\circ}\text{C}$ variability at shallow depth horizons (e.g., at 30 m; Fig. 1). Below 50 m, however, the variability was less than 1 $^{\circ}\text{C}$ and the mean for this period in the upper 700 m of Croker Passage was within $\pm 0.7^{\circ}\text{C}$ of 0 $^{\circ}\text{C}$. The vertical salinity range over this depth was 33.89–34.57‰. At times “brash” ice and icebergs were encountered during sampling, but the area of the sampling rectangle was for the most part clear of obstructive ice.

Zooplankton Composition and Abundance

A total of 106 zooplankton species were identified from Croker Passage samples. The list is incomplete, as a number of hydromedusae and oikopleurinae were not identified because of their poor condition. Also, all plankton from the 30 l bottle catches was not identified to species, though most of the cyclopoids were *Oncaea curvata* and the majority of calanoid copepodites were *Microcalanus pygmaeus* and *Metridia gerlachei*. The abundance data in Table 2 indicate that while the plankton was diverse, relatively few species accounted for most of the numbers and biomass. The numerically dominant (>1000 individuals/ 100 m^3) metazoan species, as determined from the plankton net collections, were all

species, 100–1000 individuals/ 100 m^3 , were the copepods *Calanoides acutus*, the pair of *Oithona* species and *Stephos longipes*; the ostracod *Conchoecia belgicae*; and the polychaete *Pelagobia longicirrata*. The principal biomass species, i.e., >40 mg DW/ 100 m^3 , were *Metridia gerlachei*, *Calanoides acutus* and *Euchaeta antarctica* (copepod). Subdominants (5–40 mg DW/ 100 m^3) were *Microcalanus pygmaeus*, *Oncaea antarctica*, *Rhincalanus gigas* (copepod), *Conchoecia belgicae*, *Thysanoessa macrura* (euphausiid) and *Pelagobia longicirrata*.

The size distribution of zooplankton taken in the 0–1000 m sweeps (Fig. 2A) clearly revealed that most of the zooplankton was small, <1 mm. The power curve $Y = 8238 X^{-3.14}$ ($r = 0.99$; $P < 0.001$) well represented the general pattern of decrease in abundance (Y) with increasing zooplankton size (X). Biomass distribution, on the other hand, was polymodal (Fig. 2B), with major maxima in the <1 mm and the 4–4.9 mm size fractions. The biomass distribution of the major taxa by size class (Fig. 3) showed that the <1 mm fraction was constituted

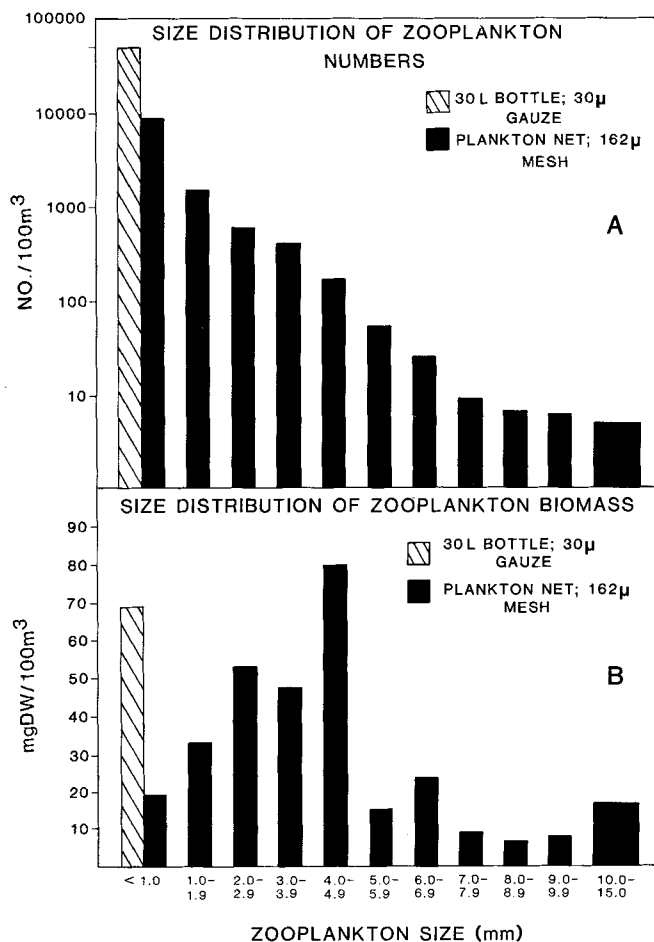


Fig. 2. Size distribution of zooplankton (A) numbers and (B) biomass in Croker Passage, March–April 1983, based on the average measurements of zooplankton from five 0–1000 m oblique plankton net tows and from 30 l bottle casts

