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A quantitative scuba-diving survey of the sublittoral macrobenthos at subantarctic Marion Island

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Summary. A SCUBA-diving survey of the macrobenthos of hard substrata in the sublittoral zone at subantarctic Marion Island was conducted during March and April 1988. Dense beds (12 $kg\,m^{-2}$) of the kelp *Macrocystis laevis* occur in depths > 5 m. *Durvillaea antarctica* is found along the infralittoral fringe and *Desmarestia rossi* and *Durvillaea* sp. occur in a narrow zone from 3 m–6 m. Under-storey algae (chiefly rhodophytes) tend to decrease in biomass with depth, with mean values of 1.57 $kg\,m^{-2}$ at 5 m, 0.75 $kg\,m^{-2}$ at 10 m and 0.49 $kg\,m^{-2}$ at 15 m. Encrusting coralline algae are particularly abundant in shallow areas ($\bar{x} = 0.92$ $kg\,m^{-2}$) but are insignificant in deeper areas. Total biomass of macrozoobenthos increased with depth with mean values of 0.12 $kg\,m^{-2}$ at 5 m, 0.34 $kg\,m^{-2}$ at 10 m and 0.46 $kg\,m^{-2}$ at 15 m. Polychaetes, crustaceans, echinoderms, molluscs, sponges and bryozoans dominated the macrozoobenthos in terms of biomass. Approximately 200 species of macrobenthic animals were recorded and numerically, polychaetes, crustaceans, molluscs, nematodes and echinoderms dominated. The sublittoral benthos at Marion Island is compared with that occurring at other subantarctic and Antarctic islands, in particular, the Kerguelen Island group. Zoogeographic trends and the possible effects of nutrient input from seabird guano are briefly discussed.

Introduction

Subantarctic Marion Island is located at 46°54′S 37°45′E adjacent to Prince Edward Island in the Southern Ocean. The nearest mainland, the coast of South Africa, is situated 2000 km to the north west, and the Crozet Island group lies some 925 km to the east.

Marion Island has a land area of 290 km^2 and a coastline of about 70 km. The coast consists chiefly of cliffs and rocky platforms although there are several boulder beaches and a few black volcanic sand beaches. Swell height, particularly on the western coast of the island, is usually large because of exposure to the full force of the "roaring forties" but even during spring tides the tidal range is < 1 m. Sea temperature ranges from 2.8°–7°C (Fuller 1967). Because of its isolated position and recent volcanic origin 276 000 years ago (McDougal 1971) the marine biota associated with the island is of particular interest.

Visits by the Challenger expedition in 1873 and the Discovery II expedition in 1935 provided the first scientific records of the benthos and fishes from Marion Island. A preliminary account of the littoral ecology was given by Fuller (1967) and was followed by an investigation of zonation patterns and species composition of littoral benthos by De Villiers (1976). Blankley (1982) and Blankley and Grindley (1985) studied trophic relationships in the littoral zone and Haxen and Grindley (1985) assessed production of the kelp *Durvillaea antarctica* which occurs in the infralittoral zone. Research in the sublittoral zone around Marion and Prince Edward Islands commenced in 1982 and during regular research cruises the benthos has been sampled by dredging and remote controlled underwater photography (Branch et al., in preparation). The macrobenthos of the shallow sublittoral zone (< 20 m) could not, however, be investigated by these techniques and in March and April 1988 a team of SCUBA divers visited Marion Island with the objective of determining the abundance and biomass of the seaweeds and animals occurring on hard substrata in this zone.

Materials and methods

The macrobenthos was sampled at three transect sites along the eastern coast of Marion Island, namely Bullard's Bay, Trypot Point and Transvaal Cove (Fig. 1). Bullard's Bay is situated about two kilometres south-west of East Cape and is fringed by a boulder beach and a rocky platform. A large colony (200 000 pairs) of macaroni penguins lives on the shore surrounding the bay and from this rookery there is considerable run-off of guano into the sea. The Trypot Point sampling site is situated two kilometres north-west of East Cape where high cliffs abutt the sea. The Transvaal Cove

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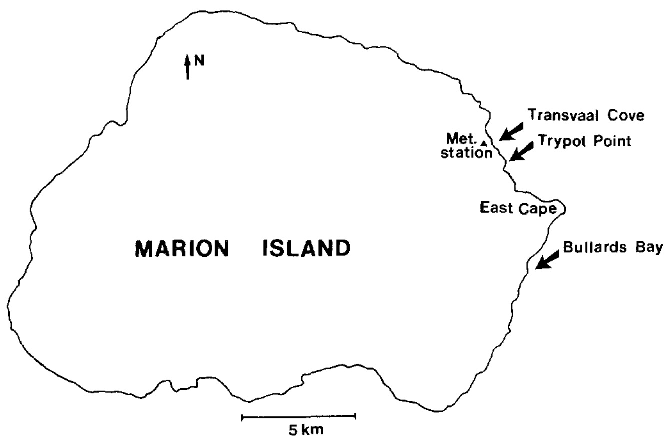

Fig. 1. Map of Marion Island showing the locations of the three study sites

sampling area extended offshore from the boulder beach adjacent to the meteorological station on the island.

At each of these sites the macrobenthos was collected from four replicate 0.1 m^2 quadrats at depths of 5 m, 10 m and 15 m. At these depths the substratum is dominated by a rocky bottom. Using paint scrapers, pairs of divers cleared the benthos within each quadrat from the substratum into 1 mm mesh collecting bags. The samples were preserved in 10% formalin and later washed through a 1 mm screen to remove sand and sorted into major taxa under a dissecting microscope. With the aid of keys to the benthos of Marion Island (Arnaud and Branch 1992; Branch et al. 1992a, b, in preparation) the majority of macrozoobenthic species occurring in the samples were identified. The total number of specimens of each species was counted and expressed as number m^{-2}. Wet mass m^{-2} was determined for each major taxon by weighing all the specimens in each sample. Dry mass was not determined because the material was required for further taxonomic analysis. Individual species are not listed in this paper but they are given together with their habitats and depth ranges in the above mentioned keys.

Holdfast and stipe numbers of the kelp *Macrocystis laevis* were counted in replicate 16 m^2 quadrats at 10 m depth at the three sites and biomass m^{-2} calculated from the mean mass of a sample of whole kelp plants removed from the water and weighed (see Attwood et al. 1991). Counts were also made of all large starfish and octopus occurring in these 16 m^2 quadrats. Numbers of *Durvillaea* sp. stipes occurring in two replicate 16 m^2 quadrats at 3–4 m depth were counted at each of the three sites and biomass m^{-2} determined from the mean mass of a sample of 11 stipes. The biomass of *Desmarestia rossi* m^{-2} was determined by clearing three replicate 0.25 m^2 quadrats at 3–4 m depth at the three sites and weighing all the *D. rossi* plants in the sample. Dry masses for *D. rossi* and *Durvillaea* sp. were determined by drying samples in an oven for 48 h at 70 °C.

