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A krill-dominated micronekton and macrozooplankton community in Croker Passage, Antarctica with an estimate of fish predation

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Abstract

A micronektonic and macrozooplanktonic community was sampled with midwater trawls in the Croker Passage, vic. Antarctic Peninsula. Species composition suggested the area was a faunal transition zone between oceanic and nearshore communities. In a comparison between the study area and two oceanic areas, four of the top five numerically dominant species were identical (*Euphausia superba, Salpa thompsoni, Thysanoessa macrura* and *Sagitta gazellae*). In the nearshore region a mysid (*Antarctomysis ohlinii*) replaced the oceanic chaetognath *Euhrohnia hamata* in numerical ranking. *E. superba* was primarily responsible for the much higher nearshore biomass values when compared with those of oceanic regions (52.6 vs 2.4–3.1 g DM/m^2). The ctenophore *Callianira antarctica*, the mysid *A. ohlinii*, and the pelagic nototheniid fish *Pleuragramma antarcticum* were important neritic biomass species. Some oceanic species, notably *S. thompsoni* and the mesopelagic fish *Electrona antarctica*, were also important contributors to total micronektonic biomass. Fish predation by *P. antarcticum* and *E. antarctica* on *E. superba* (assuming constant fish and krill populations through the season that was sampled, the austral fall (90 d), and using our daily consumption values) is estimated at 2.5% and 2.9% of the total krill numbers, respectively, mostly on the juvenile segment of the population.

Krill densities vary considerably in time and space, while available data suggest that pelagic fishes show less seasonal and spatial change. The most likely explanation for those observations is that the fishes are reliably more vulnerable to sampling gear than krill, but it also implies a consistent low level of fish predation on krill throughout the year, particularly on juveniles.

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1. Introduction

Descriptions of Antarctic pelagic ecosystem ecology have focused on the shallow-dwelling krill, *Euphausia superba* (e.g. El-Sayed, 1971; Ross et al., 1996; Quetin et al., 1996; Hofmann et al., 1998; Lascara et al., 1999), largely due to its overwhelming dominance in nearshore communities (Hopkins, 1985a, b) and clear importance to the nutrition of birds and mammals (Ainley and DeMaster, 1990; Cherel and Kooyman, 1998; Ainley, 2002). Less is known about Antarctic pelagic communities considered as a whole, particularly the interactions of krill and their micronektonic predators, the relative abundance of macrozooplankton other than krill, and the importance of deeper-living or vertically migrating species (Robison, 2003). Deeper-living macrozooplankton and micronekton contribute substantially to the biomass of open-ocean Antarctic systems, sometimes exceeding krill in abundance (Lancraft et al., 1989, 1991; Pakhomov et al., 1996). Despite big differences in the relative importance of krill and other macrozooplankton from place to place in the seasonal sea-ice zone, regional comparisons of micronekton and macrozooplankton abundance are still quite rare (Piatkowski, 1985a, b; Hopkins and Torres, 1988; Lancraft et al., 1989, 1991; Hopkins et al., 1993 a, b; Pakhomov et al., 1996).

Whether offshore or in continental shelf waters, pelagic species form an important trophic link between apex predators and herbivores. The bottom fauna is inaccessible to many diving species on the Antarctic continental shelf because its typical 500 m depth (Eastman, 1993) is beyond their reach. Thus, because of their pelagic distribution, micronekton are an important source of food for flighted seabirds (Ainley et al., 1991) and shallow diving penguins such as the Gentoo, Adelie, and Chinstrap (Bengtson et al., 1993; Williams, 1995; Ainley, 2002). They also form a significant part of the diet of deeper divers such as emperor penguins (Cherel and Kooyman, 1998), and crabeater, Ross, Weddell and leopard seals (Øritsland, 1977; Lowry et al., 1988).

The present study investigated the micronekton and macrozooplankton community in the upper 1000 m of a nearshore pelagic Antarctic environment to provide a basis for comparisons with offshore systems and to give information on accessibility of micronekton to upper trophic levels. In turn, the study considers fish as intermediate trophic level predators to estimate predation pressure of fishes on krill.

2. Materials and methods

Micronekton and macrozooplankton were sampled during the austral fall (March and April 1983) using a modified opening–closing Tucker trawl off R/V HERO. The sampling site was the island-bound Croker Passage, an area consisting of two deep-water basins (maximum depth = 1200 m) in the Palmer Archipelago just north of Anvers Island, Antarctica (Fig. 1). Brash ice was frequently encountered but most sampling was conducted in open waters.

The trawl had a 4.8 m^2 effective mouth opening and a 6 mm (1.1 cm stretched) mesh (Hopkins, 1985b). It was opened and closed with clock-actuated release mechanisms (Davies and Barham, 1969) with filtration volumes monitored by dial-type flowmeters only when the trawl was open. Depth was estimated by wire angle triangulation during the tow and documented by attached time–depth recorders. While depth control was variable due to unavoidable changes in ship speed, only discrete zone tows were used in this study to better characterize patterns of vertical distribution, biomass, and abundance. Trawling was at speeds between 2 and 3 knots.

