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Rhodolith Bed Composition in the Southwestern Gulf of California, México

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Abstract The composition of rhodolith beds, relative abundance of species and growth-forms, was evaluated in relation to a depth gradient and substratum along the southwestern Gulf of California. Replicate transects were established in twelve rhodolith beds to evaluate the species and growth form distribution in relation to depth (2-7, 7-12 and 12-20 m) and habitat (sand vs. rock). Four species with four growth-forms were determined: *Lithophyllum margaritae* which ranged in growth-form from fruticose, fructifoliose to foliose; *Lithothamnion muelleri* where the growth-form range was lumpy to fruticose; in both *Neogoniolithon trichotomum* and *Mesophyllum engelhartii* where only fruticose growth-form was observed. *Lithophyllum margaritae* was the most abundant species in relation to depth in the sandy habitat and *Lithothamnion muelleri* was dominant in the shallow rocky areas. The presence of *N. trichotomum* was limited to shallow sandy beds and *M. engelhartii* was limited to the deeper areas. Growth-forms also showed a variation with depth and substrata, in where fruticose forms dominate in sandy areas, lumpy forms dominate in rocky habitats and foliose forms were more abundant in the deeper areas. The differences in the abundance of each species and growth form might be explained by a combination of biological features; growth rate, density of reproductive structures and calcification rate in relation to environmental features such substrate type (rock vs. sand), water motion and light.

Key words: Rhodolith beds, Growth-forms, *Lithophyllum*, *Lithothamnion*, *Neogoniolithon, Mesophyllum*

Introduction

Rhodolith beds are widely distributed, forming extensive communities of free-living coralline algae in a wide range of depths (Foster, 2001). They are known to collectively create a fragile, structured biogenic matrix (Foster *et al*., 1997). This matrix provides habitat for diverse assemblages of invertebrates and algae (Cabioch, 1969; Keegan, 1974; Steller *et al*., 2003). Rhodolith beds are one of the major nearshore biogenic sediment producers (Mabesone *et al*., 1972; Wilson and Bosence, 2003), and are useful for the interpretation of distinct paleo-environments (Carannante *et al*., 1988; Freiwald *et al*., 1991; Foster *et al*., 1997; Basso, 1998).

Rhodoliths have a wide bathymetrical and geographical distribution (review by Foster, 2001), but very little is known about the species composition of the beds on ecological or geographical scales. Individual rhodoliths might be formed by a single species (Payri, 1997; Riosmena-Rodríguez *et al*., 1999) or a group of species (Basso, 1998). In turn rhodolith beds can be composed of a single dominant species ex. *Hydrolithon reinboldii* (Payri, 1997) or a combination of several dominate species such as *Lithothamnion corallioides* and *Phymatolithon calcareum* and *Lithothamnion glaciale* in Scotland (Birkett *et al*., 1995). The proportions in which these species are present vary both spatially and temporally (Birkett *et al*., 1995), although no specific evaluation has been made in relation to environmental conditions. It is commonly found that fruticose growth-form are most common form shallow water beds (Kempf, 1970; Adey and McKibbin, 1970; Bosence, 1985; Piller and Rasser, 1996) and foliose forms in deep water beds although this has not been intentionally

evaluated. Studies have suggested that species and growth form composition are variable, and these variations have been attributed to distinct environment conditions (Blunden *et al.*, 1977; Bosence, 1983; Steller and Foster, 1995). In many areas the species composition of beds is compromised due to the poor taxonomic status of the species involved.

In the Gulf of California, Steller and Foster (1995) have shown that rhodolith morphology is related to a depth gradient. Foster *et al.* (1997) described that beds are organized in two environments (wave and current beds) linked with depth and water motion; also the beds are distributed in two substrates sandy and rocky-sandy areas, where blunt morphologies dominate in exposed areas with high wave action. Steller *et al.* (2003) suggested that beds are composed of three species (*Neogoniolithon trichotomum*, *Lithothamnion muelleri* and *Lithophyllum margaritae*) and dominated by *L. margaritae*. These conclusions were based on limited spatial and geographical sampling and no growth-form evaluation was presented.

