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Ecological patterns of polychaete assemblages associated with the Mediterranean stony coral *Cladocora caespitosa* (Linnaeus, 1767): a comparison of sites in two biogeographic zones (Adriatic and Aegean Sea)

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Abstract

The Mediterranean stony coral *Cladocora caespitosa* (Linnaeus, 1767) is a well-known habitat builder, and as such hosts a diversified faunal assemblage. Although polychaetes are one of the most abundant and diverse macrobenthic groups associated with *C. caespitosa* colonies, our knowledge of their ecological features in this association is still limited. The aim of this paper was to gather and compare the most comprehensive data available on polychaetes associated with *C. caespitosa* in the Adriatic and the Aegean Seas, and to test for differences between these geographic areas. To this end, differences were tested in terms of: (i) richness and structure of polychaete assemblages; (ii) feeding and functional traits of assemblages; (iii) the main factors influencing those aspects, (iv) the relationship between polychaete assemblages richness and *Cladocora* colony size, estimated richness. Differences were observed between the Adriatic and the Aegean assemblages, in terms of richness, species composition and relative proportion of the dominant feeding guild (filter feeders most abundant in the Aegean and carnivores in the Adriatic) and motility mode (sessile most abundant in the Aegean and motile in the Adriatic). Conversely, cosmopolitan and Atlanto-Mediterranean species dominated the assemblages in both geographic areas, and the same Species-Area Relation model proved to be effective for richness estimation in both geographic areas.

Keywords: Benthic ecology; Habitat builder species; Polychaeta; Mediterranean Sea.

Introduction

The Mediterranean stony coral *Cladocora caespitosa* (Linnaeus, 1767) is the only native colonial and obligate zooxanthellate coral in the Mediterranean Sea (Zibrowius, 1980); it is present throughout the basin but is only locally abundant (Peirano *et al.*, 1998). It lives in different environments, from shallow photophilic algal communities to deeper circalittoral zones (e.g., Chefaoui *et al.*, 2017; Kersting *et al.*, 2017). The species is particularly sensitive to different types of environmental changes, either anthropogenic or natural (Rodolfo-Metalpa *et al.*, 2005; Kružić *et al.,* 2012; Kersting *et al.*, 2015) and is vulnerable to catastrophic events due to slow growth dynamics (Kersting *et al.*, 2014). Population declines have been recorded in many areas of the Mediterranean Sea (Kersting *et al.*, 2013; Kružić *et al.,* 2014). Consequently, the species has been classified as "Endangered" in the IUCN Red List (Casado de Amezua *et al.*, 2015). This species is a well-known habitat builder; it is physiologically and morphologically similar to the typical tropical reef-building corals, and as such hosts a diverse faunal assemblage (Zibrowius, 1980; Peirano *et al.*, 1998). Given the endangered state of the host, a method to estimate species richness for associated macrofauna in a non-destructive way was recently proposed (Pitacco *et al.*, 2017; Pitacco *et al.*, 2019). This method consists in the application of a Species-Area Relationship (SAR) model, based on the Arrhenius equation (Arrhenius, 1921), which describes one of the most fundamental ecological relationships, i.e., a positive correlation between the size of an area and the number of species encountered in it. This method has been widely used for biodiversity estimates, in particular in large-scale terrestrial environments (Neigel, 2003). However, estimating the richness of coral associated macrofauna based on the colony size is also efficient (Pitacco *et al.*, 2017, 2019). Nevertheless, available literature about macrobenthic fauna associated with *C. caespitosa* is still fragmented, and often limited to a single taxonomic group (e.g., echinoderms,

Zavodnik, 1976; polychaetes, Arvanitidis & Koukouras, 1994), and few areas of the Mediterranean, i.e., the Adriatic (e.g., Sciscioli & Nuzzaci, 1970; Pitacco *et al.*, 2014, 2019), the Ionian (Lumare, 1965) and the Aegean Seas (Koukouras *et al.*, 1998). Very few works have analyzed the entire macrobenthic associated community to species level: one in the Ionian Sea (Lumare, 1965), two in the Adriatic Sea (Pitacco *et al.*, 2014, 2019) and two in the Aegean Sea (Koukouras *et al.*, 1998; Antoniadou & Chintiroglou, 2010). Those works note that polychaetes are one of the most abundant and diverse macrobenthic groups associated with *C. caespitosa* colonies. Moreover, polychaetes also represent one of the most important taxonomic groups associated with *C. caespitosa* in terms of biomass (Schiller, 1993). Due to this high abundance and diversity and to the well-known functional diversity of polychaetes in general, this group likely plays important ecological roles in *C. caespitosa* colonies. Nonetheless, there are very few studies concentrated on the polychaete fauna of Mediterranean stony coral (Sciscioli & Nuzzaci, 1970; Arvanitidis & Koukouras, 1994; Chintiroglou, 1996). Thus, the aim of this paper is to increase our knowledge of polychaete assemblages associated with *C. caespitosa* in the Mediterranean from the following aspects: (i) structure of polychaete assemblages; (ii) feeding and functional traits of assemblages; (iii) main factors influencing those aspects; and (iv) relationship between polychaete assemblages and colony size, and SAR model application.

Materials and Methods

Study areas and sampling methods

Due to the aforementioned lack of available literature, the only comparable studies in terms of methodology and taxonomic resolution were restricted to the Adriatic and the Aegean Seas. Data on polychaete fauna associated with *C. caespitosa* from the Northern Adriatic Sea were obtained from Pitacco *et al.* (2019), whereas data from the Aegean Sea were retrieved from the following papers: Arvanitidis & Koukouras (1994), Chintiroglou (1996), and Koukouras *et al.* (1998) (Table 1). The datasets were merged and the species list was updated according to the current nomenclature of the World Register of Marine Species (WoRMS Editorial Board, 2019). After the merger, methodological differences that could bias the comparison were considered. In the Adriatic Sea, the exact abundance of species of the subfamily Spirorbinae was not calculated; therefore, this group was not included in the quantitative comparisons. Moreover, data from Pitacco *et al.* (2014) were considered only for qualitative analyses (species composition and frequency), since colony size was not comparable.

Data from seven different sampling sites were analyzed (Fig. 1), five from the Gulf of Trieste (Northern Adriatic Sea) and two from a site off the Chalkidiki peninsula (Northern Aegean Sea), with five colonies sampled at each site in the Gulf of Trieste, and seven along the Chalkidiki peninsula.

Table 1. Codes, geographic coordinates, depths, water temperature (T), total volume of colonies (V_{tot}) and sampling dates of sampling sites and referent publication.

Region	Site	Code	Latitude (N) Longitude (E)	Depth (m)	T (°C)	V_{tot} (cm^3)	Sampling date	Reference
Adriatic Sea	Debeli Rtič	DR	45°35'28'' 13°42'88''	5-6	22 - 23	100 - 940	19.9.2012	Pitacco *et al.* (2019)
	Cape Ronek	RR	45°32'25'' 13°36'56''	6-9	21 - 25	85 - 680	9.7.2012	Pitacco *et al.* (2019)
	Strunjanček	ST	45°32'5'' 13°36'10''	4-6	24 - 26	150 - 535	22.8.2012	Pitacco *et al.* (2019)
	Pacug	PA	45°31'34'' 13°35'24''	5-7	23 - 23	110 - 820	10.9.2012	Pitacco *et al.* (2019)
	Piranček	PR	45°31'38'' 13°34'30''	7-9	21 - 25	140 - 1715	24.7.2012	Pitacco *et al.* (2019)
	Ronek bank	GR	45º32'34'' 13° 37' 01''				5.11.2010	Pitacco *et al.* (2014)
Aegean Sea	Pirgadikia	Pir	40°20'01'' 23°43'2''	3-5	26 - 27	460 - 4670	19.7.1987	Arvanitidis & Koukouras (1994), Chintiroglou (1996), Koukouras *et al.* (1998)
	Vourvourou	Vou	40°13'29'' 23°46'09''	15-19	24 - 26	465 -1970	23.7.1987	Arvanitidis & Koukouras (1994), Chintiroglou (1996), Koukouras *et al.* (1998)

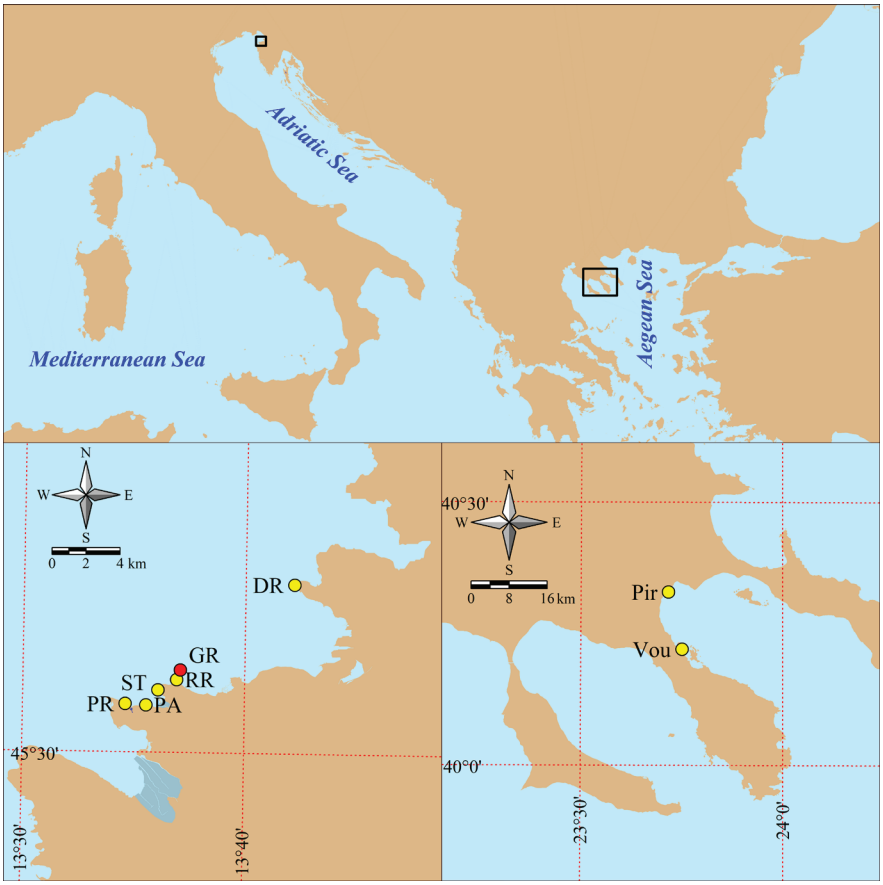

Fig. 1: Map of sampling sites. DR =Debeli Rtič, RR = Cape Ronek, ST = Strunjanček, PA = Pacug, PR = Piranček, Vou = Vourvourou, Pir = Pirgadikia, GR = Ronek bank (in red; qualitative data only).

