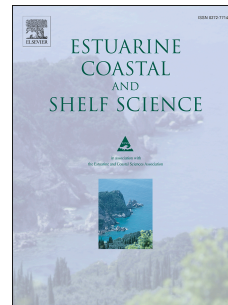


# Journal Pre-proof

Disentangling heterogeneity and commonalities in nantidal Mediterranean lagoons through environmental features and macrozoobenthic assemblages

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PII: S0272-7714(19)31033-9

DOI: <https://doi.org/10.1016/j.ecss.2020.106688>

Reference: YECSS 106688

To appear in: *Estuarine, Coastal and Shelf Science*

Received Date: 9 November 2019

Revised Date: 14 January 2020

Accepted Date: 1 March 2020

Please cite this article as: Gravina, M.F., Cabiddu, S., Como, S., Floris, A., Padedda, B.M., Pusceddu, A., Magni, P., Disentangling heterogeneity and commonalities in nantidal Mediterranean lagoons through environmental features and macrozoobenthic assemblages, *Estuarine, Coastal and Shelf Science* (2020), doi: <https://doi.org/10.1016/j.ecss.2020.106688>.

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Journal Pre-proof

1     **Disentangling heterogeneity and commonalities in nanotidal Mediterranean**  
2     **lagoons through environmental features and macrozoobenthic assemblages**

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17 **Abstract**

18 A comprehensive set of physiographic and environmental features, anthropogenic pressures, as well as  
19 the soft-bottom macrozoobenthic assemblages were analyzed in seven nanotidal lagoons located in the  
20 Sardinia island (western Mediterranean Sea). We hypothesized that the common typology, and the  
21 restricted climatic and geographical settings of the studied lagoons could be reflected in a limited  
22 environmental and biological heterogeneity, leading to homogeneous or consistent patterns of  
23 ecological variability. To test our hypothesis, we (i) evaluated the extent of environmental heterogeneity  
24 of the lagoons under scrutiny to single out the main features accounting for most of the variation among  
25 them, and (ii) analyzed the within- and among-lagoons' variation in macrozoobenthic assemblages to  
26 identify common patterns and/or a pool of recurrent species, peculiar to distinctive zones within  
27 individual lagoons. In terms of physiographic/environmental features, freshwater inputs, minimum  
28 salinity and chlorophyll-*a* were the best explanatory variables arranging the lagoons in three distinct  
29 clusters. The environmental integrative index (EII), based on the anthropogenic pressures, further  
30 allowed a significant separation of the lagoons, with Santa Gilla and Casaraccio being the most and the  
31 least impacted ones, respectively. In all of the investigated lagoons, the distribution of dominant  
32 macrozoobenthic species was mainly related to the land-sea gradient, the degree of confinement and  
33 the organic enrichment of sediments. Accordingly, we identified four major pools of most distinctive  
34 species (60 out of a total of 211 species/taxa found), including (i) opportunistic species, (ii)  
35 brackish/halolimnobic species, (iii) species typical of coastal sheltered waters, and (iv) properly marine  
36 species. We also identified differences in the macrozoobenthic community composition among lagoons,  
37 mostly attributable to the origin of the assemblages, and the dispersal ability and colonization  
38 adaptability of individual species. Our results show that single benthic macroinvertebrate species are  
39 useful indicators for characterizing the within-lagoon heterogeneity, whereas the assemblage's  
40 composition best highlights differences among lagoons. We, thus, raise the need for a thorough analysis  
41 of the benthic biodiversity, including the species-specific life history and autecology of the dominant  
42 species, to enhance our comprehension of local spatial patterns and the connectivity between lagoons.  
43 Overall, the present study demonstrates the usefulness of our approach to disentangle heterogeneity  
44 vs. commonalities within and among nanotidal lagoons.

45

46 **Key words:** Benthic macroinvertebrates; Biodiversity; Spatial variation; Sediments; Organic matter

47

## 48 1. Introduction

49 In contrast to early models exhibiting an overall uniformity of brackish-water benthic assemblages as  
50 monotonous biocoenoses (Pérès and Picard, 1964) and a mono-factorial distinctness among basins  
51 simply based on salinity (Remane, 1934; Venice System, 1959), recent studies have highlighted  
52 unexpected levels of environmental and biological heterogeneity of coastal lagoons (Basset et al., 2007;  
53 2008; Como et al., 2007; Magni et al., 2019). The Guelorget and Perthuisot model (1992) was based on a  
54 descriptive approach of habitat, zones, and landscape variation in Mediterranean brackish-water  
55 biotopes. From a hydrodynamic point of view, the emerged gradient varies from “choked” to  
56 “restricted” and to “leaky” lagoons, underlining the dominant role of flushing and marine connection  
57 (Guelorget and Perthuisot, 1992; Sacchi and Occhipinti Ambrogi, 1992). The resulting hydrological  
58 gradient is reflected in the distribution and texture of sediments, with suspended solids rich in fine  
59 sediments and organic matter (OM) settling where hydraulic energy is low (De Falco et al., 2004;  
60 Molinaroli et al., 2009). This gradient is known to influence greatly the distribution and composition of  
61 lagoon macrozoobenthic assemblages (Como et al., 2007; Magni et al., 2008a, 2015), also in relation to  
62 the physiographic characteristics of the system (Basset et al., 2006; Tagliapietra and Ghirardini, 2006).

63 Expanding upon the concepts of confinement (Guelorget and Perthuisot, 1992) and organic  
64 enrichment (Pearson and Rosenberg, 1978), Tagliapietra et al. (2012) proposed a unified conceptual  
65 framework of habitat saprobity in coastal lagoons. The term “saprobity” was first developed for  
66 freshwater systems more than a century ago (Kolkwitz & Marsson, 1909; Sládeček, 1967) and is referred  
67 to as a “state descriptor” of an aquatic ecosystem resulting from the input and decomposition of OM  
68 and the removal of the system’s catabolites. Thus, it is viewed as a selection factor for species diversity;  
69 the higher the saprobity the more impaired the system, with progressively poorer and less diverse  
70 benthic communities dominated by species increasingly tolerant to reducing conditions and toxicity  
71 (Tagliapietra et al., 2012). At the same time, the large environmental variability typical of the lagoon  
72 ecosystems tend to select species and communities which are able to cope with disturbed conditions  
73 and to re-colonize relatively quickly. As an example, it has been shown that  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of  
74 benthic consumers did not vary significantly before and after a dystrophic event, indicating that the  
75 benthic assemblages and the relations among different trophic levels were quickly restored (Magni et  
76 al., 2008b). In addition to saprobity, salinity is as an additional driver of selection structuring the  
77 macrozoobenthic assemblages in brackish environments, particularly at the oligohaline and hyperhaline  
78 extremes (Foti et al., 2014). These results are consistent with the recognition that transitional waters  
79 (TWs) are characterized by a combination of high heterogeneity and ecotone-related common  
80 properties such as engineering and ecological resilience (Basset et al., 2013).

81 Within the European Water Framework Directive 2000/60/EC (WFD; 2000/60/EC), three  
82 macrotypes of TWs have been defined: two macrotypes for tidal systems according to the salinity range

83 variation and one macrotype for the non-tidal systems. For the Mediterranean region, Tagliapietra and  
84 Ghirardini (2006) suggested introducing a subdivision of the non-tidal lagoons into nanotidal (with  
85 average tide <0.5 m) and microtidal (with average tide 0.5–1.0 m) systems so allowing their better  
86 characterization based on three main physical factors, i.e. coastal typology, tidal range and climate.  
87 However, no studies have evaluated so far the heterogeneity and commonalities of nanotidal lagoons  
88 within a limited geographical range from both an environmental and biological perspective.  
89 Furthermore, while a classification of macrozoobenthic assemblages at higher taxonomic level has been  
90 suggested for monitoring purposes in coastal lagoons (e.g. Mistri and Munari, 2008; Pitacco et al., 2018),  
91 little relevance has been given to the analysis of the autecology of dominant benthic species, which may  
92 help disentangling heterogeneity and commonalities within and among lagoons.

93 In the present study, we focused on seven nanotidal lagoons distributed along the coast of the  
94 Sardinia island (western Mediterranean). We hypothesized that the restricted climatic and geographical  
95 settings of those lagoons may be reflected in a limited environmental and biological heterogeneity. To  
96 test this hypothesis, we (i) evaluated the extent of physiographic/environmental heterogeneity and  
97 anthropogenic pressures of the lagoons under scrutiny to single out the main features accounting for  
98 most of the variation among lagoons; and (ii) analyzed the patterns of variation in macrozoobenthic  
99 assemblages within and among the lagoons to identify common features among them and/or a pool of  
100 recurrent species peculiar to distinctive zones within individual lagoons. We expected that benthic  
101 species of different origin and characteristics (i.e. opportunistic, brackish/halolimnobic, common in  
102 sheltered waters and marine) would be distributed according to the environmental features of  
103 individual lagoons or zones within a lagoon, as well as according to the individual species' life strategies,  
104 all these factors influencing the connectivity among lagoons.

105

## 106 **2. Material and Methods**

### 107 *2.1. Lagoons investigated*

108 Seven lagoons distributed along the Sardinian coast and covering a surface area of about 51.7 km<sup>2</sup>,  
109 representing more than half of the total surface area of Sardinian TWs, were investigated. They include  
110 the lagoons of Casaraccio and Calich in the north-western sector, Cabras, Mistras and Santa Giusta in  
111 the western sector, Santa Gilla in the southern sector, and Tortoli in the eastern sector (Fig. 1). Cabras  
112 and Santa Gilla are the largest lagoons in terms of surface area and catchment area, respectively (Table  
113 1). All the lagoons under scrutiny are nanotidal (average tide <0.5 m; Tagliapietra and Ghirardini, 2006),  
114 have a water depth ranging from about 1 to >3 m and are characterized by a *Csa* climate (i.e.  
115 Mediterranean Mild with dry, hot summer) according to the Koeppen–Geiger–Pohl Climatic  
116 Classification system (e.g. Peel et al., 2007). Most of them have an important fishery (Cabras, Mistras,  
117 Santa Giusta and Tortoli lagoons) and aquaculture activities, including shell fisheries (Calich, Mistras,

118 Santa Gilla and Tortoli lagoons) and/or fishing bait production (Santa Gilla lagoon); they also benefit  
119 from one or more protection measures (Table 1). A brief description of each lagoon and the sampling  
120 stations is provided below. Further details and sources of the dataset used in the present study are  
121 given in Table 2.