The aims of this study are to: 1) describe the species and growth-form composition of the beds in the southwestern Gulf of California, México; 2) determine if there is any relationship of species and growth-form composition with depth, substrate and/or geographic distribution.

Material and Methods

To understand the species and growth form composition of rhodolith beds, 12 beds occurring between Santa Rosalia to Los Cabos were selected. The beds were chosen to represent different depths (2-7, 7-12, 12-20), type of bed (current vs. wave), habitat (only sandy vs. mixture of sand-rock) and geographical location (north vs. south). All the selected beds are described in Riosmena-Rodriguez *et al.* (2006, Fig. 2, Table 1). At each site two unrelated random 50m transects were laid out along the sea floor at the planned depth. The first 50 intercepted plants, bigger than 2cm diameter, with good purple-pink coloration, were collected, from both transects.

The samples were dried in the shade and determined to species level based on Riosmena-Rodríguez *et al.* (2006, Figs 3-5, Table 1). After this, each species was classified into growth-forms in accordance with Woelkerling *et al.* (1993). The mean of the relative abundance was measured as the proportion of each species and growth-form were clumped at each treatment (depth, substrate type, wave-current and habitat) and calculated (Table 2). Statistically significant differences in the species and growth-forms were assessed with ANOVA and Kruskall-Wallis tests. Tukey and Nemenyi's tests (Zar, 1996) were used to find *a posteriori* groups of means that differed significantly.

Results

The rhodolith beds are generally dominated by the species *Lithophyllum margaritae* and fruticose is the most common growth form (Table 2, Figs 1- 3). *Lithophyllum margaritae* and *Lithothamnion muelleri* have the widest range of growth forms and depth distribution present in the area (Table 2, Figs 1- 4). A clear trend was observed in relation to depth in where *L. margaritae* was the dominant among the 3 species present in all depths (Figs 1 -3), with significant differences among species at the two lower depths (Figs 2.3; $p = 0.05$) and no significant difference between species (Fig. 1). *Neogoniolithon trichotomum* was only present in the shallow depth (2-7m); *Mesophyllum engelhartii* was only present in the deeper areas (over 20m), and the proportion of *L. muelleri* was greater in the shallow (2-7m) and middle regions than the deeper areas (20m, Fig. 1).

The three growth-forms identified in the samples of *Lithophyllum margaritae* were found in all depths although there was variation in the proportions found between depths (Figs 4-6). The proportion of the fruticose form was consistent between 2-7 and 7-12m but significantly different than

Table 1. Principal features of each of the sampling localities. Depth, type of bed and main substrate are presented using the number used in Riosmena-Rodriguez *et al*., (2007).