Sampling was performed by SCUBA diving, in the Gulf of Trieste in 2012, at 4-9 m depth, and off the Chalkidiki peninsula in 1987 at 3-5 and 15-19 m depth (Table 1). The sampling and processing methods are described in Pitacco *et al.* (2019) and Koukouras *et al.* (1998). In both cases, research focused on the entire invertebrate community, with both sessile and motile species associated with coral. The additional site (Ronek bank, Fig. 1) in the Adriatic Sea, considered for qualitative analyses only, was close to Cape Ronek, but at greater depths, between 12 and 21 m depth (Pitacco *et al.*, 2014).

Environmental variables and **Cladocora** *colonies biometry*

Sampling depth, water temperature, number of sampled colonies (n), and total volume of colonies (V_{tot}) were recorded for all sampling sites. Colony microhabitat variables, i.e., percentage of living polyps (LP), interstitial volume (V_{int}), percentage of algal cover (alg), sponge cover (spg), and percentage of sediments trapped inside the colony with respect to V_{int} (sed), were available only for the Adriatic sites.

Classification in functional and biogeographic groups

Each polychaete species was assigned to one of the following 12 categories derived from a combination of motility pattern, feeding mode and the morphology of feeding structure, following Fauchald & Jumars (1979) and Jumars *et al.* (2015): HMJ = herbivore motile jawed, BMX = burrowing motile non-jawed, BSX = burrowing sessile non-jawed, CMJ = carnivore motile jawed, CMX = carnivore motile non-jawed, CDJ = carnivore discretely motile jawed, FST = filter-feeders sessile tentaculate, FSP = filter-feeders sessile pumping, SMJ = surface deposit feeders motile jawed, SMT = surface deposit feeders motile tentaculate, SDT = surface deposit feeding, discretely motile tentaculate, SST = surface deposit feeding sessile tentaculate. Overall 5 different feeding guilds: subsurface deposit feeders/burrowing (B), carnivores (C), herbivores (H), filter feeders (F), surface deposit feeders (DF), and 3 motility patterns: motile (M), discreetly motile (D) and sessile (SE) were found.

A biogeographic analysis was performed in order to estimate whether geographic distance could explain the differences in species composition. The species were assigned to the following biogeographic categories, according to the relevant literature (Bianchi, 1981; Barnich & Fiege, 2003; Musco & Giangrande, 2005; Bakalem *et al.*, 2020): aa = amphi-Atlantic, am = Atlantic-Mediterranean, amip = African Atlanto- Mediterranean and Indo-Pacific, amr = Atlantic-Mediterranean and Red Sea, amp = Atlan-

to-Mediterranean and Pacific, amrip = Atlanto-Mediterranean, Red Sea and Indo-Pacific, c = cosmopolitan, d = disjunct distribution, iam = Indo-Atlanto-Mediterranean, m = endemic Mediterranean, mrip = Mediterranean, Red Sea and Indo-Pacific.

Taxa assigned to two or more groups, or that could not be assigned to a group, were marked as NA (Not Assigned) in the subsequent analyses.

Data analysis

In order to enable comparisons between the two geographic areas, the sampling depths were classified into arbitrary ranges: 3-6 m, 6-8 m and 15-19 m.

Frequency of occurrence (%F) was calculated for each species. The identities of the most frequent species (>50% of frequency) were compared, between the Adriatic and the Aegean Seas, and between different sampling depths.

Species richness (S), abundance (N), the Shannon & Wiener diversity index (H′), and the Pielou index of equitability (J) (Clarke & Warwick, 2001) were calculated for each colony. In this paper, we chose to use total volume (V_{tot}) as the *Cladocora* colony size descriptor, being the only possible one to compare data reported from the Adriatic and the Aegean Seas. Feeding richness (Sf) was calculated as the number of feeding groups per colony, and feeding diversity (Hf) was calculated with the Shannon diversity index, using feeding richness instead of taxa richness.

To test whether the biometric characteristic of the colonies and the diversity descriptors analyzed (S, N, H', J', Sf, Hf) varied among the two geographic areas, depth ranges, and colony size classes, the Chi square test applied to the Kruskal-Wallis test (KW) by ranks and the pairwise post-hoc Wilcoxon test (W) were perfomed. The non-parametric Spearman Rank-order coefficient (r_s) (Spearman, 1907) was used to check for collinearity between depth and colony size.

PERMANOVA and PERMDISP analyses were performed to test the significance of the differences in structure of polychaete assemblages between geographic areas (2 factors, fixed: Adriatic and Aegean Seas), depth range (three factors, random: 3-6 m, 6-8 m, 15-19 m), and colony size classes (two factors, fixed: small: <1 dm^3, big: >1 dm^3). The threshold between small and big colonies was chosen on the basis of the cumulative curve for polychaete richness with increasing sampling volume, which reached the asymptote for a sampling volume of 1dm^3. The same statistical analyses were performed using the abundances of each feeding, functional and biogeographical group. The analyses were based on the Bray-Curtis similarity of square root transformed data, and on the Jaccard similarity index, with presence-absence data to test the variability of beta diversity. To calculate the *p* values for PERMANOVA and PERMDISP, we used 9999 permutations. Non- metric MDS graphs were created based on Bray-Curtis similarity of square root transformed data. Groups obtained from clusters built using the group average method were included in the MDS graphs. The species best explaining the dissimilarity among the obtained cluster groups were identified through SIMPER analysis.

Distance-based linear models (DISTLM) were used to test whether the variations in polychaete communities are explained by abiotic data. DISTLM does a partitioning of variation in a data cloud described by a resemblance matrix, according to a multiple regression model (Legendre & Anderson, 1999). Depth and colony volume were used as predictor variables, and the resemblance of species/abundance, functional traits and biogeography matrices were used as response variables.

Since a positive relationship between colony size and richness of polychaete assemblages has already been reported for both the Adriatic (Pitacco *et al.*, 2019) and the Aegean Sea (Arvanitidis & Koukouras, 1994), in this work the two datasets were combined. Regression analysis was performed using log-transformed variables (polychaete richness S_{tot} and colony size V_{tot}), after checking against strong deviations from the assumptions of normality with the Shapiro test (Shapiro & Wilk, 1965). The 95% confidence interval and prediction intervals were calculated and plotted for the entire dataset. The relationship between diversity indices, richness and abundance of the main feeding/functional groups and colony size were tested with the non-parametric Spearman Rank-order coefficient (r_s) (Spearman, 1907).

A p-value < 0.05 was chosen as a significance threshold. Calculations were performed with the PRIMER v6 + PERMANOVA software package (Clarke & Gorley, 2006; Anderson *et al.*, 2008), and vegan package (Oksanen *et al.*, 2008) for R software package v3.6.1 (R Development Core Team, 2008).

Results

Environmental and biometric data

The main abiotic and biotic characteristics of sampling sites are presented in Table 1. Colony size (V_{tot}) did not show significant differences between samples from the Adriatic and the Aegean Seas (KW chi-squared = 0.415, $p > 0.05$), or between depth ranges (KW chi-squared = 0.261, $p > 0.05$) or sampling sites (KW chi-squared = 3.390, $p > 0.05$). Colony size (V_{tot}) was not significantly correlated with depth in neither the Adriatic (r_s = - 0.015, p = 0.943) nor the Aegean (r_s = - 0.053, p = 0.856).

Polychaete assemblage composition and structure

In the Northern Adriatic Sea, 110 polychaete taxa from 22 families were reported, with 90 determined to species level. 99 taxa (82 species) were recorded from shallow *Cladocora* beds (4 - 9 m), while 43 taxa (27 species) from the deeper biogenic bank (12 - 21 m). In the Aegean Sea, 87 taxa from 27 families, with 75 taxa determined to species level were recorded. Altogether, 124 species of polychaetes from 30 families were reported from both areas,

with 40 species co-occurring in colonies from both the Adriatic and Aegean Sea sampling sites (Supplementary Material, Table S1).

The most diverse families in both areas were: Syllidae (overall 32 species; 11 Aegean, 28 Adriatic), Serpulidae (16 species; 10 Aegean, 10 Adriatic), Polynoidae (10 species; 5 Aegean, 9 Adriatic), Eunicidae (10 species; 7 Aegean, 6 Adriatic) and Terebellidae (9 species; 7 Aegean, 9 Adriatic) (Fig. 2). At the Aegean sites, the most abundant family was Serpulidae (42% of the total abundance), followed by Syllidae (11%) and Sabellidae (8%), while at the Adriatic sites the most abundant families were Eunicidae and Syllidae, each representing 18% of total abundance, followed by Serpulidae (16%) and Nereididae (12%) (Fig. 2).

Species frequency differed between sites in both geographic areas (Table 2). Some species such as *Vermiliopsis infundibulum* (Philippi, 1844) and *Pseudopotamilla reniformis* (Bruguière, 1789) were frequent only at the Aegean sites while other species, such as *Spirobranchus triqueter* (Linnaeus, 1758), *Serpula concharum* Langerhans, 1880, and *Harmothoe areolata* (Grube, 1860) were frequent only at the Adriatic sites. Conversely, some species were frequent in both areas; for instance, *Hydroides pseudouncinata pseudouncinata* Zibrowius, 1968, *Vermiliopsis striaticeps* (Grube, 1862), *Serpula vermicularis* Linnaeus, 1767, *Ceratonereis costae* (Grube, 1840), *Harmothoe spinifera* (Ehlers, 1864), *Notomastus latericeus* Sars, 1851 and *Haplosyllis spongicola* (Grube, 1855) (Table 2). The composition of the most frequent species also differed between sampling depths within the sampling areas (Table 2), but the pattern was not consistent in both geographic areas.

Significant differences in polychaete assemblage richness (S), abundance (N), and diversity (Shannon index, H') were observed between the sites from different geographic areas (Fig. 3, Supplementary Material, Table S8). On average, richness of polychaete taxa (S) was higher at the Adriatic Sea sites (37 ± 9 SD) compared to the Aegean Sea sites (28 ± 7 SD), and the same pattern was observed for abundance (Adriatic: 227 ± 168 SD; Aegean: 135.5 ± 67.5) and Shannon diversity index (Adriatic: 2.9 ± 0.3 SD, Aegean: 2.7 ± 0.2 SD). In the Adriatic, richness (45 ± 7 SD), abundance (320 ± 132 SD) and diversity (3.16 ± 0.16 SD) were significantly higher in bigger than 1 dm^3 colonies than in smaller colonies (less than 1 dm^3) (S = 29 ± 7 SD, N = 142 ± 86 SD, H' = 2.80 ± 0.30 SD), whereas in the Aegean the figures did not vary significantly with colony size (Fig. 3, Supplementary Material, Table S8). Colonies bigger than 1dm^3 at the Adriatic sites displayed significantly higher richness, abundance, and diversity than colonies bigger than 1 dm^3 in the Aegean (S = 27 ± 8 SD, N = 124 ± 49 SD, H' = 2.76 ± 0.29 SD), whereas richness, abundance and diversity associated with small colonies did not vary between the two geographic areas (Fig. 3, Supplementary Material, Table S8). Richness, abundance, and diversity did not differ significantly between sampling depths, for both the Adriatic and the Aegean Sea (Fig. 3, Supplementary Material, Table S8), but the shallower samples from the Adriatic (3-6 m) showed significantly higher diversity (3.03 ± 0.33) than the samples from the Aegean at the same depth (2.77 ± 0.16).

