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Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts

E. A. Pakhomov, R. Perissinotto, C. D. McQuaid

Southern Ocean Group, Dept of Zoology and Entomology, Rhodes University, PO Box 94, Grahamstown, 6140, South Africa

ABSTRACT: The composition, distribution, abundance, biomass and size-structure of macroplankton/micronekton communities at the Subtropical Convergence (STC) and the Antarctic Polar Front (APF) regions were investigated during the South African Antarctic Marine Ecosystem Study (SAAMES II, January–February 1993; SAAMES III, June–July 1993). A total of 115 and 32 macroplankton/micronekton species were found in the epipelagic zones of the STC and APF, respectively. Cluster analysis based on species composition indicated the occurrence of 3 different plankton communities: one in the STC region, another to the north of the APF and the third to the south of the APF. Although the APF and the STC were investigated in different seasons, average abundance and biomass were similar in both regions. Tunicates, euphausiids, decapods and myctophiid fishes dominated the total stock of the 2 frontal regions, in terms of both abundance and biomass. Both fronts exhibited considerable fluctuations in the abundance and biomass levels which appeared to covary with the spatial distribution of the phytoplankton stock in the area. The dominant size-classes were composed of a small group of 5 to 30 mm siphonophores, tunicates and euphausiids and a larger group of 40 to 80 mm euphausiids, chaetognaths, vertically-migrating decapods and myctophiid fishes.

KEY WORDS: Subtropical Convergence · Antarctic Polar Front · Macrozooplankton · Micronekton · Biomass · Abundance · Taxonomy · Community structure

INTRODUCTION

The Southern Ocean is subdivided into several thermohaline zones by 4 major circumpolar fronts (Deacon 1982, Lutjeharms & Valentine 1984, Lutjeharms 1985) which exhibit enhanced biological activity, compared to the adjacent waters (Allanson et al. 1981, Lutjeharms et al. 1985, Chapman et al. 1987, Laubscher et al. 1993).

The Subtropical Convergence (STC), dividing the subtropical and subantarctic waters, forms one of the strongest horizontal temperature gradients of this ocean. North of this, the region directly south of Africa is exposed to the influence of the Agulhas Current system. The interaction of the Agulhas Retroflection Current (ARC) with the northern border of the STC causes a high degree of variability in currents and meridional heat transport by warm-core eddies that often cross the STC (Olson & Evans 1986, Chapman et al. 1987, Gordon et al. 1987). The Antarctic Polar Front (APF), dividing the Subantarctic and Antarctic zones, is the second main circumpolar front in the Southern Ocean (Deacon 1982, Lutjeharms & Valentine 1984).

Physical transport mechanisms, phytoplankton new production, grazing food chains and vertical migrations of zooplankton, provide the basis for the transport of fixed carbon into the deep ocean. This is known as the 'biological carbon pump' (Longhurst & Harrison 1989). The oceanic fronts not only have a substantial influence on the total productivity of the pelagic subsystem of the Southern Ocean, they may also contribute significantly to the removal of large amounts of fixed carbon to deep ocean waters. In a recent model of the Antarctic ecosystem, Huntley et al. (1991) suggested that up to 80% of the net primary production may be consumed directly by the meso- and macrozooplankton. During the last decade, research activities in the Southern Ocean have increased rapidly and investigations on the macrozooplankton/micronekton component have been focused mainly on the community level. Neritic (Fukuchi et al. 1985, Tanimura et al. 1986, Tuker & Burton 1990), marginal-ice zone (Hopkins et al. 1989, Hosie & Stolp 1989, Lancraft et al. 1989, Siegel et al. 1992) and open oceanic communities (Hopkins 1985, 1987, Piatkowski 1987, Siegel & Piatkowski 1990, Boysen-Ennen et al. 1991, Pakhomov 1991, Hosie 1994) in the different sectors of the Southern Ocean have been the subject of the most intensive investigations. However, the communities of the Subantarctic, the APF and the STC zones have been largely neglected and are still poorly known. Within these areas, only the waters around island masses have received some attention (Miller 1982a, b, 1985, Boden & Parker 1986, Perissinotto & McQuaid 1992, Pakhomov 1993a).

This study was, therefore, designed with the aim of improving the information on the composition, distribution, abundance, biomass and size-structure of the macrozooplankton/micronekton communities in the main frontal zones of the Southern Ocean.

MATERIALS AND METHODS

Samples were collected during 2 cruises of the South African Antarctic Marine Ecosystem Study (SAAMES) aboard the SA 'Agulhas' (Voyages 70 and 72). The first survey, SAAMES II, took place during the period 21 January to 4 February 1993 in the region of the Antarctic Polar Front (APF), between latitudes of 47° and 53° S (longitude 0° to 10° E). On the second occasion, SAAMES III, during the period 25 June to 12 July 1993, the work was carried out at the Subtropical Convergence (STC) in the region of the Agulhas Retroflection Current, between latitudes of ca 39° and 44° S (longitude 10° to 22° E) (Fig. 1). During each cruise, three 36 h stations across the APF and the STC were undertaken in the middle, in the southern and in the northern vicinity of the frontal regions, respectively. At each station, trawls were carried out at regular intervals of ca 2 to 3 h. In addition, in the region of the STC 3 transects through a warm-core eddy (WCE) were made with trawls at intervals of ca 8 to 12 h (Fig. 1). A total of 9 samples from the region of the APF and 30 samples from the region of the STC were collected and analyzed.

Macrozooplankton and micronekton were collected using a Rectangular Midwater Trawl (RMT-8) with a nominal mouth area of 8 m^2 and mesh size of 4.5 mm (Baker et al. 1973). The volume filtered by the trawl was determined by multiplying the effective mouth area of the trawl by the distance travelled. This was calculated from the ship's speed and the period of trawling, after the trawl was opened in the water. In calculating the volume filtered, the effect of towing speed was also taken into account (Roe et al. 1980, Pommeranz et al. 1982). Towing speed varied between 1.5 and 4 knots. Usually, the trawl was towed obliquely between 0 and 300 (± 100) m. The depth and the opening and closing of the trawl were controlled by a Universal Underwater Unit (U^3, Robertson et al. 1981). Samples were preserved in 4 % buffered formalin and examined in the laboratory. Catches were sorted, counted and analyzed for taxonomic identification, body length (with an accuracy ≈ 1 mm) and displacement volume. The dry weight of the main macroplanktonic and micronektonic groups from the different hauls were obtained by oven-drying specimens for 36 h at 60 °C.

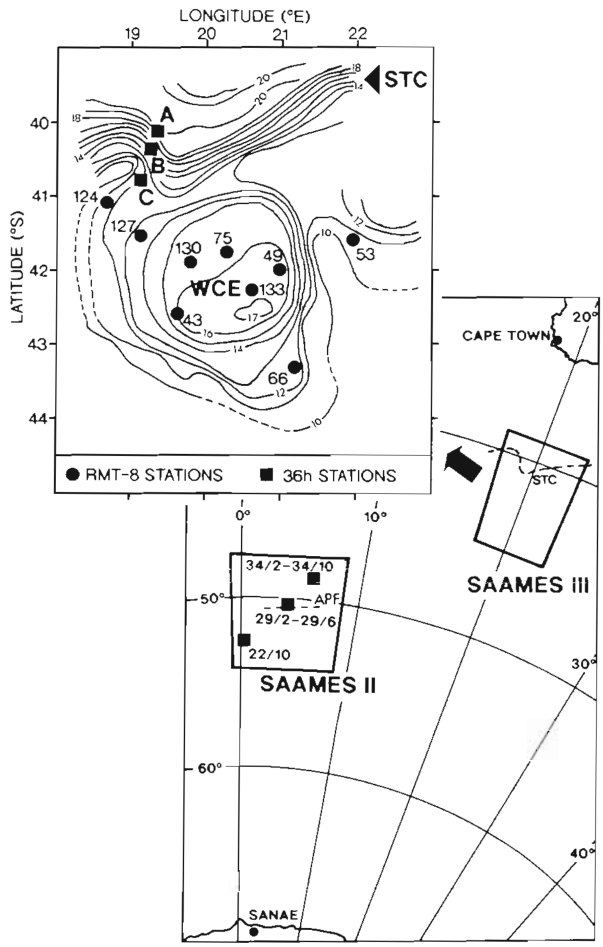

Fig. 1. Sea surface isotherms and macroplankton/micronekton stations occupied by the SA 'Agulhas' during January–February 1993 (SAAMES II) and June–July 1993 (SAAMES III; adapted from Lutjeharms et al. 1994). STC: Subtropical Convergence; WCE: warm-core eddy. A: STC Stn A (from 84/1 to 88/3); B: STC Stn B (from 106/1 to 110/2); C: STC Stn C (from 101/2 to 105/1)

A pre-calibrated 120 kHz echo-sounder (Simrad EK-500) was used for the detection of plankton acoustic backscattering. This was operated in conjunction with an echo-integrator with output on a colour printer. This gave a depth-stratified quantitative estimate of acoustic reflectivity (S_a, $m^2 nm^{-2}$) along the survey path every 30 min.