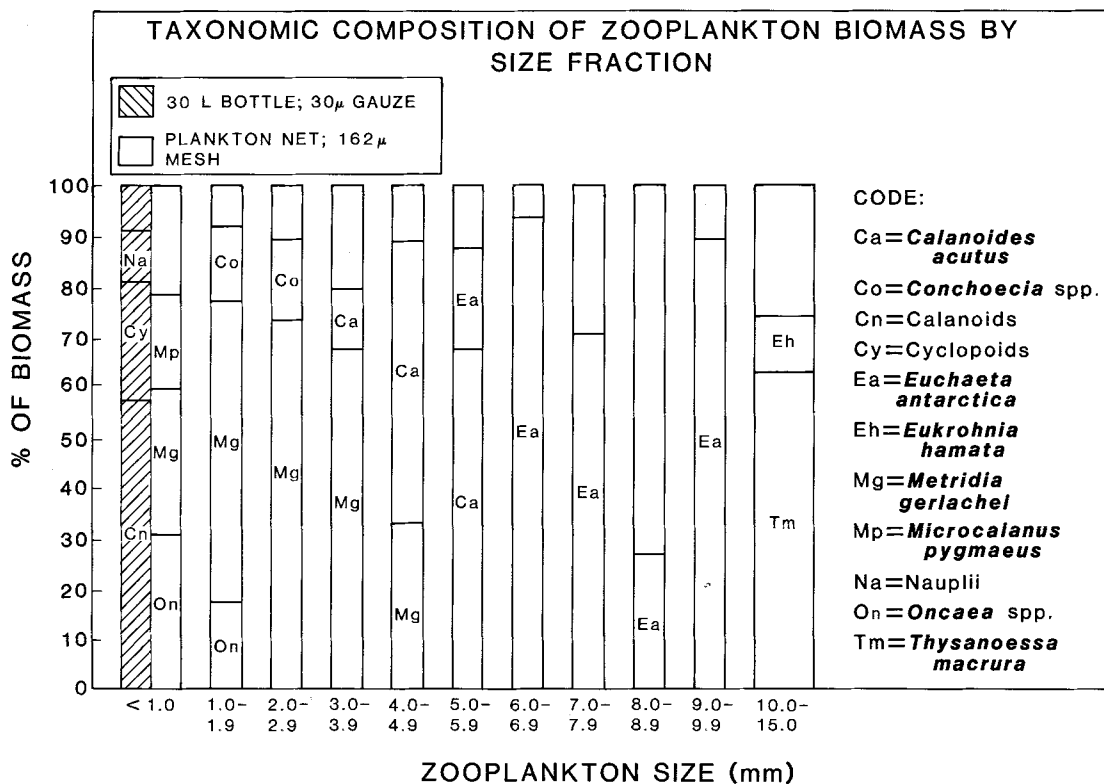


Fig. 3. Taxonomic composition of zooplankton by size class based on the average results of analyses of five 0–1000 m oblique plankton tows. Unlabelled portions of each bar composed by biomass of the remainder of the zooplankton

mostly by cyclopoids (primarily *Oncaea curvata*) and copepodites of *Metridia gerlachei* and *Microcalanus pygmaeus*. The size fractions from 1–3.9 mm were constituted mostly by various stages of *Metridia gerlachei*. The 4–5.9 mm size range, which included the second biomass peak, was composed primarily of *Calanoides acutus*. *Euchaeta antarctica* and *Thysanoessa macrura* constituted the major share of biomass in the 6–9.9 mm and the 10–15 mm fractions, respectively.

The total number of zooplankton >1 mm in the upper 1000 m was estimated at 2800/100 m³ from the 162 μ mesh net catches. Zooplankton <1 mm on the basis of 30 l bottle casts was 51,000/100 m³, or 18 times the abundance of 1–15 mm zooplankton. The biomass of 1–15 mm zooplankton, as obtained with the species size-weight regressions was 0.29 g DW/100 m³ and the <1 mm metazoan plankton biomass was estimated at 0.07 g DW/100 m³.

Vertical Distribution

A multiple plankton net system was unavailable for this study, hence vertical distribution information was cumulated single tow at a time in the period 12 March, 1983 to 11 April, 1983. Most of the vertical zonation results, however, were based on tows obtained in a relatively

Table 1. Data on the plankton tows made in Croker Passage in March–April, 1983 which were used in this study. D = day; N = night; T = twilight

Sample no.	Local time	Date	Depth	Volume filtered (m ³)
1	1825–2210(N)	12. 3. 83	0–1000	3878
4	1945–2323(N)	13. 3. 83	0–1000	4200
8	2012–0020(N)	14. –15. 3. 83	0–1000	4936
11	0210–0430(N)	16. 3. 83	630–820	2696
12	1501–1711(D)	16. 3. 83	750–820	3469
13	2237–0047(N)	16. –17. 3. 83	775–1000	2853
14	0406–0551(N)	17. 3. 83	300–400	2386
15	1546–1731(D)	17. 3. 83	230–480	2635
16	2133–2238(N)	18. 3. 83	130–200	2795
17	0958–1024(D)	8. 4. 83	0–100	977
18	0930–1045(D)	8. 4. 83	100–200	2362
19	1220–1335(D)	8. 4. 83	200–300	2654
20	1558–1708(D)	8. 4. 83	340–550	2699
21	2120–2150(N)	8. – 9. 4. 83	0–100	897
22	2300–0013(N)	9. 4. 83	200–300	2641
24	1645–2033(T)	9. 4. 83	0–1000	5192
25	2203–2313(N)	9. 4. 83	450–550	1852
26	0927–1037(D)	10. 4. 83	350–550	4147
27	1237–1347(D)	10. 4. 83	480–570	1859
28	1602–1712(D)	10. 4. 83	600–770	1792
29	2157–2307(N)	10. –11. 4. 83	550–650	3082
30	1046–1156(D)	11. 4. 83	800–1000	1817
31	1409–1519(D)	11. 4. 83	330–470	1830
32	1630–2020(T)	11. 4. 83	0–1000	5625