Results

The mean total biomass of macrobenthos (excluding canopy-forming algae) at different depths at the three study sites at Marion Island is given in Table 1 and ranged from 0.7 kg m^{-2} to 3.9 kg m^{-2}. In general, biomass of algae decreased with depth whereas biomass of zoobenthos increased with depth.

Algae

Distinct zonation of algae with depth was evident in the shallow sublittoral zone. At the infralittoral fringe the kelp *Durvillaea antarctica* occurs in a narrow band. Haxen and Grindley (1985) recorded extremely high mean values of 28 kg to 161 kg wet mass m^{-2} for this kelp, highest values occurring at sheltered sites. Encrusting coralline algae cover the rocks and boulders in the shallower parts of the sublittoral zone. At 5 m depth mean biomass m^{-2} of encrusting corallines varied from 264 g at Transvaal Cove to 1699 g at Bullard's Bay but decreased markedly with depth at all three sites (Table 1). A narrow zone from 3–6 depth is dominated by two algae, the large bushy phaeophyte, *Desmarestia rossi* and the kelp *Durvillaea* sp. The latter has previously been termed *D. willana* (Attwood et al. 1991) but there is doubt about its identity. C. Hay (personal communication) suggests that it may be a subtidal variety of *D. antarctica* similar to that recorded by Klemm and Hallam (1988) at Macquarie Island. Morphologically, it is very different from the intertidal *D. antarctica* at Marion Island and we refer to it as *Durvillaea* sp. to distinguish it. Biomass of *D. rossi* and *Durvillaea* sp. was high in this zone reaching peak values of 18.1 kg and

Table 1. Mean biomass in g wet mass m^{-2} (with SE) of macrobenthos (excluding *M. laevis*) in the shallow sublittoral zone at Marion Island

	Bullard's Bay	Trypot Point	Transvaal Cove
5 m depth			
Coralline algae	1 699.25 (471.05)	795.88 (600.58)	264.28 (190.79)
Other algae	2 113.63 (554.47)	1 832.00 (451.73)	368.43 (188.07)
Zoobenthos	177.93 (41.01)	67.54 (23.53)	127.48 (19.39)
Total	3 990.81 (960.50)	2 695.42 (460.59)	760.19 (227.13)
10 m depth			
Coralline algae	132.00 (32.95)	64.38 (12.37)	4.18 (2.33)
Other algae	845.38 (219.04)	905.37 (301.19)	499.80 (70.55)
Zoobenthos	345.15 (60.34)	309.11 (46.40)	361.18 (5.84)
Total	1 322.53 (198.07)	1 278.86 (253.47)	865.16 (58.71)
15 m depth			
Coralline algae	0.13 (0.13)	0.88 (0.71)	0.00 (0.00)
Other algae	674.58 (85.73)	128.88 (65.520)	663.10 (290.53)
Zoobenthos	321.44 (32.18)	598.24 (136.56)	455.25 (46.01)
Total	996.15 (69.71)	727.96 (167.71)	1 118.36 (284.39)

Table 2. Biomass (g) of the phaeophytes *Desmarestia rossi* and *Durvillaea* sp. from 3–4 m depth at Marion Island

	No. of quadrats	Mean wet mass m^{-2}	S. E.	Mean dry mass m^{-2}	S. E.
Desmarestia rossi					
Bullards Bay	3	12973	3282	2799	613
Trypot Point	3	18133	4575	3468	1093
Transvaal Cove	3	14333	2007	2716	759
Durvillaea sp.					
Bullards Bay	2	3234	66	550	10
Trypot Point	2	8869	721	1505	122
Transvaal Cove	2	5001	361	848	62

8.8 kg m^{-2} respectively (Table 2). These values are equivalent to dry masses of 3.5 kg and 1.5 kg m^{-2}. Dense beds of the kelp *Macrocystis laevis* occur along the eastern coast of Marion Island in depths from about 5–20 m. Total area of these kelp beds was 5.5 km^2 and there were on average 0.88 holdfasts per m^{-2} (Attwood et al. 1991). The mean wet mass of a *Macrocystis laevis* plant (holdfast, stipes and fronds) was 13.2 kg, thus giving a mean biomass for this kelp of 11.6 kg m^{-2}. In terms of dry mass this equates to 1.3 kg m^{-2}.

Under-storey algae (chiefly rhodophytes) also contributed a significant proportion of the total algal biomass in the shallow sublittoral. At 5 m depth at Bullard's Bay and Trypot Point these algae were particularly abundant, reaching about 2 kg m^{-2} (Table 1). The dominant rhodophyte species were *Schizoseris* sp., *Cryptopleura* sp., *Ballia callitricha* and *Myriogramme* sp. whilst the chlorophyte *Codium* sp. and the phaeophyte *Halopteris* sp. were also abundant.

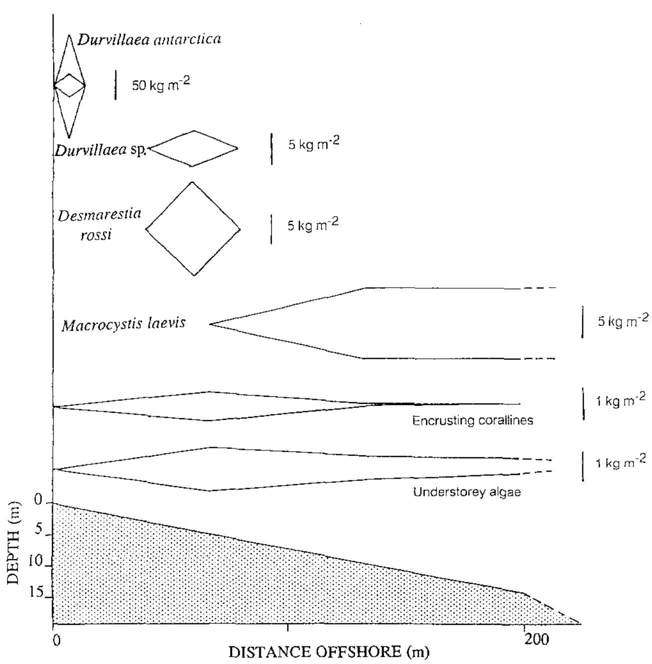

Fig. 2. Schematic representation of the mean wet biomasses of algae in relation to depth in the shallow sublittoral zone at Marion Island. Data derived from Tables 1 and 2, *Durvillaea antarctica* values from Haxen and Grindley (1985) and *Macrocystis laevis* values from Attwood et al. (1991)

Figure 2 is a schematic representation of the mean distribution and biomass of algae in the shallow sublittoral on the east coast of Marion Island. It emphasises the domination of the shallows by *Durvillaea antarctica*, the existence of a narrow zone of *Durvillaea* sp. and *Desmarestia rossi* in 3–6 m and the development of massive beds of *Macrocystis laevis* further offshore.