To compare the plankton communities from the APF and the STC regions, cluster analysis was carried out using Jaccard similarity index (Jaccard 1902) coupled with pair-group single linkage (nearest neighbour clustering):

$$K_J = C/(A + B - C)$$

where K_J is the coefficient of similarity, A and B are the number of species in the respective areas and C is the number of species common to the 2 areas. Data from all samples collected at the 36 h stations were pooled for the purpose of this analysis.

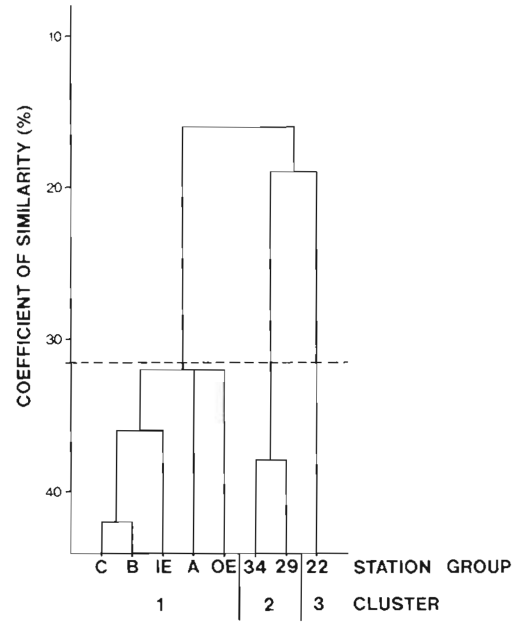

Fig. 2. Dendrogram based on similarity coefficients among RMT-8 samples according to macroplankton/micronekton species composition. A: STC Stn A; B: STC Stn B; C: STC Stn C; IE: inside warm-core eddy (Stns 43, 49, 75, 130 & 133); OE: outside warm-core eddy (Stns 53, 66, 124 & 127); 22: APF Stn 22/10; 29: APF Stns 29/2 to 29/6; 34: APF Stns 34/2 to 34/10

RESULTS

Composition, abundance and biomass

A total of 115 and 32 macrozooplankton and micronekton species were found in the epipelagic zone of the STC and APF, respectively (Table 1). The highest number of species (63) was recorded at Stn A, immediately north of the STC (winter), and the lowest (8) at Stn 22, immediately south of the APF (summer).

Selecting an arbitrary distance level of 31.5%, 3 clusters describing sample groups of similar geographical origin were obtained (Fig. 2). Cluster 1 covered the STC region, while Cluster 2 included the centre of the APF and the area immediately north of it. Cluster 3 contained only 1 station, located immediately south of the APF. Very low coefficients of similarity (0.02 to 0.16) were obtained when APF and STC regions were compared. However, within the APF region coefficients of similarity ranged from 0.11 to 0.38, and within the STC from 0.22 to 0.42 (Fig. 2).

In the APF region, tunicates and euphausiids dominated the catch and together accounted for 93.7% and 84.2% of total abundance and biomass, respectively (Table 2). Fishes constituted about 13% of the total biomass, although their contribution to total abundance was ≤1% (Table 2). At Stn 22 (Cluster 3) *Euphausia superba* was the most abundant species (Fig. 3C), with concentrations of 4.5 ind. m^{-2} and 475 mg dry wt m^{-2}. The most abundant species at Stns 29 & 34 (Cluster 2) tended to be *Salpa thompsoni*, which reached densities of up to 26.7 ind. m^{-2} and 325 mg dry wt m^{-2} (Stn 29, Fig. 3C). This species contributed more than 80% to the total abundance and biomass. The euphausiids *Euphausia vallentini* and *E. triacantha* were the next most abundant species in this zone (Fig. 3C). The nighttime sample of Stn 34 was dominated by myctophiids, which accounted for ca 71% of total biomass. The total macroplankton/micronekton abundance at the APF ranged from 0.3 to 29.9 ind. m^{-2}, with an average of 8.7 ind. m^{-2}. Total biomass was 2 to 495 mg dry wt m^{-2}, mean 184 mg m^{-2} (Fig. 3A, B, Table 2).

In the STC region (Cluster 1) tunicates, siphonophores, euphausiids and chaetognaths were the most abundant groups (Table 3, Fig. 4C). During daytime, about 90% of total biomass was accounted for by tunicates but, although their abundance increased at night, their contribution decreased to ca 50% due to the migrations of fish, decapods and euphausiids which made up 26, 10 and 8% of the total, respectively (Table 3).

Eight species were identified in the tunicate group. Of these, *Pyrosoma* sp. and *Iasis zonaria* were the most abundant and frequently encountered (Table 1). Doliolidae, which the hyperiid *Phronima sedentaria* uses as a hide, were the next most frequent group of tunicates. The dominant chaetognaths were *Sagitta gazellae*, *S. hexaptera* and *Eukrohnia hamata*. Within the siphonophore group, 17 species were identified but the bulk of their abundance was made up of *Chelophies appendiculata*, *Hippopodius hippopus* and *Lensia*

Table 1. Species composition and frequency of occurrence (%) of the macrozooplankton/micronekton in the RMT-8 samples collected during Voyages 70 and 72 aboard the SA 'Agulhas' The identification of species in brackets is not conclusive

