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DOMINANCE ANALYSES OF GORGONIAN (OCTOCORALLIA: GORGONACEA) POPULATIONS ON SINGAPORE CORAL REEFS

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Abstract

Fourteen sites on reefs in Singapore were sampled to elucidate gorgonian distribution and community structure. Species richness and mean colony density varied from 9-17 species and 4.8-28.2 colonies per square metre, respectively. Mean species richness and colony density for all sites on Singapore reefs that support gorgonian growth was 13 species per site and 15.3 colonies per square metre, respectively. The Plexauridae, Ellisellidae, and Subergorgiidae were the most dominant families. Subergorgia suberosa and Ctenocella (Umbracella) sp. A were the dominant species numerically, as well as being ubiquitous throughout the survey sites. For other species, a wide spectrum of distributional characteristics exists from few but ubiquitous, to numerous but found at only a few sites.

Introduction

Coral reefs in Singapore are of the fringing or patch type. In general, four distinct zones are present on reefs in Singapore: the reef flat which is exposed at the lowest tides; the reef slope, which is relatively steep (about 30° declination); the reef crest between the reef flat and the reef slope; and the reef bottom, where the reef slope levels out. On most reefs in Singapore, the reef bottom occurs at a depth of about 12-15m. Distinct depth zonation of the flora and fauna on Singapore coral reefs is evident, both in terms of scleractinian corals, which are generally confined to the upper 10m (reef flat, crest, and upper slope) of reefs in Singapore (Goh et al., 1994), as well as of the non-scleractinian component of the reef flora and fauna (Goh and Chou, 1994a, b). Below the 10m depth, the fauna consists mainly of gorgonians and sponges (Goh and Chou, 1994b), of which the former are more conspicuous, and can visually dominate the zone.

Gorgonians have a worldwide distribution, being found in polar, temperate, sub-tropical and tropical latitudes, in depths ranging from the inter-tidal to the deep ocean trenches, and in temperatures ranging from -1°C to 30°C (Alderslade, 1984). To date, 31 species of gorgonians have been reported from Singapore (Goh and Chou, 1996). Gorgonian distribution on reefs south of the main island was observed to be related to the availability of suitable substrata (Goh and Chou, 1994a), although no quantitative evidence was provided. In that study, three distinct bathymetric zones of gorgonian distribution were observed, viz., crest, slope, and bottom, based on species composition and relative abundance. In addition, the greatest species richness and abundance occurred in the bottom zone where gorgonians form the dominant community. This distinct zonation pattern of gorgonians in Singapore was reiterated and statistically confirmed in a subsequent analysis using multi-dimensional scaling and cluster analysis (Goh et al., 1997).

The present study aims to establish a dominance hierarchy of gorgonian species in order to better understand the ecological position of each species within the community. Gorgonians have not only been found to be the dominant fauna on the lower slope and bottom of reefs in Singapore (Goh and Chou, 1994a), but also to harbour a wide range of associated organisms (Goh et al., in press). Consequently, elucidating gorgonian community structure has implications for understanding the ecology of a wide variety of other coral reef organisms.

Materials and Methods

Fourteen sites on the reefs of Singapore's southern offshore islands (Fig. 1) were surveyed to elucidate distributional patterns of the gorgonian fauna in Singapore. At each site, six 1x1m^2 quadrats were positioned along a 11m long transect line, at a constant depth, parallel to the reef crest. Quadrats were placed 1m apart on the transect line (Goh and Chou,