Zoobenthos

Biomass. The general trend for an increase in zoobenthos biomass with depth in the sublittoral zone (Table 1) is reflected in Fig. 3. Mean biomass values for zoobenthos were remarkably similar in the kelp beds at 10 m and 15 m depths at all three sites, with the exception of the 15 m samples at Trypot Point which had the highest mean wet biomass (598 g m^{-2}). Trypot Point also had the lowest mean wet biomass (68 g m^{-2} at 5 m depth).

The dominant zoobenthic groups were Annelida, Bryozoa, Crustacea, Mollusca, Echinodermata and Porifera which comprised > 93% of the zoobenthic biomass at

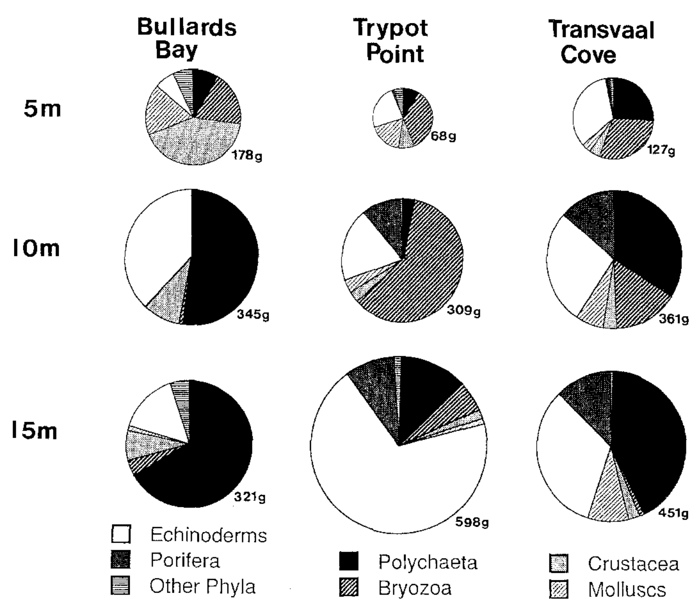

Fig. 3. Biomass of macrozoobenthos from the sublittoral zone at Marion Island. Area of pie diagrams is proportional to mean biomass m^{-2} at 5 m, 10 m and 15 m depths at the three sites

all three sites (Fig. 3). With increased depth, Annelida (mainly polychaetes) increased in both absolute biomass and proportional representation and at 15 m depth at Bullards Bay and Transvaal Cove contributed 216 g and 192 g respectively to the total wet biomass m^{-2}. Bryozoa contributed a greater proportion to the total wet biomass in the shallower depths and were profuse at 10 m at Trypot Point where the mean wet biomass of Bryozoa was 186 $g\,m^{-2}$. Porifera only contributed significantly at Trypot Point and Transvaal Cove (10 m and 15 m) where mean values varied from 32 g to 55 $g\,m^{-2}$.

In general, biomass of echinoderms increased with depth, with Holothuroidea and Echinoidea contributing most to the total echinoderm biomass. Holothurian biomass was extremely low at 5 m at all stations but increased markedly at Transvaal Cove (10 m and 15 m) and at Trypot Point (15 m) reaching a maximum mean wet biomass of 255 $g\,m^{-2}$ at the latter (Fig. 4). Echinoid biomass also peaked at 15 m depth at Trypot Point (141 $g\,m^{-2}$). Mean wet biomass of Asteroidea was less than 12 $g\,m^{-2}$ at all stations except at 10 m depth at Bullards Bay where starfish biomass reached 54 $g\,m^{-2}$. Ophiuroidea contributed only a small percentage to total echinoderm biomass but attained mean wet biomass values of 12 to 16 $g\,m^{-2}$ in the kelp beds at Transvaal Cove and Trypot Point.

Molluscs were represented by Amphineura, Gastropoda and Bivalvia (Fig. 4). Chitons were particularly

