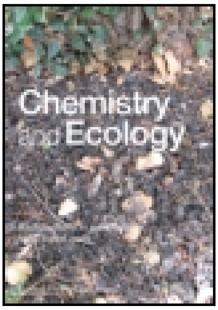

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Zooplankton responses to hydrological and trophic variability in a Mediterranean coastal ecosystem (Lesina Lagoon, South Adriatic Sea)

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Spatial and temporal variability in zooplankton was studied at eight stations located in the Lesina Lagoon (South Adriatic Sea) Salinity, temperature, dissolved oxygen and chlorophyll *a* (in the lagoon) at these stations were also assessed. The zooplankton community was characterised by clear seasonal oscillations and mostly represented by copepods and their larvae. The dominant copepod species were *Calanipeda aquaedulcis* and *Acartia tonsa*, which exhibited spatial–temporal segregation in the lagoon. *C. aquaedulcis* copepodites seemed to be better adapted to oligotrophic and oligohaline conditions compared with the *A. tonsa* population. The invasive species *A. tonsa* has completely replaced the formerly abundant *Acartia margalefi*. A positive correlation was found between abundances, total species numbers and trophic state. An increasing abundance trend was shown from the lagoon towards the sea. The highest diversity indices were recorded at the two channel inlets, during high tide due to the absence of a clear dominance of one or more coastal species and the co-occurrence of species of lagoon and marine origin.

Keywords: Lesina Lagoon; Mediterranean Sea; zooplankton assemblage; spatial–temporal distribution; trophic state; alien species

1. Introduction

Brackish coastal lagoons appear to be original entities, belonging to the paralic domain, and their features are strongly dependent on their interactions related to their location between land and sea. They are subjected to internal and irregular variations, which modulate their biocoenosis. The scientific community has studied these ecosystems and their limiting forcing factors for over half a century, describing their high spatial, temporal and biological heterogeneity due to their transitional properties [1–3]. In particular, Carrada et al. [4] emphasised the need for further investigation on space and time distribution patterns of biocenosis, on the interaction network connecting zooplankton to other trophic levels, and on the exchange of plankton between the lagoon and the adjacent sea. Furthermore, coastal lagoons are highly susceptible to eutrophication events that,

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in recent years, have caused a deterioration in water quality, with deleterious consequences for biological communities [5] and danger for public health [6]. Anthropogenic impact might often be the main cause of eutrophication events in these ecosystems in relation to human activities such as agriculture [7,8], urbanisation, industrialisation [9–11] and aquaculture [12]. Therefore, and also as a consequence of ever-increasing exploitation and alterations in natural resources that cause and enhance the variability in these transitional environments (e.g. fishing and aquaculture), the EU Water Framework Directive [13] established guidelines for water resource management with well-defined objectives for the protection of groundwater, and inland, estuarine and coastal waters. This framework requires Member States to assess the Ecological Quality Status of transitional and coastal waters by 2006 and obtain good ecological status by 2015.

In order to implement the legislation on these transitional environments and comply with the EU Water Framework Directive, studies on zooplankton structure and distribution patterns were carried out, within the framework of the 'MIDAN Project' with the main aim of the 'physical–chemical and biological characterisation of the Lesina Lagoon to identify a nursery area for some commercial fish species'. To date, studies concerning the zooplankton community of this lagoon are few and fragmentary [14,15]. The Lesina Lagoon is a nontidal lentic lagoon [16,17] representing a peculiar ecosystem subjected to continual hydrodynamic and environmental changes related to the opening, closing or partial obstruction of its two artificial channels, Acquarotta and Schiapparo, affecting water exchange with the neighbouring Adriatic Sea. Guerloget and Perthuisot [2] argue that its nearness to the point of contact with the adjacent sea is one of the main factors responsible for within-lagoon faunistic changes. This is followed by the degree of confinement of the lagoon system and, consequently, the degree of heterogeneity in species composition. In addition, its hydrological balance is greatly dependent on meteorological conditions [18]. In recent years, the Lesina Lagoon has experienced a progressive eutrophication, with occasional dystrophic crises [19]. In terms of trophic state and water quality, recent studies have highlighted space–time variability in this ecosystem which passes from a good state, in the areas near the channels, to a bad state in those closed to freshwater inputs, especially during the winter months [17]. Therefore, environmental changes reflect changes in the zooplankton community. This lagoon is the site of intensive aquaculture which could favour the introduction of alloctonous species, such as *Acartia tonsa*, reported for the first time in the Lesina Lagoon by Sei and Ferrari [15], with the consequent disappearance of the formerly abundant *Acartia margalefi*.

The aims of this study were: (1) to show space and time zooplankton variability in relation to environmental conditions, in order to provide detailed information about the actual ecological status of the lagoon; (2) to relate zooplankton distribution to the trophic state defined for this nontidal lentic ecosystem; and (3) to test the hypothesis of a confinement of this ecosystem comparing zooplankton communities in the three environments (lagoon, the two channels, in different tidal conditions, and the adjacent coastal marine waters).

2. Materials and methods

2.1. *Study area*

Lesina Lagoon (41.88°N and 15.45°E) is located in the southern Adriatic Sea on Cape Gargano (Figure 1). It has an area of 5100 ha, extending east–west for ∼22 km and with a width of 3 km within the Gargano National Park. In 1995, the lagoon was declared a Site of Community Importance (IT9110015). The lagoon is separated from the Adriatic Sea by a 1–2-km wide and 18-km long beach ridge and is connected to the sea through two tidal channels (Acquarotta to the west, 2 km long, 6–10 m wide, 0.8–2 m deep and Schiapparo to the east, 1 km long, 25 m wide, 1.5–3 m deep). The two channels are protected on the seaward side by gabions, and their beds are lined

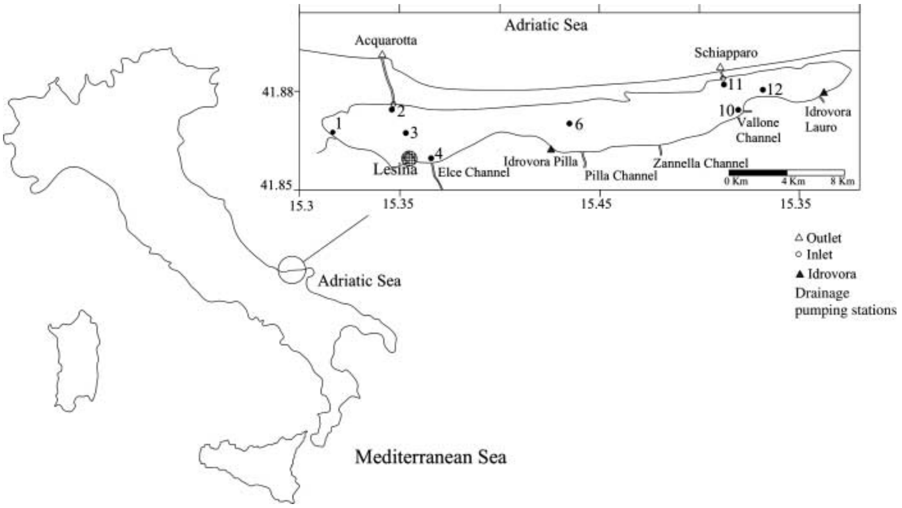

Figure 1. Study area and sampling stations.

with concrete, as are the banks at the seaward end. Since 1998–1999, sluices and 10 mm grills have been located perpendicular to each channel at the lagoon end, in order to prevent adult fish from escaping, but reducing inward and outward water flux. Lesina Lagoon receives a moderate freshwater input from minor seasonal streams, mostly located in the south-eastern area. About 80% of the annual freshwater budget is discharged into the eastern part of the lagoon (Francavilla pers. comm.). Therefore, the western part generally exhibits higher salinity values than the eastern area. The large size of the lagoon, in relation to the low depth, limits the beneficial effects of incoming sea water [20,21]. The low tidal range (0.156 m) of the southern Adriatic Sea, combined with the moderate freshwater inputs and the low efficiency of water exchange with the sea, suggests that the hydrological balance in the Lesina Lagoon is strongly affected by atmospheric conditions (wind and rain). Over the last 10 years, rainfall (400–700 mm a year) has tended to be concentrated in autumn–winter, even though strong rainfall events have been recorded in spring. The residence time of the water is estimated to be ~70–100 days [22]. The main sources of anthropogenic pressure are partially treated wastewaters from three municipalities of 30,000 inhabitants discharged into the lagoon by Elce Channel (8000 inhabitants), the river Lauro and Idrovora Lauro (drainage pumping station); intensive vegetable farming and wheat extend on the western side of the lagoon. In addition, three intensive aquaculture plants are located along the coast and their wastewaters are discharged into the lagoon. On the western shore, a cattle farm of ~1500 head is situated near Acquarotta Channel.

