Nekton community of the Scotia Sea as sampled by the RMT 25 during austral summer

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ABSTRACT: The nekton community was sampled by a Rectangular Midwater Trawl (RMT 25) over the upper 1000 m of the Scotia Sea during January 1991. A total of 81 nekton and micronekton species were collected from 2 sites, one in the oceanic western Scotia Sea (Stn 1) and the other on the northwestern slope of the South Georgia shelf (Stn 2). Species composition, abundance, biomass and day/night vertical distribution were investigated. Crustaceans were the most important group in terms of species numbers (28 species) followed by mesopelagic fish (24), molluscs (15) and coelenterates (11). Species diversity increased with depth and was higher at Stn 2 (76 species) than at Stn 1 (62 species). Biomass in the upper 1000 m was considerably higher at Stn 1 (94.6 g wet wt m^{-2} during daytime, 87 g wet wt m^{-2} during night) than at Stn 2 (10.2 and 23.7 g wet wt m^{-2}, respectively), mostly due to dense concentrations of the tunicate *Salpa thompsoni* (41.6 g wet wt m^{-2} during night). The other main contributors to the high biomass at Stn 1 were coelenterates (28.3 g wet wt m^{-2} during night) and mesopelagic fish (4.9 g wet wt m^{-2} during night). Euphausiids (*Euphausia triacantha* and *E. superba*) accounted for 1.5 g wet wt m^{-2} at Stn 2 during night, with *E. triacantha* the more important of the two (1.4 g wet wt m^{-2}). Except for *Bathylagus antarcticus* all common mesopelagic fishes showed a marked diurnal vertical migration (i.e. *Electrona antarctica*, *Gymnoscopelus braueri*, *Krefftichthys anderssoni*, *Protomyctophum bolini*). During daylight they stayed in the core of the Circumpolar Deep Water (CDW; 400 to 800 m) and at night they were mainly distributed in the Antarctic Surface Water (ASW; 0 to 400 m). Other species with pronounced vertical migration were the hydromedusa *Calycopsis borchgrevinki*, the squid *Brachioteuthis* ?*picta*, and the euphausiid *Euphausia triacantha*. The scyphomedusae *Atolla wyvillei* and *Periphylla periphylla* and the crustaceans *Cyphocaris richardi*, *Gigantocypris mulleri* and *Pasiphaea scotiae* did not appear to migrate and remained concentrated in the CDW. Spatial variability was analysed by multivariate data analyses (clustering techniques) and related to hydrography. Four main groups, characterised by different nekton communities, were derived: (1) a lower mesopelagic nekton community from the deeper layers of the CDW, apparent at both stations, (2) an upper mesopelagic nekton community from the core of the CDW, apparent at both stations, (3) an epipelagic nekton community from the ASW over the South Georgia slope (Stn 2) and finally (4) an epipelagic nekton community from the ASW of the oceanic Scotia Sea (Stn 1). The performance of the midwater trawl is discussed as it has a substantial impact on the catchability of the nekton. The presented data provide new information on the structure and spatial variability of Antarctic nekton communities and emphasise the geographical and vertical discontinuities between communities.

KEY WORDS: Nekton community · Southern Ocean · Pelagic ecosystem · Antarctic food chain · RMT 25

INTRODUCTION

It has been suggested that the Southern Ocean can no longer be considered a single ecosystem (Clarke 1985, Hempel 1985). In fact there is a pronounced hydrographic and biogeographic latitudinal zonation separating the region into 3 large-scale subsystems: the ice free oceanic 'West Wind Drift' (hereinafter referred to as Antarctic Circumpolar Current, ACC) extending from the Subtropical Front in the north to the northern limit of the pack ice, the 'East Wind Drift' with seasonal pack ice cover, and the shelf water zone immediately around the Antarctic landmass with almost permanent ice cover (Hempel 1985). The nekton samples analysed in the present study were all obtained from the Scotia Sea (Fig. 1), which is charac-
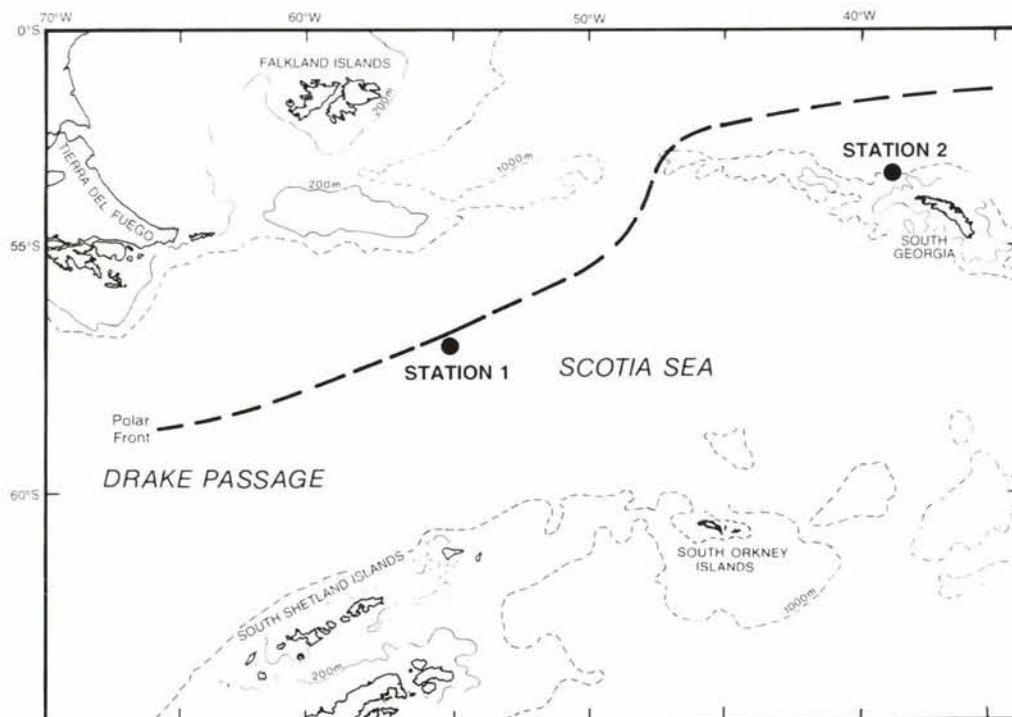
Fig. 1. Atlantic sector of the Southern Ocean showing the Polar Front relative to Stn 1 (13 to 15 January 1991) and Stn 2 (28 to 30 January 1991)

terised by a high zooplankton diversity (copepods, small euphausiids and salps predominating; Mackintosh 1934, Foxton 1966, Hempel 1985), and occurs in the most northerly of the 3 sectors.

Despite intensive investigations of the zooplankton and macrozooplankton communities of the Atlantic sector of the Southern Ocean (e.g. Hopkins 1985a, Atkinson & Peck 1988, Boysen-Ennen & Piatkowski 1988, Hopkins & Torres 1988, Piatkowski 1989a, b, Siegel & Piatkowski 1990, Siegel et al. 1992, Hopkins et al. 1993) the ecology of the micronekton or the nekton communities has received relatively little attention (Lancraft et al. 1989, 1991). Of all known species of Antarctic fish, 25 % live in the meso- and bathypelagic regions of the Southern Ocean (Kock 1992) and form a substantial part of the nekton community. Although the general biogeography of these species has been described (Hulley 1981, McGinnis 1982, Gon & Heemstra 1990) their detailed ecology is largely undescribed. In recent years the most abundant group, the myctophids, which occur in dense concentrations in the Scotia Sea, have begun to be exploited commercially (Filin et al. 1991, Kozlov et al. 1991). They are also important in the diet of a number of vertebrate predators, particularly king penguins (e.g. Adams & Klages 1987, Adams & Brown 1989, Cherel & Ridoux 1992) and this highlights their importance in the Antarctic food web. The nekton community also contains large populations of coelenterates (Larson 1986, Larson & Harbison 1990) and populations of large

pelagic shrimps for which there are few ecological data (Clarke & Holmes 1987, Iwasaki & Nemoto 1987). Squid are also important components of the nekton community, especially the ommastrephid *Martialia hyadesi* (Rodhouse & Yeatman 1990, Rodhouse 1991). This forms the principal prey item for a number of vertebrate predators (Croxall & Lishman 1987, Rodhouse et al. 1987, 1990, 1992a, Rodhouse & Prince 1993), which are together estimated to consume some 340 000 t of *M. hyadesi* per year in the Scotia Sea (Rodhouse et al. 1993). In turn, *M. hyadesi* feeds on other members of the nekton community, for example myctophids and euphausiids (Rodhouse et al. 1992b). In addition to the myctophids, *M. hyadesi* is also considered to be a resource with potential for future commercial exploitation (Rodhouse 1990). In the absence of any true epipelagic families of fish in the Antarctic (Kock 1987, 1992) the ommastrephid squids of the Scotia Sea appear to fill the niche occupied elsewhere in the world's oceans by pelagic fish such as carangids, clupeids and scombrids.

