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Spatial and temporal distributions of the sponge fauna in southern Italian lagoon systems

C. LONGO, F. CARDONE, M. MERCURIO, C. NONNIS MARZANO, C. PIERRI and G. CORRIERO

Department of Biology, University of Bari "Aldo Moro", Via Orabona, 4 - 70125 BARI, Italy

Corresponding author: caterina.longo@uniba.it

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Abstract

The present work focused on the taxonomic composition, spatial distributions, and temporal distributions of the sponge fauna from the main lagoon systems of southern Italy: Lesina, Varano, Taranto, Alimini, Faro, Ganzirri, Tindari and Marsala. Overall, 62 sponge species were recorded, belonging to the classes Demospongiae (52 species), Calcarea (8) and Homoscleromorpha (2). All the lagoon systems studied hosted sponges, even if with marked differences. Species richness varied from one (Lesina) to 45 (Marsala). A large number of the species recorded during this study (52%) was found only at a single site, whereas a species only (*Halichondria (H.) panicea*) was present in all the environments studied. Sponges colonised all available substrates. Salinity was the ecological factor that best explained the spatial distribution of sponges, even though the wide heterogeneity of sponge assemblages, strongly suggests an important role of stochastic factors acting on pre- and post-settlement phases. Comparison of the present data with lists available from the literature shows that sponge assemblages from most of the studied lagoons were quite persistent. However, in some of the lagoons remarkable extinction processes, probably related to massive and prolonged anthropogenic pressures, have contributed to large changes in the sponge patterns.

Keywords: Porifera, Mediterranean lagoons, taxonomy pattern, spatial distribution, temporal distribution.

Introduction

Lagoons are high sedimentation environments, typically poor in natural hard substrates, with a few exceptions (e.g. mangrove roots, phanerogam rhizomes, mollusc shells, calcified bryozoan skeletons). However, in the last centuries, human activities have led to the introduction of stone debris, ropes and material lost by farmers and by the artisanal fisheries, sometimes causing major structural changes in lagoon environments (Cardone *et al.*, 2014; Gristina *et al.*, 2015). In highly trophic environments, both natural and introduced hard substrates are usually colonised by peculiar macrozoobenthic communities mainly dominated by filter-feeders, which often form rich and stratified assemblages (Nonnis Marzano *et al.*, 2007; Cardone *et al.*, 2014; Gristina *et al.*, 2015).

Porifera may be very abundant within lagoon hard benthic communities. Rützler *et al.* (2000) surveyed 95 species of sponges in a 3-hectare lagoon of Belize, pointing out how in such environments sponges provide substrate, shelter, and defence for many other organisms and positively affect habitat structure. Similarly, rich sponge assemblages are also associated with natural and artificial hard substrates in some western Mediterranean lagoons (Corriero, 1989; Corriero *et al.*, 2007; Longo *et al.*, 2004).

In lagoon environments, however, there are several sponge species able to also colonize soft sea bottoms. These sponges usually originate by asexual fragmentation, the detachment of individuals from hard substrates during storms,

or through localised infections by pathogens or predator bites (Wulff, 1985). They may live loose on the sediment, partially or completely buried in it, thanks to some special adaptations that mitigate the occlusion of aquiferous system caused by sediment grains. Some species incorporate foreign bodies that allow them to stabilize themselves on the mobile substrate (Cerrano *et al.*, 2004), while others adopt adaptive shape modifications to live in unattached conditions, displaced over sediment or rolling on it (Mercurio *et al.*, 2006).

According to literature, the lagoon systems in the western Mediterranean richest in sponges are the Mar Piccolo of Taranto (north-western Apulia), with 45 species (Scalera *et al.*, 1976; Pulitzer-Finali, 1983; Longo *et al.*, 2004) and the Marsala Lagoon (north-western Sicily), inhabited by 47 species (Corriero, 1989; 1990). Twenty-five species of sponges were recorded by Topsent (1925) for the Etang de Thau (Gulf of Lion), 20 species, with high coverage of hard bottoms, were reported for the lagoon of Venice (north-eastern Italy) (Sarà, 1960; Corriero *et al.*, 2007), 18 and 17 for the basins of Fusaro (north-western Campania) (Siribelli, 1963) and Faro (north-eastern Sicily) (Labate & Arena, 1964), respectively. By contrast, the more confined coastal lakes displaced along the Italian coast usually host a lower number of sponge species. In particular: four and three species are respectively reported for Alimini (south-eastern Apulia) and Varano (north-eastern Apulia) coastal lakes, six and four for the lagoon systems of Ganzirri and Tindari (north-eastern Sicily), and only one sponge species is reported for both the

lakes of Lesina (north-eastern Apulia) and Ugento (south-western Apulia) (Labate & Arena, 1964; Nonnis Marzano *et al.*, 2003b; Cardone *et al.*, 2014). No other relevant data referring to the occurrence of the sponge fauna in the western Mediterranean lagoons are noted from the literature.

The aim of the present paper is to improve the knowledge of Mediterranean lagoon sponge fauna by comparing the sponge assemblages from the main lagoon systems of the southern Italian coast. The research analyzes the pattern of sponge assemblages in light of the main ecological traits and evaluates the resilience of sponge assemblages in the studied environments.

Materials and Methods

Data collection, spatial and temporal scales of the datasets

Data refer to the following Italian lagoon systems (Fig. 1): Lesina (LES), Varano (VAR), Taranto (TAR), Alimini (ALI), Faro (FAR), Ganzirri (GAN), Tindari (TIN) and Marsala (MAR). They included closed and semi-enclosed wetlands, from saline to brackish waters. Sampling was performed from 2004 to 2012, and in particular: in 2004 at Tindari; in 2006 at Faro and Ganzirri; in 2010 at Taranto and Marsala; in 2012 at Lesina, Varano, and Alimini. At each site a different number of stations was considered, depending upon the dimensions and morphology of the lagoon, and on habitat patchiness. In particular, two stations were considered at Faro and Ganzirri, three at Alimini and Tindari, and four stations at the remaining sites (Lesina, Varano, Taranto, and Marsala) (Fig. 1). In each station (100 x 100 m in size) the presence of sponges was carefully detected by SCUBA divers, considering all the substrates present. Sponge samples were collected for taxonomic identifications, that were performed in the laboratory following standard procedures (see Corriero, 1990; Longo *et al.*, 2004; Mercurio *et al.*, 2004).

The list of the analysed environmental parameters (those available for all studied environments) is presented in Table 1. The parameters are: 1) surface area of the basin; 2) number of freshwater inlets; 3) number of marine channels; 4) maximum depth; 5) minimum salinity; 6) mean salinity; 7) maximum salinity; 8) salinity stability; 9) sinuosity of the water body; 10) presence of *Posidonia oceanica* meadows; 11) presence of other phanerogams (number of species); 12) presence of rocky substrates; 13) presence of artificial substrates; 14) openness; 15) minimum water temperature; 16) mean water temperature; and 17) maximum water temperature. The salinity stability was computed as the measure of the percentage variation of range values compared to the main values (100 % = salinity end points equal to main value; 0 = extreme variation of salinity, from freshwater to hyperhaline). Sinuosity is expressed as the ratio between the perimeter of the lagoon and the circumference of a

circle having the same surface of the lagoon. Openness is the ratio (expressed in percentage) between the measurement of the surface area of the outlet and the perimeter; in a completely isolated ecosystem, the openness will be equal to 0%. Environmental data were collected from published articles (see Nonnis Marzano *et al.*, 2007; Barbone & Basset, 2010; Giangrande *et al.*, 2012; Basset *et al.*, 2013; Caruso *et al.*, 2013; Cardone *et al.*, 2014). Biotic and abiotic data were organised into two matrices: a presence/absence matrix with sponge data, and an abiotic data matrix with environmental parameters.

Taxonomic records gathered from field research were coupled with literature data in order to evaluate the trends of the taxonomic patterns through time. Articles retrieved were further screened according to sampling design and taxonomic resolution (taxa classified down to species level) of the present paper. Literature data refer to sampling performed in the years 2000 and 2007 for Lesina Lagoon (Nonnis Marzano *et al.*, 2003a, b; Cardone *et al.*, 2014), 2007 for Varano and Alimini (Cardone *et al.*, 2014); 1976-1983 and 2001-2004 for Taranto (Scalera Liaci *et al.*, 1976; Pulitzer Finali *et al.*, 1983; Longo *et al.*, 2004), 1964 for Faro and Ganzirri (Labate & Arena, 1964); 1984 for Tindari (Corriero, unpublished data); and 1990 and 2001 for Marsala (Corriero, 1990; Mercurio *et al.*, 2004). Taxonomic revision was carried out according to World Porifera Database (part of the World Register of Marine Species, <http://www.marinespecies.org/>), updated with the revised classification of Demospongiae by Morrow & Cárdenas (2015).