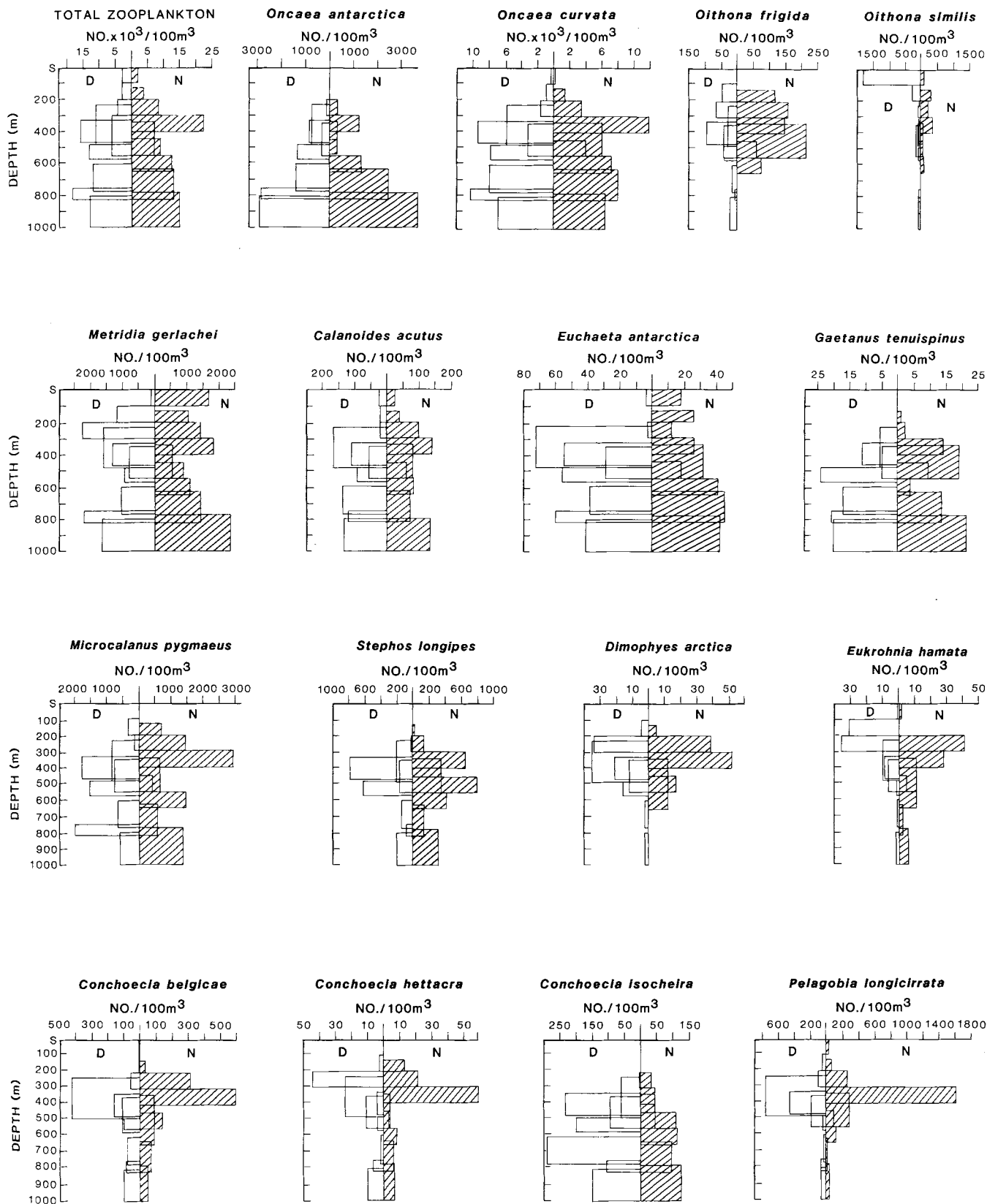


Fig. 4. Vertical distribution of the principal zooplankton species in Croker Passage (see "Results" for criteria). N = night; D = day; + = present in low numbers

short span of four days, 8–11 April. This period included virtually all of the daytime discrete zone tows and four tows in evenly spaced zones in the upper 700 m at night, including the crucial 0–100 m zone (Table 1). The vertical distribution patterns in Fig. 4, then, are considered as representative of April. These patterns indicate that the most abundant zooplankton species had broad vertical distributions in Croker Passage in the fall of 1983. Of those species $>10/100\text{ m}^3$ in numbers and $>1\text{ mg DW}/100\text{ m}^3$ in biomass only *Oithona frigida*, *Gaetanus tenuispinus* (copepod) and *Conchoecia hettacra* were not found from the surface to 1000 m. The abundant species, however, had relatively low population densities in the upper 200 m, with the exception of *Oithona similis* which was at maximum densities in this zone. Seven of the 16 abundant species in Fig. 4 seemed most concentrated in the 200–500 m zone, these being *Microcalanus pygmaeus*, *Stephos longipes*, *Oithona frigida*, *Conchoecia belgicae*, *C. hettacra*, *Pelagobia longicirrata* and *Dimophyes arctica* (calycophoran siphonophore). The maximum for $<15\text{ mm}$ *Eukrohnia hamata* (chaetognath) was slightly shallower, at 100–400 m. Of the numerically dominant species, only *Oncaea antarctica* had highest population densities at depths greater than 500 m. The vertical distribution of total zooplankton reflected that of *Oncaea curvata*, which alone constituted over half the zooplankton numbers.

Diel vertical migration among the most important species was not clearly evident, though *Euchaeta antarctica* and *Metridia gerlachei* appeared to be considerably more abundant in the upper 200 m and 100 m, respectively, at night, and *Oithona similis* in the upper 100 m during the day. The 27 uncommon species in the 1 to

$10/100\text{ m}^3$ range also generally had broad vertical distributions. Seven species, the copepods *Aetideopsis minor*, *Calanus propinquus*, *Ctenocalanus citer*, *Scaphocalanus farrani*, *Spinocalanus abyssalis* var. *pygmaeus*, the euphausiid *Thysanoessa macrura* and the pteropod *Spongiobranchaea australis*, were found throughout the water column. Three species in the group were collected only from the upper 650 m of the water column, the copepod *Scolecithricella minor*, and the tunicates *Fritillaria borealis* and *Salpa thompsoni*. Large (i.e., $>15\text{ mm}$) specimens of the latter species were found as well in trawl catches from greater depths.