Taxon	Subtropical Convergence region					Polar Front region		
	Inside eddy	Outside eddy	36 h stations A	B	C	36 h stations 22	29	34
Hydromedusae								
1. *Pegantha margaton*	–	–	25.0	–	–	–	–	–
2. *P. triloba*	–	–	12.5	14.3	16.7	–	–	–
3. *Pegantha* sp.	20.0	–	12.5	14.3	–	–	–	–
4. Hydromedusae gen. sp.	20.0	–	25.0	28.6	33.3	–	–	40.0
Scyphomedusae								
5. *Periphylla periphylla*	–	–	–	14.3	–	–	–	–
Siphonophora								
6. *Chelophyes appendiculata*	100.0	75.0	87.5	42.9	83.3	–	–	–
7. *Diphyes dispar*	20.0	–	–	–	–	–	–	–
8. *Diphyes (antarctica)*	–	–	37.5	–	–	+	33.3	–
9. *Muggiaea (atlantica)*	20.0	–	–	–	–	–	–	–
10. *Hippopodius hippopus*	20.0	–	62.5	14.3	16.7	–	–	–
11. *Hippopodius* sp.	–	–	12.5	–	–	–	–	–
12. *Marrus antarcticus*	–	–	12.5	–	–	–	–	–
13. *Marrus* sp.	–	25.0	–	–	–	–	–	–
14. *Eudoxoides spiralis*	40.0	–	12.5	14.3	16.7	–	–	–
15. *Agalma okeni*	–	–	62.5	–	–	–	–	–
16. *Ceratocymba sagittata*	–	–	50.0	–	–	–	–	–
17. *Ceratocymba (dentata)*	–	–	12.5	–	–	–	–	–
18. *Abilopsis (tetragona)*	20.0	–	12.5	–	–	–	–	–
19. *Lensia (hostile)*	–	50.0	–	100.0	100.0	–	–	–
20. *Melophysa (melo)*	–	–	–	14.3	–	–	–	–
21. *Vogtia* sp.	20.0	–	–	–	–	–	–	–
22. *Amphicaryon* sp.	–	–	12.5	–	–	–	–	–
23. Nectophora (undet.)	40.0	25.0	62.5	28.6	83.3	+	–	80.0
Ctenophora								
24. *Pleurobrachia pileus*	–	–	12.5	14.3	16.7	–	33.3	–
Polychaeta								
25. *Tomopteris* sp.	–	25.0	–	–	–	–	–	–
26. *T. carpenteri*	–	–	–	–	–	+	–	–
Euphausiacea								
27. *Euphausia similis*	–	50.0	–	57.3	83.3	–	–	–
28. *E. spinifera*	60.0	75.0	–	85.8	66.7	–	–	–
29. *E. recurva*	20.0	25.0	62.5	42.9	–	–	–	–
30. *E. superba*	–	–	–	–	–	+	–	–
31. *E. vallentini*	–	–	–	–	–	–	33.3	20.0
32. *E. triacantha*	–	–	–	–	–	–	100.0	60.0
33. *Euphausia* sp. (furcilia)	–	–	12.5	14.3	–	–	–	–
34. *Nematoscelis megalops*	80.0	75.0	12.5	71.5	66.7	–	–	–
35. *Thysanoessa gregaria*	–	–	–	14.3	–	–	–	–
36. *T. macrura*	–	–	–	–	–	–	33.3	–
37. *Thysanoessa* spp.	20.0	25.0	–	28.6	–	–	33.3	40.0
38. *Thysanopoda pectinata*	20.0	–	25.0	–	–	–	–	–
39. *Stylocheiron maximum*	–	–	25.0	–	–	–	–	–
Amphipoda								
40. *Phronima sedentaria*	20.0	25.0	–	28.6	16.7	–	–	40.0
41. *Tetrathyrus forcipatus*	–	25.0	–	–	–	–	–	–
42. *Rhabdosoma whitei*	–	–	12.5	–	–	–	–	–
43. *Streetsia mindanaonis*	–	–	12.5	–	–	–	–	–
44. *Platyscelis ovoides*	–	–	12.5	–	–	–	–	–
45. *Paraphronima crassipes*	–	–	–	14.3	–	–	–	–
46. *Parathemisto gaudichaudii*	–	–	–	–	–	–	66.7	100.0
47. *Primno macropa*	–	–	12.5	14.3	–	–	–	60.0
48. *Vibilia antarctica*	–	–	–	–	–	+	66.7	20.0
49. *Vibilia* sp.	–	–	12.5	28.6	–	–	–	–
50. *Cyllopus magellanicus*	–	–	–	–	–	+	66.7	–
51. *Lanceola syana*	–	–	–	–	–	–	–	20.0
52. Gammaridea gen. sp.	–	–	–	14.3	–	–	–	–
Decapoda								
53. *Hymenodora glacialis*	20.0	25.0	–	–	16.7	–	–	–
54. *Systelaspis debilis*	40.0	25.0	37.5	14.3	–	–	–	–
55. *Funchalia woodwardi*	–	–	12.5	–	–	–	–	–
56. *Acanthephyra pelagica*	20.0	–	–	28.6	16.7	–	–	–
57. *Pasiphaea* sp.	–	–	–	14.3	–	–	–	–
58. Sergestidae gen. sp.1	60.0	75.0	25.0	28.6	33.3	–	–	–
59. Sergestidae gen. sp.2	40.0	25.0	25.0	–	16.7	–	–	–
60. Brachiura (larvae)	60.0	–	–	14.3	–	–	–	–
61. Phyllosoma (Palinuroidea)	20.0	25.0	25.0	–	–	–	–	–
Stomatopoda								
62. Stomatopoda (larvae)	20.0	–	37.5	28.6	16.7	–	–	–
Pteropoda								
63. *Diacria quadridentata*	20.0	–	–	–	–	–	–	–
64. *Cymbulia sibogae*	40.0	25.0	–	14.3	16.7	–	–	–

Table 1 (continued)

Taxon	Subtropical Convergence region Inside eddy	Outside eddy	36 h stations A	B	C	Polar Front region 22	36 h stations 29	34
65. *Cymbulia* sp.	20.0	–	25.0	–	–	–	–	–
66. *Cresies virgula*	–	–	12.5	–	–	–	–	–
67. *Limacina retroversa*	–	–	12.5	–	–	–	–	–
68. *L. helicina*	–	–	–	85.8	16.7	–	–	–
69. *Clio pyramidata*	20.0	–	–	–	–	–	–	20.0
70. *Clio* sp.	–	–	12.5	–	–	–	–	–
71 *Spongiobranchia australis*	–	–	–	–	–	–	33.3	80.0
72. *Hyalocylis striata*	–	–	12.5	–	–	–	–	–
Heteropoda								
73. *Pterotrachea* sp.	–	50.0	62.5	14.3	–	–	–	–
Cephalopoda								
74. *Moroteuthis knipovichi*	–	–	–	–	16.7	–	–	20.0
75. *Histioteuthis marohista*	–	–	–	–	16.7	–	–	–
76. *H. atlantica*	–	–	–	–	16.7	–	–	–
77. Histioteuthidae (larva)	–	–	–	14.3	–	–	–	–
78. Teuthoidea (larva 1)	–	–	12.5	–	–	–	–	–
79. Teuthoidea (larva 2)	–	–	12.5	–	–	–	–	–
80. Teuthoidea gen. sp.	–	–	12.5	–	–	–	–	–
Chaetognatha								
81. *Sagitta gazellae*	40.0	75.0	37.5	85.8	100.0	–	100.0	100.0
82. *S. hexaptera*	60.0	–	25.0	14.3	–	–	–	–
83. *S. macrocephala*	40.0	–	37.5	–	–	–	–	–
84. *Sagitta* sp.	40.0	–	62.5	28.6	–	–	–	–
85. *Eukrohnia hamata*	40.0	–	62.5	42.9	33.3	–	33.3	80.0
86. *Eukrohnia* sp.	–	–	12.5	–	–	–	–	–
Tunicata								
87. *Pyrosoma* sp.	100.0	100.0	100.0	28.6	66.7	–	–	–
88. Doliolidae (tunica)	100.0	25.0	25.0	42.9	–	–	–	60.0
89. *Salpa fusiformis*	20.0	25.0	50.0	–	–	–	–	–
90. *S. thompsoni*	–	50.0	–	–	–	+	100.0	40.0
91. *Iasis zonaria*	40.0	25.0	50.0	28.6	16.7	–	–	–
92. *Ihlea magalhanica*	–	25.0	–	14.3	16.7	–	–	–
93. *Thalia orientalis*	20.0	–	–	–	–	–	–	–
94. Salpidae gen. sp.	–	25.0	–	–	–	–	–	–
95. *Oikopleura* sp.	20.0	–	–	–	–	–	–	–
Osteichthyes								
96. Anguilliformes (*Leptocephalus* sp.)	60.0	–	12.5	–	–	–	–	–
97. *Electrona subaspera*	–	25.0	–	–	–	–	–	–
98. *Electrona* sp.	–	–	–	–	–	+	–	–
99. *Diaphus taaningi*	20.0	75.0	12.5	14.3	33.3	–	–	–
100. *D. efflugens*	20.0	–	–	–	–	–	–	–
101. *D. lutkeni*?	–	–	25.0	–	–	–	–	–
102. *Diaphus* sp.	–	–	–	28.6	–	–	–	–
103. *Protomyctophum bolini*	–	–	–	–	–	–	33.3	20.0
104. *P. choriodon*	–	–	–	–	–	–	–	20.0
105. *P. luciferum*	–	25.0	–	–	–	–	33.3	–
106. *P. normani*	–	25.0	–	–	–	–	–	–
107. *Protomyctophum* sp.	–	–	12.5	28.6	50.0	–	66.7	20.0
108. *Krefftichthys anderssoni*	–	–	–	–	–	–	33.3	–
109. *Gymnoscopelus* sp.	20.0	25.0	–	14.3	–	–	–	20.0
110. *Benthosema suborbitale*	–	–	12.5	–	–	–	–	–
111. *Benthosema* sp.	–	–	–	–	16.7	–	–	–
112. *Hygophum hanseni*	–	25.0	–	–	–	–	–	–
113. *Lampadema* sp.	–	–	–	–	16.7	–	–	–
114. Myctophidae unknown	–	–	25.0	–	–	–	–	–
115. *Notolepis coatsi*	–	–	–	–	–	–	–	20.0
116. *Argyropelecus hemigymnus*	40.0	25.0	25.0	–	–	–	–	–
117. *A. aculeatus*	–	–	12.5	–	–	–	–	–
118. *Lobianchia dofleini*	–	50.0	–	–	–	–	–	–
119. *Luciosudis normani*	40.0	–	–	–	16.7	–	–	–
120. *Margerthia obtusirostra*	–	–	12.5	–	–	–	–	–
121. *Gonostoma elongatum*	20.0	–	–	–	–	–	–	–
122. *Anoplogaster cornuta*	–	–	12.5	–	–	–	–	–
123. *Indiacanthus atlanticus*	–	–	–	14.3	–	–	–	–
124. *Eustomias* sp.	20.0	–	–	–	–	–	–	–
125. *Sio nordenskjoldii*	20.0	–	–	–	–	–	–	–
126. *Scopelosaurus kreffti*?	–	–	–	–	16.7	–	–	–
127. *Astronesthes* sp.	–	–	–	–	–	–	–	20.0
128. *Chauliodus* sp.	–	25.0	–	–	16.7	–	–	–
129. *Ceratias* sp.	–	–	–	14.3	–	–	–	–
130. *Vincinguerria* sp.	40.0	–	–	–	33.3	–	–	–
131. *Bathylagus* sp.	20.0	–	–	14.3	–	–	–	–
132. Fish eggs	–	–	62.5	28.6	16.7	–	–	–
No. of samples	5	4	8	7	6	1	3	5