122  
123 *2.1.1. Casaraccio lagoon*  
124 The Casaraccio lagoon is connected to the Gulf of Asinara through a 4-6 m large and 400 m long artificial  
125 channel. Water exchange between the lagoon and the Gulf is further limited by artificial barriers  
126 (*Lavorieri*) to control the fish catch. Freshwater input is very low throughout the year owing to the  
127 presence of a few temporary creeks only, and consistent with the lagoon's hyperhaline state. Four  
128 sampling stations (Cs1, Cs2, Cs3 and Cs4, Fig. 1) were selected along a gradient of water renewal at  
129 progressive distance from the lagoon inlet where stations Cs1 and Cs2, characterized by sandy  
130 sediments, were located. By contrast, the innermost and most confined station Cs4 was characterized  
131 by muddy sediment, while the intermediate station Cs3 had muddy-sand sediments (see also Floris,  
132 2003). This lagoon has no significant anthropogenic impacts.

133  
134 *2.1.2. Calich lagoon*  
135 The Calich lagoon extends parallel to the coast with an opening to the sea occupied by a small touristic  
136 harbor. The lagoon is connected to the sea through the Fertilia channel, a natural opening enlarged  
137 during reclamation work between 1938 and 1948. However, water exchange is impaired by the lagoon's  
138 elongated conformation. Two natural tributaries (Rio Barca and Rio Fangal), and one artificial channel  
139 (Canale Uruni) provide a major freshwater input, affected by the discharge of industrial and domestic  
140 sewage. Moreover, a large part of the surrounding area is used for agricultural purposes and fishing  
141 activities are practiced. Five sampling stations (Ca1, Ca2, Ca3, Ca4, and Ca5, Fig. 1; see also Floris, 2003)  
142 were investigated. Stations Ca1 and Ca3 were located in proximity to Rio Barca and Rio Fangal,  
143 respectively, while station Ca2 was located between the two tributaries, all of them on muddy  
144 sediment. The other two stations, Ca4 and Ca5, characterized by sandy-mud and sandy sediments  
145 respectively, were located at the lagoon inlet (Ca4) and in the channel connecting the lagoon with the  
146 sea (Ca5).

147  
148 *2.1.3. Cabras lagoon*  
149 The Cabras lagoon is the largest Sardinian lagoon in terms of surface area (Table 1). Most of the  
150 freshwater input to the lagoon originates upland from the Rio Mare e Foghe, with a minor tributary, Rio  
151 Tanui, located in the lagoon's southern sector. In the late 1990s, artificial barriers (*Lavorieri*) were  
152 constructed along the "*scolmatore*" (spillway) to control the fish catch. The lagoon only connection to

153 the Gulf of Oristano are three narrow creeks flowing into a larger channel (Padedda et al., 2010). The  
154 water exchange between the lagoon and the gulf is very limited, favoring the accumulation of  
155 particulate (De Falco et al., 2004; Magni et al., 2004; Como et al., 2007) and dissolved (Specchiulli et al.,  
156 2018) organic matter. The lagoon is subjected to considerable inputs of domestic and agricultural  
157 discharges. For the present study, four sampling stations (Cb1, Cb2, Cb3 and Cb4, Fig. 1; see also Magni  
158 et al., 2004, 2005) were selected along two different gradients of salinity and saprobity, the latter  
159 determined by a series of interlinked environmental features, including trophic and hydrodynamics  
160 conditions which characterize different sectors of the lagoon (Magni et al., 2005, 2008a; Foti et al.,  
161 2014). Accordingly, station Cb1 was sandy, station Cb3 was muddy-sand, while stations Cb2 and Cb4  
162 were muddy.

163

#### 164 2.1.4. *Mistras lagoon*

165 The Mistras lagoon, adjacent to the Cabras lagoon, is an artificially semi-enclosed system with no  
166 riverine inputs. It was connected to the Cabras Lagoon until the 1970s, but now only has an opening to  
167 the Gulf of Oristano through its mouth. Salinity can be much higher than adjacent marine waters due to  
168 strong evaporation in the summer (Specchiulli et al., 2018). Fishing activities are practiced, and the  
169 surrounding area is used for agricultural purposes. Three sampling stations were selected in three  
170 different soft-bottom sandy habitats, including a *Cymodocea nodosa* dominated area (Mi1), a  
171 macrophyte dominated area (Mi2) and an area without vegetation (Mi3) (Fig. 1; see also Fenzi, 2013).  
172 For consistency among stations, all samples were collected in bare sediments at some distance from the  
173 vegetation where present.

174

#### 175 2.1.5. *Santa Giusta lagoon*

176 The Santa Giusta lagoon is separated from the Gulf of Oristano by a long-shore bar and is located in an  
177 agricultural area for intensive rice production. Moreover, this lagoon is subjected to considerable inputs  
178 of domestic and industrial discharges, and different fishing activities are practiced. During the last few  
179 decades, several human interventions have profoundly modified the lagoon ecosystem. The lagoon has  
180 been subjected to dystrophic events following anoxia and sulphide development in the summer of 2004  
181 and 2010, both reducing drastically the macrozoobenthos and fish population (Magni et al., 2008b).  
182 Samples were collected in November 2009 in three areas, here named Sa1, Sa2, Sa3 (Fig. 1; see also  
183 Floris, 2003; Magni et al., 2008b), according to a hierarchical sampling design described in Floris (2003)  
184 and Tataranni et al. (2009) which included twelve stations with two replicates in each area. All stations  
185 have sandy-muddy bottoms.

186

#### 187 2.1.6. *Santa Gilla lagoon*



188 The Santa Gilla lagoon comprises the largest catchment among the Sardinian lagoons (Table 1). It is  
189 connected with the Cagliari Gulf in the Sardinian southern coast through one channel, while in the north  
190 it receives two freshwater inflows from Flumini Mannu and Cixerri. The lagoon is located between the  
191 historical and industrial ports of Cagliari city, each serving a different type of traffic. This lagoon has  
192 been exposed, for several decades, to the discharge of industrial wastes, as well as to municipal  
193 untreated urban and industrial sewage, and other anthropogenic related activities, including airports,  
194 railways, oil refinery, and incinerators (Cottiglia, 1995). Moreover, the main fluvial inputs to the lagoon  
195 have carried for a long time heavy metal-enriched waste waters resulting from the mining activities  
196 carried out in its watershed areas (Atzeni et al., 1998; Esposito et al., 2018). Three stations were  
197 sampled seasonally on four dates along a salinity gradient. Station Si1 was located at the marine pole  
198 and is characterized by muddy-sand sediments, while Station Si3 was the most confined one and  
199 subjected to freshwater inputs (Si3), with Si2 at an intermediate location. Both Si2 and Si3 have muddy  
200 sediments (see also Cabiddu et al., 2013, Atzori et al., 2018).

201

#### 202 *2.1.7. Tortoli lagoon*

203 The Tortoli lagoon is located on the eastern coast of Sardinian and is connected with the sea through  
204 two channels in its central and southern area, while the freshwater inputs enter the lagoon from Rio  
205 Girasole (Rio Mannu) through a bulkhead system in its northern area. Agricultural and urban sewage  
206 waters inflow from the surrounding continental areas, and fishing activities are practiced. The central  
207 area of the basin is 1 m depth, while the surrounding channels are 2-2.5 m depth. The samples were  
208 collected at six stations, seasonally on four dates. Three stations (To2, To3, To4) were located in the  
209 internal area of the lagoon and have sandy sediments; To1 and To5 were located in proximity of the  
210 central and southern of the channel, respectively, towards the sea and had both muddy-sand sediments;  
211 To6 was located in the Rio Girasole and has sandy-mud sediments.

212

#### 213 *2.2. The dataset*

214 The physiographic/environmental data and the anthropogenic pressures for the seven investigated  
215 lagoons were obtained from numerous sources, including published papers, Ph.D. theses and local  
216 official reports, supported by the authors' previous studies and extensive knowledge of the investigated  
217 lagoons (e.g. Magni et al., 2008a,b; Padedda et al., 2012; Cabiddu et al., 2014; Atzori et al., 2018).

218 Four major environmental variables, i.e. sediment grain size composition and organic matter  
219 (OM) content, degree of confinement and salinity, were categorized and analyzed in combination with  
220 the biotic data (see section 2.3). Sediment texture of individual stations was classified into four main  
221 categories (mud: sand <10%, mud >90%; sandy-mud: mud >50%, sand <50%; muddy-sand: mud <50%,  
222 sand >50%; and sand: sand >90%, mud <10%) according to Folk (1954). Similarly, four categories were

223 made for the OM content (low:  $\leq 3\%$ , medium: 4-7%, high: 8-11%, and very high:  $\geq 12\%$ ) according to  
224 Hyland et al., 2005 and Magni et al., 2008a, 2009. Three categories were assigned to the confinement  
225 level (low, medium and high) based on our extensive knowledge of the studied lagoon and previous  
226 papers (e.g. Magni et al., 2008b; Padedda et al., 2010; Cabiddu et al., 2014; Foti et al. 2014), and salinity  
227 (low:  $\leq 10\text{‰}$ , medium: 11-29‰, high:  $\geq 30\text{‰}$ ) considering its variation relative to our sampling dates  
228 (Table 2) rather than to the overall salinity range reported for each lagoon (Table 1).

229 As for macrozoobenthos, the numbers of individuals of each species (or lowest practical taxon) in  
230 a sample were recorded by station and lagoon for a total of 420 samples (Table 2). The macrozoobenthic  
231 data were updated (e.g. new species name assignment when needed), standardized (e.g. total  
232 abundance given per- $\text{m}^2$  basis as density, taxonomic consistency checked across different studies) and  
233 merged into a common dataset for subsequent analysis (see also Magni et al., 2009). All samples, except  
234 those from Santa Gilla lagoon, were sieved on a 0.5 mm mesh size (Table 2).

235

### 236 2.3. Data analysis

237 In order to assess the heterogeneity among the investigated lagoons, an integrated approach was  
238 adopted using environmental data, anthropogenic stress estimates and faunistic data.