Twenty-one discrete tows (12 days and 9 nights) filtered a total of 520 477 m^3 of water, with roughly half being filtered in each diel period. Nearly the entire water column was sampled as 1000 m was the maximum depth of towing (see Table 1 for collection information). The collections were first fixed in a buffered 10% formaldehyde solution and then stored in the laboratory in a 50% isopropyl alcohol solution.

Except for one collection (tow 21) each entire sample was sorted with all micronekton and macrozooplankton (organisms greater than 20 mm) identified, enumerated, and their wet

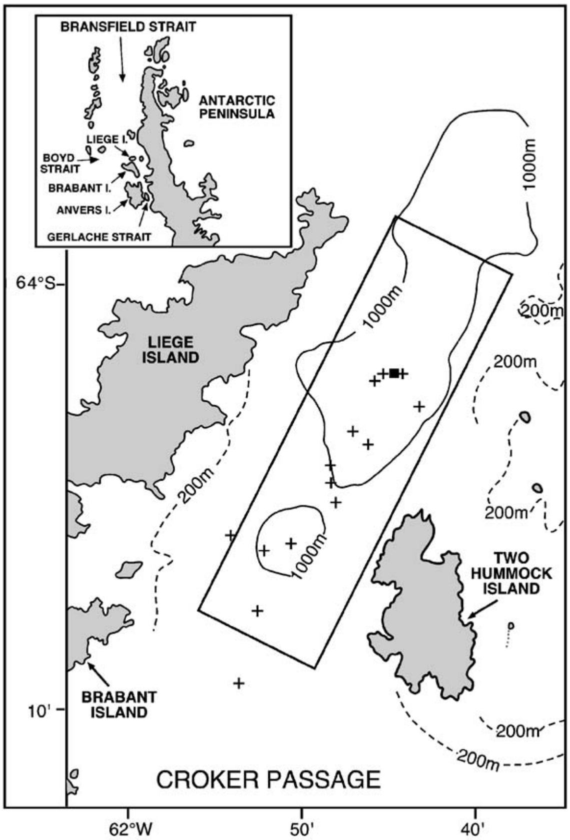

Fig. 1. The study area in Croker Passage. All trawling took place within the rectangle shown. + = XBT profiles. Solid square represents salinity station (8 April 1983).

masses (WM) recorded (±0.001 g). Tow 21 was a large-volume (16 l) shallow night tow consisting primarily of *E. superba*, so a 2-l subsample of the tow was treated as above and then prorated to whole sample values. Because ctenophores do not preserve well, they were counted after each tow, their volume measured, and then were discarded. Tentative identification of the ctenophores indicated that most were *Callianira antarctica* with a few *Beroe* sp. making up the remainder. Some organisms were removed, prior to weighing, for a food web study (Hopkins, 1985a); the weights of these were estimated with length–mass curves (Lancraft, unpubl. data). Wet mass (WM) was converted to dry mass (DM) by subtracting water content. The latter was estimated by drying specimens at 60 °C to constant mass (Donnelly et al., 1990).

For every tow, the biomass/m^3 of each taxon was calculated by dividing its biomass in the sample by the volume of water filtered in that tow. Biomass/m^3 was multiplied by the depth range (in meters) of that tow to yield an integrated biomass over the depth range of the tow. Integrated biomass values for 200 and 1000 m depth strata (mg WM/m^2 and mg DM/m^2) were calculated by summing integrated biomass values for all tows down to those depths (Lancraft et al., 1989). When tows overlapped, a mean was taken for the overlapping strata. Integrated abundance (number/m^2) values were calculated in an identical manner. Daytime catch values were generally lower than those for nighttime catches (Table 2; Fig. 2A and B), suggesting net avoidance was a bias. Nighttime values were therefore used as the best indicators of abundance and biomass.

To estimate the impact of fish predation on *E. superba*, stomach contents were examined in a range of size classes of *Electrona antarctica* and *Pleuragramma antarcticum*, and the number and lengths of krill in the gut contents were noted. While net feeding may be a bias in the determination of pelagic fish diets (Lancraft and Robison, 1980), only krill with obvious signs of digestion were counted in this study, thereby eliminating krill potentially consumed in the trawl cod end. The size of prey and the degree of digestion indicated that most of the fish fed daily. Predation pressure (number krill consumed/day/100 m^2) was estimated for each fish size class by multiplying the number of krill consumed per fish by the abundance of that size class in the total fish population. All size classes for each fish species were then summed to determine the total predation impact by that species on the krill population. Krill biomass consumed (mg DM/day/100 m^2) was estimated by multiplying average lengths of krill prey by their dry masses and treating those values like the abundances. Four hundred specimens of *E. superba* were randomly selected from a variety of tows and measured to determine the spectrum of prey lengths available to fish predation. All krill length measurements were from the tip of the rostrum to the end of the telson, slightly different