Table 2. Abundance and biomass of the major groups of the macroplankton/micronekton in the Antarctic Polar Front region during January–February 1993 (0 to 300 m)

Group	Abundance (ind. m^{-2} ± SD)	%	Biomass (mg dry wt m^{-2} ± SD)	%
Medusae	0.003 ± 0.006	<0.1	0.244 ± 0.485	0.1
Siphonophora	0.084 ± 0.119	1.0	0.633 ± 0.784	0.3
Ctenophora	0.003 ± 0.008	<0.1	0.467 ± 1.400	0.3
Polychaeta	0.006 ± 0.017	0.1	0.033 ± 0.033	<0.1
Euphausiacea	0.894 ± 1.506	10.2	60.660 ± 155.762	32.9
Amphipoda	0.250 ± 0.198	2.9	3.111 ± 3.642	1.7
Pteropoda	0.017 ± 0.022	0.2	0.389 ± 0.654	0.2
Cephalopoda	0.001 ± 0.004	<0.1	0.178 ± 0.533	0.1
Chaetognatha	0.132 ± 0.092	1.5	0.644 ± 0.787	0.3
Tunicata	7.293 ± 10.217	83.5	94.622 ± 136.076	51.3
Osteichthyes	0.052 ± 0.076	0.6	23.444 ± 39.984	12.7
Total	8.7 ± 10.6	100.0	184 ± 191	100.0

(hostile). Other common macroplankton were euphausiids, mostly *Nematoscelis megalops*, *E. spinifera*, *E. recurva* and *E. similis*, and decapod shrimps, mainly *Systelaspis debilis* and Sergestidae. Myctophiids consistently dominated the fish community at both fronts.

Total macroplankton abundance in the STC region varied from 0.2 to 6.9 ind. m^{-2} (average 1.6 ind. m^{-2}) during the daytime and from 1.3 to 10.6 ind. m^{-2} (average 4.2 ind. m^{-2}), during the nighttime (Table 3, Fig. 4). The total biomass range was 3 to 1227 mg dry wt m^{-2} (mean 101 mg m^{-2}) and 26 to 755 mg m^{-2} (mean 234 mg m^{-2}) during the day and night, respectively (Table 3, Fig. 4A, B).

Distribution

The spatial distribution of the macroplankton/micronekton at the APF was characterized by a sharp increase in the abundance of *Salpa thompsoni* (Fig. 3C) at the centre of the APF (Stn 29), compared to the stations located immediately north and south of the front, where abundance levels of tunicates were similar and relatively low (Fig. 3C). However, total biomass decreased regularly across the APF, moving from the south to the north of the front (Fig. 5A). This was due mainly to the disappearance of *Euphausia superba*, which constituted the bulk of the macroplankton at Stn 22 (Fig. 3C), south of the surface expression of the APF.

Sharp changes in abundance and biomass were also found along the transect crossing the STC (Fig. 5B). Total abundance decreased dramatically from north to south of the front and correlated positively with the drop in temperature but negatively with the increase in chlorophyll *a* concentration (Fig. 5B). The highest peaks in total biomass were observed in the centre of the STC and immediately south of it. No significant differences (*t*-test, $p > 0.1$) were observed in the levels of biomass and abundance between stations inside and outside the warm-core eddy (Fig. 4B). However, community structure within the eddy was different from that of surrounding waters. In particular, meroplank-

Table 3. Abundance and biomass of the major groups of the macroplankton/micronekton in the Subtropical Convergence region during June–July 1993 (0 to 300 m)

Group	Daytime				Nighttime			
	Abundance (ind. m^{-2} ± SD)	%	Biomass (mg dry wt m^{-2} ± SD)	%	Abundance (ind. m^{-2} ± SD)	%	Biomass (mg dry wt m^{-2} ± SD)	%
Medusae	0.036 ± 0.055	2.2	3.627 ± 0.269	3.6	0.051 ± 0.078	1.2	2.007 ± 4.040	0.9
Siphonophora	0.409 ± 0.378	24.5	1.386 ± 1.582	1.4	1.095 ± 1.282	26.3	3.487 ± 4.312	1.5
Ctenophora	0.008 ± 0.025	0.5	0.352 ± 0.933	0.3	0.002 ± 0.008	0.1	0.080 ± 0.309	<0.1
Polychaeta	–	–	–	–	0.002 ± 0.008	0.1	0.003 ± 0.010	<0.1
Euphausiacea	0.113 ± 0.129	6.9	0.663 ± 0.949	0.7	1.170 ± 1.042	28.1	18.960 ± 24.466	8.1
Amphipoda	0.008 ± 0.015	0.5	0.055 ± 0.140	<0.1	0.032 ± 0.053	0.8	0.703 ± 2.302	0.3
Decapoda	0.012 ± 0.026	0.7	0.647 ± 0.149	0.6	0.216 ± 0.179	5.2	22.127 ± 21.448	9.5
Stomatopoda	0.027 ± 0.044	1.6	0.493 ± 1.141	0.5	0.009 ± 0.019	0.2	0.093 ± 0.234	<0.1
Pteropoda	0.028 ± 0.034	1.7	0.204 ± 0.465	0.2	0.042 ± 0.071	1.0	1.137 ± 2.389	0.5
Heteropoda	0.006 ± 0.018	0.4	0.100 ± 0.314	0.1	0.018 ± 0.028	0.4	2.313 ± 6.882	1.0
Cephalopoda	0.009 ± 0.023	0.5	0.287 ± 0.759	0.3	0.012 ± 0.026	0.3	7.887 ± 25.626	3.4
Chaetognatha	0.211 ± 0.142	12.8	0.358 ± 0.390	0.4	0.172 ± 0.164	4.1	0.316 ± 0.453	0.1
Tunicata	0.698 ± 1.535	42.5	90.000 ± 313.45	89.5	1.188 ± 2.257	28.5	114.047 ± 175.64	48.8
Osteichthyes	0.079 ± 0.097	4.8	2.433 ± 2.975	2.4	0.153 ± 0.088	3.7	60.460 ± 76.613	25.9
Total	1.6 ± 1.7	100.0	101 ± 312	100.0	4.2 ± 3.2	100.0	234 ± 224	100.0