239 Among the environmental data, the structural descriptors of the lagoons considered in the  
240 present study were expanded upon the study of Basset et al. (2006) and included: catchment area,  
241 surface area, water volume, mean and max depth, annual freshwater inflow, salinity type (Venice  
242 System, 1959), dominant primary producers, annual mean of nutrient and chlorophyll-*a* (Chl-*a*)  
243 concentrations, and protection measures. The surface area of all Sardinian lagoons was calculated with  
244 the support of a geographic information system on the most recent vector cartography provided by the  
245 Sardinian regional authority (RAS, 2017).

246 To estimate the degree of anthropogenic stress of the studied lagoons, we applied an  
247 environmental integrative index (EII) based upon existing knowledge and best professional judgment.  
248 This index, divided into four classes (absence to very low = 0; low = 1; moderate = 2; high = 3), was  
249 quantified for each lagoon as the sum of partial component metrics. Pressures included: agriculture  
250 input, domestic and industrial discharge, land reclamation, water abstraction, power generation, port  
251 activity, navigation, dredging, fishery. The same approach has been already applied successfully in other  
252 Mediterranean lagoons (Lugoli et al., 2012; Orfanidis et al., 2014; Fabbrocini et al., 2017). Owing to the  
253 subjective element in the approach, we acknowledge that a comparison with other studies should be  
254 made with caution. On the other hand, we contend that the pressure index obtained for the seven  
255 lagoons of the present study provides valuable information within the context of this study as it has  
256 been consistently determined using the same criteria.

257 Such physiographic/environmental variables and the anthropogenic pressures data were analyzed  
258 by means of Principal Component Analysis (PCA) using the correlation matrix (Gower, 1966). ANOSIM  
259 was used to test significant differences among the groups highlighted in the PCA plot and the linear  
260 Pearson correlation was computed to the main environmental variables and stress measures significant  
261 in explaining the ordination model.

262 Furthermore, in order to examine the patterns in variation among lagoons the benthic  
263 macroinvertebrate metrics were used as biotic descriptors. In particular, the taxonomic composition and  
264 density data of macroinvertebrate assemblages were inspected by means of the non-metric  
265 multidimensional ordination model (nMDS) with the additional purpose to examine the dis/similarity  
266 among the lagoons on the basis of both biotic (macrozoobenthic density) and environmental (sediment  
267 OM content and grain size composition, confinement and salinity) descriptors. The correlations between  
268 the environmental variables and the nMDS points were presented in the plot as vectors from the origin.  
269 Moreover, the within-lagoon pattern of macrozoobenthic assemblages' spatial variation was also  
270 investigated. For each lagoon the faunal density data were inspected by means of cluster analysis. The  
271 UPGMA method was used to produce clusters embracing the sampling stations on the basis of the  
272 average distance in terms of taxonomic composition. Analysis of similarities (ANOSIM) was performed to  
273 investigate variation in macrozoobenthos composition within the sampling stations of each lagoon and  
274 among the lagoons as a whole (Clarke, 1993). The Similarity Percentage (SIMPER) test (Clarke and  
275 Warwick, 2001) was used to determine the contribution of each species/taxon, cutting-off 90%, to the  
276 total dissimilarity between samples. Each species identified by SIMPER was assigned to one of four main  
277 ecological categories (i.e. common in coastal sheltered waters, brackish, opportunistic and properly  
278 marine) based on our expert knowledge and the published literature (e.g., Parenzan, 1974, 1976; and  
279 Doneddu and Trainito, 2005, for molluscs; Riggio, 1996; Ruffo, 1982; and Sconfiatti, 2004, for  
280 crustaceans; and Giangrande et al., 2005; Gravina et al., 1989; Cardone et al., 2014; and Giangrande and  
281 Gravina, 2015, for polychaetes).

282

### 283 **3. Results**

#### 284 *3.1. Physiographic/environmental features and anthropogenic pressures*

285 The main physiographic and environmental features of the investigated lagoons are summarized in  
286 Table 1 and illustrated in Fig. 2a. The PCA ordination in the plane of the first two components arranged  
287 the seven lagoons into small lagoons (surface of  $< 1 \text{ km}^2$  and volume of  $1 < \text{Mm}^3$ , i.e. Casaraccio and  
288 Calich), medium lagoons (surface of  $1\text{-}15 \text{ km}^2$  and volume of  $2\text{-}16 \text{ Mm}^3$ , i.e. Tortoli, Mistras and Santa  
289 Giusta) and large lagoons (surface of  $>15 \text{ km}^2$  and volume of  $18\text{-}38 \text{ Mm}^3$ , i.e. Santa Gilla and Cabras)  
290 ones. A similar lagoons' arrangement was given in relation to the freshwater inflow with minimum  
291 freshwater inputs in Casaraccio, medium inputs in Tortoli and Santa Giusta, and maximum inputs in

292 Santa Gilla and Cabras. The ANOSIM tests revealed significant differences among these clusters  
293 according to the lagoon surface ( $R = 0.96$ ,  $P < 0.05$ ), volume ( $R = 0.76$ ,  $P < 0.05$ ) and freshwater inputs ( $R$   
294  $= 0.90$ ,  $P < 0.05$ ). The lagoon surface, volume and freshwater inflow showed a significant correlation  
295 with the component 1, while minimum salinity and Chl- $a$  were significantly correlated with component 2  
296 (Table 3).

297 The environmental integrative index (EII) of each lagoon, based on the anthropogenic pressures,  
298 is shown in Table 4 and illustrated in Fig. 2b. The PCA ordination discriminated lagoons with an EII  $< 1$   
299 (Casaraccio, Mistras, Tortoli) from those with an  $> 1$  EII  $< 1.5$  (Calich, Cabras) and those with an EII  $> 1.5$   
300 (Santa Giusta, Santa Gilla). The ANOSIM test confirmed these results, revealing significant differences  
301 between these two groups ( $R = 0.57$ ,  $P < 0.5$ ). The EII was strongly correlated with component 1 ( $P <$   
302  $0.001$ ), which included various anthropogenic stressors such as industrial discharges ( $P < 0.001$ ),  
303 agriculture input ( $P < 0.05$ ), industrial land reclamation ( $P < 0.05$ ), power generation ( $P < 0.05$ ), dredging  
304 ( $P < 0.05$ ) and port activity ( $P < 0.001$ ) (Table 5). Santa Gilla was the most impacted lagoon, whereas the  
305 Casaraccio one had the highest degree of naturalness.

306  
307 *3.2. Macrozoobenthic assemblages and faunal composition*  
308 In the seven examined lagoons 211 taxa were found, of which 52.8% were polychaetes, followed by  
309 crustaceans (25.0%), molluscs (15.6%), ascidians (2.3%), anthozoans and echinoderms (1.9%), and  
310 chironomids, oligochaets and phoronids ( $< 1\%$  each). The one-way ANOSIM test revealed the differences  
311 among the seven examined lagoons and their significant separation on the basis of the macrozoobenthic  
312 assemblage composition, with a global  $R = 0.887$ , a mean rank within of 41.98, and mean rank between  
313 of 209.9,  $P = 0.0001$ .

314 The MDS ordination model confirmed this separation, arranging the stations in convex hulls  
315 corresponding to the individual lagoons. There was little overlap among lagoons as a result of the  
316 pronounced peculiarity of biocoenoses of each lagoon (Fig. 3). The abiotic variables constraining the  
317 ordination pattern observed, i.e. sediment grain size and organic matter content, confinement and  
318 salinity, highlighted further a spatial differentiation of the lagoons. In particular, the Mistras lagoon was  
319 located on the left-side hand of the model corresponding to high salinity and high confinement, with no  
320 overlap with the other lagoons. Casaraccio was also found on the left-side hand of the model, but on a  
321 lower position owing to high salinity but low confinement, and with the four stations very close one to  
322 each other. By contrast, Cabras was located on the right-side of the model, corresponding to low and  
323 medium salinity, with no overlapping with other lagoons, but with the four stations indicating two major  
324 distinct patterns. In particular, two one-another-close stations located in the upper-side of the model  
325 were characterized by high confinement and high organic enrichment, and muddy conditions.  
326 Differently, the other two stations in the lower side of the model were related to low and medium

327 confinement and were characterized by progressively lower organic and mud contents. The hulls  
328 corresponding to the other lagoons (i.e. Santa Giusta, Santa Gilla, Calich and Tortoli) were located in an  
329 intermediate central position, with individual stations arranged to the main gradients, i.e. high  
330 confinement and organic and mud content (upper side) or salinity (left-, lower-side).

331 The SIMPER analysis identified 60 species, out of a total 211 taxa found in all lagoons, which were  
332 responsible for the 90% cumulative contribution of the distinction within each investigated lagoon (Tab.  
333 6). These 60 most distinctive species, 38 of which were found in two or more lagoons, included four  
334 main groups. The first group of species, e.g. *Cyathura carinata*, *Hediste diversicolor*, *Cerastoderma*  
335 *glaucum*, is typical of brackish water systems (marked "B" in Table 6); they were the most common and  
336 were found in more than three lagoons. On the other hand, other halolimnobic species, e.g. *Corophium*  
337 *orientale* and *Lekanesphaera hookeri*, were exclusive to the Cabras lagoon. The second group, including  
338 *Abra segmentum*, *Nainereis laevigata*, *Neanthes acuminata*, *Abarenicola claparedi*, *Gammarus*  
339 *insensibilis* and *Monocorophium sextone*, embraces species commonly inhabiting coastal sheltered areas  
340 (marked "C" in Table 6), most of them found in three-four lagoons; the third group includes properly  
341 marine species (marked "M" in Table 6) such as *Loripes orbiculatus*, *Protodorvillea kefersteini*, *Dexamine*  
342 *spinosa*. Finally, the fourth group included some opportunistic species (marked "O" in Table 6),  
343 commonly found in at least three lagoons, i.e. *Polydora ciliata*, *Prionospio cirrifera*, *Capitella capitata*,  
344 *Heteromastus filiformis* and Chironomidae; in addition other opportunistic species, *Prionospio*  
345 *multibranchiata*, *Pseudopolydora antennata*, *Malacoceros fuliginosus*, *Streblospio shrubsolii* occurred in  
346 two lagoons. Overall, *A. segmentum* ("C") and *C. capitata* ("O") were found in all investigated lagoons,  
347 *N. laevigata* ("C"), *C. glaucum* ("B") and *G. insensibilis* ("C") were found in six lagoons (Table 6).