Study areas

Lesina

The lagoon of Lesina (Foggia, Apulia) (Fig. 1A) is an elongated coastal basin separated from the sea by a sand bar and stretching for approximately 22 km west to the east, with a maximum width of 2.2 km. It communicates with the sea by means of two artificial channels, the western one longer and narrower than the eastern channel. Usually, the water flow in both channels is limited on the lagoon side by sluices and partially obstructed grilles once used for fishing purposes. Freshwater inflows are due to small tributaries mainly located in the eastern sector of the basin. The combination of sea water and freshwater inflows produces a salinity gradient with values decreasing from west to east (Nonnis Marzano *et al.*, 2007).

Varano

The lagoon of Varano (Foggia, Apulia) (Fig. 1B) is the largest in southern Italy. The basin is surrounded on three sides by steep hills while the north side facing the sea is a bar of sand dunes. Two artificial channels, located at the eastern and western extremities of the sand bar respectively, provide a connection with the Adriatic Sea. The lagoon and the neighbouring coastal area are exploited by mussel farming.

Taranto

The Mar Piccolo of Taranto (Apulia) (Fig. 1C) consists of two distinct basins connected to the open sea through an outer semi-enclosed basin. The Mar Piccolo is characterised by low seawater turnover, with moderate currents, more intense in the first inlet than in the second (Capasso *et al.*, 1989). The second inlet receives freshwater inflow from some small streams. Dissolved oxygen shows wide seasonal variability, and oxygen deficits can occur in the deep layers, thus leading to seasonal dystrophic crises (Gaino *et al.*, 2010). Hard substrates are very abundant and diversified, mainly consisting of stones and debris of human origin, ropes and material abandoned by mussel farmers and fishermen. Rich assemblages of filter feeders (mainly poriferans, hydrozoans, polychaetes, bryozoans, bivalves, crinoids, and ascidians) characterise macrozoobenthos of hard substrates, forming multilayered assemblages (Gristina *et al.*, 2015).

Alimini

The Alimini Grande Lake (Lecce, Apulia) (Fig. 1D) is a salt-marsh separated from the sea by sand dunes. In the south-western area the main freshwater contributor is Lake Alimini Piccolo, a water body connected to the main basin by a 1,300 m-long channel. Moreover, the lake receives freshwater inputs in its north and north-west portions. Freshwater fluxes vary seasonally. The lake shores are generally rocky and a gradient from sandy to silty bottoms can be observed from the shore to the centre of the basin. Marshy areas are distributed mainly in the northern area of the basin. The very low nutrient values reported for the basin suggest an oligotrophic state, albeit not supported by the values of other trophic state descriptors estimated.

Faro

Faro Lake (Messina, Sicily) (Fig. 1E) is located on the Cape Peloro Peninsula, in the north-easternmost part of Sicily, between the Tyrrhenian and the Ionian seas. Although characterised by small dimensions, it represents the deepest coastal basin in Italy, reaching a maximum depth (28 m) in the funnel-shaped eastern part. By contrast, the shallower western side does not exceed 3 m in depth. The lake is characterised by a meromictic regime, with anoxic and sulphide-rich waters generally confined below 15 m depth. Exceptional seawater inflows cause strong alterations of the anoxic layer and temporary die-offs of aerobic organisms (Giuffrè & Pezzani, 2005).

Ganzirri

Ganzirri (Messina, Sicily) (Fig. 1F) is a brackish coastal lake having the appearance of a long (1,670 m) and narrow (200 m on average) stream tube parallel to the coast (Manganaro *et al.*, 2011). Due to its location, it gathers a considerable amount of freshwater from the

land. As a consequence, salinity and temperature variations induced by climatic conditions are remarkable.

Tindari

The Tindari ponds are located along the Tyrrhenian coast of Sicily (Province of Messina) (Fig. 1G). This area was characterised by a marked morphological evolution that produced rapid changes in number, shape, and dimensions of the ponds in a few years (Leonardi *et al.*, 2000). It currently includes five brackish-water ponds showing hydro-biological features related to indirect inputs of both marine and continental waters (Leonardi *et al.*, 2000). The ancient and more confined ponds (Marello, Mergolo, and Verde) are sensitive to the effects of continental waters, while the recent and external ones (Fondo Porto, Porto Vecchio) have typical marine characteristics. Data were collected from Verde (a), Porto Vecchio (b), and Mergolo (c) ponds (Fig. 1G). The Verde pond is the most eutrophic, with occasional dystrophic crises (Caruso *et al.*, 2010). The Porto Vecchio pond is characterised by oligotrophic waters with occasional seasonal increases in nutrient levels. Its origin dates back to the 1980s, and is due to the natural evolution of the coastal line. The Mergolo pond shows intermediate trophic values, close to those reported for the Porto Vecchio pond (Caruso *et al.*, 2010).

Marsala

Marsala Lagoon (Trapani, Sicily) (Fig. 1H) is characterised by high water exchange with the sea, mainly through the southern opening, which reduces thermohaline oscillations. However, the presence of a barrier of the phanerogam *Posidonia oceanica* greatly decreases the wave action even in the outermost part of the lagoon (Corriero, 1989). The bottom is covered by fine sediments, with considerable portions of coarse sand. Hard substrates are scarce, mainly represented by algal or animal calcareous concretions and by phanerogam rhizomes. The benthic fauna shows the highest values of taxonomic richness among Italian lagoon environments (Basset *et al.*, 2006), with demosponges representing a very important component of the macrozoobenthos (Corriero, 1989; 1990; Mercurio *et al.*, 2004).

Statistical analysis

Relationship among environmental parameters and Porifera richness was estimated using a Generalised Linear Mixed Models (GLMM). The taxa richness, weighted by the sample size, was used as binomial descriptor of biodiversity, being suitable to accurately estimate the similarity among sites. As predictors (fixed effect) of sponge richness all 17 environmental parameters were included in the model. GLMM offer a flexible approach to model the sources of variation and correlation that arise from grouped data by combining the properties of linear mixed models, which incorporate random ef-

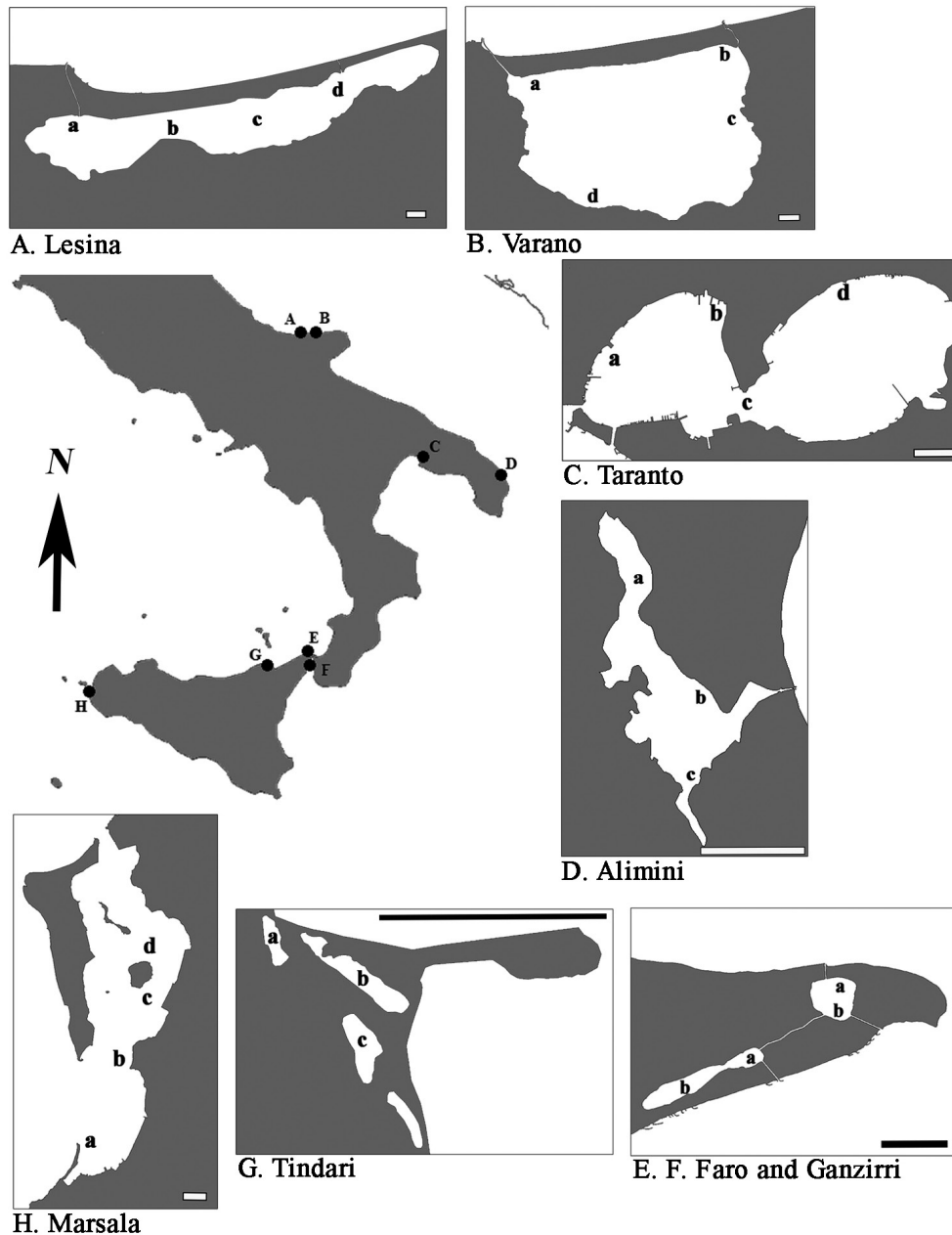


Fig. 1: Distribution of the lagoon systems studied. Small letters indicate sampling sites. Scale bar = 1 km.