| Locality	Sampling depth (m)	Type of bed	Main Substrate	Bed number in Figure 1 of Riosmena- Rodriguez et al. (2006)
1. Cardón	2-7, 7-12	Wave	Sandy	26
2. Requesón	2-7, 7-12	Wave	Sandy	27
3. Pocitos	2-7, 7-12	Wave	Sandy	29
4. Coloradito	2-7, 7-12	Wave	Sandy	30
5. Coronado I	7-12	Wave	Sandy	32
6. Coronado II	12-20	Current	Sandy	33
7. Diguet	12-20	Current	Sandy	42
8. Diana	12-20	Current	Sandy	44
9. San Francisco	12-20	Current	Sandy	45
10. San Lorenzo	12-20	Current	Sandy	48
11. Calerita	2-7	Wave	Rock/sandy	49
12. Punta Perico	12-20	Current	Rock/sandy	53
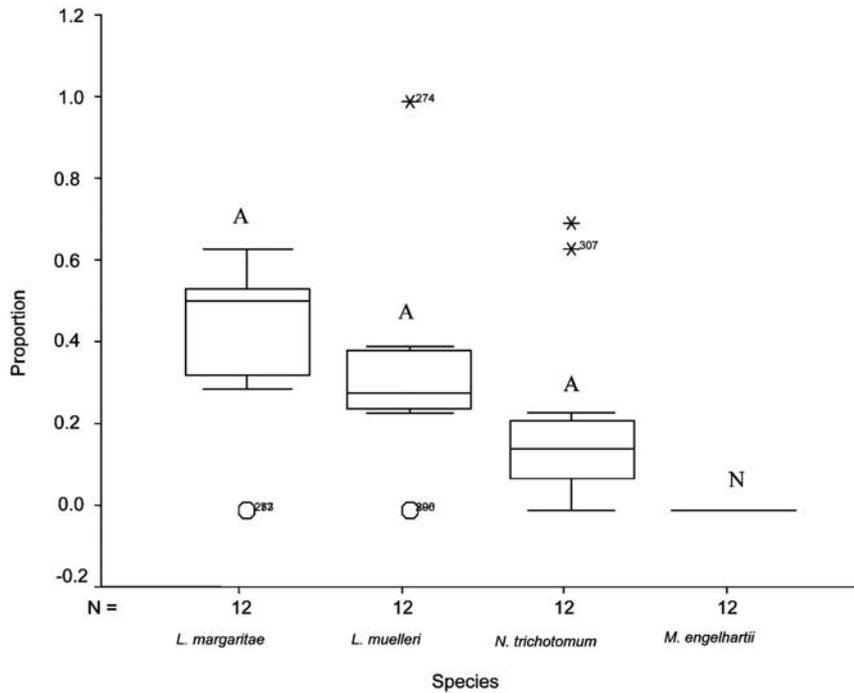
Fig. 1. Proportion of rhodolith bed forming species between 2-7m depth. Box plots denoted by a different capital letter differ significantly by ANOVA test ($p \leq 0.05$) with post-hoc Tukey test, asterisks and circles represent the significant group. Bars represent standard deviation.