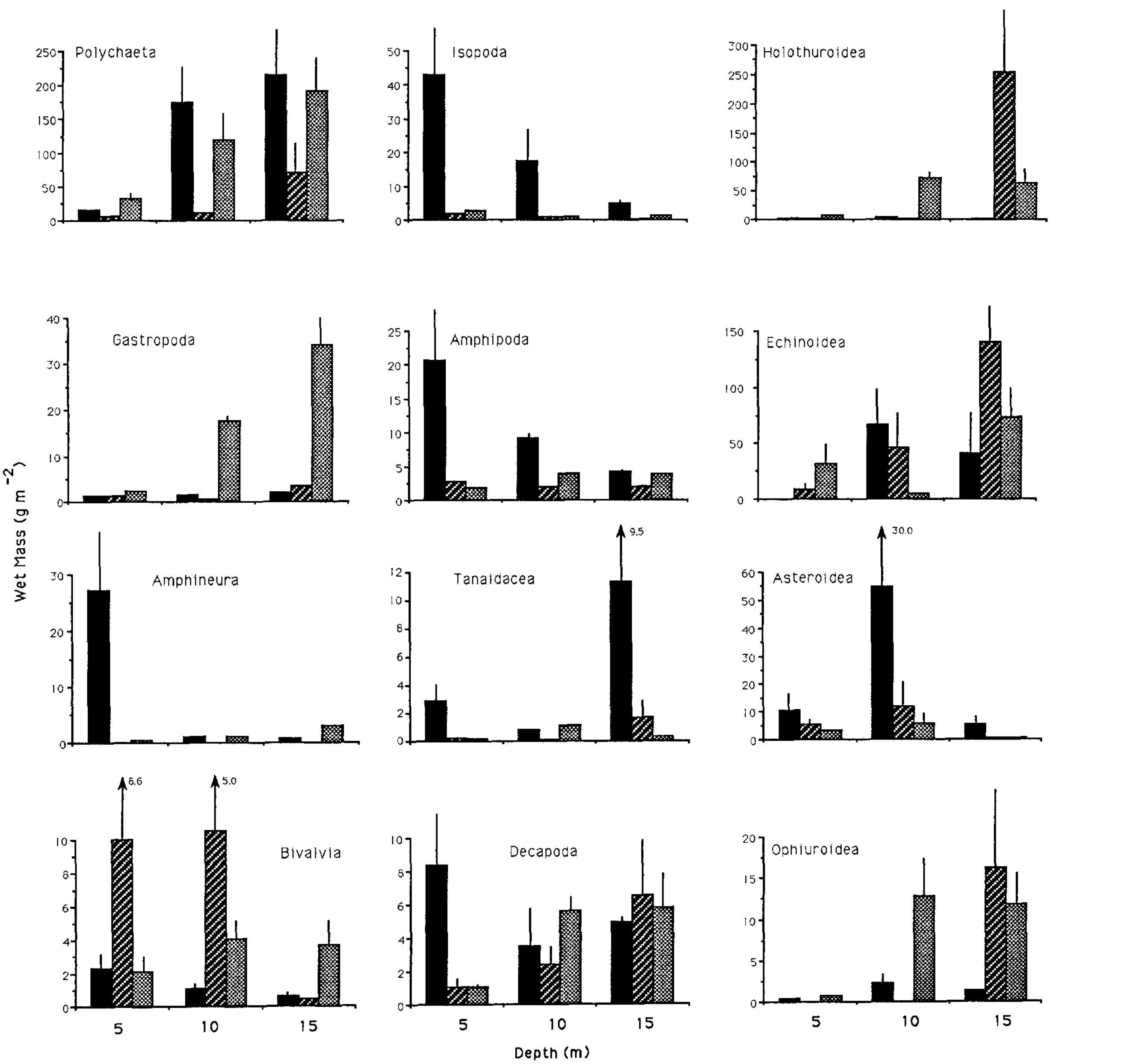

Fig. 4. Mean biomass m^{-2} of macrozoobenthos at three depths in the Marion Island sublittoral zone. Standard error of the means indicated by *vertical bars* and histogram shading as follows: *black* Bullards Bay, *cross-hatched* Trypot Point and *dots* Transvaal Cove

plentiful in the shallow water at Bullards Bay attaining a mean biomass value of 27 $g\,m^{-2}$. Gastropod biomass showed a marked increase with depth at Transvaal Cove, reaching a mean wet biomass value of 34 $g\,m^{-2}$ at 15 m. Biomass values for bivalves were generally low at all sites (<4 $g\,m^{-2}$) reflecting the small size of most of the species occurring at Marion Island in the shallow sublittoral zone.

Though a few specimens of Ostracoda and Copepoda were collected, four malacostracan orders, namely Isopoda, Amphipoda, Decapoda and Tanaidacea dominated the crustacean component of the shallow sublittoral benthos (Fig. 4). Isopod, amphipod and decapod biomasses were highest at 5 m depth at Bullards Bay and attained means of 43 $g\,m^{-2}$, 21 $g\,m^{-2}$ and 8 $g\,m^{-2}$ respectively. Tanaid mean biomass reached 11 $g\,m^{-2}$ at 15 m depth at Bullards Bay.

Species richness

Approximately 200 species of macrobenthic animals were recorded during this study (Table 3). Polychaetes were the most species-rich group, with 34 species distinguished, followed by Gastropoda (26 species), Amphipoda (23 species), Isopoda (19 species), Bryozoa (15 species), Bivalvia (14 species), Asteroidea (10 species) and Hydrozoa (10 species). Although Echinoidea and Holothuroidea represented a significant percentage of the total sublittoral zoobenthic biomass they were each only represented by a single species.

The total number of species found in the four replicate 0.1 m^2 quadrats for each depth at the three study sites are also given in Table 3. The number of polychaete species ranged from 14–21 with about 10 species recorded per quadrat at all depths. Gastropod species richness appeared higher at Transvaal Cove than at the other two sites with 19 species recorded at 10 m depth.

Numerical abundance

A total of 46 769 animals was extracted from the macrobenthic samples. Polychaeta were numerically dominant, constituting 37.2% of the total (Fig. 5). Crustacea were the next most abundant taxon, representing 29.3% of all the animals sampled, with Amphipoda the most abundant order. Nematodes contributed 14.9% to the total number of animals collected though the biomass of these organisms was negligible. Molluscs made up 13.3% of the total with three classes (Bivalvia, Gastropoda and Amphineura) contributing about equally. Echinoderms amounted to 3.2% with Holothuroidea contributing the greatest number of animals within this phylum. Taxa which contributed the remaining 2.1% of total numbers were Anthozoa, Nemertea, Sipunculoidea, Platyhelminthes, Pycnogonida, Acari, Brachiopoda and Ascidiacea. Bryozoa, Hydrozoa and Porifera were not included in numerical analyses.

The highest mean number of polychaetes was reached at Bullards Bay where 15 982 m^{-2} and 11 007 m^{-2} were

Table 3. Species richness of macrozoobenthos in the shallow sublittoral zone at Marion Island. Values indicate total number of species found in four replicate 0.1 m^2 quadrats for each depth at the three study sites (BB = Bullards Bay, TP = Trypot Point, TC = Transvaal Cove). Total number of species recorded for each taxon during the study is given in the last column and total number of species for each depth and site is given at the foot of the table

Taxon	BB 5 m	BB 10 m	BB 15 m	TP 5 m	TP 10 m	TP 15 m	TC 5 m	TC 10 m	TC 15 m	Total no.
Porifera	0	1	1	1	3	3	2	3	2	5
Hydrozoa	0	0	4	0	1	4	3	8	7	10
Anthozoa	1	1	1	1	1	0	1	1	0	2
Platyhelminthes	Species not distinguished									?6
Nematoda	Species not distinguished									?10
Nemertea	1	0	1	1	1	1	1	1	1	1
Sipunculida	0	0	1	1	0	1	0	1	1	1
Oligochaeta	1	1	1	1	1	1	1	1	1	1
Polychaeta	20	14	15	18	16	21	15	16	19	34
Ostracoda	0	0	0	1	0	1	0	1	0	1
Copepoda	0	0	0	0	1	0	0	1	1	1
Tanaidacea	5	5	5	5	4	5	3	7	4	8
Isopoda	11	6	4	7	4	9	6	6	4	19
Amphipoda	12	13	11	13	8	7	8	9	9	22
Decapoda	1	1	2	1	1	2	1	1	2	2
Acari	0	2	2	0	0	1	0	0	0	2
Pycnogonida	1	0	1	0	0	0	0	2	2	3
Bryozoa	5	4	7	8	1	8	6	10	11	15
Brachipoda	0	0	1	0	2	2	0	2	1	2
Amphineura	2	1	1	2	1	2	2	2	1	2
Gastropoda	3	5	6	8	8	11	10	19	8	26
Bivalvia	6	6	4	3	5	5	5	7	4	14
Asteroidea	4	2	1	4	3	2	4	4	1	10
Ophiuroidea	2	3	1	2	0	2	1	1	2	3
Echinoidea	0	1	1	1	1	1	1	1	1	1
Holothuroidea	1	1	1	1	1	1	1	1	1	1
Ascidiacea	1	1	0	1	1	1	1	1	1	1
Total no.	77	68	72	80	64	91	72	106	84	187 + 16