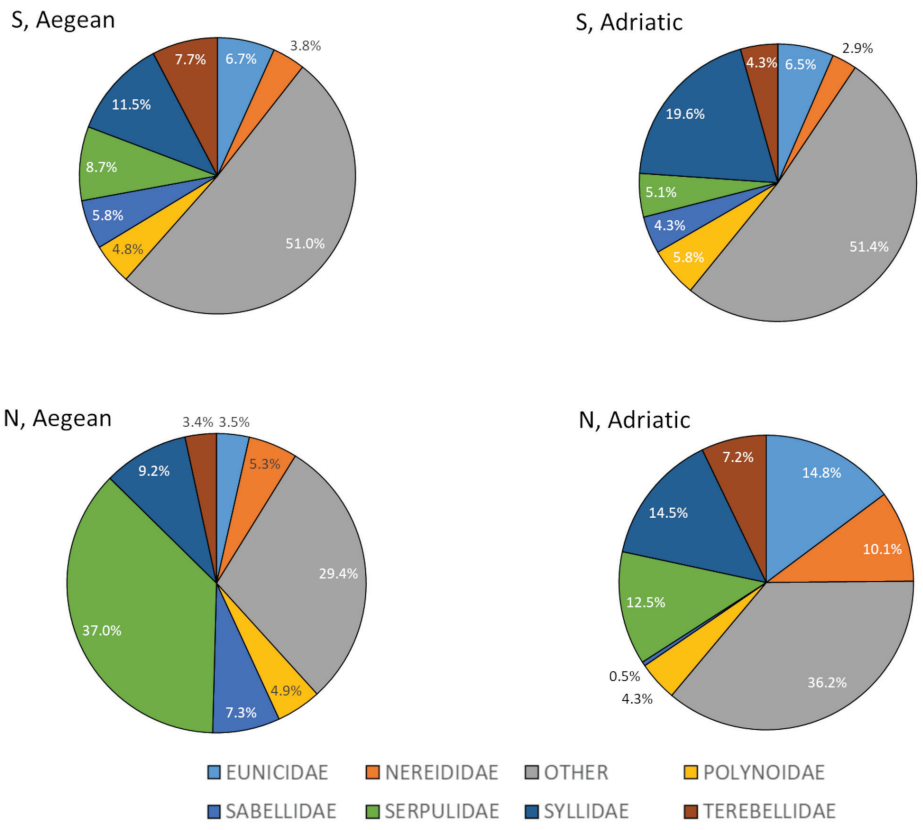

Fig. 2: Cumulative species richness (S) and abundance (N) of polychaetes for the dominant polychaete families in the Adriatic (right) and the Aegean Sea (left).

Table 2. Frequency of the most frequent species (>50% of frequency) found in the two areas analyzed, at the different sampling depths. n = number of samples.

Geographic area	**Adriatic sea**	**Aegean Sea**		
Depth range	4 - 9 m	12 - 21 m	3 - 5 m	15 - 19 m
n	25	3	7	7
Reference	Pitacco *et al.*, 2019	Pitacco *et al.*, 2014	Arvanitidis & Koukouras 1994; Chintiroglou, 1996	Arvanitidis & Koukouras 1994; Chintiroglou, 1996
Most frequent species				
Ceratonereis costae (Grube, 1840)	84%	100%		86%
Cirriformia tentaculata (Montagu, 1808)	72%	67%		
Dodecaceria concharum Örsted, 1843	92%	100%		
Eunice vittata (Delle Chiaje, 1828)	96%	100%		
Haplosyllis spongicola (Grube, 1855)	64%	100%		71%
Harmothoe areolata (Grube, 1860)	56%	100%		
Harmothoe extenuata (Grube, 1840)	84%			
Harmothoe spinifera (Ehlers, 1864)		67%	100%	86%
Hydroides pseudouncinata pseudouncinata Zibrowius, 1968	56%	67%	100%	86%
Leodice torquata (Quatrefages, 1866)	92%			
Lepidonotus clava (Montagu, 1808)			100%	
Lumbrineris coccinea (Renier, 1804)	68%	100%		
Lumbrineris latreilli Audouin & Milne Edwards, 1833	60%	100%		
Lysidice ninetta Audouin & H Milne Edwards, 1833	96%	100%		
Lysidice unicornis (Grube, 1840)	88%	67%		
Nereis rava Ehlers, 1868	80%	100%		
Notomastus latericeus Sars, 1851	88%	67%	86%	
Palola siciliensis (Grube, 1840)	68%	100%		
Polycirrus aurantiacus Grube, 1860				86%
Psamathe fusca Johnston, 1836			100%	
Pseudopotamilla reniformis (Bruguière, 1789)			57%	71%
Scoletoma impatiens (Claparède, 1868)	60%	67%		
Serpula concharum Langerhans, 1880	84%	100%		
Serpula vermicularis Linnaeus, 1767		67%	71%	
Spirobranchus polytrema (Philippi, 1844)			100%	
Spirobranchus triqueter (Linnaeus, 1758)	84%	100%		
Syllis alternata Moore, 1908	56%			
Syllis ferrani Alós & San Martín, 1987	72%			
Syllis gerlachi (Hartmann-Schröder, 1960)	72%			
Syllis hyalina Grube, 1863				86%
Syllis spp.		100%		
Syllis variegata Grube, 1860	96%			
Trypanosyllis zebra (Grube, 1860)	68%			
Vermiliopsis infundibulum (Philippi, 1844)			100%	100%
Vermiliopsis striaticeps (Grube, 1862)	84%	100%	100%	100%

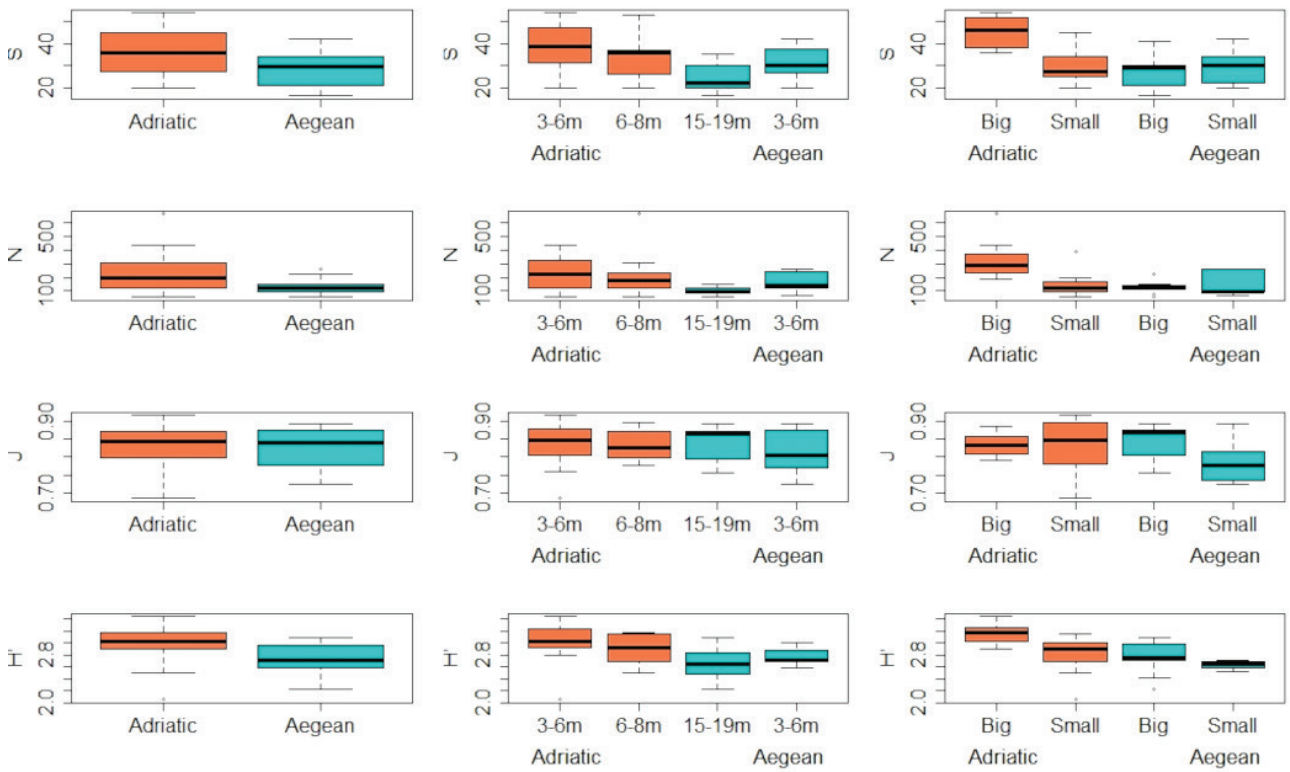

Fig. 3: Boxplot showing variability in the average values of diversity descriptors of polychaete assemblages between geographic areas (left), depth ranges (central) and colony sizes (right). S = polychaete richness, N = polychaete abundance, J = Pielou equitability index, H'= Shannon diversity index.