Table 1. Main structural environmental parameters: 1 Surface (km²); 2 n° of freshwater inlets; 3 n° of seawater inlets; 4 max depth (m); 5 min, 6 mean and 7 max salinity (PSU); 8 salinity stability (%); 9 sinuosity (%); 10 presence/absence of *Posidonia oceanica*; 11 presence/absence of other phanerogams; 12 presence/absence of rocky substrates; 13 presence/absence of artificial substrates; 14 openness (%); 15 min, 16 mean and 17 max water temperatures (°C) (Mancinelli *et al.*, 2005; Nonnis Marzano *et al.*, 2007; Barbone & Basset, 2010; Giangrande *et al.*, 2012; Basset *et al.*, 2013; Caruso *et al.*, 2013; Cardone *et al.*, 2014).

| Lagoon | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|----------|-------|---|---|-----|----|------|----|----|-----|----|----|----|----|-----|----|------|----|
| Lesina | 51 | 1 | 2 | 1.5 | 5 | 22.5 | 51 | 68 | 2.0 | 0 | 2 | 0 | 1 | 0.1 | 3 | 16.5 | 32 |
| Varano | 60.50 | 1 | 2 | 6 | 24 | 24.8 | 29 | 95 | 1.2 | 0 | 2 | 0 | 1 | 0.1 | 7 | 19.1 | 28 |
| Taranto | 21.76 | 1 | 1 | 13 | 37 | 36 | 38 | 71 | 1.3 | 0 | 3 | 1 | 1 | 0.2 | 8 | 18.2 | 27 |
| Alimini | 1.40 | 1 | 1 | 3.4 | 22 | 29 | 35 | 11 | 2.2 | 0 | 1 | 1 | 1 | 0.2 | 5 | 19.0 | 25 |
| Faro | 0.26 | 1 | 2 | 28 | 34 | 36 | 38 | 55 | 1.1 | 0 | 1 | 1 | 0 | 0.4 | 14 | 29 | 34 |
| Ganzirri | 0.33 | 1 | 2 | 6.5 | 31 | 32.3 | 35 | 80 | 1.7 | 0 | 0 | 1 | 0 | 0.3 | 14 | 24.6 | 29 |
| Tindari | 0.02 | 0 | 0 | 3.4 | 29 | 34 | 39 | 88 | 2.7 | 1 | 2 | 1 | 0 | 0.0 | 10 | 21.1 | 28 |
| Marsala | 20 | 0 | 2 | 2.0 | 38 | 39.3 | 40 | 97 | 1.8 | 1 | 5 | 1 | 0 | 5.8 | 12 | 19.7 | 28 |

fects, and generalised linear models which handle non-normal data (Bolker *et al.*, 2009). All the environmental parameters have been previously standardised using *Decostand* command of package *Vegan* (Oksanen *et al.*, 2013). All the possible combinations were examined to evaluate the fit of different predictor variables. Models were compared using the Akaike's Information Criterion correction for finite sample sizes (AICc), which provides a measure of the relative importance of the predictor variables. As there were a number of well-supported models for each response variable, model averaging was performed on all models within a 95% AICc confidence interval. This method has numerous advantages since it does not require to define an arbitrary threshold for support of the best model, as in the traditional approaches. Furthermore, model averaging provides a measure of the importance of explanatory variables in the models (Burnham & Anderson 2002). The relative importance (RI) of variables are calculated as the sum of the Akaike weights of the models in which the variable appears; better models have larger Akaike weights, and a variable that contributes more to model fit will thus have a higher RI value.

The pattern of sponge distribution along environmental parameters highlighted by AICc and across different lagoons was estimated using a Canonical Correspondence Analysis (CCA, Legendre & Legendre 1998). One particularly attractive feature of a CCA triplot is that species are ordered along the canonical axes following their ecological optima. This allows a relatively easy ecological interpretation of species assemblages. This data, even though collected for the investigation on sponge species occurrence, can be biased by different sampling efforts, as some stations had no sponge species, and furthermore, ecological and spatial autocorrelation among stations can occur. To prevent the effect of confusing factors it was decided to consider the sponge richness as a whole within lagoons without spatial replicates. The pattern of sponge distribution within and among lagoons was estimated using a metric multidimensional scaling such as the Principal Component Analysis (PCoA) on the matrix of species-lagoon interactions (matrix of presence-absence) without recourse to environmental parameters. PCoA allows to order samples in matrices with many zero values (common situation in the matrices of occurrence). Stations without sponge species have been removed from the matrix. To estimate the temporal stability of the Porifera assemblages within lagoons from a quantitative point of view, the specific richness and the presence of persistent species at the beginning and at the end of a period of observation was compared and evaluated using the data of the present work as well as literature data. The pattern of sponge distribution among time series was estimated using a PCoA. Significance of variables in determining variation of distances has been tested using a permutation MANOVA test (Anderson, 2001) on the scores of ordination models.

All the analyses presented in this study used R statistical software (R Core Team, 2015).

Results

Sponge taxonomic patterns

Overall, 62 sponge species, belonging to the classes Demospongiae (52), Calcarea (8), and Homoscleromorpha (2), were recorded at the studied lagoon sites (Table 2). For the Demospongiae, all three subclasses (Verongimorpha, Keratosa and Heteroscleromorpha) are represented and among the 22 orders currently considered to be valid (van Soest, 2015) thirteen are represented in the study sites. The order Dictyoceratida is the most represented, with 5 families, 6 genera, and 11 species. The orders Haplosclerida (5 families, 5 genera and 8 species), Poecilosclerida (3 families, 4 genera, and 8 species), Clionaida (1 family, 2 genera, and 6 species) and Suberitida (2 families, 3 genera, and 6 species) species are also well represented. The orders Tethyida (2 families, 2 genera, and 4 species), Bubarida (1 family, 1 genus, and 2 species) and Dendroceratida (1 family, 1 genus, and 2 species) are present with few species. Finally, the Axinellida, Chondrillida, Polymastiida, Tetractinellida and Verongida are present with one species only. Within the Calcarea, both the known subclasses of Calcinea and Calcaronea are represented, with one order each (Clathrinida and Leucosolenida, respectively) of the five currently considered to be valid (van Soest, 2015), including 6 families, 6 genera and 8 species. The order Clathrinida is represented by three species while the order Leucosolenida is represented by five species. Within this latter order, the presence of the alien invasive species *Paraleucilla magna*, already reported from Taranto (Longo *et al.*, 2004; 2007) and Faro (Bertolino *et al.*, 2014), is still remarkable. The class Homoscleromorpha is represented by its sole known order (Homosclerophorida), two families (Oscarellidae, Plakinidae), two genera, and two species.

Sponge distribution at a spatial scale

All the lagoon systems studied hosted sponges, even if with marked differences in species richness (Table 2). Marsala hosted 45 species, 17 of which (38% of the total richness) were exclusive to this lagoon. Thirty-one species were found at Taranto, seven of which (23%) exclusive to this site; 12 at Faro, with four exclusive species (33%); nine at Alimini, with two exclusive species (22%); five at Tindari with two exclusive species (40%). Ganzirri, Varano, and Lesina respectively hosted six, five, and one species and did not show any exclusive species (Fig. 2). On the whole, 52% of the species recorded during this study were "unique species" (species only found at a single site, *sensu* Colwell & Coddington, 1994), while approximately 31% were represented by "duplicates" (species present at two sites, *sensu* Munari & Mistri, 2008) (Fig. 3).