Table 1
Data on trawl tows taken during March–April 1983 in Croker Passage

Tow no.	Local time	Date (mm.dd.yy)	Depth (m)	Vol. fil. (m^3)
9	1352–1552 (D)	3.15.83	450–850	38 579
10	2010–2225 (N)	3.15.83	550–820	25 771
11	0210–0430 (N)	3.16.83	630–820	35 744
12	1501–1711 (D)	3.16.83	750–820	35 063
13	2237–0047 (N)	3.16–17.83	775–1000	32 010
14	0406–0551 (N)	3.17.83	300–400	26 362
15	1546–1731 (D)	3.17.83	230–480	25 495
16	2133–2238 (N)	3.18.83	130–200	25 115
17	0958–1024 (D)	4.8.83	0–100	15 114
18	0930–1045 (D)	4.8.83	100–200	21 628
19	1220–1335 (D)	4.8.83	200–300	22 154
20	1558–1708 (D)	4.8.83	340–550	19 460
21	2120–2150 (N)	4.8.83	0–100	8556
22	2300–0013 (N)	4.9.83	200–300	31 142
25	2203–2313 (N)	4.9.83	450–550	18 851
26	0927–1037 (D)	4.10.83	350–550	28 813
27	1237–1347 (D)	4.10.83	480–570	22 009
28	1602–1712 (D)	4.10.83	600–770	18 272
29	2157–2307 (N)	4.10–11.83	550–650	30 178
30	1046–1156 (D)	4.11.83	800–1000	18 365
31	1409–1519 (D)	4.11.83	380–470	21 796
Total day tows				28 6748
Total night tows				23 3729
Total				52 0477

D = day; N = night.

from the total length used by Mauchline and Fisher (1969), but used several times previously in the literature (Fraser, 1936; Einarsson, 1945; Nemoto, 1957). Regressions of size vs. dry mass for *E. superba*, *E. antarctica*, and *P. antarcticum* are reported in Table 4.

3. Results

3.1. Species composition and vertical distribution

Forty-three species of micronekton and macrozooplankton were collected in the Croker Passage (Table 2) during 1983. Single specimens of two other species of fish (*Bathylagus antarcticus* and *Electrona carlsbergi*) (Fig. 3) were collected by trawl tows in a previous cruise to the Croker Passage study area during 1982, bringing fish diversity to a total of 11 species. Except for the nototheniid *P. antarcticum,* the liparid *Careproctus georgianus,* and the bathydraconid *Cryodraco antarcticus*, all of the fish were mesopelagic oceanic species. Gammarid amphipods were the second most diverse group with a total of ten species. Cephalopods, because of their avoidance capabilities, were probably under-represented. The mouth area of the net employed during the study was small (4.8 m^2) relative to the most commonly used midwater trawls (RMT-8, 8 m^2, Mother Tucker trawl, 9 m^2, MOC 10, 10 m^2) but was very effective for its size. Comparison of fish lengths with those in other studies (Lancraft et al., 1989, 1991; Pakhomov et al., 1996) showed that the smaller net captured the larger size classes quite well and total biomasses were similar to or greater than those from other reports.

Most of the fauna resided fairly deeply, with abundance peaks centering below 200 m. *E. superba* was a notable exception in that it was

Table 2
Taxonomic composition and diel vertical distribution of Croker passage micronekton and macrozooplankton

Species	*n*	Day range (Peak)	*n*	Night range (Peak)
Fish				
Electrona antarctica	65	230–850 (380–850)	30	130–820(200–400)
Electrona carlsbergi[a]				
Pleuragramma antarcticum	31	230–1000 (500–1000)	48	130–1000(130–200)
Protomyctophum bolini	2	230–480		
Gymnoscopelus nicholsi	1	450–850	2	130–650
Notolepis coatsi			1	450–550
Cyclothone microdon			3	775–1000
Bathylagus antarcticus[a]				
Melanostigma gelatinosum[a]				
Careproctus georgianus[a]				
Cryodraco antarcticus[a]				
Crustaceans				
Euphausia superba	1001	0–850 (0–100)	64787	0–1000(0–100)
Thysanoessa macrura	353	0–1000 (200–1000)	585	130–1000(200–650)
Cyphocaris richardi	108	0–1000 (450–850)	116	130–1000(210–550)
Eurythenes gryllus	10	800–1000	1	775–1000
Eurythenes obesus	1	750–820	1	550–650
Eusirus propeperdentatus	63	230–1000 (350–850)	59	300–1000 (300–820)
Eusirus perdentatus			4	200–300
Eusirus microps	9	230–570	10	130–650
Orchomene plebs	36	230–1000 (230–570)	46	130–1000 (300–400)
Orchomene rossi	11	0–550	20	130–650 (130–200)
Epimeriella macronyx	57	230–850 (450–850)	3	450–650
Parandania boecki	2	750–820	5	775–1000
Themisto gaudichaudi	2	0–300	8	0–300 (0–100)
Pasiphaea scotiae			2	550–650
Antarctomysis ohlinii	866	230–1000 (750–1000)	1201	210–1000 (660–1000)
Antarctomysis maxima			1	550–820
Dactlyamblyops hodgsoni	1	800–1000	5	630–1000
Molluscs				
Galiteuthis glacialis	1	380–470	3	450–1000
Brachioteuthis picta			1	130–200
Alluroteuthis antarcticus			2	550–820
Psychroteuthis glacialis	1	350–550	1	450–550
Macrozooplankton				
Sagitta gazellae	931	0–1000 (860–1000)	972	130–1000 (300–1000)
Sagitta marri	54	450–1000 (750–1000)	48	550–1000 (630–1000)
Eukrohnia hamata	457	200–1000	446	200–1000
Tomopteris carpenteri	54	0–850 (240–470)	29	130–650 (300–400)
Tomopteris septentrionalis	1	450–850		
Salpa thompsoni	4377	0–1000 (200–1000)	3536	0–1000 (0–650)
Callianira Antarctica	178	230–1000	159	0–1000
Atolla wyvillei	1	600–770	4	550–1000
Periphylla periphylla	2	750–1000	2	300–1000
Calycopsis borchgrevinki	16	340–850 (340–550)	5	300–820
Diphyes Antarctica	111	100–850(100–300)	95	130–820 (200–400)

[a] These species were collected in tows not listed in Table 1.