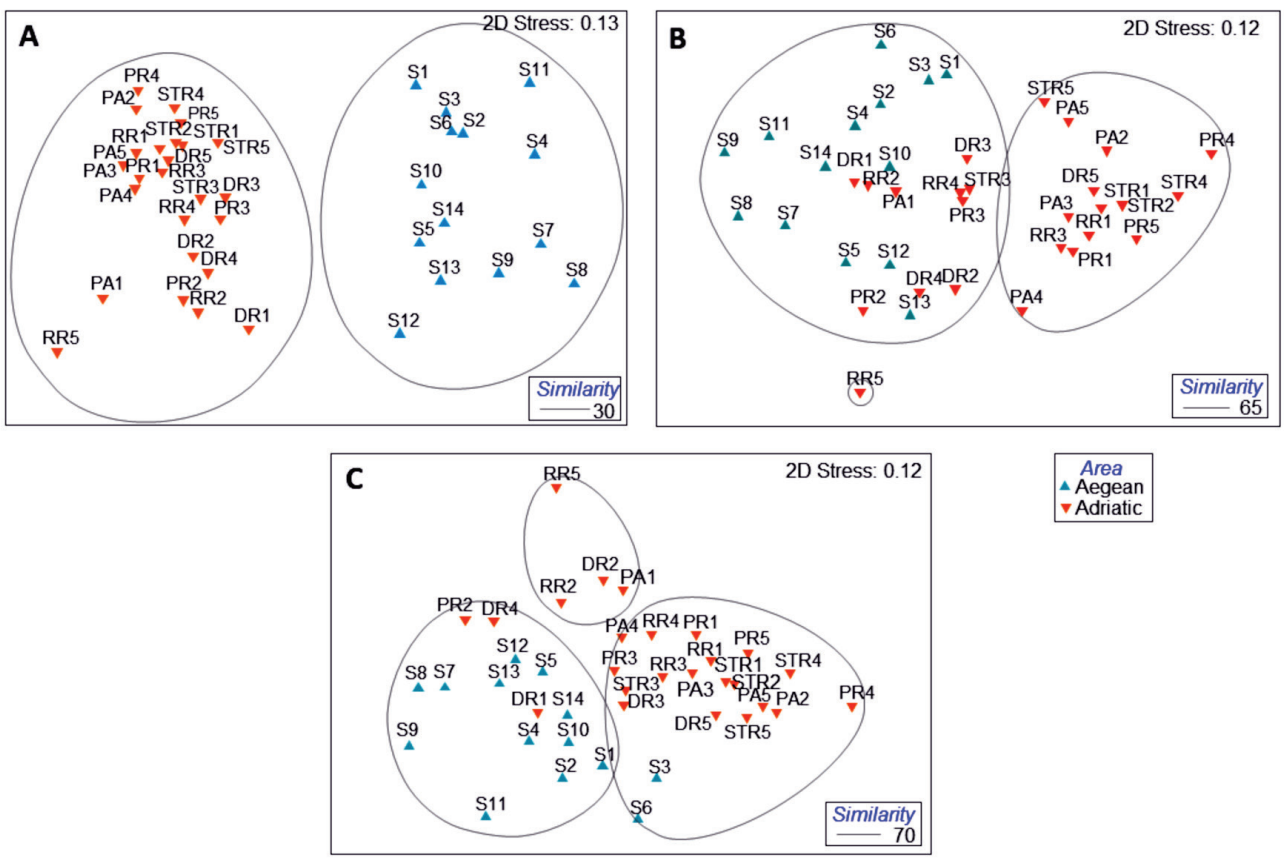

Fig. 4: Non-metric MDS ordination plot comparing the structure of polychaete assemblages for samples from the Adriatic and the Aegean Sea, based on (A) species abundances data, (B) abundances of feeding guilds, and (C) abundance of biogeographic groups. Groupings derived from cluster analyses are shown (grey line). For the Aegean Sea n =7, for the Adriatic Sea n=5.

Equitability (Pielou index, J) did not vary significantly with depth, colony size or geographic area (Fig. 3, Supplementary Material, Table S8).

Cluster analysis (Fig. 4A) did not reveal a clear difference in the structure of polychaete assemblages associated with *C. caespitosa* between the Adriatic and Aegean sites and this was confirmed by the PERMANOVA results (Table 3). No difference in data dispersion between the two areas was observed (PERMDISP, Table 3). To test the effect of depth and colony size on polychaete assemblage structure, the two areas were considered separately. In the Aegean Sea there was a significant difference in polychaete assemblage structure between depth ranges (PERMANOVA, Table 3), but not between the two size classes (PERMANOVA, Table 3). In both cases, no difference in dispersion was observed (PERMDISP, Table 3). Conversely, in the Northern Adriatic Sea, significant differences were observed between colony size ranges, but not between depths (PERMANOVA, Table 3). Data dispersion also differed between size classes (PERMDISP, Table 3), with higher dispersion in small colonies (35.2 ± 1.6 SE) compared to bigger ones (27.4 ± 0.6 SE), indicating that the observed significant differences in polychaete abundance between *Cladocora* colony size classes, could be biased by the differences in the dispersion of the samples. The MDS graph (Supplementary Material, Fig. S1) confirmed differences in terms of both position and dispersion between size classes. The same patterns were observed for presence-absence data (PERMANOVA and PERMDISP based on the Jaccard similarity index, Table 3). In the Adriatic Sea, presence-absence data and data dispersion differed only among size ranges (Table 3), with the highest dispersion observed in colonies smaller than 1 dm^3 (35.2 ± 1.6 SE) rather than in bigger colonies (27.4 ± 0.7 SE). Again, significant PERMDISP analyses indicate that the observed differences

Table 3. PERMANOVA and PERMDISP testing results for differences in structure of polychaete assemblages based on abundance (Bray-Curtis similarity) and presence-absence data (Jaccard similarity). df = degrees of freedom; SS = sums of squares; MS = mean squares; Pseudo-F = pseudo-F ratio; res = residuals; F = F-ratio; P = permutational probability. Significant P-values ($p < 0.05$) are in bold.

	Bray-Curtis similarity					**Jaccard similarity**				
	Permanova					Permanova				
Source	df	SS	MS	Pseu-do-F	*P*	df	SS	MS	Pseu-do-F	*P*
Total data										
Area	1	25930	25930	19	**0.0001**	1	25730	25730	13.6	**0.0001**
Res	37	51632	1395.5			37	70153	1896		
Total	38	77561				38	95883			
Aegean data										
Size classes	1	1359.7	1359.7	0.98	0.485	1	1747	1746.7	0.9	0.619
Depth ranges	1	3096.1	3096.1	22	**0.0256**	1	3224	3223.8	16	0.067
Depth x Size	1	1956.8	1956.8	1	0.1555	1	1917	1916.7	1	0.513
Res	10	13917	1391.7			10	19689	1968.9		
Total	13	19871				13	26600			
Adriatic data										
Size classes	1	6258.5	6258.5	58	**0.0001**	1	5041	5041.1	30	**0.0001**
Depth ranges	1	1312.5	1312.5	12	0.2268	1	1972	1972.2	12	0.222
Depth x Size	1	1491	1491	14	0.1302	1	1874	1873.5	1	0.297
Res	21	22813	1086.3			21	34725	1653.6		
Total	24	31761				24	43554			
	PERMDISP					PERMDISP				
factor		*df*	F	*P*			*df*	F	*P*	
Total data		1	1.35	0.303			1	0.95	0.395	
Aegean data										
Depth ranges		1	0.94	0.401			1	2.26	0.177	
Size classes		1	0.002	0.977			1	1.98	0.28	
Adriatic data										
Depth ranges		1	0.002	0.969			1	0.002	0.97	
Size classes		1	19.37	**0.0001**			1	25.61	**0.0001**	

could be due to data dispersion.

The differences in the polychaete assemblage' structure between the Adriatic and the Aegean Sea were both due to the different abundances of the most frequent species (SIMPER, Supplementary Material, Table S2), such as *S. concharum, H. pseudouncinata pseudouncinata, V. infundibulum, Syllis variegata* Grube, 1860 and others, and to different species composition in the two areas. In fact, some species were present only in the Aegean Sea, such are *Psamathe fusca* Johnston, 1836, *Spirobranchus polytrema* (Philippi, 1844) and others, while others were found only in the Adriatic Sea, such as *Syllis ferrani* Alós & San Martín, 1987, *Harmothoe extenuata* (Grube, 1840) and others.

In the Aegean Sea, the differences between sampling depths were mostly due to different abundances of the species present at both depths (SIMPER, Supplementary Material, Table S3), in particular, *H. pseudouncinata pseudouncinata, N. latericeus, P. reniformis, S. vermicularis* and *S. polytrema* that were more abundant at 3-5 m depth, and *C. costae* that was more abundant at 15-19 m depth. In the Aegean, *H. pseudouncinata pseudouncinata, C. costae, S. vermicularis and P. reniformis* were slightly more abundant in colonies smaller than 1 dm^3, while *V. striaticeps* was slightly more abundant in colonies bigger than 1 dm^3 (SIMPER, Supplementary Material,Table S3).

In the Adriatic Sea, the difference between small and big colonies was mainly due to the different abundances of the following species: *N. latericeus*, *C. costae*, *Eunice vittata* (Delle Chiaje, 1828), *S. ferrani*, *Nereis rava* Ehlers, 1868, *Syllis gerlachi* (Hartmann-Schröder, 1960), *Lysidice unicornis* (Grube, 1840), *Lysidice ninetta* Audouin & H Milne Edwards, 1833 and several unidentified Terebellidae species, which were more abundant in big colonies, and *S. concharum* that was more abundant in small colonies (SIMPER, supplementary Material, Table S4). Moreover, *N. latericeus*, *S. ferrani* and *S. gerlachi* were much more frequent (up to 100%) in bigger colonies than in smaller ones (about 50-60%). *S. concharum, C. costae, N. rava*, and *L. ninetta* were more abundant at 3-6 m, whereas *N. latericeus*, *E. vittata* and *S. triqueter* were more abundant at 6-8 m depth (SIMPER, Supplementary Material, Table S4).

The results of DISTLM analysis (Supplementary Material, Table S5) show that variations in polychaete assemblages, when considering total species abundance, can be only partially explained by sampling depth and colony volume. A correlation was in fact found between the species/abundance matrix and both depth and volume ($p < 0.05$), but the sequential test showed that together they explained only a small portion of total variation (13%). The same analysis, performed on the two datasets separately, showed that for the samples from the Aegean sites, depth was the main factor influencing polychaete assemblages ($p < 0.05$), while colony volume was the main factor affecting polychaete assemblages in samples from the Adriatic sites (Supplementary Material, Table S5).

Functional diversity

Motile jawed carnivores (CMJ), discretely motile jawed carnivores (CDJ), and sessile filter-feeders (FST) were the dominant functional groups in terms of abundance at the sampling sites in both geographic areas. However, while at the Aegean sites filter feeders represented the most abundant feeding guild (51.3% of total abundance), colonies in the Northern Adriatic were dominated by carnivores, in particular by CMJ (33.8%), followed by CDJ (22.7%) (Fig. 5A). As regards taxa richness instead, CMJ dominated both at the Aegean (28.6%) and the Adriatic sites (36.1%), followed by FST (20.8% in the Aegean and 10.2% in the Adriatic) and CDJ (16.9% in the Aegean and 18.5% in the Adriatic) (Fig. 5A). The dominant motility mode differed in terms of abundances between all the sites, with sessile species were most abundant in the Aegean Sea (56%) and motile polychaetes were most abundant in the Northern Adriatic (48%). Conversely, motile polycheates dominated in terms of taxa richness in both geographic areas, with 43.2% at the Aegean sites and 64.5% at the Adriatic sites (Fig. 5B).