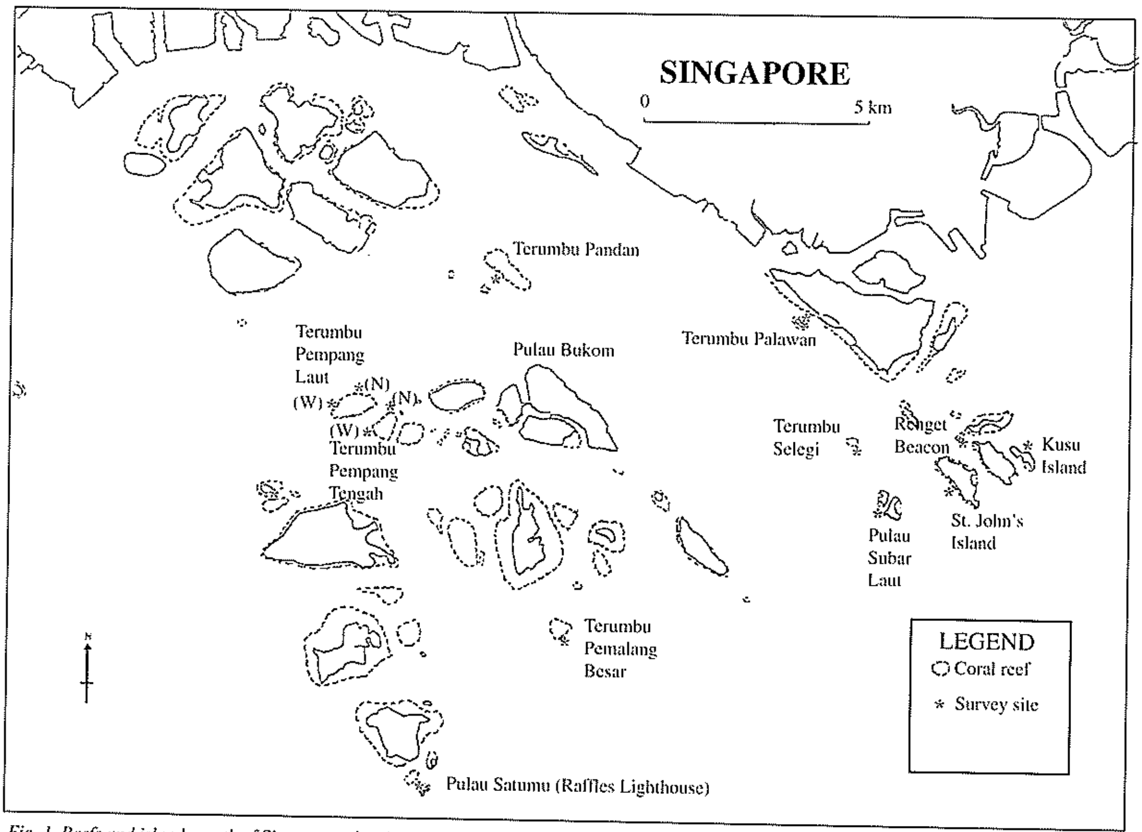

Fig. 1. Reefs and islands south of Singapore, showing survey sites.

1994a) and adjacent quadrats were positioned on opposite sides of the transect line to further reduce the effect of clumping, a known characteristic of gorgonians. The depth at which the transect line was placed was recorded with reference to the reef crest (ranging from 4.5m to 12.1m below the reef crest; mean for 14 sites: 8.5m) to enable replication of the study regardless of the height of the tide. This depth generally corresponded to the ecological zone at the reef bottom for each survey site where abundance and richness of gorgonians are known to be maximal (Goh and Chou, 1994a; Goh et al., 1997). At St. John's Island, Pulau Subar Laut, and Raffles Lighthouse, the transect line was placed on the lower reef slope as the reef bottom was beyond the depth where safe and effective sampling could be carried out using SCUBA techniques. The abundance and richness of gorgonians at the depths where these transects were conducted was visually assessed to be similar to that at the reef bottom.

All gorgonian colonies within the quadrats were counted; colonies that could not be identified were also included in the counts as a separate category. Results thus reflect distributional patterns of the entire gorgonian community at each site, and not just for several selected species. Mean colony density (per m^2) at each site was calculated using the six replicate $1m^2$ quadrat samples.

Results and Discussion

Overview of Distribution Parameters

Of the 31 known species from Singapore (Goh and Chou, 1996), a total of 25 (including three previously unrecorded species) were recorded in this study. Species richness and mean density (colonies per m^2) of gorgonians varied at each site from 16 species and 28.2 colonies per m^2 at St. John's Island, 17 species and 16.5 colonies per m^2 at Terumbu Selegi, to not a single colony at Pulau Salu (Table 1). Mean site species richness and colony density

Table 1. Species richness and mean colony density of gorgonians for each of the 14 survey sites.