Lesina Lagoon exhibits strong seasonal variations of temperature (ranging from 7–8 °C in winter to 26-28 °C in summer) and salinity (between 11 and 34, in the same season) [20,21].

2.2. *Sampling methods*

In the Lesina Lagoon, zooplankton samples were collected every month from June 2006 to May 2007 (with a gap in August 2006), during the morning (between 8:00 and 12:00), in eight sampling stations: 1, 3, 6 and 12 located along the central longitudinal transect, 4 and 10 on the southern shore, and 2 and 11 near the western and eastern channels, respectively (Figure 1). Because most stations were located in shallow waters, a plankton net was towed horizontally between the surface and the bottom, avoiding contact with the sediment, for 5 min at a speed of $\sim 1\ \mathrm{m \cdot s^{-1}}$, all around each station point.

At the two channels, zooplankton samplings were performed monthly from October 2006 to June 2007. Every month, samples were collected twice a day (8:00–10:00 during the daytime and 17:30–20:00 at sunset), a maximum of 12 h before/after lagoon samplings, from two stations located at the inlets of the two channels towards the lagoon, named 'channel' stations. In September 2006, sampling was carried out once a day. The tidal current direction was registered using a visual method according to hydrometric levels: northward (out coming tide from the lagoon = low tide) and southward direction (incoming tide from the sea= high tide).

At the outlets of the two channels ('Sea' stations), zooplankton samplings were taken monthly from June 2006 to May 2007 with gaps in August, December and March. A net was towed horizontally between the surface and 1–2 m depth.

All samples were collected by towing a plankton net with a mouth area of 0.25 $\mathrm{m^2}$ and mesh size 200 μm, equipped with a flowmeter (Hydrobios), suspended just below the inner mouth perimeter of the net. Samples were preserved in formaldehyde (4% final concentration). Environmental parameters (salinity, dissolved oxygen and temperature) were measured using a multiparameter probe (YSI 6920, with temperature/conductivity, dissolved oxygen (DO), pH and shallow depth powered by a YSI 650 MDS) simultaneously to all zooplankton samplings at every station. In the lagoon, chlorophyll *a* (Chl*a*) was also measured by collecting water samples. Chlorophyll *a* processing methods are described in Roselli et al. [17].

2.2.1. *Laboratory methods*

Zooplankton organisms were counted using a stereoscopic microscope, for subsamples ranging from 1/100 to 1/25 of the entire sample, depending on the abundance of the sample. Whole samples were analysed for rare species. Adult copepods were identified to the species level, where possible, and copepodid stages to genus level. Specimens belonging to other zooplankton groups were classified at higher taxonomic levels, with the exception of cladocerans, identified at the genus level. Amphipoda, Mysidacea and Ostracoda were not taken into account in counting total abundance and performing statistical analysis. Rotifera were not sampled due to the large mesh size of the net used. Abundance values were expressed as individuals per cubic meter ($\mathrm{ind \cdot m^{-3}}$).

2.3. ***Data analysis***

2.3.1. *Multivariate analysis*

Principal component analysis (PCA) was performed on Euclidean distances of normalised environmental parameters (temperature, salinity, Chl*a*, DO) measured in the Lesina Lagoon, to test for time and space patterns of these factors. Carlson's [23] Trophic State Index TSI (Chl*a*) was used to evaluate trophic state in the lagoon, according to following equation [24]:

$$\mathrm{TSI(CHL)} = 30.6 + \ln(\mathrm{ChL}).$$

The Simprof (similarity profile) routine was run to test for evidence of structure in an a priori unstructured set of samples from the three environments investigated. For this aim, abundance data from each ecosystem were previously averaged by month to delete the time factor. Channel stations were averaged taking into account the tide in order to evaluate differences related to this factor. Data were log transformed and cluster analysis with Simprof at 0.05 significance level was performed on a Bray–Curtis similarity matrix.

To explore spatial and temporal distribution patterns of zooplankton assemblages in the lagoon, multidimensional scaling (MDS) analysis was performed on a Bray–Curtis similarity matrix obtained from square-root transformed abundance data to allow the less-abundant species to exert some influence on the calculation of similarities. An ANOSIM two way-test was performed to estimate the differences between stations. The same one-way test was used to evaluate differences between station groups relating them to their position along the north–south and east–west axes. All these analyses are Primer β-6 software options [25]. Canonical correspondence analysis, an option in a Past software package [26], was performed on abundance data, transformed by sample normalised length and log-transformed environmental parameters, to relate zooplankton taxa and copepod species to hydrological and trophic conditions in the lagoon. In the two channels, similarities in copepod assemblages were estimated by cluster analysis performed on a Bray–Curtis similarity matrix obtained from square root transformed data with tide as a factor. Differences between tide and season groups were evaluated with the ANOSIM test. Simper analysis was used to identify those copepod species mostly contributing to similarities between sample groups.

2.3.2. *Univariate analysis*

Some aspects of biodiversity were evaluated by using species richness (S), as total number of crustacean species, and Shannon index (H') [27] in all the three environments.

Spatial and temporal patterns of these indices were calculated in each of the three environments. Zooplankton assemblage spatial and temporal distribution patterns were related to environmental factors (DO, Chl$a$, temperature and salinity) using Spearman's correlation coefficients measured for all zooplankton taxa and copepod species.

3. Results

Main mesozooplankton taxa and species found in the three investigated environments with their overall mean abundances are listed in Table 1. Three clusters identifying different biotic structures were distinguished by Simprof (at 0.05 significance level) in cluster analysis (Figure S1 – available online only): a proper lagoon ecosystem, grouping all the stations located inside the Lesina Lagoon and channel stations in low tide, at 48% of similarity; and at higher similarity level. Another group was constituted by channel stations in high tide and the last by 'Sea' stations. The lagoon ecosystem had the lowest Shannon index and species richness values; highest values were shown by channel group of samples in high tide (Figure S1), in the smaller box on the right side). In the lagoon, salinity oscillated between an absolute maximum of 23.9 at station 2 and minimum of 6.0 at station 12 in May and January, respectively. The mean annual trend, shown in Table 1, showed higher mean values in the western stations compared with the eastern stations (Table 1). Temperature values showed wide seasonal variations due to the shallow character of the study area, but were generally homogeneous throughout the lagoon (Table 2). Chl$a$ exhibited higher values in summer at station 1 (Table 2). On average, DO (Table 2) ranged from a maximum in December to a minimum in May. Spatial variation (Table 2) for this parameter did not show great differences, but peaks were measured at stations 4 and 11.

In the ordination plot of the environmental data set (Figure S2 – available online only), PCA showed a clear separation of cooler (autumn–winter) and warmer months (late spring–summer). PC1 and PC2 axes accounted for the greatest percent (32.7 and 30.5%, respectively) of total variance. Chl$a$ and temperature were positively correlated to the first axis (the highest eigenvectors: 0.71 and 0.70, respectively), and salinity and DO showed higher eigenvectors (-0.70 and 0.70, respectively) on PC2.

Table 1. Main mesozooplankton taxa, copepod and cladoceran species identified in lagoon, channels and sea with their mean abundances (ind·m^{-3}) in each environment.