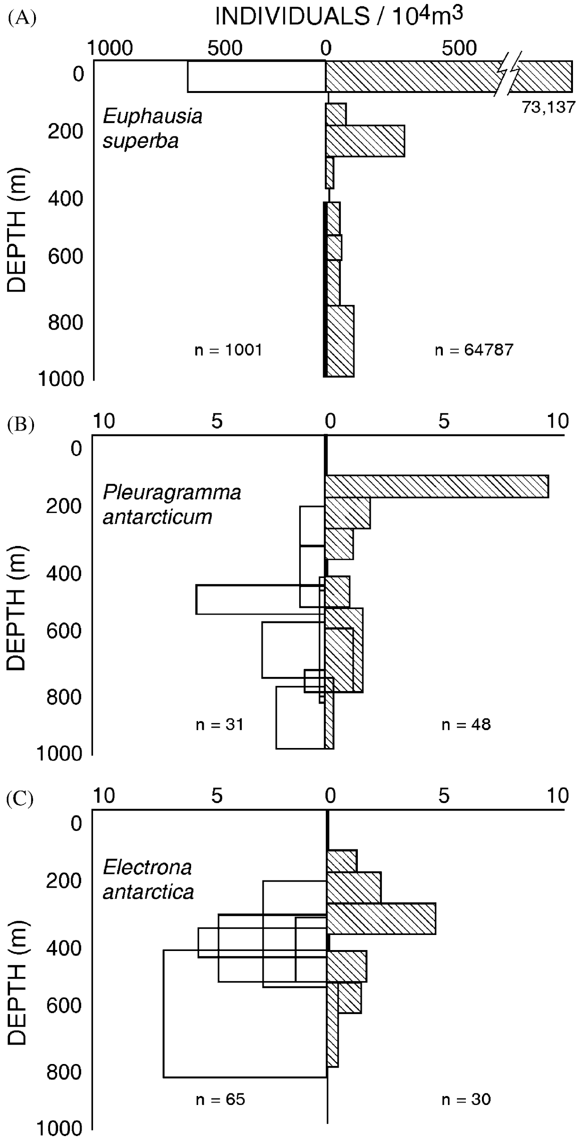

Fig. 2. Diel depth abundance patterns (individuals/$10^4\,m^3$) of *Euphausia superba* (A) and its major fish predators *P. antarcticum* (B) and *Electrona antarctica* (C) in the Croker Passage. Shaded bars are night abundances, n = total number of individuals in day or night samples.

most abundant in the upper 100 m (Fig. 2A). Most of the micronekton and all of the macrozooplankton had wide vertical depth distributions, which, for a few, broadened slightly during the day. Notable deep-living non-migrators were *Thysanoessa macrura* and *Antarctomysis ohlinii*.

The only species exhibiting strong diel vertical migration patterns were the dominant fishes (*P. antarcticum* and *E. antarctica*, Fig. 2B and C). During the night their overall vertical distributions were not significantly different (Kolmogorov–Smirnov test, $p > .05$). However, the nighttime abundance peaks of the fish were separated, with *P. antarcticum* (130–200 m) being more shallowly distributed than *E. antarctica* (200–400 m). The fish also had non-overlapping distributions during the day (Kolmogorov–Smirnov test, $p < .001$). The gammarid amphipod, *Cyphocaris richardi*, and the only tunicate found in the study (*S. thompsoni*) also showed weak diel vertical migration patterns.

3.2. Abundance and biomass

E. superba was the most abundant species in Croker Passage, with an integrated abundance of 787.9 individuals for every square meter of surface (Table 3) in the upper 200 m. Below this depth *E. superba* abundance dropped off precipitously to $8.1/m^2$ (difference between integrated 0–200 m and 0–1000 m values), for a total of $796.0/m^2$ in the entire sampled water column (0–1000 m). The second most abundant species, *S. thompsoni*, was more evenly distributed with 12.7 individuals/m^2 in the upper 200 m and $7.3/m^2$ residing below 200 m, totaling $20.0/m^2$ for the 0–1000 m range. The next four numerically subdominant species (*A. ohlinii*, *Sagitta gazellae*, *T. macrura*, and *Eukrohnia hamata*, in order of descending abundance) were all most abundant below 200 m. *E. superba* and the other five species made up 99.5% of the total micronekton and macrozooplankton abundance. *E. superba* alone accounted for 95.5% of all numbers. With *E. superba* excluded, the other five dominant species accounted for 89.3% of the total, while with *E. superba* they account for only 4.0%. This underscores how strongly *E. superba* dominated the Croker Passage community.