348 In terms of within-lagoon variability, we found consistently across all lagoons a cluster grouping  
349 inner stations with elevated degree of confinement and a cluster grouping more marine stations (for  
350 details Section 2.1). At the freshwater end, two stations were especially evident in each cluster, i.e. Cb1  
351 for Cabras and To6 at for Tortoli, respectively (Fig. 4). The ANOSIM test confirmed significant differences  
352 among the groups of stations revealed within each lagoon by the cluster analysis (Table 7). The  
353 biological contribution to the within-lagoon heterogeneity was apparent both in terms of number and  
354 composition of species (Fig. 5 and Table S1, respectively). In particular, the total number of species  
355 collected at each station showed a generalized decreasing trend along the outer-inner gradient  
356 irrespective of the lagoon (Fig. 5). Furthermore, among the four ecological categories (marine, coastal,  
357 brackish, opportunistic) in which individual species were grouped, the greatest contribution to the  
358 within-lagoon variation in species richness was due to the marine species (Fig. 5). In particular, the  
359 species composition also highlighted notable within-lagoon differences, with the marine species being  
360 numerically more abundant at the seaward stations, while the brackish and opportunistic species being  
361 more representative at the inner stations (Table S1).

362

363 **4. Discussion**

364 The present study demonstrated major differences, but also commonalities, among and within lagoons  
365 from both an environmental and biological point of view. First of all, significant differences among  
366 lagoons were related to their physiographic characteristics (e.g. size and volume) as already reported by  
367 Basset et al. (2006) on a larger geographical scale, including lagoons with a wider surface extension than  
368 those investigated here. In addition, we found that a high heterogeneity among the investigated lagoons  
369 was also associated with differences in freshwater inputs, minimum salinity and Chl-*a* concentrations in  
370 the water column. As per the anthropogenic pressures, the Environmental Integrative Index (EII)  
371 highlighted how large lagoons with the most extended watersheds are the ones which suffer the most  
372 serious impacts. Santa Gilla and Santa Giusta are the lagoons most affected by pollution, land  
373 reclamation (Santa Gilla only) and habitat exploitation due to port and fisheries activities. Indeed, both  
374 lagoons are close to two important urban areas which for decades have identified the lagoons as  
375 receptacles of any kind of pollutant discharge. Being sheltered with respect to the adjacent marine  
376 areas, they have been exploited for the storage of boats, representing an additional source of pollution  
377 through the leaching of paints and the leaks of fuel and lubricants from marine engines, and navigation  
378 causing mechanical disturbance to the lagoons' sediments. Calich and Cabras, instead, suffer a moderate  
379 impact due to domestic and agriculture pressures and to fin-fisheries. There, the main anthropogenic  
380 impact is the nutrient discharge of the two respective large watersheds, intensively exploited for  
381 agriculture and with a natural land cover almost disappeared. The impact of fishing is minimal because it  
382 is carried out intensively in the framework of fixed fishing structures (Cabras) or due to the small  
383 number of fishermen (Calich). Furthermore, Tortoli and Mistras are subjected to low levels of  
384 anthropogenic pressures being exploited only by small fisheries. In particular, Mistras is characterized by  
385 a nearly absent catchment area, whereas Tortoli has a reduced human presence and a low level of  
386 alteration of the natural forest land cover. Finally, Casaraccio, located in a barren and uninhabited  
387 territory, is the least exploited among the investigated lagoons, owing to its highest degree of  
388 naturalness.

389 Also the comparative analysis of the macrozoobenthic assemblages allowed us assessing an  
390 elevated degree of differentiation among lagoons. From the original dataset of 211 taxa found in total in  
391 all lagoons, a restricted pool of 38 species was common to two or more lagoons and included  
392 opportunistic species (29%), brackish/halolimnobic species (16%), species typical of coastal sheltered  
393 waters (34%) and properly marine species (21%). The remaining 22 of the 60 widely occurring species  
394 belonged exclusively to a single lagoon taxocoenosis and were mostly properly marine species. Likewise,  
395 the majority of more rare species (not considered here) which constituted the assemblages of each  
396 single lagoon were characteristics of marine waters.

397 Indeed, the rich pool of species of marine origin which characterized the lagoonal assemblages of  
398 the present study helps explaining the unexpected high degree of biodiversity in systems known for  
399 having a reduced number of species (Magni et al., 2009). It is known that marine species are  
400 overwhelmingly dominant in waters with a wide salinity range (Whitfield et al., 2012). Furthermore, the  
401 species distribution can be explained not only in relation to the salinity gradient, but also considering  
402 other environmental factors. For instance, Farina et al. (2018) showed that currents and winds, at the  
403 large-scale, and residual circulation cells and hydrodynamic energetic level at local scale, influence the  
404 recruitment and distribution of sea-urchin populations along the Western Sardinian shelf. We believe  
405 that biotic factors such as species' biological traits (e.g., reproductive modes) also play an important role  
406 in the dispersal of the species found in the present study and, thus, the extent of connectivity among  
407 the lagoons. In fact, most of these marine species, which occur in a single lagoon, are crustaceans  
408 peracarids, which lack pelagic larvae (e.g. *Apocorophium acutum*, *Elasmopus pocillimanus*,  
409 *Microdeutopus algicola*, *Iphinoe trispinosa*, *Apseudes latreilli*). The same holds true for the mollusk *Abra*  
410 *tenuis*, recorded only in the Mistras lagoon, which is a directly developing aplanic species (Holmes et al.,  
411 2004), whereas the congeneric *A. segmentum*, found in all the seven investigated lagoons, produces  
412 planktonic larvae. Among polychaetes, *Perinereis rullieri* is characterized by the disappearance of the  
413 epitokous stage with free spawning and planktonic larvae in contrast with the congeneric *P. cultrifera*  
414 which is a species common in coastal/sheltered waters, reproducing with epitokal metamorphosis  
415 (Prevedelli and Simonini, 2003); *Myriochele heerii* is capable of asexual reproduction by fission (Oliver,  
416 1984), this latter reproduction mode being also developed in the phoronid *Phoronis psammofila* (Emig,  
417 1972), both species found only in the Tortoli lagoon.

418 Brackish species, even though in limited number, were also responsible for the differentiation  
419 among lagoons. In the present study, three of the seven brackish species occurred exclusively in the  
420 Cabras: *Monocorophium orientale*, *Lekanesphaera hookeri* and *Idotea chelipes*. All of these three species  
421 lack pelagic larvae and ensure their dispersal through the passive transport of adults, such as rafting on  
422 floating objects (Gutow et al., 2006). Alternative means of passive dispersal can also explain the  
423 distribution of the gastropod *Hydrobia acuta* which occurred in two choked lagoons, namely Cabras and  
424 Mistras. This species lacks the planktonic phase and profits from passive vectors such as filamentous  
425 algae and birds' feet for dispersal of adults and eggs capsules (Barnes, 1999). Finally, we also found that  
426 opportunistic species, typically occurring in organically enriched coastal and lagoon systems (e.g. Como  
427 and Magni, 2009; Kanaya et al., 2015), contributed to the differentiation among the investigated  
428 lagoons, most of them being common to not more than three lagoons, with only *Capitella capitata*  
429 being common to all lagoons. Notwithstanding their typical traits of r-strategists and in spite of their  
430 ubiquitous character, the opportunistic species colonized the lagoons differently, likely according to the  
431 local variation in environmental features, such as hydrodynamics, sedimentary organic matter contents,

432 oxygen concentration and salinity (Barnes, 1980; Hyland et al., 2005; Can et al., 2009; Schirosi et al.,  
433 2010; Farina et al. 2018) as well as biological factors, such as larval supply and recruitment, predation  
434 and competition (Come and Magni, 2009; Giangrande et al., 2017). As an example, *Malacoceros*  
435 *fuliginosus* occurred only in Casaraccio and Tortoli, *Prionospio multibranchiata* characterized Calich and  
436 Santa Giusta, *Pseudopolydora antennata* was found in Santa Giusta and Santa Gilla, and *Streblospio*  
437 *shrubsolei* in Calich and Santa Gilla. These differences are consistent both with the chance arrival of the  
438 species and with their capability to maintain their own population levels by competition with other  
439 species within the same benthic assemblage.

440 Our study reveals also that the majority of the benthic assemblages within each lagoon is  
441 autochthonous. We infer that the species populations would be principally maintained both by their  
442 high reproductive rates and short life-cycles and by their particular life strategies, such as benthic-direct  
443 development and suppression of pelagic phases (Giangrande et al., 2017). Moreover, the most  
444 constraining environmental factors (e.g. salinity, confinement, sediment organic enrichment)  
445 conditioned the spatial colonization of the species within each lagoon, explaining most of the biological  
446 variability. On the other hand, we hypothesize that the faunal exchanges between the lagoon and the  
447 sea, mostly explaining commonality, would be restricted to the number of species with long-living  
448 pelagic larvae commonly occurring also in marine coastal waters or to the species using passive  
449 transportation (phoresy) for their dispersal. This hypothesis is corroborated by previous results reported  
450 for the Acquatina brackish lake (Apulia, Italy) where polychaetes' larvae of marine origin were absent,  
451 almost entirely replaced by polychaetes with short-living larvae typical of lagoon species (Giangrande  
452 and Rubino, 1994). Our hypothesis is also consistent with the idea that in nanotidal lagoons larval export  
453 from the lagoon towards the sea is lacking or severely reduced, but at the same time the short larval  
454 phase typical of lagoonal species favor the establishment of dense autochthonous populations.

455 We also report here a significant within-lagoon variability, which was similarly found across  
456 lagoons and was related to the main environmental gradients typically found in coastal lagoons. In  
457 particular, the macrozoobenthic assemblage in each investigated lagoon changed spatially according to  
458 the land-sea gradient and the confinement level, with a significant differentiation among the stations  
459 located at the marine pole and the lagoon's innermost sectors. In each lagoon, a similar gradient  
460 highlighted a typical decline in species richness from the marine to the most confined pole, as is typically  
461 found in these ecosystems (Guelorget and Pethuisot, 1992; Cardone et al., 2014; Giangrande and  
462 Gravina, 2015). However, in each lagoon changes along this gradient were associated with a different  
463 species composition.