	Abundance		
Zooplankton taxa	Lagoon	Channels	Sea
Appendicularia	–	3.2 (± 11.3)	228.0 (± 738.7)
Cirripedia larvae	8.8 (± 52.3)	68.8 (± 330.5)	16.8 (± 35.8)
Chaetognatha	–	9.3 (± 11.3)	64.9 (± 185.9)
Copepoda larvae	13.0 (± 80.1)	0.5 (± 9.1)	7.4 (± 12.4)
Decapoda larvae	0.0 (± 0.1)	4.5 (± 14.0)	4.6 (± 9.1)
Echinodermata larvae	–	0.1 (± 0.6)	5.0 (± 11.3)
Foraminifera	–	–	4.9 (± 12.9)
Hydromedusae	0.6 (± 2.2)	2.1 (± 10.7)	13.0 (± 26.9)
Mollusca Bivalvia larvae	0.5 (± 2.0)	19.1 (± 62.1)	453.7 (± 1188.1)
Mollusca Gasteropoda larvae	0.2 (± 0.4)	0.9 (± 2.0)	162.3 (± 579.6)
Mysidacea larvae	0.0 (± 0.1)	–	–
Polychaeta	0.1 (± 0.3)	0.2 (± 0.7)	4.9 (± 20.6)
Polychaeta larvae	0.4 (± 1.0)	146.1 (± 198.2)	388.6 (± 768.4)
Siphonophora	–	–	61.4 (± 246.8)
Teleostea larvae	0.1 (± 0.2)	0.3 (± 0.7)	0.2 (± 0.8)
Cladocera			
Daphnia sp.	1.2 (± 10.2)	–	–
Penilia avirostris	0.0 (± 0.1)	0.4 (± 1.6)	104.2 (± 226.5)
Podon intermedius	–	0.1 (± 0.4)	0.7 (± 2.9)
Evadne spinifera	0.0 (± 0.0)	0.4 (± 1.9)	21.3 (± 80.5)
Evadne tergestina	–	0.0 (± 0.1)	1.6 (± 4.3)
Podon polyphemoides	–	–	1.1 (± 4.2)
Copepoda			
Poecilostomatoida			
Corycaeus brehmi	–	1.1 (± 5.1)	7.4 (± 21.1)
Corycaeus giesbrechti	–	0.3 (± 0.1)	2.6 (± 10.3)
Corycaeus latus	–	–	5.0 (± 20.6)
Coryna granulosa	0.0 (± 0.2)	–	0.1 (± 0.2)
Farranula rostrata	–	0.1 (± 0.6)	0.1 (± 0.5)
Oncaea media	–	0.8 (± 4.8)	2.5 (± 10.1)
Oncaea minuta	–	0.5 (± 2.5)	12.7 (± 51.4)
Cyclopoida			
Cyclopoida spp.	0.3 (± 0.9)	0.2 (± 0.6)	–
Oithona similis	–	3.7 (± 14.1)	6.3 (± 12.8)
Oithona nana	–	1.3 (± 3.5)	12.4 (± 32.6)
Oithona plumifera	–	1.3 (± 5.5)	0.5 (± 0.1)
Oithona brevicornis	–	2.1 (± 10.1)	2.8 (± 5.1)
Harpacticoida			
Harpacticoida spp.	–	10.0 (± 34.8)	4.7 (± 10.6)
Clytemnestra scutellata	–	0.2 (± 0.1)	0.5
Euterpina acutifrons	0.0 (± 0.1)	5.7 (± 20.8)	37.1 (± 107.5)
Monstrilloida spp.	–	0.1 (± 0.3)	1.2 (± 3.9)
Calanoida			
Acartia clausi	0.0 (± 0.1)	5.2 (± 13.5)	176.8 (± 231.9)
Acartia grani	–	0.7 (± 3.5)	4.5 (± 17.7)
Acartia negligens	–	–	0.1 (± 0.6)
Acartia tonsa	10.6 (± 6.8)	0.5 (± 1.6)	16.5 (± 37.5)
Calanipeda aquaedulcis	342.9 (± 1825.7)	55.7 (± 201.7)	0.3 (± 0.8)
Calocalanus styliremis	0.0 (± 0.0)	0.0 (± 0.0)	0.5 (± 0.3)
Centropages typicus	0.0 (± 0.2)	0.2 (± 0.8)	0.5 (± 0.6)
Centropages ponticus	0.0 (± 0.0)	12.2 (± 54.3)	25.6 (± 37.0)
Clausocalanus furcatus	–	0.5 (± 2.5)	1.0 (± 4.2)
Mecynocera clausi	–	–	0.0 (± 0.0)
Nannocalanus minor	–	0.0 (± 0.0)	1.0 (± 4.0)
Paracalanus parvus	0.0 (± 0.0)	7.2 (± 25.8)	46.0 (± 94.2)
Temora stylifera	–	0.6 (± 2.5)	8.0 (± 26.0)

Note: Standard deviations are given in parentheses.

Table 2. Temporal and spatial trends of environmental parameter mean values in the Lesina Lagoon.

	Salinity		Temperature (°C)		Chl*a* (μg·L^{-1})		Dissolved oxygen (%)	
	Mean	± SD	Mean	± SD	Mean	± SD	Mean	± SD
Months								
Jun	–	–	25.5	1.1	9.0	14.4	125.6	12.22
Jul	12.6	1.7	27.1	0.9	7.6	4.6	90.0	19.19
Aug	–	–	–	–	–	–	–	–
Sep	14.0	2.2	22.4	0.8	2.6	1.4	100.2	11.28
Oct	13.7	1.5	17.4	0.8	4.0	2.0	110.2	8.20
Nov	13.3	2.5	19.0	0.5	2.7	1.1	111.3	17.73
Dec	12.1	2.9	10.2	0.4	1.9	0.6	130.9	21.06
Jan	11.0	3.0	9.5	1.8	2.6	1.9	69.9	12.73
Feb	11.1	3.5	13.0	0.9	2.5	2.4	104.8	7.89
Mar	14.9	2.3	9.6	0.5	3.6	1.4	95.6	9.27
Apr	11.9	3.2	18.1	0.9	1.8	1.8	100.5	9.74
May	16.8	3.5	24.5	0.7	3.4	1.2	65.6	16.74
Stations								
L01	13.86	1.60	18.04	7.30	9.9	15.6	97.16	20.45
L02	16.07	3.63	17.57	7.10	4.1	3.1	99.39	18.37
L03	14.55	2.16	17.74	7.05	3.8	2.3	99.85	18.87
L04	12.53	2.13	17.61	6.20	4.6	4.0	108.45	32.18
L06	11.55	1.48	17.49	6.20	3.2	1.4	92.64	28.11
L10	10.83	3.69	18.43	5.92	2.9	1.7	97.09	24.26
L11	12.40	2.97	17.76	6.32	3.6	2.4	107.84	23.03
L12	10.13	2.93	18.22	6.67	2.9	1.4	100.83	22.09

In the lagoon, the zooplankton assemblage was constituted by 14 taxa with average abundances that were relatively low. The seasonal trend (Figure 2a) was characterised by wide oscillations. The highest peak in abundances was recorded in February, but zooplankton densities were relatively low thoughout the year. An abrupt decline in abundance was observed in early winter, reaching lowest values in December. Copepoda reached highest densities in February, contributing to the greatest percentage of zooplankton (Figure 2b). Relatively important abundances of Copepoda larvae (76.1 ind·m^{-3}) were recorded in March. This month was characterised by the presence of a higher number of zooplankton taxa, such as freshwater Cladocera, belonging to the genus *Daphnia*, and Cirripedia larvae. Among the copepod populations, two calanoid species permanently inhabited the lagoon: *Acartia tonsa* and *Calanipeda aquaedulcis*. The former was less abundant than the latter, reaching higher mean abundances in June and September with a population core of 34.9 ind·m^{-3} in June at station 3. It exhibited an oscillating abundance trend during all the year (Figure S3 – available online only). In winter, *C. aquaedulcis* was the overwhelming species, showing a maximum in February (Figure S3), and a population core of 10,540 ind·m^{-3}, at station 4. Other calanoid species were occasionally present in the lagoon such as *Calocalanus styliremis*, in December, and *Centropages* copepodites, in May, with very low mean abundances.