Table 2. List of the sponge species recorded at the eight lagoon sites based on both the present – in bold – and literature data (Labate & Arena, 1964; Scalera Liaci *et al.*, 1976; Pulitzer Finali *et al.*, 1983; Corriero, 1990; Nonnis Marzano *et al.*, 2003 a, b; Longo *et al.*, 2004; Mercurio *et al.*, 2004; Cardone *et al.*, 2014).

| Taxa | Taranto 1976-83 | Taranto 2001-2004 | Taranto 2010 | Alimini 2007 | Alimini 2012 | Faro 1964 | Faro 2006 | Ganzirri 1964 | Ganzirri 2006 | Tindari 1984 | Tindari 2004 | Marsala 1990 | Marsala 2001 | Marsala 2010 |
|---|-----------------|-------------------|--------------|--------------|--------------|-----------|-----------|---------------|---------------|--------------|--------------|--------------|--------------|--------------|
| Calcarea | | | | | | | | | | | | | | |
| <i>Clathrina coriacea</i> (Montagu, 1814) | | | | | | | | | | | | * | * | * |
| <i>Clathrina rubra</i> Sarà, 1958 | | | * | * | | | | | | | | * | * | * |
| <i>Leucandra crambessa</i> Haeckel, 1872 | * | * | * | * | | | | | | | | * | * | * |
| <i>Leucetta solida</i> (Schmidt, 1862) | * | * | | | | | | | | | | * | * | * |
| <i>Leucosolenia microspinata</i> Longo, 2009 | | | | | | | | | | * | | | | |
| <i>Leucosolenia variabilis</i> (Haeckel, 1870) | * | * | * | * | | | | | | | | * | * | * |
| <i>Paraleucilla magna</i> Klautau, Monteiro & Borojevic, 2004 | | | * | * | | | | | * | | | * | * | * |
| <i>Sycon ciliatum</i> (Fabricius, 1780) | * | * | * | * | | | | | | | | * | * | * |
| <i>Sycon raphanus</i> Schmidt, 1862 | | | | | * | | | | | | | | | |
| Homoscleromorpha | | | | | | | | | | | | | | |
| <i>Oscarella lobularis</i> (Schmidt, 1862) | | | * | * | | | | | | | | * | * | * |
| <i>Plakina monolopha</i> Schulze, 1880 | | | * | * | | | | | * | | | * | * | * |
| <i>Plakortis simplex</i> Schulze, 1880 | | | | | | * | | | | | | | | |
| Demospongiae | | | | | | | | | | | | | | |
| <i>Aaptos aaptos</i> (Schmidt, 1864) | | | | | | | | | | | | * | * | * |
| <i>Acarinus tortilis</i> Topsent, 1892 | * | | | | | | | | | | | * | * | * |
| <i>Aplysilla rosea</i> (Barrois, 1876) | | * | * | * | | | | | | | | * | * | * |
| <i>Aplysilla sulfurea</i> Schulze, 1879 | | * | * | * | | | | | | | | * | * | * |
| <i>Aplysina aerophoba</i> (Nardo, 1833) | | | | | | | | | | | | * | * | * |
| <i>Batzella inops</i> (Topsent, 1891) | | * | * | * | | | | | | | | * | * | * |
| <i>Cacospongia mollior</i> Schmidt, 1862 | | | * | * | | | | | | | | * | * | * |
| <i>Chalinula limbata</i> (Montagu, 1814) | | | | | | | | | | | | * | * | * |
| <i>Chalinula reuteroides</i> Schmidt, 1868 | | | | | | | | | | | | * | * | * |
| <i>Chondrilla nucula</i> Schmidt, 1862 | | | | | | | | | | | | * | * | * |
| <i>Cinachyrella tarentina</i> (Pulitzer-Finali, 1983) | * | | | | | | | | | | | * | * | * |
| <i>Ciocalypia penicillus</i> Bowerbank, 1862 | | | | | | | | | | | | * | * | * |
| <i>Clathria (Clathria) toxistyla</i> (Sarà, 1959) | | | | | | | | | | | | * | * | * |
| <i>Clathria (Clathria) toxivaria</i> (Sarà, 1959) | | | | | | | | | | | | * | * | * |
| <i>Clathria (Microciona) cleistochela</i> (Topsent, 1925) | * | * | * | * | | | | | | | | * | * | * |
| <i>Clathria (Microciona) gradalis</i> (Topsent, 1925) | * | * | * | * | | | | | | | | * | * | * |
| <i>Cliona celata</i> Grant, 1826 | * | * | * | * | | | | | | | | * | * | * |
| <i>Cliona copiosa</i> Sarà, 1959 | | | * | * | | | | | | | | * | * | * |
| <i>Cliona rhodensis</i> Rützler & Bromley, 1981 | | | | | | | | | | | | * | * | * |
| <i>Cliona</i> cf. <i>schmidti</i> (Ridley, 1881) | | | | | | | | | | | | * | * | * |
| <i>Cliona viridis</i> (Schmidt, 1862) | * | * | * | * | | | | | | | | * | * | * |
| <i>Cliothisa hancocki</i> (Topsent, 1888) | * | * | * | * | | | | | | | | * | * | * |
| <i>Dictyonella incisa</i> (Schmidt, 1880) | | * | * | * | | | | | | | | * | * | * |
| <i>Dictyonella pelligera</i> (Schmidt, 1864) | | * | * | * | | | | | | | | * | * | * |
| <i>Dysidea avara</i> (Schmidt, 1862) | | * | * | * | | | | | | | | * | * | * |
| <i>Dysidea fragilis</i> (Montagu, 1814) | * | * | * | * | | | | | | | | * | * | * |
| <i>Dysidea incrustans</i> (Schmidt, 1862) | * | * | * | * | | | | | | | | * | * | * |
| <i>Eurypon clavatum</i> (Bowerbank, 1866) | * | * | * | * | | | | | | | | * | * | * |

(continued)

Table 2 (continued)

| Taxa | Marsala 2010 | Marsala 2001 | Marsala 1990 | Tindari 2004 | Tindari 1984 | Ganzirri 2006 | Ganzirri 1964 | Faro 2006 | Faro 1964 | Alimini 2012 | Alimini 2007 | Taranto 2010 | Taranto 2001-2004 | Taranto 1976-83 | Varano 2012 | Varano 2007 | Lesina 2011 | Lesina 2007 | Lesina 2000 | 1 | 1 | 1 | 3 | 5 | 30 | 22 | 31 | 4 | 9 | 17 | 12 | 6 | 6 | 4 | 5 | 41 | 47 | 45 | | | | | | | | | | |
|--|--------------|--------------|--------------|--------------|--------------|---------------|---------------|-----------|-----------|--------------|--------------|--------------|-------------------|-----------------|-------------|-------------|-------------|-------------|-------------|---|---|---|---|---|----|----|----|---|---|----|----|---|---|---|---|----|----|----|---|---|---|---|---|---|---|---|---|---|
| <i>Eurypon viride</i> (Topsent, 1889) | * | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| <i>Geodia cydonium</i> (Jameson, 1811) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | | | | |
| <i>Halichondria (Halichondria) bowerbanki</i> (Burton, 1930) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | | | |
| <i>Halichondria (Halichondria) panicea</i> (Pallas, 1766) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | | |
| <i>Halichondria (Halichondria) semitubulosa</i> (Lieberkuhn, 1859) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | | |
| <i>Haliclona (Haliclona) simulans</i> (Jonsthor, 1842) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | |
| <i>Haliclona (Reniera) cinerea</i> (Grant, 1826) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | |
| <i>Haliclona (Reniera) mediterranea</i> (Griessinger, 1971) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | |
| <i>Haliclona (Rhizonera) rosea</i> (Bowerbank, 1866) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | |
| <i>Haliclona (Soestella) mucosa</i> (Griessinger, 1971) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | |
| <i>Haliclona palmata</i> (sensu Lieberkuhn, 1859) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | | |
| <i>Hymeniacidon perlevis</i> (Montagu, 1814) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | |
| <i>Ircinia variabilis</i> (Schmidt, 1862) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | |
| <i>Ircinia reticulata</i> Pulitzer Finali & Pronzato, 1981 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | |
| <i>Mycale (Aegogropila) contarenii</i> (Lieberkuhn, 1859) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | |
| <i>Mycale (Aegogropila) retifera</i> (Topsent, 1924) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | |
| <i>Mycale (Aegogropila) rotalis</i> (Bowerbank, 1874) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | | |
| <i>Myxilla (Myxilla) rosacea</i> (Lieberkuhn, 1859) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Oceanapia decipiens</i> (Sarà, 1958) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Oceanapia isodictyiformis</i> (Carter, 1882) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Phorbas topsenti</i> Vacelet & Perez, 2008 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Pione vasitifica</i> (Hancock, 1849) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Polymastia penicillus</i> (Montagu, 1814) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Protosuberites epiphyllum</i> (Lamarck, 1815) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Pseudosuberites sulphureus</i> (Bowerbank, 1866) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Raspaciona aculeata</i> (Jonsthor, 1842) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Sarcotragus pipetta</i> (Schmidt, 1868) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Sarcotragus spinosulus</i> Schmidt, 1862 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Scalarispongia scalaris</i> (Schmidt, 1862) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Siphonochalina</i> sp. | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Spirastrella cunctatrix</i> Schmidt, 1868 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Spongia (Spongia) officinalis</i> Linnaeus, 1759 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Spongia (Spongia) virgulosa</i> (Schmidt, 1868) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Spongosorites intricatus</i> (Topsent, 1892) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Suberites carnosus</i> (Johnston, 1842) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Tedania (Tedania) anhelans</i> (Vio in Olivi, 1792) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Terpios fagax</i> Duchassaing & Michelotti, 1864 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Tethya aurantium</i> (Pallas, 1766) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| <i>Tethya citrina</i> Sarà & Melone, 1965 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Tethya meloni</i> Corricio, Gadaleta & Bavestrello, 2015 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Tethyspira spinosa</i> (Bowerbank, 1874) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Timea crassa</i> (Topsent, 1900) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Timea stellata</i> (Bowerbank, 1866) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| <i>Timea unistellata</i> (Topsent, 1892) | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | |
| No. of taxa | 1 | 1 | 1 | 1 | 1 | 3 | 5 | 30 | 22 | 31 | 4 | 9 | 17 | 12 | 6 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