Total nighttime dry biomass (Table 3) in the epipelagic zone (0–200 m) was high (48 791 mg DM/m^2) due to the intense concentration of *E. superba* in that zone. The night time dry biomass from the surface to 1000 m for all species was 52 606 mg DM/m^2. Without *E. superba,* biomass values for the 0–200 m and 0–1000 m zones

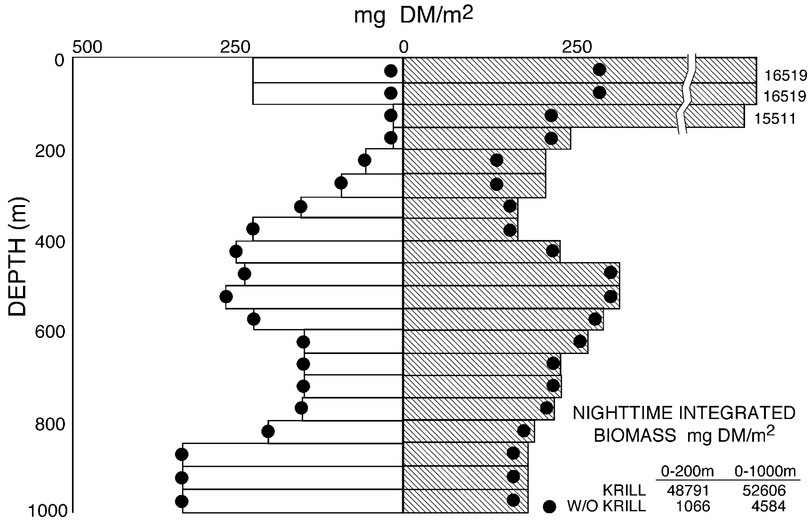

Fig. 3. Croker Passage community biomass (mg DM/m^2), 0–1000 m. Shaded bars are biomasses determined from night tows. Filled circles represent biomass in depth stratum without *Euphausia superba*.

decreased to 1066 and 4584 mg DM/m^2, respectively (Fig. 4). Dense concentrations were evident in the 0–200 m zone on the ship's fathometer during the day as well but our daytime catches were reduced because of gear avoidance.

E. superba was the biomass dominant in the 0–1000 m column, accounting for 91.3% of the total dry mass with 48 022 mg DM/m^2 (Table 3). Ctenophores (mostly *C. antarctica*), *A. ohlinii, S. thompsoni, P. antarcticum*, and *E. antarctica* were the subdominants, in order of decreasing biomass. Wet mass (WM) biomass patterns varied only in the reversal of the ranking of *A. ohlinii* and *S. thompsoni* because of the latter's greater water content.

While *E. superba* dominated the upper 200 m, its dry biomass below 200 m (297 mg DW/m^2; 0–1000 m value minus 0–200 m value) was exceeded by that of the ctenophores (1597 mg DM/m^2), *A. ohlinii* (746 mg DM/m^2) and *P. antarcticum* (307 mg DM/m^2) and was only slightly above that of *E. antarctica* (282 mg DM/m^2) and *S. thompsoni* (223 mg DM/m^2).

3.3. Predation

Stomach contents from a total of 133 specimens of *E. antarctica* and 37 specimens of *P. antarcticum* were examined for krill prey. The two species consumed similar numbers and sizes of krill (Table 4). Average number of krill/stomach (varying from 0.7 to 2.6) increased with fish length. Mean krill prey size ranged from 24.2 to 28.5 mm with the average size also increasing with larger fish. Maximum abundances of krill taken from the trawl were in the 30–32 mm size fraction, with the average being 31.1 mm (Fig. 4). The average size of krill consumed by the fishes was smaller than the mean size of trawl-caught krill, suggesting a positive selection for smaller krill (Fig. 4). The estimated daily consumption of total krill numbers by *E. antarctica* was 0.027%, which translates to 0.017% of the total krill biomass. *P. antarcticum* captured slightly larger krill, ingesting a slightly larger fraction of krill population numbers (0.033%) and higher biomass than *E. antarctica* (0.026%, Table 5).

4. Discussion

The Croker Passage species list was that of a modified open-ocean community (Lancraft et al., 1989, 1991) mixed with nearshore species. Fish diversity was low in contrast to the oceanic Antarctic systems like the Scotia Sea and Weddell

Table 3
Integrated biomass and numerical abundance of Croker Passage micronekton and macrozooplankton