Regarding zooplankton spatial distribution (Figure 3a), the highest mean abundances occurred at station 4, whereas the lowest were at stations 1 and 10. The highest abundance of freshwater Cladocera was recorded at station 12, with the lowest salinity (Table 1). Copepoda larvae were the dominant group at station 6, representing the highest percentage of zooplankton in this station (Figure 3b).

MDS analysis (Figure 4), performed on mesozooplankton abundance data at each station, resulted in a great similarity among all samples, but at 30% similarity three groups were separated: the first, grouping autumn–winter months; the second and the third, spring and summer months, respectively. An ANOSIM test revealed greater significant differences between season groups (Global R: 0.27, $p = 0.001$; Table 3) than spatial ones (Global R: 0.13, $p = 0.01$; Table 3) in the

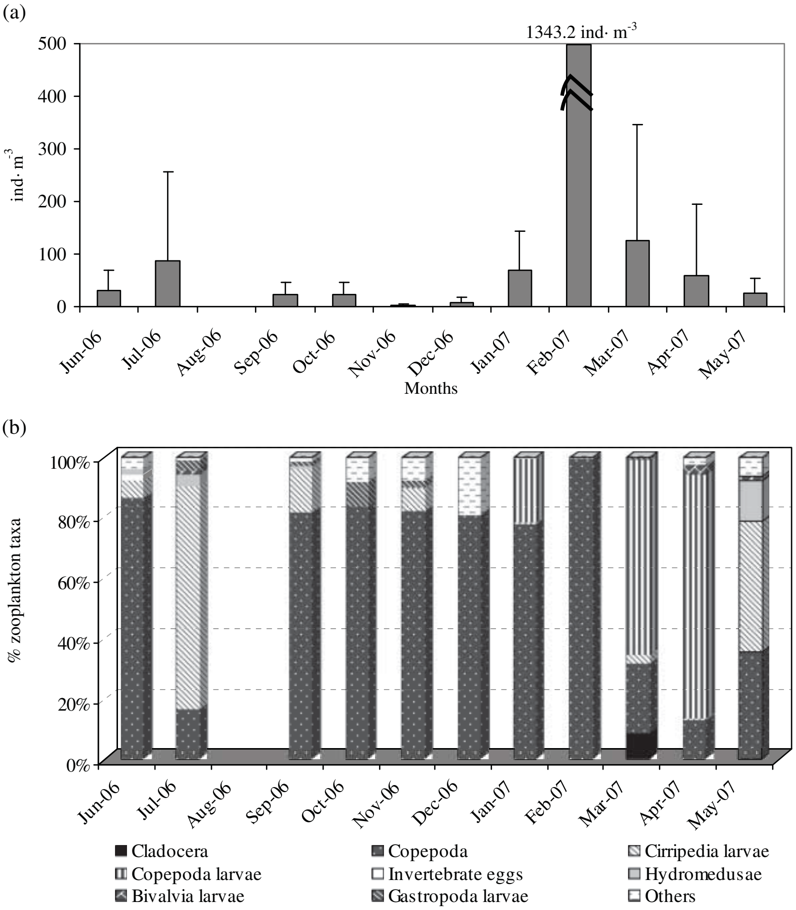

Figure 2. (a) Temporal zooplankton mean abundance trends and (b) relative contribution (%) of each zooplankton group in the Lesina Lagoon.

same season, but the station that differed significantly from almost all others was station 1. Stations 6 and 11 were significantly different from the ones on the southern side of the lagoon (Table 3). Northernmost and southernmost groups of stations exhibited more significant differences (*R*: 0.05, $p = 0.014$) than easternmost and westernmost ones (*R*: 0.02, $p = 0.22$).

In Canonical Correspondence Analysis (CCA) ordination (Figure 5), the first axis exhibiting the highest eigenvalue (0.26 with $p \leq 0.01$) was positively correlated with temperature, and to a lesser extent with Chl*a* and salinity. Thus it was related to seasonal succession of zooplankton groups, with more thermophilic species/taxa corresponding to higher coordinates, and colder-living ones to lower coordinates. The second axis (eigenvalue 0.13, $p \leq 0.01$) was negatively correlated to DO. Among the main zooplankton taxa, temperature was the most important factor explaining cladoceran and Copepoda larvae space and time patterns (Spearman's coefficient $R = -0.35$ and -0.36, $p < 0.001$, respectively). Cirripedia larvae were positively related to temperature, Chl*a* and salinity (Spearman's coefficient $R = 0.23$, $p = 0.03$; $R = 0.22$ and $R = 0.21$, $p = 0.04$, respectively). Within the copepod community, *A. tonsa* was significantly correlated to temperature and Chl*a* (Spearman's coefficient $R = 0.57$ with $p < 0.001$, and 0.26 with $p = 0.02$, respectively), *C. aquaedulcis* adults did not show any relation to the hydrological gradient, whereas its juvenile stages were inversely related to temperature and Chl*a* (Spearman's

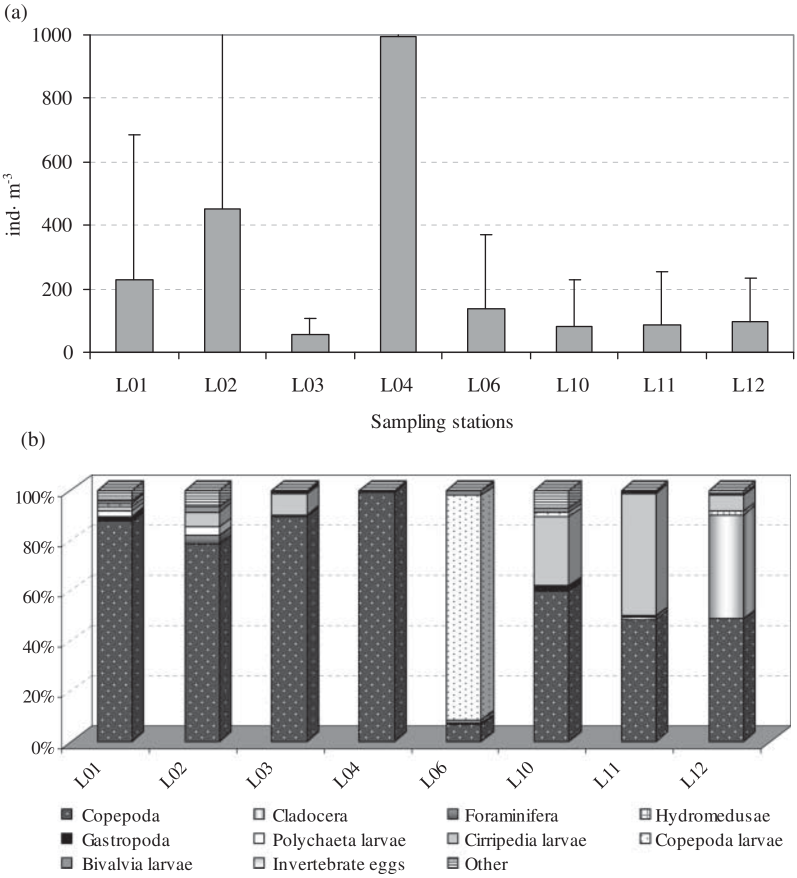

Figure 3. (a) Spatial zooplankton mean abundance trends and (b) relative contribution (%) of each zooplankton group in the Lesina Lagoon.