The most frequent and abundant carnivores were *E. vittata*, *S. variegata*, *Leodice torquata* (Quatrefages, 1866) and *L. ninetta* in the Adriatic Sea, and *H. spinifera*, *Lepidonotus clava* (Montagu, 1808), *Syllis hyalina* Grube, 1863, *L. ninetta*, *Lumbrinereis latreilli* Audouin & Milne Edwards, 1833 and *C. costae* in the Aegean Sea. The most frequent and abundant filter feeders were *S. concharum*, *S. triqueter* and *V. striaticeps* in the Adriatic Sea, *V. striaticeps*, *V. infundibulum*, and *H. pseudouncinata pseudouncinata* in the Aegean Sea. The most frequent and abundant surface deposit feeders were *Dodecaceria concharum* Örsted, 1843 and *Cirriformia tentaculata* (Montagu, 1808) in the Adriatic Sea, and *P. fusca* in the Aegean Sea, while the dominant subsurface deposit feeders was *N. latericeus* in both the Adriatic and the Aegean Sea.

Among motile species, the most frequent and abundant polychaetes at the Adriatic sites were *E. vittata*, *S. variegata*, *L. torquata* and *L. unicornis*, while *H. spinifera* and *L. clava* were the most frequent and abundant at the Aegean sites. As regards sessile species in the Adriatic, the most frequent were *D. concharum*, *S. concharum*, and *S. triqueter*, whereas *V. infundibulum* and *H. pseudouncinata pseudouncinata* were the most frequent species in the Aegean Sea, and *V. striaticeps* in both the Adriatic and the Aegean Sea. Among discretely motile polychaetes at the Adriatic sites, the most frequent were *C. costae* and *N. rava*, whereas *L. latreilli* and *P. fusca* were the most frequent at the Aegean sites. The motile polychaete *L. ninetta* was frequent and abundant in both geographic areas.

The richness and diversity of feeding guilds (Fig. 6) were significantly higher at the Adriatic than at the Aegean sites (Supplementary Materials, Table S6). In both the Adriatic and the Aegean Sea, richness and abundance of feeding guilds did not differ significantly with depth, but at the deeper sites in the Aegean the values were significantly lower than at the Adriatic sites (Fig. 6, Supple-

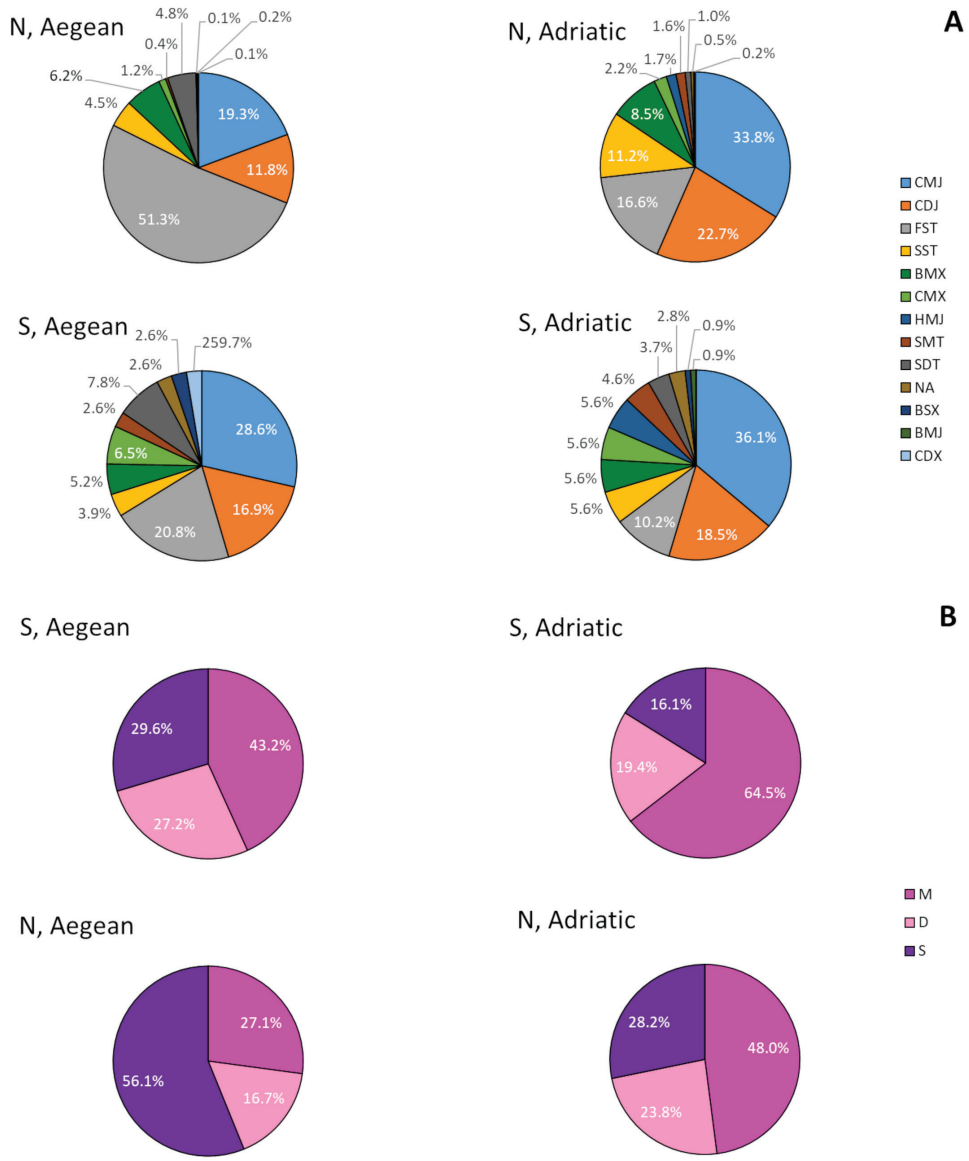

Fig. 5: Cumulative richness (S) and abundances (N) of feeding groups (A) and motility modes (B) in the Aegean (left) and the Adriatic Sea (right). HMJ = herbivore motile jawed, BMX = burrowing motile non-jawed, BSX = burrowing sessile non-jawed, CMJ = carnivore motile jawed, CMX = carnivore motile non-jawed, CDJ = carnivore discretely motile jawed, FST = filter-feeders sessile tentaculate, FSP = filter-feeders sessile pumping, SMJ = surface deposit feeders motile jawed, SMT = surface deposit feeders motile tentaculate, SDT = surface deposit feeding, discretely motile tentaculate, SST = surface deposit feeding sessile tentaculate; M = motile, D = discretely motile, and S = sessile.

mentary Materials, Table S6, A7). In the Aegean, feeding richness did not vary significantly between the two colony size classes, while in the Adriatic it was higher in bigger colonies (Fig. 6, Supplementary Materials, Table S6, S7). Feeding richness in big colonies in the Adriatic was higher than in the Aegean colonies of both size classes (Fig. 6, Supplementary Materials, Table S6, S7). Feeding diversity did not differ between small and big colonies in both the Adriatic and the Aegean, but feeding diversity in big Adriatic colonies was higher than in the Aegean colonies of both size classes (Fig. 6, Supplementary Materials, Table S6, S7).

Considering the abundance of the different feeding guilds, cluster analysis revealed that polychaete assemblages were divided into three groups: one group composed solely of the Northern Adriatic samples, one group consisting of samples from both the Aegean and the Adriatic Sea, and the last one represented only by site RR5 (Fig. 4B). The results of DISTLM analysis (Supplementary Material, Table S5) show that sampling depth and colony volume partially explain the variations between polychaete feeding guilds. A correlation was in fact found between functional group matrix and both depth and volume ($p < 0.05$), but the sequential test showed that together they explained only a small portion of the total variations (25%).

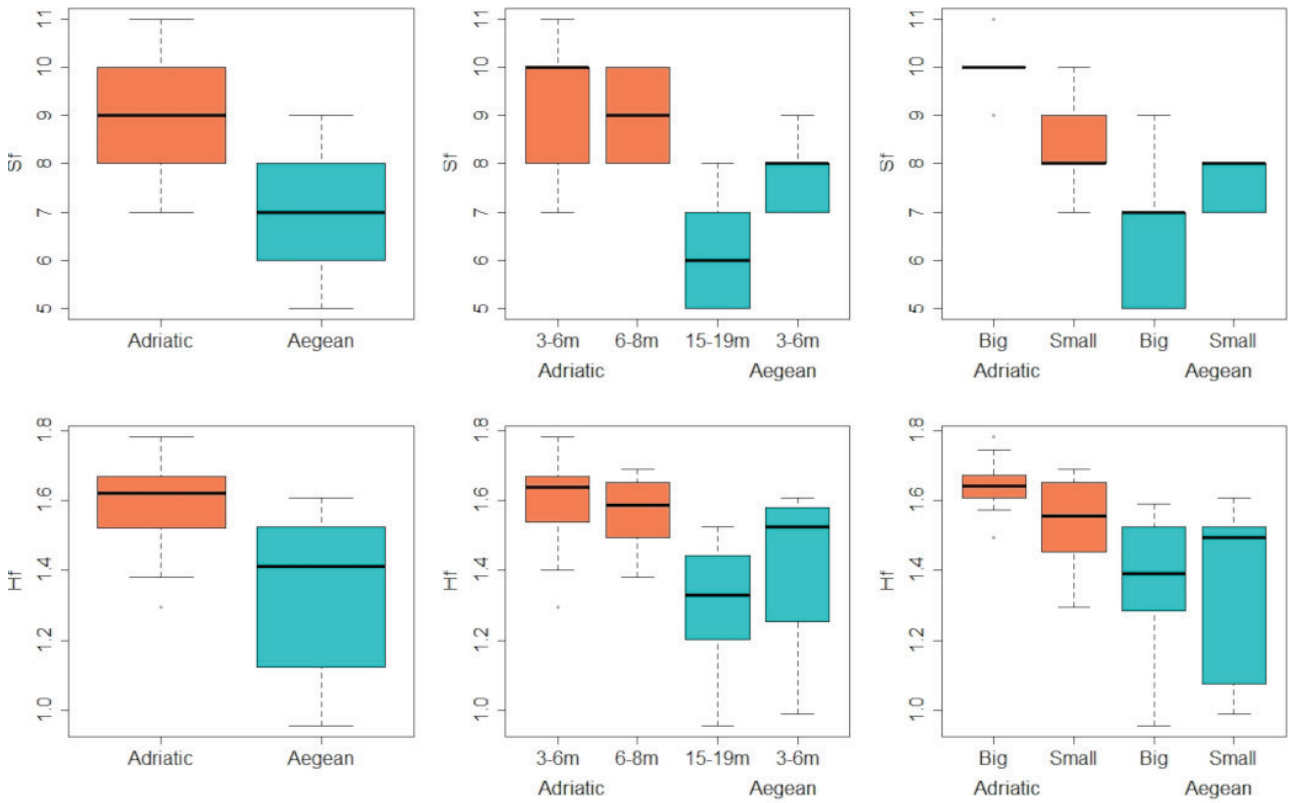

Fig. 6: Average feeding richness (Sf) and feeding diversity (Hf) overall in the two geographic areas (left), at the different depth ranges (central) and in colonies with different sizes (right).