464 Our results pinpoint that the within-lagoon heterogeneity of the macrozoobenthos described  
465 above superimposes the among-lagoon heterogeneity and emerges as a peculiar and natural property of  
466 the investigated set of lagoons. Regards the causes of these patterns, we hypothesize that the within-



467 lagoon heterogeneity is mostly sustained by stochastic factors, mainly related to the local geographical  
468 characteristics and coastal hydrodynamics. These factors influence the timing of arrival and dispersal  
469 phases of both larvae and adults, which may successfully colonize the different lagoons according to  
470 their specific adaptability and life strategies. In this regard, we suggest that the causes of the high  
471 heterogeneity within each lagoon should be investigated in terms of lagoon origin, geographical  
472 features and hydrodynamics, all of these factors being able to constrain the connectivity among lagoons,  
473 as well as in terms of dispersal ability and life history traits of the benthic species. These latter aspects  
474 are, indeed, the main factors influencing the species colonization strategy and their adaptability to the  
475 local environmental conditions. Our suggestion finds foundation also on the documented importance  
476 of both geographical and biological factors in determining the macrozoobenthos distribution in hard  
477 bottom communities of other Mediterranean lagoons (Cardone et al., 2014; Nonnis Marzano et al.,  
478 2010). With our contentions in mind, we propose that the relative proportions of each main component  
479 (marine, common in sheltered waters, halolimnobic, opportunistic) of the macrozoobenthic  
480 assemblages can be considered valuable ecological indicators of the within-lagoon heterogeneity; thus  
481 on the local spatial scale, the assemblages change consistently across lagoons along the confinement  
482 and salinity gradients. At the same time, the taxonomic composition of macrozoobenthic assemblages  
483 characterizes the among-lagoon heterogeneity/communality, with the assemblages changing according  
484 to their origin and the species' biological traits. Our results confirm and emphasize the complexity of  
485 coastal lagoons and highlight the efficacy of macrozoobenthic species as environmental indicators,  
486 especially when their autecology is duly considered (Zettler et al., 2013). We believe that this approach  
487 is best suited for characterizing the natural conditions of TWs and assessing their environmental quality  
488 (Magni et al., 2009; Van Hoey et al., 2010).

489 In conclusion, our study is pivotal in that it highlighted for the first time both heterogeneity and  
490 common patterns in nanotidal lagoons located within a restricted climatic and geographical setting.  
491 Indeed, our analysis applied to an extensive dataset set including physiographic and environmental  
492 features, anthropogenic pressures and macrozoobenthic assemblages, proved its efficiency in shedding  
493 light on local spatial patterns within a lagoon and the potential connectivity with other lagoons.  
494 Furthermore, our results confirm that biodiversity studies carried out at the lowest taxonomic level (i.e.  
495 species identity) help explaining the heterogeneity and complexity of the lagoons. Thus, we propose the  
496 adoption of such an approach to boost future management and conservation programs.

497

#### 498 **Acknowledgements**

499 We would like to thank Marcello Giorgi, University of Rome "Tor Vergata", for technical support in data  
500 analysis procedures. We also thank our handling Editor, Professor Mike Elliott, and two anonymous  
501 reviewers for their valuable suggestions and careful reading of the manuscript.

- 502
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719 **Table 1.** Physiographic and environmental features of the seven lagoons investigated.

Lagoon	Transitional District	Catchment area (km <sup>2</sup> )	Surface (km <sup>2</sup> )	Volume (Mm <sup>3</sup> )	Mean depth (m)	Max depth (m)	Annual freshwater inflow (Mm <sup>3</sup> yr <sup>-1</sup> )	Salinity range	Main primary producers	Chl- <i>a</i> annual mean concentration (µg l <sup>-1</sup> )	DIN annual mean concentration (mmol m <sup>-2</sup> )	PO <sub>4</sub> annual mean concentration (mmol m <sup>-2</sup> )	Protection measures
Casaraccio	Gulf of Asinara	11.7	0.85	1	1.2	2	1	16-42	Phy-P, Phy-B	3	39.64	7.9	SCI, SPA, R
Calich	Gulf of Alghero	432	0.97	1	1.2	2	43	2-33	Phy-P, Phy-B	12	14.85	1.02	SCI, SPA, OPF
Cabras	Gulf of Oristano	459.2	22.3	38	1.7	2.1	76	2-42	Phy-P	17-40	16.75	2.02	SCI, SPA, R, OPF
Mistras	Gulf of Oristano	0	4.1	2	0.5	2	0	32-59	Phy-P, Phy-B	3	4.66	1.71	SCI, SPA, R, OPF
Santa Giusta	Gulf of Oristano	137.6	8	16	1	3	8	15-42	Phy-P, Phy-B	5	7.24	0.17	SCI, SPA
Santa Gilla	Gulf of Cagliari	2238	13	18	1	3	80	15-35	Phy-P, Phy-B	8	7.24	0.17	SCI, SPA, R, OPF
Tortolì	Southeastern coast	99.8	2.5	4	1	2	15	8-38	Phy-P	1	10.49	2.29	SCI

720 Protection measures: SCI: Site of Community Importance; SPA: Special Protection Area; R: Ramsar Site; OPF: Oasis of Faunistic Protection. Phy-P = Phytoplankton; Phy-B = Phytobenthos.

721 **Table 2.** Details and sources of the dataset used in the study.

Lagoon	Lagoon code	Sampling stations (n)	Replicates per station (n)	Sampling times (n)	Sampling dates	Total samples (n)	Sampler type	Sampler area (cm <sup>2</sup> )	Mesh size (mm)	Reference
Casaraccio	Cs	4	3	5	Mar, Jun, Sep, Dec 1994; Mar 1995	60	Box corer	170	0.5	Floris, 2003
Calich	Ca	5	3	4	Mar, Jul, Dec 1995; Mar 1996	60	Box corer	170	0.5	Floris, 2003
Cabras	Cb	4	6	4	Jul-Aug 2001 and Jan-Feb 2002 <sup>§</sup> ; Jul-Aug 2010 and Jan-Feb 2011 <sup>ϕ</sup>	96	Ekman-Birge grab	216	0.5	Magni et al., 2005 <sup>§</sup> ; Foti et al., 2014 <sup>ϕ</sup>
Mistras	Mi	3	4	4	Apr, May 2010; Oct, Nov 2010	48	Box corer	170	0.5	Fenzi, 2013
Santa Giusta	Sa	3	24	1	Nov 2002	72	Box corer	170	0.5	Floris, 2003
Santa Gilla	Si	3	3	4	Jul, Oct 2010; Jan, Mar 2011	36	Van Veen grab	500	1	Cabiddu et al., 2014
Tortoli	To	6	2	4	Jul, Nov 2003; Feb, Jun 2004	48	Van Veen grab	500	0.5	Gravina unpublished

722 **Table 3.** Correlation coefficient  $R$  among physiographic/environmental features of the studied lagoons (see Table  
 723 1), and the components from PCA. \*  $P < 0.05$ ; \*\*  $P < 0.001$ , ns = not significant.

	Component 1	Component 2
Surface	0.87*	-0.42 ns
Volume	0.78*	-0.60 ns
Mean Depth	0.33 ns	-0.31 ns
Max Depth	0.26 ns	0.34 ns
Freshwater inflow	0.99 **	-0.48 ns
Min Salinity	-0.39 ns	0.77 *
Max Salinity	-0.34 ns	0.03 ns
Mean DIN	-0.19 ns	-0.41 ns
Mean PO <sub>4</sub> <sup>3-</sup>	-0.34 ns	-0.20 ns
Mean Chl- $a$	0.81 *	-0.85 *

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724 **Table 4.** Type and magnitude of anthropogenic pressures and environmental indicator index (EII) for each studied lagoon.

Lagoon	Non-point pollution source	Point pollution source		Habitat loss		Industry		Ports			Fisheries		Total pressures	Pressure index (EII)
	Diffuse agriculture input	Domestic discharge	Industrial discharge	Land reclamation (urban)	Land reclamation (industrial)	Water abstraction	Power generation	Port activity	Navigatio n	Dredging	Fin- fisherie s	Shell- fisherie s	Sum	Mean
Casaraccio	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calich	2	3	1	1	0	0	0	1	0	0	1	1	10	1.43
Cabras	2	2	0	0	0	0	0	0	1	1	2	0	8	1.23
Mistras	1	0	0	0	0	0	0	0	0	1	1	1	4	0.62
Santa Giusta	2	3	1	0	0	0	0	1	1	1	2	1	12	1.85
Santa Gilla	2	2	3	1	3	0	2	2	1	2	2	2	22	3.38
Tortoli	1	0	0	0	0	0	0	0	1	0	2	2	6	0.92

725 An environmental integrative index (EII) expressed as the sum of component metrics (CM) quantified the total anthropogenic stress at each location and sampling site in four levels: 0—absence to  
726 very low; 1—low; 2—moderate; 3—high.  
727 An ‘expert judgment’ approach based on the existing knowledge for the seven studied lagoons: Casaraccio (Floris, 2003; ARPAS, 2009), Calich (RAS, 1994a; Consorzio di Bonifica della Nurra, 1998;  
728 Hydrocontrol and AMGA, 2001a,b,c,d; Floris, 2003), Cabras (Magni et al., 2004, 2005, 2008a; Padedda et al., 2012), Mistras (Fenzi, 2013) Santa Giusta (Hydrocontrol and AMGA, 2001a,b,c,d; Floris,  
729 2003; Magni et al., 2008b), Santa Gilla (RAS, 1994a; Degetto et al., 1997; Hydrocontrol and AMGA, 2001a, b, c, d; Cabiddu et al., 2013, 2014; Atzori et al., 2018) and Tortoli (Hydrocontrol and  
730 AMGA, 2001a,b,c,d).

731 **Table 5.** Correlation coefficient  $R$  among environmental stressors of the studied lagoons (see Table 4) and the  
 732 components from PCA. \*  $P < 0.05$ ; \*\*  $P < 0.001$ , ns = not significant.