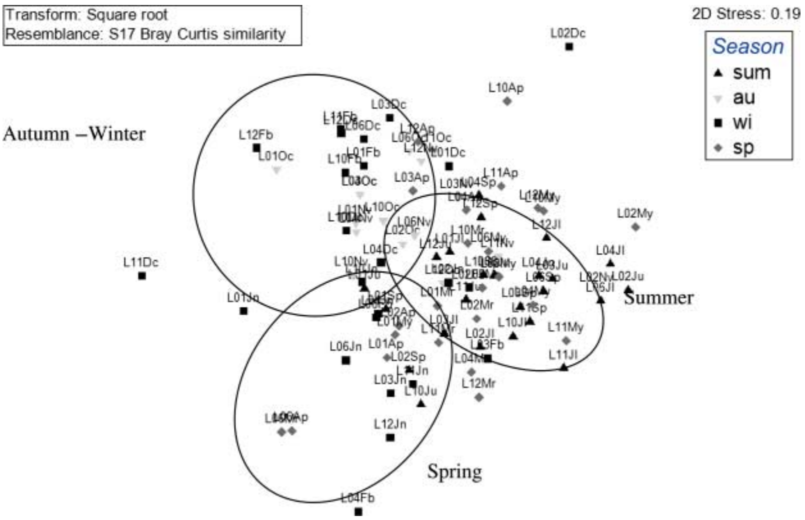

Figure 4. Multidimensional Scaling (MDS) performed on mesozooplankton abundance data set from lagoon samples, plotted by factor ‘Season’ (sum = summer, au = autumn, wi = winter, sp = spring).

Table 3. Results from ANOSIM test for differences between season and station groups across seasons.

	R	Significance (p)
Group		
sum, au	**0.542**	**0.001**
sum, wi	**0.398**	**0.001**
sum, sp	**0.208**	**0.026**
au, wi	−0.068	0.7
au, sp	**0.323**	**0.027**
wi, sp	**0.213**	**0.026**
Stations		
L01, L02	0.18	0.87
L01, L03	**0.32**	**0.03**
L01, L04	**0.382**	**0.011**
L01, L06	**0.461**	**0.021**
L01, L10	**0.331**	**0.011**
L01, L11	**0.416**	**0.016**
L01, L12	0.185	0.123
L02, L03	0.00	0.466
L02, L04	0.09	0.247
L02, L06	0.079	0.318
L02, L10	0.124	0.201
L02, L11	0.084	0.228
L02, L12	0.112	0.224
L03, L04	−0.169	0.963
L03, L06	0.056	0.352
L03, L10	0.056	0.317
L03, L11	−0.14	0.894
L03, L12	−0.034	0.543
L04, L06	0.191	0.097
L04, L10	**0.247**	**0.03**
L04, L11	**0.337**	**0.015**
L04, L12	0.034	0.386
L06, L10	**0.337**	**0.026**
L06, L11	0.202	0.12
L06, L12	0.079	0.349
L10, L11	−0.051	0.677
L10, L12	−0.045	0.658
L11, L12	−0.197	0.904

Note: Significant Rho values are shown in bold.

coefficient $R = -0.36$ and -0.22, $p = 0.001$ and 0.04, respectively). Trophic State Index (TSI), based on Chl$a$, varied seasonally and spatially, ranging from an absolute maximum (70.1) at station 1 in June, to a minimum (23.7) at station 12 in April. On average, the highest values were generally recorded in summer, coinciding with the second peak in zooplankton abundances (Figure 6a). The easternmost stations were generally characterised by lower values than westernmost ones (Figure 6b), partially resembling the zooplankton abundance spatial trend. Thus, zooplankton abundances were positively correlated to the trophic index (Spearman's $R = 0.23$; $p < 0.03$). Comparison between TSI and species richness (S) spatial and temporal trends showed closer similarity (Figure 6c,d) and were positively related (Spearman's $R = 0.24$, $p = 0.02$). The Shannon index showed low values in colder months, ranging from 0.1 in February to 1.1 in December. The highest value (1.7) was measured at stations 2 and 10, in July. This index did no show significant correlation to TSI ($R = 0.13$, $p < 0.2$).

In the channels, environmental parameters varied greatly with the tidal current. Temperatures reached the maximum in July and the minimum in March (Table 4). Salinity was strongly dependent on the tide, with lower values during low tide, and the highest ones during high tide.

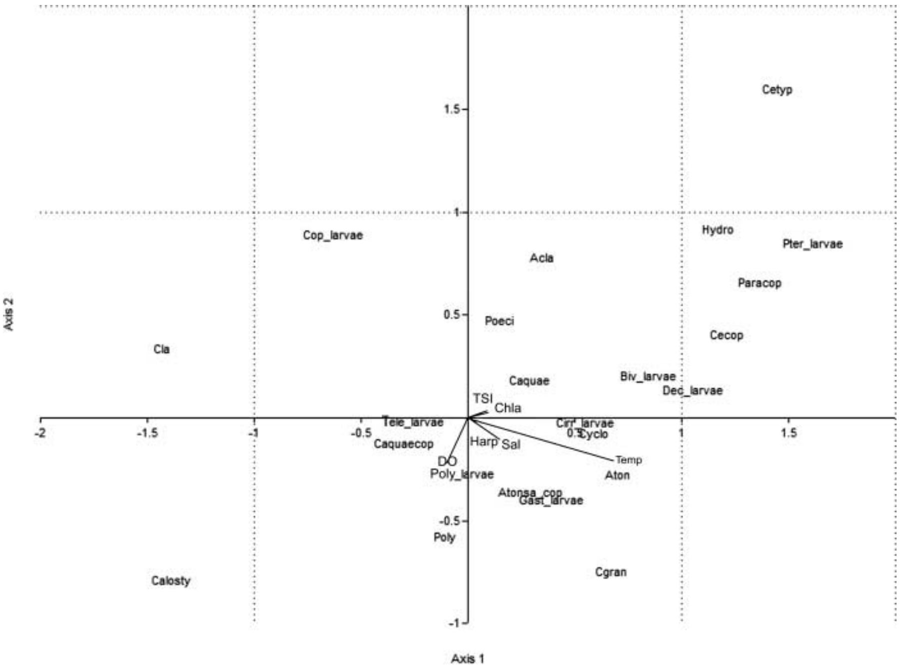

Figure 5. Canonical Correspondence Analysis (CCA) performed on mesozooplankton abundance and environmental parameter data sets from the Lesina Lagoon. In the plot, environmental factor abbreviations are as follows: Temp = temperature, DO = dissolved oxygen, Chl*a* = chlorophyll *a* and TSI = Trophic State Index; zooplankton taxa were abbreviated as follows: Aton = *Acartia tonsa*, Atonsa cop = *Acartia tonsa* copepodites, Acla = *A. clausi*, Caquae = *Calanipeda aquaedulcis*, Caquae cop = *C. aquaedulcis* copepodites, Cetyp = *Centropages typicus*, Cecop = *Centropages* copepodites spp., Paracop = *Paracalanus* copepodites spp., Calosty = *Calocalanus styliremis*, Cgran = *Coryna granulosa*, Cyclo = Cyclopoida, Poeci = Poecilostomatoida, Cop_larvae = Copepoda Larvae, Cla = Freshwater Cladocera, Poly = Polychaeta, Poly_larvae = Polychaeta larvae, Cirr_larvae = Cirripedia larvae, Gast_larvae = Gastropoda larvae, Pter_larvae = Pteropoda larvae, Biv_larvae = Bivalvia larvae, Dec_larvae = Decapoda larvae, Hydro = Hydromedusae, Tele_larvae = Teleostea larvae.

Dissolved per cent oxygen saturation was lower during the night time. On average, this factor ranged from a maximum in December to a minimum in May at Acquarotta and Schiapparo channels, respectively (Table 4).