Over half (56) of the species identified were rare, i.e., $<1/100\text{ m}^3$, 37 of which were copepods. Among the latter group, 10 were taken only in 0–1000 m oblique sweeps and another 15 in mesopelagic collections from below 500 m. Only three of the rare copepod species, *Euchirella rostromagna*, *Haloptilus ocellatus* and *Pleuromamma robusta*, occurred in catches from shallower than 300 m. As for rare species other than copepods, the two least abundant ostracods, *Conchoecia brachyaskos* and *C. imbricata*, and the mysid *Dactylamblyops hodgsoni* (?) were only taken below 600 m. Amphipods showed a range of vertical patterns, with *Primno macropa* and *Cyphocaris richardi* having comparatively broad distributions, *Parathemisto gaudichaudii* and *Hyperiella macronyx* being taken mostly in the upper half of the water column, and *Orchomene plebs* occurring more in middepth collections. Of the six polychaete species, *Tomopteris septentrionalis* and *Typhloscolex mulleri* had broad vertical ranges, whereas *Maupasias caeca* and *Rhynchonerella bongraini* were in collections from shallower than 500 m. *Travisopsis levinseni* was in interme-

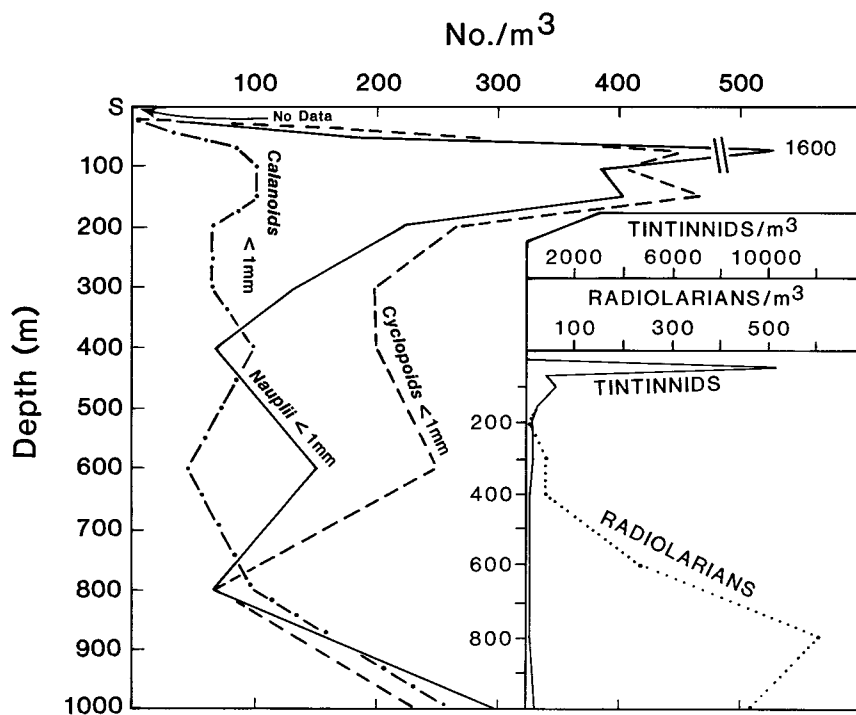


Fig. 5. Vertical distribution of metazoan and two groups of protozoan plankton $<1\text{ mm}$ in Croker Passage, March–April 1983, based on 30 l bottle casts (30 μ gauze). No surface data available

Table 2. Zooplankton species taken from Croker Passage, Antarctic Peninsula with 162 μ mesh plankton nets in the austral fall, March – April, 1983. Abundance values represent an average for five oblique 0 – 1000 m tows. Depth ranges based on the discrete zone plankton collections. Asterisk (*) indicates present only in 0 – 1000 m oblique tows. ¹ Counts based on individual bracts etc., since colonies never taken intact. + The dominant biomass species, but all were in the micronekton size range (>17 mm)