Thus, any model of the Southern Ocean pelagic ecosystem will be incomplete without a consideration of the composition, abundance and standing stock of the nekton. This paper describes the nekton community of the Scotia Sea, defining community according to Mills (1969) as 'a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups'.

This study examines the nekton community of the upper 1000 m at 2 sites in the Scotia Sea using hauls made with an opening/closing midwater trawl. The first of these was oceanic (Stn 1), while the other occurred on the northwestern slope of the South Georgia shelf (Stn 2). Both stations were located in the northern Scotia Sea close to the main path of the ACC. The ACC is the major oceanographic feature of the Southern Ocean and is an extensive, eastward flowing circumpolar current (e.g. Whitworth 1983, Hellmer et al. 1985, Stramma & Peterson 1990), responsible for the circumpolar distribution of zooplankton and micronekton species. It flows into the Scotia Sea through the Drake Passage before being deflected to the north of South Georgia. The upper waters of the ACC comprise Antarctic Surface Water (ASW) and Subantarctic Surface Water separated by a band of Antarctic Intermediate Water (AIW) and underlain by a thick band of Circumpolar Deep Water (CDW). The AIW is limited to the north by the Subantarctic Front (SAF) and to the south by the Polar Front (PF). Both sample sites occurred to the south of the PF, a region considered to be highly productive (Ainley & DeMaster 1990).

We report on the spatial distribution patterns of the nekton species at these 2 sites and compare the stations using clustering techniques. Detailed analyses on the biomass spectra of the nekton community and their implications for the upper pelagic food web in the Antarctic are described in the companion article by Rodhouse et al. (1994).

MATERIALS AND METHODS

Sampling. Nekton samples were collected with an opening/closing rectangular midwater trawl with a design aperture of 25 m² (RMT 25) according to the design principle described by Baker et al. (1973). The trawl consists of 2 nets, opened and closed using release gear connected to an IOS type acoustic net monitor (Harris 1969). The release gear had 4 operational jaws allowing the nets to be rigged so that opening the second net was independent of closing the first. This enabled separate layers to be sampled. The design mouth-angle of the net is 45° and, for the purpose of calculating water volume sampled, it was assumed that this angle was maintained at the towing speed of 3 knots. The nets were built in 3 sections of reducing mesh size: 19, 10 and 5 mm, measured along 1 side of the square. All the meshes were of woven, knotless construction. Actual panel sizes are shown in Fig. 2 together with the design mouth area for each mesh section. The cod-ends employed on these nets are the standard type used with the RMT 1+8 system (Baker et al. 1973).
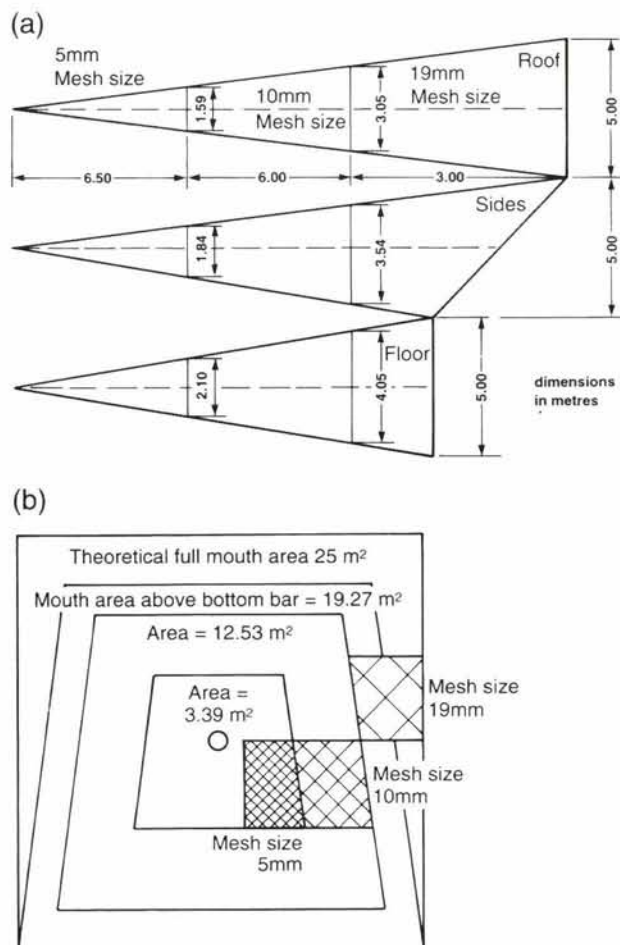

Fig. 2. The British Antarctic Survey's RMT 25. (a) Size and shape of the 3 panels of netting. (b) Mouth areas for each mesh size

A total of 20 RMT 25 samples were collected in the austral summer at Stn 1 in the oceanic Scotia Sea (bottom depth 4100 m; 13 to 15 January 1991), and at Stn 2 on the northwestern slope of South Georgia (bottom depth 1500 m; 28 to 30 January 1991) (Fig. 1). At Stn 1 all net hauls fell within a rectangle ranging from 57° 03.8' S to 57° 08.7' S, and from 55° 08.6' W to 55° 25.9' W; at Stn 2 all net hauls fell within a rectangle ranging from 53° 22.5' S to 53° 39.1' S, and from 38° 31.9' W to 38° 55.7' W. Each 200 m layer from the surface to 1000 m was sampled twice at each station, once in daylight and once at night, as defined by sunrise and sunset. The RMT 25 was deployed in downward oblique hauls. While it was fishing the net was lowered slowly and continuously through the target layer. The duration of a standard haul within one layer was 2 h but in some cases this was extended for up to 1 h. The mean volume filtered per 2 h haul was 260 000 ± 48 000 m³. Flowmeter data were used to correct all samples to a standard volume of 10 000 m³.

Between the RMT 25 hauls temperature and salinity profiles were obtained for the top 1000 m using a Neil Brown Mark III CTD.

Treatment of samples. The total volume of each net sample was measured and in the case of large samples, sub-samples were taken prior to sorting. Nekton organisms, arbitrarily defined as metazoans > 10 mm in body size, were identified to the lowest posssible taxonomic unit. Siphonophores, copepods, small polychaetes, amphipods and chaetognaths, which occurred regularly in the samples, were considered too small to be sampled quantitatively by the RMT 25 and were discarded after sorting. Ctenophores were also excluded from further calculations because they could not be collected as whole specimens. The total number of each nektonic species was recorded and the total volume of each species determined by displacement. Biomass was expressed in standing stock (g wet wt m^{-2}, mg wet wt m^{-2}) assuming 1 g approximately equals 1 ml (displacement volume). Species relative abundance was expressed in individuals per 10 000 m^3 water volume filtered (ind. $10^{-4} m^{-3}$).

Treatment of data. Agglomerative hierarchical cluster analysis was used to differentiate and group the 20 samples from the 2 stations. The analyses followed a multi-step strategy for the study of multi-species distribution patterns (Field et al. 1982). In order to avoid overemphasizing rare and random occurrences the data set was reduced to the 58 taxa that occurred in at least 3 samples. Data were arranged in an $(n \times m)$-matrix with n representing the 20 samples and m representing the relative abundances (ind. $10^{-4} m^{-3}$) of the 58 nekton taxa. All species abundances were log_{10}-transformed to smooth the large abundance values of a few species. Similarity between sample pairs was expressed by the Bray-Curtis Index; this index groups the samples according to both presence and abundance of species. This is the most appropriate method for marine ecological data sets (Field et al. 1982). The clustering of samples followed the Complete Linkage Method. Cluster analyses and calculations of ecological indices were carried out using the software package COMM adapted for personal computers (Piepenburg & Piatkowski 1992). More information on the various clustering procedures and their effects on classification results is compiled by Romesburg (1984).