Zooplankton abundances and species composition showed marked monthly oscillations at the two channel stations. A total of 24 taxa were identified. Zooplankton peaks in abundance (almost completely due to Cirripedia larvae) were recorded in June during high and low tide, at Schiapparo and in March, during high tide at Acquarotta, whereas the lowest densities were measured in December at Acquarotta and Schiapparo, during low tide (Figure 7). On average, the most abundant zooplankton groups were: Copepoda, Cirripedia larvae, Polychaeta larvae and Bivalvia larvae. Stronger oscillations characterised copepod abundances and species composition due to tidal successions. Cluster analysis performed on the copepod abundance data set (Figure 8) indicated two groups of samples separated at 30% of similarity level: low- and high-tide sample groups. The former were generally characterised by lower abundances and a smaller number of species (15) than the latter. According to SIMPER analysis, the species which most accounted for similarity between samples of low tide were *C. aquaedulcis*, contributing to 79.3% of similarity, and *A. tonsa* (16.5%). In the high-tide sample group, a total of 29 copepod species were identified. SIMPER analysis showed that the species that most accounted for similarity among high tide samples were: *Acartia clausi* (23.2%), *Centropages ponticus* (19.9%), *Paracalanus parvus* (15.0%) and *Oithona nana* (10.4%). The most significant differences between groups of samples were due to

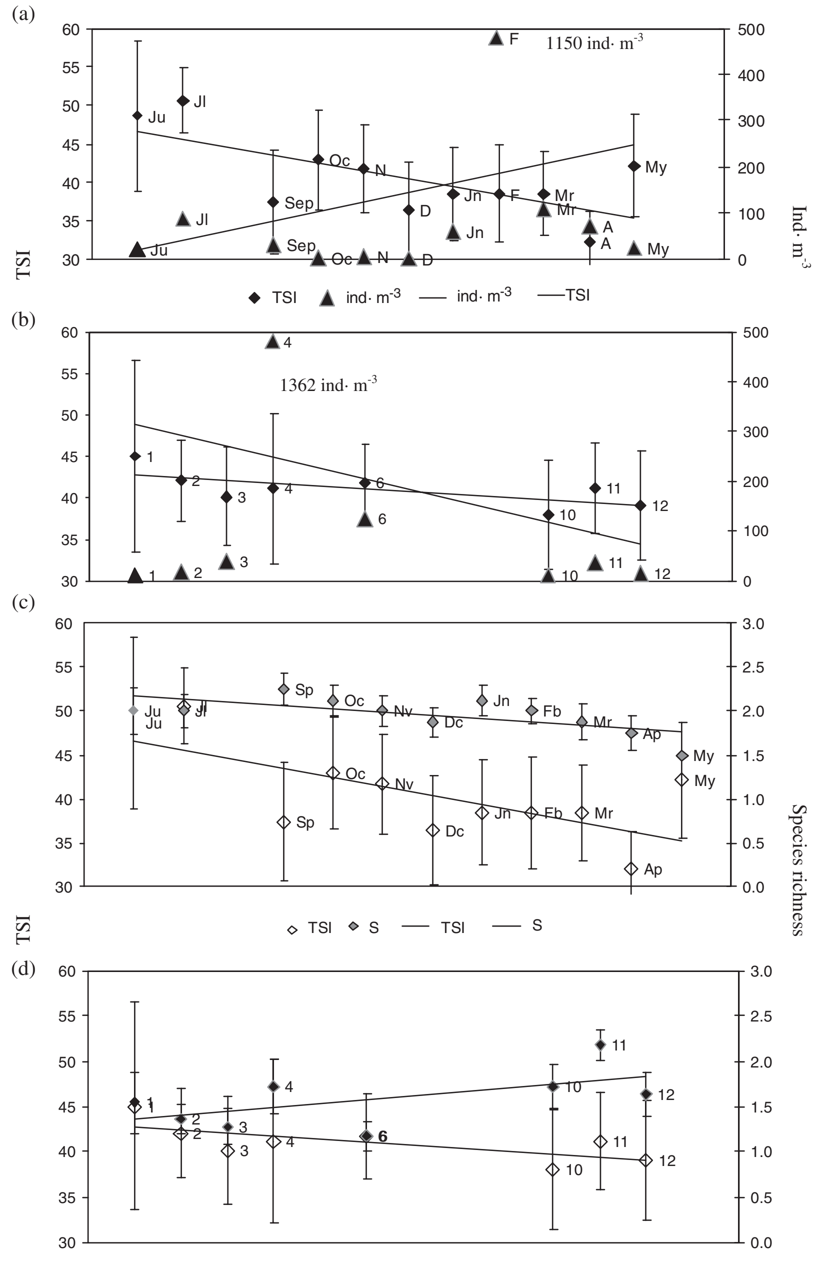

Figure 6. Trophic State Index (TSI) relations with zooplankton abundances in Lesina Lagoon over (a) time and (b) space; and with species richness (total number of species) over (c) time and (d) space.

seasonality (ANOSIM test result: $R = 0.24$, $p < 0.01$), rather than tide ($R = 0.33$, $p > 0.05$). Shannon index generally exhibited wide oscillations with the highest values in March (2.3 and 2.4) both at Acquarotta and Schiapparo Channels, respectively during high tide. Lower values were recorded in winter and spring during low tide (range: 0.3–0.7).

At the outlets of the two channels along the South Adriatic Sea coast, temperatures ranged from a maximum of 25 °C in summer to a minimum of 11 °C in winter, whereas salinity was more stable during the year varying from 37.6 to 36.2. A total of 27 zooplankton groups and

Table 4. Temporal and spatial trends of environmental parameters of averaged daily measures, in the two channels (S = Schiapparo, A = Acquarotta).

Sampling month and location	Temperature (°C)	Salinity	Dissolved oxygen (%)
OctS	19.5 (± 2.2)	13.1 (± 1.4)	86.9 (± 30.4)
OctA	19.3 (± 2.2)	16.7 (± 0.7)	85.5 (± 22.2)
NovS	13.4 (± 0.8)	10.9 (± 0.3)	210.9 (± 1.8)
NovA	12.0 (± 1.8)	15.5 (± 0.8)	141.3 (± 0.0)
DecS	10.9 (± 0.4)	11.1 (± 0.1)	188.6 (± 48.4)
DecA	10.4 (± 0.5)	14.9 (± 0.1)	155.1 (± 19.9)
JanS	11.9 (± 0.4)	16.5 (± 8.9)	75.1 (± 6.2)
JanA	12.0 (± 0.1)	13.8 (± 0.1)	63.1 (± 3.1)
FebS	13.0 ($n = 1$)	15.0 (± 7.1)	–
FebA	13.4 ($n = 1$)	12.5 (± 3.5)	–
MarS	11.5 (± 3.0)	25.5 (± 16.3)	99.5 (± 0.7)
MarA	11.9 (± 1.1)	29.0 (± 11.3)	98.5 (± 9.2)
AprS	18.5 (± 0.6)	24.5 (± 16.3)	96.5 (± 9.2)
AprA	19.3 (± 0.6)	17.8 (± 4.6)	120.0 (± 9.9)
MayS	22.6 (± 1.4)	27.8 (± 12.1)	51.9 (± 3.6)
MayA	22.8 (± 0.2)	27.0 (± 8.1)	51.1 (± 10.0)
JunS	25.4 (± 1.8)	29.5 (± 11.5)	110.9 (± 13.4)
JunA	25.8 (± 0.5)	31.5 (± 6.1)	121.4 (± 47.9)

Note: Standard deviations are given in parentheses.

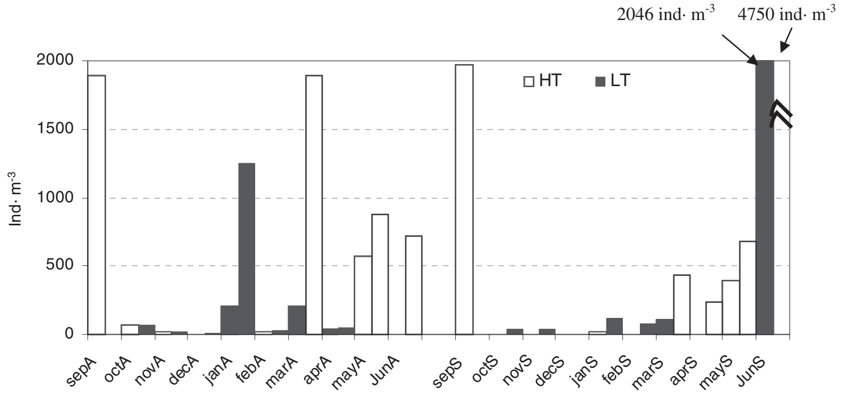

Figure 7. Temporal trends in total zooplankton abundances in channel stations relative to the tide (HT = high tide; LT= low tide). On the x-axis, station name groups month, indicated by three letters, and channel of sampling (with the initial of the channel, A for Acquarotta and S for Schiapparo).