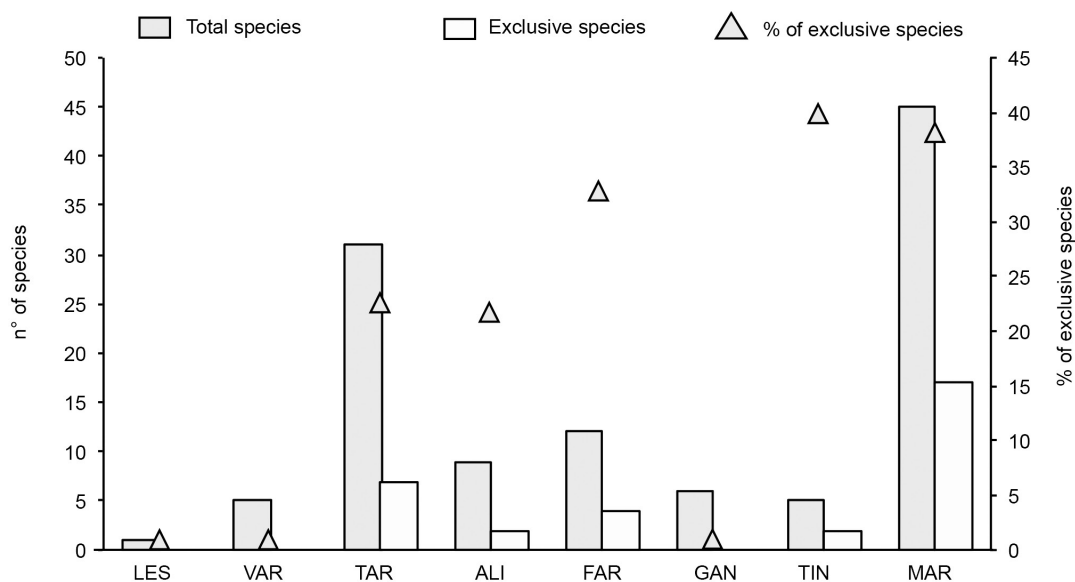


Fig. 2: Numbers of sponge species (total and exclusive species), within the lagoon systems under study.): Lesina (LES), Varano (VAR), Taranto (TAR), Alimini (ALI), Faro (FAR), Ganzirri (GAN), Tindari (TIN), Marsala (MAR).

Six species were found at three of the eight study sites, whereas only a few species were recorded in more than half of the study sites. In particular, *Halichondria* (*Halichondria*) *panicea* was the only species present in all the environments studied, while *Hymeniacidon perlevis* was found in six of the sites and *Halichondria* (*H.*) *bow-erbanki*, *Oceanapia isodictyformis*, and *Sycon raphanus* occurred in half of the studied lagoons.

Sponge distribution and environmental parameters

The GLMMs and the related AICc show that the sponge species richness essentially depends on five of the 17 environmental parameters tested (Fig. 4). Both salinity minimum and salinity stability are able to explain

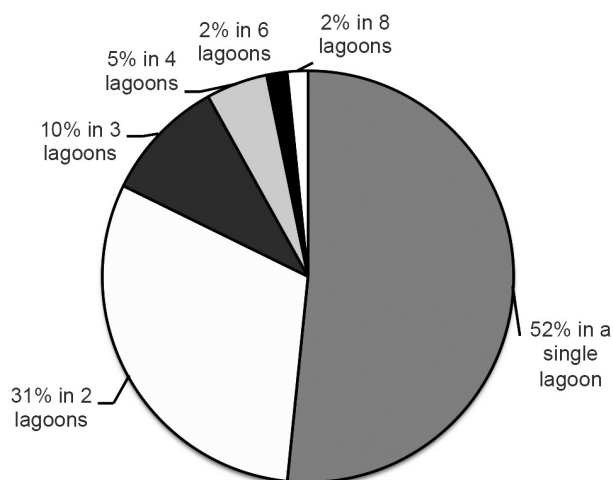


Fig. 3: Distribution of unique, duplicate, and common sponge species among the lagoon systems.

sponge species richness, giving a similar contribution and being present in 100% of the averaging models. The mean salinity was removed from the model because it strongly correlated with the minimum salinity ($r > 0.9$). The presence of phanerogams and the openness make a similar and moderate contribution (RI values 0.65 and 0.53, respectively), while lagoon surface (found in two of the five models) is the parameter which least contributes to the sponge species richness. The pattern of lagoon distribution and species occurrence related to the five significant environmental variables is shown in Figure 5. The two principal axes explain 67% of data variance. Three of the five environmental parameters (salinity minimum, salinity stability and openness) show a strong correlation with each other and opposite to lagoon surface. There is no direct correlation between phanerogams and the remaining four parameters. Both Taranto and Marsala show high openness, large surface area, high salinity minimum, and greater salinity stability, whereas Alimini displays the widest salinity variation. The remaining lagoons are generally characterised by lower values of openness, number of phanerogam species, salinity minimum, and surface area, and among them Tindari shows the lowest values for all the variables considered.

Regarding the distribution of species in relation to the five environmental factors highlighted by AICc test, CCA shows that, although a part of the species appears to be randomly distributed, others seems to be linked to one or more factors. In particular, a first group of species including *Cliona schmidtii*, *C. celata*, *C. rhodensis*, *Pione vastifica*, *Dysidea avara*, and *Sacrotragus spinosulus*, is positively related to the number of phanerogam species. A second group includes *Leucosolenia microspinata*, *Eurypon*

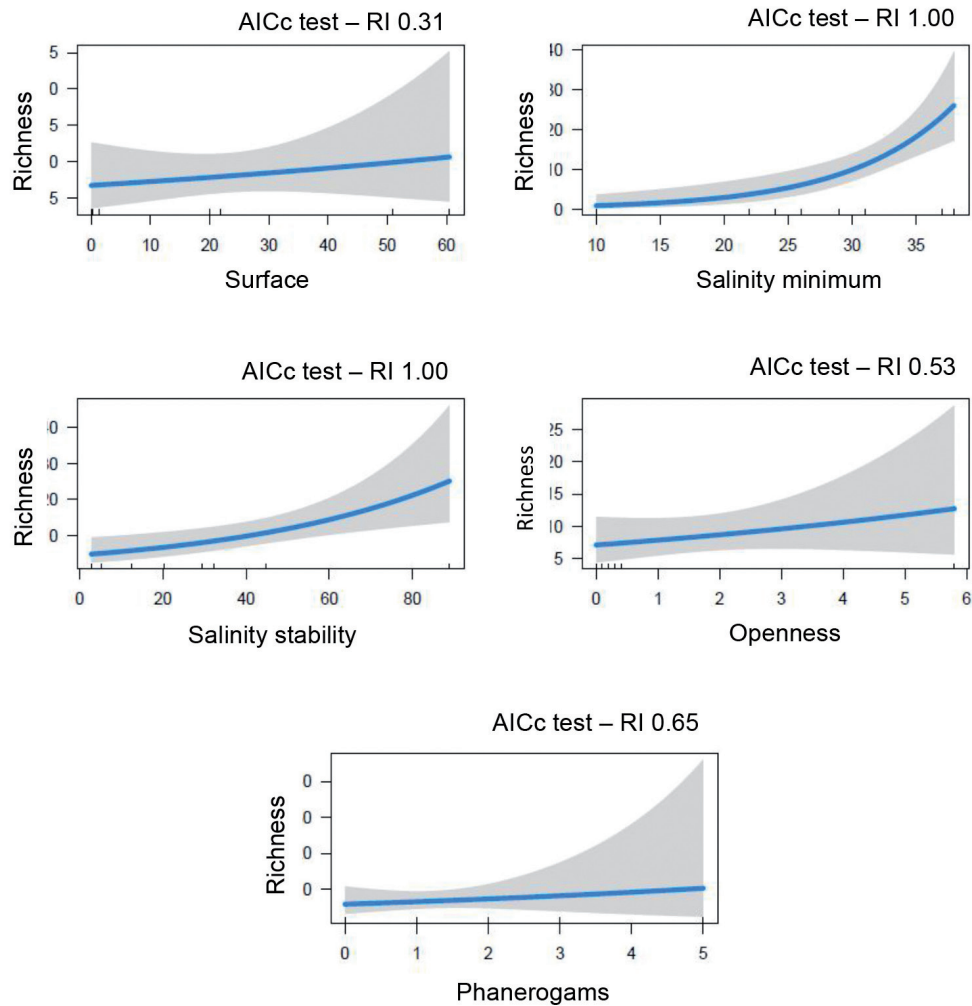


Fig. 4: Plots of the Generalised Linear Mixed Models (GLMMs) built using different potential predictor variables: species richness (dependent variable) and five of the 17 environmental parameters (independent variables).

viride, *Polymastia penicillus*, *Halichondria (H.) panicea*, *Ircinia variabilis*, and *Paraleucilla magna* whose presence is positively linked to high values of minimum salinity, to salinity stability, and openness. The lagoon surface, although it represents one of the factors able to explain the specific richness, does not directly influence the occurrence of any sponge species. Other species are distributed without any obvious connection with the five main factors. The PCoA (Fig. 6; Pseudo F = 2.781, $p < 0.001$) shows a first separation along the first axis between Marsala and Taranto that are distributed along the positive values of the axis and the remaining lagoons which are distributed around negative values. The second axis further divides these groups, with Marsala and Taranto being distributed according to opposite values of the axis (Fig. 6). Taranto shows a sponge assemblage with a homogenous distribution except for station d, the innermost and the most confined (Fig. 1C), showing a sponge assemblages more similar to that of Faro and Ganzirri. The Alimini stations are grouped and separated from the remaining lagoons because of a diversified and conservative sponge assemblage occurring within the biotope. The remaining lagoons show

remarkable data overlap that makes them indistinguishable from each other.