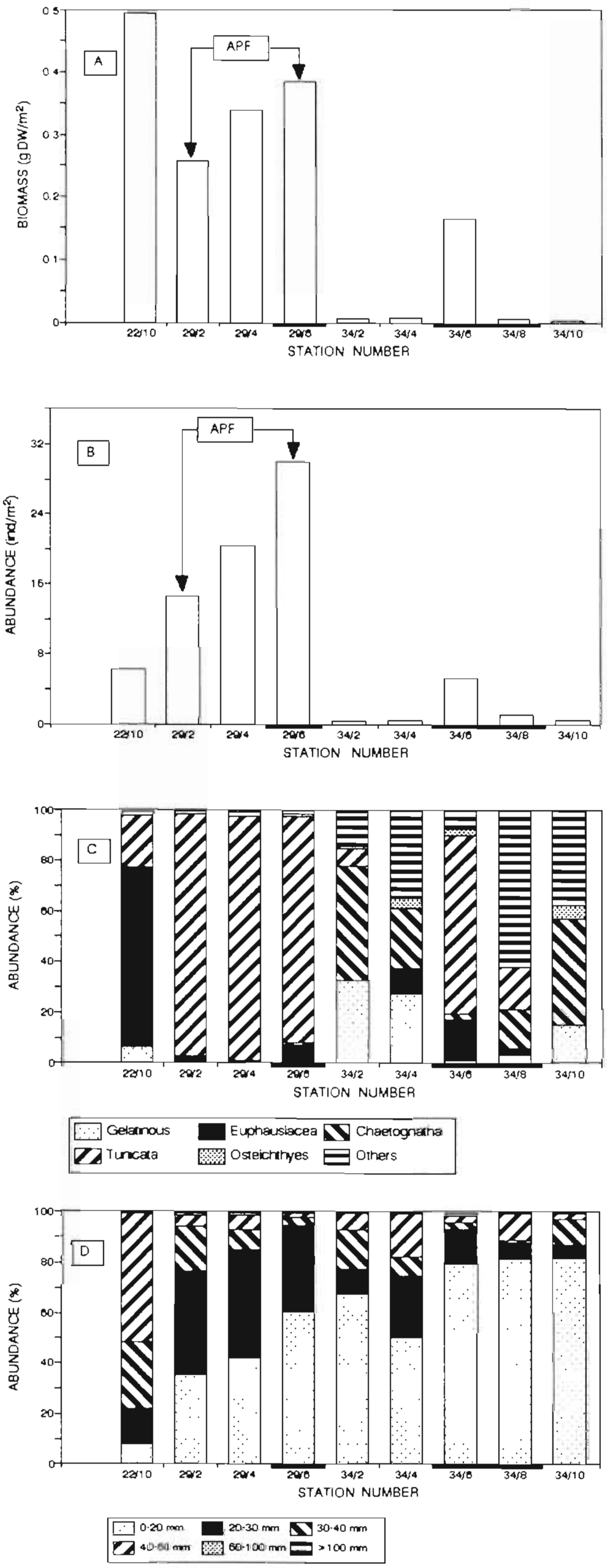

Fig. 3. Total biomass (A), abundance (B), percentage taxonomic (C) and size (D) composition of the macroplankton/micronekton community of the APF zone during January–February 1993. Period of darkness is indicated by thickening of the horizontal axis

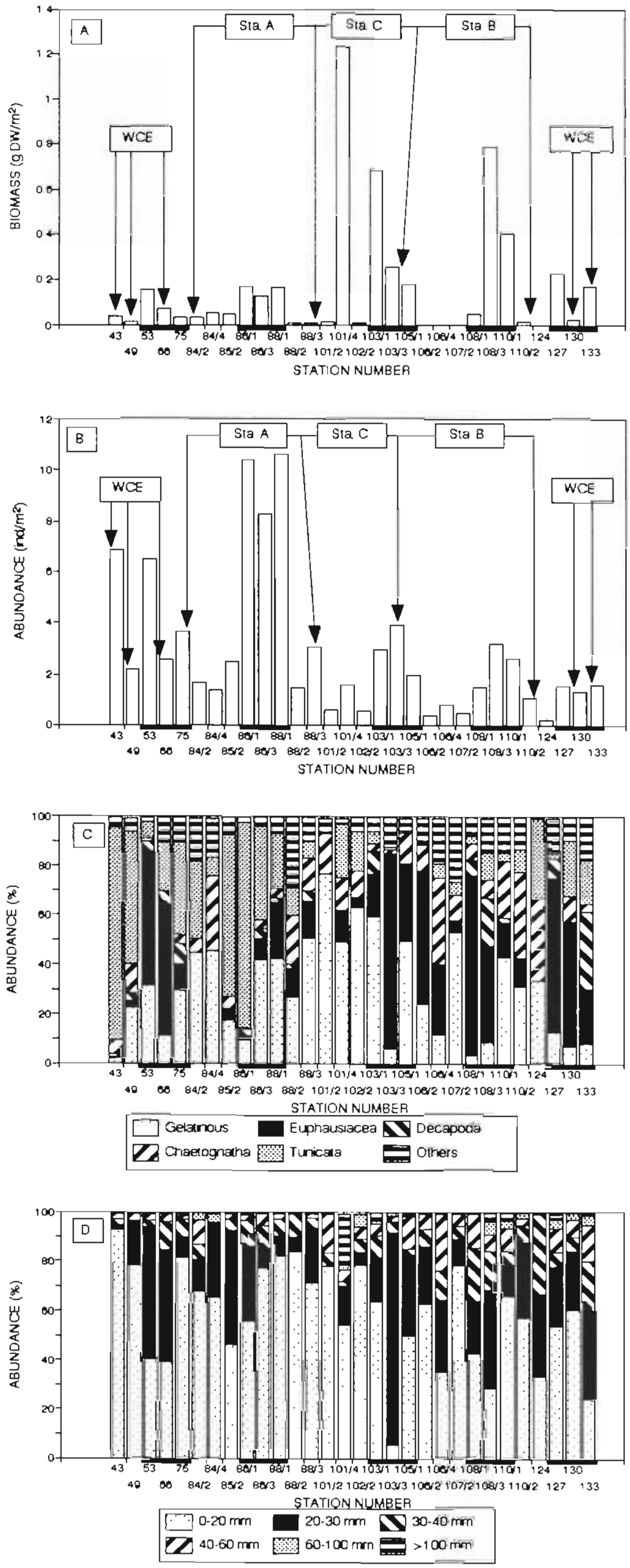

Fig. 4. Total biomass (A), abundance (B), percentage taxonomic (C) and size (D) composition of the macroplankton/micronekton community of the STC zone during June–July 1993. Period of darkness is indicated by thickening of the horizontal axis

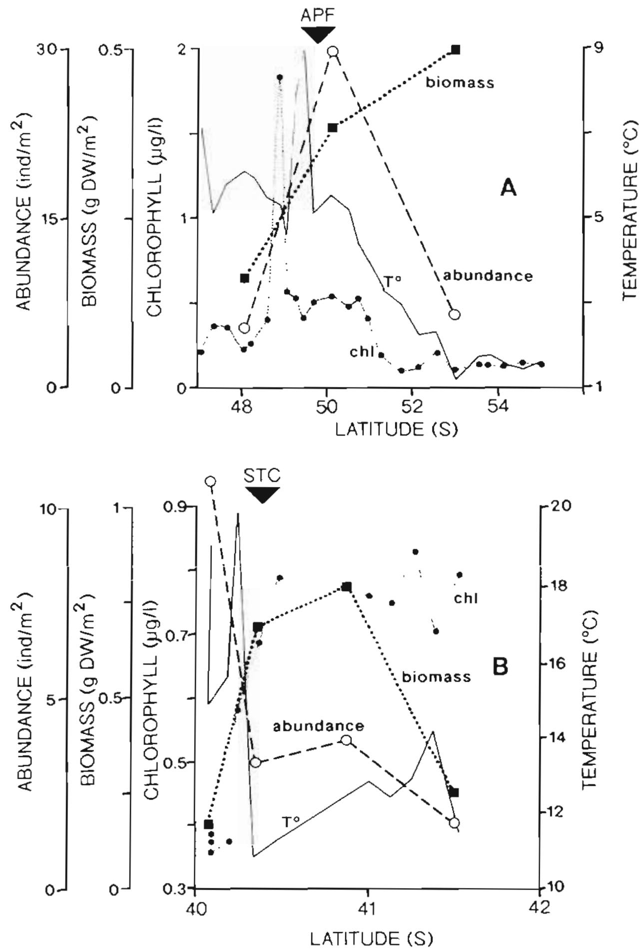

Fig. 5. Changes in surface chlorophyll *a* concentration (chl), surface temperature (T°), macroplankton/micronekton abundance and biomass across (A) the APF and (B) the STC zones

tonic larvae of subtropical origin (larvae of Stomatopoda, Brachiura and Phyllosoma) were common inside the eddy but completely absent outside (Table 1).

Size composition

Within the APF zone 5 to 35 mm tunicates made up most of the local stock. There was also a minor peak in abundance of animals in the size range of 40 to 60 mm largely due to high densities of *Euphasuia superba* (Fig. 6A, B). The size distribution of total biomass exhibited 2 modal peaks. The first in the 20 to 30 mm range was due to tunicates and euphausiids and the second, 40 to 60 mm, was due mostly to euphausiids. The 60 to 80 mm size group was dominated by myctophiid fish, large tunicates and chaetognaths (Fig. 6C, D). Stn 22 (Cluster 3) was dominated by euphausiids with length of 40 to 60 mm which accounted for about 80% of the total abundance (Fig. 3C, D). On the other hand, Stns 29 & 34 (Cluster 2) were dominated by smaller organisms, of lengths ranging from 5 to 30 mm (Figs. 3D & 6A).

In the STC region, the 0 to 20 mm size fraction accounted for most of the daytime abundance. A significant increase in the proportion of 20 to 40 mm animals (up to 90% of total abundance at Stn 103/3; Fig. 4D) was observed in nighttime samples. The distribution of size versus abundance shows a predominance of taxonomic groups of small size (5 to 30 mm): siphonophores, tunicates and euphausiids. The contribution of chaetognaths was highest in the 40 to 50 mm size range. The relative proportion of fishes increased substantially above the length of 60 mm (Fig. 7A, B). The tail of the size distribution diagram is due to large *Pyrosoma* sp. (length up to 100 to 300 mm) and deep water fish of the Stomiidae. The distribution of size versus biomass exhibits 3 peaks and is skewed to the right (Fig. 7C). The first peak (20 to 30 mm) is mostly due to euphausiids (*Euphausia spinifera* and *E. similis*), the second (40 to 80 mm) to decapods and chaetognaths, while the third peak (80 to 100 mm) is composed of a mixture of myctophiid fishes and decapods. As for the abundance diagram, about 80% of the total biomass in the tail size classes is due to large colonial *Pyrosoma* sp. (Fig. 7C, D).