RESULTS

Hydrography

Fig. 3 shows temperature and salinity against depth and temperature against salinity at each of the 2 sample sites. There are marked similarities between the profiles; at both stations a 200 to 300 m layer of cool, fresh ASW overlies warmer, more saline CDW and there is a pronounced temperature-minimum in the upper waters due to the seasonal warming at the surface. Fig. 1, which shows the general position of the PF in the Scotia Sea, also shows the exact position of the PF relative to Stn 1 (determined from an XBT transect between the Falkland Islands and Stn 1). Both stations were to the south of the PF.

At Stn 1 temperature decreases from 2.9 °C at the surface to a minimum of −0.7 °C at 160 m and then increases to 2°C at the core of the CDW around 600 m (Fig. 3). There apears to be a relatively constant salinity gradient between about 100 and 400 m. A marked change in both the temperature and salinity gradients occurs at 400 m. Below 600 m temperature and salinity are relatively uniform and vary little with depth. Similar features are apparent at Stn 2 with a pronounced temperature inversion in the surface waters and salinity increasing rapidly to about 400 m. Again, the temperature and salinity gradients alter around 400 m and little change in either variable is evident below 600 m.

The water column may be subdivided as follows: (1) 0–200 m, the bulk of the ASW with a pronounced temperature inversion; (2) 0–400 m, the region of greatest salinity (and thus density) change; (3) 200–400 m, the depth range over which most mixing between ASW and CDW occurs; (4) 400 m, the depth at which a marked change in temperature and salinity gradient occurs; (5) 400–600 m, the core of the CDW and the depth range over which salinity and temperature gradients are lower; (6) 600–1000 m, relatively uniform conditions.

Species composition

A total of 81 nekton and micronekton species were collected from the 2 sites. The sample size and depth range of each species, divided into day and night samples, are summarised in Table 1. Eight species, the pteropods *Clione limacina*, *Limacina helicina*, *Peraclis valdiviae*, *Spongiobranchaea australis* and *Thliptodon antarcticus* and the crustaceans *Euphausia frigida*, *Thysanoessa macrura* and *Vibilia antarctica*, were considered too small to be quantitatively sampled by the RMT 25. They are included in Table 1 but are not considered in later community analyses.

Diversity was slightly higher at Stn 2 (South Georgia slope) with 76 species, of which 19 (25%) were only found there. At Stn 1 (the oceanic Scotia Sea) 62 species were recorded, of which 5 (8%) were collected in that area only. Crustaceans were the most diverse group with a total of 28 species, followed by
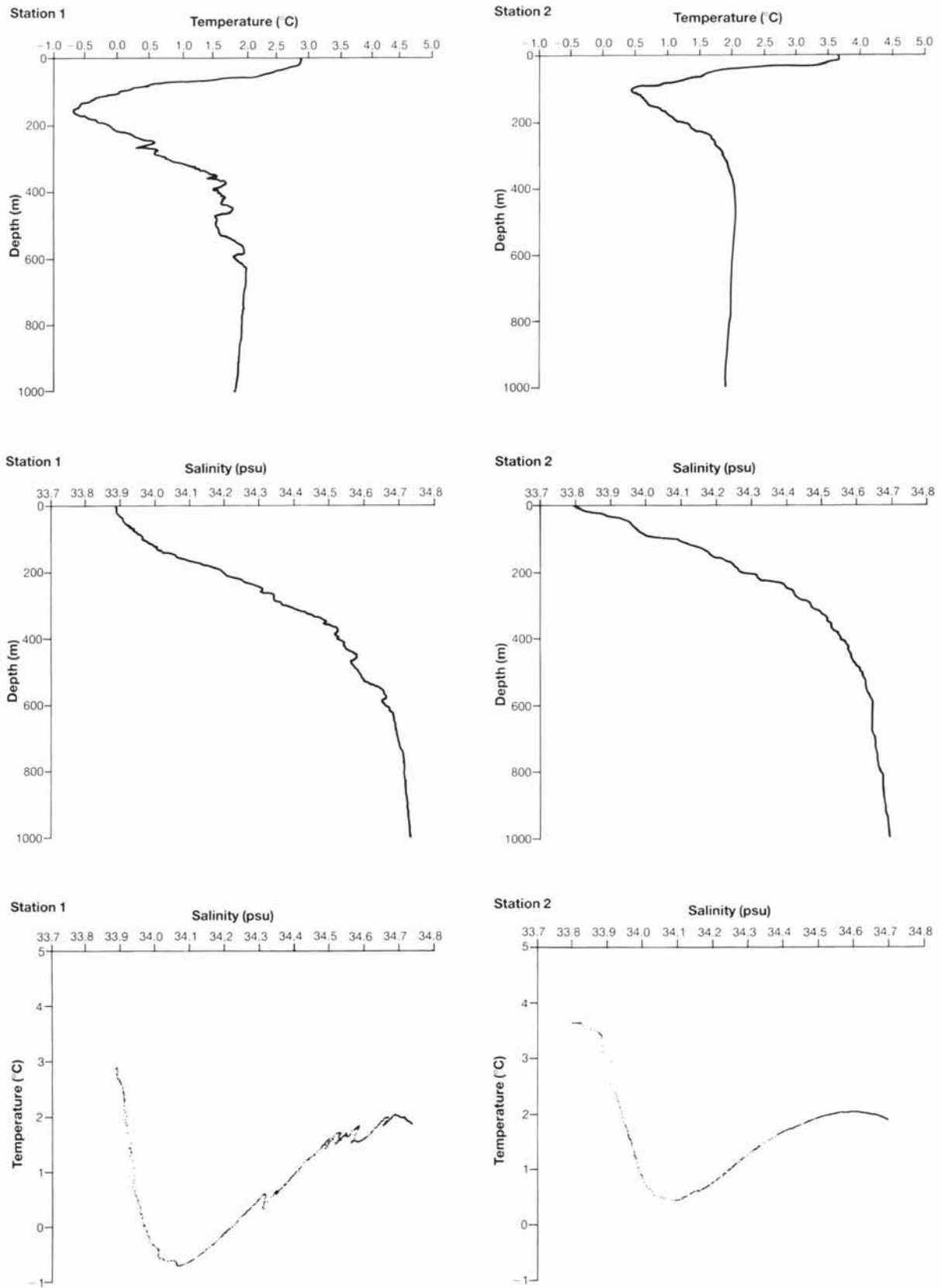
Fig. 3. Hydrographic profiles and temperature/salinity diagrams at the sample sites

Table 1. Nekton and micronekton species list and vertical distributions. n: sample size from discrete tows. *Species not quantitatively sampled by RMT 25