Survey Site	Species Richness	Mean Density (colonies per m^2)
Kusu Island	9	11.3
Renget Beacon	10	22.7
St. John's Island	16	28.2
Pulau Subar Laut	14	8.8
Terumbu Selegi	17	16.5
Terumbu Palawan	15	20.2
Terumbu Pandan	13	7.2
Terumbu Pemalang Besar	15	25.7
Raffles Lighthouse	15	20.3
Terumbu Pempang Tengah (North)	13	17.7
Terumbu Pempang Tengah (West)	9	4.8
Terumbu Pempang Laut (North)	11	6.8
Terumbu Pempang Laut (West)	14	9.0
Pulau Salu	0	0
Mean (for 13 sites; excl. P. Salu)	**13**	**15.3**

was 13 species and 15.3 colonies per m², respectively for sites in Singapore that support gorgonian settlement and growth (the site at Pulau Salu is excluded because it did not support any gorgonian colonies). This compares with a total of 39 species (for more than 20 sites) and 2.8-36.2 colonies per m² in Puerto Rico (Yoshioka and Yoshioka, 1989a). These researchers also reported that their results for colony densities were comparable or greater than those in Jamaica (Kinzie, 1973) and Florida (Goldberg, 1973).

Table 2. Dominance hierarchy for gorgonian species in Singapore, based on number of colonies and number of sites where species can be found.

		Abundance			Ubiquity		
Family	**Species**	**# of colonies**	**% of total #**	**Rank[1]**	**# of sites present**	**% presence[2]**	**Rank[3]**
Anthothelidae	*Solenocaulon* sp. A	2	<1	-	2	15.4	-
Subergorgiidae	*Subergorgia suberosa*	250	23.8	1	13	100	1
	S. mollis	8	<1	-	4	30.8	-
Melithaeidae	*Acabaria robusta*	12	1.1	-	6	46.2	-
Acanthogorgiidae	*Acanthogorgia* sp. C	1	<1	-	1	7.7	-
Plexauridae	*Echinomuricea pulchra*	32	3.0	-	5	38.5	-
	Astrogorgia cf. *rubra*	7	<1	-	5	38.5	-
	Astrogorgia sp. A	1	<1	-	1	7.7	-
	Astrogorgia sp. B	3	<1	-	2	15.4	-
	Echinogorgia sp. A	87	8.3	5	11	84.6	3
	Echinogorgia sp. B	89	8.5	4	11	84.6	3
	Echinogorgia sp. C	78	7.4	8	9	69.2	4
	Echinogorgia sp. D	79	7.5	7	11	84.6	3
	Echinogorgia sp. E	11	1.0	-	5	38.5	-
	Euplexaura sp. A	2	<1	-	1	7.7	-
	E. cf. *pinnata*	6	<1	-	3	23.1	-
	Plexaurid sp. A	106	10.1	3	9	69.2	4
Ellisellidae	*Junceella (Junceella)* sp. A	85	8.1	6	12	92.3	2
	J. (Dichotella) cf. *gemmacea*	75	7.1	9	13	100	1
	Ctenocella (Ctenocella) pectinata	11	1.0	-	7	53.8	-
	C. (Umbracella) cf. *umbraculum*	49	4.7	10	12	92.3	2
	C. (Umbracella) sp. A	161	15.3	2	12	92.3	2
	C. (Ellisella) laevis	2	<1	-	1	7.7	-
Unidentified	Unknown sp. A	19	<1	-	8	61.5	-
	Unknown sp. B	19	<1	-	7	53.8	-

Note: 1. Based on the percentage of the total number of colonies present at the 14 sites; only 10 highest ranking species shown for clarity.
2. Based on the 13 sites where gorgonians were found (Pulau Salu was excluded because no gorgonians were found at the site).
3. Based on the percentage of the total number of sites where species is present; only 10 highest ranking species shown for clarity.

Numerical Dominance and Ubiquity

When considering dominance relationships between species, at least two aspects need to be discussed: numerical dominance and ubiquity. The numerical dominance of a species is directly related to its ability to propagate (whether sexually or asexually) and grow quickly within a relatively small area (a single reef). The ability of a species to recruit at a large number of reefs (ubiquity) is a function of its fecundity, larval dispersal efficiency, and larval settlement and survival rates.