	Component 1	Component 2
Environmental indicator index	0.99**	0.04 ns
Agriculture input	0.76*	0.43 ns
Domestic discharge	0.59 ns	0.25 ns
Industrial discharge	0.94**	-0.32 ns
Land reclamation (urban)	0.71 ns	-0.49 ns
Land reclamation (industrial)	0.85*	-0.27 ns
Power generation	0.85*	-0.36 ns
Port activity	0.93**	-0.27 ns
Navigation	0.54 ns	0.71 ns
Dredging	0.76 *	0.01 ns
Fin-fisheries	0.64 ns	0.72 ns
Shell-fisheries	0.59 ns	-0.04 ns

733

734 **Table 6.** List of the 60 species identified by the SIMPER analysis (individual contribution of > 0.5%) responsible for  
 735 90% of the distinction between lagoons. Higher taxon: Cn = Cnidaria; P = Polychaetes; B = Bivalves; G = Gastropods;  
 736 Ch = Chironomids; C = Crustaceans; Ph = Phoronids. Black/white-coded species category: O = opportunistic; C =  
 737 common in coastal sheltered waters; B = brackish; M = properly marine. Species assignment to one of four main  
 738 ecological categories was based on our expert judgment and according to the published literature (for details see  
 739 section 2.3 of Materials and Methods). Species occurrence indicates the number of lagoons where an individual  
 740 species was found.

Species	Higher taxon	Species category	Species occurrence	Casarcio	Calich	Cabras	Mistras	Santa Giusta	Santa Gilla	Tortoli
<i>Capitella capitata</i> (Fabricius, 1780)	P	O	7	✓	✓	✓	✓	✓	✓	✓
<i>Abra segmentum</i> (Récluz, 1843)	B	C	7	✓	✓	✓	✓	✓	✓	✓
<i>Naineris laevigata</i> (Grube, 1855)	P	C	6	✓	✓		✓	✓	✓	✓
<i>Cerastoderma glaucum</i> (Poiret, 1789)	B	B	6	✓	✓		✓	✓	✓	✓
<i>Gammarus insensibilis</i> Stock, 1966.	C	C	6	✓	✓	✓		✓	✓	✓
<i>Neanthes acuminata</i> (Ehlers, 1868)	P	C	5	✓	✓			✓	✓	✓
<i>Loripes orbiculatus</i> Poli, 1795	B	C	5	✓	✓		✓	✓		✓
Chironomidae	Ch	O	5	✓	✓	✓	✓			✓
<i>Abarenicola claparedi</i> (Levinsen, 1884)	P	C	4	✓			✓	✓		✓
<i>Hediste diversicolor</i> (O.F. Müller, 1776)	P	B	4		✓	✓			✓	✓
<i>Polydora ciliata</i> (Johnston, 1838)	P	O	4			✓		✓	✓	✓
<i>Prionospio cirrifera</i> Wirén, 1883	P	O	4		✓	✓			✓	✓
<i>Monocorophium sextone</i> (Crawford, 1937)	C	C	4	✓	✓			✓	✓	
<i>Heteromastus filiformis</i> (Claparède, 1864)	P	O	3		✓				✓	✓
<i>Phylo foetida</i> (Claparède, 1868)	P	C	3	✓	✓			✓		
<i>Podarkeopsis capensis</i> (Day, 1963)	P	M	3		✓			✓	✓	
<i>Protodorvillea keferteni</i> McIntosh, 1869)	P	M	3	✓	✓		✓			
<i>Hydrobia acuta</i> (Draparnaud, 1805)	G	B	3			✓	✓		✓	
<i>Cyathura carinata</i> (Krøyer, 1847)	C	B	3		✓	✓			✓	
<i>Dexamine spinosa</i> (Montagu, 1813)	C	M	3	✓	✓					✓
<i>Gammarus aequicauda</i> (Martynov, 1931)	C	C	3			✓	✓	✓		
<i>Microdeutopus anomalus</i> (Rathke, 1843)	C	C	3	✓	✓			✓		
<i>Microdeutopus gryllotalpa</i> Costa, 1853	C	C	3				✓		✓	✓
<i>Monocorophium insidiosum</i> (Crawford, 1937)	C	B	3			✓			✓	✓
<i>Tanais dulongi</i> (Audouin, 1826)	C	O	3	✓				✓		✓
<i>Paranemonia cinerea</i> (Contarini, 1844)	Cn	C	2	✓						✓
<i>Aricidea cerrutii</i> Laubier, 1866	P	M	2	✓	✓					
<i>Cirriformia tentaculata</i> (Montagu, 1808)	P	C	2					✓	✓	
<i>Malacoceros fuliginosus</i> (Claparede, 1868)	P	O	2	✓						✓
<i>Perkinsyllis anopthalma</i> (Capaccioni & San Martín, 1990)	P	M	2	✓	✓					
<i>Prionospio multibranchiata</i> Berkeley, 1927	P	O	2		✓			✓		
<i>Protoaricia oerstedii</i> (Claparède, 1864)	P	M	2	✓	✓					
<i>Pseudopolydora antennata</i> (Claparède, 1869)	P	O	2					✓	✓	
<i>Streblospio shrubsolii</i> (Buchanan, 1890)	P	O	2		✓				✓	
<i>Venerupis corrugata</i> (Gmelin, 1791)	B	M	2				✓			✓
<i>Chondrochelia savignyi</i> (Kroyer, 1842)	C	M	2	✓	✓					
<i>Cymodoce truncata</i> Leach, 1814	C	M	2				✓	✓		
<i>Monocorophium acherusicum</i> Costa, 1851	C	C	2					✓	✓	
<i>Alitta succinea</i> (Leuckart, 1847)	P	C	1			✓				
<i>Hilbigneris gracilis</i> (Ehlers, 1868)	P	M	1		✓					
<i>Myriochele heeri</i> Malmgren, 1867	P	M	1							✓
<i>Nephtys hombergii</i> Savigny in Lamarck, 1818	P	M	1							✓
<i>Perinereis rullieri</i> Pilato, 1974	P	M	1				✓			
<i>Sphaerosyllis pirifera</i> Claparede, 1868	P	M	1		✓					
<i>Sphaerosyllis taylori</i> Perkins, 1981	P	M	1		✓					
<i>Spiochaetopterus costarum</i> (Claparède, 1869)	P	M	1							✓
<i>Abra tenuis</i> (Montagu, 1803)	B	M	1				✓			
<i>Caecum clarkii</i> Carpenter, 1859	G	M	1							✓
<i>Parvicardium exiguum</i> (Gmelin, 1791)	B	M	1							✓
<i>Apocorophium acutum</i> (Chevreux, 1908)	C	M	1							✓
<i>Apeudes latreilli</i> (Milne Edwards, 1828)	C	M	1	✓						

<i>Caprella scaura</i> Templeton, 1836	C	M	1					√		
<i>Elasmopus pocillimanus</i> (Bate, 1862)	C	M	1					√		
<i>Idotea chelipes</i> (Pallas, 1766)	C	B	1		√					
<i>Iphinoe trispinosa</i> (Goodsir, 1843)	C	M	1					√		
<i>Lekanesphaera hookeri</i> (Leach, 1814)	C	B	1		√					
<i>Microdeutopus algicola</i> Della Valle, 1893	C	M	1					√		
<i>Monocorophium orientale</i> (Schellenberg, 1928)	C	B	1		√					
<i>Sphaeroma serratum</i> (Fabricius, 1787)	C	M	1				√			
<i>Phoronis psammophila</i> Cori, 1889	Ph	M	1					√		
<b>Number of species identified by SIMPER</b>				<b>22</b>	<b>27</b>	<b>15</b>	<b>16</b>	<b>20</b>	<b>22</b>	<b>30</b>
<b>Total number of species</b>				<b>61</b>	<b>66</b>	<b>25</b>	<b>39</b>	<b>83</b>	<b>63</b>	<b>101</b>

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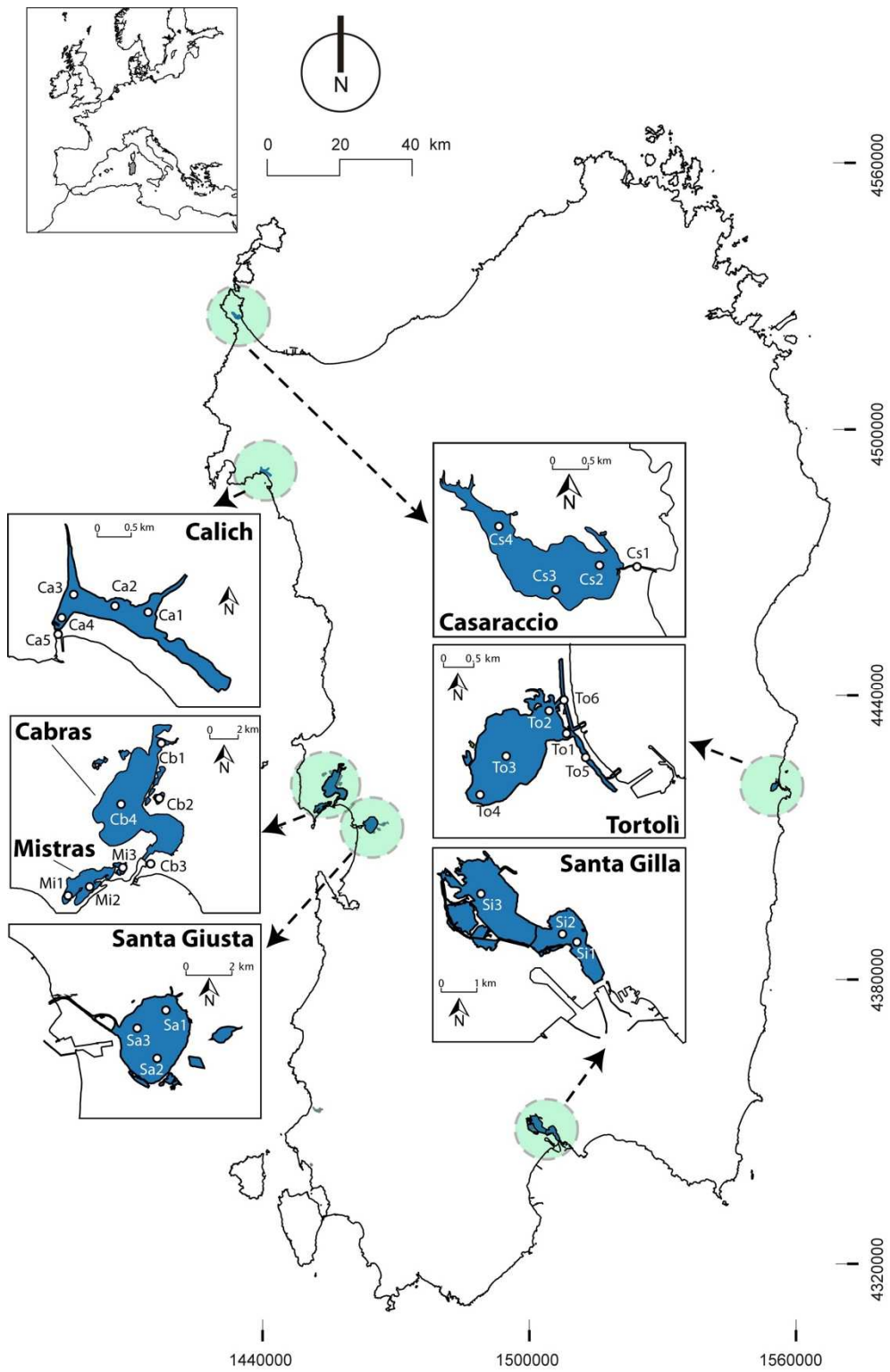
744 **Table 7.** Results of ANOSIM (ANalysis Of Similarities) between the sampling stations of the seven Sardinian  
 745 lagoons, based on Bray-Curtis distance measure with  $R$  and relative  $P$  value after Bonferroni correction. Summary  
 746 results of the test are shown in the Results paragraph.