| Species | Scotia Sea (Stn 1) | | | | South Georgia (Stn 2) | | | |
| | Day | | Night | | Day | | Night | |
	n	Range (m)	n	Range (m)	n	Range (m)	n	Range (m)
Coelenterata								
Calycopsis borchgrevinki	90	200 – 800	345	0 – 800	162	0 – 1000	178	0 – 1000
Colobonema sericeum	1	800 – 1000		–	1	400 – 600	2	400 – 800
Crossota brunnea	5	600 – 800	6	400 – 600	35	400 – 1000	36	400 – 1000
Halicreas minimum	126	600 – 1000		–	24	400 – 1000	80	400 – 1000
Pantachogon haeckeli		–		–		–	22	200 – 800
Hydromedusae indet.	1	0 – 200	39	0 – 200	1	0 – 200		–
Atolla wyvillei	256	200 – 1000	281	200 – 1000	201	0 – 1000	149	200 – 1000
Desmonema gaudichaudi	2	200 – 600	2	200 – 400	1	0 – 200		–
Pandea rubra	4	800 – 1000		–		–	3	800 – 1000
Periphylla periphylla	147	200 – 1000	148	400 – 1000	48	200 – 1000	69	0 – 1000
Stygiomedusa gigantea	1	200 – 400	1	200 – 400	1	200 – 400	3	0 – 1000
Nemertinea								
Obnemertes maximovi	2	800 – 1000		–	1	800 – 1000	7	400 – 800
Mollusca								
Clio pyramidata		–		–	3	200 – 400	3	0 – 200
Clio piatkowskii	12	600 – 1000	8	600 – 1000	5	200 – 1000	16	0 – 1000
Clione limacina		–	23	0 – 200		–	6	200 – 800
Limacina helicina		–		–	1	400 – 600	14	600 – 1000
Peraclis valdiviae		–		–	1	400 – 600		–
Spongiobranchaea australis		–		–	3	400 – 1000	7	200 – 600
Thliptodon antarcticus		–		–		–	1	400 – 600
Alluroteuthis antarcticus	2	800 – 1000	3	800 – 1000	1	800 – 1000		–
Bathyteuthis abyssicola	1	800 – 1000		–		–		–
Brachioteuthis ?picta	7	600 – 1000	8	0 – 800	15	200 – 1000	24	0 – 1000
Chiroteuthis sp.		–		–	1	800 – 1000		–
Galiteuthis glacialis	5	600 – 1000	9	400 – 1000	6	200 – 1000	3	600 – 1000
Histioteuthis eltaninae		–	1	400 – 600		–		–
Mastigoteuthis psychrophila		–		–	4	400 – 1000	2	800 – 1000
Psychroteuthis glacialis	1	600 – 800	1	0 – 200		–		–
Polychaeta								
Tomopteris carpenteri		–		–	14	200 – 400	13	0 – 400
Ostracoda								
Gigantocypris mulleri	141	600 – 1000	66	400 – 800	119	200 – 1000	78	200 – 1000
Euphausiacea								
Euphausia frigida	3	400 – 600		–	104	0 – 200	98	0 – 200
Euphausia superba	13	400 – 600	4	200 – 600	112	0 – 800	95	0 – 800
Euphausia triacantha	1944	0 – 1000	453	0 – 800	2333	0 – 1000	10833	0 – 800
Thysanoessa macrura		–	56	0 – 600	313	0 – 200	127	0 – 400
Decapoda								
Acanthephyra pelagica	26	200 – 400	17	400 – 600	42	200 – 800	41	200 – 1000
Gennadas kempi	15	600 – 1000		–	20	400 – 1000	39	400 – 800
Pasiphaea grandicula	1	600 – 800	21	0 – 800	2	400 – 1000	3	400 – 800
Pasiphaea scotiae	42	600 – 1000	86	200 – 1000	48	200 – 1000	35	200 – 1000
Petalidium foliaceum	66	600 – 1000	8	800 – 1000	54	400 – 1000	32	200 – 1000
Sergestes arcticus	11	600 – 800		–	1	400 – 600	2	400 – 600
Stereomastis suhmi		–	1	600 – 800	4	400 – 800		–
Mysidacea								
Boreomysis sp.		–		–	1	800 – 1000	1	600 – 800
Gnathophausia gigas	21	600 – 1000	19	200 – 1000	12	400 – 1000	14	400 – 1000

Table 1 (continued)

| Species | Scotia Sea (Stn 1) | | | | South Georgia (Stn 2) | | | |
| | Day | | Night | | Day | | Night | |
	n	Range (m)	n	Range (m)	n	Range (m)	n	Range (m)
Amphipoda								
Cyphocaris richardi	44	600 – 1000	173	0 – 1000	117	400 – 1000	129	200 – 1000
Danaella mimonectes		–		–		–	2	200 – 600
Eurythenes obesus		–		–	11	400 – 1000	9	0 – 1000
Eusiroides stenopleura	7	800 – 1000	3	400 – 600	3	400 – 1000	7	400 – 800
Parandania boecki	43	600 – 1000	26	200 – 800	72	400 – 1000	110	200 – 1000
Cyllopus lucasii	21	0 – 600	15	200 – 600	92	0 – 600	75	0 – 600
Hyperia antarctica	8	400 – 600	4	600 – 800	6	400 – 800	3	200 – 800
Hyperia macrocephala		–		–		–	3	0 – 200
Lanceola sp.	2	200 – 1000		–	1	800 – 1000	3	600 – 1000
Megalolanceola stephenseni	1	800 – 1000		–		–		–
Pegohyperia princeps	5	600 – 800	4	600 – 1000	5	400 – 1000	8	200 – 1000
Scypholanceola aestiva		–		–		–	1	400 – 600
Themisto gaudichaudii	108	0 – 800	266	0 – 1000	13287	0 – 1000	6570	0 – 800
•Vibilia antarctica		–		–	2	200 – 400	7	0 – 600
Tunicata								
Salpa thompsoni	25361	0 – 1000	17297	0 – 1000	8	0 – 800	7	0 – 800
Vertebrata (Pisces)								
Nansenia antarctica	15	400 – 800	6	400 – 800	6	0 – 800	9	200 – 600
Bathylagus antarcticus	43	600 – 1000	275	200 – 1000	70	200 – 1000	42	0 – 1000
Cyclothone spp.	48	400 – 1000	16	0 – 1000	17	400 – 1000	48	200 – 1000
Borostomias antarcticus	4	600 – 800	6	0 – 1000	9	200 – 800	6	200 – 1000
Stomias ?gracilis	1	600 – 800	8	0 – 600		–	1	400 – 600
Benthalbella elongata	5	600 – 1000	1	600 – 800	2	400 – 800	9	200 – 1000
Notolepis coatsi	5	400 – 1000	8	400 – 800	7	200 – 800	13	0 – 1000
Electrona antarctica	67	200 – 1000	125	0 – 1000	202	0 – 1000	161	0 – 1000
Electrona carlsbergi	7	600 – 800	89	0 – 800	5	0 – 600	4	200 – 600
Gymnoscopelus bolini		–	4	600 – 1000	2	200 – 600	3	200 – 800
Gymnoscopelus braueri	74	400 – 1000	162	0 – 1000	99	400 – 1000	274	0 – 800
Gymnoscopelus fraseri		–	7	0 – 200	14	0 – 1000	1	0 – 200
Gymnoscopelus nicholsi	1	800 – 1000		–	12	0 – 600	7	0 – 200
Krefftichthys anderssoni	53	0 – 1000	229	200 – 1000	277	0 – 1000	200	0 – 1000
Lampanyctus achirus	10	600 – 800	12	400 – 1000	14	400 – 1000	19	200 – 1000
Protomyctophum andriashevi		–		–		–	1	0 – 200
Protomyctophum bolini	75	200 – 800	131	0 – 800	132	0 – 800	130	0 – 600
Protomyctophum choriodon		–		–	8	0 – 600	36	0 – 200
Protomyctophum gemmatum	5	400 – 600	2	400 – 600		–		–
Melanonus gracilis		–		–	1	400 – 600		–
Nemichthys ?scolopaceus	1	400 – 600		–	2	400 – 800		–
Cyanomacrurus piriei	2	800 – 1000	2	800 – 1000	5	400 – 1000	9	400 – 1000
Poromitra crassiceps	9	600 – 1000	4	800 – 1000	9	200 – 1000	8	600 – 1000
Paradiplospinus gracilis		–		–	4	200 – 1000	4	0 – 1000

mesopelagic fish with 24 species. Molluscs were represented by 15 species, of which 8 were cephalopods. Coelenterates occurred with 11 species. Two of them, *Desmonema gaudichaudi* and *Stygiomedusa gigantea*, were large scyphomedusae.

The tunicate *Salpa thompsoni* was present in very dense aggregations at Stn 1 and outnumbered all other species (Table 1). It was relatively scarce at Stn 2. At Stn 1 the crustaceans were dominated by the euphausiid *Euphausia triacantha*, whereas the hyperiid amphipod *Themisto gaudichaudii* was the most

abundant crustacean at Stn 2. No dense swarms of the Antarctic krill *Euphausia superba* were present in the areas investigated. Fish numbers were dominated by myctophids (*Electrona antarctica*, *Gymnoscopelus braueri*, *Krefftichthys anderssoni*) at both stations.