33 species were identified, with abundance ranges shown in Figure S4 (available online only). On average, copepods represented 73.0% of the total zooplankton. Other important groups were Bivalvia larvae (7.9%), Polychaeta larvae (6.7%) and Appendicularia (3.9%). Within the copepod assemblage, a total of 28 species were identified. Among adult copepods, *A. clausi* was the overwhelming species in almost every season, with mean abundances ranging from a maximum in spring (249.1 ind·m^{-3}) to a minimum (4.3 ind·m^{-3}) in winter, when abundances were similar to *Corycaeus brehmi* (10.6 ind·m^{-3}) and *P. parvus* (5.3 ind·m^{-3}). Remarkable *A. tonsa* abundances were recorded in autumn, with a peak in November (153 ind·m^{-3}) at Acquarotta outlet, and in spring, with maximum abundance of 53.0 ind·m^{-3}, in April at the Schiapparo outlet, becoming the third most abundant species in spring. The Shannon index temporal trend showed lower values at the sea compared to channel stations. Higher values were recorded in fall and early winter (1.5) and lowest in summer (varying between 0.2 and 0.5).

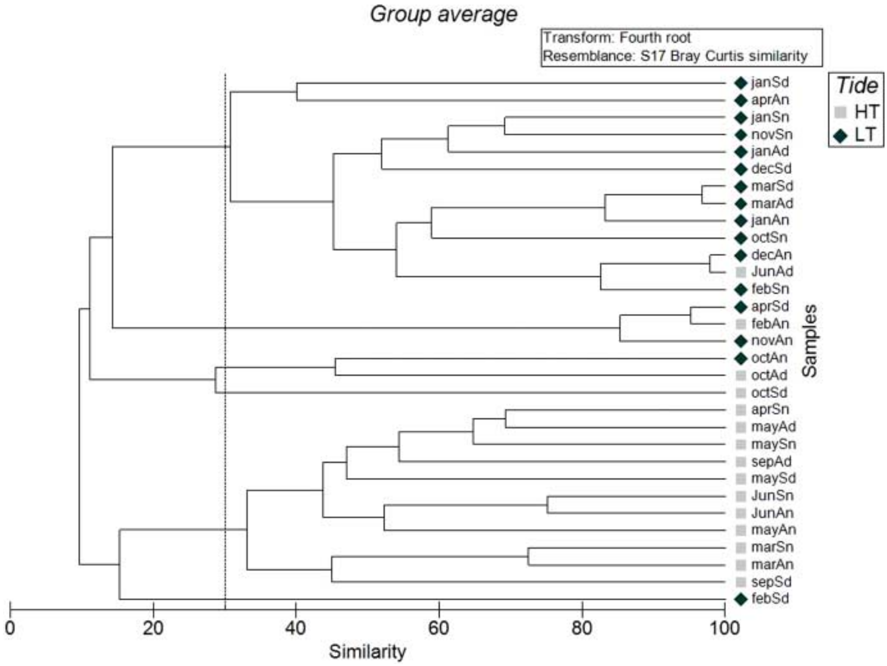

Figure 8. Cluster analysis performed on abundance data set at channel stations, using tide (HT = high tide; LT = low tide), as a factor. Station name groups month, indicated by three letters, channel by the initial of the channel, A for Acquarotta and S for Schiapparo, and time (n = night, d = day) of sampling.

4. Discussion

4.1. *Zooplankton structure*

In the investigated area, three ecosystems were distinguishable that are different for zooplankton structure and environmental parameters: lagoon, channels and marine coastal area.

Lesina Lagoon is a nontidal lentic ecosystem characterised by zooplankton abundances fluctuating within a range partly similar to that found in other similar Mediterranean ecosystems, located in different geographic zones, such as Lakes Ganzirri and Faro (abundance maximum of 9034 and 2314 ind$\cdot$m^{-3}, and minimum of 2 and 4 ind$\cdot$m^{-3}, respectively); [28], Stagnone di Marsala (3979 ± 4957 ind$\cdot$m^{-3}) [29]. In the former environment, highest abundances were recorded in summer, whereas in the Lesina Lagoon, highest abundances were found in winter, as well as in ‘Le Cesine’ coastal pond [30]. In particular, in this coastal pond the copepod assemblage was dominated by *C. aquaedulcis* as in our investigated area, in the same season.

Lesina Lagoon zooplankton assemblage is characterised by clear seasonal oscillations. Three temporal groups were identified by multidimensional scaling analysis and confirmed by significant coefficients resulted from the ANOSIM test: autumn–winter season, spring and summer seasons. Overall, zooplankton was mostly characterised by copepods and their naupliar stages, even though these smaller stages might be underestimated due to the mesh size of the net used. Due to their stenohaline character, cladocerans are restricted to the easternmost stations because of the lower salinity values in this area due to higher amounts of freshwater input during the colder months. This is as demonstrated by the inverse relationship with temperature in the CCA plot. Copepods are represented by two calanoid estuarine species *A. tonsa* and *C. aquaedulcis*, permanently inhabiting the Lesina Lagoon, and reported in the literature as having broad tolerance limits [31]. Together, these species are considered direct food competitors [32] which co-exist [33]. In Lesina

Lagoon, coexistence of *A. tonsa* and *C. aquaedulcis* is favoured by space and time segregation, because the former is more abundant in summer and autumn, whereas the latter is more abundant in winter. This temporal separation is strongly related to seasonal trends in temperature and salinity. *A. tonsa* has a relatively higher abundance in summer and autumn which could be explained by the stronger marine input from the Acquarotta Channel, especially in summer [20]. This species can adapt to wide ranges in temperature (11–25 °C) [34] and salinity (11–37) [35]. However, according to Holste and Peck [36] and Leandro et al., [37], the major factor affecting *A. tonsa* egg production rate, growth and development is temperature, as also confirmed by the higher Spearman's coefficient for this parameter in this study. This species appears to have a life cycle common to other congeneric species which produce resting eggs in winter due to unfavourable conditions [38,39]. In winter, the simultaneous diminution in temperature and salinity might inhibit *A. tonsa* development and give rise to the best conditions for growth in the *C. aquaedulcis* population. *C. aquaedulcis* is known to occur preferentially during colder months [40]. Its main reproductive period has been reported as March and April [41]. Our findings, in February–March, of great numbers of copepod nauplii (probably, hatched from *C. aquaedulcis* eggs) and copepodite stages, are in agreement with the literature referred to previously. In the Spanish Veta la Palma wetlands, where both species occur, *C. aquaedulcis* reaches maximum abundances in summer [42], even though that ecosystem seems to be similar to ours (average depth: 30 cm; temperature range: 11.8–23.5 °C; salinity range: 7–15). Marques et al. [43] also reported the highest probability of occurrence of this species in warmer waters, compared with colder waters for *A. tonsa*, with opposite trends with respect to those found in the Lesina Lagoon.

A. tonsa and *C. aquaedulcis* showed preferential habitats in the lagoon: the former is almost completely restricted to stations affected by marine waters with higher salinity and the latter is preferentially distributed in the most confined area of the Lesina Lagoon, mainly influenced by freshwater inputs.