A total of 1195 colonies comprising 22 of the 31 known gorgonian species from Singapore (Goh and Chou, 1996) were recorded in this study; three additional undescribed species are also recorded here. The species-by-species analysis of relationships among gorgonians in Singapore (Table 2) showed that *Subergorgia suberosa* and *Ctenocella* sp. A were the two most abundant species (23.8% and 15.3% of all colonies recorded, respectively). In terms of ubiquity, both *S. suberosa* and *Junceella* cf. *gemmacea* were found at all sites that supported gorgonian growth. Another species of *Junceella, Junceella* sp. A, together with *Ctenocella* sp. A and its close relative *Ctenocella* cf. *umbraculum* were also ubiquitous, all three being found at 92.3% of the sites supporting gorgonians. Taking into account both abundance and ubiquity, *S. suberosa* and *Ctenocella* sp. A were the two most dominant species on Singapore reefs. The numerical dominance and ubiquity of these two species imply that they are successful, both in terms of competition for space on a given reef site (numerical dominance), as well as in the ability to recruit at different sites (ubiquity). One contributing factor for the dominance of *S. suberosa* could be the comparatively rapid growth rate in this species (Goh and Chou, 1995).

While similarities in species rankings based on the different systems occur, differences in rankings for *Junceella* cf. *gemmacea* and *Ctenocella* cf. *umbraculum* also reveal some ecological characteristics of these species. *Junceella* cf. *gemmacea* was only ranked 9 in terms of numerical dominance (accounting for 7.1% of the total number of colonies counted) but was found at all sites that supported gorgonian growth (Table 2). Similarly, *Ctenocella* cf. *umbraculum* was only ranked 10 numerically (4.7% of the total number of colonies counted), but was found at all but one of the sites that supported gorgonians. These observations reveal that the two species are able to efficiently disperse larvae and to recruit at many sites, but may not be able to compete with other species for space within the context of a particular reef. On the other hand, a previously uncollected (for Singapore) species, tentatively called Plexaurid sp. A, had a much higher numerical dominance (ranked 3) than these two species, making up more than 10% of all the colonies recorded, but was found at only nine of the sites. The distributional pattern of this species suggests that it is an efficient competitor for space and other resources once it is established on a particular reef. In terms of larger scale dispersal between reefs, it appears to be less effective compared with other less abundant species. Pheromones have been implicated in the gregarious settlement of marine invertebrate larvae (Burke, 1986), and these adult-associated chemical cues may also explain the small scale but high density distribution of species like Plexaurid sp. A. Reproduction by fragmentation, as reported in *Junceella fragilis* (Walker and Bull, 1983) could explain the distribution of Plexaurid sp. A, but no evidence for this has been observed thus far.

At the family level, the Plexauridae (502 colonies recorded) and Ellisellidae (383 colonies recorded) were the most abundant. This dominance is reiterated by the taxonomic richness of these two families in comparison with other gorgonian families in Singapore: the Plexauridae is represented by 13 distinct species while there are six ellisellid species (Goh and Chou, 1996). The Subergorgiidae was the next most abundant family with 258 colonies recorded (mainly contributed by *Subergorgia suberosa*).

Community Structure: Relationships with Site Carrying Capacity and Species Richness

To study if gorgonian community structure affected dominance relationships among species, sites were differentiated by their colony carrying capacity and species richness. The colony carrying capacity of a site was defined in this study as the mean density of gorgonians (regardless of species) at that site;

Table 3. Comparison of mean number of colonies per species between sites with high/low colony carrying capacity and high/low species richness.

	Site Colony Carrying Capacity[2]				Site Species Richness[3]			
	High		Low		High		Low	
Species[1]	**Mean[4]**	**Rank**	**Mean[4]**	**Rank**	**Mean[4]**	**Rank**	**Mean[4]**	**Rank**
F. Subergorgiidae								
Subergorgia suberosa	20.3	1	23.5	1	17.1	1	27.1	1
F. Plexauridae								
Echinomuricea pulchra	3.8	10	0.25	-	2.6	-	0.6	-
Echinogorgia sp. A	8.0	4	5.9	9	7.7	6	6.3	8
Echinogorgia sp. B	7.7	5	6.0	8	8.7	4	4.7	9
Echinogorgia sp. C	6.9	6	6.5	5	6.8	8	6.5	6
Echinogorgia sp. D	6.0	8	9.8	3	8.0	5	7.5	3
Plexaurid sp. A	10.4	3	6.4	6	9.6	3	7.3	5
F. Ellisellidae								
Junceella (Junceella) sp. A	6.7	7	6.2	7	6.9	7	7.5	3
J.(Dichotella) cf. *gemmacea*	6.0	9	7.0	4	6.8	9	6.1	7
Ctenocella (Umbracella) cf. *umbraculum*	3.4	-	5.6	10	4.1	10	4.7	9
C. (Umbracella) sp. A	12.3	2	13.6	2	13.3	2	12.4	2

Note: 1. For clarity, only the top ten ranked species are shown in this table.
2. Sites with high colony carrying capacities are defined as those where the density of colonies is greater than the mean (=92 colonies per m^2) for the 13 sites where gorgonians were found (Pulau Salu was excluded because no gorgonians were found at the site). Low site carrying capacity reflects the situation where colony density is less than or equal to 92 colonies per m^2.
3. Sites with high species richness are defined as those where the species richness is greater than the mean (=13 species per site) for the 13 sites where gorgonians were found (Pulau Salu was excluded because no gorgonians were found at the site). Low site species richness reflects the situation where species richness is less than or equal to 13 species per site.
4. Mean = mean percentage composition of species with respect to total number of colonies at the sites in the relevant categories.

species richness was likewise defined as the mean number of species at that site. Assuming no recent external disturbances (and since we have been visiting these reefs on a regular basis for the past seven years, this assumption is reasonable), site carrying capacity is therefore a reflection of the ability of the site to support gorgonians while site species richness is an indicator of the level of competition at that site.

Species were initially categorised according to the following: sites with high/low carrying capacity (higher or lower than mean colony density), and sites with high/low species richness (higher or lower than mean species richness). The ten most dominant species at each of these categories of sites were listed (Table 3). Only three families (Subergorgiidae, Plexauridae, and Ellisellidae) were represented in any of these lists, further establishing their dominance on Singapore reefs. *Subergorgia suberosa* and *Ctenocella* sp. A were again the two most dominant species in all four site categories examined. *Echinogorgia* sp. D and *Junceella* cf. *gemmacea* were better represented in communities where the site carrying capacity was low, increasing in rank from '8' to '3' and '9' to '4', respectively. At sites with low species richness, *S. suberosa*, *Junceella* sp. A, and *Ctenocella* cf. *umbraculum* became more dominant, each increasing their share of the total site composition (in terms of number of colonies) compared with sites where species richness was higher than average. In particular, *Junceella* sp. A also significantly improved on its rank from '7' to '3'. All other species decreased in occurrence when comparing sites with high versus low species richness.

Sites were further differentiated based on different combinations of site colony carrying capacity and species richness (Table 4). This enabled a more precise differentiation of sites, e.g., two sites, both of which support a large number of colonies could be differentiated based on the fact that one has high inter-specific competition while the other exhibits low levels of inter-specific competition. *Subergorgia suberosa* was found to maintain its dominance over other species in all these combinations of site carrying capacity or species richness. This species appears to be particularly well adapted to environmental conditions in Singapore compared to other gorgonian species. Alternatively, this species may simply be the most efficient coloniser of newly available space and is subsequently able to hold on to the place where it has settled. However, this latter explanation necessitates periodic major disturbances such as typhoons or hurricanes that will 'clear' previous colonisation, and these do not occur in Singapore. The specific environmental parameters that control gorgonian distribution in Singapore have not been established as yet, although water depth (Bayer, 1961), irradiance levels (Grigg, 1974), availability of substrata (Bayer, 1961; Kinzie, 1973; Jordan, 1989), bottom sediment transport (Yoshioka and Yoshioka, 1989a), topographic relief (Yoshioka and Yoshioka, 1989a, 1989b) and strength of surge action (Kinzie, 1973; Birkeland, 1974; Jordan, 1989) are known to affect local distributional patterns of gorgonians. What is clear is that at sites where some species were limited (as reflected in low site species richness) by site-specific environmental factors, *S. suberosa* took up a significantly higher percentage of the available space compared to sites with a high species richness, regardless of the carrying capacity of the site. At sites where both the colony carrying capacity and species richness were high, and at sites where these were both low, *Ctenocella* sp. A was the second most dominant species. At more 'intermediate' sites where the carrying capacity was high but species richness low, and vice versa, this dominance was reduced. The same pattern was also seen in Plexaurid sp. A. These two species may have a higher tolerance for environmental conditions that other species do not do well in, but are not able to be as successful when environmental conditions do not exclude these competitors. At sites with high carrying capacity and high species richness, the relative competition factor is reduced by the larger number of potential sites for settlement.

Conclusions/Summary

Gorgonian species richness and mean colony density ranged from 9-17 species per site and 4.8-28.2 colonies per m^2, respectively. Among the six gorgonian families (Goh and Chou, 1996) found in Singapore, the Plexauridae, followed by the Ellisellidae and the Subergorgiidae, was the most dominant

Table 4. Comparison of mean number of colonies per species between sites with different combinations of colony carrying capacity and species richness.

	High Colony Carrying Capacity[2]				Low Colony Carrying Capacity[2]			
	High Richness[3]		Low Richness[3]		High Richness[3]		Low Richness[3]	
Species[1]	**Mean[4]**	**Rank**	**Mean[4]**	**Rank**	**Mean[4]**	**Rank**	**Mean[4]**	**Rank**
F. Subergorgiidae								
Subergorgia suberosa	16.6	1	29.5	1	18.5	1	26.0	1
F. Plexauridae								
Echinomuricea pulchra	3.6	10	1.4	-	0	-	0.4	-
Echinogorgia sp. A	7.8	5	8.5	4	7.4	6	5.2	9
Echinogorgia sp. B	9.6	4	2.9	10	6.6	7	5.7	7
Echinogorgia sp. C	6.6	7	7.5	6	7.5	5	6.0	6
Echinogorgia sp. D	6.7	6	4.3	8	11.2	4	9.1	3
Plexaurid sp. A	11.9	3	6.5	7	3.8	10	7.8	4
F. Ellisellidae								
Junceella (Junceella) sp. A	5.5	8	9.5	2	5.5	9	6.5	5
J.(Dichotella) cf. *gemmacea*	4.6	9	9.5	2	12.2	2	4.4	10
Ctenocella (Umbracella) cf. *umbraculum*	3.5	-	3.0	9	5.6	8	5.6	8
C. (Umbracella) sp. A	14.1	2	7.9	5	11.5	3	14.6	2

Note: 1. For clarity, only the top ten ranked species are shown in this table.
2. Sites with high colony carrying capacities are defined as those where the density of colonies is greater than the mean (=92 colonies per m^2) for the 13 sites where gorgonians were found (Pulau Salu was excluded because no gorgonians were found at the site). Low site carrying capacity reflects the situation where colony density is less than or equal to 92 colonies per m^2.
3. Sites with high species richness are defined as those where the species richness is greater than the mean (=13 species per site) for the 13 sites where gorgonians were found (Pulau Salu was excluded because no gorgonians were found at the site). Low site species richness reflects the situation where species richness is less than or equal to 13 species per site.
4. Mean = mean percentage composition of species with respect to total number of colonies at the sites in the relevant categories.

in terms of number of colonies. Even when sites were categorised according to site carrying capacity and species richness, and each group was considered separately, only 11 species (all from these three families) were found in the top ten ranked positions.

In general, *Subergorgia suberosa*, followed by *Ctenocella* sp. A dominated other gorgonian species, both in terms of abundance and ubiquity. The implication of this is that they are not only successful competitors for space, but also efficiently disperse larvae that can colonise new sites. In particular, this dominance was found to be irrespective of the carrying capacity or species richness present at a particular site. For *S. suberosa*, this dominance was maintained in all categories when sites were grouped according to all possible combinations of high/low site colony carrying capacity and high/low site species richness. *Ctenocella* sp. A maintained its overall standing as the second-most dominant gorgonian species in Singapore at sites where both the carrying capacity and species richness were high and also at sites where these were both low. This dominance appeared to be diminished at sites with high carrying capacity but low species richness and vice-versa.

Junceella cf. *gemmacea* and *Ctenocella* cf. *umbraculum* were ranked poorly for numerical dominance, but had a ubiquitous distribution. They may not be able to dominate other species with respect to space within an established gorgonian community at a particular site, but are able to be dispersed widely. Plexaurid sp. A showed a reverse distribution pattern, being numerically dominant but relatively poorly distributed.

Echinogorgia sp. D and *Junceella* cf. *gemmacea* were significantly more dominant at sites with low versus high carrying capacity. At sites with low species richness, *Subergorgia suberosa*, *Ctenocella* cf. *umbraculum* and *Junceella* sp. A were more dominant than at sites with high species richness.

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