Vertical distribution of numerically dominant species

Most species occurred over a wide depth range and were caught at depths down to 1000 m, with numbers
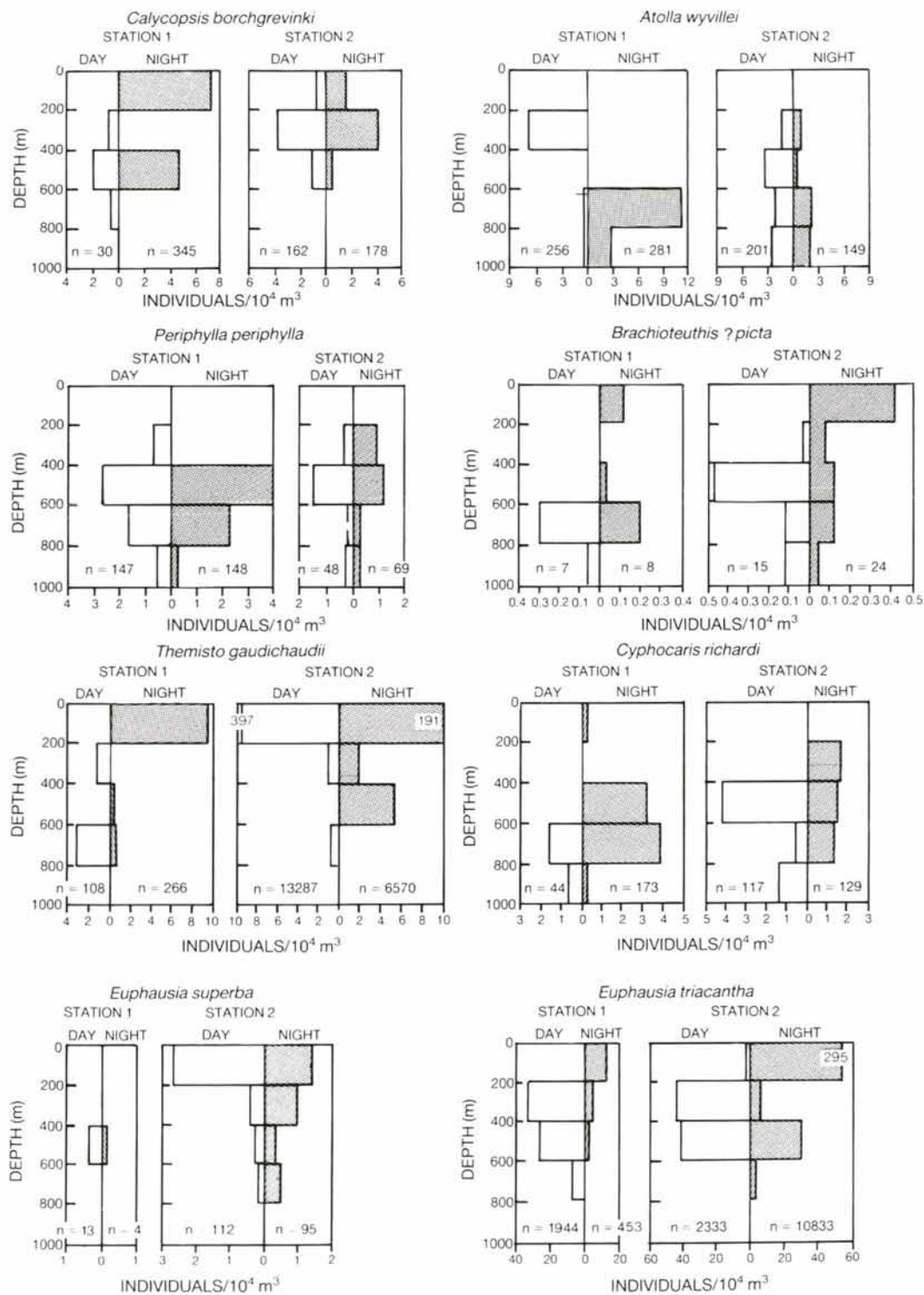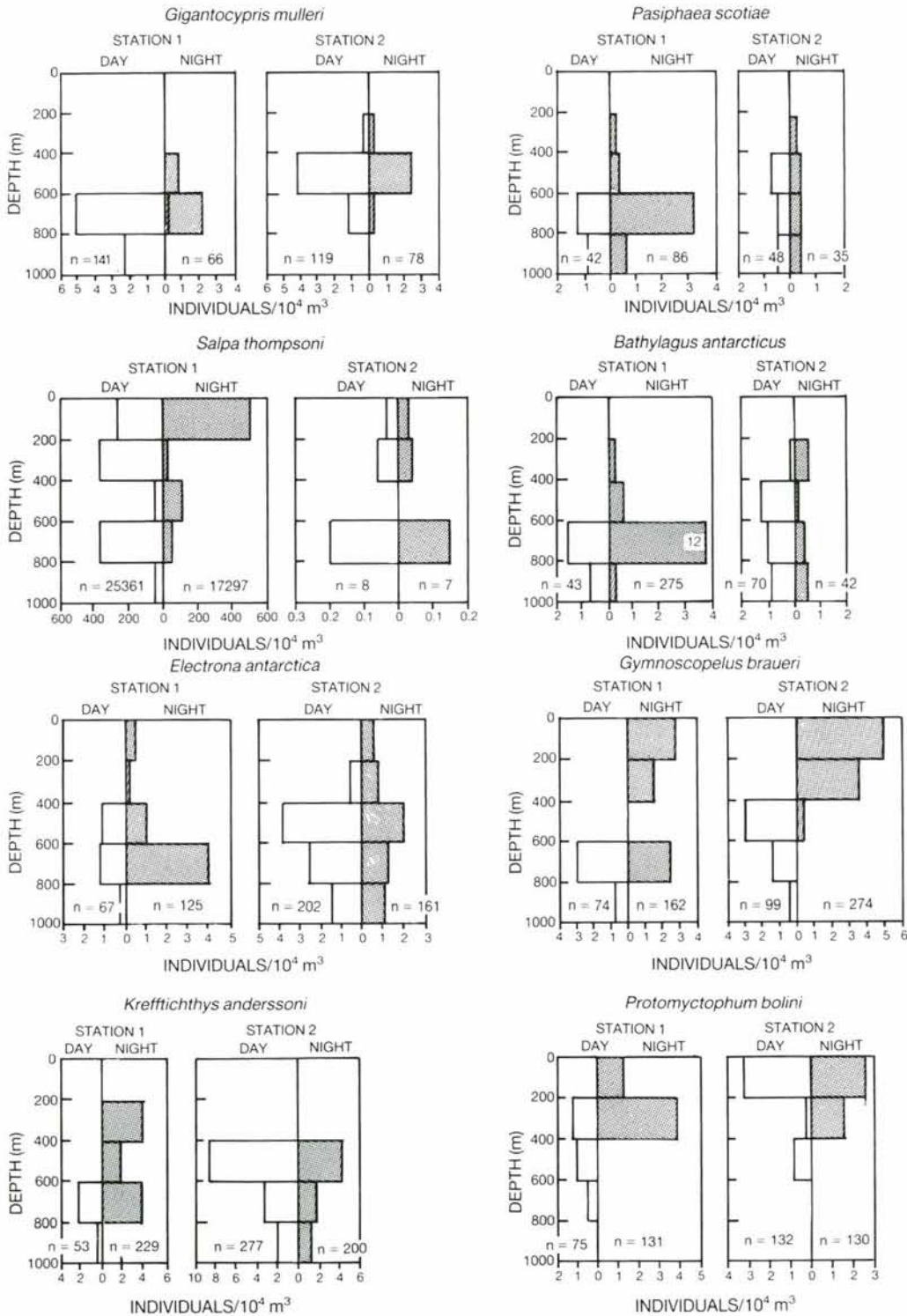
Fig. 4 (this and facing page). Vertical distribution of numerically most abundant species. n: no. of specimens collected

decreasing in the deepest layer during night hauls. The majority of species were not present in the upper 200 m (Table 1), although the number of species caught in this layer increased during the night. Most species were rare, i.e. <1 ind. 10^{-4} m^{-3}.