Species	0–200 m			0–1000 m		
	mg DM/m^2	mg WM/m^2	no./1000 m^2	mg DM/m^2	mg WM/m^2	no./1000 m^2
Pisces						
Electrona antarctica	28	91	11	310	990	122
Pleuragramma antarcticum	223	1190	88	530	2834	175
Protomyctophum bolini				2	9	9
Gymnoscopelus nicholsi	16	81	4	26	128	5
Notolepis coatsi				<1	1	6
Cyclothone microdon				1	4	6
Subtotal	267	1362		869	3966	
Euphausiacea						
Euphausia superba	47725	174814	787885	48022	175905	796014
Thysanoessa macrura	24	82	257	75	252	2209
Subtotal	47749	174896		48097	176157	
Amphipoda						
Cyphocaris richardi	7	28	48	87	344	465
Eurythenes gryllus				31	121	6
Eurythenes obesus				<1	1	2
Eusirus propeperdentatus				49	235	262
Eusirus perdentatus				3	15	13
Eusirus microps	<1	2	4	5	26	38
Orchomene plebs	1	2	7	21	56	194
Orchomene rossi	11	28	48	15	40	63
Epimeriella macronyx				<1	3	10
Parandania boecki				14	44	30
Themisto gaudichaudi	1	6	58	1	7	64
Subtotal	20	66		226	892	
Mysidacea						
Antarctomysis ohlinii				746	3720	5053
Antarctomysis maxima				3	16	4
Dactlyamblyops hodgsoni				<1	3	27
Subtotal				749	3739	
Thaliacea						
Salpa thompsoni	346	8450	12665	569	13887	20014
Coelenterata						
Ctenophores	404	4163	220	2001	20627	762
Atolla wyvillei				11	260	16
Periphylla periphylla				5	267	11
Calycopsis borchgrevinki				2	34	20
Diphyes antarctica	<1	21	48	1	74	353
Subtotal	404	4184		2020	21262	
Others						
Galiteuthis glacialis				16	136	17
Brachioteuthis picta	4	34	4	4	34	4
Alluroteuthis antarcticus				15	131	10
Psychroteuthis glacialis				1	11	6
Sagitta gazellae	<1	9	29	33	678	4112

Table 3 (*continued*)

Species	0–200 m			0–1000 m		
	mg DM/m^2	mg WM/m^2	no./1000 m^2	mg DM/m^2	mg WM/m^2	no./1000 m^2
Sagitta marri				<1	4	186
Eukrohnia hamata				2	37	2074
Tomopteris carpenteri	1	4	7	5	35	125
Subtotal	5	47		76	1066	
Total	48791	189005		52606	220969	

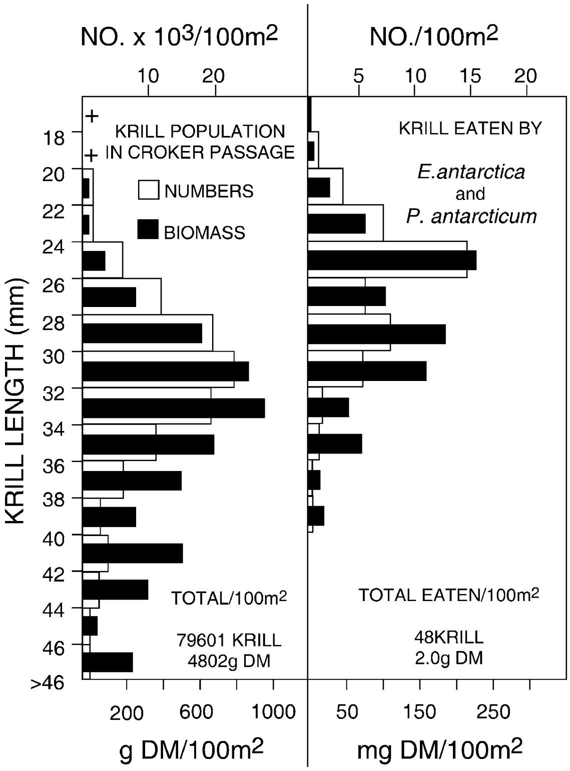

Fig. 4. Comparison of abundance, biomass, and length composition of the total Croker Passage *Euphausia superba* population and the *E. superba* eaten by fish.

Sea (Lancraft et al., 1989, 1991). Mesopelagic species like *B. antarcticus*, myctophids other than *E. antarctica,* and large mesopelagic predatory fish were notably absent or occurred in reduced numbers in Croker Passage. *P. antarcticum*, an endemic pelagic nototheniid, replaced the mesopelagic species in abundance in the nearshore environment, a pattern also observed by Slosarczyk and Cielniaszek (1985) over the Antarctic Peninsula shelf, Williams (1985) in Prydz Bay, and Dewitt (1970) in the Ross Sea.

Restricted circulation from the Bellingshausen Sea over the continental shelf into Croker Passage, as indicated by its lack of a well-developed Upper Circumpolar Deep Water zone (temperatures $>1.5\,^{\circ}$C at a depth of 200 m, Fig. 5), a water mass typically found in the Bellingshausen Sea and Bransfield Strait (Grelowski and Tokarczyk, 1985; Smith et al., 1999), may exclude the deeper-living oceanic fauna from the Croker Passage. *A. ohlinii*, a robust pelagic mysid completely absent from the mesopelagic zone of oceanic areas (Lancraft et al., 1989, 1991),was abundant in the Croker Passage, suggesting a strong neritic influence. The high diversity and, in some cases, high abundance (*Eusirus propeperdentatus*) of benthopelagic gammarid amphipods also registered the influence of land on the Croker Passage community.

A regional biomass comparison of Antarctic pelagic ecosystems (this study and Lancraft et al., 1989) shows that the most obvious difference was the overwhelming dominance of *E. superba* in the nearshore area (Table 6). Ctenophores (*C. antarctica*) also were more important in Croker Passage, decreasing in the blue water study areas of the Scotia and Weddell Seas. *A. ohlinii* and *P. antarcticum*, both nearshore species, also greatly increased the overall biomass of Croker Passage.