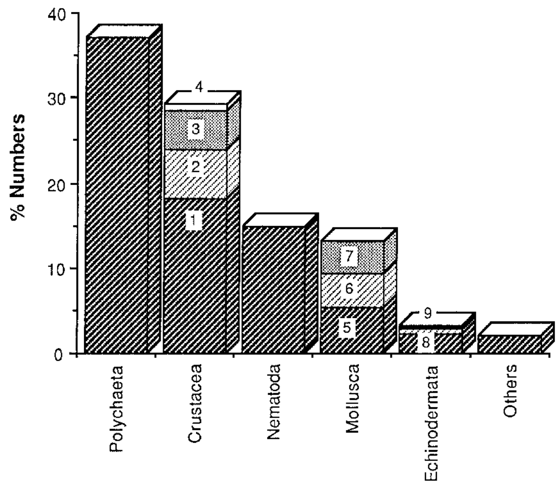

Fig. 5. Percentage contribution of major zoobenthic taxa to the total number of animals collected from 36 × 0.1 m^2 quadrats in the Marion Island sublittoral zone. (*1* Amphipoda, *2* Isopoda, *3* Tanaidacea, *4* Decapoda, *5* Bivalvia, *6* Gastropoda, *7* Amphineura, *8* Holothuroidea, *9* Ophiuroidea + Asteroidea + Echinoidea)

recorded at 10 m and 15 m depths respectively (Fig. 6). These high numbers were chiefly due to the abundance of the small sedentary polychaete *Rhynchospio glutea* at these sites. Other numerically dominant sedentary polychaetes were *Axiothella quadrimaculata, Orbiniella minuta, Thelepus setosus, Boccardia polybranchia, Polycirrus hamiltoni, Oriopsis limbata* and *Notomastus* sp. Abundant errant polychaetes were *Platynereis australis, Typosyllis variegata* and *Exogone heterosetosa.*

Among the crustaceans, amphipod and isopod numbers were highest at Bullards Bay where at 5 m depth they attained mean densities of 9442 m^{-2} and 4197 m^{-2} respectively (Fig. 6). The numerically dominant species of Amphipoda comprised *Jassa falcata, Atyloella magellanica, Haplocheira barbimana* and *Cylindryllioides mawsoni* whilst the numerically dominant Isopoda were the flabelliferan *Dynamenella eatoni* and the asellotans *Joeropsis marionis* and *Joeropsis curvicornis.* Tanaid numbers were also highest at Bullards Bay with *Zeuxoides pseudolitoralis, Allotanais hirsutus* and *Apseudes spectabilis* the most abundant species. Two species of decapods were recorded, the numbers of the crab *Halicarcinus planatus* increasing with depth whereas the shrimp *Nauticaris marionis* was only recorded at 15 m depth.

The chiton *Hemiarthrum setulosum* was particularly abundant in the shallow water at Bullards Bay, attaining a mean density of 3760 m^{-2} (Fig. 6). Amongst the bivalves, *Kidderia minuta*, which was usually found associated with under-storey rhodophytes, was numerically dominant, attaining densities of 2315 m^{-2} at Trypot Point. The larger *Gaimardia trapesina*, though rare in the cleared benthic quadrats, is in reality extremely abundant in the canopy of the *Macrocystis* beds, being attached to fronds of this kelp. A mean density of 73 *G. trapesina* specimens per frond was recorded on kelps collected in 10 m of water in Transvaal Cove. Gastropods attained their highest densities (1852 m^{-2}) at 10 m in Transvaal Cove. The small *Jeffreysia edwardiensis* and the larger whelk *Trophon declinans* were the most abundant gastropods though the limpet *Nacella delesserti* was common in shallow water. Specimens of *Octopus* sp. were observed by divers at all three sites in depths > 10 m.

Holothuroidea were the most abundant echinoderms and the single species recorded, *Pseudocnus laevigatus*, attained densities of 1235 m^{-2} (Fig. 6). *Ophiurolepis martensi* was the numerically dominant ophiuroid and had a mean density of 210 m^{-2} at Trypot Point (15 m) and 232 m^{-2} at Transvaal Cove (10 m). The single species of sea urchin found at Marion Island, *Pseudechinus marionis*, reached a mean density of 50 m^{-2} in 15 m depth at Trypot Point. Asteroid densities were highest at Bullards Bay (70 m^{-2}) chiefly due to the abundance of the small starfish *Anteliaster scaber.* Echinoids, ophiuroids and holothuroids tended to increase in numbers with depth while asteroids diminished. Counts of larger starfish (> 5 cm diameter) which would probably have been under-represented in the cleared 0.1 m^2 quadrats were made in eight 16 m^2 quadrats at the three study sites. Six species of these larger starfish were noted with densities ranging from 0.4–1.5 m^{-2} (Table 4).