The vertical depth ranges of 16 major nekton species (Fig. 4) suggest some distinct diel vertical migratory patterns. With the exception of *Atolla wyvillei*, *Periphylla periphylla*, *Cyphocaris richardi*, *Gigantocypris mulleri* and *Pasiphaea scotiae* which had their abun-

Gigantocypris mulleri

Pasiphaea scotiae

Salpa thompsoni

Bathylagus antarcticus

Electrona antarctica

Gymnoscopelus braueri

Krefftichthys anderssoni

Protomyctophum bolini

dance peaks in the CDW and showed no clear indication of a vertical movement, all species exhibited an upward migration during the night.

The hydromedusa *Calycopsis borchgrevinki* showed a strong vertical migration at Stn 1 where it ascended

from the 200–600 m layers during the day to the upper 0–200 m layer during night. The squid *Brachioteuthis* ?*picta* occurred mainly below 600 m at Stn 1; at Stn 2 it showed a pronounced vertical migration from the CDW during the day into the surface ASW during the

night. *Euphausia superba*, very rare at Stn 1, was quite common at Stn 2 with higher concentrations in the surface layer during daylight than at night. At both stations *E. triacantha* showed a pronounced vertical migration into the surface layer during the night, where it was nearly absent during daylight. The very abundant tunicate *Salpa thompsoni* exhibited a strong vertical migration at Stn 1; during daylight it was distributed over a wide depth range while at night it concentrated in the upper 0–200 m.

All the common mesopelagic fish migrated vertically. At both stations the myctophids *Electrona antarctica*, *Gymnoscopelus braueri*, *Krefftichthys anderssoni*, *Protomyctophum bolini* and the bathylagid *Bathylagus antarcticus* ascended from the deeper layers during daylight to the surface layers during night. This pattern was particularly marked for *G. braueri*, but only weakly exhibited by *B. antarcticus*.

Standing stock biomass

The total nekton biomass per unit area (g wet wt m^{-2}) for each 200 m layer is given in Table 2. At Stn 1 the maximum nekton biomass occurred during daylight in the 2 upper layers, with evidence of diel vertical migration from 200–400 m during daylight (37.2 g wet wt m^{-2}) to 0–200 m at night (33.0 g wet wt m^{-2}). There was also a pronounced peak in biomass in the 600–800 m layer in both daylight and darkness (21.8 and 19.2 g wet wt m^{-2}, respectively), although there was no evidence of diel vertical migration at this depth. At Stn 2, the nekton biomass was much lower with a maximum of 7.8 g wet wt m^{-2} at 800–1000 m during the night. There was little evidence of diel vertical migration between any of the layers but biomass in all layers was consistently higher in hauls made during the night than in daylight, which suggests an upward migration into the upper 1000 m from layers below.

The standing stock values (mg wet wt m^{-2}) for the major taxonomic groups and the most abundant species illustrate that only a relatively few species constitute the majority of the biomass (Table 3). At Stn 1 the tunicate *Salpa thompsoni* was the major species in terms of biomass (41 570 mg wet wt m^{-2}; 0–1000 m); however, at Stn 2 the species was virtually

Table 2. Nekton biomass from RMT 25 samples. Standing stock in g wet wt m^{-2}

Depth range (m)	Stn 1		Stn 2	
	Day	Night	Day	Night
0 – 200	25.2	33.0	1.2	3.6
200 – 400	37.2	17.8	1.2	2.6
400 – 600	4.4	12.0	1.2	5.0
600 – 800	21.8	19.2	3.0	4.7
800 – 1000	6.0	5.0	3.6	7.8
0 – 1000	94.6	87.0	10.2	23.7

absent. At both sites coelenterates (*Periphylla periphylla*, *Atolla wyvillei*) and mesopelagic fish (*Bathylagus antarcticus*, *Electrona antarctica*, *Gymnoscopelus braueri*) comprised the majority of the biomass. The crustaceans *Euphausia triacantha* and *Themisto gaudichaudii* were major contributors at Stn 2 only (Table 3).

Table 3. Biomass (mg wet wt m^{-2}) of major taxonomic groups and selected dominant species calculated from RMT 25 hauls performed during night

Group/Species	Stn 1		Stn 2	
	0–200 m	0–1000 m	0–200 m	0–1000 m
Coelenterata	462	28 333	725	15 126
Mollusca	18	235	28	158
Euphausiacea	24	41	1 197	1 461
Decapoda	41	633	0	336
Amphipoda	2	137	769	895
Tunicata[a]	28 632	41 570	2	11
Pisces	487	4 922	489	4 216
Others[b]	3 334	11 129	390	1 497
Calycopsis borchgrevinki	150	423	54	277
Atolla wyvillei	0	9 694	0	1 641
Periphylla periphylla	0	10 675	15	11 117
Brachioteuthis ?picta	17	63	25	75
Gigantocypris mulleri	0	73	0	64
Euphausia triacantha	24	38	1 180	1 420
Acanthephyra pelagica	0	79	0	223
Pasiphaea scotiae	0	510	0	46
Cyphocaris richardi	2	72	0	26
Parandania boecki	0	59	0	35
Themisto gaudichaudii	28	35	766	781
Bathylagus antarcticus	0	2 361	9	628
Borostomias antarcticus	4	103	0	176
Electrona antarctica	39	441	57	895
Electrona carlsbergi	270	292	0	27
Gymnoscopelus bolini	0	219	0	228
Gymnoscopelus braueri	62	302	243	817
Krefftichthys anderssoni	0	486	1	309
Protomyctophum bolini	54	164	74	101
Cyanomacrurus piriei	0	175	0	309

[a] Consists of *Salpa thompsoni* only
[b] Also includes not quantitatively collected species

Community analysis

The results of the cluster analysis are shown in a dendrogram (Fig. 5). The ordinate represents the groupings or clusters of samples and the abscissa the percentage similarity. The samples are grouped according to both presence and abundance of species. Thus, the clusters derive from the similarity of the nekton composition in the different samples and reflect the different nekton communities responsible for the sample groupings.

At an arbitrary similarity level of 40%, 4 major net haul clusters and 1 single sample emerge (Fig. 5). Four communities can be derived. Cluster 1 groups the 4 deepest nekton samples (800–1000 m) of both stations plus the night sample for the 600–800 m layer at Stn 2. It represents the lower mesopelagic nekton community. Cluster 2 represents samples from the 400–600 m and 600–800 m layers of both Stns 1 and 2. It represents an upper nekton community, and although similar to the lower mesopelagic community, it is richer in species and biomass. In Cluster 3 the 4 net hauls from
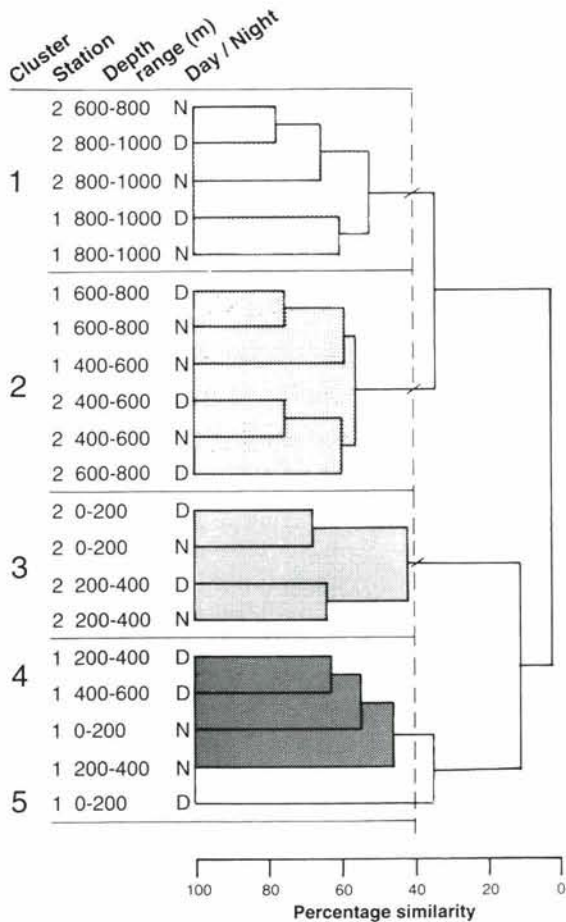
Fig. 6. Extension of the nekton communities as revealed by cluster analysis (see Fig. 5)

the upper layers (0–200 m, 200–400 m) of Stn 2 are grouped together. This cluster characterises the epipelagic (0–400 m) nekton community of the South Georgia slope region. Cluster 4 is a similar grouping, but is restricted to samples from Stn 1. This cluster also includes the daylight sample from the 400–600 m layer at Stn 1 and describes the epipelagic nekton community of the oceanic Scotia Sea. The daylight sample from the upper surface layer (0–200 m) of Stn 1 was an outlier which could not be grouped into any of the existing clusters. A diagram of the distribution of communities is given in Fig. 6.