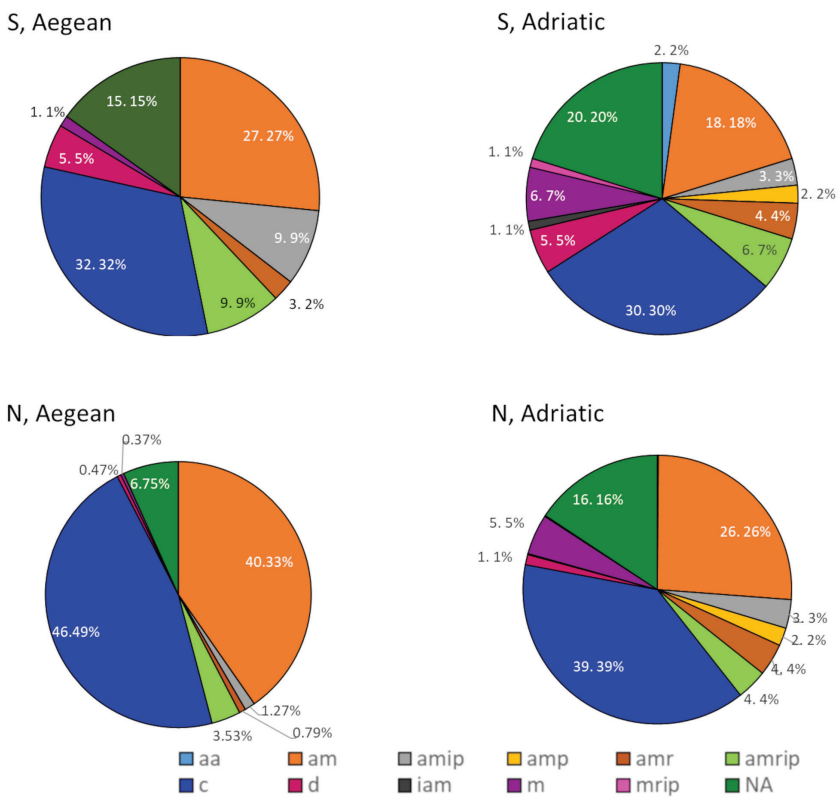

Fig. 7: Cumulative richness (S) and abundances (N) of the polychaetes assigned to the different biogeographic categories in the Aegean (left) and the Adriatic Sea (right). aa = amphi-Atlantic, am = Atlanto-Mediterranean, amip = African Atlanto Mediterranean and Indo-Pacific, amr = Atlanto-Mediterranean and Red Sea, amp = Atlanto-Mediterranean and Pacific, amrip = Atlanto-Mediterranean, Red Sea and Indo-Pacific, c = cosmopolitan, d = disjunct distribution, iam = Indo-Atlanto-Mediterranean, m = endemic Mediterranean, mrip = Mediterranean, Red Sea and Indo-Pacific.

Biogeography

Cosmopolitan polychaetes (c) dominated the assemblage in both studied areas (Fig. 7), as regards both richness (32% in Aegean sites, 30% in Adriatic sites) and abundance (46% in Aegean sites, 39% in Adriatic sites), followed by Atlanto-Mediterranean species (am), showing higher percentages of both richness and abundance at the Aegean sites (27% of richness, 40% of abundance) than at the Adriatic sites (18% of richness, 26% of abundance). Amphi-Atlantic (aa), Indo-Atlanto-Mediterranean (iam), and Mediterranean, Red Sea and Indo-Pacific (mrip) polychaetes were found only at the Adriatic sites, while there was no biogeographic group exclusive of the Aegean sites (Fig. 7). The most abundant species found exclusively at the Aegean sites (*P. reniformis*, *P. fusca* and *S. hyalina*) are cosmopolitan (c), whereas the most abundant species found exclusively at the Adriatic sites are endemic of the Mediterranean (m) (*S. ferrani*), cosmopolitan (c) (*S. gerlachi*) and Atlantic-Mediterranean and Pacific (amp) (*H. extenuata*).

Multivariate analyses showed that considering the abundance of the different biogeographical groups, polychaete assemblages were divided into groups, corresponding, to the two geographical areas analysed, with few exceptions (sites DR1, DR4 and PR2 grouped with Aegean sites, and sites S3 and S6 grouped with Adriatic ones) (Fig. 4C). A significant difference between the Adriatic and Aegean Sea sites was confirmed by the PERMANOVA results (df = 1, Pseudo-F = 13.7, p = 0.0001), and no difference in data dispersion between the two areas was observed (PERMDISP: df = 1, F = 0.936, p = 0.363). SIMPER results (SIMPER, Supplementary Material, Table S8) show that those differences were mainly due to the different abundance of the two most dominant groups present in both areas (cosmopolitan and Atlanto-Mediterranean), and that the dissimilarity between the Aegean and Adriatic sites was low (33.90). The results of DISTLM analysis (Supplementary Material, Table S5) show that sampling depth and colony volume partially explain biogeographical group variations. A correlation was in fact found between biogeographic matrix and both depth and volume ($p < 0.05$), but the sequential test showed that together they explained only a small portion of the total variations (23%).

Colony size effect

Polychaete species richness increased with increasing colony size (Table 4), and this relationship did not seem to be significantly influenced by geographic area (Fig. 8A) and sampling depth (Fig. 8B). The regression line ($\log(S) = 0.186*\log(V_{tot}) + 2.206$) was successfully fit for the complete dataset (Adjusted $R^2 = 0.225$, $p = 0.001$). Data distribution did not deviate significantly from the assumption of normality (Shapiro test, $p > 0.05$), and the model did not show significant deviations from the homogeneity of residuals. Almost all observed values fitted between the upper and lower limits of the prediction interval (Fig. 8), with the only exception being two samples collected at the Vou site (Aegean Sea), between 15 and 19 m depth.

Species abundance (N) and the Shannon diversity in-

Table 4. Spearman coefficients (r_s), p-value and significance levels of the correlations between colony size (V_{tot}) and biotic indices and functional traits of polychaete assemblages. S_{tot} = total richness, N_{tot} = total abundance, H' = diversity index, J' = Pielou index, Sf = feeding richness, Hf = feeding diversity. Richness of the different functional groups: M_S = motile, D_S = discretely motile, SE_S = sessile, C_S = carnivores, DF_S = surface deposit feeders, B_S = subsurface deposit feeders/burrowing, F_S = filter feeders, H_S = herbivores, Abundances of the different functional groups: M_N = motile, D_N = discretely motile, SE_N = sessile, C_N = carnivores, DF_N = surface deposit feeders, B_N = subsurface deposit feeders/burrowing, F_N = filter feeders, H_N = herbivores.

		r_s	p		r_s	p
Indices						
	S_{tot} vs V_{tot}	0.51	< 0.001	**N_{tot} vs V_{tot}**	0.48	< 0.01
	H' vs V_{tot}	0.49	< 0.01	**J' vs V_{tot}**	-0.01	> 0.05
	Sf vs V_{tot}	0.30	> 0.06	**Hf vs V_{tot}**	0.20	> 0.06
Motility	**Richness**			**Abundances**		
	M_S vs V_{tot}	0.34	< 0.05	**M_N vs V_{tot}**	0.53	< 0.001
	D_S vs V_{tot}	0.71	< 0.001	**D_N vs V_{tot}**	0.53	< 0.001
	SE_S vs V_{tot}	0.11	> 0.05	**SE_N vs V_{tot}**	0.19	> 0.05
Feeding	**Richness**			**Abundances**		
	C_S vs V_{tot}	0.47	< 0.01	**C_N vs V_{tot}**	0.464	< 0.01
	DF_S vs V_{tot}	0.353	< 0.001	**DF_N vs V_{tot}**	0.474	< 0.001
	B_S vs V_{tot}	0.29	> 0.05	**B_N vs V_{tot}**	0.559	< 0.001
	F_S vs V_{tot}	0.13	> 0.05	**F_N vs V_{tot}**	-0.13	> 0.05
	H_S vs V_{tot}	0.08	> 0.05	**H_N vs V_{tot}**	0.08	> 0.05

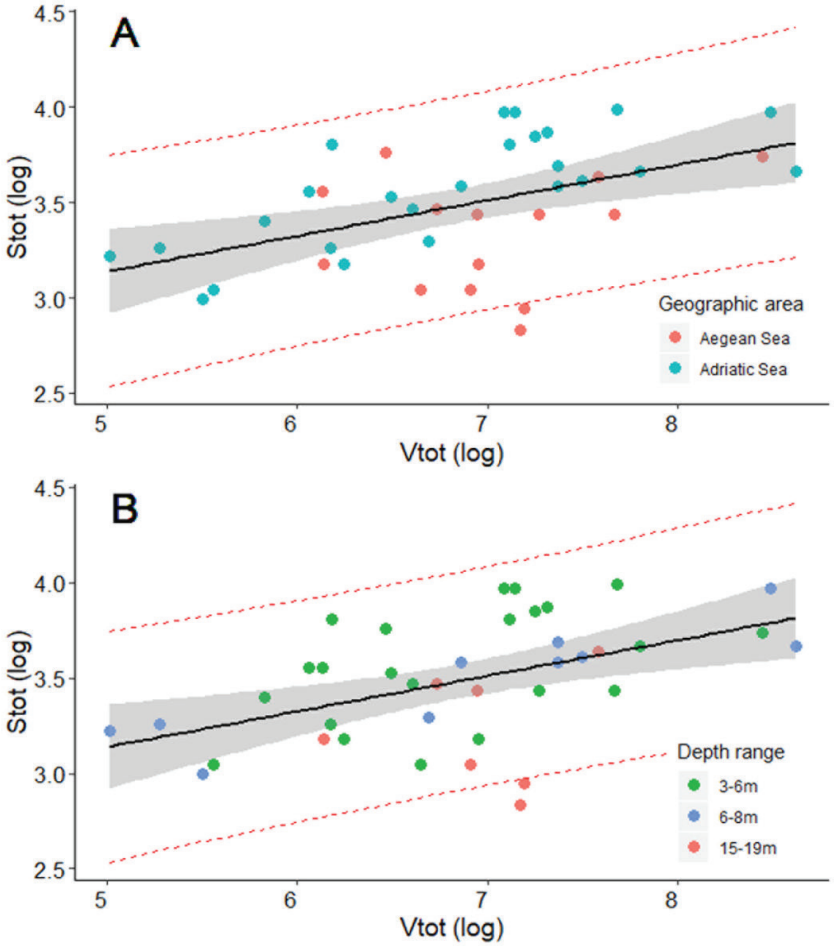

Fig. 8: Relationship between polychaete species richness and colony size, displaying geographic areas (A) and sampling depth (B). Stot = total species richness; Vtot = colony size (cm^3). Grey band = 95% confidence interval; dashed red line = prediction interval.

dex (H') increased with increasing colony size as well, while there was no correlation between the Pielou index (J) and colony size (Table 4).