Vertical migrations

The main taxonomic groups of macroplankton and micronekton (i.e. euphausiids, decapods and fish) showed a clear pattern of vertical migration in both frontal regions (Figs. 3 & 4), with significant differences between average abundance and biomass in daytime and nighttime samples (*t*-test, $p < 0.001$). Total macroplankton/micronekton abundance was also significantly different (*t*-test, $p < 0.05$) between daytime and nighttime samples. However, biomass differences were not significant (*t*-test, $p > 0.1$). Hydroacoustic data show that macroplankton/micronekton backscattering increased in nearsurface waters (0 to 100 m) at night at all stations in both regions. During the day, however, maximum backscattering intensity was found between 100 and 250 m, and often even deeper (Fig. 8).

DISCUSSION

Recent investigations have shown that frontal regions contribute substantially to the total productivity of the Southern Ocean (Allanson et al. 1981, Lutjeharms et al. 1985, El-Sayed 1988, Laubscher et al. 1993). Enhancements in the activity and abundance of

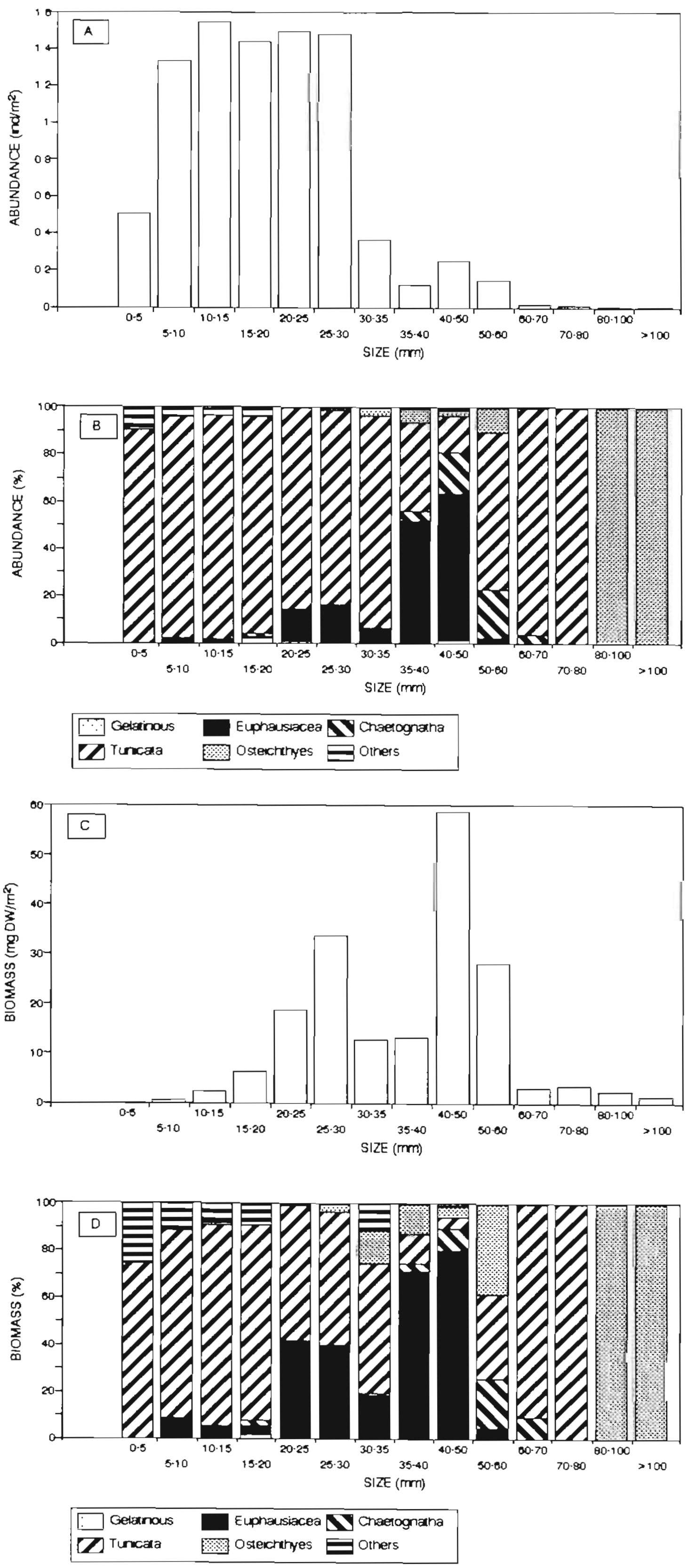

Fig. 6. Total and percentage distribution of macroplankton/micronekton abundance (A & B) and biomass (C & D) versus size at the APF zone during January–February 1993

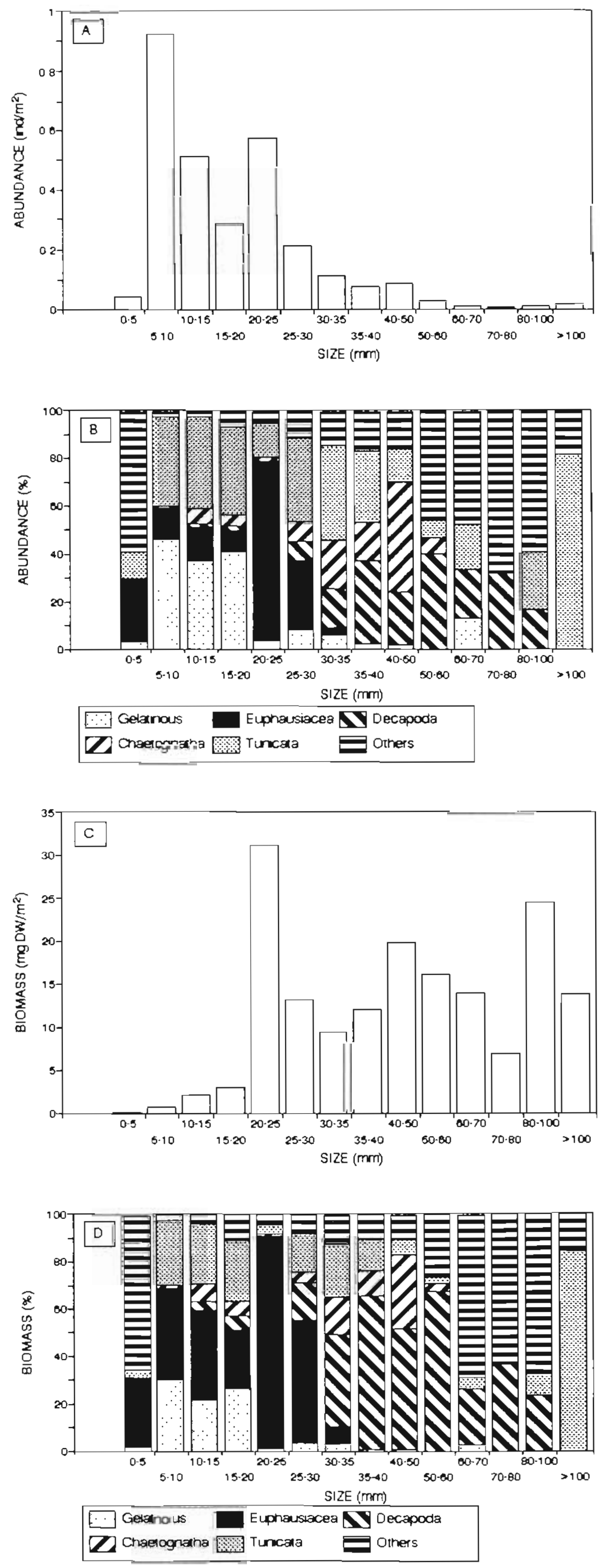

Fig. 7. Total and percentage distribution of macroplankton/micronekton abundance (A & B) and biomass (C & D) versus size at the STC zone during June–July 1993