The characteristics of the assemblages in each depth/time stratum in terms of the number of species, the dominant species and its percentage dominance and a diversity index (Shannon & Weaver 1963) were compiled for each sample (Table 4). At Stn 1 *Salpa thompsoni* was the dominant species in all samples. This species was of low importance at Stn 2, where the dominant species varied for the different layers. Species number and diversity increased with depth and reached higher values at Stn 2.

DISCUSSION

Net performance

In calculating nekton relative abundance and biomass densities from RMT 25 samples, it should be noted that the effective mouth area of the net is dependent upon the mouth angle during fishing. The nominal mouth area of 25 m^2 is only achieved when the mouth angle is 45°. The actual mouth area is dependent on towing speed since the bottom bar weight remains constant but the net drag is proportional to the square of velocity. Roe et al. (1980) showed that for an RMT 8 there is a speed range over which the mouth angle remains constant (2.6 to 8.0 knots). Our net, having larger meshes making up the majority of its filtering area, would be expected to have a proportionally lower drag and so reach a similar mouth angle plateau at a higher speed. Thus, for horizontal towing at

Fig. 5. Cluster analysis dendrogram (Bray-Curtis Index, complete linkage)

Table 4. Number of species, dominant species, its percentage dominance and diversity index $H' = -\Sigma(n/N)\ln(n/N)$ after Shannon (Shannon & Weaver 1963) with n = relative abundance of each species in the sample and N = total relative abundance of all species in the sample

Stn	Sampling depth (m)	Day or night	No. of species	Dominant species	Percentage dominance	Diversity index
1	0 – 200	D	6	Salpa thompsoni	99.8	0.017
1	0 – 200	N	17	Salpa thompsoni	92.8	0.391
1	200 – 400	D	13	Salpa thompsoni	88.8	0.460
1	200 – 400	N	21	Salpa thompsoni	54.4	1.611
1	400 – 600	D	17	Salpa thompsoni	53.8	1.151
1	400 – 600	N	28	Salpa thompsoni	84.7	0.803
1	600 – 800	D	36	Salpa thompsoni	89.6	0.635
1	600 – 800	N	31	Salpa thompsoni	49.1	1.912
1	800 – 1000	D	34	Salpa thompsoni	66.2	1.531
1	800 – 1000	N	22	Salpa thompsoni	41.5	2.088
2	0 – 200	D	16	Themisto gaudichaudii	97.4	0.171
2	0 – 200	N	25	Euphausia triacantha	58.7	0.859
2	200 – 400	D	27	Euphausia triacantha	80.3	0.946
2	200 – 400	N	35	Euphausia triacantha	22.4	2.613
2	400 – 600	D	48	Euphausia triacantha	49.2	2.132
2	400 – 600	N	44	Euphausia triacantha	50.5	2.105
2	600 – 800	D	35	Krefftichthys anderssoni	18.7	2.741
2	600 – 800	N	42	Euphausia triacantha	15.8	2.951
2	800 – 1000	D	37	Petalidium foliaceum	13.7	2.883
2	800 – 1000	N	32	Atolla wyvillei	19.5	2.795

3 knots we are confident that the mouth angle was close to 45°. However, exact information on the mouth angle of the net can only be achieved if the inclination of the net will be measured directly during the haul.

With the mouth at its design angle the bottom bar trails 5 m behind the top bar. Oblique haul techniques will thus increase mouth area during downward hauls and decrease mouth area during upward hauls.

With the larger mesh panels at the front of the net the 25 m² mouth area may not be appropriate for calculating the densities of those species able to escape through the larger mesh sizes. However, given the probability that the net will exert a herding effect this problem is complex and cannot be addressed further in the present study.

Finally, the performance of the RMT 25 may also be influenced by the angled mouth design in that objects, such as rigging wires, monitor and release gear, pass over the organisms and, if detected, may elicit an escape response before the organisms actually enter the net. Net avoidance is most likely to be a problem in well lit water but it may also occur at depth where bioluminescence, stimulated by the net gear, may indicate the presence of the net.

Distribution patterns and community structure

The composition of pelagic ecosystems varies considerably in space and time, resulting in an extremely heterogeneous distribution of key species (Haury et al.

1978, Omori & Hamner 1982). Thus, the results of the present study obtained from hauls at 2 considerably different sites within the Scotia Sea and during only 6 d of January 1991 should be considered simply as a snapshot in time of one important trophic level of the Antarctic pelagic ecosystem. Our study provides a sound basis for any further investigation of the Antarctic nekton community, a previously widely ignored element of the Southern Ocean ecosystem, even though restricted spatially and temporally. In fact, the opening/closing version of the RMT 25 revealed for the first time detailed information on the vertical structure and species-specific biomass levels of the Antarctic nekton community.

The present study is the first examination of the summer nekton community in the Scotia Sea and provides the most comprehensive nekton and micronekton species list reported for the Southern Ocean. It was found that large numbers of mesopelagic fish which also contained a number of rare forms (Gon & Heemstra 1990) were responsible for the high nekton diversity. Both Stns 1 and 2 were situated outside the zone influenced regularly by seasonal pack ice, in which Euphausia superba, the Antarctic krill, dominates the pelagic ecosystem (Hempel 1987) and so, as expected, relatively small numbers of E. superba were recorded. However, krill distribution is notoriously patchy and we may, by chance, have missed sampling through a swarm leading to a low recorded abundance in this study. Mesopelagic fish, salps, coelenterates, decapod crustaceans and amphipods were the predominant

nekton organisms, both in terms of numerical abundance and biomass. These typical nekton groups have been observed to form distinct faunal assemblages in midwater (e.g. Auster et al. 1992) and, if in high densities, are responsible for the development of so-called deep-scattering layers (Milliman & Manheim 1968).

At both sites our species list described a typical Antarctic oceanic nekton fauna which included several species previously reported from adjacent regions (Mackintosh 1934, Lancraft et al. 1989, 1991). This list also contained a number of species, such as the nemertean *Obnemertes maximovi*, the decapods *Pasiphaea grandicula* and *Sergestes arctica*, and the hyperiid amphipods *Megalolanceola stephensi* and *Scypholanceola aestiva* which have been reported only sporadically from the Southern Ocean.

At both stations species diversity increased considerably with depth (Table 4) and this is attributed to the species-rich CDW below about 400 m (Fig. 3). A number of typical mesopelagic species occurred there which avoided the surface layers (i.e. the scyphomedusae *Atolla wyvillei* and *Periphylla periphylla*, the squid *Mastigoteuthis psychrophila*, the ostracod *Gigantocypris mulleri*, the decapod *Gennadas kempi*, the amphipod *Eusiroides stenopleura*, and the fish *Cyanomacrurus piriei* and *Poromitra crassiceps*).

One of the most striking results from our studies was that cluster analysis grouped samples from the CDW (400–1000 m) from both study sites into the same communities (Clusters 1 and 2; Fig. 5). In contrast, samples from the upper layers (0–400 m), which were characterised by ASW and waters where mixing between ASW and CDW occurred, were geographically separate (Clusters 3 and 4; Fig. 5).

The communities present at Stns 1 and 2 were the lower mesopelagic nekton community, with numerous species typical of the deep layer (800–1000 m) of CDW (Cluster 1), and the upper mesopelagic nekton community mainly restricted to the 400–800 m layers of CDW (Cluster 2). The latter, higher depth strata, were richer in biomass and species abundance than the lower CDW level (Table 2, Fig. 4). We attribute this to (1) most mesopelagic species having their peak distribution in the core of the CDW in about 500–600 m, and (2) the diurnal migration of several species from the deepest layers into the 400–800 m layers. However, this pattern was not consistent. At Stn 1 the daylight 400–600 m sample was grouped in the surface cluster (Cluster 4) by its low species number, and at Stn 2 the nighttime 600–800 m sample was grouped with the lower mesopelagic community (Cluster 1) probably by the high portion of mesopelagic species that have their distribution centre in the deeper layers.