The distribution of sponges in the studied lagoon systems according to the availability of substrates is reported in Table 3. In all lagoons, the sponges colonize rocks, artificial substrates, soft bottoms, algal beds (both sessile and unattached algae), and phanerogam leaves. In addition, at Marsala, the hard rhizomes of *P. oceanica* are also largely exploited by sponges, whereas at Lesina an additional biological substrate usually hosting sponges is represented by the reefs of the polychaete tube worm *Ficopomatus enigmaticus*. No relationships between sponge species richness and difference in availability of substrates in the lagoon systems were highlighted by the statistical analysis. Generally, rocky substrates, when present, show the highest diversity of sponge species, together with the rhizomes of *P. oceanica* (Marsala) and artificial substrates (Taranto). Usually, in a same lagoon, sponge species associated with soft substrates differ from those inhabiting hard substrates; conversely, no appreciable differences in species composition were observed between artificial and rocky substrates. The number of sponge

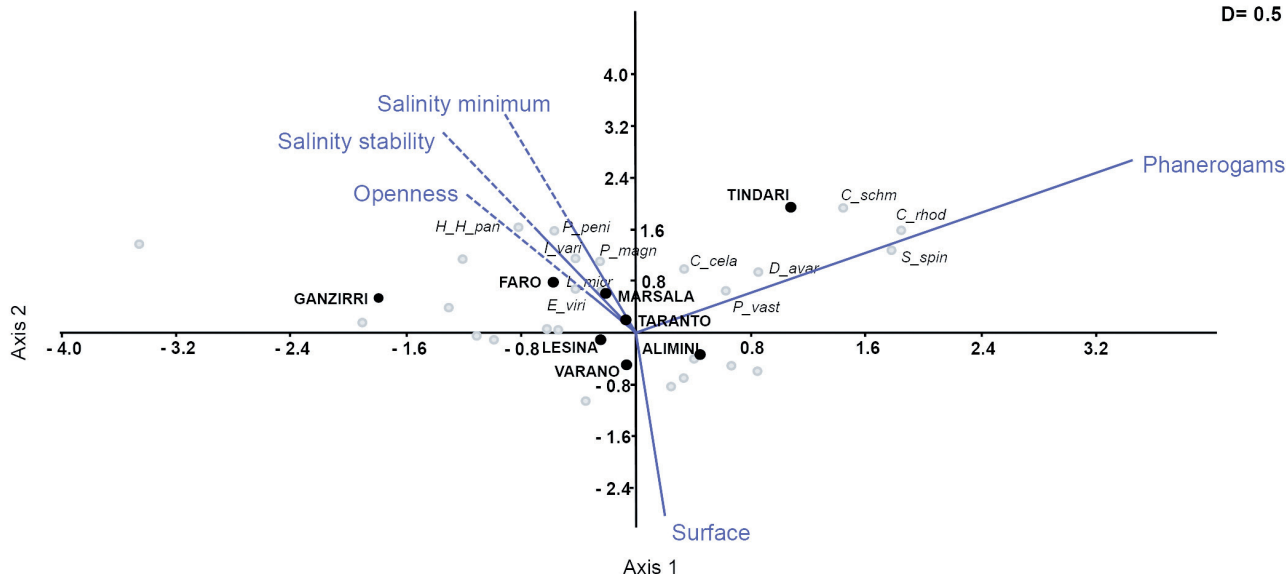


Fig. 5: CCA triplot of sponge species within lagoons constrained by five over 17 environmental parameters. Species abbreviations: *C_cela* (*Cliona celata*), *C_rhod* (*Cliona rhodensis*), *C_schm* (*Cliona schmidtii*), *D_avar* (*Dysidea avara*), *E_viri* (*Eurypon viride*), *H_H_pan* (*Halichondria (Halichondria) panicea*), *I_vari* (*Ircinia variabilis*), *L_micr* (*Leucosolenia microspinata*), *S_spin* (*Sarcotragus spinosulus*), *P_peni* (*Polymastia penicillus*), *P_magn* (*Paraleucilla magna*), *P_vast* (*Pione vastifica*).

species exclusively associated to only one substrate is very low; in particular at Marsala, *Cliona copiosa* and *Chalinula renieroides* were exclusively found on soft bottoms and *P. oceanica* leaves, respectively; at Tindari, *Eurypon viride* was found exclusively in association with algal beds.

Temporal distributions of the sponge assemblages

Figure 7 shows the variation in species richness and the persistence of the sponge assemblages occurring at the study sites during the time interval considered. The time intervals for each site were the following: Varano and Alimini 5 years; Lesina 12 years; Tindari and Marsala 20 years; Taranto 34 years; Faro and Ganzirri 42 years.

The percentage of persistent species in the eight lagoons (i.e. species reported by the oldest literature record that were also found during the present study) varied between 24 and 100% (Fig. 7). Indeed, all the species reported by the oldest available literature from the lagoons of Lesina, Varano, Alimini and Tindari were also found during the present investigation. Marsala, characterised by the highest species richness, showed approximately 94% of persistent species recorded after a time interval of 20 years (1990-2010). On the contrary, at Taranto and Ganzirri, persistent species were nearly 43 and 50%, respectively, whereas at Faro we found the lowest persistence of the sponge assemblage, with 24% of persistent species after a 42-year time interval.

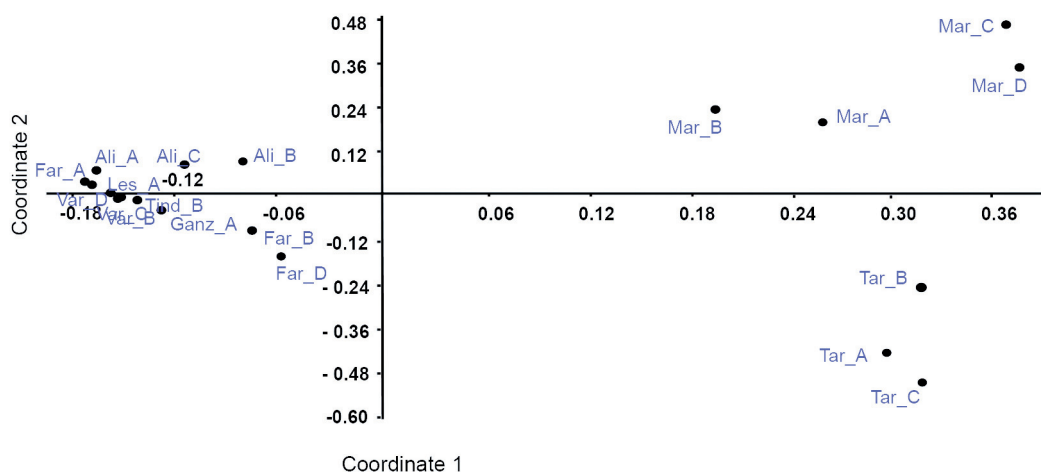


Fig. 6: PCoA biplot of a Bray-Curtis dissimilarity matrix of the presence/absence data of sponge species among stations. Lesina (LES), Varano (VAR), Taranto (TAR), Alimini (ALI), Faro (FAR), Ganzirri (GAN), Tindari (TIN), Marsala (MAR).