The top five most abundant species in all three regions are the same except for the replacement of

Table 4
Diets of dominant fishes, with comparisons to published information

Fishes			*Euphausia superba*			Daily ration		
Size (n)	Size at midrange (mm)	DM (g) at midrange	No./stom. mean (range)	Size (mm) mean (range)	DM (g) in stomach	Daily ration (% DM) This study	Daily ration (% DM) Pakhomov et al. (1996)	Daily ration (% DM) Rowedder (1979)
Electrona antarctica								
60–69 (11)	65	1.190	1.4 (0–2)	24.2 (20–27)	0.045	3.752		
70–79 (45)	75	1.947	1.4 (0–5)	24.5 (19–33)	0.046	2.382		
80–89 (50)	85	2.993	2.2 (0–8)	26.0 (17–39)	0.087	2.916		
90–99 (27)	95	4.387	1.7 (0–5)	26.3 (19–35)	0.070	1.592		
Total (133)		Mean (range)	1.7 (0–8)	25.3 (17–39)	0.062	2.660	1.86 (0.46–3.45)	5
Pleuragramma antarcticum								
<100 (7)	90	1.062	0.7 (0–3)	26.0 (25–27)	0.028	2.616		
101–125 (10)	113	2.323	0.7 (0–4)	27.8 (21–32)	0.034	1.465		
126–150 (10)	139	4.738	2.6 (0–6)	28.0 (15–39)	0.129	2.726		
>150 (10)	160	7.689	2.4 (0–13)	28.5 (17–34)	0.126	1.636		
Total (37)		Mean (range)	1.6 (0–13)	27.6 (15–39)	0.076	2.111	no data	no data

Dry mass of *Electrona antarctica* computed from the length mass regression: y (mass, g) $= 0.0000007 \times$ (standard length, mm)$^{3.437}$, $r^2 = 0.954$, $n = 222$. Dry mass of *Pleuragramma antarcticum* computed from the length mass regression: y (mass, g) $= 0.0000002 \times$ (standard length, mm)$^{3.441}$, $r^2 = 0.977$, $n = 46$. Dry mass of *Euphausia superba* computed from the length mass regression: y (mass,g) $= 0.000006 \times$ (length, mm)$^{3.037}$, $r^2 = 0.978$, $n = 480$.

Table 5
Predation on krill by dominant fishes

Fishes			*Euphausia superba*		
Size (n)	% Abund.	No.eaten/d (/100 m^2)	DM eaten/d (g DM/100 m^2)	% total krill population eaten/d	
				(no./100 m^2)	(g DM/100 m^2)
Electrona antarctica					
60–69 (11)	8.42	1.4	0.045		
70–79 (45)	31.58	5.4	0.179		
80–89 (50)	42.11	11.3	0.448		
90–99 (27)	17.89	3.7	0.152		
Total (133)	100	21.8	0.796	0.027	0.017
Pleuragramma antarcticum					
<100 (7)	15.38	1.9	0.075		
101–125 (10)	41.03	5	0.243		
126–150 (10)	19.23	8.8	0.437		
>150 (10)	24.36	10.2	0.535		
Total (37)	100	25.9	1.232	0.033	0.026

Estimates of krill removed from the total population (per 100 m^2) by *Electrona antarctica* and *Pleuragramma antarcticum*. Data on total krill numbers from Fig. 4, masses calculated using regressions in legend of Table 4.

the chaetognath *E. hamata* with the mysid *A. ohlinii* in the Croker Passage (Table 7). The general uniformity of important species in Croker Passage when compared with offshore regions and the notable differences in species composition support the contention that the Croker Passage area is a transition zone between oceanic mesopelagic and nearshore pelagic fauna.

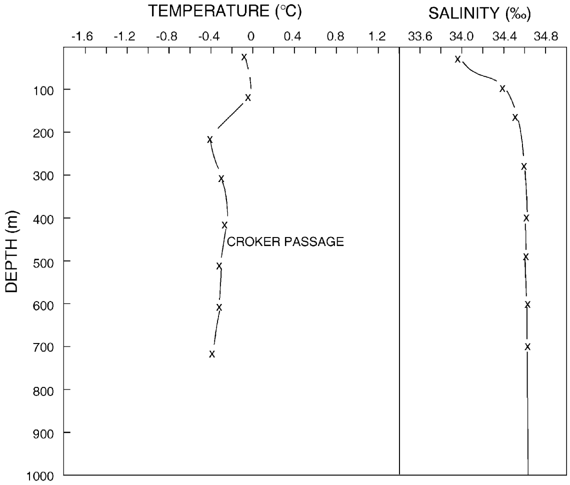

Fig. 5. Hydrographic data from the Croker Passage study area (Hopkins 1985b). Note temperatures below 0 °C at depths of 200 m and greater.

Many estimates of krill biomass in the upper 200 m have been taken from areas north of the study site using nets (Piatkowski, 1985a, b; Siegel, 1986; Worner, 1979, to name only a few) as well as acoustical methods (Rakusa-Suszczewski, 1982; Macaulay et al., 1984; Kalinowski et al., 1985). Our mean abundance of 788 individuals/m^2 falls into the range of previous Antarctic Peninsula studies (Piatkowski, 1985a; Worner, 1979) while our net captured wet biomass values (175 g WM/m^2) are moderate compared to acoustical biomass estimates (Rakusa–Suszczewski, 1982; Macaulay et al., 1984; Kalinowski et al., 1985; Lascara et al., 1999). Using a separate set of oblique tows taken during the same cruise as this study, Hopkins (1985a) estimated the *E. superba* biomass for 0–1000 m at 55 g DM/m^2, a value quite close to ours (48 g DM/m^2) considering the differences in methodology.

Table 6
Regional comparison of biomass (mg DM/m^2) dominants in the 0–1000 m range

Species	Scotia Sea Spring ’83	Weddell Sea Fall ’86	Croker Passage Fall ’83
Euphausiacea			
Euphausia superba	1077	667	48 022
Thysanoessa macrura	15	24	75
Subtotal	1092	691	48 097
Thaliacea			
Salpa thompsoni	1156	159	569
Pisces			
Electrona antarctica	314	273	310
Gymnoscopelus nicholsi	0	0	26
Gymnoscopelus braueri	128	86	0
Gymnoscopelus opisthopterus	81	304	0
Bathylagus antarcticus	216	283	0
Pleuragramma antarcticum	0	0	530
Subtotal	739	946	866
Ctenophora	<1	99	2001
Mysidacea	<1	<1	749
Amphipoda	16	6	226
Others	129	476	98
TOTAL	3132	2377	52 606

Table 7
Regional comparison of top five numerically dominant species (number/m^2)

Scotia Sea	Weddell Sea	Croker Passage
Salpa thompsoni (145.33)	*Euphausia superba* (6.05)	*Euphausia superba* (796.01)
Euphausia superba (4.34)	*Salpa thompsoni* (5.62)	*Salpa thompsoni* (20.01)
Sagitta gazellae (1.88)	*Eukrohnia hamata* (2.73)	*Antarctomysis ohlinii* (5.05)
Thysanoessa macrura (0.91)	*Sagitta gazellae* (2.08)	*Sagitta gazellae* (4.11)
Eukrohnia hamata (0.85)	*Thysanoessa macrura* (1.31)	*Thysanoessa macrura* (2.21)

With few exceptions, during the austral fall in the Croker Passage macrozooplankton and micronekton species were primarily distributed below 200 m as were their zooplankton prey, much of which had migrated to typical winter depths (Hopkins 1985a, b). Of the abundant species, only *E. superba* and, at night, the vertically migrating taxa (*S. thompsoni, E. antarctica,* and *P. antarcticum*) were abundant above 200 m (Table 2). *E. superba* and *S. thompsoni* inhabited the surface waters (salps only at night) to feed mainly on phytoplankton (Hopkins 1985b) while the fish, living just below the krill, are important nocturnal predators on *E. superba* (Dewitt and Hopkins, 1977; Hopkins, 1985a). Kock (1987) suggested that mesopelagic fish, contrary to earlier beliefs (e.g., Laws, 1985), were more important krill predators than cephalopods.

Our values for daily ration of the two dominant fishes agree quite well with numbers available from other studies (Table 4). Both *Electrona* and *Pleuragramma* had mean daily ingestion rates of between 2% and 3% of dry mass (2.66% and 2.11% respectively), whereas Pakhomov et al. (1996) estimated 1.86% for *Electrona*, and Rowedder (1979) estimated 5% for *Electrona* during the summer. An energy budget constructed for the third year of life of *Electrona*, using growth data based on microincremental aging techniques and published respiration measurements, showed excellent agreement (87%) between energy expenditures and an ingestion rate of 2.44% dry mass (Greely et al., 1999), further corroborating the numbers in Table 4. Rowedder (1979) numbers are likely most typical of maximal summer ingestion rates. Both Rowedder (1979) and the present study showed an overwhelming dominance of krill in the diet of fishes, whereas the fishes of Pakhomov et al. (1996) showed a preference for Calanoid copepods. Fishes likely take krill when they are available, switching to copepods when krill are more scarce.

Previous estimates of pelagic fish predation on krill (Kock, 1985; Laws, 1985), based on feeding through half the year, suggest that 15% of the krill population is annually consumed by fish. If winter feeding intensity is near that of summer feeding, then predation impact would be somewhat higher. Information on winter feeding rates is scarce and contradictory, with some indicating slower winter feeding for nototheniids (Chekunova and Naumov, 1982; Linkowski et al., 1983) and mesopelagic fish (Lancraft et al., 1991) while others observed active winter–spring feeding by nototheniids (Daniels, 1982; Tarverdiyeva, 1972). For the present study, assuming constant fish and krill populations through the season that was sampled, the austral fall (90 d), and using our daily consumption values, *E. antarctica* and *P. antarcticum* would ingest 2.5% and 2.9% of the total krill numbers, respectively, just during the fall season. Most of the predation was only on the juvenile segment of the population.

Krill densities vary considerably in time and space (Nast, 1986; Lascara et al., 1999), while available data suggest that pelagic fishes show less seasonal and spatial change (Table 5; Lancraft et al., 1991). What is most likely is that the fishes are reliably more vulnerable to sampling gear than krill, but it also implies a consistent low level of predation pressure by fishes throughout the year, particularly on juvenile krill.

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