The richness and abundances of motile (M) and discretely motile (D) polychaetes increased with colony size, while richness and abundance of sessile polychaetes (SE) were not significantly related with colony size (Table 4).

The richness and abundance of carnivores (C), surface deposit feeders (DF) and abundance of subsurface deposit feeders/burrowers (B) increased with colony size (Table 4). Conversely, no significant relationship was found between the richness and abundance of filter feeder polychaetes (F) and herbivorous (H) polychaetes and colony size ($p > 0.05$). Moreover, no significant relationship was found between feeding richness (Sf) and feeding diversity (Hf) on the one hand and colony size on the other hand (Table 4).

Discussion

Polychaete assemblages associated with *C. caespitosa* showed quite high overall richness in both the the Adriatic and the Aegean Seas, compared to other Mediterranean corals. Given the differences in sampling and data processing, our results are not directly comparable with the data reported for other Mediterranean coral species; however, at least from a qualitative point of view, *C. caespitosa* seems to be the Mediterranean coral supporting the richest polychaete assemblage so far. As regards shallow water corals, Terrón-Sigler *et al*. (2014) have listed 27 polychaete taxa associated with *Astroides calycularis* (Pallas, 1766) at Marina del Este beach (Spain). Regarding mesophotic and deep water corals, Kipson *et al*. (2009) have reported 45 taxa of polychaetes associated with a coralligenous community dominated by the red gorgonian *Paramuricea clavata* (Risso, 1826) in the central part of the Eastern Adriatic Sea (Croatia). Mastrototaro *et al*. (2010) have listed 24 species of polychaetes associated with white coral banks dominated by *Madrepora oculata* (Linnaeus, 1758) and *Lophelia pertusa* (Linnaeus, 1758) in the Ionian Sea, off Cape Santa Maria di Leuca (Italy). Chimienti *et al*. (2020) found 29 polychaete species associated with *Antipathella subpinnata* llis and Solander, 1786 at Tremiti Islands (Italy), while Chimienti (2020) reported 5 polychaete species associated with *Eunicella verrucosa* (Pallas, 1766) in the Ligurian Sea (Italy). The high diversity of *Cladocora* associated polychaete assemblages in our study is likely due to the complex structure of the coral. In fact, we distinguished three main microhabitats in the colonies, namely, hard substrate suitable for epilithic and endolithic species, interstitial space for small motile organisms, and trapped sediment for the more typical soft bottom species (Pi-

tacco *et al.*, 2014). In general, scleractinian corals host the richest and most diversified associated polychaete assemblages because of their typical three-dimensional structure (Molodtsova *et al.*, 2016). High richness of polychaete assemblage associated with *C. caespitosa* could be related to the low toxicity of polyps (Chintiroglou, 1996). Martins Garcia *et al.* (2008) suggested that the position of the sting cells in the gastro-vascular cavity of scleractinian corals could explain the bigger diversity of their associated fauna, compared to the fauna associated with the so-called "branching fire coral" (*Millepora alcicornis* Linnaeus, 1758), a colonial hydrozoan whose polyps create a barrier to larval colonization, given that the sting cells are located in the epidermis.

According to a recent review, the most diverse and abundant polychaete families found associated with *C. caespitosa*, correspond to the most common and rich cnidarian-associated families (Molodtsova *et al.*, 2016): Polynoidae, Syllidae, Serpulidae, and Eunicidae. These families are also typical of hard bottoms in the Mediterranean, with Syllidae ranking first place (Somaschini, 1988; Tena *et al.*, 2000; Giangrande *et al.*, 2003; Giangrande *et al.*, 2004; Mikac *et al.*, 2020). The richest families were the same in both studied areas, but the diversity of Syllidae was much higher in the Adriatic Sea.

As regards polychaetes, some individuals with less than half the average adult size (e.g., *S. vermicularis* and *L. torquata*), the stolons of some species of genera *Syllis* and *Trypanosyllis* and some individuals of *Pileolaria* spp. incubating eggs in the operculum, were observed (*personal observations*), indicating the importance of *C. caespitosa* colonies for the recruitment of polychaetes. Previous research has shown that colonies of *C. caespitosa* play an important role as a nursery habitat for molluscs (Pitacco *et al.*, 2017).

Considering species composition and abundance data, the polychaete assemblages associated with *C. caespitosa* varied clearly between the Adriatic and the Aegean sites. Those variations were due to the different abundance of common species, but also to different species composition, with some species found exclusively in one of the two areas. In fact, only 40 species were found in the fauna of both areas.

Part of the discordance in the composition of polychaete fauna in the two areas could be due to the fact that there is a difference of almost twenty years between the two research projects. The Aegean samples were taken in 1987 and published for the first time in 1994. Thus, the knowledge on taxonomy of Mediterranean polychaetes available the latest by 1994 was used to identify the polychaetes from the Aegean Sea. On the other hand, the samples from the Slovenian coast were taken in 2010 (Pitacco *et al.*, 2014) and in 2012 (Pitacco *et al*., 2017, 2019), and published for the first time in 2014. In fact two species reported for the Adriatic Sea in this research were only described after 1994, i.e., *Flabelliderma cinari* Karhan, Simboura & Salazar-Vallejo, 2012 and *Parasabella tommasi* (Giangrande, 1994). Other species, such as sabellid *Parasabella langerhansi* (Knight-Jones, 1983), and syllids *Syllis beneliahuae* (Campoy & Alquézar, 1982), *Syllis columbretensis* (Campoy, 1982), *Syllis ferrani* Alós & San Martín, 1987 and *Syllis gerundensis* (Alós & Campoy, 1981) were described just few years before the Aegean polychaetes were analysed. Consequently, knowledge on their taxonomy and distribution was scarce at the time. While *P. langerhansi* was recorded by Giangrande for the first time in the Mediterranean as late as 1994, the four syllids mentioned above were described from the Spanish coast of the Mediterranean Sea. Important identification manuals (such are San Martín, 2003 and Barnich & Fiege, 2000) were published in the meantime, shedding light on the taxonomic status and distribution of some species already present in the Mediterranean and reporting species previously not mentioned in the Mediterranean. Differences in the datasets in this research might partly be due to the differences in the identification manuals used; this could be particularly true for species such as *Harmothoe fragilis* Moore, 1910, *Harmothoe gilchristi* Day, 1960 and the aforementioned syllids.

The analyses of biogeographical groups confirmed the difference between the two areas; however, the dissimilarity between them was low. The assemblages were dominated by cosmopolitan and Atlanto-Mediterranean species at both the Aegean and Adriatic sites, and the differences between the two areas were mainly due to their different abundances. Three biogeographical groups, Amphi-Atlantic (aa), Indo-Atlanto-Mediterranean (iam), and Mediterranean, Red Sea and Indo-Pacific (mrip), were found exclusively in the Adriatic Sea, and all of them were represented by one or two species only. Our results are consistent with the biogeographical analysis of Mediterranean polychaetes performed by Arvanitidis *et al.* (2002); in the Mediterranean and the Black Sea, the most represented were cosmopolitan and Atlanto-Mediterranean polychaetes. Conversely, Arvanitidis *et al*. (2002) did not find a significant difference in the proportion of biogeographical groups among different areas of the Mediterranean, and high similarity in the biogeographical affinity of polychaetes between the Adriatic and the Aegean Sea. Musco & Giangrande (2005) observed a similar pattern for Mediterranean syllids. This similarity between the two areas was explained, in part, by the co-occurrence of similar ecological features, such as shallow water, distance from Gibraltar, low temperature and salinity (Arvanitidis *et al.*, 2002). Thus, currently available literature on the biogeographical affinity of polychaetes does not explain the differences in species composition between the two areas observed during this study. Some species were not assigned to a group due to the lack of knowledge on species distribution such as, e.g., *Flabelliderma cinari* Karhan, Simboura & Salazar-Vallejo, 2012 to date known only from few locations in Slovenian and Turkish waters (Pitacco & Karhan, 2019). Currently, there are doubts about the assignment of cosmopolitan status to so many polychaete species. According to Hutchings & Kupriyanova (2018), some studies suggest that cosmopolitan polychaetes do exist, but are rare. In fact, the cosmopolitan distribution of several species found herein (i.e., *Lysidice ninetta* Audouin & H Milne Edwards, 1833, *Perinereis cultrifera*

(Grube, 1840), *Arabella iricolor* (Montagu, 1804), *Phyllodoce madeirensis* Langerhans, 1880, *Haplosyllis spongicola* (Grube, 1855), *Syllis alternata* Moore, 1908, *Syllis gracilis* Grube, 1840 and *Trypanosyllis zebra* (Grube, 1860)) should be questioned since their morphology is hardly distinguishable (Scaps *et al*., 2000; Maltagliati *et al*., 2001; Iannotta *et al*., 2006, 2009; Lattig *et al*., 2007; Lattig & Martín, 2009; Carr *et al*., 2011; Zanol & Ruta, 2015; Álvarez-Campos *et al*., 2016, 2017; Faulwetter *et al*., 2017; Ravara *et al*., 2017; Langeneck *et al*., 2020). On the other hand, the cosmopolitan status of some other species is currently questioned as they might represent species complexes, i.e., *Ditrupa arietina* (O. F. Müller, 1776), *Exogone naidina* Örsted, 1845, *Salvatoria clavata* (Claparède, 1863), *Syllis armillaris* (O.F. Müller, 1776), *Trypanosyllis aeolis* Langerhans, 1879) (López *et al*., 2001; San Martín, 2003; Hartley, 2014; Álvarez-Campos *et al*., 2017; Langeneck *et al*., 2018). Moreover, some species classified as cosmopolitan have complicated taxonomy or are purely identified and therefore erroneously reported in different geographic sectors (i.e., *Heteromastus filiformis* (Claparède, 1864), *Lumbrineris coccinea* (Renier, 1804), *Lumbrineris latreilli* Audouin & Milne Edwards, 1833) (Carrera-Parra, 2006; Capaccioni-Azzati & El-Haddad 2015). In-depth integrated studies would be necessary to solve the status of the above listed species and, presumably, their cosmopolitan status will likely be derelict in the future based on further research and knowledge.