	Casaraccio	Calich	Cabras	Mistras	Santa Giusta	Santa Gilla	Tortoli
Mean rank within	422	65.55	26.95	17.5	944.4	26.5	112.2
Mean rank between	6058	154.5	77.28	50.5	1686	40.9	162.6
$R$	0.37**	0.94**	0.839**	0.99**	0.58**	0.44*	0.366**

747 \*  $P < 0.05$ , \*\*  $P < 0.001$ ; Permutation N=9999.

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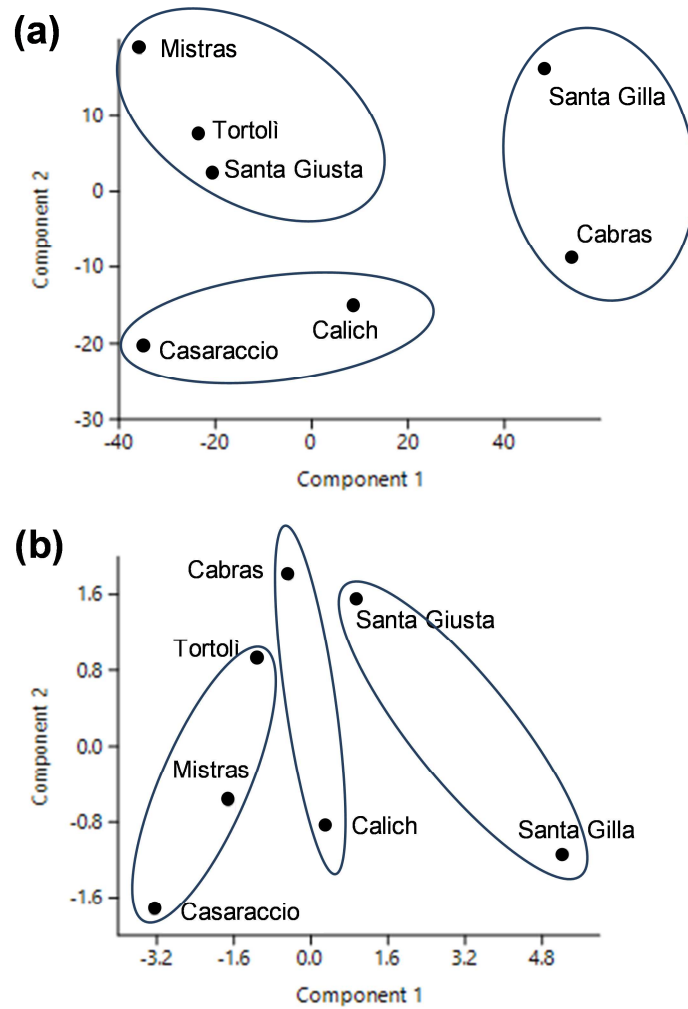


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750 **Fig. 1.** Studied lagoons and location of the sampling stations within each lagoon (Sardinia, western  
 751 Mediterranean Sea).

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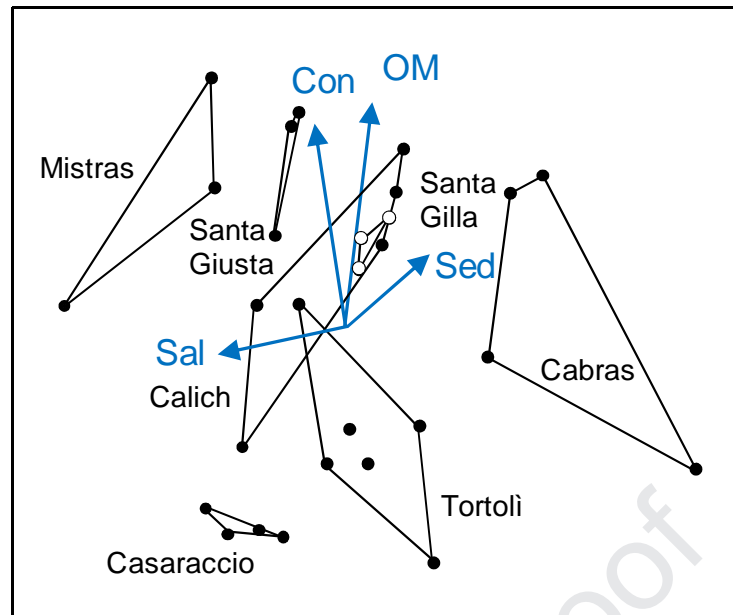


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755 **Fig. 2.** Ordination model produced by Principal Component Analysis on (a) physiographic/environmental  
 756 similarity (percentages of variance: 75.7 for component 1 and 12.2 for component 2), and (b)  
 757 anthropogenic pressures similarity among the studied lagoons (percentages of variance: 60.2 for  
 758 component 1 and 16.4 for component 2) (data from Table 1 and 4, respectively).

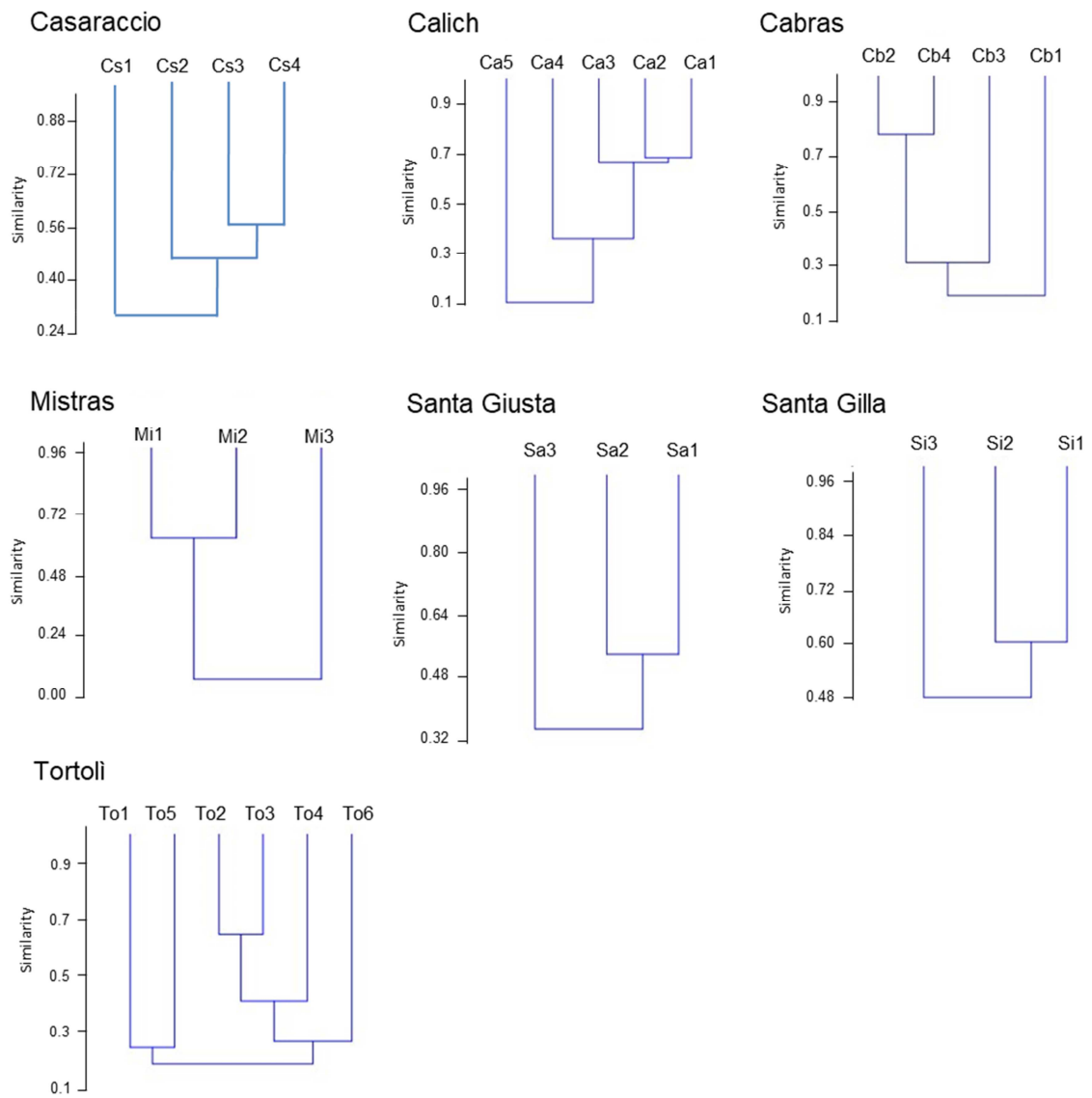
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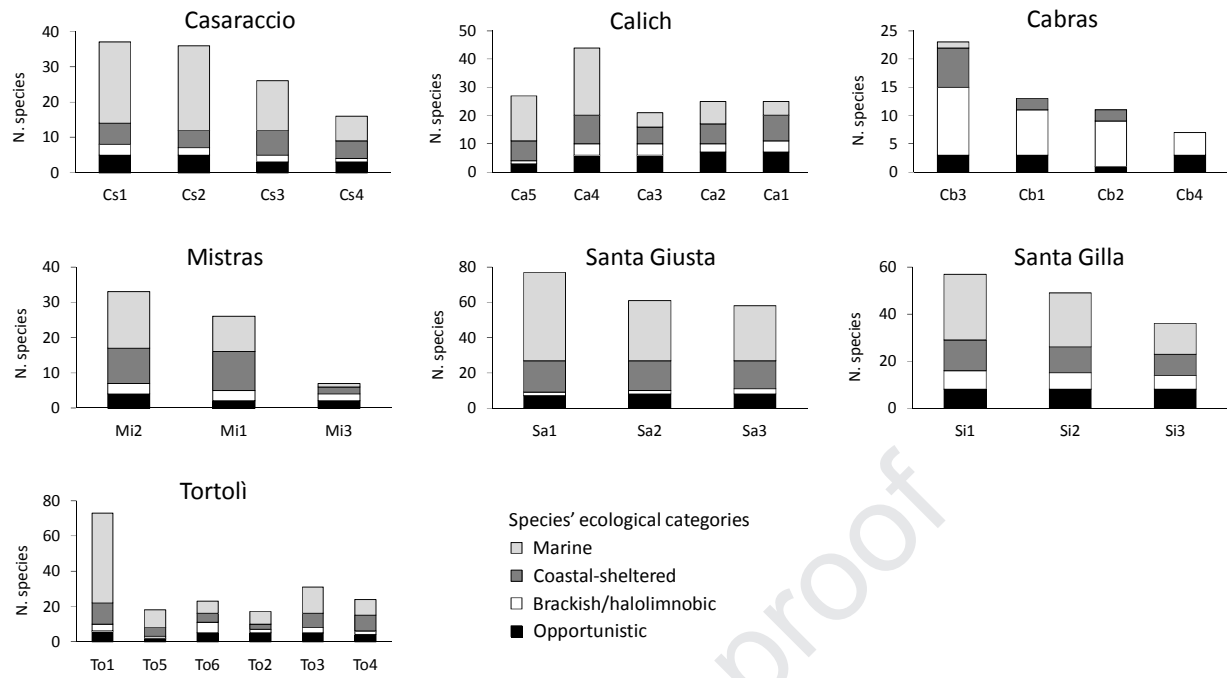
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762 **Fig. 3.** nMDS ordination model on the macrozoobenthic taxa most contributing by SIMPER for  
 763 dissimilarity within each lagoon: 1, Casaraccio; 2, Calich; 3, Cabras; 4, Mistras; 5, Santa Giusta; 6, Santa  
 764 Gilla (open circles); 7, Tortoli. Dark dots are the station-points. Sal = salinity; Con = confinement; OM =  
 765 sediment organic matter; Sed = sediment granulometry.