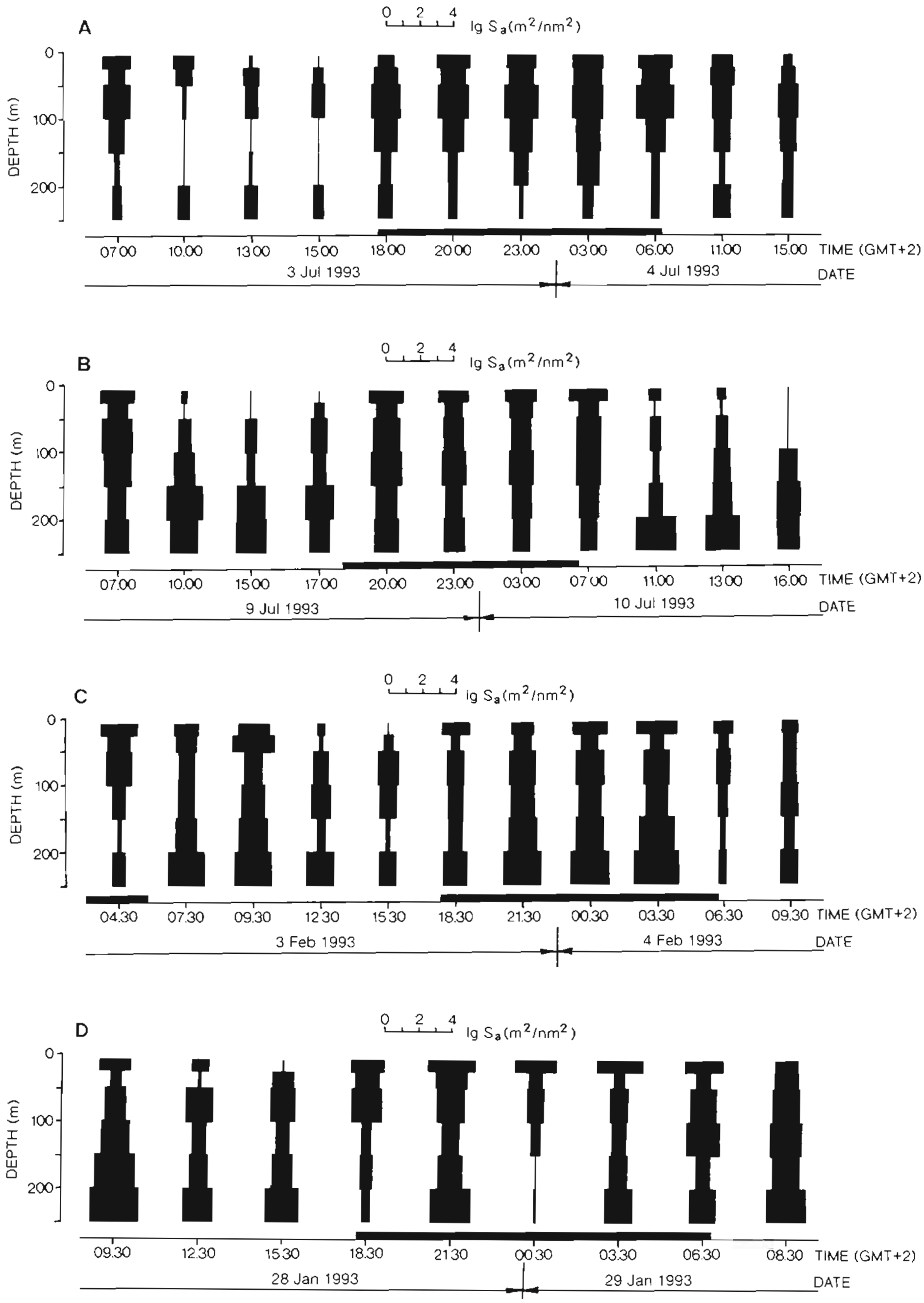

Fig. 8. Vertical distribution of planktonic backscattering intensity (120 kHz) at the STC (A & B) and the APF (C & D) zones. A: STC Stn A; B: STC Stn B; C: APF Stn 34; D: APF Stn 22. Period of darkness is indicated by thickening of the horizontal axis

birds and mammals have often been observed in the proximity of Southern Ocean fronts in conjunction with an increase in primary production (Shuntov et al. 1982, Batytskaja & Shurunov 1983, Abrams 1985, Cockcroft et al. 1990). The macroplankton and the micronekton are the intermediaries which channel primary and secondary productivity to the highest trophic levels. These components occupy, therefore, a key position in the Southern Ocean carbon cycle and reliable estimates of the efficiency of the biological pump can be obtained only after their community structure is identified and their stocks and consumption rates are correctly assessed.

The species richness (115) observed in the STC zone during the winter cruise was much higher than the value of 56 previously recorded in the Gough Island region (Miller 1982b), which lies just south of the STC. In our study the number of species was actually closer to the values usually observed at higher latitudes, in the vicinity of the Antarctic continent, where species richness varies between ca 60 and 140, depending on the sector considered (Mackintosh 1934, Hardy & Gunther 1935, Dolzhenkov 1975, Piatkowski 1987, Pakhomov 1991, Hosie 1993). A total of 32 species of macroplankton/micronekton were found in the APF zone during the summer cruise. Species richness at the APF is well within the range reported in the literature for this region. Specifically, 41, 47 and 30 species were reported for the areas around the Prince Edward Archipelago (Miller 1982a, Boden & Parker 1986), the Kerguelen Archipelago (Koubbi 1993, Pakhomov 1993a, Piatkowski 1993) and the open ocean at 57° S in the Atlantic sector (Pakhomov 1991), respectively. Most of the species found during both surveys are common and exhibit circumpolar distribution in the Southern Ocean (Baker 1954).

The STC and the APF have some environmental features in common and, in particular, they represent the 2 main sites where dense, cold surface waters sink under warmer, less dense waters (Deacon 1982, Lutjeharms 1985). They are also regarded as strong biogeographical boundaries, demarcating the subtropical, Subantarctic and Antarctic pelagic realms of the Southern Ocean (Rustad 1930, Naumov et al. 1962, Dolzhenkov 1982). The taxonomic analysis of our samples confirms the marked differences between the macroplankton/micronekton communities of the STC and the APF regions. All stations from the STC survey were included in the first group of the cluster analysis (Fig. 2). The highest species similarity was found between stations situated in the centre of the STC and immediately south of it. On the other hand, the lowest coefficient of similarity was obtained between the station located to the north of the STC and outside the warm-core eddy. This is a well-known effect due to a drastic reduction in the number of subtropical species observed at the edge of warm-core eddies (Angel & Fasham 1983, Davis & Wiebe 1985). Thus, although the STC is a strong biogeographical front, eddy shedding results in many tropical and subtropical species penetrating through the STC in the Subantarctic region (Lutjeharms 1988). For example, the subtropical hyperiid *Phronima sedentaria*, which is usually not encountered south of the STC (Vinogradov et al. 1982), was found during this survey, as far south as the northern border of the APF. However it is likely to be a zone where these species are not able to reproduce successfully.

The second cluster included mainly euphausiids and salps found north of the APF. The euphausiid *Euphausia triacantha* is a common species in the southern part of the Subantarctic zone (Lomakina 1964) and is most concentrated at the APF. On the other hand, the APF zone represents the southern boundary of distribution of the subantarctic krill *E. vallentini* (Lomakina 1964). Indeed, both of these euphausiids were observed in the middle of the APF and immediately north of it. The salp *Salpa thompsoni* was also found in abundance in our samples from the APF. This species is widely distributed in the Subantarctic and Antarctic zones (Foxton 1966) and appears to occur as far south as the pack ice (Piatkowski 1987, Lancraft et al. 1991, Siegel et al. 1992). During this survey, the abundance of *S. thompsoni* decreased dramatically south of the APF, with maximum concentrations coinciding with the increase in surface temperature, chlorophyll biomass and primary production (R. Laubscher unpubl.) observed in the middle of the APF.

The third grouping of the cluster analysis was dominated by the Antarctic krill *Euphausia superba* which exhibits a distribution range limited to the north by the surface expression of the APF (Marr 1962, Lomakina 1964, Mackintosh 1973, Grachev 1991). It was found only at Stn 22, immediately to the south of the APF. Also, the macroplankton composition at this station was very similar to the typical oceanic community described for the Weddell Sea and the Antarctic Peninsula region (Piatkowski 1987, Siegel & Piatkowski 1990, Boysen-Ennen et al. 1991). Our results on the taxonomic composition and distribution of the macroplankton/micronekton support, therefore, the recent conclusions of Lancraft et al. (1991) and Siegel et al. (1992) that *E. superba* is most abundant in the Scotia, Weddell Seas and in the proximity of the APF, while *Salpa thompsoni* is most abundant to the north, in open ocean waters. Salps, with copepods, also dominate the total zooplankton stock of the Subantarctic zone and Polar Frontal Zone (PFZ) (Foxton 1966, Maruyama et al. 1982, Voronina 1984, Grachev 1991).