The total number of polychaete taxa associated with *C. caespitosa* reported for the Adriatic Sea was higher than for the Aegean Sea. This could partly be attributed to the fact that some species present only in the Adriatic Sea were originally described or reported from the Mediterranean Sea or included in the important identification manuals after 1994, as already discussed above. Moreover, the higher number of Adriatic Sea colonies analyzed could explain the higher total number of species recorded. Average polychaete richness was higher at sites in the Adriatic than in the Aegean Sea, as well. This could be partly due to a superimposed sampling depth effect, since some colonies sampled deeper in the Aegean Sea showed the lowest species richness. Variations in the richness and diversity (H') of polychaete assemblages in the Adriatic Sea were related primarily to colony size, while those in the Aegean to sampling depth. DistLM analyses performed on the data from the two areas confirmed that depth was the main factor structuring polychaete assemblages in the samples from the Aegean, whereas colony size was the main factor influencing polychaete assemblages in the samples from the Adriatic. These results are undoubtedly due to the different focus of the compared studies, and the different distribution of the Mediterranean stony coral itself in the two areas. In Slovenian waters, most of the *Cladocora* colonies are located within the first 10m depth; sampling encompassed a narrower depth range, but a wider range of colony size, thus enabling testing of the differences of the polychaete fauna between different sized colonies. On the other hand, in the Aegean Sea, *Cladocora* colonies are distributed in a wider depth range and, therefore, it was possible to test the differences between associated polychaete fauna living in colonies at different depths (shallower, 3-5 m and deeper, 15-19 m colonies). DistLM analyses performed on the whole dataset confirmed the importance of both factors, i.e., depth and colony size, in structuring the polychaete assemblages; however, together they explained only a small portion of the total variance of polychaete assemblages.

In the Adriatic Sea, polychaete assemblages associated with colonies bigger and smaller than 1 dm^3, differed in terms of species richness, diversity, abundance patterns, and dispersion of presence/absence data, with bigger colonies hosting richer, more diverse and more abundant polychaete assemblages. The index of equitability (J') did not reveal any relationship with colony size, implying that the polychaete assemblages are well-structured even in small colonies, and that the variability of overall diversity was mainly related to the variability of species richness. Beta diversity was higher for small colonies, than for bigger ones. A previous study on decapod crustaceans associated with the tropical coral *Pocillopora damicornis* (Linnaeus, 1758) has highlighted the importance of small colonies for associated fauna, showing that two small colonies can host more species than a single big colony with a volume equal to the sum of the two smaller ones (Abele & Patton, 1976). The explanation provided by the authors was based on the Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1967), considering coral colonies as island-like habitats and assuming that the frequency of occurrence is a good indication of dispersal ability. If the number of good colonizers (i.e., the most frequent) is higher than the equilibrium number (total number of species resulting from the equilibrium between immigration and extinction) in the small colonies, then those colonies are expected to host the same species (i.e., the most frequent), and bigger colonies are expected to host a higher number of species. Conversely, Abele & Patton (1976) found few species that are considered good colonizers (>80% of frequency), less than the equilibrium number for most colonies (even the smaller ones). Consequently, a different species composition between two small colonies and their cumulative number of species higher than a single colony of comparable volume were expected.

The dominant feeding modes considering both abundances and taxa richness were CMJ, CDJ, and FST in all cases. The same dominance was observed at different depths in the Aegean Sea (Chintiroglou, 1996), and at a deeper site of the Gulf of Trieste (Pitacco *et al.*, 2014). Motile carnivores dominated the assemblages in terms of taxa richness in samples from both geographic areas. Nevertheless, while carnivores were the most abundant group in the Adriatic, filter feeders were the most abundant in the Aegean Sea. Colonies of *C. caespitosa* are known to hold in their interstitial spaces high nutrient levels (Schiller, 1993) and a rich microbial community (Rubio-Portillo *et al.*, 2018), deriving mainly from coral produced mucus. The combined effect of coral-produced food availability and reduced water flow velocity among corallites create a specific environment more or less in-

dependent from surrounding waters (Schiller, 1993), providing food for deposit feeders and shelter for juveniles, and this availability of prey attracts carnivores. The dominance of carnivores could be also related to the age of the colony, and indicative of a stable environment. In fact, investigations on polychaete colonization on tropical dead coral showed that the percentage of carnivores is low at the beginning of colonization, and then increases with time (Hutchings & Peyrot-Clausade, 2002). The high abundance of sessile filter feeders, was also reported for other phyla associated with temperate corals, such as molluscs (Crocetta & Spanu, 2008; Pitacco *et al.*, 2017), and could be related to food availability in the water column. The distribution of *C. caespitosa* in shallow water is known to be related to both seabed morphology and to the supply of nutrients and carbonate (e.g., Kružić & Benković, 2008; Kersting & Linares, 2012; Zunino *et al.*, 2018). A number of authors (e.g.,Hovland *et al*., 2002; Mastrototaro *et al*., 2010) have reported that deep-sea coral reefs establish themselves where there is a continuous and regular supply of concentrated food and nutrients, and that this flow is a crucial factor not only for corals themselves, but also for associated suspension feeders. The coexistence of suspension feeders of different taxa, typically associated to corals, requires a certain level of trophic specialization for the distribution of resources (Sarà, 1986).

Composition in terms of feeding guilds is consistent with composition in terms of motility modes. Motile polychaetes (mainly carnivores) were dominant in terms of taxa richness in both areas. Sessile polycheates (mainly filter feeders) were most abundant in the Aegean and motile polychaetes in the Adriatic. The high presence of sessile species is due to the fact that the coral provides hard substrate to settle. The different proportions found in the Adriatic and the Aegean Seas could be related to different factors, such as larval dispersal, timing of colonization or competition for space or for food after settlement (Sarà, 1986). Moreover, sessile filter feeders consisted mainly of Serpulidae, which are typically gregarious. Gregariousness is a cooperative behaviour that could increase colonization success, thus contributing to the unpredictability of hard bottom colonization dynamics (Sarà, 1986). Differences observed in terms of richness and diversity of feeding modes (Sf and Hf), reflected a pattern of general richness and diversity: they were higher in the Northern Adriatic and in shallow areas.

In previous studies it was reported that in the Adriatic Sea macrobenthic assemblages associated with *C. caespitosa* followed SAR (Species/Area Relationship) models based on the Arrhenius equation (Arrhenius, 1921), thus enabling to estimate the richness of associated macrofauna in a non-destructive way, based solely on colony size (Pitacco *et al.*, 2017, 2019). Colony size was the best predictor of the richness of associated invertebrates, and the same SAR model was predictive even when the richness of associated mollusc and polychaete assemblages were considered separately (Pitacco *et al.*, 2019). In this research, despite the difference in richness between the Adriatic and the Aegean Sea, colony size in terms of V_{tot} proved to be a good proxy for polychaete richness, and the regression line obtained from the complete dataset was predictive for both areas, with only few exceptions represented by some of the deepest samples. The independence of SAR models from the geographic area was proved also for decapod crustaceans associated to the tropical coral *P. damicornis* in two distinct regions of Panama (Abele, 1976). The common pattern of the Species-Volume Relation, SVR *sensu* Belmaker (2009), found in the Northern Adriatic and the Aegean Sea, suggests that polychaete richness in corals of comparable colony size is similar between the two studied areas, even if species composition differs. Although the present data come from two restricted areas, and information from other Mediterranean regions would undoubtedly be necessary to validate this method, our results suggest that the same SAR model could be applied successfully to polychaetes associated with *C. caespitosa* in other areas of the Mediterranean Sea. Colony size distribution and colony morphology of *C. caespitosa* is not universally homogeneous in the Mediterranean Sea, and differences between sites are likely related to different hydromorphological conditions, in particular sea currents, wave action and sedimentation rate (Schiller, 1993; Kružić & Benković, 2008). Those differences in colony biometrics have been documented for different sites along the Slovenian coast in the Adriatic (Zunino *et al.*, 2018) but no recent information on coral biometry is available for the Aegean, notwithstanding the important presence of this species in the form of both banks and beds (Peirano *et al.*, 1998; Chefaoui *et al.*, 2017). It has been reported for the Adriatic Sea (Kružić *et al.*, 2008, 2014; Zunino *et al.*, 2018), and for other areas of the Mediterranean (Rodolfo-Metalpa *et al.*, 2005; Kersting *et al.*, 2013, 2015), that populations of *C. caespitosa* are affected by different types of anthropogenic pressures. Those pressures, such as the colonization of non-indigenous algae that cause colony recession (Kružić *et al.*, 2008) and thermal anomalies that provoke bleaching and mortality events (Jiménez *et al.*, 2014; Kružić *et al.*, 2014; Kersting *et al.*, 2015), could lead to a severe decline. Given those threats and the ecological importance of *C. caespitosa* populations, their mapping and monitoring of their ecological status should be extended to other areas of the Mediterranean.

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Supplementary data

The following supplementary information is available online for the article:

Fig. S1: Non-metric MDS ordination plot, based on species abundance data, comparing structure of polychaete assemblages between samples with different colony size from the Adriatic Sea.
Table S1. Taxon list with feeding guilds (TG) and biogeography groups assigned, and mean abundance and standard error (SE) of each taxa at the two sites in the Aegean (PIR, VOU) and the five sites in the Adriatic (RR, PR, STR, PA, DR).
Table S2. Results of SIMPER analyses (cut-off 90%) used to identify taxa that mostly contribute to (A) polychaete similarity within geographic areas, (B) polychaete dissimilarity between geographic areas.
Table S3. Results of SIMPER analyses (cut-off 90%) used to identify taxa that mostly contribute to (A) polychaete similarity within the same depth and size class, (B) polychaete dissimilarity between depths and size classes in the Aegean Sea.
Table S4. Results of SIMPER analyses (cut-off 90%) used to identify taxa that mostly contribute to (A) polychaete similarity within the same depth and size class, (B) polychaete dissimilarity between depths and size classes in the Adriatic Sea.
Table S5. Results of DISTLM analyses testing the response of biological data to environmental variables.
Table S6. Results of KW chi-squared testing differences of biological indices between areas, depths and colony sizes.
Table S7. Results of pairwise comparisons testing differences of biological indices between areas.
Table S8. Results of SIMPER analyses (cut-off 100%) used to identify biogeographic groups that mostly contribute to similarity (A) within Aegean and Adriatic, and (B) dissimilarity between Aegean and Adriatic Sea.