In the Lesina Lagoon, the presence of coastal species (*A. clausi*, *P. parvus*, *C. ponticus*, *C. styliremis*, etc.) can be considered occasional and mainly due to the dominant winds (Mistral and other western winds) that transport these species into the lagoon in winter and spring [20]. In fact, these species may not inhabit the lagoon, probably because of the salinity barrier due to reduced water exchange with the sea. For these reasons, the diversity indices in the lagoon are lower than those in the channels and adjacent sea. They are also comparable with similar ecosystems such as the neighbouring Varano Lagoon where three Acartiidae species (*A. clausi*, *Paracartia latisetosa* and *A. margalefi*) were identified by Quarta et al. [14] and Acquatina Lake where *Paracartia latisetosa*, *A. margalefi*, *Pteriacartia josephinae* and *A. italica* occur [44]. The number of coexisting congener species could depend on the space heterogeneity and seasonal succession of their populations [28,45–47]. Almost all these species are reported as eurybiotic, r-strategy type species, capable of producing resting eggs, typical of unstable coastal lagoon environments exposed to sudden variations in abiotic factors [44,45,48]. Therefore, the Lesina Lagoon appears more confined (*sensu* [2]) than the above-cited ecosystems. The record of only *A. tonsa* within the congener Acartiidae species association supports the assumption of the confinement of this lagoon [45].

Channels represent transitional environments between the lagoon and the sea, characterised by biotic and abiotic factors highly dependent on tidal phases, as evident in the cluster analysis. Their mixing gives rise to peculiar features with typical zooplankton assemblages for each tidal phase. The low-tide group of samples has a lagoon origin and can be identified by the lower salinity and dominance of *C. aquaedulcis*. This in turn will depend on the abundance oscillations of this species related to seasonal successions into the lagoon. The high-tide group with marine origin is identified by its higher salinity and is characterised by a copepod species composition similar to the coastal assemblage. The former group has slightly higher abundances than those in the lagoon, probably because of mixing effects between lagoon and marine waters. Hence, the overlapping of marine and lagoon species and, at the same time, higher zooplankton abundances support increasing diversity indices with respect to the lagoon and sea. However, densities during high tide are markedly lower than those found at sea, but characterised by the overwhelming dominance of *A. clausi*, similar to coastal marine assemblage. In this case, the diversity index decreases. Therefore, our results show an increasing trend of abundances from the lagoon to the sea, in agreement with findings of Comaschi-Scaramuzza and Martino [49].

4.2. *Trophic state and human impact*

The Lesina Lagoon is an ecosystem with continuous changes in hydrology and trophic state due to both natural vulnerability (reduced water exchange with the neighbouring Adriatic Sea, high residence time, scarce tidal range and freshwater loads) and anthropogenic pressures (agriculture, aquaculture, wastewater treatment plants, watershed resident population with its discharge, and natural and/or human-regulated channel). Zooplankton community responds promptly to all these changes. The Lesina lagoon has been recently defined by Roselli et al. [17] as an oligomesotrophic–mesotrophic system ($30 < \mathrm{TSI} < 50$) which is in agreement with the low zooplankton abundances found in our study and their significant correlation to the trophic state. In fact, the summer peak in zooplankton abundances was coincident with Chl*a* values. *A. tonsa* adults and copepodids, the most important component of the summer peak, seem strongly dependent on the trophic state of the lagoon being positively correlated to Chl*a*. By contrast, the winter peak in abundance at station 4 is almost completely sustained by *C. aquaedulcis* copepodites which are inversely correlated to trophic state. This species appears adapted to more oligotrophic conditions due to their feeding preferences constituted by heterotrophic prey based on picoplankton, dinoflagellates and ciliates [50], as suggested by the low Chl*a* values measured in winter in the Lesina Lagoon. By contrast, copepod naupliar stages seem to be most affected by temperature, preferring colder than warmer waters.

Species richness increases with increasing trophic index, as demonstrated by the significant correlation between months and stations. In high food availability conditions probably competition is lower. Our results are dissimilar to those reported for temperate Mediterranean brackish lagoons that demonstrate a decrease in species richness with increasing salinity [51]. In our case, lower values of species richness were recorded in winter than in summer when salinity increased. The spatial trend in the lagoon showed higher values in westernmost and more saline stations compared to easternmost stations.

Since 1990, the Schiapparo and Acquarotta Channels have been partially obstructed by wooden barriers. Moreover, the latter channel is continuously subjected to opening/closing by means of natural sea-driven sandbar formation. These changes may have caused a decrease in salinity and the disappearance of *A. margalefi*, reported in the Lesina Lagoon by Quarta et al. [14], and its substitution with *A. tonsa*. In Imbossica Lagoon, the same species was also recorded after human-induced sandbar opening or closing that caused changes in the predominant water conditions, mainly related to trophic state and salinity [52]. The strong dependence of *A. tonsa* from trophic state of the lagoon was demonstrated by the significant Spearman's correlation coefficient with this factor. Differences in salinity ranges may also explain the absence of *A. tonsa* in similar coastal lagoons such as Varano Lagoon and Acquatina Lake [53,54]. These two ecosystems show salinity oscillations within ranges higher than those recorded in the Lesina Lagoon during this study. Our salinity measurements are also lower than those reported by Ficca [20] and Caroppo [55] for the same lagoon. This might have also have favoured the colonisation of *A. tonsa* in this lagoon. This is an invasive species that appeared in Europe in the first half of the twentieth century and has since progressively colonised most European seas and estuaries. The species was possibly transported by ship ballast water [56] from North America, where it is commonly found [57]. However, the fact that *A. tonsa* prevails in areas with intense aquaculture, such as the Lesina

Lagoon, suggests an introduction associated to human activity [58–60]. In Lake Faro (north-eastern Sicily, Mediterranean Sea), an area devoted to mussel farming, where two Acartiidae species have occurred to date (*A. margalefi* and *P. latisetosa*), has experienced a similar pattern of species substitution, with *A. margalefi* progressively being displaced by the invasive *A. tonsa* (Brugnano et al., pers. comm.).

Comparison with previous studies on zooplankton abundances in the Lesina Lagoon are not possible because there are insufficient data before our study to establish the seasonal cycle of *A. tonsa* and *C. aquaedulcis*. Thus, we are unable to evaluate the effects of an introduction of *A. tonsa*. Abundances at the station in front of the Acquarotta channel in May and June can be compared only with those, clearly three orders of magnitude lower, recorded by Sei and Ferrari [15], in the same months and locations. This would support the hypothesis of an ongoing change in the trophic and/or hydrological state of the Lesina Lagoon. Furthermore, no mention of the occurrence of *C. aquaedulcis* in the Lesina Lagoon was made by the same authors. At least two reasons must be indicated for this species not being found by these authors: they sampled in the period of minimum abundances of *C. aquaedulcis*; there were strong oscillations in the dominance of one of the two species in relation to seasonal freshwater flow and so, to hydrological balance of the lagoon. In Chesapeake Bay with a salinity range (12–18) similar to that in our study area, linear mixed-effects models showed a negative correlation between freshwater inputs and *A. tonsa* abundance in the oligohaline region, but not in higher salinity regions [61]. However, long-term bio-monitoring programmes demonstrated strong oscillations in *A. tonsa* abundances, related mostly to salinity and temperature trends [47]. By contrast, decreasing grazer abundances can alter top-down control of the food web and the fate of phytoplankton during summer blooms in terms of Chl*a*. This would generate a chain reaction on upper trophic levels, because copepods can be important components of the diet of bentho-pelagic invertebrates [62] and planktivorous juveniles of fishes, being the lagoon a nursery area for numerous fish and crustacean species of commercial value [63]. In the same way, human management of the lagoon with the construction of barriers to prevent fish escaping from this area may have caused an increase in the number of predators and the subsequent decline of their planktonic prey with an altered bottom-up control.

Hence this study provides information about the current ecological status of this lagoon and its channels, useful to develop a more complete management plan, taking into account changes in copepod communities related to human activities. Zooplankton constitutes a sensitive tool for monitoring environmental changes in coastal lagoons because the populations react immediately in trophic status and salinity variations [64,65]. Although zooplankters are very important components of shallow ecosystems, sometimes acting as keystone species, they have not been considered as biological elements for the classifications of ecological status in 'EU Water Framework Directive'. This fact can be considered mystifying [66] and several attempts have recently been made in Mediterranean shallow waters to assess the potential of some zooplankton groups as indicators of ecological status (e.g. [67,68]).

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