Although the APF and the STC zones were investigated in different seasons, the mean abundance and biomass of macroplankton/micronekton were very similar in the 2 regions. Biomass levels recorded at the STC and APF during this study are comparable to the mean values usually found in the open Subantarctic and PFZ of the Southern Ocean (Tables 2, 3 & 4). Within the 2 fronts, maximum biomass levels were higher than in the interfrontal zones. However, these levels were lower than those reported for the same fronts in other studies (Table 4). Also, south of the APF biomass levels were higher than those generally observed in subantarctic waters, with the exception of island shelves where levels are comparable to those found at the oceanic fronts (Table 4).

The STC region exhibited considerable fluctuations in the abundance and biomass levels of macroplankton/micronekton which appeared to covary with the spatial distribution of the phytoplankton stock in the area. Within the APF region, only total abundance matched the distribution of chlorophyll and primary production, while biomass increased throughout the APF zone, from north to south.

Table 4. Mean macrozooplankton biomass in different areas of the Southern Ocean

Source	Region, season, layer	Mean biomass (g dry wt m^{-2})
	Subantarctic, open waters	
Hopkins (1971)	Subantarctic, annual, 0-1000 m	0.805 [a]
	Antarctic Convergence, annual, 0-1000 m	0.885 [a]
Dolzhenkov (1975)	Pacific Ocean, summer, 0-100 m	0.057
Maruyama et al. (1982)	Pacific Ocean, Subantarctic front, summer, 0-300 m	1.304
Muravjova (1982)	Pacific Ocean, mountain range Gerakl, winter, 0-100 m	0.012
	Pacific Ocean, mountain range Gerakl, summer, 0-100 m	0.024
Barchatov (1985)	Pacific Ocean, summer, 0-200 m	0.131
	Subtropical Convergence, summer, 0-200 m	4.4 (max)
	Subantarctic, around islands	
Miller (1982a)	Prince Edward Islands, winter, 0-50 m	0.007
Miller (1982b)	Gough Island, early summer, 0-50 m	0.013
Perissinotto & McQuaid (1992)	Prince Edward Islands, shelf, summer, 0-300 m	2.62-2.86
Pakhomov (1993a)	Kerguelen Archipelago, summer 1988, 0-200 m	0.498
Semelkina (1993)	Kerguelen Archipelago, autumn 1987, 0-500 m	1.155 [b]
	winter 1987, 0-500 m	0.156 [b]
	summer 1988, 0-500 m	0.558 [b]
	Antarctic, south of the Antarctic Polar Front	
Hopkins (1987)	McMurdo Sound, summer, 0-800 m	0.21-0.8
Hopkins et al. (1989)	Scotia Sea (AMERIEZ), ice edge, winter, 0-1000 m	0.245
Lancraft et al. (1989)	Scotia Sea (AMERIEZ), open water, winter, 0-1000 m	2.4-3.1
Boysen-Ennen et al. (1991)	Weddell Sea, summer, 0-300 m	1.2-3.4
Lancraft et al. (1991)	Scotia Sea (AMERIEZ), open water, winter, 0-1000 m	2.978
Pakhomov (1991)	57° 00' S, 20° 00' W, summer, 0-150 (200) m	0.023-1.32
Siegel et al. (1992)	Scotia Sea (EPOS), winter, 0-60 m	0.076-0.435
Pakhomov (1993b)	Indian Ocean, Ob & Lena banks, summer, 0-200 m	0.442
	Indian Ocean, Ob & Lena banks, spring, 0-500 m	0.170 [c]

[a] From vertical tows (copepods excluded)
[b] From vertical tows (euphausiids & amphipods only)
[c] From vertical tows (*Salpa thompsoni* only)

Within the Atlantic sector of the Southern Ocean, immediately south of the APF region, the macroplankton/micronekton biomass is generally dominated by the large stock of *Euphausia superba* (Marr 1962, Mackintosh 1973). During our survey, no RMT-8 tows were made south of Stn 22, at the southern edge of the APF. However, according to the results of Bongo net tows, which will be presented elsewhere, the biomass of *Euphausia superba* decreased dramatically south of this station. Thus, it is likely that the total macroplankton/micronekton biomass followed the same pattern, showing enhanced levels only in close proximity to the APF and decreasing sharply south of it.

It must be stressed that while the seasonal influence on the productivity of the region of the APF is very marked (Voronina 1984, El-Sayed 1988, Comiso et al. 1993, Semelkina 1993), the STC is relatively uniform throughout the year. At the primary trophic levels in particular, the area of the STC exhibits little variation in the phytoplankton stock in the different seasons (Allanson et al. 1985, Comiso et al. 1993, Weeks & Shillington 1994). Thus, while macroplankton/micronekton assemblages at the APF are expected to differ substantially, both qualitatively and quantitatively, between winter and summer, it is likely that they change little at the STC during the annual cycle.

The most abundant macroplankton/micronekton feeding groups in both frontal regions were herbivorous tunicates and euphausiids. In the STC region, carnivorous siphonophores and chaetognaths constituted the second largest proportion. In terms of biomass, tunicates, euphausiids, decapods (STC only) and fish dominated the stock. The first 3 groups are generally regarded as dominant throughout the Southern Ocean (Maruyama et al. 1982, Miller 1982a, b, Piatkowski 1987, Pakhomov 1989, Lancraft et al. 1991, Siegel et al. 1992). Fishes, however, are mostly represented by the family Myctophidae and are most densely concentrated between the STC and the APF, particularly in the area of the Subantarctic Front (Chindonova 1987, Zemsky 1987, Maslennikov et al. 1990). In this zone, mesopelagic myctophiids may reach biomass levels of up to 10 to 11.3 g dry wt m^{-2}, and estimates of mean biomass are in the range of 1.3 to 2.5 g dry wt m^{-2} (Linkowski 1983, Zemsky 1987). Similar values, ca 0.7 to 11.0 g dry wt m^{-2}, have also been observed in the marginal ice zone (Lancraft et al. 1989). Our estimates of myctophiid biomass are significantly lower than these values. In the STC region, average nighttime biomass was 0.06 g dry wt m^{-2} (max 0.302 g m^{-2}), while at the APF this reached a maximum of 0.117 g m^{-2}. This discrepancy in the biomass levels of myctophiids between our study and others is probably due to the fact that only the 0 to 300 m upper layer was sampled during our survey. Previous estimations have been made using data from much deeper sampling depths, and often from areas with extremely high aggregations of mesopelagic fish. Our data on myctophiid biomass are, therefore, only partly comparable with estimates from other studies.

The macroplankton/micronekton size composition was also similar for both the APF and the STC regions. Both fronts were dominated by mid-size opportunist filter-feeders, such as tunicates and euphausiids, probably as a result of the high primary productivity rates of these regions. The carnivore component was represented by small siphonophores and larger chaetognaths, decapods and myctophiids (vertical migrators).

Grachev (1991) has recently shown that the general size structure of the Southern Ocean zooplankton community changes dramatically moving along a north-south transect. Particularly, in the APF region the proportion of macroplankton/micronekton decreases sharply, while the total biomass does not change significantly due to a parallel increase in mesoplankton biomass. Boysen-Ennen et al. (1991) have shown that the macroplankton community of the Weddell Sea is dominated by 5 to 10 mm sized salps and 20 to 40 mm euphausiids. Our data are consistent with these results and it is, therefore, possible that the same size classes dominate through much of the Southern Ocean.

Most of the groups of macroplankton/micronekton of the APF and the STC undergo diurnal vertical migrations. This feature may play an important role by effectively removing a major portion of the photosynthetically fixed CO_2 from surface to deep water through nighttime grazing at the surface and the production of faecal pellets below the euphotic zone during daytime. On the other hand, micronektonic fishes, decapods, cephalopods and euphausiids are effectively consumed by marine birds and mammals (Ainley et al. 1988, Huntley et al. 1991, Hopkins et al. 1993). Therefore, the APF and especially the STC region may promote, through their high macroplankton/micronekton biomass, an increase in the abundance of the top predators and, consequently expand the carbon flow through the trophic pyramid. This would lead to increased respiratory losses of CO_2 to the atmosphere, thereby diminishing the efficiency of the biological pump (Huntley et al. 1991).

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