Table 3. Substrates exploited by sponges (number of collected species) within the lagoon systems studied.

| | Lesina | Varano | Taranto | Alimini | Faro | Ganzirri | Tindari | Marsala |
|--|--------|--------|---------|---------|------|----------|---------|---------|
| <i>P. oceanica</i> (leaves, rhizomes) | | | | | | | | 21 |
| Other phanerogams (leaves) | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 3 |
| Algal beds | 1 | 2 | 5 | 2 | 6 | 3 | 2 | 7 |
| <i>F. enigmaticus</i> reefs | 1 | | | | | | | |
| Rocky substrates | | 3 | 26 | 3 | | | | 28 |
| Artificial substrates | 1 | 1 | 14 | 1 | 5 | 3 | 1 | 4 |
| Soft bottoms | 1 | 1 | 5 | 1 | 2 | 2 | 2 | 9 |

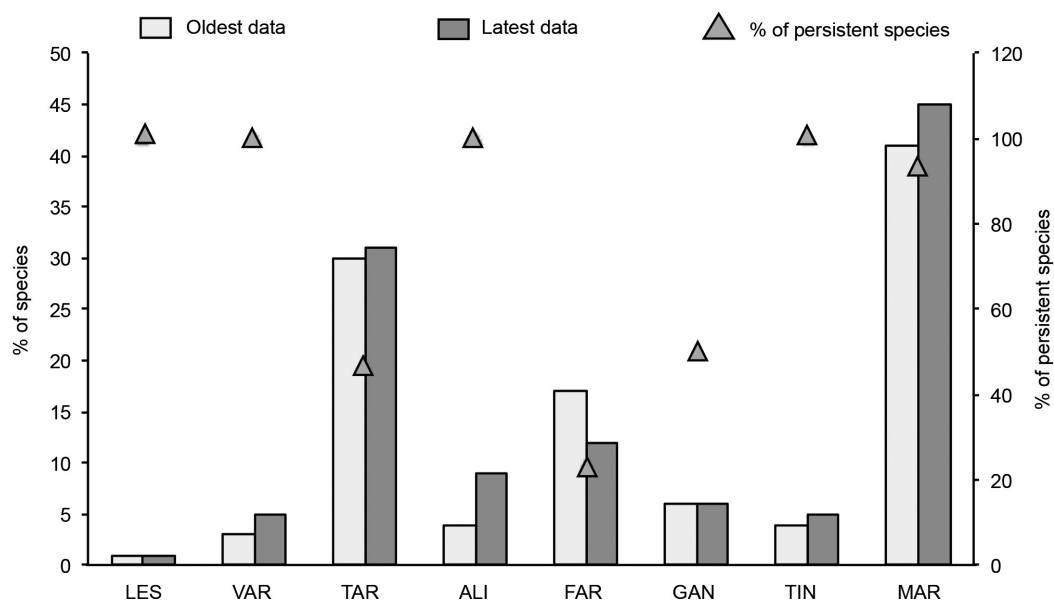


Fig. 7: Temporal comparison of species richness (bars), and, in percentages, persistence of species over time (black triangles) in the study sites. Labels on the x-axis refer to the study lagoons.

Regarding sponge species richness, Lesina, Taranto and Ganzirri showed rather conservative values, without remarkable changes in the number of species over time. At Varano, Alimini, Marsala and Tindari an increase in the number of poriferans was observed, likely due to a higher accuracy in the data sampling and the taxonomic analysis. At Faro we observed a marked decrease in number of species, although this was registered after a rather long time interval of 42 years.

The analysis of time series scaling (Fig. 8) showed a separation of two lagoons (Taranto and Marsala) from all the others. Differences are not casual (Pseudo F = 1.851, $p < 0.001$) and reflect the diverse composition of specific populations of sponges (Fig. 7). Thereafter Taranto and Marsala separated in a clear manner according to the first axis. All remaining lagoons separated from the first two with a negative value of the first axis and showed an overlap that does not allow visualising of a clear pattern.

Lesina

The only species recorded in this basin is *Halichondria (Halichondria) panicea*, already present in 2000. In accordance with the literature (Nonnis Marzano *et al.*, 2007), the species was mostly distributed in the western part of the basin, at higher salinity values. This site, in summer 2008, was strongly affected by a severe dystrophic event (Basset *et al.*, 2013).

Varano

Of the five species found in 2012, two records were new for this lagoon: *Hymeniacidon perlevis* and *Sycon raphanus*.

Taranto

Of the 31 species found during the present investigation, only three were new records for this environment (*Clathrina rubra*, *Sarcotragus pipetta*, and *Spongia (Spongia) virgultosa*). Moreover, it was possible to con-

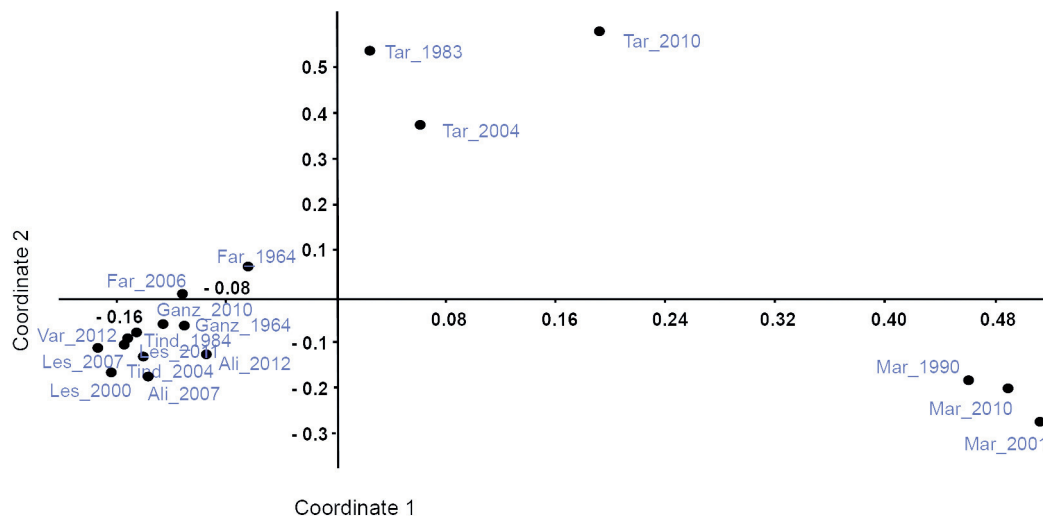


Fig. 8: PcoA on the species/time matrix, the first two axes explain 44% and 14% of variance, respectively. Lesina (LES), Varano (VAR), Taranto (TAR), Alimini (ALI), Faro (FAR), Ganzirri (GAN), Tindari (TIN), Marsala (MAR).

firm the massive presence of the alien calcareous sponge *Paraleucilla magna*, already recorded at Taranto since 2001 (Longo *et al.*, 2004; 2007).

In general, a remarkable change in species composition of the sponge assemblage has occurred at Taranto at the end of the last centuries. Indeed, of the 30 species recorded during the period 1976-1983 (Scalera Liaci *et al.*, 1976; Pulitzer Finali, 1983), only seven were also reported by Longo *et al.* (2004), who recorded a total of 22 species for the time interval 2001-2004. Changes in sponge assemblages could be probably due to the intense industrialization of the area and to the increased presence of mollusc and fish farms as sources of habitat modification (Caroppo *et al.*, 1994).

Alimini

Of the nine species found during the present study, five (*Cliona celata*, *C. rhodensis*, *C. cf. schmidtii*, *Sarcotragus spinosulus*, *Sycon raphanus*) were new records for the lagoon.

Faro

From the 12 sponge species recorded during the present study, only four (*Halichondria (H.) panicea*, *H. (H.) bowerbanki*, *Hymeniacidon perlevis* and *Suberites carnosus*) were also present in 1964, while eight species were new records for this environment. Thirteen out of 17 species listed in the literature have disappeared from the basin within the last 42 years. The occurrence of the alien species *P. magna*, reported in 2012 by Bertolino *et al.* (2014), is noteworthy, and confirms the fact that this area may be considered as a hot-spot for the entry and spread of alien species in the Central Mediterranean (Cosentino *et al.*, 2009). As it happens at Taranto, these faunistic changes are probably due both to the anthropogenic impacts arising from extensive urbanization along

the shore (Giangrande *et al.*, 2012) and to the presence of mollusc aquaculture farms as sources of habitat modification.

Ganzirri

Of the six species found in the basin during the present study, three (*Halichondria (H.) bowerbanki*, *Haliclona (Reniera) cinerea* and *Hymeniacidon perlevis*) were persistent species already present here in 1964, and three (*Chalinula renieroides*, *Halichondria (H.) panicea*, *Suberites carnosus*) were new records for this site.

Tindari

Three demosponge species (*Hymeniacidon perlevis*, *Halichondria (H.) panicea*, *Oceanapia isodictyiformis*) and one calcisponge (*Leucosolenia microspinata*) were recorded in 1984, whereas after twenty years a further demosponge (*Eurypon viride*) was detected.

Marsala

The comparison between the current species composition of the sponge assemblages and that reported in the literature (Corriero, 1990; Mercurio *et al.*, 2004) shows remarkable persistence of the sponge fauna from Marsala Lagoon: of the 45 species surveyed in 2010, 43 were also present in 2001 and 38 of these since 1990. Among the species not previously recorded, there is a new species belonging to the genus *Tethya*, *T. meloni*, recently described by this research group (Corriero *et al.*, 2015a). By contrast, the disappearance of a few species of demossponges is remarkable, since in the past they were represented by high or very high number of individuals. In particular: *Phorbas topsenti* that probably disappeared at the end of the last century after a large epidemic event (Corriero & Gaino, unpublished data), and *Chalinula*

limbata, that was recorded in association with leaves of the phanerogam *Posidonia oceanica* (Corriero, 1990), now in regression within this lagoon.

Discussion

On the whole, the lagoon systems of southern Italy are suitable environments for sponges, since they host approximately 12% of the 509 sponge species reported for all the Italian coasts (Pansini & Longo, 2008). It is interesting to note that whilst the class Calcarea represents 7.8% of the whole Italian sponge fauna, the studied lagoon systems host a higher percentage of Calcarea (12.9% of the species recorded).