	Depth range (m)	no/ 100m ³	mg DW/ 100m ³		Depth range (m)	no/ 100m ³	mg DW/ 100m ³
Copepoda							
<i>Aetideopsis minor</i>	0–1000	7	2.08	<i>Undinella brevipes</i>	330–775	<1	<0.01
<i>Arietellus simplex</i>	750–1000	<1	<0.01	<i>Xanthocalanus gracilis</i> (?)	130–1000	1	0.13
<i>Bathycalanus bradyi</i>	*	<1	<0.01	Ostracoda			
<i>Calanoides acutus</i>	0–1000	101	60.65	<i>Conchoecia antipoda</i>	230–1000	4	0.56
<i>Calanus propinquus</i>	0–1000	5	2.76	<i>Conchoecia belgicae</i>	0–1000	114	12.31
<i>Candacia falseipera</i>	750–1000	<1	<0.01	<i>Conchoecia brachyaskos</i>	775–1000	<1	<0.01
<i>Candacia maxima</i>	330–470	<1	<0.01	<i>Conchoecia hettacra</i>	100–1000	13	1.21
<i>Centraugaptilus rattrayi</i>	300–400	<1	<0.01	<i>Conchoecia imbricata</i>	630–820	<1	0.01
<i>Cephalophanes frigida</i>	*	<1	0.11	<i>Conchoecia isocheira</i>	0–1000	79	1.89
<i>Cornucalanus robustus</i>	630–1000	<1	<0.01	<i>Conchoecia skogsbergi</i>	230–1000	1	0.05
<i>Ctenocalanus citer</i>	0–1000	18	0.14	Euphausiacea			
<i>Euaugaptilus laticeps</i>	750–820	<1	<0.01	<i>Thysanoessa macrura</i>	0–1000	4	11.03
<i>Euchaeta antarctica</i>	0–1000	43	46.71	[<i>Euphausia superba</i>] ⁺			
<i>Euchaeta barbata</i>	750–820	<1	<0.01	Amphipoda			
<i>Euchaeta biloba</i>	550–650	<1	<0.01	<i>Cylopus lucasii</i>	*	<1	<0.01
<i>Euchaeta rasa</i>	550–650	<1	<0.01	<i>Cyphocaris richardi</i>	230–1000	<1	0.41
<i>Euchaeta similis</i>	750–1000	<1	0.54	<i>Eusirus propeperdentatus</i>	300–1000	1	1.84
<i>Euchiella rostromagna</i>	130–550	<1	<0.01	<i>Hyperietta dilatata</i>	130–820	3	0.96
<i>Farrania frigida</i>	*	<1	<0.01	<i>Hyperietta macronyx</i>	0–570	<1	<0.01
<i>Gaetanus antarcticus</i>	*	<1	<0.01	<i>Orchomene plebs</i>	100–650	<1	0.56
<i>Gaetanus intermedius</i>	630–1000	<1	<0.01	<i>Parathemisto gaudichaudii</i>	130–200	<1	<0.01
<i>Gaetanus tenuispinus</i>	130–1000	10	2.51	<i>Primno macropa</i>	0–820	<1	<0.01
<i>Haloptilus ocellatus</i>	200–1000	<1	0.10	<i>Scina</i> sp.	230–650	<1	<0.01
<i>Haloptilus ozycephalus</i>	*	<1	<0.01	<i>Vibilia stebbingi</i>	*	<1	<0.01
<i>Heterorhabdus austrinus</i>	130–1000	5	1.00	Mysidacea			
<i>Heterorhabdus compactus</i>	750–820	<1	<0.01	<i>Antaretomysis ohlinii</i>	350–820	1	1.84
<i>Heterorhabdus farrani</i>	300–1000	3	0.95	<i>Dactylamblyops hodgsoni</i> (?)	630–1000	<1	<0.01
<i>Heterostylites major</i>	750–820	<1	<0.01	Coelenterata			
<i>Lubbockia aculeata</i> (?)	*	<1	<0.01	<i>Diphyes antarctica</i> ¹	230–1000	4	0.85
<i>Lucicutia clausi</i>	750–820	<1	<0.01	<i>Dimophyes arctica</i> ¹	0–1000	11	1.44
<i>Lucicutia curta</i>	800–1000	<1	<0.01	<i>Haliereas</i> sp.	*	<1	0.02
<i>Lucicutia macrocera</i>	800–1000	<1	<0.01	<i>Pyrostephos vanhoeffeni</i> ¹	200–1000	4	0.45
<i>Lucicutia ovalis</i>	450–1000	2	0.04	<i>Solmundella</i> sp.	550–1000	<1	<0.01
<i>Lucicutia wolfendeni</i>	750–1000	<1	<0.01	Polychaeta			
<i>Metridia curticauda</i>	230–1000	3	0.30	<i>Maupasia caeca</i>	0–550	<1	<0.01
<i>Metridia gerlachei</i>	0–1000	1906	122.90	<i>Pelagobia longicirrata</i>	0–1000	113	10.28
<i>Microcalanus pygmaeus</i>	0–1000	1148	5.15	<i>Rhynchonerella bongraini</i>	100–200	<1	<0.01
<i>Mimocalanus cultrifer</i>	*	<1	<0.01	<i>Tomopteris carpenteri</i>	*	<1	<0.01
<i>Oithona frigida</i>	100–1000	102	1.65	<i>Tomopteris planktonis</i>	100–1000	3	0.80
<i>Oithona similis</i>	0–1000	450	1.15	<i>Tomopteris septentrionalis</i>	200–1000	<1	<0.01
<i>Oncaea antarctica</i>	0–1000	1350	7.26	<i>Travislopsis levinseni</i>	230–650	<1	<0.01
<i>Oncaea curvata</i>	0–1000	5694	4.21	<i>Typhloscoler mulleri</i>	100–1000	<1	<0.01
<i>Onchocalanus magnus</i>	*	<1	<0.01	Mollusca			
<i>Onchocalanus wolfendeni</i>	750–1000	<1	<0.01	<i>Clione antarctica</i>	130–650	<1	<0.01
<i>Oithria</i> sp.	350–550	<1	<0.01	<i>Limacina helicina</i>	130–200	<1	<0.01
<i>Pleuromamma robusta</i>	230–820	<1	0.04	var. <i>antarctica</i>			
<i>Pseudochirella hirsuta</i>	750–1000	<1	<0.01	<i>Spongiobranchaea australis</i>	0–1000	3	0.09
<i>Pseudochirella mawsoni</i>	*	<1	<0.01	Chaetognatha			
<i>Racovitzanus antarcticus</i>	0–820	<1	0.10	<i>Eukrohnia hamata</i>	0–1000	16	2.16
<i>Rhincalanus gigas</i>	100–1000	4	5.45	<i>Sagitta gazellae</i>	100–200	<1	<0.01
<i>Scaphocalanus farrani</i>	0–1000	1	0.11	<i>Sagitta marri</i>	200–1000	1	0.42
<i>Scaphocalanus antarcticus</i>	600–1000	<1	0.17	Tunicata			
<i>Scaphocalanus parantarcticus</i>	*	<1	<0.01	<i>Fritillaria borealis</i>	0–550	4	0.04
<i>Scaphocalanus verwoorti</i>	130–1000	12	0.78	<i>Salpa thompsoni</i>	0–650	2	1.03
<i>Scolecithricella altera</i> (?)	130–1000	2	0.14				
<i>Scolecithricella dentipes</i>	230–1000	2	0.33				
<i>Scolecithricella emarginata</i>	800–1000	<1	<0.01				
<i>Scolecithricella minor</i>	0–650	10	0.18				
<i>Scolecithricella cenotelis</i>	630–1000	<1	0.01				
<i>Spinocalanus abyssalis</i>	330–1000	1	0.02				
<i>Spinocalanus abyssalis</i> var. <i>pygmaeus</i>	0–1000	3	0.02				
<i>Stephos longipes</i>	0–1000	253	1.31				
<i>Temorites brevis</i>	450–650	<1	<0.01				

diate depth samples from 200–650 m. The two pteropods, *Limacina helicina* and *Clione antarctica*, were taken at depths shallower than 650 m. The chaetognath *Sagitta gazellae* also occurred in shallow collections, though larger individuals, i.e., >15 mm, did occur in our deeper trawl samples.