Although the mean density of nematodes reached figures of over 6000 m^{-2} at Bullards Bay, numbers were considerably lower at the other two sites. Though generally not considered to be macrobenthic marine organisms, many of these nematodes were in excess of 20 mm in length. Amongst the other minor phyla, a small unidentified ascidian attained a mean density of 407 individuals

Table 4. Counts of large zoobenthic organisms occurring in 16 m^2 kelp quadrats at 10 m depth at three sites in the Marion Island sublittoral zone

Locality	Bullards Bay		Trypot Point		Transvaal Cove			
Replicates	a	b	a	b	a	b	c	d
Cephalopoda								
Octopus sp		sample					1	
Asteroidea		lost						
Anasterias rupicola	1							
Smilasterias scalprifera	2							
Undescribed sp. (MAR 16.F3)	2		7	1	2	2	2	
Pteraster affinis	1		17	16				
Diplasterias meridionalis					6	10	5	5
Porania antarctica					1	1		

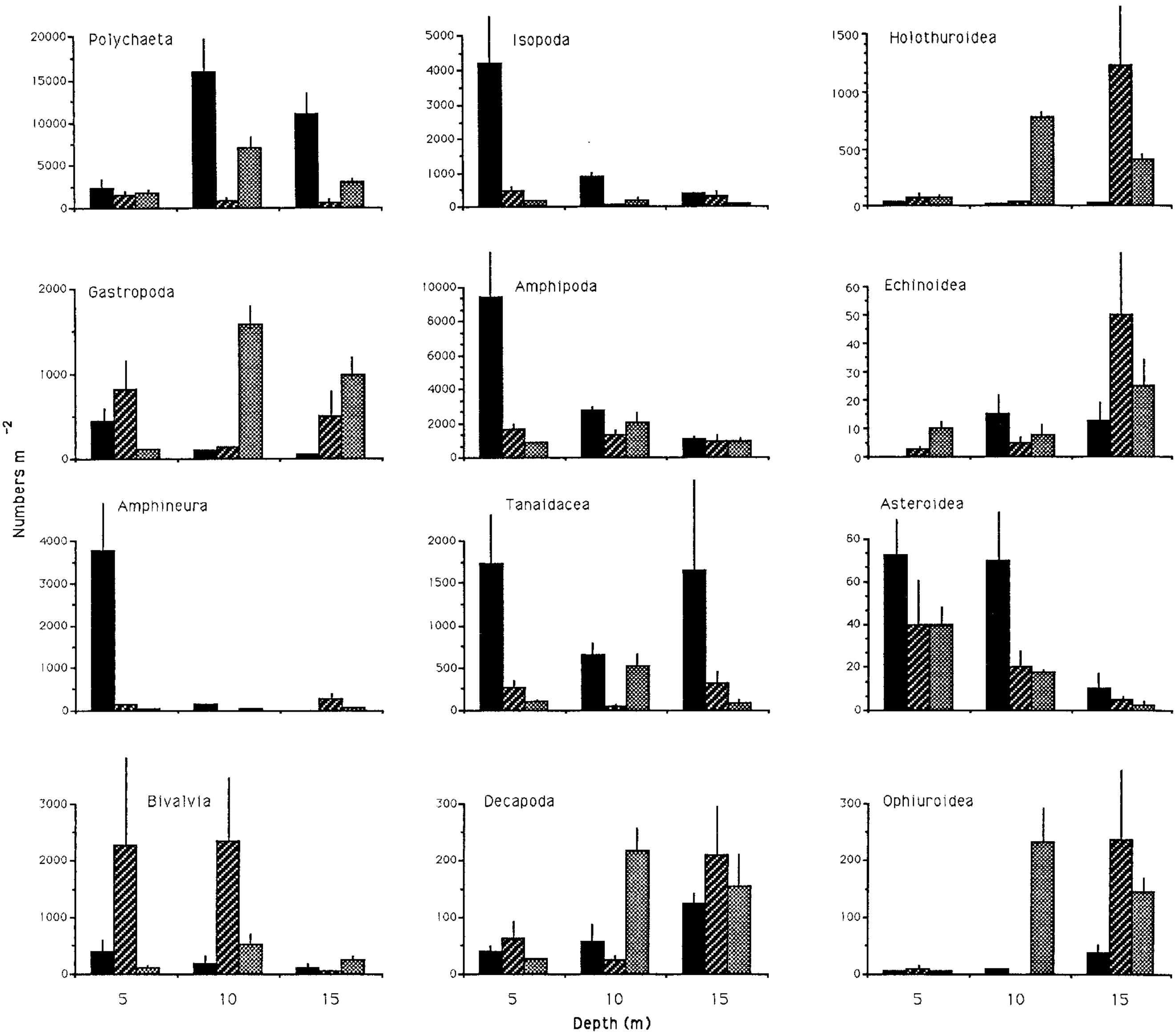

Fig. 6. Mean numerical abundance m^{-2} of macrozoobenthos at three depths in the Marion Island sublittoral zone. Standard error of the means indicated by *vertical bars* and histogram shading as follows: *black* Bullards Bay, *cross-hatched* Trypot Point and *dots* Transvaal Cove

m^{-2} at 15 m depth at Bullards Bay. Nemertean worms were also most abundant at Bullards Bay (275 m^{-2} at 15 m) and the single sipunculid species *Golfingia margaritacea* attained a maximum mean density of 97 m^{-2} at this site as well.

Among the bryozoans occurring in the sublittoral zone, *Bicrisia edwardsiana* was found in 70% of the samples, *Hippothoa* sp. in 58%, *Figularia philomela* in 47% and *Fenestrulina majuscula in* 44%. The dominant hydrozoan, *Serturella picta*, occurred in 36% of the samples, with *Symplectoscyphus subdichotomus* and *Myriothela meridiana* also common.

Discussion

Since the advent of SCUBA-diving, sublittoral benthic research in Antarctica and at the subantarctic islands has shown major advances with several studies relying on divers to make observations and collect samples from a variety of localities and habitats including under fast ice (Neushul 1964; Grua 1964; Peckam 1964; Everson and White 1969; Gruzov and Pushkin 1970; Propp 1970; Dayton et al. 1970; Grua 1971; Hardy 1972; White and Robins 1972; Gallardo et al. 1975; De Laca and Lipps 1976; Richardson 1979; Platt 1979; Nakajima et al. 1982; Castilla 1985).

Many of the above references relate to the distribution of benthic algae, and the presence of infralittoral *Durvillaea antarctica*, shallow-water encrusting corallines, *Desmarestia* spp. and *Macrocystis* kelp beds appears to characterise the phytobenthos at most subantarctic islands (Smith and Simpson 1985; Knox 1987; Arnaud 1989; Kingsford et al 1989; Selkirk et al. 1990). Besides figures for kelp there are, however, few values for the biomass of sublittoral algae at subantarctic islands in the literature. The dominant alga in the sublittoral at Marion Island was *Macrocystis laevis*, for which a mean wet biomass of 11.6 kg m^{-2} was recorded. Individual plants of *M. laevis* at Marion Island had a similar biomass to those at Kerguelen Island where *M. pyrifera* plants ranged from 3.4 kg to 22.5 kg (Delepine 1976). On the Antarctic Peninsula De Laca and Lipps (1976) recorded a peak dry biomass of 0.8 kg m^{-2} for *Desmarestia menziesii*, which is considerably less than the 2.7–3.4 kg m^{-2} dry biomass found for *Desmarestia rossi* in the shallows at Marion Island. Wet biomass values for under-storey algae at Marion Island in 5–10 m depth (0.37–2.11 kg m^{-2}) are comparable to values found at Signy Island, South Orkneys, where White and Robins (1972) recorded a mean of 1.33 kg m^{-2} at depths of 2–10 m and Richardson (1979) found a mean of 0.98 kg m^{-2} and a maximum of 2.05 kg m^{-2} at 6–8 m.

On Marion Island algal biomass was significantly higher at Bullards Bay (especially at 5 m) than at the other two sites, with encrusting corallines particularly profuse. This site was situated near a large rookery of macaroni penguins (200 000 pairs) and it is possible that the increase in biomass of algae here is related to increased nutrient input from guano run-off. In the South Shetland Islands Tatur and Myrcha (1983) recorded changes in the chemical composition of guano run-off from the rookeries, with volatile ammonia lost to the atmosphere and some phosphorus retained on land. Despite this, they found that at rookeries close to the sea almost all of the guano deposit may be washed into the sea during heavy rains. Bosman and Hockey (1986) have shown that intertidal community structure on islands off the west coast of South Africa is profoundly influenced by nutrient input from seabird guano.

The general use of grabs operated from boats and research ships to determine biomass values for zoobenthos near the subantarctic islands and the Antarctic shelf is reflected in the literature. For example, Desbruyeres and Guille (1973) recorded a zoobenthic biomass of 61 g m^{-2} at 20 m depth near a *Macrocystis* bed at Kerguelen Island. Platt (1979) documented values of 34–226 g m^{-2} at 9–12 m in soft bottom areas around South Georgia and Jazdzewski et al. (1986) measured 80–90 g m^{-2} on gravel and stones at 15 m depth at the South Shetland Islands. Using hand-corers, divers sampled the infauna at Signy Island in the South Orkneys and recorded mean biomass values of 307–788 g m^{-2} at depths of 0–35 m (Hardy 1972). In rocky areas at the same island, the zoobenthic biomass averaged 168 g m^{-2} at 6 m and 700 g m^{-2} at 26 m (White and Robins 1972). Quantitative collections of zoobenthos on hard substrata by divers at the Antarctic Haswell Islands revealed biomass to be low in the ice-scoured shallows (20–25 g m^{-2}) but to increase markedly to 450 g m^{-2} between 6 and 25 m (Propp 1970). Nakajima et al. (1982) reported a biomass of 46–109 g m^{-2} at 1.5–8 m depth and 438 g m^{-2} at 10 m in Lutzow-Holm Bay at the Syowa Station in Antarctica.

No biomass values could be found in the literature for shallow sublittoral benthic communities on hard substrata at any of the subantarctic islands. However, the above figures for Antarctic zoobenthos are comparable with the mean biomasses found at the three sites at Marion Island (68–598 g m^{-2}). The trend at Marion Island for zoobenthic biomass to increase with depth is also reflected in many of the above Antarctic studies. The low zoobenthic biomass at 5 m depth at Trypot Point at Marion Island is probably a result of the extensive water movement at this site due to the reflection of waves from the cliff base. All four replicate samples there had very little accumulated organic matter or sediment, in contrast to most of the samples collected at 10 m and 15 m within the *Macrocystis* beds. The biomass m^{-2} within the kelp beds was similar at all three sites with only the 15 m station at Trypot Point showing a higher biomass due chiefly to the exceptional abundance of holothurians in two of the replicates.

Polychaetes, echinoderms, crustaceans, molluscs, bryozoans and sponges dominated the zoobenthos at Marion Island and studies at the subantarctic Kerguelen Islands, some 2 400 km to the east, have revealed the same groups to be dominant (Grua 1971; Arnaud 1974; Arnaud 1989). At Kerguelen Island the large errant polychaete *Platynereis magalhaensis* (= *P. australis*) and the sedentary polychaetes *Thelepus setosus*, *Neoleprea streptochaeta* and *Boccardia polybranchia* were abundant amongst seaweeds on hard substrata in shallow waters between the shore and the *Macrocystis* beds (Duchene 1984). These polychaetes were also common in the same habitat at Marion Island but, in addition, tiny spionids (*Rhynchospio glutea*), sabellids (*Oriopsis limbata*) and orbinids (*Orbiniella minuta*) were also abundant. At 5 m depth at Marion Island the mean numbers of polychaetes ranged from 1 552 to 2 420 m^{-2} which is similar to the mean of 1 645 m^{-2} recorded at Kerguelen Island. Within the kelp beds there, *Platynereis* and several syllid species dominated and the mean density of polychaetes was 1 840 m^{-2}. *Platynereis* was also abundant in the kelp beds at Marion Island, occurring at all three sampling sites. Other dominant polychaetes varied between sites. At Bullards Bay the abundance of *Rhynchospio glutea* and *Axiothella quadrimaculata* contributed substantially to the overall polychaete density of 15 982 m^{-2}: an order of magnitude greater than that found at Kerguelen. At Transvaal Cove these two species were less prolific but the several other species (e.g. *Polycirrus hamiltoni*, *Notomastus* sp., *Thelepus setosus* and *Oriopsis limbata*) were abundant, resulting in mean densities ranging from 3 050 to 7 075 m^{-2}. At Trypot Point densities of polychaetes were lower, with means ranging from 692 to 910 m^{-2}.

Echinoderms have also been studied in detail at Kerguelen Island, where 36 species were recorded from grab samples at depths between 5 and 180 m (Guille 1977). Greatest abundance occurred in the detrital sediments at 17 to 32 m depth, adjacent to *Macrocystis* beds, with up to 640 individuals m^{-2}. This figure is comparable to the echinoderm densities found in the kelp beds at Marion Island which, though varying widely, averaged 577 individuals m^{-2}. Only seven species co-occurred in the two studies, namely the ophiuroid *Ophiacantha vivipara* and the asteroids *Anasterias rupicola*, *Pteraster affinis*, *Diplasterias meridionalis*, *Leptychaster kerguelenensis*, *Smilasterias scalprifera* and *Porania antarctica*. A further three genera, *Amphiura*, *Ophiurolepsis* and *Henricia* were common between the two studies. The holothurian *Pseudocnus laevigatus*, recorded at Kerguelen by Arnaud (1974), also occurs at both islands. Four species of sea-urchins occur in the *Macrocystis pyrifera* beds at Puerto Toro in the Beagle Channel, Chile (Castilla 1985) compared to a single species, *Pseudechinus marionis*, at Marion Island.

As in the case at Marion Island, numerous amphipods and isopods are associated with seaweeds and *Macrocystis* debris at Kerguelen Island (Grua 1971; Duchene 1984). Thirteen of the gammaridean amphipod species associated with *Macrocystis* holdfasts and fronds at Kerguelen (Arnaud 1974) were also found in the sublittoral at Marion Island. The sphaeromatid isopod *Exosphaeroma gigas* is also common to both islands (Duchene 1984), as is the tubiculous tanaid *Allotanais hirsutus* which abounds in intertidal muddy sands at Kerguelen Island with densities of 56 000 to 146 000 m^{-2} (Delille et al. 1985). Only a single species of crab, *Halicarcinus planatus*, has been recorded in the shallow sublittoral at both Marion and Kerguelen Islands (Arnaud 1974; Duchene 1984) and Richer de Forges (1977) has highlighted the importance of *Macrocystis* holdfasts as a habitat for ovigerous females and juveniles of this species.

Both chiton species found in the Marion Island sublittoral (*Hemiarthrum setulosum* and *Terenochiton kerguelenensis*) are widespread in the Antarctic and subantarctic (Gaillard 1971). The extremely high numbers of *H. setulosum* recorded among the encrusting coralline algae at 5 m at Bullards Bay far exceed the maximum densities found in the *Durvillaea antarctica* zone at both Marion Island (Blankley and Grindley 1985) and Macquarie Island (Simpson 1976). Simpson (1976) records that coralline algae are the preferred food of *H. setulosum*. He also considers that cover provided by *Durvillaea antarctica* is essential for these small chitons in the infralittoral zone. However, at 5 m depth at Bullards Bay, beyond the *D. antarctica* zone, high biomasses of encrusting corallines and large numbers of chitons (particularly *H. setulosum*) were recorded. Evidently *H. setulosum* does not depend on *D. antarctica* in the sublittoral zone.

Although the small bivalves *Kidderia minuta* and *Kellia nuculina* were extremely abundant in the sublittoral zone at Marion Island, large bivalves were absent. This is in sharp contrast to the situation at Kerguelen Island where dense beds of the mussels *Aulacomya ater* and *Mytilus edulis* occur in depths from 5 m–70 m and may attain biomass values of 10 kg m^{-2} (Grua 1971; Arnaud 1974). With the exception of *Cyclopecten* all other bivalve genera found in the sublittoral at Marion Island during this study have also been recorded from Kerguelen Island. Similarly, only one gastropod genus occurring at Marion Island (*Jeffreysia*) was not found at Kerguelen Island (Gaillard 1971; Cantera and Arnaud 1984). With the exception of the limpet *Nacella delesserti* and the whelk *Trophon declinans*, most gastropods occurring at Marion Island were extremely small in size ($<$ 5 mm). From the intertidal and shallow subtidal areas at Marion Island, Blankley and Grindley (1985) reported mean densities of *N. delesserti* to be 75 m^{-2} and 93 m^{-2} respectively. In the present study mean densities at 5 m at Trypot Point and Transvaal Cove were similar with 58 m^{-2} and 65 m^{-2} respectively but limpet densities at Bullards Bay were much higher, with a mean of 240 m^{-2}, possibly related to the increased algal abundance at this site. From the vertical stacks of limpets observed in the shallow sublittoral at Marion Island it appears that they spawn in the same manner as that described by Picken and Allen (1983) for *Nacella concinna* at Signy Island.

Octopus sp. occurs commonly at Marion Island and is probably a major predator in the sublittoral zone. However, despite frequent sightings by divers, there is no quantitative information on this species.

Bryozoans, hydrozoans and sponges, though difficult to quantify numerically, were common in the sublittoral at Marion Island as at most subantarctic and Antarctic islands (Dell 1972). At Kerguelen Island dense accumulations of sponge spicules on the sea-floor at depths as shallow as 5 m provide a habitat for a rich and diverse fauna (Arnaud 1974). At Marion Island, however, there was no evidence of similar sponge spicule accumulations in the shallow sublittoral. Two genera of hydrozoans (*Sertularella* and *Halecium*) and nine genera of bryozoans (*Menipea*, *Fenestrulina*, *Beania*, *Hippothoa*, *Smittina*, *Tricellaria*, *Osthimosia*, *Tubulipora* and *Cellaria*) found in the sublittoral at Marion Island have also been collected at Kerguelen Island (Redier 1971; D'Hondt and Redier 1977).

Despite the paucity of data on the benthic biomass of the sublittoral zone at most islands in the subantarctic region, sufficiently detailed sampling has been undertaken at both Marion and Kerguelen Islands to show their stong affinities, confirming earlier views that they both belong to the same subregion i.e. the Kerguelen subregion (Hedgpeth 1970; Cantera and Arnaud 1984; White 1984; Knox 1987).

The general pattern of biomass distribution at Marion island also accords with that recorded elsewhere in the Antarctic and subantarctic. The benthic biomass is high and consists predominantly of algae which decline in biomass with depth whereas zoobenthic biomass increases with depth. Despite the extremely high numerical abundance of some zoobenthic species overall zoobenthic biomass is not particularly high because many of the species are extremely tiny. This tendency is particularly clear amongst the polychaetes, amphineurans, bivalves and gastropods, and runs contrary to the previously perceived trend towards gigantism in Antarctic benthic communities (White 1984).

Notable absentees from Marion Island were barnacles and large bivalves. Their absence is particularly striking in view of the abundance of other filter-feeders. Indeed, filter-feeders, detritivores and consumers of macrophytic debris make up the bulk of the zoobenthic biomass.

Recent attention has been focussed on the possible existence of an "island effect" enhancing the productivity of phytoplankton in the vicinity of Marion Island (Boden 1988). To this enhanced phytoplankton productivity can be added the production of macro-algae around the island (Haxen and Grindley 1985; Attwood et al. 1991). Their productivity per unit area is approximately 2–3.5 times that of the phytoplankton but much of the material they produce may be cast ashore or transported away from the island. Despite this high primary production and the considerable sublittoral zoobenthic biomass measured in the present diving survey at Marion Island, we remain largely ignorant of the pathways and rates of transfer between primary and secondary production. Perissinotto and McQuaid (1990) have, however, suggested that the vertically migrating planktonic larvae of benthic species such as *Nauticaris marionis* may act as a link between pelagic primary and benthic secondary production. The latter may be much lower than anticipated from the biomass because of the low rates of turnover in cold waters (White 1984; Blankley and Branch 1984, 1985). One of the priorities for the future should be to elucidate these pathways and rates.

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