Within Demospongiae, the order Dictyoceratida is the most represented (11 species, 17.7% of the species list), in contrast to the known taxonomic composition of the Mediterranean sponge fauna, where Poecilosclerida are dominant (Pansini & Longo, 2003). Moreover, the number of species belonging to the order Tetractinellida found during the present study is very low, when compared with records related to other Mediterranean sponge assemblages in different environments (Corriero *et al.*, 2004). In the studied lagoons, therefore, abundance ratios among demosponge taxa are distinctive and the Mediterranean most common sponge orders, namely Poecilosclerida and Tetractinellida, are scarcely represented, probably due to selective processes related to the stressing environmental factors typically affecting these environments.

A feature which may explain such richness in sponge species is the evidence that, differently from shallow open waters, sponges are able to colonize a wide range of habitats and substrates in lagoon environments. Indeed, besides inhabiting rocky substrates, often of anthropogenic origin, several sponges in lagoon environments used to live in association with frondose algae and phanerogams, both utilised as a substrate and as a filter against the intense light radiation. At Lesina, for example, *Halichondria (H.) panicea* is able to colonize the thalli of the unattached alga *Valoniopsis egagropyla*. According to Nonnis Marzano *et al.* (2003b; 2007), the sponge varies its distribution in the lake with time, in accordance with salinity variations, thanks to the currents which induce movements of the algal beds. At Tindari, where rocky substrates are lacking, *Eurypon viride* and *H. (H.) panicea* live closely associated with thalli of several algal species (mainly *Anadyomene stellata*, *Chaetomorpha* sp., *Laurencia* sp., *Polisiphonia* sp., *Valonia* sp.) and phanerogam leaves (*Cymodocea nodosa*). At Marsala, nearly 50% of the 45 recorded sponge species lives in association with macroalgae and phanerogams, sometime forming close relationships, as in the case of *Geodia cydonium* and the thallus of the rhodophyte *Rytiphloea tinctoria* (Mercurio *et al.*, 2006). Artificial substrates (mainly: poles, nylon ropes and fishing nets, plastic and glass waste) are also widely colonised by sponges. This

feature, previously described by Corriero *et al.* (2007) for Venice lagoon, is very impressive at Taranto, where multilayered assemblages of sponges, together with other benthic filter feeders (mainly bivalves, polychaetes and ascidians), cover the artificial substrates scattered on the soft bottoms. Interestingly, these results also indicate that the species composition of sponges from artificial substrates was quite similar from those on rocky ones. Such observations disagree with the findings of Lim *et al.* (2009) that artificial structures may not necessarily be surrogates for natural hard substrates for sponges. It is conceivable that both at Taranto and Venice the stratified layers of benthic organisms, in particular the bivalve shells that cover the surface of artificial substrates, may facilitate the larval attachment by sponges, and account for the wide exploitation by sponges on this natural secondary substrate (Corriero *et al.*, 1991).

Finally, in all the lagoons studied, several sponge species are able to live on soft bottoms due to specialised adaptations for withstanding the effect of being covered by sediments and for remaining anchored in place. These adaptations mainly consist in the ability to incorporate sand into their structure, thus improving stability and changes of the body shape. These features, previously described in sponges from Red Sea (Ilan & Abelson, 1995) and Caribbean lagoons (Cerrano *et al.*, 2004), are well emphasised at Marsala, where the number of sponges inhabiting soft bottom is very remarkable.

The sponge assemblages investigated during the present research are different among the eight studied lagoon sites, disagreeing with both the traditional model of Pérès & Picard (1964) which considers the Lagoon Euryterm and Euryhaline (LEE) as a typically monotonous biocoenosis, and the theory of the Paralitic Domain (Guélorget & Perthuisot, 1983) which predicts a typical biological uniformity in sheltered marine and brackish ecosystems. On the contrary, our results are in accordance with more recent literature (Cardone *et al.*, 2014) that emphasised the heterogeneity of benthic fauna from the Mediterranean transitional waters.

Even though all the studied lagoons hosted sponges, wide differences in species richness and faunistic patterns occur: lagoons with larger seawater inlets (Marsala, Taranto) harbour a very rich and diversified sponge fauna, while more confined systems (Lesina, Varano, Tindari) host a few sponge species.

There are some environmental factors considered which better explain the distribution of sponges in lagoon. In particular, the sponge species richness seems to be positively related to the salinity and to the number of phanerogam species. The salinity seems to be the ecological factor that best explains the spatial distribution of sponges, more in its minimum and its stability values than in the maximum values, explaining the species occurrence within lagoons. According to Nonnis Marzano *et al.* (2003b), an annual mean salinity close to 15 PSU seems to limit the distribution of *H. (H.) panicea*

at Lesina. Also in Venice Lagoon salinity seemed to be the main ecological factor responsible for the distribution of sponges. Here, the species richness is directly related with the increase of salinity values, and, according to Corriero *et al.* (2007), an annual mean salinity value close to 17 PSU constitutes the lowest distributional limit for a few demosponges (*Hymeniacidon perlevis*, *H. (H.) panicea*, *H. (H.) bowerbanki*, *Haliclona palmata*, *Dysidea fragilis* and *Tedania anhelans*). Phanerogam leaves play an important role as source of substrate for several encrusting sponge species in most of the lagoons examined. In addition, at Marsala, the rhizomes of *Posidonia oceanica* host a rich assemblage of benthic species, both invertebrates and algae with calcareous structures, which favour the occurrence of a large number of boring clionid species.

However, the structure of sponge assemblages, apart from geographical differences among the sites, is evidently also affected by other ecological factors, acting on pre- and post-settlement phases, such as availability of propagules, dispersion mechanisms, competition, etc. This complexity of events, changing in both time and space, leads to the creation of sponge communities which are anything but monotonous, so that in each lagoon nearly half of the species are unique, not being found in any other biotope examined.

The comparison of time series data showed that sponge assemblages are quite persistent in most of the lagoon systems considered. This trait characterises both lagoons with marked environmental fluctuations (i.e. Varano, Alimini, Tindari and Lesina, this last recently affected by a strong dystrophic event), where Porifera are represented by a few species, and Marsala, where wide communication with the sea occurs and the sponge assemblage exhibits high values of species richness. According to the literature, the sponge species inhabiting lagoons with high environmental fluctuations are usually characterised by short life cycles, rapid growth and high mortality (Nonnis Marzano *et al.*, 2003a; Gaino *et al.*, 2010), whereas at Marsala the sponge species with longer life cycles prevail (Mercurio *et al.*, 2007), thus suggesting that resilience is a trait independent from the sponge life cycle. However, not all sponge assemblages showed persistence traits, since at Taranto, Faro and Ganzirri we observed a remarkable extinction process that have brought to the disappearance of more than half (50% at Ganzirri, nearly 57% at Taranto and 76% at Faro) of the sponge species reported in the literature in a time interval ranging from 34 (Taranto) to 42 (Faro and Ganzirri) years. Even though sampling or taxonomic bias should partially affect this result, the deep temporal changes in the sponge patterns may be more likely related to intense habitat modifications due to massive and prolonged anthropogenic pressures that affect such lagoons. In particular, the Mar Piccolo of Taranto is historically affected by the severe impact of industrial emissions and sewage, that, together with heavy intercontinental shipping traf-

fic and the presence of several mussel and oyster farms, have defined a drastic decrease in seawater quality and a significant increase in dystrophic events (Caroppo *et al.*, 1994). Similarly, at Faro, human activities have caused major environmental changes, and in the last four decades the result of reckless overbuilding and uncontrolled speculation has largely erased the natural landscape, with accretions of building and urban expansion (Manganaro *et al.*, 2011). In both sites, the above-mentioned activities have caused not only the direct decay of the local benthic communities, but also they facilitate the introduction of several exotic species (Bertolino *et al.*, 2014; Corriero *et al.*, 2015b), thus further contributing to the change in the faunistic patterns.

In other cases massive disease phenomena affecting one or more sponge species can have played a key role in faunistic pattern changes of lagoon Porifera. According to the literature, the frequency of reports of sponge disease is clearly increasing in recent years, and the role of such phenomena in determining severe changes of sponge communities on a global scale has been ascertained (Webster, 2007). In lagoon environments, however, sponge disease should be a very strong threat, able to produce deep changes in sponge assemblages, since in these confined partially-enclosed environments the recolonization is an uncertain and very slow process, due to the lack of an adequate larval supply. Data collected in the present research does not allow one to relate sponge disappearance to epidemic events in those lagoons where major faunistic changes occurred (i.e. Faro, Ganzirri and Taranto); conversely, at Marsala, the small changes in sponge pattern are mainly due to the complete disappearance of two species, very abundant in the recent past (*Phorbas topsenti* and *Halichondria (H.) semitubulosa*), both affected by strong epidemic events at the end of the last century (Corriero & Gaino, unpublished data).

Finally, it is noteworthy that many temporal changes in sponge patterns are likely due to the implementation of research, in terms of more taxonomic effort, new technologies, exploration of new habitats and localities, and a combination of these factors. Obviously, the increase of research effort positively affects taxonomic knowledge, in terms of both new described species, as at Taranto and Marsala, but also in terms of a general increase in recording and, therefore, of sponge richness. In the present research this is evident at Taranto, where the use of trained divers for sampling allows the detection of many undescribed species from an unexploited habitat.

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