766 **Fig. 4.** Results of cluster analysis based on macrozoobenthic density data of each studied lagoon.



767

768 **Fig. 5.** Total number of species collected at each station within each lagoon and divided into four main  
 769 ecological categories. Stations were ordered according to their location along the outer-inner gradient  
 770 (see Fig. 1).

771 **Supplementary Table S1.** Total abundance (ind. m<sup>-2</sup>) per station of the species which mostly contributed to the  
 772 benthic community variability of the stations within each lagoon (species list extrapolated from Table 6). Stations  
 773 within each lagoon are ordered according to the outer-inner gradient (see Figs. 1 and 5). Species category: O =  
 774 opportunistic; C = common in coastal sheltered waters; B = brackish; M = properly marine.

<b>Casaraccio Lagoon</b>	Cs1	Cs2	Cs3	Cs4	
<i>Aricidea cerrutii</i> M	60	360	4	10	
<i>Capitella capitata</i> O	988	1628	3812	3045	
<i>Malacoceros fuliginosus</i> O	2228	236	12	10	
<i>Naineris laevigata</i> C	4	16	0	0	
<i>Neanthes acuminata</i> C	340	16	4	0	
<i>Abra segmentum</i> C	0	0	32	45	
<i>Cerastoderma glaucum</i> B	0	16	8	35	
Chironomidae O	4	4	0	155	
<i>Apseudes latreilli</i> M	56	4	0	0	
<i>Chondrochelia savignyi</i> M	88	0	60	0	
<i>Dexamine spinosa</i> M	44	0	0	0	
<b>Calich Lagoon</b>	Ca5	Ca4	Ca3	Ca2	Ca1
<i>Aricidea cerrutii</i> M	5	265	0	0	0
<i>Capitella capitata</i> O	95	20	30	10	0
<i>Hediste diversicolor</i> B	0	0	645	675	310
<i>Naineris laevigata</i> C	10	365	0	0	15
<i>Neanthes acuminata</i> C	85	695	0	0	0
<i>Protodorvillea kefersteini</i> M	110	5	0	0	0
<i>Sphaerosyllis taylori</i> M	20	245	0	0	0
<i>Streblospio shrubsolii</i> O	0	0	140	140	345
<i>Cerastoderma glaucum</i> B	0	15	30	60	40
<i>Cyathura carinata</i> B	0	25	265	70	90
<i>Dexamine spinosa</i> M	40	0	0	0	0
<b>Cabras Lagoon</b>	Cb1	Cb3	Cb2	Cb4	
<i>Alitta succinea</i> C	118	60	14	1080	
<i>Capitella capitata</i> O	4	140	0	22	
<i>Hediste diversicolor</i> B	0	630	1088	264	
<i>Polydora ciliata</i> O	0	0	0	74	
<i>Abra segmentum</i> C	0	10	22	0	
<i>Hydrobia acuta</i> B	18	132	94	1142	
Chironomidae O	8	150	128	388	
<i>Gammarus aequicauda</i> C	16	1430	4	0	
<i>Idotea chelipes</i> B	0	1446	0	0	
<i>Lekanesphaera hookeri</i> B	0	1698	22	0	
<i>Monocorophium orientale</i> B	8028	1896	2	0	
<b>Mistras Lagoon</b>	Mi2	Mi1	Mi3		
<i>Capitella capitata</i> O	26	4	622		
<i>Naineris laevigata</i> C	25	241	0		
<i>Perinereis rullieri</i> M	222	130	0		
<i>Abra tenuis</i> M	122	74	2057		
<i>Cerastoderma glaucum</i> B	41	24	444		
<i>Hydrobia acuta</i> B	0	0	470		
<i>Venerupis corrugata</i> M	18	0	0		
<i>Cymodoce truncata</i> M	4	4	0		
<i>Gammarus aequicauda</i> C	133	226	18		
<i>Microdeutopus gryllotalpa</i> C	215	448	19		
<i>Sphaeroma serratum</i> M	31	359	0		
<b>Santa Giusta Lagoon</b>	Sa1	Sa2	Sa3		
<i>Capitella capitata</i> O	25	195	220		
<i>Cirriformia tentaculata</i> C	420	30	160		
<i>Naineris laevigata</i> C	8	52	847		
<i>Prionospio multibranchiata</i> O	372	1428	3062		
<i>Abra segmentum</i> C	293	2318	278		

<i>Cerastoderma glaucum</i> B	28	508	40	775
<i>Cymodoce truncata</i> M	2745	2555	4482	
<i>Microdeutopus anomalus</i> C	103	1493	15	776
<i>Monocorophium acherusicum</i> C	550	248	0	
<i>Monocorophium sextonae</i> C	3023	1970	0	
<i>Tanais dulongii</i> O	48	146	40	

<b>Santa Gilla Lagoon</b>	Si1	Si2	Si3
<i>Cirriformia tentaculata</i> C	216	345	12
<i>Hediste diversicolor</i> B	422	241	512
<i>Heteromastus filiformis</i> O	61	44	109
<i>Neanthes acuminata</i> C	90	7	0
<i>Polydora ciliata</i> O	78	294	236
<i>Streblospio shrubsolii</i> O	2557	2032	1935
<i>Abra segmentum</i> C	80	173	2198
<i>Hydrobia acuta</i> B	7	3	269
<i>Caprella scaura</i> M	265	36	0
<i>Microdeutopus gryllotalpa</i> C	88	49	22
<i>Monocorophium acherusicum</i> C	151	73	2

<b>Tortoli Lagoon</b>	To1	To5	To6	To2	To3	To4
<i>Heteromastus filiformis</i> O	83	73	15	13	15	3
<i>Malacoceros fuliginosus</i> O	0	0	75	0	0	3
<i>Myriochele heeri</i> M	360	0	0	0	0	0
<i>Nephtys hombergii</i> M	28	150	0	160	130	20
<i>Spiochaetopterus costarum</i> M	378	0	0	0	0	0
<i>Abra segmentum</i> C	268	15	25	58	53	70
<i>Caecum clarkii</i> M	38	0	0	0	0	0
<i>Iphinoe trispinosa</i> M	20	3	0	3	3	0
<i>Apocorophium acutum</i> M	38	5	15	148	125	8
<i>Microdeutopus algicola</i> M	103	0	0	0	3	58
<i>Monocorophium insidiosum</i> B	3	0	343	188	10	34

**Gravina\_et\_al\_ECSS\_Highlights**

- Environmental features and macrobenthic assemblages investigated in seven Mediterranean lagoons.
- Within-lagoon common patterns related to salinity, confinement and organic enrichment.
- Among-lagoon differences determined by individual species.
- Species' autecology helps explaining local spatial patterns and connectivity among lagoons.
- Our approach sheds light on heterogeneity and commonalities within and among lagoons.

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**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: