Spatio-temporal variability of benthic macrofauna in a coastal lagoon assessed by ecological interaction networks

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Keywords: Benthic macrofauna, Coastal lagoon, Community structure, Networks, Spatio-temporal variability

Abstract: An ecological survey of the benthic communities was carried out, at both spatial and temporal scales, in Papapouli Lagoon, the first ecotouristic park in Greece by applying for the first time, ecological network analysis. The application of ecological network analysis provided novel information on the quality of interactions among species, undetected by the most frequently used methods. The sorting of substrate samples enabled the identification and density determination of 40,036 individuals belonging to 31 different taxa, although, strong dominance of only a few species was observed. "Deposit feeders" were the dominant trophic group in all sampling sites and seasons while "suspension feeders" exhibited relatively the lowest abundance. The periodic opening of the sea inlet seems to be of crucial importance. In coastal lagoons, where there is constant communication with the sea, benthic fauna patterns seem to change according to the sea-land gradient. However, in intermittently closed lagoons, such as Papapouli Lagoon, a more homogenous pattern is evident. The obtained networks showed that when communication with the sea is interrupted all the benthic fauna patterns tend to be destabilized and centralized around one species, which in most cases is a "deposit feeder". When the inlet opens and communication with the sea is restored, the benthic composition seems to be more cohesive, especially in the most distant regions. Knowledge generated by network analysis should provide a valuable tool in order to assess potential environmental changes and assist management decisions.

Introduction

Coastal lagoons are shallow water collections, partially isolated from the sea by barriers created by both the deposition of sediment and the wave action (Bird 1994). Due to their isolation and low depth, coastal lagoons vary considerably in physico-chemical parameters on a seasonal basis. Their interface position, between land and sea, makes them particularly susceptible to both marine and terrestrial influences (Colombo 1977).

Lagoon ecosystems are of high ecological interest primarily because of their productivity, which plays a key role in the reproduction and development of many species. Their high productivity is based mainly on the primary production of the phytobenthos and, to a lesser extent, on phytoplankton resulting directly in the consumption of the largest part of the organic matter produced by the benthic macrofauna (Santos et al. 1997, Wainright et al. 2000). Their economic value is also substantial as they are considered as suitable habitats for aquaculture and fisheries (Rogdakis et al. 2010). However, these activities often result in ecosystem degradation due to accumulation of pollutants, degradation of water quality, and increase of organic matter triggering eutrophication and dystrophic episodes (Lacerda 1994, Spaulding 1994, Mogias and Kevrekidis 2005).

Lagoons usually are characterized by a high degree of spatial and temporal variability. Environmental differences in space and time are usually responsible for differences in the diversity and composition of macroinvertebrate communities. Consequently, natural environmental differences generate variation in the functional diversity and community patterns of macroinvertebrates (Schmera et al. 2013).

Information on the spatial and temporal patterns of the benthic faunal community is crucial in order to guide management and refine predictions about potential environmental changes due to anthropogenic impacts (Arias and Darke 1994, Constable 1999, Ysebaert and Herman 2002, Salas et al. 2006, Munari et al. 2009, 2010, Dutertre et al. 2013).

To date, a wide variety of methods of community structure analysis have been implemented (Arvanitidis et al. 2005a,b, 2009, Munari et al. 2009). However, over the last few years, the multispecies modeling approach such as keystone species complex and ecological interaction networks has gained ground due to the fact that these models take into account the interactions among the members of the community and can provide information on concomitant changes within the community following species removal or replacement (Proulx et al. 2005, Ortiz et al. 2013). In this way, they represent useful tools for screening and determining the set of variables that should be considered in relevant field experiments.

Network analysis is thought to be suitable for any kind of web interactions such as genes and proteins but also populations and individuals (Proulx et al. 2005, May 2006). Until relatively recently, network approaches have been used extensively in the study of social and technological networks (Albert et al. 1999, Scott 2000, Kleinberg 2008). Their implementation in biology has been confined to the study of foodwebs and metabolic networks (Jeong et al. 2000, Dunne et al. 2008, Ings et al. 2009, Johnson et al. 2009, Anderson et al. 2011, Liu et al. 2011, Pah et al. 2013) while applications to communities are still rare (Vasas and Jordán 2006, Fuller et al. 2008, Kapagianni et al. 2010, Boutsis et al. 2011).

In coastal lagoons, the benthic macrofauna is mainly represented by three groups of species: i) marine species that occur in areas with direct or indirect communication with the sea, ii) "opportunistic" species, which appear usually in regions enriched with organic matter, and iii) typical euryhaline species of brackish water, which are best adapted to the fluctuating environmental conditions (Lardicci et al. 2001). According to Guelorget and Perthuisot (1992), the most important factor which shapes species composition and community structure is the degree of confinement. "Confinement" is dependent on communication with the sea and the freshwater inflow, and is expressed as the time of renewal of marine-origin components. According to "confinement" model the fauna inhabiting paralic environments are assigned to six well-defined zones along the sea-land gradient (Guelorget and Perthuisot 1992). The limits of these zones may show a seasonal shift indicating the dynamic character of the lagoonal environment (Koutsoubas et al. 2000a).

Here, we describe and analyze the benthic macrofauna of a brackish water lagoon form the North Aegean Sea. We use "confinement" theory in order to i) detect any spatial and temporal variability of the benthic macrofauna pattern according to spatio-temporal changes in the communication with the sea, and ii) assess the driving forces that alter its structural and functional characteristics in different ways. For this purpose, we describe the benthic community and additionally we implement, for the first time in brackish ecosystems, network analysis to get a deeper insight into the features associated with its structural connectedness.

Materials and methods

Study area

Papapouli Lagoon, the first ecotouristic park in Greece, is a brackish water lagoon located at the SW part of Thermaikos gulf in the North Aegean Sea (Fig. 1). The surface of the area is about 3 km² while the total basin occupies an area of about 13.5 km². It is a shallow lagoon with maximal depth of 1.8 m. The lagoon is formed under the influence of Papapouli River as well as of saline inflows from the Aegean Sea. A significant part of the waters from the southern side of Mount Olympus end up in this area (Koukaras 2010). Papapouli Lagoon is separated from the sea by a sand barrier of 630 m in length and 30-70 m in width. It is a chocked lagoon, separated from the sea via two inlets, both situated on the eastern side allowing limited water exchange. The first one, located in the NE side of the lagoon, is always closed while the second one, located in the SE part, is opened periodically according to the intensity and the direction of the wind. This second inlet is usually closed from June to December. In early January, the degree of communication with the sea changes as a result of the inlet opening due to the intense wave action. This directly results in sediment transport from the sea, thus altering the morphology of the inlet. In spring, the inlet remains open, but the wave action is reduced and a smaller but constant communication with the sea is observed. Thus, in Papapouli Lagoon the communication with the sea varies spatially and seasonally. Papapouli Lagoon also acts as a drainage ditch of the surrounding area. Until 2009 no official management had been applied. Nowadays, Papapouli Lagoon is an ecotouristic park used for educational activities, entertainment as well as for fish farming. Papapouli Lagoon is of great importance as it has been declared as Wildlife Refuge.
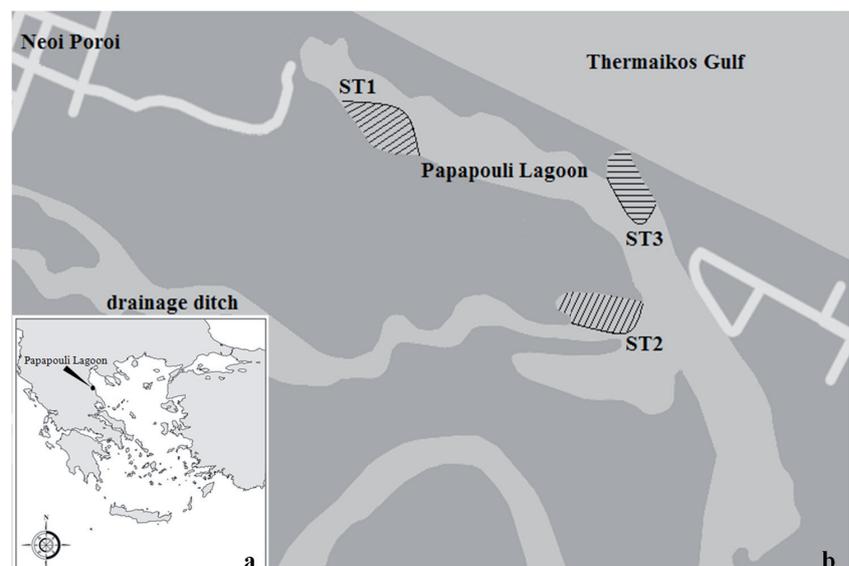

Figure 1. (a) Geographical location of the study site in Greece, **(b)** Map of the Papapouli Lagoon showing the sampling stations.

Sampling methods and laboratory techniques

Seasonal sampling was performed in autumn (October 2011), winter (January 2012) and spring (April 2012) in three different stations (ST1, ST2, ST3). Each station was selected according to its distance from the sea (Fig. 1). Station ST1 is the most remote with an average distance from the sea of about 400 m. Station ST2 is near the NE opening (200 m) which also accepts freshwater inputs, while station ST3 is located on the inner part of the inlet (40 m), which usually remains open from January to June. Each station was further divided in three approximately equal regions and from each region a composite sample was collected in order to account for spatial heterogeneity. Each composite sample consisted of a mixture of three individual samples, each one randomly collected inside each region of each station with a modified van Veen grab, covering a surface of 400 cm² (20 cm × 20 cm) and penetrating to a depth of 20 cm (Larimore 1970). A total of three genuine composite replicate samples, per season, were taken from each one of the three sampling stations. The samples were sieved through a 500 μm size mesh and preserved in 10% formalin (Eleftheriou and McIntyre 1976). Additional sediment samples were taken with a small corer for particle size analysis and estimation of organic carbon. These samples were preserved at –20°C. Water temperature, salinity, dissolved oxygen, pH, and depth were measured with a CTD auto recorder (DKK-TOA, Japan). In the laboratory, the presence of vegetation in each sample was noted and the benthic fauna was sorted, identified to species level (where possible), and classified to at least one of the following trophic groups according to the nature and origin of food: 1) herbivores (H), feeding on macroalgae and/or phanerogams; 2) carnivores (C), feeding on various sessile or motile invertebrates; 3) suspension feeders (Sf), feeding on suspended organic particles in the water column; 4) deposit feeders (Df), feeding on detritus on the substratum at the bottom of the lagoon. Species belonging to more than one trophic group were assigned by dividing the number of their individuals by the number of trophic groups in which they could be included (Fauchald and Jumars 1979, Boaventura et al. 1999, Cancela da Fonseca et al. 2001, Bazairi et al. 2003, Carvalho et al. 2005). The assignment of each taxon to the appropriate trophic group was performed according to Fauchald and Jumars (1979), Webb et al. (1987), Koutsoubas et al. (2000b), Mistri et al.(2001a), Kelly et al. (2002), Fidalgo e Costa et al. (2006), Chintiroglou et al. (2008), Dolbeth et al. (2009).

Grain size analysis of the sediment was carried out according to the methods described by Buchanan (1984). For the estimation of the organic carbon (%) in the sediment, the wet oxidation titration procedure using an acid dichromate system was used (Allen 1974).

Data analysis

To verify the effect of sampling period and sampling site (independent variables) as well as of their interaction on the abiotic variables (dependent variables) repeated measurements ANOVA was applied. For the determination of hydrodynamics, the coefficient of variation in sediment was used. All analyses regarding grain size estimations were performed with GRADISTAT v.6.0 package (Blott and Pye 2001).

Analysis of variance (ANOVA) was used to study differences in the abundance of each trophic group among samples, both temporally and spatially. Prior to the analyses, tests of homogeneity of variances were carried out and data were log-transformed (Zar 1984, Clarke and Green 1988). The Fisher LSD test was used for *post hoc* comparisons. Spearman's correlation coefficient was used to investigate possible relationships among trophic groups and abiotic variables. All statistical analyses were conducted with STATISTICA v.7, Tulsa, USA, Statsoft (Hill and Lewicki 2007).

Network analyses

In network analysis, for the construction of community matrices, the abundance data of the benthic species were used on the basis of their joint occurrence. The niche overlap index of MacArthur and Levins (1967) was used in order to calculate the probability of joint occurrence, which is defined by

$$a_{ij}= \Sigma p_{ik}p_{jk} / \Sigma p_{ik}^2$$

where a_{ij} is the overlap between species i and j while p_{ik} and p_{jk} are the probabilities of species i and j, respectively, to occur in site k. Moreover, the matrix used for the construction of the networks is not symmetric, which means that $a_{ij} \neq a_{ji}$. The intensity of the benthic species relation is indicated by the degree of the species' habitat overlap. The more frequent their joint occurrence, the higher their habitat overlap and the more intense their relation. The presented interactions between species, on the basis of co-existence, do not necessarily represent cause-effect relationships. In our data set, whenever the overlap of two species was found to be below 5% of the maximum recorded one, the species co-occurrence was considered non-significant and the corresponding entry in the matrix was set to zero. In order to construct graphs for the benthic fauna networks, data were analyzed by the network analysis software UCINET 6 (Borgatti et al. 1999). In the reproduced networks, the nodes represent benthic species belonging to specific trophic groups while the edges (ties), which connect these nodes, represent the joint occurrence of species in samples.

The estimation of certain metrics, provided by graph theory for the assessment of network connectedness or the structural importance of certain nodes/species, was used to analyze the structure of benthic fauna networks. There are several metrics which can be used for the estimation of network cohesion. Among them, we estimated density and distance since they are considered to be the simplest and most commonly used parameters of network cohesion. The density of a network expresses the degree of network connectedness. Density is equal to the total of all weights of ties, present in the network, divided by the maximum number of possible ties, if all nodes were significantly correlated with all the others (Jordano et al. 2006, Wey et al. 2008). We used the distance metric since by considering the distance that a species has from others we can capture the aspect of how differ-

Table 1. Mean values of abiotic data across the sampling seasons and sampling stations. The distance of each station from the sea is also given. The effects of sampling season and sampling station on abiotic variables as well as their interaction are also shown (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ns: not significant). ♦: presence of mixed photophilic algae, ○: presence only of *Ulva* sp., A: autumn, W: winter, S: spring.

| | Sampling stations | | | | | | | | | | | |
| | ST1 | | | ST2 | | | ST3 | | | *p*-value | | |
	A	W	S	A	W	S	A	W	S	Spatial	Temporal	Interaction
Water												
Temperature (ºC)	15	6	17.2	15	6	17	15.3	7.2	17.1	**	***	**
Salinity (psu)	15.6	29.2	29.2	15.7	28.1	19.6	15.77	36.6	33.2	***	***	***
Dissolved oxygen (mg/l)	8.37	7.25	8.43	8.35	7.42	8.1	8.27	7.9	8.49	*	***	*
pH	8.05	8.02	7.85	7.99	8	7.78	8.01	8.0	7.85	*	***	ns
Depth (cm)	23	34	24	34	27	27	11	21	43	***	***	***
Sediment												
Median diameter (µm)	416.9	876.4	378.7	28.09	308.5	39.56	666.2	424.1	387.08	***	***	***
Organic carbon (%)	2.14	1.16	2.08	2.80	1.67	2.81	1.15	1.40	2.37	***	***	***
Hydrodynamics	Poor	Poor	Poor	Very poor	Moderate	Very poor	Moderate	High	High			
Vegetation	♦	♦	♦	♦	♦	♦	○	♦	♦			
Distance from the sea (m)	410.96			205.19			38.53					

ent species are embedded in networks and not just the direct connections from one species to the next one. The distance between two nodes is the number of ties contained in the shortest path that connects them. In valued networks, like the ones of the present study where ties have a certain weight, the distance between two nodes is defined as the strength of the weakest tie along the path between them (Hanneman and Riddle 2005).

On the other hand, centrality indicates how a given network is focalized on specific nodes. Individual and network centrality metrics were estimated for each interaction network, separately. The simplest centrality metric, degree centrality, was used in order to assess the centrality of each individual node within each network and thereby to assess the structural importance of each node (Freeman 1979, Friedkin 1991). The degree centrality approach is regarded as a measure of connectedness and argues that species that have more connections are more likely to be dominant because they can directly affect other species. Additionally, the number of weighted ties of each node with the other nodes of the network is also represented by "degree centrality". An idea of the distribution of a species in samples can be gained by the number of nodes/species to which a node/species is adjacent.

In order to assess the overall structure of each network, the eigenvector centrality was estimated which depends on both the number and the quality of ties (Hanneman and Riddle 2005). More specifically, we chose the eigenvector approach in an effort to find the most central species (i.e., those with the minimum distance from others) in terms of the "global" or "overall" structure of the network, and to pay less attention to patterns that are more "local." Thus, we can have

a general idea of the network structure. Eigenvector centrality metric operates by assigning higher scores to nodes that are connected with well-connected neighbors than to nodes connected with impoverished ones (Newman 2008). For each network, eigenvector centrality was compared to the maximum possible centrality that characterizes the corresponding "star network", i.e., a network with the same nodes but with only one focal node connected with all others, whereas these latter are connected only to the focal node. Thus, in highly centralized networks very few central nodes dominate and these networks risk fragmentation in case of damaged central nodes.

Results

Abiotic variables

The average values of abiotic variables of water and sediment as well as the presence of vegetation at the three stations in each seasonal sampling are given in Table 1. The effects of sampling season and sampling station separately were significant for all the abiotic variables. The interaction effect of sampling season×sampling station was significant for all the variables with the exception of pH.

Temperature values varied among seasons according to the usual air temperature and correlated highly with the dissolved oxygen in the water (Table 2). Dissolved oxygen varied significantly mainly among seasons, with winter values being much lower than those recorded in autumn and spring. Merely, in station ST3 values remained quite constant through the seasons. Reduced concentrations of dissolved oxygen,

Table 2. Results of nonparametric Spearman correlation analysis. Bold values denote environmental variables that are strongly corre- lated (*p*<0.05). H: Herbivores, C: Carnivores, Df: Deposit feeders, T: Temperature (°C), S: salinity (psu), DO: Dissolved oxygen (mg/l), OC: organic carbon (%), MD: mean particle size (μm).

	H	C	Df	T	S	DO	OC	MD
H	1.000	**0.864**	-0.362	0.028	0.464	0.035	0.082	0.146
C		1.000	-0.311	-0.045	0.472	-0.120	-0.229	0.428
Df			1.000	-0.271	**-0.760**	0.083	-0.220	0.087
T				1.000	0.006	**0.763**	0.579	-0.307
S					1.000	-0.129	-0.174	0.221
DO						1.000	0.501	-0.183
OC							1.000	**-0.822**
MD								1.000

which are responsible for the establishment of anoxic condi- tions and phenomena like dystrophic crisis, did not overcome (i.e., towards lower values) the usual threshold levels for the benthic macrofauna survival.

Salinity seems to be influenced by freshwater inflows from Papapouli River as well as by saline inflows from the sea. Salinity varied seasonally with the highest values record- ed in winter when the inlet opened while the lowest ones were observed in autumn (inlet closed). During autumn, salinity remained constant in all stations. During winter and spring, average values of salinity ranged from 36.6 psu to 33.2 psu in station ST3 and from 28.1 psu to 19.6 psu in station ST2 while in station ST1 no fluctuation was detected.

The pH differed significantly among seasons with val- ues in spring being much lower than those of the other two seasons. The pattern of the depth-change varied significantly, both spatially and seasonally. Stations ST1 and ST2 had ap- proximately the same depth while in station ST3 the lowest depth was recorded. In ST3, depth ranged from 11 cm to 43 cm from autumn to spring, respectively. Controversially, in station ST2 the greatest depth was recorded in autumn (34 cm) while during the other two seasons it dropped to 29 cm. In station ST1, the highest depth was observed in win- ter while among the other seasons no significant differences were detected.

The concentration of organic carbon in the sediment was the highest in spring samples. Regarding sites, the highest values were observed in station ST2. In particular, ST1 and ST2 presented the same pattern with the highest concentra- tions of organic carbon recorded in autumn (ST1: 2.14%, ST2: 2.80%) and spring (ST1: 2.08%, ST2: 2.81%) while the lowest ones in winter (ST1: 1.16%, ST2: 1.67%). Station ST3 showed a different pattern with the concentration of organic carbon in the sediment being increased from autumn (1.15%) to spring (2.37%). The results of the nonparametric Spearman correlation analysis showed a strong negative correlation (ρ = -0.822, *p* < 0.05) (Table 2) between the mean diameter of the sediment particle size (MD) and organic carbon.

The coefficient of variation in sediment, which gener- ally provides a fair aspect of hydrodynamics, showed poor hydrodynamic conditions in station ST1, very poor in ST2

(with one exception during the winter season), and moderate to high in ST3. Those conditions may represent changes fol- lowing the opening of the inlet.

Several photophilic algae along with some epiphytes were detected in all stations. Among these algae, species from the *Gracilaria* and *Ceramium* genera are included. An exception comprised the station ST3 during autumn sampling where only algae of the genus *Ulva* were present.

Distribution of taxa

The sorting of substrate samples enabled the identifica- tion and density determination of 40,036 individuals belong- ing to 31 different taxa. Amphipods, polychaetes, bivalves, chironomids, and oligochaetes were the dominant taxo- nomic groups. Most of the macrobenthic species recorded in Papapouli Lagoon have a wide spatial distribution and were not characteristic of a single site. All species recorded are among the typical fauna of a Mediterranean lagoon. The species *Corophium orientale, Gammarus crinicornis, Hediste diversicolor, Abra segmentum, Hydrobia acuta, Capitella capitata,* larvae of *Chironomus salinarius*, and Tubificidae sp. were present in all stations and seasons. The species *Myosotella myosotis* and *Donacilla cornea,* characteristic of marine environments, were present only in stations ST1 and ST3, respectively.

The distribution of taxa among the feeding categories along with spatio-temporal differences among samples is given in Table 3.

"Deposit feeders" were the dominant trophic group in all sampling sites and seasons while "suspension feeders" ex- hibited the lowest abundance. An exception was detected in station ST3 during autumn sampling where the "suspension feeders" were the second dominant trophic group. In all sam- pling sites and seasons, the second dominant trophic group was "herbivores" followed by "carnivores". However, in sta- tion ST3 in winter sampling the second dominant group was "carnivores" while "herbivores" were the third. The percent- age contribution of each trophic group to the total community is given in Table 3.

Table 3. Mean abundance (±SE) of the benthic trophic groups (ind/400cm²) and statistical differences according to station and season. P-values as well as Fisher LSD values for each trophic group are given. The % contribution of each trophic group to the total community is also given (*: $p<0.05$, **: $p<0.01$, ***: $p<0.001$, ns: not significant). A, W, S as in Table 1.

Station	Deposit feeders		Suspension feeders		Carnivores		Herbivores	
	abundance	% con.	abundance	% con.	abundance	% con.	abundance	% con.
ST1A	1936.6 (±167.8)	92.45	14.0 (±5.3)	0.67	71.1 (±26.2)	3.5	73.3 (±24.3)	3.38
ST1W	861.4 (±70.8)	73.15	5.8 (±0.9)	0.5	153.8 (±68.8)	13.27	156.3 (±68.8)	13.09
ST1S	900.3 (±280.3)	79.65	5.7 (±4.7)	0.5	108.1 (±52.8)	10.29	116.3 (±50.2)	9.56
ST2A	2141.1 (±413.2)	96.22	4.0 (±1.0)	0.18	24.1 (±22.0)	2.52	56.1 (±18.0)	1.08
ST2W	1152.2 (±66.8)	96.74	1.8 (±0.6)	0.15	16.3 (±13.4)	1.74	20.7 (±13.8)	1.37
ST2S	719.7 (±119.4)	92.08	5.8 (±1.0)	0.75	18.2 (±9.7)	4.85	37.9 (±11.9)	2.33
ST3A	3062.9 (±255.3)	96.65	84.0 (±14.0)	2.65	13.9 (±3.6)	0.26	8.2 (±2.2)	0.44
ST3W	767.9 (±243.4)	75.61	26.5 (±18.1)	2.61	111.4 (±32.9)	10.81	109.8 (±32.7)	10.97
ST3S	289.6 (±25.3)	55.37	12.8 (±2.8)	2.45	107.3 (±61.5)	21.63	113.1 (±59.4)	20.54
Spatial	ns		***		**		*	
Temporal	***		*		ns		ns	
Interaction	**		ns		ns		*	

Samples showed a statistically significant dispersion regarding all four trophic groups (repeated measurements ANOVA results; Table 3). In "deposit feeders", seasonal distribution was detected with the lowest abundance observed in spring and the highest in autumn. The lowest values were detected in station ST3. The combined effect of season and site was also significant ($p < 0.01$). This pattern seems to follow the inflow of seawater when the inlet is open, with station ST3 being influenced first and station ST1 last. Strong negative correlation with salinity was also detected (Table 2).

Regarding "herbivores", the combined effect of season and site was also significant ($p < 0.05$). Spatially, ST1 station showed significantly higher values than the other two stations. Seasonally, differences were only observed between autumn and winter samples. The lowest values for autumn samples were recorded in station ST3 while for winter samples in station ST2. The Spearman correlation coefficient showed a high positive correlation with the trophic group of "carnivores".

In "carnivores" significant differences were detected only spatially. Stations ST1 and ST3 showed the greatest abundances of "carnivores" while the lowest one was recorded in station ST2.

Concerning the "suspension feeders", temporal and spatial differentiation among samples was obvious. More specifically, highest values were observed in autumn while the lowest ones were detected in winter and spring samples. High values of spatial variance among samples were detected in station ST3. Differences in values between ST1 and ST2

Table 4. Cohesion and centrality metrics for marine benthic networks for each season in all the three sampling sites. A, W, S as in Table 1.

Site	Average density	Average distance	Eigenvector centrality %
ST1A	0.179	1.024	93.32
ST1W	0.261	1.438	49.21
ST1S	0.224	1.228	72.35
ST2A	0.183	1.048	94.74
ST2W	0.182	1.110	93.35
ST2S	0.189	1.133	91.23
ST3A	0.165	1.014	98.27
ST3W	0.211	1.182	74.51
ST3S	0.178	1.110	93.61

were relatively low and of no significance. No correlations with other trophic groups or abiotic variables were detected.

Benthic fauna networks

The benthic fauna interaction networks at each sampling station in all three sampling seasons are presented in Figs 2-4 for ST1, ST2, and ST3 stations, respectively. Cohesion metric parameters for each site are presented in Table 4. The average density values of ST1W, ST1S, and ST3W were higher compared with those of the other sampling sites. Similarly, the values of average distance presented an analogous trend, with ST3A showing the lowest values.

All networks in stations ST2 and ST3 (with the exception of ST3W, 74.5%) were highly centralized yielding an eigenvector centrality value ranging from 91 to 98% of the maximum possible centrality (Table 4). ST1W and ST1S networks showed considerably lower values (49 and 72%, respectively), with the exception of ST1A that presented much higher values.

Since centrality is not only a network property but also refers to individual nodes, we present in Table 5 the degree centrality scores of the most central benthic species. According to these values, all the ST2 networks, in all sampling seasons, were highly centralized around one central node-species, the "deposit feeder" *Corophium orientale*. ST3S and ST3A networks were also greatly centralized. However, in each sampling season, the species that presented the highest values of degree centrality differed. In ST3S it was the "herbivore" *Gammarus crinicornis*, in ST3A the deposit feeder *Capitella capitata*, while in ST3W the "deposit feeder" *Corophium orientale*. The ST1A network presented the same pattern with the ST2 network, as *Corophium orientale* also showed the highest values of degree centrality compared with the other species. In ST1S and ST1W the pattern differed as in each case more than one species presented similar degree centrality scores. In all three networks, ST1W, ST1S,

and ST3W, the highest degree centrality scores were shown by two "deposit feeders" and one "herbivore species". The "herbivore" species in all three networks was the species *Gammarus crinicornis*. Species of the genus *Gammarus* have also been recorded for their occasionally carnivorous and detritivorous nature (Kelly et al. 2002). In network ST1W, the "deposit feeders" were represented by the species *Capitella capitata* and *Corophium orientale* while in ST3W they were represented by *Corophium orientale* and larvae of the insect *Chironomus salinarius*.

Discussion

According to Barnes (1994) lagoons are usually divided in the outer and the inner area most affected by sea and land, respectively. In Papapouli Lagoon these two areas, according to the abiotic variables, were differentiated with stations ST1 and ST3 being more affected by the sea while station ST2 being influenced by the inland part of the lagoon. Stations ST1 and ST3 were characterized by sandy sediments but also by increased values of salinity when the sea inlet was open while station ST2 was characterized by organically enriched muddy sediments reflecting higher terrestrial influence. Thus, station ST1 seems to be more marine than terrestrially af-
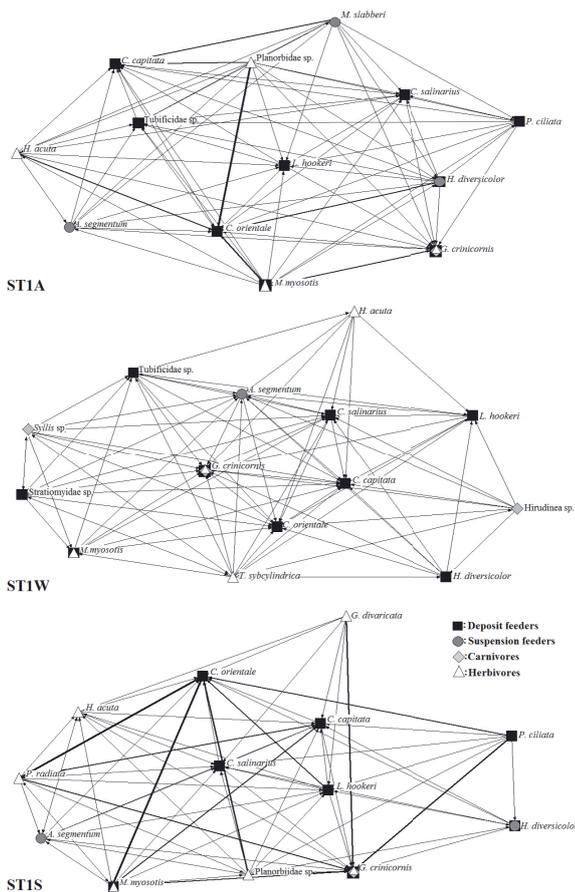

Figure 2. Spatio-temporal benthic fauna networks in station ST1. The multishapes in the species *Gammarus crinicornis, Hediste diversicolor* and *Myosotella myosotis* represent their subsumption in more than one trophic groups.
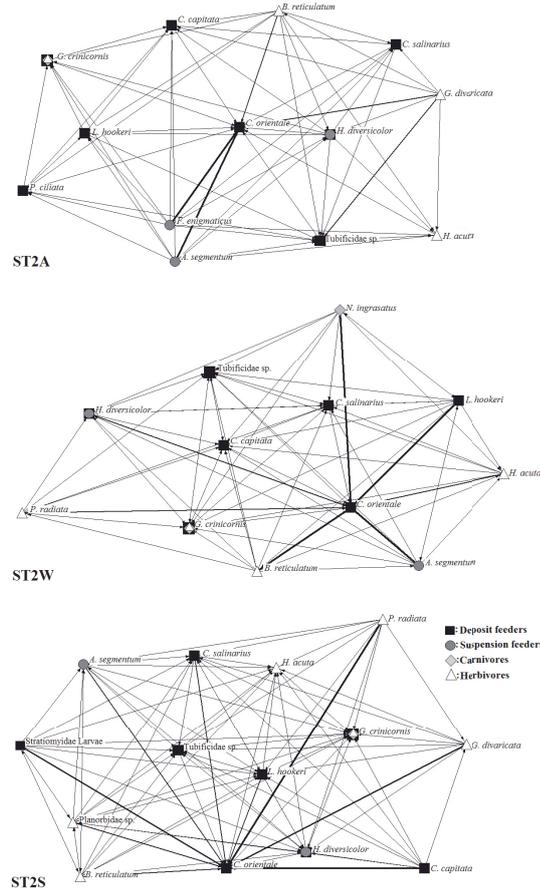
Figure 3. Spatio-temporal benthic fauna networks in station ST2. The multishapes in the species *Gammarus crinicornis* and *Hediste diversicolor* represent their subsumption in more than one trophic groups.
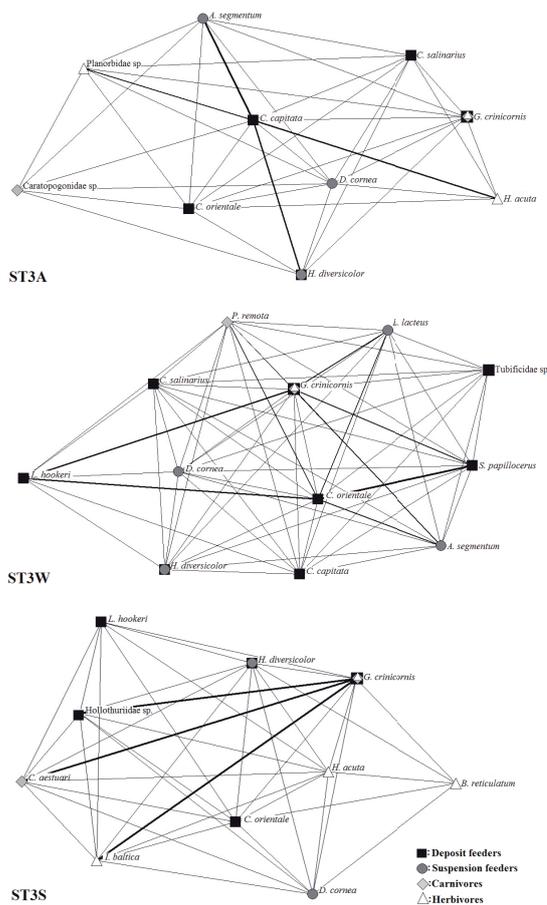
Figure 4. Spatio-temporal benthic fauna networks in station ST3. The multishapes in the species *Gammarus crinicornis* and *Hediste diversicolor* represent their subsumption in more than one trophic groups.

fected although it is farther from the sea inlet than station ST2. Guelorget and Perthuisot (1983) introduced the "confinement" model, which suggests that confinement is not only influenced by the distance from the sea inlet but it also results from the combined effects of all hydrological and morphological factors which control the relationship between each region within a lagoon and the sea. The combined effect of these variables can act as a threshold for the distribution of species (Koutsoubas et al. 2000a).

On the basis of macrofauna composition, the outermost area (station ST3) showed a different faunal composition compared with the innermost part, corresponding to the model of "confinement" proposed by Guelorget and Perthuisot (1992).

In station ST3 benthic macrofauna ranged from zone III to zone IV characterized by the occurrence of both brackish water (e.g., *C. orientale, A. segmentum, H. acuta*) and marine species (e.g. *S. papillocercus, D. cornea*). Cognetti and Maltagliati (2000) suggested that euryhaline marine species whose populations have developed a tolerance to unpredictable changes in habitat as well as stenohaline marine species, which have developed euryhaline populations, usually settle in brackish habitats which communicate directly with the

sea. In the other two stations, the benthic macrofauna ranged from zone IV to V with the presence of typical brackish species such as *C. orientale* and Tubificidae sp. Freshwater species such as the gastropods Planorbiidae were also present. Seasonal shifts from one zone to another were observed according to the periodic opening of the inlet.

Overall, 31 species were collected during the three sampling periods. In all stations, 9 out of the 31 species were always present. These species are considered as common brackish-water species, which characterize transitional habitats such as lagoons. Cognetti and Maltagliati (2000) reported that typical brackish communities are composed of the same euryhaline species, especially when they are in the same biogeographical region. Their occurrence is affected by their tolerance to the variation of certain abiotic variables such as temperature, availability of oxygen, and the substrate. Seasonal fluctuations in their abundance could be attributed to their life cycle and other factors such as selective predation and interspecific competition (Van Dolah 1978, Nicolaidou and Karakiri 1989, Sarda et al. 1996, Wright et al. 1996, Bologna 2007). Similar results have been reported for other Mediterranean lagoons (Nicolaidou et al. 1985, 2006, Barnes 1994, Reizopoulou et al. 1996, Cognetti and Maltagliati 2000, Koutsoubas et al. 2000a, Mistri et al. 2001b, Reizopoulou and Nicolaidou 2004).

Network analysis showed that the benthic fauna networks of the three stations in the three sampling seasons differed regarding the number of nodes-species but presented similarities regarding the number of interactions as well as centrality.

The smallest and least complex networks were detected in station ST3. Particularly, ST3A and ST3S networks had the lowest number of nodes-species (10) and all cohesion estimated metrics were also found to be among the lowest (average density, average distance). All ST2 and the ST1A networks presented an intermediate profile as they all had higher number of nodes (12-14) while all other network metrics regarding centrality and cohesion were very similar to those of the ST3A and ST3S networks, if not a little higher. On the other hand, ST1W, ST1S, and ST3W were the most cohesive, strong and complicated networks. Moreover, their number of nodes-species was high (12-14) as well. This pattern may be influenced by the neighboring of station ST3 with the sea and its direct connection during winter and spring where new species enter the lagoon (Koutsoubas et al. 2000a, Mogias and Kevrekidis 2005).

Regarding cohesion metrics, reduced average network density and distance reflect a shift towards fewer and weaker direct relationships instead of many indirect ones, which could imply a disruption of several interactions among benthic fauna species. This is an indication of disorganized interactions and a further indication of increased network fragility (Stamou et al. 2011). On the other hand, increased average tie density and distance indicate an increase in indirect ties between the nodes of the network.

ST3A, ST3S, all ST2, and ST1A networks presented increased eigenvector score of centralization (91-98%). Increased centrality shows the importance of few focal nodes

Table 5. Degree centrality scores of the five central benthic species within each interaction network.

ST1					
AUTUMN		**WINTER**		**SPRING**	
Species	**Degree of centrality**	**Species**	**Degree of centrality**	**Species**	**Degree of centrality**
Corophium orientale	20.218	*Capitella capitata*	25.862	*Corophium orientale*	26.996
Capitella capitata	5.200	*Gammarus crinicornis*	19.942	*Gammarus crinicornis*	21.040
Gammarus crinicornis	2.686	*Corophium orientale*	12.824	*Capitella capitata*	5.184
Tubificidae sp.	3.028	*Chironomus salinarius*	2.158	*Chironomus salinarius*	1.856
Lekanesphaera hookeri	0.533	*Abra segmentum*	0.231	*Lekanesphaera hookeri*	1.671
ST2					
AUTUMN		**WINTER**		**SPRING**	
Species	**Degree of centrality**	**Species**	**Degree of centrality**	**Species**	**Degree of centrality**
Corophium orientale	24.832	*Corophium orientale*	41.630	*Corophium orientale*	36.836
Tubificidae sp.	4.817	*Capitella capitata*	4.930	*Gammarus crinicornis*	2.927
Capitella capitata	2.950	*Gammarus crinicornis*	1.370	*Hydrobia acuta*	0.852
Gammarus crinicornis	1.837	*Chironomus salinarius* (larvae)	1.833	Tubificidae sp.	0.690
Lekanesphaera hookeri	0.465	Tubificidae sp.	1.809	*Hediste diversicolor*	0.479
ST3					
AUTUMN		**WINTER**		**SPRING**	
Species	**Degree of centrality**	**Species**	**Degree of centrality**	**Species**	**Degree of centrality**
Capitella capitata	30.237	*Corophium orientale*	28.202	*Gammarus crinicornis*	36.429
Corophium orientale	2.836	*Gammarus crinicornis*	14.208	*Corophium orientale*	7.430
Donacilla cornea	1.017	*Chironomus salinarius* (larvae)	4.119	*Hediste diversicolor*	1.103
Gammarus crinicornis	0.194	*Donacilla cornea*	1.501	*Lekanesphaera hookeri*	0.315
Chironomus salinarius (larvae)	0.129	*Capitella capitata*	0.129	*Hydrobia acuta*	0.146

as significant elements for the stability of the network (Wey et al. 2008), and their elimination may break up the network into smaller subgroups (Lusseau and Newman 2004, Stamou et al. 2011). These focal nodes, presenting high degree centrality values with increased importance as intermediaries, are identified as bottlenecks (Lusseau et al. 2006, Boutsis et al. 2011) and their existence is decisive for the whole network stability and connectivity and, eventually, its robustness (Wey et al. 2008). Increased importance of few nodes makes networks more fragile, due to the risk of fragmentation if the focal nodes are damaged.

In Mediterranean lagoons, spatio-temporal variability in benthic macrofauna patterns is also known to be affected by landscape patchiness. Opportunistic species as well as habitat-selective species are responsible for most part of the macrobenthic patchiness. Each microhabitat allows some specific taxa to maintain a significant population size, which is a prerequisite for ensuring a long-term survival of these species in the lagoon (Ludovisi et al. 2013). However, in our case we tried to reduce the spatial heterogeneity using samples of different habitats within the same station.

Generally, in all networks with the exception of ST3S network, all the central species belonged to the "deposit feeder" group. All ST2 and the ST1A networks were highly centralized around one central node, the "deposit feeder" *C. orientale*. This could be attributed mainly to the fine sedi-

ment as well as to its high concentration of organic carbon. According to Gray (1981) the concentration of organic carbon in sediment provides a good estimate of the availability of food. Both the above factors are of crucial importance for the establishment of "deposit feeder" species (Cancela da Fonseca et al. 2001). Moreover, given that *C. orientale* lives in tunnels near the surface of the sediment, it is obvious that the establishment of these species can be favored in fine sediments.

On the other hand, the increased values of centrality in the ST3A and ST3S networks were due to the high centralization around the "deposit feeder" *C. capitata* and the species *G. crinicornis,* respectively. *Capitella capitata* is an "opportunistic species" facilitating the quick exploitation of the increased organic load (Pearson and Rosenberg 1978, Borja et al. 2000, Malea et al. 2004). "Opportunistic" species follow an r-strategy life span and, thus, have the ability to colonize temporary or disturbed habitats where competition is weak (Amanieu et al. 1979). Species of the genus *Gammarus* have been recorded mainly as "herbivore" species, which, by grazing on macrophytes, contribute to macrophyte fragmentation and subsequent decomposition (Menéndez and Comín 1990). These species have also been recorded as "deposit feeders" but also as "predators" (Mackneil et al. 1997). *Gammarus crinicornis* was also a very important component of ST1S network. The increased importance of this species as a network component, particularly in spring networks, could be associ-

ated with its high abundance during that period of the year as well as with its "herbivore" nature and, thus, with phyto-benthos biomass (Kevrekidis 1988). Photophilic algae along with epiphytes that are settled among their thalli are known to comprise a palatable resource of food for Gammaridae species which actively feed on their host plant (Mancinelli and Rossi 2001, Byers et al. 2012).

Finally, in ST1W, ST1S, and ST3W the centrality values were respectively lower (49-74%), more benthic fauna species seem to play important roles as key players, and networks consist of species from more than one different trophic groups (deposit feeders, herbivores). Such large and highly connected networks are considered more robust against disturbances (Allesina et al. 2009). Although "deposit feeders" and "herbivores" seem to have an important role in shaping species interactions within the benthic community, "carnivores" and "suspension feeders" were restricted only to the radial part of the networks due to the fact that their abundance did not increase enough in order to occupy a central position. However, "suspension feeders" presented their highest number of individuals in the outermost part of the lagoon where hydrodynamics ranged from moderate to high. It has previously been shown that the dominance of this trophic group is determined by hydrodynamics (Sanz 1986, Pearson and Rosenberg 1987, Bódis et al. 2011) and the sediment grain size (Sanders 1958, Young and Rhoads 1971, Jaramillo 1984, Probert 1984). Concerning "carnivores", they reached their maximal proportion at the outer part of Papapouli Lagoon (ST3) as well as in station ST1, especially in winter and spring where the sea-inlet was open. Their high abundance in these stations could be attributed to the relatively high abundance of "herbivores" as a positive correlation between them has been detected. According to Pearson and Rosenberg (1987), many carnivores are related more to their prey distribution than to other abiotic variables.

According to redundancy theory, the gain or loss of a species may have large effects on community composition. However, when these changes concern species which overlap in function to a sufficient degree that the removal of one species will be compensated by the others, they may provoke negligible overall consequences on ecosystem processes (Walker 1992, Lawton and Brown 1993, Mistri et al. 2001a). Thus, the level of redundancy may be used as a measure of assemblage resilience (Chapin et al. 1995). Our data showed that when stress from environmental changes is reduced the community composition does not change much, with the species *Corophium orientale* being always the center of the network, regardless of the season (station ST2). When the environmental changes are moderate, the network is more cohesive and stable with more than one species occupying the central nodes of the network (station ST1). However, when the environmental changes are intensive species overlap in the central nodes of the networks seasonally (station ST3). These overlaps concern species which are functionally equivalent to a sufficient degree because all the changes occur among exclusively or occasionally "deposit feeder" species. Since redundancy reflects the resistance of the community to the change of its functional structure (Lawton and Brown 1993),

we can assume that the benthic communities in stations (e.g., ST3) that are under high stress due to the intensive change of the abiotic variables are quite resistant to disturbance.

Although our results represent a short-term dynamics of these systems, they show that the knowledge generated by network analysis should provide a valuable tool in order to assess potential environmental changes and inform management decisions. However, further experimental studies and modeling using other multispecies approaches such as those based on artificial neural networks or keystone species complex (Muttil and Chau 2007, Jordán et al. 2008, Ortiz et al. 2013) should be performed. Moreover, in order to get a holistic idea of all the interactions among the species, a more detailed sampling protocol is needed to gain information also on phytoplankton, zooplankton, pelagic fauna and vegetation. This could be very useful because it could facilitate the determination of any compartments (Krause et al. 2003) allowing more punctual predictions to be made for the stability of the studied networks.

Conclusions

Our results represent a single case study from Papapouli Lagoon and show that the degree of communication with the sea in the studied lagoon affects most of the environmental variables as well as the benthic community structure. In intermittently closed lagoons such as Papapouli Lagoon a more homogenous pattern is evident with the exception of the outer part of the lagoon. However, in order to generalize our results in a larger spatial scale more work including data from additional lagoons with similar geomorphological characteristics is needed.

The application, for the first time in a lagoon ecosystem, of network analysis has provided novel information on the quality of interactions among species. The obtained networks showed that when communication with the sea is interrupted all the benthic fauna patterns tend to be destabilized and centralized around one species, which in most cases was a "deposit feeder". When the inlet opens and the communication with the sea is restored, the benthic composition seems to be more cohesive, especially in the most distant regions.

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