The surface layers were clearly geographically separate, although their large-scale hydrography was similar. ASW characterised the upper 200–300 m of the water column at both stations, with a seasonally warmed upper surface layer of ca 60 m (>2.0°C). Higher species numbers and diversities caused by the proximity of South Georgia (the 'island effect') probably explained the conspicuous grouping of the slope samples into the South Georgia epipelagic nekton community (Cluster 3). Small-sized species such as the pteropod *Clio pyramidata* and the polychaete *Tomopteris carpenteri* were only found in this community. *Themisto gaudichaudii* and *Euphausia triacantha* were numerically very abundant and *E. superba*, known to be typical in the area (Ward et al. 1990), was also a common component (Table 1, Fig. 4). Although close to the shelf of South Georgia this community should not be considered neritic as no benthic, benthopelagic or meroplanktonic stages of typical demersal species were present.

The surface samples of Stn 1 were grouped into the epipelagic community of the Scotia Sea (Cluster 4) which also included the daylight sample at 400–600 m layer as described above. This community presented an impoverished fauna that was less diverse than the corresponding community at South Georgia and considerably affected by large concentrations of *Salpa thompsoni*. Numerically this tunicate dominated all samples at Stn 1 (Table 4) while at Stn 2 it was virtually absent. *S. thompsoni* is a highly variable component in the pelagic system of the Southern Ocean (Everson 1984, Piatkowski 1985a, b) and its locally restricted, high abundance had a strong influence when characterising the Stn 1 community. The species is extremely patchy and can outnumber all other species by a small-scale rapid multiplication through asexual reproduction during times of favourable food supply, i.e. algal blooms (Foxton 1966). The relatively clear separation of the communities (Clusters 1 to 4) was biased by one outlier sample. The daylight 0–200 m catch at Stn 1 was grouped separately from all other samples due to the lowest species number and diversity encountered (Table 4).

Biomass levels were expressed in wet weight to emphasise the importance of gelatinous forms in the nekton community. Except for the deepest layer (800–1000 m) total biomass was one order of magnitude higher in the oceanic Scotia Sea than at the South Georgia slope (Table 2). This difference was mostly due to the large numbers of *Salpa thompsoni*, *Atolla wyvillei* and *Periphylla periphylla* at the oceanic site. In particular, *S. thompsoni* contributed a major share of the biomass at Stn 1 with 87% in the 0–200 m layer, and 48% in the upper 1000 m during the night collections. The biomass of mesopelagic fish was similar at both stations over 0–1000 m, with 4.92 g wet wt m^{-2} at Stn 1 and 4.16 g wet wt m^{-2} at Stn 2 (Table 3), but was

more important in relative terms at the latter where it accounted for 18% of the biomass, as opposed to 6% at Stn 1. Euphausiids, notably *Euphausia triacantha*, were the principal components of the biomass at Stn 2 where they comprised 6% of the nekton biomass (1.46 g wet wt m^{-2} in 0–1000 m). We consider our biomass estimations to be reasonably accurate since, apart from the fast swimming cephalopods, the gelatinous forms, crustaceans and the sluggish mesopelagic fish are readily sampled by the large RMT 25. Biomass estimates for the highly mobile species such as squid (e.g. *Brachioteuthis ?picta* with only 75 mg wet wt m^{-2}, 0–1000 m, Stn 2) are likely considerable underestimates since there is evidence to suggest large numbers of squid in the area, particularly ommastrephids (Rodhouse & Yeatman 1990, Rodhouse 1991). Moreover, squid form the principal dietary component of many top predators in the South Georgia area (e.g. Croxall & Lishman 1987, Rodhouse et al. 1987, 1990, 1992a, Rodhouse 1991, Rodhouse & Prince 1993).

The nekton biomass levels for the South Georgia slope region (23.7 g wet wt m^{-2}, 0–1000 m, during the night) are in the same range as others reported for similar micronekton/nekton assemblages in the area. Lancraft et al. (1989) estimated 28.2 g wet wt m^{-2} (0–1000 m, night tow) for Weddell Sea and 31.0 g wet wt m^{-2} (0–1000 m, night tow) for open waters near ice edge zones in southern Scotia Sea during summer. Even during winter micronekton community biomass has been reported at 22.9 g wet wt m^{-2} (0–1000 m, nighttime) below the partially consolidated pack ice in the vicinity of the Weddell-Scotia Confluence (Lancraft et al. 1991). As in our study, salps, coelenterates and mesopelagic fish were found to contribute the major proportion of the nekton biomass. However, the high biomass levels found in the oceanic Scotia Sea during the present study (Table 2, Stn 1) far exceed all earlier estimations. Our data further suggest a substantial increase in biomass for the surface layers during the night, mostly due to animals migrating from the CDW to the productive upper layers (Table 2, Fig. 4). At the South Georgia slope there is even some evidence for a migration of nekton from below 1000 m into the upper layers, since total biomass for the upper 1000 m is increased by more than a factor of 2 during the night (Table 2).

In contrast with previous studies, where *Salpa thompsoni* was reported to show a weak vertical migration (Piatkowski 1985a, b, Lancraft et al. 1989), this study showed a very marked upward migration during the night (Fig. 4). However, this could also have been due to a patchy distribution, i.e. during the night hauls a particularly dense concentration happened to be sampled in the top 200 m. A patchy distribution pattern could also explain the comparatively dense concentration of *Euphausia superba* during a daylight haul in the upper 200 m at Stn 2 (Fig. 4).

Calycopsis borchgrevinki, *Euphausia triacantha* and the dominant mesopelagic fish all showed a migration, ascending from the core of the CDW into the surface layers during darkness. For the mesopelagic fish this migration pattern confirms the results of Torres & Somero (1988). For *Electrona antarctica*, *Gymnoscopelus braueri*, *Krefftichthys anderssoni* and *Protomyctophum bolini* (4 myctophid species also comprising the key members of the fish biomass in our study) they reported a daytime centre of distribution between 200–600 m and an upward shift into the upper 200 m at night. They further conclude that the diel upward movement of fish can result in a displacement of nearly 20% of the total fish biomass into the upper surface layer at night. This upward shift can be mostly explained as a feeding migration as there is evidence that Antarctic myctophids feed mainly on copepods, euphausiids, amphipods and euphausiid larvae (Rowedder 1979, Hopkins 1985b, Gerasimova 1991, Lancraft et al. 1991), all abundant in this area (Atkinson & Peck 1988, Atkinson et al. 1990, Ward et al. 1990).

Food web implications and conclusions

The nekton community described in this study comprises a major component of the Southern Ocean pelagic ecosystem. Its biomass distribution implies a more diverse food web than previously realised, with mesopelagic fish, coelenterates, decapod crustaceans and squid as major links between the zooplankton and top predators. A similar non-krill-dominated Antarctic food chain has been recently suggested for the coastal Weddell Sea (Boysen-Ennen et al. 1991) with the pelagic Antarctic silverfish *Pleuragramma antarcticum* as the main link between zooplankton and top predators.

Accepting that myctophids, the main group within the mesopelagic fish, feed primarily on small zooplankton such as copepods (e.g. *Metridia gerlachei*), ostracods (e.g. *Conchoecia* spp.) and euphausiid larvae (Hopkins 1985b, Lancraft et al. 1991) and that myctophids form a substantial component of the diet of Antarctic top predators (Croxall & Lishman 1987, Ainley et al. 1991), then they should be regarded as a crucial link within a non-krill-dominated Antarctic food chain. However, the feeding patterns of nekton community members other than myctophids need more study; the diets of decapod crustaceans and coelenterates are not fully documented and a recent study shows that squid, especially the ommastrephid *Martialia hyadesi*, preys heavily on myctophids (Rodhouse et al. 1992b), which makes trophic interactions within the nekton community relatively complicated.

We propose the nekton community of the Scotia Sea to be of major importance to the pelagic ecosystem and suggest a food chain with zooplankton — nekton (mesopelagic fish, squid, coelenterates and decapod crustaceans) — top predators as an important alternative to the more conventional Antarctic food chain, where krill is assumed to be consumed directly by the top predators.

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