The vertical distribution patterns of metazoan plankton <1 mm (Fig. 5) show a strong peak for copepod nauplii at 75 m and for cyclopoids at 75–150 m. A modest peak for calanoid copepodites occurred at 1000 m. All three groups had minimum densities at 25 m, there being no data for the surface. The two abundant kinds of protozoans in our preserved catches showed opposite patterns, which tintinnids being most prevalent at 50 m and radiolarians at 800 m. Foraminiferans were absent from the 30 l bottle collections.

Discussion

With the exception of the calanoid *Öothrix* (= *Neoscolecithrix*) sp., all of the species listed in Table 2 have been previously reported from the Southern Ocean. This appears to be the first record of this genus south of the Polar Front. While not challenging tropical-subtropical oceanic habitats in species variety, (e.g., Owre and Foyo 1967 list over 200 species of copepods alone in the upper 900 m of the Florida current) zooplankton in Croker Passage was moderately diverse (e.g., 64 copepod species listed in Table 2) despite the basin's limited size and depth. This can be related to deep water connections with the open Southern Ocean through the Boyd and Bransfield Straits. Evidence for such connections was the large number of pan-oceanic meso-bathypelagic copepods taken in our deep tows (e.g., see Vervoort 1951, 1957). Though sampling was in close proximity to land, there was little influence on catch composition from the benthos. The amphipod *Orchomene plebs*, however, was found in plankton net and trawl catches, this species being associated with the ice as well as with open water (Hurley 1965; Bellan-Santini 1972).

The vertical distribution patterns in Fig. 4 show that in March–April, 1983, all of the abundant species, with the exception of *Oithona similis*, were concentrated at depths below 200 m. The descent of zooplankton into the mesopelagic zone to overwinter is well known for high latitudes in both hemispheres (e.g., Foxton 1956; Beyer 1962; Vinogradov 1970). My earlier results, based on *RV Eltanin* collections from the Pacific sector (Hopkins 1971) showed the descent to occur in May, a month later than in 1983 in Croker Passage. Foxton's (1956) data for 64°S (close to the latitude of Croker Passage) from different sectors of the Southern Ocean showed that there is considerable regional variation in the relative amount of zooplankton in the upper 100 m in any given month. The mean pattern for all transects, however, showed descent to intermediate layers also occurring one month later than was apparently the case in Croker Passage in 1983.

Andrew's (1966) data for *Calanoides acutus* from *RV Discovery* collections indicated initiation of descent as early as February for this species but his vertical patterns for May agreed best with the present March–April data. Summer vertical distribution patterns in the upper 1000 m are unknown for Croker Passage, consequently it is impossible to state when the descent from the upper 100–200 m began. Nor can the possibility be discounted that the March–April pattern is representative of the entire year. On the basis of what is known of seasonal migration cycles in the Southern Ocean (e.g., Foxton 1956; Hopkins 1971; Voronina 1973 among others), however, concentration of zooplankton in the upper 100 m during the austral summer would be predicted as would descent from the epipelagic zone at some time in the fall. The factor(s) initiating the apparent early descent in Croker Passage are unknown.

As most of the zooplankton had occurred below the epipelagic zone in March–April, it is informative to consider the state of maturity of populations of the most prevalent species in relation to the onset of winter. The ratios in Table 3 give some idea of the proportion of immature stages in species populations and were computed by dividing the adult female length of each species into the mean length of individuals in the population as obtained from the measurements of specimens in aliquots. The ratios cover a wide spectrum, 41–93%, with the top 3 biomass species showing contrasting patterns. *Metridia gerlachei* was well represented by all copepodite stages, *Euchaeta antarctica* was intermediate in population maturity and *Calanoides acutus* was present only in late stages. The population size structure of *Calanoides acutus* was similar to the April–May patterns Andrews (1966) showed for this species. The ratios were biased in some instances because of smaller size of adult males as compared to females in conjunction with a high proportion of males in the population of some species, e.g., as in the two *Oncaea* species and *Metridia gerlachei*. Many early copepodites of both sexes of these three species, however, were seen. Thirteen of the 32 species listed had ratios of 80% or better, indicating that comparatively few early copepodite stages of this group were present at the onset of winter.

The data in Fig. 4 and Table 2 indicate unquestionably that the vertical distributions for the abundant species were broad both day and night. There is also some suggestion that portions of the populations of *Euchaeta antarctica* and *Metridia gerlachei* moved into the epipelagic zone at night. Hardy and Gunther (1935) recorded an upward migration at night for these two species as well. Andrews (1966) reported diel vertical migration in *Calanoides acutus*, though this was not apparent in either Hardy and Gunther's (1935) or the present data. The large concentration of *Oithona similis* in the upper 100 m during the day is thought to be more the result of patchiness than diel migration since Vinogradov (1970) reported this species as remaining in the epipelagic zone during winter in the Northwest Pacific.

Table 3. Indices of population maturity of 32 species as derived from comparison of the median length of individuals in each species population to the length of adults (female)

Species	Median length adult female length %	Species	Median length adult female length %
<i>Eukrohnia hamata</i>	41	<i>Rhincalanus gigas</i>	77
<i>Metridia gerlachei</i>	48	<i>Aetideopsis minor</i>	78
<i>Thysanoessa macrura</i>	52	<i>Ctenocalanus citer</i>	79
<i>Conchoecia belgicae</i>	52	<i>Oithona similis</i>	80
<i>Sagitta marri</i>	56	<i>Calanoides acutus</i>	81
<i>Stephos longipes</i>	60	<i>Lucicutia frigida</i>	82
<i>Oncaea antarctica</i>	62	<i>Gaetanus tenuispinus</i>	82
<i>Hyperiella dilatata</i>	62	<i>Conchoecia isocheira</i>	82
<i>Euchaeta antarctica</i>	62	<i>Scaphocalanus verwoorti</i>	85
<i>Oncaea curvata</i>	63	<i>Oithona frigida</i>	85
<i>Microcalanus pygmaeus</i>	64	<i>Heterorhabdus austrinus</i>	86
<i>Conchoecia antipoda</i>	64	<i>Heterorhabdus farrani</i>	86
<i>Xanthocalanus gracilis</i> (?)	72	<i>Racovitzanus antarcticus</i>	87
<i>Conchoecia hettacra</i>	76	<i>Spinocalanus abyssalis</i> v. <i>pygmaeus</i>	92
<i>Metridia curticauda</i>	77		
<i>Calanus propinquus</i>	77	<i>Scolecithricella minor</i>	93
		<i>Scaphocalanus farrani</i>	93

The three principal biomass species, i.e., *Metridia gerlachei*, *Calanoides acutus* and *Euchaeta antarctica*, combined accounted for 74% of the biomass of net-caught plankton in the upper 1000 m. *Metridia gerlachei* alone accounted for 39%. In *RV Eltanin* collections from open ocean areas south of the Polar Front in the Pacific sector, *Metridia gerlachei* ranked fourth in biomass behind *Rhincalanus gigas*, *Calanoides acutus* and *Calanus propinquus* (Hopkins 1971). In *RV Discovery* collections this species was of secondary importance in terms of biomass (MacKintosh 1934), which in part probably resulted from its escapement through the relatively coarse graded meshes of the Discovery N70 and N100 nets (~0.2–0.5 mm for N70; ~1–4 mm for N100). *Rhincalanus gigas*, the biomass dominant in *RV Eltanin* collections and the numerical dominant in *RV Discovery* (N70) samples, was not abundant in Croker Passage. Also, Kaczmaruk (1983) reported this species as being uncommon in Weddell Sea samples, and few were found in our 1983 oblique 0–700 m collections from Bird Basin in the Ross Sea (unpublished data). This species, then, as Raymont (1963) suggested, appears to be of greater importance in the West Wind Drift than closer to the continent in the East Wind Drift system. Voronina (1973) warns that *Rhincalanus gigas* may have a broader latitudinal pattern of abundance than is apparent from earlier studies because much of the population remains below 500 m until late spring and then peaks in epipelagic waters later than, for example, *Calanoides acutus*. Sampling in Croker Passage, however, included virtually the entire water column, and was during the fall. It is unlikely, then, that a significant portion of the *Rhincalanus gigas* population was missed.

Total biomass in the upper 1000 m in the Southern Ocean has been summarized in an earlier paper (Hopkins

1971) in which standing stocks in the West Wind Drift south of the Polar Front were estimated at 2.1–2.7 g DW/m². In Croker Passage, which is in the East Wind Drift system, the biomass as determined from the plankton net collections was somewhat higher, 3.1 g DW/m². For perspective it is useful to compare Croker Passage standing stock with that in the Gulf of Mexico, an oligotrophic subtropical environment wherein similar collection and analysis techniques were used (Hopkins 1982). Upper 1000 m values for Croker Passage were 0.7 g DW/m² for <1 mm and 2.9 g DW/m² for >1 mm zooplankton; the respective values for the Gulf of Mexico at 27°N 86°W were 0.4 and 1.2 g DW/m², with the standing stock for Croker Passage being considerably greater. Zooplankton numerical abundance in Croker Passage, on the other hand, was less than in the Gulf. The numbers for the <1 mm and >1 mm fractions in Croker Passage were 511,000 and 28,600/m², respectively, and in the Gulf, 1,386,000 and 47,000/m², respectively. By dividing these abundances into the above corresponding biomasses it becomes apparent that Croker Passage zooplankton individuals were larger on average than Gulf of Mexico zooplankton. The characteristically larger size of zooplankton at high latitudes has been noted by others (Sewell 1948; Raymont 1963) and certainly holds true in this particular comparison. Undoubtedly a complicating factor here is that Gulf of Mexico data were from summer, presumably an active period of secondary production, when larval stages were abundant whereas data from Croker Passage were from the fall long after the spring bloom, and when fewer larval stages were present. Evidence for the latter is that the Gulf population of <1 mm metazoans was 94% copepod nauplii; in Croker Passage nauplii were only 42% of this size fraction.

Differences in the macroplankton-micronekton fraction of biomass (i.e., >15 mm) are even more striking. In the Gulf this fraction was estimated at 0.7 g DW under a square meter of sea surface (Hopkins and Lancraft 1984), or 44% of the <1 mm and >1 mm zooplankton combined. In Croker Passage, an ecosystem dominated by krill, the micronekton in terms of *Euphausia superba* biomass alone was determined at 55 g DW/m² (based on an average of 7 oblique 0–1000 m Tucker Trawl sweeps), which exceeds the total zooplankton standing stock by a factor of 15. The ratios, then, for the two areas for metazoan plankton <1 mm to zooplankton >1 mm to macroplankton-micronekton >15 mm are 1.0:4.5:85.0 for Croker Passage and 1.0:3.0:1.8 for the eastern Gulf of Mexico. This comparison is biased to a small degree towards a high value in the eastern Gulf for the >1 mm zooplankton. Organisms up to 25 mm were included in zooplankton analyses of Gulf samples; the contribution of 15–25 mm plankton, however, to the total biomass for the 1–25 mm fraction was only 10–15%. The inordinately large macroplankton-micronekton component in Croker Passage, of course, results from the fact that krill (and *Salpa thompsoni*, the other important macroplankton-micronekton biomass species not included in the standing stock estimate) are small particle grazers, feeding at base-level in the trophic structure (Nemoto and Harrison 1981).

As indicated above, *Euphausia superba* accounted for most of the pelagic animal biomass. Despite the enormous standing stock of krill in Croker Passage relative to zooplankton, and their high population densities in swarms (e.g., Hamner et al. 1983), their large size precludes utilization as live prey by most zooplankton and smaller macroplankton-micronekton predators. Their major predators in the pelagic environment are mammals, birds, cephalopods and fishes (see Knox 1970; El-Sayed 1971; Green 1977; Nemoto and Harrison 1981, for ecosystem models). Instead, the principal caloric value of krill to the zooplankton population at least in the austral fall in Croker Passage, on the basis of extensive diet analysis, appears to be as molts and debris (Hopkins, in press).

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References

- Andrews KJH (1966) The distribution and life history of *Calanoides acutus* (Giesbrecht). *Discovery Rep* 34:117–162
- Bellan-Santini D (1972) Invertébrés marins des 12. et 15. expéditions antarctiques françaises en Terre Adélie. 10. Amphipodes gamma-riens. *Tethys* (Suppl) 4:157–238
- Beyer F (1962) Absorption of water in crustaceans, and the standing crop of zooplankton. *Rapp PV, Reun Cons Int Explor Mer* 153:79–95
- Davies TE, Barham EG (1969) The Tucker opening-closing micronekton net and its performance in a study of the deep scattering layer. *Mar Biol* 2:127–131
- El-Sayed SZ (1971) Dynamics of trophic relations in the Southern Ocean: Research in the Antarctic. *Am Assoc Adv Sci* 73–91
- Foxton P (1956) The standing crop of zooplankton in the Southern Ocean. *Discovery Rep* 28:193–235
- Green KA (1977) Ecosystem modeling for the southern ocean. *Antarct J US* 12:34–55
- Hamner W, Hamner PP, Strand SW, Gilmer RW (1983) Behavior of Antarctic krill, *Euphausia superba*: Chemoreception, feeding, schooling, and molting. *Science* 220:433–435
- Hardy AC, Gunther ER (1935) The plankton of the South Georgia whaling grounds and adjacent waters 1926–1927. *Discovery Rep* 11:1–456
- Hopkins TL (1971) Zooplankton standing crop in the Pacific sector of the Antarctic. In: Llano GW, Wallen IE (eds) *Biology of the Antarctic seas*. *Am Geophys Union* 17:347–362
- Hopkins TL (1982) The vertical distribution of zooplankton in the eastern Gulf of Mexico. *Deep-Sea Res* 29:1069–1083
- Hopkins TL (in press) Food web of an Antarctic midwater ecosystem. *Mar Biol*
- Hopkins TL, Baird RC (1975) Net feeding in mesopelagic fishes. *Fishery Bull US* 73:908–914
- Hopkins TL, Lancraft TM (1984) The composition and standing stock of mesopelagic micronekton at 27°N86°W in the eastern Gulf of Mexico. *Contrib Mar Sci* 27:143–158
- Hurley DE (1965) A common but hitherto undescribed species of *Orchomonella* (Crustacea Amphipoda: Family Lysianassidae) from the Ross Sea. *Trans R Soc NZ, Zool* 6:107–113
- Kaczmaruk BZ (1983) Occurrence and distribution of the Antarctic copepods along the ice shelves in the Weddell Sea in summer 1979/1980. *Meeresforsch* 30:25–41
- Knox GA (1970) Antarctic marine ecosystems. In: Holdgate MW (ed) *Antarctic ecology*. Academic Press, London, pp 69–96
- Lovegrove T (1962) The effect of various factors on dry weight values. *Rapp PV Reun Cons Int Explor Mer* 153:86–91
- Mackintosh NA (1934) Distribution of the macroplankton in the Atlantic sector of the Antarctic. *Discovery Rep* 9:65–160
- Motoda S (1959) Devices of simple plankton apparatus. *Mem Fac Fish Hokkaido Univ* 7:73–94
- Nemoto T (1968) Feeding of baleen whales and krill, and the value of krill as a marine resource in the Antarctic. In: *Proc Symp Antarct Oceanogr*. Scott Polar Res Inst, Cambridge, England, pp 240–253
- Nemoto T, Harrison G (1981) High latitude ecosystems. In: Longhurst AR (ed) *Analysis of Marine ecosystems*. Academic Press, London, pp 95–126
- Omori M (1978) Some factors affecting dry weight, organic weight and concentrations of carbon and nitrogen in freshly prepared and in preserved zooplankton. *Int Rev Gesamten Hydrobiol* 63:261–269
- Ostapenya AP, Shushkina EA (1973) Caloricity of net plankton and energy equivalents of the body mass of some tropical activity of pelagic communities in the tropical oceans (Engl transl), *Nauka*, pp 190–197
- Owre HB, Foyo M (1967) Copepods of the Florida current. *Fauna Caribaea*, vol 1 Crustacea. Part 1. Copepods. *Inst Mar Sci, Univ Miami*, pp 1–137
- Raymont JEG (1963) *Plankton and productivity in the oceans*. Pergamon Press, London, 660 pp
- Sewell RBS (1948) The free-swimming planktonic Copepods. *Geographical distribution*. *Sci Rep Murray Exped* 8 (Zool) 3:317–592
- Tranter DJ (1982) Interlinking of physical and biological processes in the Antarctic Ocean. *Oceanogr Mar Biol, Annu Rev* 20:11–35
- Vervoort W (1951) Plankton copepods from the Atlantic sector of the Antarctic. *Verh K Akad Wet Amsterdam (Tweede Sectie)* DJ 47:1–156
- Vervoort W (1957) Copepods from the Antarctic and sub-antarctic plankton samples. *Rep BANZ Antarct Exped (B)* 3:1–160
- Vinogradov ME (1970) Vertical distribution of the oceanic zooplankton IPST translation. *US Dept Interior Doc No TT 69-59015*, 339 pp
- Voronina NM (1973) Vertical structure of a pelagic community in the Antarctic Oceanology (Engl transl). *12:415–420*