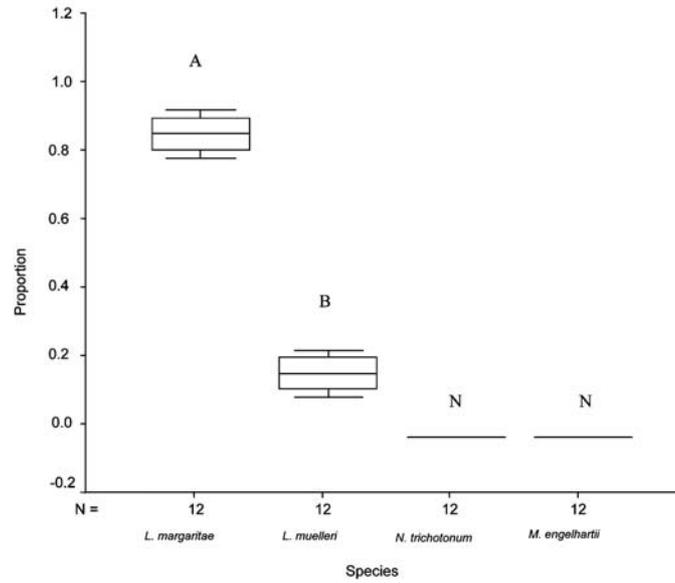
Fig. 2. Proportion of rhodolith bed forming species between 7-12m depth.
Meaning of symbols and letters are the same as in Fig.1.
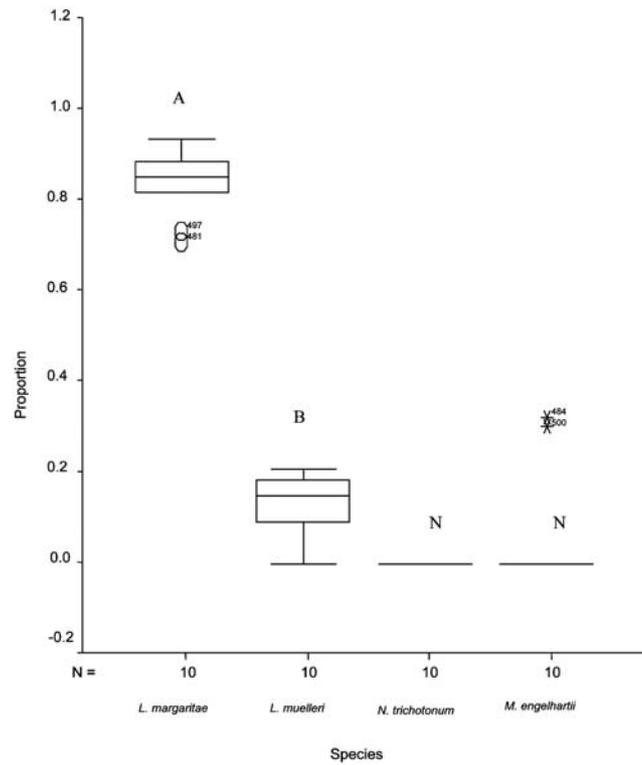
Fig. 3. Proportion of rhodolith bed forming species between 12-20m depth.
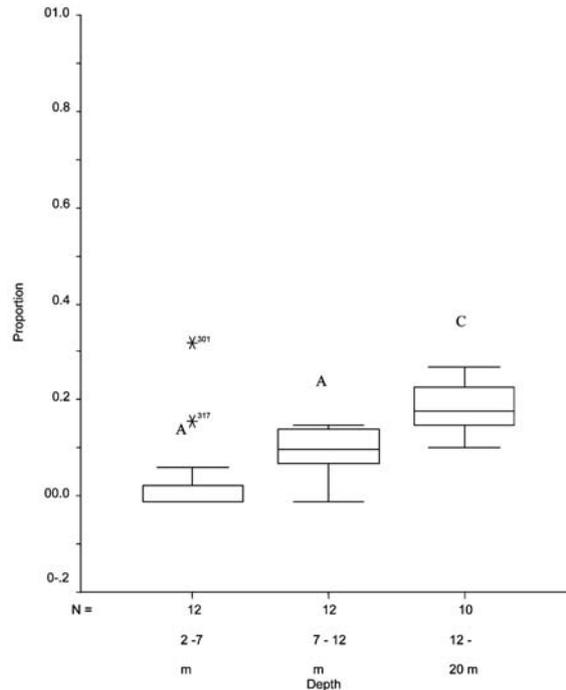Meaning of symbols and letters are the same as in Fig.1.
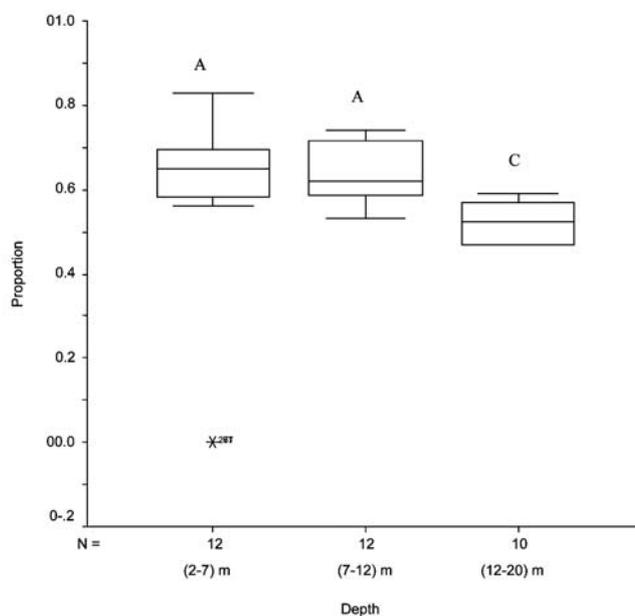
Fig. 4. Proportion of fructicose morphology of *L. margaritae* by depth. Box plots denoted by a different capital letter differ significantly by K-W test (p ≤ 0.05) with post-hoc Dunn. Bars represent standard deviation.
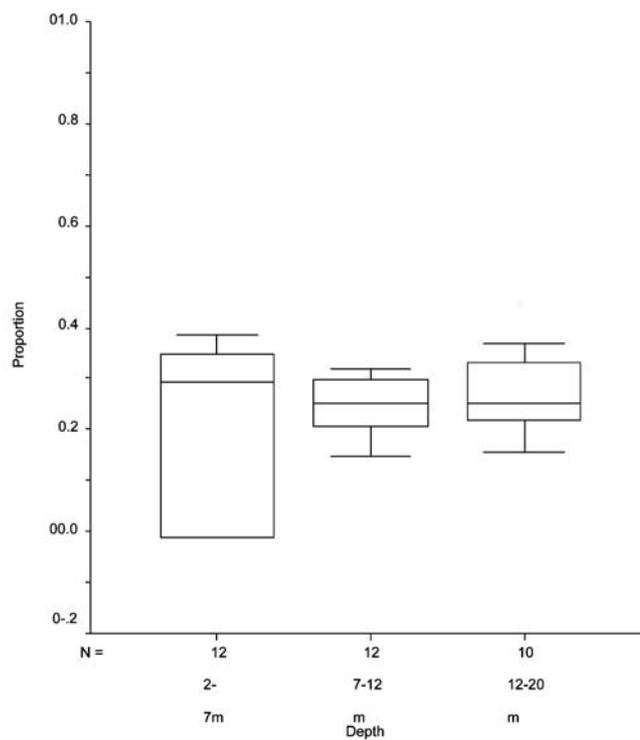

Fig. 5. Proportion of fructifoliose morphology of *L. margaritae* by depth. Meaning of symbols and letters are the same as in Fig.4.

Table 2. Composition of the species and growth form in each environmental condition. Data are mean ± standard deviation, *NP* = Not present. The fist number shows the proportion of the growth morphologies for each species in the corresponding environment. The total number printed in bold, shows the proportion of each species at various environmental conditions.

Specie	Growth-form	Depth			Substratum		Bed type	
		2-7 m	**7-12 m**	**12-20 m**	**Sand**	**Rock**	**Wave**	**Current**
		N (12)	N (12)	N (10)	N (30)	N (4)	N (24)	N (10)
L. margaritae (0.68±0.24)	Fructicose	0.56±0.27	0.64±0.07	0.52±0.05	0.62±0.09	0.25±0.29	0.60±0.20	0.52±0.05
	Fructifoliose	0.23±0.17	0.26±0.06	0.28±0.07	0.27±0.10	0.18±0.21	0.24±0.13	0.28±0.07
	Foliose	0.05±0.10	0.11±0.05	0.20±0.05	0.12±0.10	0.07±0.08	0.08±0.08	0.20±0.05
	Total	**0.42±0.21**	**0.84±0.04**	**0.83±0.07**	**0.73±0.18**	**0.35±0.36**	**0.63±0.26**	**0.83±0.08**
L. muelleri (0.22±0.22)	Lumpy	0.30±0.30	0.04±0.10	0.26±0.07	0.15±0.17	0.50±.0.57	0.17±0.28	0.26±0.22
	Fructicose	0.54±0.40	0.96±0.10	0.54±0.11	0.78±0.27	*NP*	0.75±0.36	0.54±0.33
	Total	**0.37±0.31**	**0.16±0.04**	**0.11±0.07**	**0.18±0.09**	**0.50±0.57**	**0.27±0.25**	**0.11±0.07**
N. trichotonum (0.075±0.17)	Fructicose	0.83±0.38	*NP*	*NP*	0.33±0.48	*NP*	0.42±0.50	*NP*
	Total	**0.21±0.22**	**NP**	**NP**	**0.09±0.17**	**NP**	**0.11±0.19**	**NP**
M. engelhartii (0.018±0.07)	Lumpy	*NP*	*NP*	0.05±0.10		0.11±0.14		0.05±0.10
	Fructicose	*NP*	*NP*	0.15±0.32	*NP*	0.39±0.44		0.15±0.32
	Total	**NP**	**NP**	**0.06±0.13**	**NP**	**0.15±0.18**	**NP**	**0.06±0.13**

Fig. 6. Proportion of foliose morphology of *L. margaritae* by depth. Box plots denoted by a different capital letter differ significantly by K-W test (p ≤ 0.05) with post-hoc Dunn Test, asterisks represents the significant group. Bars represent standard deviation.
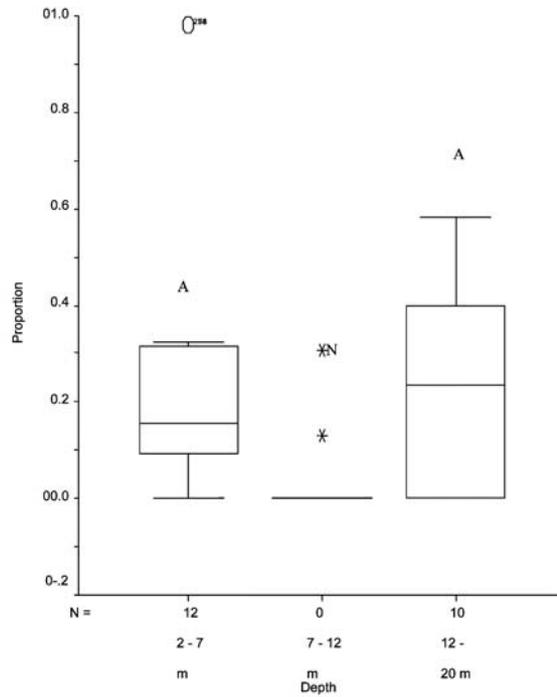
Fig. 7. Proportion of lumpy morphology of *L. muelleri* by depth. Box plots denoted by a different capital letter differ significantly by K-W test (p ≤ 0.05) with post-hoc Dunn Test, asterisks represent the significant group. Bars represent standard deviation.
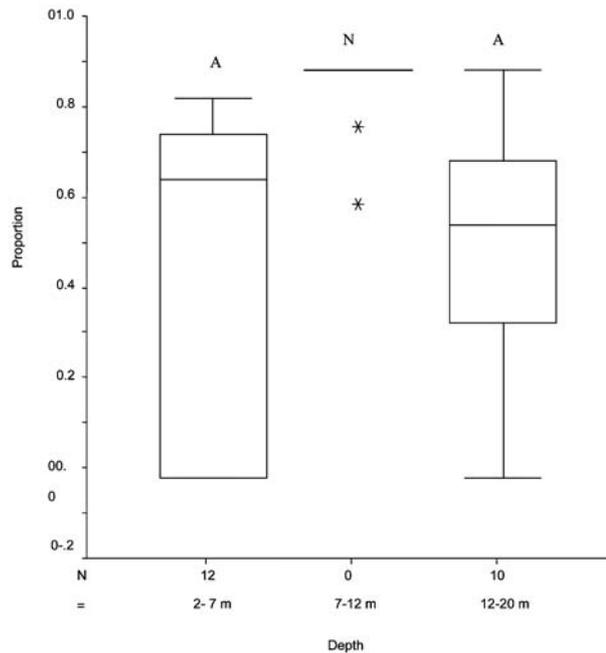
Fig. 8. Proportion of fructicose morphology of *L. muelleri* by depth. Meaning of symbols and letters are the same as in Fig.4.

the proportion found at 20m. The proportions of the foliose forms inversely corresponded with the proportions of the fruticose form showing significant differences between shallow beds in relation to the deeper areas (Fig. 6). The proportion of the fructifoliose form remained relatively stable between depths and no significance differences were observed (Fig. 5).

Fruticose and lumpy growth-forms were observed in *L. muelleri*, both were present at the extremes of the surveyed depths but not common in the middle range (Figs 7 - 8). The lumpy growth form was more widely dispersed in the deeper water (Fig. 7) where as the fruticose form was more widely dispersed in the shallow areas (Fig. 8). Comparisons of the abundance of species between the current vs. wave beds (Table 2) showed a clear distinction between the forms seen, an example of this is the restriction of *Neogoniolithon trichotomum* to the upper areas (2-7m).

In relation to substrate type (Table 2) the dominance of *Lithothamnion muelleri* is clear in relation to all species, except for *L. margaritae*, in shallow water. The presence of *Mesophyllum engelhartii* in deep areas is noticeable but not significant. The absence of *Neogoniolithon trichotomum* is noticeable and significant in relation to the other species (Table 2). The growth form composition in each substrate type had similar trends in where blunt forms dominate rocky/sandy habitats and fruticose dominates in the sandy areas (Table 2).

Discussion

One of the major problems in working with rhodoliths and coralline algae in general is the identification of specimens to the generic or specific level. The classification within the order Corallinales has changed from the recognition of one or two families (living and fossil) in the early 20th century to four families at the beginning of the 21st century (Harvey *et al*., 2003). At the generic level, the changes have been more dramatic and a major evaluation (Woelkerling 1988) was necessary to settle many of the classical problems. Boundaries of genera and species remain a common problem best solved by regional monographs using consistent diagnostic features (Riosmena-Rodriguez *et al*., 1999; Harvey *et al.,* 2003). Two of the major problems are that many growth-forms can occur in the same species (Woelkerling *et al*., 1993; Riosmena-Rodriguez *et al*., 1999) and a single rhodolith can be formed by several species (Basso, 1998).

Once taxonomic approaches are based on anatomical structures, and the evaluation of these structures is done (Riosmena-Rodríguez *et al*., 2007, Table 1) it is possible to understand patterns of distribution. In our study several species are present but it is the high morphologically variable *L. margaritae* show foliose, fruticose, lumpy growth forms, or combinations of them (Riosmena-Rodríguez *et al*., 2007, Fig. 3), that dominants the sandy habitats in the southern part of the study area (Fig. 1- 3 Table 2). Similarly *Phymatolithon calcareum*, which also has great morphological variability, (Cabioch, 1966) is one of the dominant species with a wide bathymetric and geographic distribution, found along the Northeastern Atlantic ranging from the temperate areas (Irvine and Chamberlain, 1994), the Mediterranean (Cabioch *et al*., 1992) to the Canary Isles (Afonso-Carrillo and Gil-Rodriguez, 1982) and the Northeastern Pacific (Konar *et al*., 2006). Fruticose and lumpy morphologies have been described for *Hydrolithon reinboldii* (Payri, 1997), which is found widely in the Indo-Pacific. Based on the above observations, most of the species around the world range from fruticose to lumpy forms with a transition from mostly fruticose plants to more abundance of foliose plants (i.e. *L. orbiculatum* from British Isles). In our study the foliose plants were relative more abundant in deeper areas, supporting the early ideas of Kempf (1970).

The observed differences in depth distribution might be explained by a combination of environmental factors such as water motion (Steller and Foster, 1995); temperature/irradiance that

might affect the growth and reproduction rate (Leukart, 1994); and the calcification rate (Payri, 1997; Payri *et al.*, 2001). The effect of the environment on coralline algal morphology and distribution is widely recorded (Steneck and Adey, 1976; Steller and Foster, 1995). Light/temperature is highly temporal variable in the southern part of the Gulf with the major change happening around 30m (Alvarez-Borrego, 1983; Caceres-Martínez *et al.*, 1992). The growth rates for most of the species are known (Rivera *et al.*, 2003; Steller, 2003), with *M. engelhartii* being the exception. The highest growth rate belongs to *Neogoniolithon trichotomum*, which grows 5.5mm per year, followed by *Lithophyllum margaritae* (2.2mm per year) (Steller, 2003) and *Lithothamnion muelleri* (0.87mm per year) (Rivera *et al.*, 2003). Considering growth rate alone, *N. trichotomum* should be dominant in sandy areas rather than *L. margaritae* and *L. muelleri* but the evident calcification is less in the first than in the later 2 species (this can be observed when decalcification is developed as in Riosmena-Rodriguez *et al.*, 1999) suggesting that it would be easier to break apart or suffer from physical damage. Also, when the relative density of conceptacles in each species is evaluated *L. margaritae* has the highest density of tetrasporangial conceptacles, mostly tetrasporangial, and in *N. trichotomum* conceptacles are not common at all (Riosmena-Rodriguez, pers. obs.). The lower amount calcium per individual and thus its ability to grow faster than *L. muelleri* and reproduce more often than *N. trichotomum* explain the higher density of *L. margaritae* in sandy habitats. The dominance of *L. muelleri* in rocky habitats can be explained by its relatively better survivability in relation to abrasion.

A similar trend can be reasoned for the dominance of the fruticose growth forms in our areas and elsewhere (Irvine and Chamberlain, 1994; Payri, 1997; this study). The fruticose form may have greater resistance to physical damage caused by water movement and better energy efficiency derived from photosynthesis than the other growth forms. The circular-oval shape of the fruticose form enables it to capture light from any angle and provides some resistant to breakage. While lumpy (coarse) or foliose (thinner) growth-forms have unequal surfaces with longer or wider sides that might be able to capture light in one direction. Foliose plants are orientated to receive light mostly from the upper layers and lose out on the scattered reflections in the superficial waters, a possible adaptation to deep areas but one that results in an increase in fragility. Lumpy plants may better adapted to rocky areas are more abundant.

Acknowledgements

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